

# A New Genus of Elephant Fish (Holocephali: Callorhynchidae) from the Late Jurassic of Central Russia

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**Abstract**—This article describes *Moskovirhynchus robustus* gen. et sp. nov., a new genus and species of elephant fish from two Upper Jurassic (Boreal middle Volgian Substage, *virgatus* Zone) localities of Moscow and the Moscow region, based on isolated mandibular, palatine and vomerine dental plates. The dentition of the new genus bears a morphological resemblance to that of the Recent elephant fish genus *Callorhynchus* Lacepède, 1798, but is characterized by a mosaic combination of primitive (on palatine tooth plates) and advanced (on both palatine and mandibular plates) dental characters—e.g., presence of asymmetrical bifurcated median tritor on mandibular plates and reduced tritors on palatine plates (an advanced condition for callorhynchids) together with a well-developed aboral area of palatine plate (a primitive condition). The new taxon, known only from dental elements, represents the oldest representative of the Callorhynchidae *sensu stricto*.

**Keywords:** Chimaeriformes, Chimaeroidei, tooth plates, Volgian stage, Moscow, Moscow Region

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## INTRODUCTION

Isolated dental plates of chimaeroid fishes (Chimaeroidei) from the Jurassic of the Russian Plate were discovered early on (Bogolyubov, 1912), but systematic collection did not begin until the end of the twentieth century (Averianov, 1992). Fifteen Jurassic localities are now known from this area (all in the European part of Russia) from the Middle (Bathonian, Callovian) and Upper (Volgian Stage) Jurassic (Popov, 2003, 2005; Popov and Beznosov, 2006; Popov and Shapovalov, 2007). The Callovian association is the most abundant and taxonomically diverse, comprising six to seven genus-level taxa of callorhynchids and “edaphodontids” from seven localities (Popov, 2005).

Isolated dental plates are known from the Boreal Volgian Stage of this area for chimaeroids “Edaphodontidae” gen. et sp. indet. (possibly, a taxon close to *Elasmodus* sp., E.V. Popov, pers. observ.) and *Ischyodus* cf. *schuebleri* Quenstedt, 1858 (both—(?) lower Volgian Substage, Kargort section in the Komi Republic, Russia: Popov and Beznosov, 2006), *Stoilodon* sp. (*nikitini* Zone of the middle Volgian Substage of Gorodishchi section in the Ulyanovsk Region, Russia: Popov and Efimov, 2012) and *Brachymylus bogolubovi* Averianov, 1992 (middle Volgian Substage of Moscow, Russia: Bogolyubov, 1912; Averianov, 1992). Several members of the association have been

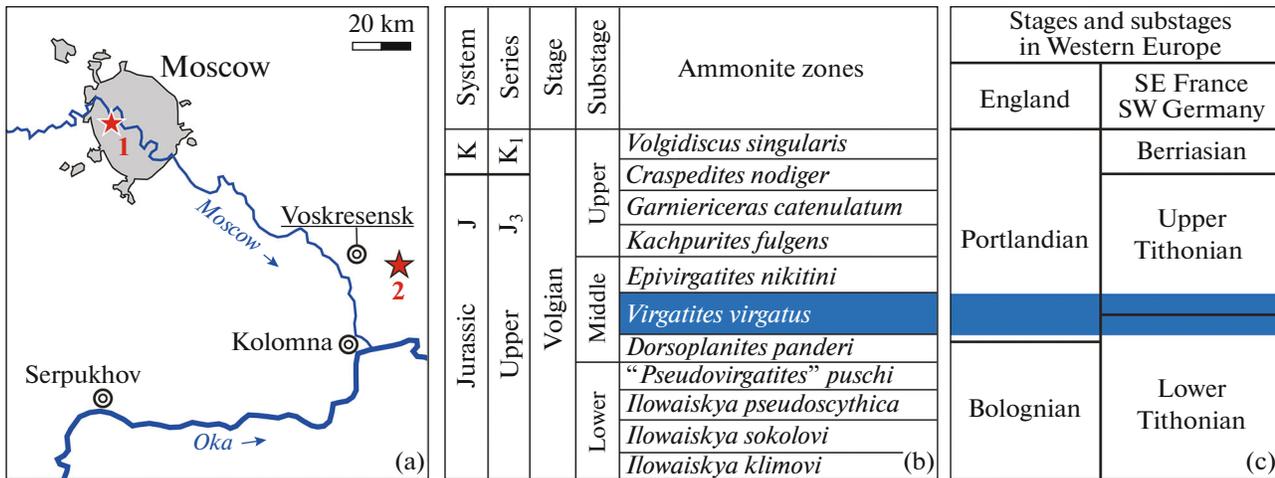
described from the middle Volgian (*virgatus* Zone) substage of the Upper Jurassic of Moscow and the surrounding region, including two callorhynchids: *Callorhynchus* sp. and *Brachymylus* sp.—and two “edaphodontids”: *Ischyodus* cf. *townsendi* Buckland, 1835 and *Elasmodectes* sp. (the latter taxon can now be reidentified as *Stoilodon* sp.; see also: Popov and Efimov, 2012, p. 74). The *Callorhynchus* sp. derived from this association is redescribed in this article as a new genus of elephant fishes (Callorhynchidae s. s.): *Moskovirhynchus robustus* gen. et sp. nov.

The figured tooth plates are housed at the Regional Earth Sciences Museum of the Saratov State University (SGU, no. 155).

