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Dental microtomographic evidence for functional heterodonty in the upper jaw of a Late Jurassic pycnodont actinopterygian fish

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This study describes the detailed analysis of an exceptionally well-preserved specimen of pycnodont fish vomerine teeth from the Upper Jurassic limestones of the Owadów-Brzezinki Quarry Lagerstätte in central Poland (Tomaszów Mazowiecki area). X-ray microtomography (μ-CT) revealed the details of the pycnodont tooth morphology and histology. Using the non-destructive technique of X-ray microtomography for exploring the internal structure of fossil teeth in 3D, we were able to recognize individual skeletal tissues. Petrodentine (a specific hypermineralized type of dentine) is present in the pycnodont teeth. This skeletal tissue is common in durophagous vertebrates. The presence of petrodentine in the specimen investigated is interpreted by comparison with extinct and extant dipnoans, which are also durophagous fish and are among the closest ecological analogues of pycnodonts. Microtomography revealed unexpected patterns in the internal architecture and tissue density of the upper jaw. Specifically, the posterior region of the vomer displays higher bone density and significantly larger, more heavily mineralized teeth compared to the anterior portion. These findings suggest a greater biomechanical resistance of the posterior upper jaw to crushing forces. The material described supplements knowledge of Late Jurassic ichthyofaunas and ecosystems in the central and eastern parts of the European Archipelago.

Key words: pycnodonts, Actinopterygii, dentition, histology, feeding adaptations, durophagy

INTRODUCTION

The fossil record of the Jurassic pycnodont actinopterygians (Neopterygii, Pycnodontiformes) is poor in Poland. Remains of this group are mainly known from Upper Jurassic deposits (Kin et al., 2013). The only place in Poland where Upper Jurassic actinopterygian fish fossils occur in significant quantities is Owadów-Brzezinki Quarry (Fig. 1). The quarry is located 18 km south-east of the town of Tomaszów Mazowiecki, in the northern part of the Mesozoic boundary of the Holy Cross Mountains. The Upper Jurassic (Tithonian/Middle Volgian) carbonate deposits of Owadów-Brzezinki Quarry are famous for their well-preserved fossils of marine and terrestrial organisms (Kin and Błażejowski, 2012; Kin et al., 2012, 2013). These limestones are the youngest Upper Jurassic strata in the epicratonic area of Poland (Kutek, 1994; Kin et al., 2013). The fossils include diverse oysters, ammonites, horseshoe crabs, crustaceans and terrestrial insects (Kin and Błażejowski, 2012; Kin et al., 2012, 2013). The Owadów-Brzezinki deposits have also yielded an abundant vertebrate fauna including ophthalmosaurid ichthyosaurs, turtles, crocodylomorphs, pterosaurs and large actinopterygian fishes (Kin et al., 2013; Błażejowski et al., 2015; Tyborowski et al., 2016; Tyborowski, 2016, 2017).

A preliminary investigation of the collection shows the presence of three different taxonomic groups of actinopterygians: halecomorphs (isolated teeth, jaws and skull bones of caturids and furids), pachycormiforms (isolated teeth, jaw bones and skull elements) and pycnodonts (jaws, teeth and articulated skeletons). Pycnodonts (Pycnodontiformes) are a monophyletic group of durophagous and shallow-water actinopterygians (Nursall, 1996; Kriwet, 2005). Their jaws bore flat and rounded teeth – an adaptation to crushing hard-shelled organisms such as bivalves or brachiopods (Kriwet, 2005). Pycnodonts are known from many Upper Jurassic (Kimmeridgian/Tithonian) localities (Fürsich et al., 2007; Ebert, 2016).

We describe for the first time the application of X-ray microtomography (μ-CT) as a noninvasive tool for investigating the morphology and histology of pycnodont vomerine teeth. The analyses carried out allow us to put forward a new hypothesis concerning the functional and strength differentiation of the up-

