Late Silurian fish microfossils from Ramsåsa (sites D and 'south of church'), Skåne, south Sweden

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The microvertebrate assemblages from Ramsåsa sites D and 'south of church', Skåne, south Sweden are described for the first time. Analysis of these microvertebrate assemblages from the Öved Sandstone Formation of Skåne indicates a Ludlow rather than Pridoli age. One of two faunas from Ramsåsa site D contained the zonal fossil *Thelodus sculptilis* and the other *T. sculptilis* in association with *Paralogania ludlowiensis* and *Thelodus carinatus*. The presence of *T. carinatus* is the youngest record of this species in Laurussia, and indicative of the transitional phase between the *Andreolepis hedei* and *T. sculptilis* Zones of the East Baltic Microvertebrate Standard. A fauna with *Thelodus parvidens*, from south of Ramsåsa church, proved only broadly datable as Ludlow (Whitcliffian). *T. parvidens* is the dominant species in the three faunas. Several *Thelodus* scale variants are described and compared within species concepts of *Thelodus parvidens* and form overlap between scales of histologically similar *Thelodus* taxa in the Late Ludlow of the region is considered. The analysis of the morphological features of the trunk scales of the acanthodian *Nostolepis striata* is continued. Scale forms of *Gomphonchus volborthi* and other, unidentified acanthodian scales are described and compared. The interregional correlation of the Scanian fish faunas on the basis of recent faunal data is surveyed.
A contribution to IGCP 406: Circum-Arctic Palaeozoic Vertebrates

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Introduction

Microvertebrate assemblages from Ramsåsa sites D and 'south of church', Scania, south Sweden are described for the first time. The fossils derive from three samples housed in the fish collections of the Palaeozoology section of the Swedish Museum of Natural History in Stockholm. The exposures at Ramsåsa which yielded the samples were not the best accessible (Moberg, 1910: 140). They were in Grönwall's (1897) zone

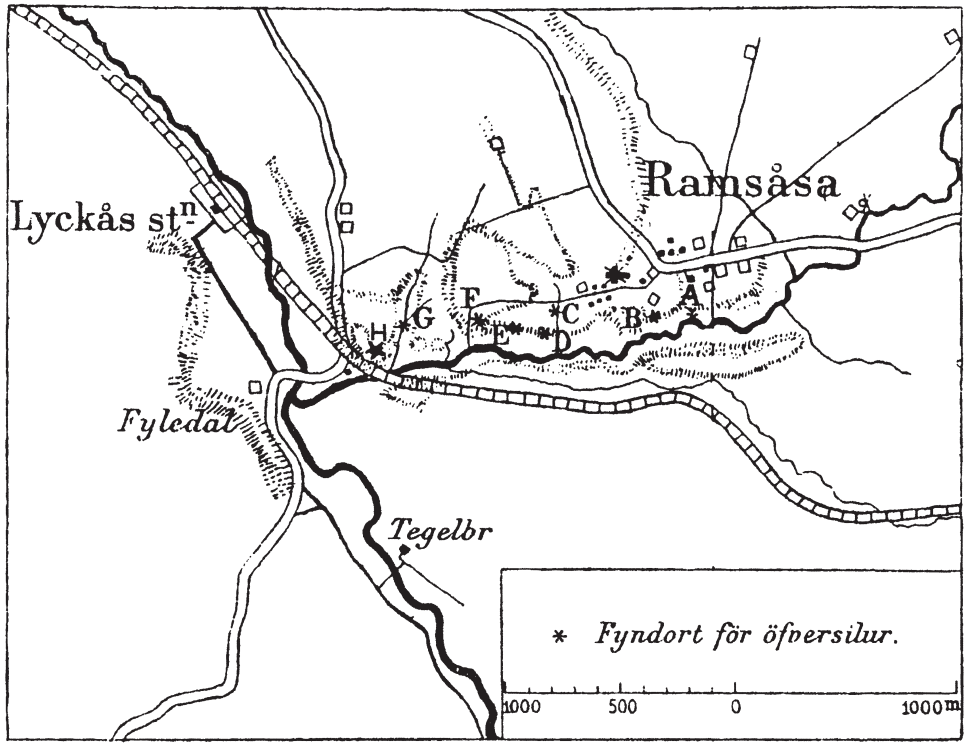

Fig. 1. Outcrops in the Öved Sandstone Formation in the Ramsåsa area (adapted from Grönwall, 1897).

4 (site D), and possibly zone 3 (site 'south of church') (Moberg, 1910: 140), now grouped together in the Öved Sandstone Formation (Jeppsson & Laufeld, 1986), the younger of the two formations that make up the Upper Silurian Öved-Ramsåsa Group. For a discussion on the age of the ÖSF, dated as Pridoli by Jeppsson & Laufeld (1986), see Vergoossen (1999b), and the correlation sections in this volume.

The rocks at Grönwall's (1897) locality B, south of Ramsåsa church (Fig. 1), are red limestone and reddish greenish mottled limestone (Larsson, 1979). The NRS rock sample from south of the church was a mottled limestone with thin intercalated mudstone layers that were harder to dissolve; the rock was greyish green with one purplish surface.

Grönwall (1897: 218-219) described three exposures from locality D, of which two yielded fish remains: the second exposure '*Onchus*' sp. and 'scales and teeth of fish', the third '*Onchus*' sp. Larsson (1979) designated the three shallow outcrops Ramsåsa 4-6 and recorded the following lithologies: reddish brown, soft mudstone and red thinly bedded limestone (Ramsåsa 4); soft red mudstone (Ramsåsa 5); reddish brown silty mudstone (Ramsåsa 6). Jeppsson (1974) and Larsson (1979) didn't mention fish fossils from their Ramsåsa D samples. Jeppsson (1974) dissolved c. 900 g of rock, from which he recorded 65 conodonts in total (two from D1, 63 from D3). These numbers are very low. By comparison the NRS samples from site D, of which the precise sampling spots are unknown, were rich in fish scales (see below) and contained rare con-

odont fragments. For faunal (other than vertebrates) and stratigraphical references concerning Ramsåsa sites 4-6 see Larsson (1979).

Abbreviations, symbols and definitions

Abreviations:

hv Helvetesgraven variant
NRS Museum of Natural History, Palaeozoology Department, Stockholm
ÖSF Öved-Sandstone Formation
rhv Ramsåsa H variant
right (left, top and bottom, in the description of figured scales): see Vergoossen (2002b)

costatiform: *Thelodus* head scales with a crown of alternating folds and radial ridges that converge distally, dorsally or posteriorly in a pointed top or a dorsal ridge. Shorter intermediate ridges may be present. This term excludes smooth-crowned forms of *Thelodus costatus* sensu Gross, 1967 with notched crown rims.

dorsal view (in illustrations): is the same as crown view, but has been preferred in compounds such as laterodorsal, anterodorsal etc.

flat: in contrast to deep and round, swollen or hemispherical.

glabrous: *Thelodus* scales with smooth crowns that have no notched, ridged, or folded rims, e.g. particular cephalopectoral scales of *T. parvidens.*

horizontal: in contrast to sloping, slanting, or vertical.

Material and registration

Ramsåsa, locality 'south of church'

The NRS collections contained one, small, registered block with a site/collection sticker reading: 'Q 606 Ramsåsa block s kyrkan E. Stensiö 1924' (registration number and geographic position hand-written). The map (Fig. 1) shows Grönwall's locality B in that place. The term 'block' may indicate that a loose rock was picked up, but more precise information on the site, or a site letter, are lacking. All the Scanian rocks in the Palaeozoic fish collection with 'E. Stensiö 1924' on their sticker, have either a letter for the site or some other site information. The rock weighed 69 g and contained c. 30 scales (28 glabrous *Thelodus parvidens* scales, one *T. bicostatus* scale, and one scale of Acanthodii, morph 1 cf. *Gomphonchus volborthi*) of poor preservation and easily destroyed with a wet brush. Non-vertebrate fossils included ostracodes, tentaculites and possibly crinoid remains.

Ramsåsa, locality D

The two small rocks available from this locality carried site/collection stickers with the name of E. Stensiö 1924. One rock had a written registration number, Q 685, the other had no registration number. Both rocks were given a serial working number: SW 4 and SW 24 respectively. Rock Q685/ SW 4 weighed c. 54 g and was a fine-grained red-brown, sandy, micaceous limestone, with cast of many fossils, especially ostracodes. Most of the scales were destroyed during acid processing. A first bath in diluted acetic acid (10%) had not sufficiently 'cleaned' the scales. An attempt to

remove the adhering particles from most of the material in a second bath of 5% acetic acid proved destructive. A small number of scales (c. 500) survived for identification. These had been treated in a second bath of 10% acetic acid that had been used before.

There was a handwritten identification note with sample SW 24 reading '*Thelodus* scales'. The handwriting differed from that on the collection sticker. Apart from microvertebrates, the residue contained fragments of brachiopods or bivalves, ostracodes, and rare gastropod, ?phyllocarid, and conodont fragments. Weight: 13.6 g; fraction 0.212 mm sieve width had a total weight of 207 mg (dry unsorted residue) and contained 45 fish remains identifiable to species level per 1.7 mg residue: thelodonts: 42 (*Thelodus parvidens*, glabrous crowns: 38; forma *costatus*: 3; forma *trilobatus* 1); acanthodians: 3 (*Nostolepis striata*: 2; acanthodian gen. et sp. ?, morph 1: 1).

Methods

To facilitate picking, the residues were sieved into fractions with the following mesh widths: 0.106-0.212-0.355-0.425-0.5-0.710-0.850 mm. The latter two yielded practically no material. Gradually it became clear that from 0.5 mm downwards considerable differences in faunal composition could occur between the fractions. For instance, among the thelodonts in SW 24 the number of glabrous *T. parvidens* scales in the 0.355 mm fraction was more than eight times higher than in the 0.106 mm fraction, whereas the number of trilobatiform scales in the 0.355 mm fraction was five times lower than in the 0.106 mm fraction. *T. sculptilis* scales were most efficiently picked from the 0.106 mm fraction. In the fractions larger than 0.212 mm this species became extremely rare. The acanthodian remains also increased in number and diversity from 0.5 mesh width downwards: indeed the only complete but moderately preserved acanthodian tooth whorl came from the 0.106 mm fraction. Stellate and coronate tesserae were only collected from the 0.212 mm fraction down. These findings were unexpected. In the literature no distinction is usually made between taxa or taxon variants within several size groups, apart from general statements about the smallest and largest scale size of a particular species.

Systematic descriptions

The fish remains discussed here, mainly scales and scale groups, are considered para-, scio- or scleritome taxa because complete fish showing the diversification of the squamation on the body, and ontogenetic series of such fish, are not yet available for any of the taxa. For this reason classification above the genus level has, as a rule, been avoided. The discussion especially focuses on those remains whose classification within conventional microvertebrate systematics is unresolved.

Thelodonti

Thelodus parvidens Agassiz, in Murchison, 1839, sensu Märss, 1986
Pls 1-6; Pl. 7, figs. 40b-41b, 44-47a; Pl. 8, figs. 47b-50.

This designation refers to the species in its widest possible sense, in contrast to *Thelodus parvidens* Agassiz, sensu Gross, 1967 (also used in this paper), which only

refers to smooth-crowned scales as described by Agassiz and comparable with the type material, and represents the most restricted concept of the species.

Head scales

Costatiform (oral) scales (figs. 1-6): These scales have a crown of several alternating folds and radial ridges that converge distally, dorsally or posteriorly into a pointed top or a dorsal ridge. Shorter intermediate ridges may be present. The term has a more restricted morphological reference than the morphology of *Thelodus costatus* (Pander, 1856) sensu Gross 1967, because it excludes forms with notched crowns (e.g. Gross, 1967: pl. 1: 9, 11).

Parts of the crown of rectangular scale P8909 (fig. 1) have broken off. The crown has circa seven, sharp (radial) main ridges, which rise from the neck ab centro. Then they curve back centrad at sharp angles (almost 90° in some ridges) and converge into a dorsal ridge (fig. 1b). Distally the ridges are straight, their greatest convexity is low in the crown. There is at least one short intermediate ridge (fig. 1a, right) in what is probably the anterolateral crown. Vertical neck low, with faint posterolateral vertical riblets. A thickened rim (approximately of same height as neck) forms the base.

The crown of P8910, a tiny scale (fig. 2), is more rectangular than the crown in fig. 3b. Five radial ridges converge in a short, semicircular, dorsal ridge. One of the ridges (on the right in fig. 2) is, in fact, the continuation of a pair of shorter ridges which converge in the lower crown part. All the ridges rise from the neck ab centro and then curve back centrad in the lower crown part, at angles of almost 90°. Neck and base low, transition indistinct.

Another tiny scale, P8911 (fig. 3), has a round crown ('bonnet' type) with five, sharp, radial ridges that converge distally. The ridges curve up from near the upper base, a clear neck cannot be distinguished. This upper basal surface slopes down and widens out ventrad. The base is rounded hexagonal.

Scale P8912 (fig. 4) has a round crown with seven distally converging radial main ridges. Distally the crown is blunted. There is one short intermediate ridge low in the crown (to the right in the photo).

The crown of P6913 (fig. 5) deviates from the bonnet type in that it has widened out on one side (fig. 5a). The crown has several worn radial ridges that bend upwards and ascend from the neck and converge into a blunted, mid dorsal ridge (fig. 5b). The ridges on the elongated crown side are much longer than the others (fig. 5a). The greatest convexity of the ridges lies half way up (fig. 5b). All around, the crown is larger than the neck but does not overhang it. The neck is low, vertical and smooth. A basal rim separates the upper basal platform from the rest of the deep and robust, oval base that is slightly concave where the pulp hole is situated (fig. 5b). The base makes up one third of the total scale height.

In side view (fig. 6b) the crown of P8914, a worn scale, is somewhat rectangular. The base has a similar shape (fig. 6a). Six blunted, radial crown ridges bending upwards from the neck converge pointwise distally. The greatest convexity of the ridges is close to the neck. All around, the crown is slightly larger than the neck but does not overhang it. The vertical neck has faint, vertical ribbing, and is moderately high all around, making up about 20% of total scale height. A narrow upper basal zone is marked off by a faint basal rim. The base is rounded in one half, and more angular in the other (fig. 6a). Base low, flat and horizontal.

Remarks: Two types of crowns have been observed: those in which the crown in its lower part bends for some distance away from the neck and curves back centrad at a sharp angle; the further away a crown ridge bends from the neck, the more wing-like it may be developed (figs. 1b, 2). Such crowns can be larger than the base. This scale variant might be transitional to *T. traquairi* scales. In the other type of crown the ridges do not bend away from the neck so markedly and the upward curve is less angular: in those scales the crown is well contained within base (fig. 6a).

Pugniform scales (= *Thelodus pugniformis* Gross, 1967) (figs. 7-9): The peculiar, vertical orientation of many pugniform crowns that resemble a ping-pong bat or baseball catcher's glove might have served to block the flow of water rather than to provide free and smooth passage for it. Even in the variant that I published from Helvetesgraven (Vergoossen, 1999b: pl. 1: 5), which has a horizontal crown and a median dorsal crown keel directed anteroposteriorly, such a function is feasible depending on how the scale was fixed in life position. Instead of interpreting that specimen as transitional to the common, smooth-crowned cephalopectoral *T. parvidens* scale sensu Märss 1986, it is also possible to argue that the keel is a further specialisation to 'cleave' the water flow. Gross (1967: 17) suggested a very restricted occurrence on the head (mouth region), but did not indicate why. Gross also thought that this scale type might derive from several *Thelodus* taxa: *T. parvidens, T. traquairi, T. schmidti*. To these Karatajute Talimaa (1978) added *T. marginatus* (= *T. carinatus* sensu Fredholm, 1988a) and *T. sculptilis.* Märss (1986) included the pugniform scale type as oral scales in the body zonation scheme for *T. laevis* (op. cit.: text-fig. 18: 1) and *T. parvidens* (ibid.: text-fig. 19: 6).

Gross (1967: pl. 2: 11) illustrated a scale with a posterior crown edge that has several lobes ('cockscomb-like'), and one with a shallowly notched distal crown edge (op. cit.: pl. 2: 7).

Fredholm (1990: fig. 6E) showed a pugniform *T. schmidti* scale with five distal lobes. Scale P8915 (fig. 7) is trilobed, with a prominent median lobe that overhangs neck and base (fig. 7c). The neck is high. Midventrally, where the pulp hole is, the base is concave (fig. 7c). A similar basal feature was illustrated in some scales by Gross (1967: pl. 2: 8a, 9b, 10a, 12) and by Märss (1986: pl. 21: 5). A concave base may have spanned arched cartilage. This, together, with the peculiar shape of the scales, could indicate oral, pharyngeal or branchial derivation.

Bilobed scale P8917 (fig. 9) has a strikingly concave base. The distal crown edge has a median fold which divides the upper crown into two equally sized lobes. Gross (1967: pl. 2: 12) figured a bilobed specimen where a fold in the distal crown edge is situated off centre (towards lateral) producing two lobes of unequal dimensions. One of the lateral crown edges is damaged (fig. 9a) showing radiating dentinal tubules?

The distal crown edge of P8916 has been worn down and flattened (fig. 8b) and was perhaps trilobed originally (cf. fig. 8a). The anterior base is thickened.

Cephalopectoral scales

Bicostatiform scales (= *Thelodus bicostatus* Hoppe, 1931, sensu Gross, 1967) (figs. 10-20)

Gross (1967) thought that these scales were part of *T. parvidens* or *T. trilobatus.* Fredholm (1989: 33) considered bicostatiform scales diagnostic of *T. parvidens*. Märss

1986 (pl. 21: 3) illustrated a scale demonstrating a combination of costatiform and bicostatiform features.

P8918 (fig. 10) and P8919 (fig. 11) show the characteristic forms of horizontal crown smaller than base, and with a raised, parallel, median ridge pair. There are minor differences in preservation and in size of the several features between the scales.

In P8920 (fig. 12) the two median crown ridges ascend steeply from near base level anteriorly, where the fold between the ridges is constricted. The ridges soon bend to horizontal and continue more or less parallel to posterior. On each side the ridge pair is flanked by one, stepped down, more or less parallel lateral ridge which begins posteriorly to the median pair and at a higher level, and ascends more gently. Neck and base are low. Posterolateral neck and base poorly preserved, or broken off.

P8921(fig. 13) is a similar specimen, but the preservation of the lateral ridges and the crown rims is poor so that these features are hard to distinguish in anterior view (fig. 13a). The median ridge pair ascends less steeply. The base, with anteromedian swelling, is deeper anteriorly than posteriorly.

In P8922 (fig. 14) the median fold is almost three times narrower. The crown ridges and crown rims converge into a posterior cusp (cf. the specimen in fig. 15b).

P8923 (fig. 15) has a distinct neck all around (well visible in side view, fig. 15b) and vertical, straight neck ribs laterally and posteriorly (fig. 15b). A higher neck especially affects the vertical position where the anteromedian ridge pair of the crown begins: this beginning has been uplifted. Compare in this respect the scales in figs. 15b or 17b with that in fig. 14b. The presence of lateral ridges is unclear: a lateral ridge would seem to be absent on the right (fig. 15a), where the lower lateroposterior part of the crown has broken off, however (fig. 15b). Base low, extended forward and slightly thickened forward (fig. 15b).

The presence of lateral crown ridges is also unclear in P8924 (fig. 16). The posterior crown tip overhangs the neck. This neck is well-developed all around, slightly higher posterior than anterior, and with vertical ribs laterally (fig. 16a). The neck is somewhat higher than the base: together they make up circa half the total scale height. The base has a slight anteromedian swelling (fig. 16b).

The crown of P8925 (fig. 17) is so broad that it amply overhangs neck and base lateroposteriorly. Even the right lateral ridge sticks out far over base laterally. The anteromedian constriction of the base (fig. 17a) indicates a tendency towards spur formation (fig. 17b).

The crown of P8926 (fig. 18) shows anterior bifurcation in one ridge of the median pair: actually two shorter ridges curve up from the anterior neck and converge approximately at the same level on the crown where the lateral ridges begin (fig. 18b). Compare this with the short rib to the right of and lateral to the median ridge pair in P8927 (fig. 19). Bicostatiform crowns with bifurcating median ridges, plus lateral ridges might represent a transitional phase to a costatiform crown type. The neck is better developed posterolaterally than anteriorly. The lateral ridges curve up from the lateral crown rim (fig. 18b) and run parallel to this rim (fig. 18a) rather than to the median ridge pair (cf. the lateral ridges parallel to the median ridge pair of P8925, fig. 17a; here the space between crown rim and lateral ridge is also wider). Perhaps the lateral ridges originated in bifurcations of the lateral crown rims? With continuing growth, the crown rim and lateral ridge grew further apart and their parallel course

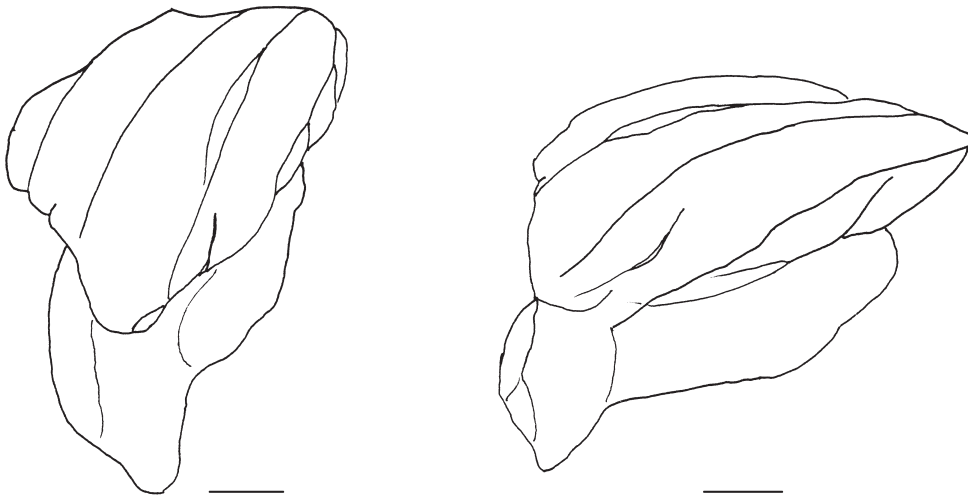

Fig. 2. *Thelodus parvidens* sensu Märss, 1986, bicostatiform scale (P8927) with one ridged crown rim, anterior and lateral views; sample Ramsåsa D, SW 24; size of bar is 0.1 mm.

was undone by the increasing curvature of the crown rim. Serial thin-sectioning may provide evidence for this idea. The base is a low ring constricted anteromedially (fig. 18a), which may indicate a tendency to spur formation, or ventrad growth (fig. 18b).

P8927 (fig. 19; Fig. 2) is interpreted as bicostatiform, but its basal spur is an unusual feature. The specimens described by Gross (1967: 18) had no spur and I know of no other records. The assignation to *T. parvidens* is doubtful because parallel crown ridges may also occur in *T. carinatus*. The fold between the median pair of crown ridges narrows by more than 50% in the posterior crown half. From the point where the constriction occurs, the median ridges follow a parallel course in posterior direction. Anterior to the constriction the ridges follow a converging course. One lateral ridge flanks the median pair on each side. The left lateral ridge is as high as the median pair, but the right lateral ridge is lower. The lateral crown rims are irregular in their posterior part. On the right rim, infoldings and faint ridging can be observed (best visible in fig. 19b and exaggerated in the drawing of Fig. 2) parallel to the short, oblique, anterior riblet to the right of the median ridge pair. The anteromedian basal spur is twisted to the right (fig. 19c) and directed ventrad. The whole scale shows a tendency towards rightward asymmetry and rightward morphological modification. This only specimen needs to be histologically tested.

The median and lateral subparallel crown ridges in P8928, a rhombic scale (fig. 20), are of equal height. The anterior part of the ridges and the distinction between crown and neck are better observable in lateral view (fig. 20b) than in anterior view (fig. 20a), where they have been obscured. The lateroposterior neck has well-preserved vertical and convex riblets (fig. 20c).

Other cephalopectoral scales (figs. 21-27): In the body zonation schemes of Märss (1986) the cephalopectoral scales of the *Thelodus* species from the East Baltic Silurian

consist mainly of smooth-crowned scales in several variations, and in some species also of scales that have few, longitudinal ridges (*T. laevis* Pander, 1856, sensu Märss, 1986, *T. parvidens* Agassiz, sensu Märss, 1986) or grooves (*T. sculptilis* Gross, 1967, *T. admirabilis* Märss, 1982). The ridges cover the entire length of the crown, the grooves are shorter. In *T. parvidens* the term '*bicostatus*' (from *T. bicostatus* Hoppe, 1931, sensu Gross, 1967), or its derivative bicostatiform, is available to distinguish morphologically between the ridged crowns and the smooth-crowned variants. For the latter no morphological terminology is available. The term 'cephalopectoral' not only lacks distinctive morphological reference, but in the case of the smooth-crowned *T. parvidens* variants also refers to a hypothetical position on the body of these scales. To distinguish the smooth-crowned cephalopectoral variants morphologically from each other and from bicostatiform and trunk scale groups and to facilitate the discussion, new descriptive terminology is introduced in this and following sections. 'Glabrous' is used for *Thelodus* scales with crowns that are smooth and without notched, or ridged, or folded rims. The combination 'incised glabrous' refers to smooth crowns that have notched rims, or rims with alternating short ridges and folds. 'Antero-incised' means notched/ridged and folded on the anterior crown rim. 'Postero-incised' means notched/ridged and folded on one/both lateroposterior crown rims, etc.

According to Märss (1982: 114), it cannot be stated with certainty whether smooth cephalopectoral scales from the *T. sculptilis Zone* upwards belong to *T. parvidens*, *T. sculptilis,* or *T. admirabilis*. These species are histologically not distinctive. According to Fredholm (1988a) the smooth-crowned scales of *T. parvidens* and *T. carinatus* are impossible to determine without histological preparation. These factors complicate identification of the glabrous scales in the Ramsåsa D/SW 24 fauna, since the above species, except *T. admirabilis*, are all present. All *Thelodus* scales tested for their histology and with their inner structure preserved well enough, show dentinal tubules arising from the pulp canal and following a straight course up. Dentinal tubules that are strongly curved in their central part (as in e.g. *T. laevis* sensu Märss, 1986 and also thought to be a feature of *T. carinatus* scales by Fredholm, 1988a) have not been observed in material from Ramsåsa D. It is assumed that the glabrous variants discussed below belong to *T. parvidens*, unless stated otherwise and until different data become available. See also section on *T. carinatus*.