## LOCALITIES AND MATERIAL

The tooth plates of the new genus of elephant fishes described here come from two localities in Central Russia within the boundaries of Moscow and Moscow Region (Fig. 1a):

(1) Kuntsevo. Gullies (N 55°44′33.5″, E 37°26′27.6″; N 55°44′40.3″, E 37°26′16.8″) on the right bank of Moscow River near the Kuntsevo Archaeological Site (Fili—Kuntsevo Park) in Moscow. Jurassic deposits are represented here by sandy clays and sands with phosphorites and abundant inverte-



**Fig. 1.** (a) Localities with remains of *Moskovirhynchus* gen. nov. in Central Russia (Moscow and the surrounding region); localities: (1) Kuntsevo; (2) LFR 7-2-bis quarry; (b) paleontological zonation of the Volgian stage of European Russia (after Rogov, 2010, 2014; Kiselev et al., 2018), stratigraphic range of the new chimaeroid genus is shown in color; (c) correlation of the *Virgatites virgatus* Zone with stratigraphic units of England (after Cope, 1993), France and Germany (after Schweigert, 2007; Bulot et al., 2014).

brate fossils of the middle Volgian Substage (*virgatus* and *nikitini* Zones) (Fig. 1b). Overlying them are the generally similarly structured but more sandy deposits of the upper Volgian Substage (*fulgens*, *catenulatum* and *nodiger* Zones) and of the Hauterivian stage of the Early Cretaceous (Gerasimov, 1971; Rogov, 2017; Tesakova, 2017). The closest nearby Jurassic sections along the Moscow River (Khoroshevo, Studeny Ovrage in Mnevnik; both now unavailable) have been known as classic Jurassic sections since the end of the eighteenth century (Starodubtseva, 2006). They have repeatedly been studied by geologists (e.g., Rouillier, 1845; Trautschold, 1861, 1870; Nikitin, 1883; Rozanov, 1912) and served as common destinations for geological fieldtrips (Pavlov, 1946, Aprodov and Aprodova, 1963; Gerasimov, 1967). The chimaeroid tooth plates were collected by one of the authors (K.M. Shapovalov) in the 1990s by wet-sieving fossil-rich dark-grey clayey sands (“shell bed”) of the topmost *virgatus* Zone, (the top part of bed 1 in: Tesakova, 2017).

In addition to the new chimaeroid species, this bed has also yielded tooth plates of *Brachymylus* sp. (SGU, no. 155/78) and *Ischyodus* sp. (SGU, no. 155/79). Other fossils coming from this bed (as well as the overlying middle Volgian *nikitini* Zone beds and upper Volgian *fulgens* Zone beds) include numerous shark fossils (teeth, spines), bones, scales and numerous otoliths of bony fishes, teeth of marine reptiles, various invertebrates: bivalve, gastropod, scaphopod and cephalopod mollusks, brachiopods and echinoderms (their spines form most of the enclosing “shell bed”).

The section interval discussed here has also been described from temporary exposures opened during construction in the nearby neighborhoods of Moscow (Malenkina and Shkolin, 2009; Shkolin and Malen-

kina, 2015) and several remaining natural outcrops in the region around Moscow (Rogov, 2017).

(2) LFR 7-2-bis. The now abandoned quarry no. 7-2 bis (N 55°23'36", E 38°51'02.6") of the Lopatinsky Phosphorite Mine in the Voskresensk District of the Moscow Region. Volgian deposits (total thickness about 3 m) in the quarries of this mine are sandy and clayey middle Volgian (*panderi*, *virgatus* and *nikitini* Zones) beds of small thickness (1.5–2 m), containing phosphorites and sandy upper Volgian beds (sands, sandstones with phosphorites) (Mitta, 1993; Gerasimov et al., 1995; Rogov, 2017). Volgian deposits are lying over Oxfordian clays and are overlain by sandstones of the lower Cretaceous Ryazanian Regional Stage (Mitta, 2005).

Material of *Moskovirhynchus robustus* gen. et sp. nov. from Kuntsevo locality is represented by six tooth plates of variable preservation, including the holotype SGU, no. 155/75 and a vomerine plate (SGU, no. 155/74) belonging to a juvenile individual; from quarry LFR no. 7-2-bis two tooth plates: the relatively large left palatal plate (SGU, no. 155/64), as well as an incomplete right mandibular plate belonging to a juvenile individual (SGU, no. 155/73). Other chimaeroid taxa have been identified from the same locality (Popov and Shapovalov, 2007): *Brachymylus* sp. and “edaphodontids” “*Ischyodus*” cf. *townsendi* Buckland, 1835 and *Elasmodectes* sp. [the latter taxon was later reidentified as (?) *Stoilodon* sp.: see Popov and Efimov, 2012]. The entire fossil material comes from the tailings of the strip mine (*ex situ*) and most likely dates to the middle Volgian, *virgatus* Zone, judging from the frequency of ammonites belonging to this zonal assemblage found at the sites where chimaeroid plates were collected (K.M. Shapovalov, pers. observation, 1990s). Collections were made by K.M. Shapovalov in 1997–1999.

The middle Volgian *virgatus* Zone is currently believed to correlate (Rogov, 2010, 2014; Kiselev et al., 2018) with the lower part of the Portlandian Stage in England (the entire *Glaucolithites glaucolithus* Zone and parts of the *Galbanites okusensis* and *Progalbanites albani* Zones) (Cope et al., 1980; Cope, 2013), or the lower part of the upper Tithonian (the lower part of the *Micracanthoceras ponti* Zone) and the topmost lower Tithonian of southwestern Germany and southeastern France (Schweigert, 2007; Bulot et al., 2014) (Fig. 1c; see also the zonal correlation chart for the Volgian Stage in: Arkhangel'sky et al., 2019, text-fig. 2).

