



Late Silurian fish microfossils from Helvetesgraven, Skåne (southern Sweden) (I)*

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Abstract

The fauna from a Late Silurian residue sample from Övedskloster (Skåne) is listed. It comprises scales of 'Agnatha' (rare osteostracan scales, and the thelodonts *Thelodus parvidens*, '*T. traquairi*', *T. sculptilis*, *T. admirabilis*, and '*Loganellia cuneata*') and of Gnathostomata (the acanthodians *Nostolepis striata*, *Gomphonchus sandelensis*, *Poracanthodes? lehmani* sp. nov., and *Poracanthodes* cf. *punctatus*, tesseræ of the head and other specialised elements of the squamation; and the osteichthyan *Andreolepis hedei*). This fauna is considered to be as old as, or slightly younger than that from the complex of sedimentary rocks along the Anglo-Central Urals margin of the Laurussian continent affected by the Ludfordian *A. hedei* Event. This event marks the transition between the *hedei* and *sculptilis* Zones of the Microvertebrate Standard Zonation and can be correlated with the *snajdri* Conodont Interval Zone. The evidence favours a simultaneous palaeogeographical appearance of the punctatiform and porosiform poracanthodid acanthodians within the Baltica region of Laurussia.

Introduction

In the present contribution, the fauna of an unregistered residue sample from 'Övedskloster', kept in the Naturhistoriska Riksmuseet (Palaeozoology section, Stockholm, NRS), is listed; the geographical reference to Övedskloster is probably a less accurate indication for the second quarry at Helvetesgraven (see below). The biostratigraphical implications of the fauna are discussed and the fauna is compared with that from 'Övedskloster', described by Lehman (1937). Palaeontological comments and brief descriptions are included, but complementary details will be published elsewhere.

The outcrops at Helvetesgraven (Figure 1) and adjacent localities are in the Early Pridolian Öved Sandstone Formation, which is part of the Late Silurian Öved-Ramsåsa Group (Jeppsson & Laufeld 1986). The Öved Sandstone (Figure 2(a)) comprises sandstones,

shales and subordinate thin limestone bands with marine faunas, in which the increasing importance of the bivalves indicates a shallowing-upward trend (Jeppsson & Laufeld 1986). The type locality is the (second) quarry at Helvetesgraven, which was flooded several decades ago. A reddish sandstone is still exposed in a few small sections. Pieces of bone-bed from the dump piles at the quarry were placed in the *Ligonodina elegans* Conodont Zone by Jeppsson (1974, 1982). In Skåne, this zone represents the youngest Silurian. Within this zone, Jeppsson (1974; see also Jeppsson & Laufeld 1986) distinguished a local fauna with *Hindeodella steinhornensis* new subspecies 2 (Figure 2(a), *H.s.* n. sp. 2), which he placed in a new local zone on the basis of the conodonts from Helvetesgraven. This local zone represents a fauna that Jeppsson (1974: p. 12 and table 1) considered slightly less 'advanced' than the one from his sample Ramsåsa F 66.

The unregistered residue of which I studied the fish fauna, was labelled 'Övedskloster' in T. Ørvig's hand-

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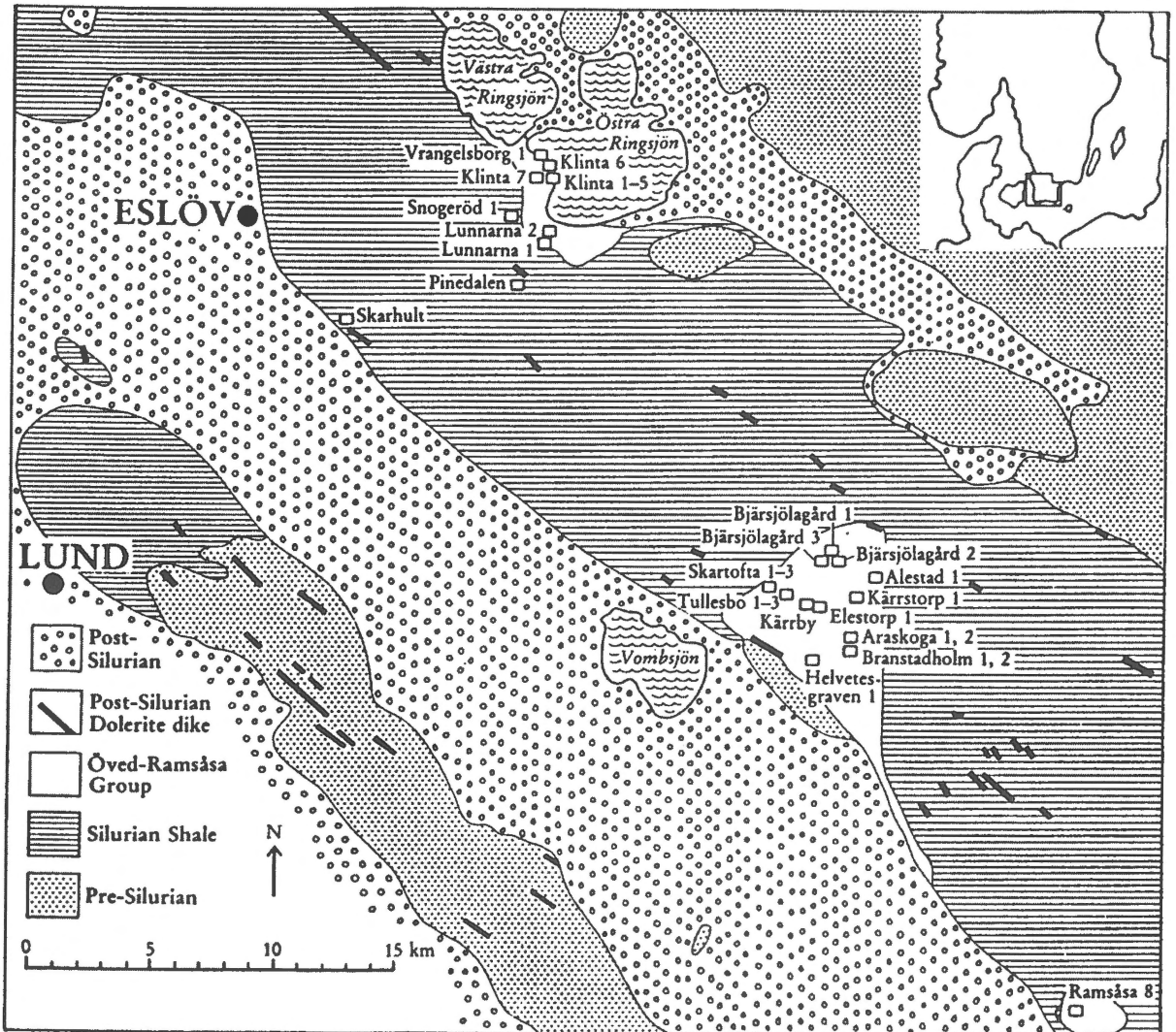
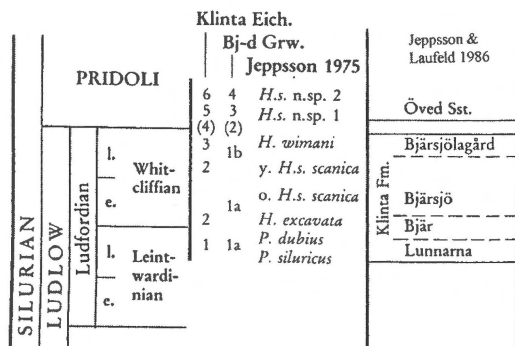


Figure 1. Map of Skåne (from Jeppsson & Laufeld 1986), showing the Helvetesgraven site.

writing and was kept in the cabinet where Ørvig's thin sections and other residue samples are stored in the NRS. The sample contained few loose, red sediment particles, and reddish white fossils, sometimes with particles of sediment adhering to them. I assume that the rock that yielded the fish remains was collected at the type locality. The printed stickers on the rocks in the NRS collection bear the combined site name 'Övedskloster-Helvetesgraven'. The problems related to collecting from the outcrops at Helvetesgraven were summed up by Jeppsson & Laufeld (1986). Ørvig may have received the residue or rock from a source outside the NRS; no notes relating to the residue could be traced in the NRS.

