

Upper Silurian thelodonts from Severnaya Zemlya Archipelago (Russia)

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ABSTRACT

Thelodonts have been found in the Bol'shaya, Matusevich, Obryvistaya, Pod"emnaya, Spokojnaya, Ushakov rivers and Cape October sections of October Revolution Island, and Komsomolets and Pioneer islands sections, Severnaya Zemlya Archipelago, Russia. Two new families, one new genus and six new species belonging to the orders Katoporida and Thelodontida are described from the Upper Silurian. Seven taxa are re-described. Scattered scales of *Loganellia cuneata* (Gross, 1947), *Paralogania* ex gr. *martinssoni* (Gross, 1967), *Paralogania menneri* n. sp., *Valiukia flabellata* n. gen., n. sp., *Phlebolepis elegans* Pander, 1856, *Thelodus visvaldi* n. sp., *Thelodus matukhini* n. sp., *Thelodus* ex gr. *schmidti* (Pander, 1856), *Thelodus* sp. indet. and *Lanarkia?* sp. are characteristic for the Ludlow part of the sequence (Ust-Spokojnaya Formation of October Revolution Island and its analogue on Pioneer and Komsomolets islands). *Thelodus parvidens*(?), *Loganellia cuneata*, *Paralogania wilsoni* n. sp., *P. kachanovi* n. sp., *Paralogania* sp. cf. *P. borealis* (Karatajūtė-Talimaa, 1978), *Goniporus alatus* (Gross, 1947) and *Nikolivia elongata* Karatajūtė-Talimaa, 1978 are distributed in the sections of Krasnaya Bukhta Formation on October Revolution Island and coeval strata of Pioneer Island (Pridoli). *Thelodus visvaldi* n. sp. is also present in Wenlock of Pioneer Island.

KEY WORDS

Thelodonti,
Upper Silurian,
Severnaya Zemlya Archipelago,
scale morphology,
histology.

RÉSUMÉ

Thélodontes du Silurien supérieur de l'Archipel de Severnaya Zemlya (Russie).

Des Thélodontes ont été récoltés dans les vallées des rivières Bol'shaya, Matusevich, Obryvistaya, Pod"emnaya, Spokojnaya, Ushakov ainsi que dans les sections du Cap Octobre de l'Île de la Révolution d'Octobre et des îles Komsomolets et Pionnier. Deux nouvelles familles, un nouveau genre et six nouvelles espèces du Silurien supérieur appartenant aux ordres des Katoporida et des Thelodontida sont décrits. Sept taxons sont redécrits. Les écaillés isolées de *Loganellia cuneata* (Gross, 1947), *Paralogania* ex gr. *martinsoni* (Gross, 1967), *Paralogania menneri* n. sp., *Valiukia flabellata* n. gen., n. sp., *Phlebolepis elegans* Pander, 1856, *Thelodus visvaldi* n. sp., *Thelodus matukhini* n. sp., *Thelodus* ex gr. *schmidti* (Pander, 1856), *Thelodus* sp. indet. et *Lanarkia* ? sp. sont caractéristiques de la partie Ludlow de la séquence (Formation Ust-Spokojnaya de l'Île de la Révolution d'Octobre, et son homologue des îles Pionnier et Komsomolets). *Thelodus parvidens* (?), *Loganellia cuneata*, *Paralogania wilsoni* n. sp., *P. kachanovi* n. sp., *Paralogania* sp. cf. *P. borealis* (Karatajūtė-Talimaa, 1978), *Goniporus alatus* (Gross, 1947) and *Nikolivia elongata* Karatajūtė-Talimaa, 1978 sont distribuées dans les sections de la Formation de Krasnaya Bukhta de l'Île de la Révolution d'Octobre et dans les strates équivalentes de l'Île Pionnier (Pridoli). *Thelodus visvaldi* n. sp. est également présent dans le Wenlock de l'Île Pionnier.

MOTS CLÉS

Thelodonti,
Silurien supérieur,
Archipel de Severnaya Zemlya,
morphologie des écaillés,
histologie.

INTRODUCTION

Isolated scales of thelodonts have been found at numerous levels in the Upper Silurian sequence of the October Revolution, Pioneer and Komsomolets islands of Severnaya Zemlya Archipelago. The research level of the deposits varies in the sections. The interval between samples was different and therefore there is an incomplete picture of the vertical distribution of thelodont species and assemblages even from the main Upper Silurian sections on October Revolution Island. The upper part of the Ust-Spokojnaya Formation (Ludlow) on the banks of the Matusevich River (outcrop 2) is the best one. The samples from the Ludlow part of the deposits cropping out on the Ushakov and Spokojnaya rivers also yielded a great number of well preserved scales. Thelodonts of Ludlow age were discovered in the rocks of October Cape (sample MF 34-1, formation not defined). The Krasnaya Bukhta Formation, Pridoli, is

represented in the Krasnaya Bay and Spokojnaya River area of the eastern part of the October Revolution Island (see Märss & Karatajūtė-Talimaa 2002: fig. 1).

The Silurian of Pioneer Island was discovered and studied by B. A. Klubov and E. I. Kachanov during a field trip in 1976 (Klubov *et al.* 1980: fig. 1, I-II, III and V areas). The 210 m thick beds of dolomitic and oncolitic limestones were dated as Ludlow (members 1-2 of the I-II and III areas), and a 90 m thick complex (member 3 of the V area) was treated as Pridoli. Samples with vertebrate microremains of these rocks were given to V. Karatajūtė-Talimaa and identifications made by her were also included.

New and previously known data on vertebrate microremains, mainly thelodonts, and conodonts allows a precise dating of the Silurian deposits. Based on conodonts (Männik 2002), a considerable part of the Lower Silurian (members 1-4) corresponds to the middle? and upper Llandovery. Member 7 (40 m thick), because of

SYSTEM		Series	Member	Thickness (m)	Samples	Samples with thelodonts	Area	Thelodonti indet.	Loganelliidae indet.	Loganella n. sp. 1	Loganella sp. indet.	Loganella cuneata (Gross, 1947)	Paralogania sp. indet.	Paralogania klubovi Märss & Karatjütë-Talimma, 2002	Paralogania ex gr. martinsoni (Gross, 1967)	Paralogania kachanovi n. sp.	cf. Valiukia sp. indet.	Thelocus sp. (n. sp.?)	Thelocus visvaldi n. sp.	Thelocus ex. gr. schmidti (Pander, 1856)	Thelocus parvidens(?) Agassiz, 1839	Apsidognathus sp. Ozarkodina confluens bucerus (Virra, 1983)		
SILURIAN	Pridoli	3		90	90	12	V																	
				100																				
				100-110																				
	Ludlow	2		200-210	200-210	8-E 9-ж 8-д-1 5-M, 5M-1	I-II																	
				100																				
				110																				
	Wenlock	7		40	40	6-Б 6-А 8-г, 8-г-1 8-д 5-д 5-и 5-к 5-г-2 5-к 5-г-1 5-Е, 5Е-2	III																	
				100																				
				70																				
	Llandovery	4		50	50	4-В 4-А, Б 3 2-Х 2-и 2-К-2 2-ж 2-д 2-А	I																	
				30																				
				100																				
Llandovery	1		70	70	7-А 10-В 10-А 7-Б	I-II																		
			30																					
			70																					

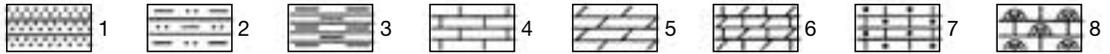


FIG. 1. — Distribution of thelodonts in the Silurian section of Pioneer Island; 1, sandstone; 2, sandstone and silty sandstone; 3, argillite; 4, biomorphic limestone; 5, dolomite; 6, dolomitic limestone; 7, oolitic limestone; 8, stromatoporoidal limestone (after Klubov *et al.* 1980: fig. 2; modified). Cyrillic letters in fig. 2 of Klubov *et al.* 1980 are in present paper transliterated as follows: A = a; B = b; В = v; г = g; д = d; E = e; 3 = zh; и = i; K = k; M = m; H = kh.

the enclosed vertebrate species, can be treated as Ludlow and not as Wenlock. In this way, the volume of the latter is strongly reduced if com-

pared with that in Klubov *et al.* (1980). Most likely, only members 5 and 6 (170 m thick in the III area) can be attributed to the Wenlock.

In Fig. 1 the distribution of thelodonts in the Silurian of Pioneer Island is given. The lithological column, the number of samples and areas are as they were given in Klubov *et al.* (1980: fig. 2). Some samples did not yield phosphatic remains or they were not studied. In addition, the material of the expedition of E. N. Lenkin to Pioneer Island in 1974 was used to determine the Ludlow thelodont assemblages. Scales of thelodonts were also found in a few rock samples from Komsomolets Island (samples collected by A. F. Khapilin in 1974). They all come from the Ludlow part of the Upper Silurian.

The formations distinguished within the Silurian of October Revolution Island cannot with certainty be traced on the other islands of the archipelago but series are determined and correlated by thelodonts and other early vertebrates.

Distribution of thelodont taxa in the Ordovician to Devonian sections of October Revolution and Srednij islands is given in the paper by Märss & Karatajūtė-Talimaa (2002: fig. 1). Distribution of outcrops and stratigraphical subdivision of the Upper Silurian series on Severnaya Zemlya is reported by Männik *et al.* (2002).

SYSTEMATICS

In this work the thelodonts taxonomy established by Gross (1967) and Karatajūtė-Talimaa (1978, 1997) has been used.

The scales having collection numbers as combinations of letters Pi and numbers are housed in the Institute of Geology, Tallinn, and those with LIG 35 followed by specimen number are stored in the Lithuanian Institute of Geology, Vilnius.

Subclass THELODONTI Kiaer, 1932

Order KATOPORIDA Gross, 1967

Family LOGANELLIIDAE Karatajūtė-Talimaa, 1997

Genus *Loganellia* Turner, 1991

TYPE SPECIES. — *Loganellia scotica* (Traquair, 1898).

Loganellia cuneata (Gross, 1947)

(Fig. 2J-R)

MATERIAL EXAMINED. — About 50 scales from the Ust-Spokojnaya Formation, Ludlow, and over 100 scales from the Pridoli part of the sequence.

REMARKS

The synonymy of *Loganellia cuneata* s.l. is given by Turner (1976) and Märss (1986). Karatajūtė-Talimaa (1978) described *Loganellia* (= *Logania*) *cuneata* from the Pridoli of North Timan. The scales with postero-lateral spines of the crown were not included in the morphological set of this species (*L. cuneata* s.str.). Later Karatajūtė-Talimaa (1997) revised the taxonomy of loganelliid thelodonts and gave morphological criteria for the genera *Loganellia* and *Paralogania*. To the genus *Loganellia* were ascribed only forms having a squamation of simple, ribbed scales as described by Gross (1947, 1967).

DESCRIPTION AND COMMENTS

Rare scales of *Loganellia cuneata* associated with numerous scales of the genus *Paralogania* (*P. ex gr. martinsoni* and *P. menneri* n. sp.) in the samples 2-23, and 47-14 on October Revolution Island, and in the sample 5d on Pioneer Island of Ludlow part of the sections. *L. cuneata* scales are better represented in the Krasnaya Bukhta Formation of October Revolution Island (samples 51a, 51b, and 45 of talus) and in the Pridoli of Pioneer Island (sample 12).

In Fig. 2J-R the scales from the middle part of the Ust-Spokojnaya Formation are displayed (Matusevich River, sample 2-23). They are mostly comparable with *L. cuneata* from the uppermost Pridoli of Lithuania. Relatively short scales with convex base are similar with those from the Beyrichienkalk (Gross 1967: taf. 3, fig. 16; and *obliteratus*-type in Gross 1947). The scales are small to medium-sized (0.4-0.8 mm long, rarely 1.2 mm). The central area is narrow, with a medial furrow. The central area is separated from the lateral ones by deep down-

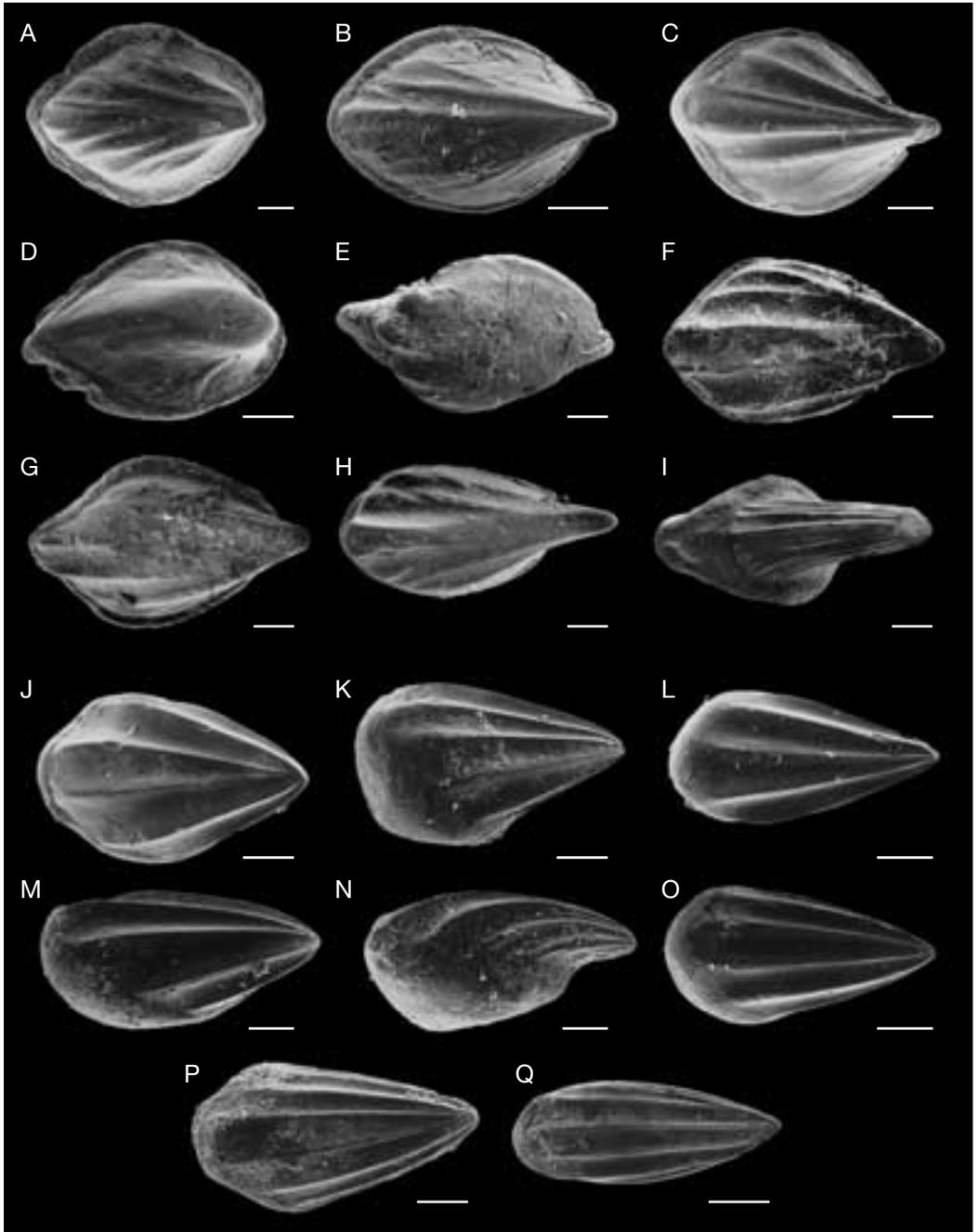


FIG. 2. — **A-I**, *Thelodus matukhini* n. sp., scales in crown view; **A**, LIG 35-859; **B**, holotype, LIG 35-860; **C**, LIG 35-861; **D**, LIG 35-862; **E**, Pi 7552; **F**, Pi 7550; **G**, Pi 7547; **H**, Pi 7551; **I**, Pi 7557; **A-D**, sample 18041-14, Komsomolets Island, Ludlow, Upper Silurian; **E-I**, sample MF 34-1, cape October (Otyabrskij), October Revolution Island, Ludlow, Upper Silurian; **J-Q**, *Loganelia cuneata* (Gross, 1947); **J**, **L**, **O-Q**, scales in crown view; **K**, **M**, scales in oblique lateral crown view; **N**, a scale in lateral view; **J-Q**, LIG 35-863-LIG 35-870; sample 2-23, Matusevich River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. Scale bars: A, C, E-H, J-P, 0.1 mm; B, D, I, Q, 0.2 mm.

stepped groove. Lateral crown areas bear two to three, rarely four pairs of longitudinal ridges. They extend up to the tapered posterior crown apex. On the lower side of the crown, behind the convex base, the longitudinal ridges are short and fine (Fig. 2N). In some scales the central crown area consists of two longitudinal areas separated by a ridge (Fig. 2R). In all studied scales the base is convex, pulp opening hardly visible. Scales with spur-like projection anteriorly of the base were not found.

The size and proportions of the crown and base of *L. cuneata* from the Ludlow and Pridoli of Severnaya Zemlya are not fully similar. *L. cuneata* scales from the Pridoli (Pioneer Island, sample 12) are larger; the base is rather small, slightly shifted forwardly but the crown, on the contrary, is large and with sharp longitudinal ridges.

Genus *Paralogania* Karatajūtė-Talimaa, 1997

TYPE SPECIES. — *Paralogania kummerowi* (Gross, 1967).

Paralogania ex gr. *martinssoni* (Gross, 1967)
(Figs 3A-M; 4; 5; 6A-E)

SYNONYMY. — See Turner (1976), Karatajūtė-Talimaa (1978) and Märss (1986b).

MATERIAL EXAMINED. — Over 1000 scales of good to very good preservation.

OCCURRENCE. — Samples MF 157-4, Spokojnaya River; MF 34-1, Cape October; MF 11-1, 2-1, 2-2, 2-7, 2-8, 2-19, 2-20, 2-21, 2-23, Matusevich River; Sample 31-1, Ushakov River, October Revolution Island, Ust-Spokojnaya Formation; 5055e, 2055zh, 2087, 2463, 2803, 5m, 5m-1, 5d, 5zh-1, 8d-1, 8g, 8g-1, 8g-2, 9zh, Pioneer Island; 18066-5, 20568, Komsomolets Island, Severnaya Zemlya Archipelago, Ludlow, Upper Silurian.

DESCRIPTION AND COMMENTS

On Severnaya Zemlya the scales of very variable morphology of *P. martinssoni* have been found in the Ludlow rocks. Märss (1986b: figs 12-14) gave evidence that *L. martinssoni* scales significantly change in morphology from the Wenlock, Rootsiküla Stage up to the Ludlow, Paadla Stage of Estonia. Karatajūtė-Talimaa

(1997: 14) noted that the scales of *P. martinssoni* vary in different localities. We tend to think that the name *P. martinssoni* embraces more than one species. Because of uncertainty, in this work we treat this species as *P. ex gr. martinssoni*.

Scales of small to medium size. Head scales (Figs 4A; 5A, B) rounded to oval with crenulated margins around the crown. Crown surface flat and smooth. Transitional scales (Figs 3A; 4B-J, O; 5C-J, O) with anterolateral or without notches, postero-lateral edges smooth or with short spines. Trunk scales (Figs 3B-H; 4K-N, P, R-Z; 5J-N, P-U) with characteristic smooth and flat medial plate of crown and two to eight spines on the postero-lateral vertical crown portion, and a single medial spine beneath the posterior apex of the crown plate. More posteriorly the scale crowns and the scales itself become narrower (Fig. 3L, M). Fig. 3M exhibits a scale with a strange upwards directed posterior crown apex. The scale in Fig. 3I most possibly comes from a fin because of its very narrow elongate configuration. There are scales with rather wide crown that is ridged longitudinally (Fig. 3J, K), each ridge ending with a pointed apex; the latter is often broken. Their position in the squamation is not known. Some scales have a rib above the spines (Fig. 3G-I, L) similar to those we know in *P. ludlowiensis* (Gross, 1967) and *P. consimilis* (Märss & Karatajūtė-Talimaa 2002: fig. 5). The microstructure of *P. martinssoni* is typical for *Paralogania* with sinuous dentine canals, that continue with rather straight dentine tubules (Fig. 6A-E).

