Late Silurian fish microfossils from Klinta and Rinnebäcks Bro (Scania, south Sweden), with remarks on the morphology of *Nostolepis striata* trunk scales

J.M.J. Vergoossen

Vergoossen, J.M.J. Late Silurian fish microfossils from Klinta and Rinnebäcks Bro (Scania, south Sweden), with remarks on the morphology of *Nostolepis striata* trunk scales. – Scripta Geol., 123: 71-92, 1 fig., 4 pls, Leiden, February 2002.
J.M.J. Vergoossen, Paleontologie, Biologisch Centrum Rijksuniversiteit Groningen, Kerklaan 30, NL 9751 NN Haren, The Netherlands (E-mail: J.M.J.Vergoossen@ biol.rug.nl).

Key words: Fish scales, Osteostraci, Heterostraci, Thelodonti, Acanthodii, nostolepid trunk scale variation, correlation, Whitcliffian, Sweden
The microvertebrate faunas from ten small pieces of rock from the Öved Sandstone Formation at Klinta (1-10) yielded osteostracan, heterostracan, thelodont, and acanthodian remains, dated here as Whitcliffian. The most important age indicators are the heterostracan *Archegonaspis* and the thelodont zonal fossil *Thelodus sculptilis*. The latter taxon is also present in a small Whitcliffian fauna from the Öved Sandstone Formation at Rinnebäcks bro, together with other thelodont and acanthodian remains. From Rinnebäcks bro no previous records of Silurian fish fossils exist. In an attempt to gain a better understanding of nostolepid trunk scale variation and to develop an instrument to assess this variation, seven *Nostolepis striata* trunk scales from Klinta are described and discussed on the basis of 42 morphological features. Some of these features enable detailed comparison between *N. striata* trunk scale variants and with scales of allied nostolepid taxa.
A contribution to IGCP 406: Circum-Arctic Palaeozoic Vertebrates.

Contents

Abbreviations and definitions

Abbreviations:

FAR forward projection of anteromedian crown riblets
KL 1-10 numbers of Klinta samples
NRS Palaeozoology Department of the Swedish Museum of Natural History, Stockholm
pcr posteriorly converging (anteromedian crown) riblets
pdr posteriorly diverging (anteromedian crown) riblets
RB Rinnebäcks bro

age marker: *Thelodus admirabilis* is not a zone fossil in the Microvertebrate Standard Zonation, but in the East Baltic standard sequence it virtually has the same range as the zone fossil *T. sculptilis*.

erratics: Upper Silurian East-Baltic-derived erratics

right: (left, top and bottom, in the description of figured scales): orientation in the figure.

trunk: in the section on *Nostolepis striata* and allied nostolepid acanthodian scales this term has been used because a more topospecific indication of the position of the scales on the body cannot be given. Evidence to prove that all the scales labelled as trunk scales actually derive from that part of the fish, is not available.

Previous research

Turner (1984) recorded a fish fauna of 68 scales (identifiable to species level) 'from the grey - red cornstone' by Lake Ringsjön, Klinta. This fauna comprised 'grey scales' of *Thelodus parvidens* (44 specimens, 91 % of fauna), *T. costatus* (3), *T. trilobatus* (1), *Nostolepis striata* (18), *Gomphonchus sandelensis* (2), and cephalaspid? bone fragments. Turner also reported finds of ostracodes and conodonts. There are no records of Silurian microvertebrates from Rinnebäcks bro.

Klinta

Geology (see Vergoossen, 2002a: text-fig. 1)

Jeppsson & Laufeld (1986) treated the lithology and conodont-based biostratigraphy of the area around Klinta. Practically all the outcrops at Klinta (Jeppsson & Laufeld, 1986: fig. 5, sites Klinta 1-7) fall within the Whitcliffian Bjär Member of the Klinta Formation (upper Leintwardinian to upper Whitcliffian), Öved-Ramsåsa Group. The Bjär Member comprises soft shales similar to the *Colonus* shale with intercalations of hard, grey, micaceous shale and subordinate detrital limestone. Only from their site Klinta 7 Jeppsson & Laufeld (1986: 37) reported till containing large quantities of calcareous, red-weathered Öved-Ramsåsa sandstone boulders from the Pridoli Öved Sandstone Formation, Öved-Ramsåsa Group. Jeppsson & Laufeld (1986) didn't mention fish remains from the Klinta area.

Material and registration

The microvertebrate faunas for the present study were obtained from 10 unregistered, small pieces of red, calcareous sandstone all labelled 'Klinta, E.A. Stensiö, 1924' and stored in the fish collection of the Palaeozoology Department of the Swedish Museum of Natural History, Stockholm (NRS). One identification label (KL 10) read 'bone fragment indet.' and on others (KL 5-6) was written '*Thelodus* scales'. Exact derivation and stratigraphical level of the samples are unknown. Their total weight was 234 g. The rocks were dissolved in 10% acetic acid and yielded brachiopod or bivalve fragments and ostracod moulds in addition to the fish remains. The smallest fractions (< 0.3 mm) were the most diverse, and yielded practically all the scales of the zonal fossil *Thelodus sculptilis.* Scales larger than 0.5 mm were absent. The figured specimens are kept in the NRS (numbers prefixed P).

Preservation

On the whole the preservation of the material from Klinta is poor when compared with that from Helvetesgraven (Vergoossen, 1999b). Thelodont scales are better preserved than acanthodian remains. In all samples from Klinta the crown and neck of the thelodont scales is a bright, shiny white and the base is dull orange brown. Sometimes the crown is wholly or partially wrapped up in a, dark greyish red, ferruginous crust. The pulp hole may be filled with the same ferruginous accretion. The base is softer, more susceptible to destruction than the neck and crown. This difference in fossilisation promotes the separation of the crown and neck from the base. Isolated crown-necks were regularly found but isolated bases occurred less frequently. The base may disintegrate when manipulated with a wet brush. The thelodont scales show no signs of transport such as rounding. This is best observed on *Thelodus parvidens* crowns, where the fractures are always sharp and angular. A particular type of preservation in isolated *T. parvidens* crowns is that of a ring-shaped or tubular wall in the place where the pulp hole was. Scales of taxa with delicate processes, such as the anterior basal spur (in trilobatiform *Thelodus* or *Loganellia* scales) or the sharp posterior points of multilobed crowns (as in forma *trilobatus*) are seldom found complete, but the basal spur may be better preserved than the multilobed crown, as finds of specimens with fragile, thin, curved basal spurs indicate. Complete multilobed crowns have not been collected. Bases with spurs have not been found isolated.

Twofold colouration and different preservation of crown/neck and base are rarer in acanthodian scales, and far less distinct. The acanthodian scales may have a uniform, dull, brown-red colour: the same colour as the rock matrix, which makes some scales hard to detect, even in the residue fractions. In the acanthodian scales there is also a tendency for the base and crown to become dissociated. *Nostolepis striata* crowns are readily identified, even from small fragments, and also by immersion in anise oil. Other acanthodian crowns are harder to identify, also because chemical (corrosion) rather than mechanical processes seem to have obscured or destroyed morphological and histological features: marked signs of transport have not been observed on the acanthodian scales either (cf. Vergoossen, 2002a, on the preservation

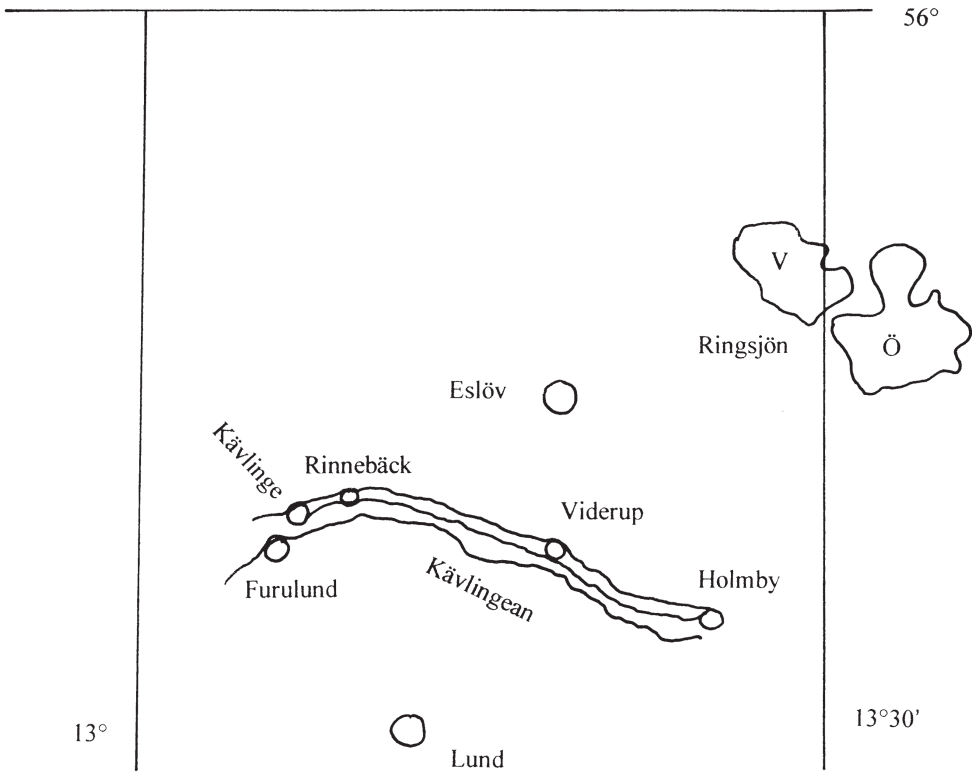

Fig. 1. Sketch map of the Rinnebäcks Bro area (adapted from a map from Bonniers Världatlas).

of acanthodian scales from Ramsåsa H). Thus the category 'Acanthodii scales gen. et sp. indet.' (Table 1) in particular refers to other taxa than *N. striata*.

