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A large platypterygiine ichthyosaur from the Late Cretaceous of Poland and its macropredatory adaptations

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ABSTRACT:

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The discovery of a well-preserved rostral cross-section of a platypterygiine ichthyosaur in Cenomanian deposits at Annopol, Poland, provides new insights into the anatomy, functional morphology, and ecological role of this group during the Late Cretaceous. The specimen, identified as Platypterygiinae indet., preserves articulated teeth, a visible interpremaxillary cavity, and neurovascular canal openings, enabling detailed anatomical and comparative analyses. The robust dentition, featuring blunt crowns and deep implantation, suggests adaptations for a hypercarnivorous diet focused on hard and bony prey, such as marine turtles, smaller ichthyosaurs and large actinopterygian fish. Comparative analysis reveals close affinities with other Platypterygiinae, such as *Platypterygius australis* (Kear, 2005) and *Pervushovisaurus* spp., while highlighting distinctions from more generalist ophthalmosaurids like *Ophthalmosaurus* spp. The ecological role of the Annopol ichthyosaur as an apex predator mirrors that of modern marine predators, such as orcas and great white sharks, emphasizing its dominance in Cenomanian marine ecosystems. Its presence reflects the productivity and complexity of these environments, while its extinction at the Cenomanian–Turonian boundary underscores the combined impact of environmental disruptions, including ocean anoxia. This study enhances our understanding of the adaptive strategies, sensory biology, and ecological significance of Late Cretaceous ichthyosaurs, providing a key reference for exploring the evolutionary and ecological dynamics of marine reptiles during a critical period in Earth's history.

Key words: Ichthyosauria; Platypterygiinae; Palaeoecology; Feeding adaptations; Cenomanian.

INTRODUCTION

Ichthyosaurs, a diverse clade of highly specialised marine reptiles, are emblematic of the adaptive radiations that characterised the Mesozoic marine ecosystems. Their evolution, spanning from the Early Triassic (Olenekian) to their extinction in the Late Cretaceous (Cenomanian), reflects significant ecological and morphological changes driven by environmental shifts and biotic interactions (Fischer *et al.* 2016; Stubbs and Benton 2016). Among the ichthyosaurs, the family Ophthalmosauridae persisted into the Cretaceous, exemplifying a group that successfully adapted to changing marine ecosystems. Platypterygiinae, a subclade of ophthalmosaurids, is particularly notable for its global distribution and ecological importance during the Late Jurassic and Early Cretaceous (Arkhangelsky 1998; Bardet *et al.* 2016). The fossil record of Cretaceous ichthyosaurs is geographically widespread but fragmentary, particularly for cranial material, which holds critical information about feeding strategies and ecological roles. In Europe, significant discoveries have been made in regions such as the Albian–Cenomanian deposits of Annopol in Poland (Bardet *et al.* 2016), the Hauterivian–Aptian strata of Germany (Fischer 2012; Fischer *et al.* 2012), and the Lower Cretaceous units of northern Italy (Serafini *et al.* 2022). These finds have provided a glimpse into the diversity of platypterygiines, including their cranial adaptations, but comprehensive studies of their rostral morphology remain limited.

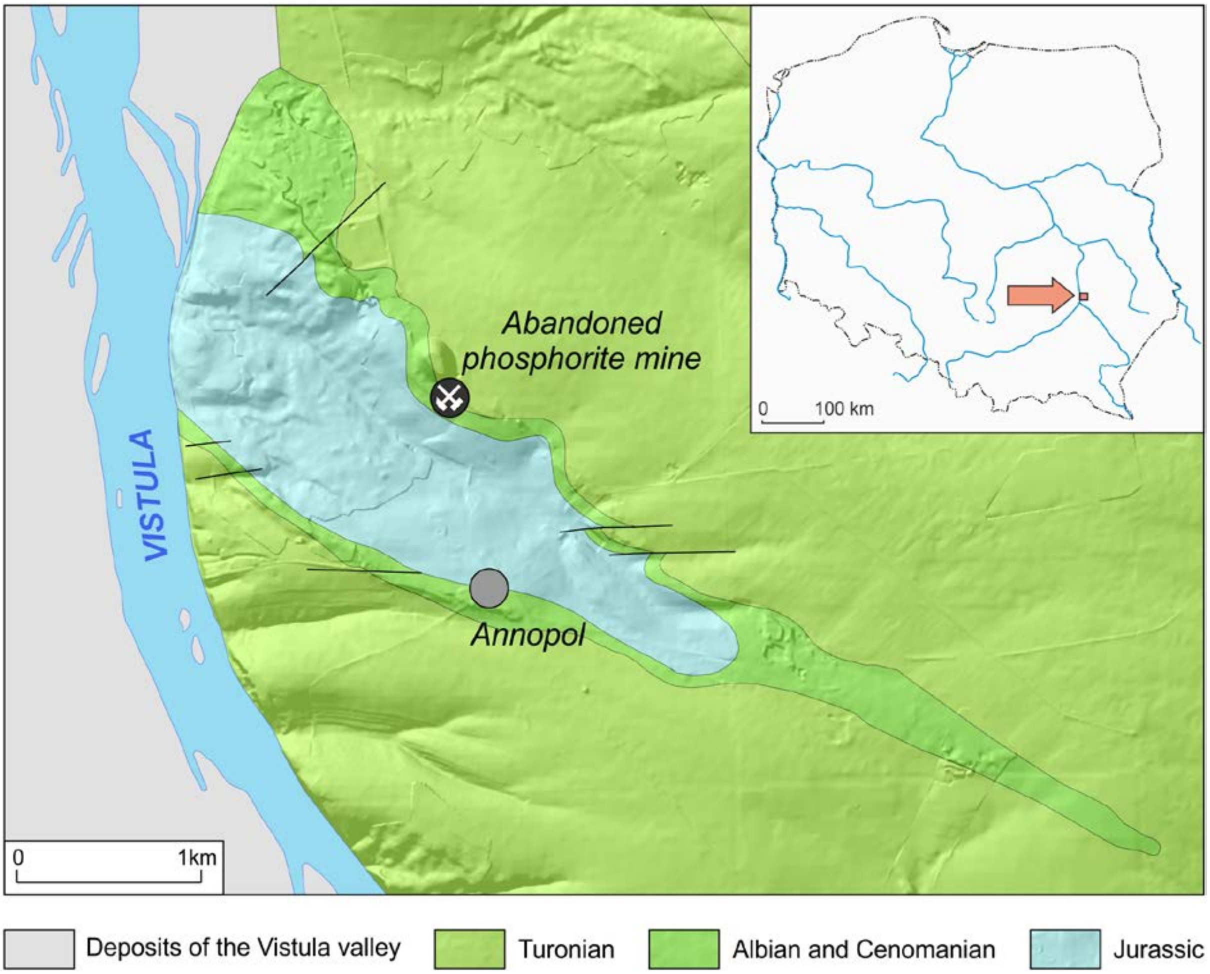
Rostral structures in aquatic reptiles, including ichthyosaurs, play a pivotal role in various ecological and functional contexts. The morphology of the snout influences hydrodynamics, prey capture mechanisms, and sensory capabilities (Ibrahim *et al.* 2014; Álvarez-Herrera *et al.* 2020). For ichthyosaurs, the arrangement of teeth, neurovascular pathways, and cranial foramina within the rostrum provide insights into their feeding strategies and adaptations to specific ecological niches (Serafini *et al.* 2022). Studies of rostral anatomy in other ichthyosaurs, such as *Platypterygius hercynicus* Kuhn, 1946, have demonstrated the complexity of these systems and their potential role in prey detection and capture (Kolb and Sander 2009). Recent investigations into the neurovascular systems of many aquatic tetrapods have highlighted their sensory adaptations, such as electro- and mechanoreception, which could have facilitated the detection of prey in turbid environments (Czech-Damal *et al.* 2012; George and Holliday 2013). In ichthyosaurs, evidence of complex rostral vascularization suggests analogous capabilities, underscoring the ecological significance of snout morphology (Serafini *et al.* 2022). However, few ichthyosaur fossils preserve fine details of the rostral anatomy, making specimens with articulated teeth, visible cranial cavities, and intact foramina exceptionally valuable (Tyborowski *et al.* 2020).

