New Wenlock–Pridoli (Silurian) acanthodian fishes from Lithuania

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Five new monotypic acanthodian genera and five new species are described from the Silurian (Wenlock to Pridoli) of Lithuania. Two new genera and species, *Vesperalia perplexa* and *Fecundosquama basiglobosa*, belong to climatiiform and three, *Arenaceacanthus arcuatacanalis*, *Bracteatacanthus assiduus*, and *Rohonilepis breviornatus*, to ischnacanthiform acanthodians. *Vesperalia perplexa* has high-crowned scales with ridges that cross the entire surface or frequently fade mid-crown and after a smooth area continue on the posterior edge. Stranggewebe in the crowns of *V. perplexa* scales has large oriented lacunae and a well-developed system of main vascular canals. *Fecundosquama basiglobosa* scales have an undeveloped neck, a crown with only marginal sculptural incisions and have an unusually large deep base. Simple bone-like mesodentine in the crowns of *F. basiglobosa* scales lacks principal vascular canals. *Arenaceacanthus arcuatacanalis* has diagnostic scales with anterior ridges that fade out at one-third of crown length, and crowns composed of simple acellular meso- and durodentine with the original arcuate radial vascular canals over the base. *Bracteatacanthus assiduus* scale crowns have short ridges of asymmetric profile and an antero-median sulcus, whereas scales of *Rohonilepis breviornatus* have sharp symmetric subradial crown ridges sloping towards the base. Scale crowns of *B. assiduus* and *R. breviornatus* are composed of dentine and durodentine, but the former is distinguished by a second area of multibranched radial vascular canals positioned high in the neck.

Key words: Acanthodii, Climatiiformes, Ischnacanthiformes, morphology, histology, Silurian, Lithuania.

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Introduction

Acanthodians are extinct Palaeozoic fishes and had their acme during the Late Silurian and entire Devonian ("The Age of Fishes"). Disarticulated microremains of acanthodians, such as scales, fin spines, teeth or fragments of ossified dermal bones are commonly represented in carbonate and terrigenous Old Red facies.

The most common taxa recognised from isolated scales are the Silurian acanthodian genera *Nostolepis* Pander, *Gomphonchus* Gross, and *Poracanthodes* Brotzen; they are present in almost all Silurian vertebrate assemblages worldwide. These genera were first discovered in Lithuania at the beginning of the 1970s by V. Karatajūtė-Talimaa during her taxonomic and biostratigraphic study of thelodonts. A. Brazauskas (Vilnius University) recently dissolved rock core samples for conodont biostratigraphic research and the fishes studied here were donated from this comprehensive series of core samples. The acanthodians in this study were taken from many samples representing entire Silurian, but unfortunately the Llandovery and the lower part of Wenlock still lack scales with acanthodian characteristics.

Despite a long history of collecting Silurian acanthodians in Lithuania, their scales were never subject to detailed taxonomically studies using both morphologic and histologic characters. Some publications discussed the biostratigraphic significance of scale assemblages and facies dependency (Karatajūtė-Talimaa et al. 1987; 1999), but these were preliminary and often incomplete faunal data were reported.

The present taxonomic study is principally based on cores from fifteen boreholes from Lithuania (Fig. 1) which contained acanthodian associations from Wenlock to Pridoli. Included in the study also are finds from additional boreholes representing the top of the Pridoli, from a previous study of acanthodians from Silurian/Devonian boundary beds.

This paper represents the second one in a series describing new climatiid and ischnacanthid scale taxa; new nostolepids are described in the first paper (Valiukevičius 2003).

The acanthodian collection is housed in Vilnius, at the museum of the Institute of Geology and Geography (abbreviated LIGG), and is numbered 25-A.

Systematic palaeontology

Order Climatiiformes Berg, 1940
Family Climatiidae Berg, 1940
Genus *Vesperalia* nov.

Derivation of name: From Latin *vesper*, evening, referring to the late discovery of the genus during the study.

Type species: *Vesperalia perplexa* gen. et sp. nov.

Age and geographic distribution: Rietavas Beds of the Jūra Formation, Pridoli, Late Silurian; West Lithuania.

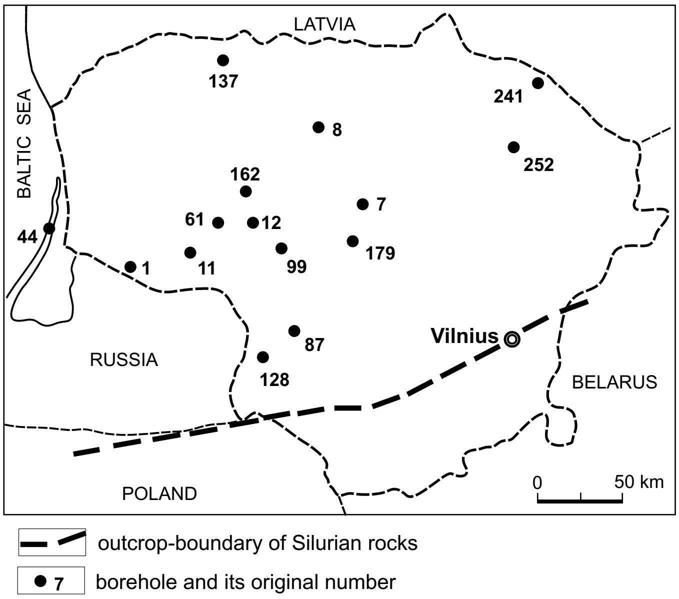

Fig. 1. Sketch map showing location of the boreholes yielding the majority of the material studied. Borehole and its original number: 1-Stoniškiai, 7-Krekenava, 8-Stačiūnai, 11-Šešuvis, 12-Kunkojai, 44-Nida, 61-Viduklė, 87-Sutkai, 99-Gėluva, 128-Vilkaviškis, 137-Liepkalnis, 162-Kurtuvėnai, 179-Ledai, 241-Butkūnai, 252-Svėdasai.

Diagnosis.—As for *Vesperalia perplexa* gen. et sp. nov., the only species.

Vesperalia perplexa gen. et sp. nov.

Figs. 2, 3.

Holotype: LIGG 25-A-2413, trunk scale (Fig. 2A).

Type locality: Stoniškiai-1 borehole, depth 1211.0–1217.0 m.

Type horizon: Rietavas Beds of the Jūra Formation, Pridoli, Upper Silurian.

Range: Type horizon only.

Derivation of name: From Latin *perplexus*, tangled, intricate.

Material.—Total about 600 scales.

Diagnosis.—*Vesperalia* with high-crowned scales, porous neck and thick crown with a sculpture of four to six linear or wavy longitudinal ridges, of which two converging ones may form a raised medial area. Ridges usually cross the entire length of the crown or fade out mid-length, continuing after a smooth area on the posterior edge of the crown. Scales grow superpositionally or both superpositionally and areally. Stranggewebe with unusually large oriented lacunae and simple mesodentine form both posterior and anterior parts of the crown. The crown contains a system of complicated and enlarged vascular canals.

Description.— Most trunk scales have rounded rhomboidal crowns varying from isometric to elongate, with length of 0.5–0.87 mm and width of 0.61–0.9 mm. The length and width of the larger scale specimens is 0.93–1.47 mm and 0.95–1.4 mm, respectively. The crown surface is broad and flat, with slightly downsloped lateral and anterior margins. Four to six sharp sub-parallel straight or wavy ridges extend the whole crown length. The ridges become more robust towards the scale base.They are usually of the same height across the crown but may be more pronounced and higher posteriorly (Fig. 2C, D, G). The two most conspicuous ridges converge at the posterior tip of the crown and may form a slightly raised

