{p 89}[†] **E. I. Vorobyeva & H. D. Obrucheva**

RHIZODONT CROSSOPTERYGIAN FISHES (FAM. RHIZODONTIDAE) FROM THE MIDDLE PALEOZOIC DEPOSITS OF THE ASIAN PART OF THE USSR[*]

Scales and teeth of crossopterygian fishes (Crossopterygii) belonging to family Rhizodontidae (order Osteolepiformes) are widely distributed in the Middle Paleozoic deposits of the Asian part of the USSR. The majority of finds have been referred to genus *Strepsodus*, often meaning *Strepsodus siberiacus* Khabakov, erected on the basis of rather characteristic sculptured scales from the Lower Carboniferous Bystraya and Nadaltay Formations in the Minusa depressions of Krasnoyarsk Region (Khabakov, 1927; Obruchev, 1955; Vorobyeva, 1962).

Genus *Strepsodus*, type species *Strepsodus sauroides* Binney (Woodward, 1909), is typical of the Lower and Middle Carboniferous of Europe, where it is usually found as disarticulated skeletal elements, especially the shoulder girdle and vertebrae (Andrews, Westoll, 1970). Species of *Strepsodus* are also known from the Lower Carboniferous of North America and Australia, primarily represented with scales. The Australian forms, in particular *Strepsodus decipiens* (Woodward, 1906), differ from European and American ones by their thinner ornament, approaching *Strepsodus siberiacus* in this respect. New finds of this latter species including, besides scales, the cranial bones, shoulder girdle and teeth, give grounds for its allocation to a separate genus of rhizodont crossopterygian, *Pycnoctenion* gen. nov. (type species *P. siberiacus*), which is probably generically close to *Strepsodus*. As will be shown, genus *Pycnoctenion*, like *Strepsodus*, comprises large fishes possessing rather bulky dermal bones, and characterized by several structure

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[†] Numbers in curled brackets refer to original page numbers.

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peculiarities unique to the family, such as absence of cosmine in the integument, cycloid scales, intensive branching of the sensory canals in the skull and presence of a pair of tusks at the anterior end of the lower jaw.

Species assigned to *Pycnoctenion*, besides those from the Krasnoyarsk Region, are found in the USSR in Yakutia and Central Asia. They might be [conditionally] divided into two groups by the scale sculpture: with thicker or thinner ornament. The latter resemble the Australian "*Strepsodus*" species (*S. decipiens*) in this, indicating that the Australian forms may fit into *Pycnoctenion*.

The obvious similarity of the scales from a number of *Pycnoctenion* species from the USSR (*P. jacuticus*, *P. tuwensis*) with P. siberiacus makes grounds for the parallelization of the deposits in which they were found with the Nadaltay and Bystraya Formations of the Minusa Depressions. This can be confirmed by presence, alongside *Pycnoctenion*, in these deposits (especially in the Emyaksin Formation of Yakutia) of another typically Carboniferous genus of crossopterygian, *Rhizodopsis*, represented in Minusa by *R. savenkovi* Obruchev.

It is quite possible that the distribution of *Pycnoctenion*, like that of *Rhizodopsis*, is limited to the Carboniferous, and thus might be used for the correlation of Carboniferous deposits.

However, representatives of the family as a whole are probably distributed into the Devonian of USSR; this is in particular indicated by the finds of rhizodont-type scales in the Kokhay Formation of Kazakhstan, described below as *Propycnoctenion nephroides*.

{p 90} Order OSTEOLEPIFORMES

Family RHIZODONTlDAE Traquair, 1881

Genus *Pycnoctenion* Vorobyeva, gen. nov.

Etymology. Name from *pycnos* (Greek) = dense and *ctenion* (Greek) = crest.

Strepsodus (non Young, 1886): Woodward, 1906, p. 16, Pl. 7, Fig. 2, 3, 8; Khabakov, 1927, p. 303-305, Pl. 15, Fig. 4, 7, 10; Obruchev, 1954, p. 328, 329; 1955, p. 6, Pl. 26, Fig. 2; Vorobyeva, 1962, p. 216, Pl. C-27, Fig. 7; Vorobyeva and Obruchev, 1964, p. 297, Pl. IV, Fig. 5, 6 (*pars*).

