Acta Geologica Polonica, Vol. 67 (2017), No. 3, pp. 393–403
DOI: 10.1515/agp-2017-0018

Isolated pliosaurid teeth from the Albian–Cenomanian (Cretaceous) of Annopol, Poland

DANIEL MADZIA[1] and MARCIN MACHALSKI[2]

[1, 2] *Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, PL-00-818 Warsaw, Poland.*
E-mail: daniel.madzia@gmail.com; E-mail: mach@twarda.pan.pl

In commemoration of Andrzej Radwański (1935–2016)

ABSTRACT:

Madzia, D. and Machalski, M. 2017. Isolated pliosaurid teeth from the Albian–Cenomanian (Cretaceous) of Annopol, Poland. *Acta Geologica Polonica*, **67** (3), 393–403. Warszawa.

Brachauchenine pliosaurids were a cosmopolitan clade of macropredatory plesiosaurs that are considered to represent the only pliosaurid lineage that survived the faunal turnover of marine amniotes during the Jurassic–Cretaceous transition. However, the European record of the Early to early Late Cretaceous brachauchenines is largely limited to isolated tooth crowns, most of which have been attributed to the classic Cretaceous taxon *Polyptychodon*. Nevertheless, the original material of *P. interruptus*, the type species of *Polyptychodon*, was recently reappraised and found undiagnostic. Here, we describe a collection of twelve pliosaurid teeth from the upper Albian–middle Cenomanian interval of the condensed, phosphorite-bearing Cretaceous succession at Annopol, Poland. Eleven of the studied tooth crowns, from the Albian and Cenomanian strata, fall within the range of the morphological variability observed in the original material of *P. interruptus* from the Cretaceous of England. One tooth crown from the middle Cenomanian is characterized by a gently subtrihedral cross-section. Similar morphology has so far been described only for pliosaurid teeth from the Late Jurassic and Early Cretaceous. Even though it remains impossible to precisely settle the taxonomic distinctions, the studied material is considered to be taxonomically heterogeneous.

Key words: *Polyptychodon*; Plesiosauria; Pliosauridae; Teeth; Albian; Cenomanian; Annopol; Poland.

INTRODUCTION

Following detailed reassessment of the phylogenetic relationships within the Plesiosauria, it has been proposed that only three plesiosaur clades survived the Jurassic–Cretaceous transition (Benson and Druckenmiller 2014). The Cretaceous plesiosauroids were represented by xenopsarians, a clade formed by leptocleidians and elasmosaurids, and a single cryptoclidid species *Abyssosaurus nataliae* Berezin, 2011. The pliosaurid lineage, in turn, supposedly persisted in the form of Brachaucheninae. All other plesiosaurs were hypothesized to became extinct by the end of the Jurassic.

Brachauchenines belonged to thalassophonean pliosaurids, a clade of gigantic macropredatory amniotes and significant components of Middle Jurassic to early Late Cretaceous marine ecosystems (e.g. Kear 2003; Knutsen 2012; Knutsen *et al*. 2012; Benson *et al*. 2013; Schumacher *et al*. 2013; Benson and Druckenmiller 2014; Fischer *et al*. 2015; Madzia 2016; Páramo-Fonseca *et al*. 2016). Despite the fact that members of the clade Brachaucheninae represented the apex predators for more than 60 Ma, their fossil record is relatively poor. In Europe, it is dominated by isolated teeth known from numerous localities (e.g. Owen 1851; Papazzoni 2003; Marcinowski and Radwański 1983; Kear *et al*. 2014; Bardet *et al*. 2016; Fischer *et al*. 2016; Madzia 2016; Sachs *et al*. 2017). In most cases, the material was attributed to the taxon *Polyptychodon* Owen, 1841a. However, a recent reappraisal of the original material of *P. interruptus* Owen, 1841b showed that the teeth associated with the taxon do not bear any autapomorphies and most likely belonged to different species or possibly even members of different larger clades (Madzia 2016). As a result, it was recommended that other specimens attributed to *P. interruptus* should be reconsidered as well. Such a study has already been carried out on material from the lower (lower middle?) Turonian of Opole, southwest Poland (Sachs *et al*. 2016a, 2016b). This material includes four teeth assigned to *P. interruptus* by Leonhard (1897). Based on the general morphology of these teeth, Sachs *et al*. (2016a, 2016b) suggested that they resemble those of polycotylids.

The aim of this study is to describe and discuss the taxonomic and phylogenetic significance of a small collection of pliosaurid teeth, all but one belonging to the "*Polyptychodon*" type. This material originates from the upper Albian–middle Cenomanian part of the Cretaceous sedimentary succession exposed at Annopol, central Poland. This contribution is an addition to a series of papers on the Cretaceous biota from Annopol, resulting from recent exploration of this important Polish "Fossil-Lagerstätte" (Machalski and Kennedy 2013; Machalski and Martill 2013; Popov and Machalski 2014; Kennedy and Machalski 2015; Kapuścińska and Machalski 2015; Fraaije *et al*. 2015; Machalski and Wilmsen 2015; Bardet *et al*. 2016; Machalski and Olszewska-Nejbert 2016; Dubicka and Machalski 2017; Siversson and Machalski 2017). An important part of the studied material comes from the collection of late Prof. Andrzej Radwański, who was so successfully involved in earlier investigations of the Annopol fossils, depositional environments, and biostratigraphy (Radwański 1968; Marcinowski and Radwański 1983, 1989).

