Late Jurassic teeth of possible cryptoclidid origin from the Owadów-Brzezinki Lagerstätte, Central Poland (#80921)

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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 Upper Jurassic sites in Central Poland, with a wide array of fossil fauna present, both vertebrate and invertebrate. It has recently attracted attention due to discoveries of large-bodied marine reptiles fossils representing ichthyosaurs, turtles, and marine crocodylomorphs, but until now one characteristic Mesozoic marine group was not present: plesiosaurs. In this short report we would like to report the presence of the plesiosaur, with four isolated teeth displaying a set of characteristics typical for this group, with distinguishing apicobasal ridging pattern and elongated, conical shape. Based on Principal Coordinates Analysis (PCoA), of the largest and most complete specimen ZPAL R.11/OB/T4 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 between Boreal and Tethyan faunas, once again expanding the broad spectre of fossil taxa present in this site, and together with previous findings of plesiosaur material in a nearby region, providing evidence for presence of Cryptoclididae in Jurassic of Central Poland.

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Abstract

Owadów-Brzezinki is currently one of the most promising Upper Jurassic sites in Central Poland, with a wide array of fossil fauna present, both vertebrate and invertebrate. It has recently attracted attention due to discoveries of large-bodied marine reptiles fossils representing ichthyosaurs, turtles, and marine crocodylomorphs, but until now one characteristic Mesozoic marine group was not present: plesiosaurs. In this short report we would like to report the presence of the plesiosaur, with four isolated teeth displaying a set of characteristics typical for this group, with distinguishing apicobasal ridging pattern and elongated, conical shape. Based on Principal Coordinates Analysis (PCoA), of the largest and most complete specimen ZPAL R.11/OB/T4 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 between Boreal and Tethyan faunas, once again expanding the broad spectre of fossil taxa present in this site, and together with previous findings of plesiosaur material in a nearby region, providing evidence for presence of Cryptoclididae in Jurassic of 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, an iconic order of predators with compact four-flippered bodies and necks of varying lengths. They are known in the fossil record from the Upper Triassic up ~~of~~ the Upper Cretaceous (Williston, 1914; Benson et al., 2013b; Wintrich et al., 2017). Especially the Upper Jurassic is well known from many findings of taxa belonging to this group, and in Jurassic of Europe plesiosaurs had been found mainly in Germany, France, Switzerland, and the United Kingdom (O'Keefe, 2004; Vincent et al., 2007; Benson & Bowdler, 2014; Foffa et al., 2018a; Sachs et al., 2019), also with a high prominence in the arctic Svalbard (Knutsen et al., 2012; Benson et al., 2013a; Roberts et al., 2017; Roberts et al., 2020). However, this group is rather poorly represented in Poland

(Madzia et al., 2021 and references therein), historical accounts of isolated teeth from ~~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), a 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 plesiosaurian an remains have been described from this site. The palaeontological site of the Owadów-Brzezinki ~~is~~ referred to as a ~~new Upper Jurassic~~ "taphonomic window" providing insights on the distribution of Late Jurassic vertebrates of Central European archipelago.

In this short article we report the presence of Plesiosauria, based on the discovery of four isolated plesiosaur 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 palaeontological site is one of the most important recent palaeontological discoveries from Poland (Kin et al., 2013; Błażejowski et al., 2016). Unusually well-preserved fossils of marine and terrestrial organisms of Late Jurassic (Tithonian) age, many of them new to science, provide a good opportunity to study 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) and xiphosuran arthropods (Kin & Błażejowski, 2014; Błażejowski, 2015; Błażejowski et al., 2019, 2020), constituting one of the largest accumulation of Jurassic horseshoe crabs discovered so far. Most prominent taxa of vertebrates discovered so far are represented by the ichthyosaur *Cryopterygius kielanae* (Tyborowski, 2016, which has been also placed in *Undorosaurus* by Zverkov & Effimov, 2019, and Zverkov & Jacobs, 2021) 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 horizon 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 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 its palaeogeographic 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).

METHODS AND TERMINOLOGY

All teeth have been prepared manually. Specimens were coated with sublimed ammonium chloride to accentuate the fine structure of the enamel, and then photographed using a Nikon D5 (55mm f/2.8) digital camera (Fig. 2 A-G1). The collected material is housed at the Institute of Palaobiology, Polish Academy of Sciences in Warsaw (ZPAL R. 11). The tooth description terminology is based on marine reptiles teeth studies (Zverkov et al., 2018; 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 of the animal's mouth; distal – inwards into the animal's mouth; labial – towards the animal's lips; lingual – towards the tongue.

