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Systematics and dental system reconstruction of the durophagous chondrichthyan *Lagarodus* JAEKEL, 1898.

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ABSTRACT:

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The type species of the Carboniferous chondrichthyan genus *Lagarodus* JAEKEL, 1898 is changed to *Psammodus specularis* TRAUTSCHOLD, 1874 because of an identification error in TRAUTSCHOLD (1874). Five morphotypes: *angustus*, *specularis*, *cubicus*, accessory, and orobranchial are recognised. Tooth morphology, configuration of wear surfaces, growth traces on the basal surface and comparison with extant analogues were used to reconstruct the dentition.

K**ew words:** Chondrichthyans, *Lagarodus*, Carboniferous, Systematics, Dental system.

INTRODUCTION

In 1864 G. ROMANOWSKY described a chondrichthyan tooth-based species, *Psammodus angustus*, from the Lower Carboniferous (Serpukhovian) of the Moscow Region (Podmokloye village). Unfortunately, his description does not sufficiently emphasize the distinguishing characters; the drawings (p. 159, tab. 3, fig. 6) are unclear (Text-fig. 1). The type specimen was lost.

TRAUTSCHOLD (1874) ascribed the tooth elements from the Moscovian, Middle Carboniferous of Myachkovo quarry (Moscow Region) to the same species. He also erected a new species, *Psammodus specularis*, and noted that these two dental types might belong to the same fish on the basis of histological and morphological similarities. In the same paper, smaller elements constructed on the same pattern were designated as "*P. cubicus*" without formal description, but were also said to be close to the two previous forms. Thin sections for "*P. angustus*" and "*P. specularis*" were published to demonstrate the similarity. This position was later supported by WOODWARD (1889).

JAEKEL (1898) transferred *Psammodus angustus* to a new genus *Lagarodus*, which since then became widely used in the literature (OBRUCHEV 1964, STAHL 1999, ELLIOTT & *al.* 2004).

Later authors neglected TRAUTSCHOLD's (1874) valid species names in favour of "*angustus*". M. HANSEN (1986, unpublished dissertation, *fide* STAHL 1999) and STAHL (1999) regarded the "*angustus*" and "*specularis*" types as belonging to the same fish; later ELLIOTT & *al.* (2004) assigned the "*cubicus*" ("small square teeth") variety to it.

Revision of the Middle Carboniferous and newly collected Upper Carboniferous (Moscovian-Kasimovian) material from the Moscow Region demonstrated that teeth from the Lower Carboniferous differed in morphology. Re-examination of ROMANOWSKY's (1864) drawing reveals that in his specimen the coronal part of the tooth curves basally, forming a roll rather than the sharp wedge-like wing characteristic of TRAUTSCHOLD's (1874) specimens. For this reason TRAUTSCHOLD's (1874) identification of his Middle Carboniferous teeth as *Psammodus angustus* and the

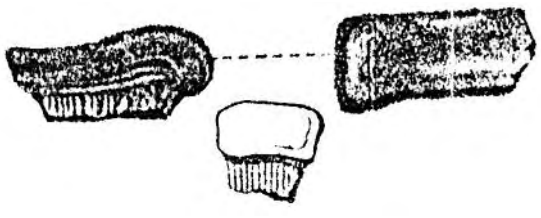

Fig. 1. "*Psammodus*" *angustus* ROMANOWSKY, 1864. Tooth in various projections. From ROMANOWSKY, 1864, slightly modified

subsequent generic re-assignment of these teeth to *Lagarodus* JAEKEL, 1898, is regarded as erroneous (LEBEDEV & LYAPIN 2001).

According to Article 70, paragraph 70.3.2, of the ICZN (1999), the generic name *Lagarodus* should be conserved for the valid species *Psammodus specularis* TRAUTSCHOLD, 1874 (*versus* LEBEDEV & LYAPIN 2001) and the species name *angustus* ROMANOWSKY, 1864 would be applied only to the Lower Carboniferous form. However, until new material is found in the type area localities, "*Psammodus angustus*" would remain a "*nomen dubium*", because the drawing and very short description are insufficient to confirm the attribution to this genus or to enable assignment to another genus.

