

A New Genus of Elephant Fishes (Holocephali: Callorhynchidae) from the Upper Callovian of the Volga Rigion near Saratov, Russia

E. V. Popov

Research Geological Institute, Saratov State University, Bol'shaya Kazach'ya ul. 120, Saratov, 410012 Russia

e-mail: popovev@info.sgu.ru

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Abstract—*Duffinodus nikolaii* gen. et sp. nov., a new genus of elephant fishes (Chimaeroidei, Callorhynchidae) based on the right mandibular dental plate and the left vomerine plate from the Middle Jurassic (Upper Callovian, *Quenstedticeras lamberti* Ammonite Zone) from the Dubki quarry in the vicinities of Saratov (Saratov Province, Russia) is described. An emended diagnosis for the family Callorhynchidae Garman, 1901 based on dental plates is presented. The family consists of four or six genera: *Callorhynchus* Lacépède, 1798, *Brachymylus* Woodward, 1892, *Pachymylus* Woodward, 1892, *Duffinodus* gen. nov., *?Eomanodon* Ward et Duffin, 1989 and *?Bathytheristes* Duffin, 1995. A modified morphological nomenclature of the chimaeroid dentition is proposed.

INTRODUCTION

Jurassic chimaeroids from Russia are insufficiently known, and information on these fishes is based upon isolated finds of dental plates (Bogolyubov, 1912; Obruchev, 1964; Averianov, 1992) and egg capsule imprints (Test *et al.*, 1962; Obruchev, 1966; Nesson and Averianov, 1996a). In this respect, a find of chimaeroid dental plates, the mandibular and the anterior upper (vomerine) ones, in the abandoned quarry near the village of Dubki close to Saratov is of some interest. A section of the quarry, which is mostly flooded, is composed of Callovian–Oxfordian clays and superimposed sands including the basal conglomerates of the Volgian Stage of the Jurassic. The quarry section yielded diverse invertebrate fauna (Seltser, 1999; Baraboshkin *et al.*, 2001) and elasmobranch teeth (Popov *et al.*, 2001).

The dental plates under description were found in 2000 by M.S. Arkhangelsky and N.N. Il'in close to the water level (text-fig. 1c, in Popov *et al.*, 2001) in the southeastern part of the quarry. The same level of the section yielded numerous ammonites characteristic of the Upper Callovian *Quenstedticeras lamberti* Zone (Middle Jurassic), including the zonal species. The analysis of the foraminiferan assemblage from the horizon immediately overlapping the shell breccia level (Popov *et al.*, 2001, text-fig. 1c, level III) demonstrated the presence of the species of the Upper Callovian *Lenticulina tumida*–*Epistomina elschankaensis* Zone; apart from the index species, numerous foraminifers *Pseudolamarkina rjasanensis* Myatl., *Epistomina mosquensis* Uhlig, *Saracenaria engelsensis* Kosyz. and others were determined (G.N. Startseva, personal communication). Thus, this level is dated as the Upper Call-

ovian Substage of the Middle Jurassic, *Quenstedticeras lamberti* Zone (*Zonal'naya stratigrafiya...*, 1991).

Dental plates described in this paper were referred to a single species on the basis of the correlation of their morphological characters: slight and similar degree of reduction of the descending lamina and a primitive condition of the tritoral pattern (presence of knoblike dermal structures, the absence of an outer tritoral series along the labial margin of the vomerine plates and symphyseal tritor at the mandibular plate beak, etc.). The same characters, and the position of the outer tritor on the aboral part of the mandibular plate suggest the attribution of this species to a new genus within the elephant chimaeroid family Callorhynchidae Garman, 1901.

The described material is stored at Saratov State University (SGU), collection no. 155.

TERMINOLOGY AND REMARKS ON THE MORPHOLOGY OF CHIMAEROID DENTAL PLATES

The author of the present paper developed a new terminology for morphological structures of chimaeroid dental plates (Popov, 1999), taking into account recommendations of Patterson (1992) (regarding the terminology of surfaces and directions), Newton (1878) (tritors terminology), and T. Ørving, 1985) (pleromin type). This terminology is applied to described plates (Fig. 1). Some terms are explained below.