Rinnebäcks bro

One small sample of fossiliferous, red, shaly limestone, weighing 20 g and labelled 'Rinnebäcks bro, Moberg, 1890' (bro = bridge) was present in the Silurian fish collections of the NRS, registration P702. Exact derivation and stratigraphic level of the rock are unknown. 'We have been unable to find a useful map incorporating Rinnebaecks Bro, it does not seem to be the best known of localities — Jan (Bergström) had not heard of it…… I will send a copy of an ordinary map showing approximately where the locality must be', Werdelin (NRS, pers. comm.).

Along Kävlinge river there runs a small stream named Rinnebäck (Fig. 1). The outcropping bedrock at Rinnebäck is Triassic (Kågeröd beds), which is underlain by Silurian (Ulf Shived, Swedish Geological Survey, pers. comm. 'Could Moberg have picked a lose slab at this place?'). Acid dissolution of rock as above. Apart from the fish remains, the residue yielded ostracod moulds, gastropods, tentaculites, fragments of brachiopods or bivalves, conodonts, echinoderms. No fish remains were found in

the fractions larger than 0.5 mm or smaller than 0.3 mm. The fauna is poorer than those from Klinta, but less rock was available for dissolution: about 8% of the rock total available from Klinta. The preservation of the scales is worse than that from Klinta and entire *Nostolepis* scales may disintegrate when touched with a wet brush. But generally the preservation is similar for shared taxa, with the exception of the thelodont basal spurs, which are incomplete in the few specimens found. The figured specimens are kept in the NRS (registration numbers prefixed P).

Systematic descriptions

Osteostraci
Pl. 1, fig. 1.

Two small and thin bone fragments were found in KL 5, the largest, P8878, measuring c. 0.45 × 0.28 mm (length × width). The fragments show the upper and middle layers. The external openings (pores?) are c. 0.02 × 0.03 mm in size and are arranged in longitudinally parallel rows separated by worn, low and narrow ridges. The rows are mainly one opening wide. The longitudinal ridges follow a slightly irregular rather than a straight course. The openings also show parallel arrangement widthwise, but no continuous widthwise ridges were formed. More or less similar remains were figured from the Öved Ramsåsa Sandstone from Helvetesgraven (Vergoossen, 1999b).

Heterostraci
Archegonaspis cf. *lindstroemi* Kiaer, 1932
Pl. 1, figs. 2-3.

Eleven heterostracan bone fragments were found in KL 4, and the largest (P8879) is figured here. Its size is about 1.5 × 0.7 × 0.3 mm (length × width × height). The surface consists of slightly convex, smooth, longitudinal and parallel ridges of more or less equal width (from 0.20 to 0.23 mm; suggesting a density of 4-5 ridges per mm). The ridges are separated by rows of micro surface openings of the vascular canal system that lead ventrally to wider, more or less oval, longitudinal canals (arrow in fig. 2). The rows are as a rule one opening wide. Large rectangular to quadrangular cavities under the ridges indicate the cancellous layer (fig. 2). The cavities are not as wide as the ridges. The thickness of the ridges is well visible in the illustrations. The fragments are reminiscent of the *Archegonaspis lindstroemi* scales from the Leintwardinian? of Gotland (Fredholm, 1988a).

Thelodonti
Thelodus parvidens Agassiz, in Murchison, 1839, sensu Märss, 1986
Pl. 1, figs. 4-12; Pl. 2, figs. 13-14.

Scales with smooth and unnotched crowns of variable shape dominate. Here the rhomboid crown (fig. 6, KL 5) is contrasted with the more rectangular crowns of slenderer scales (figs. 4-5, KL 5; fig. 8, Rinnebäcks bro). In relatively rare cases the basal

ring has a shallow groove (more grooves are more seldom) that crosses the basal ring and runs from the pulp opening to the base-neck interval. This could imply that a side canal branched off from the main vascular supply to the pulp, thus connecting the pulp to the space around the neck of the scale (where, supposedly, the sensory line canals ran in some thelodonts), or to the base of the neighbouring scale in the corium. This phenomenon has been noticed before (Gross, 1967: pl. 1: 1b, 19b) but received little attention. In Upper Silurian (Ludlow-Pridoli) scales of the Baltic area I have not yet observed it in specimens of e.g. *Katoporodus, Goniporus, Paralogania*, or *Loganellia*. Karatajute-Talimaa (1978) figured a '*Logania' cuneata* specimen from the 'Downton' of Lithuania (op. cit.: pl. 26: 2b) with two basal grooves, a scale of '*Logania*'*? kadvoiensi* (op. cit.: pl. 13: 6) and a scale of *Helenolepis obruchevi* (op. cit.: pl. 10: 12b), each with one basal groove, from S2 of Tuva (former USSR). From the Devonian (D1), Karatajute-Talimaa (1978) figured one specimen of *Nikolivia oervigi*, two specimens of *N. elongata* and one of *Turinia pagei* (op. cit.: pl. 47: 3b, pl. 44: 3b, pl. 43: 6b, pl. 34: 2b, respectively), all of the order of the Thelodontida sensu Karatajute-Talima, 1978, with a similar basal groove. Perhaps these off-branching canals were more common in (or/and have been more figured from) scales with *Thelodus* type of histology? The phenomenon would also seem to be restricted to particular variants, especially the smooth-crowned type, and I have not observed it, for example, in scales with an anterior basal spur such as specimens of forma *trilobatus*. Finally there would seem to be an ontogenetic restriction: in young scales with a wide open base and very narrow basal rim, or in old scales with a deep base and a closed or practically closed pulp opening, basal grooves connecting the pulp opening with the space around the neck have not been noticed. Further investigations are needed.

Forma *costatus* (= *Thelodus costatus* Pander, 1856) sensu Gross, 1967: No high-crowned *costatus* scales with converging crown ridges were collected, only nine, more flattened smooth crowns with rims of alternating notches and short ridges. In specimen P8882 (fig. 7, KL 6) the crown edges bend ventrad and the lateroposterior or anterior crown edge is notched.

Forma *bicostatus* (= *Thelodus bicostatus* Hoppe, 1931) sensu Gross, 1967 (fig. 9, KL 2): Six scales were collected.

Forma *trilobatus* (= *Thelodus trilobatus* Hoppe, 1931) sensu Gross, 1967 (figs. 10-11, KL 5; fig. 12, KL7; figs. 13-14, KL 2): In frequency these scales rank second among the collected thelodont scales: 30 vs more than 500 smooth-crowned *Thelodus parvidens* specimens picked from (and an estimated double that number present in) the entire material from Klinta and Rinnebäcks bro. In some scales (P8885, figs. 10-11) the crown ridges have been almost completely eroded away so as to suggest a smooth crown.

Thelodus sculptilis Gross, 1967
Pl. 2, figs. 15-19.

These scales are rare: 17 in total were collected. Still, they have been found in six out of nine faunas from Klinta (fig. 17, cephalopectoral scale; figs. 18-19: trunk scales), and in the sample from Rinnebäcks bro (figs. 15-16: oral scales). The preservation is poor. KL 5 yielded the largest number of scales: seven. The posterior neck may have vertical riblets of irregular height (fig. 18).

Thelodus traquairi Gross, 1967
Pl. 2, figs. 20-21.

The absence of these scales from the Klinta samples, which were specially searched for their presence, is unexpected, since they were regularly found in other Scanian samples (Helvetesgraven, Vergoossen, 1999b; Ramsåsa H, Vergoossen, 2002a). The illustrated scale could be assigned to *T. traquairi* on the basis of comparison with contemporaneous material from Ramsåsa H and Ringerike ('9 g'; Oslo Basin).

Loganellia cuneata (Gross, 1967)
Pl. 2, figs. 22-24; Pl. 3, fig. 25.

Only seven *Loganellia* scales were identified: six specimens of *L. cuneata* from Klinta and one specimen from Rinnebäcks bro (*Loganellia* sp. indet.). They are not all of the precaudal type shown in the illustrations. It has not been possible to back up the identifications by histological evidence.

Acanthodii
Nostolepis striata Pander, 1856
Pl. 3, figs. 26-36; Pl. 4, fig. 37.

