

## EARLY PERMIAN CHONDRICHTHYANS OF THE MIDDLE AND SOUTH URALS

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**ABSTRACT** – Very diverse Early Permian chondrichthyan assemblages occur in the Asselian to Artinskian of the Middle and South Urals. They include numerous symmoriid teeth of “*Denaea*” *decora* Ivanov, *Cobelodus obliquus* sp. nov., *Stethacanthus* and *Denaea*; the teeth of the ctenacanthoid *Heslerodus*; the teeth of the synechodontiform *Synechodus antiquus* sp. nov.; and the teeth of taxa of doubtful affinities – *Adamantina foliacea* Ivanov, *Cooleyella* cf. *C. fordi* (Duffin & Ward), *Cooleyella* sp. A., as well the scales and denticles of various types. Two new species, *Cobelodus obliquus* and *Synechodus antiquus*, are described herein. The Early Permian chondrichthyan assemblages of Urals include a few taxa occurring only in that interval, as well taxa which were distributed in the Carboniferous and persisted into the Early Permian, such as *Stethacanthus*, *Cobelodus*, *Denaea*, “*Denaea*”, *Lissodus*, *Heslerodus*, “*Symmorium*”, *Petalodus*, *Cooleyella* and *Adamantina*. This occurrence of a synechodontid is the oldest in the world. The symmoriid sharks disappeared in the Middle Permian. The Permian shark faunas of the Urals contain a diverse assemblage of symmoriids, ctenacanthoids and synechodontiforms, but there are no xenacanthids were common in the Permian assemblages of Western Europe and North America.

**Key words:** Early Permian, chondrichthyans, Urals, Russia.

**RESUMO** – Assembléias muito diversificadas de condrictes do Permiano inferior ocorrem no Asseliano ao Artinskiano dos Urais Central e Sul. Elas incluem numerosos dentes simorídeos de “*Denaea*” *decora* Ivanov, *Cobelodus obliquus* sp. nov., *Stethacanthus* and *Denaea*; dentes do ctenacantóide *Heslerodus*; dentes do sinecodontiformes *Synechodus antiquus* sp. nov.; dentes de taxa de afinidades incertas: *Adamantina foliacea* Ivanov, *Cooleyella* cf. *fordi* (Duffin & Ward), *Cooleyella* sp. A, bem como escamas e denticulos de vários tipos. Duas espécies novas, *Cobelodus obliquus* e *Synechodus antiquus* são aqui descritos. A assembléia de condrictes do Permiano inferior dos Urais inclui, também, uns poucos táxons que ocorrem apenas naquele intervalo, além de alguns que já estavam presentes durante o Carbonífero e persistiram no Permiano inferior, tais como *Stethacanthus*, *Cobelodus*, *Denaea*, “*Denaea*”, *Lissodus*, *Heslerodus*, “*Symmorium*”, *Petalodus*, *Cooleyella* e *Adamantina*. A ocorrência de um sinecodontídeo é a mais antiga do mundo. Os tubarões simorídeos desapareceram no Permiano médio. A fauna permiana de tubarões dos Urais contém uma diversificada assembléia de simorídeos, ctenacantos e sinecodontiformes, mas nenhum xenacantídeo, que, por sua vez, eram comuns nas assembléias permianas da Europa ocidental e da América do Norte.

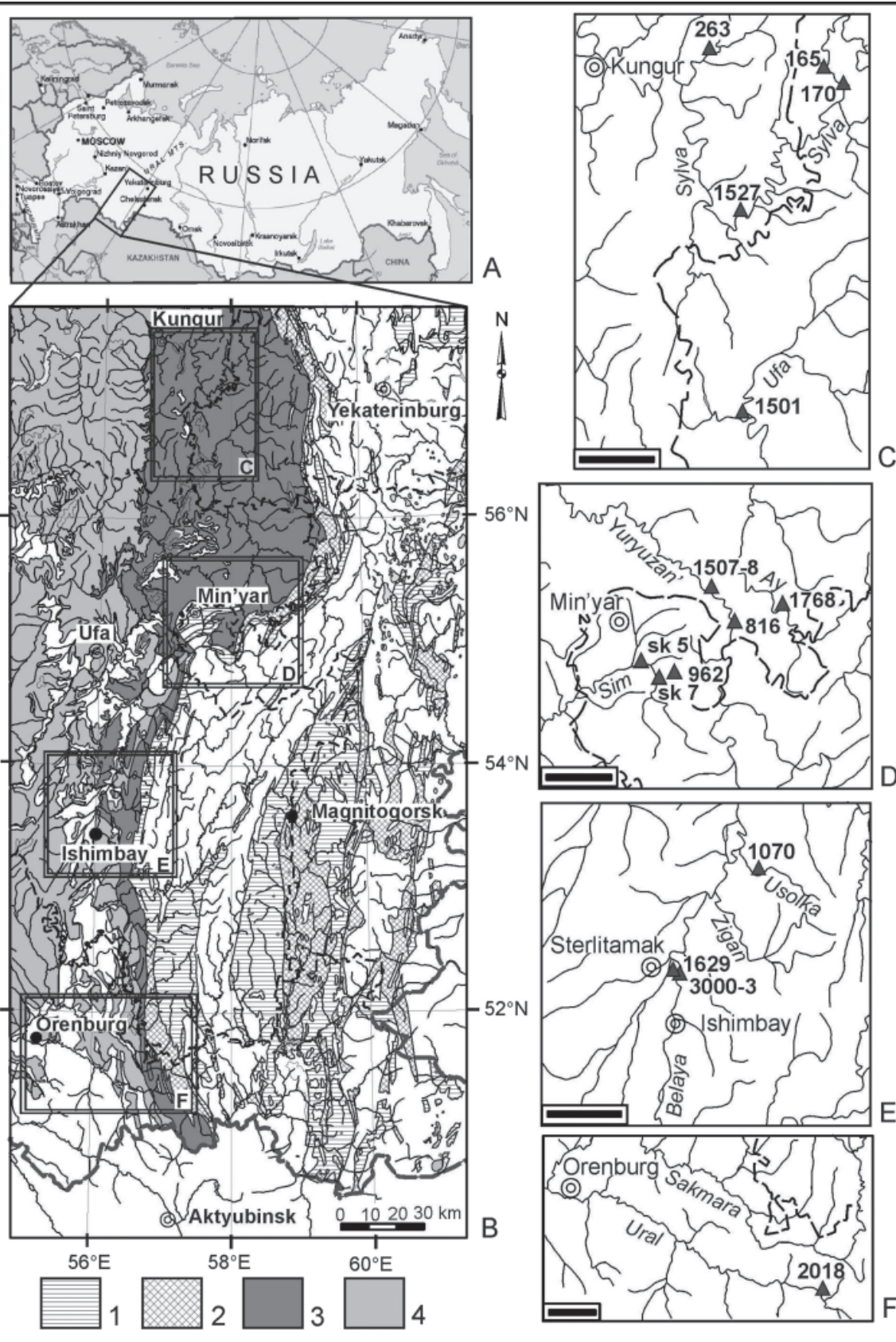
**Palavras-chave:** Permiano inferior, condricties, Rússia.

