

New Late Silurian to Middle Devonian acanthodians of the Timan-Pechora region

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ABSTRACT:

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New Přidoli to Eifelian acanthodian scales from various structural units of the Timan-Pechora region are described. Among 15 new species and 1 new genus, there are: 10 new species of nostolepids, common members of most of the biostratigraphic associations, the monospecific genus *Monospina* gen. nov., a single new species of *Cheiracanthoides* (all *Climatiida*), *Diplacanthus pechorensis* sp. nov. (*Diplacanthida*), and two new species of *Gomphonchus* (*Ischnacanthida*). Besides morphologic descriptions the taxa are also characterised histologically. Acanthodian taxa with scale crowns and bases composed of cellular bone, or very similar tissue, proposed as a primitive feature in their evolution, are reported for the first time.

Key words: Acanthodians, Nostolepids, *Climatiids*, *Diplacanthids*, *Ischnacanthids*, Late Silurian, Early Devonian, Middle Devonian.

INTRODUCTION

This paper provides the taxonomic description of the new Late Silurian to Middle Devonian acanthodians of the Timan Pechora Region, NE European Russia, based primarily on isolated scales, and rarely on teeth or fin spines. Acanthodian remains of this type are common elements of the vertebrate microremains in the vertebrate material from that region. As the former studies have shown their high biostratigraphic potential, not only for local subdivision and correlation, but also for wider inter-regional correlations, it seemed advisable to undertake their systematic study, in order to provide the basis for a more rational classification, and consequently, their better use in stratigraphical practice.

Some characteristic acanthodian assemblages from the Timan-Pechora region were the subject of a preliminary study by the author already in the late 1980s (VALIUKEVICIUS 1988). Subsequently, I have studied the stratigraphic ranges and zonal assemblages of acanthodians from the Lower Devonian of the Varandey-Adzva area

and Khorejver Depression (north-east of the region) (VALIUKEVICIUS 1993).

New studies of the Timan-Pechora faunas were undertaken in context of the IGCP Project 328 "Palaeozoic Microvertebrate Biochronology and Global Marine and Non-marine Correlation" (1991-1996) (VALIUKEVICIUS 1995, VALIUKEVICIUS & KRUCHEK 2000). Recently (1996-2000) the Timan-Pechora region, as one of the arctic reference regions, was included into the IGCP scientific Project 406 "Circum-Arctic Palaeozoic Vertebrates", and the description presented herein is mainly the outcome of this project.

The studied collection includes about 500 samples with acanthodians, coming from different structural units of the Timan-Pechora region (Text-fig. 1), from the top-most Silurian (Přidoli) to the basal Middle Devonian (see Text-fig. 2).

The collection studied herein is housed in the Museum of the Institute of Geology and Geography, Vilnius. Its catalogue number is 20-A. For the descriptive morphologic and histologic terminology see DENISON (1979).

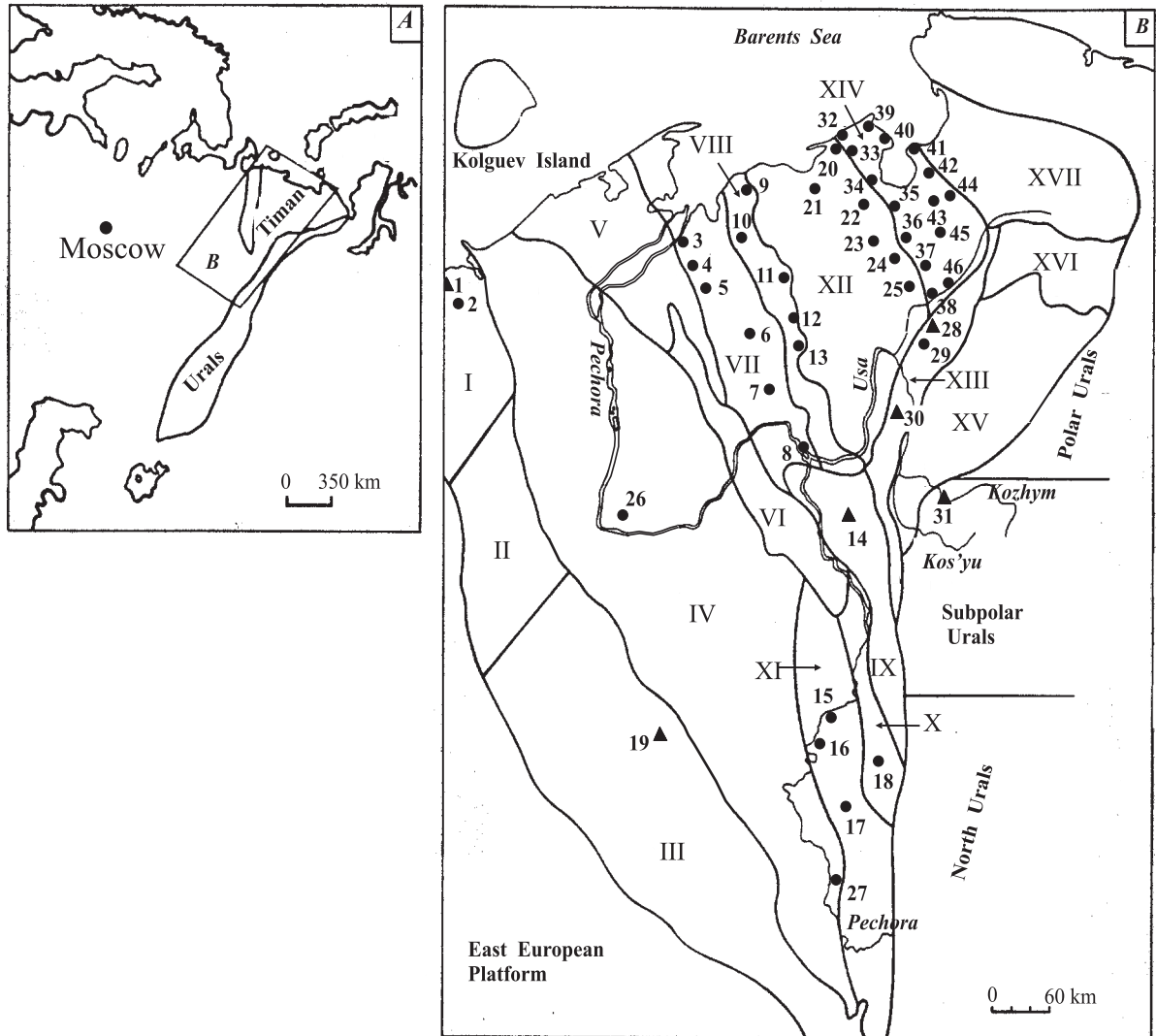


Fig. 1. Sketch map showing location of Timan-Pechora region and the Urals on the north-eastern part of the East European Platform (A) and division of the region into structural-facies areas (I-XVII, after IVANOV 1999) with the localities (1-46) of studied acanthodians (B)

I – North Timan Ridge, II – Middle Timan Ridge, III – South Timan Ridge, IV – Izhma-Pechora Syncline, V – Malaya Zemlya-Kolguev Monocline, VI – Pechora-Kozhva Megaswell, VII – Denisov Depression, VIII – Kolva Megaswell, IX – Bol'shaya Synia Depression, X – Middle Pechora Uplift, XI – Upper Pechora Depression, XII – Khorejver Depression, XIII – Chernyshev Ridge, XIV – Varandey-Adz'va structural area, XV – Kos'yu-Rogovaya Depression, XVI – Vorkuta Uplift, XVII – Korotaikha Depression. 1 – Velikaya River, 2 – Indiga, 3 – Kumzha, 4 – Vaney Vis, 5 – Sev. Shapkina, 6 – Verkhnyaya Laya, 7 – Mishvan', 8 – Andriushkin, 9 – Vangurey and Yuzhn. Vangurey, 10 – Yareiyu, 11 – Inzyrey, 12 – Khar'yaga, 13 – Vozey, 14 – Bol'shaya Synia River, 15 – Vuktyl, 16 – Sev. Savinobor, 17 – Yur-Vozh, 18 – Verkhnyaya Soch', 19 – Ukhta River, 20 – Varknavt, 21 – Yuzhn. Sadayaga, 22 – Olen'ya, 23 – Sev. Khosedayu, 24 – Zap. Yareiyaga, 25 – Kolva, 26 – Nizevaya, 27 – Pal'yu, 28 – Der-Shor River, 29 – Adz'va, 30 – Shar'yu River, 31 – Kozhym River, 32 – Varandey, 33 – Toravey, 34 – Naul' and Labagan, 35 – Sed'yaga, 36 – Yareiyaga, 37 – Osovey, 38 – Khosedayu, 39 – Medynka and Toboy, 40 – Miadsey, 41 – Ust'-Talota, 42 – Tamiakha, 43 – Zap. Lekeiyaga, 44 – Sev. Saremboy, 45 – Niadeiyu, 46 – Tcherpayu. Black circles – boreholes, black triangles – outcrops

SYSTEMATIC PALAEONTOLOGY

Class Acanthodii BERG, 1922
 Order Climaatiiformes BERG, 1940
 Family Climaatiidae BERG, 1940

Genus *Nostolepis* PANDER, 1856

DIAGNOSIS: see in R. DENISON (1979).

TYPE SPECIES: *Nostolepis striata* PANDER, 1856.

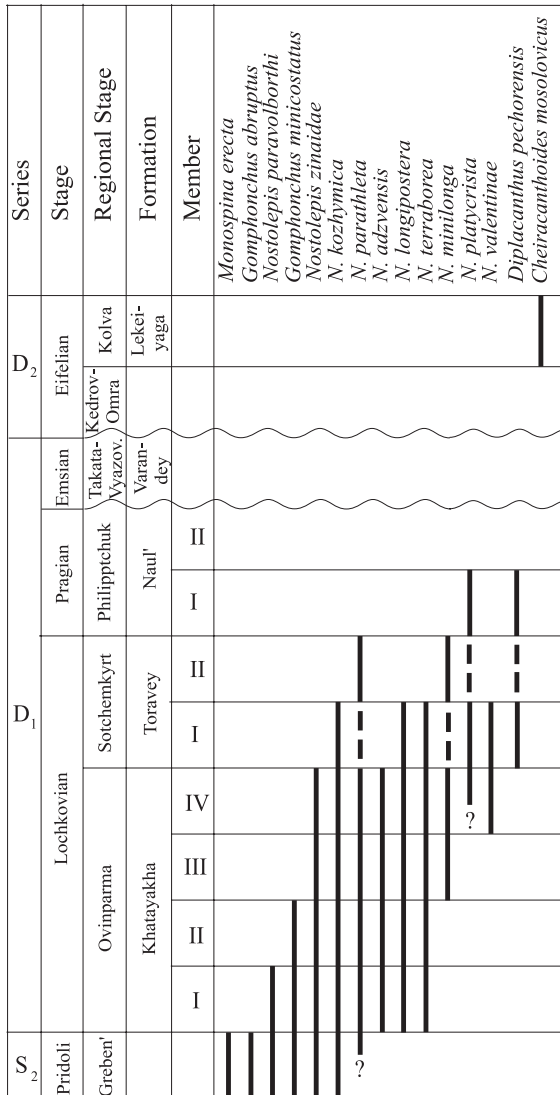


Fig. 2. Stratigraphic ranges of the new acanthodian taxa. Formations are taken from the Varandey-Adzva structural area

Nostolepis zinaidae sp. nov.
(Text-figs 3 A-M, 4 A-F, 5 A-C, 6 A-C)

- 1988. *Nostolepis* sp. no. 2; J. VALIUKEVICIUS, p. 603, table 2.
- 1993. *Nostolepis* sp. nov. 2; J. VALIUKEVICIUS, p. 29.
- 1995. *Nostolepis* sp. nov. 2; J. VALIUKEVICIUS, p. 395, text-fig. 4.
- 2000. *Nostolepis* sp. nov. 2; J. VALIUKEVICIUS & S. KRUCHEK, p. 281, text-fig. 6.

HOLOTYPE: LIG 20-A-1639, trunk scale (Text-fig. 3 I).

ETYMOLOGY: In honour of Zinaida Petrovna YUREVA (Arkhangelsk, Russia).

TYPE LOCALITY: The Kozhym River section, outcrop 236, samples 16-42.

TYPE HORIZON: Lower Devonian, Lochkovian, Ovinparma Formation, members 1-2.

MATERIAL: Over 35 000 body (head and trunk) scales including specimens from the lateral line, rare head tectal plates and tesserae, several fragments of fin spines and 9 palatine teeth.

DIAGNOSIS: *Nostolepis* with head tesserae ornamented by concentric or straight pyramidal ridgelets; trunk scales of moderate size, ornamented with pronounced radial or subradial ridges converging into the longest centrals, in some forming a wide, anteriorly ridged medial area. Scales composed of highly cellular bone in base, *Strangewebe* with long lacunae and simple mesodentine in crown similar to bone tissue. Pectoral or prepectoral fin spines with wide proximal rib and one pair of lateral ribs, and short oblique tubercle rows at the basal part posteriorly; dorsal? spine with enlarged proximal rib making a half of spine width and two pairs of lateral ribs. Small monocuspid palatine teeth, rarely with lateral denticles.

DESCRIPTION: The head tesserae and the tesserae-like scales, of variable shape (from circular, oval, rhomboid-oval, rectangular, triangular to multiangular multilobed), consist of the flat, ornamented crown plate, the low neck and the almost flat or slightly convex, rarely concave basal plate. The tesserae with the small, latero-posterior crown overhang predominate. The crowns are wider (0.55-0.76 mm) than long (0.37-0.51 mm). Three principal crown types in respect of their ornamentation may be distinguished: (1) crowns with the flattened and low concentric ridgelets separated by shallow and wider groovelets; both bent parallel to the posteriorly rounded crown margin (Text-fig. 3 B); (2) crowns with wavy uneven striae, running radially from the central one, which is slightly elevated or has the form of a rounded or multiangular bulb (Text-fig. 3 C); and (3) crowns with sharp, 3-5 subpyramidal ridgelets, with pointed apices, on each crown fold, becoming multilobed in the posterior part of the crown (Text-fig. 3 A). The first and the third types of tesserae grow areally, to one side, when the younger growth lamella was protruding previous one posteriorward from below. Growth occurs only distally from the primordial lamella. In contrast, the second type of tesserae are characterised by the areal, to all sides directed crown growth.

The head tesserae-scales have a higher neck, thicker crown plate and a less convex base. The crown plate is flat or slightly concave, rounded to rhomboid or rounded quadrangular in outline, with length slightly less than

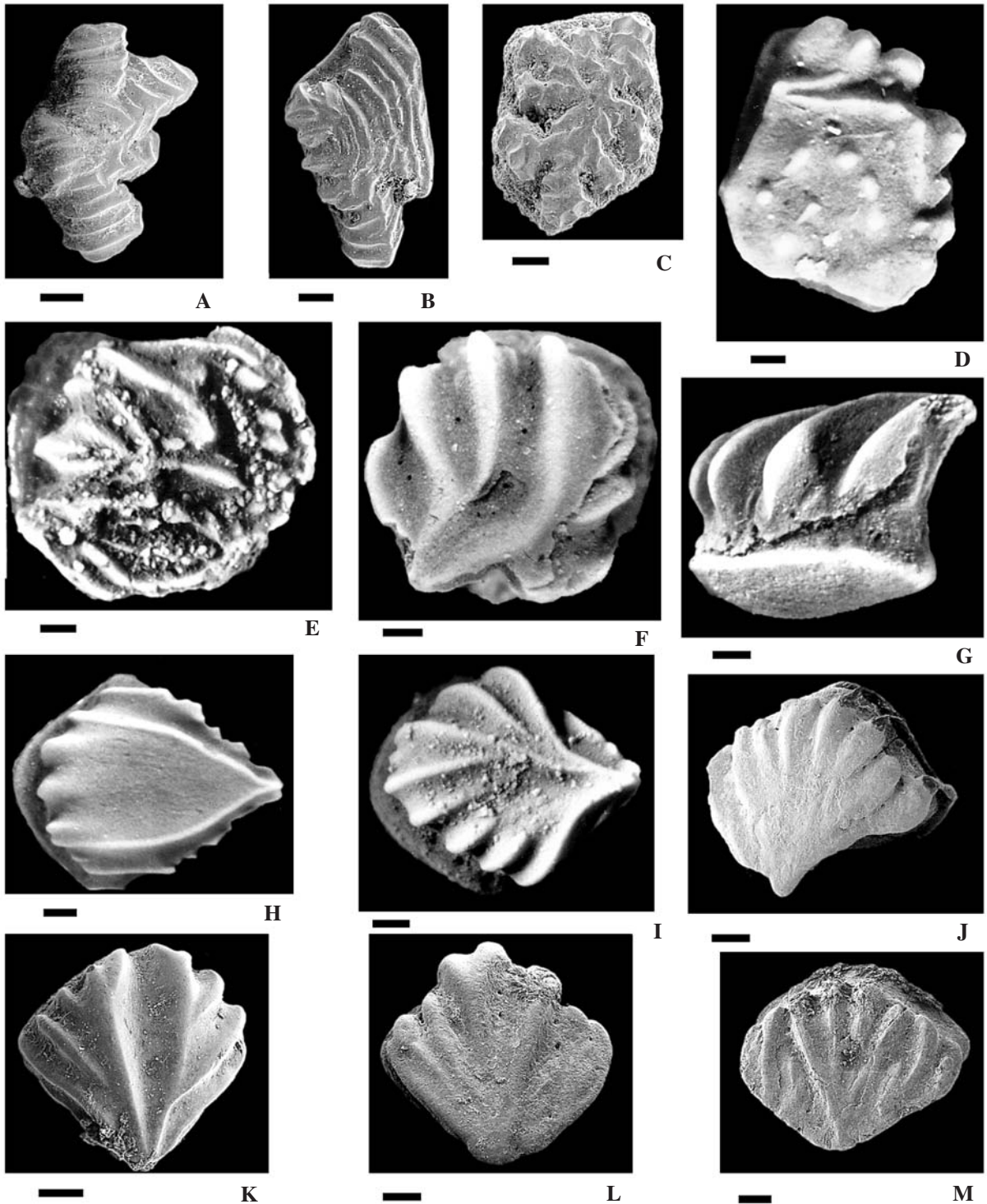


Fig. 3. Tesserae and scales of *Nostolepis zinaidae* sp. nov.; A-C – head tesserae, crowns, anterior to left: A – specimen LIG 20-A-2329; B – LIG 20-A-2328; C – LIG 20-A-2335; D, E – head scales, same orientation: D – LIG 20-A-1674; E – LIG 20-A-1637; F-M – body scales: F, G – lateral line? scale LIG 20-A-1631, crown, anterior upward (F) and side, anterior to left (G); H-M – trunk scales, crowns: H – LIG 20-A-1681; I – holotype, LIG 20-A-1639, anterior to left for both specimens; J – LIG 20-A-2176; K – LIG 20-A-2173; L – LIG 20-A-2174; M – LIG 20-A-2177, anterior upward for all. The Kozhym River section, outcrop 236: beds 16-18 (A, B, F, G) and bed 42 (C, E, I); Saremboj-2 borehole, depth 3344-3352.8 m (D, H); Tcherpayu-22 borehole, depth 2046.7-2052.6 m (J-M). Lower Devonian, Lochkovian: Khatayakha Formation (D, H and J-M) and Ovinparma Formation, members 1-2 (A-C, E-G, I). Bar: 0.1 mm

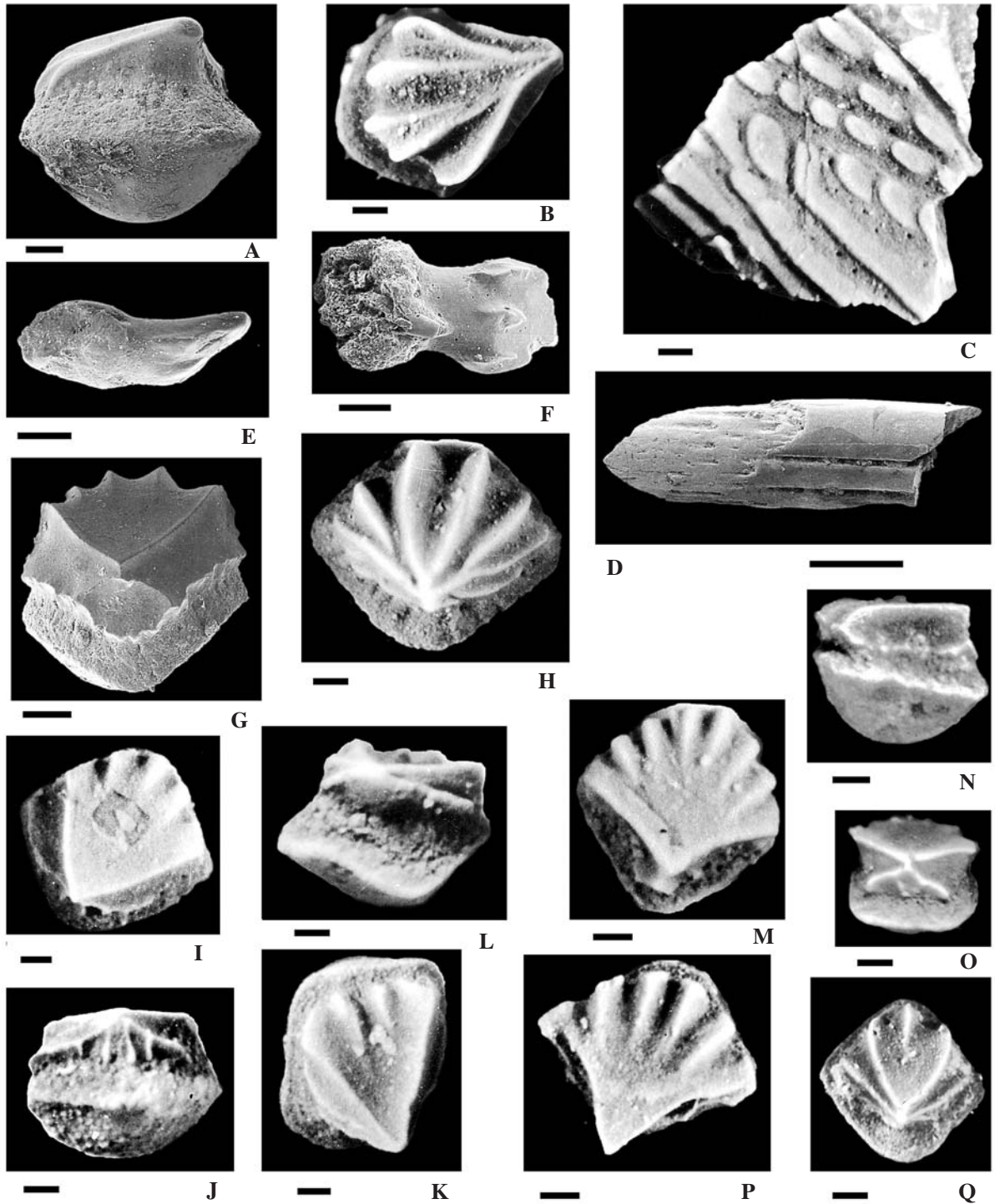


Fig. 4. A-F – *Nostolepis zinaidae* sp. nov.; A, B – trunk scales, anterior to left: A – LIG 20-A-2175 (side), B – LIG 20-A-1640 (crown); C, D – fragments of fin spines: C – pectoral or prepectoral? spine, LIG 20-A-1836, proximal to left; D – unidentified spine, LIG 20-A-2340, proximal upward; E, F – palatine teeth, lateral view, apex to right: E – LIG 20-A-2339; F – LIG 20-A-2338. Tcherpayu-22 borehole, depth 2046.7-2052.6 m (A) and the Kozhym River section, outcrop 236, bed 42 (B-F). Lower Devonian, Lochkovian: Khatayakha Formation (A) and Ovinparma Formation, Member 2 (B-F). Bar: 0.1 mm, except for D – 1 mm. G-Q – *Nostolepis adzvensis* sp. nov.; Trunk scales, crowns, anterior upward (G-I, K, M, P-Q), posterior neck view (J, L, O) and lateral view, anterior to left (N): G – LIG 20-A-2233; H – LIG 20-A-1512; I, J – LIG 20-A-1508; K, L – LIG 20-A-1507; M, N – holotype, LIG 20-A-1509; O – LIG 20-A-1920; P – LIG 20-A-1510; Q – LIG 20-A-1877. Varandey-7 borehole, depth 4200-4212 m (G); Saremboy-2 borehole, depth 3532-3539.1 m (H); North Saremboy-17 borehole, depth 3954-3961 m (I-P); Inzyrey-204 borehole, depth 4521-4525.4 m (Q). Lower Devonian, Lochkovian, Khatayakha Formation. Bar: 0.1 mm

width (0.6-0.85 mm and 0.8-1 mm respectively). The crown is ornamented with scattered circular bulbs, of variable height, and ridges. The latter are situated usually along the lateral margins (Text-fig. 3 D). Sometimes the ridges are uneven, with variable length and height, running radially or subradially on the antero-median part of the crown. They are randomly or concentrically distributed on the posterior part (Text-fig. 3 E). Short lateral radial ridges may converge into the central one.