Type species—*Strepsodus siberiacus* Chabacov, 1927, Lower Carboniferous, Bystraya Formation; Krasnoyarsk Region.

Diagnosis. Fishes with thin, strongly overlapping, rounded scales, covered with thin radial crests, not uncommonly subdivided into anterior and posterior sectors. The dermal skull bones have tuberculated or striated ornament. Large symphyseal bones seem to have been present. Large fang-shaped grasping tusks are situated at the anterior end of the lower jaws. The precoronoids are shifted to the anterior edge of the jaw. The precoronoid fossa is absent. The small, marginal teeth are gracile, with simple wall folding and a hollow pulp cavity. The tusks possess large folds at the base, often with lateral cutting edges on the upper half and complicated folding: the bone enters up to the end of the fold branches; the pulp cavity is filled with osteodentine bars.

The cleithrum has a high and narrow dorsal branch and may fuse with the clavicle. The clavicle possesses a well-developed ascending process.

Comparison. *Pycnoctenion* differs from other genera by dermal bone sculpturing, tooth shape (especially the presence of large folds at the base of the tusks) and some peculiarities of the shoulder girdle construction. By the scale structure it is the closest genus to *Strepsodus*, from which it differs by relatively thin and dense arrangement of crests on the non-overlap scale area, presence of osteodentine in the tooth pulp cavities, comparatively narrow dorsal process of the cleithrum and, [as appear], weak development of the dorsal plate.

Species list. Seven species: *Pycnoctenion decipiens* (Woodward, 1906); *P. rybinskensis* sp. nov.; *P. jacuticus* sp. nov.; *P. siberiacus* (Chabacov, 1927); *P. tuwensis* sp. nov.; *P. tuberculata* sp. nov.; *P. litvinovitschae* sp. nov.

Remarks. *Pycnoctenion* remains which are indeterminable at the specific level are known also from the Soros Formation (?Lower Carboniferous) of Yakutia.

Distribution. Lower Carboniferous, Tournaisian, Visean and Namurian; Australia, Western Siberia, Tuva, Yakutia, Kazakhstan.

Pycnoctenion siberiacus (Chabacov, 1927)
Fig. 1; Pl. IX, Fig. 1-7.

Strepsodus siberiacus: Khabakov, 1927, p. 303-305, Pl. 15, Fig. 4, 7, 10; Obruchev, 1954, p. 328, 329; 1955, p. 46, Pl. 26, Fig. 2; Vorobyeva, 1962, p. 216, Pl. C-27, Fig. 7; Vorobyeva and Obruchev, 1964, p. 297, Pl. 4, Fig. 5, 6 (*pars*).

Holotype. A scale; Minusa trough, Yenisey R., 5.5 km downstream from Kop village; Lower Carboniferous, upper part of the Bystraya Formation; Khabakov, 1927, Pl. 15, Fig. 4.

Description. The scales (Pl. IX, Fig. 5-7) are very thin; oval, rounded, ovoid or angular in shape, 7-10 mm long. The ossification center coincides with the geometrical one, or is displaced anteriorly. The internal surface is smooth or has a longitudinal crest at the center. The crest may be short or constitute up to half the scale length. {p 91} 8-13 concentric lines run round the scale, each 28-31 mm long. The anterior and posterior sectors of the external surface are covered with thin, sharp-tipped crests arranged in radial rows, projecting from the ossification center. Each sector makes up from 1/5 to 1/2 of the scale surface, usually about 1/3. The anterior sector is covered with straight or, less often, slightly meandering crests. The posterior sector has coarser crests (1.5 times wider), wound along, sometimes bifurcating or insignificantly diverging at the periphery, becoming thinner towards the center. Due to branching, the number of crests varies posteriorly from 70 to 200; only rarely does it not exceed 50. The width of the furrows

between the crests is usually equal to the crest thickness, but may be 3-4 times thicker. The furrows may expand towards the periphery. The transitional zone between sectors is covered with concentric rows of crests, bearing tubercles and anastomosing between each other forming a network.

The squamosal (Pl. IX, Fig. 2) is comparatively long, attaining its maximum depth posteriorly, where it is 1.5 times longer than deep. Its ossification center is displaced to the dorsal half, the jugular line canal (cju) is slightly bent. Judging by the bone configuration and contact notches for the postorbital (iPo), maxilla (iMx) and jugal (iJu), the first two bones are rather deep, the third one is low. The maxilla had an abrupt and deep posterior edge.