On the diversity and identification of *Nostolepis striata* trunk scales

Only specimens from Klinta are figured because they are preserved best. After *Thelodus parvidens*, trunk scales of *Nostolepis striata* are the commonest fish fossils in the samples from Klinta and Rinnebäcks bro, with 180 specimens collected. The material is less diverse than the *N. striata* scales from Helvetesgraven (Vergoossen, 1999b) or Ramsåsa site H (Vergoossen, 2002a). None of the seven trunk scales here illustrated agrees in every detail with the dozens of forms that have been depicted from Scania and the Baltic region before. This makes the identification of *N. striata* and allied trunk scales arbitrary and confusing: a coherent, distinctive, diagnostic description for so much morphological variation is difficult to provide, and it is impractical to record the differences for each scale. Brotzen (1934) and Lehman (1937) worked out a taxonomy based on such type of detail, but their approach was rejected by Gross (1947). Gross (1947, and especially 1971) considerably widened the species concept, both morphologically and histologically, but at the same time managed to define a workable and satisfactory framework for *N. striata* that suited his aims and times. He (1947) illustrated a fair number of *N. striata* variants, mostly trunk scales, but thought that their form range was so wide that not all the variations could be shown. This was also unnecessary because *N. striata* was an easily recognisable species (Gross, 1971: 7). However, with loads of new material becoming available world-wide as a result of invigorated research during the last decades, it is precisely this wide form range of *N. striata* (including the trunk scales — never adequately illustrated), together with the world-wide occurrence and long time range of the species (Wenlock-Emsian) that has enabled researchers to give a personal and individualised interpretation of the species concept, no doubt inspired by histological findings and pressures to produce biostratigraphical results.

Currently, the trunk scales of *N. striata*, always the most numerous scale type in samples, can hardly be used for biostratigraphical purposes within the Silurian-Devonian, because with so much morphological variation, the species concept, or rather the restrictions of the concept, are no longer clear (the histological aspects are not discussed here). What we need most now are comprehensive and well-illustrated surveys of the variation ranges of *N. striata*, and allied taxa, preferably from one sample and stratigraphical level per survey, and including the smallest and largest fractions. As a matter of fact I have one large sample from an Upper Silurian East-Baltic-derived erratic ('*Poracanthodes punctatus* Zone', Vergoossen, 1999a) containing *Nostolepis striata* scales, and scale forms similar to scales of *N. alta* Märss, 1986 (uppermost Silurian), *N. minima* Valiukevicius, 1994, *N. arctica* Vieth, 1980, *N. applicata* Vieth, 1980, *Canadalepis linguiformis* Vieth, 1980 (Lower Devonian) besides several, undescribed others, which may all be interpreted as distinct variants within one taxon, some with gradual transitions between them (modified or specialised scales such as tesserae, squamae umbellatae and proniae, etc. are not discussed here). Not until this variability has been sorted out, can any of these taxa be redefined or used with a high degree of accuracy and reliability. The present practice (cf. Valiukevicius, 1998) focuses on the species definition and description of one distinctive trunk scale form group from one or more sites plus a few conspicuous variants, without considering 'minor' variations (1), transitions to other form groups/species (2) and shared intraspecific forms (3). This is a practical approach, but it is a simplification that does not do justice to the factual diversity and complexity of the *Nostolepis* material (cf. the situation for the poracanthodids that are currently being revised: Vergoossen, 1999a, 2002a).

Whether the scales from Klinta here treated are all *Nostolepis striata* scales sensu Gross cannot be decided at the moment. Scales agreeing with the specimens described and illustrated by Gross (1947, 1971), or variations thereof (cf. e.g. figs. 26, 31), are certainly present, but on the other hand such a typical specimen as in Gross (1947: pl. 26: 5; with rhomboid crown, short radial anterior crown riblets, crown only slightly inclined and not protruding over neck posteriorly, neck all around and a pair of lateral neck ribs converging into the posterior crown tip) is hard to find in any Scanian material examined by me so far and was, interestingly, not figured from Scania by Lehman (1937). Scales with denticulated lateral crown rims (e.g. Gross, 1947: pl. 26: 11-12) have not been collected from Klinta, nor from Rinnebäcks bro. This could be due in part to the poor preservation (but see below). Although Gross (1947) synonymised the genus *Diplacanthoides* with *Nostolepis* on histological grounds (including the taxa created by Lehman, 1937; mostly specifically indeterminate according to Denison, 1979, but see Valiukevicius, 1998), Scanian *Nostolepis striata* scales (cf. the ones in figs. 30, 32, 37) may differ remarkably morphologically from the specimens shown by Gross (1947, 1971; see also Vergoossen 1999b, 2002a). In addition it is difficult to distinguish separate form groups, also in the Scanian material: not only is each scale different from any other, but they are also linked by transitions. I agree with Gross (1971: 7) that it makes no sense trying to describe and figure all the morphological differences, but only in so far as this would mean having to refer each different scale to a separate taxon. Contrary to Gross, I think that understanding the morphological variation in the squamation of *N. striata*, may be the key to understanding the late Ludlovian to Lochkovian Laurussian (especially Baltic) nostolepids, or at least

those nostolepids whose squamation shows close affinity to *N. striata* (also histologically: the listed taxa are of similar nostolepid type, with the possible exception of *Canadalepis linguiformis*), such as the *elegans* scale group, *Nostolepis alta, N. applicata*, *N.* (aff.) *arctica, N. athleta* Valiukevicius, 1994, *N. laticristata* Valiukevicius, 1994, *N. minima, N. multicostata* Vieth, 1980, *N.* aff. *multicostata, C. linguiformis, Endemolepis inconstans* Valiukevicius, 1998. *N. linleyensis* from the lower Pridoli of Much Wenlock (GB; Miller & Märss, 1999) is not regarded here as a taxon closely allied to *N. striata.* The inclusion of the taxon in the genus *Nostolepis* is questionable, partly for the same reasons that Vergoossen (1999c: 64) advanced for '*Nostolepis*' *robusta*. A detailed treatment of this issue is outside the scope of this paper.

In order to establish which variables determine *Nostolepis striata* trunk scale variation and to weigh their significance, a concise description of the seven figured *N. striata* trunk scales (P8896-P9902) is given, in support of the similarities and differences visible in the SEM images. Features not visible in the scans are omitted. From the descriptions a check list of 42 features is deduced, enabling a more detailed comparison of the morphology of the scales of *N. striata* and allied taxa, and their variation ranges. Next it is attempted to make such a comparison for some of the listed features. The list can be further elaborated, also by consulting Twain & Zidek (1982), to include features of variants that have not been described here, such as: rhomboid shape of crown — elaboration of feature 3; radial orientation of anterior crown riblets — elaboration of feature 22; etc.

Descriptions of the figured *Nostolepis striata* trunk scales

The specimens were selected from the 106 *N. striata* trunk scales obtained from the samples KL 2 (62 scales) and KL 5 (44 scales) because they differed from the scales figured by Gross (1947, 1971, 1973) and for their distinct but relatively small morphological variability. The larger the samples, the larger the number of differences and the more extreme they may become.

Asymmetric scale P8896 (figs. 26-27): Triangular crown, slightly concave and with horizontal orientation. Curved (convex) rims. Anterior crown margin straight and parallel to the left anterior margin of the base. Four short, oblique and longitudinal, parallel, anterior riblets curve up from the basal platform. One lateral ledge (convex in outline), starting at level of right, lateral basal corner (fig. 26) and converging posteriorly into crown. Low lateroposterior neck. Crown fills up entire base and does not project over base. Rhomboid, low base. The two large openings in the lateral crown (fig. 27) between upper rim of crown and lateral ledge are probably artefacts.

Asymmetric scale P8897 (figs. 28-29): Triangular crown, slightly concave and slightly inclined. Curved (convex) rims. Anterior margin of crown parallel to left anterior margin of base (fig. 28). It has three forward projecting short, oblique and longitudinally parallel anterior riblets. Two pairs of straight lateral neck ribs, of which the first starts at the level of the lateral basal corners and ends halfway the length of the crown. The second pair starts immediately behind where the first ends and converges posteriorly into the crown. Crown fills up entire base and projects over base only with posterior tip. Rhomboid, low base.

Symmetric scale P8898 (fig. 30): Narrow, longitudinally elliptical crown, slightly concave and inclined. Curved rims (less convex), bending inward anteriorly. Anterior

margin of crown starts close to median anterior corner of base. One pair of curved (slightly convex) lateral neck ledges, starting at level of lateral basal corners and converging posteriorly into crown plate. Crown does not fill up entire base: there is a free, smooth, sloping, lateroposterior, upper basal zone. Rhomboid, low base.
Remark: Scales with a narrow and elongate crown (cf. also P8902, figs. 36-37) were collected less frequently. The present, poorly preserved specimen is the only one that resembles scales of the '*elegans*' form group (Vergoossen, 1999b), but the base is convex in stead of flat.

