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REDESCRIPTION OF *PROGNATHODON LUTUGINI* (SQUAMATA, MOSASAURIDAE)

D.V. Grigoriev

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

ABSTRACT

Dollosaurus lutugini (Yakovlev, 1901) is the only valid species known from the territory of the former USSR. It was described from Campanian deposits of Eastern Ukraine on the basis of an incomplete skeleton. This study provides a description of an osteological material including the previously undescribed epipterygoid and squamosal. Phylogenetic analysis of a data matrix of 37 terminal taxa and 135 characters shows that *D. lutugini* and *Prognathodon solvayi* Dollo, 1889 are sister taxa. *P. lutugini* is distinct from *P. solvayi* by possession of smooth enamel surface of teeth, depression of anteriormost trunk vertebrae condyles, larger relative length of cervical vertebrae, and a distinct, horizontally interdigitating articulating surface of the splenial and angular. We conclude that *D. lutugini* is in *Prognathodon* clade; generic name of *Dollosaurus* Yakovlev, 1901 is a subjective junior synonym of the *Prognathodon* Dollo, 1889.

Key words: Campanian, Cretaceous, *Dollosaurus*, Mosasauridae, phylogeny, *Prognathodon*

ПЕРЕОПИСАНИЕ *PROGNATHODON LUTUGINI* (SQUAMATA, MOSASAURIDAE)

Д.В. Григорьев

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

РЕЗЮМЕ

Dollosaurus lutugini (Yakovlev, 1901), описанный по неполному скелету из кампанских отложений Восточной Украины, является единственным видом мозазавров с территории СССР. Приводится полное морфологическое описание всего остеологического материала, включая ранее не описанные верхнекрыловидную и чешуйчатаю кости. Филогенетический анализ 37 таксонов мозазавров, основанный на распределении 135 признаков, показал, что *D. lutugini* является сестринским таксоном *Prognathodon solvayi* Dollo, 1889. От последнего вида *D. lutugini* отличается наличием бугорков и ямок на сочленовной поверхности между пластинчатой и угловой костями, более ровной поверхностью зубов, большим дорсовентральным сжатием мыщелков переднетуловищных позвонков и большей относительной длиной шейных позвонков. Поскольку *D. lutugini* попадает в кладу видов *Prognathodon*, родовое название *Dollosaurus* Yakovlev, 1901 является младшим субъективным синонимом рода *Prognathodon* Dollo, 1889.

Ключевые слова: кампан, мел, *Dollosaurus*, Mosasauridae, филогения, *Prognathodon*

INTRODUCTION

In the Cretaceous, large portions of the Eurasian plate were covered by the epicontinetal seas, but the fossil record of the marine reptiles in general and mosasaurs in particular from Russia and the whole territory of the former Soviet Union is still inadequate. Many fragmentary remains of mosasaurs have been found in the Upper Cretaceous sediments in the Lower Volga basin (Saratov and Penza provinces), along the rivers Ural, Pechora, Don, in the deposits of the Turgai strait in Kazakhstan, in Uzbekistan, and Azerbaijan (Pravoslavlev 1914; Rozhdestvenskii 1947; Prizemlin 1988; Pervushov et al. 1999; Storrs et al. 2000).

Currently, *Dollosaurus lutugini* is the only valid species of mosasaurs described from the former Soviet Union (Yakovlev 1905; Storrs et al. 2000). This species, based on a partial skeleton including a fragmentary skull, was found in 1898 by geologist L.I. Lutugin on the bank of Severskii Donets River near the Krymskoe village (Slavyanoserbsk District, Lugansk Province of Ukraine) (Fig. 1) in the Late Campanian deposits (Storrs et al. 2000). Since that time, the phylogenetic position of *Dollosaurus* had been variously interpreted and to the present day it is still unclear (Lindgren 2005).

In this contribution, we redescribe the holotype material of *Dollosaurus lutugini* including newly recognized elements. We also provide an updated phylogenetic analysis and taxonomic revision of this taxon, and an updated skeletal reconstruction.

Institutional abbreviations. CCMGE – Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia.

MATERIAL AND METHODS

The holotype of *Prognathodon lutugini* (CCMGE 818) is mounted in the exhibition hall of the Chernyshev's Central Museum of Geological Exploration in Saint-Petersburg. The mounting was done by Tsaregradskii (1935) based on the reconstruction of *Clidastes liodontus* Merriam, 1894 published by Williston (1898). Here I provide a novel reconstruction of this skeleton based on newly recovered phylogenetic position of this species. During the original conservation, the bones were covered with polyvinyl butyral (PVB). The PVB has now lost much of its adhesive properties and the bones have begun to crumble. To preserve bones from further decay, they were covered with a new application of PVB. The skeletal elements are disarticulated, and thus the exact position of particular vertebrae within the vertebral column is unknown; however, the vertebrae can be sorted by morphology and relative size, allowing estimates of approximate position within the vertebral column. As the exact position of the vertebrae cannot be identified, their location on the reconstruction diagram corresponds to their initial allocation made by Tsaregradskii (1935). Since Tsaregradskii's (1935) study, some of the bones, such as the premaxilla and scapula, were lost. The epipterygoid and squamosal, previously unreported, were recognized in the present study. The osteological terminology is based mainly on Russell (1967) and the systematics follow Leblanc et al. (2012). The photos of teeth have been taken at different depth levels and combined using Helicon Focus 5.3 ×64.

SYSTEMATICS

Order Squamata Oppel, 1811

Family Mosasauridae Gervais, 1853

Subfamily Mosasaurinae Gervais, 1853

Genus *Prognathodon* Dollo, 1889

***Prognathodon lutugini* (Yakovlev, 1901)**
(Figs. 1–14)

Clidastes (?) *lutugini* sp. n.: Yakovlev, 1901, p. 515
Dollosaurus lutugini: Yakovlev, 1905, p. 135
Prognathodon lutugini: Lingham-Soliar, 1989, p. 142

Holotype. CCMGE 818, partial skeleton including portions of the premaxilla, right and left pterygoid, epipterygoid, right and left squamosals, right dentary fused with splenial and prearticular, left dentary, right and left coronoid, right and left splenials, right angular fused with prearticular and left angular, isolated teeth, disarticulated cervical, dorsal, and caudal vertebrae, disarticulated phalanges, rib fragments, and coracoid.

Locality and horizon. An outcrop on Severskii Donets River near the Krymskoe village, Slavyanoserbsk District, Lugansk Province of Ukraine. The glauconite sands of *Belemnitella mucronata* zone, upper Campanian, Upper Cretaceous (Tsaregradskii 1935).

Fig. 1. Map of the Ukraine and neighbouring territories with star indicating the *Prognathodon lutugini* locality near the Krymskoe Village, Lugansk Province.

Revised diagnosis. *Prognathodon lutugini* differs from all other *Prognathodon* taxa by splenial-angular surface with distinct horizontal tongues and grooves, vertebral condyle shape (condyles of anterior trunk vertebrae slightly depressed, height to width ratio is 0.75) and vertebral length proportions (cervical vertebrae are almost equal in size to the longest vertebrae in the column, maximum cervical vertebrae length – 72 mm, maximum dorsal vertebrae length – 80 mm). Also differs from all other *Prognathodon* species except *P. solvayi* Dollo, 1889 by dentary tooth count (13), but can be excluded from referral to *P. solvayi* by possession of relatively smooth enamel surface. Differs from *P. kianda* Schulp et al., 2008 by absence of dentary anterior projection and larger anterior pterygoid teeth (compared to the marginal dentition). Differs from *P. waiparaensis* Welles et Gregg, 1971 and *P. solvayi* by tooth surface not striated medially. Also differs from *P. kianda* and *P. currii* by presence of carinae serration on tooth. Differs from *P. saturator* and *P. rapax* Hay, 1902 by the shape of vertebral condyle (condyles of posterior trunk vertebrae not higher than wide).