Dental plates of the suborder Chimaeroidei are complex structures (Didier *et al.*, 1994; Stahl, 1999). Each presents oral (*ort*) and aboral parts (*abt*) (Figs. 1a, 1d, 1e, 1g). These parts are morphological equivalents of

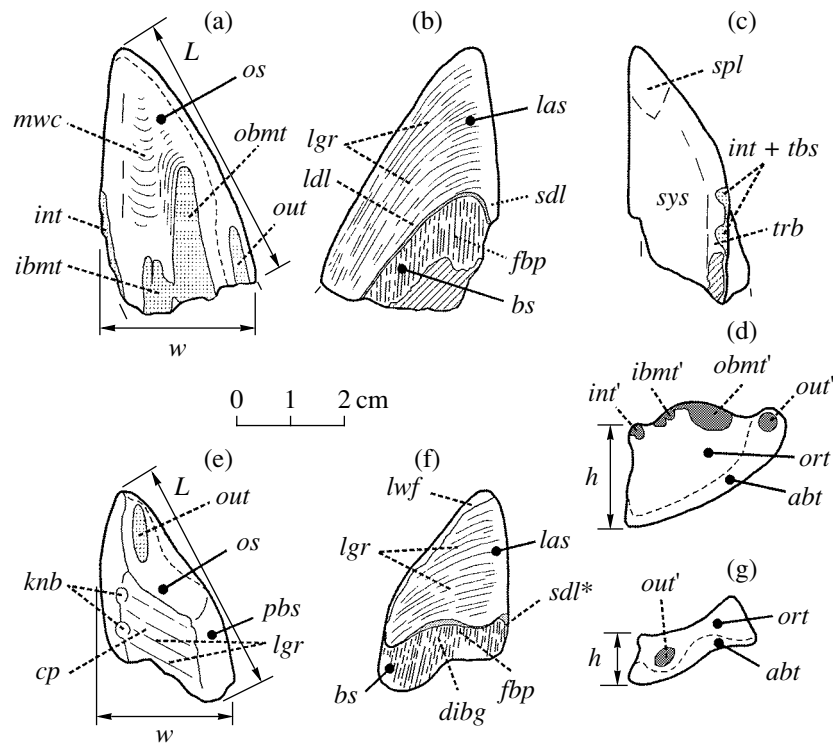


Fig. 1. Terminology and measurements of the mandibular and anterior upper jaw (vomarine) dental plates of *Duffinodus nikolai* sp. nov., used in the text. (a)–(d) right mandibular dental plate: (a) occlusal view, (b) basal view, (c) symphyseal view, and (d) lingual profile; (e)–(g) left anterior upper jaw (vomarine) plate: (e) symphyseal–occlusal view; (f) basal view; and (g) lingual profile. Designations: (os) occlusal surface, (las) labial surface, (sys) symphyseal surface, (bs) basal surface, (pbs) parabasal surface of the vomarine plate, (ort) oral part of the plate, (abt) aboral part of the plate, (ldl) lateral descending lamina, (sdl) symphyseal descending lamina, (sdl*) damaged symphyseal descending lamina, (obmt) outer branch of the median tritor, (out) outer tritor, (ibmt) inner branch of the median tritor, (int) inner tritor, (tbs) tritoral buds, (knb) knobs, (spl) symphyseal platform; (mwc) mesial wear cavity, (cp) central platform of the occlusal surface of the vomarine plate, (lwf) labial wear facet, (dibg) distobasal groove of the basal surface, (lgr) growth lines of the enamel-like dermal tissue, (fbp) basal perforation field, (L) mesiodistal length, (h) maximum depth of the symphyseal surface, (w) maximum width of the specimen; (int', ibmt', obmt', out') pleromin bodies exposed at the occlusal surface of the plate in the form of corresponding tritors or their branches; dotted line shows boundaries of the oral and aboral parts of the plates on (a and e) the occlusal surfaces and (d and g) lingual profiles; oblique shading marks damaged areas.

two individual teeth of the ancestral form, one of which (=aboral part of the plate) became strongly reduced and coupled to another in the course of evolution (Didier *et al.*, 1994). This hypothesis is corroborated by the position of the outer tritor on the aboral part of the calrhinchid mandibular plate established here (see below).

