Systematics of the cretaceous-paleogene chimaeroid fish of the genus elasmodus (chondrichthyes, holocephali)

Article in Paleontological Journal · January 2001

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Paleontological Journal, Vol. 35, No. 3, 2001, pp. 289–300. Translated from Paleontologicheskii Zhurnal, No. 3, 2001, pp. 65–75.

Systematics of the Cretaceous–Paleogene Chimaeroid Fish of the Genus *Elasmodus* (Chondrichthyes, Holocephali)

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Received April 7, 1999

Abstract—The genus *Elasmodus* comprises nine species including *E. tsheganicus* sp. nov. *Elasmodus* remains are known from the Albian–Eocene interval, predominantly from the Old World. Fossil material of this genus has been found in fourteen localities in Russia, Kazakhstan, Uzbekistan, and Ukraine. The *Elasmodus* fishes were sclerophagous and had probably partially shifted towards vertebrate carrion feeding. The extinction of this genus was due to global cooling and sea regression at the end of the Eocene.

INTRODUCTION

The genus *Elasmodus* Egerton, 1843 includes peculiar chimaeroid fish known from the middle of the 19th century from the Paleogene of England and the Senonian of Belgium (Agassiz, 1843; Egerton, 1843; Woodward, 1891a). The first *Elasmodus* remains in Russia were found by L.S. Glickman in the Cenomanian of Saratov during 1947–1952. This material was studied by T. F. Eichhorn, who attributed these remains to "*Elasmodus khosatzky* Eichhorn" (unpublished manuscript; the most complete specimens from this collection are not preserved). Later, this species was described as *E. sinzovi* Averianov, 1994 (Averianov and Glickman, 1994). Material from the territory of the former USSR almost doubles the known history of the genus, and significantly expand our ideas on its taxonomic variety and geographical distribution (for earlier reviews see: Nessov and Averianov, 1996; Averianov *et al.*, 1999). This paper presents information obtained from new finds. The genus *Elasmodus* is revised and the distribution, evolution, adaptations, and causes of the extinction of these fish are discussed.

The genus *Elasmodus* resembles other "edaphodontids" (this family includes the genera *Ischyodus*, *Edaphodon* and, tentatively, *Elasmodus*) by the tritoral pattern of the tooth plates, but differs from them in the presence of lamellar tritors along the cutting edge of the dentition (outer tritors of the vomerine plate, lateral tritor of the palatine plate, and outer tritor of the mandibular plate). This distinction was the reason to establish the genus and erect its name (from the Greek *elasma*—plate). The lamellar tritor, in comparison to the usual one composed of tubular dentine, demonstrates a more specialized and advanced condition. Tritoral lamellae consist of fused dentine tubules arranged in even rows, which in the usual tritors are randomly spaced and do not merge (Ørvig, 1985). Only in a few extinct chimaeroids are the tritors chiefly lamellar (e.g., in the Jurassic genera *Ganodus* and *Eomanodon*); the majority demonstrate tritors composed of tubular dentine. Strengthening of the lamellar tritors along the cutting edge of the dentition in *Elasmodus* suggests some peculiarities of these chimaeroids' diet, which distinguishes them from contemporaneous "edaphodontids."

MATERIAL

The material described in the present paper is stored in the collections of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN PC); F.N. Chernyshev Central Research Geological Prospecting Museum (TsNIGR museum), St. Petersburg; and the Institute of Animal Zoology and Genofund of the Academy of Sciences of Kazakhstan, Almaty (IZK). The tritor designation scheme of the tooth plates of *Elasmodus* is shown in Fig. 1.

SYSTEMATIC PALEONTOLOGY

CLASS HOLOCEPHALI BONAPARTE, 1831

Order Chimaeriformes Patterson, 1965

Family "Edaphodontidae" Owen, 1846

Genus *Elasmodus* Egerton, 1843

Elasmodus: Egerton, 1843a, p. 156.
Psaliodus: Egerton, 1843a, p. 156.

Type species. *E. hunteri* Egerton, 1843.

Diagnosis. Mesial tritor at the mandibular plate short rostrocaudally, parallel to the symphysial edge, and composed of tubular dentine. Outer tritors consist of lamellar dentine. Anterior outer tritor very wide, mesial outer tritor less wide. Posterior outer tritor consists of several (up to five–six) short columns. Palatine plates massive, bearing four–five tritors. Anterior internal, posterior internal, and mesial tritors elongated to various degrees and consist of tubular dentine. Lateral tritor long, consisting of lamellar dentine. Vomerine tritors subrectangular, bearing few (three–four, up to seven–eight at the maximum) outer tritors composed of lamellar dentine.

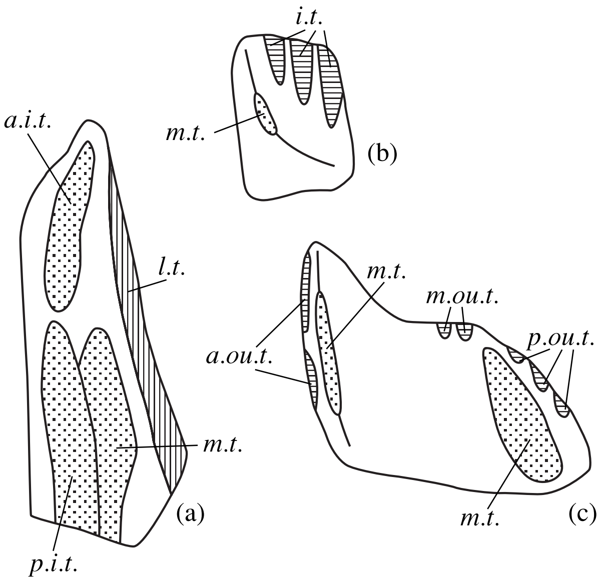


Fig. 1. The diagram of tritor identification in the chimaeroid tooth plates of the genus *Elasmodus*: (a) palatine plate, (b) vomerine plate, (c) mandibular plate; (a) and (b) ventral, (c) dorsal. Tritor designations: *a.i.t.*—anterior inner tritor, *a.ou.t.*—anterior outer tritor, *i.t.*—internal tritor, *l.t.*—lateral tritor, *m.ou.t.*—mesial outer tritor, *m.t.*—mesial tritor, *ou.t.*—outer tritor, *p.i.t.*—posterior inner tritor, *p.ou.t.*—posterior outer tritor, *s.t.*—symphysial tritor. Tritors composed of tubular dentine are dotted.