### INTRODUCTION

The Permian chondrichthyans of Russia have not been adequately studied, especially the occurrence of Early Permian sharks was mentioned rare. A preliminary analysis of taxon distribution was recently reported by the author (Ivanov, 2000). The abundant and taxonomically diverse chondrichthyan assemblages were found in the Early Permian interval from Asselian to Artinskian of the Middle and South Urals. The studied material was obtained from dissolved samples collected for conodonts, which allowed the precise stratigraphic level of the samples to be defined. The specimens are housed in the Palaeontological Museum of St. Petersburg University (PM SPU).

### LOCALITY INFORMATION

The localities of Early Permian chondrichthyans in the Middle and South Urals are distributed within the Pre-Uralian foredeep: in the Sylva, Yuryuzan'-Ay, Belaya and Aktyubinsk depressions (Figure 1). The shark remains as well abundant marine invertebrates occur largely in the carbonate deposits of six regional stages (R. S.): Kholodny Log (Asselian), Tastuba and Sterlitamak (Sakmarian), Burtsevka, Irgina and Sarga (Artinskian). The chondrichthyan assemblages observed herein come from the following sections:



**Figure 1.** A, General location of area; B, Geological map showing four regions where studied material was collected: 1, Devonian; 2, Carboniferous; 3, Early; 4, Late Permian rocks; C-F, maps of the Early Permian chondrichthyan localities: Middle (C) and South (D-F) Urals. Scale bars = 10 km (C-F).

**Middle Urals**

**Section 165.** Sverdlovsk District, Sylva River, right bank, 3 km north of Platonovo village; the chondrichthyan remains are found in the nodular limestones of Sarga R. S., Artinskian.

**Section 170.** Sverdlovsk District, Sylva River, left bank, 2 km downstream of Platonovo village; the chondrichthyan remains are found in the nodular limestones of Sarga R. S., Artinskian.

**Section 263.** Perm' District, Barda River (right affluent of the Sylva River), right bank, near Voskresensy village; the chondrichthyan remains are found in the nodular limestones of Sarga R. S., Artinskian.

**Section 1501.** Sverdlovsk District, Ufa River, upstream from Krasnoufimsk, near Sarana village; the chondrichthyan remains are found in the detrital limestones of Sarga R. S., Artinskian.

**Section 1527.** Perm' District, Sylva River Basin, Chikalinsk quarry; the chondrichthyan remains are found in the reef limestones of Sarga R. S., Artinskian.

**South Urals**

**Section 816.** Bashkortostan, Yuryuzan' River, right bank, near Musatovo village; the chondrichthyan remains are found in the marls and detrital limestones of Irgina R. S., Artinskian.

**Section 962** (= sk 3). Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim town in the direction of Chelyabinsk; the chondrichthyan remains are found in the silt marls and carbonate nodules of Sterlitamak R.S., Sakmarian.

**Section 1070.** Bashkortostan, Dal'niy Tyul'kas Creek (left affluent of the Usolka River), southward from Krasnousol'sk; the chondrichthyan remains are found in the marls and detrital limestones of Burtsevka and Irgina R. Stages, Artinskian.

**Sections 1507, 1508.** Bashkortostan, road cut of Chulpan – Mesyagutovo, near Maloyaz; the chondrichthyan remains are found in the detrital limestones of Tastuba R.S., Sakmarian.

**Section 1629.** Bashkortostan, Belaya River, near Sterlitamak, 300 m northward from Tra-Tau Hill (“shikhan”), the chondrichthyan remains are found in the clay-rich limestones and marls of Sarga R.S., Artinskian.

**Section 1768.** Bashkortostan, Ay River, right bank, 0.5 km from Anzyak Creek entry to upstream; the chondrichthyan remains are found in the limestones and marls of Sarga R.S., Artinskian.

**Section 2018.** Orenburg District, Ural River, right bank, 2 km west northward from Nikol'skoe village; the chondrichthyan remains are found in the sandy and clayish limestones of Kholodny Log R.S., Asselian.

**Sections 3000-3003.** Bashkortostan, Belaya River, near Sterlitamak, 300 m northward from Tra-Tau Hill; the chondrichthyan remains are found in the reef limestones of Sakmarian, Sterlitamak R.S., Sakmarian.

**Section sk 5.** Chelyabinsk District, , road cut of Sim – Min'yar, 1 km western of Simskaya station; the chondrichthyan remains are found in the detrital limestones of Tastuba R.S., Sakmarian.

**Section sk 7.** Chelyabinsk District, Sim River, right bank,

near Sim town; the chondrichthyan remains are found in the nodular limestones of Tastuba R.S., Sakmarian.

The detailed description of most of the sections above cited is given by Chuvashov *et al.*, 1990, Davydov & Popov, 1991, and Shamov *et al.*, 1995.

**CHONDRICHTHYAN FAUNA**

The chondrichthyans are represented by the isolated teeth, scales, denticles and the fragment of a hybodontoid spine. Most of the microremains are well preserved; the tissues of the teeth and scales of several localities are practically unchanged and completely transparent (Figure 4). The distribution of taxa is given in the Table.

Teeth have been assigned to the symmoriid *Cobelodus obliquus* sp. nov., *Stethacanthus* sp., *Danaea* sp., “*Danaea*” *decora* Ivanov; the ctenacanthoid *Heslerodus* sp., the synechodontiform *Synechodus antiquus* sp. nov.; the indeterminate hybodontoid, as well to the taxa of doubtful affinities – *Adamantina foliacea* Ivanov, *Adamantina* sp., *Cooleyella* cf. *C. fordi* (Duffin & Ward), *Cooleyella* sp. A. “*Danaea*” *decora* (Figure 3K-P) and *Adamantina foliacea* (Figure 3J) are described in detail by author from the Early Permian of Middle and South Urals (Ivanov, 1999). The description of the new taxa, *Cobelodus obliquus* and *Synechodus antiquus*, are presented below.

