

A comparison of teeth in Tithonian, Late Jurassic, predatory actinopterygian fishes from Owadów-Brzezinki Lägerstätte and its palaeoecological implications

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The Owadów-Brzezinki palaeontological site is known for its very well-preserved fossils of Late Jurassic vertebrates, such as numerous fossil fish teeth and occasional dental bones. Some of these represent well-studied taxa, including the most common large predatory fish, with notable examples of caturoids (such as *Strobilodus* sp.) and pachycormids (*Orthocormus teyleri*). The current study presents the microstructure and histological features of the teeth of the selected specimens of the above taxa. They are determined through examinations of tooth cross-sections under thin microscopic observations and by the usage of scanning electron microscopy (SEM). The above inspections, combined with aspects of external tooth morphology, allowed us to determine the palaeoecology of the aforementioned taxa of large predatory fish. It is concluded that examined Caturioidea displayed a rather homogenous dentition belonging to the intermediate cut/slash guild, characterized by an internal orthodontin histology with prominent incremental Andresen growth lines of differing form, indicating living in a highly variable, unstable environment. The teeth of pachycormid specimen (*O. teyleri*) can be characterized as having denteon-based orthodontin histology, with a rapid rate of tooth eruption and a heterodont, elongated specialist dentition of the piercing guild. The observed structural differences in the teeth suggest a different niche distribution between the taxa studied. They help to explain how these predatory ray-finned fishes may have coexisted both in the local environment of the Owadów-Brzezinki and in the wider, more global context of Late Jurassic shallow marine environments. In addition, the tooth samples are characterised by pronounced surface bioerosion with traces of *Mycellites ossifragus* durophagous fungal activity, indicating an intense bioerosion caused by these microorganisms after the death of the fish.

Key words: Actinopterygii, Caturioidea, teeth, predatory, microstructure, histology, niches, Late Jurassic, Poland, Owadów-Brzezinki Quarry.

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Introduction

The study of fossil teeth is one of the most engaging fields of paleobiology, due to the multiplicity and quality of information they provide regarding the ecology of the vertebrates from which they came. In addition, their mechanically resistant structure and chemical composition allow them to be preserved often in an almost unchanged state, creating some

of the most promising objects for paleontological research. Generally, the most common fossil material through which the Actinopterygii clade is represented, comes from the teeth that ray-finned fish usually replace during their lifetime (Berkovitz and Shellis 2017). The teeth of predatory fishes are found particularly often, since they are both very numerous in each individual and frequently exchanged. The Late Jurassic period can be especially promising when studying predatory Actinopterygii, as we have exquisitely preserved

fossils from this time that can be closely compared with living ecologically equivalent species (Tyborowski 2017). The fossils of Late Jurassic ray-finned fishes are therefore valuable in reconstructing ancient food chains. Understanding the similarities in the ecologies of modern and Late Jurassic animals can add value to the study of present day/extant marine settings by providing a perspective on how evolutionary pressures force similar adaptations in different groups of Actinopterygii.

The first part of the material analysed in this study belongs to the superfamily Caturioidea, included in the clade Halecomorphi belonging to the infraclade Holostei which is widely distributed in both the Cenozoic and Mesozoic (Lambers 1994, 1998; Grande and Bemis 1998). Halecomorphi, due to their placement in the Holostei, are characterized by a more basal cranial bone arrangement (Grande and Bemis 1998). Caturioidea were widespread macropredatory hunters of Jurassic and Early Cretaceous (López-Arbarello and Ebert 2023). Although the specimens of the Caturioidea are globally distributed (Schaeffer and Patterson 1984), they are most often found in the Upper Jurassic sediments of Europe (Woodward 1893; Lambers 1994, 1999; López-Arbarello and Ebert 2023).

Another family, Pachycormidae, represented here by *Orthocormus tayleri*, also includes prominent macro-predators (Arratia 2004; Arratia and Schultze 2013). This family is known from Jurassic and Cretaceous sediments (Friedman et al. 2010; Maxwell et al. 2020; Cooper et al. 2022) and besides predators includes filter-feeders i.e., the famous filter-feeding *Leedsichtys problematicus* (Liston 2004). The predatory members of Pachycormidae family are characterized by an elongated, toothed rostrum, scythe-shaped pectoral fins, reduced pelvic fins and a prominent, nearly symmetrical caudal fin (Liston et al. 2019). They are recognised as fast-moving, open-water predators (Arratia and Schultze 2013).

In this research, optical and transmitted electron microscopy were used to study the dental microstructure and histology of two actinopterygian families with prominent Late Jurassic predatory taxa: Caturioidea (*Strobilodus* sp. and Caturioidea indet.) and Pachycormidae (*Orthocormus tayleri*). These ray-finned fish fossils come from strata exposed in the Owadów-Brzezinki quarry, which is considered a counterpart (Kin et al. 2012) to the famous Solenhofen Plattenkalk (Lambers 1994, 1998; Arratia and Schultze 2013), belonging to the distinctive facies of the Solenhofen Archipelago paleogeographic region. While pachycormids genus of *Orthocormus* is known mainly from this paleogeographic European region (Lambers 1988; Arratia and Schultze 2013), fossils of caturioids are observed in numerous places around the world (Woodward 1893; Müller 2011; Bogdan et al. 2013; López-Arbarello and Ebert 2023). Along with assessing the overall tooth morphology and microstructure, observations are being made to clarify how these large predatory ray-finned fishes of similar size coexisted. In addition, the analysis may indicate a link between tooth characteristics and the feeding strategy of the predators studied.

Institutional abbreviations.—ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting

Since becoming a well-known attraction in recent years, Owadów-Brzezinki quarry (51°22'27" N, 20°8'11" E; Fig. 1), first described by Kin et al. (2013), has been established as one of the richest Late Jurassic (Tithonian) fossil sites in Central-Eastern Europe and one of the most impressive Lagerstätten in Poland, bearing a wide spectrum of well-preserved taxa, including a significant number of vertebrate fossils, some of which were recognized as macro predatorial.

The site is located in the north-western margin of the Holy Cross Mountains, in the north-eastern limb of the Tomaszów Syncline. The uppermost part of the Brzostówka Marl Member of the Pałuki Formation and the overlying limestone of the Kcynia Formation, including the Sławno Limestone Member, *Corbulomima* Limestone and a fragment of “serpulid” beds, are exposed in the Owadów-Brzezinki section (Kutek 1994; Błażejowski et al. 2016; Fig. 1). The section shows a gradual marine regression revealed by a transition from offshore to coastal and lagoonal settings, but its uppermost part was deposited during a short-term marine transgression and the re-appearance of coastal environments (Błażejowski et al. 2016, 2023; Wierzbowski et al. 2016).

At the moment, the Owadów-Brzezinki Quarry is the only place in extra-Carpathian Poland where upper Tithonian strata are available for study. The exposed carbonate sequence belongs to the Kcynia Formation and can be divided into four successive units (Kin et al. 2013; Błażejowski et al. 2016). Thick-bedded chalky and micritic limestone of the unit I and unit II, which contain marine fauna, were included into the Sławno Limestone Member by Matyja and Wierzbowski (2016). Overlying well-bedded micritic limestone of unit III, which contain common *Corbulomima* bivalves and were formed in lagoonal environment, are, informally, called the *Corbulomima* Limestone (Fig. 1) according to the earlier classification (cf. Kutek 1994). Unit III is highly fossiliferous and has yielded the specimens that are the subject of this study (Fig. 1). The occasional anaerobic conditions and the accompanying set of biochemical processes were of particular importance for the preservation of the extraordinary paleontological discoveries (Wierzbowski et al. 2016; Błażejowski et al. 2019, 2020). As a result, the remains of organisms accumulated in the lagoon waters and were perfectly preserved in the fossil state. A narrow interval of unit IV from the uppermost part of the Owadów-Brzezinki section consists of oyster-bryozoan-serpulid organodetrital limestone assigned to the “serpulid” beds, which were formed in coastal settings (cf. Matyja and Wierzbowski 2016; Wierzbowski et al. 2016).

According to the stratigraphical studies of Kutek (1994) and Matyja and Wierzbowski (2016) based on ammonite

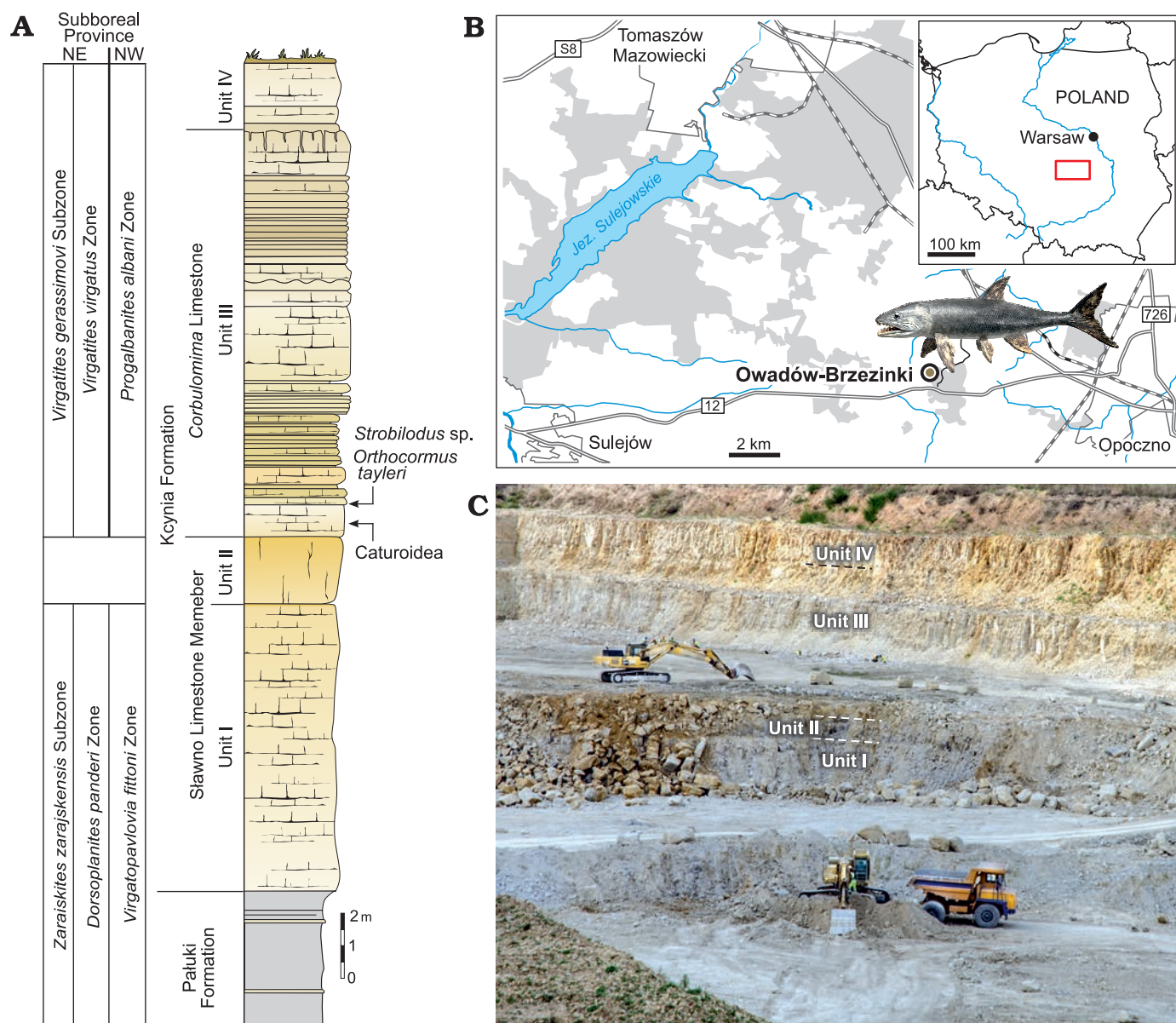


Fig. 1. A. Lithological succession and biostratigraphy of the Owadów-Brzezinki Quarry. The topmost part of the Pałuki Formation and overlying limestone of the Kcynia Formation (Units I–IV). B. Road map with the location of the Owadów-Brzezinki site and its proximity to Tomaszów Mazowiecki in Central Poland. C. General view of the Owadów-Brzezinki section (i.e., Unit III and most fossiliferous *Corbulomima* Limestone occurring in the middle of the quarry wall).

