

**A synoptic review of the vertebrate fauna from the “Green Series” (Toarcian)  
of northeastern Germany with descriptions of new taxa: A contribution to  
the knowledge of Early Jurassic vertebrate palaeobiodiversity patterns**

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## 1. Introduction

During the Toarcian, wide areas of central and western Europe were covered by a shallow epicontinental shelf sea that was subdivided into several basins, referred to as the Central European epicontinental Basin (CEB) (RÖHL and SCHMID-RÖHL, 2005). The CEB formed the southern part of a transcontinental seaway that connected the low-palaeolatitude Tethys Ocean in the south with the high-palaeolatitude Boreal Sea in the north. It was inhabited by a broad variety of marine vertebrates, including rich and diverse faunas of bony and cartilaginous fish, and secondarily marine reptiles, as known from numerous fossil localities spread over Europe. The bulk of these finds have been recovered from basinal organic-rich mudstones and marlstones of western Europe. In particular, the Posidonia Shale Formation in southwestern Germany and the Whitby Mudstone Formation in eastern England produced many well-preserved specimens of fish and marine reptiles, and has received considerable research attention since the first half of the 19<sup>th</sup> century (e.g., BRONN, 1830; QUENSTEDT, 1847; WOODWARD, 1896, 1897, 1898, 1899; HAUFF, 1921; VON HUENE, 1922; BENTON and TAYLOR, 1984; GROßMANN, 2007; MAISCH, 2008; MAXWELL, 2012). Conversely, little attention has been paid to vertebrate remains recovered from lower Toarcian beds of northeastern Germany due to the scarcity of productive localities up to date. In this region, Early Jurassic strata only crop out in the abandoned clay pits of Grimmen and Dobbartin in Mecklenburg-Western Pomerania (Fig. 1A), both giving access to thick stacks of lower Toarcian clays, which are assigned traditionally to the so-called “Green Series”. These distinct accumulations were deposited at the northern edge of the North German Basin near to the neighboring Polish Basin, which both formed parts of the northern CEB (Fig. 1C), documenting a marine marginal ecosystem immediately following the onset of the Toarcian-Oceanic Anoxic Event.

The “Green Series” clay deposits of Grimmen and Dobbartin are renowned for their rich and diverse terrestrial insect fauna that has attracted palaeoentomologists since the end of the 19<sup>th</sup> century (see ANSORGE, 2003). Likewise, fish and marine reptile material has been reported from the “Green Series” for over 100 years (e.g., GEINITZ, 1884, 1900a, b; JAEKEL, 1929; THIES, 1989; ZESSIN, 1995, 1998, 2001; MAISCH and ANSORGE, 2004), but little detailed taxonomic research has been conducted, and a comprehensive study on the “Green Series” vertebrate fauna has not been provided so far. The only literature that can be recommended is THIES (1989) who gave a comprehensive review on the basal neopterygian fish *Lepidotes* of Grimmen and Dobbartin, and MAISCH and ANSORGE (2004) who summarized the scarce ichthyosaur material from Dobbartin.



The present doctoral dissertation comprises new studies on the “Green Series” vertebrate assemblage that contribute to fill the gap of knowledge regarding its taxonomic and systematic diversity and its relevance for understanding Early Jurassic vertebrate life.

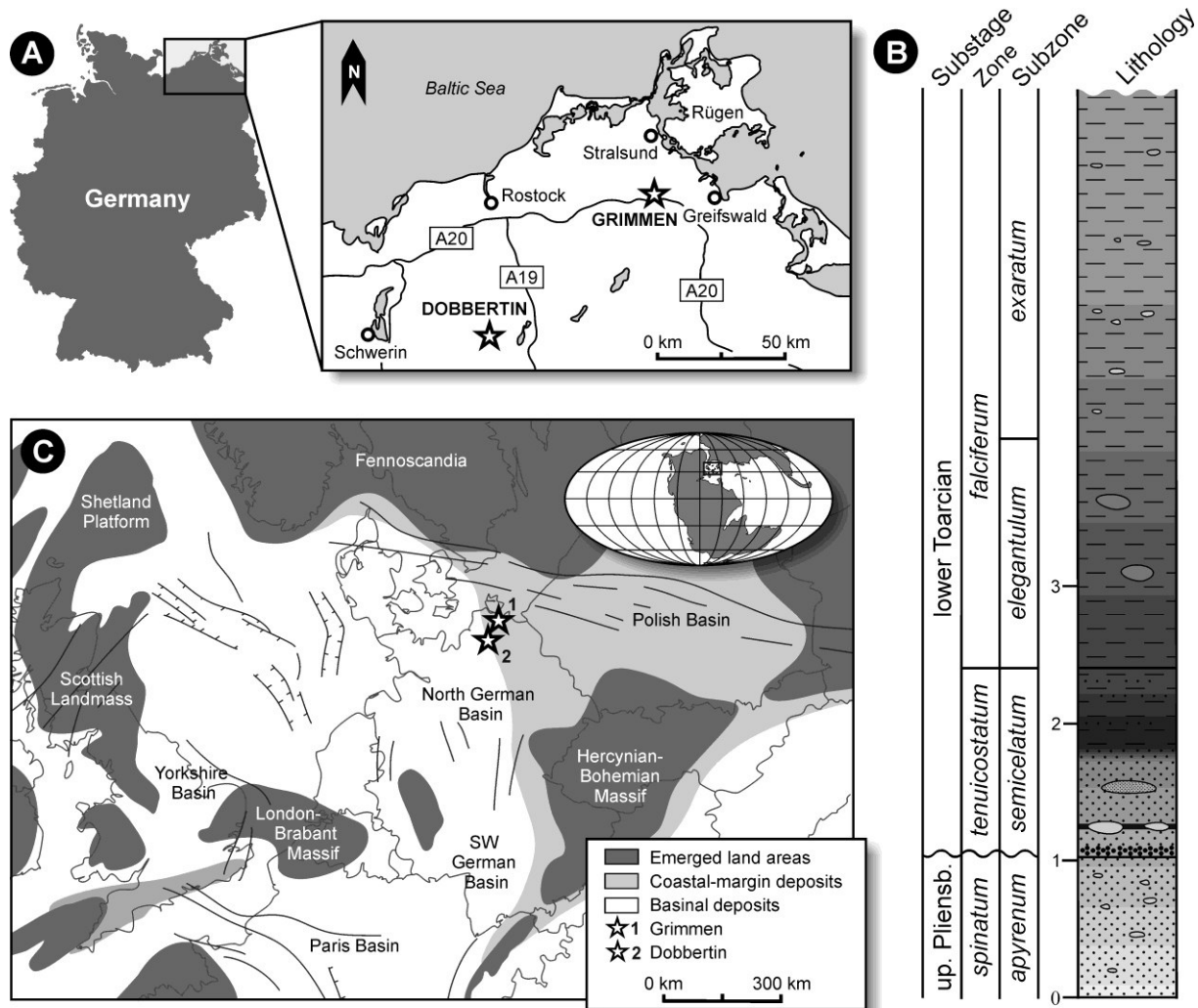


Figure 1. **A**, Geographical location map; **B**, Stratigraphic standard section of the late Early Jurassic succession exposed in the Grimmen clay pit (wavy line indicates hiatus at the Pliensbachian-Toarcian transition); **C**, Rough reconstruction of Toarcian palaeogeography of central and western Europe (modified from PIENKOWSKI, 2004; RÖHL and RÖHL-SCHMID, 2005; KORTE et al., 2015).

## 2. Geological and Stratigraphic Framework

Although laterally persistent, outcrops of Mesozoic strata are rare in northeastern Germany (e.g., KATZUNG, 2004). Early Jurassic strata only crop out in the abandoned open-cast clay pits of Grimmen and Dobbertin, both representing parautochthonous successions of upper Pliensbachian to lower Toarcian marine sediments that were glacially dislocated during Pleistocene ice

advances (see ERNST, 1967, 1991, 1992; ANSORGE and OBST, 2015; ANSORGE and GRIMMBERGER, 2016). The litho- and biostratigraphy of the exposed successions have already been described in the literature (ERNST, 1967, 1991, 1992; PRAUSS, 1996; ANSORGE, 2007; ANSORGE and OBST, 2015).

Fine-grained sands containing fine- to coarse-grained, bioclastic-rich sand bodies represent the upper Pliensbachian interval of Grimmen (ERNST, 1967, 1991; ERNST *in* GRÜNDEL, 1999). Pyrite and carbonate concretions, less commonly siderite concretions, are present. The fauna is rich in marine invertebrates, but also remains of actinopterygian and chondrichthyan fishes occur (ERNST, 1967, 1991; HERRIG, 1969a, b; KUTSCHER, 1988; GRÜNDEL, 1999; BUCHHOLZ, 2012).

Biostratigraphically, the sandy interval has been correlated with the *apyrenum* subzone (lower *spinatum* zone) based on ammonite evidence (ERNST, 1991; BUCHHOLZ, 2012). The Pliensbachian-Toarcian transition is omitted by a hiatus, probably caused by erosion and non-deposition (RÖHL and SCHMID-RÖHL, 2005), and therefore, the uppermost *spinatum* zone (*hawskerense* subzone) and probably much of the lower Toarcian *tenuiscostatum* zone (*paltum* to *clevelandicum* subzone) are absent (ERNST, 1991). The lower Toarcian interval shows a retrogradational stratal pattern, consisting of fine-grained sands that pass upwards into black bituminous, laminated silty clays referred to the latest *tenuiscostatum* zone (*semicelatum* subzone), and finally into a thick stack of pure clays containing fossiliferous concretions, used to assign the clay deposits to the lower *falciferum* zone (*elegantulum* to *exaratum* subzone) (Fig.1B). This clay interval represents the lower part of the “Green Series”, which is restricted to northeastern Germany reaching thicknesses of several tens of meters (SCHUMACHER and SONNTAG, 1964; STOERMER and WIENHOLZ, 1965; LEHMKUHL, 1970).

Unlike the “Green Series” clay deposits of Grimmen, those of Dobbartin are biostratigraphically not well-constrained, and in consequence, they can solely be dated to the *falciferum* zone on the basis of current data (ANSORGE, 2003; ANSORGE and OBST, 2015). Given the tectonic disturbances that took place during glacial dislocation, the original thicknesses of the “Green Series” clay deposits of both Grimmen and Dobbartin cannot be firmly determined.

Unlike the usually compressed fossil material from the more famous lower Toarcian deposits of Europe, the “Green Series” fossil assemblage stands out for including specimens that are preserved three-dimensionally in concretions (Fig. 2) occurring interbedded within the clay. This kind of preservation gives access to minute and often unidentifiable, morphological features.

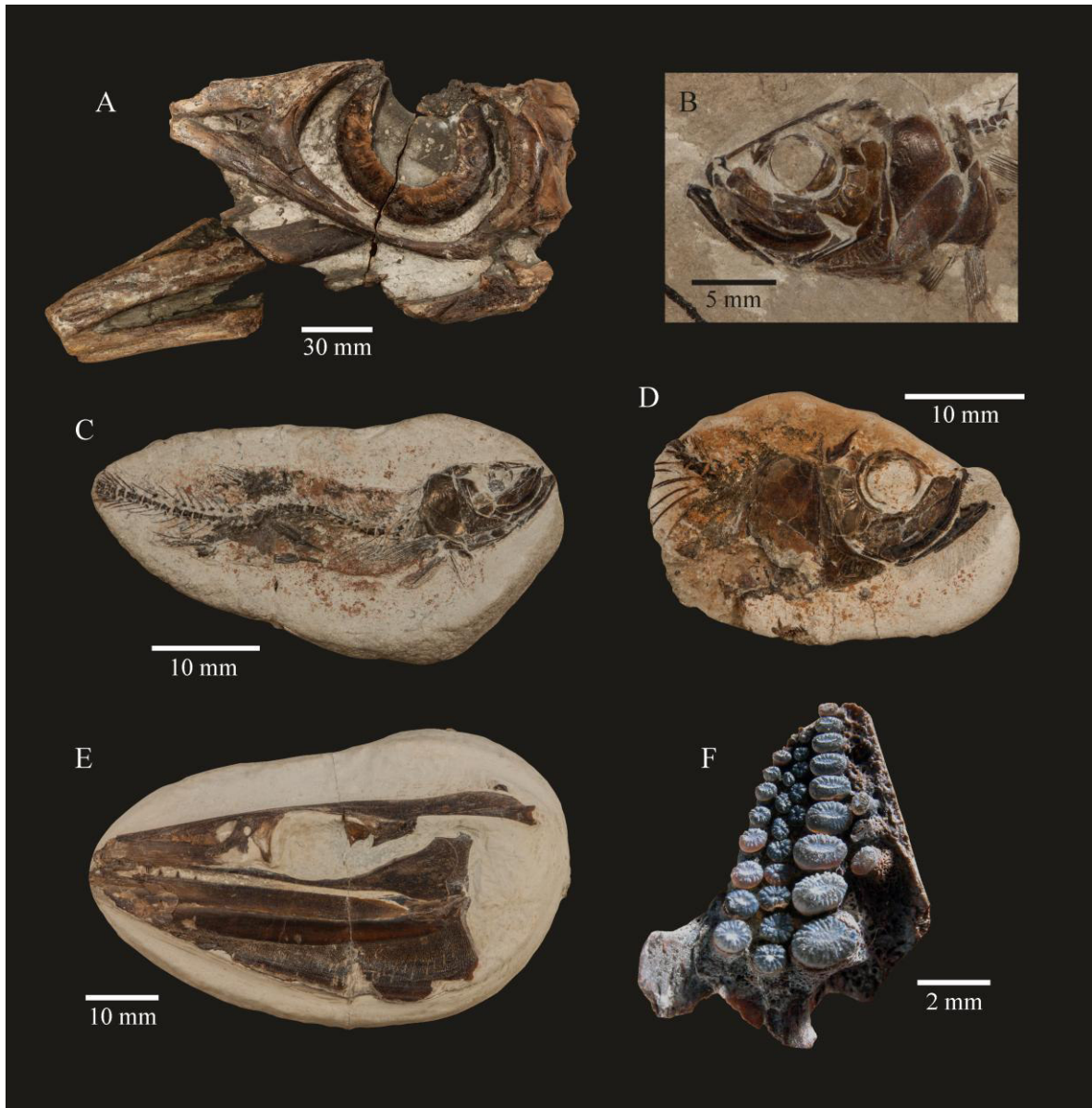


Figure 2. Vertebrates from the “Green Series”. **A**, skull of *Stenopterygius* cf. *quadriscissus* (GG 436) in left lateral view; **B**, skull of *Leptolepis normandica* (GG 431/2a) in left lateral aspect; **C**, almost complete specimen of *Leptolepis coryphaenoides* (GG 431/7) in right lateral view; **D**, skull of *Leptolepis jaegeri* (GG 431/16) in right lateral view; **E**, skull of *Saurorhynchus hauffi*, sp. nov. (GG 20001) in left lateral aspect; **F**, *Grimmenodon aureum*, gen. et sp. nov. (holotype, GG 437), left prearticular bone with dentition in occlusal view.

Based on the presence of a rich but taxonomically impoverished ammonite fauna and the scarcity of typical stenohaline invertebrates, brackish-marine water conditions were inferred for the time of deposition of the “Green Series” (ERNST, 1991; ANSORGE, 2003, 2007). Reduced salinity conditions are also confirmed by occurrences of conchostracans (ANSORGE, 2003; pers. obs.). Apart from having produced a rich and diverse fauna of terrestrial insects, the “Green Series” has

also yielded a spider (SELDEN and DUNLOP, 2014) that was washed into the epicontinental shelf sea. This indicates a near-shore depositional environment. Abundant plant and wood remains (ERNST, 1967; ANSORGE, 2007) also support the interpretation of a near-shore setting during the time of deposition. In addition, the lower Toarcian of Grimmen also produced a basal thyreophoran dinosaur, *Emausaurus ernsti*, which was described based on a single specimen containing cranial and postcranial elements (HAUBOLD, 1990). These remains were initially recovered from a concretion from the *tenuicostatum* zone.

Significantly, the boundary between the *tenuicostatum* and *falciferum* zones coincides with the height of the Toarcian Oceanic Anoxic Event (T-OAE), which is considered to be one of the most dramatic environmental disruptions that took place during the Mesozoic, and massively impacted marine biota (e.g., LITTLE and BENTON, 1995; CASWELL et al., 2009; DERA et al., 2010; CASWELL and COE, 2014). The exposed “Green Series” clay deposits of Grimmen and Dobbartin therefore document a marine marginal ecosystem immediately following onset of the T-OAE.

### 3. Material and Methods

In an effort to generate new and reliable data on the diversity of vertebrates in the lower Toarcian “Green Series”, accessible fossil material from different institutional collections were investigated and analyzed (for an annotated list of examined specimens see Suppl. Table). For comparative purposes, collection-based studies of fossil vertebrate material from time-equivalent deposits of Europe were carried out. The fossil specimens examined during the course of this project were photographed and interpretative line-drawings were produced. In addition, detailed measurements were taken. In order to expose particular morphological features, in some cases mechanical and/or chemical preparation techniques were required. Photographs were obtained using digital cameras and digital microscopes. In some cases, micro-computed tomography (micro-CT) was used to study internal anatomical structures. The micro-CT scans used in present study were conducted at the Department of Paleontology of the University of Vienna, Austria, and the Zoological Institute and Museum of the University of Greifswald.

**Institutional Abbreviations:** **BGR**, Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover; **DMM**, Deutsches Meeresmuseum, Stralsund; **GG**, Institut für Geographie und Geologie, Ernst-Moritz-Arndt-Universität Greifswald; **GPIH**, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg; **GPIT**, Geologisch-Paläontologisches Institut, Eberhard Karls Universität Tübingen; **GZG**, Geowissenschaftliches Zentrum, Georg-August-Universität Göttingen; **HMG**, Heimatmuseum Grimmen; **IPUW**, Institut für Paläontologie, Universität Wien; **JME**, Jura-Museum Eichstätt; **MfN**, Museum für

Naturkunde Berlin; **MV**, Geologische Landessammlung Sternberg, Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern; **NL**, Natureum Ludwigslust; **NLMH**, Niedersächsisches Landesmuseum Hannover; **NMB**, Staatliches Naturhistorisches Museum Braunschweig; **PLM**, Pommersches Landesmuseum, Greifswald; **SMNS**, Staatliches Museum für Naturkunde Stuttgart; **UMH**, Urweltmuseum Hauff.

#### 4. Results and Conclusions

The collection-based examinations performed in the course of this project led to the recognition of a wide range of vertebrate taxa (see Table 1), and subsequently, four studies on different fossil vertebrate clades from the lower Toarcian “Green Series” were worked out.

Table 1: Synopsis of vertebrate taxa from the lower Toarcian “Green Series” of Grimmen and Dobbertin (based on material housed in institutional collections; see Suppl. Table 1).

<b>Dinosauria</b>	<b>Osteichthyes</b>
<b>Sauropodomorpha</b>	<b>Actinopterygii</b>
<b>Sauropoda</b>	<b>Saurichthyiformes</b>
<b>Gravisauria</b>	<b>Saurichthyidae</b>
Gravisauria indet.	<i>Saurorhynchus hauffi</i> , sp. nov.
	<i>Saurorhynchus</i> sp.
<b>Ichthyopterygia</b>	<b>Lepisosteiformes</b>
<b>Ichthyosauria</b>	<i>Lepidotes elvensis</i> (BLAINVILLE, 1818)
Ichthyosauria indet.	<b>Dapediiformes</b>
<b>Parvipelvia</b>	<i>Tetragonolepis semicincta</i> BRONN, 1830
<b>Neoichthyosauria</b>	<i>Dapedium</i> sp.
<b>Thunnosauria</b>	<b>Pycnodontiformes</b>
<i>Stenopterygius</i> cf. <i>quadriscissus</i>	<i>Grimmenodon aureum</i> , gen. et sp. nov.
<b>Sauropterygia</b>	<b>Teleostei</b>
<b>Plesiosauria</b>	<b>Leptolepidae</b>
Plesiosauria indet.	Leptolepidae sp. 1
cf. Plesiosauria indet.	<i>Leptolepis coryphaenoides</i> (BRONN, 1830)
<b>Neoplesiosauria</b>	<i>Leptolepis normandica</i> NYBELIN, 1962
<b>Plesiosauroidea</b>	<i>Leptolepis jaegeri</i> AGASSIZ, 1844
Plesiosauroidea indet.	<i>Leptolepis</i> sp. 1
	cf. <i>Proleptolepis</i> sp.
<b>Crocodyliformes</b>	<b>Chondrichthyes</b>
<b>Mesoeucrocodylia</b>	<b>Euselachii</b>
Mesoeucrocodylia indet.	<b>Hybodontiformes</b>
<b>Thalattosuchia</b>	Hybodontiformes indet.
Thalattosuchia indet.	
<b>Teleosauridae</b>	
<i>Steneosaurus bollensis</i> (JAEGER, 1828)	

These deal with various fields in recent palaeontological research on Early Jurassic vertebrates, including taxonomy, palaeobiogeography, palaeoecology, and palaeobiology. In addition, a taxonomic revision of the Early Jurassic belone-like bony fish *Saurorhynchus* was performed. The main results of these studies are summarized below.

#### 4.1 Dinosaurs

One of the most striking outcomes of this project is that the “Green Series” vertebrate assemblage is composed of both marine and terrestrial components. STUMPF et al. (2015) reported fragmentary basal sauropod dinosaur remains from the “Green Series” of Grimmen (**Paper 1**), representing the second dinosaur record from this site, in addition to the basal thyreophoran *Emausaurus ernsti*.

Sauropoda is a taxonomically diverse group of herbivorous dinosaurs that include the largest terrestrial animals ever to have existed on Earth (SANDER and CLAUSS, 2008; SANDER et al., 2011). They were the dominant herbivores in global terrestrial ecosystems throughout much of the Mesozoic, from the Middle Jurassic to the end of the Cretaceous (MANNION et al., 2011). The early history of sauropod dinosaurs is still poorly understood and has been controversially discussed in recent decades (e.g., UPCHURCH, 1998; UPCHURCH et al., 2004, 2007a; YATES, 2007; ALLAIN and AQUESBI, 2008). The Early Jurassic dinosaur record is represented by a small number of named species with unambiguous sauropod affinities (WILD, 1978; COOPER, 1987; HE et al., 1998; UPCHURCH et al., 2007b; ALLAIN and AQUESBI, 2008; BANDYOPADHYAY et al., 2010; MCPHEE et al., 2015).

The “Green Series” sauropod material consists of two fragmentary specimens, a dorsal neural spine and four associated pelvic girdle elements, which were found during the last quarter of the 20<sup>th</sup> century, but remained unstudied due to their fragmentary condition. Notably, the material represents the second sauropod body fossil record from the Early Jurassic of Europe, in addition to *Ohmdenosaurus liassicus*, which was described based on a tibia, astragalus, and calacaneum from the lower Toarcian Posidonia Shale Formation of southwestern Germany (WILD, 1978).

Based on the observed set of morphological characters, the “Green Series” material can clearly be referred to Gravisauria, indicating close morphological resemblances to the late Early Jurassic basal gravisaurian sauropod *Tazoudasaurus naimi* (ALLAIN and AQUESBI, 2008). Moreover, the Grimmen sauropod material is suggestive of osteological immaturity on account of being rather

small in size as compared to the corresponding elements of other sauropods. Otherwise, the possibility of insular dwarfism cannot be ruled out with certainty momentarily.

Although the lack of overlapping elements hinders a detailed comparison to *Ohmdenosaurus liassicus*, it has to be noted that the latter taxon more closely resembles the Middle Jurassic gravisaur *Rhoetosaurus brownei* than other basal sauropods (NAIR and SALISBURY, 2012). In consequence, these different taxonomic affinities suggest the presence of at least two sauropod taxa in the lower Toarcian terrestrial ecosystems of Europe. However, this must be regarded as tentative until more complete material is available in order to provide a closer assessment of their systematic relationships, and therefore the material from the “Green Series” is left in open nomenclature and simply referred to as Gravisauria indet.

The occurrence of dinosaur remains in marine depositional settings requires transportation processes. The traditional explanation for dinosaurs in marine settings is that they were washed into the marine realm via coastal freshwater runoff (BUFFETAUT, 1994). Alternative hypotheses invoke the influence of marine predators (BENTON et al., 1995). For example, *Emausaurus ernsti* was suspected to be a “Speiballen” (i.e., a compacted mass of indigestible stomach contents; see THIES and HAUFF, 2013) regurgitated by a large marine reptile (ERNST in HAUBOLD, 1991) since it was initially found as a densely compacted pile of disarticulated cranial and postcranial elements preserved in a concretion.

## 4.2 Marine Reptiles

Marine reptiles formed a common component in the lower Toarcian marine vertebrate communities, occupying the higher trophic levels within the marine food web including the top positions (BÖTTCHER, 1989). The lower Toarcian marine reptile record from northern Germany is poorly known, especially in comparison to the rich faunas obtained from England and southwestern Germany (BENTON and TAYLOR, 1984; GODEFROIT, 1994; URLICHS, 1994). The presence of marine reptiles in the “Green Series” is known for more than a century, but little research on this assemblage has been performed up to now. GEINITZ (1900a, b) reported four articulated caudal centra of an ichthyosaur from the “Green Series” of Dobbertin. This specimen was later referred to *Stenopterygius ‘zetlandicus’* by VON HUENE (1922), and refined by MAISCH and ANSORGE (2004) to ‘Neoichthyosauria indet.’ These authors also reported an incomplete ichthyosaur skull from the “Green Series” of Dobbertin, which they assigned to *Stenopterygius* cf. *quadriscissus*. ZESSIN (1995, 1998, 2001) and ZESSIN and KREMPIEN (2010) reported

ichthyosaur and crocodyliform remains from the “Green Series” of Grimmen. These papers, however, do not provide any detailed morphological or systematic descriptions. Further marine reptile material from northern Germany is known from the Posidonia Shale Formation of Brunswick and from Toarcian-aged erratics near the town of Ahrensburg, Schleswig-Holstein, incorporating largely poorly documented material (ERNST, 1920; OERTEL, 1925; WUNNENBERG, 1928, 1950; WINCIERZ, 1967; LEHMANN, 1971; SACHS et al., 2016).

STUMPF (2016) reported a previously undocumented marine reptile assemblage from the “Green Series” of Grimmen and Dobbertin (**Paper 2**). This assemblage includes cranial and postcranial material of ichthyosaurs, plesiosaurs, and thalattosuchian crocodyliforms (the latter two taxa being described in detail for the first time from the “Green Series”), confirming the presence of a diverse fauna of marine reptiles in the lower Toarcian marginal marine ecosystems of the North German Basin south of Fennoscandia immediately following the onset of the T-OAE. Notably, the new material includes an incomplete skull referable to the geographically widespread thalattosuchian *Steneosaurus bollensis*, vertebrae of plesiosauroid plesiosaurs, and a partial skull that probably pertain to a new and unnamed ichthyosaur taxon.

The general compositional character of the “Green Series” marine reptile fauna resembles that from other lower Toarcian European localities (e.g., BENTON and TAYLOR, 1984; GODEFROIT, 1994; URLICH et al., 1994). Unfortunately, the fragmentary nature of the material does not allow to test hypotheses of lower Toarcian marine reptile palaeobio-geography. Nevertheless, the presence of plesiosaur remains assignable to Rhomaleosauridae and Microcleididae in lower Toarcian-aged erratics of Ahrensburg (SACHS et al., 2016), combined with the occurrence of a possible non-microcleidid plesiosauroid in the “Green Series” suggests that at least three distinct plesiosaur taxa were present in the marine marginal ecosystems extending south of Fennoscandia. Moreover, it seems likely that plesiosaurs were a relatively common component in the North German Basin during lower Toarcian times (see Fig. 3). This is intriguing because it would contrast with our current understanding of lower Toarcian marine reptile faunas, which indicates that plesiosaurs were particularly less dominant as compared to ichthyosaurs and thalattosuchians (BENTON and TAYLOR, 1984; GODEFROIT, 1994; URLICH et al., 1994). This discrepancy could be attributable to specific ecological and/or biological constraints, but more likely corresponds to preservation biases. More research is therefore needed in order to provide more definitive data on the marine reptile diversity from the Toarcian of northern Germany.



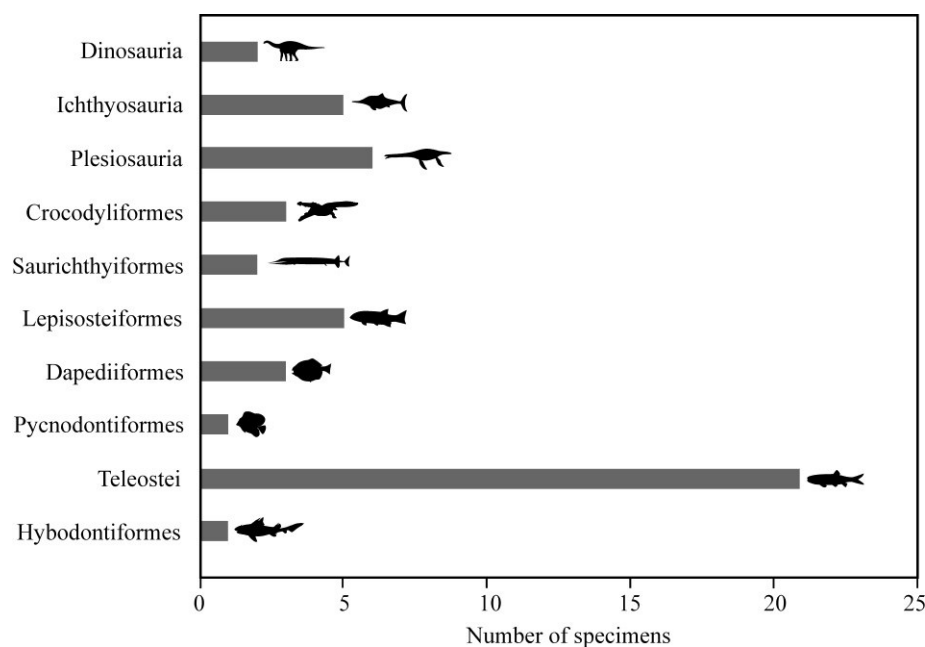


Figure 3. Composition of the “Green Series” vertebrate fauna (total number of fossil specimen is 48; see also Suppl. Table).

### 4.3 Fishes

Bony fishes form the dominant component of the “Green Series” vertebrate fauna, comprising at least eleven actinopterygian taxa belonging to five clades (see Table 1). Material of cartilaginous fish is, conversely, rare and represented by two fragmentary specimens, which can be assigned to Hybodontiformes indet. (an incomplete fine spine and a few placoid scales contained in a concretion; the latter specimen is held in the private collection of J. ANSORGE). The “Green Series” actinopterygian fauna is by far dominated by members of the family Leptolepidae (Teleostei). Reports of leptolepids in the “Green Series” of Grimmen and Dobbertin have been made since the late 19<sup>th</sup> century (e.g., GEINITZ, 1884; JAEKEL, 1929; NYBELIN, 1974; ANSORGE, 2007), but no detailed anatomical accounts have been provided so far.

#### 4.3.1 Leptolepidae

In the course of the present doctoral thesis, KONWERT and STUMPF (in press) compiled the first comprehensive study about the leptolepid fishes recovered from the “Green Series” (**Paper 3**). This study led to the recognition of six taxa based on cranial material, including *Leptolepis coryphaenoides*, *L. normandica*, *L. jaegeri*, a possible *Proleptolepis* and two yet unnamed taxa that were provisionally described as Leptolepidae sp. 1 and *Leptolepis* sp. 1, respectively, until more material is available.

From the known fossil record, fishes of the family Leptolepidae first appeared in the early Lower Jurassic (Sinemurian: ARRATIA and SCHULTZE, 1999; FOREY et al., 2010). They are common in the Early Jurassic of Europe (e.g., BRONN, 1830; AGASSIZ, 1832; RAYNER, 1937; WENZ, 1968; NYBELIN, 1974), but also were reported from the Lower Jurassic of South America (ARRATIA, 1987; ARRATIA and SCHULTZE, 1999). Notably, several synapomorphies of modern teleosts appear in this clade for the first time (ARRATIA, 1997, 1999, 2013, 2015). However, controversial issues concerning the taxonomic and morphological diversity of Leptolepidae still prevail.

An important step in order to clarify the taxonomic content of Leptolepidae was achieved by NYBELIN (1974), who defined Leptolepidae as including the Jurassic genera *Proleptolepis* (represented by three species from the early Lower Jurassic: *P. furcata* [type species], *P. elongata* and *P. megalops*) and *Leptolepis* (represented by six species from the late Early Jurassic: *L. coryphaenoides* [type species], *L. normandica*, *L. jaegeri*, *L. saltviciensis*, *L. autissiodorensis* and *L. nathorsti*, and one species from the Middle Jurassic: *L. woodwardi*), as well as the Late Jurassic species *Leptolepides sprattiformis* and *Tharsis dubius*. Subsequent phylogenetic studies, however, demonstrated that *Leptolepides* and *Tharsis* are not closely related to *Leptolepis* and *Proleptolepis*, and no support for the family was found (e.g., PATTERSON and ROSEN, 1977; ARRATIA, 1997, 1999, 2015). ARRATIA and THIES (2001) introduced a new teleost, ‘*Longileptolepis*’ *wiedenrothi* (= *Paraleptolepis wiedenrothi*; ARRATIA, 2003), based on a single specimen from the lower Toarcian Posidonia Shale Formation of northwestern Germany. A phylogenetic analysis conducted by ARRATIA and THIES (2001) revealed that *Longileptolepis* is nested between *Proleptolepis* and *Leptolepis*, of which the latter taxon is the most advanced. ARRATIA and HIKUROA (2010) revised the taxonomic content of Leptolepidae and restricted it to *Leptolepis*, *Proleptolepis* and *Longileptolepis* based on a set of uniquely derived postcranial characters. However, despite recent advances in understanding the taxonomic and morphological diversity of Leptolepidae, some taxa still need to be described in detail to complete our understanding of the early history of Teleostei. For instance, the distinction of species within the genus *Leptolepis* is still problematic, since the characters used in the literature are often insufficient and ambiguous, which make specific identification difficult.

The “Green Series” leptolepid assemblage is significant in revealing distinct combinations of morphological characters for use in differentiation between the species *Leptolepis coryphaenoides*, *L. normandica*, and *L. jaegeri*. While *Leptolepis coryphaenoides* and *L. normandica* show rather low levels of morphological disparity, *L. jaegeri* is readily distinguished from the

former species by its upper jaw morphology and dentition. These findings stand in strong contrast to WENZ (1968), who synonymized most of the late Early Jurassic species with *Leptolepis coryphaenoides*, arguing in favor of intraspecific variation.

One notable difference to previously published studies is that the preopercle was found to be variable in shape within *Leptolepis coryphaenoides* and *L. normandica*: i.e., presence/absence of a notch at the posteroventral margin of the bone. This is intriguing because among leptolepids, the presence of a notch at the posteroventral margin of the preopercle was previously considered as a diagnostic character of *Proleptolepis* and *Longileptolepis* (NYBELIN, 1974; ARRATIA and THIES, 2001). On the other hand, contrasting with *Leptolepis coryphaenoides* and *L. normandica*, within the material referred to *L. jaegeri*, a notch at the posteroventral margin of the preopercle was found to be absent, and it is possible that this difference, among others, may later prove to be of phylogenetic relevance.

Compared to the palaeobiogeographic data available for Early Jurassic leptolepids (NYBELIN, 1974), the “Green Series” material referred to *Leptolepis coryphaenoides*, *L. normandica*, and *L. jaegeri* expands the palaeobiogeographic distributions of these species far northwards, suggesting that they had a broad distribution within the CEB during Toarcian times. The presence of a specimen reminiscent of *Proleptolepis* is of particular note, since specimens attributed to this genus have been previously reported only from the Sinemurian of England and Portugal (NYBELIN, 1974; ANTUNES, 1974; FOREY et al., 2010). This suggests that *Proleptolepis* might had a wider temporal as well as spatial distribution than previously thought.

Viewed from a palaeoecological perspective, leptolepids potentially occupied a lower trophic level within the Early Jurassic marine vertebrate communities. Their comparatively small size and generalized morphology suggest that they were actively swimming animals with predominantly planktivorous dietary preferences. Notably, most leptolepids from the “Green Series” are represented by isolated skulls, while complete skeletons are rare. This type of preservation could be related to processes of decay, as suggested by URLICHS et al. (1994) or, alternatively, was biomechanically produced, perhaps by preying cephalopods (see EBERT et al., 2015). Direct evidence of predation on leptolepids is exemplified by fossil gastric contents, such as seen in a specimen of the bony fish *Saurorhynchus* recovered from the lower Toarcian Posidonia Shale Formation of southwestern Germany (URLICHS et al., 1994).

#### 4.3.2 Revision of *Saurorhynchus*

*Saurorhynchus* material also occurs in the “Green Series”, known from two specimens. More productive localities are known in England (Sinemurian, Toarcian: GARDINER, 1960; FOREY et al., 2010) as well as in north- and southwestern Germany (Toarcian: HAUFF, 1938; THIES, 1985). The family Saurichthyidae, to which the genus *Saurorhynchus* belongs, is a morphologically distinctive group of actinopterygian fishes, ranging from the Late Permian to Middle Jurassic (ROMANO et al., 2012; MAXWELL, 2016). Elongate skulls with acuminate jaws, long and slender bodies, posteriorly situated median fins and symmetrical tail fins characterize saurichthyid fishes (e.g., STENSIÖ, 1925; RIEPEL, 1985; ROMANO et al., 2012). They are usually interpreted as ambush predators based on ecomorphological evidence (e.g., LOMBARDO and TINTORI, 2005; ROMANO et al., 2012; KOGAN et al., 2015). However, some saurichthyids are interpreted as efficient surface-cruising predators (WU et al., 2011).

Early Jurassic saurichthyids are usually considered less morphologically disparate and taxonomically diverse than their Triassic relatives, consisting of only two valid species, *Saurorhynchus acutus* and *S. brevirostris* spanning the Early Jurassic. Historically, both species were differentiated almost entirely based on cranial ratios (WOODWARD, 1895; HAUFF, 1938; GARDINER, 1960). A taxonomic revision of *Saurorhynchus* from the Early Jurassic of England and Germany conducted by MAXWELL and STUMPF (in press) led to the identification of four species based on cranial osteology: *S. acutus*, *S. brevirostris*, *S. anningae*, sp. nov., and *S. hauffi*, sp. nov. (**Paper 4**).

While *S. brevirostris* and *S. anningae*, sp. nov. are known only from the Sinemurian of England, *S. acutus* and *S. hauffi*, sp. nov. shared a broad European distribution in the Toarcian immediately following the onset of the T-OAE, from Germany to England. The Sinemurian-aged *Saurorhynchus anningae*, sp. nov. and *S. brevirostris*, in particular, show disparity in cranial fineness as well as in tooth and jaw morphology. In contrast, the Toarcian-aged *S. acutus* and *S. hauffi*, sp. nov. show much lower levels of disparity, differing from each other in cranial morphology, dermal ornamentation, and position of the lateral extrascapular.

The four species are united by the presence of a dermohyal, dorsal position and multiple descending branches of the mandibular sensory canal and the pattern of dermal ornamentation composed of pitting and reticulation with a reduced or absent ganoine layer rather than parallel ganoine ridges and tubercles, to the exclusion of all Triassic saurichthyids.

The Sinemurian-aged *Saurorhynchus anningae* is the most divergent from the other *Saurorhynchus* species. Notably, it displays a suite of features that are almost certainly plesiomorphic, based on their wide distribution among Triassic saurichthyids, such as the shape of the mandible (i.e., posterior edge of mandible straight or only weakly sinusoidal, becoming gradually rounded ventrally), denticles on the parasphenoid rostrum ventral to the orbit, and squamation developed further anteriorly in the caudal region.

The Toarcian-aged *Saurorhynchus hauffi* also exhibits some unusual features, including retention of fringing fulcra on the median fins. Their presence in a Jurassic saurichthyid is somewhat unexpected (ROMANO et al., 2012), and may later prove to be of phylogenetic relevance.

The “Green Series” yielded a single specimen referable to *Saurorhynchus hauffi*, sp. nov. (Fig. 2E). This specimen is of special interest because it is three-dimensionally preserved, separating it from the other known cranial *Saurorhynchus hauffi* material, which in most cases has undergone considerable compaction, and future micro-CT based research on GG 20001 may prove to be of great significance in understanding the endocranial morphology of *S. hauffi*.

#### 4.3.3 Pycnodontiformes

Apart from encompassing fossil specimens of exceptional preservation, the “Green Series” actinopterygian assemblage is particularly important for including a new genus and species of pycnodontiform fish, *Grimmenodon aureum*, described by STUMPF et al. (in review) based on a diagnostic left prearticular dentition from the “Green Series” of Grimmen (**Paper 5**) (Fig. 2F). In addition, STUMPF et al. reported an isolated indeterminate pycnodontiform tooth crown from the upper Pliensbachian of the same site. Significantly, *Grimmenodon aureum*, gen. et sp. nov. is the second unambiguously identified pycnodontiform species from the Early Jurassic, in addition to *Eomesodon liassicus* from the early Lower Jurassic of western Europe (SAINT-SEINE, 1949; GARDINER, 1960). The new material adds to the particularly scarce record of early pycnodontiform fishes, suggesting that the Early Jurassic diversity of pycnodontiform fishes was larger than previously assumed and probably equaled that of the Late Triassic.

Pycnodontiform fishes form a morphologically and ecologically distinctive group of basal neopterygians, ranging from the Late Triassic to the middle Eocene (NURSALL, 1996, 1999, 2010; ARRATIA, 1999; POYATO-ARIZA, 2015). They are characterized *inter alia* by generally densely arranged molariform teeth on the unpaired vomer in the upper and the paired prearticulars in the lower jaws, which form an efficient crushing dentition, indicating durophagous feeding habits in

a wide range of pycnodontiforms (KRIWET, 2001a). So far, ca. 700 species have been described belonging to more than 45 genera (KRIWET, 2001c, 2005); only about 80 species are known from disarticulated or articulated skeletons. All remaining species are based on isolated dentitions or even teeth, but many taxa based on isolated dental material remain ambiguous. Nevertheless, LONGBOTTOM (1984), KRIWET (1999, 2005, 2008), POYATO-ARIZA and BERMÚDEZ-ROCHAS (2009), and SHIMADA et al. (2010) among others demonstrated that the morphology and arrangement of teeth on the vomer and prearticulars in pycnodontiform fishes provide unique combinations of characters and even allow identifying autapomorphic traits for taxa assignment and establishing reliable diagnoses.

The prearticular dentition of *Grimmenodon aureum*, gen. et sp. nov. is distinct from that of all other known pycnodontiforms by displaying unique tooth and ornamentation patterns. It bears five well-defined longitudinal tooth rows without intercalating teeth. The main row is well-defined and flanked medially by one tooth row and laterally by three tooth rows, with the first lateral row being inconspicuous and restricted to the anterior half of the tooth plate. The teeth are strongly ornamented in occlusal view, showing a considerably wide variability of ornamentation patterns. The indeterminate pycnodontiform tooth crown from the upper Pliensbachian, conversely, lacks any ornamentation, which seem to differentiate it from *Grimmenodon aureum*, gen. et sp. nov.

Tooth development in pycnodontiform fishes has been controversially discussed in the literature for more than 100 years. For instance, NURSALL (1996) proposed that pycnodontiforms formed a single generation of molariform teeth without replacement of individual teeth. Other authors suggested that the number of teeth was increased by the addition of larger ones formed posterior to functional teeth simultaneously to caudally directed bone growth (e.g., WOODWARD, 1893, 1895; THURNMOND, 1974; POYATO-ARIZA and WENZ, 2005), a view supplemented by LONGBOTTOM (1984) who proposed both an anterior and posterior additional tooth development, in which the anterior teeth were replaced by small irregularly arranged teeth.

In an effort to assess new information on the tooth development in pycnodontiform fishes, *Grimmenodon aureum*, gen. et sp. nov. was studied using micro-CT. The obtained data revealed the absence of neither non-functional teeth nor developing tooth germs preserved within the prearticular tooth plate. On the other hand, the posterior-most tooth in the main prearticular row in *Grimmenodon aureum*, gen. et sp. nov. is partially covered by spongy bone, which might suggest that this tooth was not fully functional and still developing at the time of death. In

conclusion, no replacement teeth were formed within the tooth-bearing bone but the authors hypothesize that new teeth were rather added posteriorly to functional teeth during bone growth. From a palaeoecological perspective, the recognition of a pycnodontiform fish in the lower Toarcian “Green Series” alters the perception of faunal and palaeoecological interactions in the marine vertebrate fauna obtained from this unit, separating it from all other time-equivalent European marine vertebrate communities (WENZ, 1968; HAUFF and HAUFF, 1981; URLICHS et al., 1994; DELSATE, 1999; VINCENT et al., 2013; WILLIAMS et al., 2015). This disparity, combined with the interpretation that these localities largely document more open-marine depositional environments, is in good accordance with the interpretation that pycnodontiforms were predominantly linked to marginal marine environments, as inferred from palaeobiogeographical and ecomorphological evidence (e.g., KRIWET, 2001a, b; POYATO-ARIZA, 2005; MARTÍN-ABAD and POYATO-ARIZA, 2013). This specific distribution pattern can be probably related to diverse environmental and/or biological constraints, such as swimming capacities and the availability of preferred food resources, but also to preservation biases (POYATO-ARIZA, 2005).

With regard to the robust molariform dentition seen in the prearticular of *Grimmenodon aureum*, gen. et sp. nov., this taxon appears to have been well-adapted to durophagy. In this context, it is interesting to note that the “Green Series” also yielded specimens of the neopterygian fishes *Dapedium*, *Tetragonolepis* and *Lepidotes*, whose dentitions are interpreted as being indicative of at least facultative durophagous feeding habits (e.g., QUENSTEDT, 1847; WOODWARD, 1897; THIES, 1991; SMITHWICK, 2015) (see Fig. 4). In consequence, based on indirect evidence, it seems reasonable to conclude that *Grimmenodon aureum*, gen. et sp. nov. was in competition with taxa like *Dapedium* and *Lepidotes*, and may have used alternative strategies in order to partition food resources efficiently and avoid direct competition.

From the known fossil record, pycnodontiforms first appeared in the Late Triassic of central Europe (KRIWET, 2001b), and three genera and species, *Brembodus ridens*, *Eomesodon hoferi*, and *Gibbodon cenensis*, were reported from the upper Norian marine deposits of the northern Tethys margin (GORJANOVIĆ-KRAMBERGER, 1905; TINTORI, 1981). Additional Norian pycnodontiform records of uncertain affinities but different from the three other Triassic pycnodontiforms were reported from epicontinental sea deposits of Belgium and Luxembourg (DELSATE and KRIWET, 2004). Isolated teeth from the Rhaetian of France assigned to *Gyrodus milinum* by HENRY (1876) represent teeth of *Colobodus* sp. Therefore, at least four different pycnodontiform taxa occurred prior to the Triassic-Jurassic mass extinction event, which is con-

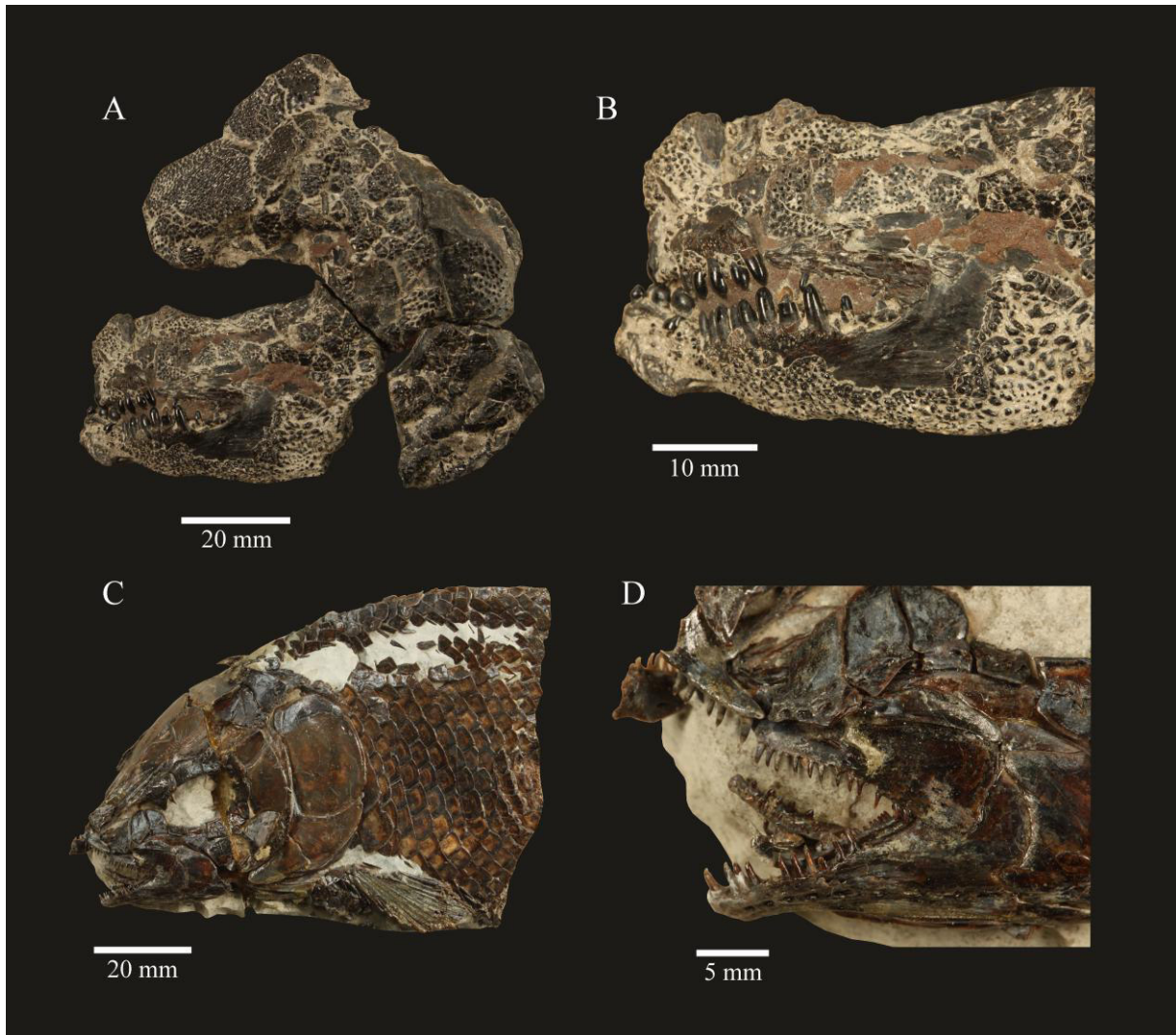


Figure. 4. Fishes from the “Green Series”. **A, B**, incomplete skull of *Dapedium* sp. (GG 441) in left lateral view (**A**), and close-up view of dentition (**B**); **C, D**, incomplete specimen of *Lepidotes elvensis* (GG 435) in left lateral aspect (**C**), and close-up view of dentition (**D**).

sidered to be one of the most dramatic environmental disruptions that took place during the Phanerozoic, with a loss of almost 50% of marine genera and significant terrestrial faunal and floral turnovers (e.g., RAUP and SEPKOSKI, 1982; YOUNG et al., 2014).

Early Jurassic pycnodontiform records are very rare and restricted to western Europe (SAINT-SEINE, 1949; GARDINER, 1960; DELSATE et al., 2002; DUFFIN, 2010). Obviously, the pycnodontiforms *Gibbodon* and *Brembodus* vanished before, or in conjunction with the Triassic-Jurassic mass extinction event. Only the genus *Eomesodon* can be considered to have crossed this boundary and is present with a single species, *E. liassicus*. Consequently, the apparent taxonomic diversity reduction in the Early Jurassic supports the supposition that pycnodontiform fishes also



were affected by the Triassic-Jurassic mass extinction event. However, the new pycnodontiform material from the Pliensbachian and Toarcian of Grimmer increase the standing diversity of pycnodontiforms in the Early Jurassic significantly. When corrected for sample size differences (excluding ambiguous taxa), it is evident that Early Jurassic pycnodontiform fish diversity more or less equaled that of the Late Triassic accepting the poor collection effort and restricted facies occurrences during the Early Jurassic. Nevertheless, it is hypothesized that pycnodontiform fishes were not or only marginally affected by the Triassic-Jurassic mass extinction event according to our current knowledge.

By the Middle Jurassic, pycnodontiform fishes seemingly became more abundant and diverse but still are represented mainly by isolated remains of several genera occurring in almost all stratigraphic stages (e.g., AGASSIZ, 1833–1844; SAUVAGE, 1867, 1880a, b; WOODWARD, 1892, 1895; GALTON et al., 1980; KRIWET et al., 1997). The taxonomic validity of most of these taxa, however, remains ambiguous for the moment but indicate nevertheless a possible increase in diversity and that pycnodontiforms achieved a very wide distribution early in their evolutionary history. More detailed analyses of these remains will provide a better understanding of early pycnodontiform diversity patterns in the future.

## **5. Prospectus**

The results derived from the present study provide new insights into the taxonomic, systematic, and ecological diversity of Early Jurassic European vertebrates, and hence offer promising clues for understanding Lower Jurassic vertebrate palaeobiodiversity patterns. Nevertheless, many taxa – especially bony fishes – still remain understudied, and therefore more research is needed in order to complete our current understanding of Early Jurassic vertebrate life. This should incorporate detailed re-examinations of available collection material including species-level revisions. In addition, imaging and statistical methods such as computed tomography and morphospace analyses should be applied more frequently as they offer exciting opportunities for future studies.

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**Supplementary Table.** Inventory of vertebrate fossils from the “Green Series” assessed for this study.

Taxon	Repository	Description	Locality/stratigraphic age
Gravisauria indet.	GG 411/1-4	Iliac acetabular process, distal right pubis, proximal left ischium, proximal right ischium	Grimmen, <i>falciferum</i> zone
Gravisauria indet.	GG 412	Dorsal neural spine	Grimmen, <i>falciferum</i> zone
<i>Stenopterygius</i> cf. <i>quadriscissus</i>	GG 436	Incomplete skull	Dobbartin, <i>falciferum</i> zone
Ichthyosauria indet.	NL uncatal.	Partial skull and associated postcranial elements	Grimmen, <i>elegantulum</i> subzone
Ichthyosauria indet.	GHM uncatal.	Presacral centrum	Grimmen, <i>falciferum</i> zone
Ichthyosauria indet.	GG 444	?sacral centrum	Grimmen, <i>exaratum</i> subzone
Ichthyosauria indet.	GG 422/1	?sacral centrum	Grimmen, <i>falciferum</i> zone
Plesiosauroidea indet.	GG 422/2	Cervical centrum	Grimmen, <i>falciferum</i> zone
Plesiosauroidea indet.	GG 422/3	Caudal centrum	Grimmen, <i>exaratum</i> subzone
Plesiosauria indet.	EMR uncatal.	Phalanx	Grimmen, <i>falciferum</i> zone
Plesiosauria indet.	GG 422/4	Three caudal vertebrae and other postcranial elements	Grimmen, <i>elegantulum</i> subzone
Plesiosauria indet.	GG 422/5	Cervical rib	Dobbartin, <i>falciferum</i> zone
Plesiosauria indet.	DMM 3989	Dorsal vertebrae and other postcranial elements	Grimmen, <i>elegantulum</i> subzone
cf. Plesiosauria indet.	MV 200250	Gastralia	Grimmen, <i>elegantulum</i> subzone
<i>Steneosaurus bollensis</i> (JAEGER, 1828)	GG 422/6	Incomplete skull and associated osteoderm	Grimmen, <i>falciferum</i> zone
Thalattosuchia indet.	PLM uncatal.	Partial rostrum with teeth	Grimmen, <i>falciferum</i> zone
Meoecrocodylia indet.	GG 422/7	Cervical vertebra	Grimmen, <i>falciferum</i> zone
Hybodontiformes indet.	GG 448	Fragmentary fin spine	Grimmen, <i>exaratum</i> subzone
<i>Saurorhynchus hauffi</i> sp. nov.	GG 20001	Incomplete skull	Grimmen, <i>exaratum</i> subzone
<i>Saurorhynchus</i> sp.	GG 447	Incomplete skull	Grimmen, <i>exaratum</i> subzone
<i>Lepidotes elvensis</i> (BLAINVILLE, 1818)	GG 435	Skull with pectoral girdle and part of the postcranial skeleton	Grimmen, <i>exaratum</i> subzone

<i>Lepidotes elvensis</i> (BLAINVILLE, 1818)	BGR I 4502	Skull with pectoral girdle and part of the postcranial skeleton	Dobbertin, <i>falciferum</i> zone
<i>Lepidotes</i> sp.	GG 440	Incomplete skull	Dobbertin, <i>falciferum</i> zone
<i>Lepidotes</i> sp.	GG 445	Incomplete skull	Grimmen, <i>exaratum</i> subzone
<i>Lepidotes</i> sp.	GG 449	Almost complete specimen	Grimmen, <i>exaratum</i> subzone
<i>Tetragonolepis</i> <i>semicincta</i> BRONN, 1830	GG 446	Incomplete specimen	Grimmen, <i>exaratum</i> subzone
<i>Dapedium</i> sp.	GG 441	Incomplete skull	Dobbertin, <i>falciferum</i> zone
<i>Dapedium</i> sp.	GG 450	Incomplete skull	Dobbertin, <i>falciferum</i> zone
<i>Grimmenodon aureum</i> gen. et sp. nov.	GG 437	Left prearticular with dentition	Grimmen, <i>exaratum</i> subzone
Leptolepidae sp. 1	GG 431/5a, b	Incomplete skull, preserved in part and counterpart	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis</i> <i>coryphaenoides</i> (BRONN, 1830)	GG 431/3	Incomplete skull	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis</i> <i>coryphaenoides</i> (BRONN, 1830)	GG 431/7	Almost complete specimen	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> <i>coryphaenoides</i> (BRONN, 1830)	GG 431/19	Skull with pectoral girdle	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> <i>coryphaenoides</i> (BRONN, 1830)	GG 431/20	Incomplete skull	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis</i> <i>coryphaenoides</i> (BRONN, 1830)	NRM P 6091 (cast of MNH P 23834)	Incomplete skull	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis normandica</i> NYBELIN, 1962	GG 431/2a, b	Skull with pectoral girdle and a few abdominal vertebrae, preserved in part and counterpart	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis jaegeri</i> AGASSIZ, 1832	GG 431/1	Skull with pectoral girdle	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis jaegeri</i> AGASSIZ, 1832	GG 431/6	Skull with pectoral girdle	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis jaegeri</i> AGASSIZ, 1832	GG 431/9a, b	Skull (acid prepared)	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis jaegeri</i>	GG 431/10	Almost complete specimen	Grimmen, <i>exaratum</i> subzone

AGASSIZ, 1832			
<i>Leptolepis jaegeri</i> AGASSIZ, 1832	GG 431/15	Incomplete skull	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis jaegeri</i> AGASSIZ, 1832	GG 431/16	Skull	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.1	GG 431/4a	Skull with pectoral girdle	Dobbertin, <i>falciferum</i> zone
<i>Leptolepis</i> sp.1	GG 431/17	Skull	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.1	GG 431/18	Skull	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.	GG 431/21	Left parietal	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.	GG 431/11	Skull with pectoral girdle	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.	GG 431/12	Almost complete specimen	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.	GG 431/14	Almost complete specimen	Grimmen, <i>exaratum</i> subzone
<i>Leptolepis</i> sp.	MV 202614	Isolated caudal fin	Grimmen, <i>exaratum</i> subzone
cf. <i>Proleptolepis</i> sp.	MV 202612	Fragmentary skull	Grimmen, <i>exaratum</i> subzone

## **Publications included in this dissertation**

**PAPER 1:** STUMPF, S., J. ANSORGE, and W. KREMPIEN. 2015. Gravisaurian sauropod remains from the marine late Early Jurassic (Lower Toarcian) of North-Eastern Germany. *Geobios* 48(3):271–279.

Author contribution: The project was conceived and designed by S. S. who also analyzed the data, prepared all figures/tables, wrote and revised the manuscript. J. A. and W. K. found part of the fossil material, and J. A. participated in the writing of the geological/stratigraphic part.

**PAPER 2:** STUMPF, S. 2016. New information on the marine reptile fauna from the lower Toarcian (Early Jurassic) “Green Series” of North-Eastern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 280(1):87–105.

**PAPER 3:** KONWERT, M., and S. STUMPF. In Press. Exceptionally preserved Leptolepidae (Actinopterygii, Teleostei) from the late Early Jurassic Fossil-Lagerstätten of Grimmen and Dobbertin (Mecklenburg-Western Pomerania). *Zootaxa*.

Author contribution: The project was conceived and designed by M. K. and S. S. Both authors acquired and analyzed the data, prepared the figures, wrote and revised the manuscript.

**PAPER 4:** MAXWELL, E. E., and S. STUMPF. In Press. Revision of *Saurorhynchus* (Actinopterygii: Saurichthyidae) from the Early Jurassic of England and Germany. *European Journal of Taxonomy*.

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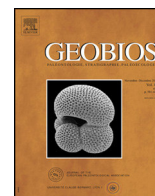
STUMPF, S, J. ANSORGE, and W. KREMPIEN. 2015. Gravisaurian sauropod remains from the marine late Early Jurassic (Lower Toarcian) of North-Eastern Germany. *Geobios* 48(3):271–279.

**PAPER 1**



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## Original article

# Gravisaurian sauropod remains from the marine late Early Jurassic (Lower Toarcian) of North-Eastern Germany<sup>☆</sup>



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## ABSTRACT

Basal sauropod remains recovered from the shallow-marine Lower Toarcian (*Harpoceras falciferum* ammonite zone) “Green Series” clay of Grimmen (North-Eastern Germany) are reported, representing, along with the inclusion of *Ohmdenosaurus* from the coeval Posidonia Shale of Southern Germany, the second unambiguous record of Early Jurassic sauropod body fossil remains from Europe. The material consists of two specimens: four partially preserved pelvic girdle elements and a dorsal neural spine, which were found during the last quarter of the 20th century, but remained unstudied due to their fragmentary condition. Based on the observed set of characters, both specimens can clearly be referred to Gravisauria, indicating close morphological resemblance to the late Early Jurassic Moroccan taxon *Tazoudasaurus*. The material is suggestive of derivation from one (or two?) ontogenetically immature individual(s) on account of being rather small in size compared to the corresponding elements of other basal sauropods; nevertheless, the possibility of phyletic dwarfism cannot be ruled out due to the Lower Toarcian palaeogeography. Given the fragmentary nature of the available material and the uncertainty as to whether both specimens belong to the same individual, the specimens are simply regarded as Gravisauria gen. et sp. indet. until more complete material is available.

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## 1. Introduction

The famous Lower Toarcian Posidonia Shale of Southern Germany is best known for its rich invertebrate and vertebrate faunas (e.g., Dames, 1895; Huene, 1922; Hauff and Hauff, 1981; Rieggraf et al., 1984; Urlichs et al., 1994; Großmann, 2007; Maisch, 2008). Exceptional well-preserved specimens of secondarily marine reptiles as ichthyosaurs and marine crocodiles are the highlights of many museum collections throughout the world. In addition to marine reptiles, also rare dinosaur remains have been recorded from the Lower Toarcian of Germany. The dinosaur material reported so far includes only two diagnostic taxa: the basal sauropod *Ohmdenosaurus liasicus* Wild, 1978, from the Posidonia Shale of Ohmden near Holzmaden (Baden-Württemberg, Southern Germany), and the basal thyreophoran *Emausaurus ernsti* Haubold, 1990, from coeval beds of Grimmen (Western Pomerania, North-Eastern Germany). Additionally, von Huene (1966) considered a fragmentary dorsal vertebra from an erratic boulder derived from the “Green Series” clay found near

Ahrensburg (Schleswig-Holstein, Northern Germany) as *Megalosauridae* indet., but as already implied by Carrano et al. (2012), this specimen is actually best identified as *Saurischia incertae sedis*, as it manifests characters found in dorsal vertebral centra of both theropods and sauropods (i.e., a convex anterior articulation surface and a distinct pleurocoelous fossa).