Asymmetric scale P8899 (fig. 31): Triangular crown, slightly concave and inclined. Curved (convex) rims bending inward anteriorly. The right rim bends inward more than the left. Anterior crown margin straight. There is a smooth zone between the anterior crown and the rounded anterior margin of the base. Three short anterior riblets, of which two are longitudinally parallel, and the third is more or less parallel to the inward bending right rim of the crown. Two curved lateral ledges to the right of the right rim of the crown. The outer and shorter ledge more strongly curved than the inner. The inner ledge is more or less parallel to the crown rim, except for the inward bending part of this rim. One lateral ledge (less broad) on the left, parallel to the left crown rim, except for the inward bending part of this rim. The ledges start at level of lateral basal corners and converge into crown plate at different positions: posterior (inner ledge on the right), further anterior (ledge on the left), halfway (outer ledge on the right). Moderately high posterior neck. Crown fills up entire base (behind the free anterior zone), and projects over base only with its rear part. Projection about 1/3 of crown length. Rhomboid base, deeper than in the above scales.
Remark: This scale is a variation on some of the forms shown by Gross (cf. 1947: pl. 26: 8-9).

Asymmetric scale P8900 (figs. 32-33): Triangular crown, slightly concave and inclined. Left rim curved (convex) and bending inward anteriorly, right rim straight. Anterior crown margin slightly irregular. There is a narrow free zone between the anterior crown and the rounded anterior basal rim. The anterior surface of the crown faces left. Six short anterior crown riblets, also directed towards the left (more or less so). The rather broad, lateral surfaces, give the crown a pyramidal aspect (fig. 32). Each lateral surface has a short anteromedian riblet, which is oriented towards the median scale part. Lateroposterior neck with a few openings low in the neck and increasing in height posteriorly, where it is moderately high. Crown fills up entire base (behind the narrow free anterior zone). Posterior projection over base negligible. Rhomboid and moderately deep, convex base.
Remark: In crown morphology this scale shows a certain affinity to the crown of coronate tesserae (cf. Gross, 1971: pl. 3: 10, 16, 19).

Slightly asymmetric scale P8901 (figs. 34-35): Broad triangular crown, slightly concave and slightly inclined. Curved (convex) rims bending inward anteriorly, and constricting anterior crown. Anterior margin of crown has two forward projecting, short, anteriorly converging riblets, and there is one very short anterior riblet parallel to right crown rim. A narrow sculpture-free zone separates the anterior crown from the rounded anterior basal rim. The anterior surface of the crown plate faces right. One convex lateral ledge (on the left in fig. 34) running obliquely from level of lateral basal corner in posterior direction. Moderately high posterior neck. Crown fills up entire

base (behind the narrow free anterior zone) and does not project over base. Rhomboid and moderately convex base.

Slightly asymmetric scale P8902 (figs. 36-37): Narrow and elongate trapezoid, originally probably triangular crown, moderately inclined. Curved (slightly convex) rims bending inward anteriorly, and constricting anterior crown. Anteromedian crown partly elevated and bordered by two sharp parallel ridges and with one central, short longitudinal, anterior riblet (fig. 37). Where the left rim of the crown bends inward (fig. 36) there is another short, longitudinal, anterior riblet. The crown is placed slightly off centre, and its anterior surface faces left (fig. 36). There is a free basal zone all around the crown. One narrow, curved (convex) lateral ledge on each side of the crown, converging posteriorly into the crown. These ledges begin at the level of the lateral corner of the base (left ledge) or further posteriorly (right ledge, hardly visible in fig. 36). Moderately high posterior neck. Posterior crown part projecting over rhomboid, convex, low base.

Feature list

The following features were deduced from the descriptions above (absolute size measurements have not been included): 1: crown: symmetric-asymmetric; 2: asymmetric crown: surface facing left or right; 3: shape of crown: triangular-ellipsoid; 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, or convex; 12: crown rims: bending inwards and constricting anterior crown, or not; 13: lateral crown rims: narrow (ridge-like) — broad (ledge-like); 14: lateral crown rims: plain-ornamented; 15: number of lateral crown rims: left-right; 16: starting position of most anterior lateral crown rims: at the level of the lateral corners of base-further anterior/posterior; 17: lateral crown rims: straight or curved (convex-concave); 18: lateral crown rims: bending inwards, or not; 19: lateral crown rims: converging into posterior crown tip, or well below tip; 20: anterior crown margin: straight-irregular, with 'Vorkrönchen' or 'Nebenkrönchen' ; 21: anterior riblets: present (their number) or absent; 22: orientation of anterior riblets: towards lateral left — towards lateral right — longitudinal — mixed (specify further); 23: orientation of anterior riblets: all parallel (to what?), or partly parallel (to what?); 24 forward projection of anteromedian riblets: these riblets parallel — posteriorly diverging — posteriorly converging; 25: crown: filling entire upper basal platform, or part of platform; 26 free, unornamented zone of basal platform: anterior-anterolateral-lateral-posterolateral-posterior-all around crown; 27 distance between crown and basal rim (further specified in relation to 26): narrow-wide; 28 surface between crown and basal rim (not the neck; further specified in relation to 26): concave-flat-convex-sloping; 29 neck: lateral-posterior-lateroposterior; 30: neck: low-moderately high-high; 31: neck openings: none-tiny-medium-large (size relative to 0.1 mm bar); 32: neck ribs, developed as: sharp ridges — ribbons (= broader) — sheets (= still broader); 33: neck ribs: straight-curved; 34: neck ribs: on the left — on the right — posterior — on the left and right — on the left, right and posterior; 35: neck ribs:

number; 36: neck ribs: as long as the lateral neck — shorter — mixed (specify further in relation to 34); 37: starting point of neck ribs: near base level — higher in the neck — near the end point of a more anterior neck rib; 38: 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; 39: neck ribs, converging: into posterior crown point — into posterior part of crown rim — into the median part of the crown rim — into the anterior part of the crown rim — into lateral crown rim (low-halfway-high) — into another neck rib; 40: base: concave-flat-convex; 41 base: low-moderately deep-deep; 42: shape of base: rhomboid or otherwise.

General and taxon-related remarks on some listed features

Symmetric or asymmetric crown (feature 1) — The scales of *Nostolepis striata* and allied taxa are asymmetric (longitudinally) and often this is obvious. However, the degree of asymmetry is rather variable and may be so slight that one tends to overlook it, and may regard it as symmetric. When a scale is called symmetric in this volume, it is approximately symmetric.

(Latero)posterior projection of crown (features 6-7) — One may distinguish between *N. striata* scales whose crowns do not project over base and scales showing diverse degrees of projection. It is likely that such distinctions are linked up with body topography, even though no specific places on the body can be suggested here relating to these differences. The crown of *N. striata* and allied nostolepid scales never reaches the degree of crown projection so conspicuous and common in the scales of *N. gracilis* Gross, 1947.

Crown rims (features 11, 12) and lateral crown rims (features 13-19) — A distinction must be made between crown rims and lateral crowns rims on the one hand, and neck ribs on the other. Crown rims are the most anteriorly starting limits of the lateroposterior crown plate. The lateral crown rims form lateroposterior, often lowered or terraced, extensions of the crown plate. The first pair of lateral crown rims begins further posteriorly, the second still further back etc. Neck ribs do not contribute to the increase in crown plate surface. Lateral crown rims are a characteristic feature of many *N. striata* and allied trunk scales and are present in all of the scales figured here. For *N. striata* scale types without lateral crown rims, see Vergoossen (2002a: figs. 62-63; 58-59 with neck rib; 64-65 with neck ribs; 2000: pl. 1: 6); two other illustrations in the latter paper clearly show the difference between a crown with a neck rib (fig. 7) and with a lateral crown rim (fig. 8). All the *N. striata* trunk scales figured by Gross (1947: pl. 26) have lateral crown rims. All the scales of the *N. arctica* type material figured by Vieth (1980: pl. 5: 1-9) have lateral crown rims, and the same is true for the figured *N.* aff. *arctica* scales (Valiukevicius, 1998: pl. 3: 16-21). Lateral crown rims can be observed in at least three (out four) specimens of the figured *N. multicostata* type material (Vieth, 1980: pl. 4: 1-2, 4). For lateral crown rims in *N.* aff. *multicostata* see Valiukevicius (1998: pl. 4: 3, 5, 6). Lateral crown rims are also present in *N. minima* (Valiukevicius, 1998: pl. 3: 1-9, all the figured scales), *Nostolepis* sp. (op. cit.: pl. 2: 1-4, all the figured specimens), *N. athleta* (ibid.: pl. 5: 13), *N. laticristata* (ibid.: pl. 6: 8-9, all the figured scales). Scales of *N. alta* may have lateral crown rims (Märss, 1986: pl. 28: 12-14). On the other hand, in the type material of

Canadalepis linguiformis the lateral crown rims are absent in all the figured specimens with a single crown (Vieth, 1980: pl. 7). Of the *C. linguiformis* scales figured by Valiukevicius (1998: pl. 3: 3-8) only the scale in fig. 3 has lateral crown rims.

