A New Ophthalmosaurid Ichthyosaur from the Late Jurassic of Owadów-Brzezinki Quarry, Poland

Author: Tyborowski, Daniel

Source: Acta Palaeontologica Polonica, 61(4) : 791-803

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.00252.2016

A new ophthalmosaurid ichthyosaur from the Late Jurassic of Owadów-Brzezinki Quarry, Poland

DANIEL TYBOROWSKI

Tyborowski, D. 2016. A new ophthalmosaurid ichthyosaur from the Late Jurassic of Owadów-Brzezinki Quarry, Poland. *Acta Palaeontologica Polonica* 61 (4): 791–803.

A new Late Jurassic ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. is described from carbonate deposits of Owadów-Brzezinki Quarry, Central Poland, corresponding in age to the Agardhfjellet Formation (Tithonian, Middle Volgian) of the Svalbard Archipelago. The new species is represented by three-dimensionally preserved bones which display several features characteristic for *Cryopterygius*; including appendicular skeleton, pectoral girdle and perhaps neural arches. The morphology of the Polish form is distinct enough from *Cryopterygius kristiansenae* from the Svalbard Archipelago to warrant erection of a new species. The size of the bones of *Cryopterygius kielanae* sp. nov. indicates that this species was smaller than the type species. Its diagnostic anatomical features include a humerus with prominent and well developed dorsal process located in the middle of the dorsal surface of the bone, prominent deltopectoral crest, relatively broad femur and absence of the wide groove on the quadrate articular condyle. The discovery of a new ophthalmosaurid ichthyosaur of the genus *Cryopterygius* in Poland suggests that the Owadów-Brzezinki area was a transition zone between the tropical Tethys Ocean and the Arctic basin during the Late Jurassic.

Key words: Ichthyosauria, Ophthalmosauridae, Late Jurassic, Poland, Owadów-Brzezinki Quarry.

Daniel Tyborowski [paleodanieltyborowski@gmail.com], Museum and Institute of Zoology, Polish Academy of Sciences, ul. Wilcza 64, 00-679 Warszawa, Poland.

Received 15 February 2016, accepted 4 June 2016, available online 17 August 2016.

Introduction

The Upper Jurassic (uppermost Lower Tithonian = Middle Volgian) Fossil-Lagerstätte exposed in the Owadów-Brzezinki Quarry is one of the new paleontological localities which have been described in recent years on Polish territory. The locality yields a perfectly preserved complex of marine and terrestrial organisms similar in its taxonomic diversity and palaeoenvironment to the south German Solnhofen-Eichstätt area (Seilacher 1970; Kin and Błażejowski 2012; Kin et al. 2013; Błażejowski et al. 2016). The fossils discovered so far in the area of the Owadów-Brzezinki Quarry include horseshoe crabs (Kin and Błażejowski 2014), lobster-like decapod crustaceans (Feldmann et al. 2015), diverse insects represented by dragonflies, beetles, and grasshoppers (Bechly and Kin 2013) as well as the remains of various fish and isolated pterosaur teeth (Kin et al. 2013; Błażejowski et al. 2015). Marine reptiles are amongst the rarest macrofossils in the Jurassic and Cretaceous deposits of Poland, and to date are represented only by isolated vertebrae (Hirszberg 1924), teeth (Lomax 2015) and poorly preserved skull bones (Bardet et al. 2016). However, in recent years, excavations have provided very rich material of skeletal remains belonging to large marine reptiles (Tyborowski et al. 2016). Numerous vertebrae, ribs, limb bones, skull fragments, and teeth belonging to the ichthyosaurs (Ichthyosauria: Ichthyopterygia), turtles (Cryptodira: Testudinata) and marine crocodylomorphs (Thalattosuchia: Crocodylomorpha) have been discovered in Owadów-Brzezinki Quarry. Morphological analysis of the ichthyosaur bones, leads to a conclusion that they represent a new species of the ophthalmosaurid ichthyosaur *Cryopterygius.* The species *Cryopterygius kristiansenae* is known from the Upper Tithonian deposits of the Svalbard Archipelago. The aim of this paper is to describe a new species, *Cryopterygius kielanae*, from the uppermost Lower Tithonian Kcynia Formation at the Owadów-Brzezinki Quarry, near Tomaszów Mazowiecki in Central Poland (Fig. 1).

Institutional abbreviations.—GMUL, Geological Museum of the University of Lodz, Poland.

Geological setting

The study area is located approximately 18 km southeast of Tomaszów Mazowiecki (Central Poland; Fig. 1). All sediments cropping out in the Owadów-Brzezinki Quarry are

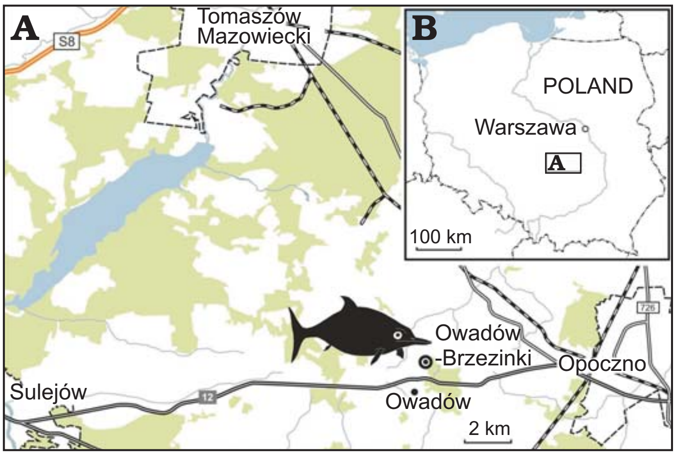

Fig. 1. General map of Poland with the location of the studied area (**B**). Location of the Owadów-Brzezinki Quarry (**A**).

of Tithonian (Middle Volgian) age (Kutek 1994; Matyja and Wierzbowski 2016). At the moment, Owadów-Brzezinki Quarry is the only place in the extra-Carpathian Poland where Tithonian strata are available to study. The exposed carbonate sequence belongs to the Kcynia Formation and can be divided into four successive units (Błażejowski et al. 2016). Unit I represents a massive, laminated, fine-grained limestone with a total thickness of approximately 9.1 m. This unit contains a rich and diverse fauna of invertebrates and vertebrates. Deep-burrowing bivalves *Pleuromya* accompanied by oysters *Deltoideum* and an unidentified trigoniid bivalve, rhynchonellid and terebratulid brachiopods, small gastropods, and ammonites are common, especially in the lower part of this unit. Numerous skeletal remains belonging to the representatives of marine reptiles including *C. kielanae* have been found (Tyborowski et al. 2016) in this unit. The sediment of the oldest unit probably formed in the environment of a vast and shallow sea bay or a lagoon, which remained open to a deeper basin. The remains of ichthyosaurs and ammonites were probably posthumously transported to the bay from the open sea. The overlying 2 m thick unit II is represented by thinly-bedded, fine-grained limestone with occasional distinctive parallel lamination and mass occurrence of calcareous polychaete tubes at one horizon. This part of the sequence is rich in decapod crustaceans (lobsters). Measuring approximately 13 m thick, unit III consists of thinly laminated limestone, in places like lithographic limestone. The limestone of this unit is rich in bivalves of the genera *Corbulomima* and *Mesosaccella* and other marine and terrestrial organisms such as horseshoe crabs *Limulus darwini*, large actinopterygian halecomorphs (*Furo microlepidotes* and *Caturus* jaw bones and teeth), pycnodontiforms (post-cranial skeleton and many isolated teeth and jaw bones), dragonflies (family Eumorbaeschnidae), grasshoppers (family Prophalangopsidae), beetles, ammonites, and rhamphorhynchid pterosaurs (Kin et al. 2012; Kin and Błażejowski 2012, 2014). A rich collection of microfossils has also been found in this unit. The unit III sediments formed in a shallow, tropical lagoon environment. At the top of the quarry section is unit IV, approximately 2 m thick, an organodetritic limestone where bivalves, bryozoans, polychaetes, and rarely ammonites were found.

Taphonomy of the bone-bearing horizon.—The discovery of numerous associated marine vertebrate individuals within a narrow stratigraphic horizon in Owadów-Brzezinki Quarry is another example of a marine vertebrates bonebed in the Jurassic fossil record (Martill 1993). The Owadów-Brzezinki bonebed is a mixed assemblage of ophthalmosaurid ichthyosaurs and other marine and semiaquatic vertebrate taxa such like members of Actinopterygii, Testudinata, and Crocodylomorpha (Tyborowski et al. 2016). The studied material of the new ophthalmosaurid ichthyosaur can be assigned to two different taphonomic categories: (i) disarticulated but associated parts of the skeleton, (ii) isolated bones and bone fragments. Disarticulated parts of the skeleton are represented by the fin and pectoral girdle bones, an accumulation of vertebrae and a fragmentary part of the rostrum. The fracture of the rostrum suggests vertical or subvertical landing of an ichthyosaur body on the sea floor and a relatively hard touchdown. Similar situations have been described from other Jurassic localities (Wahl 2009). Disarticulation of the rest of the skeleton parts is an effect of the activity of scavengers and sea currents. The activity of scavengers is supported by the presence of teeth marks on the surface of some ribs. The isolated bones are represented by vertebrae, neural arches, complete teeth, tooth crowns, tooth roots, broken ribs, and skull bones. All the isolated bones are well preserved. All of the described bones belong to a single individual. This is indicated by the size of the bone elements and their accumulation in the same horizon in one place within a few square meters. Skeletons belonging to other individuals have been found in other sectors of the quarry. The Owadów-Brzezinki bonebed shows some evidence of transport before burial. It contains disarticulated partial skeletons and isolated skeletal elements. The carcasses of the marine reptiles may have drifted post mortem into the bay from the open sea. In the bay the carcass sank to the bottom and was buried.