Paralogania menneri n. sp.
(Figs 7; 8)

HOLOTYPE. — Transitional(?) scale LIG 35-878 (Fig. 7J, K).

ETYMOLOGY. — Named in honour of Dr. V.V. Menner, Moscow, Russia, one of the organizers of field work to the October Revolution Island in 1978.

SYNONYMY. — *P. menneri* n. sp. scales were earlier identified as *Paralogania* sp. nov. 2 (Karatajūtė-Talimaa 1997: fig. 9C, D; Talimaa 2000); and as *Paralogania* sp. 1 (Märss & Karajūtė-Talimaa 2002: fig. 1).

MATERIAL EXAMINED. — More than 5000 scales of good preservation. Especially rich in different morphological

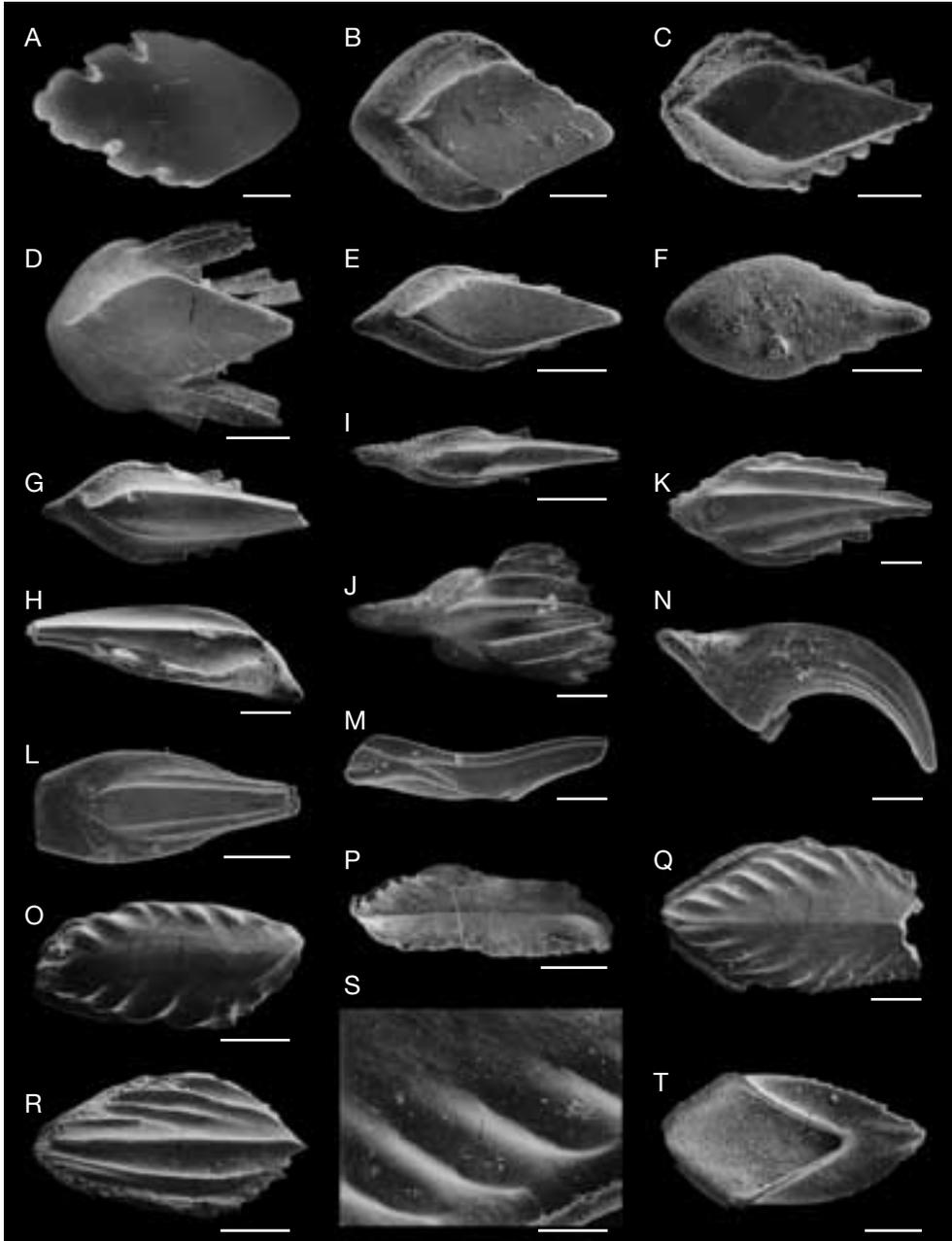


FIG. 3. — **A-M**, *Paralogania* ex gr. *martinssoni* (Gross, 1967); **A**, transitional scale; **B-H**, **L**, **M**, trunk scales; **I**, fin scale; **J**, **K**, scales of unknown position; **A-E**, **G**, **I-L**, scales in crown view; **F**, a scale in base view; **H**, **M**, scales in lateral view; **N**, *Laarkia*? sp., a scale in lateral view; **O-T**, *Phlebolepis elegans* Pander, 1856; **O-R**, scales in crown view; **S**, magnified scale of Fig. 3Q showing the finely striated crown margin; **T**, scale in base view; **O-Q**, **S**, cephalo-pectoral scales; **R**, precaudal scale; **T**, precaudal? scale; **A**, Pi 7612; **B**, Pi 7609; **C**, Pi 7610; **D**, Pi 6845; **E**, Pi 7616; **F**, Pi 7617; **G**, **H**, Pi 7615; **I**, Pi 6847; **J**, Pi 6846; **K**, Pi 7608; **L**, LIG 35-900; **M**, LIG 35-901; **N**, LIG 35-902; **O**, Pi 7564; **P**, Pi 7560; **Q**, Pi 7562; **R**, Pi 7563; **S**, Pi 7562; **T**, Pi 7566; **A-K**, sample MF 11-1, Matusevich River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow; **L-N**, sample 5m-1, Pioneer Island; **O-T**, sample MF 157-4, Spokojnaya River, October Revolution Island, Ludlow, Upper Silurian. Scale bars: A-D, F, G, K, S, 0.1 mm; E, H-J, M-O, Q, R, T, 0.2 mm; L, P, 0.3 mm.

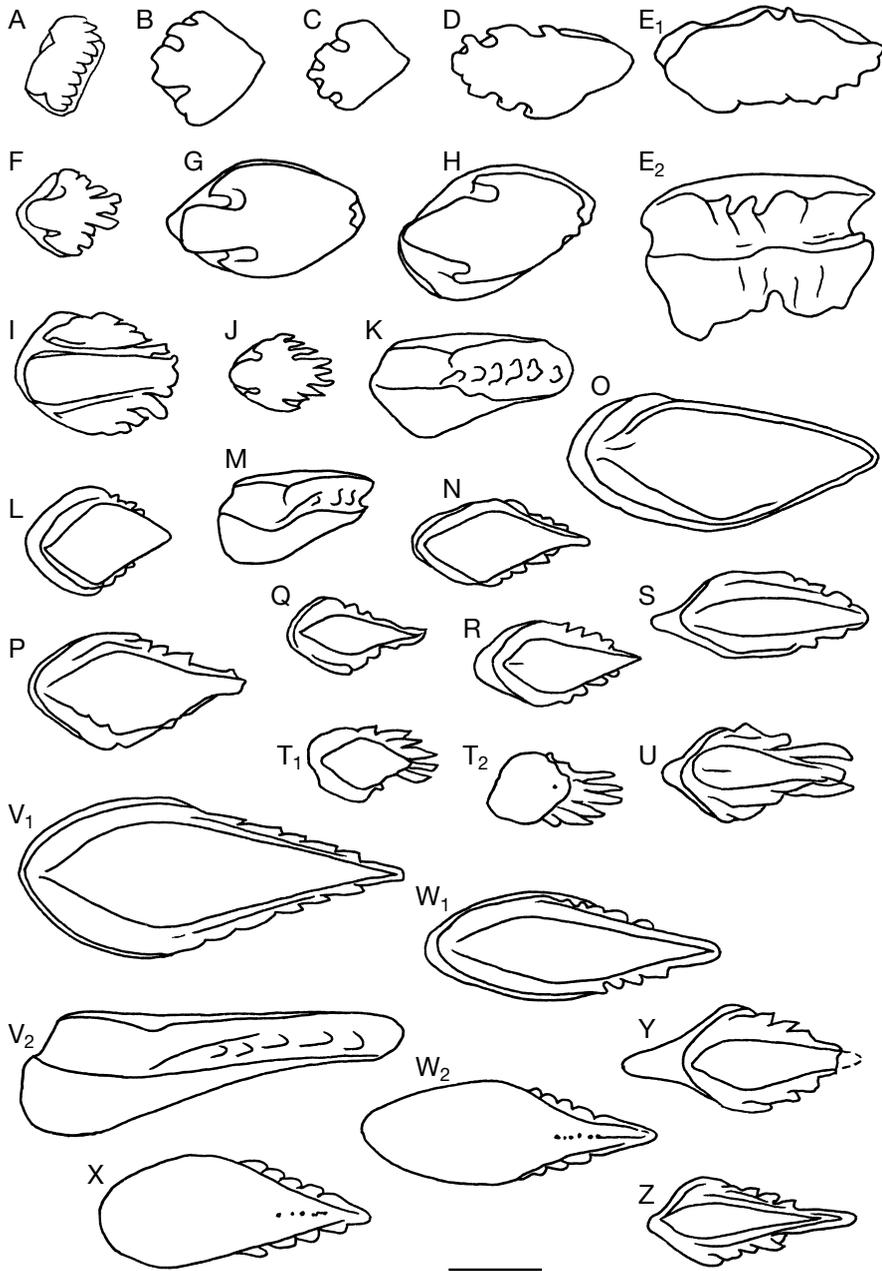


FIG. 4. — Set of scales of *Paralogania* ex gr. *martinssoni* (Gross, 1967); **A**, head scale; **B-J**, **O**, transitional scales; **K-N**, **P**, **R-Z**, trunk scales; **Q**, fin scale; **A-D**, **E₁**, **F-J**, **L**, **N-T₁**, **U**, **V₁**, **W₁**, **Y**, **Z**, scales in crown view; **E₂**, **K**, **M**, **V₂**, scales in lateral view; **T₂**, **W₂**, **X**, scales in base view; **A**, LIG 35-007; **B**, LIG 35-001; **C**, LIG 35-002; **D**, LIG 35-005; **E**, LIG 35-006; **F**, LIG 35-008; **G**, LIG 35-009; **H**, LIG 35-010; **I**, LIG 35-0013; **J**, LIG 35-031; **K**, LIG 35-016; **L**, LIG 35-017; **M**, LIG 35-014; **N**, LIG 35-021; **O**, LIG 35-012; **P**, LIG 35-023; **Q**, LIG 35-024; **R**, LIG 35-022; **S**, LIG 35-025; **T**, LIG 35-019; **U**, LIG 35-018; **V**, LIG 35-028; **W**, LIG 35-029; **X**, LIG 35-030; **Y**, LIG 35-033; **Z**, LIG 35-032; **A-I**, **K-W**, sample 8d-1, Pioneer Island, Ludlow, Upper Silurian; **J**, **X-Z**, sample 5m-1, Pioneer Island, Ludlow, Upper Silurian. Scale bar: 0.5 mm.

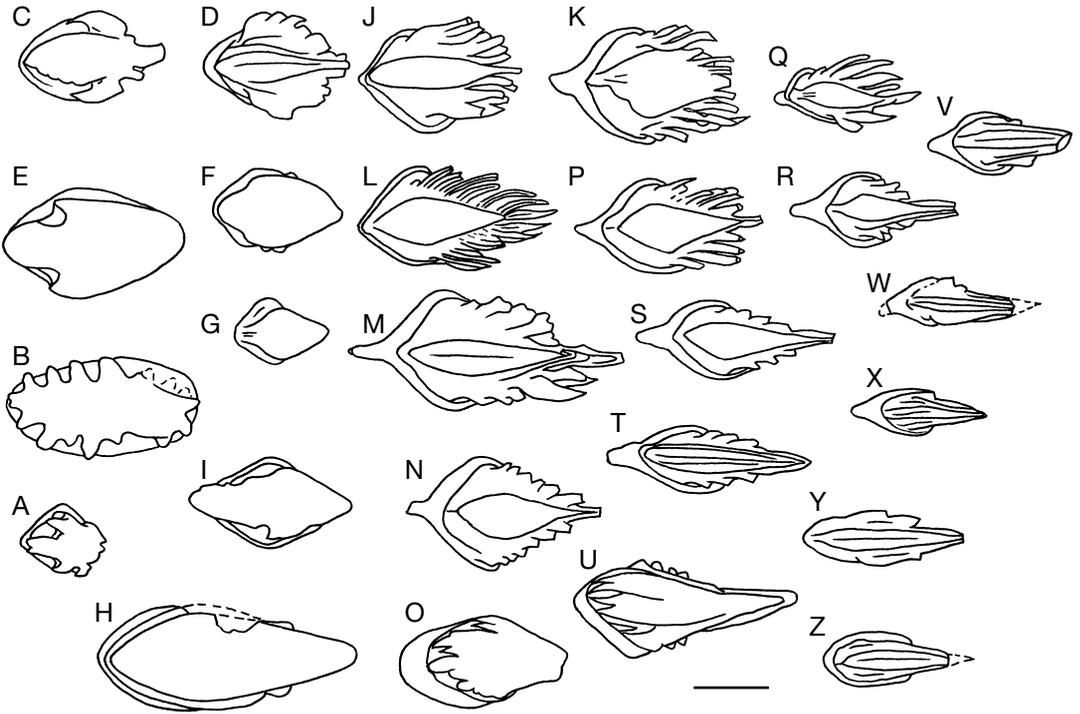


FIG. 5. — Set of scales of *Paralogania* ex gr. *martinssoni* (Gross, 1967); **A, B**, head scales; **C-I, O**, transitional scales; **J-N, P-U**, trunk scales; **V-Z**, fin scales; **A**, Pi 5605; **B**, Pi 5590; **C**, Pi 5607; **D**, Pi 5609; **E**, Pi 5611; **F**, Pi 5613; **G**, Pi 5617; **H**, Pi 5595; **I**, Pi 5591; **J**, Pi 5604; **K**, Pi 6772; **L**, Pi 5588; **M**, Pi 5606; **N**, Pi 5601; **O**, Pi 5600; **P**, Pi 6773; **Q**, Pi 6775; **R**, Pi 6776; **S**, Pi 6774; **T**, Pi 5612; **U**, Pi 5614; **V**, Pi 6779; **W**, Pi 5949; **X**, Pi 6777; **Y**, Pi 6778; **Z**, Pi 5948; sample 2055 zh, Pioneer Island, upper part of Ludlow, Upper Silurian (drawings after Märss 1986b: fig. 14). Scale bar: 0.5 mm.

varieties of scales is the sample 14-47 from the Spokojnaya River, October Revolution Island.

TYPE LOCALITY AND AGE. — Samples 47-14, Spokojnaya River, October Revolution Island, Severnaya Zemlya Archipelago, Ust-Spokojnaya Formation, Ludlow, Upper Silurian; 18041-14, Komsomolets Island, Ludlow, Upper Silurian.

DIAGNOSIS. — Head scales rounded or oval with crenulated margins. The length of the scales is between 0.3-0.9 mm. Transitional scales are of two morphological types. Type “A” has characteristic for loganelliid scales. They have rhomboidal or oval crowns with deep notches anteriorly, and with one or several projections (spines) of the posterior margin. The length of the scales represents 0.4-0.8 mm. Among type “B”, the scale crowns have a posterior median spine. In some of such scales the spine can be relatively long, e.g., if the average length of the scales is 0.6-0.8 mm then with the spine it can reach 1.1 mm. The crown is anteriorly wide, rhomboidal or rounded, with a

median and one to three lateral areas. The surface of the medial area is smooth and that of the spine is finely striated. Some trunk scales have short rhomboidal crowns with a smooth medial area, and with short base (length 0.5-0.75 mm); postero-laterally of the crown is situated one row of short spines four to five in number, and instead of a posterior spine a longitudinal ridge is present. The main part of trunk scales consists of scales with long (length up to 1.7 mm) but narrow crown and relatively short base, wide in the central part. A lot of scales are with spur-like projection anteriorly of the base. Posteriorly the crowns of many scales are longitudinally finely striated. Histology typical for *Paralogania*.

DESCRIPTION

Morphology

Head scales small (0.3-0.5 mm), oval, rarely rounded, with finely crenulated crown margins (Fig. 8A, B). Larger scales, with length up to

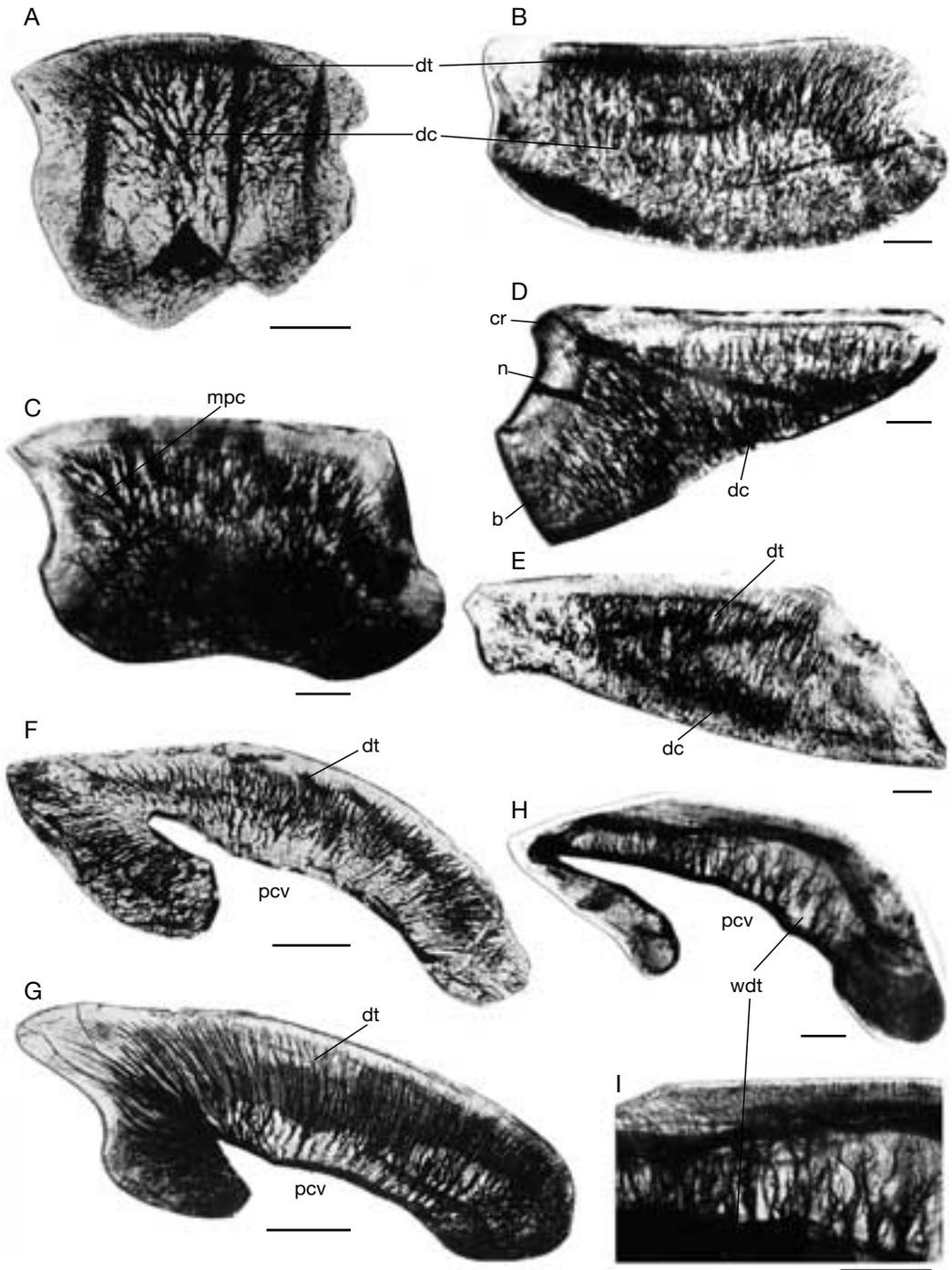


FIG. 6. — Microstructure of the scales; **A-E**, *Paralogania* ex gr. *martinsoni* (Gross, 1967); **F, G**, *Thelodus* sp. indet.; **H, I**, *Lanarkia*? sp.; **A**, Pi 6378; **B**, Pi 6362; **C**, Pi 6370; **D**, Pi 6368; **E**, Pi 6446; **F**, Pi 6377; **G**, Pi 6373; **H, I**, Pi 6371; sample 2055 zh, Pioneer Island, upper part of Ludlow, Upper Silurian. Abbreviations: **b**, base; **cr**, crown; **dc**, dentine canal; **dt**, dentine tubules; **mpc**, main pulp canal; **n**, neck; **pcv**, pulp cavity; **wdt**, wide dentine tubules. Scale bars: 0.1 mm.