Most of the samples for the study of the Scanian fish fauna by Lehman (1937) were collected by Stensiö in 1924. Lehman's material from Övedskloster came from the second quarry at Helvetesgraven (Jeppsson & Laufeld 1986; compare Lehman 1937: 9). For these reasons I shall refer to Helvetesgraven as the site that yielded the faunas. Since Lehman (1937: 5) stated that a small part of his material had been collected by Grönwall, or even before Grönwall, it cannot be entirely excluded that rocks from other outcrops in the vicinity have been involved.

A.



B.

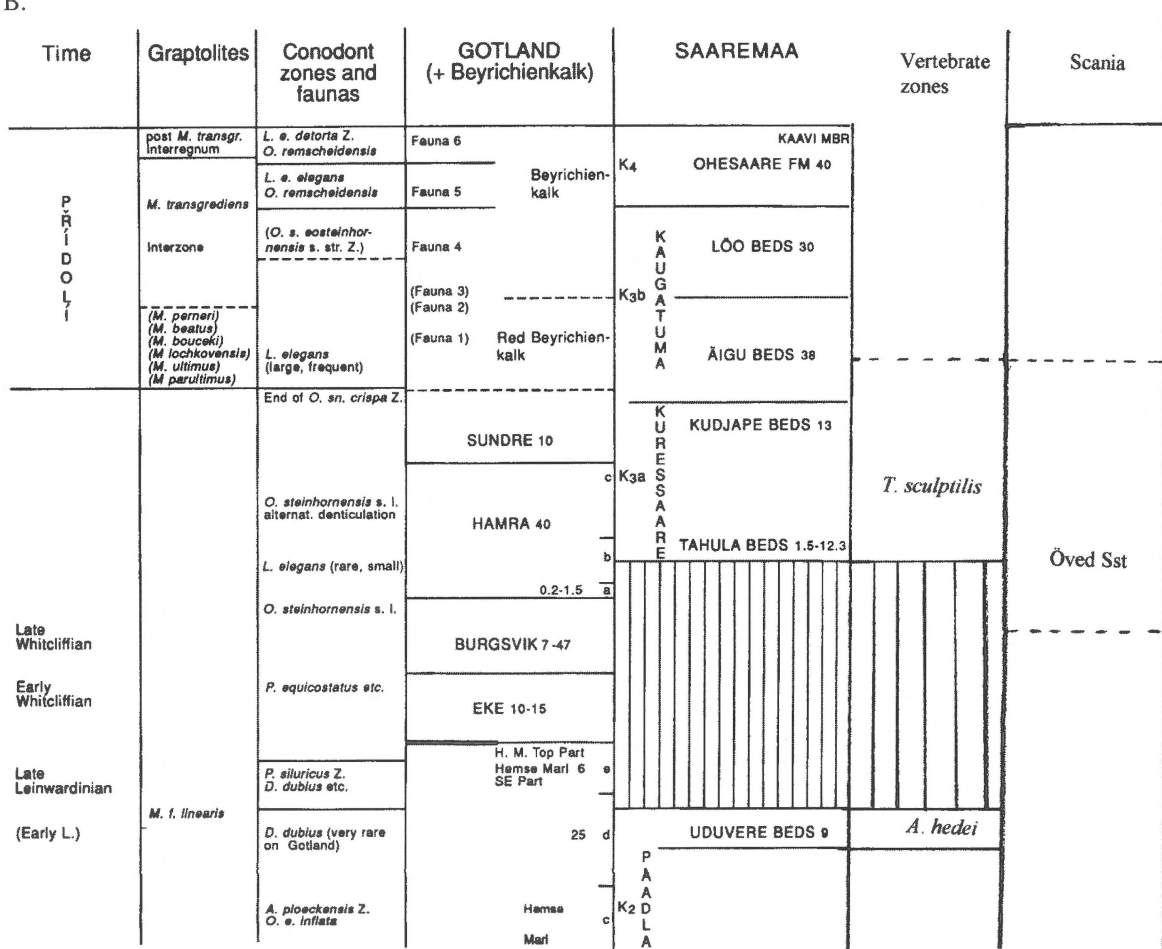


Figure 2. Stratigraphy of Skåne. A: Late Silurian stratigraphy according to Jeppsson & Laufeld (1986). B: Possible range of the Öved Sandstone suggested in this paper and projected on the correlation chart by Jeppsson et al. (1994).

History of research

Lehman (1937) described the Late Silurian fish microfauna from Helvetesgraven in combination with that from nearby Ramsåsa (Figure 1). He compared the two faunas by their lists of taxa (Lehman 1937: 86–88) and by the number of identified scales (Lehman 1937: 33, 56–57). His taxa were based on a total of 378 thelodont and acanthodian scales from both localities, as well as spines, teeth and other remains. The faunal list for Helvetesgraven is about 50% shorter (26 taxa, including 6 possible occurrences; a total of 56 scales) than that for Ramsåsa (53 taxa, including 3 possible occurrences; a total of 322 scales). Lehman (1937: 82) remarked that the acanthodians were better represented than thelodonts at Helvetesgraven, whereas it was just the other way round at Ramsåsa. Lehman (1937: 86–88) listed the following taxa from Helvetesgraven: thelodont scales (11, assigned to 8 scale taxa): *Thelodus laevis* Pander aff. *planus*, *T. glaber* Pander, *T. parvidens* Agassiz; the presence of the following 5 taxa was uncertain: *T. laevis*, *T. carinatus* Pander, *T. schmidti* Pander, *T. goebeli* Pander and *T. trilobatus* Hoppe (large variety); acanthodian scales (45, assigned to 9 taxa): *Gomphodus sandelensis* Pander, *Poracanthodes margaritatus* Lehman, *Diplacanthoides compressus* Lehman, *D. furcatus* Brotzen, *D. insignis* Brotzen, and *D. multicostatus* Lehman; the presence of the following 3 taxa was possible: *Gomphodus volborthi* Rohon, *Diplacanthoides elegans* Brotzen, and *D. sinuosus* Lehman; acanthodian spine taxa (5): *Onchus purchisoni* Agassiz, *O. tenuistriatus* Agassiz, *O. roemeri* Hoppe, *O. curvatus* Pander, and *Onchus? brotzeni* Lehman. In addition, the occurrence of cyathaspid, cephalaspid and arthrodire remains, as well as the possible presence of elasmobranch teeth, were recorded. Lehman's taxon names will be discussed below.