Material

The specimen under this study was found by Marcin Krystek from the GMUL, during the field research of the Jurassic localities of Central Poland in 2003. All remains were found in unit I. Skeleton of the ichthyosaurs typically has between 90–100 vertebrae (McGowan and Motani 2003). The skeleton from Owadów-Brzezinki Quarry has 42 vertebral centra, which indicates that it represents roughly half of the axial skeleton. Several skull bones are preserved, including a large portion of the lower jaw with visible tooth impressions. Isolated teeth were also found. The pectoral girdle is represented by a scapula, coracoid and clavicles. The limbs are represented by a humerus, radius, ulna, femur and numerous fin bones (metacarpals and phalanges). Most of the bones are not covered by carbonate sediment, which greatly facilitates observation of their morphology. The collected material is housed in the GMUL.

Systematic palaeontology

Order Ichthyosauria Blainville, 1835

Family Ophthalmosauridae Baur, 1887

Genus *Cryopterygius* Druckenmiller, Hurum, Knutsen, and Nakrem, 2012

Type species: *Cryopterygius kristiansenae* Druckenmiller, Hurum, Knutsen, and Nakrem, 2012; Tithonian of Svalbard Archipelago.

Cryopterygius kielanae sp. nov.

Etymology: In honour to Zofia Kielan-Jaworowska (1925–2015), world-renowned Polish researcher of Mesozoic mammals.

Holotype: GMUL 3579-81, a fragment of the lower jaw, isolated teeth, fragments of pterygoid and quadrate, parts of the cervical, dorsal, and caudal vertebral column, most of the left pectoral girdle, right clavicle, right forefin, and left femur.

Type locality: Owadów-Brzezinki Quarry of Nordkalk GmbH, Sławno, vicinity of Tomaszów Mazowiecki (Central Poland); 51°22’34.53” N, 20°08’07.86” E.

Type horizon: Upper Jurassic (the uppermost Lower Tithonian = Middle Volgian), the lower part of the Kcynia Formation, the Sławno Limestone Member.

Diagnosis.—Medium size ophthalmosaurid ichthyosaur (estimated 3.5–4 m of total body length; based on comparisons of pectoral girdle and forefin size in other more complete ophthalmosaurids; the humerus and scapula are similar in size to those of *Janusaurus lundi*, which is estimated to be a medium-sized species), and is smaller in length than type species. Absence of a deep and wide ventral groove on the quadrate articular condyle (quadrate articular condyle divided by a deep and wide groove in *Ophthalmosaurus icenicus*, *Sveltonectes insolitus*, *Acamptonectes densus*, and *Platypterygius australis*). Humerus with tall and prominent dorsal process located in the middle of the dorsal surface of the bone, rather than less prominent dorsal process located at the posterior margin of the dorsal surface of the bone in *C. kristiansenae*. Humerus with prominent deltopectoral crest, rather than very weakly developed deltopectoral crest in *C. kristiansenae* (relatively low dorsal process and deltopectoral crest in *Ophthalmosaurus icenicus*, *Aegirosaurus leptospondylus*, and *Caypullisaurus bonapartei*). Humerus with two distal facets (three distal facets in *Ophthalmosaurus icenicus*, *Brachypterygius extremus*, *Caypullisaurus bonapartei*, *Undorosaurus gorodischensis*, *Aegirosaurus leptospondylus*, *Janusaurus lundi*, and *Acamptonectes densus* humeri). Proximal and distal ends of the femur anteroposteriorly broader in *C. kielanae* than in *C. kristiansenae* (relatively narrower femur in *Ophthalmosaurus icenicus* and *Janusaurus lundi*).

Description.—*Skull*: The skull bones of *Cryopterygius kielanae* are represented by the right pterygoid, left quadrate and part of the lower jaw.

Pterygoid: The pterygoid bone is rectangular and is anteriorly and posteriorly incomplete (Fig. 2A). The posterior part of the pterygoid is thickened and forms short trigonal processes. The medial part of the dorsal surface of the bone is flat. The bone forms the medial edge of the interpterygoid vacuity. The maximum preserved anteroposterior length of the pterygoid is 128 mm.

Quadrate: As in other ophthalmosaurids the quadrate is a concentric, lunate-shape bone, it may be that more than half of the dorsal quadrate is missing (Fig. 2B). The occipital lamella is broken. The ventral part of the quadrate forms a wide articular condyle. The condyle is prominent and convex ventrally. The articular condyle has no deep and wide groove. The maximum mediolateral width of the articular surface of the condyle is 64 mm. The dorsal part of the quadrate is the thinnest part.

Mandible: The preserved part of the lower jaw is the posterior part of right ramus. The jaw fragment is anteriorly and posteriorly incomplete. The maximum length of the preserved part of the lower jaw is 245 mm. The maximum height of the preserved fragment of the lower jaw is 66 mm. A fragment of the lower jaw consists of a dentary bone and surangular bone (Fig. 3). On the upper edge of the dentary bone, a longitudinal dentary groove 16 mm deep is present. This groove extends along the entire preserved portion of the lower jaw. The width of the dental groove is 26 mm. Inside the groove the tooth impressions are visible (Fig. 3A). The tooth impressions are oval in shape. The diameter of the impressions is 10 mm. All of the tooth impressions are located on the lingual wall of the dental groove. The maximum length of the surangular preserved fragment is 126 mm. A portion of the lateral surangular is visible at the anterior part of the jaw fragment. The distinguishing features of the surangular are lacking. The fossa surangularis appears well developed.

Dentition: Nine isolated teeth belonging to *C. kielanae* were found. The teeth were found in the vicinity of the preserved lower jaw fragment. Only one is preserved complete (root and crown; Fig. 4). Most of the teeth are preserved in the form of roots with broken crowns. The isolated crowns are also present. The complete tooth measures 32 mm in apicobasal length. The root measured 21 mm in length. The length of the crown is 11 mm. The crowns are conical and robust. All the teeth are curved lingually and nearly circular in cross section. There is no indication of prominent carinae. Crowns have ornamentation in the form of gentle apicobasal grooves.

Axial skeleton: Forty-two vertebrae are preserved in the holotype of *C. kielanae*. These vertebrae are preserved as the isolated centra (Fig. 5). Four neural arches from the mid-dorsal region are also preserved. None of the neural arches are fused to the centra or with its neighbour. One of them has preserved the neural spine. Given that the typical vertebral count of ichthyosaurs is 90–100 (McGowan and

