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Late Jurassic teeth of possible cryptoclidid origin from the Owadów-Brzezinki Lagerstätte, Central Poland

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Owadów-Brzezinki is currently one of the most promising Late Jurassic sites in Central Poland, with a wide array of fossil fauna present and exciting new discoveries made every year. It has recently attracted attention due to discovery of large-bodies marine reptile remains, representing ichthyosaurs, turtles, and marine crocodylomorphs, but to this moment one characteristic Mesozoic marine group was not present: plesiosaurs. In this short report we would like to acknowledge presence of the Plesiosauria, with four isolated teeth displaying a set of characteristics typical for this group, with characteristic apicobasal ridging pattern and elongated, conical shape, together with previous findings of plesiosaur material in nearby sites, enabled us to classify the examined teeth as belonging to the family Cryptoclididae, This discovery provides further evidence for the importance of the site as the area of mixing of Boreal and Tethyan faunas, once again expanding the broad spectrum of fossil fauna present in this site, and providing further evidence for presence of Cryptoclididae in Late Jurassic Central Poland.

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Abstract

Owadów-Brzezinki is currently one of the most promising Late Jurassic sites in Central Poland, with a wide array of fossil fauna present and exciting new discoveries made every year. It has recently attracted attention due to discovery of large-bodied marine reptile fossils, representing

ichthyosaurs, turtles, and marine crocodylomorphs, but to this moment one characteristic Mesozoic marine group was not present: plesiosaurs. In this short report we would like to acknowledge presence of the Plesiosauria, with four isolated teeth displaying a set of characteristics typical for this group, with characteristic apicobasal ridging pattern and elongated, conical shape, together with previous findings of plesiosaur material in nearby site, it enabled us to classify the examined teeth as belonging to the family Cryptoclididae, This discovery provides further evidence for the importance of the site as the area of mixing of Boreal and Tethyan faunas, once again expanding the broad spectrum of fossil fauna present in this site, and providing further evidence for presence of Cryptoclididae in Late Jurassic Central Poland.

Keywords: Owadów-Brzezinki, Late Jurassic, marine reptile, teeth, Cryptoclididae

INTRODUCTION

One of the most charismatic groups of Mesozoic marine reptiles are without a doubt plesiosaurs, a characteristic order of fossil predators with compact four-flippered bodies and necks of varying lengths, which can surely be dubbed one of the symbols of the Mesozoic Era. They are known in the fossil record from the Upper Triassic up to ~~the end of~~ the Upper Cretaceous (Williston, 1914). Especially the Late Jurassic is well known from many findings of taxa belonging to this group, and in Europe plesiosaurs had been found mainly in Germany, Switzerland, and the United Kingdom (Bardet et al., 2008; Benson & Bowdler, 2014; Foffa et al., 2018a; Sachs et al., 2019), also with a high prominence in arctic Svalbard (Benson et al., 2013; Roberts et al., 2017). However, this group is rather poorly represented in Poland (Madzia et al., 2021 and references therein), isolated teeth being historically reported from the Aalenian of Wolin (Deecke, 1907), Bathonian of Jastrząb (Rehbinder,1913) and Oxfordian of the Zalas Quarry (Molenda, 1997; Borszcz & Zatoń, 2009; Lomax, 2015; Bardet et al., 2015) and Wapiennik (Groß, 1944; Tyborowski, 2019), vertebrae from the Callovian of Brzostówka (Hirszberg, 1924) and Kimmeridgian of Piekło (Pusch, 1837; Hirszberg, 1924), partial cranium from the Oxfordian of Częstochowa (Maryańska, 1972; Tyborowski, 2019), unspecified remains from the Oxfordian of Inowrocław (Jentzsch, 1884), and various unpublished remains from the (?)Bathonian of Faustianka, Bathonian of Ogrodzieniec, Callovian of Bolęcin, Oxfordian of Mirów, and undetermined Jurassic strata of Młynka (Madzia et al., 2021). Recently, a pectoral vertebra ascribed to Plesiosauria has been described from the Kimmeridgian site of Krzyżanowice, located near the Owadów-Brzezinki site (Tyborowski & Błażejowski, 2019), with possible placement in the family Cryptoclididae (Madzia et al., 2021).

The Owadów-Brzezinki quarry has recently become a well-known and promising fossil-bearing site (Błażejowski et al., 2020), with numerous finds of Late Jurassic vertebrate animals (Tyborowski et al., 2016). The marine reptile group in this faunal assemblage is represented by ophtalmosaurid ichthyosaurs, metriorhynchid crocodylomorphs (Tyborowski et al., 2016), pancryptodiran turtles (Szczygielski et al., 2018), but so far no Plesiosauria an remains have been described from this site. The palaeontological site of the Owadów-Brzezinki *is referred to* as a ~~new~~ “taphonomic window” of Late Jurassic, providing insights on the evolution of life on Earth in the local palaeogeographical and paleoenvironmental context.

In this short report, we ~~acknowledge the presence of Plesiosauria, based on the discovery of~~ four isolated teeth, which display characteristic features for this clade, with possible placement in the family Cryptoclididae.

