



Early Jurassic Diversification of Pycnodontiform Fishes (Actinopterygii, Neopterygii) after the End-Triassic Extinction Event: Evidence from A New Genus and Species, *Grimmenodon aureum*

Authors: Stumpf, Sebastian, Ansorge, Jörg, Pfaff, Cathrin, and Kriwet, Jürgen

Source: Journal of Vertebrate Paleontology, 37(4)

Published By: The Society of Vertebrate Paleontology

URL: <https://doi.org/10.1080/02724634.2017.1344679>




BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

EARLY JURASSIC DIVERSIFICATION OF PYCNODONTIFORM FISHES (ACTINOPTERYGII, NEOPTERYGII) AFTER THE END-TRIASSIC EXTINCTION EVENT: EVIDENCE FROM A NEW GENUS AND SPECIES, *GRIMMENODON AUREUM*

SEBASTIAN STUMPF ^{*,1} JÖRG ANSORGE,¹ CATHRIN PFAFF ² and JÜRGEN KRIWET ²

¹Institute of Geography and Geology, University of Greifswald, Friedrich-Ludwig-Jahn-Straße 17A, 17489 Greifswald, Germany, sebastian.stumpf@stud.uni-greifswald.de; ansorge@uni-greifswald.de;

²University of Vienna, Department of Palaeontology, Geozentrum, Althanstraße 14, 1090 Vienna, Austria, cathrin.pfaff@univie.ac.at; juergen.kriwet@univie.ac.at

ABSTRACT—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 northeastern 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 early Lower Jurassic 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 greater than previously assumed and probably equaled that of the Late Triassic. 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 prearticular of *Grimmenodon aureum*, gen. et sp. nov. Our results show that no replacement teeth were formed within the tooth-bearing bone but rather were added posteriorly to functional teeth.

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

Citation for this article: Stumpf, S., J. Ansorge, C. Pfaff, and J. Kriwet. 2017. Early Jurassic diversification of pycnodontiform fishes (Actinopterygii, Neopterygii) after the end-Triassic extinction event: Evidence from a new genus and species, *Grimmenodon aureum*. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2017.1344679.

INTRODUCTION

Extinct pycnodontiform fishes (the ‘pycnodonts’), which are a morphologically and ecologically distinctive group of basal neopterygians (Nursall, 1996b, 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 jaw and the paired prearticulars in the lower jaw. 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 water- to freshwater-influenced deposits of Mesozoic and Palaeogene ages (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 taxa consequently remains ambiguous. Nevertheless, Longbottom (1984), Kriwet (1999, 2005,

*Corresponding author.

© Sebastian Stumpf, Jörg Ansorge, Cathrin Pfaff, and Jürgen Kriwet.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

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 taxon assignment and establishing reliable diagnoses. The importance of recognized autapomorphic characters in phylogenetic analyses, however, needs to be tested.

The oldest remains of pycnodontiform fishes, which comprise both complete skeletons and isolated dentitions, are known from 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 mass extinction event, conversely, is extremely scarce. So far, a single species and at least 12 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 after the Triassic-Jurassic extinction event was greater than previously assumed.

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

GEOLOGICAL AND STRATIGRAPHIC SETTING

Although laterally persistent in northeastern Germany, outcrops of Mesozoic strata are rare (e.g., Katzung, 2004). Early Jurassic strata only crop out in the abandoned open-cast clay pits of Grimmen and Dobbartin (Fig. 1A), both representing parautochthonous successions of upper Pliensbachian to lower

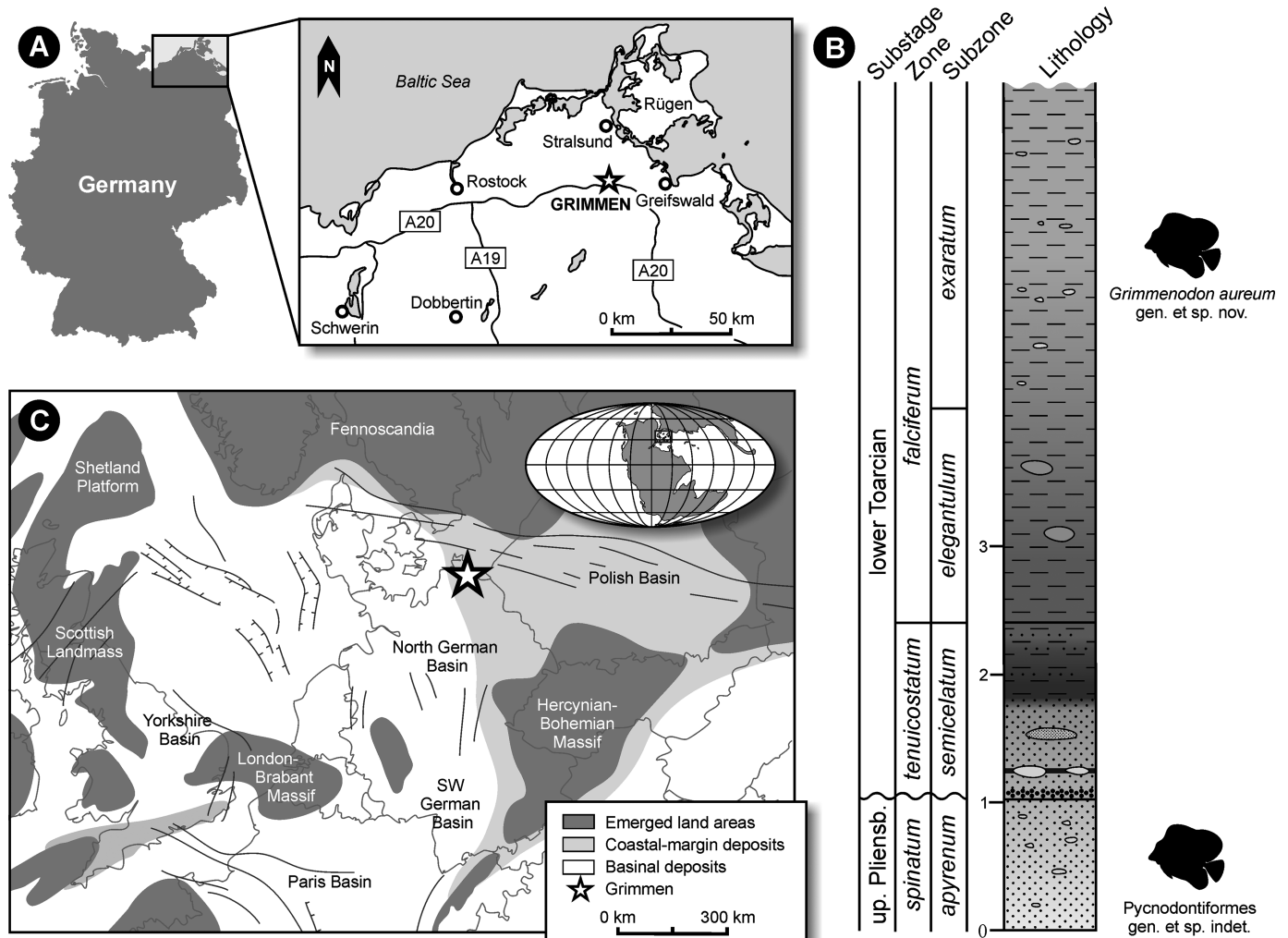


FIGURE 1. **A**, geographical location map. **B**, stratigraphic standard section of the late Early Jurassic succession exposed in the Grimmen clay pit (wavy line indicates hiatus at the Pliensbachian-Toarcian transition), with stratigraphic position of *Grimmenodon aureum*, gen. et sp. nov., GG 437,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

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, respectively, of the Grimmer clay pit (Fig. 1B).

Paleogeographically, the late Early Jurassic succession exposed in the Grimmer clay pit was deposited at the north-eastern edge of the North German Basin (NGB), which was one of the many sub-basins 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 have been described in detail by Ernst (1967, 1991), Prauss (1996), and Ansorge (2007). The upper Pliensbachian interval of Grimmer 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 paper).

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 due to 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 northeastern 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; Röhl and Schmid-Röhl, 2005).