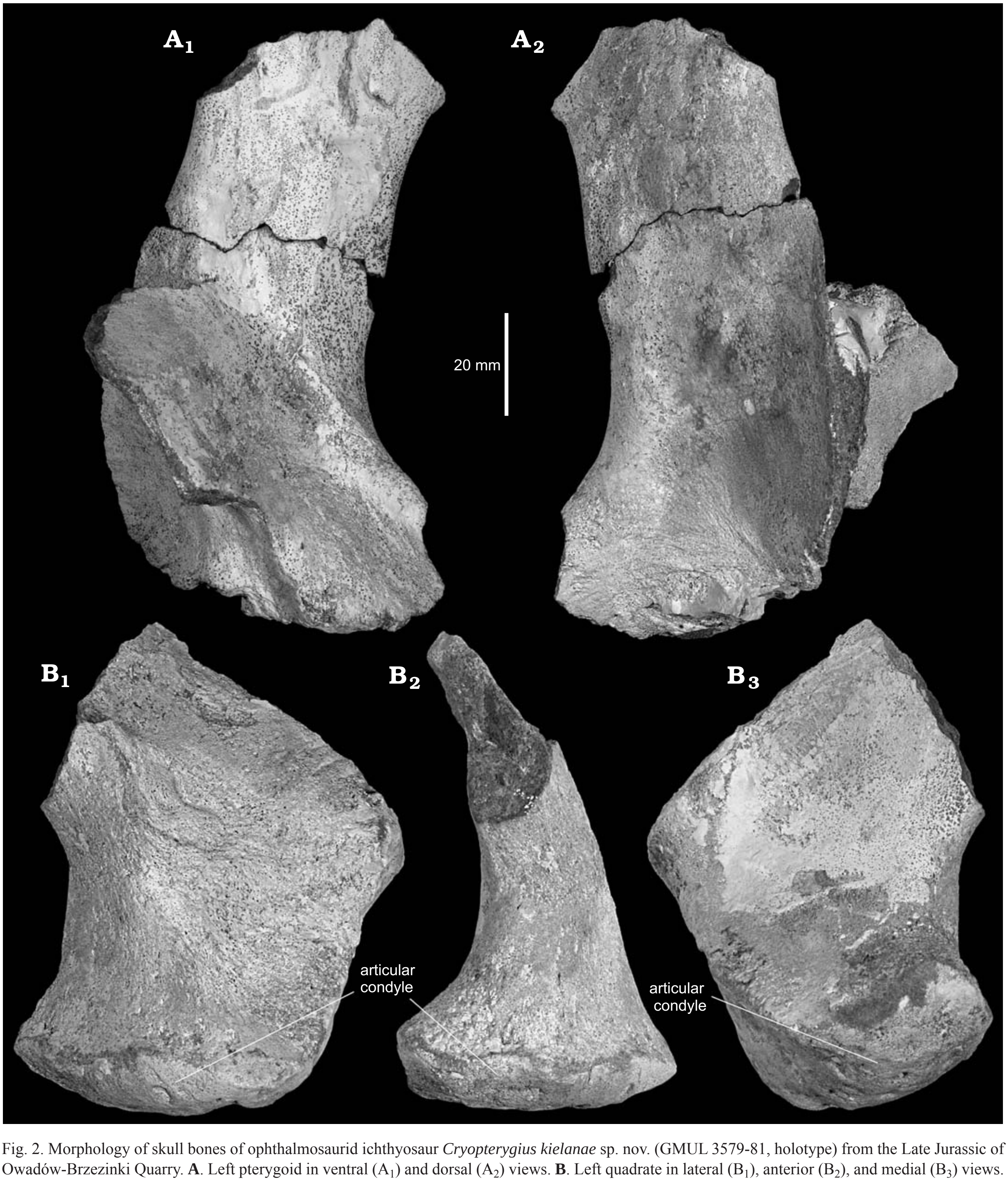

Fig. 2. Morphology of skull bones of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry. **A**. Left pterygoid in ventral (A_1) and dorsal (A_2) views. **B**. Left quadrate in lateral (B_1), anterior (B_2), and medial (B_3) views.

Motani 2003), the *C. kielanae* holotype includes about one-half of the vertebral column. The specimen includes: 4 cervical vertebrae (including atlas-axis complex), 11 dorsal vertebrae and 27 caudal vertebrae.

Atlas-axis complex: The atlas-axis complex is completely fused together (Fig. 5A). There is a sutural boundary between the atlas centrum and axis centrum. The atlas centrum is longer anteroposteriorly than the axis centrum

Fig. 3. Rostrum fragment of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry; in "dental/apical" (**A**) and right-lateral (**B**) views.

(Table 1). The diapophyses (dorsal rib facet) of the atlas centrum and axis centrum cannot be discerned. A single apophysis, probably parapophysis (ventral rib facet) of the atlas centrum is visible in the anterior half of the atlas. The parapophysis of the axis centrum is visible at the posterior edge of the atlas-axis complex. All of the atlas-axis complex parapophyses are visible in the mid-height of the centra. The floor of the neural canal of the atlas-axis complex is 12 mm wide in the anterior edge of the atlas centra and 24 mm wide in the posterior edge of the axis centra.

Cervical vertebrae: All of the cervical centra are dorsoventrally taller than anteroposteriorly long, and they are as laterally wide as dorsoventrally high (Fig. 5B). The diapophysis and parapophysis are visible at the anterior edge of the centra. The diapophyses are confluent with the facets for the neural arches anteriorly on the top of the centra. All of the cervical centra parapophyses are located in the mid-height of the centra. The floor of the neural canal of the cervical centra is 25 mm wide.

Dorsal vertebrae: Passing from the anterior to the posterior regions of the dorsal backbone, centra tend to increase in size in all dimensions (Fig. 5C). In all dorsal centra the two rib facets are visible. The diapophyses and parapophyses from the anterior dorsal centra are dorsally located. The diapophyses from the anterior dorsal centra are still confluent with the facets for the neural arches. The diapophyses and parapophyses become situated more ventrally on centra towards the posterior of the dorsal region. The diapophyses on centra from the posterior part of the dorsal region are losing their contact with the facets for the neural arches. Also, the diapophyses from this region becomes reduced. The floor of the neural canal of the dorsal centra is 20 mm in wide.

Table 1. Selected skeleton measurements (in mm) of *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype).

Atlas centrum anteroposterior length	26
Axis centrum anteroposterior length	11
Cervical centra anteroposterior length	24
Smallest dorsal centrum anteroposterior length	24
Largest dorsal centrum anteroposterior length	28
Smallest caudal centrum anteroposterior length	8
Largest caudal centrum anteroposterior length	25
Scapula maximum proximodistal length	193
Scapula maximum anteroposterior width, proximal blade	78
Scapula maximum anteroposterior width, distal blade	34
Scapula, coracoid facet length	20
Scapula, glenoid facet length	40
Humerus maximum proximodistal length	118
Humerus maximum anteroposterior width, proximal end	62
Humerus maximum heigh, proximal end	65
Humerus maximum anteroposterior width, distal end	83
Humerus maximum heigh, distal end	41
Humerus minimum anteroposterior width, midshaft	50
Radius maximum proximodistal length	42
Ulna maximum proximodistal length	50
Femur maximum proximodistal length	76
Femur maximum anteroposterior width, proximal end	42
Femur maximum anteroposterior width, distal end	57
Femur minimum anteroposterior width, midshaft	36

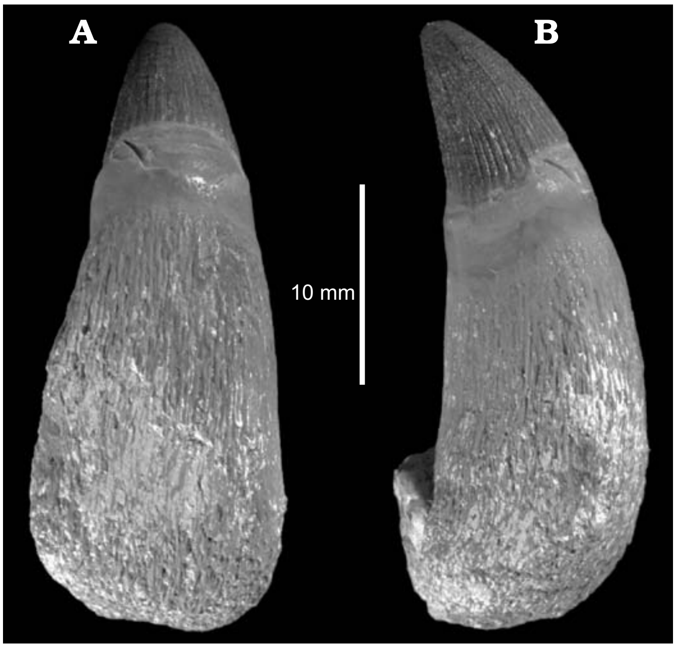

Fig. 4. Ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry; tooth in labial (**A**) and anterior (**B**) views.

Caudal vertebrae: Twenty-seven caudal vertebrae of *C. kielanae* are preserved (Fig. 5D–F), fifteen of which are preflexural vertebrae; twelve of them are postflexural vertebrae. The preflexural centra of *C. kielanae* are the largest of all the vertebral centra (Table 1). The postflexural centra are laterally compressed and have a characteristically oval shape in anterior and posterior views. All of the preflexural centra have only one rib facet visible, probably the parapophysis. No rib facets are present in postflexural centra. The floor of the neural canal of the preflexural centra is 15 mm in wide. The floor of the neural canal of the postflexural centra is 7 mm in wide. The apical centra are not preserved.

Neural arches: Only five neural arches from the mid-dorsal region are preserved. The neural spines are present in two of these but the apical part of the one spine is eroded. One of the preserved neural spines has a V-shaped apical notch. However, the specimen was found in the other layer than the rest of the skeleton and cannot determine whether it belongs to that individual. Height of the neural arches measured from base of the pedicel at the neurocentral boundary to the midpoint of the spine along the lateral surface is 57 mm.

Ribs: The preserved ribs of the *C. kielanae* are very disarticulated. All are broken. Some are figure of 8 shaped in cross section and taper gradually to their distal ends. Some of the rib has bite marks and small grooves suggesting post-mortem activity of the scavengers.

Pectoral girdle: The pectoral girdle of *Cryopterygius kielanae* is better known from the left side, which includes a nearly complete scapula and part of the clavicle. On the right side of the pectoral girdle only a part of the coracoid and clavicle are preserved.

Scapula: The scapula comprises a proximal blade that is anteroposteriorly expanded, and a narrow distal blade (Fig. 6A). The articular surface of the proximal blade includes an anterior, non-articular surface, the coracoid facet and the glenoid facet. The anterior, non-articular surface of the proximal blade supports the acromial process. The coracoid facet is relatively thin compared to the glenoid facet (Table 1) and anterior, non-articular surface and is also shorter than the glenoid facet. The acromial process is poorly preserved, being incomplete dorsally. The proximolateral surface of the scapula has a broad concavity with forms approximately one-third of the total scapula length. The acromial process forms the anterior margin of this concavity. The distal blade is broken ventrally. The posterior margin of the distal blade is incomplete.

Coracoid: The right coracoid is not well preserved (Fig. 6B). The preserved part is from the intercoracoid facet region. The maximum mediolateral width of the preserved part of the coracoid is 116 mm. Length of intercoracoid facet is 103 mm. The intercoracoid facet probably forms the anterior half of the medial margin.