GEOLOGICAL SETTING

The Owadów-Brzezinki quarry (51°22’27” N, 20°8’11” E) is an active open-pit marl and limestone mine, located in central Poland in the Łódzkie Voivodeship (Opoczno County) in the NW margin of the Holy Cross Mountains (Fig. 1). This paleontological site is one of the most important recent paleontological discoveries from Poland (Kin et al., 2013; Błażejowski et al., 2016). Unusually well preserved fossils of marine and terrestrial organisms of the Late Jurassic (Tithonian) age, many of them new to science, provide a good opportunity for studying the taphonomy of the ecosystem, evolution and migration of taxa, and paleoenvironmental changes (cf. Błażejowski et al., 2016, 2019; Wierzbowski et al., 2016). Especially interesting is the fact that new species, endemic to this site, are constantly discovered, such as the lobster-like decapod crustaceans (Feldmann et al., 2015; Błażejowski et al., 2016) or especially ~~Xiphosura~~ arthropods (Kin & Błażejowski, 2014; Błażejowski, 2015; Błażejowski et al., 2019, 2020), constituting one of the largest accumulation of Jurassic horseshoe crabs discovered so far. Endemic taxa of vertebrates are represented by the ichthyosaur *Cryopterygius kielanae* (Tyborowski, 2016) and the pancryptodiran turtle *Owadowia borsukbialynickae,*(Szczygielski et al., 2018). Other vertebrate taxa are represented by Actinopterygii and Elasmobranchii (Kin et al., 2013; Błażejowski et al., 2015) and marine crocodylomorphs (Błażejowski et al., 2016), with additional shore fauna represented by insects, terrestrial crocodylomorphs, and possibly pterosaurs (Kin et al., 2013). The Owadów-Brzezinki section is located within both the Brzostówka marls of the topmost part of the Pałuki Formation (Fm) and the overlying limestones of the Kcynia Fm (Błażejowski et al., 2016). The uppermost part of the Pałuki Fm and the overlying limestones of the Kcynia Fm, including the Sławno Limestone Member (Mb), "*Corbulomima* limestones", and a fragment of "serpulid" beds, exposed in the section (Kutek 1994; Matyja & Wierzbowski, 2016). The sedimentary pattern observed in the Owadów-Brzezinki section indicates a gradual marine regression revealed by a transition from offshore to coastal and lagoonal settings but its uppermost part was deposited during a short-term marine transgression and the re-appearance of coastal environments (Błażejowski et al., 2016; Wierzbowski et al., 2016).

The uppermost part of the Brzostówka Marl Mb of the Pałuki Fm from the Owadów-Brzezinki quarry (ca. 4 m thick) consists of black, blue-greyish and yellow-bluish marls with the intercalation of thin oyster-bearing and marly limestone beds (Błażejowski et al., 2016; Wierzbowski et al., 2016). The marls yielded abundant marine microfossils, bivalves, ammonites, decapod crustaceans and fish (Błażejowski et al., 2016). The overlying limestones of the Kcynia Fm have been subdivided into four lithological units (cf. Błażejowski et al., 2016).

According to the stratigraphical studies of Kutek (1994) and Matyja & Wierzbowski (2016) based on the ammonite fauna, the lower part of the Owadów-Brzezinki deposits is dated to the regularis horizon (the uppermost part of the Brzostówka Marl Mb of the Pałuki Fm) and zarajskensis horizon (unit I of the Sławno Limestone Mb of the lowermost part of the Kcynia Fm) of the Zarajskensis Subzone of the Scythicus (Panderi) Zone of the Middle Volgian, as well as to the Fittoni Zone from the "Bolonian" zonation of England (Matyja & Wierzbowski 2016). The upper part of the Owadów-Brzezinki section (units III and IV belonging to the "*Corbulomima* limestones" and "serpulid" beds, respectively) has, in turn, been assigned to the both the Gerassimovi Subzone of the Virgatus Zone of the Middle Volgian and the Albani Zone of the "Portlandian" (Matyja & Wierzbowski, 2016). Owadów-Brzezinki has recently attracted much attention not only due to the exquisite quality and quantity of preserved fossils, but also due to paleogeographic significance – this site is proposed to encompass an important area, located on the border of the Boreal/Subboreal and Tethyan realms, where the mixing of temperate and tropical faunal biota occurred (Błażejowski et al., 2016, 2022; Matyja & Wierzbowski, 2016).

MATERIAL, METHODS AND TERMINOLOGY

All teeth have been prepared manually. Specimens coated with ammonium chloride were photographed using a Nicon D5 (55mm f/2.8) digital camera (Fig. 2A-G1). The collected material is housed at the Institute of Palaeobiology, Polish Academy of Sciences in Warsaw (ZPAL R. 11). The tooth description terminology is based on Madzia (2020), with the following terms used: apical – towards the apex of the tooth crown; basal – towards the tooth crown base; mid-crown – approximately centrally between the crown apex and base; mesial – towards the anterior direction in the animal's mouth; distal – inwards the animal's mouth; labial – in the direction of animal's lips; lingual – towards the tongue.

Material: four isolated teeth, labelled ZPAL R.11/OB/T1-T4

Locality and horizon: Owadów-Brzezinki (Central Poland), Tithonian, upper Pałuki Fm and lower part of the Unit 1 of the Kcynia Fm.

Specimens were collected during various fossil excavations. ZPAL R.11/OB/T1, ZPAL R.11/OB/T2 and ZPAL R.11/OB/T3 were collected from dark grey marls belonging to the Pałuki Fm, while the best preserved ZPAL R.11/OB/T4 has been found in the limestone at the base of the Kcynia Fm, within a few centimetres above the boundary with the Pałuki Fm, which consists of chalky limestones representing the Unit I. Due to collection of specimens in different time and strata, connected with exploitation of the quarry, it is most likely that ZPAL R.11/OB/T1–T3 and certainly ZPAL R.11/OB/T4 belonged to different individuals. The specimens are partially encased in rock and the matrix was not removed to not damage specimens which at the time limits the observable characteristics of the specimens. The enamel of the teeth and overall morphology are generally excellently preserved, even though all the specimens are incomplete. While apicobasal ridges are very prominent, with sharp, prominent edges and of regular form, the enamel appears mostly smooth, with no additional striae present. Ridging is visible on the mesial, labial, lingual and distal faces of the preserved fragments. All teeth can be described as conical in overall morphology, with ovaloid cross section. Independently of the color of the host rock, all reported specimens appear to have the same dark brown coloration. This is easily explainable in the case of specimens ZPAL R.11/OB/T1-T3, as they were acquired from similar strata of the same formation, but in the case of specimen ZPAL R.11/OB/T4, coming from the Unit I of the Kcynia Fm, it has more interesting implications, and it appears that the fossilization process led to a similar outcome in both cases –it is explainable by fact that the Unit I has been described by Wierzbowski et al. (2016) as deposited in a standard marine setting, transitional to nearshore environments of the upper units, so the conditions have been similar. This form of preservation is also typical for other teeth from this interval.