DESCRIPTION

Premaxilla. The premaxilla was described by Tsaregradskii (1935) but currently it cannot be located in the CCMGE collection (there are also no figures of premaxilla in the previous publications). This bone was also mentioned by Russell (1967). According to the Tsaregradskii's description, the premaxilla was present by only a very tip of the bone, in which the base of the teeth could be seen. On the medial side of the bone the articulation surface with maxilla was detected. The tooth on the tip of the bone was protruding at some angle, premaxilla broadly arcuate anteriorly, without forming a predental rostrum (Tsaregradskii 1935).

Pterygoid. Both bones are incomplete, and the right pterygoid is almost completely a gypsum restoration with two original teeth. The left pterygoid is more complete, but all processes are broken off, except the basisphenoid process (Fig. 3). The tooth-bearing segment is straight and supports at least seven teeth (three teeth preserved on the left pterygoid and two on the right). The most posterior alveolar margin on the right pterygoid is very small. Teeth arise from a thin pronounced vertical ridge. Anterior pterygoid teeth are relatively large, and comparable to the marginal teeth in size (pterygoid teeth are up to 46 mm,

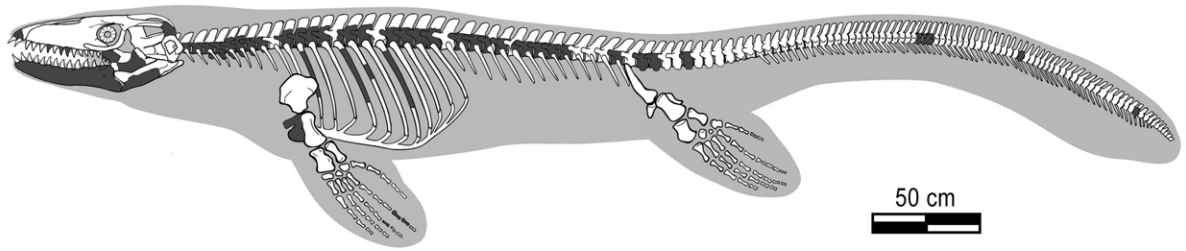

Fig. 2. Reconstruction of *Prognathodon lutugini* based on cranial and postcranial features of *P. saturator* (redrawn from Dortangs et al. 2002). Presented skeletal elements are marked by grey.

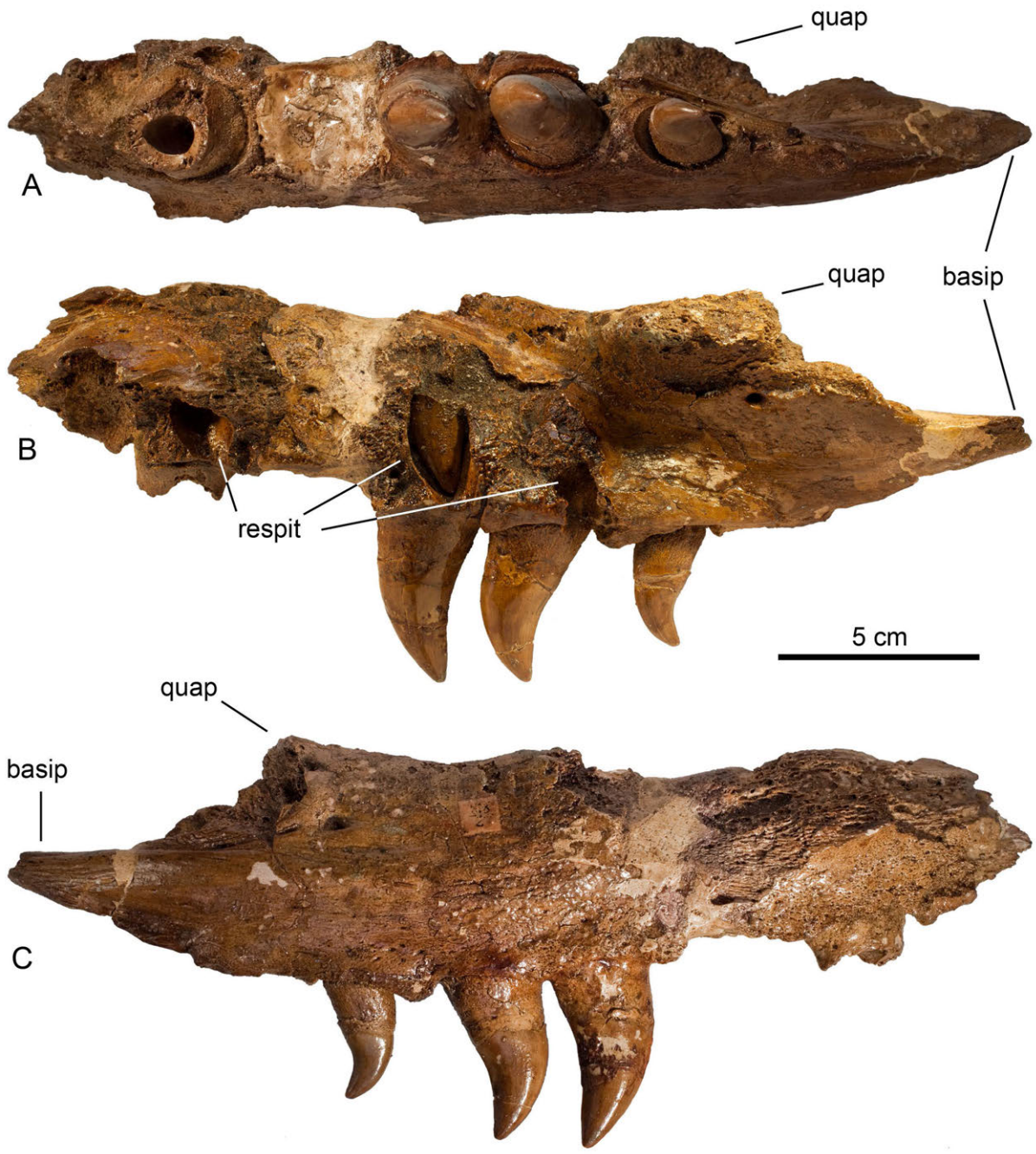

Fig. 3. *Prognathodon lutugini* (CCMGE 818), left pterygoid in ventral (A), lateral (B) and medial (C) views. Abbreviations: basip – basisphenoid process of pterygoid; quap – quadratic process of pterygoid; respit – resorption pit on tooth base.

Fig. 4. *Prognathodon lutugini* (CCMGE 818), epipterygoid in different views (A, B, C).

