A lepidosauromorph specimen from the Middle Jurassic (Bathonian) Moskvoretskaya Formation of the Moscow Region, Russia

Pavel P. Skutschas[1,2*], Andrey G. Sennikov[3], Elena V. Syromyatnikova[2,3], Dmitriy D. Vitenko[1,2], Igor A. Parakhin[1], Roman A. Bapinaev[1,2], and Susan E. Evans[4]

[1]*Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, St. Petersburg, Russia*

[2]*Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia*

[3]*Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia*

[4]*Department of Cell and Developmental Biology, University College London, London, UK*

*Correspondence author. E-mail: skutchas@mail.ru, p.skutschas@spbu.ru.

Abstract

A fragmentary diapsid left maxilla from the Bathonian Peski locality in Moscow Region, previously referred to Choristodera, is identified as Lepidosauromorpha indet. This specimen represents the first fossil record of basal lepidosauromorphs in the Middle Jurassic of European Russia. Among basal lepidosauromorphs, the maxilla from the Peski locality resembles those of the Middle Triassic *Fraxinisaura* and the contemporary Middle Jurassic (Bathonian) *Marmoretta* in subpleurodont tooth implantation, a relatively low dorsal process, and high keeled teeth with gently recurved apices and striae on the lingual side. This similarity suggests possible close relationships of *Fraxinisaura*, *Marmoretta* and the Peski form. The recognition of a basal lepidosauromorph in the fauna of the Peski locality extends the known geographical range of the Bathonian non-lepidosaurian lepidosauromorphs and demonstrates their wide Laurasian distribution at this time. It is additional evidence that Bathonian vertebrate faunas of Europe and Western Siberia were similar in composition.

Keywords: Lepidosauromorpha, Middle Jurassic, Bathonian, Moscow Region, Russia

Introduction

The Middle Jurassic continental vertebrate faunas of European Russia became first known with the discovery of the Bathonian Peski locality in the Moscow Region (Alekseev et al. 2001; Alifanov and Sennikov 2001; Sennikov et al. 2005a, b; Starodubtseva et al. 2008). The uniqueness of the Peski fauna is determined, in part, by its geographic position. The Peski locality is situated between Asian (e.g., the Balabansai Formation localities in Kyrgyzstan and the Berezovsk Quarry locality of the Itat Formation in Krasnoyarsk Region, Siberian Russia) and Western European (e.g., the Kirtlington Cement Quarry locality of the Forest Marble Formation in England and the Kilmaluag Formation localities in Scotland) localities containing diverse faunas of continental vertebrates of Bathonian age (Evans and Milner 1994; Evans and Waldman 1996; Averianov et al. 2005, 2010, 2016; Panciroli et al. 2020). Thus, the Peski locality is potentially important in understanding the distribution and composition of Middle Jurassic vertebrate faunas throughout Eurasia. Although the Peski locality has been known for a relatively long time (more than 20 years), the material of many vertebrate groups remains undescribed. One of these groups is Lepidosauromorpha, represented by undescribed lizard remains and a fragment of maxilla that more closely resembles non-lepidosaurian lepidosauromorphs from the UK and Germany. The main aim of this study is to describe and determine the taxonomic affiliation of this partial lepidosauromorph maxilla from the Peski locality.

Institutional abbreviations

PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

Geological setting and associated vertebrate assemblage

The fragmentary lepidosauromorph maxilla was discovered at the Peski locality in the Kolomensky District of Moscow Region on the territory of the Peski Industrial Complex of Construction Materials (Novopeskovskii Quarry). The fossil-bearing deposits of the Peski locality belong to the Moskvoretskaya Formation (Meshchera Horizon) and they consist of dark gray, black, and green clays, clay siltstones with lenses of clay gravel, and light gray and

yellowish wavy or oblique sands with interlayers of siltstones that occur in a series of karst cavities, fissures, and depressions in Late Carboniferous limestones (Myachkovskian Horizon, Moscovian Stage) (Alekseev et al. 2001; Sennikov et al. 2005a, b; Paschenko et al. 2018). The fossils of the Peski locality are represented by micro- and macrovertebrate, macroinvertebrate, and macro- and microflora (spores and pollen) remains. The Peski locality has been dated as late Bathonian based on the pollen assemblage (Alekseev et al. 2001).