The occlusal, or biting surface *sensu lato* is the functional inner surface of the dental plate, which may bear the tritors. Patterson (1992) recommended using this descriptive term; however, he did not subdivide the occlusal surface into the properly functional wear surface, and the unworn surface not used in the course of functioning dental plates and partly coated with soft mouth tissues during the fish lifetime. If the dental plate is well preserved, its unworn part is clearly defined by the presence of compact glossy tissue on its surface, which is not observed on the functional wear surface. Ward and Grande (1991, text-fig. 2) designate the same surfaces as “occlusal” and “postocclusal.”

The unworn part of the occlusal surface in the vomarine plates forms a concave central (occlusal) platform. As a result of occlusion, a wear ledge is frequently formed between this platform and the worn area of the occlusal surface in the lingual part of the latter.

The right and left dental plates in a fish jaw may either contact each other or remain separated. In the former case, such contact occurs at the mesial corner of each plate where the contact areas are formed. These areas are variable in shape and distal extent and are named here the symphyseal platforms (Fig. 1c, *spl*) (for example, in the mandibular plates of the chimaeroid genus *Edaphodon* Buckland, 1838).

The vomarine dental plates are characterized by convex subrectangular or trapezoid cross section, in contrast to the subtriangular shape of the mandibular and palatine plates. Therefore, there is one more surface in these plates placed between the basal, labial, occlusal, and lingual surfaces. It is usually named the articulator platform for the palatine plate (Newton, 1878). However, Dean (1906, pp. 125, 126) demon-

strated that, in juveniles of some chimaeroids (genus *Harriotta* Goode et Bean, 1895), the vomerine and palatine plates do not contact and only slightly overlap in the individuals of later ontogenetic stages. The absence of a true extended articulation between these dental plates in juveniles is also observed in the figures of the chimaerid dentition (Didier *et al.*, 1994, text-fig. 5). For these reasons, the term parabasal surface is proposed to designate a such surface (Fig. 1e, *pbs*).

The occlusal surface of the vomerine dental plate is concave, its unworn area limited by the plate margins and the wear ledge is suggested to be designated as the central platform (Fig. 1e, *cp*).

The nutrition of the aboral part of the plate was obviously accomplished through numerous small canals and pores piercing the descending lamina basally. Some of these canals, usually presented as small longitudinal grooves, may be located on the basal surface and form the basal perforation field (Figs. 1b and 1f, *fbp*), which is well developed in primitive chimaeroids (for example, callorhinchids). This field looks like the basal surface striation (Averianov, 1992).

The basal surfaces of the dental plates may bear one or two longitudinal grooves. One groove, the longitudinal axis of which is displaced distally, is present on the vomerine plate of the new form; it is termed here the distobasal groove (Figs. 1f, 1g, *dibg*).

Growth lines (Figs. 1b, 1e, 1f, *lgr*) are subtransversal, parallel to each other, and are fine glossy ridges separated by grooves of similar appearance. They are observed on the labial surface and unworn part of the occlusal plate surface, but only if the compact glossy tissue is preserved. These lines mark the stage and possibly seasonal growth of dental plates, which should correlate with the general growth of the fish body. Unequal interval size between the growth lines of the central platform of the occlusal and labial surfaces of the vomerine plate in *Duffinodus* might indicate faster growth of the oral part of the plate than that of the aboral one.

The labial wear facet (Fig. 1f, *lwf*) is usually a narrow wear surface (formed as a result of lifetime functioning of the dentition) on the labial surface of some dental plates along their labial margin. In contrast to consistently erased occlusal surface, it is unstable in appearance.

The pleromin bodies inside any dental plate occur on one or several levels. Two levels or storeys are conditionally recognized, i.e., the labial storey, including all tritons extending to the labial margin, and the lingual storey, including all other tritons. Traditionally, the tritons of the labial storey are termed outer (including the symphyseal tritor), and those of the lingual storey are inner tritons (including the median one). In callorhinchids, the tritons of the labial storey are absent or only slightly developed.