The crowns of the lateral line scales (Text-fig. 3 F, G) are rounded quadrangular or oval in outline, slightly inclined and ornamented with strong, high and rounded longitudinal and radial ridges, curved downward anteriorly. The two longest medial, laterally bent, sometimes distally pointed ridges, continue to the posterior edge forming an asymmetrical crown ornamentation. Smaller radial ridges (2-3 pairs) converge into medials.

The trunk scales vary according to the crown ornamentation. The dominant forms have rhombic or rhomboid crowns (wide and round anterior margins and elongated, narrow posterior margins). The ornamentation consists of anteriorly widened radial ridges, fading out at the mid-length of the crown or extending to its posterior end (Text-figs 3I-L, 4B). The central area of the crown is often dominated by the two medial, longitudinal ridges (Text-fig. 3K). Usually the marginal ridges are the longest (Text-figs 3I, 4B), rarely they are of the same shape and length as the other ridges (Text-fig. 3J).

Text-fig. 3H illustrates the most common scales. They are supposedly from the tail or near-tail area. Their crown consists of a wide triangular and slightly elevated medial part, carrying short and rounded anterior ridges, and narrow symmetric lateral slopes with additionally ornamented (multispined) marginal rims. These scales have a postero-lateral crown overhang. The centrally swollen base is displaced anteriorly.

The scales in Text-fig. 3M have regularly rhombic crowns, without the base overhang, the two longest radial ridges, pointed posteriorly, with 1-2 short anterior ridgelets in between, and a variable number of converging, randomly distributed lateral ridges, separated from the longest ones by a groove. The posterior half of the crown bears short ridges.

All scale varieties, besides the last one, are very similar in size. Crown length varies from 0.58 mm to 0.82 mm and width from 0.57 to 0.7 mm. The last variety is slightly wider than long (0.6-0.77 mm and 0.43 and 0.58 mm respectively).

Associated were found the fin spines. The first type of fin spine (Text-fig. 4C), supposedly pectoral or prepectoral, is ornamented with a rounded and wide longitudinal rib on the leading edge and one pair of smaller ribs on each side. The remaining spine part is covered with

oblique rows of tubercles, elongated in outline and not overlapping. Another fin spine, horseshoe-shaped in transverse section, has an unusually large, wide, rounded proximal rib, and two pairs of narrow laterals, with deep and sharp grooves in between (Text-fig. 4D). The insertion portion is about 2 mm long, defining a shallow spine insertion into the animal body. It has highly vascularized bone tissue.

The small monocuspid palatine teeth (Text-figs 4E, F), 0.45 mm long, bent slightly antero-posteriorly, are of ellipsoidal basal transverse section and articulated with a plate of porous bone tissue. Rare specimens carry small and sharp, oblique lateral denticles.

The scales similar to the holotype (Text-fig. 5C) show a flattened, low-pyramidal base, composed of highly cellular bone tissue containing plenty of large angular osteocytes, with short winding processes. The thin and dense growth lamellae are penetrated by Sharpey's fibres of moderate length. The apex of the base cone bears remarkably elongated and horizontally oriented osteocytes, following the growth lamellae, thus emphasizing the similarity of the tissue to crown mesodentine. The posterior part of the crown is composed of 3 thick growth lamellae [including the first, primordial lamella] made of *Stranggewebe* (mesodentine tissue with elongated, horizontally oriented lacunae); the small anterior portion of the crown is composed of simple mesodentine. The tissue contains numerous, densely packed angular osteocytes. The superficial durodentine is only supposed to develop in the youngest growth lamella.

The scale with a wide medial crown area and weak ornamentation differs from those described above in the flattened base apex, the absence of *Stranggewebe* in the crown (present only in fragments in the primordial lamella), the presence of enlarged radial vascular canals over the base, and in upward directed ascending vascular canals (Text-fig. 5A, B). Due to densely packed osteocytes in the bone-like simple mesodentine, no dentinal canals occur, except for the outer strips of growth lamellae, penetrated by upward directed dentine tubules (Text-fig. 5B).

The crown *Stranggewebe* of the ?lateral line scale (Text-fig. 6A) is penetrated by a system of wide radial and ascending dentine canals. Each of the growth lamellae contains the narrow lateral strips of simple mesodentine, with unoriented osteocytes and lacunae. Typical simple mesodentine is missing in the anterior part of the crown.

The scale with the longest and narrowest crown (Text-fig. 6B, C) does not differ histologically from the last described.

REMARKS: Through the high and sharp crown ornamentation, *Nostolepis zinaidae* sp. nov. differs from all of the known species of the genus. From the slightly similar

Nostolepis sp. A (MÄRSS 1997, pl. 6, figs 2, 3, 13), from the lower Lochkovian of the Central Urals (Russia), it differs in its higher morphological diversity and in the scales with two dominating medial ridges, or with randomly distributed ridges, on the posterior part of the crown. *N.* sp. A also differs in possessing rounded, low, less prominent ridges. Modification of the crown mesodentine with densely packed osteocytes has not been observed previously.

STRATIGRAPHIC RANGE: Upper Silurian (Přidoli, Greben' Regional Stage) through Lower Devonian (Lochkovian, the lower part of Ovinparma Regional

Stage, the Ovinparma and Khatayakha formations and their facial correlatives). The Lochkovian part is assigned to the *remscheidensis* conodont Zone (DEULIN 1991).

Nostolepis adzvensis sp. nov.
(Text-figs 4G-Q, 7A-B)

1988. *Nostolepis* sp. no. 3; J. VALIUKEVICIUS, p. 604, table 2.

1993. *Nostolepis* sp. nov. 3; J. VALIUKEVICIUS, p. 28.

1995. *Nostolepis* sp. nov. 3; J. VALIUKEVICIUS, p. 395, text-fig. 4.

2000. *Nostolepis* sp. nov. 3; J. VALIUKEVICIUS & S. KRUCHEK, p. 281, text-fig. 6.

HOLOTYPE: LIG 20-A-1509, trunk scale, crown and side views (Text-fig. 4M-N).

ETYMOLOGY: From Adzva township (Komi Republic, Russia).

TYPE LOCALITY: North Saremboj-17 borehole, depth 3954-3961 m.

TYPE HORIZON: Lower Devonian, Lochkovian, Khatayakha Formation.

MATERIAL: This is one of the most common taxa, often forming monospecific occurrences. Over 28 000 trunk scales.

DIAGNOSIS: *Nostolepis* with rhomboid scales of moderate size, with 3-6 fading out or posteriorly pointed crown ridges; rarely with triangular lingual and ridged medial area; a pair of oblique neck ridges converge to the lateral crown margins making "starlet"-like structure at the posterior crown-neck junction. Crowns with pointed ridges composed of bone-like simple mesodentine with numerous osteocytes; those with fading out ridges composed of simple mesodentine, *Stranggewebe*, and superficial durodentine.

DESCRIPTION: The scales are rhomboid in shape, with slightly inclined crowns, quadrangular necks becoming higher posteriorly, and convex rhomboid bases. The sizes of bases and crowns are similar. The crowns are usually isometric (0.4-0.66 mm), rarely wider than long (0.66 and 0.6 mm respectively), and exceptionally longer than wide (0.52 mm against 0.32 mm). The crown plate is tabulate, rarely slightly concave or convex, ornamented with 3 (Text-fig. 4I) to 6 (Text-fig. 4M), anterior, subradial distinct ridges, fading out midway along the crown length. Also common are specimens with 4-6 sharp ridges, running radially over

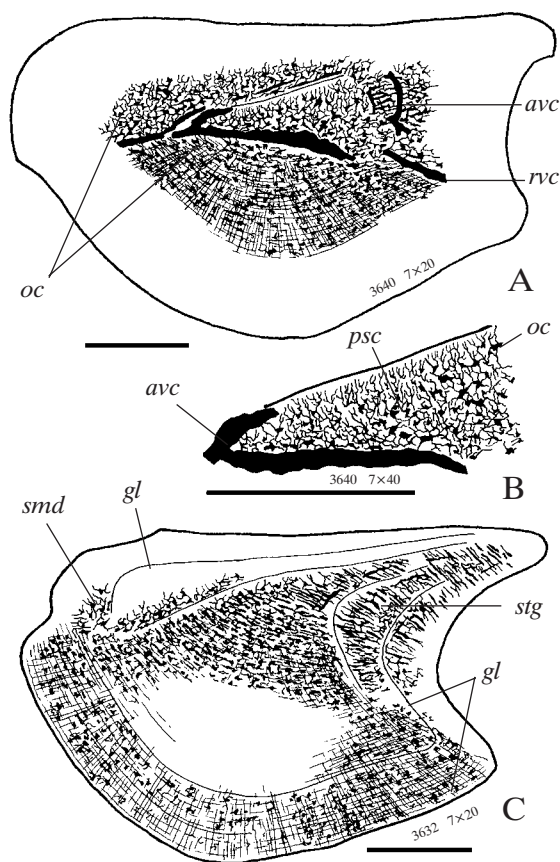


Fig. 5. *Nostolepis zinaidae* sp. nov.; histologic structure of scales. A – vertical longitudinal section of a specimen with weakened crown ornamentation (like that in Fig. 3 H). Thin section 3640; B – magnified central area of crown in primordial scale of the same specimen; C – vertical longitudinal section of the specimen similar to the holotype with high and sharp crown ridges. Thin section 3632. Tcherpayu-22 borehole, depth 2046.7-2052.6 m. Lower Devonian, Lochkovian, Khatayakha Formation. Bar: 0.1 mm. *Avc* – ascending vascular canal; *gl* – growth lamella; *oc* – osteocyte cavity; *psc* – primordial scale; *rvc* – radial vascular canal; *smd* – simple mesodentine; *stg* – *Stranggewebe* (mesodentine with oriented lacunae)

the whole crown, pointed posteriorly (Text-fig. 4H). Some have elongated and concave crowns, with posterior base overhang, a triangular medial area, and 2-3 short anterior ridgelets (Text-fig. 4K). Crown margins and a pair of clearly oblique neck ridges arising from the lateral base corners (Text-fig. 4 L, O, J, Q) point together to the posterior, giving a “starlet”-like picture. Below the posterior neck walls bear 2-4 vertical, parallel (Text-fig. 4J) or radial (Text-fig. 4G, O) ridgelets. Rarely neck ridges continue almost parallel to the crown rim and run in the middle between the crown rim and the base rim.

The crowns of the scales with long and posteriorly pointed ridges are composed of simple bone-like mesodentine, similar to that in *N. zinaidae* sp. nov. 3-4 thick growth lamellae show dense cellular tissue (Text-fig. 7A), apart from osteocyte spaces containing only short tubular

processes and lacking a system of enlarged vascular canals. This tissue continues up to the top of the youngest growth lamella. The moderately high-pyramidal base is composed of bone with numerous osteocytes and arranged in dense, thin growth plates, penetrated by Sharpey’s fibres.

The crowns of the scales with fading out ridges are composed of *Stranggewebe* and simple bone-like mesodentine (Text-fig. 7B), arranged into up to 8, distinctly thinner growth lamellae. *Stranggewebe* with fragments of large ascending vascular canals composes the posterior part of the crown, including the primordial scale. Almost all of the growth lamellae contain peripheral strips of simple mesodentine, portions of which increase posteriorly. The bone-like simple mesodentine of the crown and the bone tissue of the base do not differ from those of the above mentioned varieties. The central (being the

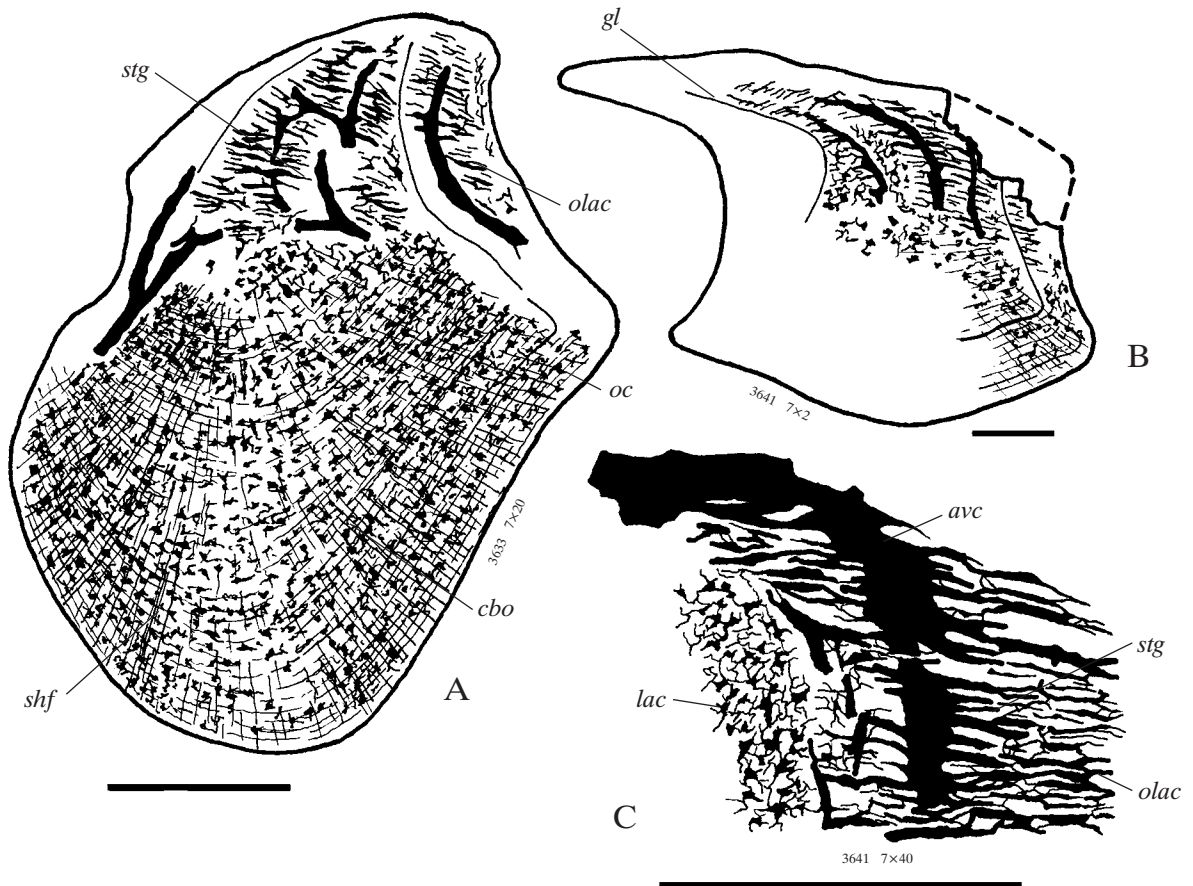


Fig. 6. *Nostolepis zinaidae* sp. nov.; histologic structure of scales. A – vertical longitudinal section of a specimen from the supposed lateral line, with asymmetric uneven crown ridges (like that in Fig. 3 F-G). Thin section 3639; B – vertical longitudinal section through a scale with the most elongated and narrowed crown (like that in Fig. 4 B). Thin section 3641; C – magnified central area in crown of the same specimen. Locality, horizon and bar – the same as for Fig. 5. Avc – ascending vascular canal; cbo – cellular bone; gl – growth lamella; lac – lacuna; oc – osteocyte cavity; olac – oriented lacuna; shf – Sharpey’s fibres; stg – *Stranggewebe*

thinnest) areas of the growth lamellae, apart from the primordial one, may be completely composed of durodentine (Text-fig. 7B).

REMARKS: Earlier (VALIUKEVICIUS 1994), I included *Nostolepis* sp. no. 3 (= *Nostolepis adzvensis* sp. nov.) into the synonymy of *Nostolepis laticristata*. More detailed study of the specimens from Timan-Pechora showed, however, that these two taxa are separate. In contrast to *N. adzvensis*, having highly cellular base bone, penetrated with long regularly streamed Sharpey's fibres, the base bone is almost acellular in *N. laticristata*, with characteristic variably streamed short Sharpey's fibres (VALIUKEVICIUS 1994, text-fig. 62:3-4). The crown mesodentine in *N. laticristata* is composed of upward directed

and clear branches of dentine canals, containing lacunae, and lacks the *Stranggewebe*.

Several specimens from the ?late Lochkovian of the Red Canyon River Formation of Arctic Canada, identified as *Gomphonchus* sp. cf. *G. hoppei* GROSS (VIETH 1980, pl. 8, fig. 17, 19 and 20), are very close morphologically, including the presence of the posterior neck structures. The sectioned scales, however, show simple mesodentine without lacunae in the crowns and almost acellular base bone (VIETH 1980, text-fig. 24 A-C).

Nostolepis adzvensis sp. nov. is also comparable with the Gondwanan species, *N. guangxiensis* WANG, described from the early Emsian Ertang Formation, central Guangxi, China. Both species are similar in the presence of oblique neck ridges and structures on the posterior neck. In contrast to *N. adzvensis*, however, the Chinese species (WANG 1992, pl. 1, figs 3-4) has, however, more regular and less pronounced rhombic scale crowns, ornamented with fading out anterior ridges. Moreover, its crown is not elongated and lacks either a lingual medial area or high posteriorly pointed ridges. Both species differ also in the histological characteristics of their crown tissues. *Stranggewebe* in *N. guangxiensis* (WANG 1992, pl. 1, fig. 5A-B) is absent, and its crown is composed of simple mesodentine with "...a few cell spaces, netty dentine tubules and well-developed system of fine vascular canals" (WANG 1992, p. 298). The wavy dentine network with prolonged canals and the enlarged lacunae spaces are clearly seen in both the anterior and posterior crown parts. The bone-like mesodentine with numerous osteocytes and only short processes, characteristic of *N. adzvensis*, is missing in the Chinese species.

N. guangxiensis, referred erroneously to the genus *Gomphonchus*? (BURROW 1997), is also known from the topmost Lochkovian-Pragian (*pesavis-sulcatus* conodont Zones) of the Trundle beds of the Jerula and Gleninga formations in central New South Wales, Australia. The Australian species (BURROW 1997, pl. 1, figs 4-8 and pl. 4, figs 1-6) is more diverse in crown ornamentation, including bifurcated ridges on the upper crown plate, and "...lateral slopes usually having three ridges each, though these may bifurcate close to the neck" (BURROW 1997, p. 65). Its histologic structure is poorly known. BURROW (op.cit.) mentioned rare scattered lacunae in the apex of the base cone, ascending vascular canals in each of the growth zones, dentine tubules filling most of the crown, and durodentine between the tubules and in the superficial growth plate. On the basis of these characters, he referred these scales provisionally to *Gomphonchus*. Subsequently, however, in the Addendum, distributed privately in October 1997, he redrew some of the scales previously published, demonstrating the lack of the ascending vasculars of the *Gomphonchus*-type, and con-

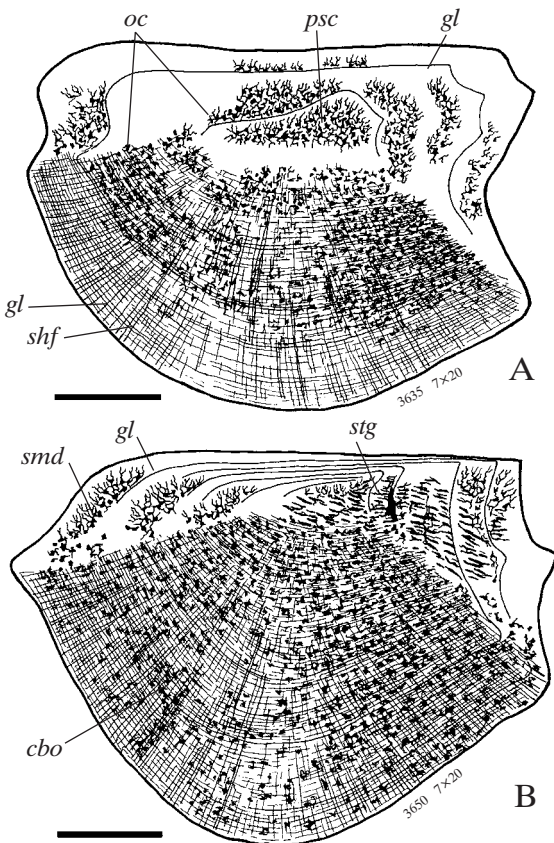


Fig. 7. *Nostolepis adzvensis* sp. nov.; Histology of scales. A – vertical longitudinal section of a specimen with high and pointed ridges at the posterior crown. Thin section 3635; B – vertical longitudinal section through a scale with short and fading out crown ridges (like positioned in Fig. 4 P). Thin section 3650. Tcherpayu-22 borehole, depth 2046.7-2052.6 m. Lower Devonian, Lochkovian, Khatayakha Formation. Bar: 0.1 mm. Cbo – cellular bone; gl – growth lamella; oc – osteocyte cavity; psc – primordial scale; shf – Sharpey's fibres; smd – simple mesodentine; stg – *Stranggewebe*.

sequently correcting his former interpretation, concluding that the scales derived from a climatiiform rather than from an ischnacanthiform acanthodian, which is fully confirmed here.

STRATIGRAPHIC RANGE: Only type horizon and its age analogue – the Ovinparma Formation; *remscheidensis* conodont Zone.

Nostolepis kozhymica sp. nov.
(Text-figs 8 A-J, 9 A-E)

1988. *Nostolepis* sp. no. 4; J. VALIUKEVICIUS, p. 604, table 2.

1993. *Nostolepis* sp. nov. 4; J. VALIUKEVICIUS, p. 29.

1995. *Nostolepis* sp. no. 4; J. VALIUKEVICIUS, p. 395, text-fig. 4.