The newly discovered platypterygiine ichthyosaur rostrum from the Cenomanian deposits of Annopol, Poland, represents a rare example of such preservation. This specimen, which includes articulated teeth, a visible interpremaxillary cavity, and trigeminal nerve foramina, offers a unique opportunity to investigate the functional morphology of this group during the Late Cretaceous. The Annopol site itself is significant, having yielded a rich assemblage of marine reptiles, including large predatory taxa (ichthyosaurs, pliosaurs, elasmosaurs) that coexisted in the Albian–Cenomanian seas of Central Europe (Bardet *et al.* 2016). Previous studies on ichthyosaur rostra have often focused on isolated elements, leaving many aspects of cranial morphology and its ecological implications unexplored. The Annopol specimen provides a more complete perspective, allowing for a detailed assessment of rostral function in feeding. By comparing this specimen to other well-documented platypterygiine taxa, such as *Pervushovisaurus campylodon* (Fischer, 2016) from Germany and *Platypterygius australis* (Kear, 2005) from Australia, it is possible to place the Annopol ichthyosaur within a broader evolutionary and ecological framework (Kear 2005; Fischer *et al.* 2016).

This study aims to address several critical questions regarding the morphology and ecology of Late Cretaceous ichthyosaurs: 1) to provide a detailed description of the rostrum, emphasizing its cranial and dental features, including the arrangement of teeth, cranial cavities, and neurovascular foramina; 2) to compare the specimen with other platypterygiine ichthyosaurs; and 3) to explore the role of the rostral features in feeding strategies and ecological interactions. By addressing these objectives, this study contributes to our understanding of the adaptive strategies that allowed platypterygiine ichthyosaurs to thrive during the Late Cretaceous. Furthermore, it highlights the importance of high-resolution anatomical analyses in reconstructing the palaeobiology of extinct marine reptiles.

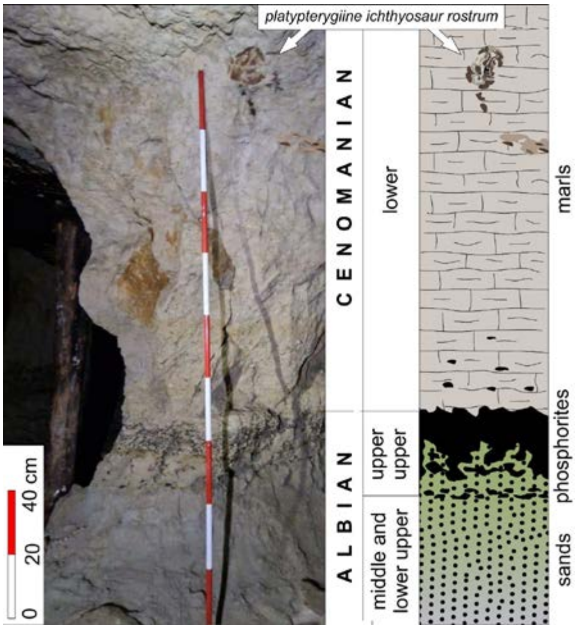
GEOLOGICAL SETTING

The Annopol Anticline (formerly the Rachów Anticline) is a geological structure located on the right bank of the Vistula River (Text-fig. 1), in the Mesozoic margin of the Holy Cross Mountains (Samsonowicz 1925, 1934; Pożaryski 1947; Text-fig. 1). The area is characterised by a unique stratigraphy, resulting from the mid-Cretaceous transgression and episodes of low sea level, which favoured the concentration of phosphorites (Machalski and Kennedy 2013). It is distinguished by the relatively small thickness of Cretaceous sediments compared to neighbouring areas, owing to its location on a submarine uplift – the so-called Annopol outcrop (Cieśliński 1976). The oldest exposed rocks in the region are Upper Jurassic limestones and dolomites (Kimmeridgian), upon which rest the transgressive sediments of the lower and middle Albian and the Cenomanian (Text-fig. 1), consisting mainly of glauconitic sands, marls, and phosphorites (Samsonowicz 1925, 1934; Pożaryski 1947). The Cretaceous sediments rest unconformably on the Upper Jurassic basement, indicating the presence of a sedimentary hiatus (Cieśliński 1959). The



Text-fig. 1. Simplified geological map of the Annopol Anticline in Poland, with location of the phosphorite mine where the specimens are preserved. Insert shows the location of the study area in Poland. Modified after Walaszczyk (1987).

Annopol phosphorites occur in two main horizons (lower and upper), separated by a poorly consolidated sand layer. The lower phosphorite horizon is rich in large, sand-bedded phosphorite nodules, containing numerous fossils of Albian ammonites. The upper phosphorite horizon contains smaller phosphorite nodules in a marly matrix, showing evidence of intense bioturbation (Cieśliński 1959; Marcinowski and Radwański 1983). The succession of the Annopol Anticline documents the dynamic evolution of the sedimentary basin during the mid-Cretaceous (Text-fig. 2). In the Albian, the region was located on a shallow marine shelf, influenced by erosion and reworking processes, leading to the formation of complex phosphate deposits. During the Cenomanian, further deepening of the basin occurred, resulting in the deposition of glauconitic marls followed by lower Turonian limestones, indicative of a progressive marine transgression (Machalski *et al*. 2023). The high glauconite content and the presence of phosphorites suggest conditions favourable for diagenesis in an environment of reduced sedimentation and frequent sediment reworking (Machalski and Kennedy 2013). The biostratigraphy of the succession of the Annopol Anticline is based on the analysis of fossils (ammonites, inoceramid bivalves, and foraminifera), allowing for a high-resolution stratigraphy. Ammonites play a key role in the Albian and are widely distributed in sediments of this age (Cieśliński 1959). The most important ammonite species include *Hoplites dentatus* (Sowerby, 1821) and *Mortoniceras inflatum* (Sowerby, 1818), which are characteristic of the lower and middle Albian (Marcinowski and Wiedmann 1990). Additionally, numerous fossils of belemnites



Text-fig. 2. Photograph of the underground gallery of Annopol mine with location of specimen ZPAL V38/50, and stratigraphic interpretation.