GENERAL BACKGROUND

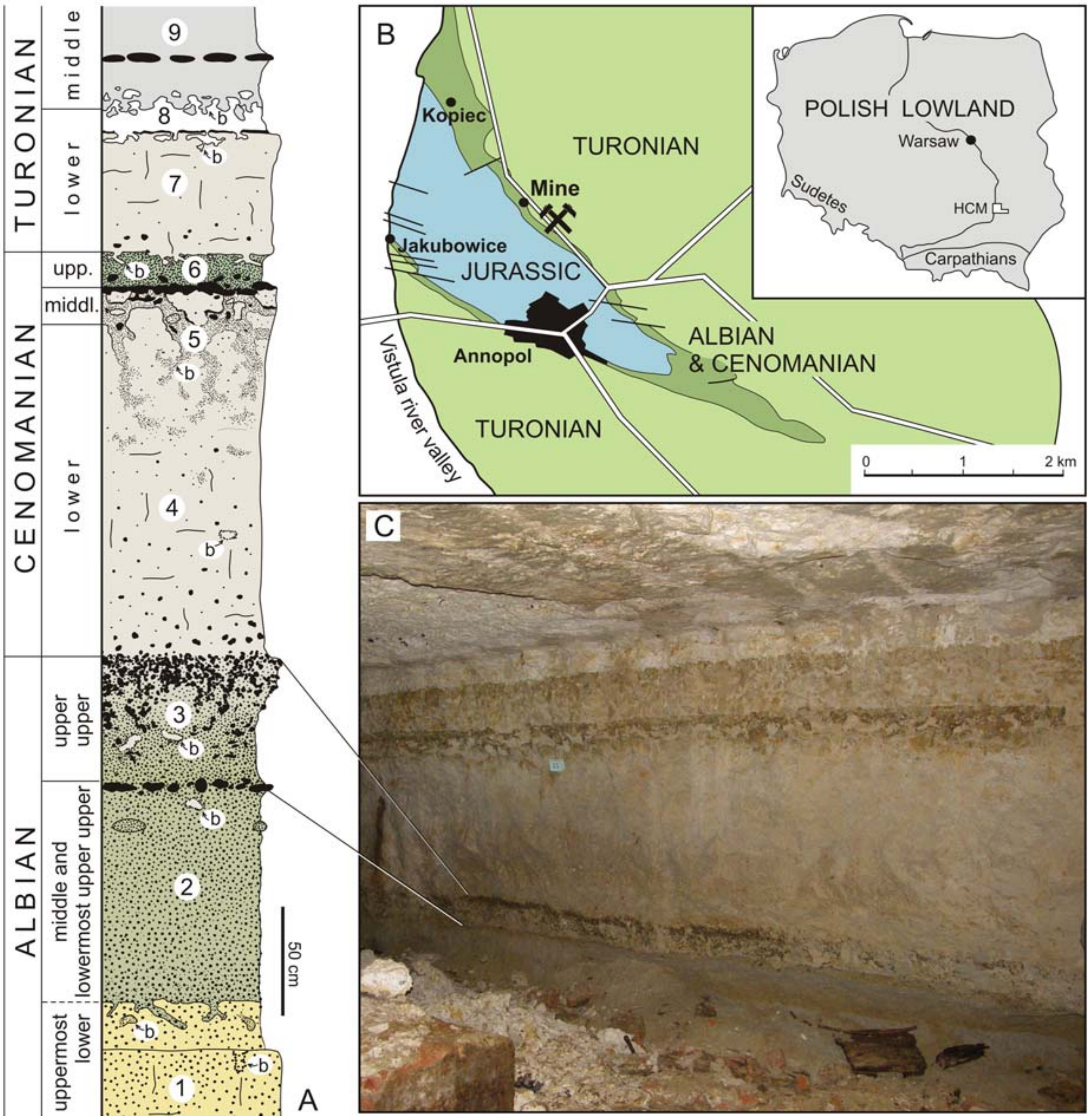
The Cretaceous (uppermost lower Albian–lower Turonian) condensed, phosphorite-bearing marine succession (Text-fig. 1A–C) is exposed along the limbs of the Annopol anticline on the east bank of the Wisła River, central Poland (Samsonowicz 1925, 1934; Marcinowski and Radwański 1983; Walaszczyk 1987; Machalski and Kennedy 2013). The Albian–Turonian strata exposed at Annopol comprise a series of thin transgressive units, capped by layers of reworked phosphatic nodules and clasts, hardgrounds, and burrowed omission and/or erosional surfaces, reflecting a series of regression maxima (Text-fig. 1A; Machalski and Kennedy 2013; Dubicka and Machalski 2017). The most recent data on the stratigraphy of the Annopol succession, based on ammonites and foraminifera, are presented in Machalski and Kennedy (2013), Kennedy and Machalski (2015), and Dubicka and Machalski (2017); the latter work also includes a bathymetric interpretation of the succession based on the foraminiferal spectra and facies development.

Unit 3 (Text-fig. 1A) is the most fossiliferous interval at Annopol (e.g. Popov and Machalski 2014; Bardet *et al*. 2016). This unit is composed of highly glauconitic, marly sands with nodular phosphates concentrated in its upper part (Text-fig. 1A). Unit 3 was deposited during a transgressive pulse in the late Albian ("Vraconnian" *sensu* Amédro 2002), in a relatively shallow-marine, highly productive, phosphogenic environment (Walaszczyk 1987; Dubicka and Machalski 2017). Together with a layer of phosphate nodules and clasts at the top of the underlying unit 2, unit 3 was referred to as "the Phosphorite Bed" by previous authors (e.g. Marcinowski and Wiedmann 1985; Marcinowski and Radwański 1983, 1989).

Another highly fossiliferous interval in the Annopol succession is a composite hardground near the top of the Cenomanian. This interval comprises the topmost part of unit 4 and highly residual unit 5, restricted to infillings of large crustacean burrows produced at the top of unit 4, see Text-fig. 1A). The reader is referred to Walaszczyk (1987), Machalski and Wilmsen (2015), and Dubicka and Machalski (2017) for more detailed descriptions of this interval.

The fossil assemblages from Annopol comprise invertebrate and vertebrate remains. Over 2,700 vertebrate fossils, represented mainly by isolated skeletal elements (teeth, bones), were collected in 2008–2015, during fieldwork led by one of us (M.M.). Most of the material is from the abandoned underground phosphorite mine *Jan 1* and from the surface locality Kopiec (gathered by screenwashing of sediment from the "Phosphorite Bed"; see Popov and Machalski 2014 and Bardet *et al*. 2016 for description of the screenwashing procedures).

The vertebrate assemblages from Annopol comprise remains of bony fish, sharks and rays (Siversson and Machalski 2017; Newbrey, Machalski, Siversson and Martin-Abad *unpublished*), chimaeroids (Popov



Text-fig. 1. A – The Cretaceous succession of the Annopol anticline (modified after Machalski and Kennedy 2013), based on the sections exposed at Kopiec (lower part) and in the abandoned underground mine *Jan 1* (upper part). **B** – Sketch-map of the Annopol anticline with main fossil sites and its location within Poland. **C** – Field photo of a representative outcrop of the Cretaceous succession in the underground phosphorite mine (indicated is the upper Albian "Phosphorite Bed"). Abbreviations: b – burrow; HCM – Holy Cross Mountains

and Machalski 2014), protostegid turtles (Kapuścińska and Machalski 2015, platypterygiine and ophthalmosaurine ichthyosaurs (Bardet *et al*. 2016), pliosaurid and elasmosaurid plesiosaurs (Bardet *et al*. 2016), as well as extremely rare and fragmentary remains of pterosaurs (ornithocheiroids and/or azhdarchoids; see Machalski and Martill 2013). Most of these fossils have been collected from unit 3 at the top of the Albian.

