Campanian and Maastrichtian mosasaurid reptiles from central Poland

MARCIN MACHALSKI, JOHN W.M. JAGT, RUDI W. DORTANGS, ERIC W.A. MULDER, and ANDRZEJ RADWAŃSKI

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Isolated marginal teeth and tooth crowns of Late Campanian and Late Maastrichtian mosasaurid reptiles (Squamata, Platynota) from the Wisła River valley area, central Poland, are described and illustrated. These comprise two Late Campanian taxa from Piotrawin quarry: *Prognathodon* sp. and Plioplatecarpinae sp. A., and four late Late Maastrichtian taxa from Nasiłów quarry: *Mosasaurus* cf. *hoffmanni* Mantell, 1829, *M.* cf. *lemonnieri* Dollo, 1889c, "*Mosasaurus* (*Leiodon*) cfr. *anceps*" *sensu* Arambourg (1952), and Plioplatecarpinae sp. B. In addition, the previously described fragmentary jaw with associated teeth of the Late Campanian age from Maruszów quarry (west of the Wisła River area), is reassigned to *Mosasaurus* cf. *hoffmanni*. This specimen suggests that *M. hoffmanni* or a closely related (ancestral?) species already appeared in Europe during the Late Campanian (well-documented European occurrences of *M. hoffmanni* are Late Maastrichtian in age). At least part of the described mosasaur material is likely to stem from periodic feeding in the area (broken-off or shed tooth crowns) or from floating carcasses (complete teeth and jaw fragments).

Key words: Reptilia, Squamata, Platynota, Mosasauridae, Upper Cretaceous, Campanian, Maastrichtian, Poland.

Marcin Machalski [mach@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL 00-818 Warszawa, Poland;
John W.M. Jagt [john.jagt@nhmmaastricht.nl], Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, P.O. Box 882, NL-6200 AW Maastricht, the Netherlands;
Rudi W. Dortangs, Hoofdstraat 36, NL-6436 CG Amstenrade, the Netherlands;
Eric W.A. Mulder [eric292@gmx.net], Museum Natura Docet, Oldenzaalsestraat 39, NL-7591 GL Denekamp, the Netherlands;
Andrzej Radwański, Instytut Geologii Podstawowej, Wydział Geologii UW, Al. Żwirki i Wigury 93, PL 02-089 Warszawa, Poland.

Introduction

During the Late Cretaceous, in epicontinental seas worldwide, mosasaurid reptiles occupied the top position in the food chain. In recent years, fossils of these marine lizards have attracted much attention, especially in attempts to reconstruct phylogenetic relationships within the Squamata (DeBraga and Carroll 1993; Lee 1997; Caldwell 1999; Zaher and Rieppel 1999; Rieppel and Zaher 2001).

Other aspects in recent mosasaur studies include analyses of distribution patterns, which have led to the realisation that numerous species across the Atlantic (Atlantic Coast of the USA *versus* northern Europe) are either synonymous or closely related (Gallagher 1993; Mulder 1999), and that certain species within Europe were more widespread than previously thought (e.g., Bardet and Pereda Suberbiola 1996; Bardet and Tunoğlu 2002).

In comparison to other areas in Europe, e.g., southern Sweden (Persson 1959; Lindgren 1998; Lindgren and Siverson 2002), the Maastricht area in the Netherlands (Mulder et al. 1998; Kuypers et al. 1998) and the Mons Basin in southern Belgium (e.g., Lingham-Soliar 1996, 1999, 2000), mosasaurids are rare in the Upper Cretaceous deposits of Poland. Only fragmentary remains of a jaw and a single tooth were described by Sulimski (1968) and isolated teeth and tooth crowns reported by Radwański (1985). The aim of the present paper is to describe mosasaurid material from central Poland, collected mostly by A. Radwański and M. Machalski, as well as to discuss that reported on by Sulimski (1968).

Material

The new mosasaurid material represents isolated marginal teeth and tooth crowns collected at two quarries, Piotrawin and Nasiłów, situated in the Wisła (Vistula) River valley area (Fig. 1). The specimens from Piotrawin come from the Upper Campanian opoka (siliceous limestone) representing the *Nostoceras hyatti* Zone (= *N. pozaryskii* Zone of Błaszkiewicz 1980, see Kennedy 1993; Machalski 1996a). The material from Nasiłów comes from two horizons: the upper Upper Maastrichtian marly opoka (*Belemnella kazimiroviensis* Zone, see Christensen (1996) for standard belemnite zonation of the Maastrichtian Stage) and the Danian greensand, containing a mixture of Danian and reworked late Late Maastrichtian fossils (see Pożaryska 1965; Hansen et al. 1989; Radwański 1996; Machalski 1996b, 1998; Machalski and Jagt 1998). There is no doubt that the mosasaurid material from the

greensand, all phosphatised and damaged to some extent, is reworked, and is of late Late Maastrichtian age.

The mosasaurid skeletal remains previously described by Sulimski (1968) comprise a fragmentary jaw from sandy glauconitic opoka representing the Upper Campanian *Nostoceras hyatti* Zone, and not "uppermost Maastrichtian" as claimed by Sulimski (1968), from Maruszów, west of the Wisła River valley sections (see Błaszkiewicz 1980: fig. 1 and Fig. 1 herein), as well as a single tooth from the upper Upper Maastrichtian marly opoka of Nasiłów.

Institutional abbreviations.—IGPUW AR, Institute of Geology, University of Warsaw, Warsaw (collection A. Radwański); IRScNB, Royal Belgian Institute of Natural Sciences, Brussels; MKD, Natural History Museum, Department of the Muzeum Nadwiślańskie, Kazimierz Dolny; MNHN, National Museum of Natural History, Paris; MZ, Museum of the Earth, Polish Academy of Sciences, Warsaw; NHMM, Natural History Museum Maastricht, Maastricht; OGP, Oertijdmuseum de Groene Poort, Boxtel; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

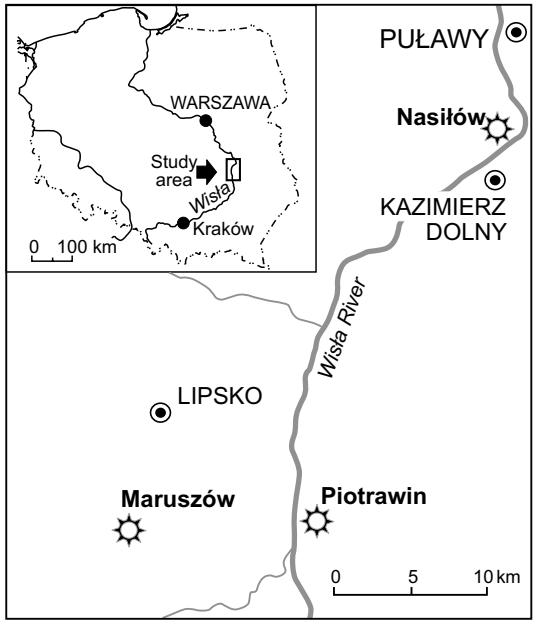


Fig. 1. Location of outcrops in central Poland (starlets), which have yielded the mosasaur remains referred to in the text.

Taxonomic potential of mosasaurid teeth

Identification of mosasaur taxa on the basis of isolated teeth and tooth crowns is fraught with difficulties. Current mosasaur taxonomy relies on cranial features (e.g., frontal, quadrate) and on postcranial elements (e.g., coracoid, scapula, vertebrae, paddle structure). Only exceptionally are dental features included in descriptions or diagnoses of taxa, e.g., in the durophagous species (e.g., Dollo 1913; Russell 1975).

The taxonomic potential of teeth in many mosasaurid species remains to be evaluated on the basis of detailed descriptions of teeth belonging to more complete, diagnostic skeletal remains. In particular, changes in morphology (facetting, carinae, height/width ratio) between anterior, lateral and posterior marginal teeth should be studied. The same holds true for the pterygoid dentition. Moreover, whenever possible, ontogenetic changes should be considered.