In contrast to plain lateral rims, which are common, ornamented lateral rims seem to be a much-restricted feature in *Nostolepis striata* scales, although Gross (1971: 7) remarked that ornamented rims (op. cit., pl. 6: 1-2) are 'not seldom'. The ornament may be dentate or consist of one or more rows of spinae (thorny outgrowths). This ornament is absent in the Scanian scales studied by me. The absence cannot be due to preservation alone, since the scales from the Helvetesgraven sample (Vergoossen, 1999b) are well preserved. The absence is not primarily a quantitative matter either, since in total enough *N. striata* scales are available in the Scanian samples. Factors that might play a role (also in combination with each other or with environmental factors) are: 1) the size of the scales: this is unlikely because in late Ludlovian to Pridolian scales from erratics this feature is also present in scales smaller than 0.5 mm; 2) body topography: the scales grew in a relatively small area on the body; 3) scale ontogeny: the question may be raised when, during the ontogeny of the scale, the lateral rims got their characteristic denticulations or when the rows of spinae were formed. For instance, I know of no histological evidence of the presence of denticulations in growth lamellae older than the lamella that was last or last but one, added to the crown (see also Vergoossen, 1999a: 243); 4) taxon-related restrictions: dentate or spinose lateral crown rims have not been recorded from the '*elegans*' scale group, *N. applicata*, *N.* (aff.*) arctica, N. athleta, N. laticristata, N. minima, N.* (aff.) *multicostata*, *Canadalepis linguiformis,* and *Endemolepis inconstans*, but denticulation of lateral crown rims occurred in *N. alta* (Märss, 1986: pl. 28: 10; pers. obs. from unpublished erratic material).

Anterior crown riblets (features 20-23) — A direct relationship has been observed between the number of anterior crown riblets and the width of the crown (without lateral extensions): the narrower the crown (in proportion to its length), the fewer riblets; this observation is not a law applicable to each *Nostolepis striata* scale. The size of the scale as such seems irrelevant, since also very small scales may have high numbers of anterior riblets. Absence of anterior riblets in scales with broad crowns would be unusual in *N. striata* and allied forms. A low number or absence of anterior riblets in narrow and anteriorly constricted *N. striata* crowns is to be expected, also in scales of the '*elegans*' group (cf. fig. 30) or *N. arctica*, which often have elongate, narrow and constricted crowns, and in *Canadalepis linguiformis*. In the studied Scanian material absence of anterior riblets in scales identified as *N. striata* seems rare.

There is also a relationship between the place of the scale on the body and the orientation of the anterior riblets: depending on the asymmetry of the scale crown (linked to body topography and distance from midline) riblets may show orientation to the left, when the scale was situated right of midline, or to the right, when the scale was situated left of midline. The anterior riblets closest to the crown rims, may show a tendency towards an orientation parallel with the orientation of the crown rims. There is no consistent parallel or radial arrangement (convergent towards the posterior crown tip) of the anterior riblets, as in some other contemporaneous Silurian-Devonian acanthodian taxa (e.g. radial in poracanthodids, parallel in *Cheiracanthoides*).

'Vorkrönchen' or 'Nebenkrönchen' (feature 20) — This is a structure on the ante-

rior crown margin resembling an additional little crown. Gross (1971: 7) wrote that not seldom a new, small rib centre formed on the anterior crown margin resembling a 'Nebenkrönchen' (an extra little crown). Gross (1973: pl. 36: 7) figured a 'Downtonian' *Nostolepis striata* scale from an erratic with a 'Vorkrönchen'. He also described and figured 'Vorkrönchen' from 'cladodont' scales, where the structure is linked with apposed growth onto the anterior crown and represents the newest growth increase. I have never collected *N. striata* trunk scales with a 'Vorkrönchen'. To my knowledge apposed 'Vorkrönchen' have not been recorded from the Silurian-Devonian taxa allied to *N. striata* (see above). *N. applicata* is a special case in that similar scales are probably part of the Late Silurian *N. striata* squamation in erratic assemblages. *N. applicata* has scales with several crowns, of which some may be apposed, but this is not the structure discussed here.

Forward projection of anteromedian riblets (FAR) (feature 24) —. This is a special arrangement of the anterior crown riblets, often two or three riblets right in the middle of the anterior crown margin, and should be distinguished from a 'Vorkrönchen'. Gross (1947: pl. 26: 10a) figured a nice example. Such an arrangement is absent in many *Nostolepis striata* variants (see e.g. op. cit.: pl. 26: 5-8; 11-12, 14-15) and may never have formed in these, because some of the variants (e.g. ibid.: the group of scales in pl. 26: 5-7, 15 and the group of scales in pl. 26: 11-12, 14) almost certainly derive from other places on the body (judging from their general shape) than the scales with forward projected anterior riblets (e.g. ibid.: pl. 26: 10). FAR may be present in very small scales, but whether this means it also occurs in the youngest growth phases cannot be decided at the moment. In the studied Scanian material the number of scales with FAR is low in comparison to those without.

None of the scales here figured has FAR with an arrangement of posteriorly converging riblets (pcr); pcr imitates the common crown shape of the trunk scale. An arrangement of posteriorly diverging riblets (pdr, fig. 34) stands in contrast with the common crown shape. At the microlevel the effects of these two different shapes on the water flow across the scale crown may have been virtually opposed. It is for this reason that they deserve attention. Nothing is known about the (relative) frequency of either shape in nostolepid scales, or about their restriction to particular scale variants (in particular body regions in particular nostolepid taxa). Scales with pcr have been figured less frequently than those with pdr. A pcr arrangement was illustrated from: *Diplacanthoides trilobatus* (Lehman, 1937: fig. 31; IV A, Ramsåsa F), *Nostolepis minima* (Valiukevicius, 1998: pl. 1: 9). Pdr was shown in: *D. compressus* (Lehman, 1937: fig. 6, Helvetesgraven), *D. sinuosus?* (ibid.: fig. 62, Helvetesgraven), *Nostolepis striata* (Vergoossen, 2000a: pl. 1: 6). In its general shape, the pdr arrangement is reminiscent of the beak-like, forward projecting anteromedian fold in the crown of other acanthodian taxa, cf. e.g. '*Gomphonchus* (aff.) *hoppei*' (Valiukevicius, 1998: pl. 2: 5-7, 18). Perhaps these structures had the same function?

Scales with forward projecting anteromedian parallel riblets have been figured predominantly, e.g. *Nostolepis striata* (Valiukevicius, 1998: pl. 1: 3-4; Vergoossen, 2002a: fig. 58), *N. minima* (Valiukevicius, 1998: pl. 1: 7), *N.* aff. *arctica* (ibid.: pl. 3: 20; this is probably a *N. striata* scale); *N. applicata* (Vieth, 1980: pl. 4: 7, 11). The scales of *Canadalepis linguiformis* Vieth (1980: pl. 7) have no forward projecting anteromedian rib set; such a set would seem a very unlikely structure for some of the narrow

crown variants of this taxon (e.g. Vieth, 1980: pl. 3: 11, 12). Valiukevicius (1998) figured six *C. linguiformis* scales without FAR (pl. 3: 3-6, 8) and one scale with forward projecting anteromedian parallel riblets (pl. 3: 7).

No forward projecting anteromedian riblets have been recorded or figured from: scales of the '*elegans*' form group (Vergoossen, 1999b, 2002a), *Nostolepis arctica* (Vieth, 1980: pl. 5), *N. multicostata* (Vieth, 1980, pl. 4), *N.* aff. *multicostata* (Valiukevicius, 1998: pl. 4, except fig. 2, but this is a heavily damaged scale and certainly does not look like *multicostata*), *N. athleta* (Valiukevicius, 1998: pl. 5), *N. alta* (Märss, 1986: pl. 28; pers. obs.), *Endemolepis inconstans* (Valiukevicius, 1998: pl. 6).

Neck ribs (features 32-39) — Gross (1947, 1971) did not describe or figure neck ribs in *Nostolepis striata* scales. In the small Scanian scales often high magnifications are needed to discover neck ribs. Neck ribs are distinct from lateral crown rims because they are essentially part of the (lateroposterior) neck morphology and their most anterior or lowest point is always situated in the neck, below the outermost crown rim. Neck ribs become also part of the crown morphology when they run into the crown, for instance with their posterior end (fig. 29, posteriormost neck rib). Of the scales here figured, the specimen from Klinta 5 in fig. 29 is the only one with neck ribs; these neck ribs are oblique, or parallel to the outer crown rim. Longer and shorter neck ribs, oblique and parallel to the outer crown rim, have also been figured from *N. arctica* by e.g. Vieth (1980: pl. 5: 1b, 2b, 4b, 7c). For the parallel sort of neck rib see also two *N. striata* scales from Ramsåsa H (Vergoossen, 2002a: figs. 58, 65). These figured specimens of both *N. striata* and *N. arctica* are all trunk scales, with a considerable inclination of the crown in some specimens; they are not scales transitional to scales or tesserae of the head because they show no resemblance to such tesserae. It is unknown how regular or irregular both sorts of neck ribs, or their combination, are in *N. striata* scales. Among Ludlovian to Lochkovian acanthodian scales the combination might be a topospecific attribute restricted to some scales of some nostolepid taxa. Among the thelodonts, *Loganellia* scales may have similar neck ribs. Series of very short oblique neck ribs (called 'caudale Ripchen') occur in *N. multicostata* (Vieth, 1980: pl. 4: 3b). More or less parallel oblique neck ribs were figured by Lehman (1937: figs. 37 A, C) from *Diplacanthoides decoratus* (Ramsåsa F).