Turner (1984) mentioned a sample from the 'Övedskloster sandstone from Helvetesgraven' yielding one ostracode, the thelodonts *Thelodus parvidens*, *Loganella ludlowiensis* Gross (= *Paralogonia ludlowiensis*), *Loganella* sp., and acanthodian scales. As a rule, in post second world war biostratigraphical evaluations, the fish fauna from Helvetesgraven was not treated separately from that of Ramsåsa (among others, Märss 1986b: fig. 46).

Lehman's nomenclature: the taxa from Helvetesgraven

None of the scales from the Helvetesgraven site identified by Lehman (1937) have been traced in the collection of the NRS. A comparison of Lehman's material with the new material can therefore be made only on the basis of his text and illustrations. Only Lehman's (1937) figures 55–63 (acanthodian scales), 77 (acanthodian teeth) and 83–84 (acanthodian spines) show the morphology of material from the site. Turner (1976, 1984: table 5.2) was the first fish researcher who tried to assess and update Lehman's nomenclature for the thelodonts. Of the taxa found with certainty at Helvetesgraven, she assigned *Thelodus glaber* to *T. parvidens* (see also Gross 1967) and *T. laevis* aff. *planus* to *T. costatus*. Of the taxa possibly present at Helvetesgraven she assigned the scales of *T. schmidti* to *T. sculptilis*, *T. traquairi* and *T. schmidti*. The scales of *T. goebeli* were assigned to *T. sculptilis* and *T. schmidti*. Turner (1984) assigned the scales of *T. carinatus* to *T. sculptilis*, and those of *T. laevis* to *T. parvidens*.

T. schmidti scales, which were partly grouped with the redefined *T. carinatus* Pander and partly with the redefined *T. laevis* by Märss (1986b), are easily distinguished by their histology (dentinal tubules strongly curved rostrad). No scales with such shape of the tubules have been found in the NRS residue.

Lehman (1937: 35) followed Brotzen's (1934) classification of acanthodian scales from an Early Devonian erratic conglomerate from Germany. The taxa were mainly based on morphological features allowing of only little morphological variation (see Lehman 1937: 35–36). In addition, several histological types were distinguished (Lehman 1937: 70). The majority of the identified taxa in Lehman's material from Helvetesgraven belonged to the genus *Diplacanthoides*, with a 'diplacanthid' type of histology. Gross (1947) showed that Brotzen's *Diplacanthoides* is identical with *Nostolepis*. Denison (1979) also included Lehman's new *Diplacanthoides* taxa – as specifically indeterminable – within *Nostolepis*. A thin section through a scale of *D. multicostatus* (Lehman 1937: pl. 7, fig. 8) clearly shows the histological structure of a *Nostolepis* scale. Lehman was the first to recognise *Nostolepis? dentoides* Hoppe as an acanthodian from a thin section through a scale (Lehman 1937: 71, pl. 5, fig. 3). Although he interpreted the histological structure of *D. multicostatus* and that of *N. dentoides* as typical 'diplacanthid', he also be-

lieved that the histological structures were distinct, representing different taxa, which is understandable if one compares the two photographs. Lehman's remark (1937: 71) that the histological structure of *Nostolepis* was not found in Skåne must be considered in this context.

In the NRS residue, a morphologically distinct group of scales (Plate II, Figures 16–17) is present that best matches both the specimen of *Diplacanthoides elegans* figured by Brotzen (1934: pl. 1, fig. 11) and those figured by Lehman (1937: figs. 57, 59). Lehman (1937: 41) wrote that his *D. elegans* scales differed from the one figured by Brotzen, and the question mark behind the taxon name (Lehman 1937: 41, 87) indicates his doubts about this identification. My taxonomic interpretation of these scales is discussed, together with the other *Diplacanthoides* taxa, in the palaeontological section on *Nostolepis striata*.

Of the poracanthodids, Lehman (1937) only described *Poracanthodes margaritatus* from Helvetesgraven. Gross (1947) did not regard *P. margaritatus* as an acanthodian scale; he based his view on the evidence of two similar scales which he had collected from Beyrichienkalk erratics. I have never seen such scales.

Of the five acanthodian spine taxa listed by Lehman (1937), two were restricted to Helvetesgraven in his opinion. *Onchus curvatus* (Lehman 1937: fig. 83) and *Onchus (?) brotzeni* (Lehman 1937: fig. 84). The first was equated with *N. striata* / *Climatius curvatus* by Gross (1947) and the second was labelled as 'incertae sedis' by Denison (1979). The NRS residue did not contain any spine remains identifiable to species level.

Methods

The weight of the residue was 5–6 g. The residue was divided into two fractions with a sieve (0.425 mm mesh width), which were then compared. The weight of the finest fraction was approx. 5 g. The number of fish microfossils identifiable to species level in 0.011 g of the finest residue was 266 (137 thelodont, 129 acanthodian), yielding an estimated number of more than 120 000 identifiable fish remains for the entire finest fraction. Due to time pressure, only a small part of the sample could be examined, but the faunal list represents all the common taxa in the sample. It is not known why the residue is so much biased in favour of the finest remains, among which are the smallest tesseræ and poracanthodid scales ever recorded. The specimens with 'P' num-

bers are stored in the fish collections at the Palaeozoology section of the NRS. Registration numbers preceded by 'JV' refer to the author's collection kept at the Paleontologische Werkkamer (Biologisch Centrum Rijksuniversiteit Groningen).

Fauna

The taxa/groups in the Helvetesgraven fauna listed underneath are marked with one asterisk (*) if they represent a first record for this locality, and with two asterisks (**) if they represent a new taxon/group.

'Agnatha'

Osteostraci

* cf. *Hemicyclaspis*

Thelodonti (5 scale species)

Thelodus parvidens, including

* *pugniformis*

* *bicostatus costatus trilobatus* forms

* '*T. traquairi*' GROSS 1967

* *T. admirabilis*

* *T. sculptilis*

* *Loganellia cuneata* sensu Märss 1986b, including

* *cruciformis* scales

Gnathostomata

Acanthodii (at least 4 scale species)

Nostolepis striata group of (flank) scales, of great morphologic diversity and probably including new *Nostolepis* taxa
nostolepid spine fragments

* nostolepid-like tooth whorls

Gomphonchus sandelensis

* tesseræ stellatae sensu Gross 1971

* tesseræ coronatae sensu Gross 1971

* other plates of the head/shoulder girdle region

* squamæ proniae

* squamæ umbellatae sensu Gross 1971

** *Poracanthodes? lehmani* nov. sp.

** *Poracanthodes* sp. cf. *P. punctatus*

* isolated teeth ('Dornzähne' sensu Gross 1957)
ischnacanthid (= '*Gomphodus*' sensu Gross 1957) tooth whorls

** ischnacanthid (cf. '*Gomphodus*' sensu Gross 1957) tooth whorl, new morphovariant 1

** ischnacanthid tooth whorl, new morphovariant 2

* dentition cones sensu Valiukevicius 1992

Osteichthyes (1 scale species)

* *Andreolepis hedei*

Apart from fish fossils, the sample yielded rare conodonts, gastropods, phyllocarid and other invertebrate fragments. (Note added in proof: recent inspection of the residue from an unregistered NRS rock sample from Helvetesgraven confirmed the presence of the fish taxa mentioned above.)