Ideally, when more or less complete skulls are available of any particular mosasaur taxon, the full sets of (preserved) mandibular and pterygoid teeth should be described in detail and illustrated in buccal (labial, external), lingual (internal) and occlusal aspects. Ultimately, this would allow isolated teeth to be identified with much greater precision than is possible to date. Sakurai et al. (1999) tabulated differences in dentition of a mosasaur species; it is along these lines that more work needs to be done.

On the other hand, numerous mosasaur taxa are based on isolated teeth only (e.g., Dollo 1913; Arambourg 1952; Russell 1967, 1975). Despite these difficulties, we have attempted to refer isolated teeth and tooth crowns from the Polish Campanian and Maastrichtian to particular mosasaurid taxa. Whenever possible, we have based our identifications on direct comparison with better known material from the Maastrichtian type area near Maastricht, the Netherlands. However, as none of the features of the studied dental material is strictly diagnostic at the specific level, we have decided to leave in open nomenclature even those specimens which find a good match in comparative material of well-known species.

Systematic palaeontology

Genus *Mosasaurus* Conybeare in Parkinson, 1822: 298

Type species: *Mosasaurus hoffmanni* Mantell, 1829: 207, by monotypy.

Mosasaurus cf. *hoffmanni* Mantell, 1829

Figs. 2–6.

Material.—Two teeth (IGPUW AR-1, IGPUW AR-2), found together and possibly belonging to a single individual, and one tooth crown (IGPUW AR-3), from the Danian greensand at Nasiłów (redeposited late Late Maastrichtian material). Two tooth crowns (IGPUW AR-4, OGP 1254) from the upper Upper Maastrichtian opoka at Nasiłów. A fragmentary jaw and isolated tooth crowns (ZPAL R. I/1–5), representing a single individual, from the Upper Campanian of Maruszów, previously recorded as *Mosasaurus* sp. (sp. A) by Sulimski (1968: 245, pl. 1; pl. 2: 1–4, refigured herein as Figs. 4–6). Comparative material from the type Maastrichtian area (type area of *Mosasaurus hoffmanni*) includes NHMM 004984-2, 007129, 006684-3b, 1997262, 1997266, and 1997267.

Description.—The best-preserved specimen is an anterior (?premaxillary) tooth, IGPUW AR-2 (Fig. 2B), 100.3 mm in height (including root, with small resorption pit). It is asymmetrically bicarinate, with a deeply U-shaped cross section, and with markedly unequal lingual and buccal surfaces. The buccal surface is more or less flat, with 2–3 facets (best visi-

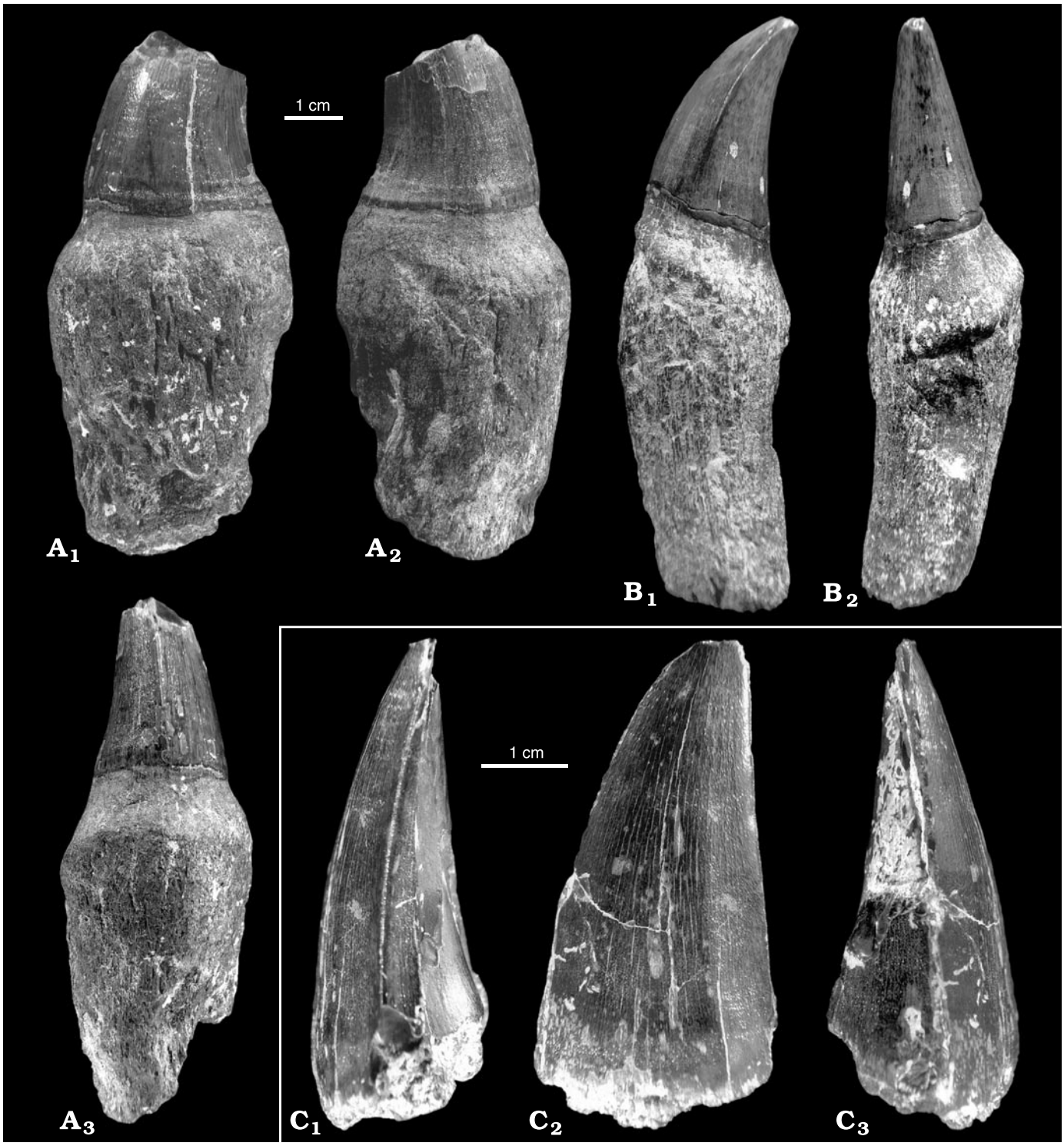


Fig. 2. *Mosasaurus* cf. *hoffmanni* Mantell, 1829, from the Danian greensand at Nasiłów (redeposited late Late Maastrichtian material). **A**. IGPUW AR-1 in buccal (A_1), lingual (A_2), and anterior (A_3) views. **B**. IGPUW AR-2 in posterior (B_1) and lingual (B_2) views. **C**. IGPUW AR-3 in posterior (C_1), buccal (C_2), and anterior (C_3) views.

ble proximally); on the lingual surface the facets are less well developed, and their number cannot be determined precisely. Both the anterior and posterior carinae are well developed, with minute serrations over their entire length. The crown has a marked posterior and lingual recurvature. The enamel shows beading, best developed proximally.

IGPUW AR-1 (Fig. 2A) is a massive lateral tooth, 89.6 mm in total height (as preserved), including the incomplete root. It has an elliptical cross section, with both buccal and lingual surfaces showing barely visible facets and beading. Both posterior and anterior carinae show minute serrations. The crown is moderately posteriorly and lingually recurved.