Clay deposits referred to the ‘Green Series’ crop also out in the abandoned Dobbertin clay pit. However, unlike those exposed at Grimmer, 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 Grimmer and Dobbertin 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, marine-brackish 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; S.S., pers. observ.). The fauna mainly comprises actinopterygians (e.g., Jaekel, 1929; Malzahn, 1963; Thies, 1989; Ansorge, 2007; Ansorge and Obst, 2015; Konwert and Stumpf, 2017; Maxwell and Stumpf, 2017), followed by marine reptiles (Maisch and Ansorge, 2004; Stumpf, 2016) and rare chondrichthyans (Ansorge, 2007). These faunal elements occur alongside an extraordinarily rich terrestrial entomofauna (Ansorge, 1996, 2003), indicating the presence of suitable environments nearby. The ‘Green Series’ of Grimmer has 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 nearshore depositional environment, as proposed by Ernst (1967, 1991) and Ansorge (2003).

Significantly, the boundary between the *tenuiscostatum* 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 the onset of the T-OAE.

MATERIALS 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 (J.A.) 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, lending it a somewhat gilded appearance. The second specimen, MV 202615, an isolated pycnodontiform tooth crown, 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 Grimmer site, which started in 1959–1960 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-computed tomography (micro-CT) device (Bruker/Skyscan 1173 housed at the Department of Palaeontology, University of Vienna). With an image pixel size of 7.13 μm and an X-ray beam set at 50 kV, 160 μA , the average of three frames were taken under the rotation step of 2°.

Following the description of the new taxon, we provide a review of the Early and Middle Jurassic fossil record of pycnodontiforms and finally compare the standing diversity with that of the Late Triassic.

Terminology—The morphological terminology used in the text follows that of Nursall (1996b, 1999). Consequently, we use the term ‘coronoid process’ here, although this structure cannot be considered homologous to the coronoid process in non-pycnodontiform neopterygians, where it is formed by the dentary, the surangular, and/or the angular.

SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Cope, 1887

NEOPTERYGII Regan, 1923

PYCNODONTIFORMES Berg, 1937

GRIMMENODON, gen. nov.

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

Diagnosis—Pycnodontiform fish showing the following unique combination of morphological characters: Prearticular with rather short and narrow symphysis; coronoid process rather low in dorsoventral directions; 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.

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

GRIMMENODON AUREUM, sp. nov.

(Figs. 2, 3)

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

Holotype—GG 437, left prearticular bone with dentition.

Locality and Horizon—Abandoned open-cast clay pit of Grimmen (Mecklenburg-Western Pomerania, Germany); *Harpoceras exaratum* subzone (*Harpoceras falciferum* zone, lower Toarcian, Early Jurassic) (see Ansorge, 2007).

Diagnosis—As for genus (by monotypy).

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

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 symphysis 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 wall that demarcates part of the posteromedial margin of the bone. The coronoid process is rather low in dorsoventral height, 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 posterolaterally beyond the tooth plate to form an elevated and anteroposteriorly elongated ridge in ventral view

(Fig. 2A, C), which is consistent with Nursall's (1996b) 'coronoid ridge.' 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 (Fig. 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 (Fig. 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 positioned 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 the 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. The furrow is medially demarcated by the bony lamella that extends posteriorly from the symphysis part of the posteromedial 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 the main teeth) and have 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 with 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 with those arranged in the first and second lateral rows. 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 the 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

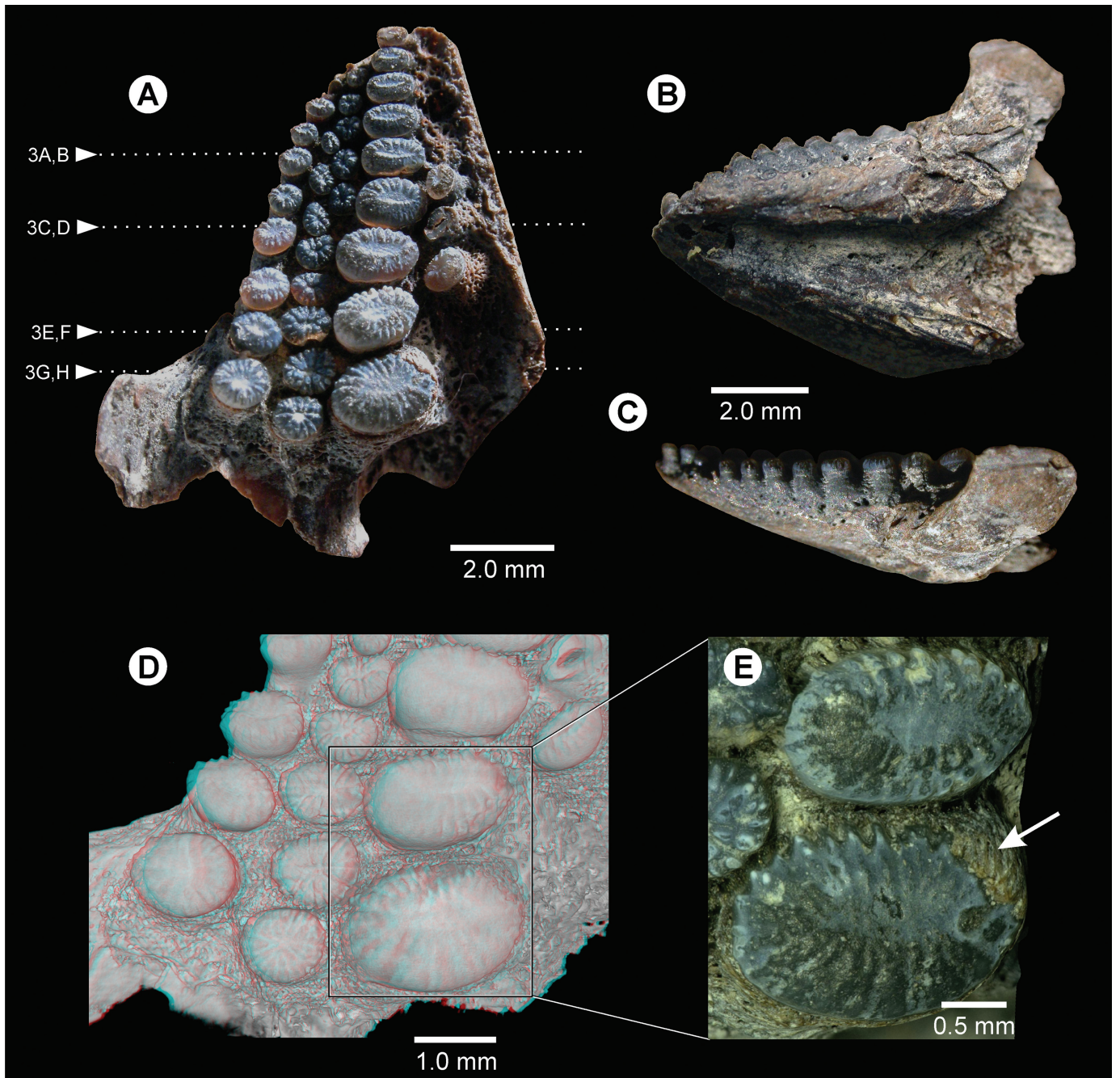


FIGURE 2. *Grimmerodon aureum*, gen. et sp. nov., GG 437, holotype, an isolated, almost complete left prearticular with dentition from the lower Toarcian of Grimmen, Mecklenburg-Western Pomerania, Germany, in **A**, occlusal (the positions of micro-CT-generated transverse slices [see Fig. 3] are indicated [3A, B–3G, H]), **B**, ventral oblique, and **C**, lateral views (anterior to the left). **D**, 3D model from micro-CT scan showing the posterior part of the tooth plate (image presented as red-cyan stereo anaglyph; use red-cyan glasses to view). **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).

of the teeth slightly overhang the dorsolateral margin of the prearticular (Fig. 2B).

The teeth are mounted on pedicles, which are clearly visible in lateral view, and numerous minute foramina are irregularly aligned along the dorsolateral surface of the prearticular (Fig. 2C). Internally, the tooth-bearing bone exhibits an irregularly spongy texture (Fig. 3), similar to the condition seen in a sectioned prearticular of *Gyrodus cuvieri* Agassiz, 1844, figured by Nursall (1996b:fig. 8; see also Kriwet, 2005:fig. 23). However, the micro-CT transverse slice shows spatial differences in the

development of the internal spongy bone, in particular in the symphyseal region, where the irregularly arranged spongy bone is more strongly developed and even more densely packed, which is probably accompanied by enhanced jaw adductor forces (see Kriwet, 2001c, 2004). In addition, the coronoid process and the posteromedially extending bony wall show a slightly more regularly arranged spongy bone texture, giving a somewhat fibro-lamellar appearance to it (Fig. 3E–H).

The minute foramina aligned along the dorsal margin of the lateral surface below the third lateral tooth row of the

TABLE 1. Morphometric data (in mm) of *Grimmenodon aureum*, gen. et sp. nov., GG 437, holotype.