Osteostraci

cf. *Hemicyclaspis* (Plate I, Figure 3)

Pitted scales with an ornament of parallel smooth ridges separated by one or two rows of pores are not uncommon in Late Silurian sediments from the Baltic region. The overlap area for the adjoining scale is on the right in Plate I, Figure 3. According to P. Janvier (pers. comm., 1998), such scales are highly suggestive of *Hemicyclaspis*, which occurs in the Burgsvik Sandstone on Gotland.

Thelodonti

Thelodus parvidens group of scales

This group (Plate I, Figures 4–8) consists, among others, of rare, smooth crowned *T. parvidens* scales that possess a spiny posterior crown edge and swollen anterior base (Plate I, Figure 4). *Trilobatus* scales are well represented and variable in shape (Plate I, Figure 7). One variant is the scale type that Lehman (1937: pl. 2, fig. 23) named *T. querceus* (Plate I, Figure 8). Turner (1984) referred such scales to *T. trilobatus*. Märss (1986b: fig. 20, no. 32–36) included similar scales as postpectoral scales in the morphological variation scheme for *T. parvidens* but, whereas the specimens in Märss have smooth downstepped outermost lateral wings, this feature is not so clearly developed in the NRS specimens and was not depicted by Lehman (1937: pl. 2, fig. 23) either.

I found no scales of the form that Lehman (1937: fig. 24) collected from Ramsåsa and named *Thelodus clavaeformis*. It has an oval or rhomboid crown plate with antero-posteriorly directed crown ridges of more or less equal length and its posterior edge is not cut up. The *clavaeformis* variant is not represented in Märss's (1986b: fig. 20) scheme for *T. parvidens* and morphologically it would not seem to fit in as postpectoral sensu Märss (1986a). It is, indeed, hard to place such scales anywhere within Märss's scheme when one considers the general diagnosis for variants from

the five body regions (Märss 1986a). Turner (1984) assigned *clavaeformis* to *T. trilobatus*, but gave no arguments. Until more data will become available, it might be best to keep Lehman's names to indicate such variants.

Cephalo-pectoral *bicostatus* forms (Plate I, Figure 6) are relatively rare in the sample, and so are the oral *pugniformis* scales. In some of these (Plate I, Figure 5), the crown widens out posteriorly to form a platform below the sharp-edged top. According to Turner (pers. comm. 1998), such forms are transitional to ordinary flank scales.

'*T. traquairi*' Gross 1967 (Plate I, Figure 9)

Since high, horn-like scales (Gross 1967: pl. 4, figs 10a, 11a, 14, 15a) were not found – possibly because the fraction of the sample investigated is too fine-grained – I did not identify these scales as *Lanarkia* sp. Gross (1967: 19) noted that '*T. traquairi*' occurs frequently at Ramsåsa, but not seldom in a slightly different (geniculate) form (Gross 1967: pl. 4, figs 16–18). Such variants were not found either, but the general shape of the scales from Helvetesgraven falls within the variation range illustrated for the type species. The scales are rare in the residue.

T. sculptilis (Plate I, Figures 11–12)

Routine anise oil immersion revealed that the youngest growth zones of the crown have the appearance of a *parvidens* crown in some cephalopectoral scale types (in such specimens as figured by Märss 1986b: figs 21/7; 22/8, 14). The morphological differentiation into a *sculptilis* crown takes place from the 3rd or 4th growth zone onwards.

Two taxonomic implications of this observation might be that young *sculptilis* scales are indistinguishable from young *parvidens* scales, and that *parvidens*-like scales are part of the *T. sculptilis* squamation. Märss (1986b) did not include the *parvidens* scale type in her squamation schemes for *T. sculptilis*. This needs to be further examined.

Acanthodii

Nostolepis striata group of scales and
Diplacanthoides elegans (Plate II, Figures 15–17)

Vergoossen (1999, in press a) suggested that *Diplacanthoides elegans* Brotzen is probably identical with the Early Devonian *Nostolepis arctica* Vieth. One

scale figured by Lehman (1937: pl. 3, fig. 57) would seem to represent specimens with a narrow and elongated central part of the crown (Vieth 1980: pl. 5, figs 2, 3, 7, 9), which are also present in the NRS residue. In some of Vieth's scales in which the crown is not so steep (e.g., Vieth 1980: pl. 5, figs 4–5), it forms a more or less rounded anterior rectangle with the base. I have not found such scales, but one seems to be figured in Lehman (1937: fig. 59C').

In the Swedish scales, the base is often flat and I have rarely observed short lateral ribs (cf. Vieth 1980: pl. 5, figs 1b, 3b, 4a, 7c, 8a), which may have been influenced by the colour and dimensions of my material (see below). For the time being I prefer to regard *D. elegans* / *N. arctica* as an Early Devonian taxon, in agreement with Valiukevicius' (1998) distributional data for *N. cf. arctica* and with my own observations on *arctica* scales across the Siluro-Devonian boundary in the Welsh Borderland, UK (Vergoossen 1999, in press a). The Swedish *Diplacanthoides elegans*-like scales, a distinct form group within the available Swedish material, are treated here as the 'elegans' scale group within the Late Silurian nostolepids, until this problem will have been further addressed.

Valiukevicius (1998) assigned *D. elegans* to *N. striata* without arguments. Lehman only recorded *D. elegans*? from Helvetesgraven ('Övedskloster') in a table (Lehman 1937: 87), but he mentioned it also from Ramsåsa in his text (Lehman 1937: 41).

Other *Diplacanthoides* taxa from Helvetesgraven

I found no scales resembling *D. multicostatus* (large and easily recognised; Lehman 1937: fig. 63, p. 96), *D. sinuosus*? (smaller, still recognisable; Lehman 1937: fig. 62, p. 96) or *D. compressus* (a small but conspicuous form; Lehman 1937: fig. 61, p. 96). Scales looking like *D. furcatus* (Lehman 1937: fig. 66) have been observed in the large fraction and are assigned to *N. striata* (compare Gross 1947: pl. 26, fig. 9), in agreement with Valiukevicius (1998).

The inconspicuous scales of *D. insignis* (Lehman 1937: figs 33, 65) were not spotted in the large fraction and are difficult to spot in the small size fraction: immediate recognition of the diagnostic, morphological characteristics of the *Diplacanthoides* taxa in the small size fraction is commonly difficult, due to the small dimensions of the scales and the poorly contrasting surface features resulting from the uniform opaque white colour. Strong magnifications are needed, in combination with lighting from several angles.

As new material of these taxa from Helvetesgraven is lacking for a proper evaluation, I respect Lehman's names for the time being, under the restriction that *Diplacanthoides* has a *Nostolepis*-type histology sensu Gross (1947, 1971, 1973; compare Valiukevicius 1998: 30).