THE MATERIAL

The pliosaurid teeth described in the present paper are all represented by tooth crowns in various state of preservation. This material stems from collections housed in two institutions: 1) Stanisław Józef Thugutt Geological Museum, Faculty of Geology, University of Warsaw (abrreviated MWGUW); 2) Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL). These collections are characterized below in terms of their provenance and dating of specimens:

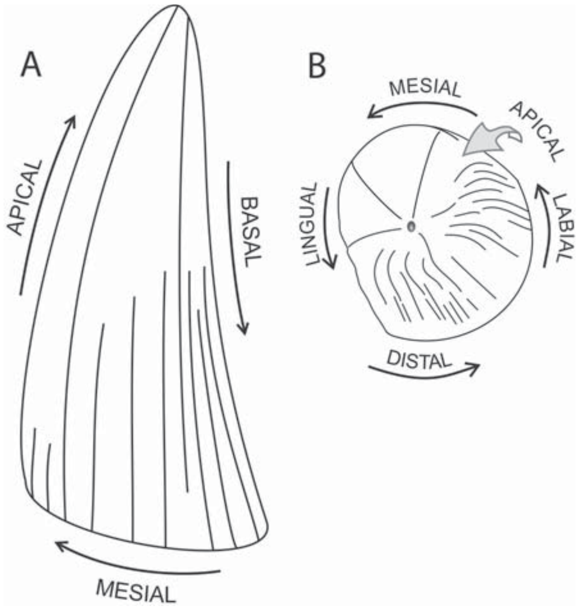
MWGUW collection. Five teeth in this collection were gathered by Prof. Andrzej Radwański. The precise location of these specimens in the Annopol area is not available. As far as their age is concerned, specimens MWGUW 009757–61, illustrated formerly in Marcinowski and Radwański (1983, pl. 8) were described as originating from the "Middle/ Upper Albian phosphorites of Annopol-on-Vistula" (Marcinowski and Radwański 1983, caption to pl. 8). Based on their preservation and character of the matrix adhering to or infilling cavities in these specimens, we assume that this material most likely originated from unit 3 (Text-fig. 1A) and, therefore, is probably of late late Albian age (cf. Bardet *et al.* 2016). A single specimen, MWGUW 009761, comes from the middle Cenomanian unit 4, as evidenced by the distinctive matrix adhering to its apical part.

Three additional MWGUW specimens, numbered MWGUW ZI/60/001, 019, and 020, were collected before World War II by Jan Samsonowicz, a geologist who discovered the Annopol anticline in 1923. No precise provenance data within the Annopol area and succession are available for the MWGUW collection. However, all the three teeth reveal preservation typical of unit 3 (Text-fig. 1A) and are therefore probably of late late Albian age (cf. Bardet *et al.* 2016).

ZPAL collection. Four pliosaurid tooth crowns are present in this material (ZPAL V.38/443, 893, 894, and 2034). Specimen ZPAL V.38/2034 originated from screenwashing of sands from the "Phosphorite Bed" at Kopiec and is probably of late late Albian age (cf. Bardet *et al.* 2016). Three Cenomanian tooth crowns were found *in situ* in the underground mine *Jan 1*. Amongst these, ZPAL V.38/894 originated from the topmost part of the lower Cenomanian unit 4, and the other two, ZPAL V.38/893, and ZPAL V.38/443, are from the middle Cenomanian unit 5 (Text-fig. 1A).

DESCRIPTION OF THE MATERIAL

The terminology of the anatomical orientation of pliosaurid teeth follows that of Smith and Dodson (2003): apical, toward the apices of the tooth crown or the tooth base; basal, toward the *cervix dentis*; distal, away from the tip of the snout; labial, toward the lips; lingual, toward the tongue; mesial, toward the tip of the snout (see Text-fig. 2).

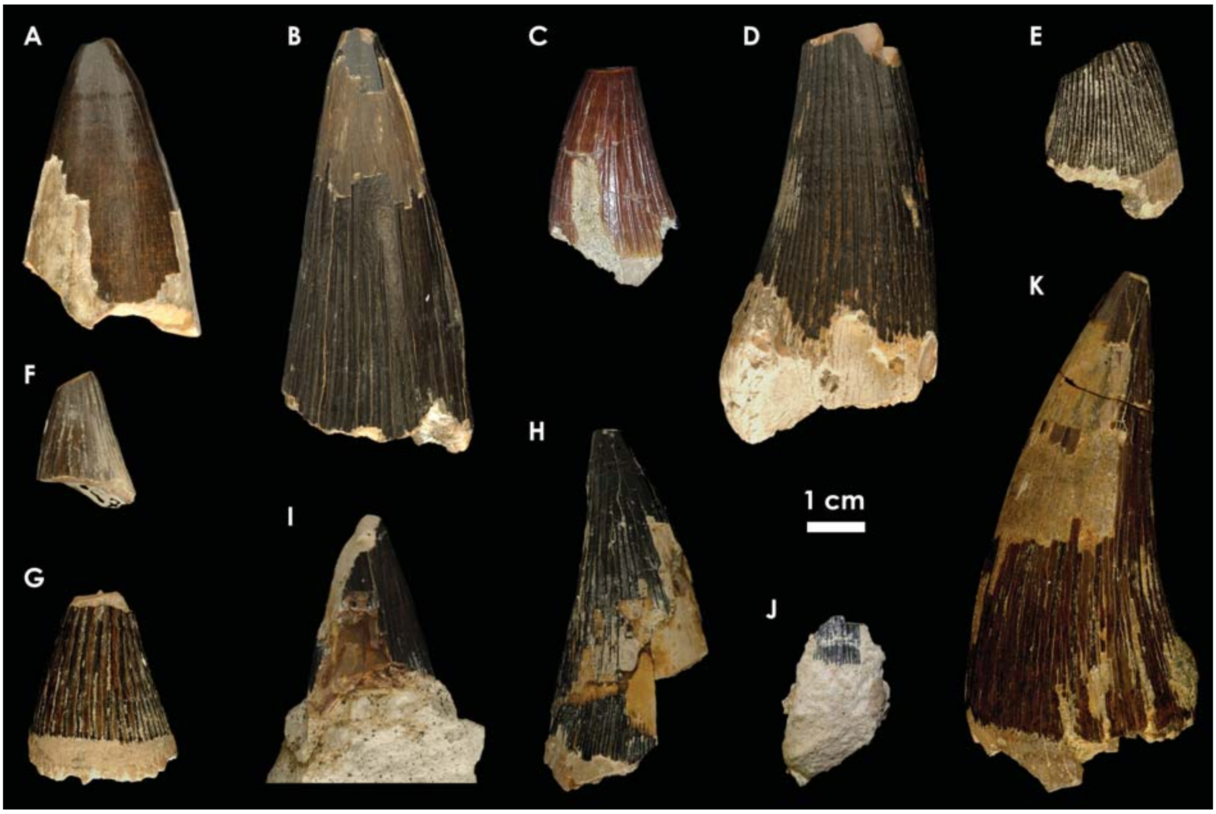


Text-fig. 2. Tooth anatomical orientation in idealized plesiosaur tooth (after Madzia 2016). **A** – Plesiosaur tooth crown in labial view. **B** – Apical view of plesiosaur tooth crown

