Devonian acanthodians from Severnaya Zemlya Archipelago (Russia)

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ABSTRACT
Acanthodians from the stratigraphic interval of late Pridoli (Late Silurian) to Givetian (Middle Devonian) are studied. Based on 48 acanthodian taxa, biostratigraphic zones are established within the late Pridoli (*Poracanthodes punctatus* Zone, Krasnaya Bukhta Formation) and Lochkovian (*Nostolepis minima* Zone), the latter divided into two subzones: *Poracanthodes menneri* (Severnaya Zemlya Formation) and *Diplacanthus poltnigi* n. sp. (Pod"emnaya Formation). Two more biostratigraphic units are characterised by index species, but they have no acanthodian-based boundaries (separated by intervals without effective acanthodian characteristics). These are beds with *Watsonacanthus costatus* n. sp. typical for the Emsian Rusanov and lower Al'banov formations, and Eifelian? or Eifelian/Givetian? beds with *Diplacanthus solidus* n. sp. (Vstrechnaya Formation). Five new genera and 14 new species are described. They are based on articulated specimens from the topmost Severnaya Zemlya Formation (*Acritolepis ushakovi* n. gen., n. sp., *A. urvantsevi* n. gen., n. sp., *Acanthacanthus ornatus* n. gen., n. sp., *Nostolepis decora* n. sp., *N. fragilis* n. sp., *Acanthopora transitans* n. gen., n. sp. and *Acanthospina irregulare* n. gen., n. sp.) or on isolated scales identified from different formations (*Nostolepis timanica* n. sp., *N. watsoni* n. sp., *Watsonacanthus costatus* n. sp., *Diplacanthus poltnigi* n. sp., *D. solidus* n. sp., *Gomphonchus nordicus* n. sp. and *Arcticacanthus bicostatus* n. gen., n. sp.).

KEY WORDS
Acanthodii,
Lower to Middle Devonian,
Severnaya Zemlya Archipelago,
Russia,
new genera,
new species.

RÉSUMÉ
Les acanthodiens dévoniens de l'archipel de Severnaya Zemlya (Russie).
Les acanthodiens présents dans l'intervalle stratigraphique du Pridoli supérieur (Silurien supérieur) au Givétien (Dévonien moyen) sont étudiés. À partir de 48 taxons d'acanthodiens, les zones stratigraphiques du Pridoli supérieur (Zone à *Poracanthodes punctatus*, Formation de Krasnaya Bukhta) et du Lochkovien (Zone à *Nostolepis minima*) ont été établies. Cette dernière zone est divisée en deux sous-zones : *Poracanthodes menneri* (Formation de Severnaya Zemlya) et *Diplacanthus poltnigi* n. sp. (Formation de Pod"emnaya). Deux autres unités biostratigraphiques ont été définies par des espèces index : l'unité à *Watsonacanthus costatus* n. sp. rattachée aux formations emsiennes de Rusanov et de l'Al'banov inférieur et l'unité à *Diplacanthus solidus* n. sp. (Formation de Vstrechnaya) d'âge Eifélien ? ou Eifélien/Givétien ? Ces unités sont délimitées par des intervalles non définis car ne présentant pas d'acanthodiens stratigraphiquement caractéristiques. Cinq nouveaux genres et 14 nouvelles espèces sont décrits. Ils sont basés sur des spécimens articulés du sommet de la Formation de Severnaya Zemlya (*Acritolepis urvantsevi* n. gen., n. sp., *A. ushakovi* n. gen., n. sp., *Acanthacanthus ornatus* n. gen., n. sp., *Nostolepis decora* n. sp., *N. fragilis* n. sp., *Acanthopora transitans* n. gen., n. sp. et *Acanthospina irregulare* n. gen., n. sp.) ou sur des écailles isolées récoltées dans différentes formations (*Nostolepis timanica* n. sp., *N. watsoni* n. sp., *Watsonacanthus costatus* n. sp., *Diplacanthus poltnigi* n. sp., *D. solidus* n. sp., *Gomphonchus nordicus* n. sp. et *Arcticacanthus bicostatus* n. gen., n. sp.).

MOTS CLÉS
Acanthodii,
Dévonien inférieur et moyen,
archipel de Severnaya Zemlya,
Russie,
nouveaux genres,
nouvelles espèces.

INTRODUCTION

The end of the 1970s was the most successful period of field sampling of Severnaya Zemlya acanthodians. Detail field work on the October Revolution Island in 1978 allowed the discovery of the first Early Devonian articulated acanthodians ever known from Arctic Russia and until now they remain the only elements for biogeographical correlation with other regions. Rock samples for microremains were collected in 1978. Acetic acid dissolution of these samples has enriched the collection of acanthodian microremains (scales and spine fragments) referred to in this article. Apart from this material, samples collected by E. Kachanov and M. Gagiev (Magadan, Russia), on Pioneer Island in 1976, and by E. Mark-Kurik (Tallinn, Estonia) and A. Khapilin (St. Petersburg, Russia), on Komsomolets Island in 1979, have also been included in this study.

The uninterrupted bed-by-bed sampling of Lower and Middle Devonian rock sequence, mainly represented by Old Red Sandstone facies, was impossible because of the hardly cemented, siliceous and mainly non-carbonate rocks. Therefore acanthodians are restricted to selected stratigraphic levels. Microremains of other fish groups could also be recovered only from dissoluble rocks. Thus large or smaller parts of several formations did not deliver any information on acanthodians; this concerns the Givetian Vatutin Formation, the lower part of Vstrechnaya Formation (Eifelian?) and the upper Al'banov Subformation (Emsian). Despite a sufficiently detail sampling, the lower part of Pod''emnaya Formation (Lochkovian) has yielded only three transitional acanthodian

species. Thus with biostratigraphic respect, it is conventionally joined with its well characterised upper part. The absence of acanthodian-based biostratigraphic unit for the Spokojnaya Formation (Pragian), is due to similar reasons. The gaps in the acanthodian vertical distribution reveal occurrences of beds with index species but without acanthodian-based joint boundaries.

Denser nearly bed-by-bed sampling for microremains has been done within the Eifelian formations in order to establish an assemblage-based correlation with well documented related facies of the Baltic basin. These intervals concern the outcrop 5, beds 48-153 and outcrop 7, beds 2-18 along the Matusevich River (58 samples in the Al'banov-Vstrechnaya-Vatutin formations) and several levels at the Ushakov River (26 samples from the outcrops 25, 26 and 27 in Al'banov-Vstrechnaya formations).

An incomplete stratigraphic distribution of taxa did not allow us to establish an acanthodian zonal scheme for the entire time interval under study. Zonation is acceptable only for the Pridoli (Late Silurian) and the Early Devonian (Lochkovian). Pridolian acanthodians are included for comparison with the earliest Devonian assemblage and certainty of acanthodian-based regional boundary of Pridoli/Lochkovian.

SYSTEMATICS

Only the new acanthodian taxa are described. For the known species photographic illustrations are provided and their stratigraphic distribution is summarised in Tables 2 and 3.

An exception is made for the poracanthodids, due to difficulties to identify their species, since the Severnaya Zemlya examples demonstrate several differences from the published material. Short descriptions and discussions on morphologic and histological characters are summarised in Remarks.

The whole collection is stored in the Museum of Lithuanian Institute of Geology and Geography (LIG) in Vilnius, under catalogue number 35.

Order CLIMATIIFORMES Berg, 1940
Suborder and Family indet.

Genus *Acritolepis* n. gen.

TYPE SPECIES. — *Acritolepis ushakovi* n. gen., n. sp.

ETYMOLOGY. — From *Acritos* (Greek): stumbling, mixed; and *lepis* (Greek): scale.

OTHER SPECIES INCLUDED. — *Acritolepis urvantsevi* n. gen., n. sp.

AGE. — Early Devonian, early Lochkovian.

DIAGNOSIS. — Small-sized moderately deep-bodied climatiid with lowly erected longitudinally six-ribbed dorsal spines, long thick-walled eight-ribbed pectoral spines and slender cylindrical scapula. Spines composed of highly vascularised bone and mesodentine. Prepectoral spines, tectal plates of the shoulder girdle region and jawbones with teeth are present. Body scale crowns flattened and elongated with short anterior ridges, composed dominantly of Stranggewebe and simple mesodentine.

DISCUSSION

The taxonomic position of *Acritolepis* n. gen. among Climatiiformes is hardly recognisable. Fin spines in most representative Climatiidae are short and stout, sometimes robust, mainly ornamented by beaded, nodose or tuberculated ribs, rarely with distal denticles. Smooth, moderately slender ribs are only present in *Euthacanthus* Powrie, 1864 (Denison 1979). The presence of two dorsal fin spines, proposed by Gagnier & Wilson (1995, 1996b) in the precise diagnosis of the order, remains almost the only feature occurring in *Acritolepis* n. gen., but their shape and insertion points are only comparable to *Vernicomacanthus* Miles, 1973 (long anterior dorsal inserted behind the pectorals and posterior dorsal inserted behind pelvic spine). The posterior dorsal spine is longer than the anterior one, a feature mentioned in *Brachyacanthus* Egerton, 1860, *Lupopsyrus* Bernacsek & Dineley, 1977 and *Brochoadmones* Bernacsek & Dineley, 1977, which essentially differ by other peculiarities. The first two genera are characterised like *Acritolepis* n. gen. by a position of the posterior dorsal spine opposite the anal. The new genus is especially distant from most Climatiidae by lack of intermediate spines.

TABLE 1. — Measurements in mm of *Acritolepis ushakovi* n. gen., n. sp.

Specimen LIG-	Visible spine length					Length between		
	Pectoral	Pelvic	Anal	Dorsal anter.	Dorsal poster.	Rostr.-Dors. anter.	Dorsals	Dors. poster.-Caud.
35-380 (holotype)	14.6	10.1	9.3	11.9	10.2	20.0	17.8	16.2
35-348			3.1	14.9	17.0		17.0	16.0
35-384				20.5	9.0		23.8	
35-371	16.0		11.0					

Specimen LIG-	Height at the		Visible length	Supposed length	Depth/ supposed length ratio
	Dorsal anter.	Dorsal poster.			
35-380 (holotype)	15.1	16.0	54.0	70-73.0	0.22
35-348		14.8	39.5	60-62.0	0.24
35-384			59.0	80-83.0	
35-371					

A dermal shoulder girdle is developed in many genera (Miles 1966, 1973; Denison 1979). Rare exceptions are the highly specialized *Brochoadmones* (Bernacsek & Dineley 1977; Gagnier & Wilson 1996a) and *Kathemacanthus* Gagnier & Wilson, 1996 (Gagnier & Wilson 1996b). One or two pairs of prepectoral spines are present also in most genera, excepted *Erriwacanthus* Ørvig, 1967 and *Climatius* Agassiz, 1845, which possess three pairs of spines. In *Acritolepis* n. gen. distinct dermal shoulder plates cannot be recognized, but they are supposed according to associated fragments of plates with stellate tubercles or other comparatively high tectal elements. An articulation of pectorals to scapulocoracoid can also be supposed. Jaw bones bear ankylosed teeth (main cusps with intercusps) which are close to *Nostolepis* Pander, 1856 (Gross 1957), but this occur in other genera (*Parexus* Agassiz, 1845, *Vernicomacanthus*, *Ptomacanthus* Miles, 1973, *Climatius* and *Brochoadmones*) supplied with tooth whorls, which have not been observed in *Acritolepis* n. gen. It differs also from *Nostolepis* by the squamation: poorly ridged crowns of scales, peculiarities of dentine composition, mesodentine and bone ("*Nostolepis*"-type histology) demonstrate many similarities, but a possession of tooth whorls, spines with nodose ridges lacking inserted base and presence of intermediate spines, does not occur in *Acritolepis* n. gen. This indicates a distant relationship. This can supposedly also be said for *Canadalepis* Vieth, 1980 (Vieth 1980) of which the histological structure of scales remains insufficiently studied (see Discussion in description of *A. urvantsevi* n. gen., n. sp.).

By its relatively deep body (maximum depth to length ratio of 0.22-0.24, if we are not mistaken in our reconstruction of the missing parts), its high scapula, long strongly ribbed fin spines, deeply inserted dorsals, the posterior one situated approximately opposite the anal, the new genus is close to representatives of the Diplacanthidae (Denison 1979). The main differences observed in *Acritolepis* n. gen. are as follows: presence of teeth, a cylindrical scapula (it is angulate in diplacanthids), absence of intermediate spines, reduced inserted parts of the spines and lower insertion angle. Scale histology in

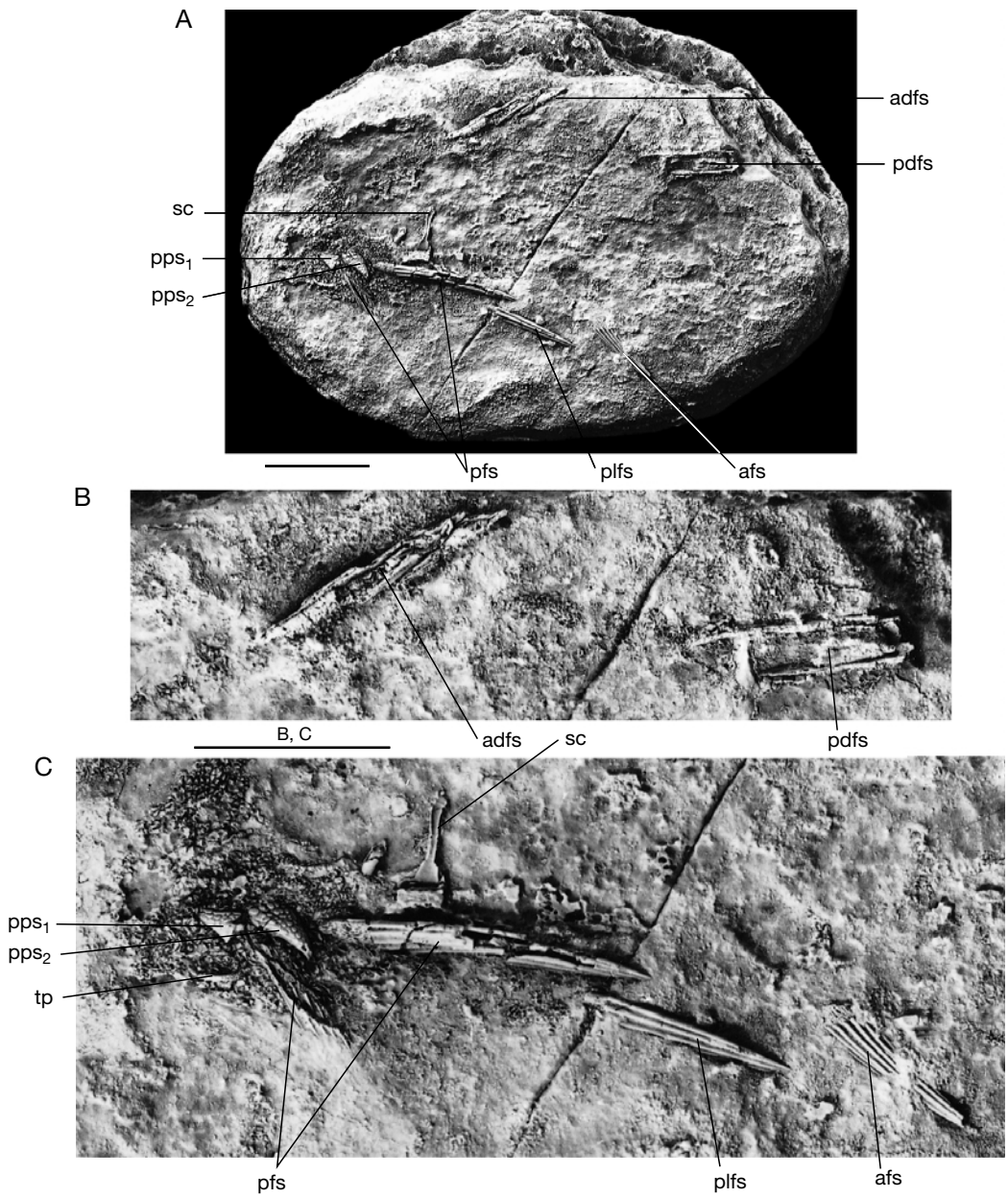


FIG. 1. — *Acritolepis ushakovi* n. gen., n. sp., Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation; **A**, general lateral view, anterior to left, holotype (LIG 35-A-380); **B**, enlarged area with anterior and posterior dorsal fin spines; **C**, enlarged area with paired pectoral and prepectoral, unpaired pelvic and anal spines, scapula, head covering plates-tesserae and squamation. Abbreviations: **adfs**, anterior dorsal fin spine; **afs**, anal fin spine; **pdfs**, posterior dorsal fin spine; **pfs**, pectoral fin spine; **plfs**, pelvic fin spine; **pps$_1$**, **pps$_2$**, first and second prepectoral spines; **sc**, scapula; **tp**, tectal plate. Scale bars: 10 mm.

diplacanthids (*Diplacanthus* Agassiz, 1844, *Rhadinacanthus* Traquair, 1888, *Ptychodictyon* Gross, 1973) with its characteristic style of principal vascular canals (penetrating especially the base), lack of Stranggewebe, etc. (Valiukevičius 1985, 1995b), has lead to propose a separate order Diplacanthiformes. All above mentioned affinities and differences lead to maintain the new genus in an uncertain taxonomic position.

Acritolepis ushakovi n. sp.
(Figs 1-12)

HOLOTYPE. — LIG 35-A-380. Adult specimen missing head and tail, in lateral view. Articulated anterior and posterior dorsal, pectoral, pelvic and anal fin spines, two prepectorals, scapula, head covering plates, tesserae-scales, trunk scales (Figs 1; 2). Matusevich River, outcrop 1, bed 21.

PARATYPES. — LIG 35-A-384: articulated dorsal fin spines in lateral view and squamation in dorsal view (Fig. 4A-C, E); LIG 35-A-385: spine fragments, tesserae-scales and trunk scales; LIG 35-A-390: jawbone with teeth in lateral view (Fig. 3A), disarticulated scales and denticulate tectal plates; LIG 35-A-404: articulated specimen in lateral preservation exposing squamation (trunk scales, tesserae-scales, tesserae) and fragments of spines, fully dissolved during preparation; LIG 35-A-348: specimen in lateral view with dorsal fin spines, fragment of anal spine and squamation (Fig. 2B). All specimens from the Spokojnaya River, outcrop 41, bed 12; LIG 35-A-371: articulated specimen with pectoral and anal(?) fin spines in inner view, scapula, tesserae and tectal plates of prepectoral area and intact scales (small and enlarged, tesserae-like); LIG 35-A-386: specimen exposing jawbone, articulated teeth (main cusps, intercusps and palatine), denticles, branchial(?) cones, tectal plates, denticulate tesserae-scales and tesserae of polyodontode type (Fig. 3B, C). Both specimens from the Matusevich River, outcrop 1, bed 21.

ETYMOLOGY. — In honour of one of the first discoverer and researcher of Severnaya Zemlya Archipelago: G. A. Ushakov (Russia).

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 1, bed 21; Spokojnaya River, outcrop 41, bed 12. Top of the Severnaya Zemlya Formation, Lower Devonian, lower Lochkovian.

DIAGNOSIS. — Moderately deep-bodied climatiid with two lowly erected dorsal fin spines, long pectorals, two pairs of prepectorals; no intermediates; anal spine opposite to posterior dorsal, and pelvic midway between pectorals and anal; spines longitudinally ribbed, composed of acellular bone and highly vascularised mesodentine (outer part); slender, cylindrical scapula with wide procoracoid? blade; jaw bones with ankylosed principal cusps and intercusps of trabecular dentine; tuberculate or denticulate tectal plates, polyodontode tesserae and denticulate tesserae-scales composed of mainly acellular bone (basal parts), vascularised osteon-bearing cellular bone (middle) and mesodentine (superficial layer); uniform body scales with short-ridged and flattened crowns, composed of durodentine (superficial strip), simple mesodentine and Stranggewebe restricted to each growth lamella, and bases of variable cellular bone.

DESCRIPTION

Body shape and proportions

Described from specimens missing head and tail, preserved laterally flattened, *Acritolepis ushakovi* n. gen., n. sp. is a moderately deep-bodied (maximum depth to supposed length ratio of 0.22-0.24), small-sized (up to 80-83 mm long, based on proportions with the longest anterior dorsal spine in LIG 35-A-384) climatiid with two poorly erected, deeply inserted dorsal fin spines, the posterior longer and wider. The pectoral spines are longer than dorsals and inserted in a low lateral position. It possesses two pairs of prepectoral spines, and short anal and pelvic spines. The anal spine lays opposite or just in front of posterior dorsal, and pelvic one at midway between pectorals and anal. Measurements on Table 1.

Fin spines

Pectoral spines are thick-walled, with a single central cavity, open at parabasal part. They are slightly curved and ornamented with six to eight longitudinal ribs on each side (Figs 1C; 2A). The last three distal ribs near the inserted portion may be interrupted (tuberculated) or short, converging (Fig. 6A). Deep grooves separate them. The holotype demonstrates a shallow insertion (inserted part represents 2.2 mm of a whole 14.6 mm spine length). Spines are sharpened and show in section at the base a flattened horseshoe form, a rounded isosceles triangle in the middle part and blunt triangle form at the tip. Prepectoral spines (Fig. 2A) are different both in size and proportions; it is why they are treated as two pairs. The anterior is 1.6 mm in length with

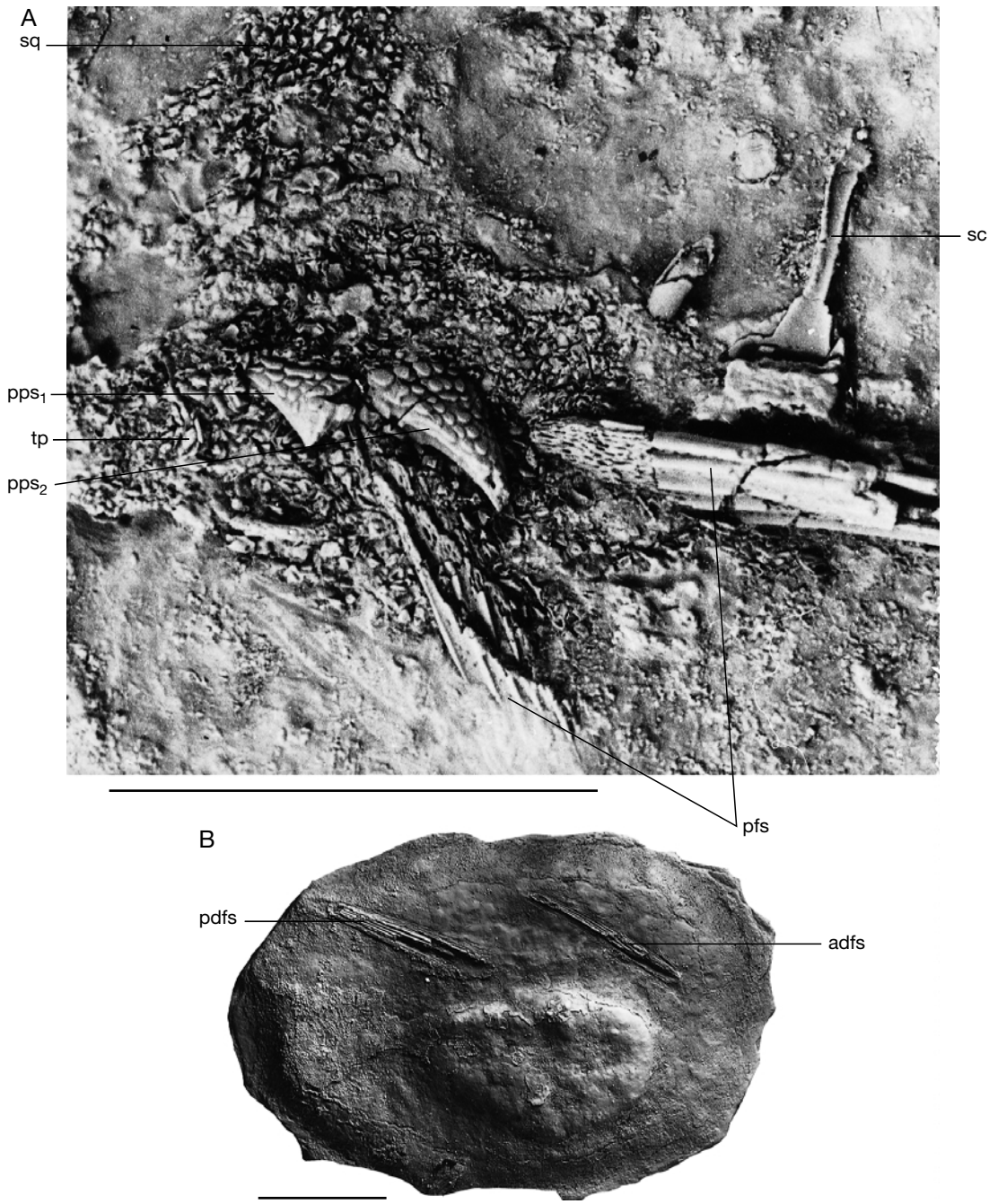


FIG. 2. — *Acritolepis ushakovi* n. gen., n. sp., Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **A**, detailed rostral part of the holotype (LIG 35-A-380) with tuberculated prepectorals, head tesserae and tectal plates, lateral view; **B**, paratype (LIG 35-A-348), lateral preservation, anterior to right, anterior and posterior dorsal fin spines, fragment of anal spine, squamation. Abbreviations: **adfs**, anterior dorsal fin spine; **pdfs**, posterior dorsal fin spine; **pfs**, pectoral fin spine; **pps_1**, **pps_2**, first and second prepectoral spines; **sc**, scapula; **sq**, squamation; **tp**, tectal plate. Scale bars: 10 mm.

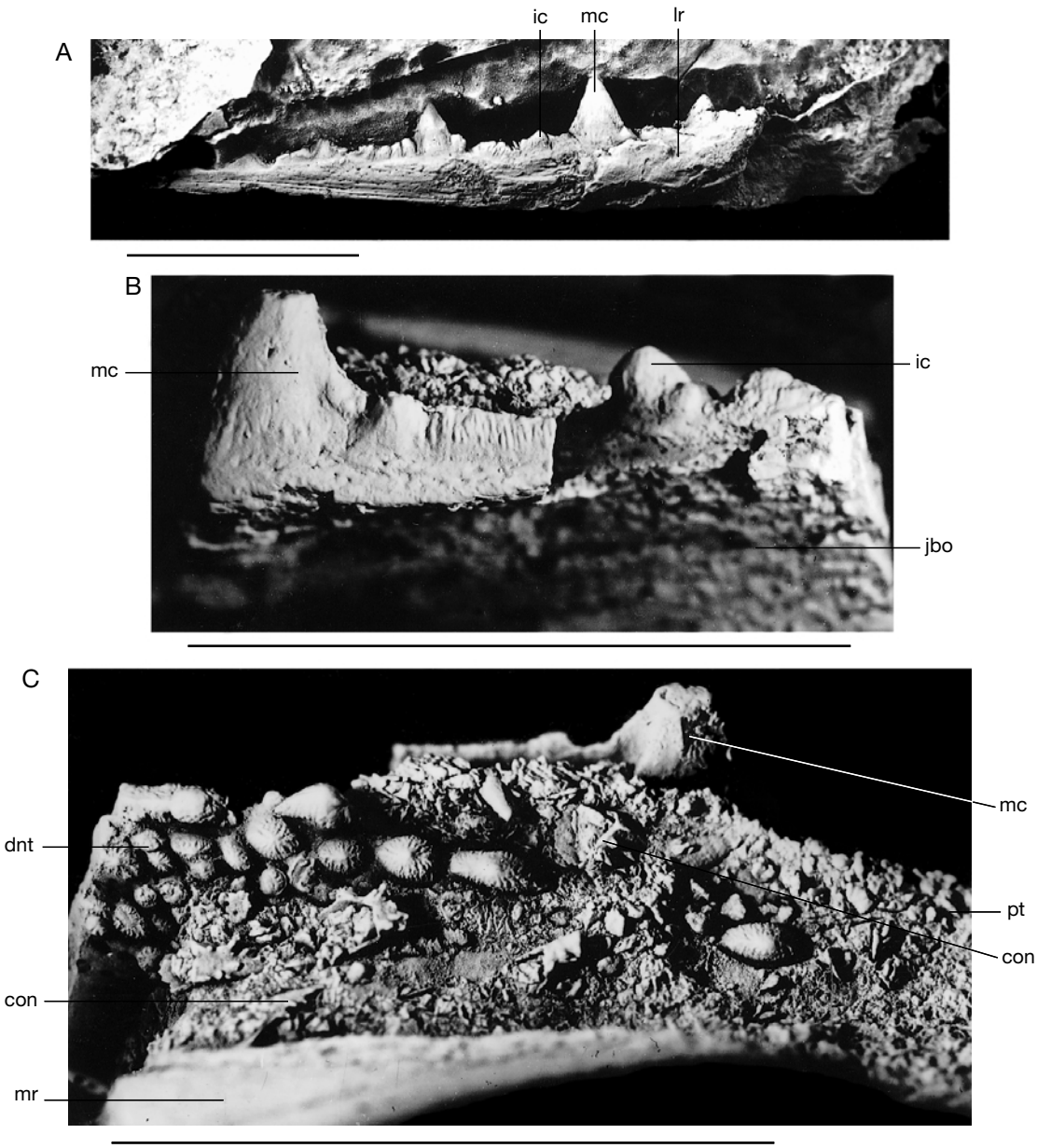


Fig. 3. — *Acritolepis ushakovi* n. gen., n. sp.; **A**, jawbone with the main and intercusps, lateral view, paratype (LIG 35-A-390), Spokojnaya River, outcrop 41, bed 12; **B**, **C**, jawbone with teeth of the lateral row, denticles, palatine teeth and branchial? cones in lateral view (**B**) and medial-occlusal view (**C**), paratype (LIG 35-A-386), Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation. Abbreviations: **con**, branchial? cone; **dnt**, denticle; **ic**, intercusp; **jbo**, jawbone; **lr**, lateral tooth row; **mc**, main tooth cusp; **mr**, medial ridge; **pt**, palatine tooth. Scale bars: 10 mm.

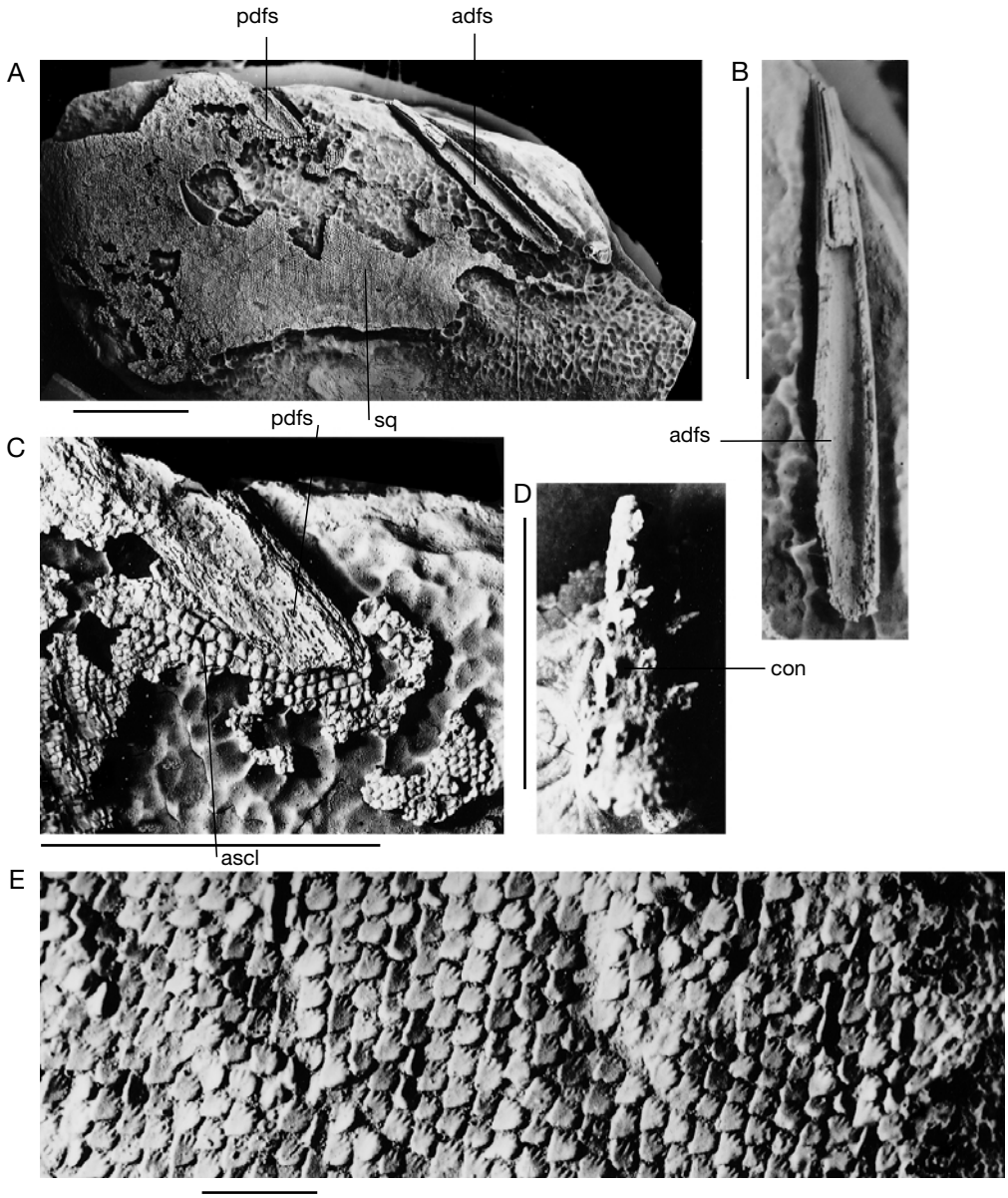


FIG. 4. — *Acritolepis ushakovi* n. gen., n. sp., Severnaya Zemlya Formation; **A**, paratype (LIG 35-A-384), lateral view, dorsal fin spines and squamation, anterior to right; **B**, magnified anterior dorsal fin spine of the same specimen; **C**, posterior dorsal fin spine with enlarged asymmetrical scales of the same specimen, Spokojnaya River, outcrop 41, bed 12; **D**, branchial? cone (LIG 35-2099) from the paratype LIG 35-A-386, Matusevich River, outcrop 1, bed 21; **E**, enlarged area of squamation with myomeric structures in the central part of paratype LIG 35-A-384, dorsal view, Spokojnaya River, outcrop 41, bed 12. Abbreviations: **adfs**, anterior dorsal fin spine; **ascl**, asymmetric magnified scales; **con**, branchial? cone; **pdfs**, posterior dorsal fin spine; **sq**, squamation. Scale bars: A-C, 10 mm; D, E, 1 mm.

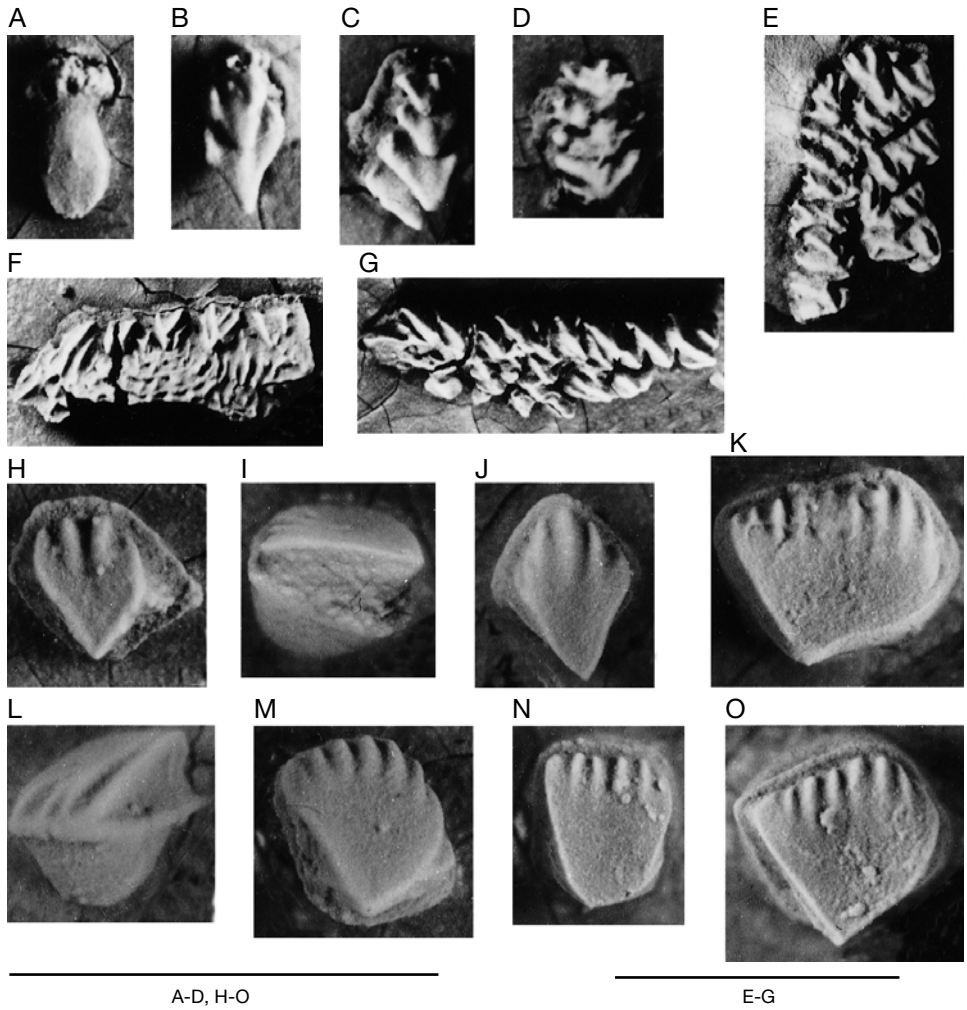


FIG. 5. — *Acritolepis ushakovi* n. gen., n. sp.; **A**, palatine tooth with bony base (LIG 35-2103); **B**-**D**, denticulate tesserae-scales of one-sided areal growth, crowns; **B**, LIG 35-2106; **C**, LIG 35-2105; **D**, LIG 35-2100; **E**-**G**, polyodontode-type tesserae of areal growth from the head area, crowns; **E**, LIG 35-2104; **F**, LIG 35-2102; **G**, LIG 35-2101, paratype LIG 35-A-386, Matusevich River, outcrop 1, bed 21; **H**-**O**, scales; **A**-**G**, scales from the paratype LIG 35-A-404, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **H**, LIG 35-2047, normal trunk scale, crown; **I**, LIG 35-2045, side view; **J**, LIG 35-2041, scale from the tail area, crown; **K**, LIG 35-2044, specialized asymmetrical tessera-like scale, crown; **L**, LIG 35-2042, trunk scale, side view; **M**, LIG 35-2046, asymmetrical scale, crown; **N**, LIG 35-2040, scale from the tail area, crown; **O**, LIG 35-2039, trunk scale, crown. Scale bars: 1 mm.

a base length of 2.4 mm and ratio of base length/spine length about 1.59. The second, situated closer to pectoral spines, show a length of 2.1 mm and a base length of 3.4 mm, with a ratio base length/spine length of about 0.6. Randomly distributed and extensively overlapping rounded tubercles compose their ornamentation. An arrangement in lines is partly seen on the second one. The most complete dorsal spines preserved on paratype LIG 35-A-348 have a length of 14.9 mm (for the anterior spine) and about 17 mm (for the posterior). Their basal width is 1.5 mm and 2.3 mm respectively. The biggest anterior dorsals might reach 23 mm in length (on paratype LIG 35-A-384) and posterior dorsals 26-27 mm. These spines are slightly

curved posteriorly, moderately erected, hollow, of a flattened rounded triangular form in section (Fig. 6B). Their sculpture is made of six longitudinal ribs. Specialized enlarged scales (Fig. 4A, C) surround the deeply inserted spine part. Pelvic and anal spines are shorter than pectorals (Fig. 1C), with six longitudinal ribs on each side. In morphological features they look identical to pectorals. The anal spine is inserted in the body musculature at a higher angle than dorsals. Large pore openings of vascular canals lay within the grooves on dorsal and pectoral spines.