The *Danaea* teeth from the Kholodny Log Regional Stage (section 2018) are distinctly similar to the teeth of typical representative of the genus, such as type-species *Danaeaournieri* Pruvost (author's study of original collection), *Danaea* sp. (Savitskiy *et al.*, 2000) and others. These teeth are characterised by a cladodont crown bearing long slender cusps, surrounding a triangular base. The cusps are rounded in the cross section and recurved lingually; the lateral and intermediate cusps are almost equal in height. The base has convex occlusal and slightly concave basal sides and bears a single small, distinct, prominent, round button on the lingual edge of occlusal side, and one small labio-basal tubercle. The foramina of the main vascular canal are present on the button edge and in the centre of basal surface. These teeth differ greatly from the teeth of “*Danaea*” *decora* (Ivanov, 1999) and “*D.*” *meccaensis* (Williams, 1985) in another type of the tooth connection system (Ivanov, 1997, 2001).

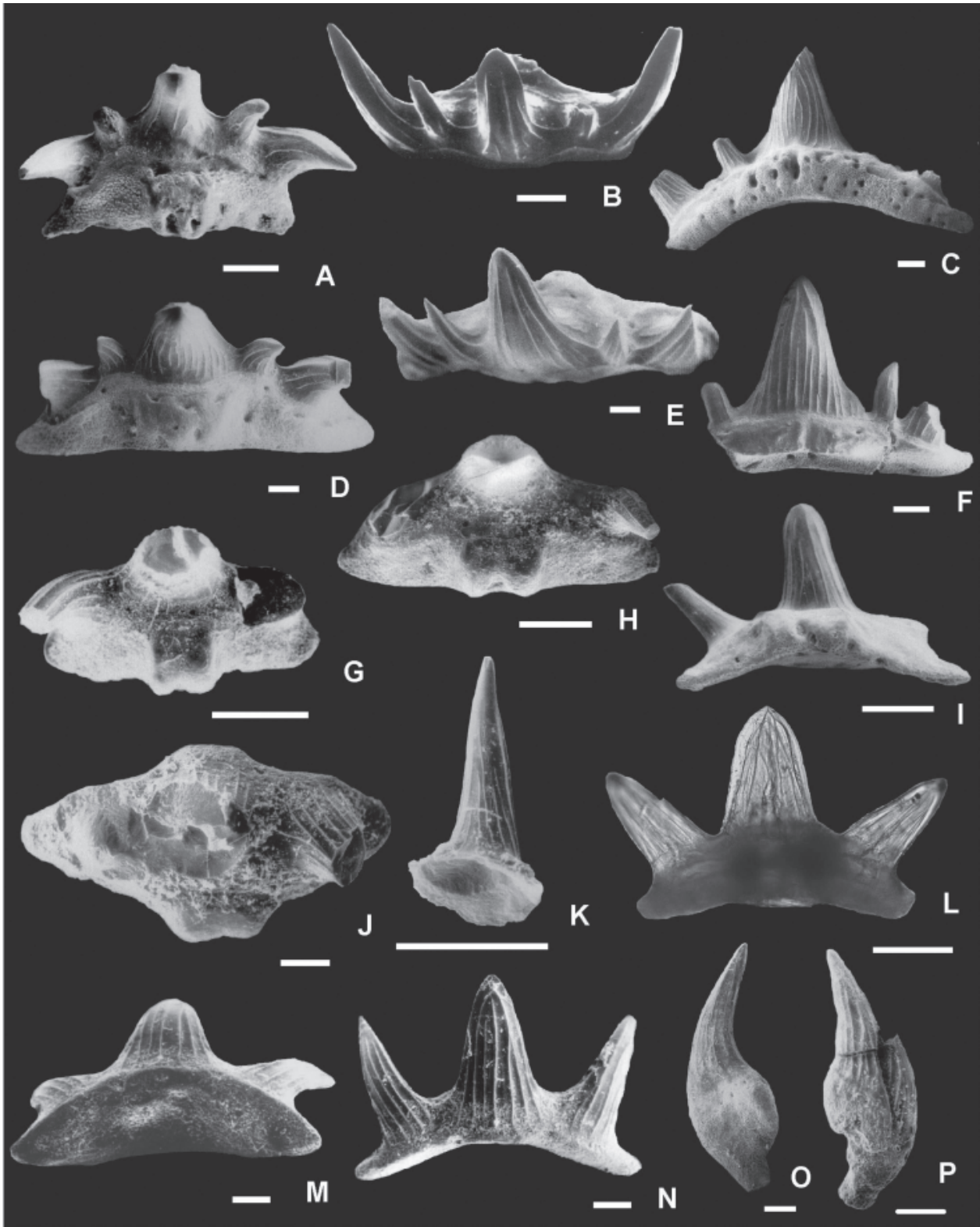
The tooth of *Stethacanthus* from the Burtsevka Regional Stage (section 1070) is similar to teeth of *Stethacanthus altonensis* (St. John & Worthen, 1875) but differ in the slight extension of lingual torus and the distal position of the button.

The *Heslerodus* teeth from the Kholodny Log and Sarga Regional Stages (sections 165, 1768 and 2018) have a crown structure typical for teeth of *H. divergens* (Trautschold) redescribed by Ginter (2002) but the base is practically flat and the labio-basal projections are not developed.