### TOOTH PLATE TERMINOLOGY

Descriptive terminology and measurements were proposed by the first author (Popov, 1999, 2003; Popov and Beznosov, 2006; Popov and Shapovalov, 2007; Popov and Machalski, 2014; Popov et al., 2019), a key to the main descriptive terms and measurements is shown in Figs. 2 and 3.

When the anterolateral tritor was absent on the callorhynchid mandibular plate and, therefore, the plate could not be placed in the ontogenetic series the same way this is done for the “edaphodontids” (Popov and Beznosov, 2006; Popov and Shapovalov, 2007; Popov and Machalski, 2014), we used measurements of the length of the symphyseal platform (Ls) at the contact between left and right mandibular plates (Fig. 2a). In the case of palatine and vomerine plates we used the maximum mesiodistal length (L) of the specimen as a relative index (Fig. 2e), although this index is less reliable.

### SYSTEMATIC PALEONTOLOGY

The classification of chimaeroid fishes (from superfamily level up) follows Nelson (2006). The composition of the family Callorhynchidae Garman, 1901 follows the authors' concept (Popov, 2003; Popov et al., 2019).

#### CLASS CHONDRICHTHYES

#### SUBCLASS HOLOCEPHALI

#### Superorder Holocephalomorpha

#### Order Chimaeriformes

#### Suborder Chimaeroidei

#### Superfamily Callorhinchoidea Garman, 1901

#### Family Callorhynchidae Garman, 1901

#### Genus *Moskovirhynchus* Popov et Shapovalov, gen. nov.

**Etymology.** From the Moscow River, in the banks of which the material was discovered, and the Greek *rhynchus* (beak); masculine.

**Type species.** *Moskovirhynchus robustus* gen. et sp. nov.

**Diagnosis.** (Based on the dental system; the asterisk (\*) indicates apomorphic characters). Callorhynchid known from small-sized mandibular, palatine, and vomerine tooth plates. Field of basal perforation is well-developed on all tooth plates. Mandibular tooth plates have vascular tritors: the median tritor is wide, bifurcated, with a well-developed inner branch (\*). The inner tritor is moderately developed. The outer tritor is narrow. Palatine tooth plates are robust and tall and have a greatly developed aboral part which is 1.5–2 times larger than the height of the oral part of the tooth plate; the single rounded inner tritor of vascular pleromin is displaced towards the symphyseal margin (\*). Vomerine tooth plates are subtriangular, laterally compressed, with a well-developed symphysis which is occlusally rotated and forms a symphyseal crest in occlusion; tritors are absent (\*).

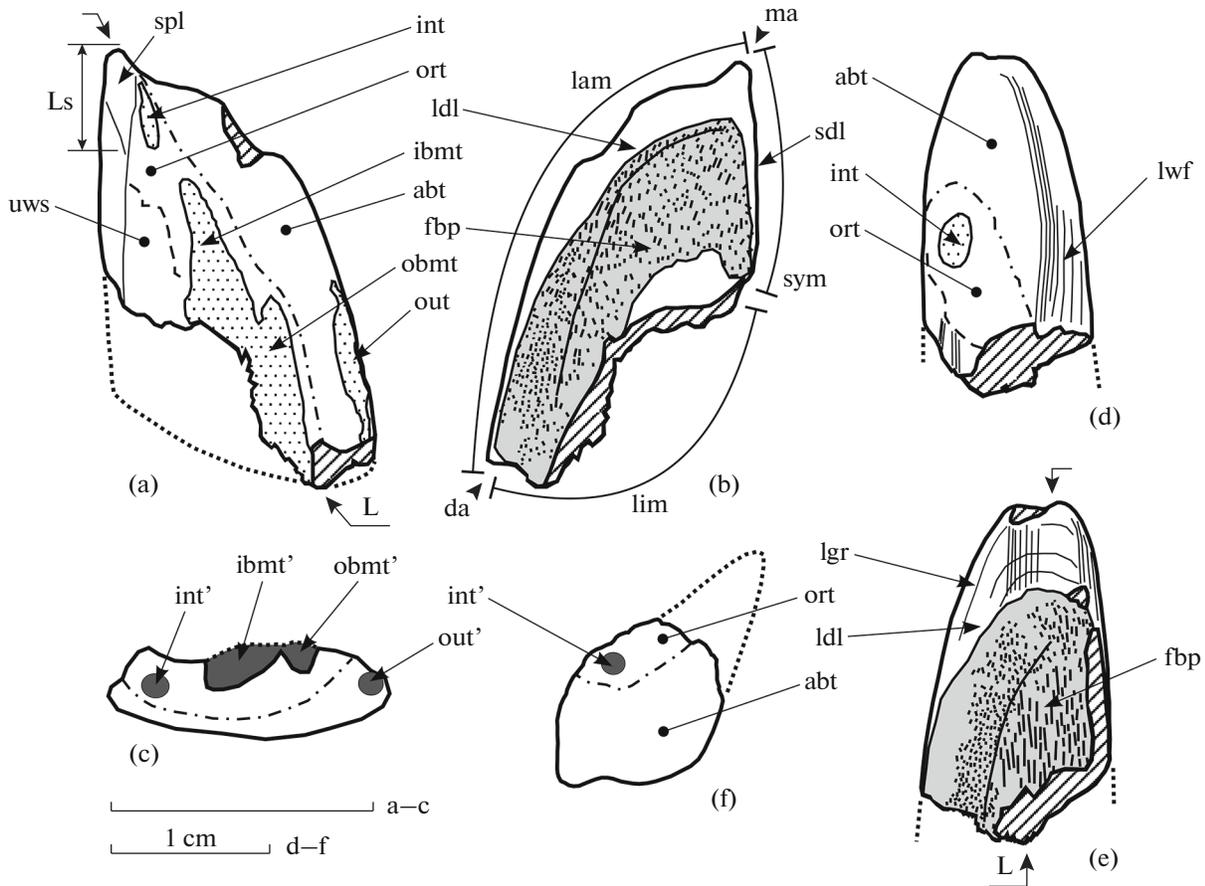
**Species composition.** Type species from Central Russia, *virgatus* Zone, middle Volgian, Upper Jurassic.