The histological structure of spines is uniform. Two thirds of their walls are composed of dense, thin-lamellar acellular bone, lining the central cavity, which may be of a complicated configuration at the basal part (Fig. 8A). The outer third (ribbed spine part) is composed of highly vascularised mesodentine containing large longitudinal canals, contracted in mature spines by concentric denteons (Fig. 8A, B). Superficial canal openings connect with denteons of deeper layers. A network of short winding mesodentine tubules of "*Nostolepis*"-type includes a small number of lacunae.

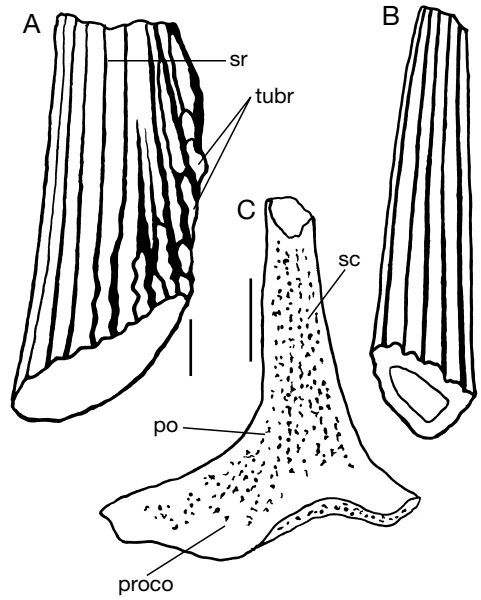


FIG. 6. — *Acritolepis ushakovi* n. gen., n. sp., drawings of selected elements of paratypes; **A**, part of pectoral? spine with longitudinally ribbed anterior and interruptedly ribbed (tuberculated) distal part (LIG 35-2138), paratype LIG 35-A-385, Spokojnaya River, outcrop 41, bed 12; **B**, middle? part of dorsal spine (LIG 35-2133); **C**, scapulocoracoid with openings of vascular canals (LIG 35-2124); **B**, **C**, from paratype LIG 35-A-371, Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation. Abbreviations: **po**, pore opening; **proco**, procoracoid; **sc**, scapula; **sr**, spine rib; **tubr**, tuberculated rib. Scale bars: 1 mm.

Shoulder girdle

A slender scapula of cylindrical form slightly narrowing upwards represents the dermal shoulder girdle; it measures 4 mm in height in the holotype (Fig. 1C) and 4.5 mm in LIG 35-A-371 (Fig. 6C). A wide basal blade (procoracoid?) with a deep groove for the pectoral spine(?) articulation makes a low cone with a parabasal diameter of about 4.1 mm (Fig. 6C). Its perichondral bone is highly vascularised; openings of large vascular canals on scapula walls are distributed randomly or in lines.

Dentition

The dentition is represented only by fragments of dentigerous jawbones with teeth of the main lateral row (32 mm long in paratype LIG 35-A-390 and 13.1 mm long in LIG 35-A-386); it also exposes ornamented denticles and palatine teeth. Firmly ankylosed principal cusps (five seen in LIG 35-A-390) of lateral biting edge have a triangular longitudinal and stretched rhombic transverse basal form with a rounded outer line. It bears an emerged inner keel, and shows sharp side flanges (Fig. 3A). The maximum cusp height is 2.1 mm in the first specimen and about 3.5 mm (with broken tip) in the second. It decreases in size in a row frontward. Main cusps may bear smaller lateral cusps. Three to four (Fig. 3A) intercusps are about one third as high as principals, essentially blunter and ornamented by vertical wavy interrupted groovelets (striated). Mesial side of the lateral ridge is covered by blunt striated denticles of irregular shape and height. Their parabasal form in transverse section changes from circular to oval. Several denticles are displaced between the lateral and mesial ridges (Fig. 3C). This area also bears randomly situated palatine teeth (Fig. 5A) of flattened and elongated sharp-flanged lingual form. They do not exceed 0.4 mm in length.

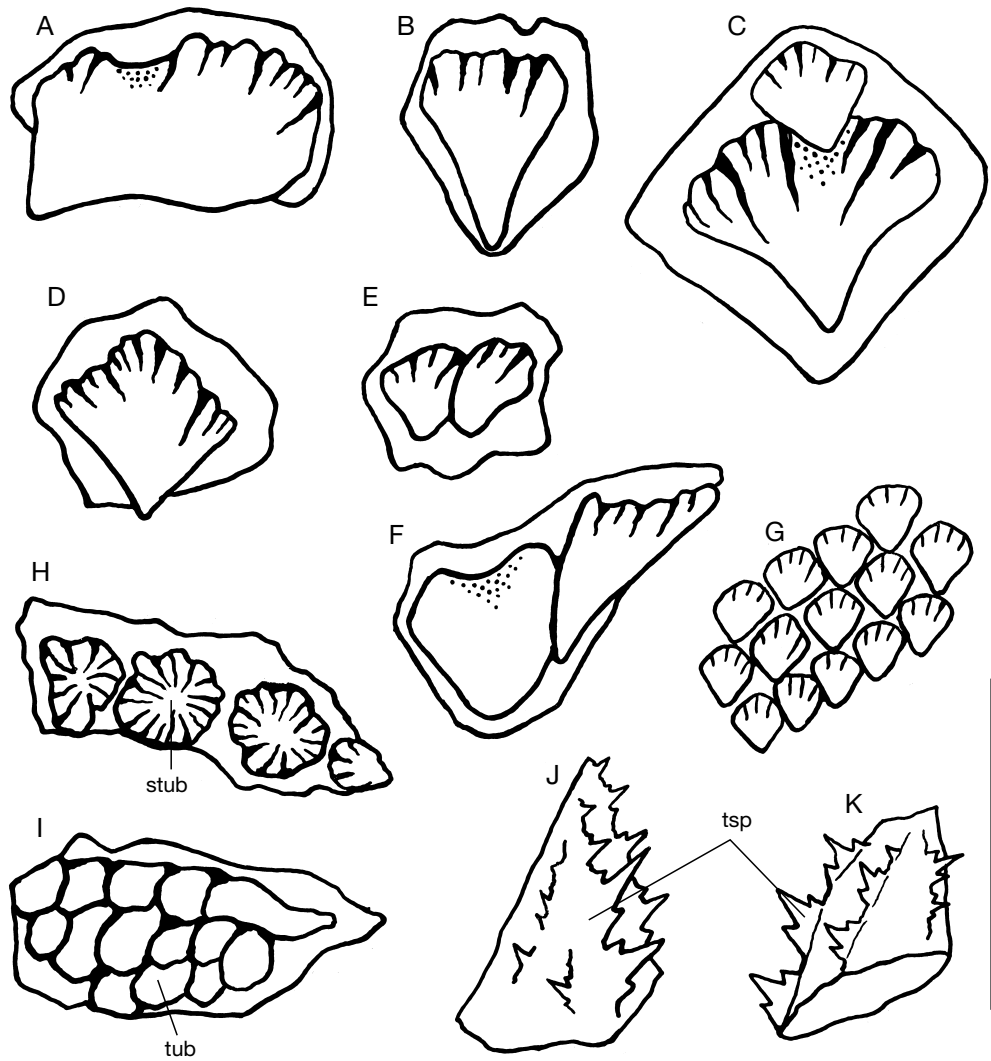


FIG. 7. — *Acritolepis ushakovi* n. gen., n. sp., drawings of selected elements of paratypes; **A**-**F**, head tesserae, crowns, anterior upwards; **A**, asymmetrical, two-crowned (LIG 35-2126); **B**, LIG 35-2125; **C**, rhombic, two-crowned, small anterior as a secondary scale (LIG 35-2137); **D**, LIG 35-2129; **E**, **F**, two-crowned, sidegrown; **E**, LIG 35-2127; **F**, LIG 35-2130; **G**, trunk scales, arrangement in lines without overlap (LIG 35-2134); **H**, **I**, tectal plates, with separated starlet-like striated denticles (**H**, LIG 35-2136) and with extensively overlaped unornamented tubercles (**I**, LIG 35-2131); **J**, **K**, branchial? cones with tricuspidate denticles, LIG 35-2122 (**J**) and LIG 35-2123 (**K**); **A**, **B**, **D**-**G**, **I**, from paratype LIG 35-A-371; **C**, from paratype LIG 35-A-385; **J**, **K**, from paratype LIG 35-A-386, Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation; **H**, from paratype LIG 35-A-390, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation. Abbreviations: **stub**, stellate tubercle; **tsp**, tricuspidate spinelet; **tub**, tubercle. Scale bar: 1 mm.

The teeth are composed of trabecular dentine (Fig. 9C) showing principal ascending canals and their obliquely upstream sideward branches. For principal cusps the material is supposed to be of specialized flange dentine (no section have been done).

Branchial? cones

The jawbone interridge area in LIG 35-A-386 bears separate random, hollow and thin-walled cones (Figs 3C; 4D; 7J, K); they are ornamented by linear perpendicularly or obliquely-directed mainly tricuspid spinelets.

Tectal plates and tesserae

The rostral area (anterior to shoulder girdle) of specimens (holotype, also LIG 35-A-371, LIG 35-A-386, LIG 35-A-390) is covered with three types of tesserae and plates. Polygonal irregularly shaped plates with extensively overlapping, rounded, flattened, unornamented tubercles (Fig. 7I) and with ridged stellate tubercles distributed without overlap (Fig. 7H) dominate on the shoulder girdle of the holotype (Fig. 1C). A first sort of plates resembles prepectorals in their ornament, whereas the second bears blunt denticles resembling those from the mesial side of lateral jawbone ridge. All plates are composed of three tissue layers (Fig. 9A, B): 1) basal: laminar, mainly acellular bone; 2) middle: highly vascularised cellular bone with distinct osteon structures filling gradually the principal vascular canals during growth; and 3) superficial (ornamented): certain "*Nostolepis*"-type mesodentine with dense network of winding, mainly up streamed dentine canals with lacunae-like widenings.

Polyodontode tesserae (Fig. 5E-G), the second plate type, are short and wide (1-1.4 mm). They are composed of numerous small odontodes growing in areal style. Like ordinary scales they have moderately convex bases and low necks. Some of these tesserae are distinguished by an anterior row of higher, separate odontodes, the remaining crown part consisting of poorly distinct odontodes: they are densely grown together into one compact flattened plate, concentrically striated by wavy grooves, lining the distal edge (Fig. 5F). This tesserae type is supposedly mainly connected with rostral head areas, represented in specimens exposing jawbones and dentition (LIG 35-A-386, LIG 35-A-390). Both varieties of the second-type tesserae have basal plates made of acellular thin-lamellar bone (Fig. 12A, B) and crowns with a slightly different composition. Crowns of the first variety show typical "*Nostolepis*" mesodentine with a network of winding dentine tubules, including lacunae (Fig. 12A). The junction strip between base bone and crown mesodentine contains principal circular vascular canals constricted by concentric denteons. The same mesodentine is only present in anterior odontodes in tesserae of the second type (Fig. 12B). These are secondary odontodes (added later). The main part, including primordial lamella, is composed of thin-lamellar dentine without vascular canals, except for the principal circular ones, located higher in the neck.

The third type is represented by denticulate tesserae-scales with one-side (posterior) areal growth (Fig. 5B-D). They are small (0.3-0.4 mm long) and represent transitional forms passing to typical trunk scales. Several (dominant 3-4)

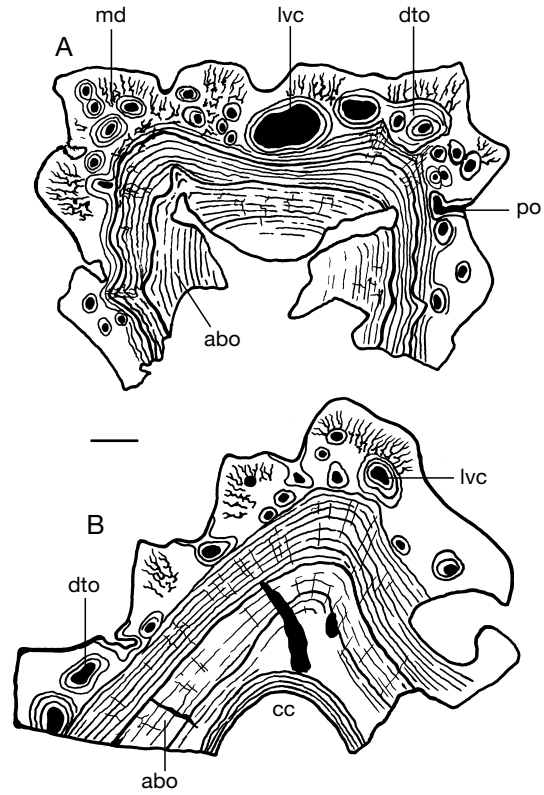


FIG. 8. — *Acritolepis ushakovi* n. gen., n. sp., mature spine histology, anterior upwards, from paratype LIG 35-A-404, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **A**, transverse section through the basal part, thin section 3490; **B**, transverse section through the middle part, thin section 3489. Abbreviations: **abo**, acellular bone; **cc**, central cavity; **dto**, denteon; **lvc**, longitudinal vascular canal; **md**, mesodentine; **po**, pore opening. Scale bar: 0.1 mm.

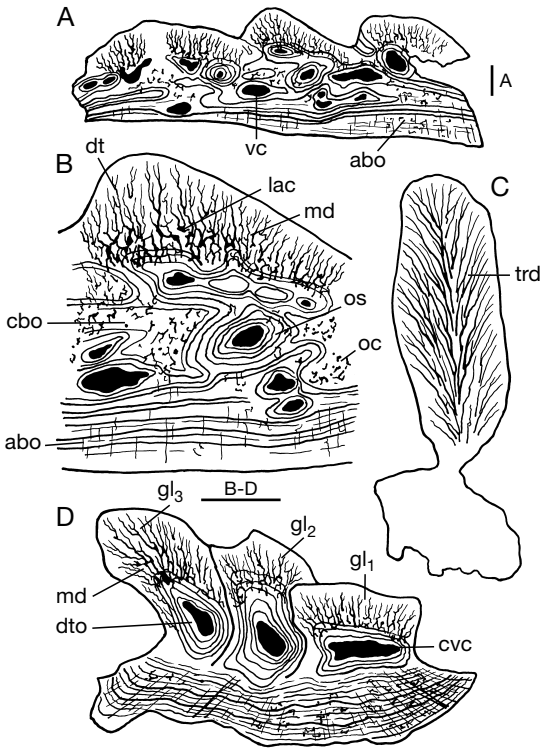


FIG. 9. — *Acritolepis ushakovi* n. gen., n. sp., histologic structure of separated elements, Severnaya Zemlya Formation; **A**, vertical section through the tectal plate with starlet-like stellate tubercles (LIG 35-2136), (see Fig 7H), thin section 3499; **B**, magnified area of the same plate, microstructure of the central tubercle; **A**, **B**, paratype LIG 35-A-390, Spokojnaya River, outcrop 41, bed 12; **C**, trabecular dentine of the palatine tooth (see Fig. 5A), thin section 3501; **D**, vertical longitudinal section through the denticled tessera-scale of one-sided areal growth (see Fig. 5C), anterior to right, thin section 3500; **C**, **D**, paratype LIG 35-A-386, Matusevich River, outcrop 1, bed 21. Abbreviations: **abo**, acellular bone; **cbo**, cellular bone; **cvc**, circular vascular canal; **dt**, dentine tubule; **dto**, denteon; **gl_1**, **gl_2**, **gl_3**, lamella of areal growth; **lac**, lacuna; **md**, mesodentine; **oc**, osteocyte cavity; **os**, osteon; **trd**, trabecular dentine; **vc**, vascular canal. Scale bars: 0.1 mm.

show unornamented or radially ridged crowns with extensive overlaps (up to half of length) joined by a common base. Base's bone contains rare osteocyte cavities (Fig. 9D); the neck area includes major circular vascular canals surrounded by wide strip of concentric denteons. The external mesodentine does not differ from that of other plates and tesserae.

Squamation

Except for the head and shoulder area, squamation is surprisingly uniform. Trunk scales small (0.17-0.32 mm long), with two to six parallel, short, rounded ridges, prolonging up to one third of crowns length, which is down sloping anteriorly. Low neck and convex, centrally or slightly anteriorly vaulted base (Fig. 5H-O) separated from the neck by a rim of sub-rhombic outline. Scales, recognized as tail scales, are narrower and longer (Fig. 5J, N). At the posterior dorsal spine in LIG 35-A-384 (Fig. 4C) we can see small area of magnified, slightly asymmetric scales with increased number of ridges (eight) like figured on Fig. 5K. Scales displaced densely in oblique lines without overlap (Fig. 4E). Trunk and tail scales composed of cellular bone (base), durodentine and mesodentine (crown) (Fig. 10). Superpositional growth type. Cellular bone extremely thin-lamellar, with well defined long Sharpey's fibres of longitudinal and perpendicular orientation (Fig. 10D, F) and inconstant number of osteocyte cavities. Simple mesodentine composes anterior, whereas Stranggewebe the posterior parts of every growth lamella, including primordial. Their number does not exceed four. Stranggewebe surrounded by outer strips of simple networked mesodentine. Osteocyte cavities and lacunae meet high, even in the superficial layer of primordial lamella, but never in the last formed, which are partly composed of durodentine. Scales only rarely show presence of large circular vascular canals (Fig. 10A) displaced over the base.

The scale-like crowned tesserae (Fig. 7A-F) consist of ridged rhombic, leaf-shaped elongated or widened asymmetrical crown, on a variable base exceeding crowns measurements. Tesserae may be two-crowned (Fig. 7C, E, F) side grown or grown antero-posteriorly, with smaller secondary proximal crown (Fig. 7C). These are found on the head area. One-crown tesserae are similar to trunk scales in histological structure (Fig. 11B). Differently from them, base plate composed of highly cellular bone and crown contained better developed enlarged radial and ascending vascular canals. Two-crowned (without overlap) tesserae (Fig. 11A) show histological structure

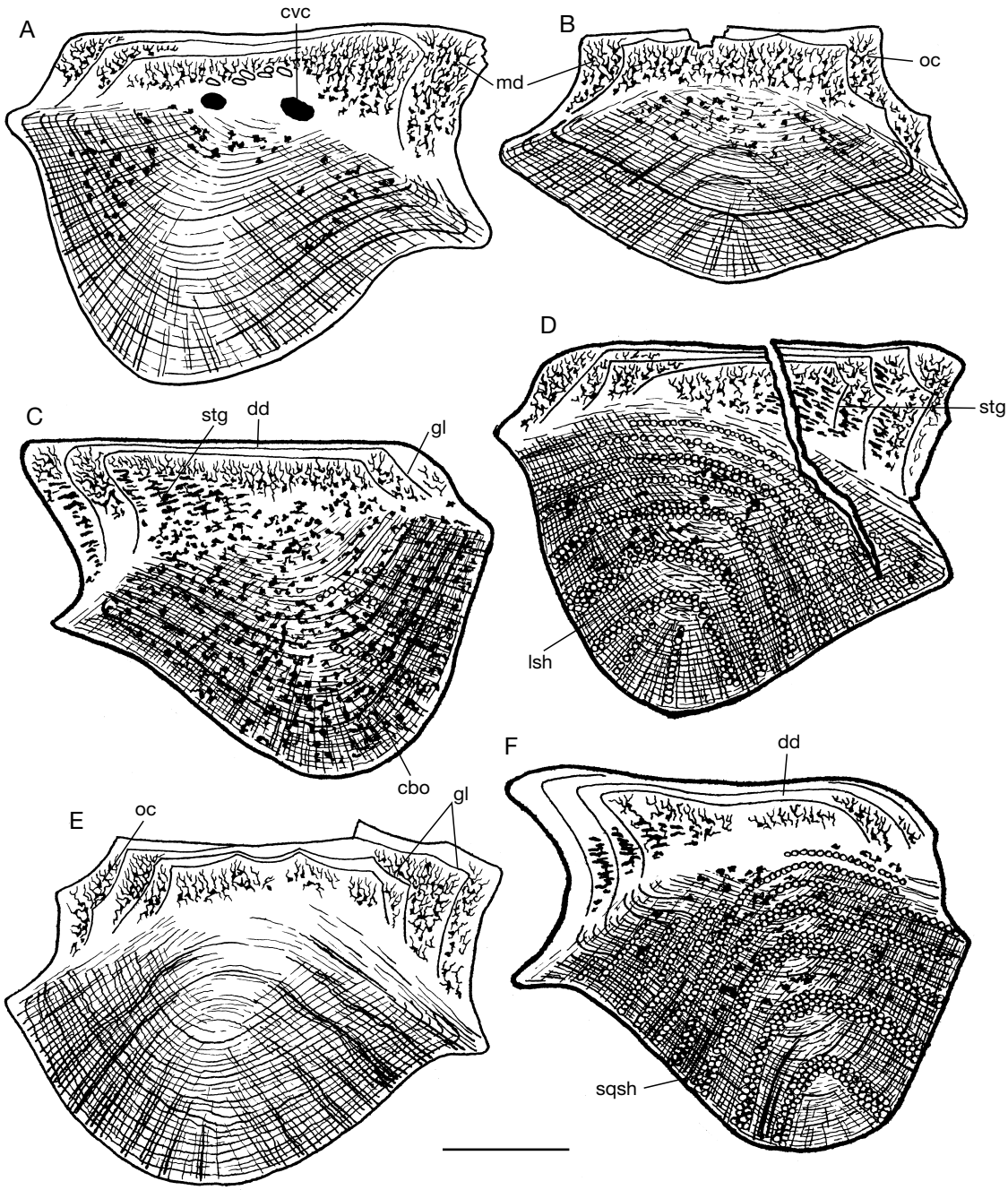


FIG. 10. — *Acritolepis ushakovi* n. gen., n. sp., scale histology, from paratype LIG 35-A-404, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **A**, vertical longitudinal section through the asymmetrical trunk scale (see Fig. 5K), thin section 3359; **B**, vertical transverse section through the central part of small elongated tail scale (see Fig. 5J), thin section 3363; **C**, **D**, vertical longitudinal sections through the central part of trunk (**C**, thin section 3355) and tail scale (**D**, thin section 3358); **E**, vertical transverse section through the head scale (see Fig. 5H), thin section 3360; **F**, vertical longitudinal section through the less ornamented (with two short ridgelets) trunk scale, thin section 3357. Abbreviations: **cbo**, cellular bone; **cvc**, circular vascular canal; **dd**, durodentine; **gl**, growth lamella; **lsh**, longitudinal Sharpey's fibres; **md**, mesodentine; **oc**, osteocyte cavity; **sqsh**, transverse Sharpey's fibers; **stg**, Stranggewebe (oriented mesodentine). Scale bar: 0.1 mm.

of two trunk scales with separate convex bases, later joined by additional common basal plate. Both basal parts composed of thin-lamellar acellular bone resembling tectal tesserae of polyodontode type. Superposed lamellae (up to five) in the crown are composed of a simple mesodentine with enlarged principal circular vascular canals and a dentine tubule network with osteocytes.

DISCUSSION

Acritolepis ushakovi n. gen., n. sp. is closest to *A. urvantsevi* n. gen., n. sp. Despite the less complete preservation of the latter, several morphological elements and their histological structure can be compared. Uniting affinities are as follows: massive, thick-walled pectoral spines with a single central cavity and distinct longitudinal ribs, do not exceed eight on each side; deep grooves in-between containing in pectoral and dorsal spines numerous openings of vascular canals; rounded triangular flattened or isosceles triangular section; presence of prepectorals ornamented by extensively overlapping tubercles; slender cylindrical scapula with wide procoracoid? blade, containing openings of vascular canals; shape and proportions of body scales with poorly ridged lingual crowns, arranged in lines without overlap; Stranggewebe in crowns composing posterior parts of every growth lamella including the primordial one and surrounded by simple mesodentine strip; presence of large longitudinal vascular canals in spines.

However, the differences between species compared seem more essential. These are: deep insertion of pectoral spines in *A. urvantsevi* n. gen., n. sp. versus the shallow insertion in *A. ushakovi* n. gen., n. sp.; one pair of prepectorals in the first versus two in the second; spine histological structure composed of three distinct layers in *A. urvantsevi* n. gen., n. sp.: 1) basal bone with increased cell number and decreased number of vascular canals; 2) middle, also highly cellular bone with principal vascular canals restricted in mature spines by concentric osteons; and 3) superficial mesodentine with network of tubules and numerous osteocytes even at the outer strip. In *A. ushakovi* n. gen., n. sp. two thirds of spines are composed of a thin-lamellar acellular bone, and only the ribbed part is made of highly vascularised mesodentine containing few osteocytes; a higher density of denteons occur in the outer strip. Scales of *A. urvantsevi* n. gen., n. sp. bear less ridges (up to four), and are more elongated; the number of growth lamellae in crowns does not exceed three; there is a simple networked mesodentine with a diversified system of principal vascular canals and osteocytes even at the outer strips of the last growth lamella; the crown mesodentine gradually merges into cellular bone of scale base. *A. ushakovi* n. gen., n. sp. scales bear more ridges (up to eight) and crowns are more flattened; up to four to five growth lamellae; extremely thin-lamellar base bone with irregular (mainly small) number of osteocytes; simple mesodentine without system of principal vascular canals; the osteocytes never reach the outer strips of at least the two latest growth lamellae.

BIOSTRATIGRAPHIC SIGNIFICANCE

A. ushakovi n. gen., n. sp. is a key species of the *Poracanthodes menneri* Subzone, based on association of articulated acanthodians from the topmost part of Severnaya Zemlya Formation. It characterises the lower part of the *Nostolepis minima* Zone, traced throughout the regions worldwide. Age is early Lochkovian. Tentatively correlates to the *woschmidti* Zone of the standard conodont scale.

Acritolepis urvantsevi n. sp.
(Figs 13-16)

HOLOTYPE. — LIG 35-A-382. Anterior part of the trunk with paired pectoral and prepectoral fin spines, fragmentary scapula, tesserae-like plates and squamation preserved laterally (Fig. 13A, B). Pod"emnaya River, outcrop 67, bed 12.

ETYMOLOGY. — In honour of one of the first discoverer and researcher of Severnaya Zemlya Archipelago: N. N. Urvantsev (Russia).

OTHER MATERIAL EXAMINED. — LIG 35-A-381 and LIG 35-A-402: parts of unidentified fin spines in ventral preservation and squamation. Matusevich River (both), outcrop 1, bed 21. Another specimen LIG 35-

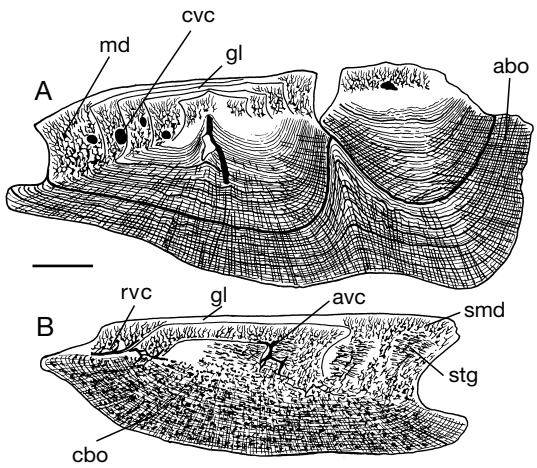


FIG. 11. — *Acritolepis ushakovi* n. gen., n. sp., histology of tessera-scales, Severnaya Zemlya Formation; **A**, vertical longitudinal section through the central part of two-crowned tessera, thin section 3491, paratype LIG 35-A-404, Spokojnaya River, outcrop 41, bed 12; **B**, vertical longitudinal section through the slightly asymmetrical tessera-scale (see Fig. 7A), thin section 3492, paratype LIG 35-A-371, Matusevich River, outcrop 1, bed 21. Abbreviations: **abo**, acellular bone; **avc**, ascending vascular canal; **cbo**, cellular bone; **cvc**, circular vascular canal; **gl**, growth lamella; **md**, mesodentine; **rvc**, radial vascular canal; **smd**, simple mesodentine; **stg**, Stranggewebe (oriented mesodentine). Scale bar: 0.1 mm.

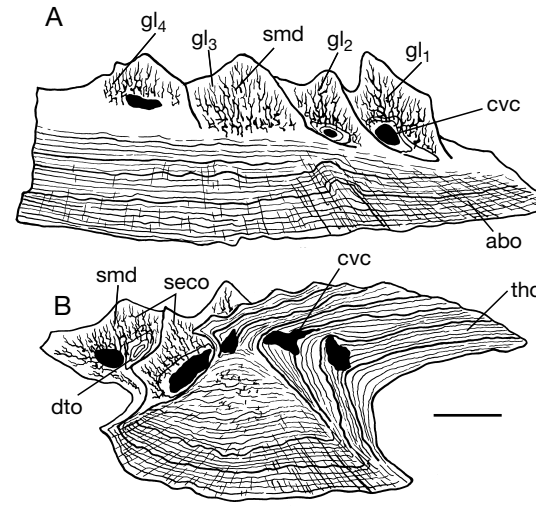


FIG. 12. — *Acritolepis ushakovi* n. gen., n. sp., histology of polyodontode-type tesserae, from paratype LIG 35-A-386, Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation; **A**, vertical transverse section through the tessera like figured on Fig. 5G, thin section 3502; **B**, vertical longitudinal section through the tessera with the secondary growth area on the crown (see Fig. 5F), thin section 3503. Abbreviations: **abo**, acellular bone; **cvc**, circular vascular canal; **dto**, denteon; **gl_1**, **gl_2**, **gl_3**, **gl_4**, lamellae of areal growth; **seco**, secondary odontode; **smd**, simple mesodentine; **thd**, thinlamellar dentine. Scale bar: 0.1 mm.

A-383: poorly exposing squamation alone. Spokojnaya River, outcrop 41, bed 12.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 1, bed 21; Spokojnaya River, outcrop 41, bed 12 and Pod"emnaya River, outcrop 67, bed 12. Top of the Severnaya Zemlya Formation, Lower Devonian, lower Lochkovian.

DIAGNOSIS. — Climatiid with long, deeply inserted, uniformly eight-ribbed pectoral fin-spines, wide basal tuberculated prepectoral spines and rounded slender scapula. Outer mesodentine of spine with numerous osteocytes. Middle and basal layers made of vascularised cellular bone with fragmentary osteons. Scales with elongated crowns, down sloping anteriorly; with two to three short anterior ridges. Composed of Stranggewebe and simple mesodentine. It shows a diversified system of principal vascular canals at the junction of base and crown.

DESCRIPTION

Poorly articulated specimens exhibiting a shoulder girdle with fragment of scapula, pectoral spines and mostly distorted squamation. Body measurements and proportions are indistinct.

Fin spines

Pectoral spines (Figs 13A, B; 15A) thick-walled, massive, slightly caudally bent with eight uniform, sharply distinct smooth ribs separated by deep grooves. Ribs and grooves are approximately of the same width, quadrangular, with a slightly rounded profile through the whole spine length. Preserved parts (22.6 mm for spine fossilized laterally just downward the prepectoral, and 20.7 mm for other, oriented ventrally) are hollow, with single fully closed central cavity. In transverse sections the spine (Fig. 15A) shows a slightly rounded triangular form with parabasally widened sides (about 3 mm). The inserted portion (about 6.3 mm) demonstrates a deep insertion in the body.

Spine histology contains cellular bone and mesodentine structures. The thin superficial layer (ridged part) is formed of mesodentine (Fig. 14A, B) with a dense network of short, winding dentine tubules; it contains lacunae and osteocytes even at

the surface. Middle spine part is composed of cellular bone, densely penetrated by osteocyte cavities and linear fibers. Large longitudinal vascular canals and elongated cell structure (Fig. 14D) are constricted in mature spines by concentrically thin-laminated osteons, better seen in transverse sections (Fig. 14B). Large pore openings, distributed in grooves are visible on the spine surface. They continue into deeper levels of the middle layer as wide irregular vascular canals (Fig. 14A). The basal layer, lining the spine cavity, is approximately of the same volume as the middle one, formed of bone with increased cell number and less numerous enlarged vascular canals.

Prepectoral spine (Fig. 15D) shows a sharp tip and a wide basal triangular form in lateral view. It is slightly asymmetrical. Its total length is 5.0 mm, base length, 4.1 mm and the ratio of base length to spine length is about 0.82. 10 longitudinal rows of rounded and oval tubercles – beaded ridges – are present (Fig. 15D). Tubercle size decreases both toward the sides and the tip. Basal parts of tubercles are mostly extensively overlapped and thus to the tip, their turned margin has a higher angle in profile.

The histological structure of mesodentine and cellular bone composing this spine is similar to that of pectoral ones, except for osteon formation (Fig. 14C).

Shoulder girdle

The unarticulated scapula is present over the pectoral spine. Its visible part is round, 3.3 mm high and shows a base diameter of 3.2 mm. Just above the base, its diameter is reduced to half. On the walls pointed openings of large vascular canals (Fig. 15C) are seen. They penetrate the perichondral bone and are regularly distributed in lines.

Squamation

In the specimens, only small areas show an intact scale cover. This squamation is mainly distorted and represented by isolated scales or small articulated scale groups (Fig. 15B). Two morphological scale varieties can be recognized. First: enlarged examples with multiangular isometric, rhombic, often elongated or widened scales, slightly convex base and aside to other ones with twice or more times reduced crown (Fig. 13E, F). Maximum diameter of the base reaches 1.5 mm. The crown is anteriorly low and the neck is either absent or very low. The wide medial, slightly concave area gives to this crown a sort of tongue shape. Crowns are devoid of ornamentation or with two or three very short blunt ridges. This scale variety is mainly observed to the left (anteriorward) of pectoral fins in the holotype and treated as head scales. They represent a morphological transition to tesserae-like scales or plates, like those known in climatiids. The second variant (Fig. 13C, D, G, H) recognized as trunk scales shows the following features: crown size varies from 0.2 mm to 1.2 mm and crown is flat or slightly concave in the central part (Fig. 13C). Rhombic, elongated or leaf-formed with rounded and widened anterior margin, they are ornamented (up to one third of the crown length) with three to four short parallel ridges, and possess a sharpened posterior margin, sloping slightly upward and overhanging the base (Figs 13H; 15B). Their base is moderately convex (Fig. 13D), centrally or anteriorly vaulted. A low and stout neck is separated from the base by a well developed rim of rhombic or sub-circular outline.

The scale histology of both morphological varieties is practically uniform. Head scales or tesserae-like scales (Fig. 16A, E) as well as trunk scales (Fig. 16B-D, F) are composed of oriented (Stranggewebe after Gross 1971) and simple mesodentine, characteristic of the "*Nostolepis*"-type histology. Both varieties contain widened main circular and radial vascular canals, located at the junction between the base and crown (Fig. 16E, F). Ascending canals, rising from them, develop wide principal branches in every growth lamella, of which the number does not exceed three. Growth is superpositional. Oriented mesodentine composes the large posterior scales area primordial lamella included. Horizontally elongated lacunae are displaced densely to each other without leaving any space for dentine tubule connections. The outer strips of lamellae are composed of a simple mesoden-

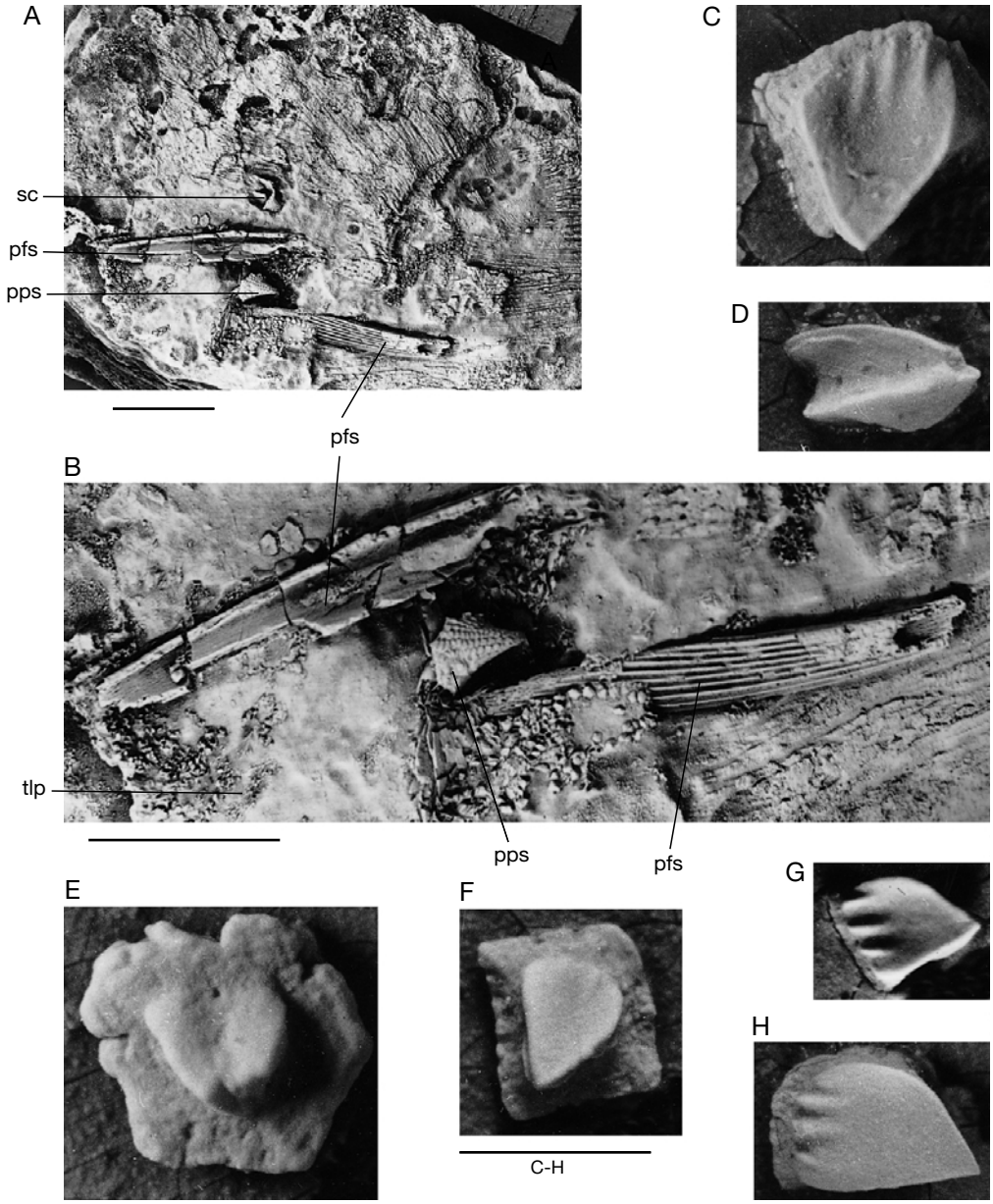


FIG. 13. — *Acritolepis urvantsevi* n. gen., n. sp.; **A**, **B**, holotype (LIG 35-A-382), Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, paired pectoral and prepectoral fin spines, tessera-like plates and squamation, preserved in lateral view, anterior to left; **B**, magnified area with pectoral and prepectoral fin spines; **C**-**H**, scales and tesserae; **C**, LIG 35-2049, normal trunk scale, area behind the pectoral spine, crown; **D**, LIG 35-2053, scale from the same area, lateral view; **E**, LIG 35-2048, tessera-like plate, area of prepectoral spine, crown; **F**, LIG 35-2051, tessera-scale from the same area, crown; **G**, LIG 35-2097, scale from the mostly rightward distanced area; **H**, LIG 35-2052, slightly asymmetrical trunk scale. All scales from the holotype specimen. Abbreviations: **pfs**, pectoral fin spine; **pps**, prepectoral spine; **sc**, scapula; **tlp**, tessera-like plate. Scale bars: A, B, 10 mm; C-H, 0.5 mm.

