Diversity of tissues in acanthodians with *Nostolepis*-type histological structure

JUOZAS VALIUKEVIČIUS and CAROLE J. BURROW

Valiukevičius, J. and Burrow, C.J. 2005. Diversity of tissues in acanthodians with *Nostolepis*-type histological structure. *Acta Palaeontologica Polonica* 50 (3): 635–649.

Acanthodian scales with *Nostolepis*-type histological structure are separated into five groups based on the presence/absence and extent of stranggewebe, odontocytic and syncitial mesodentine networks, cellular unipolar mesodentine, bone-like mesodentine and durodentine in scale crowns. Two new families of acanthodians are erected, based primarily on histological structure of scales: the Vesperaliidae (stranggewebe extending throughout the scale crown) and the Acritolepidae (bone-like mesodentine in the scale crown). The latter family includes species erected for articulated fish. The families Tchunacanthidae and Lenacanthidae are united in the single family Tchunacanthidae, characterized by having scale crowns with mesodentine formed mainly by unipolar cells. A sixth group, which we exclude from the *Nostolepis*-type, has scale crowns composed of dentine without lacunae, plus durodentine, and bases with only rare osteocyte cavities. The new groups promote the revision and reassignment of many "nostolepid" taxa, in particular removing many species from the genus *Nostolepis*. Four new genera are erected: *Pechoralepis* (including part of *Nostolepis*), assigned to Acritolepidae nov.; and three genera assigned to an indeterminate family, which scales are composed of only odontocytic mesodentine without stranggewebe: *Nostovicina* (including part of *Nostolepis*), *Nobilesquama* (including part of *Nostolepis*), and *Peregrinosquama* (including part of *Watsonacanthus*). Histological structures are considered the primary characters of taxonomical value when based on isolated scales. Unfortunately, scale histology is unknown for most articulated acanthodians.

Key words: Dentine, mesodentine, stranggewebe, bone, Acanthodii, *Nostolepis*, Silurian, Devonian.

Juozas Valiukevičius [valiukevicius@geo.lt], Institute of Geology and Geography, T. Ševčenkos 13, 03223 Vilnius, Lithuania;
Carole J. Burrow [C.Burrow@uq.edu.au], Department of Zoology and Entomology, University of Queensland, Queensland 4072, Australia.

Introduction

In the terminology of the odontode regulation theory (Ørvig 1967, 1968, 1977; Karatajūtė-Talimaa 1998), acanthodian scales are characterized by a complicated odontodium which, in distinction from some other groups of vertebrates, "originates at the boundary between epidermis and mesoderm, and consists of dentinoidal crown and bony basal plate [...]" (Karatajūtė-Talimaa 1998: 35). Most acanthodian scales grew from the scale primordium (primordial scale) by a complete superposition on older odontodes, both crowns and bases, of spherical lamellae covering the previously formed layers. The scale primordium is not necessarily small, sometimes occupying a large portion of the fully formed scale; it supposedly developed during the embryonic stage of an animal. Contrary to the opinion of Karatajūtė-Talimaa (1998), we note that the numbers of growth lamellae in crowns do not reflect the ontogenetic developmental stage of the animal. Some "climatiid" acanthodian taxa show only two or three growth lamellae in fully formed, adult specimens. In most acanthodians, growth lamellae in crowns and bases are not aligned: those of the crown are fewer, and frequently have a thickness corresponding to that of the second order growth lamellae in scale bases (our observation; see also Karatajūtė-Talimaa and Smith 2003), which encompass numerous (four to twelve) dense and thin laminae of the first order.

Rare acanthodian taxa have flank scales with crowns which grew areally, or both areally and superpositionally. The areal addition of the younger growth zones either completely encircle the primordium or, more rarely, extend bilaterally, or just posteriorly by addition of a younger and larger odontode protruding from below the previous one. The latter growth type often increases the broadness or length of the crown without increasing its height. Such scales with areal growth characterize taxa in several of the groupings which we describe here. Rare acanthodian species, for example *Acanthodes bridgei* Zidek, 1976, are known from growth series of juvenile and adult fishes, which show that scales developed first on the caudal peduncle, then on the anterior flank next to the lateral line.

Thus in acanthodiforms "the size of the body scales diminishes toward the head, as well as both upward and downward from the main lateral line" (Zidek 1976: 29). The scales increase in size throughout ontogeny. In non-acanthodiform acanthodians with superpositional growth of flank scales

(e.g., *Acritolepis* spp.), the scales decrease in size from the pectoral to the caudal region. Nearly all acanthodians have areal growth scales and/or tesserae on the head.

Acanthodian scales of the *Nostolepis* histological type (*sensu* Gross 1947) have crowns composed of mesodentine (with or without lacunal widenings and interspersed osteocyte cavities), with some also having stranggewebe (*sensu* Gross 1971) and durodentine. "Mesodentine" is a term originally used by Ørvig (1958) for the osteostracan dentinous tissue comprising a network of odontocytes and their randomly-directed processes. Gross (1971) applied the term to the similar dentinous tissue in *Nostolepis* scales. We follow Ørvig (1967) in considering mesodentine as a tissue intermediate between dermal bone and dentine. This tissue also sometimes incorporates polygonal osteocyte cavities with radiating processes. We designate this tissue as simple mesodentine. Smith and Sansom (2000) disagreed with Ørvig (1967), and asserted that mesodentine was not a transitional form between bone and dentine. Karatajūtė-Talimaa and Smith (2003: 298) suggested that "in the future new terms should be used such as odontocytic (cellular) dentine and syncitial dentine, for a joined network of branching tubules without cell spaces". In light of the range of variants we observe in *Nostolepis*-type crown tissues, we prefer to retain the term mesodentine in its prior sense, to acknowledge that in at least some of its manifestations it is not a "true" dentine. We will apply their adjective "odontocytic" to mesodentine with lacunal widenings, and "syncitial" to mesodentine lacking lacunae.

Whereas Smith and Sansom (2000) regarded bone and dentine as two completely different tissues, and the range of dentinous tissues a result of phenotypic plasticity or loose developmental controls, our investigations of acanthodian histology show a series of crown dentine types between a tissue indistinguishable from bone through orthodentine. Whether this series reflects a "phylogenetic progression" or variable development, we feel that it is still useful to retain the classical terms mesodentine and semidentine for cellular dentinous tissues.

As well as simple mesodentine, stranggewebe (*sensu* Gross 1971: sometimes referred to as oriented mesodentine) forms posterior parts of scale crowns. Stranggewebe is a tissue comprising enlarged and very elongate lacunae oriented horizontally, with only rare interconnecting tubules. The characteristic feature of the tissue is the identical appearance of lacunae in horizontal, transverse or longitudinal section, indicating that they comprise two sets, running longitudinally and transversely. The only alternative possibility is that they are disc-shaped and oriented at an angle to the horizontal, but as they never appear circular or even oval in cross-section, this is unlikely.

The superficial durodentine (sometimes called enamel-like dentine or enameloid, but not an enamel), is a canal-free dentine, often showing growth laminae, which is found in some taxa with *Nostolepis*-type scale histology. Sometimes the tissue is clear but not laminated or birefringent, presumably when it is not hypermineralized and crystals are randomly oriented, but in most cases it is birefringent when viewed under crossed Nicols.

Scale bases grow superpositionally into the mesoderm and are composed of a laminar bone with varying concentrations of osteocyte cavities, usually more numerous in the upper part. Most cell lacunae are oriented parallel to growth lines, being longer and most regularly oriented in the upper part of the cone (equivalent to the base of the primordial scale) making a tissue of similar appearance to stranggewebe. Sharpey's fibres, which attach scale bases to the corium, run perpendicular to growth lines in two systems at right angles to each other, and are seen as circular spaces in cross section and as long lines in longitudinal section.

Institutional abbreviations.—LIGG, Lithuanian Institute of Geology and Geography, Vilnius, Lithuania; MNB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; SMNH, Naturhistoriska Riksmuseet, Stockholm, Sweden.

Principal characters of five *Nostolepis*-type structural groups

The first structural group.—This group encompasses scales composed of typical stranggewebe and simple odontocytic mesodentine distributed in crowns according to the classical *Nostolepis*-type defined by Gross (1971). Stranggewebe is developed in the posterior crown part and the scale primordium (Fig. 1A, C). This tissue occupies most of each growth lamella and is sometimes covered by a mantle of simple mesodentine (Fig. 1B, D). Osteocyte cavities are seen throughout the crown or just alongside the superficial thin mesodentinal layer (Fig. 1D). An odontocytic mesodentine fills all of the anterior parts of the growth lamellae succeeding the primordium and incorporates osteocyte cavities even superficially. Durodentine is not usually developed, but is sometimes formed over the central crown. Scale crowns in most taxa also have a system of enlarged ascending, circular and radial vascular canals. Scale bases are usually moderately deep and highly cellular.

Flank scales grew by superposition in most taxa included in this grouping except for in *Nostolepis robusta* (Brotzen, 1934) and *Climatius reticulatus* Agassiz, 1845 in which areal growth zones form the crown. This areal growth (and some morphologic characters more characteristic of chondrichthyans) indicate that *Nostolepis robusta* should be reassigned to a different genus.

Taxa with this structure include:
Euthacanthus macnicoli Powrie, 1864
Nostolepis striata Pander, 1856 (*sensu stricto*)
N. gracilis Gross,1947
N. costata Goujet, 1976
N. arctica Vieth, 1980

