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Permian Chondrichthyans of the Kanin Peninsula, Russia[1]

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Abstract—Chondrichthyan fish remains reported from the Permian (Kazanian) deposits of the Chiosha Bay, and the lower course of the Nadtey River of the Kanin Peninsula (Nenets Autonomous District, Arkhangelsk Region, Russia) include dental elements and scales belonging to *Stethacanthus* cf. *S. altonensis* (St. John et Worthen, 1875), Symmoriiformes gen. indet., "*Ctenacanthus*" sp. and "*Lissodus*" sp., Euselachii gen. indet., *Adamantina benedictae* Bendix-Almgreen, 1993 and *Kanodus robustus* sp. nov. The latter genus is assigned to the previously monotypic family Psephodontidae. The record of *Stethacanthus* in the Middle Permian of Russia is its youngest occurrence worldwide, whilst the occurrence of Adamantina benedictae in the Middle Permian of the Kanin Peninsula is older than the Greenland record.

Keywords: Chondrichthyes, Permian, Kanin Peninsula, Russia

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INTRODUCTION

Fossil fish remains have been reported from the Permian deposits of the Kanin Peninsula, in the northern part of Nenets Autonomous District, Arkhangelsk Region, Russia, in several publications. The teeth of *Helodus* sp. and a fin spine of *Xystracanthus* sp. were mentioned but not illustrated in Lyutkevich (1955). Minikh (2006) described one incomplete tooth of a stethacanthid shark, and numerous scales and squamation fragments of actinopterygians. A diverse chondrichthyan assemblage has been cited by the present authors (Ivanov, Lebedev, 2007).

The outcrops of shallow-water marine Permian deposits are located along the seashore on the northwestern coast of Chiosha Bay (shelf area of the Barents Sea), between the mouth of the Nadtey River and Yarnisalya Cape, as well as in the lower course of the Nadtey River. Detailed descriptions of outcrops, stratigraphical data and correlation are given in two recent publications (Grunt et al., 2002; Afanasieva et al., 2006).

Chondrichthyan remains have been reported from several localities.

(1) Outcrop 1 of Afanasieva et al. (2006) is situated near the mouth of the Nadtey River, at the Nadteysalya Cape. Fish remains including chondrichthyans and actinopterygians were found in a sequence of interbedded sandstones and sandy limestones with abundant brachiopods, bivalves, and crinoids (bed 2 of Afanasieva et al., 2006). Chondrichthyan remains were collected by T. Grunt and E. Malysheva, and comprise a tooth fragment of *Stethacanthus* sp., buccopharyngeal denticles of Symmoriiformes gen. indet., a tooth and isolated cusp of *Adamantina benedictae* Bendix-Almgreen, and scales of Euselachii gen. indet. The strata exposed at these outcrops belong to beds containing the brachiopod *Burovia fredericksi* and have been tentatively correlated with the Ufimian (Afanasieva et al., 2006).

(2) Outcrop 7 of Afanasieva et al. (2006) is located between the mouths of the Nadtey and Krutaya rivers, to the west of the former. Bed 1 is composed of carbonate siltstone and contains ostracods, crinoids, and diverse actinopterigyan and chondrichthyan remains. The latter are represented by teeth of *Stethacanthus* cf. *S. altonensis* (St. John et Worthen); a spine-brush complex and buccopharyngeal denticles of Symmoriiformes gen. indet.; teeth and scales of *Adamantina benedictae*; a tooth of "*Lissodus*" sp.; scales of Euselachii gen. indet. The specimens were collected by T. Grunt and E. Malysheva. The correlation of this outcrop is disputed. Afanasieva et al. (2006) assign this part of the section to the beds with the brachiopod *Bajtugania kaninense* and it is tentatively correlated with the Urzhumian Stage.

(3) A tooth of "*Ctenacanthus*" sp. was found in the outcrop on the left bank of the Nadtey River, 4 km upstream from mouth of the river. The bed with the shark remains is assigned to the Kazanian.

(4) The outcrop on the left bank of the Nadtey River, 4km upstream from mouth of the river has yielded a tooth of "*Ctenacanthus*" sp. The bed with the

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shark remains is assigned to the Kazanian. The specimen was collected by Yu. Gubin.

(5) Bed 1 of outcrop 18 between the Nadtey River and Yarnisalya Cape (in the description by A. Sultanaev, 1972) belongs to the Kazanian (Stepanov et al., 1975) and contains a tooth plate of *Kanodus robustus* Lebedev sp. nov.

(6) Teeth of *Stethacanthus* cf. *S. altonensis* and a tooth plate of *Kanodus robustus* were collected by O. Shilovskiy from a sandstone layer in the outcrop between Nadtey River and Yarnisalya Cape, close to the cape. This layer relates to the beds with the brachiopod *Kaninospirifer borealis* and is assigned to the Kazanian (Afanasieva et al., 2006).

The stratigraphical correlation of Permian deposits in the Kanin Peninsula is controversial, but the assignment of a Kazanian age to the strata is beyond question. However the correlation of part of the Permian sequence with the Urzhumian Stage is arguable because the status of the Ufimian Stage in Russia is still under discussion. Most Permian workers assign the interval of the Solikamian Regional Stage to the Kungurian (Kotlyar, 2009), whilst the correlation of the Sheshmian Regional Stage (upper part of the Urzhumian Stage) is still under debate.

Chondrichthyan remains from these outcrops are represented by isolated teeth, tooth plates, denticles and scales. The specimens described here were collected at different times by T. Grunt, Yu. Gubin, E. Malysheva, O. Shilovskiy, and A. Sultanaev. Institutional abbreviations of museum collections are: GMM—Geological-Mineralogical Museum of the Kazan' State University (Kazan', Russia), GI KSC—Geological Institute, Komi Scientific Centre (Syktyvkar, Russia); NHMD—Natural History Museum of Denmark (Copenhagen, Denmark); PIN—Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia); PM SPU—Paleontological Museum of St. Petersburg State University (St. Petersburg, Russia).

SYSTEMATIC PALEONTOLOGY

CLASS CHONDRICHTHYES HUXLEY, 1880

SUBCLASS ELASMOBRANCHII BONAPARTE, 1838

Order Symmoriiformes Zangerl, 1981

Family Symmoriidae Dean, 1909

Genus *Stethacanthus* Newberry, 1889

Cladodus: Agassiz, 1843 in part, p. 196.
Physonemus: McCoy, 1848 in part, p. 117.
Lambdodus: St. John and Worthen, 1875 in part, p. 283.
Stethacanthus Newberry, 1889, p. 198.
Ctenacanthus: A. Minikh, 1999 in part, p. 135.
Gutturensis: Sequeira and Coates, 2000, p. 155.
Akmonistion: Coates and Sequeira, 2001, p. 439.
Pinegia: A, Minikh, 2004, p. 129.
Pinegocaptus: A. Minikh, 2006, p. 180.

Type species: *Physonemus altonensis* St. John et Worthen, 1875.

Remarks. The genus *Stethacanthus* has been previously assigned to the family Stethacanthidae (Lund, 1974; Zangerl, 1981). A new family, the Falcatidae was erected by Zangerl (1990). However, Maisey (2009) analysed the morphology of fins and spine-brush complexes in symmoriiforms and suggested combining the families Stethacanthidae and Symmoriidae based on the presence of a paired semicircular pelvic cartilage. If this proposal is followed, the Stethacanthidae is a junior synonym of the Symmoriidae.