2000. *Nostolepis* sp. nov. 4; J. VALIUKEVICIUS & S. KRUCHEK, p. 281, text-fig. 6.

HOLOTYPE: LIG 20-A-1686, trunk scale, crown view (Text-fig. 8E).

ETYMOLOGY: For the Kozhym River, subpolar Urals.

TYPE LOCALITY: The Kozhym River section, outcrop 236, samples 14-42.

TYPE HORIZON: Lower Devonian, Lochkovian, 1-2 members of the Ovinparma Formation.

MATERIAL: Over 5500 trunk and 42 supposed head scales.

DIAGNOSIS: *Nostolepis* with isometric or elongated rhomboid scales, having convex to deep bases and slightly protruding crowns. Crowns flat, ornamented with 6-8 strong, fading out anterior ridges, two pairs of which continue and point posteriorly, forming lateral areas; up to 3 oblique neck ridges on each side. Scale bases composed of densely lamellar cellular bone; crowns composed of mesodentine with networked tubules, numerous osteocytes, and *Stranggewebe*, both penetrated by a system of wide principal vascular canals, of which the most important is the second strip (the first is just over the base) of radial ones located high in the neck.

DESCRIPTION: The trunk scales, with an almost horizontal crown plate, are isometric rhomboid to rhomboid in outline, with elongated posterior, and wide, rounded anterior margins, rarely ellipsoidal or circular. The most common scales are as wide as long (0.36-0.78 and 0.43-0.81 mm respectively). Rare ellipsoidal crowns are longer than wide: 0.62-0.75 and 0.46-0.52 mm. The short poste-

rior crown overhang is visible in most of the trunk scales. The crown plate is thick, flat, ornamented with subparallel to subradial ridges, sloping downward anteriorly to the base rim. 6-8 strong and rounded anterior ridges continue subradially and fade out, not reaching halfway along the crown length (Text-fig. 8B, D). In some cases the two pairs of the posteriorly pointed longest marginal ridges form low symmetric lateral slopes (Text-fig. 8A, H-J) with multilobed to spiny margins. The marginal ridges run obliquely from the side base corners to the posterior crown tip, forming up to 3 neck ridges on each side (Text-figs 8A, E, J). Some of the crowns have distinct subradial, sharp anterior ridges (Text-fig. 8A), fading out halfway along the crown length. The scale bases are of rhombic outline, centrally convex, sometimes deep, slightly protruding beyond the crowns antero-laterally.

The supposed head scales (Text-fig. 8G) with round rhomboid, ellipsoid to circular, slightly convex crowns, are ornamented with 2-3 symmetric pairs of pointed, radial ridges, with wide and high anterior edges. 1-2 medial ridgelets are shorter and fade out at one-third of the crown length.

All of the scale varieties have compact bases, composed of highly cellular, densely lamellar bone, and the crowns are composed of simple mesodentine and *Stranggewebe*. The vascular system in the crowns includes wide radials, circulars and ascendings, forming the principal canal net (Text-fig. 9A, B, D). The peripheral strips of the growth lamellae are composed of simple mesodentine with numerous osteocytes, observed even in the superficial layers. The holotype-like specimens show the maximum *Stranggewebe* area (Text-fig. 9B-C) in the posterior part of the crown, embracing the primordial scale, whereas those with the lowered lateral crown slopes show only fragmentary *Stranggewebe* (Text-fig. 9A, D-E). In all of the examined scales, the *Stranggewebe* contains less pronounced *Stranglakunen* than in *Nostolepis adzvensis*. A distinctive feature of the scales is the presence, high in the crown, of the second strip (the first is located just over the base cone) with wide radial vascular canals opening on the posterior neck (Text-fig. 9E).

REMARKS: The only form showing some similarity to *N. kozhymica* sp. nov. is *Nostolepis multicostata* VIETH (VIETH 1980, pl. 4, figs 1-5), from Member A of the Red Canyon River Formation (late? Lochkovian) of Arctic Canada. It differs, however, in the higher number of ridges and their variable shape, and also in the histologic structure, particularly of the crown tissues. *N. multicostata* lacks the *Stranggewebe*, and its simple mesodentine without radial vascular canals contains only few lacunae (VIETH 1980, text-fig. 16A-C).

For comparative remarks to *Nostolepis platycrista* sp.

nov. and *Nostolepis minilonga* sp. nov. see descriptions of the respective species.

STRATIGRAPHIC RANGE: Timan – Pechora region; it ranges from the Přidoli (Upper Silurian) to the upper part, but not to the top, of the Lochkovian (Lower Devonian); the youngest representatives found in the lower member of the Toravey Formation (see Text-fig. 2). An interval representing the *remscheidensis* and *optima* conodont zones (DEULIN 1991).

Nostolepis parathleta sp. nov.
(Text-figs 10 A-H, 11 A-B)

2000. *Nostolepis* sp. n. 33; J. VALIUKEVICIUS, p. 134, text-fig. 1.

HOLOTYPE: LIG 20-A-2237, trunk scale (Text-fig. 10A).

ETYMOLOGY: Due to the resemblance to *Nostolepis athleta* VALIUKEVICIUS (1994).

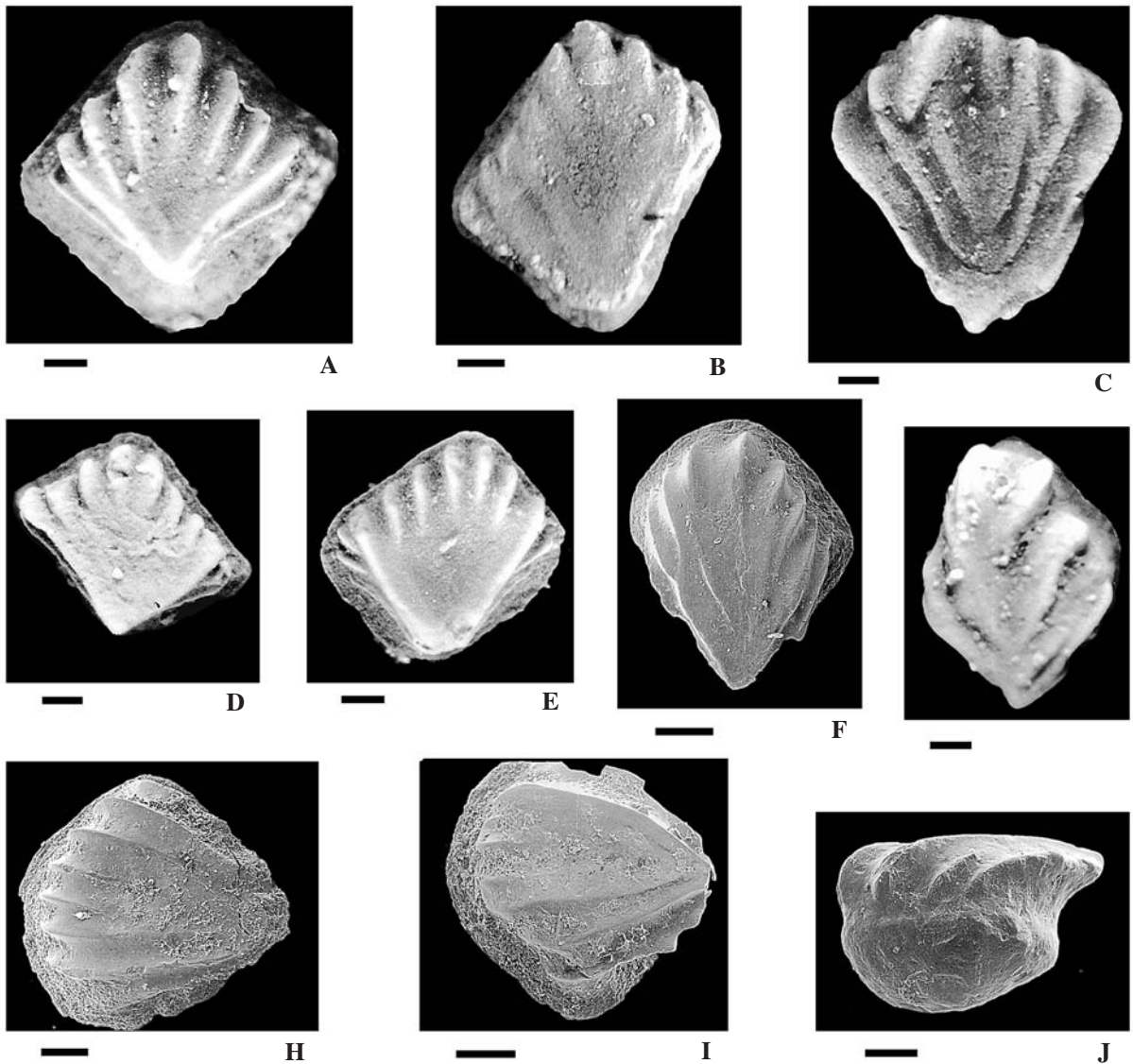


Fig. 8. *Nostolepis kozhymica* sp. nov.; Trunk (A-F, H-J) and head (G) scales, crowns, anterior upward (A-G) or to left (H-I) and scale side view (J): A – LIG 20-A-1702; B – LIG 20-A-1835; C – LIG 20-A-1635; D – LIG 20-A-1703; E – holotype, LIG 20-A-1686; F – LIG 20-A-2210; G – LIG 20-A-1636; H – LIG 20-A-2241; I – LIG 20-A-2240; J – LIG 20-A-2361. Vuktyl-58 borehole, depth 6003-6008 m (A, D); Labagan-76 borehole, depth 4117-4123 m (B); the Kozhym River section, outcrop 236, beds 16-18 (C, G); Vozey-84 borehole, depth 3116-3130 m (E); West Lckeyiyaga-46 borehole, depth 3101-3109 m (F); North Saremboy-19 borehole, depth 3117-3124 m (H-I); Vaney Vis-1 borehole, depth 4145.5-4151.9 m (J). Lower Devonian, Lochkovian: Khatayakha Formation (A-B, D-E), Ovinparma Formation (C, G), Toravey Formation (F, H-I) and Kumzha Formation (J). Bar: 0.1 mm.

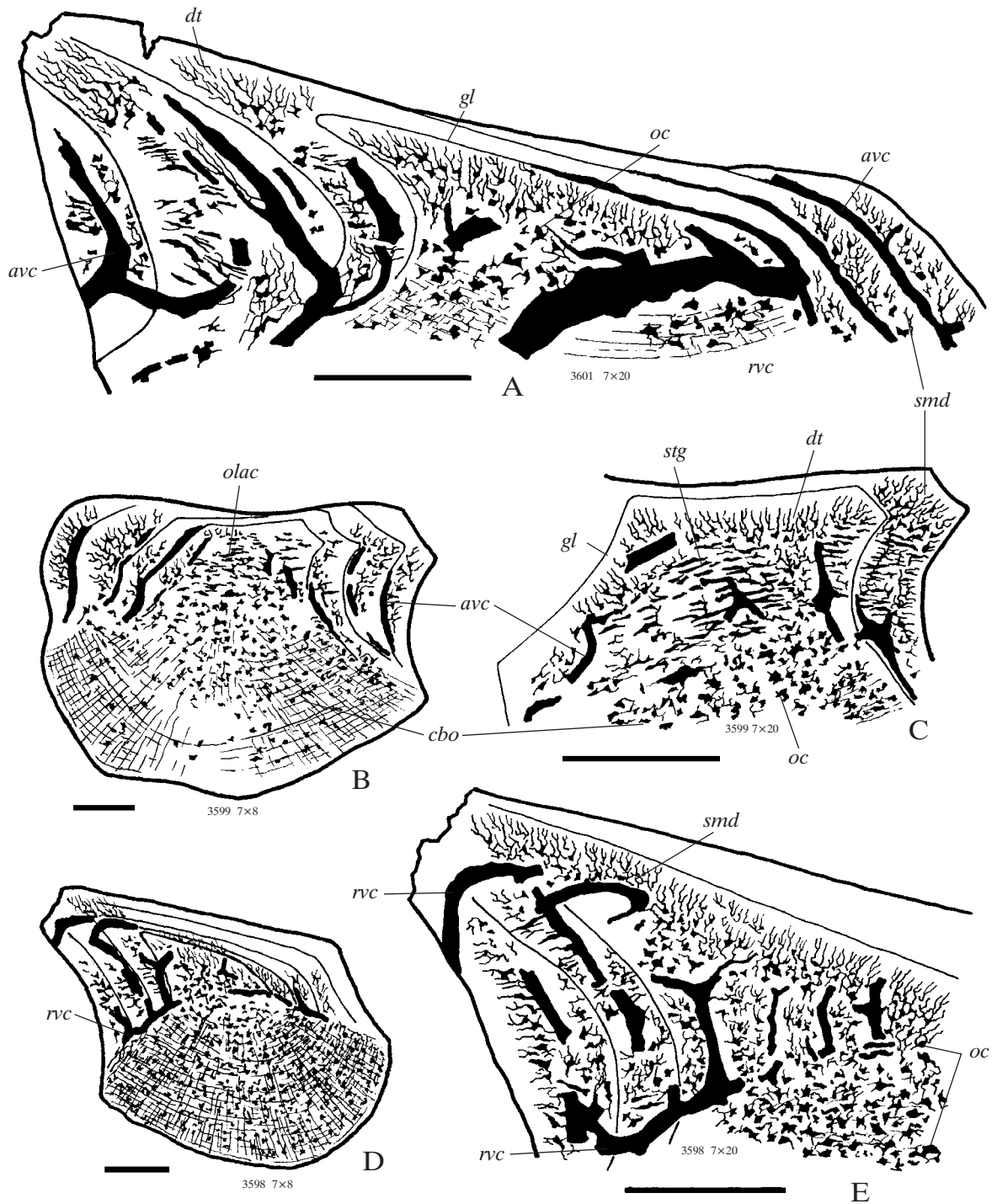


Fig. 9. *Nostolepis kozhymica* sp. nov.; Histology of scales. **A** – vertical longitudinal section through the crown of a specimen like that in Fig. 8 C. Thin section 3601; **B** – vertical transverse section of a specimen similar to the holotype. Thin section 3599; **C** – magnified area embracing primordial scale of the same specimen; **D** – vertical longitudinal section of a specimen with elongated lateral and short, fading out medial crown ridges (like that in Fig. 8 I). Thin section 3598; **E** – magnified left part of crown (primordial scale with a base fragment) of the same specimen. Miadsey-1 borehole, depth 3619-3626 m. Lower Devonian, Lochkovian, Toravey Formation, Member 1. Bar: 0.1 mm. *Avc* – ascending vascular canal; *cbo* – cellular bone; *dt* – dentine tubule; *gl* – growth lamella; *oc* – osteocyte cavity; *olac* – oriented lacuna; *rvc* – radial vascular canal; *smd* – simple mesodentine; *stg* – *Stranggewebe*.

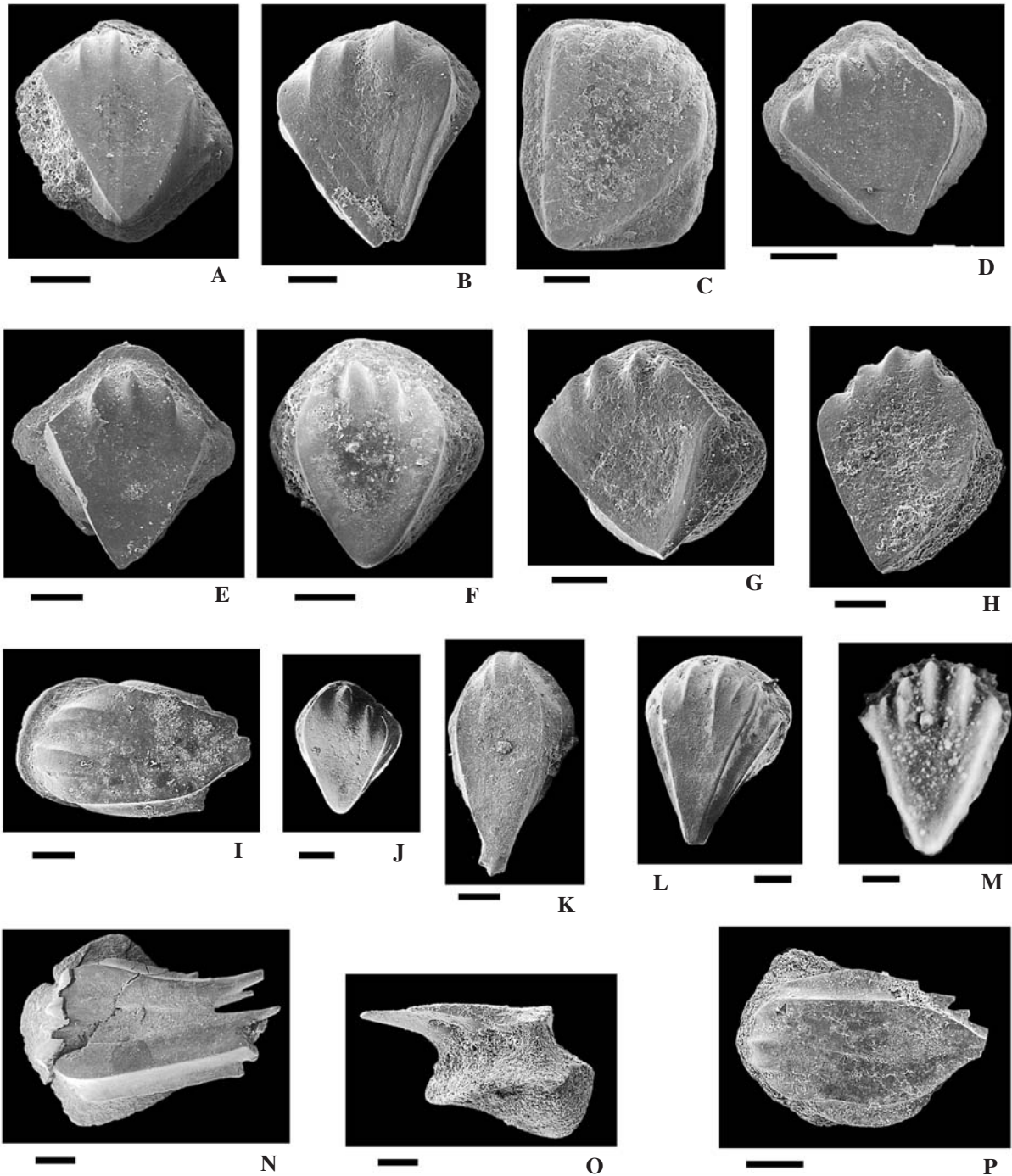


Fig. 10. **A-H** – *Nostolepis parathleta* sp. nov.; Trunk scales, crowns, anterior upward: A – holotype, LIG 20-A-2237; B – LIG 20-A-2248; C – LIG 20-A-2236; D – LIG 20-A-2308; E – LIG 20-A-2307; F – LIG 20-A-2198; G – LIG 20-A-2246; H – LIG 20-A-2247. Varandey-7 borehole, depth 4092-4099 m (A, C, F); Sed'yaga-4 borehole, depth 3144-3156 m (B, G-H); Värknävt-7 borehole, depth 4126-4143 m (D-E). Lower Devonian, Lochkovian: Toravey Formation (A-C, F-H) and Khatayakha Formation, members 1-2 (D-E). Bar: 0.1 mm

I-P – *Nostolepis longipostera* sp. nov.; Trunk scales, crowns, anterior to left (I, N, P) or upward (J-M), and scale side view, anterior to right (O): I – holotype, LIG 20-A-2183; J – LIG 20-A-1954; K – LIG 20-A-2317; L – LIG 20-A-1953; M – LIG 20-A-1872; N – LIG 20-A-2314; O – LIG 20-A-2315; P – LIG 20-A-2184. Verkhnyaya Sotch-1 borehole, depth 2622-2623 m (I, P); Inzyrey-205 borehole, depth 4578.5-4584.9 m (K, N-O); Sed'yaga-3 borehole, depth 3171-3177 m (J, L); Ust'Talota-1 borehole, depth 3318.8-3322.2 m (M). Lower Devonian, Lochkovian: Khatayakha Formation, members 1-2 (J-O) and Ovinparma Formation (I, P). Bar: 0.1 mm

TYPE LOCALITY: Varandey-7 borehole, depth 4092-4099 m.

TYPE HORIZON: Lower Devonian, Lochkovian, the lower (terrigenous-carbonate) Member of the Toravey Formation.

MATERIAL: Over 4250 scales, supposedly all trunk specimens.

DIAGNOSIS: *Nostolepis* with scales ornamented by short and flattened anterior ridges extending to a quarter of crown length; neck ridges present on one or both sides, or absent; scale bases moderately deep, extending all around the crowns. Scale crowns composed of bone-like networked mesodentine with plenty of osteocytes and *Stranggewebe* with long *Stranglakunen*, occupying posterior or crown part; bases composed of thin-lamellar cellular bone.

DESCRIPTION: The scales are of moderate size with the crown slightly longer than wide (0.33-0.61 and 0.3-

0.52 mm respectively). The crown plate is almost flat, rarely slightly concave. The crowns vary from rhomboid, with sharp corners (Text-fig. 10D-E, G), to drop-shaped or ellipsoidal with inwardly bent lateral rims (Text-fig. 10F, H). The posterior part of the crown is narrower, without base overhang. 3-5 low, flattened, parallel anterior ridges continue over less than a quarter of the crown length. They are straight or medially bent and slope slightly baseward. The ridges are very regularly spaced along the entire anterior margins. Rarely they are located on a single side only (Text-fig. 10D). Several specimens have neck ridges (Text-fig. 10G) flanking the narrow lateral slopes, that may widen at the lateral crown corners. The common asymmetric slopes (or a slope) are present only on one side. The antero-centrally convex and moderately deep base is of rhombic or quadrangular outline, sometimes wider than long; it extends all around the crown or does not protrude beyond its posterior tip.

The 3-4 thick growth lamellae of the crown are composed of simple mesodentine resembling bone tissue, penetrated densely by short, winding dentine tubules and numerous osteocytes even in the superficial layers (Text-fig. 11B). Widened ascending and radial (over the base) vascular canals are present. The posterior part of the crown, including the primordial scale, is composed of *Stranggewebe* with long *Stranglakunen* (Text-fig. 11A). The thin-lamellar bone, penetrated by long Sharpey's fibres and numerous osteocytes, form a low-pyramidal or almost flat base.

REMARKS: *Nostolepis athleta* VALIUKEVICIUS from the Lochkovian and Pragian of Taimyr, has a better developed ridged medial area with multilobed to spiny lateral slopes (VALIUKEVICIUS 1994, pl. 19, figs 12-15). Moreover, its scale bases are larger, deeper and more advanced anteriorward. Histologically, *N. athleta* has up to 7 growth lamellae in the scale crowns, it lacks the *Stranggewebe* and the principal system of vascular canals, and its crown has neither the simple mesodentine with dense ascending canals, nor the lacunae or osteocytes (VALIUKEVICIUS 1994, text-fig. 65:1-2).

For comparison with *N. adzvensis* see description above.

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, Khatayakha and Toravey formations or their facial correlatives.

Nostolepis longipostera sp. nov.
(Text-figs 10 I-P, 12 A-D)

2000. *Nostolepis* sp. n. 30; J. VALIUKEVICIUS, p. 134, text-fig. 1.