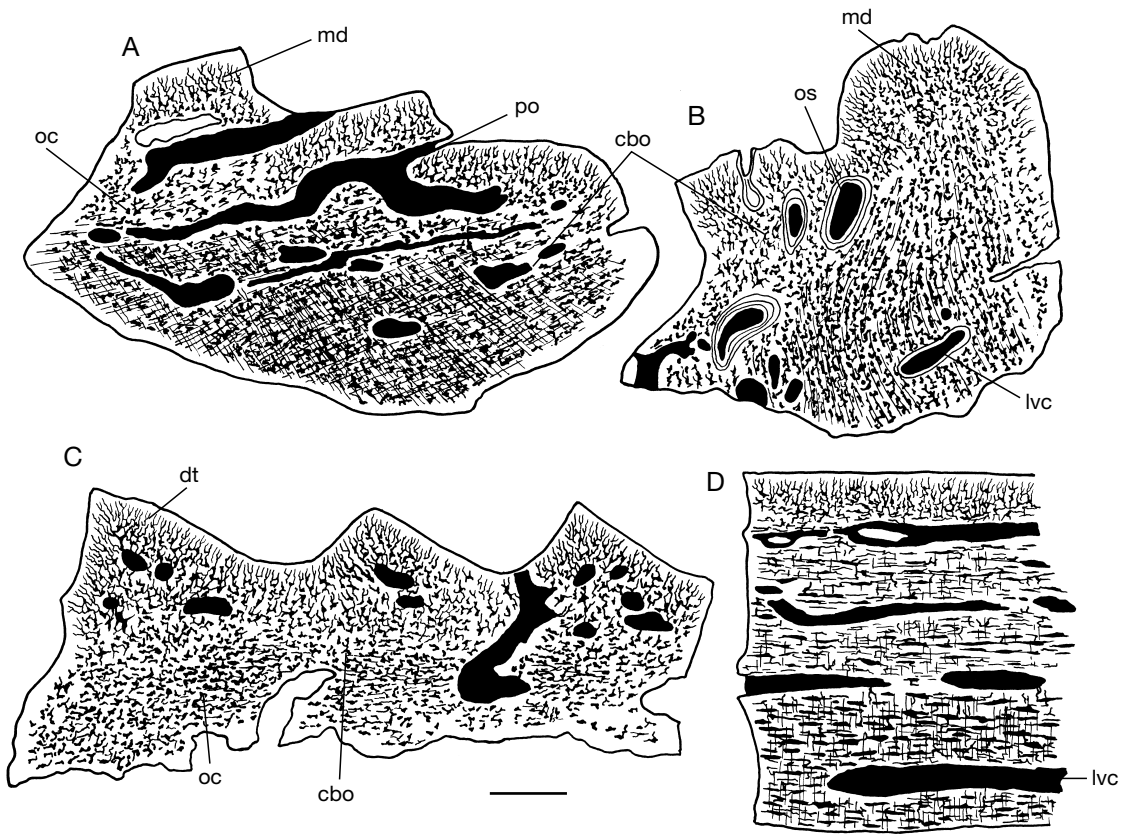


FIG. 14. — *Acritolepis urvantsevi* n. gen., n. sp., histological structure of fin spines, Severnaya Zemlya Formation; **A**, transverse section through the basal part of pectoral spine containing pore openings in the grooves, thin section 3475; **B**, transverse section through the two-ribbed fragment of pectoral spine (supposedly, middle part), thin section 3481; **C**, transverse section through the fragment of tuberculated prepectoral spine, thin section 3473; **D**, longitudinal section through the single-ribbed fragment of pectoral spine, thin section 3472; **A**, **C**, **D**, holotype (LIG 35-A-382). Pod"emnaya River, outcrop 67, bed 12; **B**, specimen LIG 35-A-402. Matusevich River, outcrop 1, bed 21. Abbreviations: **cbo**, cellular bone; **dt**, dentine tubule; **lvc**, longitudinal vascular canal; **md**, mesodentine; **oc**, osteocyte cavity; **os**, osteon; **po**, pore opening. Scale bar: 0.1 mm.

tine with a network of winding, narrow dentine tubules and numerous osteocytes with short processes. An analogous type of tissue composes entirely the anterior crown area. The crown mesodentine gradually turns into the cellular bone of base. The base tissue is extremely thin-layered with a maximum number of multiangular or slightly rounded osteocyte cavities.

DISCUSSION

Acritolepis urvantsevi n. gen., n. sp. is comparable to *Nostolepis striata* Pander, 1856 and *Canadalepis linguiformis* Vieth, 1980 only by several selective features. Less sculptured "Kronenplättchen" (tesserae coronate) (Gross 1971: pl. 5, figs 5-7, 10) of *N. striata* are distantly similar by their large inconstantly shaped base, their anteriorly lowered crown with small numbers of short and blunt ridges. Scales grown together or distinct tesserae of the new species do not meet. Unfortunately, the histological structure of "Kronenplättchen" observed by the author is very fragmentary, with the supposition they could be close to *N. striata* body scales. The vascular canals piercing the base, are not found in *A. urvantsevi* n. gen., n. sp. Fin spines

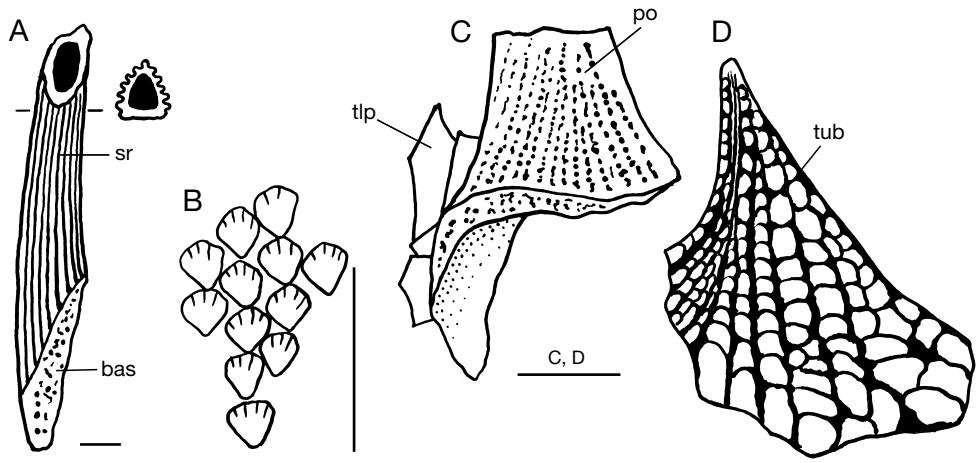


FIG. 15. — *Acritolepis urvantsevi* n. gen., n. sp., drawings of selected elements, Severnaya Zemlya Formation; **A**, pectoral spine in lateral view with transverse section through median part; **B**, trunk scales, arrangement in lines; **C**, basal portion of scapula with linear openings of vascular canals; **D**, magnified prepectoral spine; **A**, **C**, **D**, holotype (LIG 35-A-382). Pod"emnaya River, outcrop 67, bed 12; **B**, specimen LIG 35-A-402, Matusevich River, outcrop 1, bed 21. Abbreviations: **bas**, basal (inserted) spine part; **po**, pore opening; **sr**, spine rib; **tlp**, tessera-like plate; **tub**, tubercle. Scale bars: A, 2 mm; B-D,1 mm.

of the compared species are rather different. Short and stout, tuberculated spines of *N. striata* (Gross 1971: pl. 8, figs 2-26) are distantly close only to prepectorals of *A. urvantsevi* n. gen., n. sp. Longitudinally smooth-ribbed spines like pectorals of *A. urvantsevi* n. gen., n. sp. have not been described in *N. striata*. The main spine histological structure is comparatively similar. Superficial mesodentine of the new species contains more numerous osteocytes and a more complicated network of dentine tubules. Middle and basal bony layers are characterised by a magnified tissue vascularisation; osteon structures are only fragmentarily observable (compare with Gross 1971: text-fig. 14A-E), whereas they show a great density in the cellular bone of mature spines in *N. striata*.

Morphological similarity of *A. urvantsevi* n. gen., n. sp. and *Canadalepis linguiformis* is only restricted to the general shape and crown ornamentation of tesserae-like scales with developed basal plates (Vieth 1980: pl. 7, figs 9-18). Essential differences occur in the histological structure. In *C. linguiformis* the Stranggewebe is absent (Vieth 1980: text-fig. 23A-D), the simple mesodentine contains rare osteocytes and lacuna-like widenings of dentine tubules. The main system of diversified vascular canals, characteristic for *A. urvantsevi* n. gen., n. sp., does not exist in *C. linguiformis*. The cellular base bone of new species contains a larger numbers of osteocytes.

BIOSTRATIGRAPHIC SIGNIFICANCE

Identical to *Acritolepis ushakovi* n. gen., n. sp.

Family CLIMATIIDAE Berg, 1940
Genus *Nostolepis* Pander, 1856

Nostolepis decora n. sp.
(Figs 17; 18)

HOLOTYPE. — LIG 35-A-346. A specimen preserved laterally, exposing only squamation, with the head and tail areas, fin spines also missing (Fig. 17A).

ETYMOLOGY. — From *Decorus* (Latin): beautiful, lovely.

LOCALITY AND AGE. — October Revolution Island: Pod"emnaya River, outcrop 67, bed 12. Lower Devonian, lower Lochkovian, Severnaya Zemlya Formation.

DIAGNOSIS. — Small-sized nostolepid with leaf-like scales, having anteriorly down sloping crowns with

two long, posteriorly pointed ridges, forming an elevated medial area. Lowered lateral notched areas present. Two enlarged pores open latero-distally on the neck. Crown composed of Stranggewebe with large lacunae and, in only a small proximal area, of simple networked mesodentine.

DESCRIPTION

This description is based on the holotype which is the only representative of this species.

Squamation

Scales are distributed densely in oblique lines with small extensive overlap. Trunk scales have oval or leaf-like crowns with a rounded, widened anterior and tapered, pointed posterior edge. The largest crowns reach in length 0.65 mm. They slope down anteriorly with a prevailing low angle, sometimes to 45°. We always distinguish a medial area of elongated triangular form (Fig. 17C, E) to stretched strip (Fig. 17F) with two blunt, magnified and higher ridges pointing and protruding posteriorly beyond the base. Slightly concave plates between them may be ornamented with one or two shorter ones. Somewhat lower notched lateral crown areas join upward uneven, rarely "denticulate", sides (Fig. 17F, G). The base is moderately convex, anteriorly vaulted, with a prevailingly low neck. Rare examples (mostly with higher neck) contain two enlarged pore openings on the latero-distal neck walls. Two longitudinal lines of enlarged scales (especially widened, to 0.75 mm) with asymmetrically ridged crowns may be defined as lateral line scales (Fig. 17B) or tesserae-scales with often wavy or interrupted ridges of both inconstant number and shape (Fig. 17H). Their crowns do not show a division into medial and lateral areas. Their neck may also contain two pore openings.

Trunk scales, normal (Fig. 18A) and extremely elongated (Fig. 18C), as well as asymmetrical lateral line scales (Fig. 18F), are composed of classical Stranggewebe in crowns with horizontally stretched long lacunae, connected with principal circular, radial and ascending vascular canals. They present no surrounding strips of simple mesodentine. Medial area shows two lamellae of superpositional growth (Fig. 18D), whereas laterals join sideward (areal). Crown contains simple mesodentine with plenty of osteocytes and a small number of dentine tubules composes the minor proximal crown area only. It turns gradually into the highly cellular base bone. Scales from the lateral line (Fig. 18F) or the special tesserae-scales (Fig. 18B) have a complicated system of enlarged vascular canals, leaving almost no space for dentine tubules or lacunae.

Branchial? plates

Rare pointed fragments of plates with slightly convex or flat thin base and randomly displaced oblique or vertical sharply-tipped spinelets demonstrate a dentine structure (Fig. 18E) with a main (pulpar) ascending canal in the centre and small branching tubules. Their base is supposedly composed of mesodentine. By these features they differ from branchial? cones of *Acritolepis* n. gen.

DISCUSSION

By its original crown ornamentation, including the two-ridged medial area and lateral notched "wings", but also by the latero-distal neck pore openings (no pores on crowns surface), *Nostolepis decora* n. sp. differs from all known nostolepids. A distant similarity arises only with one morphological variety of normal trunk scales of *N. striata* Pander, 1856, figured by Gross (1947: pl. 26 (7), figs 10, 11; 1971: pl. 6, figs 1, 2). The latter have parallel and numerous converging anterior ridges on the flat and wide medial crown area, and also regularly shaped narrow notched lateral areas, which may contain a double line of notches.

BIOSTRATIGRAPHIC SIGNIFICANCE

Identical to the representatives of *Acritolepis* n. gen.

Nostolepis fragilis n. sp.
(Figs 19; 20A-G; 21; 22)

Nostolepis sp. no. 7 – Valiukevičius 1988a: 604, 605.

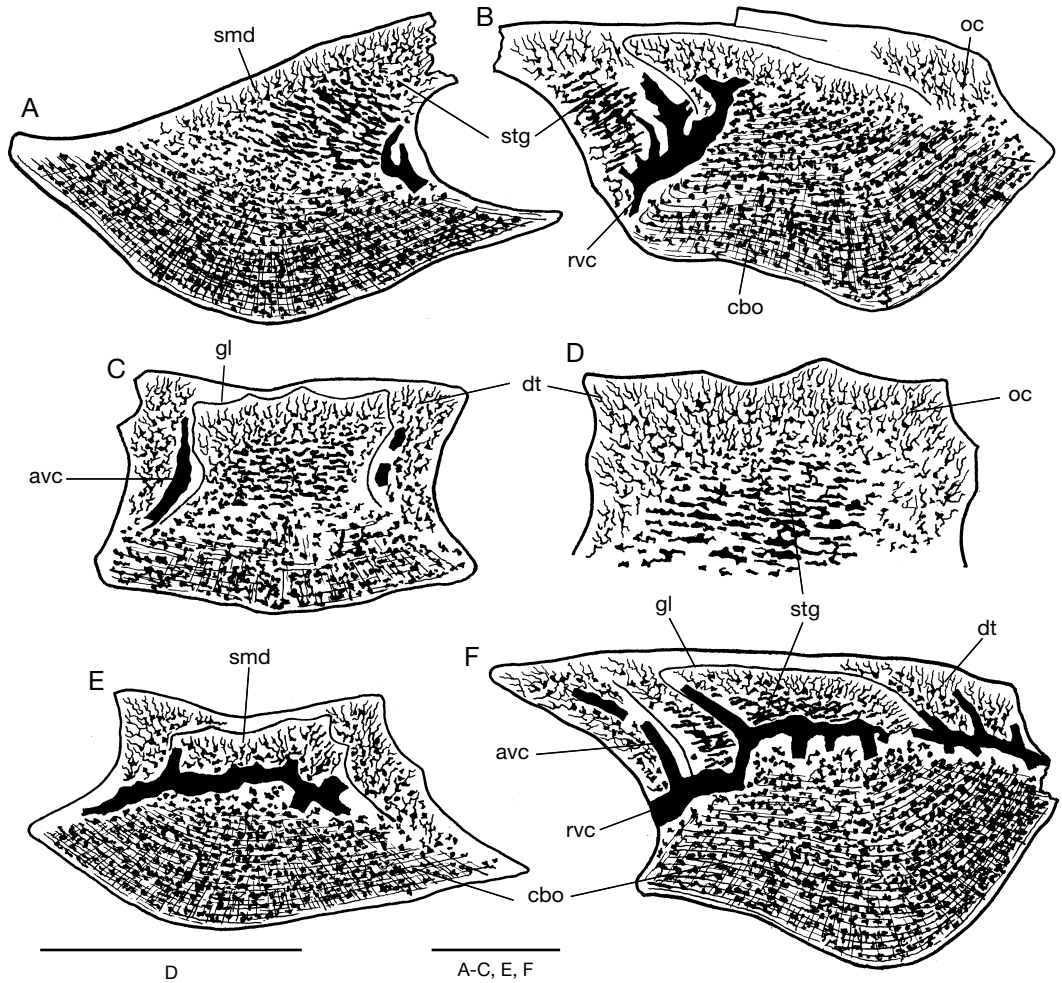


FIG. 16. — *Acritolepis urvantsevi* n. gen., n. sp., histology of scales, all scales from the holotype (LIG 35-A-382), Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, vertical longitudinal section through the tessera-scale with multiangular base, thin section 3351; **B**, vertical longitudinal section through the elongated trunk scale, thin section 3348; **C**, vertical transverse section through the central part of normal trunk scale, thin section 3347; **D**, magnified area of the primordial growth lamella of the same scale; **E**, vertical transverse section through the anterior part of tessera-like scale with quadrangular base, thin section 3349; **F**, vertical longitudinal section through the normal trunk scale, thin section 3350. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **dt**, dentine tubule; **gl**, growth lamella; **oc**, osteocyte cavity; **rvc**, radial vascular canal; **smd**, simple mesodentine; **stg**, Stranggewebe (oriented mesodentine). Scale bars: 0.1 mm.

HOLOTYPE. — LIG 35-A-353. Fragmentary specimen preserved in lateral view with two fragments of pectoral spines, two ventral fin spines and squamation (Fig. 19A, B). Matusevich River, outcrop 1, bed 21.

ETYMOLOGY. — From *Fragilis* (Latin): fragile, referring to squamation.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 1, bed 21. Lower Devonian, lower Lochkovian, Severnaya Zemlya Formation.

DIAGNOSIS. — Nostolepid with two stout ventral (intermediate?) fin spines with nodose ridges and longitudinally ribbed pectoral ones, composed of cellular bone and mesodentine (the ribbed part only). Scales with crowns anteriorly down sloping at a high angle, ornamented with two ridges, forming a medial area, and two symmetrical side ridges; base concave with a deep posterior fossa. One or two growth lamellae in crown composed of simple mesodentine with vascular tubules, distantly resembling the lacunae of Stranggewebe.

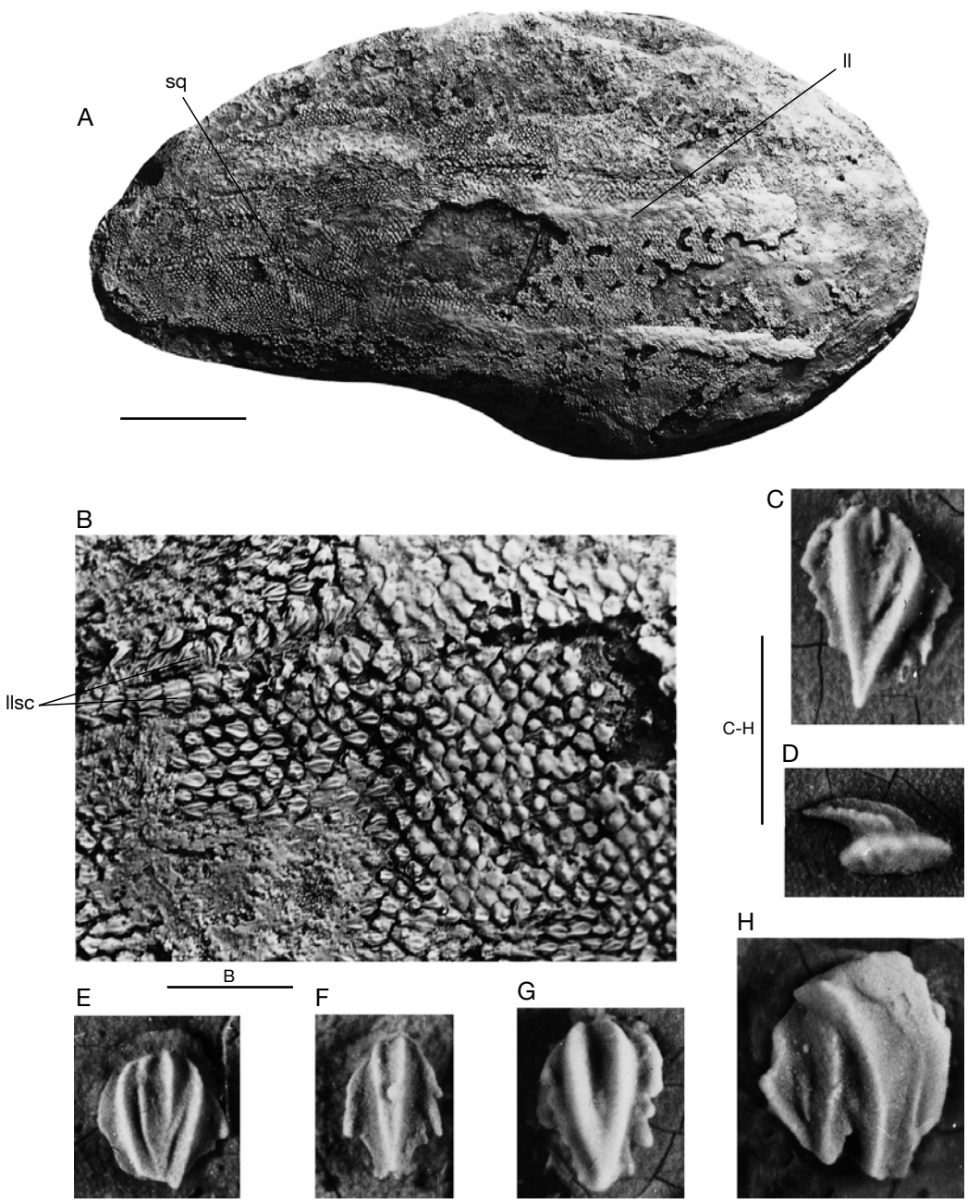


FIG. 17. — *Nostolepis decora* n. sp., all scales from the holotype specimen, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, holotype (LIG 35-A-346) in lateral preservation, squamation, anterior to right; **B**, enlarged area of the same specimen, trunk scales and magnified asymmetric scales along the lateral line; **C**-**G**, trunk scales; **C**, LIG 35-2030, crown; **D**, LIG 35-2025, side; **E**, LIG 35-2031, crown; **F**, LIG 35-2032, crown; **G**, LIG 35-2033, crown (anterior upwards for all crowns); **H**, tessera-scale from the lateral line, crown, LIG 35-2026. Abbreviations: **ll**, lateral line; **llsc**, scale from lateral line; **sq**, squamation. Scale bars: A, 10 mm; B, 2 mm; C-H, 0.5 mm.

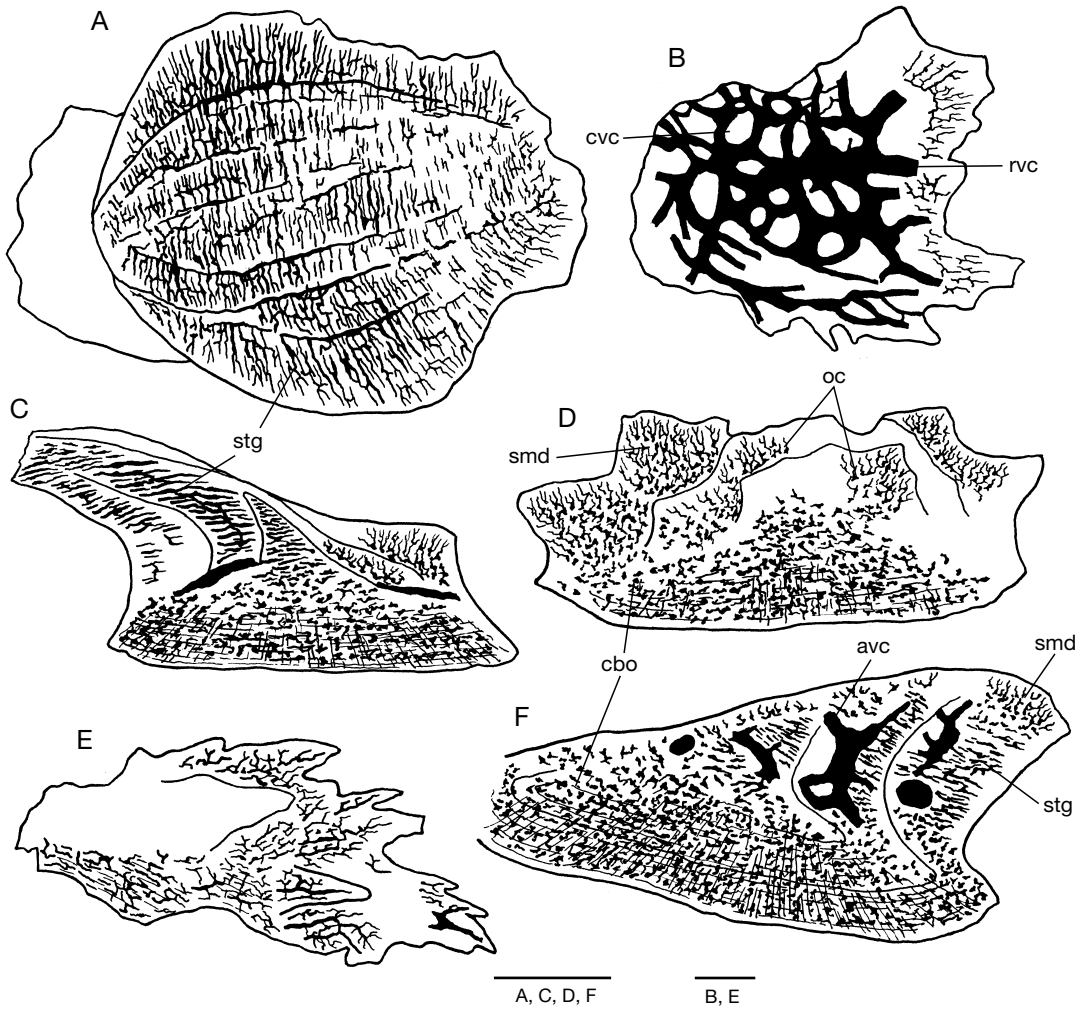


FIG. 18. — *Nostolepis decora* n. sp., histologic structure of trunk scales, tesserae-scales and denticled branchial? plates; **A**, normal trunk scale (like figured on Fig. 17G) in anise oil, crown, LIG 35-2077; **B**, tessera-scale (see Fig. 17H) in anise oil, crown, LIG 35-2076; **C**, vertical longitudinal section through the central part of scale with posteriorly pointed elongated crown (see Fig. 17C), thin section 3447; **D**, vertical transverse section through the anterior part of stretched scale with linked upward, notched lateral areas (see Fig. 17F), thin section 3449; **E**, slightly recurved denticled plate in anise oil, LIG 35-2075; **F**, vertical longitudinal section through the asymmetrical tessera-scale from the lateral line, thin section 3448. For locality and stratigraphic assignement see Fig. 17. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **cvc**, circular vascular canal; **oc**, osteocyte cavity; **rvc**, radial vascular canal; **smd**, simple mesodentine; **stg**, Stranggewebe (oriented mesodentine). Scale bars: 0.1 mm.

DESCRIPTION

Species described from the single holotype specimen.

Fin spines

The best preserved spines are the two ventral fin spines (intermediate?) following one another with a distance of about 10 mm. The first one measures 7.3 mm in length, the second *c.* 8.0 mm. These spines are stout, anteriorly with a narrowed oval cross section, almost without curvature, hollow, only slightly inserted or missing an insertion base. They bear four robust nodose ridges on each side (Fig. 19B). The two anterior

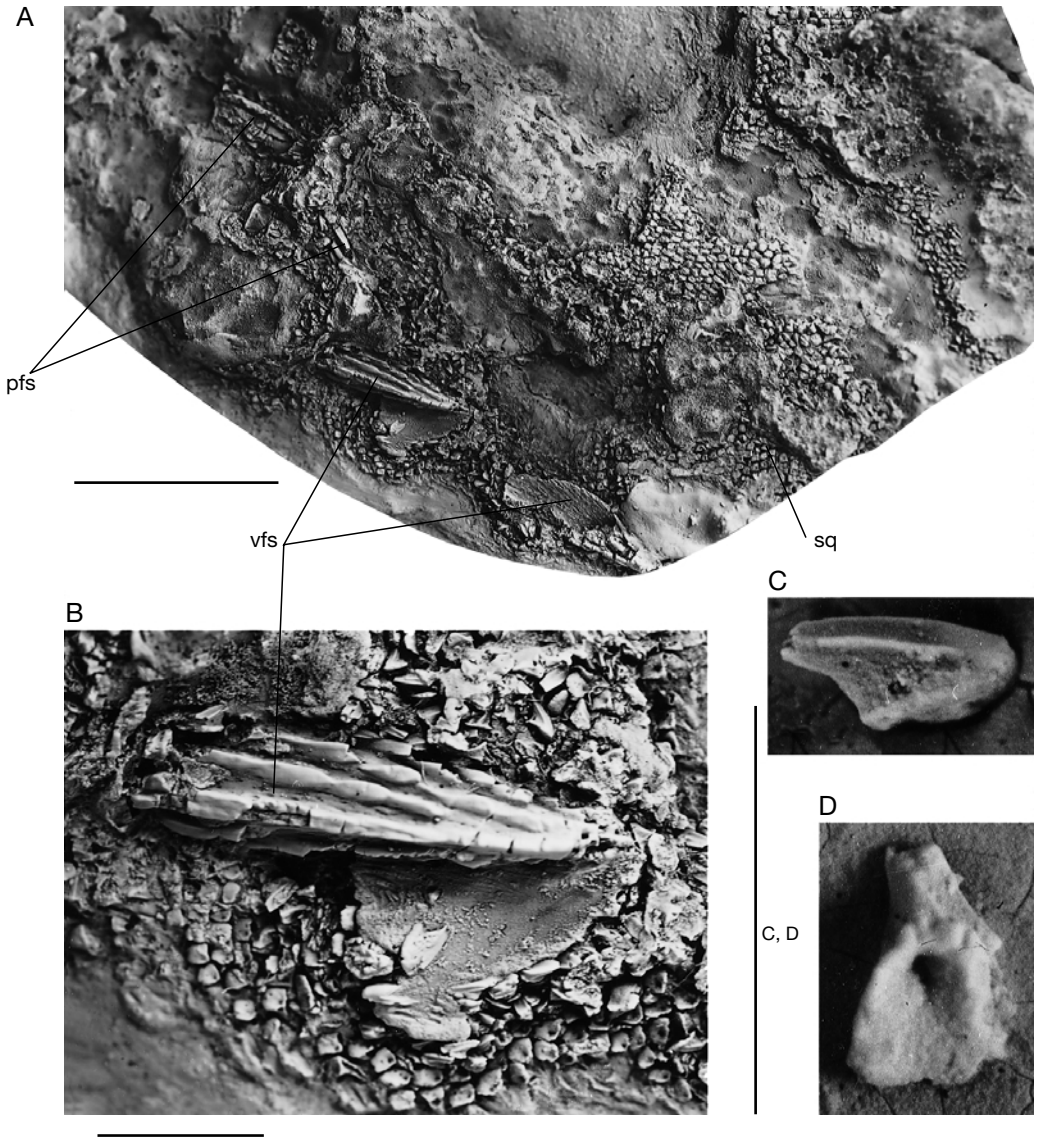


FIG. 19. — *Nostolepis fragilis* n. sp., Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation; **A**, **B**, holotype (LIG 35-A-353); **A**, in lateral preservation, anterior to left, supposed fragments of pectoral fin spines, two ventral spines and squamation; **B**, magnified first ventral spine and squamation; **C**, trunk scale, side, anterior to right, LIG 35-2061; **D**, trunk scale, base, anterior to page bottom, LIG 35-2063. Abbreviations: **pfs**, pectoral fin spine; **sq**, squamation; **vfs**, ventral fin spine. Scale bars: A, 10 mm; B, 3 mm; C, D, 1 mm.

ones, which do not reach the top end, meet on the anterior margin in a typical V-shape pattern. Nodes increase in length both anteriorly and basally. Grooves between ridges are deep and wide, with numerous pore openings.

In front and above the first ventral are displaced two fragments of the supposed pectoral spines. Their length are respectively 4.0 mm and 1.3 mm. The latter, closer to the ventral spine, bears three longitudinal ribs, the proximal one

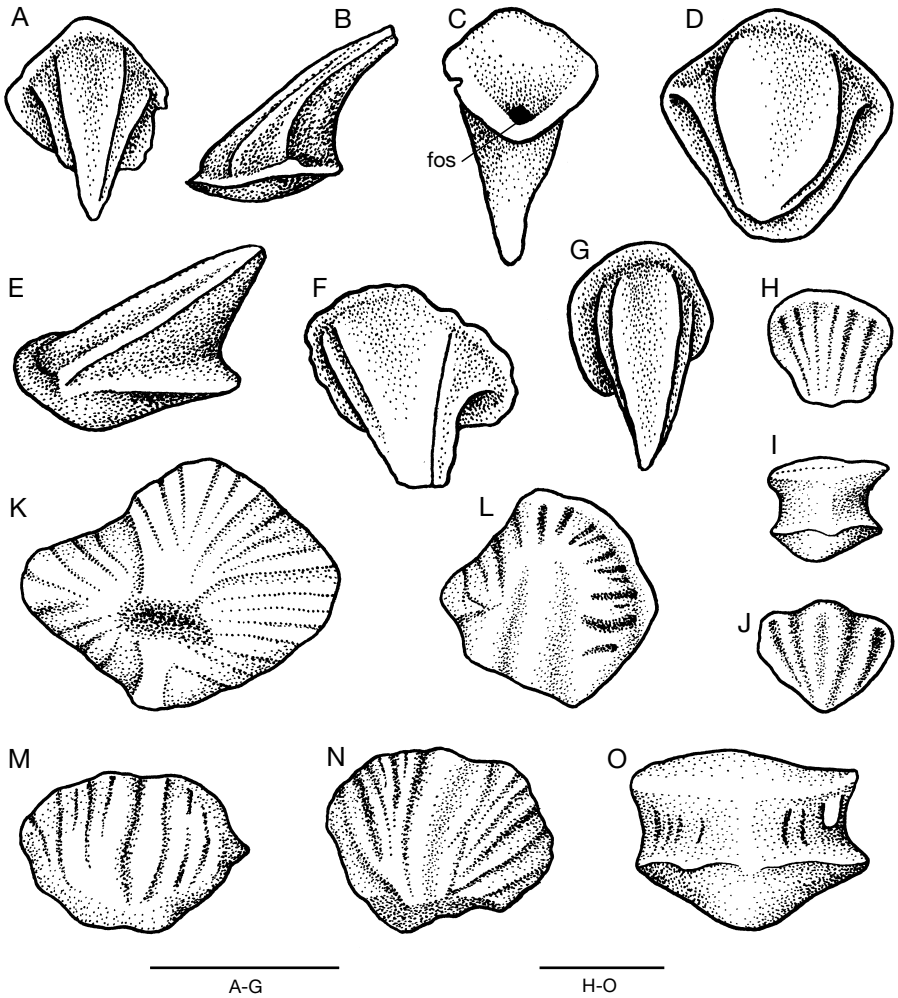


FIG. 20. — Drawings of scales; **A**-**G**, *Nostolepis fragilis* n. sp., holotype; **A**-**C**, LIG 35-1275, crown (**A**), side (**B**) and base (**C**), anterior upwards (**A**, **C**) and to left (**B**); **D**, **E**, LIG 35-1276, crown (**D**, anterior upwards) and side (**E**, anterior to left); **F**, **G**, LIG 35-1277 and 35-1279, crowns, anterior upwards. For locality and stratigraphic arrangement see Fig. 19; **H**-**J**, *Diplacanthus solidus* n. sp.; **H**, **I**, holotype, LIG 35-1283 crown (**H**, anterior upwards) and side (**I**, anterior to left); **J**, LIG 35-1285, crown, anterior upwards, Matusevich River, outcrop 5, bed 151 (top), Vstrechnaya Formation; **K**, **L**, *Diplacanthus carinatus* Gross, 1973, crowns, anterior upwards; **K**, LIG 35-1254; **L**, LIG 35-1282, Matusevich River, outcrop 5, bed 149, Vstrechnaya Formation; **M**-**O**, *Cheiracanthus* sp. cf. *Ch. longicostatus* Gross, 1973; **M**, LIG 35-1286, crown, anterior upwards; **N**, **O**, LIG 35-1284 crown, anterior upwards (**N**) and side, anterior to left (**O**). Matusevich River, outcrop 5, bed 153 (**M**) and top of bed 151 (**N**, **O**), Vstrechnaya Formation. Abbreviation: **fos**, fossa. Scale bars: 0.5 mm.

being enlarged, quadrangular in cross section, and separated from its neighbour by a very deep, wide groove containing some pore openings.

All spines are composed of highly vascularised cellular bone (Fig. 22A, B) and, only in their ribbed part, of mesodentine with characteristically up streamed dentine tubules.

Squamation

Scales show small crown overlaps. Scales with elongated sub-rhombic crowns (0.4-0.6 mm long) dominate. They possess sharp and posterior tapering edges sloping at an angle of 30-50° toward the horizontal base (Figs 19C; 20B). Proximal crown part slopes downward to the

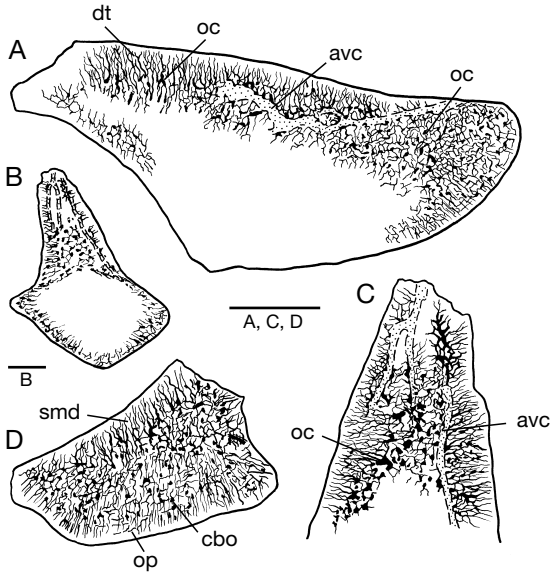


FIG. 21. — *Nostolepis fragilis* n. sp., scale histology, holotype; **A**, vertical longitudinal section through elongated scale, thin section 692; **B**, vertical transverse section through elongated scale, thin section 695; **C**, magnified area of crown of the same scale; **D**, vertical longitudinal section through the widened scale, thin section 691. Dotted canals better seen with slightly changed focus. For locality and stratigraphic arrangement see Fig. 19. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **dt**, dentine tubule; **oc**, osteocyte cavity; **op**, osteocyte process; **smd**, simple mesodentine. Scale bars: 0.1 mm.