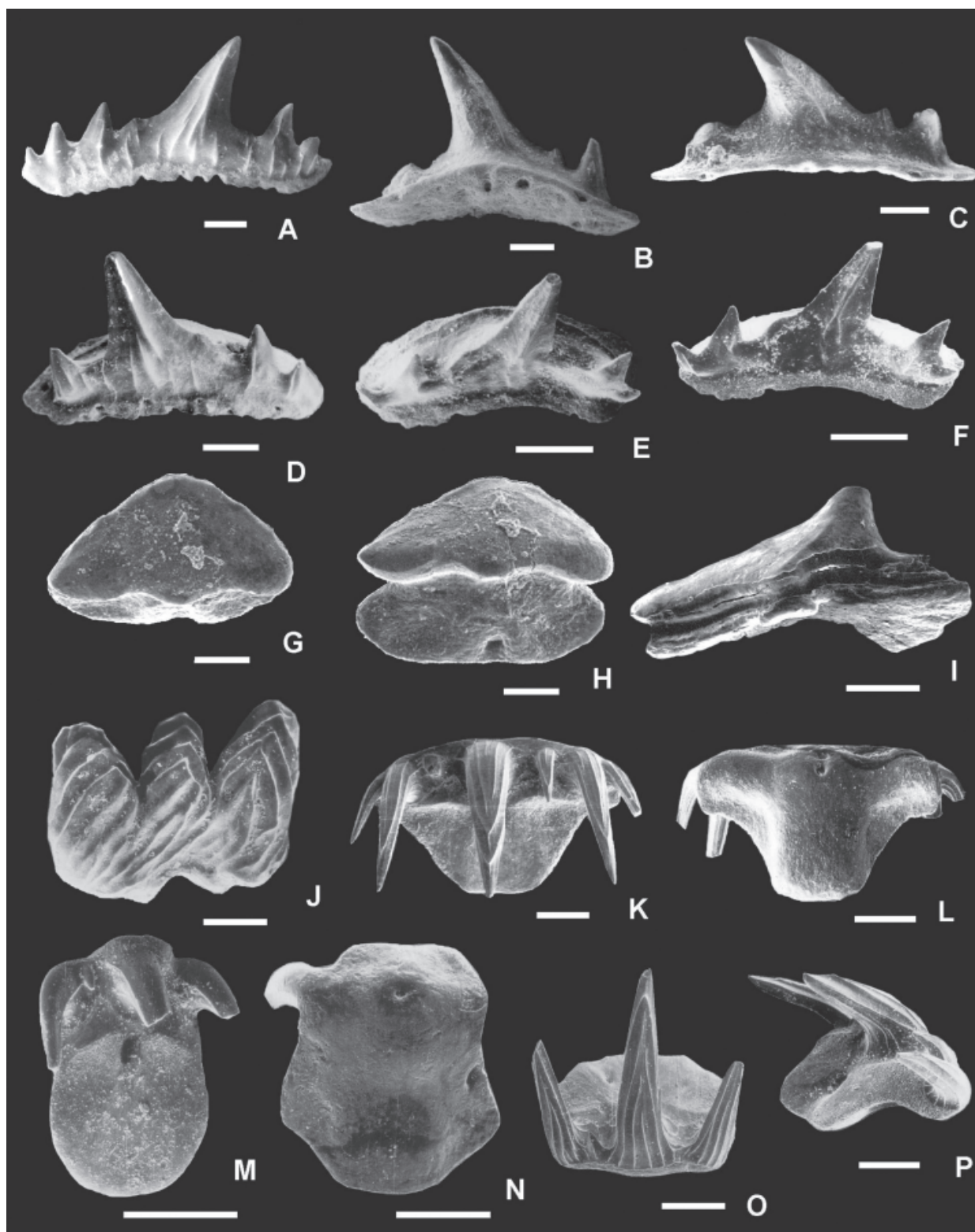
The teeth occurring in the Sarga Regional Stage (section 1501) and belonging to *Adamantina* possess well-developed labio-basal tubercles, a shallow labial depression, and a five-cusped crown with smooth labial side.

The teeth of *Cooleyella* cf. *C. fordi* from the Irgina and





**Figure 2.** A-L, *Cobelodus obliquus* sp. nov., teeth; A-B, holotype, PM SPU 39-1. A, occlusal and B, oblique labial views; C, PM SPU 39-2, lingual view; D-E, PM SPU 39-3, in occlusal (D) and oblique labial (E) views; F, PM SPU 39-4, labial view; G, PM SPU 39-5, occlusal view; H, PM SPU 39-6, occlusal view; I, PM SPU 39-7, lingual view; J-K, PM SPU 39-8, occlusal view (J) and left lateral cusp from this tooth (K); L, PM SPU 39-9, tooth immersed in aniseed oil, lingual view; M-N, PM SPU 39-10 in oblique basal (M) and labial (N) views; O, P, *Cobelodus* sp.; O, PM SPU 39-11, monocuspid denticle, lateral view; P, PM SPU 39-12, bicuspid denticle, lateral view. A-F, I, L, South Urals, Sim, section 962, Sakmarian, Sterlitamak Regional Stage (R.S.); G, H, J-K, M-O, South Urals, Tra-Tau Hill, section 1629, Artinskian, Sarga R.S.; P, PM SPU 39-12, South Urals, Dal'niy Tyul'kas Creek, section 1070, Artinskian, Irgina R.S. Scale bars = 0.25 mm.



**Figure 3.** A-F. *Synechodus antiquus* sp. nov., teeth. A, holotype, PM SPU 39-13, labial view; B-C, PM SPU 39-14 in oblique lingual (B) and lingual (C) views; D, PM SPU 39-15, labial view; E-F, PM SPU 39-16; in oblique occlusal (E) and labial (F), views; G-H, *Cooleyella* cf. *fordi* (Duffin & Ward), tooth, PM SPU 39-17, in occlusal (G) and oblique lingual (H) views; I, *Cooleyella* sp. A, tooth, PM SPU 39-18, labial view; J, *Adamantina foliacea* Ivanov, tooth, PM SPU 6-82, labial view; K-P, “*Denaea*” *decora* Ivanov, teeth; K, holotype, PM SPU 6-74, occlusal view; L, PM SPU 6-81, basal view; M, PM SPU 39-19, occlusal view; N, PM SPU 39-20, basal view; O, PM SPU 39-21, labial view; P, PM SPU 6-78, lateral view. A-F, South Urals, Tra-Tau Hill, section 1629, Artinskian, Sarga R.S.; G, H, South Urals, Tra-Tau Hill, section 3000, Sakmarian, Sterlitamak R.S.; I, South Urals, Nikol’skoe, section 2018, Asselian, Kholodny Log R.S.; J, Middle Urals, Sylva River, section 165, Artinskian, Sarga R. S.; K-L, O-P, South Urals, Sim, section 962, Sakmarian, Sterlitamak R.S.; M, South Urals, Sim River, section sk 7, Sakmarian, Tastuba R.S.; N, South Urals, Simskaya station, section sk 5, Sakmarian, Tastuba R.S. Scale bars = 0.25 mm.

Sterlitamak Regional Stages (sections 1070 and 3003) diverge from the type material of the species (Duffin & Ward, 1983) by the weakly prominent central cusp, blunt and short basal flange (Figure 3G, H). Another tooth assigned as *Cooleyella* sp. A (Figure 3I) from the Kholodny Log Regional Stage (section 2018) differs from the known representatives of genus in the presence of transversal ridge crossing the labial side of the crown, a poorly development of basal flange.

The hybodontoid tooth found in the Sarga Regional Stage (section 1501) resembles the monocuspid teeth of *Tristychius* (Dick, 1978, text-figure 25A-E).