Element	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

Abbreviations: **aMxWT/MxLT**, average of relative length proportions; **LR1**, first lateral tooth row; **LR2**, second lateral tooth row; **LR3**, third lateral tooth row; **MdR**, medial tooth row; **MR**, main tooth row; **MxLT(R)**, maximum length of teeth and variation of measurements (refers to the shortest length available) and variation of measurements; **MxWT(R)**, maximum width of teeth (refers to the greatest length available, regardless of tooth orientation) and variation of measurements (as indicated by '(R)'); **NTM**, number of complete teeth preserved in tooth row.

tooth-bearing bone communicate via short bony tubes with internal spaces in between the spongy bone, as visible in the digitally reconstructed micro-CT transverse sections of the prearticular (Fig. 3C, D). However, it should be noted that the spaces within the posterior portion of the prearticular are partially filled with matrix, which has a density that is slightly less than the surrounding bone tissue (Fig. 3E–H). Occasionally, these matrix-filled areas are enriched in an indeterminate material of high density (Fig. 3G, H) similar to the pyrite that covers parts of the occlusal surface of the bone (Fig. 3C, D).

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 bone tissue, and there is no indication of developing tooth germs or non-functional teeth inside the tooth-bearing bone adjacent to or below erupted teeth. Distinction between circumpolar dentine, pallial dentine, and acrodin cap (see Kriwet, 2005) was not possible based on the micro-CT scan.

COMPARISON AND DISCUSSION

So far, only a single Early Jurassic pycnodontiform species, *Eomesodon liassicus* (Egerton, 1855) 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* (J.K., pers. observ.). 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 is, however, considered 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, because the fossil specimens pictured by Pászti (2004:figs. 1, 2) are not actually pycnodontiforms. Moreover, it is to be noted that Pászti's (2004:fig. 3) line drawing of "*Eomesodon* sp." is adapted from that of *Stemmato-dus rhombus* (Agassiz, 1844) 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* (Agassiz, 1844), *E. trigonus* (Buckland, 1837), *Macromesodon bucklandi* (Agassiz, 1844), *M. discoides* (Agassiz, 1844), *M. oblongus* (Agassiz, 1844), *M. tenuidens* (Woodward, 1890), and *Proscinetes biserialis* (Agassiz, 1844) (Woodward, 1890, 1892, 1895). In addition, isolated dentitions attributed to different species of *Macromesodon* also were reported from the Bathonian of France, including *M. bathonicus* (Sauvage, 1880b), *M. boloniensis* (Sauvage, 1867), *M. discoides*, *M. gervaisi* (Sauvage, 1867), and *M. radiatus* (Agassiz, 1844) (Sauvage, 1867, 1880a, 1880b). Furthermore, pycnodontiform teeth of Bathonian age were described from France (Kriwet et al., 1997) and Italy (Bassani, 1885). The taxonomy of Bathonian pycnodontiforms, however, is very poorly understood. For instance, as 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* (Agassiz, 1834), *M. gibbosus* (Wagner, 1851), and *M. surgens* (Poyato-Ariza and Wenz, 2002) 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

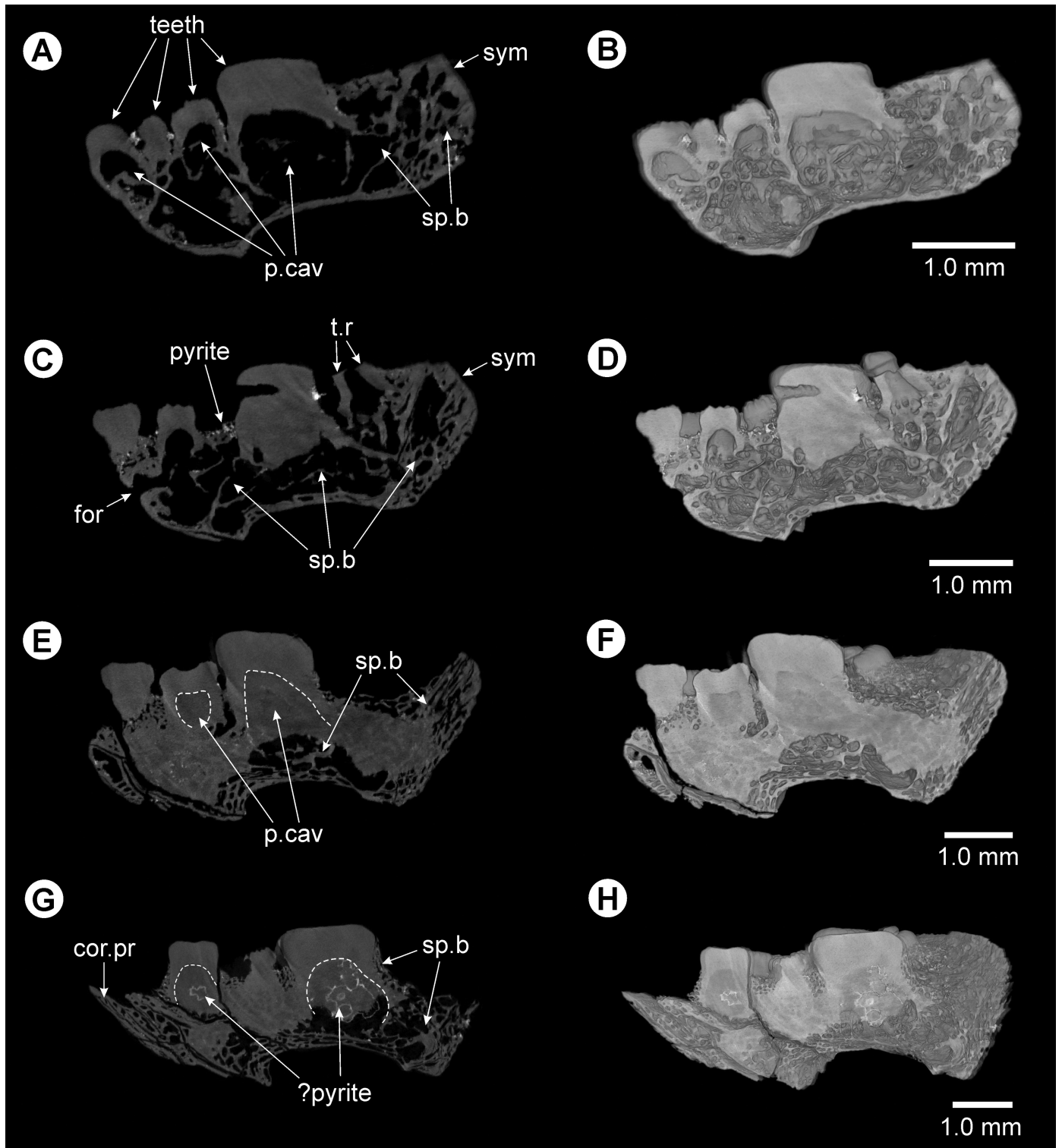


FIGURE 3. *Grimmerodon aureum*, gen. et sp. nov., GG 437, holotype, from the lower Toarcian of Grimmen, Mecklenburg-Western Pomerania, Germany. **A–H**, digitally reconstructed 2D and 3D transverse slices from micro-CT scan (the positions of the transverse section planes are shown in Fig. 2A; **B**, **D**, **F**, and **H** are presented as red-cyan stereo anaglyphs, use red-cyan glasses to view). Dashed lines indicate boundary of pulp cavities. **Abbreviations:** cor.pr, coronoid process; for, foramen; p.cav, pulp cavity; sp.b, spongy bone; sym, symphysis; t.r, tooth root.

Stonesfield, Oxfordshire, England, as well as in *Macromesodon gervaisi* (Sauvage, 1867:pl. 2, fig. 4; 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 whether 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, 1844:pl. 19, fig. 10).

Pycnodontiform remains of Callovian age have been rarely reported in the literature. For instance, Kriwet (2008) figured an isolated left prearticular of an indeterminate species of *Athrodon* Sauvage, 1880b, recovered from the Callovian of Falaises des Vaches Noires near Dives-sur-Mer, Calvados, France. Unlike in *Grimmenodon*, gen. et sp. 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* Woodward, 1895, from the Callovian Peterborough Member (formerly named 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-dimensionally 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 the 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 7–10 cm at the time of death, when compared with *Gyrodus* and *Proscinetes* (Licht, 2009; Licht et al., 2015). The strong occlusal sculpturing of the teeth is suggestive of an immature ontogenetic stage, because the vomerine and prearticular dentitions of pycnodontiforms usually become 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 discussed in the literature for many years. For instance, Nursall (1996b) 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 a 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 of their new taxon *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 indicate a similar mode of tooth development as described in the ginglymodian 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 for 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 support 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* Linnaeus, 1758 (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 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 rows.