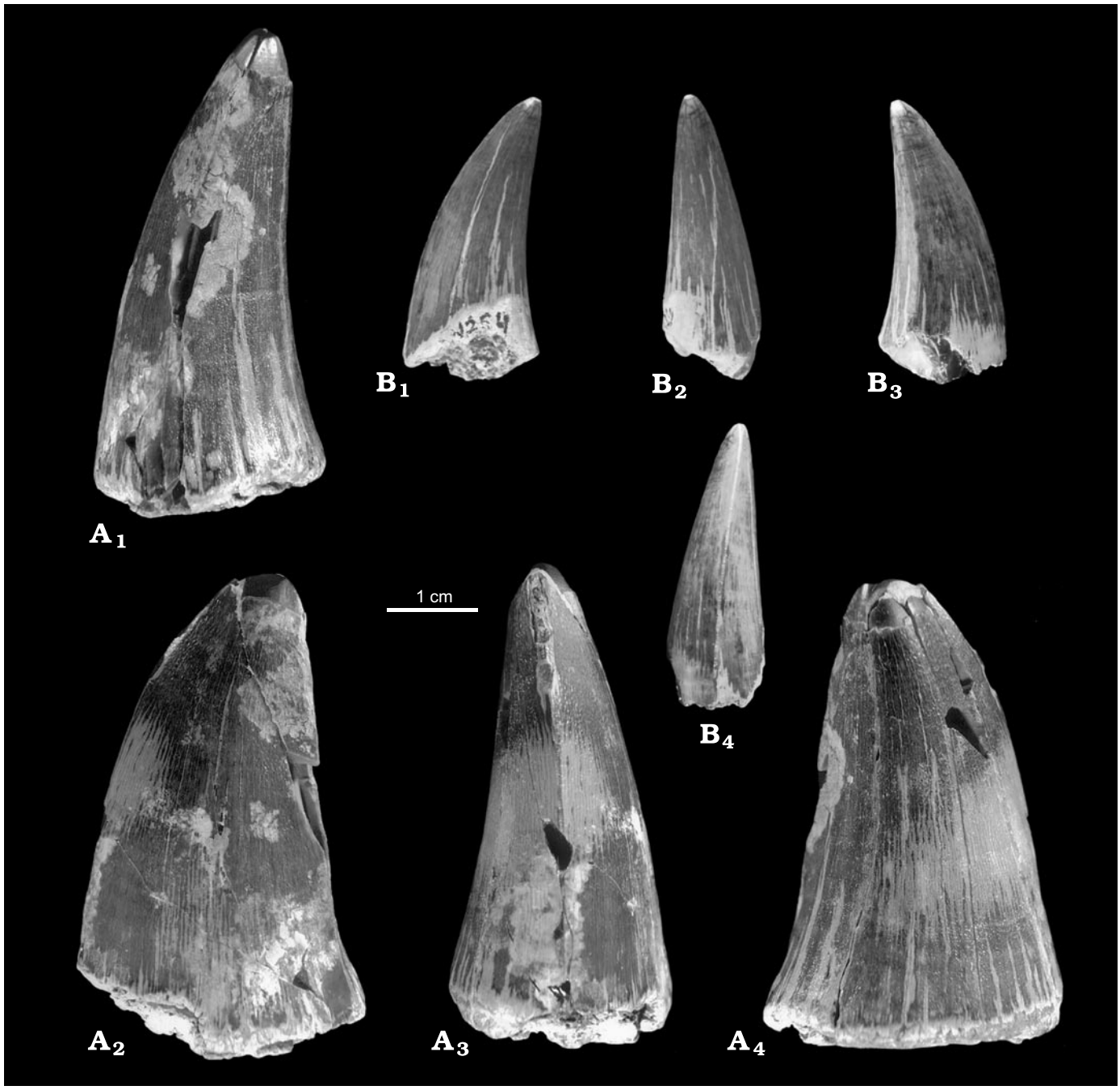


Fig. 3. *Mosasaurus* cf. *hoffmanni* Mantell, 1829, from the upper Upper Maastrichtian opoka at Nasiłów. **A**. IGPUW AR-4 in posterior (A_1), buccal (A_2), anterior (A_3), and lingual (A_4) views. **B**. OGP 1254 in lingual (B_1), posterior (B_2), buccal (B_3), and anterior (B_4) views.

IGPUW AR-3 (as preserved 57.0 mm in height; see Fig. 2C) and IGPUW AR-4 (as preserved 51.6 mm in height; see Fig. 3A) show elliptical cross sections, and appear to have occupied a comparable position in the dental or maxillary ramus. These specimens have more clearly developed facets, on both the buccal and lingual surfaces, and show distinct beading of the enamel.

OGP 1254 (Fig. 3B) is a comparatively small (from a subadult individual?), bicarinate tooth crown (31.5 mm in height, as preserved), 14.2 mm in width (at the base). In cross section it is more or less elliptical, with the lingual and buccal surfaces markedly unequal. The buccal surface is faintly convex, with 3 unequal facets; on the lingual surface there are up to 9 such facets, narrower and especially marked proximally, reaching to just above mid-height; beading is well visible. Both carinae are well developed, the anterior one being more pronounced, with minute serrations over their entire lengths. The crown is moderately lingually, but more clearly posteriorly recurved.

Teeth and tooth crowns in the Upper Campanian specimen ZPAL R. I/1–5 (Figs. 4–6) show a U-shaped cross section, with both the buccal and lingual surfaces facetted, with