Species composition. Nine species: *E. rossicus* Averianov, 1999 (Albian of Russia); *E. sinzovi* Averianov, 1994 (Cenomanian–Santonian of Russia); *E. avirostrus* Averianov, 1999 (Campanian–? Maastrichthian of Kazakhstan); *E. zharyk* Averianov, 1999 (Campanian of Kazakhstan); *E. khosatzkyi* Averianov, 1999 (Campanian of Kazakhstan); *E. greenoughi* Agassiz, 1843 (Campanian–Maastrichthian of Western Europe); *E. hunteri* Egerton, 1843 (Paleocene–Eocene of Europe and USA); *E. kempi* Ward, 1977 (Eocene of Great Britain), and *E. tsheganicus* sp. nov. (Eocene–? Oligocene of Kazakhstan).

Occurrence. Cretaceous (Albian–Maastrichthian) and Paleogene (Paleocene–? Oligocene) of Eurasia and North America.

***Elasmodus rossicus* Averianov, 1999**

Plate 10, figs. 1–3

Elasmodus rossicus: Averianov and al., 1999, p. 135, pl. 1, fig. 5.

Holotype. TsNIGR museum, no. 3/12868, right mandibular plate; Russia, Belgorod Region, Gubkin (Lebedi quarry); sands close to the main phosphorite bed of the Upper (?) Albian, outcrop GLE-5.

Description. A species of *Elasmodus* with comparatively robust mandibular plates with a long symphysis. Distance from the symphysis to the mesial tritor is about equal or slightly larger than the rostrocaudal diameter of the latter. Palatine plates are very narrow. Vomerine plates bear a single outer lamellar tritor and one symphysial tritor composed of tubular dentine.

The anterior end of the mandibular plate is strongly bent mesially. The “beak” is very much expressed in the specimen ZIN PC no. 4/30. The symphysial tritor is absent. The mesial tritor is rather wide and faces backwards. The mesial outer tritor is single and it is less than half as wide as the anterior outer tritor. There are two–four posterior outer tritors; they are missing in juvenile individuals. There is a slightly expressed strip of dense dentine (“ascending plate,” a primitive character, see Patterson, 1992) at the external side of the mandibular plate below the oral edge. The striation at the surface contacting the mandibular cartilage is directed perpendicular to the external edge. Mandibular plates of juvenile individuals are rather thin and gracile. The palatine plate is very narrow. Anterior inner, posterior inner, and mesial tritors are fused. Posterior inner and mesial tritors are elongated and of about equal size. In the vomerine plate, the symphysial edge is very short and the lateral edge is very massive. The symphysial tritor is rounded and very small. Dentine lamellae of the outer tritor are parallel to the symphysial edge.

Occurrence. Epicontinental sea of the Late(?) Albian of the Russian Platform.

Material. Apart from the holotype, specimens ZIN PC nos. 1-11/30, 13/30 and 14/30, 9 mandibular, 2 palatine, and 2 vomerine plates, Gubkin (Lebedi and Stoilo quarries).

***Elasmodus sinzovi* Averianov, 1994**

Plate 10, figs. 4–7; Plate 11, figs. 1 and 2

Elasmodus sinzovi: Averianov and Glickman, 1994, p. 121, text-fig. 1.

Elasmodus sp.: Averianov, 1997, p. 79.

Holotype. TsNIGR museum, no. 5/12868, right mandibular plate; Russia, Saratov Region, Saratov; the base of the “sponge horizon”, Upper Turonian–Lower Santonian.

Explanation of Plate 10

Figs. 1–3. *Elasmodus rossicus* Averianov, 1999, tooth plates (×1.25): (1) specimen ZIN PC no. 1/30, left mandibular plate: (a) dorsally, (b) ventrally; (2) specimen ZIN PC no. 2/30, right mandibular plate: (a) ventrally, (b) dorsally; (3) specimen ZIN PC no. 3/30, left palatine plate: (a) ventrally, (b) dorsally; Gubkin, Upper (?) or Lower–Middle Albian.

Figs. 4–7. *Elasmodus sinzovi* Averianov, 1999, tooth plates (×1.25): (4) specimen ZIN PC no. 3/13, fragmentary right palatine plate, ventrally; (5) specimen ZIN PC no. 2/13, fragmentary left mandibular plate, dorsally; Sinenkiye, Lower Cenomanian; (6) specimen ZIN PC no. 2/38, fragmentary left palatine plate, ventrally; (7) specimen ZIN PC no. 1/38, left mandibular plate: (a) dorsally, (b) ventrally, Saratov, Upper Cenomanian.