Specimen description

ZPAL R. 11/OB/T4: The largest and best-preserved specimen (Fig. 2 A-D) characterized by complete crown, measuring 47 mm in length, with an apicobasal crown height of 34 mm. The base of the teeth can be measured at 11 mm in mesiodistal length, with mid-crown length of 9 mm while apex comes to a straight point, measuring 2 mm in length. The apicobasal length/mesiodistal length ratio (AP/MD) can be measured at 3.09. The overall shape of the crown can be described as conical, elongated with slight lateral compression, leading to ovaloid shape in cross section. It is the only specimen that has a part of the root preserved, which is very helpful in further identification. The root can be described as rather narrow, only slightly wider than the teeth base at the 13 mm in mesiodistal length. Exposed sections consist of lingual, mesial and distal faces, with also excellently visible apical face, in which the slightly ovaloid cross-section is visible. The apex appears strongly recurved. Apicobasal ridges are finer, but still very prominent, in contrast to coarser ridges present in specimen ZPAL R.11/OB/T3, and they appear rather irregular in pattern, with some of the ridges present through all the crown length, and some only in certain segments. In the basal section, the ridging appears to transcend apically at a slight angle, especially in lingual plane, while the apical section is devoid of ridging, which disappears 2 mm from the apex. There is a shallow, but wide groove present at a lingual plane of root.

ZPAL R. 11/OB/T3: This specimen (Fig. 2 E, F), measuring 24 mm in total length, consist of mostly intact crown with part of the apex and base missing. Measuring 10 mm in length at mid-section and 12 mm in mesiodistal length near the base, specimen appears especially robust, with nearly conical cross section. Labial, distal and apical faces with part of lingual, are exposed. It has well-preserved apicobasal ridges, which appear strikingly prominent in this case, with very high density of the structures present in this specimen. This prominence can be attributed to excellent preservation of enamel in this specimen. Those structures, in contrast to smaller teeth, appear to be slightly irregular in form. The mesiodistal curvature can be characterized as moderate.

ZPAL R. 11/OB/T2: Measuring 25 mm in total length, this specimen (Fig. 2 F) has preserved complete crown, with the root missing. Shape can described as strongly conical, with minor mesiodistal compression. This specimen has exposed labial and mesial face. Mid-crown length in mesiodistal plane can be measured at 6 mm, with basal mesiodistal length at 8 mm. The crown AP/MD can be measured at 3.125. Apicobasal ridges appear straight and regularly developed, while mesiodistal curvature is only slight.

ZPAL R. 11/OB/T1: The smallest of the featured specimens and also least preserved (Fig. 2 G), measures 16 mm in total length with mesiodistal mid-crown length of 6 mm. Preserved part of the crown of the tooth can be characterized as conical, slightly ovaloid in cross section. Only the upper portion of the tooth crown is preserved and the apex of the tooth is missing. Nevertheless, even fully preserved, this specimen is supposed to be of smaller size than other examined teeth. The exposed faces include labial, mesial and distal. Teeth curvature in mesiodistal plane can be characterized as slight. Apicobasal ridges appear especially prominent in distal plane and they can be described as less densely packed than in larger specimens.

DISCUSSION

The shape of the discovered teeth (Fig. 3) is generally elongated, slightly recurved with a ovaloid cross-section. Roots are not preserved (ZPAL R.11/OB/T1-T3) or poorly preserved (T4), but the preserved portion of the root of T4 indicates narrow, elongated roots. This characteristic, linked to the relative elongation of the teeth, may suggest adaptations to piscivorous diets. This hypothesis can be supported by paleoenvironmental data, as there appear to numerous taxa of Actinopterygii and Elasmobranchii discovered at the location (Kin et al., 2013, Błażejowski et al., 2015) that could enable this kind of diet. Additionally, the presence of a pointed apex (preserved in ZPAL R.11/OB/T4) provides further evidence for piscivory (Massare, 1987). Mesozoic marine reptilian teeth exhibit a wide array of morphologies (Massare, 1987), which represent their varied ecological niches. Considering the relative proportions of the crowns and visible wear of apices, described teeth can be characterized as belonging to Pierce II/generalist guild by Massare (1987; 1997), which characterize marine reptiles preying on small fish.

There is a variation in plesiosaur teeth, as they can develop as long, longitudinally curved cones or long and robust conical structures, with a smooth or striated crown surface (Foffa et al., 2018b; Madzia & Cau, 2020). One of the defining characteristics of the Plesiosauromorpha, in contrast to Ichthyosauria and Crocodylomorpha, is the presence of very prominent apicobasal ridges often accompanied by shearing carinae (Massare, 1987; Lomax, 2015). Long-necked ~~plesiosaurids~~, which include for example the genera *Plesiosaurus* or *Cryptoclidus* are characterized by their characteristic tooth shape, which can be described as elongated and conical with pointy apices (Massare, 1987). Another very important characteristic noted by Massare is the basal diameter to crown height ratio often greater than 3.5 and never less than 3.

The examined teeth exhibit the following characteristics, which suggest their affiliation with the Plesiosauria. Especially striking characteristic is presence of strong apicobasal ridges, which are present along the length of the entire tooth crown, excluding the apex region and apical fusion of the ridges with the carinae-like ridges forming in mesial and distal regions, which can be felt by hand examination due to increased sharpness in this region. Furthermore, the apicobasal ridges are narrow and sharp, as is typical of the Plesiosauria (Massare, 1987) in contrast to ~~ichthyosaurid~~ ridges, which are characterized by a folded dentine structure called plicidentine, which results in consequent folded structure of the enamel (Maxwell et al., 2011; MacDougall et al., 2014). Ichthyosaur typical pattern is associated with rather wide regular ridges of the enamel, in contrast to the sharp ridges of specimens in this study. The teeth appear slightly ovaloid in cross section, in contrast to the simple conical teeth observed in the endemic ichthyosaur *C. kielanae* (Tyborowski, 2016). The crown AP/MD ratio is 3.125 for ZPAL R. 11/OB/T2 and 3.09 for ZPAL R. 11/OB/T4 which is within the spectrum of ratios described by Massare (1987) as characteristic for plesiosaurian teeth (although it should be noted that due to the basal shape being not conical but ovaloid this value could vary according to the plane of measurement, with lesser ratio in the mesiodistal than in the labiolingual plane).