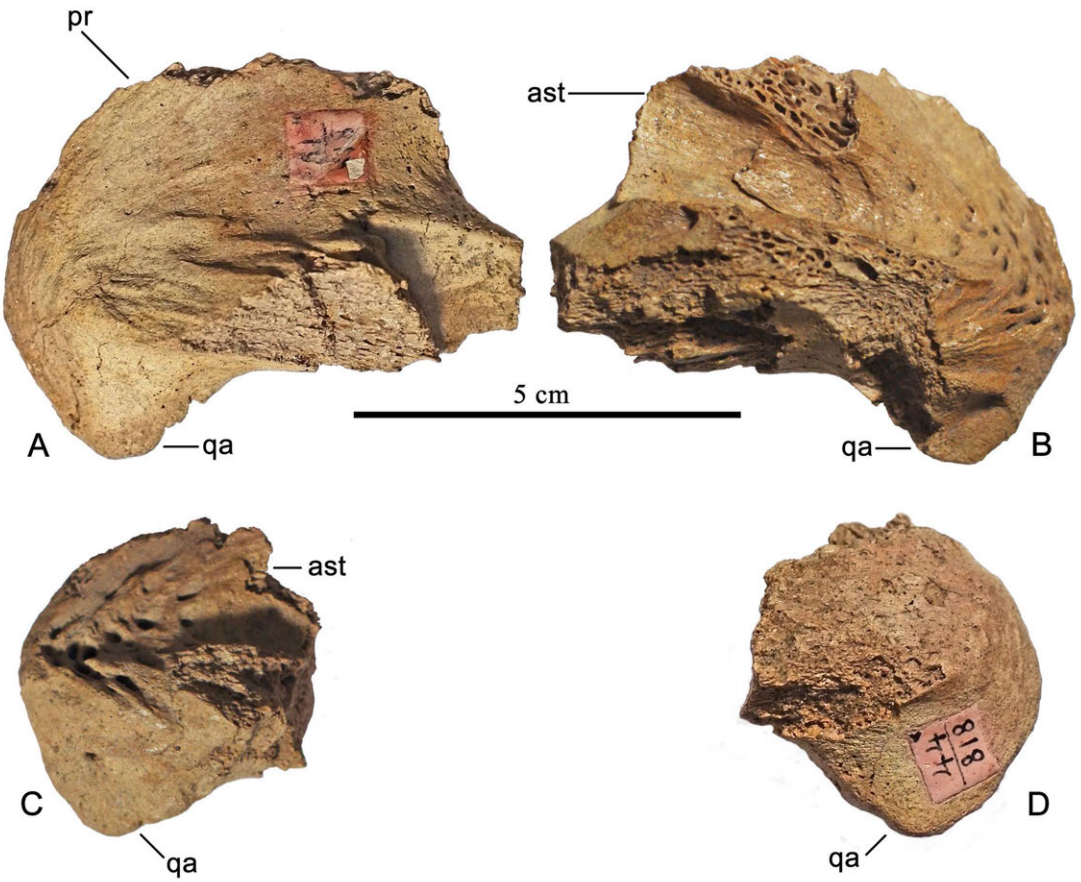

Fig. 5. *Prognathodon lutugini* (CCMGE 818), right (A, B) and left (C, D) squamosals in lateral (A, C) and medial (B, D) views. Abbreviations: ast – articulation with supratemporal; pr – parietal ramus; qa – quadrate articulation.

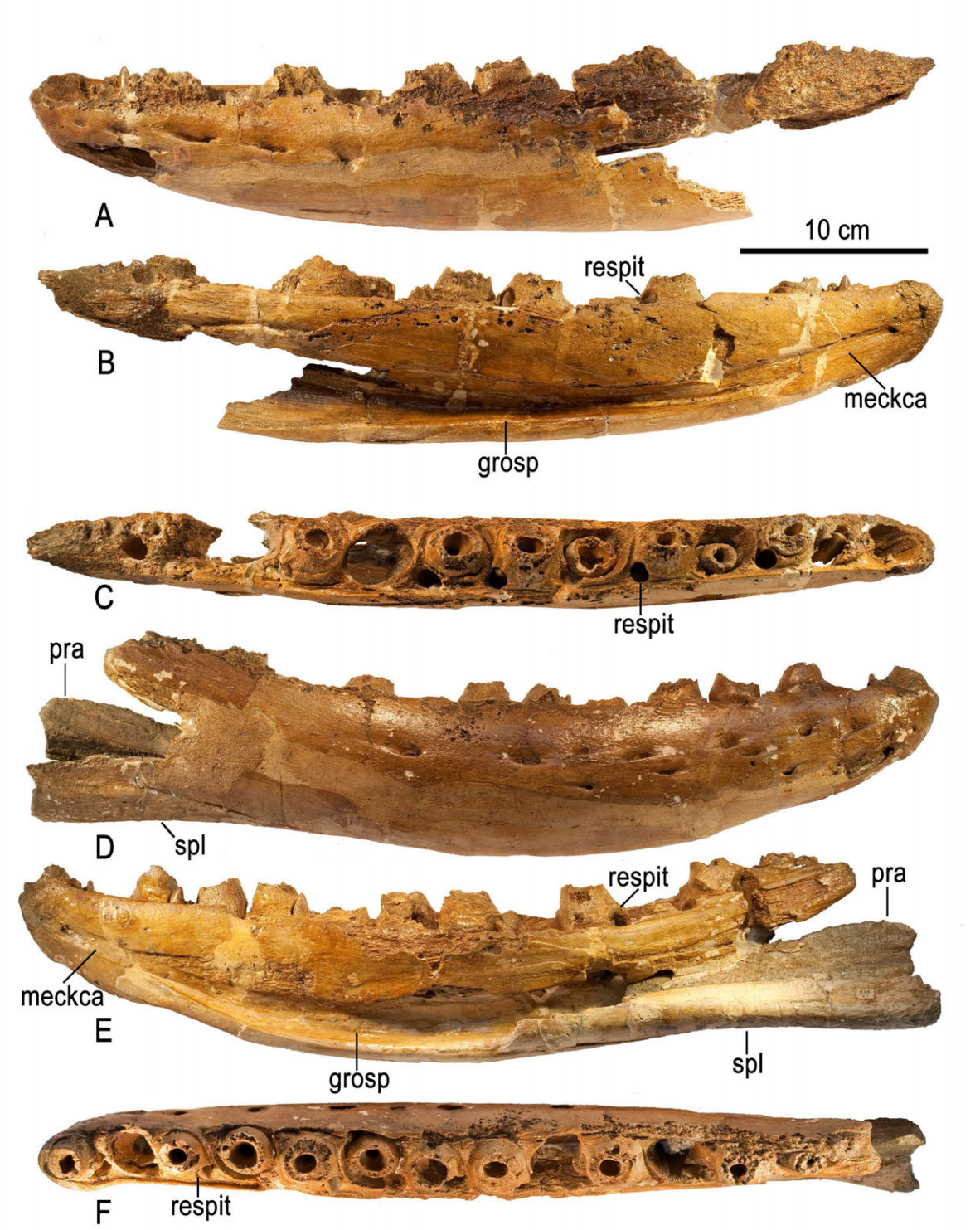

Fig. 6. *Prognathodon lutugini* (CCMGE 818), left (A-C) and right (D-F) dentaries in lateral (A, D), medial (B, E), and dorsal (C, F) views; B. Abbreviations: grosp – groove for splenial; meckca – Meckelian canal; pra – prearticular; respit – resorption pit on tooth base; spl – splenial.

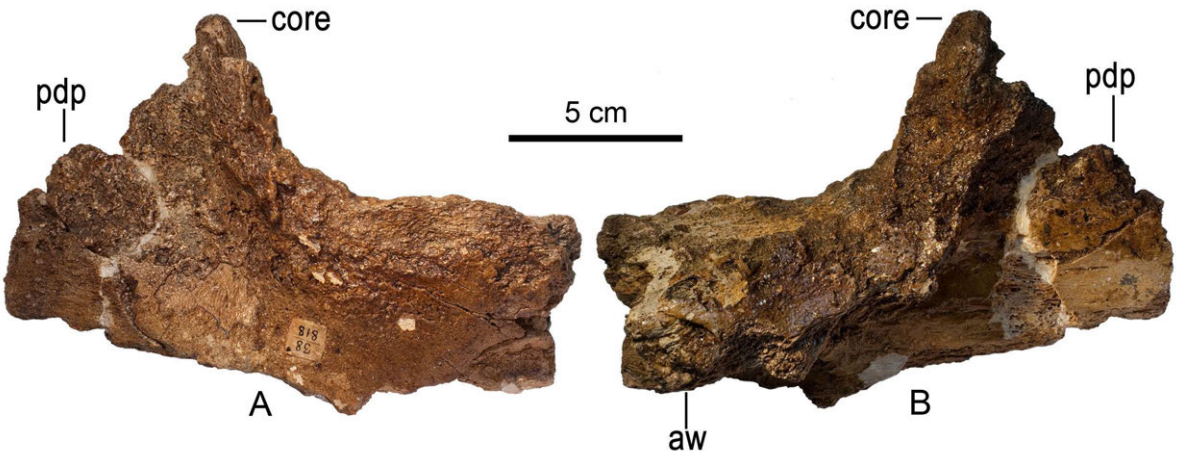

Fig. 7. *Prognathodon lutugini* (CCMGE 818), right coronoid in lateral (A) and medial (B) views. Abbreviations: aw – anteromedial wing; core – coronoid eminence or apex; pdp – posterodorsal process.