Stethacanthus cf. _S. altonensis_ (St. John et Worthen, 1875)

Plate 9, Figs. 1–4

Description. Medium to large teeth possess a cladodont crown and a lingually extended base. The central cusp is incurved lingually, considerably higher and wider than the other cusplets. Intermediate cusps, if present in the crown, are smaller than the lateral ones. Cusps are rounded in cross section or slightly flattened labio-lingually. They are separated from each other by narrow spaces and do not form a single crown. Each cusp bears the same ornamentation of numerous tiny, closely-spaced cristae extending from the base to the cusp tip. The boundary between the cusps and base is distinct and accentuated by a narrow groove which is arched and runs close to the labial rim in the central cusp.

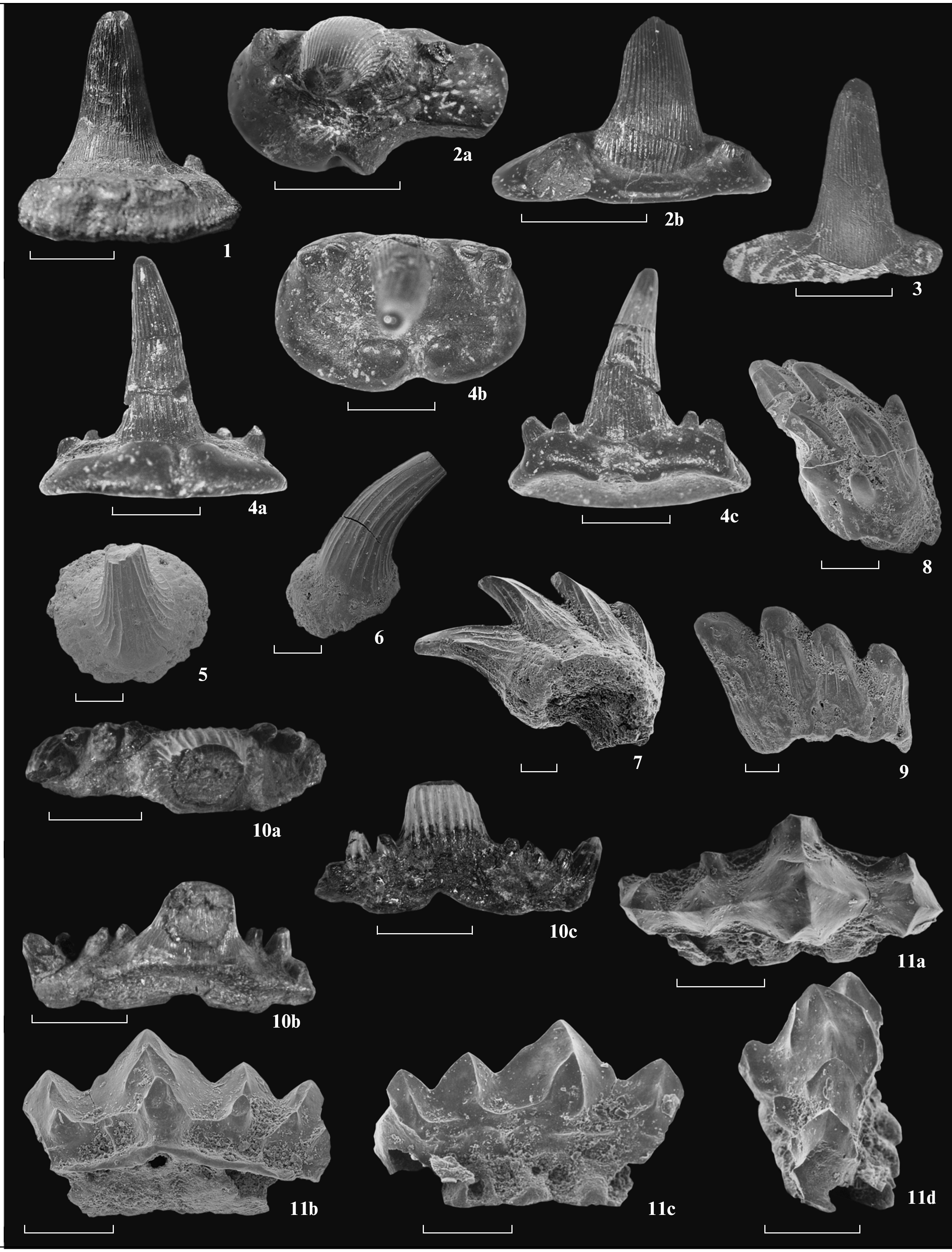
The tooth base is oval, mesio-distally elongated, and convex on the occlusal side and concave on the basal side, with rather thick lingual and thin labial parts. The oval, mesio-distally elongated apical button is located at the lingual rim. The labial margin of the base bears a wide and short labio-basal projection. The width of the projection is equal to that of the central cusp.

The lingual face of the base is wave-shaped. The vascular canals open around the apical button on the occlusal side, sometimes separated from the button itself. The central part of the basal concavity is perforated by several canal openings.

The sizes of the teeth vary from 12 to 23 mm in height and from 14 to 26 mm in width. The smaller teeth have intermediate cusplets and a higher lingual surface under the central cusp. The large teeth possess a tricuspid crown with the central cusp and apical button occupying the greater part of the tooth; the labial part of the base is considerably thinner in smaller teeth.

Remarks. The teeth described herein are assigned to *Stethacanthus* cf. *S. altonensis* (St. John et Worthen) because they are not substantially different from those of the type species. However, Ginter et al. (2010) correctly noted that there are at least three informal groups of *Stethacanthus* teeth with minor differences in the tooth morphology. These authors referred 10 species to the genus *Stethacanthus* that had

Plate 9



earlier been assigned to *Cladodus*. A decision on species validity will only be possible after the complete revision of all taxa that have been ascribed to the genus *Stethacanthus*.

Ginter et al. (2010) analyzed the taxa of stethacanthids and considered the genera *Akmonistion* and *Gutturensis* as junior synonyms of the genus *Stethacanthus*. Minikh (2004) described a new genus *Pinegia* based on isolated teeth from the Permian of European Russia and included two species: *P. grunti* A. Minikh and *P. rosanovi* (A. Minikh) assigned previously to the genus *Ctenacanthus* (Minikh, 1999). "*Pinegia*" proved to be a preoccupied name and was replaced by *Pinegocaptus* A. Minikh (2006). Minikh found reasons to erect the new genus and compared the described specimens with the teeth of *Stethacanthus resistens* Ginter from the Late Devonian of Poland (Ginter, 2002A) instead of comparing them with the type species *S. altonensis* (St. John et Worthen). This is problematic, because the teeth of the latter cannot be distinguished from the Permian teeth in Minikh's collection. *S. resistens* was attributed recently to *Cladodoides wildungensis* (Jaekel) from the Late Devonian of Germany (Ginter et al, 2010). We consider *Pinegocaptus* to be a junior synonym of the genus *Stethacanthus*.