Plate 10

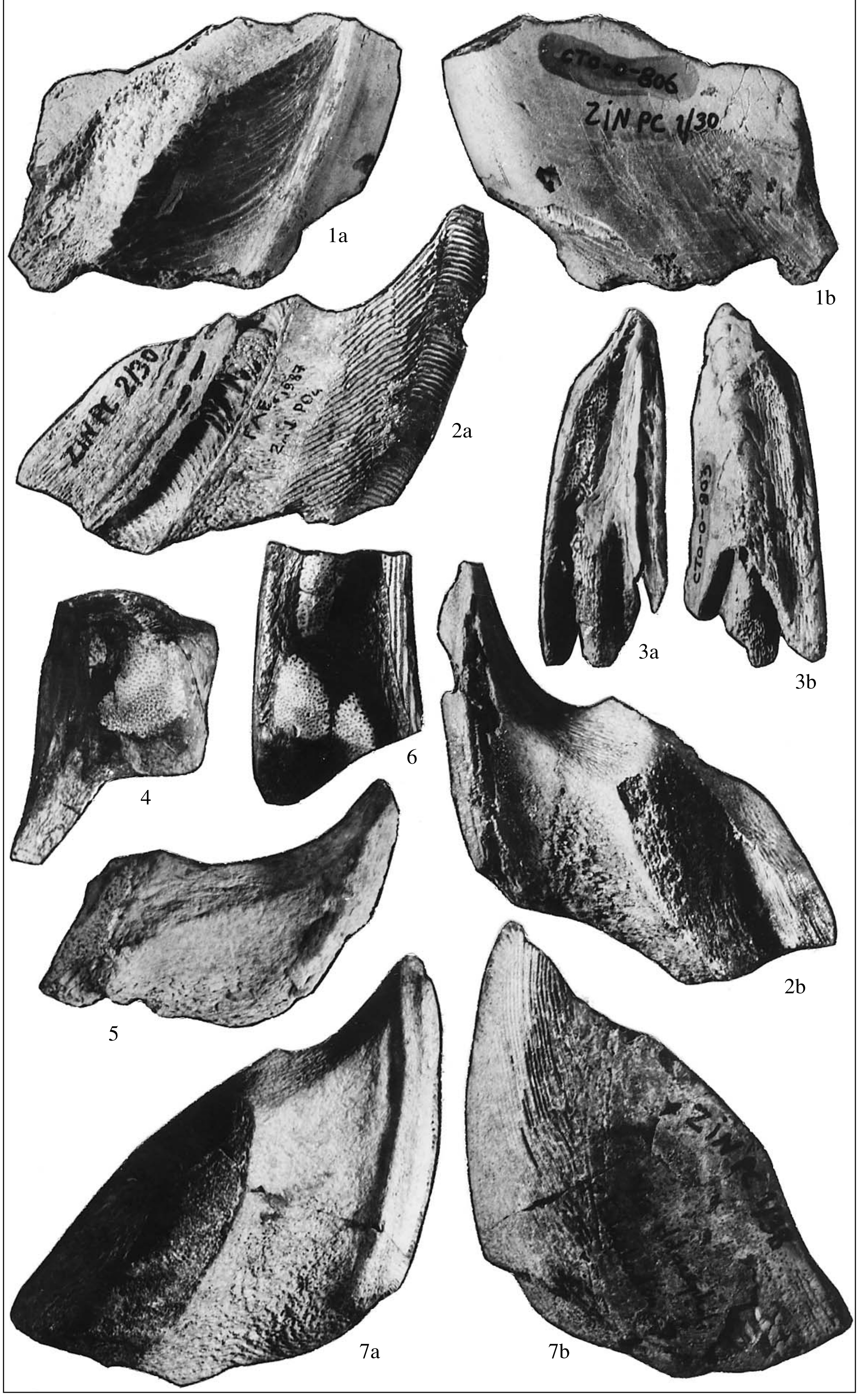
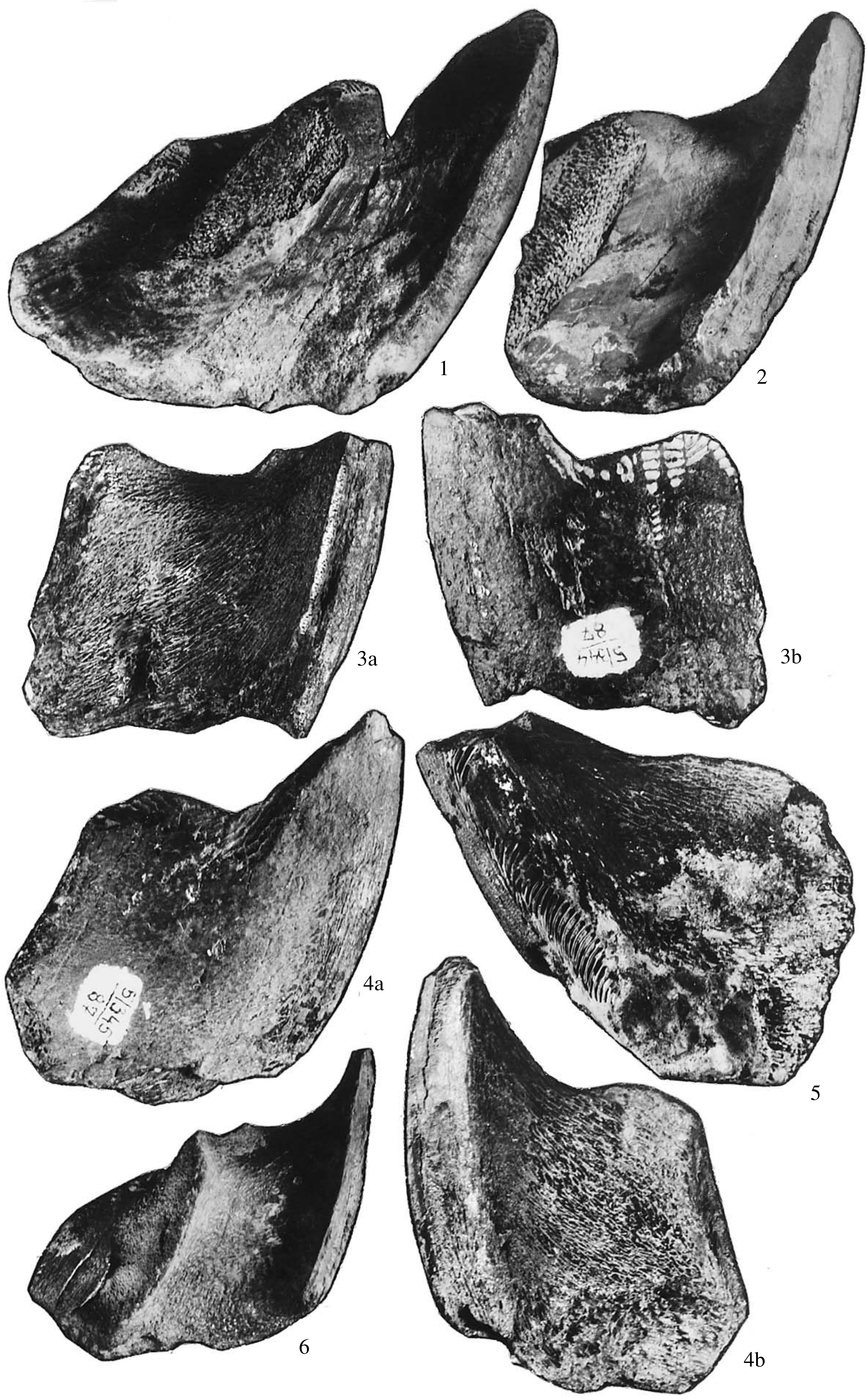


Plate 11



Explanation of Plate 11

Figs. 1 and 2. *Elasmodus sinzovi* Averianov, 1999, tooth plates (×1.25): (1) specimen ZIN PC no. 3/11, left mandibular plate, dorsal, Kikino, Upper Santonian; (2) specimen ZIN PC no. 1/3, fragmentary left mandibular plate, dorsal; Polpino, Turonian.

Figs. 3–5. *Elasmodus avirostrus* Averianov, 1999, tooth plates (×1.25): (3) paratype IZK no. 5/344/87, fragmentary left mandibular plate: (a) dorsal, (b) ventral; (4) paratype IZK no. 5/345/87, fragmentary right mandibular plate: (a) ventral, (b) dorsal; (5) specimen IZK no. 5/231/86, fragmentary right mandibular plate dorsal; Kushmurun, Upper Campanian –? Lower Maastrichtian.

Fig. 6. *Elasmodus khosatzkyi* (?) Averianov, 1999, left mandibular plate, dorsally (×1.25), specimen ZIN PC no. 2/36; Kachar, Lower Campanian.

D e s c r i p t i o n. A species of *Elasmodus* with comparatively robust mandibular plates with a long symphysis. The distance from the symphysis to the mesial tritor is about 1.5 times larger than the rostrocaudal diameter of the latter. The palatine plates are wide. The mesial tritor is much shorter than the posterior inner tritor. The vomerine plate bears seven–eight outer tritors, and there is no symphysial tritor.

The anterior extremity of the mandibular plate is strongly angled mesially. The "beak" may be well expressed, but is usually low. The mesial tritor is oval, wide, and faces backwards. The mesial outer tritor is the only one, and there are from three to six posterior outer tritors. The striations at the surface contacting the mandibular cartilage are parallel to the external edge. The mandibular plates of juvenile individuals are comparatively thin. The palatine plates are robust and rather wide.