The Peski locality has yielded a diverse vertebrate assemblage, which (besides lepidosauromorphs) includes chondrichthyan (sharks *Hybodus* sp. and chimaeras *Ischyodus* cf. *egertoni*) and osteichthyan (the dipnoan *Ceratodus segnis* and the actinopterygians *Lepidotes* sp., *Ptycholepis* sp., Coccolepididae indet., Dapediidae indet.) fishes, brachyopoid temnospondyls (cf. *Gobiops* sp.), salamanders (Caudata indet.), the basal turtle *Heckerochelys romani*, a neosuchian crocodyliform (Neosuchia indet.), theropod dinosaurs (Tetanurae indet.), and a mammaliaform synapsid (Morganucodontidae indet.) (Krupina 1995; Alekseev et al. 2001; Alifanov and Sennikov 2001; Gambaryan and Averianov 2001, Bragina 2005; Sennikov et al. 2005a, b; Sukhanov 2006; Popov and Shapovalov 2007; Starodubtseva et al. 2008; Paschenko et al. 2018).

Fishes are represented by isolated bones, complete or partial skeletons (actinopterygians), and fin spines and teeth (chondrichthyans). Among tetrapods, the remains of the aquatic turtle *Heckerochelys romani* have the best preservation and completeness. *Heckerochelys* is represented by numerous (more than 150) isolated shell and non-shell postcranial bones and a partial skeleton with a fragmentary skull (Sukhanov 2006). Other terrestrial vertebrates are known from rare isolated and often abraded bones and teeth (Alekseev et al. 2001; Alifanov and Sennikov 2001; Sukhanov 2001, Sukhanov 2003, 2006; Sennikov et al. 2005a, b; Starodubtseva et al. 2008; Paschenko et al. 2018). The fragment of the maxilla of the lepidosauromorph described below was initially identified by V.R. Alifanov as belonging to the primitive choristodere *Cteniogenys* ? sp. (Sennikov et al. 2005a, b; Starodubtseva et al. 2008), and this assignment was accepted by subsequent workers (e.g., Paschenko et al. 2018).

Systematic palaeontology

Diapsida Osborn, 1903

Sauria Macartney, 1802, sensu Gauthier, Estes, and de Queiroz, 1988

Lepidosauromorpha Gauthier, Estes, and de Queiroz, 1988

Lepidosauromorpha incertae sedis

Figures 1-2

Specimen. PIN 4767/7, fragmentary left maxilla. One tooth (Fig. 2A, B) was broken during the preparation of PIN 4767/7 and stored separately from the main specimen.

Locality and age. The Peski locality, Kolomenskii District, Moscow Region. The Moskvoretskaya Formation, Middle Jurassic (upper Bathonian).

Description. The specimen PIN 4767/7 is represents the anterior portion of the left maxilla, with a posterior part of the premaxillary process (= anterior process; = premaxillary ramus) and the anteriormost part of the dorsal process (= facial process) (Fig. 1). The premaxillary process is slender and dorsoventrally low (Fig. 1C, D, F). The dorsal process is weakly developed. The dorsal edge of the premaxillary process and the anterior part of the dorsal process are smooth forming a distinct long continuous narial margin (Fig. 1C, D). The narial margin is parallel to the supradental shelf and the dental edge of the premaxillary process (Fig. 1D) and smoothly curves dorsally in the anterior part of the dorsal process.

The lateral surface (Fig. 1C) is smooth with two large neurovascular foramina for the passage of the superior alveolar nerve and vessels. The more anterior neurovascular foramen is larger than the posterior one and is situated on the premaxillary process. The more posterior neurovascular foramen lies at the level of the anterior part of the dorsal process, where the narial margin is most curved dorsally.

The medial surface (Fig. 1D) of the bone has a distinct, relatively wide groove that is situated close and parallel to the narial margin. The supradental shelf is well-developed.