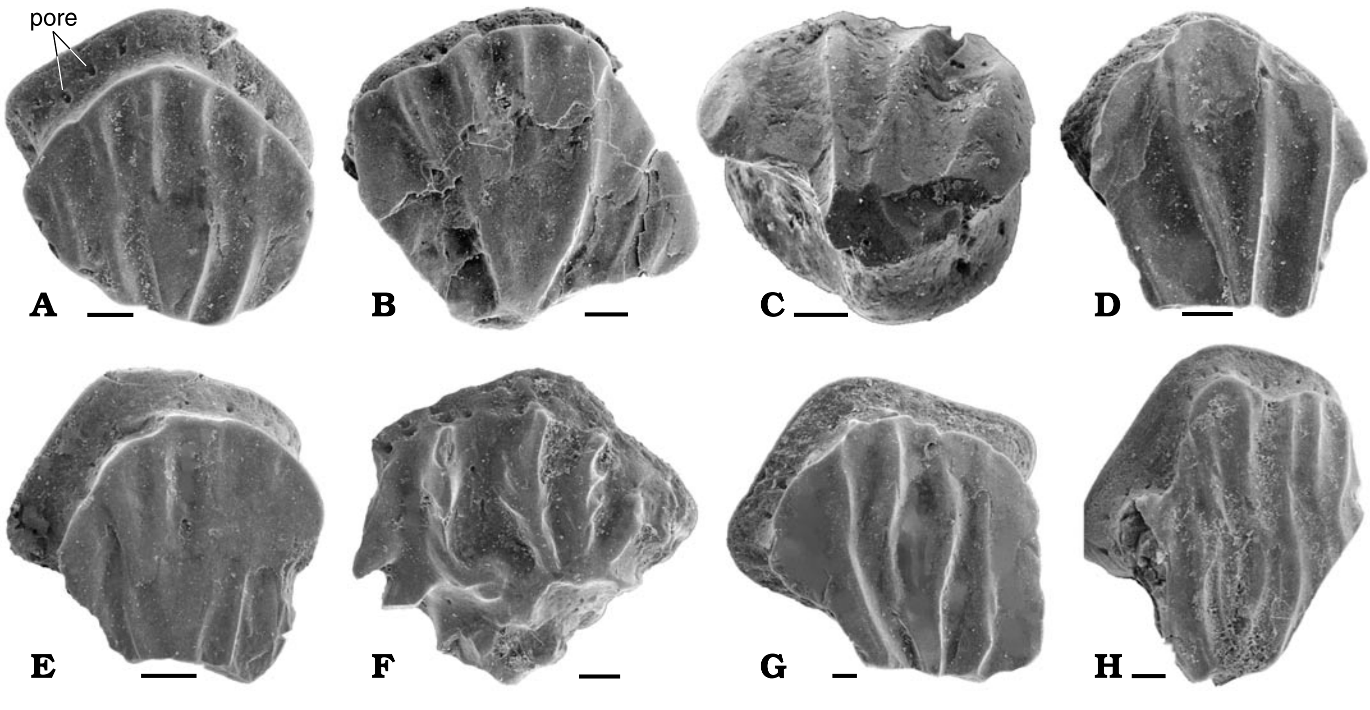

Fig. 2. *Vesperalia perplexa* gen. et sp. nov. SEM micrographs, trunk scales except for F, head? scale, crown views, anterior upwards: holotype, LIGG 25-A-2413 (**A**), LIGG 25-A-2416 (**B**), LIGG 25-A-2417 (**C**), LIGG 25-A-2418 (**D**), LIGG 25-A-2420 (**E**), LIGG 25-A-2422 (**F**), LIGG 25-A-2421 (**G**), LIGG 25-A-2414 (**H**). Scale bars 0.1 mm. Nida-44 borehole, depth 1213.0 m (A, E–H) and Stoniškiai-1 borehole, depth 1211.0–1217.0 m (B–D). Upper Silurian, Pridoli, Rietavas Beds of the Jūra Formation.

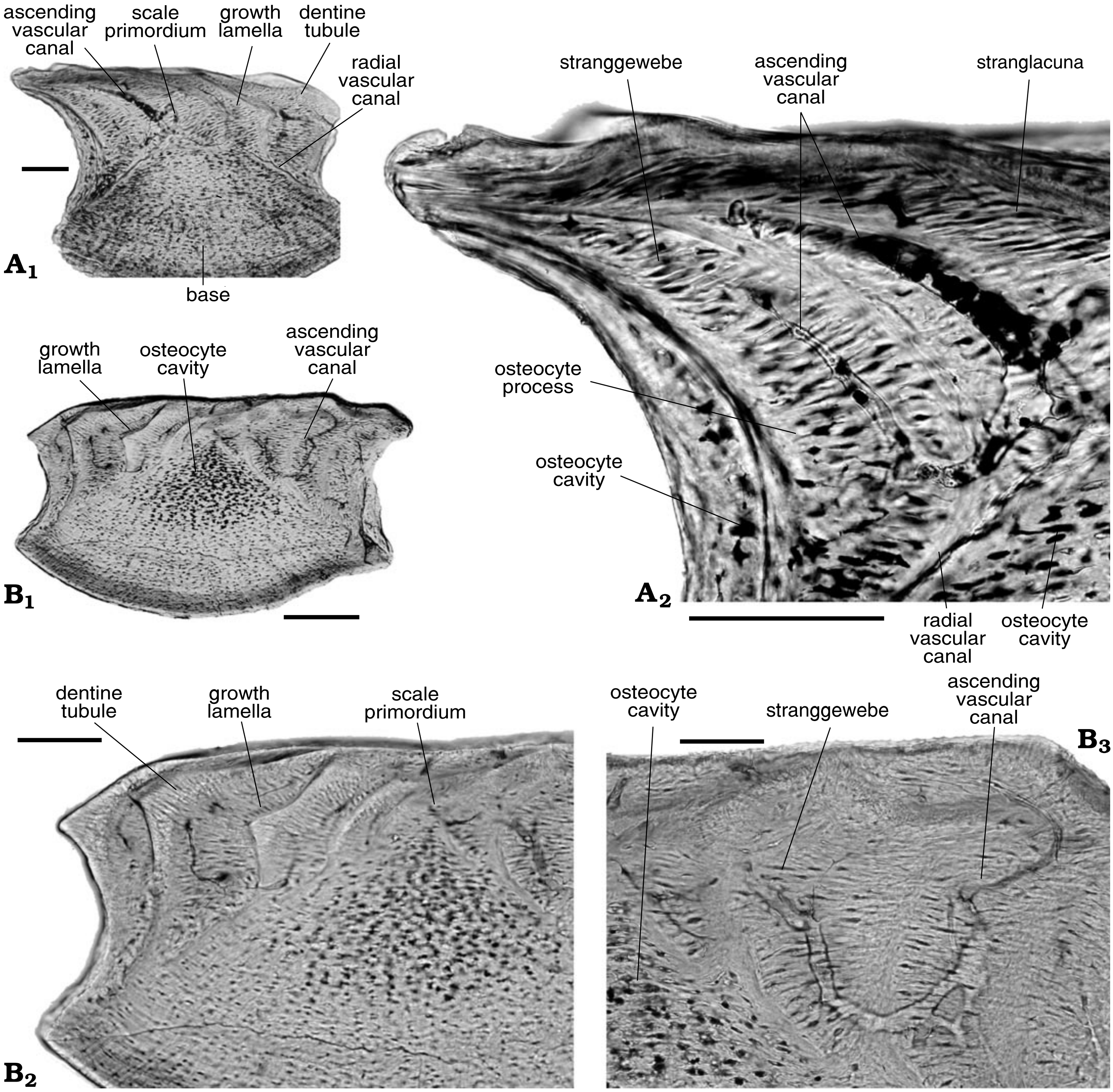

Fig. 3. *Vesperalia perplexa* gen. et sp. nov. Microstructure of scales in vertical longitudinal (**A**) and transverse (**B**) sections. A_1. Holotype-like scale with uniform bent, sub-parallel ridges prominent at the anterior and posterior edges of the crown, and almost fading out near the crown center. Thin section LIGG 3678. A_2. Detail of posterior edge of crown and a small portion of base of the same scale. B_1. Widened scale with flattened ridges like those in Fig. 2E. Thin section LIGG 3679. B_2. Detail of the left part of the same scale. B_3. Detail of the right part of the same scale. Scale bars 0.1 mm. Stoniškiai-1 borehole, depth 1211.0–1217.0 m. Upper Silurian, Pridoli, Rietavas Beds of the Jūra Formation.

triangular medial plateau (Fig. 2B, D), which has a sculpture of weak anterior ridgelets (Fig. 2B) or has an anteriorly widened shallow groove (Fig. 2D). The holotype and other specimens have ridges that fade out at the mid-length of the crown and after a central smooth area, continue and increase in height posteriorly (Fig. 2A, E). Of particular interest are the specimens with crown ridges and grooves on the anterior and posterior areas that do not join, but are shifted laterally relative to the long axis of the scale (Fig. 2E). The grooves between ridges are of irregular depth and width, and sometimes form deeper troughs at their anterior end (Fig. 2E, G, H).

Scale necks are tall and contain large linearly opening basal pores on all the walls, with up to four on each side (Fig. 2A, E). The scale base is rhombic in outline, moderately to greatly convex, usually protruding slightly beyond the crown antero-laterally. The deepest point of the base is centrally positioned.

Putative head scales (very rare in the studied samples) have isometric rhomboid, thickened crowns (up to 0.65–0.82 mm long and wide) and low porous necks as compared to trunk scales. Head scale crowns have three to four prominent, robust and rounded ridges of even height extending over the entire crown length. These robust ridges bend medially towards the posterior edge (Fig. 2F), but do not join each other. Additional lateral oblique riblets occur on the side of each ridge. The postero-lateral crown edge is multicuspid with several (up to four on each side) rough spinelets.

The histology of all *V. perplexa* scales (Fig. 3) is uniform. Crowns are composed of stranggewebe (mesodentinal tissue containing elongate, linearly oriented lacunae and incorporating osteocytes; for histologic terminology see Gross 1971 and Denison 1979) and simple mesodentine arranged in four thick growth lamellae. The growth type differs slightly among scales. Scales with interrupted ridges (Fig. $3A_1$, B_1) demonstrate a superpositional growth in only the two oldest lamellae, whereas the two youngest are added areally. Scales with continuous ridges grow superpositionally.

The stranggewebe is characterized by enlarged and elongate stranglacunae with interconnecting short processes. An unevenly thick mantle of simple mesodentine is superficial to the stranggewebe in each growth lamella (Fig. $3B_2$). In scales of this species, the stranggewebe develops with a similar intensity not only in the posterior part of the crown, as it is characteristic of most climatiids, but also in its anterior parts (Fig. $3A_1$).

The basal part of the neck has rare, typical mesodentine osteocyte cavities. The principal vascular system is formed of enlarged radial vascular canals positioned over the base, and wide ascending and slightly branched main canals supplying each growth lamella (Fig. $3A_2$, B_3). This system is complicated in the earliest/oldest lamellae because of additional branchings.

