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GIANT *MOSASAURUS HOFFMANNI* (SQUAMATA, MOSASAURIDAE) FROM THE LATE CRETACEOUS (MAASTRICHTIAN) OF PENZA, RUSSIA

D.V. Grigoriev

Saint Petersburg State University, Universitetskaya Emb. 7-9, 199034 Saint Petersburg, Russia;
e-mail: grigoriev_dmitry@mail.ru

ABSTRACT

This study provides a morphological description of the fragmentary skull of a mosasaur discovered in 1927 in the Upper Cretaceous (Maastrichtian) deposits in the city of Penza (Russia). Some bones from the original material had been lost since their discovery; their description is based on plaster casts. The Penza mosasaur displays characteristic features of *Mosasaurus hoffmanni* such as the posterior carina that shifts from a somewhat lateral position in the anterior teeth to a posterior position further along the tooth row, a frontal with convex lateral margins, and a powerfully built dentary. This is the first unequivocal record of this taxon from Russia. *M. hoffmanni* from the Penza is one of the largest mosasaurs ever known with an overall length of the body about 17 m.

Key words: Maastrichtian, Cretaceous, Penza, *Mosasaurus hoffmanni*, Mosasauridae

ГИГАНТСКИЙ *MOSASAURUS HOFFMANNI* (SQUAMATA, MOSASAURIDAE) ИЗ ПОЗДНЕГО МЕЛА (МААСТРИХТА) ПЕНЗЫ, РОССИЯ

Д.В. Григорьев

Санкт-Петербургский Государственный Университет, Университетская наб. 7-9, 199034 Санкт-Петербург,
Россия; e-mail: grigoriev_dmitry@mail.ru

РЕЗЮМЕ

Приведено детальное морфологическое описание фрагментарного черепа мозазавра, найденного в 1927 г. в верхнемеловых отложениях (маастрихт) г. Пенза, Россия. Часть оригинальных костей была впоследствии утрачена; их описание выполнено по сохранившимся гипсовым слепкам. На основании изменения положения зубной карины от передних к задним зубам, лобной кости с выгнутыми боковыми сторонами и массивных зубных костей пензенская особь отнесена к *Mosasaurus hoffmanni*. Это первая достоверная находка данного вида на территории России. Мозазавр из Пензы был одним из крупнейших представителей семейства, с длиной тела достигавшей не менее 17 м.

Ключевые слова: маастрихт, мел, Пенза, *Mosasaurus hoffmanni*, Mosasauridae

INTRODUCTION

In the Russian territory and adjacent countries, mosasaurs are predominantly known from fragmentary specimens, predominantly isolated bones. More or less complete mosasaur skeletons are extremely rare. Such findings include a partial skeleton of *Prognathodon lutugini* Yakovlev, 1901 from the Campanian deposits in East Ukraine (Yakovlev 1905; Grigoriev 2013); a partial strongly deformed skeleton from the Maastrichtian locality Rasstrigin (the right-bank part of the Volgograd Region) (Lavrentiev 1930; Yarkov 1993), lost during World War II; a partial skeleton from the Maastrichtian locality Sergievka

(the right-bank part of the Saratov Region), which has been defined by Bayarunas (1914) as a *Mosasaurus* sp. and which was severely damaged during a fire; and a partial skeleton from the early Maastrichtian site Nevezhkino-1 (Saratov Region), which has also been damaged (Pervushov et al. 1999).

One of the most complete findings, which has been preserved till our time almost undamaged, is a mosasaur skull found in Penza (Fig. 1). This skull is remarkable because of its large size and for the historical circumstances of its discovery.

In 1927, political exile, the socialist revolutionary M.A. Vedenyapin found the bones of a large marine reptile at the outskirts of Penza in a ravine where Red Army soldiers trained in machine gun shooting. Excavations were started at the site of Vedenyapin's finding. The entire population of Penza soon began speaking about the excavations. In a church, a preacher gave a sermon that these were the bones of the animal that did not go on Noah's Ark, and many interested people would often crowd around the excavations. Vedenyapin would lecture on the geological past of Penza. According to Vedenyapin, there were 10s of thousands of people one day. There were thefts of the findings, after which a militiaman was appointed to guard the excavation site. When more bones were stolen at night, a Red Army patrol was sent to carry out day-and-night security. The works were performed quickly because of rains, which could cause landslides on the slope. Lower jaw bones, scapula, vertebrae, and ribs were found during the excavations. To ensure better preservation of the found material, it was placed in boxes together with the matrix and sent to the Saint Petersburg Geological Committee (Archive of the Penza Regional Museum; Arkhangelsky et al. 2012).

According to the A.N. Ryabinin's entry in the inventory book of Chernyshev's Central Museum of Geological Exploration the bones were assigned to *Mosasaurus giganteus* Sömmerring, 1816. N.P. Stepanov mounted the skull, after which it was exhibited in Chernyshev's Central Museum of Geological Exploration, Saint Petersburg (Fig. 2). An exact plaster copy was sent to the Penza Regional Museum. Unfortunately, the skull exposed in Saint Petersburg suffered the same fate as some of the bones from the excavations: all small and unsecured bones and teeth were stolen by visitors of the museum. The skull has been covered with a bell glass only relatively recently (oral communication from the museum staff T.V. Vinogradova and N.M. Kadlets).

It is necessary to note that some mosasaur remains were found at the same site before Vedenyapin's finding. In 1925, the right part of a lower jaw with teeth, apparently a caudal vertebra with processes, quadrate, and several teeth were found at the same site. From photos, this material was assigned to *Mosasaurus giganteus* or *Mosasaurus camperi* by Tsaregradskii (1926). Earlier, in 1918, during digging in a cellar in Penza (at Dvoryanskaya street, presently Krasnaya street), 11 mosasaur vertebrae were found. All of the found materials were transferred to the Penza Regional Museum but were later lost (Archive of the Penza Regional Museum).

Institutional abbreviations. CCMGE – Chernyshev's Central Museum of Geological Exploration, Saint-Petersburg, Russia; IRSNB – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; PRM – Penza Regional Museum, Penza, Russia; TMP – Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

MATERIAL AND METHODS

The original skull of the Penza specimen (CCMGE 10/2469) is mounted in the exhibition hall of Chernyshev's Central Museum of Geological Exploration in Saint Petersburg (Figs 2, 3, 5A, B). An unassembled plaster copy of the same specimen (PRM 2546) is exhibited in the Penza Regional Museum. During the mounting of the original skeleton by N.P. Stepanov, the bones were covered with a very thick layer of polyvinyl butyral (PVB), and it is therefore very difficult or sometimes impossible to define the contacts between certain bones on the original material. Because the mosasaur skull is exposed in the museum, it was impossible to dissolve the PVB and study some bones in detail due to their rigid attachment to the frame. Unlike the original material, in most cases, it is possible to trace these contacts on plaster casts. In addition, the original material was damaged by museum visitors. Thus, all the original teeth from the mandibles were stolen (the plaster casts of the teeth on the original mandibles do not correspond to the real teeth that were set in their places because they were made after the theft, unlike the Penza casts). The right angular-surangular-coronoid-articular-prearticular unit was heavily damaged on the edges, and the left angular, parietals, left postorbitofrontal, left squamosal and element of the scapula-coracoid (It is impossible to determine

Fig. 1. Locality of *Mosasaurus hoffmanni* (PRM 2546), indicated by a star in the city of Penza (Penza Region, Russia).

whether it is scapula or coracoid) have been lost. Additionally, the skull mounted in Saint Petersburg has incorrectly placed bones. For example, the right splenial was oriented backwards, and right dentary fragments are set in the wrong order (Fig. 5A). A detailed study of this specimen is possible only because a plaster copy was preserved as were some original photographs. For the reconstruction of the skull (Fig. 4A–C), all available data were used. A photo of the skull (Figs 2, 3) made right after the mounting in 1927 was used in addition to the existing original and plaster copy material. Through this pictures, the correct position of the dentary fragments was restored. This photo was also used for the splenial reconstruction (9C, F), which was not entirely preserved in the original or plaster material. Apparently, in the photos, it is possible to observe mistakes made during the mounting (shown by the arrows in Figs 2 and 3). For example, the left angular is placed on the right side, thereby increasing the height of the right posterior mandibular unit, and the dentary is pushed too far forward, thus creating a false impression of its total length. In Fig. 3, the arrow and dotted line shows incorrectly fitted bone to the articular. In this study, photos of bones with protruding elements have been taken at different depth levels and combined using Helicon Focus 4.2.9 X64 (Focus stacking software that increase the depth of field in an image).

