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# Evolution of the Cretaceous Lamnoid Sharks of the Genus *Eostriatolamia*

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**Abstract**—The "archaic" tooth form and comparatively few tooth rows are characteristic of the Cretaceous sharks of the genus *Eostriatolamia* (Odontaspididae). This is in contrast to the conditions in the Cenozoic sand sharks and thus makes it possible to regard this as a valid genus. The evolution and systematics of *Eostriatolamia* are reconsidered, in particular, on the basis of statistical methods. The cluster and principal component analyses were used to process a large quantity of teeth from 17 samples from the Albian-Campanian. Six or seven species are included in the genus *Eostriatolamia*: *E. gracilis* (Albian of Europe and Kazakhstan), *E. striatula* (Aptian–Albian of Europe), *E. subulata* (=*E. amonensis?*) (Cenomanian of Europe, Kazakhstan and ?USA), *E. venusta* (=*E. samhammeri?*, =*E. sanguinei?*) (Santonian–Early Campanian of Europe, ? Late Campanian of USA), *E. segedini* (=*E. aktobensis?*) (Santonian–Early Campanian of Kazakhstan), *?E. lerichei* (the latest Early Campanian–beginning of the Late Campanian of Kazakhstan) and *E. holmdelensis* (Late Campanian of the USA).

## INTRODUCTION

Teeth of small sand sharks of the family Odontaspididae often dominate in the Cretaceous marine vertebrate oryctocomplexes. Their distinguishing character, in particular, are the barely expressed crests on the internal part of the crown. These teeth were originally described as the species of the genus *Lamna* (*L. gracilis* Agassiz, 1843, *L. subulata* Agassiz, 1843, *L. venusta* Leriche, 1906). The Albian *L. gracilis* and the Cenomanian *L. subulata* were later commonly assigned to the genera *Odontaspis* (Pictet and Campiche, 1858; Sauvage, 1880) or *Scapanorhynchus* (Woodward, 1889, 1912; Priem, 1896; Leriche, 1902). The species from the Albian of Lithuania similar to *L. gracilis* was described as *Odontaspis* (*Synodontaspis*) *striatulus* (Dalinkevicius, 1935). The Santonian species *L. venusta* was regarded as a separate genus *Eostriatolamia* Glückman, 1979, which also included *L. gracilis*, *L. subulata, Oxyrhina angustidens* Reuss, 1845, *E. segedini* Glückman et Zhelezko, 1979 and *E. lerichei* Glückman et Zhelezko, 1979 (Glickman and Zhelezko, 1979; Glickman, 1980). One more *Eostriatolamia* species *E. aktobensis* Zhelezko, 1988 from the Lower Santonian of Mugodzhary (Zhelezko, 1988) was described later.

The Late Cretaceous species *O. angustidens*, clearly distinguished from the other forms listed above by absence of lateral cones and a smooth lingual part of the tooth crown was used to erect the new genus *Paranomotodon* Herman in Cappetta et Case, 1975 (Cappetta, Case, 1975a) and is currently referred to the thresher sharks (Alopiidae). In the latest paper on the fossil chondrichthyan fishes (Capetta, 1987) the genus *Eostriatolamia* is questionably synonymized with the genus *Synodontaspis* White, 1931 (the senior available name for the sharks of this genus is *Carcharias* Rafinesque, 1810: ICZN, 1987, Opinion no. 1459). At the same time Capetta (1987) noted, that *L. venusta*, the type species of the genus *Eostriatolamia*, is morphologically close to *Synodontaspis striatula* (Dalinkevicius, 1935). Even earlier *L. venusta* had been referred to the genus *Plicatolamna* Herman, 1975 (=*Cretodus* Sokolov, 1965) (Herman, 1977). The systematic position of the Albian-Cenomanian *L. gracilis* and *L. subulata* was not fixed in Capetta's system. He only specified, that *"Scapanorhynchus" subulatus* should belong to the family Odontaspididae (Capetta, 1987, p. 93).

As may be seen from the foregoing text, the systematic position of the small Cretaceous sand sharks is treated by different authors ambiguously. One of the reasons is, probably, the complete absence of modern methods of statistical material processing from the paleontological practice of identification of chondrichthyan fish fossil remains. This is largely due to the difficulty of making sufficient numbers of measurements of shark teeth. This problem may be solved by a method of shark teeth measurements introduced by Glickman (1980 and below). This article summarizes the results of the statistical processing of a large quantity of fossil sand shark teeth from various horizons of the Cretaceous of Russia, Lithuania and Kazakhstan. The validity of the genus *Eostriatolamia* and the evolution of its species composition are discussed.

## MATERIAL

The studied material is stored in the collections of the Darwin Museum, Moscow (DM).

973 complete shark teeth of the genus *Eostriatolamia* from the following 17 samples were measured:

(a) Sullukapy, Mangyshlak Peninsula, Kazakhstan. Outcrop 128, beds 18 and 17b. Upper Albian. Coll. DM, unnumbered. Collected by V.I. Zhelezko. *n* = 14.

