inclination characterizes the tri-partite crown, which has the shape of a three-cusped tooth. A narrow and smooth median section is flanked by two wide, but shorter, lateral wings. The crown narrows towards the base, forming a short but pronounced neck. Several large canal openings perforate the neck on both sides. When the scales are grown together, differentiation of the base is not visible, and only the different crown units are seen. One well preserved specimen shows a group of three scales with welded bases (Fig. 28A). The main part is formed by a large scale, with two smaller scales growing on the anterior part. Another specimen shows a row of overlapping scales of different sizes with several large neck canal openings on both the anterior and posterior side (Fig. 28C).

Remarks. Since few scales were available, histological investigations were not made. Chondrichthyes indet. may be a growing polyodontodia of *Ctenacanthus* type in the scheme of Karatajute-Talimaa (1992).

Some vertebrate remains of unknown origin, treated under Incertae Sedis may also be comparable with true chondrichthyans (Fig. 43D, H, J).

Occurrence. Lochkovian, Monument, Hall Land, North Greenland.

Acanthodii

Order Climatiida Berg 1940
Family Climatiidae Berg 1940

Genus *Nostolepis* Pander 1856

Type species. *Nostolepis striata* Pander 1856, Late Silurian (Pridoli), Ohesaare Formation, Saaremaa, Estonia.

Diagnosis. Small and large scales with smoothly downbent anterior part of crown; neck less pronounced in anterior part; crown anteriorly ornamented by posteriorly converging or parallel strongly expressed ridges and ribs; superpositional growth with simple mesodentine in crown and irregular branching tubules rising from radial, circular and ascending vascular canals; cellular bone in base usually with numerous cell cavities.

Species content. *Nostolepis striata* Pander 1856; *N. alta* Märss 1986a; *N. applicata* Vieth 1980; *N. arctica* Vieth 1980; *N. athleta* Valiukevicius 1994; *N. costata* Goujet 1976; *N. curiosa* Valiukevicius 1994; *N. curta* Valiukevicius 1994; *N. gaujensis* Valiukevicius 1998; *N. gracilis* Gross 1947; *N. guangxiensis* Wang Nian-zhong 1992; *N. infida* Valiukevicius 1994; *N. kernavensis* Valiukevicius 1985; *N. lacrima* Valiukevicius 1994; *N. laticristata* Valiukevicius 1994; *N. matukhini* Valiukevicius 1994; *N. minima* Valiukevicius 1994; *N. multangula* Valiukevicius 1994; *N. multicostata* Vieth 1980; *N. robusta* (Brotzen 1934); *N. spina* Valiukevicius 1994; *N. taimyrica* Valiukevicius 1994; *N. tareyensis* Valiukevicius 1994; *N. tcherkesovae* Valiukevicius 1994.

Range. Early Silurian (Wenlock) – Middle Devonian (Eifelian).

***Nostolepis halli* sp. nov.**
Fig. 29A–G; Fig. 30

Derivation of name. In honour of Charles Francis Hall, the leader of the U.S. North Polar Expedition 1871–73, who died and was buried in Hall Land. Also referring to the main fossil locality close to his grave.

Holotype. MGUH VP 3567 from GGU sample 82738 (Fig. 29A, B).

Figured material. MGUH VP 3567–3571, 3631 from GGU sample 82738.

Other material. About 60 scales from GGU samples 82734, 82736, 82737, 82738 and 298937.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Diagnosis. Homogeneous set of medium-sized scales, about 1 mm, with low rhomboidal crown, bent down anteriorly towards base and anteriorly diffuse neck; crown smoothly ridged anteriorly with intermediate furrows; lateral wings folded up; large convex base, displaced anteriorly, with lower posterior part; mesodentine tissue in crown with irregular branching tubules; cellular bone in base with few osteocyte cavities and process tubules.

Scale morphology. Like the other acanthodians, the scales of *Nostolepis halli* sp. nov. are quite poorly preserved. They are brown-yellow to dark brown, medium sized and vary in length from about 0.5–1 mm.

The set of scales is homogeneous and no clearly differentiated scale types seem to be present.

The rhomboidal or sector-shaped crown is smooth, flat or slightly convex (Fig. 29A–F). Postero-lateral crown margins are straight and meet in a posteriorly pointing crown apex. Smaller specimens may have postero-lateral margins that make a curve towards the centre of the scale before they meet (Fig. 29C, F). On a slightly lower level, at the postero-lateral sides, a small dorso-lateral wing is visible on each side in the best preserved specimens (Fig. 29A, B, D, E). The wing is folded along a median line with its lateral margins pointing upward. This in cross section V-shaped wing is characteristic of the species. Anteriorly 7–10 smooth ridges separated by short, shallow furrows run backwards towards the centre of the upper crown surface. They converge slightly but do not join before they disappear in the flat crown surface. The ridges are also evenly distributed on each side of an imaginary median line and bend gently down towards the neck and the base. Due to the presence of ribs and furrows, the anterior crown margin appears crenulated or notched in a dorsal view. On the upper crown surface it is often possible to see each layer of growth. The crown is higher posteriorly, which gives a slightly posteriorly rising inclination. Posteriorly the low neck is much more pronounced than in the indistinct lower anterior part. The neck is smooth and neither pore openings nor neck furrows are visible. The transition between the neck and the anterior crown furrows is very gentle and the neck is only pronounced near the lower ends of the intermediate ridges. Usually the base is much wider than the crown and is much higher anteriorly. A large part of the swollen displaced base projects at the front.

Scale histology. The upper crown surface in most scales of *Nostolepis halli* is poorly preserved but overlapping, sometimes visible in the antero-dorsal upper part of the crown, indicating a superpositional type of growth; up to seven growth lamellae are visible and superposed on the embryonic scale (Fig. 30A). Each lamella in the crown contains irregular branching tubules of mesodentine type (Fig. 30B). The proportionally large base is composed of layers of cellular bone with round or flattened osteocyte cavities and tubules of irregularly distributed short branching processes (Fig. 30A). The flattened cavities are, together with associated tubules, generally arranged along the longitudinal axis of the basal layers. Each layer or zone is laminated and continuous with one on the crown. Long tubules of Sharpey's fibres are developed perpendicular to these basal layers.

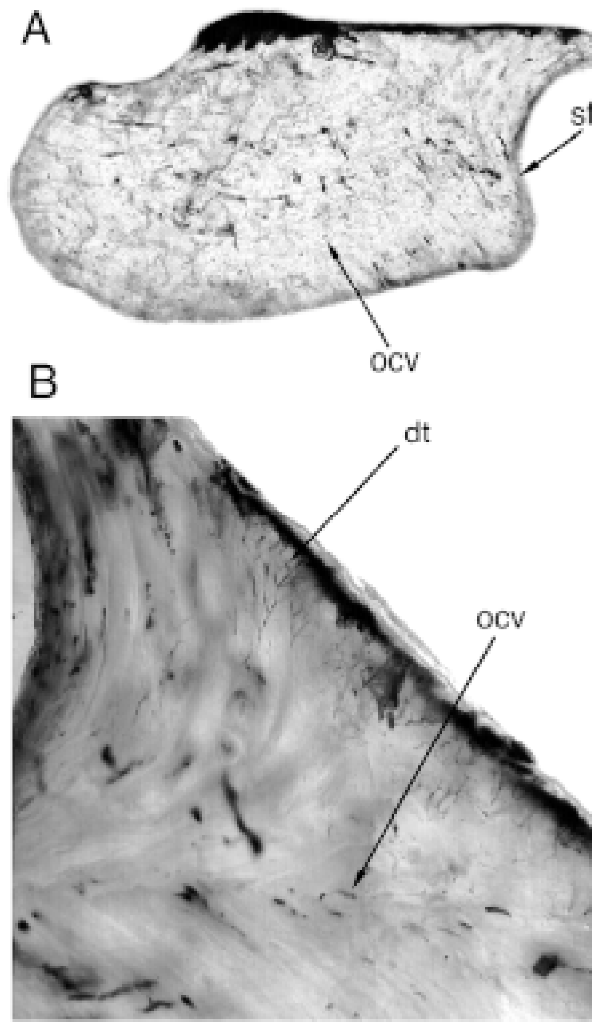


Fig. 30. *Nostolepis halli* sp. nov. Histology of the scale.
A: Scale in vertical longitudinal section, MGUH VP 3571, × 98.
B: Scale in vertical longitudinal section, close up of crown, MGUH VP 3631, × 325.
All specimens from GGU sample 82738, Halls Grav.
dt: dentine tubules; **ocv**: osteocyte cavities; **sf**: tubules of Sharpey's fibres.

Scale dimensions. Length 0.5–1.1 mm; width 0.5–1.0 mm.

Remarks. The Greenland species is delimited from comparable species by the up-bent shape of the lateral wing. Lateral structures of other species of *Nostolepis* are instead expressed as vertical, diagonal or horizontal ribs. The smaller *Gomphonchus* cf. *G. hoppei*, reported by Vieth (1980) from the Lochkovian strata of the Canadian Arctic, has a general morphology more similar to *N. halli* than the traditional *G. hoppei*. Its

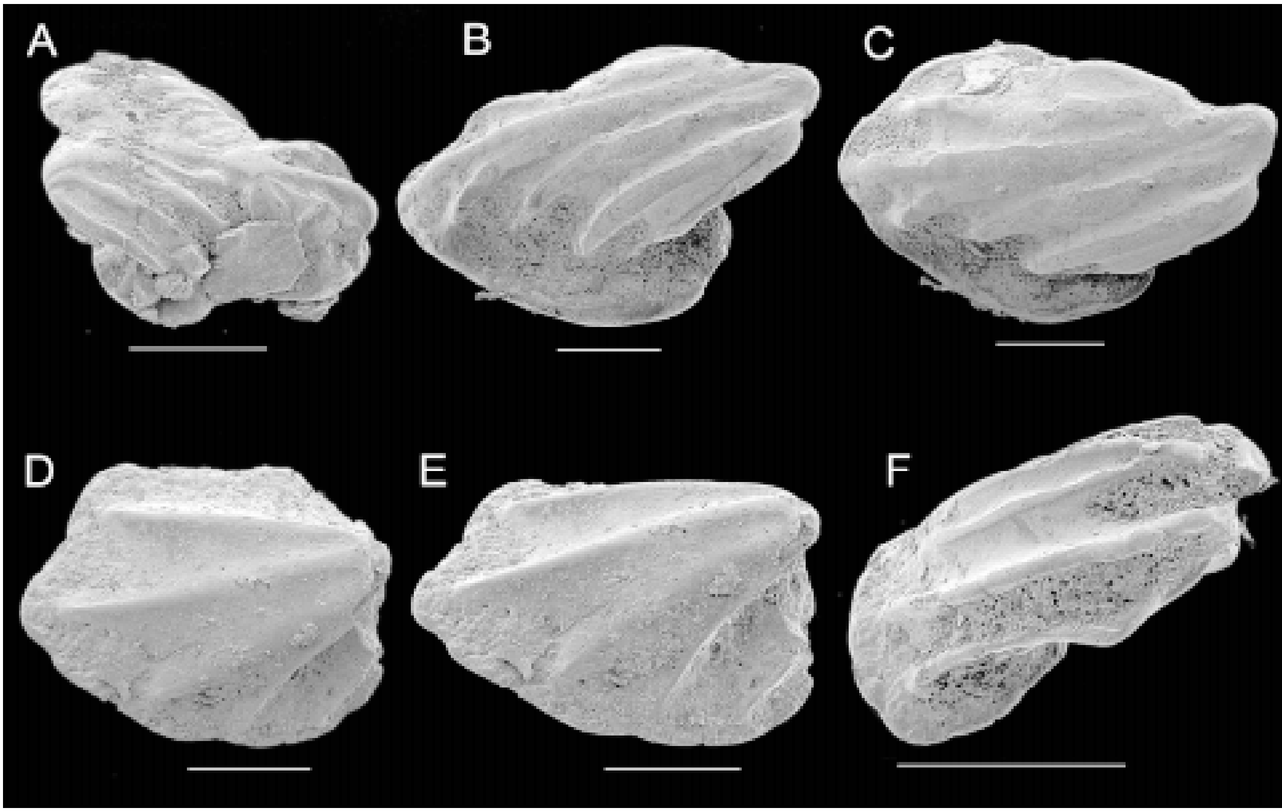


Fig. 31. Climatiida indet. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Head? scale in oblique crown view, MGUH VP 3558. **B**: Trunk scale in oblique crown view, MGUH VP 3560. **C**: Scale in crown view, MGUH VP 3560. **D**: Scale in crown view, MGUH VP 3557. **E**: Scale in oblique crown view, MGUH VP 3557. **F**: Scale in oblique crown view, MGUH VP 3559.
MGUH VP 3557–3559 from GGU sample 82736, Halls Grav; MGUH VP 3560 from GGU sample 82738, Halls Grav.

illustrated histology suggests it is probably also of *Nostolepis* but its lateral ridges are clearly different from the wings of *N. halli*.

Occurrence. Pridoli, Halls Grav, Hall Land, North Greenland.

Climatiida indet.
Figs 31, 32

Figured material. MGUH VP 3557–3559 from GGU sample 82736, MGUH VP 3560, 3561 from GGU sample 82738.