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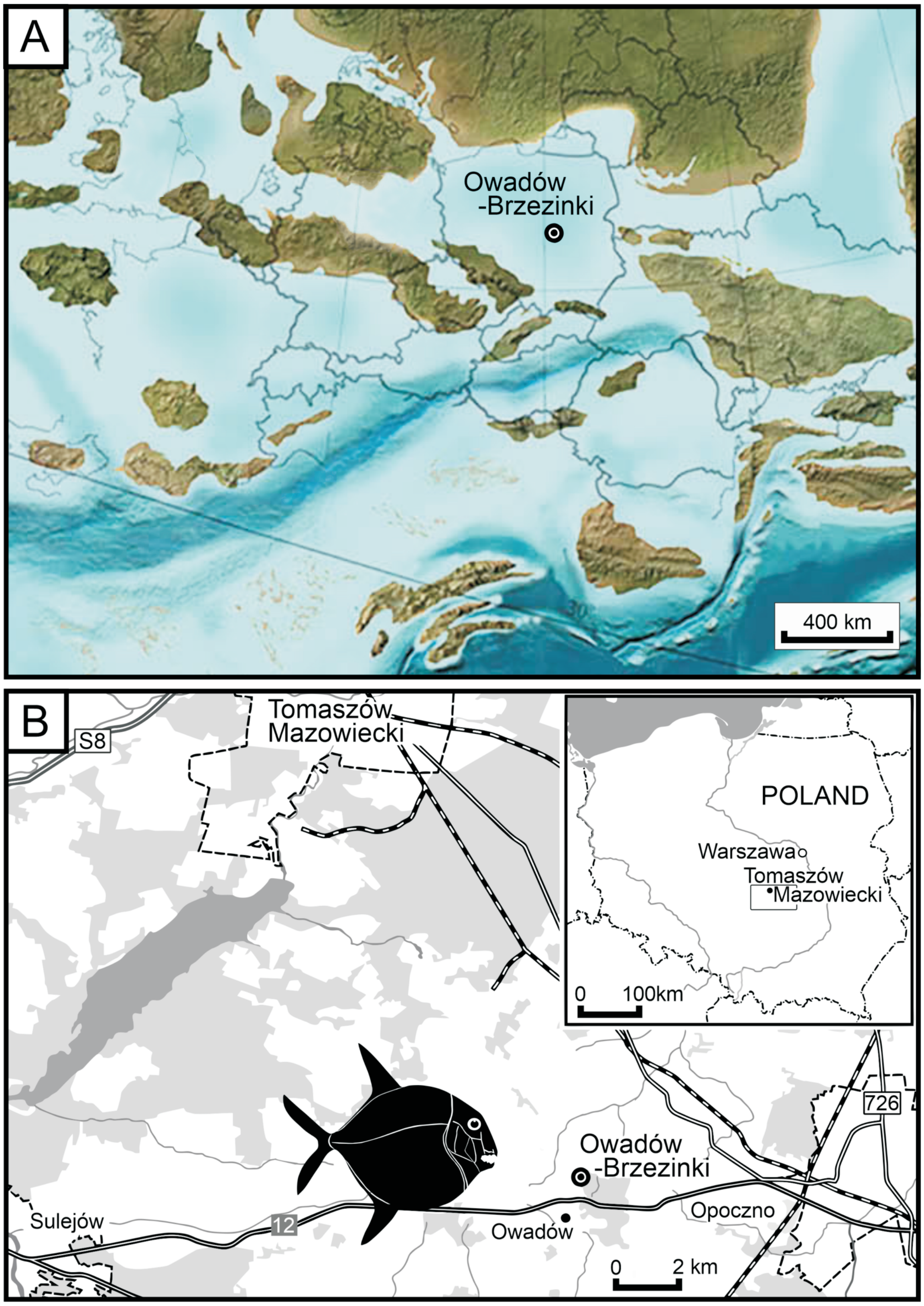

Fig. 1. Location of Owadów-Brzezinki Quarry

A – palaeogeographic map of the area during the Late Jurassic (map reconstruction from Ron Blakey, Colorado Plateau Geosystems, Arizona, USA; cpgeosystems.com/paleomaps.html); **B** – sketch map of the Owadów-Brzezinki Quarry area

per jaw teeth of pycnodonts. Additionally, a comparison of the microtomographic results seems to suggest that there were also significant functional differences in the adaptations of the upper and lower jaws in different pycnodont species.