and bivalves of the family Inoceramidae occur in Albian sediments, providing further biostratigraphic data (Cieśliński 1987). In the Cenomanian, the primary index fossils are bivalves of the family Inoceramidae, including *Inoceramus crippsi* Mantell, 1822 and *Inoceramus pictus* Sowerby, 1829, which allow for precise dating of the succession (Cieśliński 1987). Additionally, Cenomanian deposits contain numerous fossils of cartilaginous fish, including shark teeth and chimaeras, offering further biostratigraphic insights (Radwański 1968; Popov and Machalski 2014). Bivalves representing *Mytiloides* spp. and *Inoceramus* spp. are widely distributed in Turonian deposits (Machalski and Kennedy 2013). Furthermore, numerous ammonite fossils, including *Collignoniceras woollgari* Mantell, 1822, are characteristic of this stage (Marcinowski 1980). In recent years, research in the Annopol Anticline has yielded significant discoveries, greatly enhancing our understanding of the geological structure, depositional environments, and biostratigraphy of the region. Notably, fossil remains of large marine reptiles, including ichthyosaurs and plesiosaurs, have provided valuable new insights into Albian and Cenomanian marine ecosystems (Bardet *et al*. 2016). Furthermore, new stratigraphic studies within the phosphorite interval have led to a more refined understanding of the sedimentary basin's evolution during this period (Machalski *et al*. 2023).

MATERIAL AND METHODS

The palaeontological material described here consists of an ichthyosaur rostrum visible in transverse section and a fragment of an ichthyosaur mandible visible in longitudinal section, exposed along a wall of the underground gallery of an abandoned phosphate mine in Annopol (Text-figs 3–6). Judging by the elements' similar size and proximity, we interpret them as belonging to the same individual. Stratigraphically, the elements are located in the upper part of the lower Cenomanian marls (unit 4 of Bardet *et al*. 2016; Text-fig. 2). In Bardet *et al*. (2016), the catalogue number ZPAL V38/50 is assigned to the rostrum in transverse section; however, these remains are not currently stored in any scientific collection due to the fact that they cannot be extracted from the mine wall. Access to these fossils is still possible by entering the mine. The photos used for this publication were taken by GG and AK, who carefully examined and measured the material.

SYSTEMATIC PALAEONTOLOGY

Order Ichthyosauria de Blainville, 1835
Clade Neoichthyosauria Sander, 2000
Clade Thunnosauria Motani, 1999
Family Ophthalmosauridae Baur, 1887
Subfamily Platypterygiinae Arkhangelsky, 2001
sensu Fischer *et al*., 2012

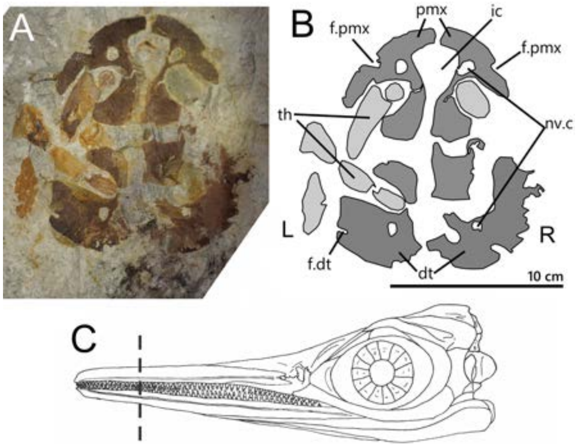
Platypterygiinae indet.
(Text-figs 3–6)

REFERRED MATERIAL: ZPAL V38/50, including an articulated partial rostrum exposed in transverse section in the sediment matrix (marl) of the upper part of a wall of the Annopol underground gallery (Text-figs 3–5), and an articulated partial mandible of presumably the same individual exposed in longitudinal section (Text-fig. 6). ZPAL V38/50 was previously illustrated in Bardet *et al.* (2016) but not described; the partial mandible is here illustrated and described for the first time.

LOCALITY AND HORIZON: Annopol mine located in Lubelskie Voivodeship, south-eastern Poland; lower Cenomanian, unit 4 in Bardet *et al.* (2016).

DESCRIPTIVE AND COMPARATIVE ANATOMY:

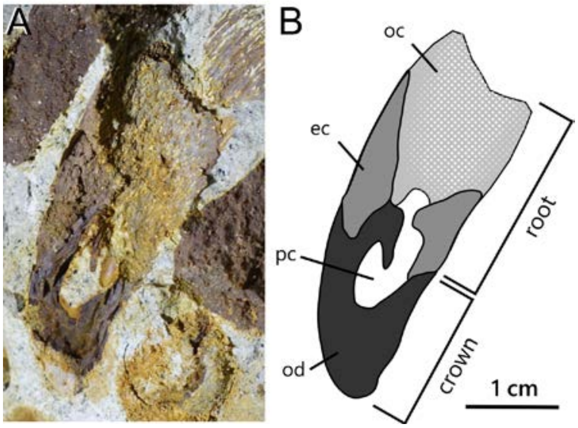
Overall morphology. The specimen's rostrum is preserved in transverse section, whereas part of the mandible is exposed in longitudinal section. The transverse section of the rostrum consists of the left and right premaxilla, the left and right anterior dentary, with one tooth visible in each of the upper and lower jaws. Based on the preserved elements, this should correspond to the anterior region of the animal's snout. The entire cross-section is 15 cm high and 11 cm wide at the level of the occlusal plane. Since the right side of the skull is in a slightly worse state of preservation than the left side, and the proportions of the bones on the right side seem to be slightly disturbed, it can be concluded that the cross-section is not perfectly perpendicular to the axis of the skull but deviates slightly from the left-right plane. The entire cross-section of the rostrum is oval in shape – its ventral edge is stouter and wider, taking an almost angular shape, while the dorsal edge is characterised by a much slenderer morphology, with a distinct curvature (Text-fig. 3A, B). Judging by the morphological features and anatomical structure of the bones that make up the preserved fragment of the ichthyosaur rostrum, our interpretation is that the visible cross-section through the jaws is located in the anterior part of the animal's snout, close to the symphysis (Text-fig. 3C).



Text-fig. 3. Platypterygiine ichthyosaur from Annopol mine; ZPAL V38/50, transverse section of the mid-anterior part of the rostrum. A – specimen preserved in the underground gallery; B – anatomical interpretation of the specimen; C – reconstructed skull of the animal with putative location of the cross-section. Reconstruction based on the skull of *Platypterygius longmani* Wade, 1990 from Kear (2005). Abbreviations: dt – dentary; f.dt – fossa dentalis; f.pmx – fossa premaxillaris; ic – interpremaxillary cavity; nv.c – neurovascular canals; pmx – premaxilla; th – teeth; L – left side; R – right side.