The median tritor of the mandibular plate possessing a complex noncylindrical profile (Fig. 1d) and

forming a fork (bifurcation) on the occlusal surface is called compound and forms two branches, the outer (*obmt*) and inner (*ibmt*) branches (Fig. 1a).

In longitudinal section, the tritons of the chimaeroid dental plates are usually shaped like subcylindrical columns with entire and parallel symphyseal and lateral margins. In certain cases, the "pulsing" (interrupted) formation of the tissue along one of these margins form pleromin processes, the tritoral buds (Fig. 1c, *tbs*). Symphyseal tritoral buds are found in the palatine plates of the callorhinchid *Pachymylus leedsi* Woodward (Woodward, 1892, pl. 3, fig. 1b) and *Duffinodus nikolaii* gen. et sp. nov.; the lateral ones occur in the mandibular dental plates of the "edaphodontid" "*Ganodus*" *dentatus* Egerton (Stahl, 1999, text-fig. 152a).

There is an unusual superficial structure along one of the functional margins of the dental plates of some chimaeroids; this is a longitudinal row of knobs, containing the elements of vascular pleromin (pleromin knobs), or without those. In the latter case, they are termed simply knobs (Fig. 1e, *knb*). Such knobs are present along the symphyseal occlusal margin of the vomerine plate in *Duffinodus nikolaii* gen. et sp. nov.

The tritons of the dental plates might be divided into two groups by the degree of their disposition: individual (single) tritons and tritoral series. A tritoral series is a group of individual tritoral bodies, usually medium-sized or small, which tend to be arranged in series (their number is more than, or equal to 3). The series is usually placed in a certain part of the functional occlusal surface, carries out the corresponding function (usually, cutting or fine crushing), and is clearly separated from another series or a group of individual tritons. On the functional surface, such a series is frequently represented by numerous small tritoral bodies or pleromin units placed in echelon manner but originating from different tritoral bodies. They may also be arranged as transversal filaments. In the dental plate section, such a series is recognized by linear, almost linear, or the grouped position of tritoral bodies of approximately the same diameter.

SYSTEMATIC PALEONTOLOGY

Superfamily systematics of chimaeroid fishes is accepted after Didier (1995).

Order Chimaeriformes

Suborder Chimaeroidei Patterson, 1965

Superfamily Callorhinoidea Didier, 1901

Family Callorhinchidae Garman, 1901

Type genus. *Callorhinchus* Lacépède, 1798.

Diagnosis. Dental plates rather stout, largely of the crushing type, with well developed or incompletely (focally) mesially reduced descending lamina. Basal perforation field usually well developed. Tritons of dental plates mainly composed of vascular pleromin. In mandibular dental plates, outer tritor placed on aboral

part of plate; tritons of labial storey absent or poorly developed. Median and 0–2 inner tritons present.

Palatine dental plates having one compound or two tritons. Descending lamina clearly divided into symphyseal and lateral parts.

Vomerine dental plates usually with one tritor; tritoral series absent.

Distribution. Lower Jurassic–Recent; Europe, South America, Australia, and New Zealand; oceans of the Southern Hemisphere.

Composition. Genera *Callorhinchus* Lacépède, 1798, *Brachymylus* Woodward, 1892, *Pachymylus* Woodward, 1892, *Duffinodus* gen. nov., *Eomanodon* Ward et Duffin, 1989, and *Bathytheristes* Duffin, 1995.

Remarks. The family, starting from the time of its establishment, was for a long time considered to be monotypic, including the some extant genus *Callorhinchus* Lacépède, 1798 (Garman, 1901; Berg, 1940; Obruchev, 1964; Patterson, 1965; Nelson, 1976; Carroll, 1988; etc.). Ward and McNamara (1977) extended the family composition, including there two Jurassic genera, *Brachymylus* Woodward, 1892 and *Pachymylus* Woodward, 1892. These genera were considered to be closely related to the genus *Callorhinchus* based on "...the presence of a single body of pleromic dentin, forming tritons on the oral surface and exhibiting laminar ornamentation on the inner surface" (Ward and McNamara, 1977, p. 593). Probably, the authors kept in mind general robustness and a small number of tritons on the occlusal surfaces of the plates (primitive condition) and presence of well-pronounced basal perforation field (as a consequence of the well developed descending lamina).