The osteological terminology is based predominantly on Russell (1967), and the systematics follow Palci et al. (2013).

SYSTEMATICS

Order Squamata Oppel, 1811

Family Mosasauridae Gervais, 1853

Subfamily Mosasaurinae Gervais, 1853

Genus *Mosasaurus* Conybeare, 1822

***Mosasaurus hoffmanni* Mantell, 1829**
(Figs 2–12)

Material. *Original material*: CCMGE 10/2469, a partial skull including two dentaries, with one preserved replacement tooth in the alveolar margin on the left ramus (?), right and left splenials, the right

Fig. 2. Laboratory assistant Stepanov N.P. and prepared skull of the Penza specimen. Year 1929. The single arrow shows the incorrectly positioned left angular. The two arrows and the dotted line between them illustrate the correct position of the posterior end of the dentary.
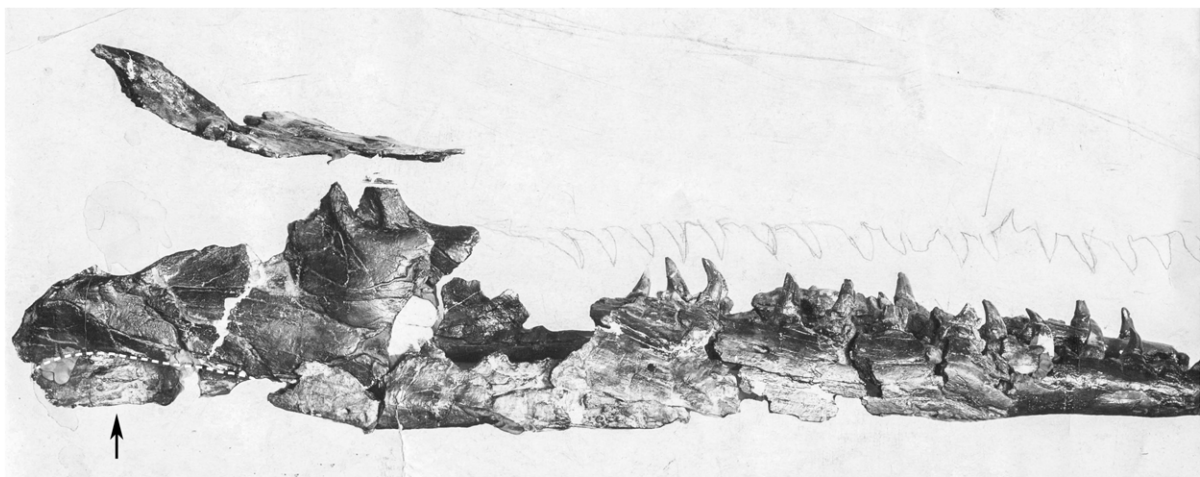

Fig. 3. Prepared skull of the Penza specimen. The dotted line and arrow indicate the incorrectly fitted undefined bone to the articular.
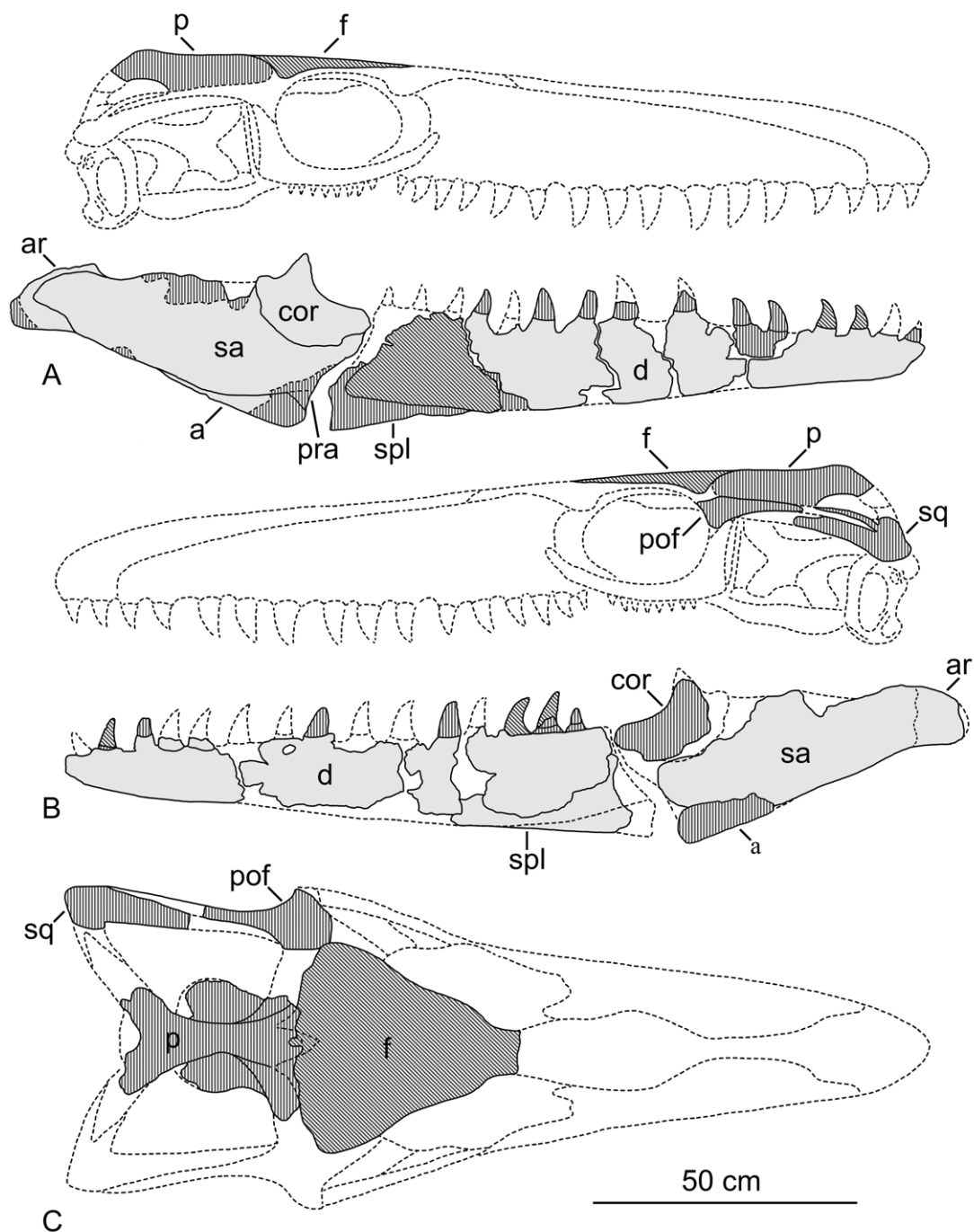
Fig. 4. Reconstruction of *Mosasaurus hoffmanni* (CCMGE 10/2469, PRM 2546) in the right lateral (A), left lateral (B) and dorsal (C) views. Redrawn from Lingham-Soliar (1995). The presented skeletal elements are marked in gray. Oblique hatching represents skeletal elements recovered exceptionally from the archival photos (Figs 2 and 3). Vertical hatching represents the skeletal elements that were not preserved in the original material but that are presented in the form of plaster casts. The dotted line indicates missing portions of the skull. Abbreviations: a, angular; ar, articular; cor, coracoid; d, dentary; f, frontal; p, parietal; pof, postorbitofrontal; pra, prearticular; sa, surangular; spl, splenial; sq, squamosal.