Here, we report basal sauropod remains from the Lower Toarcian of North-Eastern Germany consisting of a dorsal neural spine and four partially preserved pelvic girdle elements, including a preacetabular process of an ilium, a right pubis and two ischia – right and left. The bones were found isolated in the former clay pit of Grimmen during the last quarter of the 20th century, and remained unstudied due to their fragmentary condition. Recently, the dinosaurian nature was verified by the first author (Stumpf, 2012). In this paper, the skeletal elements are described and their taxonomic affinities are discussed.

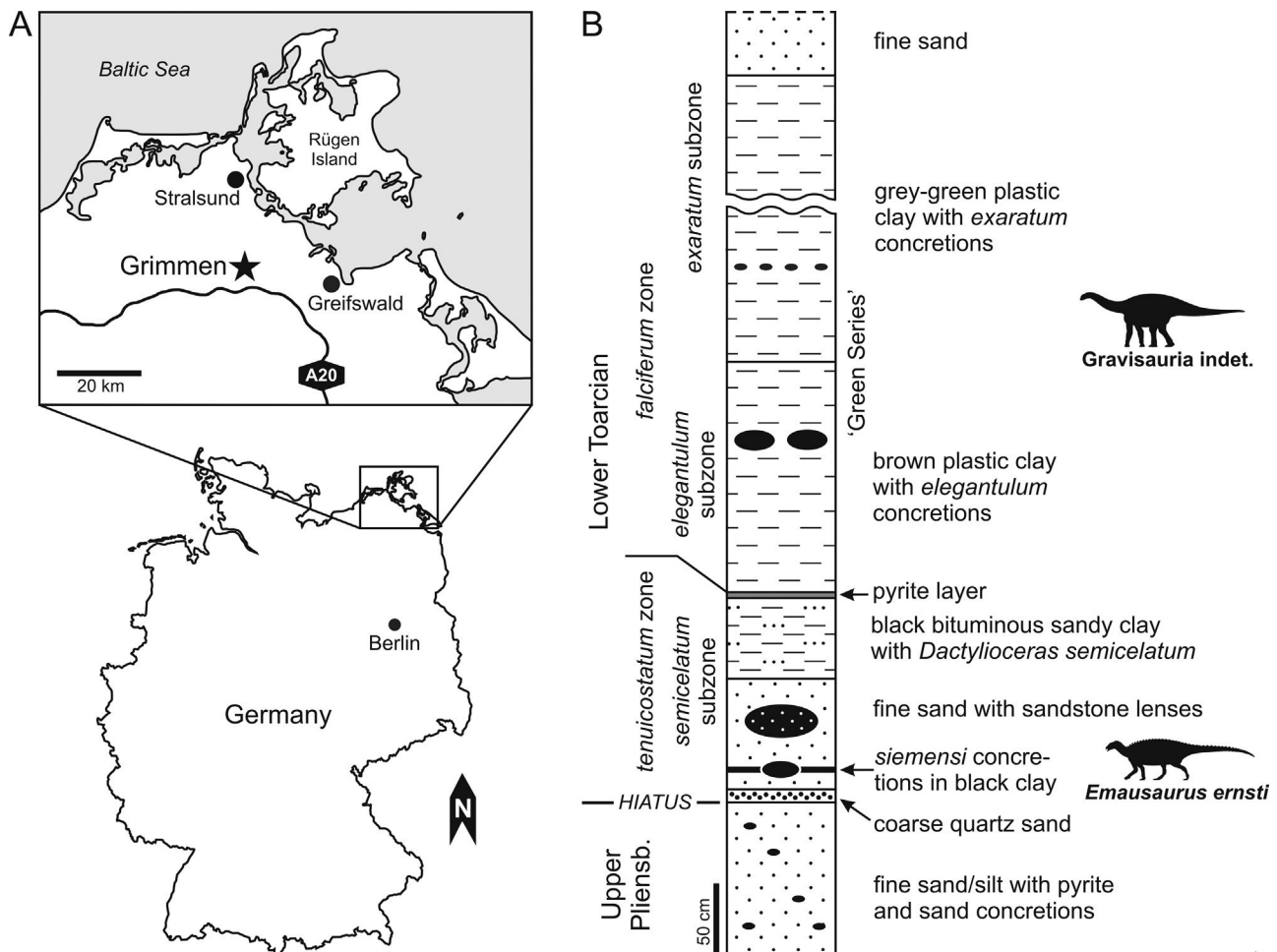
## 2. Geological setting

The sauropod remains were discovered in the former clay pit of Grimmen, Western Pomerania, North-Eastern Germany (Fig. 1(A)). The clay was mined in a Pleistocene dislocated raft with exposed Upper Pliensbachian to Lower Toarcian shallow-marine sediments

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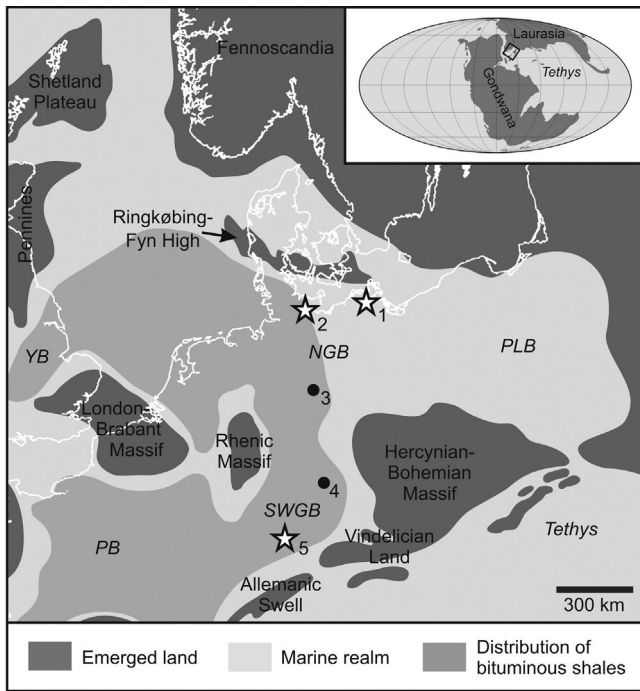
**Fig. 1.** Geographical and geological setting. **A.** Geographic location map. **B.** Stratigraphic standard section of Upper Pliensbachian to Lower Toarcian sediments of Grimmen (Western Pomerania, NE Germany). The stratigraphic positions of the dinosaur remains are indicated.

(Ernst, 1967, 1991; Ansorge, 2007; Fig. 1(B)). In 1995, clay extraction activities ended and today the deeper parts of the pit are flooded.

The oldest sediments exposed are Upper Pliensbachian sands. Following a hiatus, the Lower Toarcian (*tenuicostatum* zone) is built of a coarse- to fine-grained sand of shallow-marine origin. Within the sand, a thin clay layer contains carbonate concretions with *Lobolyceras siemensii*, indicating the *semicelatum* subzone. Then the sedimentary input became more fine-grained and finally, pure clay of the so-called “Green Series” of the *falciferum* zone was deposited in a restricted basin south of the Fennoscandian mainland. In the basal part of the “Green Series” clay is a distinct layer of carbonate concretions yielding monospecific iridescent ammonites of *Eleganticeras elegantulum* (*elegantulum* subzone). Higher up in the glaciotectionic disturbed section, grey plastic clay with a layer of flat small carbonate concretions follows, rarely exceeding 10 cm in diameter. These concretions, rich in marine invertebrates and terrestrial insects (Ansorge, 1996, 2003, 2007), yield the type ammonite of the *exaratum* subzone (*Harpoceras exaratum*). As the marine fossils clearly indicate, the depositional area of the “Green Series” was brackish with reduced salinity. This is exemplified by the absence of stenohaline invertebrates such as echinoderms and belemnites and an impoverished ammonite fauna poor in species, but with a high number of individuals (Ernst, 1967, 1991; Lehmkuhl, 1970). In the uppermost part of the section, the sedimentation of the “Green Series” clay turns into deposition

of fine quartz sand, indicating a reduction of water depth during sea level regression. Due to the lack of macrofossils, the age of the sand can only be assumed to belong also to the *falciferum* zone.

In Early Jurassic times, the depositional area was situated at the north-eastern margin of the North German Basin that covered much of Northern Germany (Fig. 2). In the northern part of the island of Rügen, Early Jurassic sediments are primary absent. This zone might be an emerged land area belonging to the Ringkøbing-Fyn High (Petzka et al., 2004), a probable source area for the terrestrial elements of the Grimmen taphocoenosis in addition to the Fennoscandian mainland. The deposition of bituminous Posidonia Shale in the deeper part of the basin turns to the North-East into plastic clay of the “Green Series”. Both types of sediments interfinger in the western parts of the states of Mecklenburg-Western Pomerania and Brandenburg (Petzka et al., 2004; Tessin, 2010). Like the Posidonia Shale, the “Green Series” clay also contains carbonate concretions, indicating coeval carbonate precipitation in the whole basin. The concretions of North-Eastern Germany can be correlated with those of the Brunswick area, Lower Saxony (Weitschat, 1973). Following Röhl and Schmid-Röhl (2005), the “Unterer Stein” of Southern Germany (Holzmaden area, Baden-Württemberg) corresponds to the *siemensii* concretions of Northern Bavaria (e.g., Schesslitz; Fig. 2). Consequently, the dating of both horizons into the *exaratum* subzone allows a correlation with *borealis* concretions of Brunswick area and *exaratum* concretions of Grimmen.



**Fig. 2.** Lower Toarcian palaeogeography of Central Europe. Localities mentioned in the text are indicated; localities with dinosaur remains are marked by a star. 1. Grimmen, Western Pomerania; 2. Ahrensburg, Schleswig-Holstein; 3. Schandelah, Lower Saxony; 4. Schesslitz, Bavaria; 5. Ohmden, Baden-Württemberg. NGB: North German Basin; PB: Paris Basin; PLB: Polish Basin; SWGB: South-West German Basin; YB: Yorkshire Basin. Map modified after Maisch and Ansorge (2004) and Pieńkowski (2004); insert map modified after Smith et al. (1994).

Besides marine and terrestrial invertebrates, the exposed sediments in Grimmen have yielded a considerable amount of marine vertebrate fossils, including remains of sharks, actinopterygians and marine reptiles (Ansorge, 2007; Zessin and Krempien, 2010; Stumpf, 2012). In addition to the marine vertebrates, the basal thyreophoran dinosaur *Emausaurus ernsti* was described from a carbonate concretion coming from the lowermost (*semicelatum* subzone) Lower Toarcian sequence (Haubold, 1990).

### 3. Material and methods

The new sauropod remains described herein come from the plastic clay of the “Green Series” of the *falciferum* zone. Since they were not associated with a carbonate concretion with guiding fossils, the precise age, however, cannot be firmly established due to glaciotectionic deformation of the entire section. The individual bones are fragmented and have suffered from erosion in some cases, which is likely to be the result of a combination of damage prior to the burial and distortion generated by glaciotectionic deformation stresses. Internally, void spaces are filled by sparitic calcite.

The first skeletal elements of the herein reported material were found by Wilfried Krempien and Wolfgang Zessin in 1978/1979. This material includes an iliac preacetabular process, a distal right pubis, and a proximal left ischium. Since all elements were found disarticulated but spatially associated, the material is interpreted to belong to a single individual. Independently to the previous finds, a proximal right ischium was discovered by Jörg Ansorge in 1985. Given the identical morphology and matching size of the overlapping portions of both ischia, the right ischium is assumed to belong to the earlier detected bones. Additionally, a dorsal neural spine was found by Stefan Liebermann in 1993.

Some of the pelvic elements were already figured by Zessin and Krempien (2010: figs. 8, 9, 11), but labelled as “indeterminate saurian limb bone fragments”. Through the courtesy of the collectors, the skeletal elements were donated to the Institute of Geography and Geology of the University of Greifswald, where the material is housed with inventory numbers GG411/1–4 and GG412. The nomenclature for vertebral laminae and associated fossae used in the text is based on Wilson (1999) and Wilson et al. (2011).

### 4. Systematic palaeontology

DINOSAURIA Owen, 1842  
SAURISCHIA Seeley, 1887  
SAUROPODOMORPHA von Huene, 1932  
SAUROPODA Marsh, 1878  
GRAVISAURIA Allain and Aquesbi, 2008  
GRAVISAURIA gen. et sp. indet.

Figs. 3–5

**Material:** Iliac preacetabular process (GG411/1); distal right pubis (GG411/2); proximal left ischium (GG411/3); proximal right ischium (GG411/4); dorsal neural spine (GG412).

**Locality:** Former clay pit of Grimmen (54°7'53.53" N, 13°3'29.88" E), Western Pomerania, North-Eastern Germany.

**Stratigraphic origin:** *Harpoceras falciferum* zone, Lower Toarcian, Early Jurassic.

**Measurements:** See Table 1.

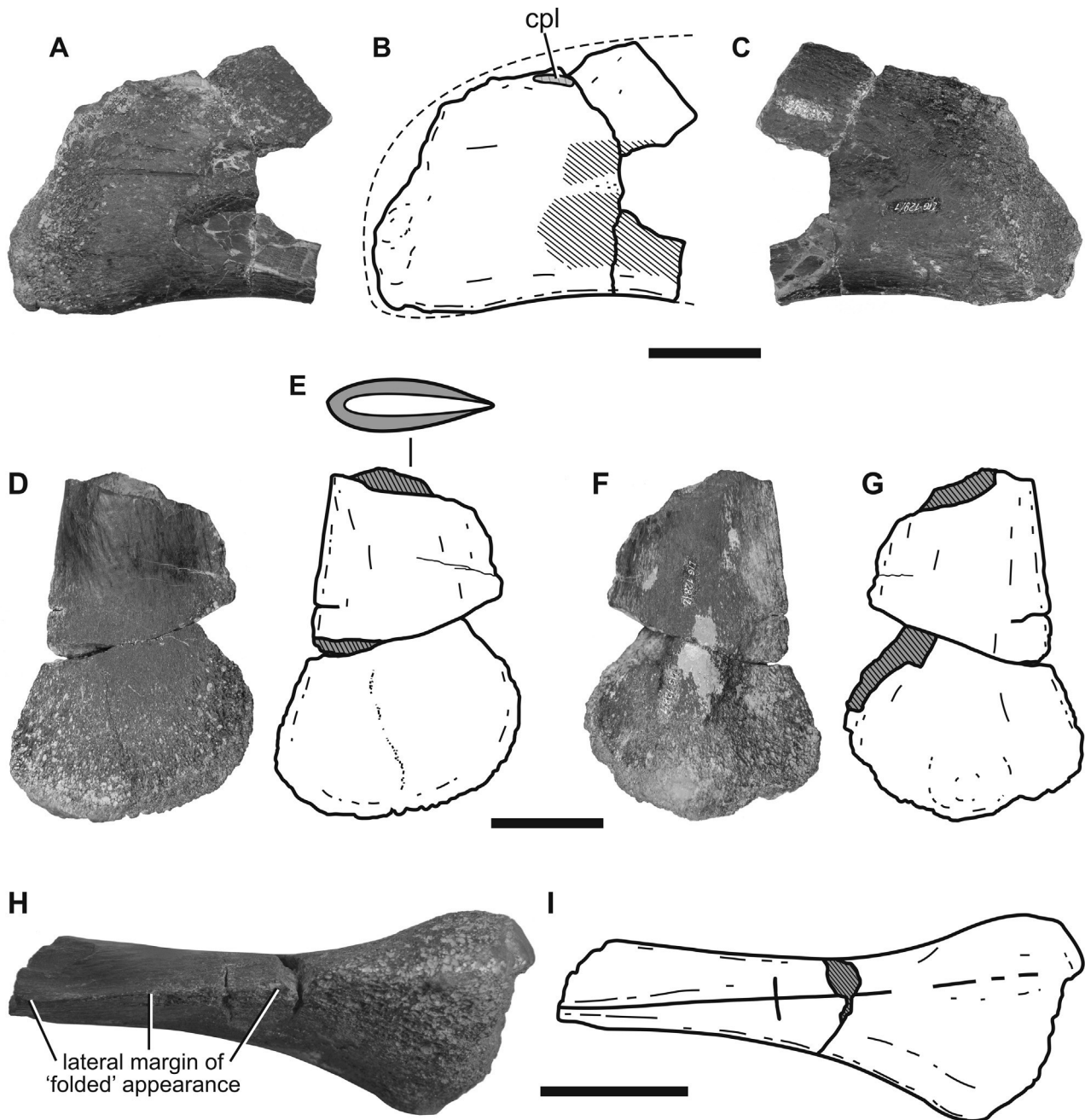
**Description:** As preserved, the iliac preacetabular process (GG411/1; Fig. 3(A–C)) forms an elongated and dorsoventrally well-developed subtriangular structure, being transversally narrow along its length, but slightly thickened at its tip. Unfortunately, it is not possible to say whether it represents a right or a left one. Whereas the dorsal margin is incomplete and slightly eroded, the ventral margin is mildly concave in lateral aspect and rounded in transversal section. Although dorsally incomplete, the iliac preacetabular process appears to have been anteriorly pointed rather than terminating with an anteriorly rounded expansion; however, this remains conjectural due to preservation. GG411/1 bears a fusiform, spiral-shaped coprolite attached close to its dorsal margin, measuring 12 mm in total length (Fig. 3(A, B)). Its morphology is consistent with referral to bony fish having a spiral valve (Hunt et al., 1994; Northwood, 2005); instead, coprolites

**Table 1**

Measurements (in mm) of the pelvic bone elements GG411/1–4 and the dorsal neural spine GG412 from the Lower Toarcian of Grimmen, Western Pomerania, NE Germany.

Element	Dimension	Measurements
Iliac preacetabular process GG411/1	Maximum anteroposterior length	116
	Maximum dorsoventral height	149
Distal right pubis GG411/2	Proximodistal length	161
	Anteroposterior length of distal end	117
Proximal left ischium GG411/3	Transverse width of distal end	66
	Length of the iliac peduncle	55
Proximal right ischium GG411/4	Proximodistal length	109
	Width across proximal end	134
Dorsal neural spine GG412	Length of pubic peduncle	55
	Length of iliac peduncle	53
	Length of chord across acetabulum	53
	Dorsoventral height	104
	Anteroposterior length of distal end	38
	Transverse width of distal end	41



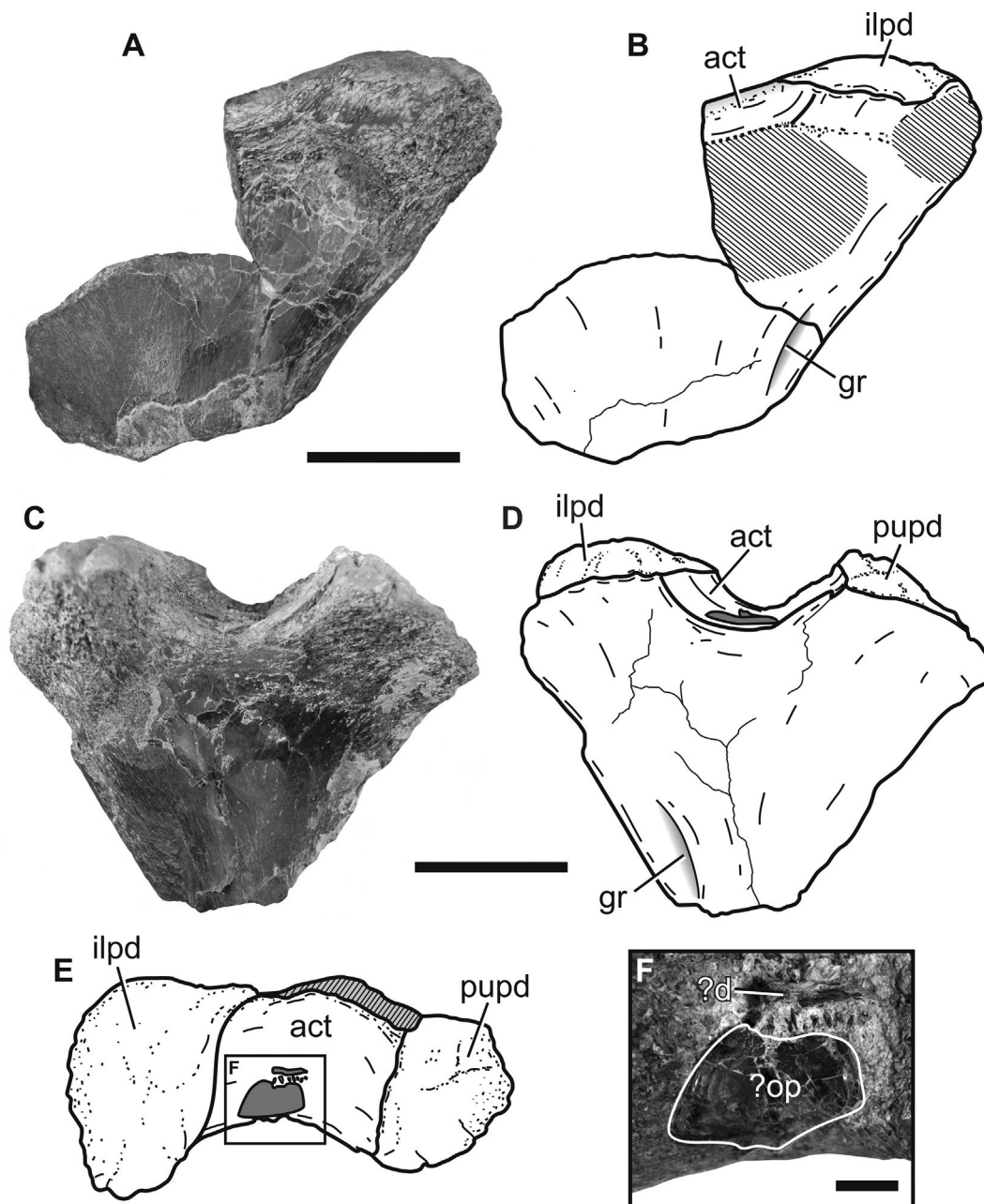


**Fig. 3.** *Gravisauria* gen. et sp. indet., GG411/1–2, Lower Toarcian of Grimmen (Western Pomerania, NE Germany). **A–C.** Iliac preacetabular process GG411/1 in ?lateral (A, B) and ?medial (C) view. **D–I.** Distal right pubis GG411/2 in anterior (D, E), posterior (F, G), and lateral (H, I) view. cpl: coprolite. Scale bars: 5 cm.

attributed to sharks display a heteropolar mode of spiraling (McAllister, 1985).

The distal half of a rather slender right pubis is preserved (GG411/2; Fig. 3(D–I)). The preserved portion of the pubic shaft is broad laterally and becomes gradually thinner towards its medial edge; the pubic symphysis, however, is irregularly preserved. In lateral aspect, the pubic shaft has a “folded” appearance (Fig. 3(H, I)). The internal bone structure can be seen from the fracture surface, demonstrating that it consists of an inner anteroposteriorly-flattened region made up of cancellous bone and an outer compact cortex, which becomes medially thinner. The distal end is strongly anteroposteriorly expanded relative to the shaft, exhibiting a convex rugose distal extreme which is subtriangular in outline.

A left proximal ischium (GG411/3; Fig. 4(A, B)) and a right proximal ischium (GG411/4; Fig. 4(C–E)) are preserved. The following description is mainly based on GG411/4, as it is more complete and considerably better preserved – though it has undergone some deformation, as indicated by compactional cracks. Both, the iliac and pubic peduncle are separated by the slightly incised acetabulum, which has an upstanding medial rim. Laterally attached to the acetabulum of GG411/4, two isolated bony fish remains are identifiable, including a possible lower jaw fragment which bears a single row of broken teeth and a ganoid specimen, presumably representing a right operculum (Fig. 4(E, F)). The iliac peduncle is transversally enlarged and rugose, slightly overhanging the lateral and medial surface of the proximal plate. It has a subtriangular outline, which slightly faces medially, with the

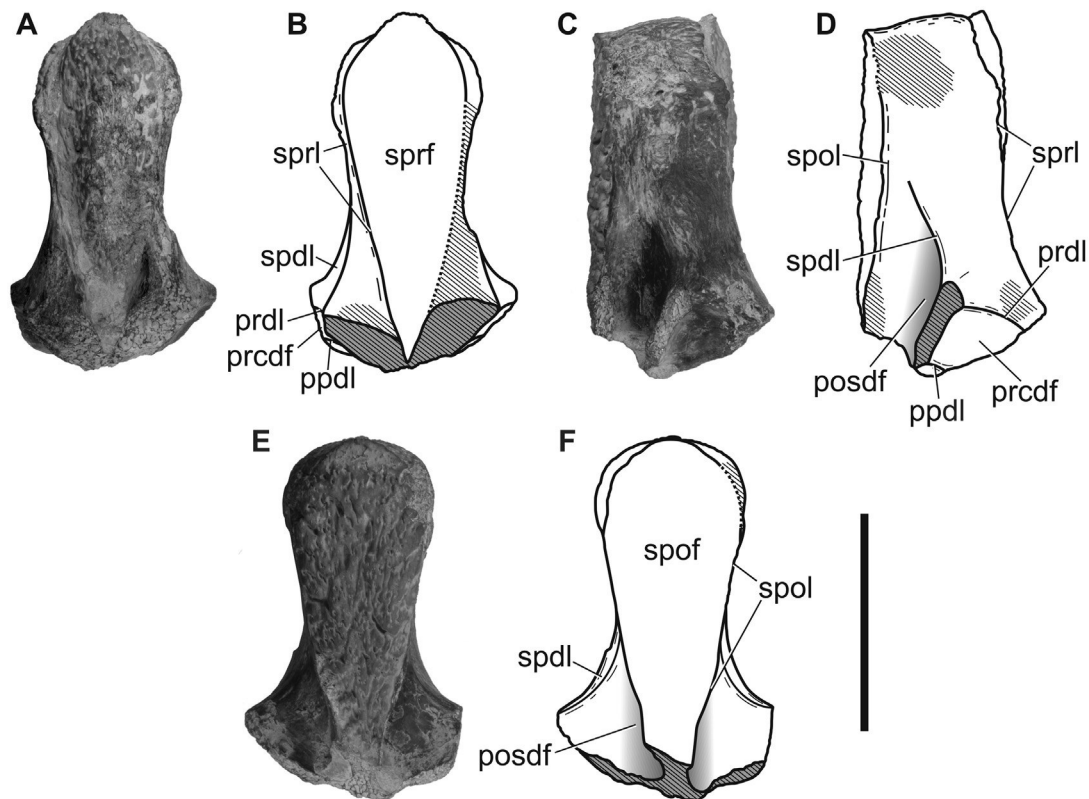


**Fig. 4.** *Gravisauria* gen. et sp. indet., GG411/3–4, Lower Toarcian of Grimmen (Western Pomerania, NE Germany). **A, B.** Proximal left ischium GG411/3 in lateral view. **C–E.** Proximal right ischium GG411/4 in lateral (C, D) and proximal (E) view. **F.** Close-up view of bony fish remains seen in GG411/4. act: acetabulum; d: dentary; gr: groove; ilpd: iliac peduncle; op: operculum; pupd: pubic peduncle. Scale bars: 5 cm (A–E), 5 mm (F).

long axis anteromedially oriented, creating a short anterior expansion which contributes to the medial acetabular rim. The pubic peduncle is rugose too, but it is less robust than the iliac peduncle and becomes transversally thinner in ventral direction; its terminal extent is missing due to breakage. The preserved portion of the ischial shaft is subtriangular in cross-section, with a broad and rounded dorsal margin and a sharp ventral margin. As seen in the broken surface, the outer compact cortex is broad dorsally and becomes thinner towards the ventral margin. A distinct groove is present, extending along the dorsolateral margin, showing rugosities and striations, probably representing the insertion site for the *M. flexor tibialis internus* 3 (Borsuk-Białynicka, 1977; Hutchinson, 2002).

The preserved neural spine (GG412; Fig. 5) is considered to come from the middle to posterior part of the dorsal vertebral series

based on its shape and the presence of a spinal laminae system composed of spinoprezygapophyseal, spinopostzygapophyseal and spinodiapophyseal laminae. GG412 is particularly robust and slightly spatulate in both anterior and posterior aspects. In dorsal view, it is subrectangular in outline, being transversally wider than anteroposteriorly long. GG412 is built up from both the spinopre- and spinopostzygapophyseal laminae that extend vertically along the anterolateral and posterolateral margins, respectively; they are subparallel in lateral aspect. Whereas the spinoprezygapophyseal laminae are particularly stout, the spinopostzygapophyseal laminae are formed by slightly developed ridges. The spinodiapophyseal lamina is well-defined and joins the neural spine laterally at approximately mid-height, but fails to contact the spinopostzygapophyseal lamina (Fig. 5(C, D)). The neural spine architecture of GG412 includes a distinct dorsoventrally elongated



**Fig. 5.** Gravisauria gen. et sp. indet., dorsal neural spine GG412, Lower Toarcian of Grimmen (Western Pomerania, NE Germany). **A, B.** Anterior view. **C, D.** Right lateral view. **E, F.** Posterior view. posdf: postzygapophyseal spinodiapophyseal fossa; ppdl: paradiapophyseal lamina; prcdf: prezygapophyseal centrodiapophyseal fossa; prdl: prezygapophyseal lamina; spdl: spinodiapophyseal lamina; spof: spinopostzygapophyseal fossa; spol: spinopostzygapophyseal lamina; sprf: spinoprezygapophyseal fossa; sprl: spinoprezygapophyseal lamina. Scale bar: 5 cm.

postzygapophyseal spinodiapophyseal fossa, bounded anteriorly by the spinodiapophyseal lamina and posteriorly by the spinopostzygapophyseal lamina. It also includes a shallowly-developed prezygapophyseal centrodiapophyseal fossa, which is bounded dorsally by the prezygapophyseal lamina and ventrally by the paradiapophyseal lamina; but there is no sign of the presence of a prezygapophyseal spinodiapophyseal fossa. Both the spinopre- and spinopostzygapophyseal fossae bear prominent rugosities for the attachment of interspinal ligaments, extending ventral to the base of the spine.

**Remarks:** The pelvic girdle elements GG411/1–4 can be clearly placed among the Sauropoda, on account of the presence of an elongated and strongly dorsally expanded iliac preacetabular process, and because of the anteroposteriorly expanded distal pubic end with a convex rugose surface. Although GG411/1–4 does not preserve any synapomorphic characters to clarify its phylogenetic position within Sauropoda, the iliac preacetabular process GG411/1 is consistent with referral to Gravisauria, since it is the first sauropod clade to have extensive and strongly dorsoventrally developed iliac preacetabular processes, contrasting with the plesiomorphic condition of non-gravisaurian sauropodomorphs (e.g., *Yunnanosaurus* [Young, 1942]; *Melanorosaurus* [Galton et al., 2005]; *Lessemsaurus* [Pol and Powell, 2007]), in which this process displays an anteroposteriorly shortened and less extensive dorsoventral development.

The right pubis GG411/2 also indicates a gravisaurian affinity, as it bears a distal end that is strongly anteroposteriorly expanded relative to the shaft, resembling the morphology of the corresponding portions of the pubes of *Vulcanodon* (Cooper, 1984), *Tazoudasaurus* (Allain and Aquesbi, 2008), *Barapasaurus* (Bandyopadhyay et al., 2010) and more advanced sauropods, separating it

from non-gravisaurian sauropodomorphs, which have less expanded distal pubic ends (e.g., *Jingshanosaurus* [Zhang and Yang, 1994]; *Aardonyx* [Yates et al., 2010]; *Antetonitrus* [McPhee et al., 2014]; *Lessemsaurus* [Pol and Powell, 2007]). Furthermore, the distal end of GG411/2 has a convex rugose distal acetabular rim that is subtriangular in outline with the transverse width 0.56 times that of the anteroposterior length, a condition, which is very similar to that seen in *Tazoudasaurus*, both in morphology and proportion (Allain and Aquesbi, 2008: tabl. 5). Significantly, the lateral shaft margin of GG411/2 has a “folded” appearance, presumably representing an autapomorphy of GG411/1–4 as this morphology contrasts with the general condition seen in sauropodomorphs, in which the pubes are laterally rounded.

The ischia GG411/3–4 resemble those of *Tazoudasaurus* in exhibiting a subtriangular iliac peduncle which create a short anteriorly directed expansion to reach the medial acetabular rim (Allain and Aquesbi, 2008) – a feature differing from *Vulcanodon*, in which the iliac peduncle forms a distinct anterolaterally directed expansion (Cooper, 1984). As in other sauropods (e.g., *Tazoudasaurus* [Allain and Aquesbi, 2008]; *Cetiosaurus* [Upchurch and Martin, 2003]; *Neuquensaurus* [Otero, 2010]), GG411/3–4 bear distinct grooves that extend along their dorsolateral margins. The presence of such an ischial groove is also known to be present in sauropod outgroups including basal sauropodomorphs, theropods and ornithischians (Langer, 2003; Yates, 2003). Unfortunately, the ontogenetic stage of GG411/1–4 remains unresolved, but the rather small sizes of the individual bones suggest that they derive from an ontogenetically immature individual.

Overall, GG411/1–4 indicates close resemblance to the basal gravisaurian *Tazoudasaurus*, especially regarding the shape and proportions of the distal pubic end combined with the development



of the ischial proximal plate. Unfortunately, the preservation of the iliac preacetabular process (GG411/1) is not adequate enough to compare it meaningfully with that of the latter taxon, in which this process terminates in a lobe-shaped expansion (Allain and Aquesbi, 2008), contrasting distinctly with the general condition of non-neosauropodan sauropods where the iliac preacetabular process is subtriangular in profile. The presence of a potential autapomorphy in GG411/1–4 (a “folded” pubic shaft) suggests that it represents a new taxon distinct from known gravisaurian sauropods. However, given the incompleteness and fragmentary nature of the available material, a new name is not erected and it is here considered as an indeterminate gravisaurian sauropod until more material is available. The fossil association of disarticulated sauropod and bony fish remains including a coprolite probably represents a localized accumulation generated by hydraulic transport and reworking, suggesting that the material remained exposed on the seabed for some time prior to burial.

The presence of spinoprezygapophyseal, spinopostzygapophyseal and spinodiapophyseal laminae on the dorsal neural spine clearly demonstrates the sauropod identity of GG412. Amongst sauropods it can be positively referred to Gravisauria because of being distally transversally wider than anteroposteriorly long (Allain and Aquesbi, 2008), a character stage previously considered to be diagnostic of Eusauropoda (Wilson and Sereno, 1998; Wilson, 2002). This condition differs from that of non-gravisaurian sauropods such as *Antetonitrus* (McPhee et al., 2014) and *Lessemsaurus* (Bonaparte, 1999), in which the dorsal neural spines retain the plesiomorphic condition of basal sauropodomorphs in being laterally compressed – though this feature also manifests itself in some basal sauropods more derived than the latter taxa (e.g., *Isanosaurus* [Buffetaut et al., 2000]; *Shunosaurus* [Zhang, 1988]). The presence of a distinct spinoprezygapophyseal lamina which extends vertically along the anterolateral margin of the spine also indicates a gravisaurian affinity, separating GG412 from more basal sauropodomorph outgroups, which lack spinoprezygapophyseal laminae or display only incipiently developed laminae.

The above discussed characters of GG412, combined with the development of strong rugosities on both the anterior and posterior faces instead of pre- and postspinal laminae found in *Macronaria* and *Diplodocoidea* (Salgado et al., 1997; Upchurch, 1998; Carballido et al., 2011), most closely resemble dorsal neural spines of *Tazoudasaurus* (Allain and Aquesbi, 2008), *Cetiosaurus* (Upchurch and Martin, 2002), *Spinophorosaurus* (Remes et al., 2009), and *Patagosaurus* (Bonaparte, 1986). Further evidence supporting the placement of GG412 within Gravisauria is indicated by the presence of a well-developed spinodiapophyseal lamina, since this character stage is present in the dorsal neural spines of *Tazoudasaurus* and more derived sauropods (Allain and Aquesbi, 2008; Wilson et al., 2011). Exceptions to this include *Kotasaurus* (Yadagiri, 2001), *Spinophorosaurus* (Remes et al., 2009), *Cetiosaurus* (Upchurch and Martin, 2002) and *Shunosaurus* (Zhang, 1988), which lack spinodiapophyseal laminae or display only weakly developed ridges. GG412 is reminiscent of middle dorsal neural spines of *Tazoudasaurus* in exhibiting a spinodiapophyseal lamina that fails to contact the spinopostzygapophyseal lamina (Allain and Aquesbi, 2008), suggesting that GG412 can be excluded from the (*Barapasaurus* + (*Patagosaurus* + (Omeisauridae + (*Jobaria* + Neosauropoda)))) clade of Wilson (2002), in which these laminae merge to form a composite lateral lamina. Notably, GG412 morphologically differs from *Tazoudasaurus* and more advanced sauropods in lacking a prezygapophyseal spinodiapophyseal fossa, which probably represents an autapomorphic feature. Furthermore, the prezygapophyseal centrodiapophyseal fossa as even the prezygo- and the paradiapophyseal lamina are less well-developed in

GG412, as compared to those seen in dorsal neural spines of other gravisaurian sauropods. However, the morphological variation of sauropod neural spine laminae and fossae depending on the ontogenetic stage and placement of the vertebra within the dorsal series (see Wedel, 2003; Allain and Aquesbi, 2008; Carballido et al., 2012; Carballido and Sander, 2013) reveals that these features are of dubious diagnostic significance. Regrettably, GG412 does not provide any information in order to determine its ontogenetic stage, but as it is the case in GG411/1–4, its comparatively small size is indicative of belonging to a not fully grown individual. Consequently, given the possibility of ontogenetic bias and the uncertainty as to whether GG412 + GG411/1–4 belong to a single individual (which at least cannot be ruled out), the dorsal neural spine GG412 is also simply regarded as an indeterminate gravisaurian sauropod.

## 5. Discussion

The Lower Toarcian vertebrate assemblage of Grimmer requires transportation processes of allochthonous elements. Therefore, the sauropod remains may be remnants of drifting carcasses that have been washed by rivers draining the Fennoscandian mainland into the epicontinental sea, or alternatively, originated from the Ringkøbing-Fyn High. In contrast, the compacted pile of disarticulated cranial and postcranial elements of the basal thyreophoran *Emausaurus* found in a carbonate concretion has been suspected to be a Speiballen (i.e., a compacted mass of indigestible stomach contents) regurgitated by a large marine reptile (Ernst in Haubold, 1991; see Thies and Hauff, 2013 for a review of Jurassic vertebrate Speiballen).

The presence of skeletal elements of two sauropods of similar size, taxonomic affinities and stratigraphic age suggests that they derive from a single individual; however, this remains conjectural. In the light of being comparably small in size compared to the corresponding elements of other basal sauropods, it might be possible that the sauropod remains reported here originate from not completely ontogenetically mature individuals. The Ringkøbing-Fyn High as a potential source area, however, also gives credence to the idea of phyletic dwarfism (*sensu* Gould and MacFadden, 2004), but further material is crucially needed to test this hypothesis.

The Grimmer sauropod material add to the highly incomplete Early Jurassic sauropod record, being the second unambiguous body fossil record from Europe – even though rich sauropod ichno-assemblages have been reported from the Early Jurassic of Italy (Dalla Vecchia, 1994; Avanzini et al., 2008), Poland (Gierliński, 1997; Gierliński and Sawicki, 1998; Gierliński and Pieńkowski, 1999; Gierliński et al., 2004), and Romania (Pieńkowski et al., 2010). Although the lack of overlapping elements prevents a detailed comparison of GG411/1–4 and GG412 to *Ohmdenosaurus*, which has been described on the basis of a partial right hindlimb (including a tibia, astragalus and calcaneum) from the Lower Toarcian Posidonia Shale of Southern Germany (Wild, 1978), it is noteworthy that the Grimmer sauropod material shows closest morphological similarities to the Early Jurassic (Pliensbachian-Toarcian) Moroccan taxon *Tazoudasaurus*, while *Ohmdenosaurus* most closely resembles the probable non-eusauropodan gravisaur *Rhoetosaurus* from the Middle Jurassic of Australia in having a comparably slender tibia and a dorsoventrally compressed astragalus (see Nair and Salisbury, 2012). So, these different taxonomic affinities suggest the occurrence of at least three sauropod taxa (or a possible minimum of two taxa) in the Lower Toarcian of Germany; but this must be regarded as tentative until more complete material is available in order to provide a closer assessment of their systematic relationships.



## 6. Conclusions

The herein described sauropod remains recovered from the shallow-marine Lower Toarcian “Green Series” clay of Grimmer (Western Pomerania, North-Eastern Germany) are clearly referable to Gravisauria, indicating close morphological resemblance to *Tazoudasaurus*. Along with the inclusion of the basal thyreophoran *Emausaurus*, they represent the second dinosaur record from this site. Despite being fragmentary and indeterminate, this material is significant as it constitutes the second unambiguous occurrence of Early Jurassic sauropod body fossils from Europe, adding to the particularly scarce record of basal sauropods as a whole.

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**PAPER 2**

# New information on the marine reptile fauna from the lower Toarcian (Early Jurassic) “Green Series” of North-Eastern Germany

Sebastian Stumpf

With 6 figures and 2 tables

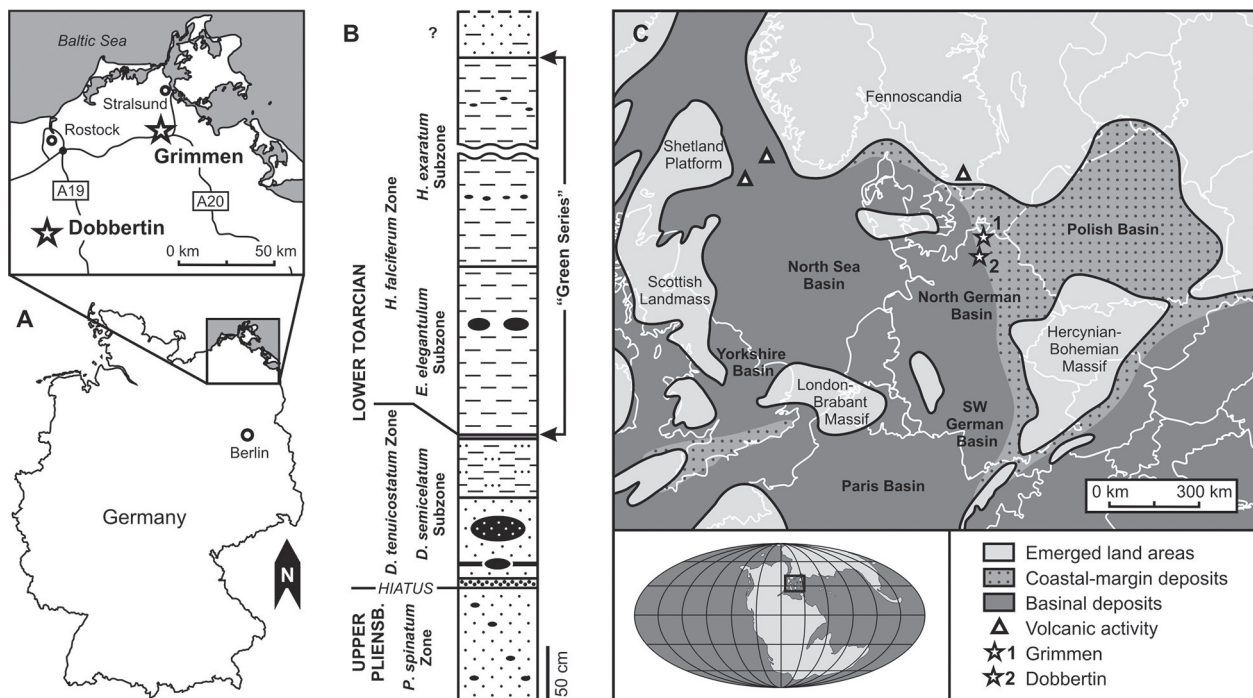
**Abstract:** The marine lower Toarcian (Early Jurassic) formations outcropping in Europe are widely known to have produced diverse faunas of secondarily marine reptiles, especially coming from black bituminous shales and marlstones of Western Europe. Conversely, little attention has been paid to marine reptile material recovered from time-equivalent beds of North-Eastern Germany due to the scarcity of productive localities. Here, a previously undescribed marine reptile assemblage comprising ichthyosaur, plesiosaur and thalattosuchian crocodyliform remains from the marine marginal lower Toarcian (the *Harpoceras falciferum* ammonite Zone) “Green Series” of North-Eastern Germany is reported, complementing previous records of these groups from Northern Germany with an early Toarcian age. Although fragmentary and largely indeterminate, this material is significant in indicating the presence of a probable new and unnamed ichthyosaur taxon. Moreover, the marine reptile material described herein is significant because it includes the first reliable report of both plesiosaurs and thalattosuchian crocodyliforms from the lower Toarcian of North-Eastern Germany, confirming their presence in this region during Toarcian times.

**Key words:** Ichthyosauria, Plesiosauria, Thalattosuchia, Toarcian, North-Eastern Germany.

## 1. Introduction

The European record of Toarcian (Early Jurassic) marine vertebrates includes abundant fossils of secondarily marine reptiles. The bulk of these finds have been recovered from lower Toarcian black bituminous shales and marlstones of Western Europe since the beginning of the 18<sup>th</sup> century (FRAAS 1891; BENTON & TAYLOR 1984; GODEFROIT 1994). Conversely, little attention has been paid to marine reptile remains recovered from time-equivalent beds of North-Eastern Germany. In this region, the lower Toarcian crops out only in the Pleistocene dislocated deposits of Grimmen and Dobbertain (Mecklenburg-Western Pomerania), both exposing a thick package of pure clay, referable to as the “Green Series”. Although these clay deposits have been

studied for more than a century (e.g., GEINITZ 1880, 1884, 1894; JAEKEL 1925; ERNST 1967, 1991, 1992; ANSORGE 1996, 2007; SELDEN & DUNLOP 2014; STUMPF et al. 2015), the marine reptile material thoroughly studied so far is limited to two ichthyosaur specimens coming from the “Green Series” of Dobbertain. The first mention of ichthyosaur remains from the lower Toarcian “Green Series” clay deposits of Dobbertain was given by GEINITZ (1900a, b) who notes the presence of four articulated caudal centra. This specimen was later referred to *Stenopterygius* ‘*zetlandicus*’ (= *S. triscissus*) by VON HUENE (1922), and recently refined by MAISCH & ANSORGE (2004) to Neoichthyosauria indet. MAISCH & ANSORGE (2004) additionally assigned a partial skull to *Stenopterygius* cf. *quadrisissus*. The presence of marine reptile material in the lower Toarcian “Green



**Fig. 1.** (A) Geographical map showing the positions of the Early Jurassic localities of Dobbartin and Grimmen. (B) Stratigraphic standard section of the upper Pliensbachian to lower Toarcian succession of Grimmen. (C) Toarcian palaeogeography of Central and Western Europe (maps modified from SMITH et al. 1994; PIEŃKOWSKI 2004; RÖHL & SCHMID-RÖHL 2005; DERA et al. 2011; KORTE et al. 2015).

Series” of Grimmen is known since the second half of the 20<sup>th</sup> century (ZESSIN 1995, 1998, 2001; ZESSIN & KREMPIEN 2010), but has never been studied in any detail.

In the present paper a previously undescribed marine reptile assemblage comprising ichthyosaur, plesiosaur and thalattosuchian crocodyliform remains from the lower Toarcian “Green Series” is reported, with comments on their significance in understanding the lower Toarcian marine reptile fauna from Northern Germany.

## 2. Geological and stratigraphic setting

Although laterally extended in North-Eastern Germany, the Early Jurassic only crops out in the abandoned clay pits of Grimmen and Dobbartin (Mecklenburg-Western Pomerania; Fig. 1A), both exposing a parautochthonous succession of upper Pliensbachian to lower Toarcian marine strata that were glacially dislocated during the Pleistocene ice advances (ERNST 1967, 1991, 1992). The

Early Jurassic strata exposed in the Grimmen clay pit most probably originate from the “Grimmener Wall” anticline (GEHL 1965), which is located a few kilometres north of the actual position. The Early Jurassic strata outcropping at Dobbartin is, otherwise, assumed to derive from the top of the Krakow salt structure, located about 10 kilometres north-east of the actual position (WIENHOLZ 1957). Given the glaciotectonic deformation of the entire sections and the present outcrop situations, their original thicknesses cannot be firmly established.

The Early Jurassic stratigraphic sequence outcropping in the Grimmen clay pit (Fig. 1B) is characterized by a hiatus at the Pliensbachian/Toarcian transition (i.e., the upper part of the upper Pliensbachian *P. (Pleuroceras) spinatum* Zone and probably much of the lower Toarcian *D. (Dactylioceras) tenuicostatum* Zone are absent; ERNST 1991). The lower Toarcian interval mainly consists of fine-grained sand that passes upwards into black bituminous, laminated silty clay and pure clay, reflecting a retrograding near-shore depositional environment (ERNST 1967, 1991;



**Table 1.** Inventory of lower Toarcian marine reptile remains assessed for this study.

Taxon	Description	Specimen number	Locality	Stratigraphic age	Figure
Ichthyosauria indet.	Partial skull and associated postcranial elements	NLWL uncatalogued	Grimmen clay pit	<i>E. elegantulum</i> Subzone	2A, B
Ichthyosauria indet.	Presacral centrum	GHM uncatalogued	Grimmen clay pit	<i>H. falciferum</i> Zone	2C-G
Ichthyosauria indet.	?sacral centrum	GG 422/1	Grimmen clay pit	<i>H. falciferum</i> Zone	2H-L
Plesiosauroidea indet.	Cervical vertebra	GG 422/2	Grimmen clay pit	<i>H. falciferum</i> Zone	3A-D
Plesiosauroidea indet.	Caudal centrum	GG 422/3	Grimmen clay pit	<i>H. exaratum</i> Subzone	3E-H
Plesiosauria indet.	Phalanx	EMR uncatalogued	Grimmen clay pit	<i>H. falciferum</i> Zone	3I
Plesiosauria indet.	Three caudal vertebrae and other postcranial elements	GG 422/4	Grimmen clay pit	<i>E. elegantulum</i> Subzone	3J-L
cf. Plesiosauria indet.	Gastralia	MV 200.250	Grimmen clay pit	<i>E. elegantulum</i> Subzone	3M, N
Plesiosauria indet.	Cervical rib	GG 422/5	Dobbartin clay pit	<i>H. falciferum</i> Zone	4
<i>Steneosaurus bollensis</i>	Partial skull and associated osteoderm	GG 422/6	Grimmen clay pit	<i>H. falciferum</i> Zone	5
Mesoeucrocodylia indet.	Cervical vertebra	GG 422/7	Grimmen clay pit	<i>H. falciferum</i> Zone	6A-F
Thalattosuchia indet.	Rostrum with teeth	PLM uncatalogued	Grimmen clay pit	<i>H. falciferum</i> Zone	6G-I

PRAUSS 1996). The top of the Early Jurassic section is represented by fine-grained sand with intercalated clay streaks containing plant remains (ERNST 1991; PRAUSS 1996), indicating a reduction of water depth during relative sea-level fall. The precise stratigraphic position of this sandy interval, however, is unknown due to the lack of index fossils, but according to the sequence stratigraphic framework proposed by ZIMMERMANN et al. (2015), an upper lower Toarcian age is probable. The lower Toarcian sedimentary succession outcropping at Dobbartin is reminiscent of that exposed at Grimmen, but some lithological units lack biostratigraphically significant ammonites (ERNST 1992; ANSORGE & OBST 2015). The stratigraphic ages of these units, however, can be broadly determined by means of lithostratigraphy and ammonite associations (see ANSORGE & OBST 2015 and references therein).

The marine reptile-bearing sequences exposed at Grimmen and Dobbartin are represented by thick packages of pure clay containing fossiliferous carbonate concretions, used to date the clay deposits biostratigraphically to the lower Toarcian *H. (Harpoceras) falciferum* Zone (ERNST 1967, 1992). These distinct accumulations are referred to the traditionally called “Green Series”, which reaches thicknesses of several tens of metres in North-Eastern Germany (SCHUMACHER & SONNTAG 1964; STOERMER & WIENHOLZ 1965; LEHM-KUHL 1970). The “Green Series” clay, which is sup-

posed to be in part a weathering product of the Early Jurassic basalt volcanism in Skåne (Southern Sweden) (ZIMMERLE et al. 1994; see also BERGELIN et al. 2011), was laid down at the northeastern edge of the North German Basin south of Fennoscandia (Fig. 1D). These clay deposits markedly differ from the time-equivalent black bituminous shales and marlstones known from sections in the deeper parts of the Central European Basin (JENKYN 1988; DE GRACIANSKY et al. 1998; RÖHL & SCHMID-RÖHL 2005). In Poland, the “Green Series” is absent and replaced by the Ciechocinek Formation, which represents a shallow, brackish-marine accumulation deposited in the Polish Basin (PIEŃKOWSKI 2004; LEONOWICZ 2009, 2011).

Macrofossils originating from the lower Toarcian “Green Series” deposits are rare and usually contained in syngenetic carbonate concretions that occur interbedded within the clay. Unlike the concretions originating from the “Green Series” of Grimmen, which can be correlated with the *E. (Eleganticeras) elegantulum* and *H. (Harpoceras) exaratum* Subzone (ERNST 1967), those deriving from the “Green Series” clay deposits of Dobbartin can solely be dated to the *H. falciferum* Zone on the basis of current data (ANSORGE 2003; ANSORGE & OBST 2015). Based on the presence of a rich but taxonomically impoverished ammonite fauna and the lack of typical stenohaline invertebrates, such as echinoderms and soft-bodied cephalopods, reduced

salinity conditions have been inferred for the time of deposition of the “Green Series” (ERNST 1991; ANSORGE 2003, 2007). However, it should be noted that the *H. falciferum* Zone coincides with the Toarcian Oceanic Anoxic Event (T-OAE) which massively impacted marine biota (e.g., CECCA & MACCHIONI 2004; CASWELL et al. 2009; DERA et al. 2011; CASWELL & COE 2015). Nevertheless, the occurrence of rare conchostracans demonstrates a freshwater influence during deposition of at least parts of the “Green Series” (ANSORGE 2003; pers. obs.). The marine vertebrate fauna mainly consists of actinopterygian fishes (e.g., JAEKEL 1925; MALZAHN 1963; THIES 1989), followed by marine reptiles. These faunal elements occur alongside an extraordinary rich fauna of terrestrial insects (see ANSORGE 2003 for a recent summary), indicating the presence of suitable environments nearby. The “Green Series” of Grimmen has also yielded abundant plant and wood remains, as well as a spider and sauropod dinosaur remains (ERNST 1967; SELDEN & DUNLOP 2014; STUMPF et al. 2015) that must have been washed into the marine realm, suggesting a near-shore depositional setting as proposed by ERNST (1967, 1991) and ANSORGE (2003). In addition, the lower Toarcian of Grimmen has also produced the thyreophoran dinosaur *Emausaurus ernsti* (HAUBOLD 1990). This specimen specifically originated from the *D. tenuicostatum* Zone.

The marine reptile material described herein was collected directly from the lower Toarcian “Green Series” clay deposits of Dobbertin and Grimmen by both geoscientists and amateur collectors, and is now held in numerous public institutions of Mecklenburg-Western Pomerania (see Table 1 for specimen list).

**Institutional abbreviations:** EMR, Erdölmuseum Reinkenhagen; GG, Institut für Geographie und Geologie, Universität Greifswald; GPIH, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg; HMG, Heimatmuseum Grimmen; NLWL, Natureum Ludwigslust; MV, Geologische Landessammlung Sternberg, Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern; PLM, Pommersches Landesmuseum, Greifswald.

**Anatomical abbreviations:** aac, atlas-axis complex; aof, antorbital fenestra; apr, anterior process; art, articular; as, articulation surface; bo, basioccipital; br, broken edge; bs, basisphenoid; c, centrum; d, dentary; hy, hyoid; j, jugal; l, lacrimal; lg, limb girdle element; mc, meckelian canal; mx, maxilla; n, nasal; na, neural arch; nd, narial duct; nvf, neurovascular foramina; os, osteoderm; pl, palatine; pna, pedicle of neural arch; ppr, posterior process; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; r, rib; rt, replacement tooth; sa, surangular; st, supratemporal; t, tooth.

### 3. Systematic palaeontology

#### 3.1. Ichthyosaurs

Ichthyosauria DE BLAINVILLE, 1835

Ichthyosauria indet.

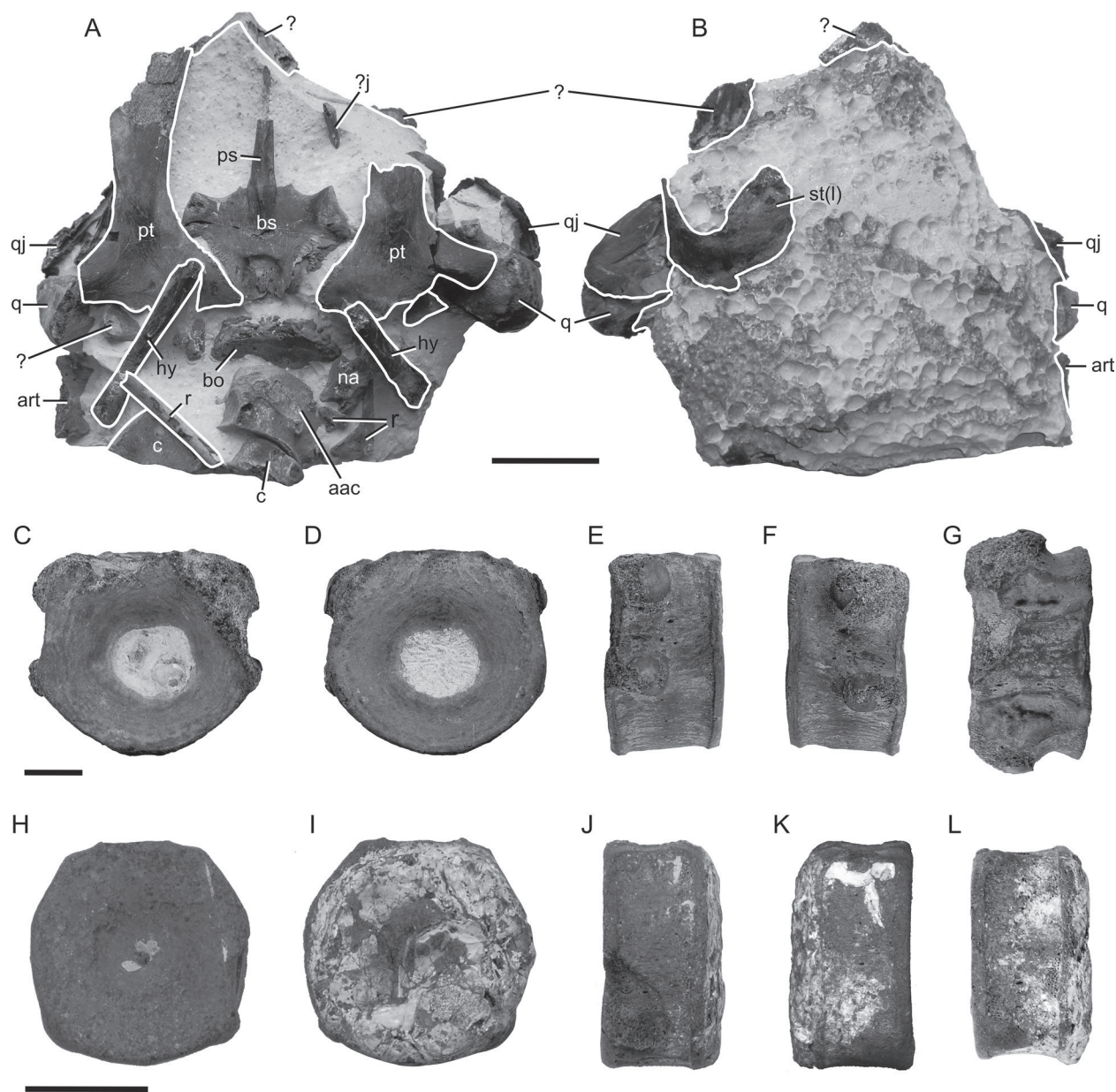
Fig. 2

**Referred specimen:** NLWL uncatalogued, a partial skull and associated postcranial elements preserved in a concretion (Fig. 2A, B). The specimen was found in 1995 by W. ZESSIN (see ZESSIN 1995), and partly prepared by J. ANSORGE by means of chemical preparation.

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*E. elegantulum* Subzone, *H. falciferum* Zone).

**Description:** Preserved in a concretion from the *E. elegantulum* Subzone, ca. 210 x 200 x 80 mm in size, the specimen is mostly visible in ventral aspect. NLWL uncatalogued is partially disarticulated and slightly compressed dorsoventrally. NLWL uncatalogued includes the following cranial elements: both hyoids, both pterygoids, the parabasisphenoid, the basioccipital, both quadrates, both quadratojugals, the left supratemporal, the right articular and other cranial elements that require further preparation to allow a precise anatomical assignment. Associated postcranial bones preserved in the concretion include the atlas-axis complex, two vertebral centra and three ribs. In addition, the matrix contains superabundant shells of the supposedly holoplanktonic coelodiscid gastropod *Coelodiscus minutus* (see TEICHERT & NÜTZEL 2015).

**Skull:** The pterygoids are broken, both lacking their anterior portions; the right one is more complete than the left and is concave on both its lateral and medial sides. The pterygoid is enlarged posteriorly, creating a lateral and a medial wing. The medial lamellae of the pterygoids are slightly rugose and separated from the basisphenoid. The articular condyles of the right and left quadrate are exposed, both being largely covered by the lateral projecting wings of the pterygoids. The right quadrate condyle has a subrectangular outline in lateral view with a slightly concave facet for the contact with the quadratojugal. Only a part of the occipital lamella of the right quadrate is visible in lateral aspect. The quadratojugals are partially preserved and disarticulated. The basisphenoid is pentagonal in outline, becoming rapidly narrower towards its posterior end. The basiptyergoid processes are large and laterally expanded. The anterior margins of the basiptyergoid processes form wide convexities that are separated from the anteromedial trabecular cartilage depression by small anteriorly projecting processes. The posterolateral surfaces of the basisphenoid are rugose for the attachment of intervening connective tissue for articulation with the quadrate rami of the pterygoids. The foramen for the carotid artery piercing the basisphenoid is unpaired and set within the posterior half of the bone. Posterior to the carotid foramen, the basisphenoid bears a shallow groove, which leads into the carotid foramen. The parasphenoid is fully fused to the basisphenoid



**Fig. 2.** Ichthyosaur remains from the lower Toarcian “Green Series” of Grimmer. (A, B) Skull and associated postcranial elements, *Ichthyosauria* indet. (NLWL uncatalogued) in ventral (A) and dorsal (B) view. (C–G) Presacral centrum, *Ichthyosauria* indet. (GHM uncatalogued) in anterior (C), posterior (D), left lateral (E), right lateral (F) and dorsal (G) aspect. (H–L) ?Sacral centrum, *Ichthyosauria* indet. (GG 422/1) in anterior (H), posterior (I), left lateral (J), right lateral (K) and ventral (L) view. Scale bars: (A, B) 5 cm; (C–G) 1 cm.

with no trace of a sutural contact; the anterior portion of the parasphenoid is missing. The preserved portion of the parasphenoid bears a ventral sagittal keel. The basioccipital is still largely covered by matrix, exposing its ventral surface and part of the extracondylar area. The extracondylar area, as preserved, is extensive and perforated by a pair of

lateral foramina. The ventral surface of the basioccipital is strongly rugose and slightly concave. The hyoids are robust and stout; while the right one is incomplete anteriorly, the left one is broken anteriorly and posteriorly. The right articular is exposed; it is incomplete laterally and transversally compressed. Its anterior surface is slightly rugose for articulation



with the quadrate. On the opposite side of the concretion, the right supratemporal is exposed in dorsal view, being situated close to the left quadratojugal. The supratemporal, as preserved, is 'U'-shaped, forming an extensive lateral ramus and a delicate medial ramus; both lacking their anteriormost extends. The ventral supratemporal ramus is covered by matrix.