The simple mesodentine enclosing stranggewebe in the outer parts of lamellae contains a characteristic net of winding dentine tubules with many osteocyte cavities even in the superficial layers (Fig. $3A_2$, B_2). Durodentine is absent.

Scale bases are composed of cellular bone arranged in very thin and dense growth lamellae with plenty of osteocyte cavities and medium to long Sharpey's fibre traces. The osteocyte density increases towards the tip of pyramidal base, where they become oriented along the growth lines, and approximate the structure of both bone tissue and stranggewebe (Fig. $3B_2$).

Discussion.—The trunk scales of *Vesperalia* differ from those of all known climatiids in having a high and linearly porous neck distinct from the convex base by a sharp rim and irregular ridges ornamenting the horizontal plate of the crown. They also have wide, pronounced, often wavy subparallel ridges; the two central ridges may form an elevated medial area and point towards the posterior end of the crown. Ridges of some scale specimens are developed along the anterior and posterior edges of the crown, leaving the median part of the crown unsculptured a character not previously observed in acanthodians. Histological microstructure corresponds to the *Nostolepis*-type, distinguished by very large ascending and radial vascular canals, unusually elongate lacunae of stranggewebe covered by a mantle of osteocyte-rich mesodentine in scale crowns (the tissue has bone-like characteristics).

The *Nostolepis*-type histology suggests that *Vesperalia perplexa* gen. et sp. nov. can be asigned to the climatiids as presently classified. Based on morphologic characters, particularly the distribution of crown ridges, the scales of *V. perplexa* differ from known nostolepids, and should be considered generically distinct. Other morphological features, that are worth mentioning are the high and porous necks (not characteristic of most climatiids), and the crown sculpture of interrupted ridges. In addition, both superpositional and areal growth types are developed in scales of *V. perplexa*. It is obvious, that the replacement of the superpositional growth by the areal one takes always place after the formation of two the oldest lamellae (of four), and can not be attached to the ontogenetic development stage (younger or older) of scales. Histologically, scales are distinguished from those of other Climatiiformes not only by an exhuberant development of stranggewebe, a unique character among climatiids, but also by the particularly large oriented lacunae, clearly separated strips of stranggewebe and thick mantle of simple mesodentine in growth lamellae.

There are no closely related climatiids to be compared. According to several characters, *Vesperalia perplexa* gen. et sp. nov. resembles representatives of *Endemolepis* and *Tareyacanthus* (Valiukevičius 1994, 1998). The former, represented by a single species *Endemolepis inconstans* Valiukevičius, 1998, ranges across the Silurian–Devonian boundary in the Baltic, is distinguished by crown ridges of changeable form and length (sharp narrow, broad rounded, single or meeting in pairs, frequently with additional oblique branchings) extending the entire crown length, except for a diagnostic, narrow, unornamented anterior strip (Valiukevičius 1998: pl. 6: 3–7). Two known Devonian representatives of *Tareyacanthus*, *T. magnificus* Valiukevičius, 1994 (pl. 23: 9–14) from Taimyr Peninsula (Russia) and *T. dissectus* Valiukevičius, 1998 (pl. 3: 22–24 and pl. 4: 7–9) from the Stoniškiai Formation of the Baltic coast, have scales ornamented with high, sharp parallel or slightly fan-shaped ridges (up to eight per scale), that may bifurcate anteriorly and are separated by deep grooves. The histologic microstructure of both taxa is only comparable with *Vesperalia perplexa* gen. et sp. nov. as they all have a complicated system of principal vascular canals in crowns, but the details mentioned previously distinguish *Vesperalia* and its single species from all known climatiids.

Occurrence.—Stoniškiai-1 borehole, depth 1211.0–1217.0 m; Nida-44: 1213.0 m and Šešuvis-11: 1005.0–1015.2 m.

Genus *Fecundosquama* nov.

Derivation of name: *fecundus* (Latin) fertile, fruitful, referring to the richness and statistic dominance in samples, and *squama* (Latin) scale.

Type species: *Fecundosquama basiglobosa* gen. et sp. nov.

Age and geographic distribution: Minija Regional Stage and the lower part of the Jūra Regional Stage, Pridoli, Late Silurian; Lithuania.

Diagnosis.—As for *Fecundosquama basiglobosa* gen. et sp. nov., the only species.

Fecundosquama basiglobosa gen. et sp. nov.

Figs. 4, 5.

Gomphonchus sp. A; Märss 1997: pl. 2: 13–15.

Holotype: LIGG 25-A-2405, trunk scale (Fig. 4A).

Type locality: Kurtuvėnai-162 borehole, depth 1052.2–1072.4 m.

Type horizon: The upper part of Minija Regional Stage (Varniai Beds or their correlatives) to the lower part of Jūra Regional Stage (lower part of the Jūra or Lapės formations).

Range: Minija Regional Stage to the lower part of Jūra Regional Stage.

Derivation of name: From Latin *basis*, base and *globosus*, round, globose, referring to the scale base shape.

Material.—More than 50 000 scales.

Diagnosis.—*Fecundosquama* scales having low horizontal crowns with crenulated sculpture anteriorly or around the entire crown margin, lacking a neck; deep convex base present. Scale crowns composed of simple bone-like mesodentine with abundant osteocyte cavities and enlarged vascular canals present in the oldest growth lamellae only. Crown mesodentine merges gradually into highly cellular thin-lamellar bone in the base that is penetrated by long traces of Sharpey's fibres.

Description.—Scales have a very low crown and a large, convex base protruding beyond the crown on all sides. Crown length varies from 0.35 to 0.7 mm, and can be 0.3 to 0.77 mm wide. The isometric rhomboid crown plate of trunk scales (Fig. 4A, B, E) is almost flat, very slightly curved downwards at the anterior margins, and posteriorly the crowns are elongated and rhomboidal to elipsoidal. The anterior margin of the crown has short but comparatively wide notches which extend to the surface of the scale base. The number of notches varies from 5 to 6 (Fig. 4E) to 10 (Fig. 4B). The putative head scales (Fig. 4C, D) differ from the trunk scales in having isometric rhomboid to round crowns with notches on all margins. The deep, convex scale base is rhomboid to round in outline, with a prominent lateral rim at the deepest point projecting anterior to the crown. In rare cases the deepest point of the base is situated posteriorly, so the base protrudes beyond the posterior margin of the crown (Fig. 4E). Scales lack necks.

Simple mesodentine crown tissue (neither stranggewebe nor durodentine present) and cellular bone in scale bases can be seen in the sectioned scales. Up to six thin lamellae of superpositional growth in crowns are composed of bone-like mesodentine containing numerous multi-angular osteocyte spaces even in the latest, outer lamella (Fig. $5A_2$) and short radiating and winding dentine tubules form a fine network. The scale primordium does not differ from others in respect to tissue structure. Most scales sectioned have no enlarged vascular canal system in crowns (Fig. $5A_1$, B_1), and only one (Fig. $5C_1$, C_2) demonstrates wide radial vascular canals in the two oldest growth lamellae. There is no sharp boundary between the crown mesodentine and bone of the base: the first tissue grades gradually into the second. The cellular bone of the base is composed of numerous very fine growth zones (Fig. $5A_1$, A_2) penetrated by long Sharpey's fibre traces (Fig. $5B_2$, B_3) and enclosed abundant osteocyte cavities with short cell processes. Osteocytes are oriented along growth lines.

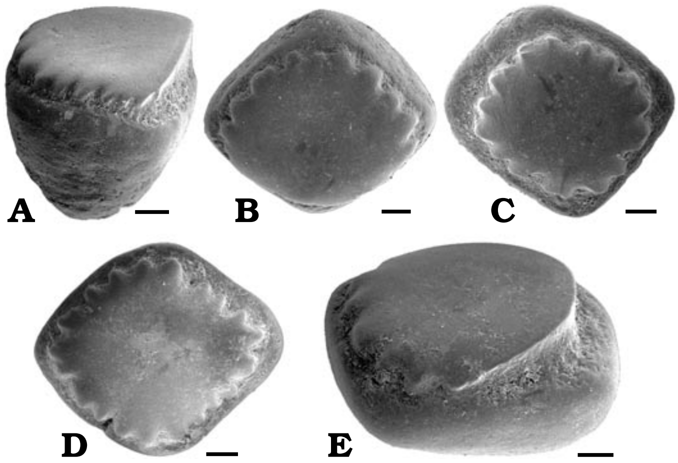

Fig. 4. *Fecundosquama basiglobosa* gen. et sp. nov. SEM micrographs of scales. **A**, **B**, and **E**. Trunk scales. **A**. Holotype, LIGG 25-A-2405, antero-lateral view, anterior to the left. **B**. LIGG 25-A-2407, crown view, anterior upwards. **E**. LIGG 25-A-2406, lateral view, anterior to the left. **C**, **D**. Head? scales, crown views, anterior upwards. **C**. LIGG 25-A-2409. **D**. LIGG 25-A-2408. Scale bars 0.1 mm. Gėluva-99 borehole, depth 681.6 m. Upper Silurian, Pridoli, Vievis Formation.