Principal Coordinates Analysis (PCoA) was used to explore the morphospace occupied by the specimen ZPAL R.11/OB/T4. This sample was the largest and with the most complete crown, hence it was deemed the only specimen viable for such an analysis. The PCoA enables to explore multiple morphological characteristics of the teeth at once. This feature makes it one of the most optimal tools for systematic placement based on dental material alone, provided that the data scope is sufficient. In this study, we used the modified data matrix of Madzia et al. (2021), which was originally published by Foffa et al. (2018b). However, we included the group of Ichthyosauria that were missing from the modified matrix, but present in the original one, as it is found in the fossil strata of the analyzed site (Tyborowski, 2016). The PCoA was conducted using PAST 4.10 software (Hammer et al, 2001). The continuous and discrete characters, which are used in this data matrix, can be found in the supplement of Foffa et al. (2018b). The continuous characters used in this analysis have been ~~Z-transformed. Consequently,~~ Gower similarity index (Gower, 1971) was employed, since it is well suited for data with both continuous and discrete variables, as noted by Madzia et al. (2021). The modified dataset with included ZPAL R.11/OB/T4 data is available in supplementary file (SM_OW), and raw PCoA results, containing eigenvalues and diagrams, can be found in Supplement 2.

SYSTEMATIC PALAEONTOLOGY

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

PLESIOSAUROIDEA Gray, 1825

CRYPTOCLIDIA Ketchum & Benson, 2010

CRYPTOCLIDIDAE Williston, 1925

CRYPTOCLIDIDAE indet.

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 at different times 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 the matrix, which was not removed to avoid damaging 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 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 oval-to-subcircular 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) is characterized by complete crown measuring 47 mm in total length (including part of preserved root), with an apicobasal crown height of 28.6 mm. The base of the tooth can be measured at 10.23 mm in mesiodistal length (ML), 8 mm in labiolingual length (LL) with mid-crown length of 7 mm. The apex comes to a straight point, measuring 2 mm in length. The apicobasal length/basal diameter (ML+LL/2) - crown ratio (CR) can be measured at 3.13. 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. This specimen is characterized by a very sharp enamel boundary between tooth crown and root. The root can be described as proportionally narrow in diameter when compared to crown, only slightly wider than the teeth base the 13 mm in mesiodistal length. Exposed sections consist of lingual, mesial and distal faces, with ~~an also excellently~~ visible apical face, in which the slightly ovaloid cross-section is visible. The apex appears strongly recurved, and the overall curvature of the tooth is 1.21 (convex/concave surface ratio). 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, which appears rather regular in shape and we consider it to be integral characteristic of root. The ridging appears more prominent on the lingual rather than labial face.

ZPAL R. 11/OB/T3: This specimen (Fig. 2 E), measuring 24 mm in total length, consists 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 sub-circular 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 in comparison to ZPAL R. 11/OB/T4.

ZPAL R. 11/OB/T2: Measuring 23 mm in total length, this specimen (Fig. 2 F) has preserved almost complete crown, with the root missing. ~~Shape~~ can described as strongly conical, with minor labiolingual compression. This specimen has exposed labial and mesial face. Mid-crown length in mesiodistal plane can be measured at 6 mm, with ML at 8 mm and LL at 6.3 mm. The ~~crown~~ CR ~~can be measured at~~ 3.21. Apicobasal ridges appear straight and regularly developed, while mesiodistal curvature is only slight. The crown appears to possess slightly worn apex.

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. The preserved part of the crown 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 if fully preserved, this specimen would likely to be of smaller size than the previously described teeth. The missing apical section in this case can likely be result sign of tooth wear. 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 (e.g. ZPAL R. 11/OB/T3).