Other material. About 35 scales from GGU sample 82734, 82736, 82737, 82738.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Scale morphology. The small and variably shaped climatiid scales are a rare component of the collections from the Halls Grav locality. The crown has a high inclination from the larger base and narrows towards the posteriorly pointing end (Fig. 31). In upper view, the crown is convex or almost flat with ridges which converge posteriorly. The scales may have as many as eight ridges converging from the base towards the posterior crown apex. One scale type has a cone-shaped crown with distinct ridges, converging from the base to the slightly posteriorly pointing apex (Fig. 31D, E). Some of the ridges run more at the lateral areas. The neck is mostly weakly developed. Another type, probably from the body, has a flatter more elongated or rhomboidal crown with less inclination and a more pronounced neck (Fig. 31B, C). In this type, the ridges run more on the median upper surface of the crown with only very few on the lateral areas. They bend down anteriorly towards the neck and lateral ridges are much shorter. In basal view the posteriorly overhanging crown is almost smooth and shows only

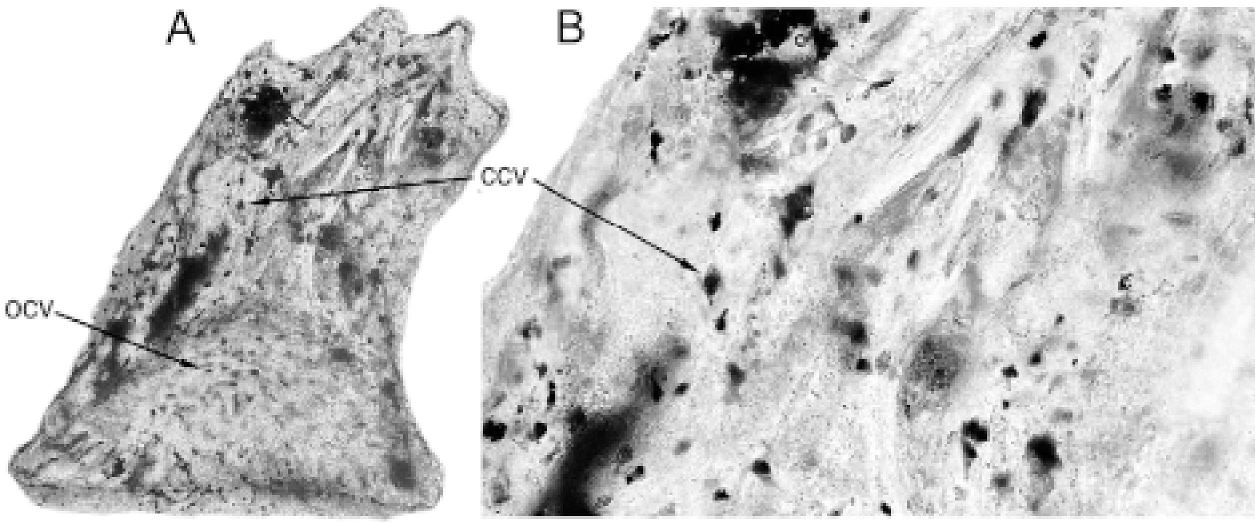


Fig. 32. Climatiida indet. Histology of scale.
A: Scale in vertical longitudinal section, MGUH VP 3561, × 177. **B**: Scale in vertical longitudinal section, close up of crown, MGUH VP 3561, × 590.
MGUH VP 167 from GGU sample 82738, Halls Grav.
ccv: cavities in crown; **ocv**: osteocyte cavities.

very weak striations. All scales have a round or irregular base which is often very thin. In basal view the scales are flat, convex or just slightly concave. Less regular scales, almost triangular in outline, appear to be composed of three smaller welded scales (Fig. 31A) and may be derived from the head region.

Scale histology. The large embryonic scale has perhaps only one or two growth zones added on the top and sides (Fig. 32). The base of the embryonic scale has many round osteocyte cavities with bone cell processes (Fig. 32A). Sharpey's fibres are present in the lower part of the base. The crown is poorly preserved in available sections but shows several rounded cell cavities with spreading tubules (Fig. 32B).

Scale dimensions. Length 0.3–0.7 mm; width 0.2–0.6 mm.

Remarks. Although the histological information is limited, it indicates similarities with the most primitive acanthodian structures found in *Euthacanthus* Powrie 1864 from the Lower Devonian of Scotland (Denison 1979). Morphologically these scales are more similar to *Climatius* Agassiz, 1845 and *Nostolepis* Pander 1856. The base of *Climatius* has no (or very few) bone cell cavities (Ørvig 1967; Denison 1979).

Occurrence. Pridoli, Halls Grav, Hall Land, North Greenland.

Order Ischnacanthida Berg 1940
Family Ischnacanthidae Woodward 1891

Genus *Gomphonchus* Gross 1971

Type species. *Gomphodus sandelensis* Pander 1856 (type by monotypy); Late Silurian (Pridoli), Ohesaare Formation, Saaremaa, Estonia.

Diagnosis. Small and large scales (0.3–1.3 mm) with low or convex base, often displaced anteriorly; low or elevated rhomboidal crown with low inclination; smooth or ornamented with radiating ridges and furrows; superpositional growth with dentine in crown; cellular and acellular bone in base and outer enameloid layer on crown; long fine branching ascending vascular canals rising from neck towards crown centre in each dentine growth layer; fine network of horizontal and radial canals in crown.

Species content. *Gomphonchus sandelensis* (Pander 1856); *G. alveatus* Vieth 1980; *G.*? bogongensis Burrow 1997; *G. hoppei* (Gross 1947); *G. liujingensis* Wang Nian-zhong 1992; *G. tauragensis* Valiukevicius 1998; *G.*? *turnerae* Burrow 1995.

Range. Early Silurian (Wenlock) – Early Devonian (Emsian).

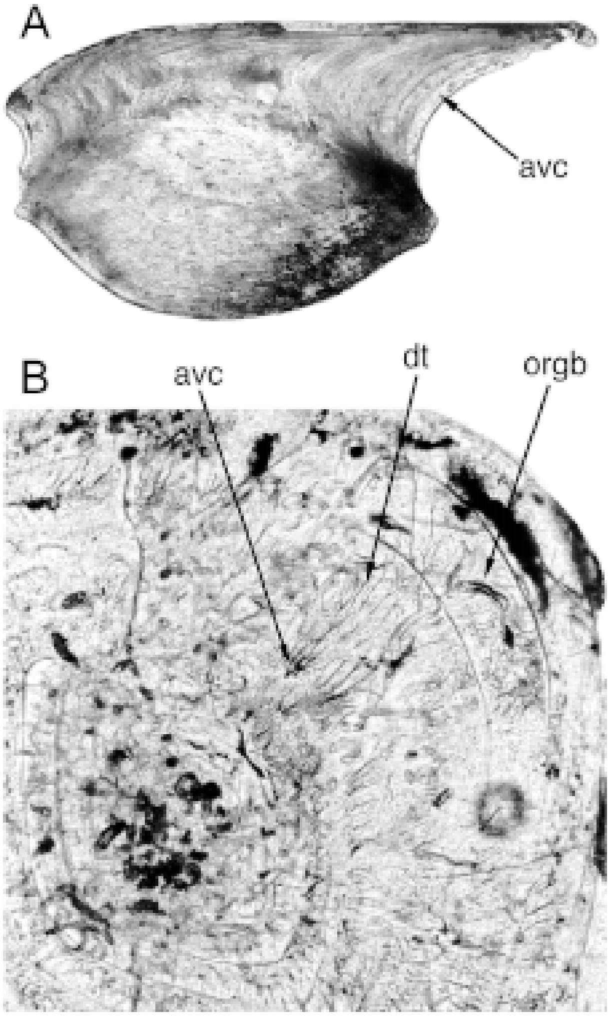


Fig. 33. *Gomphonchus* cf. *G. sandelensis*. Histology of the scale.
A: Scale in vertical longitudinal section, MGUH VP 3566, × 216.
B: Scale in horizontal crown section, MGUH VP 3632, × 191.
All specimens from GGU sample 82738, Halls Grav.
avc: ascending vascular canals; **dt**: dentine tubules; **orgb**: organism borings or burrows.

Remarks. Gross (1971) concluded, contrary to earlier views (Gross 1947), that several specimens of the type species, *G. sandelensis*, have bone cells in the basal tissue. Often specimens lack this distinct character, probably due to differences in preservation. J. Valiukevicius (1995; personal communication 1998) suggests that *Gomphonchus* may have both cellular and acellular bone in the base.

***Gomphonchus* cf. *G. sandelensis* (Pander 1856)**
Fig. 29H–L, I; Fig. 33

Syntypes. *Gomphodus sandelensis*, Pander 1856, table. 6, fig. 15–17. Late Silurian (Pridoli), Ohesaare Formation, Saaremaa, Estonia. The types have been lost.

Figured material. MGUH VP 3562 from GGU sample 319264, MGUH VP 3563–3566, 3632 from GGU sample 82738.

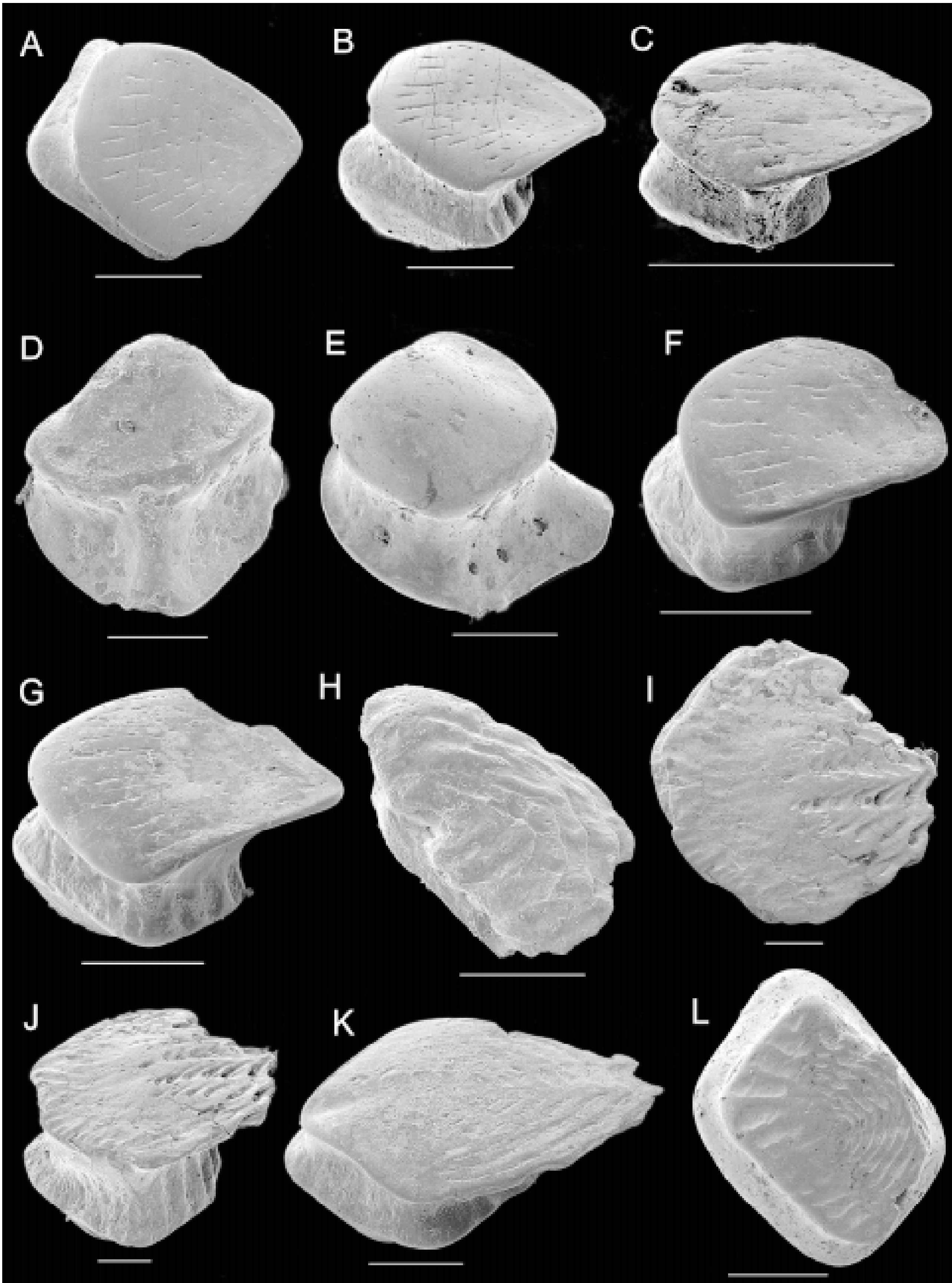
Other material. Hundreds of specimens from GGU samples 82734, 82736, 82737, 82738, 298937 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Small and large scales (0.3–1.2 mm) with low inclined and flat rhomboidal crown; smooth or anteriorly ridged upper crown surface; crown bending slightly down anteriorly; neck high and distinct with posterior vertical ridges; base convex, often displaced anteriorly; superpositional growth with long, fine, little branching, ascending vascular canals; acellular bone in the base.

Scale morphology. Scales of *Gomphonchus* cf. *G. sandelensis* are very rare and vary in colour from yellowbrownish to darker brown. They are poorly preserved, often with broken crown edges, and are represented by one main morphotype. Scale length equals crown length and varies between 0.2 and 1.0 mm. The crown is rhomboidal in shape with rounded corners. The

Fig. 34. *Poracanthodes*. SEM photomicrographs. Scale bars equal 0.2 mm.
A–**G**. *Poracanthodes* cf. *P. punctatus*. **A**: Scale in crown view, MGUH VP 3572. **B**: Scale in oblique crown view, MGUH VP 3572. **C**: Scale in oblique crown view, MGUH VP 3573. **D**: Scale in postero-basal view, MGUH VP 3574. **E**: Scale in oblique basal view, MGUH VP 3575. **F**: Scale in oblique crown view, MGUH VP 3576. **G**: Scale in oblique crown view, MGUH VP 3577.
H–**L**. *Poracanthodes* cf. *P. porosus*. **H**: Scale in oblique crown view, MGUH VP 3583. **I**: Scale in crown view, MGUH VP 3596. **J**: Scale in oblique crown view, MGUH VP 3596. **K**: Scale in oblique crown view, MGUH VP 3582. **L**: Scale in crown view, MGUH VP 3584.
MGUH VP 3572–3577, 3584 from GGU sample 82738, Halls Grav; MGUH VP 3582 from GGU sample 82736, Halls Grav; MGUH VP 3583, 3596 from GGU sample 319264, Monument.


A
B
C
D
E
F
G
H
I
J
K
L

anterior corner is more rounded than the pointed posterior end. The most anterior part of the crown often bends down slightly towards the base. Often concentric layers are evident, due to abrasion, on the smooth crown surfaces, which are flat or slightly convex. The clear bilateral symmetry is often lost in these scales (Fig. 29H). From the flat dorsal surface and the sharp edges, the crown slopes with a low angle towards the crown centre and bends back again, forming a quite distinct and high neck. The neck is evenly high all around the scale, given by very little or no visible inclination. Posteriorly, the lower part of the neck has vertical ribs with intervening openings of the dentine canals. Small dentine canal or tubule openings are visible all around the neck. The junction between the neck and the base is characterized by a well marked rim. In basal view, the base is oval or rhombic with rounded corners and often clear concentric striping. The high vaulted base is narrower than the crown, often with the swelling displaced anteriorly.

Scale histology. Many scales are poorly preserved and the histological structures are often disturbed by irregular canals formed by boring organisms (Fig. 33B). *G.* cf. *G. sandelensis* has a superpositional type of growth with at least 8 layers superposed on the embryonic scale (Fig. 33A). Narrow ascending canals in each dentine layer divide and send off few side-branches of finer tubules (Fig. 33B). Osteocyte cavities are not clearly visible in the base. Numerous tubules of Sharpey's fibres in the base run radially and perpendicularly from the outer surface towards the centre.

Scale dimensions. Length 0.2–1.0 mm; width 0.2–1.0 mm.