Premaxilla. The left premaxilla is much better preserved than the right one. It shows a characteristic bipartite shape in cross-section, reminiscent of the lowercase letter 'h' (Text-fig. 3A, B). Here, one can distinguish the superficial part of the bone with the preserved outline of its outer edge, as well as the internal part, which in its upper part forms the ventral and lateral walls of the interpremaxillary cavity, while its lower part borders the right premaxilla, and from the ventral side forms the vault of the bony palate. The dorsal outline of the premaxilla, is gently convex in cross-section (Text-fig. 3A). The outer surface of the left bone appears to be relatively smooth, in contrast to the surface of the right bone, which is characterised by greater irregularity. The bone can be divided into an outer region, which includes the area dorsal and lateral to the dental groove, and an internal region, medial to the preserved tooth (Text-fig. 3). The dental groove has a semi-elliptical shape in cross-section. The width of the dental groove at its widest point is 2 cm. The length of the socket is 5 cm. The lateral and medial walls are approximately of similar height on the left bone, while the medial wall of the right bone is eroded in its distal part, making it appear slightly shorter than the lateral wall. The contact between the two premaxillae on the ventral side of the interpremaxillary cavity is vertical and about 6 cm long. The articular connection of the two bones on the dorsal side of the interpremaxillary cavity is much thinner and does not exceed 1 cm in thickness. A cross-section through the internal region of both premaxillae has a characteristic 'ear-like' shape, with a widened ventral part and a narrower dorsal part, which is also the bottom of the alveolar groove and forms the ventral edge of the interpremaxillary cavity (Text-fig. 3A, B). On the dorsolateral surface of both premaxillae, there is a visible notch, which marks the presence and position of the fossa praemaxillaris; this is a longitudinal groove that in many parvipelvians extended along the entire premaxilla (Kear 2005; Delsett *et al.* 2019). About 1 cm below the fossa praemaxillaris, on the side, there is a small, circular opening with a diameter of 0.8 cm. The corresponding canal in the right premaxilla is located at a greater depth, approximately 2 cm, due to dislocation. It is separated from the interpremaxillary cavity by a thin layer of bone, which does not exceed 1 mm in thickness. The opening of the right premaxilla has a different shape from its left counterpart and takes the form of an equilateral triangle with rounded apexes.We interpret these openings as canals of the neurovascular system, as identified in other ichthyosaurs, as well as in crocodilians, mosasaurs, plesiosaurs, and predatory dinosaurs (Ibrahim *et al.* 2014; Lomax *et al*. 2019; Álvarez-Herrera *et al*. 2020).

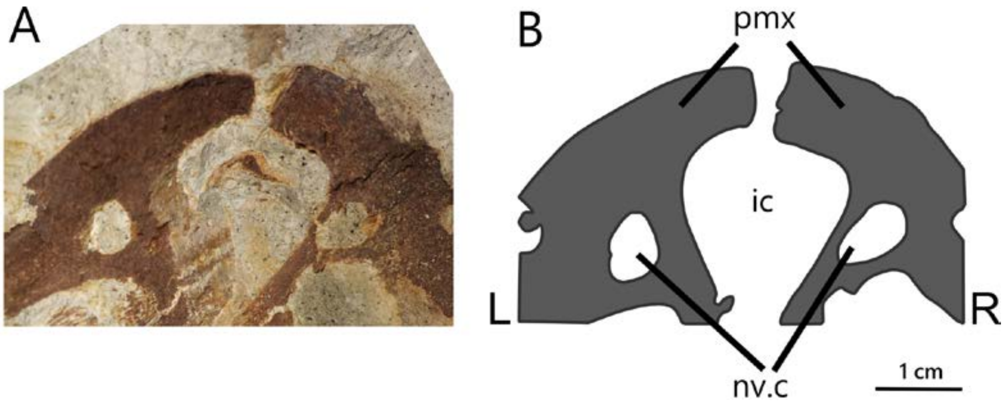
Dentary. The left dentary is also better preserved than its right counterpart (Text-fig. 3A, B). The thickness of both dentaries in the central part of the mandible is 6 cm. Similarly to the premaxilla, the dentary bone in cross-section has a bipartite structure. It consists of a larger ventrolateral region and a smaller dorsal region, the upper edge of which is also the floor of the oral cavity (Text-fig. 3B). The division of the dentary into these two regions results from the presence of the tooth alveolus, which, like the corresponding alveolus on the premaxilla, has a semi-elliptical outline. The alveolus of the dentary is, however, slightly shallower than the alveolus of the premaxilla and reaches a depth of about 4 cm. The lateral wall of the left dentary is clearly higher than the medial wall. The medial wall is almost vertical close to the base of the alveolus, while it is curved laterally in the dorsal part. This is comparable to the condition in *Platypterygius australis* and *Undorosaurus*? *kristiansenae* Druckenmiller, Hurum, Knutsen and Nakrem, 2012 as opposed to *Keilhauia* sp. of Delsett *et al.* (2019). The lateral margin of the dentary is slightly concave, and in its ventral part, just above the edge of the bone, there is a cross-section through a small teardrop-shaped hole (Text-fig. 3A, B). Most likely, this hole is a remnant of the blood vessels that ran along the jaw of the ichthyosaur during its life, which fed the external tissues covering the bone. However, it cannot be ruled out that nerves also ran through this hole. Such longitudinal channels (fossa dentalis) containing small holes on the dentary occur in many taxa among ichthyosaurs: *Platypterygius australis*, *Pervushovisaurus campylodon*, and Ophthalmosauridae indet. of Delsett *et al*. (2019). In the deeper part of both dentaries, just at the medial edge of their ventral region, there are oval foramina, similar in size to the openings of the neurovascular system in the premaxillae. The presence of such openings also on the lower jaw indicates an extensive sensory system in the anterior part of the snout. Both bones are in mutual articulation only in the narrow part of the ventral side of the mandible, forming the bony floor of the lower jaw. From the internal side, the left and right dentary bones are not in contact with each other and are separated by a gap, arranged parallel to the medial edges of both bones. This space is about 5 cm high and 1 cm wide. It connects with the oral cavity at an angle of almost 90º, forming a 'T'-shaped cavity in cross-section. The space between both dentaries was likely filled with connective tissue.



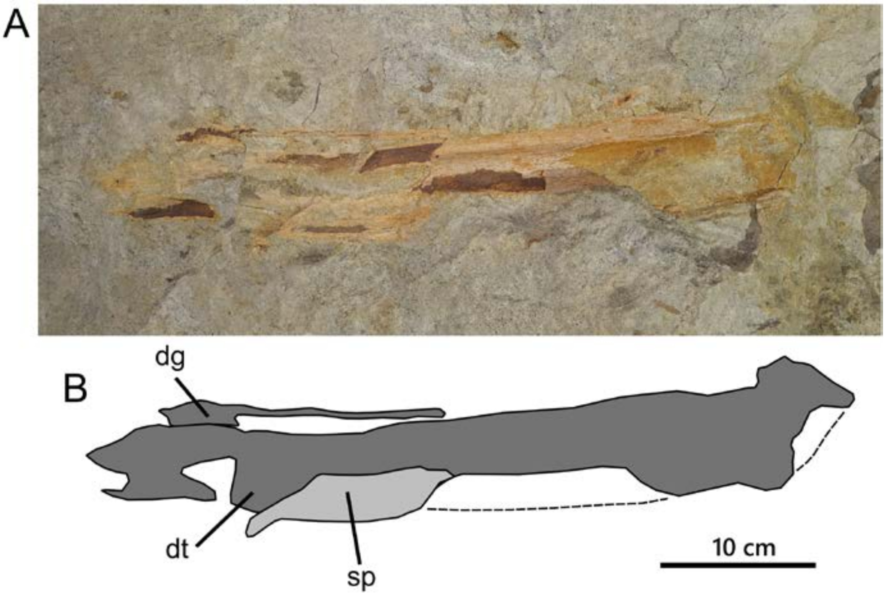
Text-fig. 4. Dentition of specimen ZPAL V38/50. A – functional tooth from the upper jaw of the specimen, exposed in coronal section in Annopol mine; B – dental tissue interpretation; the reconstruction is solely based on tissue distribution from Maxwell *et al*. (2011). Abbreviations: ec – external cementum; oc – osteocementum (pulpal cementum); od – orthodentine (dentine); pc – pulp cavity.