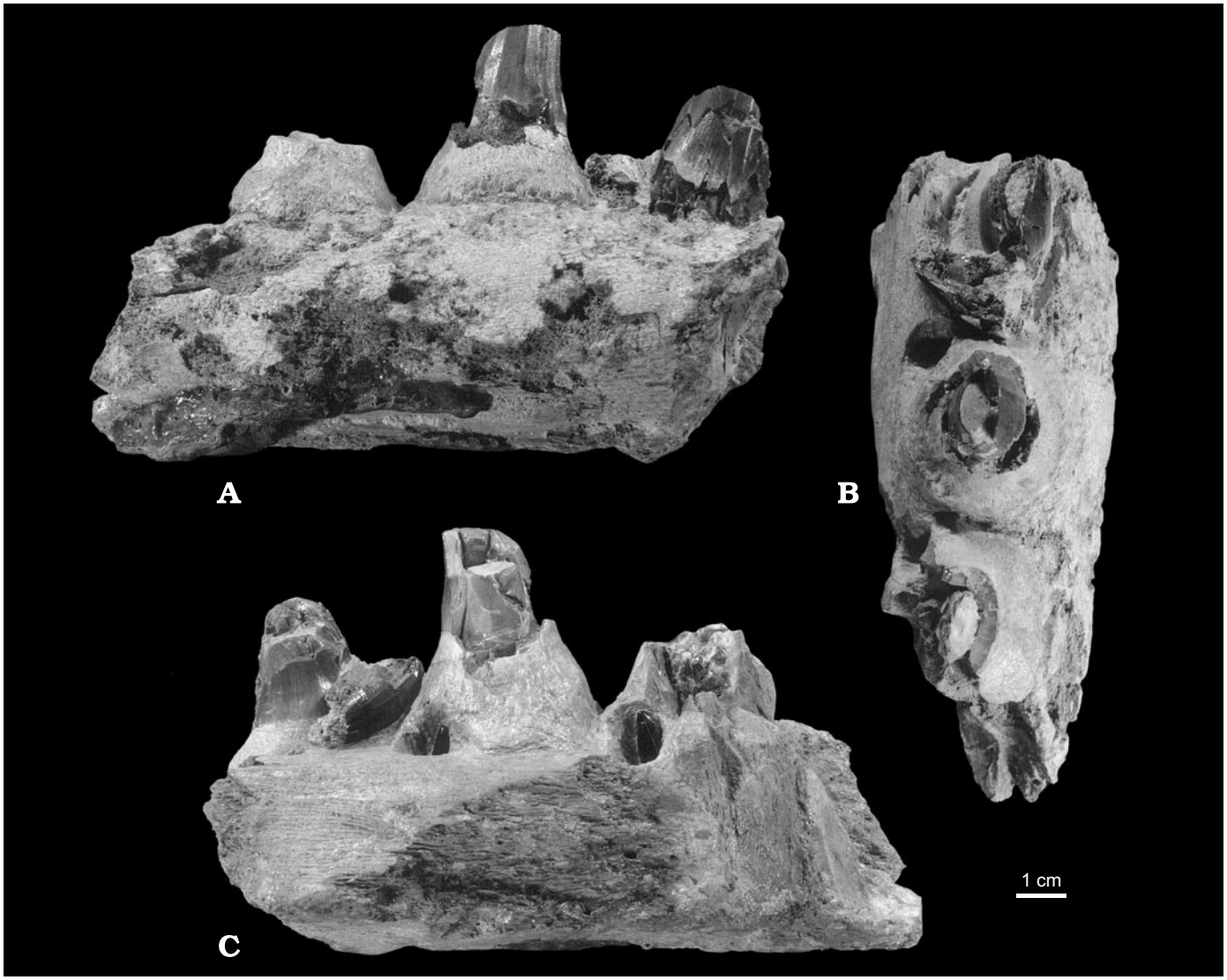


Fig. 4. *Mosasaurus* cf. *hoffmanni* Mantell, 1829, from the Upper Campanian opoka at Maruszów, ZPAL R.I/1, partial upper jaw in buccal (**A**), occlusal (**B**), and lingual (**C**) views.

buccal facets wider and more distinct than those on the lingual side. They also show well-developed anterior and posterior carinae, a slight posterior recurvature and a more pronounced lingual recurvature. Enamel beading is less pronounced than in the Late Maastrichtian specimens, but does occur in patches, both proximally and distally.

Discussion.—Typical anterior and median-posterior teeth of adult specimens of *M. hoffmanni* are robust, bicarinate, have asymmetrical crowns (lingual side more inflated) with a few wide "prismatic" facets on the buccal side of the crown, and more numerous facets on the lingual side; they also reveal beading of the enamel (Lingham-Soliar 1995; Jagt et al. 1995; Kuypers et al. 1998). The posterior teeth are more symmetrical, but are still characterised by beaded enamel and distinct facets (op. cit.). The beading of the enamel was held to be diagnostic of teeth of *M. hoffmanni* by Kuypers et al. (1998). However, it occurs in African and Polish specimens herein referred to as "*Mosasaurus* (*Leiodon*) cfr. *anceps*" and in one of the Polish specimens referred to as *M.* cf. *lemonnieri* as well (see below).

The Late Maastrichtian specimens IGPUW AR-1–4 from Nasiłów fall within the range of dental variation of adult specimens of *M. hoffmanni* from the environs of Maastricht. The single tooth from the upper Upper Maastrichtian opoka of Nasiłów (MZ VIII/Vr-66), referred to by Sulimski (1968) as *Mosasaurus* sp. (sp. B), also falls within the adult category of *M. hoffmanni.*

Teeth of subadult *M. hoffmanni* are more slender. Specimen OGP 1254 from Nasiłów may belong here. The size of the tooth crowns of the Upper Campanian specimen ZPAL R. I/1–5 from Maruszów suggests that these remains originate from a subadult individual as well. It is well matched by smaller sized material of *M. hoffmanni* from the Maastrichtian type area (e.g., Kuypers et al. 1998: pl. 1: 5, 6).

Stratigraphic and geographic range.—In the Maastrichtian type area, the lowermost well-documented occurrence of *M.*

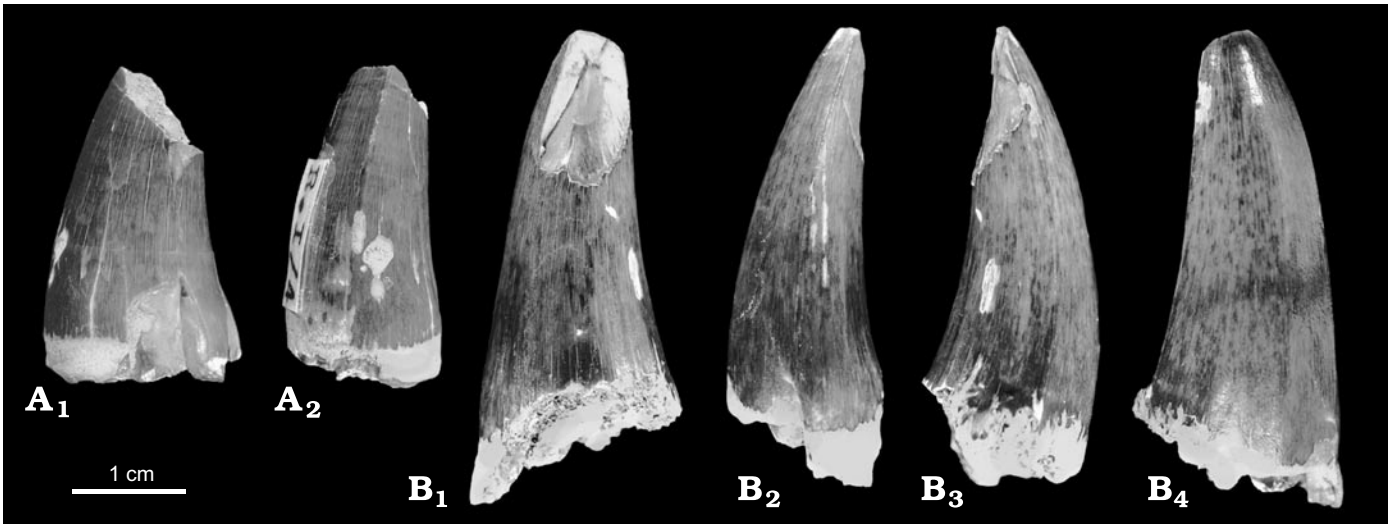


Fig. 5. *Mosasaurus* cf. *hoffmanni* Mantell, 1829, from the Upper Campanian opoka at Maruszów. **A**. ZPAL R.I/4 in lingual (A_1) and anterior (A_2) views. **B**. ZPAL R.I/2 in lingual (B_1), anterior (B_2), posterior (B_3), and buccal (B_4) views.