**Postcranial skeleton:** The atlas-axis complex is exposed in left lateral view; the atlantal diapophysis is still embedded in matrix. The atlas is completely fused to the axis by the means of a sigmoidal suture. Unlike the atlas, which is damaged anteriorly, the axis is well-preserved with a moderately concave posterior articulation surface and a distinct ventral facet for the articulation with the axial intercentrum. Two further centra are present, but broken. A neural arch is exposed nearby the atlas-axis complex; its distal neural spine is covered by the left hyoid. Out of a total number of three ribs preserved in NLWL uncatalogued, only one is in a good state of preservation and is bicipitate. The ribs are rounded in cross-section.

**Identification:** Five valid ichthyosaur genera are currently recognized from the Toarcian stage of Europe (MAISCH 1998a, 2008; MAISCH & MATZKE 2000): *Temnodontosaurus*, *Suevoleiathan*, *Eurhinosaurus*, *Stenopterygius* and *Hauffiopteryx*. Of these, *Temnodontosaurus* can be clearly differentiated from NLWL uncatalogued on account of its basisphenoid, which retains the plesiomorphic condition of non-neoichthyosaurian ichthyosaurs in possessing a paired carotid foramen piercing the ventral surface of the bone (MAISCH 1998b; MAISCH & MATZKE 2000; MARTIN et al. 2012). *Temnodontosaurus* can also be distinguished from NLWL uncatalogued based on the presence of short basiptyergoid processes on the basisphenoid (MAISCH 2002; MARTIN et al. 2012), a condition shared with *Suevoleiathan* and *Stenopterygius* (FRAAS 1891: pl. 5, fig. 3; pl. 10, fig. 1; BROILI 1909: fig. 4). *Stenopterygius* also differs from NLWL uncatalogued in exhibiting two shallow grooves, which lead into the unpaired carotid foramen perforating the ventral surface of the basisphenoid (MAISCH 1998b; MAISCH & MATZKE 2000). In *Hauffiopteryx* and *Eurhinosaurus*, the precise morphology of the basisphenoid is unknown, thus preventing detailed comparisons. However, the basioccipital is ventrally notched in these two latter taxa (see MCGOWAN 1979: fig. 8; MAXWELL et al. 2012: character 24), contrary to the condition in NLWL uncatalogued, in which the ventral surface of the basioccipital is only slightly concave.

Consequently, NLWL uncatalogued lacks diagnostic features that would allow a referral to any valid Toarcian genus of the Ichthyosauria. Perhaps the most important feature in NLWL uncatalogued is the presence of markedly laterally expanded basiptyergoid processes on the basisphenoid, as this feature is only currently known in members of the Ophthalmosauridae (FISCHER et al. 2013: character 19), suggesting that this specimen represents a new and unnamed taxon. However, given the incomplete and fragmentary nature of NLWL uncatalogued, this specimen is here simply considered as an indeterminate ichthyosaur until more material comes to light.

**Referred specimen:** GHM uncatalogued, a presacral centrum (Fig. 2C-G); GG 422/1, a ?sacral centrum (Fig. 2H-L). GHM uncatalogued was collected by H. SCHNEIDER, who kindly donated it to the GHM in 1987.

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** GHM uncatalogued is a biconcave disc that has subpentagonal outline in both anterior and posterior aspect, with distinct bony rims that form the anterolateral and posterolateral margins of the centrum. The di- and parapophyses are well developed and connected to the anterior marginal rim of the centrum; the diapophyses are confluent with the neural arch facets dorsally, the parapophyses are situated at mid-height on the centrum body.

GG 422/1 forms a rounded disc with slightly developed exterior bony rims. Whereas the anterior articulation surface is concave and displays a marked notochordal pit, the posterior articulation surface is covered by a highly compacted mass of aragonitic molluscan shell fragments of uncertain affinities. Both the di- and parapophyses are confluent, forming single, ventrolaterally oriented apophyses; there are no ventral haemal arch facets.

**Identification:** Whereas the fusion between the diapophyses and neural facets in GHM uncatalogued indicates that this specimen is identifiable as belonging to the anterior presacral region, GG 422/1 is considered to come from either the sacral or the anterior caudal region based on the presence of single, ventrolaterally positioned apophyses and the lack of ventral haemal arch facets (see MCGOWAN & MOTANI 2003). Both specimens are referred to Ichthyosauria indet.

**Fig. 3.** Plesiosaur remains from the lower Toarcian "Green Series" of Grimmen. (A-D) Cervical vertebra, Plesiosauroidea indet. (GG 422/2) in anterior (A), posterior (B), left lateral (C) and ventral (D) view. (E-H) Caudal centrum, Plesiosauroidea indet. (GG 422/3), in anterior (E), right lateral (F), left lateral (G) and dorsal (H) view. (I) Phalanx, Plesiosauria indet. (EMR uncatalogued) in ?dorsal view. (J-L) Three caudal vertebrae and other postcranial elements, Plesiosauria indet. (GG 422/4) in various aspects; (M, N) Gastralium, cf. Plesiosauria indet. (MV 200.250) in ?ventral aspect (M) and close-up view on broken gastralium (N). Scale bars: (A-M) 5 cm, (N) 0.5 cm.

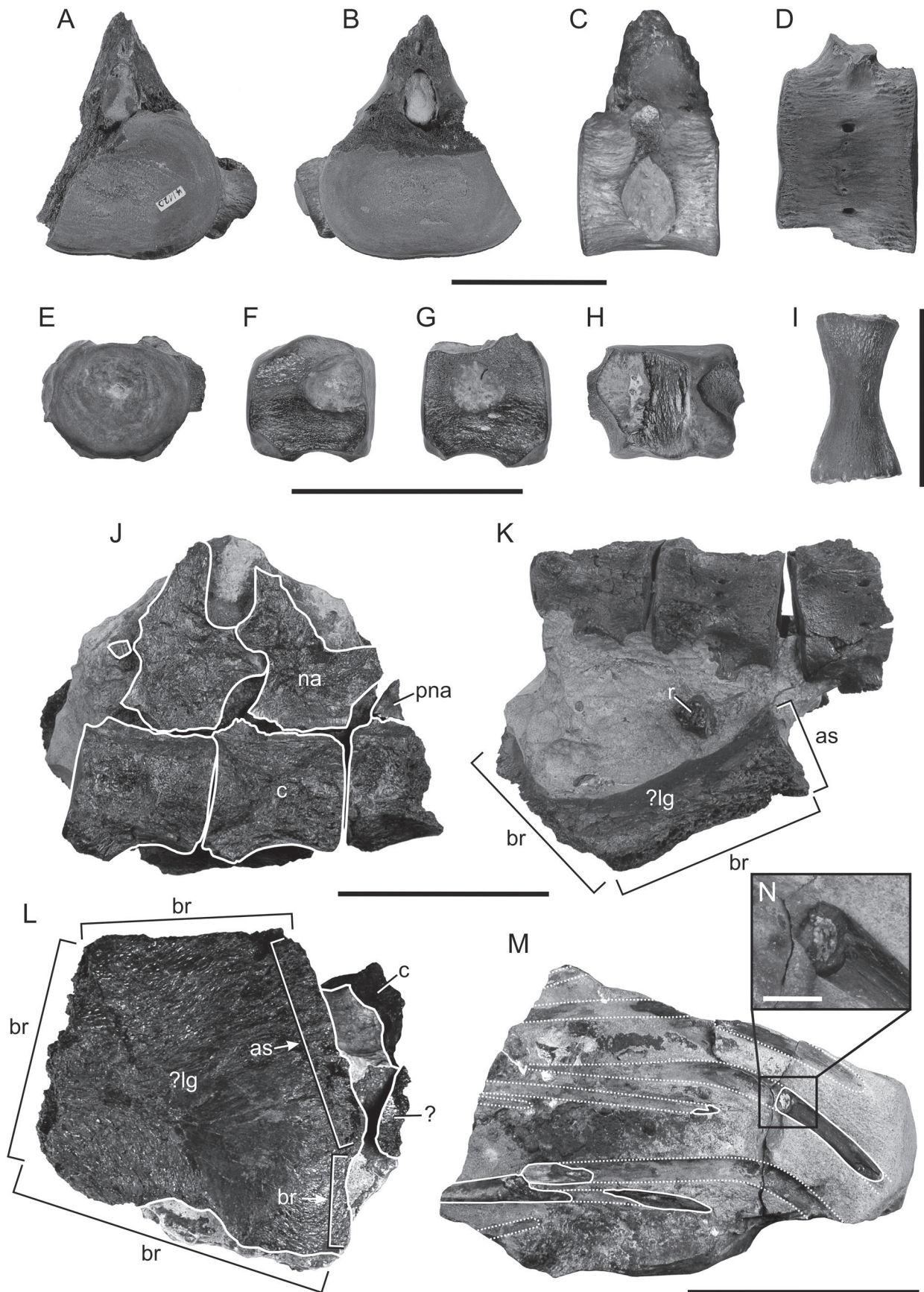


Fig. 3.



**Table 2.** Centrum measurements (mm) of the marine reptile material from the lower Toarcian “Green Series” clay of Grimmen (\* incomplete centrum).

Taxon	Specimen number	No.	Length	Width	Height
Ichthyosauria indet.	GHM uncatalogued	-	18.5	35.4	33.4
Ichthyosauria indet.	GG 422/1	-	8.4	18.8	18.7
Plesiosauroidea indet.	GG 422/2	-	45.5	62.8*	44.9
Plesiosauroidea indet.	GG 422/3	-	28.1	31.8	24.9
Plesiosauria indet.	GG 422/4	“1”	22.4*	30.6*	24.8
		“2”	29.5	29.3*	25
		“3”	29.4	22.5*	24.9
Mesoeucrocodylia indet.	GG 422/7	-	43.4	35.5	36

### 3.2. Plesiosaurs

Plesiosauria DE BLAINVILLE, 1835

Neoplesiosauria KETCHUM & BENSON, 2010

Plesiosauroidea WELLES, 1943

Plesiosauroidea indet.

Fig. 3A-H

**Referred specimen:** GG 422/2, an incomplete cervical vertebra (Fig. 3A-D).

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** The vertebral centrum of GG 422/2 is broken obliquely, lacking most of its right lateral portion. Although the centrum width could not precisely be determined due to breakage, the preserved centrum dimensions clearly demonstrate that in life it was wider than long and high (see Table 2). GG 422/2 bears gently concave articulation surfaces with abrupt-angled, slightly rugose edges. The articulation surfaces seem to have been somewhat constricted medially. The ventral surface is transversally flat, without keel or groove. The ventral paired nutritive foramina (= foramina subcentralia *sensu* STORRS 1991) are widely separated with three smaller foramina between them. GG 422/2 displays a raised, slightly posterolaterally facing rib facet which is situated nearly at mid-height on the centrum body. The rib facet is suboval in outline, rugose and has a raised rim; there is no sign of a presence of a longitudinal ridge. The neural arch is damaged, lacking the pre- and postzygapophyses and most of the distal neural spine. The neural canal is suboval. The anterior and posterior surface of the neural spine seem to have been occupied by a vertically oriented groove just above the neural canal. The neurocentral suture is ‘V’-shaped in left lateral view and partially obscured by bony fusion.

**Identification:** GG 422/2 is considered to come from the posterior cervical series based on the widely separated paired ventral foramina, combined with the mid-height position of the rib facet on the centrum body (see BROWN 1981). The longer than high centrum proportion of GG 422/2 is consistent with the diagnosis of Plesiosauroidea proposed

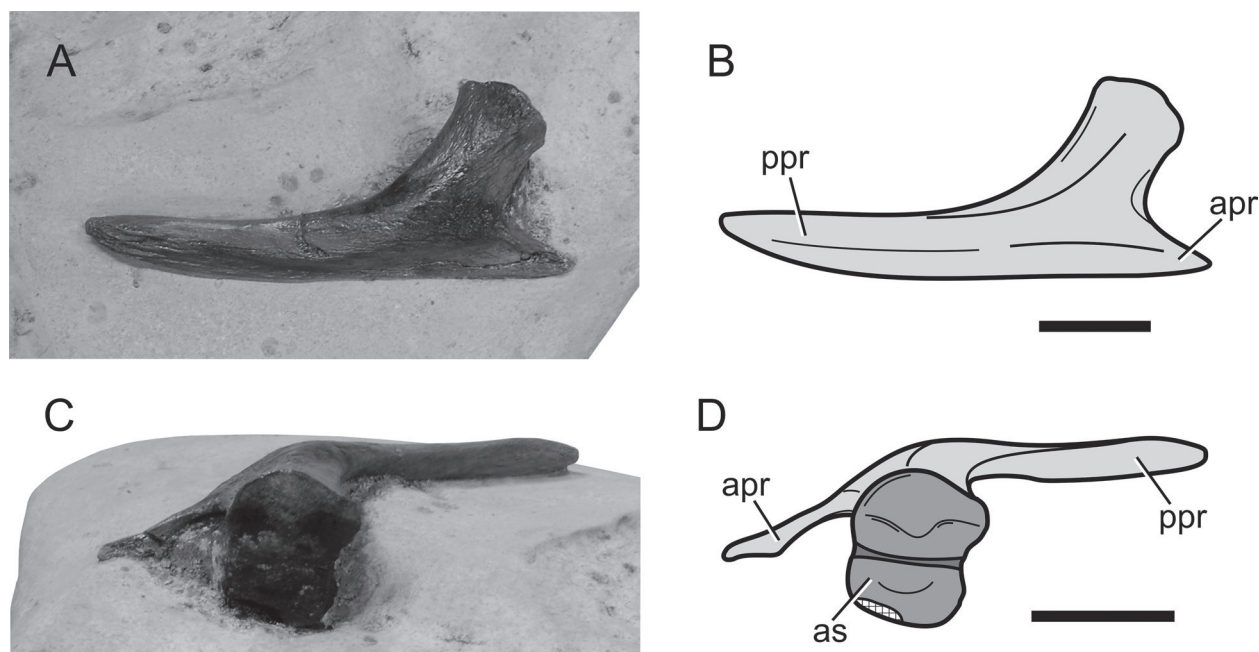
by BROWN (1981). Likewise, the centrum body is wider than high, a feature typical for Toarcian plesiosauroids (BENSON et al. 2012: character 133).

On the other hand, GG 422/2 bears a single-headed rib facet, which would be unusual for an Early Jurassic plesiosaur, as it constitutes a character state found in derived plesiosauroids (Cryptoclidia and Elasmosauridae: KETCHUM & BENSON 2010). However, this feature is likely compatible with the ‘co-joined’ condition introduced by DRUCKENMILLER & RUSSELL (2008) (e.g., *Westphaliasaurus*: SCHWERMANN & SANDER 2011: fig. 8). Therefore, it appears quite probable that GG 422/2 can be referred to a non-microcleidid plesiosauroid, since microcleidids are characterized by, among other features, exhibiting clearly separated posterior cervical rib facets (BENSON et al. 2012: character 123). In consequence, GG 422/2 is here simply ascribed to Plesiosauroidea indet. Concerning the ontogenetic age of GG 422/2, it is consistent with attribution to an osteologically mature individual based on the highly fused condition of the neurocentral suture (*sensu* BROWN 1981).

**Referred specimen:** GG 422/3, a caudal centrum (Fig. 3E-H). The specimen was originally found partially encased in a concretion from the *H. exaratum* Subzone by E. KOPPKA, and freed from matrix by his son J. KOPPKA, who recently donated it to the GG.

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*H. exaratum* Subzone, *H. falciferum* Zone).

**Description:** GG 422/3 is wider than long and high (see Table 2) and slightly amphicelous. The articulation surfaces are suboval in outline and bear central notochordal pits. GG 422/3 displays prominent, ventrally projecting haemal arch facets, which are situated on both the anteroventral and posteroventral margins; the posterior ones being larger than the anterior ones. The rib facets are rounded, slightly rugose and positioned at mid-height without contacting the neural arch facets. The right rib facet contacts the anterolateral margin of the centrum while the left one does not. The right neural arch facet is reduced as compared to its left counterpart, forming a depression, which is separated from the lateral margin of the floor of the neural canal, smoothly merging into the lateral surface of the centrum body. The left neural arch facet is prominent and subtriangular in outline, with



**Fig. 4.** (A-D) Cervical rib, *Plesiosauria* indet. (GG 422/5) from the lower Toarcian “Green Series” of Dobbertin in lateral (A, B) and proximal (C, D) view. Scale bars: 1 cm.

the medial margin being in contact with the neural canal floor along almost entire length. The left/right asymmetry present in GG 422/3 is suggestive of a hypoplastic pattern, which possibly can be explained by a developmental issue (see WOLFERS & HOEFFKEN 1974).

**Identification:** The vertebral morphology of GG 422/3 is compatible with that of *Plesiosauroidea* (*sensu* BENSON et al. 2012), in particular the presence of suboval articulation surfaces and wider than high centrum proportions. Further evidence supporting the placement of GG 422/3 within *Plesiosauroidea* is indicated by the possession of rib facets that are located at centrum mid-height without contacting the neural arch facets, and ventrally projecting haemal arch facets, as these features are evident in *Seeleyosaurus*, *Microcleidus homalospondylus* and *M. (= Hydorion) brachypterygius* (see BENSON et al. 2012). Accordingly, GG 422/3 is here regarded as an indeterminate plesiosauroid plesiosaur. Given the unfused condition of the vertebral processes, GG 422/3 can be clearly referred to an individual that was osteologically immature at the time of death (*sensu* BROWN 1981).

*Plesiosauria* DE BLAINVILLE, 1835

*Plesiosauria* indet.  
Figs. 3I-L, 4

**Referred specimen:** EMR uncatalogued, a phalanx (Fig. 3I).

**Locality and horizon:** Grimmer clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** EMR uncatalogued is slightly dorsoventrally flattened, proportionally short (i.e., its maximum proximodistal length is less than twice its maximum mediolateral width) and constricted in the middle, resulting in an hourglass-shaped appearance. The articulation facets are flat and somewhat rugose with raised margins; the articular margins form abrupt angles with the phalangeal shaft.

**Identification:** The phalangeal morphology of EMR uncatalogued, with its hourglass-shaped appearance combined with the presence of a slightly dorsoventrally flattened mid-shaft cross-section, is consistent with referral to *Plesiosauria* (e.g., BARDET et al. 1999; BENSON et al. 2015a, b), but a more precise identification is not possible and the specimen is here assigned to an indeterminate plesiosaur. Based on the presence of well-defined articulation surfaces, a referral of EMR uncatalogued to an osteologically mature individual is considered likely (see STORRS 1997).

**Referred specimen:** GG 422/4, a concretion containing three caudal vertebrae, a possible limb girdle fragment and other postcranial elements (Fig. 3J-L).

**Locality and horizon:** Grimmer clay pit. Lower Toarcian (*E. elegantulum* Subzone, *H. falciferum* Zone)

**Description:** GG 422/4 is a partly prepared concretion from the *E. elegantulum* Subzone that contains a sequence of three

articulated caudal vertebrae resting on their left lateral sides. All the vertebrae are broken obliquely. Despite being incomplete, the preserved vertebral centra dimensions (see Table 2) demonstrate that they were wider than long and high in life. As far as can be judged, the centra are slightly amphicoelous with central notochordal pits and abrupt-angled edges, ventral nutritive foramina, raised haemal arch facets that are situated on the posteroventral margins (absent in centrum “one”), and distinct rib facets. The absence of haemal arch facets in centrum “one” might indicate that it originates from the anterior caudal region. Excepting the neural arch of centrum “one”, which is only represented by a small piece of its left pedicle, the neural arches associated with centra “two” and “three” are broken along the sagittal plane, but articulated. The neural arches are not fused to the centra. On the opposite side of the concretion, a subrectangular, plate-like bone fragment is exposed that bears a distinct articulation surface, displaying a rugose and pitted texture (maximum length along articulation surface = 58.6 mm); all the remaining margins are broken. Although precise identification of this element is hampered due to its poor state of preservation, its overall morphology suggests that it belongs to either the pectoral or pelvic girdle. Further elements preserved in the concretion include a caudal rib visible in cross-section and a small bone fragment of uncertain affinity.

**Identification:** The wider than high caudal centrum proportions (inferred in GG 422/4) are typical of many plesiosauroids (e.g., *Westphaliasaurus*: SCHWERMANN & SANDER 2011; *Seeleyosaurus*: DAMES 1895), but also occur in some pliosauroids (see BENSON et al. 2012). Accordingly, a definitive attribution of GG 422/4 remains equivocal and the specimen is here ascribed to Plesiosauria indet.

GG 422/4 is consistent with referral to an osteologically immature individual based on the unfused condition of the vertebral processes and the incompletely ossified articulation surface of the girdle element (*sensu* BROWN 1981).

**Referred specimen:** GG 422/5, a right cervical rib resting on a concretion (Fig. 4).

**Locality and horizon:** Dobbertin clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** GG 422/5 is a carbonate concretion that contains a right cervical rib resting on its ventral side. The rib has a distinct anterior process and an elongated posterior process, with the rib shaft being suboval in cross-section. The facet for the articulation with the cervical centrum is divided in two by a longitudinal groove.

**Identification:** GG 422/5 is consistent with referral to Plesiosauria based on the possession of two co-joined facets for articulation with the cervical centrum, and the presence of a distinct anterior and a larger posterior process (e.g., *Stratesaurus*: BENSON et al. 2015a: fig. 15). In contrast, the cervical ribs of thalattosuchian crocodyliforms are somewhat ‘T’-shaped in lateral view, with the anterior process being as long as the posterior process (e.g., MUELLER-TÖWE 2006; PIERCE & BENTON 2006; MARTIN & VINCENT 2013). Accordingly, GG

422/5 is referred to Plesiosauria indet. This is a significant specimen, as it constitutes the first plesiosaur record from the Early Jurassic of Dobbertin.

cf. Plesiosauria indet.

Fig. 3M, N

**Referred specimen:** MV 200.250, an incomplete gastralia basket contained in a concretion.

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*E. elegantulum* Subzone, *H. falciferum* Zone).

**Description:** MV 200.250 represents a broken piece of a concretion originating from the *E. elegantulum* Subzone that contains an incomplete gastralia basket, consisting of apparently five rows of gastralia, of which the majority are preserved as impressions. As far as can be judged, the most complete gastralia row consists of three gastralia. Unfortunately, given to the incompleteness of the specimen, it is not quite clear whether the gastralia are preserved in dorsal or ventral view. The most lateral gastralia show a distinct curvature in the coronal plane, becoming somewhat flattened distally. In at least one row of gastralia, the articulation between two elements is preserved, illustrating that the medial one bears laterally extended excavation for the articulation with the adjacent gastralia. As seen in one broken surface, the gastralia are made up of compact cortex and an inner core that is made up of cancellous bone; the void spaces are filled with calcite.

**Identification:** The specific arrangement of the gastralia combined with the marked curvature of the most lateral elements most closely resembles that of plesiosaur gastralia baskets (e.g., *Plesiosaurus*: STORRS 1997; *Cryptoclidus*: BROWN 1981), and the presence of compact cortical bone (which is typical of plesiosaur bones; e.g., WIFFEN et al. 1995; CRUICKSHANK et al. 1996; STREET & O’KEEFE 2010) does not contradict an assignment of MV 200.250 to Plesiosauria. Consequently, MV 200.250 is here tentatively referred to an indeterminate plesiosaur. Assuming this identification to be correct, its overall size, as compared relative to those of other known plesiosaurs, suggests belonging to a small immature individual.

### 3.3. Crocodyliforms

Crocodyliformes BENTON & CLARK, 1988

Mesoeucrocodylia BENTON & CLARK, 1988

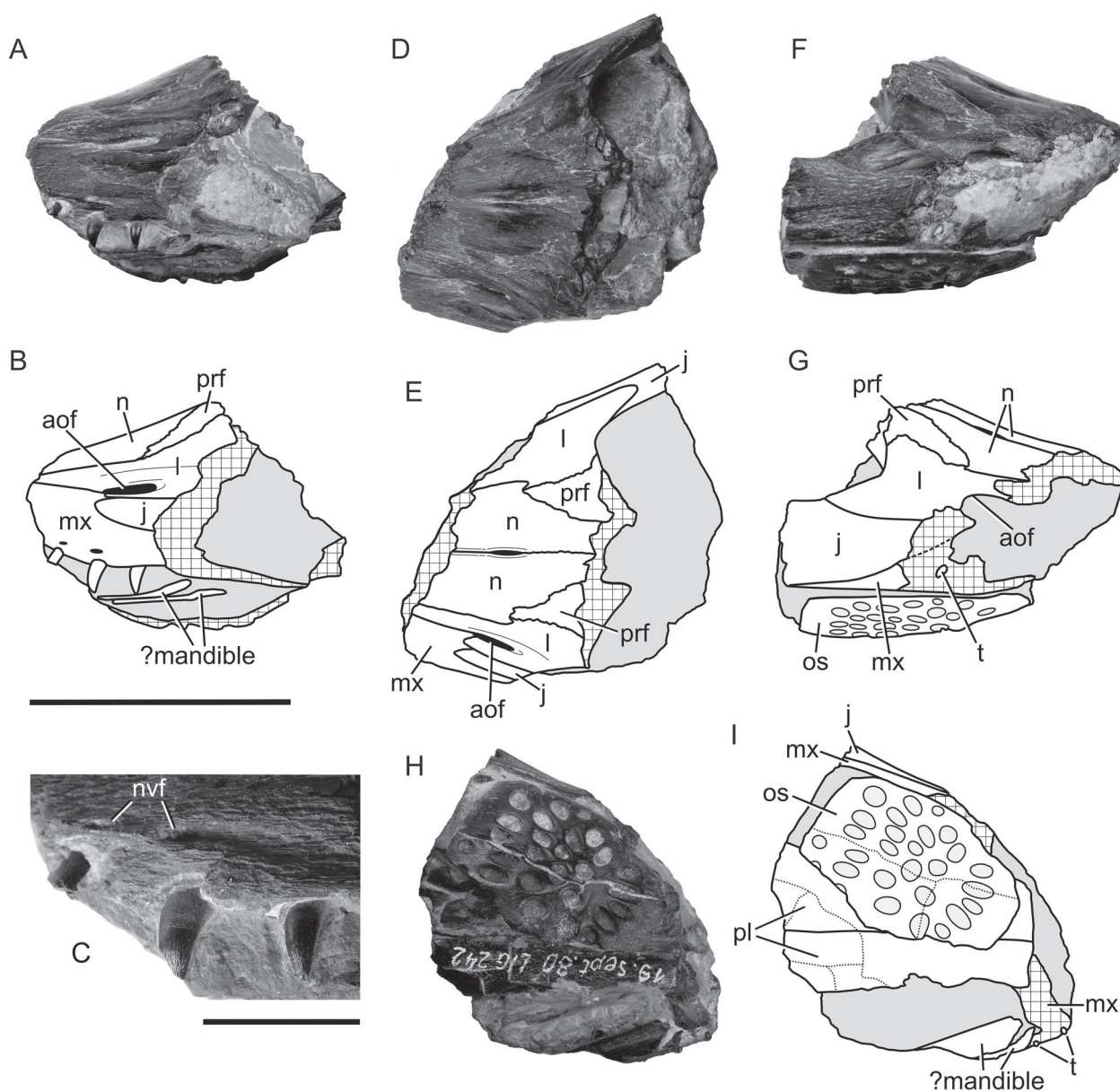
Thalattosuchia FRAAS, 1901

Teleosauridae GEOFFROY SAINT-HILAIRE, 1831

Genus *Steneosaurus* GEOFFROY SAINT-HILAIRE, 1825

**Type species:** *Steneosaurus megistorhynchus* GEOFFROY SAINT-HILAIRE, 1825





**Fig. 5.** (A-I) *Steneosaurus bollensis* (GG 422/6) from the lower Toarcian “Green Series” of Grimmen in left lateral (A, B) view, close-up view on the teeth (C), dorsal (D, E), right lateral (F, G) and ventral (H, I) view. Scale bars: (A, B; D-I) 5 cm, (C) 1 cm.

*Steneosaurus bollensis* (JAEGER, 1828)

Fig. 5

**Diagnosis:** See MUELLER-TÖWE (2006).

**Referred specimen:** GG 422/6, a partially preserved skull and an osteoderm preserved in a concretion. The specimen was found in 1980 by W. KREMPIEN and figured by ZESSIN

(2001) and ZESSIN & KREMPIEN (2010), but not yet thoroughly studied. Recently, it was kindly donated, through the courtesy of the collector, to the GG.

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** The cranium is articulated and perfectly pre-

served in three dimensions. It includes the anterior part of the skull roof and a part of the palate; the rostral and posterior skull region are missing. Ventrally attached to the palate, the specimen preserves an osteoderm and two indeterminate bones, which could correspond to the mandible.

**Skull:** The left maxilla is partially preserved; the rostral portion and the posteriormost extension are missing. Anterodorsally, it meets the lacrimal in a straight suture and tapers off between the lacrimal and the jugal to produce a short and delicate process, which contributes to the anterior portion of the small, slit-like antorbital fenestra. The posterior portion of the bone is dorsally lined by the jugal. The bone preserves two neurovascular foramina, positioned dorsal to the oral margin. Three maxillary teeth are preserved, of which only the most posterior one is complete. They are apically recurved with pointed apices. Their enamel is covered by fine vertical striations with a single smooth carina extending along the posterior edge. The right maxilla is only represented by its posteriormost extension, which borders the jugal dorsally. Its anterior part is damaged, exposing a broken tooth root. The paired nasals are incomplete anteriorly and posteriorly. The median nasal suture is slightly serrated posteriorly and plane anteriorly. Anterolaterally, the nasals contact the lacrimals in a straight suture and the prefrontals in a complexly serrated suture posterolaterally. The anterior portions of both the right and the left prefrontal are preserved and are triangular in outline. Medially, they meet the nasals in a serrated suture and the lacrimals in an oblique suture laterally. The lacrimals are incomplete anteriorly and posteriorly. They are bordered by the nasals anteromedially and by the prefrontals posteromedially. The right lacrimal forms almost the entire anterior border of the orbit and meets the jugal laterally. The left lacrimal is in contact with the maxilla anterolaterally, overlaps the jugal posterolaterally, and contributes to the posterior portion of the antorbital fenestra. Both the right and the left jugal are only poorly preserved. The right jugal meets the lacrimal in a straight suture ventrally and forms the ventral margin of the orbit. The left jugal is bordered by the maxilla anteriorly and is overlapped by the lacrimal dorsomedially. Anteriorly, the bone forms an acute angle, dorsally overlapping the maxilla; its contact with the antorbital fenestra is minimal. Of the palatal bones, only parts of the palatines are preserved, meeting each other in a straight median suture. The maxillae, when seen in ventral view, are largely obscured by rock matrix.

GG 422/6 includes two indeterminate bone fragments close to the left maxilla, best visible in ventral aspect, which probably correspond to the mandibular ramus.

**Postcranial skeleton:** Ventrally attached to the palate, GG 422/6 bears an isolated osteoderm, which is exposed in dorsal view. The osteoderm is incomplete and subrectangular in outline, showing an ornamentation pattern of round to ovoid pits. Unfortunately, this osteoderm does not preserve enough information to judge whether it belongs to the dorsal or ventral osteodermal shield.

**Identification:** At present, three valid crocodyliform genera have been reported from the lower Toarcian formations outcropping in Europe (MUELLER-TÖWE 2006): *Pelagosaurus*,

*Platysuchus* and *Steneosaurus*. The latter is represented by three Toarcian species: *Steneosaurus bollensis*, *S. gracilirostris* and *S. brevior*.

Concerning the pattern of arrangement of the cranial bones, GG 422/6 perfectly matches with representatives of *Steneosaurus* (WESTPHAL 1962; MUELLER-TÖWE 2006), separating it from *Pelagosaurus*, which has an antorbital fenestra that is bordered by the lacrimal and maxilla (PIERCE & BENTON 2006), and *Platysuchus*, in which the jugal is excluded from contact with the orbital margin (MUELLER-TÖWE 2006). This condition, however, has also been reported in specimens of *Steneosaurus bollensis* (WESTPHAL 1962; WALKDEN et al. 1987; GODEFROIT 1994), but it has been recently shown by MUELLER-TÖWE (2006) that in the majority of specimens, the jugal contacts the border of the orbit, separating the lacrimal from the postorbital. The lack of ornamentation on the nasal, lacrimal, jugal and the anterior portion of the prefrontal also indicates that GG 422/6 does not belong to *Pelagosaurus* or *Platysuchus*, as both taxa are characterized by extensive sculpturing of almost the entire skull (WESTPHAL 1962; MUELLER-TÖWE 2006; PIERCE & BENTON 2006), thus giving further support for referral of GG 422/6 to *Steneosaurus*. Excepting the large variation in overall skull proportions, the cranial osteology of *Steneosaurus* remains remarkably uniform which makes identification of partial skulls difficult. Nevertheless, the reduced, slit-like antorbital fenestra present in GG 422/6 indicates that it can be referred to *Steneosaurus bollensis*, separating it from *S. gracilirostris* and *S. brevior*, which possess relatively large and rounded antorbital fenestrae (WESTPHAL 1962; MUELLER-TÖWE 2006). Moreover, *Steneosaurus gracilirostris* can also be readily distinguished from GG 422/6 based on the presence of extensive ornamentation made up of densely-packed small, rounded pits on the prefrontal (MUELLER-TÖWE 2006). Hence, as evident from its overall cranial morphology, GG 422/6 is here referred to the most common and palaeobiogeographically widespread Toarcian species of *Steneosaurus*, *S. bollensis*. Although highly incomplete, the preserved maximum antorbital width (i.e., skull width at the anterior border of orbits) of about 50 mm, as compared to those provided by MUELLER-TÖWE (2006) for at least 32 complete skulls of *Steneosaurus bollensis*, demonstrates that GG 422/6 can be clearly referred to an immature individual.

Thalattosuchia FRAAS, 1901

Thalattosuchia indet.

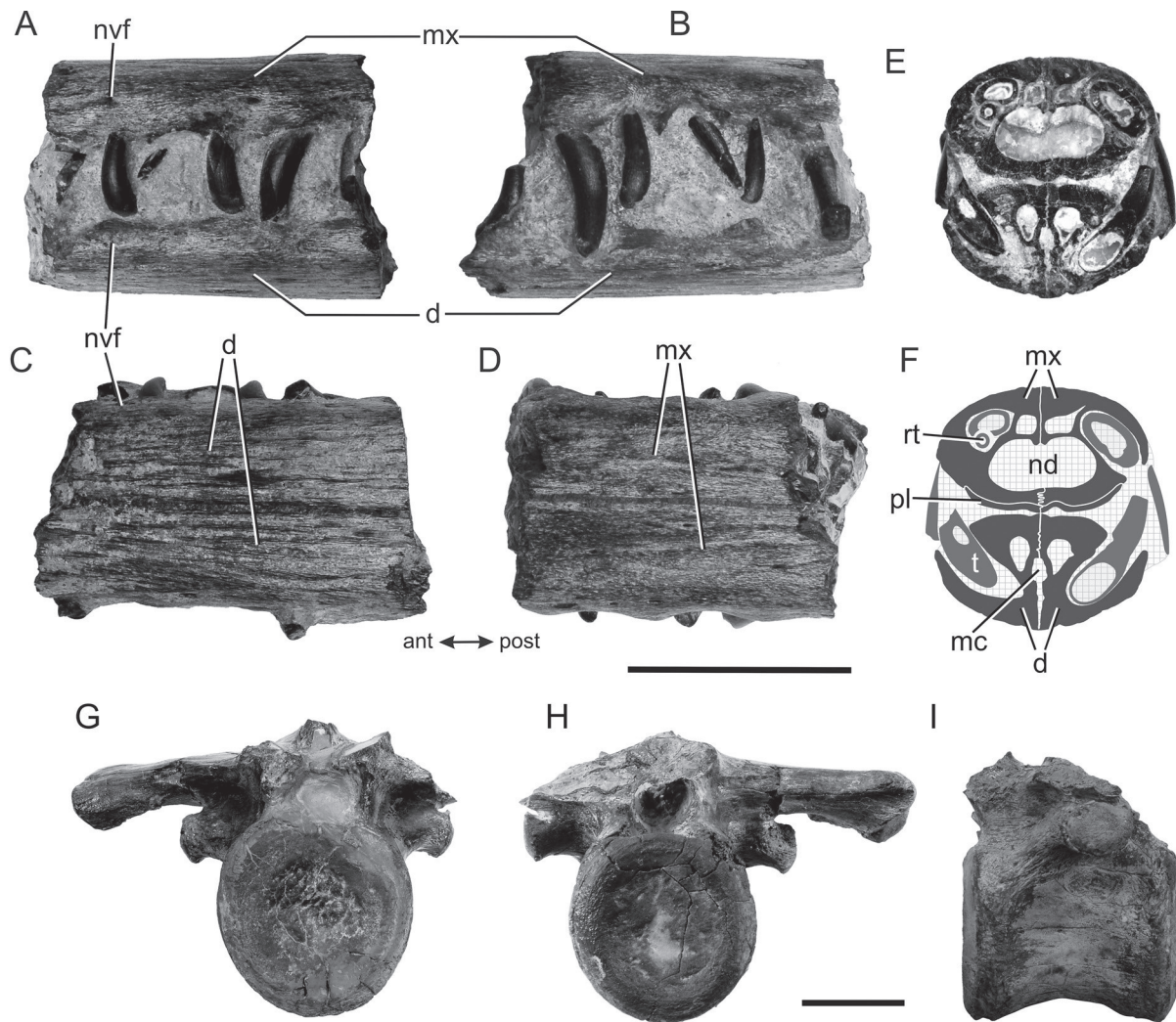
Fig. 6A-F

**Referred specimen:** PLM uncatalogued, a carbonate concretion containing a partial rostrum with teeth (Fig. 6A-F). The specimen was collected by H. SCHNICK in the 1983 and later purchased by the PLM.

**Locality and horizon:** Grimm clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** PLM uncatalogued represents a weathered carbonate concretion containing a single fragment of rostrum





**Fig. 6.** Crocodyliform remains from the lower Toarcian “Green Series” of Grimmen. (A–F) Rostrum, *Thalattosuchia* indet. (PLM uncatalogued) in left lateral (A), right lateral (B), ventral (C), dorsal (D) and posterior (E, F) aspect. (G–I) Cervical vertebra, *Mesoeucrocodylia* indet. (GG 422/7) in anterior (G), posterior (H) and left lateral (I) view. Scale bars: 2 cm.

that includes parts of the cranium (maxillae and palatines) preserved in occlusion with the mandibular rami (dentaries). PLM uncatalogued preserves twelve teeth, in which the maxillary teeth regularly alternate with the dentary teeth. The tooth crowns are slender and recurved; no apices are preserved. The tooth enamel is ornamented by fine vertical striations with a single smooth carina running along the posterior edge. Both the maxillary and dentary rostrum are transversally elliptical in cross-section, with the median maxillary suture and the median suture separating the dentaries forming a shallow groove visible in dorsal and ventral view, respectively. Several small neurovascular foramina are present, aligned along the lateral surfaces of the maxillae and dentaries. Whereas the dorsal surface of the maxillae

lacks any traces of sculpturing, the dentaries show an ornamentation pattern along the ventral surface that consists of strongly defined, longitudinally directed furrows. The palatines are only visible in the posterior cross-section, forming thin sheets of bone ventrally adjacent to the maxillae. The posterior transverse breaks provide insights into the internal rostral anatomy, with the internal vacuities being filled with sparitic calcite. The nasal duct passing through the maxillary rostrum is large, somewhat bilobate in outline and is situated between the alveoli, which are occupied by teeth. The left maxillary alveolus preserves a replacement tooth that is dorsally enclosed by the enamel of the older tooth. As clearly inferred from the cross-sections, tooth implantation was thecodont. Two further cavities are present dorsomedially.



ally adjacent to the alveoli. The dentary rostrum displays three vacuities, the Meckelian canal, which is formed by both dentary bones and two further ones, each one of them being situated between the Meckelian canal and the alveolus, respectively.

**Identification:** The tubular appearance of PLM uncatalogued, the thecodont implantation of the teeth, combined with the tooth morphology and the internal rostral anatomy indicate that it can be positively referred to a longistrine thalattosuchian crocodyliform (e.g., BUFFETAUT et al. 1981; VIGNAUD 1995), but its incompleteness precludes further systematic identification. The size of PLM uncatalogued, as compared to the corresponding portions of the rostra of other Toarcian thalattosuchians, is indicative of a juvenile individual.

Mesoeucrocodylia BENTON & CLARK, 1988

Mesoeucrocodylia indet.

Fig. 6G-I

**Referred specimen:** GG 422/7, a partially preserved cervical vertebra (Fig. 6G-I). It was found in 2001 by M. LOH, who kindly donated it to the GG.

**Locality and horizon:** Grimmen clay pit. Lower Toarcian (*H. falciferum* Zone).

**Description:** The vertebral centrum of GG 422/7 is longer than high and wide (see Table 2) and slightly amphicœlous, with thickened anterior and posterior margins, giving an hourglass-shaped appearance to the centrum in ventral aspect. In lateral view, the ventral margin of the centrum is slightly concave anteroposteriorly. The neural arch is fused to the centrum, with the neurocentral sutures being partially closed. GG 422/7 lacks most of the neural spine and the left diapophysis. The di- and parapophyses are clearly separated and are located at the base of the neural arch, indicating that GG 422/7 comes from the anterior dorsal series (see ANDREWS 1913). The parapophyses are short, bear distinct articulation facets for the attachment of the capitulum of the ribs; they are positioned just below the diapophyses. The diapophysis forms a horizontal process, which projects far laterally, being three times the length of the parapophysis. Its articulation facet for the attachment of the tubercle of the rib is slightly thickened distally, having circular outline in lateral view.

**Identification:** The vertebral morphology of GG 422/7, with its anteroposteriorly elongated, hourglass-shaped and slightly amphicœlous vertebral centrum, is consistent with a mesoeucrocodylian origin (SALISBURY & FREY 2000), but a more detailed identification is hampered by the absence of cranial elements. Consequently, it is here simply identified as belonging to an indeterminate mesoeucrocodylian crocodyliform. Given the partially closed condition of the neurocentral sutures, GG 422/7 is considered to come from an osteologically immature individual (*sensu* BROCHU 1996).

## 4. Discussion

The lower Toarcian “Green Series” of North-Eastern Germany represents a specific facies, yielding rare marine reptile remains that contribute to our knowledge of Early Jurassic marine life in marginal settings. The fossil assemblage presented herein complements previous records of marine reptiles remains from northern Central Europe with an Early Jurassic age (GEINITZ 1900a, b; ERNST 1920; OERTEL 1925; LEHMANN 1971; MOTHS 1994; MAISCH & ANSORGE 2004; SMITH 2008; SACHS et al. 2016), which remain particularly scarce, especially in comparison to the rich faunas obtained from the Early Jurassic formations outcropping in Western Europe (e.g., HAUFF 1921; HAUFF & HAUFF 1980; BENTON & TAYLOR 1984; GODEFROIT 1994, 1996; BENTON & SPENCER 1995). Although based on a small number of fragmentary specimens, this material is significant as it includes the first reliable reports of plesiosaurs (including both juvenile and adult specimens) and thalattosuchian crocodyliforms from the lower Toarcian “Green Series” of North-Eastern Germany, confirming their presence in the marginal ecosystems of the North German Basin south of Fennoscandia during Toarcian times. Moreover, the material described herein is noteworthy in indicating the presence of a probable new and unnamed ichthyosaur taxon.

Contemporaneous records of marine reptiles from Northern Germany outside the state of Mecklenburg-Western Pomerania are known from Pleistocene erratics in the vicinity of Ahrensburg (Schleswig-Holstein), and the Posidonia Shale Formation of the Brunswick area (Lower Saxony), incorporating largely poorly documented remains of ichthyosaurs, plesiosaurs and thalattosuchian crocodyliforms (ERNST 1920; OERTEL 1925; WUNNENBERG 1927, 1950; WINCIERZ 1967; LEHMANN 1971; LIERL 1990; HAUFF et al. 2014; SACHS et al. 2016). The Ahrensburg material is of special interest because it is interpreted as deriving from a distal, prodeltaic environment (SACHS et al. 2016). The preglacial provenance of the Ahrensburg erratics was recently discussed by SACHS et al. (2016), who consider an offshore Baltic Sea occurrence between the Danish Island of Bornholm and Mecklenburg-Western Pomerania to be most probable.

ERNST (1920) published the first report of Early Jurassic marine reptile remains from Pleistocene erratics in the vicinity of Ahrensburg, briefly noting the presence of crocodyliform osteoderms and ichthyosaur remains in erratics referable to the “*Acutus*-(*Schroederi*-) Zone” (= *D. tenuicostatum* Zone; LEHMANN 1968). He assigned this material to ‘*Stenosaurus*’ (= *Steneosau-*

rus) sp. and *Ichthyosaurus* sp., respectively. OERTEL (1925) mentioned vertebrae of ‘*Thaumatosauros*’ (= *Meyerasaurus*) sp. in erratics attributable to the “*Radiosa-Affinis-Zone*”. Ammonites occurring in these erratics include specimens of *Dumortiera pseudoradiosa* (ERNST 1920), the index of the upper Toarcian *D. pseudoradiosa* Subzone. LEHMANN (1971) briefly described an incomplete ichthyosaur skull, which he assigned to *Ichthyosaurus* sp., but also suggested affinities to ‘*Leptopterygius*’ (= *Temnodontosaurus*) *platyodon*. Furthermore, he mentioned an ichthyosaur coracoid and associated rib fragment preserved in a carbonate concretion referable to the *H. falciferum* Zone (see SACHS et al. 2016). This specimen was recently re-assessed by SACHS et al. (2016), who tentatively assigned it to the rhomaleosaurid plesiosaur *Meyerasaurus* sp. LEHMANN (1971) also briefly described a plesiosaur specimen consisting of three articulated dorsal vertebrae (GPIH uncatalogued) that were, according to the label found enclosed with GPIH uncatalogued (pers. obs.), freed from a concretion of the *E. elegantulum* Subzone. LEHMANN (1971) assigned this specimen to *Plesiosaurus* sp., but he also noted that it could probably be referred to ‘*Plesiosaurus*’ (= *Microcleidus*) *homalospondylus* on the basis of “size, morphology and stratigraphic age”. Recently, SACHS et al. (2016) tentatively identified GPIH uncatalogued as *Seeleyosaurus* sp., particularly based on the dorso-ventral elongation of the neural spines, coupled with the absence of anteroposterior constrictions at the base of the spines; however, it should be noted that this assignment is mainly based on photographs provided by LEHMANN (1971: pl. 3, pl. 4, fig. 1) since the specimen could not be relocated by the authors. Just recently, I retrieved the specimen at the GPIH, which made a more detailed re-examination possible. This re-examination revealed the presence of anteroposteriorly constricted neural spine bases (*contra* SACHS et al. 2016), a feature regarded as diagnostic for *Microcleidus* (BENSON et al. 2012: character 142). SACHS et al. (2016) also reported indeterminate microcleidid plesiosaur material, which can be dated to the upper Toarcian *G. (Grammoceras)* *thouarsense* Zone.

The presence of fossil remains assignable to probable *Meyerasaurus* and *Microcleidus*, coupled with the occurrence of a possible non-microcleidid plesiosauroid at Grimmen indicates the existence of three plesiosaur taxa in the lower Toarcian marine marginal ecosystems extending south of Fennoscandia. Moreover, it seems likely that plesiosaurs were a relatively common component in the marine marginal environments south of

Fennoscandia during Toarcian times (and perhaps also beyond; see SMITH 2008). If correct, this would contrast with our current understanding of Toarcian marine reptile faunas, which indicates that plesiosaurs were particularly less dominant when compared to ichthyosaurs and thalattosuchians (HAUFF 1921; BENTON & TAYLOR 1984; GODEFROIT 1994, 1996; FISCHER et al. 2011; VINCENT et al. 2013; WILLIAMS et al. 2015). This discrepancy could be attributable to specific ecological and/or biological constraints, but more likely corresponds to preservation biases. More material is therefore needed in order to provide more definitive data on the marine reptile diversity from the Toarcian of northern Central Europe.

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**PAPER 3**

Exceptionally preserved Leptolepidae (Actinopterygii, Teleostei) from the late Early Jurassic Fossil-Lagerstätten of Grimmen and Dobbertin (Mecklenburg-Western Pomerania, Germany)

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## **Abstract**

Exceptionally well-preserved fishes of the family Leptolepidae (Actinopterygii, Teleostei) from the late Early Jurassic Fossil-Lagerstätten Grimmen and Dobbertin (Mecklenburg-Western Pomerania, NE Germany) are reported and detailed anatomical descriptions are given. The described material specifically derives from the “Green Series”, which represents a specific facies that falls within the lower part of the early Toarcian *Harpoceras falciferum* ammonite Zone. Complete skeletons are rare, and most specimens are represented by isolated skulls. Most of the skulls are fully articulated and show only a low degree of compaction, while some specimens are almost three-dimensionally preserved. The leptolepid fauna comprises *Leptolepis coryphaenoides*, *L. normandica*, *L. jaegeri*, a possible *Proleptolepis*, and two other taxa, which are described in open nomenclature. Several anatomical characters, such as the shape of premaxilla, maxilla, dentary, preopercle, the cephalic sensory canals, and the dentition of the jaws, are discussed and compared to former studies. The new material provides novel insights into morphology, diversity and paleobiogeography of leptolepid fishes. The records of *Leptolepis coryphaenoides*, *L. normandica* and *L. jaegeri* from Grimmen and Dobbertin represent the northeastern-most occurrences of these species from Europe, suggesting that they inhabited the whole central European epicontinental sea during the early Toarcian. The possible occurrence of *Proleptolepis* in the lower Toarcian of Grimmen suggests that this genus might have had a much wider paleobiogeographical and temporal distribution, since specimens attributed to *Proleptolepis* have previously been reported only from the Sinemurian of western Europe.

**Key words:** *Leptolepis*, *Proleptolepis*, Toarcian, Green Series, Grimmen, Dobbertin.



## Introduction

Teleostei forms the most species-rich group of vertebrates with about 27000 extant species (Nelson 2006). First appearing in the Middle Triassic, teleosts attained a cosmopolitan distribution at the end of the Jurassic (Arratia 2004, 2013, 2015a). Several synapomorphies of modern teleosts (Leptolepidae plus more advanced teleosts) such as the presence of cycloid scales; ossified autocentra, constricting the notocord; two ural centra; and 19 principal caudal rays appear the first time in Leptolepidae (Arratia 1997, 1999, 2013, 2015a). The stratigraphic range of Leptolepidae is Early to Middle Jurassic (Nybelin 1974, Arratia & Hikuroa 2010) and they probably had a world-wide distribution (see Woodward 1900, Arratia & Hikuroa 2010, Arratia 2015b). Thus, members of the family Leptolepidae represent a major step in the evolution of teleosts and are of great interest for evolutionary and palaeobiogeographic studies (e.g., Patterson & Rosen 1977; Arratia 1997, 1999; 2013, 2015a; Arratia & Hikuroa 2010; Sferco *et al.* 2015). Early Jurassic leptolepids are very abundant in western and central Europe, especially in the Toarcian, where numerous specimens have been found (e.g., Bronn 1830; Agassiz 1832; Hauff 1921; Rayner 1937; Wenz 1968; Nybelin 1974; Williams *et al.* 2015). An important step in order to clarify the taxonomic content of Leptolepidae and its genera was achieved by Nybelin (1974). Otherwise, some taxa still need to be described in detail to complete our understanding of the early history of teleosts. For instance, the distinction of species within the genus *Leptolepis* is still problematic, since the characters used by Nybelin (1974) are, in many ways, wide distributed and ambiguous, which make specific identification difficult. Aggravating this situation, most species within *Leptolepis* are still poorly known due to the scarcity of well-preserved material. The objective of this paper is twofold: to describe the leptolepid fauna from the lower Toarcian “Green Series” of Grimmen and Dobbertin and to identify discrete characteristics in order to further clarify the taxonomy, anatomy, and palaeobiogeography of Early Jurassic leptolepids from Europe.

## Geological and stratigraphic setting

Although laterally extended in north-eastern Germany, Early Jurassic sediments only crop out in the abandoned open-cast clay pits of Grimmen and Dobbertin (Mecklenburg-Western Pomerania; Fig. 1A), both exposing a parautochthonous succession of upper Pliensbachian to lower Toarcian sediments that were glacially dislocated during the Pleistocene ice advances (Ernst 1967, 1991, 1992). The lower Toarcian marine vertebrate-bearing sequences exposed at Grimmen and Dobbertin are represented by thick packages of pure clay containing fossiliferous carbonate concretions. These distinct accumulations are referred to the traditionally called “Green Series”, which reaches thicknesses of several tens of meters in North-Eastern Germany (Schumacher & Sonntag 1964; Stoermer & Wienholz 1965; Lehmkuhl 1970). The “Green Series” clay deposits have been biostratigraphically dated to the *Harpoceras falciferum* Zone based on ammonites found associated with the concretions that occur interbedded within the clay (Ernst

1967, 1992). Unlike the concretions originating from the “Green Series” of Grimmen, which can be correlated with the *Eleganticeras elegantulum* and *Harpoceras exaratum* Subzones (Ernst 1967), those deriving from the “Green Series” clay deposits of Dobbertin can solely be dated to the *Harpoceras falciferum* Zone on the basis of current data (Ansorge 2003; Ansorge & Obst 2015). Based on the presence of a taxonomically impoverished ammonite fauna and the absence of typical stenohaline invertebrates (e.g., belemnites and soft-bodied cephalopods), reduced salinity conditions have been concluded for the time of deposition of the “Green Series” (Ernst 1991; Ansorge 2003, 2007). However, it is to be noted that the *Harpoceras falciferum* Zone coincides with the Toarcian Oceanic Anoxic Event, which massively impacted marine ecosystems (e.g., Caswell *et al.* 2009; Dera *et al.* 2011; Caswell & Coe 2014). The occurrence of rare conchostracans, otherwise, demonstrates a freshwater influence during deposition of at least parts of the “Green Series” (Ansorge 2003; Stumpf pers. obs.). These occur alongside an extraordinary rich entomofauna (see Ansorge 2003 for a recent summary), indicating the presence of suitable environments nearby. The vertebrate fauna mainly consists of actinopterygians, ichthyosaurs, plesiosaurs, thalattosuchians (e.g., Geinitz 1884; Jaekel 1929; Malzahn 1963; Thies 1989; Maisch & Ansorge 2004; Ansorge 2007; Stumpf 2016) and recently described sauropod remains (Stumpf *et al.* 2015). The most common vertebrates recovered from the “Green Series” are teleosts. Geinitz (1884) published the first report of teleosts from the “Green Series”, briefly noting on fishes from Dobbertin, which he assigned to *Leptolepis “bronni”* and *Leptolepis “concentricus”*, respectively. Jaekel (1929) described a head from Dobbertin, which he attributed to *Leptolepis “bronni”* (herein identified as *Leptolepis jaegeri*; see below). Later, Nybelin (1974: pl. 9, fig. 3) figured a cast of a partial head of *Leptolepis coryphaenoides* from Dobbertin (this specimen was assessed for this study; see below). Just recently, Ansorge & Obst (2015: fig. 15b) figured a *Leptolepis “bronni”* from Dobbertin (herein ascribed to *Leptolepis normandica*). Teleosts from the lower Toarcian “Green Series” of Grimmen were figured and identified as *Leptolepis* sp. by Ansorge (2007: fig. 13-4) and Zessin & Krempien (2010: fig. 16, 17).

The material described herein is preserved within or on the outer surface of small to medium-sized, laminated micritic concretions that were collected directly from the “Green Series” clay deposits of Grimmen and Dobbertin by both geoscientists and amateur collectors. While the teleost-bearing concretions recovered from the “Green Series” clay deposits of Grimmen can be correlated with the *Harpoceras exaratum* Subzone (Ansorge 2007) (Fig. 1b), those originating from the “Green Series” of Dobbertin can solely be dated to *Harpoceras falciferum* Zone based on the data currently available (Ansorge 2003; Ansorge & Obst 2015). Although resembling each other, the concretions from the *Harpoceras exaratum* Subzone of Grimmen are much smaller, as compared to the Dobbertin concretions, reaching sizes of up to 10 cm size. As a consequence, complete or near-complete specimens are rare. Most of the herein described specimens are represented by almost completely articulated heads. These often

occur associated with the pectoral girdles, abdominal vertebrae and scales. Apart from articulated specimens, isolated teleostean bones are frequent, incorporating large amounts of vertebrae that are consistent with referral to Leptolepidae (*sensu* Arratia & Hikuroa 2010). The fossil material contained within concretions is almost perfectly three-dimensionally preserved, with the void spaces being filled with micrite and/or sparitic calcite. This kind of preservation indicates an early diagenetic formation prior to compaction of the surrounding clay. Conversely, the specimens preserved on the outer surfaces of the concretions have undergone compaction. The specimens, especially those from Dobbartin, are coated with pyrite, which gives a somewhat golden appearance to the bones.

### **Taxonomic background**

Fishes of the genus *Leptolepis*, in its modern taxonomic sense (Nybelin 1974), are small teleosts, restricted to the Lower to Middle Jurassic (Nybelin 1974, Arratia & Hikuroa 2010). The first description of a fish of the genus *Leptolepis* Agassiz, 1832 (*sensu* Nybelin 1974) was provided by Bronn (1830), who described several specimens of a small fossil fish from the Lower Jurassic of Neudingen (Baden-Württemberg, Germany) and named this fish *Cyprinus coryphaenoides*. Two years later, Agassiz (1832) realized that the assignment to *Cyprinus* was incorrect. He included the species in his new genus *Leptolepis* and, however, renamed the species *Bronnii*. In the same work, he briefly described two new species, *L. Jaegeri* and *L. longus* (both from Zell, Baden-Württemberg, Germany). Agassiz (1832) also referred fishes from the Upper Jurassic Plattenkalk deposits of Bavaria (Germany), previously assigned to *Clupea* by de Blainville (1818), to *Leptolepis*. In the work of Agassiz (1833–1844), he briefly described *L. tenellus* from the Lower Jurassic of Badisch-Oberland (Baden-Württemberg, Germany) and *L. caudalis* from the Lower Jurassic of England, as well as other species from the Middle and Late Jurassic. Furthermore, he included *Leptolepis* in his order Ganoides, based on the assumption that the scales are covered with a layer of ganoine. Müller (1845) observed concentric lines on the scales of *Leptolepis*, but followed the incorrect interpretation of Agassiz, that the scales are covered with ganoine, and consequently excluded *Leptolepis* from his new subclass Teleostei. In the following century, lots of small fossil fishes were described and assigned to *Leptolepis*, ranging from the Upper Triassic to Upper Cretaceous, from all over the world (e.g. *L. macropthalmus* Egerton, 1845; *L. concentricus* Egerton 1849; *L. constrictus* Sauvage, 1873; *L. affinis* Sauvage 1873; *L. pronus* Sauvage, 1873; *L. pachystetus* Sauvage, 1873; *L. autissiodorensis* Sauvage, 1892; *L. talbragarensis* Woodward, 1895; *L. lowei* Woodward, 1895; *L. disjectus*, Woodward, 1895; *L. africana* Gardiner, 1960; *L. normandica* Nybelin, 1962; *L. koonwarri* Waldman, 1971). As a consequence, *Leptolepis* became a wastebasket taxon for the reception of small Mesozoic fishes of generalized teleostean morphology. One hundred-thirty years after the erection of the genus *Leptolepis*, Nybelin (1962) reestablished the correct specific name for Agassiz's (1832) *L. "bronnii"*,

which is *L. coryphaenoides*, following the rule of priority. Nybelin (1962) also erected a new species, *L. normandica*, based on material from the Toarcian of France and England.

Later, in a revision of the Toarcian material from France, Wenz (1968) synonymized most of the Toarcian species previously attributed to *Leptolepis* (including *L. normandica*) with the type species *L. coryphaenoides*, treating observed anatomical differences as intraspecific variations. This use of *L. "coryphaenoides"* in a wide sense was accepted by Patterson (1975) and in part by Tintori (1977) and Patterson & Rosen (1977). The confusion concerning the taxonomy, diversity and synonymy of Leptolepidae was, in many aspects, clarified by Nybelin (1974) with his "Revision of the Leptolepid Fishes". Nybelin realized that the genus *Leptolepis* has to be interpreted in a strict sense, and restricted the content of the genus to the type species *L. coryphaenoides* and closely allied fishes (*L. normandica*, *L. jaegeri*, *L. saltviciensis*, *L. autissiodorensis*, *L. woodwardi* and *L. nathorsti*), ranging in age from Toarcian to Bathonian. He excluded many species with the erection of new genera (*Proleptolepis*, *Seefeldia*, *Leptolepides*), or reestablished formerly used generic names (*Ascalabos*, *Tharsis*). Beside this, he also erected the genus *Proleptolepis*, including three new species (*P. furcata*, *P. elongata* and *P. megalops*). Furthermore, Nybelin also gave a new definition of the family. Leptolepidae *sensu* Nybelin (1974) contains the Early Jurassic genera *Leptolepis*, *Proleptolepis*, and the Late Jurassic genera *Leptolepides* and *Tharsis*. Later phylogenetic studies, however, demonstrated that *Leptolepides* and *Tharsis* are not closely related to *Leptolepis* and *Proleptolepis*, and no support for the family was found (e.g. Patterson & Rosen 1977; Arratia 1997, 1999, 2015a; Arratia & Tischlinger 2010). Arratia & Thies (2001) introduced a new teleost, *Longileptolepis wiedenrothi* (= *Paraleptolepis wiedenrothi*, Arratia 2003), based on a single individual from the lower Toarcian of Salzgitter-Haverlahwiese (Lower Saxony, Germany). A phylogenetic analysis conducted by Arratia & Thies (2001) revealed that *Longileptolepis* is nested between *Proleptolepis* and *Leptolepis*, with the latter taxon being the most advanced. Arratia & Hikuroa (2010) reported Leptolepidae indet. from the Callovian of Antarctica and showed that leptolepids probably were globally distributed. Furthermore, they assigned *Leptolepis*, *Proleptolepis* and *Longileptolepis* to Leptolepidae on the base of three uniquely derived characters (vertebrae with thin and smooth autocentra, autocentra and chordacentra not constricting the notochord, lack of cavities for adipose tissue in the walls of the autocentra). Despite recent advances in understanding the taxonomic and anatomical diversity of Leptolepidae, the distinction of species within the genus *Leptolepis* s. str. remains problematic. Additionally, the invalid species name *Leptolepis "bronni"* is still mistakenly used in the literature (e.g., Keller 1976; Hauff & Hauff 1981; Hauff *et al.* 2014; Ansorge & Obst 2015).

## Methods

Most of the fossils from Grimmen and Dobbartin were mechanically prepared with the help of pneumatic preparation tools, fine steel needles of different sizes, and soft brushes by the authors, J. Ansorge, and S.