A new concept of family composition was suggested by Stahl (1999), who included in its structure many genera, mostly from the Mesozoic; some genera were earlier placed in the family Edaphodontidae Owen, 1846. The genera were grouped in two subfamilies, the Callorhinchinae Garman, 1901 (*Callorhinchus* Lacépède, 1798, *Brachymylus* Woodward, 1892, *Ischyodus* Egerton, 1843, *Pachymylus* Woodward, 1892, and *Ptyktoptychion* Lees, 1986) and Edaphodontinae Owen, 1846 (genera *Edaphodon* Buckland, 1838, *Leptomylus* Cope, 1869, and *Paredaphodon* Casier, 1966). In addition, two genera, *Eomanodon* Ward et Duffin, 1989 and *Ganodus* Agassiz, 1843, were referred to this family only tentatively. Major characters used for such grouping were the presence and the extent of reduction of the descending lamina on the dentition plates. However, the reduction of the descending lamina is a character of general trend in the suborder evolution; this is associated with the transition of the chimaeroid dentition from crushing-breaking to breaking-cutting and cutting types, accompanied by the development of numerous small tritoral pads or no tritons at all (genus *Rhinochimaera* Garman, 1901 of the family Rhinochimaeridae Garman, 1901). Probably, the reduction of this lamina was accompanied by

the appearance of the labial storey tritons and modification of morphofunctional characteristics of the dentition developed in parallel in various phylogenetic lineages of chimaeroids. For example, reduction of the descending lamina in morphogenesis of the genus *Ischyodus* was noted by Ward and Grande (1991).

Therefore, the composition of the family Callorhinchidae Garman, 1901 suggested by Stahl seem to be insufficiently grounded. The researcher included in this family not only primitive callorhinchids (*Callorhinchus*), but also chimaeroids possessing more advanced dentition (*Ischyodus*) and even obviously specialized forms, such as *Edaphodon* and *Leptomylus*.

The family composition proposed in the present study includes the genera *Callorhinchus*, *Brachymylus*, *Pachymylus*, and *Duffinodus* gen. nov. as well as two genera known by sole palatine dental plates, i.e., *Eomanodon* from the Pliensbachian of England (Ward and Duffin, 1989) and *Bathytheristes* from the Toarcian of Germany (Duffin, 1995).

The plate of *Eomanodon simmsi* Ward et Duffin, 1989 is characterized by the morphology typical of callorhinchids: the larger part of the plate is occupied by two isolated tritons, the lateral flange of the plate is most likely a segment of a well-developed lateral descending lamina. The lamellar structure of tritons composed of compact pleromin does not obstruct the attribution of the genus to callorhinchids, as this character may change in ontogeny. The small dental plate size also confirms this.

The dental plate of the chimaeroid *Bathytheristes gracilis* Duffin, 1995 is characterized by the deep lateral lamina and clearly differentiated, however, comparatively low symphyseal descending lamina. At the same time, the basal perforation field is absent and the tritoral structures are reduced. There is only one tritor consisting of vascular pleromin, which is shifted towards the mesial angle of the plate.

The absence of additional material on these genera, including the more significant taxonomically mandibular dental plates, and information on the structure of the basal surface of the plate in *Eomanodon simmsi* does not make it possible to unequivocally solve the problem of the familial assignment of these genera.

Genus *Duffinodus* Popov, gen. nov.

Etymology. In honor of the paleoichthyologist Dr. Christopher Duffin (Great Britain) and from the Greek *odus* (tooth).

Type species. *Duffinodus nikolaii* sp. nov.

Diagnosis. Callorhinchid possessing crushing-breaking dentition. Mandibular dental plate robust, with deep symphysis and short beak. Inner, unsegmented outer, and compound (bifurcated) median tritons composed of vascular pleromin. Vomerine dental plate massive and subtriangular, with narrow outer tritor of vascular pleromin.