The maxillary fragment PIN 4767/7 has four teeth (two broken and two preserved) and one empty alveolar space (Fig. 1D, E). The teeth are closely spaced (about 7-8 per 5 mm), conical, and have rounded bases. The teeth become slightly larger posteriorly, at the level of the dorsal process. The tooth implantation is weakly pleurodont. The preserved teeth are long (equal or greater in height to the dorsoventral height of the premaxillary process) and with their apices gently recurved lingually (the anterior tooth) or slightly posterolingually (Fig. 1E). The apices have low anterior and posterior keels that reach the top of the tooth (Fig. 2A, B). There are up to eight striae between these keels on the lingual surface of the tooth. The striae have different

lengths: some of them reach the apex of the tooth, but some end before reaching the apex (Fig. 2C). The labial surface of the apices is smooth (Fig. 1C).

Comparisons and discussion

The fragmentary maxilla PIN 4767/7 from the Peski locality can be assigned to the Lepidosauromorpha based on the presence of pleurodont tooth implantation (e.g. Evans 1991; Schoch, Sues, 2018; see discussion of pleurodonty in LeBlanc et al. 2020). It differs from those of choristoderes (including the Bathonian basal choristodere *Cteniogenys*) in tooth implantation (pleurodont in PIN 4767/7 vs. subthecodont in choristoderes), the rounded bases of the teeth (vs. mediolaterally expanded base in choristoderes), the presence of the striae only on the lingual surface of the tooth crowns (striae equally pronounced on both the lingual and labial sides in non-neochoristoderan choristoderes), and in the presence of a smooth lateral bone surface with relatively large neurovascular foramina (vs. sculptured lateral surface with several rows of relatively small neurovascular foramina that open into short grooves in choristoderes) (e.g. Evans 1990; Evans and Klembara 2005; Skutschas 2008). As a result, the previous assignment of PIN 4767/7 (Sennikov et al. 2005a, b; Starodubtseva et al. 2008) to Choristodera is not supported by this study and there is currently no evidence of the presence of choristoderes in the Peski vertebrate fauna.

The fragmentary maxilla PIN 4767/7 differs from that of most squamates (including UK Middle Jurassic taxa like *Bellairsia* and *Oxiella*) in having a less pronounced labial wall (= weakly pleurodont implantation, see e.g. Evans 1998 for comparisons) and differs from rhynchocephalians with pleurodont teeth in having taller, sharper, gracile and less crowded teeth (see Jenkins et al. 2017 and references therein) and, additionally, by lacking any external bone sculpture (present in some rhynchocephalians, e.g. Early Jurassic *Gephyrosaurus*, see Evans 1980).

Among basal lepidosauromorphs (= “non-lepidosaurian lepidosauromorphs”), the fragmentary maxilla PIN 4767/7 most closely resembles that of the Middle Triassic *Fraxinisaura* (Schoch and Sues 2018) and the contemporary Middle Jurassic (Bathonian) *Marmoretta* (Evans 1991; Waldman and Evans 1994) in the structure of the maxilla (low labial wall, relatively low dorsal process, and long premaxillary process bordering an extended narial margin) and the maxillary teeth (relatively high crowns with gently recurved apices, the presence of striae on the lingual side; anterior and posterior keels). The similarities could be the result of close relationships of all these taxa, given that *Fraxinisaura* may be the sister taxon of *Marmoretta* (Schoch and Sues,

2018; Griffiths et al. (in press)). Despite this similarity, the fragmentary nature of PIN 4767/7 (namely, the absence of the tab-like anterior portion of the premaxillary process, dorsal part of the dorsal process, and posterior portion of the bone) does not permit further detailed comparison. Pending the discovery of additional material, we conservatively identify PIN 4767/7 as Lepidosauromorpha indet.

The Middle Jurassic record of basal lepidosauromorphs is scarce and it is limited to Bathonian localities in the UK (*Marmoretta oxoniensis* in the Kirtlington Cement Quarry locality of the Forest Marble Formation in England; *Marmoretta* sp. and two undescribed lepidosauromorph species (lepidosauromorph species A and lepidosauromorph species B sensu Panciroli et al. 2020) in the Kilmaluag Formation, Scotland) (Evans 1991; Waldman and Evans 1994) and Siberian Russia (Lepidosauromorpha indet. in the Berezovsk Quarry locality of the Itat Formation in Krasnoyarsk Region) (Averianov et al. 2016). Our find extends the known geographical range of the Bathonian non-lepidosaurian lepidosauromorphs and demonstrates their wide Laurasian distribution at this time.