GEOLOGICAL BACKGROUND

The section is located within the Brzostówka marls of the Pałuki Formation and overlying limestones of the Kcynia Formation (Matyja and Wierzbowski, 2016). The main part of the section is composed of Kcynia Formation limestones and can be subdivided into four units (Kin et al., 2013), each with its specific fossil assemblage. The sedimentary pattern observed in the Owadów-Brzezinki section indicates shallowing of the depositional environment from offshore to nearshore/lagoonal settings (Kin and Błażejowski, 2012; Kin et al., 2013), whereas unit IV bears evidence of a return to more open marine conditions (Kin et al., 2013). Such transitions allow for comparative studies with other sites of similar palaeoenvironmental facies (Kin et al., 2013; Tyborowski et al., 2016). The vertebrate fossils are mostly disarticulated or isolated and occur mainly in two fossil-bearing units (Unit I and III), both of which correspond to the Zarajskites Subzone of the Scythicus Zone of the middle Volgian (i.e. the uppermost Lower Tithonian). The sequence of the Kcynia Formation was dated on the basis of ammonites (Kin et al., 2013; Matyja and Wierzbowski, 2016).

The source strata for the material described represents the upper part of the Kcynia Formation (Unit III in Kin et al., 2013; Matyja and Wierzbowski, 2016). According to Kin et al. (2013), this unit has a transitional palaeoenvironmental character reflecting a shallow-marine and lagoonal setting. Thus, the palaeoenvironment recorded in the upper part of the Owadów-Brzezinki Quarry should be considered as a natural habitat for pycnodonts. Unit III consists of well-bedded micritic limestones. The lowermost part of Unit III comprises thick-bedded, hard, yellow limestones. The overlying beds are paler in colour and very fossiliferous ("corbulomima horizon"). Numerous specimens of horseshoe crabs (Kin and Błażejowski, 2014) were found in Unit III in association with an enormously rich assemblage (mass-accumulations) of soft-shelled bivalves (either protobranchs or corbuloids), various fish and marine reptiles, rare ammonites, decapod crustaceans, land insects (dragonflies, beetles, grasshoppers) and isolated pterosaur teeth (Kin et al., 2013).

MATERIAL AND METHODS

The material described herein was collected during excavations in 2015–2018, conducted by Daniel Tyborowski. The material assigned to the Pycnodontidae indet. comprises an isolated vomerine bone with teeth. The Jurassic pycnodont teeth were scanned at the Microtomography Laboratory in the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, using an X-ray micro-computed tomography scanner *Zeiss XRadia MicroXCT-200*. X-ray microtomography is based on differences in attenuation of the X-ray beam propagation through different objects such as different types of skeletal tissue (e.g., bone, orthodentine, osteodentine, enamel). It provides an opportunity for detailed analysis of the pycnodont fish teeth. The computed image is of such good quality that it is possible to study teeth microstructures preserved in the rock matrix. The fragmentary condition of the specimen is insufficient for phylogenetic analysis beyond the proposed taxonomic attribution.

This specimen is housed at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, abbreviated ZPAL V/OB/1964.

SYSTEMATIC PALAEONTOLOGY

Osteichthyes Huxley, 1880
Actinopterygii Cope, 1887
Neopterygii Regan, 1923
Pycnodontiformes Berg, 1937
Pycnodontoidei Nursall, 1996
Pycnodontidae Agassiz, 1832
Pycnodontidae indet. (Figs. 2–4).

M a t e r i a l. – Isolated vomerine dentition of pycnodont actinopterygian fish. The specimen is stored under number ZPAL V/OB/1964 at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw.

D e s c r i p t i o n. –The specimen examined consists of the small vomerine dentition (Fig. 2), which measures ~15 mm in length and from 1 mm in height (in its anterior region) to 3.5 mm in height (in its posterior region). Five longitudinal tooth rows can be seen (Fig. 2A). The main tooth row is composed of four teeth. All of them are subcircular. They are widely spaced. Teeth from the second and fourth rows are oval or sub-rectangular and gently elongated. Three teeth are visible in the second row and four teeth can be seen in the fourth row. Teeth from all the rows form a series of regularly increasing size in the posterior direction (Fig. 2B). The anterior teeth are eroded and have on their surface grooves and cavities (Fig. 2B). A natural cross-section of the tooth row is visible on a broken ridge of the specimen (Fig. 3A). The pulp cavities of the teeth can be seen. They have an isometric shape and dentine surrounds them (Fig. 3A–D). Under the cavities the bone has a spongy appearance (Fig. 3C, D). Hypermineralized tissue stretches from the pulp cavities up to the occlusal surface of the teeth. This tissue has a lighter colour and higher density than the dentine (osteodentine, orthodentine) and is very similar to acrodentine or enamel (Fig. 3A, B). The pulp cavities of the teeth of the main tooth row are of approximately the same size as those of the medial and lateral rows (Fig. 3C). The size of the pulp cavities increases from anterior to posterior in the jaw (Fig. 3C, D). The interior of the tooth-bearing bone shows no evidence of non-functional teeth, and the pulp cavities present are hollow inside.