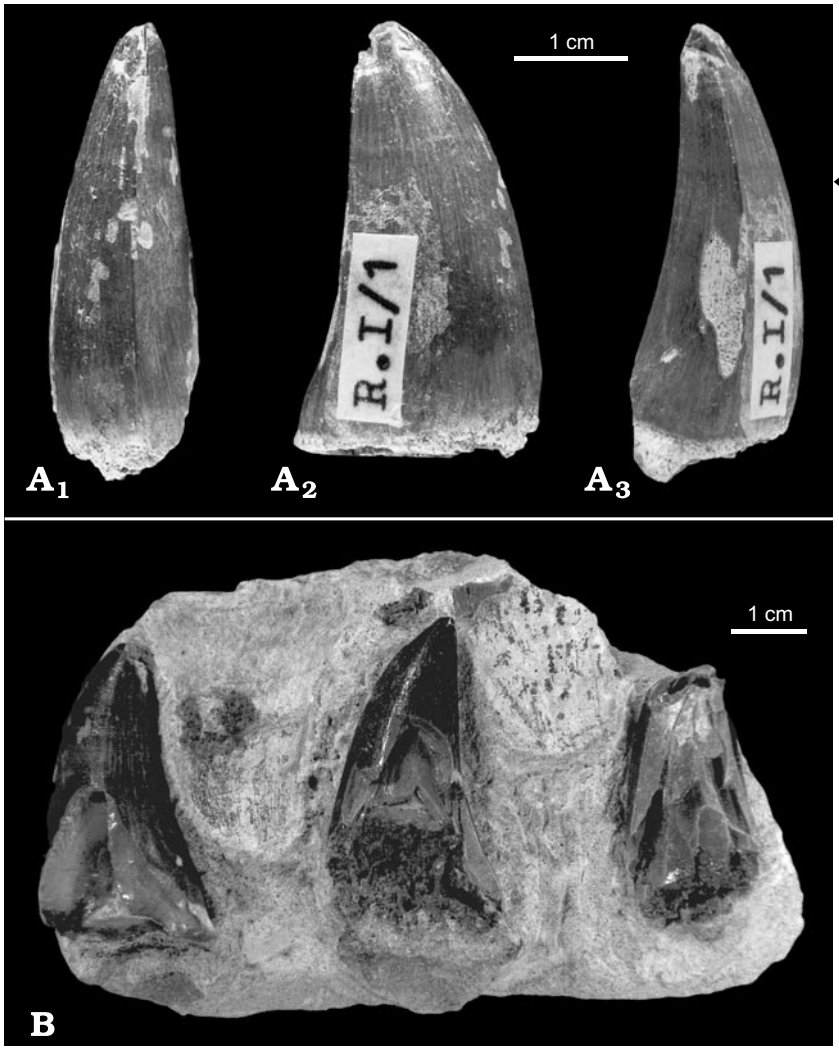


Fig. 6. *Mosasaurus* cf. *hoffmanni* Mantell, 1829, from the Upper Campanian opoka at Maruszów. **A**. ZPAL R.I/1, left-hand side tooth in B in anterior (A_1), buccal (A_2), and posterior (A_3) views. **B**. ZPAL R.I/1, three tooth crowns preserved in original jaw position (although jaw bone is not preserved).

hoffmanni, based on the diagnostic skeletal material, is within the upper half of the Lanaye Member (Gulpen Formation, lower Upper Maastrichtian *Belemnitella junior* Zone). However, finds of isolated teeth and tooth crowns from the Vijlen Member (Gulpen Formation, Lower Maastrichtian) in the Haccourt-Lixhe area (Liège, NE Belgium), suggest that *M. hoffmanni* or a closely related species made its first appearance in the area earlier. The species is fairly common in the Emael and Nekum members (Maastricht Formation, Upper Maastrichtian), in particular in the Eben Emael (Bassenge) area (Liège). The type of *M. hoffmanni* (MNHN AC 9648) is from the upper third of the Nekum Member (Bardet and Jagt 1996). The species ranges up to the K/Pg boundary. Reworked tooth crowns have been recorded from the basal Geulhem Member (Houthem Formation) of Early Paleocene age (Kuypers et al. 1998).

Other records of *M. hoffmanni* include the Upper Campanian to Upper Maastrichtian of New Jersey (USA) (Mulder 1999 synonymised *Mosasaurus maximus* Cope, 1869, with *M. hoffmanni*), the uppermost Maastrichtian of Missouri (Campbell and Lee 2001), the Maastrichtian of Alabama (Kiernan 2002), Bulgaria (Tzankov 1939; see also Nikolov and Westphal 1976), northern Denmark (Bonde 1997; Jagt personal observation), Congo (Zaire) (Lingham-Soliar 1994b), Niger (Lingham-Soliar 1991), and Turkey (Bardet and Tunoğlu 2002). Persson (1959: 462, fig. 10; pl. 15: 1, 2) recorded *M.* cf. *hoffmanni* from the

Lower Campanian of southern Sweden. This material, however, refers to *Tylosaurus ivoensis* (Persson, 1963) (see Lindgren and Siverson 2002).

In Europe, well-documented remains of *M. hoffmanni* appear to be confined to Upper Maastrichtian strata. However, the specimen from Maruszów suggests that *M. hoffmanni* or a closely related (ancestral?) species appeared in Europe as early as the Late Campanian. This may be confirmed only by more diagnostic finds.

Mosasaurus cf. *lemonnieri* Dollo, 1889c

Fig. 7.

Material.—Three tooth crowns ZPAL R. 9/1, ZPAL R. 9/2, and ZPAL R. 9/5 from the upper Upper Maastrichtian opoka at Nasiłów. Comparative material from the Maastrichtian type area includes NHMM 001463, NHMM 1997269, NHMM 1997299, and NHMM 1997304.

Description.—Best preserved is ZPAL R. 9/1 (Fig. 7B), which is bicarinate and measures 30 mm in height, and 14.7 mm in width (at the base). In cross section the crown is elliptical with the lingual surface more inflated. Both anterior and posterior carinae are well developed, with minute serrations visible only distally. The crown has a slight posterior recurvature, but more pronounced lingual recurvature. The buccal surface shows four facets of unequal width, the lingual surface 7. The facets are separated by distinct ridges or striae (resulting in their slight concavity) and reach to just above mid-height of the crown.

Specimens ZPAL R. 9/2 (Fig. 7A) and ZPAL R. 9/5 (Fig. 7C), although fragmentary, reveal the same morphology. ZPAL R. 9/5 shows traces of beading proximally.

Discussion.—*Mosasaurus lemonnieri* seems to be closely related to *M. hoffmanni* (Lingham-Soliar 2000). Its teeth are usually more slender and smaller than those of adult *M. hoffmanni*. Tooth facets in *M. lemonnieri* are separated by distinct ridges (striae *sensu* Lingham-Soliar 2000). As a result, the facets are slightly concave rather than flat or slightly convex as in *M. hoffmanni* (Meijer 1984). Moreover, the facets on both sides of the crown are approximately of the same width, whereas in *M. hoffmanni* they are much wider on the buccal side (Dollo 1924; Meijer 1984; Kuypers et al. 1998). It should also be noted that some specimens of *M. lemonnieri* from the Mons Basin (especially IRScNB 3109) reveal crowns with a near-smooth surface (Kuypers et al. 1998). These, however, are absent in the Polish material under discussion.

Stratigraphic and geographic range.—The original material of *M. lemonnieri* is from the lower Lower Maastrichtian *Belemnella obtusa* Zone of the Mons Basin, southern Belgium. In the Maastrichtian type area, the lowermost occurrence of the species is at the base of the Valkenburg Member (Maastricht Formation, lower Upper Maastrichtian *Belemnitella junior* Zone). It is not common, and does not range up into the Meerssen Member, let alone to the K/Pg boundary (Mulder et al. 1998).

Mosasaurus lemonnieri was much less widely distributed than *M. hoffmanni.* There are no well-documented records of this species outside Belgium and the Netherlands. Tooth crowns from the Maastrichtian of Zaire (Congo) referred to as cf. *Mosasaurus lemonnieri* by Lingham-Soliar (1994b: fig. 1g–j) differ in having approximately six buccal and 12–14 lingual striae, and in lacking the lingual recurvature of the crowns, typical of the species. They resemble specimen MKD. MP-18 from the upper Upper Maastrichtian of Nasiłów herein