Principal Coordinates Analysis

The data matrix provided by Foffa et al. (2018b) is an excellent tool for comparing the tooth morphologies of Jurassic marine reptiles, due to possessing large dataset of various morphological characters of different taxa. Furthermore, this dataset can be easily supplemented with additional tooth specimens for comparison, and it can be utilized to perform PCoA. Hence, such method can be used to assess the possible taxonomic relationship of the examined teeth based on the closest morphological analogues. The morphospaces occupied by different taxonomic groups of marine reptiles are often distinctive, allowing ~~a~~ rough ~~classification~~ of the teeth ~~specimen~~. We have been able to score 19 out of possible original 20 characters used in study by Madzia et al. (2021) for specimen ZPAL R. 11/OB/T4. In the first analysis, we compared the specimen ZPAL R. 11/OB/T4 against all the major Jurassic toothed marine reptile groups provided by Foffa et al, (2018b) as the spectrum of fossil vertebrates teeth at the Owadów-Brzezinki site is wide and we cannot exclude other possible groups, and in the second analysis against sole Plesiosauria.

It can be observed on the morphospace occupation ~~graph~~ (Fig. 3 A) that crocodylomorphs are mainly grouped on the negative side of the y axis and on the negative side of the x axis, while all Plesiosauria are grouped on the positive side of the x axis. Ichthyosaurs occupy the morphospace near the central part. Specimen ZPAL R. 11/OB/T4 does not fit exactly into any morphospace, but it is closest in relation to Plesiosauridae. It should be noted that at this moment dataset is rather scant for Plesiosauroidea, characterized by few specimens with often highly incomplete scores, especially when compared to pliosaurids (Foffa et al., 2018b supplement). This may result in a smaller morphospace occupied in this analysis, in contrast to the real morphological diversity of the group.

The next graph (Fig. 3 B) depicts the occupation of the morphospace of ZPAL R. 11/OB/T4 in relation to other plesiosaurian taxa. Comparison with inferred more closely related taxa (based on observed morphology) enables a more detailed localization of the specimen in morphospace. The negative side of the x axis is occupied by Pliosauridae, while the positive side displays the morphospace inhabited by Plesiosauroidea. As can be seen in this analysis, ZPAL R. The 11/OB/T4 specimen under investigation is localized in Plesiosauroidea morphospace with a very similar position to cryptoclidid *Tricleidus seeleyi.* Meanwhile, other taxa are placed much further away, with the other closest taxa of established taxonomic position being also cryptoclidid: *Cryptoclidus eurymerus*. Based on this location, it can be presumed that the examined teeth belong to cryptoclidid plesiosaur.

It should be noted that ridging patterns of the examined teeth are indeed very similar to *Tricleidus* (Foffa et al., 2018a, fig. 3 D1-4), but *Tricleidus seeleyi* is characterized by circular, more conical shape of the teeth, which differ in parameters of the labiolingual compression and curvature (Foffa et al., 2018b supplement) from the examined specimens. However, we should not exclude that this compression is an diagenetic effect and that we are indeed dealing with *Tricleidus* teeth, perhaps belonging to other species than *T. seeleyi,* with a more sturdy and curved dentition. This would extend the range of this taxon beyond Callovian, as at this moment it is known only from specimen NHMUK R3539 (Andrews, 1910). Also, the sample size for Foffa et al. (2018b) is one tooth specimen, so this aspect should also be taken into consideration with respect to possible anisodonty. Still, the most probable scenario is that the animal from this study exhibited a similar dental morphology in some aspects due to similar feeding strategy, and we are dealing with other taxa. Dental and cranial characteristics of aquatic tetrapods are strongly convergent in shape (Fisher et al., 2017) when a similar niche is exploited, and with this in consideration, using such a tool for establishing taxonomic position also bears a margin of error.

Palaeobiogeographic context and morphological characteristics in comparison to other cryptolclidid dental material

Cryploclididae are a family of plesiosaurs mostly recognized from Middle to Late Jurassic (Roberts et al., 2020), well represented in the fossil record, also from England and Svalbard (Knutsen et al., 2012; Benson & Bowdler, 2014; Foffa et al., 2018a; Roberts et al., 2017; Roberts et al., 2020). They constituted one of the dominant groups of plesiosaurs in Middle and Late Jurassic of Northern Hemisphere until decline at the Jurassic-Cretaceous Transition (Benson & Druckenmiller; 2013). As such, from palaeobiogeographical context this family should also be likely to inhibit Owadów-Brzezinki, as large marine reptiles of Mesozoic margin of Holy Cross Mts are considered to have been mainly of Boreal realm provenance (Tyborowski, 2016). Therefore one of the closest analogues to the Owadów-Brzezinki site in the context of plesiosaur species identification can be the Upper Jurassic Kimmeridge Clay. This site also encompasses the Tithonian, belonging to the Boreal province, and bears various marine reptile taxa (Benson & Bowdler, 2014; Foffa et al., 2018a), often those of plesiosaurs. It should be noted that the Kimmeridge Clay represents a much larger time interval than the site in this study. 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