(b) Kanev, Ukraine. Upper Albian. Coll. DM, no. 7. Collected by O.A. Erlanger. *n* = 18.

(c) Burluk River, Miroshniki, in the vicinity of Kamyshin, Volgograd Region. Outcrop 2 (Glickman, 1957). Upper Albian. Coll. DM, no. 1. Collected by L.S. Glickman. *n* = 9.

(d) Village of Vareikiai, *Sventoji* River, Lithuania. Greenish-gray aleurolites of the Jiesia Formation. Upper Albian. Coll. DM, no. 112. Collected by R. Mertiniene. *n* = 26. Type locality for *Odontaspis (Synodontaspis) striatula* Dalinkevicius, 1935.

(e) Saratov. White quartz sand. Lower Cenomanian. Coll. DM, nos. B-482, B-490, B-883, B-981 and B-987. Collected by L.S. Glickman. *n* = 125.

(f) Saratov. The Lower Phosphorite horizon. Upper Cenomanian. Coll. DM, nos. 55 (B-908), B-1021, B-1041, B-1044. Collected by L.S. Glickman. *n* = 134.

(g) Saratov. The Upper Phosphorite horizon. Upper Cenomanian. Coll. DM, nos. B-972, B-975. Collected by L.S. Glickman. *n* = 109.

(h) Ebeity Ravine, Tas-Kuduk, Mugodzhary, Kazakhstan. Outcrop 167, layer 11. Upper Cenomanian. Coll. DM, no. 52. Collected by L.S. Glickman and V.I. Zhelezko. *n* = 36.

(i) Sagyz River, Mugodzhary, Kazakhstan. Outcrop 111, layer 5 (Zhelezko and Segedin, 1972). Nogaity Member. Upper Cenomanian. Coll. DM, no. 45. Collected by L.S. Glickman and V.I. Zhelezko. *n* = 58.

(j) Shiili River, Emba River Basin, Mugodzhary, Kazakhstan. Outcrop 78. Koldenen-Temir Formation, Zhurun Beds. Lower Campanian. Coll. DM, nos. 124 and 191. Collected by V.I. Zhelezko. *n* = 134. Type locality for *Eostriatolamia lerichei* Glückman et Zhelezko, 1979.

(k) Zharyk River (Ilek River), Mugodzhary, Kazakhstan. Outcrop 105. Koldenen-Temir Formation, Kublei Beds. Upper Santonian. Coll. DM, no. 436. Collected by V.I. Zhelezko. *n* = 41.

(l) Tyk-Butak River, Or' River Basin, Mugodzhary, Kazakhstan. Layer 2. Lower Campanian. Coll. DM, no. 161. Collected by V.I. Zhelezko, R.A. Segedin and L.S. Glickman. *n* = 36.

(m) Tyk-Butak River, Or' River Basin, Mugodzhary, Kazakhstan. Layer 3. Upper Santonian. Coll. DM, no. 165. Collected by V.I. Zhelezko and L.S. Glickman. *n* = 73. Type locality for *Eostriatolamia segedini* Glückman et Zhelezko, 1979.

**Table 1.** Matrix of normalized Euclidean distances between 17 samples of the *Eostriatolamia* shark genus. Samples: (a) Sullukapy; (b) Kanev; (c) Burluk; (d) *Sventoji*; (e) Saratov (white quartz sands); (f) Saratov (the Lower Phosphorite horizon); (g) Saratov (the Upper Phosphorite horizon); (h) Ebeity; (i) Sagyz; (j) Shiili; (k) Zharyk; (l) Tyk-Butak (layer 2); (m) Tyk-Butak (layer 3); (n) Alymtau; (o) Kublei (outcrop 65); (p) Kublei (outcrop 66); (r) Ulety

| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| a | 0.00 | | | | | | | | | | | | | | | |
| b | 2.75 | 0.00 | | | | | | | | | | | | | | |
| c | 3.06 | 3.76 | 0.00 | | | | | | | | | | | | | |
| d | 9.48 | 11.80 | 8.91 | 0.00 | | | | | | | | | | | | |
| e | 1.89 | 2.11 | 2.21 | 10.18 | 0.00 | | | | | | | | | | | |
| f | 2.76 | 1.40 | 3.02 | 11.29 | 1.44 | 0.00 | | | | | | | | | | |
| g | 2.20 | 3.99 | 1.93‘ | 8.32 | 2.14 | 3.31 | 0.00 | | | | | | | | | |
| h | 1.60 | 2.90 | 1.99 | 9.04 | 1.42 | 2.43 | 1.80 | 0.00 | | | | | | | | |
| i | 3.66 | 1.45 | 4.36 | 12.57 | 2.57 | 1.57 | 4.65 | 3.55 | 0.00 | | | | | | | |
| j | 11.56 | 13.78 | 10.70 | 2.78 | 12.03 | 13.08 | 10.17 | 10.95 | 14.38 | 0.00 | | | | | | |
| k | 7.92 | 10.10 | 7.17 | 3.19 | 8.32 | 9.33 | 6.46 | 7.30 | 10.64 | 3.93 | 0.00 | | | | | |
| l | 6.91 | 8.86 | 5.88 | 4.27 | 7.08 | 8.05 | 5.47 | 6.03 | 9.30 | 5.23 | 1.88 | 0.00 | | | | |
| m | 9.90 | 11.97 | 8.87 | 2.60 | 10.22 | 11.24 | 8.49 | 9.14 | 12.51 | 2.18 | 2.64 | 3.36 | 0.00 | | | |
| n | 12.50 | 14.54 | 11.33 | 3.95 | 12.78 | 13.84 | 11.05 | 11.73 | 15.10 | 2.07 | 5.24 | 6.05 | 2.80 | 0.00 | | |
| o | 6.73 | 9.07 | 6.42 | 3.60 | 7.31 | 8.43 | 5.47 | 6.26 | 9.65 | 5.07 | 1.65 | 2.08 | 3.79 | 6.33 | 0.00 | |
| p | 4.02 | 6.04 | 3.94 | 7.13 | 4.23 | 5.20 | 2.55 | 3.61 | 6.45 | 8.57 | 4.69 | 4.00 | 7.06 | 9.69 | 3.77 | 0.00 |
| r | 7.30 | 9.43 | 6.44 | 3.75 | 7.58 | 8.63 | 5.78 | 6.60 | 9.91 | 4.64 | 1.03 | 1.20 | 3.08 | 5.70 | 1.43 | 4.01 |

(n) Alymtau Range, Chimkent Chuli, Kazakhstan. Lower Darbaza Subformation. The uppermost Lower Campanian. Coll. DM, nos. 267, 268, 269. Collected by V.D. Prinada, G.A. Belen'kii, A.V. Sochava and A.O. Averianov. *n* = 103.

(o) Kublei River, Mugodzhary, Kazakhstan. Outcrop 65 by the village of Dmitriyevskii, layer 8 (Glickman *et al.*, 1970; Zhelezko *et al.*, 1979; Zhelezko, 1988). The Zharyk Formation (?). Uppermost Lower–lowermost Upper Campanian. Coll. DM, nos. 417 and 424. Collected by R.A. Segedin and V.I. Zhelezko. *n* = 12.

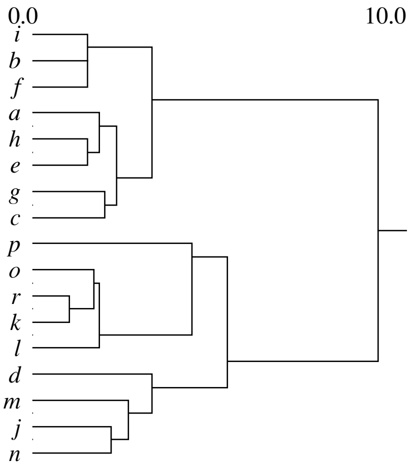

**Fig. 1.** Dendrogram of 17 samples of *Eostriatolamia*, similarity based on the matrix of euclidean distances (Table 1). Samples: (*a*) Sullukapy; (*b*) Kanev; (*c*) Burluk; (*d*) *Sventoji*; (*e*) Saratov (white quartz sands); (*f*) Saratov (the Lower Phosphorite horizon); (*g*) Saratov (the Upper Phosphorite horizon); (*h*) Ebeity; (*i*) Sagyz; (*j*) Shiili; (*k*) Zharyk; (*l*) Tyk-Butak (layer 2); (*m*) Tyk-Butak (layer 3); (*n*) Alymtau; (*o*) Kublei (outcrop 65); (*p*) Kublei (outcrop 66); (*r*) Ulety.

(p) Kublei River, Mugodzhary, Kazakhstan. Outcrop 66. Koldenen-Temir Formation, Zhurun Beds. Lower Campanian. Coll. DM, nos. 151 and 166. Collected by V.I. Zhelezko. *n* = 31.

(r) Ulety River, Mugodzhary, Kazakhstan. Outcrop 75, layer 4. Koldenen-Temir Formation, Zhurun Beds. Lower Campanian. Coll. DM, no. 128. Collected by V.I. Zhelezko. n = 14.

Teeth were measured by the following technique. Each tooth outline was drawn on squared paper using a photoenlarger so that the tooth size would equal 100 mm. Each tooth was subject to 11 measurements: measurements a1–a10 (relative tooth width measured at a distance equal to every 10% of the height from the top is calculated in percents from the tooth height) were taken from the tooth outline on squared paper, and h, the absolute tooth height, measured in millimeters from the specimen itself. The average values of measurements a1–a10 and h were calculated for each of the 17 samples. These average values were processed by the following methods of multidimensional statistics: (1) cluster analysis (Aldenderfer and Blashfield, 1989), based on the euclidean distances matrix between the samples (Table 1); hierarchical dendrogram, constructed by the algorithm "average" (Figs. 1 and 2) principal component analysis (Kim and Mueller, 1989). Calculations were produced by IBM computer with the help of DATA, CLUSTER, CORR, FACTOR, and GRAPH modules making part of the SYSTAT statistical programs package.