the splenial should be turned backwards

20 cm

Fig. 5. Preserved original *Mosasaurus hoffmanni* (CCMGE 10/2469) material in the right lateral (A) and left lateral (B) views. The arrow indicates the correct position of the dentary fragment. All represented teeth are plaster copies that do not correspond to the real teeth.

angular in articulation with the right surangular, coronoid, articular and prearticular, left surangular, articular and prearticular in the articulation as well.

Plaster copy: PRM 1-5/2546, right dentary consisting of five parts with eight teeth sitting in the alveolar margins; PRM 6-10/2546, left dentary consisting of six parts with three teeth sitting in the alveolar margins and one separate tooth with the root; PRM 13,14/2546, right and left splenials; PRM 16/2546, right angular in articulation with the right surangular, coronoid, articular and prearticular; PRM 15/2546, left angular; PRM 18/2546, left coronoid; PRM 17/2546, left surangular in articulation with the articular and prearticular; PRM 19/2546 left postorbitofrontal; PRM 22/2546, left squamosal; PRM 21/2546, parietals; PRM 23/2546, element of the scapula-coracoid. In addition, it is known that there were frontals and ribs initially; however, they are not preserved to the present day.

Locality and horizon. The specimen was collected in the outcrop in the Prolom ravine within the city of Penza, near the Mironositskoe cemetery (Fig. 1). The exact modern position of the locality is unknown. Now on this site most likely the Prolomnaya street passes, and the locality no longer exists.

The highest horizons of the Maastrichtian (Upper Cretaceous) of the *Belemnitella americana* zone are exposed along the Sura River in the city of Penza area. They are represented by micaceous quartz glauconitic aleurite (depth of deposits – 18–20 m) along with *B. lanceolata* Schloth. and *B. americana* Mart. (Chibrikova 1954). Tsaregradskii (1926) notes that the oyster genus *Ostrea praesinzowi* Archangelsky, 1905 (guide fossil for Maastrichtian (Glazunova 1972)) was also found in these deposits. An unusual microfaunal complex was found in the same layer and comprises the guide fossil for the Turonian (*Bolivinita couvigeriniformis* Keller), Santonian (*Reussia subrotundata* Cuschm. et Phomas) and Maastrichtian (*Bolivina incrassata* Reuss) stages, suggesting all the deposits listed above were eroded and took part in the resedimentation of the *B. americana* zone (Chibrikova 1954).

DESCRIPTION

Postorbitofrontal. The left postorbitofrontal is preserved only in the form of a plaster copy (Fig. 6A–C). The articulation for the postorbital process of the parietal is broken at the base. The articulation

for the frontal posterolateral is also absent, and the tip of the squamosal process is slightly broken off. The postorbitofrontal is straight and narrow, and the oblique suture between the postorbitofrontal and squamosal is at least 215 mm long, begins under the jugal process and is represented as a sulcus posteriorly turning in a laterally compressed process sandwiched between the squamosal laminas. The jugal process is triangular in outline and extends to approximately the same length as the main body of the postorbitofrontal. It gradually tapers off to the squamosal process. The jugal process is 50 mm long. There are no signs of a postorbitofrontal transverse dorsal ridge. Overall length of the postorbitofrontal is 286 mm.

Squamosal. There is a preserved plaster copy of the left squamosal (Fig. 6D–G). All processes except for the quadrate process are more or less broken off. The squamosal is comma shaped, tall and laterally compressed. The postorbitofrontal process occupies most of the squamosal. The suture with the postorbitofrontal is represented by the thin, deep sulcus. The medial wall of this sulcus is somewhat shallower than the lateral wall. The squamosal and postorbitofrontal together are slightly arched dorsally. The parietal and quadrate processes are positioned relative to each other at an angle of 90 degrees. Length of the squamosal is 255 mm.

Frontal. The original material or casts of the frontals did not survive; however, in photos (Figs 2, 3) taken in 1927, they are distinctly visible. The bones can be observed in two photos in lateral and dorsolateral views. However, a lack of image resolution and limited viewing angles do not allow for an accurate description, but it is still possible to obtain some information from the photos. Relying on the photos, it is possible to infer that the frontals are broad and short with sinusoidal sides. In the anterior part of the frontals, a low midline dorsal keel is present.