(Foffa et al., 2018a). The elongated form of the teeth examined here closely corresponds to the Cryptoclididae teeth from the Coralline Gap Formation (which underlies the Kimmeridge Clay) that were described by Foffa et al., (2018a). Cryptoclididae have also been found in the Slottsmøya Member of the Agardhfjellet Formation (Roberts et al., 2017) in Svalbard, which is of Tithonian-Berrasian age, also belonging to the Boreal province.

It is postulated that there are at least four taxa of plesiosaurs *sensu stricto* (long-necked) present in the Kimmeridge Clay (Benson & Bowdler, 2014) that ought to be included in the family Cryptoclididae. The latest work by Foffa et al. (2018a) postulates that the Cryptoclididae from the Coralline Group, which sits below the Kimmeridge Clay, are represented by the *Muraenosaurus, Tricleidus, Cryptoclidus* and *Kimmerosaurus*. *Cryptoclidus* exhibits reduced ridging and *Kimmerosaurus* is characterized by almost absent reduced ridging of the teeth, while the herein examined teeth are characterized by ridging present almost throughout the whole length of the labial, distal, mesial and, lingual surfaces, excluding only the apex region. 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. *Mureanosaurus* dentition is much more elongated and conical (e.g. Foffa et al., 2018a; Foffa et al., 2018b supplement) than that of studied specimens. *Tricleidus* apicobasal ridging pattern is very similar (Foffa et al., 2018a), with apical portion of mesial face characterized by reduction of ridging, and other surfaces of crown distinguished by prominent ridging. Nevertheless, as was previously noted, the teeth of *Tricleidus* are circular in cross section, which differs them from the labiolingually compressed teeth from this study. *Tricleidus* teeth are also much more elongated (Foffa et al., 2018b supplement), with higher CR. CR however can also vary in same specimen, as plesiosaurs exhibit anisodonty (eg. Sassoon et al., 2015; Kear et al., 2017).

There are also members of the Cryptoclididae family present from Spitzbergen represented by dental material - *Spitrasaurus larseni* (Knutsen et al., 2012) and *Ophtalmothule cryostea* (Roberts et al., 2020). *S. larseni* dental material is represented by very gracile crowns, D-shaped in cross-section (Kutsen et al., 2012), quite dissimilar in an overall morphology to the specimens presented here. *O. cryostea* dental material exhibits more similar proportions to the studied teeth (Roberts et al., 2020, fig. 11), but the ridging pattern is comparatively fine and more prominent on labial surface, while the examined specimens tend to show more pronounced ridging on lingual faces instead.

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; Knutsen et al., 2012; Roberts et al., 2017), and also dubious species *C. sclerodirus* (Bogolubow, 1911, negated by Persson, 1962).Such this widespread presence makes this genus a likely candidate, however, both species are only mainly known from the postcranial skeleton, only with reported lower mandible fragment of C. *svalbardensis* (Roberts et al., 2017). and the lack of information on their dental morphology poses a problem.

Summary

Based on the results of PCoA, inferred teeth morphology, and to a lesser degree comparison with closely related faunal assemblages from the Boreal province of the United Kingdom and Svalbard sites, the featured specimens can be ascribed to the animal from Cryptoclididae family. It must be stressed that classification based just on fossil teeth can bear a wide margin of error

(Benson et al., 2013a), 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). The most likely candidate at this moment seems to be *Tricleidus*, because the morphospace occupied by ZPAL R. 11/OB/T4 is very closely localized to tooth specimen from NHMUK R3539, although there are also very notable differences in morphology between these two dentitions. Other option includes *Colymbosaurus* of which dental material has yet to be discovered. Additionally, the possibility of an entirely new genus should also not be ruled out. However, more fossil material will be required for a more certain diagnosis than just establishing material as belonging to cryptoclidid.