**Comparison.** The new genus differs from the most similar extant genus *Callorhynchus* Lacepède, 1798, which is also known from fossils (Stahl, 1999; Otero et al., 2013; Cicimurri and Ebersole, 2015), in the pronounced bifurcation of the median tritor with a more developed inner branch of the mandibular tooth plate, the more robust palatine tooth plate with a single, undeveloped small tritor, a taller descending lamina and generally a more developed aboral part of the palatine tooth plate; a more laterally compressed vomerine tooth plate with an occlusally rotated symphyseal surface and totally lacking tritors (in *Callorhynchus* one tritor is usually present: Averianov, 1997; Herman et al., 2001).

*Moskovirhynchus* gen. nov. differs from the Middle Jurassic *Pachymylus* Woodward, 1892 in the presence of the inner tritor and the bifurcation of the median tritor of the mandibular tooth plate; the smaller inner tritor of the palatine tooth plate, the greater displacement of this tritor away from the symphyseal margin and the absence of symphyseal pleromin processes. Vomerine tooth plates are unknown for *Pachymylus*.

The new genus differs from the Middle Jurassic *Duffinodus* Popov, 2003 in the lesser height of the symphysis and the less robust mandibular tooth plate, which has a more developed inner branch of the median tritor (in *Duffinodus* the outer branch is most pronounced, while the inner one is shorter and mesially segmented), the mesial position of the inner tritor; the more laterally compressed vomerine tooth plate with an occlusally rotated symphysis that forms a symphyseal crest and lacks occlusive tritors. Palatine tooth plates are not known for *Duffinodus*.

*Moskovirhynchus* gen. nov. differs from the Middle Jurassic *Brachymylus* Woodward, 1892 in the absence of a symphyseal tritor on the mandibular tooth plate, the bifurcation of the median tritor on the mandibular tooth plate, and a better developed symphyseal half of



**Fig. 2.** Morphological interpretation of mandibular and palatine tooth plates of *Moskovirhynchus robustus* gen. et sp. nov. and terminology used in text; (a–c) SGU, no. 155/65, right mandibular (L18, Ls3.2) plate: (a) symphyseal-occlusal view, (b) basal view, (c) lingual cross-section; Moscow, Kuntsevo; Upper Jurassic, middle Volgian, *virgatus* Zone; (d–e) SGU, no. 155/66, left palatine (L19.8) plate: (d) occlusal view, (e) basal view, (f) lingual cross-section; Moscow Region, Lopatinsky Phosphorite Mine no. 7-2-bis; Upper Jurassic, middle Volgian, *virgatus* Zone. Abbreviations: damaged surfaces and parts of the plate cross-hatched; vascular pleromin of trititors stippled; laminar pleromin in grey; orientation of missing parts of tooth plates as dotted line. Abbreviations: ('), int', syt' etc. pleromin bodies of the corresponding trititors in lingual cross-section; abt, aboral part of the plate; da, distal angle; fbp, field of basal perforation (light grey fill); ibmt, inner branch of median tritor; int, inner tritor; L, mesiodistal length; lam, lateral descending lamina; lgr, growth lines on the surface of "compact glossy tissue", lim, lingual margin; Ls, length of symphyseal platform on mandibular plate; lwf, labial wear facet; ma, mesial angle; obmt, outer branch of median tritor; ort, oral part of plate; out, outer tritor; sdl, symphyseal descending lamina; spl, symphyseal surface; sym, symphyseal margin; uws, unworn part of the occlusal surface.