Unfortunately, the larger part of TRAUTSCHOLD's collection was lost during World War II, and for this reason a neotype for *Lagarodus* [*Psammodus*] *specularis* (TRAUTSCHOLD, 1874) is chosen here.

The systematic position of *Lagarodus* JAEKEL, 1898 was obscure for a long time. Earlier classifications placed it in the Psammodontiformes based on a tooth morphology suggestive of a durophagous habit (OBRUCHEV 1964, STAHL 1999).

LEBEDEV & LYAPIN (2001) suggested its attribution to the family Orodontidae based on several morphological characters. However, whilst demonstrating a specific durophagous pattern, *Lagarodus* shows significant differences from psammodonts. For this reason, the creation of a new family Lagarodontidae is proposed here. Its ordinal attribution requires further

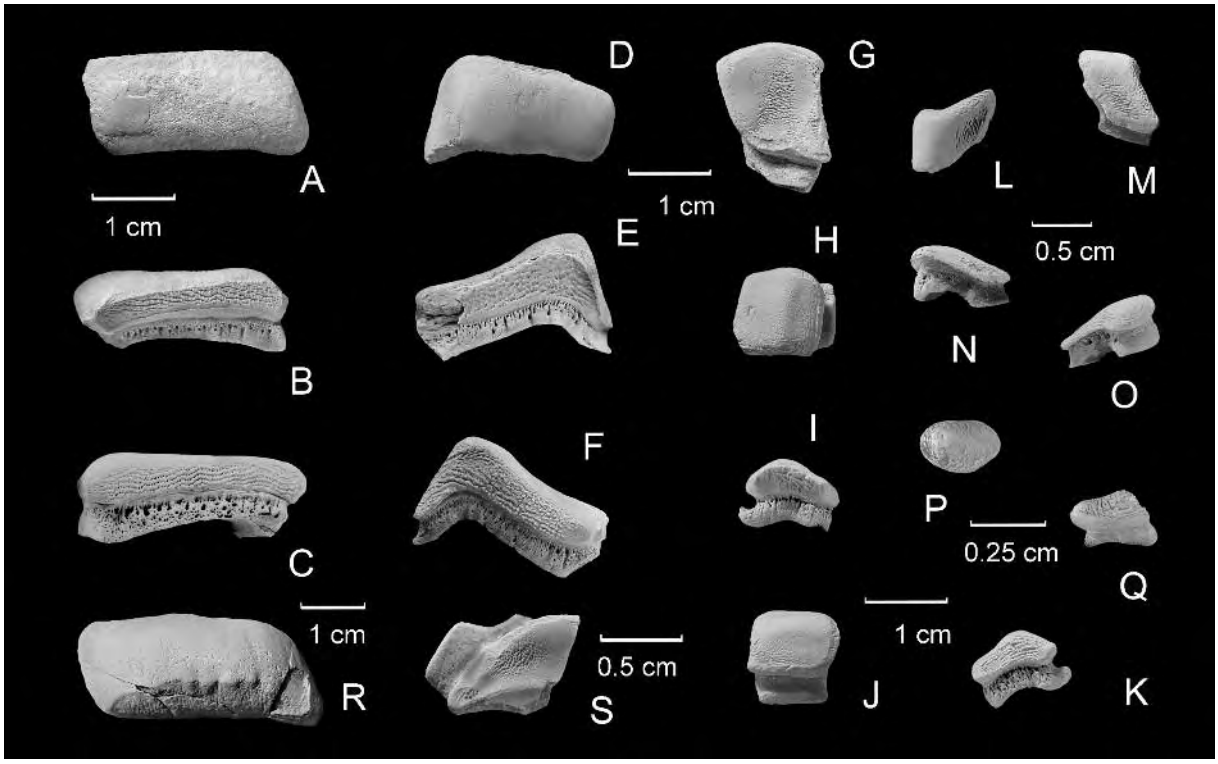

Fig. 2. *Lagarodus specularis* (TRAUTSCHOLD, 1874): A-C – neotype PIN 1704/2, *specularis* tooth morphotype, Kolomna District, Myachkovo quarry, ? Domodedovo Formation; D-G – specimen PIN 2804/666, *angustus* tooth morphotype, Ramenskoye District, Kamennaya Tyazhina quarry, ? Peski Formation; H-K – specimen PIN 2804/821, *cubicus* tooth morphotype, Kolomna District, Peski quarry, Novlinskoye Series; L-O – specimen PIN 2804/873, accessory tooth morphotype, Kolomna District, Peski quarry, Novlinskoye Series; P-Q – specimen PIN 2804/869, ? orobranchial tooth morphotype, Kolomna District, Peski quarry, Novlinskoye Series; R – specimen PIN 2804/1855, *specularis* morphotype tooth bearing tuberculated ridge at the crown, Ramenskoye District, Kamennaya Tyazhina quarry, ? Peski Formation; S – specimen PIN 2878/22, incomplete tooth of accessory morphotype demonstrating wear surfaces resulting from occlusion, Kolomna District, Peski quarry, Novlinskoye Series. All Moscow Region, Middle Carboniferous, Moscovian, Myachkovo Regional Stage

examination of tooth histology, which will be published in future. The family may definitely be attributed to the elasmobranchs, since *Lagarodus* displays such fundamental features as the arrangement of the teeth in growing series (shown by growth shifting marks on the aboral surface of the base) and the presence of enameloid on the unworn crown surfaces (in contrast to *Psammodus*, for example *P. rugosus* AGASSIZ, 1838, PIN 1488/55).