Gomphonchus volborthi

I consider this taxon a valid species, possibly older than *G. sandelensis* (Vergoossen 1999, in press a). Lehman (1937) mentioned its possible presence at Helvetesgraven, but I did not find it. Contrary to what Valiukevicius (1998: 30) wrote, the taxon was not erected by Lehman but by Rohon (1893, *Theolepis volborthi*). Valiukevicius assigned Lehman's scales to *N. striata* without arguments. However, *volborthi* scales have a *Gomphonchus*-type histology (pers. obs.; Hoppe 1931; Rohon 1983: 37, fig. 7; Gross 1947).

Tesserae stellatae

Tesserae stellatae varying in crown ornament from isolated, triangular denticles in stellate arrangement (Plate II, Figure 18) to similarly arranged 'arms' of fused denticles on a thin, often penta- or hexagonal plate with marginal accretional lines are not rare, and their dimensions can be a lot smaller than hitherto recorded: the smallest specimens collected from the NRS residue measure 0.22×0.22 and 0.22×0.28 mm but have one slightly damaged edge. The smallest undamaged specimen measures 0.36×0.24 mm. Variants with a small central tubercle and ring- or wedge-shaped sculptures around it (Gross 1971: pl. 2, figs 17–18, 27) were not found.

Tesserae coronatae, and other plates from the head/shoulder-girdle region

These tesserae are among the smallest found in the sample. One rounded, monotuberculate platelet measures 0.16×0.26 mm, and an elongate platelet with three tubercles in line is 0.3×0.2 mm in size. The 'horseshoe' variant (Gross 1971: pl. 3, figs 10, 16, 19, 21, 23–25) has not been observed, although the ornament on some forms comes close to it (cf. Plate II, Figure 19; this pentagonal plate also bears three isolated triangular denticles with round basal outlines). In the available material coronate plates show transitions to stellate plates, and vice versa.

Squamae proniae/‘Pultschuppen’ sensu Gross 1971, non Gagnier et al. 1989

Scales assigned to this form group may be wider than long (as the specimen in Plate II, Figure 20) and may have a stellate arrangement of the tubercles in the upper (posterior) crown part, separated by a distinct groove from the obliquely striped, lower (anterior) crown part. The stellate arrangement, so characteristic of the tesseræ stellatae, also occurs in specimens from East Baltic-derived erratics from the northern Netherlands (pers. obs.), but has never been recorded. This may indicate that squamæ proniae are transitional to the tesseræ stellatae and derive from a region of the head neighbouring the tesseræ stellatae, i.e. they were part of the outer squamation rather than deriving from the oropharyngeal cavity, as Gross (1971) suggested. Stellate-like tesseræ are, however, also known from the anterior part of climatiid tooth whorls (Miles 1973, *Ptomacanthus anglicus*: fig. 13b).

In nostolepid whorls, the base may be developed like an arched plate rather than a whorl (pers. obs.). The peculiar basal shape of many squamæ proniae (inverted V) approaches the shape of such tooth plates. For this reason, climatiid/nostolepid squamæ proniae might have been situated in the mouth close to the tooth plates and whorls.

Poracanthodes? lehmani nov. sp.

Ischnacanthida Berg 1940

Poracanthodidae Vergoossen 1997

Poracanthodes Brotzen 1934

Type species: *Poracanthodes punctatus* Brotzen 1934 (revised diagnosis in Vergoossen in press b).

Poracanthodes? lehmani nov. sp. (Plate II Figures 22–26, Plate III, Figure 27)

Derivation of name – in honour of J.-P. Lehman, who first studied the fish remains from Skåne.

Material – Holotype P 8818 (Plate II, Figures 22–23) from the Tahula beds, Estonia. Paratypes P 8819 (Plate II, Figures 24–25), P 8820 (Plate II, Figure 26), P 8821 (Plate III, Figure 27), and P 8822 (slide with 17 specimens) from Helvetesgraven, Sweden (all flank scales).

Type locality and horizon – Tahula 709 drilling, depth 7.8 m; Tahula beds, Kuressaare Regional Stage – *Thelodus sculptilis* Zone before appearance of *T.*

admirabilis; Ludfordian, Silurian; Saaremaa, Estonia (Märss 1986b).

Distribution – apart from the type locality, the species is known from Helvetesgraven, low in the Öved Sandstone Formation, at the transition between *Andreolepis hedei* and *T. sculptilis* Zones, Ludfordian, Silurian.

Morphological description – The description is chiefly based on the holotype, a mature flank scale (Plate II, Figures 22–23). Rhomboid shape of crown. The anterior lateral rims of the crown meet anteromedially at a right angle. There are more than 25 short, radial, dentate ridges along the anterior margin. The crown is not or only slightly inclined and smooth in front of the ridges. This smooth area is very narrow. Each ridge forms an obtuse angle with each new growth lamella, except in the central part of the anterior crown, where approximately three ridges lie within the oldest crown part. These ridges are longest. The crown shows eleven growth lamellae, which lie separated from each other from their lateral corners onwards in posterior direction. These free lying lamellae have been apposed, whereas superpositional growth occurs in the crown area in front of the free lamellae. When the scale grows older, superpositional growth increases in posterior direction, especially in the anterior crown centre, and tends to obliterate former apposition here. Each growth lamella has a dentate posterior edge and is smooth anterior to the dentation. Up to ten radial canals open out very high on the posterior neck, immediately under the crown surface. The neck is high all around and slightly constricted. Anterior neck smooth. Posterior crown overhang varies from negligible to 50% of scale length. Base swollen; swelling placed centrally but not projected in front of crown. Measured scales vary in size from 0.17 × 17 mm (Plate III, Figure 27) to 0.6 × 0.6 mm.

Histology: the histological preservation of the *Poracanthodes? lehmani* scales from Helvetesgraven is poor; and material from Tahula was not available for histological study. The histology was studied in thin sections and by aniseed oil immersion but the picture remains too unclear for definite assignment of the scales to *Poracanthodes*. Osteocyte spaces are present in the base. Two to ten radial canals, widening out in posterior direction, may occur. The radial canals, usually two, begin behind the primary growth zones and their number increases during growth. The ra-

dial canals are regularly connected by arcade canals, and arcade canals may be interconnected, but only the faintest indications for the presence of pore canals rising from the arcade canals have been observed. Thin dentinal canals ascend from the anterior neck and bend in horizontal direction in each new crown layer. The uppermost crown layers show these dentinal canals radiating from the anterior crown margin across several growth zones towards the crown centre, as in all gomphonchids and poracanthodids. The dentinal canals ascending from the posterior neck, end between the radial canals in the lower crown parts, where they are straight and oriented longitudinally and horizontally.

Modifications occur in small and presumably juvenile scales (Plate II, Figure 26; Plate III, Figure 27), and in transitional scales, but their morphological and histological pattern is basically the same.

Poracanthodes cf. punctatus

These Swedish flank scales (Plate III, Figures 28–30) differ from those of the type species (revised diagnosis in Vergoossen in press b) in the following respects: their small size (approx. 0.25 mm in width and 0.2 mm in length for the scale in Plate III, Figure 28, and 0.6×0.3 respectively for the scale in Plate III, Figure 29); the low number of growth zones (usually around 5); the crown has no median sulcus or anterior ridges and is wider than long (instead of vice versa), and is not inclined; the anterior crown edge is markedly rounded instead of angular; the base is never as convex, and the basal swelling is central instead of displaced anteriorly. In the type species the upper basal rim at the posterior neck-base interval is always straight. Crenulation of this rim, as seen in some of the NRS scales (Plate III, Figure 29) and affected by the low entry of vascular canals, has never been recorded. More often than not crenulation is combined with an almost flat base. In many of these features, the Swedish scales resemble those from the latest Pridolian of Manbrook, Welsh Borderland, UK (Vergoossen 1999: fig. 15; in press a: fig. 26; see also in press b: figs 32–33).