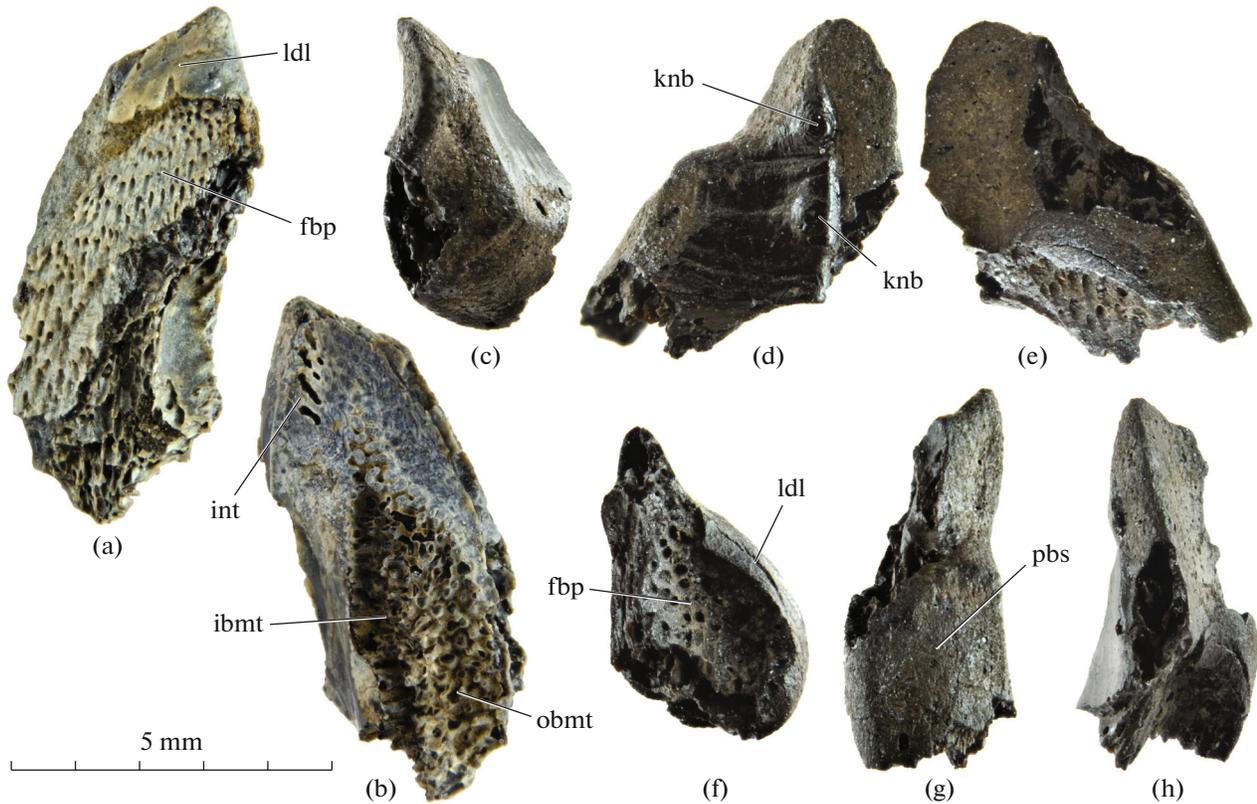
the lateral descending lamina; the presence of a single tritor of the palatine tooth plate (*Brachymylus* has two well-developed vascular trititors). Vomerine tooth plates are unknown for *Brachymylus*.

The new genus differs from the Early Jurassic "*Brachymylus*" *latus* Duffin, 1996, known only from a mandibular tooth plate, in the degree of reduction of the occlusal trititors, the presence of an outer tritor and a different morphology of bifurcation in the median tritor, with better developed and deep inner branch, the less robust mandibular tooth plate, and the symphyseal part of the lateral descending lamina that is less reduced in height.

*Moskovirhynchus* gen. nov. differs from the Early Jurassic genera *Bathytheristes* Duffin, 1995 and *Eomanodon* Ward et Duffin, 1989, known only from pala-

tine tooth plates, in the more robust morphology of the palatine tooth plate, the absence of laminated pleromin in the structure of the tritor (*Bathytheristes* has one laminated tritor, *Eomanodon* has two larger laminated trititors), the better developed aboral part of the tooth plate.

**Remarks.** Mandibular plates of *Moskovirhynchus* gen. nov. greatly resemble those of *Callorhynchus*, differing mainly in the morphology of the bifurcation of the median tritor, which in modern and fossil species of the latter genus is absent even as a morphological aberration (Stahl, 1999; Kriwet and Gazdzicki, 2003; Otero et al., 2013). Considering that mandibular tooth plates are the most diagnostic dentition element in chimaeroid fishes (Stahl, 1999; Popov, 2003), *Moskovirhynchus* gen. nov. and *Callorhynchus* can be



**Fig. 3.** Tooth plates belonging to juvenile individuals of the Late Jurassic *Moskovirhynchus robustus* gen. et sp. nov.: (a), (b) SGU, no. 155/73, incomplete right mandibular (L8.3, Ls2.3) plate: (a) basal view, (b) occlusal view; Moscow Region, LFR-7-2-bis; Upper Jurassic, middle Volgian, ?*virgatus* Zone.; (c–h) SGU, no. 155/74, right vomerine (L 6.7) plate: (c) mesial view, (d) symphyseal-occlusal view, (e) basal view, (f) lingual view, (g) parabasal view, (h) apical view; Moscow, Kuntsevo; Upper Jurassic, middle Volgian, *virgatus* Zone. Scale applies to all figures. Abbreviations: pbs, parabasal surface of the vomerine plate; knb, knobs (without pleromin); other abbreviations as in Fig. 2.

considered the closest among all callorhynchid genera within the scope used here (Popov, 2003; Popov et al., 2019). The composition of the family Callorhynchidae requires further revision, which is beyond the scope of this article, but the two genera (*Callorhynchus* and *Moskovirhynchus*) can be considered Callorhynchidae sensu stricto. *Moskovirhynchus*, therefore, is the oldest member of the modern elephant fish known from tooth plates. The next most recent taxon is *Callorhynchus borealis* Nessov et Averianov, 1996 from the late Albian (Early Cretaceous) of Central Russia (Nessov and Averianov, 1996) which is the oldest known species of elephant fish of the genus *Callorhynchus*.

*Moskovirhynchus robustus* Popov et Shapovalov, sp. nov.

Plate 9, figs. 1–6

*Callorhynchus* sp.: Popov and Shapovalov, 2007, text-fig. 3a–3e, pl. 1, figs. 1–3; Popov et al., 2019, text-fig. 4C.

**Etymology.** Lat. *robustus* ‘solid, robust’; a characteristic of the palatine tooth plate compared with fossil and extant elephant fish of the genus *Callorhynchus*.