DISCUSSION

Mesozoic marine reptilian teeth exhibit a wide array of morphologies (Massare, 1987), which represent their varied ecological niches. The shape of the discovered teeth (Fig. 4) is generally elongated, slightly recurved with a sub-circular cross-section. Roots are not preserved (ZPAL R.11/OB/T1-T3) or poorly preserved (ZPAL R.11/OB/T4), but the preserved portion of the root of ZPAL R.11/OB/T4 indicates narrow, elongated roots, barely wider than a crown. This characteristic, linked to the relative elongation of the teeth, may suggest adaptations to piscivorous diet (Massare, 1987, 1997). 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). However, the interesting aspect of the teeth should be noted, as the teeth exhibit relative lateral compression, with ML/LL ratio of 0.78 for ZPAL R.11/OB/T4 and 0.79 for ZPAL R.11/OB/T2. This ratio is rather unusual for plesiosaur, which are more often characterized by circular cross-section of teeth (Foffa et al., 2018b supplement), which are more typical characteristic of obligatory piscivores (Massare, 1987). 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. The morphospace analysis by Fisher et al., (2022) concludes that generally predators possessing teeth of complicated structure, such as richly ornamented teeth of these specimens, are small prey specialists, because predators of large prey have been found to possess generally teeth simple in morphology (the exception to this rule appear to be Pliosauridae).

There is a variance 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 Plesiosauria, in contrast to Ichthyosauria and Crocodylomorpha, is the presence of very prominent apicobasal ridges which in some cases also accompanied by shearing carinae (Massare, 1987; Lomax, 2015). Long-necked Plesiosauroidea, are characterized by their elongated and conical teeth with pointy apices (Massare, 1987; Massare, 1997). 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. An especially striking characteristic is the 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. Furthermore, the apicobasal ridges are narrow and sharp, as is typical of the Plesiosauria (Massare, 1987) in contrast to ichthyosaur ridges, which are characterized by a folded dentine structure called plicidentine, which results in a 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 from study appear sub-circular in cross section, in contrast to the simple conical teeth observed in the endemic ichthyosaur *C. kielanae* (Tyborowski, 2016). The crown CR ratio is 3.21 for ZPAL R. 11/OB/T2 and 3.33 for ZPAL R. 11/OB/T4 which is within the spectrum of ratios described by Massare (1987) as characteristic for plesiosaurian teeth.

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 winding and complicated in larger specimens. This can be possibly ascribed either to: 1) tooth allometry, as larger size requires more structural support to handle the stress induced by struggling prey (McCurry et al., 2019); 2) 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 from this study. 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.

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., 2013a) and is recognized as a valid practice of taxonomic identification (Brown, 1981). Application of multivariate methods, including PCoA, enables us to increase the precision of such classifications. Still, without utilizing the skeletal material, establishing taxonomic position can be largely imperfect. 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 Cryptoclididae family. Therefore, the finding of vertebral column in adjacent site (Tyborowski & Błażejowski, 2019, Madzia et al., 2021) along with the teeth described in this report complement each other and provide evidence for strong presence of Cryptoclididae in Late Jurassic Central Poland.

CONCLUSIONS

The results of the principal coordinate analysis (PCoA), together with palaeobiogeographic and morphological data, provide strong evidence for the described teeth as belonging to plesiosaur placed in the Cryptoclididae family. 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 palaeo 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, 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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Figure captions

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.

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).

Figure 3 ZPAL R.11/OB/T4 (black star) morphospace occupation among marine reptiles of Jurassic, visualization of results of PCoA, segregation along principal coordinates 1 and 2. Based on modified dataset from Madzia et al., (2021) with included Ichthyosauria, originally from Foffa et al., 2018b. (A) Compared to all major groups from Foffa et al., 2018b study. (B) Compared against Plesiosauria. Animal silhouettes from phylopic.org: Plesiosauroidea and Geosaurinae (T. Michael Keesey; CC BY 3.0) Metriorhynchinae (Gareth Monger; CC BY 3.0). Animal silhouettes of Pliosauridae and Metriorhynchidae based on Dmitry Bogdanov (CC BY 3.0). Teleosauroidea modified from Young et al. (2016).

Figure 4 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.

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.