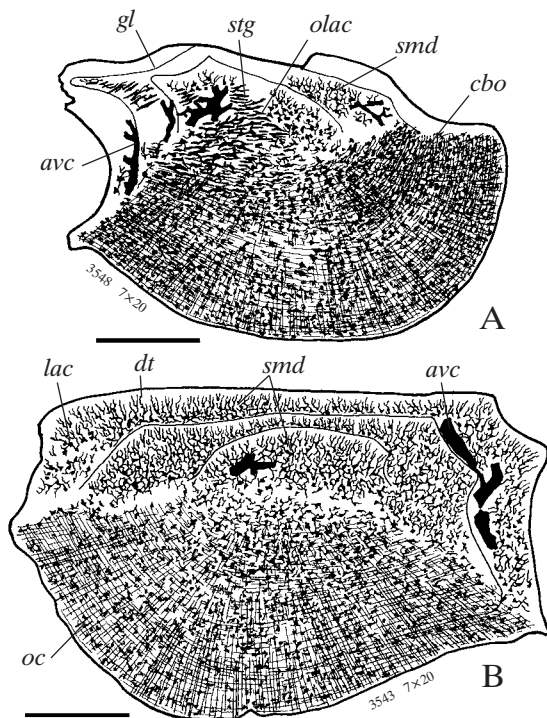


Fig. 11. *Nostolepis parathleta* sp. nov.; Histologic structure of scales in vertical longitudinal sections. A – thin section 3548; B – thin section 3543. Varknavt-23 borehole, depth 4278-4285 m. Lower Devonian, Lochkovian, Formation not certain defined, supposed Khatayakha. Bar: 0.1 mm. *Avc* – ascending vascular canal; *cbo* – cellular bone; *dt* – dentine tubule; *gl* – growth lamella; *lac* – lacuna; *oc* – osteocyte cavity; *olac* – oriented lacuna; *smd* – simple mesodentine; *stg* – *Stranggewebe*

HOLOTYPE: LIG 20-A-2183, trunk scale (Text-fig. 10I).

ETYMOLOGY: Due to the distinctly elongated posterior part of the scale crown.

TYPE LOCALITY: Varknavt-5 borehole, depth 4082-4089 m.

TYPE HORIZON: Lower Devonian, Lochkovian, members 1-2 of the Khatayakha Formation.

MATERIAL: About 3300 scales.

DIAGNOSIS: *Nostolepis* with elongated scales, flat crowns, ornamented with 2-4 fading out, short anterior ridges, flanked by a pair of longest ones. Crowns composed of modified mesodentine (?orthodentine) and long ascending and radial vascular canals; simple mesodentine developed in primordial scale, and durodentine centrally – in all growth lamellae after primordial. Bases composed of almost acellular bone.

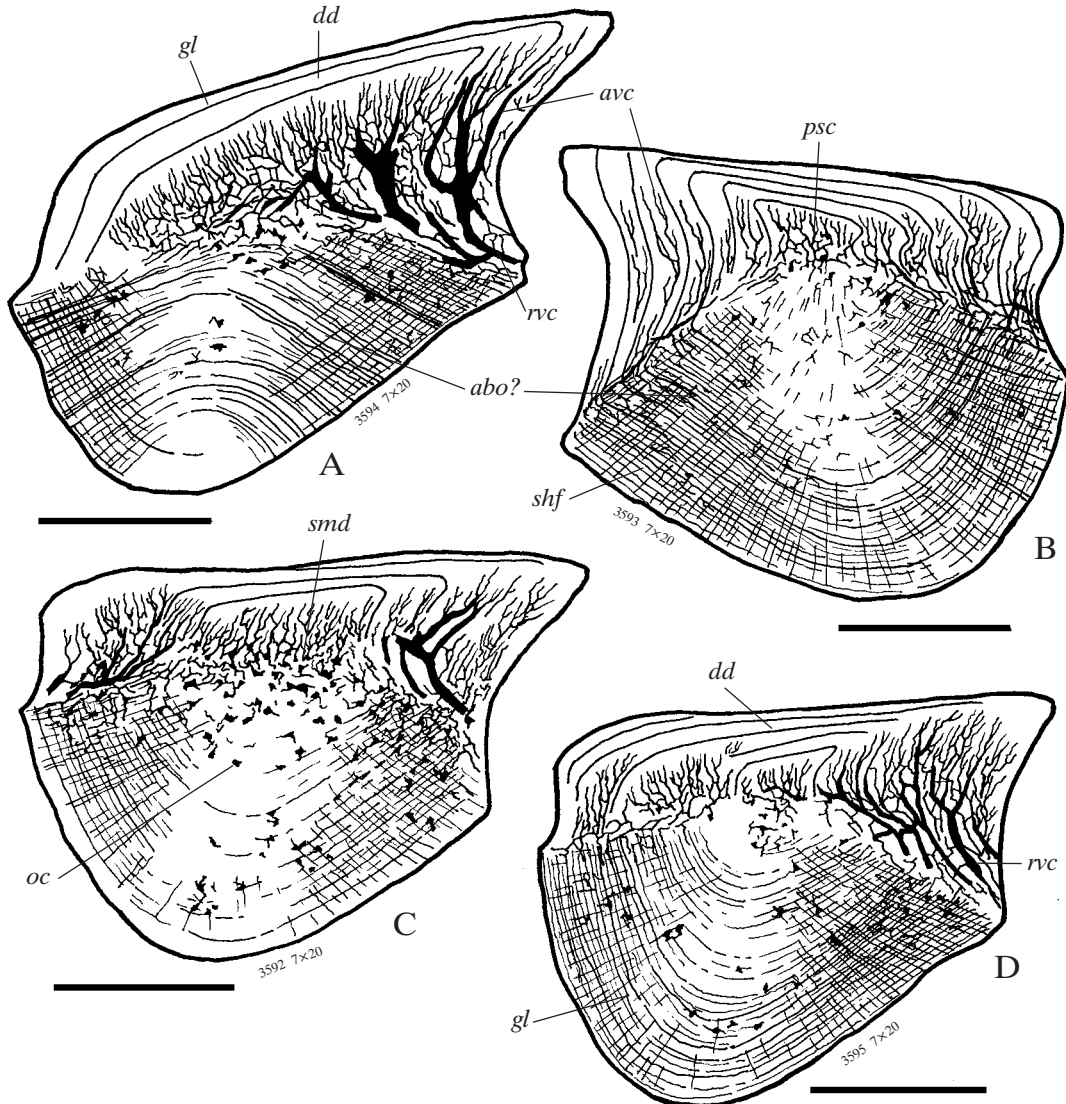


Fig. 12. *Nostolepis longipostera* sp. nov.; Histology of scales in vertical longitudinal sections. A – the specimen similar to the holotype with narrow lowered lateral areas. Thin section 3594; B – scale with short anterior crown ridges, without lateral slopes (like that in Fig. 10 M). Thin section 3593; C – scale with the most elongated crown and long lateral ridges flanking shallow medial concavity (like that in Fig. 10 N). Thin section 3592; D – scale with weak crown ornamentation, like that in Fig. 10 K. Thin section 3595. Varknavt-5 borehole, depth 4082-4089 m. Lower Devonian, Lochkovian, Khatayakha Formation, Member 2. Bar: 0.1 mm.

Abo? – acellular? bone; *avc* – ascending vascular canal; *dd* – durodentine; *gl* – growth lamella; *oc* – osteocyte cavity; *psc* – primordial scale; *rvc* – radial vascular canal; *shf* – Sharpey's fibres; *smd* – simple mesodentine.

DESCRIPTION: The scales are elongated (crown length: 0.4-0.75 mm, width 0.29-0.44 mm) with ellipsoidal, rarely rhombic to triangular outline. The crowns are flat, with a wide and rounded anterior margin and a narrow posterior tip. The crowns overhang the bases posteriorly. The ellipsoidal specimens have rounded side corners (Text-figs 10I, K, P), with its widest portion at the crown's midlength. The narrow, slightly sloping, symmetric lateral areas occur in numerous scales, rarely additional posterior spinelets occur (Text-fig. 10P). The 2-4 fading out short central ridges continue subparallel to one-third of the crown length. Rarely they occur only in an extremely narrow anterior strip (Text-fig. 10K). The longest, ellipsoidally bent ridges, forming the medial area, point to the posterior crown tip or diverge near to it (Text-fig. 10I, K, P). Rare specimens have an asidely bent and well elevated medial area without anterior ribbing, but with shallow longitudinal concavity and much more lowered lateral slopes, flanked by the neck ridges (Text-fig. 10N). The scale neck is moderately high, clear on all sides. The deep base, with the latero-anterior swelling, protrudes slightly beyond the crown. Rarely, the bases are located far to the anterior, with the deepest portion protruding beyond the anterior crowns.

The scale crown is composed of durodentine and modified mesodentine, located in up to eight superimposed growth lamellae. Characteristic simple mesodentine is observed only in the primordial scale or in the two oldest lamellae (Text-fig. 12B-C). It contains rare, random osteocytes and clear upward directed winding dentine tubules. The younger growth lamellae are composed of modified mesodentine with distinct main branches of radial (over the base, Text-fig. 12A) and ascending vascular canals (Text-fig. 12A, C-D), densely interwoven with dentine tubules. The tissue becomes intermediate in character between meso- and orthodentine. This concerns mainly the posterior part of the crown; the anterior part shows normal mesodentine structures (Text-fig. 12D). Neither *Stranggewebe* nor lacunae were observed. The central crown area of all of the growth lamellae, besides the primordial one, is composed of durodentine (Text-fig. 12B, D). The almost acellular, densely lamellar bone of the flattened low-pyramidal base is pierced by long Sharpey's fibres and contains single random osteocytes, the number of which may increase tipward (in the primordial scale, Text-fig. 12C).

REMARKS: *Nostolepis longipostera* sp. nov. resembles *N. minima* VALIUKEVICIUS, known from the early Lochkovian of Taimyr, Baltic and other regions. *N. minima* scales are similar, with flat, slightly elongated crowns, weakly ridged medial area, and with oblique lateral ridges flanking lowered side slopes (VALIUKEVICIUS 1994, pl. 21, figs 10-12; 1998, pl. 1, figs 5-9). Both species differ in the histologic structure. *N. minima* shows "Nostolepis"-type

histology with characteristic mesodentine, *Stranggewebe* in the scale crowns (VALIUKEVICIUS 1998, pl. 12, figs 2-6), and highly cellular bone in the bases. The specimens from Taimyr repeat virtually all of the characters with the exception of the reduced *Stranggewebe* area (VALIUKEVICIUS 1994, text-fig. 75:1-4).

Nostolepis timanica, described from the Severnaya Zemlya Archipelago (VALIUKEVICIUS 2003, figs 25-26), and occurring commonly in the Lochkovian to the Emsian of the Timan-Pechora region, differs clearly from *N. longipostera*. In contrast to the latter, its scales never have laterally sloped crown areas, their crown plate is medially concave, with anterior rounded ridges of variable shape and length, and they are quite distinct histologically.

Histologically, *N. longipostera* resembles *Watsonacanthus costatus* VALIUKEVICIUS from the Emsian of Severnaya Zemlya (VALIUKEVICIUS 2003): both have modified mesodentine, an intermediate tissue between meso- and orthodentine, with long ascending and branching radial canals over the base, and lack osteocytes, lacunae and *Stranggewebe* in the crowns. *W. costatus* differs in having clear cellular bone in the scale bases (VALIUKEVICIUS 2003, fig. 32). These are far advanced anteriorly in relation to the crown plate. The species is also distinguished by sharp radial outer ridges and the lack of neck ridges.

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, Khatayakha Formation and the lower (terrigenous-carbonate) Member of the Toravey Formation or their facial correlatives.

Nostolepis platycrista sp. nov.
(Text-figs 13 A-E, 14 A-C)

2000. *Nostolepis* sp. n. 29; J. VALIUKEVICIUS, p. 134, text-fig. 1.

HOLOTYPE: LIG 20-A-1634, trunk scale (Text-fig. 13A).

ETYMOLOGY: From *platy* (Greek) – wide and *crista* (Latin) – ridge, referring to crown ornamentation.

TYPE LOCALITY: Toboy-11 borehole, depth 3382-3389 m.

TYPE HORIZON: Lower Devonian, Lochkovian, the lower (terrigenous-carbonate) Member of Toravey Formation.

MATERIAL: About 260 scales.

DIAGNOSIS: *Nostolepis* with isometric scales of moderate size having 6-8 widened, rounded, sometimes bifur-

cated, anteriorly slightly downsloping ridges, running half-way of crown length. Scale bases deep, projecting to somewhat beyond the anterior crown margin. Bases composed of cellular bone with variable number of osteocytes. Crowns composed of simple mesodentine with long and straight networked ascending vascular canals and contain osteocytes only in the neck area.

DESCRIPTION: The species has isometric scales with rhomboid crowns, high necks and deep bases. The crowns are horizontal, as long as wide, varying from 0.39 to 0.81 mm. The anterior margin of the crown is rounded to angulate, the posterior one is slightly elongated, with small base overhang. The 6-8 strong, wide, rounded, straight, subparallel to subradial anterior ridges fade out

halfway along the crown length. They slope slightly downward to the anterior base (Text-fig. 13B) with almost no reduction of the neck height. Rare specimens have shortly bifurcated medial ridges (Text-fig. 13D). The crown side corners are downsloped, and a pair of marginal ridges may converge radially into the crown rims (Text-fig. 13C). Neck ridges never occur. Sometimes the last but one pair of the ridges becomes the longest and points posteriorly (Text-fig. 13A). The deep, centrally vaulted base of the isometric rhomboid outline projecting to or somewhat beyond anterior crown margin.

The specimens similar to the holotype (with one pair of the longest posteriorly pointed ridges) show crown mesodentine (Text-fig. 14A) slightly differing from that of the other scale varieties. The ascending vascular canals

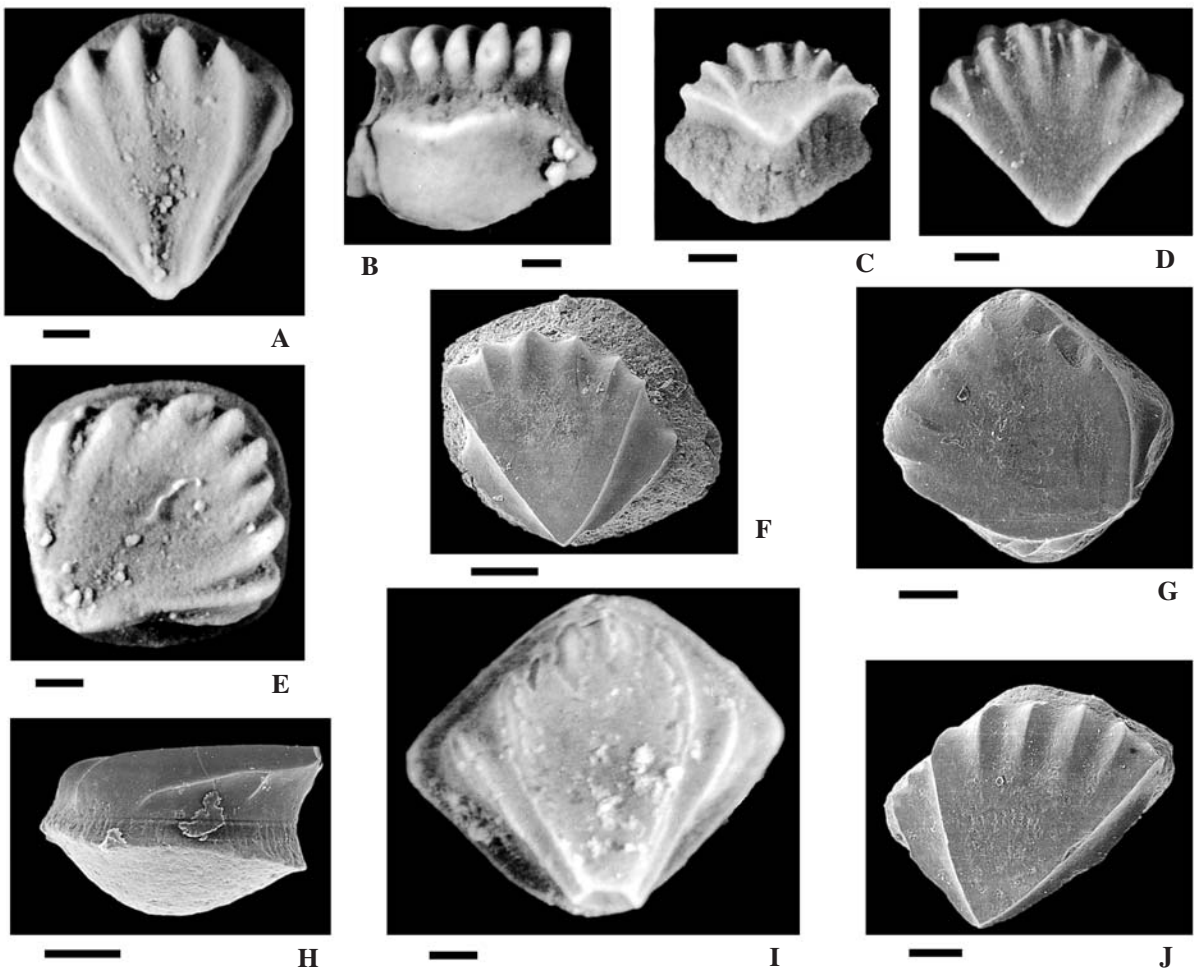


Fig. 13 **A-E** – *Nostolepis platycrista* sp. nov.; Trunk scales, crowns, anterior upward (A, C-E) and scale anterior side view (B): A – holotype, LIG 20-A-1634; B – LIG 20-A-1874; C – LIG 20-A-1871; D – LIG 20-A-1873; E – LIG 20-A-1633. Toboy-11 borehole, depth 3382-3389 m (A, E); North Saremboj-19 borehole, depth 3117-3124 m (B-D). Lower Devonian, Pragian, Naul' Formation, Member 1 (A, E) and Lochkovian, Toravey Formation, Member 1 (B-D). Bar: 0.1 mm. **F-J** – *Nostolepis terraborea* sp. nov.; Trunk scales, crowns, anterior upward (F-G, I-J) and scale side view, anterior to left (H): F – holotype, LIG 20-A-2251; G – LIG 20-A-2212; H – LIG 20-A-2254; I – LIG 20-A-1889; J – LIG 20-A-2252. Toravey-25 borehole, depth 4251-4255 m (F, H, J); West Lekeiyaga-46 borehole, depth 3101-3109 m (G); Sed'yaga-4 borehole, depth 3144-3156 m (I). Lower Devonian, Lochkovian, Toravey Formation, Member 1. Bar: 0.1 mm

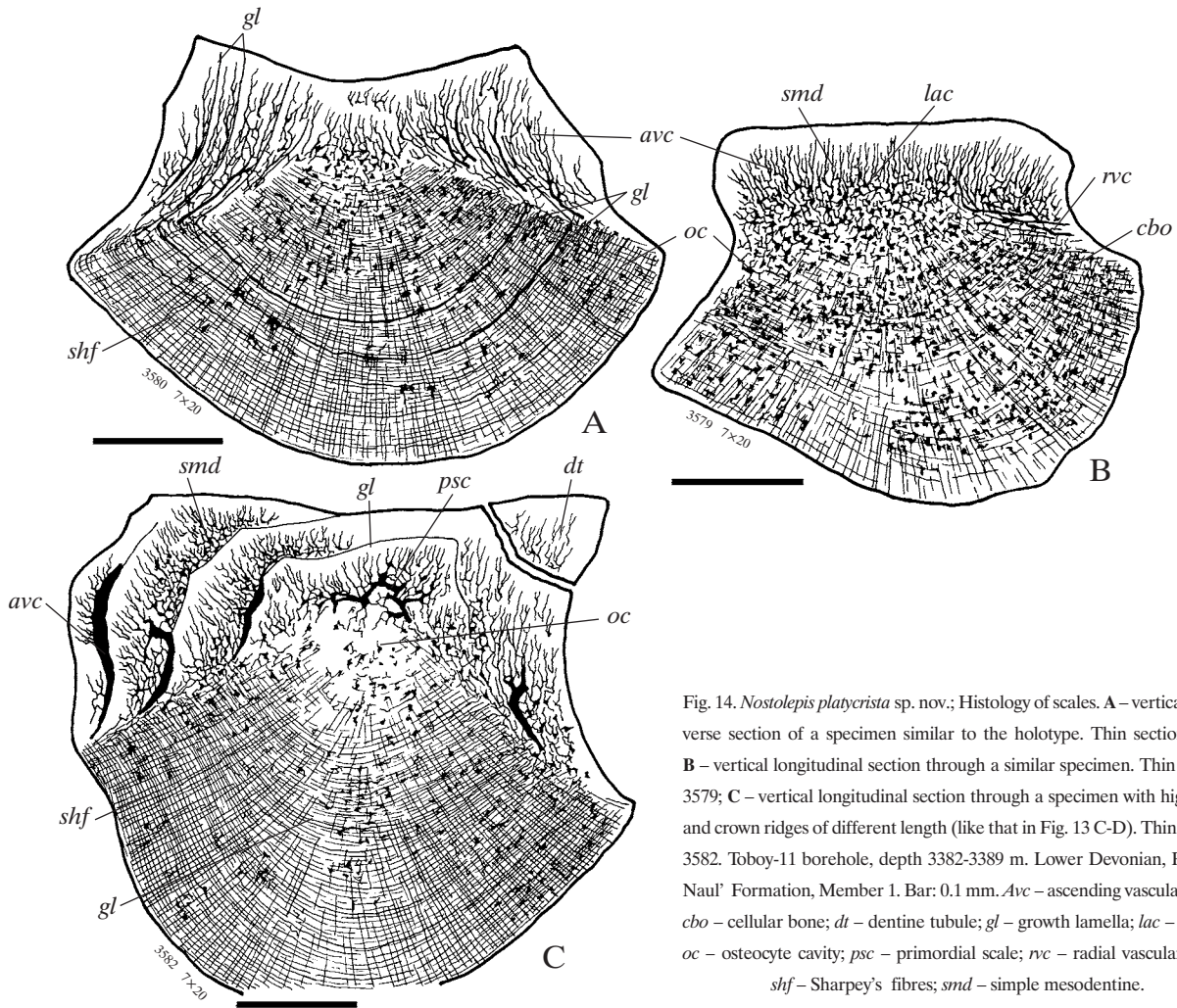


Fig. 14. *Nostolepis platycrista* sp. nov.; Histology of scales. A – vertical transverse section of a specimen similar to the holotype. Thin section 3580; B – vertical longitudinal section through a similar specimen. Thin section 3579; C – vertical longitudinal section through a specimen with high neck and crown ridges of different length (like that in Fig. 13 C-D). Thin section 3582. Toboy-11 borehole, depth 3382-3389 m. Lower Devonian, Pragian, Naul' Formation, Member 1. Bar: 0.1 mm. Avc – ascending vascular canal; cbo – cellular bone; dt – dentine tubule; gl – growth lamella; lac – lacuna; oc – osteocyte cavity; psc – primordial scale; rvc – radial vascular canal; shf – Sharpey's fibres; smd – simple mesodentine.

are long, more linearly upstreamed and they contain wide main and interwoven side branches. The osteocyte cavities occur exclusively in the primordial scale.

Other scale varieties have the crowns composed of a simple mesodentine, densely penetrated with uniform dentine tubules, with the osteocytes in the neck area (Text-fig. 14B). Higher in the crown occur ascending canals similar to the first variety. The scales with the deepest base and the highest neck have clear superpositionally lamellar crowns and wide principal ascending and radial vascular canals located in the basal parts of growth lamellae (Text-fig. 14C). This also concerns the primordial scale. The variable number of osteocytes in the bases is caused, most probably, by the fossilization and preservation conditions.