The extremely rare form P8930 (fig. 22) is a heart-shaped, posterolaterally incised, glabrous scale with a midposterior point. The crown is slightly convex with a few notches and very short, ridges on one lateral crown edge (on the left in fig. 22b). Neck high, smooth and concave. The shape of the flat base is the same as that of the crown. On the unnotched lateral side (fig. 22b) the crown and base are probably slightly damaged, but the damage has hardly affected the original heart shape. The specimen derives from a specific place on the body, perhaps it is one scale of a pair surrounding an opening (sensory pit ?).

Fig. 23 shows a kidney-shaped, anterolaterally incised, glabrous scale, P8931. The shape is achieved by an anteromedian constriction or inward (= centrad) folding of the scale, which is especially well visible on the base (fig. 23b). The scale is circa twice wider than long. It could have flanked an opening, or might be the result of fusion of two separate scales. The crown is slightly convex and has an anterolateral crown rim with notches and short radial ridges. The posterior rim is smooth. The crown slightly

overhangs the neck. Distinct steep neck (about a quarter of total scale height) with faint vertical ribs. A narrow upper basal zone, bordered by a rim, surrounds the neck. The base is a low and flat.

P8932 (fig. 24), a rectangular, incised glabrous scale, has a convex crown whose edge is lobed rather than ridged (as the anterior crown rims of the scales in figs. 67a, 76b) or notched (as the posterior crown rims of the scale in fig. 76b, or Gross, 1967: pl. 1: 7). The lobes look like drops (cf. the different shape of the lobes in the *T. costatus* scale, Gross, 1967: pl. 1: 11). The right side has more lobes than the left side. Main (central) crown area smooth. Crown overhangs neck all around. The vertical, smooth neck is approximately as high as the flat base.

The rhombic, anterolaterally incised, glabrous scale P8933 (fig. 25) has shallow notches along the entire anterolateral crown edge. This shape might lead on to that of P8984 (fig. 76). The crown edges curve ventrad, more so anteriorly than posteriorly, whereas the median crown is relatively flat. The anteromedian crown is not extra or distinctly marked by a ridge pair, triangular lobe, larger fold nor deeper notches, etc. The midposterior crown is pointed. The vertical neck has lateroposterior vertical riblets and is surrounded by an upper basal rim. The base is low and flat.

A rhombic, midanteriorly incised, glabrous scale is P8934 (fig. 26). The slightly convex crown with a central depression that results from damage has a smooth, rounded rim, except anteromedially where two shallow notches mark off an inconspicuous lobe. The crown overhangs the neck all around. Low basal rim. The crown of this scale differs from that of P8962 (fig. 54), a mid-anteriorly incised glabrous *Thelodus sculptilis* scale, by the shallowness of the anteromedian notches, the absence of radiating ridges and by the fact that the anteromedian crown is not projected forward (cf. Märss, 1986: text-fig. 20: 8).

The midanteriorly and anterolaterally incised, glabrous crown of P8935 (fig. 27) is more convex than the crown of P8934 (fig. 26a). The two, short anteromedian ridges and shallow intermediate fold (fig. 27b) are more prominent than the few short ridges and shallow notches to the left (fig. 27a). The prominence is in part produced by the somewhat deeper incision to the right of the median ridge pair. The crown reaches its greatest convexity and width near midlaterally, and also its greatest ventrad extension. The crown overhangs neck and base. The vertical neck is higher than the neck of P8934 (fig. 26) and has vertical lateroposterior riblets. The base is a flat, narrow ring. This scale might also represent a transitional form to *T. sculptilis* scale P8962 (fig. 54) or it might be a *T. carinatus* scale (cf. the *T. carinatus* scales in fig. 67 and in fig. 7a, Fredholm, 1988a; this latter is incised glabrous and almost round and by its morphology this might also be a *T. parvidens* scale).

The anterior crown edge of P8929 (fig. 21) is rounded and must have had a radial ornament of shallow folds and short ridges. Perhaps the lateral crown edges also had this ornament. Beyond the ridges the crown is smooth. The most characteristic feature of the pentagonal crown are its midlateral and midposterior constrictions: the first is crescent-like and occurs immediately round the anterolateral corners of the crown (fig. 21b; in fig. 21a the crescent is well visible on the left). The second constriction makes the posterolateral crown edges concave and produces a midposterior, rounded tip (fig. 21b). In anterolateral view (fig. 21a), the concavity of the posterolateral edges is hardly visible. The greater part of the crown surface is flat (fig. 21b). The neck is low

and vertical. The basal contours follow those of the crown and its constrictions: this is well visible in posterior view (fig. 21b). The base is larger than the crown, moderately deep and with an upper basal rim. Only the rounded posterior crown tip overhangs neck and base.

Trunk scales

By this conventional designation attention is drawn to three glabrous variants. The terms cephalopectoral and postpectoral have been avoided because the distinctive criteria are not clear in the case of the variants described below. Cephalopectoral *Thelodus* scales are thought to have an oval smooth and flat crown surface, and postpectoral scales have a crown with longitudinal ridges and posterior short spines and a short anterior basal spur (Märss, 1982: 114), but the termini are not always applied without ambiguity. See for example the treatment of such features in *Thelodus parvidens* scales by Märss (1986): compare the cephalopectoral scales in pl. 21: 7-9 with the cephalopectoral scales in text-fig. 20: 9, 11, 13 and the postpectoral scales in text-fig. 20: 18-19.

Though finds of these variants are not common in the Ramsåsa D samples, they have been regularly collected in the smallest fractions (<0.355 mm). The terms calcarate, or spurred, glabrous have been used to distinguish forms with an anteromedian basal spur (cf. Märss, 1986: pl. 21: 7).

Variant 1: spurred and rhizoid glabrous scales (figs. 28-32): The crown of P8936 (fig. 28) extends over base laterally and posteriorly. The scale has a straight anterior crown edge. The neck is high all around, about 2/3 of total scale height, and square anteriorly. There is a short, markedly dorsally flattened (fig. 28a), triangular, anteromedian basal spur, at an angle of little less than 180° to the base. Low, oval, flat, ring-shaped base.

The entire crown plate of P8937 (fig. 29b) is convex, but the ventrad curve is strongest along the lateral edges. Compare with the crown of P8942 (fig. 34), which is more convex, and more evenly so. The anteromedian crown edge is angular (fig. 29b). The crown extends over base laterally and posteriorly. The anteromedian base is slightly constricted (fig. 29b). This is an indication of spur formation, which is directed almost horizontally, as in the base of P8936 (fig. 28a).

The anterolateral edge of the crown of P8938 (fig. 30) is strongly curved ventrad, even more so than in the preceding scale, but the central crown is not curved. In lateral view (fig. 30b) the anteromedian, ventrad basal thickening and beginning of spur formation (directed vertically) is best observed. The rest of the base is a flat plate with a central pulp opening.

The convex, rhombic crown of P8939 has a rounded anterior rim on the right (fig. 31a) and a straight anterior rim on the other side (fig. 31b). The strongest convexity of the crown is in the anteromedian part (fig. 31b). The low, smooth neck (about 15% of total scale height) narrows ventrad. Crown and neck extend over base laterally and posteriorly. The base is deep anteromedially where a distinct constriction marks off an anteriorly rounded, robust spur pointing ventrad. In lateral view (fig. 31b) the upper or dorsal surface of the spur corresponds with the anterior spur surface of P8938 in lateral view (fig. 30b), but these surfaces show a marked difference in dorsoventral inclination: perpendicular in P8938 (fig. 30b) and considerably less steep in P8939 (fig.

31b). The basal development of the latter scale is reminiscent of a specimen of *T. laevis* (Gross, 1967: pl. 1: 14), which has a forward projected, tongue-like anterior basal lobe.

P8940 (fig. 32) has a flat base widening out in anterior direction and with beginning rhizoid formation anteriorly. Although rhizoid formation is a common basal feature in many thelodont taxa, it has seldom been illustrated in glabrous *Thelodus* scales. A second specimen was collected from sample Q 685.

Variant 2: multicuspid glabrous scales (= with multicuspid posterior crown edge) (figs. 33-36): The crown may be bicuspid, tricuspid or have more cusps. A multicuspid glabrous scale from Helvetesgraven was figured by Vergoossen (1999b: pl. 1: 4) and a tricuspid scale figured by Märss (1986: pl. 21: 9) belongs to this variant. Turner (2000: pl. 4: 6-8) figured three multicuspid specimens from 'typical *Thelodus parvidens* Assemblage from Ludlow to early Pridoli' in Britain: fig. 8, Upper Bringewood Formation; fig. 6, Lower Whitcliffe beds; and fig. 7, early Pridoli.

The crown of P8941 (fig. 33) is slightly convex. The posterior crown edge has two sharp, median, posterior points. The neck is ribbed, steep and slightly concave. The crown extends over base lateroposteriorly. Neck/base transition gradually sloping and marked by faint upper basal rim. Oval, flat base, with irregular (fractured?) anterior edge (on one side).

Scale P8942 (fig. 34) has an oval, convex, tricuspid crown with the median point sharpest and longest. The crown widely overhangs the neck, which is faintly ribbed. Base wide open and destroyed on the side shown in the photo.

The crown of P8943 (fig. 35) is less convex than that of P8942 (fig. 34) and tricuspid. The lateral cusps are better developed than those seen in fig. 34. The crown increases in width posteriorly, as the crowns of the scales in figs. 39-41, but contrary to those in figs. 34, 36, 38. The neck is well-developed all around, with posterior ribs, and delimited by an upper basal rim. Base low, with anteromedian thickening.

The multicuspid, oblong crown of P8944 (fig. 36) is flat, has three distinct posterior cusps on one side, and several, less distinct and broken ones on the other. The blunted, midposterior cusp is largest. Well-developed neck all around. Neck base transition obliterated. The oval base is flat.

Variant 3: spurred, multicuspid glabrous scales (figs. 37-41): This variant combines features of variants 1 and 2, and was also figured by Märss (1986: text-fig. 20: 18-19). A *Thelodus trilobatus* scale that might belong here, or with variant 1, was illustrated by Turner (2000: pl. 5: 5) from the Upper Whitcliffe Formation, Ludlow.

The multicuspid oval crown of P8945 (fig. 37) is rather plane, overhanging the base laterally and posteriorly. The irregular left posterior crown edge shows traces of five cusps. The crown edge to the right of the largest, posteromedian cusp seems smooth. The high neck (c. 40% of total scale height) has posterior, vertical ribbing and is separated from the base by a basal rim. The short, conical, anteromedian basal spur is directed ventrad at a high obtuse angle.

The multicuspid rhombic crown of P8946 (fig. 38) is plane but for the anterior part, which is curved towards base. The anterior crown rim is round. The lateroposterior crown has many, mostly broken off, little cusps. The midposterior point is largest. High neck (c. 1/3 of total scale height) with short, vertical lateroposterior riblets. The

flat basal plate has an irregular outline and a distinct anteromedian constriction (fig. 38a) introducing a short nose-like spur.

The corroded, damaged scale in fig. 39 (P8947) has a plane, rectangular multicuspid crown showing traces of four or five cusps along the posterior edge (fig. 39b). High neck (c. 50% of total scale height) all around. The flat basal plate is prominently projected forward of crown and with anteromedian point bent ventrad (fig. 39b), an indication of beginning spur formation?

The corroded, damaged, more or less symmetric, multicuspidate scale P8948 (fig. 40) has a crown that increases in width posteriorwards and is not quite plane. The anterolateral crown edge is slightly bent ventrad. The posterior crown edge has about seven, broken cusps of which the midposterior is the largest. Well-developed neck all around. Faint basal rim at neck/base transition (fig. 40b). The flat base has a midanterior spur with a slight, ventrad bend.

Scale P8949 (fig. 41) is symmetrical and has a slightly inclined, smooth crown that widens out posteriorly. Posterior crown edge has 7-8 cusps. The crown overhangs the base laterally and posteriorly. Low, smooth, steep neck all around. A narrow, upper basal zone with outer rim surrounds the neck but posteriorly the neck/base interval has become obscured by sediment. The short, nose-like (fig. 41b) anteromedian basal spur, which measures c. 20% of total base length, is oriented ventrad. The base is low.

Discussion — Scale P8939 (fig. 31), variant 1, differs in two features from all the other scales (variants 1-3): the crown does not overhang the neck laterally and posteriorly; the other difference is the shape of the neck, which decreases in size from dorsad to ventrad.

The variants 2 and 3 fit better within the glabrous *Thelodus parvidens* squamation sensu Gross, 1967 than the independent *T. trilobatus* scale type sensu Gross, 1967 (with median crown fold), which was included in the body zonation scheme for *T. parvidens* by Märss (1986: 42) as a postpectoral scale type. Of the postpectoral scales figured in that scheme, none resembles any of the variants discussed here. The scale form most approaching such variants is, in the terminology of the present paper, a tricuspidate variant 3 specimen (Märss, 1986: text-fig. 20:18) with largest midposterior cusp: unfortunately such a scale was not collected from any Ramsåsa fauna dealt with in this volume. The body zonation schemes obviously have drawbacks (see also Vergoossen, 2002a), the most fundamental being that they are essentially composites, i.e. scales from several sites, stratigraphic levels and possibly slightly varying age, mature and young scales and overlapping forms of several taxa may have been combined. Some of the postpectoral forms in the scheme for *T. parvidens* possibly represent scales with abraded crowns (e.g. Märss, 1986: text-fig. 20: 21, 24) assignable to other taxa (e.g. op. cit.: figs. 22-27 referable to *T. sculptilis*).

Fredholm (1988a, fig. 8E), who followed Märss (1986), illustrated a small, smooth-crowned, 'trilobatiform' scale from limestone unit e at Milklint 3, *Polygnathoides siluricus* Conodont Zone (Leintwardinian), Gotland, resembling glabrous variants 2 and 3, but instead of a neck all around (as in all the Scanian specimens), the specimen from Gotland seems to have no anterior neck. That scale was illustrated together with more traditional *Thelodus trilobatus* scales (Fredholm, 1988a: figs. 8F, H) from the same conodont zone but from a different site (Gogs 1, Hemse Marls), and the three scales were included in *T. parvidens* without discussion.

Scales whose crown ornament has been strongly abraded may be confused with the variants treated above. Such specimens have been regularly collected and could be assigned to *T. sculptilis* (figs. 42-43) or to *T. trilobatus.*

Apart from the general observation that the variants 1-3 comprise small scales, and often have a thin, or low, open base, and might thus be relatively young scales, no further statements can be made about the growth phases represented among these variants because no ontogenetic data are available.

Other glabrous trunk scales (P8952, fig. 44): The oblong, inclined crown has a midposterior point and is thrice longer than wide. Crown edges damaged. Laterally and posteriorly the crown overhangs the base (fig. 44a). The anterior crown is curved ventrad. Smooth, vertical neck all around, posteriorly increasing to twice its anterior height and with a midposterior keel. The neck is surrounded by a flat and narrow upper basal zone with low basal rim; oval, flat base. Compare a similar specimen from Ramsåsa H (Vergoossen, 2002a: fig. 13), which has posterior neck ribs and a crown anterolaterally overhanging the base. These scales may not be cephalopectoral because they are so narrow.

Trilobatiform scales that have a crown with a median fold (= *Thelodus trilobatus* Hoppe, 1931) (figs. 45-50). These scales are assignable to *T. parvidens* sensu Märss, 1986 as postpectoral scales and to *T. trilobatus* sensu Gross, 1967 as an independent taxon. They cannot be assigned to *T. parvidens* sensu Gross, 1967. After the introduction of the body zonation scheme by Märss (1982) and the reinvestigation of '*Thelodus macintoshi*' by Turner (1986) and its subsequent assignation to *T. parvidens*, Gross' taxonomic concepts on *T. parvidens* and *T. trilobatus* were abandoned, but not completely and by everyone (cf. Turner, 2000). In this section the scales of *T. trilobatus* are treated as a separate form group, irrespective of their classification, to contrast them with scales described above (the spurred or multicuspid glabrous variants).

P8953 (fig. 45) is a scale with a tricusped, horizontal crown. The anterior crown is markedly constricted anteromedially where the median fold begins. The fold is distinctly projected forward of the rest of the crown and over the neck anteromedially. The fold is flanked by raised ridges that converge posteriorly and end as one ridge in the midposterior and largest cusp. The lateral crown halves, which each end in a posterior cusp, are smooth. Well-developed neck all around. The flat base has an anteromedian constriction introducing a short, rounded, nose-like spur hat is oriented horizontally and lies in line with the base.

The multicuspid crowns of P8954 (fig. 46), and esp. of P8955 (fig. 47), lack such a prominent, anteromedian forward projection of the median fold as seen in the crown of P8953 (fig. 45). Anteromedially the fold curves ventrad and is constricted (the fold in P8953, fig. 45, lacks these features). As a result, there is no room for an anterior neck in these scales. The lateroposterior edge of the right crown half (fig. 46a) possibly carried a couple of cusps and that crown half also possessed a lateral ridge parallel to longitudinal axis of the crown (fig. 46b). The lateral ridge is not raised to the level of the median ridge pair but situated lower. The anteromedian basal spur (fig. 46) is longer and slenderer than in the preceding scale and directed slightly ventrad but is not introduced by a distinct anteromedian basal constriction.

The slightly inclined crown of scale P8955 (fig. 47) widens out posteriorwards (fig.

47a). The right lateral crown rim begins further posteriorly than the left (fig. 47a). The anteromedian pair of sharp ridges ascends from upper base level (fig. 47a) towards posterior, where they converge and end in the midposterior cusp. Cusp and median ridges bend to the left (esp. the right ridge). The median ridge pair is flanked on the right side by one lateral ridge, which runs parallel to the right ridge of the median pair and ends in a cusp. Lateral cusp and ridge bend left. The lateral ridge is not situated much lower than the median ridge pair. The multicuspid posterior crown edge is broken, but two long cusps are still intact. Length of cusps is c. 1/3 of total crown length. Well-developed lateroposterior neck. Upper basal rim around oval and low base. The anteromedian basal spur distinctly curves ventrad but contrary to the posteriormost crown, the spur is not bent to the left.

Scale P8956 (fig. 48) is rather similar to the preceding one but with a lateral ridge flanking the median pair on each side and parallel to the median pair. Again the ridges in the right scale half bend to the left, but more weakly so. The base is low, flat and horizontal. The anteromedian basal constriction introducing spur formation is well noticeable. The spur is thicker. Its ventral surface lies almost in line with that of the base and the curvature of its dorsal surface is more gradual.

The crown of P8957 (fig. 49) has a median fold subdivided by a long subridge. The subridge converges into the left ridge of the median pair in the posterior crown half. Mid posterior cusp straight. Almost straight lateral ridges, but in the cusp the left lateral ridge curves away (to the left) from the course it had up to that point. Spur directed more ventrad, but for the rest this scale is rather similar to the preceding one.

Scale P8958 (fig. 50) has a multicuspid posterior crown and a basal spur, which is bent to the right. The spur also has a median ridge (fig. 50b). The crown has round anterior and lateral rims, is much wider than the preceding scales and without anteromedian constrictions. The anteromedian pair of crown ridges and the left lateral crown ridge ascend perpendicularly from the neck. The lateral crown ridge begins at the same latitudinal level as the median ridges. In all these features the specimen differs from most of the preceding scales. A vague and shallow fold can be traced on the right crown half (fig. 50b), which may have been flanked originally by a lateral ridge. The remains of such a ridge can be seen on the right anterior crown edge in Fig. 50a. The right crown half is slightly arched (fig. 50b), another feature in which this specimen differs from the preceding scales. In the height of the ridges relative to the rest of the crown the scales resembles P8953 (fig. 45). Well-developed neck all around. Lateroposterior base low and flat. The base widens and thickens towards anterior (fig. 50b).

Remarks: The glabrous (calcarate) multicuspid scales show greater affinity to the glabrous scales of *Thelodus parvidens* sensu Gross 1967 than do the scales of *T. trilobatus* sensu Gross, 1967 (with median fold plus flanking ridge pair). This affinity supports Gross' (1967) restricted species concept of *T. parvidens* (i.e. with the exclusion of *Thelodus trilobatus*) as much as it supports the wide species concept of *T. parvidens* introduced by Märss, 1986 (i.e. with the inclusion of *T. trilobatus* and other forms). Hypothetically, a *T. parvidens*-like fish with completely smooth squamation is as plausible as one with only costatiform, bicostatiform and trilobatiform scales, to mention just two of the several combinations that can be made with the available scales from Ramsåsa D.

Scanian *Thelodus trilobatus* scales are morphologically very diverse, and only a small part of this diversity has been mapped here. It is not unreasonable, also from the point of view of their diversity, to suggest that they might belong to an independent *T. trilobatus* taxon. For instance, on the analogy of the anteromedian basal spur in many scales across the whole body of the genus *Lanarkia* (Märss & Ritchie, 1998) the spur in the scales of an independent *T. trilobatus* fish may have had a wide distribution across the body rather than being restricted to the posterior trunk region, as in *Thelodus parvidens* sensu Märss, 1986.

In general the anteromedian basal spur in *T. trilobatus* scales may bend ventrad at any angle between the extremes of 90° (perpendicular) and 180° (horizontal). A spur orientation close to 90° is, however, very uncommon. The spur may be both directed ventrad and projected forward strictly anteromedially, or bend away from anteromedially to the left or right. The bend to the right or left may be considerable. In cross section the spur may be anything between thin and thick, thin goes with a more flattened or slender shape and thick with a more spherical shape. There may be just an indication of a spur, or the spur may have a considerable length. I did not observe doubled spurs as Gross (1967: pl. 2: 14) did in *T. trilobatus.* All these different spur features may give information on at least four subjects: 1) the ontogenetic phase of the scale (Is a spur, or indication thereof, always present from the earliest growth phase of a scale? Can a spur disappear or become disguised in the course of growth as a result of growth impulses that change from specific spur formation to a more general, anteriorly biased, basal formation?); 2) growth space: restricted or more ample capacity for vertical or horizontal expansion in the corium, for instance linked up with the presence or absence of cartilaginous bone; 3) the degree of curvature of the body; and 4) the place on the body where the scale grew, which plays an important role in the body zonation schemes (but cf. *Lanarkia* — Märss & Ritchie, 1998).

There is a basal growth bias in favour of an anterior direction in many scales of the *Thelodus* taxa treated in this paper, except in some oral scales or in very young scales. A similar bias is seen in contemporaneous acanthodian trunk scales. I cannot think of a reason why this should be so. Spur or rhizoid formation do not occur in acanthodian scales, but the following basal features are shared: deeply swollen anteromedian base (in older acanthodian scales) and considerable projection of base forward of crown (especially in poracanthodids). S. Turner (pers. com.) wrote: 'I think this growth bias has to do with spacing and hydrodynamic pressures on areas of the outer surface. Possibly anterior spurs develop at places of maximum drag thus holding the scales more firmly. This tendency of scales with spurs to appear more elongated in the horizontal plane is taken to extremes in the Gondwanan turiniids (cf. the Bolivian *Turinia gondwana* Turner, in Gagnier et al., 1988). But why this does not happen so clearly in modern sharks I cannot say. Which is why I used basal growth features as a synapomorphy for the Thelodonti (Turner, 1991). Of course, as you say, other groups do show this growth bias occasionally.' However, the anterior growth bias is not restricted to spur formation, which is an elaboration of the feature. The feature would seem to be more general, for scales across a large part of the body. In addition, Turner's arguments do not fully consider the position of the growth bias, i.e. the preference for the midanterior part of the base (also in scales without spurs) to another part of the base. Neither do her arguments consider

phylogenetic and geographic aspects on the generic and species levels. Silurian *Thelodus* preceded Devonian *Turinia*, and the living conditions of *Thelodus* species from the (East-)Baltic region may have differed from those of *Turinia gondwana* from Bolivia.

Thelodus sculptilis Gross, 1967
Pl. 8, figs. 51-54a; Pl. 9, fig. 54b.

Märss (1986: text-figs. 21-22) distinguished between Ludlow morphological scale series of *T. sculptilis* from Estonia (Tahula beds) and from Scania (Öved-Ramsåsa beds), but included them in the same species.

Oral and/or cephalopectoral scales

In P8959 (fig. 51) the crown has a median fold on the anterior crown edge and a smooth, midposterior nose-like peg. The lateral ridges, directed posteriorwards, almost reach the smooth longitudinal axis of the crown. A rounder scale (approaching cruciform shape) with a more ridge-like midposterior peg, is seen in fig. 52.

Cephalopectoral scales

Scale P8961 (fig. 53) has a crown with an anteromedian fold that ascends from the neck and fades out where the smooth midposterior nose-like peg begins. Anterior to the conspicuous constriction that forms the peg, the crown is wide, smooth and wing-like. The anterior crown edge is rounded, bending towards the neck and with few, shallow folds lateral to the central fold. The posterior crown tip has a slanting ventral keel (fig. 53b) and overhangs the vertical neck, which is low anteriorly and increases in height lateroposteriorly where it also shows a few vague ribs (fig. 53b). Narrow, slightly sloping, upper basal zone all around; the zone is somewhat wider lateroposteriorly, where also a weak rim may be observed (fig. 53a). Base rounded rhombic and open.

Some cephalopectoral scales combine a smooth crown with two shallow anterolateral incisions and a smooth anteromedian lobe (Märss, 1986, text-figs. 21: 7, from Estonia; 22: 10, from Scania). When there is only one such lateral notch (op. cit.: text-fig. 20: 9), or two on the left and one on the right (ibid. 20: 8), the scales are referred to *Thelodus parvidens*. The reasons for this different treatment are not clear and the examples illustrate the ambiguity of these identifications. Other scales have a smooth crown with a midanterior lobe that has one notch, in addition to one notch on each anterolateral rim (ibid.: 21: 10, from Estonia). A smooth scale with only a midanteriorly notched crown lobe, and no lateral rim notches (midanteriorly incised glabrous, P8962, fig. 54), is here described. It is transitional to glabrous scales. The smooth crown is slightly convex, and little inclined. The outline of the crown is almost round (fig. 54a). On the anteromedian crown edge two blunted, radiating ribs flank a fold. This rib structure sticks out forward over neck and base (fig. 54b). On each side of the structure the crown seems to be slightly infolded (fig. 54b). The crown overhangs the neck all around. The vertical neck has vertical ribs and rests on a sloping, narrow upper basal zone (fig. 54a). The rhombic base is thin and has angular lateral corners (fig. 54a).