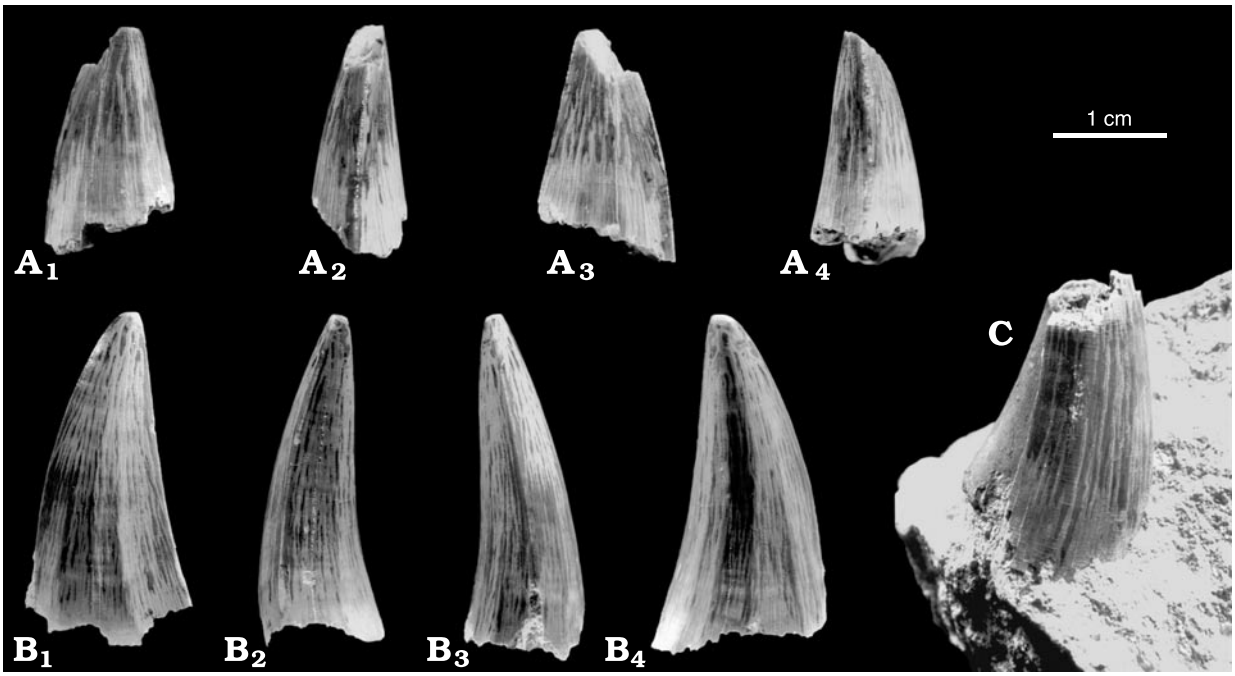


Fig. 7. *Mosasaurus* cf. *lemonnieri* Dollo, 1889c, from the upper Upper Maastrichtian opoka at Nasiłów. **A**. ZPAL R. 9/2 in lingual (A_1), anterior (A_2), buccal (A_3), and posterior (A_4) views. **B**. ZPAL R. 9/1 in buccal (B_1), posterior (B_2), anterior (B_3), and lingual (B_4) views. **C**. ZPAL R. 9/5 in oblique buccal view.

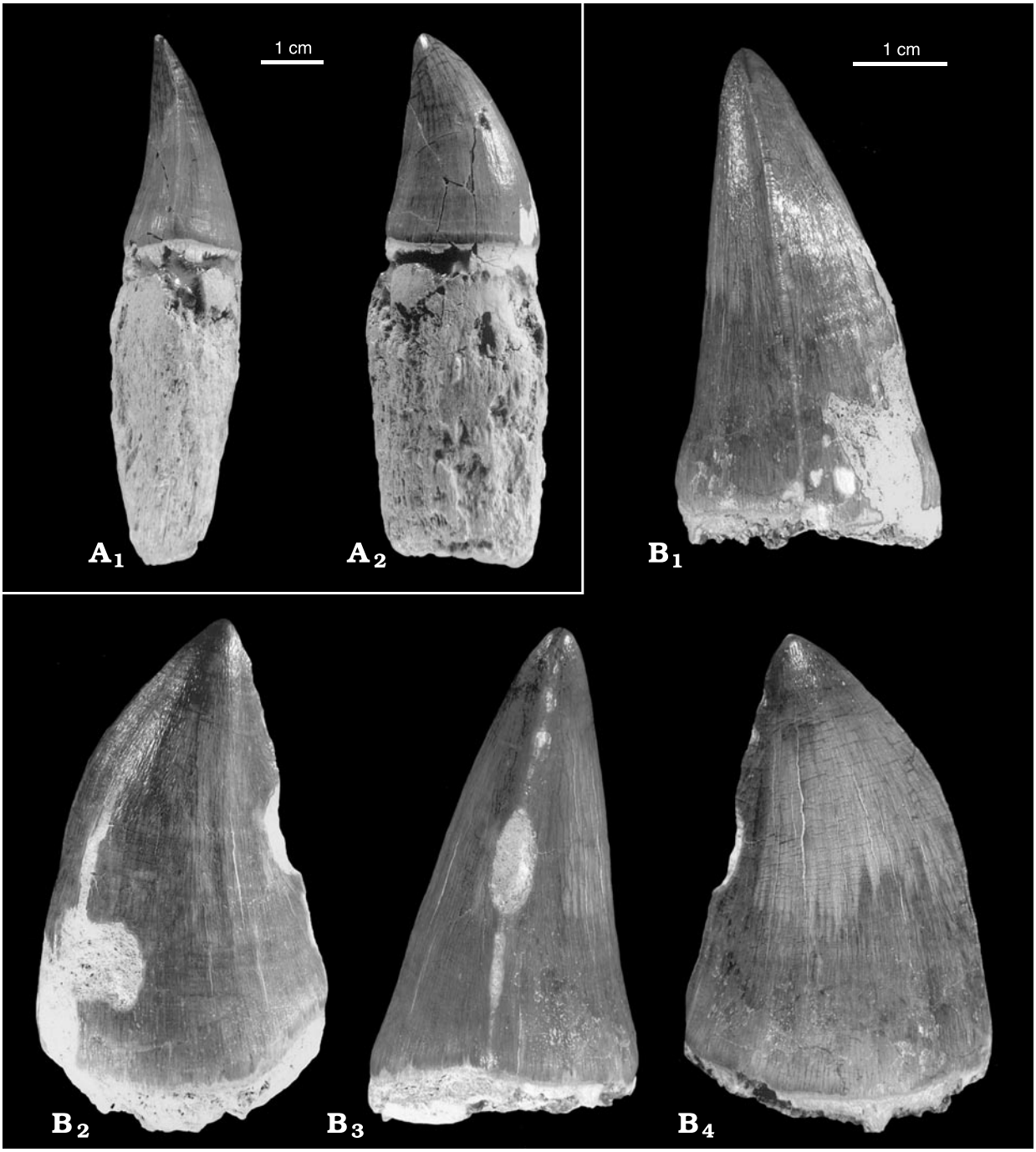


Fig. 8. "*Mosasaurus* (*Leiodon*) cfr. *anceps*" *sensu* Arambourg (1952), from the upper Upper Maastrichtian opoka at Nasiłów. **A**. ZPAL R. 9/3 in posterior (A_1) and buccal (A_2) views. **B**. ZPAL R. 9/4 in anterior (B_1), buccal (B_2), posterior (B_3), and lingual (B_4) views.

referred to as Plioplatecarpinae sp. B (see below). However, some of the tooth crowns in the type series of *Mosasaurus beaugei* Arambourg, 1952 (pl. 39: 13–21) from the Maastrichtian of Morocco may be related, especially the more laterally compressed ones showing a slight lingual recurvature.

"*Mosasaurus* (*Leiodon*) cfr. *anceps*" *sensu* Arambourg (1952)

Fig. 8.

Material.—A single tooth ZPAL R.9/3 and a tooth crown ZPAL R. 9/4 from the upper Upper Maastrichtian opoka at Nasiłów. Comparative material from the Maastrichtian type area includes NHMM 007129.

Description.—Specimen ZPAL R. 9/3, a lateral tooth, measures 85.8 mm in height (inclusive of root), and shows well-developed anterior and posterior carinae, both with minute serrations (Fig. 8A). In cross section it is elliptical, with buccal and lingual surfaces subequal, the latter more

broadly rounded. Facetting is not well developed, but is more clearly seen on the lingual surface. The crown is faintly posteriorly recurved, and more strongly so lingually. Enamel beading is present, but poorly developed.