The teeth (Text-figs 3 and 4) were measured using a digital caliper. The following parameters are given in the text of the description chapter (below): CH, crown height, the distance between the distalmost point at the base of the tooth crown and the crown apex; WLR, width-to-length ratio, measured adjacent to the *cervix dentis* (the parameter is roughly equivalent to CBR *sensu* Smith, Vann and Dodson 2005; applied as in Madzia 2016). Photographs of specimens were taken using a digital single-lens reflex camera Nikon D1X.

Each tooth crown is provided with its probable original position in the jaws. This was determined based on the curvature of the crowns which is generally indicative of the side (i.e., left/right). Identification of the exact tooth-bearing element from which it originated (i.e., premaxilla, maxilla, or dentary) is currently regarded as impossible for the majority of the specimens.

MWGUW 009757. Left premaxillary/maxillary or right dentary tooth crown, previously figured by Marcinowski and Radwański (1983, pl. 8, fig. 17) and in Text-fig. 3A herein. The tooth crown is incomplete. Presumably, the preserved part constitutes the apical half of the crown with the remainder being broken off. It is robust and slightly curved linguodistally. Its apex is worn. The total CH of the tooth crown cannot be measured accurately but



Text-fig. 3. Pliosaurid teeth from the Albian–Cenomanian of Annopol. **A** – MWGUW 009757 [LV], **B** – MWGUW 009758 [LV], **C** – MWGUW 009760 [LV], **D** – MWGUW 009759 [LV], **E** – MWGUW ZI/60/019 [LGV], **F** – MWGUW ZI/60/020 [LV], **G** – MWGUW ZI/60/001 [LV?], **H** – ZPAL V.38/893 [LV], **I** – ZPAL V.38/443 [LGV], **J** – ZPAL V.38/894 [?], and **K** – ZPAL V.38/2034 [LV]. Abbreviations: LV, labial view; LGV, lingual view

the preserved part is approximately 40 mm height and the WLR is around 0.95. The distribution of the apicobasal ridges is very uneven. Mesiolabially, only a single partial ridge is visible. It is situated on the labial part of the tooth crown adjacent to its apex. The lack of the ridges is possibly caused by the fact that a substantive part of the basal portion of the tooth crown is missing. Similar unridged tooth crowns were observed in the collection from the Cambridge Greensand Member (see e.g. Madzia 2016, fig. 5). Apically, their mesiolabial surface is largely unridged, but its basal part usually includes ridges. In these crowns, however, Madzia (2016) observed a possible pattern consisting of three ridges running on the entire crown height. Linguodistally, the ridges of MWGUW 009757 are present and relatively distantly-spaced. Only a single lingually positioned ridge is developed throughout the whole apicobasal height. None of the observed ridges are branching. The surface is rather smooth but very indistinct vermicular striae can be observed around the entire circumference of the crown. Likewise, the enamel of MWGUW 009757 is very slightly undulated transversely. Probably late late Albian in age.

MWGUW 009758. Left premaxillary/maxillary or right dentary tooth crown, previously figured by Marcinowski and Radwański (1983, pl. 8, fig. 19) and in Text-fig. 3C herein. The tooth crown is almost complete. It lacks only a short basal part, a mesiolabial segment of the enamel, and the apex. It is slightly curved linguodistally. The CH of the preserved part is ~61.25 mm, with WLR of about 0.95. The distribution of the apicobasal ridges is uneven. Mesiolabially, only three ridges, separated by a series of shorter ones, reach the apex. Such morphology is consistent with the possible pattern observed by Madzia (2016, fig. 5) in the Cambridge Greensand Member collection. Linguodistally, the ridges are more closely-spaced and most of them extend from the *cervix dentis* up to the apex. None of the observed ridges are branching. The enamel exposed between the adjacent ridges bears smooth to relatively rough vermicular striae. Probably late late Albian in age.

MWGUW 009759. Left premaxillary/maxillary or right dentary tooth crown, previously figured by Marcinowski and Radwański (1983, pl. 8, fig. 20) and in Text-fig. 3E herein. The tooth crown is reasonably complete, lacking only a part of the apex. It is slightly curved linguodistally. The CH of the preserved part is approximately 50 mm, with WLR of about 0.9. The apicobasal ridges are distributed rather regularly. Most of the assessable ridges extend through the whole apicobasal height of the preserved part of the tooth crown. The mesiolabially positioned ridges are more distantly-spaced than their linguodistal counterparts. None of the observed ridges are branching though some of the basalmost ones are somewhat scattered around the entire circumference near the *cervix dentis*. The enamel surface is only partially exposed. It contains rather smooth vermicular striae. Mesiolabially, they become rough on the basal half of the tooth crown. Probably late late Albian in age.

MWGUW 009760. Right premaxillary/maxillary or left dentary tooth crown, figured in Text-fig. 3D. The tooth crown is nearly complete. It lacks a small part of its basal portion, a mesiolabial segment of the enamel, and a part of the apex which is worn off. It is slightly curved linguodistally. The CH of the preserved part is ~30 mm; WLR is ~1. The ridges are present around the entire circumference of the tooth crown but their extent and density differ. Mesiolabially, the apicobasal ridges are shorter, reaching approximately two-thirds of the crown height, and they are slightly more distantly-spaced. Linguodistally, three ridges reach the apicalmost part of the preserved portion of the crown. However, due to the missing apex it is unknown whether they were developed up to the apex. None of the observed ridges are branching. The enamel surface is not well exposed but very slight vermicular striae can be observed where the surface is unridged. Probably late late Albian in age.