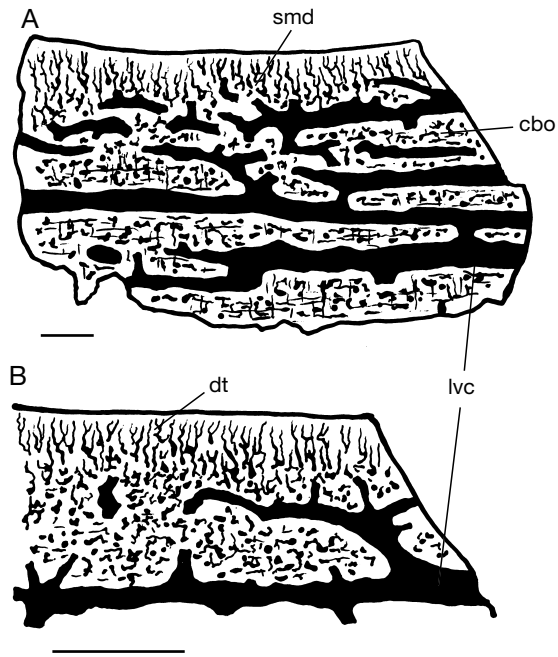


FIG. 22. — *Nostolepis fragilis* n. sp., spine histology; **A**, longitudinal section through the fragment of supposed pectoral spine, thin section 3504; **B**, magnified area at the right edge of the same section. For locality and stratigraphic arrangement see Fig. 19. Abbreviations: **cbo**, cellular bone; **dt**, dentine tubule; **lvc**, longitudinal vascular canal; **smd**, simple mesodentine. Scale bars: 0.1 mm.

base outline. The distal pointed edge may overhang the base on twice their length (Fig. 20C). Short, widened crowns (Fig. 20D) and enlarged bases met rarely. Two long ridges delimit a large medial crown area, surrounded by a pair of lateral areas, somewhat lowered (Fig. 20D, G) or connected to the base sides at right angle (Fig. 20B). The rhombic base is small, anteriorly vaulted (Fig. 20E) and posteriorly depressed, with a deep fossa (Figs 19D; 20C).

Scales are made of a moderately cellular bone (base) and mesodentine showing only one or two growth lamellae (crown). Enlarged radial and ascending vascular canals (Fig. 21A, C) are present with arising and mainly superficially directed winding dentine tubules. They contain widenings similar to the lacunae in Stranggewebe. The crown mesodentine looks similar to bone tissue of the base due to the presence of osteocytes even high in the crown and in well preserved bases.

DISCUSSION

By their crown downsloping anteriorly at a high angle, overhanging the base and by their medial area, outlined by two long ridges, the scales of *Nostolepis fragilis* n. sp. are similar to *N. arctica* Vieth, 1980 (Vieth 1980: pl. 5, figs 1-9). But at the difference of the new species, *N. arctica* scales are larger, more massive and bear more ridges. Additional ridges may also be present on lateral areas. Except for medials and one pair of laterals, *N. fragilis* n. sp. has no extra ornamental details. Its concave and fossulated base strongly differs from the convex and centrally vaulted ones of *N. arctica*. Scale crowns with their increased number of growth lamellae (five),

their more diversified system of principal vascular canals and the presence of typical Stranggewebe are characteristic for *N. arctica* (Vieth 1980: fig. 20A-E).

BIOSTRATIGRAPHIC SIGNIFICANCE

Identical with representatives of *Acritolepis* n. gen.

Nostolepis watsoni n. sp.
(Figs 23A-F; 24)

HOLOTYPE. — LIG 35-2020. Scale (Fig. 23A). Pioneer Island, sample P-10-1. Lower Devonian, Member 8 (Klubov *et al.* 1980).

PARATYPES. — LIG 35-1937, 1938, 1940, 1968 and 1969: scales (Fig. 23B-F). All from the same sample as the holotype.

ETYMOLOGY. — In honour of D. M. S. Watson, acanthodian researcher.

MATERIAL EXAMINED. — 83 scales.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 5, bed 55; Spokojnaya River, outcrop 48, beds 5, 7 and outcrop 49, bed 11; Pod"emnaya River, observation point 26-3. Pioneer Island: samples P-12-7, 12-12, 10-1, 9-1 and observation point 2478. Lower Devonian, Emsian, Rusanov and Al'banov formations of the October Revolution Island and supposed analogues, in age, of the first one on Pioneer Island (Members 6-8).

DIAGNOSIS. — *Nostolepis* with scales of moderate size, rhombic crowns ornamented by six short, rounded, sub-parallel or sub-radial ridges, low neck and strongly anteriorly advanced base. Extremely thin-lamellose cellular to acellular base bone, with a simple network of mesodentine and Stranggewebe in crown which can be replaced by dentine.

DESCRIPTION

Species described from disarticulated scales. Their size varies in length from 0.4 to 0.85 mm. Crown is rhombic, with a slightly elongated posterior area. Six short, rounded, sub-parallel or sub-radial converging ridges (Fig. 23A, B) occur along the proximal margin. Another scale variety (Fig. 23D, F) shows more regularly parallel, lower and longer ridges reaching the middle crown part. The scale base is massive, strongly vaulted anteriorly and protruding the crown (Fig. 23A, C). A distinct sub-rhombic rim, separating it from a very low neck that thickens posteriorly, outlines it. Postero-lateral neck walls may bear vertical grooves.

The two noted scale varieties have a slightly different histological structure. The short-ridged crowns (like the holotype) are composed of mesodentine with a typical network of tubules interconnected with osteocyte spaces (Fig. 24C, D). The small posterior area demonstrates a Stranggewebe only superficially developed. It never occurs in the primordial lamella. The extremely thin-layered base is composed of cellular bone. The second scale variety has bases consisting of almost acellular bone and crowns made of dentine (Fig. 24A, B). The number of growth lamellae is the same: eight. Ascending vascular canals are smooth, with long widened principal and shorter side branches. No lacunae or osteocytes are met. A complex central knot (Fig. 24A) of dentine canals is seen in the primordial growth lamella.

DISCUSSION

By its crown ornamentation and its specific, largely advanced, massive and anteriorly vaulted base, *Nostolepis watsoni* n. sp. is comparable to several representatives belonging to different genera. The closest one is *Nostolepis* sp. B defined by Vyushkova from the Telengitian upper Salairka beds and Belovo Horizon of Salair (Vyushkova 1992: pl. 1, figs 7-9, pl. 3, fig. 1). The histological structure of scales has not been investigated. Morphologic differences concern the more numerous and regular subparallel ridges occurring in the Salair specimens. This is also supposedly said about the weakly ridged scales of *Trundlelepis cervicostulata* morphotype 2 (Burrow 1997), identified from the Lochkovian Trundle beds of New South Wales, Australia (Burrow 1997: pl. 1, fig. 17a, b, pl. 3, fig. 3). As opposed to *N. watsoni* n. sp., they bear six to 12 anterior ridges, and about 10% of scales contain crown pore openings, which are not observed in *N. watsoni* n. sp. *Trundlelepis cervicostulata* scale bases are also composed of cellular (Burrow 1997: fig. 5C and explanatory

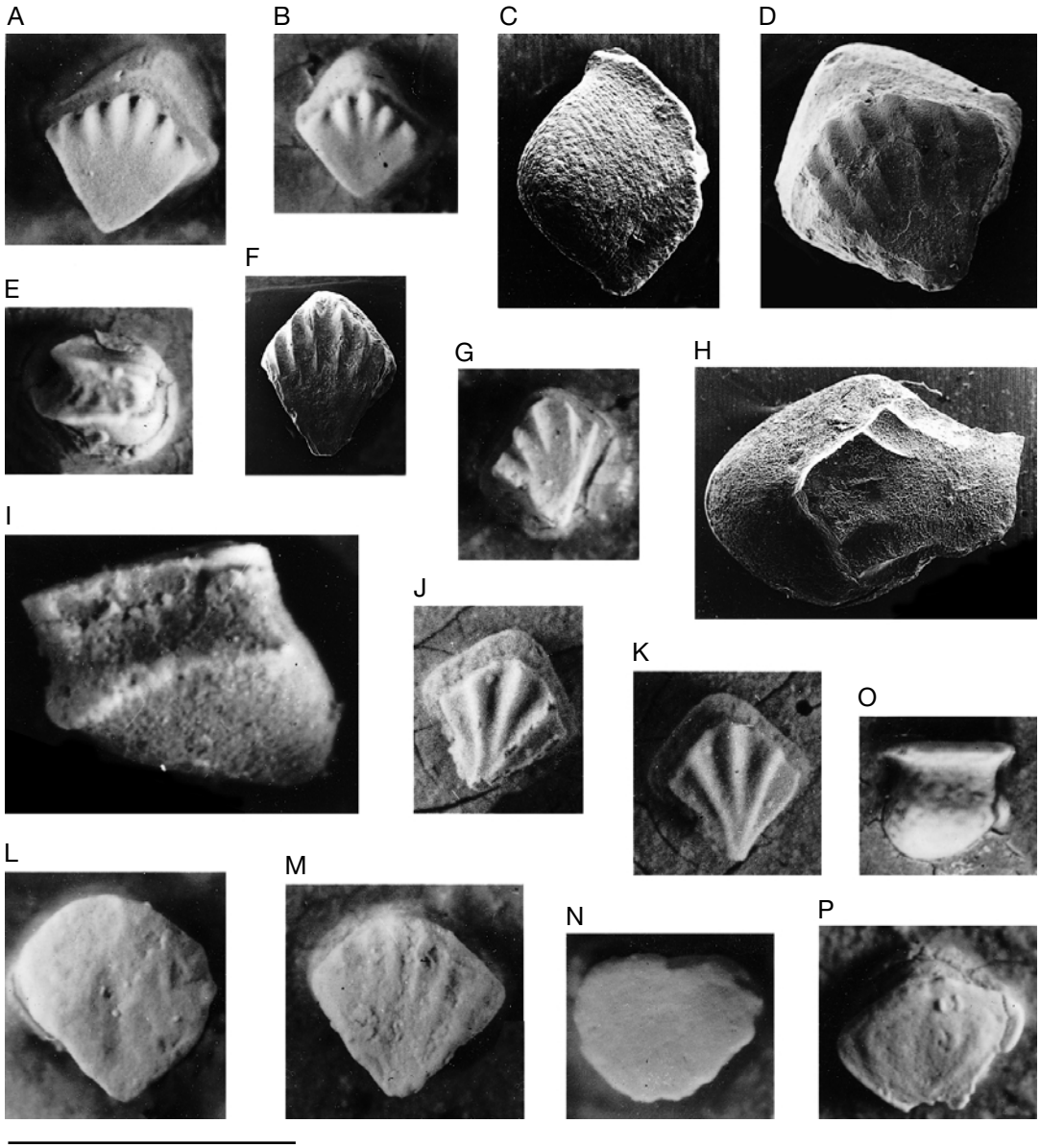


FIG. 23. — **A**-**F**, *Nostolepis watsoni* n. sp., scales, Pioneer Island, sample P-10-1, Lower Devonian, Member 8. (Here and further members of the Pioneer Island geological sequence taken after Klubov *et al.* 1980); **A**, holotype, LIG 35-2020, crown; **B**, LIG 35-1968, crown; **C**, LIG 35-1938, base; **D**, LIG 35-1937, crown; **E**, LIG 35-1969, side; **F**, LIG 35-1940, crown; **A**, **B**, **D**, **F**, anterior upwards; **C**, to left; **E**, to right; **G**-**K**, *Watsonacanthus costatus* n. sp., scales; **G**, LIG 35-1967, crown; **H**, LIG 35-2140, crown; **I**, LIG 35-1422, side; **J**, LIG 35-1993, crown; **K**, holotype, LIG 35-2074, crown; anterior upwards (**G**, **K**, **J**), to the left (**H**) and to right (**I**); **G**-**I**, Pioneer Island, sample P-10-1, Lower Devonian, Member 8; **J**, **K**, October Revolution Island, Spokojnaya River, outcrop 48, bed 5, lower Al'banov Subformation; **L**, **M**, Acanthodii indet., scales, crowns, anterior upwards; **L**, LIG 35-1997; **M**, LIG 35-1998, Komsomolets Island, outcrop 18077, bed 9, Spokojnaya Formation; **N**-**P**, *Gomphonchus nordicus* n. sp., scales; **N**, LIG 35-2006, crown, anterior upwards; **O**, LIG 35-2008, side, anterior to left; **P**, holotype, LIG 35-2007, crown, anterior upwards, Pioneer Island, sample 12-76, Upper Silurian, Pridoli, Member 3. Scale bar: 1 mm.

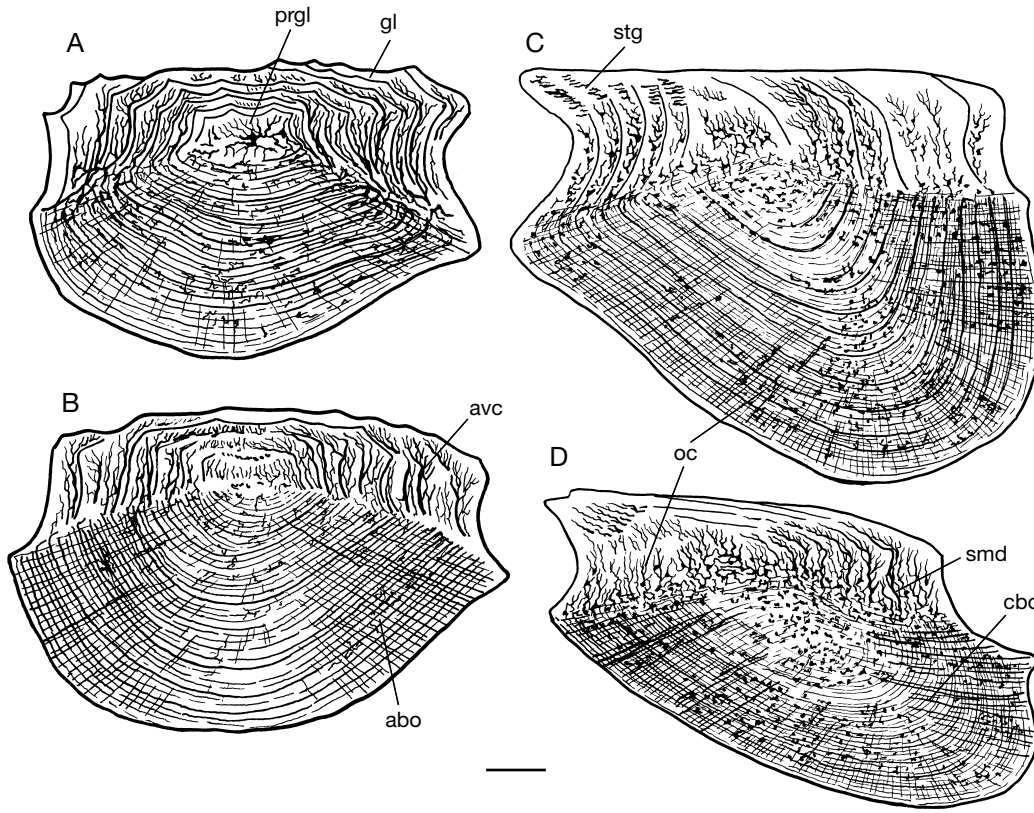


FIG. 24. — *Nostolepis watsoni* n. sp., scale histology, Pioneer Island, sample P-9-1, Lower Devonian, Member 8; **A**, **B**, vertical transverse sections through the scales with elongated flattened ridges (see Fig. 23 D), thin sections 3286 (**A**) and 3266 (**B**); **C**, **D**, vertical longitudinal sections through the scales with short, rounded, higher ridges (see Fig. 23A), thin sections 3267 (**C**) and 3268 (**D**). Abbreviations: **abo**, acellular bone; **avc**, ascending vascular canal; **cbo**, cellular bone; **gl**, growth lamella; **oc**, osteocyte cavity; **prgl**, primordial growth lamella; **smd**, simple mesodentine; **stg**, Sranggewebe (oriented mesodentine). Scale bar: 0.1 mm.

fig. 5-3 in addendum 1997) to acellular bone (fig. 5D and fig. 5-4). Their simple mesodentine (figs 5-2 and 5-5 in addendum 1997) in crown contains short winding dentine tubules with lacunae expansions comparable only to the first variety of scales in *N. watsoni* n. sp. Stranggewebe or dentine tissue with long ascending vascular canals is not seen in *T. cervicostulata*.

Several morphologic similarities unite *N. watsoni* n. sp. with the scales of *Cheiracanthoides* sp. indet. from the Emsian La Grange Limestone of Armorican Massif, France (Vidal *et al.* 1994: fig. 4.11). However the crown ridges of figured specimen seem sharper when compared to *N. watsoni* n. sp. The histological structure of these scales is not taken into account.

By most morphologic and histological features *Nostolepis watsoni* n. sp. resembles scales of *Watsonacanthus* Valiukevicius, 1979. It can be marked as an intermediate form between certain *Nostolepis* and *Watsonacanthus* lineages. By its converging rounded and flattened ridges it is closer to *W. oervigi* Valiukevicius, 1979 (pl. 11, figs 1-8, pl. 12, figs 1-4). *W. oervigi* scale bases are characterised by a highly cellular bone (Valiukevičius 1979: fig. 1a-d; 1994: fig. 75.5), containing dense multiangular osteocytes, and a simple mesodentine network in crowns without forming main branches. Stranggewebe has also not been observed.

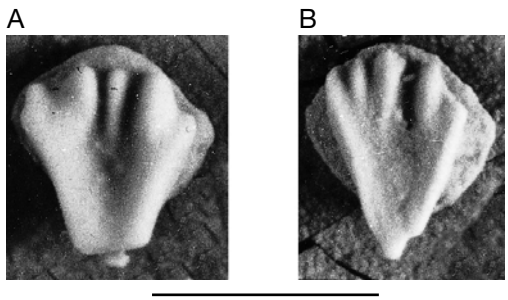


FIG. 25. — *Nostolepis timanica* n. sp., scales, crowns, anterior upwards, Pioneer Island, sample P-10-1, Lower Devonian, Member 8; **A**, LIG 35-2022; **B**, holotype, LIG 35-2023. Scale bar: 0.5 mm.

BIOSTRATIGRAPHIC SIGNIFICANCE

Key species of the beds with *Watsonacanthus costatus* n. sp. based on acanthodian, a dispersed scale assemblage, an age analogue of the nominate acanthodian zone, marked earlier as *Watsonacanthus oervigi* Zone can be proposed. On Severnaya Zemlya Archipelago it is attached to the Rusanov Formation and lower Al'banov Subformation. The Conodont-grounded age, based on ranges of the dominating *Pandorinellina expansa* (Uyeno & Mason, 1975), *P. exigua exigua* (Philip, 1966) with a smaller numbers of *Pelekysgnathus* Klapper & Johnson, 1980 and *Steptotaxis* Uyeno & Klapper, 1980, gives an Emsian age, within the *dehiscens-inversus* zones of the standard conodont scale.

Nostolepis timanica n. sp.
(Figs 25; 26)

HOLOTYPE. — LIG 35-2023. Scale (Fig. 25B). Pioneer Island, sample P-10-1. Lower Devonian, Member 8.

ETYMOLOGY. — After Timan-Pechora region, where the species has been identified first.

MATERIAL EXAMINED. — 60 scales.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 4, bed 3; Spokojnaya River, outcrop 40, bed 27. Pioneer Island: samples P-9-1 and 10-1. Lower Devonian, Lochkovian to Emsian, Pod"emnaya to Rusanov formations.

DIAGNOSIS. — A *Nostolepis* with minute scales with elongated, horizontally flattened crowns with three to four short, converging anterior ridges of both inconstant form and length. Simple mesodentine in crown with typical canal network or with long, smooth ascending and branchy radial vasculars resembling those of dentine-type tissue. Bone of base highly cellular.

DESCRIPTION

Species described from isolated scales. Their size varies in length from 0.2 to 0.45 mm. Crowns have an elongated triangular form with rounded and widened anterior edge and tapered posterior, overhanging base. Three to four stout, rounded sub-parallel anterior ridges of inconstant form and length converge but do not reach medial crown part. Two thirds of the crown surface are flat, unornamented, only with a shallow longitudinal medial concavity. Crown plate is horizontal. Scale bases are rhombic; differently convex anterior and side margins are protruding crown. Most convex ones are centrally vaulted. We observe up to four growth lamellae in the crown composed of uniform simple mesodentine. Several specimens demonstrate comparatively long, smooth main branches of ascending vascular canals (Fig. 26C, D), less characteristic for the "*Nostolepis*"-type histology. Mesodentine canal network includes medium numbers of osteocyte spaces, increasing in primordial lamella (Fig. 26B, E). Enlarged and branching radial dentine canals occur at the base-crown junction. Base bone is highly cellular, uniformly thin lamellar, with long Sharpey's fibres.

DISCUSSION

Nostolepis timanica n. sp. follows *N. striata* Pander, 1856-*N. minima* Valiukevicius, 1994 phylogenetic lineage of nostolepids. It differs from the close *N. minima* by its weaker ridges both in number and strength, including loss of oblique neck ridges. *N. timanica* n. sp. has no lateral crown ridges, like those pointing distally in *N. minima* (Valiukevičius 1994: pl. 21, figs 10-12; 1998: pl. 1, figs 5-9). Furthermore differences occur in histological structure. *N. minima* scale crowns are composed of a simple mesodentine with a more bushy canal network and a Stranggewebe (scales from the

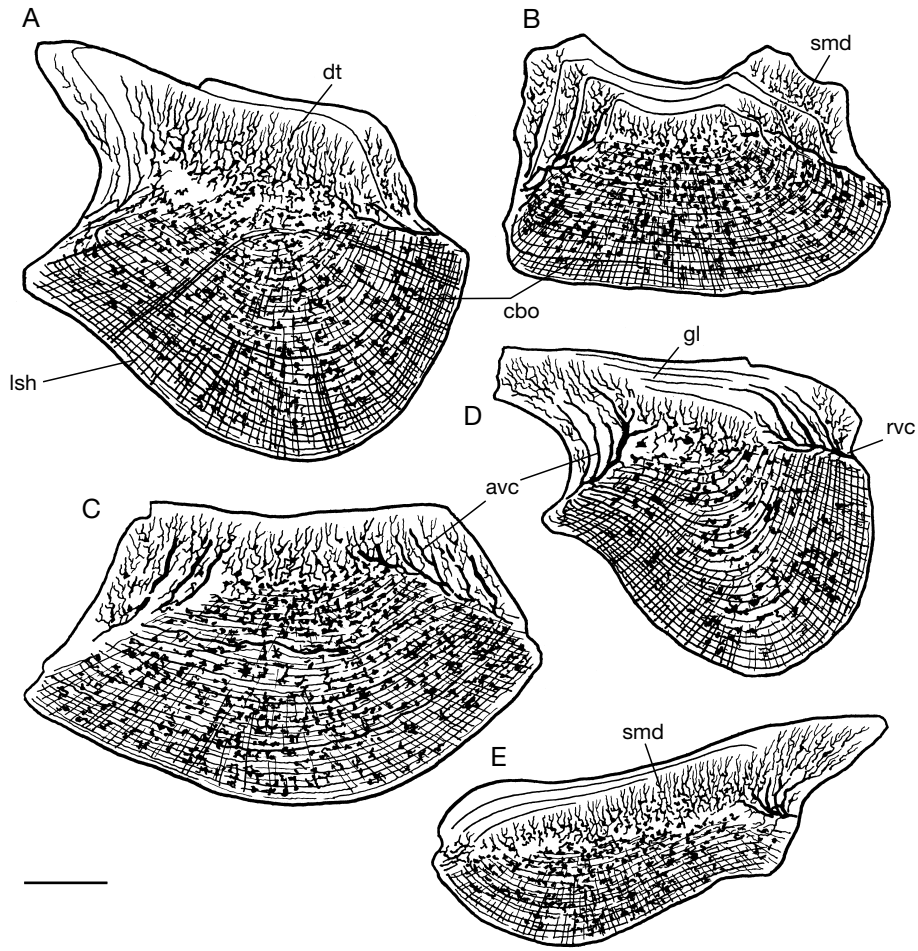


FIG. 26. — *Nostolepis timanica* n. sp., scale histology, Pioneer Island, sample P-10-1, Lower Devonian, Member 8; **A**, vertical longitudinal section through the central part of scale, anterior to right, thin section 3375; **B**, vertical transverse section through the anterior part of scale, thin section 3376; **C**, vertical transverse section through the posterior scale part, thin section 3377; **D**, **E**, vertical longitudinal sections through the scale with maximum vaulted, convex base (**D**) and maximum flattened scale (**E**), anterior to right (**D**) and to left (**E**), thin sections 3378 and 3379. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **dt**, dentine tubule; **gl**, growth lamella; **lsh**, longitudinal Sharpey's fibres; **rvc**, radial vascular canal; **smd**, simple mesodentine. Scale bar: 0.1 mm.

Tareya River section, Tajmyr; Valiukevičius 1994: fig. 75.4) only fragmentary developed: it can completely fill all posterior area of crowns (scales from the type Baltic region; Valiukevičius 1998: pl. 12, figs 2-4), embracing also the primordial growth lamella. *N. timanica* n. sp. shows no Stranggewebe, and ascending or radial vascular canals are sometimes more characteristic of true dentine than mesodentine style.

BIOSTRATIGRAPHIC SIGNIFICANCE

Long-ranging species, occurring into the *Nostolepis minima* (upper part) Zone assemblage (*Diplacanthy poltnigi* Subzone), upper part of Lochkovian (Pod"emnaya Formation). The latest representatives are found on Severnaya Zemlya Archipelago within the age analogues of the Rusanov Formation on Pioneer Island, in beds with *Watsonacanthus costatus* n. sp. (Emsian).

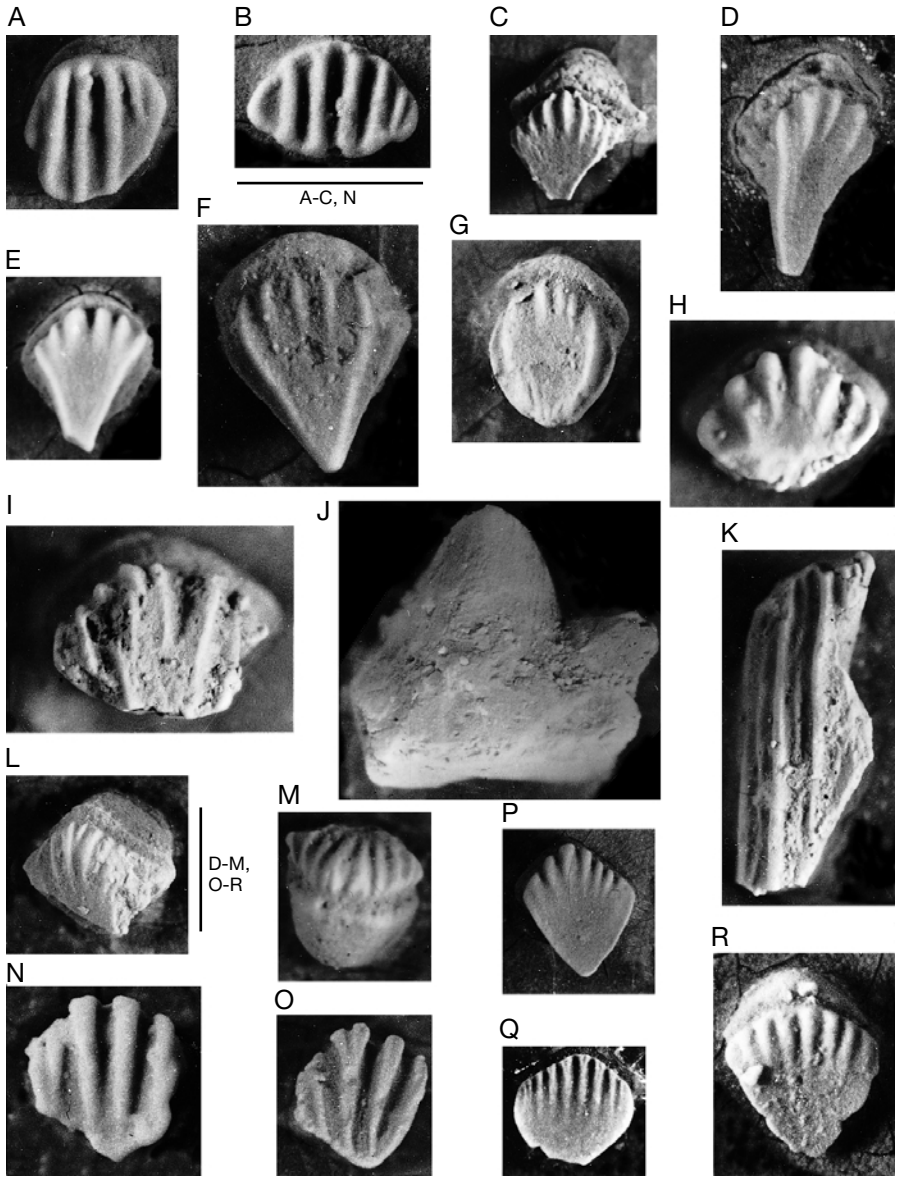


FIG. 27. — **A**, **B**, *Nostolepis* sp. cf. *N. gracilis* Gross, 1947, scales, crowns, anterior upwards; **A**, LIG 35-2068; **B**, LIG 35-2067; Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation; **C**-**E**, *Nostolepis taimyrica* Valiukevicius, 1994, scales, crowns, anterior upwards; **C**, LIG 35-2021; **D**, LIG 35-1971; **E**, LIG 35-1996; Pioneer Island, sample P-10-1 (**C**, **D**), Lower Devonian, Member 8 and Ushakov River, outcrop 25, bed 1 (**E**), lower Al'banov Subformation; **F**, **G**, *Nostolepis striata* Pander, 1856, scales, crowns, anterior upwards; **F**, LIG 35-2012; **G**, LIG 35-2011; Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation; **H**-**K**, *Nostolepis* sp. cf. *N. multicostata* Vieth, 1980; **H**, **I**, scales, crowns, anterior upwards; **H**, LIG 35-1983; **I**, LIG 35-2010; **J**, LIG 35-1979, jawbone fragment with main tooth cusps; **K**, LIG 35-1977, spine fragment, lateral view, anterior to left; Spokojnaya River, the right bank outcrop – analogues of outcrop 4, higher the 11th bed on the Matusevich River (**H**) and Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation; **L**, **M**, *Nostolepis* sp. cf. *N. multangula* Valiukevicius, 1994, scales, oblique crown-side views, anterior upwards (**L**) and downwards (**M**); **L**, LIG 35-2018; **M**, LIG 35-1992; Pioneer Island, outcrop 980, sample 980^{a}, age unidentified (**L**) and Spokojnaya River, outcrop 48, bed 5 (**M**), lower Al'banov Subformation; **N**, **O**, *Tareyacanthus* sp. cf. *T. dissectus* Valiukevicius, 1994, scales, crowns, anterior upwards; **N**, LIG 35-2004; **O**, LIG 35-1972. Pioneer Island, sample P-9-1 (**N**) and P-10-1 (**O**); Lower Devonian, Member 8; **P**, **Q**, *Cheiracanthoides borealis* Valiukevicius, 1994, scales, crowns, anterior upwards; **P**, LIG 35-2001; **Q**, LIG 35-1780; Pioneer Island, sample P-9-1 (**P**) and P-10-1 (**Q**), Lower Devonian, Member 8; **R**, *Cheiracanthoides comptus* Wells, 1944, scale, crown, anterior upwards, LIG 35-1973; Pioneer Island, sample P-10-1, Lower Devonian, Member 8. Scale bars: 0.5 mm.

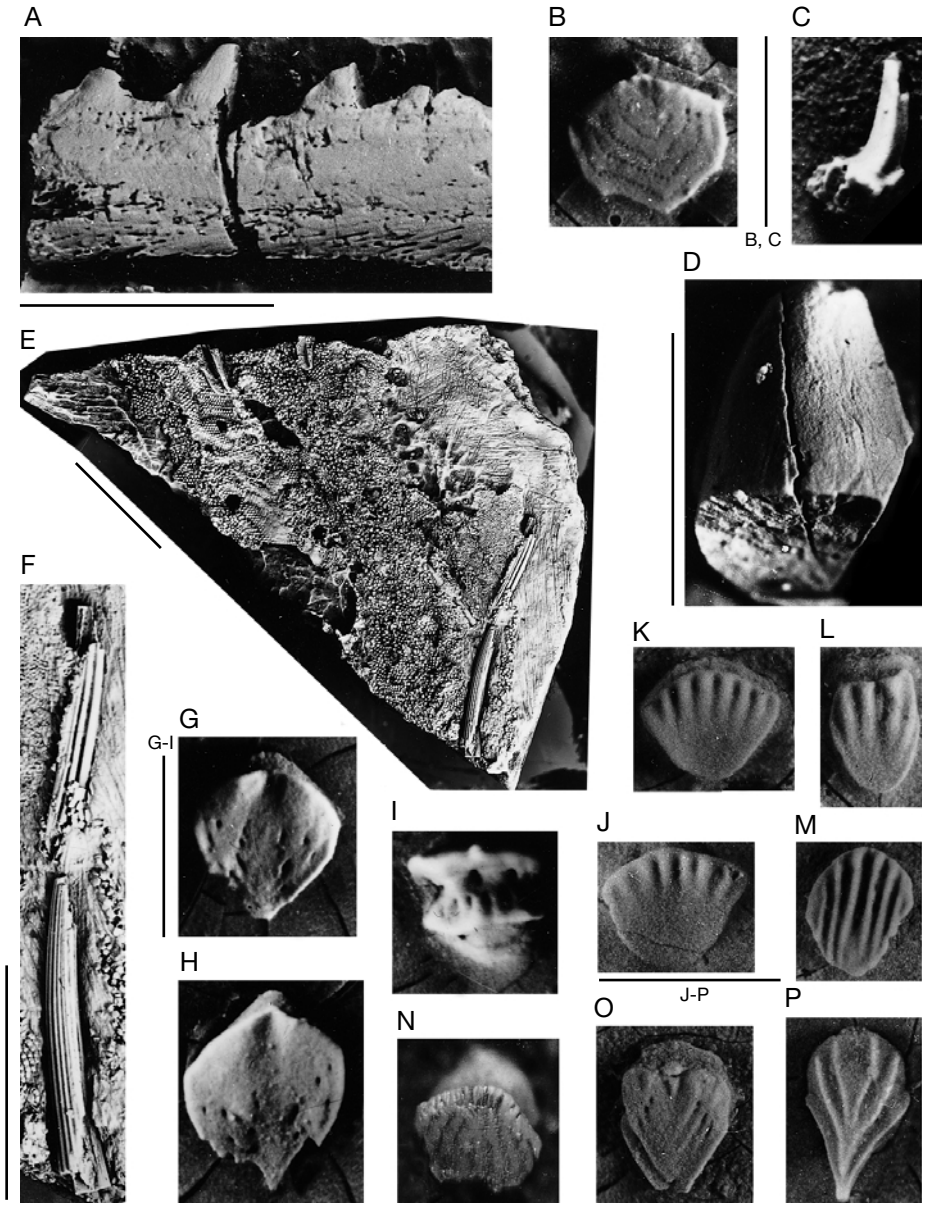


FIG. 28. — **A**-**D**, *Poracanthodes punctatus* Brotzen, 1934; **A**, jawbone fragment with tooth cusps of the main row, lateral view, LIG 35-A-391; **B**, scale, crown, anterior upwards, LIG 35-2087; **C**, palatine tooth, lateral view, LIG 35-2084; **D**, fragment of main cusp, lateral view, LIG 35-2083; microremains; **B**-**D** from the same paratype LIG 35-A-391, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **E**-**I**, *Poracanthodes* sp. cf. *P. subporosus* Valiukevicius, 1998; **E**, articulated squamation and fin spines, lateral preservation, paratype LIG 35-A-376; **F**, magnified fragments of spines of the same specimen; **G**-**I**, scales from the same paratype; **G**, crown, anterior upwards, LIG 35-2094; **H**, crown, anterior upwards, LIG 35-2092; **I**, side, anterior to right, LIG 35-2091; Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **J**-**L**, *Cheiracanthoides* sp., scales, crowns, anterior upwards; **J**, LIG 35-2071; **K**, LIG 35-2072; **L**, LIG 35-2073; Pioneer Island, sample 12-76, Upper Silurian, Pridoli, Member 3; **M**, *Nostolepis* sp. cf. *N. gracilis* Gross, 1947, scale, crown, anterior upwards, LIG 35-2066, Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation; **N**, **O**, *Poracanthodes* sp. cf. *P. porosus* Brotzen, 1934, scales, crowns, anterior upwards, LIG 35-2009 and 35-2069, Pioneer Island, sample 12-76, Upper Silurian, Pridoli, Member 3 (**N**) and October Revolution Island, Spokojnaya River, outcrop 41, bed 1, Krasnaya Bukhta Formation (**O**); **P**, *Nostolepis* sp., scale, crown, anterior upwards, Pioneer Island, sample P-10-1, lower Devonian, Member 8. Scale bars: A, E, F, 10 mm; B, C, G-P, 0.5 mm; D, 1 mm.