Discussion.—This new genus and species is based on scales with clear morphologic (center of flat crown without ridge ornamentation, fine ridges confined to crown margins, no neck, deep convex base protruding beyond crown on all sides) and histologic characters (neither stranggewebe nor durodentine present in crowns, vascular canal system weakly developed, well-developed net of bone-like mesodentine with many osteocyte spaces, forming a gradual transition to cellular bone in scale bases). The comparatively short stratigraphic range of *Fecundosquama basiglobosa* gen. et sp. nov. together with diagnostic features makes it a potentially good biostratigraphic taxon for more detailed vertebrate zonations of the Late Silurian.

F. basiglobosa gen. et sp. nov. has outstanding diagnostic features, and no related taxa are known to date. In terms of histology, there are some known climatiids similar *F. basiglobosa* in some ways, for example, bone-like mesodentine, absence of stranggewebe or reduced principal vascular canal system. The presence of such scale characters was demonstrated in a study on phylogenetical development of nostolepids from the Timan-Pechora region spanning the Late Silurian–Early Devonian (Valiukevičius 2000). All the characters together in *F. basiglobosa*, especially the distinctive features of bone tissue in scale bases (density and fine-lamellar cellular bone and gradual transition to the crown mesodentine), are observed in acanthodians for the first time.

Märss (1997) presented morphologically similar specimens (histology not examined) from the same region of the Baltic, in the Dubovskoye borehole of the Kaliningrad District (former East Prussia). The rocks are from the Kaugatuma Stage, Pridoli, from depth 1064.7–1085.5 m and originally were identified as *Gomphonchus* sp. A (Märss 1997: fig. 4). These scales are referred to *F. basiglobosa* gen. et sp. nov. Some characters (low horizontal crown, no neck, large convex base and proportions of crown/base development) demon-

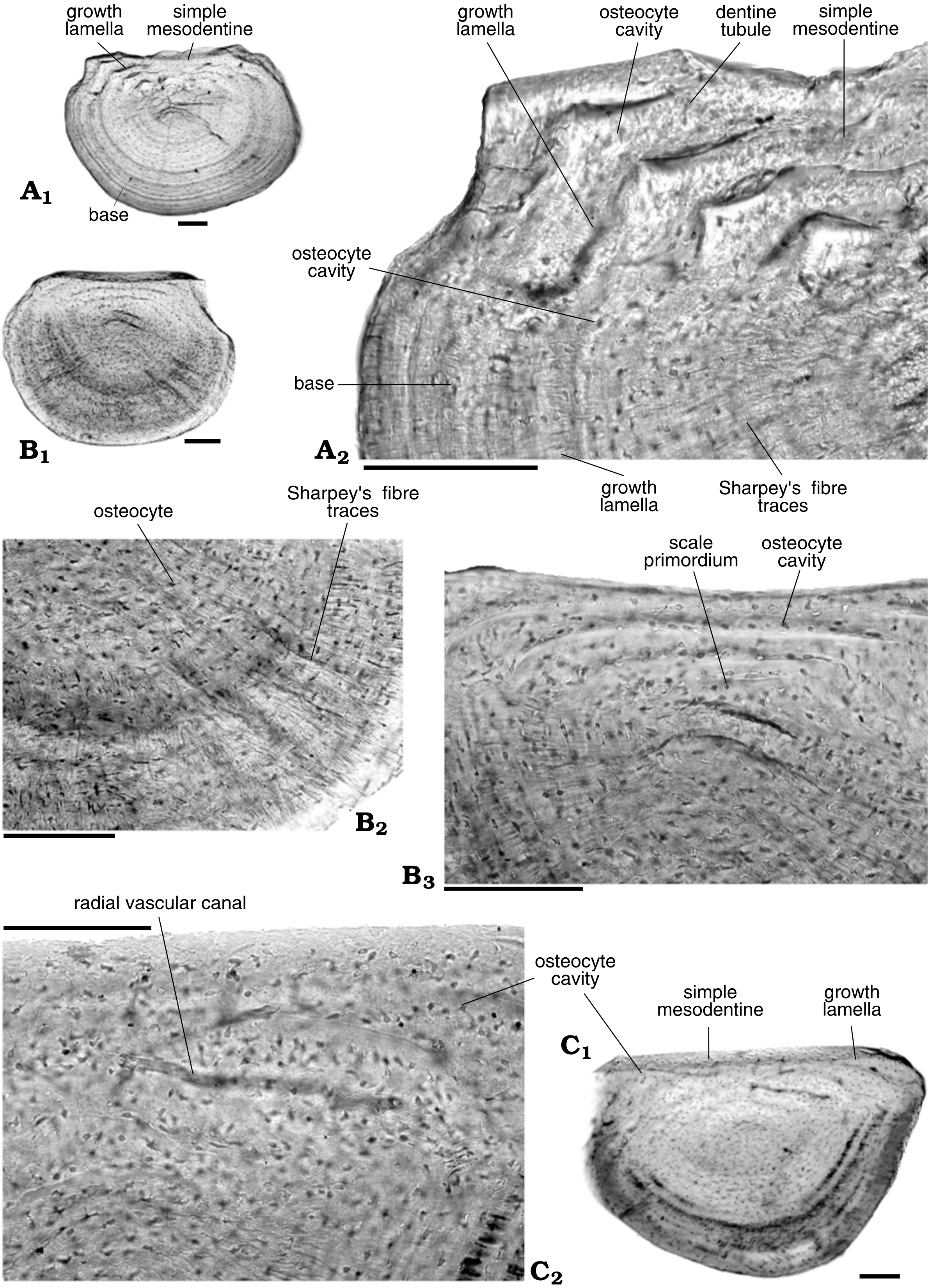

Fig. 5. *Fecundosquama basiglobosa* gen. et sp. nov. Microstructure of trunk scales in vertical transverse (**A**) and longitudinal (**B**, **C**) sections. A_1. Thin section LIGG 3683. A_2. Detail of the left part of the same scale. B_1. Thin section LIGG 3686. B_2. Detail of the right part of the base of the same scale. B_3. Detail of the central part of crown and bordering base area of the same scale. C_1. General view, thin section LIGG 3687. C_2. The same scale, detail of the right part of crown and bordering base area. Scale bars 0.1 mm. Kurtuvėnai-162 borehole, depth 1052.2 m. Upper Silurian, Pridoli, Jūra Formation (A_1, A_2 and B_1–B_3) and Ledai-179 borehole, depth 537.7 m. Upper Silurian, Pridoli, Lapės Formation.

strate similarity between these scales, however, the scales are not identical. The Dubovskoye specimens (Märss 1997: pl. 2: 13–15) not only have notches on the anterior part of the crown, but also have short surface ridgelets. The main difference between *F. basiglobosa* and the Dubovskoye scales is the presence of small bulbs or sometimes cone-like spinelets displaced in lines on the postero-lateral crown walls in the latter. These specimens, in my opinion, are similar to and might belong to *F. basiglobosa*, what suggests a climatiid rather than an ischnacanthid affinity for the Dubovskoye scales.

Occurrence.—Ledai-179 borehole, depth 537.4–547.6 m; Gėluva-99: 681.6–685.3 m; Sutkai-87: 609.3–615.3 m; Kurtuvėnai-162: 1052.2–1072.4 m; Stoniškiai-1: 1311.0– 1359.0 m; Šešuvis-11: 1072.9–1119.5 m; Liepkalnis-137: 892.1–893.9 m; Vilkaviškis-128: 706.2–714.0 m.

Order Ischnacanthiformes Berg, 1940

Family Ischnacanthidae Woodward, 1891

Genus *Arenaceacanthus* nov.

Derivation of name: From Latin *arenaceus*, small and *acanthus*, thorn.

Type species: *Arenaceacanthus arcuatacanalis* gen. et sp. nov.

Age and geographic distribution: Lower Silurian, Wenlock, Gėluva Regional Stage, Upper Silurian, Ludlow, Dubysa and Pagėgiai regional stages, to Pridoli, Minija Regional Stage, Lithuania.

Diagnosis.—As for only species *Arenaceacanthus arcuatacanalis* gen. et sp. nov.

Arenaceacanthus arcuatacanalis gen. et sp. nov.

Fig. 6.

Cheiracanthoides sp. nov. 1 and *Cheiracanthoides* sp. nov. 3; Valiukevičius in Karatajūtė-Talimaa et al.1987:67–68.

Holotype: LIGG 25-A-2443, trunk scale (Fig. 6A).

Type locality: Ledai-179 borehole, depth 547.6 m.

Type horizon: Upper Silurian, Pridoli, Vievis Formation.

Range: From Lower Silurian, Wenlock Gėluva Regional Stage, through Upper Silurian, Ludlow, Dubysa and Pagėgiai regional stages, to Pridoli, Minija Regional Stage.

Derivation of name: From Latin *arcuatus*, bent, curved, referring to characteristic form of branching radial vascular canals.

Material.—96 scales.

Diagnosis.—*Arenaceacanthus* with tiny scales and a crown sculpture of 6 to 8 short, low, parallel or fan-like anterior ridges. Scale crown composed of simple acellular mesodentine and durodentine, and base of acellular bone. Vascular system distinguished by multibranched net-like ascending and enlarged arcuate radial canals at the base/crown junction.

Description.—Tiny scales with well developed medium to high neck. Crown plate is horizontal, with a posteriorly elongate rhomboid to elipsoidal or round outline, 0.3 to 0.54 mm in length and 0.3 to 0.5 mm wide, with a sculpture of 6 to 8 short parallel anterior ridgelets that fade out at one-third of the crown length. Ridgelets are low, of angular profile and separated by shallow grooves. Scales with parallel or sub-parallel ridgelets (Fig. 6A, B) are more common as compared to those with radiating ones (Fig. 6D). Up to half the length of the crown overhangs base posteriorly. Scale bases are rhomboid in outline, with a sharp junction with the neck. Bases are moderately to deeply convex and project, at the deepest point, anterior to the crown.