Remarks. *G.* cf. *G. sandelensis* differs from the type material by not having the distinct neck ribs anteriorly and the anterior ribs of the upper crown surface. A few scales from the Halls Grav locality are found which might come from the head region. The true taxonomical affinity, however, is unknown and they could be related to any of the acanthodian scale taxa.

Occurrence. *G.* cf. *G. sandelensis*, Pridoli–Lochkovian, Hall Land, North Greenland; *G. sandelensis*, Wenlock–Pridoli, Saaremaa, Estonia and Latvia; Ludlow, Gotland, Sweden; Pridoli, Scania, Sweden; Pridoli, Timan-Pechora region, north-eastern part of European Russia; Pridoli, erratic boulder, Germany; Lower Devonian, Arctic Canada; Lochkovian, Spain.

Genus *Poracanthodes* Brotzen 1934

Type species. *Poracanthodes punctatus* Brotzen 1934. Lower Devonian? erratic boulder (Bey. 36), the lowlands of northern Germany. Later designated as type species by Gross (1971), see also Valiukevicius (1992).

Diagnosis. Large and small scales with flat rhomboidal crown; ornamented crown with short parallel or radial ridges on anterior part, alternatively unornamented; posterior part of crown smooth or often with concentric grooves and multicuspidate ridges; pore canal system with radial pore, arcade pore and pore canals; pore canals open on upper crown surface with numerous pores arranged in radial or concentric rows; crown composed of dentine and mesodentine; base composed of acellular bone or bone with osteocyte cavities. (Modified from Valiukevicius 1992.)

Species content. *Poracanthodes punctatus* Brotzen 1934; *P. gujingensis* Wang Nian-zhong & Dong Zhi-zhong 1989; *P. menneri* Valiukevicius 1992; *P. porosus* Brotzen 1934; *P. subporosus* Valiukevicius 1998.

Range. Late Silurian (Ludlow) – Early Devonian (Lochkovian).

Remarks. For a long time *Poracanthodes* was considered to represent lateral line scales of *Gomphonchus* (Gross 1971; Denison 1979), an idea subsequently changed by the find of articulated specimens of *Poracanthodes menneri* with a complete squamation of poracanthodiform scales (Valiukevicius 1992). Valiukevicius (1995) also introduced a *Poracanthodes* type of histology for scales, including several genera such as *Poracanthodes*, *Gomphonchus* (only *G. hoppei*), *Ectopacanthus* and *Lietuvacanthus*. This grouping is not stable for taxonomical usage since, for example, several species within *Poracanthodes* differ by either having superpositional or areal growth which should serve as a character to split up the now well established genus *Poracanthodes*. Revision is also prompted by the presence of cellular or acellular bone tissue. Vergoossen (1997) proposed a taxonomical revision of poracanthodid acanthodians but this cannot be completely adapted, since his reassignment of the type species *Poracanthodes punctatus* to *P. porosus* and the new *Brotzenolepis punctatus* is inadmissible following the International Code of Zoological Nomenclature (Ride *et al*. 1985, Article 61a) and thereby not valid. Although the validity of the genus *Poracanthodes* has

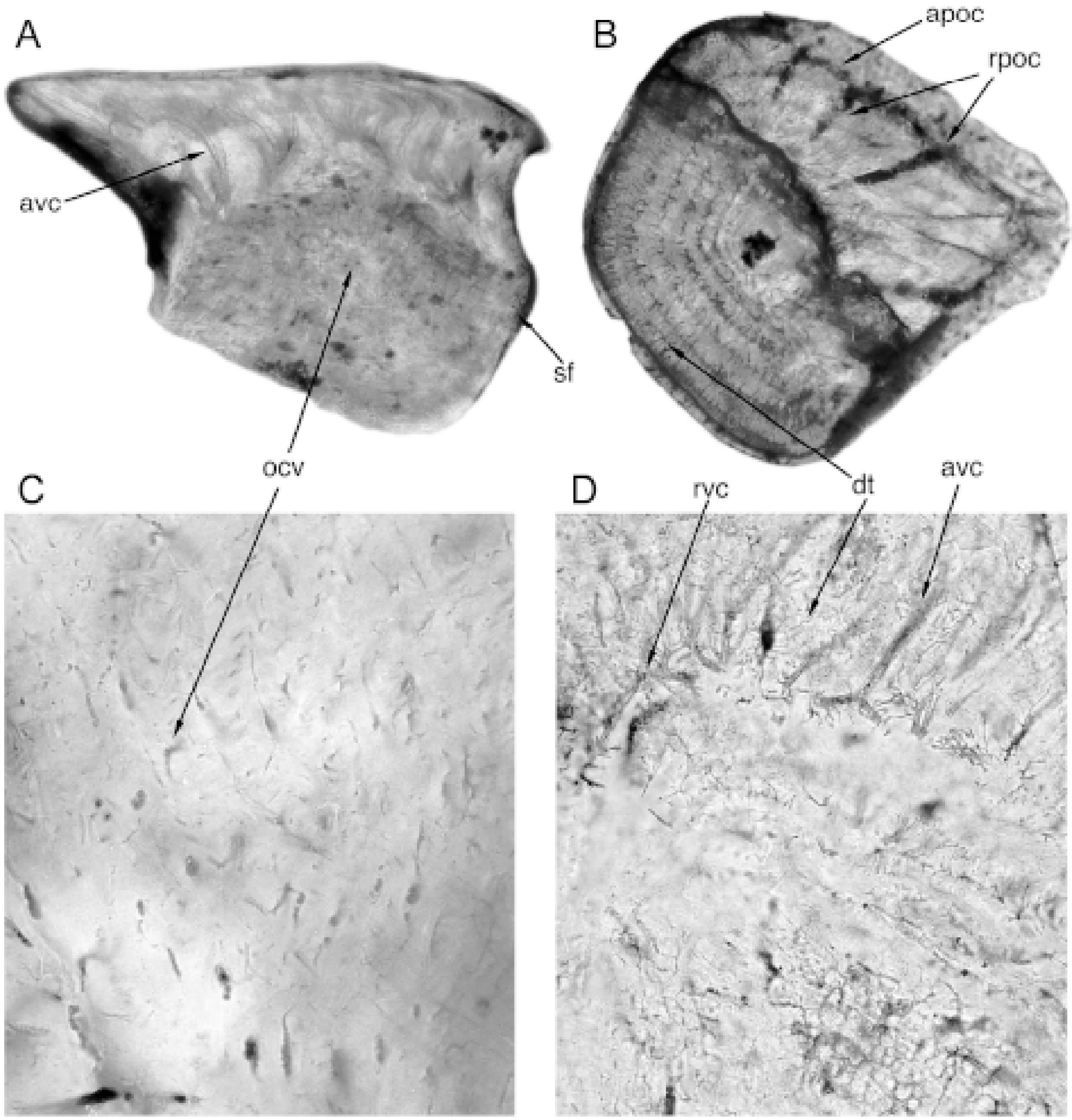


Fig. 35. *Poracanthodes* cf. *P. punctatus*. Histology of the scale.
A: Scale in vertical longitudinal section, MGUH VP 3578, × 174. **B**: Scale in horizontal crown section, MGUH VP 3579, × 152. **C**: Scale in vertical longitudinal section, close up of basal tissue, MGUH VP 3580, × 548. **D**: Scale in vertical longitudinal section, close up of crown, MGUH VP 3581, × 514.
All specimens from GGU sample 82738, Halls Grav.
apoc: arcade pore canals; **avc**: ascending vascular canals; **dt**: dentine tubules; **ocv**: osteocyte cavities; **rpoc**: radial pore canal; **rvc**: radial vascular canals; **sf**: tubules for Sharpey's fibres.

been questioned, it became definitely valid when Valiukevicius (1992) designated *P. punctatus* as the type species.

Poracanthodes cf. *P. punctatus* Brotzen 1934

Fig. 34A–G; Fig. 35

1986a *Poracanthodes* aff. *punctatus* Brotzen – Märss, p. 57, plate 32, figs 6, 7, 9.

Syntypes. *Poracanthodes punctatus*, Brotzen 1934, plate 3, figs 1, 8. Lower Devonian? erratic boulder (Bey. 36), the lowlands of northern Germany. The material seems to be lost.

Figured material. MGUH VP 3572–3581 from GGU sample 82738.

Other material. Hundreds of specimens from GGU samples 82734, 82736, 82737, 82738, 298937, 298960 and 319264.

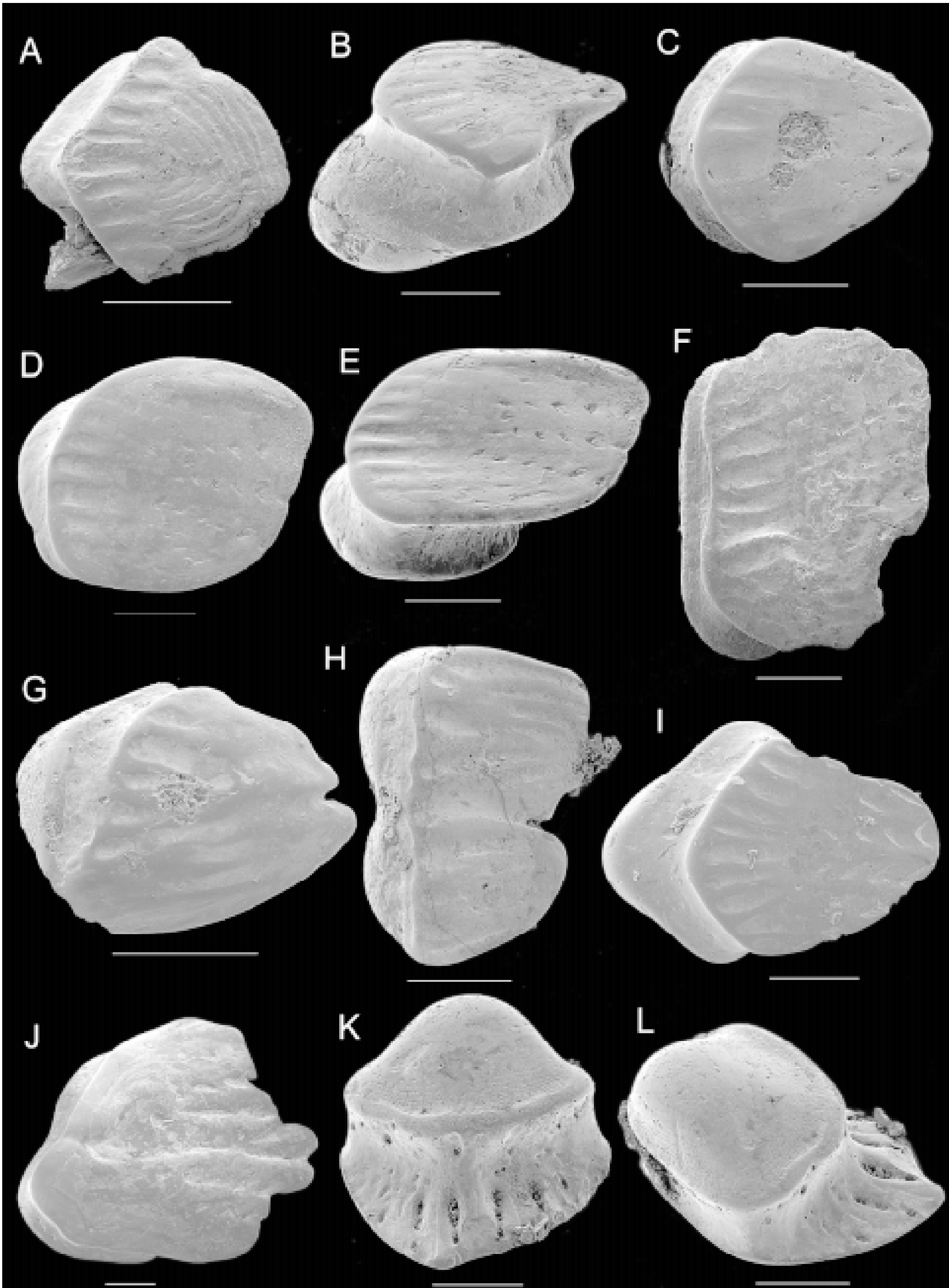
Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Small and large poracanthodid scales with rhomboidal crown; anterior crown margin round or angular; anterior part smooth, rarely with short ridges, often with median sulcus; crown surface with concentric rows of tiny pores, parallel to the postero-lateral crown margins; high neck with posterior openings for radial pore canals above openings for vascular canals; superpositional type of growth; pore canal system with radial pore canals connected by arcade pore canals; pore canals run from arcade canal to openings in the upper crown surface.

Scale morphology. Scales of *Poracanthodes* cf. *P. punctatus* vary in colour from dirty white to amber brown or dark brown. They are quite well preserved and highly variable in size, 0.2–0.9 mm in length. The crown shape is smoothly rhomboidal with a rounded anterior outline and a longer, pointed posterior part (Fig. 34A–C, F, G). The crown has a very low inclination but anteriorly the flat or slightly convex crown bends down slightly towards the base. Small pores are visible on the otherwise smooth upper surface. They have an almost concentric orientation in the posterior part, following the growth lamellae. Pores on the central anterior part of the upper crown surface are arranged along narrow slits or furrows of different length. They have an antero–posterior orientation and may be difficult to separate morphologically from the anterior part of the more concentric rows. Just below the acute margins, the crown gets narrower, forming a high distinctive neck. Large openings of four or six radial canals are visible on the part of the neck that joins the lower side of the crown (Fig. 34D, E). Smaller vascular canal openings, on a lower level on the neck, occur posteriorly where vertical slits or furrows are also developed at the basal part of the neck. The base is round or rhomboidal and follows the shape of the crown. The base and the neck are clearly separated by a brim. Posteriorly the crown is larger and projects over the base. The anteriorly displaced base, which seldom projects anteriorly, is usually higher in the frontal part. Growth lines are sometimes clearly visible at the basal surface.

Scale histology. The scales show superpositional growth with up to nine lamellae superposed on the embryonic scale, but due to their thinness these are sometimes difficult to detect in the upper posterior part of the crown. External morphological characters also suggest superpositional growth. The crown is composed of dentine with narrow ascending vascular canals rising from the basal part in each growth zone (Fig. 35A). These dentine canals branch into fine dentine tubules, forming a complex and multibranched dentine pattern (Fig. 35D). Each ascending canal joins with the dentine canal in the next lamellae by larger horizontal dentine canals. These radial vascular canals must not be confused with the larger radial pore canals that belong

Fig. 36. *Poracanthodes* cf. *P. porosus*. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Scale in crown view, MGUH VP 3585. **B**: Scale in oblique crown view, MGUH VP 3586. **C**: Scale in crown view, MGUH VP 3587. **D**: Scale in crown view, MGUH VP 3588. **E**: Scale in oblique crown view, MGUH VP 3588. **F**: Scale in crown view, MGUH VP 3597. **G**: Scale in crown view, MGUH VP 3589. **H**: Two joint scales in crown view, MGUH VP 3590. **I**: Scale in crown view, MGUH VP 3591. **J**: Scale in crown view, MGUH VP 3592. **K**: Scale in postero-basal view, MGUH VP 3593. **L**: Scale in oblique basal view, MGUH VP 3593.
MGUH VP 3585–3593 from GGU sample 82738, Halls Grav; MGUH VP 3597 from GGU sample 319264, Monument.