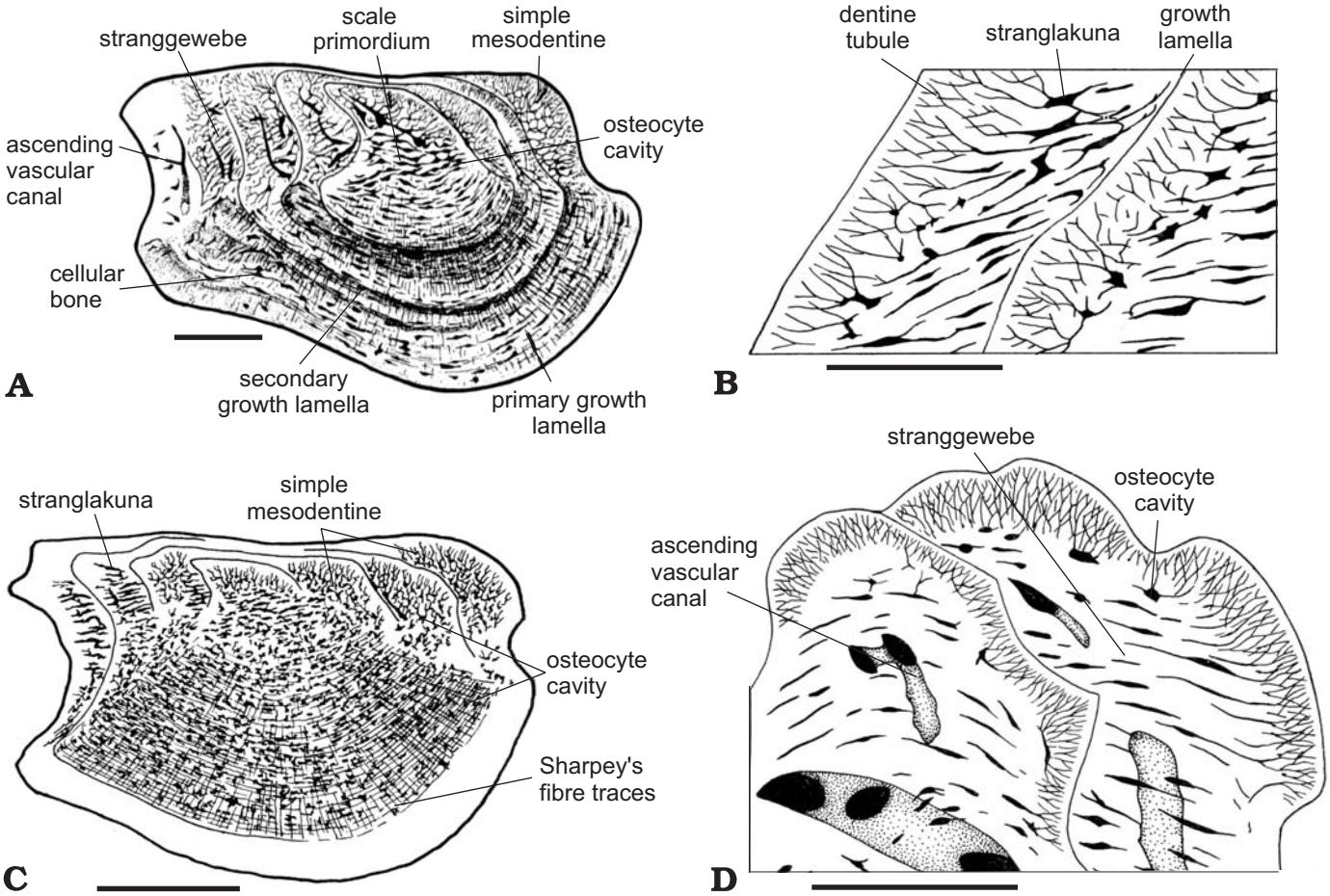

Fig. 1. First type of *Nostolepis* histological structure, with stranggewebe (posterior crown part), simple odontocytic mesodentine network (anterior crown part) and cellular bone (base). **A**, **B**, **D**. *Nostolepis striata* Pander, 1856 in vertical longitudinal sections. **A**. All types of tissues and ascending vascular canals (Ørvig 1967: text-fig. 5A); SMNH, thin section S 1044. **B**. Posterior part of crown with stranglakunae layer covered by a layer of odontocytic mesodentine (Gross 1971: fig. 2G); MNB, thin section 3658. **D**. Posterior part of scale containing a system of principal wide vascular canals, and a superficial layer of syncitial mesodentine (Gross 1971: fig. 6A); MNB, thin section 3935. **C**. *Nostolepis terraborea* (Valiukevičius 2003b: fig. 15C); LIGG, thin section 3644. Simple odontocytic mesodentine network and long stranglakunae in a scale without principal vascular canals. Scale bars 0.1 mm.

N. kernavensis Valiukevičius, 1985
N. alta Märss, 1986
N. minima Valiukevičius, 1994
N. taimyrica Valiukevičius, 1994
N. linleyensis Miller and Märss, 1999
N. decora Valiukevičius, 2003a
N. parathleta Valiukevičius, 2003b
N. kozhymica Valiukevičius, 2003b
N. terraborea Valiukevičius, 2003b
N. amplifica Valiukevičius, 2003c
N. magnicostata Valiukevičius, 2003c
N. consueta Valiukevičius, 2003c
N. musca Valiukevičius, 2003c
Tareyacanthus magnificus Valiukevičius, 1994
T. dissectus Valiukevičius, 1998
Nostolepoides platymarginata Burrow, 1997
Cheiracanthoides comptus Wells, 1944
C. proprius Valiukevičius, 1985
C. rarus Valiukevičius, 1994
C. borealis Valiukevičius, 1994
C. estonicus Valiukevičius, 1998
C. nativus Valiukevičius, 1998
C. planus Valiukevičius, 1998
C. wangi Burrow et al., 2000
C. dolosus Burrow et al., 2000
C. mosolovicus Valiukevičius, 2003b
Endemolepis inconstans Valiukevičius, 1998.

Taxa lacking the system of principal vascular canals:
Nostolepis matukhini Valiukevičius, 1994
N. tcherkesovae Valiukevičius, 1994.

Taxa showing areal crown growth:
Nostolepis robusta (Brotzen, 1934)
Climatius reticulatus Agassiz, 1845.

The second structural group.—This group is characterized by having stranggewebe extending through the entire scale crown (Fig. $2A_1$, B_1). The oriented lacunae (i.e., stranglakunae) are of maximal length, aligned with the strang-

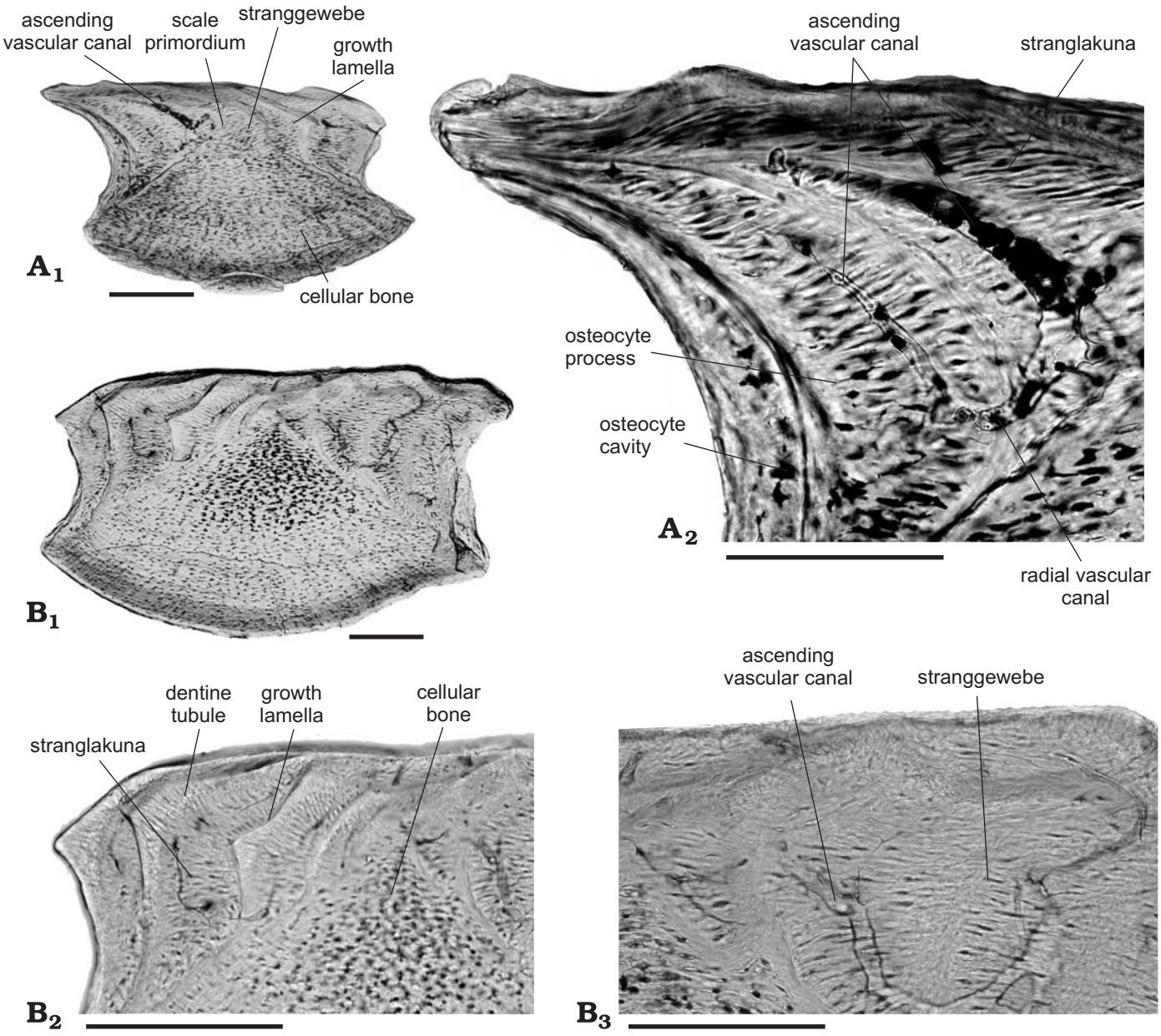

Fig. 2. Second type of *Nostolepis* histological structure, with maximum stranggewebe extent, exemplified by *Vesperalia perplexa* (Valiukevičius 2004: fig. 3A, B). **A**. LIGG, thin section 3678. A_1. Vertical longitudinal section of scale showing long and dense stranglakunae with short processes and interspersed osteocyte cavities, with no simple mesodentine. A_2. Wide ascending and radial vascular canals. **B**. LIGG, thin section 3679. B_1. Scale in vertical transverse section; orientation of stranglakunae and superficial dentine tubules in an odontocytic mesodentine, and a dense concentration of osteocyte cavities in the apex of base cone (B_2); stranglakunae and the vascular system of the right crown part (B_3). Stoniškiai-1 borehole, Lithuania, Pridoli, Silurian. Scale bars 0.1 mm.

lakunae of adjacent growth zones; they are joined together by short canaliculi (Fig. $2A_2$, B_3) and are connected with the enlarged ascending vascular canals that arise from the wide radial and circular canals. Only thin superficial parts of the crown growth lamellae are composed of simple mesodentine, in which dentine tubules are directed more or less perpendicular to growth lines (Fig. $2B_2$). Durodentine is absent. Growth of scale crowns is both superpositional and areal. Highly cellular bone composes the whole scale base, but osteocyte concentration increases distinctly in the apex of the base cone (Fig. $2B_1$, B_2).

Only two taxa have this structure:
Acanthacanthus ornatus Valiukevičius, 2003a (areal growth)
Vesperalia perplexa Valiukevičius, 2004.