Up to six crown growth lamellae consisting of net-like mesodentine (Fig. $6E_1$) show superpositional growth, are very thin towards crown edges and considerably thicker in the neck. Thin superficial durodentine strips (Fig. $6F_2$) are seen in two to three of the youngest growth lamellae. A dense network is formed of ascending vascular canals, long principal branches, many smaller branchings and interspersed dentine tubules (Fig. $6E_2$). No osteocyte spaces have been observed in crown tissue. The radial vascular canals at the base/neck junction are multibranched, winding and arc towards the base (Fig. $6E_1$, E_2). These arcuate radial canals make interconnections with small canaliculae in the base. The oldest growth lamella does not differ in this respect from the younger ones, but sometimes contains an enlarged vascular knot (Fig. $6F_2$) with thin dentine tubules emanating from all sides. Scale bases are composed of moderately dense acellular bone pierced by short winding canaliculae, which are mostly orientated along the growth lines. Sharpey's fibre traces are preserved only in short segments which may be due to preservation conditions.

Discussion.—Most ischnacanthid scale taxa were poorly studied with the exception of *Gomphonchus* (Pander) and *Poracanthodes* Brotzen. Previously scales with short, parallel, fading crown ridges and a lack of details of microstructure, were attributed to the genus *Cheiracanthoides* Wells. This practice was perpetuated in a biostratigraphic review of the Silurian acanthodians of Lithuania (Karatajūtė-Talimaa et al. 1987), where scales like those of *Arenaceacanthus arcuatacanalis* were identified as *Cheiracanthoides* sp. nov. 1 and *C.* sp. nov. 3. Thin-sectioned scales show clearly that the putative *Cheiracanthoides* scales do not belong to a climatiiform acanthodian. Here, such scales are considered to be from an ischnacanthiform, as suggested by their histology and the similarity of vascular canals differing from climatiiforms and acanthodiforms.

Summing all the distinctive characters of *Arenaceacanthus arcuatacanalis*, it has no closely related taxa within the family Ischnacanthidae. The crown ornamentation of *A. arcuatacanalis* scales is unlike that of known ischnacanthids and, to the contrary, more characteristic of the climatiiform *Cheiracanthoides.* Otherwise, the histological characteristics of the vascular system in scales (arcs of radial canals at the base/neck junction, network of ascending vascular canals interspersed with dentine tubules, the style of mesodentine in sum) distinguishes *A. arcuatacanalis* from other ischnacanthids. Only the details of the branching of the vascular canals makes *A. arcuatacanalis* scales comparable to representatives of the genera *Poracanthodes* Brotzen*, Gomphonchus* Gross or *Lietuvacanthus* Valiukevičius. The arcuate radial canals over the base are unique to *A. arcuatacanalis*.

Occurrence.—Ledai-179 borehole, depth 544.1–567.6 m; Gėluva-99: 735.2–806.0 m; Sutkai-87: 666.6 m; Kurtuvėnai-162: 1132.0 m; Butkūnai-241: 416.4–457.0 m; Viduklė-61: 1124.0–1161.6 m.

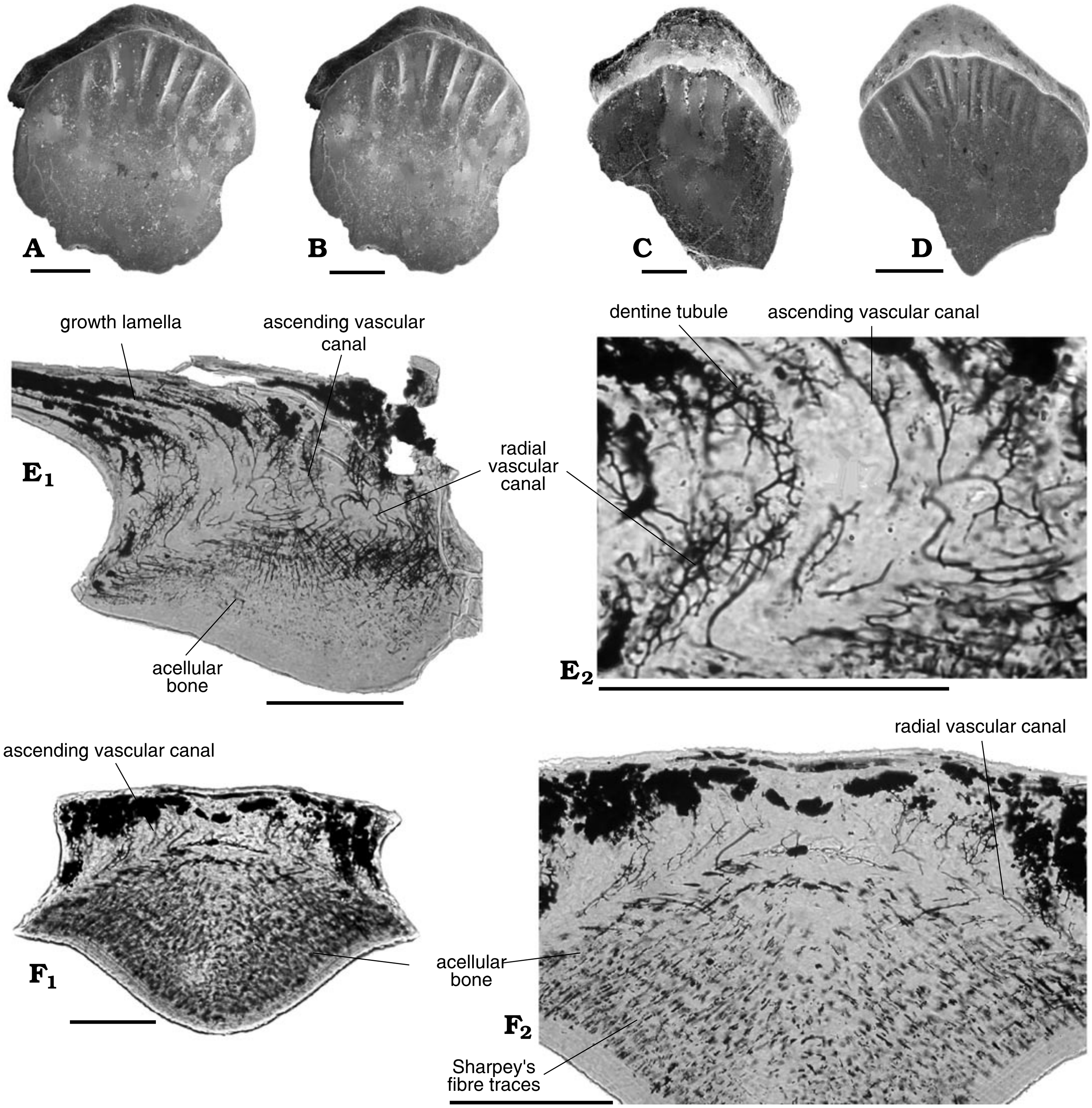

Fig. 6. *Arenaceacanthus arcuatacanalis* gen. et sp. nov. **A**–**D**. SEM micrographs of trunk scales, crown views, anterior upwards. **A**. Holotype, LIGG 25-A-2443. **B**. LIGG 25-A-2444. **C**. LIGG 25-A-2446. **D**. LIGG 25-A-2447. **E**, **F**. Microstructure of scales in vertical longitudinal (**E**) and vertical transverse (**F**) sections. E_1. General view, thin section LIGG 3731. E_2. Detail of the left side, the lower part of crown and bordering base strip of the same scale. F_1. Thin section LIGG 3733, general view. F_2. Enlarged main part of the same scale. Scale bars 0.1 mm. Ledai-179 borehole, depth 547.6 m. Upper Silurian, Pridoli, Vievis Formation.

Genus *Bracteatacanthus* nov.

Derivation of name: From Latin *bracteatus*, deceptive, delusive and *acanthus* (Latin) thorn.

Type species: *Bracteatacanthus assiduus* gen. et sp. nov.

Age and geographic distribution: Rietavas Beds of the Jūra Formation, Pridoli, Upper Silurian; West Lithuania.

Diagnosis.—As for only species *Bracteatacanthus assiduus* gen. et sp. nov.

Bracteatacanthus assiduus gen. et sp. nov.

Fig. 7.

Holotype: LIGG 25-A-2453, trunk scale (Fig. 7D).

Type locality: Nida-44 borehole, depth 1213.0 m.

Type horizon: Rietavas Beds of the Jūra Formation, Pridoli, Upper Silurian.

Range: Found only at type horizon.

Derivation of name: From Latin *assiduus*, regular, constant, referring to morphological uniformity of scales.

Material.—Approximately 100 scales.

Diagnosis.—*Bracteatacanthus* having small rhomboidal scales with a sculpture of 6 to 8 short crown ridges of asymmetric profile and an antero-median sulcus. The most convex part of the base projects in advance of crown. Crown composed of dentine with long ordinary ascending and multibranched radial vascular canals, part of which are situated high in the neck; thin outer durodentine strips present. Acellular bone in base very dense, with thin growth lamellae.