Scales transitional to ?head or ?shoulder-girdle regions have also been found. They are not known from the British material.

Ischnacanthid toothwhorls

Although the size of the whorls (Plate III, Figures 31–34) is smaller (> 0.425 mm) than the minimum size (0.5 mm) of the '*Gomphodus/Gomphonchus*' whorls indicated by Gross (1957, 1971), their morphology

matches Gross's descriptions and illustrations, with two notable, rare exceptions:

New morphovariant 1 (Plate III, Figures 31–32) – This whorl (about 0.35 mm in length and 0.3 mm in width) has a median longitudinal row of teeth, and, almost at right angles to this, another row on each side. All teeth on the whorl are smooth and round in cross-section. Longitudinally there are six main teeth, which are bent in posterior direction. The number of side cusps flanking these main teeth increases in posterior direction. The most anterior main teeth 1 & 2 have no sides cusps; main teeth 3–5 are flanked by one small cusp on each side (tricuspid rows); main tooth 6 is flanked by a pair of diminishing small cusps on each side (pentacusp row). A smooth zone (increasing in width posteriorly) separates the longitudinal tooth row from the latitudinal ones, which are multicusp but poorly preserved so that the total number of cusps and their precise arrangement is unclear. All cusps, including the largest teeth, in each lateral row are bent towards the centre of the whorl rather than in posterior direction. It is this feature that distinguishes this tooth spiral from all the known spirals. Unless this spiral is a complex, fused structure of three and originally distinct spirals, it cannot have grown in the way suggested by Gross (1957) or Ørvig (1973: fig. 2(a)). No openings for vascular vessels are visible in the longitudinal tooth series; it would seem that there is one such opening near the largest tooth of each latitudinal row. The base is thin, concave and considerably arched, in shape almost like a yarmulka.

New morphovariant 2 (Plate III, Figures 33–34) – This worn whorl, of which the anterior part has broken off, is characterized and distinguished by a single median, longitudinal row of four round to oval teeth without sidecusps on a thin, concave, gently arched basal plate that widens out posteriorly. The teeth have all broken off near the base. They become more oval in posterior direction and in cross-section show openings for ascending canals. The largest posterior tooth is encircled by a single row of openings for vascular canals, most of which are roughly equal in size but two latero-posterior openings (Plate III, Figure 33) are notably larger.

I found a similar whorl among large quantities of '*Gomphonchus*' whorls in East Baltic-derived erratic JV 970000 from Oosterhaule (Friesland, the Netherlands: Pridoli, *B. punctatus* Zone). In the latter, the teeth show no longitudinal striae.

The new whorl type can be interpreted as a rare variant, which together with the more common whorls, makes up the whorl dentition in one animal; its rarity might reflect a special position (see Ørvig 1973); or as an independent taxon. In both cases it is meaningful to refer to different whorl forms by distinct terminology, e.g., the brush or hedgehog variant (for the 'Gomphodus' whorls sensu Gross 1957) and the comb or hairpin variant for the present whorls. H.-P. Schultze (pers. comm., 1998) commented that this tooth whorl looks like a porolepiform rather than an acanthodian whorl, but porolepiform remains such as the characteristic rhombic scales were not collected from either the Helvetesgraven residue or the erratic block (Vergoossen in press b). Porolepiform remains are unknown from the Baltic Silurian.

Osteichthyes

Andreolepis hedei

Only small, fragile, flank scales (Plate III, Figure 35) with separated crown ridges (cf. Gross 1968) and pseudofulcral scales (Janvier 1971, 1978) were found, usually broken. The largest and most complete flank scale was about 1.6 mm in length and 0.5 mm wide.

Age, correlation and biostratigraphy

Besides scales of *P. ?lehmani*, which derive from a level in the Tahula beds of Estonia below the appearance of *T. admirabilis*, the following taxa are relevant to the age determination of the fauna. The two zonal fossils *A. hedei* and *T. sculptilis*; *T. admirabilis* and cf. *Hemicyclaspis*. According to Märss (1992) the co-occurrence of these taxa on the Anglo-Uralian margin of Laurussia is typical of the short-ranging *A. hedei* Event, which marks the transition between the *hedei* and *sculptilis* zones of the Silurian Vertebrate Standard Zonation. The event falls within the *snajdri* Conodont Interval Zone in the Late Ludfordian (Märss et al. 1995).

The co-occurrence of *A. hedei* and *T. sculptilis* was only known so far from the Tabuska Beds on the western slope of the Central Urals (Märss 1992: fig. 2), which is at the easternmost end of the Anglo-Uralian margin. The fauna from Helvetesgraven, which is right at the heart of this continental margin, has the second co-occurrence of the zonal fossils on record. Excavated from erratic boulder no. 0.410 from the Warsaw

province (Märss 1992), *T. admirabilis* was not known along this continental margin from outside the East Baltic region, where it appears in the Tahula beds (Kuressaare regional stage, Ludfordian) at a slightly higher level than *T. sculptilis* (Märss 1992: fig. 2). In the fauna from Helvetesgraven, *T. admirabilis* outnumbered *T. sculptilis* (about 2:1 in the part of the material picked so far), which might imply that the fauna is perhaps younger than any of the Laurussian faunas affected by the *hedei* Event as shown in Märss's fig. 2. The presence of *Hemicyclaspis*-like scales in the assemblage from Helvetesgraven provides further faunal links to the fauna from the Ludfordian Burgsvik Sandstone on Gotland.

What makes the fauna from Helvetesgraven unique on the Anglo-Uralian margin of Laurussia is the co-occurrence of these four taxa, which all point towards a Late Ludfordian age, either coeval with the *hedei* Event as defined by Märss (1992) or (slightly) younger. Such an age differs from the conodont dating (Pridolian) for the Öved Sandstone (Figure 2(a)) and fits in better with the upper part of the Klinta Formation, of which the Bjärsjölagård Member (Figure 2(a)) was correlated with part of the Burgsvik Sandstone on the basis of the conodonts (Jeppsson & Laufeld 1986). Outcrops in the Klinta Formation have not been recorded from the Helvetesgraven area. The age indicated by the fish remains is closer to that of the older *L. elegans* conodont fauna, which was correlated with the Estonian Tahula Beds by Jeppsson et al. (1994) (see Figure 2(b)). The fauna from the NRS Helvetesgraven residue is correlated here with part of the hiatus below these beds, because of the presence of *A. hedei*. Until further data will become available, it is concluded that:

- there are at least two bonebeds in the area, ranging in age from Late Ludfordian (the lower bonebed) to the youngest Lower Pridolian in Scania (the upper bonebed);
- the Öved Sandstone (inclusive of the lower bonebed) is partly of the same age as the top of the Klinta Formation (cf. Figure 2(a)).