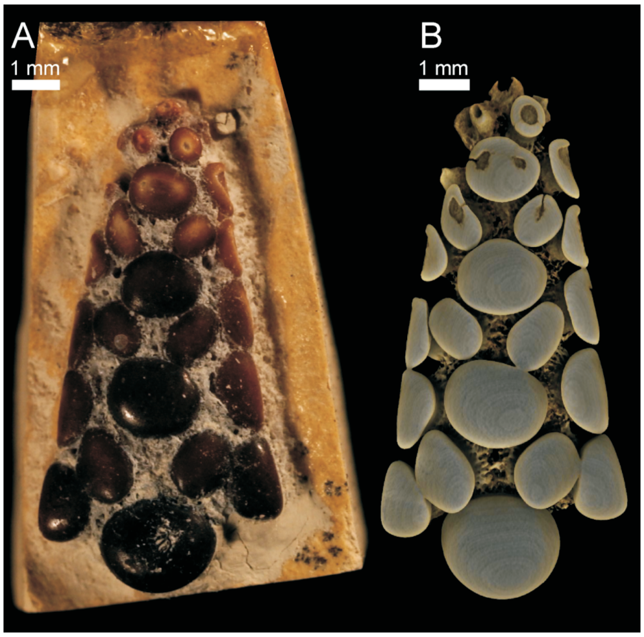

Fig. 2. Pycnodont fish (Pycnodontidae indet.) remains from the Upper Jurassic of Owadów-Brzezinki Quarry

A – occlusal view of the vomerine dentition;
B – 3D model from micro-CT scan of the tooth plate

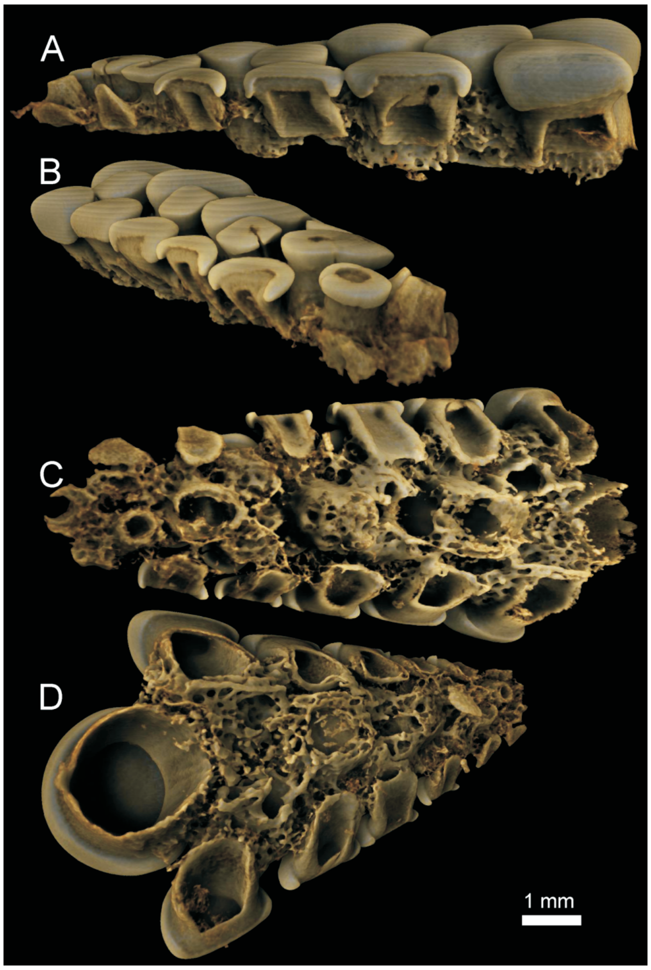

Fig. 3. Micro-CT scans of the pycnodont fish (Pycnodontidae indet.) vomerine dentition from the Upper Jurassic of Owadów-Brzezinki Quarry

A – lateral, **B** – right-anterior, **C** – ventral, **D** – ventral-posterior views

C o m p a r i s o n. – The vomerine dentition shows some similarities to the typical tooth morphology and arrangement of *Coelodus* species (Nursall, 1996):

– an occlusal surface gently convex from side to side;
– main teeth broader than long;
– main teeth broader than the lateral teeth;
– main teeth oval;
– lateral teeth oval to sub-rectangular.