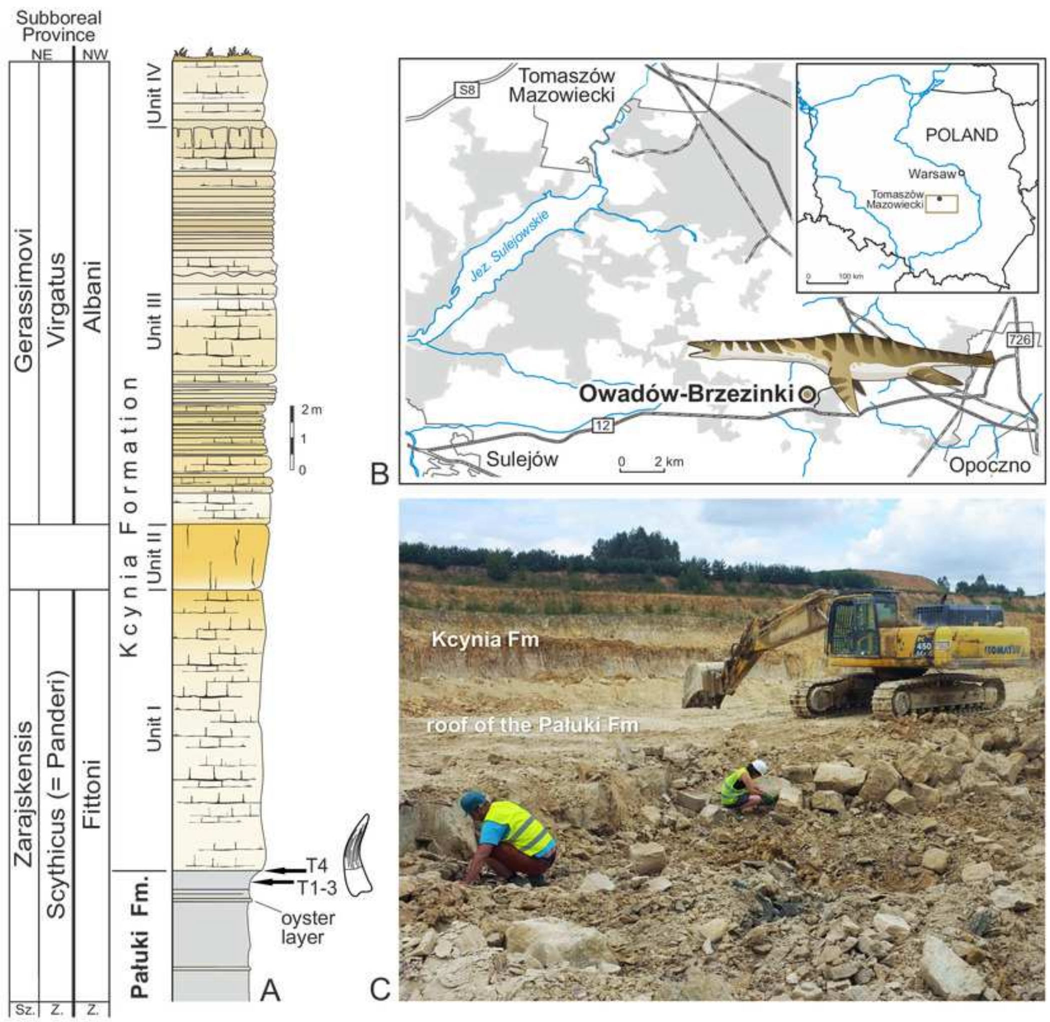

Subboreal Province
NE
NW
Gerassimovi
Virgatus
Albani
Zarajskensis
Scythicus (= Panderi)
Fittoni
Sz.
Z.
Z.
Kcynia Formation
Unit IV
Unit III
Unit II
Unit I
Pałuki Fm.
T4
T1-3
oyster layer
2 m
1
0
A
Tomaszów Mazowiecki
S8
Jez. Sulejowskie
POLAND
Warsaw
Owadów-Brzezinki
12
726
Sulejów
0 2 km
Opoczno
B
Kcynia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