One of the most peculiar characteristics of many aquatic predator teeth is the presence of apicobasal ridges (McCurry et al., 2019), which develop longitudinally in various forms and are sometimes accompanied by winding striae on the surface of the teeth. These structures have yet to be understood in depth, although it is suggested that they enhance the mechanical properties of teeth in an aquatic setting (Ciampaglio et al., 2005; McCurry et al., 2019). The apicobasal ridges are often used as an identification characteristic (Brown, 1981), which, in addition to overall morphology, enables one to roughly distinguish genera if the only available material are teeth. In the examined samples, the apicobasal ridges appear to form along the almost entire apicobasal length of the tooth crown (except for the very apex) and are present medially, lingually, labially, and distally, encompassing the entire circumference of the teeth. Excluding the ridging, crowns surfaces appear smooth, with no visible striation. It is very characteristic that in the studied specimens, the ridges appear continuously more prominent in larger teeth, and the structure generally also becomes more refined and complicated in larger specimens. This can be ascribed either to: a) tooth allometry, as larger size requires more structural support to handle the stress induced by struggling prey; b) variation exhibited in different stages of the life of an animal, with ridges becoming more prominent in larger, older specimens, or 3) some form of heterodonty, with larger teeth of a single individual exhibiting more prominent ridges. Additionally, a similar relationship can be observed in tooth curvature, which becomes more prominent in larger teeth. However, this may be an effect of preservation, as smaller teeth are less intact, especially compared to ZPAL R.11/OB/T4, and due to this condition it could be very difficult to judge the curvature *in vivo*, with additional possibility of diagenetic processes influencing the shape and pronouncing the curvature in larger specimens.

It would be a very fascinating thought experiment to imagine the size of the full animal, to which specimen ZPAL R.11/OB/T4 belonged, because of its large size. However, Massare (1987) noticed that plesiosaur teeth are proportionally large in relation to skull width, with tooth height to gullet (mouth width) ratio greater than 0.3, so in this case even massive teeth could belong to a mid-sized specimen. It should also be taken into consideration that proportions of the skull size to body ratio may vary considerably in this group of animals, as it encompasses a wide-spectra of head to body ratios (O'Keefe, 2002).

CLASSIFICATION

Superorder: SAUROPTERYGIA Owen, 1859

Order: PLESIOSAURIA de Blainville, 1835

Superfamily: CRYPTOCLIDIA Ketchum and Benson, 2010

Family: CRYPTOCLIDIDAE Williston, 1925

CRYPTOCLIDIDAE indet.

Based on the inferred teeth morphology and comparison with closely related faunal assemblages from the boreal province of the United Kingdom and Svalbard sites, the featured specimens can probably be ascribed to the family Cryptocleididae. It must be stressed that classification based just on fossil teeth can bear a wide margin of error (Benson, et al., 2013), as teeth are very prone to wear due to their extensive usage, and due to large variation in morphology displayed even intraspecifically and even in one specimen (heterodonty, wear, or development pathologies).

One of the closest analogues to the Owadów-Brzezinki site in the context of species identification can be the Late Jurassic Kimmeridge Clay, which also encompasses the Tithonian, belonging to the Boreal province, bearing various marine reptile taxa, also plesiosaurs. It should be noted that the Kimmeridge Clay represents a much larger time interval than the site in this study, nevertheless, it still provides the best analogue in this situation. Although the Solnhofen Plattenkalk provides a good analogue due to its of Tithonian age, no plesiosaur remains have been found in this formation so far, making Kimmeridge Clay the best European analogue in this case. The Kimmeridge Clay and formations of similar age in the United Kingdom exhibit two families of plesiosaurs: the long-necked Cryptoclididae and the large-headed macro predatory Pliosauridae. It should be noted that the teeth of the Pliosauridae are much more common than those of the Cryptoclididae (Foffa et al., 2018a). The preserved root fragment in specimen T4 suggests a rather narrow and elongated root, which, along its with oval cross section and no strong trihedral or sub-trihedral outline which is typical for the genus *Pliosaurus* (Benson et al., 2013), rules out this taxon even despite its presence in coeval strata. Furthermore, the elongated form of the teeth closely corresponds to the Cryptoclididae teeth described by Foffa et al. (2018a) from the Coralline Gap Formation, which underlies the Kimmeridge Clay. Cryptoclididae have also been found in the Slottsmya Member of the Agardhfjellet Formation (Roberts et al., 2017) in Svalbard, which is of Tithonian age, also belonging to the boreal province, therefore providing further evidence for the placement of the specimens in the family Cryptoclididae family. It is postulated that there are at least four taxa of plesiosaurs *sensu stricto* (long-necked) present in the Kimmeridge Clay (Benson and Bowdler, 2014), which are supposed to be included in the family Cryptoclididae, but only *Colymbosaurus* and *Kimmerosaurus* are well described. Only *Kimmerosaurus i*s known from teeth remains, because *Colymbosaurus* fossils consist only of the postcranial skeleton (Benson & Bowdler, 2014). The most recent work by Foffa et al. (2018a) postulates that the Cryptoclididae from the Coralline Group, which sits below the Kimmeridge Clay, are represented by the genera: *Muraenosaurus, Tricleidus, Cryptoclidus*, and *Kimmerosaurus. Cryptoclidus* and *Kimmerosaurus* exhibit incomplete ridging on all of the circumference of the teeth, while the herein examined teeth are characterized by ridging present throughout the length of the labial, distal, mesial and, lingual surfaces, excluding only the apex region, in effect making these genera unlikely candidates. The observed ridging pattern, is much more similar to that seen in *Muraenosaurus* or *Tricleidus*, because those taxa exhibit complex and complete ridging on all faces of their teeth. Another possibility is the genus *Colymbosaurus*. There are two valid species of *Colymbosaurus*: *C. megadeirus* from England (Seeley, 1869; Benson & Bowdler, 2014), *C. svalbardensis* from Svalbard (Persson, 1962; Roberts et al., 2017), and also dubious species *C. sclerodirus* (Bogolubow, 1911, negated by Persson, 1962), and this widespread presence makes this genus a likely candidate, but the problematic aspect here is that both species are only known from the postcranial skeleton, so we are not familiar with their dental morphology. Additionally, a possibility of entirely new genus should not be ruled out.