The lower jaw is represented by a fragment from the precoronoid region, sculptured with longitudinally extended anastomosing crests forming a small network and striated ornament.

The tusks (Pl. IX, Fig. 1) are up to 20 mm high have a basal diameter of about 10-12 mm. They are straight or slightly recurved, rounded in cross section and thick-walled. The lower half bears wide, rounded, strongly convex longitudinal crests. The lower third is covered with bony matter.

The marginal teeth have no visible folds on the outside and are bent slightly inwards. The ratio of height to basal diameter is about 1:3. The microstructure of the large marginal teeth base (diameter 6-7 mm) and tusks (diameter 10-11 mm) is similar and differs only in the number of main folds on the perimeter (14-15 and 25-28 respectively). The main folds are divided at the end by moderately wide bony bars (fig. 1), which penetrate into all the lateral branches of the folds. From the periphery the folds are often subdivided into two or three and the bony bars (zn) penetrate inside the crevices between them up to 1/3 the length of the main fold. The lateral branches of the main folds vary in number (usually from 4 up to 8) and are sometimes barely discernible. Occasionally they bear secondary branches, though no more than two. The pulp cavity is filled at the base of the larger marginal teeth and tusks by osteodentine bars, from 1/5 to 1/3 the diameter of the tooth. Thick osteodentine plates (os), surrounding the cavity are distinct in the upper folded half of the teeth. The ascending process of the cleithrum is narrow and slightly shorter than the ventral plate, fusing with clavicle anteriorly.

Size. Specimen PIN # 784/2: squamosal length - 70 mm.

Distribution. Lower Carboniferous, Tournaisian; Krasnoyarsk Region, Bystraya, Altay and Nadaltay Formations of the Minusa trough.

Material. More than 100 scales, dermal skull, shoulder girdle bones and teeth from a number of sites in the Minusa trough: Abakan River, Kamyshta Creek; Northern Minusa, Iltekovka village; the right bank of the Yenisey close to Igrysh village; Medvedskoye and Krivenskoye villages; the right bank of Yenisey, Oskin Klyuch Creek; the right bank of Chulym River, Syr River, Tryasuchaya River; collected by various geological crews, coll. PIN # 784, 781. The most complete material occurs from Iltekovka village site, Collected by V. S. Meleshchenko.

{p 92} *Pycnoctenion rybinskensis* Vorobyeva, sp. nov.

Pl. X, Fig. 6

Etymology. Named after a site in the Rybinsk depression.

Holotype. A scale, PIN # 1741/23; Krasnoyarsk Region, North-east margin of the Rybinsk depression close to Malaya Kamala village; Lower Carboniferous, the upper part of Charga–?lower part of the Krasnogoryevskaya Formation; Pl. X, Fig. 6.

Description. The scales are moderately thin, rounded, heart-shaped or ovoid, 13-25 mm in diameter. The center of ossification coincides with the geometric one, or is shifted forwards. A longitudinal crest corresponds to it on the internal side of the scale.

Up to 16 incremental lines may be counted on the scales measuring 23 mm in diameter. The posterior sector has its apex slightly behind the ossification center; it occupies about 1/5-1/4 of the scale surface and is equal to or half the size of the anterior surface. Their are 30-34 crests, slightly wound up with smooth tops, occasionally

branchy or faltering, sometimes anastomosing; the more lateral crests are shorter and simpler. The furrow width is usually 1.5 times more than the crest thickness or is equal to it. The anterior sector is less pronounced, ornamented with thin radial tuberculated crests. The sectors are divided by a stripe of striated/concentric crests, forming a networked ornament.

Size (holotype). Scale length - 30 mm.

Comparison. Differs from the type species *P. siberiacus* in having more rough crests, comparatively smaller in number on the non-overlapped surface and absence of tubercles over them.

{p 93} **Remarks**. The number of crests on the posterior sector of the scale approaches that of some species of *Strepsodus* from the Lower Carboniferous of Northern America—*S. dawsoni* Hay and *S. hardingi* (Dawson).

Material. About 20 scales from the type locality, coll. PIN # 1741.

Pycnoctenion jacuticus Vorobyeva sp. nov.
Fig. 2; Pl. X, Fig. 1-4; Pl. XI, Fig. 1.