**Table 2.** Correlation of characters to the first three principal components

| Measurements | F1 | F2 | F3 |
|---|---|---|---|
| a1 | 0.941 | –0.038 | –0.298 |
| a2 | 0.938 | –0.037 | –0.338 |
| a3 | 0.961 | 0.011 | –0.266 |
| a4 | 0.973 | 0.092 | –0.187 |
| a5 | 0.979 | 0.158 | –0.067 |
| a6 | 0.980 | 0.146 | 0.095 |
| a7 | 0.962 | 0.026 | 0.233 |
| a8 | 0.961 | 0.000 | 0.266 |
| a9 | 0.963 | 0.019 | 0.206 |
| a10 | 0.930 | 0.011 | 0.344 |
| h | 0.420 | –0.907 | 0.023 |
| Dispersion, % | 85.215 | 8.009 | 5.533 |

## RESULTS

Studied samples are clearly separated into 2 groups (Fig. 1) following the results of the cluster analysis: (1) the Albian and Cenomanian *Eostriatolamia,* except the sample from the Albian of Lithuania ("d") and (2) Santonian and Campanian *Eostriatolamia*, as well as the sample from the Albian of Lithuania. The latter sample is closer to the samples "j" and "m", collected from the type localities for *E. lerichei* and *E. segedini* correspondingly. Both samples are very similar and do not differ sharply from other Santonian–Campanian samples.

These two sample groups also differ in the results of the principal component analysis (Fig. 2, Table 2). Moreover, in this case the Albian samples became separated from the Cenomanian ones in the principal component space F1 × F2 (Fig. 2a). The first principal component characterizes the tooth width at the measured levels (measurements a1–a10), the second principal component is related to the tooth height. In the principal component space F1 × F3 the Santonian–Campanian samples are also clearly separated from the Albian–Cenomanian ones, but the latter do not differ from each other. In both principal component spaces the sample from the Albian of Lithuania (*E. striatula*) is sharply separated from the Albian–Cenomanian and from the Santonian-Campanian samples (Figs. 2a and 2b).

The tooth width, related to the value of the principal component 1, remained almost unchanged in the evolution of *Eostriatolamia* (Fig. 3) during the Cenomanian in comparison with the Late Albian. Without taking into account the *E. striatula* sample from the Albian of Lithuania ("*d*"), they then increased significantly by the Santonian, slightly decreased during the Early Campanian and increased again by the beginning of the Late Campanian. It is noteworthy that the distinct width increase of the tooth crowns in *Eostriatolamia* correlates with the significant marine transgression that occurred during the Early Turonian, and some reduction of this parameter corresponds to the sea level drop during the Early Campanian (Shopf, 1982).

## DISCUSSION

Cooperative results of both statistical analyses suggest that: (1) the Albian (*E. gracilis*) and the Cenomanian (*E. subulata*) samples are rather close to each other, but may nevertheless be separated. This enables a valid recognition of both species; (2) the Albian *E. striatula* differs adequately from *E. gracilis*) and *E. subulata*, as well as from the Santonian-Campanian samples and permits consideration of this taxon as a valid species, and (3) the Santonian-Campanian samples form a single group (*E. venusta*, *E. segedini*, and *E. lerichei*), well distinguished from the Albian-Cenomanian forms. The material from the *E. aktobensis* type locality (Kublei River, outcrop 65, the lower part of Koldenen-Temir Formation) was not studied by us. However, judging by a previous description (Zhelezko, 1988), this species does not possess essential morphological distinctions from "*E. segedini*".

As noted by Capetta (1987, p. 91), the majority of teeth, referred by Glickman (1980) to *E. venusta*, differ significantly from the shark teeth of this species from the Santonian of Belgium, which are morphologically close to "*Synodontaspis*" *striatula* from the Albian of Lithuania. In fact, the typical *E. venusta* from Belgium (Leriche, 1929; Herman, 1977) meets the description of *E. lerichei* more, than that of *E. venusta* (Glickman and Zhelezko, 1979; Glickman, 1980) by a number of characters (large size, anterior teeth up to 20 mm long, the crests are absent from the internal side of the crown, and the anterior and lateral teeth usually demonstrate one lateral cone on both sides).

It is not improbable, however, that a peculiar *Eostriatolamia* species (present in the samples "*k*", "*l*", "*m*", "*p*", and "*r*"), characterized by smaller size, than that of *E. venusta*, slightly smaller width of tooth crowns, presence of vertical striations on the internal side of the crowns and, usually, two lateral cones on both sides and absence of short vertical crests at the crown base externally (sometimes present only at the bases of lateral cones) existed during the Late Santonian–Early Campanian in the Tethys. This species, yet unrevealed by the statistical methods applied here (probably, because of the small amount of studied material), should be named *E. segedini* (=*E. aktobensis?*). In North America the species morphologically similar to the latter was described as *Odontaspis holmdelensis* Capetta et Case, 1975 from the Upper Campanian of New Jersey, USA (Capetta and Case, 1975a).