M a t e r i a l. Five isolated teeth of varied preservation (some teeth are partially broken or rather abraded); Kanin Peninsula, Chiosha Bay, outcrop 1, at Nadteysalya Cape, bed 2; "Ufimian", beds with the brachiopod *Burovia fredericksi*; outcrop between Nadtey River and Yarnisalya Cape; Kazanian, beds with the brachiopod *Kaninospirifer borealis;* outcrop 7, between the mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*.

***Symmoriiformes* gen. indet.**

Plate 9, Figs. 5–9

D e s c r i p t i o n. The material includes two types of dermal denticles. The first type of denticle belongs to the spine-brush complex of symmoriiform sharks (Pl. 9, Figs. 5, 6). Each has a curved posteriorly crown that is spine-like, long, and rounded in cross section. The crown surface is ornamented with distinct cristae. The denticle base is either rounded or oval, with convex external and flat basal faces.

The buccopharyngeal denticles vary in shape. Most of them have a multicuspid crown with striated, conical cusps arranged in a single row. The cusps consecutively overlap each other progressively increasing in height. Such denticles have been attributed to the formal taxon "*Stemmatias* (*Stemmatodus*) *simplex*" (St. John and Worthen, 1875). Some of these denticles have a spiral arrangement of cusps and a curved base with strongly concave basal face (Pl. 9, Fig. 7), but others possess straight rows of densely placed cusps and a flat basal face (Pl. 9, Fig. 9). The compound crown of rare denticles is composed of three cusp rows (Pl. 9, Fig. 8), in which the cusps of the central row are higher than the lateral ones. Such denticles were described as "*Stemmatias cheiriformes*" by St. John and Worthen (1875), now a formal taxon.

R e m a r k s. The denticles of the spine-brush complex are known in the symmoriiforms *Stethacanthus* (Lund, 1974; Coates and Sequeira, 2001), *Orestiacanthus* (Lund, 1984), *Falcatus* (Lund, 1985) and *Damocles* (Lund, 1986) but only some denticles forming the spine-brush complex in *Stethacanthus* possess a curved crown (Coates and Sequeira, 2001).

The buccopharyngeal denticles of "*Stemmatias*"-type have been described in several symmoriiforms: *Cobelodus* (Zangerl and Case, 1976), *Stethacanthus* (Williams, 1985; Coates and Sequeira, 2001), and *Symmorium* (Williams, 1985).

M a t e r i a l. Seven denticles; Kanin Peninsula, Chiosha Bay, outcrop 1, at Nadteysalya Cape, layer 2; "Ufimian", beds with the brachiopod *Burovia fredericksi*; outcrop 7, between the mouths of the Nadtey and Krutaya rivers, bed 1; ?Urzhumian, beds containing the brachiopod *Bajtugania kaninense*.

E x p l a n a t i o n o f P l a t e 9

Figs. 1–4. *Stethacanthus* cf. *S. altonensis* (St. John et Worthen, 1875), teeth: 1—PM SPU 52-1, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*; lingual view; 2—GMM 839/80; outcrop between Nadtey River and Yarnisalya Cape; Kazanian, beds with the brachiopod *Kaninospirifer borealis*: 2a—occlusal and 2b—labial views; 3—GI KSC 1/322, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*, labial view; 4—PM SPU 52-2, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*: 4a—lingual, 4b—occlusal and 4c—labial views.

Figs. 5–9. Symmoriida gen. indet.; outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*: 5, 6—denticles from the spine-brush complex: 5—PM SPU 52-3, crown view; 6—PM SPU 52-4, lateral view; 7–9—buccopharyngeal denticles: 7—PM SPU 52-5, lateral view; 8—PM SPU 52-6, oblique lateral view; 9—PM SPU 52-7, lateral view.

Fig. 10. "*Ctenacanthus*" sp., tooth, PIN 4472/9; Nadtey River left bank of upstream 4 km from the river mouth; Kazanian: 10a—occlusal, 10b—lingual and 10c—labial views.

Fig. 11. "*Lissodus*" sp., tooth, PM SPU 52-8; outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*: 11a—occlusal, 11b—labial, 11c—lingual and 11d—lateral views.

Scale bars: Figs. 1, 3–10 mm; Figs. 2, 4, 10—5 mm; Figs. 5, 6—500 μm; Figs. 7–9, 11—200 μm.

Order Ctenacanthiformes Glikman, 1964

Family Ctenacanthidae Dean, 1909

Genus *Ctenacanthus Agassiz*, 1843

"*Ctenacanthus*" sp.

Plate 9, Fig. 10

D e s c r i p t i o n. This cladodont tooth has a high and wide central cusp flanked by a pair of moderate lateral cusps and six small intermediate cusplets. One pair of intermediate cusplets is higher than the two adjacent pairs. The central and lateral cusps are inclined and curved lingually, whilst the axes of the intermediate cusplets are almost vertical. All cusps are covered by strong, sub-parallel cristae on the labial side and by a tiny striation on the lingual side. The cusp bases of the lateral and central cusps are arranged in one longitudinal line, but the intermediate cusplets are differentially displaced labially. The labial surface of the tooth is sinuous and bears a shallow, medial labial depression that continues on the basal side of the tooth. The base has two labio-basal tubercles that are prominent, oval, elongated mesio-distally, and separated from each other by a narrow groove that extends the labial depression. The long axes of tubercles lie in the same plane.

R e m a r k s. The described tooth very much resembles the teeth of "*Ctenacanthus*" *costellatus* Traquair illustrated by Ginter (2002B, Fig. 4A). The teeth of "*C.*" *costellatus* described by Moy-Thomas (1936) differ considerably from the type specimens of Traquair's collection (Ginter et al., 2010). This taxon needs a revised description. The tooth described as *Saivodus* sp. by Hodnett et al. (2012, Fig. 6G) is similar in labial view to the tooth from the Permian of the Kanin Peninsula.

The ctenacanthiform sharks comprise two groups based on distinct tooth morphologies. The teeth of the first group containing the genera *Cladodus, Ctenacanthus, Goodrichthys, Saivodus*, and *Tamiobatis* (Ginter et al, 2010), possess a short base, a shallow labio-basal depression, a single, strongly elongated apical button and one or two labio-basal projections. *Glikmanius* (Ginter et al., 2005), *Heslerodus* (Ginter, 2002B), *Kaibabvenator* and *Nanoskalme* (Hodnett et al., 2012), as well "*Ctenacanthus*" *costellatus* (Ginter, 2002B) belong to the second group. Their teeth have a longer, trapezoidal base, a deeper labio-basal depression, two rounded apical buttons and two labio-basal tubercles. The family Heslerodidae was erected by Maisey (2010) based on the genus *Heslerodus*. Hodnett et al. (2012) suggested that *Glikmanius, Kaibabvenator* and *Nanoskalme* should also be placed in this family. In our opinion, the part of the specimens, identified earlier as "*Ctenacanthus*" *costellatus* should be established as a new genus and assigned to the Heslerodidae.

M a t e r i a l. One incomplete tooth with a broken lingual part of the base; Kanin Peninsula, Nadtey River, left bank 4km upstream from the river mouth; Kazanian.

