morphologically quite variable, but include a few scales that resemble *Loganellia* cf. *L. tuvaensis* from the Halls Grav locality. The Lochkovian Drake Bay Formation of Prince of Wales Island has a few taxa which can be compared with the Chester Bjerg Formation fauna, including *Canonia grossi*, *Nikolivia* and *Gomphonchus sandelensis* (Vieth 1980). The differences, however, between the faunal composition of the Chester Bjerg Formation and the fauna of similar age in the Baillie–Hamilton and Cornwallis Island sections are striking (author's observations of the material of Märss *et al.* 1997, 1998).

In conclusion, the thelodont assemblages seem to be the most age diagnostic remains from the vertebrate-yielding localities of the Chester Bjerg Formation. The Halls Grav locality contains *Loganellia* cf. *L. tuvaensis* and *Nikolivia* sp., indicating a Late Silurian age for this assemblage which also shows new thelodont taxa such as *Paralogania foliala* sp. nov. and *Praetrilogania grabion* gen. et sp. nov. *Canonia* cf. *C. grossi* from Monument suggests an Early Devonian age and the fauna is complemented by the new taxa *Loganellia almgreeni* sp. nov., *Praetrilogania grabion* gen. et sp. nov. and *Thulolepis striaspina* gen. et sp. nov. It is possible that the apparent succession of faunas from Halls Grav to Monument may prove to be of biostratigraphic utility in the Silurian–Devonian boundary interval. The acanthodians, including one new species of *Nostolepis*, one problematic climatiid, one species of *Gomphonchus* and variable poracanthodiforms, cannot give a more precise age than Late Silurian – Early Devonian for both localities, although future taxonomical revision of the poracanthodiforms may change that. The heterostracans, osteostracans and anaspids from the Chester Bjerg Formation are not useful age determinants, since they are poorly preserved and are not yet reliable for comparison of Circum-Arctic strata.

Systematic palaeontology

Most of the major clades listed in Figure 4 are considered monophyletic and reflect the latest studies of interrelationships of the Craniata (Janvier 1996a, b). Thelodonts were excluded from this classification due to their questionable validity as a separate clade (Janvier 1981, 1996a, b; Wilson & Caldwell 1998), but Turner (1991) has argued for their monophyly based on evidence from scale morphology. New material has revealed greater variation in body morphology than previously thought (Wilson & Caldwell 1998), but the true affinity and relationship of thelodonts and their typical scales still remains open. Thelodonts are here described initially as a separate group, within the classification of the better known craniate clades. Classification of higher thelodont taxa is based on works by Karatajute-Talimaa (1978, 1997).

Several different thelodont classifications of morphological scale varieties within a species have been used. The traditional head, transitional and body (trunk) scale classification was re-defined by Märss (1982, 1986b) to oral, cephalo-pectoral, postpectoral, precaudal and pinnal scale types, based on studies of articulated specimens of *Phlebolepis elegans*. Further knowledge about the scale variation in comparison with the position on the body has been achieved by studies on the squamation of articulated thelodonts from the Silurian of Scotland by Märss & Ritchie (1998). In the present study, head, transitional and trunk scale classification has been used as a basis, with complementary classification when possible. Acanthodian taxonomical classification follows Denison (1979) with some modification at the generic level.

Thelodonti

Order Katoporida Karatajute-Talimaa 1978
Family Loganiidae Karatajute-Talimaa 1978

Genus *Loganellia* Turner 1991

Type species. *Thelodus scoticus* Traquair 1898; Lower Silurian (Llandovery), Patrick Burn Formation, Logan Water, Lesmahagow, Lanarkshire, Scotland. Later designated as type species for genus *Logania* by Gross (1967a). The diagnosis for *Loganellia scotica*, includ-

ing body morphology, was revised by Märss & Ritchie (1998).

Diagnosis. Scales vary from small to large (0.1–2.0 mm); head scales round or oval with serrated crown edges; median part of crown surface is smooth and flat; shallow pulp cavity placed centrally on the base; transitional scales oval or rhomboidal, oblong, with crown of 'oak leaf' type; pulp canal usually not developed; trunk scales rhomboidal, wedge-shaped and oblong; crown consists of rhomboidal median part with flat surface or longitudinal groove; ridged lateral part which is shorter and narrower; trunk scales with posteriorly extending pulp canal or concentration of wider dentine canals; base of mature trunk scales is usually high. (Modified from Karatajute-Talimaa 1997.)

Species content. *Loganellia scotica* (Traquair 1898); *L. asiatica* (Karatajute-Talimaa 1978); *L. cuneata* (Gross 1947); *L. einari* Märss 1996; *L. grossi* Fredholm 1990; *L. incompta* (Karatajute-Talimaa 1990); *L. sibirica* (Karatajute-Talimaa 1978); *L. tuvaensis* (Karatajute-Talimaa 1978); *L. aldridgei* sp. nov. Turner in press; *L. avonia* sp. nov. Turner in press.

Range. Early Silurian (early Llandovery) – earliest Devonian.

Remarks. Since the earlier proposed genera names *Logania* (Gross 1967a) and *Loganella* (Turner & Peel 1986) are preoccupied *Loganellia* Turner 1991 is used as a replacement name.

Loganellia cf. *L. tuvaensis* (Karatajute-Talimaa 1978)

Figs 5–7

1978 *Logania tuvaensis* sp. nov. Karatajute-Talimaa, pp. 79–78, plate 18, figs 1–6; plate 19, figs 1–13; pict. 18, figs 1–3; pict. 19, fig. 7.
1986 *Loganella* cf. *L. tuvaensis* – Turner & Peel, p. 82, fig. 3D, E.
1990 *Logania tuvaensis* – Karatajute-Talimaa, plate 10.

Holotype. *Logania tuvaensis*, LitNIGRI, scale No. T-395 (Karatajute-Talimaa 1978, plate 18, fig. 1a–c). Upper Silurian, Pridoli, river Elegest sample 236, Pichi-shui Beds, Tuva region, south of Siberia in Russia.

Figured material. Head and rostral scales; MGUH VP 3394–3397 from GGU sample 82738, MGUH VP 3398–3400 from GGU sample 298937, MGUH VP 3433 from GGU sample 82736. Transitional scales; MGUH VP 3401, 3402 from GGU sample 82738, MGUH VP 3403–3410, 3431, 3432, 3434 from GGU sample 298937. Trunk scales; MGUH VP 3411–3413, 3415 from GGU sample 82738, MGUH VP 3414, 3416–3424 from GGU sample 298937, MGUH VP 3435, 3436 from GGU sample 82736. Posterior trunk scales; MGUH VP 3425 from GGU sample 82738, MGUH VP 3426–3430 from GGU sample 298937.

Other material. Several thousand scales are available from GGU samples 82734, 298938, 298950, 298953, 298954, 298960 and 298963 and about five questionable scales from GGU sample 319264.

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

Diagnosis. Loganiid scales, medium size, up to 1.2 mm long, with rhomboidal or sagittate crown; flat horizontal median crown area with smooth margins; vertical lateral part with one short lateral ridge inclining from base towards a posterior apex; base convex and displaced anteriorly with diffuse posterior pulp aperture, alternatively evenly convex with central pulp aperture; dentine tissue with irregular branching dentine tubules and narrow dentine canals; pulp canal not developed; posteriorly concentrated wider dentine canals extend towards crown apex; basal layer thick with tubules of Sharpey's fibres. (Translated and modified from Karatajute-Talimaa 1978.)

Scale morphology. The scales are medium sized, varying in length between 0.4–1.2 mm, and the majority of those examined represent a mature stage of development. They are mainly well preserved, white, yellow to dark brown in colour and seem not to be waterworn. Some samples, however, contain heavily etched specimens probably due to weathering of the rock.

The rare head or rostral scales (Fig. 5A, C, D; Fig. 6.1–7) are rounded or slightly elongated and have a smooth flat or slightly convex crown with up to 14 almost vertical ribs and notches on the crenulated margins. Scales which are more elongated are less symmetrical with deeper notches ascending from the anterior crown margin toward the centre of the crown. Some of these scales have a crown that resembles an

oak leaf (Fig. 5D). The neck is weakly developed at the connection of the sharp junction between the crown and base of the rostral scales. The swollen base is usually as large and deep as the crown. In mature scales the centrally situated pulp openings are often relatively wide and deep, if compared with the trunk scales.

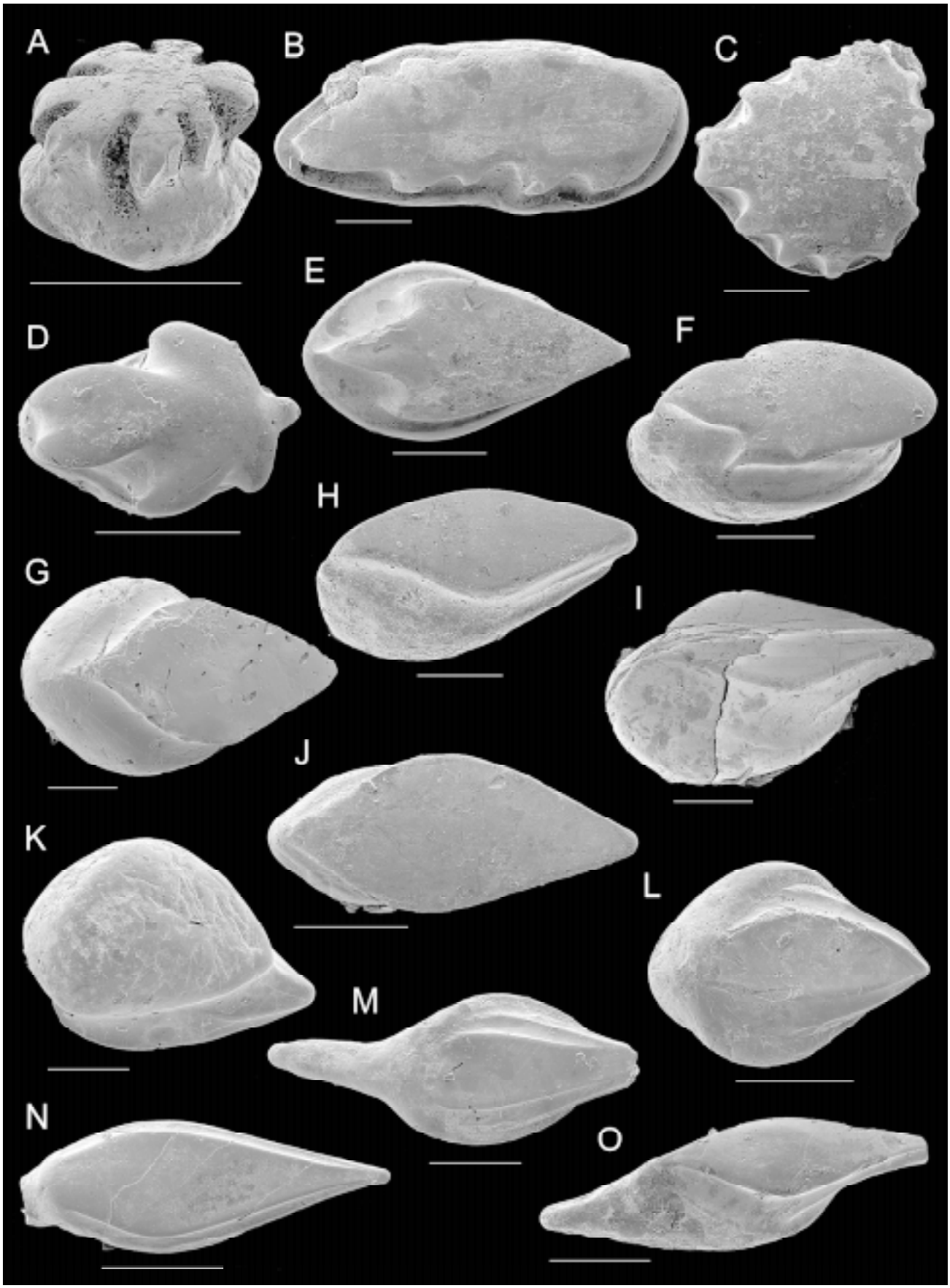
There are two types of transitional scales. The first type represented by some asymmetric scales has leaf-shaped or navicular crowns similar to rostral scales but with notches concentrated on the anterior part at the crown margin. Secondly, there are symmetrical scales, sometimes with a pair of notches on the anterior crown margin. Transitional scales of the first type (Fig. 5B; Fig. 6.8–11) could be included together with the group of head scales, but they are relatively larger. The oval base is often slightly larger than the crown which is oval to elongated and sometimes very asymmetrical. Deep notches are directed towards the centre of the flat or slightly convex crown and are situated along the anterior and central margin. When a pulp opening or depression is visible on the deep base it has a central position and is quite often elongated. Transitional scales of the second type (Fig. 5E, F; Fig. 6.12–15) are much more abundant than the first type. They are relatively large, oval or elongated with a flat and smooth crown forming a rhomboidal, sagittate or oval platform. The extension of the crown margins is longer in the posterior part forming a low angled posterior point. In the middle of the anterior part of the crown the smooth left and right margins bend horizontally towards the centre of the crown, forming an edge-cutting notch or vertical groove, sometimes flanked by a vertical lateral ridge. In some scales only the notch is visible, not the ridge, and vice versa. Anteriorly, where the crown becomes narrower, the upper crown surface bends down towards the neck. The narrowing sometimes results in a sharp anterior point or apex before the bent down portion. The lateral sides of the crown, likewise lateral areas, are almost vertical and bend slightly inwards, forming a sharp junction towards the base. A high neck is therefore represented just above this junction.

In some scales a tiny lateral wing runs on each side from the centre of the neck towards the posterior point of the crown. This feature is typical for most trunk scales, suggesting that these scales are located more posteriorly. Some of the smaller forms may come from the area of the dorsal fin (Fig. 6.18, 19). Scale forms between transitional scales of type one and type two are also present. The large oval and convex base is broader but shorter than the crown and is thicker in its central part, or rarely in its anterior part. The deep anterior part of the base is also a character more common in trunk scales. The small pulp opening is located posteriorly when the base is deepest anteriorly or located centrally when the base is deepest in the central part. Dentine canals are sometimes recognisable as small holes or depressions on the surface of the base (Fig. 5K).

The crown of trunk scales (Fig. 5G–K; Fig. 6.16, 17, 20–26) is wide in the central part and smoothly rhomboidal with a flat upper surface. The extension of the margins is undisturbed and often straight, giving the crown an angular feature. Postero-laterally the margins are longer and more stretched than antero-laterally, and they meet at a lower angle, forming a sharply pointed, but still rounded, posterior apex. Anteriorly the margins often bend down towards the base, where they meet with a less sharp angle than at the posterior apex. The lateral sides of the crown are vertical and slightly concave, forming a high neck. Typical for this type of scale is the lateral ridge running on each side from the posterior apex towards the central part of the scale and the neck base junction. These ridges are tiny and rarely reach as far back as to the lateral corner of the rhomboidal crown. The base is wider than the crown and anteriorly displaced. Anteriorly the base is much deeper than posteriorly and in some scales a weak and poorly developed anterior basal process is developed. In mature scales, a tiny pulp aperture is

---

Fig. 5. *Loganellia* cf. *L. tuvaensis* (Karatajute-Talimaa 1978). SEM photomicrographs. Scale bars equal 0.2 mm.
A: Head or rostral scale in oblique crown view, MGUH VP 3394. **B**: Transitional scale in crown view, MGUH VP 3403. **C**: Head or rostral scale in crown view, MGUH VP 3395. **D**: Head or rostral scale in crown view, MGUH VP 3396. **E**: Transitional scale in crown view, MGUH VP 3401. **F**: Transitional scale in oblique crown view, MGUH VP 3402. **G**: Trunk scale in crown view, MGUH VP 3414. **H**: Trunk scale in oblique crown view, MGUH VP 3411. **I**: Trunk scale in oblique crown view, MGUH VP 3412. **J**: Trunk scale in crown view, MGUH VP 3413. **K**: Trunk scale in basal view, MGUH VP 3415. **L**: Posterior trunk scale in crown view, MGUH VP 3424. **M**: Posterior trunk scale in crown view, MGUH VP 3426. **N**: Posterior trunk scale in crown view, MGUH VP 3425. **O**: Posterior trunk scale oblique crown view, MGUH VP 3427.
MGUH VP 3394–3396, 3401, 3402, 3411–3413, 3415, 3425 from GGU sample 82738, Halls Grav; MGUH VP 3403, 3414, 3424, 3426, 3427 from GGU sample 298937, Halls Grav.