Liebermann. Some specimens were acid prepared by J. Ansorge, using acetic acid with concentrations of 7 % to 10 %. Specimen GG 431/9 a and b was transferred on epoxy resin and than acid prepared by J. Ansorge. Drawings were made with the help of stereoscope microscopes. Most of the photographs were taken under coverage with ethanol (99%), with Fujifilm Finepix S 1600 and Zeiss AxioCam HR3 cameras. All measurements were taken by M. Konwert with a vernier caliper.

**Terminology.** The terminology of the skull roof follows the homologization of Schultze (2008). The terms used for hyoid arch, urohyal, and suspensorium are from Arratia & Schultze (1990, 1991). The terminology of the caudal skeleton and vertebral count follows Nybelin (1963), Arratia & Schultze (1992), as well as Schultze & Arratia (2013). The terminology of the fin elements follows Arratia (2008).

**Nomenclature of *Leptolepis* “*bronni*”, *L. “coryphaenoides”* and *L. coryphaenoides*.** With this work, we largely agree with the taxonomy and nomenclature of Nybelin (1962, 1974). Nybelin (1962) realized that the initial, and thus correct, name for the type species of *Leptolepis* is *L. coryphaenoides*. The formerly used name *L. bronni* was established by Agassiz (1832) for a species previously described by Bronn (1830) as *Cyprinus coryphaenoides*. Furthermore, Nybelin (1962) realized that *L. “bronni”* is a collective species, consisting of at least *L. coryphaenoides* (Bronn, 1830) and *L. normandica* Nybelin, 1962. Thus, descriptions of *L. “bronni”* (e.g. Woodward 1895, Jaekel 1929, Rayner 1937) may be a blend of at least these species. When we cite these publications, we retain the use of the name “*bronni*”, to avoid confusion with the valid species. Wenz (1968) accepted *coryphaenoides* as valid species name, but she interpreted the species *L. “bronni”*, *L. normandica* and others (*L. pachystetus*, *L. constrictus*, *L. pronus*, *L. affinis*) as synonyms of the type species *L. coryphaenoides*, and thus, she treated the anatomical differences between *L. coryphaenoides* and *L. normandica* as intraspecific variations. We do not agree with this interpretation. *L. coryphaenoides sensu* Wenz (1968) is, in our opinion, also a collective species, including at least *L. coryphaenoides (sensu* Nybelin 1962, 1974) and *L. normandica* Nybelin, 1962. When we name *L. coryphaenoides* in the wide sense of Wenz (1968), we use quotation marks (“*coryphaenoides*”) to avoid confusion with *L. coryphaenoides* in the strict sense of Nybelin (1962, 1974).

**Adult and juvenile specimens.** The herein examined specimens of *Leptolepis* comprises fishes of different sizes. The maximal known total length of *L. coryphaenoides* is 85 mm (Bronn 1830). Nybelin (1974) stated an almost equal length of 77 mm standard length for *L. coryphaenoides* and 74 mm standard length for *L. normandica*. *L. jaegeri* is described as larger than *L. “bronni”* by Agassiz (1832). This was confirmed by Nybelin (1974), who stated a length of more than 100 mm for this species. Specimens which are evidently smaller then these sizes are herein interpreted as juveniles or subadults. As already discussed by Wenz (1968), small individuals of *Leptolepis* possess a lower number of tubules in the preopercular sensory canal than large specimens. This character is herein interpreted as indicative for juvenile

specimens. Also the state of ossification of the vertebral autocentra changes during ontogeny (e.g., Konwert 2011, Arratia 2016). In fact, poorly ossified autocentra were herein observed in small specimens of *Leptolepis*. Consequently, we interpret these specimens as juveniles or subadults.

**Institutional Abbreviations.** **NHM** British Museum (Natural History), London; **GG** Institut für Geographie und Geologie, Ernst-Moritz-Arndt Universität Greifswald; **MHNP** Muséum national d'Histoire naturelle, Paris; **NRM** Naturhistoriska Riksmuseet, Stockholm; **SNHM** Staatliches Naturhistorisches Museum Braunschweig; **MV** Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern, Geologische Landessammlung Sternberg.

**Material.** The following material was used for this study:

**GG:** Undetermined fishes (from Grimmen): GG 431/7; GG 438/8a, b; GG 431/9a, b, c; GG 431/10; GG431/11; GG 431/12; GG 431/13; GG431/14; GG 431/15; GG 431/16; GG431/17; GG 431/18; GG 431/19; GG 431/21. Undetermined fishes (from Dobbertin): GG 431/1; GG 431/2; GG 431/3; GG 431/4a, b; GG 431/5; GG 431/6; GG 431/11; GG 431/20. *Leptolepis* “*bronni*” (from Holzmaden): GG21.224; GG21.220; GG21.221; GG21.222; GG21.223; GG21.225; GG21.227. “*Pholidophorus*” sp.: GG21.219 (Dormettingen); GG21.226 (Dorset).

**MV:** Undetermined fishes (from Grimmen): MV 202612, MV 202613, MV 202614.

**NRM:** *Leptolepis jaegeri* Agassiz, 1832: NRM P. 6483a, b (neotype, from Holzmaden). *Leptolepis coryphaenoides* (Bronn, 1830): NRM P. 6091 (cast of MNH P 23834, Dobbertin); NRM P 6500 (Holzmaden); NRM P 7810 (Salzgitter); NRM P 7811 (Salzgitter). *Leptolepis nathorsti* Woodward, 1900 (from Svalbard): NRM P 1314; NRM P 1316 (lectotype); NRM P 1317.

**SNHM:** *Leptolepis* sp. (from Schandelah and Hondelage): 19 uncataloged specimens.

## **Systematic Palaeontology**

Actinopterygii Cope, 1887

Teleostei Müller, 1845 (*sensu* Arratia, 1999)

### **Leptolepidae Pictet, 1854**

**Content.** *Leptolepis coryphaenoides* (Bronn, 1830); *L. normandica* Nybelin, 1962; *L. jaegeri* Agassiz, 1832; *L. saltviciensis* Simpson, 1855; *L. autissiodorensis* Sauvage, 1892; *L. woodwardi* Nybelin, 1974; *L. nathorsti* Woodward, 1900; *Proleptolepis furcata* Nybelin, 1974; *P. elongata* Nybelin, 1974; *P. megalops* Nybelin, 1974; *Longileptolepis wiedenrothi* (Arratia & Thies, 2001).



**Geographical distribution.** Lower to Middle Jurassic Sediments of: Spitsbergen, Svenskøja (Svalbard, Norway); Neudingen, Holzmaden, Zell, Boll (Baden-Württemberg, Germany); Dobbartin, Grimmen (Mecklenburg-Western Pomerania, Germany); Salzgitter, Schandelah, Hondelage (Lower Saxony, Germany); Le Cain, Curcy (Normandie, France); Dumbleton, Gretton, Iminster (England, Great Britain); Bergamo (Lombardy, Italy); Quebrada Vaquillas Altas, Quebrada la Carreta (Chile); Antarctic peninsula (Antarctica); Sao Pedro de Muel (Portugal) (data from Wenz 1968; Nybelin 1974; Tintori 1977; Arratia & Thies 2001; Arratia & Hikuroa 2010; Arratia 2015b; Antunes *et al.* 1981; this paper).

**Stratigraphical distribution.** Lower Jurassic, Senimurian, *Asteroceras obtusum* Zone to late Middle Jurassic, Callovian.

### **Leptolepidae sp. 1**

Figure 2; Plate 1A, B

**Material.** GG 431/5a, b isolated head missing postcranial bones, preserved in part and counterpart. Many of the bones are missing but molds of the bones are preserved on both slaps, showing their outlines and ornamentation.

**Geographical distribution.** Former clay pit of Dobbartin, Mecklenburg-Western Pomerania, Germany.

**Stratigraphical distribution.** Lower Jurassic, lower Toarcian “Green Series”, *Harpoceras falciferum* Zone.

### **Description.**

Cranial bones (Fig. 2; Pl. 1B): The parietal is incompletely preserved, but the impressions of the bone on GG 431/5a and b show that the anterior portion of the bone was thin and elongate. The posterior part is broad with an undulating posterior margin. The surface of the bone is ornamented with several fine grooves. The postparietal is not preserved. The pterotic is somewhat L-shaped with a broad ventral and a thin dorsal limb, the latter is mainly formed by a heavily ossified bony ridge. Some short vertical grooves are present on the surface of the bone, the most posterior one, that is deeper and broader than the previous ones, seems to be the middle pit line. A short section of the parasphenoid is preserved in the specimen, it is thin and heavily ossified. The posterior margin of the extrascapula is damaged, but the impression of this bone on GG 431/5b shows that it was semicircular, with a straight anterior margin.

Upper and lower jaws (Fig. 2; Pl. 1B): The jaws are only known from impressions on the rock. The maxilla is long and slightly convex, at least its anterior part must have been ornamented with

longitudinal grooves and ridges. The impressions on GG 431/5b indicate the presence of teeth at least in the posterior part of the maxilla, their size remains unknown. Two supramaxillae are present. They are placed dorsal to the maxilla. The posterior supramaxilla bears a well marked, spine-like anterodorsal process. According to the impressions, both must have been covered with a strong ornamentation of longitudinal grooves and ridges. The molds of the dentary and angular are uninformative.

Circumorbital bones (Fig. 2; Pl. 1A): The bones of the circumorbital series are known from impressions of the supraorbital and the left and right infraorbital 1. The dermosphenotic (fig. 2; pl. 4B, E) is preserved in GG 431/5a, as well as its impression in GG 431/5b. The supraorbital is elongate with a sharp anterior tip. Its medial margin is sharply angled along its entire length. The possible presence of a posterior supraorbital is unknown. The infraorbital bone 1 was large and broad, with its anterior portion deeper than the posterior. The dermosphenotic is very large for basal teleosts (about 10% of head length), it is somewhat triangular and expands in anterodorsal direction.

Opercular bones and branchiostegal rays (Fig. 2; Pl. 1B): The opercular series consists of opercle, subopercle, preopercle; the interopercle was not observed. The opercle is the largest bone of the series, it bears a strongly ossified ridge at its anterior margin. The articulation with the subopercle is oblique. Some irregular shaped grooves are present on the surface of the bone. The subopercle is about as half as deep as the opercle and slightly broader. Its ventral and posteroventral margins are convex. The preopercle consists of a long dorsal and a ventral limb, both forming an angle of  $110^\circ$ . The dorsalmost part of the preopercle is only formed by the bony tube of the preopercular sensory canal. There is a well-marked notch in the posterior margin, and a small process in the anterior margin. Three incompletely preserved, plate-like branchiostegal rays are present ventral to the opercular bones.

Sensory canal system (Fig. 2; Pl. 1A, B): All preserved sensory canals are bone enclosed. The preserved part of the supraorbital canal runs along the parietal and forms a slight curve posterior to the orbit. The supraorbital canal ends at the posterior margin of the parietal. The canal probably continues on the postparietal. The canal does not give off any tubules, but four pores are observed. The infraorbital canal is positioned near the dorsal margin of infraorbital 1, at least five tubules are present in this bone. These are long and thin, nearly reaching the ventral margin of infraorbital 1. The infraorbital canal ends at the anterior margin of the dermosphenotic. On the dermosphenotic, the infraorbital canal gives off four tubules, all are directed dorsally, ending close to the dorsal margin of the bone. The infraorbital sensory canal is posteriorly continuous with the otic canal. The otic canal runs along the dorsolateral margin of the pterotic. This canal does not have tubules but two pores are present. The supratemporal canal runs near the anterior margin of the extrascapula, it gives off at least five long tubules that probably reached the posterior margin of the extrascapula. A short part of the middle pit line is probably present in the posterior

part of the pterotic. The preopercular canal runs near the anterodorsal margin of the ventral limb of the preopercle, and along the center of the dorsal limb. At least eight tubules are present in the ventral limb of the preopercle, their length increases in posterior direction. They end near the ventral respectively posterior margin of the preopercle. One long tubule was observed in the ventral portion of the dorsal limb of the preopercle. A single pore is present in the dorsal portion of the preopercular canal.

Identification: Although poorly preserved and lacking the postcranial skeleton, GG431/5a, b can be assigned to Leptolepidae based on the presence of two relatively large supramaxillae that are placed at the dorsal margin of the maxilla and the L-shaped preopercle. The specimen cannot be assigned to any existing species of Leptolepidae, since the undulating posterior margin of the parietal, the L-shaped pterotic, and the number of tubules in the infraorbital canal in the dermosphenotic seem to be unique among leptolepids.

### ***Proleptolepis*-like**

Figure 3, Plate 1C

**Material.** MV 202612, fragmentary head preserved in medial view.

**Geographical distribution.** Former clay pit of Grimmen, Mecklenburg-Western Pomerania, Germany.

**Stratigraphic distribution.** Lower Jurassic, lower Toarcian “Green series”, *Harpoceras falciferum* Zone, *Harpoceras exaratum* Subzone.

### **Description.**

Opercular series (Fig. 3; Pl. 1C): The opercle, subopercle, preopercle, and interopercle are preserved in the specimen. The opercle is poorly preserved. Its anterior margin is formed by a well-ossified ridge. The broad and deep subopercle is very large. The overall size seems to be equal to the size of the opercle, or it was slightly larger. The anterodorsal and anterior margins of the subopercle are straight, whereas the ventral and posterior margins are convex. The dorsal part of the preopercle is not preserved, but its mold allows to evaluate its outline. The bone is formed by a dorsal, vertical oriented, and a ventral, horizontal oriented limb; both limbs form an angle of about 120°. Anteriorly, at the confluence of both limbs there is a broad, convex process. Although the ventral margin of the bone is covered by the interopercle, the exposed part suggests the ventral limb of the preopercle to be very deep. In the posterior margin of the bone, at about the confluence of both limbs, a deep, sharp notch is present. The fragments and the molds interopercle suggest that it was large and triangular. Its length exceeds the

length of the ventral limb of the preopercle. The ventral and posterior margins of the bone form an angle of about 90°.

Infraorbital 3 and suborbital (Fig. 3; Pl. 1C): Anteriorly to the preopercle, there are fragments of a canal bearing, dermal bone. In order to the large size and the position of these remains, they are identified as belonging to infraorbital 3. Between the posterior margin of infraorbital 3 and the impression of the preopercle, there are two bone fragments. According to their position these fragments are interpreted as remains of a suborbital bone.

Sensory canal system (Fig. 3; Pl. 1C): The infraorbital sensory canal is only known from a single, trifurcated tubule in the remains of infraorbital 3. The preopercular canal runs close to the anterior respectively dorsal margins of the bone. Its canal gives off at least 10 unbranched tubules. Some more might be covered by the interopercle. The dorsal part of the canal gives off a single, posteriorly directed, long tubule. This seems to end at or close to the posterior margin of the preopercle. Two short and thin tubules are present at the confluence of both limbs, an additional short tubule is directed anteriorly.

Identification: The shape of the preopercle and the large size of the subopercle prevent an assignment to any species of *Leptolepis*. A large subopercle is found in *Longileptolepis wiedenrothi*, *Proleptolepis furcata* and *P. megalops*. As described above, MV 202612 bears a deep notch in the posterior margin of the preopercle. A shallow notch is present in *Longileptolepis wiedenrothi* (Arratia & Thies 2001) and some species of *Leptolepis* (see below). A deep notch in the posterior margin of the preopercle, similar to the described specimen, is only present in *Proleptolepis*. Thus, MV 202612 indicates closest morphological resemblance to *Proleptolepis*. However, given the incomplete nature of the specimen it is here considered as an indeterminate Leptolepidae until more material is available.

### ***Leptolepis* Agassiz, 1832**

**Type species.** *Leptolepis coryphaenoides* (Bronn, 1830).

**Content.** *L. coryphaenoides* (Bronn, 1830); *L. normandica* Nybelin, 1962; *L. jaegeri* Agassiz, 1832; *L. autissiodorensis* Sauvage, 1892; *L. saltviciensis* Simpson, 1855; *L. woodwardi* Nybelin 1974, *L. nathorsti* Woodward, 1900.

**Geographical distribution.** Lower to Middle Jurassic sediments of: Spitsbergen, Svenskøja (Svalbard, Norway); Neudingen, Dormettingen, Holzmaden, Zell, Boll (Baden-Württemberg, Germany); Dobbartin, Grimmen (Mecklenburg-Western Pomerania, Germany); Salzgitter, Schandelah, Hondelage (Lower Saxonia, Germany); Le Cain, Curcy (Normandy, France), Dumbleton, Gretton, Ilminster

(England, Great Britain); Bergamo (Lombardy, Italy) (data from Wenz 1968; Nybelin 1974; Tintori 1977; this paper).

**Stratigraphical distribution.** Lower Jurassic, lower Toarcian to Middle Jurassic, Callovian.

***Leptolepis coryphaenoides* (Bronn, 1830)**

Figures 4A, B, 6; Plates 2A–C, 3A, B

Synonyms:

*Cyprinus coryphaenoides* Bronn, 1830: pl. 1.

*Leptolepis Bronnii* Agassiz, 1832: p. 146.

*Leptolepis bronnii* Quenstedt, 1858: pl. 33 figs. 8–11.

*Leptolepis bronni* Rayner, 1937 (in part): figs. 1–14.

*Leptolepis coryphaenoides* Nybelin, 1962: fig. 1A.

*Leptolepis coryphaenoides* Nybelin, 1963: fig. 9.

*Leptolepis coryphaenoides* Wenz, 1968 (in part): figs. 79–107, pls. XL–XLVIII.

*Leptolepis coryphaenoides* Patterson, 1968 (in part): figs. 9 A–C.

*Leptolepis coryphaenoides* Nybelin, 1974: figs. 4A–B; 5A–K; 6A–L; 7D–G; 8; pls. VI–X; XI, figs. 1, 4–5.

*Leptolepis coryphaenoides* Patterson, 1975 (in part): figs. 58, 89–91, 127, 128A, 132B, 144.

*Leptolepis coryphaenoides* Taverne, 1975: fig. 1.

*Leptolepis coryphaenoides* Nybelin, 1976: pl. 1, fig. 4–5.

*Leptolepis coryphaenoides* Tintori, 1977: figs. 1–4.

*Leptolepis coryphaenoides* Patterson & Rosen, 1977: figs. 32B–C, 33C.

*Leptolepis coryphaenoides* Schultze & Arratia, 1989: fig. 6A.

*Leptolepis coryphaenoides* Arratia & Schultze, 1990: fig. 10A–E.

*Leptolepis coryphaenoides* Arratia, 1994: pl. 7 figs. A–B.

*Leptolepis coryphaenoides* Wild, 1994: fig. 85.

*Leptolepis coryphaenoides* Arratia & Lambers, 1996: fig. 14C.

*Leptolepis coryphaenoides* Arratia, 1996a: fig. 1D.

*Leptolepis coryphaenoides* Arratia, 1996b: figs. 5A, 6B.

*Leptolepis coryphaenoides* Arratia, 1997: figs. 76A, B, 82A, 83B, 88B, 89A–C, 90A.

*Leptolepis coryphaenoides* Delsate, 1997: pl. 1, 3A–B.

*Leptolepis coryphaenoides* Arratia, 1999: fig. 13.

*Leptolepis coryphaenoides* Kriwet, 2001: fig. 4.7H.

*Leptolepis normandica* Arratia & Thies, 2001: fig. 12B.

*Leptolepis coryphaenoides* Arratia & Thies, 2001: fig. 12D.

*Leptolepis coryphaenoides* Bean, 2006: figs. 9H–I, 19A.

*Leptolepis normandica* Bean, 2006: fig. 18A.

*Leptolepis coryphaenoides* Arratia & Herzog, 2007: fig. 7C.

*Leptolepis coryphaenoides* Arratia, 2008: fig. 7B, 22.

*Leptolepis coryphaenoides* Arratia, 2009: fig. 14A.

*Leptolepis coryphaenoides* Arratia & Hikuroa, 2010: figs. 7A–D.

*Leptolepis coryphaenoides* Arratia, 2013: figs. 97D, 99A, 100A–B.

*Leptolepis coryphaenoides* Schultze & Arratia, 2013: figs. 5B, 9A, B, 21B.

*Leptolepis coryphaenoides* Arratia & Schultze, 2015: fig. 768A.

*Leptolepis coryphaenoides* Arratia, 2015: figs. 4A, C, 10C, 11D, 15C.

**Material.** GG 431/3 slightly disarticulated, incomplete head, from Dobbertin; GG 431/7 subadult, almost complete specimen, missing most of the caudal fin, from Grimmen; NRM P 6091 (cast of MNH P.



23834) fragmentary head, from Dobbertin; GG431/19 isolated head with pectoral girdle, from Grimmen; GG431/20 incomplete head, from Dobbertin.

**Geographical distribution.** Neudingen, Holzmaden, Zell, Boll (Baden-Württemberg, Germany); Dobbertin, Grimmen (Mecklenburg-Western Pomerania, Germany); Curcy (Normandy, France), Dumbleton, Gretton, Ilminster (England, Great Britain); Bergamo (Lombardy, Italy) (data from: Wenz 1968; Tintori 1977; Nybelin 1974; this paper).

**Stratigraphical distribution.** Lower Jurassic, Toarcian, at least *Harpoceras falciferum* Zone.

### **Description.**

Cranial bones (Figs. 4A, B; Pl. 2A): A short part of the mesethmoid was observed in GG 431/7, most of it is covered by infraorbital 1. The parietals form most of the skull roof. They are poorly preserved in GG 431/7 but the remnants show that they were narrow anteriorly but broader in its posterior portion. The postparietals are not preserved. In GG 431/7 the pterotic is subrectangular, with a smooth surface. The pit lines were not observed. The extrascapula seems to be semicircular, with a straight anterior margin.

Upper Jaw (Figs. 4A, B, 5; Pl. 2A, 3A, B): The upper jaw consists of maxilla, premaxilla and two supramaxillae. The triangular premaxilla is very small and elongate, with the ascending process being low and narrow. A single row of very small teeth is present along the oral margin of the premaxilla. The maxilla is the largest bone of the upper jaw. It is moderately long and deep. Its posterior margin reaches the center of the quadrate. The ventral margin is convex, especially its posteroventral margin shows a strong curvature. A single row of miniscule teeth is present on the ventral margin of the maxilla. A well-ossified ridge is present along the lateral margin of the bone. In GG 431/3 several small longitudinal grooves are present on the lateral surface of the maxilla. These were not observed in GG 431/7 but this might be due to the fact that GG 431/7 is a subadult specimen and thus, the bone might not be fully developed. Most of the dorsal margin of the maxilla is covered by the supramaxillae. The anterior supramaxilla is elongate, with a sharp anterior tip. A low ridge is present along the lateral margin of the bone. The main body of the posterior supramaxilla is somewhat triangular in GG 431/7 but ovoid in GG 431/3. A long, spine-like anterior process emerges from about the center of the bone. The anterior tip of the process is covered by the first infraorbital in both specimens, so its length is unknown. The posterior supramaxilla shows an ornamentation of several grooves, running parallel to the dorsal and ventral margins of the bone.

Lower Jaw (Figs. 4A, B; Pl. 3A): Most of the lower jaw is covered by the maxilla in the observed specimens. The dentary forms most of the ventral margin of the lower jaw. The oral margin ascends with an angle of about 40° in respect to the ventral margin of the dentary. Two very small teeth are preserved

on the dentary of GG 431/7. The ventral margin of the dentary is slightly convex and the mandibular sensory canal runs close the ventral margin of the bone. Posterodorsally, the dentary articulates with the angular. The exposed part of the angular shows a distinct ornamentation of grooves and ridges.

Circumorbital bones (Figs. 4A, B, 5; Pl. 2C): The circumorbital series is incomplete in all examined specimens. The large and elongate infraorbital 1 is subtriangular, with its anterior margin deeper than the posterior margin. Infraorbital 2 is very thin, mainly carrying the infraorbital sensory canal. It is slightly shorter than infraorbital 1. Infraorbital 3 is the largest bone of the series. It is subrectangular with a concave anteroventral and convex dorsal and posterior margins. Infraorbitals 4 and 5 are preserved in NRM P 6091. Both are of equal size and shape. They are small and subrectangular. The ventral part of the dermosphenotic is preserved in NRM P 6091 but its exact shape remains unknown. A single suborbital is present between infraorbitals 3 to 5, dermosphenotic, the preopercle and the opercle. It is elongate and bears a well-marked notch in its posterior margin. The ventral part of the thin and delicate anterior sclerotic bone is preserved in GG 431/7. The anterior part of the anterior supraorbital was observed in GG 431/7. It is thin and elongate. A very small, poorly ossified bone lies laterally to the anterodorsal tip of infraorbital 1 and the anterior tip of the parietal of GG431/7, which might be a remnant of the antorbital.

Hyoid- and Palatoquadrate arches (Figs. 4A, B; Pl. 2A): The dorsal part of the hyomandibula is exposed in GG 431/7 and the complete bone in GG 431/3. Anteriorly, it bears a thin lamella, and well-marked opercular and preopercular processes posteriorly. The main body of the quadrate is triangular. It bears a well-defined condyle for the articulation with the lower jaw. The posteroventral process of the quadrate is elongated; its posterior part is broken in GG 431/3 and covered by the preopercle in GG 431/7. Thus, its length remains unknown, but it is at least as long as the main body of the quadrate. The symplectic was not observed. The ventral part of the metapterygoid is exposed in GG 431/7. Its dorsal portion is covered by infraorbital 3 and its ventral margin is less broad than its dorsal part, as well as the dorsal part of the quadrate. An elongate, chondral bone lies ventrally to the preopercle in GG 431/7. This bone was identified as posterior ceratohyal. The number of the branchiostegal rays remains unknown due to poor preservation, but the more posterior ones seem to be longer and much broader than the anterior ones.

Opercular bones (Figs. 4A, B, 5; Pl. 2A–C): From the opercular series the opercle, subopercle, preopercle, and interopercle are preserved in the specimens. A suprapreopercle (see Nybelin 1962, 1974) is absent in specimen GG 431/7. The condition remains unknown in the other specimens. The opercle is the largest bone of the series. A well ossified ridge is present along its anterior margin. Several fine growth lines are running parallel to the ventral posterior and dorsal margins of the bone. The anterior, ventral and posterior margins of the bone are straight, whereas the dorsal margin is convex. Contrary to

the descriptions of Nybelin (1962, 1974), the anterior and posterior margins are not parallel. This is also true for specimen NRM P 6091 (MNH P 23834 in Nybelin 1974) which was assigned to *L. coryphaenoides*. The subopercle is slightly broader than the opercle but less deep. Several fine growth-lines are present parallel to the ventral and posterior margins of the bone. The preopercle is L-shaped. The ventral and dorsal limbs form an angle of a  $110^\circ$  with each other. The dorsal-most part of the dorsal limb of the preopercle is well preserved in GG 431/7. It seems to be only formed by the tube-like ossification of the preopercular sensory canal, and reaches the otic sensory canal dorsally. In GG 431/3, there is an indistinct notch in the posterior margin of the preopercle. Most of the interopercle is covered by the preopercle in both specimens, so not much is known about this bone.

Sensory canal system (Figs. 4A, B, 5; Pl. 2A–C): Only the cephalic sensory canals are known. The trunk canal is not preserved in the examined specimens. All sensory canals are running in tube-like ossifications. A short, poorly preserved part of the supraorbital canal is preserved on the posterior part of the parietal of GG 431/7. Its shape remains unknown. The infraorbital canal runs along the center of infraorbital 1. The canal is not preserved in GG 431/3 but impressions on the surface of the bone indicate the presence of at least four tubules, which seem to end close to the ventral margin of the infraorbital 1. The canal continues in the dorsal margin of infraorbital 2, no tubules were observed. On infraorbital 3, the canal runs near the anterior margin of the bone. It gives off two to four tubules which end at about the center of the bone. These are not branched in the juvenile specimen GG431/7, but strongly branched in NRM P 6091 and GG 431/19. In NRM P 6091 and GG 431/19, the canal continues close to the anterior margins of infraorbitals 4 and 5. The canal gives off one to two tubules in infraorbital 4 and one in in infraorbital 5. All tubules in infraorbitals 4 and 5 are unbranched, posteriorly directed and close to the posterior margins of the respective bones. The canal on the dermosphenotic is only known from NRM P 6091. In this bone the canal seems to trifurcate. The anterior, dorsal directed part of the canal is undoubtedly the anterodorsal branch of the canal. One of the posteriorly, respectively posterodorsally directed “branches” must be a tubule, the other the true posterior branch. A decision cannot be made on the basis of specimen NRM P 6091 because of the defective state of the dermosphenotic. Nybelin (1974:40) interpreted the ventral one as a posterior directed tubule, since he observed an equivalent tubule in another specimen (BMNH 19642). Thus, we follow Nybelins interpretation. The mandibular canal is well preserved in GG 431/3. It runs near the ventral margin of the dentary. Three pores are present on the ventral margin of the canal. The canal continues in the ventral part of the angular, the posterior opening is not visible. It is probably placed at the medial side of the bone. The preopercular canal runs close to the dorsal/anterior margin of the preopercle. In GG 431/3 it gives off at least 11 tubules (on the left preopercle), some of them are very broad and at least six of them are branched up to four times. The very broad tubules might be the result of fusion of adjacent tubules. All tubules end close to the ventral or

posterior margin of the preopercle. In GG 431/7 the preopercular canal gives off 10 tubules, only two of them are branched. The preopercular canal reaches the otic canal dorsally. The otic canal runs along the dorsolateral margin of the pterotic, a single, dorsally directed, short tubule is present. Posteriorly, the otic canal is continuous with the supraoccipital canal. This runs close to the anterior margin of the extrascapula. The number of tubules and the continuation with the posttemporal canal is unknown because of poor preservation. The canals in the posttemporal and supracleithrum are not preserved.

Vertebral column and associated bones (Pl. 2A): The following description is based on GG 431/7, a subadult specimen. Bones of the vertebral column can change their shape and often fuse with other bones during ontogeny. For descriptions of adult individuals of *Leptolepis* see e.g. Rayner (1937), Wenz (1968), Nybelin (1962, 1974), Arratia (1991, 1997), and Arratia & Hikuroa (2010). The total number of vertebrae, as well as the number of abdominal and caudal vertebrae are unknown, because the anteriormost vertebrae are covered by the opercle, others are covered by scales. The autocentra are slightly longer than broad, each being slightly constricted in its middle part. Their surface is smooth, without any ornamentation. The parapophyses are fused to their respective centrum, they are subtriangular in shape and are as long as their centra. Both halves of the abdominal neural spines are unfused but are fused in the caudal region. The ribs are thin, at least the anterior ribs seem to reach the ventral margin of the abdomen. Thin, elongate epineural processes are associated with the anterior abdominal neural arches. Epipleural bones seem to be absent. All neural arches seem to be unfused with their respective centrum in GG 431/7. Arratia (1991, 1997) described the abdominal neural arches as to be unfused, but the caudal neural arches as fused to their centra in *L. coryphaenoides*. Therefore, the herein observed unfused caudal neural arches of GG 431/7 are interpreted as an ontogenetic condition. The last six neural spines and the last five hemal spines are distally expanded. The neural spines are thin, their length remain unknown.

Pectoral girdle and fin (Figs. 4A, 5; Pl. 2A): The pectoral girdle is complete in GG 431/7, but many of the bones are poorly preserved. Most of the posttemporal is covered by the opercle, so its shape is unknown. This is also true for the supracleithrum that seems to be elongate. The dorsal limb of the cleithrum is covered by the subopercle, the ventral limb is directed anteroventrally. Its anterior tip and its posterior margin are bent in medial direction. Several fine grooves run parallel to the margins of the cleithrum, which seem to be growth lines. Postcleithrum 1 is an elongate bone, that seems to articulate with the supracleithrum dorsally and overlaps the postcleithrum 2 ventrally. Postcleithrum 2 is broad and seems to be triangular. The dorsal part of postcleithrum 3 is covered by the left pectoral fin. Its ventral part is triangular. The pectoral fin is located close to the ventral margin of the body. The following description is based on the right pectoral fin of GG 431/7. Sixteen pectoral fin rays are present. Most of them are segmented and branched in their distal portions. Two, maybe three small, elongate scales seem to be associated with the last pectoral fin ray. There are four poorly preserved proximal radials. Three are

elongate, the fourth is short and about twice as broad as the others. The anterior part of the coracoid is narrow and elongate. Anteriorly it reaches the anteroventral tip of the cleithrum. The posterior part of the coracoid is about as twice as broad as the anterior portion. A small part of the scapula is exposed in GG 431/7, but most of it is covered by the cleithrum, so its shape remains unknown.

Pelvic girdle and fin (Pl. 2A): The pelvic fin is placed at about 50% of standard length. The basipterygium is triangular, with a strongly ossified ridge along its lateral edge. Eleven fin rays plus an elongate pelvic splint are present. The distal portions of the pelvic fins are poorly preserved, but at least some of the lepidotrichia were segmented distally.

Dorsal and anal fin (Pl. 2A): Both, the dorsal and anal fins are poorly preserved. The dorsal fin consists of at least 11 fin rays. The number of precurent rays is unknown. At least ten fin rays are present in the anal fin, the first three are precurent rays. Fulcra are absent in the dorsal and anal fins.

Squamation (Pl. 2A): Several, comparatively large cycloid scales are preserved in GG 431/7. Their shape is circular in the dorsal part of the abdominal region, but some scales in the ventral part of the abdomen show an oval outline. However, all scales show complete circuli.

Remark: Nybelin (1974: pl. IX, fig. 3) figured a cast of a fragmentary head of a *L. coryphaenoides* from the Dobbertin Lagerstätte with the collection number MNH P 23834. This cast was found in the collection of the Naturhistoriska Riksmuseet in Stockholm, but with the different collection number NRM P 6091. The labels indicate that the collection number MNH P 23834 refers to the original specimen.

Identification: The above described specimens share the presence of branched tubules in the preopercular canal. Nybelin (1974) listed three species of *Leptolepis* which possess branched tubules in the preopercular sensory canal, *L. coryphaenoides* (Bronn, 1830), *L. saltviciensis* Simpson, 1855 and *L. autissiodorensis* Sauvage, 1892. Nybelin (1974) also points out that *L. saltviciensis* might represent juvenile stages of *L. autissiodorensis*. The preopercles of *L. saltviciensis* and *L. autissiodorensis* are almost equal in shape. They are less broad and more crescentic than in *L. coryphaenoides*. Furthermore, the tubules in the preopercular canal are shorter, the number of tubules is higher and fewer branched tubules are present in *L. saltviciensis* and *L. autissiodorensis*. The herein described specimens GG 431/3, GG 431/19, GG 431/20 and NRM P 6091 have relatively broad preopercles and relatively low numbers of tubules in the preopercular canal. Therefore, they are assigned to *L. coryphaenoides*. This assignment is also supported by the presence of miniscule teeth on the maxilla and premaxilla, as well as the presence of a small premaxilla in GG 431/3, as described in *L. coryphaenoides* by Nybelin (1974). Specimen GG 431/7 shows a comparatively narrow preopercle, as described in *L. saltviciensis* and *L. autissiodorensis* (Nybelin 1974). Otherwise, GG 431/7 is considered as a juvenile and the preopercle might not be fully

developed. The specimen differs to *L. autissiodorensis* in the low number of tubules in the preopercular canal of 10 (more than 22 in *L. autissiodorensis*). The miniscule teeth on maxilla, premaxilla and dentary, as well as the small premaxilla of GG 431/7 are consistent with referral to *L. coryphaenoides*. Thus, GG 431/7 is also assigned to *L. coryphaenoides*.

***Leptolepis normandica* Nybelin, 1962**

Figure 6; Plates 1E, 2D, 3C

Synonyms:

*Leptolepis concentricus* Egerton, 1849 (in part): p.35.

*Leptolepis pachystetus* Sauvage, 1874: pl. VII, figs. 2, 3.

*Leptolepis bronni* Woodward, 1895: p. 504.

*Leptolepis normandica* Nybelin, 1962: fig. 1B.

*Leptolepis normandica* Nybelin, 1963: fig. 10.

*Leptolepis coryphaenoides* Wenz, 1968 (in part): figs. 91, 92B, 94A, pl. XLII, XLIII fig. C.

*Leptolepis normandica* Nybelin, 1974: figs. 1A, B; 2; 3 A–C; 7A–C; pls. I–IV; V figs. 1–5; IX figs. 2, 3; XXX fig. 1.

*Leptolepis normandica* Nybelin, 1976: pl. 1, fig 3.

*Leptolepis normandica* Delsate, 1997: figs. 1–5; pl. 1, figs. 1, 4A–C; pl. 2, figs. 5–9.

*Leptolepis normandica* Arratia, 1984: fig. 7E.

*Leptolepis coryphaenoides* Arratia & Thies, 2001: fig. 12C.

*Leptolepis normandica* Bean, 2006: figs. 9E–G.

*Leptolepis coryphaenoides* Bean, 2006: fig 18B.

*Leptolepis bronni* Ansorge & Obst, 2015: fig. 15B.

**Material.** GG 431/2a, b, articulated head with pectoral girdle and few abdominal vertebrae, preserved in part and counterpart. The specimen is associated with four insect wings, including the holotypes of *Protorhyphus stigmaticus* Handlirsch, 1920 and *Parablattula reticulata* Handlirsch, 1920.



**Geographical distribution.** Curcy, May (Normandy, France); Dumbleton, Alderton (Gloucestershire, England); Dobbartin (Mecklenburg-Western Pomerania, Germany); Barscharage (Luxembourg); ?Holzmaden (Baden-Württemberg, Germany) (data from: Wenz 1968; Nybelin 1962, 1974; Delsate 1997; this paper).

**Stratigraphical distribution.** Lower Jurassic, Toarcian, at least *Harpoceras falciferum* Zone.

### **Description.**

Cranial bones (Fig. 6; Pl. 1E): Most of the cranial bones are poorly or not preserved. Most of the cranial roof is formed by the parietal. It is narrow and elongate in its anterior portion. The posterior portion is damaged. It seems to have been much broader than the anterior part. Anteriorly, the parietal articulates with the mesethmoid. Remnants of the postparietal, pterotic and endocranial bones are preserved but are uninformative. The mesethmoid is short, but the lateral wing is large. It extends in anterolateral and posterolateral directions. The posterior part of the lateral wing is covered by infraorbital 1, so its posterior length is unknown. The nasal bone lies slightly dislocated below the supraorbital. The exposed part of this bone is its posterior portion, which is thin and tube-like, mainly carrying the supraorbital sensory canal. The lateral ethmoid is narrow, elongate, and poorly ossified.

Upper jaw (Fig. 6; Pl. 3 C): The upper jaw consists of premaxilla, maxilla and two supramaxillae. The premaxilla is small. It bears a well marked, broad ascending process. A single row of at least eleven, long, but very narrow teeth are present on the oral margin of the premaxilla. The maxilla is the largest bone of the upper jaw. It is long, reaching the posterodorsal margin of the quadrate. The bone is convex ventrally and concave dorsally. A well ossified ridge is present along the lateral margin of the bone. An elongate groove is present on the lateral surface, running parallel to the ridge. Some short grooves are running diagonal to the dorsally and ventral margins of the maxilla at about the center of the bone. The dorsal margin of the maxilla bears an elongate surface for the articulation of the supramaxillae. A single row of several small, needle-like teeth is present along the ventral margin of the maxilla. Each tooth is associated with a small groove. The ventral portions of both supramaxillae are broken and their dorsal margins are covered by infraorbital bones. Thus, the exact shapes of both bones are unknown. The anterior supramaxilla seems to have been elongated, with a sharp anterior tip. The remaining part of the posterior supramaxilla indicates a more or less trapezoidal shape, an anterior process seems to arise from the anteroventral portion of the bone and extends anterodorsally. Its length remains unknown. The surface of the posterior supramaxilla is strongly ornamented. The ornamentation consists of several grooves, running more or less parallel to the ventral margin of the bone and some low tubercles.

Lower jaw (Fig. 6; Pl. 3C): The lower jaw is formed laterally by the dentary and angular. Most of both bones is covered by bones of the upper jaw. Most of the ventral margin of the lower jaw is formed by the dentary. The oral margin ascends with an angle of about 30° in respect to the ventral margin of the bone. Four very small teeth were observed on the oral margin. The exposed part of the angular is poorly preserved in the specimen, so not much is known about it.

Palatoquadrate and hyoid arches (Fig. 6): The quadrate and a small portion of the entopterygoid are the only exposed bones of the palatoquadrate arch in the specimen. The main body of the quadrate seems to be triangular, as in the other species of *Leptolepis*. The posteroventral process of the quadrate is longer than the main body, but its posterior part is covered by the preopercle, so its length remains unknown. Some poorly preserved branchiostegals are present ventral to the interopercle, these seem to be elongate and laterally flattened.

Orbital bones (Fig. 6; Pl. 1E): The orbital bones are nearly completely preserved, lacking only the posterior supraorbital, the dermosphenotic, and the antorbital. The anterior portion of the anterior supraorbital is preserved in the specimen. It shows a sharp anterior tip and is sharp angled along its lateral margin. The second supraorbital is not preserved. Both sclerotics are preserved. Both are semicircular shaped, and at least the posterior is very broad. They have probably surrounded the eye completely. Infraorbital 1 is subrectangular, with its anterior part being deeper than the posterior margin. Infraorbital 2 is about as long as infraorbital 1, but thin, just a little bit broader than the infraorbital sensory canal. Infraorbital 3 is the largest bone of the infraorbital series. Posteriorly, it reaches the preopercle. It is convex at its ventral and concave at its posterior margins. The dorsal margin of infraorbital 3 is partly overlapped by infraorbital 4. Infraorbital 4 is subrectangular, with a convex ventral margin, which overlaps infraorbital 3. The ventral margin of infraorbital 5 is straight, and as broad as the dorsal margin of infraorbital 4. The bone narrows in dorsal direction. The dorsal margin of the bone is not preserved. One suborbital is present whereas an “accessory” suborbital (see Nybelin 1974) is absent. The bone covers the space between the infraorbitals and the opercle and preopercle. The anterior margin of the bone is covered by infraorbitals 3 to 5. The posterior margin of the suborbital bears a distinct notch. A small notch is also present in the dorsal margin, probably for the passage of the preopercular sensory canal.

Opercular bones (Fig. 6; Pl. 1E): The opercular series consists of opercle, subopercle, preopercle and interopercle. The opercle is the largest bone of the series. Its anterior, ventral and posterior margins are straight, but it is convex and bent in medial direction dorsally. Some fine growth lines were observed. The subopercle is about as half as deep as the opercle, but slightly broader. Its posteroventral margin is convex. The preopercle is L-shaped, with a long dorsal and a shorter ventral limb, both form an angle of about 110°. The posterior margin of the preopercle shows a vague notch. In the anterior margin, near the

confluence of both limbs, the preopercle bears an anterior process. A suprapreopercle, as described by Nybelin (1974), was not observed. It is either absent or completely covered by the suborbital. Most of the interopercle is covered by the preopercle, so its exact shape is unknown. Its ventral margin is as long as the ventral limb of the preopercle.

Sensory canal system (Fig. 6; Pl. 2D): The sensory canal system is known from the mandibular, preopercular, infraorbital, and a very short portion of the supraorbital canals. All preserved parts are by bone. All tubules are unbranched. The mandibular canal runs close to the ventral margin of the dentary. The canal is poorly preserved and does not allow a proper description. The preopercular canal runs close to the dorsal margin of the ventral limb and along the center of the dorsal limb of the preopercle. It gives off twelve tubules, nine of them are present in the ventral limb. These tubules increase in length posteriorly, and point in posteroventral direction. The tubules in the ventral limb end close to the ventral margin of the bone or reach the margin. At the confluence of dorsal and ventral limb, two tubules, pointing in posterior and posterventral directions are present. These are much shorter than the preceding ones and do not reach the posterior margin of the preopercle. A very short, anteriorly directed tubule is also present at the confluence of both limbs. A single tubule is present in the ventral part of the dorsal limb. This points in posterodorsal direction and does not reach the posterior margin of the preopercle. The infraorbital canal runs close to the dorsal, or anterior margin of the infraorbital bones. The infraorbital canal is not preserved in infraorbital 1, but impressions on the bone show its position. The canal gives off at least four tubules, which apparently have reached the ventral margin of the bone. The canal continues close to the center of infraorbital 2. It gives off four tubules on infraorbital 3, which are directed posteroventrally. The first one is much shorter than the other tubules. Two tubules are present in infraorbital 4; they point posteriorly. The ventral one is long, ending close to the posterior margin of the bone; the dorsal tubule is evidently shorter. The infraorbital canal does not seem to give off any tubules in infraorbital 5.

Vertebral column and associated bones (Pl. 1F): Seven abdominal vertebrae are exposed in the specimen, but it is assumed that few others are covered by the opercle. The autocentra are slightly longer than broad, each being slightly constricted in its middle part. Their surface is smooth, without ornamentation. The parapophyses are large, about as broad as their respective centrum. The parapophyses are fused to the autocentra lateroventrally and bear a short, very thin process at its lateroventral margin. The processes point posteroventrally. Ribs are not preserved. The neural arches are not fused to their centra. Each arch bears a thin epineural process, which is directed posteriorly. The epineural processes are united with the neural arches also by thin bony lamellae. These lamellae exceed in anterior and dorsal direction and form a small anterodorsal process. The neural spines are thin and form an angle of about 45° with the vertebral column. Supraneural bones are not preserved.

Pectoral girdle and fin (Fig. 6; Pl. 1E): The preserved bones of the pectoral girdle are: cleithrum, supracleithrum, and two postcleithra. The cleithrum is composed of two limbs, a vertical dorsal and a horizontal ventral one. The dorsal limb seems to be longer than the ventral one. Several fine grooves and ridges, running parallel to the posterior margin of the bone are present. These seem to be growth lines. The elongate supracleithrum is hardly damaged. A long and narrow bone is present posterior to the cleithrum. This bone is identified as postcleithrum 1. A second postcleithrum is present ventrally to postcleithrum 1. This element is incompletely preserved, so that its shape remains unknown. Several lepidotrichia of the pectoral fin (probably originating from both fins) lie ventrally and posteriorly to the cleithrum, they are poorly preserved. At least some rays are segmented.

Remark: Nybelin (1974) pointed out that *L. normandica* Nybelin, 1962 might be identical with *L. pachystetus* Sauvage, 1873. This assumption is based on the relatively low number of unbranched tubules in the preopercular sensory canal and a similar shaped opercle in both species. Due to Sauvage's insufficient description and the loss of the holotype of *L. pachystetus* the identity of both species cannot be confirmed (see Nybelin 1974). The herein examined specimens of Leptolepidae sp. 1, *Proleptolepis*-like, *Leptolepis* sp. 1 and *L. jaegeri*, do also have a relatively low number of unbranched tubules in the preopercular sensory canal, but differ from *L. normandica* in other characters. This shows that the number and shape of the tubules cannot be used as sole character for the identification of the species. Furthermore, we disagree with Nybelin's (1962, 1974) interpretation of the shape of the opercle in *L. normandica* (see below). For these reasons, we retain the use of the name *L. normandica*, following the nomenclature of Nybelin (1962, 1974).

### ***Leptolepis jaegeri* Agassiz, 1832**

Figures 7A–C; 8A–C; 9A, B; 10A, B; 11; Plates 1D; 2E; 3D; 4A–C

Synonyms:

*Leptolepis Jaegeri* Agassiz, 1832: p. 146

*Leptolepis Jaegeri* Agassiz, 1833–1844 (vol. 2): p. 13

*Leptolepis jaegeri* Woodward, 1895: p. 505

*Liassolepis bronni* (nomen nudum) Jaekel, 1929: fig. 3

*Leptolepis coryphaenoides* (in part) Wenz, 1968: figs. 92A, 95A

*Leptolepis jaegeri* Nybelin, 1974: figs. 9, 10A–C; pls. XII, XIII fig. 3

*Leptolepis bronni* Ansorge & Obst, 2015: fig. 15C

**Material.** NRM P 6483a, b (neotype) from Holzmaden; GG 431/1 isolated head with pectoral girdle, preserved in 3D, from Dobbartin; GG 431/6 isolated head with pectoral girdle, from Grimmen; GG 431/9a isolated head preserved in 3D prepared from left side, from Grimmen, acid prepared specimen; GG431/9b same individual as GG 431/9a, right side of the head in lateral view; GG 431/10 almost complete, juvenile specimen from Grimmen; GG 431/15 incomplete head from Grimmen; GG 431/16 isolated head from Grimmen.

**Geographical distribution.** Zell, Holzmaden (Baden-Württemberg, Germany); Dobbartin, Grimmen (Mecklenburg-Western Pomerania, Germany); Le Cain (Normandy, France); ?Dumbleton (Gloucestershire, Great Britain) (data from: Agassiz 1832, Nybelin 1974, this paper).

**Stratigraphical distribution.** Lower Jurassic, Toarcian, at least *Harpoceras falciferum* Zone, *Harpoceras exaratum* Subzone.

### **Description.**

General description: Small, slender teleost, maximal known head-length 22 mm. Pelvic fins placed at about 50 % of SL, origin of dorsal fin slightly posterior to pelvic fin. Anal fin placed at about 70 % of standard length. Body covered with cycloid scales.

Cranial bones (Figs. 7A, B; 8A–C; 9A, B; 10A, B; Pls. 1D; 2E; 3D; 4A–C): The mesethmoid is well preserved in GG 431/9a, the anterodorsal margin of this bone is short. The ventral lamella of the mesethmoid extends posterior from the lateral and point to the anterior tip of the lateral etmoids. The anterior tip of the lateral wing of the mesethmoid is in contact to the anteromedial tip of the bone, forming a mesethmoidal foramen. The nasal bones are small. They articulate with the parietal laterally. The posterior portion of the nasal bone is mainly formed by the tube-like ossification of the supraorbital sensory canal, whereas it is triangular in its anterior portion. The parietals form most of the skull roof. They are narrow and elongate in their anterior part. The suture between both parietals is smooth. The parietals articulate with the mesethmoid anteriorly; the nasal bones, supraorbital and dermosphenotic laterally; the pterotic posterolaterally; and the postparietal posterodorsally. The postparietal bones seem to be subrectangular. The anterior and middle pit lines are present in the posterior portion of the bone. The pterotic forms most of the lateral aspect of the skull roof. Its exact outline remains unknown, because of poorly preservation. The middle pit line was observed on the right pterotic of GG 431/1. The narrow lateral ethmoids are well preserved in GG 431/9a, b. They articulate with the parietals and do not reach the parasphenoid ventrally. A short anteroventral process points to the posteroventral lamella of the mesethmoid. The parasphenoid is elongate and narrow. It articulates with the vomer anteriorly, the

entopterygoid ventrally and with endocranial bones posterodorsally. A tooth plate is fused to the parasphenoid slightly anterior to the ascending processes of the parasphenoid, at the ventral margin of the bone. At least six teeth are present at the right margin of the plate, some more are medially placed. The teeth are comparatively large, conical and point posteroventrally. The short vomer articulates with the parasphenoid ventral to the mesethmoid. The vomer bears at least seven, comparatively large, conical teeth. The vomerine teeth are arranged in two rows and point posteroventrally. The orbitosphenoid is preserved in GG 431/9a. It is located dorsal to the orbit and does not exceed anteriorly or ventrally. Posteriorly, the orbitosphenoid sutures with the pterospheneid, which forms the medial aspect of the posterodorsal margin of the orbit. The extrascapula is preserved in GG 431/1 and GG 431/16, but the state of preservation is poor in both specimens. In specimen GG4321/9a, some bones of the braincase are preserved. The prootic forms most of the lateral and anteroventral aspects of the braincase, it sutures with the basioccipital posteroventrally, with the pterospheneid and basisphenoid anteriorly, and with exoccipital posteriorly. The articulation of the prootic with the parasphenoid remains unknown because of poor preservation. The prootic-exoccipital suture runs vertical and is almost straight. The exoccipital forms the posterolateral and posterior aspects of the braincase, it sutures the basioccipital ventrally. The exoccipital-basioccipital suture is clearly visible in the anterior portion of the anteroventral portion of the exoccipital but was not observed in the posterior part of the bone. This may indicate a fusion of both bones, late in ontogeny. The basioccipital forms the ventral and the posteroventral part of the posterior braincase. The epiotic forms the posterodorsal and most probably, a part of the posterior aspect of the braincase. The autosphenotic and pterotic are not preserved in GG431/9a.

Hyoid arch (Fig. 8A, 9B): The posterior ceratohyal preserved in GG431/9b, but most of the bone is covered so its shape remains unknown. The groove for the afferent hyoidean artery runs close to dorsal margin of the bone. A small facet, probably for the articulation of the interhyal, is present on the posterodorsal margin of the posterior ceratohyal. The anterior ceratohyal is fenestrated, the groove for the afferent hyoidean artery is continuous with the fenestra and leaves the bone at its anterior margin. Most of the dorsal hypohyal is covered by the ventral hypohyal, the shape and size of the bone remains unknown. The anterodorsal tip of the dorsal hypohyal bears two small depressions anteriorly. The ventral hypohyal is a massive, subrectangular bone. A deep groove for the afferent hyoidean artery is present. It runs in anteriorly, but turns ventrally at about the center of the bone. The afferent hyoidean artery pierced the bone and exited it at its medial side. An elongate bone, which is probably the displaced urohyal, lies dorsal to the anterior ceratohyal in GG 431/9b. Several very small, conical teeth are present on the complete surface of the bone. A broad bone is present anterior to the hypohyals, this is either the basihyal or a basihyal tooth plate. Its anterodorsal surface is sparsely covered with conical teeth. The size of the teeth varies. The teeth near the medial and lateral margins of the bone are larger than those in the center of the

bone. Some branchiostegal rays are preserved in both lateral sides of GG 431/1 and in GG 431/15. They are long and seem to broaden in posterior direction.

Palatoquadrate arch (Figs. 8A, B; 9A, B; 10A, B; Pls. 3D; 4B, C): The metapterygoid is almost completely preserved in GG 431/9a, it is large and subrectangular. The ventral margin of the bone seems to be slightly convex. The anterior portion of the bone is directed medially to meet the entopterygoid. The processus basalis forms the anterodorsal tip of the bone. The processus metapterygoideus lateralis is short but well defined. It arises from the anterodorsal margin of the metapterygoid and points dorsally. The quadrate is triangular, the posterodorsal margin is broad and slightly concave. The posteroventral process of the quadrate is narrow and much longer than the main body of the quadrate. The symplectic is elongate, it is narrow in its anterior portion and broadens posteriorly. The entopterygoid is large, it forms most of the ventral margin of the orbit. Several small teeth are present on the medial side of the entopterygoid. The ectopterygoid is elongate and narrow, it bears an articulation facet for the autopalatine anteriorly. The lateral surface of the bone is edentulous, but teeth may be present at its medial side. The autopalatine is large, it is as deep as the ectopterygoid. The posterior part of the bone is directed posterodorsally. The autopalatine seems to articulate with the ectopterygoid.

Upper jaw (Figs. 7A–C; 8A, B; 9A, B; 10A, B; Pls. 3D; 4A–C): The Upper jaw consists of premaxilla, maxilla and two supramaxillae. The premaxilla is large (in comparison with *L. coryphaenoides*) and bears a high ascending process. A single row of comparatively large, conical teeth is present on the oral margin of the bone. In specimen GG 431/1 at least 11 teeth are present on the right premaxilla. The maxilla is the largest bone of the upper jaw. It is long and reaches to the center of the quadrate. The maxilla is convex ventrally and concave dorsally. The articular process is well defined and resembles the length of the premaxilla, it is narrow and directed anteromedially. A prominent bony ridge is present along the lateral side of the anterior portion of the maxilla. The posterior part of the bone is smooth. Fifty-six teeth conical are preserved along the ventral margin of the left maxilla of GG 431/1; and 60 in GG 431/15 but several teeth are missing in both specimens. The former number of teeth must have been about 70. The teeth in the anterior part of the maxilla are slightly larger than these in the posterior part of the bone. The supramaxillae large. The anterior supramaxilla is fusiform with a sharp anterior tip. The posterior supramaxilla is slightly larger than the anterior one. A long, spine-like anterodorsal process arises from the center of the bone. It articulates with the dorsal margin of the anterior supramaxilla. The lateral surface of the posterior supramaxilla is ornamented with several longitudinal grooves and bony ridges.

Lower jaw (Figs. 7A, B, 8, B; 9A, B; 10 A, B; Pls. 3D; 4A–C): The lateral aspect of the lower jaw is formed by the dentary and angular. Most of the ventral margin of the lower jaw is formed by the



dentary. The oral margin of the dentary ascends gently in direction of the coronoid process. In GG431/1, GG 431/9a and GG 431/16, the oral margin of the dentary possess a low, broad dorsal process. The “leptolepid” notch is present just anterior to the coronoid process, it is deep and narrow. The high and heavily ossified coronoid process is placed at about 50 % of the length of the dentary. The dorsal margin of the bone is formed by the coronoid process and a long posteriodorsal process. The posterodorsal tip of the dentary almost reaches the quadrate. A single row of at least 12, comparatively large teeth are present at the oral margin of the dentary. The dentary teeth are conical and slightly curved in posterior direction. In GG 431/16, the dentary teeth posterior to the process on the oral margin of the dentary are thin and straight. The angular inserts in the space between the posterodorsal process and the ventral margin of the dentary. The lateral aspect of the bone is formed by a thin sheet of bone. The ventral portion of the angular is heavily ornamented with several grooves and ridges. The state of fusion of angular, articular and retroarticular remains unknown.

Orbital bones (Figs. 8A–C; 9A, B; 10A, B; Pls. 1D; 3D; 4B, C): Two supraorbital bones are present. The anterior supraorbital is narrow and elongate and bears a sharp anterior tip. Anteriorly, the bone almost reaches infraorbital 1. The posterior supraorbital bone is preserved in GG 431/16. It is elongate, but much smaller than the anterior supraorbital. A very small, slightly dislocated bone is present in the olfactory region of GG 431/9b. It is flat and carries a sensory canal. In order to its shape and position, the bone is identified as the antorbital bone. Infraorbital 1 is a large bone, its anterior margin is deeper than the posterior margin. Infraorbital 2 is narrow and elongate, not much broader than its part of the infraorbital sensory canal. Infraorbital 3 is the largest bone of the series. It is rectangular and about as twice as broad as deep; its posterior margin reaches the preopercle. The ventral part of infraorbital 4 overlaps the anterodorsal part of infraorbital 3, it is about as broad as deep. Infraorbital 5 is subrectangular and about as large as infraorbital 4. The dermosphenotic is preserved in GG431/8b and GG 431/16. It is large and articulates with infraorbital 5 ventrally. Its anteroventral margin is concave and the dorsal and posterior margins are convex. The anterior margin of the suborbital is covered by the infraorbitals 3 to 5, and its posterior margin overlaps the dorsal part of the preopercle. A notch is present in the posterior margin of the bone. An “accessory” suborbital bone is absent. The anterior and posterior sclerotic bones are preserved in GG 431/16. Both bones are semi-circular and apparently have formed a complete ring around the eye.

Opercular bones (Figs. 7A, B; 8A, B; 9A, B; 10 A, B; Pls. 2E; 4A–C): The opercle, subopercle, interopercle and preopercle are preserved. The opercle is the largest bone of the series. It is trapezoidal shaped. The anterior, ventral, and posterior margins are straight. The dorsal margin is medially directed and seems to be slightly convex. The anterior margin is formed by a bony ridge. The suborbital is large, its depth is about 2/3 of the opercle. It is evidently broader than the opercle. The ventral and posterior

margins of the subopercle are convex. The preopercle is composed of a dorsal and a ventral limb, which form an angle of about  $110^\circ$ . The bone expands ventrally and posteriorly. Thus, it is deeper and broader than in other species of the genus. The dorsal limb narrows dorsally, its dorsal-most part is covered by the suborbital. There is no notch in the posterior margin of the preopercle. A small anterior process in the anterior margin of the preopercle is present in GG 431/1, GG 431/8b, GG 431/9a, and GG 431/15. The process is absent in NRM P 6483a and GG 431/16. A suprapreopercle was not observed. Most of the interopercle is covered by the preopercle, it seems to be as long and as deep as the ventral limb of the preopercle.

Sensory canal system (Figs. 7A, B; 8A–C; 9A, B; 10A, B; Pls. 1D; 2E; 4B, C): All sensory canals run bone enclosed on the surface of the bones, with exception of the mandibular canal. The supraorbital runs along the parietals. Anteriorly, it continues on the nasal bones. Posteriorly, the infraorbital canal reaches up to the center of the postparietal, where it is continuous with the anterior pit line. The canal does not give off any tubules, but at least three pores are present in the dorsal surface of the posterior part of the canal of GG 431/1. The anterior pit line is continuous with the posterior opening of the supraorbital sensory canal, it is short and meets the posterior and middle pit lines near the posterior margin of the postparietal. The posterior pit line is short and runs medially. It ends close to the suture of both postparietals. The middle pit line is continuous with the posterior pit line. Which runs laterally and reaches on the pterotic, where it runs ventrally. Its length remains unknown due to poor preservation. The anterior-most part of the infraorbital canal was observed in the antorbital in GG 431/9b, the possible presence of tubules remains unknown. The infraorbital canal runs close to the dorsal margin of infraorbital 1. Five tubules are present in infraorbital 1, they end close to the ventral margin of the bone. There is no evidence of tubules, leaving the canal in infraorbital 2. The canal continues near the anterodorsal and anterior margins of the infraorbitals 3 to 5. The canal gives off two to three tubules in infraorbital 3. A single tubule is bifurcate in infraorbital 3 in GG 431/8. Two or three short tubules are present in infraorbital 4. Tubules are absent in infraorbital 5 of GG 431/16 but a single tubule is present in the bone in GG 431/8. The infraorbital canal continues in the dermosphenotic where it splits in the anterior and posterior branch. The anterior branch seems to end at the anterior margin of the bone. Two tubules are present in the dermosphenotic of GG 431/8b and at least one in GG 431/16. The tubules are dorsally directed and seem to reach the dorsal margin of the bone. The posterior branch is short and is continuous with the otic canal. The opening of the canal is placed on the medial side of the dermosphenotic, in its posterior portion. The otic canal is poorly preserved in all specimens, it runs close to the ventral margin of the pterotic. The supratemporal canal is preserved in GG 431/16, it runs close to the anterior margin of the extrascapula and gives off at least three tubules. The posttemporal canal close to the ventral margin of the posttemporal. A single, very short, dorsally directed tubule is present in GG

431/1. The canal continues in the supracleithrum where it runs posteroventrally. It leaves the bone at its posterior margin. The mandibular canal is best preserved in GG 431/9b. It runs within the bone close to the ventral margin of the dentary. Five pores are present in the mandibular canal, they are arranged with almost equal distances to each other. The canal continues within the ventral part of the angular. The posterior opening seems to be at the medial side of the bone. The preopercular canal runs close to the dorsal and anterior margins of the preopercle. The canal gives off 11 to 13 unbranched tubules. They run in posteroventrally and posteriorly. With exception of the dorsal-most one or two tubules, these are directed posterodorsally. The distal tips of the tubules are broader than their proximal portions. Most of the tubules are very long and reach the ventral or posterior margins of the bone, or end very close to the margins of the preopercle. In specimen GG 431/9a and GG 431/15, the distal parts of some tubules in the ventral limb of the preopercle overlap the distal part of the subsequent tubule. The trunk canal is not preserved.

Vertebral column and associated bones (Pl. 4A–C): The total number of vertebrae as well as the numbers of abdominal and caudal vertebrae remain unknown due to poor preservation. The autocentra are longer than high, and are slightly constricted in the middle. The surface of the autocentra is smooth, without any ornamentation. In anterior/posterior view the autocentra are thin and ring-like, and do not or just slightly constrict the notochord. The parapophyses are fused to the centra ventrally. They are subtriangular and as long as their centra. A short process is present at the lateral margin of each parapophysis. The ribs are poorly preserved in the examined specimens. They are thin, slightly curved, and seem to end close to the ventral margin of the body. A single supraneural bone is preserved in GG431/10. The bone is thin, elongate and seems to be straight. The number of supraneurals remains unknown. The abdominal neural arches are not fused to their centra in the juvenile specimen GG 431/10. The condition is unknown in adult individuals. Both halves of the abdominal neural spines are separate, whereas the caudal neural spines are fused. The hemal arches and spines are poorly preserved so not much is known about these bones.