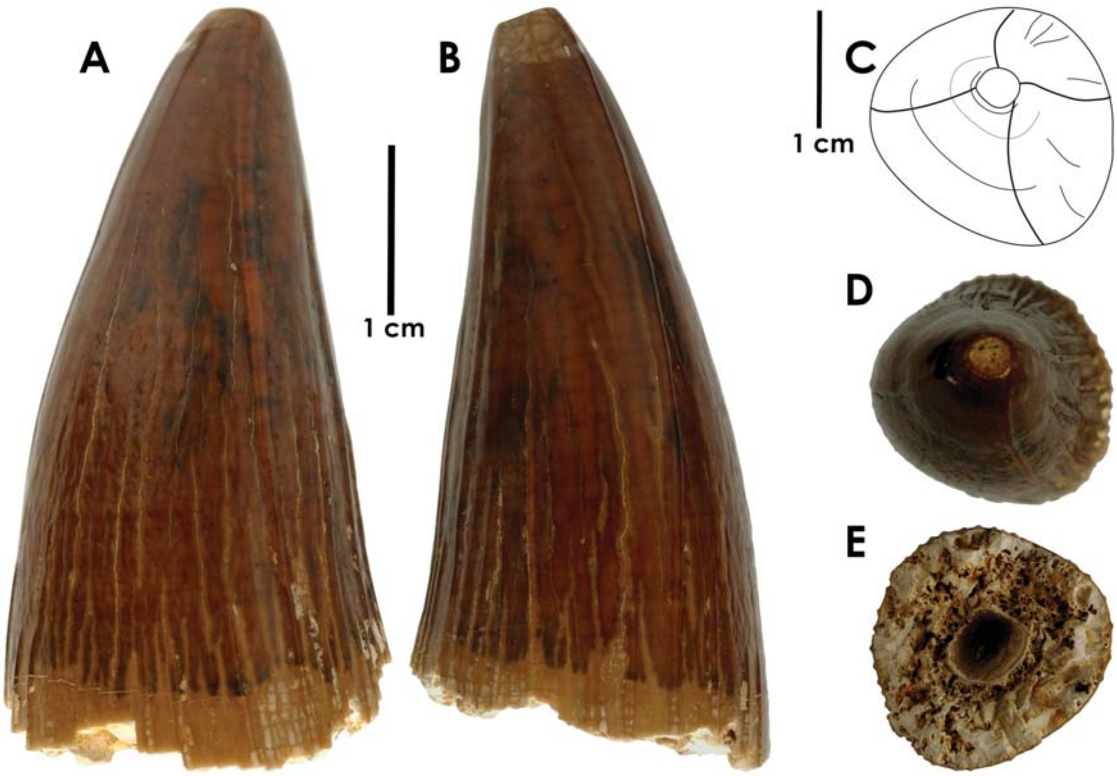
MWGUW 009761. Right premaxillary/maxillary or left dentary tooth crown, figured in Text-fig. 4A–C. The tooth crown is complete, only a small part of its apex is worn off. It is slightly curved linguodistally. The CH is ~35.7 mm; WLR is around 1. Unlike all other tooth crowns described in the present study, MWGUW 009761 is gently subtrihedral in cross-section. Only four ridges reach the apex. Two are situated linguodistally and separated by a few shorter ridges developed on the basal half of the crown. The other two ridges are placed mesiolabially. They are separated by an almost flat surface with six observable ridges that are developed on a short basalmost segment. None of the observed ridges are branching. The surface is smooth apically but roughens on the basal half of the tooth crown. Middle Cenomanian in age.

MWGUW ZI/60/001. Probably right premaxillary/maxillary or left dentary tooth crown, previously figured by Bardet *et al*. (2016, fig. 7b, c) and in Text-fig. 3H herein. Only approximately two-thirds of the basal part of the tooth crown is preserved. The crown is slightly curved linguodistally. The apex is worn and partially crushed off. The CH of the preserved part is approximately ~22.3 mm; the WLR is ~0.94. The ridges are developed rather evenly along the entire circumference. The mesially positioned ridges are more distantly-spaced. The vertical extent cannot be assessed due to the missing apex but most of the observable ridges reach the apicalmost preserved part. Distally, the basal section of the tooth crown is partially covered by matrix whose removal might have caused some destruction of the enamel. At least three of the ridges present in this part seem to be branching near the *cervix dentis*. The enamel surface is not sufficiently exposed and preserved between the adjacent ridges to enable its assessment. Nevertheless, some shallow structural elements resembling vermicular striae are observable. Probably late late Albian in age.

MWGUW ZI/60/019. Right premaxillary/maxillary or left dentary tooth crown, figured in Text-fig. 3F. Only a basal half of the crown is preserved. The CH is unmeasurable but the WLR is about 0.93. The apicobasal ridges are distributed regularly though they are more distantly-spaced labially. None of the observed ridges are branching. The enamel surface is partially exposed labially where it is roughening. Probably late late Albian in age.

MWGUW ZI/60/020. Probably left premaxillary/maxillary or right dentary tooth crown, figured in Text-fig. 3G. Only an apical part is preserved. Neither the CH nor the WLR can be measured. The distribution of the apicobasal ridges is uneven. The ridges are more distantly-spaced on the mesial half. Most of the ridges present on the preserved part of the specimen seem to reach the apex. None of the observed ridges are branching. The enamel surface is poorly exposed. Still, mesially, rather smooth vermicular striae can be observed. Probably late late Albian in age.

ZPAL V.38/443. Left premaxillary/maxillary or right dentary tooth crown, figured in Text-fig. 3J. Only a narrow mesial and a distal segment of the tooth crown is assessable. The crown is slightly curved. The total



Text-fig. 4. Specimen MWGUW 009761 from the middle Cenomanian of Annopol. **A** – labial, **B** – lingual, **C**, **D** – apical, and **E** – basal view

CH cannot be measured nor estimated accurately. The preserved part is ~27 mm high. The WLR cannot be assessed. The apicobasal ridges are distributed relatively evenly on the preserved basal sections along the entire circumference. None of the observed ridges are branching. Only limited parts of the enamel surface are exposed. They contain very shallow vermicular striae. Middle Cenomanian in age.

ZPAL V.38/894. Tooth crown of uncertain position, figured in Text-fig. 3K. Only a small linguo-/labiobasal part of the tooth crown is preserved. Neither the CH nor the WLR can be assessed. A short segment of closely-spaced ridges is observable. None of the ridges are branching. The surface between the adjacent ridges is very poorly visible and cannot be properly assessed. Early Cenomanian in age (this is the only record of a pliosaurid tooth from the lower Cenomanian of Annopol known to us).

ZPAL V.38/893. Left premaxillary/maxillary or right dentary tooth crown, previously figured by Bardet *et al*. (2016, fig. 7a) and in Text-fig. 3I herein. Only the labial half of the tooth crown is reasonably complete. The lingual half lacks a considerable basal portion. The crown is slightly curved linguodistally. The apex is worn. The CH of the preserved part is approximately 60 mm; the WLR cannot be assessed due to the missing parts. The apicobasal ridges are distributed relatively evenly along the entire circumference. Mesiolabially, three ridges seem to reach the apex though they are poorly preserved. Other ridges terminate approximately two centimeters below the apex. Linguodistally, the ridges reach more apically. Basally, the labiodistally positioned ridges are very closely-spaced. None of the observed ridges seem to be branching. The surface between the adjacent ridges is very poorly visible and cannot be properly assessed. Middle Cenomanian in age.