C O H O R T EUSELACHII HAY, 1902

S u p e r f a m i l y Hybodontoidea Owen, 1846

Family Lonchidiidae Herman, 1977

Genus *Lissodus* Brough, 1935

"*Lissodus*" sp.

Plate 9, Fig. 11

D e s c r i p t i o n. This small tooth possesses a multicuspid, monolithic crown and typical euselachian base. The crown is composed of a high central cusp, paired moderate intermediate and lower lateral cusps arranged pyramidally. The cusps are conic, sharp-edged and roughly quadrate in cross section. They bear ornamentation consisting of coarse vertical ridges descending from the cusp tip, and sometimes branching downward. These ridges do not reach the crown/base boundary. The bases of the vertical ridges are linked together on both the labial and lingual faces. The distinct, longitudinal occlusal crest can be traced along the full length of the crown and passes through the cusp apices. A prominent labial peg and accessory projections are located on the labial side of the tooth crown, at the basal part of the cusp. Small nodes are found on the labial surface of each cusp, between the cusp apices and projections or peg. A narrow, distinct longitudinal ridge borders the labial edge of the crown and a crown shoulder is developed. The base is extended lingually, and inclined linguo-basally, with a concave basal part. Numerous vascular canals open at the lingual edge. A longitudinal row of canal openings is located on the central part of the basal surface.

R e m a r k s. This tooth is most similar to the some morphotypes of "*Lissodus*" *wirksworthensis* Duffin from the Viséan of England (Duffin, 1985) but differs from that taxon by its more distinctly separated cusps. One tooth belonging to morphotype 1 of *Lissodus* sp. from the Tournaisian of Ireland (Duncan, 2004, Fig. 3E) resembles the tooth described herein, but the Permian specimen has lower intermediate and lateral cusps, and additionally, a lingual buttress.

Rees and Underwood (2002), in analyzing Mesozoic lonchidiid sharks' teeth, suggested that the Palaeozoic taxa formerly ascribed to *Lissodus* might be separated into two new genera after the revision of all Palaeozoic species. We provisionally ascribe the Kanin specimen to "*Lissodus*" until such a revision is done.

M a t e r i a l. One isolated tooth with a partly broken base; Kanin Peninsula, Chiosha Bay, outcrop 7, between the mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds containing the brachiopod *Bajtugania kaninense*.

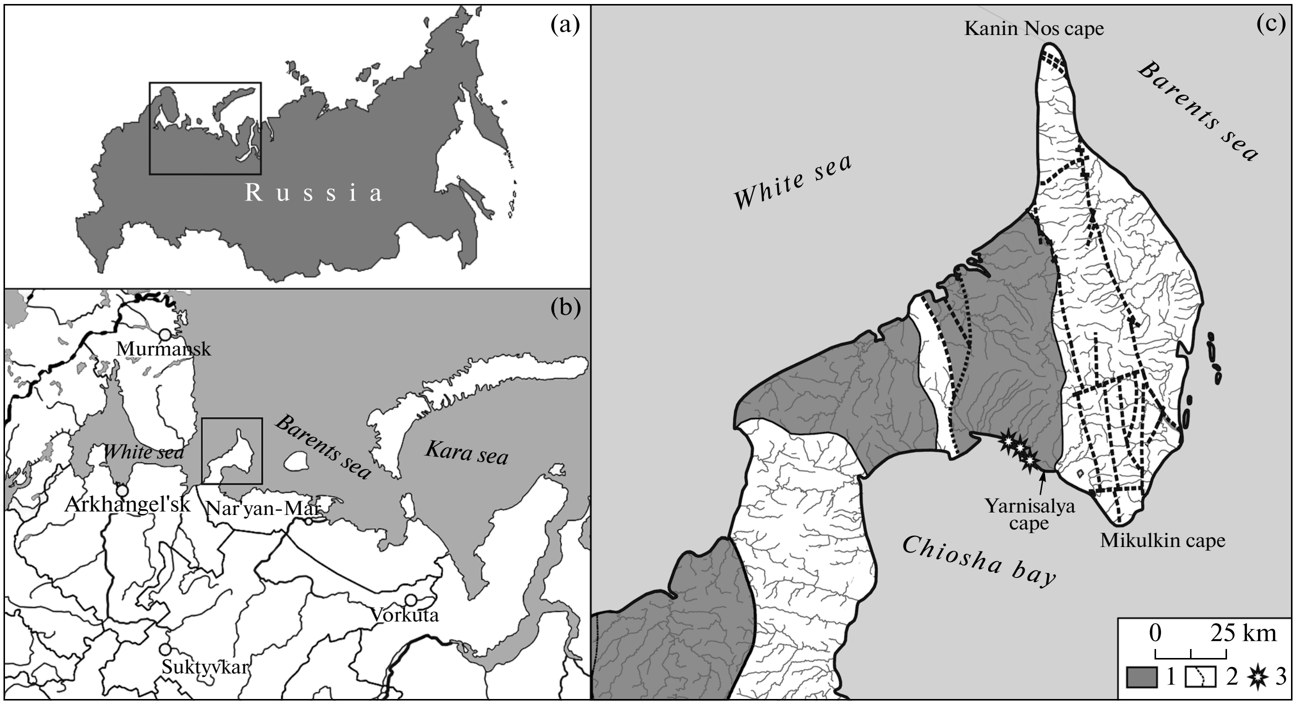


Fig. 1. Permian chondrichthyan localities in the Kanin Peninsula. Keys for (c): (1) Permian or undivided Upper Paleozoic deposits, (2) fault, (3) locality.

***Euselachii* gen. indet.**

Plate 10, Figs. 1–5

D e s c r i p t i o n. Three scale morphotypes are present in the described collection. The scales of morphotype 1 have an apically elongated crown (Pl. 10, Fig. 1). The crown bears strong ridges with longitudinal, intervening medial grooves. The ridges are parallel to each other, extended along the length of the crown. The central ridge reaches to the base and is more prominent than the lateral ones. The scale neck is well developed, and narrow. The base has cone-shaped external and flat basal sides.

The scales of morphotype 2 possess a flat crown with a serrated margin, a short neck and a low, conical base (Pl. 10, Fig. 2).

The scales of morphotype 3 (Pl. 10, Figs. 3–5) show the greatest diversity and abundance. These placoid scales have a posteriorly-inclined crown ornamented by between one and three prominent short ridges which arise from the neck and disappear on the posterior part of the crown. The medial ridge may be larger than lateral ones or of the same size. The posterior edge of the crown is sinuous. The scale neck is low in the posterior part and high posteriorly, and bears numerous canal openings. The base is thin and flat.

R e m a r k s. The scales of morphotype 1 are often assigned to hybodontiform sharks (e.g., Reif, 1978). Scales resembling morphotype 2 were described as *Complanicorona* by Johns et al. (1997) from the Triassic of British Columbia. The scales of morphotype 3 are similar to those of some neoselachian sharks. Such scales were described by Johns et al. (1997) under the taxonomic name *Glabrisubcorona*.

M a t e r i a l. 12 scales; Kanin Peninsula, Chiosha Bay, outcrop 1, at the Nadteysalya Cape, layer 2 "*Ufimian*", beds containing the brachiopod *Burovia fredericksi*; outcrop 7, between the mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*.

ELASMOBRANCHII ORD. INDET.