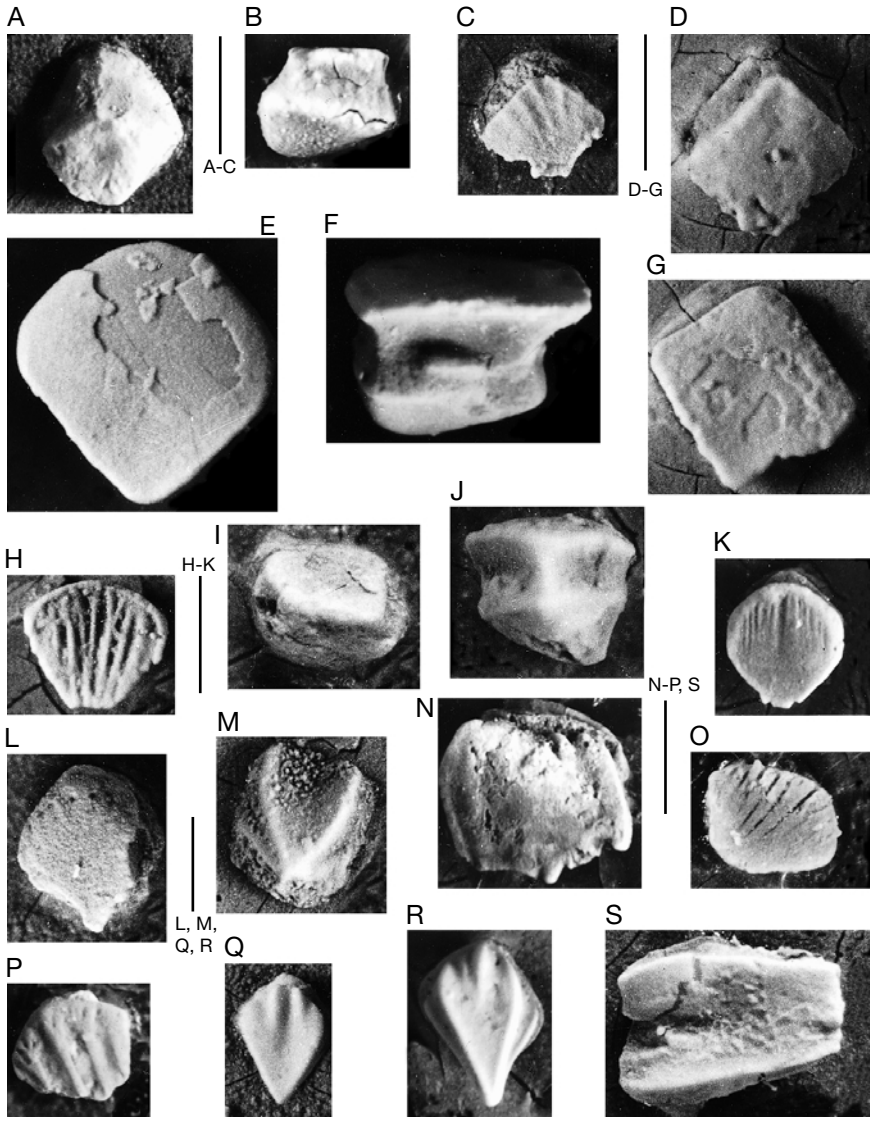


FIG. 29. — **A**, **B**, *Gomphonchus sandelensis* (Pander, 1856), scales; **A**, LIG 35-2000, crown, anterior upwards; **B**, LIG 35-1662, side, anterior to left; Komsomolets Island, outcrop 18077, bed 9, Spokojnaya Formation (**A**) and October Revolution Island, Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation (**B**); **C**, **D**, *Gomphonchus* sp. cf. *G. hoppei* (Gross, 1947), scales, crowns, anterior upwards; **C**, LIG 35-1990; **D**, LIG 35-1991; Spokojnaya River, outcrop 41, bed 1, Krasnaya Bukhta Formation; **E**-**G**, *Acanthoides*? sp. C of Valiukevičius 1985, scales; **E**, **F**, LIG 35-1415, crown, anterior upwards (**E**) and side, anterior to left (**F**); **G**, LIG 35-1974, crown, anterior upwards; Spokojnaya River, outcrop 48, bed 5 (**E**, **F**) and Pioneer Island, the sample with *Tollichthys polaris* and *Luetkeichthys borealis* original specimens, Al'banov Formation; **H**, *Markacanthus* sp. cf. *M. alius* Valiukevicius, 1988, scale, crown, anterior upwards, LIG 35-2019, Matusevich River, outcrop 5, bed 149; **I**, *Acanthoides*? sp. B of Valiukevičius 1985, scale, oblique crown-side view, LIG 35-1995, Matusevich River, outcrop 5, bed 151; **J**, *Acanthoides*? sp. D of Valiukevičius 1985, side, anterior to right, LIG 35-1994, Matusevich River, outcrop 5, bed 133; **K**, **L**, *Cheiracanthus* sp. cf. *Ch. brevicostatus* Gross, 1973, scales, crowns, anterior upwards; **K**, LIG 35-1868; **L**, LIG 35-2070; Matusevich River, outcrop 5, bed 149, Vstrechnaya Formation (**H**-**L**); **M**, *Nostolepis laticristata* Valiukevicius, 1994, scale, crown, anterior upwards, LIG 35-1966; **N**, *Pruemolepis wellsi* Vieth-Schreiner, 1983, scale, crown, anterior upwards, LIG 35-1675; **O**, *Diplacanthus poltnigi* n. sp., holotype, scale, crown, anterior right-obliquely-upwards, LIG 35-1789; Matusevich River, outcrop 4, bed 3 (**M**-**O**), Pod"emnaya Formation; **P**, *Diplacanthus* sp. cf. *D. gravis* Valiukevicius, 1988, scale, crown, anterior left-obliquely-upwards, LIG 35-1985, Matusevich River, outcrop 5, bed 151, Vstrechnaya Formation; **Q**, **R**, *Nostolepis minima* Valiukevicius, 1994, scales, crowns, anterior upwards, LIG 35-2054 (**Q**) and LIG 35-1880 (**R**); Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **S**, *Nostolepis* sp. cf. *N. arctica* Vieth, 1980, scale, crown, anterior to left, LIG 35-2064, Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation. Scale bars: 0.5 mm.

Genus *Acanthacanthus* n. gen.

TYPE AND ONLY SPECIES. — *Acanthacanthus ornatus* n. gen., n. sp.

ETYMOLOGY. — Twice repeated *acantha* (Greek): thorn.

AGE. — Early Devonian, early Lochkovian.

DIAGNOSIS. — As for the type and only known species.

Acanthacanthus ornatus n. sp. (Figs 30A, B; 31)

HOLOTYPE. — LIG 35-A-347. Specimen preserved in lateral view, exposing only the squamation (Fig. 30A, B). Spokojnaya River, outcrop 41, bed 12.

ETYMOLOGY. — From *ornatus* (Latin): ornamented, decorate.

LOCALITY AND AGE. — The single holotype specimen. Lower Devonian, lower Lochkovian, top of the Severnaya Zemlya Formation.

DIAGNOSIS. — Climatiid with large-sized scales of elongated rhombic or drop-shaped crown, ornamented by two posteriorly pointed radial ridges, separating lateral lowered crown areas, and one to two pairs of radial, also acute ridges on the flattened medial area. Crown composed of dominating Stranggewebe, containing wide ascending vascular canals, forming large knots-chambers at the junction with circular canals. Base bone thin-lamellar and moderately cellular.

DESCRIPTION

Scales with rhombic, elongated-rhombic or drop-shaped crowns 0.7-1.2 mm long. The anterior margin is widened, posteriorly stretched, distantly overhanging base, at a low angle relative to it. Rare examples are as wide as long. Crown plates are flat or slightly longitudinally convex. Two symmetrical marked radial ridges cross over the whole crown; they point posteriorly and separate narrow lowered lateral areas. One or two pairs of medial ridges are running parallel to laterals point centralwards but do not reach the posterior edge of crown. All ridges are rounded, not sharp. The shorter central ridges form sometimes a small forecrown-like area, essentially protruding others. The scale neck is low anteriorly and somewhat higher posteriorly; the rhombic base, anteriorly convex, strongly advances. Scales are set densely in lines, with small overlap areas.

Scale crowns demonstrate superpositional (mainly on the two earliest lamellae of the medial area) and areal growth (lateral lamellae, up to four) (Fig. 31A-D). Almost all crowns are composed of Stranggewebe with large stretched lacunae, and only the two latest growth lamellae contain strips of simple networked mesodentine (Fig. 31B, D). It also composes the very restricted anterior crown area (Fig. 31E). Osteocytes are observed even in the latest – lateral – lamellae (Fig. 31D). Characteristic widened ascending vascular canals; at crossing points with circular ones they make large knots-chambers (Fig. 31B, D) and are connected with oriented lacunae or outward-streamed dentine tubules. The Stranggewebe of crown gradually turns into base bone with average cell cavities pierced by long Sharpey's fibres and densely lined by thin growth lamellae.

DISCUSSION

Through their characteristic crown ornamentation *Acanthacanthus ornatus* n. gen., n. sp. scales differ from all the known Climatiidae. Distant affinities are noted with scales of *Climatius reticulatus* Agassiz, 1845, which show radially ridged crowns, but the symmetrical pairs of ridges are not sharp (Denison 1979: figs 16C, 17B). Another comparable taxon, *Nostolepis costata* Goujet, 1976, shows high, sharp, sometimes posteriorly pointed ridges and has lowered lateral areas (Goujet 1976: pl. 62, figs 1-10). But these ridges are of an inconstant length – from short to extend over all the crown – or symmetrically meeting in pairs. By their characteristic vascular canal widening, named "pulp chambers" by Denison (1979), *Acanthacanthus ornatus* n. gen., n. sp. is comparable to *N. costata*, however these last scales are composed of simple mesodentine, without Stranggewebe (Goujet 1976: text-fig. 55A-D) and *Euthacanthus macnicoli* Powrie, 1864 (Denison 1979: fig. 10A), of which it distinctly differ by the mesodentine structure.

BIOSTRATIGRAPHIC SIGNIFICANCE

Key species of the *Poracanthodes menneri* Subzone, a unit based on association of articulate acanthodians from the topmost part of the Severnaya Zemlya Formation. It corresponds to the lower part of the *Nostolepis minima* Zone, widely traced through the regions. Age is early Lochkovian. Tentatively correlated to the *woschmidti* Zone of standard conodont scale.

Genus *Watsonacanthus* Valiukevicius, 1979

Watsonacanthus costatus n. sp.
(Figs 23G-K; 32)

Watsonacanthus oervigi Sobolev, Karatajute-Talimaa & Valiukevicius, 1988: pl. 1, figs 12, 13. — Valiukevičius 1994: 165, pl. 22, figs 1-5, text-figs 75.5, 76.1-4; 1995a: 394, 397, text-figs 2, 4, 6.

HOLOTYPE. — LIG 35-2074. Scale (Fig. 23K). October Revolution Island, Spokojnaya River, outcrop 48, bed 5.

PARATYPES. — LIG 35-1967, 2140, 1422, 1993: scales (Fig. 23G-J).

ETYMOLOGY. — From *Costatus* (Latin): ridged, with reference to the crown ornamentation.

MATERIAL EXAMINED. — 35 scales.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 5, bed 55; Spokojnaya River, outcrop 48, beds 5-7 and outcrop 49, bed 11. Pioneer Island: samples P-9-1 and 10-1. Lower Devonian, Emsian, lower Al'banov Subformation of the October Revolution Island and supposed age analogues of the Rusanov Formation on the Pioneer Island (Member 8).

DIAGNOSIS. — *Watsonacanthus* with scales ornamented by three to six sharp radial ridges pointing posteriorly or converging at crown midlength. Neck low, base massive, strongly anteriorly protruding crown. Scale crown composed of simple mesodentine network without principal canal branches and lacunae (anterior part, primordial lamella included), and dentine containing long ascending and radial vascular canals (posterior part). Base bone lowly cellular.

DESCRIPTION

Species described from isolated scales. Small and medium-sized scales with crown length of 0.4-0.8 mm, dominate. Rare examples exceed 1 mm. Crown is of a rhombic, rarely elongated-rhombic (Fig. 23H) form, flat. Maximum elongated crowns overhang bases posteriorly. Three to six sharp radial ridges, highered anteriorly and gradually lowered, may point at the posterior edge or converge at the crown midlength. Their anterior transverse sections make characteristic triangle forms. Base massive, rhombic in outline, anteriorly vaulted and strongly protruding crown. Neck low.

Maximum six lamellae of superpositional growth in crown composed of simple networked mesodentine (anterior part, including primordial lamella) and dentine (posterior part). Mesodentine without principal branches of canals (Fig. 32B, C) and without lacunae. Rare osteocyte spaces observed only in primordial lamella (Fig. 32A). Posterior crown part penetrated by long widened ascending canals with numerous smaller side branches. For this of dentine composed part characteristic also long, multibranched radial vascular canals displaced at the junction strip between base and crown (Fig. 32B, C). Extremely thin-lamellar base bone includes small numbers of osteocytes.

DISCUSSION

Detailed study of *Watsonacanthus* scales from Tajmyr and Severnaya Zemlya has led to a final opinion assigning them to separate species differing from *W. oervigi* of Spitsbergen (Valiukevičius 1979). *W. costatus* n. sp. has essentially higher, sharper and mostly longer crown ridges. *W. oervigi* differs both by its crown and base tissue structure. Simple networked mesodentine lacking main vascular canals composes entirely three to four growth lamellae in crown of *W. oervigi*. It includes osteocytes (Valiukevičius 1994: text-fig. 75.5). Dentine-type tissue has not been observed. Scales from Tajmyr are identical in their morphological features to those of Severnaya Zemlya, but they differ in their crown mesodentine structure, which exhibits lacunae and osteocytes in the earliest growth lamellae (Valiukevičius 1994: text-fig. 76.1-4). Stranggewebe is developed in very restricted area.

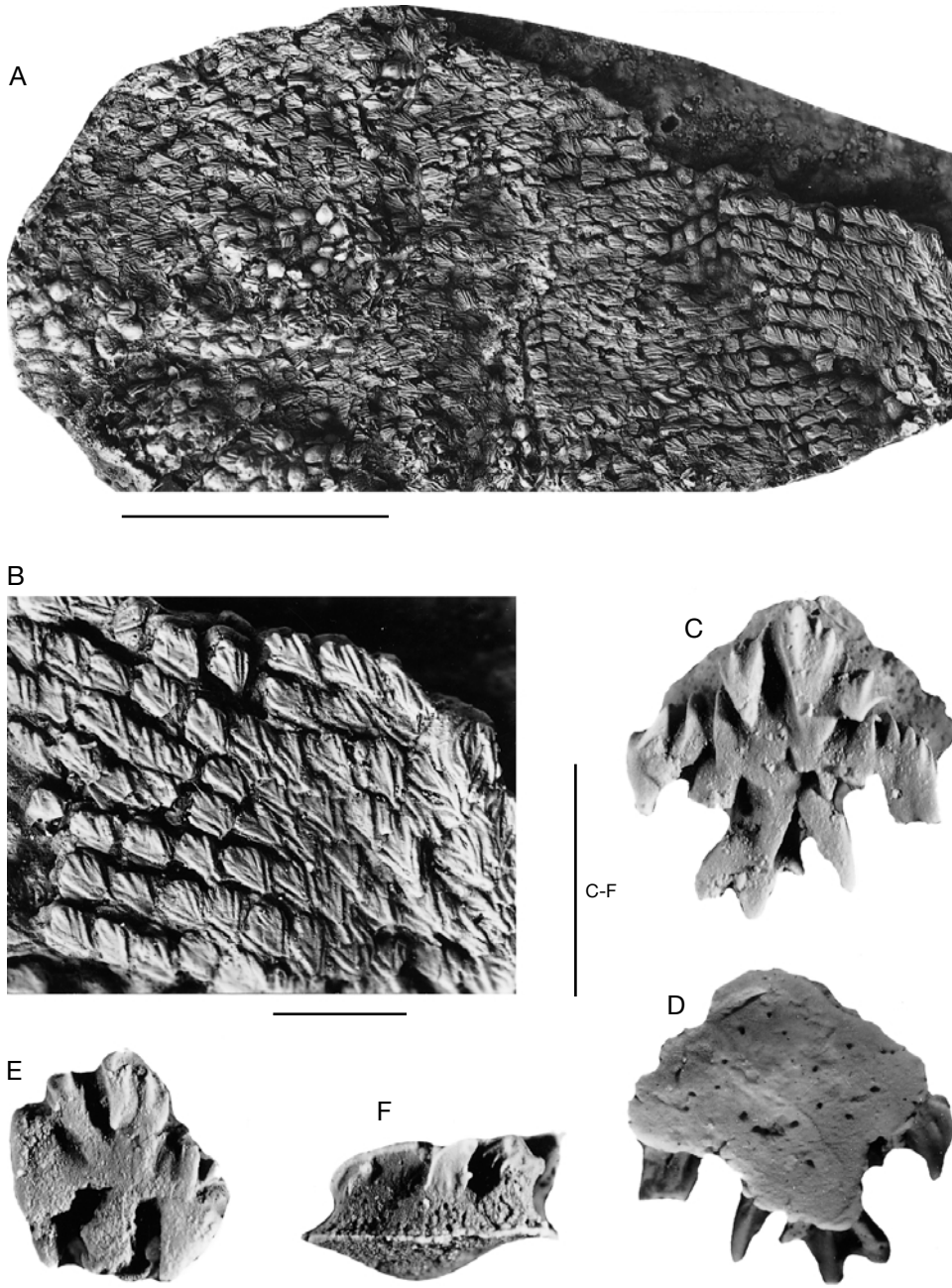


FIG. 30. — **A**, **B**, *Acanthacanthus ornatus* n. gen., n. sp., Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **A**, holotype, specimen LIG 35-A-347 in lateral preservation, squamation, anterior to left; **B**, enlarged area (right corner) of the same specimen, scales, crowns; **C**-**F**, *Acanthospina irregulare* n. gen., n. sp., scales, specimen LIG 35-A-345, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **C**, **D**, LIG 35-1245, crown (**C**) and base (**D**), anterior upwards; **E**, **F**, LIG 35-1246, crown (**E**), anterior upwards and side (**F**), anterior to left. Scale bars: A, 10 mm; B, 2 mm; C-F, 1 mm.

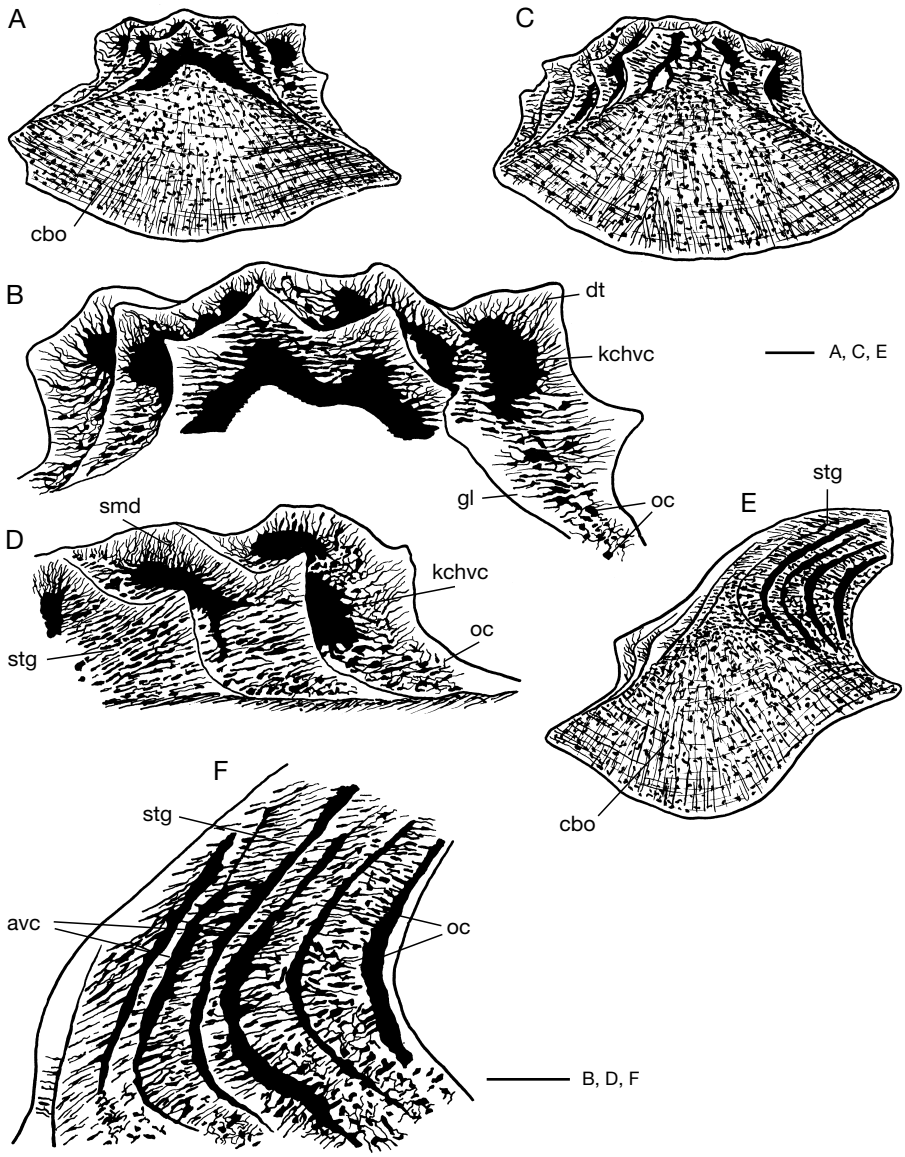


FIG. 31. — *Acanthacanthus ornatus* n. gen., n. sp., scale histology, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, vertical transverse section through the central part of medium wide scale, thin section 689; **B**, enlarged crown of the same section; **C**, vertical transverse section through the mostly widened scale, thin section 688; **D**, magnified right crown area of the same section; **E**, vertical longitudinal section through the maximum elongated scale, thin section 687; **F**, magnified crown area of the same scale. All scales from the holotype specimen LIG 35-A-347. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **dt**, dentine tubule; **gl**, growth lamella; **kchvc**, knot-chamber of vascular canals; **oc**, osteocyte cavity; **smd**, simple mesodentine; **stg**, Stranggewebe (oriented mesodentine). Scale bars: 0.1 mm.

W. sibiricus scales (Valiukevičius 1994: pl. 22, figs 7, 8) differ from the species under consideration by their tiny size and the flatness of scales, ornamented by a pair of short medial ridges and two pairs of longer lateral ones almost reaching the posterior edge, but with no posterior point.

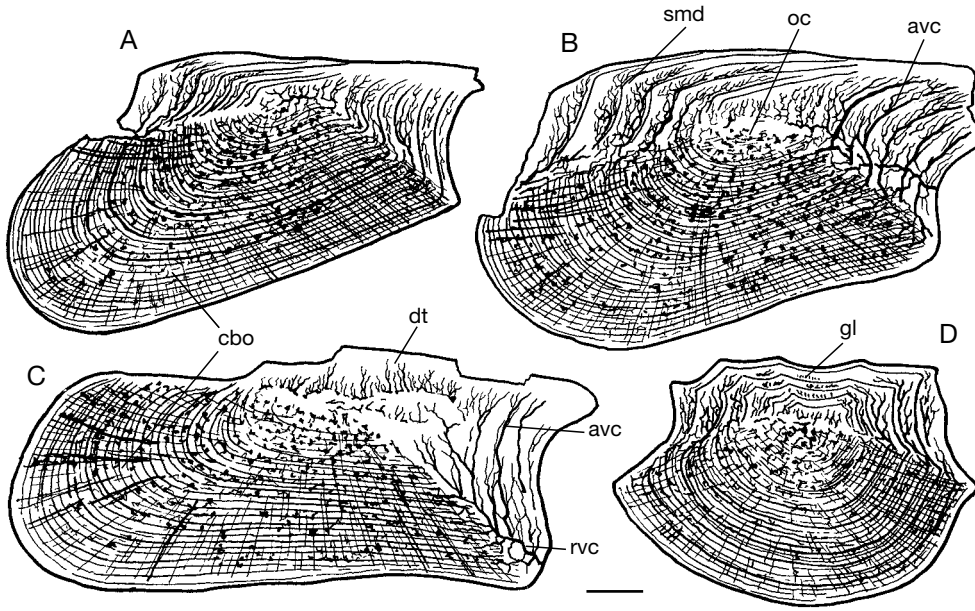


FIG. 32. — *Watsonacanthus costatus* n. sp., scale histology, Pioneer Island, sample P-10-1, Lower Devonian, Member 8; **A**-**C**, vertical longitudinal sections of scales, anterior to left, thin sections 3289 (**A**, scale like figured on Fig. 23K), 3302 (**B**, scale with shorter ridges) and 3303 (**C**, scale like figured on Fig. 23H); **D**, vertical transverse section through the central part of scale like figured on Fig. 23K. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **dt**, dentine tubule; **gl**, growth lamella; **oc**, osteocyte cavity; **rvc**, radial vascular canal; **smd**, simple mesodentine. Scale bar: 0.1 mm.

BIOSTRATIGRAPHIC SIGNIFICANCE

Index species among the acanthodian assemblage. It allows to distinguish on Severnaya Zemlya Archipelago the early Emsian beds with *Watsonacanthus costatus* n. sp. (lower Al'banov Subformation on October Revolution and Pioneer islands and Member 8, supposed Rusanov Formation on the Pioneer Island). In Tajmyr (Dolgan beds, formerly *Favosites regularissimus* Zone) and Timan-Pechora (Varandei Formation) regions – index species for the nominate acanthodian Zone (earlier *W. oervigi*; Valiukevičius 1995a: text-figs 2-6). It corresponds on Pioneer Island to *dehiscens-inversus* and in Tajmyr to *gronbergi-inversus* zones of the standard conodont scale.

Order DIPLACANTHIFORMES Berg, 1940

Acanthodian fishes having scales of the "*Diplacanthus*"-type histological structure (Valiukevičius 1985, 1995b).

Family DIPLACANTHIDAE Woodward, 1891
Genus *Diplacanthus* Agassiz, 1844

Diplacanthus poltnigi n. sp.
(Figs 29O; 33)

Nostolepis gracilis — Vieth 1980: 32, 33, pl. 5, fig. 14a, b (partim).

Diplacanthus longispinus — Poltnig 1984: 114, 115, pl. 2, figs 1-7.

HOLOTYPE. — LIG 35-1789. Scale (Fig. 29O). Matusevich River, outcrop 4, bed 3.

ETYMOLOGY. — In honour of Dr. W. Poltnig, Karl-Franz University of Graz, Austria.

MATERIAL EXAMINED. — 10 scales.

LOCALITY AND AGE. — Out of the holotype locality, Spokojnaya River, outcrop 40, beds 21 and 27. Lower Devonian, Lochkovian, Pod"emnaya Formation.

DIAGNOSIS. — *Diplacanthus* with small rhombic scales, with crown ornamented by 10 to 23 deep, linear, sub-parallel grooves, extending over all its length or converging at the extreme posterior area. Crown composed of mesodentine with long ascen-

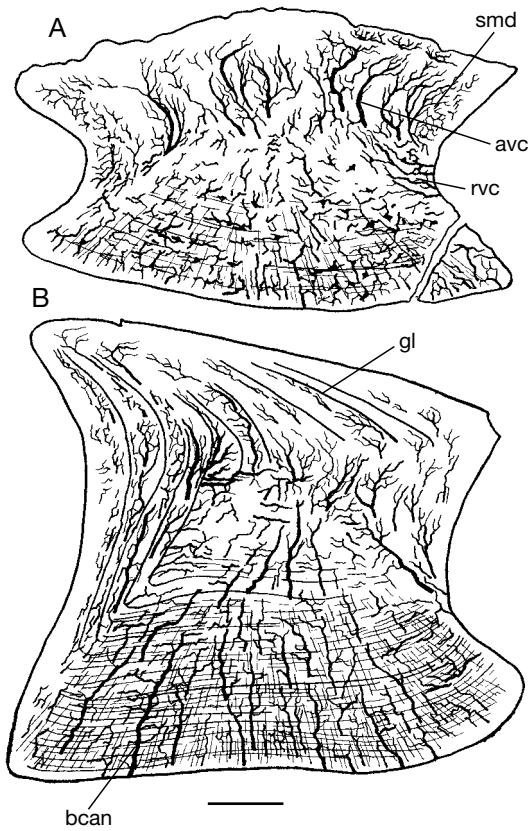


FIG. 33. — *Diplacanthus poltnigi* n. sp., scale histology, Matusevich River, outcrop 4, bed 3, Pod"emnaya Formation; **A**, vertical transverse section through the central part of scale like holotype, thin section 921; **B**, vertical longitudinal section through the scale with maximum high neck and flattened base, thin section 922. Abbreviations: **avc**, ascending vascular canal; **bcan**, vascular canal piercing base of scale; **gl**, growth lamella; **rvc**, radial vascular canal; **smd**, simple mesodentine. Scale bar: 0.1 mm.

ding vascular canals and small side tubules. Complex centripetal radial canals over the base. Acellular base bone penetrated by long and branchy upstreamed vascular canals.

DESCRIPTION

Species described from isolated scales. Crowns are sub-rhombic, rounded-rhombic to oval, flat, 0.4-0.8 mm long, with width generally exceeding the length. Crowns are ornamented with 10 to 12 deep, linear, sub-parallel, U-formed grooves, slightly deepened anteriorly; in scales from other regions up to 23 grooves can occur. No visible ridges. Grooves extend overall crowns, rarely more shallow posteriorly. Scale bases are usually as large as the crowns, slightly convex with a moderately high necks. Rare examples with very high necks have almost flat bases.

Scale crowns are made of mesodentine close to dentine by several features. One encounters up to eight growth lamellae penetrated by long principal ascending vascular canals, connected by small winding side branches. Primordial lamella contains a complicated knot of vascular canals (Fig. 33B). Neither lacunae of canals nor superficial durodentine are observed. Multi-branched centripetal radial canals occur at the junction strip between base and crown (Fig. 33A). Sharpey's fibres and numerous long and wide ascending vascular canals (Fig. 33B) similar to the ones in crown pierce the thin-lamellar acellular bony base.

DISCUSSION

We suppose this taxon has been described under different names from the Canadian Arctic (Vieth 1980) and Graz, Austria (Poltnig 1984). In the first case it is identified as *Nostolepis gracilis* Gross, 1947, but rather differs from the latter by its crown ornamentation. The Canadian specimens are ornamented with very numerous grooves (to 23). The histological structure of this sort of scale has probably not been studied because the published figures (Vieth 1980: text-fig. 19A-C) are supposedly linked to typical *N. gracilis* – with crown pores and certain "*Nostolepis*"-type tissue collected together with them in fossil samples. The scales from Graz, defined as *Diplacanthus longispinus* Agassiz, 1844 (Poltnig 1984: pl. 2, figs 1-7), cannot be ascribed to this species for the same reason – they have no ridges, but only deep linear grooves (11-16 as marked) on crowns. In comparison, *D. longispinus* (Gross 1947: pl. 6, figs 1, 2) is ornamented with numerous gradually posteriorly lowering sharp ridges, disposed in a fan-like pattern and separated by wide shallow grooves.

Scales of the known *Diplacanthus* species, *D. crassisimus* Duff, 1842 (Denison 1979: fig. 21A-C) and

D. kleesmentae Valiukevicius, 1986 (Valiukevičius & Karatajūtė-Talimaa 1986: pl. 1, figs 8, 9, pl. 3, fig. 8, pl. 4, fig. 6), have scales with ridges or grooves concentric to the postero-lateral margins of crowns, or possessing thick crowns with high posterior medial keel and radiating lower lateral ridges and grooves like in *D. carinatus* Gross, 1973 (Gross 1973: pl. 36, figs 8-10; Valiukevičius 1985: pl. 1, figs 1-5, pl. 3, figs 1-4, pl. 11, figs 7-9, pl. 13, figs 5-8) or in less carinated *D. gravis* Valiukevicius, 1988 (Valiukevičius 1988b: pl. 8, figs 1-4). At least, *D. horridus* Woodward, 1892 has crowns with posteriorly converging ridges like *D. longispinus*. The histological structure of investigated *Diplacanthus* scales, belonging to the "*Diplacanthus*"-type, differs in *D. kleesmentae* (Valiukevičius & Karatajūtė-Talimaa 1986: text-fig. 4.4-6) by its high network in crown mesodentine with winding principal ascending canals and smaller branchings containing lacunae, and also by their multibranched radial canals over the base. *D. carinatus* is distinguished by bushy knots of branchy, radially oriented horizontal vascular canals and by arched forms of circular canals (Valiukevičius 1985: text-fig. 15.8). In *D. longispinus*, one observes long, parallel, regularly symmetrically branched horizontal vascular canals (Gross 1947: text-fig. 14A, B). In *D. gravis* it is composed of three to four growth lamellae of mesodentine with irregularly placed ascending tubes, sometimes forming a bush, long subparallel horizontal vascular canals with characteristically ascending dentine tubules and complicated radials (Valiukevičius 1988b: text-fig. 1a-e). The species under description differs from the known taxa of the genus both by its parallel grooves on crown (without ridges) and a more abundant dentine-like tissue composing them.

BIOSTRATIGRAPHIC SIGNIFICANCE

Long-ranging species. In Severnaya Zemlya Archipelago it is met only within the upper part of *Nostolepis minima* Zone (*Diplacanthus poltnigi* n. sp. Subzone), a Lochkovian (Pod"emnaya Formation) association. In Canadian Arctic (locality 18) it is distributed in the Red Canyon River (A) Formation, dated as upper? Lochkovian (Vieth 1980) or upper Lochkovian/Pragian (Langenstrassen & Schultze 1996). The youngest finds occur in Waldsdorf from Graz (Austria), the latest Emsian after Poltnig (1984).

Diplacanthus solidus n. sp.
(Figs 20H-J; 34)

HOLOTYPE. — LIG 35-1283. Scale (Fig. 20H, I). Matusevich River, outcrop 5, bed 151 (top).

ETYMOLOGY. — From *Solidus* (Latin): solid, compact, referring to scale shape.

MATERIAL EXAMINED. — 12 scales.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 5, beds 136-153; Ushakov River, outcrop 27, bed 16. Middle Devonian, Eifelian?, Vstrechnaya Formation.

DIAGNOSIS. — *Diplacanthus* having small scales with triangle, trapezoid- to leaf-like crown and high neck. Two to four pairs of symmetric narrow linear grooves expanding slightly radially over all crown, except for a smooth rim along the proximal margin. Crown mesodentine resembles dentine by its style of ascending and horizontal vascular canals. Radial canals over the base almost not developed.

DESCRIPTION

Species described from isolated scales. They are small in size (0.3-0.4 mm), with rounded triangular, trapezium-like (with rounded and widened anterior edge), to leaf-like crown, a high neck and a slightly convex, centrally vaulted, base. Crown is ornamented with two to four symmetric pairs of linear grooves, crossing through the all length, in a slightly radially or fan-like pattern. Grooves increase in depth and width anteriorly. Along the proximal margin a narrow smooth strip (Fig. 20H) may be present. Another variety of scales has comparatively wide medial area with a shallow longitudinal concavity (Fig. 20J), marked by a central pair of grooves. All grooves seem wider as in other *Diplacanthus*. A smooth proximal rim is absent. In several specimens the postero-lateral neck walls contain two rounded bulbs.

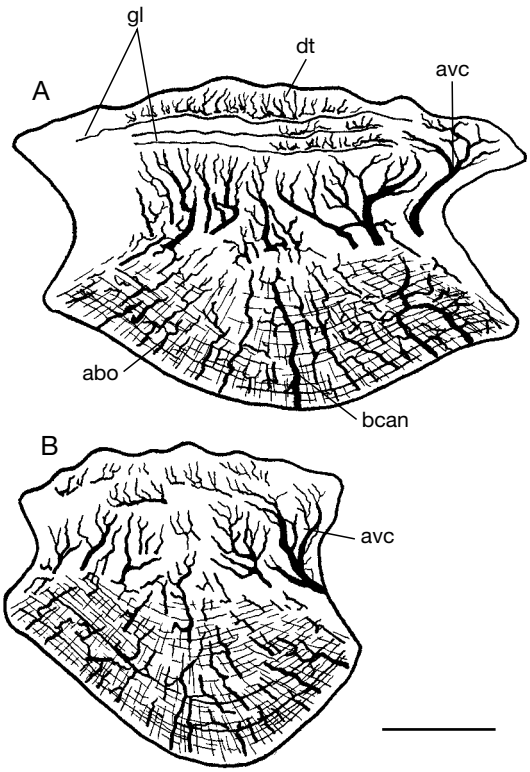


FIG. 34. — *Diplacanthus solidus* n. sp., scale histology, vertical transverse sections through the central parts of scales, Matusevich River, outcrop 5, bed 151, Vstrechnaya Formation; **A**, thin section 667; **B**, thin section 668. Abbreviations: **abo**, acellular bone; **avc**, ascending vascular canal; **bcan**, vascular canal piercing base of scale; **dt**, dentine tubule; **gl**, growth lamella. Scale bar: 0.1 mm.

By their shape the ascending vascular canals in crowns are closely resembling these of dentine: long, smooth, with principal branch, basally placed in each growth lamella (Fig. 34A, B), numbering four. Smaller horizontal branches contain numerous short upstreamed dentine tubules. Long and wide vascular canals, centripetally oriented towards the flattened pyramidal tip, also pierce the base.

DISCUSSION

The new species differs from the above-described *D. poltnigi* n. sp. by the reduced number and more radially directed narrower grooves, the presence of an unornamented anterior strip on scale crowns and a higher neck. Histological structure of the compared species is close by the style of vascular canals ascending and penetrating the base, and by the lack of lacunae in crowns. Their principal difference concerns the neck radial canals: they are multibranched, complicated in *D. poltnigi* n. sp. and almost not developed in *D. solidus* n. sp. See also the discussion of preceding species to compare them to other *Diplacanthus* taxa.

BIOSTRATIGRAPHIC SIGNIFICANCE

Index species of the beds with the *Diplacanthus solidus* n. sp. acanthodian association, occurring from the upper part of Vstrechnaya Formation (Middle Devonian, Eifelian?) on Severnaya Zemlya Archipelago. The species is also met in Baltic area within the *Nostolepis kernavensis* (Eifelian, *kockelianus* Zone of conodont standard) and *Diplacanthus gravis* (Givetian) acanthodian zones.

Order ISCHNACANTHIFORMES Berg, 1940
Family ISCHNACANTHIDAE Woodward, 1891
Genus *Gomphonchus* Gross, 1971

Gomphonchus nordicus n. sp.
(Figs 23N-P; 35)

HOLOTYPE. — LIG 35-2007. Scale (Fig. 23P). Pioneer Island, sample 12-76.

ETYMOLOGY. — From *Nordicus* (Latin): nordic, referring to the area of origin.

MATERIAL EXAMINED. —About 115 scales.

LOCALITY AND AGE. — October Revolution Island: Spokojnaya River, outcrop 41, bed 1, outcrop 45, bed 20, sample from talus (supposedly top of outcrop 45) and outcrop 51a, bed a. Pioneer Island: sample 12-76. Upper Silurian, Pridoli: Krasnaya Bukhta Formation of the Spokojnaya River series and supposed age analogues on Pioneer Island (Downton, Member 3 as taken by Klubov *et al.* 1980).