Among the new incoming taxa characteristic of the faunal transition from the *hedei* to *sculptilis* zones, Märss (1992: 210) mentioned '*Poracanthodes porosus*', but not *Poracanthodes punctatus* nor '*P. aff. punctatus*' sensu Märss 1986b (see Burrow et al. in press; see also Valiukevicius 1998: 43). The first-named has now been redefined as *Radioporacanthodes* nov. gen. *porosus*, type species of the porosiform poracanthodid acanthodians (Vergoossen in press b;

see also Vergoossen 1997) and is probably a Late Pridolian taxon preceded by several older porosiform taxa (see Vergoossen 1999, in prep.). *P. punctatus* is the type species of the punctatiform poracanthodids (Vergoossen in press c; see also Vergoossen 1997).

Porosiforms have, so far, not been found in the NRS residue from Helvetesgraven and have not been reported from the Burgsvik Sandstone and Oolite Beds on Gotland either (Märss 1992); their absence might be due to environmental factors (cf. Märss 1997). The punctatiform poracanthodids are represented, however, by at least one, but more likely two taxa. This observation favours a simultaneous first appearance of punctatiform and porosiform poracanthodids within the complex of sedimentary rocks of the *A. hedei* Event in the Baltic region of Laurussia.

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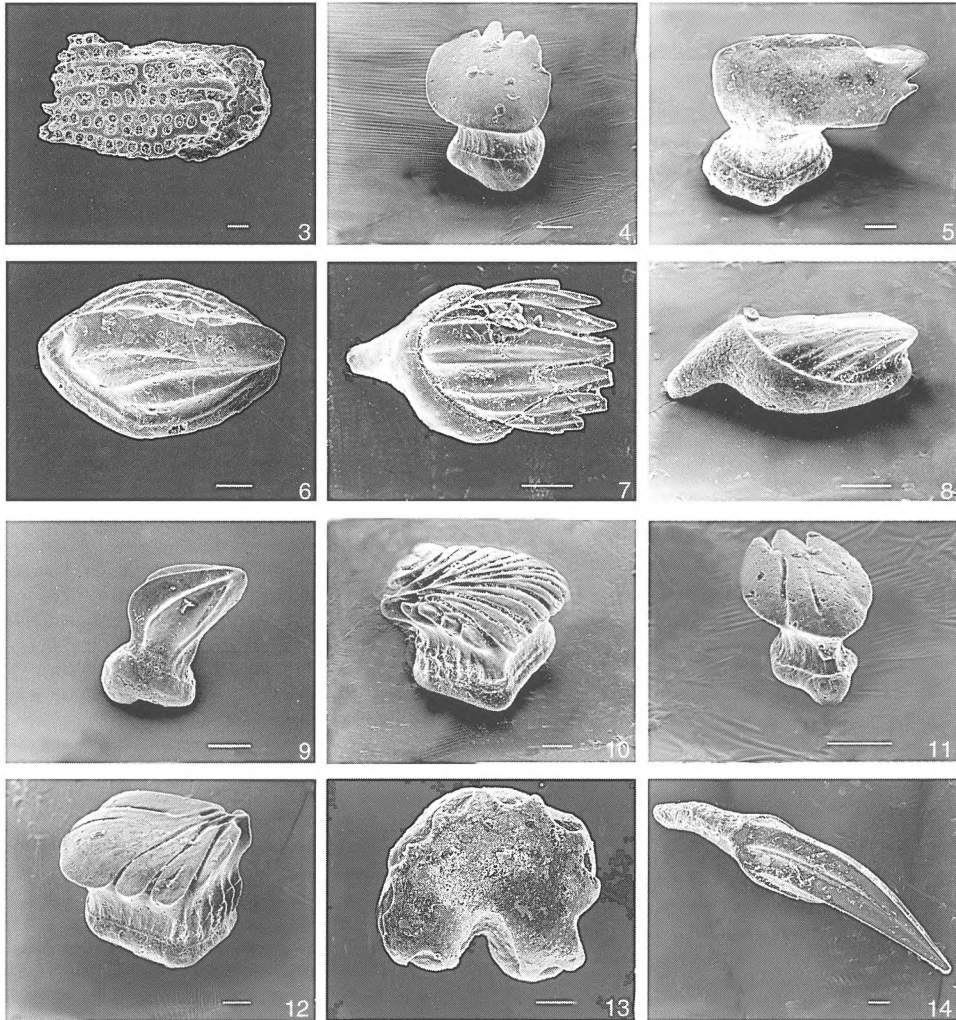


Plate I. Late Silurian microfossil fish specimens are from Helvetesgraven. Scale bars equal 100 OU. Figure 3: cf. *Hemicyclaspis*, crown view, P 8800. Figure 4: *Thelodus parvidens*, smooth crowned scale with indented posterior crown, anterior view, P 8801. Figure 5: *T. parvidens*, pugniformis variant, lateral view, P 8802. Figure 6: *T. parvidens*, bicostatus variant, crown view, P 8803. Figure 7: *T. parvidens*, conventional *trilobatus* form, crown view, P 8804. Figure 8: *T. parvidens* = '*T. querceus*' Lehman, lateral view, P 8805. Figure 9: '*T. traquairi*' Gross 1967, lateral view, P 8806. Figure 10: *T. admirabilis*, lateral view, P 8807. Figure 11: *T. sculptilis* (compare Figure 4), anterior view, P 8808. Figure 12: *T. sculptilis*, scale with three slits in the posterior crown, lateral view. These slits lie in continuation of the crown furrows that are deep anteriorly but become very shallow posteriorly. Such specimens pass into *T. admirabilis* scales, P8809. Figure 13: *Loganellia cuneata* sensu Märss 1986b. Cephalopectoral scale that gave passage to a sensory line canal, crown view, P 8809. Figure 14: *L. cuneata*, postpectoral scale, crown view, P 8810.