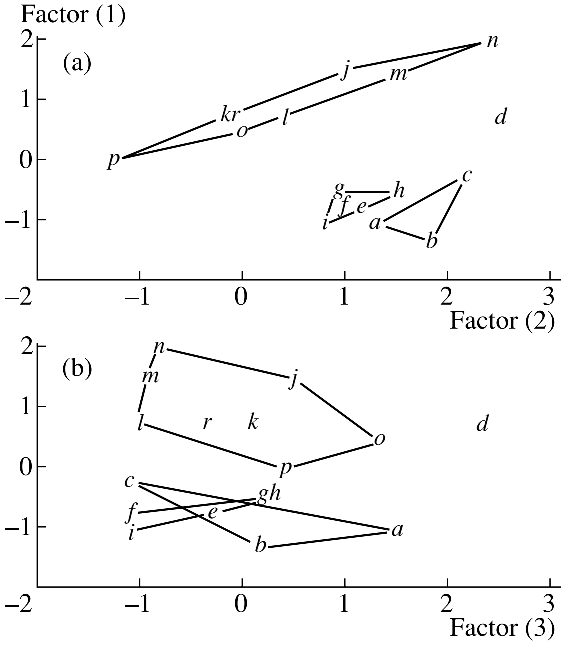

**Fig. 2.** Distribution of 17 samples of *Eostriatolamia* in the factor space F1 and F2 (a) and F1 and F3 (b). For samples see Fig. 1.

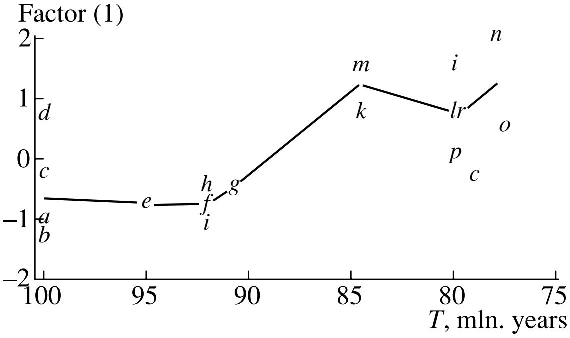

**Fig. 3.** Distribution of 17 samples of *Eostriatolamia* in the space factor 1 × geological time (T). For samples see Fig. 1.

Two *Eostriatolamia* species *E. striatula* and *E. gracilis* inhabited the Early Cretaceous epicontinental seas in Europe. *E. striatula*, whose teeth were distinguished by a comparatively wider crown and strongly expressed striae on the internal tooth sides is known, apart from the Albian of Lithuania, from the Late Aptian (Gargasian) of France (Capetta, 1975). *E. gracilis* (Fig. 4), remarkable for narrower crowns with considerably expressed striae on the internal side is known beside from the Albian of the Russian platform, for example, from the Albian of Northern France (Leriche, 1902). In the Tethys the *E. gracilis* descendants hardly changed during the Cenomanian (*E. subulata*, Fig. 5), but approximately from the Early Turonian their teeth evolved with a stronger emphasis on a cutting function (the crown became considerably expanded) and the body size of these sharks enlarged. As a result, the tooth morphotype described as "*E. segedini*" appeared. The size increase and strengthening of the cutting function

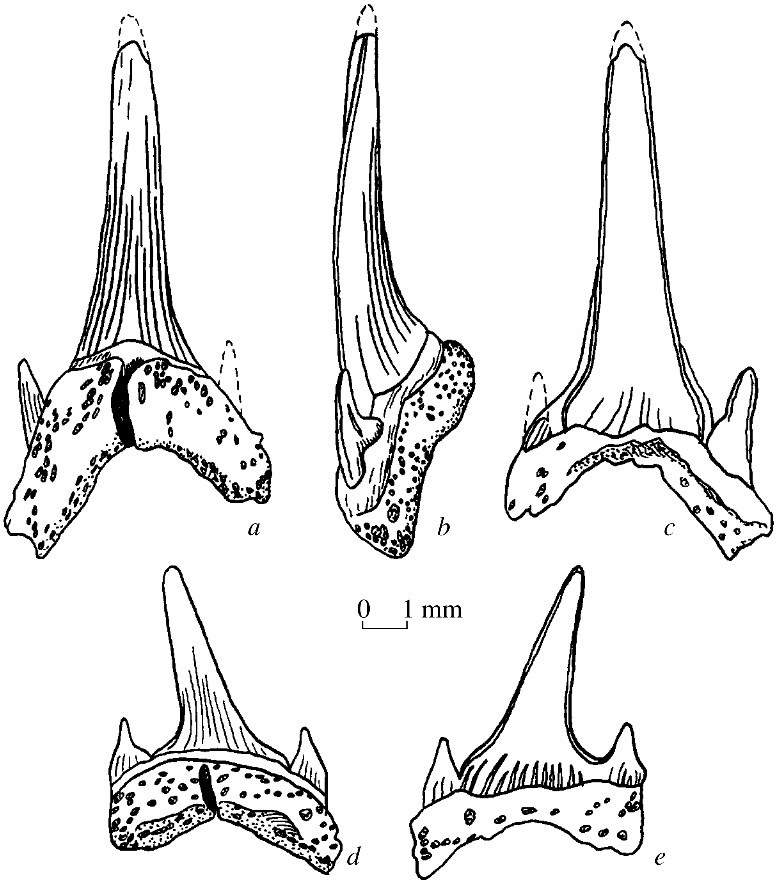

**Fig. 4.** Anterior: (*a–c*) and lateral: (*d*) and (*e*) teeth of *Eostriatolamia gracilis* (Ag., 1843): (*a*) and (*d*) internally, (*b*) laterally, (*c*) and (*e*) externally. Belgorod Region, Gubkin, Upper Albian. Scale bar 1 mm.