ZPAL V.38/2034. Right premaxillary/maxillary or left dentary tooth crown, previously figured by Bardet *et al.* (2016, fig. 6) and in Text-fig. 3L herein. The tooth crown is complete but its preservation is relatively poor. Except for a rather narrow labiodistal segment, the apical half of the crown lacks most of its outer enamel surface. The apex is very slightly worn. The crown is distinctly curved linguodistally. The CH of the preserved part is ~73 mm; the WLR is 0.88. The apicobasal ridges are distributed relatively evenly though they are slightly more distantly-spaced on the mesiolabial face of the crown. Only a short labial part of the outer enamel is preserved near the apex. It shows three ridges reaching the apex. None of the observed ridges are branching. The surface between the adjacent ridges contains rather smoothly developed vermicular striae. Probably late late Albian in age.

DISCUSSION

Robust plesiosaur teeth originating from the mid-Cretaceous strata of the European Archipelago have commonly been regarded as representing a single pliosaurid taxon, *Polyptychodon interruptus* Owen, 1841b. A recent reappraisal by Madzia (2016) showed, however, that the original material attributed to *P. interruptus* is most likely too variable to belong to a single taxon. This conclusion was further regarded as being supported by the considerable time span between the oldest and youngest specimens assigned to *P. interruptus*, likely to exceed 35 Ma (early Aptian to ?middle Santonian).

Except for a single tooth crown, the studied specimens fall within the morphological variability observed by Madzia (2016) in the collection of the late Albian (to early Cenomanian? see Machalski 2017) teeth from the lower Cenomanian Cambridge Greensand Member of the West Melbury Marly Chalk Formation, England. Even though Madzia (2016) suggested that the Cambridge collection most likely includes members of different taxa, he was unable to set sharp morphological boundaries between particular tooth crowns. Madzia (2016) observed, nevertheless, that some of the crowns possess a possible taxonomically relevant arrangement of the apicobasal ridges (see Madzia 2016, fig. 5). Such an appearance, involving three mesiolabially positioned ridges running through the entire crown height, was observed in the studied material as well.

One of the tooth crowns (MWGUW ZI/60/001) seems to possess at least three branching ridges on the distal half near the *cervix dentis*. A lack of branching ridges was sometimes used to distinguish *P. interruptus* from its North American relatives (VanLoh and Bell 1998; Angst and Bardet 2016). However, the distribution and character of the branching ridges are known to be variable (Schumacher 2008; Madzia 2016). Nevertheless, the apicobasal ridges still need to be studied in detail to properly evaluate the potential taxonomic relevance of their appearance.

One middle Cenomanian tooth crown from Annopol (MWGUW 009761) differs from all other specimens in its gently subtrihedral cross-section. For a long time, the Cretaceous pliosaurids, members of the clade Brachaucheninae, could have been easily distinguished from their Late Jurassic relatives based on, among other things, the cross-sectional shape of their tooth crowns. Brachauchenines, such as *Brachauchenius lucasi* Williston, 1903 or *Megacephalosaurus eulerti* Schumacher *et al.*, 2013, originally described from the Turonian (Upper Cretaceous) of Kansas (USA), have conical tooth crowns with suboval to subcircular cross-sections (Madzia 2016). On the other hand, the teeth of Late Jurassic pliosaurids [a lineage consisting of *Pliosaurus* Owen, 1841a, see also Knutsen (2012) and Benson *et al.* (2013), and perhaps *Gallardosaurus* Gasparini, 2009; with the latter possibly being referable to the former (Benson *et al.* 2013)] have crowns with characteristic subtrihedral to trihedral cross-sections. There was no definitive evidence for a transitional (subtrihedral/trihedral) tooth crown morphology between the basal thalassophoneans with conical teeth, such as *Liopleurodon ferox* Sauvage, 1873, and the mid- to Late Cretaceous brachauchenines. Recently, Zverkov (2015) reported on a tooth crown (h-216; Faculty of Geology, Lomonosov Moscow State University) originating from the lower Valanginian of Crimea. In contrast to all other pliosaurid teeth that have been known to date from the Cretaceous strata, this specimen exhibited a tooth crown morphology with distinctly flattened labial surface, similar to the teeth of the Late Jurassic taxon *Pliosaurus*, thus suggesting that two pliosaurid lineages (*Pliosaurus* and Brachaucheninae) crossed the Jurassic–Cretaceous boundary. Nevertheless, a subsequent study by Fischer *et al.* (2015), describing a new peculiar pliosaurid *Makhaira rossica* from the upper Hauterivian of Russia, with tooth crowns possessing subtrihedral-trihedral cross-sectional shape, suggested that such a morphology could actually have been typical of the "transitional" Late Jurassic to Early Cretaceous pliosaurids, including the basal brachauchenines. The interrelationships within the clade Pliosauridae still remain to be settled. Nevertheless, the specimen MWGUW 009761 from the middle Cenomanian of Annopol might represent the youngest reported occurrence of pliosaurids with tooth crowns possessing subtrihedral cross-sectional shape.

In the light of the preliminary results of Sachs *et al.* (2016a, 2016b), who attributed some "*Polyptychodon*" teeth to Polycotylidae rather than to Pliosauridae, a brief comparison between the teeth of pliosaurids and polycotylids is provided here in order to better assess the taxonomic composition of the teeth from the Albian–Cenomanian of Annopol. The teeth of polycotylid taxa with well-preserved dentition, such as *Dolichorhynchops* (Schmeisser McKean 2012) are often comparable in size but much more slender and distinctly curved. In some polycotylids, such as *Polycotylus latipinnis* Cope, 1869, *Plesiopleurodon wellesi* Carpenter, 1996, or *Edgarosaurus muddi* Druckenmiller, 2002, some teeth from certain tooth positions are more robust than other teeth. Yet, when these teeth are compared to the studied material from the Albian–Cenomanian of Annopol, they still seem to be much more slender. Considering these differences, it currently seems unlikely that any of the teeth described herein could be assigned to Polycotylidae. Also, in contrast to the case of pliosaurids, which were further represented in the material from the mid-Cretaceous strata of Annopol by a large vertebral centrum (MWGUW ZI/60/2; Bardet *et al*. 2016), no polycotylid material has been identified.