Etymology. Named after its location in Yakutia.

Holotype. PIN # 2805/100, lower jaw; Yakutia, left bank of the Viluy River, 150 m downstream from the mouth of Onkuchakh Creek; ?Lower Carboniferous, upper part of the Emyaksin Formation; fig. 2; Pl. X, Fig. 4.

Description. The scales are thin, rounded or slightly elongated, 10-16 mm in diameter; the ossification center is usually shifted to the posterior half. The internal surface is smooth or bears a longitudinal median ledge, which equals up to 1/3 of the scale length.

The external side is completely covered with radial crests, the non-overlapped surface constitutes less than 1/3 of the total scale area and is represented by a wide, short posterior sector with its apex behind the ossification center. This sector is sculptured by thin, low, sometimes faltering crests with smooth sharp-edged tops, and which meander and branch only slightly. The total number of crests does not exceed 40. The furrows between the crests are 2 - 2.5 times wider than the crests. The anterior sector makes up about 1/3-1/2 of the total surface, not always clearly defined and covered with straight or, less often, slightly meandering crests, being about three times thinner than those in the posterior sector. The crests are divided by thin furrows, with widths equal to or slightly less than their thickness, and are covered with small, conical tubercles, which sometimes fuse with their bases. Incremental lines are well traced on both scale surfaces.

The lower jaw (Fig. 2; Pl. X, Fig. 4) is rather short; it is 4.5 times longer than deep. The dentary forms the larger part of the anterior jaw edge and bears a wide overlap surface for the symphyseal bones. The anterior process of the precoronoid almost reaches the anterior margin of the dentary. The intercoronoid fossa is small. The vertical coronoid laminae do not project above the dentary oral edge.

The maxilla (fig. 2) is deep; it is 4 times longer than deep in the middle. The posterior edge is long and slightly convex.

Teeth. The tooth apices are recurved or sometimes straight (Pl. X, Fig. 3), with a smooth surface. Lateral cutting edges are usually present on the upper half of the tusks and give their tips a blade-like appearance. The tooth walls are thick on top, become slightly thinner towards the proximal third. The lower two thirds of the wall bare large, often double folds. In the middle of the folds crests may be observed, which turn into sharp edges at the apex. {p 94} The folds strongly diverge at the tusk base; the bony bars between them are wide and [situated in several files] (Pl. XI, Fig. 1).

The sculpturing on the lower jaw (fig. 2) consists of separate tubercles and on the cleithrum consists of long wound up crests with smooth tops.

Size (holotype). The lower jaw length is 80 mm.

Comparison. In scale structure this species is closest to *P. rybinskensis*, from which it differs by thinner and larger overlapped scales and the posterior position of ossification centers. It differs from other species by the absence of tubercles on the crests of the posterior sector as well as possessing large overlap areas. It differs from the type species in the characters listed above and also by the smaller quantity of the crests, wider protrusion of the bone between the tooth folds and the tuberculated sculpturing of the lower jaw bones.

Material. Besides the holotype, about 20 scales and isolated teeth from the type site, collected by G. S. Fradkin, V. V. Menner and the author, coll. PIN # 2847. Also 15 scales from Viliuy River, Emyaksin-Khayata locality, collected by A. T. Averchenko, coll. PIN # 2845.

Pycnoctenion tuwensis Vorobyeva, sp. nov.

Pl. XI, Fig. 2.

Etymology. Named for its location in Tuva.

Holotype. PIN # 789/2; scale; North-east Tuva, right bank of the Yenisey River, 180 m upstream from Seyba village, site number 1002; Lower Carboniferous, Tournaisian, Suglugkhem Formation; Pl. XI, Fig. 2.

Description. The scales are 3.5 to 30 mm long, and of angular, rounded, ovoid or oval shape. The ossification center is usually shifted forwards and a short ledge corresponds to it at the internal surface. Concentric incremental lines are widely spaced (7 rings on the scale attaining 30 mm in diameter) and interrupt on some scales the ornament crests of the non-overlapped surface. The anterior ornamented sector proceeds from the scale center, is not always distinct and may occupy up to 1/4 of the non-overlapped surface. The posterior sector is covered with much rougher, tuberculated and insignificantly

wound, sometimes branching crests. It occupies 1/5-1/4 of the scale surface. 30-35 crests may be counted on its posterior edge, the grooves being twice as wide as the crests.