fauna (Fig. 1), the lower part of the Owadów-Brzezinki deposits is dated to the *Zaraiskites regularis* horizon (the uppermost part of the Brzostówka Marl Member of the Pałuki Formation) and *Zaraiskites zarajskensis* horizon (unit I of the Slawno Limestone Member of the lowermost part of the Kcynia Formation) of the *Zarajskensis* Subzone of the *Dorsoplanites panderi* Zone of the Middle Volgian, as well as to the *Virgatopavlovia fittoni* Zone from the “Bolonian” zonation of England (Matyja and Wierzbowski 2016; Błażejowski et al. 2023). The upper part of the Owadów-Brzezinki section (units III and IV belonging to the *Corbulomima* Limestone and “serpulid” beds, respectively) has, in turn, been assigned to the both *Virgatites gerassimovi* Subzone of the *Virgatites virgatus* Zone of the Middle Volgian and the *Progalbanites*

albanii Zone of the “Portlandian” (Matyja and Wierzbowski 2016; Błażejowski et al. 2023).

Bony fish remains are one of the most common fossils found at the site (Kin et al. 2013), and they are particularly represented by numerous teeth found in the limestone of Kcynia Formation, being often present in the sediments of the normal marine setting of Unit I. However, they are exceptionally abundant in the sediments of the shallower settings of Unit III; in most cases, these teeth are almost microscopic in scale, barely noticeable with the naked eye, but alongside these tiny specimens there are also larger teeth ranging from a few millimetres to a few centimetres in length. Those are sometimes found still intact in the jawbones of fossilized fish (Błażejowski et al. 2015; Tyborowski 2017).

Material and methods

The material for the study (Fig. 2) consists of fossil fragments of jaw bones representing two important groups of predatory bony fishes: Caturioidea (*Strobilodus* sp.) and Pachycormidae (*Orthocormus teyleri*), and in the case of indetermined caturioids also three isolated teeth found in the sediments. The collected material is housed at the Institute of Palaeobiology, Polish Academy of Sciences in Warsaw (ZPAL P. 16/O-B).

The preparation of the material was done at the Institute of Geological Sciences of Jagiellonian University in Kra-

ków. The teeth were cut in the vertical and horizontal planes, then cleaned and polished. Three isolated teeth from indetermined caturioids and four from the anterior region of the dentary fragment of *Strobilodus* sp. (ZPAL P. 16/O-B/FT1–FT3), were selected for thin sections. Two of the isolated teeth were cut in a vertical plane, while the dentary teeth and one isolated teeth specimen were cut in horizontal planes. In the case of maxillary teeth, the cuts were made in the basal, mid-crown and apical planes. Horizontal thin sections of the *O. teyleri* teeth were sampled from the marginal row of dentary teeth in the posterior section of the left dentary

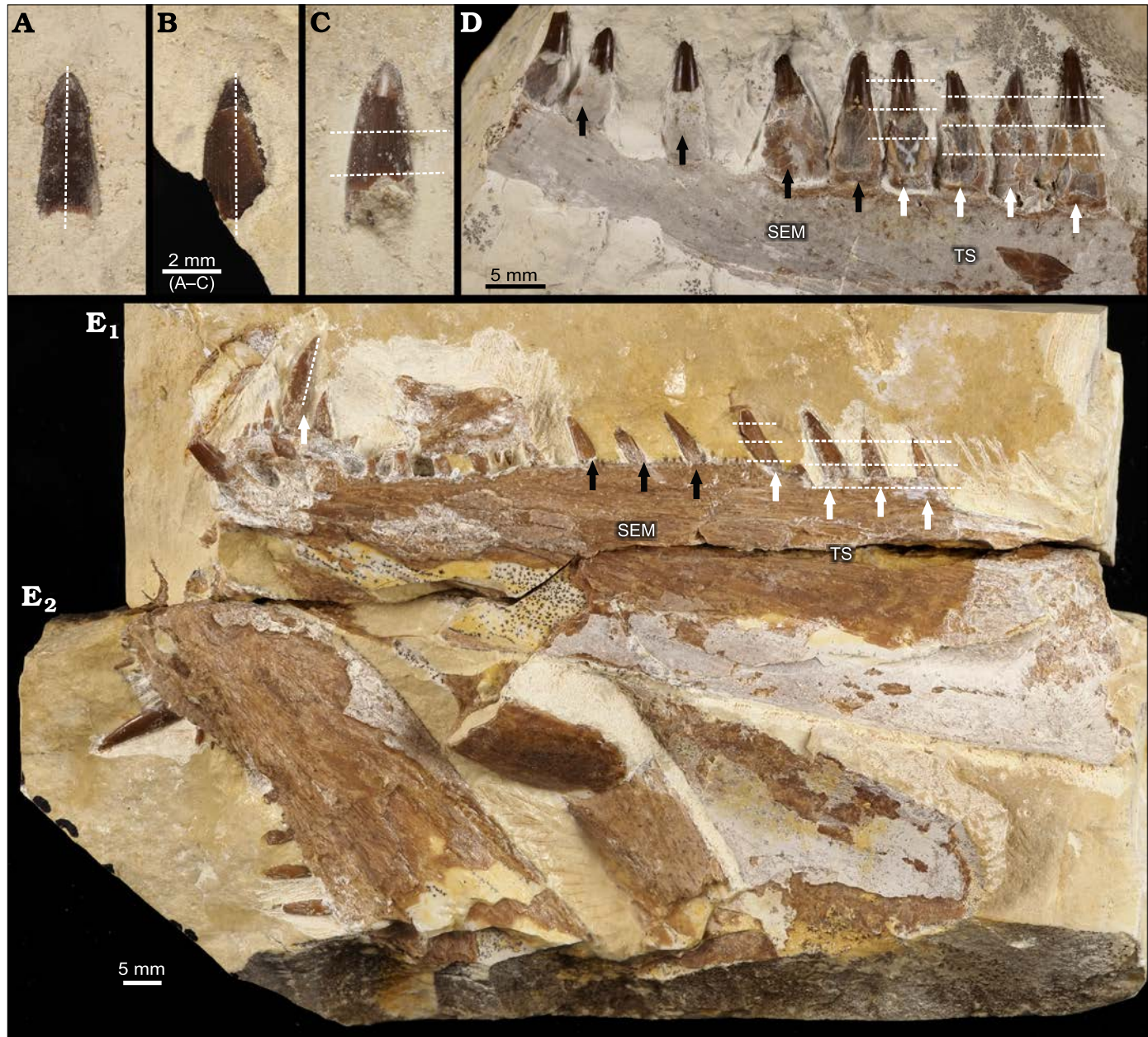


Fig. 2. Studied specimens of actinopterygian fishes from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. A–C. Loose teeth of Caturioidea indet. A. ZPAL P. 16/O-B/FT1. B. ZPAL P. 16/O-B/FT2. C. ZPAL P. 16/O-B/FT3. D. Caturioid *Strobilodus* sp., ZPAL P. 16/O-B/2, right dentary in lateral view. E. Pachycormid *Orthocormus teyleri* Lambers, 1988, ZPAL P. 16/O-B/3, left dentary (E₁) and right dentary (E₂) in lateral view. Dashed white lines indicate thin-sectioning plane; white arrows indicate which teeth were sampled for thin-sectioning (TS), black arrows indicate which samples were chosen for SEM analysis.

(ZPAL P.16./O-B/3). The vertical thin section was sampled from the symphyseal tusk. The fragments were polished and impregnated with resin. The samples were examined at 10×, 25× and 100× magnifications using a transmitted light microscope equipped with a Nikon Eclipse E600-POL camera. The thin sections are currently housed at the Institute of Geological Sciences of Jagiellonian University, with collection numbers NG/PAL/VERT/OB/C1–C7 for Caturioidea (ZPAL P. 16/O-B/FT1–FT3) and NG/PAL/VERT/OB/O1–O4 for Pachycormidae (ZPAL P. 16/O-B/3).

Scanning electron microscopy was realized using a HITACHI S-4700 instrument fitted with the NORAN VANTAGE microanalysis system. Four *Strobilodus* sp. (ZPAL P.16./O-B/2) teeth from the posterior section of the preserved fragment of dentary bone and three *O. teyleri* dentary (ZPAL P.16./O-B/3) teeth coming from the central part of the marginal tooth row were selected for SEM examination. These teeth were etched in a 10% acetic acid solution for ten minutes to accentuate the fine enameloid and dentin structures.

The terminology for tooth description is based on the Berkvitz and Shellis (2017) methodology used in describing fish teeth, using the following terms: apical, towards the apex of the tooth crown; basal, towards the tooth crown base; mid-crown, approximately centrally between base and apex of teeth; mesial, towards the anterior direction in animals' mouth; distal, inwards the animals' mouth; labial, in direction of animals' lips; lingual, towards the tongue.

Systematic palaeontology

Class Actinopterygii Klein, 1885

Infraclass Holostei Müller, 1846

Clade Halecomorphi Cope, 1872

Order Amiiformes O.P. Hay, 1929

Superfamily Caturioidea Owen, 1860

Genus *Strobilodus* Wagner, 1851

Type species: Strobilodus giganteus Wagner, 1851 (sensu López-Arbarello Ebert 2023), Painten (Germany), Kimmeridgian.

Strobilodus sp.

Fig. 2D.

Material.—Right dentary, ZPAL P.16./O-B/2 from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland.

Description.—The study material consists of an incomplete right dentary bone, with preserved medial and partially preserved posterior section, with nine intact teeth. This bone measures 59 mm in the anteroposterior plane, 11 mm in the dorsoventral plane and 6 mm in the labiolingual plane. Its shape can generally be characterized as elongated and moderately gracile. In the anterior region, the bone is rectangular, while in the medial plane it is slightly curved dor-

sally. The robustness of the bone gradually decreases in the ventral direction. There is a prominent indentation along the ventral margin of the bone in the central region, identified as ventral groove housing sensory canal. The whole bone texture is rather rough and compact. Two teeth are missing from the alveoli of the described specimen (Fig. 2D).

The teeth of the specimen can be characterized as conical, with a thick basal part and with a diameter that drastically decreases at the mid-crown. In the mid-crown and apical parts, the shape is much more gracile and elongated. In the apical plane, the cross section can be characterized as rounded with slight labiolingual compression, characterized by carinae present from the mid crown to the apex, while the basal cross section is rather round. The length of the teeth varies slightly in the described dentary, with larger and more

Table 1. Teeth crown lengths and width (in mm). Tooth row of *Strobilodus* sp.: A. Teeth rows of *Orthocormus teyleri*: P, parasymphyseal and symphyseal; M, mariginal; (d), damaged.