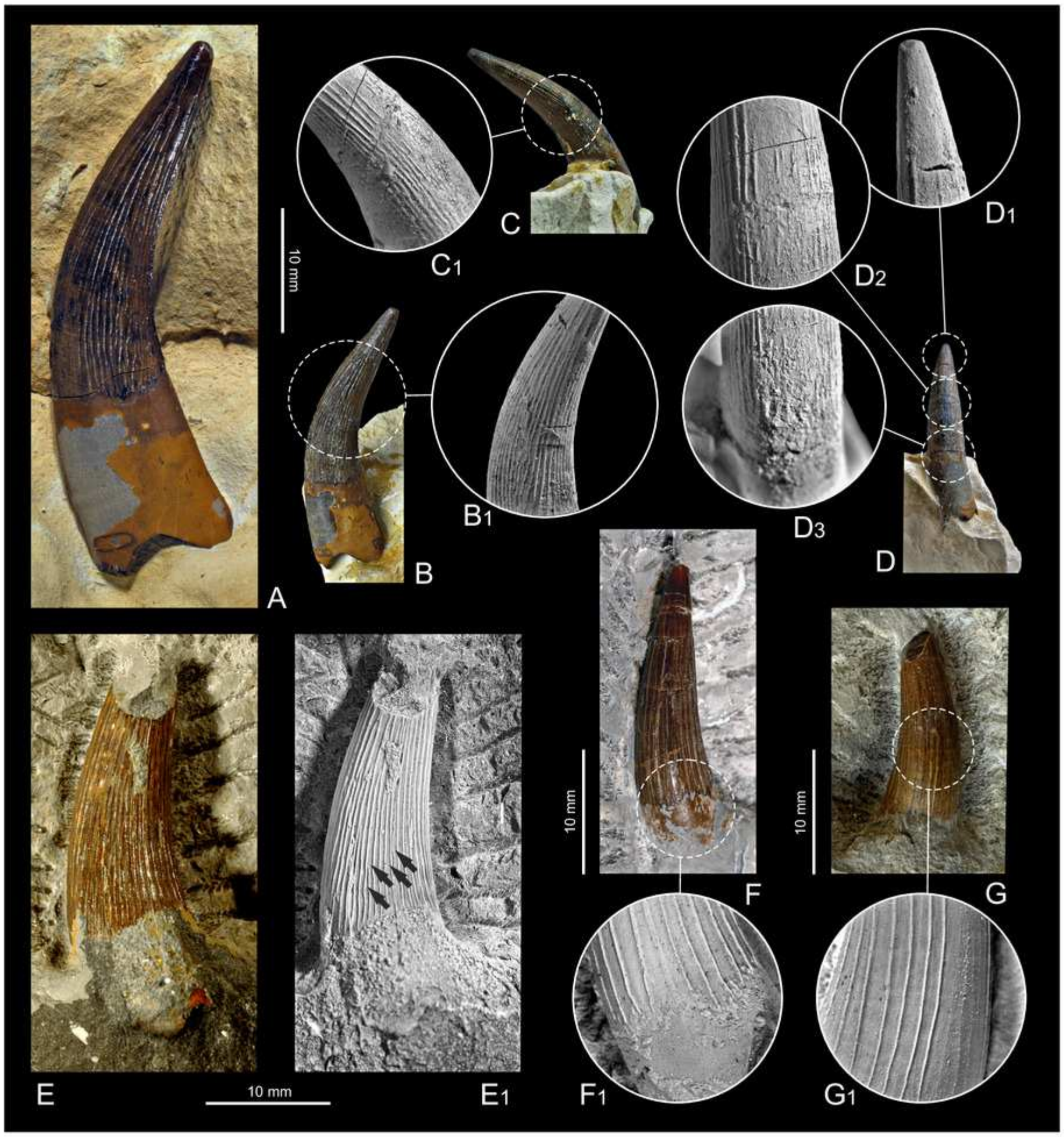

A
B
B1
C
C1
D
D1
D2
D3
E
E1
F
F1
G
G1
10 mm
10 mm
10 mm
10 mm

Figure 3

ZPAL R.11/OB/T4 (black star) morphospace occupation among marine reptiles of Jurassic, visualization of results of PCoA, segregation along principal coordinates 1 and 2.

Based on modified dataset from Madzia et al. (2021) with included Ichthyosauria, originally from Foffa et al. (2018b). (A) Compared to all major groups from Foffa et al. (2018b) study. (B) Compared against Plesiosauria. Animal silhouettes from phylopic.org: Plesiosauroidea and Geosaurinae (T. Michael Keesey; CC BY 3.0) Metriorhynchinae (Gareth Monger; CC BY 3.0). Animal silhouettes of Pliosauridae and Metriorhynchidae based on Dmitry Bogdanov(CC BY 3.0). Teleosauroidea modified from Young et al. (2016).