Clavicles: All preserved fragments of the left clavicle measure 80 mm in length. The left clavicle is broken from proximal and distal edge. The right clavicle is better preserved but is also anteriorly and posteriorly broken. The maximum length of the right clavicle is 152 mm. The bones are gently curved dorsally and posteriorly. The right clavicle has a facet for the scapula and the visceral surface of the bone is gently dented.

Forefin: The morphology of the *Cryopterygius kielanae* forefins is best understood from the right forefin, which includes a complete humerus, complete radius and ulna, and most of the metacarpals and phalanges (Fig. 7). Most of them were found as disarticulated elements. The forefin is relatively small compared to total body length of *C. kielanae*. The length of the preserved part of the forefin is 300 mm, although distalmost phalanges are missing so the estimated total length of the forefin is 350 mm.

Humerus: The distal end of the humerus is wider than proximal end in maximum anteroposterior width (Fig. 8). The anteroposterior width and dorsoventral height of the humerus proximal articular surface are nearly identical. The proximal articular surface is very irregular, suggesting a considerable investment in articular cartilage. The distal end of the humerus is anteroposteriorly longer (Table 1) than dorsoventrally high. The dorsal process is broken but still more prominent than the deltopectoral crest (McGowan and Motani 2003). The dorsal process is situated on the proximal half of the bone and it measures approximately 50 mm long and maximum 20 mm wide. It arises near the posterodorsal surface, and ends suddenly by the midpoint of the shaft (Fig. 8). The deltopectoral crest is also prominent but is smaller than the dorsal process. The deltopectoral crest is situated ventrally on the proximal half of the humerus and is located at the anterior margin of the bone. The humerus has only two large distal facets for the radius and ulna. The radial

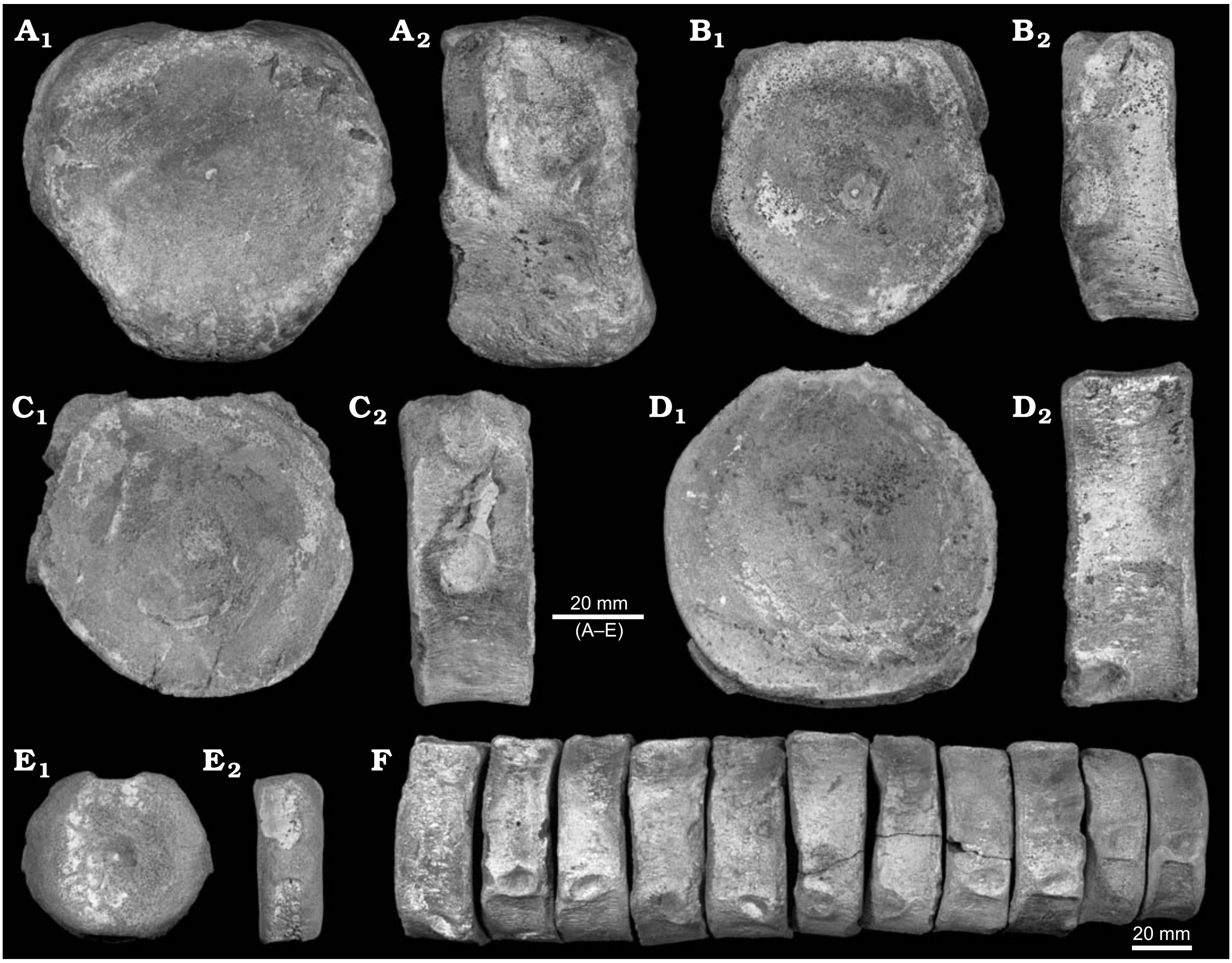

Fig. 5. Morphology of isolated centra of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry. Atlas-axis complex (**A**), cervical (**B**), dorsal (**C**), preflexural caudal (**D**), and postflexural caudal (**E**) centra, preflexural caudal spine (**F**); in anterior (A_1–E_1) and left-lateral (A_2–E_2, F) views.

facet is smaller than the ulnar facet. Anteroposterior length of the radial facet is 45 mm. Anteroposterior length of the ulnar facet is 52 mm. The facet for a preaxial accessory element is absent. Probably a preaxial accessory element does not directly articulate to the humerus. The radial and ulnar facets meet at an angle of 60°, looking from the dorsal view.

Zeugopodium and autopodium: The radius and ulna are the two largest bones anteriorly and posteriorly located. The posterior articular surface of both elements is gently rounded. Both bones are polygonal. All of them are broader than long. The radius is slightly smaller than the ulna (Table 1; Fig. 7). The anterior surface of the radius is curved and covered with small hummocks. The preaxial accessory element, radiale, intermedium, ulnare, distal carpals, metacarpals and phalanges are found as disarticulated elements in one layer. They were identified on the basis of Motani's (1999) criteria. The preaxial accessory element is teardrop-shaped. It is anteroposteriorly broadest and dorsoventrally thinnest proximally. The anterior margin of the preaxial accessory element is thinner than the posterior margin. It bears a posterior facet for the radius. The radiale, intermedium and ulnare are polygonal and broader than long. They are approximately of the same size. The interpretation of homology of the distal carpals and metacarpals is ambiguous. Probably the metacarpal V contacts the ulnare and the distal carpal 4. The proximal phalanges are rectangular and pentagonal.

Hindfin: The hindfin bones of *C. kielanae* are represented only by the left femur (Maxwell et al. 2012; Fig. 9). The distal end of the femur is wider than the proximal end (Table 1). Anteriorly, the femur is broad, but tapers posteriorly to a thin, blade-like posterior margin. The proximal articular surface is undulating and very irregular, and bears prominent hummocks, suggesting a considerable investment in articular cartilage just like on the humerus. From the anterior view and posterior view the femur is nearly symmetrical. The