A
B
C
D
E
F
G
H
I
J
K
L

to the pore canal system of porosiform acanthodian scales. The pore canals are best visible as openings on the crown surface where they form the typical pattern of *P.* cf. *P. punctatus*. Four or six large radial pore canals extend from the centre and open on the neck, close to the lower crown surface (Fig. 35B). On a slightly higher level concentric arcade pore canals are developed, following each growth lamellae. The base has growth layers parallel to the subsurface, composed of cellular bone with round or spindle-shaped osteocyte cavities (Fig. 35C) which are arranged along the boundaries of the individual layers. The basal tissue also contains fibres and short multibranched canals. Perpendicular to the layers and the parallel fibres both long and short tubules of Sharpey's fibres are developed.

Scale dimensions. Length 0.2–0.9 mm; width 0.2–1.0 mm.

Remarks. *Poracanthodes punctatus* Brotzen 1934 from erratic boulders of the North German lowlands differs from present material by not having clear narrow longer slits on the anterior part of the crown surface. Other specimens from erratic boulders of similar age also lack this character and may also differ by having a deeper sulcus in the anterior part of the crown (Gross 1947, 1971; Märss 1986a). Scales from the Late Silurian (Pridoli) Kaugatuma Stage of Estonia, referred by Märss (1986a) to *P.* aff. *P. punctatus*, are morphologically similar to the scales from North Greenland.

Some of the head scales of unknown affinity (Fig. 43A–C) may belong to *Poracanthodes* cf. *P. punctatus* or other acanthodian taxa.

Occurrence. *Poracanthodes* cf. *P. punctatus*, Pridoli–Lochkovian, Hall Land, North Greenland; *Poracanthodes punctatus*, Pridoli–Lochkovian, Estonia and Latvia; Pridoli, Manbrook, Welsh Borderland, Great Britain; Early Devonian, erratic boulder, lowlands of northern Germany.

***Poracanthodes* cf. *P. porosus* Brotzen 1934**

Fig. 34H–L; Fig. 36; Fig. 37

1976 '*Gomphodus*' and '*Poracanthodes*' types – Bendix-Almgreen, fig. 443G–I, K.

Holotype. *Poracanthodes porosus* Brotzen 1934, plate 3, fig. 2, Lower Devonian? erratic boulder (Bey. 36), lowlands of northern Germany. Material seems to be lost.

Figured material. MGUH VP 3582 from GGU sample 82736, MGUH VP 3584–3595 from GGU sample 82738, MGUH VP 3583, 3596, 3597 from GGU sample 319264.

Other material. Thousands of scales are available from GGU samples 82734, 82736, 82737, 82738, 298937, 298953, 298954, 298960, 298963 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Small and large scales with superpositional or areal growth; rhomboidal crown with smooth or ridged anterior part; zigzag growth pattern on posterior part of crown; upper crown surface with radial rows of large pores; pore canal system with pore canals which run from the wide radial pore canals towards upper crown surface; radial pore canal openings on the upper part of the neck.

Scale morphology. Scales of *Poracanthodes* cf. *P. porosus* are very common in all the vertebrate yielding samples from the Chester Bjerg Formation. They are badly preserved and the posterior part of the crown is usually broken or completely destroyed. The colour of the scales varies from white to dark brown within the same sample. There is a high variability in size among this morphologically homogeneous group of scales, but it is still possible to detect several basic types.

The most common type has a posteriorly protruding crown which may be smoothly rhomboidal or rounded and sometimes with a more irregular shape (Fig. 36C–L), which may be due to two scales that have grown together (Fig. 36H). The crown is usually flat with a very low plane inclination, but it may be slightly convex or concave (Fig. 36D, E, G, H). Up to six rows of pore openings run radially or longitudinally from the centre towards the posterior margin of the otherwise smooth crown surface, but clear pores are absent in some specimens (Fig. 36G, H). Up to eight wider, deeper furrows with intermediate ridges are developed and extend from the centre towards the anterior crown margin. The upper crown surface often appears heavily worn and the ornamentation is only weakly visible. In some specimens it is possible to detect a faint zigzag growth pattern in the posterior part of the crown (Fig. 36C, I). The well pronounced neck is quite low and perforated by small and larger pores in the anterior part (Fig. 36K, L). The smaller pore openings are concentrated on a median level, representing the openings of radial vascular canals. The larger openings are arranged in short slit-like rows on the lower side of the crown and towards the neck. They represent the radial pore canal and associated pore canals. The anteriorly protruding base is strongly convex and separated from the crown and its neck by a well marked rim. The anterior part of the concentrically striped base is higher and more vaulted than the posterior part.

A few scales have a more elongated rhomboidal shape of the crown and show a clear zigzag pattern in the posterior part of the crown (Fig. 34K). The anterior part is smooth, often with a marginal sulcus.

A second scale type differs mainly by the ornamentation of the upper crown surface. It lacks the weak zigzag pattern in the posterior part of the crown. Instead these scales have concentric grooves parallel to the postero-lateral margins (Fig. 34L; Fig. 36A). The pore canal openings are still arranged radially and perpendicular to these grooves. In the anterior part of the crown up to eight regular wide furrows with intermediate ridges are developed.

The third distinct scale type has a more rounded crown with short irregular and weakly developed ridges on the anterior part of the upper crown surface (Fig. 34I, J). Pore canal openings are arranged in radial rows that run from the centre towards the posterior margin. Between the rows are ridges, which are cut by concentric growth lines that give an overlapping zigzag growth pattern. The scales have neck pores and ridges on the posterior part of the clear and relatively high neck.

Scale histology. The first and most common type of scale has superpositional growth with at least six layers superposed on the embryonic scale. The second type probably has superpositional growth while the third type most likely has areal growth. The dentinous crown has ascending vascular canals rising from the basal part which branch into finer dentine tubules in each growth zone (Fig. 37A). The pore canal system of these porosiform scales is characterized by up to six wide radial pore canals (Fig. 37B). Several wide pore canals extend from the radial pore canals towards the upper crown surface, where they are visible as large pore openings. No arcade canals are found in the North Greenland forms. The radial pore canals open on the lower crown surface, close to the neck (Fig. 36K, L). The smaller openings of the radial vascular canals open on the neck. The base has growth layers composed of cellular bone with round or spindle-shaped osteocyte cavities parallel to the subsurface (Fig. 37A). Both long and short tubules of Sharpey's fibres are developed perpendicular to the layers and the parallel fibres.

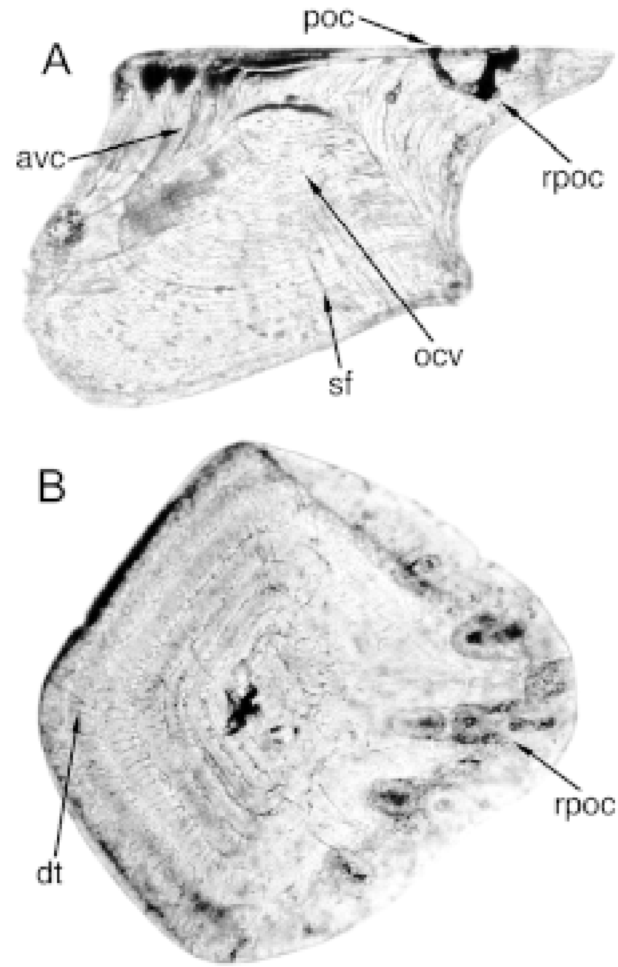


Fig. 37. *Poracanthodes* cf. *P. porosus*. Histology of the scale. **A**: Scale in vertical longitudinal section, MGUH VP 3594, × 122. **B**: Scale in horizontal crown section, MGUH VP 3595, × 127. Both specimens from GGU sample 82738, Halls Grav. **avc**: ascending vascular canals; **dt**: dentine tubules; **ocv**: osteocyte cavities; **poc**: pore canals; **rpoc**: radial pore canal; **sf**: tubules for Sharpey's fibres.

Scale dimensions. Length 0.2–1.0 mm; width 0.2–1.0 mm.

Remarks. Valiukevicius (1992) showed that the variability among scales from different parts of the body of *Poracanthodes menneri* from the Lower Devonian of Severnaya Zemlya is not notably large which, together with histological characters, suggests that scales referred here to *P.* cf. *P. porosus*, probably belong to several species. The three basic types of *P.* cf. *P. porosus* from the Chester Bjerg Formation mainly differ in the ornamentation in the anterior part of the crown and by growth type. The first and most common type shows regular ridges and furrows on the anterior part of the crown. This type is similar to *Poracanthodes subporosus* Valiukevicius 1998 by appearing to have superpositional growth, but differs notably by the anterior crown ornamentation. The second scale type (Fig. 34L, 36A) has the same regular anterior ridges and furrows, but differs from the first type by having concentric grooves without any clear radially oriented pores. These two types may together be sufficiently diagnostic to establish a new taxon, but since poracanthodid taxonomy is still controversial, it is preferable to keep their affinity open for future revision of the group. There are, however, a few scales that show closer morphology to *P. porosus* s.s. The last described morphotype (Fig. 34I, J) is similar to scales of specimens of *P. menneri* found in the Lower Devonian of Severnaya Zemlya (Valiukevicius 1992). Related isolated scales are also found in the eastern Baltic and the central Urals (Märss 1997).

Occurrence. *Poracanthodes* cf. *P. porosus*, Pridoli–Lochkovian, Hall Land, North Greenland; *Poracanthodes porosus*, Pridoli–Lochkovian, Estonia and Latvia; Lower Devonian, erratic boulders, Germany; Pridoli, Manbrook, Welsh Borderland, Great Britain.

Acanthodii indet.
Spine fragments
Figs 38–40

Figured material. MGUH VP 3598 from GGU sample 82736, MGUH VP 3599–3603 from GGU sample 82738, MGUH VP 3604, 3605 from GGU sample 298937.

Other material. Hundreds of small fragments, mostly poorly preserved, from GGU samples 82734, 82736, 82737, 82738, 298937, 298954, 298963 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Morphology. Despite the fragmental preservation of the fin spines from the Chester Bjerg Formation, the ornamentation of smooth longitudinal ribs suggests a common morphology. These fragments are derived from both the proximal and distal parts of the spines and show different stages of development (Figs 38, 39).

A well preserved proximal fragment of an assumed juvenile spine, triangular in cross section, exposes a quite short maybe broken base and a posteriorly wide open central pulp cavity (Fig. 38C, D). Five broad, evenly sized, spine ribs run parallel towards the broken terminations. The ribs have a characteristic smooth surface and are rounded in cross section. The distal part of this particular spine is lacking but the equivalent stage is represented by many other fragments, with five to seven slender ribs that converge towards the apex (Fig. 38E, G–I). Fragments from the distal part have a closed central cavity and a posterior shallow furrow or slit of variable width and size. They are often round or oval in cross section, but can also be triangular and more laterally flattened. It is difficult to tell if the several types of fragments that represent distal terminations are from old or young spines. Several larger fragments with seven ribs have similar cross sections and the same gross morphology, but they represent the middle part of older spines (Fig. 40).

Most fragments have the same general morphology with evenly sized ribs that in the most distal part converge and join to form wider ribs. Some fragments, however, from distal and other parts have ribs of variable size. The variation may involve smaller ridges occurring as striations on the larger anterior ribs (Fig. 38G) or larger lateral ridges (Fig. 38H, I). Some fragments are slightly curved.

One slender fragment has narrow noded ribs, which is a character common for spines of climatiids (Fig. 38A, B). Between each rib small pore holes are visible.

Histology. Due to the fragmental preservation it is difficult to define old or young spine fragments by only looking at the general morphology. Old scales have an immature proximal part and mature middle and distal parts. Most spines under discussion seem to be quite young and histological characters indicating maturity are mainly visible in distal fragments.