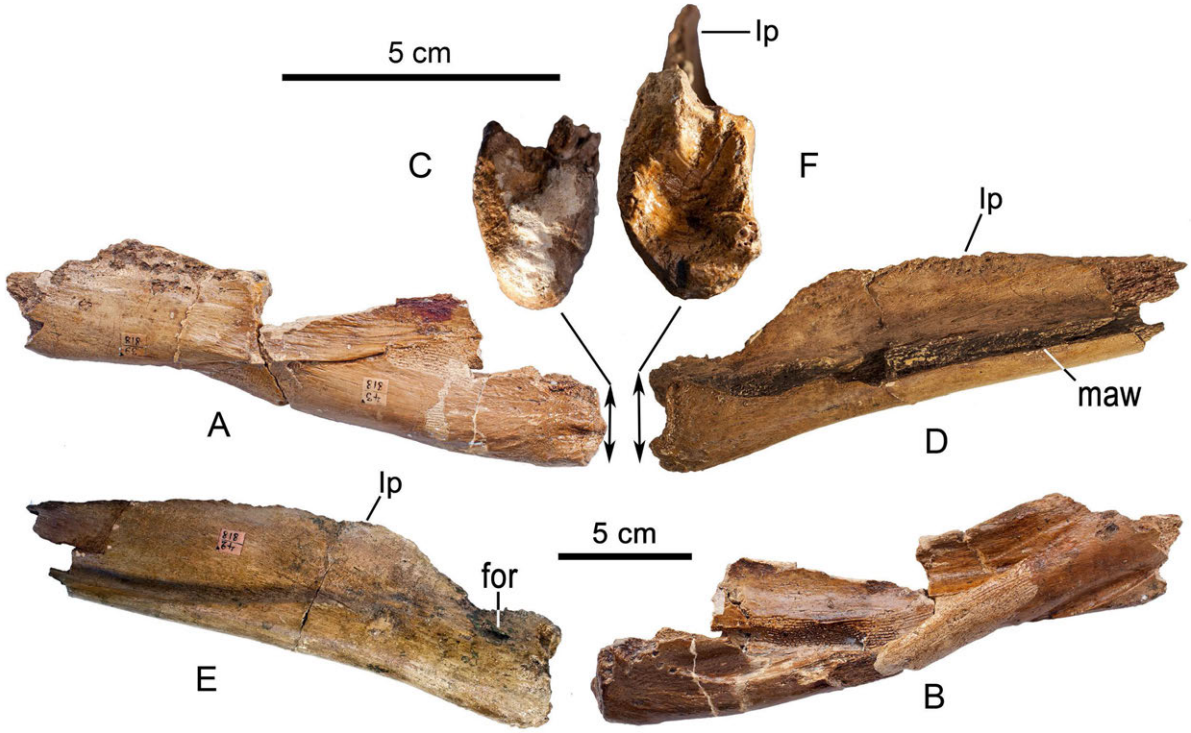

Fig. 8. *Prognathodon lutugini* (CCMGE 818), left angular (A, B, C) and splenial (D, E, F) in medial (A, D), lateral (E, B) and posterior (C, F) views. Abbreviations: for – foramen; lp – lateral process; maw – medial ascending wing.

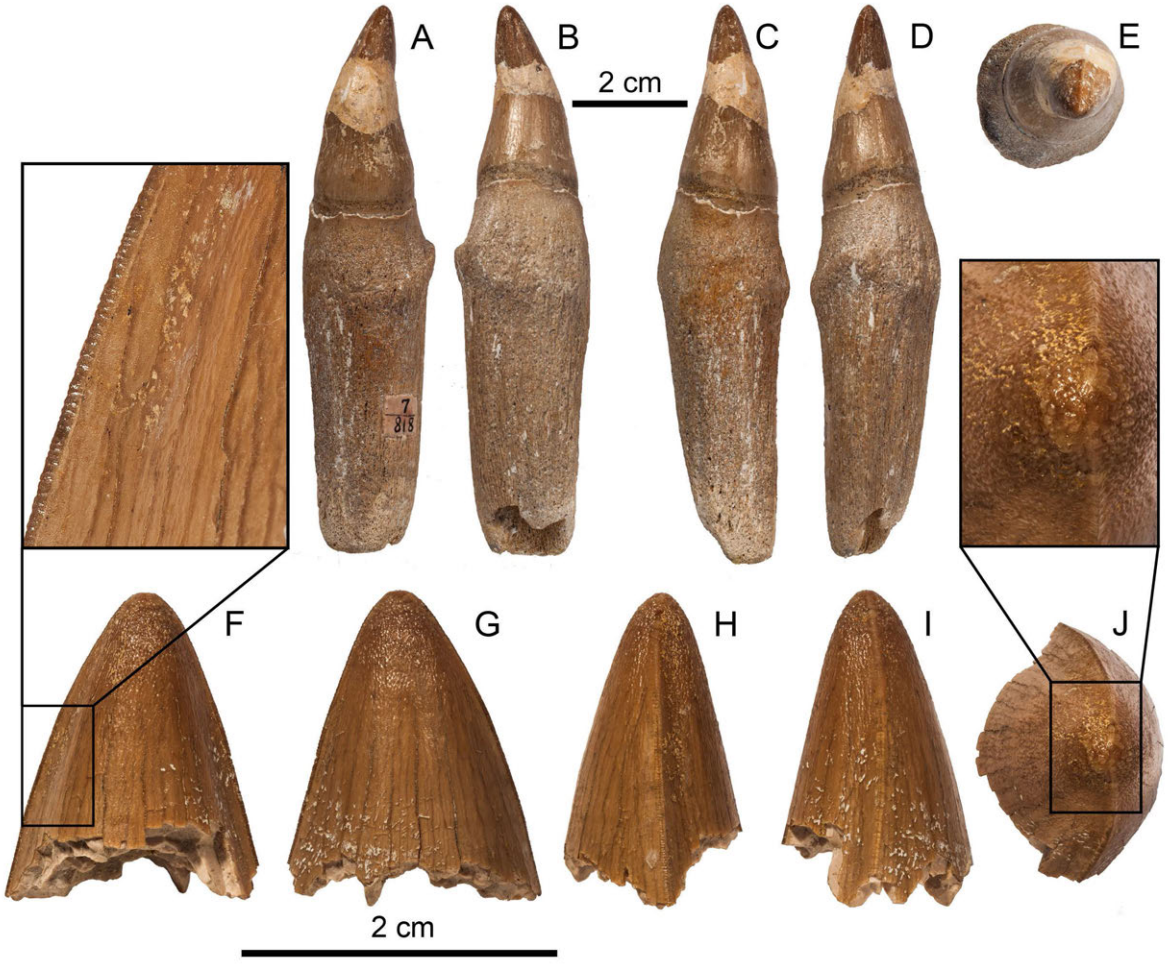

Fig. 9. *Prognathodon lutugini* (CCMGE 818), teeth in lingual (A, F), buccal (B, G), anterior (C, H), posterior (D, I) and apical (E,J) views. Callouts show enlarged fragments of the tooth carina with serration and wrinkles at the tip of the crown.

and marginal are up to 54 mm). The teeth are moderately recurved, the curvature increases posteriorly along the pterygoid. The posteriormost (sixth) tooth is recurved up to 40 degrees, whereas the most anterior (fourth) tooth is up to 20 degrees. The teeth are slightly laterally compressed and the crowns have well defined posterior carina without serration. Few resorption pits are present. A small replacement tooth is located in the resorption pit of the fourth pterygoid tooth. The ventral surface of basisphenoid process is nearly smooth. The base of the quadratic ramus originates between the fifth and sixth tooth. There are foramina above the sixth tooth on the lateral surface of the pterygoid and above the position between sixth and seventh tooth on the medial surface.