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

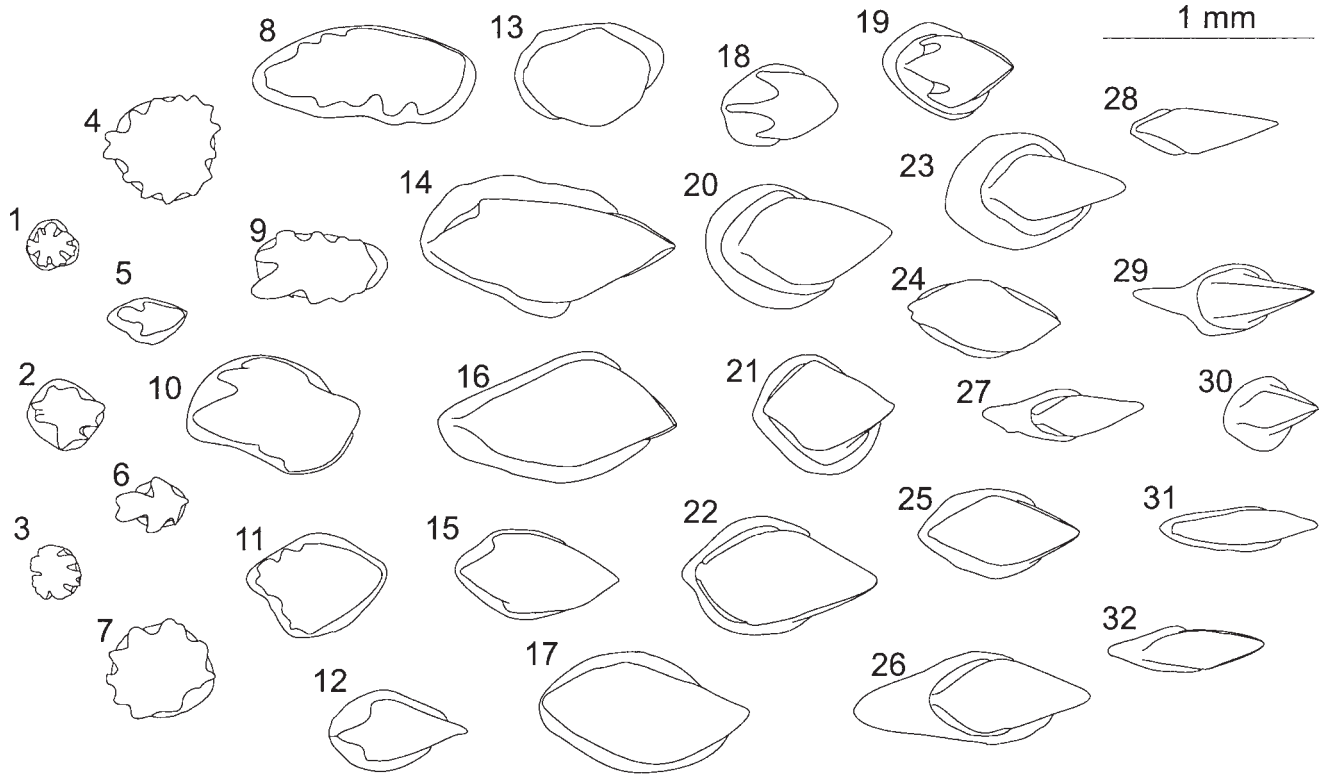


Fig. 6. *Loganellia* cf. *L. tuvaensis* (Karatajute-Talimaa 1978). The main morphological scale varieties in crown view.
1: Head or rostral scale, MGUH VP 3394. **2**: Head or rostral scale, MGUH VP 3398. **3**: Head or rostral scale, MGUH VP 3397. **4**: Head or rostral scale, MGUH VP 3395. **5**: Head or rostral scale, MGUH VP 3399. **6**: Head or rostral scale, MGUH VP 3396. **7**: Head or rostral scale, MGUH VP 3400. **8**: Transitional scale, MGUH VP 3403. **9**: Transitional scale, MGUH VP 3404. **10**: Transitional scale, MGUH VP 3405. **11**: Transitional scale, MGUH VP 3406. **12**: Transitional scale, MGUH VP 3407. **13**: Transitional scale, MGUH VP 3408. **14**: Transitional scale, MGUH VP 3409. **15**: Transitional scale, MGUH VP 3410. **16**: Trunk scale, MGUH VP 3416. **17**: Trunk scale, MGUH VP 3417. **18**: Transitional scale, MGUH VP 3431. **19**: Transitional scale, MGUH VP 3432. **20**: Trunk scale, MGUH VP 3414. **21**: Trunk scale, MGUH VP 3418. **22**: Trunk scale, MGUH VP 3419. **23**: Trunk scale, MGUH VP 3420. **24**: Trunk scale, MGUH VP 3421. **25**: Trunk scale, MGUH VP 3422. **26**: Trunk scale, MGUH VP 3423. **27**: Posterior trunk scale, MGUH VP 3427. **28**: Posterior trunk scale, MGUH VP 3428. **29**: Posterior trunk scale, MGUH VP 3426. **30**: Posterior trunk scale, MGUH VP 3424. **31**: Posterior trunk scale, MGUH VP 3429. **32**: Posterior trunk scale, MGUH VP 3430.
MGUH VP 3394–3397 from GGU sample 82738, Halls Grav; MGUH VP 3398–3400, 3403–3410, 3414, 3416–3424, 3426–3432 from GGU sample 298937, Halls Grav.

situated posteriorly, when not completely overgrown. Younger scales, which are very rare, have a larger opening in the centre. During scale-growth the basal layer grows posteriorly and in the end, if visible at all, a tiny hole is left posteriorly (Fig. 5K). In the area where the former main cavity was, it is possible to trace small dentine canal openings on the basal surface.

Smaller and more elongated scales with a strongly pointed posterior apex indicate a position on the most posterior part of the body (Fig. 5L–O; Fig. 6.27–32). Some of them are specialized by having lower and less vertical lateral parts of the crown (Fig. 5L, M; Fig. 6.29, 30). These scales have a crown with a flat or slightly concave median region, flanked by wide single or double-ridged lateral areas. Scales of both types have quite often an anterior basal process. When compared with other scales of *L.* cf. *L. tuvaensis,* this type of scale has a more extreme morphology, which may indicate a fin edge squamation. The first and more general type of posteriorly placed scales is thereby probably situated more anteriorly on the fin or posteriorly on the tail.

Scale histology. Histological structure seen among the set of scales is less variable than their morphology. Crowns of head scales (Fig. 7A) are penetrated by several branching dentine tubules, which tend to be more abundant in the median part. Towards the base, ap-

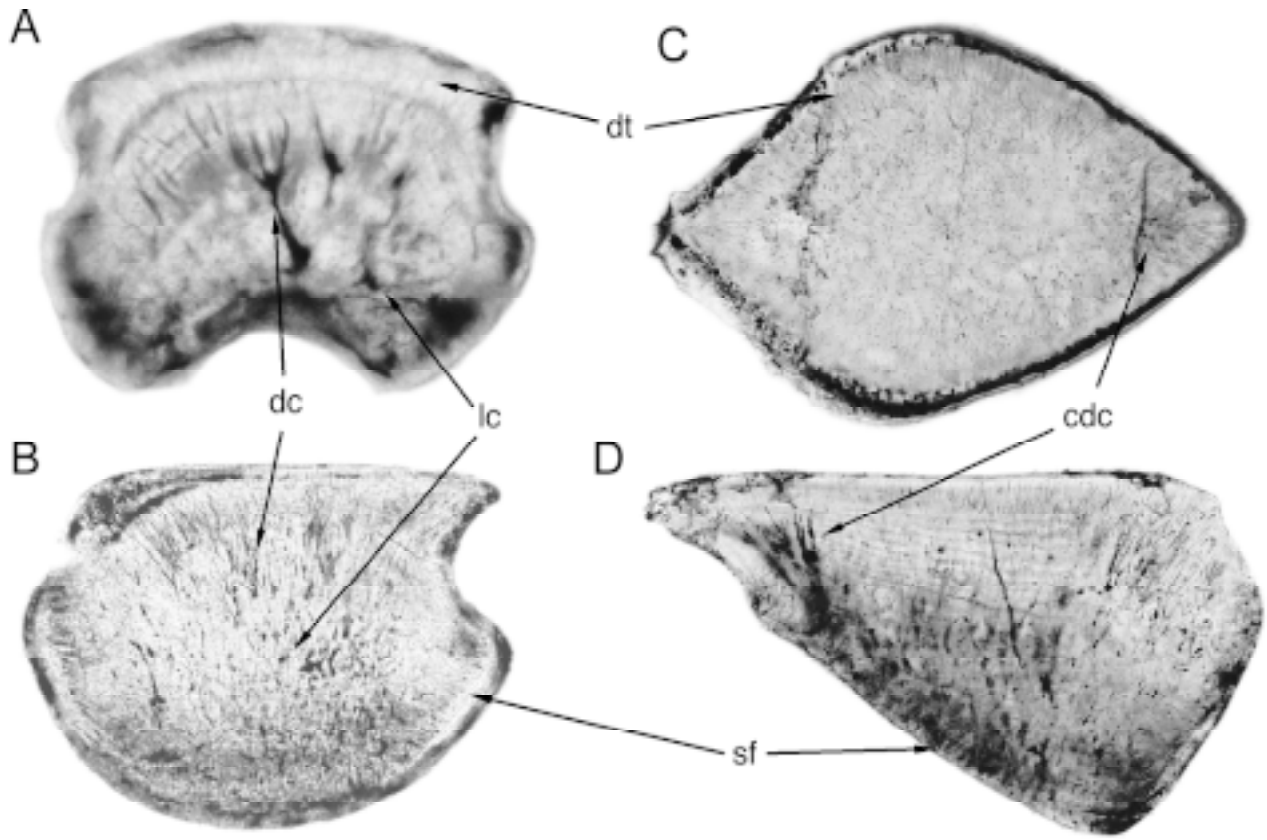


Fig. 7. *Loganellia* cf. *L. tuvaensis* (Karatajute-Talimaa 1978). Histology of the scales.
A: Head or rostral scale in vertical longitudinal section, MGUH VP 3433, × 203. **B**: Transitional scale in vertical longitudinal section, MGUH VP 3434, × 111. **C**: Trunk scale in horizontal crown section, MGUH VP 3435, × 83. **D**: Trunk scale in vertical longitudinal section, MGUH VP 3436, × 94.
MGUH VP 3433, 3435, 3436 from GGU sample 82736, Halls Grav; MGUH VP 3434 from GGU sample 298937, Halls Grav.
cdc: concentration of dentine canals; **dc**: dentine canals; **dt**: dentine tubules; **lc**: odontoblast joining lacunae; **sf**: tubules for Sharpey's fibres.

proximately at neck level, the tubules converge to wide straight dentine canals and lacunae. A pulp canal is not visible, but a shallow central pulp cavity is preserved until the head scales reach full maturity by full development of basal tissue. In mature scales, the dense basal tissue with well developed tubules for Sharpey's fibres forms a quite high convex base.

A high base is also characteristic for the mature transitional scales (Fig. 7B), which usually have a uniform basal thickness. A central depression is sometimes visible at the base where canals and lacunae converge. The branching dentine tubules are straight and regular in the uppermost part of the crown. Towards the central part of the scale they are thicker and more scarce and irregular, and when joining they often form lacuna-like cavities.

Trunk scales of *L.* cf. *L. tuvaensis* have a concentration of thicker tubules, canals and lacuna-like cavities in the posterior part of the crown (Fig. 7C, D). They extend from a small depression or aperture in the base, caused by the junction of canals, towards the posterior part of the crown. This concentration is equivalent to the typical short pulp canal usually found in other loganiid scales. The basal tissue is thicker in the anterior part, which also reflects the height of the anteriorly displaced base. Where the basal tissue is thicker, there is also a higher amount of irregularly oriented tubules of Sharpey's fibres.

Scale dimensions. Length 0.4–1.2 mm; width 0.2–0.7 mm.

Remarks. Karatajute-Talimaa (1978) originally described *Loganellia tuvaensis* as a quite homogeneous set of scales, collected in sections by the river Elegest in the Tuva region, south of Siberia, Russia. In comparison with original material and a complementary morpho-

logical set (Karatajute-Talimaa 1990), the material from North Greenland clearly is morphologically much more diverse with forms not described earlier, as detected by Turner & Peel (1986). It is also clearly morphologically different from the related taxon, *L. incompta* (Karatajute-Talimaa 1990), by having less expressed lateral wings. The largest differences between the original material and the scales under discussion are found among the transitional scales, and especially in the presence of smaller scales from the most posterior part of the body. The present material also shows lower inclination of the crown, as well as smaller and shorter lateral ridges. The difference may reflect the enormous amount of material available from the Chester Bjerg Formation, giving new information about scale forms, but the differences are not sufficient to establish a new species.

Occurrence. *Loganellia tuvaensis*, Pridoli, Tuva, south of Siberia in Russia; *Loganellia* cf. *L. tuvaensis*, Pridoli–Lochkovian, Halls Grav, Hall Land, North Greenland.

Loganellia almgreeni sp. nov.

Figs 8–10

Derivation of name. For Svend Erik Bendix-Almgreen, Geological Museum, Copenhagen, Denmark, for his studies of Greenland vertebrates.

Holotype. Trunk scale; MGUH VP 3449 from GGU sample 319264 (Fig. 8G; Fig. 9.8).

Figured material. Head scales; MGUH VP 3437. Transitional scales; MGUH VP 3440–3448, 3459. Trunk scales; MGUH VP 3449–3458. Scales from the leading edge of the fin or around the eye; MGUH VP 3438, 3439. All from GGU sample 319264.

Other material. About 100 scales, moderately well preserved, from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Diagnosis. Small loganiid scales with a high convex anteriorly displaced base; smoothly rhomboidal or oval flat crown with a pair of anterior notches or furrows running posteriorly towards a single crown apex; rhomboidal or sagittate median crown area; central or slightly posterior pulp aperture; branching and slightly irregular dentine tubules converging towards a narrow pulp cavity and canal.

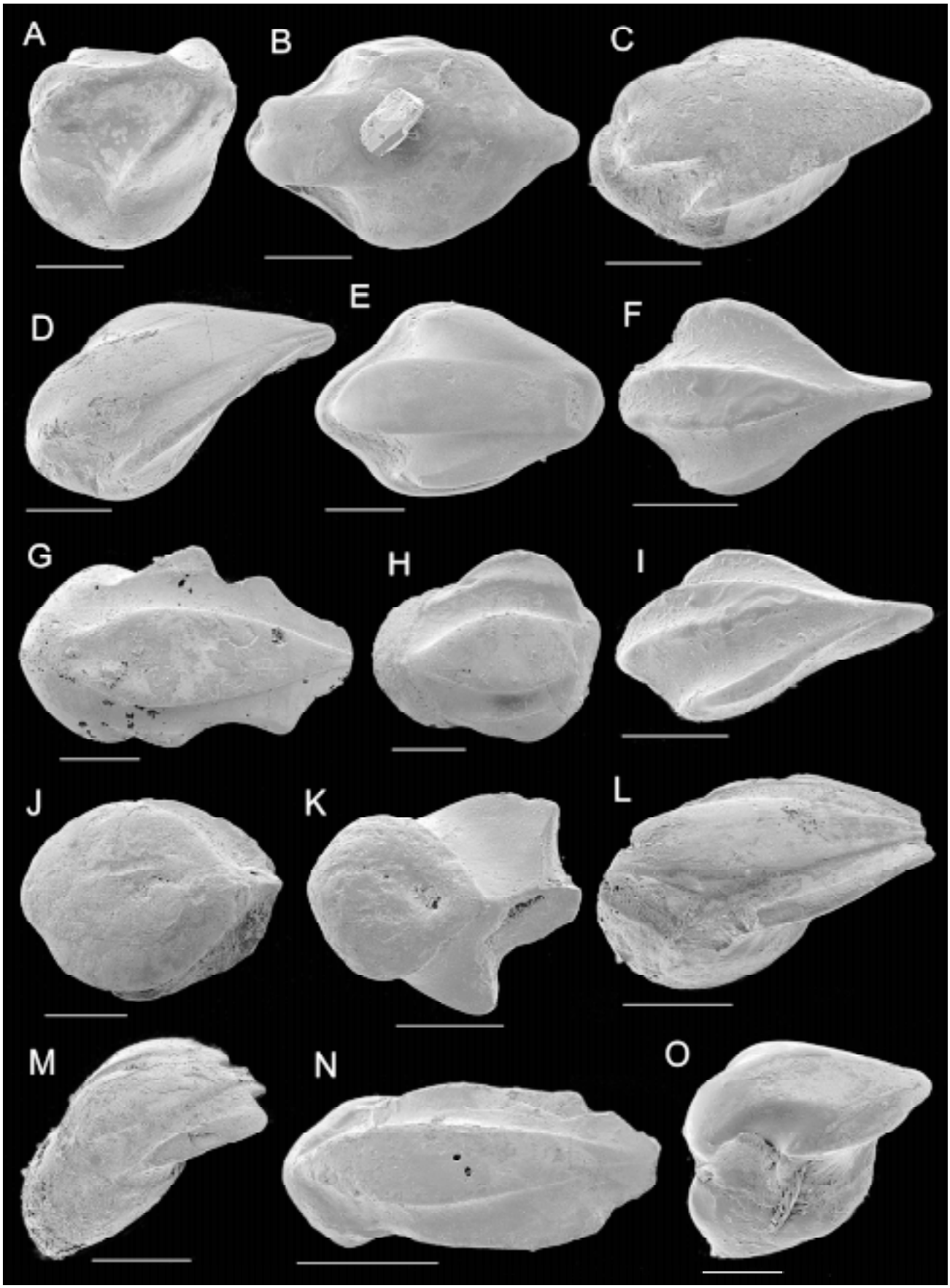
Scale morphology. The scales of *Loganellia almgreeni* sp. nov. are small and do not exceed 0.5 mm in length. They are well preserved, although the apex sometimes is broken, and are variably pale brown in colour.