Pectoral girdle and fin (Fig. 1A, Pl. 4A–C): The pectoral girdle is poor preserved in all examined specimens. The posttemporal, supracleithrum and cleithrum. The posttemporal consists of a well ossified dorsal limb and a thin ventral limb, which mainly carries the posttemporal canal. Most of the supracleithrum is covered by the opercle, the bone is comparatively broad and elongate. The cleithrum is composed of a narrow dorsal limb, which is oriented vertically; and a ventral, almost horizontal limb. The anterior tip of the ventral limb bends ventrally. A narrow, and elongate postcleithrum articulates with the cleithrum along its posterior margin, it is assumed to be the first postcleithrum. Other postcleithra were not preserved. Seventeen pectoral fin rays are preserved in GG 431/6, the first one is evidently broader

than the others. The fin rays are segmented, and at least some of them are branched in their very distal portions.

Pelvic fin (Pl. 4A): The pelvic fin is placed at about 55% of standard length. The preservation of the pelvic girdle and fin in NRM P 6483 a, b and GG 431/10 is too poor to give a description.

Dorsal fin (Pl. 4A): The dorsal fin is placed at about 57% of standard length. The numbers of the pterygiophores and lepidotrichia remain unknown due to poor preservation. In NRM P 6483b (neotype), the first pterygiophore is formed of three processes which point anteroventrally. At least the two anterior processes are connected by a thin ossification.

Anal fin (Pl. 4A): The anal fin is poorly preserved in GG 431/10. It is placed at about 73% of standard length. The fin consists of at least one precurrent and ten principal lepidotrichia. The precurrent ray is significantly shorter than the principal rays. All principal anal rays are segmented and branched in their distal portions. The number and shape of the pterygiophores remains unknown.

Caudal Skeleton and fin (Fig. 11, Pl. 4A): The description of the caudal skeleton is based in GG 431/10, a juvenile specimen. The ural and preural autocentra are poorly preserved. The fragments of the autocentra show that they were thin with smooth surfaces. The neural and hemal arches are not fused to the respective autocentra. At least the neural arches of preural centra 1 to 3 bear a sharp anterior process at their bases. The neural spine of preural centrum 3 is long, it ends close to the dorsal margin of the body. The neural spines form an angle of about 40° with the dorsal margin of the vertebra. The neural spine of preural vertebra 2 is not preserved. The neural spine of the first preural vertebra is short, about as half as long as the spine of preural vertebra 3. The hemal spines of preural vertebrae 1 and 2 bear short anterior processes. Two ural vertebrae are present, both are poorly preserved so their exact shapes remain unknown. The first ural centrum is longer than the preural centra and supports two hypurals. Two neural spines are present on ural centrum 1+2. The anterior one is about as long as the neural spine of preural vertebra 1, whereas the posterior spine of ural centrum 1+2 is evidently shorter. The second ural centrum is evidently smaller than ural centrum 1+2. Nine hypurals are present. The first one is the largest bone of the series and bears a spine-like anterior process. Anterior processes are absent in the other hypurals. Hypural 1 and 2 are not fused at their bases. The hypurals decrease in size posteriorly. Three epurals are present. They are thin and elongate. The dorsal tips of the epurals are covered by the epaxial basal fulcra, so their length remain unknown. Seven uroneurals are present, all are elongate and the first three are slightly sigmoidal shaped. The anterior tip of the first uroneural is broken, so its length remains unknown. The first three uroneurals reach at least the anterior margin of the first ural centrum. Uroneurals 1 and 2 bear a thin membranous outgrowth at their anterodorsal margins. A single, plate-like dorsal caudal scute is present. The ventral caudal scute is incompletely preserved, so its size and shape remain unknown. Eight

epaxial basal fulcra are present. The anterior ones are short, but their length increases posteriorly. An elongate fringing fulcrum is preserved in GG 431/10. The total number of fringing fulcra in the dorsal lobe remains unknown due to poor preservation. Fringing fulcra are absent in the ventral lobe of the caudal fin. There are 10+9 principal caudal rays. A short dorsal process is present on the proximal segment of principal ray 8. The proximal portion of the first segment of principal ray 10 is dorsally and ventrally expanded. Eight precurrent fin rays are present in the ventral lobe of the caudal fin. Six of them are segmented. The segmentation of all fin rays is straight or slightly sigmoidal. 'Urodermals' are not preserved.

**Squamation (Pl. 4A):** The body is covered with thin cycloid scales. Most of them show circular or oval outlines. In GG 431/10 the scales in the anterolateral part of the body are larger than the other scales. They are about as twice as high than broad, but also show circuli. The scales are devoid of ganoine.

**Identification:** The above described specimens are comparable with *Leptolepis jaegeri* sensu Nybelin (1974), particular based on the shapes of premaxilla, dentary, preopercle, and the presence of comparatively large, conical teeth on maxilla, premaxilla and dentary. The holotype of *L. jaegeri* is lost (Nybelin 1974; Maxwell, pers. comm.). Therefore, Nybelin (1974) designated NRM P 6483a, b as neotype. However, the neotype is poorly preserved and the assignment to *L. jaegeri* is apparently only based on “Its larger size and the locality (...)” (Nybelin 1974: 64). In the initial description *L. jaegeri* is described as: “Broader, larger, with larger scales.” (than *L. “bronni”*) (Agassiz 1832: 146, translated). The shape of the scales in the neotype is unknown due to the poor state of preservation of the specimen. Comparatively large scales were observed in the anterior part of the body of specimen GG 431/10. Thus, Nybelin’s assignment is most probably correct.

### ***Leptolepis* sp. 1**

Figures 8A, B; Plate 4E

**Remark.** The herein examined specimens GG 431/4, GG 431/17 and GG 431/18 show anatomical similarities to *L. jaegeri* concerning the shape of the maxilla, premaxilla and the dentition of these bones. The preopercle and the dentition of the dentary are different to those in the neotype of *L. jaegeri* (NRM P 6483a, b). We are not yet sure if these differences have to be interpreted as intraspecific variations of *L. jaegeri* or if the specimens represent another species. We will give a description in a separate contribution.

### **Discussion of selected characters**

We had not the possibilities to see all type specimens of the respective species which we discuss below. Thus, our comparisons are based on descriptions of following authors, when needed: Rayner (1937),

Jaekel (1929), Nybelin (1962, 1963, 1974, 1976), Wenz (1968), Tintori (1977), Arratia & Thies (2001), Arratia (1997, 2003).

**Dermosphenotic and its part of the infraorbital canal.** The dermosphenotic is missing in most of the specimens of the herein described specimens, but it is preserved in *Leptolepidae* sp.1 (GG 431/5 Fig. 2; Pl. 1A, B), and *Leptolepis jaegeri* (GG 431/8, Pl. 1D and GG 431/16, Fig. 10B, Pl. 4C). The ventral part of the bone is present in one specimen of *L. coryphaenoides* (NRM P 6091, Fig. 5). In *Leptolepidae* sp. 1 (GG 431/5) and *L. jaegeri* (GG 431/8 and GG 431/16) the dermosphenotic is large, broader than high, and the infraorbital sensory canal gives off two or four tubules, respectively, all directed postero-dorsally. This characteristic pattern seems to be unique among leptolepid fishes. The shape of the dermosphenotic of *L. "bronni"* is described and drawn by Rayner (1937: fig. 3) as a small, roughly Y-shaped bone. She also described an anterodorsal branch of the infraorbital canal, but she did not mention or drew any tubules. The bone is not described by Nybelin (1962), but drawn as relatively small. In his reconstruction of *L. coryphaenoides*, the anterior branch of the infraorbital canal ends at the anterodorsal margin. The dermosphenotic of *L. "coryphaenoides" sensu* Wenz (1968) is described as small and triangular. The respective part of the infraorbital canal is described with an anterior branch, directed anterodorsally to the supraorbital canal. Tubules are not mentioned in the text. In contrast to the description, a large dermosphenotic, which is higher than broad, with two posterodorsal directed tubules, giving off in the anterodorsal branch, are drawn in her reconstruction of MHNP 1962-30-1 (Wenz 1968: fig. 96). The photograph of this specimen (Wenz 1968: pl. XLV, fig. B) suggests that this reconstruction is correct. Nybelin (1974: 12) described the dermosphenotic of *L. normandica* as "higher than broad" and the corresponding part of the infraorbital canal as Y-shaped, bearing an "antero-dorsal directed tubule" (Nybelin 1974: 24). According to his reconstruction (Nybelin 1974: fig.1) and the photograph (Nybelin 1974: pl. II, fig. 1), this "tubule" is the anterodorsal branch of the infraorbital canal in the dermosphenotic as it was described by other authors (Rayner 1937, Wenz 1968, this paper). Nybelin (1974) noted that a single, posteriorly directed tubule is rarely present. If present, it is placed ventrally to the branching of the canal. The reconstructions of the dermosphenotic and its part of the infraorbital canal of *L. coryphaenoides* of later authors (e.g. Taverne 1975, Arratia & Thies 2001; Arratia & Schultze 2015, Arratia 2015a) agree with Nybelin (1974). The dermosphenotics of *Proleptolepis furcata* and *P. megalops* have an almost equal shape, they are higher than broad and elongate. As in the species of *Leptolepis*, Nybelin (1974:83, 107) described an anterodorsal directed "tubule" in *P. furcata* and *P. megalops*, which is herein interpreted as the anterior branch of the infraorbital canal. In both, *P. furcata* and *P. megalops*, a single long tubule is present, directed in dorsal, or anterodorsal direction. The dermosphenotics of *L. saltviciensis*, *L. autissiodorensis*, *L. nathorsti*, *L. woodwardi*, *P. elongata* and *Longileptolepis wiedenrothi* are unknown. In conclusion: the shapes of the dermosphenotic and its part of the infraorbital sensory canal are almost equal in *L. coryphaenoides* and *L. normandica*, but different to the dermosphenotics of *P.*

*furcata* and *P. megalops* which show striking similarities, but in both groups, the bone is very different from these of the herein described specimens of *Leptolepidae* sp. 1 and *Leptolepis jaegeri*.

**Tubules in the supraorbital canal.** In most leptolepids the supraorbital sensory canal gives off some tubules. They are short, always unbranched and medially directed, but also specimens without tubules in the supraorbital canal are known. Rayner (1937: fig. 2) drew three tubules in *Leptolepis "bronni"*, but mentioned that the presence of tubules in the supraorbital canal is not a constant feature. Wenz (1968) reported specimens of *L. "coryphaenoides"* which possess tubules in the supraorbital canal (Wenz 1968: fig. 86A), but she also drew specimens without tubules (Wenz 1968: figs. 82A, B; 83; 84; 86B). Nybelin (1962, 1974) observed tubules in *L. coryphaenoides* (Nybelin 1974: fig. 4A, B; pls. VII, fig 3; VIII, fig. 2), *L. normandica* (Nybelin 1974: fig. 1A, B; pls. I; V, figs. 1, 2, 3), *L. nathorsti* (Nybelin 1974: figs. 13, 14A, B; pl. XX, figs. 1, 2), *Proleptolepis furcata* (Nybelin 1974: fig. 15A, B) and *P. megalops* (Nybelin 1974: figs. 20; 21A, B). The herein examined specimens of *Leptolepidae* sp. 1 (GG 431/5a, Fig. 2, Pl. 1A, B), *Leptolepis jaegeri* (GG 431/1, Fig. 8C) and *L. sp.1* (GG 431/4, GG 431/18) do not possess any tubules in the supraorbital canal. Unfortunately, the condition remains unknown in the specimens of *L. coryphaenoides* and *L. normandica* from Grimmen and Dobbertin. The only specimen of the herein examined material which clearly shows tubules is an isolated parietal (GG 431/21, Fig. 13). The overall shape of the specimen suggests that it most probably belongs to the genus *Leptolepis*. The arrangement of the tubules resembles that in *L. normandica* as described by Nybelin (1974). In summary: the supraorbital canals of *L. coryphaenoides*, *L. normandica*, *L. nathorsti*, *Proleptolepis furcata* and *P. megalops* give off short, medially directed, unbranched tubules. In *Leptolepidae* sp. 1, *Leptolepis jaegeri* and *L. sp.1*, tubules are absent in the supraorbital canal. The supraorbital sensory canals of *Leptolepis woodwardi*, *L. saltvicensis*, *L. autissiodorensis*, *Proleptolepis elongata* and *Longileptolepis wiedenrothi* are unknown.

**Suborbital.** One or two suborbital bones are present in all leptolepid fishes s. st., occupying the space between infraorbital bones 3 to 5, the preopercle and the opercle. The presence of two suborbitals, both of about equal size, is reported in *Longileptolepis wiedenrothi* (Arratia & Thies 2001). *Proleptolepis furcata*, *P. megalops* and *P. elongata* bear also two suborbital bones, a large one and a small "accessory" one in the anterodorsal corner of the above described space (see Nybelin 1974). All *Leptolepis* species, in which the respective part of the head is known (*L. coryphaenoides*, *L. normandica*, *L. jaegeri*), have a single, elongate suborbital, which is vertically oriented. In all of the herein described specimens of *Leptolepis*, we have found a well-marked notch in the posteroventral margin of the suborbital. The notch was not mentioned by any other author but was shown in *Proleptolepis* by Nybelin (1974: figs. 15A, 20). The herein examined specimens of *Leptolepis normandica* (GG431/2, Fig. 6, Pl. 1E) and *Leptolepis* sp.1



(GG 431/4a, Fig. 12A; GG431/17; GG431/18) show a small, half-circular notch in the dorsal margin of the bone, which seems to provide space for the passage of the preopercular canal.

**Shape of opercle.** The shape of the opercle, especially the angle between its anterior and posterior margins, was used by Nybelin (1962, 1974) as diagnostic character to distinguish between *L. coryphaenoides* and *L. normandica*. He described the anterior and posterior margins of the opercle of *L. coryphaenoides* as running almost parallel to each other, whereas these margins form a distinct angle in *L. normandica*. This character was already discussed by Wenz (1968: 212), who interpreted these different shapes as intraspecific variations or as artifacts of preservation. In the herein described specimens of *L. coryphaenoides* (GG 431/7, Fig. 4A, Pl. 2A; NRM P 6091: Fig. 5; GG431/19, GG431/20) and *L. normandica* (GG 431/2, Fig. 6; Pl. 1E) the situation is contrary to Nybelin's descriptions; but other distinct characters (e.g. the shape of the premaxilla, number and shape of tubules in the preopercular sensory canal) support our assignments to the respective species. Additionally, some of Nybelin's specimens of *L. coryphaenoides* (BMNH 32465, Nybelin 1974: pl. VII, fig. 1; NRM P 7810, Nybelin 1974: pl. X, fig. 1) show an opercle with oblique anterior and posterior margins as described in *L. normandica*. Thus, Nybelin's descriptions seem to be incorrect. We interpret the different shapes of the opercle as variable within the respective species.

**Shape of the preopercle.** In leptoepid fishes the preopercle is composed of two well-defined limbs. The dorsal one narrows in dorsal direction, the ventral one is directed anterior or anteroventrally. A distinct notch in the posteroventral margin of the preopercle is present in *Proleptolepis* (Nybelin 1974) and *Longileptolepis* (Arratia & Thies 2001). It was previously interpreted as absent in *Leptolepis* (Nybelin 1974, Arratia & Thies 2001). Also previous and later authors described and/or figured the preopercle in *Leptolepis* with an entire posteroventral margin (e.g. Rayner 1937, Wenz 1968, Nybelin 1962, 1974, Taverne 1975, Tintori 1977, Arratia & Schultze 2015, Arratia 2015a). The presence of this notch was used as a diagnostic character for *Proleptolepis* (Nybelin 1974) and for *Longileptolepis* (Arratia & Thies 2001). The shape of the notch is different in both genera, the notch is deep in *Proleptolepis* but it is less pronounced or shallow in *Longileptolepis*. With the herein described material, we have found a shallow notch, similar to that in *Longileptolepis*, in the specimens of Leptoepidae sp. 1 (GG 431/5: Fig. 2), *Leptolepis* sp. 1 (GG 431/4, Fig. 12A), *L. coryphaenoides* (GG 431/3, Fig. 4B, Pl. 2B), and *L. normandica* (GG 431/2, Fig. 6, Pl. 2D). A deep notch, similar to that in *Proleptolepis*, is present in the *Proleptolepis*-like specimen (MV 202612: Fig. 3, Pl. 1B). A notch in the posterior margin of the preopercle is absent in specimens of *L. coryphaenoides* (GG431/7, Fig. 4A; GG431/19, Pl. 2C), all specimens of *L. jaegeri* (NRM P 6483, Fig. 7A, B; GG431/1, Fig. 8B, Pl. 2E; GG 431/9, Fig. 9A; GG431/15, Fig. 10A) and in *L. nathorsti* (NRM P 1316, lectotype). Thus, the presence or absence of a notch in the posteroventral margin

of the preopercle cannot be used as a diagnostic character, and has to be interpreted as a variable within the genus *Leptolepis*, as well as within in the species *L. coryphaenoides* and *L. normandica*.

**Suprapreopercle.** A suprapreopercle was described in *L. normandica* by Nybelin (1962, 1974). Arratia (1997) reported the presence of this bone also in few specimens of *L. coryphaenoides*. A suprapreopercle was not observed in the herein examined material, but we cannot exclude the presence of this bone, since most of our specimens are fully articulated heads. If a suprapreopercle is present it is completely covered by the suborbital. It is definitely absent in the specimens of *Leptolepidae* sp.1 (GG 431/5, Fig. 2, Pl. 1A) and *L. coryphaenoides* (GG 431/3, Fig. 5B and GG 431/7, Fig. 5A).

**Shape of premaxilla.** The premaxilla of *L. "bronni"* is briefly described by Rayner (1937: 51) as a small bone with an "upward enlargement", but nothing is said about the size of this ascending process. The reconstruction of Rayner (1937: fig. 3) suggests a low and narrow process. Wenz (1968) described the premaxilla of *L. "coryphaenoides"* as small, with a low dorsal process. *L. coryphaenoides sensu* Nybelin (1974) has a premaxilla, which is smaller than in *L. normandica* and the ascending process also is more slender than in *L. normandica*. The bone in *L. normandica* is described as small, with a broad ascending process. We agree with these descriptions. In the specimens of *L. coryphaenoides* from Grimmer (GG 431/7, Fig. 5A) and from Dobbertin (GG 431/3, Fig. 5B, Pl. 3A), the premaxillae are small, and the ascending process is low and narrow. In the specimen of *L. normandica* from Dobbertin (GG 431/2: fig. 6, pl. 3C) the premaxilla is a small bone, but its ascending process is comparatively high and broad. In *L. jaegeri sensu* Nybelin (1974: 59) the bone is described with a high ascending process and with "its postero-lateral portion is proportional shorter than in *L. normandica* and *coryphaenoides*.", but his reconstruction of *L. jaegeri* (Nybelin 1974: fig. 9) shows a bone which is in all aspects larger than the premaxillae in *L. coryphaenoides* and *L. normandica*. This reconstruction reflects our results. In the *L. jaegeri* specimens from Dobbertin (GG 431/1, Figs. 8A, B, Pl. 4B; GG 431/6) and the specimens from Grimmer (GG 431/9, Figs. 9A, B; GG 431/15, Fig. 10A, Pl. 3D; GG431/16, Fig. 10B, Pl. 4C) the premaxillae are long, broad and bear a high and broad ascending process, which is almost as high as the length of the ventral part of the premaxilla. The three species of *Proleptolepis* show premaxillae of almost equal shapes. They are small, short but high, almost triangular and bear a small ascending process. The bone is slightly larger in *P. megalops* (Nybelin 1974: 95, 81, 101). Thus, the shape of the premaxillae of *Proleptolepis* is very different from that in *Leptolepis*. The premaxilla of *Longileptolepis wiedenrothi* has a "long, well-developed ascending process" (Arratia & Thies 2001: 170). According to their drawing and reconstructions, the ventro-lateral part of the bone, as well as the process are thin. Thus, it differs from the other species of *Leptolepidae*. The premaxillae of *Leptolepis autissiodorensis*, *L. saltviciensis*, *L. nathorsti* and *L. woodwardi* are unknown.

**Shape of maxilla.** In all species of leptolepids the maxilla is long with a more or less convex ventral margin. In all species of *Leptolepis* there is a prominent ridge along the lateral surface of the bone, especially in its anterior portion (the maxilla of *L. woodwardi* is unknown). In *L. coryphaenoides* and *L. normandica*, the maxilla has an almost equal shape. In both species the ventral margin of the bone is strongly convex, the posterior tip of the bone is rounded and points in posterodorsal direction (Figs. 4A, B, 6, Pl. 3 A–D). This shape was also observed in *L. sp. 1* (GG 431/4, Fig. 12; GG 431/17, GG 431/18), *L. nathorsti* and *Proleptolepis*. The maxilla is less deep and less convex in *L. jaegeri* (Figs. 8B, 9A, 10A, B; Pls. 3D, 4C) than in the above listed taxa. Furthermore, the posterior tip is less rounded and points in posterior direction. Although the maxilla is poorly preserved in *Longileptolepis wiedenrothi* (see Arratia & Thies 2001), its shape seems to resemble that in *L. jaegeri*.

**Dentition of premaxilla.** The dentition of the premaxilla differs in leptolepid fishes. About twelve fine teeth were observed in *L. “bronni”* by Rayner (1937). The premaxillary teeth of *L. “coryphaenoides”* are described as: “The oral border of the bone presents one dozen of small, identical teeth” (Wenz 1968: 214, translated). Nybelin (1974) described the premaxillary teeth of *L. coryphaenoides* and *L. normandica* as small and fused at their bases in the anterior portion of the bone, but being separate posteriorly. Fusion of teeth was not observed by any other author, and is not present in any specimen of the herein examined material. We agree with the descriptions of Rayner (1937) and Wenz (1968). In the herein examined specimens of *L. coryphaenoides* (GG 431/3, Fig. 4B, Pl. 3A and GG 431/7, Fig. 4A) and *L. normandica* (GG 431/2, Fig. 6, Pl. 3C), the oral margin of the premaxilla bears a single row of about twelve minuscule, needle-like teeth. This is comparable with the dentition of *Proleptolepis* (see Nybelin 1974). Few conical teeth are present on the premaxilla of *Longileptolepis wiedenrothi* (Arratia & Thies 2001). The dentition of the premaxilla of *L. jaegeri* is described by Nybelin (1974) as a single row of 12 to 14 small teeth. The photographs of Nybelin's specimen of *L. jaegeri* (Nybelin 1974: pl. XII, figs. 1 and 2) are retouched, the dentition of the premaxilla and dentary do not resemble the original state of the neotype NRM P 6483. However, his reconstruction (Nybelin 1974: fig. 9) shows comparatively large, conical teeth. This agrees with our results concerning the neotype of *L. jaegeri* (Fig. 7A), in which we have observed few comparatively large, conical teeth pointing ventrally. Also the specimens of *L. jaegeri* from Dobbartin (GG 431/1, Fig. 8A, B; Pl. 4B) and Grimmen (GG431/15, Fig. 10A, Pl. 3D; GG431/16, Fig. 10B, Pl. 4C) show relatively large, conical teeth on the oral margin of the premaxilla. Similar teeth are present in premaxilla of *L. sp.1* (GG 431/17, Pl. 4E; GG 431/18). Thus, the premaxillary teeth are very small and needle-like in *Proleptolepis*, *Leptolepis coryphaenoides* and *L. normandica* but slightly larger and conical in *Longileptolepis wiedenrothi* and *Leptolepis jaegeri* and *L. sp. 1*.

**Dentition of maxilla.** Maxillary teeth are not mentioned or drawn by Rayner (1937) in her description of *L. “bronni”*. Very small teeth along the whole ventral margin of the dentary in *L.*

“*coryphaenoides*” were described by Wenz (1968). The maxillary teeth of *L. normandica* and *L. coryphaenoides* are “a boarder of fused teeth” (Nybelin 1974: 13), nothing is said about their size, but his reconstructions and photographs of *L. normandica* and *L. coryphaenoides* indicate that they are very small. We agree with the presence of very small teeth in *L. coryphaenoides* and *L. normandica*, but found no evidences for a fusion of teeth. The maxillae of *L. nathorsti*, *Proleptolepis furcata*, *P. megalops* and *P. elongata* show very small teeth along the ventral margin of the maxilla (Nybelin 1974), and also the maxilla of *Longileptolepis wiedenrothi* carries small conical teeth (Arratia & Thies 2001). The maxilla of the neotype of *L. jaegeri* (NRM P 6483) is not preserved, but it is present in the specimens GG 431/1 (Fig. 8B), GG431/15 (Fig. 10A, Pl. 3D) and GG431/16 (Fig. 10B, Pl. 4C). The dentition is damaged in all specimens. Jaekel (1929) described specimen GG 431/1 and counted 60 to 80 teeth, which seems to be a plausible range. The teeth of *L. jaegeri* are also small, but conical and considerably larger than in the above mentioned species. We observed identical teeth on the maxilla of *L. sp. 1* (GG 431/4, Fig. 12B).

**Dentition of dentary.** About six very small teeth are mentioned and drawn in the anterior-most part of the dentary of *L. “bronnii”* by Rayner (1937). This was assumed to be also true for *L. normandica* by Nybelin (1974). No teeth were mentioned or drawn in *L. coryphaenoides* by Nybelin (1962, 1974). Wenz (1968) apparently did not observe any teeth in the dentary of *L. “coryphaenoides”*. We agree with the description of Rayner (1937). In *L. coryphaenoides* GG 431/7 (Fig. 4A) at least two very small teeth are preserved in the anterior portion of the dentary, but some seem to be broken. Also in the herein examined specimen of *L. normandica* (GG 431/2, Fig. 6A), some very small teeth are preserved in the anterior portion. Very small dentary teeth are also present in *Proleptolepis furcata*. The condition is unknown in *P. megalops*, *P. elongata* (Nybelin 1974), as well as in *Longileptolepis wiedenrothi* (Arratia & Thies 2001) and *Leptolepis nathorsti*. Teeth seem to be absent in the dentary of *Leptolepis woodwardi* (Nybelin 1974). Already Nybelin (1974) observed comparatively large, conical teeth on the oral margin of the dentary of *L. jaegeri*. We agree with this interpretation. At least ten, comparatively large, conical teeth are present along the complete oral margin of the herein examined specimens of *L. jaegeri* (Figs. 7C, 8A, B, 9A, B, 10A, B; Pl. 3D, 4B, C). In conclusion, about six, very small teeth are present in the anterior portion of the dentaries of *L. normandica*. Whereas the posterior portion of the oral margin of the dentary seems to be edentulous. This seems to be also true for *L. coryphaenoides* and *Proleptolepis furcata*. In *Leptolepis jaegeri*, the complete oral margin bears relatively large, conical teeth.

**Number and shape of tubules in the preopercular sensory canal.** The number and shape of tubules in the preopercular canal is a main character that Nybelin (1962) induced to describe *L. normandica*. Nybelin (1962, 1974) discussed two groups of *Leptolepis* species, one in which the tubules in the preopercular canal are always unbrached (*L. normandica*, *L. jaegeri*, *L. woodwardi* and *L. nathorsti*) and another group with branched tubules (*L. coryphaenoides*, *L. saltviciensis* and *L. autissiodorensis*).

Wenz (1968) also found and described specimens with branched as well as unbranched tubules. She found that young individuals show a lower number of tubules in the preopercular canal than adult specimens. Consequently, she interpreted this as a variable ontogenetic condition. The presence/absence of branched tubules was interpreted by her as inner-species variation in *L. "coryphaenoides"*. We agree with Wenz (1968) in the aspect of the ontogenetic changes. Although, most of the juvenile specimens from Grimmen and Dobbartin (GG 431/12, GG 431/14) cannot be assigned to any species, they all show lower numbers of tubules than adult individuals. The branching of the tubules cannot be interpreted as variable within the respective species, since neither of our specimens of *L. normandica* (Fig. 6, Pl. 2D), *L. jaegeri* (Figs. 7A, B, 8A, B, 9A, B, 10A, B; Pl. 3B, C), *L. sp. 1* (Fig. 12A, B), *Leptolepidae sp. 1* (Fig. 2), nor *Proleptolepis*-like (Fig. 3, Pl. 1C) show even a single branched tubule in the preopercular canal. In contrast, all specimens of *L. coryphaenoides* (Fig. 4B; Pl. 2B, C), including young individuals (GG 431/7, Fig. 4A), possess branched tubules.

**Caudal skeleton.** As already described by Nybelin (1963, 1974), Wenz (1968), Patterson & Rosen (1977) and Arratia (1991), the composition of the caudal skeletons of *L. coryphaenoides* and *L. normandica* do not differ significantly. The herein described caudal skeleton of *L. jaegeri* (GG431/10, Fig. 11) resembles those of *L. coryphaenoides* and *L. normandica* in the presence of fringing fulcra in the dorsal lobe of the caudal fin and the absence of fringing fulcra in the ventral lobe. Moreover, the possession of nine hypurals in *L. jaegeri* is comparable with *L. coryphaenoides* (up to ten). The number of uroneurals is seven in *L. jaegeri*, which is in the range of *L. coryphaenoides* and *L. normandica* (seven to eight). The first ural centrum (U1+2) of GG 431/10 bears two short neural spines. Arratia (1991) reported a single neural spine on the first ural centrum of some specimens of *L. coryphaenoides*. The caudal skeleton in *Proleptolepis elongata* differs from that in the *Leptolepis* species in the presence of eleven hypurals (up to ten in *L. coryphaenoides*) and the presence of fringing fulcra in the ventral lobe of the caudal fin (absent in *Leptolepis*). *Longileptolepis wiedenrothi* also bears fringing fulcra in the ventral lobe. The other characters are unknown in this species (see Arratia & Thies 2001).

### **Geographical and stratigraphical distribution of Leptolepidae**

The earliest fossil records of fishes of the family Leptolepidae are known from the early Lower Jurassic of South America and Europe, incorporating indeterminate "proleptolepids" from the early to middle Sinemurian of Chile (Arratia 1987; Arratia & Schultze 1999; these specimens were recently refined to Leptolepidae indet. by Arratia 2015b), and *Proleptolepis* from the upper Sinemurian of England (Nybelin 1974; Forey *et al.* 2010). Additionally, Antunes *et al.* (1981) reported leptolepid fishes from the upper Sinemurian of Portugal, which they ascribed as *Proleptolepis sp.* These occurrences suggest that leptolepids have attained a wide, perhaps cosmopolitan distribution by the beginning of the Early Jurassic.

The marine late Early Jurassic (Toarcian) outcroppings in Europe have yielded numerous specimens of leptolepid fishes. Important localities include the Svalbard Archipelago in the Arctic Sea, England, France, Luxembourg and Germany (Rayner 1937; Wenz 1968; Nybelin 1974; Delsate 1997, this contribution). The youngest record of Leptolepidae is represented by a recently described indeterminate leptolepid from the upper Middle Jurassic (middle to late Callovian) of Antarctica (Arratia & Hikuroa 2010).

The “Green Series” of Grimmer and Dobbertin documents a diverse leptolepid fauna, immediately following the onset of the Toarcian Oceanic Anoxic Event. The possible record of *Proleptolepis* in the lower Toarcian “Green Series” of Grimmer is significant, as specimens attributed to this genus have previously been reported from strata of upper Sinemurian age of England and Portugal (Nybelin 1974; Antunes *et al.* 1981; Forey *et al.* 2010). Although the herein described specimen MV 202612 cannot be assigned to *Proleptolepis* with certainty, this specimen suggests that the genus might have been also present in the Toarcian. The “Green Series” leptolepid fauna is also significant, because it includes the northeastern-most records of *Leptolepis coryphaenoides*, *L. normandica* and *L. jaegeri* from Europe. Specimens assigned to *L. coryphaenoides* were previously only known from the lower Toarcian of England, France and Germany (Nybelin 1974), while *L. normandica* was only known from lower Toarcian strata of England, France and Luxembourg (Nybelin 1974; Delsate 1997). The presence of *L. jaegeri* in the “Green Series” of Grimmer and Dobbertin is of particular interest, since this rare species was previously only known from the lower Toarcian of Southwestern Germany. The identification of these three taxa in the lower Toarcian “Green Series” of Grimmer and Dobbertin suggests that they had a wide paleobiogeographic distribution within the Toarcian European Epicontinental Sea, with *L. coryphaenoides* and *L. normandica* being most widespread (Fig. 14). The precise stratigraphic ages are unknown for the majority of leptolepids historically collected from the Toarcian of Europe. The herein examined fishes from Grimmer originate from a nodular horizon (correlative with the *Harpoceras exaratum* Subzone) that occurs interbedded within the “Green Series” clay, thus representing a relatively short period of time. This leads to the assumption that the different species also lived contemporaneous. However, more research is needed in order to provide more definitive data on the taxonomy, diversity and palaeobiogeography of Toarcian leptolepids. The Toarcian species *Leptolepis autissiodorensis* Simpson, 1855 and *L. saltviciensis* Sauvage, 1892 (which might only be a synonym of *L. autissiodorensis*, see Nybelin 1974) and *L. nathorsti* Woodward, 1900, were not found among the fishes from Grimmer and Dobbertin. A true absence of these species cannot be verified because the number of the available specimens from these localities is too low to give a reliable statistical statement.

### **Preservation and taphonomy**

Most of the fossil fishes recovered from the lower Toarcian "Green Series" of Grimmer and Dobbertin are represented by isolated, almost completely articulated heads. The presence of isolated heads and tails originating from small teleosts is known from several late Jurassic fossil Lagerstätten of the Solnhofen-type (e.g., Solnhofen, Langenaltheim, Blumenberg, Eichstätt; Viohl 2015, Konwert pers. obs.). This type of preservation is interpreted as originating from decaying carcasses by Viohl (2015) and, alternatively, as bitten off by cephalopods by Ebert *et al.* (2015). Specimen GG431/2a from the "Green Series" clay deposits of Dobbertin is represented by an almost completely articulated head and some anterior abdominal vertebrae, with the last vertebra being incomplete, lacking its posterior part. This can hardly be explained by processes of decay. It therefore appears more likely that the isolated teleostean heads were biomechanically produced, perhaps by preying cephalopods, as proposed by Ebert *et al.* (2015). Apart from articulated specimens, isolated teleostean bones are commonly associated with the carbonate concretions originating from the "Green Series" clay deposits of Grimmer and Dobbertin. These occur as single or accumulated on one bedding plane. For instance, several isolated teleostean bones (i.e., vertebrae, dentaries, ceratohyals, a hyomandibula, and several indeterminable chondral and dermal bones) were found preserved on the outer surface of a single concretion (GG431/13, Pl. 4D). The vertebrae can at least be assigned to Leptolepidae based on the thin and smooth autocentra, autocentra and chordocentra not constricting the notochord and lack of cavities for adipose tissue on the walls of the autocentra (see Arratia & Hikuroa 2010). The sizes of bones vary in GG431/13, which is indicative of deriving from various individuals. Moreover, disarticulated teleostean bones also occur occasionally associated with ammonite shells and shells of the pseudoplanktonic bivalve *Pseudomytiloides dubius*, forming distinct, subcircular to oval accumulations. These fossil associations were probably generated by hydraulic transport and reworking, or more likely, reflect biomechanical production, as proposed by Ansorge (2007), who suspected these localized accumulations to be Speiballen (i.e., a compacted mass of indigestible stomach contents) regurgitated by marine reptiles. These findings suggest that leptolepids were present in abundance, forming a significant component in the marine lower Toarcian "Green Series" biota.

### **Final comments**

The herein described morphological diversity of leptolepid fishes is considered to reflect morphological patterns of distinct taxa as suggested by Nybelin (1962, 1974). The interpretation of very high intraspecific variation of several morphological characters in the type species, as proposed by Wenz (1968), is considered to be incorrect in most aspects. Although some characters are interpreted herein as variable within some taxa (e.g. the shape of opercle, the presence or absence of a notch in the posterior margin of the preopercle), most of the characters show distinct morphologies, which allows a clear



differentiation between the above listed species. With the herein provided descriptions, we have found that the following taxa are characterized by the combination of the following characters:

**Family Leptolepidae.** (1) Preopercle L-shaped, with distinct dorsal and ventral limbs; (2) two supramaxillae at dorsal margin of maxilla present; (3) vertebrae with thin and smooth autocentra (Arratia & Hikuroa 2010); (4) autocentra and chordacentra not constricting the notochord (Arratia & Hikuroa 2010); (5) lack of cavities for adipose tissue in the walls of the autocentra (Arratia & Hikuroa 2010); (6) two or one suborbital bones present, occupying the space between infraorbitals 3–5, preopercle and opercle; (7) body covered with cycloid scales.

**Genus *Leptolepis*.** (1) One suborbital present; (2) “accessory” suborbital (*sensu* Nybelin 1974) absent; (3) prominent longitudinal ridge along the lateral side of maxilla present; (4) bones of the cranial roof lack ornamentation; (5) fringing fulcra on dorsal lobe of caudal fin present; (6) fringing fulcra in ventral lobe of the caudal fin and in the other fins absent; (7) anterior and posterior sclerotics large, forming a complete ring; (8) postcleithrum 1 large and elongate.

***L. coryphaenoides*.** (1) Premaxilla small, triangular, with its anteromedial ascending process low and narrow; (2) several branched or bifurcated tubules present in preopercular canal and infraorbital canal on infraorbital 3; (3) ventral margin of maxilla intensely convex, especially in its posterior portion; (4) single row of miniscule, needle-like teeth present on premaxilla, maxilla and oral margin of dentary.

***L. normandica*.** (1) Premaxilla small, the anteromedial ascending process moderately high and broad; (2) tubules of the cephalic sensory canals always unbranched; (3) ventral margin of maxilla intensely convex, especially in its posterior portion; (4) single row of minuscule, needle-like teeth present on premaxilla, maxilla and oral margin of dentary.

***L. jaegeri*.** (1) Premaxilla large, with high and broad ascending process; (2) ventral margin of dentary slightly convex; (3) comparatively large, conical teeth present on premaxilla, maxilla, vomer, dentary; (4) coronoid process of dentary posteriorly placed; (5) notch in posterior margin of preopercle absent; (5) supraorbital sensory canal without tubules.

As described above, Leptolepidae sp. 1, *Proleptolepis*-like and *Leptolepis* sp. 1 show characters or a combination of characters, which are not described in any species of leptolepid fishes. The genus *Leptolepis* contains a multiplicity of valid and invalid species, but the descriptions, especially historical ones, are often very brief and insufficient. Furthermore, the type specimens are lost in many cases. Because of this, and the incompleteness of the specimens, we were not able to assign these fishes to an existing species or a new one.

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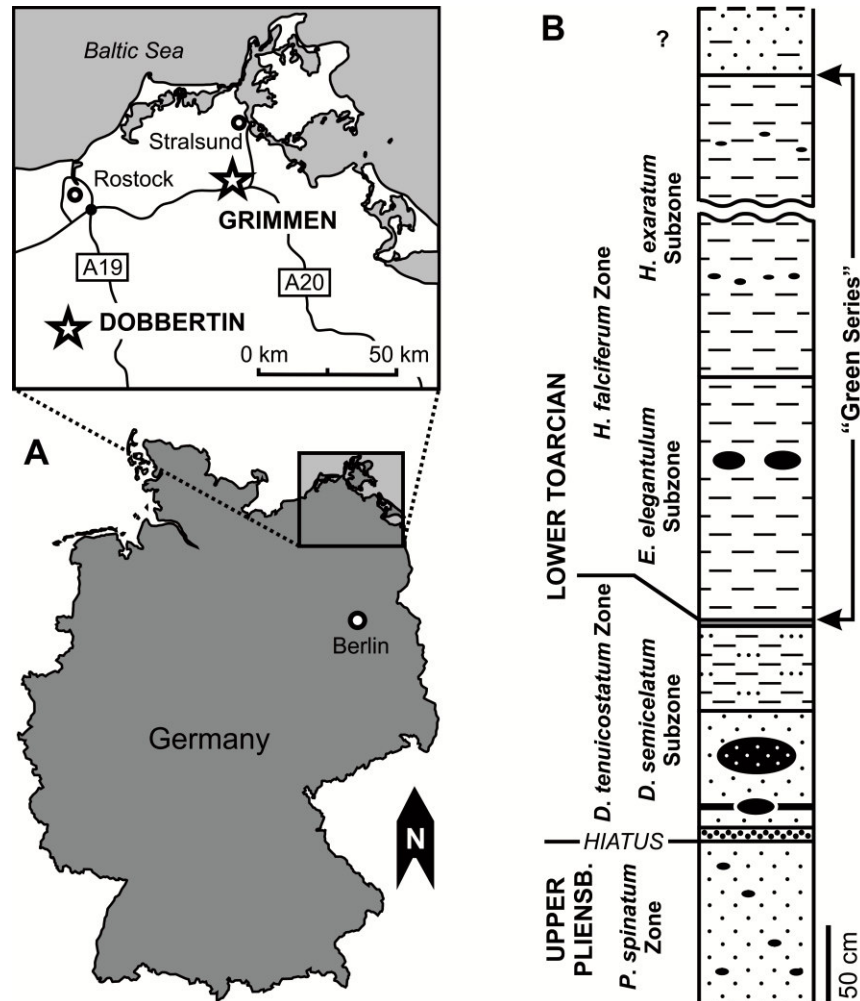
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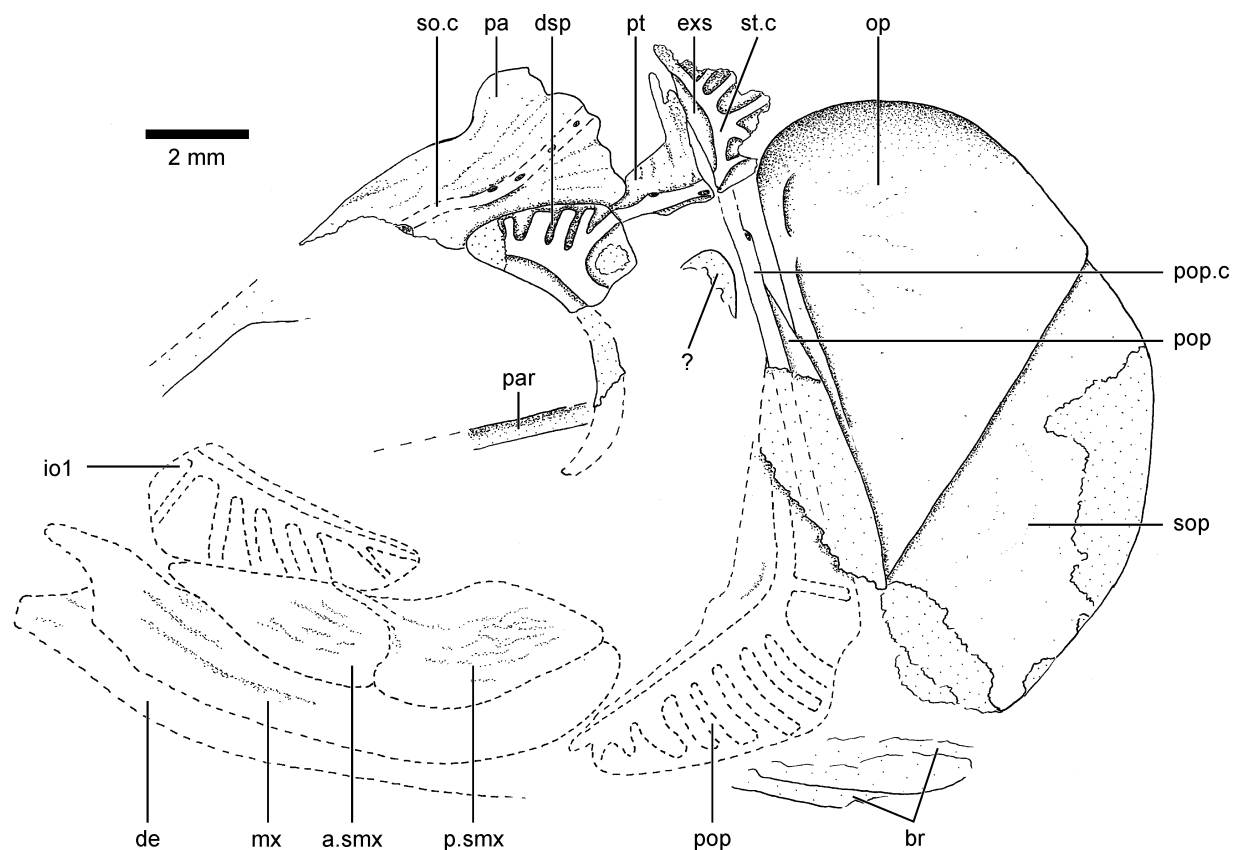
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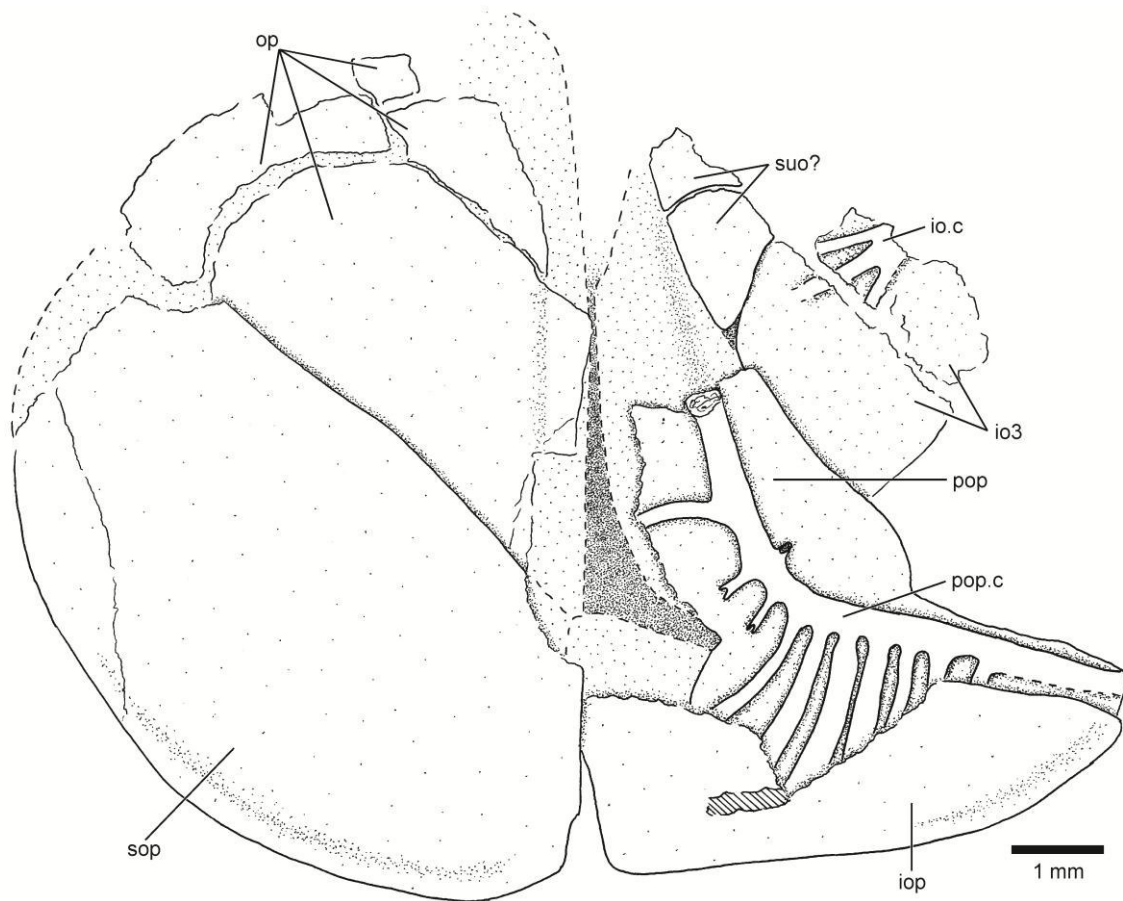
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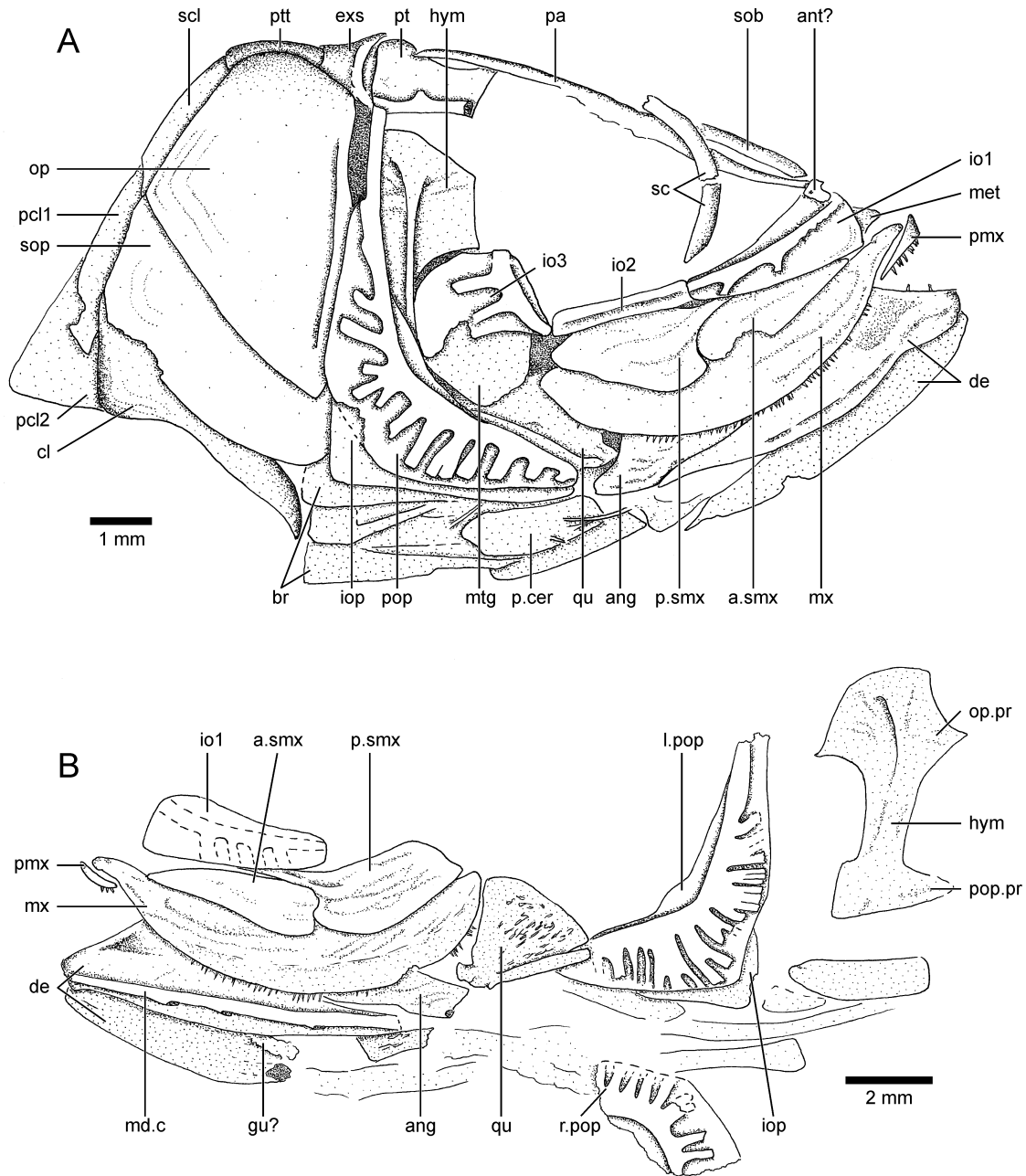
**FIGURE 1.** **A** Geographical map showing the positions of the late Early Jurassic localities of Dobbertin, Mecklenburg, and Grimmen, Western Pomerania. **B** Stratigraphic standard section of the Upper Pliensbachian to Lower Toarcian succession outcropping at Grimmen.



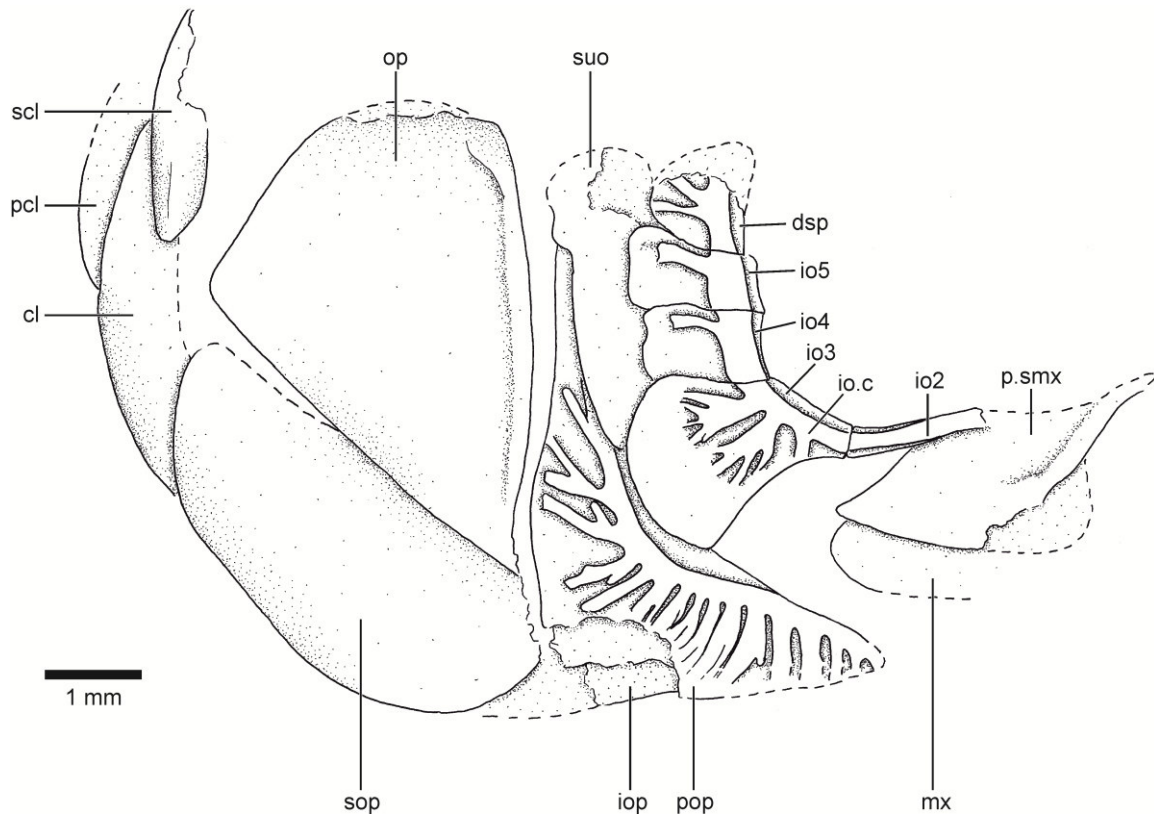
**FIGURE 2.** Leptolepidae sp. 1 (GG 431/5a) from Dobbertin. Line drawing of cranial bones and molds. Dashed lines indicate molds. Abbreviations: **a.smx**, anterior supramaxilla; **br**, branchiostegal rays; **de**, dentary; **dsp**, dermosphenotic; **exs**, extrascapula; **io1**, infraorbital 1; **op**, opercle; **pa**, parietal bone; **par**, parasphenoid; **pt**, pterotic; **pop**, preopercle; **pop.c**, preopercular sensory canal; **p.smx**, posterior supramaxilla; **sop**, subopercle; **so.c**, supraorbital sensory canal; **?**, unknown bone.



**FIGURE 3.** *Proleptolepis*-like (MV 202612) from Grimmer. Line drawing of cranial bones in medial view. Dashed lines indicate moulds. Abbreviations: **iop**, interopercle; **io3**, infraorbital 3; **io.c**, infraorbital sensory canal; **op**, opercle; **pop**, preopercle; **pop.c**, preopercular sensory canal; **sop**, subopercle; **suo**, suborbital.

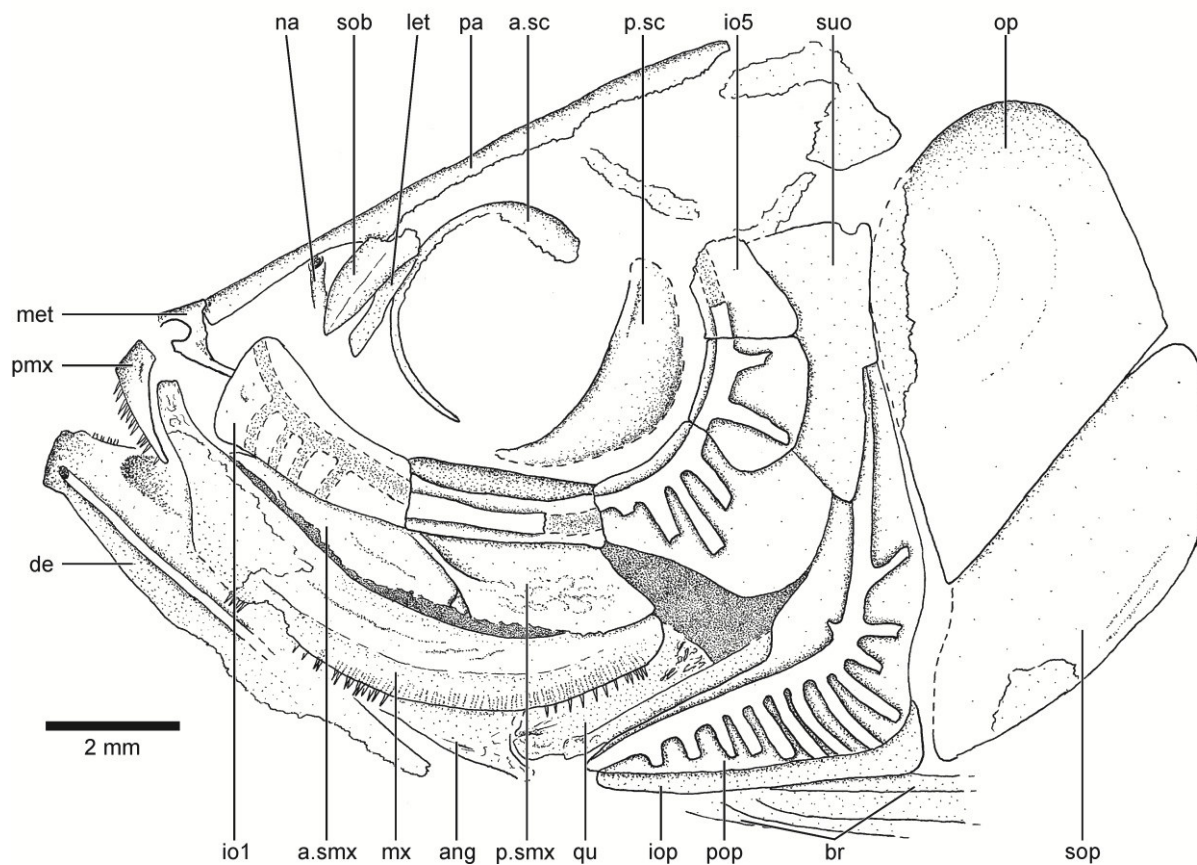


**FIGURE 4.** *Leptolepis coryphaenoides*. Line drawings of cranial bones. **A** GG 431/7, juvenile specimen from Grimmen. **B** GG 431/3, adult specimen from Dobbertin. Abbreviations: **ang**, angular; **ant**, antorbital; **a.smx**, anterior supramaxilla; **br**, branchiostegal rays; **cl**, cleithrum; **de**, dentary; **exs**, extrascapula; **gu?**, gular plate?; **iop**, interopercle; **io1**, infraorbital 1; **io2**, infraorbital 2; **io3**, infraorbital 3; **l.pop**, left preopercle; **pmx**, premaxilla; **pt**, pterotic; **ptt**, posttemporal; **hym**, hyomandibula; **md.c**, mandibular sensory canal; **met**, mesethmoid; **mtg**, metapterygoid; **mx**, maxilla; **op**, opercle; **op.pr**, opercular process of hyomandibula; **pa**, parietal bone; **pcl1**, postcleithrum 1; **pcl2**, postcleithrum 2; **pop**, preopercle; **pop.pr**, preopercular process of hyomandibula; **p.cer**, posterior ceratohyal; **p.smx**, posterior supramaxilla; **qu**, quadrate; **r.pop**, right preopercle; **scl**, supracleithrum; **sob**, supraorbital bone; **sop**, subopercle.



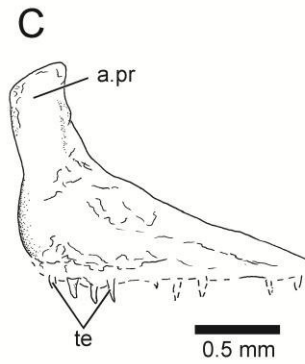
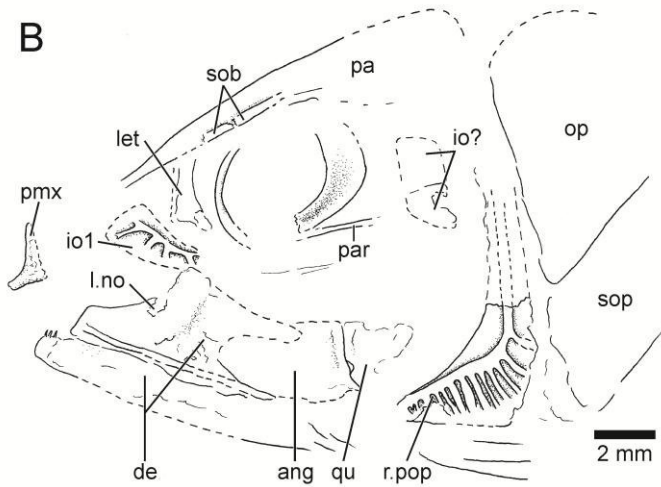
**FIGURE 5.** *Leptolepis coryphaenoides* (NRM P 6091, cast of NHM P 23834) from Dobbertin. Line drawing of cranial bones and pectoral girdle in lateral view. Abbreviations: **cl**, cleithrum; **dsp**, dermosphenotic; **io.c**, infraorbital sensory canal; **iop**, interopercle; **io2**, infraorbital 2; **io3**, infraorbital 3; **io4**, infraorbital 4; **io5**, infraorbital 5; **mx**, maxilla; **op**, opercle; **pcl**, postcleithrum; **pop**, preopercle; **p.smx**, posterior supramaxilla; **scl**, supracleithrum; **sop**, subopercle; **suo**, suborbital.