O c c u r r e n c e. Cenomanian–Santonian epicontinental sea of the Russian Platform.

M a t e r i a l. Apart from the holotype, specimens ZIN PC nos. 2/13 and 3/13, fragmentary mandibular and palatine plate, Sinenkiye 2; ZIN PC nos. 1-6/38, 5 fragmentary mandibular and one palatine plate, Saratov; ZIN PC no. 1/3, fragment of the mandibular plate, Polpino; ZIN PC no. 3/11, mandibular plate, Kikino.

***Elasmodus avirostrus* Averianov, 1999**

Plate 11, figs. 3–5

Elasmodus avirostrus: Averianov *et al.*, 1999, p. 133, pl. 1, figs. 1, 3 and 4.

H o l o t y p e. TsNIGR museum, no. 1/12868, right palatine plate; Kazakhstan, Kustanay Region, "Priozerniy" quarry close to Kushmurun railway station; Eginsai Formation, Upper Campanian–?Lower Maastrichtian.

D e s c r i p t i o n (Figs. 2a–2d). *Elasmodus* species characterized by deep and thin mandibular plates with a short symphyses. The mesial tritor is narrow. The distance from the symphysis to the mesial tritor is 5–6 times larger than the rostrocaudal diameter of the latter. The mesial tritor of the palatine plate arises posteriorly to the constriction between the anterior and posterior inner tritors. There are four outer tritors on the vomerine plate.

There are four mesial outer tritors on the mandibular plate. The posterior outer tritor is exposed at the external edge as a continuous stripe. The mesial tritor is very narrow. The very long and narrow symphysial tritor is present in one of three mandibular plates. The palatine plate is rather short, very thick, and it bears a robust symphysial edge. The anterior and posterior inner tritors are fused, but are separated with a distinct constriction. The anterior inner tritor consists of dentine tubules somewhat ordered in oblique rows; the posterior inner and mesial ones are composed of disorderly located dentine tubules. The mesial tritor is separated from the posterior inner one. The outer tritor is long and consists of regular plates (no less than six) directed parallel to the external edge. The lateral tritor at the vomerine plate is almost twice as wide as more mesial tritors. A narrow and very long symphysial tritor composed of tubular dentine runs along the symphysis.

M a t e r i a l s. Apart from the holotype, IZK no. 5/231/86, a fragment of a large mandibular plate; IZK no. 5/233/86, the vomerine plate; ZIN PC no. 1/39, the mandibular plate; IZK nos. 5/345/87 and 5/344/87; and right and left mandibular plates from the type locality.

***Elasmodus zharyk* Averianov, 1999**

Elasmodus zharyk: Averianov *et al.*, 1999, p. 135, pl. 1, fig. 6.

H o l o t y p e. TsNIGR museum, no. 2/12868, right mandibular plate; Kazakhstan, Aktyubinsk Region, Zharyk River, Emba River basin (Mugodzhary Mountains), outcrop 105 (see Glickman *et al.*, 1970); Kublei beds, Koldenen-Temir Formation, Campanian.

D e s c r i p t i o n. A large form with a deep mandibular plate and rather short symphysis. Distance from the symphysis to the mesial tritor is more than twice as large as the rostrocaudal diameter of the latter.

The symphysial tritor is not preserved in the available fragment. The mesial tritor is long and faces mesially. The outer tritor consists of closely spaced dentine plates. The striation at the surface contacting the mandibular cartilage is directed parallel to the external edge.

M a t e r i a l s. Holotype only.

***Elasmodus khosatzkyi* Averianov, 1999**

Plate 11, fig. 6

Elasmodus khosatzkyi: Averianov *et al.*, 1999, p. 136, pl. 1, fig. 7.

H o l o t y p e. TsNIGR museum, no. 4/12868, left mandibular plate; Kazakhstan, Kustanay Region, town of Zhuravlevskii, Ayat River; lower part of the Zhuravlevka Formation, Upper Campanian.