The chondrichthyan scales and denticles are very abundant and diverse. They correspond to the following types:

**Scales of Type A.** Such placoid scales belong to neoselachians (Figure 4). These scales are low, flat, and possessed by the oval to rhombic, thin crown and the small, concave base located at the anterior edge. The external surface of the crown in some scales bears a medial longitudinal ridge which is prominent along the posterior edge. Similar scales are often illustrated for Mesozoic synchodontiforms and another Mesozoic to Recent neoselachians. The mentions of those scales from the Palaeozoic are occasional (Reif & Goto, 1979; Tway & Zidek, 1982; Schultze, 1985; Ivanov, 1999).

**Scales of type B.** They have a bulb- or cone-shaped crown with stellate, denticulate, strong ridges and a rather large base with numerous marginal processes and a concavity on the basal side (Figure 5A-E). The neck is not developed in some scales. There are some scales with complex crowns

(Figure 5E). Different varieties of similar scales have been described from the Devonian to Mesozoic, and attributed mainly to hybodontoid sharks (e.g. Reif, 1978; Maisey, 1983; Turner, 1993; Rees, 2002).

**Scale of type C.** The scales of this type are characterised by a fan- or leaf-shaped crown with numerous ridges radiated from the centre of concave anterior edge (Figure 5F-I). The neck is well developed. The base is smaller than the crown, with dish-like basal surface.

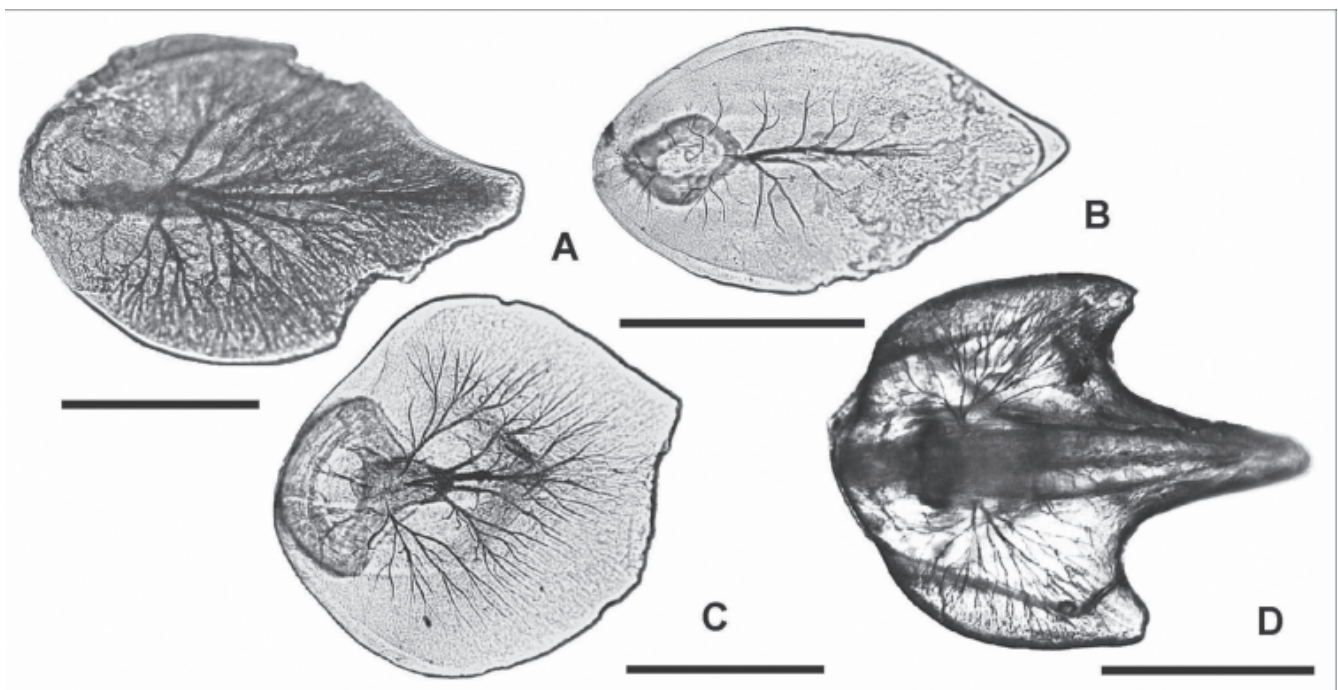
**“Petrodus” type denticles.** These dermal denticles (Figure 5J) have no precise taxonomic affinity yet (e.g. Zangerl, 1981).

**“Listracanthus” denticles.** The denticles are larger than most others; they have a compound, flattened, elongate crown and a small, often flat base (Figure 5 K, L).

**Spine-like denticles.** The denticles of this type have a long conical crown which is frequently inclined, smooth in the upper part and bearing short ridges basally (Figure 5 M, N). They rather resemble scale type I of the xenacanthid *Lebachacanthus* from the Early Permian of Germany (Soler-Gijón, 1997, Figure 4 A-C).

**Tricuspid denticles.** The rounded or oval base with three cusps is characteristic of this denticles type (Figure 5O, P). The central cusp is higher. There are some variations of the denticles: with the separated cusps placed distantly each other (Figure 5O) and with cusps compound in the flattened crown (Figure 5P).

**“Stemmatias” denticles.** These have a multicuspid crown bearing recurved cusps, and are mucous membrane or pharyngeal denticles which were described in some symmoriids such as *Cobelodus* (Zangerl & Case, 1976),



**Figure 4.** Neoselachian scales (type A) immersed in aniseed oil, focused on the dentine canals, South Urals, Tra-Tau Hill, section 3000, Sakmarian, Sterlitamak R.S.; **A**, PM SPU 39-22; **B**, PM SPU 39-23; **C**, PM SPU 39-24; **D**, PM SPU 39-25. Scale bars = 0.25 mm.



*Stethacanthus* (Lund, 1974; Zidek, 1993), *Symmorium* (Zangerl, 1981; Williams, 1985).

A small spine fragment found in the Tastuba Regional Stage (sections 1507) has the ornamentation and structure of typical hybodontoid shark spines.

## SYSTEMATIC PALAEOONTOLOGY

Class CHONDRICHTHYES, Huxley, 1880  
 Subclass ELASMOBRANCHII Bonaparte, 1838  
 Order SYMMORIIDA Zangerl, 1981  
 Family DENAEIDAE Berg, 1940  
 Genus *Cobelodus* Zangerl, 1973

**Type species.** *Styptobasis aculeata* Cope, 1894.

*Cobelodus obliquus* sp. nov.  
 (Figure 2)

**Etymology.** Latin *obliquus* means sidelong.

**Holotype.** Specimen PM SPU 39-1, an isolated tooth (Figure 2 A, B).

**Type locality and age.** South Urals, Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim town in the direction of Chelyabinsk, section 962; Sakmarian, Sterlitamak Regional Stage.