**Holotype.** SGU, no. 155/75, left mandibular (L 19.4) tooth plate; Moscow, Kuntsevo locality; Upper Jurassic, middle Volgian, *virgatus* Zone.

**Description** (Figs. 2, 3). Mandibular, palatine, and vomerine tooth plates are known for this species. Mandibular plates of adult individuals (Fig. 2a–2c; pl. 9, figs. 1–4) are characterized by a convex symphyseal surface with indistinct margins and lacking well-developed crests; the surface is expanded mesially by the symphyseal descending lamina, it bears an occlusally rotated symphyseal platform also in its mesial part. The basal surface is transversely convex, most of it occupied by descending laminae with the associated field of basal perforation. The descending laminae are not tall but long, converging near the mesial angle of the tooth plate. The lateral descending lamina is distally thickened, forming a shallow distobasal groove. The field of basal perforation is well-developed and occupies almost the entire basal surface, excluding the small lingual sector parallel to the lateral lamina. The labial surface encloses the lateral lamina in a narrow rim and has weakly-defined growth lines on the surface of the “compact glossy tissue”. The labial margin is weakly notched, with one (more rarely two) asym-



## Explanation of Plate 9

**Figs. 1–6.** Tooth plates of *Moskovirhynchus robustus* gen. et sp. nov.: (1) holotype SGU, no. 155/75, left mandibular (L19.4) plate: (1a) symphyseal-occlusive view, (1b) occlusive view, (1c) basal view, (1d) labial view, (1e) mesial view; (2) paratype SGU, no. 155/65, right mandibular (L18) plate: (2a) symphyseal-occlusive view, (2b) basal view, (2c) labial view; (3) SGU, no. 155/77, mesial fragment of left mandibular plate: (3a) basal view, (3b) occlusive view; (4) SGU, no. 155/76, distal fragment of right mandibular plate: (4a) basal view, (4b) occlusive view; Moscow, Kuntsevo; Upper Jurassic, middle Volgian, *virgatus* Zone; (5) paratype SGU, no. 155/66, left palatine (L19.8) plate: (5a) occlusive view, (5b) symphyseal view, (5c) mesial view, (5d) basal view; Moscow Region, LFR-7-2-bis; Upper Jurassic, middle Volgian, ?*virgatus* Zone; (6) SGU, no. 155/64, incomplete left palatine plate: (6a) basal view, (6b) occlusive view, (6c) mesial view; same locality as in figs. 1–4. Scale applies to all figures.

metrical lingual depression. The occlusive surface carries well-developed vascular tritons: the inner, outer and composite median tritor. The inner tritor is narrow, moderately well-developed, displaced towards the mesialmost angle of the tooth plate; the outer tritor is narrow, long and comparable in width with the inner tritor but it extends along the labial margin and is considerably set apart from the median tritor. The median tritor is bifurcated: the inner branch is wide (two to three times wider than the outer branch), long and mesially extended; the outer branch is narrow, short, does not project in plan view beyond the medial end of the outer tritor. In lingual cross-section the branches are well distinct, the axis of the inner branch is displaced towards the symphyseal margin. The boundary between oral and aboral parts of the tooth plate passes along the median tritor; the outer tritor is located in the aboral part which appears as a wide band in occlusive view. Preserved between the inner branch of the median tritor and the symphyseal margin is an unworn area with glossy covering tissue, growth lines are barely visible.

The mandibular tooth plate of a juvenile individual (SGU, no. 155/73; text-figs. 3a–3c) is the preserved central fragment of the plate with an inner and median tritor. The median tritor is mesially pointed, bifurcation is barely defined, but crushed vascular pleromin shows that the tritor is composite, with a deeper and mesially extended inner branch and a smaller and somewhat wider outer branch. The median tritor mesially reaches the inner tritor; the latter is subtriangular and shows indistinct morphology of three oblique and mesially oriented septa in the laminated structure, without pleromin fill. The distal part of the tooth plate and the outer tritor are not preserved. The labial surface preserves a mesial fragment of the lateral descending lamina. The preserved part of the basal surface is entirely covered by a field of basal perforation.

Palatal tooth plates of adult individuals (Figs. 2d–2f; pl. 9, fig. 5) are massive and tall, with a well-developed aboral part which in lingual cross-section encompasses the 2–2.5 times lower oral part. The symphyseal surface is tall, with an ill-defined symphyseal-occlusive margin; it is occlusally beveled and gradually gives way to the unworn part of the occlusive surface. Near the inner tritor the symphyseal surface is uneven, with a couple of unpronounced furrows and a longitudinal tritor torus. The basal part of the symphyseal surface has visible straight and mesially oblique growth lines. In basal plan view the tooth plate has strong relief with greatly developed and well-perforated descending laminae. The lateral lamina is very tall (up to 4 mm), converging with the less-developed symphyseal lamina in the middle part of the labial surface. From their connection, the laminae stretch out in an arch distally (lateral lamina) and towards the symphyseal-basal angle (symphyseal lamina); in the latter case the arch is more curved. The field of basal perforation is well-developed on the entire visible part of

the basal surface. The labial surface bears a moderately well-developed groove and is covered by arch-like growth lines of the tooth plate. The occlusive surface stretches mesiodistally, and is evenly and sharply mesially beveled; its labial margin is occupied by a well-developed, distally expanded labial wear facet. The middle part of the tooth plate, near the symphyseal-basal margin, carries a small, short, and oval (round in a cross-section) vascular inner tritor. The boundary between oral and aboral parts of the tooth plate on the occlusal surface is marked by a suture mesially bypassing the inner tritor and reaching the symphyseal surface.