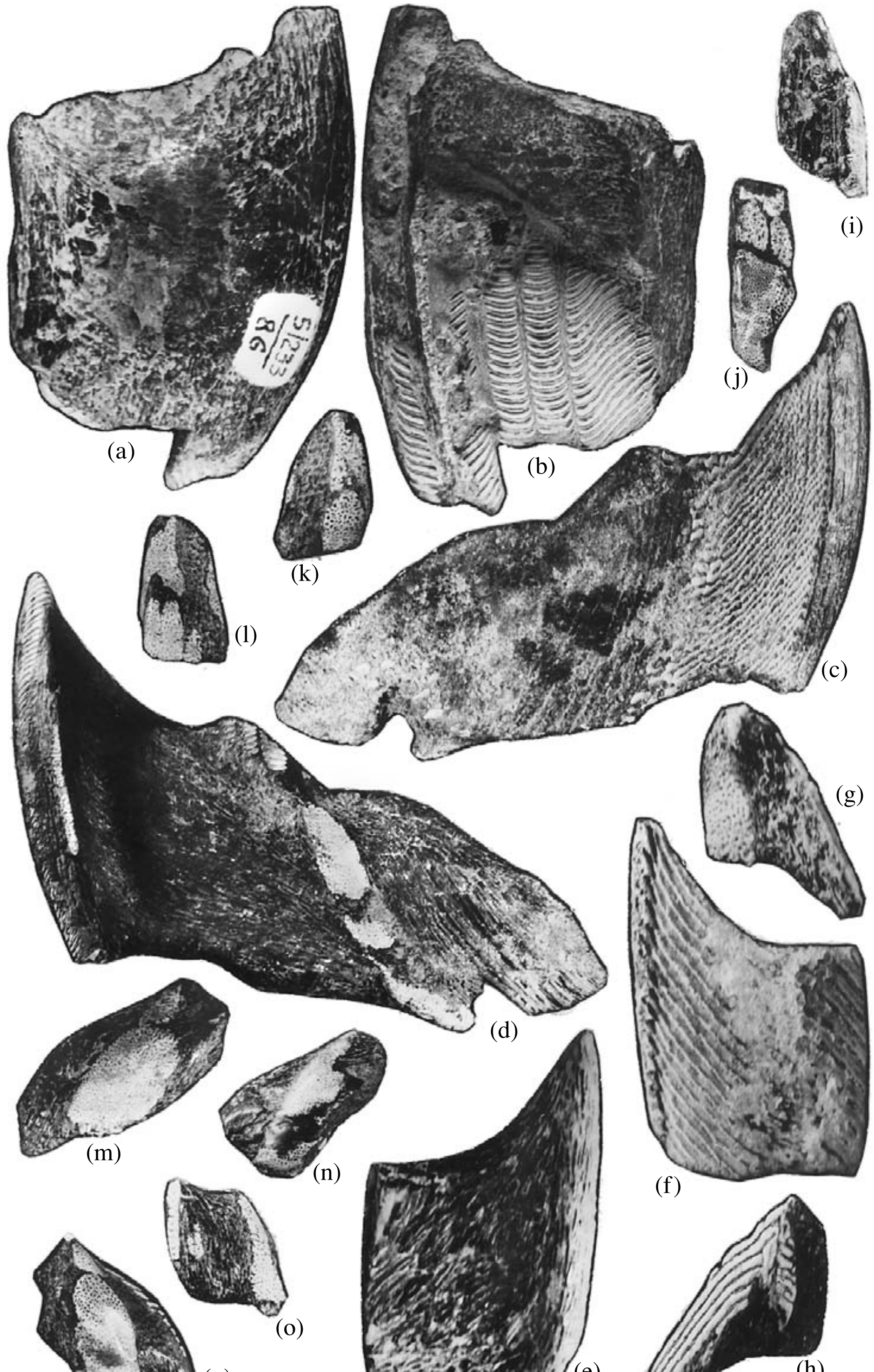


Fig. 2. Tooth plates: (a)–(d) *Elasmodus avirostrus* Averianov, 1999 (×1.25), (a) and (b) specimen IZK no. 5/233/86, right vomerine plate; (c) and (d) specimen ZIN PC no. 1/39, right mandibular plate; both Kushmurun, Upper Campanian –? Lower Maastrichtian; (e)–(h) *E. hunteri* Egerton, 1843: (e) and (f) specimen ZIN PC no. 2/40, fragmentary left mandibular plate (×3.3); (g) and (h) specimen ZIN PC no. 1/40, left palatine plate (×3.6), Malin,? Eocene; (i) and (j) *Edaphodon* sp., specimen ZIN PC no. 7/51, fragmentary left palatine plate (×1.35); (k)–(p) *Elasmodus tsheganicus* sp. nov., fragmentary plates (×1.35): (k) specimen ZIN PC no. 6/51, right palatine plate, (l) holotype ZIN PC no. 1/51, left palatine plate, (m) paratype ZIN PC no. 2/51, left mandibular plate, (n) ZIN PC no. 4/51, right mandibular plate, (o) ZIN PC no. 5/51, left mandibular plate, (p) paratype ZIN PC no. 3/51, right mandibular plate; (i)–(p) Kolenkaly Mountains, Upper Eocene – ? Lower Oligocene. (a), (d), (e), (h), (m)–(p) dorsal view, (b), (c), (f), (g), (j)–(l) ventral view and (i) medial view.

D e s c r i p t i o n. Large *Elasmodus* species possessing robust mandibular plates with very wide symphysis and rather small mesial tritor.

The symphysial tritor is not present on the mandibular plate. The mesial tritor faces backwards, and is rather small in an adult individual (individual age estimated upon the size of the holotype and well developed part of the plate located behind the mesial tritor). The distance between the symphysis and the mesial tritor is almost twice the rostrocaudal diameter of the latter. The dentine plates of the outer tritor are closely spaced. The outer tritor is exposed as a row of very small areas of lamellar dentine extended along the external edge. The striation at the surface contacting the mandibular cartilage is directed perpendicular to the external edge.

O c c u r r e n c e. The Campanian Turgai Strait (northwest Kazakhstan).

M a t e r i a l. Apart from the holotype, probably ZIN PC no. 2/36, which is an incomplete mandibular plate, Kachar.

***Elasmodus greenoughi* Agassiz, 1843**

Chimera (Elasmodus) Greenoughii [*sic*]: Agassiz, 1843, p. 350, pl. 40, figs. 11–16.

Elasmodus greenovi [*sic*]: Egerton, 1843a, p. 156; 1843b, p. 470; 1847, p. 352.

Aptychus crassus: Hébert, 1855, p. 368, pl. 28, fig. 8.

Elasmodus greenoughi: Woodward, 1891a, p. 90; 1891b, p. 112, pl. 3, fig. 17.

Elasmodus crassus: Leriche, 1906, p. 90; 1910, p. 469, pl. 6, fig. 7.

Elasmodus planus: Leriche, 1929, p. 261, text-fig. 18; Duffin, Reynders, 1995, pl. 13, figs. G and H.

L e c t o t y p e (Woodward, 1891a, p. 90). Natural History Museum (London), no. P483, an incomplete right mandibular plate. The exact locality is unknown, probably Belgium, Poudingue de Malogne, Ciply, near Mons; upper Maastrichtian.

D e s c r i p t i o n. The mesial tritor at the mandibular plate is narrow and its rostrocaudal diameter is much shorter than the distance between it and the symphysis. The mesial outer tritor is the only one. The posterior outer tritor is long and visible on the surface as a series of small tritors.

R e m a r k s. Chimaeroid tooth plates from the Campanian of Montana, USA defined as "*Elasmodus cf. greenoughi* Agassiz" (Case, 1979, p. 226, pl. 2, figs. 5 and 6) more than likely do not belong to the genus *Elasmodus*.

O c c u r r e n c e. Campanian–Maastrichtian epicontinental sea of western Europe.

***Elasmodus hunteri* Egerton, 1843**

Elasmodus hunteri: Egerton, 1843a, p. 156; 1843b, p. 470; Agassiz, 1843, p. 350; Egerton, 1847, p. 352; Dixon, 1850, p. 111, pl. 10, figs. 11 and 12; Egerton, 1852, pl. 1; Noetling, 1885, p. 11, pl. 1, figs. 2 and 3, pl. 2, fig. 6; Woodward, 1891a, p. 89; Leriche, 1902, p. 36; Dean, 1906, text-fig. 122; Leriche, 1909, p. 243, pl. 5, fig. 6; Priem, 1911, p. 23; Davis, 1937, p. 79; Casier, 1946, p. 111; Leriche, 1951, p. 502; Gurr, 1963, p. 435, text-fig. 6, pl. 24, pl. 25, fig. 3, pl. 26, fig. 4; Casier, 1966, p. 98, pl. 10, fig. 6, pl. 11, fig. 3; 1967, p. 32, pl. 7, text-fig. 27; Herman, 1972, p. 196, pl. 1, figs. 11 and 12; Ward, 1973, p. 323; 1977, text-figs. 2 and 3; Kemp *et al.*, 1990, pl. 14, fig. 4; Cvancara, Hoganson, 1993, p. 13, text-figs. 2G and 2H.

Psaliodus compressus: Egerton, 1843b, p. 471.

Elasmodus sp.: Leriche, 1902, p. 10.

L e c t o t y p e (Casier, 1966, p. 98). Natural History Museum (London), no. 43110, left mandibular plate; Great Britain, Sheppey Island; London Clays, Lower Eocene.