CONCLUSIONS

The isolated teeth from the Albian–Cenomanian (Cretaceous) strata of Annopol, Poland, have traditionally been associated with the purportedly widely distributed taxon *Polyptychodon interruptus* (Marcinowski and Radwański 1983; Bardet *et al*. 2016), despite the fact that they have never been studied in detail. Following the recent reappraisal of *P. interruptus* that called the taxonomic validity of this taxon into question (Madzia 2016), we present a description of 12 isolated tooth crowns from the upper Albian–middle Cenomanian portion of the Annopol succession and discuss their potential taxonomic and phylogenetic importance.

The morphology of all of the studied specimens, except for one, approximately corresponds with the variability observable in the late Albian (to early Cenomanian?) teeth from the lower Cenomanian Cambridge Greensand Member of the West Melbury Marly Chalk Formation, England. However, one specimen from the middle Cenomanian of Annopol is characterized by a gently subtrihedral cross-section. So far, a similar appearance has only been described for pliosaurid teeth from the Late Jurassic and Early Cretaceous (e.g. Benson *et al*. 2013; Zverkov 2015; Fischer *et al*. 2015). Because of their size and robustness, and following the comparison of the material with the teeth of some other robust-toothed plesiosaurs (polycotylids), we interpret all the teeth as belonging to Pliosauridae.

Despite the fact that the studied collection of isolated pliosaurid teeth is limited in number, we consider it to be taxonomically heterogeneous. Thus, other material historically attributed to *Polyptychodon interruptus* should be reassessed as well.

Acknowledgements

We are indebted to Matt Riley and Dan Pemberton (both Sedgwick Museum of Earth Sciences, University of Cambridge, UK) for access to the material in their care, Marian Dziewiński for pictures of the specimens, Magdalena Łukowiak for help with preparation of Text-fig. 4, and Ola Hołda-Michalska for preparation of Text-fig. 1 (all Institute of Paleobiology, Polish Academy of Sciences). We thank Sven Sachs (Naturkundemuseum Bielefeld), an anonymous reviewer, and the Editor Irek Walaszczyk for valuable comments. We thank Wiesław Liwiński (Mayor of Annopol) for his support during field work. Special thanks go to Agnieszka Kapuścińska, Michał Andziak, Witold Biernat, Maciej Duda, Grzegorz Gajek, Michał Klimek, Artur Komorowski, Zbigniew Lis, Maciej Małysiak, Tomasz Mleczek, Krzysztof Nejbert, Adam Zaremba, and the OSP Sucha Wólka fire fighters for participation in field work at Annopol. Mariusz Niechwiedowicz (Stanisław Józef Thugutt Geological Museum, Faculty of Geology, University of Warsaw) is acknowledged for his help in making the MWGUW collection available for our studies. The study was funded by the National Science Centre (Poland) grant DEC-2012/05/B/ST10/00710 to Marcin Machalski.

REFERENCES

Amédro, F. 2002. Plaidoyer pour un étage Vraconnien entre l'Albien sensu stricto et le Cénomanien (système Crétacé). *Academie Royale de Belgique, Classe des Sciences*, **4**, 1–128.

Angst, D. and Bardet, N. 2016. A new record of the pliosaur *Brachauchenius lucasi* Williston, 1903 (Reptilia: Sauropterygia) of Turonian (Late Cretaceous) age, Morocco. *Geological Magazine*, **153**, 449–459.

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

Benson, R.B.J. and Druckenmiller, P.S. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews*, **89**, 1–23.

Benson, R.B.J., Evans, M., Smith, A.S., Sassoon, J., Moore-Faye, S., Ketchum, H.F., and Forrest, R. 2013. A giant pliosaurid skull from the Late Jurassic of England. *PLOS ONE*, **8**, e65989.

Berezin, A.Y. 2011. A new plesiosaur of the family Aristonectidae from the early cretaceous of the center of the Russian platform. *Paleontological Journal*, **45**, 648–660.

Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **210**, 259–287.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society*, **14**, 1–252.

Druckenmiller, P.S. 2002. Osteology of a new plesiosaur from the lower Cretaceous (Albian) Thermopolis Shale of Montana. *Journal of Vertebrate Paleontology*, **22**, 29–42.

Dubicka, Z. and Machalski, M. 2017. Foraminiferal record in a condensed marine succession: a case study from the Albian and Cenomanian (mid-Cretaceous) of Annopol, Poland. *Geological Magazine*, **154**, 399–418.

Fischer, V., Arkhangelsky, M.S., Stenshin, I.M., Uspensky, G.N., Zverkov, N.G., and R.B. J. Benson. 2015. Peculiar macrophagous adaptations in a new Cretaceous pliosaurid. *Royal Society Open Science*, **2**, 150552.

Fischer, V., Bardet, N., Benson, R.B.J., Arkhangelsky, M.S., and Friedman, M. 2016. Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nature Communications*, **7**, 10825.

Fraaije, R.H.B., Van Bakel, B., Jagt, J.W.M. and Machalski, M. 2015. A new hermit crab from the upper Albian (Cretaceous) of Annopol. *Zootaxa*, **3955**, 588–594.

Gasparini, Z. 2009. A New Oxfordian Pliosaurid (Plesiosauria, Pliosauridae) in the Caribbean Seaway. *Palaeontology*, **52**, 661–669.

Kapuścińska, A., and Machalski, M. 2015. Upper Albian chelonioid turtles from Poland. *Geobios*, **48**, 385–395.

Kear B.P. 2003. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. *Cretaceous Research*, **24**, 277–303.

Kear, B.P., Ekrt, B., Prokop, J. and Georgalis, G.L. 2014. Turonian marine amniotes from the Bohemian Cretaceous Basin, Czech Republic. *Geological Magazine*, **151**, 183–198.

Kennedy, W.J. and Machalski, M. 2015. A late Albian ammonite assemblage from the mid-Cretaceous succession at Annopol, Poland. *Acta Geologica Polonica*, **65**, 545–553.

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

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

Leonhard, R. 1897. Die Fauna der Kreideformation in Oberschlesien. *Palaeontographica*, **44,** 11–70.

Machalski, M. 2017. The Cenomanian ammonite *Schloenbachia varians* (J. Sowerby, 1817) from the Cambridge Greensand of eastern England: Possible sedimentological and taphonomic implications. *Cretaceous Research*. Early view online. http://dx.doi.org/10.1016/j.cretres.2017.03.025

Machalski, M. and Kennedy, W.J. 2013. Oyster-bioimmured ammonites from the Upper Albian of Annopol, Poland: stratigraphic and palaeobiogeographic implications. *Acta Geologica Polonica*, **63**, 545–554.