The only vomerine tooth plate (SGU, no. 155/74; Figs. 3c–3h) belongs to a juvenile individual, judging from its size. The tooth plate is subtriangular in symphyseal-occlusal view. The labial surface is convex in its distal half and slightly S-shaped in a cross-section. The lateral descending lamina is well-developed, solid, forming the greater part of the labial surface. In its mesial third it is pressed against the basal surface and increases in height distally. The field of basal perforation is well-developed and entirely covers the preserved part of the basal surface. The symphyseal surface lies in the plane of the occlusal surface and converges with the labial surface at an angle of about 15°; their contact forms a well-defined apical crest. There are two knobs lacking pleromin along the symphyseal-occlusive margin, the distal one is somewhat larger; both do not extend beyond the unworn part of the tooth plate. The parabasal surface is tall. Occlusive tritons are absent occlusally; neither are traces of pleromin bodies found on the lingual surface.

#### Measurements (in mm)<sup>1</sup>:

Specimen	L	Ls	Hpb
SGU 155/64 [P]	27.5	–	–
SGU 155/65 (paratype) [M]	18	3.2	–
SGU 155/66 (paratype) [P]	19.8	–	–
SGU 155/73 [M]	8.3	2.3	–
SGU 155/74 [V]	6.7	–	2.7
SGU 155/75 (holotype) [M]	19.4	4.5	–
SGU 155/76 [M]	13.9	–	–
SGU 155/77 [M]	10.2	7.2	–

<sup>1</sup> Abbreviations for tooth plate measurements used in what follows: L, mesiodistal specimen length; Ls, length of the symphyseal platform of the mandibular plate; Hpb, height of the parabasal surface of the vomerine plate. Abbreviations for the type of tooth plates in the table: [M] mandibular; [P] palatine; [V] vomerine.

**Ontogenetic characters.** There is a three-fold difference in the Ls index between largest and smallest mandibular plates (SGU, nos. 155/73 and 77). The smallest tooth plate (SGU, no. 155/73) nevertheless shows a well-developed median tritor with a

deep inner branch. The branch is also well-extended mesially, reaching the distal end of the inner tritor, unlike the larger plates, where this condition is not observed. On the other hand, the bifurcation of the median tritor is ill-defined occlusally, and the morphology of the inner tritor resembles that of the laminated, rather than vascular pleromin. This is probably due to the very small size of the tooth plate, so that it can be assumed to be juvenile, and the inner tritor morphology can be considered undeveloped vascular. The morphology of larger mandibular plates (SGU, nos. 155/65, 75–77), despite some size differentiation, does not show distinct ontogenetic changes.

Palatine plates (SGU, nos. 155/64 and 66), despite differing in size by a factor of 1.5, also do not show significant morphological differences, aside from the similarly developed labial wear facet. It can be assumed that this species is characterized by a stable morphology of the dental system in ontogeny and, possibly, had a similar type of food processing and a constant food spectrum for the ontogenetic stages defined from tooth plate size.

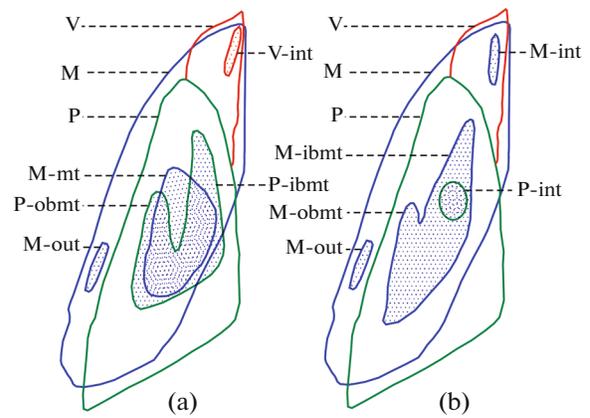
**Remarks.** The plates are assigned to the dentition of a single species based on the correlation of morphological characters (Popov, 2003), the size of the plates, as well as the similarly developed field of basal perforation on all plates, which is entirely absent in the other callorhynchid genus (*Brachymylus*) known in the middle Volgian chimaeroid assemblage of the Moscow region (Popov and Shapovalov, 2007, pl. 1, figs. 5, 6).

**Geographic and stratigraphic range.** Upper Jurassic, middle Volgian, (*virgatus* Zone) of Moscow and Moscow Region, Central Russia.

**Material:** five mandibular, two palatine, and one vomerine tooth plate, variously preserved, from two sections: Kuntsevo (SGU, no. 155/64–65, 74–77), and LFR 7-2-bis. (SGU, no. 155/66 and 73). Collected by K.M. Shapovalov in 1997–1999.

## DISCUSSION

The degree of development of the aboral part of the palatine plate of *Moskovirhynchus* gen.nov. (exceeding the oral part by a factor of 1.5–2) is analogous to the one observed in the mandibular plate of the Middle Jurassic genus *Ottangodus* from the Bajocian of France (Popov et al., 2019) and is not encountered in any other callorhynchids. It is believed that the aboral part of the plates (which in mandibular plates of the callorhynchids also carries the outer tritor) is a primitive structure for chimaeroids and may represent the vestige of an alternative tooth (Didier et al., 1994). Therefore, palatine plates of *Moskovirhynchus* gen. nov. can be considered to have a more primitive morphology in this respect than *Callorhynchus* and other genera of chimaeroid fishes. On the other hand, the palatine plates of *Callorhynchus* have the typical large compos-