Parietal. Preserved only as a plaster cast of the parietals (Fig. 7A–F). The suspensorial rami and right postorbital process are partly broken, and the left postorbital process is broken at the base. In the dorsal aspect, the main body of the bone has an hourglass shape with approximately the same anterior and posterior portions without boss in the middle. The parietal foramen is located on the anterior edge of the bone. It is relatively small (22 by 13 mm) and oval in outline. On the ventral side, it is surrounded by a barely distinguishable ridge. The depth of this
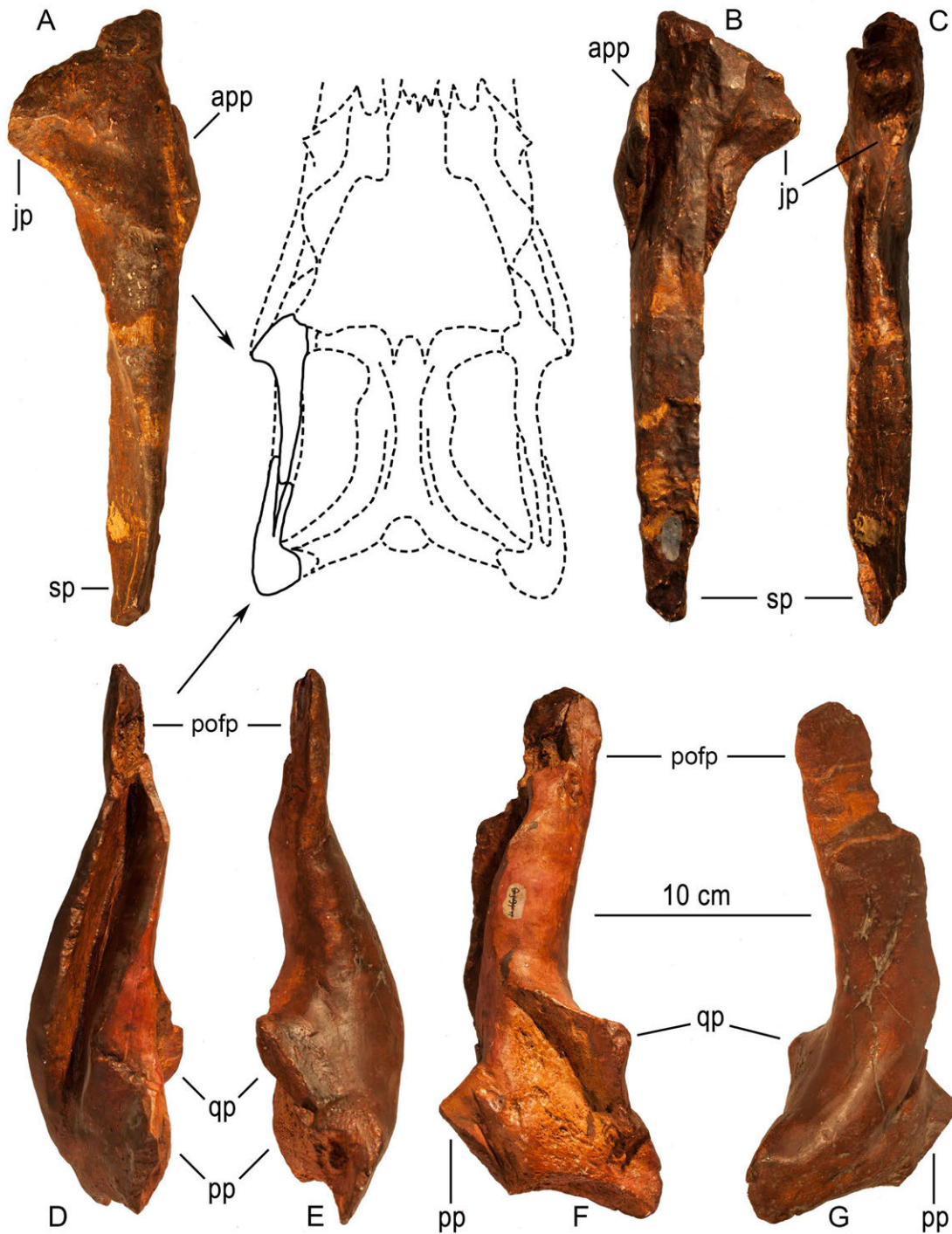
Fig. 6. *Mosasaurus hoffmanni* (PRM 2546) left postorbitofrontal (A–C) and left squamosal (D–G) in the dorsal (A), ventral (B), lateral (C), dorsomedial (D), ventrolateral (E), ventromedial (F) and dorsolateral (G) views. The reconstruction shows the position of the postorbitofrontal and squamosal of the skull. Abbreviations: app, articulation for the postorbital process of the parietal; jp, jugal process of the postorbitofrontal; pofp, postorbitofrontal process; pp, parietal process of the squamosal; qp, quadrate process of the squamosal.
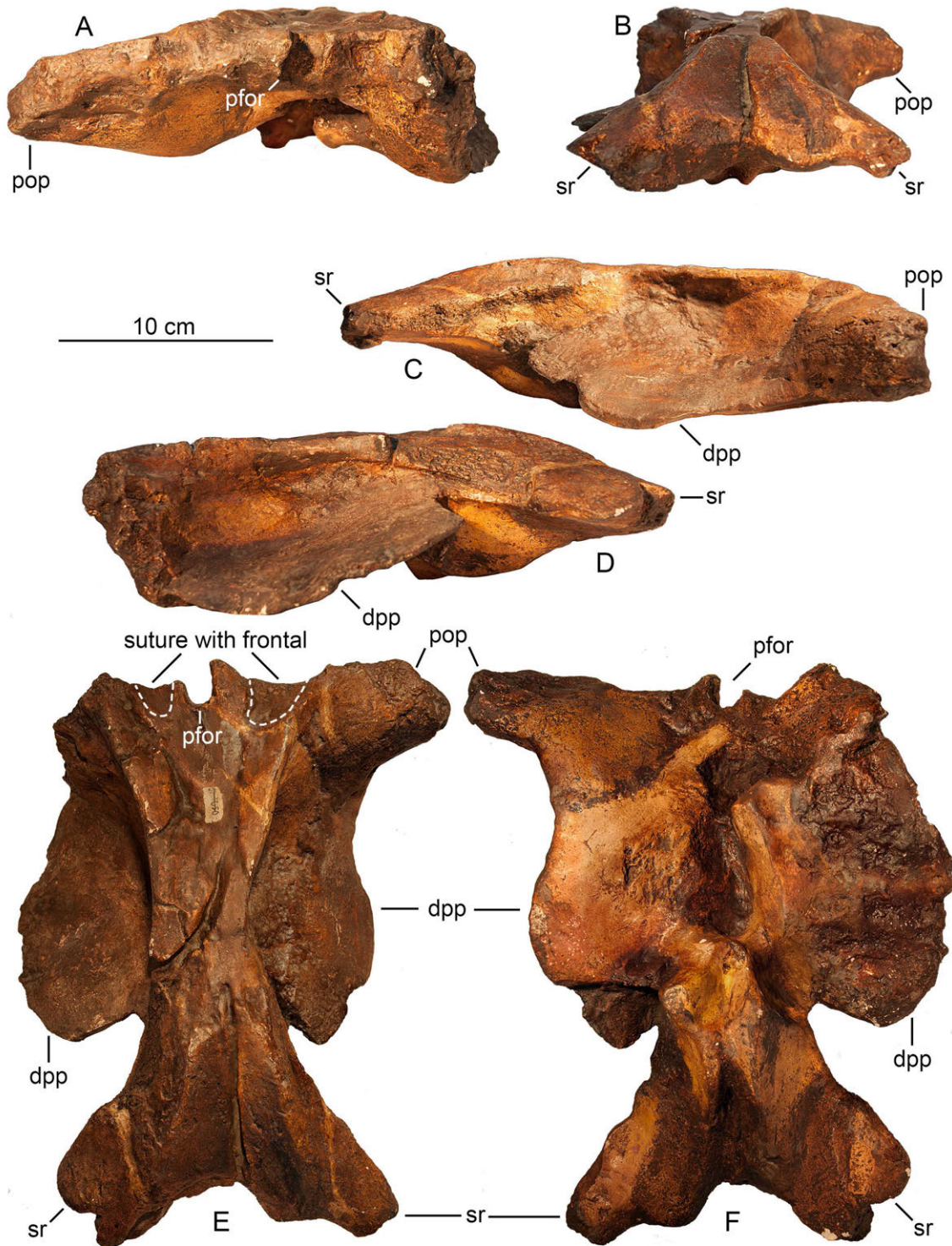
Fig. 7. *Mosasaurus hoffmanni* (PRM 2546) parietal (A–F) in the anterior (A), posterior (B), lateral (C, D), dorsal (E) and ventral (F) views. The dotted lines indicate suture surfaces with the posteriorly projecting wings of the frontal. Abbreviations: dpp, descensus processus parietalis; pfor, parietal foramen; pop, postorbital process of parietal; sr, suspensorial ramus of parietal

foramen is 25 mm. The anterior border of the parietal foramen is broken. Therefore, it is not clear whether it is formed by the parietal, or posterior edge of the frontal. There are triangular suture surfaces with the posteriorly projecting wings of the frontal arranged on the right and left of the parietal foramen (Fig 7E), which itself is fully surrounded by the parietal. From the foregoing, it can be concluded that the parietal foramen is protruding into the frontal. The parietal table bears a distinct shallow medial groove, which begins at the posterior end of the bone, and has a length of 93 mm. Robust postorbital processes ventrally and gradually becomes descensus processus parietalis. The descensus processus parietalis are concave in outline, thin and very wide (up to 63 mm) and do not reach the suspensorial rami. There are no signs of the parietal posterior shelf between the suspensorial rami.