D e s c r i p t i o n (Figs. 2e–2h). The mesial tritor at the mandibular plate is wide and its rostrocaudal diameter is no less than the distance from it to the symphysis. The external and mesial tritors at the palatine plate are strongly elongated.

The mandibular plate is thin and the distance from the symphysis to the mesial tritor is large. The palatine plate of a juvenile individual (Figs. 2g and 2h) bears a rather massive and long posterior lateral "wing" and a large tritor composed of tubular dentine. The vomerine plate bears three outer tritors approximately equal in size consisting partially of tubular and lamellar dentine. The symphysial edge is robust. There is no symphysial tritor.

O c c u r r e n c e. Late Paleocene–Eocene epicontinental sea of Europe and North America.

M a t e r i a l. ZIN PC, no. 2/40, fragmentary mandibular plate, no. 1/40 palatine plate of a juvenile individual, no. 3/40, vomerine plate, several fragments of tooth plates from the granite quarry Malin close to Penezevichi, Zhitomir Region, Ukraine. The remains are probably redeposited from Paleogene (Eocene?) deposits.

***Elasmodus kempi* Ward, 1977**

Elasmodus kempi: Ward, 1977, p. 101, text-fig. 1; Kemp *et al.*, 1990, pl. 14, figs. 5 and 6.

H o l o t y p e. Natural History Museum (London), no. P. 58710, left mandibular plate; Great Britain, Hampshire, Lee-on-the-Solent; upper part of Bracklesham Beds, Middle Eocene (Lutetian).

D e s c r i p t i o n. Middle-sized *Elasmodus* species. Tooth plates are comparatively thick. The mesial tritor at the mandibular plate is directed at an angle to the symphysial side, the mesial outer tritor is large and consists of tubular dentine. There are two well developed symphysial tritors. There are four tritors at the palatine plate, the anterior inner tritor enters the symphysial side.

O c c u r r e n c e. Middle Eocene of Great Britain.

***Elasmodus tsheganicus* Averianov, sp. nov.**

E t y m o l o g y. Species name from the Chegan Formation.

H o l o t y p e. ZIN PC no. 1/51, incomplete right palatine plate, probably of an adult individual; Kazakhstan, Aktyubinsk Region, Kolenkaly Mountains; Chegan Formation (Upper Eocene–?Lower Oligocene).

D e s c r i p t i o n (Figs. 2k–2p). Middle-sized *Elasmodus* species. The mesial tritor at the mandibular plate is directed at an angle to the symphysial side, and the mesial outer tritor is rather large and composed of tubular dentine. The palatine plate bears five tritors (the posterior inner tritor is subdivided into two tritors), and the anterior inner tritor enters the symphysial side.

C o m p a r i s o n. The new species differs from all other species of the genus (except *E. kempi*) by the oblique position of the mesial tritor at the mandibular plate, the rather large mesial outer tritor composed of tubular dentine, and the shifting of the anterior inner tritor of the palatine plate to the symphysial side. It differs from *E. kempi* by subdivision of the posterior inner tritor of the palatine plate in two tritors and a significantly shorter mesial tritor in comparison to the posterior inner tritor. The new species differs from all others of this genus in having five tritors on the palatine plate.

C o m m e n t s. Small but robust tooth plates with well developed tritoral surfaces probably belonged to adult individuals (strong development of tritors in the small plates is also characteristic of *E. kempi*). Hence, the members of the *E. tsheganicus* sp. nov. probably did not attain large size. This may have been due to hostile environmental conditions, such as dwelling in comparatively cold water.

M a t e r i a l s. Apart from the holotype, paratypes ZIN PC nos. 2/51 and 3/51, the fragmentary left and right mandibular plates, and several less complete fragments of unnumbered tooth plates in the collection ZIN PC no. 51 from the type locality.

DISCUSSION

Comments on the morphofunctional analysis of dentition, distribution, evolution, and causes of extinction in the genus *Elasmodus*.

Originally the "edaphodontids" were probably sclerophagous fish using a wide spectrum of food objects, possibly including the corpses of vertebrates (Nessov and Averianov, 1996). Specialization of *Elasmodus* dentition suggests adaptation of these chimaeroids to the usage of more specific food, which required significant cutting efforts created by tooth plate edges. At the same time, retention of tubular dentine tritors inside the mouth indicates grinding (crushing) of food objects after biting off pieces, which, however, was significantly less important than in typical "edaphodontids." The source of such particular food could be the corpses of vertebrates (marine reptiles, fish?, probably marine mammals during the Paleogene). Serious efforts should be applied for piercing the skin and biting off pieces of flesh (the cutting function of marginal lamellar tritors) and at least some for bone grinding inside the mouth (grinding function of mesial tritors consisting of tubular dentine). Presence of plesiosaur vertebrae with traces of biting attributed to chimaeroids in Kushmurun, where *Elasmodus* remains predominate among chimaeroids (there are also rare *Ischyodus* remains; unpublished data) may be regarded as indirect confirmation of such an assumption.

All known *Elasmodus* finds are restricted to the coastal zones of epicontinental seas (Fig. 3). For the first time in the record, they occur in the Albian of central Russia (*E. rossicus*) and Uzbekistan (*Elasmodus* sp.) during one of the most significant Mesozoic thermal optima (Fig. 4). Probably, their ancestors inhabited more southern areas of the Tethys, and invaded higher latitude regions with climate warming. Among chimaeroids, *Ischyodus* remains dominate during the Albian–Cenomanian interval in central Russia, *Edaphodon* and, especially, *Elasmodus* tooth plates being rarer. The further history of the last genus (during the Cenomanian–Santonian) is known only by finds on the Russian platform (*E. sinzovi*). Probably, the substitution of prevailing species among chimaeroids in the epicontinental sea of the Russian platform had occurred by the beginning of the Turonian (Averianov and Glickman, 1994), and *Ischyodus* was replaced by *Edaphodon*. Obviously, the number of *Elasmodus* individuals also increased during that time as it is these remains which were found in a number of localities that yielded only few finds of chimaeroids (Polpino, Kikino). From the Early Campanian, *Elasmodus* appears in western Europe, where it is rather rare (*E. greenoughi*); and in Kazakhstan (*E. avirostrus*, *E. zharyk* and *E. khosatzkyi*), where it predominates jointly with *Ischyodus*, while *Edaphodon* is very rare. Such a wide occurrence of the genus may result from the beginning of the Late Senonian transgression (Schopf, 1982). During the Maastrichtian, *Elasmodus* is only known with certainty from the Holland–Belgium basin (*E. greenoughi*). During the Paleocene–Eocene interval, these fish increased their range still further, and even penetrated into the remaining part of the inner epicontinental sea of North America (*E. hunteri* from North Dakota). In the east they spread to Germany, Ukraine and Kazakhstan. During the Middle–Late Eocene the living conditions of *Elasmodus* seem to worsen dramatically owing to the global cooling of the climate (Fig. 4). This was particularly due to the formation of the circum-Antarctic current, which stopped the access of warm equatorial waters to the high latitudes of the southern hemisphere (Kennett, 1977). Under these severe conditions, species formation in the Paleogene lineages of *Elasmodus* occurred by peramorphosis; that is, attaining of an adult condition of characters at earlier ontogenetic stages (McNamara, 1986). Two last species in the genus' fossil record, *E. kempi* and *E. tsheganicus* sp. nov., seem to have been influenced by this process. Marked development of tritors combined with small tooth plates is characteristic of both species. This combination suggests that these elements were allied to adult fish (in the "normal" *Elasmodus*, the tooth plates of juvenile individuals are very thin). Such peramorphous development could result from low availability of food, which did not allow chimaeroids to grow to their normal size.