The new specimen from Owadów-Brzezinki Quarry differs from those of *Coelodus* in possessing teeth with no crenulations on their surfaces. The true morphological characters of the dentition are hard to find. Thurmond (1974) gave a diagnosis of the dentitions in *Coelodus*. However, similar characters are present in *Pycnodus* dentition (Mohabey and Udhoji, 1996), but this genus is restricted to the Cretaceous-Eocene interval and *Coelodus* is a Jurassic and Cretaceous genus. Also the Late Cretaceous genus *Coccodus* has very similar vomerine dentition with similar morphology of the teeth (Nursall, 1996). However, the new specimen from Owadów-Brzezinki Quarry differs from those of *Coccodus* in possessing five longitudinal tooth rows. Internally, all of the tooth-bearing bone shows vascularization and an irregularly spongy structure (Fig. 3C, D). Similar microstructures are present in the sectioned prearticular bones of the Early Jurassic *Grimmenodon aureum* (Stumpf et al., 2017) and Late Jurassic *Gyrodus cuvieri* (Nursall, 1996; Kriwet, 2005). The new specimen from the Upper Jurassic of Poland cannot be determined more precisely than as Pycnodontidae gen. et sp. indet.

DISCUSSION

A hypermineralized tissue stretches from the pulp cavities up to the occlusal surface of the teeth. This tissue has a lighter colour then the dentine and its very similar to the petrodentine. Petrodentine is a specific hypermineralized type of dentine present in the tooth plates of dipnoan fishes (Smith, 1984; Kemp, 2001; Reisz et al., 2004). This microstructural kind of dentine ‘is formed by the continued growth of the core dentine of the cusps in the hatchling tooth plate in those species that have this tissue’ (Kemp, 2001). Growth lines are visible in petrodentine (Smith, 1984) just like in the specimen from Owadów-Brzezinki Quarry. Petrodentine is rich in calcium hydroxyapatite, almost free of collagen and free of denteons. This tissue is clearly different and distinguishable from trabecular dentine (osteodentine). The secretion of petrodentine begins in the larval stages of tooth plate development (Smith, 1984) and it is not surrounded by circumdenteonal dentine (Kemp, 2001). Twelve characters enabling distinction of petrodentine from other teeth tissues are known (Smith, 1984). Lison (1941) described petrodentine in tooth plates of extant dipnoans, but this tissue is also present in extinct forms (Smith, 1984; Kemp, 2001). Both dipnoans and pycnodonts are durophagous vertebrates (Smith, 1984; Kriwet, 2005). The presence of hard hypermineralized tissues on the occlusal surface of the teeth in those both groups is probably an adaptation to durophagy. The typical skeletal tissue in actinopterygian teeth is acrodin (Sasagawa et al., 2009; Błażejowski et al., 2015). This tissue is called the ‘acrodin cap’ or cap enameloid (Shellis and Miles, 1974;Ørvig, 1978; Wang et al., 2007). It forms the triangular and narrow crown of the tooth and it is common among active hunters like caturids or furids (Błażejowski et al., 2015). Both tissues (petrodentine and arcodin) are microstructural types of dentine. Petrodentine is just the hypermineralized kind of this tooth tissue (Smith, 1984). Probably it acted to provide a diversity of teeth tissues among different groups of actinopterygians adapted to hunt different types of prey. The active predators such as halecomorphs (e.g., caturids and furids) possess acrodin and the durophagous actinopterygians such as pycnodonts have petrodentine.

Micro-CT scans show spatial differences in the density of the internal spongy tissue of the tooth-bearing bone. The anteriormost part of the bone has a lower density than the posterior region (Fig. 4). This is indicated by the darker colour of the less dense tissue seen on μ-CT scans (Figs. 3C and 4). Thus, the posterior part of the upper jaw was more resistant to crushing and clamping of the jaw apparatus. This is corroborated by the size of the teeth. The teeth at the posterior part of the vomer are much larger than those in the symphyseal region (Fig. 2). In addition, the teeth in the back of the vomer have a much thicker layer of petrodentin than have the front teeth. This contradicts previous ideas on the lower jaws of some pycnodonts, which showed that the teeth at the front of the lower jaw and the bone supporting them were much stronger and denser than the back of the mandible (Kriwet, 2001, 2004; Stumpf et al., 2017). New data obtained through tomographic studies of the Polish specimen show that some pycnodonts may have crushed food with the posterior part of their jaws and others with the anterior part.