The third structural group.—Taxa of this group are composed of a simple mesodentine network extending through the entire crown, with no stranggewebe. The osteocyte spaces are seen in all growth lamellae (Fig. 3A, B), but sometimes their number is distinctly reduced superficially, and the tissue approaches syncitial mesodentine (Fig. 3D). The vascular canals are widest and sometimes bush-like in the scale

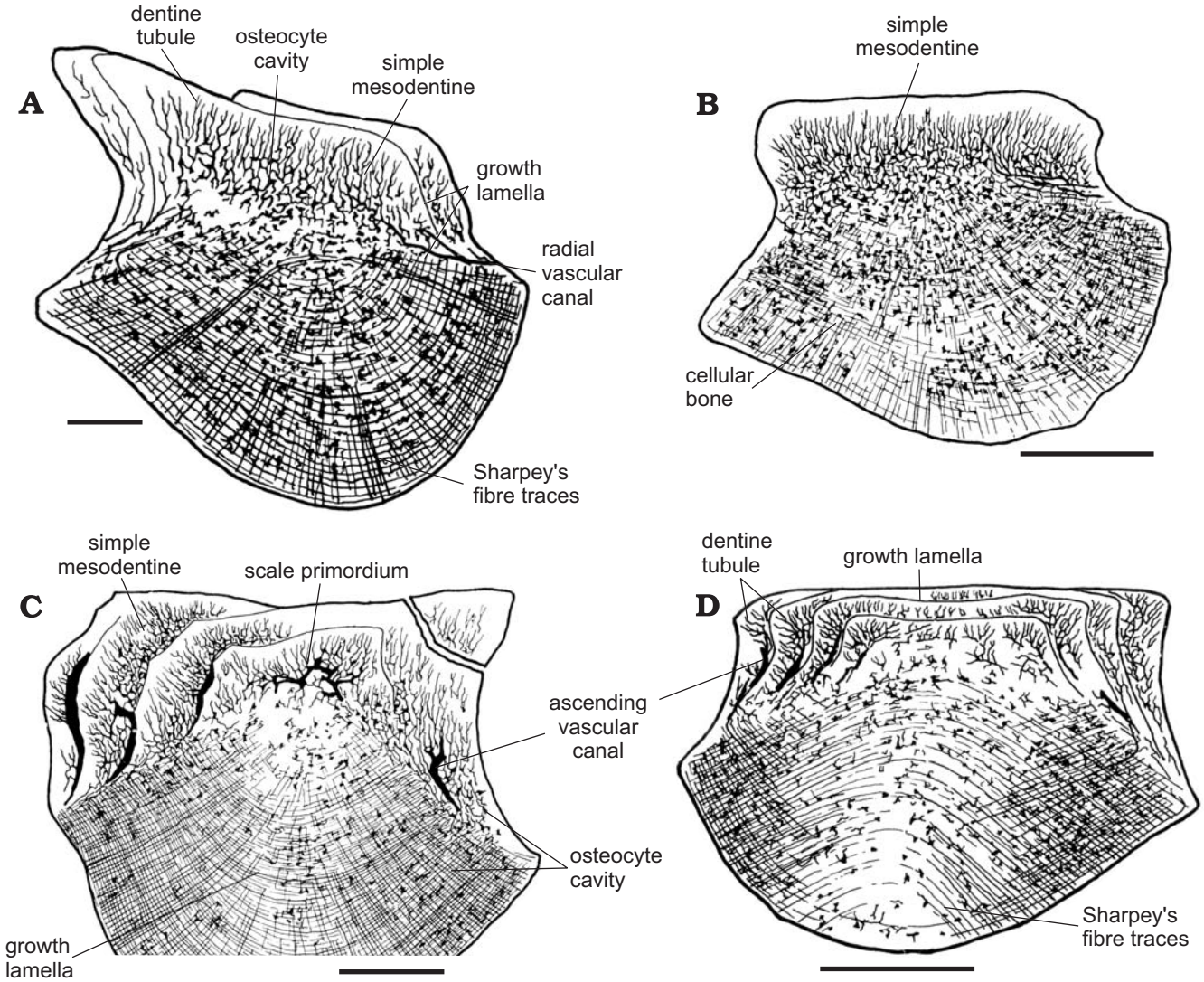

Fig. 3. Third type of *Nostolepis* histological structure, with some scales formed entirely of a simple odontocytic mesodentine (**A**–**C**) and others an almost acellular, syncitial mesodentine (**D**). Vertical longitudinal sections. **A**. *Nostolepis timanica* (Valiukevičius 2003a: fig. 26A); LIGG, thin section 3375. **B**, **C**. *Nostolepis platycrista* (Valiukevičius 2003b: fig. 14B, C); LIGG, thin sections 3579 and 3582. **D**. *Nostolepis paravolborthi* (Valiukevičius 2003b: fig. 19D); LIGG, thin section 3556. Crown mesodentine slightly odontocytic in the lower crown only (the neck area). Scale bars 0.1 mm.

primordium (Fig. 3C). Principal enlarged vascular canals are lacking in most taxa. Durodentine is not usually present, but is observed mainly as thin layers in outer laminae in several taxa. The polygonal bone cell lacunae in the base vary in density in different taxa, and are not oriented along the growth lines.

Taxa included in this group are:
Nostolepis multicostata Vieth, 1980
N. athleta Valiukevičius, 1994
N. fragilis Valiukevičius, 2003a
N. timanica Valiukevičius, 2003a
Canadalepis linguiformis Vieth, 1980
Paranostolepis glabra Vieth, 1980
Wetteldorfia triangula Vieth-Schreiner, 1983

Taxa lacking wide vascular canals:
Watsonacanthus oervigi Valiukevičius, 1979
Eifellepis werneri Vieth-Schreiner, 1983
Minioracanthus laevis Valiukevičius, 1985
Laliacanthus singularis Karatajūtė-Talimaa, 1986 (in Valiukevičius and Karatajūtė-Talimaa 1986)
?*L. ligeriensis* Vidal et al., 1994
Hanilepis wangi Wang and Dong, 1989
Taimyrolepis composita Valiukevičius, 1994
Canadalepis basdenae Burrow, 2002
?*Lijiangichthys lembodes* Wang, 2003
?*Nostolepoides mingyinensis* Wang, 2003
Nostolepis applicata Vieth, 1980 (areal growth)
N. guangxiensis Wang, 1992
N. spina Valiukevičius, 1994 (areal growth)
N. curta Valiukevičius, 1994
N. tareyensis Valiukevičius, 1994
N. halli Blom, 1999
N. platycrista Valiukevičius, 2003b
N. paravolborthi Valiukevičius, 2003b.

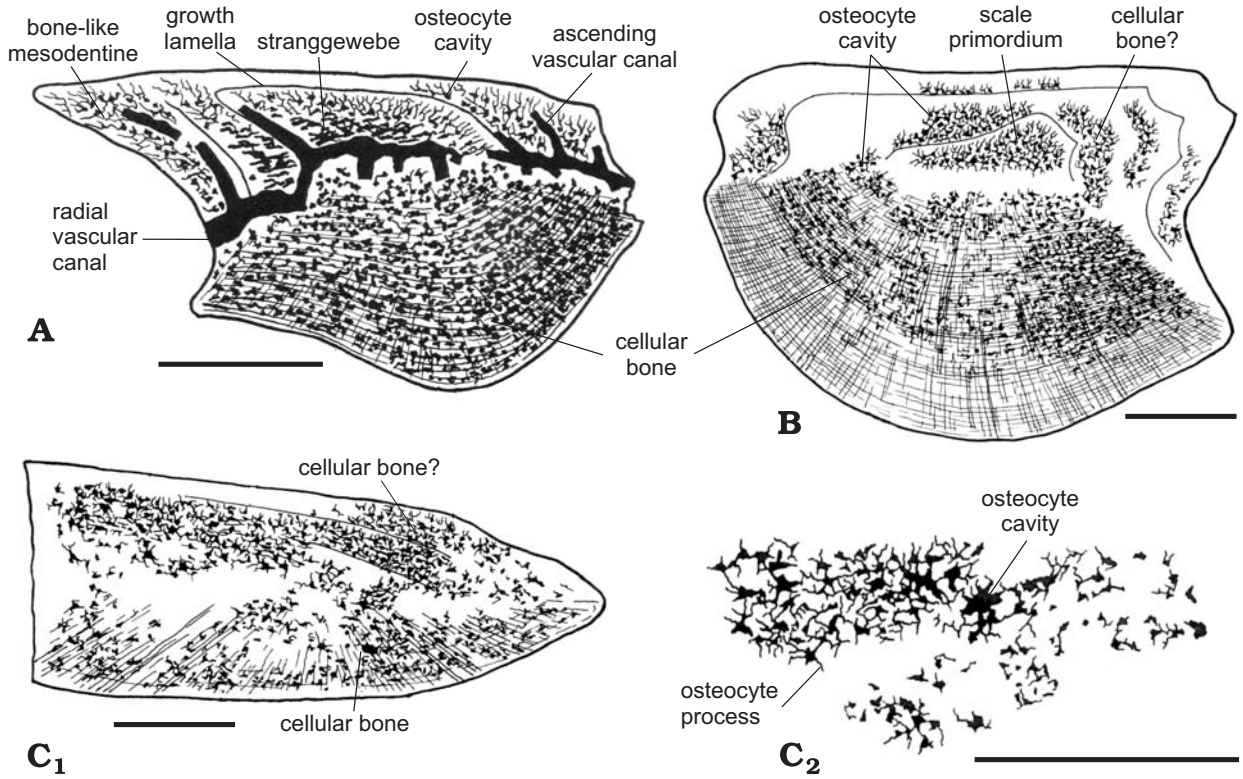

Fig. 4. Fourth type of *Nostolepis* histological structure, with crowns composed of a bone-like cellular mesodentine, or possibly cellular bone similar to that in scale bases. Vertical longitudinal sections. **A**. *Acritolepis urvantsevi* (Valiukevičius 2003a: fig. 16F); a bone-like mesodentine developed in the lower neck and crown areas not occupied by the stranggewebe; LIGG, thin section 3350. **B**. *Nostolepis adzvensis* (Valiukevičius 2003b: fig. 7A); LIGG, thin section 3635. **C**. *Monospina erecta* (Valiukevičius 2003b: fig. 22A, B); LIGG, thin section 3535. C_1. Crown tissues without vascular canals; osteocyte cavities connected to each other by short processes; crown tissue most similar to base bone. C_2. The magnified area of the anterior crown part (right corner of C_1). Scale bars 0.1 mm.

Taxa without wide vascular canals and with durodentine:
Nostolepis lacrima Valiukevičius, 1994
N. laticristata Valiukevičius, 1994
N. curiosa Valiukevičius, 1994
N. multangula Valiukevičius, 1994.

The fourth structural group.—In this group, scale crowns are composed of bone-like odontocytic mesodentine and in some taxa, stranggewebe. When present, the latter tissue is seen in the restricted posterior parts of the crown growth zones. The mesodentine in the crowns is very similar to the bone forming the base, especially in scales which lack the principal system of wide vascular canals (Fig. 4B, C). Osteocyte cavities are densely distributed in all growth lamellae, with little or no development of a "normal" mesodentinal network. Osteocyte cavities have only short processes.