Recently, Madzia et al. (2021) reviewed several fossils found at the nearby Krzyżanowice site of the Kimmeridgian age, based on previous findings (Tyborowski & Błażejowski, 2019), which included a pectoral vertebral centrum MZ VIII Vr-73 originally described as belonging to a Plesiosauria, placed in the family Elasmosauridae. The authors revised this placement, citing kidney-shaped centrum in anterior/posterior view, the circular shape of the rib facets, wide separation of the sub-central foramina and the presence of a wide neural canal in the specimen as typical characteristics for the representatives of the family Cryptoclididae. This, together with the stratigraphic context, provides one of the strongest arguments for the presence of cryptoclidid plesiosaurs in the Late Jurassic Central Poland, and the findings of teeth at the Owadów-Brzezinki site described here seem to provide further evidence for their presence. However, as mentioned earlier, the description and classification of fossil vertebrate taxa based solely on tooth material can bear a large margin of error, even if this method was previously used in classification of taxa belonging to the order Plesiosauria (Knutsen, 2012; Benson, et al., 2013) and is recognized as a valid method of taxonomic identification (Brown, 1981). Therefore, the finding of vertebral column in adjacent site Tyborowski & Błażejowski, 2019, Madzia et al., 2021) together with the teeth described in this report complement each other and provide strong evidence for presence of Crypoliciddae in Late Jurassic Central Poland.

CONCLUSIONS

In light of this discovery, further exploration is required to find more material, especially fossilized plesiosaur bones, to confirm the possible identification of the plesiosaur from Owadów-Brzezinki. Finding fossil remains of plesiosaurian presents us with a very interesting perspective, as it furthers our understanding of this site; although it has been referred as a Solnhofen-like taphonomic window (Kin et al., 2013), we can conclude that the Owadów-Brzezinki biota contained one group that the German equivalent lacks. Plesiosaurs of possible boreal origin are also interesting from a palaeogeographical point of view as they provide even more evidence for the special placement of the site at the junction between two paleo realms. This discovery bears especially large implications, as it further establishes the presence of a large and diverse assemblage of macro vertebrate fauna in this site, presenting further evidence for mixing of two different paleogeographic faunas in the region, and reveals further potential in aspect of research of evolution and ecology of large predatory marine reptiles from the Owadów-Brzezinki.

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References

Bardet N, Fernández M, Garciáa-Ramos JC, Suberbiola XP, Piñuela L, Ruiz-Omeñaca JI, Vincent P, 2008. A juvenile plesiosaur from the Pliensbachian (Lower Jurassic) of Asturias, Spain. *Journal of Vertebrate Paleontology*, **28**(1):258-263

Bardet N, Fischer V, Machalski M, 2015. Large predatory marine reptiles from the Albian–Cenomanian of Annopol, Poland. *Geological Magazine*, **153**(1):1-16

Benson RBJ, Evans M, Smith AS, Sassoon J, Moore-Faye S, Ketchum HF, Forrest R, 2013. A giant pliosaurid skull from the Late Jurassic of England. *PLoS ONE,* **8**(5): e65989

Benson RB, Bowdler T, 2014. Anatomy of Colymbosaurus megadeirus (Reptilia, Plesiosauria) from the Kimmeridge Clay Formation of the UK, and high diversity among Late Jurassic plesiosauroids. *Journal of Vertebrate Paleontology,* **34**(5):1053-1071

Brown DS, 1981. The English Upper Jurassic Plesiosauria (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. Bulletin, British Museum (Natural History), *Geology Series*, **35**(4):253-347

de Blainville MH, 1835. Description de quelques espéces de reptiles de la Californie, précédée de l'analyse d'un systèeme genéral d'Erpétologie et d'Amphibiologie. *Nouvelles Annales du Muséum d'Histoire Naturelle* **4**:236-296

Błażejowski B, 2015. The oldest species of the genus Limulus from the Late Jurassic of Poland. In: Changing global perspectives on horseshoe crab biology, conservation and management. Switzerland: Springer International Publishing, 3- 14.

Błażejowski B, Lambers P, Gieszcz P, Tyborowski D, 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

Błażejowski B, Gieszcz P, Tyborowski D, 2016. New finds of well-preserved Tithonian (Late Jurassic) fossils from Owadów–Brzezinki Quarry, Central Poland: a review and perspectives. *Volumina Jurassica*, **14**(1):123-132

Błażejowski B, Gieszcz P, Siuda R, Tyborowski, D Wierzbowski A, 2020. Geopark Owadów-Brzezinki – niezwykłe stanowisko paleontologiczne udostępnione geoturystycznie. *Przegląd Geologiczny*, **68**(1):45-49

Błażejowski B, Pszczółkowski A, Grabowski J, Wierzbowski W, Deconinck J-F, Olempska E, Teodorski A, Nawrocki J, 2022. Integrated stratigraphy and clay mineralogy of the

Owadów-Brzezinki section (Lower-Upper Tithonian transition, Central Poland): implications for correlations between the Boreal and the Tethyan domains and palaeoclimate. *Journal of the Geological Society*. Available online 7 December 2022, https://doi.org/10.1144/jgs2022-073

Bogolubow, NN, 1911. Sur l'histoire des Plesiosaures. *Mémoires de la Société impériale des naturalistes de Moscou* **29**:1-412

Borszcz, T, Zatoń M, 2009. Exploring the Jurassic at Zalas Quarry, southern Poland. *Deposits Magazine*. **20**:4-7

Ciampaglio C, Wray G, Corliss B, 2005. A toothy tale of evolution: convergence in tooth morphology among marine Mesozoic–Cenozoic sharks, reptiles, and mammals. The *Sedimentary Record,* **3**:4-8

Deecke W, 1907. *Geologie von Pommern*. Berlin: Gebrüder Borntraeger.