of the teeth in the evolution of *Eostriatolamia* are due to the significant transgression of the sea that took place in the low and middle latitudes of the Northern Hemisphere during the Early Turonian, when the sharks of this genus became compelled to adapt to life in the epipelagic biotope.

In the western part of the Atlantic a species, similar (conspecific?) to *Eostriatolamia subulata*, was described from the Cenomanian of Texas (USA) as *Odontaspis amonensis* Capetta et Case, 1975 (Capetta and Case, 1975b). This species differs from *E. subulata* by a completely smooth crown (in *E. subulata* (Fig. 5) the rudimentary striae are observed on the internal sides of the crown and short vertical crests at the base of the crown externally).

The Late Campanian species *Eostriatolamia holmdelensis* inhabited the western margin of the recently opened Atlantic ocean (east of the USA) and may be regarded as the descendant of the lineage *E. gracilis*–*E. subulata*, which also attained the evolutionary level of “*E. segedini*”. *E. holmdelensis* differs strongly from *E. segedini* by well expressed vertical striations on the internal crown surfaces, that suggests that it is a valid species. The Western European species *E. venusta* (Santonian–Early Campanian) is the most derived in terms of the enhancement of the tooth cutting function (the crown is extended as much as possible, no more than a pair of lateral cones on the anterior and lateral teeth, the striae on the internal side of the crown are already absent, since they are no longer required for tooth consolidation). This species probably originated directly from the more advanced species *E. striatula*, rather than from *E. gracilis*. Similar tooth morphotype (“*E. lerichei*”; Fig. 6) occurred in the Tethys only from the end of the Early Campanian (samples “*j*”, “*n*”, and “*o*”). Whether the “*E. lerichei*” morphotype arose in the Tethys independently from the “*E. segedini*” morphotype or whether it was a genuine *E. venusta* that gained access here from Europe it is difficult to decide now. If the first hypothesis turns out to be right, “*E. lerichei*” should be considered to be a valid species that arose in parallel with *E. venusta*. As for “*E. segedini*”, this species should probably be considered valid despite the results of the statistical analysis above.

In the western part of the Atlantic the teeth morphotype similar to *E. venusta* in many respects (large size,