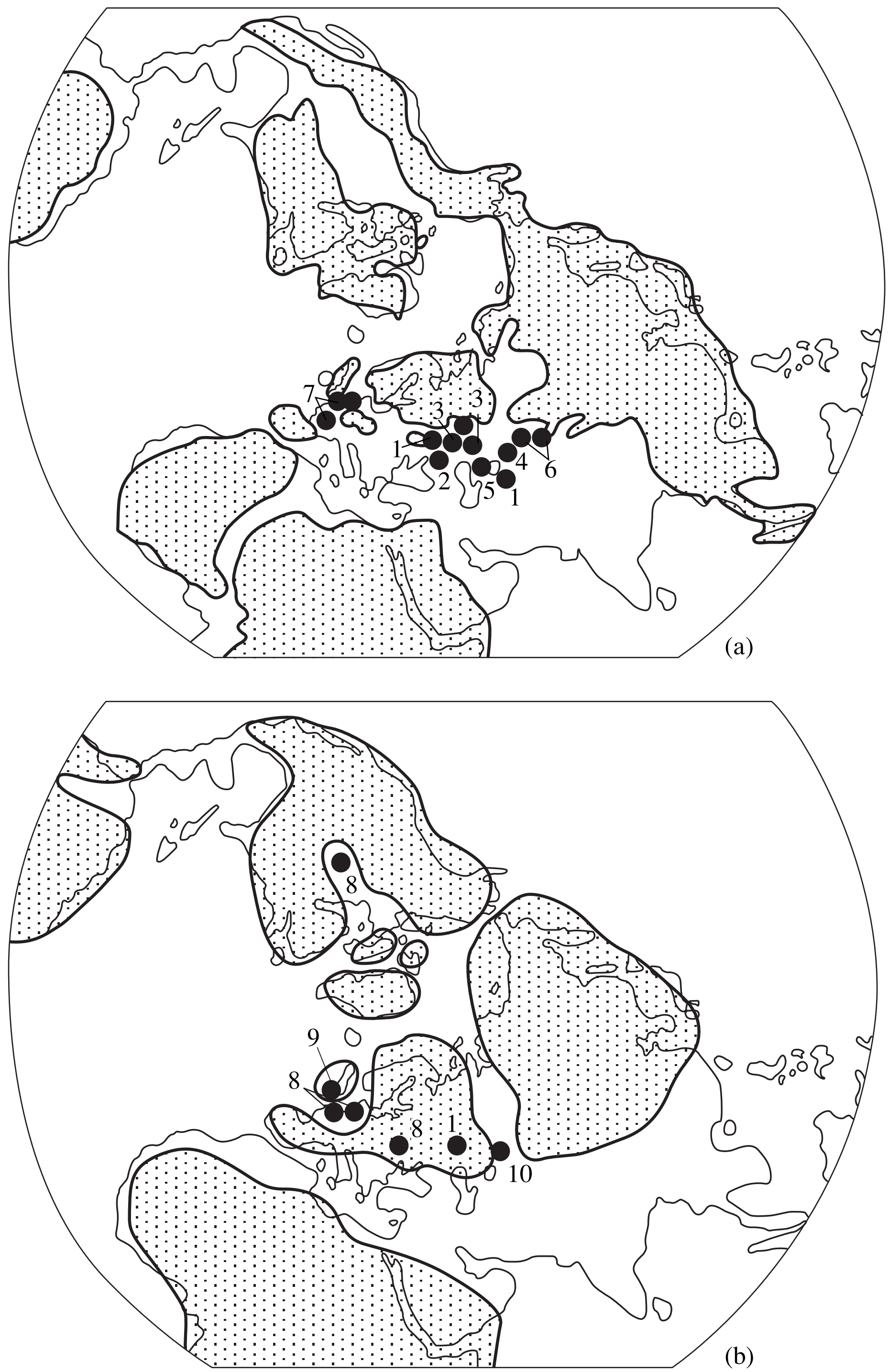


Fig. 3. Geographical distribution of chimaeroids of the genus *Elasmodus* during the Cretaceous (a) and Paleogene (b). Species: (1) *Elasmodus* sp.; (2) *E. rossicus*; (3) *E. sinzovi*; (4) *E. avirostrus*; (5) *E. zharyk*; (6) *E. khosatzkyi*; (7) *E. greenoughi*; (8) *E. hunteri*; (9) *E. kempi*; (10) *E. tsheganicus*. Dotted areas indicate approximate position of land masses. Paleogeographical reconstruction after Borzenkova (1992).

This could also be a direct consequence of the lowering of the water temperature, which caused growth delay. The palynocomplexes from the Chegan Formation indicate distinct cooling of the climate during the Late Chegan time (Akhmetiev and Zaporozhets, 1992). No real Oligocene *Elasmodus* specimens are known. In England, where the complexes of the Paleogene chondrichthyan fish are pretty well known, the youngest *Elasmodus* specimen comes from the Bartonian (the second half of the Middle Eocene; see Ward, 1980).

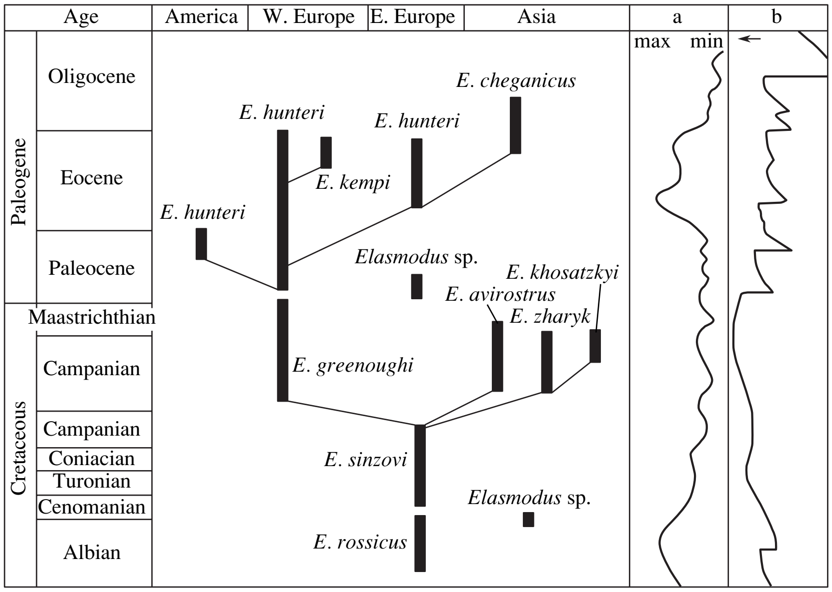


Fig. 4. Stratigraphical distribution of chimaeroids of the genus *Elasmodus*. Thin lines show possible species affinities. (a) Approximate curve of water temperature changes in the shelf seas in the middle latitudes by Borzenkova (1992) and others; (b) sea level change curve (the arrow indicates towards increase of the sea level) by Schopf (1982) (scale changed).