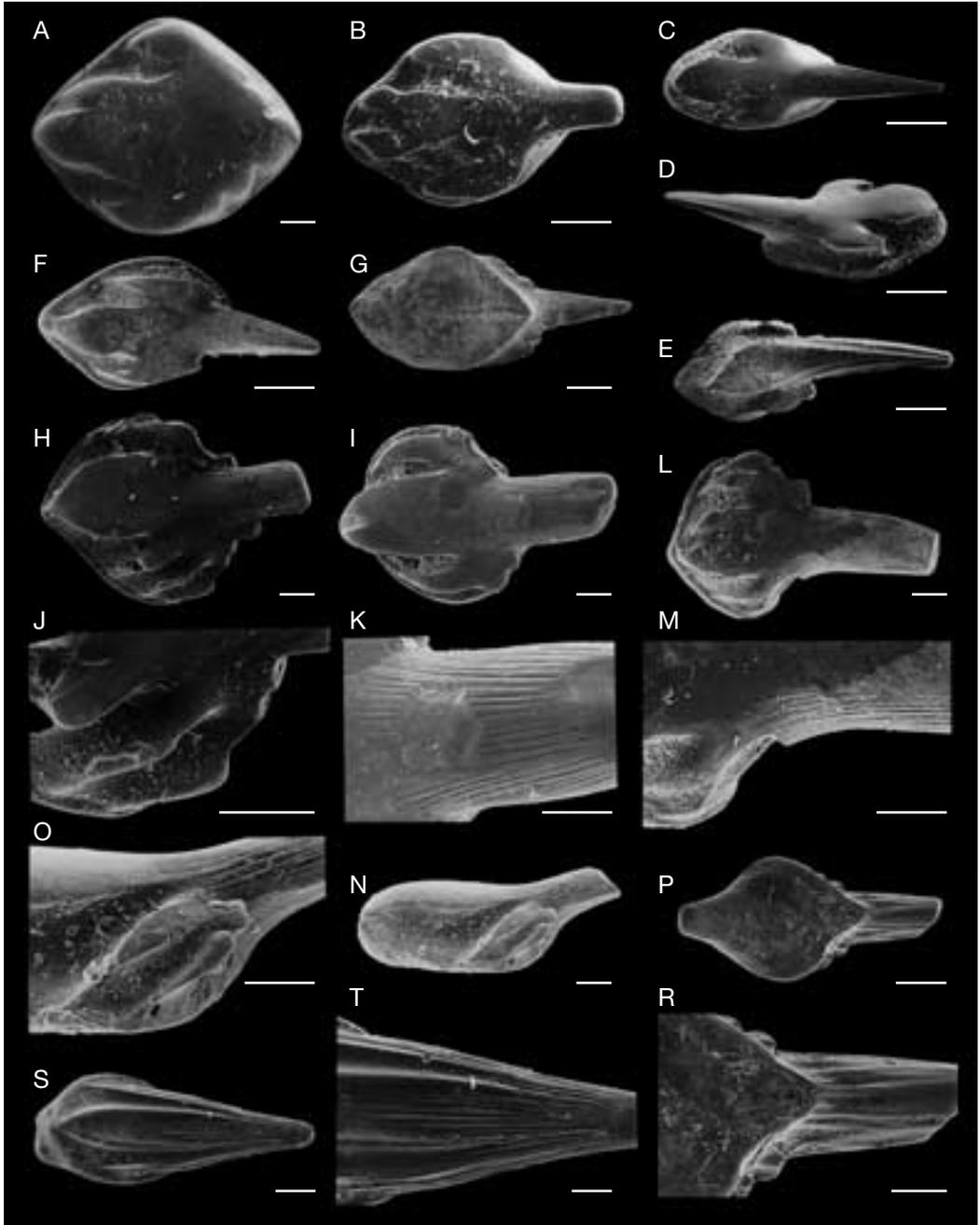


FIG. 7. — *Paralogania menneri* n. sp.; **A**, transitional scale; **B-O**, transitional(?) scales; **P-T**, trunk scales; **A-C**, **E**, **F**, **H**, **J**, **L**, **S**, scales in crown view; **D**, a scale in oblique lateral view (posterior end on the left); **G**, **P**, scales in base view; **N**, a scale in lateral view; **I**, magnified of **H**; **K**, magnified of **J**; **M**, magnified of **L**; **O**, magnified of **N**; **R**, magnified of **P**; **T**, magnified of **S**; **A**, Pi 7618; **B**, Pi 7607; **C**, **D**, Pi 7605; **E**, Pi 7604; **F**, LIG 35-871; **G**, LIG 35-872; **H**, **I**, LIG 35-877; **J**, **K**, holotype, LIG 35-878; **L**, **M**, LIG 35-879; **N**, **O**, LIG 35-880; **P**, **R**, LIG 35-881; **S**, **T**, LIG 35-882; **A-E**, sample MF 11-1, Matusevich River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow; **F**, **G**, sample 18041-14, Komsomolets Island, Ludlow; **H**, **J**, **L**, **N**, **P**, **S**, sample 47-14, Spokojnaya River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. Scale bars: **A**, **H-O**, **R**, **T**, 0.1 mm; **B-G**, **P**, **S**, 0.2 mm.

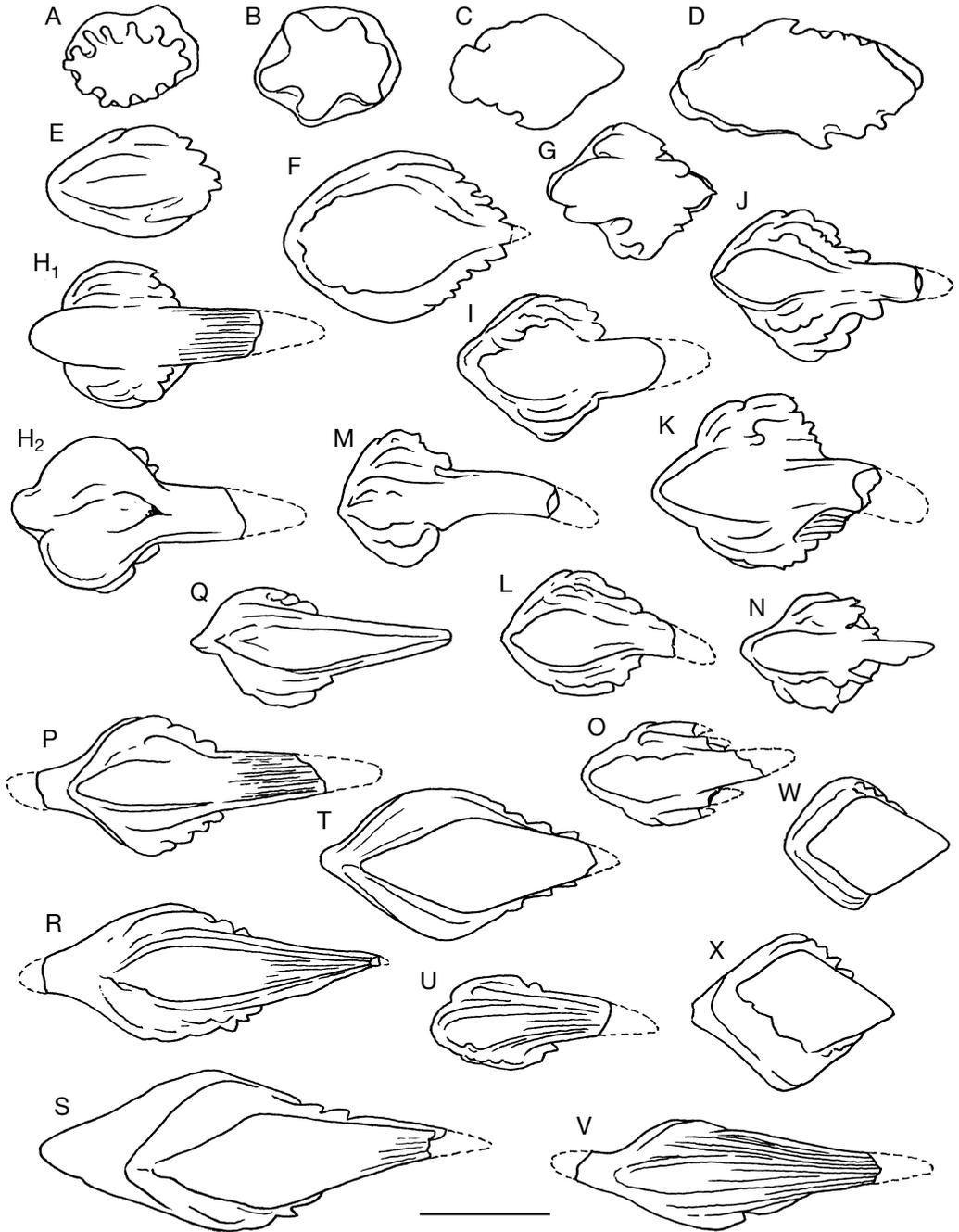


FIG. 8. — *Paralogania menneri* n. sp., morphological set of scales; **A, B**, head scales; **C-G**, transitional scales; **H-O**, transitional(?) scales; **P-X**, trunk scales; **A-H₁**, **I-X**, scales in crown view; **H₂**, a scale in base view; **A-X**, LIG 35-194-LIG 35-217; sample 47-14, Spokojnaya River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. Scale bar: 0.5 mm.

0.9 mm are rare. The base can be rather high and have small vertical rootlets. Pulp cavity in such scales is deep and opens in the centre of the base. Transitional scales have been divided into two morphological types. Type "A" consists of typical loganelliid scales with oval or rhomboidal smooth flat crown surface and shallow notches on the margins (Fig. 8C, D); the posterior part of them is tapering posteriorly into keel-like end, or their crowns have deep notches antero-laterally that divide the crown into medial and lateral areas (Figs 7A; 8E, H). Lateral areas (1-2) are relatively shorter than the medial one. The posterior crown margin bears several projections. The length of the scales of type "A" is usually less than 0.6 mm. In larger scales, with a length of about 0.8 mm, the wide and smooth central crown plate (Fig. 8F) is developed, and narrow lateral areas carry four to five short lateral spines. The base is low and a little wider than the crown. Transitional(?) scales of the morphological type "B" (Figs 7B-O; 8H-O) are particularly characteristic for the squamation of *P. menneri* n. sp. The main feature is the presence of a median posterior spine (strongly elongated central crown area) which can reach the length of the anterior, main crown part. The length of transitional(?) scales with a short spine is 0.6-0.8 mm (the length of the spine 0.15-0.25 mm) and that with a long spine is up to 1.1 mm (length of the spine 0.3-0.55 mm). The short medial spine is straight and horizontal, on the same plane as remaining crown plate. The longer spines arise posteriorly, sometimes laterally. The tips of long spines are usually broken; in well preserved scales they are sharp and long (Fig. 7C, D, F, G). Upper surface of the spine is covered with fine longitudinal striation (Fig. 7F, H, J-O), lower surface of it is usually smooth (Fig. 7G). The crown of transitional(?) scales of type "A" is rhomboidal or rounded and is divided into central and lateral areas separated by deep longitudinal notches anteriorly; its width reaches 0.45-0.6 mm. Sometimes the central area is situated far forward (Fig. 7J). The upper surface of the crown is smooth or with a short medial furrow (Fig. 7B, J, L). Laterally there can be one pair

(Fig. 7C, D, F, J), two pairs (Fig. 7O, N) or three pairs (Fig. 7H, I) of lateral areas. They are always shorter than the medial one; their margins are smooth or crenulated. Especially distinct crenulation or spines are developed on the outer margin of the most lateral area. The base which is relatively low is anteriorly a little larger than the crown and protrudes over the perimeter of the crown as a narrow strip (e.g., Fig. 7B-D, F, H, J, L). Pulp depression is elongated or triangular (Figs 7G; 8H₂).

Trunk scales of different size and form compose more than a half of the whole scale material of this species. The best example is the sample 47-14 from Spokojnaya River section. Two distinct (extreme) morphological varieties have been distinguished: 1) short rhomboidal; and 2) long and narrow, often with a spur-like projection anteriorly of the base. Besides, there are a lot of scales which length and width proportions of the crown and base are transitional between these two varieties. In Figs 7E and 8P, Q some trunk scales are shown. A relatively wide anterior part of them consists of the central and lateral areas with three to four short marginal spinelets; a spur-like projection of the base is directed anteriorwards and downwards. Such scales have the position between transitional(?) and elongated trunk scales.

Short trunk scales are up to 0.5-0.75 mm long at base width of 0.4-0.55 mm (Fig. 8W, X). Their crown is composed from a rhomboidal flat smooth area; postero-laterally of it is situated a row of short spinulets, four to five in number. The base is wider than the crown and expanded anteriorly. Fig. 8T represents a comparatively long trunk scale (length 1.0 mm) that after its features can be situated between short and wide and long and narrow scale types. The number of lateral spines is the largest (five). Beneath the postero-medial point of the crown, a longitudinal medial ridgelet, analogous to the medial spine, is developed. It begins at the posterior end of the base and continues into the posterior crown apex.

Long and narrow trunk scales reach a length up to 1.7 mm. Among them also a lot of fine and

narrow scales, still having the same proportions of the crown and base, characteristic of the relatively larger scales, have been found (Figs 7P, S; 8R, S, V). The central area of the crown is as elongated rhomb, relatively wide and flat (Fig. 8R, S) or narrow and with a furrow (Figs 7S; 8V). Postero-laterally of the crown, a row of three to four short lateral spinulets (Fig. 8S), a longitudinal ridge and a row of spinulets (Fig. 8R) or two to three longitudinal ridges (Figs 7S; 8V) can be found. The posterior part of the crown is covered with fine striation. On the lower surface a fine medial longitudinal ridge (analogous to the medial spine) is always present (Fig. 7P, R). The remaining surface is covered with longitudinal ridgelets or is smooth. The base of a number of elongated trunk scales is rhomboidal, wider than the crown and often prolonged anteriorly as a spur's shape; it can be relatively wide (Fig. 8S) or narrow (Figs 7P; 8R, V). The pulp depression is narrow and long. In many scales the pulp opening is large and situated in the posterior corner of the base.

Histology

The microstructure of the scales has been studied under anise oil immersion. Arrangement, form and width of dentine tubules are as in *Paralogania* ex gr. *martinssoni* from the Ludlow deposits of Severnaya Zemlya (Karatajūtė-Talimaa 1997: fig. 9A, B). The main pulp canal is wide and long in elongated trunk scales of *P. menneri* n. sp., and short and narrow in short trunk scales (see Karatajūtė-Talimaa 1997: fig. 9C, D). Lateral pulp canals, going into lateral spines, are not always developed.

COMPARISON

Paralogania menneri n. sp. can be attributed to the *P. kummerowi*-*P. martinssoni* group after the number and disposition of the postero-lateral spines of the trunk scales crown. Medial spine, being distinct and relatively long (or high as in *P. kachanovi* n. sp.) in the other representatives of this group, is modified in *P. menneri* n. sp. into a medial longitudinal ridgelet. Presence of special transitional(?) scales in the morphological variety

set of scales of *P. menneri* n. sp. distinguishes this species from the others of the genus. Perhaps, one characteristic is the fine longitudinal striation of the crown present only for the transitional(?) and most of the elongated trunk scales of *P. menneri* n. sp. On the scales of the closest species, *P. martinssoni*, the striation is not present. Some morphological varieties of the scales of *P. menneri* n. sp., e.g., head scales, transitional scales of type "A" and part of trunk scales (with short, rhomboidal and relatively elongated and flat crown) are present also in the morphological set of *P. martinssoni* and *P. ex gr. martinssoni*. Still, the lateral spines in trunk scales of *P. menneri* n. sp. are always short while in *P. martinssoni* they can reach a noticeable length.

Paralogania wilsoni n. sp. (Figs 9; 10)

Paralogania sp. 2 Märss & Karajūtė-Talimaa 2002: fig. 1.
HOLOTYPE. — Scale Pi 7598 (Fig. 9M).

ETYMOLOGY. — Named in honour of Dr. M. V. H. Wilson, Edmonton, Alberta University, a Furcacaudiform researcher.

TYPE LOCALITY AND AGE. — Sample MF 157-2, Spokojnaya River, October Revolution Island, Severnaya Zemlya Archipelago, Krasnaya Bukhta Formation, Pridoli, Upper Silurian.

MATERIAL EXAMINED. — Over 300 scales, relatively well preserved.

DIAGNOSIS. — Head scales with crenulated margins and a convex crown surface. Transitional scales have oak-leaf-like configuration and crown surface convex. Trunk scales anteriorly smooth in outline. Lateral portions of the crown are wide, medial crown plate smooth or with a very shallow longitudinal groove. There occur three to four proximally wide spines postero-laterally of the crown and one beneath the posterior crown apex. Dentine tubules very fine, hardly branching, and situated closely to each other. They do not form lacunae-like structures. Pulp canals present. Dentine canals start from the pulp canal. Aspentine layer in the base is thin.