The previously known occurrences of basal lepidosauromorphs in the Bathonian localities of the UK (the Forest Marble and the Kilmaluag formations) and Siberian Russia (Itat Formation) together with the new find of basal lepidosauromorphs in European Russia (Moskvoretskaya Formation) provides further evidence that the Bathonian vertebrate faunas of Europe and Western Siberia were homogeneous (see recent comparisons of the Bathonian vertebrate faunas in Paschenko et al. 2018; Panciroli et al. 2020) at least at the higher taxonomic level. The next step in our understanding of the Middle Jurassic stage of evolution of the Laurasian continental vertebrate faunas is to compare the composition of Bathonian vertebrate faunas at a lower taxonomic level (e.g. genera, species), which requires the discovery of new material and description of both new and already found (but still undescribed) material.

Acknowledgements

We thank R. Rakitov (Borissiak Paleontological Institute, Moscow) for the help with SEM micrograph of PIN 4767/7.

Funding

The work of PPS, DDV and RAB was fulfilled under financial support of the Russian Science Foundation (project 19-14-00020). The work of AGS was supported by the Russian Science Foundation (project 20–04–00070). The work of EVS was supported by the theme of the Zoological Institute of the Russian Academy of Sciences (AAAAA19-119020590095-9)

References

Alekseev AS, Agadjanian AK, Areshin AV, Barskov IS, Gordenko NV, Efimov MB, Kabanov PB, Krasilov VA, Krasnikov NM, Lebedev OA, et al. 2001. Otkrytie unikal'nogo mestonahozhdeniya sredneyurskoj fauny i flory v Podmoskov'e [Discovery of a unique locality of the Middle Jurassic fauna and flora in the Moscow Region]. Dokl Ross Akad Nauk. 377(3):359–362. Russian.

Alifanov VR, Sennikov AG. 2001. Dinozavry iz Podmoskov'ya [Dinosaurs from the Moscow region]. Dokl Ross Akad Nauk. 376(1):73–75. Russian.

Averianov AO, Lopatin AV, Krasnolutskii SA, Ivantsov SV. 2010. New docodontans from the Middle Jurassic of Siberia and reanalysis of Docodonta interrelationships. Proc Zool Inst Russ Acad Sci. 314(2):121–148.

Averianov AO, Martin T, Bakirov AA. 2005. Pterosaur and dinosaur remains from the Middle Jurassic Balabansai Svita in the northern Fergana Depression, Kyrgyzstan (Central Asia). J Palaeontol. 48(1):135–155.

Averianov A, Martin T, Skutschas P, Danilov I, Schultz J, Schellhorn R, Obraztsova E, Lopatin A, Sytchevskaya E, Kuzmin I, et al. 2016. Middle Jurassic vertebrate assemblage of Berezovsk coal mine in western Siberia (Russia). J Glob Geol. 19(4):187–204.

Bragina EN. 2005. Gibodontnaya akula *Hybodus hauffianus* Fraas, 1895 iz kontinental'nyh otlozhenij verhnego bata Podmoskov'ya [Hybodont shark *Hybodus hauffianus* Fraas, 1895 from continental deposits from the Upper Bathonian of the Moscow Region]. Izv Vuzov Geol Razved. p. 19–22. Russian

Evans SE. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of SouthWales. Zool J Linn Soc. 70: 203–264.

Evans SE. 1990. The skull of *Cteniogenys*, a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire. Zool J Linn Soc. 99:205–237.

Evans SE. 1991. A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of England. Zool J Linn Soc. 103:391–412.

Evans SE. 1998. Crown group lizards (Reptilia, Squamata) from the middle Jurassic of the British Isles. Palaeontographica, Abt. A. 250:123–54.

Evans SE, Klembara J. 2005. A choristoderan reptile (Reptilia; Diapsida) from the lower Miocene of northwest Bohemia (Czech Republic). J Vertebr Paleontol. 25(1):171–184.

Evans SE, Milner AR. 1994. Middle Jurassic microvertebrate assemblages from the British Isles, in: Fraser, N.C., Sues, H.-D. (Eds.), In the shadow of the dinosaurs. Early Mesozoic tetrapods. Cambridge University Press, Cambridge. p. 435.

Evans SE, Waldman M. 1996. Small reptiles and amphibians from the Middle Jurassic of Skye, Scotland. Museum of Northern Arizona Bulletin. 60:219–226.