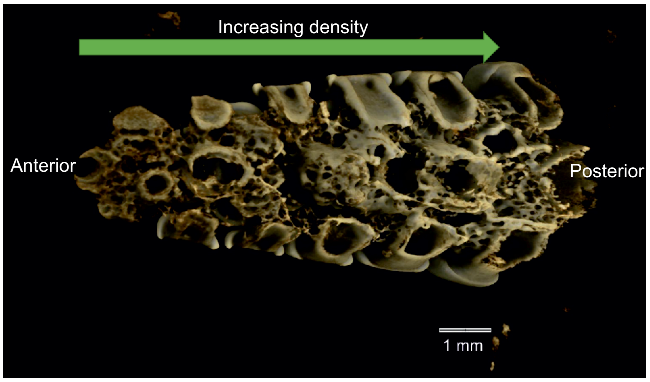

Fig. 4. Micro-CT scan of the pycnodont fish (Pycnodontidae indet.) vomerine dentition showing changes in bone density along the length of the specimen

Specimen shown in ventral view; the colour change from darker to lighter reflects an increase in tissue density

It is also possible that some pycnodonts fed in a way that is not yet fully understood, using the strength of the anterior teeth on the mandible and the posterior teeth of the upper jaw.

We hypothesize that functional heterodonty in Jurassic pycnodonts was not restricted to the lower jaw (as previously reported), but also developed independently in the palatal dentition. In the Polish specimen from Owadów-Brzezinki, μ-CT analysis reveals spatial and structural variation in vomerine tooth morphology and tissue density (Figs. 3A and 4), suggesting that the posterior region of the upper jaw was biomechanically adapted for high-stress durophagy. In contrast, previous studies (Kriwet, 2001, 2004; Stumpf et al., 2017) have demonstrated that functional heterodonty was limited to the anterior lower jaws in other pycnodont taxa. Therefore, we propose that at least some pycnodonts evolved jaw-functional asymmetry, in which the palatal and mandibular elements had distinct mechanical roles in food processing. This may reflect either a previously unrecognized evolutionary plasticity in feeding adaptations within Pycnodontiformes, or distinct ecological specializations among closely related taxa. Analogous tomographic and biomechanical studies of more complete jaw apparatuses of pycnodonts will need to be carried out to determine unequivocally which of the hypotheses presented is true.

The discovery of pycnodont material from Owadów-Brzezinki extends the known distribution of this group in Europe and highlights the ecological significance of this taxon within marginal marine environments during the Tithonian. In comparison to other Tithonian localities such as Solnhofen in Germany or Cerin in France, the presence of pycnodonts at Owadów-Brzezinki suggests faunal similarities and shared ecological niches across the European Archipelago (Ebert, 2016). Strata from the host layer contain abundant invertebrates including bivalves, gastropods and horseshoe crabs of the genus *Limulus* (Kin et al., 2013, Kin and Błażejowski, 2014). The abundance of the latter, along with previous suggestions about the diet of pycnodonts (Kriwet, 2001, 2005; Kriwet and Schmitz, 2005), suggests that they might have been a food source for some durophagous vertebrates such as pycnodonts.

CONCLUSIONS

The Late Jurassic dentition of pycnodont fish from Poland is described for the first time. The remains studied most likely belongs to a representative of the Pycnodontidae. Due to the fragmentary state of preservation of the fossil specimen analysed, a more detailed systematic position cannot be given. The new material supplements knowledge of Late Jurassic (Tithonian/Middle Volgian) ecosystems in the central and eastern parts of the European Archipelago. It also points to a marginal marine (lagoonal) environmental tolerance of the Late Jurassic pycnodont fish. The presence of this taxon at Owadów-Brzezinki Quarry indicates faunal connections with other contemporaneous localities in Europe, emphasizing the importance of this site for reconstructing Late Jurassic biodiversity and ecological patterns.

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