Epipterygoid. It is not clear if the right or left epipterygoid is preserved because the ventral and dorsal tips of the bone are crushed. The epipterygoid is S-shaped (Fig. 4). The largest end of bone seems to be dorsal. The ventral end of the bone is spatulate in shape, and in the middle, the bone becomes almost cylindrical. The surface of the bone is slightly rugose.

Squamosal. The squamosal is represented only by posterior fragments, the right being more complete (Fig. 5A, B). The squamosal is laterally compressed and tall (Fig. 5). The posterior terminus is teardrop-shaped. The squamosal has a simple vertically-oriented joint for the supratemporal. The posteroventral surface of the squamosal is concave for contact with the quadrate.

Dentary. The dentaries are almost complete, but all the teeth are broken near the base. Nevertheless, enough of the tooth crowns are preserved to suggest that crowns of posterior marginal teeth are swollen above the base. The right dentary is fused with the posterior end of the splenial and anterior blade of the prearticular (Fig. 6D–F). Both ventral and alveolar margins are concavo-convex. The dentary tooth count is 13 and at least eight tooth positions possess posteromedial subdental crypts, with replacement teeth in some of them. It is possible that some of these replacement teeth were added in subdental crypts during the mounting of skeleton. The subdental crypts are positioned posteromedially to functional teeth. The dentary terminates abruptly in front of the first dentary tooth, and although the anteriormost teeth are not preserved, it seems to be prognate. The dentary medial parapet strap is equal in height to the lateral wall of the bone. The Meckelian canal extends almost to the anterior end of bone.

Coronoid. The coronoid is saddle-shaped and has a well-developed posterodorsal process, which gives the dorsal margin of the bone a nearly 110 degree angle between the horizontal anterior end and the subvertical posterior wing (Fig. 7). Both, the anteromedial and lateral wings are broken; the lateral wing is broken at the base. There is no indication that the medial wing reaches the angular. There are distinguishable marks of the ventroposterior rim of a posteriorly rising crest (for fibre insertion) on the lateral surface of the coronoid.

Prearticular. The right anterior part of the prearticular is poorly preserved and splits into two parts. The anterior part of bone is sandwiched between the right dentary and splenial (Fig. 6D, E). The most anterior tip of the anterior part of the bone is broken under the eleventh tooth position. The second part (the middle part of the bone) is in articulation with the right angular.

Splenial. Only the posterior parts of the bones are preserved. The right splenial is in articulation with the dentary (Fig. 6D, E), and the left is disarticulated (Fig. 8E, D, F). The medial ascending wing that covers the Meckel's groove is broken at the base. The lateral process is thin, high and straight. The anterior end of the bone is broken, but according to the extension of the splenial facet on the dentary, the bone reached anteriorly to at least the third tooth position. On the lateral surface of the bone near the articulation with the angular, there is a foramen for the lingual nerve exit. The lateral process reaches 32 mm in height. The posterior-facing surface for articulation with the angular is present on the left splenial (Fig. 8F). It is laterally compressed and has distinct horizontal tongues and grooves, with a perpendicular keel.

Angular. Both paired bones are fragmentary. The left angular is more complete (Fig. 8A–C), and the right angular is in contact with the prearticular. The articulation for the splenial is in the form of a rounded "V", convex, with a median dorsal sulcus (Fig. 8C). A thin and broad wing from the labial side of angular, and a short heavy wing from the buccal side together form a narrow groove for the prearticular. A short and heavy wing arises gradually from the glenoid fossa and used to be overlapped above by the surangular.

Marginal dentition. Teeth are described, based on the isolated specimens. Preserved teeth are strongly bicarinate with a weak serration on both carinae (Fig. 9F–J). The carinae divide the tooth into lingual and labial surfaces, the lingual surface is more convex and large in comparison with the labial (Fig. 8J). There is a slight posterior and medial recurvature. The surface of the teeth is smooth, except for the minor wrinkles at the tip of the crowns. They are unfaceted and without fluting. The roots of the preserved teeth are relatively large (about 1.5 of the crown size) and barrel-shaped (Fig. 8A–E). The preserved tooth crowns are up to 54 mm tall and 25 mm wide at the base.

Cervical vertebrae. Four postaxial cervical vertebrae are preserved. Anterior and posterior zygapophyses are well developed (Fig. 10A–E). Functional zygosphenes and zygantra can be detected on two vertebrae. The vertebral hypapophyseal peduncles are presented on four vertebrae (two of them are heavily damaged); they are very short and end as small laterally compressed oval facets (Fig. 10A, C, E). These facets are posteriorly inclined and located posteriorly on the ventral surfaces of the centra. The synapophyses are large, located anteriorly on the centra, and do not extend below the ventral margin of the centrum. A strong rounded crest curves anterodorsally from the synapophysis to support the anterior zygopophysis laterally in nearly all preserved cervical vertebrae. The condyles and cotyles are weakly dorsoventrally compressed (height to width ratio is 0.85). Cervical vertebrae are almost equal in size to the longest dorsal vertebrae. The maximum length of the cervical vertebrae body is 72 mm, the height is 40 mm.