REMARKS: *N. platycrista* sp. nov., resembles closely *N. kozhymica* sp. nov. They have a similar number (6-8) and form of the fading out crown ridges, which differ only in details: the ridges in *N. platycrista* turn down and run

baseward. Neither bifurcated ridges in *N. kozhymica*, nor neck ridges or lateral crown slopes in *N. platycrista* were observed. The latter also differs in the lack of *Stranggewebe* and in the presence of narrow and uniform ascending vascular canals with a smaller number of lacunae and osteocytes in the crown (present only in the neck); a system of principal vascular canals is weakly developed or absent in the crowns of some scale varieties in *N. platycrista*.

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, Toravey Formation (*optima* conodont Zone, DEULIN 1991) through to Pragian, the lower Member of the Naul' Formation.

Nostolepis terraborea sp. nov.
(Text-figs 13 F-J, 15 A-C)

2000. *Nostolepis* sp. n. 31; J. VALIUKEVICIUS, p. 135, text-fig. 1.

HOLOTYPE: LIG 20-A-2251, trunk scale (Text-fig. 13F).

ETYMOLOGY: From *terra* – land and *borea* – north (Latin), referring to the arctic region of origin.

TYPE LOCALITY: Sed'yaga-4 borehole, depth 3144-3156 m.

TYPE HORIZON: Lower Devonian, Lochkovian, Member 1 of the Toravey Formation.

MATERIAL: Over 3400 scales.

DIAGNOSIS: *Nostolepis* with scales of moderate size, rhomboid to quadrangular in outline, slightly inclined crowns with triangular medial, anteriorly short-ridged area and distinctly lowered lateral slopes flanked by the neck ridges. Scale crowns (3-4 lamellae of superimposed growth) composed of *Stranggewebe* in posterior half, embracing primordial scale, and simple mesodentine with osteocytes even in outer layers, in anterior half. Bone in bases highly cellular.

DESCRIPTION: The scales have slightly inclined to almost horizontal, flat crowns, high posterior necks and moderately deep to deep bases, protruding slightly beyond the crowns on all sides. The crowns are isometric rhomboid, posteriorly elongated rhomboid, to quadrangular or triangular, as long as wide or slightly wider than long (0.38-0.71 and 0.34-0.7 mm respectively). The predominant forms have a clear triangular medial area (Text-fig. 13F, J) flanked by the longest ridges, which point at a posterior crown tip with a pair of neck ridges. The lateral slopes of the crown are well developed. The medial area is ornamented with 4-6 subparallel, short, sharp anterior ridges, fading out at one-third of the crown length. They slope down anteriorward almost to the base rim, thus distinctly lowering the anterior neck of the scale. The neck ridges extend obliquely from the base side corners, flanking the anteriorly widened lateral areas. Scales with an asymmetric crown shape and a lateral slope present only on one side (Text-fig. 13J) are also common.

The specialized scales (perhaps from the head area?) have a quadrangular outline (Text-fig. 13G). Their anteri-

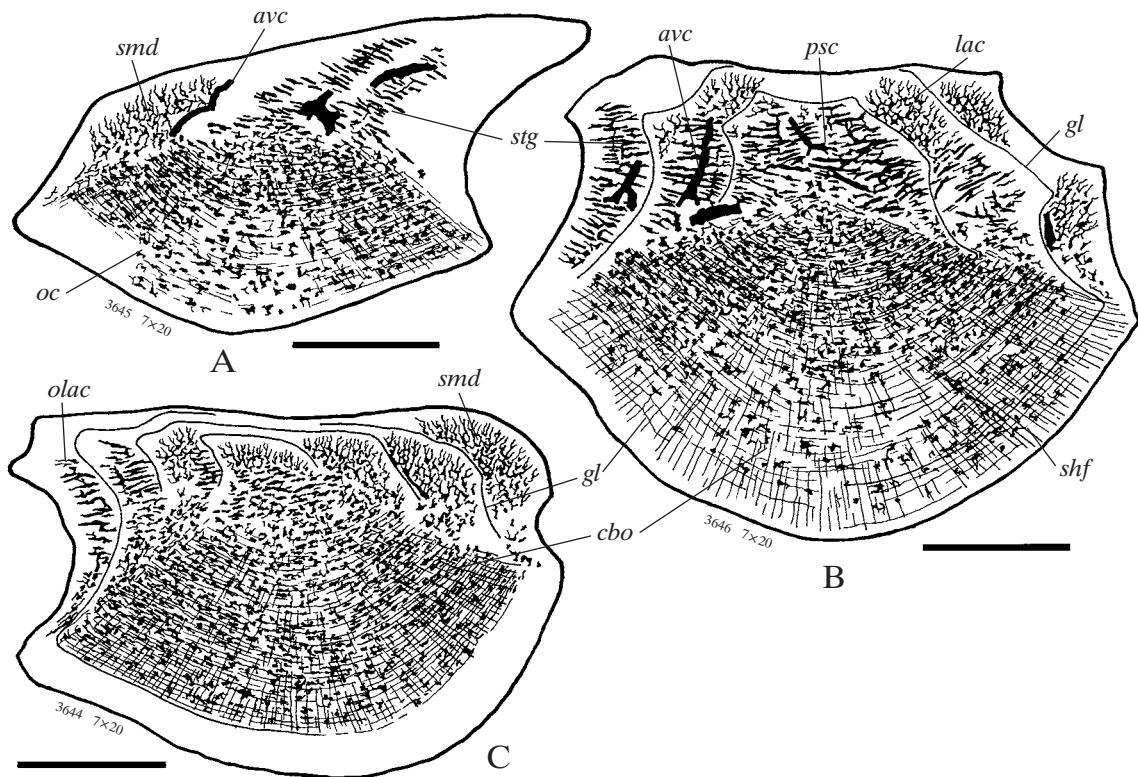


Fig. 15. *Nostolepis terraborea* sp. nov.; Histology of scales. Vertical longitudinal (A) and transverse (B) sections of a specimen similar to the holotype. Thin sections 3645 and 3646 respectively; C – vertical longitudinal section of a scale with posteriorly widened lingual crown and rounded shorter anterior ridgelets (like that in Fig. 13 G). Thin section 3644. Sed'yaga-4 borehole, depth 3144-3156 m. Lower Devonian, Lochkovian, Toravey Formation, Member 1. Bar: 0.1 mm.

Avc – ascending vascular canal; *cbo* – cellular bone; *gl* – growth lamella; *lac* – lacuna; *oc* – osteocyte cavity; *olac* – oriented lacuna; *psc* – primordial scale;

shf – Sharpey's fibres; *smd* – simple mesodentine; *stg* – *Stranggewebe*

or margin is straight, ornamented with short, low ridgelets and makes almost a right angle with the laterals that are rounded posteriorward. In contrast to the former variety, they have short lateral neck ridges, extending from the posterior neck corners and converging to the posterior crown margins.

Scales with deep, rhomboid to quadrangular, centrally swollen bases are dominant. Rare specimens have crowns overhanging the bases slightly in the posterior part.

Only small differences in histologic structure are observed between the specimens similar to the holotype and those representing supposedly the head area. The scales of the holotype (with clear lateral crown slopes) have crowns composed of *Stranggewebe* and simple mesodentine located in the 3-4 thick superimposed growth lamellae. A system of principal ascending, circular and radial vascular canals is developed (Text-fig. 15A-B). The *Stranggewebe* embraces the whole posterior crown half including the primordial scale. The *Stranglakunen* are clear and of moderate length. The simple mesodentine with winding dentine tubules contains osteocytes also in the superficial crown layers. The bone of the low-pyramidal base is highly cellular, built up of numerous thin and densely grown lamellae, penetrated by moderately long Sharpey's fibres.

The scales presumably from the head area are slightly different in the *Stranggewebe* characters. The oldest growth lamellae (primordial and the second one) are capped by wide strips of simple mesodentine similar to that of the anterior crown (Text-fig. 15C).

REMARKS: The species is similar to *Nostolepis adzvensis* sp. nov., from which it differs by the reduction of the crown ridges and the loss of the "starlet"-like ornamentation on the posterior neck. Histologically, the scales of *N. terraborea* are similar to only a single scale variety of *N. adzvensis*, that having the crowns with fading out ridges. The microstructure of the simple mesodentine is more bone-like in *N. adzvensis*, apart from osteocyte processes and short dentine tubules. The *Stranggewebe* is almost identical, but the durodentine, composing large central strips of several (after the primordial one) growth lamellae in *N. adzvensis*, is not observed in the scales of *N. terraborea*.

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, Member 2 of the Khatayakha Formation through to Member 1 of the Toravey Formation; *rem-scheidensis* and *optima* conodont Zones (DEULIN 1991).

Nostolepis minilonga sp. nov.
(Text-figs 16A-M, 17A-B)

1993. *Nostolepis* sp. nov. 22; J. VALIUKEVICIUS, p. 29.

1995. *Nostolepis* sp. no. 22; J. VALIUKEVICIUS, p. 395, text-fig. 4.

2000. *Nostolepis* sp. nov. 22; J. VALIUKEVICIUS & S. KRUCHEK, p. 281, text-fig. 6.

2000. *Nostolepis* sp. n. 22; J. VALIUKEVICIUS, p. 134, text-fig. 1.

HOLOTYPE: LIG 20-A-2238, trunk scale (Text-fig. 16A).

ETYMOLOGY: For the scale crown ornamentation, referring to its resemblance to that of *Nostolepis minima*.

TYPE LOCALITY: North Saremboj-19 borehole, depth 3127-3130 m.

TYPE HORIZON: Lower Devonian, Lochkovian, Member 1 of the Toravey Formation.

MATERIAL: Over 11 000 scales.

DIAGNOSIS: *Nostolepis* having small scales with elongated crowns overhanging bases, ornamented with three or more pairs of longitudinal ridges, of which two longest point posteriorly flanking lateral slopes; up to three anterior neck ridges on each side; four medial ridges extending to halfway along crown length; specialized scales with stout, posteriorly rounded rib, which is widened and ridged anteriorly. Two lamellae of superimposed growth in crowns composed of transitional type tissue between ortho- and mesodentine. Base bone with few osteocytes.

DESCRIPTION: The scales are small (0.28-0.55 mm long and 0.2-0.5 mm wide) with isometrically rhomboid, posteriorly lengthened and anteriorly widened rhomboid, to triangular crowns, with tapered posterior base overhang, varying from negligible to one-third of the crown length. The scale crowns are ornamented with three pairs of symmetric rounded ridges, of which the central one is the shortest, and the two lateral ones continue radially to the posterior edge (Text-fig. 16C, E). The marginal pair slopes slightly down toward the anterior, sometimes forming clear lateral areas.

The second scale variety (Text-fig. 16A-B) has multi-lobed to spiny lateral areas, separated by the longest pointed ridges, flanking elevated triangular medial area, the anterior margin of which is ornamented with 2-4 short ridgelets fading out at one-third or at the midway point of the crown length.

The third variety (Text-fig. 16D, K) is very similar to the former, but its lateral areas are gradually terraced, composed of 2-3 pairs of neck ridges, variable in length.

The fourth variety, marking a specialized scale (presumably from the lateral sensory line), has the crown with

asymmetric ornamentation (Text-fig. 16H). The 6 central-anterior ridges continuing to a halfway along the crown length, form a medial wide, strong, rounded, clearly elevated rib, overhanging the base.

Histologically, the scales of the first and of the second varieties are very similar. Their crowns are composed of the two superimposed growth lamellae (Text-fig. 17A-B), of which the oldest, the primordial one, occupies the principal space in contrast to the second one. Ascending vascular canals only, forming rare wide main branches (Text-fig. 17A). The whole crown plate is pierced by upwardly directed dentine canals, interwoven with branching and winding side tubules. Neither *Stranggewebe* nor lacunae or osteocytes occur. These characters, together with the style of dentine canals, permit the tissue to be attributed to a transitional vari-

ety between ortho- and mesodentine. The presence of the short winding tubules at the base/crown junction may indicate the development of radial vasculars here, despite the fact that they are not observed in thin sections. The scale bases are composed of compact, thin-lamellar bone, containing a low number of osteocytes. The holotype-like specimens, similarly as in the crown, demonstrate two generations of base growth (Text-fig. 17 A), differing in the thickness of the lamellae and the length of the Sharpey's fibres.

REMARKS: *Nostolepis minilonga* scales resemble those of *N. minima* (VALIUKEVICIUS 1994, pl. 21, figs 10-12); both species possess the medial crown area and the oblique neck ridges. All of the morphologic characters in *N. minilonga* are well pronounced, whereas in *N. minima*

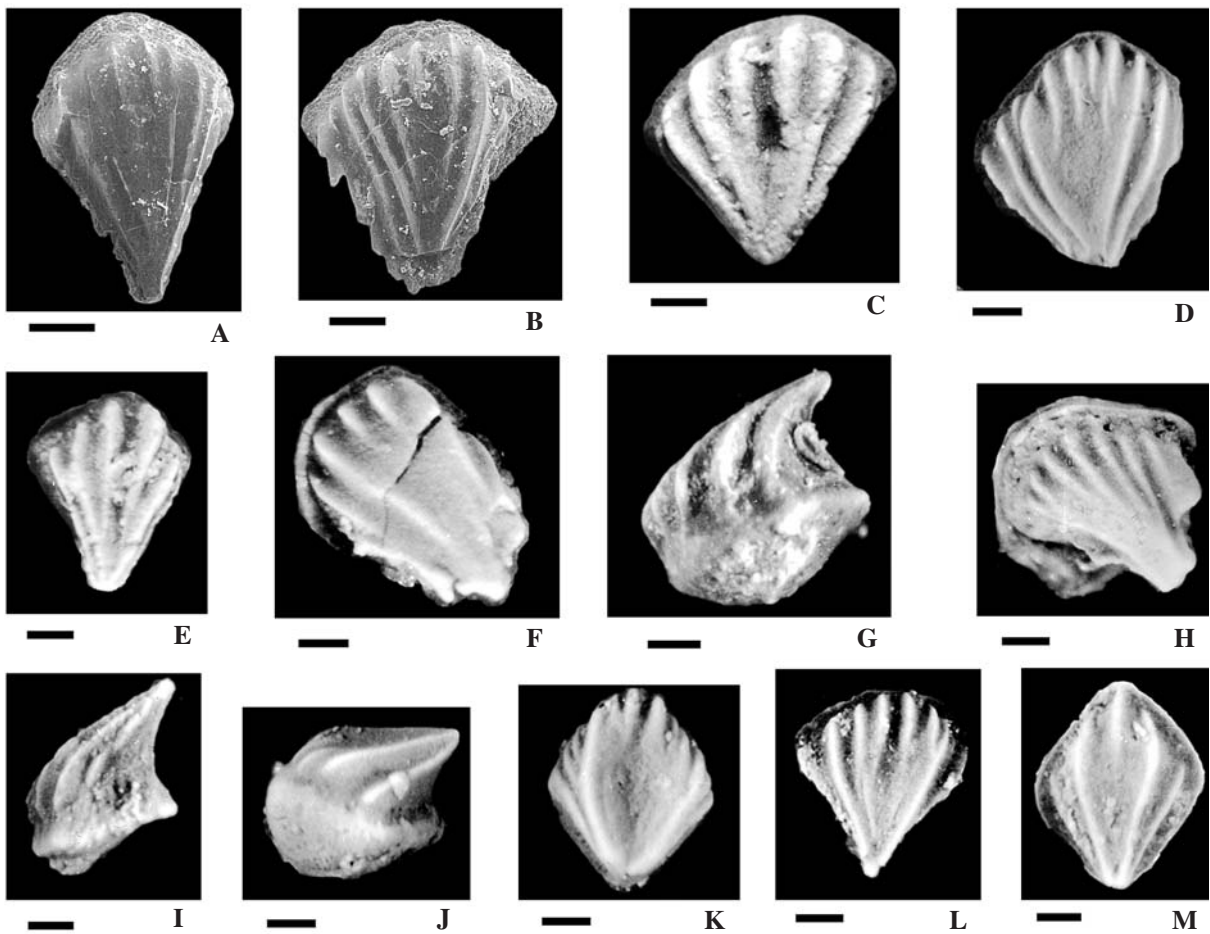


Fig. 16. *Nostolepis minilonga* sp. nov.; Trunk scales, crowns, anterior upward and scale side views, anterior to left (G, I-J): A – holotype, LIG 20-A-2238; B – LIG 20-A-2239; C and G – LIG 20-A-1676; D – LIG 20-A-1913; E and I – LIG 20-A-1670; F – LIG 20-A-1673; H – LIG 20-A-1694; J – LIG 20-A-1910; K – LIG 20-A-1888; L – LIG 20-A-1890; M – LIG 20-A-1875. North Saremboy-19 borehole, depth 3127-3130 m (A-B); Vuktyl-58 borehole, depth 6003-6008 m (C, E, G, I); West Lekeiyaga-46 borehole, depth 3101-3109 m (D); Saremboy-2 borehole, depth 3344-3352.8 m (F); Labagan-76 borehole, depth 4117-4123 m (H); West Lekeiyaga-42 borehole, depth 3230-3249 m (J); Sed'yaga-4 borehole, depth 3144-3156 m (K-L); Inzyrey-204 borehole, depth 4521-4525.4 m

(M). Lower Devonian, Lochkovian: Toravey Formation (A-B, D, F, J-L) and Khatayakha Formation (C, E, G-I, M). Bar: 0.1 mm

these are weak, rounded and short, and the crown plate is very flat.

N. minilonga is closest to *N. kozhymica* sp. nov. Both species have similar crown ornamentation, with fading out medial and pointed longest lateral ridges, and flanking side slopes. *N. minilonga* differs mostly in a relatively longer crown, in the well developed posterior base overhang, and also in the number of the longest and highest ridges (2-3 pairs) reaching the posterior crown tip.

Histologically, *N. minilonga* clearly differs both from *Nostolepis minima* (VALIUKEVICIUS 1998, pl. 12, figs 2-6) and from *N. kozhymica*. The scale crowns in the two latter species are composed of *Stranggewebe* and highly cellular mesodentine, whereas in *N. minilonga* *Stranggewebe* is absent and the crown mesodentine is of a transitional variety to orthodentine. Similarly, distinct differences occur in the case of the base bone; with numerous osteocytes in *N. minima* and *N. kozhymica*, and almost acellular in *N. minilonga*.

The dentinal tissue in the crown of *N. minilonga* resembles that in *N. longipostera* sp. nov. (see Text-fig. 12). The difference refers only to the increased number of growth lamellae and the presence of durodentine in the superficial layers in the case of the latter species.

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, Khatayakha Formation through to Pragian, Naul' Formation. The abundance zone – topmost

Khatayakha (Member 4) to the lower Toravey (Lochkovian).

Nostolepis paravolborthi sp. nov.
(Text-figs 18A-I, 19A-D)

HOLOTYPE: LIG 20-A-2322, trunk scale (Text-fig. 18H).

ETYMOLOGY: For the similarity of the general crown ridge development with that of the scales of *Gomphonchus volborthi* (ROHON, 1893) VERGOOSSEN, 1999.

TYPE LOCALITY: Olenya-3 borehole, depth 4143-4166 m.

TYPE HORIZON: Upper Silurian, Přidoli, Greben' Regional Stage, the *eosteinhornensis conodont* Zone.

MATERIAL: Ca 300 scales.

DIAGNOSIS: *Nostolepis* with small isometric scales, rhomboid crowns ornamented with subradial ridges, fading out halfway along crown length, and at anterior margin ending with widened triangular profiles. Scale crowns composed of simple mesodentine with only few lacunae in primordial lamella. Bone in bases moderately cellular.

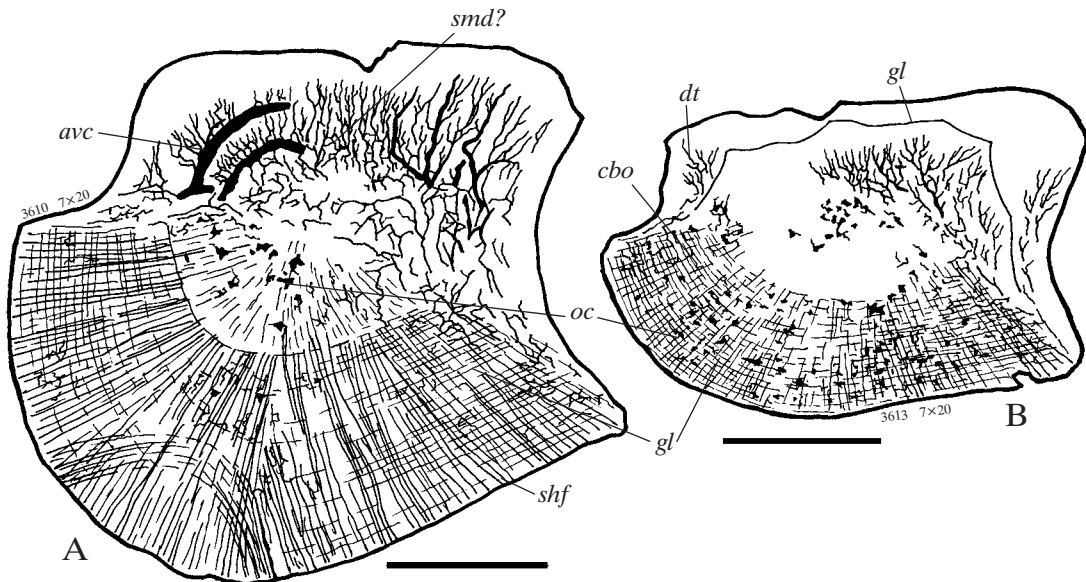


Fig. 17. *Nostolepis minilonga* sp. nov.; Histologic structure of scales in vertical longitudinal sections. A – a specimen similar to the holotype. Thin section 3610; B – specimen similar to those in Fig.16 C, E. Thin section 3613. Toboy-14 borehole, depth 3401-3416 m. Lower Devonian, Pragian, Naul' Formation, Member 1. Bar: 0.1 mm. *avc* – ascending vascular canal; *cbo* – cellular bone; *dt* – dentine tubule; *gl* – growth lamella; *oc* – osteocyte cavity; *shf* – Sharpey's fibres; *smd?* – simple mesodentine?

DESCRIPTION: The scales are small, with isometric, rhomboid crowns, slightly wider than long (0.25-0.49 mm; 0.2-0.42 mm respectively). The crown plate is flat, horizontal, with the anterior margin angulate to rounded, and the posterior one narrowed, angulate, without base overhang. The 5-8 subradial, rarely subparallel anterior ridges extend to halfway along the crown length, and fade out gradually. They are sharp and separated by wide, shallow grooves. The ridges become wider anteriorly. The anterior edges commonly become characteristically triangular (Text-fig. 18H); some ridges are anteriorly bifurcated (Text-fig. 18A). The ridges end at a crown margin and never slope down. They are mostly uniform, but some specimens have the laterals distinctly longer than medials (Text-fig. 18B, H). The scale bases are isometrically rhomboid, deep, centrally or centro-anteriorly convex, often protruding slightly beyond the crown on all sides.

The necks are well developed, high, and sometimes possess deep vertical grooves on the postero-lateral faces (Text-fig. 18F).