Machalski, M. and Martill, D.M. 2013. First pterosaur remains from the Cretaceous of Poland. *Annales Societatis Geologorum Poloniae*, **83**, 99–104.

Machalski, M. and Olszewska-Nejbert, D. 2016. A new mode of ammonite preservation – implications for dating of condensed phosphorite deposits. *Lethaia*, **49**, 61–72.

Machalski, M. and Wilmsen, M. 2015. Taxonomy and taphonomy of Cenomanian nautilids from Annopol, Poland. *Acta Geologica Polonica*, **65**, 495–506.

Madzia, D. 2016. A reappraisal of *Polyptychodon* (Plesiosauria) from the Cretaceous of England. *PeerJ*, **4**, e1998.

Marcinowski, R. and Radwański, A. 1983. The mid-Cretaceous transgression onto the Central Polish Uplands (marginal part of the Central European Basin). *Zitteliana*, **10**, 65–96.

Marcinowski, R. and Radwański, A. 1989. A biostratigraphic approach to the mid-Cretaceous transgressive sequence of the central Polish Uplands. *Cretaceous Research*, **10**, 153–172.

Marcinowski, R. and Wiedmann, J. 1985. The Albian ammonite fauna of Poland and its palaeogeographical significance. *Acta Geologica Polonica*, **35**, 199–219.

Owen R. 1841a. Odontography; or, a Treatise on the Comparative Anatomy of the Teeth; their Physiological Relations, Mode of Development, and Microscopic Structure, in the Vertebrate Animals. Volume I. Part II. Dental System of Reptiles. London: Hippolyte Bailliere, 179–295.

Owen R. 1841b. Odontography; or, a Treatise on the Comparative Anatomy of the Teeth; their Physiological Relations, Mode of Development, and Microscopic Structure, in the Vertebrate Animals. Volume II. London: Hippolyte Bailliere, 1–381.

Owen R. 1851. A monograph on the fossil Reptilia of the Cretaceous formations. London: Printed for the Palæontographical society, 1–118.

Papazzoni, C.A. 2003. A pliosaurid tooth from the Argille Varicolori Formation near Castelvecchio di Prignano (Modena Province, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, **109**, 563–565.

Páramo-Fonseca, M.E., Gómez-Pérez, M., Noè, L.F. and Etayo-Serna, F. 2016. *Stenorhynchosaurus munozi*, gen. et sp. nov. a new pliosaurid from the Upper Barremian (Lower Cretaceous) of Villa de Leiva, Colombia, South America. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, **40**, 154, 84–103.

Popov, E.V. and Machalski, M. 2014. Late Albian chimaeroid fishes (Holocephali, Chimaeroidei) from Annopol, Poland. *Cretaceous Research*, **7**, 1–18.

Radwański, A. 1968. *Ischyodus thurmanni* Pictet & Campiche and other chimaeroid fishes from the Albian–Cenomanian of the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, **13**, 315–322. [In Polish, English summary]

Sachs, S., Niedźwiedzki, R., Kędzierski, M., Kear, B.P., Jagt-Yazykova, E. and Jagt, J.W.M. 2016a. A reassessment of historical plesiosaurian specimens from the Turonian (lower Upper Cretaceous) of the Opole area, southwest Poland. In Kear, B. P., Lindgren, J., and Sachs, S. 5th Triennial Mosasaur Meeting – a global perspective on Mesozoic marine amniotes. May 16–20, 2016, Museum of Evolution, Uppsala University, Sweden, 40–42.

Sachs, S., Niedźwiedzki, R., Kędzierski, M., Kear, B.P., Jagt-Yazykova, E. and Jagt, J.W.M. 2016b. Overview of Marine Reptiles from the Turonian of the Opole area, southwest Poland. XIV Annual Meeting of the European Association of Vertebrate Palaeontologist, At Haarlem, The Netherlands, 80.

Sachs, S., Wilmsen, M., Knüppe, J., Hornung, J.J. and Kear, B.P. 2017. Cenomanian–Turonian marine amniote remains from the Saxonian Cretaceous Basin of Germany. *Geological Magazine*, **154**, 237–246.

Samsonowicz, J. 1925. Esquisse géologique des environs de Rachów sur la Vistule et les transgressions de l'Albien et du Cénomanien dans les sillon nord-européen. *Sprawozdania Państwowego Instytutu Geologicznego*, **3**, 45–118. [In Polish, with French summary]

Samsonowicz, J. 1934. Explication de la feuille Opatów (zone 45, colonne 33). Service géologique de Pologne, Carte Géologique Générale de la Pologne au 100.000-e, 1–97. Warszawa.

Sauvage, H.E. 1873. Notes sur les reptiles fossiles. 4. Du genre *Liopleurodon* Sauvage. *Bulletin de la Société Géologique de France*, **3**, 377–380.

Schmeisser McKean, R. 2012. A new species of polycotylid plesiosaur (Reptilia: Sauropterygia) from the Lower Turonian of Utah: extending the stratigraphic range of *Dolichorhynchops*. *Cretaceous Research*, **34**, 184–199.

Schumacher, B.A. 2008. On the skull of a pliosaur (Plesiosauria; Pliosauridae) from the Upper Cretaceous (Early Turonian) of the North American Western Interior. *Transactions of the Kansas Academy of Science*, **3**, 203–218.

Schumacher, B.A., Carpenter, K. and Everhart, M.J. 2013. A new Cretaceous pliosaurid (Reptilia, Plesiosauria) from the Carlile Shale (middle Turonian) of Russell County, Kansas. *Journal of Vertebrate Paleontology*, **33**, 613–628.

Siversson, M. and Machalski, M. 2017. Late late Albian (Early Cretaceous) shark teeth from Annopol, Poland. *Alcheringa*. Early view online. http://dx.doi.org/10.1080/03115518.2017.1282981

VonLoh, J.P. and Bell, G.L. 1998. Fossil reptiles from the Late Cretaceous green horn formation (Late Cenomanian–Middle Turonian) of the Black Hills Region, South Dakota. *Dakoterra*, **5**, 29–38.

Walaszczyk, I. 1987. Mid-Cretaceous events at the marginal part of the Central European Basin (Annopol-on-Vistula section, Central Poland). *Acta Geologica Polonica*, **37**, 61–74.

Williston, S.W. 1903. North American plesiosaurs. *Field Columbian Museum, Pub. 73, Geological Series*, **2**, 1–79.

Zverkov, N.G. 2015. On a typically Late Jurassic pliosaur from the Lower Cretaceous of Crimea. *The International Scientific Conference on the Jurassic/Cretaceous boundary*. Samara, Russia, 89–94.

Manuscript submitted: 20th November 2016
Revised version accepted: 15th May 2017