Gambaryan PP, Averianov AO. 2001. Femur of a morganucodontid mammal from the Middle Jurassic of Central Russia. Acta Palaeontol Polonica. 46(1):99–112.

Gauthier JA, Estes R, Queiroz K de. 1988. A phylogenetic analysis of Lepidosauromorpha, in R Estes, GK Pregill (Eds.), Phylogenetic Relationships of the Lizard Families. Stanford University Press, Stanford, California. p. 15–98.

Griffiths E, Ford D, Benson R, Evans SE. (in press). New information on the Jurassic lepidosauromorph *Marmoretta oxoniensis*. Palaeontology.

Jenkins KM, Jones M, Zikmund T, Boyde A, Daza JD. 2017. A review of tooth implantation among rhynchocephalians (Lepidosauria) J Herpetol, 51(3):300-306.

Krupina NI. 1995. Pervaya nahodka yurskih ceratodontid (Dipnoi) iz Podmoskov'ya [The first record of Jurassic ceratodontids (Dipnoi) from the Moscow Region]. Paleontol J. 2:129–131. Russian.

LeBlanc A, Paparella I, Lamoureux DO, Doschak MR, Caldwell MW. 2021. Tooth attachment and pleurodont implantation in lizards: histology, development, and evolution. J Anat. 238:1156–1178.

Macartney J. 1802. Preface and Table III; in Lectures on Comparative Anatomy. Translated from the French of G. Cuvier by William Ross, under the inspection of James Macartney. On the Organs of Motion. Longman and Rees, London.

Osborn HF. 1903. On the primary division of the Reptilia into two subclasses, Synapsida and Diapsida. Science 17:275–276.

Panciroli E, Benson R, Walsh S, Butler RJ, Castro TA, Jones M, Evans SE. 2020. Diverse vertebrate assemblage of the Kilmaluag Formation (Bathonian, Middle Jurassic) of Skye, Scotland. Earth and Environ Sci Trans of the Royal Soc of Edinburgh. 111(3):135–156.

Pashchenko DI, Kuzmin IT, Sennikov AG, Skutschas PP, Efimov MB. 2018. On the finding of neosuchians (Neosuchia, Crocodyliformes) in the Middle Jurassic (Bathonian) deposits of the Moscow Region. Paleontol J. 52(5):550–562.

Popov EV, Shapovalov KM. 2007. Novye nahodki himerovyh ryb (Holocephapli, Chimareoidei) v yuge Evropejskoj chasti Rossii [New findings of Chimeric fishes (Holocephapli, Chimareoidei] in the south of European Russia. Mod Paleontol: Class and Recent Method. p. 25–44. Russian.

Schoch RR, Sues H-D. 2018. A new lepidosauromorph reptile from the Middle Triassic (Ladinian) of Germany and its phylogenetic relationships. J Vertebr Paleontol. 38: e1444619.

Sennikov AG, Alifanov VR, Efimov MB. 2005a. A new page in the geological and paleontological history of European Russia, Dokl Mosk Ob-va Ispyt Prir. 36:128–130.

Sennikov AG, Alifanov VR, Efimov MB. 2005b. Novye dannye o geologicheskom stroenii i faune pozvonochnyh sredneyurskogo mestonahozhdeniya Peski (Moskovskaya oblast') [New data on the geological structure and vertebrate fauna from the Middle Jurassic Peski locality (Moscow Region)]. In Materialy Pervogo Vserossiiskogo soveshchaniya “Yurskaya sistema Rossii: problemy stratigrafii i paleogeografii” [First All-Russia Conference on the Jurassic System of Russia: Problems of Stratigraphy and Paleogeography], Zakharov VA, Rogov MA, Dzyuba OS (Eds.), Moscow: Geol Inst Ross Akad Nauk. p. 236– 238. Russian.

Skutschas PP. 2008: A choristoderan reptile from the Lower Cretaceous of Transbaikalia, Russia. N J. Geol Paläont Abh. 247:63–78.

Starodubtseva IA, Sennikov AG, Soroka IL, Golubev VK, Gordenko NV, Naugolnykh SV, Kandinov MN, Pavlova LA, Novikov IV. 2008. Geologicheskaya istoriya Podmoskov’ya v kollektsiyakh estestvennonauchnykh muzeev Rossiiskoi akademii nauk [Geological

History of the Moscow Region in Collections of Natural Science Museums of the Russian Academy of Sciences]. Moscow: Nauka. p. 1–229. Russian.