DIAGNOSIS. — *Gomphonchus* scales of medium size with rhombic, sub-rhombic to oval crown, high neck and convex base; crown rarely protruding anteriorly. Crown and base frequently wider than long. Flat crown with shallow central, random small lateral

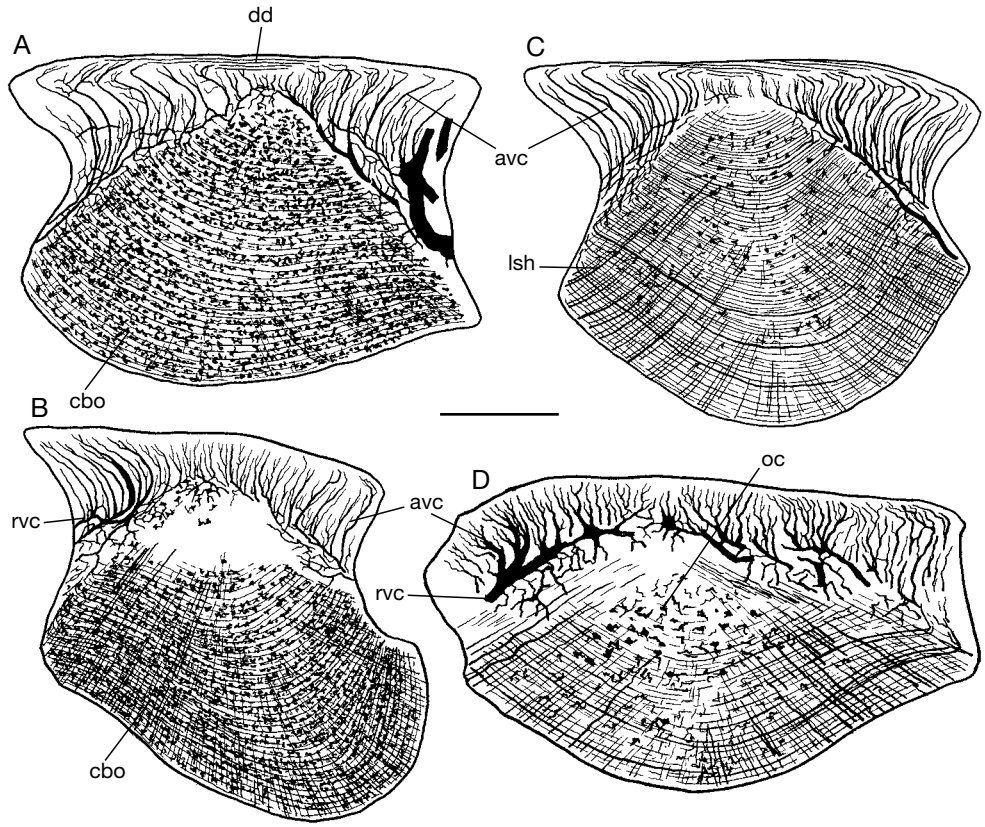


FIG. 35. — *Gomphonchus nordicus* n. sp., scale histology, Pioneer Island, sample 12-76, Upper Silurian, Pridoli, Member 3; **A**, vertical transverse section through the anterior scale part, thin section 3368; **B**, **C**, vertical longitudinal sections through the central parts of scales, thin sections 3369 (**B**) and 3367 (**C**); **D**, vertical transverse section through the flattened older? scale, thin section 3366. Abbreviations: **avc**, ascending vascular canal; **cbo**, cellular bone; **dd**, durodentine; **lsh**, longitudinal Sharpey's fibres; **oc**, osteocyte cavity; **rvc**, radial vascular canal. Scale bar: 0.1 mm.

depressions and postero-lateral concentric linear groovelets. Scale base composed of cellular bone; crown made of dentine containing smooth major ascending vascular canals, with upstreamed interspersed branches and complicated radial canals. Durodentine only developed in the central superficial crown part.

DESCRIPTION

Species described from isolated scales. Mid-size examples (0.4-0.8 mm) of scales dominate; only rare ones reach 1 mm. The crown shape varies from regularly rhombic, rhombic elongated posteriorly, rhombic widened, to leaf-like or oval. Crown plate is flat, but not even, with central slightly lowered area and small inconstantly shaped random shallow deepenings. Some parts, especially the extreme postero-lateral ones, look like the edges of the growing plates in forming concentrically linear groovelets (Fig. 23P). Several specimens have shallow convex crowns. The posterior crown tip rarely overhangs the scale base. A large amount of the material is composed of scales with widened crowns, width exceeding length. These have also strongly widened and anteriorly placed bases. Bases have a rhombic outline. The advancing crowns rarely protrude them to the front. In general, bases are centrally convex. The neck is high, frequently with vertical grooves.

Scales microstructure shows a classical cellular bone in bases and dentine in crowns. Mature scales are composed of 10 to 12 growth lamellae in crown (Fig. 35A, B), pierced by a system of well developed vascular canals: principal ascending ones are smooth, long, mainly with upstreamed intersperse branches. Centripetal multibranched radials occur just above the base and smaller branchings are directed toward the base. Part of canals may be unexpectedly widened (older scales?) (Fig. 35D). A durodentine strip is absent or developed only superficially in the scale centre (Fig. 35A, C). Several scales demonstrate a highly cellular base bone (Fig. 35A, B) and several contain only single osteocytes (Fig. 35C).

DISCUSSION

By its combination of dentine and durodentine in crown and cellular bone in base, *G. nordicus* n. sp. steps out as a specific representative of Ischnacanthidae. This species is distantly similar to *Poracanthodes punctatus* Brotzen, 1934, which also shows a transition from cellular to acellular base bone, but the crown is composed of a different mesodentine (Gross 1956: text-figs 116-118). When compared to the known *Gomphonchus* species, it is closest to *G. sandelensis* (Gross 1971: pl. 5, fig. 11, pl. 9, figs 15-17), but differs in shape, base and crown proportions (new species – alike a transitional form between *Gomphonchus* and *Acanthoides*?) and variable morphologic details of crown. The graphic illustrations of typical *G. sandelensis* scales histological structure in Gross (1971: text-figs 19E-G, 20A-E), really demonstrate acellular base bone though this author has pointed out *Nostolepis*, *Gomphonchus* and *Poracanthodes* as having cellular base bone, without definite differences (Gross 1971: 53). *G. sandelensis* possesses regularly shaped ascending canals with short upward directed interspersed branches (Gross 1971: text-fig. 20B, C), different from the long and also upstreamed ones in *G. nordicus* n. sp. *G. tauragensis*, described from the Early Devonian of Baltic, differs in its radially ridged crowns, general scale flatness, strongly advanced bases and the large area of durodentine completely composing some late grown lamellae of crowns and thin-lamellar, compact acellular bone in bases (Valiukevičius 1998: pl. 4, figs 10-16, pl. 5, fig. 1, pl. 14, figs 7, 8).

BIOSTRATIGRAPHIC SIGNIFICANCE

Key species of the *Poracanthodes punctatus* Zone, identifying upper Pridoli in different regions (Märss 1997). On Severnaya Zemlya Archipelago this zone is attached to the lower part of Krasnaya Bukhta Formation.

Genus *Poracanthodes* Brotzen, 1934

Poracanthodes punctatus Brotzen, 1934
(Figs 28A-D; 36; 37)

For synonymy see Valiukevičius (1998), and for diagnosis Gross (1947) and Valiukevičius (1998).

MATERIAL EXAMINED. — LIG 35-A-391: exposing jawbone fragment with main cusps in lateral preservation (Fig. 28A), also isolated teeth (from the jawbone and palatine, Fig. 28D, C) and scales (Fig. 28B). More than 50 isolated scales from different samples.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 2, bed 1 and outcrop 4, bed 3; Spokojnaya River, outcrop 51a, beds a-c, outcrop 45, bed 20 and sample from talus (top of outcrop), outcrop 41, beds 1 and 12. Komsomolets Island: outcrop 18077, bed 9; Pioneer Island, sample 12-76. Upper Silurian: Ludlow, Ust'-Spokojnaya Formation and Pridoli, Krasnaya Bukhta Formation. Lower Devonian, Lochkovian to Pragian, Severnaya Zemlya, Pod"emnaya and Spokojnaya formations.

REMARKS

The lower jawbone fragment is 23 mm long and up to 5 mm high stretching backwards and widening frontward medial with an oval section. It is composed of highly vascularised bone. Lateral main cusps are higher (to 3 mm) than wide, and have an oval parabasal form. They are slightly medially curved and striated by wavy groovelets. They have distinct sharp flanges supposedly on their anterior side only. Palatine teeth are tiny, elongated (to 0.3 mm), and oval in cross section, slightly recurved and present sharp sides. The main cusps are composed of

trabecular dentine (Fig. 36A, B) with multibranched widened pulpar vascular canals, restricted in mature examples by concentric denteons. They stream outerward dense and tiny branchy dentine canals (Fig. 36B). Palatine teeth demonstrate up to six growth lamellae of indeterminable dentine with enlarged vascular canals in the basal part, and a base composed of cellular bone (Fig. 36C, D).

Scales small (0.2-0.5 mm), exhibit rhombic flat crowns, containing pore openings densely distributed in concentric lines or randomly. The pore canal system consists of widened radial canals, arcade, and narrower superficial ones, opening on the surface. Vascular canals are of dentine type (Fig. 37B, C). Their base is composed of cellular bone. The osteocyte may inconstantly reduce in number. Scale growth is mainly superpositional, but sometimes appears areal? (Fig. 37C), especially in posterior scale part.

BIOSTRATIGRAPHIC SIGNIFICANCE

Long-ranging species, with spanning time from the Late Silurian to the end of Early Devonian; last occurrences on Severnaya Zemlya Archipelago are in the Spokojnaya Formation (Pragian).

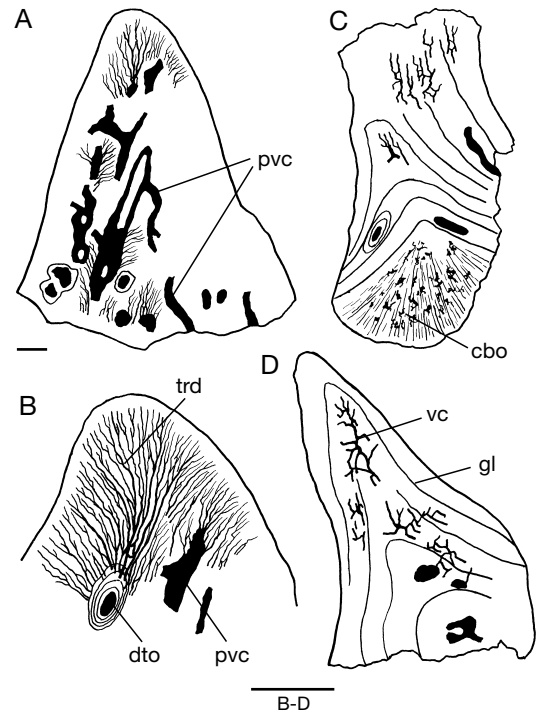


FIG. 36. — *Poracanthodes punctatus* Brotzen, 1934, histology of teeth, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **A**, longitudinal section through the main cusp, thin section 3459; **B**, magnified apex area of the same section; **C**, **D**, longitudinal sections of palatine teeth, thin sections 3461 (**C**) and 3460 (**D**), paratype LIG 35-A-391. Abbreviations: **cbo**, cellular bone; **dto**, denteon; **gl**, growth lamella; **pvc**, pulpar vascular canal; **trd**, trabecular dentine; **vc**, vascular canal. Scale bars: 0.1 mm.

Poracanthodes sp. cf. ***P. porosus*** Brotzen, 1934 (Figs 28N, O; 38)

MATERIAL EXAMINED. — 88 isolated scales.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 2, bed 1; Spokojnaya River, outcrop 51a, beds a-c, outcrop 45, sample from talus (top of outcrop) and outcrop 41, bed 1. Pioneer Island: sample 12-76. Upper Silurian, Ludlow and Pridoli, Ust'-Spokojnaya and Krasnaya Bukhta formations.

REMARKS

Severnaya Zemlya specimens differ from the typical *P. porosus* Brotzen, 1934 by less ornamented scale crowns. The Late Silurian *P. porosus* is characterised by especially ridged scales with short, parallel anterior ridges and concentrical grooves, lining the postero-lateral crown sides (Märss 1986: pl. 29, figs 11-17, pl. 30, figs 1-5). They contain pore openings both arranged in radial and concentrical lines. Severnaya Zemlya examples rarely demonstrate all these peculiarities commonly represented. Their microstructure (Fig. 38) shows a crown mesodentine of superpositional growth containing a small number of canals, but with main ascending branches. Radial, arcade and superficial pore canals may sometimes develop only on the restricted distal crown area. Densely thin-lamellar base bone includes only rare osteocyte spaces.

BIOSTRATIGRAPHIC SIGNIFICANCE

Long-ranging species, on Severnaya Zemlya Archipelago incoming into acanthodian assemblages of the Ludlow and Pridoli (Upper

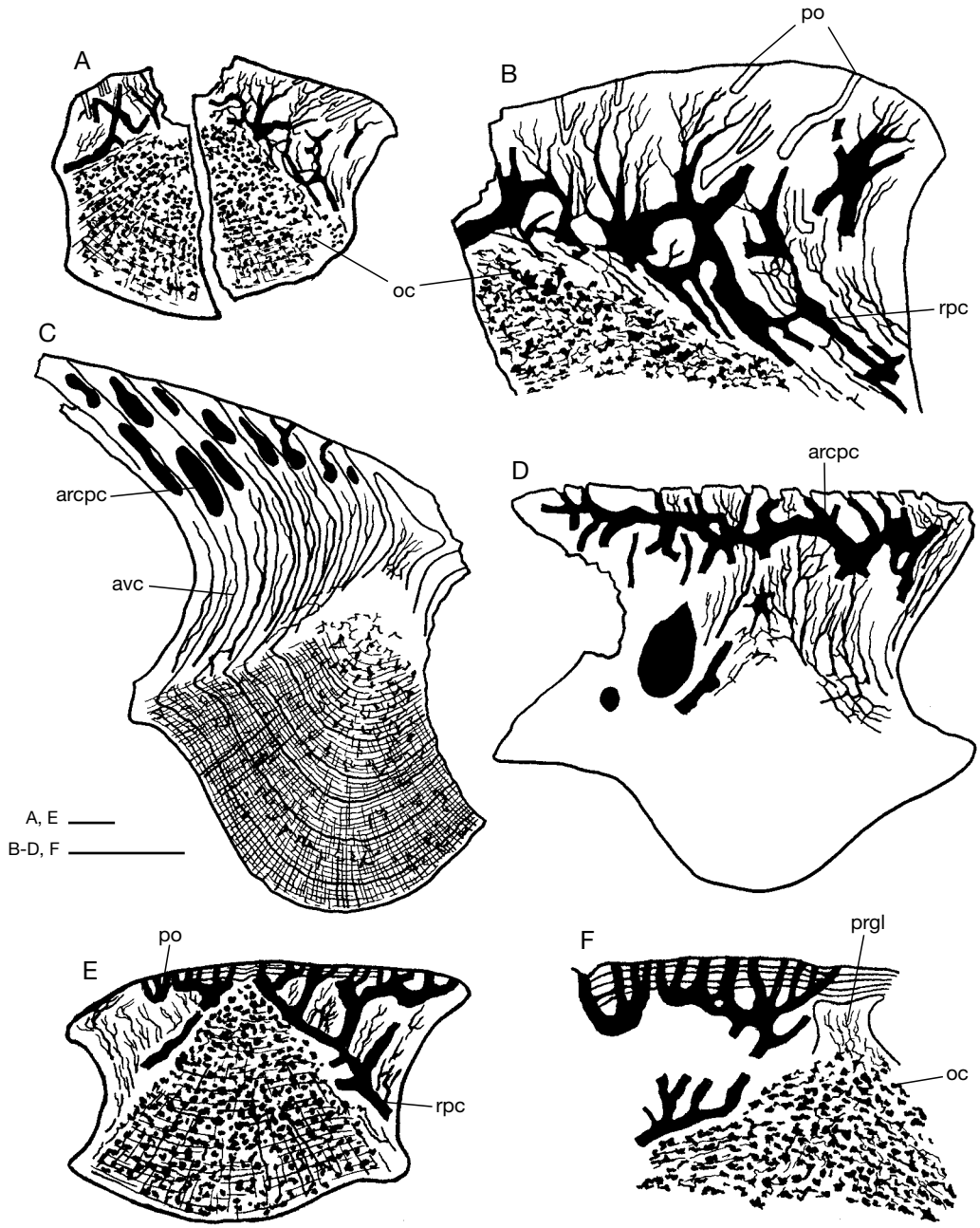


FIG. 37. — *Poracanthodes punctatus* Brotzen, 1934, scale histology; **A**, vertical longitudinal section through the old? scale with randomly displaced pores, thin section 3365; **B**, magnified right area of the same section; **C**, vertical longitudinal section through the scale with concentrically displaced pores, thin section 3462; **D**, vertical transverse section through the posterior part of scale with concentrically displaced pores, thin section 3464; **E**, vertical longitudinal section of scale, thin section 973; **F**, magnified central area of the same section. Paratype LIG 35-A-391; Pioneer Island, sample 12-76. Upper Silurian, Pridoli, Member 3 (**A**, **B**) and Spokojnaya River, outcrop 41, bed 12; Severnaya Zemlya Formation (**C**-**F**). Abbreviations: **arcpc**, arcade pore canal; **avc**, ascending vascular canal; **oc**, osteocyte cavity; **po**, pore opening; **prgl**, primordial growth lamella; **rpc**, radial pore canal. Scale bars: 0.1 mm.

Silurian), the last of which being marked as *Poracanthodes punctatus* Zone. In other regions, e.g., Baltic (Märss 1986; Valiukevičius 1998), the species extends to the Lower Devonian, Emsian.

Poracanthodes sp. cf. ***P. subporosus***
Valiukevicius, 1998
(Figs 28E-I; 39)

MATERIAL EXAMINED. — Single paratype LIG 35-A-376 (Fig. 28E): exposing poorly articulated unidentified fin spines and squamation. One more sample yields four scales.

LOCALITY AND AGE. — October Revolution Island: Spokojnaya River, outcrop 51a, beds a-c and outcrop 41, bed 12. Upper Silurian, Pridoli, Krasnaya Bukhta Formation and Lower Devonian, lower Lochkovian, Severnaya Zemlya Formation.

REMARKS

Crown pore openings are mainly organised in four radial lines, starting at midlength and extending to postero-lateral margins. Smaller numbers of scales have one to two weakly developed latero-distal groovelets, but pores are also arranged in radial lines. Referring to this, these scales are distantly comparable with the smoother ornamented and porose scales of *Poracanthodes menneri* (Valiukevičius 1992: pl. 10, fig. 2). Typical *P. subporosus*, described from the Baltic (Valiukevičius 1998: pl. 7, figs 13-22), demonstrates radial lines of pores or, rarely, pores grouped into two longitudinal areas without a strong linear arrangement. The Severnaya Zemlya specimens are dominated by large crown parts (up to the complete anterior half) devoid of pores. Their histological structure is composed of dentine and durodentine tissue (Fig. 39A, B), of a superpositional growth type; the style of radial pore canals and upstreamed superficial openings, as well as reduced cellular or acellular base bone, are without essential differences in comparison with *P. subporosus* (Valiukevičius 1998: pl. 15, fig. 9, pl. 16, fig. 1).

Fin spines, preserved articulated in paratype LIG 35-A-376, are slightly recurved, with eight longitudinal ribs on each side. The proximal rib is wider than others. Spines have a widened triangular cross section with a slightly concave base. Sectioned spine fragments show a tripartite lamination: a basal layer composed of compact acellular thin-lamellar bone; a middle layer made of bone? with increased numbers of enlarged vascular canals, restricted during the growth by well developed concentric osteons; and an outer layer made of simple mesodentine network with plenty of osteocytes (Fig. 39C, D).

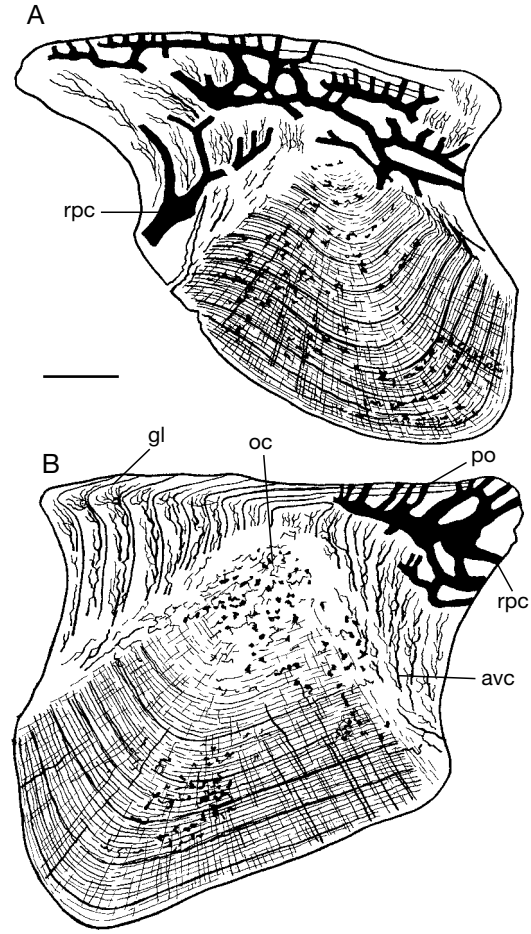


FIG. 38. — *Poracanthodes* sp. cf. *P. porosus* Brotzen, 1934, scale histology, vertical longitudinal sections of scales, Spokojnaya River, outcrop 51a, beds a-c, Krasnaya Bukhta Formation; **A**, scale with radially linear pore openings, thin section 794; **B**, scale with pore openings lined both radially and concentrically, thin section 3010. Abbreviations: **avc**, ascending vascular canal; **gl**, growth lamella; **oc**, osteocyte cavity; **po**, pore opening; **rpc**, radial pore canal. Scale bar: 0.1 mm.

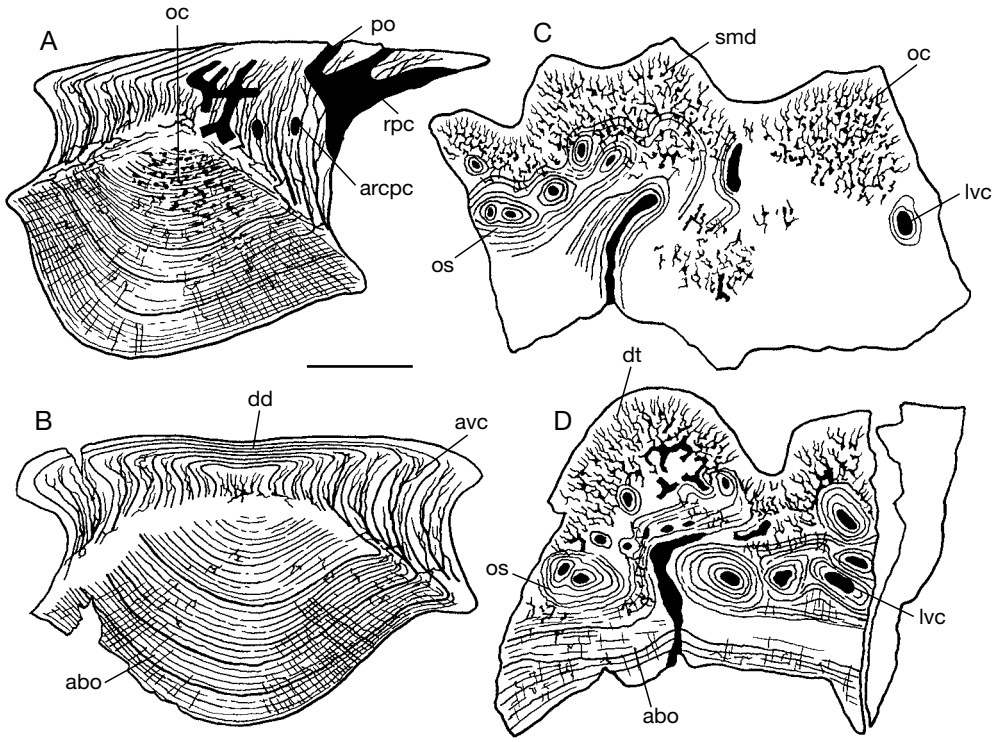


FIG. 39. — *Poracanthodes* sp. cf. *P. subporosus* Valiukevicius, 1998, scale and spine histology, from paratype LIG 35-A-376, Spokojnaya River, outcrop 41, bed 12, Severnaya Zemlya Formation; **A**, vertical longitudinal section through the central part of scale with pore canal openings on the posterior crown half, anterior to left, thin section 3465; **B**, vertical transverse section through the central part of scale with pore canal openings on the extreme posterior part only, thin section 3467; **C**, **D**, transverse sections through the unidentified fin spines, thin sections 3471 (**C**) and 3470 (**D**). Abbreviations: **abo**, acellular bone; **arcpc**, arcade pore canal; **avc**, ascending vascular canal; **dd**, durodentine; **dt**, dentine tubule; **lvc**, longitudinal vascular canal; **oc**, osteocyte cavity; **os**, osteon; **po**, pore opening; **rpc**, radial pore canal; **smd**, simple mesodentine. Scale bar: 0.1 mm.

Spine histology is rather different from that of the well known *P. menneri* (Valiukevičius 1992: fig. 11A, B), of which complicated tissue types depending on growth stages distinguish it and, *inter alia*, the structure of the middle and, particularly, the outer mesodentine layer.

BIOSTRATIGRAPHIC SIGNIFICANCE

Species appearing with the *Poracanthodes punctatus* Zone assemblage (Pridoli, Krasnaya Bukhta Formation) and spanning the Silurian/Devonian boundary associates with the *Poracanthodes menneri* Subzone (Severnaya Zemlya Formation) mainly defined by an original composition of articulated acanthodians early Lochkovian in age.

Genus *Acanthopora* n. gen.

TYPE AND ONLY SPECIES. — *Acanthopora transitans* n. gen., n. sp.

ETYMOLOGY. — From *Acantha* (Greek): spine, thorn; and *poros* (Greek): pore.

AGE. — Early Devonian, early Lochkovian.

DIAGNOSIS. — As for the type and only species.

DISCUSSION

Through the presence of some randomly displaced pore openings in crowns of its scales, this taxon may be related to *Poracanthodes*, but it is different in its modified "*Poracanthodes*"-type histology, differing both by its structure and the function duration of its pore canal sys-

tem. Several affinities are also marked with the scales identified by Gross as *Gomphonchus* or *Poracanthodes* (Gross 1971: pl. 9, figs 30, 31) from the *Beyrichia* Limestone (Upper Silurian).

Acanthopora transitans n. sp.
(Figs 40-43)

HOLOTYPE. — LIG 35-A-403: a specimen missing head and tail, preserved laterally, with a small fragment of pectoral spine, longer posterior dorsal and anal fin spines, and squamation, exposing myomeric structures (Fig. 40A-C). Matusevich River, outcrop 1, bed 21.

PARATYPES. — LIG 35-A-387: specimen 33 mm long, exposing only the squamation and a small fragment of unidentified fin spine; LIG 35-A-401: specimen about 51 mm long, exposing only squamation (Figs 40D, E; 41D-G); LIG 35-A-395: small fragment of specimen with intact scales. All from the Matusevich River, outcrop 1, bed 21. LIG 35-A-369: specimen about 58 mm long, missing head, shoulder and tail areas, preserved laterally, with parts of posterior dorsal, anal and unidentified spines and squamation (Fig. 41A-C). Ushakov River, outcrop 21, bed 9.

ETYMOLOGY. — From *Transitans* (Latin): variable, transitional, referring to a systematic position close to *Poracanthodes*.

LOCALITY AND AGE. — October Revolution Island: Matusevich River, outcrop 1, bed 21; Ushakov River, outcrop 21, bed 9. Lower Lochkovian, top of the Severnaya Zemlya Formation.

DIAGNOSIS. — Small-sized ischnacanthid with slender body and long, deeply inserted, longitudinally ribbed fin spines; two dorsal spines; pectoral spines in a low position. Three tissue layers in spines: basal acellular bone; porose, highly vascularised bone with osteons and small osteocyte numbers in the middle layer; superficial networked mesodentine with plenty of osteocytes. Scales small with rhombic crowns containing some random posterior pores. Histology of modified "*Poracanthodes*"-type: crown dentine and durodentine without radial vascular, and pore system – without radial pore canals. Pore canals function only in two latest growth lamellae, replaced by vascular canals in the earlier ones.

DESCRIPTION

Species described from articulated specimens missing head and tail areas or exposing only squamation, or part of the body behind the anterior dorsal spine. The body proportions are weakly determinable. The most completely preserved holotype specimen is a small-sized fish, which might have reached about 70-75 mm in length. Body slender: its height, both at the second dorsal and the pectoral spines amounts about 13 mm. Supposedly a long area behind the anal fin spine preserved.

Fin spines

From the holotype specimen and paratype LIG 35-A-369, it is supposed to be a long-spine fish with mid-erected spines. The anal spine of holotype is slightly recurved and might be 13 mm long (preserved 10.4 mm). The posterior dorsal (preserved on 6 mm) was inserted in a point vertically above and just behind the anal spine. Both are deeply inserted. Pectoral spine is in a low position. Its preserved part in holotype is about 2 mm. The ventral orientation does not allow to compare the ornamentation of pectoral spine with that of others. The best preserved anal spine of holotype is strongly longitudinally ribbed with enlarged, stout, sub-quadrangular proximal rib and four narrower ones on each side. Spine section is triangular, basally wide, and narrow towards the tip. Paratype LIG 35-A-369 exposes the ventrally preserved spines, supposedly belonging to a larger specimen than the holotype. Its spines are wider, one small inarticulate displaced fragment bear a sharp tip. The single central cavity is mainly open and closed only at the tip.

The spine histology shows a tripartite composition. A basal lamellar acellular bone, lines the central cavity; it is thin at the parabasal part (Fig. 42A) and thick at the tip (Fig. 42D). The middle layer is composed of very porose, highly vascularised bone with a small number of osteocytes (Fig. 42A, B). Large longitudinal vascular canals (Fig. 42E) of different length and form in mature spines are restricted by concentric osteons. The superficial mesodentine layer includes dense osteocytes and a network of winding dentine tubules (Fig. 42D, E).

Squamation

Dense lines of small body scales are displayed without overlap or with extremely small overlap areas (Figs 40E; 41C). Sometimes wavy

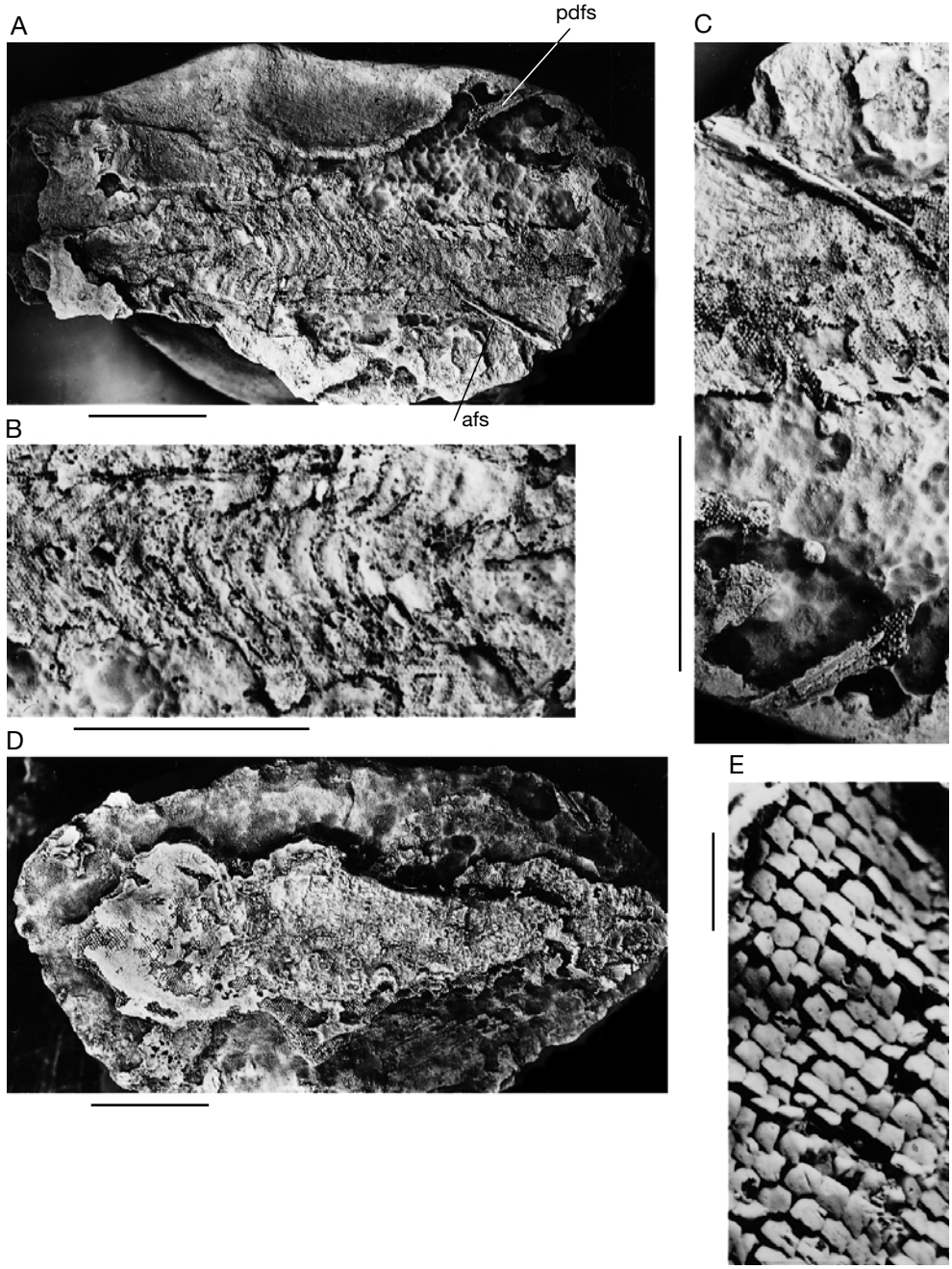


FIG. 40. — *Acanthopora transitans* n. gen., n. sp., Matusevich River, outcrop 1, bed 21, Severnaya Zemlya Formation; **A**, specimen exposing pectoral, posterior dorsal and anal fin spines and squamation with myomeric structures, lateral view, anterior to left, holotype, LIG 35-A-403; **B**, enlarged area of squamation with myomeric structures in the central part of the holotype; **C**, enlarged fin spines of the same specimen; **D**, paratype LIG 35-A-401 in lateral preservation, squamation; **E**, enlarged area of squamation of the same paratype. Abbreviations: **afs**, anal fin spine; **pdfs**, posterior dorsal fin spine. Scale bars: A-D, 10 mm; E, 1 mm.

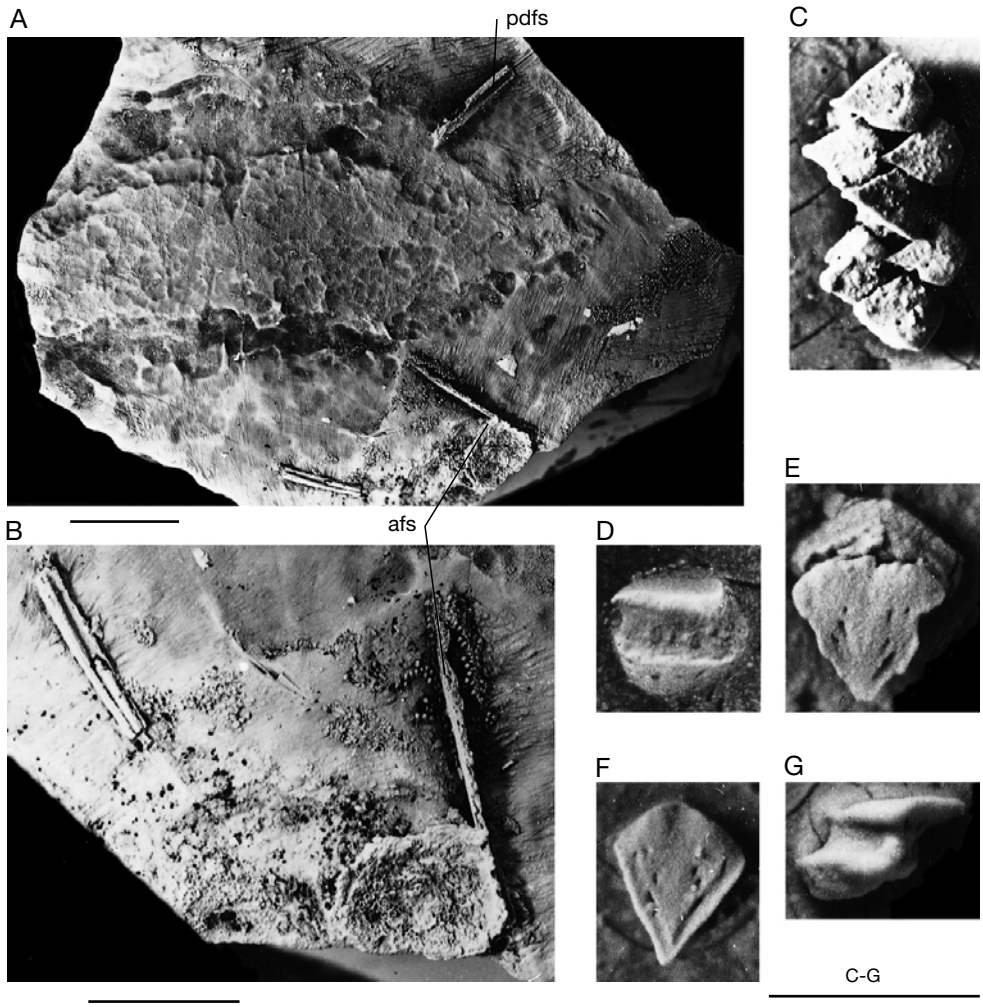


FIG. 41. — *Acanthopora transitans* n. gen., n. sp., Severnaya Zemlya Formation; **A**, posterior dorsal, anal and undeterminate fin spines and squamation, lateral view, anterior to left, paratype LIG 35-A-369; **B**, enlarged area of the same specimen with anal and undeterminated spines; **C**, intact scales from the same specimen displaced behind the anal spine; Ushakov River, outcrop 21, bed 9; **D-G**, scales; **D**, LIG 35-2058, side; **E**, LIG 35-2056, crown; **F**, LIG 35-2057, crown; **G**, LIG 35-2059, side. All scales from the paratype LIG 35-A-401; Matusevich River, outcrop 1, bed 21. Abbreviations: **afs**, anal fin spine; **pdfs**, posterior dorsal fin spine. Scale bars: A, B, 10 mm; C-G, 0.5 mm.

myomeric reflections of the body musculature can be seen (Fig. 40B). Scale crowns are of 0.18-0.40 mm long, with elongated rhombic to rounded triangular forms, flat and with small proximal depressed medial area for the pointed edge of the overlapping crown. Rare examples have shallow linear groovelets along the latero-distal margins (Fig. 41F). The crown plate contains some pore openings on its distal part. They are displayed randomly or rarely grouped in two irregular strips (Fig. 41E). Scale bases are rhombic in outline, moderately convex, with anteriorly protruding crowns (Fig. 41G). Their mid-high neck contains small pore openings on the latero-distal walls (Fig. 41D). No obvious differences or marked varieties in scale shape

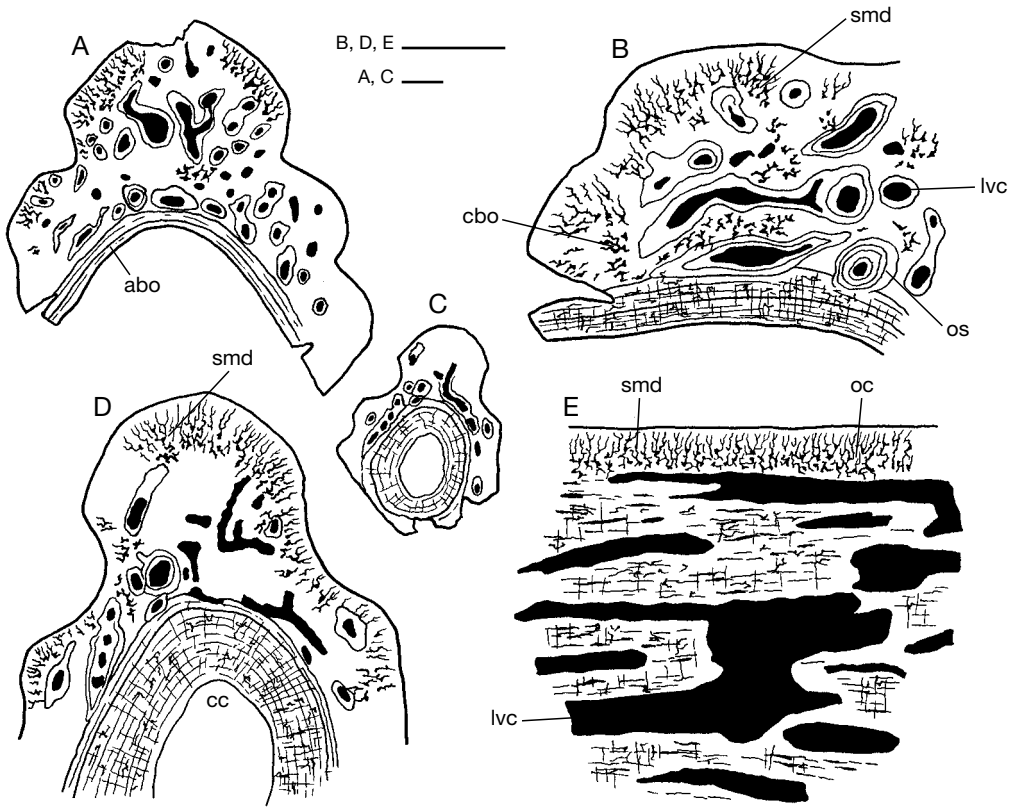


FIG. 42. — *Acanthopora transitans* n. gen., n. sp., spine histology, paratype LIG 35-A-369, Ushakov River, outcrop 21, bed 9, Severnaya Zemlya Formation; **A**, transverse section through the parabasal part, thin section 3455; **B**, magnified left corner of the same section; **C**, transverse section through the spine tip, thin section 3456; **D**, magnified proximal area of the same section; **E**, longitudinal section of spine, thin section 3458. Abbreviations: **abo**, acellular bone; **cbo**, cellular bone; **cc**, central cavity; **lvc**, longitudinal vascular canal; **oc**, osteocyte cavity; **os**, osteon; **smd**, simple mesodentine. Scale bars: 0.1 mm.

can be observed along the preserved trunk of fishes.