Thelodus traquairi Gross, 1967
Pl. 9, figs. 55-58.

These scales are not common in the samples. The morphological variation ranges within this species and within the Baltic region are poorly known. Turner (1984) illustrated horn-like *Lanarkia* scales from Ramsåsa Quarry (site F). Such scales were not present in the studied material. See also Vergoossen, 2002a.

Costatiform and other oral? scales

Some crowns of *T. traquairi* scales combine alternating radial ridges and folds with a longitudinal middorsal ridge that runs from midanteriorly to midposteriorly and may be dichotomous in anterior direction. Part of the radial ridges usually converge into the middorsal ridge. A middorsal ridge also occurs in some *Thelodus sculptilis* variants (cf. Märss, 1986: pl. 23: 2 cephalopectoral, 3 oral; and the posterior middorsal ridge in P8960, fig. 52a). But as in P8961 (fig. 53), *T. sculptilis* crowns often have longer or shorter grooves or deep and wide notches rather than alternating folds and ridges. Compare also P8966 (fig. 57, *T. traquairi*) and P8960 (fig. 52, *T. sculptilis*) for their folds and converging ridges. The distinction may sometimes be difficult to make, as also indicated by the question mark behind the species name for one scale figured by Märss (1986, pl. 23: 2). On this issue see also the next section.

Tiny scale P8963 (fig. 55) is slightly wider than long and has an almost cruciform crown (fig. 55b) on an oval, wide open base. The crown has three prominent sharp, convex ridges: one anteromedian and two lateral situated at the level of the basal corners. These ridges either curve upward from the neck to crown centre, or first follow a vertical course up from the neck before bending to the centre (fig. 55a, left ridge). The three ridges converge into a pointed distal/posterior top. In actual fact, the laterals run into the anteromedian ridge slightly before their common top (fig. 55b) and one of the lateral ridges is dichotomous anteriorly (fig. 55b, right). A fourth, straight and perpendicular, mid posterior ridge is present but less prominent (fig. 55b). Between the lateral ridges the crown extends blade or wing-like (fig. 55a). The low neck, all around and ribbed posteriorly (fig. 55a), slopes down to base: the transition is so gradual that without the neck ribs the distinction would be unnoticeable. Neck and base approximately of the same height.

The crown of P8964 (fig. 56) has two radial and raised, anteromedian ridges that ascend from the neck on a course away from the centre but soon bend centrad at angles of almost 90° and run posteriorwards for a short stretch before they converge and continue as one, straight ridge sloping up to the posterior point. Several radial lateral ridges ascend from the neck in posterior direction but only the posterolateral ridges converge into the midposterior point; the two anteriormost lateral ridges run towards the median dorsal ridge but fade out before reaching it (fig. 56). Posteroventral crown smooth. Distinct, vertical neck all around and with vertical (also convex) riblets posterolaterally (fig. 56b). Basal rim at neck base interval. Thin, flat rectangular base.

The scale with the ridged, rhombic crown in fig. 57, P8965, is longer than wide and has about nine radial longer, or shorter (intermediate) ridges. Only the longer posterolateral ridges and the median dorsal ridge converge into the midposterior, elevated

top. Most longer ridges curve up and away from the neck but soon (still in their lowermost part) bend back centrad at angles of c. 90° to slope up in posterior direction. Each of the two widest lateral ridges are situated at the level of the lateral corners of the base (fig. 57a). The almost vertical posterior crown ridges are steepest. Low, vertical neck all around. Neck-base transition unclear and sloping. Base rhombic and flat. An elevated, midposterior crown top is also seen in the specimens in figs. 56b, 74c (*Thelodus* sp.) and in a scale from the Ramsåsa H fauna (Vergoossen, 2002a: Pl. 2: 22: *T. sculptilis*).

Elongate scale P8966 (fig. 58) is longer than wide and has a more or less horizontal sharp middorsal ridge, which in the posterior crown part is bent slightly to the right (fig. 58a). This ridge curves up from the neck midanteriorly and on an oblique, forward course. Higher up it bends back to posterior twice (fig. 58b), first at an angle of c. 90° and, soon after, at an obtuse angle, to continue on an almost horizontal course. The midposterior part of the dorsal ridge is round (fig. 58b). Sharp, radial, lateral crown ridges curve upwards from the neck and run posteriorwards into the dorsal ridge (fig. 58b). The vertical neck is distinct but low all around and shows few ribs lateroposteriorly (fig. 58b). Indistinct upper basal rim (fig. 58b). The rectangular base is thin and flat.

Thelodus cf. *traquairi* Gross, 1967
Pl. 9, figs. 59-60a; Pl. 10, figs. 60b-63.

The scales described below cannot be attributed with certainty to any Baltic *Thelodus* species. They show features of both *T. traquairi* and *T. sculptilis* scales. None of the scales have anterior notches or grooves in their crowns, which makes it less likely that they should belong to *T. sculptilis*. Märss (1986: pl. 22: 7, 12) figured precaudal? scales that she referred to *T. traquairi* from the Ruhnu 500 boring (Pridoli, '*Poracanthodes punctatus* Zone'), but these specimens also show *T. sculptilis* features, although the latter species was not recorded from the boring (Märss, 1986: fig. 40). The oral scale in fig. 63 is a special case.

Oral scale P8967 has a ridged (radial ridges and dorsal ridge) crown that widens out wing-like posteriorward (fig. 59a). The crown has a raised, anteromedian fold overhanging neck and base (fig. 59b). The fold is flanked by sharp ridges that ascend from the neck in forward direction and, still in the lower crown part, curve back centrad and up, at angles of almost 90°. These two anteromedian ridges converge in the anterior crown half and continue as a single straight and sharp dorsal ridge posteriorly (fig. 59b). Three radial lateral ridges, directed posteriorwards (fig. 59a), and probably two radial lateroventral ridges, directed centrad, are also present. On the side seen in fig. 59b, one ventral and one lateral ridge converge into the ridge-like posterolateral crown rim a little below the highest midposterior crown point. The ventral posterior crown has a conspicuous midposterior, angular projection (fig. 59); compare with the midposterior crown parts of P8966 and P8968 (figs. 58b, 60b). Well-developed neck all around with robust, vertical ribs lateroposteriorly. Neck and base are more or less of equal height and together they make up half the total scale height. Base flat and rhombic.

Rhombic scale P8968 has an inclined crown (fig. 60b). The anteromedian crown fold continues into the midposterior crown point; the fold is flanked by sharp ridges

that rise almost vertically from the anterior crown rim and bend abruptly posteriorwards at angles of almost 90°. The starting point of both lateroposterior crown rims is at the converging point of a pair of short ridges that enclose a fold. The ridge pairs ascend from the lateral corners of the crown. There is a midposterior, ventral crown keel which is vertical in its uppermost and prominent part, and strongly concave (almost right-angled) in its lower part (fig. 60b). Anterolaterally the transition from crown to neck and from neck to base is indistinct. Posteriorly the vertical neck has vertical riblets. Base flat and thin.

The most remarkable feature of P8971(fig. 63) is the thin, trilobed vertical crown, which is strongly reminiscent of the pugniform scale type. Originally the crown possibly had a multicuspid, distal edge judging from the distal irregularities. A raised anteromedian, shallow fold narrowing into a peak distally, divides the crown into two smooth, lobed halves. In posterior or 'ventral' view (fig. 63b) the lateral lobes stand out wing-like. The 'ventral' crown surface is smooth and has a blunt median ridge. The transition from crown to base is gradual, indistinct and sloping posteriorly. Anteriorly, constrictions of the crown wings near base level and below the median fold (fig. 63a) indicate the presence of a very low neck. The scale has a rhombic, flat base.
Remark on multicuspid crowns: Although such crowns are thought to be a regular part of the squamation of some *Thelodus* species, there is no record of multicuspid crowns in *T. traquairi*. If this specimen was originally multicuspid it might also be a pugniform scale of *T. trilobatus* sensu Gross, 1967.

Cephalopectoral or postpectoral scales.

P8969 has a rhombic, steeply inclined crown (fig. 61) with a shallow fold between a raised anteromedian pair of ridges converging in the posterior scale half and continuing as one ridge to the midposterior crown point where also the lateral crown rims meet at an angle of almost 90°. In posterior view (fig. 61b) the crown looks like a delta fighter plane. The median fold and ridge divide the crown into two smooth wing-like halves. The dentinal tubules in this crown type are long, as also known from 'winged' *T. traquairi* and from *T. trilobatus* crowns. In anterior view (fig. 61a) the halves have two lateral angles on each lateral crown rim: the first angle is where the anterior crown rim bends up and posteriorward at c. 130° and runs almost parallel to the longitudinal axis of the scale and the median crown ridge. The second angle is a bit higher up where the lateral crown rim curves back in the direction of the longitudinal axis at c. 120°. A dichotomy of the lateral crown rim is seen at the position of the first angle in one wing (left in fig. 61a, right in fig. 61b; a converging, short lateral ridge pair). The ventral crown surface is smooth with an indistinct midposterior ridge. Well-developed neck all around, posterior neck marked by vertical riblets. Upper basal rim present. Very low rhombic base with slight anteromedian thickening and for the rest practically flat. The scale in fig. 62 shows minor variations.

Scale P8970 (fig. 62) has a rhombic, inclined crown with an anteromedian ridge that continues into the midposterior point. In lateral view (fig. 62a) a vaguer, longitudinal ridge may be seen in the middle of the right crown half and running into the posterior crown rim. As in P8969 (fig. 61), two angles are present in the lateral crown rims; the rims also show parallel orientation to the longitudinal axis/central ridge: this orientation is most conspicuous in the left lateral crown rim because it runs paral-

lel for a longer distance. The left lateral crown half is shallowly concave, the right is flatter (fig. 62b). The anterior crown rim is indistinct. The lateroposterior scale part overhangs neck and base considerably (overhang c. 35% of total crown length). The neck is high all around has a sharp dividing line midanteriorly, where the left and the right neck parts meet at an angle. The right anterior neck part is concave (fig. 62a) and widens out laterally (fig. 62b). A narrow upper basal zone surrounds the neck. The rhombic base is low.

Thelodus carinatus (Pander, 1856)
Pl. 10, figs. 64-66a; Pl. 11; Pl. 12, figs. 72b-73.

Scales of this taxon may have a *T. parvidens* type of histology, i.e. the dentinal tubules arising from the pulp canal follow a more or less straight course (Märss, 1986: pl. 20). Fredholm (1988a) included *Thelodus marginatus* Karatajute-Talimaa, 1978, which has dentinal tubules that are strongly curved in their central part (Karatajute-Talimaa, 1978: 238, fig. 3), in *T. carinatus*. Märss (1986: 86) mentioned this latter histological feature in the diagnosis of *T. laevis* (Pander, 1856) but not in that of *T. carinatus*. Fredholm (1988a) did not discuss the histology of *T. carinatus* scales from Gotland. (See also the section on *Thelodus parvidens*: other cephalopectoral scales.)

What distinguishes some of the forms described below from the ones figured by Fredholm (1988a: figs. 7, 8B) and Märss (1986: pl. 18: 6-15; pl. 20: 1-10; text-fig. 19) is that instead of a lateral ledge they have a broad, ventrad sloping, lateroposterior part beyond the highest crown point (often a triangular area on the midposterior crown), as in P8976 (Fig. 68a). The scale of *T. clavaeformis* Lehman (1937: fig. 24) may also be a *T. carinatus* scale and was assigned to *T. trilobatus* by Turner (1976). (See also Vergoossen, 1999b: 272.)

The anterior crown of the more or less rectangular scale P8972 has suffered much (fig. 64a). The dorsal crown surface has circa four radial anterolateral ridges, alternating with folds. The ridges converge to form a top in the posterior crown half. The top is situated in front of the right angle formed by lateroposterior crown rims. A smooth lateroposterior crown zone slopes up to the top (fig. 64b). The lateroposterior crown rims begin at the level of the lateral corners of the base (fig. 64b). They form a sharp boundary with the ventral crown surface. Vertical neck well-developed all around (making up more than 1/3 of total scale height), with closely spaced, posterolateral, vertical and few oblique riblets (fig. 64b). The transition from upper neck to smooth, ventral, posterolateral crown surface is marked off by these neck ribs, which extend across the whole height of the neck. Base low and flat.

The scale in fig. 65b (lateroposterior view), P8973, looks like P8972 (fig. 64b), but it is more rhombic. In anterior view (fig. 65a) it looks like a head scale, with folds between long, radial ridges that ascend from the anterior rim and reach far posteriorly. Contrary to the ridges in part of the *T. parvidens* costatiform scales, the ridges in this specimen and the one in P8972 (fig. 64a) do not curve up from the neck ab centro in their lowermost stretch, as e.g. the ridges in P8909 and P8910 (figs. 1-2) do. The highest point of the crown lies midposteriorly, where the crown rims meet (the highest point is further posterior than in the scale in fig. 64b). In their lower reach the crown rims are complex structures of a number of short converging rims: two oblique

lateral rims can be seen on the smooth ventral crown surface (fig. 65b). Such complexity represents a morphology that is transitional to a head scale. Neck vertical all around. Posterior neck higher than anterior neck, and with higher and more prominent vertical ribs. Rhombic base deeper than in P8972 (fig. 64b).

P8974 (fig. 66) has an oddly shaped, slightly tilted crown. The crown part anterior to the highest scale point (fig. 66b) is pentagonal in outline (fig. 66a). This part occupies c. 2/3 of the entire crown. An anteromedian fold is flanked by sharp ridges that bend towards the longitudinal axis of the scale where they meet (fig. 66b). The left of these ridges (fig. 66a) starts as two shorter ridges that converge near the anterior crown rim. To the right of the median fold and close to the crown rim there is a third anterior ridge, parallel to the right fold ridge and of equal length (fig. 66a). The highest scale point is where the lateroposterior sides (crown rims) of the pentangle meet, on the longitudinal axis of the scale. Posterior to the highest point, the crown surface is semicircular and smooth and slopes ventrad. This part of the crown is largely situated in the right scale half (fig. 66a). The neck is well-developed all around, lower anteriorly than posteriorly, where it is slightly concave and has concave neck riblets. The base is flat, thin and more rectangular with rounded angles.

P8975 is an oval, cephalopectoral scale (fig. 67), wider than long, and like a mushroom in shape. The crown is convex. The anterior crown edge has long, sharp, radiating ridges which curve upwards from the crown rim (fig. 67b) and run straight towards the crown centre. The ridges end just before the highest scale point, which is situated close to the middle of the crown, in the posterior crown half (fig. 67b). The ridges are clearly longer than those in P8986, a comparable specimen (fig. 78). The anteromedian pair of ridges sticks out a little further anteriorly than the other ridges (fig. 67a), and the triangular fold between this pair is the most prominent fold. The crown is smooth beyond the ridges and overhangs the low neck on all sides. Neck-base transition unclear. Base flat. The basal outline follows the undulatory outline of the crown. Compare this scale with specimens of *T. marginatus* Karatajute-Talimaa (1978: pl. 29: 2, 4).

Scale P8976 (fig. 68) is similar to P8975 (fig. 67), but the crown ridges are shorter. The two anteromedian ridges are very short and soon converge to continue as one ridge posteriorwards. The posterior crown rim is irregular. The posterior neck has sloping neck ribs (fig. 68b).

P8977 (fig. 69), with convex crown, has more ridges on the left anterior crown side than on the right, and a prominent anteromedian ridge pair and fold. In these features it resembles P8975 (fig. 67). The right crown half has a prominent, outermost posterolateral dorsal ridge, parallel to the posterolateral crown and basal rims. This ridge ends abruptly in the midposterior crown part at the point where it has begun to curve back anteriorwards. Posterior to this ridge, but lower, the narrow smooth zone of the lateroposterior crown edge extends. The edge must have been spiny, but the delicate spines have broken off (cf. Märss, 1986: pl. 18: 6). The base is rectangular, as is the crown.

Rhombic scale P8978 (fig. 70) has an inclined crown (almost twice longer than wide), whose central part is somewhat depressed. Circa six, low radiating ribs run posteriorwards from close to the upper anterobasal rim. It is not clear how far exactly each rib continues posteriorwards, but they would seem to fade out circa half way the crown, while the most lateral rib on the right crown side converges into the right

crown rim. Two midposterior carina converge in the posterior crown point. All ribs begin forward of the crown rims (fig. 70a), which ascend from close to the basal rim near the lateral corners of the base (fig. 70a). The left crown rim is markedly concave (fig. 70b). The lateral crown rims begin in the posterior scale half and border a smooth, down-stepped ledge (fig. 70a). Posterior neck only. Upper basal rim all around. Low base, slightly thicker anteromedially.

Postpectoral scale P8979 (fig. 71) has a more or less triangular crown, which is not entirely horizontal, but slightly sloping. The crown rims constrict the crown anteriorly. The left crown rim has a distinct, concave curve, also seen in P8978 and P8981 (figs. 70b, 73b) (cf. Fredholm, 1988a: fig. 7F). The central crown area is somewhat depressed and/or damaged (fig. 71b). The upper crown surface shows c. four to five thin, parallel, median ribs of roughly equal length and running from anterior into the posterior crown rim. Lateral crown rims (beginning further posteriorly than the crown rims) border a slightly downstepped, very narrow and smooth, lateral ledge (fig. 71a). The left ledge is wider than the right one. High lateroposterior neck, which is nowhere overhung by the crown. An upper basal rim marks off the transition from crown/neck to base, but the preservation of the transition is poor, and esp. the anterior details are unclear. Base low lateroposteriorly, but with robust, broken off, midanterior basal spur, oriented almost horizontally (relative to base).

Scale P8980 (fig. 72) is rather similar to the preceding one, but the crown is more rhombic and more convex because the more or less parallel median crown ribs are slightly raised and convex (fig. 72b). The five crown ribs are of unequal length because the lateral ribs begin further posteriorly than the median ones. Lateral crown rims are lacking. Anterolaterally the upper basal rim slopes ventrad, posterolaterally the rim is horizontal. Posterolateral neck obscured.

Scale P87981 (fig. 73) is longer than wide and has a slightly inclined, more or less oval crown (posterior crown part broken off). Pairs of crown ribs steeply ascend from close to the anterior upper basal rim but soon bend posteriorwards to continue up more gradually in posterior direction. Posteriorly the pairs converge and form sharp points, which curve to the right. The rib pairs bend inwards anteriorly, thus constricting the crown surface. There is a solitary rib precisely in the middle of the crown (fig. 73a) and extending far posterior. The left crown rim has a concave curve (fig. 73b). The crown has narrow, downstepped, lateral ledges (fig. 73b) bounded by the lateral crown rims that begin in the posterior scale half (fig. 73b). Low neck lateroposteriorly. Posteriorly the crown overhangs the base by c. 40% of the crown length. Base is low, with anteromedian thickening.

Range in Baltic region — Late Wenlock? Ludlow: Bringewoodian-Leintwardinian.

Occurrence in Baltic region — Gotland: Hemse Marls (SE) *Polygnathoides siluricus* Conodont Zone; Hemse Limestones: unit c?; unit d, *P. siluricus* Conodont Zone (Fredholm, 1988a). Estonia (Saarema): ?Rootsiküla Stage, Paadla Stage (Märss, 1986).

Thelodus sp. indet.
Pl. 12, figs. 74-77a; Pl. 13; Pl. 14, fig. 82c.

Here scales are described that cannot be assigned with certainty to any of the known Baltic *Thelodus* species. Between some of these scales morphological affinities

and coherence would seem to exist. In others these are not observable. Some scales may be assignable to *T. carinatus* (see below). The specimens are not regular finds.

Oral/cephalopectoral scale

The rectangular scale P8982 (fig. 74) is circa twice longer than wide, with oral (radial ridges) and cephalopectoral (smooth) crown features. The crown has a shallow anteromedian fold between a pair of ridges. The fold fades out where the ridges converge: middorsally (figs. 74a-b). Lateral radial crown ridges curve up from the neck on the left crown side. They run steeply to middorsal (fig. 74b). The smooth right side of the crown curves up from the neck and slopes up to middorsal less steeply (fig. 74b). The highest crown part lies dorsally, but there is no sharp dorsal ridge separating the lateral crown halves as in the *Thelodus traquairi* specimen P8966 (fig. 58a), which the present scale resembles in anterior view (fig. 74a). Another difference is in the posterior crown part, which is bent to the left (fig. 74a). The midposterior crown part is raised and forms a dorsal top (fig. 74c). Two narrow ledges on each side of the top are visible in fig. 74a. Such features are reminiscent of *T. carinatus* scales. The posteroventral crown surface is smooth (fig. 74c). Neck vertical, high and ribbed all round. Neck ribbing high and rather dense, ribs thin. Neck-base interval sloping. The base is low and flat.

(Antero-)incised glabrous /cephalopectoral scales

The arrow-shaped scale P8983 (fig. 75) increases up to 250% in width in posterior direction, the greatest width is at the level of lateral basal corners. Crown convex. From the flattened, smooth anterior lobe (fig. 75b) a weak middorsal ridge extends in posterior direction but becomes fainter posteriorly. In dorsal view (fig. 75a) the ridge can only be distinguished in the anterior third of the crown. The ridge marks the highest scale part (cf. P8986, fig. 78a). The lateral crown rims bear posteriorly directed short ridges and notches. The lateromedian ridges seem to be the longest and the intermediate notches the deepest but they do not reach the middorsal ridge. The crown slightly overhangs the neck all around. Neck distinct and approximately of same height as basal rim. The outline of the crown follows the outline of the base. Elongate pulp opening.

The rounded scale P8984 (fig. 76) has a convex crown. Anterolaterally the crown edge has short, radiating ridges, posterolaterally it is notched (semicircular notches, Figs. 76b, c). Anteromedially one crown ridge is positioned exactly at the long axis of the scale and here the crown sticks out farthest anteriorly and has a flattened triangular lobe (figs. 76a-b). Such an anteromedian lobe is a feature also seen in some *T. sculptilis*, *T. carinatus* (fig. 68a) and possibly *T. traquairi* scales. The crown is smooth beyond the ridges and overhangs the low, straight neck on all sides. Thin, flat base with narrow upper basal edge (fig. 76c).

Cephalopectoral or post pectoral scales

Rhombic scale P8985 (fig. 77) has a convex crown. The anteromedian crown part sticks out in front and is marked by a long median ridge (figs. 77a, b) extending to near the posterior crown rim; on each side there is one shorter, flanking ridge (fig. 77a). The anterolateral crown edge has three short radial ridges to the right and one to

the left of the median ridges (fig. 77a). The short ridges on the right become shorter laterally. Beyond the ridges the crown is smooth and slopes up to its rounded, midposterior, highest point. Fig. 77c shows the left crown rim, which is dichotomous to anterior, and the left ventral, lateroposterior crown surface, which is steep, smooth and slightly convex. Fig. 77b shows that the right crown rim is not dichotomous; the right lateroposterior crown surface is slightly damaged. Low, vertical neck all around with faint lateroposterior riblets. Anterolaterally a narrow, slightly sloping upper basal zone (fig. 77a) separates neck and base. This zone is absent posteriorly. Base flat. Compare P8985 (fig. 77b) with P8975 (fig. 67b) and P8977 (fig. 69a), both *T. carinatus* scales.

(Spurred) antero-incised glabrous/cephalopectoral or postpectoral scales

The convex crown of P8986 (fig. 78) is rounded triangular in shape. The anterolateral crown edge, which overhangs the neck, has short, curved, radial ridges and folds. The ridges are shorter than those in P8975, a *Thelodus carinatus* scale (fig. 67), which it resembles. The highest part of the scale lies near the slightly off centric end of each posteriormost ridge (fig. 78a). The smooth, steep, high posteroventral crown surface (fig. 78b) is marked off from the posterior neck area by short, vertical neck riblets. Neck and base are well preserved. The neck is slightly higher posteriorly than anteriorly. Anterior neck smooth. Low, rhombic base with upper basal rim. This scale is possibly a *T. carinatus* variant (cf. Fredholm, 1988a: fig. 7).

Compared to the preceding scale, the crown of P8987 (fig. 79) is less convex, and rounded rhombic in shape. The midposterior crown is slightly higher than the rest of the crown. The anterolateral crown edge has a few more radial ridges and folds than the scale in fig. 78 and overhangs the neck a little. The posterior crown surface is smooth, high, rounded and steep. It corresponds with the ventral crown surface in ordinary trunk scales. Low neck all around, with posterior riblets. The base is deeper, c. 50% of total scale height. The basal swelling is strongest anteromedially.

P8988 (fig. 80) is more slender than P8986 and P8987 (figs. 78-79) and has a rhombic crown that is flatter and horizontal. The crown is also more angular, both midanteriorly and midposteriorly and has few and short anterolateral crown ridges. The base is especially deep anteromedially.

Compared to P8987 (fig. 79b), the posteroventral crown part of P8989 (fig. 81b) is decidedly less steep and extends far over base posteriorly (fig. 81). The anterolateral crown is wider than in the preceding scale and an anteromedian basal spur has developed. The spur is introduced by an anteromedian constriction of the base (Fig. 81a) and directed forward and ventrad at a low obtuse angle to base. I assigned a similar, but anterolaterally wider scale to *Thelodus traquairi* (Vergoossen, 2002a: Pl. 2: 24; Pl. 3: 25).

Postpectoral? scale

Rhombic scale P8990 (fig. 82) has rounded lateral crown corners (fig. 82a) and rounded basal corners (fig. 82c). In sideview (fig. 82b) the scale resembles bicostatiform scales. The crown is slightly convex (fig. 82b) and has a median fold between an anteromedian pair of raised ridges converging into the posterior crown point. The median ridges ascend perpendicularly from the neck but soon bend abruptly posteriorwards at angles of 90° (fig. 82b). Compare this crown and its two round lateral cor-

ners (fig. 82a) with the crown of P8969, *Thelodus* cf. *traquairi* (fig. 61a), which has four and more angular lateral corners. Distinct, smooth neck all around. The anteromedian basal swelling is deep, the posterior base low. A concave midbasal 'corridor' leads to the pulp opening (fig. 82c). The orientation of the corridor indicates a slanting antero-lateral entry of the vessel(s) supplying the pulp canal rather than an entry from anterior along a more a longitudinal course, or a perpendicular entry from ventral direction.