	<i>Strobilodus</i> sp.	<i>Orthocormus teyleri</i>	
	right dentary	left dentary	right dentary
Crown apicobasal length	A1: 8	P1: 2	P1: 4
	A2: 11	P2: 2	P2: 14
	A3: 10	P3: 14	P3: 3
	A4: 11	P4: 6	P4: 1
	A5: 11	P5: 2	M1: 4
	A6: 10	P6: (d)	M2: (d)
	A7: 9	M1: 8	M3: 7
	A8: 8	M2: 3	M4: 7
	A9: 8	M3–M7: (d)	
		M8: 7	
	M9: (d)		
	M10: 9		
	M11, M12: (d)		
	M13: 11		
	M14: 8		
	M15: 6		
Crown mesiodistal width	A1: 5	P1: 0.7	P1: 1
	A2: 4	P2: 0.8	P2: 4
	A3: 4.5	P3: 1.5	P3: 1
	A4: 4.5	P4: 4	P4: 0.5
	A5: 5	P5: 1	M1: 2
	A6: 5.5	P6: 3	M2: 2.3
	A7: 3	M1: 4	M3: 2.2
	A8: 3	M2: 3	M4: 2.1
	A9: 3	M3: 1.5	
		M4: 2	
		M5: 2	
		M6: 2	
		M7: 2	
		M8: 2	
		M9: 2	
	M10: 3		
	M11: 4		
	M12: 1		
	M13: 4		
	M14: 2		
	M15: 1.5		
Crown apicobasal height/mesiodistal length ratio	2.29	2.76	

robust teeth located more anteriorly and the teeth are also better preserved in this part of the bone. Generally, the teeth can be described as roughly homodont in form and are characterized by a symmetrical shape, along with slight lingual curvature. The intact teeth studied herein have an average ratio of apicobasal height/mesiodistal length of 2.29 (Table 1).

Remarks.—The relatively narrow and anteriorly tapering dentary; robust teeth with conical acrodin caps. This specimen was first described by Błażejowski et al. (2012) as dentary, belonging to the carnivorous *Caturus* sp., and was later redescribed as left maxilla (Błażejowski et al. 2015). In current light we consider this specimen to belong to the *Strobilodus* sp., based on the latest López-Arbarello and Ebert (2023) study and interpret this specimen as dentary.

Caturoidea indet.

Fig. 2A–C.

Material.—Three partial crowns of isolated teeth (ZPAL P.16/O-B/FT1–FT3) from Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland.

Description.—*Loose teeth:* the crowns of teeth, found loosely in the sedimentary rocks of Kcynia Formation. These conical-shaped teeth are slightly mesiodistally compressed with carinae placed along the mesial and distal planes of the crown. The T1 and T2 teeth consist of the apical and mid-crown section of the teeth, while the T3 tooth consists of the mid-crown section, with part of the acrodin cap preserved (Fig. 2A–C).

Remarks.—Carinae present along the mesial and distal planes of acrodin tooth cap.

Clade Teleostomorpha Arratia, 2004

Order Pachycormiformes Berg, 1937

Family Pachycormidae Woodward, 1895

Genus *Orthocormus* Weitzel, 1930

Type species: *Orthocormus cornutus* Weitzel, 1930, Langenthalheim (Germany), Tithonian.

Orthocormus teyleri Lambers, 1988

Fig. 2E.

Material.—Left and right dentaries ZPAL P.16./O-B/3, from Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland.

Description.—*Left dentary:* the specimen under study has been previously described and identified by Tyborowski (2017: figs. 3, 5, 6) as belonging to *Orthocormus teyleri*. The bone, which consists of the left dentary, is excellently preserved in its (or the) dorsal part with only the very posterior part of the bone missing. Measuring 109 mm in the anterior-dorsal plane, 11 mm in the dorsoventral plane in the middle section and 6 mm in the labiolingual plane, the bone has a well-preserved row of teeth. The anteroventral part of the bone is incomplete, making this part much

less robust than better preserved part of the anterior right dentary. The overall shape can be described as moderately gracile in the anterior part and robust in the mesial and posterior parts, with a maximum dorsoventral height of 21 mm in this part, but this gracility of the bone, as noted by Tyborowski (2017), can be attributed to missing antero-ventral part of the bone. The anterior part is characterized by the presence of a tooth rosette with marginal and parasymphyseal tooth rows, with a prominent and strong dental battery in the row of parasymphyseal teeth, crowned with a prominent 14 mm high tusk in the apicobasal crown. The anterior rosette can be characterized as ovaloid in shape in its anterior region and elongated and rectangular in its posterior part, with the anterior part curved anterodorsally and abruptly ending with a keel on which the horizontal branch begins. The anterior part of the horizontal branch is rather straight and gracile in shape, with small peg-shaped mesial teeth. The posterior part of the horizontal branch shows distinct conical teeth in the marginal tooth row, with miniscule peg-like teeth in the ventral tooth row aligned in between.

Right dentary: The bone measures 70 mm in the anterior-posterior plane, 23 mm in the dorsoventral plane and 7 mm in the labiolingual plane. It is a very robust bone, particularly deep in the dorsoventral plane. This right part of the dentary has preserved the anterior and mesial part, and the posterior part is missing. In the anterior part of the bone, two rows of teeth are visible, parasymphyseal and marginal, forming a tooth rosette with a prominent canine-like tusk measuring 14 mm at the apicobasal crown height. This bone can be characterized by the indentation present near the parasymphyseal region, where the parasymphyseal and marginal teeth rows meet. The teeth in the row of parasymphyseal teeth row are much more robust. The bone is slightly curved in the dorsal plane, with the anterior part rounded and robust in form, while the horizontal branch is rectangular.

The shape of the teeth can be described as strongly conical and elongated in proportion, with an average ratio of apicobasal height/mesiodistal length of the complete crown of 2.76 (Table 1). Teeth can be characterized as heterodont, with a wide variation in size and morphology, with the largest teeth developed as labiolingually curved tusks and the smallest as straight-peg-shaped structures. The teeth are rather simple in their form, without any ornamentation, with carinae present only on the mesial surfaces of large tusks. The posterior teeth are mostly mesially inclined, while the symphyseal and parasymphyseal teeth are perpendicular to bone. For research purpose, only the left dental bone was sampled.

Remarks.—Some dentary teeth perpendicularly directed, but most of them inclined forward; some dentary teeth lingually curved; dentary bone with at least one, conical and slightly procumbent tooth; closely arranged dentary teeth; crown of dentary teeth with a circular base and mesiodistal oval section.

Results

Observations of microstructure in thin sections

Caturoidea.—The vertical cross section (Fig. 3A) shows two distinct layers: an inner tubular orthodontin and an outer enameloid layer. In the apical part, the teeth consist of large

caps of acrodentin, which form a very thick coating on the tops of the teeth. The ortodontin layer is tubular in structure, with slightly oblique alignment of tubules, generally perpendicular to the tooth surface. The collar enameloid layer is rather thin, consisting of a layer of about 20–30 μm thick, and is characterized by a prominent prismatic structure, while the acrodentin has a structure more similar to ortho-

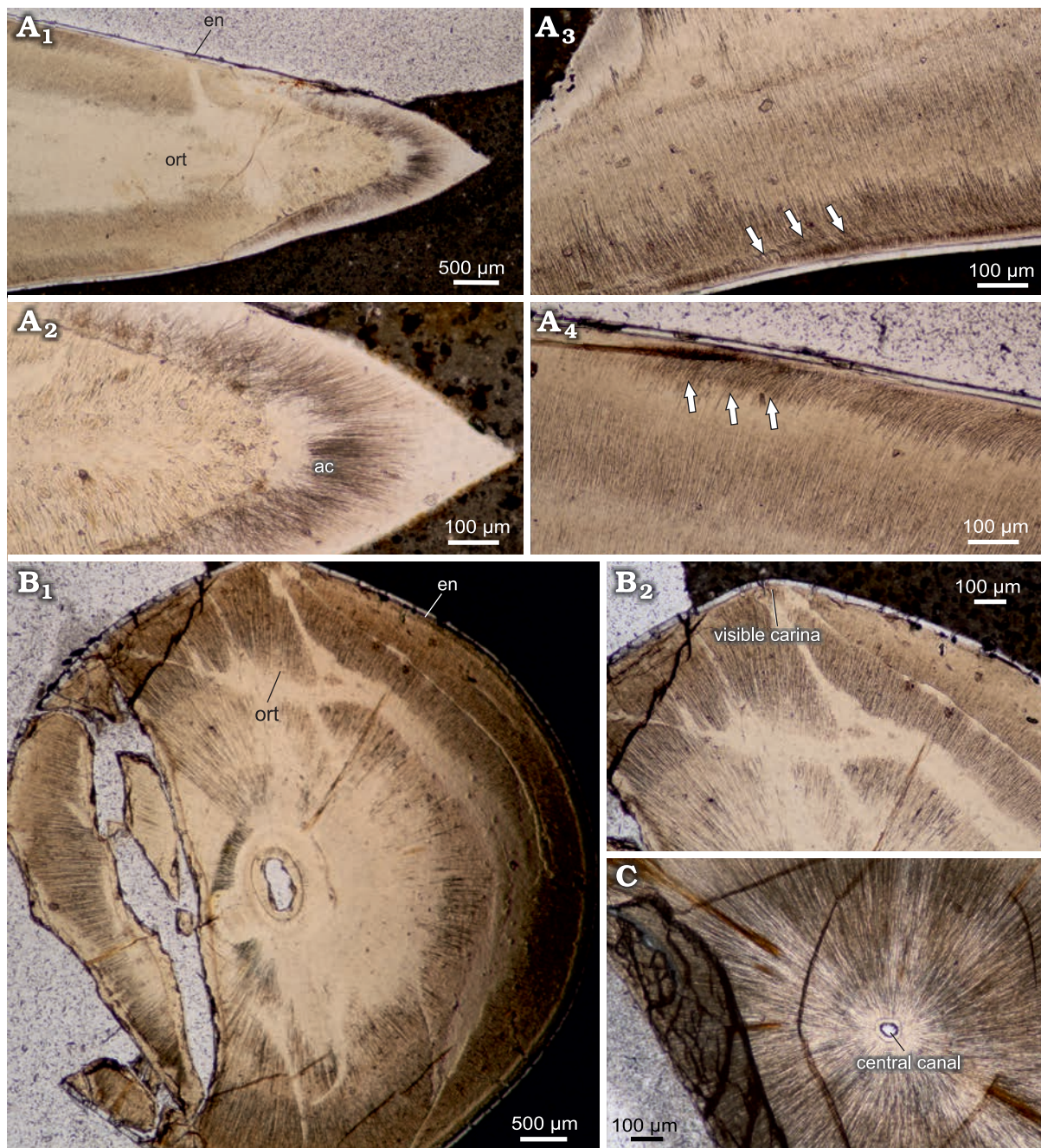


Fig. 3. Thin sections of teeth of caturoidean fishes *Caturoidea* indet. (A) and *Strobilodus* sp. (B, C) from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. A. NG/PAL/VERT/OB/C5 thin section from ZPAL P.16./O-B/FT1. A₁, general view of vertical thin section with orthodontin histology (ort) and thin enameloid layer (en); A₂, close view of apical section, with prominent acrodin cap (ac); A₃, A₄, crown mid-section with angled orthodontin tubules (highlighted) present. B, C. Horizontal cross section of *Strobilodus* sp. teeth in apical plane. Arrows indicate phenomena. B. NG/PAL/VERT/OB/C7 thin section from ZPAL P.16./O-B/FT3. B₁, overview of teeth structure, with slight mesiodistal compression and mostly solid structure; B₂, carinae present as a perturbances in mesial and distal planes of teeth. C. NG/PAL/VERT/OB/C1 thin section from ZPAL P.16./O-B/O2, small central canal surrounded by prominent dental tubules of orthodontin.