A few dozen centimetres below the cross-section through the rostrum in the wall of the underground gallery is a longitudinal section through the middle part of the ichthyosaur's lower jaw (Text-figs 2 and 6). This element is 44 cm long and about 10 cm thick (Text-fig. 6). The preserved fragment of the lower jaw is broken both on the side of the mandibular symphysis and on the side of the jaw joint. It consists of the left ramus of the mandible visible in medial view. This is evidenced by the dental groove visible in the anterior part of the specimen, which, similarly to the cross-section described above, is oriented towards the outside of the jaws (Text-fig. 6B). Thus, the anterior part of the specimen includes part of the dentary, which forms the larger portion of the preserved mandible.

Splenial. On the ventral side of the dentary, the anteromedial part of the splenial is visible (Text-fig. 6B), which protrudes slightly in this region, creating a delicate bony sinus (the 'anterior fork'), which, like in *Platypterygius australis*, is relatively shallow (Kear 2005). This feature distinguishes the Annopol specimen from ichthyosaurs such as *Ophthalmosaurus icenicus* Seeley, 1874 (Moon and Kirton 2016), *Palvennia hoybergeti* Druckenmiller, Hurum, Knutsen and Nakrem, 2012, and Ophthalmosauridae indet. (Druckenmiller *et al*. 2012; Delsett *et al*. 2019). The



Text-fig. 5. Morphology of the interpremaxillary cavity of specimen ZPAL V38/50. A – interpremaxillary cavity in transverse section as exposed in Annopol mine; B – anatomical interpretation. Abbreviations: ic – interpremaxillary cavity; nv.c – neurovascular canals; pmx – premaxilla; L – left side; R – right side.



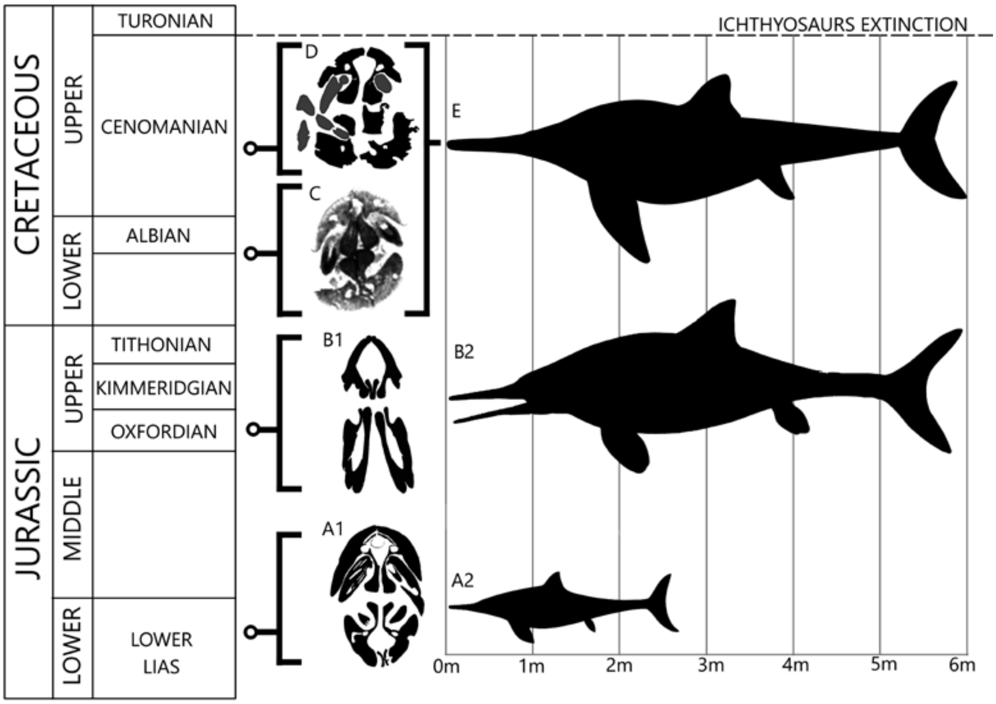
Text-fig. 6. Mandibular elements, presumably belonging to the same individual as ZPAL V38/50, located slightly below the latter, along the same gallery wall of Annopol mine. A – longitudinal section of exposed specimen; B – anatomical interpretation. Abbreviations: dg – dental groove; dt – dentary; sp – splenial.

central part of the specimen on the ventral side is covered by the surrounding rock (Text-fig. 6A), so the architecture and relative positioning of the dentary and splenial in this area are difficult to determine. The same applies to the dorsal edge of the dentary in this region – due to the covering by sediment, the dental groove is not visible.

Dentition. Two teeth are preserved on the left side of the rostrum – one on the upper jaw (premaxilla) and one on the dentary. The premaxillary tooth is much better preserved and allows for a detailed description of its internal structure (Text-fig. 4). Its root anchors deep into the dental groove, while the tip of the crown protrudes outward. It is relatively large proportionally to the jaw elements. The length of the entire tooth exceeds 6 cm and has a maximum width of about 2 cm. Both the base of the root and tip of the crown are rounded. The proportions of the root to the crown of the tooth are as follows: 2/3 for the root and 1/3 for the crown. The division into these two anatomical zones of the tooth is clearly marked by the presence of different dental tissues in each of them. The root zone is characterised by the presence of spongy and porous osteocementum (pulpal cementum). The crown of the tooth is filled with a well-mineralised and thick layer of dentine (orthodentine). From the labial side, a zone of external cementum is visible, which is wedged between the osteocementum in the root part of the tooth and between the dentine on the crown side (Text-fig. 4B). On the labial side, a thin layer of enamel is visible surrounding the outer part of the tooth. Between the orthodentine zone and the osteocementum, the pulp cavity is visible, which conforms to the external surface of the tooth (Text-fig. 4). The tooth crown is robust and blunt. On the lingual side, the edge of the crown is almost straight, while on the labial side, the edge is slightly curved. The dentine layer is thickest in the middle part of the crown and reaches up to 1 cm. The dentary tooth is less clearly defined. The tooth root is still anchored to the dental groove, while the crown is broken off and dislocated. The root zone is still discernible by the presence of porous osteocementum, while the broken crown preserves mostly orthodentine. The pulp cavity of the dentary tooth is small compared to the space occupied by the dentine, and it is approximately elliptical in shape.

Rostral cavity. The preserved cross-section of the ichthyosaur rostrum shows an empty space between the left and right premaxillae (Text-fig. 5). We interpreted this space as the interpremaxillary cavity. In the dorsal part, this cavity is wide and resembles a mushroom cap, which rapidly slims down toward the ventral part (Text-fig. 5A). This indicates that in cross-section, this cavity had the shape of an isosceles triangle with rounded vertices, oriented with the shortest side upwards. The dorsal edge of the interpremaxillary cavity is almost horizontal and parallel to the outer surface of the bone in this region. In the ventral part, the edges of the interpremaxillary cavity converge at an angle of almost 90º. A similar shape of the interpremaxillary cavity is seen in *Platypterygius australis* and *Ichthyosaurus* spp. (Kear 2005; Sollas 1916).