Paralogania ludlowiensis (Gross, 1967) and *Loganellia* sp.
Pl. 14, figs. 83-84.

Fig. 83 shows the best preserved specimen, P8291, of the two *Paralogania* scales collected. The lateral neck 'thorns' (or rather rounded 'petals' in this scale) below the neck rib (fig. 83b) are best visible in anterior view (fig. 83a). The poorly preserved scale of *Loganellia* sp. indet. (fig. 84) does not show these neck features.

Acanthodii

In both samples *Nostolepis* scales dominate among the acanthodian remains. The scales described as morph 1 in the section on the Acanthodii gen. et sp. indet. (cf. *Gomphonchus volborthi*) were found regularly, but their number is much lower. Porosiform poracanthodid scales are very rare. The presence of *Gomphonchus sandelensis* in the Ramsåsa D material is uncertain.

Nostolepis striata Pander, 1856, sensu Gross, 1947, 1971
Pl. 14, figs. 85-87; Pl. 15.

The analysis and assessment of the morphology of *Nostolepis striata* trunk scales (begun for the Klinta faunas; see Vergoossen, 2002b) is continued, and topospecific scales are also assessed. Eight illustrated specimens are described (five trunk scales, three topospecific). The selection criteria are the same as those for the *N. striata* trunk scales from Klinta. Additional criteria are that the scales should show clear morphological differences to the scales described from Klinta, and marked differences in orientation. The descriptive terminology is based on the nostolepid feature checklist (see Appendix).

Trunk scales

Asymmetric scale P8993 (fig. 85) has a crown facing right, with the anterior crown parallel to the right upper basal rim: the specimen is otherwise grossly similar to a specimen from Klinta (Vergoossen, 2002b: pl. 3: 26) with its crown facing left. The right rim of the crown is the straighter one and the left rim is wholly curved: in the Klinta specimen this is just the other way round: these rim differences are probably related to rightward and leftward asymmetry of the crown. The lateral ledges in both specimens show differences in shape and curvature: in the present scale the ledge is widest in its anteriormost part, whereas in the Klinta specimen the ledge is narrowest in its anteriormost part. The crown of the Klinta specimen has sharp anterior ridges despite the coarse-grained structure and poor preservation of the anterior scale part. Completely different preservational processes must have been at work in the present scale, where the anterior crown was probably blunted.

Symmetric scale P8994 (fig. 86) has a moderately inclined, triangular crown, roughly as broad as long, with a median anterior rib set projected slightly forward of the rest of the crown. The rib set consists of three short, sharp riblets that are subparallel. The anterior face of the crown plate is formed by a pair of convex rims (constricting the crown anteriorly) that meet in the midposterior tip and begin slightly further posterior to the anteromedian rib set. The lateral rims of the crown plate begin farthest posteriorly, at the level of the lateral basal corners, and converge into the posterior tip. The lateral rims form the outer boundaries of the lateral crown faces, which carry two riblets more or less parallel to the lateral rims of the crown. A narrow zone separates the crown from the upper basal rim anteriorly. The zone widens lateroposteriorly, where there is a low neck. Moderately convex, rhombic base, with median swelling. Only the posterior crown tip overhangs the base.

P8995 (fig. 87) is a slightly asymmetric scale with the anterior crown surface facing a little to the right and remarkably similar to a specimen from Klinta (Vergoossen, 2002b: pl. 3: 32-33) with its anterior crown surface facing left. The triangular, inclined crown plate is slightly concave. The right crown rim is curved (convex) and bends inward anteriorly, the left rim is slightly sigmoidal (fig. 87a). The anterior crown margin is irregular (fig. 87a). The anteromedian crown begins at the rounded anterior basal rim (fig. 87b). There is hardly any space between the rest of the anterior crown and the basal rim. Five short, sharp, anterior crown riblets run in different lateroposterior directions: the left two are directed towards the left crown rim, the other three towards the right rim. The rather broad, lateral crown surfaces give the crown an almost a pyramidal appearance. The right lateral surface (fig. 87b) has a short anteromedian riblet, which is oriented towards the midposterior crown tip. The left lateral surface (fig. 87a) has a short and long anteromedian riblet, also oriented to the crown tip. The lateroposterior neck has a few openings low in the neck and increases in height to posteriorly, where it is moderately high. The crown covers the entire base. The crown tip projects over the base. Rhombic base with moderate anteromedian swelling.

P8996 is an asymmetric scale with a slightly inclined, smooth, triangular crown plate facing right, longer than broad, and with an anteromedian 'beak' (fig. 88a) or a posteriorly diverging lobe (fig. 88b) rather than ribs. The left crown rim begins further posteriorly than the right, but both begin at the level of the lateral corners of the base. The greatest convexity of the crown rims is in their anteriormost part, where the crown plate is constricted by their inward bend. Beyond this point of greatest convexity, the rims run practically straight towards posterior (the left rim is a bit straighter than the right), where they form a tip that overhangs the low, lateroposterior neck. But the tip does not overhang the base (fig. 88b). The lateral crown rims begin further posteriorly than the crown rims and converge into the tip. The neck begins behind the lateral rims. There is no anterior neck. The 'beak' of the crown ascends practically from the anteromedian corner of the rhombic base. There is a narrow upper basal zone to the right and the left of the beak. This zone is largest to the left. Base moderately convex (height about a quarter of total scale height), greatest swelling anterocentrally (fig. 88b).

P8997 (fig. 89) is slightly asymmetric, with rightward asymmetry. The scale is longer than wide. The crown covers practically the entire base and the outline of the crown follows the outline of the base. The crown is low, slightly inclined and trian-

gular and has a rounded, lobed rather than ridged anterior edge. The lobes may have possessed ridges (postmortem abraded geo- or biochemically). The anterior crown edge has a folded, forward projected lobe (fig. 89b) flanked by two parallel riblets still discernable as such in lateral view (fig. 89c), and extending as far forward as the upper basal rim. This lobe is situated left of centre (figs. 89a,c). To the right of this lobe, but situated further posteriorly, there is another lobe. The riblets that flanked it are vaguely indicated in fig. 89b. The anterior crown surface is constricted by the crown rims, of which the left one is more strongly bent in its anterior stretch than the right one (fig. 89a). The crown has a shallow central depression. A pair of lateral ridges is present. These begin near the lateral corners of the base and slope upwards to posteriorly where they converge into the posterior crown point. The right one of these ridges is damaged (fig. 89c). A low concave lateroposterior neck is present. The posterior crown tip overhangs the neck. Openings (for vascular canals?) may be seen below the lateral crown ridges (figs. 89 b,c). There are three such openings in an ascending row on the right side (fig. 89c). The rhombic base is low and slightly convex.

Topospecific scales

Judging from their general shape, the following three scales may be transitional to tesserae and derive from a place on the body close to tesserae.

P8998 (fig. 90) is a slightly asymmetric, rare scale form with an asymmetric trend towards the left. The low, hardly inclined, pentagonal crown occupies practically the entire pentagonal base but nowhere sticks out over it. A minimal neck separates the anterior crown from the anterior upper basal rim (fig. 90a). Lateroposteriorly the neck is a bit higher (fig. 90b). The crown is twice longer than broad. The anterior crown edge consists of irregular lobes with c. three, short, blunt (ed ?) longitudinal riblets (fig. 90b). The length of these ribs is c. 20% of total scale length. The crown rims are straight in the anterior crown half (where they follow the basal outline) and bend centrad in the posterior half to form the crown tip. On the left side (fig. 90b) a short lateral ledge is present. The ledge begins in the posterior fifth of the scale, halfway between the crown and basal rims and converges into the crown tip. The base has a low central swelling. The pentagonal, low base and crown suggest that this scale might be transitional to a coronate tessera.

Asymmetric scale/plate P8999 (fig. 91) has an (inverted) V-shaped crown. A short, anteromedian 'embayment' (extending across c. 1/3 of total crown length) is directed posteriorwards and to the left, as is the entire anterior crown on either side of the embayment. The embayment cuts a V shape into the triangular crown, splitting off two lateral smooth legs. The left leg begins at some distance from the basal margin, further posteriorly than the right leg. The left crown rim is more strongly curved than the right and the anterior constriction of the crown is greater on the left. The left crown rim starts out on a leftward course, away from the longitudinal axis of the scale but soon curves towards midline at angle roughly between 100 and 110°. It continues its course in a straight line to converge with the right crown rim in the midposterior crown point, which has probably broken off. The left anterior crown margin is slightly concave and oblique (centrad) (fig. 91b) and consists of two indistinct lobes. The right anterior crown margin is convex, has three lobes separated by shallow grooves (not

too short) parallel to the right crown rim. The lateroposterior neck is vertical, low and increases in height posteriorly. On each side of the crown there is an oblique neck rib, which begins low in the neck at a level about halfway the longitudinal axis of the scale and joins the crown at the point where the posterior crown tip has broken off. The posteriormost crown part overhangs neck and base. A narrow upper basal zone separates the lateral neck from the basal rim (fig. 91b). Base low and rounded rhombical. The anterior basal edge is probably slightly damaged (fig. 91b). The entire anterior upper basal surface shows a convex curvature (fig. 91a). This scale or plate is probably (transitional to) a coronate tessera .

Remarks: A V-formed crown sculpture is known from some *Nostolepis striata* coronate tesserae (Gross, 1971: pl. 3: 10, 16, 23), where it may be combined with a slighty concave anteromedian basal edge (op. cit.: pl. 3: 10, 17). The V-ornament in these tesserae usually has arms with a sharp dorsal ridge and numerous short riblets all around its outer margin, and with these riblets converging into the dorsal ridge (ibid.: pl. 3). Such features distinguish the tesserae described by Gross (1971) from the present scale/plate.

The 'embayment' should not be confused with the anteromedian fold in some *Nostolepis* scales, e.g. '*Nostolepis* sp. A' (Märss, 1997: pl. 6: 5, from the Pridoli of the Central Urals). Species A is probably composed of a heterogeneous group of *Nostolepis* scales.

P9000 (fig. 92) is a rare scale form, with a steep, almost tubercular crown on an irregularly round (damaged), slightly concave base. The crown has seven, distally converging ridges. Except the midposterior one, these ridges bend slightly inwards at the crown base interval. There is a high, steep neck posteriorly, with openings (artifacts, or for vascular canals, fig. 92c) at the neck base interval. The neck base transition is indistinct but there is a narrow, sloping, upper basal zone all around — especially visible in anterior view (fig. 92a). The specimen is transitional to monotubercular platelets and (coronate?) tesserae.

Trunk scale feature checklist

The number of trunk scales selected and photographed for further morphological analysis was twice the number of scales that have been described. The scan illustrations showed that half of the scales were not preserved well enough. This poor state had remained unobserved under Wild M8 binoculars, probably as a result of small size.

The updated list is given in the appendix. The features deduced from topospecific trunk scales, possibly transitional to tesserae, received a letter code (TES). This letter code will allow distinction between features of 'ordinary' trunk scales and trunk scales transitional to other squamation types such as tesserae.

Elaboration of previously listed features (new list numbers are followed by old list numbers, if applicable): 3: pyramidal (fig. 87) — inverted V shape (fig. 91, TES) — approximately tubercular (fig. 92, TES). 21(20): lobed (figs. 89; 90, TES) — separated lobes = lobes in combination with the V-shaped crown of feature 3 (fig. 91, TES).

Additional features (new list numbers):

22: anterior crown margin with median 'bay' (fig. 91) TES: present, or absent;

27: forward projecting anteromedian lobe: lobe posteriorly diverging, or converging;

28: lateral riblets: present, or absent;

29: lateral riblets: orientation-length-number-on either lateral surface.

General and taxon-related remarks on some listed features.

Lateral crown surfaces (feature 20) and lateral riblets (features 28-29). The lateral crown surfaces (figs. 86-87) are here distinguished by their larger and broader surface from lateral ledges (fig. 85) (feature 19). Lateral riblets may occur on lateral crown surfaces (figs. 86-87). These features are also seen in a scale from Klinta (Vergoossen, 2002b: pl. 3: 32-33). Gross (1947: pl. 26: 9a) figured a *Nostolepis striata* scale (from the 'Beyrichienkalk') showing these features, and so did Valiukevicius (1998: pl. 1: 1a). The latter specimen is from the Kaliningrad district and of Lower Devonian (Lochkovian) age. A specimen of *N. arctica* Vieth (1979: pl. 5: 8) from Ellesmere Island (Lochkovian) resembles these *N. striata* scales very much.

Lobed anterior crown margin (feature 21) and forward projecting anteromedian lobe (feature 27). Valiukevicius (1998) illustrated a scale of *Canadalepis linguiformis* from Lithuania with this feature and one of *N. minima* with an anteromedian lobe (op. cit.: pl. 3: 8; pl. 1: 6, respectively), both from the Lochkovian of Lithuania. The feature was well and richly illustrated by Lehman (1937) from the following 'Downtonian' taxa, the specimens are from Ramsåsa (site F), Helvetesgraven, Saarema: *Diplacanthoides dilobatus* (fig. 29, Ramsåsa), *D. sinuosus* (fig. 38, Ramsåsa), *D. multilobatus* (fig. 39A, Ramsåsa), *D. inaequolobatus* (fig. 54, Ramsåsa), *D. insignis* (fig. 33, Ramsåsa; 58 IA, Helvetesgraven), *D. compressus* (fig. 61, Helvetesgraven), *D. trilobatus* (fig. 64, Helvetesgraven), *D. retroincisuratus* (fig. 68a, Saarema), *D. irregularis* (fig. 71 IIA, Saarema). The *D. compressus* specimen resembles P8996 (fig. 89).

The lobed anterior scale margin, as distinct from an anterior scale margin with riblets, seems a valid feature for Scanian *Nostolepis* (trunk) scales. Gross (1947, 1971) did not discuss this feature and the *N. striata* scales he figured do not show it. Neither did Valiukevicius (1998), who included the above mentioned *Diplacanthoides* taxa in the synonym list of *N. striata* without discussion, *D. irregularis* excepted. More data are needed for further assessment. For a start, it is useful to separate (well-preserved) lobed from ribbed forms in the Baltic Ludlow. However, the distinction may not always be clear-cut, also in the case of forward projection. One reason is that post-mortem geo- or biochemical abrasion may have affected the ribs. Such might be the case in some of the scales figured by Lehman (1937).

Nostolepis striata, '*elegans*' form group, Vergoossen, 1999b
(cf. '*Diplacanthoides elegans*' Brotzen, 1934; cf. *Nostolepis arctica* Vieth, 1980)
Pl. 16; Pl. 17, figs. 98b-100.

Trunk scales

The illustrated scales (figs. 93-99) fit well within Vieth's (1980: pl. 5: 1-9) Lochkovian morphological series for *N. arctica*, except that they have no neck ribs. Vieth (op. cit.) called these ribs 'lateral Rippen', of which there are often several. In her illustrated scales they are never lacking. Valiukevicius (1998) did not mention the phenomenon. One such rib is probably present in one of the specimens of *Nostolepis* aff. *arctica* (Valiukevicius, 1998: pl. 3: 18b). The flat-based nostolepid platelets of the '*elegans*' form group from Helvetesgraven (Vergoossen, 1999b: pl. 2: 16-17) have no neck ribs. The specimen figured from Klinta (Vergoossen, 2002b: Pl. 3: 30) has no neck ribs. The significance of the presence or absence of neck ribs is hard to

assess on itself. For the moment the presence of several lateral neck ribs is interpreted as feature of *N. arctica* trunk scales.

Here the trunk scales with inflated base and the scales with flat base (Vergoossen, 1999b) are both included in the *elegans* form group of *N. striata* scales. The flat-based variants are henceforth treated as plates (see below).

Scale P9004 (fig. 96) is asymmetric and has a crown facing to the right. P9003 (fig. 95), P9005 (fig. 97) and P9006 (fig. 98) are asymmetric and have crowns facing left. P9005 (fig. 97) has a broken base anteriorly. The symmetric trunk scale P9001 (fig. 93) looks like a broader variant of P9002 (fig. 94) and has a more strongly curved crown rim. Near the right crown rim the anterior crown area has a U-shaped depression (fig. 93b). The area resembles the sockets of a bivalve (fig. 93a). This feature is the most striking difference between the two scales, but it is hard to assess its significance. P9002 (fig. 94) has an anteromedian riblet.

Platelet (cf. Vergoossen, 1999b: pl. 2: 16-17)

Platelet P9008 (fig. 100) is rare and small (c. 0.25 mm long and 0.2 mm wide). The thin, damaged, polygonal (originally possibly pentagonal or hexagonal) basal plate has a more or less centrally placed, steeply inclined, triangular crown. The converging crown rims flank a concavity that is unconstricted at the crown/base interval. A little further posteriorly a pair of lateral ledges begins. These ledges have a fold and converge into the crown tip. The left ledge ascends parallel to left crown rim for half its length (fig. 100a). A broad basal zone surrounds the crown. No neck present.
Remark: The crown in this specimen, and also that in P9009 (fig. 101) looks like the crown in trunk scales rather than a tubercle, contrary to the crown in plate P9010 (fig. 102), which is distinctly tubercular. The difference is probably related to body topography: differences in the place on the body where these plates grew, i.e. for the tubercular plates closer to 'coronate' plates.

Nostolepis sp.
Pl. 17, figs. 101-104; Pl. 18, figs. 105-107.

Since there are at least two form groups of *Nostolepis striata* scales, *N. striata* and the *elegans* form group, and since not enough histological information is presently available, an a priori assignation of the scales, plates and tesserae to *N. striata* cannot be made.

Squama pronia (sensu Gross, 1971) (fig. 107)

There are three rows of poorly preserved, ridged tubercles (partly fused) parallel to the basal margin. The most distal row has partly broken off. Between the rows openings for vascular canals can be observed.

Platelets and tesserae (figs. 101-106)

Since there are at least two form groups of *Nostolepis striata* scales, *N. striata* and the *elegans* form group, and since not enough histological information is presently available, an a priori assignation of the plates and tesserae to *N. striata* cannot be made.

Platelet P9009 (fig. 101) is rare and small (c. 0.2 mm long and 0.3 mm wide), and poorly preserved. The basal plate is round, very thin and flat, with a centrally placed,

ridged crown. The ridges (at least five) converge distally. Compare coronate and shoulder girdle platelets.

The rare, monotubercular scale P9010 (fig. 102) is a coronate or shoulder girdle platelet. The thin, rhombic basal plate (c. 0.35 x 0.2 mm, measured along longest and shortest axis) is damaged on the edges. The centrally placed conical tubercle has seven convex ridges distally converging into a sharp top. At tubercle/base interval there are openings (artifacts or for entry of vascular canals) in the folds between ridges. There is a smooth upper basal zone all around which is widened to the left and right.

The rare, ovoid, monotubercular plate P9011 (fig. 103) is longer than broad, with the greatest width in posterior half. The outline of the tubercle follows that of the plate. The tubercle has seven, main and convex ridges (greatest convexity towards base) that converge into a blunt distal top. The anteromedian ridge (fig. 103b) is the longest and less steep, the other six ridges are equally high and steep but not equally spaced, so that the intermediate surface areas differ in size (fig. 103a). The area on each side of the median anterior ridge is further subdivided by parallel and slanting, anteroposteriorly directed ridges that end in the median ridge (fig. 103b), thus creating a chevron pattern. A smooth, upper basal zone, which is widest anteriorly, surrounds the tubercle. At tubercle/base interval openings may be observed (fig. 103b), either artifacts or for the entry of vascular canals. The base is slightly convex. Perhaps this tessera shows a transitional phase from conical tubercle towards the triangular type of crown in trunk scales. Coronate or shoulder girdle plate?

The multitubercular, more or less pentagonal coronate plate P9012 (fig. 104) is equipped with a semicircular 'wall' of three ridged partly fused tubercles. The outer tubercles are fused on one side, and the middle is fused on two sides. The 'wall' is situated slightly off centre (fig. 104a) and surrounded by a wide and sloping upper basal zone. The basal plate is thin and ventrally concave.

The multitubercular, complex platelet P9013 (fig. 105) is made up of four, ridged tubercles, each consisting of at least five converging ridges, on a concave, pentagonal, thin basal plate that in its outlines shows traces of fusion of two smaller platelets into a bigger one. Most anteriorly (in the photograph) a single and isolated tubercle can be observed (fig. 105b) on a strongly concave, quadrangular basal platform, which has three detached sides and is attached on one lateroposterior side in two places. The posterior platelet has a row of three tubercles lying so close together that they 'touch' or make contact by one ridge only.

Remarks: Judging from the arrangement of the tubercles this complex platelet might well have developed into an even larger tessera stellata with more platelets joining in. Although Gross (1971: 16, text-figs. 4b-c) demonstrated radial growth increase in large tesserae stellatae by simultaneous apposition of a new growth zone to all the stellate arms and all around the plate, it is conceivable that, at such an ontogenetic stage as in the present specimen, growth increase also occurred by apposition, on one side, of an entire monotubercular platelet. If this one side were the anterior side, growth would be analogous to that in tooth whorls and dentigerous jawbones. In the present specimen it is, however, impossible to establish that the semidetached monotubercular platelet is situated anteriorly. This growth issue requires histological investigations on well-preserved material.

Stellate tessera P9014 (fig. 106) is damaged. On one half of the rhombic plate with

broken edges four arms are arranged in two mirrorwise opposed, orthogonal pairs. In the parallel arms it is still possible to recognise individual, ridged tubercles and fusion has not proceeded so far as in the arms that lie in line. In nostolepid stellate tesserae, openings for vascular canals are regularly found around the arms (between the ridges, at base level) and esp. in the parts closest to the plate margins; some such openings might be present in this specimen (fig. 106b). On the other plate half the arms were probably destroyed.

Radiporacanthodes biblicus (Lehman, 1937)
Pl. 18, fig. 110.

One specimen (P9018) was collected.

Ischnacanthid spine
Pl. 20, fig. 121.

P9029 is a fragment of a slender spine bearing smooth parallel, longitudinal ribs. The ribs are semicircular in section and constricted near the thin platform that bears them. The rib on the leading edge is largest. It is flanked on each side by two ribs of decreasing width: width ratio of the three ribs (measured from leading to trailing edges and at largest cross sectional diameter) 30 : 13 : 10. The trailing edges are thin. The rear side is open and asymmetrically concave.

Acanthodii gen. et sp. indet.
Pl. 18, figs. 108-109; Pl. 19; Pl. 20, figs. 117-120.

Scales (figs. 111-120)

Although there are good morphological indications that the scales assigned to morph 1 might belong to *Gomphonchus volborthi*, histological preservation is poor and *Gomphonchus* type of histology has so far been observed only in one unfigured specimen. At present there is not enough evidence to refer some of the morphs described below to one genus or to group them together as scale variants of one species.

Morph 1, cf. *Gomphonchus volborthi* (Rohon, 1893) (figs. 111-115)

Scale P9019 (fig. 111) is a nearly symmetric trunk scale with a median depression in the rhombic crown. The anterolateral crown edge has blunted, radial ornament (originally short ridges, possibly shaped like inverted V's anteriormost?). Behind this ornament the crown is smooth. The left posterolateral crown rim is concave, the other is straight. The posterior crown tip is slightly inclined and does not overhang the concave neck. The neck is distinct all around. The anterior neck is lower than the posterior neck, which shows openings for vascular canals, and measures c. half the total scale height. The deep base has a median swelling. The base measures c. half the total scale height (from its deepest point) and is larger than the crown all around.

Scale P9020 (fig. 112) is a variant. The horizontal, rhombic crown is wider than long. Again the left posterolateral crown rim is concave and the other posterolateral rim straight. The crown tip overhangs the neck and shows the last three growth zones

(fig. 112b). The lateroposterior neck has regularly spaced openings for vascular canals in midneck position (fig. 112b, left). The left lateral corner of the base is drawn out in a sharp angle (45°): such a base is typical of some Late Silurian East Baltic gomphonchid and poracanthodid scale variants (cf. Vergoossen, 1999a: pl. 2: 24; pl. 3: 31, 35).

Another variant is P9021 (fig. 113). The crown has a marked posterior constriction; the posterior crown tip overhangs neck and base.

The more or less symmetric scale P9022 (fig. 114) has concave posterolateral crown rims, the concavity is more distinct on the left than on the right. The resulting constriction of the posterior crown is not so abrupt as in P9021 (fig. 113a). Again the posterior crown tip overhangs neck and base.

P9023 (fig. 115) is a damaged and worn variant. The rhombic, smooth crown has lateroposterior sides that are longer than the anterolateral ones, which meet at an angle of 90° anteromedially, where the crown has a short, narrow and shallow sulcus (fig. 115b). The anterolateral edge of the crown plate shows weak undulations (fig. 115b). The crown is narrower than the base. Base only slightly convex.

Morph 2, ischacanthiform scale (figs. 116-117)

Scale P9024 (fig. 116) has a smooth, horizontal, rhombic crown plate of which the left anterior edge (fig. 116a) has broken off. The left and right anterior crown rims meet anteromedially almost at right angles and there is a short, shallow fold here. Lateroposteriorly the youngest growth zone of the crown is lowered and marked off by a groove along the preceding growth zone. The neck is low anteriorly but slightly increases in height lateroposteriorly. Here remains of alternating openings (for vascular canals) and columns can be vaguely discerned. The rhombic base is larger than the crown and with central swelling.

Remarks: A posterolateral groove marking off the youngest growth zone from the rest of the crown is also known from *Gomphonchoporus hoppei* and from variant 3 scales of *Gomphonchus boekschoteni* (Vergoossen, 1999a: 236).