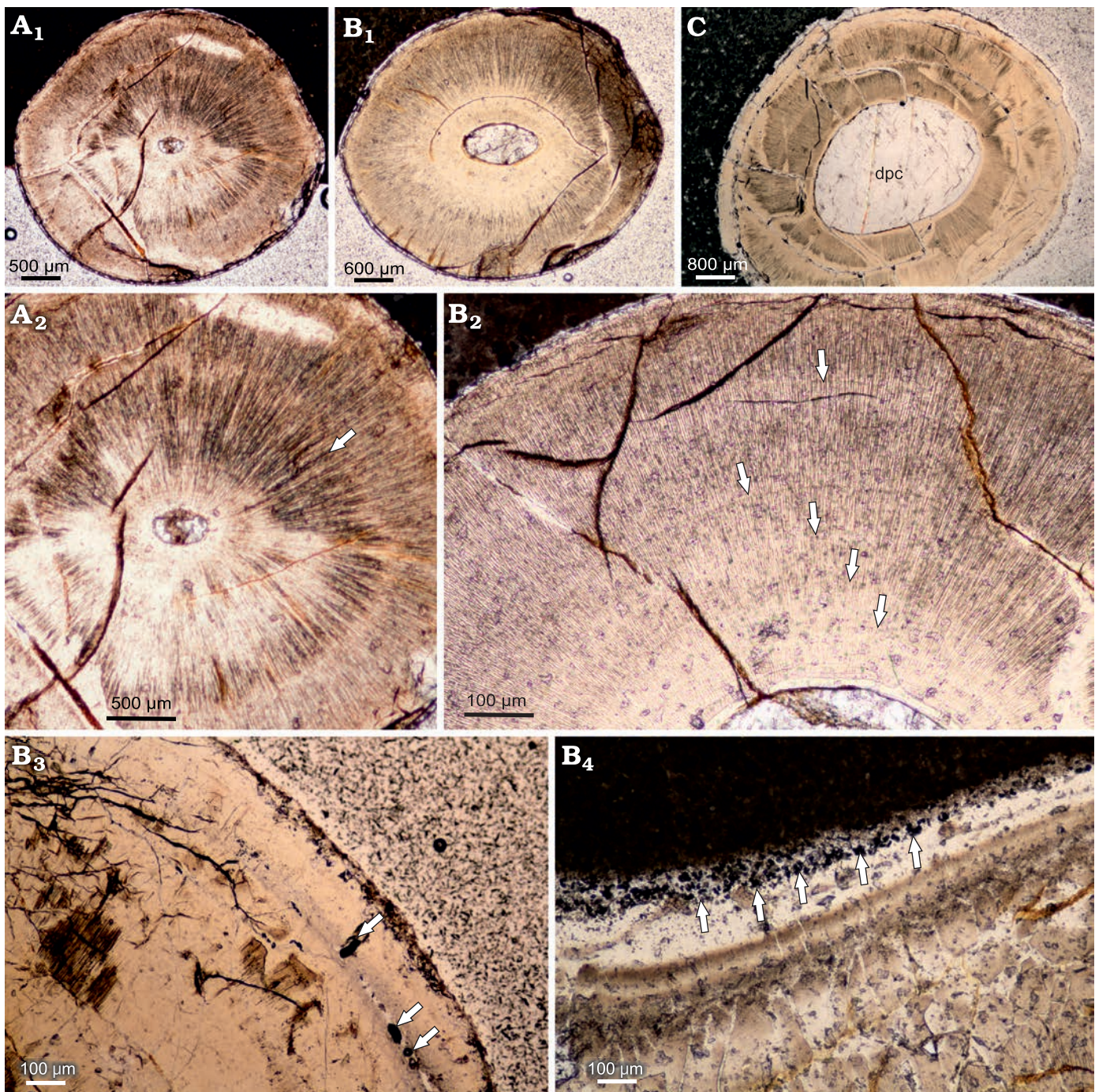


Fig. 4. Cross-sections of teeth caturioidean fishes *Strobilodus* sp. from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. A–C. NG/PAL/VERT/OB/C1–C3, respectively, thin sections from ZPAL P.16./O-B/2, in apical (A₁), mid-crown (B₁), and basal (C) planes, documenting relative increase in dental pulp cavity diameter in basal direction. Incremental growth lines: irregular (A₂) and more regular (B₂) patterns of growth are documented. Dentin drillings (arrows) present sub-superficially (B₃) and superficially (B₄).

dentin, with a slightly tubular structure, forming a massive cap enameloid at the apex. Vertical-transverse cross sections show pronounced diagenetic alteration in the centre, resulting in a reduction in the prominence of dentin tubules. The horizontal cross section (Fig. 3B) can be characterized as rounded with slight protuberances in the mesiodistal plane.

The internal structure of the teeth composed mainly of the orthodentin, which accounts for most of the cross section.

The orthodentin can be described as a highly regular structure, in the form of parallel tubules radially radiating from the centre. The observed collar enameloid layer is rather thin, measuring 30 µm at the apical cross section and about 20 µm in basal cross section. The examined teeth are characterized by a gradual increase in the diameter of the tooth in the basal direction (Fig. 4A₁, B₁, C). The basal plane surface exhibits superficial and subsurface dentin boreholes in many

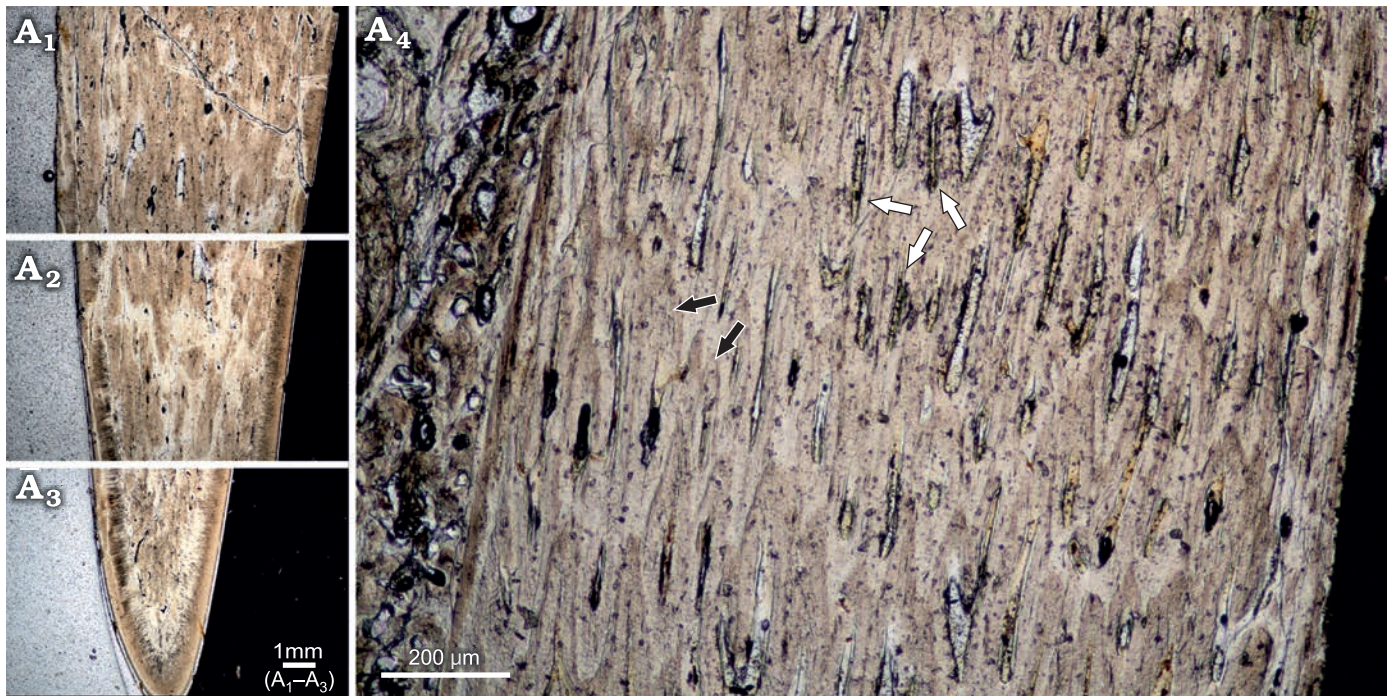


Fig. 5. Vertical cross-section of tooth of pachycormid fish *Orthocormus teyleri* Lambers, 1988, NG/PAL/VERT/OB/O1 thin section from ZPAL P. 16/O-B/3 from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. Basal (A₁), mid-crown (A₂), and apical (A₃) planes, with visible acrodin cap. Internal structure (A₄), with visible denteonal canals (white arrows) and inter-denteonal dentin (black arrows).

places (Fig. 4B₂, B₃). In the mid-crown part of the teeth, there are distinct incremental growth lines in the orthodentin layer (Fig. 4A₂, B₂). The growth lines appear either as a more prominent band dividing orthodentin into two distinct layers, as in Fig. 4A₂ or very lightly accentuated structures regularly becoming more expansive as shown in Fig. 4B₂.

***Orthocormus teyleri*.**—In vertical cross section, the teeth can be characterized as elongated and conical, having multiple internal capillary cavities, which become more numerous basally (Fig. 5). Larger capillaries are connected by an extensive network of smaller and more abundant capillaries. The examined sample shows a moderately thin acrodentin cap in apical section. The teeth are composed of three layers. The innermost osteodentin is filled with pores identified as denteonal canals (Thangadurai et al. 2022). The next is the denteons, which are divided by inter-denteonal dentin; the orthodentin layer and the outermost layer is a very thin enameloid, about 20 µm thick.

The horizontal cross section can be characterized as ovaloid, with a slight mesiodistal compression (Fig. 6). In horizontal cross section, denteons polygonal structure is clearly visible, with visible internal vascularization in series of small capillaries diverging from denteonal canals. Separation of denteons by inter-denteonal dentin is distinct. Below the orthodentin layer, a system of small capillaries surrounds inner osteodentin, exhibited as radial bundled structures. The osteodentin in basal teeth sections (Fig. 6C₂), exhibits especially prominent denteons, characterized by prominent diagenetic alteration, which highlights denteon structure. Enameloid layer is very thin in all horizontal sec-

tions, ranging on average 20 µm. The alveolar bone is visible in one of the basal thin sections, with multiple additional teeth erupting (Fig. 7) and cases of individual teeth arrested eruption on underlying specimens.

Observation of microstructure using scanning electron microscopy

Caturoidea.—The tooth enameloid of this taxa has fine small-scale longitudinal ridges (Fig. 8A, B). These form a very complex structure (Fig. 9C–H), which results in smooth ridges in the midsection of the teeth but, closer to the base of the crown, changes to a winding, more densely packed form, which then turns into fine-grained structures at the base of the teeth. The dentin layer examined in horizontal view appears as an irregular nodular structure, with small capillaries lining the layers (Fig. 10). The observed teeth in the vertical plane have a granular layered structure, where each irregular dentin layer is stacked on top of the other. In the exposed orthodentin layer there are clearly visible microborring structures, forming winding, extensive surface channel systems, with visible bifurcations (Fig. 9).