The superficial layer, forming the main part of the ribs, is the same in all fragment types (Fig. 40) and is composed of dentinous tissue with irregular branching tubules and rare joining lacunae. This dentine or perhaps mesodentine-like superficial layer gradually turns into a middle layer with concentrically laminated vascular canals. Usually this tissue, sometimes referred to as trabecular dentine (Denison 1979) but more correctly as osteodentine (Ørvig 1967), forms the main

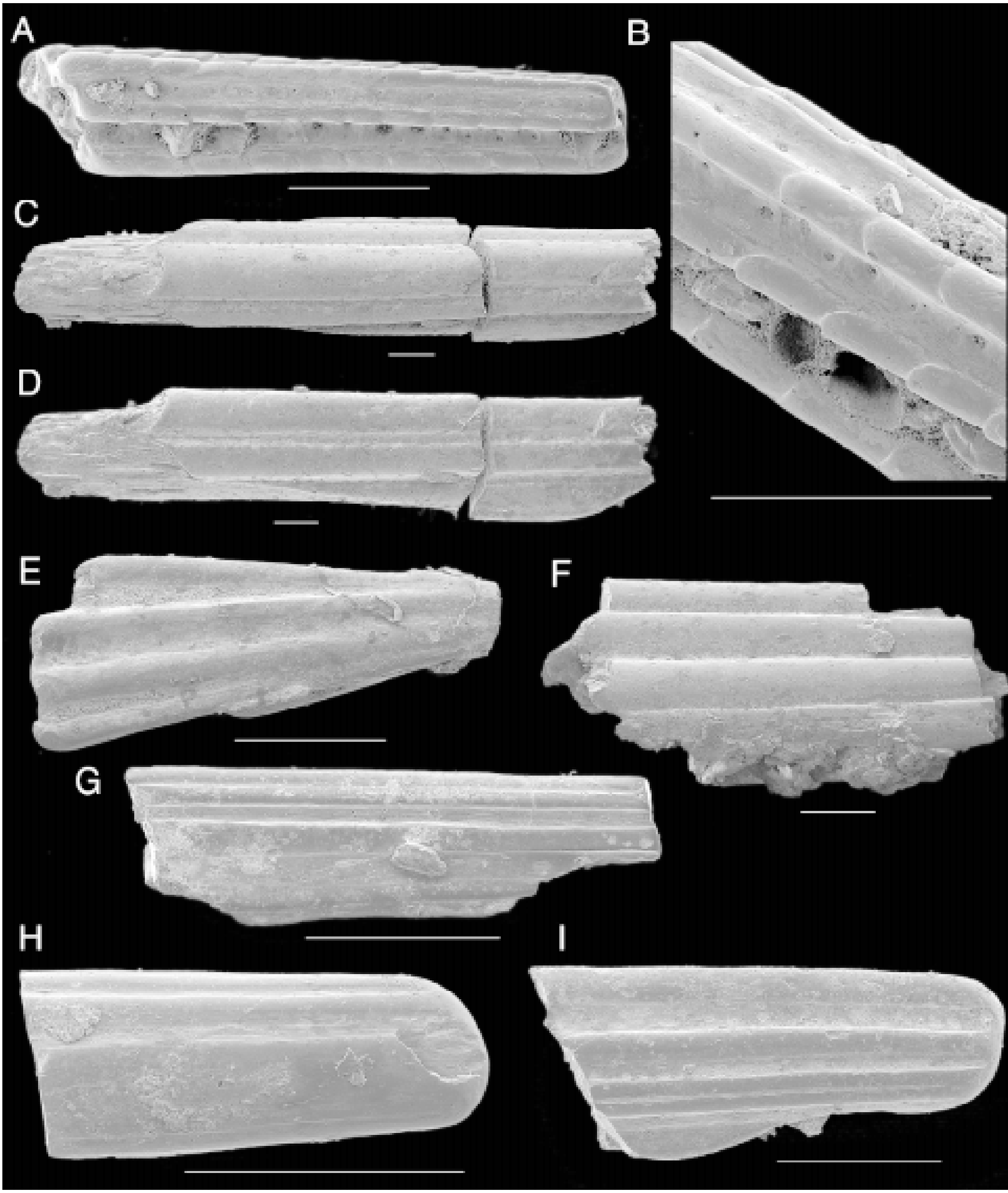


Fig. 38. Acanthodian fin spine fragments. SEM photomicrographs. Scale bars equal 0.5 mm.
A: Fragmental middle part in postero-lateral view, MGUH VP 3599. **B**: Fragmental middle part in postero-lateral view, close up of noded ribs, MGUH VP 3599. **C**: Fragmental proximal part in anterior view, MGUH VP 3604. **D**: Fragmental proximal part in lateral view, MGUH VP 3604. **E**: Fragmental middle part in lateral view, MGUH VP 3605. **F**: Fragmental distal part in lateral view, MGUH VP 3600. **G**: Fragmental distal part in lateral view, MGUH VP 3598. **H**: Fragmental distal part in lateral view, MGUH VP 3601. **I**: Fragmental middle part in lateral view, MGUH VP 3602.
MGUH VP 3598 from GGU sample 82736, Halls Grav; MGUH VP 3599–3602 from GGU sample 82738, Halls Grav; MGUH VP 3604, 3605 from GGU sample 298937, Halls Grav.

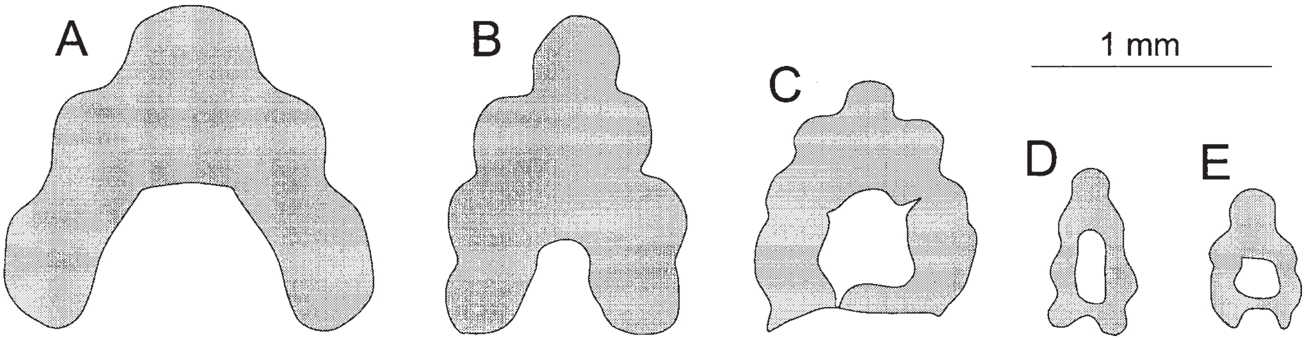


Fig. 39. Schematic illustration showing fin spine cross sections and the different stages of development. Scale bar equals 1 mm. **A**: Proximal part of immature spine. **B**: Proximal part of slightly matured spine. **C**: Middle part of immature spine. **D**: Distal part of immature spine. **E**: Distal part of slightly matured spine.

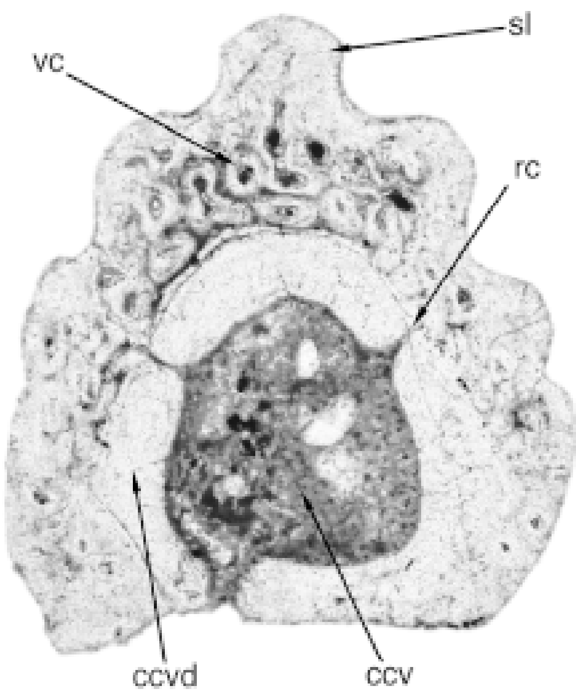


Fig. 40. Histology of acanthodian fin spine. Cross section, MGUH VP 3603 from GGU sample 82738, Halls Grav, × 82.
ccv: central cavity; **ccvd**: central cavity denteon; **rc**: radial canals; **sl**: superficial layer; **vc**: vascular canals.

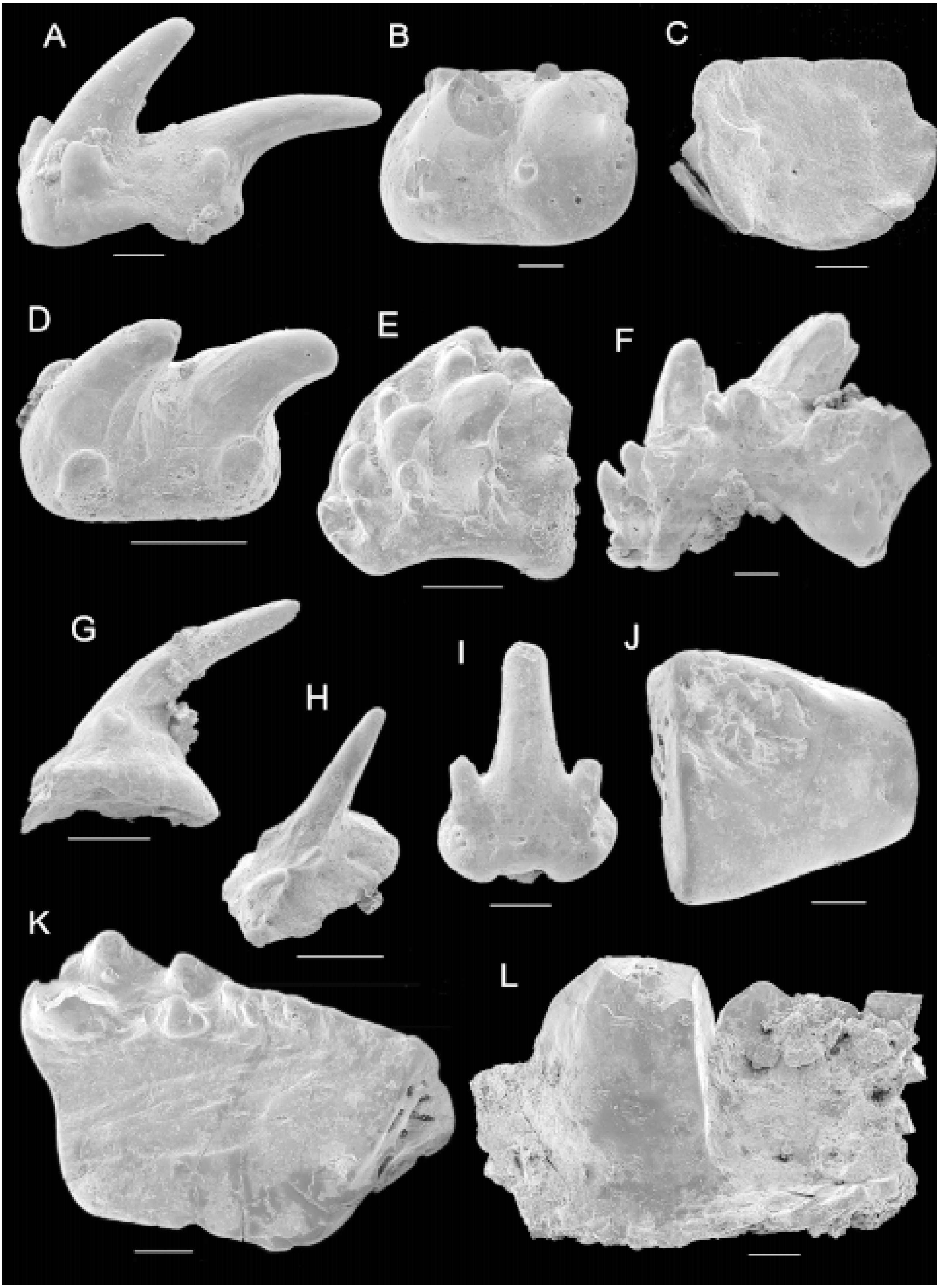
bulk of the immature spine and slightly less of the mature one. The vascular canals are predominantly longitudinal and parallel to longitudinal supporting fibres. Larger canals are concentrated in the anterior region of the spine and they may be enlarged or a number may unite to form a subcostal-like canal. It is also possible to detect differently oriented shorter canals that connect these larger canals.

Fragments from immature parts of a spine have a very thin basal layer of cellular bone lining the either open or closed central cavity. The central cavity, however, is filled by central cavity denteon at maturity. Radial canals extend from the central cavity towards the middle layer and may sometimes merge with the vascular canals.

Remarks. Despite the uniform type of morphology the spines from Chester Bjerg Formation show quite pronounced differences due to the size and maturity of the spines. There may be true taxonomical differences or reflect variation between spines from different positions on the body.

The general morphology is similar to spines of Ischnacanthidae, Acanthidae and smooth-ribbed spines of uncertain origin often placed within *Onchus* (Denison 1979). However, many different types with a wide

Fig. 41. Acanthodian dental elements. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Tooth whorl in lateral view, MGUH VP 3611. **B**: Tooth whorl in oblique upper view, MGUH VP 3606. **C**: Tooth whorl in visceral view, MGUH VP 3615. **D**: Tooth whorl in oblique upper view, MGUH VP 3607. **E**: Tooth whorl in oblique upper view, MGUH VP 3608. **F**: Tooth whorl in lateral view, MGUH VP 3616. **G**: Single tooth element in lateral view, MGUH VP 3609. **H**: Single tooth element in lateral view, MGUH VP 3610. **I**: Single tooth element in anterior view, MGUH VP 3612. **J**: Fragment of posterior part of a jaw bone in upper view, MGUH VP 3613. **K**: Fragment of middle part of a jaw bone in postero-lateral view, MGUH VP 3617. **L**: Fragment of anterior part of a jaw bone in inner lateral view, MGUH VP 3614.
MGUH VP 3606–3610 from GGU sample 82736, Halls Grav; MGUH VP 3611–3614 from GGU sample 82738, Halls Grav; MGUH VP 3615, 3616 from GGU sample 298937, Halls Grav; MGUH VP 3617 from GGU sample 319264, Monument.


A
B
C
D
E
F
G
H
I
J
K
L

time range have been referred to *Onchus*, suggesting an unsatisfactory taxonomic situation. Several of these species probably belong to *Gomphonchus*. According to Gross (1971) *Gomphonchus* is completely built up by dentine and mainly characterized by unornamented smooth ridges. The material from Greenland should therefore be of *Gomphonchus* type, but Gross (1971) included *Poracanthodes* within *Gomphonchus*, an idea now changed by the find of articulated *Poracanthodes menneri* (Valiukevicius 1992). *Gomphonchus*, as defined by Gross (1971), is known to have spines with an inserted base, while *Poracanthodes* does not (Valiukevicius 1992). The presence of *Poracanthodes* and *Gomphonchus* scales in the North Greenland material leaves the position of the spines open to discussion.

The rarity of the single spine fragment with ornamented ridges may suggest a close relation with *Nostolepis* or Climatiida indet. scales found in the same sample. Although it is unusual for Ischnacanthidae to have noded or tuberculate fin-spine ridges (Denison 1979), Gross (1971) figured such fragments referred to *Gomphonchus* from erratic boulders in Germany.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Dental elements
Figs 41, 42

1976 Tooth whorls of '*Gomphodus*' ('*Plectrodus*') type – Bendix-Almgreen, fig. 443L, M.
1976 *Nostolepis* sp. fragments of dentigerous jawbones – Bendix-Almgreen, fig. 443O, P.

Figured material. MGUH VP 3606–3610 from GGU sample 82736, MGUH VP 3611–3614, 3618 from GGU sample 82738, MGUH VP 3615, 3616 from GGU sample 298937, MGUH VP 3617 from GGU sample 319264.