Variant P9025 (fig. 117) may be a scale transitional to tessera, and is rarer than the preceding scale form. Crown and base are pentagonal. The horizontal crown inclusive of the posterior tip, covers the entire base but nowhere overhangs it. The anterior crown edge is folded (and perhaps had short, radial ridges originally, which were blunted postmortally?). The median fold is most distinct and largest (fig. 117b). The youngest complete growth zone of the crown is offset lateroposteriorly (fig. 117c). Part of the crown must be missing, judging from the presence of a fragment of another, separated and lowered, most posterior growth zone (fig. 117c). The neck is very low all around, with vestiges of lateroposterior ribbing (fig. 117b). The base is deep, making up 50% of total scale height, and with anteromedian swelling. Separated youngest growth zones are also known from *Poracanthodes? lehmani* (Vergoossen, 1999b: pl. 2: 26).

Morph 3 (figs. 118-119)

Scale P9026 (fig. 118) is asymmetric, the length axis of the crown is to the left of basal length axis. The rhombic crown plate has a marked anteromedian fold between a pair of prominent ridges, both fading out at the level of the lateral crown corners. Anteriormost the ridges are (inverted) V-shaped (fig. 118a). The right anterolateral

crown edge shows slight undulations and two faint short ridges (fig. 118b). The posterior neck is higher than the anterior neck, and has openings for vascular canals near the basal rim. Convex, rhombic base with moderate median swelling, making up c. 30% of total scale height. The crown nowhere overhangs the base.

The tiny scale in fig. 119 (P9027) is more damaged than the preceding one, the crown plate is triangular and more inclined. The anterior crown and basal rims are straighter and the base is flat.

Remark: These scales resemble Acanthodii gen. et sp. indet., variant 2 from Ramsåsa H (Vergoossen, 2002a: pl. 8: 108-109).

Morph 4 (fig. 120)

Scale P9028 might be intermediate between morphs 1 and 3. The triangular crown plate has a rounded, sharply ridged, anterior margin. The median ridge is the largest and longest of the four (fig. 120b). The ridges have the shapes of (worn) inverted V's. The anterior crown has no continuous anterior rim: between the anterior ridges the crown surface slopes into the neck without distinct barrier. The crown plate is only slightly inclined and anteriorly it bends towards the base as the ridges indicate (fig. 120b). The crown plate overhangs neck and base with its posterior tip only. The neck is concave, widening out towards the base and higher lateroposteriorly than anteriorly where it is smooth. There are openings for vascular canals in the posterior neck, in mid neck position. The rhombic base has a low, anteromedian swelling. The scale also resembles Acanthodii gen. et sp. indet., variant 3 from Ramsåsa H (Vergoossen, 2002a: pl. 7: 103).

Plates (figs. 108-109)

These very rare platelets are reminiscent of multitubercular tesserae but their acanthodian derivation remains to be demonstrated. No histological data are available.

The small, worn plate, P9016 (fig. 108) is c. 0.45 mm long and 0.5 mm wide. The basal platform is rhombic, very thin and flat, and bears five posteriorly directed, triangular, smooth(ened?), thin crown blades of which the most posterior are the largest. The anterior surface of the largest crown would seem to be shallowly concave. The crown blades do not overhang the basal platform. The undulant basal edge may indicate breakage (sharp fractures). Compare tesserae from Helvetesgraven: Vergoossen, 1999b: pl. 2: 18 (tessera stellata), 19 (tessera coronata).

The small, worn plate P9017 (fig. 109) has at least four crowns, and is c. 0.24 mm long and 0.28 mm wide. The thin basal platform is slightly concave and rounded pentagonal. The largest crown seems to be in the middle (fig. 109a). The crowns, though triangular and directed posteriorly, are not all of the same shape and do not point in the same direction and in these features the platelet also differs from P9016 (fig. 108). The basal edge is damaged.

Correlation (Tables 1-3, Figs. 3-4)

The fauna from the Ramsåsa sample 'south of church' consists of two taxa, of which only *Thelodus parvidens* sensu Märss, 1986 can be determined with certainty. In the Baltic region this species ranges from the *Andreolepis hedei* Zone, Ludlow, Leintwardinian (Märss et al., 1995) to the '*Poracanthodes punctatus* Zone', Pridoli. On Got-

Time			Grönwall, 1897	Jeppsson, 1974 Conodont Zones		Jeppsson & Laufeld, 1986	Vertebrate Zones	Öved Sandstone Fm Vergoossen, 2002a-c
PRIDOLI			4	*Hindeodella steinhornensis* nov. subsp. 2	*Ligonodina elegans*	Öved Sandstone Fm		
			3	*H. st.* nov. subsp. 1				
			2					
LUDLOW	Whitcliffian	Late		*H. wimani*		Klinta FM		
			1b				*T. sculptilis*	Ramsåsa H Ramsåsa D, Q 6 85; Klinta 2, 4-8 RB
							TRANSITION	Helvetesgraven Ramsåsa D, SW 24
				H. st. scanica				
		Early						
			1a	*H. excavata*				
	Leintwardinian	Late		*P. dubius*				
				P. siluricus				
					A. hedei			

▲

Fig. 3. Vertebrate-based correlation of the Öved Sandstone Formation (Scania, S Sweden), projected on a conodont zonation chart (modified and simplified after Jeppsson & Laufeld, 1986: fig. 3). For alternatives see the chapters on correlation (Vergoossen, 2002a-c).

Fig. 4. Vertebrate-based correlation of the Öved Sandstone Formation (Scania, S Sweden), projected on an interregional correlation chart (modified and simplified after Jeppsson et al., 1994: fig. 3). For alternatives see the chapters on correlation (Vergoossen, 2002a-c). The vertebrate data correlate best with the Late Whitcliffian *Ligonodina elegans* conodont fauna (cf. Märss, 1986: text-fig. 46).

▼

TIME		CONODONT ZONES / FAUNAS	GOTLAND	SAAREMA VERTEBRATE ZONES			SCANIA
PRIDOLI		*Ligonodina elegans detorta* Zone	Fauna 6	K4	Ohesaare Fm		
		L. e. elegans	Fauna 5				
		O. s. eosteinhornensis s. str. Z.	Fauna 4	K3b	Loo Beds		
			(Fauna 3)	Kaugatuma	Äigu Beds		
			(Fauna 2)			*T. sculptilis* Zone	
		L. elegans (large, frequent)	(Fauna 1)				
LUDLOW	Late Whitcliffian	End of *O. sn. Crispa* Zone	Sundre		Kudjape Beds		
		O. steinhornensis s.l. alternative denticulation	Hamra c				Ramsåsa, H
		L. elegans (rare, small)	b		Tahula Beds	*Archegonaspis* sp. b	Ramsåsa D (Q685), Klinta 2,4-8, RB
			a	HIATUS			
		O. steinhornensis s.l.	Burgsvik				Helvetesgraven
	Early Whitcliffian	*P. equicostatus* etc	Eke				Ramsåsa D (SW 24)
	Late Leintwardinian	*P. siluricus* Zone	*Archegonaspis* e *lindstroemi/A. hedei*				
	Early Leintwardinian		Hemse d	K2 Paadla	Uduvere Beds	*A. hedei* Zone	

Table 1. List of agnathan taxa from the Öved Sandstone Formation at sites Ramsåsa 'south of church' (Q606), D (SW24, Q685), H (P449); and Helvetesgraven (Helv; see Vergoossen, 1999b); * = glabrous scales; d = dominant; ? = presence uncertain. *T. parvidens* as the dominant species includes the formae.

Taxa	Q606	SW24	Q685	P449	Helv
Osteostraci					
Hemicyclaspis sp.				x	x
Osteostraci gen. et sp. indet.		?			x
Heterostraci gen. et sp. indet.					x
Thelodonti					
Thelodus parvidens *, including	d	d	d	x	x
forma *pugniformis*		x		x	x
forma *costatus*		x	x	?	x
forma *bicostatus*	x	x	x	x	x
forma *trilobatus*		x	x	x	x
Thelodus carinatus		x			
Thelodus traquairi		x	x	x	x
Thelodus admirabilis (age marker)					d
Thelodus sculptilis (zone fossil)		x	x	d	x
Loganellia cuneata				x	x
Paralogania ludlowiensis		x			
forma *cruciformis*					x

Table 2. List of gnathostome taxa from the same localities as in Table 1; f = fragments; rv = Ramsåsa H variant; hv = Helvetesgraven variant.

Taxa	Q606	SW24	Q685	P449	Helv
Acanthodii					
Nostolepis striata		x	x	x	x
forma *'elegans'*		x			x
nostolepid tooth whorls					f
nostolepid spines		f			f
Gomphonchus sandelensis			?	x	x
Gomphonchus volborthi		x			
stellate plates		x	x		x
coronate scales and plates		x	x	x	x
squamae proniae		x		x	x
squamae umbellatae		x		x	x
Poracanthodes? lehmani				x	x
Poracanthodes cf. *punctatus*				rv	hv
Radioporacanthodes biblicus		x		x	
'Dornzähne' sensu Gross, 1957					x
ischnacanthid tooth whorls		f		f	f
ischnacanthid spines		f	f		
dentition cones					x
Acanthodii gen. et sp. indet., morph 1	x	x	x	x	
Osteichthyes					
Andreolepis hedei (zone fossil)					x

Table 3. Overview of faunas from the lowermost Tahula beds (T — Estonia; Märss, 1992), the Burgsvik/Eke beds (BE — Gotland; Fredholm, 1989; Märss, 1992), and Scania (Vergoossen, 1999b, 2002a,b; see also the explanation of Table 1); rv = Ramsåsa H variant; hv = Helvetesgraven variant.

Taxa	T	BE	Q606	SW24	Q685	P449	Helv	Klinta1-10	Rinnebäck
Zenaspis? sp.	x								
Hemicyclaspis sp.						x	x		
Archegonaspis sp.	x							K4	
Birkiniida gen. indet. sp. A	x								
Thelodus parvidens	x	x	x	x	x	x	x	K1-2, 4-10	x
Thelodus traquairi	x	x		x	x	x	x		x
Thelodus admirabilis	x						x		
Thelodus sculptilis	x	x		x	x	x	x	K2, 4-8	x
Thelodus carinatus				x					
Loganellia cuneata	x	x				x	x	K2, 4-5	
Paralogania ludlowiensis	x	x		x					
Katoporodus tricavus	x								
Nostolepis striata	x	x		x	x	x	x	K1-2, 4-10	x
Gomphonchus sandelensis	x	x			?	x	x	K2, 5	
Poracanthodes? lehmani						x	x		
Poracanthodes cf. *punctatus* porosiforms	x	x				rv	hv	K5, 7	
Radioporacanthodes biblicus				x		x		K6	
Andreolepis hedei							x		
									P702
Total taxa	13	8	1	7	5	10	11		4
shared with Tahula			1	6	4	7	7		4
shared with Burgsvik/Eke			1	6	4	7	6		4

land, Fredholm (1988, 1989) recorded *T. parvidens* from unit d of the Hemse limestone (*Ancoradella ploeckensis* conodont range, Leintwardinian) upwards into the Sundre beds (Whitcliffian). In Scania, Fredholm (1988a: 170) reported *T. parvidens* from Vrangelsborg, Klinta Formation, Lunnarna Member (*Polygnathoides siluricus* Conodont Zone, Leintwardinian) upwards. Vergoossen (1999b) recorded the species from Helvetesgraven faunas (Öved Sandstone Formation), placed in the transition phase between the *Andreolepis hedei* and the *Thelodus sculptilis* Zones (Vergoossen, 1999b). *T. parvidens* was also recorded from the Öved Sandstone Formation at Ramsåsa H, Klinta and Rinnebäck (Vergoossen, 2002a), placed just above the transition phase. The transition phase is equivalent with a hiatus at the top of the Uduvere beds, Paadla Stage of Ludlow, in the East-Baltic sequence (Märss, 1992). Among Baltic researchers there is disagreement about the range of the hiatus: Märss (1992: fig. 1) considered the hiatus the time equivalent of part of the Whitcliffian Burgsvik/Eke beds, and more specifically of the Burgsvik Sandstone (op. cit.: fig. 2). Jeppsson et al. (1994: fig. 3) show a larger hiatus (see Fig. 4). Since the Scanian vertebrate faunas from the Öved Sandstone Formation recently studied show great affinity with the Whitcliffian Tahula beds in the East Baltic and with the Whitcliffian Burgsvik beds (Table 3) it is reasonable to restrict the age of the fauna from the Ramsåsa 'south of church' sample to Whitcliffian.

Three taxa from the Ramsåsa D faunas are crucial to the age interpretation and correlation of the samples, viz. *Thelodus carinatus* (not so rare), *Paralogania ludlowiensis*

(very rare), both only collected from sample SW 24, and *T. sculptilis* (common), collected from samples SW 24 and Q 685.

T. carinatus is the oldest of these three species. In the East-Baltic sequence it ranges from the Himmeste beds to the lower part of Uduvere beds, Paadla Stage of Ludlow (Märss, 1992; Bringewoodian-Leintwardinian: Fredholm, 1988, 1989). Of the seven taxa that occur in both beds (Märss, 1992), three (42%) are also known from the SW 24 fauna: *T. carinatus, Nostolepis striata* and '*Gomphonchus sandelensis*'. On Gotland *T. carinatus* was recorded from the Hemse d, e beds (Fredholm, 1988, 1989; Märss, 1992), Bringewoodian-Leintwardinian (Fredholm, 1988, 1989). Of the eight taxa in the *Polygnathoides siluricus* (Leintwardinian) part of these beds (Fredholm, 1988b), four (50%) are shared with the SW 24 fauna: *T. carinatus, T. parvidens*, *N. striata* and '*G. sandelensis*'; two other associated taxa are also of interest because they have been recorded recently from the Öved Sandstone Formation of Scania (Vergoossen, 1999b, 2002a): *Andreolepis hedei* and *Archegonaspis* (*lindstroemi*). See Table 3. Märss' (1992) interpretation and correlation of the Gotland succession differs for the reason stated above. Relevant within the present context is, that she recorded '*Loganellia*' [= *Paralogonia*] *ludlowiensis* in the fauna from the Hemse e beds, which she placed below the hiatus at the top of the Uduvere beds. *P. ludlowiensis* is also present in sample SW 24. This brings the number of taxa shared between Hemse e and Ramsåsa D, SW 24 to 5 out of 9 (= 55%).

Thelodus sculptilis is the youngest thelodont in the Ramsåsa D faunas. Its oldest occurrence along the Anglo-Uralian southern margin of Laurussia is in the Tabuska beds, on the western slope of the Central Urals. In the East Baltic sequence these beds are equivalent with the hiatus at the top of the Uduvere beds (Märss, 1992). Over the hiatus, towards the top of the Ludlow, lie the Tahula beds of the Kuressaare Stage, in which *T. sculptilis* first appears at the base of the sequence. The species is used as zonal fossil of the *T. sculptilis* Zone, which ranges into the lower Pridoli. The fauna associated with the first appearance of *T. sculptilis* shares more taxa with the fauna from sample SW 24 than younger occurrences of the zonal fossil. The shared taxa (7 out of 12: 58%) are: *T. sculptilis, T. parvidens, T. traquairi, Paralogania ludlowiensis*, '*Poracanthodes porosus*', *N. striata*, '*G. sandelensis*'.

On Gotland, *Thelodus sculptilis* is known from the Eke and Burgsvik beds. Of the seven taxa recorded at the base of the Eke beds, six (85%) are shared with the SW 24 fauna: *T. sculptilis, Paralogania ludlowiensis*, '*Poracanthodes porosus*', *T. parvidens* (dominant by 90%), '*G. sandelensis*', *N. striata* (Fredholm, 1989: 11-12). In the lower Burgsvik beds (Glasskär 1, biohermal limestones) *T. traquairi* is added to these (Fredholm, 1989: 43) and seven out of eight identified species (88%) are shared with the Ramsåsa D, SW 24 fauna (see also below). Of the seven taxa recorded at the base of the Burgsvik Oolite/Eke beds (Märss, 1992) five are shared (71%): *T. sculptilis, T. parvidens, P. ludlowiensis*, *N. striata*, '*G. sandelensis*'.

Only two specimens of *Paralogania ludlowiensis* were found in Ramsåsa D sample SW 24. The species is very rare in the Estonian sequence: from the Ohesaare boring at a depth of 94.45-94.48 m (Märss, 1986, fig. 41), Kuressaare Stage, lowermost Tahula beds, lowermost *Thelodus sculptilis* Zone. At the stratigraphic level in the boring where *P. ludlowiensis* occurs, 7 out of 10 taxa in the assemblage (70%) are shared with the Ramsåsa D fauna from sample SW 24: *P. ludlowiensis, Thelodus traquairi*, *T. sculptilis*, *T.*

parvidens, *Nostolepis striata*, '*Gomphonchus sandelensis*' and '*Poracanthodes porosus*'. Märss (1986, fig. 46) correlated this level with the first and only appearance of *P. ludlowiensis* with the occurrence of *P. ludlowiensis* in the Eke beds on Gotland, and with the lowermost occurrence of the species in the Ludfordian of the Welsh Borderland. Märss (1992: fig. 2) mentioned the following range of *P. ludlowiensis* on Gotland: Burgsvik Sandstone, Burgsvik Oolite and Eke beds. From the Burgsvik Sandstone Märss (1992) recorded *Zenaspis* sp., *Nostolepis striata,* '*Gomphonchus sandelensis*', *Andreolepis hedei*. Of these, only the acanthodians are shared, but *A. hedei* is known from Helvetesgraven (Vergoossen, 1999b). Table 3 (column Burgsvike/Eke) lists the taxa recorded by Fredholm (1989: 43) in the assemblage with *P. ludlowiensis* from the lower part of the Burgsvik beds (Glasskär 1, biohermal limestone). Of these taxa, the porosiforms ('*Poracanthodes porosus*' in Fredholm's list) and *T. traquairi* (= Fredholm's *Lanarkia*? sp.) are not mentioned by Märss (1992), who omitted the faunas from the biohermal limestones in her correlation table (op. cit.: fig. 2). On Gotland, the microvertebrate fauna from Glasskär 1 offers the best possibilities for correlation with the Ramsåsa D fauna from sample SW 24 because the two faunas show the greatest similarities.

Within the East Baltic, the faunas from Ramsåsa D show considerable similarity with those from the basal Tahula beds (Table 3), *Thelodus sculptilis* Zone of the Microvertebrate Standard. The low numbers of the zonal fossil, the dominance and abundance of *T. parvidens*, the extreme scarcity of *Paralogania ludlowiensis* and of the poracanthodids, the relative scarceness of *T. traquairi,* the absence of *Loganellia cuneata* and of *Katoporodus*, are arguments to suggest correlation with the Whitcliffian part of the zone, or with the transition phase to the zone. An argument in favour of the latter, at least for the fauna from Ramsåsa D sample SW 24, is the presence of *Thelodus carinatus,* which is the youngest record of this species in Laurussia so far. With *Archegonaspis* and *Andreolepis hedei*, *T. carinatus* is a remnant of older faunas also featuring these taxa. In this respect, the fauna from sample SW 24 fits well within the other Scanian vertebrate faunas recently studied (Vergoossen, 1999b, 2002b).

A special case is *Gomphonchus volborthi*. This species has been included in *G. sandelensis* ever since Gross (1947) put it there (see Vergoossen, 1999c, 2000). This practice enabled me to use *G. sandelensis* as a shared taxon in the comparison with other Baltic faunas. That *G. volborthi* occurs, for example in the Hemse beds, is obvious from the illustrations by Fredholm (1988a: fig. 9).

The microvertebrate dating of the Ramsåsa D samples differs from the conodont and tentaculite datings (Pridoli, local *Ligonodina elegans* conodont Zone) for faunas from Ramsåsa D1 and D3 by Jeppsson (1974) and Larsson (1979). To match some of the Scanian vertebrate datings (including that of the fauna from Ramsåsa D sample SW 24) with the conodont and tentaculite datings would mean, among others, to extend the ranges of *Andreolepis hedei* and *Thelodus carinatus,* plus the range of *Archegonaspis* in the Baltic region, into the Pridoli. Outside the Baltic area, Turner (2000) reported an early Pridoli occurrence of *A. hedei* from the Long Quarry Formation, south Wales, Britain. Märss (1992) correlated the Long Quarry beds with *A. hedei* with the Uduvere beds below the hiatus. A Pridoli age for the Scanian vertebrate samples would, for example, leave unexplained some of the observations that were advanced above as arguments in support of a Whitcliffian age (transition between *A. hedei* and

T. sculptilis Zones): the low numbers of the zonal fossil *T. sculptilis* (Ramsåsa D, Klinta), the dominance and abundance of *T. parvidens* (Ramsåsa south of church, D, Klinta, Rinnebäck), the scarcity of *Paralogania ludlowiensis* (Ramsåsa D fauna SW 24), the absence or extreme scarcity of *Loganellia cuneata*, and of the poracanthodids (all Scanian sites in Table 3), the absence of *Katoporodus* (all sites). It is interesting that the low numbers, scarcity or absence chiefly concern the new taxa that in the East Baltic Standard appear for the first time in the *T. sculptilis* Zone and that in Scania the low numbers of some of the older taxa such as *A. hedei* and *T. carinatus* indicate that these taxa apparently survived for a brief period of time the lower Whitcliffian Lau event, which was one (of the two) 'most devastating of the Silurian primo-secundo events' (Jeppsson & Aldridge, 2000).

Jeppsson (1974) gave the following sequence on the basis of the conodonts: Helvetesgraven, Ramsåsa H, Ramsåsa D1, Ramsåsa D3. Only the conodont fauna from Ramsåsa F represented slightly younger Pridoli. Larsson's (1979) results differ in details from Jeppsson's, but the sequence for the sites is the same. A tentative succession on the basis of the microvertebrate data might look as follows: Ramsåsa D (SW 24), Helvetesgraven, Ramsåsa D (Q 685), Ramsåsa H (see Figs. 3-4).

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Appendix

Nostolepis striata, trunk scale feature check list

1 crown: symmetric, or asymmetric
2 asymmetric crown: surface facing left, or right
3 shape of crown : triangular (trapezoid) — ellipsoid — pyramidal – [TES: inverted v-shaped — approximately tubercular]
4 shape of crown: narrow-wide (in comparison to width of base)
5 shape of crown: short-long (in comparison to length of base)
6 crown: protruding over base, or not
7 protrusion of crown: posterior tip — posterior/lateroposterior third — posterior/lateroposterior half
8 crown: inclined-horizontal
9 inclination of crown: low-moderate-steep
10 crown surface: concave-flat-convex-elevated
11 crown rims: straight-convex-sigmoidal
12 crown rims: bending inwards and constricting anterior crown, or not
13 lateral crown rims: plain, or ornamented
14 number of lateral crown rims: left — right — left and right
15 starting position of most anterior lateral crown rims: at the level of the lateral corners of base — further anterior/posterior
16 lateral crown rims: straight, or curved (convex-concave)
17 lateral crown rims: bending inwards, or not
18 lateral crown rims: converging into posterior crown tip — well below tip
19 lateral crown rims: narrow (ridge-like) — broad (ledge-like)
20 lateral crown surfaces: present, or absent
21 anterior crown margin: straight — irregular — with 'Vorkrönchen' or 'Nebenkrönchen' — lobed [TES: lobed — separated lobes in combination with v-shaped crown, feature 3]
22 [TES: anterior crown margin with median 'bay': present, or absent]
23 anterior riblets: present (their number), or absent
24 orientation of anterior riblets: towards lateral left — towards lateral right — longitudinal — mixed (specify further)
25 orientation of anterior riblets: all parallel (to what?) — partly parallel (to what?)
26 forward projection of anteromedian riblets: of parallel — posteriorly diverging — posteriorly converging anterior riblets
27 forward projecting anteromedian lobe: lobe posteriorly diverging — lobe posteriorly converging
28 lateral riblets: present, or absent
29 lateral riblets: orientation — length — number — on either lateral surface
30 crown: filling entire upper basal platform — part of platform
31 unornamented zone of basal platform: anterior — anterolateral — lateral — posterolateral — posterior — all around crown
32 distance between crown and basal rim (further specified in relation to 26): narrow-wide
33 surface between crown and basal rim (not the neck; further specified in relation to

26): concave-flat-convex-sloping
34 neck: lateral-posterior-lateroposterior
35 neck: low-high-moderately high
36 neck openings: none-tiny-medium large (size relative to 0.1 mm bar)
37 neck ribs, developed as: sharp ridges — ribbons (= broader) — sheets (= still broader)
38 neck ribs: straight-curved
39 neck ribs: on the left — on the right — posterior — on the left and right — on the left, right and posterior
40 neck ribs: number
41 neck ribs: as long as the lateral neck — shorter — mixed (specify further) — on the left — on the right
42 starting point of neck ribs: near base level — higher in the neck — near the end point of a more anterior neck rib
43 orientation of neck ribs: oblique — vertical — in continuation of a more anterior neck rib — parallel to the crown rim -parallel to the lateral crown rim(s) — parallel to other neck rib
44 neck ribs, converging into. posterior crown point — posterior part of crown rim — the median part of the crown rim — the anterior part of the crown rim — lateral crown rim (low-halfway-high) — another neck rib
45 base: concave-flat-convex
46 convex base: low-deep-moderately deep
47 shape of base: rhombic, or otherwise
48 anterior basal edge: straight-rounded-angular.