Head scales are round or irregular, with marginal notches or deep furrows that together with intermediate ridges are oriented towards the centre or slightly posterior of the convex crown (Fig. 8A; Fig. 9.1). The base is relatively deep and about the same width as the crown. Centrally situated on the base is a small pulp depression or aperture. The neck is weakly developed with the shape of a shallow furrow.

Another type of scale is here interpreted to come from the leading edge of a fin, alternatively to be situated close to or around the eye (Fig. 8F, I; Fig. 9.2, 3). This scale type is smoothly rhomboidal or saggitate with a clear posteriorly pointing apex. The whole crown has a higher inclination from the flat or concave base, which has very little basal tissue. Since most of the other scales of the same species are mature, it is possible that the lack of well developed basal tissue is characteristic for this type of scale. The narrow median part of the crown, which is furrowed along half its length, is flanked by deep wide furrows and narrow marginal ridges. With a steeper angle the furrows bend

---

Fig. 8. *Loganellia almgreeni* sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in oblique crown view, MGUH VP 3437. **B**: Transitional scale in crown view, MGUH VP 3440. **C**: Transitional scale in oblique crown view, MGUH VP 3441. **D**: Transitional scale in oblique crown view, MGUH VP 3442. **E**: Transitional scale in crown view, MGUH VP 3443. **F**: Scale from the leading edge of a fin or around the eye in crown view, MGUH VP 3439. **G**: Trunk scale in crown view, holotype, MGUH VP 3449. **H**: Trunk scale in crown view, MGUH VP 3450. **I**: Scale from the leading edge of a fin or around the eye in oblique crown view, MGUH VP 3439. **J**: Transitional scale in basal view, MGUH VP 3444. **K**: Trunk scale in basal view, MGUH VP 3451. **L**: Trunk scale in oblique crown view, MGUH VP 3452. **M**: Trunk scale in oblique crown view, MGUH VP 3453. **N**: Trunk scale in crown view, MGUH VP 3454. **O**: Transitional scale in oblique crown view, MGUH VP 3445.
All specimens from GGU sample 319264, Monument.


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

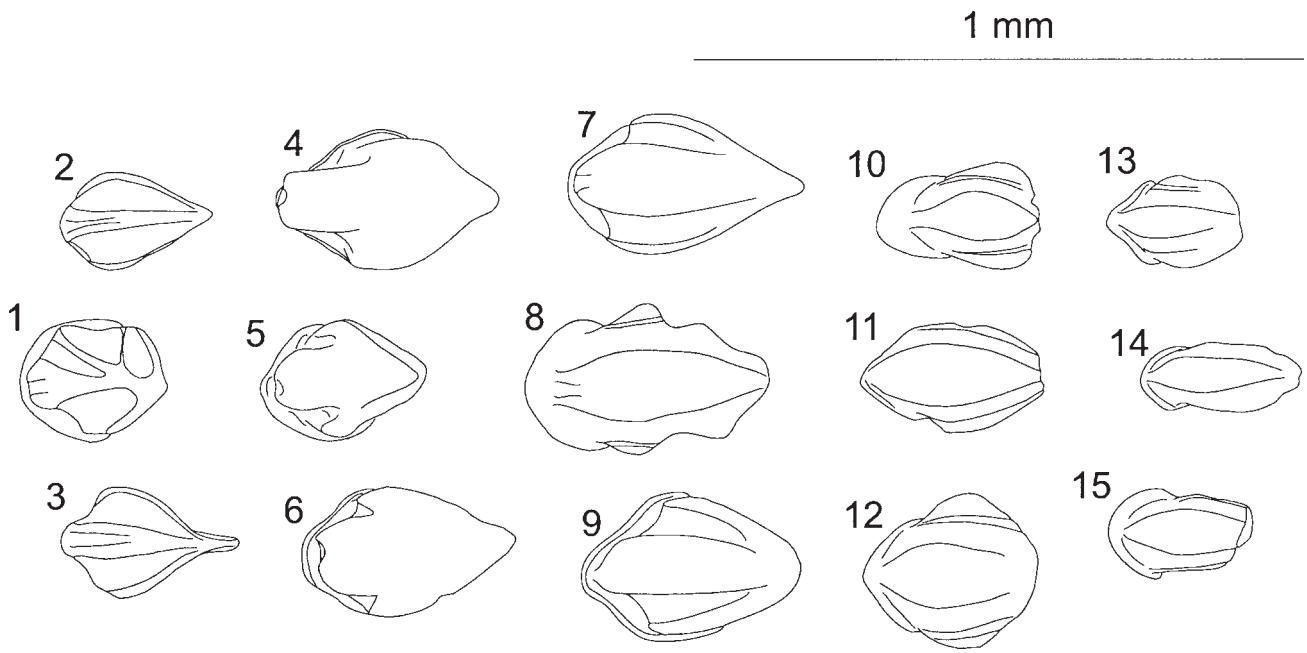


Fig. 9. *Loganellia almgreeni* sp. nov. The main morphological scale varieties in crown view.
1: Head scale, MGUH VP 3437. **2**: Scale from the leading edge of a fin or around the eye, MGUH VP 3438. **3**: Scale from the leading edge of a fin or around the eye, MGUH VP 3439. **4**: Transitional scale, MGUH VP 3440. **5**: Transitional scale, MGUH VP 3459. **6**: Transitional scale, MGUH VP 3441. **7**: Transitional scale, MGUH VP 3442. **8**: Trunk scale, holotype, MGUH VP 3449. **9**: Transitional scale, MGUH VP 3443. **10**: Trunk scale, MGUH VP 3453. **11**: Trunk scale, MGUH VP 3452. **12**: Trunk scale, MGUH VP 3450. **13**: Trunk scale, MGUH VP 3455. **14**: Trunk scale, MGUH VP 3454. **15**: Trunk scale, MGUH VP 3456.
All specimens from GGU sample 319264, Monument.

towards the basal region. This type of scale lacks a distinct neck and on the lower side of the crown a crest runs from the base towards the apex.

Transitional scales are oval or elongated, with a smooth flat or slightly convex crown forming a rhomboidal or sagittate outline (Fig. 8B–E, J, O; Fig. 9.4–7, 9). Crown margins converge posteriorly, forming a low angled point. In the middle of the anterior part of the crown the smooth margins bend horizontally towards the centre of the crown, forming a notch or short steep angled furrow. Anteriorly, where the crown margins meet in a smooth curve, the margin is disturbed by a median notch. A shallow neck is developed just above the junction between the often very high base and the vertical sides of the crown. From the posterior part of the round or oval base, on the lower side of the crown, a clear crest runs towards the apex. Pulp apertures or depressions are indistinct in mature scales, but are visible in younger scales and situated centrally or slightly posterior.

The difference between transitional and trunk scales is not large. Instead of small antero-lateral notches in the margins, larger furrows develop and run further back on the otherwise flat or slightly convex crown. The anterior median part of the crown with its small notch, also bends down towards the high base. In the more elongated trunk scales the crown cutting furrows are even more pronounced (Fig. 8G, H, K–M; Fig. 9.8, 10–13, 15). They run all the way from the anteriorly displaced base to the posterior apex. The median part of the crown is smooth, flat or slightly concave and bends down anteriorly towards the base. Here a short, shallow, antero-median furrow or notch is visible. Ridges are visible parallel to these running towards the apex, either along the margin or just in the central region of the lateral part of the crown. The smaller base is still high and convex with a tiny pulp aperture displaced posteriorly. An even sharper ridge runs on the lower side of the crown, from the clear neck and associated base to the posterior apex.

Smaller and more elongated scales with a general morphology very similar to the other trunk scales may come from the most posterior part of the tail or from the fins (Fig. 8N; Fig. 9.14).

Scale histology. *L. almgreeni* sp. nov. possesses a katoporid histology with regularly branching or anastomosing dentine tubules (Fig. 10). Towards the cen-

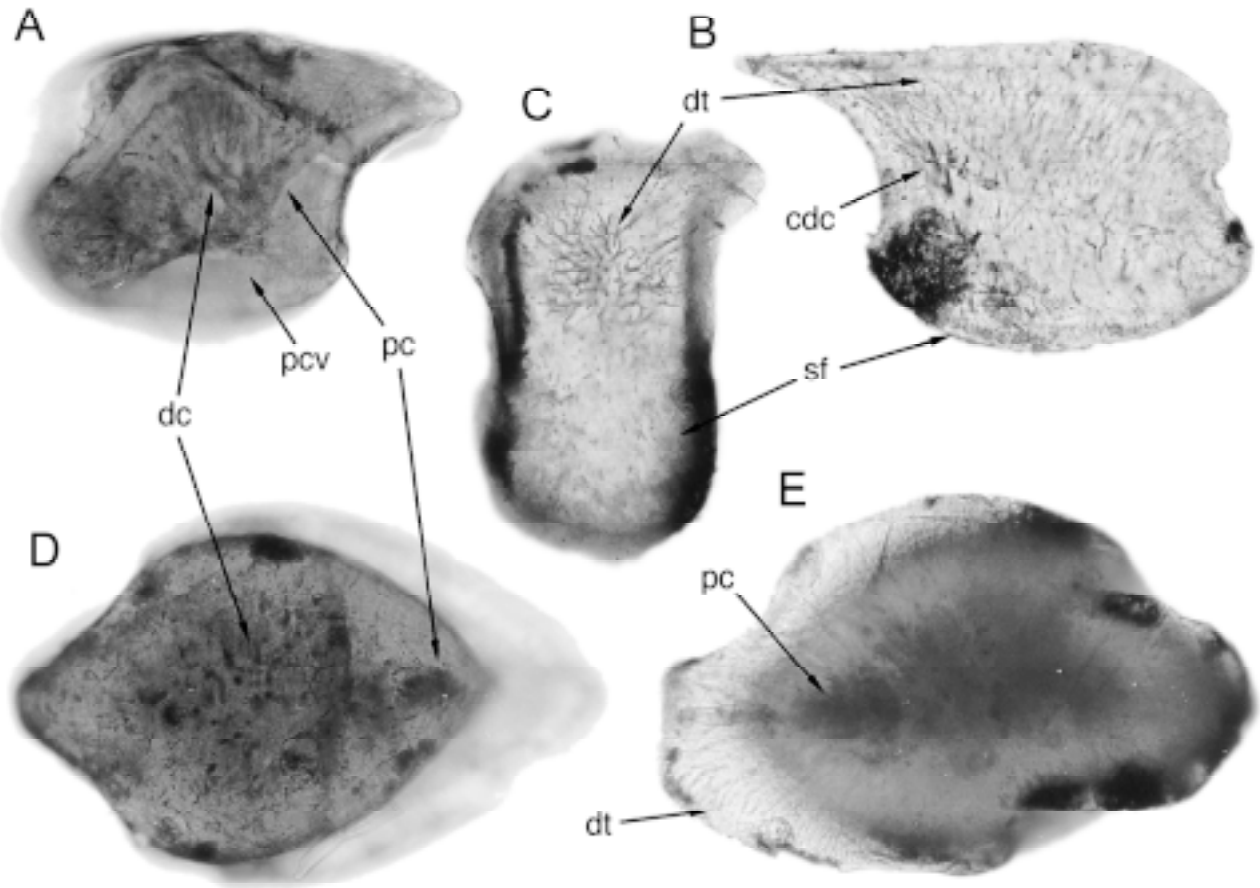


Fig. 10. *Loganellia almgreeni* sp. nov. Histology of the scales.
A: Trunk scale in lateral view, immersed in aniseed oil, MGUH VP 3457, × 199. **B**: Transitional scale in vertical longitudinal section, MGUH VP 3446, × 210. **C**: Trunk scale in vertical transversal section, MGUH VP 3458, × 206. **D**: Transitional scale in basal view, immersed in aniseed oil, MGUH VP 3447, × 176. **E**: Transitional scale in crown view, immersed in aniseed oil, MGUH VP 3448, × 164. All specimens from GGU sample 319264, Monument.
cdc: concentration of dentine canals; **dc**: dentine canals; **dt**: dentine tubules; **pc**: pulp canal; **pcv**: pulp cavity; **sf**: tubules for Sharpey's fibres.

tre of the trunk scale, the rather straight tubules attain greater thickness and pass into a relatively deep (for loganiids) and narrow pulp cavity, and short wide pulp canal (Fig. 10A). In more mature scales, when the pulp cavity is not present, the converging tubules just end in the compact base (Fig. 10B), alternatively penetrate and open onto the basal surface (Fig. 10D). Scales of *L. almgreeni* sp. nov. do not always show a clear pulp canal, but may instead show a concentration of tubules which converge towards the central pulp cavity or the compact base (Fig. 10B). Tubules of Sharpey's fibres are only found in the most distal part of the thick base and have a tendency to be oriented perpendicular to each other.

Scale dimensions. Length 0.2–0.4 mm; width 0.1–0.3 mm.

Remarks. Loganellia almgreeni sp. nov. is similar to *L. tuvaensis* (Karatajute-Talimaa 1978), *L. incompta* (Karatajute-Talimaa 1990), *L. cuneata* (Gross 1947), *L. asiatica* (Karatajute-Talimaa 1978) and *L. grossi* (Fredholm 1990) since they all have only one pair of lateral ridges or wings. In *L. almgreeni* sp. nov., however, these lateral ridges or wings are much wider and more elevated, forming more clear lateral areas. Other species within the same genus have two or more lateral ridges which also are much less pronounced than the single pair of wings present in *L. almgreeni* sp. nov. Some scales of *L. almgreeni* sp. nov. could on the other hand be confused with *Boreania minima* Karatajute-Talimaa 1985 in terms of gross morphology and histology (Fig. 8O; Fig. 10A). The similarity to the complementary set, however, as well as the higher

number of branching dentine tubules and greater irregularity of dentine tubules, support a position within the genus *Loganellia*. Some trunk scales of *L. almgreeni* sp. nov. are characterized by a central or slightly posterior pulp cavity or aperture, which is unusual for loganiid scales of other scales types than head and transitional ones.

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

Genus *Paralogania* Karatajute-Talimaa 1997

Type species. *Logania kummerowi* Gross 1967a; Upper Silurian? erratic boulder (Bey. 6), lowlands of northern Germany.

Diagnosis. Scales vary from small to large (0.3–2.0 mm); small head scales round or oval with a flat smooth crown, serrated on edges; transitional scales oval rhomboidal and very diverse in shape of crown; median crown area wedge- or spine-shaped; spiny postero-lateral part of crown; rhomboidal trunk scales with smooth and flat median crown area; postero-lateral wall of crown having either two pairs of longitudinal ridges and one underlying row of spines, one pair of longitudinal ridges and one pair of rows of thornlets or smooth postero-lateral walls; between three and eight lateral spines and one or two posteriorly median spines situated symmetrical near median line; distinct pulp cavity and canal; wide dentine canals diverging from pulp canal to lateral spines. (Modified from Karatajute-Talimaa 1997.)

Species content. *Paralogania kummerowi* (Gross 1967a); *P. borealis* (Karatajute-Talimaa 1978); *P. ludlowiensis* (Gross 1967a); *P. martinssoni* (Gross 1967a).

Range. Early Silurian (Wenlock) – Late Silurian (Pridoli).

Paralogania foliala sp. nov.

Figs 11, 12

Derivation of name. A combination of the Latin words *folium*, for leaf and *ala*, for wing, referring to the leafy appearance of the large lateral wings.

Holotype. Transitional scale; MGUH VP 3462 from GGU sample 82738 (Fig. 11B).

Figured material. Head scales; MGUH VP 3460. Transitional scales; MGUH VP 3461–3463. Trunk scales; MGUH VP 3464–3467. All from GGU sample 82738.

Other material. About 25 scales from GGU sample 82738.