Dentary. Both dentaries are incomplete (Fig. 8A–K). The most posterior parts of the bones are not preserved. The right dentary (Fig. 8A–C) is composed of six fragments (five are known from the factual material, one restored from a photograph) and the left dentary (Fig. 8D–F) of four. The bone is powerfully built. The incompleteness of the dentaries and the breaks between the dentary parts do not allow for the determination of the exact number of alveolar margins in its length. There are at least 12 teeth on the right dentary and at least 15 (12 alveolar margins on the dentary fragments with three more implied between the dentary fragments) on the left. Replacement teeth erupt in the alveolar margins (Fig. 8G). A small projection (approximately 13 mm) of the dentary anterior to the first tooth position is present. The crowns of the posterior marginal teeth are not swollen above the base. The dentary medial parapet strap is equal in height to the lateral wall of the bone. The medial surface of the dentary is slightly concave, with a deep Meckelian canal opened for the length of the dentary and beginning near the anterior tip of the bone. The original reconstruction, which can be observed in the photos (Figs 2, 3), implies that the dentary was longer, at least 200 mm (the posteriormost part has been lost). However, the existing material does not provide grounds to believe that the reconstruction was performed correctly. For maximum dentary length accepted the length of the left dentary, which has the greatest number of alveolar margins. On the basis of the most preserved posterior fragment of the left dentary, it can be assumed

that the size of the teeth is on the decline, therefore the missing dentary posterior fragment should have a small size. The alveolar margins are not concavo-convex. The right dentary as preserved has a length of 910 mm and the left of 1020 mm. Maximum height is 172 mm.

Splenial. Only the posterior parts of both splenials are preserved (Fig. 9A–G), with the medial wing on the left splenial higher compared to the right. The anterior portion (Fig. 9B, D) of the right splenial was preserved in the original material (CCMGE 10/2469), and posterior (Fig. 9A, E, G) only in a plaster copy (PRM 13/2546). The reconstruction (Fig. 9C, F) was made by combining the original and plaster materials. Due to material preservation or the features of the mounting, the lateral and medial wings of both splenials are fused together. The anterior parts of the bones are broken; however, according to the extension of the splenial facet on the left dentary, the bones reached anteriorly to at least the fourth tooth position. The right splenial is clearly expressed the surface, that should be laterally exposed in contact with the dentary. The length of this surface is 258 mm. There are no signs of a foramen for the lingual nerve on the lateral surface of the bone near the splenial articulation (likely due to the large cracks dissecting the medial side of the bone). The articulation with the angular (Fig. 9G) is present only on the right splenial, is laterally compressed (height to width ratio is 0.51) and has a smooth concave surface.

Angular. Preserved left separate angular (Fig. 9H–J) and right angular in articulation with the right surangular, coronoid, articular and prearticular (Fig. 10A–F). The right angular is in poor condition and is overlapped by the surangular 270 mm from the anterior tip of the bone, where the angular is broken off. A thin and broad wing from the medial side of the angular and a short heavy wing from the lateral side together form a narrow groove for the prearticular. There is a foramen for the angular branch of the mandibular nerve on the anterior part of the medial wing of the left angular. The articulation for the splenials is preserved on both angulars (Fig. 9J) in the form of a rounded "V" with a smooth convex surface.

Surangular. The right surangular is almost complete (with the exception of a partially broken dorsal wall). It is in articulation with the coronoid, articular, prearticular and angular (Fig. 10A, B, D). The left surangular is in approximately the same condition but articulated only with the articular
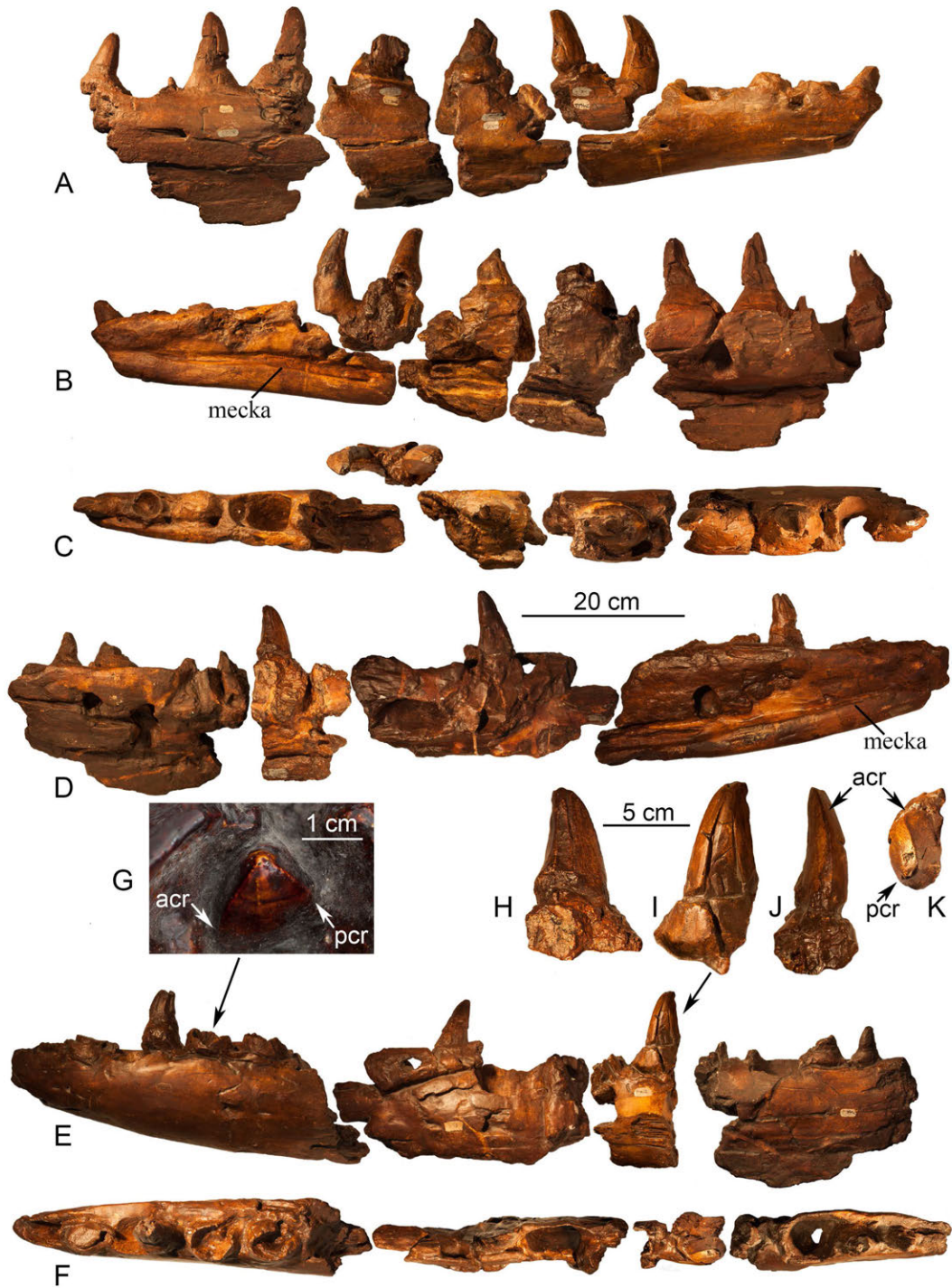
Fig. 8. *Mosasaurus hoffmanni* (PRM 2546) dentary (A–F) and teeth (J–K) in the lateral (A, E), medial (B, D), dorsal (C, F), apical (G, K), lingual (H), buccal (I) and anterior (J) views. Magnified teeth (G) are examples of the anterior (the only remaining tooth from the original material) and posterior teeth. Arrows indicate their actual positions. Abbreviations: acr, anterior carina; meckca, Meckelian canal; pcr, posterior carina.
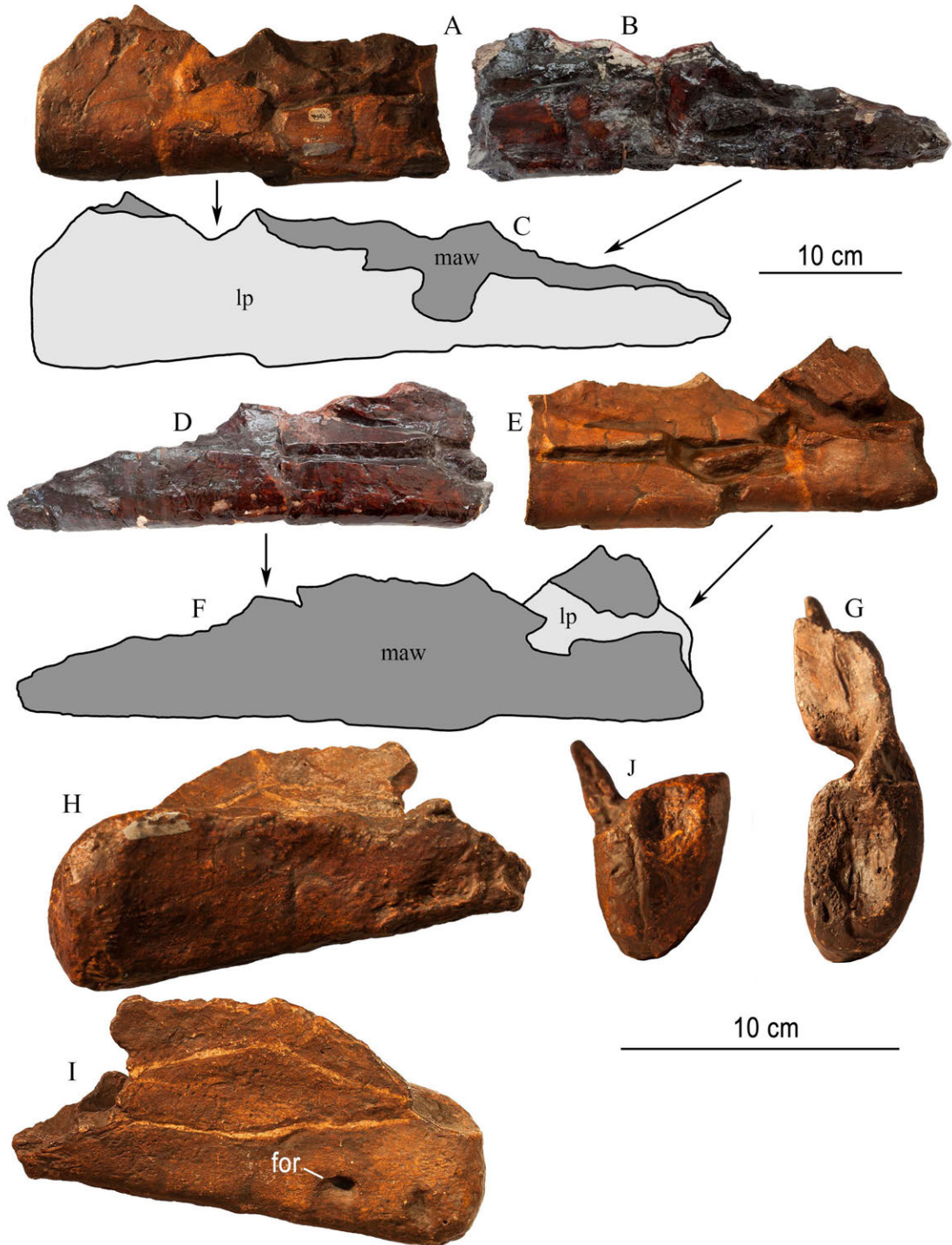
Fig. 9. *Mosasaurus hoffmanni* (CCMGE 10/2469, PRM 2546) right splenial (A–G) and left angular (H–J) in the lateral (A–C, H), medial (D–F, I), anterior (J) and posterior (G) views. Reconstruction (C, F) made by combining the original (CCMGE 10/2469 (B, D)) and plaster materials (PRM 2546 (A, E, G–J)). The arrows indicate the actual position of the skeletal elements on the reconstructions. Abbreviations: for, foramen for the angular branch of the mandibular nerve; lp, lateral process; maw, medial ascending wing.