The up to 5 superimposed growth lamellae of the crown are composed of simple mesodentine mainly with upward winding, networked dentine canals, interwoven by numerous tubules. A few lacunae are present in the primordial lamella and in the basal parts of the next one (Text-fig. 19A, C). Rare specimens demonstrate widened fragments of (also winding?) ascending vascular canals (Text-fig. 19B). Neither *Stranggewebe* nor superficial durodentine have been observed. The bone in the scale bases is compact, thin-lamellar, pierced by long Sharpey's fibres and contains moderate numbers of osteocytes.

REMARKS: *Nostolepis paravolborthi* sp. nov. is related to *Gomphonchus volborthi*. It was first described by ROHON

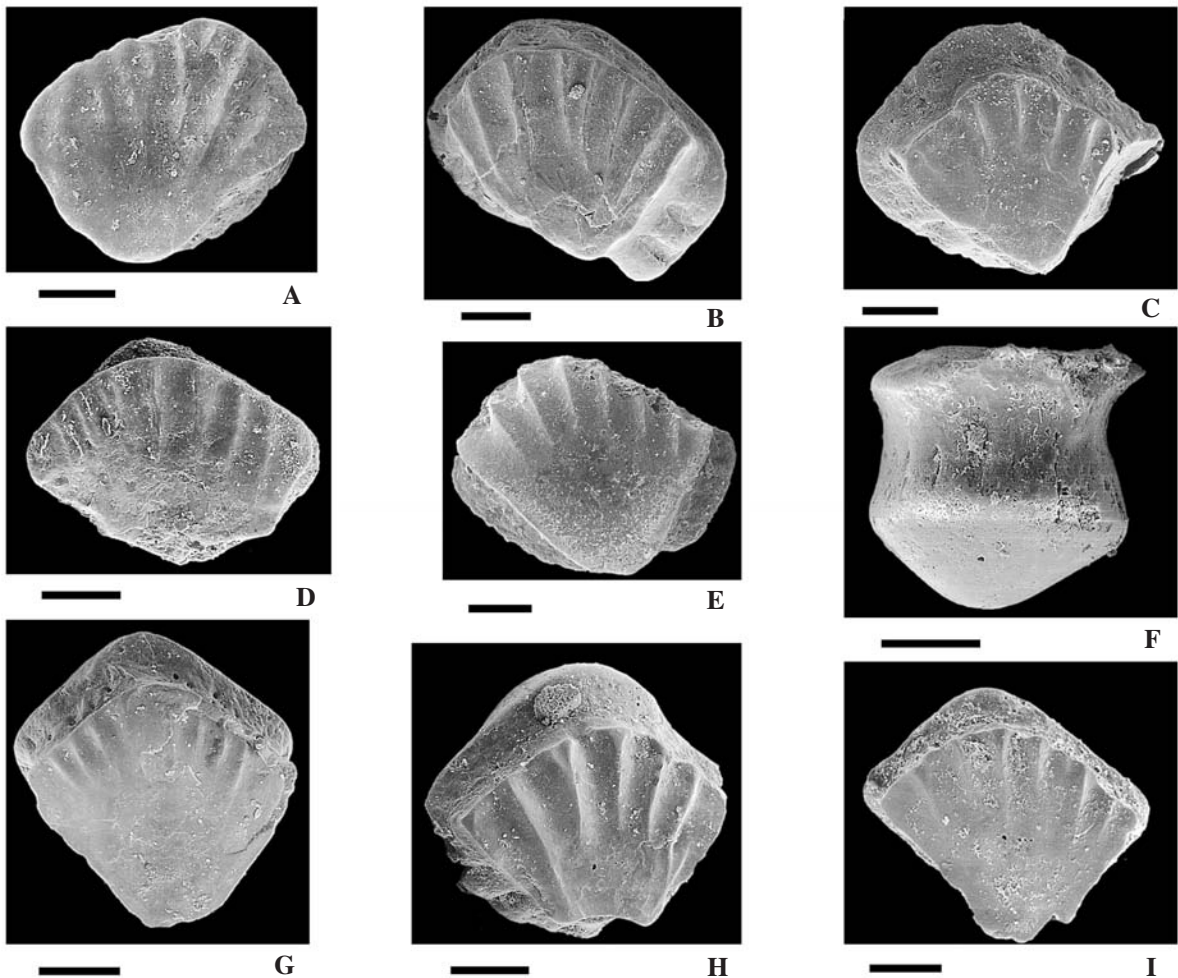


Fig. 18. *Nostolepis paravolborthi* sp. nov.; Trunk scales, crowns, anterior upward except for scale side view (F), anterior to left: **A** – LIG 20-A-2365; **B** – LIG 20-A-2325; **C** – LIG 20-A-2320; **D** – LIG 20-A-2367; **E** – LIG 20-A-2309; **F** – LIG 20-A-2369; **G** – LIG 20-A-2321; **H** – holotype, LIG 20-A-2322; **I** – LIG 20-A-2286. Olenya-2 borehole, depth 4070.8-4078.3 m (A, D-F); Olenya-3 borehole, depth 4158-4166 m (B, H) and 4143-4158 m (C, G); Vaney Vis-1 borehole, depth 4800-4808 m (I). Upper Silurian, Pridoli, Greben' Regional Stage. Bar: 0.1 mm

(1893) and accepted later by LEHMAN (1937), although his *G. volborthi* (LEHMAN 1937, pl. 3, fig. 53A, C) must be referred to *G. sandelensis* as currently understood. This species, as well as the other species of LEHMAN (1937) were questioned subsequently by GROSS (1947), who put all of his taxa into the synonymy of *G. sandelensis*. Quite recently the validity of *G. volborthi* was recognised by VERGOOSSEN (1999a, p. 43, text-figs 10-12), who reported the species from the Ludlow Bone Bed of the Welsh Borderland and from the erratics of the Netherlands. Surprisingly, he also included into the synonymy of *G. volborthi* the LEHMAN specimen referred to this species, as well as FREDHOLM's *G. sandelensis* (1988, text-fig. 9 C-D) from the Ludlow Hemse Beds of Gotland. Neither of FREDHOLM's specimens belong to *G. volborthi*; her speci-

men D is undoubtedly *G. sandelensis*, whereas the other specimen (E) may be ascribed to *Gomphonchus* sp. cf. *G. hoppei* (GROSS).

N. paravolborthi sp. nov. resembles closely *G. volborthi* (*sensu* VERGOOSSEN) in respect of the scale shape, as well as proportions and subradial crown ridge development. A very characteristic common feature is also the triangular anterior profiles of the ridges. This similarity may suggest that *G. volborthi* should actually be referred to the genus *Nostolepis*. This requires further study on sectioned specimens of *G. volborthi*.

STRATIGRAPHIC RANGE: Lower Silurian? (Adzva-1 borehole, depth 3018-3152 m) through to Upper Silurian, Pridoli.

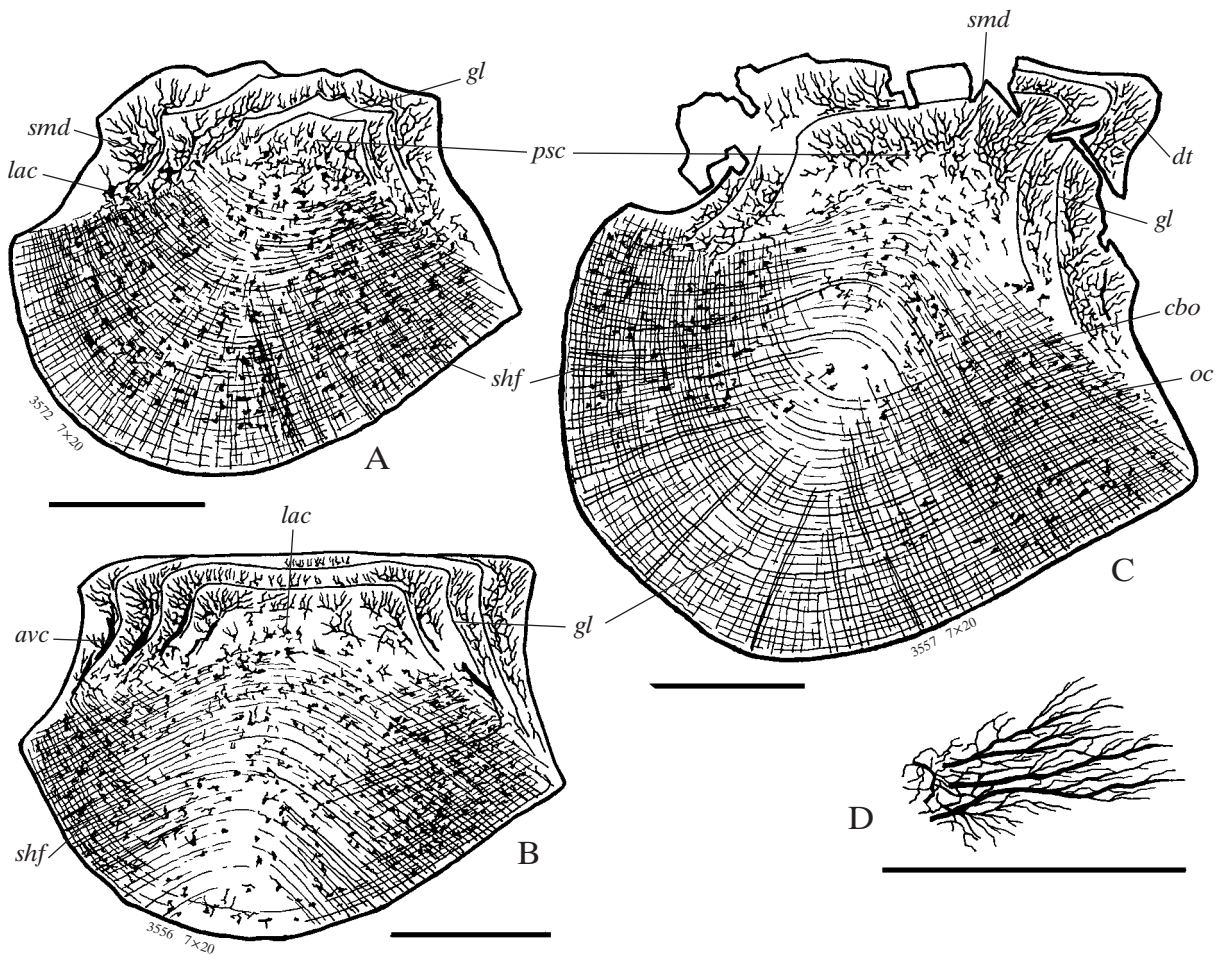


Fig. 19. *Nostolepis paravolborthi* sp. nov.; Histology of scales. Vertical longitudinal sections. A – a specimen similar to the holotype with somewhat longer crown ridges. Thin section 3572; B, C – specimens with shorter ridges, similar to that in Fig. 18 G. Thin sections 3556 and 3557 respectively; D – magnified area of crown in primordial scale (right top corner) of the last specimen. Olenya-6 borehole, depth 4049-4061 m (A) and 4089.1-4098.6 m (B-D). Upper Silurian, Pridoli, Greben' Regional Stage. Bar: 0.1 mm. *avc* – ascending vascular canal; *cbo* – cellular bone; *dt* – dentine tubule; *gl* – growth lamella; *lac* – lacuna; *oc* – osteocyte cavity; *psc* – primordial scale; *shf* – Sharpey's fibres; *smd* – simple mesodontine

Nostolepis valentinae sp. nov.
(Text-figs 20 A-G, 21 A-E)

1993. *Nostolepis* sp. nov. 23; J. VALIUKEVICIUS, p. 29.
1995. *Nostolepis* sp. no. 23; J. VALIUKEVICIUS, p. 395, text-fig. 4.
2000. *Nostolepis* sp. nov. 23; J. VALIUKEVICIUS & S. KRUCHEK, p. 281, text-fig. 6.
2000. *Nostolepis* sp. n. 23; J. VALIUKEVICIUS, p. 134, text-fig. 1.

HOLOTYPE: LIG 20-A-2253, trunk scale (Text-fig. 20 A).

ETYMOLOGY: In honour of hab. dr Valentina KARATAJUTE-TALIMAA (Vilnius).

TYPE LOCALITY: West Lekeiyaga-42 borehole, depth 3230-3249 m.

TYPE HORIZON: Lower Devonian, Lochkovian, Member 1 of the Toravey Formation.

MATERIAL: Over 420 scales.

DIAGNOSIS: *Nostolepis* with rhomboidal to ellipsoidal trunk scales with laterally protruding deep bases. Wide elevated medial area dominates crown plate, which is smooth or with one to two short anterior ridges. One to two symmetric pairs of oblique neck ridges present. ?Head scales rhomboid to quadrangular, with multi-ridged medial area, neck ridges and bases protruding beyond crowns on all sides. *Stranggewebe* in crowns with extremely long *Stranglakunen* and system of principal vasculars. Simple mesodentine highly cellular. Crown tissues with gradual transition to the base bone.

DESCRIPTION: The trunk scales have elongated rhomboidal, triangular or ellipsoidal, slightly inclined crowns (length varies from 0.24 to 0.81 mm, width from 0.21 to 0.66 mm) and bases, which protrude beyond the crowns laterally. The predominant scales have an elongated ellipsoidal or subtriangular median area, occupying the main part of the crown plate and extending clearly to the posterior tip. It may be smooth, flat and shallow, concave (Text-fig. 20D), with one (Text-fig. 20B) or two (Text-fig. 20A, C) anterior ridgelets. These slope down anteriorly together with the downcurved margins of the medial area. One or two symmetric pairs of oblique neck ridges extend from the base side corners, converging at the posterior crown tip (Text-fig. 20B), or at two-thirds of the crown length. When two pairs of neck ridges are present, the anterior-most pair is shorter (Text-fig. 20D), and converges at the midpoint (widest part) of the crown. The second pair continues obliquely from the base corners and converges at the posterior crown tip. These scales have centro-anteri-

orly convex and moderately deep bases, protruding beyond the crown plate from the sides.

Another scale variety (Text-fig. 20G) has subtriangular crowns with a long, narrow and overhanging (to one-third of the whole length) posterior part. The crown plate is without lateral slopes and neck ridges, and is ornamented with only 3-4 short rounded anterior ridgelets.

The ?head area scales (Text-fig. 20E-F) have rhomboid, quadrangular or triangular crowns and enlarged and deepened bases protruding beyond the crowns in all sides. The scales have a wide, flat median area, ornamented with 4-6 short, parallel anterior ridgelets and one or two pairs of neck ridges, flanking narrow lateral slopes. A considerable part of the material belongs to the asymmetric specimens (Text-fig. 20E).

All specimens are similar histologically. Their crowns have 2-4 growth lamellae, composed of *Stranggewebe*, and a simple bone-like mesodentine. The *Stranggewebe* has a system of widened principal ascending, radial and circular vascular canals. The longest and densest *Stranglakunen* occur in the holotype-like specimens (Text-fig. 21A-B). The simple mesodentine is highly cellular even in the superficial layers (Text-fig. 21E). It is characterised by a net of short osteocyte processes, and narrow dentine tubules. The bone of the low-pyramidal base grades into the crown tissues.

REMARKS: *Nostolepis valentinae* sp. nov. belongs to a group of nostolepids derived from the Late Silurian *Nostolepis* sp. ex gr. *N. striata* PANDER of Timan-Pechora. The lineage comprises the Lochkovian *N. minima* VALIUKEVICIUS, *Nostolepis* sp. cf. *N. multicostata* VIETH, as well as the Pragian - Emsian *N. tareyensis* VALIUKEVICIUS and *N. taimyrica* VALIUKEVICIUS. The evolution of the crown tissues in the lineage is characterised by (1) reduction of the growth lamellae and of the main system of the principal vasculars, (2) lengthening and densening of the *Stranglakunen* in the *Stranggewebe*, together with the change from simple mesodentine into more bone-like tissue with more numerous osteocytes (*Nostolepis valentinae* sp. nov.); (3) further reduction of the *Stranggewebe* area, (4) lengthening of the dentine canals in the simple mesodentine, with the formation of the upward directed, sometimes bushy branches, (5) an increase in the number of growth lamellae, and (6) the occurrence of superficial durodentine strips (as in *N. tareyensis* and *N. taimyrica* – see VALIUKEVICIUS 1994, text-fig. 61:1-4; text-fig. 58:1-6).

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, from the topmost Khatayakha through to Member 1 of the Toravey Formation.

Genus *Monospina* gen. nov.

TYPE SPECIES: *Monospina erecta* sp. nov.

ETYMOLOGY: From the Latin *mono* – one, single and *spina* – spine, thorn, referring to spiny scale crown composed of a single thorn.

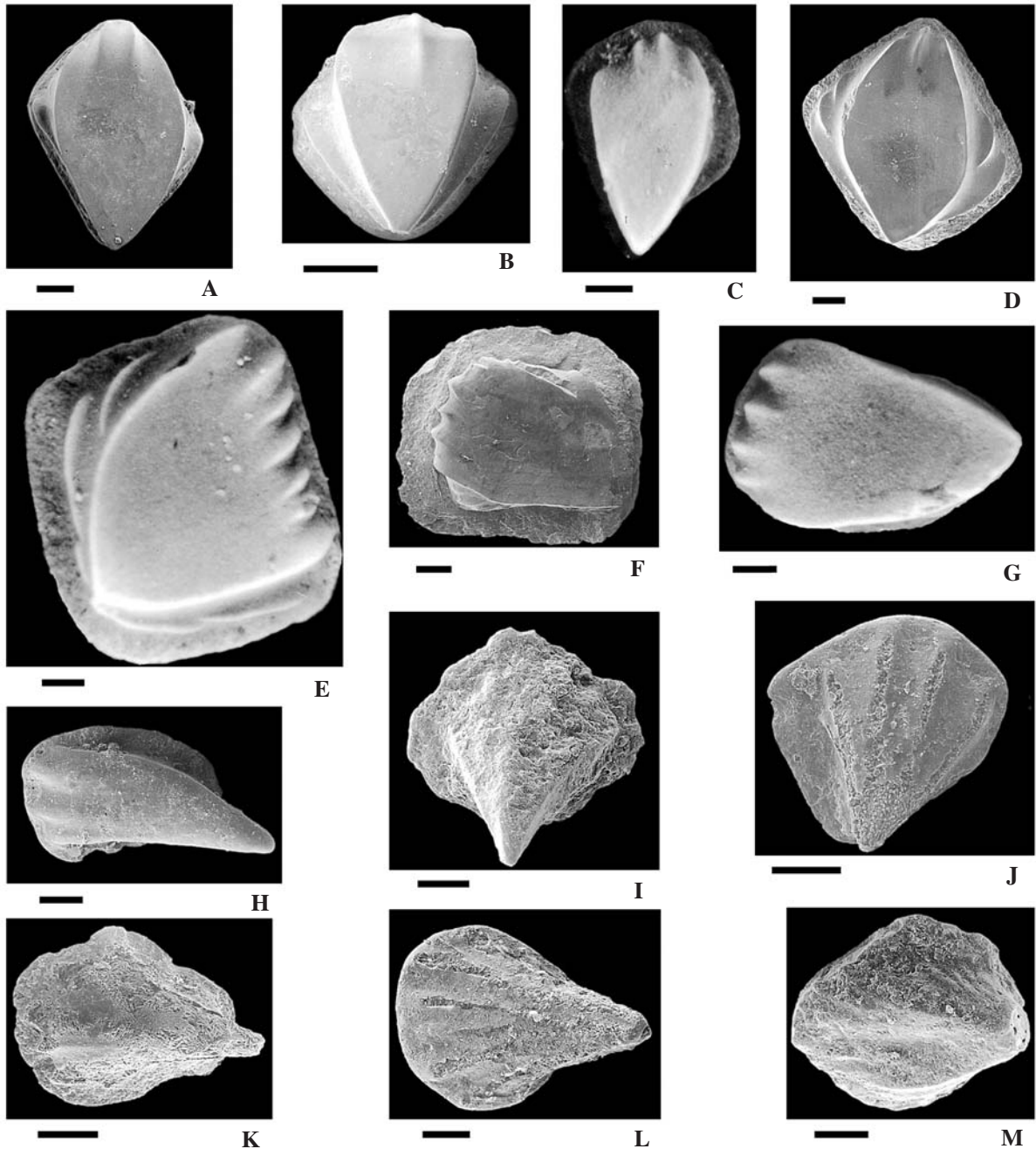


Fig. 20. **A-G** – *Nostolepis valentinae* sp. nov.; Trunk scales, crowns, anterior upward (A-D) and to left (G), and supposed head scales (E-F): A – holotype, LIG 20-A-2253; B – LIG 20-A-2197; C – LIG 20-A-1891; D – LIG 20-A-2242; E – LIG 20-A-1912; F – LIG 20-A-2275; G – LIG 20-A-1886. Toravey-25 borehole, depth 4251-4255 m (A); Varandey-7 borehole, depth 4092-4099 m (B); Sed'yaga-4 borehole, depth 3144-3156 m (C, G); North Sarembov-19 borehole, depth 3117-3124 m (D); West Lekeiyaga-42 borehole, depth 3230-3249 m (E); Värknävt-9 borehole, depth 4020-4031 m (F). Lower Devonian, Lochkovian, Toravey Formation, Member 1. Bar: 0.1 mm. **H-M** – *Monospina erecta* gen. et sp. nov.; Trunk scales, crowns, anterior to left (H, K-M) and upward (I-J): H – LIG 20-A-2324; I – LIG 20-A-2146; J – LIG 20-A-2355; K – LIG 20-A-2354; L – holotype, LIG 20-A-2356; M – LIG 20-A-2147. Olenya-3 borehole, depth 4158-4166 m (H); Indiga-379 borehole, depth 144.9 m (I, M); Vuktyl-42 borehole, depth 5945.9-5953.8 m (J-L). Upper Silurian, Pridoli, Greben' Regional Stage. Bar: 0.1 mm.

DIAGNOSIS: As for the type species.

HOLOTYPE: LIG 20-A-2356, trunk scale (Text-fig. 20L).

Monospina erecta gen. et sp. nov.
(Text-figs 20H-M, 22A-B)

ETYMOLOGY: From the Latin *erectus* – erect, referring to scale crown plate inclined to its base at a high angle.

1993. *Nostolepis* sp. nov. 19; J. VALIUKEVICIUS, p. 28.
? part 1999. *Climatiida* indet.; H. BLOM, p. 58, figs 31D-E, 32A-B.

TYPE LOCALITY: Olenya-2 borehole, depth 4070.8-4078.3 m.