Foffa D, Young MT, Brusatte SL, 2018a. Filling the Corallian gap: New information on Late Jurassic marine reptile faunas from England. *Acta Palaeontologica Polonica*: **63**(2): 287-313

Foffa D, Young MT, Stubbs TL, Dexter, KG, Brusatte SL, 2018b. The long-term ecology and evolution of marine reptiles in a Jurassic seaway. *Nature Ecology & Evolution*, **2**: 1548-1555

Feldmann, RM, Schweitzer, CE, 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

Groß K, 1944. Über den Bau der Zähne von *Pliosaurus ferox* (Sauvage). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen B*, **1944**:227-230

Hirszberg F, 1924. Sur quelques vertèbres des ichtyosauriens et des plesiosauriens du Kimmeridgien et du Portlandien des environs de Tomaszów Rawski (sur la Pilica) [in Polish, with French summary]. **Prace Polskiego Instytutu Geologicznego 1**(2–5): 199–232

Jentzsch A, 1884. Über den Jura der Gegend von Inowrazlaw. Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg **24**:41-45

Ketchum H, Benson RB, 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews*, **85**(2):361-392

Kin A, Gruszczyński M, Martill D, Marshall JD, Błażejowski B, 2013. Palaeoenvironment and taphonomy of a Late Jurassic (late Tithonian) Lagerstätte from central Poland. *Lethaia*, **46**(1):71-81

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

Knutsen EM, 2012. A taxonomic revision of the genus Pliosaurus (Owen, 1841a) Owen, 1841b. *Norwegian Journal of Geology*, **92**:259-276

Kutek, J. 1994. The Scythicus Zone (Middle Volgian) in Poland: its ammonites and biostratigraphic subdivision. *Acta Geologica Polonica*, **44**(1-2):1-34

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

Madzia D, 2020. Dental variability and distinguishability in Mosasaurus lemonnieri (Mosasauridae) from the Campanian and Maastrichtian of Belgium, and implications for taxonomic assessments of mosasaurid dentitions. *Historical Biology*, **32**(10):1340-1354

Madzia D, Cau A, 2020. Estimating the evolutionary rates in mosasauroids and plesiosaurs: discussion of niche occupation in Late Cretaceous seas. *PeerJ*, **8**:e8941

Madzia D, Szczygielski T, Wolniewicz AS, 2021. The giant pliosaurid that wasn't-revising the marine reptiles from the Kimmeridgian, Upper Jurassic, of Krzyżanowice, Poland. *Acta Palaeontologica Polonica*, **66**(1):99–129

Maryańska T, 1972. Aberrant pliosaurs from the Oxfordian of Poland. *Prace Muzeum Ziemi*, **20**:201–205

Massare JA, 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology*, **7**:121-137

Massare JA, 1997. Part VI: Faunas, Behavior, and Evolution. In: Callaway JM, Nicholls EL, eds. *Ancient Marine Reptiles*. *S*an Diego, New York, Boston, London, Sydney, Tokyo, Toronto: Academic Press, 401-421.

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

Maxwell EE, Caldwell, MW, Lamoureux DO, 2011 The structure and phylogenetic distribution of amniote plicidentine. *Journal of Vertebrate Paleontology*, **31**(3):553-561

MacDougall MJ, LeBlanc ARH, Reisz RR, 2014. Plicidentin in the Early Permian parareptile Colobomycter pholeter, and its phylogenetic and functional significance among coeval members of the clade. *PLOS One*, **9**(5):e96559.

McCurry MR, Evans AR, Fitzgerald EM, McHenry CR, Bevitt J, Pyenson ND, 2019. The repeated evolution of dental apicobasal ridges in aquatic-feeding mammals and reptiles. *Biological Journal of the Linnean Society*, **127**(2): 245-259

Molenda R, 1997. *Zalas, Bear Mountain—History of Mining, Geology, Ecology*. Kraków: Studio Graficzne Szelerewicz i S-ka.

O'Keefe FR, 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). *Paleobiology*, **28**(1):101-112

Owen R, 1859. *Paleontology*. In: *The Encyclopaedia Britannica, or dictionary of arts, sciences, and general literature. Eighth edition. Vol. XVII*. Edinburgh: Adam and Charles Black

Persson PO, 1962. Plesiosaurians from Spitsbergen. *Norsk Polarinstitutt*, **1962**: 62–68

Pusch GG, 1837. *Polens Paläontologie oder Abbildung und Beschreibung der vorzüglichsten und der noch unbeschriebenen Petrefakten aus den Gebirgsformationen in Polen, Volhynien und den Karpathen nebst einigen allgemeinen Beiträgen zur Petrefaktenkunde und einem Versuch zu*. Stuttgart: E. Schweizerbart,

Rehbinder B, 1913. Die mitteljurassischen eisenerzführenden Tone längs dem südwestlichen Rande des Krakau-Wieluner Zuges in Polen. *Zeitschrift der Deutschen Geologischen Gesellschaft* **65**:181–349.