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

Diagnosis. Small loganiid scales with large anteriorly displaced base and posteriorly positioned pulp aperture; large flat crown with triangular, elongated or rhomboidal median area, disturbed anteriorly by one short, deep, median furrow; large lateral wings forming at least three posteriorly pointing spines at same level as a median posteriorly pointing spine; dentine tubules irregular, independent and with homogeneous thickness.

Scale morphology. The morphological set of *Paralogania foliala* sp. nov. includes very small head, transitional and trunk scales which do not exceed 0.4 mm in length.

The most extreme form, probably a head or rostral scale, is round with a large round base, slightly displaced anteriorly (Fig. 11A, D). In the centre of the base, or slightly posterior, a small pulp aperture or depression is visible. The round, heavily ornamented crown is characterized by a flat narrow median part which has one deep median furrow and two short shallow furrows at the anterior margin. The lateral margins of the median area converge centrally, but they run parallel towards the posterior end before they meet. Between the median and the wide lateral crown areas two furrows are developed. These postero-lateral areas or wings are triangular and flat with three apices or spines spreading and pointing postero-laterally. They are on a slightly lower level than the median part and, on account of their delicate nature, are always broken. One median spine is developed on the posterior end of the crown. It lies just below the apex of the median part at the same lower level as the lateral wing. All furrows bend down anteriorly towards the narrow and quite high neck.

Transitional scales are less ornamented and differ from the rostral ones (Fig. 11B, C) in that the median part of the crown is larger and triangular or sector-shaped, still with a deep median anterior furrow. The two flanking furrows, seen in head scales, are less pro-

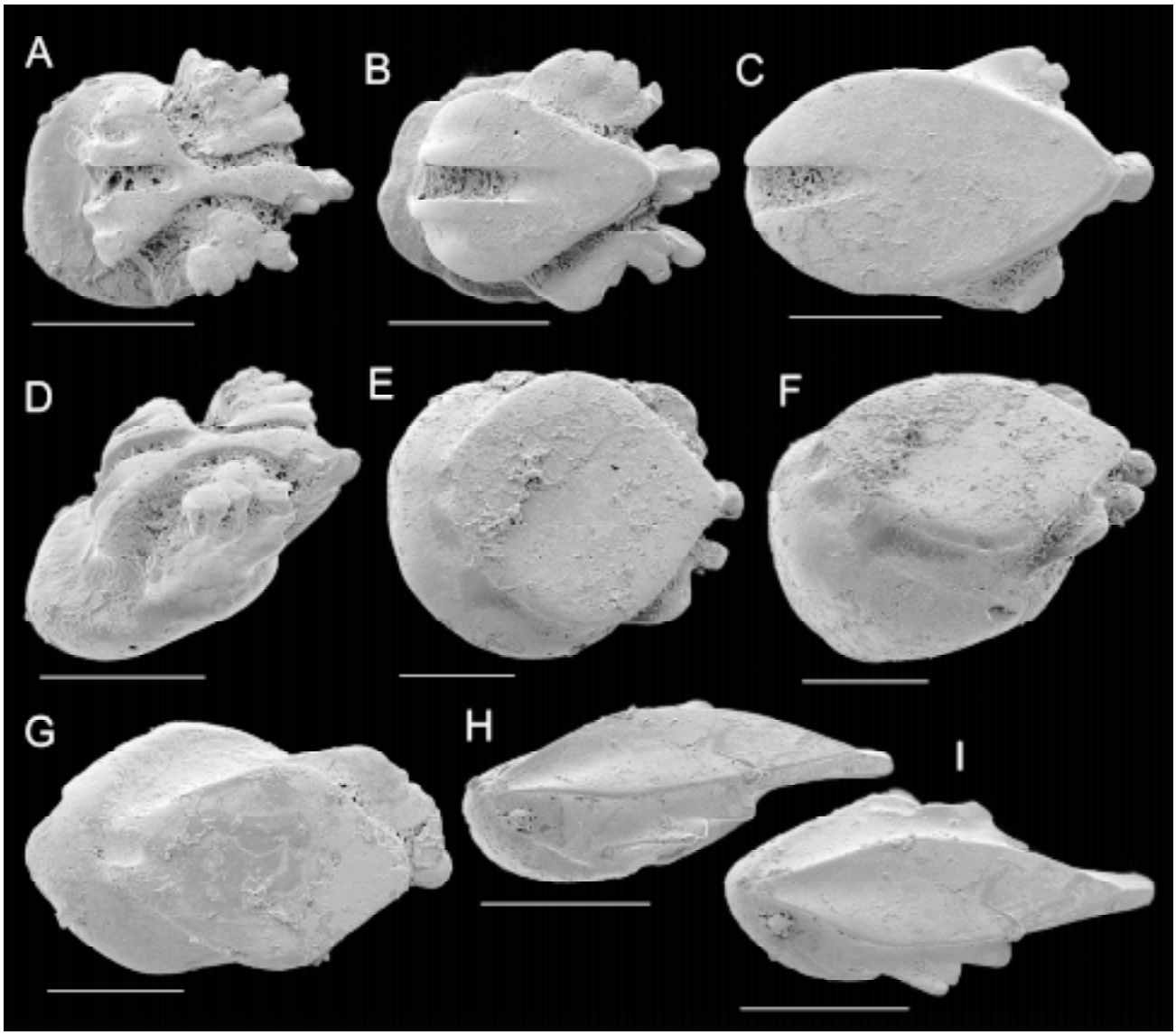


Fig. 11. *Paralogania foliala* sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in crown view, MGUH VP 3460. **B**: Transitional scale in crown view, holotype, MGUH VP 3462. **C**: Transitional scale in crown view, MGUH VP 3463. **D**: Head scale in oblique crown view, MGUH VP 3460. **E**: Trunk scale in crown view, MGUH VP 3464. **F**: Trunk scale in oblique crown view, MGUH VP 3464. **G**: Trunk scale in crown view, MGUH VP 3465. **H**: Trunk scale in oblique crown view, MGUH VP 3466. **I**: Trunk scale in crown view, MGUH VP 3466.
All specimens from GGU sample 82738, Halls Grav.

nounced. In the holotype (Fig. 11B) the median posterior spine preserves a leafy shape. The two lateral wings with spines are still wide.

The general trend, giving a less ornamented crown, continues on the larger more elongated trunk scales, in which the median section is large and round, oval or rhomboidal (Fig. 11E–G). One clear anterior furrow may be present, but it is usually just visible as a small notch. Close to the junction a clear neck is developed between the anteriorly displaced base, with its posterior pulp aperture, and the crown. The lateral wings are usually proportionally smaller.

Scales from the most posterior part or from the fins are small and elongated (Fig. 11H, I). The elongated lenticular median part of the crown is anteriorly slightly concave and bends down towards the oval base, which also is anteriorly displaced with a posterior pulp aperture. The postero-lateral wings are smaller in these scales. On the lower surface of the posterior median spine a sharp ridge or crest is developed.

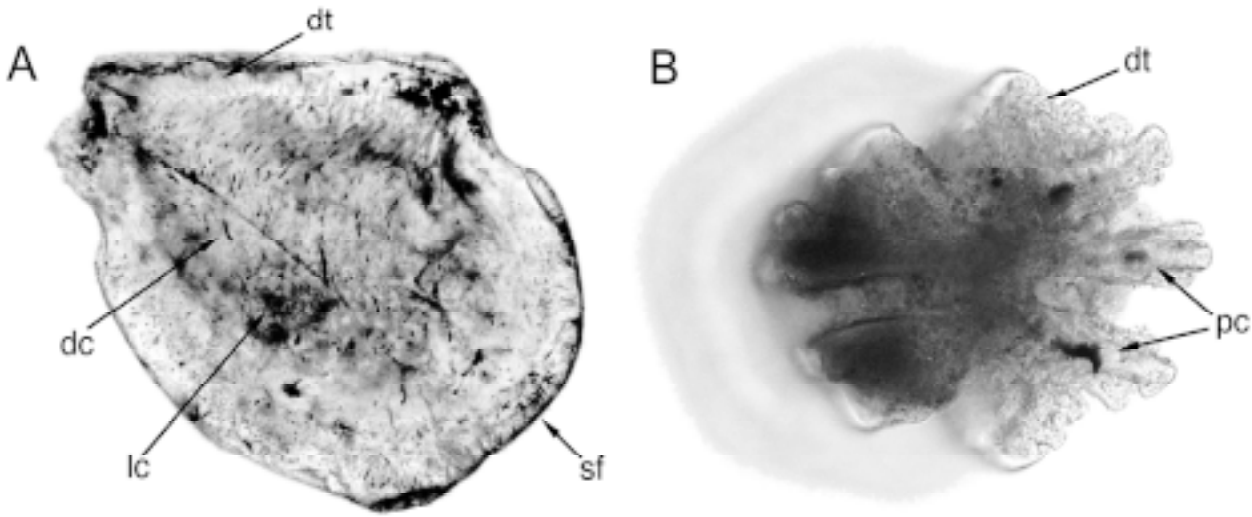


Fig. 12. *Paralogania foliala* sp. nov. Histology of the scales.
A: Trunk scale in vertical longitudinal section, MGUH VP 3467, × 219. **B**: Head scale in crown view, immersed in aniseed oil, MGUH VP 3462, × 362.
Both specimens from GGU sample 82738, Halls Grav.
dc: dentine canals; **dt**: dentine tubules; **lc**: odontoblast joining lacunae; **pc**: pulp canal; **sf**: tubules for Sharpey's fibres.

Scale histology. The dentine tissue in the crown is penetrated by irregular dentine canals and tubules (Fig. 12A). The wider tubules seem to be independent and homogeneous in thickness, seldom converging to greater thickness (it is uncertain from the few available sections if this is a feature of preservation). Several lacuna-like cavities are visible in the very irregular dentine tissue. Some tubules, however, open towards an indistinct short posterior pulp canal, which after branching can be traced into the lateral region (Fig. 12B). The basal tissue with irregular tubules of Sharpey's fibres is quite thin.

Scale dimensions. Length 0.2–0.3 mm; width 0.1–0.3 mm.

Remarks. *Paralogania foliala* sp. nov. is similar to *P. kummerowi* (Gross 1967a), *P. martinssoni* (Gross 1967a) and *P. borealis* (Karatajute-Talimaa 1978), all having one pair of lines or ridges with spines. In *P. foliala* sp. nov. these structures are much more well pronounced, forming a wide spiny wing instead of a weak line of spines. *P. ludlowiensis* (Gross 1967a) differs by usually having one fine ridge above the line of spines. The deep and short anterior crown notch, visible in some scales of *P. foliala* sp. nov. is not found in any of the other *Paralogania* species. The base of *P. foliala* differs from other species of *Paralogania* in not showing the wide anterior basal concavity.

Although it is not generally recommended to designate a transitional scale as a holotype in scale taxonomy, MGUH VP 3462 is selected since it shows the common morphological characters of the whole set of scales, such as the crown sculpture and the lateral wings with spines.

The scales of *Paralogania foliala* sp. nov. follow the same general morphological trends in the crown ornamentation as *Thulolepis striaspina* gen. et sp. nov. with respect to the sector-shaped median area and large spined lateral wings. In detail, however, they are clearly different. The lateral crown part of *Thulolepis striaspina* gen. et sp. nov. is more deeply furrowed with striated spines pointing posteriorly, while in *P. foliala* sp. nov. the lateral part is more developed as a spiny wing with a flat spreading leaf-like outline. Histological structures and base morphology of *P. foliala* sp. nov. show a close relationship with known loganiids, and especially with other species of *Paralogania* (Karatajute-Talimaa 1997). The lateral wing-like structures in *P. foliala* sp. nov. are much more pronounced and specialized than in other loganiids, but there is no further justification to establish a new genus. Histologically it shows *Paralogania* affinity, by having narrow pulp canals extending into the postero-lateral spines.

The small size and similar gross morphology promotes discussion of the squamation pattern and the relationship between *P. foliala* sp. nov. and *T. striaspina* gen. et sp. nov. The morphology may reflect a specific position on the trunk of the living animal which is

already represented among the other scale sets from the Chester Bjerg Formation. In effect this would mean that *P. foliala* sp. nov. is a specific type of scale from one of the other loganiids, while *T. striaspina* sp. nov. comes from the same position on a related thelodontid such as *Nikolivia* or *Canonia*. This idea is rejected on account of the wide variety of different forms within each morphological set for both mentioned taxa, but it can only be truly answered by new finds of articulated material.

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

Genus *Praetrilogania* gen. nov.

Derivation of name. From the Latin word *praeter*, meaning 'beyond' or 'more than', referring to the extension of the loganiid group, and the former generic name *Logania*.

Type species. Praetrilogania grabion gen. et sp. nov.

Diagnosis. Small loganiid scales with heavily ridged and furrowed crown, wider posteriorly; oval crown, often inflated, with 3–5 posteriorly pointing apices or spines; narrow median part of crown furrowed along almost the whole length; anteriorly displaced base, smaller than crown; irregular dentine tubules converge repeatedly towards canal thickness and large joining lacunae, 1–5 pulp canals extend toward 1–5 apices.

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

Remarks. *Praetrilogania* has a histological structure which is typical for scales placed within the family Katoporidae. Like *Goniporus* and *Katoporodus* it has irregular dentine tubules that often converge to almost canal thickness and up to five pulp canals. *P. grabion* gen. et sp. nov., however, differs notably by not having canal or tubule openings on the mature base and especially by its inflated crown.

Praetrilogania grabion gen. et sp. nov.

Figs 13–16

1978 *Thelodus trilobatus* – Bendix-Almgreen, fig. 443A.

1986 *Thelodus trilobatus* – Turner & Peel, p. 82, fig. 2E.

1986 *Turinia* sp. – Turner & Peel, p. 83, fig. 4.

Derivation of name. From *grabion*, the Latin word for torch, in reference to the torch-like appearance of some of the specialized head scales.

Holotype. Trunk scale; MGUH VP 3478 from GGU sample 82738 (Fig. 13K, L; Fig. 15.15).

Paratypes. Head scales; MGUH VP 3469, 3471, 3472, 3492, 3493 (Fig. 13B, C, I; Fig. 14I; Fig. 15.3, 4, 7; Fig. 16A, B). Trunk scales; MGUH VP 3473, 3475–3477, 3480, 3481, 3485 (Fig. 13D, F–H, J; Fig. 14D, E; Fig. 15.5, 8, 12, 14; Fig. 16C, D). Scales from tail or fins. MGUH VP 3486–3488, 3490 (Fig. 14A–C, H; Fig. 15.16–18, 21). All from GGU sample 82738.

Figured material. Head scales; MGUH VP 3468 from GGU sample 319264, MGUH VP 3469–3472, 3492, 3493 from GGU sample 82738. Trunk scales; MGUH VP 3473–3478, 3480, 3481, 3485 from GGU sample 82738, MGUH VP 3479, 3482–3484 from GGU sample 319264; Scales from tail or fins. MGUH VP 3486–3488, 3490 from GGU sample 82738, MGUH VP 3489, 3491, 3494 from GGU sample 319264.

Other material. About 300 well-preserved specimens have been studied from GGU samples 82734, 82736, 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. As for the genus.

Scale morphology. *Praetrilogania grabion* gen. et sp. nov. is represented by a morphological set of scales with many varieties (Figs 13–16). The scales are relatively small and do not exceed 1 mm in length. Depending on which sample the scales come from, the colour varies from dark brown to white. They are usually well preserved and only the delicate posterior edge of the crown is repeatedly broken. Scales of all varieties seem most often to be mature, since the base is inflated and the pulp aperture usually is small.

The head scales of *P. grabion* gen. et sp. nov. are morphologically quite variable. The simplest type has

a low round base and a high inflated round crown (Fig. 13A; Fig. 15.1, 2). In crown view, the scale is almost radially symmetrical and is heavily notched by furrows and ridges. Eight ridges run laterally from a narrow neck towards a meeting point in the central part of the upper crown surface. A distinct, but low, neck is formed near the base, which is low and round with a central pulp cavity. The inflated crown gives the entire scale a balloon-shaped appearance. Some scales are more bilaterally symmetrical, with the base slightly displaced anteriorly and with a small anterior basal process (Fig. 13B; Fig. 15.3). The meeting point for the lateral ridges is more posterior on the upper crown surface. This type may represent a more posterior location or specialized head scales, e.g. around the eye.

Another similar but round and inflated scale type is slender with up to ten lateral ridges (Fig. 13I; Fig. 14I; Fig. 15.7). The majority of the ridges meet in a central upper crown point or apex, but some of them, instead of meeting centrally, tend to form three smooth extensions or spines on each crown. The base is low with a slightly posterior wide pulp cavity and has a long slender basal process. Morphologically, this scale type looks like a burning torch and has motivated the specific name. This kind of ornamentation may indicate a position on the dorsal side of the head.

Less ornamented similar scales without the spines and with a slightly flattened crown, show a smoother morphology that suggests a ventral head squamation (Fig. 13C; Fig. 15.4). This scale type also has a more robust anterior process and more swollen base.