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—MV 202615 represents an isolated tooth crown. The specimen 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 indentation or ornamentation. There are no signs of breakage at the base of the tooth crown and the lower margin is continuous.

Comparison—The smooth, low oval morphology of MV 202615 is characteristic of pycnodontiform molariform teeth, although this kind of tooth crown morphology also occurs in some ginglymodian fishes (e.g., Jain and Robinson, 1963:pl. 1, fig. 7). However, teeth of ginglymodians usually bear a distinct sheath of collar ganoin that embraces the base of the tooth crown and upper part of the associated tooth neck (e.g., Olsen and McCune, 1991). The collar ganoin in molariform teeth of pycnodontiforms, conversely, is strongly reduced (Kriwet, 2005), and the teeth usually exhibit a distinct constriction at the crown-root junction. Consequently, pycnodontiform tooth crowns typically remain isolated and devoid of an associated tooth neck when broken off, unlike the condition seen in ginglymodians, where teeth mostly display at least remnants of the tooth neck and base (e.g., Mudroch and Thies, 1996; Cuny et al., 2010; Pouech et al., 2015). This provides strong support that MV 202615 can be assigned to Pycnodontiformes. The absence of ornamentation in

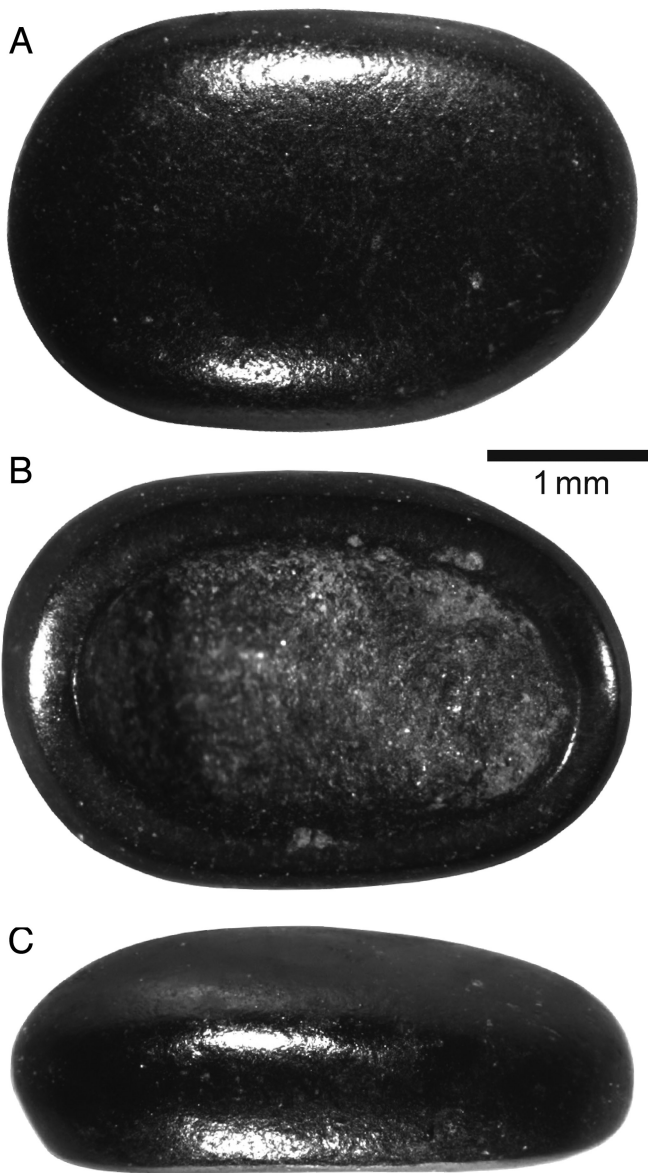


FIGURE 4. Pycnodontiformes, gen. et sp. indet., MV 202615, an isolated tooth crown from the upper Pliensbachian of Grimmen, Mecklenburg-Western Pomerania, Germany, in **A**, occlusal, **B**, basal, and **C**, lateral views.

MV 202615 most likely is due to abrasion and prevents more detailed comparisons with other known pycnodontiforms but seems to differentiate it from the new taxon described above. Consequently, 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 with the rich and diversified pycnodontiform faunas from the Late Jurassic and Late Cretaceous (Kriwet, 2001a, 2001b; Poyato-Ariza and Martín-Abad, 2013). The material constitutes the

northeasternmost records of pycnodontiform fishes from Europe known so far, 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; therefore, these forms might have inhabited more suitable areas during that time, such as the nearshore lagoonal depositional environments referred to the Baga 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, argue against an extensive postmortem transport and reworking, providing some support for the interpretation that the new taxon is autochthonous, but more material is needed to test whether *Grimmenodon aureum*, gen. et sp. nov., formed an obligatory part of the marine vertebrate biota obtained from the lower Toarcian 'Green Series'. 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 suffered massively from postmortem damage in many places (S.S., pers. observ.), suggesting reworking and redistribution generated by current activities.

The presence of a pycnodontiform fish in the lower Toarcian 'Green Series' vertebrate biota separates 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 (Nursall, 1996a; Kriwet, 2001a, 2001b; Kriwet and Schmitz, 2005; Poyato-Ariza, 2005; Martín-Abad and Poyato-Ariza, 2013). This specific distribution pattern probably can be related to diverse environmental and/or biological constraints (Poyato-Ariza and Martín-Abad, 2013), such as swimming capabilities and the availability of preferred food resources, but also to collecting biases.

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 *Pseudomytiloides dubius* (Sowerby, 1829), and the holoplanktonic coelodiscid gastropod *Coelodiscus minutes* (Schübler in Zieten, 1830–1833), as well as crustaceans. In this context, it is interesting to note that the 'Green Series' also yielded remains of the dapediiform neopterygian fish *Dapedium* Leach, 1822 (Oertel, 1921; S.S., pers. observ.), 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* Agassiz, 1832, and *Tetragonolepis* Bronn, 1830, 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

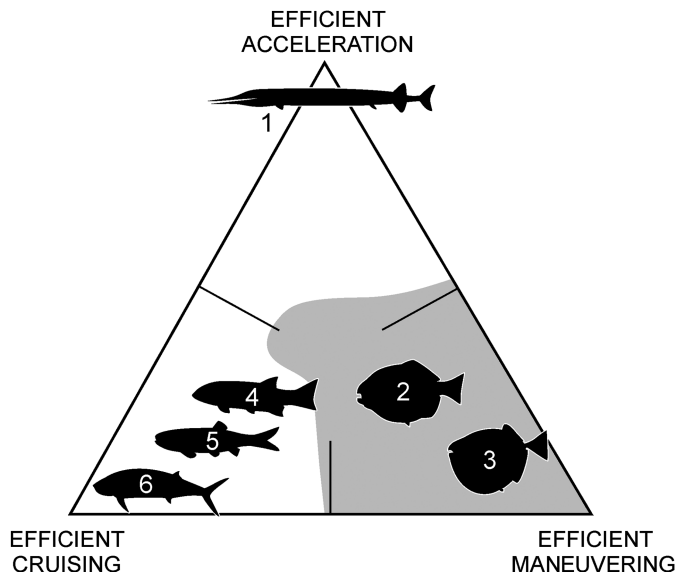


FIGURE 5. Functional morphospace of body and fin morphology defining swimming capacities (modified from Webb, 1984), as tentatively applied to the ‘Green Series’ actinopterygian ichthyofauna (1, *Saurorhynchus* Reis, 1892; 2, *Dapedium* Leach, 1822; 3, *Tetragonolepis* Bronn, 1830; 4, *Lepidotes* Agassiz, 1832; 5, *Leptolepis* Agassiz, 1832; 6, *Pachycormus* Agassiz, 1843; data from Thies, 1991; Thies and Waschkewitz, 2015; Konwert and Stumpf, 2017; S.S., pers. observ.), with tentative pycnodontiform occupation area (in light gray; adapted from Poyato-Ariza, 2005).

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 maneuvering 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 such as *Dapedium* and *Tetragonolepis* and may have used alternative strategies in order to partition food resources 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 turnover (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 rare and mainly represented by isolated vomerine and prearticular dentitions.