The following taxa belong to this structural variety:
Nostolepis zinaidae Valiukevičius, 2003b
N. adzvensis Valiukevičius, 2003b
N. valentinae Valiukevičius, 2003b
Acritolepis ushakovi Valiukevičius, 2003a
A. urvantsevi Valiukevičius, 2003a
Monospina erecta Valiukevičius, 2003b

The fifth structural group.—This group encompasses "primitive" Silurian taxa. All growth types (areal, combined areal-superpositional, and superpositional) are seen in scale crowns. Scales of all taxa have very deep globular bases with thin laminae showing easily distinguished primary- and second-order growth lamellae of cellular bone. Notably, the bases continued growing after the crown plate stopped growing (Fig. 5B). The density of osteocyte cavities varies greatly. The shape of these cells is different to that of other structural varieties; they are rounded and smaller, with no polygonal examples, and fusiform lacunae only occurring rarely, in the newest lamellae (Fig. $5A_2$). The Sharpey's fibres are long, extending radially from the base apex to the outer base lamina. The crown mesodentine incorporates rare rounded osteocyte or odontocyte cavities, mainly in the basal (inner) parts of the growth zones with only rare lacunae in the outer parts. Short and thin dentinal tubules (one to three) emanate from the cell cavities and project mainly perpendicular to the growth lines. In horizontal section, they appear as unipolar canaliculi directed outward from the lacuna. In distinction to the other structural forms, interconnecting processes are lacking.

Taxa included in this grouping are:
Lenacanthus priscus Karatajūtė-Talimaa and Smith, 2003
Tchunacanthus obruchevi Karatajūtė-Talimaa and Smith, 2003
Fecundosquama basiglobosa Valiukevičius, 2004.

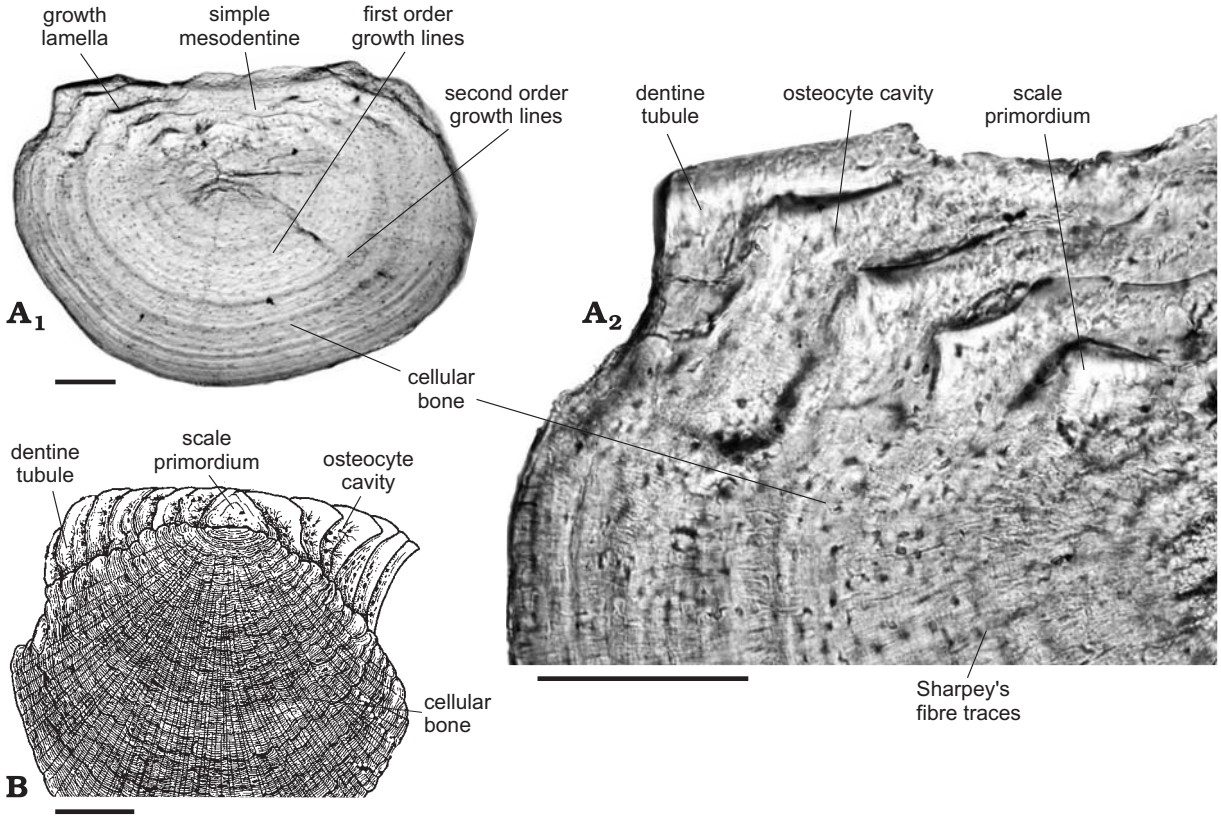

Fig. 5. Fifth type of *Nostolepis* histological structure, with cellular unipolar mesodentine in crowns and cellular bone in scale bases showing the first and second order growth lines. **A**. *Fecundosquama basiglobosa* (Valiukevičius 2004: fig. 5A, B); LIGG, thin section 3683. Thin-lamellar deep base and low crown both of superpositional growth (A_1) and rounded osteocyte cells in crowns without processe connections and unipolar outwardly emanated dentinal tubules (A_2). **B**. *Tchunacanthus obruchevi* (Karatajūtė-Talimaa and Smith 2003: fig. 18B); LIGG, thin section 1333. The short unipolar dentinal tubules in a scale crown with areal growth zones and a base which continued growing after crown growth stopped. Outcrop 135, Tchuna River, southern Siberia, upper Llandovery, Silurian. Scale bars 0.1 mm.

The sixth structural group—excluded from *Nostolepis*-type.—This group is characterized by distinct differences in histological structure to the classical *Nostolepis*-type, even though morphologically the scales are within the range shown by the genus *Nostolepis*. The scale crowns are composed of a syncitial dentine and durodentine; the bone of the base contains fewer osteocyte spaces and is sometimes almost acellular. The crown dentine differs from odontocytic and syncitial mesodentine and is similar to that of the *Acanthodes*-type structure. Ascending canals have one or two long and narrow main branches per growth lamella and are interwoven by smaller branchings, somewhat resembling syncitial mesodentine in the lowest crown area only (the neck) (Fig. 6A). Higher in the growth zones, the canals are straight, with fewer branchings, and mainly oriented perpendicular to growth lines. Dentinal lacunae and osteocyte cavities are absent. This variety is also distinguished by the presence (especially in the posterior crown part) of wide multi-branched radial vascular canals at the junction of base and crown tissues, and sometimes extending higher in the neck (Fig. 6C). Durodentine is extensively developed in the youngest growth lamellae, either forming them entirely or just present centrally composing the outer parts of the lamellae. Bone of the low, flat base cone is densely laminar, with bundles of long Sharpey's fibres and osteocyte cavities only at the apex (Fig. 6A, B) or dispersed randomly through the base space.

The following "nostolepid" taxa are characterized by this structure:

Nostolepis watsoni Valiukevičius, 2003a
N. longipostera Valiukevičius, 2003b
N. minilonga Valiukevičius, 2003b.
Watsonacanthus costatus Valiukevičius, 2003a.

Of these, only *N. longipostera* shows a relationship with the other "nostolepids" considered here in having rare scales with fragments of stranggewebe, restricted to the posteriormost part of the crown, and mesodentine-like tissue in the lower neck.

Discussion and taxonomic revision

Scale histology is unknown in several Devonian taxa presumed to be of the *Nostolepis*-type; these include climatiid taxa *Ptomacanthus* Miles, 1973, *Vernicomacanthus* Miles, 1973, and *Parexus* Agassiz, 1845 (1844), erected for articulated fish from Britain, as well as scale-based taxa including

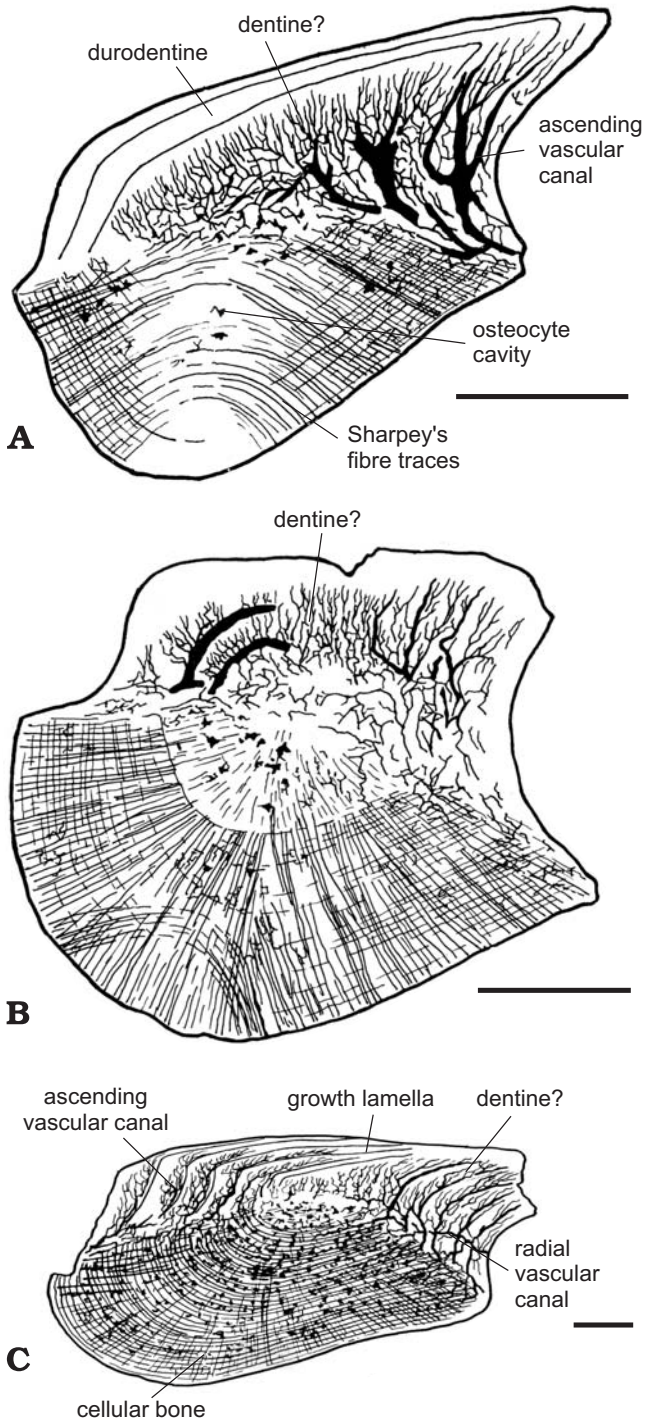

Fig. 6. Microstructure of scales of the sixth type of histological structure (not belonging to the *Nostolepis*-type). **A**. *Nostolepis longipostera* (from Valiukevičius 2003b: fig. 12A); LIGG, thin section 3594. **B**. *Nostolepis minilonga* (from Valiukevičius 2003b: fig. 17A); LIGG, thin section 3610. Multi-branched ascending vascular canals and network of non-lacunal dentinal tubules in crowns formed of a syncitial dentine with durodentine; bone in the scale bases contains only a few osteocyte cavities. **C**. *Watsonacanthus costatus* (from Valiukevičius 2003a: fig. 32B); LIGG, thin section 3302. Ascending vascular canals and the canaliculi network is slightly similar to mesodentine in the anterior crown part, and dentine-like in the posterior part, with one principal ascending branch per growth zone, and only a few interconnecting tubuli, mostly oriented upwards; cellular bone in base. Scale bars 0.1 mm.