DESCRIPTION

Morphology

There is only a few head scales in our collection (Fig. 9A). They are small (length 0.6 mm and width 0.4 mm). Their crown margins are crenulated anteriorly and serrated posteriorly; their

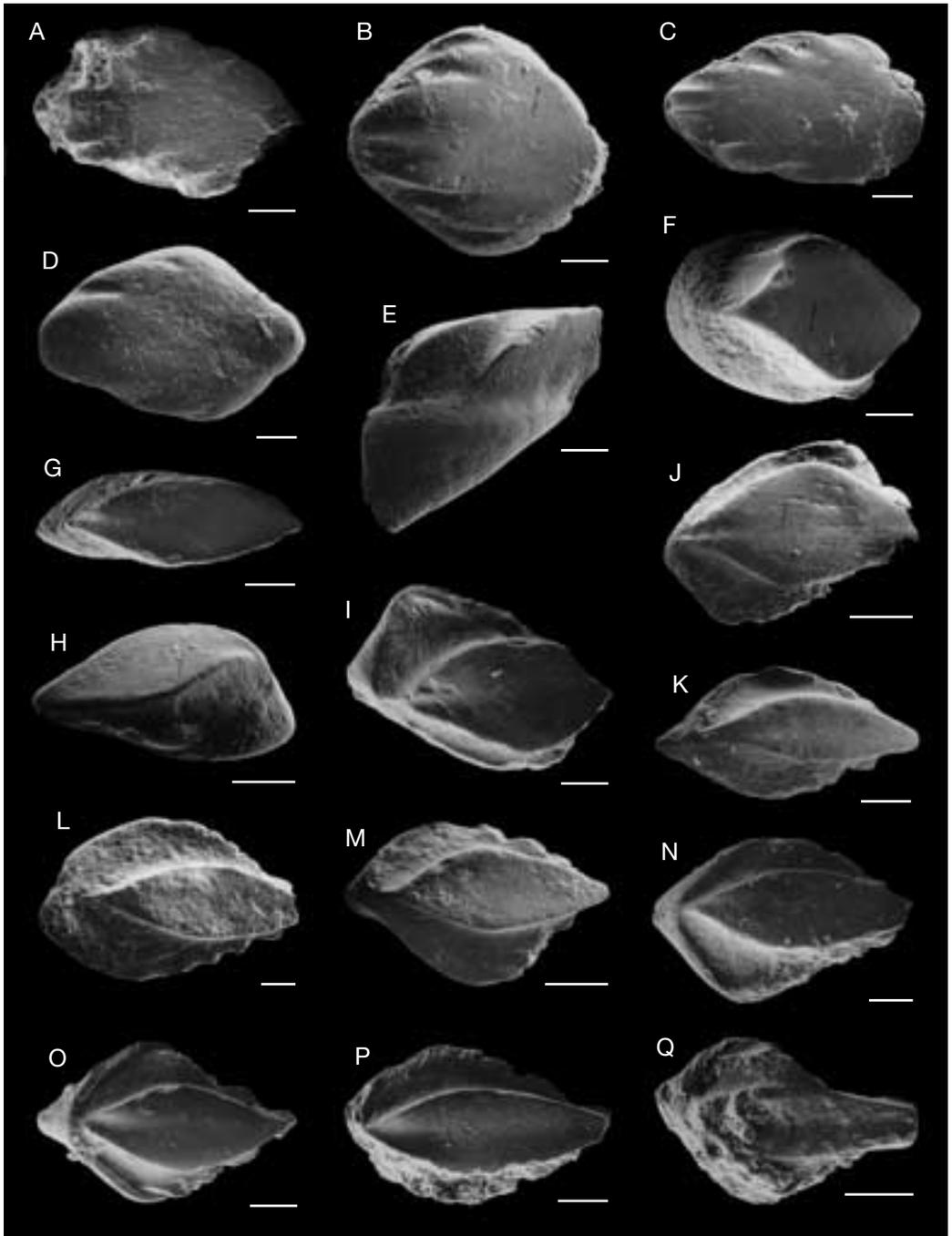


FIG. 9. — *Paralogania wilsoni* n. sp.; **A**, head scale; **B-D**, transitional scales; **E-H**, most probably the scales of leading edges of the fins; **I-P**, trunk scales; **Q**, a fin scale; **A-D**, **F**, **G**, **I-Q**, the scales in crown view; **E**, **H**, the scales in lateral view; **A**, Pi 7603; **B**, Pi 7594; **C**, Pi 7596; **D**, Pi 7601; **E**, Pi 7593; **F**, Pi 7591; **G**, Pi 7597; **H**, Pi 7602; **I**, Pi 7592; **J**, Pi 7599; **K**, Pi 7600; **L**, Pi 7595; **M**, holotype, Pi 7598; **N**, Pi 7590; **O**, Pi 7589; **P**, Pi 7587; **Q**, Pi 7588; sample MF 157-2, Spokojnaya River, October Revolution Island, Krasnaya Bukhta Formation, Pridoli, Upper Silurian. Scale bars: A-F, I, L, N-Q, 0.1 mm; G, H, J, K, M, 0.2 mm.

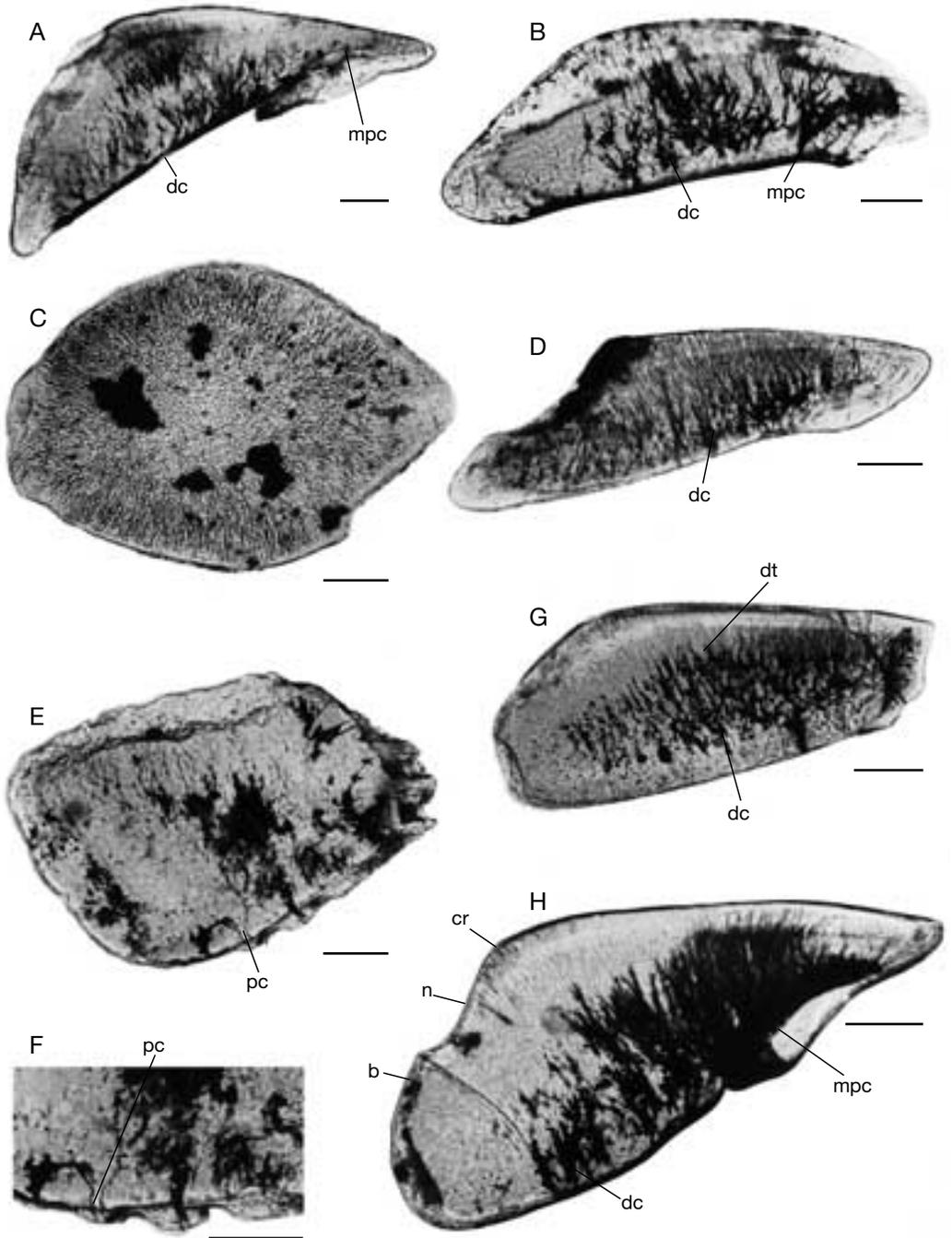


FIG. 10. — *Paralagonia wilsoni* n. sp., microstructure of the scales; **A**, Pi 7637; **B**, Pi 7638; **C**, Pi 7639; **D**, Pi 7640; **E**, **F**, Pi 7641; **G**, Pi 7642; **H**, Pi 7643; sample 157-2, Spokojnaya River, October Revolution Island, Krasnaya Bukhta Formation, Pridoli, Upper Silurian. Abbreviations: **b**, base; **cr**, crown; **dc**, dentine canal; **dt**, dentine tubules; **n**, neck; **mpc**, main pulp canal; **pc**, lateral pulp canal. Scale bars: 0.1 mm.

crown surface is slightly convex. Transitional scales (Fig. 9B-D) are 0.6-0.7 mm long, 0.4-0.6 mm wide and around 0.4 mm high. Antero-lateral notches give the scales an oak-leaf-like shape. Postero-lateral downstepped margins are slightly serrated. Base is convex in mature scales. Trunk scales (Fig. 9I-P) with length of 0.6-1.0 mm and width of 0.4-1.0 mm (holotype is 0.8 mm long and 0.5 mm wide) have slightly convex or flat smooth medial crown plate, or it can also carry a shallow longitudinal furrow. Lateral crown portions are rather wide and end posteriorly with three or four spines. The latter are rarely preserved. Trunk scales are flattened, their base has spur-like projection directed anteriorly downwards. Pulp depression is situated posteriorly in the base.

Scales with smooth flat crown plate that can have notches antero-laterally and a base high anteriorly and fading out posteriorly (Fig. 9E-H) originate from the leading fin edges. Small scales (length 0.3-0.5 mm and width 0.1-0.3 mm) probably originate from the posterior fin edges. There are two types of very small scales: with a medial crown plate and lateral portions (Fig. 9Q), or with a smooth plate only. The last ones might be scales covering the trunk: they just become small but retain the same characteristic features as trunk scales, and so do the fin scales.

Histology

Pulp canals, one main and three pairs of lateral ones, distinct (Fig. 10B, D, G, H). Main or medial pulp canal are comparatively wide, the lateral ones slightly narrower. They enter into the posterior spines (Fig. 10E, F). Dentine canals arise from the pulp canals and from the pulp depression. In the upper part of the crown they are fine, comparatively straight, in the lower part, branching and widened (Fig. 10B, D, G). Dentine tubules are very fine (Fig. 10A, C). Light thin surface layer of the crown contains numerous straight dentine tubules (Fig. 10H).

COMPARISON

Paralogania wilsoni n. sp. differs from the other species of this genus in having wide lateral por-

tions of the crown of trunk scales and, anteriorly, smoothly rounded transitional scales of oak-leaf-like outline of the crown. The scales lack a rib above the spines which is present in *P. consimilis* and *P. ludlowiensis*. *P. wilsoni* n. sp., *P. consimilis*, *P. martinsoni* and *P. kummerowi* all have only one spine beneath the posterior crown apex while *P. ludlowiensis* has two parallel spines. The head and anterior transitional scales of *P. ludlowiensis* and *P. wilsoni* n. sp. strongly differ, the former species having here a "traquairi"-type of scales on the head and trilobiform scales on the transitional body area.

Paralogania kachanovi n. sp.

(Fig. 11)

Paralogania sp. 3 Mårss & Karajütë-Talimaa 2002: fig. 1.

HOLOTYPE. — LIG 35-051, trunk scale (Fig. 11L).

ETYMOLOGY. — Named in honour of late E. I. Kachanov, Magadan, Russia, who studied the Silurian deposits on the Pioneer Island.

TYPE LOCALITY AND AGE. — Sample 12, Pridoli, Upper Silurian, Pioneer Island, Severnaya Zemlya Archipelago (see Fig. 1).

MATERIAL EXAMINED. — Over 200 scales of relatively good preservation but pyritized.

DIAGNOSIS. — Medium-sized scales (0.9-1.3 mm long). Crown margins of the head scales crenulated, crown surface flat and smooth. In the transitional scales the antero-medial crown portion separated from the lateral ones; posterior crown margin notched, crown surface flat. Trunk scales rhomboidal with one wide flat central area on the crown. Postero-lateral crown walls bear a row of six to eight spines on each side and one spine beneath the posterior crown apex. Spines are short and low, directed upwards. Posterior crown portion of smaller scales may have shallow medial groove. A short pulp canal is developed in trunk scales.

DESCRIPTION

Morphology

Head scales oval, rounded, rhomboidal, elongated and in rare cases widened (Fig. 11A-E). Asymmetric, elongated and comparatively big scales have also been found. The length of the head scales 0.5-0.9 mm, rarely up to 1.2-1.3 mm, width 0.4-0.8 mm and height 0.35-0.55 mm. Anterior crown area is distinguishable in almost

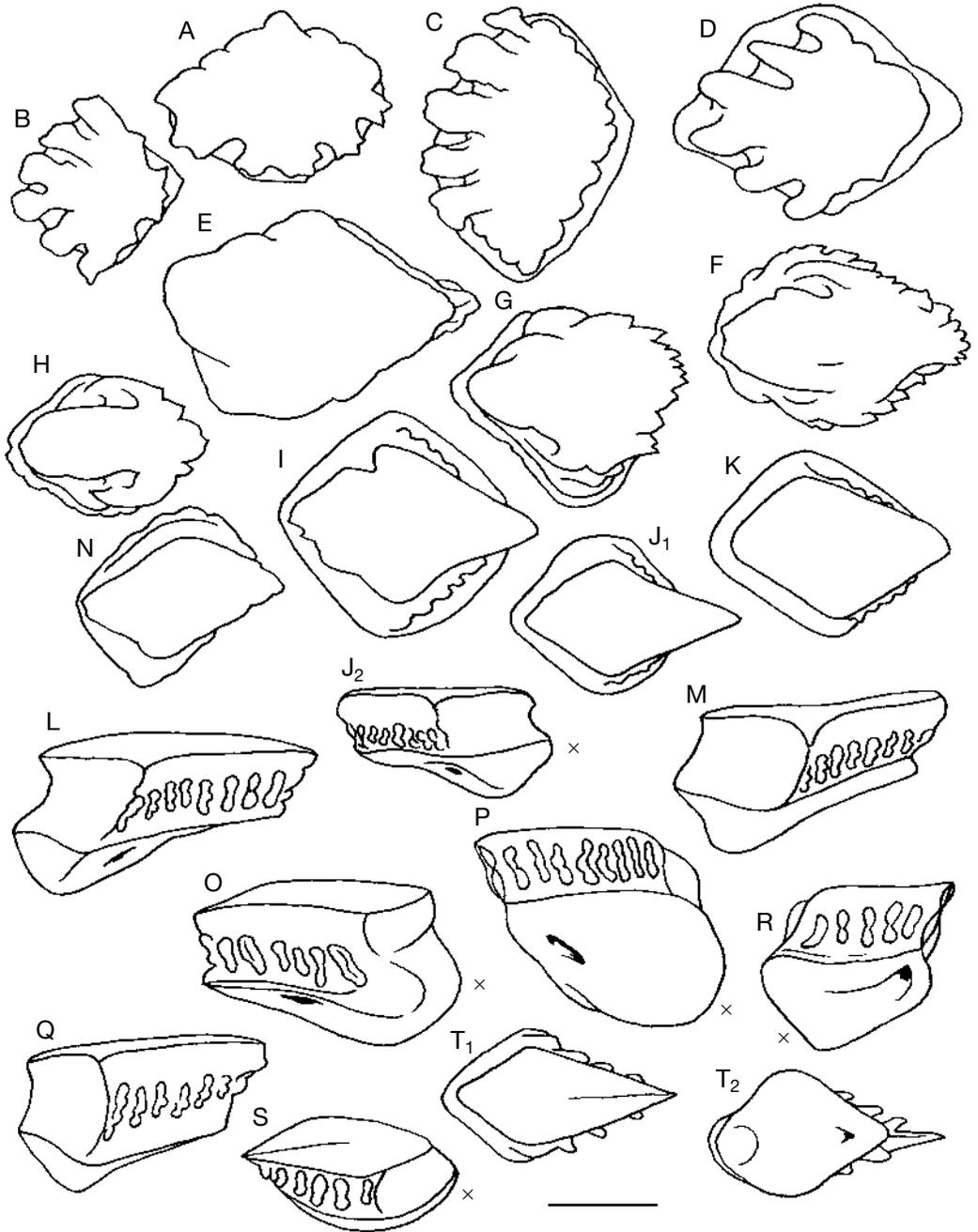


FIG. 11. — *Paralogania kachanovi* n. sp., morphological set of the scales; A-E, head scales; F-H, transitional scales; I-T, trunk scales; L, holotype; A-I, J₁, K, N, T₁, scales in crown view; J₂, L, M, O, Q, scales in lateral view; T₂, scale in base view; P, R, scales in oblique postero-lateral view; S, scale in oblique lateral view; "x" shows the anterior part of the scale; A-K, LIG 35-039-LIG 35-049; L, LIG 35-050; M-P, LIG 35-051-LIG 35-054; Q-T, LIG 35-873-LIG 35-876; sample 12, Pioneer Island, Pridoli, Upper Silurian. Scale bar: 0.3 mm.

all scales. Crown is comparatively monolithic, with flat surface, margins with deep crenulation, especially antero-laterally (Fig. 11B-D). Base is rather large and can extend beyond the perimeter of the crown. Juvenile scales with low base have a large but shallow pulp depression.

Transitional scales (Fig. 11F-H) are oval to rhomboidal. Their length can reach 0.75-0.9 mm, width 0.4-0.6 mm and height up to 0.4 mm. Crown is comparatively monolithic, with flat surface of antero-medial area and crenulated postero-lateral margins. Lateral areas of the crown are not always distinct. Base is sometimes wider than crown (Fig. 11G).

Trunk scales are rhomboidal with shortened anterior and elongated keel-like posterior areas (Fig. 11I-T). Length of the crown 0.5-0.9 mm, width 0.4-0.75 mm, height is rather constant: 0.3-0.5 mm. Height of the base is usually smaller than that of the crown. The crown of trunk scales is monolithic and composed of a smooth and flat central area with smooth margins. Antero-lateral areas of the crown (neck) are separated from the postero-lateral ones with a distinct vertical ridge. Postero-lateral crown walls bear spines, six to eight on each side, and one spine under the posterior crown apex. Spines are situated in longitudinal rows. Spines are low, directed upwards and are formed from several apices on a fused base. In Fig. 11L is drawn the scale chosen as the holotype. Its length is 0.8 mm, width 0.65 mm and height 0.35 mm: its number of spines is eight; beneath the posterior crown point the medial spine is composed of two rounded apices. Base of trunk scales is slightly shifted forwardly. The most protruding part of the base is situated anteriorly from the pulp opening. Scales with spur-like projection of the base have not been found. Triangular pulp depression is placed at the posterior corner of the base (Fig. 11P, R, T₂). Pulp opening is well defined in scales of all stages of development.

Small scales (Fig. 11S, T_{1,2}) having a narrow medial fine groove on the posterior crown surface and less lateral spines (four to six) are also present in the samples.

Histology

Short pulp canal of trunk scales distinct. Dentine tubules rather wide.

COMPARISON

P. kachanovi n. sp. scales differ from the other species of the genus in having a monolithic crown and in lacking the lateral areas of the crown on trunk scales. General proportions and flat smooth crown of trunk scales of Severnaya Zemlya species show similarity with *P. borealis* from the Pridoli of North Timan. Composition of lateral spines, their form and length/height is a unique characteristic of *P. kachanovi* n. sp. A large number of spines (up to eight) is also observed in *P. kummerowi* and *P. borealis*. *P. kachanovi* n. sp. differs from *P. wilsoni* n. sp. in its larger size, the form and width of the medial area of the crown, the number and form of lateral spines and also the form of its base (lacking the spur-like projection). *P. kachanovi* n. sp. can be attributed to the *P. kummerowi*-*P. martinsoni* group because they all have a medial spine beneath the posterior crown apex.

Paralogania sp. cf. *Paralogania borealis* (Karatajūtė-Talimaa, 1978)

DESCRIPTION AND COMMENTS

A sample from the outcrop 41, bed 1, has yielded about 20 predominantly trunk scales which crowns resembling very much the trunk scales of *Paralogania borealis* from the Eptarma Formation of North Timan (Karatajūtė-Talimaa 1978: 92-94). Together with them scales of *Goniporus alatus* and *Nikolivia elongata* are also represented. The composition of the assemblage with its lack of *Thelodus* scales and occurrence of *Nikolivia elongata* testify a completeness of the Silurian-Devonian boundary section in the Krasnaya Bay area.