Nevertheless, it is evident that pycnodontiforms first appeared in the Late Triassic of central Europe (Kriwet, 2001b), and three genera and species, *Brembodus ridens* Tintori, 1981, *Gibbodon cenensis* Tintori, 1981, and *Eomesodon hoeferi* (Gorjanović-Kramberger, 1905), were reported from the upper Norian of the northern Tethys margin. Additional Norian pycnodontiform records of uncertain affinities were reported from epicontinental seas covering Belgium and Luxembourg (Delsate and Kriwet, 2004). Isolated teeth from the Rhaetian of Grozou, France, described as *Gyrodus milinum* by Henry (1876) represent teeth

of an indeterminate species of the perleidiform fish *Colobodus* Agassiz, 1844. Therefore, at least three 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 Hettangian–Sinemurian (Saint-Seine, 1949; Gardiner, 1960; Delsate et al., 2002). 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 Triassic, taking the poor collection effort and restricted facies occurrences during the Early Jurassic into account. Nevertheless, according to our current knowledge, we hypothesize that pycnodontiform fishes were not or only marginally affected by the Triassic–Jurassic mass extinction event.

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: Bajocian: *Gyrodus* sp. (Grey-Egerton, 1869); Bathonian: *Eomesodon rugulosus*, *E. trigonus*, *Coelodus* sp., *Macromesodon bucklandi*, *M. bathonicus*, *M. boloniensis*, *M. discoides*, *M. gervaisi*, *M. oblongus*, *M. radiatus*, *M. tenuidens*, *Proscinetes biserialis*, and *Stemmatodus* sp. (e.g., Agassiz, 1844; Bassani, 1885; Sauvage, 1867, 1880a, 1880b; Woodward, 1890, 1892, 1895; Kriwet et al., 1997); and Callovian: *Mesturus leedsi*, *Gyrodus* sp., and *Athrodon* sp. (Woodward, 1895, 1896; Galton et al., 1980; Rioult and Mourdon, 1982; Kriwet, 2008). 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 nevertheless indicate 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.

CONCLUSIONS


The new Early Jurassic pycnodontiform material shows that their diversity after the Triassic–Jurassic mass extinction seemingly was greater than previously assumed. Unfortunately, however, the fossil record of Early and Middle Jurassic pycnodontiforms is strongly biased towards isolated dental remains that either have not yet been described and taxonomically identified or included in phylogenetic analyses for establishing diversification and radiation events. Therefore, it is not possible to employ robust statistical analyses. The standing diversity (i.e., raw numbers of taxa) of pycnodontiforms continuously increased from the Late Triassic to the Middle Jurassic. All Early Jurassic records are restricted to central Europe and have been recovered from few stratigraphic levels up to now. By the Middle Jurassic, pycnodontiform fishes seemingly became more abundant and taxonomically diverse and also are known from outside Europe. This, however, might not be the result of range extensions in the late Early or Middle Jurassic but most likely is related to collecting biases in the Early Jurassic. Detailed


modern morphological, taxonomic descriptions and revisions of known material, as well as additional material, are necessary to establish statistically supported diversification and diversity patterns in the future.


ACKNOWLEDGMENTS

S.S. is indebted to I. Hinz-Schallreuter (GG) for her continuous help and support. K. Obst (MV) is acknowledged for providing access to the collection in his care. S. Meng and M. Konwert (both GG), G. Kaineder (Department of Palaeontology, University of Vienna), M. Hörnig (Zoological Institute and Museum, University of Greifswald), and M. Ebert (Jura-Museum Eichstätt) are thanked for valuable suggestions and discussions. A. López-Arbarello (Bayerische Staatssammlung für Paläontologie und Geologie, Munich) and G. Arratia (University of Kansas) provided comments that improved the manuscript. S.S. was financially supported by a Ph.D. scholarship of Mecklenburg-Western Pomerania. Financial support for this project also was provided by the Austrian Science Fund (FWF: P29796-B29) to J.K.

ORCID

Sebastian Stumpf  <http://orcid.org/0000-0002-1945-2387>

Cathrin Pfaff  <http://orcid.org/0000-0001-5539-2097>

Jürgen Kriwet  <http://orcid.org/0000-0002-6439-8455>

LITERATURE CITED

- Agassiz, L. 1832. Untersuchungen über die fossilen Fische der Lias-Formation. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 3:139–149.
- Agassiz, L. 1834. Feuilleton additionel sur les Recherches sur les Poissons fossiles—part 1. Petitpierre, Neuchâtel, 20 pp.
- Agassiz, L. 1843. Recherches sur les Poissons fossiles—Vol 2, part 1. Petitpierre, Neuchâtel, 72 pp.
- Agassiz, L. 1844. Recherches sur les Poissons fossiles—Vol 2, part 2. Petitpierre, Neuchâtel, 263 pp.
- Ansonge, J. 1996. Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). Neue Paläontologische Abhandlungen 2:1–132.
- Ansonge, J. 2003. Insects from the Lower Toarcian of Middle Europe and England. Proceedings of the Second Palaeontomological Congress, Kraków, 2001. Acta Zoologica Cracoviensia 46(Supplement Fossil Insects):291–310.
- Ansonge, J. 2007. Lower Jurassic clay pit of Klein Lehmhagen near Grimmen; pp. 37–41 in R.-O. Niedermeyer, R. Dobracki, and K. Schütze (eds.), Geo-Pomerania—Excursion Guide. Biuletyn Państwowego Instytutu Geologicznego 424.
- Ansonge, J., and G. Grimmerberg. 2016. Grätensandsteine und andere Geschiebe des oberen Lias (Toarcium) aus Norddeutschland. Geschiebekunde aktuell 32:121–141.
- Ansonge, J., and K. Obst. 2015. Lias-Tongrube bei Dobbartin; pp. 227–240 in A. Börner, R.-O. Niedermeyer, and K. Schütze (eds.), 79. Tagung der Arbeitsgemeinschaft Norddeutscher Geologen—Tagungsband und Exkursionsführer. Schriftenreihe des Landesamtes für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern 1.
- Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements; pp. 265–334 in G. Arratia and H.-P. Schütze (eds.), Mesozoic Fishes 2—Systematics and Fossil Record. Verlag Dr. Friedrich Pfeil, Munich.
- Bassani, F. 1885. Avanzi di pesci oolitici nel Veronese. Atti della Società Italiana di Scienze Naturali 23:142–163.
- Bemis, K. E., and W. E. Bemis. 2015. Functional and developmental morphology of tooth replacement in the Atlantic Wolffish, *Anarhichas lupus* (Teleostei: Zoarcoidei: Anarhichadidae). Copeia 103:886–901.
- Berg, L. S. 1937. A classification of fish-like vertebrates. Bulletin de l'Académie des Sciences de l'URSS, Classe de Sciences mathématiques et naturelles 4:1277–1280.
- Bronn, H. 1830. Ueber zwei fossile Fischarten: *Cyprinus coryphaenoides* und *Tetragonolepis semicinctus* aus dem Gryphitenkalke bei Donau-Eschingen. Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1:14–30.
- Buchholz, A. 2012. Das Domerium im Lias-Aufschluss des Tontagebaues von Klein Lehmhagen bei Grimmen/Vorpommern (Nordostdeutschland)—ein Überblick. Mitteilungen der Naturforschenden Gesellschaft Mecklenburg 12:3–20.
- Buckland, W. 1829. On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations. Transactions of the Geological Society of London, Series 2 7:223–236.
- Buckland, W. 1837. Geology and Mineralogy Considered with Preference to Natural Theology. The Bridgewater Treatises of the Power, Wisdom and Goodness of God as Manifested in the Creation, Volume 5. W. Pickering, London, 727 pp.
- Casciotta, J. R., and G. Arratia. 1993. Jaws and teeth of American cichlids (Pisces: Labroidei). Journal of Morphology 217:1–36.
- Caswell, B. A., and A. L. Coe. 2014. The impact of anoxia on pelagic macrofauna during the Toarcian Oceanic Anoxic Event (Early Jurassic). Proceedings of the Geologists' Association 125:383–391.
- Caswell, B. A., A. L. Coe, and A. S. Cohen. 2009. New range data for marine invertebrate species across the early Toarcian (Early Jurassic) mass extinction. Journal of the Geological Society 166:859–872.
- Cavin, L., U. Deesri, and V. Suteethorn. 2009. The Jurassic and Cretaceous bony fish record (Actinopterygii, Dipnoi) from Thailand; pp. 125–139 in E. Buffetaut, G. Cuny, J. Le Loeuff, and V. Suteethorn (eds.), Late Palaeozoic and Mesozoic Continental Ecosystems in SE Asia. The Geological Society, London, Special Publications 315.
- Cope, E. D. 1887. Zittel's Manual of Palaeontology. American Naturalist 21:1014–1019.
- Cuny, G., A. M. Cobbett, F. J. Meunier, and M. J. Benton. 2010. Vertebrate microremains from the Early Cretaceous of southern Tunisia. Geobios 43:615–628.
- de Graciansky, P.-C., G. Dardeau, J.-L. Dommergues, C. Durlot, D. Marchand, T. Dumont, S. P. Hesselbo, T. Jaquin, V. Goggin, C. Meister, R. Mouterde, J. Rey, and P. R. Vail. 1998. Ammonite biostratigraphic correlation and Early Jurassic sequence stratigraphy in France: comparisons with some U.K. Sections; pp. 583–622 in P.-C. de Graciansky, J. Hardenbol, T. Jaquin, and P. R. Vail (eds.), Mesozoic and Cenozoic Sequence Stratigraphy of European Basins. Society for Sedimentary Geology Special Publication 60.
- Delsate, D. 1999. L'ichthyofaune du Toarcien luxembourgeois—cadre général et catalogue statistique. Travaux scientifiques du Musée National d'Histoire Naturelle de Luxembourg 30:1–101.
- Delsate, D., and J. Kriwet. 2004. Late Triassic pycnodont fish remains (Neopterygii, Pycnodontiformes) from the Germanic basin. Eclogae Geologicae Helvetiae 97:183–191.
- Delsate, D., C. J. Duffin, and R. Weis. 2002. A new microvertebrate fauna from the Middle Hettangian (Early Jurassic) of Fontenoille (Province of Luxembourg, south Belgium). Memoirs of the Geological Survey of Belgium 48:1–83.
- Dera, G., P. Neige, J.-L. Dommergues, E. Fara, R. Laffont, and P. Pellennard. 2010. High-resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian ammonites (Cephalopoda). Journal of the Geological Society, London 167:21–33.
- Duffin, C. J. 2010. Coprolites; pp. 395–400 in A. R. Lord and G. Davis (eds.), Palaeontological Association Field Guides to Fossils, Number 13—Fossils from the Lower Lias of the Dorset Coast. The Palaeontological Association, London.
- Ebert, M. 2016. The Pycnodontidae (Actinopterygii) in the late Jurassic: 2) *Turboscinetes* gen. nov. in the Solnhofen Archipelago (Germany) and Cerin (France). Archaeopteryx 33:12–53.
- Egerton, P. 1855. *Pycnodus liassicus*. Memoirs of the Geological Survey of the United Kingdom—Figures and Descriptions Illustrative of British Organic Remains, Decade VIII:1–3.
- Ernst, W. 1967. Die Liastongrube Grimmen. Sediment, Makrofauna und Stratigraphie. Ein Überblick. Geologie 16:550–569.
- Ernst, W. 1991. Der Lias im Ton-Tagebau bei Grimmen (Vorpommern). Fundgrube 27:171–183.
- Ernst, W. 1992. Der Lias der Scholle von Dobbartin (Mecklenburg). Fundgrube 28:56–70.
- Fink, W. F. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. Journal of Morphology 167:167–184.
- Friedman, M. 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous

- extinction. *Proceedings of the Royal Society B; Biological Sciences* 277:1675–1683.
- Galton, P. M., R. Brun, and M. Rioult. 1980. Skeleton of the stegosaurian dinosaur *Lexovisaurus* from the lower part of the Middle Callovian (Middle Jurassic) of Argences (Calvados), Normandy. *Bulletin trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre* 67:39–60.
- Gardiner, B. G. 1960. A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. *Bulletin of the British Museum (Natural History): Geology* 4:241–384.
- Goatley, C. H. R., D. R. Bellwood, and O. Bellwood. 2010. Fishes on coral reefs: changing roles over the past 240 million years. *Paleobiology* 36:415–427.
- Gorjanović-Kramberger, K. 1905. Die obertriadische Fischfauna von Hallein in Salzburg. *Beiträge zur Paläontologie Österreichs-Ungarns und des Orients* 18:123–224.
- Grey-Egerton, P. 1869. On two new species of *Gyrodus*. *The Quarterly Journal of the Geological Society of London* 25:379–386.
- Gründel, J. 1999. Gastropoden aus dem höheren Lias von Grimmen, Vorpommern (Deutschland). *Archiv für Geschichte der Naturwissenschaften* 2:629–672.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- Hauff, B., and R. B. Hauff. 1981. *Das Holzmadenbuch*. Holzmaden, Germany, 136 pp.
- Hauff, R. B., C. Heunisch, U. Hochsprung, J.-M. Ilger, U. Joger, M. Klopschar, R. Kosma, F. J. Krüger, D. Thies, and H. Zellmer. 2014. *Jurameer-Niedersachsens versunkene Urwelt*. Verlag Dr. Friedrich Pfeil, Munich, 96 pp.
- Henry, J. 1876. L'Infralias dans le Franche-Comté. *Mémoires de la Société d'émulation du Doubs* 10:285–476.
- Herrig, E. 1969a. Ostracoden aus dem Ober-Domerien von Grimmen westlich von Greifswald—Teil 1. *Geologie* 18:446–471.
- Herrig, E. 1969b. Ostracoden aus dem Ober-Domerien von Grimmen westlich von Greifswald—Teil 2. *Geologie* 18:1072–1101.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Scientific Meetings of the Zoological Society of London* 1880:649–661.
- Jaekel, O. 1929. *Lepidotus* und *Leptolepis* aus dem oberen Lias von Dobbertin. *Mitteilungen aus der Mecklenburgischen Geologischen Landesanstalt, Neue Folge* 3:13–25.
- Jain, S. L., and P. L. Robinson. 1963. Some new specimens of the fossil fish *Lepidotus* from the English Upper Jurassic. *Journal of Zoology* 141:119–135.
- Jenkyns, H. C. 1988. The Early Toarcian (Jurassic) anoxic event: stratigraphic, sedimentary and geochemical evidence. *American Journal of Science* 288:101–151.
- Katzung, G. 2004. Präquartärer Untergrund; pp. 38–40 in G. Katzung (ed.), *Geologie von Mecklenburg-Vorpommern*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Konwert, M., and S. Stumpf. 2017. Exceptionally preserved Leptolepidae (Actinopterygii, Teleostei) from the late Early Jurassic Fossil-Lagerstätten of Grimmen and Dobbertin (Mecklenburg-Western Pomerania, Germany). *Zootaxa* 4243:249–296.
- Koppelhus, E. B., and L. H. Nielsen. 1994. Palynostratigraphy and palaeoenvironments of the Lower to Middle Jurassic Bagå Formation of Bornholm, Denmark. *Palynology* 18:139–194.
- Kriwet, J. 1999. Pycnodont fishes (Neopterygii, †Pycnodontiformes) from the upper Barremian (Lower Cretaceous) of Uña (Cuenca province, E-Spain) and branchial teeth in pycnodontid fishes; pp. 215–238 in G. Arratia and H.-P. Schultze (eds.), *Mesozoic Fishes 2—Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, Munich.
- Kriwet, J. 2000. Revision of *Mesturus cordillera* Martill et al. 1998 (Actinopterygii, Pycnodontiformes) from the Oxfordian (Upper Jurassic) of northern Chile. *Journal of Vertebrate Paleontology* 20:450–455.
- Kriwet, J. 2001a. A comprehensive study of pycnodont fishes (Neopterygii, Pycnodontiformes)—morphology, taxonomy, functional morphology, phylogeny, and palaeobiogeography. Ph.D. dissertation, Humboldt University, Berlin, 582 pp.
- Kriwet, J. 2001b. Palaeobiogeography of pycnodontiform fishes (Actinopterygii, Neopterygii). *Seminario de Paleontología de Zaragoza* 5:121–130.
- Kriwet, J. 2001c. Feeding mechanisms and ecology of pycnodont fishes (Neopterygii, †Pycnodontiformes). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* 4:139–165.
- Kriwet, J. 2004. Dental morphology of the pycnodontid fish †*Stemmatodus rhombus* (Agassiz 1844) (Neopterygii, †Pycnodontiformes) from the Early Cretaceous, with comments on its systematic position. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 24:145–155.
- Kriwet, J. 2005. A comprehensive study of the skull and dentition of pycnodont fishes. *Zittelina* 45:135–188.
- Kriwet, J. 2008. The dentition of the enigmatic pycnodont fish, *Athrodon wittei* (Fricke, 1876) (Neopterygii, Pycnodontiformes; Late Jurassic; NW Germany). *Fossil Record* 11:61–66.
- Kriwet, J., and L. Schmitz. 2005. New insight into the distribution and palaeobiology of the pycnodont fish *Gyrodus*. *Acta Palaeontologica Polonica* 50:49–56.
- Kriwet, J., O. W. M. Rauhut, and U. Gloy. 1997. Microvertebrate remains (Pisces, Archosauria) from the Middle Jurassic (Bathonian) of southern France. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 206:1–28.
- Kutscher, M. 1988. Zur Invertebratenfauna und Stratigraphie des oberen Pliensbachien von Grimmen (DDR), Echinodermata. *Freiberger Forschungshefte, C* 419:62–70.
- Lauder, G. V., and K. F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology* 150:95–197.
- Leach, W. E. 1822. *Dapedium politum*; p. 45 in H. T. de la Beche (ed.), *Remarks on the geology of the south coast of England, from Bridport Harbour, Dorset, to Babbacombe Bay, Devon, Volume 1*. Transactions of the Geological Society of London, Series 2. Geological Society of London, London.
- Lehmkuhl, U. 1970. Makropaläozoologische Untersuchungen im Unter-Toarc des Nordteils der DDR—ein Beitrag zur Stratigraphie der 'Grünen Serie.' *Jahrbuch für Geologie* 3:243–250.
- Licht, M. 2009. The relationship of prearticular length and standard length in pycnodontiform fishes. *Studia Geologica Salmanticensia* 45:139–148.
- Licht, M., J. Kriwet, and M. Buchwitz. 2015. Body-size variation of pycnodontiform fishes from the Late Jurassic of Lower Saxony (Northern Germany) as a consequence of interspecific competition? *Paläontologische Zeitschrift* 89:891–900.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tomus I. Editio decima, reformata. Laurentii Salvii, Stockholm, 824 pp.
- Little, C. T. S., and M. J. Benton. 1995. Early Jurassic mass extinction: a global long-term event. *Geology* 23:495–498.
- Longbottom, A. E. 1984. New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali. *Bulletin of the British Museum (Natural History), Geology* 38:1–26.
- Maisch, W. M., and J. Ansorge. 2004. The Liassic ichthyosaur *Stenopterygius cf. quadriscissus* from the lower Toarcian of Dobbertin (northeastern Germany) and some considerations on lower Toarcian marine reptile palaeobiogeography. *Paläontologische Zeitschrift* 78:161–171.
- Malzahn, E. 1963. *Lepidotus elvensis* Blainville aus dem Posidonien-schiefer der Dobbertiner Liasscholle. *Geologisches Jahrbuch* 80:539–560.
- Marram, G., B. Villier, F. M. Dalla Vecchia, and G. Carnevale. 2016. A new species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the Cretaceous of Lebanon provides new insights about the morphological diversification of pycnodont fishes through time. *Cretaceous Research* 61:34–43.
- Martín-Abad, H., and F. J. Poyato-Ariza. 2013. Historical patterns of distribution in pycnodontiform and amiiform fishes in the context of moving plates. *Geologica Belgica* 16:217–226.
- Maxwell, E. E., and S. Stumpf. 2017. Revision of *Saurorhynchus* (Actinopterygii: Saurichthyidae) from the Early Jurassic of England and Germany. *European Journal of Taxonomy* 321:1–29.
- Mudroch, A., and D. Thies. 1996. Knochenfischzähne (Osteichthyes, Actinopterygii) aus dem Oberjura (Kimmeridgium) des Langenbergs bei Oker (Norddeutschland). *Geologica et Palaeontologica* 30:239–265.
- Nursall, J. R. 1996a. Distribution and ecology of pycnodont fishes; pp. 115–124 in G. Arratia and G. Viohl (eds.), *Mesozoic Fishes—Systematics and Paleoecology*. Verlag Dr. Friedrich Pfeil, Munich.