and prearticular, and the posterior end of the bone is broken right after the glenoid fossa (Fig. 10C, E, F). The element is elongated and laterally flattened, and the dorsal border of the surangular is a high thin wall that forms a coronoid buttress. This wall has a slight bend on the medial side (Fig. 10C, D). A moderate depression is preserved on the right surangular on the anterolateral edge of the bone under the anterior edge of the coronoid. This depression represents the anterior surangular foramen (Fig. 10A). The glenoid fossa is preserved on the left surangular (Fig. 10F); on the right surangular, it is damaged (outlines of the glenoid fossa on the reconstruction are drawn approximately). It is well developed, roughly oval and slightly concave. The borders of the glenoid fossa are defined by the ridge. The surangular takes part in the anterior and lateral borders of the glenoid fossa, with the rest of the fossa being formed by the articular. The surangular-articular suture extends posteriorly from the glenoid fossa. After the glenoid fossa surangular suture rises up to the posterodorsal edge of the bone, the suture runs for 75 mm along the edge, than bends on the other side and then abruptly turns anteriorly. Further tracking of the suture position is impossible because of the poor preservation. The length of the right surangular is 645 mm, left surangular is 525 mm. The surangular length occupies 75% of the dentary length (if the overall length of the dentary is approximately 1020 mm).

Coronoid. The preserved right coronoid is in contact with the surangular (Fig. 10A, B) and a plaster copy of the left coronoid. The tip of the posterodorsal process, the partial medial wall, and likely, the most anterior part are crushed. The coronoid is saddle shaped with a well-developed posterodorsal process. The dorsal border of the coronoid is concave and inclined at approximately 115 degrees. There is a "C"-shaped excavation on the medial side of the posterodorsal process (Fig. 10B). A small broken posteromedial process is present below this excavation. The anteroventral border of the lateral wing is emarginated for the anterior surangular foramen (Fig. 10A). The lateral descending wing is relatively shallow and semicircular (with the exception of the anteroventral excavation). Because of the large amount of the PVB glue on the bones, the position of the lower bound of the lateral wall may be located somewhat below those shown in the reconstruction. The medial wing descends much lower; however, the exact position of the lower boundary is undefined.

Even though the medial wing of the right angular is also partially broken, on the basis of the left angular, it can be assumed that upper medial wall of the angular should be in contact with the medial wing of the coronoid or at least that they should be in close proximity to each other. The distance between the preserved bones on the right posterior mandibular unit is 27 mm.

Maximum length of the coronoid is 180 mm; height of the lateral wing in the anterior part of the bone is 70 mm; height of the medial wing in the middle part of the bone is 150 mm. Posterodorsal process height is 50 mm.

Articular-prearticular. In the material there are right articular-prearticular presented in articulation with surangular, angular and coronoid, and missing most of the anterior part contacting with dentary (Fig. 10A, B, D), and left articular-prearticular articulated with surangular also without most of the anterior part (Fig. 10C, E, F). The prearticular is posteriorly fused with the inner surface of the articular, and they are exposed on the medial side of the surangular. It is overlapped from below by the medial wing of the angular and bounded above superficially by the coronoid. The prearticular forms the medial margin of the Meckelian canal. The retroarticular processes are broken on the original material. However, on the plaster copies, it is possible to observe that they lie in a nearly vertical orientation (almost without twisting) (Fig. 10C, D). No large foramina on the lateral face of the retroarticular processes are present on the existing material. They are roundly rectangular in outline.