Three TRAUTSCHOLD's (1874) "species" names ("*angustus*", "*specularis*" and "*cubicus*") are applied here to designate morphotypes of the species *Lagarodus specularis*. The earlier undescribed morphotype is called here "accessory".

SYSTEMATIC PALAEONTOLOGY

Subclass Elasmobranchii BONAPARTE, 1838
Order indet.
Family Lagarodontidae nov.

TYPE GENUS: *Lagarodus* JAEKEL, 1898.

DIAGNOSIS: Durophagous fishes with heterodont pavement dentition. Morphotypes are derivatives of the arch-shaped prototype; heterodonty realised by range of lateral wing development. Crowns composed of orthotrabeculine, a thick layer of enameloid coats non-occlusal crown sides. Teeth are replaced, as demonstrated by growth shifting marks at the aboral surface.

FAMILY COMPOSITION: Monotypic family.

Lagarodus JAEKEL, 1898

1874. *Psammodus* AGASSIZ; TRAUTSCHOLD, p. 289.
1898. *Lagarodus* gen. nov.; JAEKEL, p. 50.
1964. *Lagarodus* JAEKEL; OBRUCHEV, p. 249.
1999. *Lagarodus* JAEKEL; STAHL, p. 90.

TYPE SPECIES: *Psammodus specularis* TRAUTSCHOLD, 1874, Middle Carboniferous, Moscovian, Russia, Moscow Region.

DIAGNOSIS. As for the family.

GENERIC COMPOSITION. Only the type species.

REMARKS. A median tuberculated ridge on the crown of the *specularis* morphotype (PIN 2804/1855, Text-fig. 2R) is found as a rare variation. It supports the origin of this fish from an ancestor possessing arch-shaped teeth with a median ridge, like orodontiforms and some eugeneodontiforms (for example, ZANGERL 1981). The ridge runs from the central tubercle along the middle of the coronal surface.

Lagarodus specularis (TRAUTSCHOLD, 1874) (Text-figs 2-3)

1874. *Psammodus specularis* sp. nov.: TRAUTSCHOLD, p. 288, pl. 28, figs 4 a-c, pl. 39, fig. 3.
1874. *Psammodus angustus* ROMANOWSKY: TRAUTSCHOLD, p. 289, pl. 28, figs 5 a-c, pl. 39, figs 4-6.
1874. *Psammodus cubicus*: TRAUTSCHOLD, p. 290 (nom. nud.).
1889. *Psammodus angustus* ROMANOWSKY: WOODWARD, p. 99.
1889. *Psammodus specularis* TRAUTSCHOLD: WOODWARD, p. 107.
1964. *Lagarodus angustus* (ROMANOWSKY): OBRUCHEV, pl. 1, figs 1 a-c.
1999. *Lagarodus angustus* (ROMANOWSKY): STAHL, p. 90, fig. 87.