Probably, the genus became extinct in the Priabonian (Late Eocene), when the climatic cooling became most pronounced. Even if the *Elasmodus* traversed the Eocene–Oligocene boundary, the very marked, global sea regression at the Early–Late Oligocene boundary, which resulted in the almost complete disappearance of all epicontinental seas (Schopf, 1982), should have completely destroyed their habitats. After this boundary, the surviving chimaeroid groups (Chimaeridae, Rhinochimaeridae and Callorhinchidae) were confined to the cold depths of the seas and oceans, rather than the warm coastal waters of the epicontinental seas, as in the Mesozoic.

A list of localities containing the remains of *Elasmodus* in Russia, Kazakhstan, Uzbekistan, and Ukraine (in the stratigraphic sequence).

(1) Shchigry, Kursk Region, Russia. A fragmentary plate of a juvenile *Elasmodus* sp. was found in Albian sands close to the Shchigry railroad station (outcrop KShchI-1). Collected by A.O. Averianov and A.V. Panteleyev, 1995.

(2) Gubkin, Belgorod Region, Russia. About 20 tooth plates of *E. rossicus* were found in the sands of the Sekmenovka Formation of the Upper (?) Albian in the Lebedi and Stoilo iron ore quarries close to the towns of Gubkin and Starii Oskol. Collected by L.A. Nessov, 1980–1994 and A.O. Averianov, 1991–1998.

(3) Khodzhakul, Karakalpakistan, Uzbekistan. A fragmentary plate of *Elasmodus* (?) sp. was found in the sands of the lower–middle part of the Khodzhakul Formation (outcrop SKh-20), Upper Albian (Nessov, 1988). Collected by L.A. Nessov.

(4) Sinenkiye 2, Saratov Region, Russia. Fragments of tooth plates of *E. sinzovi* were found in the phosphate bearing sands (Lower Cenomanian) close to Sinenkiye Village (right bank of the Volga River, outcrop SSI-2). Collected by A.O. Averianov and A.V. Panteleyev, 1995.

(5) Saratov, Saratov Region, Russia. Rare tooth plates of *E. sinzovi* are known from the Upper Cenomanian sands in the recently recultivated quarries of Saratov ("Uvek," "Silicate factory quarry"). Some plates of *E. sinzovi* (including the holotype) were found in the yellowish gray sandstone layer (Upper Turonian–Lower Santonian) at the base of the "sponge horizon" at Lysaya Hill in Saratov (Averianov and Glickman, 1994). Collected by L.S. Glickman, 1947–1952. New specimens of *Elasmodus* from the Cenomanian of Saratov are stored in E.V. Popov's collection (Pervushov *et al.*, 1997).

(6) Polpino, Bryansk Region, Russia. The mandibular plate of *E. sinzovi* was found in the Turonian sands of the 2nd Batagi phosphorite quarry close to Bryansk (outcrop BPO-3a). Collected by A.O. Averianov and A.V. Panteleyev, 1995.

(7) Kikino, Penza Region, Russia. A tooth plate of *E. sinzovi* was found in phosphorite conglomerate (outcrop PKI-1; Upper Santonian) in a quarry close to the village of Kikino (Averianov, 1997). Collected by A.O. Averianov and A.V. Panteleyev, 1995.

(8) Kachar, Kustanay Region, Kazakhstan. A plate of *E. khosatzkyi*(?) was found in the greenish gray sands of the Eginsai Formation (outcrop KACh-5, Lower Campanian) in the Kachar quarry 50 km from Kustanay. Collected by L.A. Nessov, 1992.

(9) Kushmurun, Kustanay Region, Kazakhstan. The remains of *E. avirostrus* were found in the "Priozernyi" quarry close to the Kushmurun railway station at the base of the gray siltstone and sand beds containing phosphorites of the Eginsai Formation (Upper Campanian–?Lower Maastrichtian). Collected by B.V. Prizemlin, 1986 and 1987 and L.A. Nessov, 1992.

(10) Zhuravlevskii, Kustanay Region, Kazakhstan. The remains of *E. khosatzkyi* were found in a layer of phosphate-bearing sands of the Zhuravlevka Formation (Upper Campanian) along the Ayat River. Collected by L.A. Nessov, 1992.

(11) Zharyk, Aktyubinsk Region, Kazakhstan. The mandibular plate of *E. zharyk* was found in the Kublei beds of the Koldenen-Temir Formation at the Zharyk River in the Mugodzhary Mountains (outcrop 105; Campanian). Collected by L.S. Glickman and V.I. Zhelezko, 1968.

(12) Lysiye Gory, Saratov Region, Russia. The remains of small chimaeroids, probably juveniles of *Elasmodus* sp., were found in Danian deposits. Collected by L.S. Glickman, 1956–1967.

(13) Kolenkaly, Aktyubinsk Region, Kazakhstan. Some fragments of small tooth plates of *E. tsheganicus* sp. nov. were found in the Kolenkaly Mountains between the Emba River and Ustyurt in the deposits of the Chegan Formation (Upper Eocene – ?Lower Oligocene). The collector is unknown.

(14) Malin, Zhitomir Region, Ukraine. Granite quarry close to the Malin railway station by the town of Penezevichi. Some fragmentary plates of *E. hunteri* were found in the phosphate-bearing sands among redeposited remains of other Albian–Cenomanian, Senonian, and Paleogene vertebrates. Probably, the remains of *Elasmodus* come from the Paleogene (Eocene?). Collected by D.D. Povshednyi, 1988–1990.

ACKNOWLEDGMENTS

The author is grateful to E.V. Popov for information on the new collections of *Elasmodus* from the Cenomanian of Saratov, to A.V. Panteleyev and students of St. Petersburg University for their help during the field work, to the three anonymous reviewers for reading the manuscript and their useful comments, and to J.D. Archibald for amending the English summary. Field work of the author in 1995 was supported by the Russian Foundation for Basic Research, project no. 95-05-14186.

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