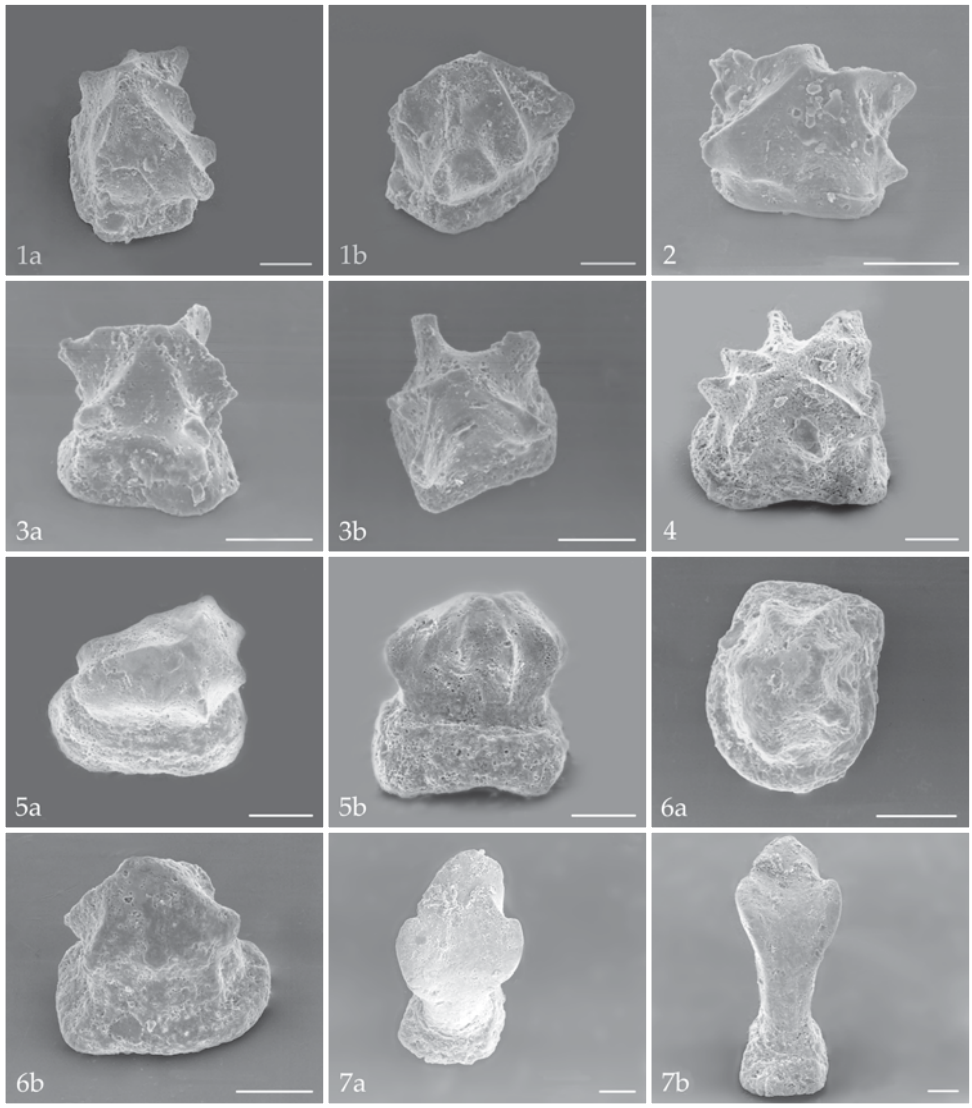

Plate 1

Figs. 1-7b. *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986
1-6: Costatiform scales; 1: P8909; a: crown view; b: lateral view; 2: P8910, crown view; 3: P8911; a: lateral view; b: crown view; 4: P8912, crown view; 5: P8913; a: crown view; b: lateral view; 6: P8914; a: crown view; b: lateral view;
7: Pugniform scale (= *T. pugniformis* Gross, 1967); P8915; a: crown view; b: anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

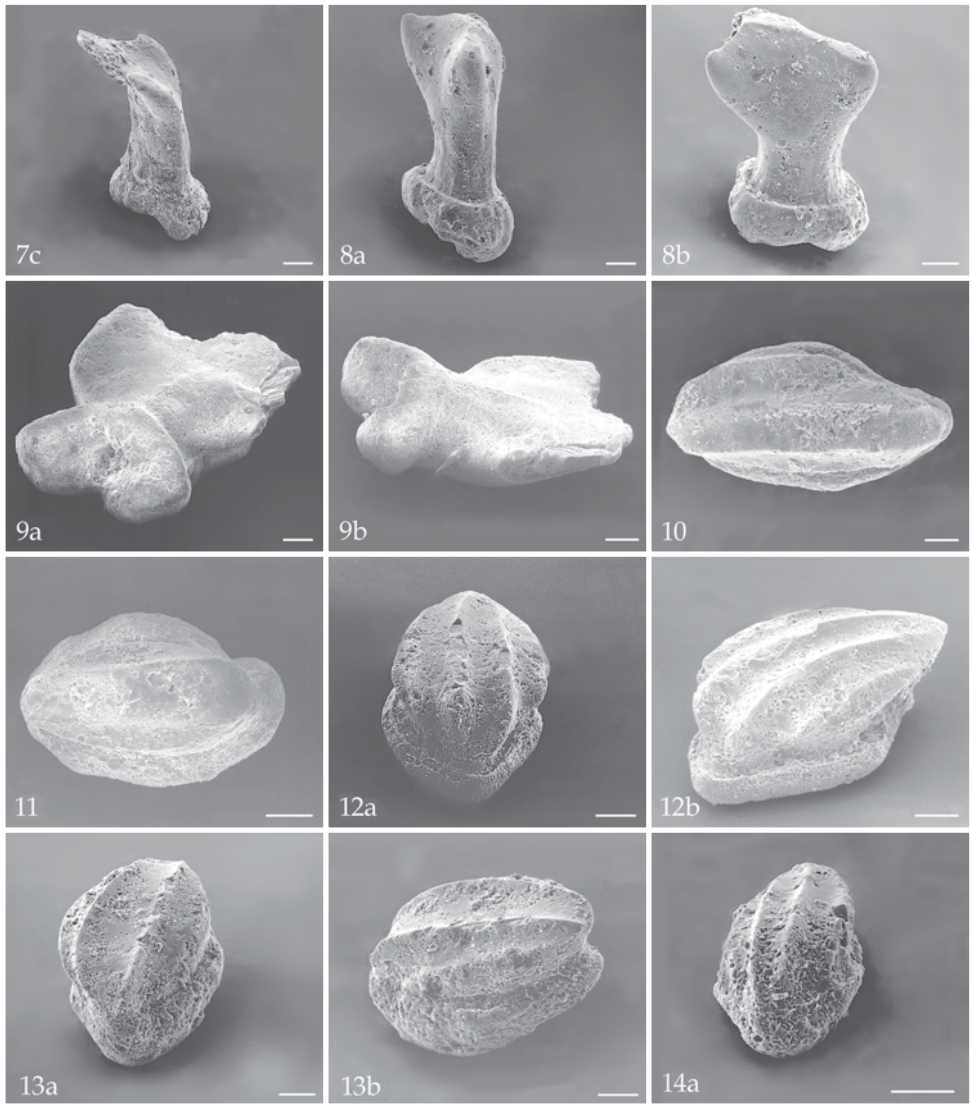

Plate 2

Figs. 7c-14a. *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986
7c-9: Pugniform scales (= *T. pugniformis* Gross, 1967); 7c: P8915; lateral view; 8: P8916; a: lateral view; b: posterior view; 9: P8917; a: ventral view; b: lateral view.
10-14: Bicostatiform scales (= *T. bicostatus* Hoppe, 1931, sensu Gross, 1967); 10: P8918, crown view; 11: P8919, crown view; 12: P8920; a: anterior view; b: anterolateral view; 13: P8921; a: anterior view; b: lateral view; 14a: P8922, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

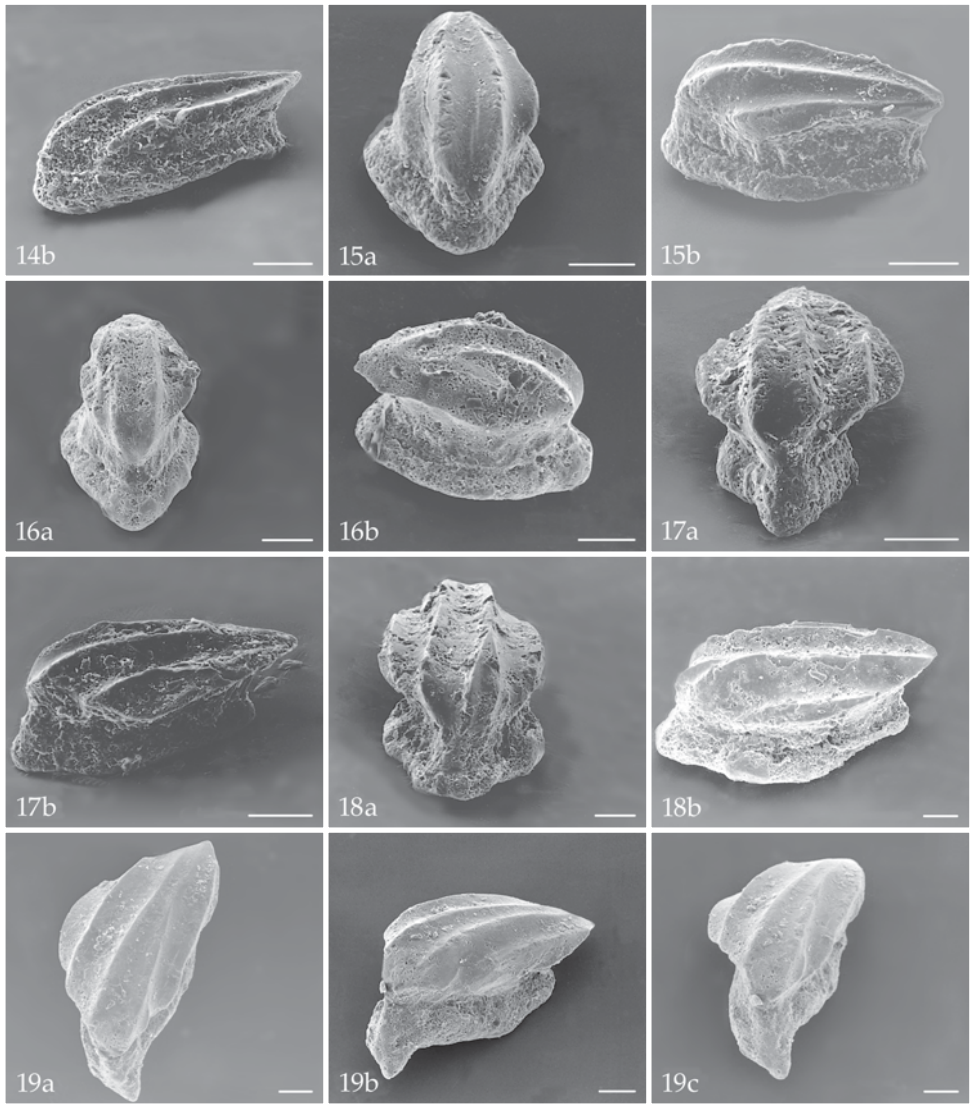

Plate 3

Figs. 14b-19. *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986
14b-19: Bicostatiform scales (= *T. bicostatus* Hoppe, 1931, sensu Gross, 1967); 14b: P8922, lateral view; 15: P8923; a: anterior view; b: lateral view; 16: P8924; a: anterior view; b: lateral view (posterior to the left); 17: P8925; a: anterior view; b: lateral view; 18: P8926; a: anterior view; b: lateral view; 19: P8927; a: crown view; b: lateral view; c: anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

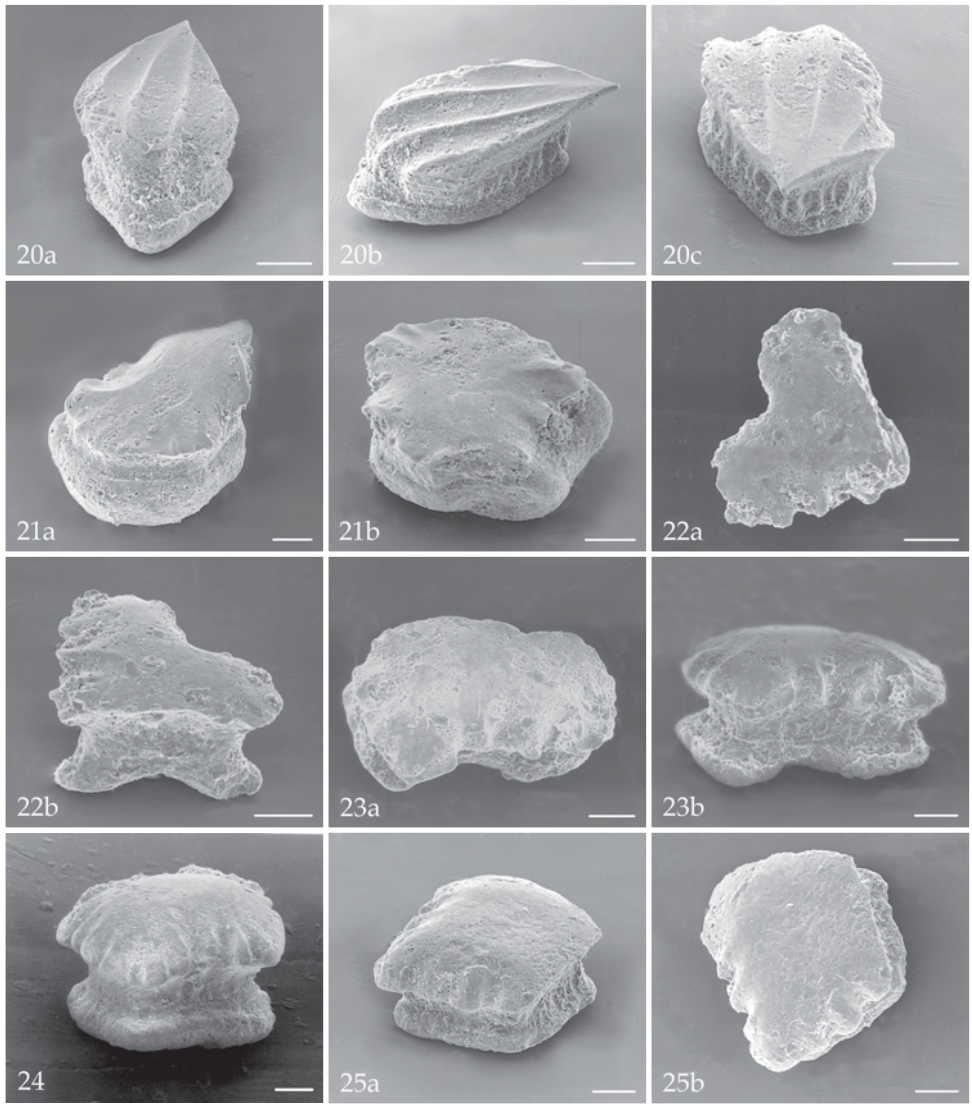

Plate 4

Figs. 20-27. *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986
20: Bicostatiform scale (= *T. bicostatus* Hoppe, 1931, sensu Gross, 1967); P8928; a: anterior view; b: lateral view; c: posterior view.
21-25: Cephalopectoral scales; 21: P8929; a: anterior view; b: posterior view; 22: posterolaterally incised, glabrous, heart-shaped scale, P8930; a: crown view; b: posterior view; 23, 25: anterolaterally incised, glabrous scale; 23: P8931; a: crown view; b: lateral view; 25: P8933; a: lateral view; b: crown view; 24: incised, glabrous scale, P8932, lateral view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

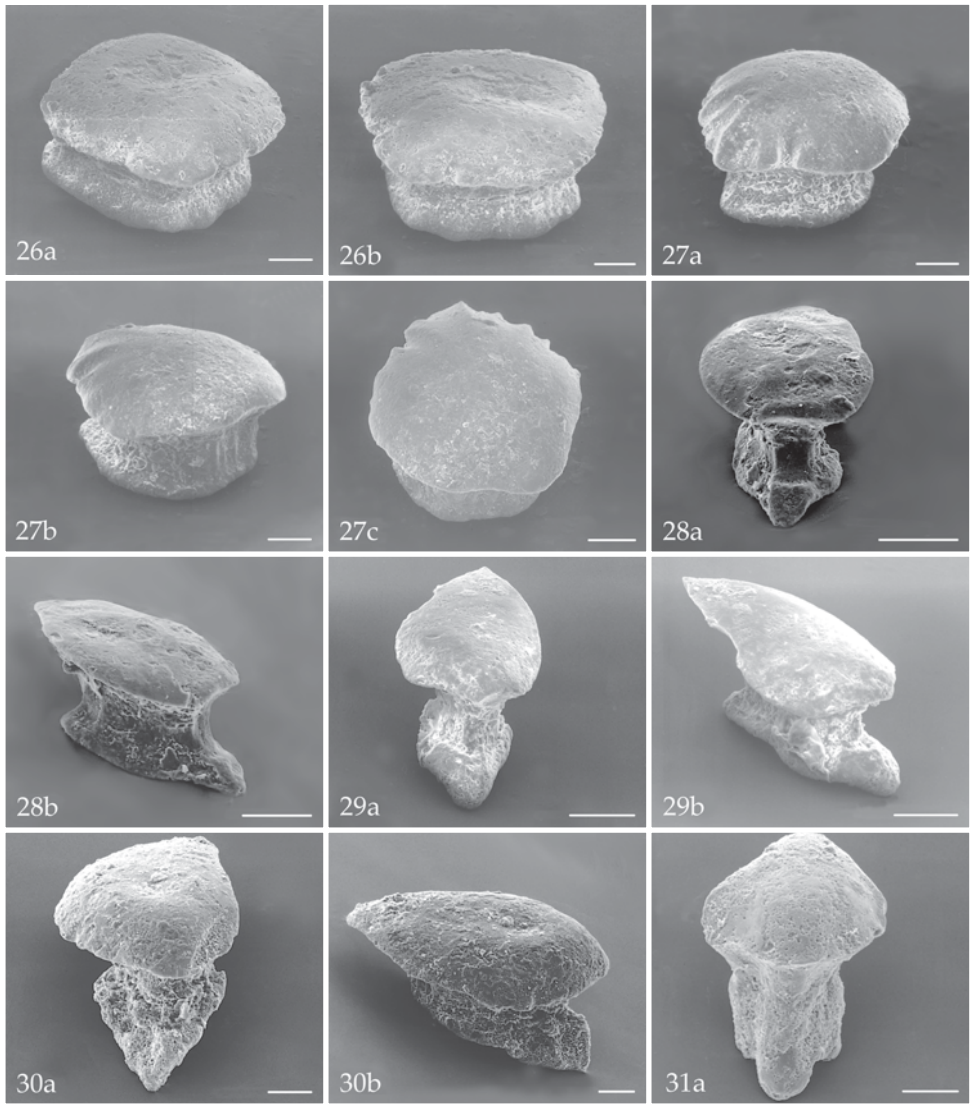

Plate 5

Figs. 26-31a. *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986, or sensu Gross, 1967?
26: Midanteriorly incised, glabrous, scale, P8934; a: anterior view; b: more lateral view; 27: midanteriorly and anterolaterally (on one side) incised, glabrous scale, P8935; a: anterolateral view; b: lateral view; c: crown view.
28-31a: Calcarate glabrous scales, variant 1; 28: P8936; a: anterior view; b: lateral view; 29: P8937; a: anterior view; b: lateral view; 30: P8938; a: anterior view; b: lateral view; 31a: P8939, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

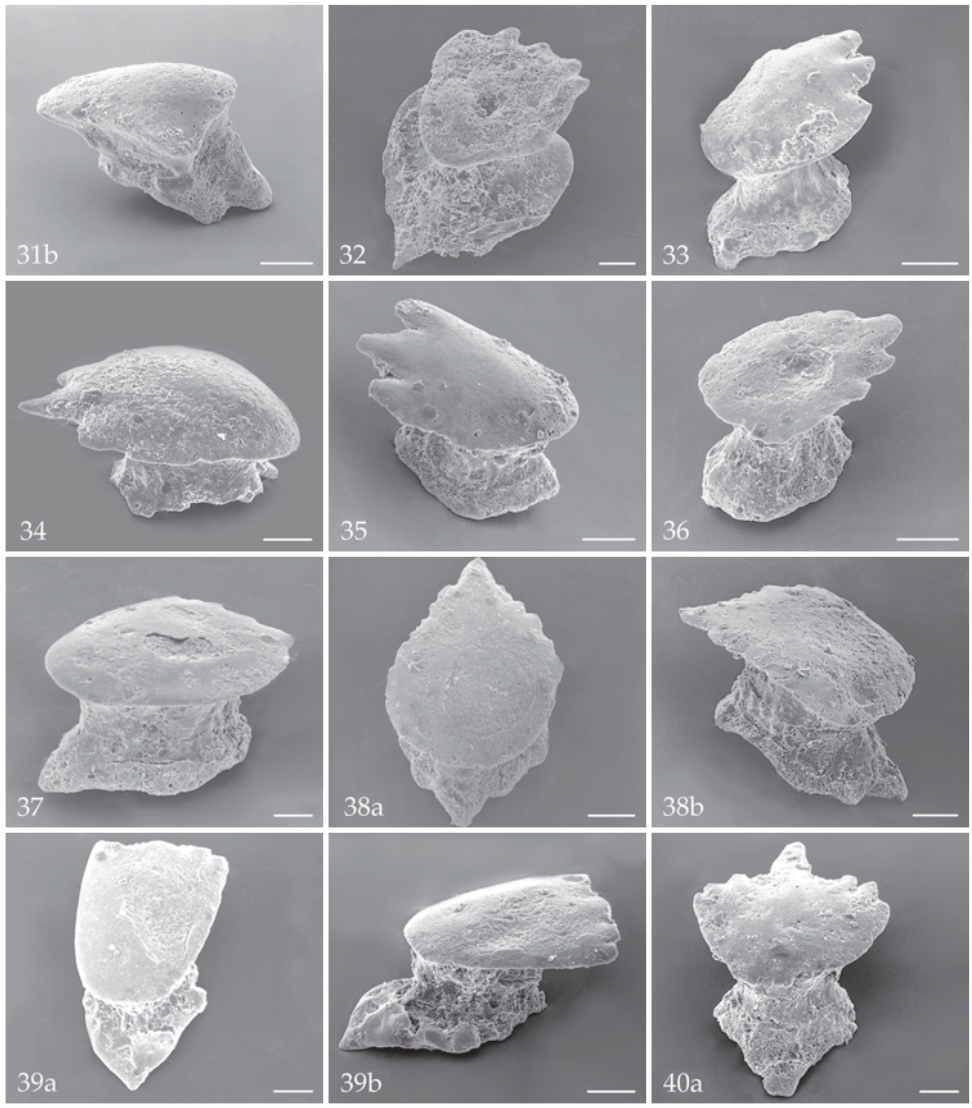

Plate 6

Figs. 32-40a: *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986, or sensu Gross, 1967?
31b: Calcarate glabrous scales, variant 1; P8939, lateral view.
32: Rhizoid glabrous scale, variant 1; P8940, ventral view.
33-36: Multicuspid glabrous scales, variant 2; 33: P8941, anterolateral view; 34: P8942, lateral view; 35: P8943, lateral view; 36: P8944, dorsolateral view.
37-40a: Calcarate, multicuspid glabrous scales, variant 3; 37: P8945, lateral view; 38: P8946; a: crown view; b: lateral view; 39: P8947; a: crown view; b: lateral view; 40a: P8948, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

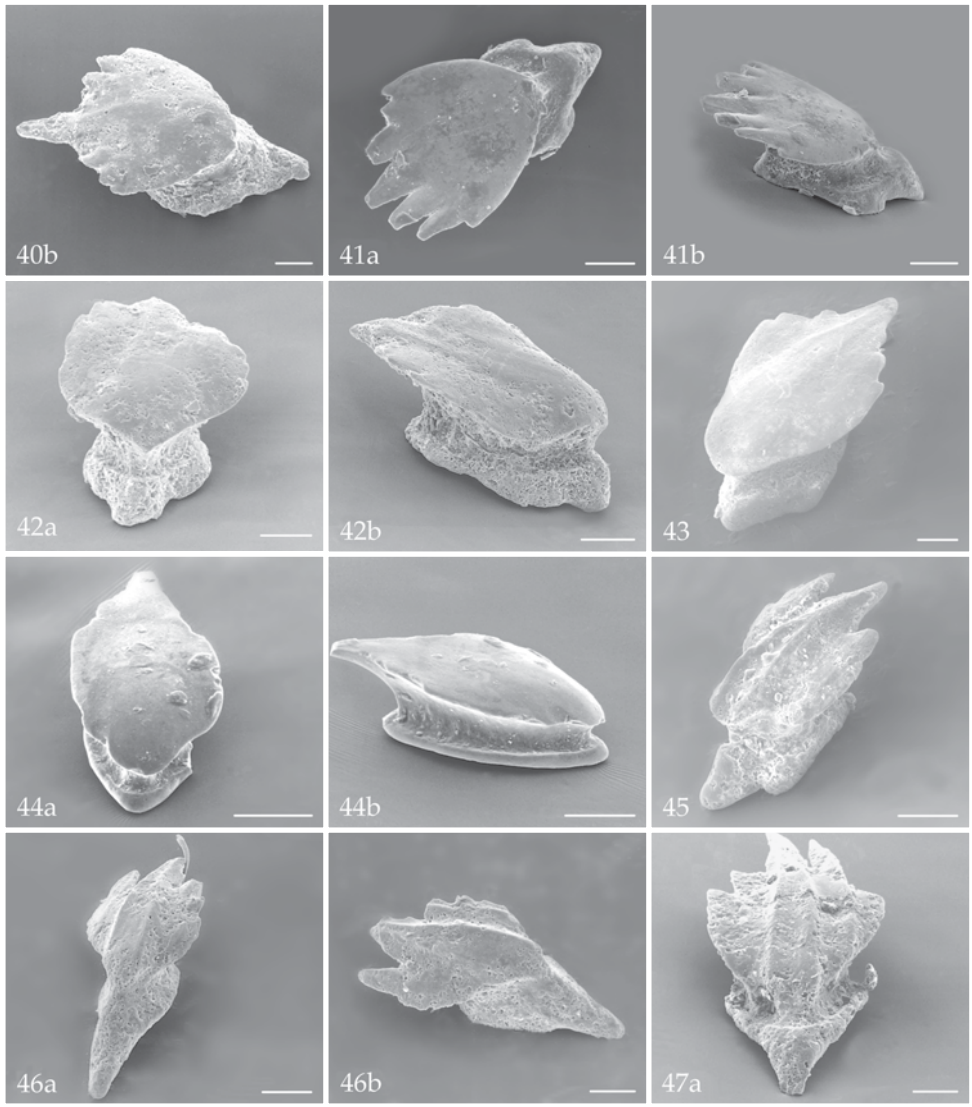

Plate 7

Figs. 40b-41b, 44: *Thelodus parvidens* sensu Märss, 1986 (or sensu Gross, 1967?)
40b-41: Calcarate, multicuspid, glabrous scale, variant 3; 40b: P8948, crown view; 41: sample Q 685, P8949; a: crown view; b: lateral view.
44: Glabrous scale, P8952; a: anterior view; b: lateral view.
42-43: Worn *Thelodus* crowns, seemingly glabrous; 42: P8950; a: anterior view; b: lateral view; 43: P8951, crown view.
45-47a: Trilobatiform scales (= *T. parvidens* sensu Märss, 1986, or *T. trilobatus* sensu Gross, 1967); 45: P8953, dorsolateral view; 46: P8954; a: anterior view; b: lateral view; 47a: P8955, anterior view.