Systematic affinities and comparison. The specimen from Annopol represents a well-preserved example of an ichthyosaur rostrum in cross-section, providing a rare opportunity to analyse the internal anatomy and relative systematic affinities within the Ophthalmosauridae (Text-fig. 7). Comparative analysis of the Annopol specimen against a wide range of Jurassic and Cretaceous ichthyosaur taxa – including *Keilhauia* spp., *Undorosaurus* spp., *Ophthalmosaurus* spp., *Brachypterygius* spp., *Palvennia* spp., *Acamptonectes* spp., *Aegirosaurus* spp., *Pervushovi-*



Text-fig. 7. Stratigraphic plot of ichthyosaurs from Europe known from well-preserved rostrum transverse sections (middle column) compared to the specimen from Annopol and putative size of the corresponding taxa (right part). A1, A2 – *Ichthyosaurus communis* de la Beche and Conybeare, 1821 (based on Sollas 1916); B1, B2 – Ophthalmosauridae indet. (based on Tyborowski *et al*. 2020); C – Platypterygiine indet. (based on Serafini *et al*. 2022); D – Platypterygiinae indet. (this study); E – Platypterygiine indet. (reconstruction made by P. Szczepaniak).

saurus spp., and other platypterygiine ichthyosaurs – highlights diagnostic features supporting its placement within Platypterygiinae. This section expands on shared characteristics, contrasting morphologies, and functional adaptations, providing a systematic and morphological framework to refine the taxonomic identification of the Annopol specimen.

The teeth of the Annopol ichthyosaur are set in semi-elliptical dental groove with well-developed lateral and medial walls, a feature characteristic of platypterygiines (Massare 1987). *Ichthyosaurus* spp. teeth, as described by Sollas (1916), are more conical and slender, with pointed crowns suited for grasping soft prey. This contrasts sharply with the blunt, robust dentition of the Annopol specimen, reflecting different dietary strategies (Sollas 1916). The dentition of the ophthalmosaurid from the Late Jurassic of Poland in Tyborowski *et al.* (2020) exhibits instead intermediate robustness, with moderately thick enamel and a less pronounced bluntness in the crown. The subrectangular, massive shape of the tooth roots is an apomorphic feature of Platypterygiinae (Fischer 2016).

The premaxillae exhibit a bipartite structure, characterised by a combination of external and internal regions. The 'h'-shaped cross-section aligns closely with taxa such as *Platypterygius australis*, *Platypterygius hercynicus*, and *Pervushovisaurus campylodon* (Kear 2005; Kolb and Sander 2009; Fischer 2012, 2016). The curvature and elongation of the premaxillae, combined with the presence of fossae praemaxillaris, are consistent with observations in *P. campylodon*, reflecting adaptations for feeding in diverse marine environments (Fischer 2016). Comparatively, *Keilhauia* spp. possess less pronounced fossae praemaxillaris, indicating a lower degree of cranial specialization (Delsett *et al.* 2019).

The outward orientation of the dental groove and the more dorsolateral positioning of teeth are indicative of a hypercarnivorous diet (Massare 1987; Kear 2005; Fischer *et al.* 2012). In contrast, taxa such as *Ophthalmosaurus icenicus* and *Undorosaurus gorodischensis* Efimov, 1999 exhibit more medially oriented dental groove, suggesting different feeding adaptations (Appleby 1956; Zverkov and Efimov 2019). The dentary's bipartite structure, with a dominant ventral region and a smaller dorsal region, closely matches *Brachypterygius extremus* Boulenger, 1904 and *Pervushovisaurus campylodon*, reinforcing its systematic placement within Platypterygiine (Kolb and Sander 2009; Fischer 2016).

The teeth of the Annopol specimen exhibit robust morphology with thick dentine and blunt crowns, consistent with platypterygiines specialised for macrophagy or in handling large prey. Comparatively, *Ophthalmosaurus* spp. and *Undorosaurus* spp. exhibit narrower and more pointed teeth, reflecting dietary specializations for softer prey (Moon and Kirton 2016; Zverkov and Efimov 2019). The Annopol specimen's dentition thus aligns with hypercarnivorous platypterygiines, differentiating it from other ophthalmosaurids with less robust dental adaptations.

The interpremaxillary cavity morphology in the Annopol specimen – triangular with rounded vertices – is a feature shared with *Platypterygius australis* and *Ichthyosaurus* sp. The deep positioning of neurovascular canals supports the presence of an advanced sensory system, consistent with observations in Platypterygiine ichthyosaurs from Italy (Serafini *et al.* 2022).

The rostral cross-section of the Annopol ichthyosaur exhibits an 'h'-shaped morphology of the premaxillae, with pronounced bipartite structures. The presence of a deep alveolar groove and a distinct neurovascular canal near the interpremaxillary cavity is a key feature. The cross-section is approximately oval, with a broader ventral edge and a slender dorsal curvature. Sollas (1916) described cross-sections of *Ichthyosaurus* spp. rostra, which have more triangular/lenticular and symmetrical profiles compared to the Annopol specimen (Text-fig. 7A). The fossae praemaxillaris were less pronounced, and the neurovascular canals were smaller and more centrally located relative to the interpremaxillary cavity. This may suggest that *Ichthyosaurus* spp. relied less on neurovascular adaptations (electroreception or mechanoreception) compared to the ichthyosaur from the Annopol (Sollas 1916). The rostral cross-sections of the specimens from the Late Jurassic (Oxfordian) of Poland described as Ophthalmosauridae indet. by Tyborowski *et al.* (2020) show a robust, nearly triangular profile (Text-fig. 7B), and similar grooves along the surface of both premaxillae, to the Annopol ichthyosaur. However, these grooves in the Morawica specimens are much shallower and less pronounced than in both *Platypterygius australis* and the Annopol specimen (Kear 2005; Tyborowski *et al.* 2020). The cross-section of platypterygiine rostra from the Northern Apennines (Serafini *et al.* 2022) are strikingly similar to the Annopol specimen (Text-fig. 7C, D). Both exhibit 'h'-shaped premaxillae with well-developed fossae praemaxillaris and neurovascular canals positioned close to the interpremaxillary cavity. The broader ventral region and slender dorsal curvature of the premaxillae are nearly identical to those of the Annopol specimen, reinforcing its placement within Platypterygiinae (Serafini *et al.* 2022).

Morphological feature	Annopol specimen (this study)	Sollas (1916)	Tyborowski *et al.* (2020)	Serafini *et al.* (2022)
rostral morphology	‘h’-shaped premaxillae, oval profile, broad ventral curvature	‘h’-shaped premaxillae, triangular/lenticular profile	‘h’-shaped premaxillae, triangular profile	‘h’-shaped premaxillae, oval profile
fossae praemaxillaris	present, well-developed	less pronounced	absent	present, well-developed
neurovascular system	triangular canals near nasal cavity	simple, shallow canals	absent	advanced, branching canals
dentition	robust, blunt	conical, slender	intermediate robustness	robust, blunt, thick enamel

Table 1. List of diagnostic features of ichthyosaurs from Europe with a well-preserved rostrum in transverse sections, including the new specimen from Annopol.