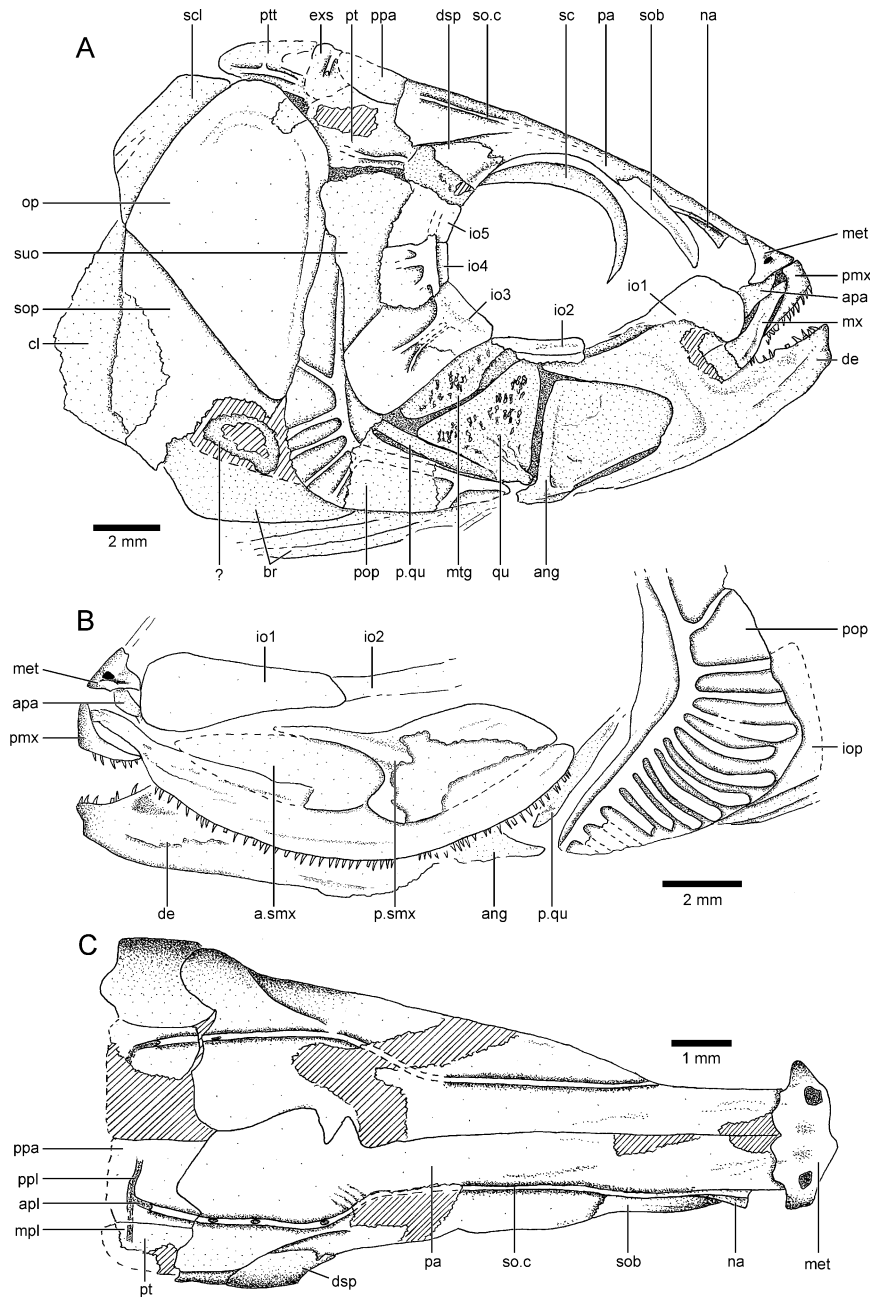


**FIGURE 6.** *Leptolepis normandica* (GG 431/2a) from Dobbertin. Line drawing of head in lateral view.

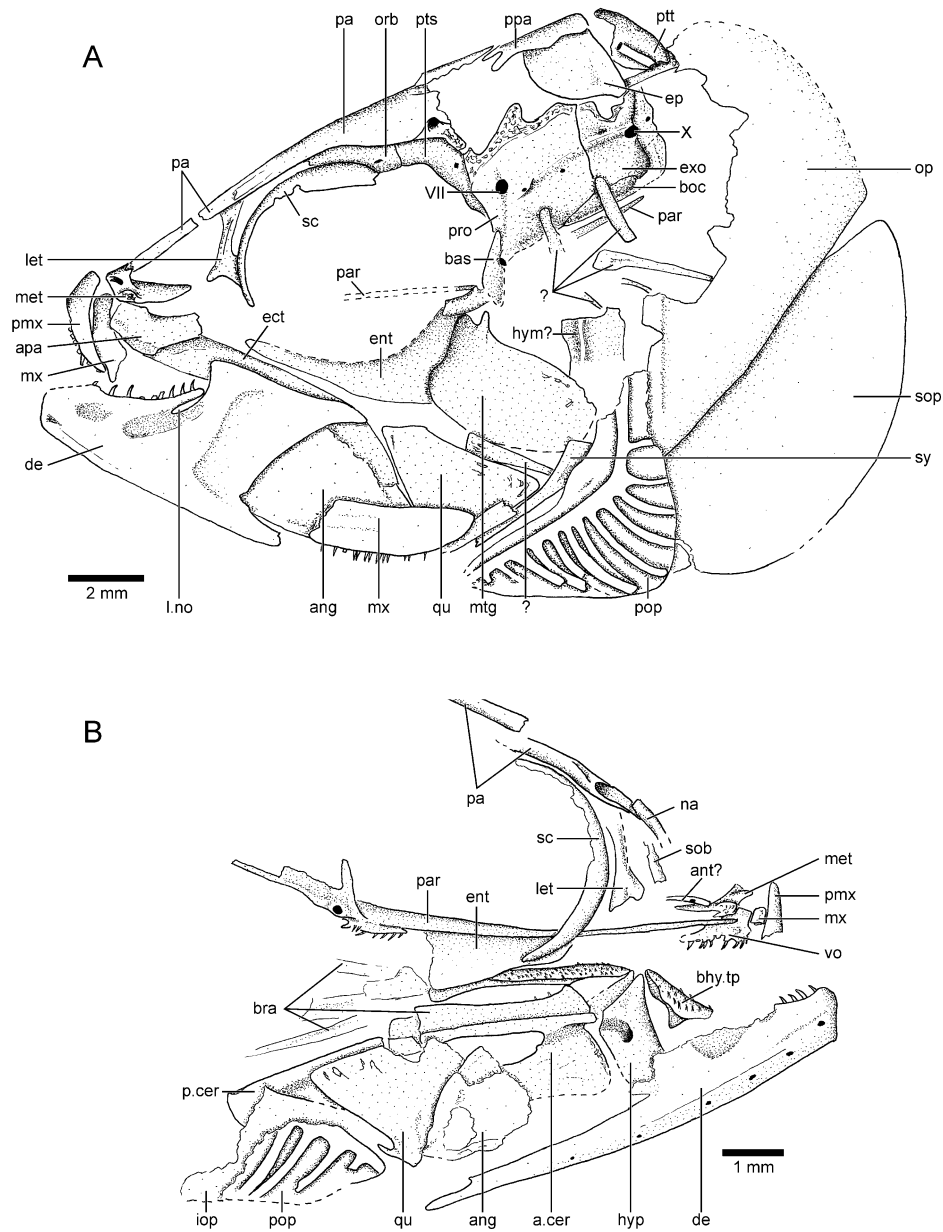
Abbreviations: **ang**, angular; **a.sc**, anterior sclerotic; **a.smx**, anterior supramaxilla; **br**, branchiostegal rays; **de**, dentary; **iop**, interopercle; **io1**, infraorbital 1; **io5**, infraorbital 5; **let**, lateral ethmoid; **met**, mesethmoid; **mx**, maxilla; **na**, nasal bone; **op**, opercle; **pa**, parietal bone; **pmx**, premaxilla; **pop**, preopercle; **p.sc**, posterior sclerotic; **p.smx**, posterior supramaxilla; **qu**, quadrate; **sob**, supraorbital bone; **sop**, subopercle; **suo**, suborbital.



**FIGURE 7.** *Leptolepis jaegeri* (NRM P 6483a, neotype) from Holzmaden. **A** photograph in lateral view (courtesy: L. Werdelin). **B** line drawing of the head in lateral view. **C** line drawing of left premaxilla. Abbreviations: **ang**, angular; **a.pr**, ascending process of premaxilla; **de**, dentary; **io1**, infraorbital 1; **io?**, infraorbital bone(s)?; **let**, lateral ethmoid; **l.no**, “leptolepid” notch; **op**, opercle; **pa**, parietal bone; **par**, **pmx**, premaxilla; parasphenoid; **qu**, quadrate; **r.pop**, right preopercle; **sob**, supraorbital bone; **sop**, subopercle; **te**, teeth.

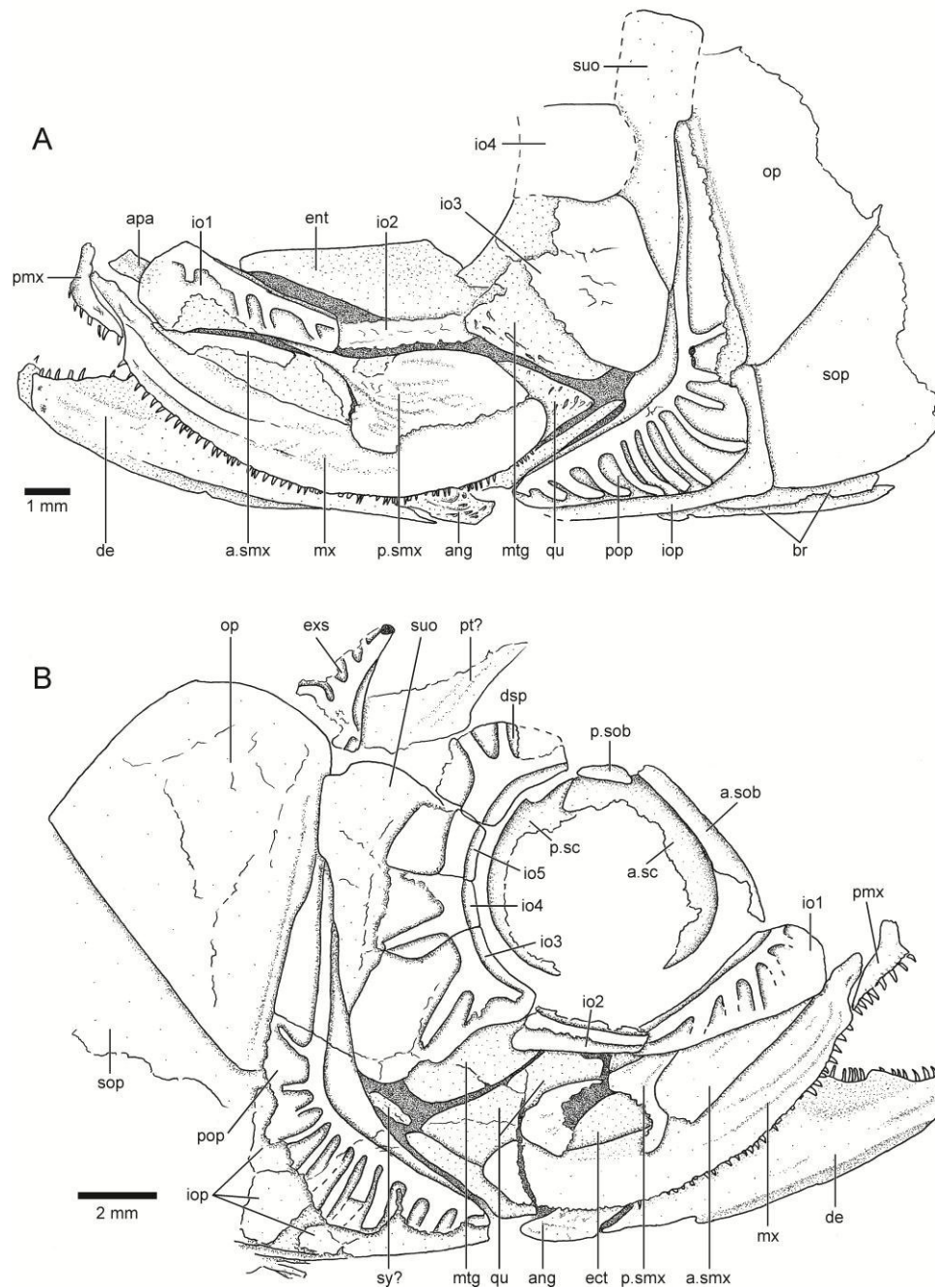


**FIGURE 8.** *Leptolepis jaegeri* (GG 431/1) from Dobbertin. **A** lateral view of right side, dashed areas indicate broken bones. **B** lateral view of left side. **C** dorsal view. Abbreviations: **ang**, angular; **apa**, autopalatine; **apl**, anterior pit line; **a.smx**, anterior supramaxilla; **br**, branchiostegal rays; **cl**, cleithrum; **de**, dentary; **dsp**, dermosphenotic; **exs**, extrascapula; **iop**, interopercle; **io1**, infraorbital 1; **io2**, infraorbital 2; **io3**, infraorbital 3; **io4**, infraorbital 4; **io5**, infraorbital 5; **met**, mesethmoid; **mpl**, middle pit line; **mx**, maxilla; **na**, nasal bone; **op**, opercle; **pa**, parietal bone; **pmx**, premaxilla; **pop**, preopercle; **ppa**, postparietal bone; **ppl**, posterior pit line; **pt**, pterotic; **ptt**, posttemporal; **p.qu**, posteroventral process of quadrate; **p.smx**, posterior supramaxilla; **qu**, quadrate; **sc**, sclerotic; **scl**, supracleithrum; **sob**, supraorbital bone; **sop**, subopercle; **so.c**, supraorbital sensory canal; **suo**, suborbital; **?**, unknown bone.

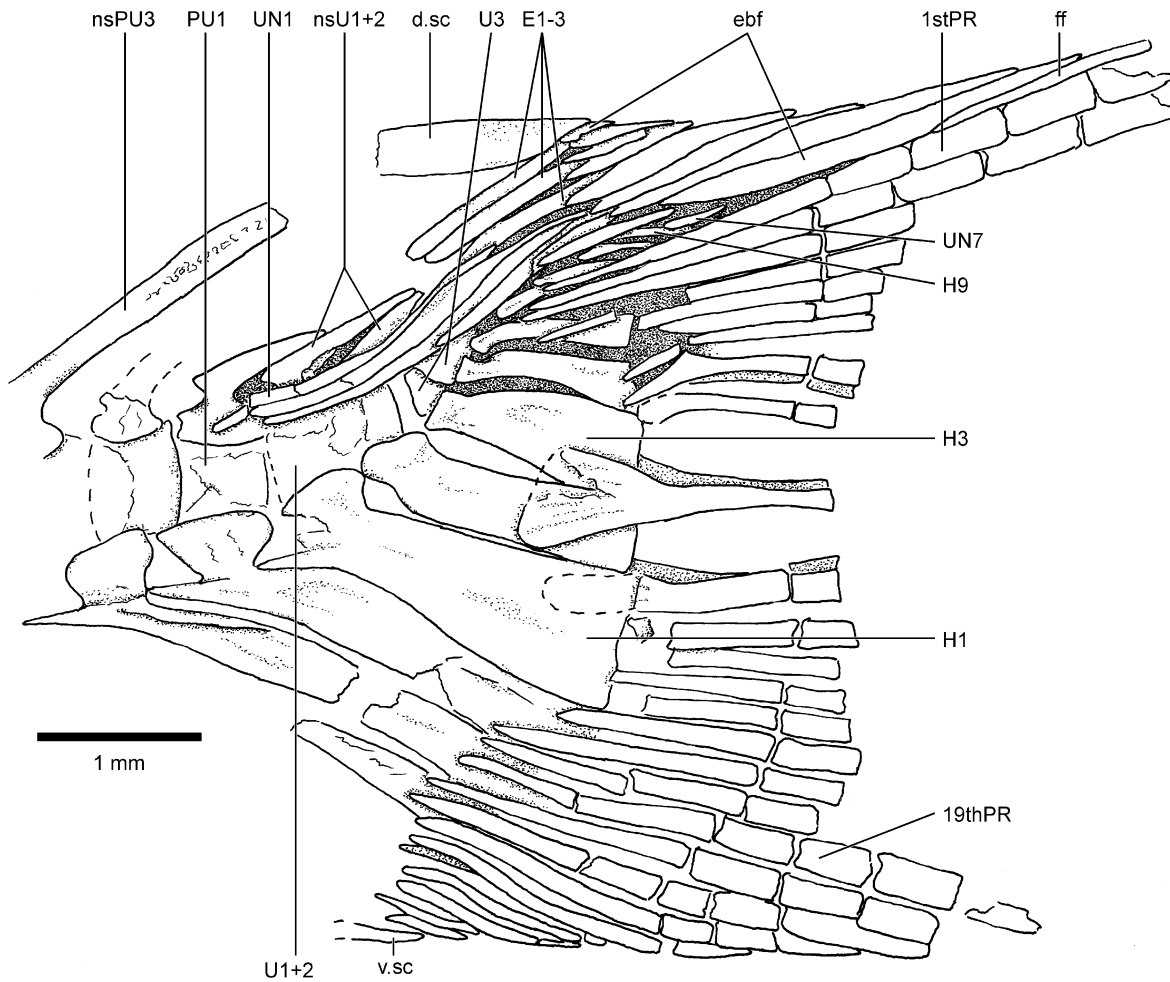


**FIGURE 9.** *Leptolepis jaegeri* (GG 431/9), from Grimmen. **A** GG 431/9a, lateral view of left side. **B** GG 431/9b, lateral view of right side. Abbreviations: **ang**, angular; **ant?**, antorbital?; **apa**, autopalatine; **a.cer**, anterior ceratohyal; **bas**, basisphenoid; **bhy.tp**, basihyal toothplate; **boc**, basioccipital; **bra**, displaced bones of branchial arches; **de**, dentary; **ect**, ectopterygoid; **ent**, entopterygoid; **ep**, epiotic; **exo**, exoccipital; **hym?**, hyomandibula?; **hyp**, hypohyal; **iop**, interopercle; **let**, lateral ethmoid; **l.no**, “leptolepid” notch; **met**, mesethmoid; **mx**, maxilla; **na**, nasal bone; **op**, opercle; **orb**, orbitosphenoid; **pa**, parietal bone; **par**, parasphenoid; **pro**, prootic; **pts**, pterosphenoid; **ppa**, postparietal bone; **ptt**, posttemporal; **sob**, supraorbital bone; **sop**, subopercle; **sy**, symplectic; **pmx**, premaxilla; **pop**, preopercle; **p.cer**, posterior ceratohyal; **qu**, quadrate; **sc**, sclerotic; **VII**, foramen for facial nerve; **vo**, vomer; **X**, foramen for vagus nerve.



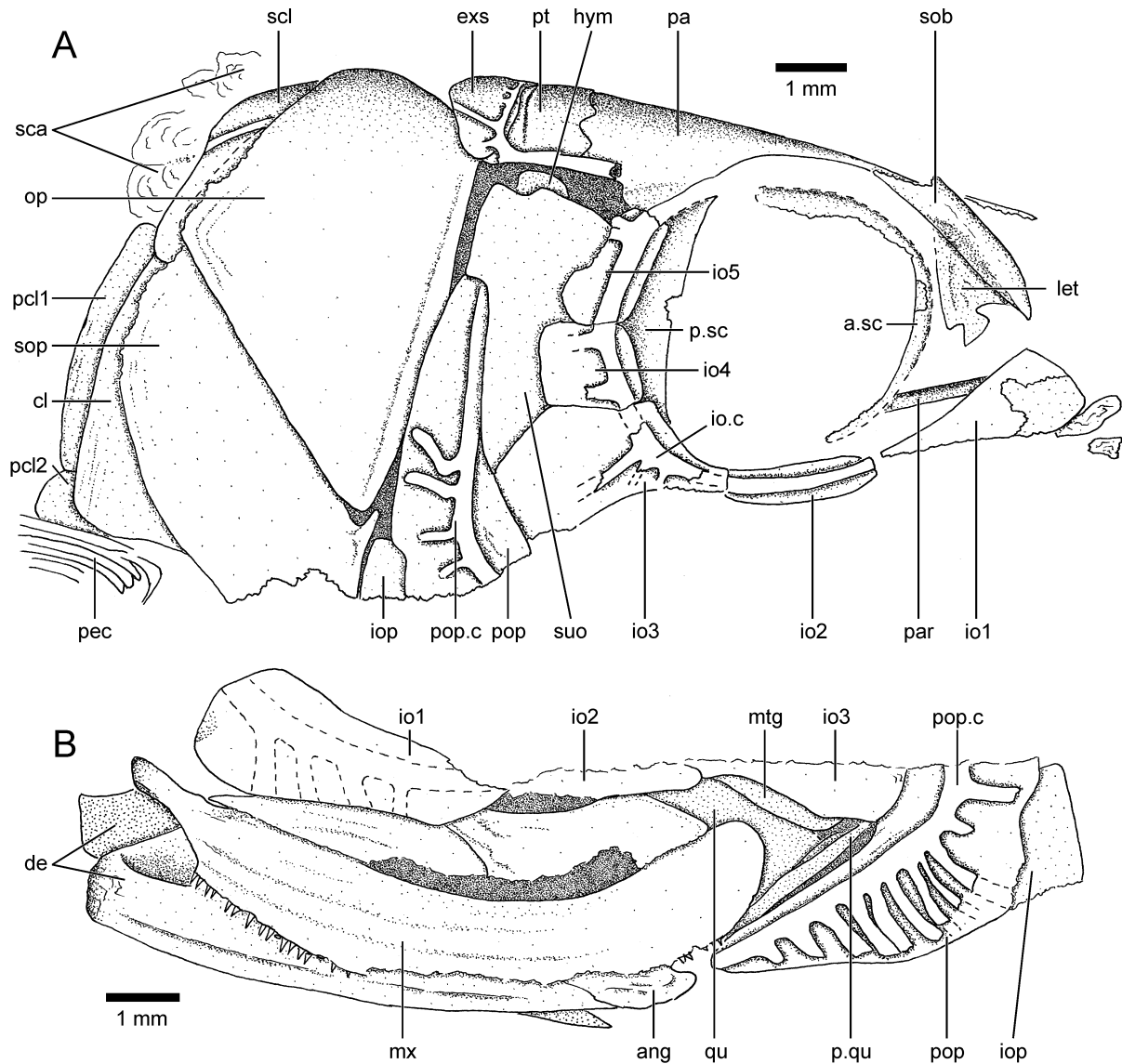


**FIGURE 10.** *Leptolepis jaegeri* from Grimmer. **A** GG 431/15 line drawing in lateral view. **B** GG 431/16 line drawing in lateral view. Abbreviations: **ang**, angular; **apa**, autopalatine; **a.sc**, anterior sclerotic; **a.smx**, anterior supramaxilla; **a.sob**, anterior supraorbital; **br**, branchiostegal rays; **de**, dentary; **dsp**, dermosphenotic; **ect**, ectopterygoid; **ent**, entopterygoid; **exs**, extrascapula; **iop**, interopercle; **io1**, infraorbital 1; **io2**, infraorbital 2; **io3**, infraorbital 3; **io4**, infraorbital 4; **io5**, infraorbital 5; **mtg**, metapterygoid; **op**, opercle; **pmx**, premaxilla; **pop**, preopercle; **pt?**, pterotic?; **p.sc**, posterior sclerotic; **p.smx**, posterior supramaxilla; **p.sob**, posterior supraorbital; **qu**, quadrate; **sop**, subopercle; **suo**, suborbital;

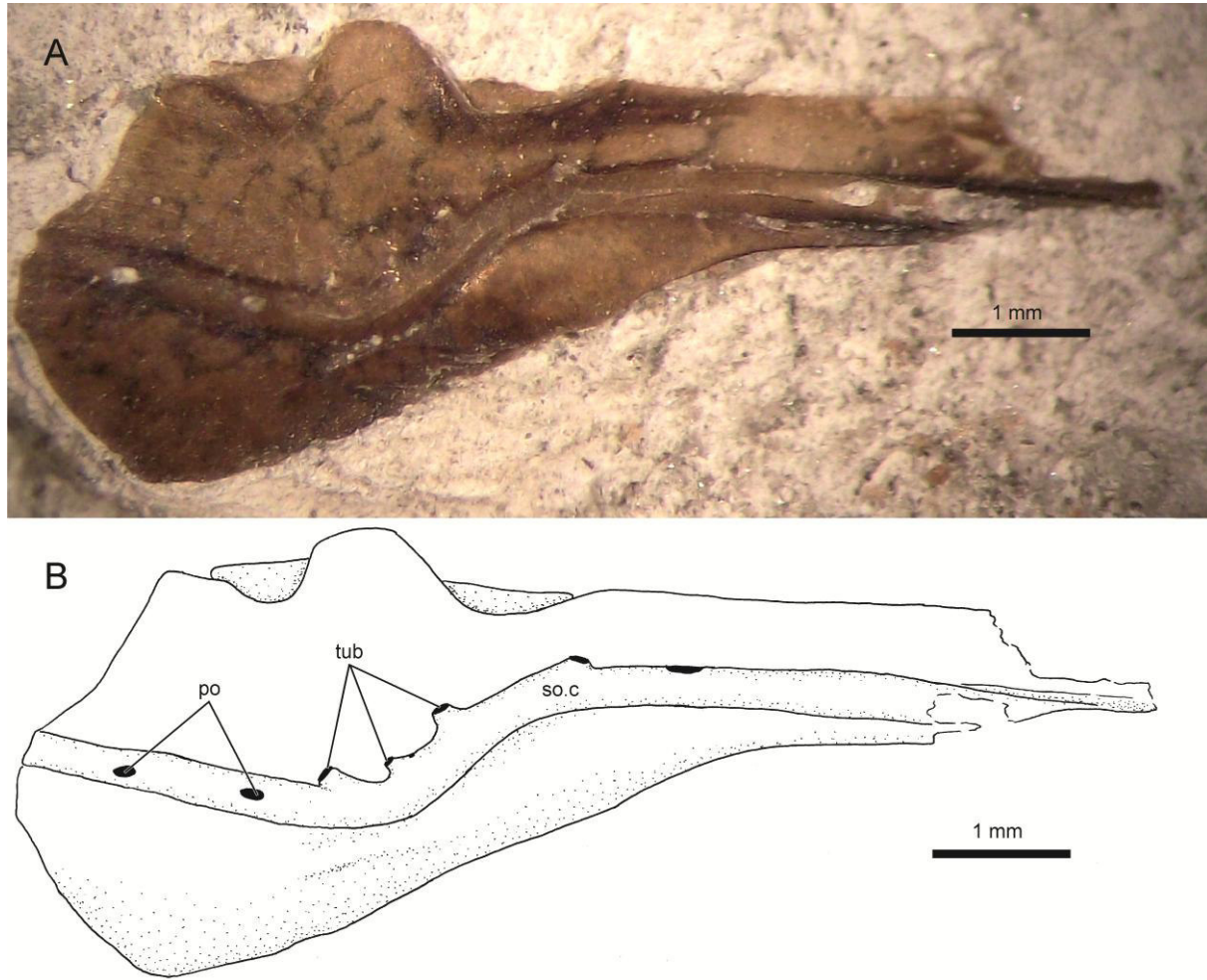


**FIGURE 11.** *Leptolepis jaegeri* (GG 431/10) from Grimmen. Line drawing of caudal skeleton.

Abbreviations: **d.sc**, dorsal caudal scute; **ebf**, epaxial basal fulcra; **E1-3**, epurals 1 to 3; **ff**, fringing fulcrum; **H1**, hypural 1; **H3**, hypural 3; **H9**, hypural 9; **nsPU3**, neural spine of preural vertebra 3; **nsU1+2**, neural spines of ural vertebra 1+2; **PU1**, preural vertebra 1; **UN1**, uroneural 1; **UN7**, uroneural 7; **U1+2**, ural vertebra 1+2; **U3**, ural vertebra 3; **v.sc**, ventral caudal scute; **1stPR**, first principal caudal ray; **19thPR**, 19th principal caudal ray.

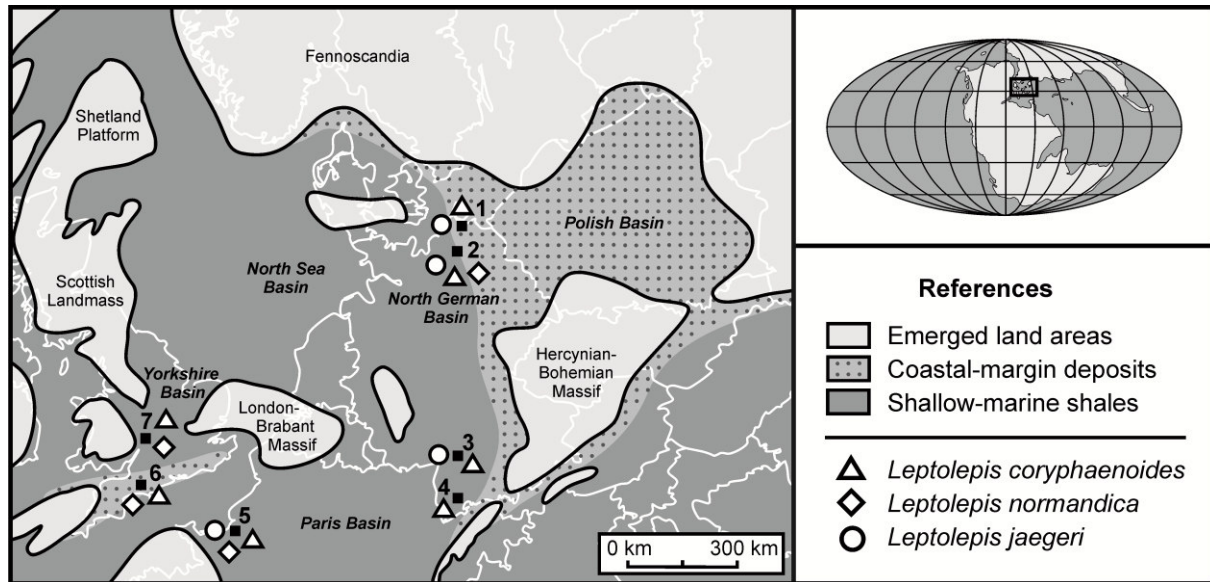


**FIGURE 12.** *Leptolepis* sp. 1 from Dobbertin. Line drawings of cranial bones. **A** GG 431/4a lateral view of right side. **B** GG 431/4b (same individual as in GG431/4a), lateral view of left side. Dashed lines indicate broken bones. Abbreviations: **ang**, angular; **a.sc**, anterior sclerotic; **cl**, cleithrum; **de**, dentaries; **exs**, extrascapula; **hym**, hyomandibula; **iop**, interopercle; **io.c**, infraorbital sensory canal; **io1**, infraorbital 1; **io2**, infraorbital 2; **io3**, infraorbital 3; **io4**, infraorbital 4; **io5**, infraorbital 5; **let**, lateral ethmoid; **mtg**, metapterygoid; **mx**, maxilla; **op**, opercle; **pa**, parietal bone; **pcl1**, postcleithrum 1; **pcl2**, postcleithrum 2; **pec**, pectoral fin; **pt**, pterotic; **pop**, preopercle; **pop.c**, preopercular sensory canal; **p.qu**, posteroventral process of quadrate; **p.sc**, posterior sclerotic; **qu**, quadrate; **sca**, scales; **scl**, supracleithrum; **sob**, supraorbital bone; **sop**, subopercle; **suo**, suborbital.

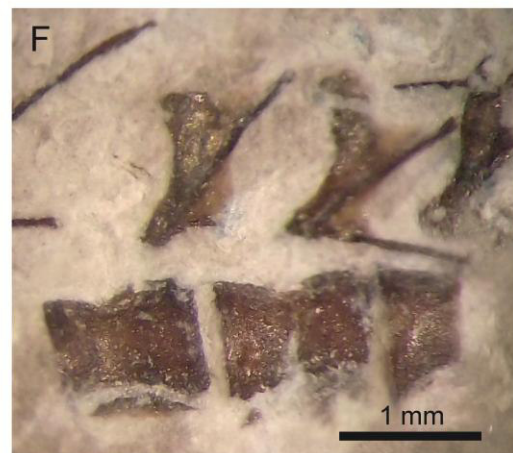
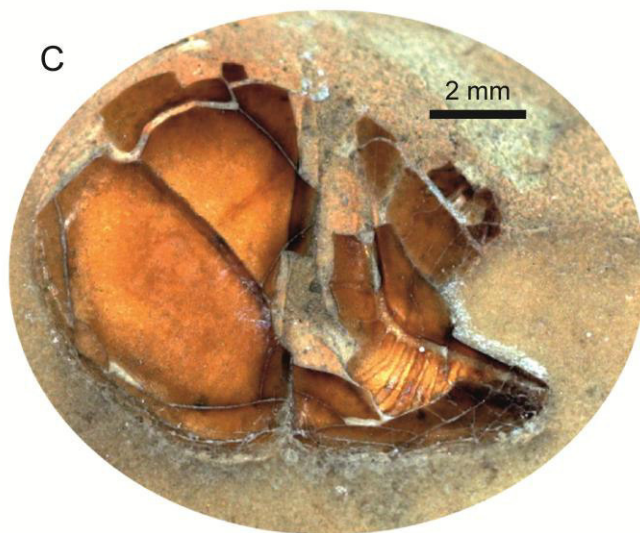
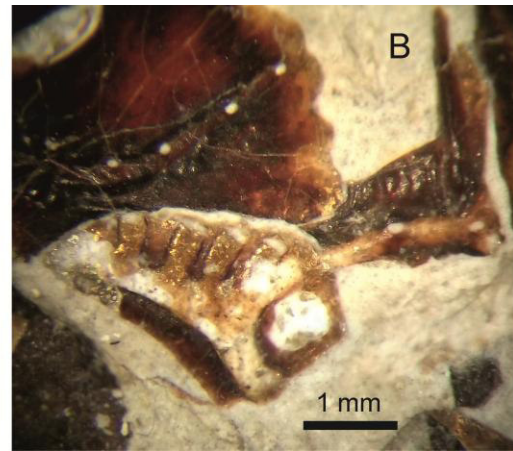


**FIGURE 13.** *Leptolepis* sp. (GG 431/21) from Grimmer, left parietal. **A** photograph in dorsal view. **B** Line drawing in dorsal view. Abbreviations: **po**, pores; **so.c**, supraorbital sensory canal; **tub**, tubules.





**FIGURE 14.** Late Early Jurassic palaeogeography of Europe (maps modified from Smith *et al.* 1994; Pieńkowski 2004; Röhl & Schmid-Röhl 2005; Dera *et al.* 2011) showing the distribution of selected Leptolepidae (data from Nybelin 1974; this contribution): **1** Grimmen, Mecklenburg-Western Pomerania, Germany; **2** Dobbertin, Mecklenburg-Western Pomerania, Germany; **3** Holzmaden, Baden-Württemberg, Germany; **4** Neudingen, Baden-Württemberg, Germany; **5** Normandy, France; **6** Iminster, Somerset, England; **7** Gloucestershire, England.



## **PLATE 1**

**A** Leptolepidae sp. 1 (GG 431/5a) from Dobbertin. Head in lateral view.

**B** Leptolepidae sp. 1 (GG 431/5a) from Dobbertin. Dermosphenotic, pterotic, and posterior part of parietal (covered with ethanol).

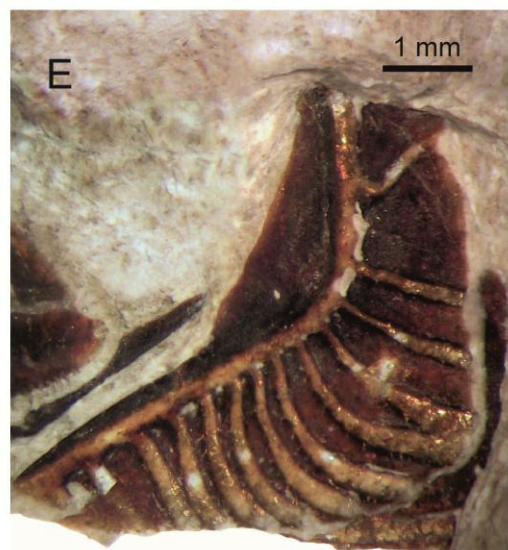
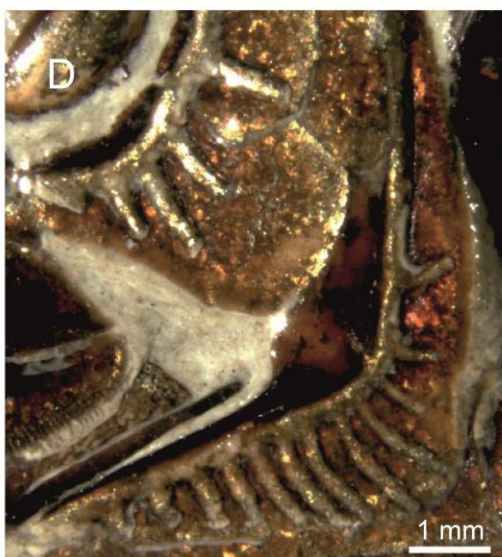
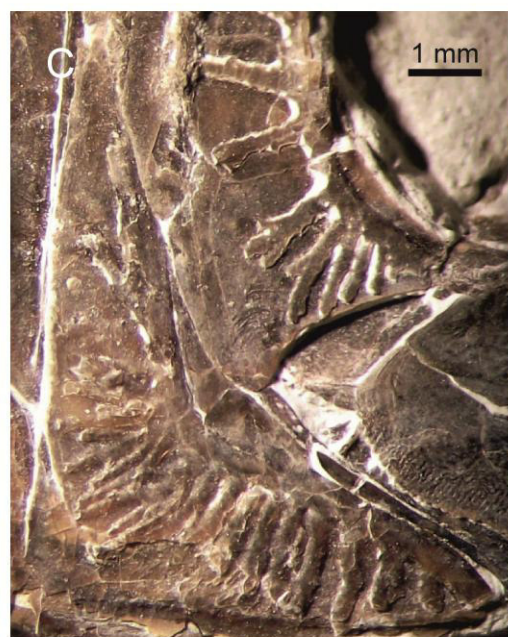
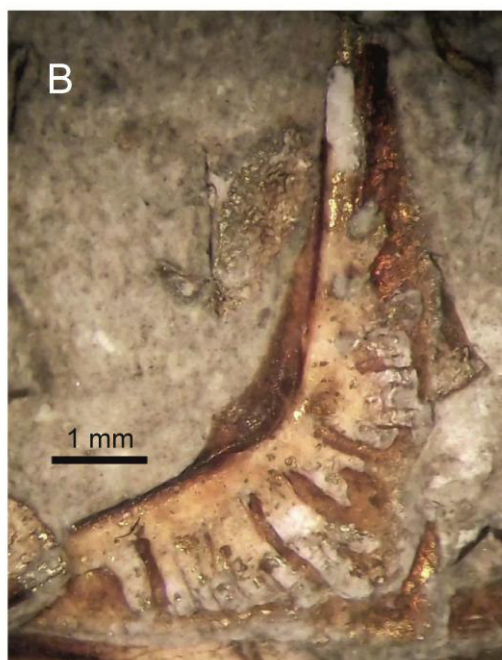
**C** *Proleptolepis*-like (MV 202612) in medial view, from Grimmen (covered with ethanol).

**D** *Leptolepis jaegeri* (GG 431/8b) from Grimmen. Dermosphenotic in medial view (covered with ethanol).

**E** *Leptolepis normandica* (GG 431/2) from Dobbertin. Specimen in lateral view.

**F** *Leptolepis normandica* (GG 431/2) from Dobbertin. Anterior abdominal vertebrae.





## **PLATE 2**

**A** *Leptolepis coryphaenoides* (GG 431/7) from Grimmen.

**B** *Leptolepis coryphaenoides* (GG 431/3) from Dobbartin. Left opercle (covered with ethanol).

**C** *Leptolepis coryphaenoides*, (GG 431/19) from Grimmen. Right opercle.

**D** *Leptolepis normandica* (GG 431/2a) from Dobbartin. Left opercle (covered with ethanol).

**E** *Leptolepis jaegeri* (GG 431/1) from Dobbartin. Left opercle (covered with ethanol).





### **PLATE 3**

Upper and lower jaws.

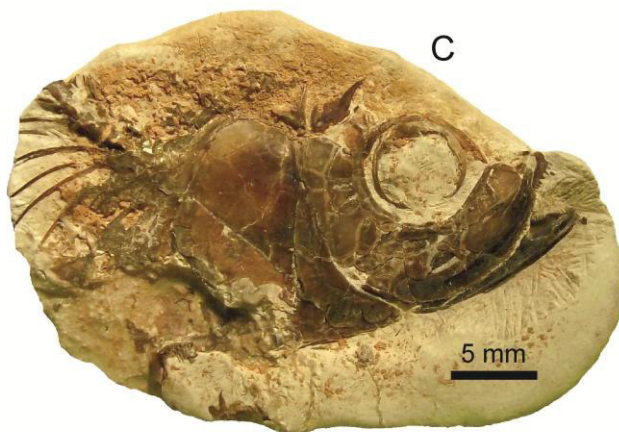
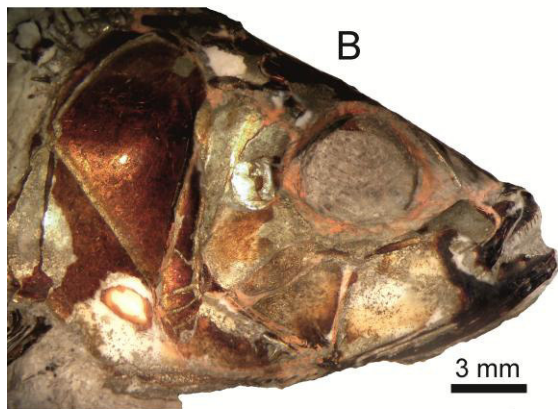
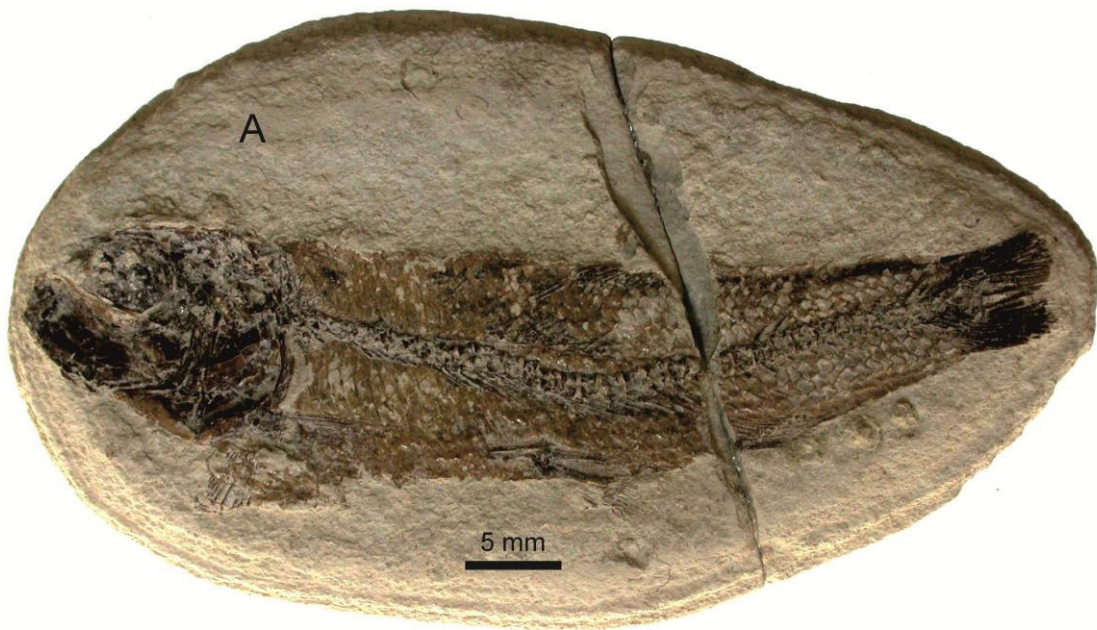
**A** *Leptolepis coryphaenoides* (GG 431/3) from Dobbartin (covered with ethanol).

**B** *Leptolepis coryphaenoides* (GG 431/19) from Grimmen (covered with ethanol).

**C** *Leptolepis normandica* (GG 431/2a) from Dobbartin.

**D** *Leptolepis jaegeri* (GG 431/15) from Grimmen (covered with ethanol).







## **PLATE 4**

**A** *Leptolepis jaegeri* (GG 431/10) from Grimmen (courtesy: J. Ansorge).

**B** *Leptolepis jaegeri* (GG 431/1) from Dobbartin. Head in right view (covered with ethanol).

**C** *Leptolepis jaegeri* (GG431/16) from Grimmen. Head in right view.

**D** Grimmen nodule with several bones of small teleosts, and the bivalve *Pseudomytiloides dubius* (GG 431/13) (covered with ethanol).

**E** *Leptolepis* sp. 1 (GG 431/17) from Grimmen.



MAXWELL, E. E., and S. STUMPF. In Press. Revision of *Saurorhynchus* (Actinopterygii: Saurichthyidae) from the Early Jurassic of England and Germany. European Journal of Taxonomy.

**PAPER 4**

Revision of *Saurorhynchus* (Actinopterygii: Saurichthyidae) from the Early Jurassic of England  
and Germany

Erin E. Maxwell<sup>1,\*</sup> and Sebastian Stumpf<sup>2</sup>

*Running Title:* Revision of *Saurorhynchus*

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*Disclaimer:* The present paper has not been submitted to another journal, nor will it be in the 6 months after initial submission to *EJT*. All co-authors are aware of the present submission.

*Abstract.* Saurichthyidae is a speciose group of fishes, ranging from the Late Permian to the Middle Jurassic. Early Jurassic saurichthyids are usually considered less morphologically disparate and taxonomically diverse than their Triassic counterparts, consisting of only two valid species. These were historically differentiated almost entirely based on cranial ratios, and both had stratigraphic ranges spanning the Early Jurassic. Here, we revise the Early Jurassic saurichthyid fishes of Europe based on restudy of the type material of *Saurorhynchus brevirostris* and *S. acutus*. We identify four species based on cranial osteology: *S. acutus*, *S. brevirostris*, *S. anningae* sp. nov., and *S. hauffi* sp. nov. *S. brevirostris* and *S. anningae* are known only from the Sinemurian of England, whereas *S. acutus* and *S. hauffi* share a broad European distribution during the Toarcian, from southwestern Germany to England. *Saurorhynchus anningae* and *S. brevirostris*, in particular, show disparity in such ecomorphologically important traits as cranial fineness, and tooth and jaw morphology. In contrast, *S. acutus* and *S. hauffi* show much lower levels of disparity, differing from each other in nostril morphology, dermal ornamentation, and position of the lateral extrascapular. The new species do not increase diversity estimates for *Saurorhynchus* in either the Sinemurian or Toarcian interval.

*Key Words.* Early Jurassic, Actinopterygii, Saurichthyidae, Posidonienschiefer Formation, Charmouth Mudstone Formation

## Introduction

Saurichthyidae is a speciose group of fishes, ranging from the Late Permian to the Middle Jurassic (Romano *et al.* 2012; Maxwell 2016). The genus *Saurichthys* encompasses all other named genera in phylogenetic analyses, but due to the long stratigraphic range and number of species, subgenera – monophyletic clades within *Saurichthys* – have been maintained for convenience (Maxwell *et al.* 2015). Jurassic saurichthyids are all considered to belong to the monophyletic *Saurorhynchus* species group (see Kogan (2016) for discussion of the higher taxonomic name *Saurorhynchus*), and are known almost exclusively from Europe, with a single reported occurrence from the Toarcian of Canada (Neuman & Wilson 1985; reviewed by Maxwell (2016)).

Saurichthyids are interpreted as piscivores based on both gastric contents and functional morphology (Rieppel 1985; Kogan *et al.* 2015; Renesto & Stockar 2015; Argyriou *et al.* 2016), and this is equally true of *Saurorhynchus* (Urlichs *et al.* 1994). However, Early Jurassic *Saurorhynchus* species appear to have been much smaller than some of their Triassic relatives (~30-50 cm vs. >100 cm in length: Romano *et al.* (2012)), and thus potentially occupied a lower trophic position. Although most saurichthyids have a long, slender body shape, *Saurorhynchus* is one of the deepest-bodied members of the clade (Maxwell *et al.* 2015). It is known only from fully marine deposits (Romano *et al.* 2012).

Historically, several species of *Saurorhynchus* have been proposed. Agassiz (1833-1843) described *S. acutus* based on a partial skull from the Toarcian of Whitby, UK. He also named “*Aspidorhynchus*” *walchneri* from the Toarcian of Baden, Germany, and *S. anningiae* from the Sinemurian of Lyme Regis, UK. The latter names were unaccompanied by descriptions, figures, or cited specimens and so are *nomina nuda*. Woodward (1895) later described a second valid species, *S. brevirostris*, based on a skull from the Sinemurian (Forey *et al.* 2010) of Lyme Regis.

*Saurorhynchus* material from the Southwest German Basin is by far the most abundant and best studied of the global occurrences. The material from Württemberg was first reported as *Aspidorhynchus walchneri* (Quenstedt 1843) and subsequently figured under the names *Belonostomus acutus* and *Saurorhynchus acutus* (Quenstedt 1856-1858; Reis 1892). However, Woodward (1895) later included all the Toarcian material from Württemberg in his new Sinemurian species *Belonorhynchus brevirostris*. When Hauff (1938) reviewed the

material from Holzmaden (Württemberg), he agreed with the species-level assessment of Woodward and classified the majority as *S. brevirostris* based on the short, deep mandible. The problem of holotypes and referred material coming from very different time intervals was compounded when Gardiner (1960) referred the bulk of the Sinemurian *Saurorhynchus* specimens to *S. acutus*. Thus, a situation was created where two species, distinguished primarily based on cranial fineness, had stratigraphic ranges spanning the Early Jurassic. This situation is especially problematic since relative cranial length, and fineness in particular, is a common axis of morphological differentiation among closely related saurichthyids (Maxwell *et al.* 2015).

Clarification of the alpha taxonomy of *Saurorhynchus* is desirable for several reasons. As the youngest representative of Saurichthyidae, a better understanding of morphology within this species group will be helpful in understanding loss of diversity and disparity within the family as a whole. From a more practical perspective, good description of the material from the classic localities of Germany and England will provide a list of characters useful for accurately identifying new finds, and thus for testing hypotheses relating to Early Jurassic biogeography and actinopterygian diversity. Moreover, *Saurorhynchus* falls in two very different positions in saurichthyid phylogeny depending on which species is studied: namely outside of the Middle Triassic Tethyan radiation when coded based on Sinemurian material referred to *S. acutus* (Wu *et al.* 2013), or nested within a clade of Middle-Late Triassic European species when coded based on Toarcian material referred to *S. brevirostris* (Maxwell *et al.* 2015). A detailed morphological study has the potential to reveal new phylogenetically informative characters that may help stabilize the position of the *Saurorhynchus* species group within Saurichthyidae. The objective of the current work is to clarify the taxonomic and morphological diversity of Early Jurassic saurichthyids from the UK and Germany following restudy of the type material of the two currently accepted species, *S. acutus* and *S. brevirostris*. We identify discrete morphological characteristics for use in specific identification of Early Jurassic saurichthyids.

## **Materials and Methods**

*Saurorhynchus* specimens from the following collections were studied, measured and photographed: GG, Institut für Geographie und Geologie, Ernst-Moritz-Arndt-Universität



Greifswald; GPIT, Geologisch-Paläontologisches Institut Tübingen; GZG, Geowissenschaftliches Zentrum, Georg-August-Universität Göttingen; MHH, Urwelt Museum Hauff; NHMUK, Natural History Museum (UK); NLMH, Niedersächsisches Landesmuseum Hannover; NMB, Staatliches Naturhistorisches Museum Braunschweig; PMU, Palaeontological collections, Museum of Evolution, Uppsala University; SMNS, Staatliches Museum für Naturkunde Stuttgart. Stratigraphic and geographic provenance were also noted, where available.

Skull bones are described using the established terminology for Saurichthyidae (e.g., Rieppel 1985) in order to facilitate comparisons within the family; however please note that some of the terminology does not reflect homology with more distantly related groups (e.g., sarcopterygians). Saurichthyids are characterized by a marginal dentition composed of large teeth alternating with smaller teeth (Griffith 1978). We use the term “laniary teeth” to refer to these larger teeth. We use the term “incisivlücken” (Hauff 1938) to describe the depressions along the marginal premaxilla and dentary into which the tips of the opposing laniary teeth fit when the jaws are closed.

## *Geology*

Early Jurassic saurichthyids are known from three formations in Germany and two from the UK, all fully marine. Less productive localities are known in France, Belgium, Luxembourg, and Canada (reviewed by Maxwell 2016); these will not be discussed here.

## UK

*Charmouth Mudstone Formation.* The *Saurorhynchus* material from the area around Lyme Regis re-examined in the present study consists of historical collections, and thus generally lacks specific stratigraphic information. Based on lithological comparisons, Forey *et al.* (2010) surmised that this material originated from the Black Ven Mudstone Member of the Charmouth Mudstone Formation (?*Caenisites turneri* to *Echioceras raricostatum* Zones; latest early Sinemurian to late Sinemurian).

*Whitby Mudstone Formation.* As with the material from Lyme Regis, the Toarcian material from Whitby also lacks detailed stratigraphic context. However, potential provenance

is restricted to the Whitby Mudstone Formation (early to middle Toarcian, *Dactylioceras tenuicostatum*, *Harpoceras serpentinum*, and *Hildoceras bifrons* Zones) (e.g., Benton & Spencer 1995).

## Germany

*Numismalismergel Formation.* The Numismalismergel Formation is a succession of marls and marly limestones extending from the *Uptonia jamesoni* Zone to the *Amaltheus stokesi* Subzone (early Pliensbachian to earliest late Pliensbachian) (Arp 2012). This formation has yielded a single *Saurorhynchus* lower jaw (SMNS 96082) exposed as part and counterpart in a broken geode from the Eastern Swabian Alb locality of Hüttlingen.

*Posidonienschiefer Formation.* In southwestern Germany, the Posidonienschiefer Formation consists of marls, marly clays, and intercalated limestones, and spans three early to middle Toarcian ammonite zones: the *tenuicostatum*, *serpentinum*, and *bifrons* Zones (Riegraf *et al.* 1984). It was deposited over 2.7-2.88 million years (Boulila *et al.* 2014). In the latest *tenuicostatum* Zone (*Dactylioceras semicelatum* Subzone), continuous deposition of organic-rich laminated black shales began, and continued through most of the *serpentinum* Zone (Röhl *et al.* 2001). Condensation horizons occur in the latest *serpentinum* Zone and the earliest *bifrons* Zone (Kauffman 1978; Röhl *et al.* 2001). The Posidonienschiefer Formation in the Southwest German Basin has been regionally subdivided into a series of beds denoted by Roman numerals with Arabic numerals as subscript. See Riegraf *et al.* (1984) for a correlation between this scheme and the ammonite zonation.

In southwestern Germany, *Saurorhynchus* specimens are known from the latest *tenuicostatum* Zone to the end of the *serpentinum* Zone (see Hauff (1938) for approximate stratigraphic distribution and raw abundance data), a range of approximately 1.5-1.62 million years (Boulila *et al.* 2014). Most of the material consists of isolated skulls and skull fragments, strongly compressed and exposed in lateral view; however rare articulated specimens have been recovered (Hauff 1938; Urlichs *et al.* 1994).

*Saurorhynchus* material is also known from the Posidonienschiefer Formation in northwestern Germany (Wunnenberg 1928; Thies 1985), from the area around Braunschweig and from the time-equivalent “Green Series” of Grimmen, northeastern Germany. Where detailed stratigraphic information is available, this material originates from the *Eleganticeras*

*elegantulum* and *Cleviceras exaratum* Subzones of the *serpentinum* Zone. Many of the specimens described by Thies (1985) are in private collections and not accessible for study, with the exception of NLMH 70598 (specimen SWG 1 of Thies), GZG.V.27931 (352-1 of Thies), GZG.V.27932 (352-2 of Thies), and GZG.V.27933 (352-3 of Thies).

*Jurensismergel Formation.* The Jurensismergel Formation consists of alternating marls and marly limestones of late Toarcian age (Nitsch *et al.* 09.10.2015). It is relatively poor in vertebrate fossils. A single partial saurichthyid rostrum recovered from the lower part of this formation is non-diagnostic below family level (SMNS 96946); a partial skull is also known from the locality of Mistelgau on the eastern edge of the Southwest German Basin (Schulbert 2013).

## Results

The type material of both currently recognized species, *Saurorhynchus acutus* and *S. brevirostris*, is from the UK. Here, we briefly review the two currently accepted species, followed by more detailed description of two new species identified during restudy of the referred material.

Actinopterygii Cope, 1887

Saurichthyidae Owen, 1860

*Saurorhynchus* Reis, 1892

***Saurorhynchus acutus*** (Agassiz, 1833-1843)

Figs 1A, 2D, 4D, 5A-B

*Belonostomus acutus* – Agassiz (1833-1843): 142, pl. 47a, fig. 4

*Acidorhynchus brevirostris* – Stensiö (1925), partim: 176

*Acidorhynchus brevirostris* – Hauff (1938), partim: pl. 22, fig. d.

*Acidorhynchus brevirostris* – Wenz (1967): pl. II, fig. A.

*Remarks.* Woodward (1895) outlined a series of characters to diagnose *S. acutus*, the majority of which cannot be observed in the type material and were drawn from observation of specimens from the much older Charmouth Mudstone Formation. Upon re-examination of the type material, Woodward (1899) clarified that the posterior (backwards) extension of the skull roof was the main feature uniting the Toarcian type and Sinemurian referred specimens, even though he had reservations that a species was likely to have such a long stratigraphic range.

Our observations suggest that the type specimen of *S. acutus* can be unambiguously differentiated from the older Sinemurian material by the short distance between the posterior edge of the orbit and the articular facet for the hyomandibula relative to the length of the orbit. These measurements fall along a single anteroposterior line, and thus are not expected to be significantly influenced by distortion. In addition, the narial opening in the *S. acutus* holotype specimen is narrower than in the material from the Charmouth Mudstone. The syntype specimen figured by Agassiz (1833-1843), NHMUK PV P 961a and its (unfigured) counterslab NHMUK PV P 36219 are non-diagnostic below family level. The holotype is consistent with a large number of *Saurorhynchus* specimens from the Toarcian of Germany, and when the additional anatomical information present in this referred material is considered it becomes clear that large differences exist between the Sinemurian and Toarcian specimens. The revised diagnosis is constructed based on the referred material from Germany, as well as on the holotype.

*Revised diagnosis.* Anterior narial opening narrow and elongate; maxilla strongly dorsoventrally compressed and ventrally deflected suborbitally such that the contact with the premaxilla occurs at an angle; posterior dorsal skull parallel to the long axis of the skull; postorbital segment approximately equal in length to the maximum depth of the lower jaw; parasphenoid edentulous ventral to the orbit; foramen for the internal carotid and efferent pseudobranchial arteries centered within the basisphenoid (sensu Wenz 1967); lateral extrascapular fused to lateral dermopterotic and not extending dorsal to the hyomandibula; posterior edge of the mandible strongly sinusoidal; angle between the posterior and ventral

edges of the mandible less than 80 degrees; subnarial laniary dentition absent; acrodin caps of the posterior laniaries straight.

*Holotype.* NHMUK PV P 4268, Toarcian of Whitby (UK) (Fig. 1A).

*Occurrence.* Early Jurassic, Toarcian, Whitby (type locality); Toarcian, *tenuicostatum* Zone, *semicelatum* Subzone to *serpentinum* Zone, Baden-Württemberg, Germany; *serpentinum* Zone, Lower Saxony, Germany (referred material).

*Referred material.* All referred material consists of isolated skulls. SMNS 56923 (Bisingen; Fig. 5A), SMNS 57039 (Holzmaden; Fig. 5B), SMNS 51009 ( $\epsilon$ II<sub>3</sub>, Ohmden), PMU 30009 ( $\epsilon$ II<sub>3</sub>, Holzmaden), SMNS 50268 ( $\epsilon$ II<sub>4</sub>, Ohmden), SMNS 87738 (Ohmden), SMNS 50924 ( $\epsilon$ II<sub>4</sub>, Holzmaden), MHH 17 ( $\epsilon$ II<sub>4</sub>, Holzmaden), SMNS 96927 ( $\epsilon$ II<sub>5</sub>, Ohmden), SMNS 96927 ( $\epsilon$ II<sub>5</sub>, Ohmden), SMNS 88007 (Holzmaden), SMNS 55324 ( $\epsilon$ II<sub>6</sub>, Holzmaden), PMU 30010 ( $\epsilon$ II<sub>6</sub>, Holzmaden), NHMUK PV P 3792 (Ohmden), NHMUK PV P 36222 (Ohmden), NHMUK PV P 36223 (Ohmden), SMNS 55319 (Ohmden), GPIT/OS/133 (Ohmden), GZG.V.27932 (*serpentinum* Zone, Schandelah).

*Description.* *Saurorhynchus acutus* is anatomically very similar to the Toarcian-aged *S. hauffi* sp. nov., described in detail in a subsequent section. The following brief description is designed only to differentiate the two species, to clarify general osteological nomenclature within *Saurorhynchus*, and to describe parts of the anatomy not preserved in *S. hauffi*.

No well-preserved postcranial material is available for *Saurorhynchus acutus*. Skull length (tip of rostrum to jaw joint, and corresponding to the length of the dermatocranium when measured along the dorsal midline) of the largest referred specimen is 125 mm (Suppl. Table 1). Assuming similar proportions to *S. hauffi*, fork length is estimated at 44 cm for large individuals of *S. acutus*. All the skulls examined in the course of this study were severely compressed, making the cranial sutures difficult to differentiate.

There is no clear evidence for interrostral bones. The anterior narial opening is an elongate anteroventrally inclined slit. When the skull is viewed dorsolaterally, it is evident based on the orientation and lipping along the anterior external narial opening that it is functionally situated more dorsally than the posterior narial opening. The suborbital bar of the maxilla is strongly dorsoventrally compressed ventral to the orbit and is also ventrally deflected such that it meets the rostromaxilla at an angle ventral to the external narial opening. This creates the impression of proportionately large, round orbits. The suture between the maxilla and premaxilla is interdigitating, differing from some of the Toarcian *Saurorhynchus* material from France and Northern Germany (Wenz 1967; Thies 1985). In some specimens, the ornamentation on the skull roof is drastically reduced and simplified, consisting mainly of pitting and being slightly more reticular only in the region of the parietals (e.g., Fig. 5B).

Unlike in *S. brevirostris*, the dorsal skull roof extends posteriorly without strong dorsal deflection. The element sutured to the posterolateral dermopterotic has been documented in *Saurorhynchus* by several authors, and has been variously interpreted as the squamosal (Reis 1892), fused suprascapular-supracleithrum (Gardiner 1960), or extrascapular (Hauff 1938). It does not participate in the cranial midline, and extends slightly further posteriorly than the dermopterotic. We interpret this element as a lateral extrascapular, following the homology discussion in Kogan and Romano (2016). The posterior elongation of the skull roof in *S. acutus* is partly accomplished through the posterior displacement of the lateral extrascapular relative to the dermopterotic (Fig. 5B,D). The lateral extrascapular and the dermopterotic are fused, such that it is difficult to see the suture along parts of its length. On the ventral surface of the dermal skull roof, two ridges run longitudinally between the orbits, dividing the interorbital surface into thirds. On the lateral side of the ridges, numerous foramina are located between the ridge and the ventral surface of the frontals. Such ridges have been interpreted as part of the neurocranium in the orbitotemporal region (Maxwell *et al.* 2016). The space between these ridges is filled with broken, cancellous bone tissue.

The palate is exposed in a single specimen (SMNS 50924). The dermopalatine extends as far anteriorly as the posterior external narial opening. It is convex in ventral view, broadening in a medial direction. It bears denticles; these are smaller and blunter than those of the other tooth bearing elements. Anteriorly, it articulates with the maxilla laterally; posteriorly it articulates with the parasphenoid medially and, posterior to this, the entopterygoid. There is no lateral palatal foramen, but because the parasphenoid is not

anteriorly expanded, a medial foramen exists between the anterior dermopalatine and parasphenoid. The ectopterygoid is very small and triangular. The portion of the parasphenoid posterior to the anterior edge of the orbit is edentulous; more anteriorly it bears small denticles.