Nostolepis gaujensis Valiukevičius, 1998 from Lithuania and *N. tewonensis* Wang et al., 1998 from China.

Acanthodian scales with *Nostolepis*-type histological structure show diverse tissue composition that should help to clarify some nomenclatural problems of tissues in lower vertebrate exoskeleton histology, as well as to revise the generic- and familial-level taxonomy of "climatiid" acanthodians. Gross (1947, 1971) used histological structure rather than morphology to characterize acanthodian genera which were known only from scales and other isolated dermal elements. Conflicts have arisen in the lower level classification because some morphologically similar specimens show wide variations in histology. This particularly concerns the *Nostolepis* species. A large number of thin sections are required to support taxonomic assignments of acanthodians. We are unsure about the Order level classification of the taxa. Based on scale structure, the first five groups would traditionally have been assigned to the Climatiiformes Berg, 1940. However, that unit is probably not monophyletic (Janvier 1996), and the presence of dentigerous jaw bones in the Acritolepidae fam. nov. could indicate their affinity with the Ischnacanthiformes Berg, 1940 (Burrow 2004). Because of the uncertainty, we have not assigned the families to orders.

The value of the six structural forms distinguished here is taxonomically variable. The first, third and fourth groups include some taxa based on articulated or partly articulated specimens: *Euthacanthus macnicoli* and *Climatius reticulatus* in the first group, *Nostolepis fragilis* in the third, and *Acritolepis ushakovi* and *A. urvantsevi* in the fourth. In all cases, we try to consider scales as part of the whole animal, so that the species recognized will fit into genera and families which are cladistically justifiable for both scales and whole animals.

Karatajūtė-Talimaa and Smith (2003) introduced a new order, the Tchunacanthida, with two new monospecific families Lenacanthidae and Tchunacanthidae defined on scales. We think that the similarities in the tissue histology in scales of *Lenacanthus* and *Tchunacanthus* (the fifth structural group presented here) support uniting these taxa in one family Tchunacanthidae, suppressing the family Lenacanthidae. The main diagnostic character for the family Tchunacanthidae is the scale crown structure, with a dentine formed of cell cavities and their unipolar processes, and without, or with restricted development, a vascular canal system. Several features used to characterize tchunacanthids are more widespread than Karatajūtė-Talimaa and Smith (2003) recognized: for example, the absence of a main vascular canal system in most taxa of the third group of acanthodians listed here; also, bone cell lacunae are found in poracanthodid acanthodian scale bases as well as in those of "climatiids", and nearly all acanthodians known from articulated specimens have head scales exhibiting areal crown growth.

Our first and third groups, which include most of the taxa, are best differentiated by the presence or absence of stranggewebe, a tissue that is unique to acanthodians. We retain the first group in the family Climatiidae Berg, 1940. Several species in the third group, formerly assigned to the genus *Nosto-*

lepis (eight from Taimyr, perhaps showing specific characters in the development of these possibly endemic taxa), and most of the other genera (*Canadalepis, Eifellepis, Hanilepis, Laliacanthus, Minioracanthus, Paranostolepis, Taimyrolepis, Watsonacanthus, Wetteldorfia*) lack stranggewebe. We assume that a family can include genera with relatively large differences in histology, and that some taxa in different phylogenetical lineages could have lost the stranggewebe structures as well as the principal vascular canal system in scale crowns, so that similar histology could reflect similar grades in different lineages. Most taxa in the third group are known only from scales, and we prefer to take a conservative approach by tentatively referring them to an indeterminate family.

The second group, represented by *Acanthacanthus* and *Vesperalia*, is distinguished by maximal extent of stranggewebe in scale crowns, and the fourth group (*Acritolepis, Monospina* and three former *Nostolepis* spp.) by the bonelike odontocytic mesodentine and densest concentration of osteocyte cavities in the crown, leaving no space for a normal mesodentine network.

The sixth group of taxa, characterized by having syncitial dentine and durodentine and lacking odontocyte and osteocyte lacunae, should be separated from the *Nostolepis*-type. This group includes acanthodians with scale structure intermediate between the *Nostolepis* and *Acanthodes* histological types, with almost acellular bone in the bases and syncitial dentine and durodentine in the crowns. Other taxa with this structural form include several species tentatively assigned to *Gomphonchus*? (Burrow and Simpson 1995; Burrow 2002). When compared to scales of *Gomphonchus* (Pander, 1856), all three "nostolepids" of this group differ in the appearance of ascending vascular canals. In this connection, there arises a problem. What is *Gomphonchus*? Histologically, its scales differ from those of articulated ischnacanthids in which scale histology has been studied, except for *Ischnacanthus gracilis* (Egerton, 1861) which has scales similar to those of *Gomphonchus sandelensis* Gross, 1971.

Another problem is the occurrence of representatives of the genus *Nostolepis* in four of the histological groups defined here. As noted earlier, Gross (1947, 1971) used histology to determine the generic relationships for isolated acanthodian scales. This approach runs counter to the classification of, for example, Devonian palaeoniscoid actinopterygian scales, where species of the same genus can show different histological structure (e.g., *Dialipina markae* Schultze, 1977, with scales having a cellular bone base and a vascular middle layer, and the younger *D. salgueiroensis* Schultze, 1968, with an acellular bone base and no vascular layer). Ørvig (1967) similarly noted histological trends from cellular to acellular bone, and mesodentine to orthodentine, within generic lineages of vertebrates. On this basis, having different *Nostolepis* spp. in different histological groupings is not necessarily a problem if other characters indicate that the species are phylogenetically related. The difficulty is that with so many acanthodian taxa (particularly *Nostolepis* spp.) based only on scales, any such relationship cannot usually be established. We propose a systematic revision of all *Nostolepis* spp., which currently embrace a very broad range of histological and morphological forms. We will follow Gross's method and use histological structure to separate off many of the species currently assigned to *Nostolepis* into several new genera. We propose the following taxonomic revision.

Systematic paleontology

Family Climatiidae Berg, 1940

Genus *Nostolepis* Pander, 1856

Comment.—We propose that the genus *Nostolepis* applies only to the representatives previously assigned to this genus which have flank scales that grew by superposition and that belong to the first histological type showing both stranggewebe and odontocytic mesodentine in scale crowns.

Type species: *Nostolepis striata* Pander, 1856; Ohesaare Cliff, Saaremaa; Ohesaare Regional Stage, Pridoli, Upper Silurian.

Species included: *N. gracilis* Gross, 1947, *N. costata* Goujet, 1976, *N. arctica* Vieth, 1980, *N. kernavensis* Valiukevičius, 1985, *N. alta* Märss, 1986, *N. minima* Valiukevičius, 1994, *N. taimyrica* Valiukevičius, 1994, *N. linleyensis* Miller and Märss, 1999, *N. decora* Valiukevičius, 2003a, *N. parathleta* Valiukevičius, 2003b, *N. kozhymica* Valiukevičius, 2003b, *N. terraborea* Valiukevičius, 2003b, *N. amplifica* Valiukevičius, 2003c, *N. magnicostata* Valiukevičius, 2003c, *N. consueta* Valiukevičius, 2003c, and *N. musca* Valiukevičius, 2003c.

Revised diagnosis.—Climatiid acanthodian with flank scales of varying size (usually > 0.5 mm) having crowns ornamented by subparallel ridges (usually < 8) of variable length; ridges are mainly stout, fading out and rarely reaching posterior crown edges; ridges are rarely bifurcated, and are rarely curved along the lateral edges; some species have raised medial area and lower lateral ledges. Flank scales grew by superposition of layers, with the crown formed of stranggewebe (posterior part) in the lamellae surrounding the primordium, and odontocytic mesodentine incorporating many osteocytes in the anterior crown part; the stranggewebe layer may be enveloped by the mesodentinal network in a growth zone; system of ascending, circular and radial vascular canals developed; bone in scale base highly cellular. The tuberculated head tesserae and tectal plates with "starlet" sculpture grew areally or both areally and superpositionally, and also have a histological structure with stranggewebe and odontocytic mesodentine. Fin spines are short with nodose ribs; they lack an insertion base and subcostal canal, and are composed of odontocytic mesodentine in the ribs and thin outermost layer; the middle layer of cellular bone and osteodentine forms the greatest thickness of the spine; a large central cavity is surrounded by a layer of finely lamellar bone.

Family Vesperaliidae nov.

Comment.—We erect the family Vesperaliidae nov. diagnosed principally by the scale histology of the second structural group (no other skeletal elements have been identified).

Type genus: *Vesperalia* Valiukevičius, 2004.

Genera included: Type genus and *Acanthacanthus* Valiukevičius, 2003a.

Diagnosis.—Acanthodians differing from the other climatiiform families in having high and unusually thick-crowned scales bearing three or four symmetrical pairs of radial, or rarely subparallel, high and robust ridges extending the entire crown length; sharp anterior crown edge; high scale neck, which sometimes has a row of pores; stranggewebe with markedly long and dense oriented lacunae composing the entire crown; thin superficial layers of odontocytic mesodentine and without durodentine; wide ascending and radial vascular canals forming chambers in crowns at the junction with the circular canals.

Discussion.—Characters shared with some of the Climatiidae are the two long, posteriorly converging ridges edging the medial area of the scale crown, but the ridges differ in the Vesperaliidae by the height and robustness of the ridges on the posterior crown part. The high scale neck with a pore row is not found in the Acritolepidae or Tchunacanthidae, and is only rarely observed in the Climatiidae. The arrangement of vascular canals and the stranggewebe are unique characters amongst acanthodians.

Genus *Acanthacanthus* Valiukevičius, 2003a

Type and only species: *Acanthacanthus ornatus* Valiukevičius, 2003a; Severnaya Zemlya Archipelago, Spokojnaya River, outcrop 41, bed 12; Lower Devonian, Lochkovian, Severnaya Zemlya Formation.

Diagnosis.—Vesperaliid acanthodian with flank scales of a large size (> 0.7 mm wide), having elongated, rhombic, flat crown plate distantly extending well beyond the base posteriorly, low neck and deep base; one or two symmetrical pairs of the longest low, flattened radial ridges run towards the posterior crown tip; longitudinally depressed medial area contains one or two pairs of short, acute ridgelets forming a separate part towards the anterior crown edge. The oldest two growth lamellae of the medial area grew superpositionally whereas the succeeding ones (up to four) attached as areal growth zones along the lateral edges, thus increasing only the breadth of scale. Scale crowns are entirely composed of stranggewebe producing very long and dense stranglacunae; only the superficial layer of this tissue weakly resembles odontocytic mesodentine in the lateral growth zones, with outwardly oriented and longer dentine tubules; unique wide knot-like chambers characterize the vascular canals in the scale primordium and junctions of the ascending and circular canals in the growth lamellae of crowns.