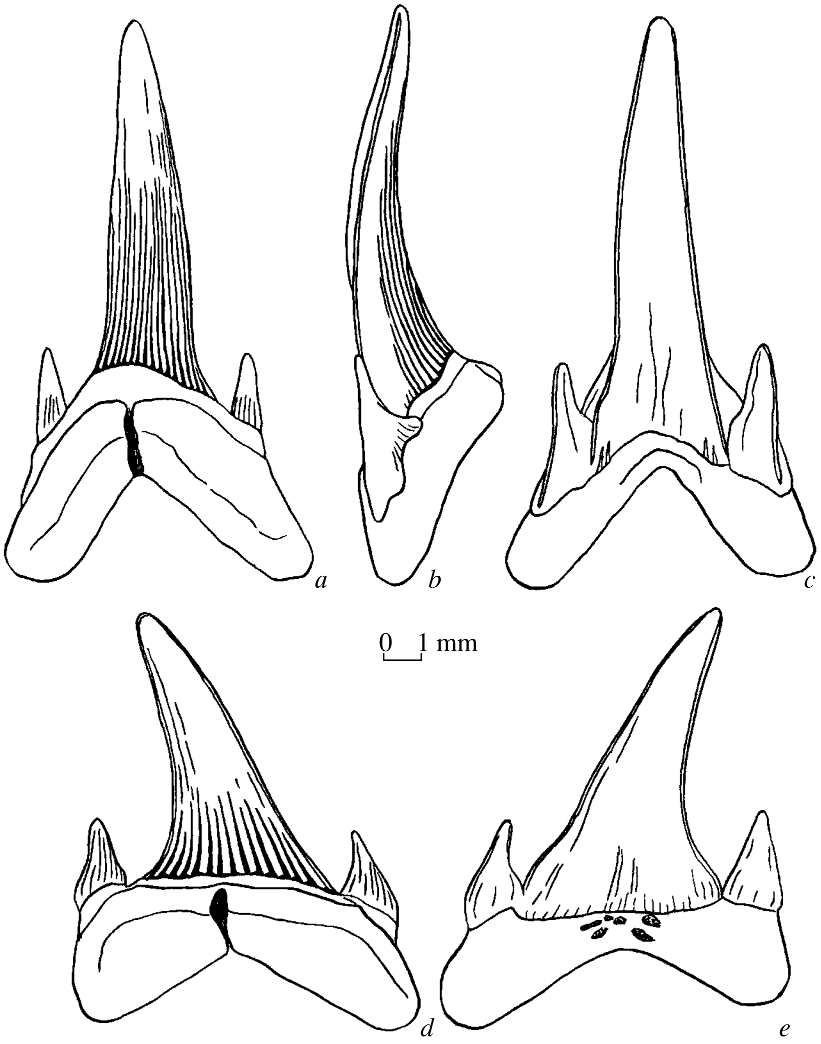

**Fig. 5.** Anterior: (*a*–*c*) and lateral: (*d*) and (*e*) teeth of *Eostriatolamia subulata* (Ag., 1843): (*a*) and (*d*) internally, (*b*) laterally, (*c*) and (*e*) externally. Saratov Region, Saratov, Upper Cenomanian (Lower Phosphorite horizon). Scale bar 1 mm.

crown base much extended, one lateral cone from each side, and the crown smooth on the internal side) was described as *Odontaspis samhammeri* Capetta et Case, 1975 from the Upper Campanian of New Jersey (USA) (Capetta and Case, 1975a) (probably, a part of the teeth of this species was referred to *Odontaspis hardingi* Capetta et Case, 1975). The American species *E. samhammeri* differs from the European *E. venusta* by the absence of short vertical crests externally at the crown base. The tooth morphotype closer to that of *E. venusta* has vertical crests externally on the crown base. It was described on the basis of few teeth from the area of the Interior Seaway of the USA (the Campanian of Montana) as *Odontaspis sanguinei* Case, 1978 (Case, 1978).

Thus, the genus *Eostriatolamia* in our opinion consists of six or seven species: (1) *E. gracilis* (the Albian of Europe and Kazakhstan), (2) *E. striatula* (Aptian–Albian of Europe), (3) *E. subulata* (=*E. amonensis?*) (Cenomanian of Europe, Kazakhstan and ?USA), (4) *E. venusta* (=*E. samhammeri?*, =*E. sanguinei?*) (Santonian–Early Campanian of Europe, ?Late Campanian of USA), (5) *E. segedini* (=*E. aktobensis?*) (Santonian–Early Campanian of Kazakhstan), (6) *?E. lerichei* (end of the Early Campanian–beginning of Late Campanian of Kazakhstan) and (7) *E. holmdelensis* (Late Campanian of the USA). It is impossible, however, to exclude completely, that some of the species listed above could in fact belong to the genus *Carcharias*, since certainly not all the species are known by sufficiently complete materials and the teeth transformations noted above could occur in parallel in these and other closely related genera.

The genus *Eostriatolamia* is not a synonym of *Synodontaspis* (=*Carcharias*), since a more advanced tooth formula and numerous tooth rows are characteristic of the latter genus (Glickman and Dolganov, 1988). The modern sand sharks, *Carcharias taurus* Rafinésque, 1810, possess a large, uncertain number of very small