All figured specimens are from sample Ramsåsa D, SW 2, unless otherwise stated. Size of bar is 0.1 mm.

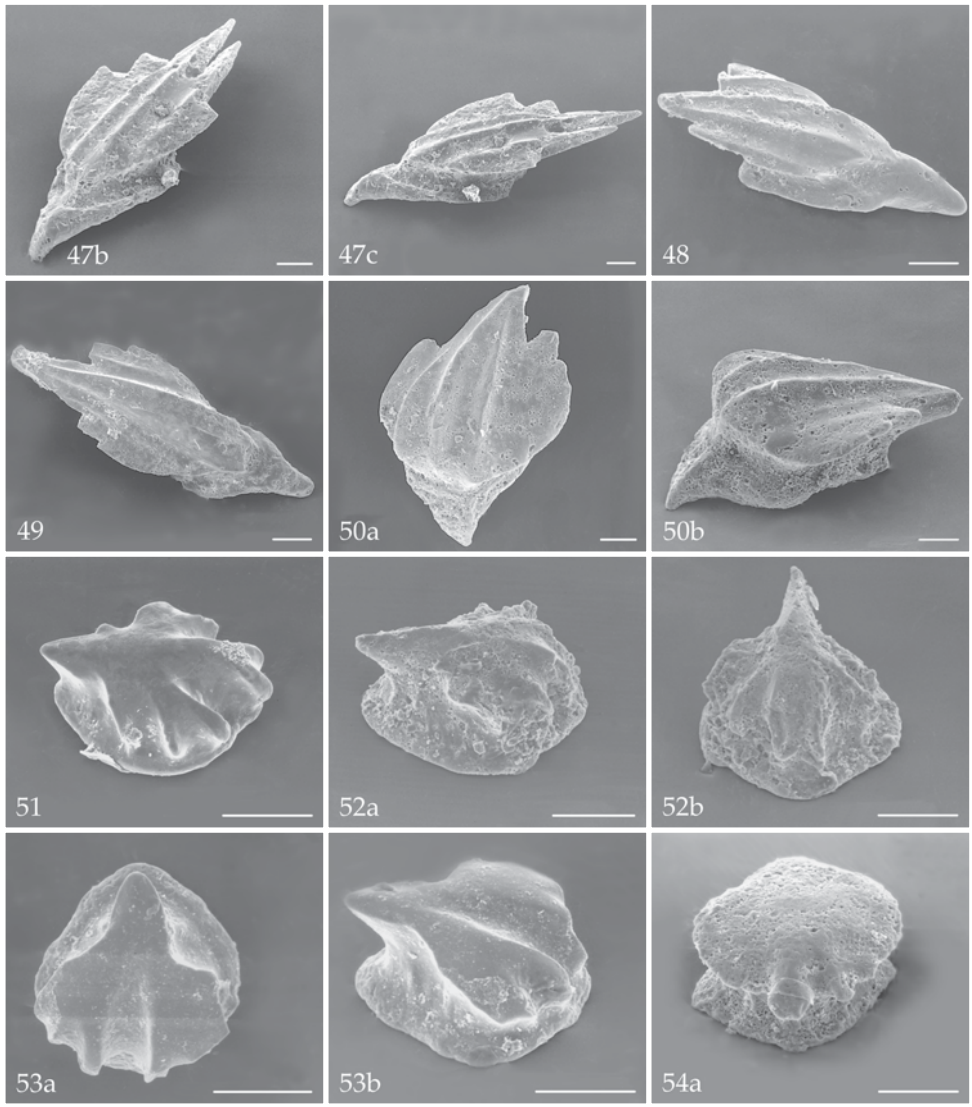

Plate 8

Figs. 47b-50: *Thelodus parvidens* Agassiz, in Murchison, 1839, sensu Märss, 1986
47b-50: Trilobatiform scales (= *T. parvidens* sensu Märss, 1986, or *T. trilobatus* sensu Gross, 1967); 47: P8955; b: anterolateral view; c: lateral view; 48: P8956, lateral view; 49: P8957, anterodorsal view; 50: P8958; a: anterodorsal view; b lateral view.

Figs. 51-54a. *Thelodus sculptilis* Gross, 1967; 51: P8959, crown view; 52: P8960; a: dorsolateral view; b anterior view; 53: P8961; a crown view; b: dorsolateral view; 54a: P8962, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

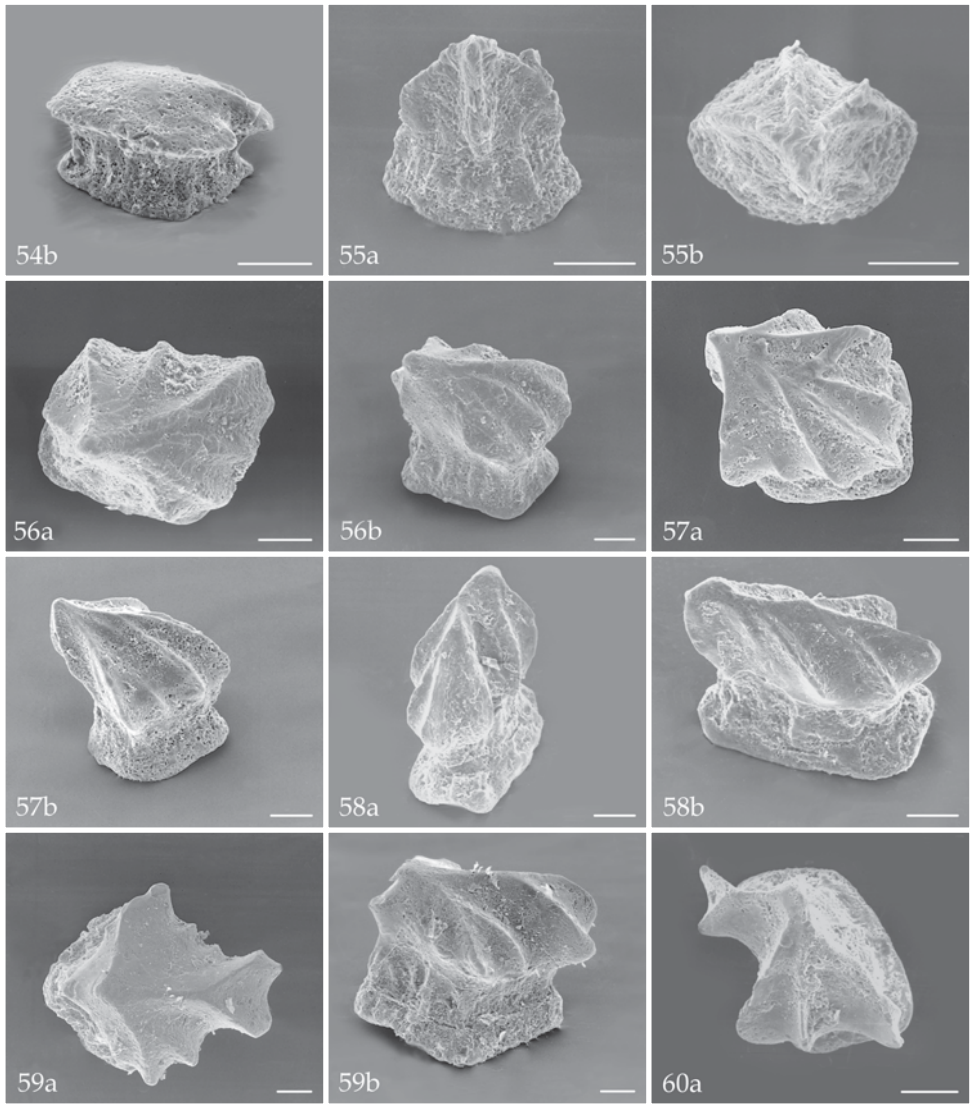

Plate 9

Fig. 54b. *Thelodus sculptilis* Gross, 1967; P8962, lateral view.

Figs. 55-58. *Thelodus traquairi* Gross, 1967, oral? scales; 55: P8963; a: posterior view; b: crown view; 56: P8964; a: crown view; b: lateral view; 57: P8965; a: crown view; b: lateral view; 58: P8966; a: anterior view; b: lateral view.

Figs. 59-60a. *Thelodus* cf. *traquairi* Gross, 1967; 59: P8967; a: crown view; b: lateral view; 60a: P8968, posterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

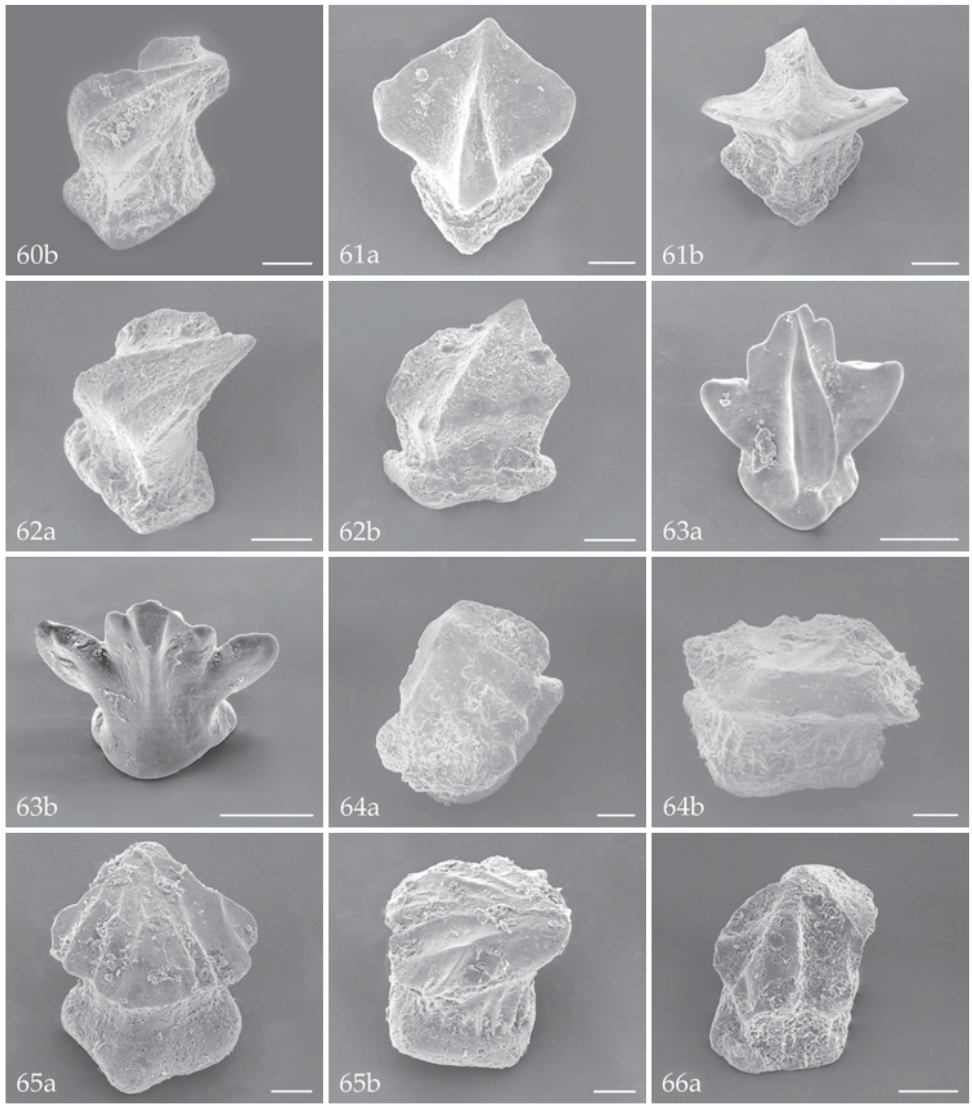

Plate 10

Figs. 60b-63. *Thelodus* cf. *traquairi* Gross, 1967; 60b: P8968, lateral view; 61: P8969; a: anterior view; b: posterior view; 62: P8970; a: lateral view; b: anterior view.
63: Pugniform scale, P8971; a: anterior view; b: posterior view.

Figs. 64-66a. *Thelodus carinatus* (Pander, 1856); 64: P8972; a: crown view; b: posterior view; 65: P8973; a: anterior view; b: lateroposterior view; 66a: P8974, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

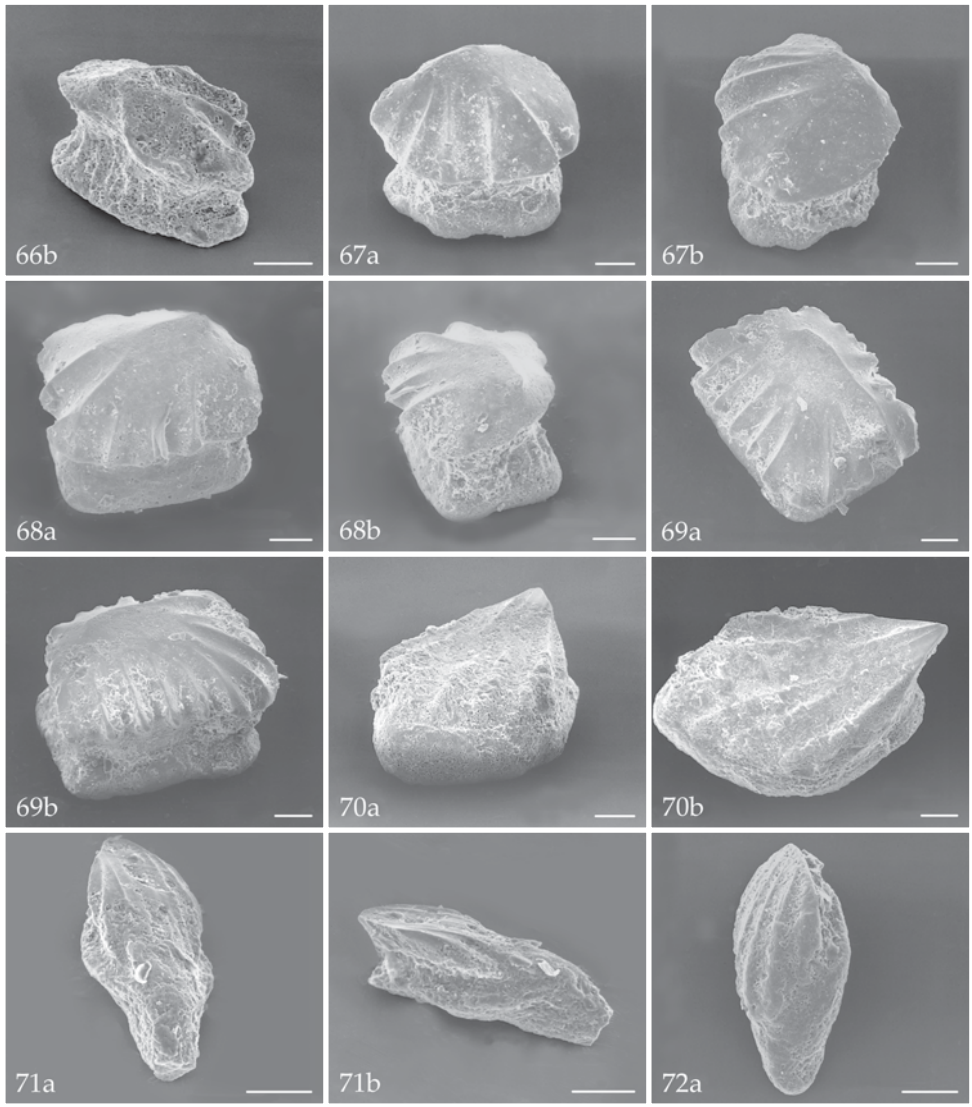

Plate 11

Figs. 66b-72a. *Thelodus carinatus* (Pander, 1856); 66b: P8974, posterolateral view; 67: P8975; a: anterior view; b: lateral view; 68: P8976; a: anterolateral view; b: posterolateral view; 69: P8977; a: crown view; b lateral view; 70: P8978; a: lateroanterior view; b: dorsolateral view; 71: P8979; a: anterior view; b: lateral view; 72a: P8980, lateroanterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

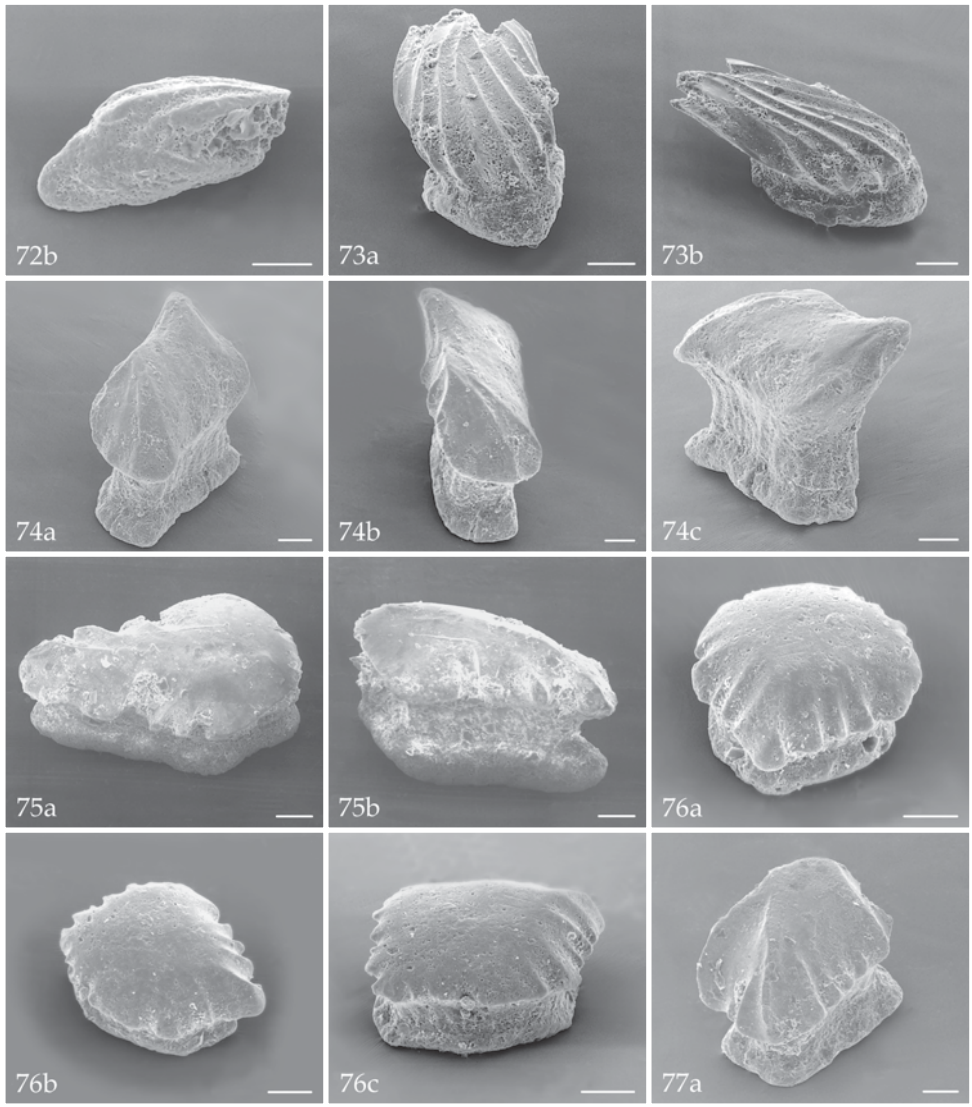

Plate 12

Fig. 72b-73. *Thelodus carinatus* (Pander, 1856); 72b: P8980, lateral view; 73: P8981; a: anterior view; b: lateral view.

Figs. 74-77a. *Thelodus* sp. indet.; 74: P8982; a: anterolateral view; b: anterior view; c: posterolateral view; 75: P8983; a: crown view; b: lateral view; 76: P8984; a: crown view from anterior; b: crown view from lateral; c: posterolateral view; 77a: P8985, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

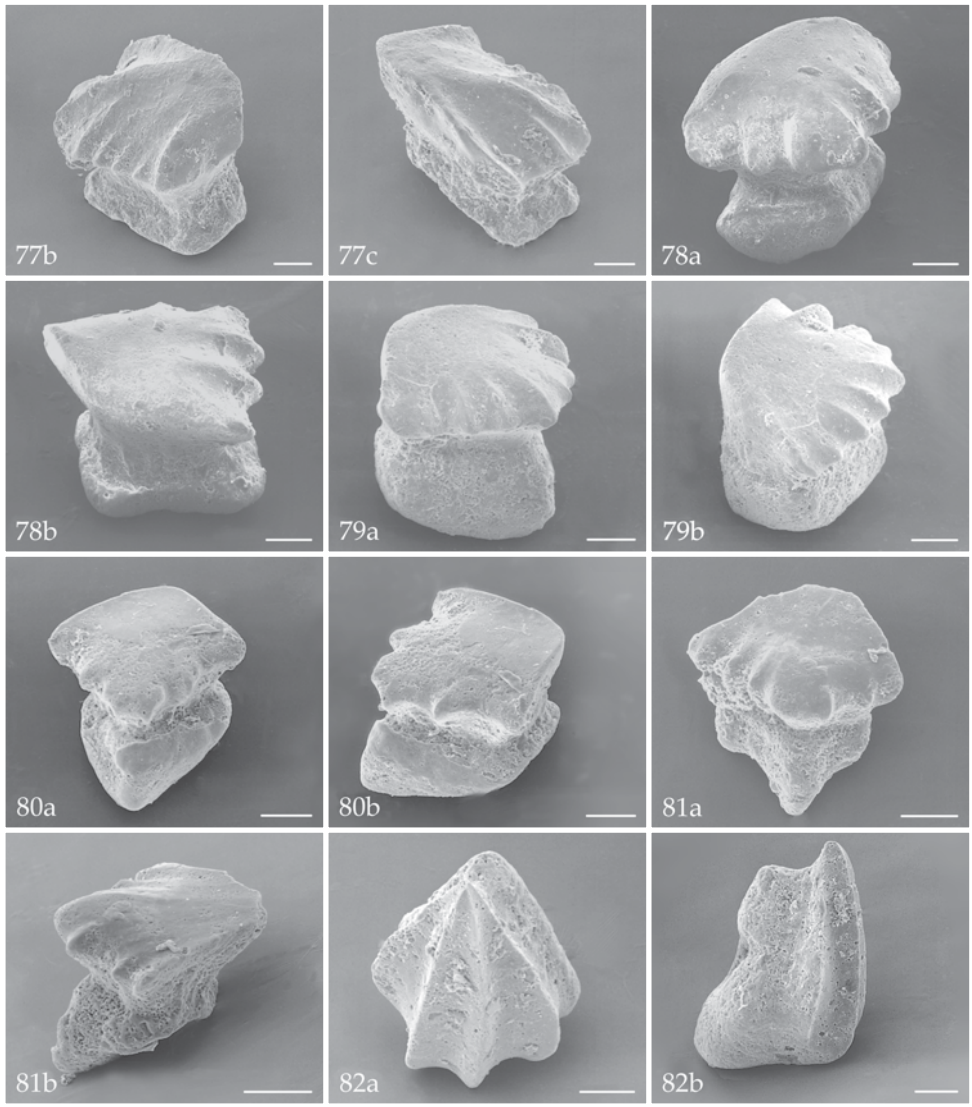

Plate 13

Figs. 77c-82b. *Thelodus* sp. indet.; 77: P8985; b: lateral view; c: lateral view, other side; 78: P8986; a: anterior view; b: posterior view; 79: P8987; a: anterolateral view; b: crown view from lateral; 80: P8988; a: anterior view; b: lateral view; 81: P8989; a: anterior view; b: lateral view; 82: P8990; a: crown view; b: lateral view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

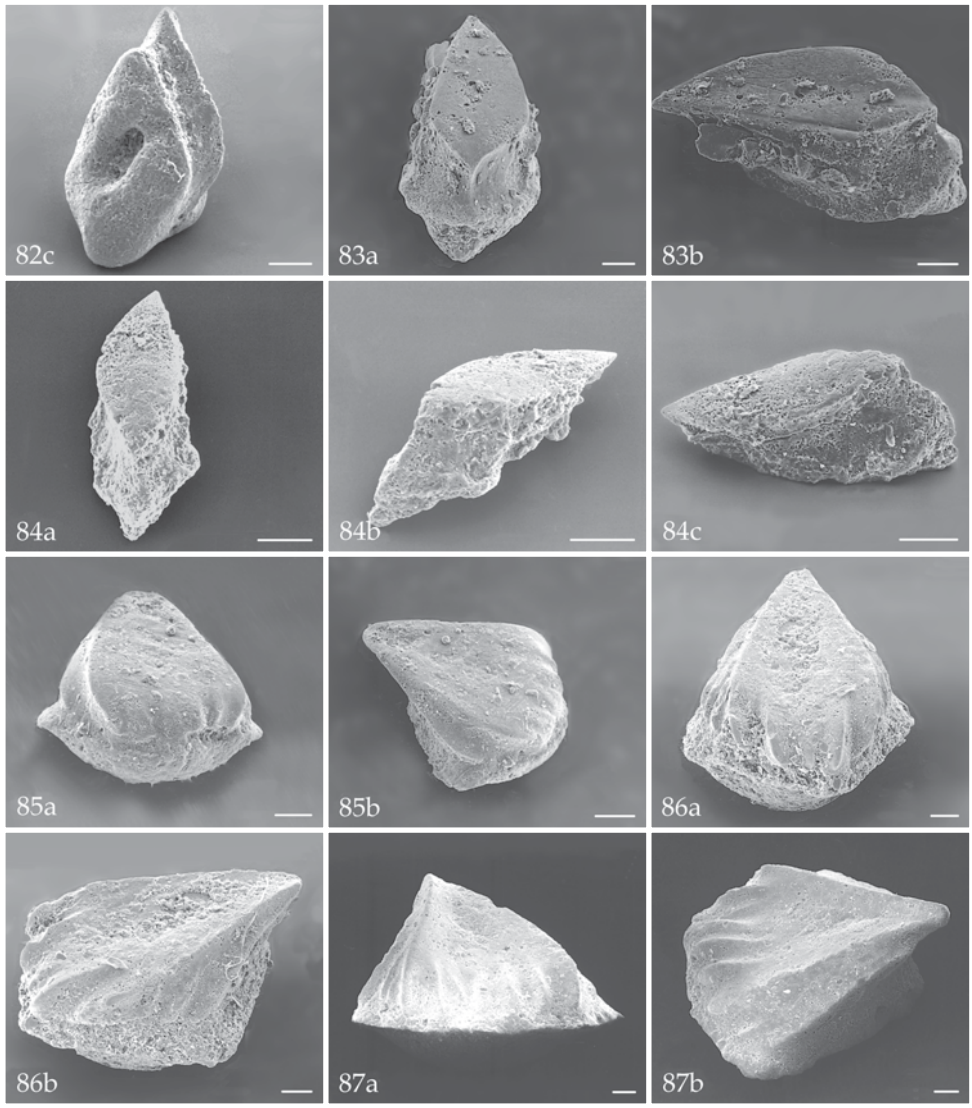

Plate 14

Fig. 82c. *Thelodus* sp. indet.; 82c: P8990, basal view.