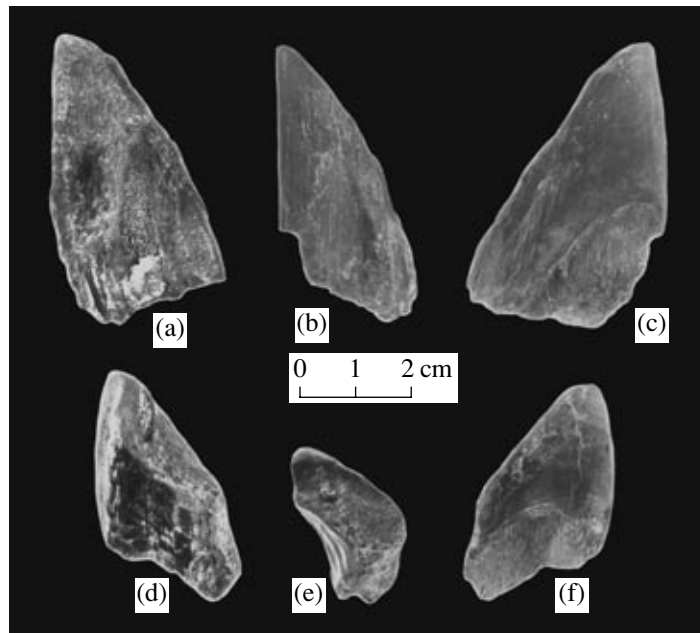


Fig. 2. Dental plates of *Duffinodus nikolaii* sp. nov. (a–c) holotype, SGU, no. 155/29, right mandibular plate: (a) occlusal, (b) symphyseal, and (c) basal views; (d–f) paratype, SGU, no. 155/30, left anterior upper jaw (vomerine) plate: (d) symphyseal-occlusal view, (e) mesial view of the occlusal surface, and (f) basal view.

Species composition. Type species.

Comparison. From the morphologically closest genus *Pachymylus* from the Middle Jurassic (Callovian) Oxford Clay of England, the new genus differs by the presence of the compound median tritor with bifurcation and the inner tritor and the absence of segmentation of the outer tritor at the mandibular plate. The vomerine dental plates of the genus *Pachymylus* are unknown.

From the extant genus *Callorhynchus* known also from the Cretaceous deposits of Russia (Nessov and Averianov, 1996b; Averianov, 1997; Stahl, 1999), the new genus differs by the robustness of the mandibular plate, the significant depth of the symphyseal surface, the presence of a compound median tritor with clear bifurcation, robustness and subtriangular shape (characteristic of the Cretaceous edaphodontid *Edaphodon*) of the vomerine dental plate, and the presence of the narrow outer tritor composed of vascular pleromin on this plate.

From the genus *Brachymylus* from the Middle Jurassic (Callovian) Oxford Clay of England (Ward and McNamara, 1977; Stahl, 1999), the new genus differs by the absence of lateral compression of the mandibular and vomerine plates and the shape and arrangement of the mesial and inner tritors of the mandibular plate and the outer tritor of the vomerine plate.

Remarks. The structure and general robustness of the mandibular dental plates in the genera *Duffinodus* gen. nov. and *Pachymylus* suggest that they should be opposed to other callorhynchid genera (in the composi-

tion accepted in this paper) and assigned to a separate subfamily.

Duffinodus nikolaii Popov, sp. nov.

Etymology. In honor of the amateur paleontologist Nikolai N. Il'in (Saratov).

Holotype. SGU, no. 155/29, incomplete right mandibular dental plate; vicinities of Saratov, village of Dubki, Dubki locality; Middle Jurassic, Upper Callovian, *Quenstedticeras lamberti* Zone.

Description (Figs. 1a–1g; 2a–2f). The species is known by the mandibular and vomerine dental plates. The mandibular dental plate (Figs. 1a–1c; 2a–2c) is massive and subtriangular and subtrapezoid when viewed from the occlusal and symphyseal surfaces, respectively.

The occlusal surface *sensu lato* includes the wear surface, except the symphyseal–lingual angle (occlusal surface *sensu stricto*). The surface is rough, unevenly cellular, and bears numerous pits and projections of the trabecular dentin.

The symphyseal surface is deep, a wide longitudinal groove runs in its upper half. A small symphyseal platform is located in the mesial part of the symphyseal surface at the end of the beak.