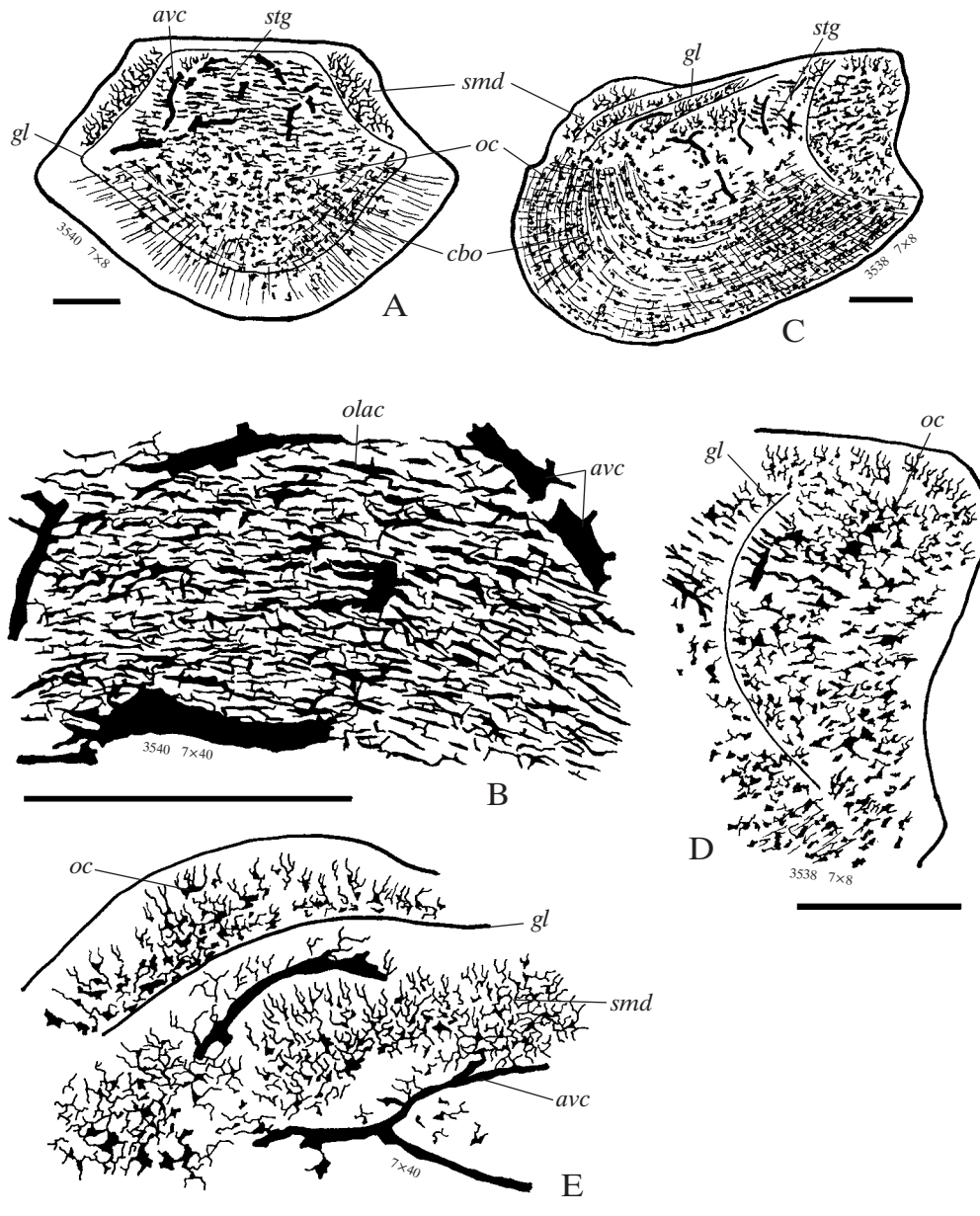


Fig. 21. *Nostolepis valentinae* sp. nov.; Histologic structure of scales. A – vertical transverse section of a specimen similar to the holotype. Thin section 3540; B – magnified area of crown in primordial scale of the same specimen; C – vertical longitudinal section through the specimen similar to that in Fig. 20 C, G. Thin section 3538; D, E – enlarged crown areas of the same specimen: D – posterior scale part, right corner; E – anterior part, primordial and two next growth lamellae. West Lekeiyaga-46 borehole, depth 3101-3109 m. Lower Devonian, Lochkovian, Toravey Formation, Member 1. Bar: 0.1 mm. *Avc* – ascending vascular canal; *cbo* – cellular bone; *gl* – growth lamella; *oc* – osteocyte cavity; *olac* – oriented lacuna; *smd* – simple mesodentine; *stg* – *Stranggewebe*

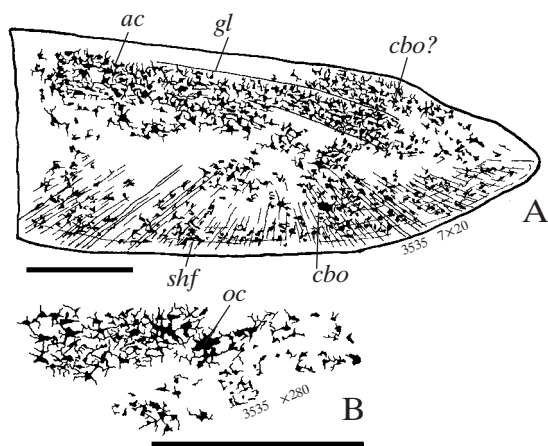


Fig. 22. *Monospina erecta* gen. et sp. nov.; Histology of scale. A – vertical longitudinal section. Thin section 3535; B – magnified crown area (left top corner) of the same specimen. Olenya-2 borehole, depth 4070.8–4078.3 m. Upper Silurian, Pridoli, Greben' Regional Stage. Bar: 0.1 mm. Cbo – cellular bone; cbo? – cellular? bone; gl – growth lamella; oc – osteocyte cavity; shf – Sharpey's fibres

TYPE HORIZON: Upper Silurian, Pridoli, Greben' Regional Stage, the *eosteinhomensis* conodont Zone.

MATERIAL: 38 scales.

DIAGNOSIS: *Monospina* with small and medium-sized scales with spiny, highly inclined crowns, sloping anteriorly to the base and pointed, cone-shaped posteriorly. Crowns ornamented with fading out anterior ridges, frequently reaching posterior tip. Scale crowns composed of cellular bone? without lengthened vascular canals.

DESCRIPTION: The scales have highly inclined, spiny crowns (angle to 40°), flat bases and lack the neck. The crowns are up to twice as long as wide (0.38–0.7 and 0.3–0.41 mm respectively), convex to cone-shaped, with rounded anterior margin and pointed posterior tip, and with large posterior overhang (Text-fig. 20H). The crown slopes anteriorly to the base plate without leaving space for the neck. The crown is ornamented with the 2–6 low subradial anterior ridges. The ridges fade out sometimes, just at the anterior strip (Text-fig. 20H), more frequently, however, they continue to the posterior part (Text-fig. 20I–J). The shorter ridges converge into the longest, outlining a cone-shaped tip (Text-fig. 20L). The scale bases are circular to rhomboid in outline, slightly convex to almost flat, rarely protruding beyond the crowns. Rare specimens have no normal bases, but flat, variably shaped basal plates (Text-fig. 20I).

Three growth lamellae composed of cellular bone? are observed in the crowns, which apart from dense, large osteocytes and their short connecting processes, are devoid of vascular canals (Text-fig. 22A–B). The crown tis-

sue is analogous to that composing the base, where it is additionally penetrated by Sharpey's fibres.

REMARKS: Conspecific with *Monospina erecta* are some of the specimens referred to as *Climatiida* indet. as reported recently by H. BLOM (1999, fig. 31D–E) from the Pridoli Chester Bjerg Formation of North Greenland. It concerns two of Blom's specimens (his fig. 31), whereas the others (31A–C) should rather be referred to *Nostolepis halli* BLOM.

BLOM's specimens differ slightly from our material in the crown ridges, which are more pronounced and higher. Wide and shallow inter-ridge grooves in the Timan-Pechora specimens are weakly developed. Histologically both the Greenland and the Timan-Pechora specimens are rather poorly known; they have, however, a uniform base tissue, three growth lamellae and large osteocytes present high in the crowns (BLOM 1991, fig. 32A–B). Moreover, besides dentine tubules, the Greenland specimens also contain wide vascular canals. Thus, their mesodentinal? crown tissue is rather different from the cellular bone? of *M. erecta* (although they considered to be conspecific).

STRATIGRAPHIC RANGE: Upper Silurian, Pridoli, Greben' Regional Stage, the *eosteinhomensis* conodont Zone.

Genus *Cheiracanthoides* WELLS, 1944

DIAGNOSIS see in R. DENISON (1979).

TYPE SPECIES: *Cheiracanthoides comptus* WELLS, 1944.

Cheiracanthoides mosolovicus sp. nov.
(Text-figs 23 A–F, 24 A–C)

1988. *Cheiracanthoides* sp. no. 6; J. VALIUKEVICIUS, p. 604, table 2.

1995. *Cheiracanthoides* sp. no. 6; J. VALIUKEVICIUS, p. 395, text-fig. 4.

2000. *Cheiracanthoides* sp. nov. 6; J. VALIUKEVICIUS & S. KRUCHEK, p. 280, text-fig. 6.

HOLOTYPE: LIG 20-A-1505, trunk scale (Text-fig. 23B).

ETYMOLOGY: From the Mosolovo Formation (Middle Devonian, Eifelian) of the Central Devonian Field, the source of the described material.

TYPE LOCALITY: West Lekeiyaga-46 borehole, depth 2677–2684 m.

TYPE HORIZON: Middle Devonian, Eifelian, Lekeiyaga Formation. Beds with *Eognathodus bipennatus bipennatus* (DEULIN 1991).

STRATIGRAPHIC RANGE: As for the type horizon.

MATERIAL: Ca 40 scales.

DIAGNOSIS: *Cheiracanthoides* with tiny rhomboid to ellipsoidal scales, flat crowns ornamented with 4-6 fading out rounded to sharp, rarely bifurcated parallel ridges, separated by shallow grooves. Up to three

growth lamellae in crowns, composed of *Stranggewebe* in posterior part with complicated *Stranglakunen*, capped superficially by strips of simple mesodentine, analogous to that of anterior crown portion. Gradual transition from mesodentine of lower crown to bone of base.

DESCRIPTION: The scales are small, not exceeding 0.39 mm in length, with isometric rhomboid, elongated rhomboid to triangular or ellipsoidal crowns overhanging bases toward the posterior. The crown plate is flat, horizontal, ornamented usually with 4-6 parallel,

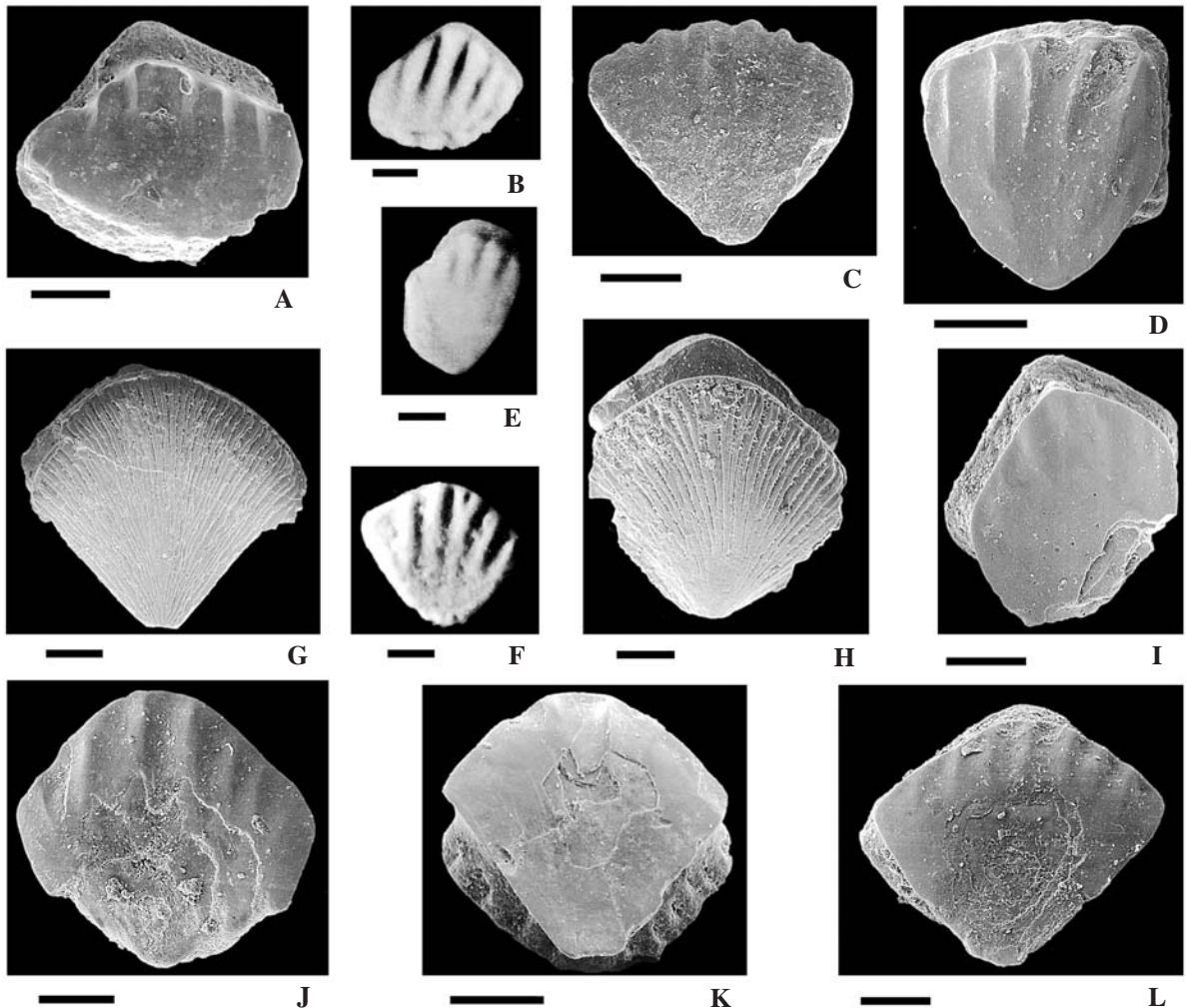


Fig. 23. **A-F** – *Cheiracanthoides mosolovicus* sp. nov.; Trunk scales, crowns, anterior upward: A – LIG 20-A-2268; B – holotype, LIG 20-A-1505; C – LIG 20-A-2211; D – LIG 20-A-2227; E – LIG 20-A-1506; F – LIG 20-A-2112. West Lekeiyaga-46 borehole, depth 2677-2684 m (A, C-D, F); West Lekeiyaga-47 borehole, depth 2647.8-2655.3 m (B, E). Middle Devonian, Eifelian, Lekeiyaga Formation. Bar: 0.1 mm. **G,H** – *Diplacanthus pechorensis* sp. nov.; Trunk scales, crowns, anterior upward: G – holotype, LIG 20-A-2217; H – LIG 20-A-2220. Toboy-14 borehole, depth 3401-3416 m. Lower Devonian, Pragian, Naul' Formation, Member 1. Bar: 0.1 mm. **I-L** – *Gomphonchus minicostatus* sp. nov.; Trunk scales, crowns, anterior upward: I – LIG 20-A-2222; J – LIG 20-A-2341; K – LIG 20-A-2280; L – holotype, LIG 20-A-2342. Olenya-3 borehole, depth 4119-4133 m (I); the Kozhym River section, outcrop 236, bed 21 (J, L); Olenya-6 borehole, depth 4049-4061 m (K). Upper Silurian, Pridoli, Greben' Regional Stage (I, K); Lower Devonian, Lochkovian, Ovinparma Formation, Member 1 (J, L). Bar: 0.1 mm

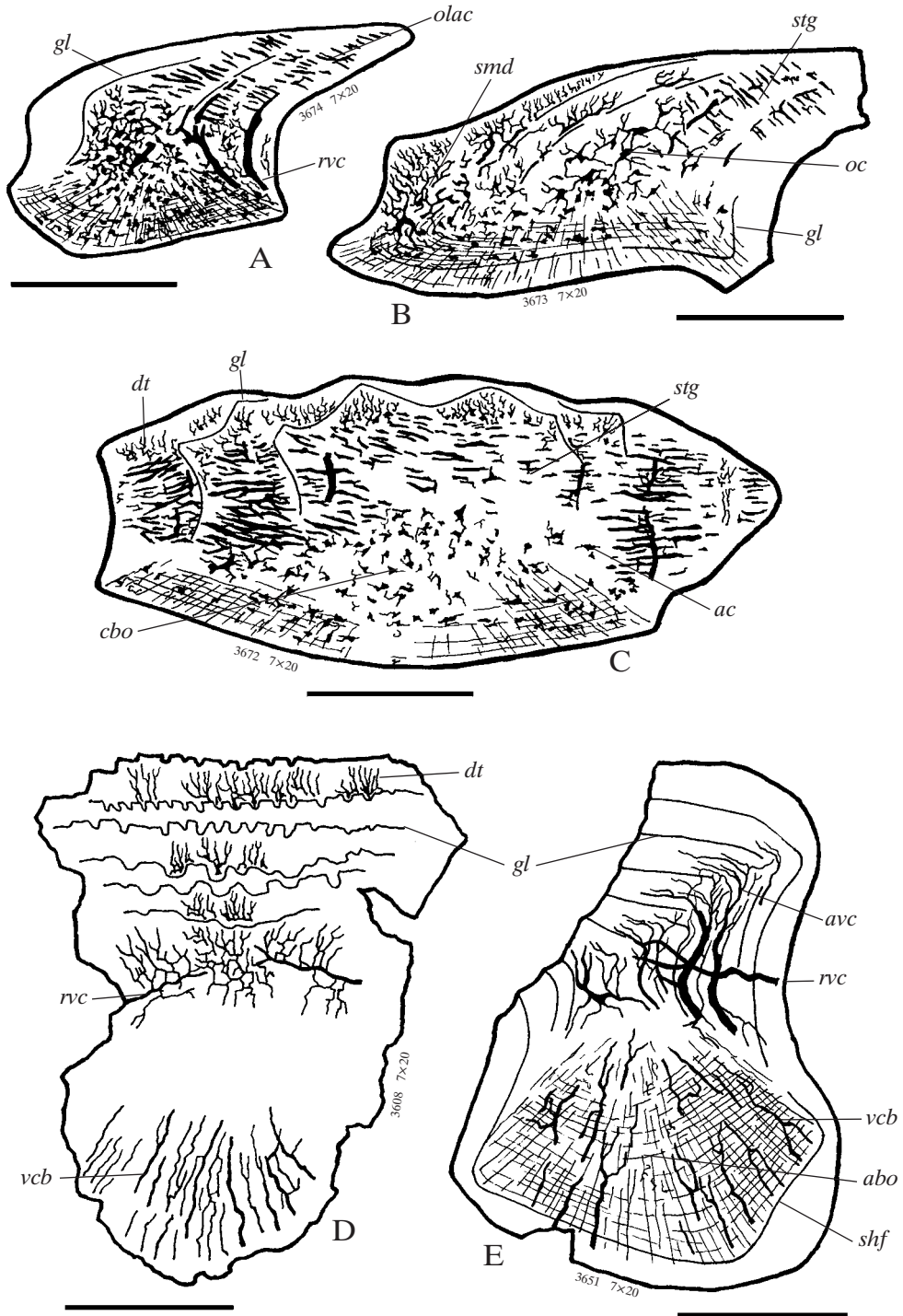


Fig. 24. Histology of scales. A-C – *Cheiracanthoides mosolovicius* sp. nov.; A, B – vertical longitudinal sections of a specimen similar to the holotype. A – thin section 3674; B – thin section 3673; C – vertical transverse section of a specimen with anteriorly bifurcated ridges (similar to that in Fig. 23 F). Thin section 3672. West Lekeiyaga-46 borehole, depth 2677-2684 m. Middle Devonian, Eifelian, Lekeiyaga Formation. Bar: 0.1 mm. D, E – *Diplacanthus pechorensis* sp. nov.; D – vertical transverse section (only central part of scale preserved). Thin section 3608; E – vertical longitudinal section, posterior part of crown missing. Thin section 3651. Toboy-14 borehole, depth 3401-3416 m (D) and Sed'yaga-4 borehole, depth 3144-3156 m (E). Lower Devonian, Pragian, Naul' Formation, Member 1 (D) and Lochkovian, Toravey Formation, Member 1 (E). Bar: 0.1 mm

Abo – acellular bone; *avc* – ascending vascular canal; *cbo* – cellular bone; *dt* – dentine tubule; *gl* – growth lamella; *oc* – osteocyte cavity; *olac* – oriented lacuna; *rvc* – radial vascular canal; *shf* – Sharpey's fibres; *smd* – simple mesodontine; *stg* – *Strangewebe*; *vcb* – vascular canal in the base of scale

rounded ridges (Text-fig. 23B, E), which become wider and higher toward the anterior margin and fade out halfway along the crown length. The specimens with the longest ridges have one-third of their surface smooth. Most of the scales are ornamented with sharp ridges, separated by wider but shallow grooves (Text-fig. 23A, D). Some of the specimens have central ridges that show clear but short anterior bifurcation (Text-fig. 23F). The neck is low but well developed, becoming slightly shorter toward the anterior. The base is small, rhomboid, slightly convex, with the anterior swell projecting just beyond the crown margin.

The scale crowns are composed of *Stranggewebe* and simple mesodentine portioned respectively in the posterior and anterior crown of the superpositionally growing lamellae, the number of which does not exceed three. The tissues contain wide radial and ascending vascular canals (Text-fig. 24A, C). The *Stranglakunen* are long, complicated, with numerous connecting narrow tubules. The *Stranggewebe* in layers is covered by peripheral strips of simple mesodentine incorporating lacunae (Text-fig. 24C), which are absent only in the extreme posterior of the crown. The numbers of unorientated enlarged osteocytes increase in the basal parts of the crown in the primordial lamella (Text-fig. 24B). The transition between the mesodentine of this part of the crown and the moderately cellular bone tissue in the low-pyramidal base seems to be gradual.

REMARKS: From *Cheiracanthoides comptus* WELLS (1944) (redescribed by GROSS 1973), from the Middle Devonian bone-beds of Ohio and Indiana, USA, *Ch. mosolovicus* sp. nov. differs in its morphological characteristics as well as histologically. The scales of *Ch. comptus* are distinctly larger, their crowns are ornamented with up to 20 uniform, parallel, fading out ridges, shallow inter-ridge grooves, rounded in the anterior edges. The ridges do not reach the anterior margin (GROSS 1973, pl. 26, fig. 24-26; pl. 27, fig. 3-4). The system of principal vascular canals in *Ch. comptus* is better developed. It contains numerous radials on each side, wide circulars and ascendings (GROSS 1973, text-fig. 4 A-D), and characteristic horizontals, located in grooves, with a bushy arrangement. The horizontals are not observed in *Ch. mosolovicus* sp. nov., whereas ascendings and radials, owing to the winding style, are represented only by short fragments.

The Middle Devonian *Ch. estonicus* (VALIUKEVICIUS 1998, pl. 8, figs 10-12), from the Eifelian of the Baltic, ascribed formerly to *Ch. comptus* (VALIUKEVICIUS 1985, pl. 3, fig. 19; pl. 8, fig. 4-5; text-fig. 3: 1-7), is also characterised by bushy horizontal, wide and long ascending, radial and circular vascular canals. Its scale crowns are

ornamented with fan-like ridges (up to thirteen), through which it differs from *Ch. mosolovicus* sp. nov. Bifurcated ridges are not observed in the scales of *Ch. estonicus*. The area of the *Stranggewebe* is approximately the same in all of the discussed taxa, occupying the posterior crown half, embracing the primordial lamella.

Ch. mosolovicus is most closely allied to *Ch. planus*, from the Silurian - Devonian boundary interval of the Baltic and Belarus (VALIUKEVICIUS 1998, pl. 3, figs 9-15; pl. 9, figs 1-5). The principal characters of the crown ornamentation are similar, except for the absence of the scale variety with sharper and more numerous (up to 12) ridges in *Ch. planus*. Histologically, both possess the same proportions and structure of *Stranggewebe* and simple mesodentine in scale crowns, except for the absence of simple mesodentine strips covering the *Stranggewebe* layers, the appearance of superficial durodentine and increased number of the growth lamellae in *Ch. planus*.