**Other material.** 37 isolated teeth from section 962, road cut of Ufa – Chelyabinsk, 1 km from Sim town in the direction of Chelyabinsk; the Sterlitamak R.S., Sakmarian; section 1070, Dal'niy Tyul'kas Creek, southward from Krasnousol'sk; the Burtsevka and Irgina R. Stages, Artinskian; section 1507, road cut of Chulpan – Mesyagutovo, near Maloyaz; the Tastuba R.S., Sakmarian; section 1629, Belaya River, near Sterlitamak, 300 m northward from Tra-Tau Hill, the Sarga R.S., Artinskian, and section 2018, Ural River, right bank, near Nikol'skoe village; the Kholodniy Log R.S., Asselian.

**Occurrence and age.** South Urals, Early Permian, Asselian – Artinskian.

**Diagnosis.** Small cladodont teeth with three to five separated cusps; central cusp slightly higher and wider than the lateral cusps, dislocated labially, labio-lingually flattened at the top; lateral cusps very curved sideward; cusps covered by numerous gentle cristae; triangular, arched base with short lingual part and acuminate lateral processes; single small, distinct apical button located distally on the lingual edge; slope fields placed alongside of the button; labio-basal edge lacking articulation elements; main canal openings located distally on the button and in the centre of basal side.

**Description.** The teeth range in size from 0.7 to 2.6 mm along the base. The crown is of cladodont type and consists of three to five cusps. The cusps are separated from each other and lingually recurved. The central cusp is slightly higher and wider than the lateral cusps; it has distinct lateral carinae and a rounded cross section toward the cusp base, which becomes oval in the middle part. The upper part of the cusp is labio-lingually compressed and obtuse. The lateral cusps and intermediate cusplets are acuminate apically and rounded

in the cross section. The base of the central cusp is slightly displaced labially; the lateral cusps are strongly curved sideward. All the cusps are ornamented by numerous, distinct cristae, which are mainly long and straight. The middle of labial and lingual faces of the central cusp bears the short gentle cristae, which are surrounded laterally by longer ones. The latter meets at the cusp top. The cusps consist of orthodentine with slightly ramifying dentine canals and covered by well-developed enameloid. The crown forms an obtuse angle with the base. The crown/base boundary is more distinct on the lingual side. The base is triangular in occlusal view, and saddle-shaped in lingual and labial views. It has the acuminate, horn-like lateral parts and slightly convex occlusal and concave basal sides. The lingual torus is short, with a straight distal margin. A single small, distinct, prominent apical button varies from rounded to almost quadrate. The button has a terminal position on the lingual torus, protruding over the lingual edge. There are the splay fields on the occlusal surface alongside the button, which bear minute papillae. The teeth lack any labio-basal articulation element but the slender thickness is visible in the five-cusped teeth. The openings of the main vascular canals are located at the lingual edge of the apical button and in the centre of basal side of the base. The small secondary canals open around the button and at the labio-basal edge, under the central cusp.

Tricuspid teeth dominated in collection. They are much smaller and have a comparatively wider central cusp, are considerably displaced labially; have a more protruded and prominent apical button and fewer canal openings. The five-cusped teeth possess a more arched base with a straight lingual margin, and longer lateral processes of the base.

**Remarks.** The mono- and bicuspid denticles (Figure 2 O, P) associating with the teeth resemble those of *Cobelodus aculeatus* and possibly belong to a new species. They are assigned herein to *Cobelodus* sp. Although *Cobelodus aculeatus* has been studied in detail, particularly the skeleton (Zangerl & Case, 1976; Zidek, 1992), the typical multicusp teeth have been a little neglected. Cope (1894, Pl. XX, Figure 3) referred only to the fragment of a tricuspid tooth of *C. aculeatus*. Drawings of such teeth were provided by Zangerl and Case (1976, Figure 16), but the authors note only the separated cusps, the slender asymmetry of the crown, and the saddle-shaped base with narrow lingual torus. The first detailed description of *C. aculeatus* teeth was presented by Hansen in his Ph. D. thesis (1986), which has allowed comparison of the new species with *C. aculeatus*.

The multicusp teeth of *C. aculeatus* differ from those of the former species in the narrow central cusp, shorter lateral cusps, the lack of a distinct apical button, the straight labio-basal margin, and the semicircular outline of lingual torus.

The attribution of the genus to the family Denaeidae is based upon the resemblance of the dental morphology of *Cobelodus*, *Denaea* and “*Denaea*” which are characterized by the slightly dominant central cusp in the crown (“undeveloped” cladodont crown), the gentle cusps

**Table 1.** Distribution of chondrichthyan taxa in the Early Permian of Middle and South Urals. **Abbreviations:** *Par*, *Parafusulina*; *Ps*, *Pseudofusulina*; *Sph*, *Sphaeroschwagerina*.