In the deposits of Krasnaya Bukhta (*bukhta* means bay in Russian) Formation on October Revolution Island and its analogues on Pioneer Island, three thelodont assemblages characterize different levels of the Pridoli. The first and oldest assemblage, established on Pioneer Island (sample 12) contains

P. kachanovi n. sp., *Loganellia cuneata* and *Thelodus parvidens*(?). The second assemblage is distributed on the higher level of the Krasnaya Bukhta Formation along the Spokojnaya River (sample 157-2 and a sample "a" from the outcrop 51a). This assemblage is composed of *Paralogania wilsoni* n. sp., *Loganellia cuneata* and *Goniporus alatus*. The third assemblage includes scales of the Late Silurian and Early Devonian thelodonts and characterizes the uppermost Pridoli (or transitional beds to the Lochkov, Early Devonian in age?).

Genus *Valiukia* n. gen.

TYPE SPECIES. — *Valiukia flabellata* n. gen., n. sp. (by monotypy).

ETYMOLOGY. — Named after Dr. Juozas Valiukevičius (Vilnius), a member of the field expedition to October Revolution Island in 1978.

OCCURRENCE. — Matusевич River, October Revolution Island, Severnaya Zemlya Archipelago, Ust-Spokojnaya Formation, Ludlow, Upper Silurian.

DIAGNOSIS. — As for species.

REMARKS

The scales figured in Märss & Karatajūtė-Talimaa 2002: figs 8I-L; 9E, referred to Loganelliidae gen. et sp. indet., belong to *Valiukia* n. gen.

COMPARISON

Morphological set of scales of genus *Valiukia* n. gen. differs from those of other genera of the family Loganelliidae (*Loganellia*, *Paralogania*, *Shielia* Märss, 1998) distributed in the Wenlock and Ludlow of Severnaya Zemlya Archipelago in several features; the most important lies on the crown structure of the transitional and trunk scales. Numerous longitudinal areas and spines are developed in the posterior part of the crown. Exclusive to *Valiukia* n. gen. they are not analogous to the postero-lateral spines of the crown of trunk scales of *Paralogania*. Some similarities can be found with the structure of the posterior part of the ridged crown of trunk scales of *Shielia* (Märss & Ritchie 1998; Märss & Karatajūtė-Talimaa 2002). Transverse ridgelets between the main ridges of different crown areas of transi-

tional scales have not been observed in the scales of other genera. The structure of the base of trunk scales, the position of pulp opening and histological features (size and distribution of dentine tubules, presence of main and lateral pulp canals) are like in scales of the genus *Paralogania*.

Valiukia flabellata n. sp.

(Figs 12-15)

Valiukia sp. 1 Märss & Karajūtė-Talimaa 2002: fig. 1.

HOLOTYPE. — Trunk scale LIG 35-844 (Fig. 14A, B) and the same restored (Fig. 12G).

ETYMOLOGY. — From the Latin word *flabellata*: fan-shaped.

TYPE LOCALITY AND AGE. — Sample 2-23, Matusевич River, Ust-Spokojnaya Formation, Ludlow, Upper Silurian.

MATERIAL EXAMINED. — Over 170 scales of different preservation.

DIAGNOSIS. — Scales very small, 0.2-0.7 mm long. Head scales rounded, irregularly shaped, with low flat crown having deep marginal cuts. Transitional scales oval, rhomboidal, sometimes rather wide. Central area of the crown is distinct anteriorly or along all its length; one or two pairs of shorter lateral areas separated from the central one by deep grooves having transverse ridgelets; the crown is posteriorly multi-pointed. Some of small transitional scales have high neck and a base smaller than the crown. Trunk scales are the largest, elongated and rhomboidal or short and oval. The central area of the crown is rhomboidal and narrow, and higher than the remaining part of it. The lateral areas, two to three on each side, are separated from each other by longitudinal ridgelets which are more distinct on the crown surface posteriorly. Postero-lateral parts of the crown are made of the very narrow longitudinal posteriorly pointed spines. The medial spine is the longest. In comparatively wide oval scales the spines are long and distributed fan-wise. On the surface of longitudinal spines, fine longitudinal ridgelets of the sculpture are distributed. On the lower surface of the crown, the longitudinal spines are tightly joined to each other and only posteriorly they end independently. Usually the longitudinal spines are situated on different levels and cover partly the neighbouring ones. The base is low, placed anteriorly, sometimes with an anterior spur-like projection. The microstructure is of loganelliid type.

DESCRIPTION

Morphology

The morphology of head, transitional and trunk scales is very different. The head scales are very

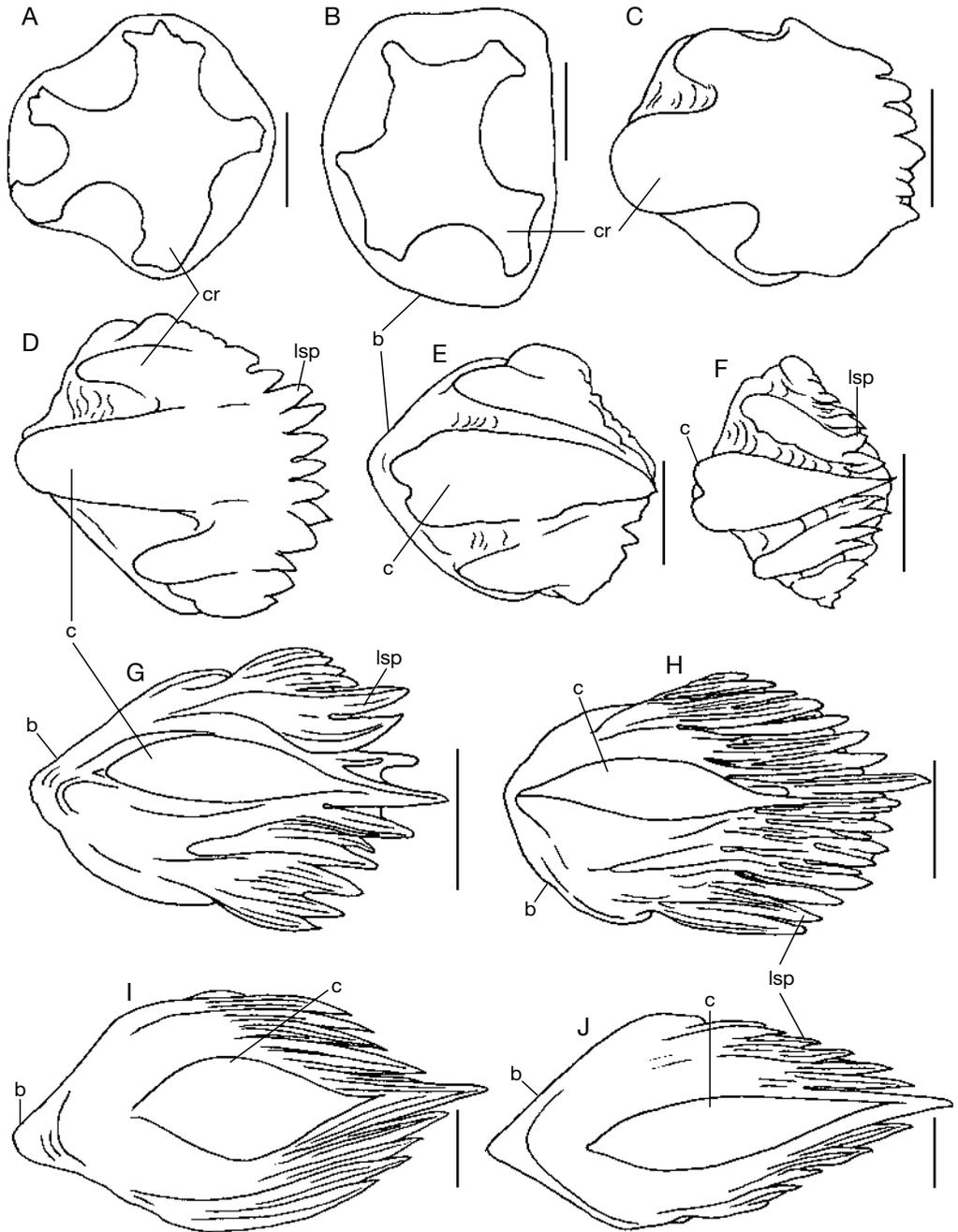


FIG. 12. — *Valiukia flabellata* n. gen., n. sp., morphological set of scales; **A, B**, head scales; **C-F**, transitional scales; **G-J**, trunk scales; posterior ends of the crown are restored; **G**, holotype, LIG 35-844 (see also Fig. 14A, B); **A-J**, LIG 35-838-LIG 35-847; sample 2-23, Matushevich River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. Abbreviations: **b**, base; **c**, central (medial) part of the crown; **cr**, crown; **lsp**, longitudinal spine of posterior part of the crown. Scale bars: 0.1 mm.

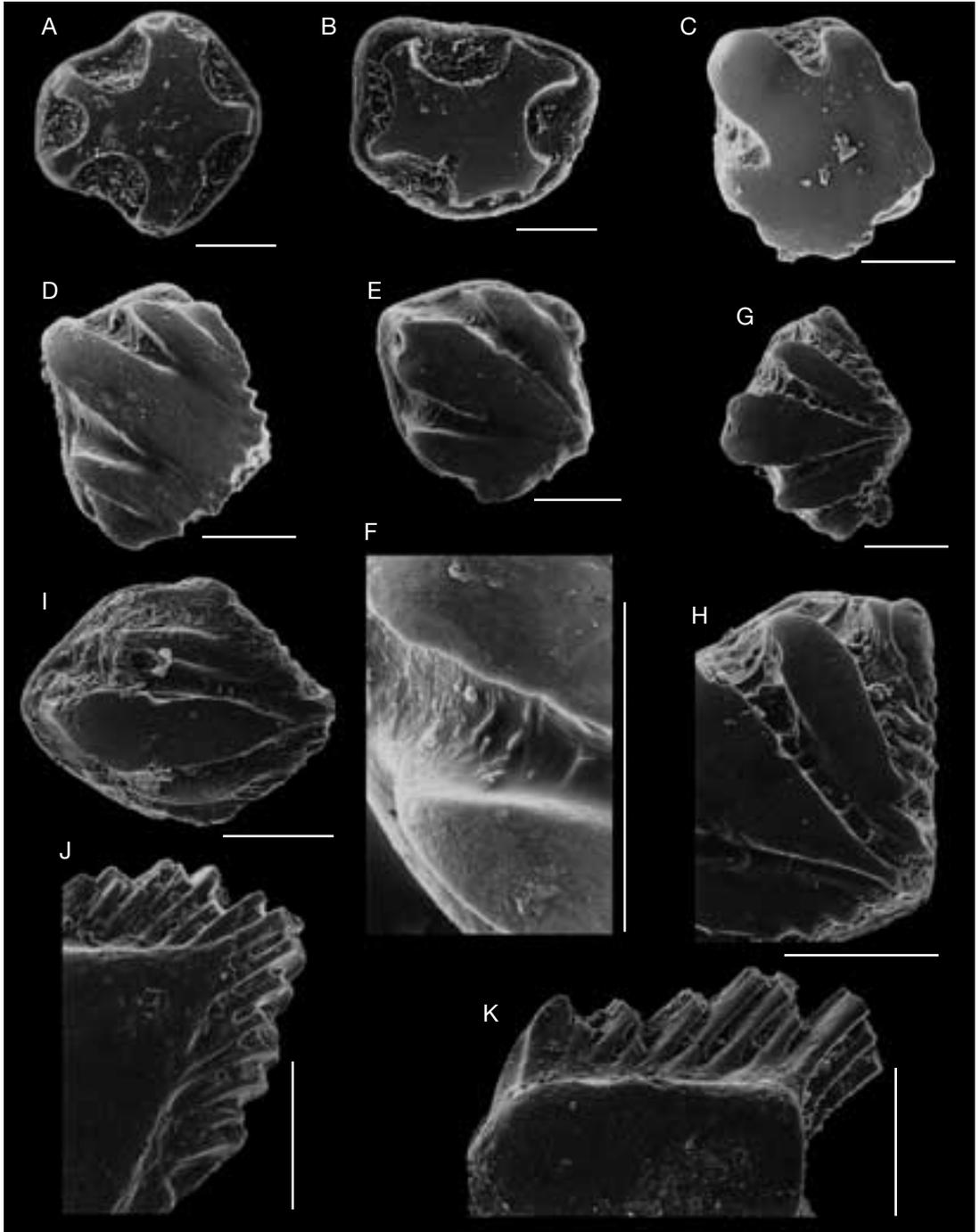


FIG. 13. — *Valiukia flabellata* n. gen., n. sp.; **A, B**, head scales; **C-H**, transitional scales; **I**, trunk(?) scale; **J, K**, posterior part of trunk scales; **A-E, G, I**, scales in crown view; **F**, magnified part of E; **H**, magnified part of G; **J, K**, scales in base view; **A-H**, LIG 35-838-LIG 35-843; **I-K**, LIG 35-848-LIG 35-850; sample 2-23, Matusevich River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. Scale bars: 0.1 mm.

small (0.2-0.3 mm in diameter), rounded, oval, sometimes of irregular shape. The crown is low, flat and with deep marginal crenulation (Figs 12A, B; 13A, B). The base is a little larger than the crown, slightly convex, and only seldom rather high. Transitional scales show some morphological varieties (Figs 12C-F; 13C-I).

In type "A" the central area of the crown is developed only in its anterior part (Figs 12C, D; 13C, D). The central area is separated from the lateral ones with deep longitudinal notches. The lateral areas, one to two on each side, are short, and separated from each other by shallow grooves. The crown surface is smooth and flat, and posterior crown margin multicuspidate. Some of the cusps are situated on the inferior level between those which are placed higher.

In type "B" the central area of the crown is completely separated from the shorter lateral areas by deep longitudinal grooves. Anteriorly of the central area is developed a shallow medial notch; posteriorly, this area is pointed and keel-like. The posterior margin of the crown multicuspidate and composed of several pointed spines (Figs 12F; 13G, H). Lateral areas are only partly (Figs 12E; 13E) or completely (Figs 12F; 13G, H) separated from each other. In several transitional scales of type "B" the crown is rather wide and rhomboidal.

In the deep grooves of both types, a peculiar morphological element, transverse ridgelets (see close-ups in Fig. 13F, G) are discovered in thelodonts for the first time. The base of the transitional scales is rhomboidal, not very high and slightly convex. Comparatively small pulp opening in the posterior corner of the base cannot always be observed. The neck of scales of type "B" is comparatively higher. The size of transitional scales is 0.2-0.35 mm but the small scales of type "B" can be even smaller than 0.1 mm.

In Fig. 13I, a transitional(?) scale with features rather similar to trunk scales is presented. The central area of its crown is narrow and higher than the rest of the scale surface like in trunk scales but the longitudinal spines on the postero-lateral part of the crown are short; in their

shape and size lateral areas of the crown are nearly the same as in transitional scales.

Trunk scales are comparatively larger and in rare cases can reach a length up to 0.65-0.7 mm, on average 0.3-0.55 mm (Figs 12G-J; 13J, K; 14). Most scales are oval to rhomboidal; they can be wide or narrow, with the crown posteriorly shifted. Central area of the crown is narrow, rhomboidal, with a flat smooth surface and separated from the lateral areas with a step being on a higher level than the remaining part of the crown. The anterior part of the central area is rather short; posterior part is pointed and can become like the medial longitudinal spine.

Among the trunk scales two morphological varieties have also been established. Type "A" contains the scales with relatively wide complicated fan-shaped crowns (Figs 12G, H; 14A-D) and type "B", the relatively narrow elongated crowns (Figs 12I, J; 14E-G, J-M).

In the crown of type "A" scales, the lateral areas, two to three on each side, are distinct. They are separated from the central area and each other by grooves. Posteriorly the crown is composed of numerous narrow longitudinal spine areas, a medial and 10 to 14 or more pairs of lateral ones. The spines are situated on different levels, some of them being on higher and some on lower levels, beneath the former. The surface of lateral areas of the crown is covered with longitudinal ridgelets that go over into the longitudinal spines. Type "A" corresponds to scales with long longitudinal fan-shaped spines. The posterior points of the spines end separately; sometimes the spine is independent along its whole length (see Fig. 12H). The base is relatively low and short, oval to rhomboidal. A relatively small pulp opening is situated in the posterior corner of it.

In the crown of type "B" trunk scales, the central area is strongly elevated when compared with remaining part of it. In Figs 12I and 14E, the same trunk scale with a rather wide crown, with oval-rhomboidal and rather wide and short central area is illustrated. In trunk scales from the posterior part of the body, the crown is elongated and its central area is narrow and

relatively high (Figs 12J; 14F, G, J, K). Lateral areas are separated from each other with ridges or furrows which are more distinct anteriorly. On the postero-lateral parts of the crown they disappear between the longitudinal ridges which become a longitudinal areas-spines. The medial spine is the longest, the lateral ones being shorter. The posterior points of the spines are usually broken. In Fig. 12 the length of all spines of the crown is restored. In type "B" trunk scales the longitudinal spines are tightly united to each other as seen in Fig. 13J, K, and only most posteriorly on the crown, they are separated. In Fig. 14L, M the scales with comparatively short longitudinal spines, five to six on each side, are presented.

Histology

The microstructure of the scales (Fig. 15A-C) has been studied using anise oil. In the crown of trunk scales the main pulp canal (mpc) and lateral branches of it, and also comparatively fine pulp canals (pc) are present. The latter go into the longitudinal spines and can be rather long (Fig. 15C). The shape and distribution of dentine tubules in the crown is similar to other loganellids.

Family KATOPORODONTIDAE
Märss, Wilson & Thorsteinsson, 2000

Genus *Phlebolepis* Pander, 1856

TYPE SPECIES. — *Phlebolepis elegans* Pander, 1856.

Phlebolepis elegans Pander, 1856
(Fig. 3O-T)

SYNONYMY. — See Turner (1976) and Märss (1986b).

MATERIAL EXAMINED. — Over 100 scales, mainly fragmentary material.

OCCURRENCE. — Samples 2-10, 2-11, 2-19, Matushevich River; 157-4, Spokojnaya River; 31-1, Ushakov River, October Revolution Island, Severnaya Zemlya Archipelago, Ust-Spokojnaya Formation, Ludlow, Upper Silurian.

DESCRIPTION AND COMMENTS

In the samples, most of the scale varieties described by Märss (1986b) have been found. As an exception, in this description we use her terminology. Oral (= rostral, the scales come from the rostrum around the mouth): scales are wide and short, with transverse angular ridge on the crown. Cephalo-pectoral (Fig. 3O-Q, S): scales are big, crown surface is smooth or with a gentle longitudinal medial ridge and short ridges antero-laterally. Postero-lateral margins of the crown is finely serrated. Crown surface has fine striation (Fig. 3S). Postpectoral scales are with a wide medial ridge and several lateral ridges on it. Precaudal scales (Fig. 3R) with a strong sharp medial and some lateral ridges. Pulp depression is always widely open. Definite fin scales are absent in our collections.

Genus *Goniporus* Gross, 1967

TYPE SPECIES. — *Goniporus alatus* (Gross, 1947).

Goniporus alatus (Gross, 1947)
(Fig. 16)

SYNONYMY. — See Gross (1967), Turner (1976) and Karatajūtė-Talimaa (1978).