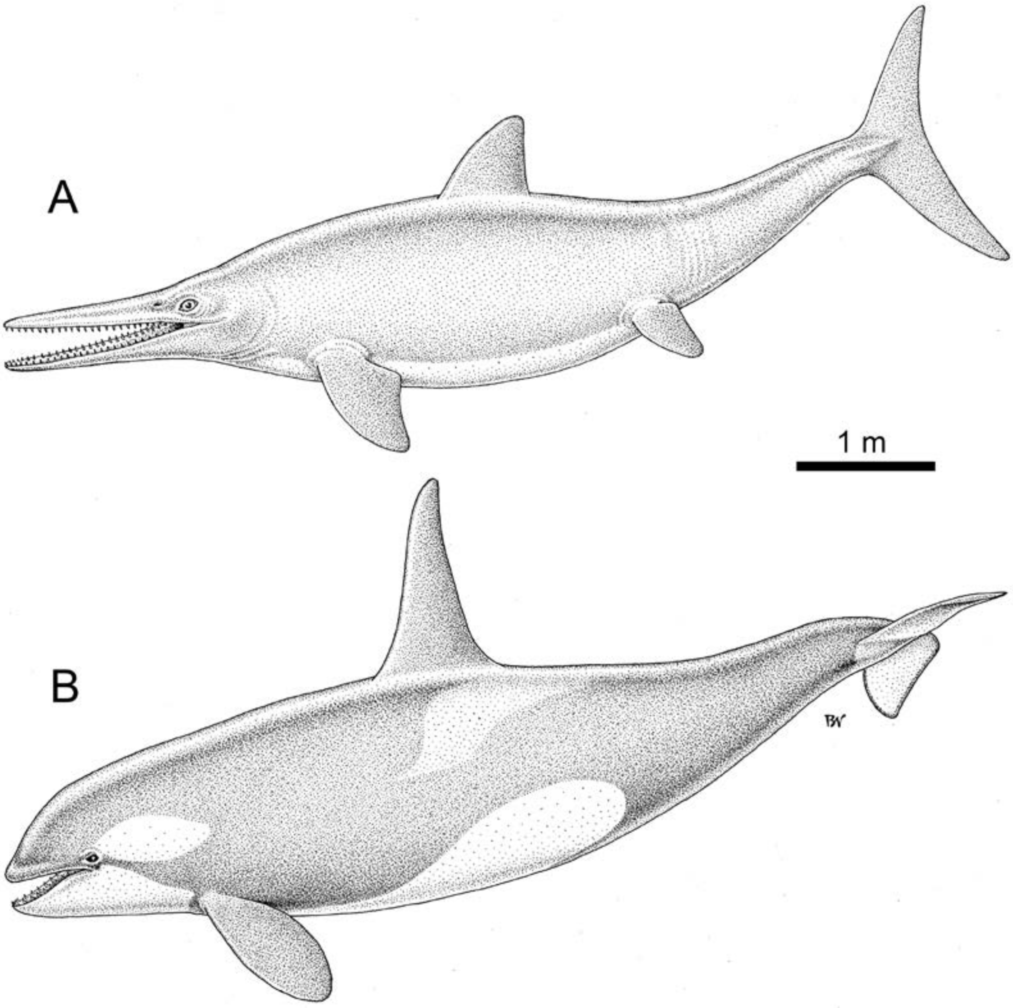
The combination of diagnostic features – including the subrectangular shape of the tooth roots (Platypterygiinae apomorphy), the ‘h’-shaped premaxillae, robust dentaries and dorsolateral tooth position – supports the placement of the Annopol specimen within Platypterygiinae (Table 1). The most diagnostic feature that allows the specimen to be classified as Platypterygiinae is the subrectangular shape of the massive tooth roots. However, the absence of more complete diagnostic cranial elements limits its precise species-level identification. Comparisons with *Platypterygius australis* and *Pervushovisaurus campylodon* preclude a definitive assignment beyond Platypterygiinae indet. (Kear 2005; Fischer 2016). The Annopol ichthyosaur shares numerous diagnostic features with the platypterygiines described by Serafini *et al.* (2022), particularly in the morphology of the premaxillae and dentition (Table 1). The ichthyosaur material from Annopol represents a significant addition to the fossil record of Late Cretaceous ichthyosaurs. Its morphology and systematic placement within Platypterygiinae provide valuable insights into cranial anatomy and dietary strategies of this clade. Future studies using advanced imaging techniques and broader comparative analyses may help refine its taxonomic resolution and contribute to a deeper understanding of platypterygiine evolution.

DISCUSSION

Ecology and comparisons with modern marine apex predators

The ichthyosaur from Annopol, identified as a large member of Platypterygiinae, likely occupied the role of an apex predator in the Cenomanian marine ecosystem. Its robust dentition, capable of processing hard and bony prey, suggests a highly specialised predator that targeted a variety of large organisms. Based on its anatomy, it likely preyed on large actinopterygian fish, sharks as well as other marine reptiles, such as marine turtles or smaller ichthyosaurs. These prey items represent taxa commonly found in Cenomanian deposits, such as those in Annopol (Kapuścińska and Machalski 2015; Bardet *et al.* 2016). In the Late Cretaceous seas, ichthyosaurs like the Annopol specimen coexisted with large pliosaurs, plesiosaurs, and sharks. These predators likely competed for similar prey resources, but the ichthyosaur’s adaptations for osteophagy suggest niche differentiation, allowing it to specialize in prey types less accessible to other large marine predators. This specialization parallels ecological partitioning observed in modern oceanic ecosystems among large predators (Massare 1987).

The Annopol ichthyosaur shares several ecological and morphological traits with modern apex marine predators, allowing for insightful comparisons regarding its role in the Cenomanian. Similar to some North Atlantic ecotypes of orcas today, the Annopol ichthyosaur likely exhibited opportunistic macropredation, taking advantage of its robust dentition to capture and process a variety of large prey. However, while orcas employ social hunting strategies to tackle large prey, ichthyosaurs possibly relied on solitary hunting, guided by tactile and electroreceptive cues, similar to extant crocodilians and some dolphins (Czech-Damal *et al.* 2012; George and Holliday 2013). The false killer whale (*Pseudorca crassidens* Owen, 1846), known for its dietary flexibility and preference for medium-to-large pelagic fish, shares dietary parallels with the Annopol ichthyosaur. The ichthyosaur’s dentition, adapted for gripping and crushing, is comparable to the robust teeth of *Pseudorca* spp., enabling it to target similarly sized prey in open marine environments (Bianucci *et al.* 2022). The great white shark’s (*Carcharodon carcharias* Linnæus, 1758) role as a macropredator aligns with the presumed ecological position of the Annopol ichthyosaur. While great white sharks use serrated teeth for tearing flesh, the ichthyosaur’s blunt dentition suggests a focus on crushing or gripping prey rather than slicing. Both predators likely occupied similar trophic levels, targeting a mix of fast-moving



Text-fig. 8. Relative size comparison of two marine apex predators. A – Platypterygiine ichthyosaur from Annopol, Poland (based on size estimated from the rostrum); B – Extant *Orcinus orca* Linnæus, 1758. Reconstructions drawn by Bogusław Waksmundzki.

pelagic prey and slower benthic organisms (Massare 1987; Jewell *et al.* 2024).