The scale histology is certainly of a modified "*Poracanthodes*"-type. Up to eight growth lamellae in crowns composed of dentine and durodentine can be identified. Ascending vascular canals are almost without principal branches. All lamellae spaces are pierced by monotonous upstreamed, interwoven dentine canals, only rarely enlarged near the base (Fig. 43A, E). No radial vascular canals are encountered in crowns. Slightly complicated mesodentine-like network of canals is identified in primordial lamella (Fig. 43C). Neither osteocytes nor lacunae or lacunae-like widenings occur in crowns. The pore canal system, including neck and superficial openings in crown, functions only within the two last growth lamellae (Fig. 43B-D), whereas in the earlier ones they are replaced by extremely widened strips of ascending vascular canals (Fig. 43B, E). This, and also the lack of radial and arcade pore canals, allows to suppose a formation of pore canal system anew in each next growth lamella. The scale bases are composed of thin-lamellar acellular bone, and exceptionally with Sharpey's fibres demonstrating no more structural elements.

DISCUSSION

The presence of pore canals and particularly of superficial openings allows to place *A. transitans* n. gen., n. sp. close to the representatives of

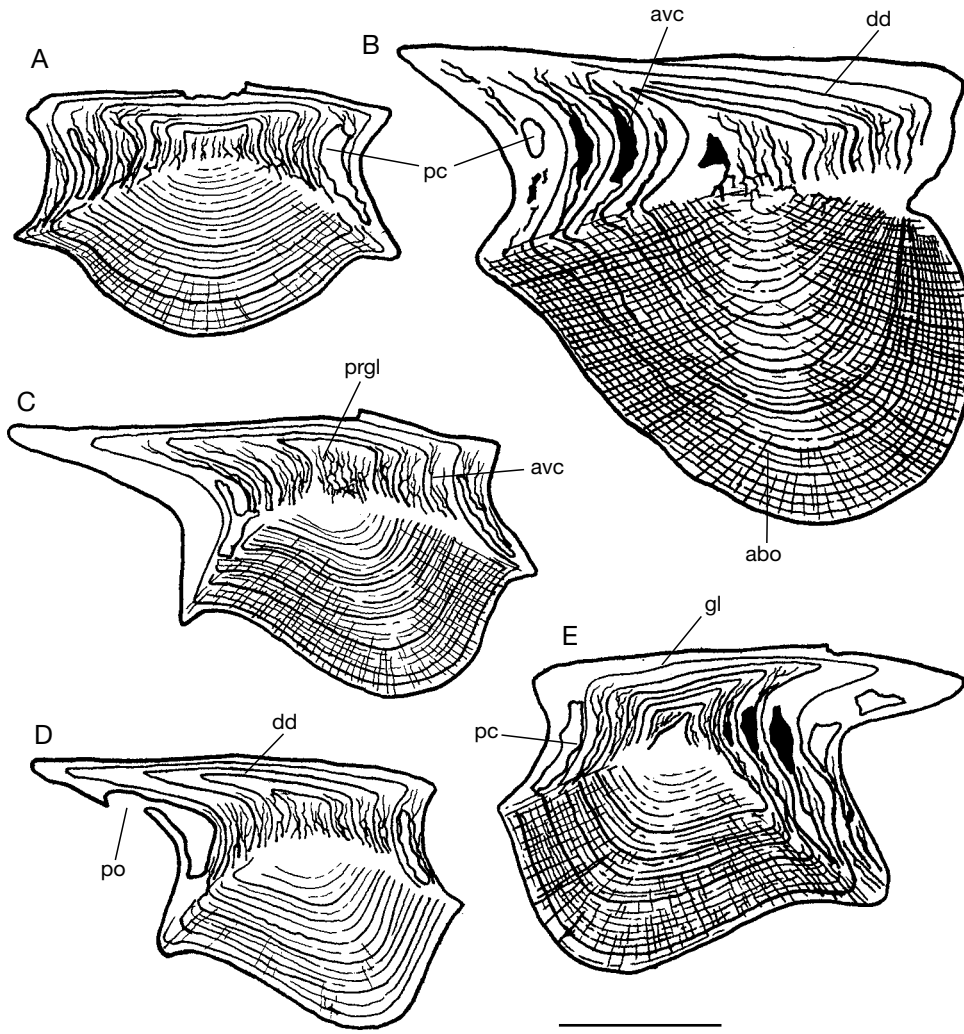


FIG. 43. — *Acanthopora transitans* n. gen., n. sp., scale histology, Severnaya Zemlya Formation; **A**, vertical transverse section through the central part of scale, thin section 3342; **B**-**E**, vertical longitudinal sections of scales, anterior to right (**B**-**D**) and to left (**E**); **B**, scale like figured on Fig. 41E, thin section 3454; **C**-**E**, scales like figured on Fig. 41F, thin sections 3341 (**C**), 3343 (**D**) and 3344 (**E**). Paratype LIG 35-A-369 (**A**, **C**-**E**); Ushakov River, outcrop 21, bed 9; and paratype LIG 35-A-395 (**B**), Matusevich River, outcrop 1, bed 21. Abbreviations: **abo**, acellular bone; **avc**, ascending vascular canal; **dd**, durodentine; **gl**, growth lamella; **pc**, pore canal; **po**, pore opening; **prgl**, primordial growth lamella. Scale bar: 0.1 mm.

Poracanthodes Brotzen, 1934. According to the pore openings, which do not cover all the crown plate, but its posterior part, *A. transitans* n. gen., n. sp. is the nearest to *P. subporosus* (Valiukevičius 1998: pl. 7, figs 13-22), but with a different pattern of pore distribution. *A. transitans* n. gen., n. sp. does not demonstrate pore openings in radial lines. Furthermore differences occur within their histological structure. The originality in tissue composition (both of crown and base) and pore canal system discriminates the taxa under comparison. The principal differences are the lack of radial pore and vascular canals, the presence of thick superficial durodentine strip in crowns and the exclusively acellular bone in scale bases of *A. transitans* n. gen.,

n. sp. Pore canal system in all known representatives of *Poracanthodes* is functioning with no interruption during the growth, whereas in *A. transitans* n. gen., n. sp. it functions only within the last lamellae, and is replaced in the earlier ones by vascular canals.

BIOSTRATIGRAPHIC SIGNIFICANCE

Key species of the *Poracanthodes menneri* Subzone, based on association of articulated acanthodians from the topmost part of Severnaya Zemlya Formation. It corresponds to the lower part of the *Nostolepis minima* Zone, widely traced through the regions. Age is early Lochkovian. Tentatively correlates to the *woschmidti* Zone of conodont standard.

Genus *Arcticacanthus* n. gen.

TYPE SPECIES. — *Arcticacanthus bicostatus* n. gen., n. sp.

ETYMOLOGY. — From Arctic: referring to the arctic origin of the fish; and *acantha* (Greek): thorn, spine.

AGE. — Early Devonian.

DIAGNOSIS. — As for type and only species.

DISCUSSION

According to highly cellular bone in bases of scales, this genus might be classified among Climatiidae or Ischnacanthidae, but the presence of an original pore canal system in crowns defines a modified "*Poracanthodes*"-type histology, thus they will be placed within Ischnacanthidae.

Arcticacanthus bicostatus n. sp.
(Figs 44A, B; 45)

HOLOTYPE. — LIG 35-2002. Scale (Fig. 44B). October Revolution Island, Pod"emnaya River, outcrop 69, bed 26.

ETYMOLOGY. — From *bicostatus* (Latin): two-ridged, referring to anteriorly bifurcated ridges on crowns.

MATERIAL EXAMINED. — 10 scales.

LOCALITY AND AGE. — October Revolution Island: Pod"emnaya River, outcrop 69, bed 26. Pioneer Island: sample P-12-7. Lower Devonian, Lochkovian, Pod"emnaya Formation to Emsian, Rusanov Formation.

DIAGNOSIS. — Ischnacanthid having mid-sized subrhombic scales, with crowns ornamented by four to six sub-parallel high ridges, extending on two thirds of its length and bifurcating anteriorly. High neck with pore openings. Dentine-like tissue of crown perforated by a pore canal system, composed of radial canals high in the neck, longitudinal canals in crown along superficial grooves, connected by uneven ascending ones formed anew in each growth lamella.

DESCRIPTION

Species described from isolated scales. Their crowns measuring 0.4-0.85 mm long are subrhombic, flat, rarely overhanging base, and often wider than long. They are ornamented with four to six longitudinal sub-parallel, anteriorly higher ridges, which are of a moderately rounded quadrangular section, strongly widened and shortly bifurcated at the anterior margin. Ridges are separated by wide grooves. Posterior third or half of the crown length is smooth. The mid-high neck, shows each three round pore openings on postero-distal walls. The rhombic outlined base rarely protrudes the crown anteriorly.

The original histological structure is not yet sufficiently investigated since the available number of scales remains too small. The crown is composed of a dentine-like tissue and the base of highly cellular bone. 10 unevenly thick lamellae of superpositional growth are present in the crown (Fig. 45B). Over the base radial vascular canals are weakly developed. They are narrow, supposedly consisting of several branches. Growth lamellae (Fig. 45A) are evenly pierced by ascending canals with monotonous and slightly more broadened longer principal branches. Some characteristic short, weakly winding ascending tubules occur in each lamella of transitional dentine-mesodentine style. The crown is pierced by a system of wide pore canals. Their openings can be observed only in the scale neck, but supposedly they are also present in the grooves of crown plate as demonstrated in sections. Radial centripetal pore canals are situated high over the base (Fig. 45B). They are multibranched, as seen on Fig. 45A (left side). From them the arising ascending pore canals are extremely uneven (Fig. 45A), with variable shape, as wide as the

radial canals. It seems they are formed anew in each new growth lamella, but continue within a principal direction during all growth (they seem to function with interruptions).

DISCUSSION

By their general crown ornamentation, these scales distantly resemble the representatives of *Cheiracanthoides* Wells, 1944, but they differ in height and in the ridges bifurcation. The highly cellular base bone might not contradict with an assignment to nostolepids but the presence of a pore canal system in crowns allows to relate *Arcticacanthus* n. gen. to the Ischnacanthidae and among them, particularly to *Poracanthodes* scales which demonstrate two sorts of base tissues: cellular and acellular bone occurring together. A modified "*Poracanthodes*"-type histology is already noted both in *Lietuvacanthus* and *Ectopacanthus*? Valiukevicius, 1998, two Early Devonian genera from the Baltic basin. The scales of *Lietuvacanthus fossulatus* have a deeply embayed anterior crown rim and a pore canal system with arcades and radials, but without upward directed canals opening on the surface (Valiukevičius 1998: pl. 6, figs 10-14, pl. 12, figs 7, 8, pl. 13, figs 1-6). On the other hand *Arcticacanthus* n. gen. scales have distinct vertical connections of radial crown pore canals, producing uneven, differently shaped ascending branches, functioning during the all scale growth. *Lietuvacanthus fossulatus* shows radial pore canals displayed in chains one above the other in every growth lamella without vertical connections or occuring only in the primordial lamella. *Ectopacanthus*? *pusillus* (Valiukevičius 1998: pl. 7, figs 8-12, pl. 14, figs 2-4), apart from differences in its crown ornamentation (smooth narrow ridges and grooves placed in fans and extending over the all crown), has a pore canal system (with arcade, radial and ascending canals) without surface openings. The pore canals rise up only to the basal part of the latest growth lamella and open in the neck.

BIOSTRATIGRAPHIC SIGNIFICANCE

Long-ranging species, occurring within the upper part of early Lochkovian *Nostolepis minima* Zone (*Diplacanthus poltnigi* n. sp. Subzone, Pod"emnaya Formation) and disappearing in the early Emsian beds with *Watsonacanthus costatus* n. sp. (age analogues of Rusanov Formation on the Pioneer Island).

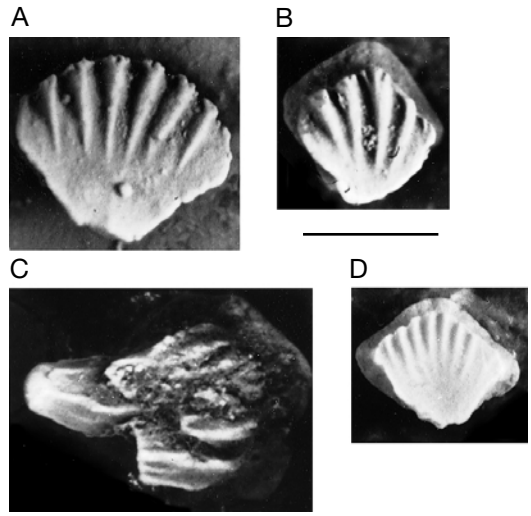


FIG. 44. — **A**, **B**, *Arcticacanthus bicostatus* n. gen., n. sp., scales, crowns, anterior upwards; **A**, LIG 35-2003; **B**, LIG 35-2002, holotype. Pod"emnaya River, outcrop 69, bed 26; **C**, *Nostolepis* sp. cf. *N. robusta* (Brotzen, 1934), scale, crown, anterior to right, LIG 35-1906. Matusevich River, outcrop 4, bed 3. Pod"emnaya Formation (**A**-**C**); **D**, *Nostolepis* sp. or *Cheiracanthoides* sp., scale, crown, anterior upwards, LIG 35-1696. Spokojnaya River, outcrop 41, bed 1; Krasnaya Bukhta Formation. Scale bar: 0.5 mm.

Acanthodii *incertae sedis*
Order and family uncertain

Genus *Acanthospina* n. gen.

TYPE AND ONLY SPECIES. — *acanthospina irregulare* n. gen., n. sp.

ETYMOLOGY. — From *acanthus* (Latin): spine, thorn; and *spina* (Latin): needle, spine, referring to spiny scales.

AGE. — Early Devonian, early Lochkovian.

DIAGNOSIS. — As for the type and only species.

DISCUSSION

Acanthodian of uncertain systematic position, with chondrichthyan-type scales (hybodontiform according to its crown morphology),

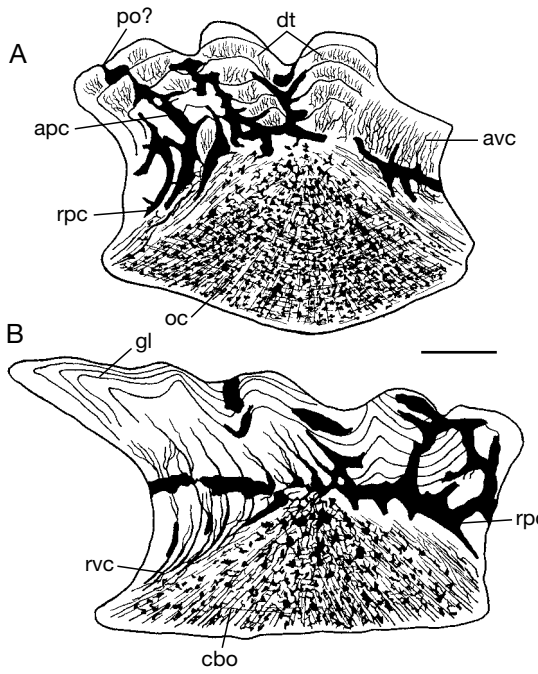


FIG. 45. — *Arcticacanthus bicostatus* n. gen., n. sp., scale histology, Pod"emnaya River, outcrop 69, bed 26, Pod"emnaya Formation; **A**, vertical transverse section; **B**, vertical longitudinal section, anterior to right, thin sections 3399 (**A**) and 3398 (**B**). Abbreviations: **apc**, ascending pore canal; **avc**, ascending vascular canal; **cbo**, cellular bone; **dt**, dentine tubule; **gl**, growth lamella; **oc**, osteocyte cavity; **po?**, pore opening?; **rpc**, radial pore canal; **rvc**, radial vascular canal. Scale bar: 0.1 mm.

composed of "*Nostolepis*"-type tissues, characteristic of acanthodian histological structure and ischnacanthid-like (particularly, *Poracanthodes*-type) teeth.

It might possibly belong to a group of climatiiform acanthodians, which, by scale morphology may be distant from the ascertained Climatiidae species.

Acanthospina irregulare n. sp.
(Figs 30C-F; 46-51)

Nostolepis sp. no. 6 – Valiukevičius 1988a: 604, 605.

"An unusually squamose acanthodian" – Valiukevičius 1997: 25.

HOLOTYPE. — LIG 35-A-344. Incomplete specimen exposing only squamation (Fig. 46G). Pod"emnaya River, outcrop 67, bed 12.

PARATYPES. — LIG 35-A-352: part of head with jawbone fragments, intact or poorly articulated teeth, one tooth whorl, isolated palatine teeth, denticles, scales and plates (Fig. 46A-F). Another small part of specimen LIG 35-A-345, exposing squamation (fully dissolved). Both specimens from the Pod"emnaya River, outcrop 67, bed 12.

ETYMOLOGY. — From *irregularis* (Latin): irregular, in reference to variable, inconstant crown ornamentation.

LOCALITY AND AGE. — October Revolution Island: Pod"emnaya River, outcrop 67, bed 12. Lower Devonian, lower Lochkovian, top of the Severnaya Zemlya Formation.

DIAGNOSIS. — Fish having large sub-rhombic to inconstantly shaped scales with high spiny denticles on crowns. Denticles rarely flattened, grown together areally. Scale necks and bases randomly porose. Crowns composed of Stranggewebe with a dense network of diversified vascular canals, partly down streamed and piercing the highly cellular bone of the scale base. Dentition of powerful sharp, high-pyramidal main cusps, smaller intercusps and rounded or flattened palatine teeth, composed of trabecular dentine with, in parabasal part, mono- or bi-branched multipulpar canals directed toward the apex. Tooth whorls also present.

DESCRIPTION

Squamation

Scales densely displayed in lines without overlaps. Their crowns vary in length from 0.4 to 1.7 mm, with a majority from 0.7-1.1 mm. In smaller examples the crowns are wider than long. The shape is inconstant in form varying from sub-rhombic (Figs 30C; 47C) to oval or elongated (Fig. 47J, K). Crowns consist of one, some or numerous areas-denticles. Multidenticle scales distinctly dominate, with well defined denticle margins (Fig. 30C) each being additionally ornamented with short anterior ridgelets (Figs 30C; 47A, H). Sometimes the denticles of medial area are flattened and fused together, resembling almost horizontal crown plate (Fig. 47A, C). This sort of crown has often well grown anterior denticles or essentially rounded starlets (Fig. 47A, C), slightly elevated and separated from the remaining crown part by larger grooves. The crowns overhang posteriorly the bases. A majority of scales have numerous, irregularly shaped denticles with longitudinal ridges

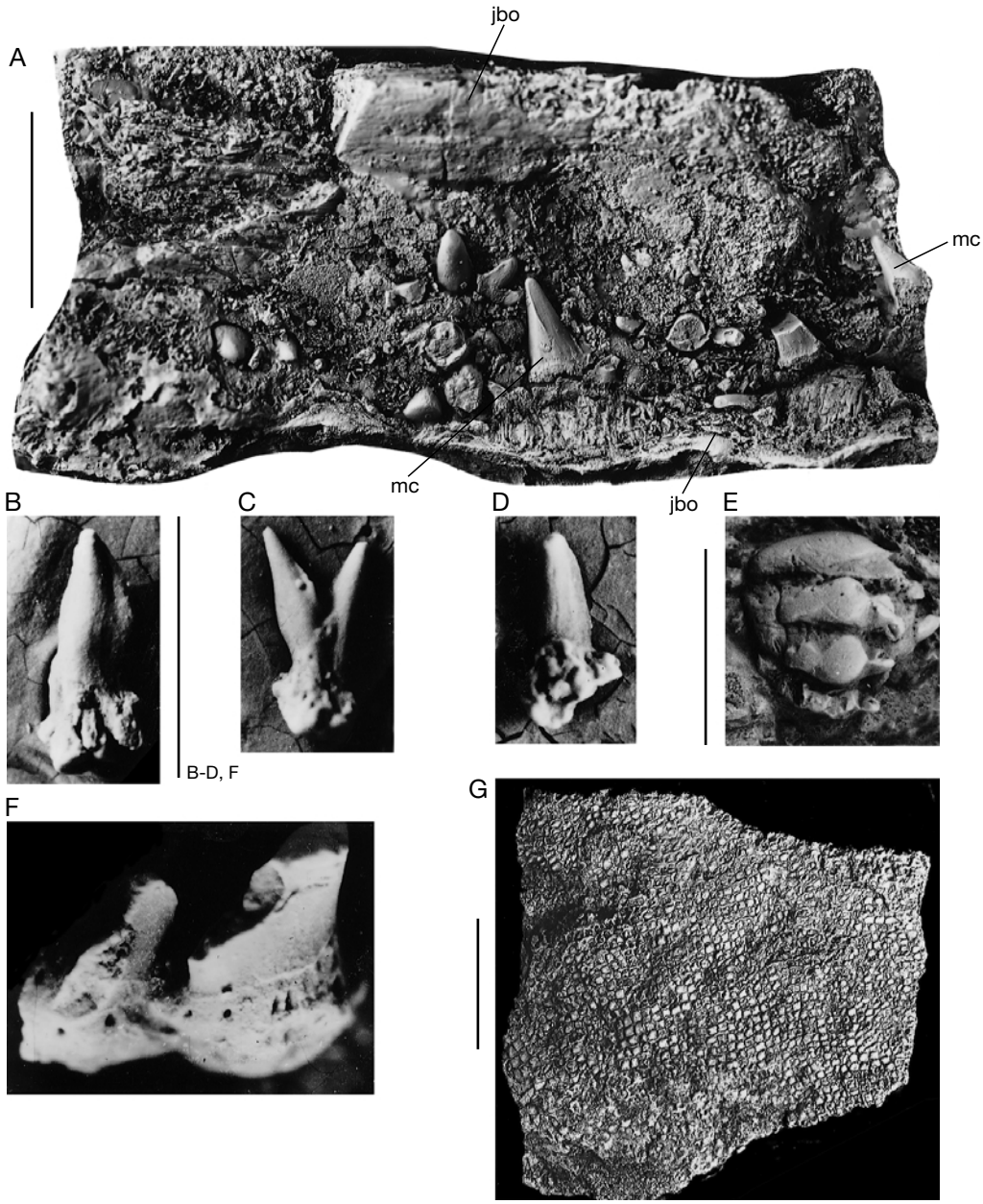


FIG. 46. — *Acanthospina irregulare* n. gen., n. sp., Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, paratype LIG 35-A-352, exposing jawbone fragments, inarticulated teeth (main cusps, palatine and whorl elements) and scales; **B**-**D**, palatine teeth, lateral view; **B**, LIG 35-2107; **C**, LIG 35-2109; **D**, LIG 35-2110; **E**, **F**, tooth whorl elements; **E**, whorl, exposed on the other rock side of the paratype LIG 35-A-352; **F**, whorl? fragment, lateral view; all microremains from the paratype LIG 35-A-352; **G**, holotype, LIG 35-A-344, scales, base view. Abbreviations: **jbo**, jawbone; **mc**, tooth main cusp. Scale bars: A, G, 10 mm; B-D, F, 1 mm; E, 5 mm.

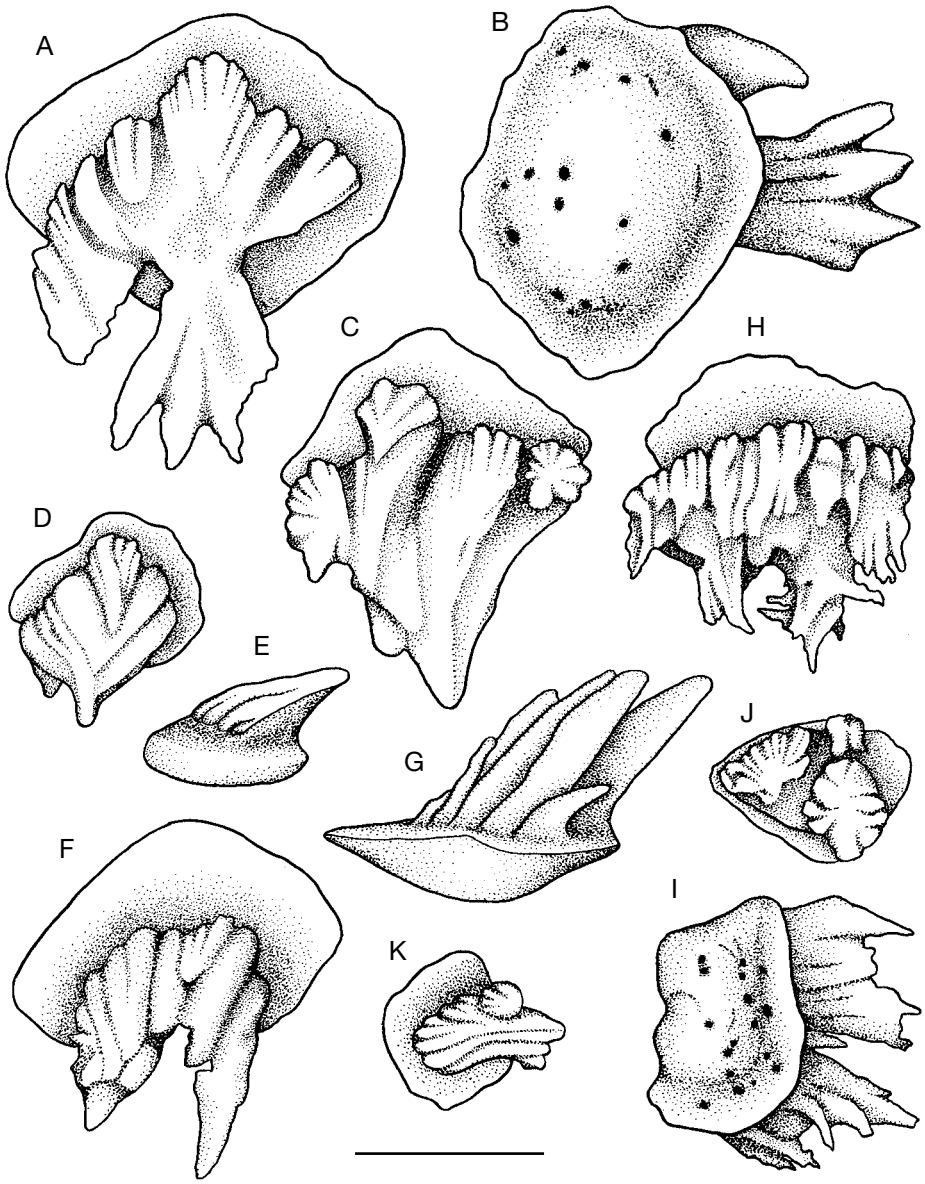


FIG. 47. — *Acanthospina irregulare* n. gen., n. sp., drawings of scales, from paratype LIG 35-A-345, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, **B**, LIG 35-1259, crown, anterior upwards (**A**) and base, anterior to left (**B**); **C**, LIG 35-1263, crown, anterior upwards; **D**, **E**, LIG 35-1269, crown, anterior upwards (**D**) and side, anterior to left (**E**); **F**, **G**, LIG 35-1265, crown, anterior upwards (**F**) and side, anterior to left (**G**); **H**, **I**, LIG 35-1270, crown, anterior upwards (**H**) and base, anterior to left (**I**); **J**, LIG 35-1261, crown, anterior upwards; **K**, LIG 35-1264, crown, anterior to left. Scale bar: 1 mm.

(Fig. 47F-H), growing on all sides of the central one and highering slightly posteriorly or rarely making a large angle with the base (Fig. 47G). Rare scales of smaller size bear an anterior fore-crown, which protrude from beneath posterior- and sideward, enlarged plates, thus pointing growth in one direction (Fig. 47D). The minority belong to tesserae-like scales with separate

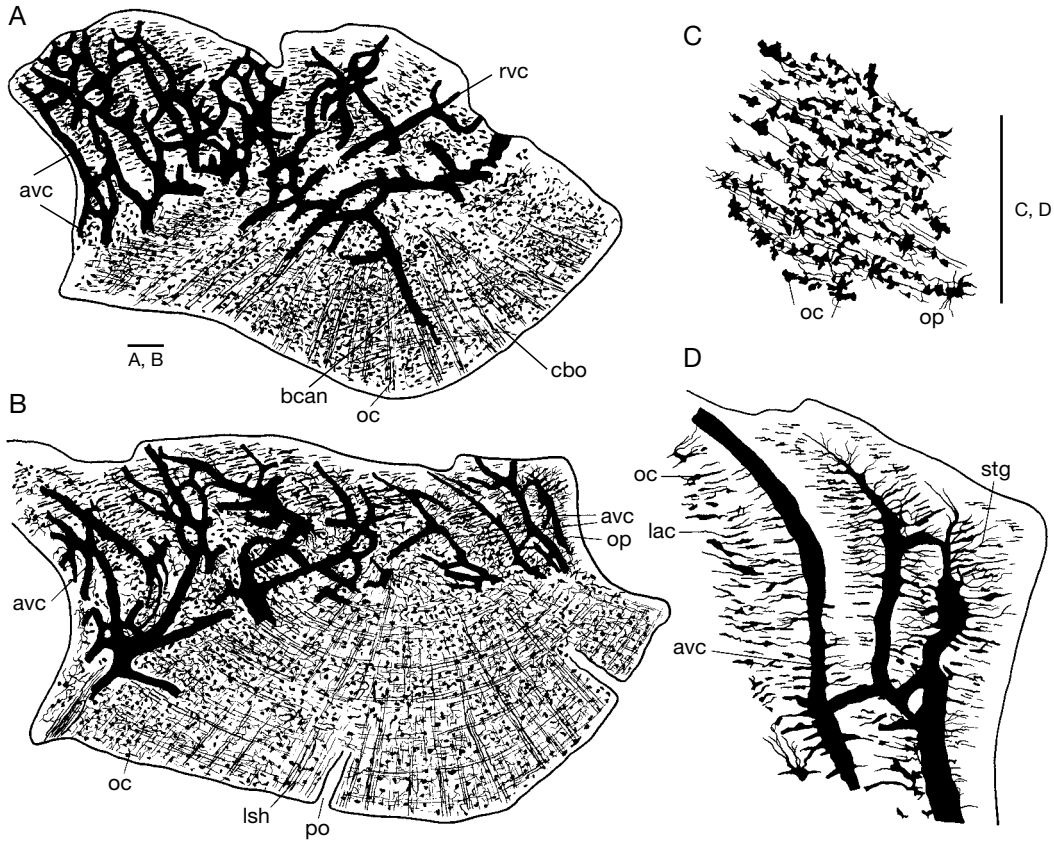


FIG. 48. — *Acanthospina irregulare* n. gen., n. sp., scale histology, vertical longitudinal sections, anterior to right, from paratype LIG 35-A-345, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, scale like figured on Fig. 47C, thin section 644; **B**, scale like figured on Fig. 47A, thin section 648; **C**, magnified base area of the same section; **D**, magnified right corner of crown of the same section. Abbreviations: **avc**, ascending vascular canal; **bcan**, vascular canal piercing base of scale; **cbo**, cellular bone; **lac**, lacuna; **lsh**, longitudinal Sharpey's fibres; **oc**, osteocyte cavity; **op**, osteocyte process; **po**, pore opening; **rvc**, radial vascular canal; **stg**, Stranggewebe (oriented mesodentine). Scale bars: 0.1 mm.

rounded and striated blunt denticles, joined with flat or slightly convex base plate (Fig. 47J). The scale neck is porose, low to mid-high. The highest crowns are distinguished by their almost absent neck, with denticles arising from the base. The base is massive, convex, rhombic, and sub-rhombic to oval or widened quadrangular, protruding the crown anteriorly and laterally. Its bottom surface exposes numerous randomly distributed large pore openings (Fig. 47B, I).

The scale histological structure is of the "*Nostolepis*"-type. Crowns are composed of areally grown lamellae with a modified mesodentine tissue. All their space is pierced by a very diversified system of dense and large (wide and long), ascending, circular and radial vascular canals, of various shapes. There is almost no place left for dentine tubules of a typical mesodentine network (Figs 48A, B; 49A, B). The largest radial canals are occurring over the base, but smaller branches are also met higher in the crowns, where they interconnect with ascendant canals and form the principal canal network. Several canals are directed baseward to open on its surface (Fig. 48A). A Stranggewebe with elongated lacunae of variable size and osteocyte spaces (Figs 48D; 49B) composes all crown. The

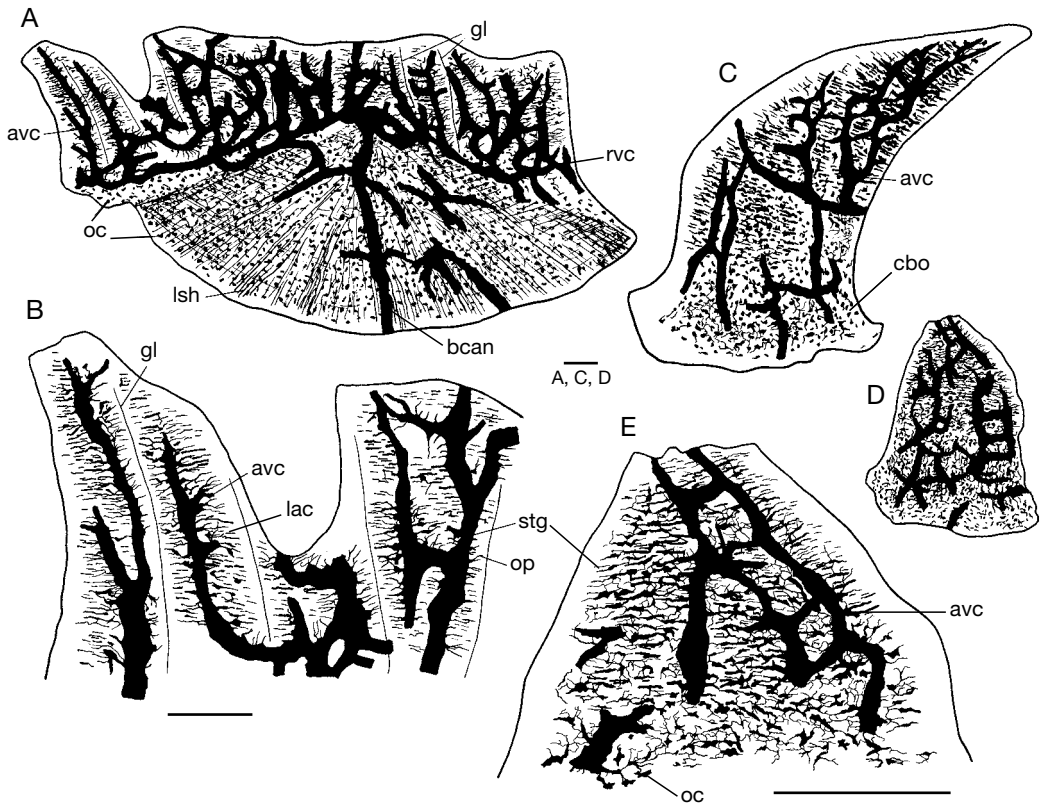


FIG. 49. — *Acanthospina irregulare* n. gen., n. sp., scale and denticle-scale histology, vertical longitudinal sections, from paratype LIG 35-A-345, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, scale like figured on Fig. 47H, thin section 652; **B**, magnified left corner of crown of the same section; **C**-**E**, monoodontodic denticle-scales, thin sections 649 (**C**) and 651 (**D**, **E**). Abbreviations: **avc**, ascending vascular canal; **bcan**, vascular canal piercing base of scale; **cbo**, cellular bone; **gl**, growth lamella; **lac**, lacuna; **lsh**, longitudinal Sharpey's fibres; **oc**, osteocyte cavity; **op**, osteocyte process; **rvc**, radial vascular canal; **stg**, Stranggewebe (oriented mesodentine). Scale bars: 0.1 mm.

base is composed of superpositionally growing highly cellular bone (Fig. 48C) with polygonal large osteocytes; vascular canals pierce it. Thorn-like scales (Fig. 49C-E) show the same tissue composition.

Dentition

Teeth fused to dermal jawbones have oval, sub-circular or, rarely, a rounded triangular parabasal section. Their arrangement relative to lateral line is destroyed. The paratype (Fig. 46A) has yielded slightly basally striated main cusps (up to 7 mm high) and smaller interspersed and lateral cusps. Teeth have a stretched high-pyramidal longitudinal section. They are rarely recurved, with sharp apexes and side flanges. Palatine teeth (Fig. 46B-D), 0.2-0.7 mm high are, thin and elongated, rounded or longitudinally flattened, and also exhibit side flanges. They are always found with a bony base of inconstant deepness and sometimes bear small blunt fragile denticles, disposed all around the palatine cusp. Two-cuspidate palatine teeth (Fig. 46C) are rarely encountered. The tooth whorl (Fig. 46E), about 4.8 mm long and to 3.9 mm wide is, massive, grouping on a slightly curved bony base three rounded main cusps (very weathered), gradually thinning in one direction. One or two cusps of smaller size are present on each side of the main cusp.

In their histological structure, the main cusps (Fig. 50) and palatine teeth (Fig. 51B) are rather identical. The basal cellular bone is highly vascularised. In parabasal part a trabecular dentine occur with multipulpar canals. Higher in crown their number reduces to one or two. Monotonous dentine weakly branched tubules arise and are directed at right angle upward and toward all sides. Sectioned blunt rounded denticles are composed of cellular bone and superficial dentine (Fig. 51A). A strip between them contains extremely enlarged vascular canals with numerous outerward ascending dentine tubules.