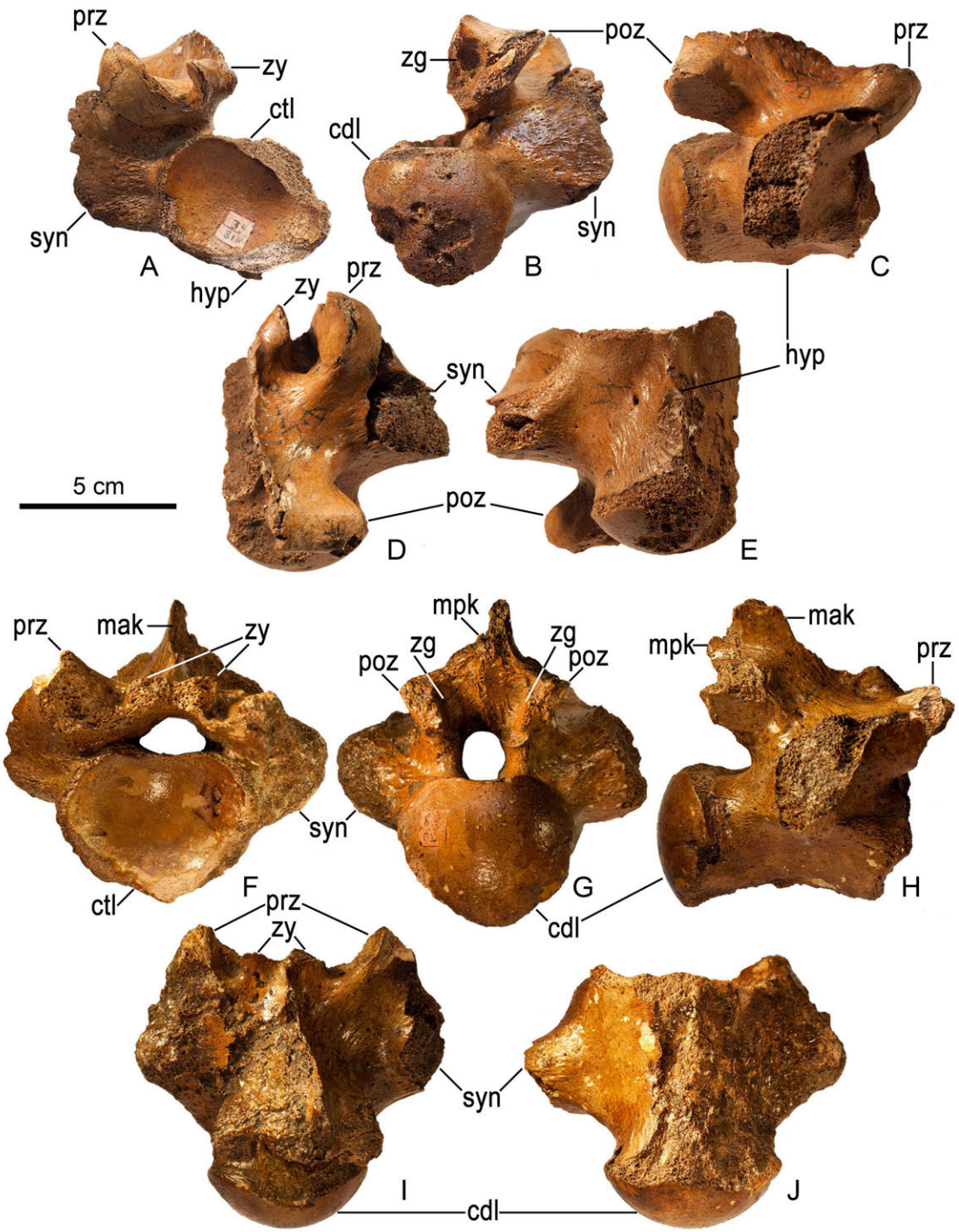

Fig. 10. *Prognathodon lutugini* (CCMGE 818), cervical (A-E) and dorsal (F-J) vertebrae in anterior (A, F), posterior (B, G), lateral (C-H), dorsal (D, I) and ventral (E, J) views. Abbreviations: cdl – condyle; ctl – cotyle; hyp – hypapophysis; mak – median anterior keel; mpk – median posterior keel; poz – postzygapophysis; prz – prezygapophysis; zg – zygosphene; zy – zygantrum.

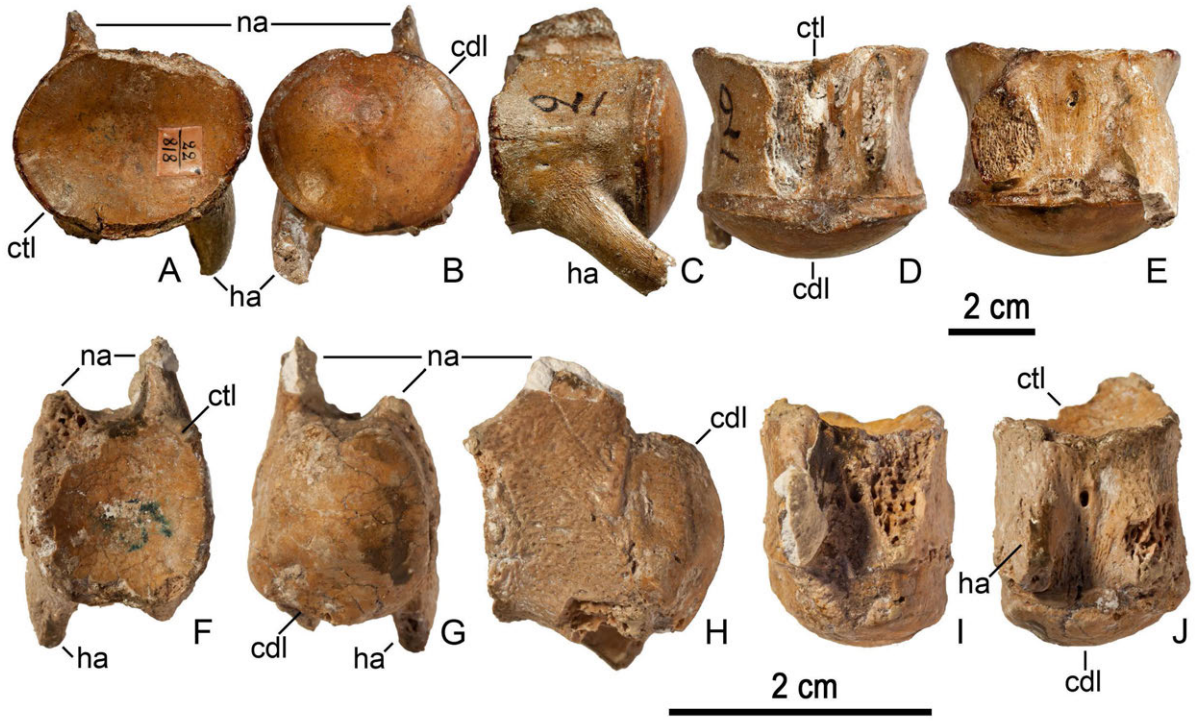

Fig. 11. *Prognathodon lutugini* (CCMGE 818), caudal vertebrae from the terminal series in anterior (A, F), posterior (B, G), lateral (C, H), dorsal (D, I) and ventral (E, J) views. Abbreviations: ha – haemal arch; na – neural arch. For other abbreviations see Fig. 10.

Dorsal vertebrae. The 26 dorsal vertebrae are represented and vary in preservation. Because the synapophyses are incompletely preserved, it is impossible to divide dorsal vertebrae into an anterior thoracic series and posterior lumbar series. The dorsal spines are also poorly preserved. Dorsal vertebrae are a little longer than the cervical. As in the cervicals, condyles and cotyles are weakly dorsoventrally compressed (height to width ratio is 0.75) (Fig. 10F–J). On some vertebrae, the synapophyses extend close to the ventral margin of the centra. The spine inclines posteriorly at about 65 degrees from horizontal. Functional zygosphenes are preserved on five vertebrae but it is impossible to determine how far back in the column. On some vertebrae there is a ridge connecting the synapophysis with the prezygapophysis (Fig. 10H). The maximum length of the dorsal vertebral body is 80 mm, height – 50 mm.

Terminal caudal vertebrae. Five terminal caudal vertebrae are presented. Dorsolateral compression of the condyles and cotyles is a little more pronounced than in the cervical and dorsal series (Fig. 11). The articulating surfaces are oval with an aspect ratio of 1.2. The lateral surfaces of the centra possess between one and five foramina arranged one above the other. Haemal arches are fused to centra and have a small lateral compression. The posteriormost and the smallest caudal vertebra (Fig. 11F–J) stand out from the other four preserved vertebrae. It is more angular and nearly square in cross-section and has no foramina on the lateral surfaces. The maximum length of the caudal vertebrae body is 43 mm, height – 43 mm.

Ribs. Many rib fragments are preserved, but none of them are complete. Two grooves run along the distal portion of the ribs from the articular head (8-shaped in cross-section), but only one groove remains behind the middle of the rib.