The anteriormost point of the angular is located on the ventral half of the lower jaw. The ventral part of the angular-dentary suture is posteroventrally angled and straight, forming a simple 'v'. The teeth are largest at the midpoint of the rostrum and become much smaller anteriorly. In no specimens was corrugation of the collar ganoine observed.

The opercle is preserved in a single specimen (PMU 30010). This element is 13.6 mm high and 13.9 mm long, and ornamented with elongate pits radiating from the palatoquadrate articulation. In overall shape it is more ovate than in *Saurorhynchus brevirostris*.

***Saurorhynchus brevirostris*** (Woodward, 1895)

Figs 1B, 2A, 4B-E, 6A

*Belonorhynchus brevirostris* – Woodward (1895), partim: 17-18, pl. II, fig. 2.

*Saurorhynchus brevirostris* – Forey *et al.* (2010): 352, pl. 65, fig. 6.

*Revised differential diagnosis.* The diagnosis is constructed based on the holotype and referred material housed at the NHMUK. This species can be differentiated from all other *Saurorhynchus* species by the following combination of characters: short, deep skull, overbite consistently present (overbite slight or absent in *S. acutus*); posterior dorsal skull roof deflected dorsally relative to the long axis of the skull (parallel in *S. acutus*); postorbital segment approximately equal in length to the depth of the lower jaw; anterior narial opening large and triangular in outline with the apex directed toward the mandible (narrow and elongate in *S. acutus*); foramen for the internal carotid and efferent pseudobranchial arteries positioned posterolaterally within the basisphenoid, exposing the large foramen of the ophthalmica magna artery on the anterolateral surface of the basisphenoid; posterior edge of the mandible weakly sinusoidal (strongly sinusoidal in *S. acutus*); angle between the posterior



and ventral edges of the mandible less than 80 degrees; subnarial laniaries well-developed with acrodin caps directed lingually (subnarial laniaries absent and all acrodin caps straight in *S. acutus*); mandibular sensory canal closer to the dorsal than ventral edge of the posterior mandible. Opercle strongly wedge-shaped; lateral supracleithrum bearing prominent anterior process pierced by a foramen; pectoral radials well-ossified.

*Holotype*. NHMUK PV OR 40726, Lyme Regis, UK (Fig. 1B). A skull with partial pectoral girdle preserved in lateral view. This specimen is probably from the Charmouth Mudstone Formation, Black Ven Mudstone Member, latest early Sinemurian to late Sinemurian (Forey *et al.* 2010).

*Remarks*. Here we restrict usage of *S. brevirostris* to material from the Lower Lias. The anterior tip of the holotype skull is missing, but in the largest referred specimen skull length (tip of rostrum to jaw joint) is 86 mm (Suppl. Table 1). Assuming similar proportions to *S. hauffi*, fork length is estimated at up to 30 cm for *S. brevirostris*.

***Saurorhynchus anningae* sp. nov.**

Figs 1C, 2B, 3A, 4A, 6B, 7A

*Belonorhynchus acutus* – Woodward (1890): pl. 8, fig. 7.

*Belonorhynchus acutus* – Woodward (1895), partim: 14-15, pl. 2, fig. 1.

*Acidorhynchus acutus* – Stensiö (1925): 178, fig. 58.

*Saurorhynchus acutus* – Gardiner (1960), partim: 272-280, figs 19-21.

*Saurorhynchus acutus* – Forey *et al.* (2010): 350-352, pl. 65, fig. 5.

*Remarks.* Agassiz (1833-1843) [pt. 2, p. 143] originally coined the name “*Belonostomus anningiae*” for *Saurorhynchus* specimens from the Lower Lias of the UK, but failed to describe the material or identify a holotype. Subsequently, Woodward (1888) figured a non-diagnostic specimen as *B. anningiae*, but did not provide a description and subsequently synonymized *B. anningiae* with *Saurorhynchus acutus* (Woodward 1895). Thus, the name *Saurorhynchus anningiae* is considered a *nomen nudum*, and is still available for the longirostrine material from the Charmouth Mudstone Formation (Sinemurian) of the UK as per the original intention of Agassiz.

*Differential diagnosis.* This species can be differentiated from all other *Saurorhynchus* species by the following combination of characters: slender, elongate skull (length to depth greater than in *S. brevirostris*); posterior dorsal skull roof essentially parallel to the long axis of the skull; postorbital segment much longer than the depth of the lower jaw (almost double) and double the length of the orbit (unlike in *S. acutus*); anterior external narial opening teardrop shaped, widening ventrally; parasphenoid rostrum bearing small denticles ventral to the orbit; foramen for the internal carotid and efferent pseudobranchial arteries displaced posteriorly relative to the basisphenoid and almost entirely enclosed by the parasphenoid (unlike in *S. brevirostris*, *S. acutus*); posterior edge of mandible straight or only weakly sinusoidal, becoming gradually rounded ventrally; angle between the posterior and ventral edges of the mandible greater than 90 degrees; acrodin caps of posterior laniaries not directed lingually (unlike in *S. brevirostris*); opercle roughly triangular in shape, tapering ventrally.

*Etymology.* Name modified from that derived by Agassiz (1833-1843) in honour of Mary Anning, an important fossil collector from Lyme Regis.

*Holotype.* NHMUK PV P 3791, a skull and pectoral girdle preserved in lateral view (Fig. 1C).

*Occurrence.* This species is currently known only from the “Lower Lias” of Lyme Regis and Charmouth, UK. Based on lithological comparisons, Forey *et al.* (2010) surmised that the *S. anningae* material at the NHMUK originated from the Black Ven Mudstone Member of the

Charmouth Mudstone Formation (*?turneri* to *raricostatum* Zones; latest early Sinemurian to late Sinemurian). The single specimen for which more specific stratigraphic provenance is available, NHMUK PV P 27569 from the *Oxynoticer as oxynotum* Zone (late Sinemurian), falls within this range.

*Description.* The material referred herein to *S. anningae* has been well-described by Gardiner (1960) as *S. acutus*. The following focuses on details in which our interpretations differ from those of Gardiner, or those structures for which additional details can be noted.

The holotype skull is only 89 mm long, however the largest skull referable to *S. anningae* is 137 mm in length (Suppl. Table 1). Assuming similar proportions to *S. hauffi*, fork length is estimated at 48 cm in the largest individuals.

The antorbital rostrum is composed of the rostromaxilla, nasaloantorbitals, and frontals. There are two external narial openings, the anterior of which is teardrop shaped and somewhat narrower than reconstructed by Gardiner. The posterior narial opening is small and circular in outline. The suture between the maxilla and premaxilla occurs ventral to the nares. Between the maxilla and the nasaloantorbital is an extremely weakly ossified area that would have borne the infraorbital canal. This space corresponds to the lacrimal, and is more anteriorly extensive than in Gardiner's reconstruction. Gardiner noted interrostral elements in some of the specimens he examined; we could not confirm the presence of these separate ossifications during restudy of the material. He also noted separate nasal and antorbital ossifications; this observation appears to be based on post-mortem breakage.

The frontal plays a small role in the dorsal edge of the orbit (Fig. 3A). Posterior to the lateral frontal is a small, triangular dermosphenotic, which carries the infraorbital sensory canal and excludes the dermopterotic from the orbit. Ventral to the dermosphenotic is a curved element forming the posterior edge of the orbit and carrying the infraorbital sensory canal; this was identified by Gardiner as the dermosphenotic but is here considered to be the penultimate infraorbital. In some of the most heavily ossified specimens, this element can be quite robust and heavily ornamented.

The lateral extrascapular extends as far anteriorly as the hyomandibula-dermopterotic articulation, unlike in *S. acutus*, and more anteriorly than in Gardiner's reconstruction. A

dermohyal is present, fused to the lateral surface of the dorsal hyomandibula (as noted by Gardiner 1960). The opercle is also as described by Gardiner.

None of the specimens examined in the present study had a well-preserved ascending process of the parasphenoid, so the posterior position of the foramen for the orbital artery could not be confirmed. Anterior to the ascending process, the parasphenoid bears denticles along its ventral surface. In lateral view, the foramen for the internal carotid and efferent pseudobranchial arteries lies ventral to the opening for the posterior myodome (Fig. 4A), rather than ventral to the anterior basisphenoid as in Toarcian species (Wenz 1967; Thies 1985).

The mandible consists of three elements in lateral view, the dentary, angular and supraangular. The configuration of the angular-dentary suture reconstructed by Gardiner (1960) is incorrect, as argued elsewhere (Griffith 1962). The angular is extensively exposed along the lateral lower jaw, and extends anteriorly approximately as far as the anterior edge of the nasaloantorbital.

The dentary and rostrompremaxilla bear large (laniary) teeth, each flanked by a pair of smaller teeth. Laniary teeth are all positioned well anterior to the external narial openings. The posteriormost laniary teeth have relatively straight crowns with acrodin caps, which fit into corresponding pits in the opposite jaw (incisivlücken). Among the posteriormost laniary teeth, the upper teeth overlap the dentary, resulting in incisivlücken on the lateral lower jaw, whereas the lower jaw is slightly narrower and so the laniaries do not project outside the mouth, resulting in an absence of incisivlücken on the lateral surface of the posterior premaxilla (Fig. 6B). The largest teeth are found in the middle of the tooth row; the anteriormost laniary teeth are quite small, similar in size to the flanking teeth. All teeth consist of an acrodin cap, a lightly corrugated region of collar enamel, and an uncorrugated base. Plicidentine appears to be developed around the very base of the tooth, but does not form external ridges above the level of the jawbone. The difference in tooth shape observed between posterior and anterior teeth in *S. brevirostris* is absent.

Few specimens are available with well-preserved postcrania. The holotype specimen preserves a discrete supracleithrum bearing ornamentation on its external surface (Fig. 1C). A triradiate cleithrum is also present. NHMUK PV P 3790 preserves the most complete postcranium. The neural arch-like elements are small and blocky, similar to those of many saurichthyids. Anteriorly, neural spines are small or absent, and elongate anterior and

posterior zygapophyses overlap to form a lattice. In the region around the median fins, neural spines appear to be present, but poor preservation makes this homology interpretation questionable. Haemal spines are preserved in a 1:1 relationship with the neural arch-like elements along the posterior part of the block, dorsal to some poorly preserved anal axonosts. The haemal spines are elongate and bifurcate ventrally. Only a single scale row is present anterior to the median fins, the mid-dorsal scale row (Fig. 7A). The scales are smooth and needle-like, tapering at their anterior and posterior ends. Posterior to the anal axonosts, a mid-ventral scale row is also present.

*Saurorhynchus hauffi* sp. nov.

Figs 1D, 2C, 4C,F, 5C-D, 6C, 7B-D

*Belonostomus acutus* – Quenstedt (1856-1858): pl. 29, fig. 8.

*Belonorhynchus brevirostris* – Woodward (1895) partim

*Belonorhynchus brevirostris* – Woodward (1899): fig. 1

*Acidorhynchus brevirostris* – Hauff (1938) partim: pl. 22, figs b,c.

*Saurorhynchus brevirostris* – Hauff and Hauff (1981): fig. 76.

*Acidorhynchus brevirostris* – Thies (1985) partim: pl. 1, figs 1, 5.

*Saurorhynchus brevirostris* – Urlichs *et al.* (1994): fig. 79.

*Saurorhynchus brevirostris* – Böttcher (1998): fig. 7.15.

*Differential diagnosis.* This species can be differentiated from all other *Saurorhynchus* species by the following combination of characters: short, deep skull; posterior dorsal skull roof deflected dorsally relative to the long axis of the skull (parallel in *S. acutus* and *S. anningae*); postorbital segment approximately equal in length to the depth of the lower jaw (approximately twice as long in *S. anningae*); overbite slight or absent (unlike in *S. brevirostris*); maxilla not ventrally deflected under the orbit (unlike in *S. acutus*); coarse,

reticular ornamentation on the dermal bones of skull roof (ornamentation reduced in *S. acutus*); parasphenoid edentulous ventral to the orbit (unlike in *S. anningae*); foramen for the internal carotid and efferent pseudobranchial arteries centered ventral to the anterior basisphenoid and oriented laterally (unlike in *S. anningae* and *S. brevirostris*); foramen for the ophthalmica magna artery situated between two ridges on the anterior surface of the basisphenoid (anterior surface of basisphenoid flat and foramen oriented anterolaterally in *S. brevirostris*); posterior edge of mandible strongly sinusoidal (straight or only weakly sinusoidal in *S. brevirostris* and *S. anningae*); angle between the posterior and ventral edges of the mandible less than 80 degrees (more than 90 degrees in *S. anningae*); mandibular sensory canal positioned along the dorsal half of the posterior mandible; anterior narial opening ovate (elongate in *S. acutus*); subnarial laniary teeth absent (unlike in *S. brevirostris*); lateral supracleithrum bearing prominent anterior process pierced by a foramen.

*Etymology.* Named in honour of Bernhard Hauff, whose doctoral dissertation described the saurichthyid fishes from the Holzmaden region.

*Holotype.* SMNS 55057 (Fig. 1D), from the Posidonienschiefer Formation horizon  $\epsilon$ II<sub>4</sub> (uppermost *semicelatum* Subzone-lowermost *exaratum* Subzone), Zell unter Aichelberg, Germany. Although the skull of this specimen is not perfectly preserved, it was selected as the holotype based on the presence of extensive postcranial material.

*Referred material.* All referred material consists of isolated skulls, unless otherwise noted. SMNS 50075 ( $\epsilon$ II<sub>3</sub>, Ohmden), MHH 2 ( $\epsilon$ II<sub>3</sub>, Holzmaden), SMNS 51007 ( $\epsilon$ II<sub>4</sub>, Dotternhausen; Fig.6C), SMNS 53980 (Ohmden; Fig. 5D), SMNS 51888 ( $\epsilon$ II<sub>4</sub>, Ohmden; Figs 4F, 5C), SMNS 55302 ( $\epsilon$ II<sub>4</sub>, Holzmaden), SMNS 58394 ( $\epsilon$ II<sub>6</sub>, Dotternhausen), SMNS 96878/1 ( $\epsilon$ II<sub>10-12</sub>, Bad Boll), GZG.V.27931 (*exaratum* Subzone, Schandelah), NMB 373 (articulated skeleton, caudal region and median fins absent; *serpentinum* Zone, Schandelah); NLMH 70598 (*elegantulum* Subzone, Haverlahwiese), GG 20001 (*exaratum* Subzone, Grimmen; Fig. 3B), NHMUK OR 39153 (Toarcian, Whitby).

*Occurrence.* Early Jurassic, Toarcian, *tenuicostatum* Zone, *semicelatum* Subzone to *serpentinum* Zone, Baden-Württemberg, Germany; *serpentinum* Zone, Lower Saxony, Germany; *exaratum* Subzone, Western Pomerania, Germany; Toarcian, Whitby, UK.

*Description.* As with *S. anningae*, material now attributed to *Saurorhynchus hauffi* sp. nov. has been previously described (Hauff 1938; Thies 1985). However, as much of the material on which the initial descriptions were based is referable to *S. acutus*, redescription is necessary. *S. hauffi* exhibits lower jaw lengths of up to 115 mm (Suppl. Table 1); this would correspond to a fish approximately 40 cm in length.

The rostromaxilla is the dominant bone in the rostrum, dorsoventrally compressed at the anterior tip and becoming strongly laterally compressed posteriorly. The posterior rostromaxilla bears a ventral process that forms an overlapping suture with the maxilla ventral to the external narial openings, as well as a dorsal process that approaches the anterior narial opening. Between these two processes, an anterior ventral process of the nasaloantorbital bearing the sensory canal is enclosed. The rostromaxilla is ornamented with longitudinal grooves. Incisivlücken are lacking at the anteriormost tip. The rostromaxilla bears approximately 30 laniary teeth. The anterior teeth are very small, and become progressively larger towards the midpoint of the jaw. The sensory pit line runs along the lateral surface of the premaxilla immediately dorsal to tooth row. The sensory pits become increasingly obscured by incisivlücken anteriorly. The presence or absence of interrostrals could not be confirmed.

The maxilla extends anteriorly as far as the first laniary tooth. The suborbital bar is dorsoventrally compressed and bears denticles on its occlusal surface. Posterior to the orbit and anterior to the deepest point of the posterior lamina, a small concave embayment is present along the ventral edge of the maxilla. The postorbital lamina is ornamented with pits, the more posterior of which are elongated in such a way that they appear directed towards the suborbital bar.

The nasaloantorbital is triangular in lateral view. The posterior end encloses two external narial openings: a small, round posterior opening and a large, oval to reniform anterior opening (Fig. 5C). Between the two narial openings runs the supraorbital sensory canal. This canal splits into two branches ventrally; the junction is contained within the nasaloantorbital. Because the lacrimal is often damaged or missing, the ventral edge of the



nasaloantorbital is often clearly exposed and has a complex morphology dictated by the orientation of the canals. There is no evidence for separate ossifications of the nasal and antorbital. The nasaloantorbital articulates with the frontal dorsally and the premaxilla ventrally. Ornamentation can be quite strong in the around the narial openings, but becomes reduced anteriorly. Between the posterior narial opening and the orbit is an area of strong dermal ornamentation associated with an element posterior to the nasaloantorbital and excluding it from contact with the anterior orbital margin. This element appears to be anamesic and is tentatively identified as a supraorbital.

The orbital series is heavily ossified. The frontal is not excluded from the dorsal edge of the orbit (Fig. 3B), in contrast to previous reconstructions (Hauff 1938; Thies 1985). The lacrimal is weakly ossified and anteroposteriorly elongate, articulating with the maxilla ventrally, premaxilla anteriorly, and nasaloantorbital and supraorbital dorsally. It transmits the infraorbital sensory canal.

The dermosphenotic is variable in size, and forms the posterodorsal edge of the orbit. It carries the infraorbital canal. Ventral to the dermosphenotic, an elongate infraorbital forms the majority of the posterior orbit and carries the sensory canal. Infraorbitals along the ventral edge of the orbit are extremely weakly ossified (just a thin tube of bone surrounding the infraorbital canal, not in direct articulation with more anterior or posterior elements), and as such are rarely preserved.

Posterior to the dermosphenotic and fused with the lateral dermopterotic, an elongate, anamesic element is sometimes preserved. As with the dermosphenotic, it is somewhat variable in terms of size. It is often missing, and even when present the sutural contact can be very difficult to see. This element is most similar to the “supraspiracular plate” of *Birgeria groenlandica* in shape, position, and the absence of a sensory canal (Nielsen 1949). The ventral dermosphenotic in *B. stensioei* (Romano & Brinkmann 2009) was later homologized with the “supraspiracular plate” of *B. groenlandica*, however the ventral dermosphenotic should contact the infraorbital and carry the infraorbital canal (Poplin 2004), which the elongate element in *S. hauffi* does not. We tentatively consider this element to be a neomorph.

The dermopterotic is a broad dorsally convex sheet of bone making up the posterior skull roof (Fig. 3B). A descending process forms an interdigitating suture with the ascending process of the parasphenoid, and creates a notch into which slots the posterior end of the neomorph. Ornamentation generally consists of pits. There is an elongate pore medial to the

hyomandibular contact indicating that the medial process of the infraorbital sensory canal was present. Anterior to this canal are the parietals. These form a large, oval ossification. Ornamentation is reticular. No evidence of sensory canals or pores could be detected.

An elongate lateral extrascapular is sutured to the lateral dermopterotic, dorsal to the hyomandibula (Fig. 5D). It transmits the posterior infraorbital canal. A medial extrascapular is also present, and together they form a v-shaped articulation with the dermopterotic.

A dermohyal was present, as the dorsal portion of the hyomandibular bears the pitted ornamentation characteristic of dermal bones (Fig. 5D). A prominent posteriorly oriented joint surface on the ventrolateral dermopterotic articulates with the hyomandibula.

The palate is not exposed in any of the skulls attributable to this species, however the parasphenoid is often well-exposed in lateral view. The parasphenoid rostrum is curved and edentulous ventral to the orbit; the posterior stem is straight and dorsally displaced. The ascending process of the parasphenoid projects dorsolaterally, and is ornamented with fine striations. The foramen for the ophthalmic artery is closer to the anterior than posterior edge of the ventral ascending process (Fig. 1D). There is no expanded tooth plate ventral to the ascending process, and the entire parasphenoid posterior to the anterior margin of the orbit is edentulous. The posterior stem of the parasphenoid is broad. Anteriorly, a central ridge and two lateral ridges are present on the ventral surface of the posterior stem; posteriorly the central ridge diminishes such that it is absent at the posterior end.

Posterior to the orbit, the large foramen for the internal carotid and efferent pseudobranchial artery is contained within the basisphenoid (Fig. 4C,F). In one specimen (SMNS 55302) this foramen is subdivided into anterior and posterior components by a pillar of bone. On the anterior surface of the basisphenoid, the large foramen for the ophthalmica magna artery is recessed in a groove laterally bordered by cristae. Posterior to the basisphenoid, the space between the ascending process and basisphenoid has been interpreted as the posterior myodome. The posterior myodome appears to be roofed by an independent ossification dividing the posterior myodome from the trigeminofacialis chamber. Dorsal to this ossification, the foramen for the ramus oticus lateralis emerges from the neurocranium.

The preopercle is relatively narrow, with the dorsal ramus being narrower than the posterior ramus. It carries the preopercular sensory canal. Unlike previous reconstructions (Hauff 1938; Gardiner 1960; Thies 1985), it is clear that the preopercular sensory canal runs along the length of the dorsal ramus as well as the posterior ramus, as in *Saurichthys*. The

dorsal edge of the preopercle bears two tiny processes, the anterior of which is directed dorsoanteriorly and the posterior of which is directed anteromedially. These presumably articulate with the hyomandibula. The suture between the posterior ramus of the preopercle and the maxilla is easy to differentiate based on the change in the direction of ornamentation at the suture. The quadratojugal is rectangular in shape and meets the maxilla anteriorly and the preopercle dorsally and posteriorly. It contacts the articular ventromedially.

The lateral lower jaw consists of four elements: a tiny articular, a small supraangular, an expanded angular, and the dentary. The articular is in contact with the supraangular anteriorly. The dorsal portion of the angular is very thin and often eroded, making it appear that the sensory canal is located near the dorsal edge of this element. However, that is not the case. The mandibular sensory canal is contained entirely within the angular, and runs closer to the occlusal jaw margin than the ventral edge. It gives rise to descending canals. The posterior edge of the angular is strongly sinusoidal, and projects posterior to the jaw joint. The angular is also strongly ornamented with pitting and some reticulation; there are a series of “growth lines” running parallel to the ventral edge. The dentary itself has a woody texture, with the grain oriented parallel to the long axis of the mandible. The ventral part of the angular-dentary suture begins as at a posteroventrally angle dorsally, but becomes deflected ventrally.

The laniary teeth are simple cones bearing an acutely pointed acrodin cap, and in general appear to be entirely unornamented and lack any differentiation between tooth base and ‘collar ganoine’ (Fig. 6C). However, a single specimen (SMNS 51007) does show extremely faint corrugation of the collar region. We consider it possible that small maximum tooth size restricts expression of the corrugation of the collar region (the specimens of *S. anningae* clearly showing a corrugated collar region are among the largest specimens, far larger than the largest *S. hauffi*). Some variability in the degree of expression must also be assumed (Gardiner 1960).

## Postcranium

*Paired fins.* The supracleithra are seldom preserved. They appear to be thin and relatively straight dorsally, ventrally bearing a prominent anterior process that is pierced by a foramen on its medial surface. There is no equivalent to this ventral anterior process of the supracleithrum within *Saurichthys*, but this morphology is shared with *S. brevirostris*. The cleithra are triradiate, with a robust posterior ramus. The paired fins are even more rarely

preserved. In NMB 373, the pectoral fins are triangular in shape, with the longest and most robust lepidotrichia located close to the leading edge of the fin. A precise count of lepidotrichia is not possible. In no specimens referred to *S. hauffi* are pelvic fins preserved.

*Axial skeleton.* The following description is based on SMNS 55057. Sixty-three abdominal and 117 caudal neural arch-like elements are preserved anterior to the caudal fin, for a total of 180 (90 vertebral segments). As indicated by the low abdominal neural arch count, the abdominal-caudal transition is displaced anteriorly relative to the anal fin (Fig. 1D). The neural arch-like elements consist of a short, robust base, a moderately long prezygapophysis and a long, tapering neural spine. The medial surface of alternating neural arches is pierced by a foramen for the intersegmental vessel (Wu *et al.* 2015). The neural spines become longer more posteriorly in the column, and become forked immediately anterior to the insertion for the dorsal fin. Posterior to the dorsal fin, the neural spines are not forked for a short distance, but become bifurcated again and posteriorly inclined towards the caudal fin. The haemal spines are short, robust hooks anteriorly, lying dorsal to the gastric mass. Some of them are also bifurcated in this region. They lengthen at the end of the abdominal cavity, and become bifurcated or even trifurcated dorsal to the anal fin (Fig. 7C). Posterior to the anal fin, the haemal spines become shorter, more robust, and posteriorly inclined.

The median fins are not complete. Eight elongate dorsal axonosts are preserved in the holotype, and no dorsal lepidotrichia. The anteriormost axonost is not differentiated relative to more posterior axonosts. Twelve anal axonosts are preserved; again the anteriormost is not differentiated (Fig. 7B). The two forks of the neural and haemal spines insert on either side of an axonost. There is a gap between the axonosts and the lepidotrichia, and a single roundish, extremely weakly ossified baseost is preserved posteriorly. Four basal fulcra are present. The preserved lepidotrichia are unsegmented and are not distally bifurcated. Fringing fulcra are present, with an arrangement similar to that described by Stensiö (1925) for the pelvic fins of *S. ornatus*, but differing in that the fringing fulcrum and distal lepidotrichium appear to be fused, especially rostrally. When fused, a suture is present between the fulcra and underlying lepidotrichia. The posterior anal fin consists of finer, soft rays. A heavily ossified element associated with more poorly ossified endochondral fragments is also preserved in this region. It is bilaterally symmetrical, forked anteriorly with each of the two rami bifurcating again. The posterior end bears three small projections, with the medial projection being slightly longer than the other two. This element is tentatively interpreted as the axonost plate (Fig.

7B), based on comparisons in shape and position with the same element in *Birgeria* (Schwarz 1970). Caudal radials are preserved, but lepidotrichia are missing.

*Squamation.* The only scale row present anterior to the median fins is the mid-dorsal scale row. Scales in this row are elongate, needle-like, and unornamented (Fig. 7C). Posterior to the median fins, no scales are present, unlike in *S. anningae* in which, at minimum, the mid-ventral row is ossified. Immediately anterior to the caudal fin, the caudal peduncle is encased in robust mid-dorsal and mid-ventral scales, which grade into basal fulcra posteriorly (Fig. 7D). The scales in the caudal peduncle are more robust than the abdominal scales, but are also smooth in texture.

*Saurorhynchus* sp.

*Numismalismergel* jaw (SMNS 96082). SMNS 96082 is the only Pliensbachian record of *Saurorhynchus* of which we are aware. Although clearly referable to *Saurorhynchus*, SMNS 96082 is distinct from *S. anningae* in the shape of the posterior mandible and position of the mandibular sensory canal, and also from *S. brevirostris*, in that the posterior edge of the mandible is more strongly sinusoidal. However, there are few features to differentiate SMNS 96082 from the Toarcian-aged *S. acutus* and *S. hauffi*. One notable difference is the development of plicidentine, which is easily visible around all tooth bases in this specimen. In Toarcian saurichthyids, plicidentine, while present at least some of the time, does not appear to be as well-developed or consistently present. However, body size/absolute tooth size may be playing a role: with a mandibular depth of 23 mm, the Numismalismergel jaw ranks among the largest *Saurorhynchus* skulls from southwestern Germany (Suppl. Table 1; Hauff 1938). As in the Toarcian material, the collar region of the teeth does not appear to be corrugated.

Comparing the jaw depth to other Toarcian *Saurorhynchus* skulls, a skull length of between 114 mm (based on PMU 30009) and 143 mm (Hauff 1938) is predicted, which would result in an estimated fork length of 40–50 cm.

## Discussion

Given the high degree of morphological and size similarity, as well as geographic and stratigraphic overlap between *S. hauffi* and *S. acutus*, it is important to examine whether differences between these two taxa are not attributable to intraspecific variation or dimorphism. Hauff (1938) acknowledged this high degree of morphological variation within Toarcian saurichthyids from Baden-Württemberg, but was unable to identify discrete characters with which to delineate species. Variation in narial morphology is poorly documented among saurichthyid fishes, but does not appear to be pronounced within Triassic species or even between closely related species (Rieppel 1985). The shape of the anterior narial opening in *S. acutus* is unique among saurichthyids. In addition to the shape of the narial opening, differences in the position of the lateral extrascapular and reduced dermal ornamentation in *S. acutus* mean that it is in practice not too difficult to distinguish *S. acutus* and *S. hauffi* based on cranial remains. It is possible that more abundant postcranial remains for both species will reveal more concrete information regarding how these two highly similar taxa coexisted in apparent sympatry.

Within the material referred to *S. acutus*, two distinct patterns of cranial ornamentation are present: a reduced pattern and a more clearly developed pattern. This reduced pattern was described in a Toarcian saurichthyid by Woodward (1899), who attributed the reduction to abrasion during preparation. Abrasion cannot be ruled out among the Posidonia Shale material, especially as several specimens show clear tooling marks from preparation, however since all *S. acutus* skulls show reduced ornamentation relative to *S. hauffi*, it is possible that these differences in ornamentation may later prove to be of taxonomic relevance.

In contrast to the relative ecomorphological homogeneity of the Toarcian species, the Sinemurian-aged *S. anningae* and *S. brevirostris* are clearly differentiated based on a multitude of features, including cranial fineness, tooth morphology, and body size. *S. brevirostris* is smaller (~30 cm fork length vs. ~50 cm fork length in *S. anningae*) and shows heterodonty between the anterior and posterior teeth, as well as a pronounced overbite. Moreover, *S. brevirostris* has a shorter, deeper skull than *S. anningae*, as well as a narrower, more ventrally tapered opercle. The opercular shape differences observed between *S. anningae* and *S. brevirostris* correlate well with those associated with variation in body fineness in saurichthyids (Wilson *et al.* 2015), implying that *S. brevirostris* may also have had a shorter, deeper body than *S. anningae*. Differences in morphology and proportions are unlikely to be related to ontogeny, since there is overlap in size between the smallest *S. anningae* specimens and mid-sized *S. brevirostris* specimens (Suppl. Table 1).

*Saurorhynchus anningae* is the most divergent from the other *Saurorhynchus* species in a suite of morphological features including anatomy of the orbitotemporal region, specifically the position of the foramen for the internal carotid and efferent pseudobranchial arteries (Fig. 4). The polarity of this feature is unclear, but differs from the other three species. However, *S. anningae* also demonstrates a suite of features that are almost certainly plesiomorphic, based on their wide distribution among Triassic saurichthyids, such as the shape of the posterior and posteroventral mandible, denticles on the parasphenoid rostrum ventral to the orbit, and squamation developed further anteriorly in the caudal region.

*Saurorhynchus hauffi* also exhibits some unusual features not previously identified in the species group, including retention of fringing fulcra on the median fins (Fig. 7B). These structures were observed and described as a ganoine layer overlying the anterior distal lepidotrichia (Thies 1985). This character could not be evaluated in other species of *Saurorhynchus* as none of the fins are well-preserved. Their presence in a Jurassic saurichthyid is somewhat unexpected (Romano *et al.* 2012), and may have implications for the position of the *Saurorhynchus* species group within saurichthyid phylogeny.

This variation within fishes referred to *Saurorhynchus* may be responsible for the two very different positions of the *Saurorhynchus* species group in phylogenetic analyses of Saurichthyidae, namely outside of the Middle Triassic Tethyan radiation when coded based on *S. anningae* (Wu *et al.* 2013), or nested within a clade of Middle-Late Triassic European species when coded based on *S. hauffi* (Maxwell *et al.* 2015). The four Early Jurassic species discussed here are united by the presence of a dermohyal, dorsal position and multiple descending branches of the mandibular sensory canal and the pattern of dermal ornamentation composed of pitting and reticulation with a reduced or absent ganoine layer rather than parallel ganoine ridges and tubercles, to the exclusion of all Triassic saurichthyids, including other species in the *Saurorhynchus* species group. Bifurcating haemal spines (observed in *S. hauffi* and *S. anningae*) may also unite this group, although the postcranial axial skeleton is unknown for *S. acutus* and *S. brevirostris*. The ‘v’-shape of the angular-dentary suture, presence of incisivlücken, pattern of the dentition consisting of a laniary tooth flanked by a pair of smaller teeth, and unsegmented lepidotrichia are all found in some of the other members of the *Saurorhynchus* species group, i.e., *Saurorhynchus deperditus*, *S. striolatus*, and *S. calcaratus* (pers. observ., Griffith 1959, 1962, 1977).

*Taphonomy.* Beardmore and Furrer (2016b) analyzed the taphonomy of saurichthyid fishes from the Middle Triassic Monte San Giorgio lagerstätte, and this study provides a basis for comparison with the taphonomic patterns observed for the Posidonia Shale saurichthyids. Specifically, Beardmore and Furrer (2016b) report frequent isolation of the head unit from the postcranium, then loss of the opercles, followed by loss of the mandible. This taphonomic gradient is associated with increasing water depth and decreasing sedimentation rates between the two formations studied (Meride and Besano Formations). The low degree of skeletal completeness observed in the Posidonienschiefer Formation saurichthyids, combined with high prevalence of the head unit in isolation, agrees well with the findings of Beardmore and Furrer (2016b) for the Besano Formation in terms of preservation, water depth, and sedimentation. In the latest *tenuicostatum* Zone, a time corresponding to sea level lowstand (Röhl & Schmid-Röhl 2005), water depths are estimated at 50 m or less in the southwest German Basin, gradually deepening to 100–150 m by the latest *serpentinum* Zone (Riegraf *et al.* 1984; Röhl *et al.* 2001). Sedimentation rates for the *serpentinum* Zone are estimated at an average of 2 mm compacted sediment / kyr at the Holzmaden locality (Martill 1993), an order of magnitude less than that of the Besano Formation and potentially explaining the much lower frequency of complete specimens and skull units associated with opercles, or even mandibles, in the Posidonienschiefer Formation. Additional loss of completeness may be related to current activity (Hofmann 1958; Brenner & Seilacher 1978; Kauffman 1978, 1981; Riegraf *et al.* 1984; Beardmore *et al.* 2012; Reisdorf *et al.* 2012; Beardmore & Furrer 2016a).

*Palaeobiogeography.* Both of the *Saurorhynchus* species from the Southwest German Basin (*S. acutus* and *S. hauffi*) are also represented in the Toarcian fish fauna from the Northwest German Basin and the Cleveland Basin (Whitby, UK). Although the skulls from Whitby lack detailed locality information, the holotype skull is in matrix containing a mass occurrence horizon of *Pseudomytiloides dubius*, suggesting a stratigraphic origin from the *serpentinum* Zone, *exaratum* Subzone (Caswell & Coe 2013), and thus is probably coeval with the material from Germany. In other words, both species shared a broad distribution in Europe in the Toarcian immediately following the onset of the early Toarcian Oceanic Anoxic Event. This pattern of broad faunal distribution within Europe during the *serpentinum* Zone in particular has been noted for ammonites, fishes, and some marine reptiles (Godefroit 1994; Benson *et al.* 2011; Dera *et al.* 2011; Wretman *et al.* 2016; Konwert & Stumpf In Review), but see Maisch and Ansorge (2004) who argue in favour of faunal provincialism.



## Conclusion

Four valid species of saurichthyid fishes were present in the Early Jurassic of Europe, *Saurorhynchus acutus*, *S. anningae*, *S. brevirostris* and *S. hauffi*. Of these, *S. brevirostris* and *S. anningae* are known only from the Sinemurian of England, whereas *S. acutus* and *S. hauffi* are restricted to the Toarcian but share a broad distribution within Europe. All species are characterized by unambiguous discrete morphological features that will be of assistance in identifying new finds of *Saurorhynchus* and improving our understanding of diversity and disparity in the youngest saurichthyids.

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Fig. 1. Holotype specimens of Early Jurassic saurichthyids. **A.** *Saurorhynchus acutus* (NHMUK PV P 4268). **B.** *Saurorhynchus brevirostris* (NHMUK PV OR 40726). **C.** *Saurorhynchus anningae* sp. nov. (NHMUK PV P 3791). **D–E.** *Saurorhynchus hauffi* sp. nov. (SMNS 55057). Photos A–C © The Trustees of the Natural History Museum, London. Scale = 20 mm (A,C); 50 mm (E).

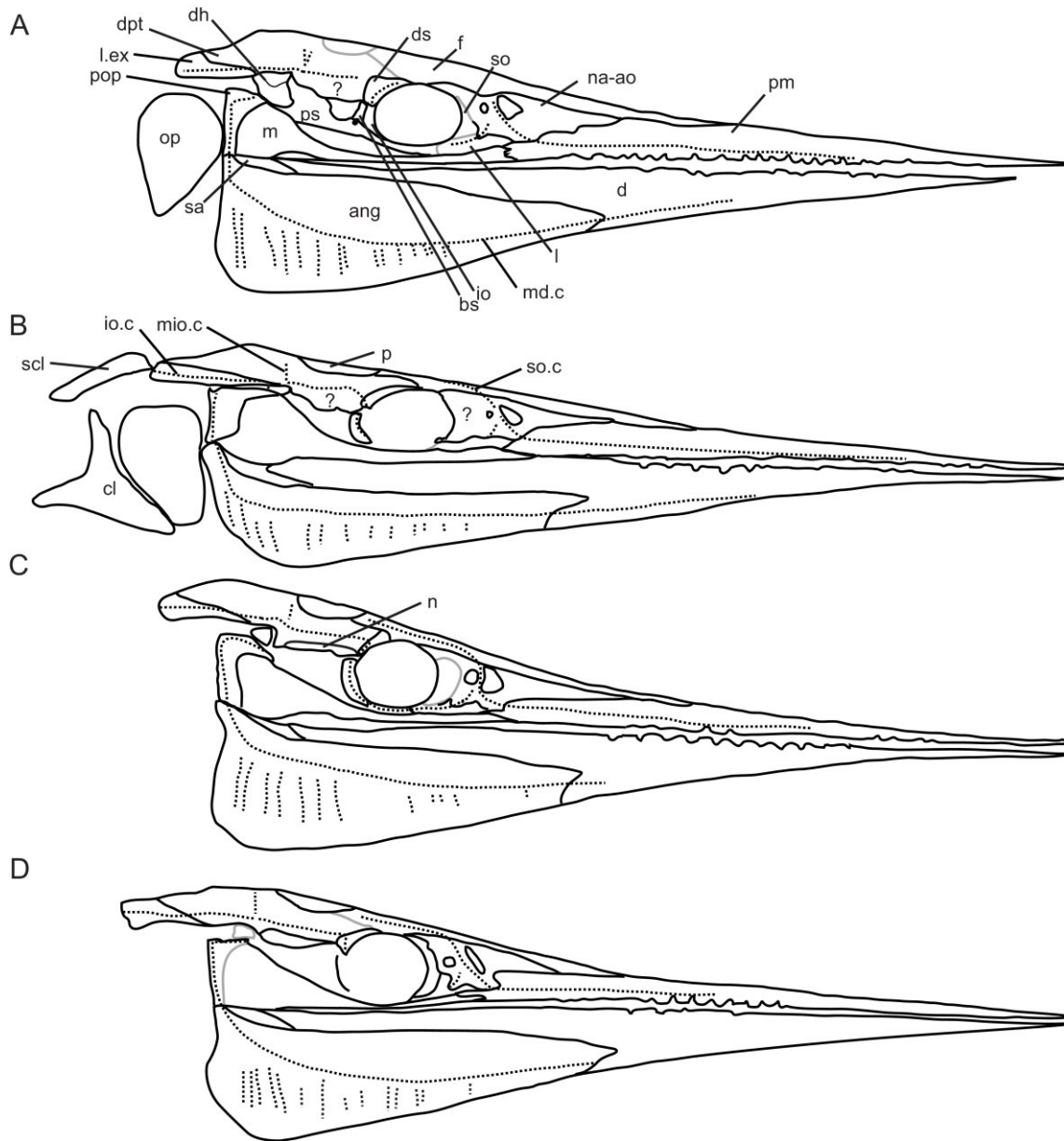


Fig. 2. Reconstruction of the dermal skull in Early Jurassic saurichthyids. **A.** *Saurorhynchus brevirostris*. **B.** *Saurorhynchus anningae* sp. nov. **C.** *Saurorhynchus hauffi* sp. nov. **D.** *Saurorhynchus acutus*. Not to scale. Dashed lines indicate sensory canals, grey lines indicate bones that were present but where the exact location of the sutural contact is unclear, and question marks indicate areas of uncertainty. Abbreviations: ang, angular; bs, basisphenoid; cl, cleithrum; d, dentary; dh, dermohyal; dpt, dermopterotic; dsp, dermophenotic; f, frontal; io, infraorbital; io.c, infraorbital sensory canal; l, lacrimal; l.ex, lateral extrascapular; m, maxilla; md.c, mandibular sensory canal; mio.c, medial branch of the infraorbital sensory canal; n, neomorph; na-ao, nasaloantorbital; op, opercle; p, parietal; pm, rostromaxilla; pop, preopercle; ps, parasphenoid; sa, supraangular; scl, supracleithrum; so, supraorbital; so.c, supraorbital sensory canal.



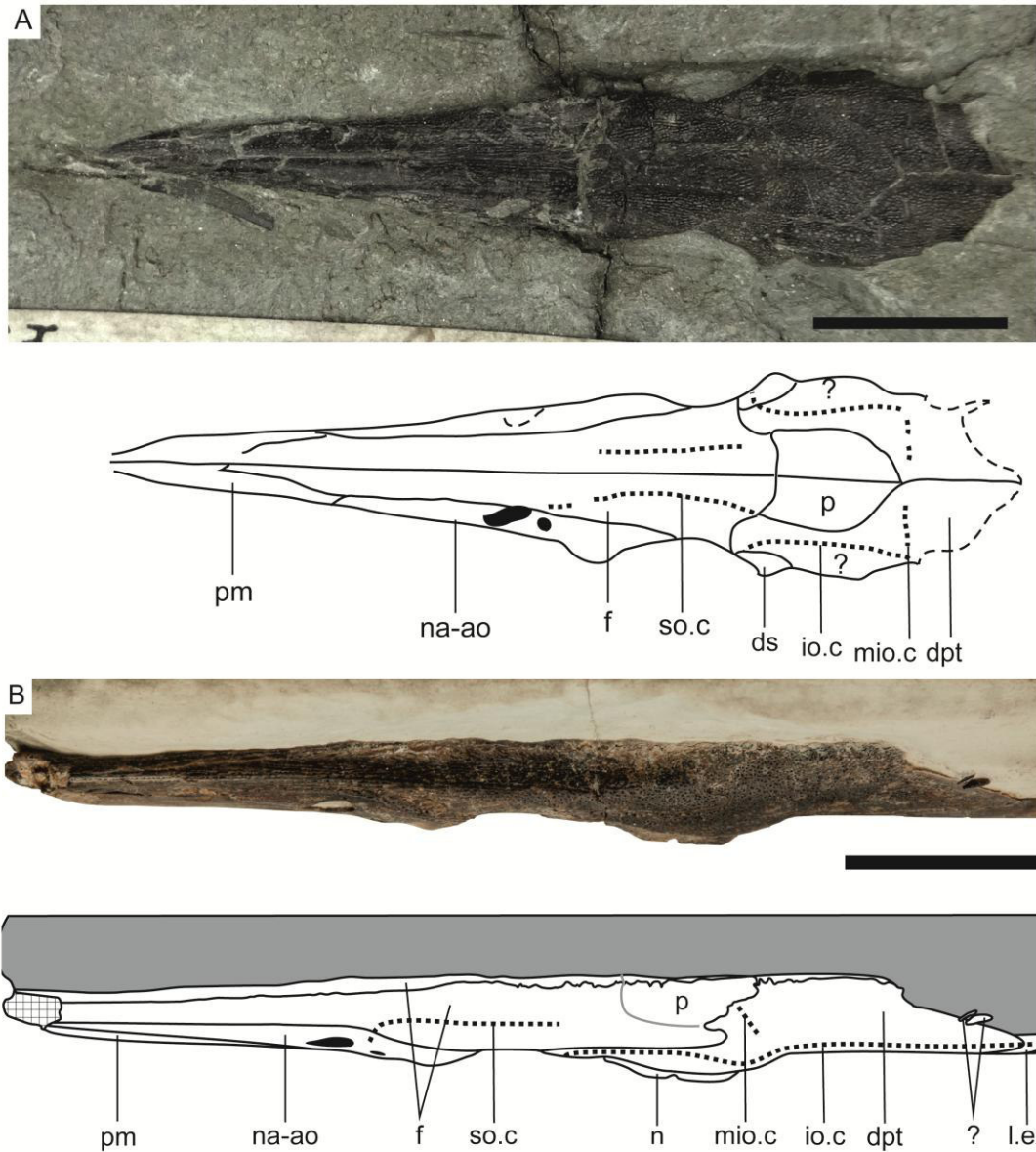


Fig. 3. Dorsal skull roof. **A**, *Saurorhynchus anningae* sp. nov. (NHMUK PV P 964); note that this skull has been dorsoventrally compressed. Photo © The Trustees of the Natural History Museum, London. **B**, *Saurorhynchus hauffi* sp. nov., three-dimensionally preserved skull GG 20001. Scale bar = 10 mm. Fine dashed lines indicate sensory canals, large dashes indicate broken or incomplete areas; grey lines indicate bones that were present but where the exact location of the sutural contact is unclear, and question marks indicate areas of uncertainty. Abbreviations: dpt, dermopterotic; dsp, dermophenotic; f, frontal; io, infraorbital; io.c, infraorbital sensory canal; l.ex, lateral extrascapular; mio.c, medial branch of the infraorbital sensory canal; n, neomorph; na-ao, nasaloantorbital; p, parietal; pm, rostrompremaxilla; so.c, supraorbital sensory canal.

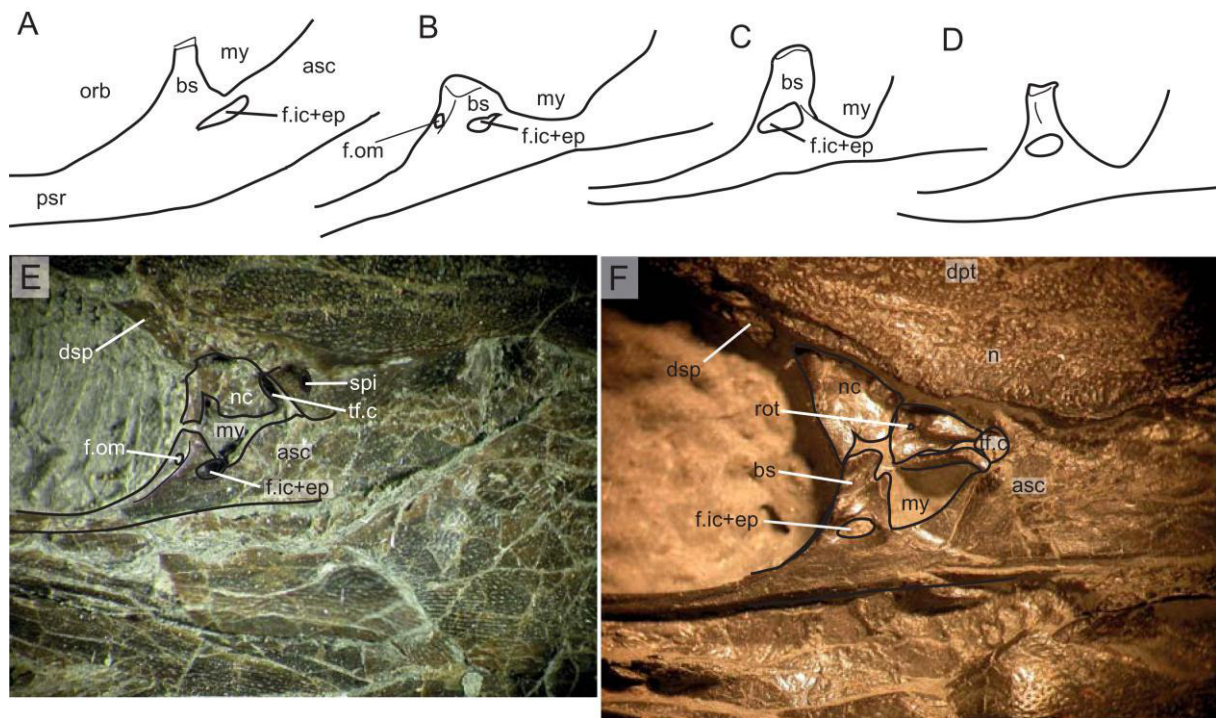


Fig. 4. Orbitotemporal region, illustrating variation in the braincase of Early Jurassic saurichthyids. **A.** *Saurorhynchus anningae* sp. nov. (based on NHMUK PV P 36227). **B, E.** *Saurorhynchus brevirostris* (photo is of NHMUK PV P 4878, mirrored). **C, F.** *Saurorhynchus hauffi* sp. nov. (photo is of SMNS 51888, mirrored). **D.** *Saurorhynchus acutus* (based on SMNS 87737). Photo E © The Trustees of the Natural History Museum, London. Scale (E–F) = 2 mm. Abbreviations: asc, ascending process of the parasphenoid; bs, basisphenoid; dpt, dermopterotic; dsp, dermosphenotic; f.ic+ep, foramen for the internal carotid artery and efferent pseudobranchial artery; f.oma, f.om, foramen for the great ophthalmic artery; my, posterior myodome; n, neomorph; nc, neurocranium; orb, orbit; psr, parasphenoid rostrum; rot, foramen for the lateral otic ramus; spi, ventral opening of the spiracular canal; tf.c, trigeminofacial chamber.



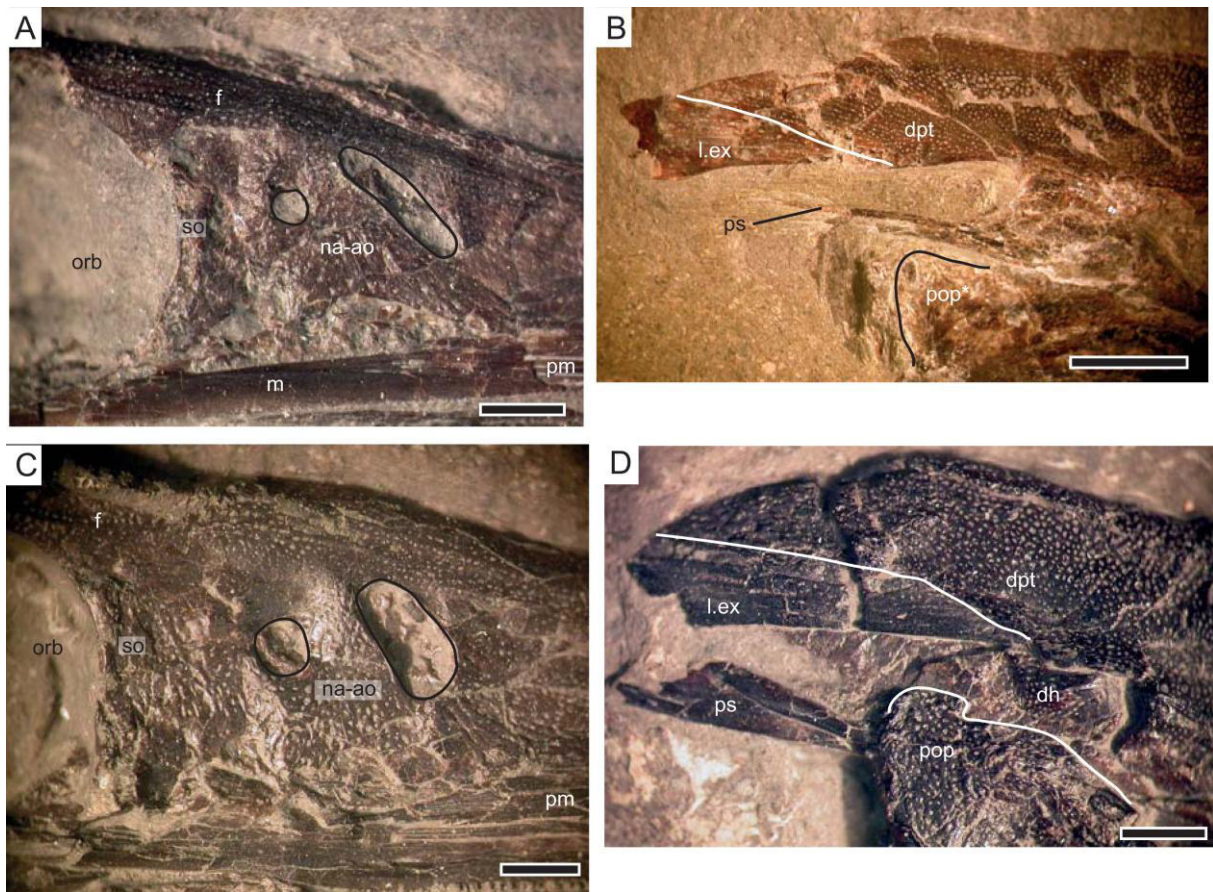


Fig. 5. Characters distinguishing *Saurorhynchus acutus* and *S. hauffi*. **A.** *S. acutus* narial region (SMNS 56923). **B.** *S. acutus* lateral extrascapular-dermopterotic contact (SMNS 57039). **C.** *S. hauffi* narial region (SMNS 51888). **D.** *S. hauffi* lateral extrascapular-dermopterotic contact (SMNS 53980, mirrored). Scale bars A, C–D = 2 mm; B = 5 mm. Abbreviations: dpt, dermopterotic; dh, dermohyal; f, frontal; l.ex, lateral extrascapular; m, maxilla; na-ao, nasaloantorbital; orb, orbit; pm, rostrompremaxilla; pop, preopercle; pop\*, damaged preopercle; ps, parasphenoid; so, supraorbital.

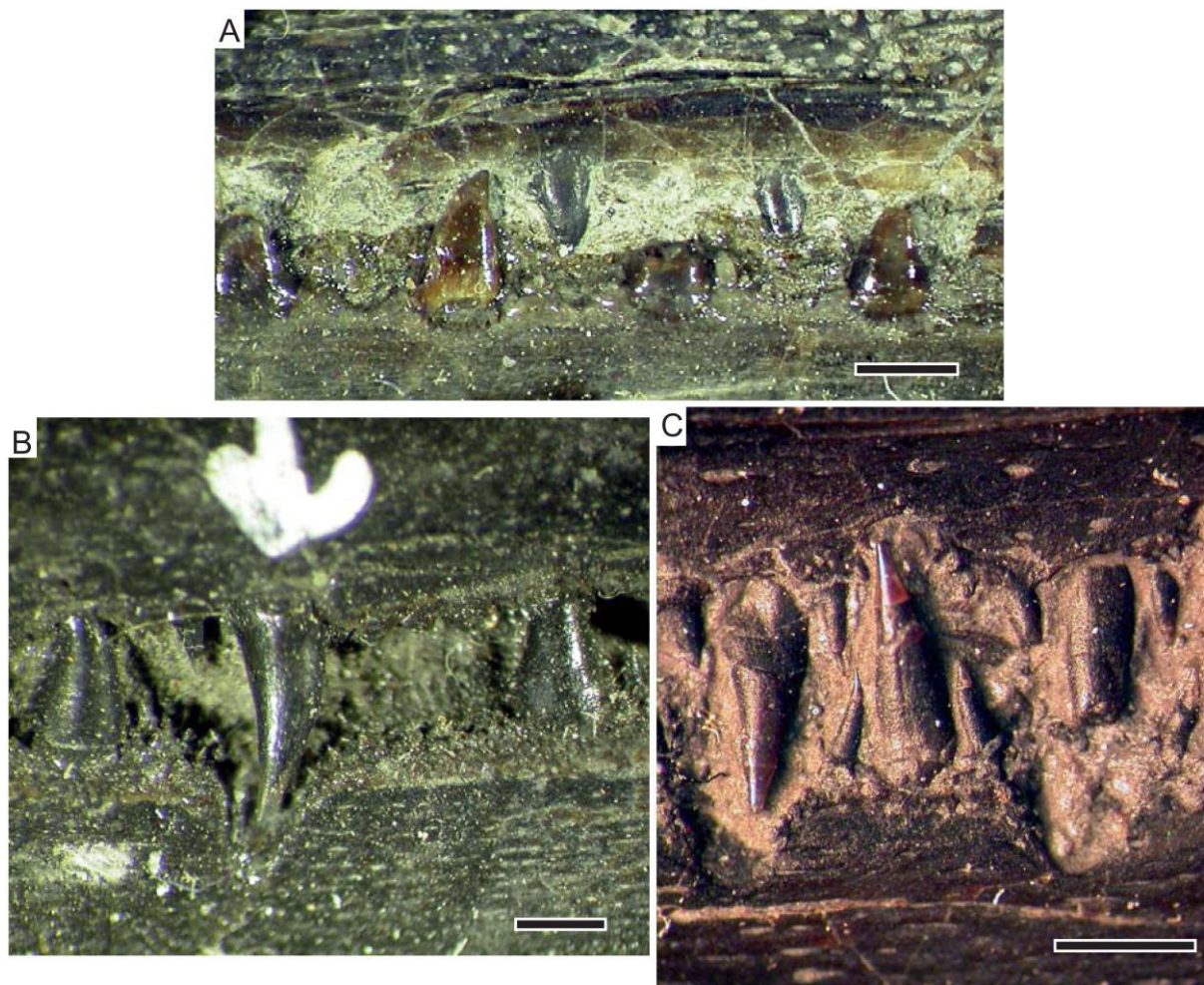


Fig. 6. Posteriormost laniary dentition. **A.** *Saurorhynchus brevirostris* (NHMUK PV P 4878), note the lingually curved crowns. **B.** *Saurorhynchus anningae* sp. nov. (NHMUK PV P 27569), note the incisivulücke associated with the premaxillary laniary tooth and the absence of lateral crypts associated with the two flanking mandibular laniaries. Photos © The Trustees of the Natural History Museum, London. **C.** *S. hauffi* (SMNS 51007), mid-rostral dentition illustrating the relationship between the incisivulücken, laniaries, and flanking smaller teeth. Scale = 1 mm



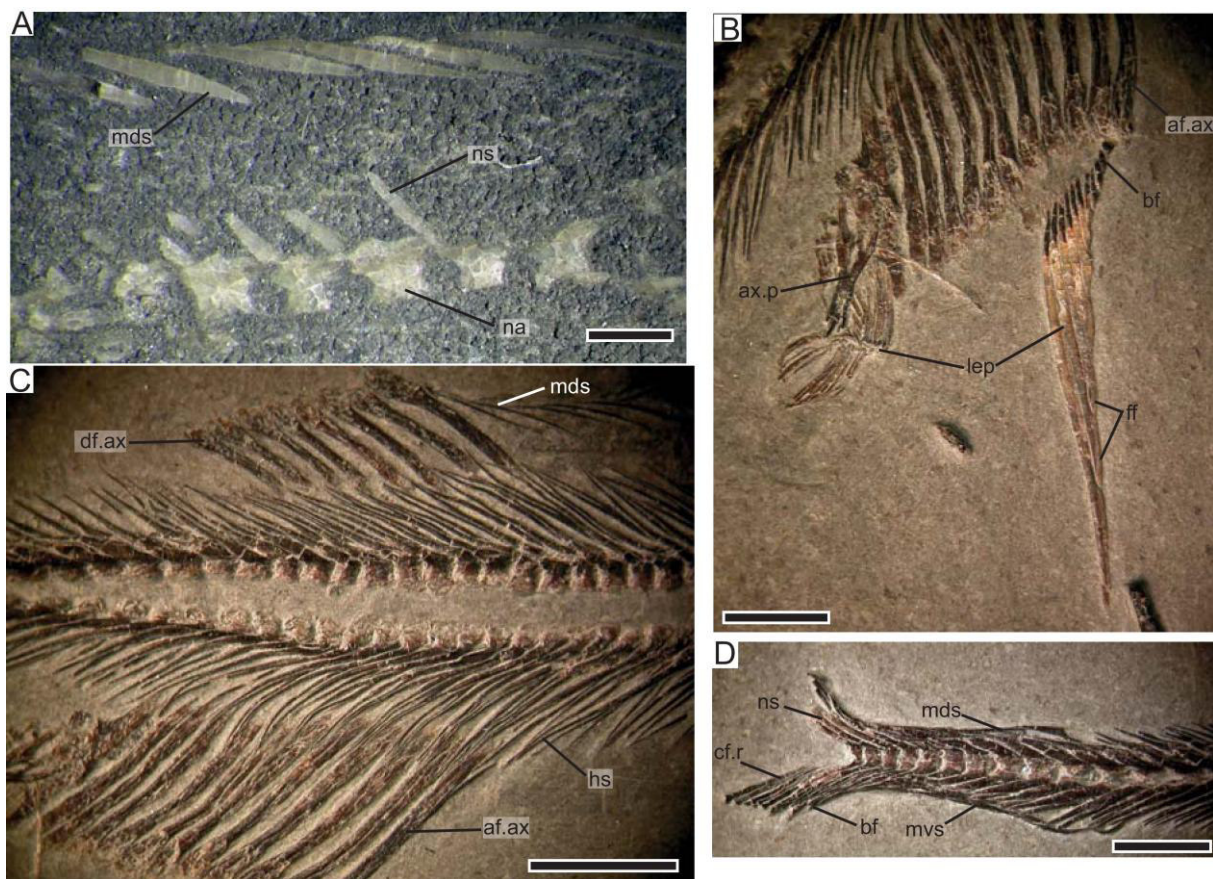


Fig. 7. Postcranium, Early Jurassic saurichthyids. **A.** *Saurorhynchus anningae*, neural arches and squamation in the posterior abdominal region (NHMUK P 3790, photo © The Trustees of the Natural History Museum, London). **B–D.** *Saurorhynchus hauffi*, SMNS 55057. **B.** lepidotrichia of the anal fin. **C.** relationship between the neural and haemal arches and the axonosts. **D.** caudal peduncle. Scale part A = 1 mm, B–D = 5 mm. Abbreviations: af.ax, axonosts of the anal fin; ax.p, axonost plate; bf, basal fulcra; cf.r, caudal fin radials; df.ax, axonosts of the dorsal fin; ff, fringing fulcra; hs, haemal spine; lep, lepidotrichia; mds, mid-dorsal scale row; mvs, mid-ventral scale row; na, neural arch; ns, neural spine.