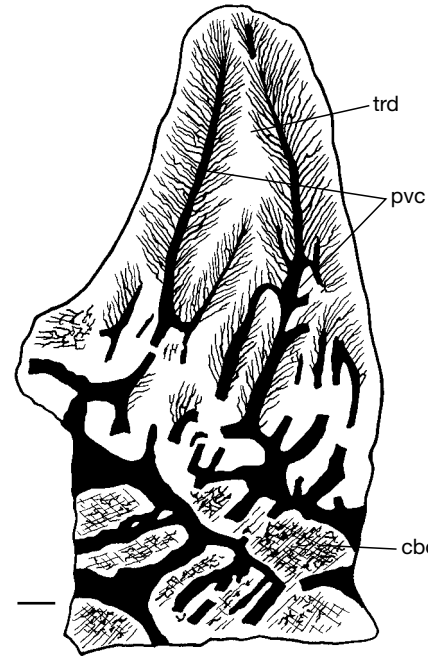


FIG. 50. — *Acanthospina irregulare* n. gen., n. sp., vertical longitudinal section through the sharply flanged tooth main cusp, thin section 3493, paratype LIG 35-A-352, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation. Abbreviations: **cbo**, cellular bone; **pvc**, pulpar vascular canal; **trd**, trabecular dentine. Scale bar: 0.1 mm.

DISCUSSION

The systematic position of *Acanthospina irregulare* n. gen., n. sp. remains uncertain. The histological structure of scales (diversified system of principal canal net, Stranggewebe composing all crown space, highly cellular and also vascularised bone in base), which can be defined as modified "*Nostolepis*"-type, is closest to that of representatives of the Climatiidae. This basic character leads to place the taxon within acanthodians. Particularly, by several histological features (growth type, style of Stranggewebe, vasculars in bases), the new taxon resembles *Nostolepis robusta* (Brotzen, 1934) (Gross 1971: text-figs 15, 16), but differs in its lack of superficial simple mesodentine strip, surrounding each growth lamella.

According to morphologic characters, especially to spiny denticles on crowns, it looks rather Chondrichthyes-like. *Acanthospina* n. gen. crowns resemble those known in certain hybodontiform chondrichthyans, e.g., *Arauzia federicoi* from the Early Devonian of Spain (Mader 1986: pl. 6, figs 1-14) or Hybodontoid gen. et sp. indet. from the Early Carboniferous of Queensland, Australia (Turner 1993: figs 12, 13). Several more essential differences occur in the shape and type of porosity of scale neck and base.

BIOSTRATIGRAPHIC SIGNIFICANCE

Key species of the *Poracanthodes menneri* Subzone, it is associated with other articulated acanthodians and occurs at the topmost part of the Severnaya Zemlya Formation. Age is early Lochkovian. Tentatively correlates to the *woschmidti* Zone of standard conodont scale.

BIOSTRATIGRAPHIC ASSEMBLAGES OF ACANTHODIANS

The Severnaya Zemlya acanthodian assemblages have been preliminary published (Valiukevičius 1988a). The species composition was then reported and a correlation of the three biostratigraphic complexes of Severnaya Zemlya was established: they belong to the first, third and sixth (Valiukevičius 1988a: table 1, p. 602) among 13 known throughout our collections from different regions. Several taxa referred to in this early publication with an open nomenclature were later described under their own

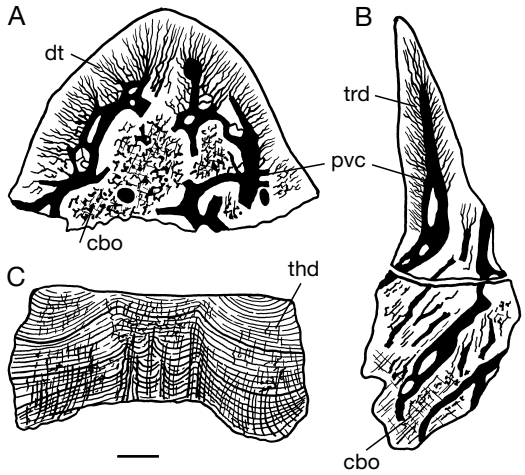


FIG. 51. — *Acanthospina irregulare* n. gen., n. sp., histology of selected elements, from paratype LIG 35-A-352, Pod"emnaya River, outcrop 67, bed 12, Severnaya Zemlya Formation; **A**, vertical longitudinal section through the blunt denticle from the jawbone, thin section 3494; **B**, vertical transverse section through the palatine tooth, thin section 3498; **C**, vertical transverse section through the porose plate from the head area, thin section 3497. Abbreviations: **cbo**, cellular bone; **dt**, dentine tubule; **pvc**, pulpar vascular canal; **thd**, thin-lamellar dentine; **trd**, trabecular dentine. Scale bar: 0.1 mm.

names, e.g., *Poracanthodes* sp. no. 3 – *P. menneri* (Valiukevičius 1992), others are shortly reported, e.g., *Nostolepis* sp. no. 6 – an unusually squamose acanthodian (Valiukevičius 1997) – and finally described in the present paper namely *Acanthospina irregulare* n. gen., n. sp. On the same line *Nostolepis* sp. no. 7 becomes *Nostolepis fragilis* n. sp., and *Cheiracanthoides* sp. no. 4 is replaced by two representatives of the new genus *Acritolepis* n. gen.: *A. urvantsevi* n. gen., n. sp. and *A. ushakovi* n. gen., n. sp.

Poracanthodes punctatus Zone is supposedly a biostratigraphic analogue of two acanthodian interval zones of the Pridoli in Baltic: *Nostolepis gracilis* and *Poracanthodes punctatus* (shallow shelf) or three: when adding *Nostolepis alta* in the deep shelf facies (Märss 1986, 1997). This zone is established from the Krasnaya Bukhta Formation on the October Revolution Island. The most complete assemblage comes from the Spokojnaya River outcrops: 51a, beds a-c; 45 and 41, bed 1. It is dominated by ischnacanthid acanthodians belonging to two genera: *Poracanthodes* (*P. punctatus* Brotzen, 1934, *P.* sp. cf. *P. porosus* Brotzen, 1934, *P.* sp. cf. *P. subporosus* Valiukevicius, 1998) and *Gomphonchus* (*G. sandelensis* (Pander, 1856), *G.* sp. cf. *G. hoppei* (Gross, 1947), *G. nordicus* n. sp.), and a smaller number of climatiids (*Nostolepis striata* Pander, 1856, *N.* sp. cf. *N. gracilis* Gross, 1947, *Nostolepis* sp. or *Cheiracanthoides* sp., *Cheiracanthoides* sp.), *Onchus*-type fin spines and *Acanthoides*? sp. (Table 2). Only *Gomphonchus nordicus* n. sp. is a key species. Others have a long-ranging occurrence, including *Gomphonchus* sp. cf. *G. hoppei* and *Poracanthodes* sp. cf. *P. porosus*, which have essentially a wider ranges in other studied regions. An almost identical assemblage is found in the sample 12-76 from Pioneer Island, which includes *Gomphonchus nordicus* n. sp., but lacks *G.* sp. cf. *G. hoppei* and *Poracanthodes* sp. cf. *P. subporosus*. The sample is supposedly attached to the age analogues of the Krasnaya Bukhta Formation.

The zone comprises likely in other studied regions only the Late Silurian range part of index species, and thus is classified as an interval range zone.

Nostolepis minima Zone is grounded by full stratigraphic range of the index species and treated as a biozone. It is attached to the Lochkovian Severnaya Zemlya and Pod"emnaya formations and composed of two distinct subzones: *Poracanthodes menneri* and *Diplacanthus poltnigi* n. sp. The latter can be only identified with certainty in the upper part of the Pod"emnaya Formation (Table 3).

Poracanthodes menneri Subzone is prevailingly established by the assemblage of articulated acanthodians from the uppermost part of the Severnaya Zemlya Formation. This stratigraphic level occurs also as an important lithological marker and is traced through the studied outcrops of all rivers on the October Revolution Island: Matusevich River, outcrop 1, bed 21, Ushakov River 21-9, Pod"emnaya River 67-12 and Spokojnaya River 41-12. This assemblage is dominated by new key taxa of climatiids: *Acritolepis urvantsevi* n. gen., n. sp., *A. ushakovi* n. gen., n. sp., *Nostolepis fragilis* n. sp., *N. decora*

n. sp., *Acanthacanthus ornatus* n. gen., n. sp., two ischnacanthids: *Poracanthodes menneri* and *Acanthopora transitans* n. gen., n. sp., and two more acanthodians of uncertain systematic position: *Acanthospina irregulare* n. gen., n. sp. and Acanthodii gen. indet. The identification and description of the latter is not taken into account since many unclear morphologic elements are still needed for an additional detailed study. This assemblage is represented most extensively on the Matusevich, Spokojnaya and Pod"emnaya rivers, whereas the Ushakov River series has yielded only both ischnacanthids and Acanthodii gen. indet. *Nostolepis minima*, identified from isolated scales and occurring together with articulated specimens (Table 2), distinguishes the Subzone belonging to the lower part of the *N. minima* Zone. *Poracanthodes menneri* Subzone is treated as a regional biozone of the index species.

Diplacanthus poltnigi n. sp. Subzone is ranked on Severnaya Zemlya Archipelago also as a regional biozone of the index species. It is distinguished by an essential renewal of the acanthodian species composition attached to the upper part of the Pod"emnaya Formation. Out of *D. poltnigi* n. sp., occur into the sequence the ischnacanthids cf. *Lietuvacanthus* Valiukevicius, 1998 (Matusevich River, outcrop 4, bed 3 and Pod"emnaya River, outcrop 69, bed 26) and *Arcticacanthus bicostatus* n. gen., n. sp. (Pod"emnaya River, outcrop 69, bed 26), and also the diagnostic climatiids: *Tareyacanthus* sp. cf. *T. dissectus* Valiukevicius, 1994, *Nostolepis timanica* n. sp., *N. laticristata* Valiukevicius, 1994, *N.* sp. cf. *N. multicostata* Vieth, 1980, *N.* sp. cf. *N. arctica* Vieth, 1980 and *Cheiracanthoides borealis* Valiukevicius, 1994. Tentative age is late Lochkovian. According to finds of index species in the Emsian of other regions, only an interval range is supposed on Severnaya Zemlya Archipelago.

Beds with *Watsonacanthus costatus* n. sp. characterise both the Emsian Rusanov Formation and the lower Al'banov Subformation. The acanthodian assemblage includes many of earlier occurrences and diagnostic acanthodians of the previous Subzone (Table 3). These are the climatiids *Cheiracanthoides borealis*, *Tareyacanthus* sp. cf. *T. dissectus*, *Nostolepis* sp. cf. *N. multicostata*, *N. laticristata*, *N. timanica* n. sp., *N.* sp. cf. *N. arctica* and the ischnacanthid *Arcticacanthus bicostatus* n. gen., n. sp. Together with them, the assemblage bears some key species. Their ranges may occur as partial because of the overlain and overlying formations or their bordering parts, which have no acanthodian characteristics. Except for *Watsonacanthus costatus* n. sp., the most valuable stratigraphic fossils are the climatiids *Nostolepis watsoni* n. sp., *N. taimyrica* Valiukevicius, 1994, *N.* sp. cf. *N. multangula* Valiukevicius, 1994 and *Cheiracanthoides comptus* Wells, 1944 (Fig. 27). An almost identical assemblage, with only single exceptions, is obtained from the outcrop 5, bed 55 on the Matusevich River and outcrop 48, beds 5-7 on the Spokojnaya River. The rock sequence of Pioneer Island has yielded *Watsonacanthus costatus* n. sp. accompanied with other diagnostic climatiids from the Devonian Member 8 (Klubov *et al.* 1980). The characteristic *Nostolepis taimyrica*, *N. watsoni* n. sp., *Cheiracanthoides comptus* and the index species have also been identified from samples distinctly belonging to the lower Al'banov Subformation: observation points 220 and 2478, and samples with the type specimens of *Tollichthys polaris* Bystrov, 1957 and *Luetkeichthys borealis* Bystrov, 1957. We suppose this acanthodian assemblage range within the Devonian Members 6-10 referred to by above-mentioned authors.

Beds with *Diplacanthus solidus* n. sp. are attached to the upper part of the Vstrechnaya Formation ascribed to Eifelian? As it was already noted, the rocks of Vstrechnaya and bordering formations along the Matusevich and Ushakov rivers have been sampled in more detail. Plenty of samples appeared unfossiliferous. The best acanthodian characteristics came from beds 136-153 of the outcrop 5 on the Matusevich River. A complete *Diplacanthus solidus* n. sp. assemblage is found here, including most valuable *Markacanthus* sp. cf. *M. alius* Valiukevicius, 1988, and all the representatives of *Diplacanthus*:

TABLE 2. — Distribution of acanthodians in samples. Figures opposite the taxon names indicate numbers of isolated scales. Abbreviations: *, the right bank outcrop, analogues of the outcrop 4, beds upwards the 11th on the Matusevich River; **, observation point 26, sample 3, Sovetskaya Bay; ***, microremains from the *Tollichthys polaris* and *Luetkeichthys borealis* type specimens (observation point 220); ****, member according to Klubov *et al.* 1980; **t**, talus; + (a), ● (b), ■ (c), articulated acanthodian species, represented by single (**a**), several (**b**) or numerous (**c**) specimens.

Locality	Outcrop	Bed	Gomphonchus nordicus n. sp.	Gomphonchus sandelensis (Pander)	Gomphonchus sp. cf. G. hoppei (Gross)	Acanthoides ? sp.	Poracanthodes punctatus Brotzen	Poracanthodes sp. cf. P. porosus Brotzen	Cheiracanthoides sp.	Nostolepis sp. cf. N. gracilis Gross	Poracanthodes menneri Valiuk.	Poracanthodes sp. cf. P. subporosus Valiuk.	Acanthopora transitans n. gen., n. sp.	Acanthodii gen. indet.	Nostolepisfragilis n. sp.	Acritolepis urvantsevi n. gen., n. sp.	Acritolepis ushakovi n. gen., n. sp.	Nostolepis decora n. sp.	Nostolepis minima Valiuk.	Acanthacanthus ornatus n. gen., n. sp.	Acanthospina irregulare n. gen., n. sp.	Nostolepis striata Pander	Nostolepis timanica n. sp.	Nostolepis sp. cf. N. multicostata Vieth	Nostolepis sp. cf. N. robusta (Brotzen)	Nostolepis laticristata Valiuk.	Nostolepis sp. cf. N. arctica Vieth	Nostolepis sp.	Pruemolepis wellsi Vieth-Schreiner	Nostolepis sp. or Cheiracanthoides sp.	Cheiracanthoides borealis Valiuk.	Arcticacanthus bicostatus n. gen., n. sp.	Climatius sp.	Tareyacanthus sp. cf. T. dissectus Valiuk.	cf. Valiuk. Lietuvacanthus	Diplacanthus poltnigi n. sp.	Gomphonchus sp. or Poracanthodes sp.	Watsonacanthus costatus n. sp.	Nostolepis tainyrica Valiuk.	Nostolepis sp. cf. N. multangula Valiuk.	Nostolepis watsoni n. sp.	Cheiracanthoides comptus Wells	Acanthoides ? sp. C Valiuk.	Acanthoides ? sp. A Valiuk.	Acanthoides ? sp. B Valiuk.	Acanthoides ? sp. D Valiuk.	Diplacanthus carinatus Gross	Diplacanthus solidus n. sp.	Diplacanthus sp. cf. D. gravis Valiuk.	Markacanthus sp. cf. M. alius Valiuk.	Cheiracanthus sp. cf. Ch. longicostatus Gross	Cheiracanthus sp. cf. Ch. brevicostatus Gross	Formation
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
October Revolution Island, Matusevich River	7	39																																											3							Gremyashchij
	5	153																																									2	10		3		1	1		Vstrechnaya
		151																																									7	4	3	4	2		3	1	
		149																																									15	9	5	1	1	3		4	
		147																																								1	8	4						1	
		145																																									1								
		136																																										1	1	3		2			
		133																																									10	8						2	
		121																																										1							
		55																																			4	3		2	1	3										Al'banov
	4	7							2																			1																								Pod"emnaya
		3		15		17	3			6									6			24	9	33	6	5	2	3	8		7			4	1	5	4																
	1	21		4							■		■	■	+	●	■		52																																		Severnaya Zemlya
	2	1		5	2		4	2																																													Ust'-Spokojnaya
		44		2																		1																															
October Revolution Island, Spokojnaya River	49	11		1																																		3			2												Al'banov
	48	7																																				4			1	2	2										
		5																				2																8		2	3	4	13										
	40	45							1																								+																				Spokojnaya
		43		4																		3																															
		38		2		2																2																					2										Pod"emnaya
		27		1		12			2	4									3				3	4					4	4	2			3		2																	
		24		2																																																	
		21		6		4																		3					1					1		3																	
		17		1																		1																															
	*r.b.,an.	4-11				9																7		12							5			2																			
	41	12					+				●	+		■		+	■		21	+																																	Severnaya Zemlya
		1	3	11	4	7	3	4	8													8								5																							Krasnaya Bukhta
	45	topt	25	113	100		36	51																																													
		11		4																																																	
		20	2	2			1																																														
	51 a	a-c	12	91	3	74	6	23	4			4																																									
October Revolution Island, Pod"emnaya River	**o.p.	26-3		7		8			1	1																													7		2												Al'banov
	69	26		4						2												3		5			2					6	+		2																		Pod"emnaya
	67	12									■			+		+	+	+	5		●																																Severnaya Zemlya
October Revolution Island, Ushakov River	24	1																																										1								Gremyashchij
	27	16																																										3	2	1						Vstrechnaya
		4																																										6						1		
	25	1																				1			4													2															Al'banov
	22	2				3																2						1																									Pod"emnaya
	21	9									●		+	+																																							Severnaya Zemlya
		1				4													3																																		
Komsomolets Island	18077	9		8		4	1																								2			3																			Spokojnaya
	18041	14				43																															3																Uncertain
Pioneer Island	14	B																																									8										13****
	P-7																																						4				42										10 Al'banov
	o.p.220					3																																	2				4										Al'banov
	o.p.2478																																					1			1	8											
	***T.p. & L.b.					35																																	6			4	9										
	P-9-1			4		3																	14								2			2				7	3		38												Rusanov
	P-10-1																						34	1			3	3			14			1				9	36		31	2	6										8
	P-10-2																														2																						
	P-12-12																																								1												7
	P-12-7																									2						4							8		2	3											6
	P-17-2			4		6																									9								3														3
	P-13-3					1																		1																													1
	12-76		73	130		50	3	8	8	2																																											S_2pr3
	980*																											1						3						2			9										Uncertain

D. carinatus, *D. solidus* n. sp. and *D.* sp. cf. *D. gravis*. On the Ushakov River the related level is only established in outcrop 27, bed 16 with *Diplacanthus carinatus* and *D. solidus* n. sp. Ranges of all these species seemingly occur as partial if compared with other studied regions.

ACANTHODIAN-BASED CORRELATION OF SEVERNAYA ZEMLYA WITH OTHER REGIONS

The *Poracanthodes punctatus* Zone assemblage from Krasnaya Bukhta Formation characterises the late Pridoli. All species, except for *Gomphonchus nordicus* n. sp., are known from the well studied Baltic basin with established sequence: *Nostolepis gracilis-Poracanthodes punctatus-Nostolepis alta* Zone. Their generalized range is determined from the upper part of the Kaugatuma and embraces the complete Ohesaare Regional Stage (Märss 1986, 1997; Karatajūtē-Talimaa *et al.* 1987). The Severnaya Zemlya acanthodian assemblage is also more or less tentatively correlated with the first biostratigraphic complex of the Greben Regional Stage of Timan-Pechora region, identified from both the outcrops (the Kozhim River, etc.) and cores of numerous borings (Valiukevičius 1993). The latter have yielded two nostolepids: *Nostolepis athleta* Valiukevicius, 1994 and *N. robusta* (Brotzen, 1934) ranging in Timan-Pechora from the latest Pridoli to Early Devonian, whereas in other regions they are found only within the Early Devonian. These exceptions (enrichment of the late Pridolian acanthodian assemblage) are only encountered in some cases, e.g., in the Olenya area.

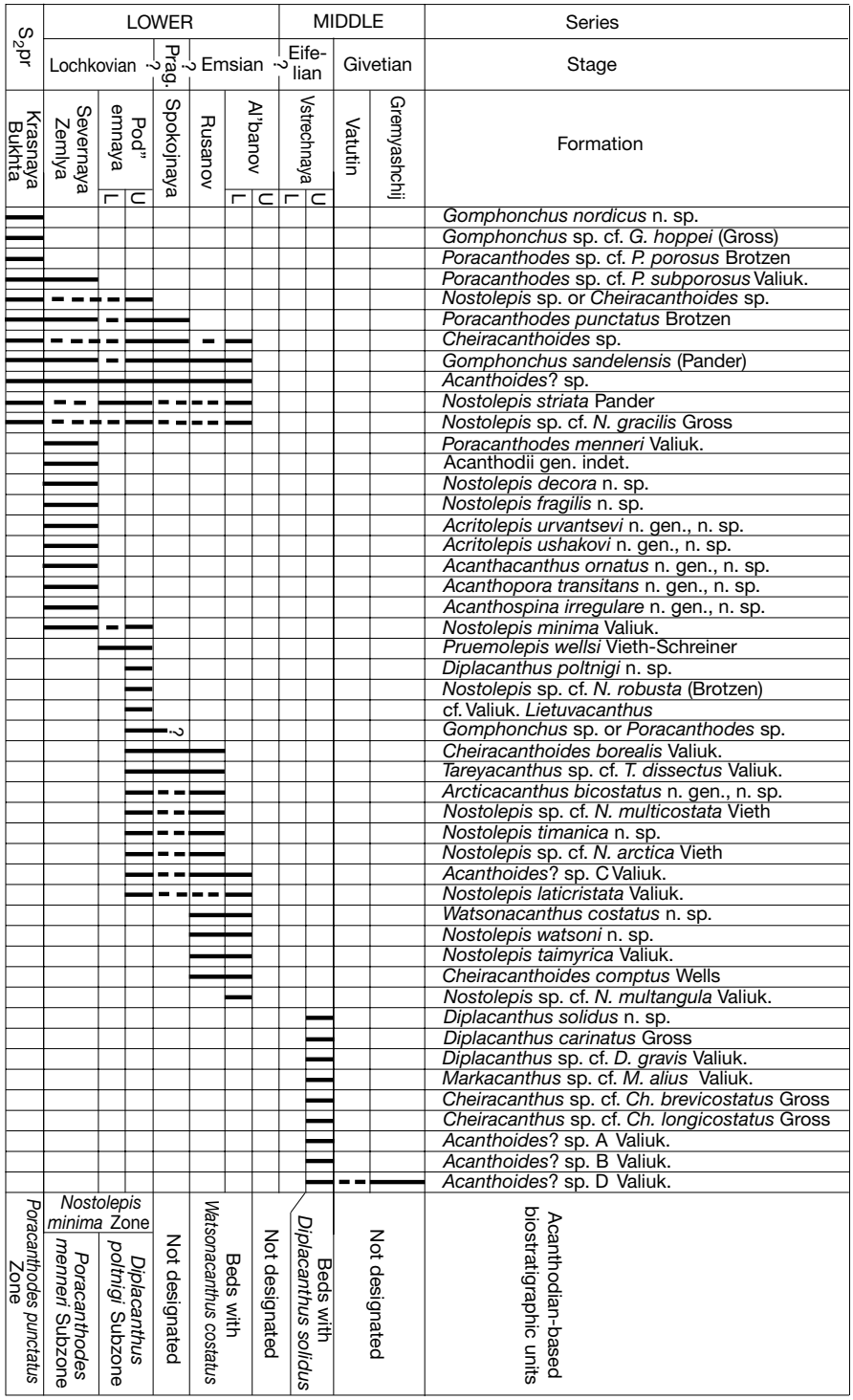
The typical *Poracanthodes punctatus* acanthodian assemblage, dominated by ischnacanthids and rare nostolepids, is established in the North Timan and attached to the Eptarma Formation (type locality is the Velikaya River outcrops).

The *Poracanthodes menneri* Subzone assemblage, represented by articulated acanthodian specimens of prevailing climatiids, has no equivalents in other regions. Its correlation is only based on the occurrence of *Nostolepis minima*, identifying the Subzone as a lower part of the *N. minima* Zone. The latter is obtained from Tilžė Regional Stage in Baltic, Borshchov and lower Chortkov in Podolia, two lower members of Khatayakha Formation (Ovin-Parma Regional Stage) in Timan-Pechora, Uryum and Tolbat beds in Tajmyr (Valiukevičius 1995a; Valiukevičius & Kruchek 2000) and Tom'chumysh Regional Stage in Salair.

The *Diplacanthus poltnigi* n. sp. Subzone assemblage is based on many nostolepids: *N. minima*, *N.* sp. cf. *N. robusta*, *N.* sp. cf. *N. multicostata*, *N. laticristata*, *N.* sp. cf. *N. arctica*, and is related to Tilžė Regional Stage in Baltic. Finds of *Diplacanthus poltnigi* n. sp. together with *Tareyacanthus* sp. cf. *T. dissectus* and cf. *Lietuvacanthus* indicate that the upper part of Pod"emnaya Formation is close to Stoniškiai of Baltic. It is attributed here to the *Lietuvacanthus fossulatus* acanthodian Zone, overlying the *N. minima* Zone. The Severnaya Zemlya acanthodian sequence demonstrates a more extensive range of *N. minima*, and *Diplacanthus poltnigi* n. sp., which has a concurrent range for its upper part. Close to *D. poltnigi* n. sp. an acanthodian assemblage is established from the upper Chortkov-Ivane-lower Dniester Regional stages of Podolia, with an equivalent in Baltic: the *Lietuvacanthus fossulatus* Zone. It includes the characteristic association of *Lietuvacanthus fossulatus*, *Tareyacanthus* sp. cf. *T. dissectus* and *Nostolepis timanica* n. sp. accompanied by species of wider ranges.

Correlations with Timan-Pechora and Tajmyr are problematic. Only *Nostolepis timanica* n. sp., if based on its first occurrences, allows to correlate the upper part of Pod"emnaya Formation with the lower Toravei in Timan-Pechora. The Tajmyr acanthodian sequence shows a *Nostolepis minima* Zone extending to the top of Lochkovian is close to that of Severnaya Zemlya. At the top of *N. minima* Zone in Tajmyr, the concurrent *N. tareyensis* Subzone, embracing Tolbat beds, is established (Valiukevičius 1995a). It includes *N. minima*, *N. laticristata*, and *N.* sp. cf. *N. arctica* as the most comparable representa-

TABLE 3. — Ranges of acanthodian species and arranged biostratigraphic units within the latest Silurian, Early and Middle Devonian.



tives of the *Diplacanthus poltnigi* n. sp. Subzone on Severnaya Zemlya. Finds of *Diplacanthus poltnigi* n. sp. (our own identifications, not taken from reference authors) in Arctic Canada (Vieth 1980) give a late Lochkovian-Pragian age and, moreover, the youngest representatives (latest Emsian) from Graz (Austria) (Poltnig 1984) need an additional study, including histological investigation, before their regional stratigraphic ranges could be determined.

The *Watsonacanthus costatus* n. sp. acanthodian assemblage is best correlated with Belovo and lower Shanda Regional stages of Salair. All five key species represented in Rusanov Formation and lower Al'banov Subformation are found in Salair accompanied by numerous species with more extended stratigraphic ranges (Vyushkova 1992). In Tajmyr this level corresponds to the Taribigai and Dolgan beds characterised by *Nostolepis multangula* and *Watsonacanthus costatus* n. sp. zones. Our opinion is based on the occurrences of both zonal index species (Valiukevičius 1994), whereas other biostratigraphically most significant taxa, e.g., *Nostolepis curta* Valiukevicius, 1994, a species phylogenetically close to *N. watsoni* n. sp., *N. taimyrica* Valiukevicius, 1994 and *Cheiracanthoides comptus* appear earlier in Tajmyr.

A close acanthodian assemblage, only including a lower number of transitional species, is found in the Varandei Formation of Timan-Pechora (Valiukevičius 1995a).

The *Diplacanthus solidus* n. sp. assemblage (the upper part of Vstrechnaya Formation) is correlated with the upper Narva-Aruküla-Burtnieki Regional stages (Eifelian-Givetian) of the Baltic area. All species identified on Severnaya Zemlya are met there. But, differently, their stratigraphic ranges are essentially wider and not equal. *Diplacanthus carinatus* and *Acanthoides*? sp. A of Valiukevičius (1985) occur in Baltic with the topmost middle Narva (*Ptychodictyon rimosum* Zone), *Diplacanthus solidus* n. sp., with the upper Narva (*Nostolepis kernavensis* Zone), whereas *D. gravis* and *Markacanthus alius*, with the Aruküla Regional Stage (*Diplacanthus gravis* Zone) (Valiukevičius 1998). All of them range through the Aruküla (Givetian). A correlation of the upper part of Vstrechnaya Formation with the Baltic upper Narva and lower Aruküla is most preferable. Related acanthodian assemblages are also known from the Kostiukovichi and lower Polotsk (Goryn beds) of Belarus. They are identified as *Nostolepis kernavensis* and *Diplacanthus gravis* zones respectively (Valiukevičius & Kruchek 2000).

SEVERNAYA ZEMLYA ACANTHODIAN ASSEMBLAGES IN RELATION TO THE DEVONIAN STANDARD CONODONT SCALE

The *Poracanthodes menneri* Subzone, composing the lower part of the *Nostolepis minima* Zone, is related to the *woschmidti* Zone of standard conodont scale. This is indirectly based on correlation of several studied regions, yielded conodonts together with acanthodians in the same samples. The datation is based on the *N. minima* ranges. This zone corresponds to the *woschmidti-postwoschmidti* conodont zones. Conodont data are known from Belarus (Brest Depression and Volyn' Monocline), where the geological series are considerably reduced, and from the more complete Podolian data, where supposedly the full *N. minima* range is dated by *woschmidti woschmidti-w. hesperius-eolaticrescens-postwoschmidti* conodont sequence (Drygant 1988).

The *Diplacanthus poltnigi* n. sp. Subzone or, more precisely, its well characterised upper part, based on our estimations of represented age analogues of the *Lietuvacanthus fossulatus* Zone (established both in Baltic and Podolia), may be dated by correlation with Podolia. There the late Lochkovian *Icriodus serus* Zone is represented; it tentatively corresponds to the *delta-pesavis* zones of conodont standard.

Beds with *Watsonacanthus costatus* n. sp. have yielded dominating *Pandorinellina exigua exigua* and *P. expansa* accompanied by a smaller number of *Pelekysgnathus* sp. and *Steptotaxis* sp. nov. C of Uyeno & Klapper (1980) from the

same samples with acanthodians (P-9-1, 10-1 and 12-12: members 7-8 on the Pioneer Island, Rusanov Formation). According to N. Sobolev (St. Petersburg), they correspond to the *dehiscens-inversus* conodont zones. Analogous dating is taken for the well correlated Belovo and lower Shanda Horizons of Salair (Vyushkova 1992) and Taribigai and Dolgan beds of Tajmyr with established conodont zonal sequence of *P. dehiscens* Philip & Jackson, 1967-*P. dehiscens* (late form)/*Steptotaxis*? *furnishi* Klapper, 1980-*Pandorinellina expansa/Steptotaxis* sp. (Sobolev 1990).

An age corresponding to the *kockelianus-varcus* zones is supposed for the beds with *Diplacanthus solidus* n. sp. The *kockelianus* conodont event is widely traced throughout the regions of the East European Platform and well established on the *Polygnathus parawebbi* or *Eognathodus bipennatus bipennatus* conodont assemblages (Kernavė in the Baltic, Kostiukovichi in Belarus, Mosolovo and Chernyi Yar in the Central Devonian Field, Lekeiyaga Formation in Timan-Pechora). According to the species present in the *Diplacanthus gravis* acanthodian Zone (known from the Aruküla and Burtnieki Regional stages in Baltic, also the lowermost Polotsk in Belarus and Staryi Oskol in the Central Devonian Field), the age of the beds may extend to the Givetian *varcus* Zone, well known from the Central Devonian Field (Aristov & Ovnatanova 1985).

CONCLUSION

The study of Late Silurian (Pridoli) to Middle Devonian acanthodians from the Severnaya Zemlya Archipelago has recovered some assemblages represented by new articulated endemic taxa and/or by isolated microremains (mainly scales) of new and known species showing certain similarity with other regions.

The latest Pridolian assemblage, *Poracanthodes punctatus* Zone, attached to Krasnaya Bukhta Formation, is represented by dominant species of *Gomphonchus* and *Poracanthodes* genera, including a new taxon, *Gomphonchus nordicus* n. sp.

The *Poracanthodes menneri* Subzone of early Lochkovian age (Severnaya Zemlya Formation) is characterised by an assemblage of articulated acanthodians. Two representatives of the new genus *Acritolepis* n. gen., *A. ushakovi* n. gen., n. sp. and *A. urvantsevi* n. gen., n. sp. of uncertain systematic position among Climatiiformes are identified here. Their general morphology, position and insertion of spines and specific histological structure of spines and scales as well as other morphologic peculiarities of the animal body do not allow to adequately place these new taxa in the system.

Acanthacanthus ornatus n. gen., n. sp. from this assemblage, according to scales with pointed radial crown ridges separating medial and lateral areas and composed prevailingly of Stranggewebe with osteocytes even in the latest growth lamella and characteristic chambers of vascular canals in crowns, is attributed to the family Climatiidae. Two additional nostolepids, *Nostolepis decora* n. sp. and *N. fragilis* n. sp., belonging also to the same family, occur here. *N. decora* n. sp. has characteristic scales with anteriorly downsloping crowns composed of elongated triangular medial area lined by two well marked ridges, and notches in lateral areas with "denticulate" margins. Medial area is grown superpositionally, whereas lateral ones join areally. *N. fragilis* n. sp. is described on articulated specimens exposing short ventral (intermediate) fin spines with nodose ridges and longitudinally ribbed pectorals, composed of cellular bone and mesodentine. Scale crowns made of simple mesodentine are ornamented with two medial and two symmetrical lateral ridges. Scale bases with deep fossa.

Acanthopora transitans n. gen., n. sp. represents a small ischnacanthid with slender body, two long, deeply inserted, longitudinally ribbed dorsal spines and similar pectorals. Its squamation consists of tiny rhombic scales with flat crowns and some randomly posterior pores. Scales exhibit a "*Poracanthodes*" histological type, but dentine and durodentine in crowns lack radial

vascular and radial pore canals. Pore canal system was functioning only in the latest lamellae, whereas in the earlier ones it is replaced by vascular canals.

Acanthospina irregulare n. gen., n. sp., an acanthodian of uncertain systematic position, is represented by high hybodontiform-like (chondrichthyan) spiny scales, composed of tissues characteristic to the "*Nostolepis*"-type histology and sharp edge teeth comparable with these of *Poracanthodes*.

The *Poracanthodes menneri* Subzone assemblage, apart from the articulated index species, includes also isolated scales of *Nostolepis minima*. The latter is widely distributed in different regions and most valuable for datation and correlation of geological series. After these finds, the subzone is assigned to the lower part of *N. minima* Zone and tentatively correlated with the *woschmidti* Zone of conodonts.

The *Diplacanthus poltnigi* n. sp. Subzone assemblage (Pod"emnaya Formation, Lochkovian) is notable by the first occurrence of three new acanthodian taxa identified on isolated scales. *Diplacanthus poltnigi* n. sp. is characterised by the absence of ridges on scale crowns. Ornamentation is represented only by deep linear sub-parallel grooves. It shows a "*Diplacanthus*"-type histology. The ischnacanthid *Arcticacanthus bicostatus* n. gen., n. sp. has scales with four to six high bifurcated anteriorly converging ridges and neck with pore openings. Dentine-like tissue of crown is pierced by diversified pore canals. Most characteristic are the ascending canals formed anew in each next growth lamella. Climatiid *Nostolepis timanica* n. sp. is described on small flattened and elongated scales with three to four short converging ridges of variable form and length. Apart from typical networked dentine tubules, the crown mesodentine contains long ascending and branchy radial vascular canals, defining a distinct dentine tissue.

According to the first appearance of *Tareyacanthus* sp. cf. *T. dissectus*, cf. *Lietuvacanthus*, the three above-mentioned new taxa and also of some other known nostolepids, this assemblage is comparable to the *Lietuvacanthus fossulatus* Zone identified in Baltic area (Stoniškiai Regional Stage) and Podolia (upper Chortkov-Ivane-lower Dniester). The Podolian series are dated by conodonts as late Lochkovian *Icriodus serus* Zone, corresponding to the *delta-pesavis* zones of conodont standard.

The *Watsonacanthus costatus* n. sp. acanthodian assemblage from Rusanov Formation and lower Al'banov Subformation (Emsian) includes two new forms related to climatiids. *Nostolepis watsoni* n. sp. is one of the intermediate members of the *Nostolepis-Watsonacanthus* phylogenetic lineage, recognized in Tajmyr and Severnaya Zemlya a series including *Nostolepis taimyrica-N. curta* Valiukevicius, 1994-*N. watsoni* n. sp.-*Watsonacanthus costatus* n. sp.-*W. sibiricus* Valiukevicius, 1994. *Nostolepis watsoni* n. sp. is determined on scales with crowns ornamented with short rounded sub-parallel or sub-radial converging ridges, and strong anteriorly advanced bases. They are composed of cellular to acellular bone in bases and both mesodentine and dentine tissues in crowns. Scales of *Watsonacanthus costatus* n. sp. are ornamented with sharp radial or converging ridges pointing posteriorly, and crowns composed of mesodentine network with reduced branches of principal vascular canals, or of dentine with long ascending and radial vasculars.

Apart from them, this assemblage contains the biostratigraphic indicators *Nostolepis taimyrica*, *N.* sp. cf. *N. multangula*, *N. timanica* n. sp. and *Cheiracanthoides comptus*. Similar acanthodian assemblages are known from Belovo and lower Shanda in Salair, Taribigai and Dolgan beds in Tajmyr and Varandei Formation in Timan-Pechora. The Severnaya Zemlya assemblage is dated by the conodonts *Pandorinellina exigua exigua*, *P. expansa*, representatives of *Pelekysgnathus* and *Steptotaxis*, collected within the same samples as the acanthodians and indicating Emsian *dehiscens-inversus* zones.

The *Diplacanthus solidus* n. sp. assemblage (upper part of Vstrechnaya Formation, Eifelian or Eifelian-Givetian?), except for the index species, is composed of two additional diplacan-

thids *Diplacanthus carinatus* and *D.* sp. cf. *D. gravis*, the cheiracanthids *Markacanthus* sp. cf. *M. alius*, *Cheiracanthus* sp. cf. *Ch. longicostatus* Gross, 1973 and *Ch.* sp. cf. *Ch. brevicostatus* Gross, 1973, and representatives of *Acanthoides*?

Diplacanthus solidus n. sp. is distinguished by scales with high neck and two to four symmetrical pairs of linear grooves extending over all crowns slightly radially or in a fan pattern. The style of vascular canals in crown mesodentine is similar to that in dentine tissue, but the canals penetrating bases are characteristic of the "*Diplacanthus*"-type histology.

Beds with *Diplacanthus solidus* n. sp. are best correlated with the Baltic upper Narva-Aruküla and Belarussian Kostiukovichi-lower Polotsk (Eifelian-Givetian) beds. They correspond to the *Nostolepis kernavensis* and *Diplacanthus gravis* acanthodian zones, the first of one being dated by the *Polygnathus parawebbi* conodont assemblage related to the *kockelianus* standard Zone.

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