Sukhanov VB. 2006. An archaic turtle, *Heckerochelys romani* gen. et sp. nov., from the Middle Jurassic of Moscow region, Russia. Danilov I.G., Parham J.F. (Eds.), Fossil turtle research. Russ J Herpetol (Supplement). 1(13):112–118.

Waldman M, Evans SE. 1994. Lepidosauromorph reptiles from the Middle Jurassic of Skye. Zool J Linn Soc. 112:135–50.

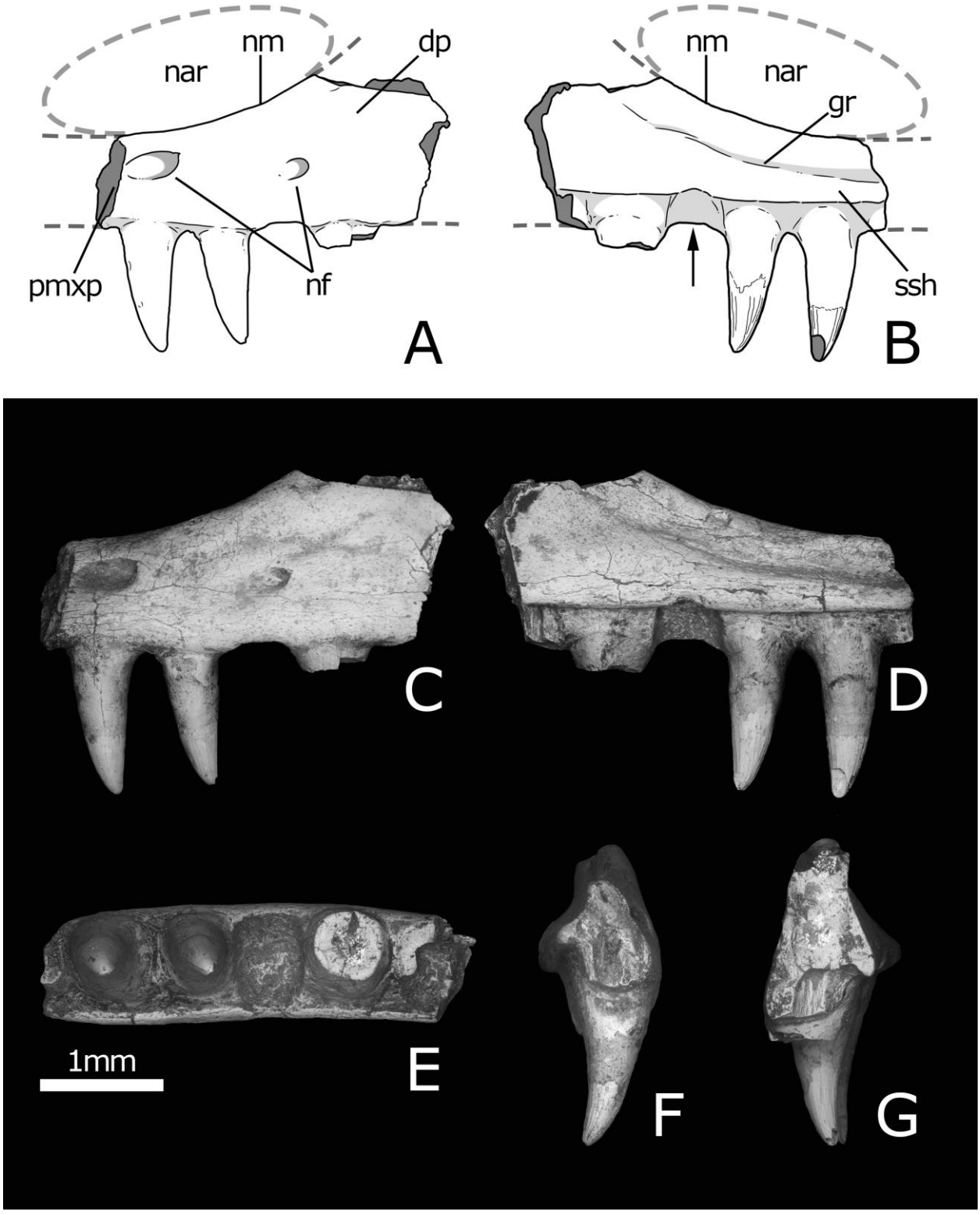

Figure 1. Lepidosauromorpha indet., PIN 4767/7, fragmentary left maxilla, in lateral (A , C), medial (B, D), ventral (E), anterior (F), and posterior (G) views. (A) and (B) – interpretative drawings. Peski