Roberts AJ, Druckenmiller PS, Delsett LL, Hurum, JH, 2017. Osteology and relationships of Colymbosaurus Seeley, 1874, based on new material of C. svalbardensis from the Slottsmøya Member, Agardhfjellet Formation of central Spitsbergen. *Journal of Vertebrate Paleontology*, **37**(1):e1278381

Sachs S, Klug C, Kear BP, 2019. Rare evidence of a giant pliosaurid-like plesiosaur from the Middle Jurassic (lower Bajocian) of Switzerland. *Swiss Journal of Palaeontology*, **138(**2):337-342

Seeley HG, 1869. *Index to the Fossil Remains of Aves, Ornithosauria, and Reptilia, from the Secondary System of Strata, Arranged in the Woodwardian Museum of the University of Cambridge*. Cambridge: Deighton, Bell, and Co.

Szczygielski T, Tyborowski D, Błażejowski B, 2018. A new pancryptodiran turtle from the Late Jurassic of Poland and palaeobiology of early marine turtles. *Geological Journal*, **53**(3):1215-1226

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

Tyborowski D, 2019. Jurassic pliosaur remains in the collections of the Museum of Częstochowa [in Polish, with English abstract]. *Rocznik Muzeum Częstochowskiego*, **18**:73–76

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

Tyborowski D, Błażejowski B, 2019. New marine reptile fossils from the Late Jurassic of Poland with implications for vertebrate faunas palaeobiogeography. *Proceedings of the Geologists' Association*, **130**(6): 741-751

Wierzbowski H, Dubicka Z, Rychliński T, Durska E, Olempska E, Błażejowski B, 2016. Depositional environment of the Owadów-Brzezinki conservation Lagerstätte (uppermost Jurassic, central Poland): evidence from microfacies analysis, microfossils and geochemical proxies. *Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen*, **282**:81-108

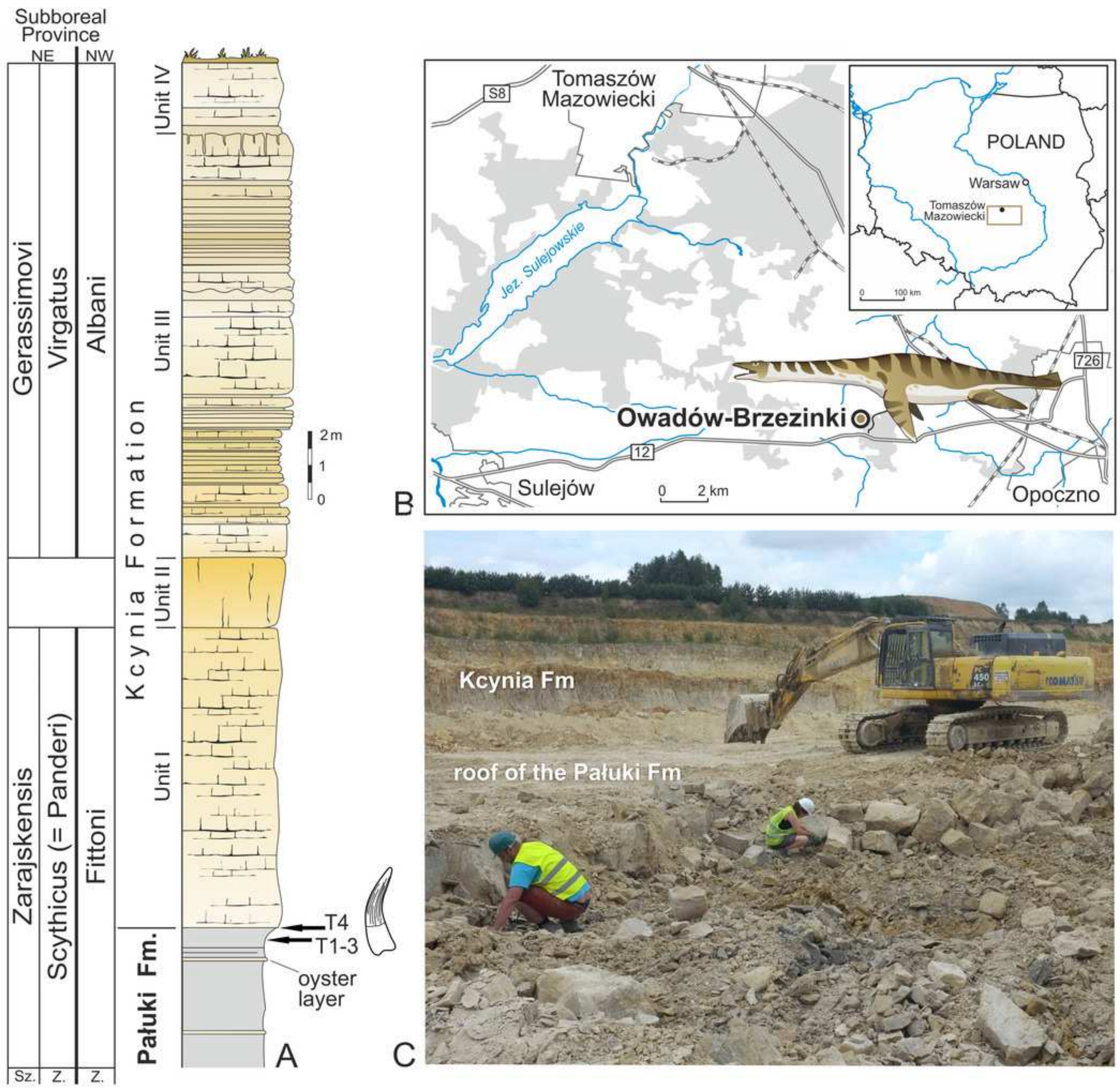
Williston SW, 1914. *Water reptiles of the past and present*. Chicago: University of Chicago Press.

Williston SW, 1925. *The osteology of reptiles*. Cambridge: Harvard University Press.

Figure 1

Map of the site and lithological succession in the study area with tooth bearing interval highlighted.

(A) Lithological succession and biostratigraphy of the Owadów-Brzezinki Quarry. The topmost part of the Pałuki Fm and overlying limestones of the Kcynia Fm (Units I-IV). (B) Road map with the location of the Owadów-Brzezinki site and its proximity to Tomaszów Mazowiecki in Central Poland. (C) General view of the Owadów-Brzezinki section (paleontological field work in the uppermost part of the Pałuki Fm). Abbreviations: Fm, Formation; Sz., Subzone; Z., Zone.