OCCURRENCE. — On Severnaya Zemlya, the scales of *G. alatus* have been found only in the Krasnaya Bukhta Formation, Pridoli, of October Revolution Island (Spokojnaya River, outcrops 51a, beds a, b, and c; 45, bed 11; 45, talus; 41, bed 1; MF 157-2). In the sections of the European biogeographic province, *G. alatus* is characteristic for the lower part of Pridoli (*Thelodus parvidens* Zone by Gross 1967; *Katoproduus tricavus-Goniporus alatus* Zone by Talimaa 2000) but also for the upper part of it (*P. kummerowi* and *K. lithuanicus-K. timanicus* Zones; see Märss *et al.* 1995). The scales of *G. alatus* are also rarely represented at the base of Lower Devonian together with the scales of *Turinia pagei* (Powrie, 1970) (Turner 1973; Märss 1986, 1997; Karatajūtė-Talimaa 1978; Talimaa 2000).

DESCRIPTION AND COMMENTS

Comparatively small oval, often rhomboidal, and flat scales. Head scales (Fig. 16A) very small (length about 0.4 mm), with crenulated crown margins. These scales are very rare in samples.

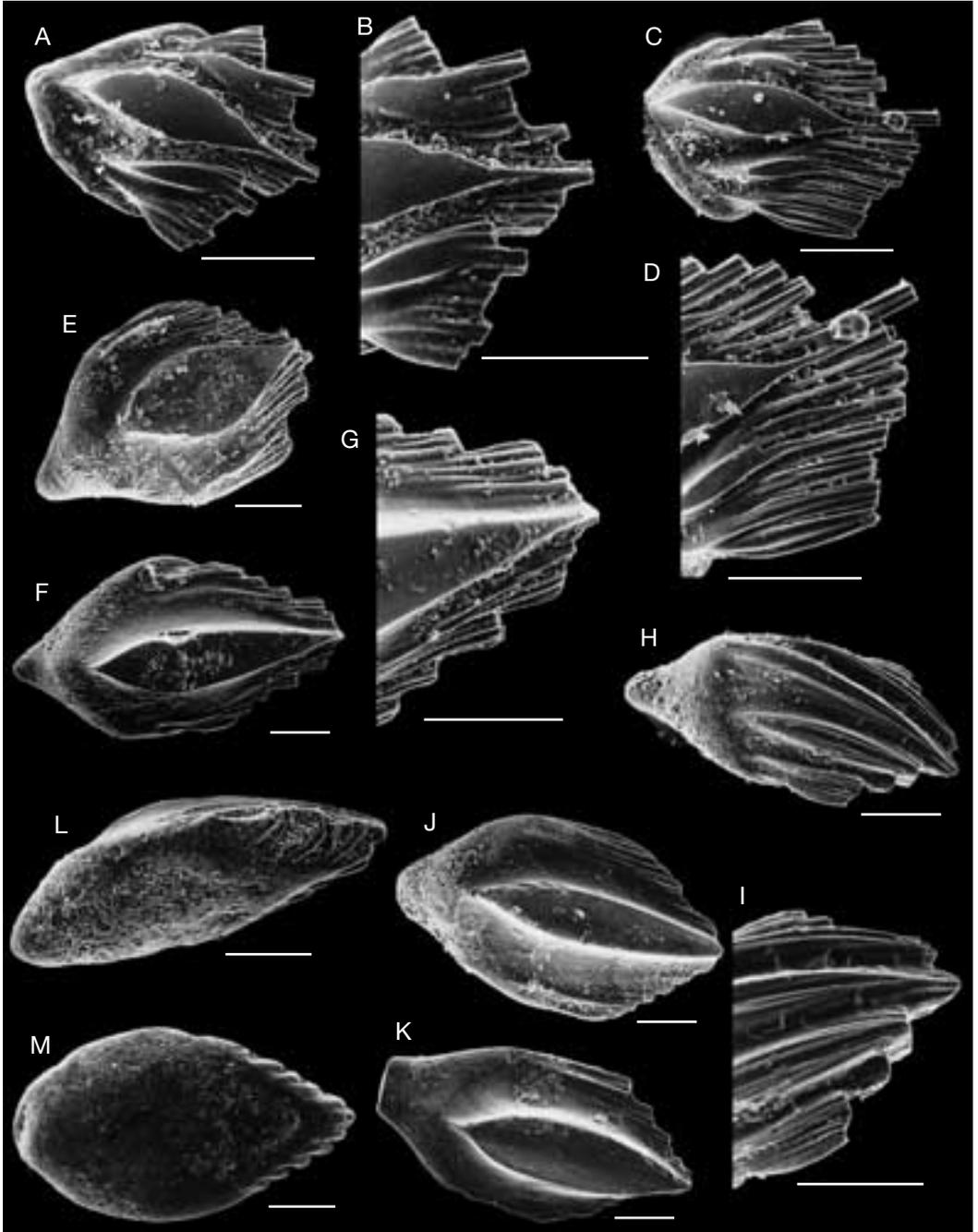


FIG. 14. — *Valiukia flabellata* n. gen., n. sp., trunk scales; **A, B**, holotype (see also Fig. 12G); **A, C, E, F, H, J, K**, scales in crown view; **B**, magnified posterior part of **A**; **D**, magnified posterior part of **C**; **G**, magnified posterior part of **F**; **I**, magnified posterior part of **H**; **L**, scale in lateral view; **M**, scale in base view; **A, B**, LIG 35-844; **C, D**, LIG 35-845; **E**, LIG 35-846; **F, G**, LIG 35-847; **H, I**, LIG 35-853; **J**, LIG 35-851; **K**, LIG 35-852; **L**, LIG 35-854; **M**, LIG 35-855; sample 2-23, Matusevich River, October Revolution Island, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. Scale bars: 0.1 mm.

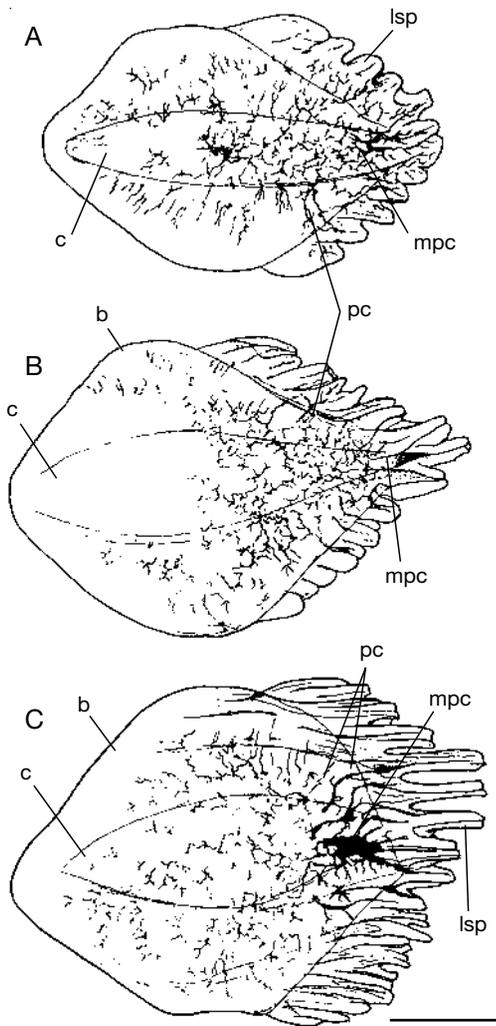


FIG. 15. — *Valiukia flabellata* n. gen., n. sp., microstructure of trunk scales in sagittal view (scale in anise oil); **A**, LIG 35-856; **B**, LIG 35-857; **C**, LIG 35-858. Abbreviations: **b**, base; **c**, central (medial) part of the crown; **lsp**, longitudinal spine of posterior part of the crown; **mpc**, main pulp canal; **pc**, pulp canal in lateral spine; sample 2-23, Matusевич River, October Revolution Island, Ust-Spokoynaya Formation, Ludlow, Upper Silurian. Scale bar: 0.1 mm.

Transitional scales are 0.5-0.65 mm long and 0.4-0.5 mm wide. They are composed of a rather monolithic flat crown with distinct central and lateral areas anteriorly on the crown only (Fig. 16B-D). Trunk scales (Fig. 16E-Q) usually predominate in the samples. Rather wide rhom-

boidal scales (Fig. 16E-I, O-Q) show a narrow central area with medial furrow and two pairs of lateral areas. Marginal areas short and wing-like. The length of the scales 0.4-0.6 mm, width 0.4-0.5 mm. The base can be convex; in this case the pulp openings are not visible. The base can be flat and low (Fig. 16G₂, O₂, P₂) or wall-like surrounding the pulp depression (Fig. 16I₂). Openings of pulp canals are situated at the postero-lateral margins of the base or in the pulp depression. The number of openings depends on the number of crown areas. Anteriorly the base has sometimes spur-like projection (Fig. 16O-Q). Small and narrow scales are composed of the central and a pair of lateral areas that are shorter and wing-like (Fig. 16J-N). The length of the scales is 0.3-0.5 mm and width 0.2-0.3 mm.

COMPARISON

After the size and form of the scales, *G. alatus* in Krasnaya Bukhta Formation, Pridoli, of Severnaya Zemlya, does not differ from the species of the same age of other regions (Welsh Borderland, erratic boulders of north German lowland, Lithuania, Latvia, Estonia, Kaliningrad District, NE Poland, North Timan, eastern part of Timan-Pechora Region, the Urals and Cornwallis Island; see Turner 1973; Märss 1997; Märss *et al.* 1998; Talimaa 2000). Still, the morphology to original most similar *Goniporus alatus* is revealed by the scales from the Pridoli of Severnaya Zemlya and Eptarma Formation of North Timan (Karatajūtė-Talimaa 1978: pl. VI, figs 6-10).

Order THELODONTIDA, Kiaer, 1932
 Family THELODONTIDAE Jordan, 1905

Genus *Thelodus* Agassiz, 1839

TYPE SPECIES. — *Thelodus parvidens* Agassiz, 1839.

Thelodus visvaldi n. sp.
 (Figs 17; 18; 19A-D)

Thelodus sp. 1 Märss & Karajūtė-Talimaa 2002: fig. 1.

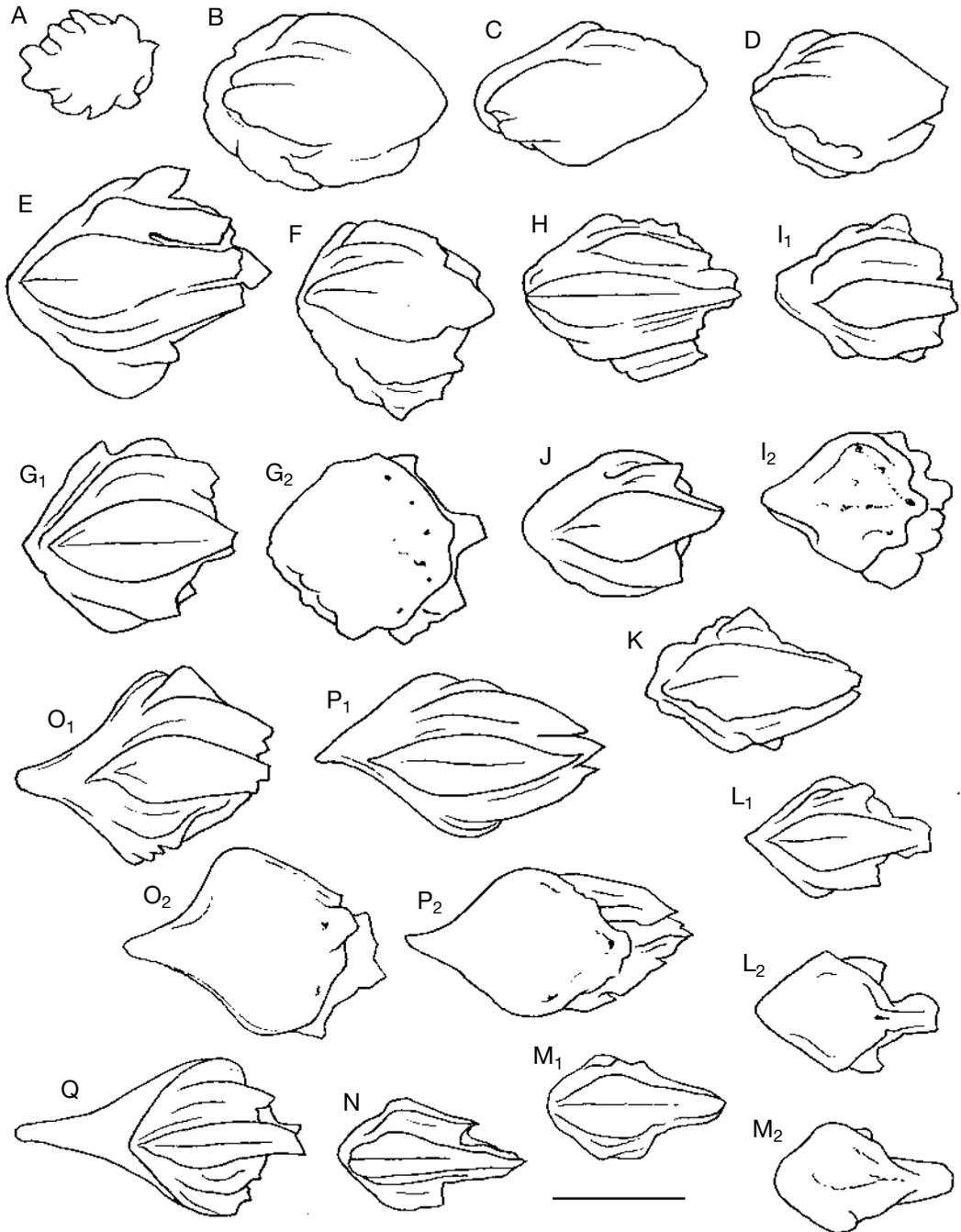


FIG. 16. — *Goniporus alatus* (Gross, 1947), morphological set of scales; **A**, head scale; **B-D**, transitional scales; **E-Q**, trunk scales; **A-G₁, H, I₁, J-L₁, M₁, N, O₁, P₁, Q**, scales in crown view; **G₂, I₂, L₂, M₂, O₂, P₂**, scales in base view. LIG 35-236-LIG 35-252; sample 41-1, Spokojnaya River, October Revolution Island, Krasnaya Bukhta Formation, Pridoli, Upper Silurian. Scale bar: 0.3 mm.

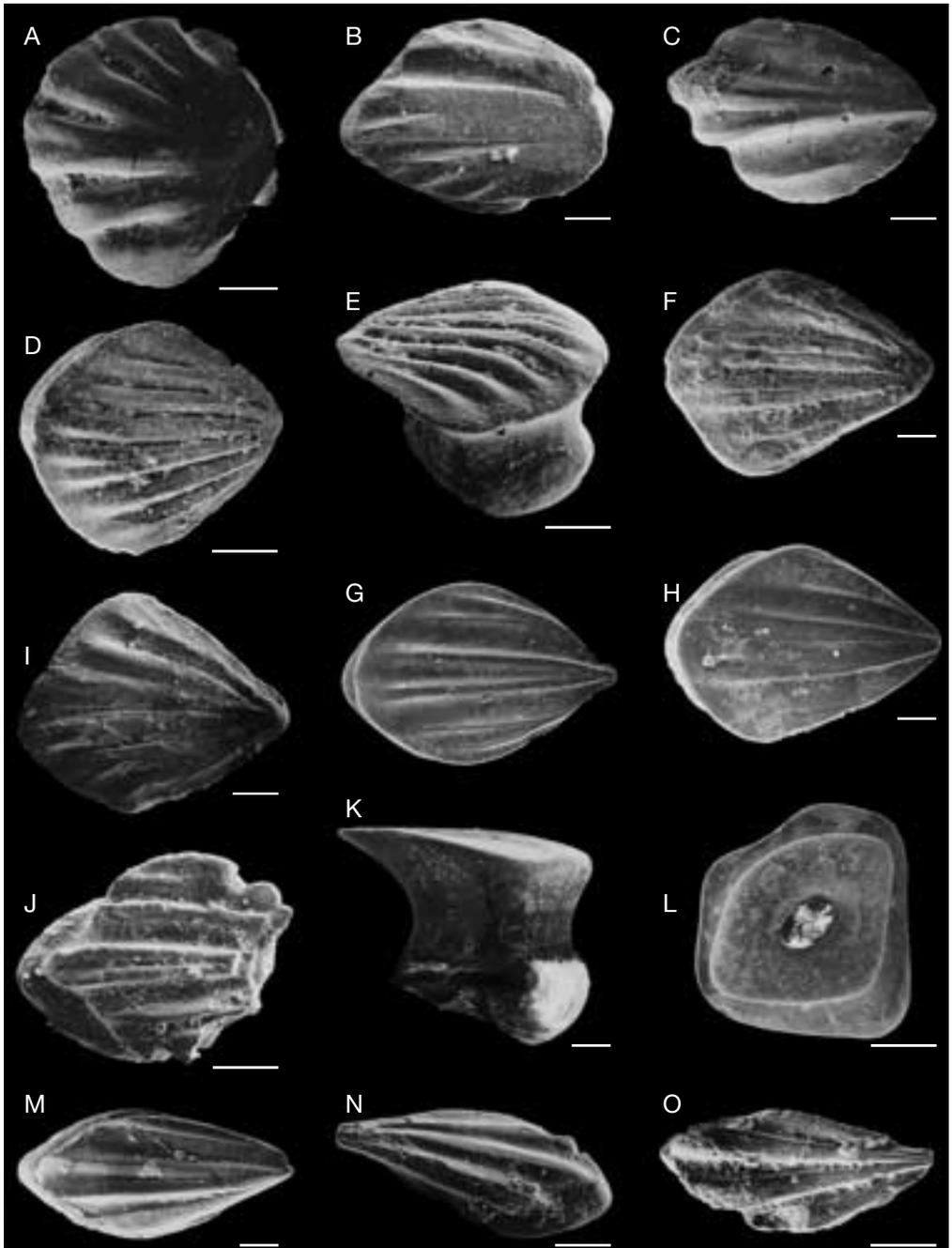


FIG. 17. — *Thelodus visvaldi* n. sp.; **A**, head scale; **B**, **D**–**I**, **K**–**O**, trunk scales; **C**, fin scale?; **J**, scale of unknown position; **A**–**D**, **F**–**J**, **M**–**O**, scales in crown view; **E**, **N**, scales in oblique lateral view; **K**, scale in lateral view; **L**, scale in base view; **A**, Pi 7541; **B**, Pi 7556; **C**, Pi 7549; **D**, **E**, Pi 7544; **F**, Pi 7542; **G**, LIG 35-903, the scale is lost; **H**, LIG 35-904; **I**, Pi 7545; **J**, Pi 7559; **K**, LIG 35-905; **L**, LIG 35-906; **M**, Pi 7553; **N**, Pi 7554; **O**, Pi 7555; **A**–**F**, **I**, **J**, **M**–**O**, MF 34-1, Cape October, October Revolution Island; **G**, **H**, **K**, **L**, 5m-1, Pioneer Island; Ludlow, Upper Silurian. Scale bars: **A**–**C**, **F**–**K**, **M**–**O**, 0.1 mm; **D**, **E**, **L**, 0.2 mm.