locality, Moscow Region, Russia; Middle Jurassic (Bathonian). Arrow points to an empty space between teeth. Abbreviations: dp, dorsal process; gr, groove; nar, naris; nf, neurovascular foramina; nm, narial margin; pmxp, premaxillary process; ssh, supradental shelf.

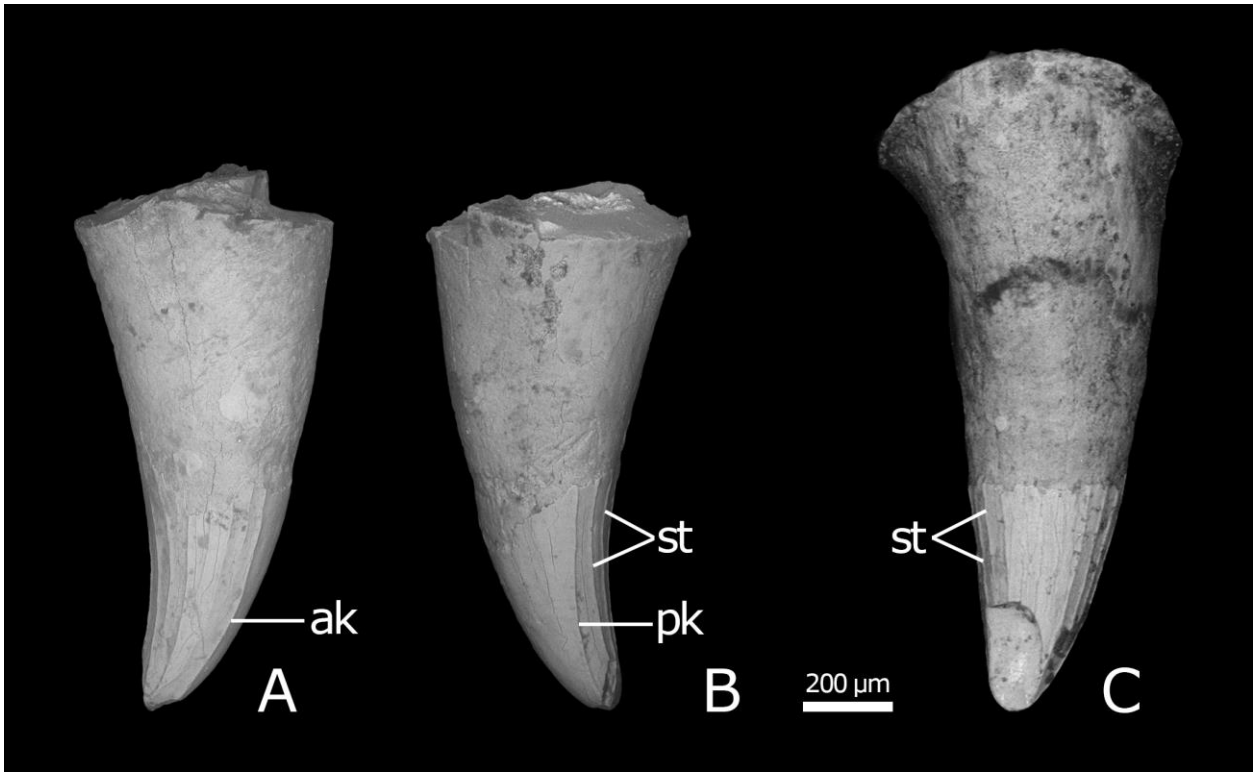

Figure 2. Lepidosauromorpha indet., PIN 4767/7, fragmentary left maxilla, close-up of tooth, in anterior (A), posterior (B), and lingual (C) views. Peski locality, Moscow Region, Russia; Middle Jurassic (Bathonian). Abbreviations: ak, anterior keel; pk, posterior keel; st, striae.