Description.—*B. assiduus* scales are small with well developed morphological elements: deeply convex base, tall neck and medium to thick crown. The crown plate is horizontal, almost isometrical, rhomboid, and sometimes with an elongate and narrow posterior flange. Crown length and width varies from 0.4–0.45 to 0.6–0.66 mm respectively. The posterior end of the crown overhangs the base only slightly. Anterior part of the crown has 6 to 8 short parallel to sub-radial ridges fading out at one-third of the crown length. The ridges are not sharp, and often have rounded outer crests (Fig. 7A) and widen anteriorly. The lateral ridge slopes are gently curved, whereas the median ones are nearly flat (Fig. 7A, D). The ridges are arranged symmetrically from the enlarged antero-median sulcus, which can form an anterior "beak" on the scale crown (Fig. 7E). The grooves in between the ridges are wide and shallow. The tall neck is porous (Fig. 7A, B) and has vertical grooves on the posterior face. The neck/base junction is outlined by a prominent rim (Fig. 7C, E). The base is rhomboidal, deeply convex, and the deepest point projects in advance of the crown.

Scales are composed of an *Acanthodes*-type histological structure. Up to ten lamellae of superpositional growth are formed of dentine and durodentine. The long ascending vascular canals are regularly oriented in the lamellae, but are not branched. A main central canal is always present (Fig. 7F_2, G_2). There are almost no upwardly directed dentine tubules in the horizontal part of crown plate. Centripetal radial vascular canals are complex and consist of several separate branched main canals, part of which are positioned unusually high in the neck (Fig. 7G_2). From the lowest of them appear some basally directed branches oriented along the growth lines of the base (Fig. 7G_2). Some of the earliest growth lamellae, not only the oldest one, have a complicated network of interwoven radial canals, ascending canals and their side branches (Fig. 7F_2). The acellular bone of the base is extensive, and forms a pyramid centrally, leaving only small space for crown dentine. Basal bone is very dense, with thin growth zones, penetrated by long Sharpey's fibre traces and contains rare short, winding vascular tubules.

Discussion.—Similar short-ridged scales from other regions have been attributed by other researchers to *Gomphonchus.* In my opinion, morphologic characters with definitive features of crown ridges and histological structure, distinguish *B. assiduus* from *Gomphonchus sandelensis* (Pander) and moreover from *G. hoppei* (Gross), and support erecting of the new genus. Whilst having *Acanthodes*-type histology, there are still diagnostic features for *Bracteatacanthus* scales which distinguish them from those of *Gomphonchus* with its characteristic cellular bone in scale bases (Denison 1979), and the composition of vascular canals in crowns.

Bracteatacanthus assiduus scales show some similarities with previously published specimens. *Gomphonchus* sp. 3 scales (Märss 1997: pl. 7: 4–9) from Hviždalka, bed 26 (Pridoli) of the Czech Republic, resemble those of *B. assiduus* based on scale shape, proportions, and several of them also by the ridge characters, which, in contrast to the Lithuanian specimens, have more relief and are sharper. Unfortunately, the Czech scales have not yet been examined histologically because of their poor preservation. Morphotype III scales of *Gomphonchus*? *turnerae* Burrow from the Jack Formation (Ludlow, *ploeckensis* conodont Zone) of Queensland, Australia also are similar to those of *B. assiduus*. The diversity of scale crowns illustrated by Burrow and Simpson (1995: fig. 2E–K) is within the range of variation of *Bracteatacanthus*, but the histological microstructure is completely different: the Australian specimens are supposedly composed of mesodentine (Burrow and Simpson 1995: fig. 3A–D). Two new *Gomphonchus* species, recently studied from Timan-Pechora region (Valiukevičius in press) differ from *B. assiduus* in that the scales have cellular basal bone and a definitive vascular canal structure in their crowns.

Occurrence.—Nida-44 borehole, depth 1213.0 m; Stoniškiai-1: 1211.0–1217.0 m; Šešuvis-11: 1005.0–1006.0 m.

Genus *Rohonilepis* nov.

Derivation of name: In honour of Victor Rohon, the Baltic acanthodian researcher of the 19th century, and fom Greek *lepis*, scale.

Type species: *Rohonilepis breviornatus* gen. et sp. nov.

Age and geographic distribution: Pagėgiai to Jūra regional stages, Ludlow and Pridoli, Late Silurian; Lithuania.

Diagnosis.—As for only species *Rohonilepis breviornatus* gen. et sp. nov.

Rohonilepis breviornatus gen. et sp. nov.

Fig. 8.

Holotype: LIGG 25-A-2459, trunk scale (Fig. 8C).

Type locality: Kurtuvėnai-162 borehole, depth 1091.3–1117.8 m.

Type horizon: Ventspils and Minija formations, Ludlow and Pridoli, Upper Silurian.

Range: Upper Silurian, Ludlow, Pagėgiai Regional Stage, to Pridoli, the lower part of Jūra Regional Stage.

Derivation of name: From Latin *brevis*, short, and *ornatus* decorated, ornamented.

Material. Total more than 2100 scales.

Diagnosis.—*Rohonilepis* with tiny scales sculptured by 6 to 10 short, sharp, symmetrical sub-parallel anterior ridges turning anteriorly toward the neck-base junction. The two longest posteriorly pointing ridges can form an elevated medial area separating narrow, lowered lateral folds. Crown dentine contains medium-branched linear ascending and simple widened

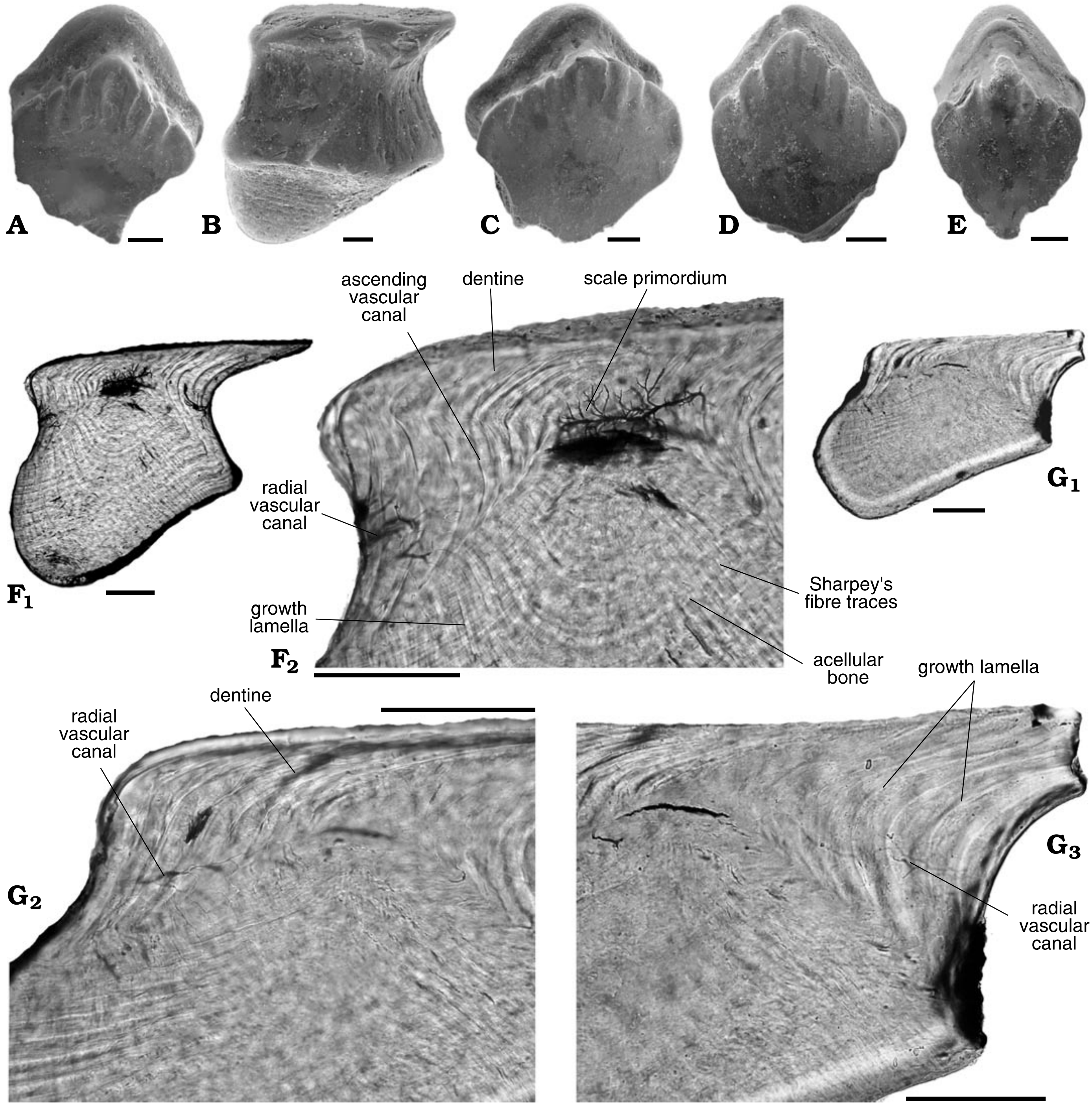

Fig. 7. *Bracteatacanthus assiduus* gen. et sp. nov. **A**–**E**. SEM micrographs of trunk scales; crown views, anterior upwards, except for **B**, lateral view, anterior to the left. **A**. LIGG 25-A-2450. **B**. LIGG 25-A-2451. **C**. LIGG 25-A-2452. **D**. Holotype, LIGG 25-A-2453. **E**. LIGG 25-A-2454. **F**, **G**. Microstructure of scales in vertical longitudinal sections. F_1. Thin section LIGG 3705, general view. F_2. Detail of the left part of crown and base apex of the same scale. G_1. Thin section LIGG 3708. G_2. Detail of the left part of crown and base apex of the same scale. G_3. The same scale, detail of the right part. Scale bars 0.1 mm. Nida-44 borehole, depth 1213.0 m. Upper Silurian, Pridoli, Rietavas Beds of the Jūra Formation.

radial vascular canals over the flat-pyramidal base, that is composed of dense acellular bone.