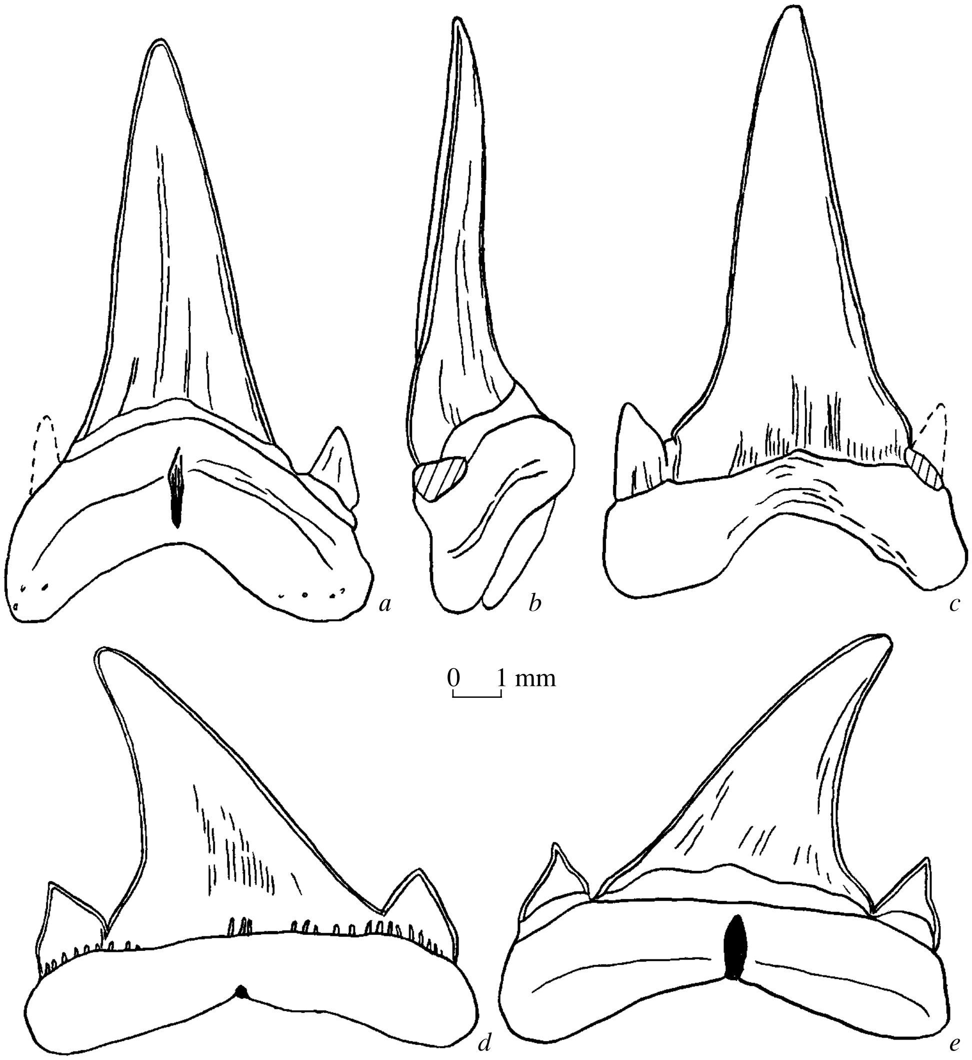

**Fig. 6.** Anterior: (*a–c*) and lateral: (*d*) and (*e*) teeth of *Eostriatolamia lerichei* Glückman et Zhelezko, 1979: (*a*) and (*e*) internally, (*b*) laterally, (*c*) and (e) externally. Lower Campanian, Alymtau, South Kazakhstan. Scale bar 1 mm.

posterior teeth, located in the corners of the mouth. These teeth, apart from the small size, are characterized by a very special crown inclined laterally. They form a sharply separated division in the jaw, probably, adapted for food crushing. In this area adjacent to the jaw articulation, the biomechanics of the jaws enable maximum pressure on the food object. A similar adaptation present in extant sand sharks (similar teeth are known in the hexanchids as well) should be considered as an advanced condition, atypical for the Cretaceous odontaspidids, assembled here in the genus *Eostriatolamia*. Small posterior teeth with a specifically slanted flattened crown are absent from the samples regarded as species of *Eostriatolamia*. This cannot be explained by insufficiently effective techniques of sample collecting, since the same sampling methods yielded the posterolateral teeth mentioned above in the Paleogene odontaspidids (at least, from the Late Paleocene) that are indisputably assigned to the genus *Carcharias*. An archaic tooth formula with a small number of slightly morphologically modified posterior teeth was obviously characteristic of sharks of the genus *Eostriatolamia*. This suggestion is supported by the evolutionary development of *Eostriatolamia*, which included the strengthening of a tooth cutting function, that is relevant to the reduction of the teeth series number. The same process is demonstrated in the evolution of the shark family Anacoracidae (Glickman, 1956, 1980; Glickman and Dolganov, 1988).

Consideration of the taxonomic structure of the genus *Eostriatolamia* was aimed at establishing true biological species, that is a set of populations genetically separated from other similar sets. Naturally, in paleontology, owing to incompleteness and limitations of the fossil record, only the so-called "paleontological species" are usually considered, e.g., by shark teeth morphotypes. The intuitive and typological approach now practically entirely prevails in the study of extinct sharks, or more precisely, their fossil teeth morphotypes. This results in a quite legitimate question, whether this represents science or has more in common with philately? (Naylor and Maisey, 1990). The way out of this situation seems to be the use of multidimensional statistics methods for the recognition of species and subspecific shark groups by their fossil teeth. One of the examples of this approach is presented in the current paper. However, the results of the use of statistical methods should be evaluated from biological positions. The fact, that tooth morphotypes are morphologically identical in various sample sets (paleopopulations) does not prove that these sets belong to a single species. In the present case the tooth morphotypes of the *E. lerichei* samples from the Campanian of Kazakhstan and *E. venusta* from the Santonian-Campanian of Europe are practically identical. Firstly, however, it is not excluded that this morphotype in *E. lerichei* developed in parallel and independently of *E. venusta*, and that this species originated not from *E. striatula*, but from *E. subulata*. Secondly, in any case the area of *E. lerichei* (eastern part of the Tethys) was isolated from that of *E. venusta* (Atlantic) by the merged continents of Africa and Europe. These circumstances make it possible to consider *E. lerichei* to be a valid biological species despite the fact that it does not differ from *E. venusta* in tooth morphology. Similarly numerous extant real biological shark species differ only insignificantly in skin color or arrangement and relative length of fins and can not be separated by tooth size and structure.

We realize that the suggested systematics of the shark genus *Eostriatolamia* would hardly satisfy stratigraphical needs, but that in any case it is possible to use fossil shark teeth reliably for biostratigraphical purposes only by learning the real evolutionary history of the biological species of these animals, however complicated it is.

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