The labial surface is comparatively smooth, it is coated by well-preserved compact glossy tissue bearing tiny and closely spaced growth lines and, in its distal half, irregularly arranged narrow longitudinal ridges. The labial margin is formed of a more compact tissue of the aboral part of the plate (descending lamina),

slightly arched, and ornamented with small tubercles. Small bits are broken off the beak tip and the distal part.

The basal perforation field covers the whole basal surface preserved, the basal surface grooves seem to be absent.

The descending lamina is moderately developed, 2–3 mm deep. This lamina is divided into the lateral and symphyseal parts; the lateral part becomes slightly deeper distally.

The following vascular tritons are present: a rather narrow outer tritor on the aboral part of the plate, the mesially forked median tritor, and the inner tritor. The median tritor is in the central part of the occlusal surface, being lingualaterally displaced; it is subdivided in two branches; the inner branch is short and superficial, it is lingually segmented into several longitudinal elements. The external branch is rather deep in lingual profile and extends far labially. The inner tritor is narrow and long; from its symphyseal side, it bears at least a couple of tritoral buds, the distance between the centers of which is about 9 mm.

At the contact of the symphyseal and occlusal surfaces, the prominent inner tritor forms a longitudinal ledge facing mostly to the symphyseal surface. Mesial to the external branch of the median tritor, the occlusal surface tends to form a ledge becoming a relatively deep, wide, and long mesial wear cavity.

The anterior left upper jaw (vomarine) dental plate (Figs. 1e–1g; 2d–2f) is subtriangular in the symphyseal–occlusal view and concave in the mesiodistal view. A large part of the occlusal surface is occupied by its unworn part shaped into a concave and asymmetric central platform. The wear surface extends as a relatively narrow band along the labial margin. The wear surface is unevenly fine-tuberculated. A conspicuous groove extends along the contact with the central area (poorly developed wear shelf) and the tubercle located in the distal part of the surface at its contact with the parabasals surface.

The symphyseal surface is slightly concave at the expense of a wide and shallow longitudinal groove. The compact glossy tissue is better developed on the central platform; it is more luminous and probably thicker than that on the labial surface. Its growth lines are spaced approximately two or three times more widely than those on the glossy tissue of the labial surface. Two rounded knobs lacking pleromin are located along the symphyseal–occlusal margin in the upper part of the symphyseal surface at a distance of 6 mm from each other.

The labial surface is subtriangular, it retains the compact glossy tissue, except for a band along the labial margin and the area near the beak. Growth lines similar in distribution and frequency to those of the mandibular plate are present in this area. A narrow labial wear facet extends along the labial margin as a

result of lifetime contact to the mandibular plate. The compact glossy tissue and trabecular dentin of the deeper layers are partly broken off along this facet.

The subrectangular parabasals surface is slightly concave.

The wide distobasal groove on the basal surface is moderately deep and displaced to the labial margin. A short longitudinal ridge corresponding to the pleromin body of the outer tritor adjoins the symphyseal side of this groove. The basal perforation field is well expressed, except for the symphyseolingual part of the basal surface.

The descending lamina is S-shaped, its lateral part is subtransversal and the longitudinal symphyseal part is poorly expressed. The lateral lamina is unevenly reduced, so that its depth varies; the maximum thickness (up to 3 mm) is observed opposite the distobasal groove.

The outer tritor is ovoid in section, it is located in the mesial part of the occlusal surface parallel to the symphyseal margin.

The posterior upper jaw (palatine) dental plates are unknown in this species.

Measurements, mm. ¹	L	h	w
Holotype SGU, 155/29	54	19	30
Paratype SGU, 155/30	45	10	25

Remarks. The holotype is a mandibular dental plate, because it possesses the following features: the deep symphysis of the plate bears a mesially placed symphyseal platform, the outer tritor is on the aboral side of the plate, general distribution pattern and the number of tritons (>2) is characteristic of mandibular plates of chimaeroids (Stahl, 1999). Such characters are not typical of the known palatine plates of callohrinchids (Woodward, 1892; Nessov and Averianov, 1996b; Stahl, 1999).

Material. The holotype and paratype SGU, no. 155/30, left anterior upper jaw (vomarine) dental plate from the type locality (collected by Il'in and Arkhangelsky, 2000).

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¹ For indices, see Fig. 1.

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