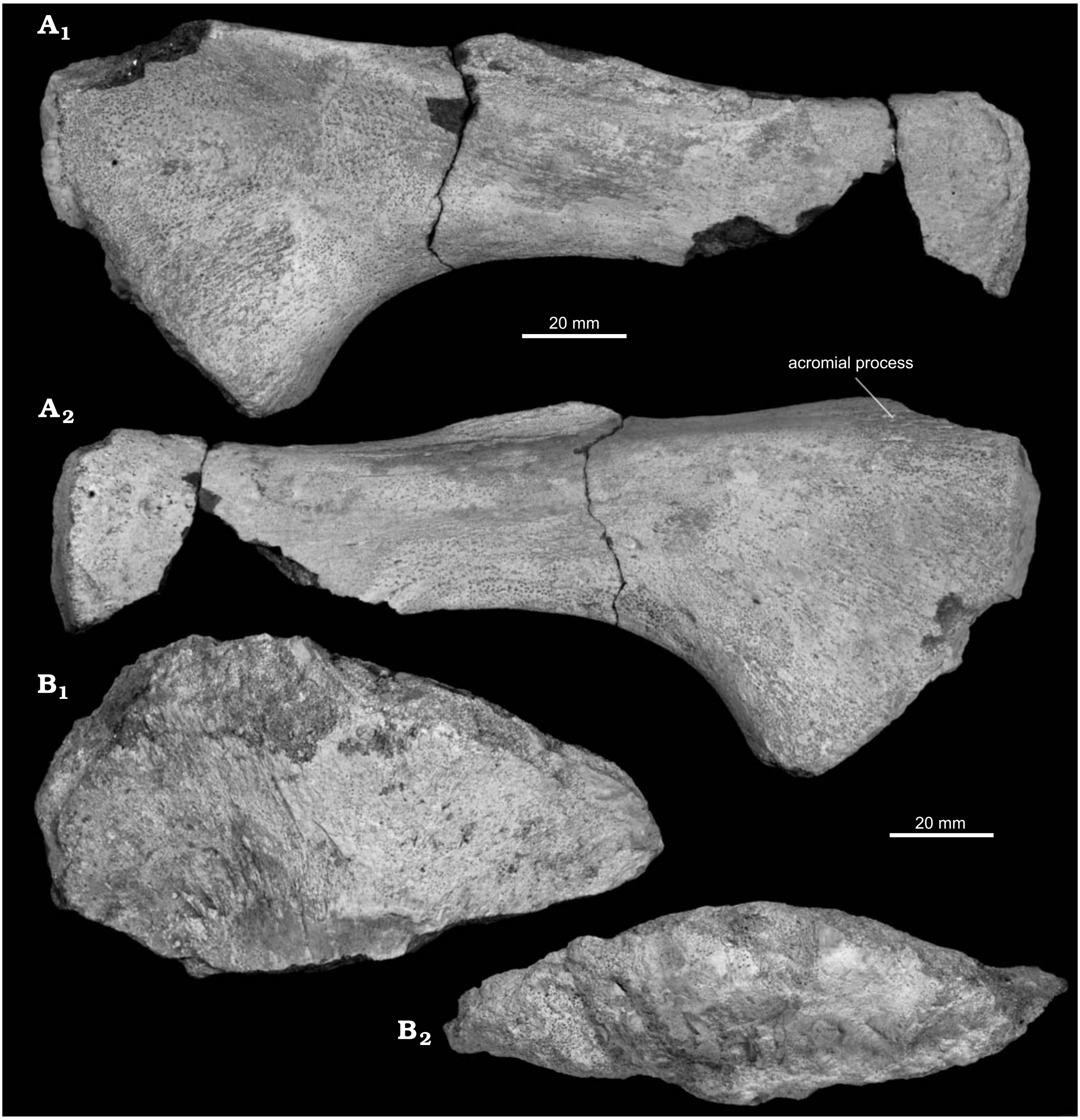

Fig. 6. Morphology of scapula and coracoid of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry. **A**. Left scapula in lateral (A_1) and medial (A_2) views. **B**. Right coracoid in lateral (B_1) and articular (B_2) views.

dorsal surface of the femur bears a low and rounded dorsal process which is located close to the anterior margin of the bone. The ventral surface bears a low, ventral process that is situated close to the anterior margin of the femur. Distally, the femur bears only two articular facets for tibia and fibula. The fibular facet is much longer than the tibial facet. Length of the tibial facet is 23 mm. Length of the fibular facet is 35 mm. Tibial and fibular facets are triangular-shaped in distal view. In dorsal view, the tibial and fibular facets of the femur meet at an angle of approximately 30°.

Remarks.—*Cryopterygius kielanae* holotype bones were found in a locality where marine reptile bones are frequently found (Tyborowski et al. 2016). The similar size and association of the bones in one sector of the quarry suggest that they belong to a single individual. Ophthalmosauridae are known from the Jurassic and Cretaceous, and include

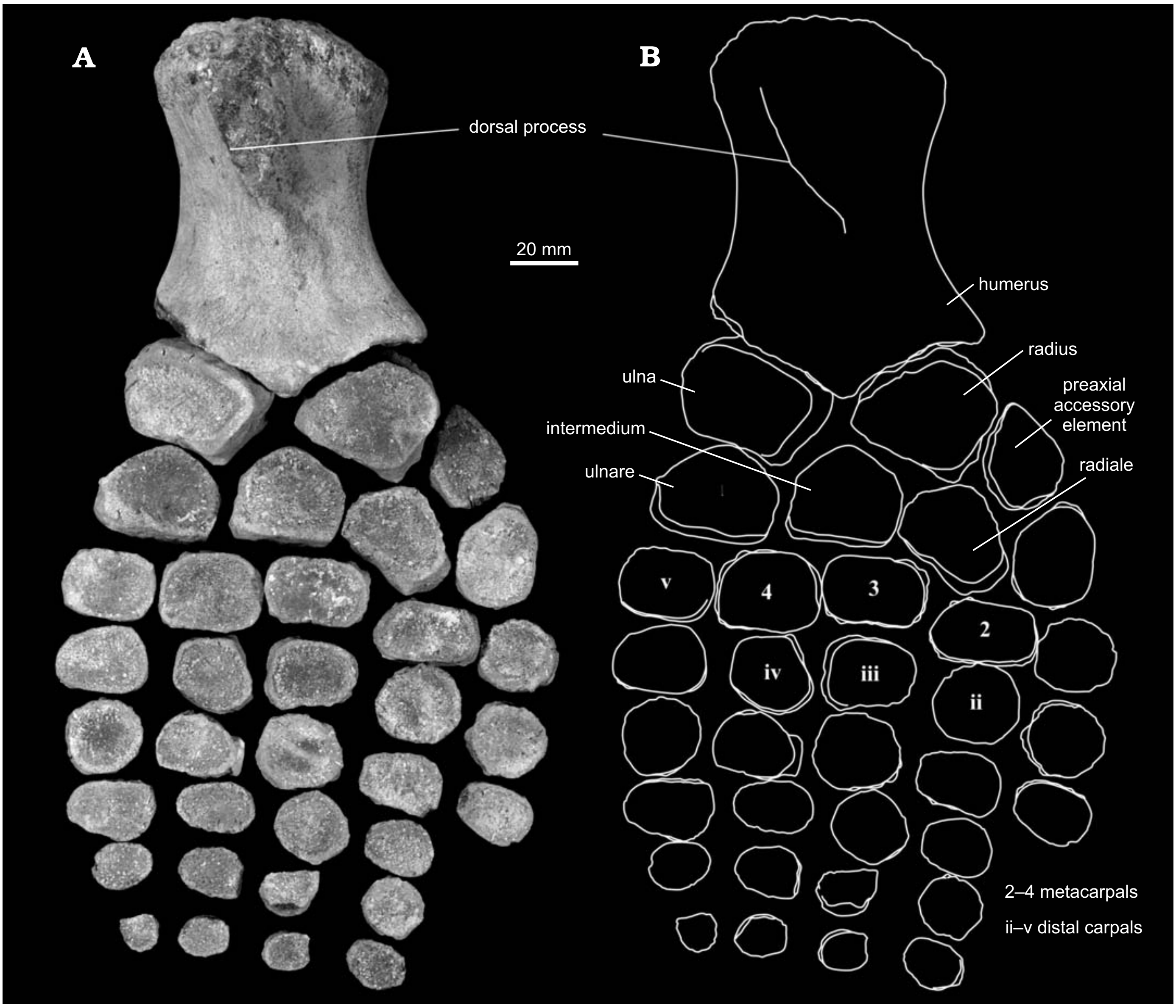

Fig. 7. Right forefin of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry; photo of the reconstruction (**A**) and explanatory drawing (**B**) in dorsal view.

taxa such as *Ophthalmosaurus* (Kirton 1983), *Aegirosaurus* (Bardet and Fernandez 2000), *Nannopterygius* (Hulke 1871), *Caypullisaurus* (Fernandez 1997), *Janusaurus* (Roberts et al. 2014), *Cryopterygius* (Druckenmiller et al. 2012), *Platypterygius* (Maxwell and Kear 2010), *Acamptonectes* (Fischer et al. 2012), *Arthropterygius* (Maxwell 2010), and *Undorosaurus* (Efimov 1999). Clearly, *C. kielanae* is a member of Ophthalmosauridae. Like the rest of the members of this group it has a preaxial accessory element in the forefin zeugopodium (McGowan and Motani 2003). The presence of a quadrate in the shape of ear is also a feature of most ophthalmosaurids (Fischer et al. 2014). As skull fragments are mostly incomplete, it is difficult to compare them with the bones of other ophthalmosaurids. The quadrate has a stapedial facet, although it is not as well developed as in other taxa such as *Acamptonectes* (Fischer et al. 2012). The articular condyle appears prominent and convex ventrally, unlike many ophthalmosaurids (*Ophthalmosaurus icenicus*, *Sveltonectes insolitus*, *Acamptonectes densus*, and *Platypterygius australis*), where the condyle is divided by a wide groove (Kirton 1983; Kear 2005; Fischer et al. 2011, 2012). The fossa surangularis is present on the surangular bone and appears well developed unlike in *Sveltonectes insolitus* (Fischer et al. 2011).