OCCURRENCE: West Lekeiyaga-46 borehole, depth 2677-2684 m; West Lekeiyaga-47: 2632.1-2655.3 m.

Order Diplacanthiformes BERG, 1940
Family Diplacanthidae WOODWARD, 1891

Genus *Diplacanthus* AGASSIZ, 1844

DIAGNOSIS see in R. DENISON (1979) and J. VALIUKEVICIUS (1985).

TYPE SPECIES: *Diplacanthus crassissimus* DUFF, 1842.

Diplacanthus pechorensis sp. nov.
(Text-figs 23 G-H, 24 D-E)

HOLOTYPE: LIG 20-A-2217, trunk scale (Text-fig. 23 G).

ETYMOLOGY: From the Pechora Plate, a structural unit of the Timan-Pechora region (Russia).

TYPE LOCALITY: Toboy-14 borehole, depth 3401-3416 m.

TYPE HORIZON: Lower Devonian, Pragian, Member 1 of the Naul' Formation.

MATERIAL: 11 scales.

DIAGNOSIS: *Diplacanthus* with isometric rhomboid scales having high necks and deep bases. Crown orna-

mented with symmetric linear bipartite ridgelets and fan-like grooves, up to twenty on each side continuing to posterior tip. Crown composed of specific mesodentine with upwardly directed bushy dentine tubules, widened ascending and radial vascular canals high in neck. Acellular bone in scale bases with tipward directed long vasculars.

DESCRIPTION: The scales are of moderate size. The crowns are isometric (0.4-0.65 mm). The crown plate is horizontal, rhomboid with rounded corners and narrowly overhanging (to one-third of crown length) the posterior tip. The antero-lateral crown margins are slightly downslanted. The crown is ornamented with symmetric linear ridgelets and grooves, up to twenty on each side, extending the length of the crown. The central ridgelets are almost parallel and converge sometimes into longer, fan-like or radial laterals (Text-fig. 23G). Many of the ridgelets continue to the extreme posterior. Most of the specimens have bipartite ridgelets, with a shallow linear groove in between (Text-fig. 23G-H). The scale neck is high, well developed, sometimes with vertical grooves on the posterior faces. The bases are rhomboid, well outlined and deep.

Histologically, the species is poorly known, but sectioned scales show a distinct "*Diplacanthus*"-type structure (VALIUKEVICIUS 1985). Up to six growth lamellae in the crown are composed of specific mesodentine with well developed ascending and radial vascular canals high in the neck (Text-fig. 24E). The upward directed and bushy, networked dentine tubules, characteristic of this histologic type (Text-fig. 24D), are located separately in the growth lamellae without any connections. The primordial scale contains a complicated knot of interwoven vasculars, part of which is widened. The acellular bone in the high-pyramidal bases is pierced by tipward-directed long vascular canals.

REMARKS: Similar Early Devonian diplacanthids are widely known albeit referred to various taxa. Good example are the scales from the ?late Lochkovian Red Canyon River (A) Formation of the Arctic Canada, identified originally as *Nostolepis gracilis* GROSS by VIETH (1980, pl. 5, figs 10-14). At least the specimen in her fig. 13 closely resembles *Diplacanthus pechorensis*. Unfortunately the histologic structure of the Canadian specimens is unknown.

Similar to *D. pechorensis* sp. nov. is *Nostolepis viethae*, described by WANG (1993), from the Early Devonian of Spain, with its type specimen represented by a scale illustrated by VIETH (1980, fig. 13). Particularly similar, with characteristic fan-like longitudinal ridges, is WANG's specimen from the middle part of the Nogueras Formation (WANG 1993, pl. 12, fig. 18).

Also similar is *Diplacanthus poltnigi* (VALIUKEVICIUS 2003), from the Lochkovian Pod'emnyaya Formation of

the Severnaya Zemlya Archipelago (Russia). From *D. pechorensis* it differs in the absence of the ridges, and in the scale crown ornamentation consisting exclusively of numerous fan-orientated grooves.

Diplacanthus longispinus AGASSIZ (POLTING 1984, pl. 2, figs 1-7) from the topmost Emsian of Graz (Austria) is regarded here as synonymous with *D. poltnigi*. Their crowns are ornamented exclusively with grooves.

STRATIGRAPHIC RANGE: Lower Devonian, Lochkovian, Member 1 of the Toravey Formation through to Pragian, Member 1 of the Naul' Formation.

Order Ischnacanthiformes BERG, 1940
Family Ischnacanthidae WOODWARD, 1891
Genus *Gomphonchus* GROSS, 1971

DIAGNOSIS see in R. DENISON (1979).

TYPE SPECIES: *Gomphonchus sandelensis* (PANDER), 1856.

Gomphonchus minicostatus sp. nov.
(Text-figs 23I-L, 25A-B)

HOLOTYPE: LIG 20-A-2342, trunk scale (Text-fig. 23L).

ETYMOLOGY: For scale ornamentation referring to minimum ridge development of the crowns.

TYPE LOCALITY: Indiga-379 borehole, depth 144.3 m.

TYPE HORIZON: Upper Silurian, P'ridoli, Greben' Regional Stage, the upper Member of the Eptarma Formation.

MATERIAL: About 160 scales.

DIAGNOSIS: *Gomphonchus* with small scales having rhomboid isometric crowns ornamented with 4-6 uniformly rounded, flattened, parallel ridges fading out at one-third of crown length. Scale bases deep, necks medium high. Crown composed of dentine with widened ascending and radial vascular canals having plenty of intermediate connecting branches; durodentine absent. Compact bone in scale bases with few osteocytes.

DESCRIPTION: The scales are small isometric, with horizontal, flat crowns, well developed moderately high necks and anteriorly deepened bases. The crowns are generally

as long as wide (0.3-0.5 mm), or slightly wider, rounded rhomboid in outline, with a small posterior base overhang. The crown plate is flat or slightly sloping at the antero-lateral margins (Text-fig. 23K-L). Its anterior strip is ornamented with 4-6 low, flattened, broad ridges, separated by wide, shallow grooves. The ridges are parallel (Text-fig. 23J, L) and fade out at one-third of the crown length. Up to 5 large vertical groovelets with central fossae (Text-fig. 23K) occur on the posterior neck faces. The scale bases are isometric, rhomboid in outline, with the anterior swollen margin projecting slightly beyond the crown.

Up to 6 lamellae of superpositional growth occur in the crowns, composed of dentine with well developed, wide ascending vascular canals, forming clear main branches connected by numerous tubules, usually directed upwards. The superficial durodentine of the crowns is not developed. Enlarged radial vascular canals are situated centripetally over the base (Text-fig. 25A). The compact thin-lamellar base bone is pierced by long Sharpey's fibres and contains rare osteocytes, which increase in number tipward in the primordial scale (Text-fig. 25B).

REMARKS: The taxon is related to *Gomphonchus mediocostatus* VERGOOSSEN, another Pridoli species from the Timan - Pechora region. Besides the scale varieties given in the original description (VERGOOSSEN 1999b, p. 234, pl. 2, figs 18-23), the material studied herein comprises specimens with short but comparatively high, subparallel or subradial ridges, fading out halfway along the crown length. Formerly, I referred these specimens to *Gomphonchus* sp. (VALIUKEVICIUS 1998, pl. 8, figs 1-6), but I now consider them conspecific with *G. mediocostatus*.

G. minicostatus sp. nov. differs from *G. mediocostatus* in the reduction of the median ridges, and in the absence of bifurcated or radial shorter laterals, converging into medials. All its ridges are uniform, flattened and parallel, fading out at the same point. Histologic affinities of the taxa are significant. *G. mediocostatus* differs in its more bushy and uniform ascending vascular canals in the crown, frequently without main branches, more numerous and thinner growth lamellae, and completely acellular bone in the bases.

STRATIGRAPHIC RANGE: Upper Silurian, Pridoli, Greben' Regional Stage, through to Lower Devonian, Lochkovian, lower part of the Ovinparma Regional Stage.

Gomphonchus abruptus sp. nov.
(Text-figs 26A-I, 27A-E)

HOLOTYPE: LIG 20-A-2148, trunk scale (Text-fig. 26I).

ETYMOLOGY: For the shape of the scale crown.

TYPE LOCALITY: The Velikaya River section, outcrop 8 e.

TYPE HORIZON: Upper Silurian, Pridoli, Greben' Regional Stage, the upper Member of Eptarma Formation.

MATERIAL: 43 scales.

DIAGNOSIS: *Gomphonchus* with scales of moderate size with rhomboid smooth crowns and obliquely steep-

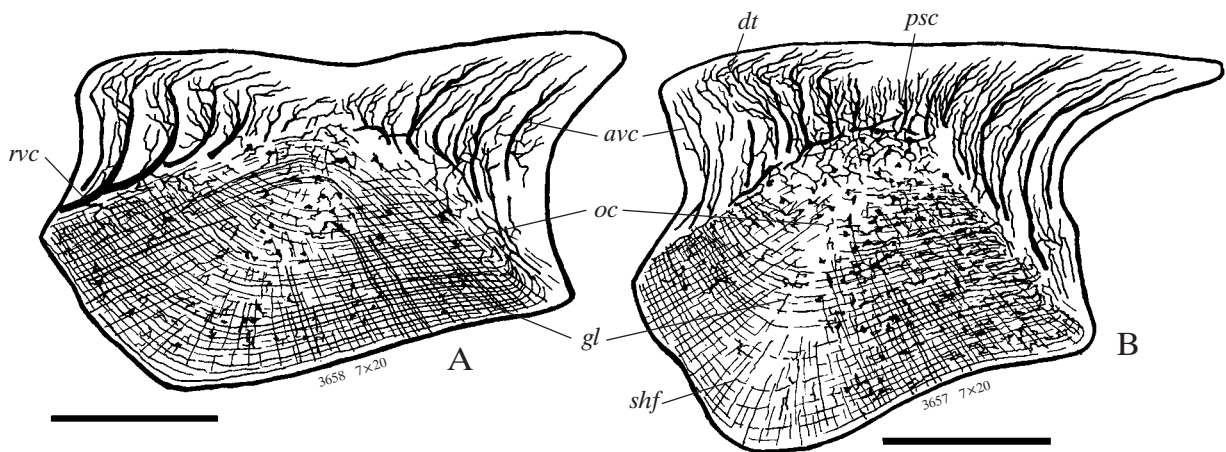


Fig. 25. *Gomphonchus minicostatus* sp. nov.; Histology of scales. Vertical longitudinal sections. **A** – thin section 3658; **B** – thin section 3657. Indiga-379 bore-hole, depth 144.3 m. Upper Silurian, Pridoli, Greben' Regional Stage, Eptarma Formation, Member 2. Bar: 0.1 mm. *avc* – ascending vascular canal; *dt* – dentine tubule; *gl* – growth lamella; *psc* – primordial scale; *rvc* – radial vascular canal; *shf* – Sharpey's fibres

ened or vertically abrupted postero-lateral margins. Scales growing areally. High-pyramidal base composed of cellular bone and crown composed of dentine. Wide radial vascular canals continue centripetally over base cone, stream up wide ascending vasculars, interwoven with dense unorientated tubules.

DESCRIPTION: The scales are of moderate size (0.46–0.7 mm), with isometric crowns, rhomboid to rhomboid rounded in outline. They are usually slightly wider than long, with well developed side corners (Text-fig. 26F). The crown plate is thick, horizontal, smooth. The postero-lateral crown margins are vertically (Text-fig. 26A, D) or obliquely (Text-fig. 26G, I) steepened. The steepening begins just behind the side corners and runs with the same or increasing intensity (Text-fig. 26G) to the posterior tip (Text-fig. 26A, D). The scale necks are high, well

developed, smooth or bearing vertical grooves on the posterior walls (up to four on each), in the central part carrying large fossae for openings of the neck radial vasculars. The bases are rhomboid, large, centrally deepened.

The scale crowns are composed of dentine arranged in up to 12 growth lamellae. Specific growth type of scales has been observed in sections. The high-pyramidal base cone almost reaches the outer crown surface in the centre (Text-fig. 27D-E). The overlap of outer growth layers in the crown plate is not observed, and thus a mostly areal growth type is proposed. The long and wide centripetal radial vasculars lie over the base (Text-fig. 27D). They send up wide main branches of ascendings located basally in each of the growth lamellae. The inter-canal space is filled up with a dense network of narrowly winding dentine tubules (Text-fig. 27E), which are not directed upwards, but are randomly orientated. Presumably only the superficial crown layer

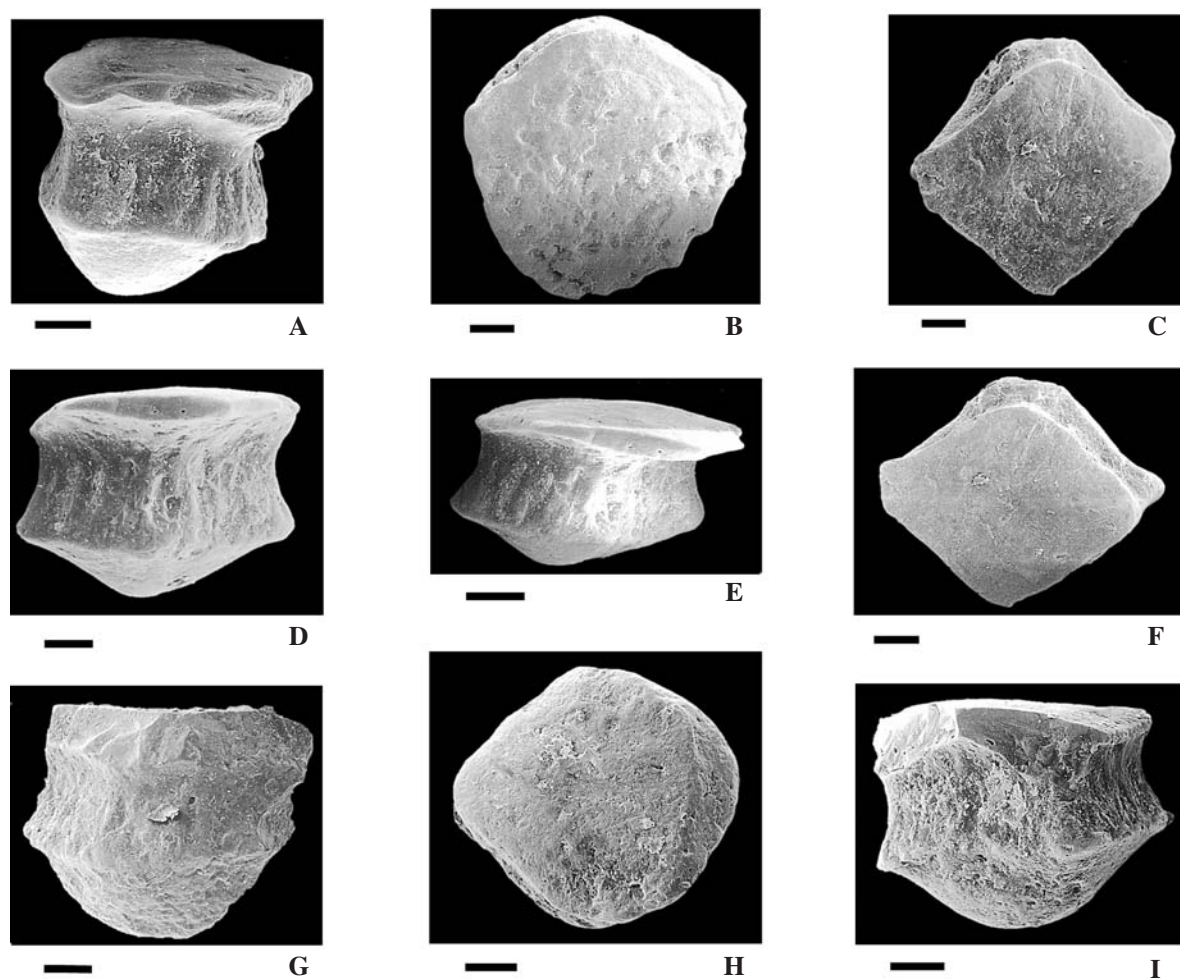


Fig. 26. *Gomphonchus abruptus* sp. nov.; Trunk scales: A – LIG 20-A-2392, side view, anterior to left; B – LIG 20-A-2396; C and F – LIG 20-A-2395 in two different orientations, crowns, anterior upward; D and E – LIG 20-A-2393, side view in two different orientations; G – LIG 20-A-2172, posterior side view; H – LIG 20-A-2149, crown, anterior upward; I – holotype, LIG 20-A-2148, posterior side view. The Velikaya River section, outcrop 8 e (A-F) and Indiga-379 borehole, depth 138 m (G) and 144.9 m (H-I). Upper Silurian, Pridoli, Greben' Regional Stage, the upper (2) Member of Eptarma Formation. Bar: 0.1 mm

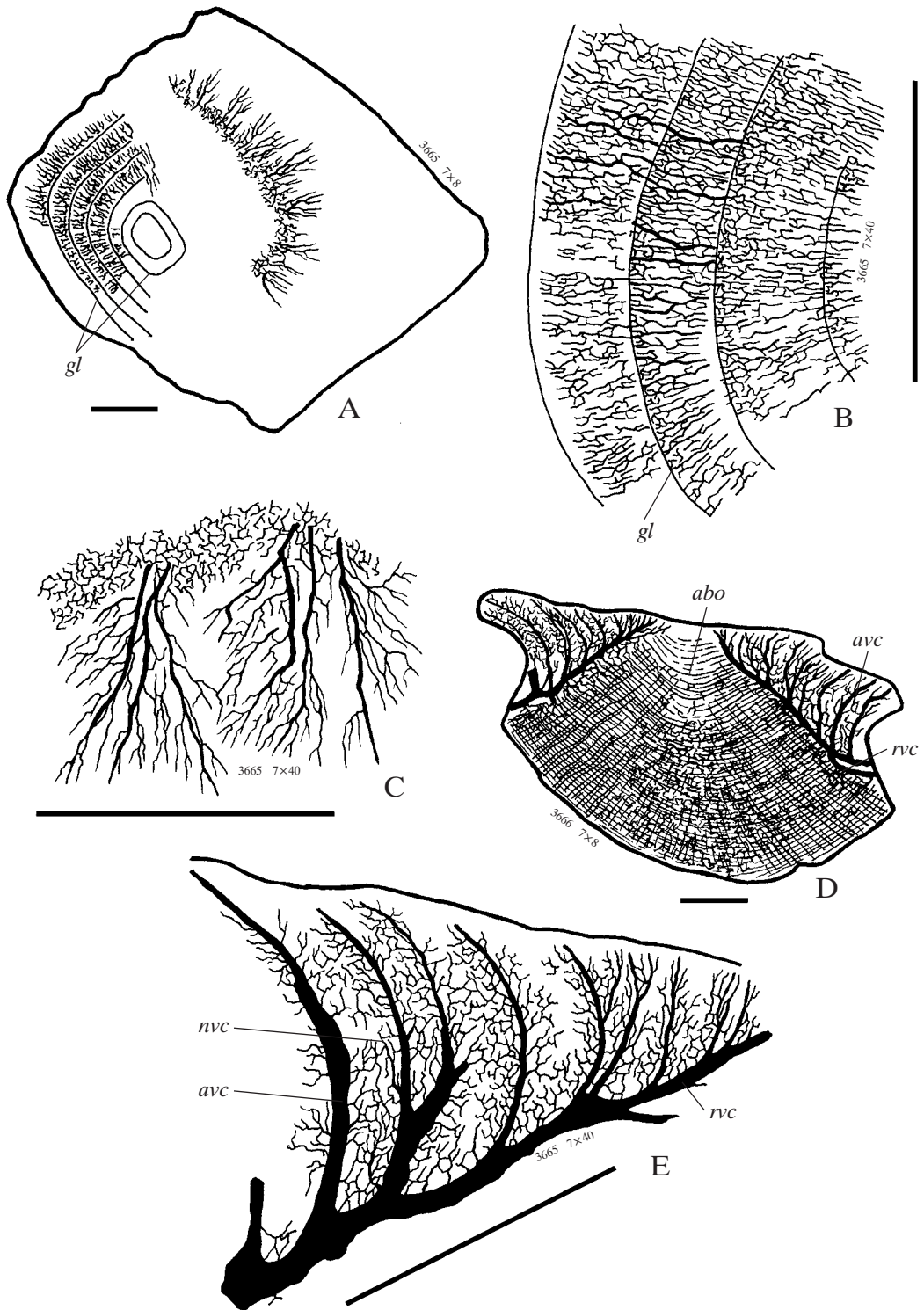


Fig. 27. *Gomphonchus abruptus* sp. nov.; Histologic structure of scales. **A** – horizontal (slightly oblique) section of a specimen through the lower part of crown. Thin section 3665; **B** – magnified left part of the same section; neck dentine canals; **C** – the same section, right part; crown dentine canals; **D** – vertical transverse section. Thin section 3666; **E** – magnified left part of crown of the same specimen. Indiga-379 borehole, depth 144.3 m. Upper Silurian, Pridoli, Greben' Regional Stage, Eptarma Formation, Member 2. Bar: 0.1 mm. *Abo* – acellular bone; *avc* – ascending vascular canal; *gl* – growth lamella; *nvc* – vascular canals in the neck; *rvc* – radial vascular canal

contains lengthened horizontal, posteriorly directed vasculars (Text-fig. 27A, C). The outer durodentine is not developed. The acellular bone in the scale bases is densely lamellar, with long Sharpey's fibres and numerous interwoven vascular processes (Text-fig. 27D).

REMARKS: *G. abruptus* sp. nov., differs from all of the other gomphonchids in its characteristic steep, postero-lateral crown margins. *Gomphonchus sandelensis* (GROSS 1971, Text-fig. 20A-E) differs, moreover, in possessing superficial durodentine in some of the youngest growth lamellae, the lack of radial vascular canals over the bases, differently shaped ascending vasculars and, particularly, in its branching tubules. For *G. sandelensis* a superpositional growth type of scale is characteristic.

G. nordicus (VALIUKEVICIUS 2003, figs 23N-P, 35A-D) from the Pridoli of Severnaya Zemlya Archipelago has unornamented scale crowns with random outer shallow concavities and postero-lateral concentric linear groovelets. It resembles *G. abruptus* sp. nov. in its dentine tissue in the scale crowns. The centripetal radial vascular canals of *G. nordicus* are well developed. Similarly as in *G. abruptus*, they reach an apex of the high-pyramidal base, which leaves centrally only a small space for thin overlapping durodentine and dentine layers. Ascending vascular canals in *G. nordicus* have mostly upward directed branchings in contrast to unorientated in *G. abruptus* sp. nov. Besides, the bone in the scale bases of *G. nordicus* varies from moderately to highly cellular.

Gomphonchus boekschoteni VERGOOSSEN, described from the East Baltic erratics, and assigned to the *Poracanthodes punctatus* Zone of the Pridoli, differs from *G. abruptus* in having smooth pear-shaped scale crowns with a variably deep antero-median sulcus and a robust, postero-medially slanting keel on the posterior neck (VERGOOSSEN 1999 b, pl. 2, figs 24-25; pl. 3, figs 26-31). The comparison of histological characteristics needs further study.

STRATIGRAPHIC RANGE: Upper Silurian, Pridoli, Greben' Regional Stage.

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