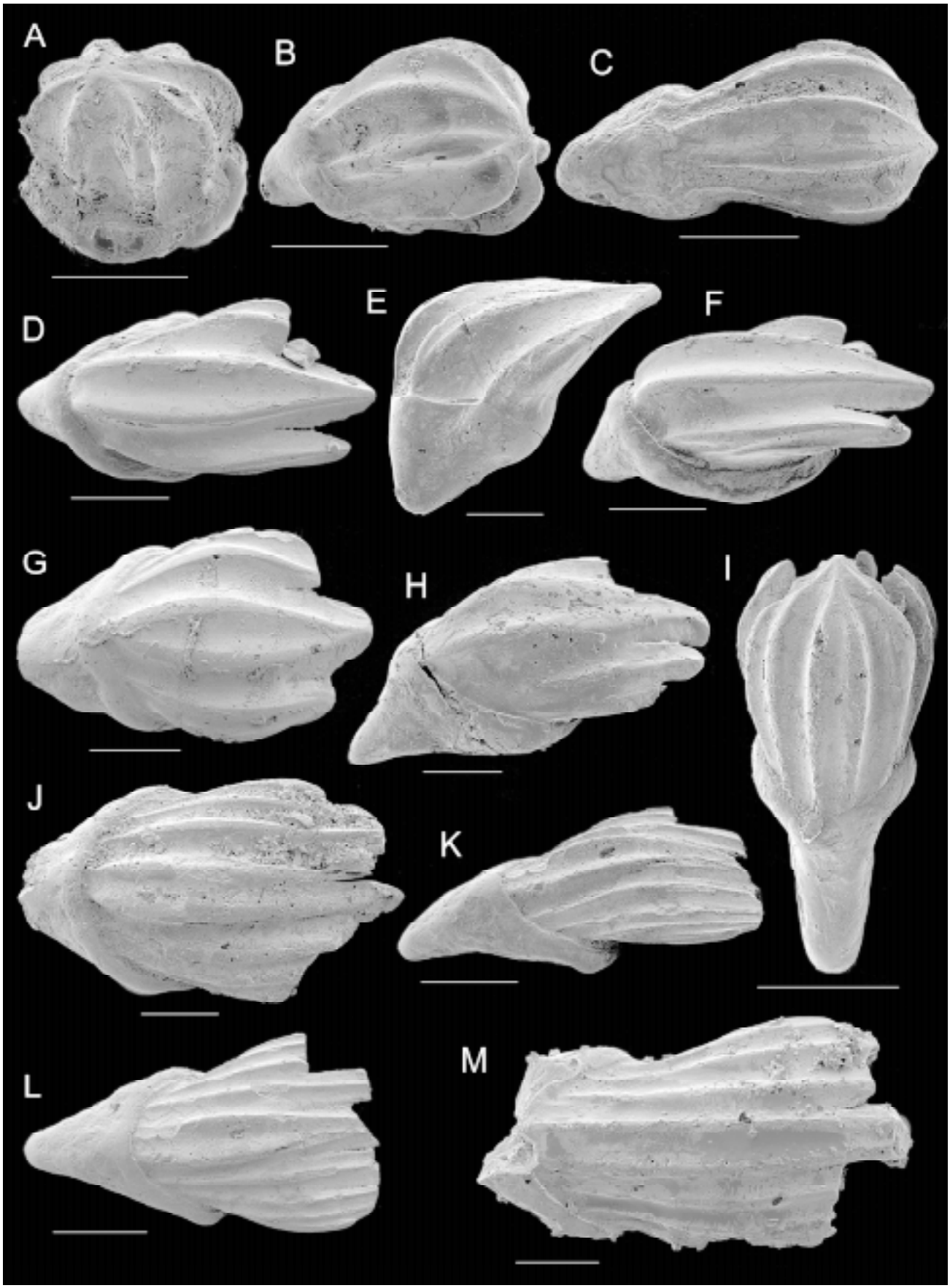
A general morphological trend with anteriorly displaced base and pulp aperture continues backward on the body (Fig. 13D–H; Fig. 15.5, 6, 8–10, 12). With these changes follows a flattening of the crown, which is oval or elongated and divided into three distinct parts; the median (wide central ridge) and the paired lateral ones. The crown is wider posteriorly and each part of the crown ends posteriorly as separated apices. They are almost always broken, however, which makes the true form of the apices uncertain. From the sharp narrow neck the distinct lenticular median part of the crown runs backwards converging on the median apex. The median part, which has a wide shallow furrow along almost its full length, is usually widest centrally. Characteristic for the lateral crown area is one or usually two ridges that run parallel towards the lateral apices. Between each ridge deep and wide intermediate furrows are developed, bent down anteriorly towards the base. The furrow closest to the median part is always wider than the outer ones. Smooth rounded ridges run from the base towards each apex on the lower side of the crown.

More specialized trunk scales of *P. grabion* gen. et sp. nov. differ mainly from previous scales by the presence of an extra lateral ridge on each side of the median crown area, followed by an increased number of apices to the total of five (Fig. 13J–M; Fig. 15.13–15). An extra pair of ridges may also occur on the lower side.

Scales from the tail are more elongated with a smoother upper side of the crown (Fig. 14A–C; Fig. 15.16–19). The crown is still wider posteriorly and ends as a smooth rounded margin and not in 3–5 apices. The median part of the crown is wider more anteriorly and the furrow is less deep. On each lateral part of the crown wide shallow furrows run parallel with one to two lateral ridges. The lower side of the crown is convex and smooth, sometimes with a sharp median crest. Displaced posteriorly is the very small pulp aperture and the convex base has sometimes developed a basal process.

Possible fin scales are small with a crown also divided into three parts (Fig. 14G, H; Fig. 15.20, 21). The lenticular median part is furrowed and converges towards a sharp posterior apex. The flanking lateral parts are characterized by a wide and anteriorly steeply down-bending furrow between the median part and a smooth margin or marginal ridge, which when present seems to follow the margin all the way towards the posterior apex. A median crest often occurs on the smooth lower crown surface. The pulp aperture is posteriorly displaced while the basal process, when present, points anteriorly.

Fig. 13. *Praetrilogania grabion* gen. et sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in oblique crown view, MGUH VP 3468. **B**: Head scale in lateral view, MGUH VP 3469. **C**: Head scale in crown view, MGUH VP 3471. **D**: Trunk scale in crown view, MGUH VP 3473. **E**: Trunk scale in antero-lateral view, MGUH VP 3474. **F**: Trunk scale in oblique crown view, MGUH VP 3473. **G**: Trunk scale in crown view, MGUH VP 3475. **H**: Trunk scale in oblique crown view, MGUH VP 3476. **I**: Head scale in crown view, MGUH VP 3472. **J**: Trunk scale in crown view, MGUH VP 3477. **K**: Trunk scale in oblique crown view, holotype, MGUH VP 3478. **L**: Trunk scale in crown view, holotype, MGUH VP 3478. **M**: Trunk scale in crown view, MGUH VP 3479.
MGUH VP 3468, 3479 from GGU sample 319264, Monument; MGUH VP 3469, 3471–3478 from GGU sample 82738, Halls Grav.


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

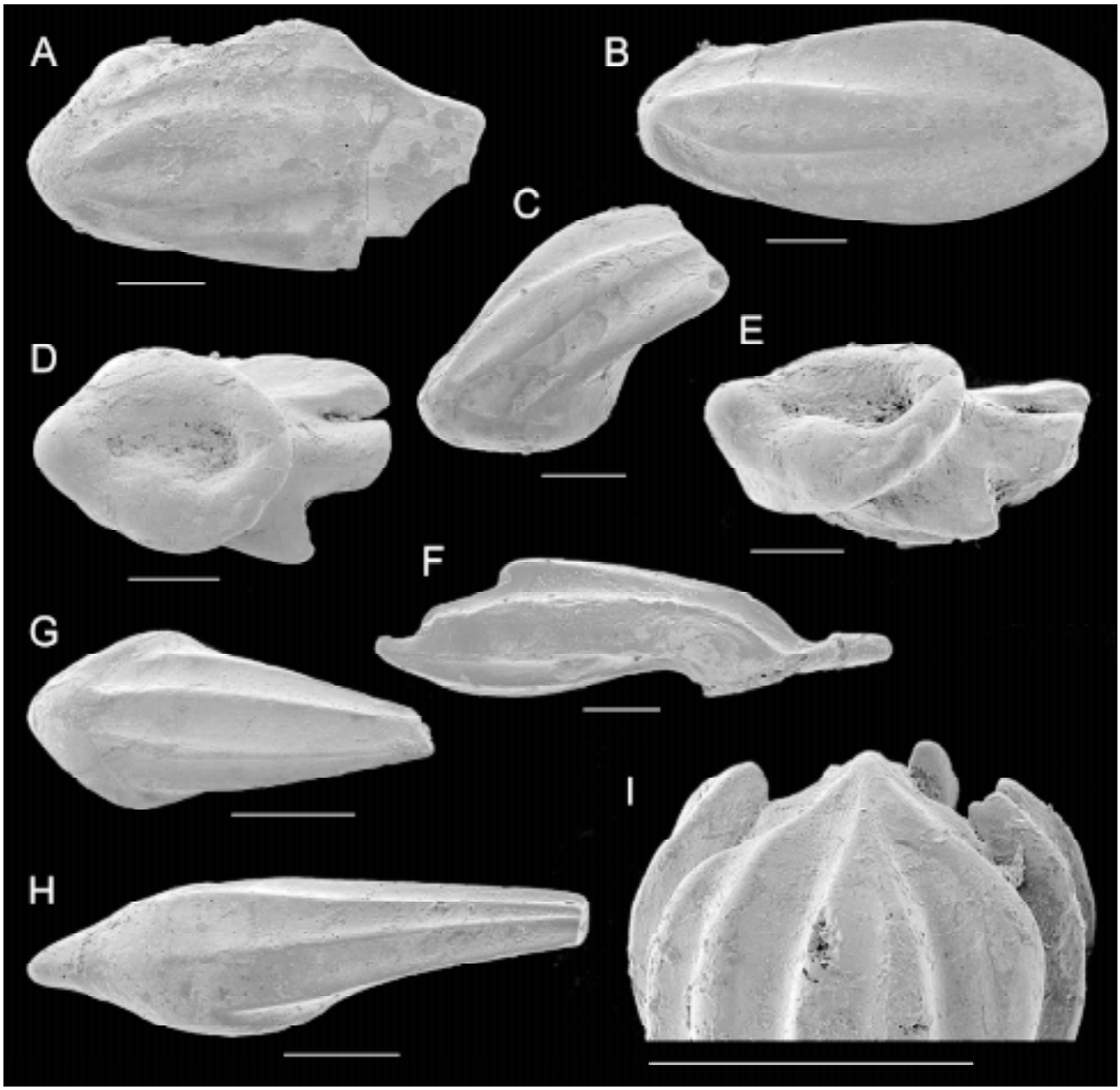


Fig. 14. *Praetrilogania grabion* gen. et sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Scale from fin or tail in crown view, MGUH VP 3486. **B**: Scale from fin or tail in crown view, MGUH VP 3487. **C**: Scale from fin or tail in oblique crown view, MGUH VP 3488. **D**: Trunk scale in basal view, MGUH VP 3485. **E**: Trunk scale in oblique basal view, MGUH VP 3485. **F**: Scale from a fin edge? in lateral view, MGUH VP 3494. **G**: Scale from fin or tail in crown view, MGUH VP 3489. **H**: Scale from fin or tail in oblique crown view, MGUH VP 3490. **I**: Head scale in crown view, close up on posterior crown edge, MGUH VP 3472.
MGUH VP 3472, 3485–3488, 3490 from GGU sample 82738, Halls Grav; MGUH VP 3489, 3494 from GGU sample 319264, Monument.

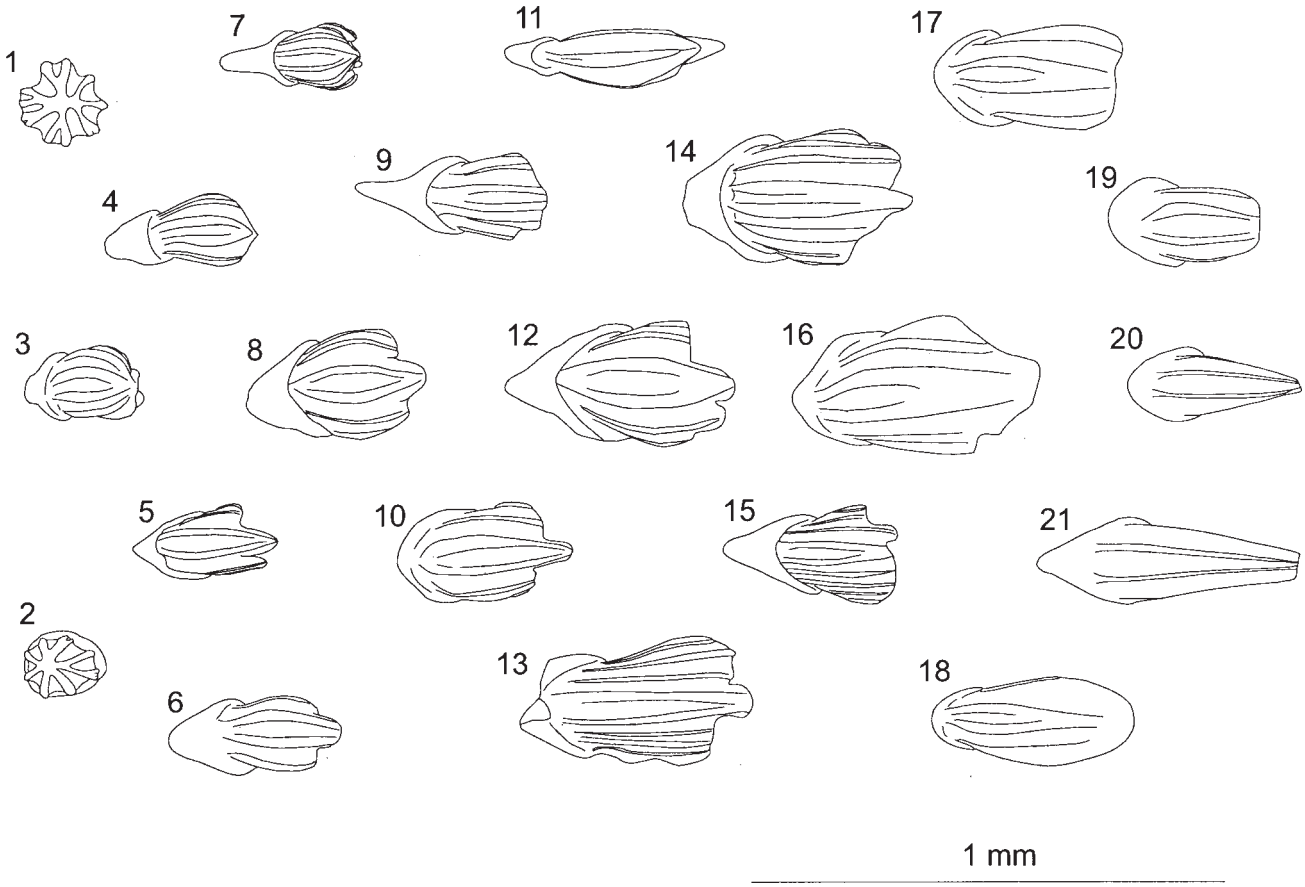


Fig. 15. *Praetrilogania grabion* gen. et sp. nov. The main morphological scale varieties in crown view.
1: Head scale, MGUH VP 3470. **2**: Head scale, MGUH VP 3468. **3**: Head scale, MGUH VP 3469. **4**: Head scale, MGUH VP 3471. **5**: Trunk scale, MGUH VP 3473. **6**: Trunk scale, MGUH VP 3482. **7**: Head scale, MGUH VP 3472. **8**: Trunk scale, MGUH VP 3475. **9**: Trunk scale, MGUH VP 3484. **10**: Trunk scale, MGUH VP 3483. **11**: Scale from a fin edge?, MGUH VP 3494. **12**: Trunk scale, MGUH VP 3476. **13**: Trunk scale, MGUH VP 3479. **14**: Trunk scale, MGUH VP 3477. **15**: Trunk scale, holotype, MGUH VP 3478. **16**: Scale from a fin or tail, MGUH VP 3486. **17**: Scale from a fin or tail, MGUH VP 3488. **18**: Scale from a fin or tail, MGUH VP 3487. **19**: Scale from a fin or tail, MGUH VP 3491. **20**: Scale from a fin or tail, MGUH VP 3489. **21**: Scale from a fin or tail, MGUH VP 3490. MGUH VP 3468, 3479, 3482–3484, 3489, 3491, 3494 from GGU sample 319264, Monument; MGUH VP 3469–3473, 3475–3478, 3486–3488, 3490 from GGU sample 82738, Halls Grav.