The pectoral girdle of the ophthalmosaurids has a wide range of intraspecific variations (Maxwell and Druckenmiller 2011), which makes comparing *Cryopterygius kielanae* to other ophthalmosaurids problematic. However, some comparisons can be made. The scapula of *C. kielanae* is generally similar to that of *Undorosaurus* (Efimov 1999) and *C. kristiansenae* (Druckenmiller et al. 2012). The distal blade of the scapula in *C. kielanae* is relatively shorter than that of

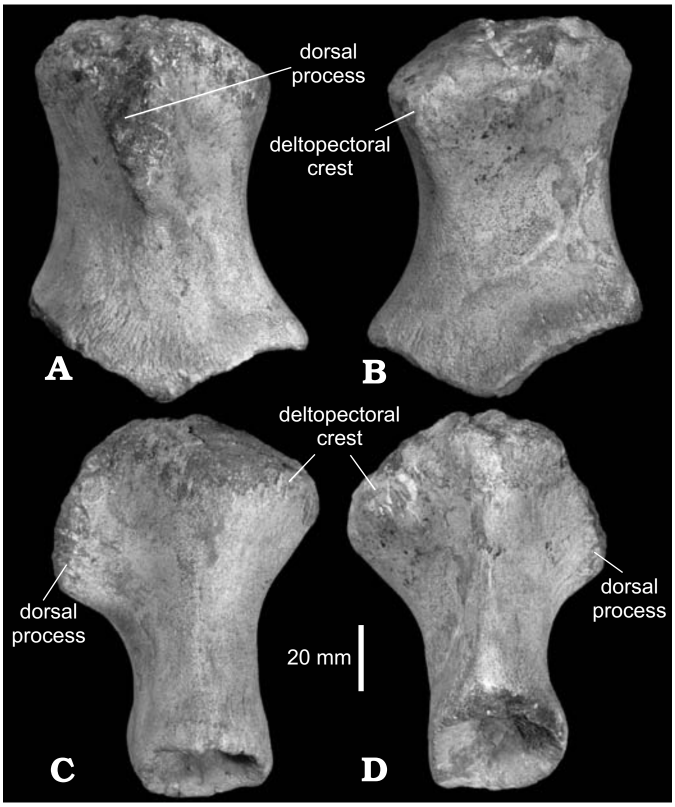

Fig. 8. Right humerus of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry; in dorsal (**A**), ventral (**B**), anterior (**C**), and posterior (**D**) views.

Caypullisaurus. The base of the acromial process is not so prominent such as *Acamptonectes* (Fischer et al. 2012). The clavicles are similar to *Janusaurus lundi* (Roberts et al. 2014) and *Ophthalmosaurus icenicus* (Kirton 1983). Both clavicles are curved dorsally and posteriorly. The visceral surface of the right clavicle is dented, as in *Janusaurus lundi* (Roberts et al. 2014).

Certainly, the forefin of *C. kielanae* is the most diagnostic part of the skeleton. The humerus has only two distal facets for radius and ulna. Most of the ophthalmosaurids have three distal facets: *Ophthalmosaurus icenicus* (Kirton 1983), *Aegirosaurus leptospondylus* (Bardet and Fernandez 2000), *Caypullisaurus bonapartei* (Fernandez 1997), *Brachypterygius extremus* (Boulenger 1904), *Undorosaurus gorodischensis* (Efimov 1999), *Janusaurus lundi* (Roberts et al. 2014), *Acamptonectes densus* (Fischer et al. 2012), and *Arthropterygius* (Maxwell 2010). The ophthalmosaurids with only two distal facets are *Cryopterygius kristiansenae* (three distal facets on the right humerus; Druckenmiller et al. 2012), *Nannopterygius enthekiodon* (Hulke 1871), *Sveltonectes* (Fischer et al. 2011), and many species of *Platypterygius* (McGowan and Motani 2003). The forefin of *Platypterygius americanus* from the Lower Cretaceous is similar to *C. kielanae* (Maxwell and Kear 2010). The proximal phalanges of *Platypterygius americanus* and *Cryopterygius kielanae* are rectangular (Maxwell and Kear 2010). The humerus of *C. kielanae* is relatively small compared to *Platypterygius hercynicus* (Kolb and Sander 2009) and *Undorosaurus gorodischensis* (Efimov 1999). The humeri of *Cryopterygius kristiansenae* and *Nannopterygius enthekiodon* are also reduced (Hulke 1871; Druckenmiller et al. 2012). Little is known about the *Nannopterygius* forefin and virtually nothing about its humeral and preaxial accessory element morphology. *Aegirosaurus leptospondylus* differs from the *C. kielanae* by the presence of three distal facets on the humerus (Bardet and Fernandez 2000). *Aegirosaurus* and *Brachypterygius* share a humerus-intermedium contact (Bardet and Fernandez 2000). The *Cryopterygius kielanae* intermedium has no contact with the humerus. *Janusaurus* also has three distal facets on the humerus (Roberts et al. 2014) and the anterior facet is the preaxial accessory element facet. *C. kielanae* also has a preaxial accessory element, but there is no preaxial accessory element facet on the humerus. The femur of *C. kielanae*, which has only two distal facets for both the tibia and the fibula, differs from the three-facet forms of *Platypterygius australis*, *Platypterygius americanus*, and *Paraophthalmosaurus kabanovi* (Maxwell and Kear 2010; Zammit et al. 2010; Arkhangelsky and Zverkov 2014).

The holotype of *C. kristiansenae* and the new ophthalmosaurid *C. kielanae* from the Owadów-Brzezinki Quarry share the following characters: (i) relatively short (proximodistally) humerus (compared to animal body) with only two distal facets for radius and ulna (three facets on the right humerus in *C. kristiansenae*), (ii) proximal phalanges rectangular or pentagonal, (iii) femur anteroposteriorly broad with only two distal facets for tibia and fibula, (iv) proximolateral surface of the scapula with a broad concavity, (v) neural arches with V-shaped apical notch in the neural spines (however, the only specimen found with this feature in Owadów-Brzezinki Quarry may not belong to this individual). Nevertheless *C. kielane* differs from *C. kristiansenae* in several aspects: (i) ulnar facet larger than the radial facet in *C. kielanae*; radial facet and ulnar facet equal in anteroposterior length in *C. kristiansenae*, (ii) tall and prominent dorsal process on *C. kielanae* humerus; low dorsal process on *C. kristiansenae* humerus, (iii) dorsal process located in the middle of the dorsal surface of the humerus in *C. kielanae*; dorsal process located at the posterior margin of the dorsal surface of the humerus in *C. kristiansenae*, (iv) prominent deltopectoral crest on *C. kielanae* humerus; very weakly developed deltopectoral crest on *C. kristiansenae* humerus, (v) femur broader in *C. kielanae* than in *C. kristiansenae*, (vi) fibular facet larger than the tibial facet in *C. kielanae*; tibial facet and fibular facet equal in anteroposterior length in *C. kristiansenae*, (vii) *C. kielanae* body significantly smaller than *C. kristiansenae* body (*C. kielanae* estimated 3.5–4 m total body length; *C. kristiansenae* estimated 5.5 m total body length).

The specimen is interpreted to be an adult, based on the articular surface of the humeral head which is convex, concavity of the distal facets, the smoothness of the humeral shaft and the advanced ossification of the forefin elements

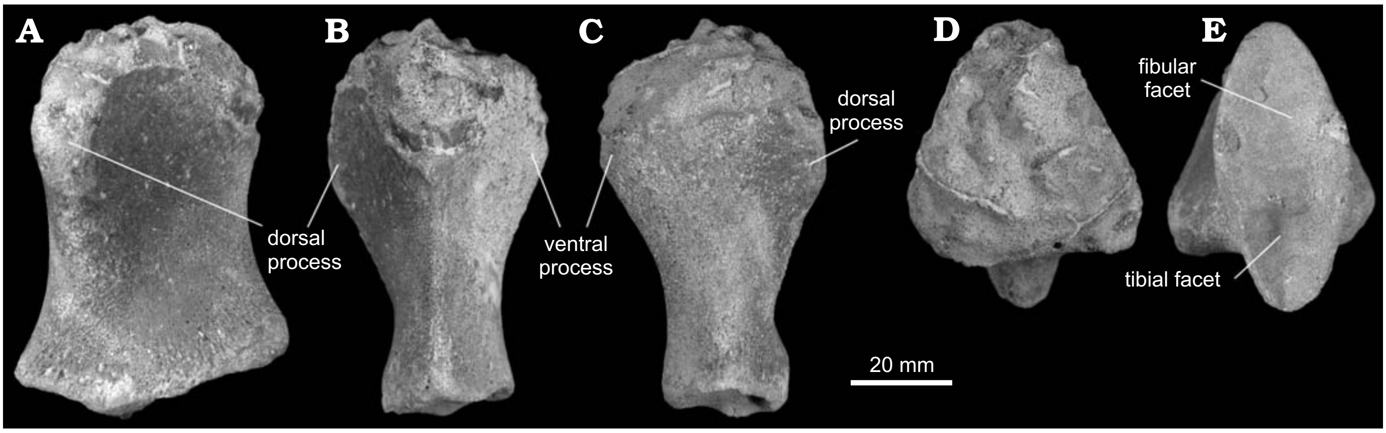

Fig. 9. Left femur of ophthalmosaurid ichthyosaur *Cryopterygius kielanae* sp. nov. (GMUL 3579-81, holotype) from the Late Jurassic of Owadów-Brzezinki Quarry; in dorsal (**A**), posterior (**B**), anterior (**C**), proximal (**D**), and distal (**E**) views.