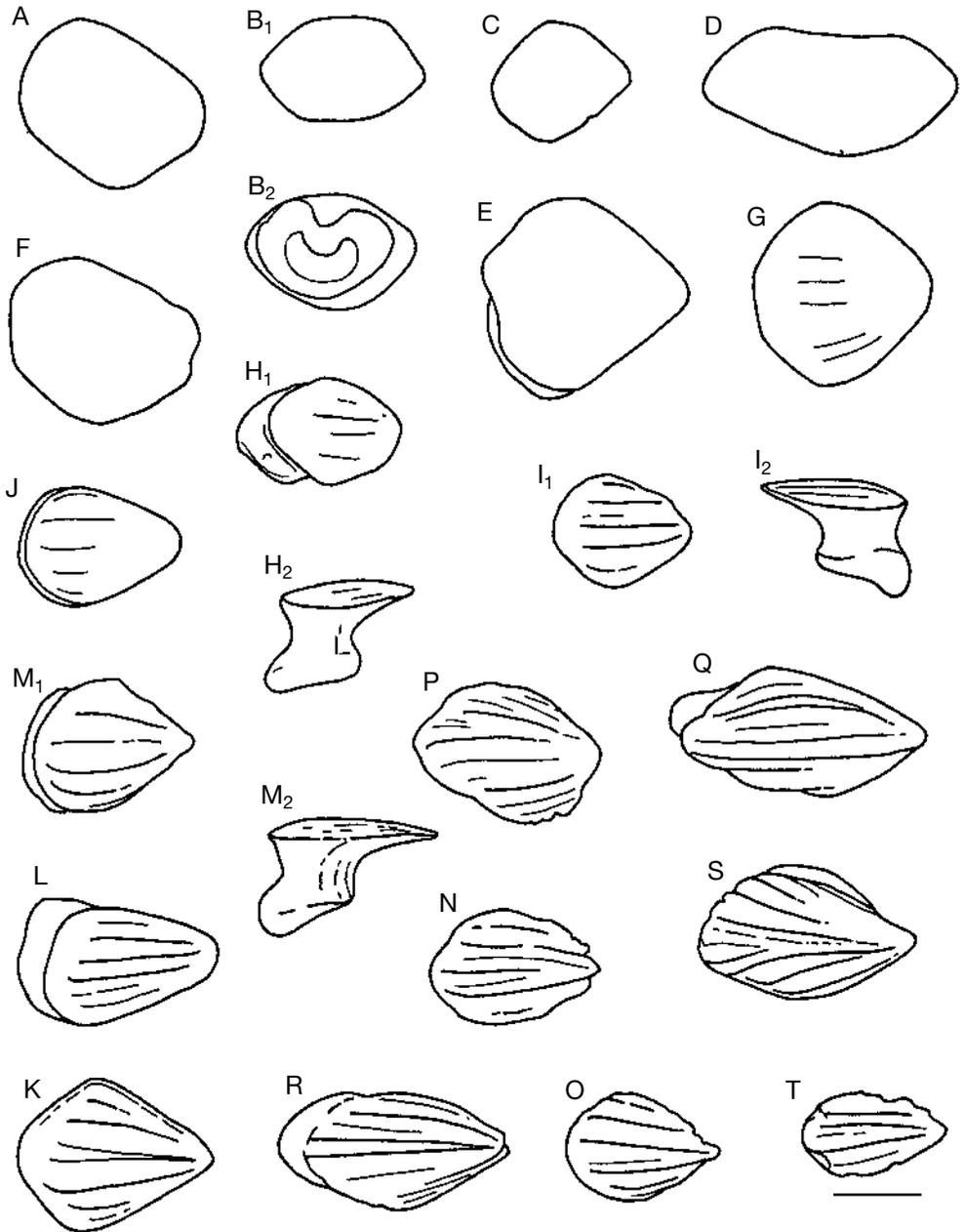


FIG. 18. — Set of scales of *Thelodus visvaldi* n. sp.; **A-G**, head scales; **H-T**, trunk scales; **A, B₁, C-G, H₁, I₁, J-M₁, N-T**, scales in crown view; **B₂**, scale in base view; **H₂, I₂, M₂**, scales in lateral view; LIG 35-120-LIG 35-139; sample 5m, Pioneer Island, Ludlow, Upper Silurian. Scale bar: 0.3 mm.

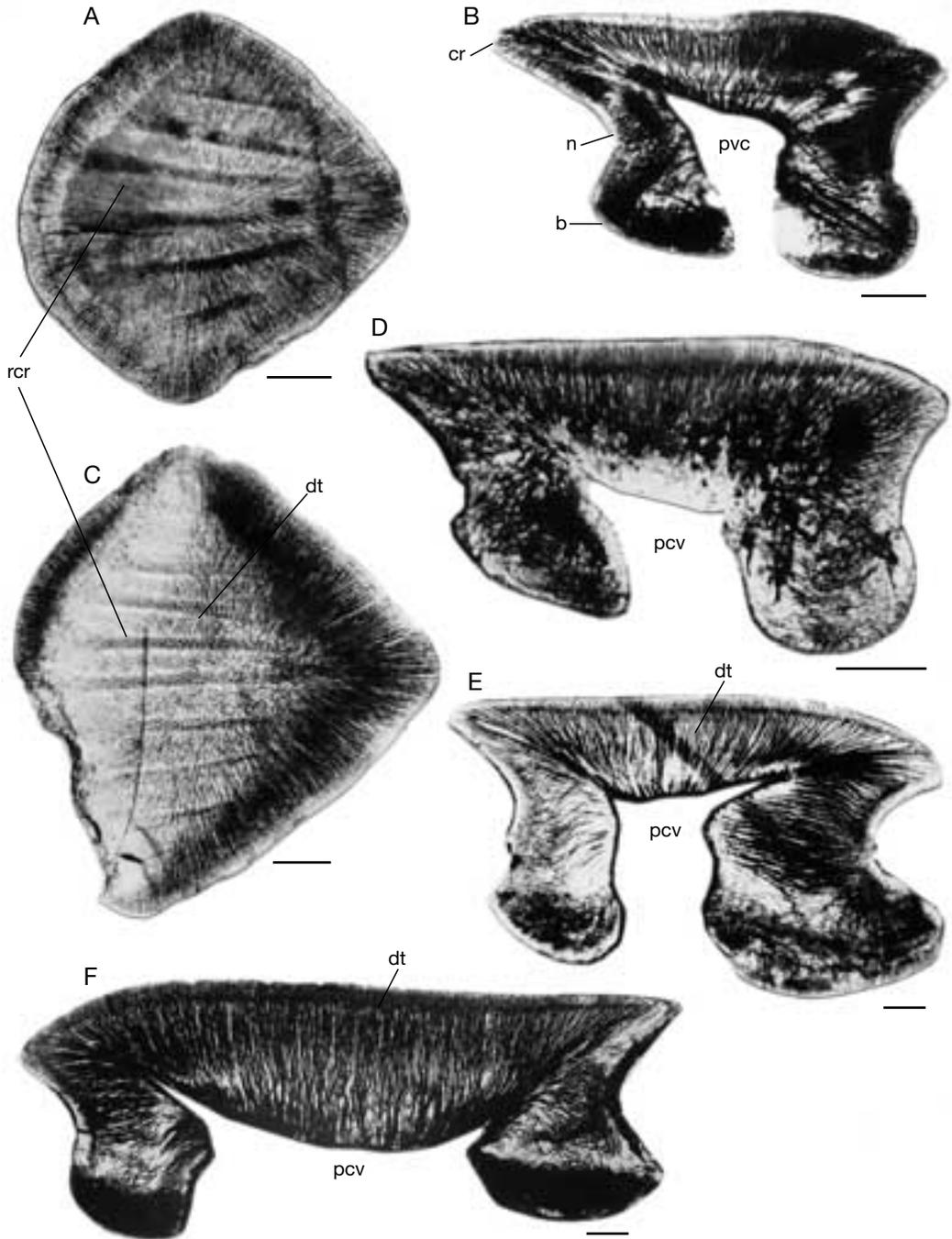


FIG. 19. — Microstructure of the scales; **A-D**, *Thelodus visvaldi* n. sp.; **E, F**, *Thelodus* sp. indet.; **A**, Pi 7644; **B**, Pi 7645; **C**, Pi 7646; **D**, Pi 7647; **E**, Pi 6445; **F**, Pi 6365; **A, C**, sample 20568, Komsomolets Island, upper part of Ludlow; **B**, sample 2-3k; **D**, MF 11-1, Matusevich River, October Revolution Island, Ust-Spokojnaya Formation; **E, F**, sample 2055zh, Pioneer Island, upper part of Ludlow, Upper Silurian. Abbreviations: **b**, base; **cr**, crown; **dt**, dentine tubules; **n**, neck; **pcv**, pulp cavity; **rcr**, ridge on the crown. Scale bars: 0.1 mm.

HOLOTYPE. — Pi 7542 (Fig. 17F).

ETYMOLOGY. — Named after Dr. Visvaldis Kuršs, Riga, Latvian State University, who participated in the field work on Severnaya Zemlya in 1978.

TYPE LOCALITY AND AGE. — Sample MF 34-1, Cape October, October Revolution Island, Severnaya Zemlya Archipelago, Ludlow, Upper Silurian.

MATERIAL EXAMINED. — About 700 scales.

OCCURRENCE. — Samples MF 34-1, Cape October; 2-3, 2-4, 2-7, 2-23, Matusевич River, October Revolution Island; 5m-1, 5d, 5i, 5zh-1,5e, Pioneer Island, Severnaya Zemlya Archipelago, Ust-Spokojnaya Formation, Ludlow, Upper Silurian. On Pioneer Island *Thelodus visvaldi* n. sp. occurs also in the Wenlock part of the section (see Fig. 1).

DIAGNOSIS. — Scale crown quadrangular to oblong, with longitudinal grooves in flat surface or with smooth flat crown surface. Between grooves, longitudinal ridges often split into two parallel ones. The neck is without vertical ridges. Typical *Thelodus* histology.

DESCRIPTION

Morphology

Crowns of head scales quadrangular or round (Fig. 17A) with short ridges and grooves anterolaterally; postero-lateral margins serrated. The scales are small, the length of head scales 0.4–0.5 mm, their width 0.3–0.5 mm. In the same sample the quadrangular scales with flat and smooth crown surface (Fig. 18A–G) are rather numerous. We tend to believe that these scales covered the body behind the rostrum and in front of the dorsal and ventral fins, and correspond to the transitional scales. The measurements of the smooth scales are: in average 0.5×0.5 mm, the maximum length 1.4 mm and width 1.0 mm. The rest of the trunk was covered with relatively high scales with a quadrangular or oblong crown that was covered with longitudinal grooves and ridges (Figs 17B, D–I; 18H–T) nearly parallel in the medial part of the crown. Ridges are often divided into two. Narrow unsculptured margins characterize the trunk scales. The measurements of the scales are: length 0.4–0.9 mm and width 0.4–0.8 mm; in the holotype (Fig. 17F) the corresponding numbers are 0.6 and 0.5 mm. The neck is distinct and relatively high. The base (Fig. 17K, L) is smaller than the crown, rhomboidal, sometimes rather wide. Narrow and small scales (Fig.

17M–O) were covering from the posterior part of the trunk. The scale in Fig. 17O is only 0.4 mm long and 0.2 mm wide.

In Fig. 17J is a very small scale, posteriorly broken (length 0.4 mm), but, still, trilobate shape is recognizable. The crown surface is typical for the new species. Its position on the body is unknown.

Histology (Fig. 19A–D)

Dentine tubules start from the pulp cavity and are directed towards the base, neck and crown (Fig. 19B, D). The tubules are comparatively wide in the lower part of the crown; they branch on some levels, and become narrower in the upper crown portion. The longest and most straight dentine tubules occur in the posterior crown portion (Fig. 19A–C).

COMPARISON

Trunk scales of *Thelodus visvaldi* n. sp. are quadrangular, their crowns carrying nearly parallel grooves and ridges in the medial part, the ridges being often bifurcated. In outline they resemble *T. sculptilis* Gross, 1967, in having relatively short scales but the latter has only few ridges on its crowns. The sculpture of both *T. visvaldi* n. sp. and *T. schmidtii* (= *T. laevis*) (Pander, 1856) is formed by longitudinal steep deep grooves and ridges but in the new species the ridges and grooves are more numerous and more parallel the medial part of the crown. The whole set of scales of *T. parvidens* is not known and in it richly ridged scales are not described. *Thelodus carinatus* (Pander, 1856) has gentle ridges on flat crown surface; some scales described here (e.g., Fig. 4J) do resemble it. Sculpture of *T. visvaldi* n. sp. and *T. admirabilis* Märss, 1982 differ in ridge/groove arrangement; the posterior prong is absent in *T. visvaldi* n. sp.

Thelodus matukhini n. sp.

(Figs 2A–I; 20)

HOLOTYPE. — Trunk scale LIG 35-860 (Fig. 2B).

ETYMOLOGY. — Named in honour of Dr. R. G. Matukhin (Novosibirsk, Russia), researcher of Severnaya Zemlya and participant of the field work to the region in 1978.

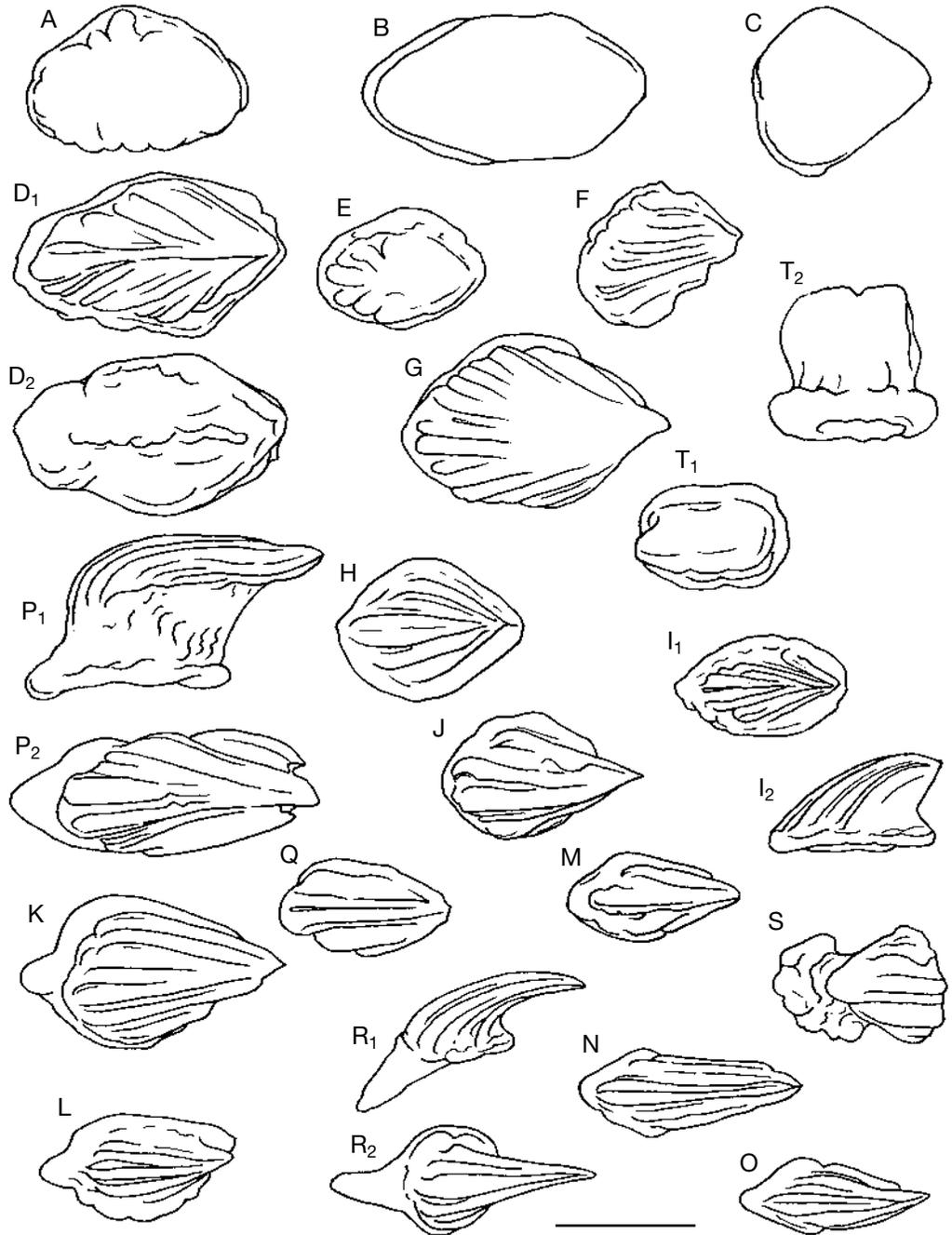


FIG. 20. — *Thelodius matukhini* n. sp., morphological set of scales; **A-C**, head scales; **D-G**, transitional scales; **H-S**, trunk scales; **T**, *pugniformis*-type of the scale; **A-C**, **D₁**, **E-H**, **I₁**, **J-O**, **P₂**, **Q**, **R₂**, **S**, **T₁**, scales in crown view; **D₂**, scale in base view; **I₂**, **P₁**, **R₁**, **T₂**, scales in lateral view; LIG 35-281-LIG 35-300; sample 18041-14, Komsomolets Island, Ludlow, Upper Silurian. Scale bar: 0.3 mm.

TYPE LOCALITY AND AGE. — Sample 18041-14, Komsomolets Island, Severnaya Zemlya Archipelago, Ludlow, Upper Silurian.

MATERIAL EXAMINED. — About 200 scales of good preservation.

OCCURRENCE. — Samples 18041-14, Komsomolets Island; *Andreolepis* sp. (*A. bedei* Gross, 1968 most probably) in this sample allows the age determination as Ludlow without any doubt; MF 34-1, Cape October area, Ludlow, Upper Silurian.

DIAGNOSIS. — Medium-sized scales (length 0.9–1.2 mm, width 0.5–0.7 mm; the length of smallest scales 0.3–0.7 mm). Head scales oval, with smooth and flat surface; their margins are sometimes crenulated. Transitional and trunk scales oval or rhomboidal. Crown surface is ridged, sometimes with longitudinal grooves with elevated spiny posterior apex. The base is not very high; it protrudes as a narrow strip behind the crown. Pulp opening large. A comparatively high neck is developed only in a few scales. Fine vertical ridgelets of the postero-lateral neck walls are present in very rare scales. Morphological set includes trilobiform and pugniform scales.

DESCRIPTION

Head scales are represented by those with oval and rhomboidal configuration and smooth surface of the crown (Fig. 20B, C), some of them having slightly crenulated margins (Fig. 20A). The base is rather low and forms a wall around large pulp opening. Rhomboidal head scales (Fig. 20C) have a base considerably smaller than the crown, a relatively high neck and a smooth surface. As transitional scale we treat rounded or elongated oval ones (Figs 2D; 20D–G). Especially characteristic are the scales with a median ridge (Fig. 20D₁) that can end with an elevated spine (Fig. 2D). Laterally from the ridge, oblique ridgelets are developed. They start at the base of the crown and are directed towards the median ridge. In some of transitional scales the anterior margin is deeply crenulated (Fig. 20E) or covered with ridgelets (Fig. 20G). Sometimes the whole crown surface is covered with fine longitudinal ridgelets (Fig. 20F). The base of transitional scales is not very high but it can be rather wide and protrude as a narrow strip over the whole perimeter of the crown (Fig. 20D₂). Pulp opening is large and elongated. The main part of the collected scales

is composed of trunk scales. Among them occur a lot of very small (0.3–0.7 mm long), narrow and elongate, and modified scales, including trilobiform (Fig. 20S) and pugniform (Fig. 20T_{1, 2}) types; the latter has laterally compressed and smooth crown surface. Characteristic *T. matukhini* n. sp. trunk scales are shown in Figs 2A–C, F–H and 20H–M. The largest scales reach the length of 1.2 mm. The crown is distinctly ridged, with a keel- or spine-like and aroson posterior apex. The central crown area is a narrow groove. Lateral to it, two to three pairs of lateral ridges are developed; they can reach the posterior tapered crown apex. Like a low and narrow strip, the base protrudes the crown perimeters. Sometimes it has short peg-like projection anteriorly, directed obliquely downwards and anteriorwards (Figs 2E; 20K, L). Pulp opening is large, often elongated and situated medially. Among trunk scales with ridged crown are often met scales with narrow or spine-like crown (Fig. 20N, O, R_{1, 2}). Some of them have a wide base with anterior spur-like projection (Fig. 20R_{1, 2}). Comparatively small part of trunk scales have a crown covered with longitudinal grooves (Fig. 20P_{1, 2}). In them, the central crown area is separated from the lateral ones by deeper grooves extending up to the posterior end of the crown (Fig. 20P₂). This variety has fine vertical ridgelets on the postero-lateral neck walls (Fig. 20P₁).