Nostolepis? sp.
Pl. 4, figs. 38-39.

Tesserae: Fragments of platelets from the head carry apposed tubercles with converging, convex ridges on a flat and thin base. At least three tubercles with detached, pointed tops can be seen in fragment P8903 (fig. 38), which measures c. 0.4 × 0.4 mm. The other fragment, P8904 (fig. 39) is slightly larger, c. 0.4 × 0.5 mm, and bears three tubercles with one common top. The ridges may bifurcate, either near the top or near the base (arrows).

Porosiforms

Three scale crowns were found; one has been identified as *Radioporacanthodes biblicus* (Lehman, 1937). For a description of this species see Vergoossen (2002a).

Acanthodii gen. et sp. indet.
Pl. 4, figs. 40-46.

Various scales (figs. 40-46)

The scans revealed greater morphological diversity of these scales than expected when observing with binoculars. The rhomboid crown of P8905 (fig. 40; KL 5) has an anteromedian fold that fades out in the posterior crown half. The fold is flanked by a pair of sharp-edged, parallel ridges, which also fade out in the posterior crown half. The median ridges are flanked by similar but shorter, lateral ridges. All the ridges start from the anterior crown edge but the details of this edge are lost. The horizontal crown slightly protrudes over the neck lateroposteriorly, but the details of the neck have not been preserved, and the base is missing. The crown morphology distinguishes this scale from the other forms. The morphology of scales P8906 (figs. 41-42; KL 10) and P8907 (figs. 43-44; KL 5) resembles that of Acanthodii gen. et sp. ?, variant 1(cf. *Gomphonchus volborthi*) from Ramsåsa H. The most peculiar scale is P8908 (figs. 45-46, KL 8). In appearance the crown resembles crowns of *Gomphonchoporus hoppei* (Gross, 1947) (Vergoossen, 1999a: figs. 40-47). From the lateral view (fig. 46) it is obvious that part of the posterior crown and neck is missing, but there are no indications for the presence of a pore canal system. Märss (pers. com.) assigned all these figured specimens to *Gomphonchus.* This needs histological corroboration.

Correlation

For correlation schemes see Vergoossen (2002c: text-figs. 3-4). All taxa from Klinta and Rinnebäcks bro, with the exception of *Archegonaspis*, are also known from the Helvetesgraven faunas, which have been placed in the late Ludlovian transition phase between the *Andreolepis hedei* and the *Thelodus sculptilis* Zones (Vergoossen, 1999b, 2002a). The youngest and the oldest age indicators in the Helvetesgraven faunas, *T. admirabilis* and *Andreolepis hedei* respectively, have not been identified in the Klinta and Rinnebäcks bro assemblages, although there is some uncertainty about the identity of P8888 (fig. 15) from Rinnebäcks bro, which might also be an oral *T. admirabilis* scale.

The presence of *Thelodus sculptilis* indicates an age at least as young as the *T. sculptilis* Zone (late Ludlow to earliest Pridoli) for the Klinta samples (KL 2, 4-8) and the Rinnebäcks bro sample. The relative scarcity of the zonal fossil, the dominance and abundance of *T. parvidens*, the scarcity or absence of *T. traquairi, Loganellia cuneata, Katoporodus* and the poracanthodids may indicate that the faunas date from low in the late Ludlovian part of the *T. sculptilis* Zone, or from the late Ludlovian transition phase to the *T. sculptilis* Zone rather than from the *T. sculptilis* Zone proper. See Vergoossen (2002a) for similar observations on the age of the Ramsåsa H fauna, which could be slightly younger than these Klinta and Rinnebäcks bro faunas because of the dominance of the zonal fossil.

Fredholm (1988a, b) placed *Archegonaspis lindstroemi* from the Hemse beds on Gotland in the Leintwardinian? (*Polygnathoides siluricus* Conodont Zone), where the taxon is always associated with *Andreolepis hedei.* The Ludlovian *Archegonaspis* sp. A from the Edole 61 borehole in Latvia (Märss, 1977) was referred to *A. lindstroemi* by Fredholm (1988a). *Archegonaspis* sp. B was briefly described (not illustrated) by Märss

Table 1. Faunal list from Helvetesgraben (H), Klinta (K1-K10) and Rinnebäcks bro (Rb = sample P702); d = dominant species. The *Thelodus parvidens* row indcates form with unnotched crown rim and smooth crown. The dominance refers to *T. parvidens* inclusive of the formae.

Taxa	H	K1	K2	K3	K4	K5	K6	K7	K8	K9	K10	Rb
Osteostraci												
Hemicyclaspis sp.	x											
Osteostraci gen. et sp. indet.	x					x						
Heterostraci												
Archegonaspis cf. *lindstroemi*					x							
Heterostraci gen. et sp. indet.	x											
Thelodonti												
Thelodus parvidens, including	x	d	d		d	d	d	d	d	d	d	d
forma *pugniformis*	x											
forma *costatus*	x		x			x	x	x	x			
forma *bicostatus*	x	x	x		x		x	x				
forma *trilobatus*	x		x		x	x	x	x	x			
Thelodus traquairi	x											x
Thelodus admirabilis (age marker)	d											
Thelodus sculptilis (zone fossil)	x		x		x	x	x	x	x			x
Loganellia cuneata including	x		x		x	x						
forma *cruciformis*	x											
Loganellia sp. indet.												x
Thelodonti gen. et sp. indet.			x		x			x				
Acanthodii												
Nostolepis striata	x	x	x		x	x	x	x	x	x	x	x
forma *'elegans'*	x					?						
nostolepid tooth whorls	x											
nostolepid spine fragments	x											
Gomphonchus sandelensis	x		x			x						
stellate plates	x											
coronate scales and plates	x											
tesserae fragments						x						
squamae proniae	x											
squamae umbellatae	x		x									
Poracanthodes? lehmani	x											
Poracanthodes cf. *punctatus*	x											
porosiforms						x		x				
Radioporacanthodes biblicus							x					
'Dornzähne' sensu Gross, 1957	x											
ischnacanthid tooth whorls	x											
ischnacanthid whorl fragments					x							
'Onchus' spine fragments	x											
whorl fragments indet.							x					
spine fragments indet.						x						
dentition cones	x											
Acanthodii gen. et sp. indet.						x	x	x	x		x	
Osteichthyes												
Andreolepis hedei (zone fossil)	x											
Pisces gen. et sp. indet.				x								

(1977) from the Kingiseppa boring (Paadla Stage, Uduvere beds, depth 3.6-18.1 m) and the Ohesaare borehole (Kuressaare Stage, Tahula beds, depth 93.21-98.8 m) in Estonia. Märss (1986: fig. 33) recorded *Archegonaspis?* sp. in the Kingiseppa boring from a depth of 10.4-18.3 m, Kuressaare Stage, Tahula beds (in the Ludlovian part of the *Thelodus sculptilis* Zone), where the taxon is associated a.o. with *T. sculptilis* and other, new incoming taxa (including *T. traquairi*) typical of the *T. sculptilis* Zone. Märss (1986: fig. 41) recorded *Archegonaspis*? sp. in the Ohesaare borehole from a depth of 93.15-99.5 m. In its lowermost occurrence in the Ohesaare boring (98.8-99.5 m), *Archegonaspis*? sp. is associated with *Andreolepis hedei*, at the top of the *A. hedei* Zone (Uduvere beds, Paadla Stage); whereas in the higher stretch of the boring (93.15-94.48 m) lowermost *T. sculptilis* Zone (Tahula beds, Kuressaare Stage), *Archegonaspis* ? sp. is associated by *T. sculptilis* and other newcomers (including *T. traquairi*, but not always).

Within the Baltic region, the presence of the genus *Archegonaspis* in sample KL 4 not only supports the (late) Ludlovian age of this fauna, but may also be an indication of the transition phase character of the KL 4 fauna. If the remains belong to *A. lindstroemi*, the KL 4 fauna might or might not be older than the Ramsåsa H fauna, but probably not older than the Helvetesgraven fauna.

The composition of the faunas from KL 1, 3, 9, 10 does not allow an evaluation within the late Ludlovian framework of the other Klinta or Scanian faunas. In general it may be said that the taxa do not contradict a Whitcliffian age.

Comparison with the fauna from Helvetesgraven (Table 1; Vergoossen, 1999b) shows that the Klinta and Rinnebäcks bro faunas are considerably less diverse.