There is one abnormal and unusual scale which might be from a fin edge (Fig. 14F; Fig. 15.11). It is long and very slender, with an extremely small base. From the base a proportionally enormous crown points backwards like an elongated balloon which thickens posteriorly. A very high central dorsal ridge runs from the narrow sharp neck to a point 3/4 of the length posterior from the base. Two smooth lateral ridges on each side extend to the posterior end where two thin ventral ridges extend to a posterior apex. Attached to the base is a large, probably broken or worn, anteriorly pointing basal process.

Scale histology. Histologically the scales are of typical katoporid type (Fig. 16). The dentine tissue is characterized by frequently branching dentine tubules or canals. Distally, in the outermost layer, dentine tubules are straight and parallel. In the next growth layer they start to converge and join to thicker tubules. This continues proximally towards the basal tissue, where the tubules have reached almost canal thickness. Most known scales are mature and have a very dense basal tissue with many irregularly oriented Sharpey's fibres. Only the larger posterior pulp canal is capable of penetrating the posterior part of the basal tissue. Some dentine tubules in the posterior part of the scale pass directly into the pulp canal which branches towards each posteriorly pointing apex. The other canals and tubules end towards the basal tissue, where they join and form larger lacunae-like cavities. In younger scales it is possible to see how finer tubules and canals pass into the shallow pulp cavity. Also in younger scales,

but less frequently, smaller lacunae are visible which are formed at the junction of branching dentine tubules and canals. Scales with a displaced base have a concentration of tubules of Sharpey's fibres in this anterior swelling.

A pulp canal is not developed in most head scales and therefore dentine tubules pass directly into a central pulp cavity. The outer layer, representing the initial cap, is usually distinct while growth lines of other layers are more difficult to detect.

Scale dimensions. Length 0.2–0.5 mm; width 0.1–0.3 mm (the total length given is less than the true, since the scales are almost always broken posteriorly).

Remarks. Trunk scales of *Praetrilogania grabion* gen. et sp. nov. are morphologically similar to those on the articulated thelodont *Shielia taiti* (Märss & Ritchie 1998). Also scales from the tail and the fins have their equivalents in both types. *Shielia taiti*, however, lacks the round inflated scales from the head region seen in *Praetrilogania grabion* gen. et sp. nov. The affinity of these scales can only be supported by comparison to the head scales of e.g. *Turinia* Traquair 1896 (Karatajute-Talimaa 1978; Turner 1986; Turner & Young 1992; Turner *et al*. 1981; Märss & Ritchie 1998). Head scales of *P. grabion* gen. et sp. nov. are in gross morphology quite similar to *Turinia*, as suggested by Turner & Peel (1986), but cannot be placed within this histologically completely different group. Included in this set are also the trunk scales earlier described by Turner & Peel (1986) as *Thelodus trilobatus*.

The most posterior trunk scales of *L. almgreeni* sp. nov. are also similar to some scales of *P. grabion* gen. et sp. nov. They differ, however, notably by lacking clear long furrows in the median part of the crown. Scales of *P. grabion* gen. et sp. nov. are generally wider in the posterior part of the crown while scales of *L. almgreeni* sp. nov. are wider closer to the centre. The base is also higher in *L. almgreeni* sp. nov. When both taxa occur together, it can be difficult to separate some of the most posterior trunk scale types. The notion that *P. grabion* gen. et sp. nov. is a separate taxon is also supported by its presence in several samples from the Halls Grav locality which do not contain scales of *L. almgreeni* sp.nov.

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

Order Thelodontida Kiær 1932
Family Nikoliviidae Karatajute-Talimaa 1978

Genus *Nikolivia* Karatajute-Talimaa 1978

Type species. *Thelodus oervigi* Karatajute-Talimaa 1968; Early Devonian (Lochkovian, D1), Ivanev horizon, sections Dobrovljany, Bedrikovtzy (upper part), Zaleschiki (lower part), Pechora (lower part), Ivane-Zolotoe (lower part), Podolia, Ukraine.

Diagnosis. Large and medium sized scales; trunk scales large with flat leaf-like, elongated, oval or wedge-liked crown, covered with longitudinal ridges; crowns often with slightly raised median area; longitudinal ridges developed on lateral areas of different width; anterior border rounded with slightly anteriorly displaced median part; posteriorly wedge-like and monolithic or split into three apices; central apex much longer than lateral; postero-lateral borders of crown smooth or slightly notched; lower crown surface smooth, flat and convex; crown of head scales high and short with thorn-like lifted end; crown of transitional scales relatively short and wide; neck on all scales low and recognisable as compact furrow; base relatively small, two to four times smaller than crown, low, round and oval, anteriorly located; pulp cavity large, wide and low with long posteriorly extending pulp canal; crown with branched, straight or slightly curved dentine tubules opening into pulp cavity and canal; proximal part of dentine tubules slightly enlarged. (Translated and modified from Karatajute-Talimaa 1978.)

Species content. *Nikolivia oervigi* (Karatajute-Talimaa 1968); *N. balabayi* Karatajute-Talimaa 1978; *N. elongata* Karatajute-Talimaa 1978; *N. gutta* Karatajute-Talimaa 1978; *N. milesi* Turner 1982.

Range. Early Devonian (Lochkovian–Pragian).

***Nikolivia* sp.**
Fig. 17E–L; Fig. 18B, C

Figured material. MGUH VP 3495 from GGU sample 298937, MGUH VP 3496–3501 from GGU sample 82738.

Other material. About 25 scales from GGU samples 82736, 82738, 298937 and a questionable occurrence from GGU sample 319264.

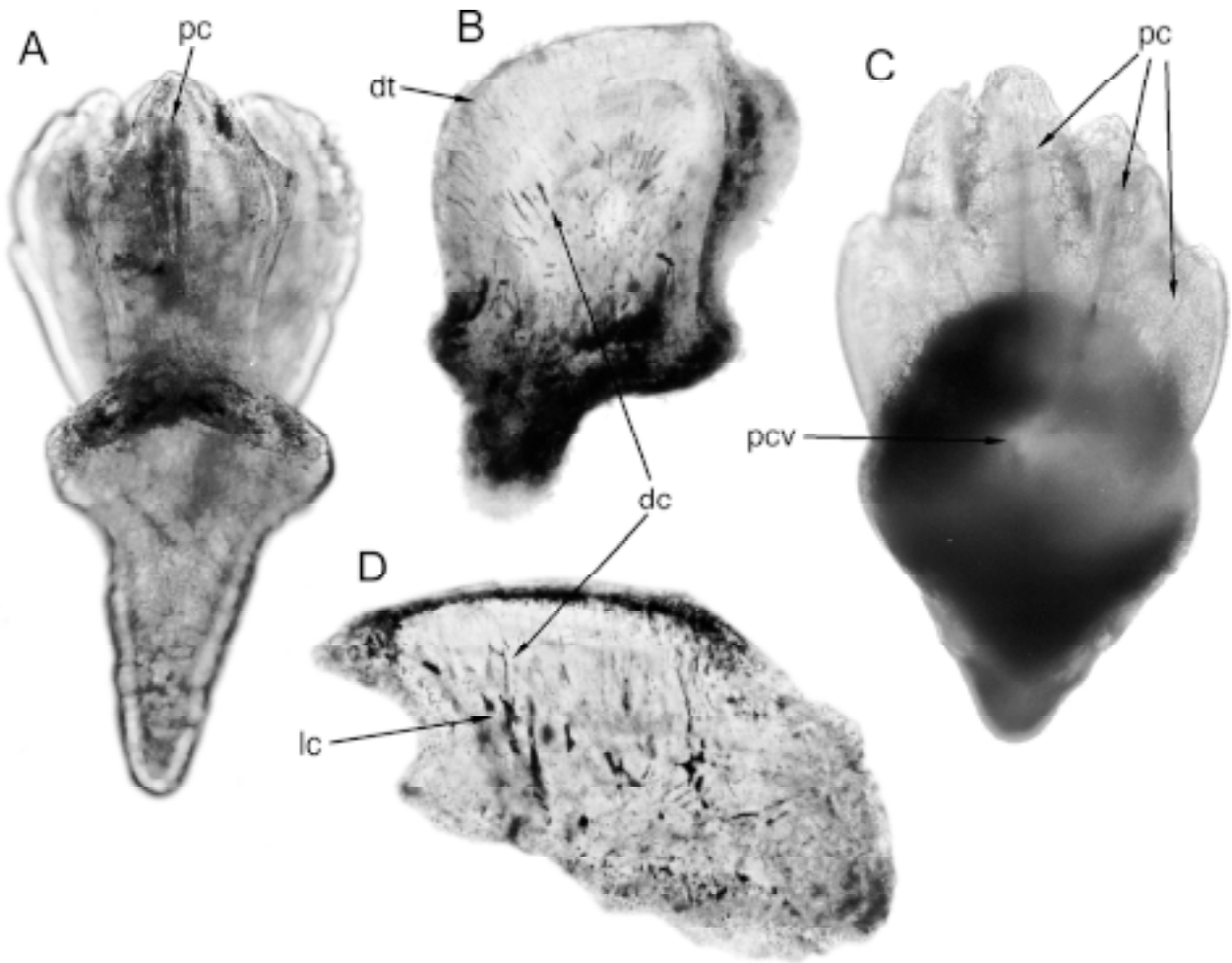


Fig. 16. *Praetrilogania grabion* gen. et sp. nov. Histology of the scales.
A: Head scale in crown view, immersed in aniseed oil, MGUH VP 3492, × 304. **B**: Head scale in vertical longitudinal section, MGUH VP 3493, × 184. **C**: Trunk scale in basal view, immersed in aniseed oil, MGUH VP 3480, × 175. **D**: Trunk scale in vertical longitudinal section, MGUH VP 3481, × 199.
All specimens from GGU sample 82738, Halls Grav.
dc: dentine canals; **dt**: dentine tubules; **lc**: odontoblast joining lacunae; **pc**: pulp canal; **pcv**: pulp cavity.

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

Scale morphology. This morphological set of nikoliviid scales is variable and may not reflect a single taxon. The low number of scales found also makes it difficult to define a consistent set and the nomenclature is therefore best left open.

A few rounded scales, presumably from the head region, have been found (Fig. 17G). They have a short crown that rises with a quite steep angle towards a posterior apex. The median area of the crown is smooth, narrow and wedge-shaped, and bends down anteriorly towards the base. The median crown area is usually flanked on the lateral sides by two pairs of lateral crown ridges or wings that run towards a weakly developed or non-existent neck. The upper one, closest to the median part, is more pronounced and wing-like. A wide open pulp cavity is visible on the typical round base.

The next scale type is less thorn-like with lower inclination of the crown (Fig. 17E, F). The median crown area is wider in the rounded anterior part and joins the base; there is no neck at this point. A larger lateral wing or ridge runs from mid-length of the base towards the posteriorly pointing apex. The apex forms the meeting point of the margins of the median part and the less pronounced lateral ridges.

One type of trunk scale is larger and more elongated, but similar to the previous one (Fig. 17H, I). The oval median crown region is proportionally very large and wide, with a flat and smooth upper surface, anteriorly meeting the base without an intervening neck. From the posterior pointing apex one pair of lateral ridges or wings runs towards the oval base, which is large and quite swollen.

A fourth scale type is shorter and more robust, with a wide slightly convex median crown area (Fig. 17J). The anterior part of the median area, which curves slightly towards the base, is slightly notched or furrowed. Laterally only one pair of wide ridges or wings is developed. This scale type, which has an oval base and low inclination of the crown, can be regarded as a typical trunk scale.

Scales from a more posterior position are elongated with a narrow concave or furrowed median crown area (Fig. 17K, L). Their size is variable and reflects their position, such that smaller scales of this type had a more posterior location. The whole crown is covered by longitudinal ridges that converge towards a posteriorly pointing apex, that includes the margin of the median crown part, as well as two or three pairs of lateral ridges. No distinct neck is developed between the crown and the elongated base, which has a wide open, or slit-shaped, aperture.

Scale histology. When immersed in aniseed oil, these scales show a typical nikoliviid histology (Fig. 18B, C). The studied young scales show a large wide pulp cavity and a pulp canal which extends posteriorly towards the crown apex. Branched, straight or slightly curved dentine tubules or canals open into the main cavity or canal. The tubules are slightly enlarged proximally towards the pulp cavity and canal.

Scale dimensions. Length 0.3–0.8 mm; width 0.2–0.5 mm.

Remarks. Problems concerning the validity of different species of *Nikolivia* were discussed by Turner (1982) in connection with her description of an articulated thelodont bearing scales that resemble different described species.

Scales of *Nikolivia* sp. from North Greenland are variable and types within this set may belong to several different species. The scale type here referred to as the most posterior one is quite similar to the holotype of *N. elongata* (Karatajute-Talimaa 1978). The other types, on the other hand, find no exact equivalent among the original set. Some of the larger scales with a large, flat, median region are also comparable to *Nikolivia gutta* Karatajute-Talimaa 1978, but have slightly larger and different lateral wings. *N. gutta* and *N. elongata* have been found together at several different localities (Karatajute-Talimaa 1978; Turner 1982) but in the absence of evidence to the contrary, the available Greenland material is all placed in *Nikolivia* sp.

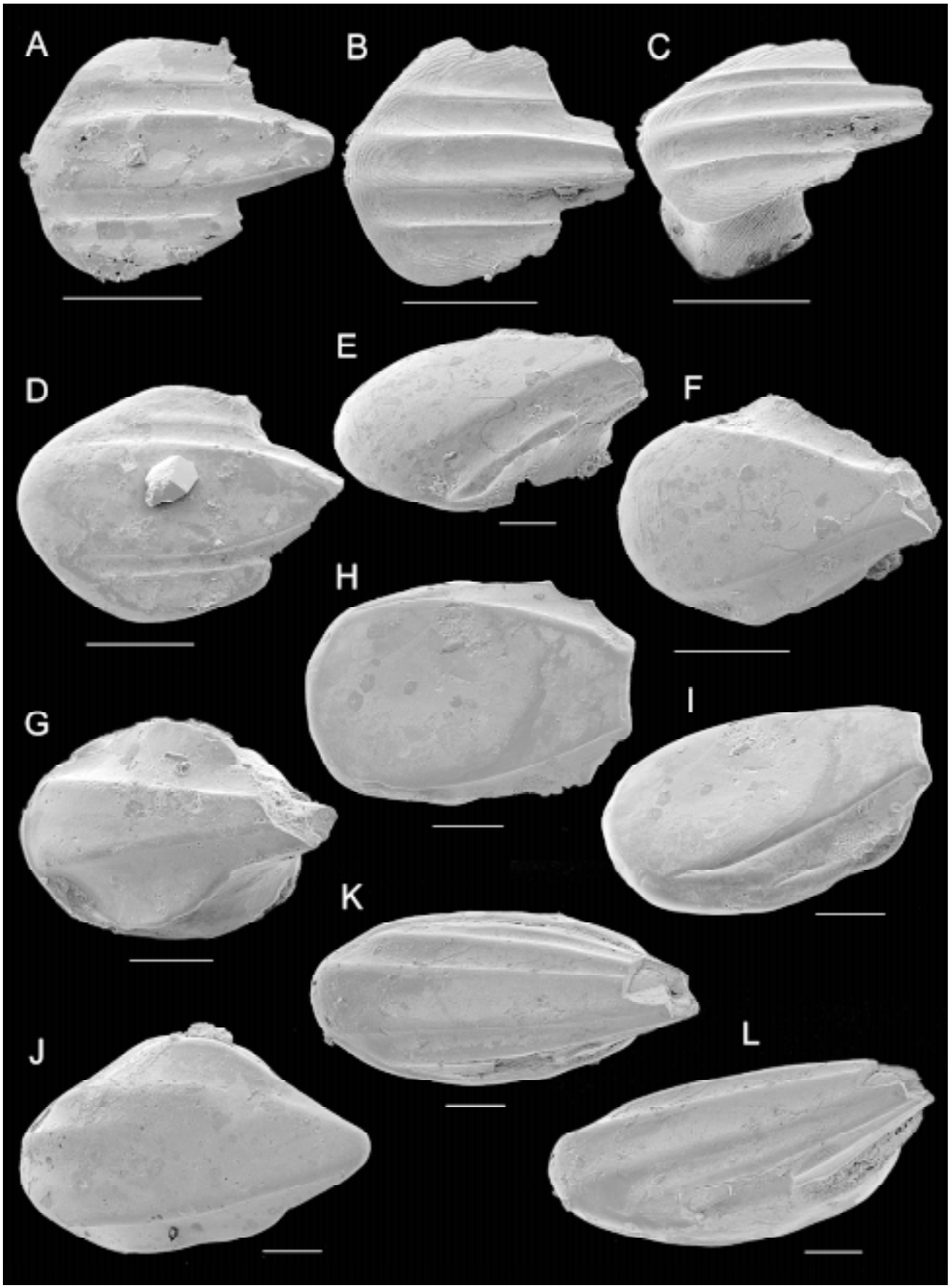
Occurrence. Pridoli-Lochkovian, Hall Land, North Greenland.