(Johnson 1977; Kear and Zammit 2014). Also the dorsal ribs with thick cortical bone are interpreted as an ontogenetic adult trait (Kear and Zammit 2014).

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Species of Tithonian ophthalmosaurids have been described from two regions of Central and North Europe. *Aegirosaurus leptospondylus* was described from the lower part of Lower Tithonian Solnhofen Formation of the Solnhofen area in Bavaria, southern Germany (Bardet and Fernandez 2000). *Cryopterygius kristiansenae*, *Palvennia hoybergeti*, *Janusaurus lundi*, and *Brachypterygius* have been described from the Middle Volgian (= Middle Tithonian) or Early Portlandian Agardhfjellet Formation of the Svalbard Archipelago in the Arctic (Angst et al. 2010; Druckenmiller et al. 2012; Gradstein et al. 2012; Hurum et al. 2012; Roberts et al. 2014). *Cryopterygius kielanae* from the Owadów-Brzezinki carbonate sediments in Poland is also Middle Volgian age (Kutek 1994; Błażejowski et al. 2016). Tithonian ichthyosaurians are also known from West Europe. *Brachypterygius extremus*, *Nannopterygius enthekiodon*, and *Ophthalmosaurus* sp. have been described from British and French Upper Kimmeridge Clay (McGowan and Motani 2003), which is Kimmeridgian–Lower Tithonian, i.e., the same age as Solnhofen and Owadów-Brzezinki. Coeval ichthyosaurs (*Undorosaurus*, *Paraophthalmosaurus*, *Brachypterygius*, *Grendelius*, and *Arthropterygius*) have also been described from the northern and southern parts of western Russia (Arkhangelsky and Zverkov 2014; Zverkov et al. 2015a, b). *Cryopterygius kielanae* is most similar to *Cryopterygius kristiansenae* based on the morphology of the forefins, parts of the pectoral girdle, femur and ribs; both taxa are known from the Middle Volgian.

The Solnhofen and Svalbard faunas both contain ichthyosaurs, however, the diversity of other reptile groups is different. In the Svalbard faunas ichthyosaurs were associated by plesiosaurians (Druckenmiller and Knutsen 2012; Knutsen et al. 2012b; Liebe and Hurum 2012) and pliosaurians (Knutsen et al. 2012a), while the Solnhofen fauna was dominated by ichthyosaurians (Bardet and Fernandez 2000), marine crocodylomorphs (Young et al. 2010) and turtles (Barthel et al. 1990). Many of the marine reptiles from the Owadów-Brzezinki Quarry, like turtles and crocodylomorphs, are members of groups already known from the Solnhofen region (Tyborowski et al. 2016; Fig. 10). Probably the shallow marine area of Owadów-Brzezinki during the Late Jurassic was a transition zone between the Arctic basin

	Solnhofen archipelago	Owadów-Brzezinki lagoon	Boreal realm
Ichthyosauria	*Aegirosaurus leptospondylus*	*Cryopterygius kielanae*	*Cryopterygius kristiansenae* *Palvennia hoybergeti* *Janusaurus lundi* *Brachypterygius*
Other marine reptiles	Testudinata Crocodylomorpha	Testudinata Crocodylomorpha	Plesiosauria Pliosauria

Fig. 10. Palaeobiogeography of the Tithonian marine reptile faunas of Central and North Europe. Red line, the possible migration routes of the boreal ichthyosaurian reptiles. Palaeogeographical map from Ron Blakey, Colorado Plateau Geosystems, Arizona, USA (http://cpgeosystems.com/paleomaps.html).

and the tropical Solnhofen lagoons located at the NW margin of the Tethys Ocean (Fig. 10).

There are two possible routes of ichthyosaurian migration from the Boreal realm to the Owadów-Brzezinki region during the Tithonian (Fig. 10). The first runs through the area of the British/French Kimmeridge Clay. The second link is through the Russian North. Both routes are known from the remains of ophthalmosaurid ichthyosaurians (McGowan and Motani 2003; Zverkov et al. 2015a, b). This hypothesis is supported by the presence of the Subboreal English (Portlandian) and Russian (Volgian) ammonites fauna in the lower part of the Owadów-Brzezinki Quarry sequence (Matyja and Wierzbowski 2016). The ophthalmosaurid ichthyosaurs of the genus *Cryopterygius* can live in both Polish and Arctic environments. The occurrence of this genus in the Owadów-Brzezinki Quarry indicates a free marine connections between the Boreal sea and that of Central Poland.

Conclusions

The ichthyosaurian bones found in the Late Jurassic of Owadów-Brzezinki Quarry in Poland represent a new species, *Cryopterygius kielanae*, morphologically different from the other ophthalmosaurid ichthyosaurs known from the Jurassic and Cretaceous. However, some similarities can be found between the new taxon and *Cryopterygius kristiansenae* from the Tithonian; Middle Volgian (Late Jurassic) of Svalbard Archipelago. The Late Jurassic ecosystem of the Owadów-Brzezinki Quarry is similar to the one known from Solnhofen area in Germany. Several groups of the marine reptiles (e.g., turtles and crocodylomorphs) are recorded in both localities (Tyborowski et al. 2016). Ichthyosaurians are known from Solnhofen region, Svalbard and Owadów-Brzezinki area but the new species *Cryopterygius kielanae* is most similar to the *Cryopterygius kristiansenae* from the Arctic region. This suggests a connection between Owadów-Brzezinki, Solnhofen and Svalbard region through the Late Jurassic. Probably the Owadów-Brzezinki area was a transition between the Arctic basin in the north and the tropical Tethys Ocean in the south and some species of ichthyosaurians could live in all these areas.

Acknowledgements

The author is grateful to Peter Walsh (University of Silesia, Sosnowiec, Poland) and Piotr Gieszcz (Association of Polish Climatologists, Warszawa, Poland) for many useful suggestion and correction of English. I would like to sincerely thank Błażej Błażejowski (Institute of Paleobiology PAS, Warszawa, Poland) for comments on the text. I appreciate the help provided in the field of Robert Siuda and Cezary Błaszczyk (both Owadów-Brzezinki Quarry, Nordkalk Company). I would like to thank Aleksandra Hołda-Michalska for computer processing of figures and Marian Dziewiński (both Institute of Paleobiology PAS) for photographing the specimens. I would like to sincerely thank the reviewers Aubrey Jane Roberts (University of Southampton, UK) and Benjamin Moon (University of Bristol, UK) for their helpful comments and for improving the manuscript. Finally I would sincerely thank to all geology students for assistance and support during fieldwork over many years. Travel and field work was supported by the Polish National Science Center grant nr UMO-2014/15/N/ST10/04818.

References

Angst, D., Buffetaut, E., Tabouelle, J., and Tong, H. 2010. An ichthyosaur skull from the Late Jurassic of Svalbard. *Bulletin de la Société Géologique de France* 181: 453–458.

Arkhangelsky, M.S. and Zverkov, N.G. 2014. On a new ichthyosaur of the genus *Undorosaurus*. *Proceedings of the Zoological Institute RAS* 318: 187–196.

Bardet, N. and Fernandez, M.S. 2000. A new ichthyosaur from the Upper Jurassic lithographic limestones of Bavaria. *Journal of Paleontology* 74: 503–511.

Bardet, N., Fischer, V., and Machalski, M. 2016. Large predatory marine reptiles from the Albian–Cenomanian of Annopol, Poland. *Geological Magazine* 153: 1–16.

Barthel, K.W., Swinburne, N.H.M., and Conway-Morris, S. 1990. *Solnhofen. A Study in Mesozoic Palaeontology*. 236 pp. Cambridge University Press, Cambridge.

Baur, G. 1887. On the morphology and origin of the Ichthyopterygia. *American Naturalist* 21: 837–840.

Blainville, H.M.D. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'érpetologie et d'amphibiologie. *Nouvelles Annales du Muséum d'Histoire Naturelle Paris* 4: 233–296.

Bechly, G. and Kin, A. 2013. First record of the fossil dragonfly family Eumorbaeschnidae from the Upper Jurassic of Poland. *Acta Palaeontologica Polonica* 58: 121–124.

Błażejowski, B., Gieszcz, P., and Tyborowski, D. 2016. New finds of well preserved Tithonian (Late Jurassic) fossils from the Owadów-Brzezinki Quarry, Central Poland: a review and perspectives. *Volumina Jurassica* 14: 123–132.

Błażejowski, B., Lambers, P., Gieszcz, P., Tyborowski, D., and Binkowski, M. 2015. Late Jurassic jaw bones of halecomorph fish (Actinopterygii: Halecomorphi) studied with X-ray microcomputed tomography. *Palaeontologia Electronica* 18.3.53A: 1–10.

Boulenger, G.A. 1904. On a new species of ichthyosaur from Bath. *Proceedings of the Zoological Society of London* 1904 (1): 424–426.

Druckenmiller, P.S. and Knutsen, E.M. 2012. Phylogenetic relationships of Upper Jurassic (Middle Volgian) plesiosaurians (Reptilia: Sauropterygia) from the Agardhfjellet Formation of central Spitsbergen, Norway. *Norwegian Journal of Geology* 92: 277–284.