	Stage	Fusulinid zone	Regional Stage	Section	Chondrichthyan remains
EARLY PERMIAN	<b>Kunurian</b>				
	Artinskian	<i>Par. solidissima</i> ,	Sarga	165, 170, 263, 1501, 1527, 1629, 1768	<b>Teeth:</b> " <i>Denaea</i> " <i>decora</i> Ivanov, <i>Cobelodus obliquus</i> sp. nov., <i>Heslerodus</i> sp., <i>Synechodus antiquus</i> sp. nov., <i>Adamantina foliacea</i> Ivanov, <i>Adamantina</i> sp., <i>Cooleyella</i> sp., <i>Hybodonthoidea</i> gen. indet. <b>Scales and denticles:</b> type A (neoselachian), type B (hybodontoid), type C, <i>Janassa</i> -like, tricuspid, <i>Cobelodus</i> , " <i>Stemmatias</i> " type.
		<i>Par. lutugini</i> – <i>Ps. juresanensis</i>	Irgina	816, 1070 (part)	<b>Teeth:</b> " <i>Denaea</i> " <i>decora</i> Ivanov, <i>Cobelodus obliquus</i> sp. nov., <i>Cooleyella</i> cf. <i>C. fordi</i> (Duffin & Ward). <b>Scales and denticles:</b> type A (neoselachian), type B (hybodontoid), type C, tricuspid, <i>Cobelodus</i> , " <i>Stemmatias</i> " and " <i>Listracanthus</i> " types.
		<i>Ps. pedissequa</i> – <i>Ps. concavutas</i>	Burtsevka	1070 (part)	<b>Teeth:</b> " <i>Denaea</i> " <i>decora</i> Ivanov, <i>Cobelodus obliquus</i> sp. nov., <i>Stethacanthus</i> sp., ? <i>Heslerodus</i> sp. <b>Scales and denticles:</b> type A (neoselachian), type B (hybodontoid), type C, tricuspid, spine-like, <i>Cobelodus</i> , " <i>Stemmatias</i> " type.
	Sakmarian	<i>Ps. urdalensis</i>	Sterlitamak	<b>962</b> (= sk 3), 3000-3	<b>Teeth:</b> " <i>Denaea</i> " <i>decora</i> Ivanov, <i>Cobelodus obliquus</i> sp. nov., <i>Synechodus antiquus</i> sp. nov., <i>Cooleyella</i> cf. <i>C. fordi</i> (Duffin & Ward). <b>Scales and denticles:</b> type A (neoselachian), type B (hybodontoid), type C, tricuspid, spine-like, <i>Cobelodus</i> , " <i>Stemmatias</i> ", " <i>Listracanthus</i> " and " <i>Petrodus</i> " types.
		<i>Ps. verneuli</i> – <i>Ps. uralica</i>	Tastuba	1507, 1508, sk 5, sk 7	<b>Teeth:</b> " <i>Denaea</i> " <i>decora</i> Ivanov, <i>Cobelodus obliquus</i> sp. nov. <b>Scales and denticles:</b> type A (neoselachian), type B (hybodontoid), type C, tricuspid, spine-like, <i>Cobelodus</i> , " <i>Stemmatias</i> " type. Fragment of hybodontoid spine.
		<i>Ps. moelleri</i>			
	Asselian	<i>Sph. sphaerica</i>	Shi-khany		
		<i>Sph. moelleri</i> – <i>Ps. fecunda</i>	Kholodny Log	2018	<b>Teeth:</b> " <i>Denaea</i> " <i>decora</i> Ivanov, <i>Denaea</i> sp., <i>Cobelodus obliquus</i> sp. nov., <i>Heslerodus</i> sp., <i>Cooleyella</i> sp. A. <b>Scales and denticles:</b> type A (neoselachian), type B (hybodontoid), type C, " <i>Stemmatias</i> " type.
		<i>Sph. vulgaris</i> – <i>Sph. fusiformis</i>			

consisting purely of the orthodontine, and the poorly or not developed elements of tooth to tooth articulation.

Subcohort NEOSELACHII Compagno, 1977  
Order SYNECHODONTIFORMES Duffin & Ward, 1993  
Family PALAEOSPINACIDAE Regan, 1906  
Genus *Synechodus* Woodward, 1888

**Type species.** *Hybodus dubrisiensis* Mackie, 1863.

*Synechodus antiquus* sp. nov.  
(Figure 3A-F)

**Etymology.** Latin, *antiquus* means ancient.

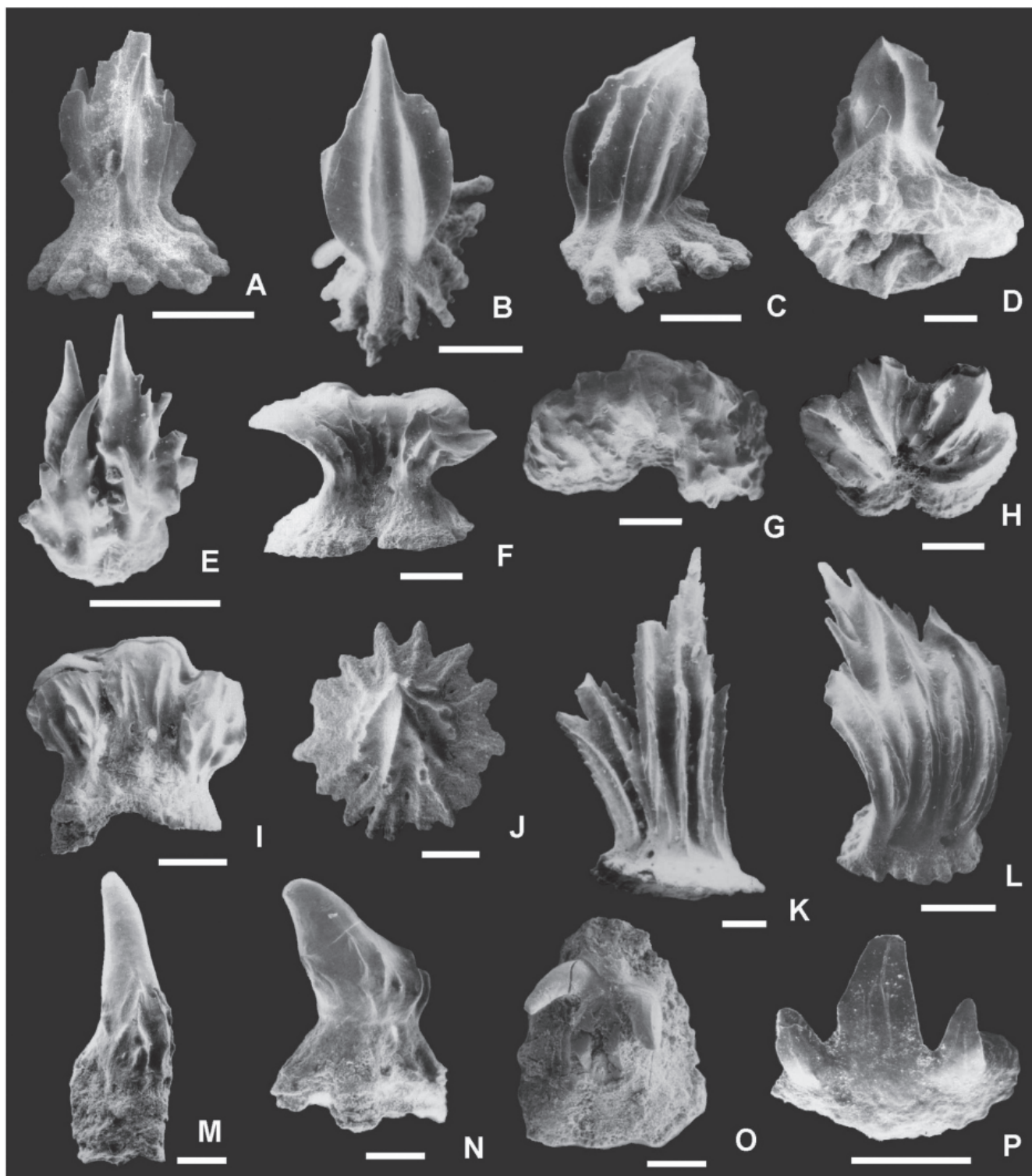
**Holotype.** PM SPU 39-13, an isolated tooth (Figure 3A).