Genus *Canonia* Vieth 1980

Type species. *Canonia grossi* Vieth 1980; Early Devonian (Lochkovian–Pragian), Member A, Red Canyon River Formation, Ellesmere Island; Drake Bay Formation, Prince of Wales Island; Member C, Stallworthy Formation, Axel Heiberg Island; all from Arctic Canada.

Diagnosis. Small, symmetrical, thelodontid scales with a small round to oval base and narrow neck; flat crown, round to oval, with three posteriorly pointing apices; wide median crown area flanked by horizontal lateral area with 0–2 longitudinal ridges or furrows, alternatively flat crown with 4–8 longitudinal ridges; anastomosing almost straight branching dentine tubules all radiate from pulp cavity; locally, mainly proximally, dentine tubules converge and join to canal thickness;

Fig. 17. *Canonia* cf. *C. grossi* and *Nikolivia* sp. SEM photomicrographs. Scale bars equal 0.1 mm.
A–**D**. *Canonia* cf. *C. grossi*. **A**: In crown view, MGUH VP 3502. **B**: In crown view, MGUH 3503. **C**: In oblique crown view, MGUH VP 3503. **D**: In crown view, MGUH VP 3504.
E–**L**. *Nikolivia* sp. **E**: Transitional scale in oblique crown view, MGUH VP 3495. **F**: Transitional scale in crown view, MGUH VP 3495. **G**: Head scale in crown view, MGUH VP 3496. **H**: Trunk scale in crown view, MGUH VP 3497. **I**: Trunk scale in oblique crown view, MGUH VP 3497. **J**: Trunk scale in crown view, MGUH VP 3498. **K**: Trunk scale in crown view, MGUH VP 3499. **L**: Trunk scale in oblique crown view, MGUH VP 3499.
MGUH VP 3495 from GGU sample 298937, Halls Grav; MGUH VP 3496–3499 from GGU sample 82738, Halls Grav; MGUH VP 3502–3504 from GGU sample 319264, Monument.


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

posteriorly, long dentine tubules or canals extend from pulp cavity towards crown. (Translated and modified from Vieth 1980.)

Range. Early Devonian (Lochkovian–Pragian).

Remarks. The original description of *Canonia* was based on a uniform group of disarticulated thelodont scales. This monospecific genus is defined by the small base and narrow neck together with the anastomosing almost straight dentine tubules, which all radiate from the pulp cavity. Following histological examination, Vieth (1980) considered *Canonia* to be of *Thelodus*-type, following Gross' (1967a) classification. Following Turner (1991), *Canonia* should be included with *Thelodus*, *Turinia*, *Apalolepis*, *Nikolivia* and others in the thelodontid histological group. *Canonia* was originally placed closest to *Nikolivia* within the family Nikoliviidae, due to the round base, overlying crown with parallel ridges and relatively straight dentine tubules or canals (Vieth 1980). Such a connection, however, is difficult to discern if one considers their diagnostic features. A small round base, narrow neck and a flat posteriorly overlying crown are characters commonly observed in *Apalolepis*. This genus, placed within another family, Apalolepidae, differs notably by having a much more delicate crown morphology. Also the histology differs in *Canonia* by having anastomosing dentine tubules and canals and by not having more than one pulp canal and curved dentine tubules. These diagnostic histological features, however, are not supported by *Canonia* scales from Severnaya Zemlya Archipelago (V. Karatajute-Talimaa, personal communication 1999). The taxonomical treatment of *Canonia* has been further complicated by new finds of articulated jawless vertebrates with thelodont scales from the Silurian and Devonian of northern Canada (Caldwell & Wilson 1995; Wilson & Caldwell 1998). Based on this new order of 'fork-tailed' agnathans, the Furcacaudiformes, Wilson & Caldwell (1998) suggest that *Canonia grossi* and other nikoliviids are found in several different genera, classified by body morphology, and thereby are not diagnostic of any particular species or genus of furcacaudiforms. They also suggest that scale-based species with furcacaudid affinity should be treated with form taxonomy, parallel to the taxonomy based on articulated specimens. It should, however, be noted that the morphological varieties of scales of furcacaudids so far is weakly characterized and many questions about the relationship between these two types of taxonomy still remain.

***Canonia* cf. *C. grossi* Vieth 1980**
Fig. 17A–D; Fig. 18A

1980 *Canonia grossi* n. gen., n. sp. Vieth, pp. 28–32, fig. 18A–H; plate 3, fig. 1–8.
1988 *Canonia* sp. – Turner & Murphy, p. 959, figs 1.22, 23, 29–34.
1993 Unnamed specimens Wilson & Caldwell, fig. 1f, g.

Holotype. *Canonia grossi*, GSC 202, juvenile scale (Vieth 1980, plate 3, fig. 1a–c), Member A, Red Canyon River Formation, Ellesmere Island, Canada.

Figured material. MGUH VP 3502–3505 from GGU sample 319264.

Other material. About 15 scales from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Diagnosis. As for the genus.

Scale morphology. The present scales of *Canonia* cf. *C. grossi* are very small and fragile, with an average size of about 0.2 mm. Nevertheless, they are well preserved and only broken at the most delicate posterior part of the crowns. Most scales seem not to be etched or water-worn and they are pale brown in colour. Two general scale types have been found of this uniform species each with a small round base, a narrow neck and a round to oval crown with three posteriorly pointing apices. The first type has a flat crown with a wide, smooth longitudinal median part which is on a slightly higher level than the horizontal lateral parts of the crown (Fig. 17D). Starting anteriorly, the margins of the median area converge to a posteriorly pointing median apex. The lateral areas, which are relatively small in the first scale type, have one pair of longitudinal ridges continuing to two lateral apices, but they are almost always broken. The second, slightly smaller, scale type differs by having a narrower median area with one wide and shallow longitudinal furrow (Fig. 17A–C). The longitudinal ridges are slightly higher on the proportionally larger lateral areas before ending posteriorly at the apices. Both scale types have a small fragile base with a wide open central pulp cavity and

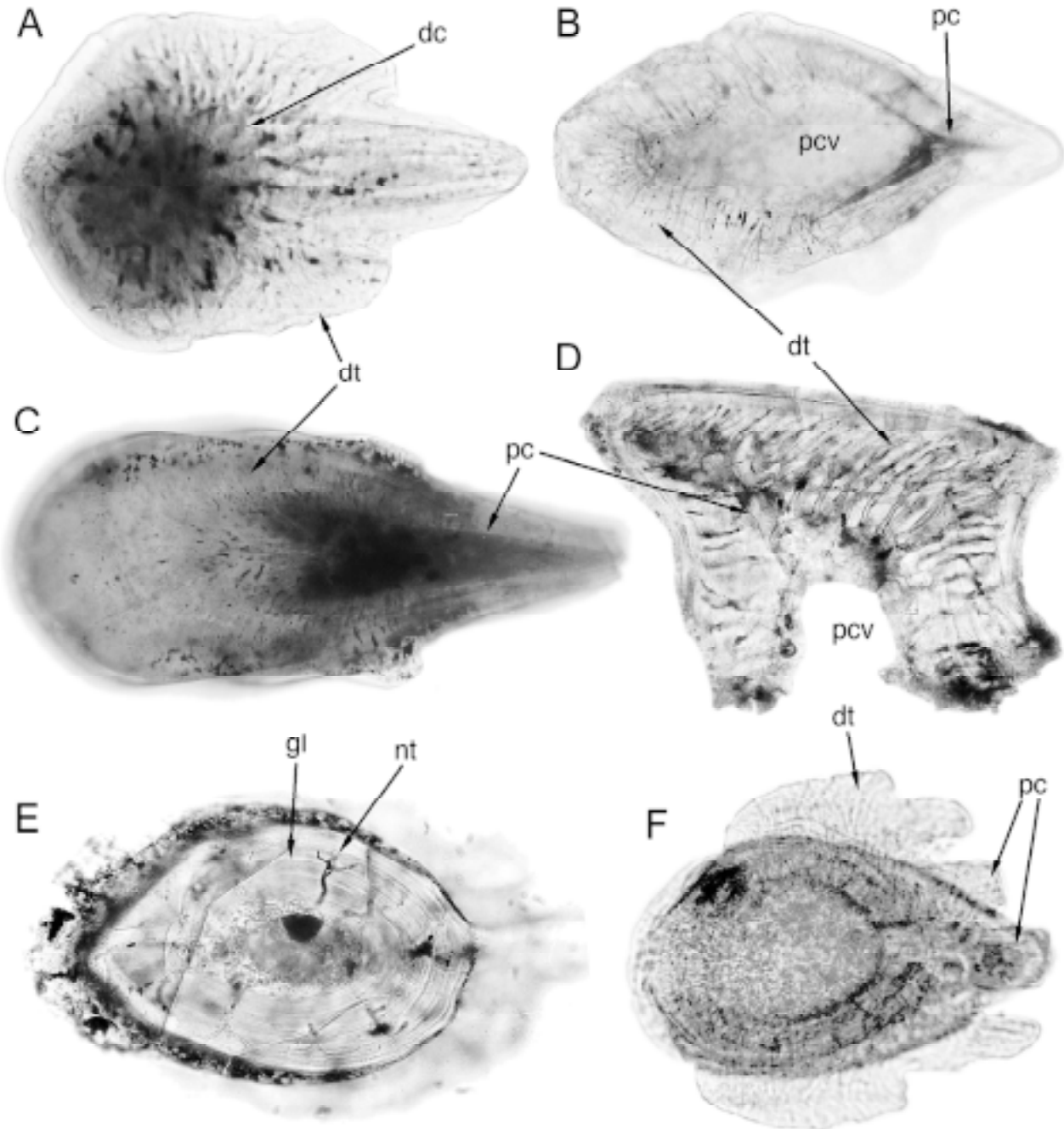


Fig. 18. *Canonia* cf. *C. grossi*, *Nikolivia* sp. and *Thulolepis striaspina* gen. et sp. nov. Histology of the scales.
A: *Canonia* cf. *C. grossi*. in crown view, immersed in aniseed oil, MGUH VP 3505, × 451.
B, **C**. *Nikolivia* sp. immersed in aniseed oil. **B**: Trunk scale in basal view, MGUH VP 3500, × 108. **C**: Trunk scale in crown view, MGUH VP 3501, × 157.
D–**F**. *Thulolepis striaspina* gen. et sp. nov. **D**: Transitional scale in vertical longitudinal section, MGUH VP 3517, × 394. **E**: Head scale in horizontal section, MGUH VP 3506, × 376. **F**: Transitional scale in crown view, immersed in aniseed oil, MGUH VP 3518, × 219. MGUH VP 3500, 3501 from GGU sample 82738, Halls Grav; MGUH VP 3505, 3506, 3517, 3518 from GGU sample 319264, Monument.
dc: dentine canals; **dt**: dentine tubules; **gl**: growth lines; **nt**: neck tubules; **pc**: pulp canal; **pcv**: pulp cavity; **sf**: tubules for Sharpey's fibres.

high narrow neck. These presumed juvenile scales are therefore probably of similar age.

Scale histology. The scales from Greenland are similar to the type material from the Canadian Arctic; they are of thelodontid type with dentine tubules all radiating from a central or anterior pulp cavity (Fig. 18A). Many dentine tubules repeatedly converge on the pulp cavity, forming a typical tree-like branching pattern. When the tubules open into the pulp cavity they have almost reached canal thickness. In the posterior part, longer but still branching dentine tubules extend from the pulp cavity towards the crown. Growth lines and tubules of Sharpey's fibres are present but difficult to see in the few specimens available.

Scale dimensions. Length 0.2–0.3 mm; width 0.1–0.2 mm.

Remarks. The general features of the material from Greenland are similar to the type material from Canada (Vieth 1980). The first type described above (Fig. 17D), with a wide and smooth median area, does not have any exact equivalent in Vieth's material, but can in general be compared to one of her most common forms, with a smooth flat central platform and only one pair of lateral crown ridges (Vieth 1980, plate 3, fig. 1). The other type described herein is similar to the second most common type described by Vieth (1980, plate 3, figs 2, 4, 6). This form, which is characterized by a narrower slightly concave median ridge, is also figured by Wilson & Caldwell (1993, fig. 1f, g) from Canada, as well as by Turner & Murphy (1988, fig. 1.22, 23, 29–34) from USA. Types with more than one pair of lateral ridges are not represented in the poor set of *Canonia* cf. *C. grossi* from the Chester Bjerg Formation (Vieth 1980, plate 3, figs 3, 5, 7, 8). Scales of *C. grossi* type are also found in residues from Severnaya Zemlya, the Timan-Pechora Region, Podolia and Spitsbergen (Talimaa in press, V. Karatajute-Talimaa, personal communication 1999). They all lie within the morphological ranges present in the type material and are all of Lochkovian age.

Occurrence. *Canonia* cf. *C. grossi*, Lochkovian, Monument, Hall Land, North Greenland; *Canonia grossi* Lochkovian–Pragian, eastern Arctic Canada; Lochkovian, Severnaya Zemlya, Russia; Lochkovian, Timan-Pechora Region, north-eastern part of European Russia; Lochkovian, Podolia, Ukraine; Lochkovian, Nevada, USA.

Family Incertae sedis

Genus *Thulolepis* gen. nov.

Derivation of name. A combination of the name Thule, referring to the original Eskimo settlement Thule in North-West Greenland (*thule* is also Latin form of the Greek word used of an island or point of land in the extreme north), and the Greek word *lepis*, for scale.

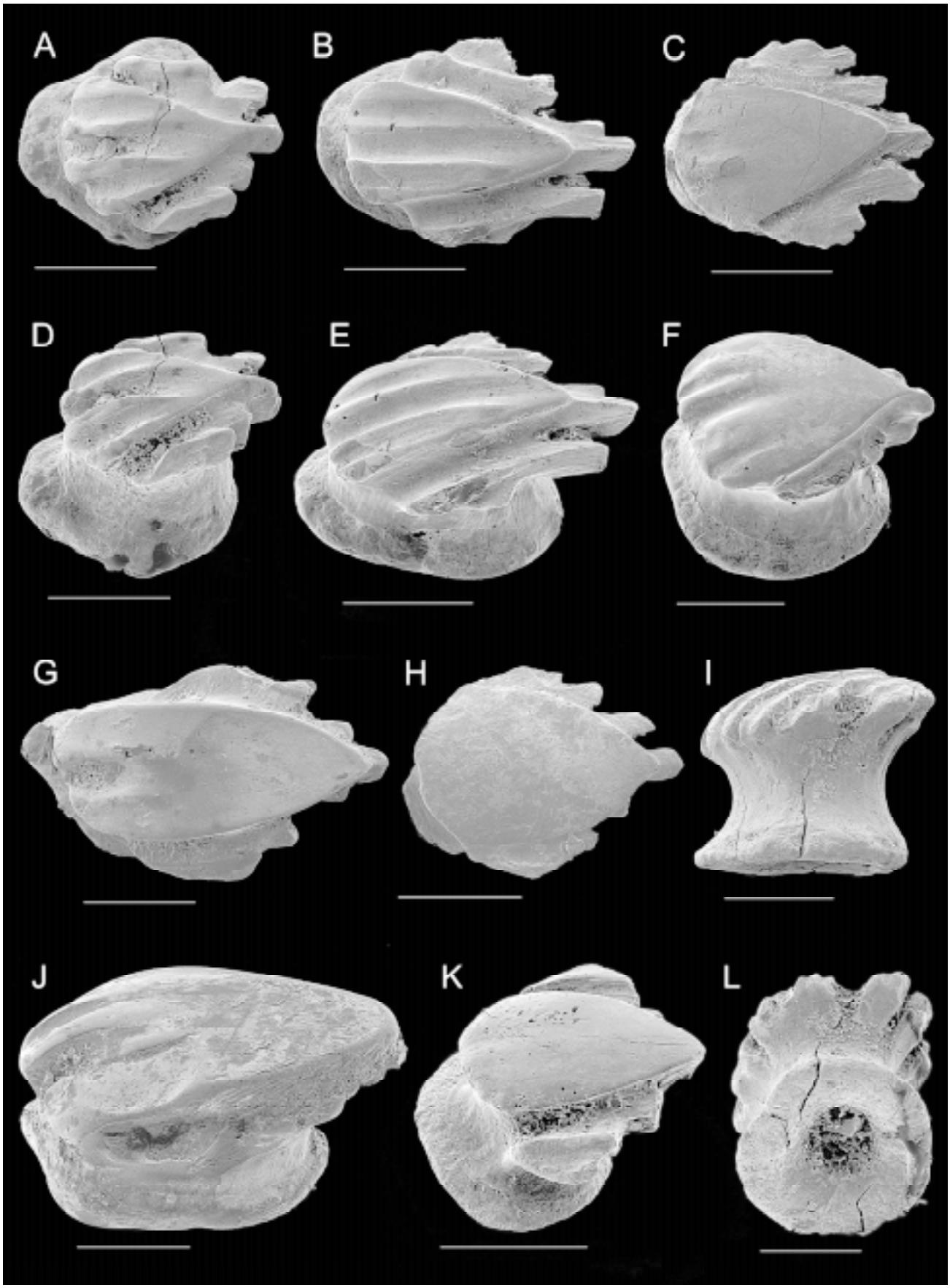
Type species. *Thulolepis striaspina* gen. et sp. nov.