NEOTYPE: Specimen PIN 1704/2, *specularis* morphotype tooth, Moscow Region, Kolomna District, Myachkovo quarry; Middle Carboniferous, Moscovian, Myachkovo Regional Stage, ?Domodedovo Formation.

REFERRED SPECIMENS: Palaeontological Institute of the RAS, Moscow, Russia (PIN); teeth in the coll. 1488, 1655, 1704, 2804, 2876 and 2878; Vernadsky State Geological Museum (SGM), coll. 56: Moscow, Ryazan', Tver' Regions, Central Russia, Middle–Upper Carboniferous, Kashira-Myachkovo Regional Stages of the Moscovian and Krevyakino-Khamovniki Regional Stages of the Kasimovian.

DIAGNOSIS. Five tooth morphotypes united into a single species based on similarity in morphology and histology. In *angustus* morphotype mesial wing strongly reduced, its surface perpendicular to that of the lateral one, central tubercle transversely elongated. Crown of *specularis* morphotype rhomboid, convex and twisted. In accessory morphotype mesial wing larger than lateral. Crowns of *cubicus* morphotype almost symmetric, shorter coronal surface sculptured. In small, possibly orobranchial, elements oval crown bears central tubercle and is ornamented.

Labial and lingual crown edges and non-occlusal coronal surfaces bear thick enameloid layer. Tubercles often fuse forming crests or network.

DISCUSSION

Reconstruction of the dentition

Based on earlier recognition of the separate *Lagarodus* tooth morphotypes as belonging to a single fish (TRAUTSCHOLD 1874; WOODWARD 1889), recent authors attempted to reconstruct its dentition (HANSEN 1986, unpublished dissertation, *fide* ELLIOTT & *al.* 2004; ELLIOTT & *al.* 2004). Both researchers accepted the arrangement of the teeth in rows and series. M. HANSEN recognised only the *specularis* and *angustus* morphotypes and placed the former in the upper and the latter in the lower jaw, in a single series along the jaw ramus. ELLIOTT & *al.* (2004) argued that lower jaw teeth would be more convex. These authors were the first to attempt an arrangement of the teeth in several rows and series in relation to a reconstructed jaw skeleton, including the *cubicus* morphotype ("small square teeth") in their reconstruction. However, this reconstruction lacks the accessory morphotype. Placing the *cubicus* morphotype elements in the symphysial region leads to an excessive amount of free space between those in such an important part of a crushing type dentition. Moreover, this arrangement does not take into account lifetime wear traces on the non-occlusive crown surfaces in the *angustus* and accessory morphotypes.

Tooth morphology, configuration of wear surfaces and comparison with extant analogues were used to reconstruct a new version of the dentition (Text-figs. 2 and 3A).

This approach is based on the following assumptions: 1) the initial morphotype for all realised variants is an arched tooth with a median ridge, as exemplified by specimen PIN 2804/1855 (Text-fig. 2R); 2) teeth should be arranged in rows and series as shown by contact areas on the lateral sides, and form a pavement dentition, and 3) elements in the series move labiad as shown by growth trace marks on the aboral sides of the bases, then become shed.

Pavement dentition in *Lagarodus specularis* is indicated by the crown structure in the accessory morphotype tooth PIN 2878/22 (Text-fig. 2S), demonstrating wear surfaces corresponding to the neighbouring teeth in the opposing jaw (LEBEDEV & ESIN 2007).

A possible modern analogue of the proposed dentition in *Lagarodus* may be seen in the Myliobatidae (Text-fig. 3). Their symphysial elements are enlarged, those in the lateral rows are small and less worn. Despite visible differences in structure, the general dentition pattern enlargement of the parasymphysial rows in the *Lagarodus* lower jaw (close fitting of the crowns, small lateral hexagonal elements) appears to be close.