The rostrum and mandible of the Annopol ichthyosaur suggest a large individual. Based on the rostrum diameter of similar platypterygiine ichthyosaurs, such as *Platypterygius australis* and *Platypterygius hercynicus*, which reached lengths of 6–9 m, it is reasonable to estimate the Annopol specimen measured approximately 7 m in total length (Kear 2005; Kolb and Sander 2009). This size places the ichthyosaur within the range of many modern apex predators:

- Orca (*Orcinus orca* Linnæus, 1758): adult males measure 6–9 m, comparable to the estimated size of the Annopol ichthyosaur (Durban *et al.* 2021; Bianucci *et al.* 2022);
- Great White Shark (*Carcharodon carcharias*): typically reaches 4–6 m, though some exceptional individuals exceed 6 m, making the Annopol ichthyosaur larger on average (Márquez-Farías *et al.* 2024);
- False Killer Whale (*Pseudorca crassidens*): generally smaller than the Annopol ichthyosaur, at 4–6 m, suggesting the ichthyosaur had a size advantage (Bianucci *et al.* 2022);
- Pilot Whales (*Globicephala* spp.): ranges from 4.5 to 6.5 m, also smaller than the Annopol ichthyosaur (Betty *et al.* 2022).

The size and robust anatomy of the rostrum of the Annopol ichthyosaur suggest it may have occupied a similar ecological role to orcas in their respective environments (Text-fig. 8).

Implications for the Cenomanian–Turonian extinction

The ichthyosaur from Annopol, as a large apex predator, represents a key component of Cenomanian marine ecosystems. Its presence, alongside other large Platypterygiinae and co-occurring marine vertebrates such as sharks and pliosaurs, suggests that these ecosystems were highly structured and capable of supporting a diverse trophic hierarchy (Bardet *et al.* 2016). The presence of apex predators typically indicates a robust ecosystem with abundant and varied prey populations, stable primary productivity, and ecological resilience (Bardet *et al.* 2016; Fischer *et al.* 2016). Cenomanian marine ecosystems, characterised by the expansion of epicontinental seas and increased marine biodiversity, likely provided the resources necessary to sustain such large predators. The ichthyosaur's adaptations for a macropredatory lifestyle, including its robust dentition and anatomical features of the sensory system, suggest it exploited a specialised ecological niche, targeting bony and large prey. This ecological specialization underscores the complexity of these ecosystems, with predators partitioning resources to avoid direct competition (Massare 1987; Kear 2005). Cenomanian ecosystems were marked by high sea levels, widespread shallow marine environments, and stable climatic conditions, which promoted high primary production and diverse marine faunas (Stubbs and Benton 2016). Ichthyosaurs, such as large platypterygiines, likely played a significant role in regulating prey populations and maintaining trophic balance. Their dominance in marine ecosystems reflects a high level of ecological stability prior to the profound changes at the Cenomanian–Turonian boundary (Bardet *et al.* 2016; Stubbs and Benton 2016). These predators were likely apex consumers, regulating populations of smaller predators and prey. Their presence indicates a top-down control mechanism that fostered biodiversity and resource stability. Such systems, however, are also highly sensitive to disruptions in primary productivity and ecosystem structure, which may have contributed to the eventual extinction of ichthyosaurs (Fischer *et al.* 2016).

The extinction of ichthyosaurs at the Cenomanian–Turonian boundary raises questions about whether this group disappeared abruptly or experienced a gradual decline. Fossil evidence suggests that ichthyosaurs were already in decline during the Albian–Cenomanian transition, with decreasing diversity and ecological specialization (Bardet 1992; Fischer *et al.* 2016). The fossil record indicates a significant reduction in ichthyosaur diversity prior to the Cenomanian–Turonian extinction event. Studies by Fischer *et al.* (2016) suggest that ichthyosaurs experienced reduced evolutionary rates and niche contraction following the Jurassic–Cretaceous transition, leaving them vulnerable to environmental changes and competition (Fischer *et al.* 2016). The specialization of Platypterygiinae, such as their reliance on a macropredatory lifestyle and deep-water hunting strategies, may have limited their ability to adapt to changing prey dynamics. The abrupt environmental shifts during the Cenomanian–Turonian boundary, including ocean anoxic events (OAE2), widespread euxinia, and temperature fluctuations, would have significantly impacted ichthyosaur habitats (Pearce *et al.* 2009). These abiotic factors likely disrupted marine food webs, reducing the availability of prey and altering ecological interactions, potentially leading to the rapid extinction of ichthyosaurs (Pearce *et al.* 2009).

Abiotic factors likely played a significant role in the extinction of ichthyosaurs. The OAE2 event led to widespread depletion of oxygen in marine environments, disrupting trophic networks and primary production (Pearce *et al.* 2009). High temperatures and increased atmospheric CO_2 levels also contributed to environmental stress, potentially exceeding the physiological tolerances of ichthyosaurs (Fischer *et al.* 2016). Ocean anoxia and euxinia would have particularly impacted deep-diving predators like the Annopol ichthyosaur, as oxygen-depleted environments reduced habitat availability and prey abundance. In addition to abiotic stressors, ichthyosaurs faced increasing competition from other marine predators. During the Late Cretaceous, large lamniform sharks and hypercarnivore actinopterygians may have contributed to ichthyosaur decline by competing for similar prey resources. Unlike the more specialised Platypterygiinae, these groups exhibited greater ecological flexibility, allowing them to thrive under changing environmental conditions (Fischer *et al.* 2016).

CONCLUSIONS

The study of the ichthyosaur rostrum from Annopol, preserved in Cenomanian deposits, provides valuable insights into the morphology, functional adaptations, and ecological role of Platypterygiinae in Late Cretaceous marine ecosystems. The exceptional preservation of this specimen, which includes articulated teeth, visible interpremaxillary cavity, and remnants of neurovascular canals, allows for a detailed reconstruction of its ecology and systematic placement. Comparative analyses of the Annopol specimen reveal morphological affinities with other Platypterygiinae, such as *Platypterygius australis* and *Pervushovisaurus campylodon*. Its robust rostral and dental adaptations confirm its placement within Platypterygiinae indet., demonstrating a high degree of specialization for capturing and processing large hard-bodied prey. These features suggest adaptations for a hypercarnivorous diet. Comparisons with modern apex predators, such as orcas and great white sharks, highlight its ecological role as a top predator in the Cenomanian marine food web. The presence of such a large, specialised predator in the Cenomanian seas reflects the ecological complexity and productivity of these environments. The ichthyosaur's role as an apex predator underscores the trophic stability of Cenomanian ecosystems, supported by high primary productivity and diverse prey resources. This study contributes to our understanding of the final evolutionary stages of ichthyosaurs, particularly their ecological roles and adaptive strategies. The Annopol ichthyosaur serves as a key reference for examining the complex interplay of environmental and biotic factors that shaped marine ecosystems during the Late Cretaceous, offering critical data for future studies on the palaeobiology of marine reptiles.

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