Acknowledgements

The author is indebted to the following persons: Ulf Borgen (Swedish Museum of Natural History) for loan of material; Ulf Shived (Swedish Geological Survey) for providing data on the geology of Rinnebäcks bro; Lars Werdelin (Swedish Museum of Natural History) for sending the map; Bert Boekschoten (Rijksuniversiteit Groningen), Carole Burrow (University of Queensland), Tiiu Märss (Tallinn Technical University) & Juozas Valiukevicius (Institute of Geology, Vilnius) for reading critically through the manuscript and making valuable suggestions; Jan Zagers (Rijksuniversiteit Groningen) for SEM photography.

References

For references see Vergoossen (2002c) at the end of this volume.

Manuscript received 23 March 2000.

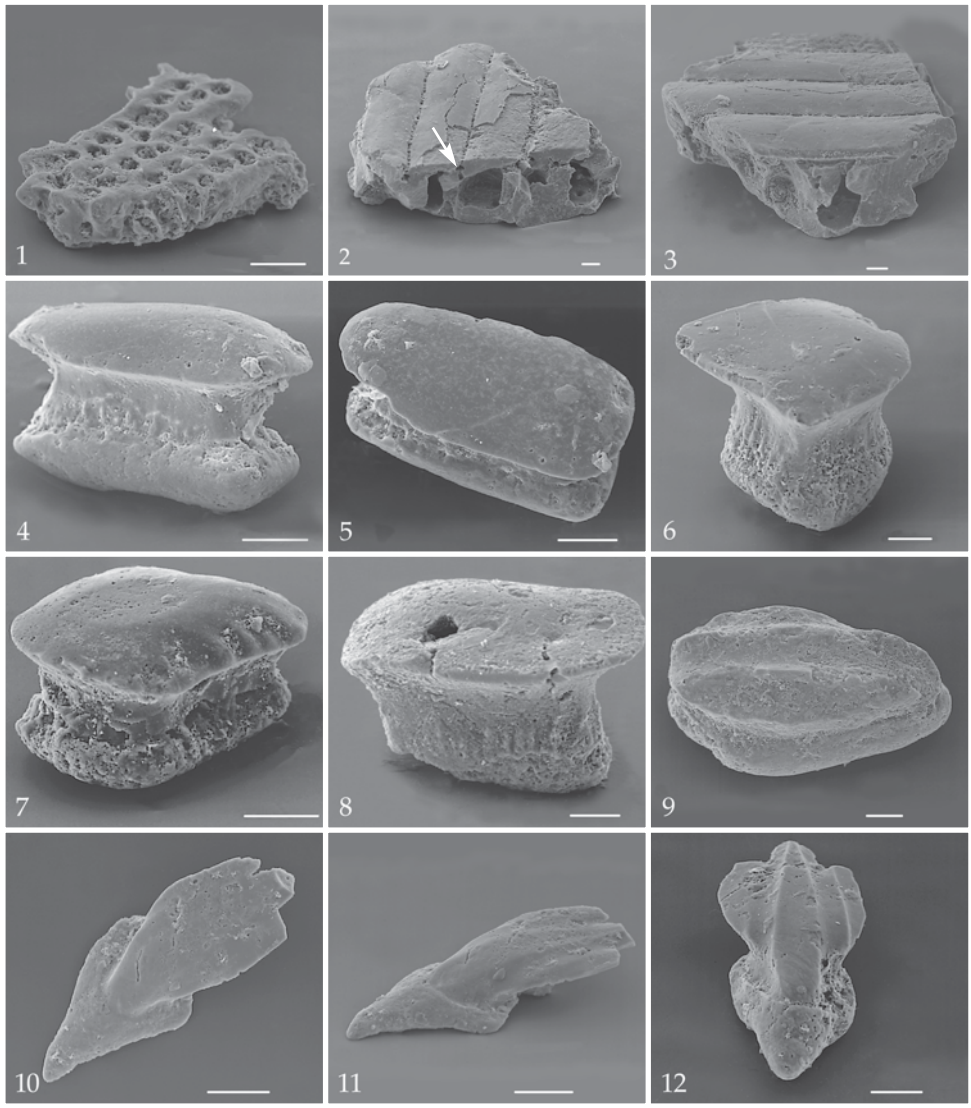

Plate 1

Fig. 1. Osteostraci; KL 5, P8878.

Figs. 2-3. Heterostraci; KL 4, plate fragment, possibly of *Archegonaspis lindstroemi* Kiaer, 1932, P8879; 2: longitudinal view; 3: lateral view. Arrow indicates longitudinal canal under the surface pores.

Figs. 4-12. *Thelodus parvidens* Agassiz, 1839; 4-5: KL 5, elongate (rectangular) scale, P8880; 4: lateral view; 5: crown view; 6: common scale type, P8881, lateral view; 7: KL 6, scale with notched lateroposterior or anterior crown, P8882, lateral view; 8: RB, elongate (rectangular) scale, P8883, lateral view.

9: Forma *bicostatus*, KL 2, P8884, lateral view.

10-12: Forma *trilobatus*, KL 5, scale with smoothened (abraded) crown, P8885, anterior view; 11: lateral view, bringing out better what has remained of the surface relief of the crown; 12: KL 7, posterior crown broken off, P8886, anterior view.

Scale bar 0.1 mm.

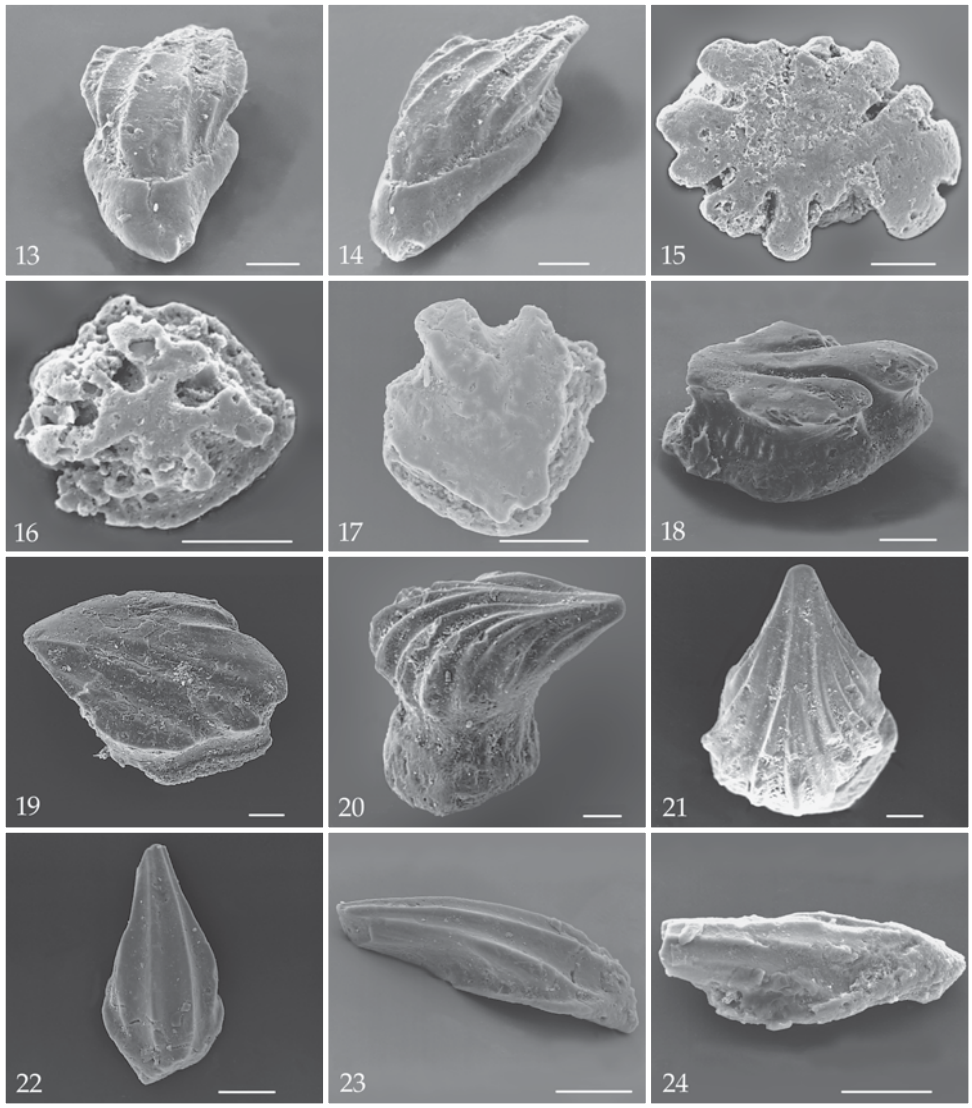

Plate 2

Figs. 13-14.*Thelodus parvidens* Agassiz, 1839, forma *trilobatus*, KL 2, posterior crown broken off, P8887; 13: anterior view; 14: anterolateral view.