- Nursall, J. R. 1996b. The phylogeny of pycnodont fishes; pp. 125–152 in G. Arratia and G. Viohl (eds.), *Mesozoic Fishes—Systematics and Paleocology*. Verlag Dr. Friedrich Pfeil, Munich.
- Nursall, J. R. 1999. The pycnodontiform bauplan: the morphology of a successful taxon; pp. 189–214 in G. Arratia and H.-P. Schultze (eds.), *Mesozoic Fishes 2—Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, Munich.
- Nursall, J. R. 2010. The case for pycnodont fishes as the fossil sister-group of teleosts; pp. 37–60 in J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson (eds.), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil, Munich.
- Oertel, W. 1921. Der Lias in Mecklenburg (Vorläufige Mitteilung). *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg* 47:1–12.
- Olsen, P. E., and A. R. McCune. 1991. Morphology of the *Semionotus elegans* species group from the Early Jurassic part of the Newark Supergroup of eastern North America with comments on the family Semionotidae (Neopterygii). *Journal of Vertebrate Paleontology* 11:269–292.
- Pászti, A. 2004. Halmaradványok az Úrkúti Mangánérc Formáció képződményeiből. *Bányászati és Kohászati Lapok, Bányászat* 137:45–46.
- Peyer, B. 1954. Ein Gebissfund von *Lepidotus* aus dem oberen weissen Jura von Thayngen, Kt. Schaffhausen (Schweiz). *Schweizerische Paläontologische Abhandlungen* 70:1–20.
- Pouech, J., J.-M. Mazin, L. Cavin, and F. J. Poyato-Ariza. 2015. A Berriasian actinopterygian fauna from Cherves-de-Cognac, France: biodiversity and palaeoenvironmental implications. *Cretaceous Research* 55:32–43.
- Poyato-Ariza, F. J. 2003. Dental characters and phylogeny of pycnodontiform fishes. *Journal of Vertebrate Paleontology* 23:937–940.
- Poyato-Ariza, F. J. 2005. Pycnodont fishes: morphologic variation, ecomorphologic plasticity, and a new interpretation of their evolutionary history. *Bulletin of the Kitakyushu Museum of Natural History and Human History, Series A (Natural History)* 3:169–184.
- Poyato-Ariza, F. J. 2015. Studies on pycnodont fishes (I): evaluation of their phylogenetic position among actinopterygians. *Rivista Italiana di Paleontologia e Stratigrafia* 121:329–343.
- Poyato-Ariza, F. J., and D. Bermúdez-Rochas. 2009. New pycnodont fish (*Acrodonichthys pasiegae* gen. et sp. nov.) from the Early Cretaceous of the Basque-Cantabrian Basin, northern Spain. *Journal of Vertebrate Paleontology* 29:271–275.
- Poyato-Ariza, F. J., and H. Martín-Abad. 2013. History of two lineages: comparative analysis of the fossil record in Amiiformes and Pycnodontiformes (Osteichthyes, Actinopterygii). *Spanish Journal of Palaeontology* 28:79–90.
- Poyato-Ariza, F. J., and S. Wenz. 2002. New insight into pycnodontiform fishes. *Geodiversitas* 24:139–248.
- Poyato-Ariza, F. J., and S. Wenz. 2004. The new pycnodontid fish genus *Turbomesodon*, and a revision of *Macromesodon* based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain; pp. 341–378 in G. Arratia and A. Tintori (eds.), *Mesozoic Fishes 3—Systematics, Palaeoenvironments and Biodiversity*. Verlag Dr. Friedrich Pfeil, Munich.
- Poyato-Ariza, F. J., and S. Wenz. 2005. *Akromystax tilmachiton* gen. et sp. nov., a new pycnodontid fish from the Lebanese Late Cretaceous of Haql and en Nammoura. *Journal of Vertebrate Paleontology* 25:27–45.
- Poyato-Ariza, F. J., M. R. Talbot, M. A. Fregenal-Martínez, N. Meléndez, and S. Wenz. 1998. First isotopic and multidisciplinary evidence for nonmarine coelacanths and pycnodontiform fishes: palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 144:65–84.
- Prauss, M. 1996. The Lower Toarcian Posidonia Shale of Grimmen, Northeast Germany—implications from the palynological analysis of a near-shore section. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 200:107–132.
- Priem, F. 1908. Étude des poissons fossiles du Bassin Parisien. *Annales de Paléontologie* 6:1–144.
- Quenstedt, F. A. 1847. Über *Lepidotus* im Lias & Würtemberg. *Friedrich Ludwig Fues, Tübingen*, 25 pp.
- Raup, D. M., and J. J. Sepkoski Jr. 1982. Mass extinctions in the marine fossil record. *Science* 215:1501–1503.
- Regan, C. T. 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proceedings of the Zoological Society of London* 1923:445–461.
- Reis, O. M. 1892. Zur Osteologie und Systematik der Belonorhynchiden und Tetragonolepiden. *Geognostische Jahreshefte* 4:143–171.
- Rioul, M., and R. Mourdon. 1982. Carrière de la Tuilerie du Fresne d'Argences (Calvados). *Bulletin trimestriel de la Société Géologique de Normandie et Amis du Muséum du Havre* 69:13–18.
- Röhl, H. J., and A. Schmid-Röhl. 2005. Lower Toarcian (Upper Liasic) black shales of the central European epicontinental Basin: a sequence stratigraphic case study from the SW German Posidonia Shale; pp. 165–189 in N. B. Harris (ed.), *Deposition of Organic-Carbon-Rich Sediments: Models, Mechanisms, and Consequences*. Society for Sedimentary Geology Special Publication 82.
- Saint-Seine, P. de. 1949. Sur la présence d'un Pycnodontidé dans le Lias inférieur du Cher. *Compte rendu sommaire des séances de la Société Géologique de France* 14:334–335.
- Sauvage, H. É. 1867. Poissons fossiles des formations secondaires du Boulonnais. *Mémoires de la Société Académique de l'arrondissement de Boulogne-sur-Mer, Série* 3:53–152.
- Sauvage, H. É. 1878. Notes sur les poissons fossiles. *Bulletin de la Société Géologique de France, Série* 3 6:623–637.
- Sauvage, H. É. 1880a. Notes sur les poissons fossiles (suite). *Bulletin de la Société Géologique de France, Série* 3 8:451–462.
- Sauvage, H. É. 1880b. Synopsis des poissons et des reptiles des terrains jurassiques de Boulogne-sur-Mer. *Bulletin de la Société Géologique de France, Série* 3 8:524–547.
- Schumacher, K.-H., and H. Sonntag. 1964. Zur Stratigraphie und Ausbildung des Lias im Norden der Deutschen Demokratischen Republik. *Geologie* 13:303–315.
- Selden, P. A., and J. A. Dunlop. 2014. The first fossil spider (Araneae: Palpimanoidea) from the Lower Jurassic (Grimmen, Germany). *Zootaxa* 3894:161–168.
- Shimada, K., T. E. Williamson, and P. L. Sealey. 2010. A new gigantic pycnodont fish from the Juana Lopez Member of the upper Cretaceous Mancos Shale of New Mexico, U.S.A. *Journal of Vertebrate Paleontology* 30:598–603.
- Smithwick, F. M. 2015. Feeding ecology of the deep-bodied fish *Dapedium* (Actinopterygii, Neopterygii) from the Sinemurian of Dorset, England. *Palaeontology* 58:293–311.
- Sowerby, 1829. *The Mineral Conchology of Great Britain; or Coloured Figures and Descriptions of Those Remains of Testaceous Animals or Shells, Which Have Been Preserved at Various Times and Depths in the Earth*, Volume 6. Printer: Richard Taylor, London, 235 pp.
- Stoermer, N., and E. Wienholz. 1965. *Mikrobiostratigraphie an der Lias/Dogger-Grenze in Bohrungen nördlich der Mitteldeutschen Hauptscholle*. *Jahrbuch für Geologie* 1:533–591.
- 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* 280:87–105.
- Stumpf, S., J. Ansorge, and W. Krempien. 2015. Gravisaurian sauropod remains from the late Early Jurassic (Lower Toarcian) of North-Eastern Germany. *Geobios* 48:271–279.
- Thies, D. 1985. Eine Gaumenbezeichnung von *Gyrodus* aus dem fränkischen Malm Gamma. *Geologische Blätter NO-Bayerns* 33/34:389–406.
- Thies, D. 1989. Sinneslinien bei dem Knochenfisch *Lepidotus elvensis* (Blainville 1818) (Actinopterygii, Semionotiformes) aus dem Oberlias (Unter-Toarcium) von Grimmen in der DDR. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 11:692–704.
- Thies, D. 1991. The osteology of the bony fish *Tetragonolepis semicincta* Bronn 1830 (Actinopterygii, †Semionotiformes) from the Early Jurassic (Lower Toarcian) of Germany. *Geologica et Palaeontologica* 25:251–297.
- Thies, D., and R. B. Hauff. 2011. A new species of *Dapedium* Leach, 1822 (Actinopterygii, Neopterygii, Semionotiformes) from the Early Jurassic of South Germany. *Palaeodiversity* 4:185–221.
- Thies, D., and J. Waschke. 2015. Redescription of *Dapedium pholidotum* (Agassiz, 1832) (Actinopterygii, Neopterygii) from the Lower Jurassic Posidonia Shale, with comments on the phylogenetic position of *Dapedium* Leach, 1822. *Journal of Systematic Palaeontology* 13:339–364.
- Thurmond, J. T. 1974. Lower vertebrate faunas of the Trinity Division in North-Central Texas. *Geoscience and Man* 3:103–129.