Diagnosis. Very small thelodontid scales, length about 0.2 mm, with ornamented or smooth sub-triangular shaped median crown area, furrowed anteriorly; ridged and furrowed dorso-lateral crown area, forming five posteriorly pointing spines or apices with small longitudinal micro-ridges; base round to oval, often smaller than crown; neck smooth high and narrow; straight or curved dentine tubules pass directly into pulp cavity; tubules converge and join to greater thickness towards pulp cavity; distinct dentine tubules in neck; 1–5 narrow pulp canals extend from pulp cavity towards spines.

Range. Early Devonian (Lochkovian).

Remarks. This genus is established for a thelodontid scale with wide, slightly curved, dentine tubules, branched narrow pulp canals and distinctive morphological characters, such as a high neck and a heavily ornamented crown. *Apalolepis* Karatajute-Talimaa 1967 (Obruchev & Karatajute-Talimaa 1967) also has bran-

Fig. 19. *Thulolepis striaspina* gen. et sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in crown view, MGUH VP 3507. **B**: Transitional scale in crown view, holotype, MGUH VP 3510. **C**: Transitional scale in crown view, MGUH VP 3512. **D**: Head scale in oblique crown view, MGUH VP 3507. **E**: Transitional scale in oblique crown view, holotype, MGUH VP 3510. **F**: Transitional scale in oblique crown view, MGUH VP 3513. **G**: Trunk scale in crown view, MGUH VP 3515. **H**: Transitional scale in crown view, MGUH VP 3514. **I**: Head scale in lateral view, MGUH VP 3511. **J**: Trunk scale in oblique crown view, MGUH VP 3516. **K**: Transitional scale? in oblique crown view, MGUH VP 3519. **L**: Head scale in basal view, MGUH VP 3511.
All specimens from GGU sample 319264, Monument.


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

ched pulp canals and curved tubules of a slightly different kind in the crown, but *Thulolepis* gen. nov. differs in terms of its higher more robust crown, larger base and posteriorly pointing spines. In crown morphology *Thulolepis* gen. nov. resembles most closely genera such as *Turinia* Traquair 1898 or *Nikolivia* Karatajute-Talimaa 1978, but the base and the neck are similar to scales of *Thelodus* Agassiz 1839. In some species of *Thelodus* it is possible to find curved dentine tubules but characters such as branched pulp canals and heavily ornamented crown are not diagnostic for *Thelodus*.

While *Thulolepis* gen. nov. shares characters with several different genera it shows no clear affinity regarding family level assignment.

***Thulolepis striaspina* gen. et sp. nov.**
Fig. 18D–F; Fig. 19; Fig. 20; Fig. 21A

Derivation of name. From Latin *stria* and *spina*, referring to the striated crown spines.

Holotype. Transitional scale; MGUH VP 3510 from GGU sample 319264 (Fig. 19B, E; Fig. 21.4).

Figured material. Head scales; MGUH VP 3506–3509, 3511. Trunk scales; MGUH VP 3515, 3516. Transitional and specialized scales; MGUH VP 3510, 3512–3514, 3517–3519. All from GGU sample 319264.

Other material. 75 head and transitional scales from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Diagnosis. As for the genus.

Scale morphology. *Thulolepis striaspina* gen. et sp. nov. is represented by probable head and trunk scales and intermediate morphologies, some of which may represent transitional scales. The scales are quite well preserved, although some are broken, and vary in colour from pale brown to dark brown or black. They are not etched or water-worn and their histological characters are well preserved. All scales are very small and only the presumed trunk scales exceed 0.3 mm in length. The more rounded head and transitional scales have a diameter about 0.2 mm.

The typical head scale is rounded with a heavily ornamented crown, a distinct and relatively high neck, and a round base which is almost as large as, or wider than, the crown (Fig. 19A, D, I, L; Fig. 20.1–3). A round wide open pulp cavity is visible at the central part of the base. The convex crown is almost round with downturned anterior ridges and furrows. These deep furrows are almost as wide as the intermediate ridges they are placed between and the number of furrows varies between one and five in different scale forms. The median furrow is mostly deeper than the flanking ones and its length varies greatly from scale to scale. One pair of deep lateral furrows, which also turns down towards the neck at the antero-lateral part, divides the median crown areas and the wide lateral crown area. These lateral regions should be regarded as a second, more posterior and slightly lower level of the crown. Posteriorly these two different crown levels intergrade to an apex and spine extension, flanked on the same lateral level by two pairs of spines. Posteriorly, on the lower side of the crown, narrow ridges run from each spine towards the base.

On the larger and more elongated trunk scales, the crowns are larger and much smoother, having only one deep short anterior furrow (Fig. 19G, J; Fig. 20.8, 9). The lateral areas of the crowns are proportionally smaller but show traces of a third pair of posteriorly pointing spines. The triangular median crown area is elongated and converges to an apex just above the posterior spine, which lies on the same level as the spiny lateral areas. Similar to the typical head scales, the trunk scales of *Thulolepis striaspina* gen. et sp. nov. have a wide, open, pulp cavity and a high narrow neck. The basal part of the trunk scales, however, follows the general trend shown in the crown by having a more elongated base and pulp opening when compared with the head scales.

Various scales lying between the morphological extremes represented by the head and the trunk scales can be regarded as transitional scales and other specializations (Fig. 19B, C, E, F, H, K; Fig. 20.5–7, 10). The main variable character is the anterior furrows of the crowns which can be less pronounced than in the typical head scale. The number and length of furrows also varies, and in some scales, the furrows are completely absent (Fig. 19H, K; Fig. 20.6, 10).

Several thin parallel ridges are visible along the surface of several of the posteriorly pointing spines, almost all of which are broken (Fig. 21A). Almost all scales have a thin base and wide open pulp cavity (Fig. 19I, L) and are of similar, relatively young, age.

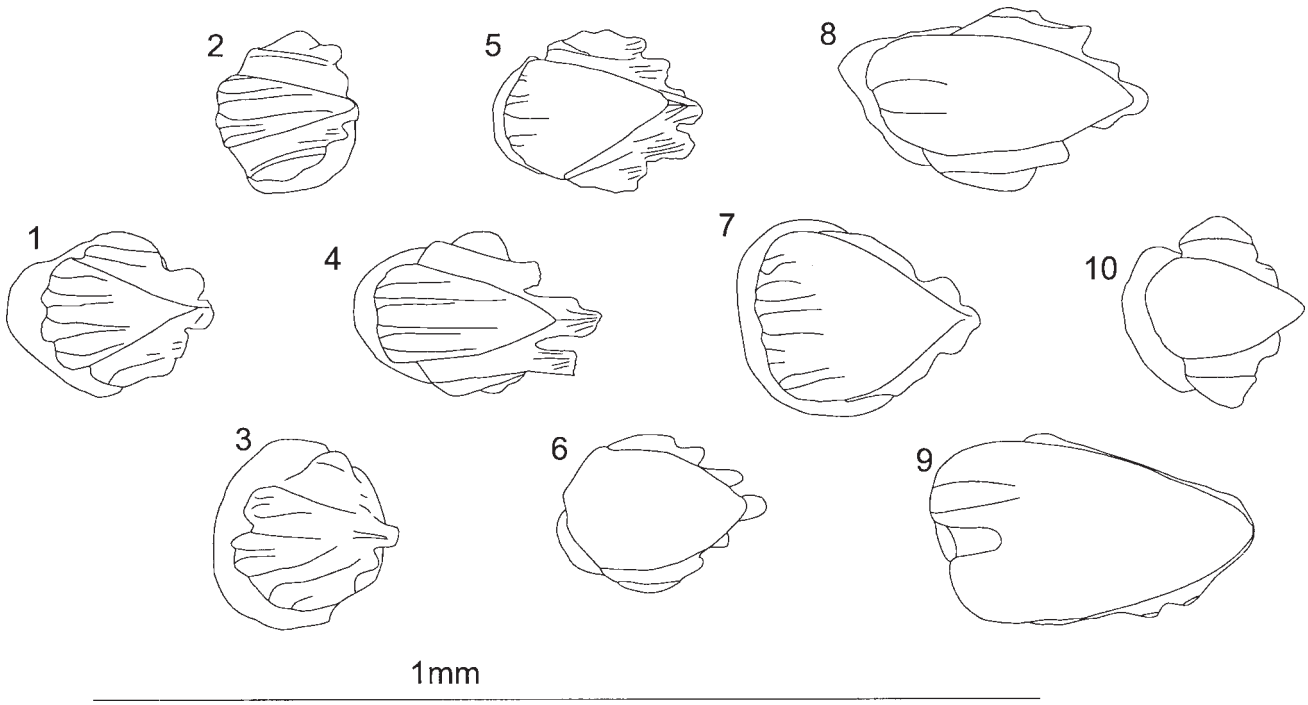


Fig. 20. *Thulolepis striaspina* gen. et sp. nov. The main morphological scale varieties in crown view.
1: Head scale, MGUH VP 3507. **2**: Head scale, MGUH VP 3508. **3**: Head scale, MGUH VP 3509. **4**: Transitional scale, holotype, MGUH VP 3510. **5**: Transitional scale, MGUH VP 3512. **6**: Transitional scale, MGUH VP 3514. **7**: Transitional scale, MGUH VP 3513. **8**: Trunk scale, MGUH VP 3515. **9**: Trunk scale, MGUH VP 3516. **10**: Transitional scale, MGUH VP 3519.
All specimens from GGU sample 319264, Monument.

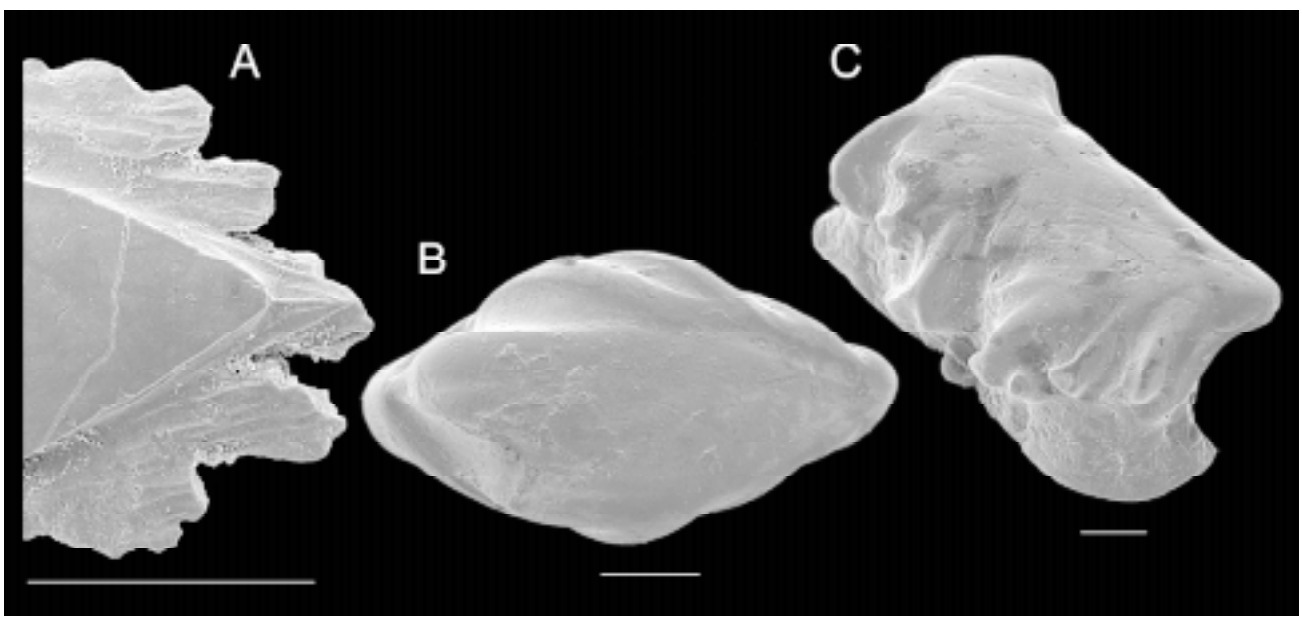


Fig. 21. Thelodont scales. SEM photomicrographs. Scale bars equal 0.1 mm.
A: *Thulolepis striaspina* gen. et sp. nov. Transitional scale in crown view, close up of posterior crown edge, MGUH VP 3512.
B, **C**. Thelodontida indet. **B**: Scale in crown view, MGUH VP 3520. **C**: Two scales grown together in oblique crown view, MGUH VP 3521.
MGUH VP 3512, 3520 from GGU sample 319264, Monument; MGUH VP 3521 from GGU sample 82737, Halls Grav.

Scale histology. The scales of *Thulolepis striaspina* gen. et sp. nov. have a typical thelodontid histology with straight or slightly curved dentine tubules passing directly into a central or slightly anterior pulp cavity (Fig. 18D–F). Some of the dentine tubules also radiate from each of the pulp canals which extend from the pulp cavity towards the postero-lateral crown spines. The converging tubules join and increase in thickness one or two times before they open into the pulp cavity. The outer layer of the crown, representing the initial cap, is proportionally thick with quite dense structure. In the neck area, towards the base, a few thicker longitudinal tubules are visible. The abundant growth lines are most clearly visible in central parts of the scales. The basal tissue is distinct with only a weak indication of tubules of Sharpey's fibres.

Scale dimensions. Length 0.1–0.4 mm; width 0.2–0.3 mm; height 0.1–0.2 mm.

Remarks. The small sample of scales of *Thulolepis striaspina* gen. et sp. nov. does not give a true picture of the proportion of scale types. Very few of the larger, presumed trunk, scales are found and there is not enough information to interpret the true squamation. The crown ornamentation of head and transitional scales is equivalent to *Thelodus admirabilis*, described by Märss (1982). *Thulolepis striaspina* gen. et sp. nov. differs notably by having a lateral wing or area on a slightly lower level and branched pulp canal.

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

Thelodontida indet.
Fig. 21B, C

Figured material. MGUH VP 3520 from GGU sample 319264 and MGUH VP 3521 from GGU sample 82737.

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

Remarks. These problematic scales show typical thelodontid characters, including a high distinct neck, robust base and a central pulp cavity. The rhomboidal or oval crown is flat and smooth, often with up to three pairs of smooth and wide lateral ridges and furrows running posteriorly with a steep angle from the neck. Scales of this type have been found growing together in pairs (Fig. 21C). They have a turiniid appearance but more material is required before their affinity can be assessed.

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

Heterostraci

Cyathaspidiformes indet.
Fig. 22A–F

1976 *Poraspis* sp.; Bendix-Almgreen, Fig. 443F.

Figured material. MGUH VP 3522 from GGU sample 82737, MGUH VP 3523, 3524 from GGU sample 82738, MGUH VP 3525, 3526 from GGU sample 298937.

Other material. About 20 fragments of variable size and preservation from GGU samples 82736, 82737, 82738, 298937.

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

Description. Fragments of Cyathaspidiformes indet. are

Fig. 22. Indeterminate Cyathaspidiformes and Pteraspidiformes. SEM photomicrographs. Scale bars equal 0.2 mm.
A–**F**. Cyathaspidiformes indet. **A**: Fragment of antero-lateral part of head shield or branchial plate in upper view, MGUH VP 3522. **B**: Median dorsal trunk scale in upper view, MGUH VP 3523. **C**: Fragment of anterior part of head shield in upper view, MGUH VP 3524. **D**: Ventro-lateral? trunk scale in upper view, MGUH VP 3525. **E**: Fragment in visceral view, MGUH VP 3526. **F**: Fragment of antero-lateral part of head shield or branchial plate, close up of tubercles in upper view, MGUH VP 3522.
G, **H**. Pteraspidiformes indet. **G**: Fragment in upper view, MGUH VP 3527. **H**: Fragment in upper view, close up of tubercles, MGUH VP 3527.
MGUH VP 3522 from GGU sample 82737, Halls Grav; MGUH VP 3523, 3524 from GGU sample 82738, Halls Grav; MGUH VP 3525, 3526 from GGU sample 298937, Halls Grav; MGUH VP 3527 from GGU sample 319264, Monument.