Figs. 15-19. *Thelodus sculptilis* Gross, 1967; 15: RB, oral scale, crown view, P8888; 16: RB, oral scale, much damaged, crown view, P8889; 17: KL 5, cephalopectoral scale, crown view, P8890; 18: KL 6, trunk scale, lateral view, P8891; 19: KL 6, trunk scale, crown relief worn down, posterior base destroyed, P8892, crown view.

Figs. 20-21. *Thelodus traquairi* Gross, 1967; RB, postpectoral scale, P8893; 20: lateral view; 21: crown view.

Figs. 22-24. *Loganellia cuneata* (Gross, 1967); 22-23: KL 5, anterior base broken off, P8894; 22: anterior view; 23: lateral view; 24: KL 2, anterior and posterior scale parts broken off, P8895, lateral view.

Scale bar 0.1 mm.

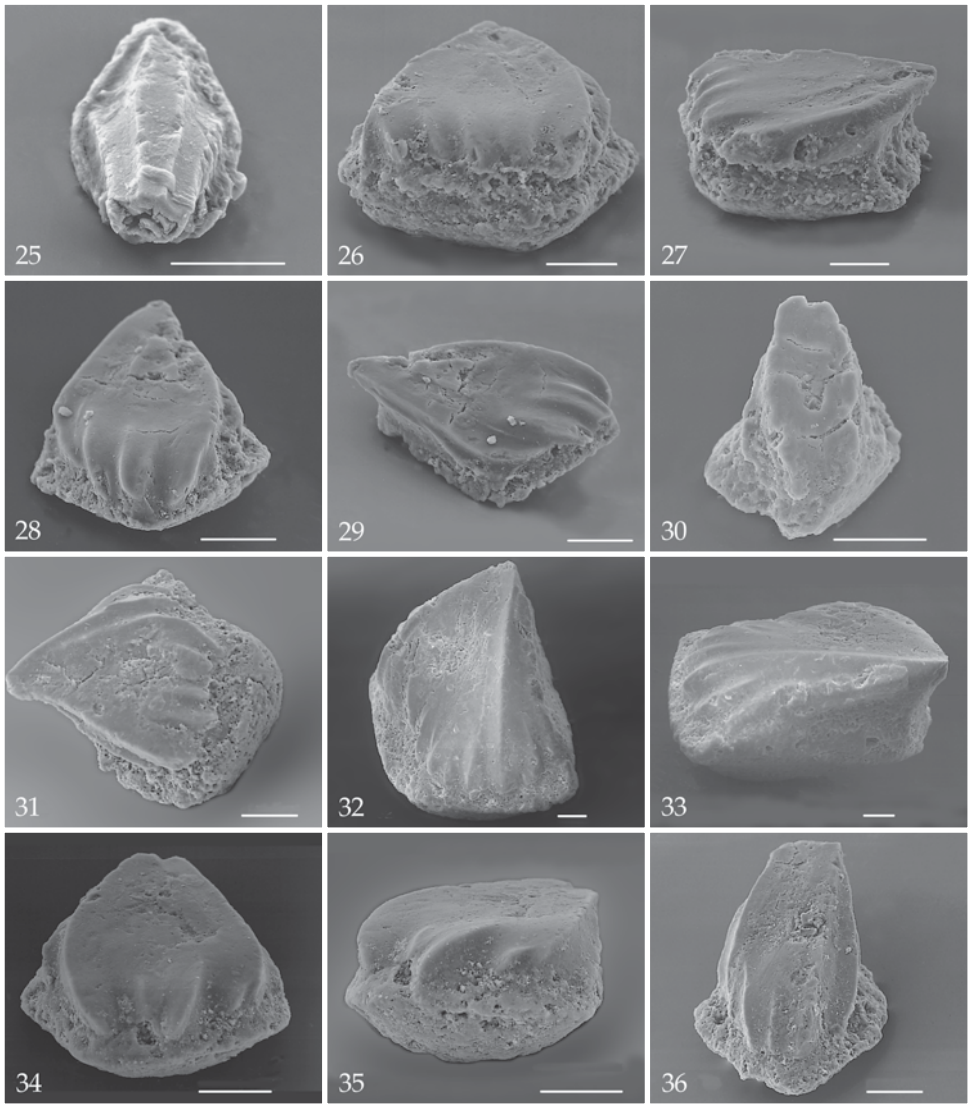

Plate 3

Fig. 25. *Loganellia cuneata* (Gross, 1967); KL 2, posterior scale part broken off, P8895, posterior view.
Figs. 26-36. *Nostolepis striata* Pander, 1856; 26-27: KL 5, P8896, 26: anterior view; 27: lateral view; 28-29: KL 5, P8897; 28: anterior view; 29: lateral view; 30: forma *elegans*? KL 5, P8898, anterior view; 31: KL 2, P8899, crown view; 32-33: KL 2, P8900; 32: crown view; 33: lateral view; 34-35: KL 2, P8901; 34: anterior view; 35: anterolateral view; 36: KL 2, P8902, anterior view.

Scale bar 0.1 mm.

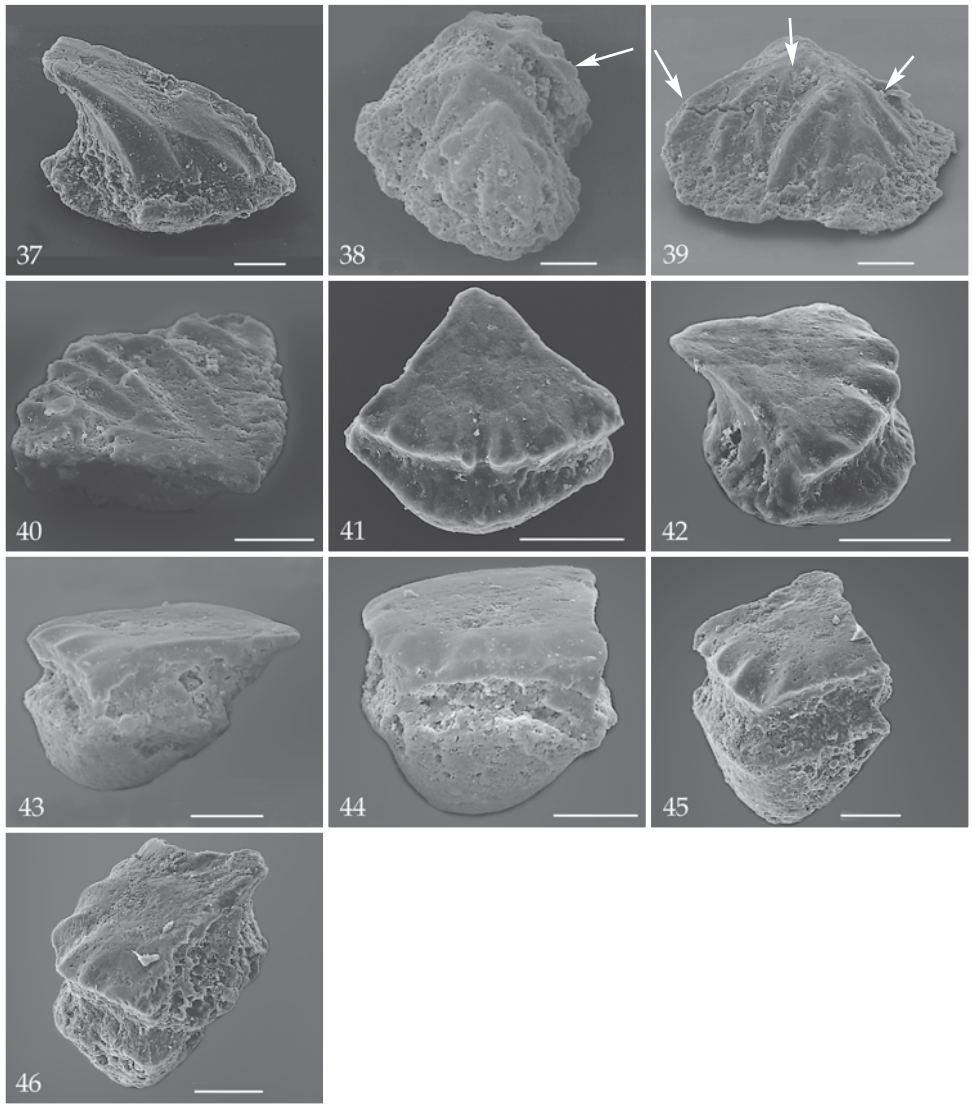

Plate 4

Fig. 37. *Nostolepis striata* Pander, 1856; KL 2, P8902, lateral view.

Figs. 38-39. *Nostolepis?* sp.; tessera; 38: KL 5, P8903, crown view; 39: KL 5, P8904, lateral view. Arrows indicate converging tubercular ridges.

Figs. 38-46. Acanthodii gen. et sp. indet; various scales; 40: KL 5, crown view from posterior, P8905; 41-42: KL 10, P8906; 41: anterior view; 42: lateral view; 43-44: KL 5, P8907; 43: lateral view; 44: antero-lateral view; 45-46: KL 8, P8908; 45: anterior view; 46: lateroposterior view.

Scale bar 0.1 mm.