COMPARISON

The most characteristic features for the scales of *Thelodus matukhini* n. sp. are the specific proportions of the crown, neck and base. Only the trunk scales of this species are characterised by the ridged keel- or spine-like crown and low wall-like base that protrudes as a narrow strip over the whole perimeter of the crown. A relatively large, often elongated pulp opening is also characteristic for the new species. Vertical ridgelets on the postero-lateral crown (or neck) wall are often present in *Thelodus schmidti* (*Thelodus* ex gr. *schmidti*), *Thelodus parvidens* and *Thelodus sculptilis* but in *Thelodus*

matukhini n. sp. they are observed only in very rare occurrences.

Theلودus ex gr. *schmidti* (Pander, 1856)
(Figs 21-23G-M)

SYNONYMY. — For *Theلودus schmidti* see Turner (1976), Karatajūtė-Talimaa (1978) and Märss (1986b).

DESCRIPTION AND COMMENTS

In the Ludlow deposits of October Revolution and Pioneer islands, levels containing abundantly scales of *Theلودus* were discovered. Morphological sets composed from scales of different levels have some similarities but establishing their identity is complicated (compare Figs 21 and 22). The authors came to the conclusion that at the present stage of the study the identification of species or, even more, establishing any new taxon is not justified. At first it is necessary to revise *Theلودus schmidti* and its closely related species, *Theلودus carinatus* and *Theلودus marginatus* Karatajūtė-Talimaa, 1978, distributed in the uppermost Wenlock and Ludlow of Europe (Estonia, Latvia, Lithuania, southern Sweden, Gotland, Norway, North Timan, bore cores of Timan-Pechora Region, the Urals [Talimaa 2000]).

Some samples from the Ludlow of Severnaya Zemlya (e.g., Spokojnaya River, sample 47-14) yield so many different morphological varieties of these scales that it is not easy to find the limits for a species of mentioned *Theلودus*. For this reason, in the present paper we treat *Theلودus* ex gr. *schmidti* s.l.

Most typical for *Theلودus schmidti* is the scale set from the Spokojnaya River, sample 47-14 (Fig. 21) and Ushakov River, sample 31-1. The scales are medium-sized, the biggest reach 1.0-1.3 mm in length, rarely 1.4 mm. Head scales (*laevis*-type) are rounded, oval or rhomboidal (Fig. 21A-D). Crown surface is usually smooth; rarely the antero-lateral margins of the crown are crenulated. Sometimes a fine striation occurs on its surface (Fig. 21F). In a few scales, fine vertical ridgelets on the postero-lateral parts of the neck were observed. The base is of moderate

height, with centrally positioned large pulp opening. A part of head scales has a base smaller than crown. The scales with strongly swollen anterior part of the base are rare (Fig. 21B).

We ascribe to the transitional scales of the group (Fig. 21G, H) the scales (type "A") with large smooth central area and narrow postero-lateral downstepped lateral ones (lateral rims). They also exist in Baltic *T. carinatus* (Märss 1986b: fig. 19: 2-4).

The trunk scales (type "B") (Fig. 21I-N) are the ones with longitudinally furrowed crowns. In part of the scales the central area of the crown is separated from the lateral rims by comparatively deep grooves; on the surface of the central area, one to three fine groovelets occur. Lateral rims can be smooth or with fine groovelets. Often the lateral rim is downstepped (Fig. 21L) like in type "A". The trunk scales of type "C" are covered with longitudinal ridgelets (Fig. 21O-X), in narrow scales their number is four to five, in wider scales it increases up to six to seven. Anteriorly ridges may bifurcate. The subdivision of scales into types "A" and "B" is rather conventional because the ridges can also be divided by rather deep grooves. Part of trunk scales has developed fine vertical ridgelets (four to eight on each side) on the postero-lateral neck wall close to the base. There is a lot of scales having smooth surface of the neck. Base is moderately high; pulp opening is large. Some scales have root-like projections of the base (Fig. 21N).

Together with typical *T. schmidti*-*T. carinatus*, in the sample also a smaller number of scales of *trilobatus*- and *pugniformis*-type are associated.

Fig. 22 presents a morphological set of scales from the Ludlow of Pioneer Island (sample 5m). Among them, head scales (Fig. 22A, B) and trunk scales of three types: type "A", characteristic for *T. carinatus* (Fig. 22C, D), type "B" (Fig. 22E-G), and type "C" (Fig. 22H, J-O, S, T), and also modified scales with strongly developed sculpture of the crown and small low base (Fig. 22I, P-R) are found. This morphological set contains all typical scales for *T. schmidti*.

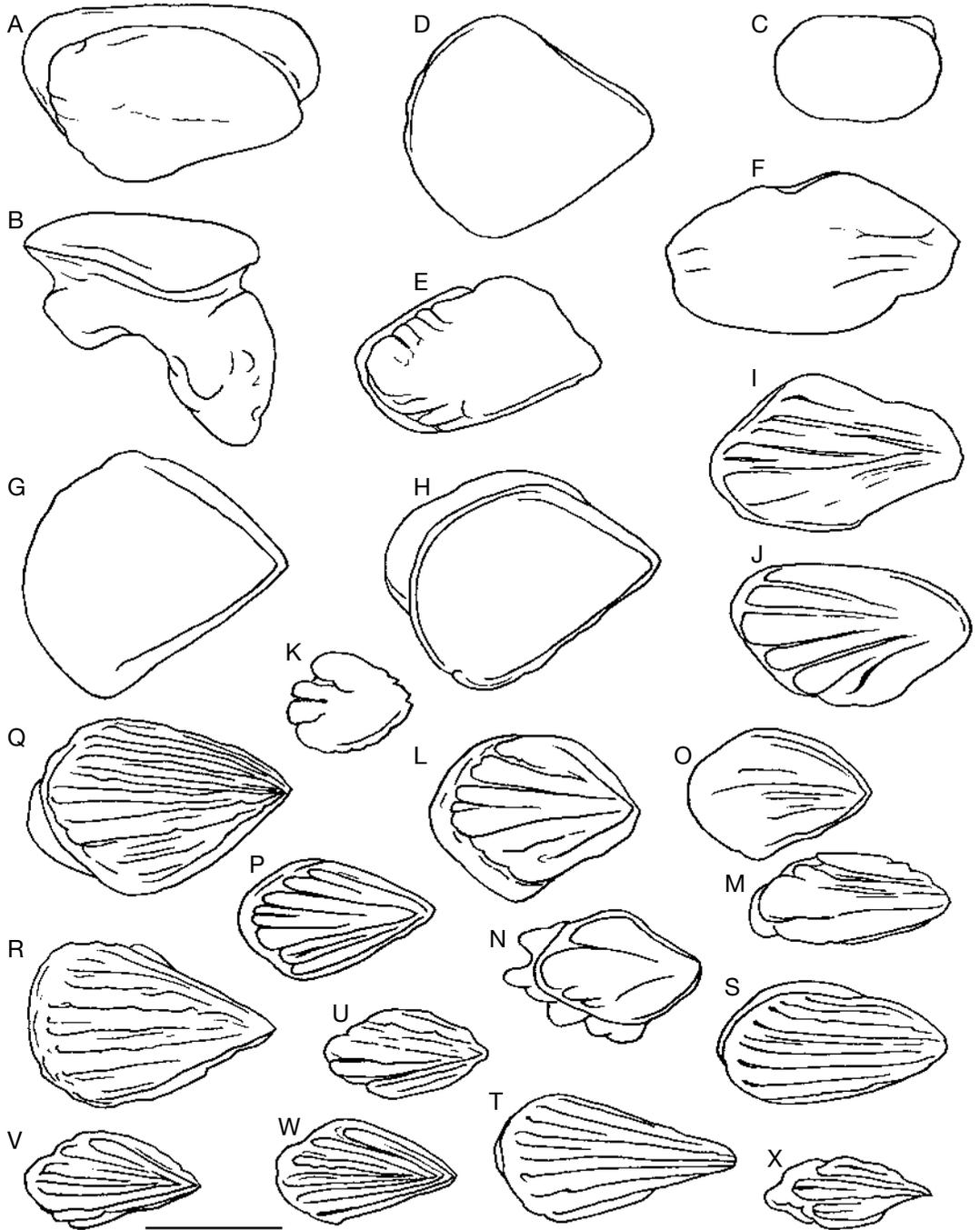


FIG. 21. — *Thelodus* ex gr. *schmidti* (Pander, 1856), morphological set of scales; **A-F, K, N**, head scales; **G, H**, trunk scales of type "A"; **I, J, L, M**, trunk scales of type "B"; **O-X**, trunk scales of type "C"; **A, C-X**, scales in crown view; **B**, scale in lateral view; LIG 35-254-LIG 35-277. Scale bar: 0.3 mm.

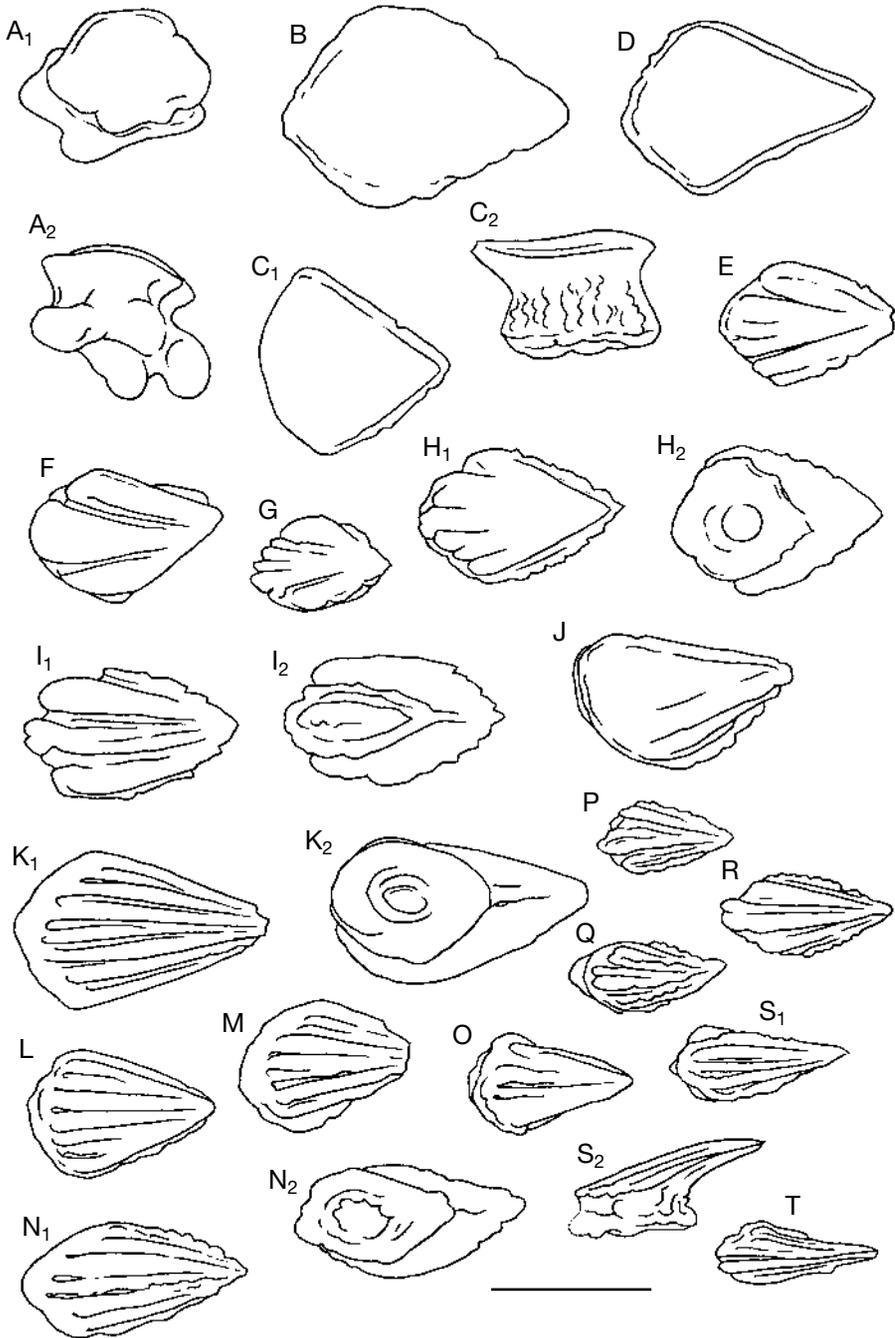


FIG. 22. — *Thelodus* ex gr. *schmidti* (Pander, 1856), morphological set of scales; **A, B**, head scales; **C, D**, trunk scales of type "A"; **E-G**, trunk scales of type "B"; **H, J-O, S, T**, trunk scales of type "C"; **I, P-R**, modified trunk scales; **A₁, B, C₁, D-G, H₁, I₁, J, K₁, L, M, N₁, O-Q**, scales in crown view; **H₂, I₂, K₂, N₂**, scales in base view; **A₂, S₂**, scales in lateral view; **C₂**, scale in posterior view; **A-T**, LIG 35-055-LIG 35-077; sample 5m, Pioneer Island, Ludlow, Upper Silurian. Scale bar: 0.3 mm.

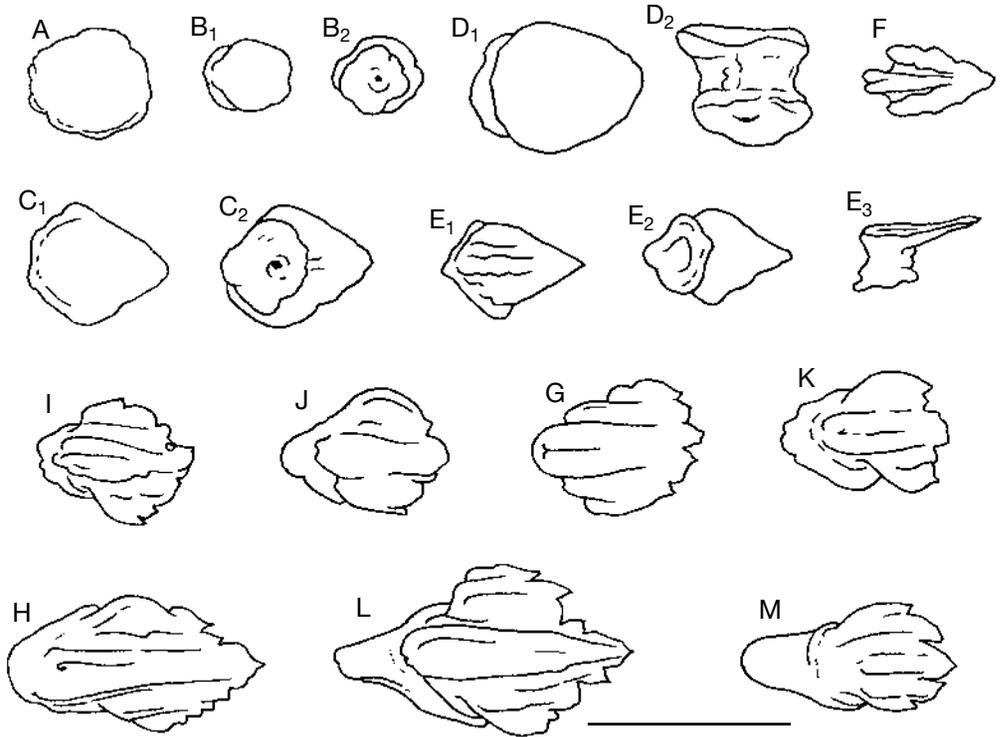


FIG. 23. — A-F, *Thelodus* sp. indet., morphological set of scales; A-D, head scales; E, F, trunk scales; A, B₁, C₁, D₁, E₁, F, scales in crown view; B₂, C₂, E₂, scales in base view; E₃, scale in lateral view; D₂, scale in posterior view; A-F, LIG 35-079-LIG 35-084; sample 5m, Pioneer Island, Ludlow, Upper Silurian; G-M, *Thelodus* ex gr. *schmidti* (Pander, 1856), trilobatifform trunk scales in crown view, LIG 35-113-LIG 35-119; sample 8d-1, Pioneer Island, Ludlow, Upper Silurian. Scale bar: 0.3 mm.

Fig. 23G-M shows trilobatifform scales from sample 8g-1, Pioneer Island. Some of them have developed spur-like projection anteriorly of the base; the crown is displaced at the back of the scale. The scales are smaller if compared with common trunk scales. The crown of trilobatifform scales is composed of a central and several pairs of lateral areas. Posteriorly, the crown is multicuspitate. Trilobatifform scales covered, most probably, a region of the body of *Thelodus schmidti* but also of *Thelodus parvidens* (see also Turner 1986 on *Thelodus parvidens* from Canada). Gross (1967: 18, 19, taf. 2: 13-21) considered *Thelodus trilobatus* Hoppe, 1931 (thin, three- to five-cuspitate crown posteriorly of the scale and long spur-like base anteriorly of it) as a good independent species for deposits of the *Thelodus parvidens* Zone, Pridoli.

Thelodus sp. indet.
(Figs 6F, G; 19E, F; 23A-F)

DESCRIPTION AND COMMENTS

On Pioneer Island in beds of Ludlow age, together with *Andreolepis hedei* were found, rather large scales with a smooth flat surface, distinct neck and base that could be identified as *Thelodus parvidens*. In the same samples also occur scales with elongated crown covered with longitudinal ridges and having comparatively wide base and pulp depression. Their microstructure reveals similar straight, proximally rather wide dentine tubules (Figs 6F, G; 19E, F). In the present work we identify them as *Thelodus* sp. indet.

Several samples of the Ust-Spokojnaya Formation on October Revolution Island (Matusevich

River, samples 2-38, 2-43; Spokojnaya River, sample 47-14; Ushakov River, sample 31-1) and Ludlow part on Pioneer (samples 5m, 5d) and Komsomolets islands (sample 18041-6) yield tiny scales which crowns reach only 0.08–0.4 mm in length. The crown of such scales is rounded, oval or rhomboidal. Neck is distinct, sometimes rather high and smooth without spinelets on the postero-lateral walls. Base is more convex anteriorly, pulp cavity central or slightly posterior. The crown surface of most of such tiny scales is smooth (Fig. 23A–D). Elongated scales that have unclear longitudinal ridgelets anteriorly (Fig. 23E₁) or grooves (Fig. 23F) have also been found.

Usually the scales described above are associated with larger scales of the *Thelodus schmidtii* type but sometimes they predominate (sample 2-38), or the whole sample is composed of tiny scales only (samples 2-43; 18041-6).

Species identification for such tiny scales is difficult. They might have been situated in a certain part of the squamation of representatives of the genus *Thelodus*, and in this case they must be treated as their corresponding species. Here they are left in open nomenclature.

Family LANARKIIDAE Obruchev, 1949

Genus *Lanarkia* Traquair, 1898

TYPE SPECIES. — *Lanarkia spinosa* Traquair, 1898.

Lanarkia? sp. (Figs 3N; 6H, I)

DESCRIPTION AND COMMENTS

In a few samples (samples 5 M-I, Pioneer Island; MF 157-2, Spokojnaya River, October Revolution Island) in the Ludlow deposits there have been found a few scales that resemble those of *Lanarkia* (Märss & Ritchie 1998). They are conical, with posterior end bending down, a crown finely ridged, wide pulp cavity, narrowing into pulp canal. A scale (Fig. 6H, I) that narrows upwards posteriorly (cuneiform scale) has

wide pulp cavity that narrows into a long pulp canal. Wide branching dentine canals in the lower part of the crown give bunches with numerous dentine tubules in the upper part of it. Dentine canals open into the pulp cavity, pulp canal and the base. To some extent they resemble the *Katoporodus*-type of histology.

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