Description.—Tiny scales with crowns that only rarely reach 0.5 mm in length and scale width varies from 0.22 to 0.38 mm. The crown plate is horizontal, with up to one-third of the posterior unsculptured part overhanging the base. A quarter to one-third of the crown length has 6 to 10 short, sharp anterior ridges with a symmetrical profile, which fade posteriorly. Crown ridges may be straight (Fig. 8D) or slightly curved towards mid-scale (Fig. 8B, C). The holotype-like specimens, with sub-parallel ridges are more abundant in samples studied, however, scales with almost parallel ridges also are known.

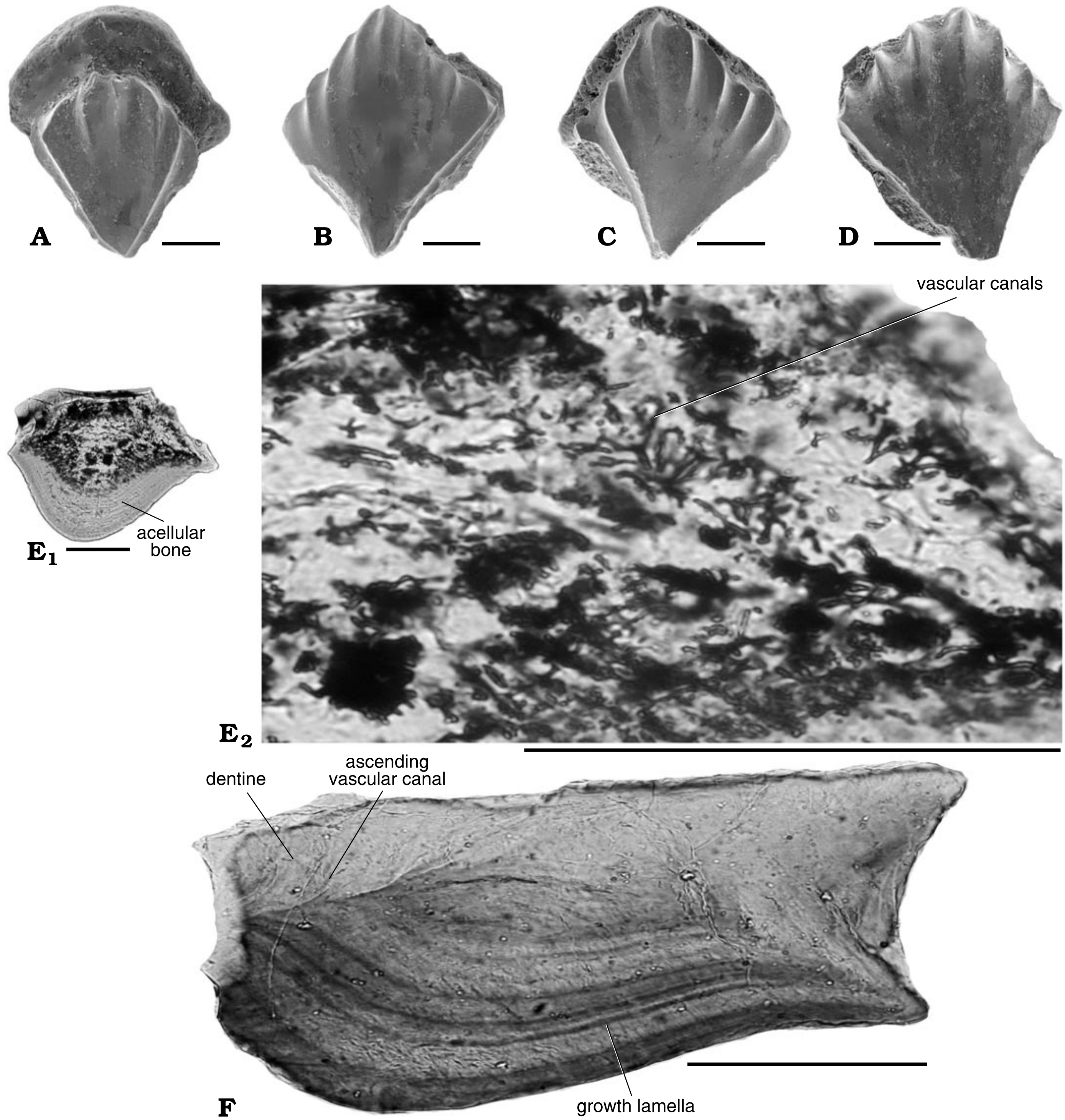

Fig. 8. *Rohonilepis breviornatus* gen. et sp. nov. **A**–**D**. SEM micrographs of scales, crown views, anterior upwards. **A**. LIGG 25-A-2457. **B**. LIGG 25-A-2458. **C**. Holotype, LIGG 25-A-2459. **D**. LIGG 25-A-2461. **E**, **F**. Microstructure of scales in vertical longitudinal sections. E_1. Thin section LIGG 3726, general view. E_2. Detail of the upper right crown part of the same scale. **F**. Thin section LIGG 3727. Scale bars 0.1 mm. Kurtuvėnai-162 borehole, depth 1103.0 m. Upper Silurian, Ludlow, Ventspils Formation.

Ridges are characteristically downwardly sloped anteriorly, sometimes reaching the base of the neck. Grooves between ridges are moderately deep and wide. Some scales have narrow lowered lateral ledges (Fig. 8A, C), separated from the remainder of the crown by the two longest, posteriorly pointing ridges. Moderately high to low neck usually has linear rows of pores. The scale base slightly protrudes beyond the crown antero-laterally, but may be also displaced far in advance of the anterior margin of the crown.

Histologic microstructure has not been sufficiently studied yet because of the preservation of the scales, but they are certainly of the *Acanthodes*-type. At least, 6 growth lamellae in crowns composed of dentine can be counted (Fig. 8F), with the oldest lamella unusually large. The vascular system is poorly defined due to re-mineralization of tissues and only short segments (Fig. 8E$_2$, F) of ascending and other vascular canals are visible. Ascending canals are moderately branched and mostly linear along growth lamellae. Radial vascular canals are simple and located just over the basal surface (Fig. 8F, right side). Durodentine has not been definitely recognized, but may be present. Acellular basal bone is dense and forms a flat-pyramid below the crown.

Discussion.—*Rohonilepis breviornatus* is comparable to the above described *Bracteatacanthus assiduus*, as histologically they both have many characters in common. The latter is distinguished by the peculiar arrangement and position of radial vascular canals in the dentine of the crown, that is definitely not present in *R. breviornatus*. Morphological differences are more substantial: asymmetrically sloped (in profile) rounded ridges do not extend baseward in *Bracteatacanthus* scales and sharper, symmetric, frequently centrally curved ridges sometimes reach the neck base in *Rohonilepis*. The lateral lower step-like margins of *R. breviornatus* scales have not been observed on those of *Bracteatacanthus*.

The sculpture of some scales of *R. breviornatus* resembles several specimens of *Gomphonchus* from the Hviždalka locality, Czech Republic (Märss 1997: pl. 7: 3, 10). Vergoossen (2002) illustrated specimens of Acanthodii gen. et sp. indet. that are similar but not as well preserved as the material figured here, but suggest, that some comparable varieties of scales might also be present in southern Sweden.

Occurrence.—Kurtuvėnai-162 borehole, depth 1091.3– 1137.5 m; Sutkai-87: 612.9–623.6 m; Gėluva-99: 654.1– 685.3 m; Stoniškiai-1: 1224.0–1308.9 m; Šešuvis-11: 1047.0–1049.5 m; Ledai-179: 525.7–544.1 m; Liepkalnis-137: 900.1–909.2 m.

Discussion and conclusions

Taxonomy

Two monotypic new genera and species of climatiiform acanthodians described here are undoubtedly placed within the family Climatiidae based on diagnostic histology. These scale-based histologic characters of the family level are as follows: few numbers of growth lamellae in scale crowns composed of mesodentine, that is represented by two main tissue varieties: simple network of dentine tubules incorporating osteocyte cavities and usually forming the anterior crown part or rarely entire crown, whereas the posterior part, the scale primordium including, is composed of stranggewebe (modified mesodentine with characteristic dense oriented and elongated lacunae); the stranggewebe is/or not enveloped by the peripheral layers of simple mesodentine in each growth lamella; the principal vascular system in crowns is formed (with few exceptions) of wide radial, circular and ascending canals; no superficial durodentine present; scale bases are composed of cellular bone.