Teeth. There is a large, poorly preserved upper part of a tusk; its outer surface bears rough crests almost to the top.

Size (holotype). Scale length 30 mm.

Comparison. The scale structure is most similar to *Pycnoctenion siberiacus*, from which it differs by a smaller number of crests on the non-overlapped surface, larger scale dimensions and, judging by number of incremental rings, also, probably, by a greater vertical extent of the tooth folding.

Distribution. Lower Carboniferous, Tournaisian, Suglugkhem Formation; North-east and central Tuva.

Material. About 20 scales and a tusk from the type locality; 10 scales from the territory of central Tuva, Kherbes, collected by the Chulym-Yenisey field crew, coll. PIN # 789.

Pycnoctenion tuberculata Vorobyeva, sp. nov.
Pl. XI,. Fig. 6.

Etymology. Name from *tuberculum* (Latin) - tubercle.

Holotype. PIN # 2879/3, scale; Western part of central Kazakhstan, Karaganda Region, Jezkazgan-Ulut precinct, Zhilandy River area, 3 km upstream from the Aktma creek inlet; Lower Carboniferous, Middle Visean, Yagovkinian Regional Stage.

Description. The scales are thin, rounded, oval or ovoid in shape and a diameter range within 13-47 mm. The ossification center coincides with the geometrical one or is shifted

forwards or, less often, backwards. {p 95} A median ledge is usually found on the internal surface, often located on the posterior half of the scale; sometimes the surface is smooth. There are 9 incremental lines on a scale 16 mm in diameter, about 25 on one 47 mm in diameter. The external surface is entirely covered with thin-wound radial crests, tuberculated on their tops. On the anterior, larger part these crests are crossed by concentric crests of a similar structure, causing the sculpture to becomes pitted. Some scales show surface subdivision into anterior and posterior sectors, the former constituting about 1/3 of the total scale surface area. The thin crests of this sector are covered by high tubercles with pointed tips, the thickness of which surpasses the width of the grooves between them. The number of crests is never less than 90-100.

Sizes. Scale length 15-23 mm.

Comparison. Similar to the type species *Pycnoctenion siberiacus*, differing from it by a less-expressed or absent anterior sector of radial crests, the pitted ornament of the overlap surface and the comparatively thin crests of the non-overlap surface. It is also similar to the Australian *P. decipiens*, from which differs by narrower crests of the posterior sector, which are not interrupted by incremental lines.

Distribution. Lower Carboniferous, Middle Visean, Yagovkinian Regional Stage, Central Kazakhstan.

Material. About 15 scales from the type locality, collected by A. B. Veimarn, coll. PIN # 2879.

Pycnoctenion litvinovitschae H. Obrucheva, sp. nov.

Pl. XI, Fig. 5, 7.

Etymology. Named after the geologist N. V. Litvinovich, who discovered the fish fauna by the Kypshak River.

Holotype. MSU 230/21, incomplete scale; Western part of Central Kazakhstan, Tselinograd Region, Southern edge of the Tengiz trough, Kypshak River; Lower Carboniferous, Upper Visean, Dalnian Regional Stage.

Description. The scales are slightly oval or rounded, with a maximum diameter of 20-32 mm and are thin. The center of ossification coincides with the geometrical one and bears an elongated flat tubercle. Incremental lines are distinctly visible. The overlap surface has radial and concentric rows of tuberculated crests. The tubercles are low and extended radially, with blunter tops closer to the non-overlap surface, fusing into short crests. The non-overlap surface forms a sector, occupying about 1/3 of the total scale surface. It is covered with slightly wavy, thin radial crests, formed by fused tubercles, not exceeding in width the tubercles of the overlap surface. The total number of crests on the non-overlap sector is around 100. The dermal bone sculpture on the lower jaw fragment consists of elongated tubercles and short crests of differing thickness, forming a striated ornament.

The teeth are large (11-12 mm high) and comparatively thin, with straight apices, four times higher than the thickness at the base. The walls bear rough flattened folds, extending almost to the top. The pulp cavity is large (Pl. XI, Fig. 7).

Sizes (holotype). Reconstructed scale size is about 20-24 mm.

Comparison. This species is close to *Pycnoctenion tuberculata*, from which differs by the blunt and elongated shape of tubercles on the crests and the absence of distinct tubercles on the posterior sector.