***Orthocormus teyleri*.**—The surface of the enameloid in this species can be characterized by the presence of prominent longitudinal ridges (Fig. 11), which appear as bump-like structures arranged linearly in the apicobasal plane. These structures are divided by visible fractures, probably of diagenetic origin. The base of the teeth is devoid of these structures, with a non-ridged granular enameloid with a dentin-like structure. The inner dentin is strongly perforated

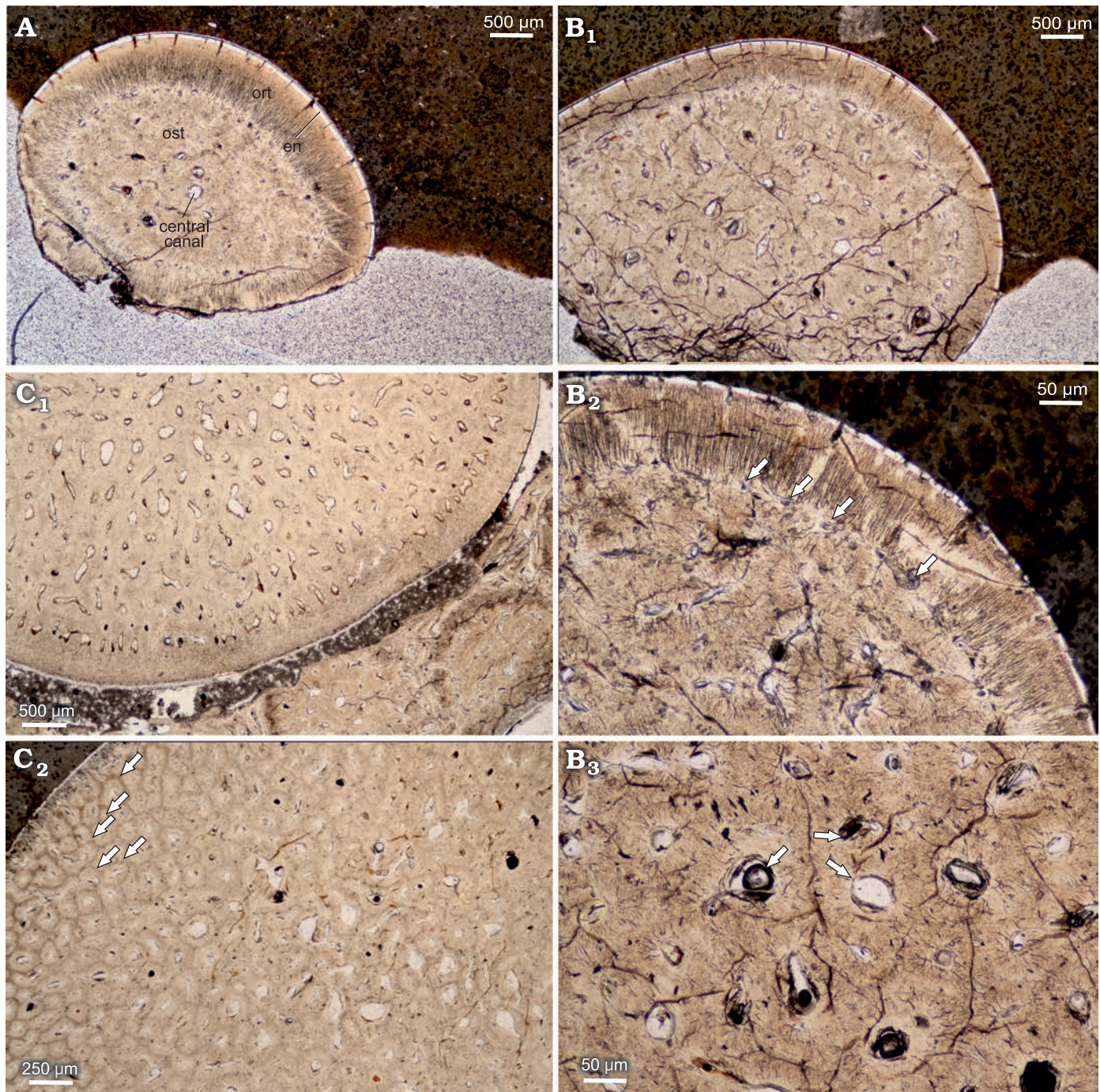


Fig. 6. Horizontal cross sections of teeth of pachycormid fish *Orthocormus teyleri* Lambers, 1988. A–C. NG/PAL/VERT/OB/O2–4, respectively, thin sections from ZPAL P. 16/O-B/3 from Tithonian, Upper Jurassic Keynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. A. Apical plane with visible osteodentin (ost), surrounded by orthodontin (ort), and outermost enameloid (en). B. Mid-crown plane. B₁, general view; B₂, osteodentin layer encircled by marginal capillaries (arrows), which contact with orthodontin; B₃, osteodentin densely packed with denteons with central denteonal canals (arrows). C. Basal plane. C₁, general view; C₂, individual denteons pronounced due to diagenetic processes (arrows).

by numerous capillary dentinal canals present in cross section in horizontal view (Fig. 11D, H). These canals appear mostly smooth internally (Fig. 11D), with only minor horizontal disturbances. In the horizontal view, the dentin shows an elaborate winding structure, with horizontal ridges perpendicular to the tooth surface, which form an irregular canal-shaped surface (Fig. 11E–G).

Discussion

Microstructural and histological comparison.—Typical teeth of ray-finned fish consist of a core, dentin and is hardened on the outer surface by enameloid. The core, filled with dental pulp during life is preserved in the fossil record as a hollow pulp cavity, which often recrystallises as in the

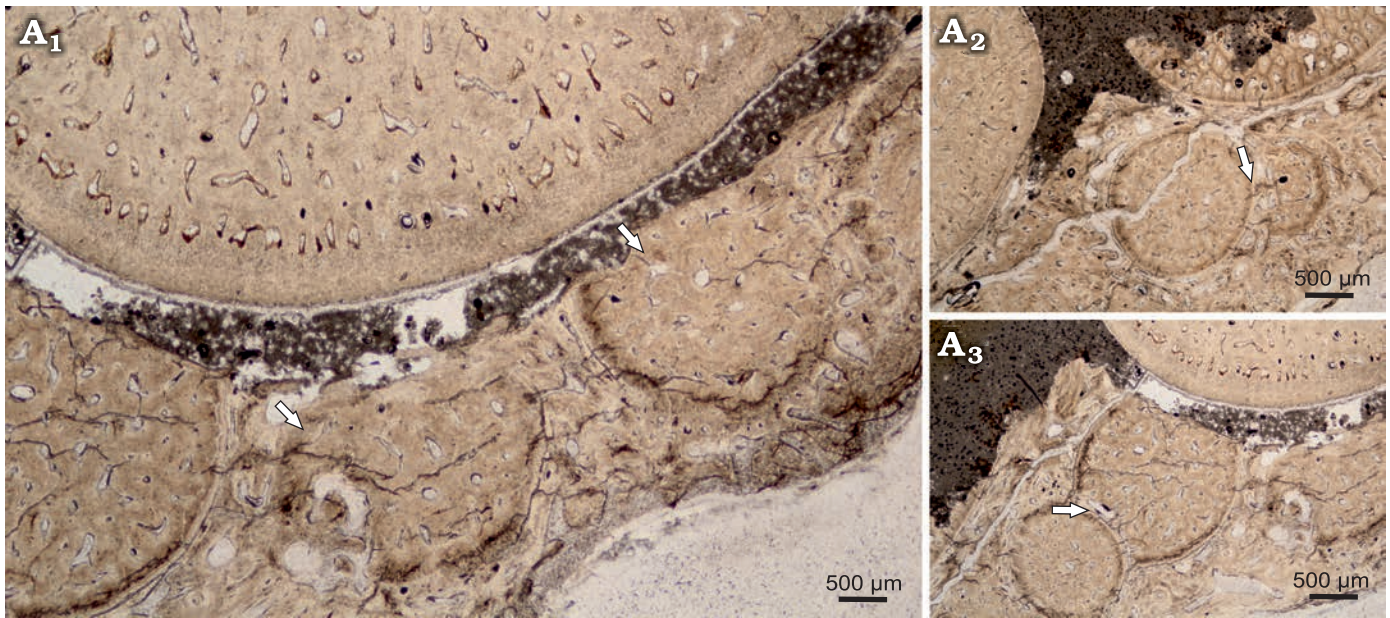


Fig. 7. Teeth eruption from alveolar bone of *Orthocormus taylori* Lambers, 1988, NG/PAL/VERT/OB/O4 thin section from ZPAL P. 16/O-B/3 from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owałów-Brzezinki, Poland. A₁, numerous teeth erupting in posterior tooth row; A₂, A₃, case of rapid teeth eruption, evidence of odontogenesis of one teeth specimen atop on the another tooth. Arrows indicate the observed phenomenon.

specimens presented herein. The cavity is surrounded by dentin, which can be either in form of tubular orthodentin or vascularised osteodentin, also called vasodentin, due to the vast internal network of canals which is more similar in structure to the bone (Ørving 1976), with the possibility of only one or both types of dentin being present (Sasagawa et al. 2009; Berkovitz and Shellis 2017; Kawasaki et al. 2021; Thangadurai et al. 2022). The outermost layer of enameloid is more similar in structure to dentin as opposed to the typical enamel of tetrapods (Sire et al. 2021), being less mineralized. In addition, in primitive actinopterygians, such as those examined in the present study, enameloid caps, also designated as acrodin, are very prominent (Shellis and Miles 1974), forming the apexes and upper regions of the teeth. The enameloid is thus formed as a cap enameloid at the apical part and a collar enameloid on the labial, lingual, distal and mesial surfaces (Kawasaki et al. 2021).

The examined caturoids teeth show a largely solid internal structure with a small central canal in the apical part, while a moderately large pulp cavity is present in the basal part. They display orthodentin histology, with the presence of strongly developed dental tubules arranged radially around the pulp cavity. Their internal structure can be described as generally similar to teeth of many predatory fish (Berkovitz and Shellis 2017), exhibiting a structure also similar to other macro-predatory aquatic taxa such as marine reptiles or crocodylians (e.g., Berkovitz and Shellis 2017; Owocki and Madzia 2020), with orthodentin building up the inner structure of the teeth, together with a prominent dental pulp cavity in the basal part. The pattern of dentin development can be described as rhythmic, since teeth show incremental growth lines.

Based on X-ray tomography of the sampled left dentary, Tyborowski (2017) discerned three histotypes present along

the tooth row of *O. taylori*: (i) “osteodentin type” with an internal structure composed of osteodentin, and no pulpal cavity, present in symphyseal and parasymphyseal teeth; (ii) “transitional type” with a noticeable pulpal cavity, surrounded by a thin layer of osteodentin, present in central part of marginal tooth row; (iii) “orthodentin type” with a well-defined pulpal cavity, and an internal structure filled with orthodentin, without visible osteodentin, located in posterior part of marginal tooth row.

The teeth of *O. taylori* were sampled from the posterior part of the maxilla, so they should not have an osteodentin pulp cavity filling. Intriguingly, however, it can be observed that most of the internal tooth structure consists of osteodentin, and only a very small cavity in the dental pulp was observed (Fig. 6A₁). This can be interpreted as an internal reinforcement of the medial teeth in the row, which means that not only the symphyseal teeth are braced, but this condition also partly corresponds to the more posterior teeth.