Other material. Several hundred tooth whorls, single teeth and jaw bone fragments from GGU samples 82734, 82736, 82737, 82738, 298937, 298953, 298954, 298960, 298963 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Tooth whorl description. Tooth whorls of the main type are bilaterally symmetrical, with a series of teeth on a curved base. They show little curvature and have only two three-cusped tooth rows on each whorl (Fig. 41A–D). They range greatly in total size, 0.5–1.5 mm in length, but the main proportions are preserved even in the smallest specimens. The tooth rows are usually equal in size, but the anterior tooth row may be slightly smaller than the other. Each row has a long slender main central cusp and a pair of smaller side cusps. The main cusp curves posteriorly and is about five times higher than the shorter and more robust side cusps. Small weakly developed ridges or striae run proximally along the main cusp. In some specimens one pair of longer lateral ridges is developed, running almost along the whole length of the main cusp. All cusps are round or oval in cross section, with a wider proximal part. The base of the whorl is round, elongated or square and usually deeply concave in basal view (Fig. 41C). Large canal openings are visible on the upper as well as the lower surface of the base. On the upper surface they are often visible as a ring along the margins of the basal part of the whorls. Due to the poor preservation and delicate structures, many specimens are found with broken cusps, exposing the central pulp canal. The colour is usually pale brown but may vary from white to dark brown.

A few specimens differ mainly by having three or four tooth rows and several variably sized side cusps. They are often irregularly oriented and the whole whorl tends to be less symmetrical (Fig. 41F). The side cusps point in different directions and decrease in size laterally. The main cusp is short and robust with small, pronounced, longitudinal ridges. The difference in height between the main cusp and the largest side cusps is less than four times. The more curved base is only anteriorly to posteriorly concave and almost convex transversely.

A third symmetric type, represented by one broken specimen, is found with at least five tooth rows (Fig. 41E). This type is much lower than the previous ones and the total number of tooth rows is unknown due to posterior breakage of the only well preserved specimen. Each row has a robust main central cusp and two pairs of side cusps, decreasing in size laterally. The size of the cusps in each row also decreases anteriorly and the cusps at front are very tiny. The base is wide, flat and less curved than the second type, with few visible canal openings.

In the large main tooth cusp in the first and most common tooth whorl, dentine surrounds a large central pulp cavity (Fig. 42), with branching dentine tubules radiating towards the outer surface which may

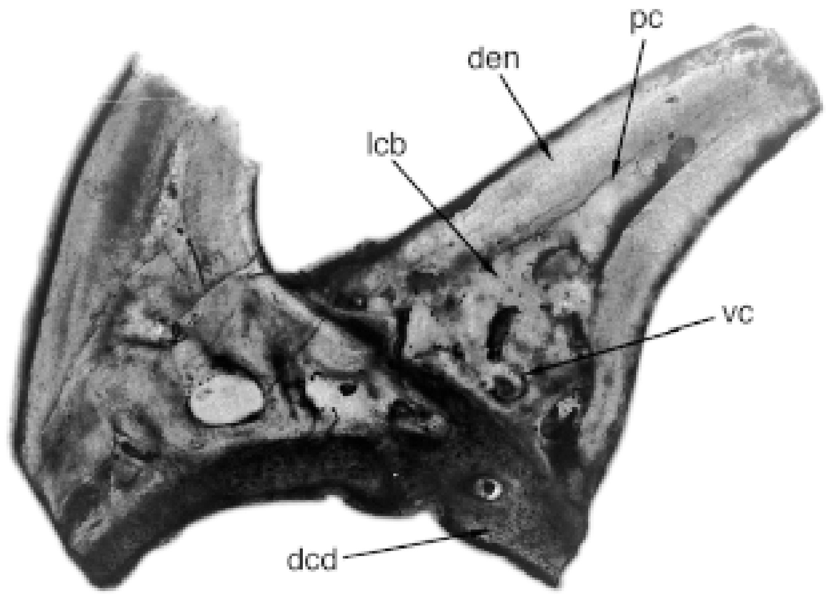


Fig. 42. Histology of acanthodian tooth whorl. Vertical longitudinal section, MGUH VP 3618 from GGU sample 82738, Halls Grav, × 91.
dcd: dense cellular bone; **den**: dentine; **lcb**: light cellular bone; **pc**: pulp canal; **vc**: vascular canal.

show a thin shiny enameloid layer. Proximally the pulp canal branches into a net of vascular canals surrounded by dentine and light cellular bone in the main body of the tooth whorl. The thin layer of basal tissue is composed of more dense cellular bone, penetrated by a few short canals.

Single tooth description. The single tooth type resembles a modified tooth whorl having only one row of cusps (Fig. 41G–I). The main single central cusp is slender and very long. It is smooth, straight or curved and has a weak striation on the proximal part. On each side and around the many times longer central cusp two, or rarely up to four smaller cusps are developed. These side cusps are not necessarily symmetrically oriented around the main cusp. A central pulp cavity is exposed when the apex of the cusps is broken (Fig. 41B). The sloping upper side of the base is round and thin, exposing large canal openings on the dorsal surface. In basal view, the base has canal openings on the deeply concave surface. Histologically, these teeth have the same basic structures seen in tooth whorls.

Jaw bone description. Jaw bones are very poorly preserved and it is difficult to find a consistent morphology among all the small fragments. One of the best preserved fragments is about 1.5 mm long and represents a fragment of the middle part of a jaw (Fig. 41K). Teeth are located on the outer half of the main jaw bone. Half the length of the lateral margin has one row of small tightly packed mono-cusped teeth, while the anterior half has two rows of two larger, separated, three-cusped teeth. Each of these consists of one larger main cusp and two smaller side cusps. Each cusp is heavily worn and more rounded than subtriangular. The inner teeth are slightly larger than the marginal ones. The jaw bone has a vertical lateral outer side and an inner side that slopes gently antero-laterally in the posterior part. In the inner anterior part the slope is initially more vertical, forming an almost L-shaped cross-section. In basal view, the jaw-bone fragment is almost square with a concave basal surface. On the broken anterior and posterior ends, several large pores and cavities after the vascular system are visible. Both marginal rows of teeth are in line with the vertical outer lateral side of the jaw bone.

Another fragment shows the anterior broken part of the jaw with a large tooth cusp and a posterior row of smaller side cusps (Fig. 41L). The fragment is 1.8 mm long. The slightly broken main cusp is 0.5 mm high, about 75% of the total jaw height, and has a subtriangular parabasal section with straight lateral and posterior sides, forming an almost perpendicular postero-lateral corner. The antero-lateral side is more rounded between the other two sharp corners. In width, the main cusp forms almost the whole part of the supporting jaw bone, which is triangular in cross section. Three laterally flattened side cusps run posteriorly along the outer lateral edge and vertical side. They have an elliptical parabasal section and are about 1/3 of the main cusp height.

A fragment from the posterior part of a jaw (Fig. 41J) is broken at both ends and is about 0.9 mm long and 1.0 mm wide. In upper view, it has a trapezoid-like shape and is narrower posteriorly. It is smooth and convex on the upper surface, with a flattened anterior area bearing small irregular rounded denticles. The denticles are very low and seem to be heavily worn. The whole fragment, however, is quite low and flat or slightly concave in basal view. Spaces after the cancellous vascular system are visible at the broken ends.

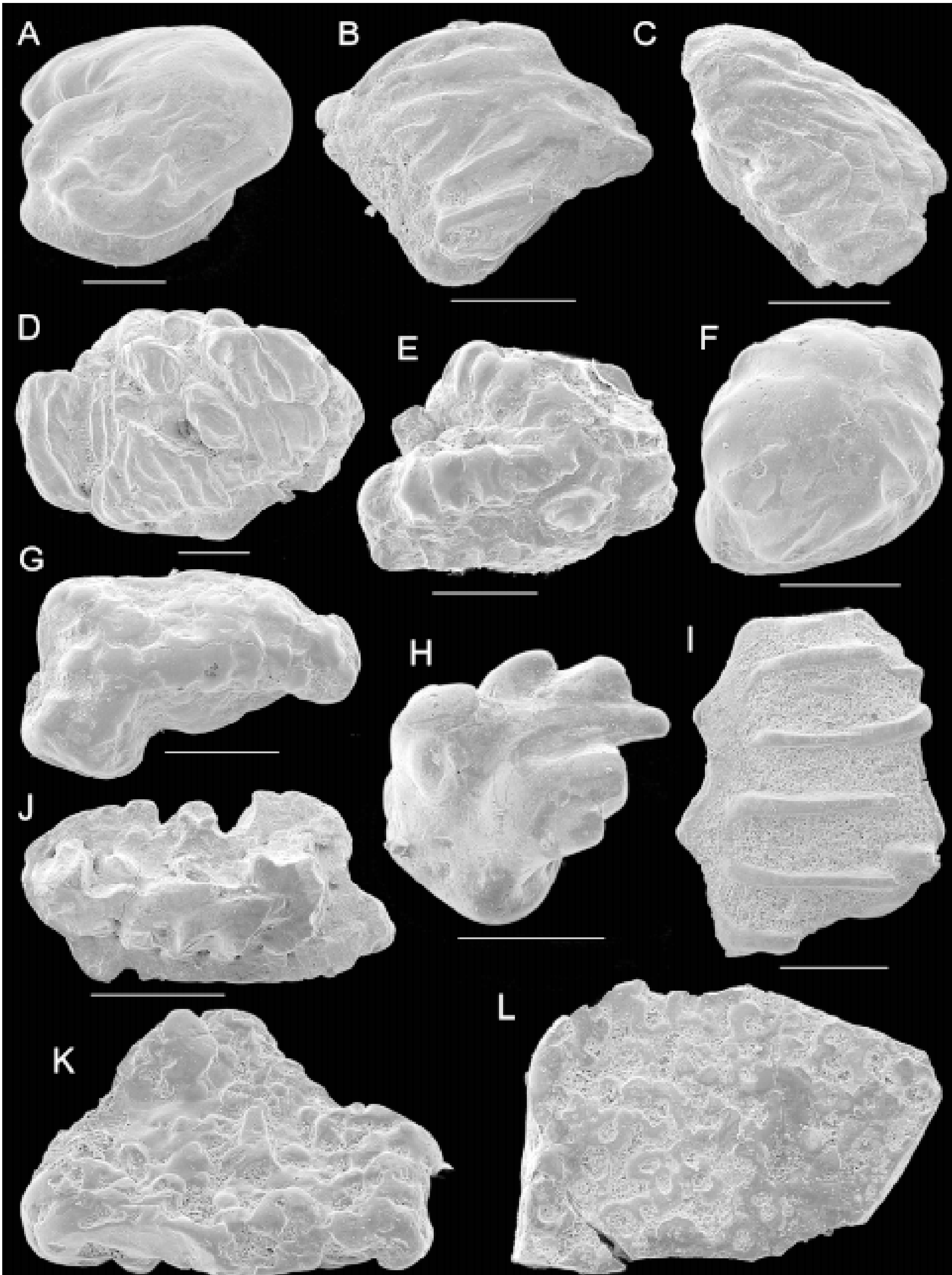
Remarks. Tooth whorls of the most common type, with only two three-cusped tooth rows (Fig. 41A–D), were referred to as *Gomphodus* by Bendix-Almgreen (1976), and are similar to the symmetric multiple tooth whorls of *Gomphonchus* (Gross 1957). The enclosed basal concavity suggests that the presence of only two tooth rows is original and not a result of breakage; this is also the dominant preservational state. Although reported by Bendix-Almgreen (1976), this form has apparently not been recorded by earlier workers. Gross (1967b) suggested that less curved whorls in *Gomphonchus* were symphysial, while heavily curved whorls with many rows where located somewhere in the mouth cavity. The evidence for this is not unambiguous and, as pointed out by Ørvig (1973), there are no clear ideas about the relation between tooth whorls and jaw bones in early ischnacanthids or climatiids. Whorls can be symphysial, located in the mouth cavity or even in the branchial region (Gross 1971; Ørvig 1973). Faunal composition and the proportion of acanthodian scales suggest that most dental elements described in this paper are ischnacanthids represented by *Gomphonchus* and poracanthodian scales. The high number of whorls or 'semi' whorls of the first type in comparison with the low number of preserved jaw bones, suggests that tooth whorls are from the mouth cavity or possibly even from the branchial region. No whorls of the type described as *Nostolepis* by Gross (1971) have been found in the material from Hall Land.

The two other types of tooth whorl, rare and with a higher number of rows, may be similarly interpreted. They are more similar to the whorls illustrated by Gross (1957) as *Gomphodus*. Burrow (1995) argued that an asymmetric tooth whorl may be parasymphysial, but not ankylosed to the jaw bone, like the tooth whorls of, for example, dipnoans. This explanation can be invoked for the rare multiple tooth whorls under discussion, but the differences between the types of tooth whorl may reflect not only different position, but also different taxonomical affinity.

The single teeth fragments from Greenland are more or less of one type and are closely related in shape and histology to the whorls with two teeth rows, indicating a common origin.

The anterior dental jaw bone fragment (Fig. 41L) is similar to the anterior part of jaw bones earlier attributed to *Nostolepis* (Gross 1957, 1971). The subtriangular parabasal section of the main cusp was originally a character differentiating it from *Gomphonchus* Gross (1957, 1971). He also based this on the idea that very few higher taxa were present in his material from the Beyrichienkalk and those present thereby fell conveniently into either *Gomphonchus* or *Nostolepis*. However, as pointed out by Denison (1976, 1979), the histology does not support this idea, since the jaw-bone attached teeth show no indication of mesodentine, which is characteristic of scales, fin spines and tooth whorls of *Nostolepis*. Gross (1971) regarded *Poracanthodes* to be specialized scales of *Gomphonchus*, but the find of the articulated *Poracanthodes menneri* described by Valiukevicius (1992) suggests that the diversity was higher than Gross (1971) originally believed. *Poracanthodes menneri* (Valiukevicius 1992) has a subtriangular parabasal section in the larger main cusps, suggesting that poracanthodiformes could contain *Nostolepis*-type jaw bones as defined by Gross (1971). This is supported by the occurrence of poracanthodiform scales and *Nostolepis*-type jaw bone fragments from

Fig. 43. Incertae sedis. SEM photomicrographs. Scale bars equal 0.2 mm.
A–**C**, **E**–**G**. Acanthodian scales and tesserae. **A**: Scale in oblique crown view, MGUH VP 3619. **B**: Scale in oblique crown view, MGUH VP 3623. **C**: Scale in oblique crown view, MGUH VP 3628. **E**: Tesserae in crown view, MGUH VP 3620. **F**: Scale in oblique crown view, MGUH VP 3624. **G**: Tesserae in oblique crown view, MGUH VP 3625.
D, **H**, **J**. ?Chondrichthyans. **D**: Unit of odontodes in oblique crown view, MGUH VP 3629. **H**: Unit of odontodes in oblique crown view, MGUH VP 3621. **J**: Unit of odontodes in crown view, MGUH VP 3630.
I: Pisces indet. Plate in upper view, MGUH VP 3626.
K, **L**. ?Actinopterygian. **K**: Plate fragment in upper view, MGUH VP 3627. **L**: Plate fragment in upper view, MGUH VP 3622.
MGUH VP 3619 from GGU sample 82736, Halls Grav; MGUH VP 3620–3627 from GGU sample 82738, Halls Grav; MGUH VP 3628–3630 from GGU sample 319264, Monument.