Marginal dentition. The description of the teeth is based predominantly on the plaster cast material (Figs 8H–K, 11A–H). On the original material, only one replacement teeth on the five tooth position is preserved on the left dentary (Fig. 8G). The teeth are posteromedially recurved, with the exception of the most posterior teeth (the twelfth tooth on the right dentary and the fifteenth tooth on the left dentary), which are slightly bent forward. The bases of the teeth protrude above the dentary almost more than one-third of the overall length of the tooth crowns. The teeth are strongly bicarinate. The plaster casts do not allow for us to hypothesize about the presence of serrations on the carinae. The lingual and labial surfaces are nearly equal on the posterior teeth (Fig. 8G). On the anterior teeth, the lingual surface is more convex and large in comparison with the labial (the
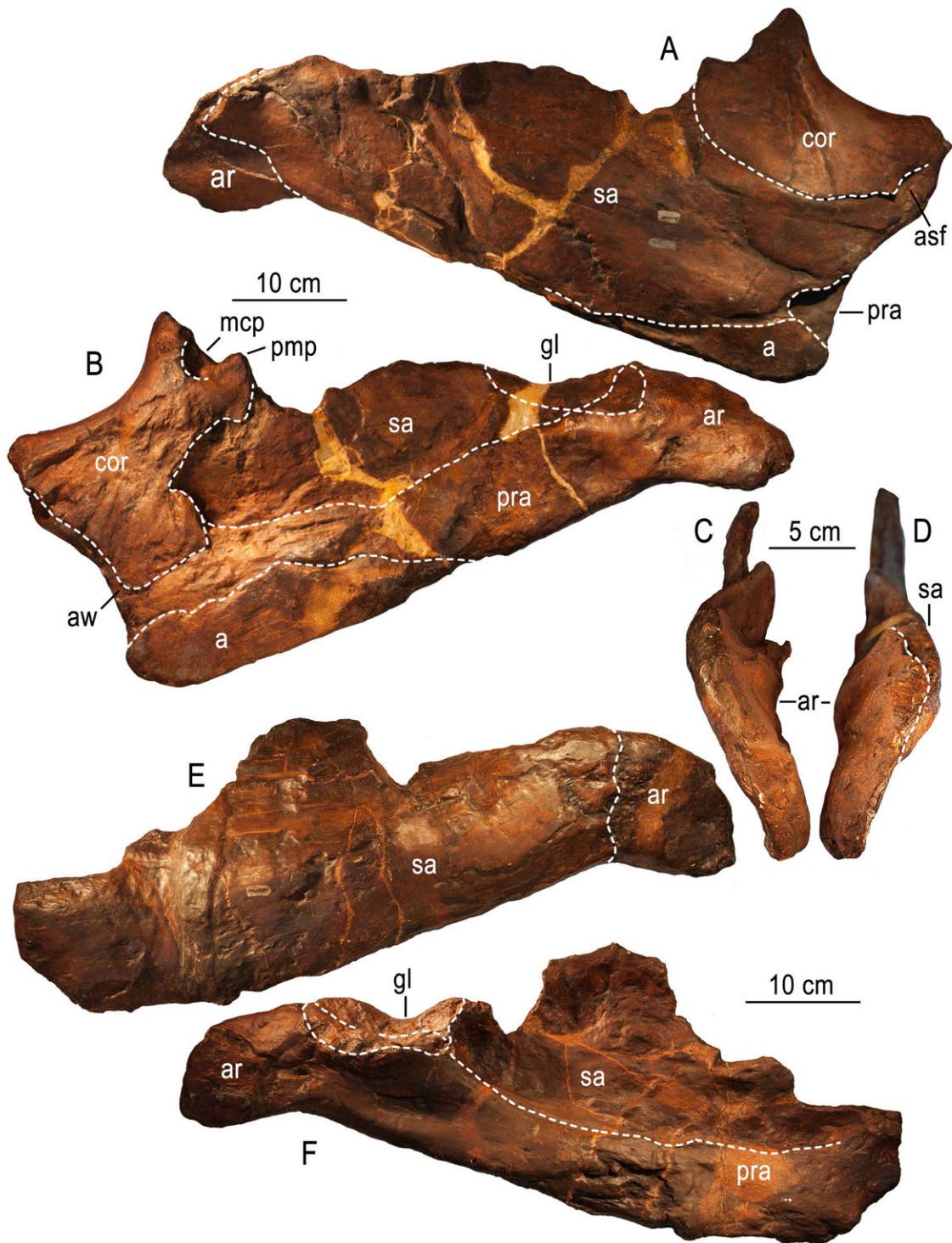
Fig. 10. *Mosasaurus hoffmanni* (PRM 2546) right (A, B, D) and left (C, E, F) posterior mandibular units in the lateral (A, E), medial (B, F) and posterior (C, D) views. Abbreviations: a, angular; ar, articular; aw, anteromedial wing; asf, anterior surangular foramen; cor, coracoid; gl, glenoid fossa; mcp, medial crescentic pit; pmp, posteromedial process; pra, prearticular; sa, surangular.

Fig. 11. *Mosasaurus hoffmanni* (PRM 2546) two right anterior teeth (A–C) and a single anterior tooth with the root (D–H) in lingual (A, D), buccal (B, D), apical (C, H), anterior (F) and posterior (G) views.

anterior and posterior carinae converge at angles up to 110 degrees). The crowns of the posterior marginal teeth are conical (Fig. 8H–K). Some crowns are distinctly faceted (for example fourth tooth on the left mandible). The teeth are up to 103 mm high (when measured together with the base protruding above the dentary) and 56 mm wide at the base.

Scapula-coracoid. The base of the scapula-coracoid element has two facets, a partly broken neck and strongly broken off fan-like blade with an unbroken posterior edge, which are preserved (Fig. 12A–E). On the basis of interposition of facets and overall morphology of the bone it is possible to state that this is the scapula-coracoid element. However,

Fig. 12. *Mosasaurus hoffmanni* (PRM 2546) scapula-coracoid element in the posterior (A), anterior (B), dorsal or ventral (C), medial (D) and ventral (E) views.

lack of the most part of the blade and absence of diagnostic elements don't allow determining whether it is scapula or coracoid or even a right or left element. The largest facet is strongly concave without traces of interdigitated suture with adjacent element of the scapula-coracoid. The main dorsal (or ventral) facet is almost flat and less than one-third in comparison with the anterior facet. The angle between the facet surfaces is approximately 130 degrees. The base with the facets is rotated by 40 degrees relative to the blade. The neck is relatively short, and the bone becomes thinner right after the facets.

DISCUSSION

A.N. Ryabinin assigned the bones to *Mosasaurus giganteus*; however, the only evidence of this is an entry in the inventory book of CCMGE. No articles or even notes with the description of this skull have ever been published.

Because the Penza specimen has powerfully built jaws, all of the Plioplatecarpinae may be removed from consideration in assessing its relationships (Konishi and Caldwell 2011). Penza specimen has a saddle-shaped coronoid with a well-developed posterodorsal process, while Plioplatecarpinae have coronoid with a slight dorsal curvature (except for *Platecarpus planifrons* (Konishi and Caldwell 2007) and *Selmasaurus johnsoni* (Polcyn and Everhart 2008)). The absence of a long anterior projection for the dentary and coronoid along with a slight dorsal curvature strikes it from the candidate list for all the Tylosaurinae (Russell 1967). Among Halisaurinae *Halisaurus ortliebi* is the most similar to the Penza mosasaur by the position of the parietal foramen, but the relatively large size of the latter and different contact between parietal and frontal (without overlapping flanges) differentiate it from the Penza specimen (Bardet et al. 2005). The specimen is clearly a Mosasaurinae due to its possession of a thin-walled surangular rising anteriorly to the posterior surface of the coronoid.