Specimen ZPAL R. 9/4 (Fig. 8B) is 45 mm in height and has a subcircular cross section, with a more broadly rounded lingual surface, well-developed anterior and posterior carinae with minute serrations, faint facets on both surfaces, and depressed areas parallel to both carinae, along the entire crown height. Enamel beading is well developed.

Discussion.—There is a good match between these specimens and material from the Maastrichtian of Morocco referred to as *Mosasaurus (Leiodon)* cfr. *anceps* by Arambourg (1952: 279, pl. 38; pl. 39: 8–11). There is also a good match with a single tooth NHMM 007129 from the Maastrichtian type area, illustrated by Kuypers et al. 1998: pl. 3: 3, 4, and ascribed to *M. hoffmanni*. All these teeth have subequal buccal and lingual surfaces (with buccal surfaces slightly more inflated), sharp and excavated cutting edges, weakly developed facets (better developed in the Polish material than in that from Morocco) and more or less clearly developed beading of the enamel. The last feature makes a significant difference in relation to teeth of the genus *Liodon* Agassiz, 1846 (= *Leiodon* Owen, 1841, *non* Swainson, 1839), which are smooth, including the type material of *Leiodon anceps* Owen, 1845 from the Upper Campanian *Belemnitella mucronata* Zone of Essex, England (Lingham-Soliar 1993).

The material described by Arambourg (1952) is in need of revision; it may represent a new mosasaurid taxon. Awaiting this revision, we provisionally denote the Polish and Maastricht specimens as "*Mosasaurus* (*Leiodon*) cfr. *anceps*" *sensu* Arambourg (1952), to stress a possible occurrence of an allegedly typically African species in Europe.

Plioplatecarpinae sp. A

Fig. 9B.

Material.—A single, fragmentary tooth crown IGPUW AR-5 from the Upper Campanian opoka at Piotrawin.

Description.—As preserved, this bicarinate tooth crown measures 38.0 mm in height, and 20.2 mm in width (at the base); the cross section is elliptical, with lingual and buccal surfaces of subequal convexity. Anterior carina sharp, well developed, the posterior carina not being preserved; no serrations visible. The crown has a slight posterior recurvature. The buccal surface shows at least seven facets of unequal width, the lingual surface 9–10; these facets do not reach mid-height. Very faint striae on both surfaces are visible; these are confined to the proximal portion of the crown; otherwise the crown shows smooth enamel. The upper portion of tooth is broken; in anterior view (Fig. $9B_2$), the slight lingual recurvature of the crown may be seen.

Discussion.—In combining facetting with proximal striae and slight lingual recurvature of the crown, the present specimen is reminiscent of teeth assigned to the genera *Plioplatecarpus* Dollo, 1882 and *Platecarpus* Cope, 1869. It is too poorly preserved to allow a more definite taxonomic assignment.

Plioplatecarpinae sp. B

Fig. 9A.

Material.—A single tooth MKD. MP-18 from the upper Upper Maastrichtian opoka at Nasiłów.

Description.—As preserved, this bicarinate tooth measures 24 mm in height, and 8.6 mm in width (at the base); in cross section it is elliptical, with subequal lingual and buccal surfaces. Both anterior and posterior carinae are well developed; serrations are preserved in patches only. The crown has a slight posterior and lingual recurvature. The buccal surface shows at least seven facets of comparable width, the lingual surface 11–12; these facets do not reach mid-height. Close to the base, very faint striae on both surfaces are visible, confined to the most proximal portion of the crown, otherwise smooth.

Discussion.—In showing a combination of well-developed facetting, a slight lingual recurvature of the crown, and basal crown striae, the present specimen is reminiscent of teeth assigned to the genera *Plioplatecarpus* and *Platecarpus*. However, it lacks the highly typical, abrupt posterior recurvature from the mid-height of the crowns, as seen in *Plioplatecarpus*. Moreover, its fine basal striae are not as pronounced as those in *P. marshi* Dollo, 1882 (especially lingually) from the Maastrichtian type area (see Dollo 1882; Lingham-Soliar 1994a; Kuypers et al. 1998). It should also be noted that some teeth from the Maastrichtian of Zaire described by Lingham-Soliar (1994b) as cf. *Mosasaurus lemonnieri*, are similar to the present specimen.

In comparison with tooth crowns here assigned to *Mosasaurus* cf. *lemonnieri* (Fig. 7), the present tooth is more slender, has more facets both buccally and lingually, and shows a lesser lingual recurvature. Plioplatecarpinae sp. A. (see above) is considerably less slender, is of larger size and has fewer facets on the lingual surface and no serrations on the carinae.

Genus *Prognathodon* Dollo, 1889a: 181

(see also Dollo 1889b: 214; *Prognathosaurus* Dollo, 1889c: 293)

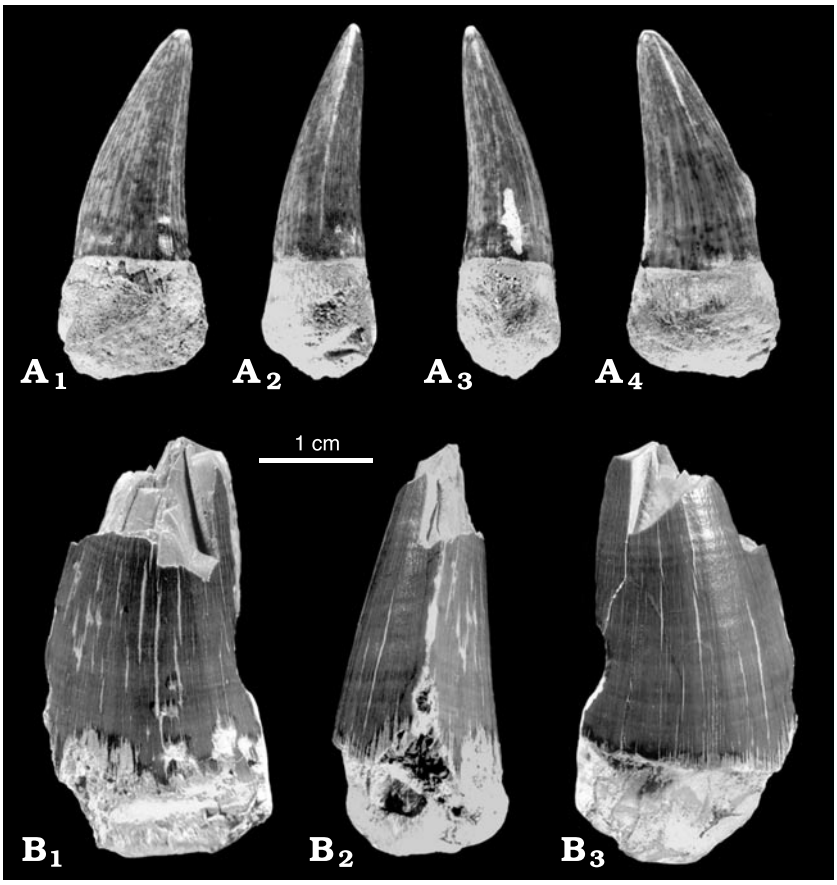
Type species: *Prognathodon solvayi* Dollo, 1889a: 181, by monotypy (see also Dollo 1889c: 293, pl. 9: 4, 5; pl. 10: 8, 9).

Prognathodon sp.

Fig. 10.

Material.—A single tooth crown IGPUW AR-6, abraded anteriorly and at the apex, from the Upper Campanian opoka at Piotrawin.