Family Jalodontidae Ginter, Hairapetian et Klug, 2002

T y p e g e n u s: *Jalodus* Ginter, 1999.

R e f e r r e d g e n e r a: *Adamantina* Bendix-Almgreen, 1993; *Isacrodus* Ivanov, Nestell et Nestell, 2012; *Jalodus* Ginter, 1999; *Texasodus* Ivanov, Nestell, Nestell, 2012.

Genus *Adamantina* Bendix-Almgreen, 1993

T y p e s p e c i e s: *Adamantina benedictae* Bendix-Almgreen, 1993.

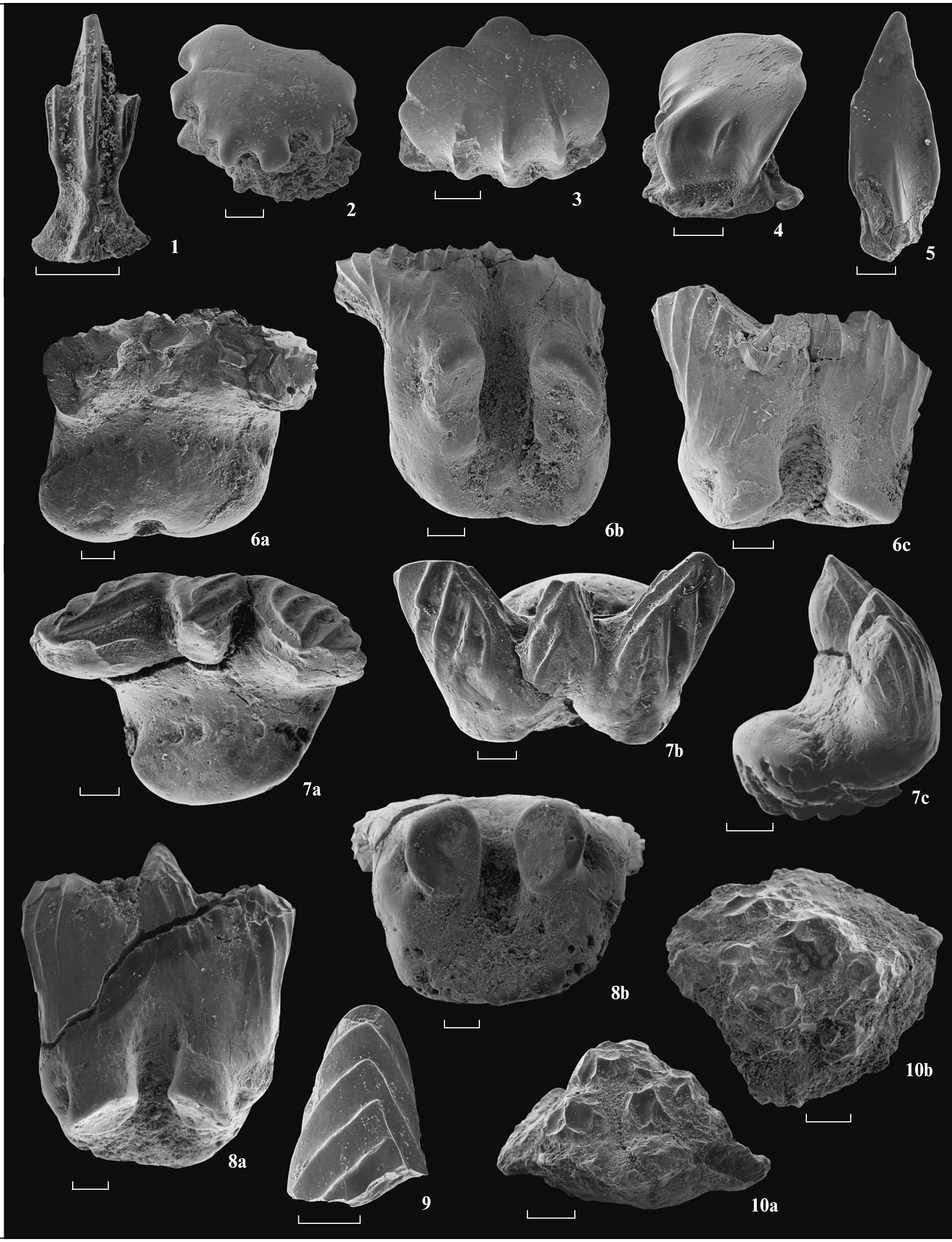
***Adamantina benedictae* Bendix-Almgreen, 1993**

Plate 10, Figs. 6–10

Adamantina benedictae: Bendix-Almgreen, 1993, s. 49–55, Figs. 3, 4; Ginter et al., 2010, p. 82, Fig. 75.

H o l o t y p e. NHMD VP 3331; East Greenland, south-east from Kap Storsch, River 14; Late Permian, Wuchiapingian, Foldvik Creek Group, Ravnefjeld Formation (Bendix-Almgreen, 1993).

Plate 10



D e s c r i p t i o n. The teeth possess a diplodont, tricuspid crown and a lingually extended base. The cusps are wide, rounded in basal cross section and slightly labio-lingually flattened at the cusp top, rather inclined lingually and fused at the base. The lateral cusps are considerably higher and wider than the central one from which they diverge mesially and distally. The labial face of the crown bears a strong ornamentation reaching to the lateral face. The ornamentation consists of coarse, spirally curved, lanceolate cristae varying from three in number on the central cusp to five on the lateral ones. The central part of the lingual face of the cusp lacks any ornamentation. The angles between the crown and base are blunt.

The tooth base is quite thick, varying from oval to almost rectangular with rounded edges, convex on the occlusal side and slightly concave on the basal side. The prominent occlusal thickness of the base is separated from the crown by a shallow longitudinal groove. The numerous vascular canals perforate the groove and form a row of foramina. The main vascular canal opens in the middle of the lingual rim. The base bears two labio-basal tubercles. They are massive, almost rounded to elongated oval, very prominent at the labio-basal rim, and have distinct margins except in the middle of the basal side. The axes of the tubercles are parallel with the lateral edges of the base. The tubercles are separated from each other by a deep and wide labio-basal depression that starts from the basal part of the central cusp in the crown and continues to the basal side of the base. One tooth (Plate 10, Fig. 6) has a slightly asymmetrical base concentrated mesiodistally.

The scale (Plate 10, Fig. 10) has convex external and basal surfaces and an almost rhomboidal base in coronal view. The scale crown consists of tubercles of different sizes arranged pyramidally; the larger central tubercles are surrounded by smaller ones. They are ornamented with curving and branching ridges formed in diamond-shaped structures. Some tubercles are fused, but sometimes separated by shallow grooves. The type series of *Adamantina benedictae* from East Greenland contains specimens with preserved squamation (Bendix-Almgreen, 1993). Two general types of scales are observed there: small and large rhomboidal ones predominate, while scales of the second type form a paired row and possibly belong to the lateral line canal. The scale from the Kanin Peninsula described herein belongs to the second type.

C o m p a r i s o n. The teeth of *Adamantina foliacea* Ivanov have three or five cusps in the crown (Ivanov, 1999). Howerver, the tricuspid teeth of later species differ from the teeth of *A. benedictae* in the higher central cusp, strongly labio-lingually flattened crown, regular lanceolate labial ornamentation, smaller rounded labio-basal tubercles, and a wider but shallow labio-basal depression.