Vesperalia perplexa, despite having an unusual crown sculpture for climatiids (interrupted ridges that are different on anterior and posterior crown parts), shows classical stranggewebe in crowns with enlarged oriented lacunae and covered by a mantle of simple net-like and highly cellular mesodentine. The expanded coverage (not only in the posterior part of the crown) of stranggewebe, is of particular interest, that has been rarely observed before.

The scales of the second species, *Fecundosquama basiglobosa*, lack crown ridges and having only marginally incised crowns, are composed of a cellular network of bone-like simple mesodentine with no stranggewebe and only rare fragments of principal vascular canals. Such a diversity of tissues might perhaps help grounding a subdivision of the family into two taxonomic units, when supported by the articulated climatiids.

The ischnacanthid affinity and histological scale-based diagnostic characters of the family can be stressed using data from an articulated *Poracanthodes menneri* (Valiukevičius 1992) and the best studied scale taxa of *Gomphonchus* (Denison 1979). Really they have different inner structure, and the similarity is only restricted by a presence of few pores in *G. hoppei* (Gross). Without deepening into taxonomical relations of taxa and accepting *a priori* that *Gomphonchus* is an ischnacanthid, the histological characters of the family are: scales composed according to two histologic types, *Acanthodes* and *Poracanthodes*; numerous growth lamellae in crowns are composed of dentine and durodentine (*Acanthodes*-type) and specified mesodentine (*Poracanthodes*-type); linear ascending and radial vascur canals form main stems that are only slightly distinguishing among other interspersed branches; mesodentine of the *Poracanthodes*-type contains multibranched ascending, radial and horizontal (in crown plate) canals often forming complex knots; neither osteocyte cavities nor lacunae present in crowns; scale bases of both histological types are composed differently, either of cellular bone (this is why the *Acanthodes*-type becomes modified) or of acellular one; scale crowns of *Poracanthodes*-type are pierced by pore canals, radial, arcade and superficially opening (sometimes they open in the neck only).

Of the three putative ischnacanthids described here, *Arenaceacanthus arcuatacanalis*, perhaps, poses more questions. This species has scales resembling those of climatiiform *Cheiracanthoides* by morphology, but has histological structure that is considerably different not only from climatiiforms, but differ also by some characters from scales of known ischnacanthiforms or acanthodiforms. Apart from specified mesodentine, scales of *A. arcuatacanalis* possess large arcuate segments of radial vascular canals at the base/ neck junction.

Scales of the two other taxa, *Bracteatacanthus assiduus* and *Rohonilepis breviornatus*, are much more similar to those of ischnacanthids with the *Gomphonchus*-like morphology, and histologically are of the *Acanthodes*-type, differing from representatives of *Gomphonchus* by the branching style of vascular canals and acellular bone in scale bases.

Biostratigraphy

Most of the taxa described here are biostratigraphically restricted to distinct formations or their parts, and the geographic distribution in Lithuania is often facies related. They

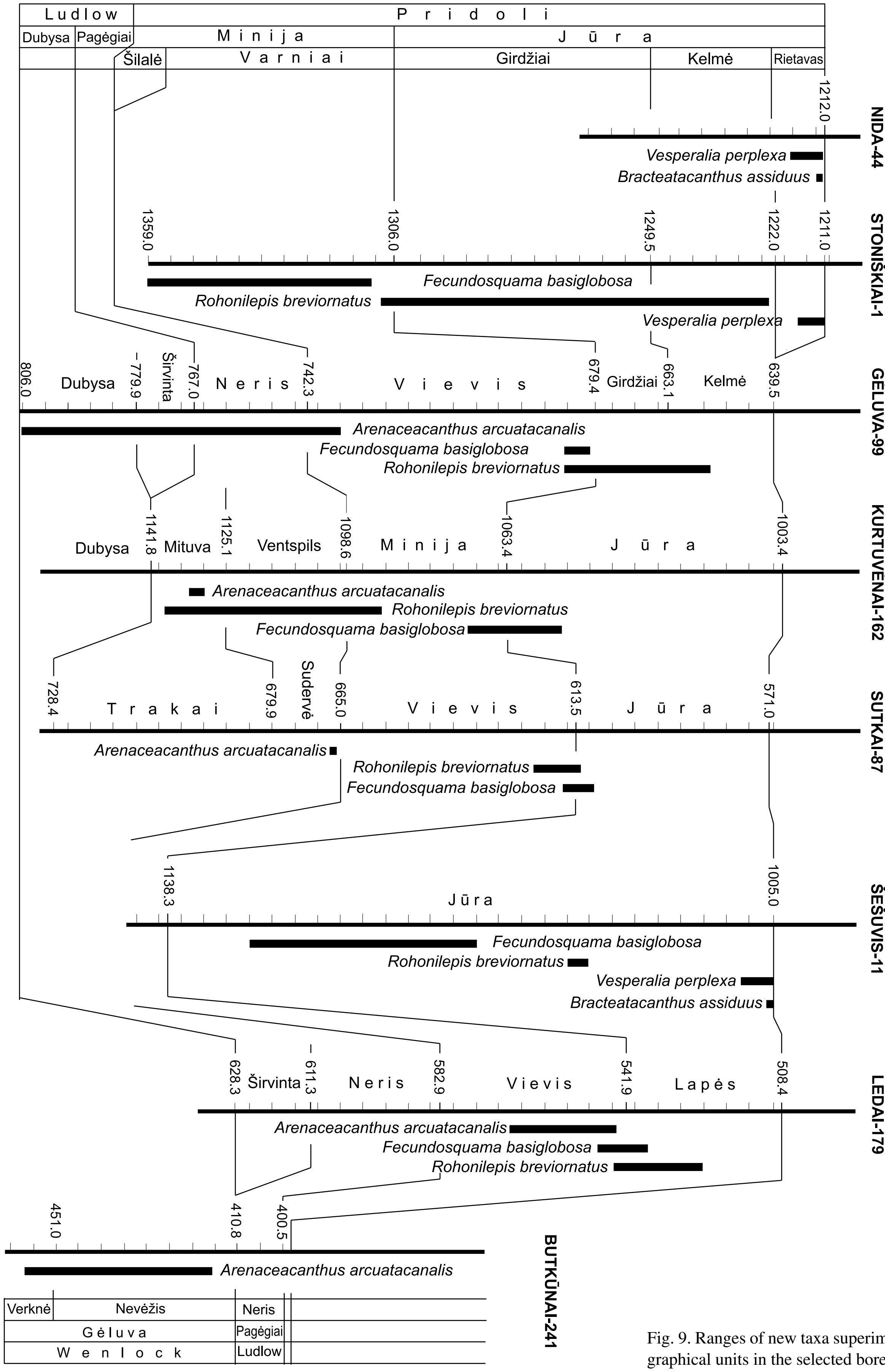

Fig. 9. Ranges of new taxa superimposed on the local stratigraphical units in the selected boreholes.

have different partial stratigraphic ranges obtained from borehole cores of different parts of Lithuania (Fig. 9). *Arenaceacanthus arcuatacanalis* is the oldest taxon, it first appears in the dolomites of the upper part of the Verknė Formation (Wenlock, the *Kockelella amsdeni* conodont Zone) in eastern Lithuania (Karatajūtė-Talimaa et al. 1987). Its acme is in the formations of the Pagėgiai and Dubysa regional stages of the Ludlow (bituminous nodular limestones, dolomitic marls and dolomites) in western and central Lithuania (see Gėluva-99 borehole, Fig. 9). It occurs in the following conodont zones: *Ozarkodina bohemica* to *O. crispa*, or sometimes in eastern Lithuania, *O. tillmani*, as an analogue of the *Kockelella variabilis*, *Polygnathoides siluricus*, and *Rotundacodina dubia* sequence of conodont zones established in the western Lithuania (Brazauskas 1987; Karatajūtė-Talimaa and Brazauskas 1994).

Fecundosquama basiglobosa is a potential marker of the Ludlow/Pridoli boundary based on its first occurrence deeply in the Varniai beds of the stratotypical Stoniškiai-1 borehole. It appears in the Minija and extends into the lower part of Jūra Regional Stage. It is characteristic for undulatory layered dolomitic marls, dolomites and limestones of the upper part of the Vievis and the lower part of Lapės formations in central and eastern Lithuania. The taxon is common in the clayey limestones and dolomitic marls of the Minija Formation to the west, spending its acme in the Varniai beds of this formation in the extreme west. The *Ozarkodina e. eosteinhornensis* conodont Zone covers this stratigraphic interval.

Rohonilepis breviornatus is more characteristic in the west of the republic, of the Girdžiai and Kelmė beds of the Jūra Formation (Pridoli), but sometimes it occurs low in the Mituva and Ventspils formations of the Pagėgai Regional Stage (see Kurtuvėnai-162 borehole) of the Ludlow Series, the *Rotundacodina dubia* and *Ozarkodina crispa* conodont zones. In sum, it appears together with *Fecundosquama basiglobosa* at the Ludlow/Pridoli boundary, but eastwards, its range becomes shorter, restricted to the uppermost Vievis and extending to the lower part of Lapės Formation (uppermost Minija to lower Jūra) in eastern Lithuania.

Vesperalia perplexa and *Bracteatacanthus assiduus* have been found only in the westernmost Lithuania, where the succession is most complete, in the Rietavas Beds (carbonate clays and clayey limestones) of the topmost Jūra Formation. Both have short stratigraphic ranges (they do not survive the Silurian/Devonian boundary) and are useful as zonal taxa for the uppermost Pridoli.

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