**Fig. 4.** Schematic reconstruction of left overlap (occlusion) of tooth plates for two callorhynchid species, not to scale: (a) *Callorhynchus callorynchus* (L., 1758), SGU, no. 155/103; eastern Pacific, West of San-Antonio, Chile; Recent; (b) *Moskovirhynchus robustus* gen. et sp. nov.; Late Jurassic of the Moscow Region. Abbreviations: outlines of tooth plates and prefixes in tritor abbreviations: M (M-), mandibular tooth plate (in blue); P (P-), palatine tooth plate (in green); V (V-), vomerine tooth plate (in red); tritor outlines: ibmt, inner branch of median tritor (with bifurcation); int, inner tritor; mt, median tritor; obmt, outer branch of median tritor (with bifurcation); out, outer tritor. Vascular pleromin of tritors is stippled.

ite median tritor with two inner branches, developed to various degrees, which is present in all extant and fossil species of this genus (Stahl, 1999; Kriwet and Gazdzicki, 2003; Otero et al., 2013). The occurrence of only a single inner tritor on the palatine plate of *Moskovirhynchus* gen. nov. (possibly, an analog of the inner branch of the median tritor of *Callorhynchus*), but smaller and symphyseally displaced, can be considered an advanced state (the evolutionary trend towards complete reduction of occlusive tritors in the dental system is most pronounced in the extant chimaeroids of the genus *Rhinochimaera*), just as the complete absence of a tritor on the vomerine plate, which is untypical for callorhynchids (Stahl, 1999; Herman et al., 2001). These characters indicate a general reduction of hypermineralized tissue (pleromin) in the dentition of the upper jaw of *Moskovirhynchus* gen. nov. and a strengthened crushing function (increased pleromin area due to the bifurcation of the median tritor) in the lower jaw dentition.

Reconstructed functional overlap (occlusion) of the tooth plates for *Moskovirhynchus* and the extant *Callorhynchus callorynchus* shows (Fig. 4), that in the first taxon the dentition had smaller overlap of occlusive median tritors. In *Moskovirhynchus*, well-developed branches of the median tritor of the mandibular plate contacted the better developed and structurally denser aboral part of the palatine plate (forming on the latter a characteristic labial wear facet and a strongly mesially inclined occlusive surface; see. Fig. 2d; pl. 9, figs. 5a, 5b, 6a, 6c). Such occlusion structure in

*Moskovirhynchus* may have served to compensate the lack of hypermineralized tissue (tritons) and/or be an adaptation to feeding on less hard prey (e.g., thin-shelled invertebrates).

The functioning of the medial part of the dental system in a way analogous to the extant *Callorhynchus* (gripping (?) food objects) was assured in *Moskovirhynchus* by an inner tritor that was displaced onto the beak of the mandibular plate. In the modern *Callorhynchus* the same effect is achieved by the morphologically similar inner tritor of the vomerine plate (in the fossil *Callorhynchus* the grip function (?) was even better developed due to the presence of inner tritons on both the mandibular and the vomerine plates which alternated in occlusion; E.V. Popov, pers. observation). The general functionality of the dental system in both genera (in the absence of cutting or alternating tritons, other types of pleromin, etc.) was likely similar.

Chimaeriform fishes (Chimaeriformes) from the end of the Jurassic are known from only several assemblages in the whole world (Stahl, 1999). The most famous of these comes from the lithographic limestones of Southern Germany (upper Kimmeridgian of Nuslingen, Baden-Württemberg; upper Kimmeridgian and lower Tithonian of the “Solenhofen Archipelago” in Bavaria). This assemblage comes from a “Konservat-Lagerstätte” (Arratia et al., 2015) and is known from numerous exceptionally preserved skeletal remains of chimaeroids *Ischyodus quenstedti* Wagner, 1857 and *Elasmodectes avitus* (von Meyer, 1862) (see Popov et al., 2013; Kriwet and Klug, 2015). The assemblage also contains isolated fossils of callorhynchids, Callorhynchidae gen. et sp. indet. (Duffin, 2018), rhinochimaerids (a small, undescribed *Harriotta* sp. in a private collection in Germany; E.V. Popov, pers. observation, 2013; the same specimen is figured as a “juvenile specimen of the chimaeroid *Ischyodus* sp.”: Mäuser, 2015, p. 525, text-fig. 1013) and the chimaeropsid *Chimaeropsis paradoxa* Zittel, 1887, a relic of the early Mesozoic group of myriacanthoid holocephalians (Riess, 1887; Woodward, 1891; Lauer et al., 2018). In England, isolated tooth plates of a single chimaeroid species, *Ischyodus townsendi* Buckland, 1835 (Woodward, 1891) are known from the Portland Beds, as well as from the basal Cretaceous Neocomian Bone-Beds (where they are redeposited). The tooth plates are particularly large (Newton, 1878, pl. 11, figs. 1–7; Woodward, 1891, pp. 64–65). In general, chimaeriform diversity in Western Europe drops down to five genera by the Tithonian (four genera of chimaeroids and one chimaeropsid genus) from the Jurassic maximum of nine genera in the Callovian (the “Oxford Clay” assemblage; Popov et al., 2012) and later six genera in the Kimmeridgian (Popov et al., 2009).

The Boreal Volgian of the Russian Plate contains sparser and more isolated chimaeroid material, which, however, enables comparisons between Western and

Eastern European assemblages. The Boreal Volgian of European Russia shows comparable diversity (five genera), but a different distribution of taxa: the absence of myriacanthoid holocephalians and rhinochimaerid chimaeroids but greater diversity of “edaphodontids” (three genera) and callorhynchids (two genera). This possibly indicates paleobiogeographic differentiation in chimaeriform assemblages at the end of the Jurassic.

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