The histology of the *O. taylori* teeth, as seen in the horizontal thin sections closely corresponds to the “osteodentin type”, with minor characteristics of the “transitional type”. However, it should be noted that these teeth were sampled from the marginal tooth row in distal parts of the maxilla. This could mean that the characteristic histology pattern observed by Tyborowski (2017) using X-ray tomography does not coincide with microscopic observations, as this type of histology would be expected from teeth located only in the symphyseal and parasymphyseal planes of the tooth row. Thus, it should be concluded that not only the parasymphyseal and symphyseal teeth show internal osteodentin histology, but so do the posterior teeth. The above conclusion also indicates that observation of traditional thin sections under light microscope is proving to be a more nuanced method

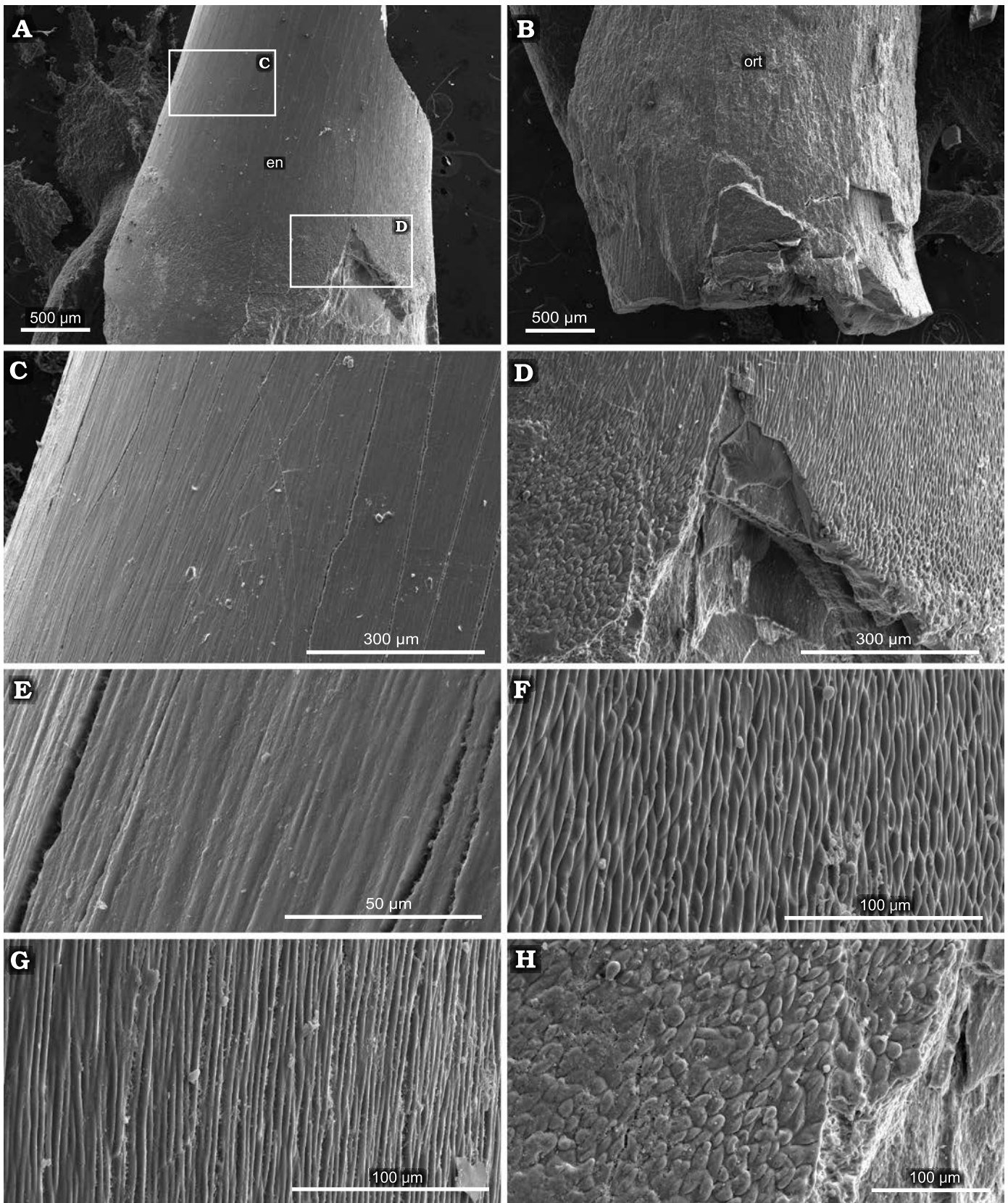


Fig. 8. SEM overview of tooth of caturiod fish *Strobilodus* sp. ZPAL P. 16/O-B/2 from Tithonian, Upper Jurassic Keynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. **A.** Mid-crown section with visible layer of enameloid (en). **B.** Basal section with exposed orthodontin (ort). **C, D.** Overview in apical-mid-crown surface. **E–H.** Changes in enameloid structure from linear through irregular to scale-like in basal direction.

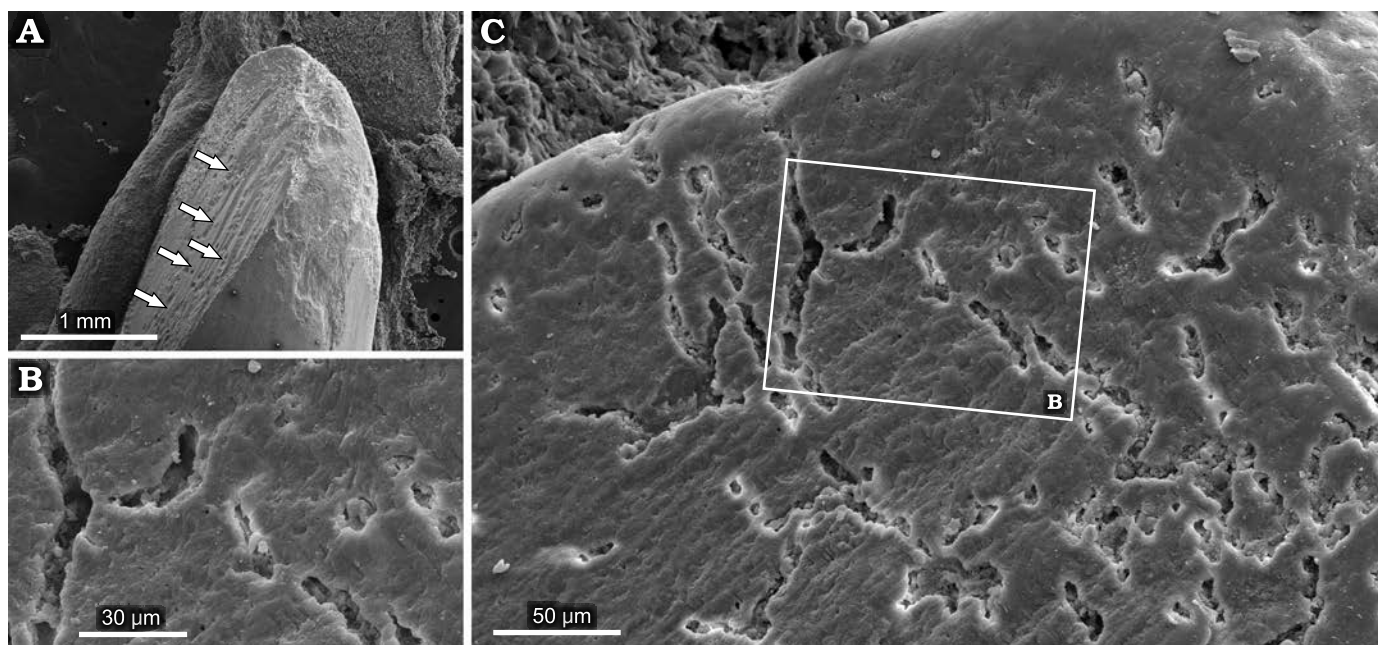


Fig. 9. Examples of superficial penetrations present in orthodontin of caturoid fish *Strobilodus* sp. ZPAL P. 16/O-B/2 from Tithonian, Upper Jurassic Kcynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. **A.** Overview of penetrated teeth with exposed dentin (borings marked by arrows). **B.** Close view of structure with visible bifurcating canals. **C.** Example of advanced bioerosion, with substantial surface area of orthodontin penetrated.

of histological examination. However, the disadvantage of this technique is the destruction of the specimen during thin-section preparation.

Finally, a striking feature of the teeth of *O. teyleri* is the polygonal structure of the osteodontin, characterized by numerous denteonal canals that serve as ossification centres for odontoblasts spreading radially to form characteristic denteons. The individual canals can pass nutrients through a series of smaller capillaries diverging from a central capillary. This system was vital for providing the nutrients needed for the rapid growth of odontoblasts. It can be suspected that the pronounced nature of the denteons in the basal parts may be influenced by diagenetic processes that highlighted the individual denteons. A very similar osteodontin structure can be observed in contemporary Atlantic wolfish (see Thangadurai et al. 2022: figs. 2, 9), with the internal vascularization occurring as multiple pores rather than as a single dental pulp cavity with a central canal.

Micro-borings present in the structure of the teeth.—

Numerous pits are visible on the surfaces of many of the observed specimens. This feature is particularly evident on SEM examination, where it can be seen that they are instead developed in the form of superficial canals. These structures only appear on surfaces with exposed dentin. Enamel in general is devoid of such structures, probably due to its higher mechanical resistance in comparison to dentin. The observed canals can be interpreted as post-mortem structures of possible fungal origin. Similar structures have been observed in the teeth of Jurassic neoselachians (Martill 1989). These micro-borings can probably be attributed to the ichnospecies *Mycellites ossifragus* Roux, 1887, known

to occur on the teeth of fossil fishes (Underwood et al. 1999), also in orthodontin. Although apatite is one of the most physically and chemically resistant biominerals, it is believed that a group of fungi have developed the ability to use this phosphate source (Martill 1989), enabling them to colonise vertebrate skeletal elements. Underwood et al. (1999) believe that the teeth and roots of bony fish such as Caturioidea often display these types of fungal origin structures, even though they are more commonly found in selachian teeth. In the tooth specimens studied, the structures observed often show the typical form of an advanced stage of colonisation, with a bifurcated, irregular branching structure on the tooth surface, sometimes involving large areas of exposed dentin. These observations suggest that many of the teeth studied were intensively colonised after the death of fish. The lagoonal environment of Unit III, from the sediments of which the specimens studied were derived, was characterised by the presence of microbial mats that enabled the preservation of horseshoe crabs (Kin and Błazejowski 2014). Possibly, this type of environment was also favourable for the development of bone-consuming fungi, which would explain the extent of colonisation present in the samples.