{p 96} **Remarks**. Taking into account the small quantity and poor preservation of the material from Kypshak it might be possible that the distinctions between *P. litvinovitschae* and *P. tuberculata* are due partly to the scales coming from a different position on the body and partly to the greater abrasion of the scales from Kypshak (producing blunt tubercle tops). We provisionally ascribe scales and a fragment of jaw from the Namurian (Baleut Regional Stage) of Jezkazgan to *Pycnoctenion*

litvinovitschae. However, these scales differ by their more elongated shape (d1/d2 = 1.6) and the posterior position of the ossification center (and thus the boss on the internal surface) and may therefore belong to a new species.

Distribution. Lower Carboniferous, Upper Visean (Dalnian Regional Stage) and, probably, Namurian (Baleutian Regional Stage) of Central Kazakhstan.

Material. Besides the holotype, their are samples containing isolated scales and fragments of jaw and teeth from the Namurian deposits, Jezkazgan precinct, collected by L. I. Kononova, coll. PIN # 2879.

Pycnoctenion sp.

Pl. XI, Fig. 3-4.

Description. The scales are thin and rounded, with a diameter of 25 mm. Incremental lines are seen distinctly on the internal surface (up to 8 circles on a scale of 24 mm diameter) and a median longitudinal crest is present. The posterior sculptured sector occupies 1/3 of the scale surface, and its angle coincides with ossification center; that is, shifted forwards. The sector is covered by closely spaced, thin, wavy, radial crests (no less than 50 on the posterior edge of the sector). However, because of the poor state of preservation, the details of the crest structure remain unclear. The anterior crest sector is not distinctly demarcated. An available fragment of a tusk is characterized by a base with large folds and smooth, striated apex.

Comparison. The described scale differs from the scales of *Pycnoctenion jacuticus* by the anterior position of the ossification center, the smaller degree of overlap and the thinner and more closely spaced crest ornament on the non-overlap surface. In this it approaches the scales of *P. siberiacus* and *P. rybinskensis*, although it differs from them by the absence of an expressed anterior sector of radial crests. In this last feature it is

similar to *P. litvinovitschae*, although it differs from it in the smaller number of crests on the posterior scale edge and in some details of the tooth structure.

Material. About 20 poorly preserved scales, prepared predominantly on the internal side; Yakutia, Kempendyay trough at the mouth of the Soros River, or 1-3.5 km upstream from the mouth of Este'ekh River; Soros Formation; collected by K. Kolodeznikov, G. S. Fradkin, coll. PIN # 2842, 2805.

Genus *Propycnoctenion* Vorobyeva, gen. nov.

Etymology. Named after the genus *Pycnoctenion*.

Type species—*Propycnoctenion nephroides* Vorobyeva, 1975; Upper Devonian, Kokhay Formation of Southern Kazakhstan.

Diagnosis. The scales are thin, rounded, not uncommonly with a notch at the anterior edge (i.e. reniform) and strongly overlapping. The non-overlap surface is covered with thin radial crests, the overlap surface with concentric crests.

Comparison. Apparently close to *Pycnoctenion*, from which it differs by the absence of radial crests on the overlap surface and presence of a notch at the anterior scale edge.

The genus is monotypic.

{p 97} *Propycnoctenion nephroides* Vorobyeva, sp. nov.

Pl. X, Fig. 5.

Etymology. Name derived from *nephros* (Greek) = kidney.

Holotype. PIN # 789/11, scale; Southern Kazakhstan, Northwest ramifications of the Kara-Tau mountain range; Kzyl-Dzhar Mountain; Upper Devonian, Kokhay Formation.

Description. The scales are 15-40 mm in diameter and rounded or shortened rostro-caudally. The center of ossification is usually strongly displaced backwards. The extent of the non-overlap surface arch makes from 1/7 up to 1/4 of the scale perimeter. The crests covering it are simple, with tuberculated tops and are separated by very thin grooves, their number varying from 4 to 50. The notch at the anterior edge often proceeds onto the internal surface with a furrow, partly occupied with the longitudinal median crest. The thin crests on the overlap surface are parallel with smooth tops bent backwards, following the notch edge. Incremental lines are visible on both sides of scales.

Size (holotype). Scale length 23 mm.