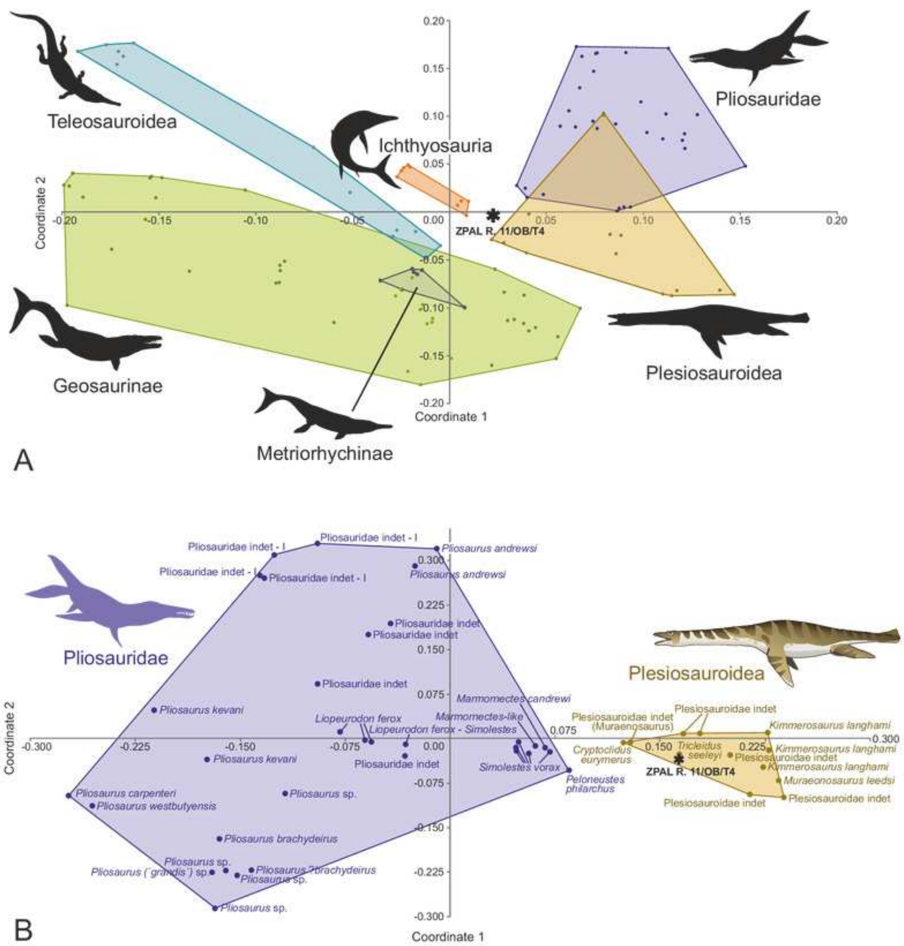
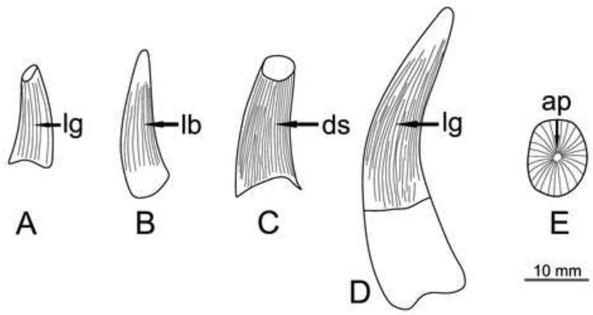

Teleosauroidea
Ichthyosauria
Pliosauridae
Plesiosauroidea
Geosaurinae
Metriorhychinae
ZPAL R. 11/OB/T4
Coordinate 1
Coordinate 2
A
Pliosauridae indet - I
Pliosaurus andrewsi
Pliosauridae indet
Pliosaurus kevani
Liopeurodon ferox
Liopeurodon ferox - Simolestes
Marmornectes candrewi
Marmornectes-like
Simolestes vorax
Peloneustes philarchus
Pliosaurus carpenteri
Pliosaurus westbutyensis
Pliosaurus sp.
Pliosaurus brachydeirus
Pliosaurus ?brachydeirus
Pliosaurus (`grandis`) sp.
Plesiosauroidae indet
(Muraenosaurus)
Cryptoclidus eurymerus
Tricleidus seeleyi
Kimmerosaurus langhami
Muraeonosaurus leedsi
ZPAL R. 11/OB/T4
Coordinate 1
Coordinate 2
B

Figure 4

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.


lg
lb
ds
lg
ap
A
B
C
D
E
10 mm