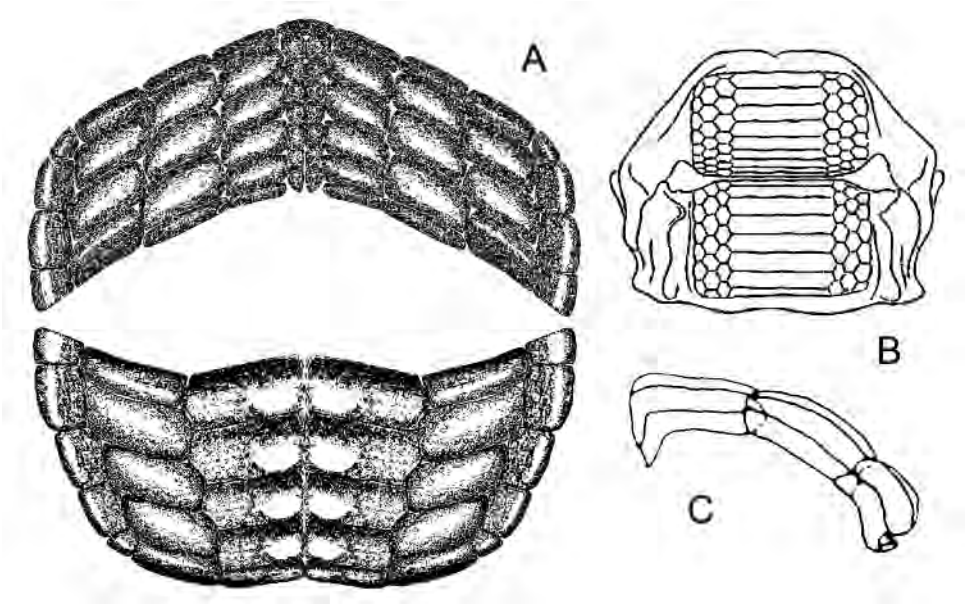

Fig. 3. A – Reconstruction of the upper and lower jaw dentition in *Lagarodus specularis* (TRAUTSCHOLD, 1874); B – dentition of the extant ray *Myliobatis aquila* L., 1758; C – *Lagarodus specularis* (TRAUTSCHOLD, 1874), suggested arrangement of the *angustus*, *specularis* and *cubicus* tooth morphotypes within dental row. Bend of the occlusal line indicates convexity of the tooth pavement. B from ZITTEL, 1923, slightly modified

In the *angustus* and accessory morphotypes insignificant wear traces over the mesial wings suggest contact with the counterpart element (Text-figs. 2G and M). Both morphotypes are interpreted as forming parasymphysial families in the upper and lower jaws (*versus* ELLIOTT & *al.* 2004). Pairs of parasymphysial teeth compares to the single symphysial element in the Myliobatidae (Text-fig. 3B).

The base margins of the *angustus*, *specularis* and *cubicus* morphotypes present more or less expressed angularity on one side and a ridge on the other (Text-figs 2B, C, E, F, I, K, N, O). If angularity defines the mesial edge, the opposite, ridge-bearing side should be lateral. This is corroborated by the *cubicus* morphotype, in which angularity at the edge of the crown bears contact surfaces (Text-fig. 2J). The lateral edge of the *angustus* morphotype closely fits the mesial edge of the *specularis* base (Text-fig. 3C). Contact areas at the mesial and lateral crown edges of the latter (Text-fig. 2B) suggest their positioning within intermediate tooth families. The number of intermediate tooth series was estimated with respect to the degree of arching within the tooth row (Text-fig. 3C). Reconstructing more than one intermediate series (*specularis* morphotype) in the lower jaw and more than three in the upper jaw leads to excessive bending of the tooth row.

Cubicus morphotype elements (Text-figs. 2H-K) are considered to be marginal as the lateral surface of their crowns are practically unworn (Text-fig. 2J), indicating that they were not in occlusion on this side. The lateral margin has no contact areas. They might be analogous to shorter teeth in the lateral tooth series in the Myliobatidae (Text-fig. 3B).