Genus *Vesperalia* Valiukevičius, 2004

Type and only species: *Vesperalia perplexa* Valiukevičius, 2004; Lithuania, Stoniškiai-1 borehole, depth 1211–1217 m; Upper Silurian, Pridoli, Rietavas Beds, Jûra Formation.

Diagnosis.—Vesperaliid acanthodian with high-crowned scales having pores around the neck and a crown plate with a sculpture of four to six linear or slightly wavy ridges, of which two converging ones may form lowly raised medial area; ridges extend the entire crown length or fade out mid-length, reemerging on the posterior edge of the crown behind a smooth area. Scales grew superpositionally or both superpositionally and areally. The stranggewebe with unusually large oriented lacunae and odontocytic mesodentine (only in narrow outer layers of growth zones) form both posterior and anterior parts of the crown; the crown has a system of widened and multiply branched ascending dentinal canals plus radial canals at the base/crown junction.

Family Acritolepidae nov.

Comment.—We erect the family Acritolepidae nov. for the taxa of the fourth histological group.

Type genus: *Acritolepis* Valiukevičius, 2003a.

Genera included: *Acritolepis*, *Monospina* Valiukevičius, 2003b, and *Pechoralepis* gen. nov. (= *Nostolepis*, partim).

Diagnosis.—Moderately deep-bodied acanthodians with dorsal spines each with 12 longitudinal ribs and long pectoral spines each with 16 ribs; insertion position of posterior dorsal spine opposite the anal spine; no ventral (prepelvic) spines; two pairs of tuberculated, wide-based prepectoral spines that are composed of a thick layer of highly vascularized acellular bone surrounding a central cavity, and cellular bone and mesodentine forming the ribs; scapula with slender shaft having a semicircular cross-section; jawbones with large triangular tooth cusps and smaller secondary cusps along the main lateral ridge and striated denticles on the mesial ledge; small palatine teeth composed of trabecular dentine; body scales with a simple spine-like shape, or with short subparallel or stout radial ridges which may form a "posterior starlet" converging into a pair of symmetric neck ridges; scale and tessera crowns composed of bone-like odontocytic mesodentine, sometimes with stranggewebe in the posterior parts of the crown growth zones; polygonal osteocyte cavities densely distributed in all growth lamellae, with little or no development of a "normal" mesodentinal network.

Discussion.—The histological structure of the prepectoral spines and the highly odontocytic crown mesodentine differ to those of all other acanthodians. The scales differ to those of the Tchunacanthidae in shape and base/crown proportions, coordinated growth of crown and base (in Tchunacanthidae, the base continued to grow after the crown stopped), and in the shape and abundance of osteocytes or odontocytes (which are rare, small and rounded in Tchunacanthidae). The acritolepids resemble the ischnacanthiforms in having dentigerous jaw bones and palatine teeth, but differ in having prepectoral spines and in the histological structure of all dermal elements.

Genus *Acritolepis* Valiukevičius, 2003a

Type species: *Acritolepis ushakovi* Valiukevičius, 2003a; Severnaya Zemlya Archipelago, Matusevich River, outcrop 1, bed 21; Lower Devonian, Lochkovian, Severnaya Zemlya Formation.

Species included: Type species and *A. urvantsevi* Valiukevičius, 2003a.

Diagnosis.—Small-sized moderately deep-bodied acritolepid acanthodian with low-angled dorsal spines bearing six

longitudinal ribs per side, long thick-walled pectoral spines with eight ribs per side, two pairs of prepectoral spines and slender cylindrical scapula. Spines composed of a thick layer of lamellar vascularized bone surrounding the large central cavity, overlain by osteodentine and odontocytic mesodentine. Dentigerous jawbones have large principal tooth cusps of a triangular shape with smaller secondary cusps between forming the lateral main tooth row, and striated blunt denticles on the lingual edge; tiny palatine teeth are also present. Flank scales grew superpositionally; they are relatively small (< 0.5 mm wide), with two to six parallel flattened uniform anterior ridges extending one-third of crown length; short neck and deep base; bone-like highly odontocytic mesodentine is composing most of the crown, with only a small area of stranggewebe in the posteriormost part of flank scale crowns. Largely varying in shape, tectal plates and tesserae of the head region are tuberculated, ridged, striated or stellate, of areal growth, polyodontode histologically, composed of lamellar acellular bone basally, cellular vascularized bone with osteon structures in the mid-layer, and odontocytic mesodentine superficially.

Genus *Monospina* Valiukevičius, 2003b

Type and only species: *Monospina erecta* Valiukevičius, 2003b; Timan-Pechora region, Olenya-2 borehole, depth 4070.8–4078.3 m; Upper Silurian, Pridoli, Greben' Regional Stage.

Diagnosis.—Acritolepid acanthodian with small and medium-sized flank scales (< 0.5 mm wide) having monospinous crowns, inclined at an angle of 40° to the bases which are flat or gently convex; scales lack necks, their pointed cone-shaped posterior crown edge far overhangs the base; two to six subradial short ridges extend back from the anterior edge, occasionally reaching the posterior part of the crown; shortest lateral ridges may converge with the longest ones; three lamellae of superpositional growth in crowns are composed of cellular bone or bone-like tissue which has dense polygonal osteocytes and short connecting processes, but is devoid of vascular canals. The tissues in crown and base of scales merge gradually to each other.

Genus *Pechoralepis* nov.

Comment.—The new genus *Pechoralepis* is erected for the former *Nostolepis* spp. of the fourth structural group.

Derivation of the name: From the Pechora Plate, the region of origin of the type species, and from the Greek *lepis,* scale.

Type species: *Pechoralepis zinaidae* (Valiukevičius, 2003b); Timan-Pechora region, Kozhym River, outcrop 236, samples 16–42; Lower Devonian, Lochkovian, Ovinparma Formation, members 1–2.

Age and geographic distribution: Upper Silurian, Pridoli, Greben' Regional Stage and Lower Devonian, Lochkovian, Ovinparma and Sotchemkyrt regional stages. Timan-Pechora region (Russia).

Species included: Type species and *Pechoralepis adzvensis* (Valiukevičius, 2003b), and *P. valentinae* (Valiukevičius, 2003b).

Diagnosis.—Acritolepid acanthodians having prepectoral pinnal plate with oblique rows of tubercles and pectoral spines with a wide leading edge ridge and one pair of lateral ribs; ventral (prepelvic) spines with a wide leading edge ridge and two pairs of longitudinal lateral ribs; head tesserae crowned by semiconcentric or stellate platelets with areal growth zones; rhomboidal to ellipsoidal trunk scales with inclined radial or subradial robust, rounded ridges converging into long medial ridges enclosing a raised central area, with one or two pairs of oblique symmetric neck ridges pointed posteriorly; stranggewebe with long and dense oriented lacunae only developed in a restricted area of the posterior crown; highly odontocytic mesodentine in the anterior part of the crown.

Discussion.—The prepectoral spines of *Pechoralepis* gen. nov. differ from those of *Acritolepis* in their sculpture. The ridgeness on scale crowns resembles that of *Vesperalia* or *Nostolepis*, but *Pechoralepis* differs in having the clear oblique neck ridges converging with those of the posteromedian crown and the best developed medial area on scale crown. The type and combination of stranggewebe and odontocytic mesodentine in the crown differ to that of other taxa.

Family Tchunacanthidae Karatajūtė-Talimaa and Smith, 2003

Comment.—This family is erected to encompass the taxa of the fifth structural group.

Type genus: *Tchunacanthus* Karatajūtė-Talimaa and Smith, 2003.

Genera included: Type genus and *Lenacanthus* Karatajūtė-Talimaa and Smith, 2003, and *Fecundosquama* Valiukevičius, 2004.

Diagnosis.—Equivalent to the Karatajūtė-Talimaa and Smith (2003) diagnosis of the order Tchunacanthida.

Genus *Tchunacanthus* Karatajūtė-Talimaa and Smith, 2003

Type and only species: *Tchunacanthus obruchevi* Karatajūtė-Talimaa and Smith, 2003; Siberia, Irkutsk amphitheatre, Tchuna River, Staroe Balturino outcrop; Lower Silurian, Upper Llandovery, Upper Balturino Subformation.

Diagnosis.—Squamation comprising head, transitional and body scales, and larger tesserae with complicated sculptured crowns and with multilobate outlines; head scales have smooth crowns with concentric growth lines; transitional body scales have crowns folded into longitudinal ridges, formed of separate tubercles; head and transitional scales have deep bases, with funnel-shaped or oblong furrows in centre and surrounding convex bosses subdivided by narrower furrows; base of body scales smaller than crown, diamond-shaped, convex; areal growth characterizes head and transitional scales; body scales have either areal-superpositional or only superpositional growth; canal system absent; crown of cellular mesodentine, with regular, rounded cell spaces, in the inner part of each dentine layer; base contains simple, small, fusiform cell spaces without processes, disposed parallel to distinct growth lines comprising very thin first order, and second-order lines.

Genus *Lenacanthus* Karatajūtė-Talimaa and Smith, 2003

Type and only species: *Lenacanthus priscus* Karatajūtė-Talimaa and Smith, 2003; South Yakutia, Niuya River outcrops and Irkutsk amphitheatre; Llandovery, Lower Silurian.

Diagnosis.—Head scales irregular, polygonal, seldom hexagonal, and rounded, with flat, or gently convex, smooth crown; edges of crown with relativly deep hollows and notches; neck feebly demarcated; base low, relatively flat but slightly convex. Transitional scales irregular, broad and short; anterior crown subdivided into two, four or seven sections. Body scales with base smaller than crown, low, polygonal or oval/diamond-shaped, with crown extended backwards to point; crown anteriorly subdivided into 3–5 sections by deep, longitudinal fissures. Areal (head), areal-superpositional (transitional) and superpositional (body) scale growth; crown of cellular mesodentine with distinct lacunae and very thin, branched tubules; base with simple cells, lacunae without branching canaliculi; system of vascular canals absent.

Genus *Fecundosquama* Valiukevičius, 2004

Type and only species: *Fecundosquama basiglobosa* Valiukevičius, 2004; Lithuania, Kurtuvėnai-162 borehole, depth 1052.2–1072.4 m; Upper Silurian, Pridoli, Minija Formation and the lower part of Jûra Formation.

Diagnosis.—Scales of moderate size (ca. 0.8 mm wide) having low horizontal crowns with crenulated sculpture of five to six notches per side anteriorly (flank) or around the entire crown margin (head scales), lacking a neck; deep convex/subglobular base protrudes beyond the crown on all sides. Scale crowns composed of odontocytic bone-like mesodentine with abundant osteocyte cavities and enlarged radial and ascending vascular canals present in the oldest growth lamellae only. Crown mesodentine merges gradually into a highly cellular thin-lamellar bone in the base that is penetrated by long traces of Sharpey's fibres.

Family indeterminate

Genus *Nostovicina* nov.

Comment.—The new genus *Nostovicina* is erected for the former *Nostolepis* spp. of the third group, in which scale crowns have only an odontocytic mesodentine lacking stranggewebe.