A
B
C
D
E
F
G
H
I
J
K
L

Late Silurian beds of Cornwallis Island, Arctic Canada (Burrow 1995; Burrow *et al*. 1997). Assignment to *Nostolepis* cannot be completely excluded since dental jaw bone is known in *Nostolepis*-like articulated acanthodians (J. Valiukevicius, personal communication 1998). Ørvig (1973) suggested, and Valiukevicius (1992), demonstrated that the upper jaw of ischnachantids also has teeth, indicating that the anterior fragment described here may be from the upper or lower jaw.

The posterior jaw fragment, whether it is from the upper or lower jaw, is similar to Silurian and lower Devonian ischnacanthids described by Gross (1971) and Burrow (1995), but the ornamentation is much more worn.

The bone fragment from a probably middle part of a jaw may belong to the same jaw type as the anterior and the posterior fragments, but the teeth are quite different. This difference may be taxonomic, but can also reflect a positional difference.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Incertae sedis

Fig. 43

Figured material. MGUH VP 3619 from GGU sample 82736, MGUH VP 3620–3627 from GGU sample 82738, MGUH VP 3628–3630 from GGU sample 319264.

Other material. Hundreds of unidentified fragments from all GGU samples processed, see Fig. 4.

Remarks. Some of the more distinctive of the many poorly preserved remains found in the residues of the Chester Bjerg Formation are mentioned here.

Several of the fragments may represent scales from the head region of acanthodians (Fig. 43A–C, F). They all have irregular ornamentation on the crown which merges into the neck anteriorly. The ornamentation may vary but the scales have the same general morphology. Some rare remains with irregular ornamentation may also be specialized scales or tesserae of acanthodians (Fig. 43E, G).

Polyodontodia-like remains (*sensu* Karatajute-Talimaa 1992) usually occur as single specimens and cannot with certainty be assigned to the true chondrichthyans (Fig. 43D, H, J). The odontodes are different in all these remains and can be rounded or three-cusped, but they all possess the characteristic neck canals.

One fragmental plate or scale has several smooth, high and narrow, elongate tubercles on a low compact basal layer (Fig. 43I). Several fragments or plates with compact tissue have irregularly shaped tubercles of similar tissue (Fig. 43K, L). These tubercles are heavily worn and show no distinctive features. They show some similarity with indeterminate fragments from Gotland, loosely assigned to *Andreolepis hedei* (Fredholm 1988).

Acknowledgements

John S. Peel is gratefully acknowledged for providing support and working facilities throughout this research at the Department of Earth Sciences, Historical Geology and Palaeontology, Uppsala University. Tiiu Märss, Tallinn, is sincerely thanked for her introduction, guidance and encouragement in the subject. Studied material was made available by the Geological Survey of Denmark and Greenland via J.S. Peel. In addition to a university research scholarship, financial support was given by the Royal Swedish Academy of Sciences and Otterborgs donationsfond. My thanks are also due to: J.O.R. Ebbestad and G. Budd for valuable discussions and advice concerning linguistic, technical and scientific problems; V. Karatajute-Talimaa, J. Valiukevicius and S.E. Bendix-Almgreen for showing material and sharing information; P.R. Dawes for information concerning the stratigraphy of Hall Land and for providing the photograph in Figure 1; and B. Jansson for laboratory preparation.

This monograph is a contribution to IGCP 328: Palaeozoic microvertebrates, and IGCP 406: Circum-Arctic Palaeozoic vertebrates.

References

Agassiz, J.L.R. 1839: Fishes of the Upper Ludlow rock. In: Murchison, R.I. (ed.): The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon Pembroke, Monmouth, Gloucester, Worcester and Stafford: with descriptions of the coal-field and overlying formations **2**, 605–607. London: John Murray.

Agassiz, J.L.R. 1845: Monographie des poissons fossiles du Vieux Grès Rouge ou Système Dévonien (Old Red Sandstone) des Iles Britanniques et de Russie. Edinburgh New Philosophical Journal **41**(17–49), 171 pp.

Armstrong, H.A. & Dorning, K.J. 1984: Silurian palynomorphs from the Chester Bjerg Formation, Hall Land, western North Greenland. Rapport Grønlands Geologiske Undersøgelse **121**, 97–103.

Bendix-Almgreen, S.E. 1976: Palaeovertebrate faunas of Greenland. In: Escher, A. & Watt, W.S. (eds): Geology of Greenland, 536–573. Copenhagen: Geological Survey of Greenland.

Bendix-Almgreen, S.E. 1986: Silurian ostracoderms from Washington Land (North Greenland), with comments on cyathaspid structure, systematics and phyletic position. In: J.S. Peel (ed.): North Greenland Lower Palaeozoic palaeontology and stratigraphy: short contributions. Rapport Grønlands Geologiske Undersøgelse **132**, 89–123.

Bendix-Almgreen, S.E. & Peel, J.S. 1974: Early Devonian vertebrates from Hall Land, North Greenland. Rapport Grønlands Geologiske Undersøgelse **65**, 13–16.

Berg, L.S. 1940: Classification of fishes, both recent and fossil. Travaux de l'Institut de Zoologie de l'Académie des Sciences de l'URSS **5**, 517 pp.

Berry, W.B.N., Boucot, A.J., Dawes, P.R. & Peel, J.S. 1974: Late Silurian and Early Devonian graptolites from North Greenland. Rapport Grønlands Geologiske Undersøgelse **65**, 11–13.

Blieck, A. 1981: Le genre *Protopteraspis* Leriche (Vertébrés, Héterostracés) du Dévonien inférieur nord-atlantique. Palaeontographica, Abteilung A **173**(5–6), 141–159.

Blieck, A. 1982: Les Hétérostracés (vertébratés agnathes) de l'horizon Vogti (Groupe de Red Bay, Dévonien inférieur du Spitsberg). Cahiers de paléontologie, 51 pp. Paris: Centre national de la recherche scientifique.

Blieck, A. & Janvier, P. 1991: Silurian vertebrates. In: Bassett, M.G., Lane, P.D. & Edwards, D. (eds): The Murchison Symposium: proceedings of an international conference on The Silurian System. Special Papers in Palaeontology **44**, 345–389.

Blieck, A., Mark-Kurik, E. & Märss, T. 1988: Biostratigraphical correlations between Siluro-Devonian invertebrate-dominated and vertebrate-dominated sequences: the East Baltic example. In: McMillan, N.J., Embry, A.F. & Glass, D.J. (eds): Devonian of the World. Canadian Society of Petroleum Geologists Memoir **14**(3), 579–587.

Blieck, A., Turner, S. & Young, G.C. in press: Devonian vertebrate biochronology and global marine/non-marine correlation. In: Blieck, A. & Turner, S. (eds): IGCP 328 final scientific report. Courier Forschungsinstitut Senckenberg.

Blom, H. in press: Silurian vertebrates from North Greenland. In: Blieck, A. & Turner, S. (eds): IGCP 328 final scientific report. Courier Forschungsinstitut Senckenberg.

Brotzen, F. 1933: *Weigeltaspis* nov. gen. und die Phylogenie der panzertragenden Heterostraci. Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B **12**, 648–656.

Brotzen, F. 1934: Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fischresten. Zeitschrift für Geschiebeforschung **10**(1), 66 pp.

Burrow, C.J. 1995: Acanthodian dental elements from the Trundle beds (Lower Devonian) of New South Wales. Records of the Western Australian Museum **17**, 331–341.

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. & Simpson, A.J. 1995: A new ischnacanthid acanthodian from the Late Silurian (Ludlow, *ploeckensis* Zone) Jack Formation, north Queensland. Memoirs of the Queensland Museum **38**(2) 383–395.

Burrow, C.J., Vergoossen, J.M.J. & Turner, S. 1997: Microvertebrate assemblages from the Late Silurian of Cornwallis Island, Arctic Canada. In: Ivanov, I., Wilson, M.H.V. & Zhuravlev, A. (eds): Palaeozoic strata and fossils of the Eurasian Arctic. Ichthyolith Issues Special Publication **3**, 6–7.

Caldwell, M.C. & Wilson, M.V.H. 1995: Comparison of the body form and squamation of 'fork-tailed' agnathans with that of conventional thelodonts. In: Lelièvre, H. *et al.* (eds): Premiers vertébrés et vertébrés inférieurs. Geobios, Mémoire Spécial **19**, 23–30.

Dawes, P.R. 1976: Precambrian to Tertiary of northern Greenland. In: Escher, A. & Watt, W.S. (eds): Geology of Greenland, 248–303. Copenhagen: Geological Survey of Greenland.

Dawes, P.R. 1984: Operation Grant Land 1965–1966; a geological exploration programme in Ellesmere Island and North Greenland. Rapport Grønlands Geologiske Undersøgelse **121**, 5–17.

Dawes, P.R. 1987: Topographical and geological maps of Hall Land, North Greenland. Description of a computer-supported photogrammetrical research programme for production of new maps, and the Lower Palaeozoic and surficial geology. Bulletin Grønlands Geologiske Undersøgelse **155**, 88 pp. + 4 maps.

Dawes, P.R. & Peel, J.S. 1984: Biostratigraphic reconnaissance in the Lower Palaeozoic of western North Greenland. Rapport Grønlands Geologiske Undersøgelse **121**, 19–51.

Denison, R.H. 1964: The Cyathaspidae. A family of Silurian and Devonian jawless vertebrates. Fieldiana, Geology **13**(5), 311–473.

Denison, R.H. 1976: Note on the dentigerous jaw bones of Acanthodii. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte **1976**(7), 395–399.

Denison, R.H. 1979: Acanthodii. In: Schultze H.-P. (ed.) Handbook of Paleoichthyology **5**, 62 pp. Stuttgart & New York: Gustav Fischer Verlag.

Dineley, D.L. & Loeffler, E.J. 1976: Ostracoderm faunas of the Delorme and associated Siluro-Devonian Formations, North West Territories, Canada. Special Papers in Palaeontology **18**, 214 pp.

Fredholm, D. 1988: Vertebrates in the Ludlovian Hemse Beds of Gotland, Sweden. Geologiska Föreningens i Stockholm Förhandlingar **110**(2), 157–179.

Fredholm, D. 1990: Agnathan vertebrates in the Lower Silurian of Gotland, Sweden. Geologiska Föreningens i Stockholm Förhandlingar **112**(1), 61–84.

Goujet, D. 1976: Les poissons. In: Les schistes et calcaires eodévoniens de Saint-Céneré (Massif Armoricain, France). Mémoires de la Société Géologique et Minéralogique de Bretagne **19**, 313–323.

Gross, W. 1938: Der histologische Aufbau der Anaspiden-Schuppen. Norsk Geologisk Tidskrift **17**(3), 191–195.

Gross, W. 1947: Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. Palaeontographica, Abteilung A **96**, 91–158.

Gross, W. 1957: Mundzähne und Hautzähne der Acanthodier und Arthrodiren. Palaeontographica, Abteilung A **109**(1–2), 1–40.

Gross, W. 1958: Anaspiden-Schuppen aus dem Ludlow des Ostseegebietes. Paläontologische Zeitschrift **32**(1–2), 24–37.

Gross, W. 1961: Aufbau des Panzers obersilurischer Heterostraci und Osteostraci Norddeutschlands (Geschiebe) und Oesels. Acta Zoologica **42**(1–2), 73–150.

Gross, W. 1967a: Über Thelodontier-Schuppen. Palaeontographica, Abteilung A **127**(1–2), 1–67.

Gross, W. 1967b: Über das Gebiss der Acanthodier und Placodermen. In: Patterson, C. & Greenwood, P.H. (eds): Fossil vertebrates. Journal of the Linnean Society of London **47**(311), 121–130.

Gross, W. 1968: Die Agnathen-Fauna der Silurischen Halla-Schichten Gotlands. Geologiska Föreningens i Stockholm Förhandlingar **90**, 369–400.

Gross, W. 1971: Downtonische und dittonische Acanthodier-Reste des Ostseegebietes. Palaeontographica, Abteilung A **136**(1–6), 1–82.

Håkansson, E., Heinberg, C. & Stemmerik, L. 1991: Mesozoic and Cenozoic history of the Wandel Sea Basin area, North Greenland. In: Peel, J.S. & Sønderholm, M. (eds): Sedimentary basins of North Greenland. Bulletin Grønlands Geologiske Undersøgelse **160**, 153–164.

Higgins, A.K., Ineson, J.R., Peel, J.S., Surlyk, F. & Sønderholm, M. 1991a: Lower Palaeozoic Franklinian Basin of North Greenland. In: Peel, J.S. & Sønderholm, M. (eds): Sedimentary basins of North Greenland. Bulletin Grønlands Geologiske Undersøgelse **160**, 71–139.

Higgins, A.K., Ineson, J.R., Peel, J.S., Surlyk, F., & Sønderholm, M. 1991b: Cambrian to Silurian basin development and sedimentation, North Greenland. In: Trettin, H.P. (ed.): Geology of the Innuitian Orogen and Arctic Platform of Canada and Greenland. Geology of Canada **3**, 109–161. Ottawa: Geological Survey of Canada (also The geology of North America **E**, Geological Society of America).

Hurst, J.M. & Surlyk, F. 1982: Stratigraphy of the Silurian turbidite sequence of North Greenland. Bulletin Grønlands Geologiske Undersøgelse **145**, 121 pp.

Ineson, J.R. & Peel, J.S. 1997: Cambrian shelf stratigraphy of North Greenland. Geology of Greenland Survey Bulletin **173**, 120 pp.

Janvier, P. 1981: The phylogeny of the Craniata, with particular reference to the significance of fossil 'agnathans'. Journal of Vertebrate Paleontology **1**(2), 121–159.

Janvier, P. 1996a: Early vertebrates. Oxford monographs on geology and geophysics **33**, 393 pp. Oxford: Clarendon Press.

Janvier, P. 1996b: The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies. Palaeontology **39**(2), 259–287.

Jeppsson, L., Fredholm, D. & Mattiasson, B. 1985: Acetic acid and phosphatic fossils – a warning. Journal of Paleontology **59**(4), 952–956.