Palaeoecological aspects inferred from observed macro- and microstructural differences.—

The shape and proportions of teeth, on a par with their microstructure, are one of the most crucial indicators of animal ecology. For studies of fossil marine predators, a classification of ecological traits based on tooth proportions has been proposed (Massare 1987; Hornung and Reich 2015; Foffa et al. 2018). This classification has been successfully applied to the fossil

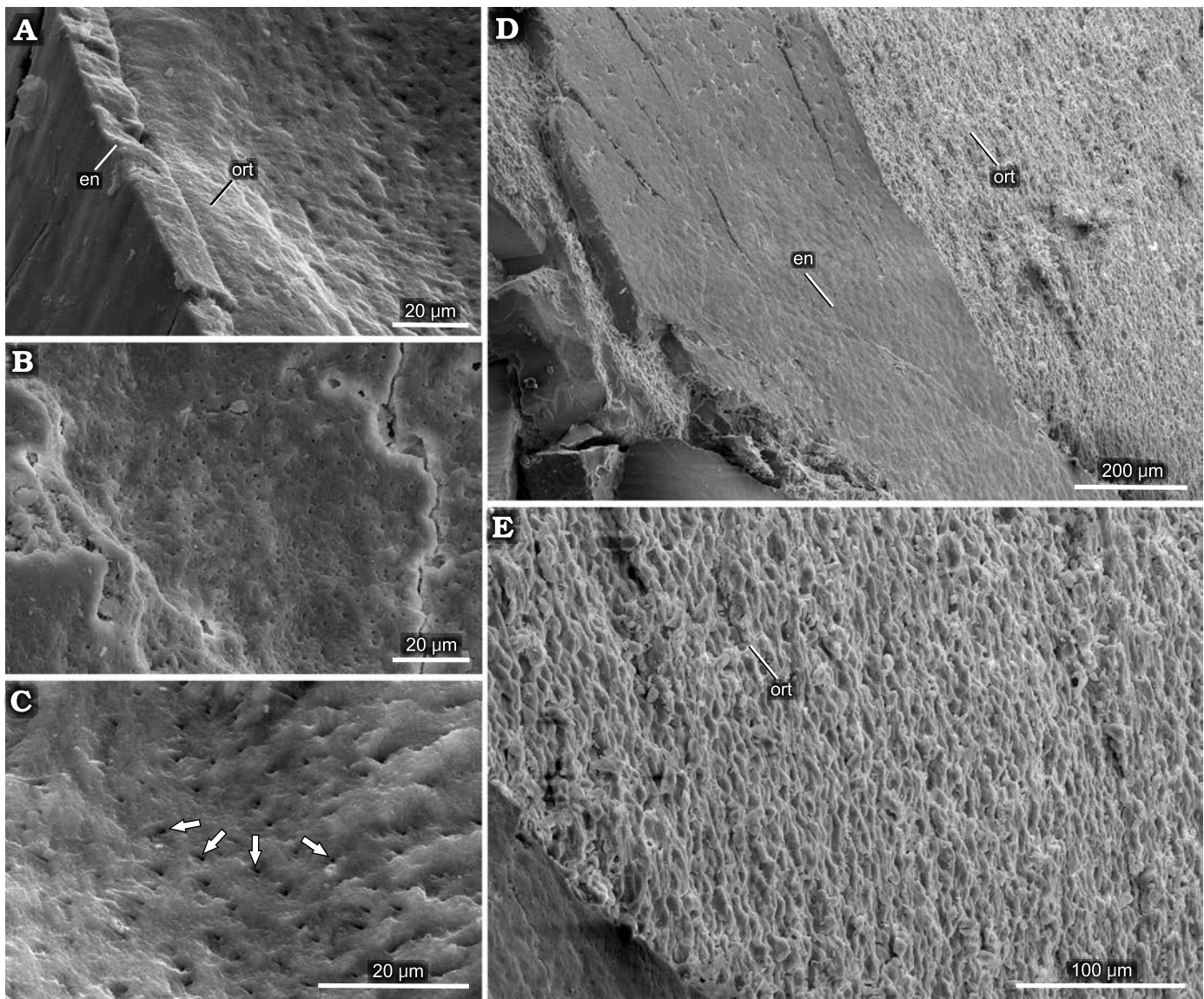


Fig. 10. Structure of orthodontin of tooth of caturoid fish *Strobilodus* sp. ZPAL P. 16/O-B/2 from Tithonian, Upper Jurassic Keynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. **A**. Boundary between orthodontin (ort) and enameloid (en). **B**, **C**. Overview of horizontal surface of orthodontin with dental tubuli (arrows). **D**. Vertical view of boundary between enameloid and orthodontin, with compact, regular enameloid and **(E)** irregular, rugose, porous orthodontin surface.

teeth of large marine reptiles, as they are often the best-preserved part of these large vertebrates and therefore provide abundant and good-quality samples to reconstruct the ecology of the organism. The palaeoecological grouping of large marine reptiles is based on the relative proportions of apicobasal, mesiodistal and labiolingual measurements along with other dental characteristics. Those include the presence of shearing carinae with three basal groups (cutting, piercing, and crushing) as well as emerging additional intermediate groups (Hornung and Reich 2015), and for the purposes of this study similar general observations can be made.

Ecological classifications of fishes, including modern ones, are based on criteria other than tooth shape (Elliott et al. 2007; Franco et al. 2008). Nevertheless, it appears that den-

tary features such as shape and proportions, including those in the extinct predatory Actinopterygii studied herein, are among the common indicators of ecology for all vertebrates (Alistair 2013). That is the case since specific adaptive pressures affect morphology regardless of the taxonomic position of the organism under investigation.

The taxa studied are often found in strata of similar facies, indicating their cohabitation in comparable environments. While both caturoids and raptorial pachycormids can be described as fast-swimming predatory fishes living in open water basins, their dental characteristics (Fig. 12), presented as macro- and microstructural features, suggest that they used different hunting strategies. This allowed these large, similar-sized predators to coexist and exploit different resources of the same environment.

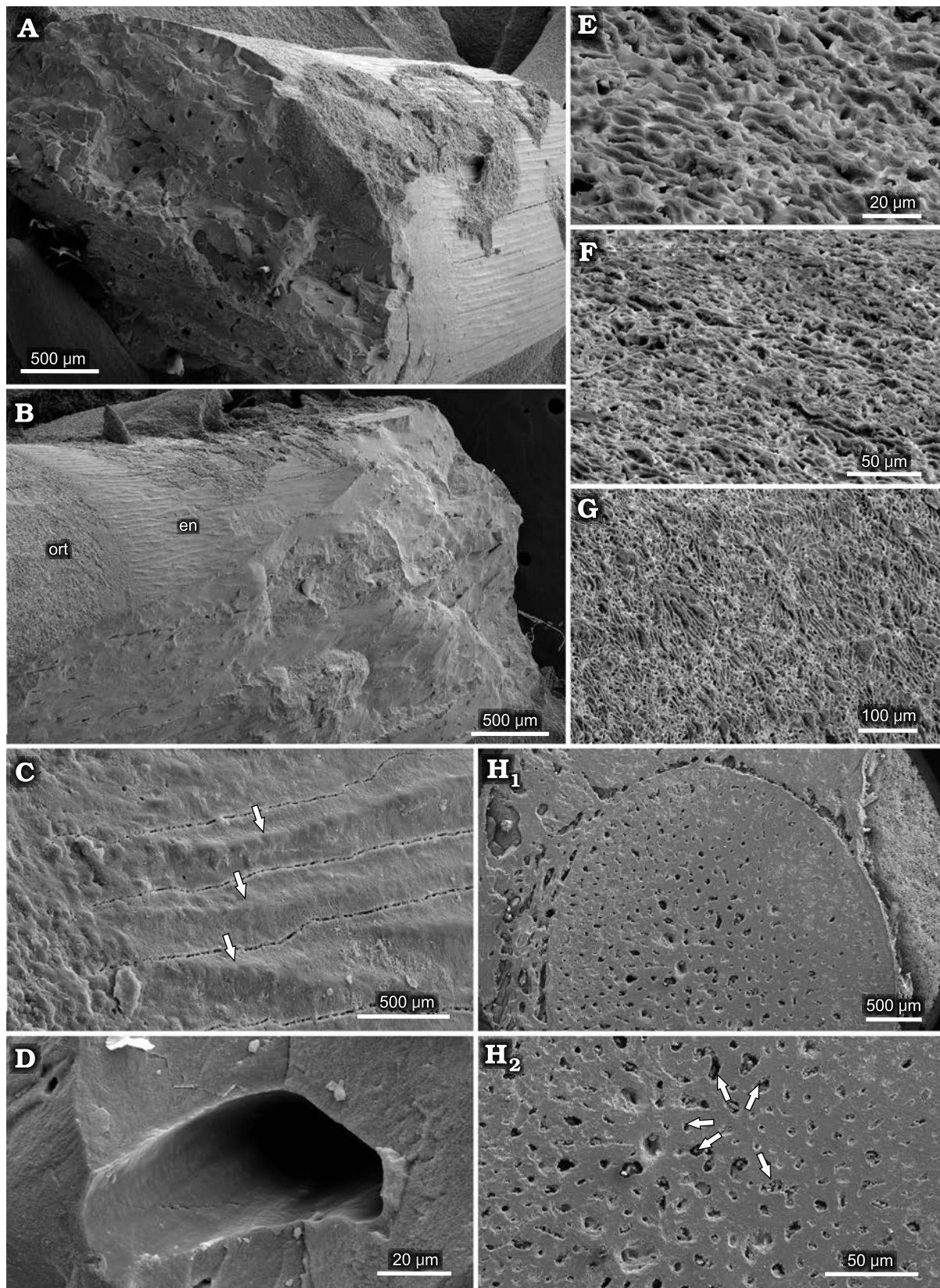


Fig. 11. Microstructure of teeth of pachycormid fish *Orthocormus teyleri* Lambers, 1988, ZPAL P. 16/O-B/3 from Tithonian, Upper Jurassic Keynia Formation, *Corbulomima* Limestone (Unit III), Owadów-Brzezinki, Poland. **A, B.** General view. **C.** Enameloid (en) and orthodentin (ort) surface with visible longitudinal ridging (marked by arrows). **D.** View of singular denteonal canal of orthodentin. **E–G.** Visible structure of orthodentin layer in vertical view, developed as series of winding, ridged irregular canals. **H.** Basal cross section in transverse plane, with visible osteodentin (H_1), arrows indicating denteonal canals (H_2).