Subboreal Province
NE
NW
Gerassimovi
Virgatus
Albani
Zarajskensis
Scythicus (= Panderi)
Fittoni
Sz.
Z.
Z.
Kcynia Formation
Pałuki Fm.
Unit IV
Unit III
Unit II
Unit I
2 m
1
0
T4
T1-3
oyster layer
A
Tomaszów Mazowiecki
S8
Jez. Sulejowskie
POLAND
Warsaw
Tomaszów Mazowiecki
0
100 km
726
Owadów-Brzezinki
12
Sulejów
0
2 km
Opoczno
B
Kcynia Fm
roof of the Pałuki Fm
C

Figure 2

Teeth specimens featured in this study.

(A-D) ZPAL R.11/OB/T4, A. Overview; (B) distal face and apicobasal ridges in close view (B1). (C) Labial face and apicobasal ridges in close view (C1). (D) Mesial face and close view of apical (D1), mid-crown (D2) and basal (D3) teeth sections. (E) ZPAL R.11/OB/T3 in distal view with prominent, sharp apicobasal ridges highlighted (E1). (F) ZPAL R.11/OB/T2 in labial view with close view of teeth base (F1). (G) ZPAL R.11/OB/T1 in lingual view with close view of mid crown apicobasal ridges (G1).

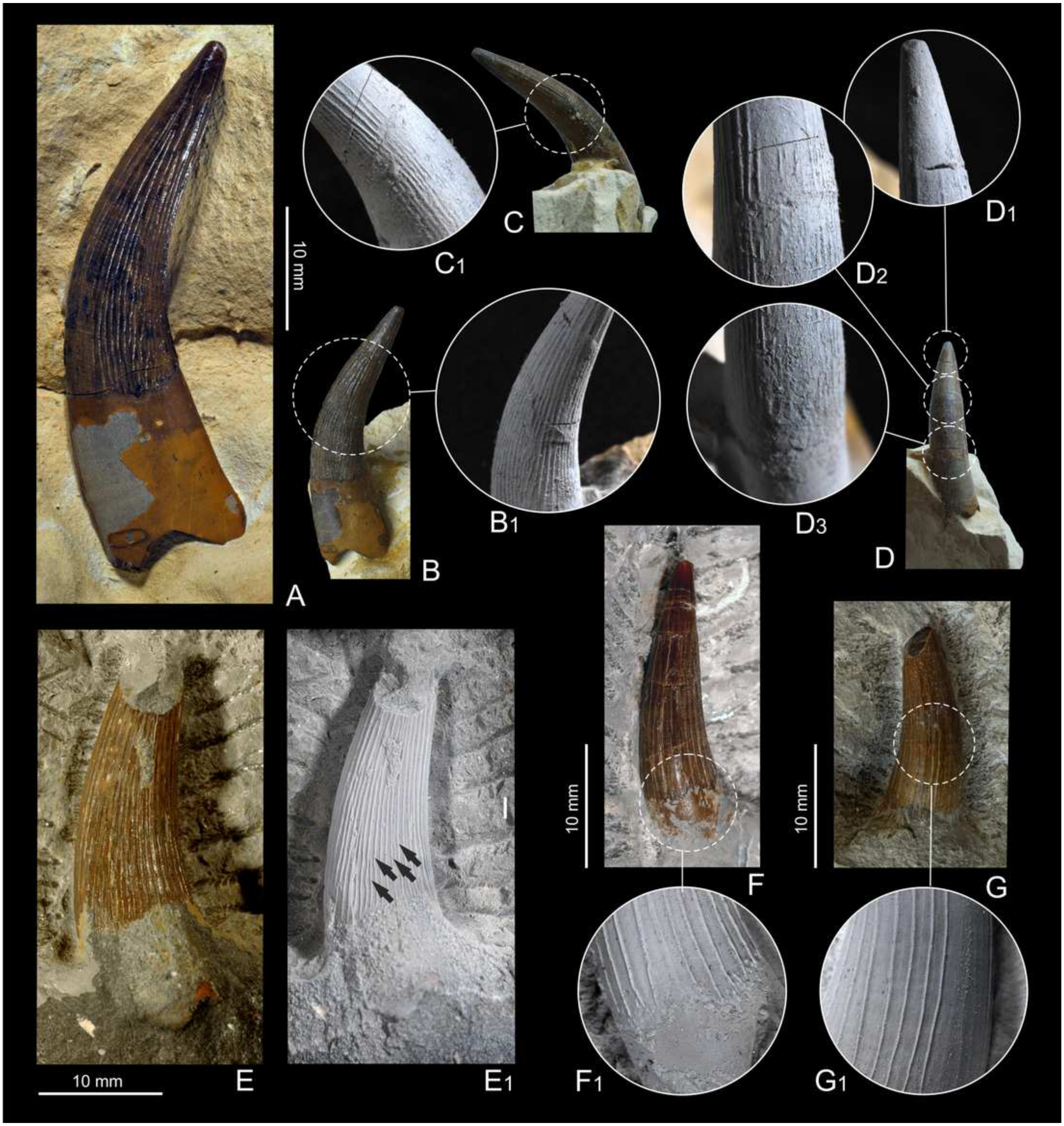

A
B
B1
C
C1
D
D1
D2
D3
E
E1
F
F1
G
G1
10 mm
10 mm
10 mm
10 mm

Figure 3

Specimen teeth sketch figure showing general morphologies, with each face highlighted.

(A) ZPAL R.11/OB/T1, lingual view. (B) ZPAL R.11/OB/T2, labial view. (C) ZPAL R.11/OB/T3, distal view. (D) ZPAL R.11/OB/T4, lingual view (E) ZPAL R.11/OB/T4, apical view. Abbreviations: lg -lingual; lb- labial; ds -distal; ap – apical.