Karatajute-Talimaa, V. 1968: New Thelodonti, Heterostraci and Arthrodires from the Chortkov horizon of Podolia. In: Essays on phylogeny and systematics of ancient fish and agnathans, 33–42. Moscow (in Russian).

Karatajute-Talimaa, V. 1978: Silurian and Devonian thelodonts of the USSR and Spitsbergen. 334 pp. Vilnius: Mokslas Publishers (in Russian).

Karatajute-Talimaa, V. 1985: Thelodonts of the Podyomnaya Formation, Lower Devonian, Gedinnian, of Severnaya Zemlya and their correlative importance. Scientific Transactions of Institutes of Higher Education of Lithuanian SSR. Geology **6**, 50–60 (in Russian with English summary).

Karatajute-Talimaa, V. 1990: Vertebrates. In: Kulikov, N.P. & Dubatolov, V.N. (eds): Silurian and Devonian of south-eastern West Siberian Plate, 59–63. Moscow: Nauka (in Russian).

Karatajute-Talimaa, V. 1992: The early stages of dermal skeleton formation in chondrichthyans. In: Mark-Kurik, E. (ed.): Fossil fishes as living animals. Academia **1**, 223–231. Tallinn: Academy of Sciences of Estonia.

Karatajute-Talimaa, V. 1997: Taxonomy of loganiid thelodonts. Modern Geology **21**, 1–15.

Karatajute-Talimaa, V.N. & Märss, T. 1997: Thelodonts from the Silurian and Lower Devonian of the Severnaya Zemlya Archipelago, Russian Arctic. In: Ivanov, I., Wilson, M.H.V. & Zhuravlev, A. (eds): Palaeozoic strata and fossils of the Eurasian Arctic. Ichthyolith Issues Special Publication **3**, 13–14.

Karatajute-Talimaa, V., Mark-Kurik, E., Kurss, V., Matuchin, R. & Menner, V. 1986: Facies relations and embedding types of vertebrates in Upper Silurian and Lower Devonian of Severnaya Zemlya. In: Kaljo, D.L. & Klaamann, E.R. (eds): Theory and practice of ecostratigraphy, 251–258. Tallin: Valgus (in Russian).

Kiær, J. 1924: The Downtonian fauna of Norway. 1. Anaspida. Videnskapsselskapets Skrifter I Matematisk-Naturvidenskaplige Klasse **6**, 139 pp.

Kiær, J. 1930: *Ctenaspis*, a new genus of cyathaspidian fishes. Skrifter om Svalbard og Ishavet **33**, 7 pp.

Kiær, J. (Heintz, A. ed.) 1932: New coelolepids from the Upper Silurian on Oesel (Esthonia). Eesti Loodusteaduse Archiiv **1**, 10(3), 8 pp. (also Publications of the Geological Institution of the University of Tartu **27**, 1–8).

Lane, P.D., Dawes, P.R. & Peel, J.S. 1980: A new Silurian *Hemiarges* (Trilobita) from North Greenland and the question of the Polaris Harbour Formation. Rapport Grønlands Geologiske Undersøgelse **101**, 45–53.

Larsen, P.-H. & Escher, J.C. 1985: The Silurian turbidite sequence of the Peary Land Group between Newman Bugt and Victoria Fjord, western North Greenland. Rapport Grønlands Geologiske Undersøgelse **126**, 46–67.

Larsen, P.-H. & Escher, J.C. 1987: Additions to the lithostratigraphy of the Peary Land Group (Silurian) in western and central North Greenland. Rapport Grønlands Geologiske Undersøgelse **133**, 65–80.

Leriche, M. 1924: Les *Pteraspis* du Dévonien de la Belgique. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie **33**, 143–159.

Long, J.A. (ed.) 1993: Palaeozoic vertebrate biostratigraphy and biogeography, 369 pp. London: Belhaven Press.

Märss, T. 1982: *Thelodus admirabilis* n. sp. (Agnatha) from the Upper Silurian of the East Baltic. Eesti NSV Teaduste Akadeemia Toimetised Geoloogia **31**(3), 112–116.

Märss, T. 1986a: Silurian vertebrates of Estonia and west Latvia. Fossilia Baltica **1**, 104 pp. Tallinn: Valgus (in Russian with English summary).

Märss, T. 1986b: Squamation of the thelodont agnathan *Phlebolepis*. Journal of Vertebrate Paleontology **6**(1), 1–11.

Märss, T. 1996: *Loganellia* (Thelodonti, Agnatha) from the Jaagarahu Stage, Wenlock, Estonia. Proceedings of the Estonian Academy of Sciences Geology **45**(4), 189–202.

Märss, T. 1997: Vertebrates of the Pridoli and Silurian–Devonian boundary beds in Europe. Modern Geology **21**, 17–41.

Märss, T. & Ritchie, A. 1998: Articulated thelodonts (Agnatha) of Scotland. Transactions of the Royal Society of Edinburgh: Earth Sciences **88**, 143–195.

Märss, T., Fredholm, D., Talimaa, V., Turner, S., Jeppsson, L. & Nowlan, G. 1995: Silurian vertebrate biozonal scheme. In: Lelièvre, H. *et al.* (eds): Premiers vertébrés et vertébrés inférieurs. Geobios, Mémoire Spécial **19**, 368–372.

Märss, T., Männik, P., Martma, T., Wilson, M.V.H., Caldwell, M.W., Thorsteinsson, R., Gagnier, P.Y. & Goujet, D. 1997: Distribution of Silurian vertebrate microremains in Baillie-Hamilton and Cornwallis Island sections, Arctic Canada. In: Wilson M.V.H. (ed.): Circum-Arctic Palaeozoic vertebrates: biological and geological significance. Ichthyolith Issues, Special Publication **2**, 20–23.

Märss, T., Caldwell, M.W., Gagnier, P.Y., Goujet, D., Männik, P., Martma,T. & Wilson, M.V.H. 1998: Distribution of Silurian and Lower Devonian vertebrate microremains and conodonts in the Baillie-Hamilton and Cornwallis Island sections, Canadian Arctic. Proceedings of the Estonian Academy of Sciences Geology **47**(2), 51–76.

Martinsson, A. (ed.) 1977: The Silurian-Devonian boundary. International Union of Geological Sciences Series A, **5**, 349 pp. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

Norford, B.S. 1972: Silurian stratigraphic sections at Kap Tyson, Offley Ø and Kap Schuchert, northwestern Greenland. Meddelelser om Grønland **195**(2), 40 pp.

Obruchev, D. & Karatajute-Talimaa, V. 1967: Vertebrate faunas and correlation of the Ludlovian – Lower Devonian in eastern Europe. In: Patterson, C. & Greenwood, P.H. (eds): Fossil vertebrates. Journal of the Linnean Society of London **47**(311), 5–14.

Ørvig, T. 1967: Some new acanthodian material from the Devonian of Europe. In: Patterson, C. & Greenwood, P.H. (eds): Fossil vertebrates. Journal of the Linnean Society of London **47**(311), 131–153.

Ørvig, T. 1973: Acanthodian dentition and its bearing on the relationships of the group. Palaeontographica, Abteilung A **143**(1–6), 119–150.

Pander, C.H. 1856: Monographie der fossilen Fische des silurischen Systems der Russisch-Baltischen Gouvernements. Obersilurische Fische. Kaiserliche Akademie der Wissenschaften, 37–91. Vienna, Austria.

Peel, J.S. & Sønderholm, M. (eds): 1991: Sedimentary basins of North Greenland. Bulletin Grønlands Geologiske Undersøgelse **160**, 164 pp.

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

Powrie, J. 1870: On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone of Forfarshire. Transactions of the Geological Society of Edinburgh **1**, 284–301.

Ride, W.D.L., Sabrosky, C.W., Bernardi, G. & Melville, R.V. 1985: International Code of Zoological Nomenclature, 3rd edition adopted by the XX General Assembly of the International Union of Biological Sciences, 338 pp. London: International Trust for Zoological Nomenclature.

Rohon, J.V. 1893: Die obersilurischen Fische von Oesel. Memoirs de l'Académie des Sciences de St. Pétersbourg **41**, 1–124.

Schøler, P. 1989: Non-toxic low-cost heavy liquid separation in the Geological Survey of Greenland. Rapport Grønlands Geologiske Undersøgelse **145**, 11–13.

Stemmerik, L. & Håkansson, E. 1991: Carboniferous and Permian history of Wandel Sea Basin, North Greenland. In: Peel, J.S. & Sønderholm, M. (eds): Sedimentary basins of North Greenland. Bulletin Grønlands Geologiske Undersøgelse **160**, 141–151.

Stetson, H.C. 1928: A restoration of the anaspid *Birkenia elegans*. Journal of Geology, **34**, 458–470.

Surlyk, F. & Hurst, J.M. 1984: The evolution of the early Palaeozoic deep-water basin of North Greenland. Geological Society of America Bulletin **95**(2), 131–154.

[Karatajute-]Talimaa, V. in press: Significance of thelodonts (Agnatha) in correlation of the uppermost Ordovician to Lower Devonian of the northern part of Eurasia. In: Blieck, A. & Turner, S. (eds): IGCP 328 final scientific report. Courier Forschungsinstitut Senckenberg.

Tarlo, L.B.H. 1964: Psammosteiformes (Agnatha) – A review with descriptions of new material from the Lower Devonian of Poland. I. General part. Palaeontologia Polonica **13**, 135 pp.

Tarlo, L.B.H. 1965: Psammosteiformes (Agnatha) – A review with descriptions of new material from the Lower Devonian of Poland. II. Systematic part. Palaeontologia Polonica **15**, 168 pp.

Traquair, R.H. 1896: The extinct vertebrate animals of the Moray Firth area. In: Harvie-Brown, J.H. & Buckley, D.E. (eds): A vertebrate fauna of the Moray Basin, 235–285. Edinburgh.

Traquair, R.H. 1898: Report on fossil fishes. Summary of progress of the Geological Survey of the United Kingdom for 1897, Memoirs, 72–76.

Trettin, H.P. (ed.) 1991: Geology of the Innuitian Orogen and Arctic Platform of Canada and Greenland. Geology of Canada **3**, 569 pp. + map vol. Ottawa: Geological Survey of Canada (also The geology of North America **E**, Geological Society of America).

Turner, S. 1973: Siluro-Devonian thelodonts from the Welsh Borderland. Journal of the Geological Society (London) **129**, 557–584.

Turner, S. 1982: A new articulated thelodont (Agnatha) from the Early Devonian of Britain. Palaeontology **25**(4), 879–889.

Turner, S. 1986: Vertebrate fauna of the Silverband Formation, Grampians, western Victoria. Royal Society of Victoria, Proceedings **98**(2), 53–62.

Turner, S. 1991: Monophyly and interrelationships of the Thelodonti. In: Chang Mee-Mann, Liu Yiu-Hai & Zhang Guo-Rui (eds): Early vertebrates and related problems of evolutionary biology, 87–119. Beijing: Science Press.

Turner, S. in press: New Llandovery to early Pridoli microvertebrates including Lower Silurian zone fossil, *Loganellia avonia* nov. sp., from Britain. In: Blieck, A. & Turner, S. (eds): IGCP 328 final scientific report. Courier Forschungsinstitut Senckenberg.

Turner, S. & Murphy, M.A. 1988: Early Devonian vertebrate microfossils from the Simpson Park Range, Eureka County, Nevada. Journal of Paleontology **62**(6), 959–964.

Turner, S. & Peel, J.S. 1986: Silurian thelodont scales from North Greenland. In: J.S. Peel (ed.): North Greenland Lower Palaeozoic palaeontology and stratigraphy: short contributions. Rapport Grønlands Geologiske Undersøgelse **132**, 79–88.

Turner, S. & Young, G.C, 1992: Thelodont scales from the Middle-Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. Antarctic Science **4**(1), 89–105.

Turner, S., Jones, P.J. & Draper, J.J. 1981: Early Devonian thelodonts (Agnatha) from the Toko Syncline, western Queensland, and a review of other Australian discoveries. BMR Journal of Australian Geology and Geophysics **6**, 51–69.

Valiukevicius, J. 1985: Acanthodians from the Narva Regional Stage of the Main Devonian Field. 144 pp. Vilnius: Mokslas (in Russian with English summary).

Valiukevicius, J. 1992: First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya. In: Mark-Kurik, E. (ed.): Fossil fishes as living animals. Academia **1**, 193–213, Tallinn: Academy of Sciences of Estonia.

Valiukevicius, J. 1994: Acanthodians and their stratigraphical significance. In: Stratigraphy and fauna of the Lower Devonian of Tareya key section (Taimyr), 131–197 and 236–243. Leningrad: Nedra.

Valiukevicius, J. 1995: Acanthodian histology: some significant aspects in taxonomical and phylogenetical research. In: Lelièvre, H. *et al.* (eds): Premiers vertébrés et vertébrés inférieurs. Geobios, Mémoire Spécial **19**, 157–159.

Valiukevicius, J. 1998: Acanthodians and zonal stratigraphy of Lower and Middle Devonian in East Baltic and Byelorussia. Palaeontographica, Abteilung A **248**(1–2), 1–53.

Vergoossen, J.M.J. 1997: Revision of poracanthodid acanthodians. In: Ivanov, I., Wilson, M.H.V. & Zhuravlev, A. (eds): Palaeozoic strata and fossils of the Eurasian Arctic. Ichthyolith Issues Special Publication **3**, 44–45.

Vergoossen, J.M.J. in press: Acanthodian and chondrichthyan microremains in the Siluro-Devonian of the Welsh Borderland, Great Britain, and their biostratigraphical potential. In: Blieck, A. & Turner, S. (eds): IGCP 328 final scientific report. Courier Forschungsinstitut Senckenberg.

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

Wang Nian-zhong 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 (in Chinese with English summary).

Wang Nian-zhong & Dong Zhi-zhong 1989: Discovery of Late Silurian microfossils of Agnatha and fishes from Yunnan, China. Acta Palaeontologica Sinica **28**(2), 192–206 (in Chinese with English summary).

Wills, L.J. 1935: Rare and new Ostracoderm fishes from Downtonian of Shropshire. Transactions of the Royal Society of Edinburgh **58**, 427–447.

Wilson, M.V.H. & Caldwell, M.W. 1993: New Silurian and Devonian fork-tailed 'thelodonts' are jawless vertebrates with stomachs and deep bodies. Nature **361**(6411), 442–444.

Wilson, M.V.H & Caldwell, M.W. 1998: The furcacaudiformes: A new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Paleontology **18**(1), 10–29.

Woodward, A.S. 1891: Catalogue of the fossil fishes in the British Museum (Natural History) **2**, 567 pp. London: British Museum.

Woodward, A.S. 1934: A new cyathaspidian fish from Upper Devonian of Corvedale. Quarterly Journal of the Geological Society (London) **90**(4), 455–567.