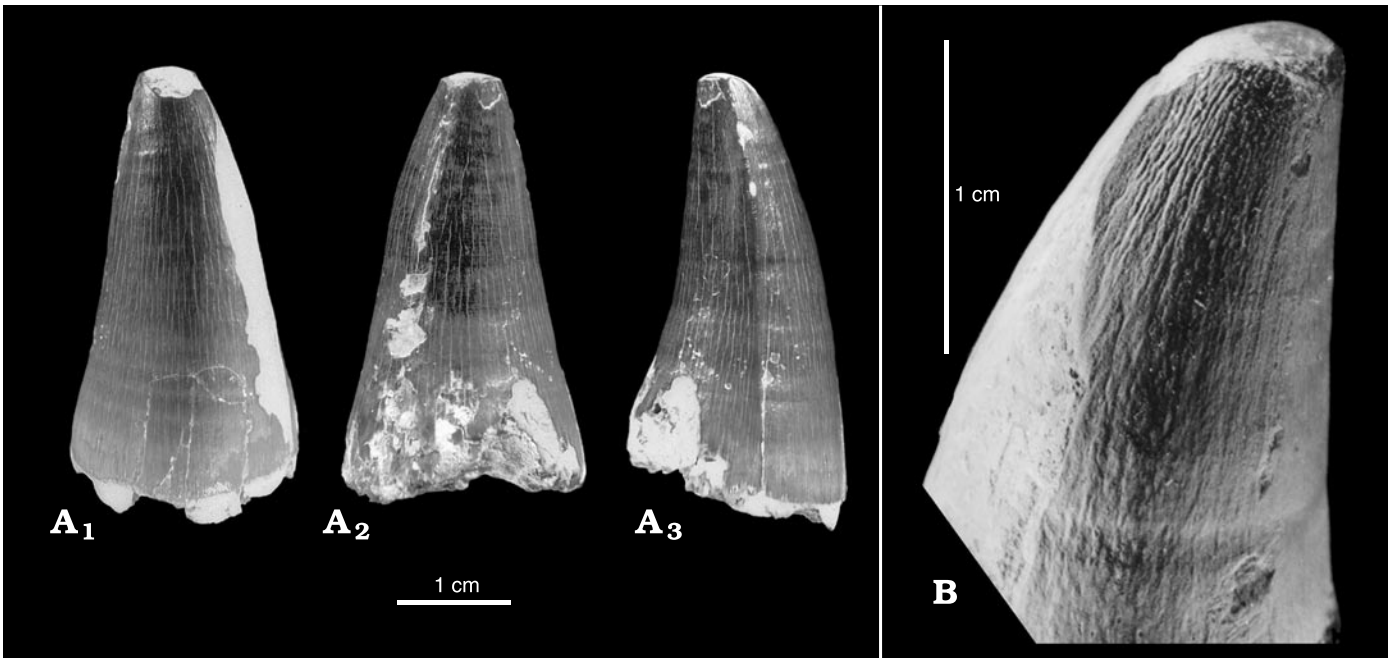
Description.—As preserved, this robust, bicarinate tooth crown measures 39.3 mm in height, and 22.0 mm in width (at the base); in cross section it is subcircular, with subequal lingual and buccal surfaces. Anterior and posterior carinae are comparatively faint, and apparently of comparable strength (although anterior carina is damaged over almost its entire length, see Fig. $10A_1$). Distally, the posterior carina shows very fine serrations (Fig. $10A_3$). The crown has a slight posterior recurvature, and shows smoothly surfaced enamel. No facets; ornament consists of very fine striae which become



← Fig. 9. **A**. Plioplatecarpinae sp. B from the upper Upper Maastrichtian opoka at Nasiłów (MKD. MP-18) in lingual (A_1), posterior (A_2), anterior (A_3), and buccal (A_4) views. **B**. Plioplatecarpinae sp. A from the Upper Campanian at Piotrawin (IGPUW AR-5) in lingual (B_1), anterior (B_2), and buccal (B_3) views.

Fig. 10. **A**, **B**. *Prognathodon* sp. from the Upper Campanian opoka at Piotrawin (IGPUW AR-6) in buccal (A_1), lingual (A_2), and posterior (A_3) views. **B**. Magnification of the apical part of the same specimen to show the anastomosed ornament mentioned in the text (specimen coated with ammonium chloride).

↓



more pronounced at crown mid-height, and which form an anastomosed pattern towards the apex (Fig. 10B).

Discussion.—In showing smoothly surfaced enamel, without facets, an ornament of very fine striae which form an anastomosing (reticulate) pattern near the tip, a slight posterior recurvature and subequal lingual and buccal surfaces, as well as in being robust and bicarinate, specimen IGPUW AR-6 finds a good match in material of late Early Campanian age from the Reims area (Champagne, France), referred to *Prognathodon giganteus* Dollo, 1904 by Bardet et al. (1997:

figs. 2, 3). Those authors stressed the presence of the characteristic anastomosed ornament near the teeth apex of *P. giganteus*. The type specimen of *P. giganteus* (IRScNB R106), from the lower Lower Maastrichtian *Belemnella obtusa* Zone of the Mons Basin, southern Belgium, reveals this ornament as well. Thus, Bardet et al. (1997) considered it to be diagnostic of *P. giganteus*. However, J. Martin (personal communication in November 2002) informs us that anastomosing ridges also occur in teeth of *Prognathodon overtonii* (Williston, 1897), and we here prefer only generic assignment for the specimen IGPUW AR-6.

Teeth of *Prognathodon solvayi* Dollo, 1889a (type IRScNB R33), also from the lower Lower Maastrichtian *Belemnella obtusa* Zone of the Mons Basin, differ in being only moderately inflated, strongly striated and slightly facetted with 7–8 facets on the buccal surface (Lingham-Soliar and Nolf 1989: figs. 20, 27).

Tooth crowns from the Maastrichtian of Zaire (Congo), illustrated by Lingham-Soliar (1994b: fig. 1e, f) and referred to as cf. *Prognathodon giganteus*, differ in having only anterior carinae.

Prognathodon currii Christensen and Bonde, 2002 from the uppermost Campanian of the Negev Desert (Israel; see Christiansen and Bonde 2002) has large and stout, subconical teeth that are ellipsoid in cross section, with blunt apices and unfacetted enamel with fine anastomosing lines apically; posterior and anterior carinae are well developed.

Teeth of *Prognathodon saturator* Dortangs et al., 2002 from the Upper Maastrichtian of the Netherlands (Dortangs et al. 2002) are more compressed, have a stronger lingual recurvature and pronounced posterior and anterior carinae.

Ecology and taphonomy

In total, the available collection of Campanian and Maastrichtian mosasaurids from central Poland comprises fourteen specimens: thirteen teeth or tooth crowns and a single fragmentary jaw. They belong to six taxa: *Prognathodon* sp., Plioplatecarpinae sp. A, and Plioplatecarpinae sp. B, *Mosasaurus* cf. *hoffmanni* Mantell, 1829 and *M.* cf. *lemonnieri* Dollo, 1889c, and "*Mosasaurus* (*Leiodon*) cfr. *anceps*" *sensu* Arambourg (1952).

The relatively high diversity of mosasaurid reptiles in Poland *vs*. the low number of specimens in total and per taxon, suggests that they represent occasional invaders or drifted carcasses rather than permanent inhabitants of the area. This is supported by the taphonomy of the mosasaurid remains from the opoka. With the exception of a single fragment of vertebral column from the Upper Campanian at Piotrawin (MKD. MP-47, not included in the present study), no vertebrae, ribs and/or appendicular skeletal elements of mosasaurs have been collected from that facies. Isolated tooth crowns from the opoka may be interpreted as broken-off or shed during periodic feeding in the area. Complete teeth and jaw fragments, in contrast, are best interpreted as stemming from floating carcasses. For obvious reasons, the conditions of the original burial of the reworked specimens from the Danian greensand are impossible to reconstruct. In summary, for reasons unknown to date (possibly depth and/or temperature related), marine lizards did not frequently visited the present-day area of central Poland.

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