Derivation of the name: From the first syllables of *Nostolepis*, and Latin *vicinalis*, neighboring, close, referring to the similarity with *Nostolepis*.

Type species: *Nostovicina fragila* (Valiukevičius, 2003a); Severnaya Zemlya Archipelago, Matusevich River, outcrop 1, bed 21; Lower Devonian, Lochkovian, Severnaya Zemlya Formation.

Age and geographic distribution: From the Upper Silurian, Pridoli, through to the Lower Devonian, Emsian. Severnaya Zemlya Archipelago, Timan-Pechora region, Taimyr (Russia), Arctic Canada, North Greenland, Baltic, China, Australia, New Zealand.

Species included: *Nostovicina applicata* (Vieth, 1980), *N. athleta* (Valiukevičius, 1994), *N. curiosa* (Valiukevičius, 1994), *N. curta* (Valiukevičius, 1994), *N. fragila* (Valiukevičius, 2003a), *N. guangxiensis* (Wang, 1992), *N. halli* (Blom, 1999), *N. lacrima* (Valiukevičius, 1994), *N. laticristata* (Valiukevičius, 1994), *N. multangula* (Valiukevičius, 1994), *N. multicostata* (Vieth, 1980), *N. paravolborthi* (Valiukevičius, 2003b), *N. platycrista* (Valiukevičius, 2003b), *N. spina* (Valiukevičius, 1994), *N. tareyensis* (Valiukevičius, 1994), and *N. timanica* (Valiukevičius, 2003a).

Diagnosis.—Acanthodians which have short longitudinally ribbed pectoral spines and two pairs of wide, stout, shallowly inserted ventral (prepelvic) spines with diagonal nodose ribs which converge with the quadrangular leading rib; high-sculptured tesserae stellatae of areal growth on the head area and small trunk scales usually showing superpositional growth; scale crowns may be flat and smooth (*Minioracanthus* Valiukevičius, 1985; *Paranostolepis* Vieth, 1980) to moderately-inclined (*Canadalepis* Vieth, 1980) bearing subparallel or rarely subradial anterior ridges which fade out posteriorly, and sometimes form a slightly raised medial area; fin spines composed of highly vascularized cellular bone and odontocytic mesodentine; crowns of tesserae and scales composed of a moderately cellular odontocytic mesodentine network mainly lacking enlarged vascular canals; some species with thin layers of durodentine developed in outer laminae; no stranggewebe in scale crowns.

Discussion.—The combination of characters which diagnose *Nostovicina* gen. nov. are variously represented in other taxa, making its affinities uncertain. The genus resembles some representatives of the Climatiidae, which are known from articulated specimens, in spine shape, but differs by the number of ventral (prepelvic) spines, e.g., *Euthacanthus* Powrie, 1864 has six pairs, *Brachyacanthus* Egerton, 1861 and *Lupopsyrus* Bernacsek and Dineley, 1977 have four pairs, and *Ptomacanthus* Miles, 1973 has three pairs. Fin spine structure resembles that of the Acritolepidae. The morphology of scales and fin spines of *N. fragila* resemble those of *Lupopsyrus pygmaeus* Bernacsek and Dineley, 1977, from the Lower Devonian of Canada, but the scales of *Lupopsyrus* are monodontode (Hanke and Wilson 2004).

Genus *Nobilesquama* nov.

Comment.—The sixth histological group of "nostolepids" does not have *Nostolepis*-type histology, and the species listed herein probably belong in a group with several other taxa, including most species tentatively referred to *Gomphonchus*?. Their higher level relationships are unclear, but histologically they appear intermediate between *Nostolepis*-type and *Acanthodes*-type. *Nobilesquama* and *Peregrinosquama* are both based on scales and erected for the former *Nostolepis*, and *Watsonacanthus* spp. in this group.

Derivation of the name: From *nobilis* (Latin) known, recognizable and *squama* (Latin) scale.

Type species: *Nobilesquama longipostera* (Valiukevičius, 2003b); Timan-Pechora region, Varknavt-5 borehole, depth 4082–4089 m; Lower Devonian, Lochkovian, Khatayakha Formation.

Age and geographic distribution: Lower Devonian, Lochkovian to lower Emsian. Timan-Pechora region, Severnaya Zemlya Archipelago and Salair (Russia).

Species included: Type species and *Nobilesquama minilonga* (Valiukevičius, 2003b), and *N. watsoni* (Valiukevičius, 2003a).

Diagnosis.—Acanthodian with rhomboid scales of moderate size, crowns carrying from two to eight short subparallel or subradial ridges of which the longest lateral symmetric pairs may point posteriorly; scale bases high and deepest centrally or more anteriorly; scale crowns composed of syncitial dentine (often orthodentine-like) with long and wide ascending and radial vascular canals, and durodentine usually developed as thick layers in each growth lamellae formed after the scale primordium; scale bases composed of bone with a very low density of osteocyte cavities, frequently almost acellular.

Discussion.—The crown ornamentation is also within the range of the revised genus *Nostolepis*, and the deep scale bases resemble those of scles of *Eifellepis* Vieth-Schreiner, 1983 and some *Laliacanthus* Karatajūtė-Talimaa, 1986, but the histology differs from these taxa, as detailed earlier. The crown tissue is similar to the *Acanthodes*-type structure, but scale bases of the latter are pierced by canals of Williamson and are completely acellular. The histological structure is closest to that of *Gomphonchus* Gross, 1971 and *Poracanthodes* Brotzen, 1934, but these taxa differ morphologically and by the latter having a pore canal system in the crown.

Genus *Peregrinosquama* nov.

Derivation of the name: From *peregrinus* (Latin) other, strange and *squama* (Latin) scale.

Type and species: *Peregrinosquama costata* (Valiukevičius, 2003a); Severnaya Zemlya Archipelago, Spokojnaya River, outcrop 48, bed 5; Lower Devonian, lower Emsian, lower Al'banov Subformation.

Age and geographic distribution: Lower Devonian, lower Emsian. Severnaya Zemlya Archipelago, Timan-Pechora region, Salair, Taimyr (Russia).

Species included: Peregrinosquama oervigi (Sobolev, Karatajūtė-Talimaa, and Valiukevičius, 1988) and *Peregrinosquama costatus* (Valiukevičius, 2003a).

Diagnosis.—Scale crowns have three to six sharp radial ridges pointing posteriorly or rarely fading out at crown midlength; neck is low, and the base is massive, protruding strongly in front of the crown; scale crowns composed of dentine with long, narrow ascending vascular/dentinal canals, of which the main branches are in the posterior part, with a syncitial mesodentine (intermediate between dentine and mesodentine) in the anterior crown part and a more orthodentine-like tissue posteriorly; crown tissues without lacunae and stranggewebe, with outer parts of growth lamellae composed of a highly refractive durodentine; finely laminar bone in scale base contains small numbers of randomly distributed osteocyte cavities.

Discussion.—Morphologically, the scales most closely resemble those of *Watsonacanthus* Valiukevičius, 1979, but histologically, scales of the latter belong to the third group of the *Nostolepis*-type structure. The ornament on scale crown resembles that of *Nostolepis, Laliacanthus, Eifellepis, Acritolepis*, and other genera, but they also differ histologically. By histological characters, *Peregrinosquama* gen. nov. is in an intermediate position between the *Nostolepis* and *Acanthodes*-types, and differs from *Nobilesquama* gen. nov. by its massive, anteriorly-protruding base, in having durodentine in all crown growth zones, and relatively narrow ascending vascular canals.

Conclusions

Of particular interest in this critique of growth and development of histological structure in acanthodian squamation is the type of scale characteristic of the Acritolepidae fam. nov., formed of bone, or bone-like tissue, both in the base and crown. We suggest that these scales formed below the ectoderm-connective tissue boundary, in the deeper layers of the corium (see Ørvig 1951: table on p. 378).

In considering the nomenclatural problems in histology, we agree with the proposal to create new terms better reflecting the essence of such tissues as dentine, mesodentine, bone-like mesodentine, but we still assert that mesodentine is a tissue intermediate between true dentine and bone, and the term "acellular mesodentine" is not applicable. We favor the terms syncitial mesodentine for a non-lacunal mesodentine-like canaliculi network, and odontocytic mesodentine for mesodentine with lacunae.

The vast majority of taxa dealt with in this paper are based on isolated scales. There is no easy solution to the problem of their taxonomic classification. Comparisons with the morphological and histological structure of scales from articulated specimens can be helpful (Valiukevičius 1992, 2003a), but unfortunately scale histology is unknown for most taxa described from such specimens, e.g., Lower Devonian acanthodians from Wayne Herbert Quarry, England (Miles 1973) and the MOTH locality, NorthWest Territories, Canada (Bernacsek and Dineley 1977; Hanke et al. 2001). In those faunas, conditions which favored morphological preservation of articulated fish were unfavorable for histological preservation. We believe that, in order to make a coherent and consistent classification based primarily on isolated scales, histological structure provides the primary characters of value taxonomically, justifying the revisions we have proposed here.

Acknowledgements

Dr. Valentina Karatajūtė-Talimaa (Vilnius) is acknowledged for helpful discussions of acanthodian histological microstructure. Reviewers of the manuscript, Drs. Hans-Peter Schultze (Berlin) and Tiiu Märss (Tallinn) are thanked for remarks and improvements. CJB acknowledges the support of an Australian Research Council Postdoctoral Fellowship 2002–2004. This is a contribution to IGCP 491 Project, "Middle Palaeozoic Vertebrate Biogeography, Palaeogeography, and Climate".

References

Agassiz, L. 1844–45. Monographie de poissons fossiles des Vieux Grès Rouges ou Système Dévonien (Old Red Sandstone) des Îles Britanniques et de Russie. 171 pp. Imprimerie de H. Nicolet, Neuchâtel.

Basden, A. 2003. Early Devonian (Emsian) vertebrate microremains from the Buchan Group, Victoria, Australia. *Proceedings of the Royal Society of Victoria* 115: 7–26.

Berg, L.S. 1940. System of agnathans and fishes, both living and fossil [in Russian]. *Proceedings of Institute of Zoology of the USSR Academy of Sciences* 5 (2): 85–517.

Bernacsek, G.M. and Dineley, D.L. 1977. New acanthodians fom the Delorme Formation (Lower Devonian) of N.W.T., Canada. *Palaeontographica A* 158: 1–25.

Blom, H. 1999. Vertebrate remains from Upper Silurian–Lower Devonian beds of Hall Land, North Greenland. *Geology of Greenland Survey Bulletin* 182: 1–80.

Brotzen, F. 1934. Erster Nachweis von Unterdevon in Ostseegebiet durch Konglomeratgeschiebe mit Fischresten. II. Teil (Paläontologie). *Zeitschrift für Geschiebeforschung* 10: 1–65.

Burrow, C.J. 1997. Microvertebrate assemblages from the Lower Devonian (*pesavis/sulcatus* zones) of central New South Wales, Australia. *Modern Geology* 21: 43–77.

Burrow, C.J. 2002. Lower Devonian acanthodian faunas and biostratigraphy of south-eastern Australia. *Memoirs of the Association of Australasian Palaeontologists* 27: 75–137.