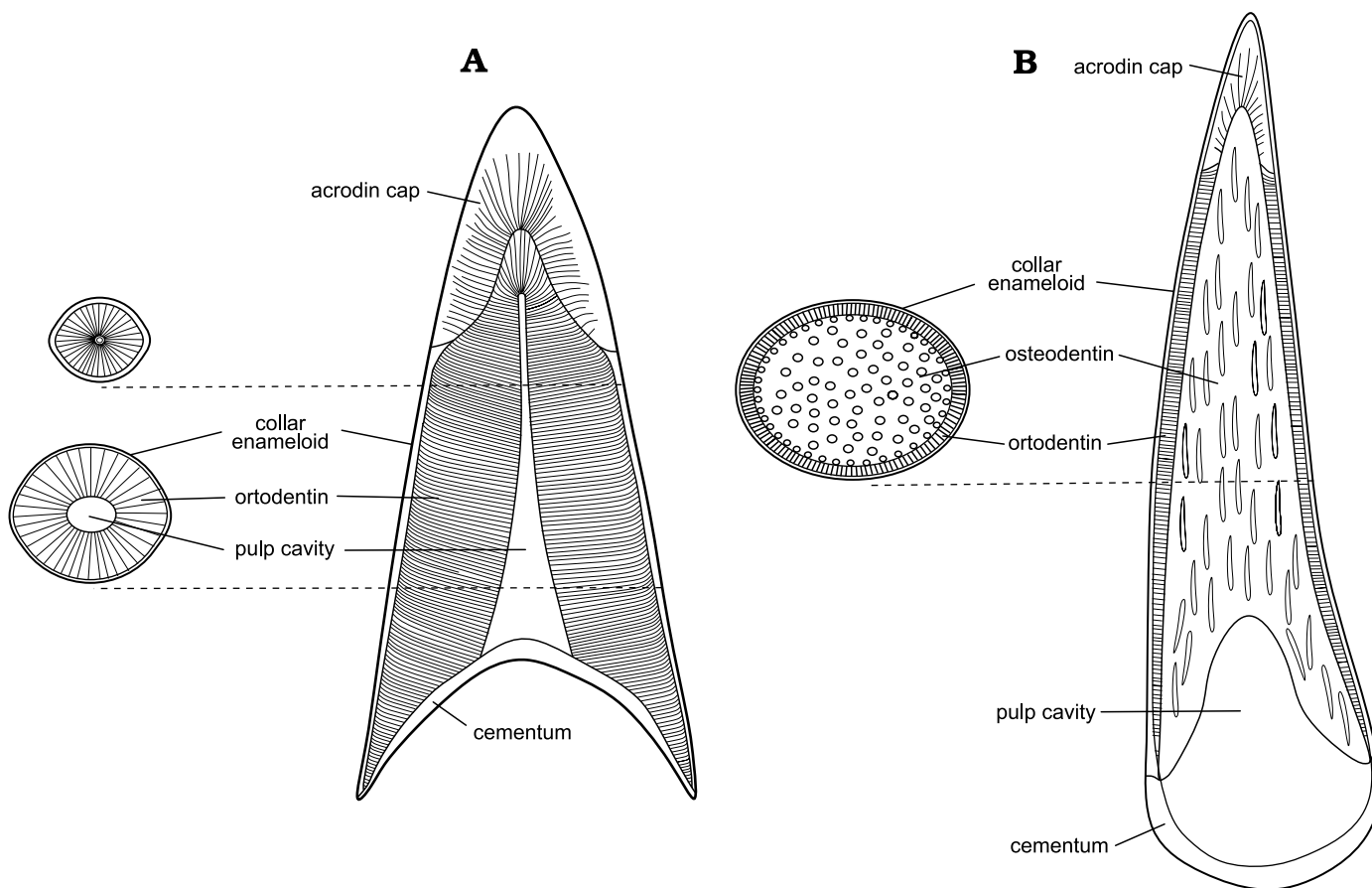


Fig. 12. Comparison of generalized teeth vertical cross sections of the studied taxa. A. Caturioidea. B. Pachycormidae. Not to scale.

The incremental growth lines are undoubtedly the most interesting aspect of the histology of the studied teeth of caturoids, as this type of structure is particularly prominent in animals inhabiting diverse environments or ones with seasonal variation. Caturoids can be considered a superfamily that was resistant to oxygen deficiency, as it is placed in the Amiiiformes (Wierzbowski et al. 2019), which often shows such adaptations. The dentin structures observed herein are interpreted as long-term increments known as the Andresen lines (Dean 2000). The apparent pattern of dentin development can be described as long-lasting endogenous biorhythms. Such characteristic of the Andresen lines identified in this case, distinguishes it from the more widely known daily incremental growth marker—von Ebner lines, which documents longer incremental cycles seen in dentin (Dean 2000).

It should be mentioned that the observed growth patterns of successive layers in all the maxillary teeth studied appear to be very irregular. These increments probably grew at different times and, therefore, the growth of dentin was regulated by a varied supply of nutrients. Although members of Caturioidea, such as *Caturus* are considered marine (Wenz et al. 1994; Kriwet et al. 1997; Pouech et al. 2014), they are also found in coastal and lacustrine paleoenvironments (Lambers 1994; Bogan et al. 2013; Martín-Abad and Poyato-Ariza 2013; Woodward 2014; Poyato-Ariza and

Martín-Abad 2020). It can therefore be assumed that they are the result of growth in an unstable habitat. Occurrences such as fluctuations in salinity and oxygenation levels may cause irregular nutrient replenishment, which would manifest as differential dentin growth. This is supported by the results of the isotopic study by Wierzbowski et al. (2019), in which oxygen stable isotope ratios from Caturioidea (referred in the study as *Caturus* sp.) teeth indicate hypersaline episodes recorded in the Unit III sediments. The observed pattern of structural growth suggests that in Caturioidea, stress conditions not only affect oxygen isotope ratios, but also control biomineralization processes. Wierzbowski et al. (2019) hypothesised that Caturioidea like modern bowfins (*Amia calva*), may be characterized as bimodally respiring and thus adapted to low-oxygen environments, which often occur in such shallow waters as those represented by the Plattenkalk sediments (Fürsich et al. 2007). The apparent differential growths observed in the dentition of studied caturoids support this theory, since episodes or periods of low oxygenation certainly affect the biological processes of the animals. This also backs the supposition that caturoids were capable of inhabiting unstable and demanding environments. Such adaptations enabled them to thrive in environments in which the more pelagic species of *Orthocormus* could not. To some extent, it gives an explanation to the numerous finds of caturoids in the fossil record worldwide.

The teeth of caturoids examined herein are characteristic for a predator with a wide range of potential prey. The presence of cutting edges (visible in the geometry of the teeth in thin-section) in the mesiodistal plane indicates that the animal had a dentition with cutting abilities. Its hunting strategy was not restricted to grasping, but the described taxon was also capable of biting off chunks of flesh, suggesting that it could handle prey larger than itself. The ratio of apicobasal crown length to mesiodistal length of 2.29 display that teeth are robust. The teeth show some minor labiolingual compression and, more importantly, the symmetrical shape of the teeth with carinae present on both the mesial and distal surfaces indicates that shearing action played an important role in the feeding strategy.

Furthermore, the geometry of the apex of the tooth can be described as conical, hinting that puncturing was also an important aspect in prey capture, as piscivory requires a degree of puncturing and adaptation to hold prey (Cohen et al. 2020). The relatively uniform dentition of the studied Caturioidea specimens can be described as villiform (Mihalitsis and Bellwood 2019), which is characteristic of piscivorous predators adapted to prey capture with an irregular or puncture-resistant integument. These features suggest that caturoids represented a member of the intermediate slash/cut guild. In contrast to internally solid teeth of *O. taylori*, the teeth of caturoids. have a rather prominent dental pulp cavity, which means that the teeth were most likely susceptible to severe trauma, even taking into account their more robust ratio of crown apicobasal height to mesiodistal length. Due to the presence of prominent carinae on both the mesial and distal sides, shearing action enabled the teeth to reduce mechanical trauma during prey capture. In this scenario, greater internal tooth strength is not required, as the priority is to tear apart prey fragments.

The most outstanding feature of *O. taylori* is the presence of multiple teeth that erupt from the alveolar bone, which demonstrates a very rapid rate of tooth replacement. This trait, combined with a persistent internal osteodentin solid core present in all dentary teeth, including mesial teeth, and not only in the symphyseal and parasymphyseal region, as postulated by Tyborowski (2017), indicates multiple adaptations to a specialized predatory lifestyle, with a possible high-impact feeding pattern balanced by a fast rate of tooth replacement. The findings of present study complements the study by Tyborowski (2017) and highlights the possible additional reinforcement of all dentary teeth in the specimen studied, as opposed to only the anterior teeth. Such an arrangement would provide further mechanical reinforcement during ram feeding, which is a proposed hunting strategy by Tyborowski (2017). Tyborowski (2017) also compares *O. taylori* ecology with modern day *Sphyrna barracuda*, and correspondingly, with a similar lifestyle to other modern predatory Actinopterygii living in open water (Harper and Blake 1991; Grubich et al. 2008). In the ram-feeding model, it should be taken into consideration that not only the anterior teeth, but also mesial teeth may come into contact with high

force when ramming into prey, hence the more posterior teeth may require additional structural support. This aspect requires further biomechanical studies to assess the possible jaw dilation in this taxon. Furthermore, it is noteworthy that a high impact feeding strategy may be possible due to the fast rate of tooth emergence observed in the alveolar bone examined in this study, in which teeth lost due to ramming can be easily replaced. The pronounced internal vascularisation of the teeth researched can be explained by the need for a rapid supply of nutrients to sustain prompt tooth development.

The teeth of *O. taylori* are strongly heterodont, and with an average elongation of 2.76 in the apicobasal/mesiodistal ratio, represent features belonging to a piercing guild animal. The teeth examined have some intermediate features related to cutting adaptation, such as a slight distal curvature, ovaloid cross-section with very little labiolingual compression, and above all the presence of mesial carinae in larger marginal teeth and symphyseal tusks. Despite this, the rather elongated proportions of the teeth, coupled with their marked variation in size, indicate an animal adapted primarily for grasping. The anterior rosette of teeth, which ends in an indentation located behind the plane of the jaw symphysis, also implies this ecology. Furthermore, the anterior symphyseal and parasymphyseal teeth are directed posteriorly, while the posterior teeth are directed anteriorly, forming a kind of trap directed at the symphyseal notch. Mihalitsis and Bellwood (2019) postulate that front fanged condition in piscivorous fishes such as in examined *O. taylori*, is an adaptation that aids in capture of fast, elusive prey. These features, combined with described tooth microstructure, allow us to conclude that this taxon, in contrast to caturoids. was probably a predator characterized by a more dynamic hunting strategy, involving the active ramming of mid-sized prey, which was retrieved by impalement through conical-shaped teeth.

Conclusions

Our observations in this study provide incentive for further microstructural analyses of fossil Actinopterygii as a tool for interpretation of their biology, especially when it comes to microstructural aspects of the predatory Jurassic fish of the families examined herein. Although both Caturioidea, and predatory pachycormids possess the elongated bodies of rapid predators that hunt from ambush (Tyborowski 2017), their dental characteristics indicate different adaptations for predation. Both tooth morphology and histology suggest niche partitioning. Due to their varied feeding strategies, these two similarly sized predatory fish taxa were able to co-exist in marine environments on a global scale, known from Late Jurassic sites such as famous Solnhofen (Germany) or, becoming increasingly important, Owadów-Brzezinki (Poland). Comparison of the microstructure and external tooth features of the aforementioned taxa allowed the following conclusions to be drawn, also concerning their palaeoecology:

(i) The examined caturoids possessed conical dentition, slightly mesiodistally compressed, with mesiodistal carinae. It is rather uniform in shape with large piercing-shearing teeth, capable not only of grasping but also of cutting chunks of flesh to retrieve a wider range of prey, representing an intermediate piercing/cutting guild. The internal tooth structure visible in cross-section consists of solid orthodontin tubules, with a moderately sized dental pulp cavity present in the basal plane and very small one in more apical plane. The specimen of *Strobilodus* sp. whose dentary was examined here probably lived in a variable environment, as reflected in the fluctuating rate of dentin growth line pattern. This was due to changes in salinity and oxygen levels, indicating a high environmental tolerance of members of the family Caturioidea. Such characteristic enabled Caturioidea to thrive in demanding environments, which may explain their worldwide presence in the fossil record;

(ii) The dentition of predatory pachycormids can be characterized as conical, slightly mesiodistally compressed, with distal curvature of the larger teeth in the parasymphaseal tooth row, along with the general anterior alignment of the posterior teeth. The elongated, conical shape of the teeth and heterodont condition suggest that this species belongs to the guild of piercing fishes. Internally, the majority of the examined internal tooth volume in the dentary consists of a small-diameter porous osteodontin structure that forms denteons with central canals to create a characteristic polygon-like structure. Their internal structure can be described as highly vascularized. Numerous growing teeth are visible in alveolar bone, indicating a very rapid rate of tooth replacement. Considering the proposed high-powered ram-type feeding strategy, these physiological features could help to replace teeth that are often lost during attacks on prey.

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