- Tintori, A. 1981. Two new pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 68:795–824.
- Ulrichs, M., R. Wild, and B. Ziegler. 1994. Der Posidonien-Schiefer und seine Fossilien. *Stuttgarter Beiträge zur Naturkunde, Reihe C* 36:1–95.
- Vincent, P., J. E. Martin, V. Fischer, G. Suan, B. Khalloufi, B. Suchéras-Marx, A. Léna, K. Janneau, B. Rousselle, and L. Rulleau. 2013. Marine vertebrate remains from the Toarcian-Aalenian succession of southern Beaujolais, Rhône, France. *Geological Magazine* 150:822–834.
- Wagner, A. 1851. Beiträge zur Kenntnis der in den lithographischen Schiefern abgelagerten urweltlichen Fische. *Abhandlungen der Mathematisch-Physikalischen Classe der königlich bayerischen Akademie der Wissenschaften* 6:1–81.
- Webb, P. W. 1984. Form and function in fish swimming. *Scientific American* 251:58–68.
- Wenz, S. 1968. Compléments à l'étude des poissons actinoptérygiens du Jurassique français. *Éditions du Centre National de la Recherche Scientifique, Paris* 15:1–276.
- Williams, M., M. J. Benton, and A. Ross. 2015. The Strawberry Bank Lagerstätte reveals insight into Early Jurassic life. *Journal of the Geological Society* 172:683–692.
- Woodward, A. S. 1890. A synopsis of the fossil fishes of the English Lower Oolites. *Proceedings of the Geological Association* 11:285–306.
- Woodward, A. S. 1892. Supplementary observations on some fossil fishes of the English Lower Oolites. *Proceedings of the Geologists' Association* 12:238–241.
- Woodward, A. S. 1893. Some Cretaceous pycnodont fishes. *Geological Magazine* 10:433–436.
- Woodward, A. S. 1895. Catalogue of the Fossil Fishes in the British Museum (Natural History)—Part 3. The Trustees of the British Museum (Natural History), London, 544 pp.
- Woodward, A. S. 1896. On some remains of the pycnodont fish, *Mesoturus*, discovered by Alfred N. Leeds, Esq., in the Oxford Clay of Peterborough. *Annals and Magazine of Natural History, Series 6* 17:1–15.
- Woodward, A. S. 1897. On the fossil fishes of the Upper Lias of Whitby—part 3. *Proceedings of the Yorkshire Geological and Polytechnic Society* 13:325–337.
- Youbi, N., A. Marzoli, H. Bertrand, E. Font, J. Dal Corso, L. Martins, J. Madeira, J. Mata, G. Bellieni, S. Callegaro, M. Kh. Bensalah, and M. Bahr. 2014. Assessing the causes of the End-Triassic biotic crisis, a review. *Comunicações Geológicas* 101:1473–1476.
- Zessin, W., and W. Krempien. 2010. Bemerkenswerte Saurier-, Krokodil- und Fischfunde aus dem Lias von Grimmen, Vorpommern. *Geschiebekunde aktuell, Sonderheft* 8:5–18.
- Zieten, C. H. von. 1830–1833. Die Versteinerungen Württembergs, oder naturgetreue Abbildungen der in den vollständigsten Sammlungen, namentlich der in dem Kabinet des Oberamts-Arzt Dr. Hartmann befindlichen Petrefacten, mit Angabe der Gebirgs-Formationen, in welchen dieselben vorkommen und der Fundorte. Verlag & Lithographie der Expedition des Werkes *Unsere Zeit*, Stuttgart, 102 pp.

Submitted November 25, 2016; revisions received May 26, 2017; accepted June 1, 2017.

Handling editor: Charlie Underwood.