Burrow, C.J. 2003. Earliest Devonian gnathostome microremains from central New South Wales (Australia). *Geodiversitas* 25: 273–288.

Burrow, C.J. 2004. Acanthodians with dentigerous jaws: the Ischnacanthiformes and *Acanthodopsis*. *Fossils & Strata* 50: 8–22.

Burrow, C.J. and Simpson, A. 1995. A new ischnacanthid acanthodian from the Late Silurian (Ludlow, *ploeckensis* Zone) Jack Formation, north Queensland. *Memoirs of the Queensland Museum* 38: 383–395.

Burrow, C.J., Turner, S., and Wang, S.-T. 2000. Devonian microvertebrates from Longmenshan, Sichuan, China: Taxonomic assessment. *In*: A. Blieck and S. Turner (eds.), Palaeozoic Vertebrate Biochronology and Global Marine/Non-marine Correlation (Final Report of IGCP 328, 1991–1996). *Courier Forschungsinstitut Senckenberg* 223: 391–451.

Egerton, P. 1861. British fossils. (Descriptions of *Tristichopterus*, *Acanthodes*, *Climatius*, *Diplacanthus*, *Cheiracanthus*). *Memoirs of the Geological Survey of the United Kingdom (British Organic Remains)* 10: 51–75.

Goujet, D. 1976. Les poissons. *In*: C. Babin, F. Bigey, J. Deunff, J. Drot, D. Goujet, H. Lardeux, J. Le Menn, J. L'Hotellier, M. Melou, A. Moreau-Benoit, P. Morzadek, F. Paris, Y. Plusquellec, J. Poncet, P. Racheboeuf, P. Taugourdeau, and M. Weyant (eds.), Les Schistes et Calcaires éodévoniens de Saint-Céneré (Massif Armoricain, France), sédimentologie, paléontologie, stratigraphie. *Mémoires de la Société géologique et minéralogique de Bretagne* 19: 312–323.

Gross, W. 1947. Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica A* 96: 91–161.

Gross, W. 1971. Downtonische und Dittonische Acanthodier-Reste des Ostseegebietes. *Palaeontographica A* 136: 1–82.

Gross, W. 1973. Kleinschuppen, Flossenstacheln und Zähne von Fischen aus europäischen und nordamerikanischen Bonebeds des Devons. *Palaeontographica A* 142: 51–155.

Hanke, G.F., Davis, S.P., and Wilson, M.V.H. 2001. New species of the acanthodian genus *Tetanopsyrus* from Northern Canada, and comments on related taxa. *Journal of Vertebrate Paleontology* 21: 740–753.

Hanke, G.F. and Wilson, M.V.H. 2004. New teleostome fishes and acanthodian systematics. *In*: G. Arratia, M.V.H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*, 189–216. Verlag Dr Friedrich Pfeil, Munich.

Janvier, P. 1996. *Early Vertebrates*. 393 pp. Oxford University Press, Oxford.

Karatajūtė-Talimaa, V. 1998. Determination methods for the exoskeletal remains of early vertebrates. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Geowissenschaftliche Reihe* 1: 21–52.

Karatajūtė-Talimaa, V. and Smith, M.M. 2003. Early acanthodians from the Lower Silurian of Asia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 93: 277–299.

Macadie, C.I. 1998. Lower Devonian fossil fishes from Reefton, New Zealand. *Records of the Canterbury Museum* 12: 17–29.

Märss, T. 1986. Silurian vertebrates of Estonia and West Latvia [in Russian with English summary]. *Fossilia Baltica* 1: 1–104.

Miles, R.S. 1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bulletin of the British Museum (Natural History), Geology* 24 (2): 111–213.

Miller, C.G. and Märss, T. 1999. A conodont, thelodont and acanthodian fauna from the Lower Pridoli (Silurian) of the Much Wenlock area, Shropshire. *Palaeontology* 42: 691–714.

Ørvig, T. 1951. Histological studies of placoderms and fossil elasmobranchs. I. The endoskeleton, with remarks on the hard tissues of lower vertebrates in general. *Arkiv för Zoologi* 2: 321–454.

Ørvig, T. 1958. *Pycnaspis splendens*, new genus, new species, a new ostracoderm from the Upper Ordovician of North America. *Proceedings of the U.S. National Museum* 108: 1–23.

Ørvig, T. 1967. Phylogeny of tooth tissues: Evolution of some calcified tissues in early vertebrates. *In*: A. Miles (ed.), *Structural and Chemical Organization of Teeth 1*, 45–110. Academic Press, New York.

Ørvig, T. 1968. The dermal skeleton, general considerations. *In*: T. Ørvig (ed.), *Current Problems of Vertebrate Phylogeny, Nobel Symposium 4*, 373–397. Almquist Wiksell, Stockholm.

Ørvig, T. 1977. A survey of odontodes ("dermal teeth") from developmental, structural, functional and phyletic points of view. *In*: S.M. Andrews, R.S. Miles, and A. Walker (eds.), Problems in Vertebrate Evolution. *Linnean Society Symposium, Series* 4: 53–75.

Pander, C. 1856. *Monographie der fossilen Fische des Silurischen Systems des Russisch-Baltischen Gouvernements*. 91 pp. Akademie der Wissenschaften, St. Petersburg.

Powrie, J. 1864. On the fossiliferous rocks of Forfashire and their contents. *Quarterly Journal of the Geological Society of London* 20: 413–429.

Schultze, H.-P. 1968. Palaeoniscoidea-Schuppen aus dem Unterdevon Australiens und Kanadas und aus dem Mitteldevon Spitsbergens. *Bulletin of the British Museum of Natural History (Geology)* 16 (7): 343–368.

Schultze, H.-P. 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläontologische Zeitschrift* 51: 152–168.

Smith, M.M. and Sansom, I.J. 2000. Evolutionary origins of dentine in the fossil record of early vertebrates: diversity, development and function. *In*: M. Teaford, M.M. Smith, and M. Ferguson (eds.), *Development, Function and Evolution of Teeth*, 65–81. Cambridge University Press, New York.

Sobolev, N., Karatajūtė-Talimaa, V. and Valiukevičius, J. 1988. Conodonts and vertebrates from the *Favosites regularissimus* Zone. *In*: N. McMillan, A. Embry, and D. Glass (eds), Devonian of the World. *Canadian Society of Petroleum Geologists Memoir* 14 (3): 535–539.

Turner, S., Burrow, C.J., and Basden, A.M. 2000. Devonian vertebrates of Queensland. *In*: A. Blieck and S. Turner (eds.), Palaeozoic Vertebrate Biochronology and Global Marine/Non Marine Correlation (Final Report IGCP 328, 1991–1996). *Courier Forschungsinstitut Senckenberg* 223: 487–522.

Valiukevičius, J. 1979. Acanthodian scales from the Eifelian of Spitsbergen. *Paleontological Journal* 4: 101–111.

Valiukevičius, J. 1985. *Acanthodians from the Narva Regional Stage of the Main Devonian Field* [in Russian with English summary]. 144 pp. Mokslas, Vilnius.

Valiukevičius, J. 1992. First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya. *In*: E. Mark-Kurik (ed.), Fossil Fishes as Living Animals. *Academia* 1: 193–213. Institute of Geology, Tallinn.

Valiukevičius, J. 1994. Acanthodians and their stratigraphic significance [in Russian]. *In*: S. Cherkesova, V. Karatajūtė-Talimaa, and R. Matukhin (eds.), *Stratigrafia i fauna nižnedevonskih otloženij Tareiskogo opornogo razreza*, 131–197 and 236–243. Vserossijskij Naučno-issledovatel'skij Institut Geologii i Mineral'nyh Ressursov Mirovogo Okeana, Sankt Petersburg.

Valiukevičius, J. 1998. Acanthodians and zonal stratigraphy of Lower and Middle Devonian in East Baltic and Byelorussia. *Palaeontographica A* 248: 1–53.

Valiukevičius, J. 2003a. Devonian acanthodians from Severnaya Zemlya Archipelago (Russia). *Geodiversitas* 25: 131–204.

Valiukevičius, J. 2003b. New Late Silurian to Middle Devonian acanthodians of Timan-Pechora region. *Acta Geologica Polonica* 53: 209–245.

Valiukevičius, J. 2003c. New Silurian nostolepids (Acanthodii, Pisces) of Lithuania. *Geologija* 42: 51–68.

Valiukevičius, J. 2004. New Wenlock–Pridoli (Silurian) acanthodian fishes from Lithuania. *Acta Palaeontologica Polonica* 49: 147–160.

Valiukevičius, J. and Karatajūtė-Talimaa, V. 1986. Acanthodian scale assemblage from the base of the Middle Devonian in the Baltic and Byelorussia [in Russian]. *In*: A. Brangulis (ed.), *Biofatsii i fauna silurijskogo i devonskih basseinov Pribaltiki*, 110–122. Vsesojuznyj Naučno-issledovatel'skij Institut Morskoj Geologii, Zinatne, Riga.

Vidal, M., Goujet, D., Janvier, P., and Lardeux, H. 1994. Micro-restes des Vertébrés du Calcaire de La Grange, Dévonien inférieur (Emsien) du Sud-Est du Massif Armoricain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 194: 321–341.

Vieth, J. 1980. Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie* 23: 1–69.

Vieth-Schreiner, J. 1983. Fisch-Schuppen und -Zähne aus der Eifeler Kalkmulden-Zone (Emsium, Eifelium). *Senckenbergiana Lethaea* 64: 129–177.

Wang, N.-Z. 1992. Microremains of agnathans and fishes from Lower Devonian of central Guangxi with correlation of Lower Devonian between central Guangxi and eastern Yunnan, south China. *Acta Palaeontologica Sinica* 31 (3): 280–303.

Wang, N.-Z. and Dong, Z.-Z. 1989. Discovery of Late Silurian microfossils of Agnatha and fishes from Yunnan, China. *Acta Palaeontologica Sinica* 28: 192–206.

Wang, N.-Z., Wang, J.-Q., Zhang, G.-R., and Wang, S.-T. 1998. The first discovery of Silurian and Early Devonian acanthodians from Zoige and Tewo Counties, West Qinling Mountains. *Vertebrata Palasiatica* 36: 268–281.

Wang, R. 1993. Taxonomie, Palökologie und Biostratigraphie der Mikroichthyolithen aus dem Unterdevon Keltiberiens, Spanien. *Courier Forschungsinstitut Senckenberg* 161: 1–205.

Wang, W. 2003. First occurrence of acanthodian microfossils from the Early Devonian of Lijiang, Yunnan, China. *Vertebrata Palasiatica* 41: 1–16.

Wells, J.W. 1944. Fish remains from the Middle Devonian Bone Beds of the Cincinnati Arch region. *Palaeontographica Americana* 3: 99–160.

Zidek, J. 1976. Kansas Hamilton Quarry (Upper Pennsylvanian) *Acanthodes*, with remarks on the previously reported North American occurrences of the genus. *The University of Kansas, Paleontological Contributions* 83: 1–41.