The coronoid of the Penza specimen bears a large vertically oriented posterior process (Fig. 10A, B), as in *Mosasaurus* or *Prognathodon*. *Clidastes* also has a significantly expanded coronoid posterior process. However, in contrast to the *Mosasaurus* and *Prognathodon*, it is more elongate with a weakly expressed descending lateral wall (Williston, 1898). In addi-

tion, the dentary is more delicately constructed in *Clidastes* (Russell 1967).

The Penza specimen has much in common with *Prognathodon* genus. For example, the posterior mandibular unit of *Prognathodon overtoni* Williston, 1897 (TMP 2007.034.0001), is similar compared to the Penza specimen (Konishi et al. 2011). The only difference is in the position of the suture between the angular-articular and surangular on the lateral side of the mandibular unit. In the Penza specimen, the articular is completely overlapped by the surangular before the glenoid suture position (Fig. 10A). Thus, the articular-angular suture position is obscured, whereas in *P. overtoni*, the surangular does not have a complete overlap of the articular and angular. In addition to the above, *P. overtoni* and other species of *Prognathodon* and also *Globidens* have concavo-convex alveolar margins, relatively straight frontal sides, the absence of tooth facets and posterior teeth with swollen crowns (Russell 1975; Bardet et al. 2005; Schulp 2006; Schulp et al. 2008).

The Penza specimen does not follow lots of characters considered by Leblanc et al. (2012) to be diagnostic for the tribe Mosasaurini: large triangular posteromedial flanges of frontal dorsally overlapping parietal table and the presence of dentary anterior projections. Furthermore, the retroarticular inflection of the Penza specimen does not fit into the Mosasaurini diagnosis. The Penza specimen's retroarticular processes lie in a nearly vertical orientation (Fig. 10C, D), whereas in Mosasaurini, they should be horizontal. However, included in the Mosasaurini tribe, *Mosasaurus lemonnieri* Dollo, 1889, does not exhibit this character either (personal observation of IRSNB R28). The retroarticular process inflection of *Mosasaurus lemonnieri* is 45 degrees, which is almost the same as the dorsoventral plane of the surangular.

Despite the above characters, the Penza specimen shares the greatest number of characters with *Mosasaurus*: a broad and short frontal, a generally rectangular to trapezoidal shape of the parietal table with sides converging but not meeting, a relatively small parietal foramen size, the absence of a parietal posterior shelf, narrow shape of the postorbitofrontal, absence of a postorbitofrontal transverse dorsal ridge, presence of a small anterior dentary projection, the dentary medial parapet strap is equal in height to the lateral wall of the bone, essentially smooth concavo-convex surfaces with an intermediate lateral compression of the splenial-angular articular

surface, very concave shape of the coronoid with a significantly expanded posterior wing, the presence of a small coronoid posteromedial process, rapidly rising anteriorly thin and high surangular coronoid buttress, surangular-articular suture position behind the condyle in the lateral view, no large foramina on the lateral face of the retroarticular process, the presence of tooth facets, non-swollen crowns of the posterior marginal teeth, and strong and elevated tooth carinae.

The closest *Mosasaurus* taxa that presents these characters are as follows: *Mosasaurus missouriensis* Harlan, 1834; *Mosasaurus conodon* Cope, 1881; *Mosasaurus lemonnieri* Dollo, 1889; and *Mosasaurus hoffmanni* Mantell, 1829.

Before comparison with this species, it is necessary to say a few words about the teeth. In the Penza specimen, there are at least 15 teeth on the dentary. This character fits almost all considered *Mosasaurus* taxa. *Mosasaurus missouriensis* has 14–15 teeth, *M. lemonnieri* has 17, *M. conodon* has 17, and *M. hoffmanni* has 14 (Bardet et al. 2004). Mulder (2004) notes that using the dentary tooth number as a character is dangerous. Considering the mechanisms of tooth replacement in mosasaurs, some intraspecific variation in the tooth number is possible. In the same paper mentioned, a *M. hoffmanni* specimen had 15 teeth. Therefore, the tooth number character was not used in the comparison with *Mosasaurus* species in this work.

In contrast to the Penza specimen, *M. missouriensis* has a shorter lateral wing of the coronoid without emargination for the anterior surangular foramen. Despite the fact that we could only observe the frontal of the Penza specimen in the side view of photos, it is clearly seen that the frontal sides are sinusoidal, unlike the straight sides of *M. missouriensis*. In addition, the articular and angular are not completely covered by the splenial (Goldfuss 1845).

The systematic relationships among the three remaining *Mosasaurus* taxa are still unclear. Baird & Case (1966) and Russell (1967) synonymized *M. lemonnieri* with *M. conodon*. This decision was made based on a lack of significant differences between the Pierre Shale (South Dakota) skeleton with the eroded skull and the Maastrichtian (Belgium and Netherlands) skeletons. The cranial portion of the diagnosis was made by Russell on the basis of the Maastrichtian *M. lemonnieri*. The comparison was conducted on the basis of Dollo's (1894) work.

However, Lingham-Soliar (1992) re-assessed the systematic status of *M. lemonnieri* as a valid taxon and noted some mistakes in Dollo's work, including the comparisons with other *M. lemonnieri* specimens. For this reason, Russell's research has been questioned. Mulder et al. (2004) suggested that *M. lemonnieri* could be a juvenile *M. hoffmanni* because the main differences between *M. hoffmanni* and *M. lemonnieri* can be observed only in "ideal cases". In addition, these specimens have almost identical quadrates.

Assuming *M. lemonnieri* is a valid taxon does not allow to compare the Penza specimen and *M. conodon* because the description of the *M. conodon* cranial material was made on the basis of the *M. lemonnieri* skull (Russell 1967). In addition, in this case, it is not possible to provide an unambiguous definition of the Penza material because it shares different characters with both *M. lemonnieri* and *M. hoffmanni*. Moreover, the Penza specimen has the most characteristic feature of the teeth in *M. hoffmanni* – the posterior carina shifts from a somewhat lateral position in the anterior teeth to a posterior position further along the tooth row (Fig. 8G–K) (Lingham-Soliar 1992, 1995; Mulder 2004). The Penza specimen shares a frontal with convex lateral margins and powerfully built dentary characters with *M. hoffmanni*, whereas *M. lemonnieri* has a slender dentary, such as in the *Clidastes* (Russell 1967; Lingham-Soliar 1992). However, depending on the animal size, it could be more robust (Lingham-Soliar 1992). The Penza specimen shares approximately the same inflection of the retroarticular processes and a similar surangular-articular lateral suture trace with *M. lemonnieri* (personal observation on IRSNB R28). Characters on which it is possible to attribute the Penza specimen to *M. hoffmanni* can be considered as more relevant than those to *M. lemonnieri*.

Even so, the author tends to agree with the opinion of Mulder et al. (2004) and Russell (1967), i.e., *M. lemonnieri* is a synonym of *M. hoffmanni*. In that case, the definition of the Penza specimen as *M. hoffmanni* is assured.

Characteristic features of the CCMGE 10/2469 are an enormous descensus processus parietalis (Fig. 7E, F) and the absence of a firmly interdigitated suture between the scapula and coracoid, such as in *M. hoffmanni* (Lingham-Soliar 1992).

There are almost no teeth under the replacement, suggesting that the specimen likely represent a mature animal.

The overall length of the skull is more than 1700 mm (the length of the right posterior mandibular unit is 690 mm, the length of the left dentary is more than 1020 mm). Thus, the total length of the animal should be approximately 17 m (using Russell's (1967) length of the *M. hoffmanni* jaw as equal to 10% of the overall body length). *M. hoffmanni* from the Penza is one of the largest mosasaurs ever known.

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