O c c u r r e n c e. Late Permian, Wuchiapingian of East Greenland and Middle Permian, Kazanian of Kanin Peninsula, Russia.

M a t e r i a l. Three isolated teeth, two fragments of tooth cusps and a scale, Kanin Peninsula, Chiosha Bay, outcrop 1, at the Nadteysalya Cape, layer 2; "Ufimian", beds with the brachiopod *Burovia fredericksi*; outcrop 7, between the mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*.

SUBCLASS EUCHONDROCEPHALI LUND AND GROGAN, 1997

Superorder Holocephali Bonaparte, 1832-41

Order Cochliodontiformes Obruchev, 1953

Family Psephodontidae Jaekel, 1898

Genus *Kanodus* Lebedev, gen. nov.

E t y m o l o g y. From the first three letters of the name of the Kanin Peninsula and the Greek όδους-tooth.

T y p e s p e c i e s. *Kanodus robustus* Lebedev, sp. nov., Russia, Arkhangelsk Region, Kanin Peninsula, Middle Permian, Kazanian.

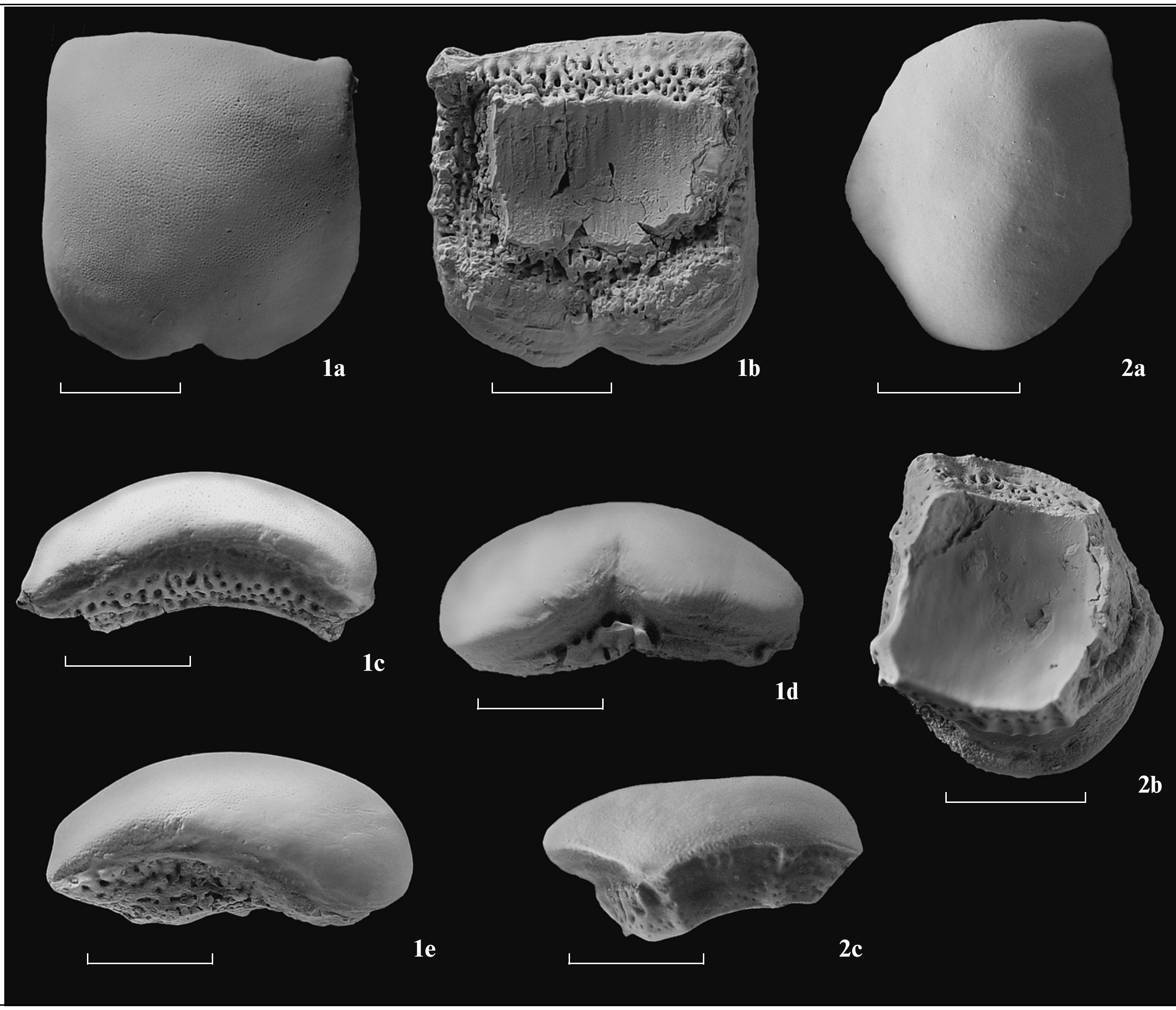
D i a g n o s i s. Psephodontid fish with robust upper and lower tooth plates of generalized "*Psepho-*

E x p l a n a t i o n o f P l a t e 1 0

Figs. 1–5. Euselachii gen. indet., scales; 1—morphotype 1, PM SPU 52-9; outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*, anterior view; 2—morphotype 2, PM SPU 52-10, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*; oblique crown view; 3–5—morphotype 3: 3—PM SPU 52-11; outcrop 1, at the Nadteysalya Cape, layer 2; "Ufimian", beds with the brachiopod *Burovia fredericksi*; anterior view, 4—PM SPU 52-12, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*, oblique lateral view; 5—PM SPU 52-13, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*, anterior view.

Figs. 6–10. *Adamantina benedictae* Bendix-Almgreen, 1993: 6–8—teeth: 6—PM SPU 52-14; outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*: 6a—occlusal, 6b—oblique basal and 6c—labial views; 7—PM SPU 52-15; outcrop 1, at the Nadteysalya Cape, layer 2; "Ufimian", beds with the brachiopod *Burovia fredericksi*: 7a—occlusal, 7b—labial and 7c—lateral views; 8—PM SPU 52-16; outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*: 8a—labial and 8b—basal views; 9—tooth cusp, PM SPU 52-17, outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*, labial view; 10—scale, PM SPU 52-18; outcrop 7, between mouths of the Nadtey and Krutaya rivers, layer 1; ?Urzhumian, beds with the brachiopod *Bajtugania kaninense*: 10a—lateral and 10b—crown views. 52-16, labial view Scale bars 200 μm.

Plate 11



Explanation of Plate 11

Figs. 1, 2. *Kanodus robustus* Lebedev, sp. nov.: 1—? lower parasymphysial tooth plate, holotype, PIN 4472/19; outcrop 18, between Nadtey River and Yarnisalya Cape, layer 1; Kazanian: 1a—occlusal, 1b—basal, 1c—labial, 1d—rostral and 1e—lateral views; 2—right upper tooth plate, GMM 839/79; outcrop between Nadtey River and Yarnisalya Cape; Kazanian, beds with the brachiopod *Kaninospirifer borealis*: 2a—occlusal, 2b—basal and 2c—lateral views. Scale bars 10 mm.

dus" design. Growth direction of the tooth plates (linguo-labial axis) perpendicular to the long axis of the jaw ramus. The squarish dome-like aspect of the aboral surface of the base shows no oblique twist which is typical of *Psephodus* tooth plates.