Coracoid. This bone was described by Tsaregradskii (1935) as "coracoid with emargination like *Clidastes*". After Tsaregradskii's description the bone was probably damaged. Amongst the osteological material in the CCMGE collection is a fragmentary specimen that generally meets the description of Tsaregradskii (1935), but currently preserves only

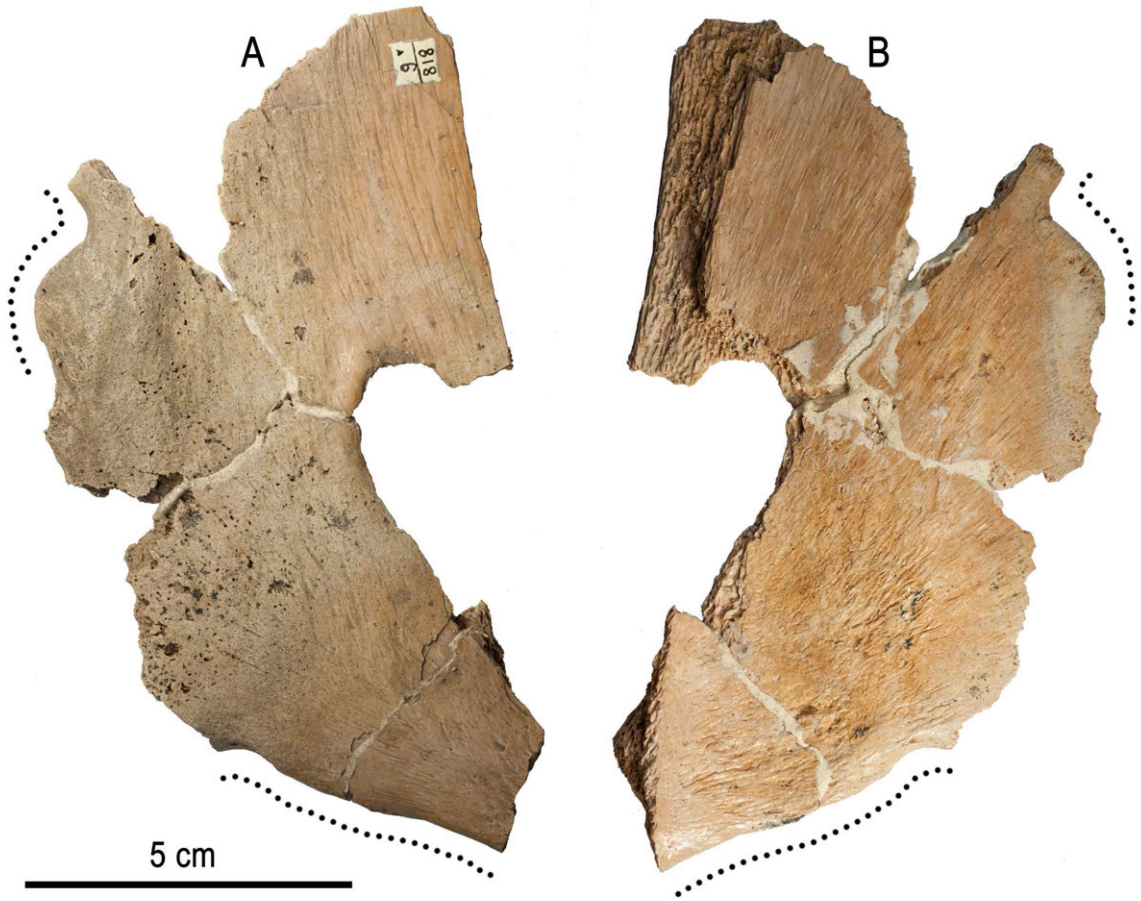

Fig. 12. *Prognathodon lutugini* (CCMGE 818), coracoid in different views (A, B). Dotted line indicates intact edges of the bone.

the anteroventral part of the very thin coracoid blade (Fig. 12). It is impossible to determine whether it is the left or right. The emargination is not preserved, but the depression on the bone surface suggests that it probably did possess a deep emargination.

Phalanges. Three phalanges are represented. They are slightly elongated, spindle-shaped with moderately expanded epiphysis, not too flattened (Fig. 13). The size of the longest one is 36 mm.

PHYLOGENETIC ANALYSIS

To assess the phylogenetic position of *P. lutugini* I used the data matrix from Leblanc et al. (2012) with one character state modification (41(?) to 41(0) for *Prognathodon kianda*). *P. lutugini* can be coded by 29

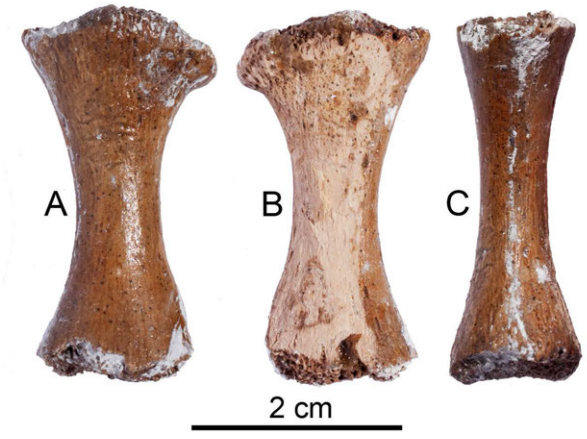

Fig. 13. *Prognathodon lutugini* (CCMGE 818), phalanx in different views (A, B, C).

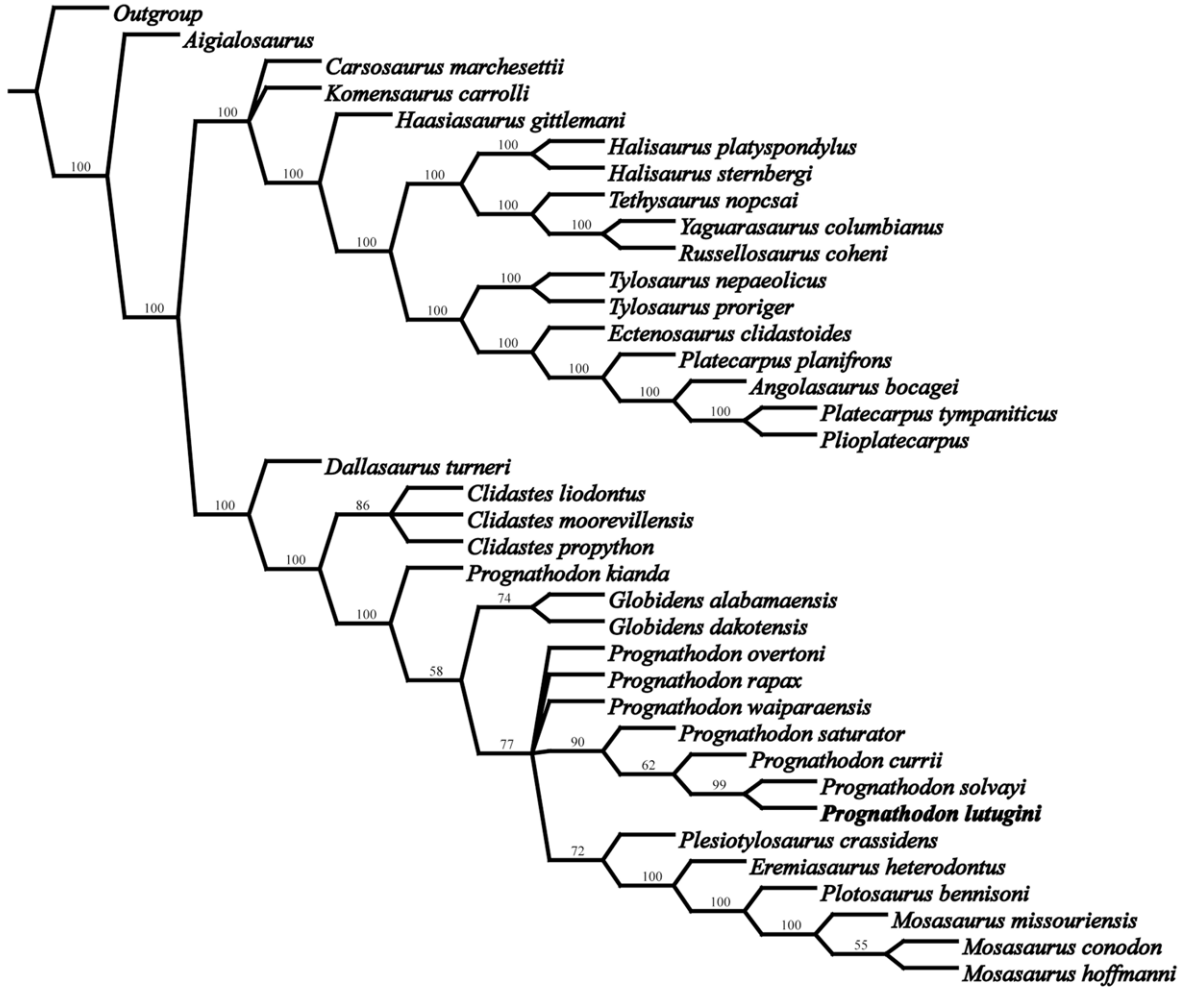

Fig. 14. The 50% majority rule consensus tree of 1755 most parsimonious trees of 409 steps, with a CI of 0.41 and an RI of 0.69.