Druckenmiller, P.S., Hurum, J.H., Knutsen, E.M., and Nakrem, H.A. 2012. Two new ophthalmosaurids (Reptilia: Ichthyosauria) from the Agardhfjellet Formation (Late Jurassic: Volgian/Tithonian), Svalbard. Norway. *Norwegian Journal of Geology* 92: 311–340.

Efimov, V.M. 1999. A new family of ichthyosaurs, the Undorosauridae fam. nov. from the Volgian Stage of the European part of Russia. *Paleontological Journal* 33: 174–181.

Feldman, R.M., Schweitzer, C.E., and Błażejowski, B. 2015. A new species of lobster (Glypheoidea: Mecochiridae) from the Late Jurassic (late Tithonian) Lagerstätte from central Poland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 275: 107–114.

Fernandez, M.S. 1997. A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin, Northwestern Patagonia, Argentina. *Journal of Paleontology* 71: 479–484.

Fischer, V., Arkhangelsky, M.S., Uspensky, G.N, Stenshin, I.M., and Godefroit, P. 2014. A new Lower Cretaceous ichthyosaur from Russia reveals skull shape conservatism within Ophthalmosaurinae. *Geological Magazine* 151: 60–70.

Fischer, V., Maisch, M.W., Naisch, D., Liston, X., Kosma, R., Joger, U., Kruger, F.X., Pardo-Perez, X., Tainsh, X., and Appleby, R. M. 2012. New ophthalmosaurid ichthyosaurs from the Early Cretaceous of Europe demonstrate extensive ichthyosaur survival across the Jurassic–Cretaceous boundary. *PLoS ONE* 7: e29234.

Fischer, V., Masure, E., Arkhangelsky, M.S., and Godefroit, P. 2011. A new Barremian (Early Cretaceous) ichthyosaur from western Russia. *Journal of Vertebrate Paleontology* 31: 1010–1025.

Gradstein, F.M., Ogg, J., Schmitz, M.A., and Ogg, G. 2012. *A Geologic Time Scale 2012*. Elsevier Publishing Company, Boston.

Hirszberg, F. 1924. Ichthyosaurian and plesiosaurian vertebrae from the Kimmeridgian and Portlandian of Tomaszów Rawski region. *Prace Polskiego Instytutu Geologicznego* 3: 200–236.

Hulke, J.W. 1871. Note on an *Ichthyosaurus* (*I. enthekiodon*) from Kimmeridge Bay, Dorset. Quarterly *Journal of the Geological Society of London* 27: 440–441.

Hurum, J.H., Nakrem, H.A., Hammer, Ø., Knutsen, E.M., Druckenmiller, P.S., Hryniewicz, K., and Novis, L.K. 2012. An Arctic Lagerstätte–Slottsmøya Member of the Agardhfjellet Formation (Upper Jurassic–Lower Cretaceous) of Spitsbergen. *Norwegian Journal of Geology* 92: 55–64.

Johnson, R. 1977. Size independent criteria for estimating relative age and the relationship among growth parameters in a group of fossil reptiles (Reptilia: Ichthyosauria). *Canadian Journal of Earth Science* 14: 1916–1924.

Kear, B.P. 2005. Cranial morphology of Platypterygius longmani Wade, 1990 (Reptilia: Ichthyosauria) from the Lower Cretaceous of Australia. *Zoological Journal of the Linnean Society* 145: 583–622.

Kear, B.P. and Zammit, M. 2014. An utero-foetal remains of the Cretaceous ichthyosaurian *Platypterygius*: ontogenetic implications for character state efficacy. *Geological Magazine* 151: 71–86.

Kin, A. and Błażejowski, B. 2012. Polish Solnhofen. *Przegląd Geologiczny* 60: 375–379.

Kin, A. and Błażejowski, B. 2014. The horseshoe crab of the genus *Limulus*: living fossil or stabiliomorph? *PLoS ONE* 9 (10): e108036.

Kin, A., Błażejowski, B., and Binkowski, M. 2012. The „Polish Solnhofen": a long awaited alternative? *Geology Today* 28: 91–94.

Kin, A., Gruszczyński, M., Martill, D., Marshall, J., and Błażejowski, B. 2013. Palaeoenvironment and taphonomy of a Late Jurassic (Late Tithonian) Lagerstätte from central Poland. *Lethaia* 46: 71–81.

Kirton, A.M. 1983. *A Review of British Upper Jurassic Ichthyosaurs*. 478 pp. Ph.D. Dissertation, University of Newcastle upon Tyne, Newcastle upon Tyne.

Knutsen, E.M., Druckenmiller, P.S., and Hurum, J.H. 2012a. A new species of *Pliosaurus* (Sauropterygia: Plesiosauria) from the Middle Volgian of central Spitsbergen, Norway. *Norwegian Journal of Geology* 92: 235–258.

Knutsen, E.M., Druckenmiller, P.S., and Hurum, J.H. 2012b. Two new species of long-necked plesiosaurians (Reptilia: Sauropterygia) from the Upper Jurassic (Middle Volgian) Agardhfjellet Formation of central Spitsbergen. *Norwegian Journal of Geology* 92: 187–212.

Kolb, C. and Sander, P.M. 2009. Redescription of the ichthyosaur *Platypterygius hercynicus* (Kuhn 1946) from the Lower Cretaceous of Salzgitter (Lower Saxony, Germany). *Palaeontographica, Abteilung A* 288: 151–192.

Kutek, J. 1994. The Scythicus Zone (Middle Volgian) in Poland: its ammonites and biostratigraphic subdivisions. *Acta Geologica Polonica* 44: 1–33.

Liebe, L. and Hurum, J.H. 2012. Gross internal structure and microstructure of plesiosaur limb bones from the Late Jurassic, central Spitsbergen. *Norwegian Journal of Geology* 92: 285–310.

Lomax, D.R. 2015. The first plesiosaurian (Sauropterygia, Pliosauridae) remains described from the Jurassic of Poland. *Palaeontologia Electronica* 18 (2): 29.

Martill, D.M. 1993. Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia: Darmstädter Beiträge zur Naturgeschichte* 2: 11–91.

Matyja, B.A. and Wierzbowski, A. 2016. Ammonites and ammonite stratigraphy of the uppermost Jurassic (Tithonian) in the Owadów-Brzezinki quarry (central Poland). *Volumina Jurassica* 14: 85–122.

Maxwell, E.E. 2010. Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, Northwest Territories, Canada. *Journal of Vertebrate Paleontology* 30: 403–415.

Maxwell, E.E. and Druckenmiller, P.S. 2011. A small ichthyosaur from the Clearwater Formation (Alberta, Canada) and a discussion of the taxonomic utility of the pectoral girdle. *Paläontologishe Zeitschrift* 85: 457–463.

Maxwell, E.E. and Kear, B.P. 2010. Postcranial anatomy of *Platypterygius americanus* (Reptilia: Ichthyosauria) from the Cretaceous of Wyoming. *Journal of Vertebrate Paleontology* 30: 1059–1068.

Maxwell, E.E., Zammit, M., and Druckenmiller, P.S. 2012. Morphology and orientation of the ichthyosaurian femur. *Journal of Vertebrate Paleontology* 32: 1207–1211.

McGowan, C. and Motani, R. 2003. *Handbook of Paleoherpetology 8. Ichthyopterygia*. 182 pp. Dr. Friedrich Pfeil, Munich.

Motani, R. 1999. On the evolution and homology of ichthyosaurian forefins. *Journal of Vertebrate Paleontology* 19: 28–41.

Roberts, A.X., Druckenmiller, P.S., Saetre, G.P., and Hurum, J.H. 2014. A new Upper Jurassic ophthalmosaurid ichthyosaur from the Slottsmoya Member, Agardhfjellet Formation of central Spitsbergen. *PLoS ONE* 9: e103152.

Seilacher, A. 1970. Understanding and importance of the Fossil-Lagerstätten. *Neues Jahrbuch Geologie Paläonologiet* 62: 34–39.

Tyborowski, D., Błażejowski, B., and Krystek, M. 2016. Reptile remains from the Upper Jurassic limestones of Owadów-Brzezinki Quarry (Central Poland). *Przegląd Geologiczny* 64 (8): 564–569.

Wahl, W. 2009. Taphonomy of a nose-dive: bone and tooth displacement and mineral accretion in an ichthyosaur skull. *Paludicola* 7: 107–116.

Young, M.T., Brusatte, S.L., Ruta, M., and De Andrade, M.B. 2010. The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. *Zoological Journal of the Linnean Society* 158: 801–859.

Zammit, M., Norris, R., and Kear, B.P. 2010. The Australian Cretaceous ichthyosaur *Platypterygius australis*: a description and review of postcranial remains. *Journal of Vertebrate Paleontology* 30: 1726–1735.

Zverkov, N.G., Arkhangelsky, M.S., and Stenshin, I.M. 2015a. A review of Russian Upper Jurassic ichthyosaurs with an intermedium/humeral contact. Reassessing *Grendelius* McGowan, 1976. *Proceedings of the Zoological Institute RAS* 319: 558–588.

Zverkov, N.G., Arkhangelsky, M.S., Pardo Perez, J.M., and Beznosov, P.A. 2015b. On the Upper Jurassic ichthyosaur remains from the Russian North. *Proceedings of the Zoological Institute RAS* 319: 81–97.