This tooth series presents at least two element types. "*Helodus*"-type elements were presumably present in the upper jaw, whilst a quadrangular, almost symmetrical tooth plate might be possibly associated with the lower jaw. An indentation is present in the middle of the lingual margin of the "lower" tooth plate. "Upper" tooth plate longer than broad, the coronal part strongly overhanging the basal part of the plate.

C o m p o s i t i o n. Type species only.

R e m a r k s. The new genus differs from the type genus of the family by possessing a symmetrical or almost symmetrical "lower" tooth plate. This suggests that the tooth plates were attached to a short, robust jaw with transversely disposed jaw rami, this being regarded a major characteristic of *Kanodus* gen. nov.

Kanodus robustus **Lebedev, sp. nov.**

Plate 11, Figs. 1–2

E t y m o l o g y. From the Latin *robustus*—thick.

H olotype. PIN no. 4472/19, ?lower parasymphyseal tooth plate; Russia, Arkhangel'sk Region, Kanin Peninsula, Chiosha Bay, between Nadtey River and

Yarnisalya Cape, outcrop 18, bed 1 by the description by A. Sultanaev, 1972; Middle Permian, Kazanian.

D i a g n o s i s. As for the genus.

D e s c r i p t i o n. The morphology of both tooth plates is suggestive of a perpendicular growth direction of the tooth plates (labio-lingual axis) relative to the axis of the jaw ramus. This is indicated by parallel growth lines on the aboral surface of the base. The base itself is strongly concave, hemispherical, suggesting that the cartilaginous jaws were very short, transversely directed and curved in the occlusal direction.

The tentative "lower" parasymphyseal tooth plate (Pl. 11, Fig. 2) is quadrangle-shaped in the plan view. The aboral surface of the base is much smaller than that of the crown, but its edges follow the outline of the latter, especially in the labial margin and part of the lateral side, where the tooth plate edge is well preserved. The tooth plate is almost symmetrical and does not show a characteristic oblique twist, which is present for example in *Psephodus dentatus* (Romanowsky, 1864) from the Tournaisian of Central Russia (Lebedev, 1996). The bilateral nature of the specimen on Pl. 11, Fig. 1 may be explained by its parasymphyseal position in the jaw, and very wide and short Meckelian cartilage.

The occlusal surface of the coronal part of the tooth plate is strongly convex. Its anterior (labial) part has two symmetrically disposed antemortem wear facets. Wear signs generally decrease linguad, towards the younger part of the tooth plate and for this reason, the lingual (posterior) quarter of the occlusal surface is almost completely covered with an almost unabraded layer of semitransparent enameloid mantling the orthotrabecular dentine that compose the bulk of the tooth plate. The incremental zones are hardly visible. The thickness of the coronal part increases linguad and reaches 10 mm, but the thickness is about 3 mm at its labial edge.

The labial margin of the coronal part is crescent-shaped; its structure is somewhat irregular. Whether one more tooth plates were situated in front (labially) of this plate, as in the upper jaw, is uncertain, because of the extreme antemortem wear which has decreased the coronal depth to a minimum. The base here is almost as thick as lingually; its surface slopes backwards abruptly. The area contacting the coronal part is compact and ornamented with weakly pronounced intercalating crests. On the basal area the crests form a mesh in which the pits house nutrient foramina.

The mesial and lateral margins are very similar in structure. The edge of the coronal part abruptly slopes down from the occlusal surface to meet the base; the vertical surface is slightly rugose, but does not show crenulations which are typical of *Psephodus*. The structure of the mesial and lateral sides of the base is similar to that of the labial margin.

The mesial and lateral margins extend posteriorly forming rounded lingual corners. The most conspicuous feature of the lingual margin is a deep symmetrical notch in the middle of the tooth plate. Within this notch the base thickens in occlusal direction. The enameloid layer of the coronal part of the tooth plate runs along the notch following its shape and almost reaches the occlusal surface. The vertical surface of the orthotrabecular dentine layer from this side is almost smooth, but the lower edge of the enameloid bears hardly visible sub-vertical rugosity. The notch suggests that the tooth plate is formed of two symmetrical parts.

The basal side of the tooth plate is only partially preserved. It is strongly concave and sculptured with labio-lingually directed swollen ridges which run parallel to each other.

In the "upper" tooth plate (Pl. 11, Fig. 2), the coronal part is pentagonal in plane view and the base is roughly square-shaped; the coronal part of the plate strongly overhangs the base. The plate is almost as long as it is wide. The occlusal surface of the coronal part is convex; it bears a swollen ridge running almost from the middle of the labial (anterior) edge towards the most arched part of the lingual (posterior) edge subdividing the occlusal surface into the mesial and lateral areas. The surface itself is smooth and shiny; it is covered with pores of the apical orthotrabecular canals. Examination of the surface in reflected light shows faint traces of incremental lines arched towards the lingual side and running from the mesial to the lateral margin.

The thickest part of the crown is the youngest, growing middle area of the lingual margin. Here it exceeds the depth of the base by approximately 1.5 times. The edge itself forms a semicircular projection strongly overhanging the base and extending from the mesio-lingual to the latero-lingual corner of the base. The lingual edge of the base is clearly separated from it and is ornamented with vertical ridges and grooves ending basally with large nutrient foramina.

The coronal part tapers on the mesial side of the plate so that only the base builds this margin. It is completely covered with large pores and 2–3 rough vertical ridges marking the contact area with the "*Helodus*"-type teeth.

The labial margin plane is strongly inclined inside. Its thick coronal part is almost smooth; the basal part bears numerous nutrient foramina. The morphology of the labial margin suggests the presence of at least one more tooth plate located in front (labially) and which contacted this area; otherwise the presence of this unworn and clearly distinct obtuse margin cannot be explained. An alternative growth pattern is demonstrated by the cochliodontids, in which the oldest (labial) part of the tooth plate forms a tapering whorl (for example, Stahl, 1999).

The lateral margin is damaged making it impossible to see the base.

The quadrangular, aboral side of the base is concave. Its surface is generally smooth, but in oblique light one can distinguish labio-lingually directed grooves marking the direction of tooth plate growth.

Occurrence. Only the type locality; possibly also the continental part of the Arkhangelsk Region, Russia (Minikh, Minikh, 1999).

Material. Holotype and GMM no. 839/79, right upper tooth plate; outcrop between Nadtey River and Yarnisalya Cape; Kazanian, beds with the brachiopod *Kaninospirifer borealis*.

DISCUSSION

Jalodontid Morphology

Recent description of new taxa from the Middle Permian of Texas, USA (Ivanov et al., 2012) makes possible the revision of the family Jalodontidae, formerly containing a single genus *Jalodus*. Now this family includes four genera: *Adamantina, Isacrodus, Jalodus*, and *Texasodus*.