Fig. 83. *Paralogania ludlowiensis* (Gross, 1967), P8991; a: anterior view; b: lateral view.

Fig. 84. *Loganellia* sp., scale, P8992; a: anterior view; b: lateral view; c: lateral view, other side.

Figs. 85-87. *Nostolepis striata* Pander, 1856, sensu Gross, 1947, 1971; trunk scales; 85: P8993; a: anterior view; b lateral view; 86: P8994; a: anterior view; b: lateral view; 87: sample Q 685, P8995; a: anterior view; b: lateral view.

All figured specimens are from sample Ramsåsa D, SW 24, unless otherwise stated. Size of bar is 0.1 mm.

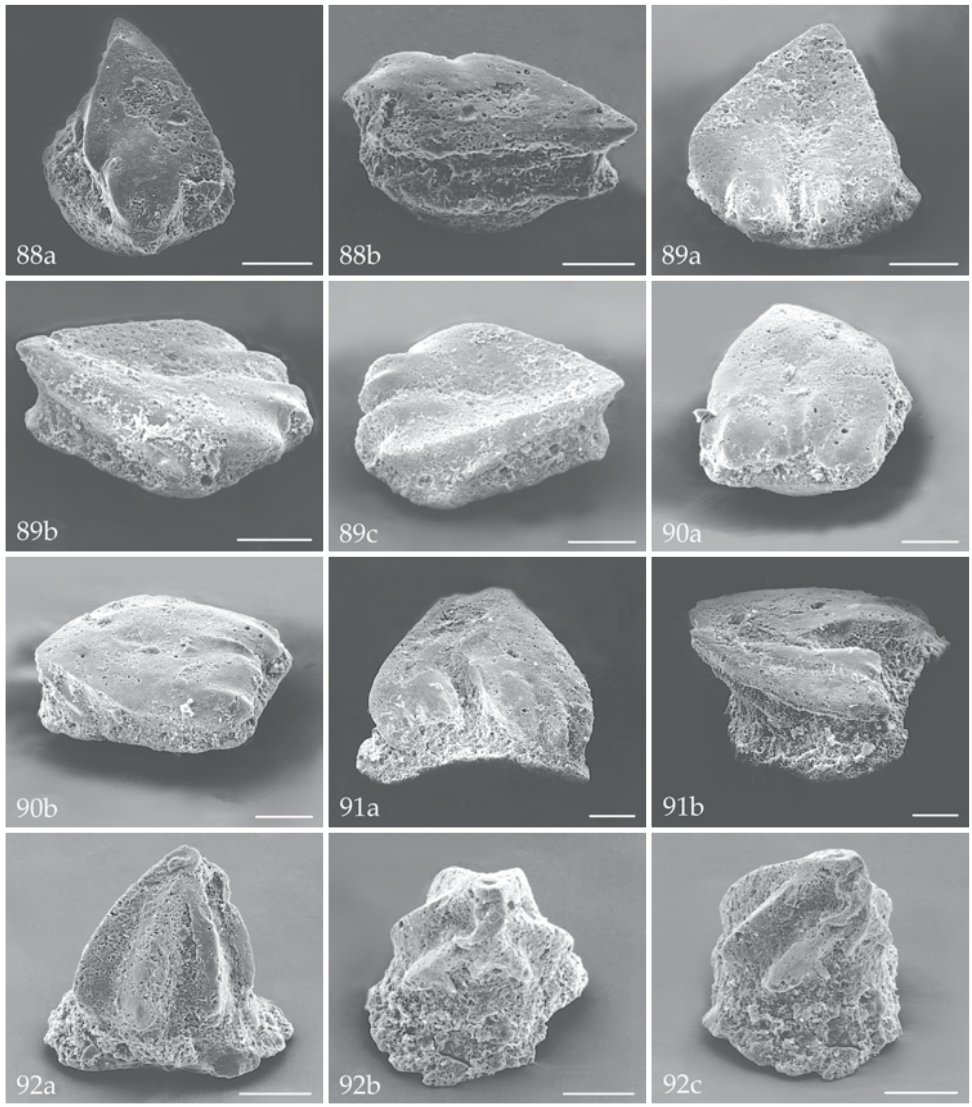

Plate 15

Fig. 88-92. *Nostolepis striata* Pander, 1856, sensu Gross, 1947, 1971
88-89: Trunk scales; 88: P8996; a: anterior view; b: lateral view; P8997; a: anterior view; b: lateral view; c: lateral view, other side.
90: Scale transitional to coronate tessera? P8998; a: anterior view; b: lateral view.
91-92: Coronate scales? 91: P8999; a: anterior view; b: lateral view; 92: P9000; a: anterior view; b: posterior view; c: more lateral and ventral posterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

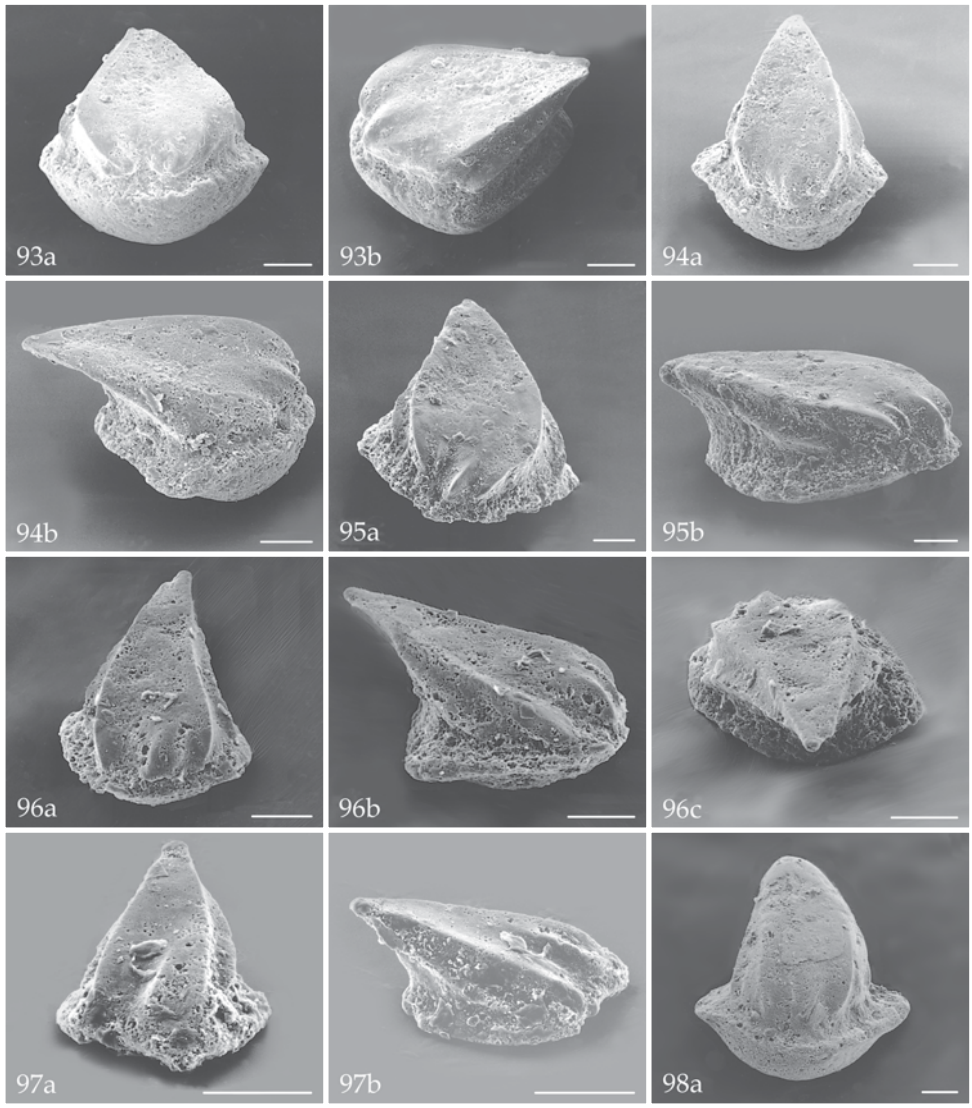

Plate 16

Figs. 94-98a. *Nostolepis striata* Pander, 1856, *elegans* form group Vergoossen, 1999
93-98a: Trunk scales; 93: P9001; a: anterior view; b: lateral view; 94: P9002; a: anterior view; b: lateral view; 95: P9003; a: anterior view; b: lateral view; 96: P9004; a: anterior view; b: lateral view; c: posterior view; 97: P9005; a: anterior view; b: lateral view; 98a: P9006, anterior view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

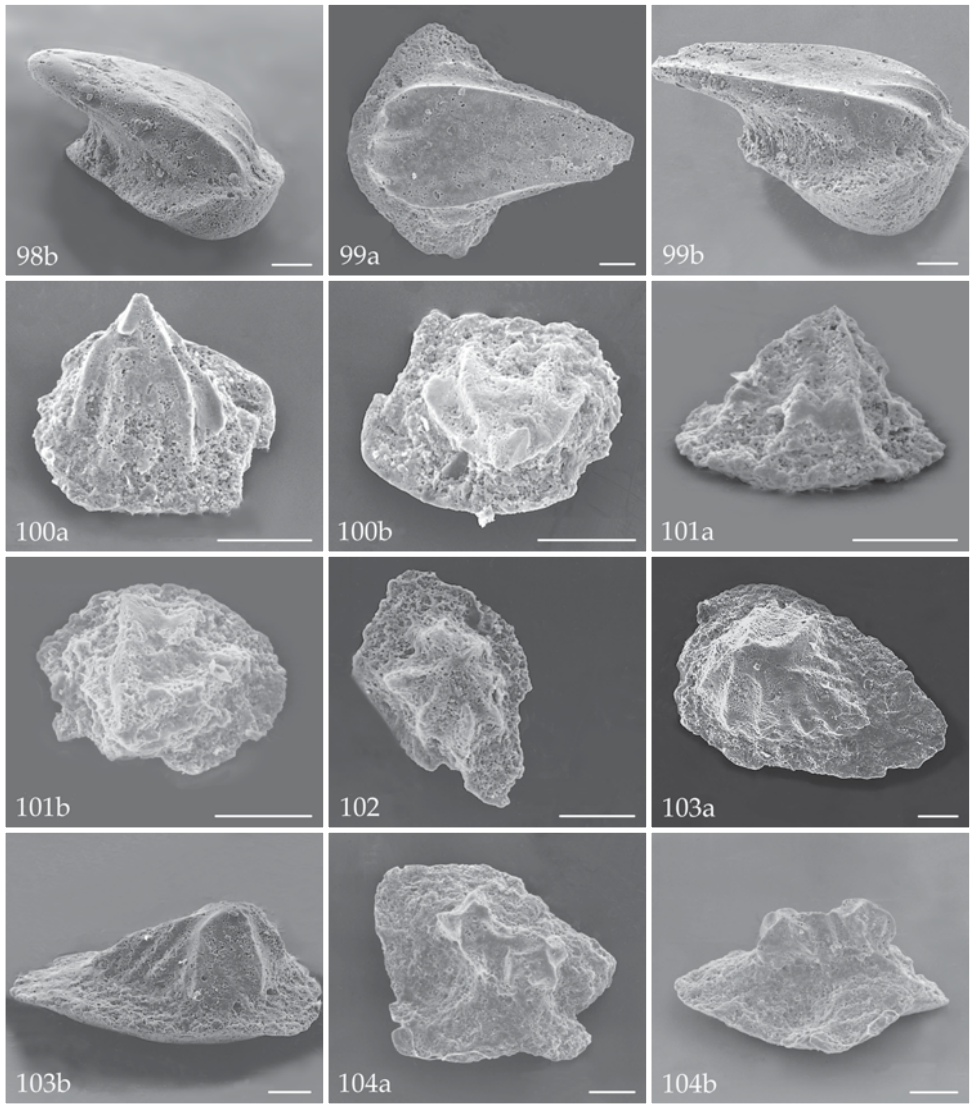

Plate 17

Figs. 98b-100. *Nostolepis striata* Pander, 1856, *elegans* form group Vergoossen, 1999
98-99: Trunk scales; 98b: P9006, lateral view; 99: P9007; a: crown view; b: lateral view.
100: Platelet, P9008; a: anterior view; b: crown view.

Figs. 101-104. *Nostolepis* sp.
101-103: Monotubercular platelets; 101: sample Q 685, P9009; a: anterior view; b: crown view; 102: P9010, crown view; 103: P9011; a: crown view; b: lateral view;
104: Multitubercular platelet, sample Q 685, P9012; a: crown view; b: lateral view.

All figured specimens are from sample Ramsåsa D, SW 24, unless otherwise stated. Size of bar is 0.1 mm.

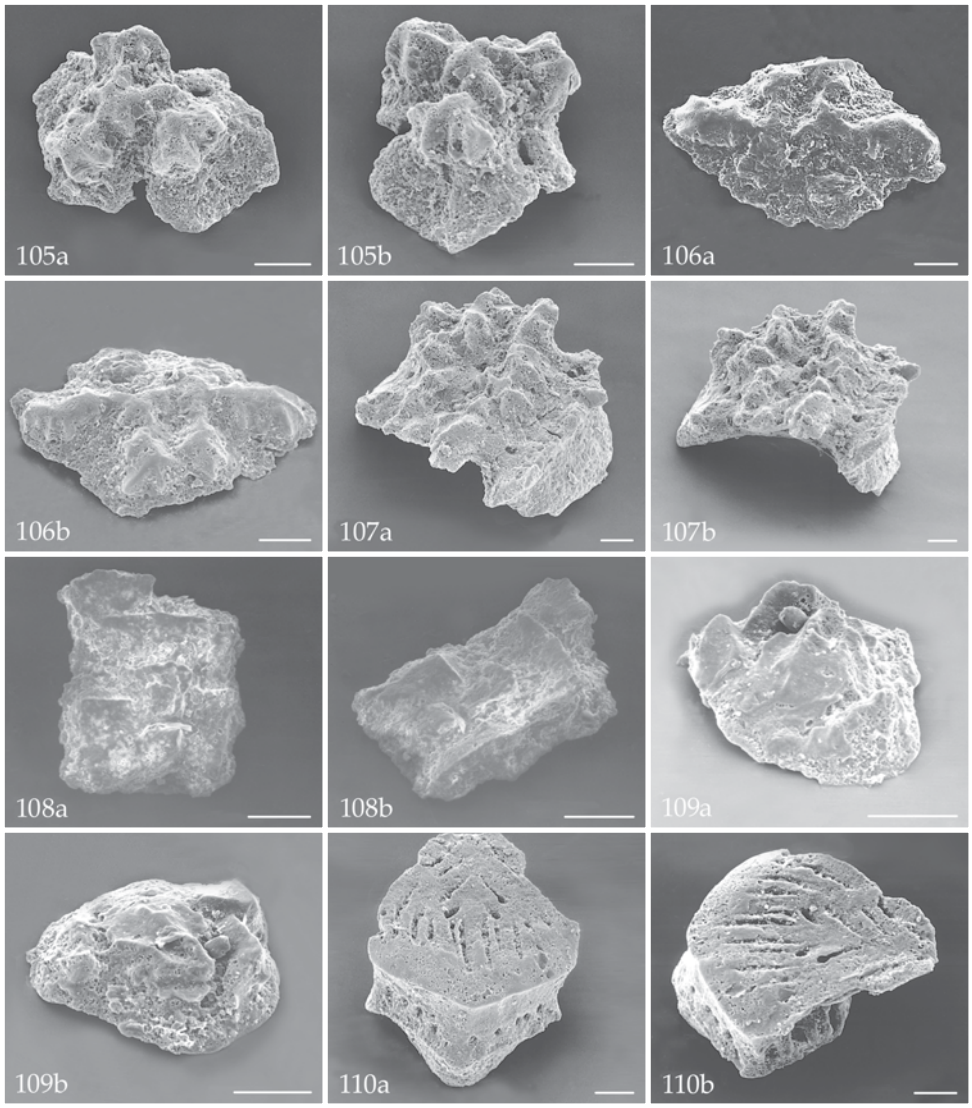

Plate 18

Fig. 105-107. *Nostolepis* sp.
105: Multitubercular platelet, P9013; a: crown view; b: lateral view.
106: Stellate plate, P9014; a: crown view, arrows indicate possible openings for vascular canals; b: more lateral view.
107: Squama pronia, P9015; a: crown view; b: lateral view.

Figs. 108-109. Acanthodii gen. et sp. indet., platelets; 108: sample Q 685, P9016; a: crown view; b: lateral view; 109: P9017; a: anterior view; b: posterior view.

Fig. 110. *Radioporacanthodes biblicus* (Lehman, 1937), P9018; a: anterior view; b: lateral view.

All figured specimens are from sample Ramsåsa D, SW 24, unless otherwise stated. Size of bar is 0.1 mm.

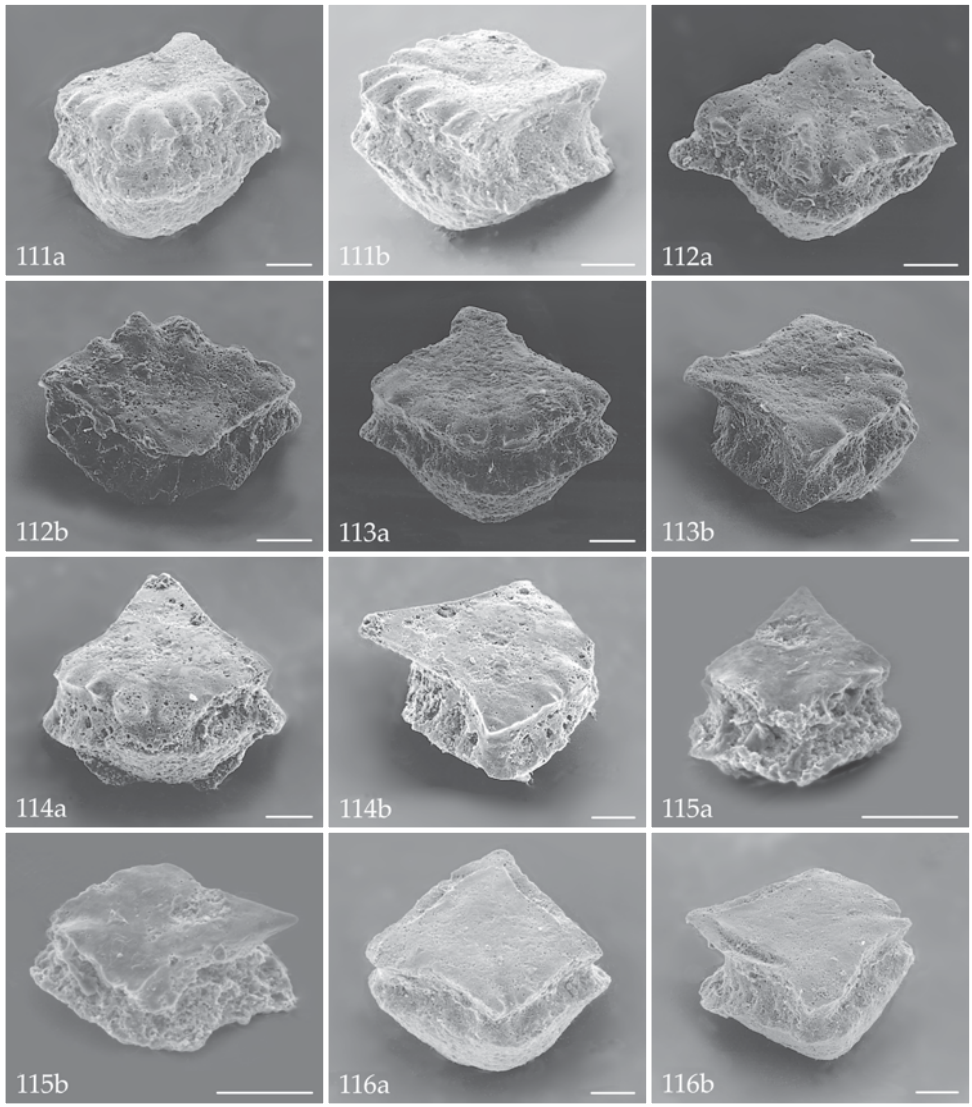

Plate 19

Figs. 111-115. Acanthodii gen. et sp. indet., morph 1, cf. *Gomphonchus volborthi* (Rohon, 1893); 111: P9019; a: anterior view; b: lateral view; 112: P9020; a: anterior view; b: posterior view; 113: P9021; a: anterior view; b: lateral view; 114: P9022; a: anterior view; b: lateral view; 115: P9023; a: anterior view; b: lateral view.

Fig. 116. Acanthodii gen. et sp. indet., morph 2, ischnacanthiform scale, P9024; a: anterior view; b: lateral view.

All figured specimens are from sample Ramsåsa D, SW 24. Size of bar is 0.1 mm.

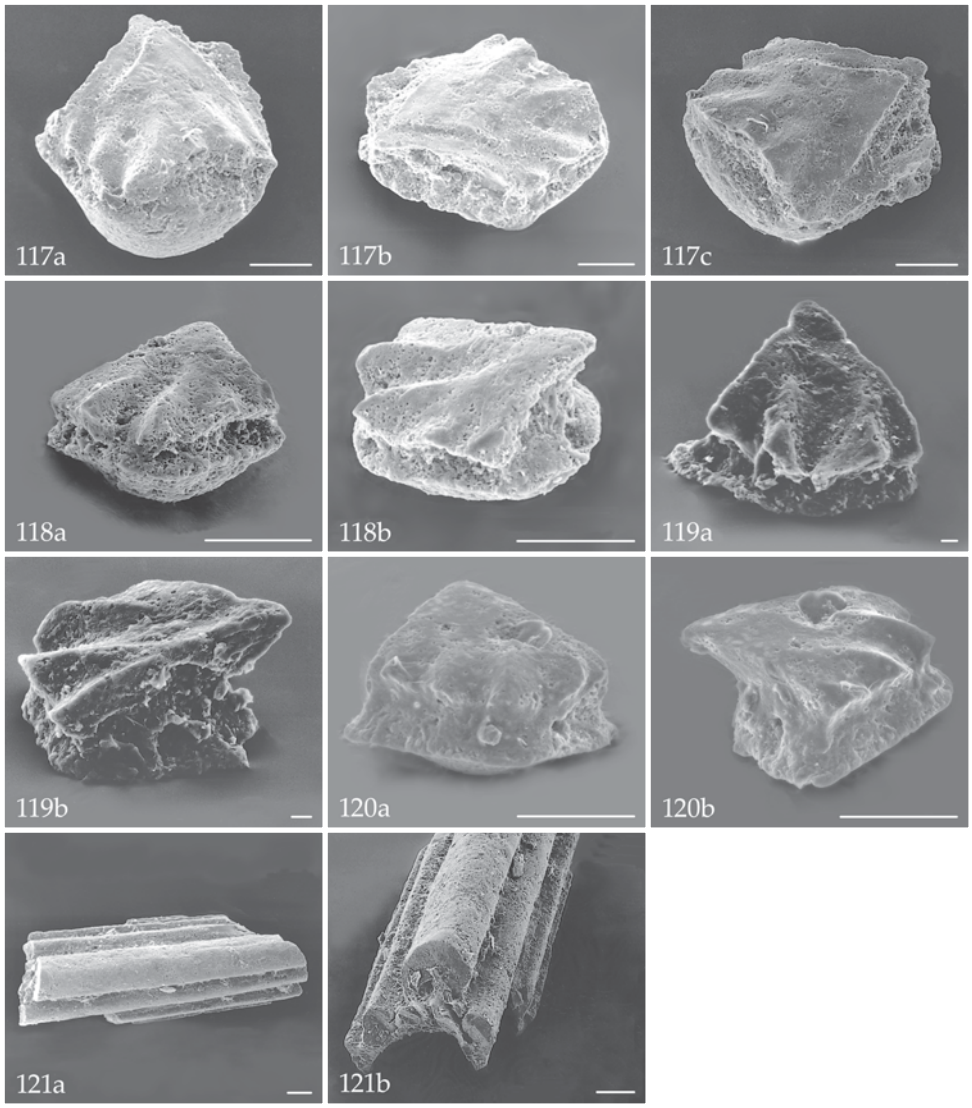

Plate 20

Fig. 117. Acanthodii gen. et sp. indet., morph 2, ischnacanthiform scale (Gross, 1947), sample Q 685, P9025; a: anterior view; b: crown view from lateroposterior; c: crown view.

Figs. 118-119. Acanthodii gen. et sp. indet., morph 3; 118: P9026; a: anterior view; b: lateral view; 119: P9027; a: anterior view; b: lateral view.

Fig. 120. Acanthodii gen. et sp. indet., morph 4, P9028; a: anterior view; b: lateral view.

Fig. 121. Ischnacanthid spine, P9029; a: view of leading edge; b: cross sectional view.

All figured specimens are from sample Ramsåsa D, SW 24, unless otherwise stated. Size of bar is 0.1 mm.