**Type locality and age.** South Urals, Belaya River, near Sterlitamak, 300 m northward from Tra-Tau Hill, section 1629, the Sarga Regional Stage, Artinskian.

**Other material.** Four isolated teeth from section 1629, Belaya River, near Sterlitamak, 300 m northward from Tra-Tau Hill, the Sarga R.S., Artinskian, and section 962, road cut of Ufa – Chelyabinsk, 1 km from Sim town in the direction of Chelyabinsk; the Sterlitamak R.S., Sakmarian.

**Occurrence and age.** South Urals, Early Permian, Sakmarian and Artinskian.





**Figure 5.** Chondrichthyan scales and denticles. **A-E**, Scales of type B (hybodontoid); **A**, PM SPU 39-26, lateral view; **B**, PM SPU 39-27, oblique anterior view; **C**, PM SPU 39-28, lateral view; **D**, PM SPU 39-29, oblique lateral view; **E**, PM SPU 39-30, anterior view; **F-I**, scales of type C; **F**, PM SPU 39-31, anterior view; **G**, PM SPU 39-32, crown view; **H**, PM SPU 39-33, crown view; **I**, PM SPU 39-34, anterior view; **J**, "Petrodus" type denticle, PM SPU 39-35, crown view; **K, L**, "Listracanthus" denticles, **K**, PM SPU 39-36, lateral view; **L**, PM SPU 39-37, oblique lateral view; **M, N**, Spine-like denticles; **M**, PM SPU 39-38, oblique lateral view; **N**, PM SPU 39-39, lateral view; **O-P**, Tricuspid denticles: **O**, PM SPU 39-40 in crown view; **P**, PM SPU 39-41, anterior view. **A-N**, South Urals, Sim, section 962, Sakmarian, Sterlitamak R.S.; **O**, South Urals, Dal'niy Tyul'kas Creek, section 1070, Artinskian, Irgina R.S.; **P**, South Urals, Tra-Tau Hill, section 1629, Artinskian, Sarga R.S. Scale bars = 0.25 mm.

**Diagnosis.** Teeth with asymmetrical, lingually inclined, labio-lingually flattened crown; lingually extended, thin base; high central cusp inclined distally; up to four mesial and up to two distal lateral cusplets; labial crown ornamentation from main ridge bifurcated basally and the accessory small ridges; lingual side poorly ornamented; labio-basal edge straight and corrugated; labial part of the base shallow; canal openings numerous in a row on labial side and some on lingual rim.

**Description.** The teeth range in size from 0.8 to 1.6 mm along the base. The teeth are elongate mesio-distally. They have a lingually inclined asymmetrical crown and lingually extended, thin base. The crown is labio-lingually compressed, possesses a high central cusp with between two and four mesial and up to two distal lateral cusplets. The central cusp and some lateral cusplets are distally inclined. The lateral cusplets are not distinctly separated from each other. The labial side of the crown is strongly ornamented. The ornamentation consists of coarse main ridges bifurcating basally on the central cusp and accessory small ridges which are absent in some teeth. The lingual side is smooth or bears up to two gentle ridges. The cusps have well-developed lateral cutting edges. The labial part of crown slightly overhangs the crown/base junction. The tooth base has shallow labial and slightly concave basal sides. The labio-basal margin of the teeth is straight, with minute undulations. Numerous vascular canals open in a row on the labial side of the base, and a few of them are situated along the lingual rim.

**Remarks.** These teeth probably correspond to the antero-lateral or lateral teeth if the jaw of an Early Permian *Synechodus* had same pattern of heterodonty.

The teeth of the new species most resemble those of *Synechodus ennikilleni* Duffin & Ward (1993) but differ from all other known species in the small number of canal openings on the lingual side of the base, the flattened crown, poorly developed lingual ornamentation, indistinct boundary between crown and base. The former teeth differ from some species in the absence of reticulate ornament and anastomosing ridges on the crown presented in many Mesozoic species of *Synechodus*.

#### PERMIAN CHONDRICHTHYAN ASSEMBLAGES

The assemblages occurring in the Asselian to Artinskian of Middle and South Urals show considerable taxonomical diversity. "*Denaëa*" *decora* and *Cobelodus obliquus* predominate over other elasmobranchian teeth in the assemblages, and the neoselachian scales and scales of type C are very abundant among another scales and denticles.

The Early Permian assemblages from the North, Nearpolar and Polar Urals include such taxa apart mentioned above: ctenacanthoid "*Symmorium*" *occidentalis* (Leidy); the hybodontoid *Lissodus*; the petalodontids *Petalodus* and *Janassa*; edestids (Ivanov, 1999, 2000).

The Early Permian chondrichthyan fauna of the Urals is represented by taxa which occur only in that interval and referred to some edestids, as well the taxa which were

distributed in the Carboniferous and persisted into the Early Permian. The latter belongs to *Stethacanthus*, *Cobelodus*, *Denaëa*, "*Denaëa*", *Lissodus*, *Heslerodus*, "*Symmorium*", *Petalodus*, *Cooleyella* and *Adamantina*. The synechodontiform neoselachians are widely distributed from the Triassic to Palaeocene. This occurrence of synechodontid sharks is the oldest in the world. The new species of *Synechodus* demonstrates a Late Palaeozoic origin for synechodontiform sharks. Symmoriids, especially "*Denaëa*" and *Cobelodus*, dominate among the Early Permian assemblages of Urals and disappeared in the Middle Permian.

Middle and Late Permian chondrichthyans are less diverse than in the Early Permian fauna. *Lissodus*, "*Symmorium*", *Janassa* were reported from the Middle and Late Permian as well (Minikh & Minikh, 1996; Malysheva *et al.*, 2000). Some taxa, hybodontoid *Polyacrodus* and sphenacanthid *Xenosynechodus egloni* Glickman appeared in the Kazanian Stage of Middle Permian (Glikman, 1980; Minikh & Minikh, 1981, 1996). Hybodontoids strongly predominate in the shark assemblages of the Middle and Late Permian age. *Lissodus*, *Polyacrodus* and synechodontids survived the Permo-Triassic biotic crisis became widely distributed in the Mesozoic chondrichthyan assemblages. The Permian shark faunas of the Urals have not yielded any xenacanthids, which were common in the assemblages of Western Europe and North America but included the diverse symmoriids, ctenacanthoids and oldest synechodontiforms.

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