In the numerous well-preserved specimens the base is often missing. These crowns are interpreted as being shed, which supports the hypothesis presented here. In these specimens the occlusal surface of the crown is worn, but the lateral is not, which excludes simple post-mortem abrasion.

The angle of the tooth series setting over the jaw ramus was reconstructed using the angle between the diagonal axis and the direction of transverse ridges over the basal surface, in other words, traces of the tooth shift resultant from differential growth of jaw and tooth series. In the *specularis* morphotype the angle is 60°, in the *angustus* and *cubicus* morphotypes, the ridges are almost perpendicular to the longitudinal axis of the tooth; in the accessory morphotype the angle reaches only 30°. This is interpreted as showing that the *specularis* tooth families were growing strongly obliquely to the long jaw axis, the accessory families slightly obliquely and the *angustus* and *cubicus* families perpendicular to it, thus defining the suggested overall shape of the dentition.

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REFERENCES

ELLIOTT, D.K., IRMIS, R.B., HANSEN, M.C. & OLSON, T.J. 2004. Chondrichthyans from the Pennsylvanian (Desmoinesian) Naco Formation of central Arizona. *Journal of Vertebrate Paleontology*, **24**, 268-280.

International Code of Zoological Nomenclature. 1999. Published by the International Trust for Zoological Nomenclature. Fourth Edition. http://www.iczn.org/iczn/index.jsp

JAEKEL, O. 1898. Über die verschiedenen Rochen-Typen. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, **5**, 44-53.

LEBEDEV, O. & ESIN, D. 2007. Palaeopathological evidence in some Permocarboniferous fishes. *In*: BLOM, H. & BRAZEAU, M.D. (*Eds*), 40th Anniversary Symposium on Early Vertebrates/Lower Vertebrates. Abstracts Volume, Uppsala, Sweden, August 13-16, 2007. *Ichthyolith Issues, Special Publication*, **10**, 59-60.

LEBEDEV, O.A. & LYAPIN, V.R. 2001. Change of the species concept of *Lagarodus angustus* (ROMANOWSKY) and the composition of the family Orodontidae (Subterbranchialia, Chondrichthyes). *In*: LEBEDEV, O.A. (*Comp*), Obruchev Symposium "Evolutionary Palaeoichthyology", p. 26, Palaeontological Institute of the RAS, Moscow, 13-16 March, 2001.

OBRUCHEV, D.V. 1964. Subclass Holocephali. Holocephalians. *In*: YU. A. ORLOV (*Ed.*), Fundamentals of Palaeontology. Agnathans, Fishes. pp. 238-266. *Nauka Publishers*; Moscow.

ROMANOWSKY, H. 1864. Description des quelques restes des poissons fossiles trouvés dans le calcaire carbonifère du gouvernement de Toula. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **37**, 157-170.

STAHL, B.J. 1999. Chondrichthyes 3. Holocephali. *In*: H.-P. SCHULTZE (*Ed.*), Handbook of Paleoichthyology, v. 4, pp. 5-164. *Verlag Dr. Friedrich Pfeil*; München.

TRAUTSCHOLD, H. 1874. Die Kalkbrüche von Mjatschkova. Eine Monographie des oberen Bergkalks. Erste Hälfte. *Nouvelles Mémoires de la Société Impériale des Naturalistes de Moscou*, **13** (19), 276-324.

WOODWARD, A.S. 1889. Catalogue of the Fossil Fishes in the British Museum (Natural History). Pt. 1. Elasmobranchii, pp. 47+474. *Taylor & Francis*; London.

ZANGERL, R. 1981. Chondrichthyes 1. Paleozoic Elasmobranchii. *In*: H.-P. SCHULTZE (*Ed.*), Handbook of Pale-

oichthyology. v. 3A, pp. 1-115. *Gustav Fischer Verlag*; Stuttgart – New York.

ZITTEL, K.A. 1923. Grundzüge der Paläontologie (Paläozoologie). 2 Abteilung: Vertebrata. 4 Auflage, pp. 3-5+1-706. *Verlag v. R. Oldenbourg*; München – Berlin.

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