Material. About 20 scales from the type locality, coll. PIN # 789.

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Plate captions

Plate IX

Fig. 1-7. *Pycnoctenion siberiacus* (Chabakov). 1 – PIN # 784/1 (x 2), premaxillary tusks; 2 – # 784/2, squamosal, imprint; 3, 4 – # 784/3-4, cleithrum and clavicle, imprints; 5 – # 784/5 (x 2), scale; North Minusa, Iltekovka Village; Lower Carboniferous, Nadaltay Formation; 6 – # 781/98 (x 3), scale; Minusa, Chulym River, Igrysh Village; 7 – # 781/99 (x 3) scale; Minusa, Oskin Creek; Lower Carboniferous, Bystraya Formation.

Plate X.

Fig. 1-4. *Pycnoctenion jacuticus* gen. et sp. nov. 1 – # 2805/101 (x 1.5), cleithrum fragment; Yakutia, Ygyatan trough, left bank of Viluy River, Onkuchakh; ?Lower Carboniferous, upper part of Emyaksin Formation; 2 – # 2845/52 (x 3), scale, Yakutia, Emyaksin-Khayata; 3 – # 2848/2 (x 2.5), tusk; 4 – holotype, # 2805/100, jaws; Onkuchakh.

Fig. 5. *Propycnoctenion nephroides* gen. et sp. nov., MSU | 103/93 (x 3), scale; South Kazakhstan, Northwest ramifications of Kara-Tau mountain range, Kzyl-Dzhar Mountain; Upper Devonian, Kokhay Formation.

Fig. 6. *Pycnoctenion rybinskensis* gen. et sp. nov., holotype PIN # 1741/23 (x 2), scale; Krasnoyarsk Region, Rybinsk trough, Malaya Kamala Village; Lower Carboniferous, Charga Formation.

Plate XI

Fig. 1. *Pycnoctenion jacuticus* gen. et sp. nov. A fragment of a thin section of the tusk base (x 50) coll. PIN # 2847; Yakutia, Ygyatan trough, Onkuchakh; ?Lower Carboniferous, upper part of Emyaksin Formation.

Fig. 2. *Pycnoctenion tuwensis* gen. et sp. nov., holotype PIN # 789/2, scale (x 3); Northeast Tuva, right bank of Yenisey River, 180 m upstream from Seyba; Lower Carboniferous, Suglugkhem Formation.

Fig. 3-4. *Pycnoctenion* sp., Yakutia, Kempendyay trough, Soros River, 1 km upstream from the mouth of Este'ekh River; ?Lower Carboniferous, Soros Formation; 3 - PIN # 2842/3-3a (x 2), scale; 4 – PIN # 2842/4 (x 4), tusk apex.

Fig. 5. *Pycnoctenion litvinovitschae* E. Obrucheva sp. nov., scale (x 2), MSU # 230/21; Central Kazakhstan, Tengiz trough, Kypshak River, Lower Carboniferous, Upper Visean, Dalnian Regional Stage.

Fig. 6. *Pycnoctenion tuberculata* gen. et sp. nov., holotype, PIN # 2879/3 (x 3), scale; Central Kazakhstan, Zhilanda River close to Aktma; Lower Carboniferous, Middle Visean.

Fig. 7. *Pycnoctenion litvinovitschae* sp. nov., PIN # 2879/4 (x 4), teeth; Central Kazakhstan, Tengiz trough, Kypshak River; Upper Visean, Dalnian Regional Stage.

Figure captions

Fig. 1. *Pycnoctenion siberiacus* (Chabakov); microstructure of marginal jaw tooth, diameter (d) 7 mm (x 14); Krasnoyarsk Region, North Minusa, Iltekovka; Lower Carboniferous, Tournaisian, Nadaltay Formation. Zn – bony bars; os – osteodentine in the pulp cavity.

Fig. 2. *Pycnoctenion jacuticus* sp. nov.; holotype, PIN # 2805/100 (x 1): a – lower jaw in medial view; b – jaw in external view; Yakutia, left bank of Viliuy River 150 m downstream from the mouth of Onkuchakh Creek; Lower Carboniferous, upper part of Emyaksin Formation. De – dentary; Dz – anterior grasping teeth; Mx – maxilla, Prc – precoronoid; od Sy – overlap area for the symphyseal bones.