(21.5%) characters from this data matrix: 1(0), 3(0), 40(1), 41(1), 59(4), 60(1), 62(2), 63(1), 64(1), 65(1), 74(1), 75(1), 76(0), 77(0), 78(1), 79(2), 80(1), 81(1), 84(1), 85(0), 89(0), 91(1), 92(1), 93(0), 94(1), 95(1), 101(1), 111(0), 126(0).

The data matrix consisting of 37 taxa and 135 characters has been analysed by a tree-search maximum parsimony ratchet algorithm using the program NONA, version 2.0 (Goloboff 1999; one million repetitions) run with Winclada version 1.00.08 interface (Nixon 1999). All characters are non-additive and all but characters 86 and 90 are phylogenetically informative. Characters 75 (presence or absence of coarse enamel ornamentation) and 78 (presence or absence of basal tooth crown inflation) were deactivated following the suggestion by Leblanc et al. (2012). The NONA analysis produced 1755 most parsimonious trees with a length of 409 steps, a consistency index of 0.41, and a retention index of 0.69. A 50% majority rule consensus tree is shown in Fig. 14.

DISCUSSION

In the original description, *P. lutugini* was referred to the Mosasaurinae based on the haemal arch fusion to the centra and the presence of zygosphenes and zygantra (Yakovlev 1901). Yakovlev (1901) noted that certain characters of the new species

were shared with *Clidastes* and *Mosasaurus* but also noted its distinctive traits (greater compression of the caudal centra and different morphology of the splenial and angular). He thought that this species is more closely related to *Clidastes* and referred to it as *Clidastes* (?) *lutugini*. Yakovlev (1901) also noted that the new species could be generically different from both these genera and provisionally proposed the generic name *Dollosaurus* if its distinctness will be supported by further research. Thus the generic name *Dollosaurus* published in Yakovlev (1901) was published as a provisional name for *Clidastes* (?) *lutugini*. This, however, does not affect the validity of the generic name *Dollosaurus*, which was published prior to 1961 (ICZN 1999: Article 11.9.3.6). In the subsequent paper, Yakovlev (1905) used the binomen *Dollosaurus lutugini* as a valid name. Except for the holotype skeleton of *Dollosaurus lutugini*, there were some other materials from the territory of the former Soviet Union described as *Dollosaurus* sp. (Prizemlin 1988; Yarkov 1993; Nesov 1997), but on closer examination these were reinterpreted as belonging to Mosasauridae indet (Pervushov et al. 1999).

Unlike Yakovlev's assumption on referring *Dollosaurus lutugini* to Mosasaurinae, Dollo (1924) and Russell (1967) included it to the subfamily Plioplatecarpinae because of the dorsally concave alveolar margin of the dentary, coronoid with greatly expanded posterior wing, extension of the splenial anteriorly into the symphysial region and the reduction in number and increase in size of the anterior pterygoid teeth. Despite the fact that none of these characteristics presented in Russell's diagnosis of Plioplatecarpinae, he suggested a close relationship of *Dollosaurus* and *Prognathodon*, a taxon Russell (1967) included within his concept of Plioplatecarpinae. Following Russell (1967), *Dollosaurus lutugini* was referred to the Plioplatecarpinae by Storrs et al. (2000) in a review article devoted to Russian marine reptiles.

Because of the presence of large zygosphenes and zygantra and enlargement of the first two dentary teeth, *Dollosaurus* was not synonymized with *Prognathodon* by Russell, but Lingham-Soliar and Nolf (1990) re-assessed some characters of *Prognathodon* and included the functional zygosphenes and zygantra character to the generic diagnosis of *Prognathodon*. Enlargement of the first two dentary teeth character is questionable because these teeth were actually broken near the base. The fused haemal arches are not characteristic for the Plioplatecarpinae but found in *Prognathodon*, which further advocates for referring of *D. lutugini* to that genus.

The systematic status of *P. lutugini* was re-examined by Lindgren (2005) on the basis of detailed comparison of the holotype (CCMGE 818) and a specimen referred to that taxon from the early Campanian deposits of Kristianstad Basin, Sweden, presented by marginal and pterygoid teeth, jawbones and caudal vertebrae. Lindgren distinguished *Dollosaurus* from *Prognathodon* and attributed it to the Mosasaurinae. Also Lindgren suggested two types of relationships between *Dollosaurus* and *Prognathodon*: the two genera represent separate offshoots of a single lineage, or *Dollosaurus* represents the most basal "*Prognathodon*-like" taxon. According to Lindgren, major differences of *Dollosaurus* from *Prognathodon* are the shape of caudal vertebrae, strong heterodonty and the absence of prominent dental peduncles. However, a closer examination of CCMGE 818 shows that a number of characters of the Kristianstad Basin specimen, noted by Lindgren as common with *D. lutugini*, are actually different.

The main characters in Lindgren's comparison of two specimens were: markedly angular caudal vertebrae centra, on which there were one or more large foramina located midway between the condyle and cotyle. Another vertebral feature was subhexagonal interarticular surfaces.

In the type material of *P. lutugini* there are six caudal vertebrae. None of them have a subhexagonal shape of articulating surfaces (Fig. 11A–E). They are oval, except of the smallest caudal vertebrae, but it is still not subhexagonal; articulating surfaces are squarer shaped (Fig. 11F, G). Also, the smallest vertebra does not have foramina on the lateral surfaces.

Lindgren (2005) wrote that it was impossible to make detailed dental examination because of poor preservation (teeth were varnished and partly plastered). However, the CCMGE 818 material was found to have teeth in good condition with roots and with well-preserved crowns (Fig. 9). The main difference of the CCMGE 818 marginal teeth is that they always have serration almost throughout the entire length of carinae in contrast to the carinae in Kristianstad Basin species that are unserrated or irregularly serrated in the posterior teeth. Also, varnish on few pterygoid teeth has been partially removed with solvent and, unlike the bicarinated pterygoid teeth of Kristianstad Basin species, CCMGE 818 has only the posterior carina.

In this connection it seems doubtful to attribute CCMGE 818 and Kristianstad Basin species to one taxon.

P. lutugini exhibits the following characters considered by Konishi et al. (2011) to be diagnostic for *Prognathodon*: first set of premaxillary teeth that are procumbent, coronoid deep and robust, 13 bicarinate dentary teeth, low pterygoid tooth count (seven), large pterygoid anterior teeth approaching the size of the marginal teeth and bearing only the posterior carinae, zygosphenes and zygantra present, haemal arch fused to caudal centrum and elongated and flat phalanges.

The phylogenetic analysis supports the referral of the species *D. lutugini* to *Prognathodon* and indicates close relationship (sister taxa) between *P. lutugini* and *P. solvayi*, but *P. lutugini* in contrast to *P. solvayi* has distinct horizontal tongues and grooves on the splenial-angular surface, the tooth surface that is not medially striated and without fluting, more depression of anteriormost trunk vertebrae condyles and bigger relative length of the cervical vertebrae.

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