The family Jalodontidae was assigned hitherto to the order Phoebodontiformes, but present study demonstrated that the jalodontids are characterized by peculiar features separating them from phoebodontiforms. Jalodontid teeth possess a crown with three to six cusps; the straight or slightly curved cusps with a distinct lanceolate ornamentation on the labial side; a thick base lacking a distinct apical button; one, two or four labio-basal tubercles separated by a short depression; the openings of main vascular canal at the lingual rim and a basal depression (Ivanov et al., 2012).

Kanodus Morphology

The establishment of a new genus *Kanodus* gen. nov. within the previously monotypic family Psephodontidae requires special comments. There are two arguments that forced us to erect the new genus. The major one is morphological and a second one is geochronological.

Symmetrical or almost symmetrical "lower" tooth plates have never been found for *Psephodus*. All previously known homological elements have been described as being rhomboid in outline (for example, Stahl, 1999) and asymmetrical. Moreover, all of them possess a characteristic twisting resulting from their growth direction which was oblique to the longitudinal jaw axis. The same comment can be made about the "upper" tooth plate in which the outline is of "traditional" *Psephodus* design, but the aboral surface of the base agrees in structure with that in the holotype: that is a general growth direction demonstrably transverse to the jaw ramus axis. These two specimens are referred to the same species and genus based on this unique feature, unknown in *Psephodus*, as well as the general robustness and similar appearance of pores on the coronal surface.

Apart from the indication of the growth direction, the hemispherical shape of the aboral surface of the base indicates a similar shape for the jaws onto which the tooth plates were apposed. In contrast to the twisted cylindrical shape in *Psephodus*, in which the jaw edge should be correspondingly semicylindrical, in *Kanodus* gen. nov. the tooth plate bearing part of the jaw should be hemispherical, requiring very short posterior parts and a transverse, highly arched and short symphyseal region in both jaws. This hypothetical structure of the jaw apparatus would not contradict the robust nature of the tooth plates themselves in regarding this fish as strongly durophagous, analogous to the condition in myliobatids (Cappetta, 1987).

There still remains uncertainty regarding the symphyseal or parasymphyseal position of the "lower" tooth plate in *Kanodus* gen. nov. The coronal part of the tooth plate is definitely symmetrical; symmetrical wear facets labially and a notch at the lingual side also support this conclusion. The aboral surface of the base also produces a bilaterally symmetrical impression; however, taking into account the incomplete preservation of a part of the base from one side, it might turn out to be slightly asymmetric, a tentative reason for regarding the holotype as possibly being parasymphyseal.

Psephodontids and Copodus

Another enigmatic Carboniferous order known only from isolated tooth plates is the Copodontiformes. The tooth plates of the members of this group are quadrilateral, almost flat or slightly convex and are often found in pairs, with posterior and anterior teeth together. Remarkably, most of the species of *Copodus* are known from the same localities yielding *Psephodus* specimens (Stahl, 1999). Whether some of the species of the only bilaterally symmetrical symphyseal *Copodus* teeth were parts of psephodontid dentitions containing symmetrical elements has never been substantiated.

In most cases, the coronal part of the teeth of the Copodontiformes is thinner than the base and extends beyond the coronal limits, contrary to the condition in *Kanodus* gen. nov. However, in *Copodus prototypus* (Davis, 1883) this is not the case and a restudy of this species may lead to a reevaluation of its position.

Distribution of taxa

A list of chondrichthyan taxa from the Permian deposits of the Kanin Peninsula is as follows:

Stethacanthus cf. *S. altonensis* (St. John et Worthen, 1875); teeth

Symmoriida gen. indet.; denticles from the spine-brush complex, buccopharyngeal denticles

"*Ctenacanthus*" sp.; tooth

"*Lissodus*" sp.; tooth

Euselachii gen. indet.; scales

Adamantina benedictae Bendix-Almgreen, 1993; teeth and scale

Kanodus robustus Lebedev, sp. nov.; tooth plates.

Stethacanthus occurs from the Late Devonian to the Middle Permian in different regions of the world. *Stethacanthus altonensis* (St. John et Worthen) is known from the Early Carboniferous (Serpukhovian) of Scotland; the Carboniferous of USA and Moscow Syneclise, Russia; the Carboniferous—Early Permian of the Urals, Russia; the Permian of the Arkhangelsk Region including the Kanin Peninsula (Ivanov, 1999; Minikh, 2004; Ginter et al., 2010). "*Ctenacanthus*" *costellatus* Traquair is found in the Viséan, Early Carboniferous of Scotland (Ginter et al., 2010).

Palaeozoic teeth of "*Lissodus*" range from the Late Devonian (Famennian) to the Middle Permian (Minikh and Minikh, 1996; Ginter et al., 2010). "*Lissodus*" *wirksworthensis* Duffin is known from the Early Carboniferous (Viséan) of England and the Kuznetsk Basin, Russia (Duffin, 1985; Rodina and Ivanov, 2002). Early Permian representatives of "*Lissodus*" are common: "*L.*" *sardiniensis* Fisher, Schnieder et Ronchi was described from the Gzhelian–Asselian of Italy; "*L.*" cf. "*L.*" *lacustris* Gebhardt—from the Asselian of Germany and "L" cf. "*L.*" *zideki*—from the Sakmarian of France (Fisher et al., 2010); "*L.*" *zideki* (Johnson)—from the Artinskian-Kungurian of Texas, USA (Johnson, 1981). "*Lissodus*" *bigibbus* A. Minikh was reported from the Kazanian, Middle Permian of Tatarstan, Russia (Minikh and Minikh, 1996).

Adamantina benedictae Bendix-Almgreen, apart from the Permian of the Kanin Peninsula, occurs in the Late Permian Ravnefjeld Formation of Eastern Greenland (Bendix-Almgreen, 1993). This formation has been assigned to the Wuchiapingian on the basis of its conodont assemblage (Rasmussen et al., 1990). The teeth of a second species of *Adamantina, A. foliacea* Ivanov, were recorded in the Tournaisian of the South Urals, the Asselian of the Polar Urals, the Artinskian of the Middle Urals, Russia, in the Late Pennsylvanian of Iowa, USA, as well as in the Roadian part of the Cutoff Formation (Middle Permian, Guadalupian) in the Guadalupe Mountains, West Texas, USA (Ivanov, 1999; Ivanov et al., 2012).

Numerous psephodontid species (until now ascribed to the genus *Psephodus*) are known mostly from the Early Carboniferous of the British Isles, Belgium, Russia and Mississippian of the United States. Only a few species survive into the Permian (*P. depressus* Waagen, 1879 and *P. indicus* Waagen, 1879) from the *Productus* limestone of Pakistan. Unfortunately, the preservation of the latter species is incomplete and the original illustrations are poor making comparison to the newly discovered materials difficult. A poorly preserved large and thick quadrilateral tooth plate is known from the Kazanian Stage of Kazan' City, Russia. *Psephodus* sp. was mentioned in faunal lists of Minikh and Minikh (1999) from the Kazanian of the Pinega River, Arkhangelsk Region, Russia.

The discovery of *Stethacanthus* in the Middle Permian of Russia is the youngest occurrence in the world. Alternatively, the occurrence of *Adamantina benedictae* in the second region, the Kanin Peninsula, in the Middle Permian is older than that in Greenland.

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