**Supplementary Table 1.** Select cranial measurements for Early Jurassic *Saurorhynchus* species

	Species	Lower jaw length	Lower jaw max. depth	Antorbita l (rostral) length	Opercle length	Opercle depth
NHMUK PV P 4268 (holotype)	<i>Saurorhynchus acutus</i>			84		
SMNS 88007	<i>S. acutus</i>			71		
SMNS 55319	<i>S. acutus</i>	95	16	72		
SMNS 56923	<i>S. acutus</i>	84		64		
SMNS 55324	<i>S. acutus</i>	93		70		
SMNS 87738	<i>S. acutus</i>			59		
SMNS 51009	<i>S. acutus</i>	125		92		
SMNS 50924	<i>S. acutus</i>	96	16	78		
SMNS 57039	<i>S. acutus</i>	102	17	78		
SMNS 96927	<i>S. acutus</i>			69		
SMNS 96927	<i>S. acutus</i>			70		
NHMUK PV P 3792	<i>S. acutus</i>	111	18	84		
NHMUK PV P 36222	<i>S. acutus</i>	110	19	84		
NHMUK PV OR 19668	<i>S. acutus</i>	100		74		
NHMUK PV OR 22528	<i>S. acutus</i>	87		68		
NHMUK PV P 36223	<i>S. acutus</i>	91		71		
GPIT 05/133	<i>S. acutus</i>		21			
GZG.V.27932	<i>S. acutus</i>		18			
PMU 30009	<i>S. acutus</i>	114	25	84		
PMU 30010	<i>S. acutus</i>	91		72	14	14
NHMUK PV OR 40726 (holotype)	<i>S. brevirostris</i>	>82	14	>57	10	13
NHMUK PV P 36233	<i>S. brevirostris</i>	80 (jaw joint to rostral tip = 86 mm)	13	64		
NHMUK PV P 4878	<i>S. brevirostris</i>	74 (jaw joint to rostral tip = 77 mm)	12	56		
NHMUK PV OR 39866	<i>S. brevirostris</i>	52 (jaw joint to rostral tip = 54 mm)	9	37		



NHMUK PV P 36232	<i>S. brevirostris</i>		15			
NHMUK PV OR 48007	<i>S. brevirostris</i>			62		
NHMUK PV P 3791	<i>S. anningae</i> (holotype)	89	10	65	9	13
NHMUK PV P 428	<i>S. anningae</i>	137	13	101		
NHMUK PV P 36227	<i>S. anningae</i>			49		
NHMUK PV P 3790	<i>S. anningae</i>	74	9			
NHMUK PV P 36226	<i>S. anningae</i>	79	10	60	7	11
NHMUK PV OR 43054	<i>S. anningae</i>	96	13	75		
NHMUK PV P 36228	<i>S. anningae</i>	94	12			
SMNS 55057 (holotype)	<i>S. hauffi</i>	97	17			
SMNS 96878/1	<i>S. hauffi</i>	91	16	68		
SMNS 55934	<i>S. hauffi</i>	84		63		
SMNS 95825	<i>S. hauffi</i>	99	17	76		
SMNS 51007	<i>S. hauffi</i>	76	15	55		
SMNS 53980	<i>S. hauffi</i>	85	15	64		
SMNS 51888	<i>S. hauffi</i>	112	17	86		
SMNS 50075	<i>S. hauffi</i>		24			
SMNS 55302	<i>S. hauffi</i>	90		66		
SMNS 55957	<i>S. hauffi</i>	101		78		
NHMUK PV OR 39153	<i>S. hauffi</i>	95	13	70		
NHMUK PV P 48441	<i>S. hauffi</i>	115		87		
GPIT 05/00833	<i>S. hauffi</i>	103	16	77		
GPIT 05/00831	<i>S. hauffi</i>	85		62		
GPIT 05/00832	<i>S. hauffi</i>	92		68		
GZG.V.27931	<i>S. hauffi</i>	101		79		
NLMH 70598	<i>S. hauffi</i>	91	14	69		
NMB 373	<i>S. hauffi</i>	102	17	78		

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**PAPER 5**

Early Jurassic diversification of pycnodontiform fishes (Actinopterygii, Neopterygii) after the end-Triassic extinction event: Evidence from a new genus and species, *Grimmenodon aureum*

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RH: STUMPF ET AL.: NEW EARLY JURASSIC PYCNODONTIFORM FISH

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ABSTRACT—Here, a new genus and species of pycnodontiform fishes, *Grimmenodon aureum*, from marginal marine, marine-brackish lower Toarcian (*Harpoceras exaratum* ammonite subzone) clay deposits of Grimmen in north-eastern Germany is described. The single specimen represents a diagnostic left prearticular dentition characterized by unique tooth arrangement and ornamentation patterns. *Grimmenodon aureum*, gen. et sp. nov. is the second unambiguously identified pycnodontiform species from the Early Jurassic, in addition to *Eomesodon liassicus* from the Sinemurian of western Europe. We also report an indeterminate pycnodontiform tooth crown from the upper Pliensbachian (*Pleuroceras apyrenum* ammonite subzone) of the same site. The material expands the Early Jurassic range of pycnodontiforms significantly northwards and confirms their presence before and immediately following the onset of the Toarcian Oceanic Anoxic Event (T-OAE) in the marginal marine ecosystems south of the Fennoscandian Shield. Moreover, the new records indicate that the Early Jurassic diversity of pycnodontiform fishes was larger than previously assumed and probably equaled that of the Late Jurassic. Therefore, it is hypothesized that the Triassic-Jurassic mass extinction event did not affect pycnodontiform fishes significantly. Micro-computed tomography was used to study the internal anatomy of the new taxon. Our results show that no replacement teeth were formed within the tooth-bearing bone but rather were added posteriorly to functional teeth during bone growth.

<http://zoobank.org/urn:lsid:zoobank.org:pub:A56BDE9C-40C4-4CFA-9C2E-F5FA35A66F2>

## INTRODUCTION

Extinct pycnodontiform fishes (the ‘pycnodonts’), which are a morphologically and ecologically distinctive group of basal neopterygians (Nursall, 1996, 1999, 2010; Arratia, 1999; Poyato-Ariza, 2015) are characterized *inter alia* by a very specific heterodontous dentition consisting of chisel- or styliform grasping teeth on the paired premaxillae and dentalosplenials, and generally densely arranged molariform teeth on the unpaired vomer in the upper and the paired prearticulars in the lower jaws. The maxillae are edentulous. Vomerine and prearticular teeth form an effective crushing dentition, indicating durophagous feeding habits in a wide range of pycnodontiforms (Kriwet, 2001a). The robust dentate jaw elements and isolated teeth are the most common remains of pycnodontiforms in the fossil record occurring nearly worldwide in most marine and even brackish to freshwater influenced deposits of Mesozoic and Palaeogene age (e.g., Longbottom, 1984; Poyato-Ariza et al., 1998; Kriwet, 1999; Poyato-Ariza and Bermúdez-Rochas, 2009; Martín-Abad and Poyato-Ariza, 2013). Disarticulated or articulated skeletons, conversely, are comparably rare. So far, ca. 700 species have been described belonging to more than 45 genera (Kriwet, 2001c, 2005); only about 80 species are known from disarticulated or articulated skeletons. All remaining species are based on isolated dentitions or even teeth.

Teeth and jaws are important functional structures but also offer significant taxonomic and evolutionary features for characterizing fishes (e.g., Fink, 1981; Lauder and Liem, 1983; Casciotta and Arratia, 1993). Nevertheless, controversial issues concerning the formation of dentitions and the taxonomic importance of tooth morphologies and arrangements in pycnodontiform fishes still prevail and detailed dental information often is omitted from species or genus diagnoses in more recent studies (e.g., Thurmond, 1974; Nursall, 1996; Poyato-Ariza and Wenz, 2005; Ebert, 2016). Therefore, knowledge of pycnodontiform tooth structures and dentitions is strongly biased towards those found isolated rather than those preserved in articulated skeletons. Additionally, Poyato-Ariza (2003) argued that pycnodontiform dentitions do not present useful character sets for phylogenetic analyses. The validity of many species and genera based on isolated teeth consequently remains ambiguous at least in many cases. Nevertheless, Longbottom (1984), Kriwet (1999, 2005, 2008), Poyato-Ariza and Bermúdez-Rochas (2009), and Shimada et al. (2010) among others demonstrated that the morphology and arrangement of teeth on the vomer and prearticulars in pycnodontiform fishes provide unique combinations of characters and even allow identifying autapomorphic traits for taxa assignment and establishing reliable diagnoses. The importance

of recognized autapomorphic characters in phylogenetic analyses needs, however, to be tested.

The oldest remains of pycnodontiform fishes, which comprise both complete skeletons and isolated dentitions, are from upper Norian (Late Triassic) marine deposits of the northern Tethys margin (what is now northern Italy and Austria) (Gorjanović-Kramberger, 1905; Tintori, 1981), and from epicontinental sea deposits of Belgium and Luxembourg (Delsate and Kriwet, 2004). They persisted into the middle Eocene when they supposedly were replaced by spiny-teleosts (Friedman, 2010; Goatley et al., 2010). During the Late Jurassic, pycnodontiform fishes seemingly rapidly diversified reaching their highest taxonomic diversity and morphological disparity in the Late Cretaceous (Kriwet, 2001b; Poyato-Ariza and Martín-Abad, 2013; Marramá et al., 2016). The Early and Middle Jurassic fossil record of pycnodontiforms in the aftermath of the Triassic-Jurassic extinction event, conversely, is extremely scarce. So far, a single species and at least 11 nominal species have been described from the Early and Middle Jurassic, respectively (see also below). Most of these species are represented by isolated vomerine and prearticular dentitions only, rendering their identification difficult. Consequently, most of the Middle Jurassic pycnodontiform species are dubious and in need of revision.

Here, we present new dental remains of pycnodontiforms from the Early Jurassic of Europe, including a new genus and species that provides evidence that the taxonomic diversity and probably morphological disparity of pycnodontiform fishes in the Early Jurassic was larger than previously assumed.

**Institutional Abbreviations**—**GG**, Institute of Geography and Geology, University of Greifswald; **MV**, Geologische Landessammlung Sternberg, Geologischer Dienst, Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern.

**Anatomical Abbreviations**—**cor.pr**, coronoid process; **for**, foramen; **lm.b**, laminar bone; **p.cav**, pulp cavity; **sp.b**, spongy bone; **sym**, symphysis; **t.r**, tooth root.

## GEOLOGICAL AND STRATIGRAPHIC SETTING

Although laterally persistent in north-eastern Germany, outcrops of Mesozoic strata are rare (e.g., Katzung, 2004). Early Jurassic strata only crops out in the abandoned open-cast clay pits of Grimmen and Dobbertin (Fig. 1A), both representing parautochthonous successions of upper Pliensbachian to lower Toarcian marine sediments that were glacially

dislocated during Pleistocene ice advances (see Ernst, 1967, 1991, 1992; Ansorge and Obst, 2015; Ansorge and Grimmberger, 2016).

The fossil fish material that forms the focus of the present study encompasses two pycnodontiform specimens, GG 437 and MV 202615, that were recovered from upper Pliensbachian and lower Toarcian strata of the Grimmen clay pit, respectively (Fig. 1B).

Paleogeographically, the late Early Jurassic succession exposed in the Grimmen clay pit was deposited at the north-eastern edge of the North German Basin (NGB), which was one of the many subbasins that covered large areas of central and western Europe during Early Jurassic times (Fig. 1C), referred to as the Central European epicontinental Basin (CEB) (Röhl and Schmid-Röhl, 2005). The litho- and biostratigraphy of the exposed succession already have been described in detail previously (Ernst, 1967, 1991; Prauss, 1996; Ansorge, 2007). The upper Pliensbachian interval of Grimmen is represented by unlithified fine-grained sand containing thin beds of silt, and subordinate lenticular streaks of clay, as well as laterally limited fine- to coarse-grained, bioclastic-rich sand bodies, which are indicative of local accumulations generated by current activity, suggesting a shallow-marine deltaic depositional environment (Ernst, 1967, 1991; Ernst *in* Gründel, 1999). Pyrite and carbonate concretions, less commonly siderite concretions, are present. The fauna is rich in marine invertebrates, comprising ammonites, bivalves, gastropods, brachiopods, scaphopods, echinoderms, ostracods, and foraminifers (Ernst, 1967, 1991; Herrig, 1969a, 1969b; Kutscher, 1988; Gründel, 1999; Buchholz, 2012). These beds also yielded a diverse vertebrate fauna, including isolated actinopterygian and chondrichthyan remains (Buchholz, 2012; this contribution).

Biostratigraphically, the sandy interval has been correlated with the *apyrenum* subzone (lower *spinatum* zone) based on ammonite evidence (Ernst, 1991; Buchholz, 2012). The Pliensbachian-Toarcian transition is omitted by a hiatus, probably caused by erosion and non-deposition (see Röhl and Schmid-Röhl, 2005). Therefore, the uppermost *spinatum* zone (*hawskerense* subzone) and probably much of the lower Toarcian *tenuiscostatum* zone (*paltum* to *clevelandicum* subzone) are absent (Ernst, 1991). The lower Toarcian interval shows a retrogradational stratal pattern, consisting of fine-grained sands that pass upwards into black bituminous, laminated silty clays referred to the latest *tenuiscostatum* zone (*semicelatum* subzone), and pure clays containing fossiliferous concretions, used to date the clay deposits to the lower *falciferum* zone (*elegantulum* to *exaratum* subzone). The clay interval is assigned to the traditionally called “Green Series”, which reaches thicknesses of several tens of meters in north-eastern Germany (Schumacher and Sonntag, 1964; Stoermer



and Wienholz, 1965; Lehmkuhl, 1970), and markedly differs from the time-equivalent black bituminous shales and marlstones known from more basinal sections of the CEB (e.g., Jenkyns, 1988; de Graciansky et al., 1998; Schmid and Schmid-Röhl, 2005).

Clay deposits referred to the “Green Series” crop also out in the abandoned Dobbartin clay pit. However, unlike those exposed at Grimmen, these clay deposits can solely be dated to the *falciferum* zone on the basis of current data (Ansorge, 2003; Ansorge and Obst, 2015). Given the tectonic disturbances that took place during glacial dislocation, the original thicknesses of the “Green Series” clay deposits of both Grimmen and Dobbartin cannot be firmly determined.

Fossils originating from the lower Toarcian “Green Series” are usually contained in syngenetic and early diagenetic carbonate concretions that occur interbedded within the clay. Based on the presence of a rich but taxonomically impoverished ammonite fauna and the scarcity of typical stenohaline invertebrates, brackish-marine water conditions have been inferred for the time of deposition of the “Green Series” (Ernst, 1991; Ansorge, 2003, 2007). Reduced salinity conditions also are confirmed by occurrences of conchostracans (Ansorge, 2003; SS pers. obs.). The fauna mainly comprises actinopterygians (e.g., Jaekel, 1929; Malzahn, 1963; Thies, 1989; Ansorge, 2007; Ansorge and Obst, 2015), followed by secondarily marine reptiles (Maisch and Ansorge, 2004; Stumpf, 2016), and rare chondrichtyans (Ansorge, 2007). These faunal elements occur alongside with an extraordinary rich terrestrial entomofauna (Ansorge, 1996, 2003), indicating the presence of suitable environments nearby. The “Green Series” of Grimmen also yielded abundant plant and wood remains, as well as the first Early Jurassic spider and basal sauropod dinosaur remains (Ernst, 1967; Selden and Dunlop, 2014; Stumpf et al., 2015) that were washed into the transepicontinental shelf sea, suggesting a near-shore depositional environment, as proposed by Ernst (1967, 1991) and Ansorge (2003).

Significantly, the boundary between the *tenuicostatum* and *falciferum* zones coincides with the height of the Toarcian Oceanic Anoxic Event (T-OAE), which is considered to be one of the most dramatic environmental disruptions that took place during the Mesozoic, and massively impacted marine biota (e.g., Little and Benton, 1995; Caswell et al., 2009; Dera et al., 2010; Caswell and Coe, 2014). The “Green Series” therefore documents a marine ecosystem immediately following onset of the T-OAE.

## MATERIAL AND METHODS

The pycnodontiform prearticular jaw bone, GG 437, described herein was initially found embedded in a carbonate concretion recovered from the lower Toarcian “Green Series” clay deposits by one of us (JA) in 2005, who subsequently extracted the specimen from the surrounding matrix using diluted acetic acid. The specimen is preserved in three dimensions, and it is coated with pyrite in many places, which gives a somewhat golden appearance to it. The second specimen, an isolated pycnodontiform tooth crown, MV 202615, was recovered by private collectors, Bernd Röber and Hannes Löser, from a temporary upper Pliensbachian bioclastic-rich coarse-grained sand body accessible during the late years of active clay mining at the Grimmen site, which started in 1959/60 and ended in 1995. The exact year of discovery is unknown.

Digital photographs were obtained using a digital compact camera (Nikon Coolpix 4500) and digital microscopes (Zeiss AxioCam HR3 housed at the GG; Keyence VHX-1000D housed at the Department of Palaeontology, University of Vienna). For descriptive purposes, various measurements were taken from GG 437, and statistical parameters were calculated using PAST 3.12 (Hammer et al., 2001). In addition, GG 437 was scanned with a Desktop-Micro-CT device (Bruker Skyscan 1173 housed at the Department of Palaeontology, University of Vienna). With an image pixel size of 7.13 $\mu$  and a X-ray beam set at 50 kV, 160  $\mu$ A, the average of three frames were taken under the rotation step of 2°.

The new Early Jurassic pycnodontiform material shows that the diversity after the Triassic-Jurassic mass extinction seemingly was larger than previously assumed. Unfortunately, however, the fossil record of Early and Middle Jurassic pycnodontiforms is strongly biased towards isolated dental remains that have not yet been included in phylogenetic analyses for establishing radiation events. Therefore, it is not possible to employ robust statistic analyses, but we rather review the Early and Middle Jurassic fossil record of pycnodontiforms and compare the standing diversity with that of the Late Triassic.

## SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Cope, 1887

NEOPTERYGII Regan, 1923

PYCNODONTIFORMES Berg, 1937

*GRIMMENODON*, gen. nov.

**Etymology**—The genus name is derived from the name of the type locality, Grimmen, and the Greek noun *odonti* (= δόντι), meaning tooth.

**Diagnosis**—Pycnodontiform fish known from a single left prearticular dentition, showing the following unique combination of morphological characters: Prearticular with rather short and narrow symphyseal articulation facet; coronoid process stout and rather low in dorsoventral dimensions; tooth plate forming a prominent posterior process; teeth oval to subcircular in occlusal outline, closely arranged in five well-defined longitudinal rows without intercalating teeth; main row flanked medially by one tooth row and laterally by three tooth rows; teeth of medial row obliquely oriented, tooth crowns with a single wrinkled wall surrounding a shallow apical furrow; teeth of main row well-defined and elevated, exhibiting a shallow and transversally directed apical furrow surrounded by a broad wrinkled wall and additional tubercles along the anterior margins; average width/length ratio of main teeth 1.58; first lateral row short and restricted to the anterior half of the tooth plate; second lateral row occupies two-thirds of the tooth plate length; teeth of the first and second lateral rows ornamented by coarse irregularly arranged tubercles that surround a rounded and deep central apical indent; teeth of the third lateral row with shallow and transversally directed apical indent bordered by an elevated and regularly tuberculated wall.

**Type Species**—*Grimmenodon aureum*, sp. nov.

*GRIMMENODON AUREUM*, sp. nov.

(Figs. 2, 3)

Pycnodontid: Ansorge 2007, 41, fig. 13–5.

**Etymology**—From Latin, golden, and refers to the somewhat golden appearance of teeth caused by spatial pyrite coatings.

**Diagnosis**—As for genus (by monotypy).

**Holotype**—GG 437, left prearticular bone with dentition.

**Type Horizon**—*Harpoceras exaratum* subzone (*Harpoceras falciferum* zone, lower Toarcian, Early Jurassic) (see Ansorge, 2007).

**Type Locality**—Abandoned open-cast clay pit of Grimmen (Mecklenburg-Western Pomerania, Germany).

**Description**—*Grimmenodon aureum*, gen. et sp. nov. is represented by an almost complete left prearticular with preserved teeth; only the anterior-most portion is missing. The

prearticular measures 10.67 mm in total length and 8.92 mm in width (maximum distance measured between the coronoid process and the medial border). The symphyseal articulation facet is rather narrow and extends posteriorly as far as the middle of the tooth plate, exhibiting a slightly rugose surface texture, probably for the attachment of interconnective tissue (see Kriwet, 2004) (Fig. 2A). More posteriorly, the symphysis continues into a faint bony lamella that defines part of the postero-medial margin of the bone. The coronoid process is stout but rather low in dorso-ventral dimensions, with a slightly convex dorsal margin that meets the posterior margin at a curved angle (Fig. 2B). The coronoid process exhibits weakly-developed ridges oriented parallel to the longitudinal axis of the tooth plate, probably for the insertion of part of the *Musculus adductor mandibulae* (see Kriwet, 2001c). The base of the coronoid process extends postero-laterally beyond the tooth plate to form an elevated and antero-posteriorly elongated lamella in ventral view (Figs. 2A, C). Posteriorly, the prearticular forms a distinct process, which is slightly incurved medially.

The prearticular dentition consists of molariform teeth closely arranged in five longitudinal rows without intercalating teeth (Fig. 2A). The teeth are strongly ornamented in occlusal view, lacking any signs of abrasion. The main row, as preserved, is elevated and comprises nine transversally elongated teeth decreasing in size anteriorly. They form a somewhat curved line in occlusal view. The spaces between adjacent teeth slightly decrease anteriorly. The main teeth are larger than any of those positioned in the medial or the lateral tooth rows, with an average width/length ratio of 1.58 (see Table 1). They are oval in occlusal outline and exhibit a transversally wide apical furrow that follows the outer contour of the crown. A broad and more or less regularly wrinkled wall surrounds the apical furrow. The radiating ridges on the surrounding wall are more strongly developed along the anterior margin, and occasionally irregularly arranged tubercles also are present along the anterior margin (Figs. 2A, D). The posterior-most tooth preserved in the main row is less elevated than the other ones aligned in the corresponding row, and its crown is partially enclosed by cancellous bone formed by the tooth plate (Figs. 2A, D, E).

The main tooth row is flanked medially by one and laterally by three tooth rows. The medial row, as preserved, includes three oval and obliquely placed teeth; the intermediate one is incomplete, lacking its crown. Medial teeth are arranged alternating with the teeth of the main row appearing almost inserted into the gaps between main teeth. They exhibit an apical indent that is surrounded by a wrinkled wall. Posterior to the medial row, the prearticular forms a deep furrow, exposing cancellous bone tissue. The furrow is medially demarcated by

the bony lamella that extends posteriorly from the symphyseal articulation along part the postero-medial margin of the bone.

The first lateral row is restricted to the anterior portion of the dentition and includes at least five teeth (Fig. 2A). They are low (not as elevated as main teeth) and display a suboval occlusal outline, with an average width/length ratio of 1.13. The three anterior-most teeth are arranged with their main axes perpendicular to the long axis of the prearticular bone, whereas those of the posterior ones are oriented parallel to its long axis. The tooth crowns display generally the same occlusal surface ornamentation, exhibiting a round apical indent that is surrounded by a broad and strongly irregularly tuberculated wall.

The second lateral row includes eight teeth and extends anteriorly as far as two-thirds of the tooth plate length (Fig. 2A). The teeth are also low compared to those of the main row and have an oval contour in occlusal view; the average width/length ratio is 1.21. The first three teeth are oriented with their main axes parallel to the long axis of the prearticular, unlike the remaining ones of the second lateral row, which are arranged perpendicular to the prearticular long axis. The teeth are ornamented by coarse and irregularly arranged tubercles that surround a rounded to suboval central apical indent. The two anterior-most teeth are slightly placed in the spaces between the teeth of the first lateral row.

The third lateral row consists of eight teeth, which display a transversally oval contour in occlusal view; at least two further teeth are missing due to breakage (Fig. 2A). The teeth are larger and more widely spaced, as compared to those arranged in the first and second lateral row. Their average width/length ratio is 1.22, similar to that of teeth of the second lateral row. The occlusal surface, however, more closely resembles that of main teeth, showing a more or less regularly wrinkled wall that surrounds a transversally wide apical furrow. The radiating ridges arranged along this margin are formed by two to three small tubercles. The lateral edges of the teeth slightly overhang the oral margin of the prearticular in both dorsal and ventral view (Fig. 2B).

The teeth are mounted on pedicles, which are well visible in lateral view, and numerous minute foramina are irregularly aligned along the oral surface of the prearticular (Fig. 2C). These foramina communicate via short bony tubes with internal void spaces in between the mineralized tissue, as visible in the digitally reconstructed micro-CT transverse sections of the prearticular (Figs. 3C, D). The tooth-bearing bone predominantly exhibits a spongy texture (Fig. 3), except for the coronoid process and the postero-medially extending bony lamella, in which the bone displays a lamellar texture (Figs. 3E–H). However, it should be noted that the void spaces within the posterior portion of the prearticular are partially filled

with sediment matrix, which has a density slightly less than the surrounding mineralized tissue (Figs. 3E–H). Occasionally, these matrix-filled areas are enriched in an indeterminable material of high density (Figs. 3G, H) similar to the pyrite that covers parts of the occlusal surface of the bone (Figs. 3C, D).

The micro-CT transverse slice shows spatial differences in the development of the internal spongy bone, in particular in the symphyseal region, where the mineralized tissue is more strongly developed and even more densely packed, as compared to the remaining portions consisting of spongy bone, which is probably accompanied by enhanced jaw adductor forces (see Kriwet, 2001c, 2004). The pulp cavities of the teeth aligned in the main row are larger and deeper than those of the medial and lateral teeth (Fig. 3). The pulp cavities are free of mineralized tissue, and there is no indication of developing tooth germs or non-functional teeth inside the tooth-bearing bone adjacent or below to erupted teeth. Distinction between circumpolar dentine, pallial dentine, and acrodin cap (see Kriwet, 2005) was not possible based on the CT scan.

**Comparison and Discussion**—So far, only a single Early Jurassic pycnodontiform species, *Eomesodon liassicus* from the Sinemurian of Barrow-on-Soar, Leicestershire, England (Egerton, 1855; Gardiner, 1960), has been described. The material consists of three poorly preserved articulated specimens. Unfortunately, the prearticular dentition of *Eomesodon liassicus* is insufficiently known to determine the total number of tooth rows, thus preventing detailed comparisons with *Grimmenodon aureum*, gen. et sp. nov. The holotype specimen of *Eomesodon liassicus*, however, exhibits a displaced molariform tooth crown showing an oval occlusal contour with a ring of widely spaced tubercles that encloses a shallow apical furrow (Egerton 1855:pl. 10, fig. 4), which is characteristic for teeth of *Eomesodon* (JK pers. obs.). This readily differentiates dentitions and teeth of *Eomesodon* from *Grimmenodon aureum*, gen. et sp. nov. Additional material referred to *Eomesodon liassicus* was reported from the Hettangian of France and Belgium, incorporating teeth and dentitions (Saint-Seine, 1949; Delsate et al., 2002). Duffin (2010:pl. 78, fig. 5) pictured a polished coprolite from the lower Early Jurassic of the Dorset Coast, England, containing inclusions of bony remains, including an incomplete, coronally broached pycnodontiform dentition that displays two rows of widely spaced and regularly rounded teeth (see also Buckland, 1829:pl. 30, figs. 2, 3a), which were previously interpreted by Buckland (1829) as suckers of a squid.

Sauvage (1878) introduced the species *Gyrodus fabrei* based on a single left prearticular recovered from Early Jurassic (probably Toarcian: Priem, 1908) strata near

Nancy, Meurthe-et-Moselle, France. This taxon, however, is considered as invalid by Kriwet (2001a), who identified it as *Eomesodon* sp. More recently, Pászti (2004) reported pycnodontiform material from the Toarcian Úrkút manganese carbonate deposits (Úrkút Manganese Formation) of Hungary. This work, however, must be regarded with the utmost caution, since the fossil specimens pictured by Pászti (2004:fig. 1, 2) are actually no pycnodontiforms. Moreover, it is to be noted that Pászti's (2004:fig. 3) line drawing of “*Eomesodon* sp.” is adapted from that of *Stemmatodus rhombus* provided by Poyato-Ariza and Wenz (2002:fig. 12).

The oldest Middle Jurassic pycnodontiform record is represented by a single partially preserved skeleton recovered from the Bajocian Middle Oolite Series of Scotland described as *Gyrodus goweri* by Grey-Egerton (1869). This species is considered as invalid by Kriwet and Schmitz (2005), because the material does not provide sufficient morphological traits to unambiguously assign it to a species and subsequently was referred to as *Gyrodus* sp. Unlike in *Grimmenodon aureum*, gen. et sp. nov., teeth of *Gyrodus*, when unworn, exhibit two crenulated apical rings with a central tubercle, and a medial or lateral apex on the inner ring (Thies, 1985; Kriwet, 2000; Kriwet and Schmitz, 2005). Moreover, *Gyrodus* can be clearly differentiated from the new taxon based on the presence of four prearticular tooth rows (Poyato-Ariza and Wenz, 2002).

A rather diverse pycnodontiform ichthyofauna was reported from the Bathonian Great Oolite Group of England, incorporating isolated dentitions of *Eomesodon rugulosus*, *E. trigonus*, *Macromesodon bucklandi*, *M. discoides*, *M. oblongus*, *M. tenuidens*, and *Proscinetes biserialis* (Agassiz, 1833–1844; Woodward, 1889, 1890, 1892, 1895). In addition, isolated dentitions attributed to different species of *Macromesodon* also were reported from the Bathonian of France, including *M. bathonicus*, *M. boloniensis*, *M. discoides*, *M. gervaisi*, and *M. radiatus* (Agassiz, 1833–1844; Sauvage, 1867, 1880a, 1880b). Furthermore, pycnodontiform teeth of Bathonian age were described from France (Gérard, 1936; Galton et al., 1980; Rioult and Mourdon, 1982; Kriwet et al., 1997) and Italy (Bassani 1885). The taxonomy of Bathonian pycnodontiforms, however, is very poorly understood. For instance, as it is yet widely accepted, the genus *Macromesodon* comprises an unnatural grouping of unrelated taxa (Kriwet, 2001a; Poyato-Ariza and Wenz, 2002, 2004). Subsequently, Poyato-Ariza and Wenz (2004) restricted *Macromesodon* to the Late Jurassic species *M. macropterus* (type species), *M. gibbosus*, and *M. surgens*, and erected the genus *Turbomesodon* for some Late Jurassic pycnodontiforms previously included in *Macromesodon*. According to the generic diagnoses provided by these authors, the

prearticular dentition of both *Macromesodon* and *Turbomesodon* comprises three tooth rows, a feature readily separating these taxa from *Grimmenodon aureum*, gen. et sp. nov., in which the prearticular teeth are arranged in five rows. Conversely, *Proscinetes biserialis*, which is known from a single left prearticular recovered from the Great Oolite of Oxfordshire, has four rows (Woodward, 1890:pl. 3, fig. 28).

The prearticular dentitions of nominal species assigned to *Eomesodon* and *Macromesodon* are considered to be similar by Woodward (1895), exhibiting one main row, one or two medial rows, and at least three lateral rows. Among the Bathonian species, the arrangement of prearticular teeth in five longitudinal rows is present in *Eomesodon rugulosus* and *Macromesodon bucklandi* (Woodward, 1890, 1895). Remains referred to these species occur most frequently in strata of the English Great Oolite Group (see Woodward, 1895). Six tooth rows are present in *Macromesodon tenuidens* (Woodward, 1890:pl. 3, fig. 23), a rare taxon known from a single right prearticular recovered from the middle Bathonian Taynton Limestone Formation of Stonesfield, Oxfordshire, England, as well as in *Macromesodon gervaisi* (Sauvage, 1867:pl. 2, fig. 4; Sauvage, 1880a:pl. 14, fig. 2) and *Macromesodon boloniensis* (Sauvage, 1867:pl. 2, figs. 2, 5) from the Bathonian of Boulogne-sur-Mer, Pas-de-Calais, France. These taxa vary in the arrangement and occlusal contour of the teeth. *Macromesodon bathonicus*, which is known from a single partially preserved left prearticular described by Sauvage (1880b:pl. 19, fig. 1), is too incomplete to ascertain that it represents a distinct species. *Macromesodon oblongus* and *M. discoides* are only known by their vomerine dentitions. Their teeth, however, markedly differ from those of *Grimmenodon aureum*, gen. et sp. nov.: e.g., regularly rounded and irregularly arranged in *M. discoides* (Woodward, 1890:pl. 3, fig. 32), and oval but oriented with their main axes parallel to the long axis of the corresponding bone in *M. oblongus* (Agassiz, 1833–1844:vol. 2, pl. 19, fig. 10).

Pycnodontiform remains of Callovian and Bajocian age have been rarely reported in the literature. For instance, Kriwet (2008) figured an isolated left prearticular of *Athrodon* sp. recovered from the Callovian of Falaises des Vaches Noires near Dives-sur-Mer, Calvados, France. Unlike in *Grimmenodon*, gen. nov., the prearticular dentition of *Athrodon* includes more than five rows of circular teeth, which are irregularly arranged and more widely spaced, with the main row being usually less well-differentiated.

The pycnodontiform *Mesturus leedsi* from the Callovian Peterborough Member (formerly named as the Lower Oxford Clay) of Peterborough, Cambridgeshire, England, is known from three-dimensional preserved cranial material (Woodward, 1895, 1896). In addition, Wenz (1968) described a three-dimensional preserved endocranium from the



Callovian of Calvados, France, which she tentatively assigned to *Mesturus* sp. The species *Mesturus leedsi* exhibits a total number of five prearticular tooth rows, including three regular and two irregularly arranged rows of low and small teeth aligned between the main and lateral one (Woodward, 1896:pl. 2, fig. 3), a character combination that easily distinguishes it from the new taxon described herein.

Thus, it is evident that the prearticular dentition of *Grimmenodon aureum*, gen. et sp. nov. is distinct from all other known pycnodontiforms in possessing an inconspicuous, anteriorly restricted first lateral row of small subcircular teeth, and a conspicuous large variability of occlusal tooth ornamentation.

**Size, ontogeny, and tooth development**—The prearticular of *Grimmenodon aureum*, gen. et sp. nov. is of comparatively small size, suggesting a hypothetical small standard length of the fish of about seven to 10 cm at the time of death when compared to *Gyrodus* and *Proscinetes* (Licht, 2009; Licht et al., 2015). The strong occlusal sculpturing of the teeth is suggestive of an immature ontogenetic stage, since the vomerine and prearticular dentitions of pycnodontiforms become usually worn during ontogeny, resulting in smooth tooth crowns during individual growth at least in the anterior portions of the dentition (see Kriwet, 2005). Tooth development in pycnodontiform fishes has been controversially discussed in the literature for many years. For instance, Nursall (1996) proposed that pycnodontiforms formed a single generation of molariform teeth without replacement of individual teeth. Woodward (1893, 1895) and Thurnmond (1974) suggested that the number of teeth was increased by the addition of larger ones formed posterior to functional teeth simultaneously to caudally directed prearticular and vomer growth, a view supplemented by Longbottom (1984), who, however, proposed both an anterior and posterior additional tooth development, in which the anterior teeth were replaced by small irregularly arranged teeth. More recently, Poyato-Ariza and Wenz (2005) described a non-functional tooth preserved *in situ* within the posterior part of the prearticular *Akromystax tilmachiton* from the Late Cretaceous of Lebanon. This tooth was found at an angle of about 90° to the occlusal surface of the corresponding bone, which might infer a similar mode of tooth development as described in the lepisosteiform fish “*Lepidotes*” (Peyer, 1954). Based on the observations obtained from *Akromystax tilmachiton*, Poyato-Ariza and Wenz (2005) suggested that a formation of posterior additional, non-successional prearticular teeth was possible in pycnodontiform fishes, probably in order to compensate simultaneous tooth abrasion, which generally first affected anterior teeth and later those positioned in the posterior part of the tooth plate. Similar teeth positioned in occlusally open sockets posterior to functional teeth are commonly present in pycnodontiforms (e.g.,

Kriwet, 2005:fig. 23). The micro-CT generated transverse slices of *Grimmenodon aureum*, gen. et sp. nov. undoubtedly reveal the absence of neither non-functional teeth nor developing tooth germs preserved within the prearticular tooth plate. Otherwise, the posterior-most tooth preserved in the main prearticular tooth row in *Grimmenodon aureum*, gen. et sp. nov. is less elevated and still partially covered by spongy bone, which might suggest that this tooth was not yet fully functional and still developing at the time of death, thus giving further credence to the interpretation of additional non-successional tooth development initiated inside the posterior part of the prearticular tooth plate. Assuming this interpretation to be correct, it is conceivable that at this stage of development, the tooth was growing in height while the spongy bone covering of the tooth crown was resorbed, similar to the condition seen in the extant durophagous teleost *Anarhichas lupus* (Bemis and Bemis, 2015). During further development, the tooth crown could grow in width and length to occupy the available space between adjacent teeth. Given to the limited available space, this stage of development was probably occasionally accompanied by a reorientation of the major tooth axes, as suggested by some teeth in the first and second lateral row.

PYCNODONTIFORMES gen. et sp. indet.

(Fig. 4)

**Referred Material**—MV 202615, an isolated tooth crown.

**Locality and Horizon**—Abandoned open-cast clay pit of Grimmen (Mecklenburg-Western Pomerania, Germany); *Pleuroceras apyrenum* subzone (*Pleuroceras spinatum* zone, upper Pliensbachian, Early Jurassic) (see Ernst, 1991).

**Description**—The tooth crown is low and oval in occlusal view with the minor axis being 1.48 times that of the major axis. The occlusal surface shows no apical indent or ornamentation.

**Comparison**—The oval occlusal outline of MV 202615 and the absence of an associated enameloid collar (= “Schmelzmanschette”; Mudroch and Thies, 1996; see also Kriwet, 2005) is typical for pycnodontiform molariform teeth. The absence of tooth ornamentation, however, prevents more detailed comparisons but seems to differentiate it from the new taxon described above. In consequence, MV 202615 is identified here as Pycnodontiformes gen. et sp. indet.

## PALEOBIOGEOGRAPHIC AND ECOLOGICAL IMPLICATIONS

The two fossil specimens described herein represent the first reliable records of pycnodontiform fishes from the late Early Jurassic, complementing previous finds of early representatives of this distinctive group of basal neopterygians, which remain particularly scarce, especially in comparison to the rich and diversified pycnodontiform faunas obtained from the Late Jurassic and Late Cretaceous (Kriwet, 2001a, 2001b; Poyato-Ariza and Martín-Abad, 2013). So far, the material constitutes the north-easternmost records of pycnodontiform fishes from Europe, confirming their presence before and immediately following the onset of the T-OAE in marginal marine ecosystems of the NGB south of the Fennoscandian Shield. However, it has to be mentioned that the fossil specimens also could be allochthonous, and therefore, these forms might have inhabited more suitable areas during that time, such as the near-shore lagoonal depositional environments referred to the Bagå Formation of Bornholm, Denmark (Koppelhus and Nielsen, 1994). The almost complete preservation and the lack of substantial signs of erosion seen in the prearticular of *Grimmenodon aureum*, gen. et sp. nov., at least, argues against an extensive post-mortem transport and reworking. Conversely, the herein described indeterminate molariform pycnodontiform tooth crown recovered from the sandy, shallow-marine upper Pliensbachian co-occurred with abundant chondrichthyan remains that have massively suffered from post-mortem damage in many places (SS pers. obs.), suggesting reworking and redistribution generated by current activities.

Significantly, the recognition of a pycnodontiform fish remain in the “Green Series” alters the perception of faunal and paleoecological interactions in the marine vertebrate biota obtained from this unit, separating it from all other time-equivalent marine vertebrate communities reported from different localities all over Europe (Wenz, 1968; Hauff and Hauff, 1981; Urlichs et al., 1994; Delsate, 1999; Vincent et al., 2013; Hauff et al., 2014; Williams et al., 2015). This disparity, combined with the interpretation that these localities largely document more open-marine depositional environments, is in good accordance with the interpretation that pycnodontiforms were predominantly linked to marginal marine environments, as inferred from paleobiogeographical and ecomorphological evidence (Kriwet, 2001a, 2001b; Kriwet and Schmitz, 2005; Poyato-Ariza, 2005; Martín-Abad and Poyato-Ariza, 2013). This specific distribution pattern can be probably related to diverse environmental and/or biological constraints, such as swimming capacities and the availability of preferred food resources, but also to preservation biases (Poyato-Ariza, 2005).

With regard to the robust molariform dentition seen in the prearticular of *Grimmenodon aureum*, gen. et sp. nov., this taxon appears to have been well-adapted to

durophagy, inferring a predominant diet of especially hard food items. Taking into consideration the fossil assemblage recovered from the lower Toarcian “Green Series”, potential food resources for durophagous fish include ammonites, the supposed facultative pseudoplanktonic inoceramid bivalve *Pseudomytoides dubius*, and the holoplanktonic coelodiscid gastropod *Coelodiscus minutus*, as well as crustaceans. In this context, it is interesting to note that the “Green Series” also yielded remains of the basal neopterygian fish *Dapedium* (Dapediiformes) (Oertel, 1921; SS pers. obs.), which is interpreted as well-adapted to durophagy, as seen in the functional morphology of the jaw and tooth morphology (Smithwick, 2015), but see Thies and Hauff (2011), who consider *Dapedium* to be a generalist feeder.

The Early Jurassic neopterygians *Lepidotes* and *Tetragonolepis*, which are considered to be at least facultative durophagous based on their dentitions (e.g., Quenstedt, 1847; Woodward, 1897; Thies, 1991), also are known from the “Green Series” (Jaekel, 1929; Malzahn, 1963; Thies, 1989; Ansorge, 2007; Zessin and Krempien, 2010). Although dental evidence is suggestive of ecological niche overlap, the disparity in morphological adaptations in *Dapedium*, *Tetragonolepis*, and *Lepidotes* is likely to have played a role in the foraging mode, and consequently, in the segregation of available food resources. Notwithstanding, the fact that the body and fin forms of *Grimmenodon aureum*, gen. et sp. nov. remain unknown, it is intriguing to note that the deep-bodied and laterally flattened dapediiform fishes *Dapedium* and *Tetragonolepis* fall within the general morphospace occupation area of pycnodontiforms (Fig. 5), which indicates taxa well-adapted to manoeuvring as well as generalist swimming forms (see Poyato-Ariza, 2005). Accordingly, based on indirect evidence, it seems reasonable to conclude that *Grimmenodon aureum*, gen. et sp. nov. was in competition with taxa like *Dapedium* and *Tetragonolepis*, and may have used alternative strategies in order to partition food resources efficiently and avoid direct competition.

## LATE TRIASSIC-EARLY JURASSIC DIVERSITY PATTERNS

The Triassic-Jurassic mass extinction event is one of the “big five” Phanerozoic extinction events with a loss of almost 50% of marine genera and significant terrestrial faunal and floral turnovers (e.g., Raup and Sepkoski, 1982; Youbi et al., 2014). The early history of pycnodontiform fishes still is poorly understood and their diversity patterns across this important biotic event have not been established so far, because many species are in need of revision or must be considered dubious. This is because pycnodontiforms from the Early and

Middle Jurassic are sparse and mainly represented by isolated vomerine and prearticular dentitions.

It nevertheless is evident that pycnodontiforms first appeared in the Late Triassic of central Europe (Kriwet, 2001b) and three genera and species, *Brembodus ridens*, *Eomesodon hoferi*, and *Gibbodon cenensis* were reported from the upper Norian of the northern Tethys margin (Gorjanović-Kramberger, 1905; Tintori, 1981). Additional Norian pycnodontiform records of uncertain affinities but different from the three other Triassic pycnodontiforms were reported from epicontinental seas covering Belgium and Luxembourg (Delsate and Kriwet, 2004). Isolated teeth from the Rhaetian of Grozou, France, assigned to the pycnodontiform *Gyrodus milinum* by Henry (1876) represent teeth of *Colobodus* sp. Therefore, at least four different pycnodontiform taxa occurred prior to the end-Triassic event.

Early Jurassic pycnodontiform records are very rare and restricted to central Europe coming from few stratigraphic levels. Obviously, the pycnodontiforms *Gibbodon* and *Brembodus* vanished before, or in conjunction with the Triassic-Jurassic mass extinction event. Only the genus *Eomesodon* can be considered to have crossed this boundary and is present with a single species, *E. liassicus*, in the Sinemurian (Saint-Seine, 1949; Gardiner, 1960). So far, no pycnodontiform records from the earliest Jurassic (Hettangian) have been reported. The apparent taxonomic diversity reduction in the Early Jurassic supports the supposition that pycnodontiform fishes also were affected by the Triassic-Jurassic mass extinction event pending further analyses employing rigorous statistical procedures. However, the new pycnodontiform remains described here come from the Pliensbachian and Toarcian and thus increase the standing diversity of pycnodontiforms in the Early Jurassic significantly. When corrected for sample size differences (excluding ambiguous taxa), it is evident that Early Jurassic pycnodontiform fish diversity more or less equaled that of the Late Jurassic accepting the poor collection effort and restricted facies occurrences during the Early Jurassic. Nevertheless, we hypothesize that pycnodontiform fishes were not or only marginally affected by the Triassic-Jurassic mass extinction event according to our current knowledge.

By the Middle Jurassic, pycnodontiform fishes seemingly became more abundant and divers but still are represented mainly by isolated remains of several genera occurring in almost all stratigraphic stages (Bajocian: *Gyrodus* sp. (Grey-Egerton, 1869); Bathonian: *Eomesodon rugulosus*, *E. trigonus*, *Coelodus* sp., *Macromesodon bucklandi* (= *M. damoni*), *M. bathonicus*, *M. boloniensis*, *M. discoides*, *M. gervaisi*, *M. oblongus*, *M. radiatus*, *M. tenuidens*, *Proscinetes biserialis*, and *Stemmatodus* sp. (e.g., Agassiz, 1833–1844; Bassani, 1885; Sauvage, 1867, 1880a, 1880b; Woodward, 1890, 1892, 1895; Kriwet et al., 1997);

Callovian: *Gyrodus* sp., *Mesturus leedsi* (Galton et al., 1980; Rioult and Mourdon, 1982)). Cavin et al. (2009) described a single right prearticular from the Middle-Late Jurassic of Mab Ching in the Khlong Min Formation, Thailand, which these authors tentatively referred to *Gyrodus* sp. The taxonomic validity of most of these taxa, however, remains ambiguous for the moment (see also above) but indicate nevertheless a possible increase in diversity and that pycnodontiforms achieved a very wide distribution early in their evolutionary history. More detailed analyses of these remains will provide a better understanding of early pycnodontiform diversity patterns in the future.

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## FIGURE CAPTIONS

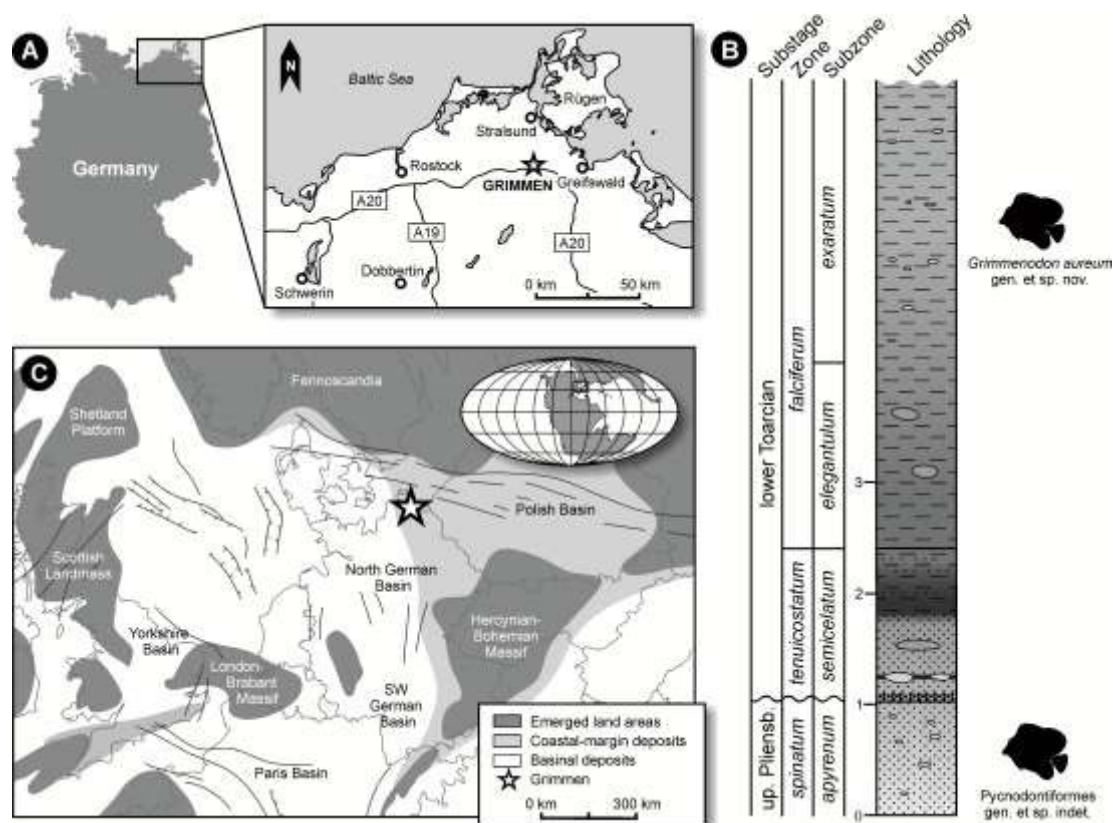


FIGURE 1. **A**, Geographical location map. **B**, Stratigraphic standard section of the late Early Jurassic succession exposed in the Grimmen clay pit (wavy line indicates hiatus at the Pliensbachian-Toarcian transition), with stratigraphic position of *Grimmenodon aureum*, gen. et sp. nov., GG 437, holotype, and *Pycnodontiformes* gen. et sp. indet., MV 202615. **C**, Rough reconstruction of Toarcian paleogeography of central and western Europe (modified from Stumpf, 2016). [Intended for page width]



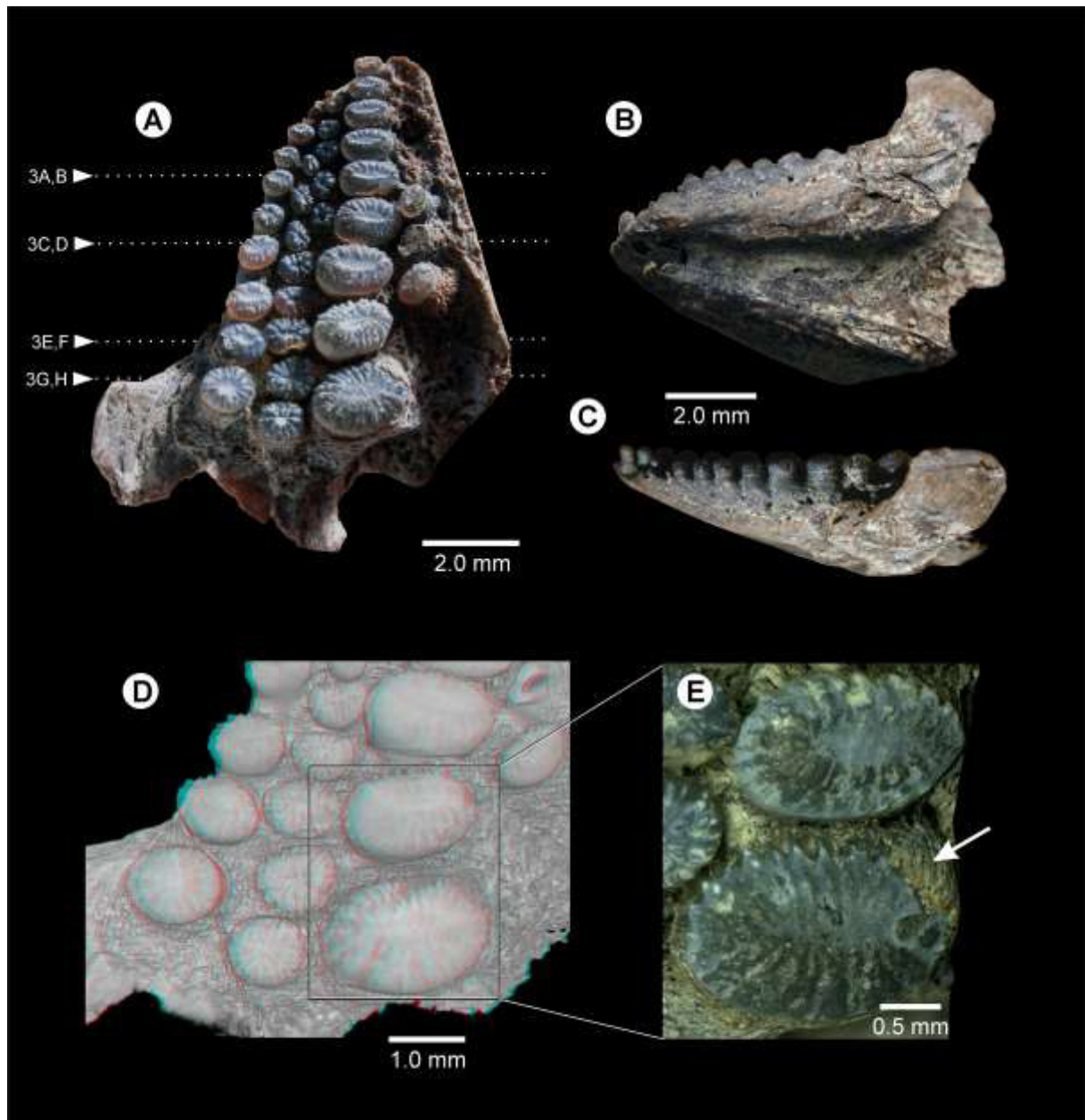


FIGURE 2. *Grimmenodon aureum*, gen. et sp. nov., GG 437, holotype, an isolated, almost complete left prearticular with dentition from the lower Toarcian of Grimmer, Mecklenburg-Western Pomerania, Germany, in (A) occlusal view (the positions of micro-CT generated transverse slices (see Fig. 3) are indicated (3A,B–3G,H), (B) ventral, and (C) oral view. D, 3D isosurface model from micro-CT scan showing the posterior part of the tooth plate. E, occlusal close-up views of the posterior-most two teeth positioned on the main row (arrows indicate spongy bone covering part of the occlusal surface). [Intended for page width]

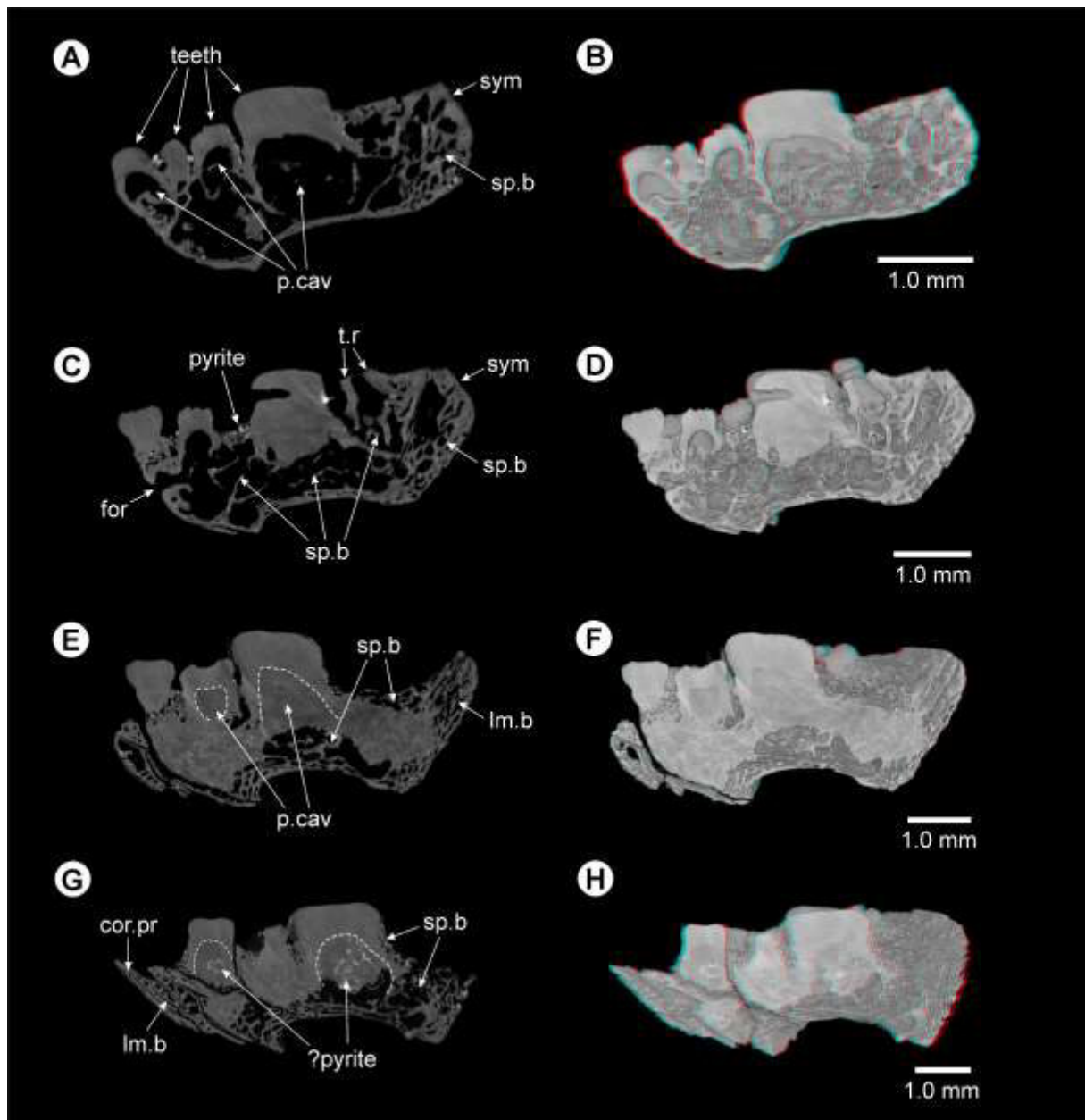


FIGURE 3. *Grimmenodon aureum*, gen. et sp. nov., GG 437, holotype, from the lower Toarcian of Grimmen, Mecklenburg-Western Pomerania, Germany. **A–H**, digitally reconstructed 2D and 3D transverse slices from micro-CT scan (the positions of the transverse section planes are shown in Fig. 2A). Light colors indicate denser materials; gray colors indicate less dense materials. Dashed lines indicate boundary of pulp cavities. [Intended for page width]

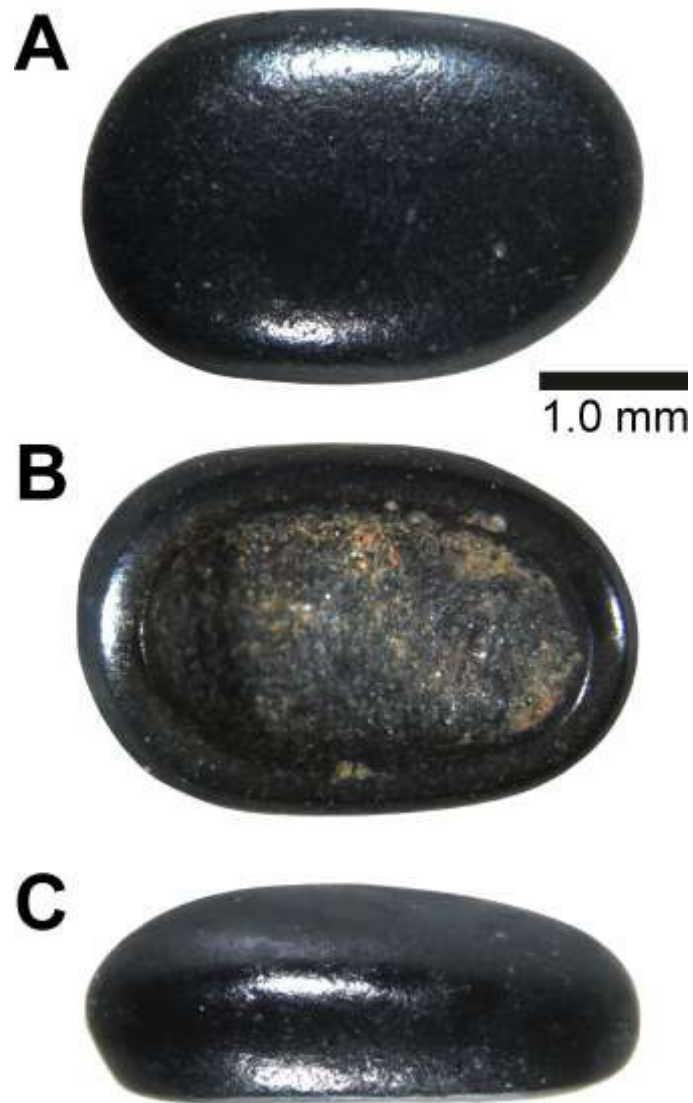


FIGURE 4. *Pycnodontiformes* gen. et sp. indet., MV 202615, an isolated tooth crown from the upper Pliensbachian of Grimmen, Mecklenburg-Western Pomerania, Germany, in (A) occlusal, (B) basal, and (C) lateral view. [Intended for column width]

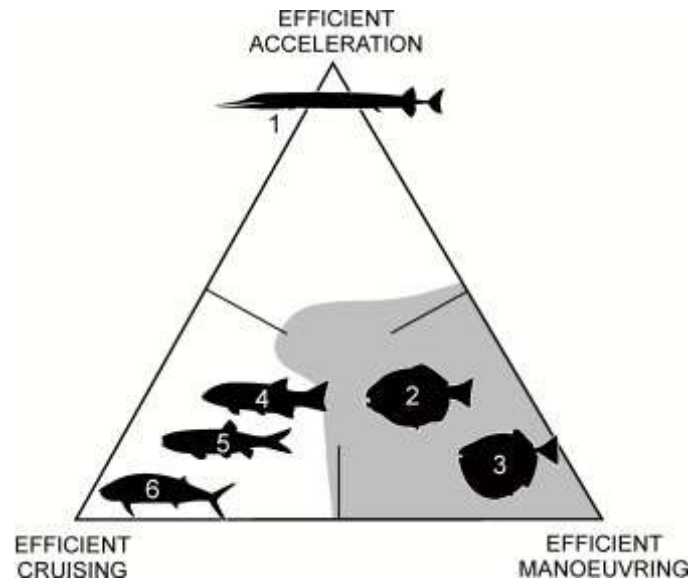


FIGURE 5. Functional morphospace of body and fin morphology defining swimming capacities (modified from Webb, 1984), as tentatively applied to the “Green Series” actinopterygian ichthyofauna (1, *Saurorhynchus* (Saurichthyiformes); 2, *Dapedium* (Dapediiiformes); 3, *Tetragonolepis* (Dapediiiformes); 4, *Lepidotes* (Lepisosteiformes); 5, *Leptolepis* (Teleostei); Pachycormiformes; data from Thies, 1991; Thies and Waschke, 2015; SS pers. obs.), with tentative pycnodontiform occupation area (shaded in light grey; adapted from Poyato-Ariza, 2005). [Intended for column width]

TABLE 1. Morphometric data of *Grimmenodon aureum*, gen. et sp. nov., GG 437, holotype (all measurements are given in mm). **Abbreviations:** **MdR**, medial tooth row; **MR**, main tooth row; **LR1**, first lateral tooth row; **LR2**, second lateral tooth row; **LR3**, third lateral tooth row; **NTM**, number of complete teeth preserved on tooth row; **MxWT(R)**, maximum width of teeth (refers to the greatest length available, regardless of tooth orientation) and variation of measurements (as indicated by (R)); **MxLT(R)**, maximum length of teeth and variation of measurements (refers to the shortest length available) and variation of measurements; **aMxWT/MxLT**, average of relative length proportions.

	NTM	MxWT(R)	MxLT(R)	aMxWT/MxLT
MdR	2	0,61-0,8 (0,19)	0,43-0,49 (0,06)	1.53
MR	9	0,53-2,27 (1,74)	0,3-1,51 (1,21)	1.58
LR1	5	0,43-0,67 (0,24)	0,38-0,56 (0,18)	1.13
LR2	8	0,45-1,02 (0,52)	0,36-0,88 (0,52)	1.21
LR3	8	0,6-1,15 (0,55)	0,41-0,98 (0,57)	1.22

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