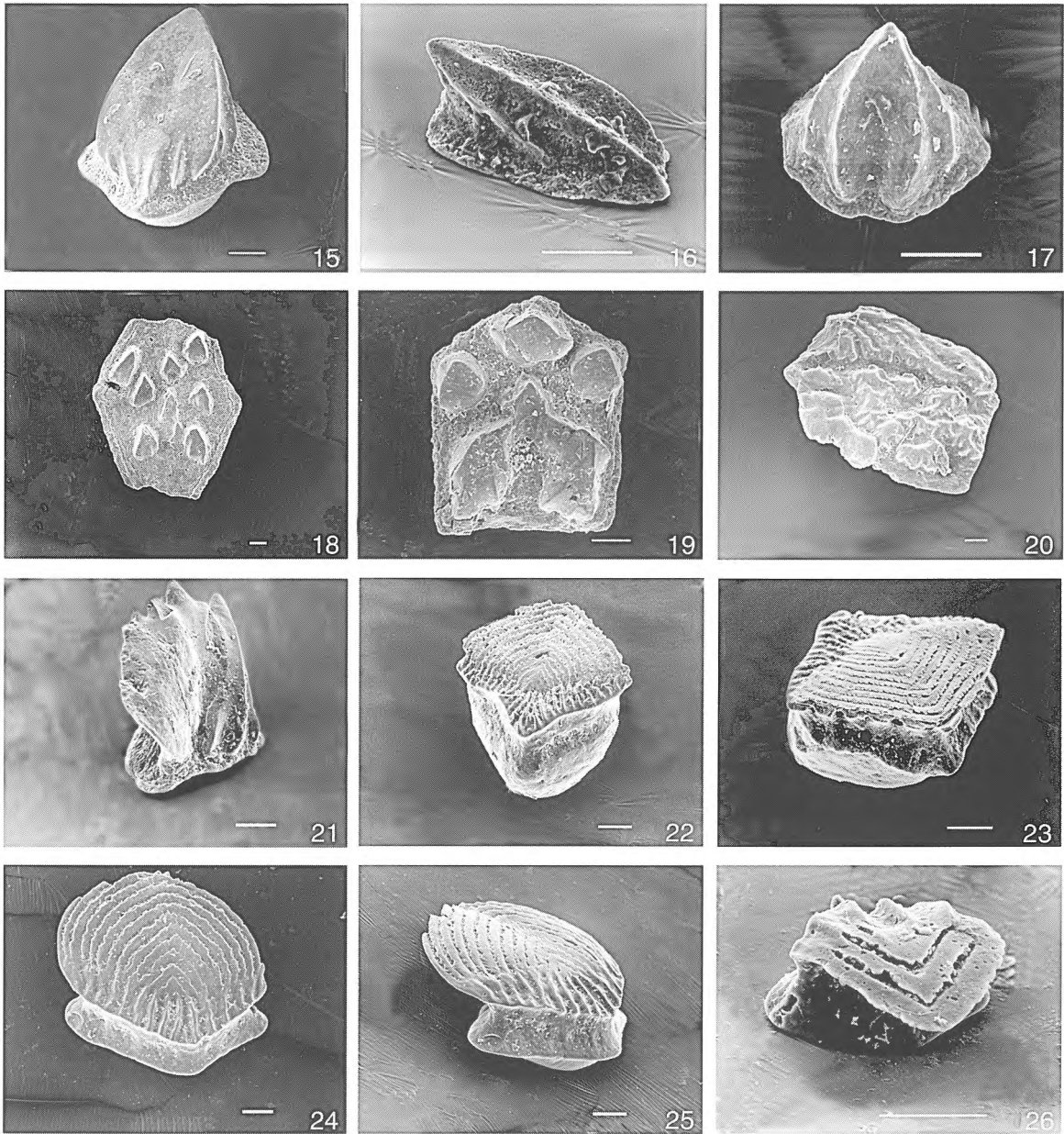


Plate II. Late Silurian microfossil fish specimens are from Helvetesgraven (unless stated otherwise). Scale bars equal 100 OU. Figure 15: *Nostolepis striata* flank scale, anterior view, P 8811. Figure 16: *Nostolepis* sp., 'elegans' form group, lateral view, P 8812. Figure 17: *Nostolepis* sp., 'elegans' form group, anterior view, P 8813. Figure 18: *Tessera stellata*, crown view, P 8814. Figure 19: *Tessera coronata*, crown view, P 8815. Figure 20: *Squama pronia*, crown view. The posterior crown part with stellate ornament is lowermost in the photograph, P 8816. Figure 21: *Squama umbellata*, anterior view, P 8817. Figure 22: *Poracanthodes? lehmani* sp. nov., holotype, anterior view, Tahula beds, Saarema, Estonia, P 8818. Figure 23: *P.? lehmani* sp. nov., holotype, posterior view, Tahula beds, Saarema, Estonia. Figure 24: *P.? lehmani* sp. nov., paratype, anterior view, P 8819. Figure 25: *P.? lehmani* sp. nov., same specimen, lateral view. Figure 26: *P.? lehmani* sp. nov., paratype, posterior view, young (?) specimen, P 8820.

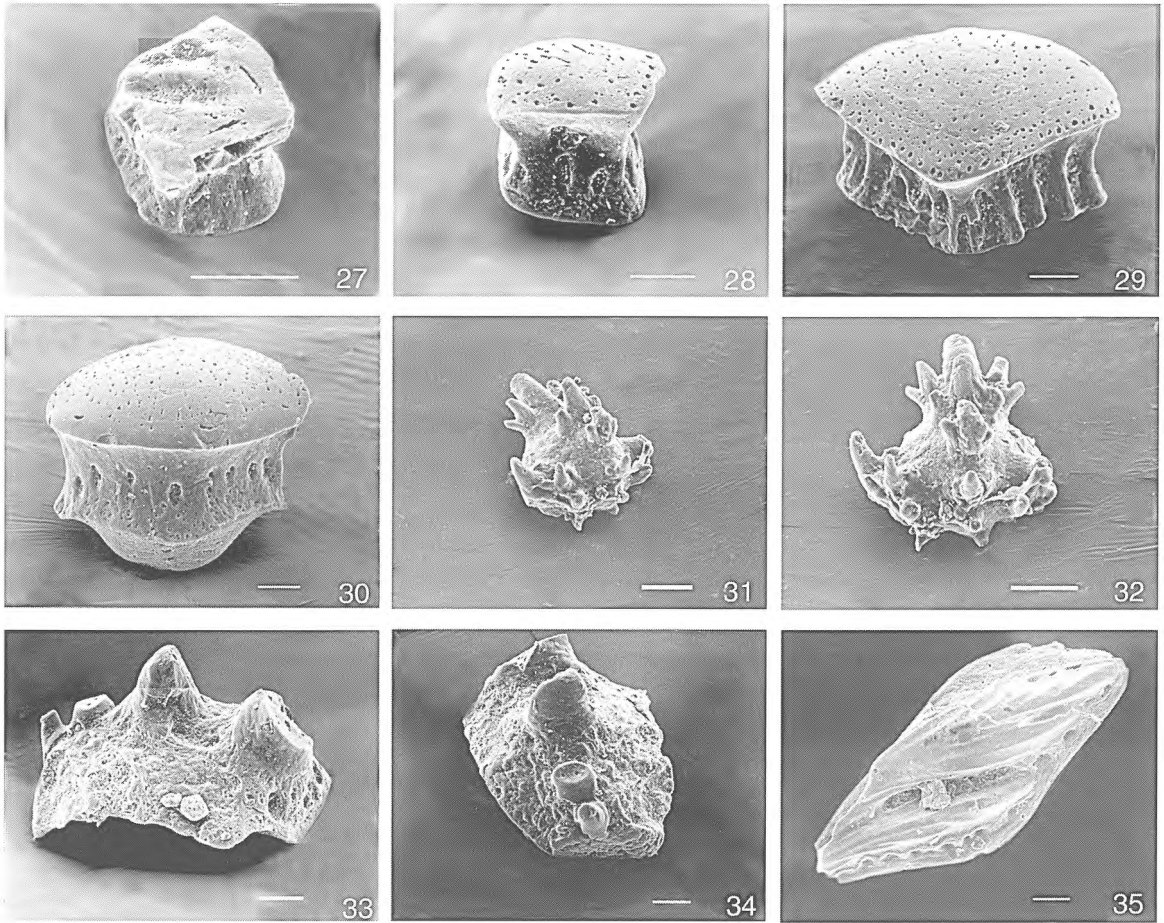


Plate III. Late Silurian microfossil fish specimens are from Helvetesgraven. Scale bars equal 100 OU. Figure 27: *P.?* *lehmani* sp. nov., paratype, latero-posterior view, young (?) specimen, P 8821. Figure 28: *Poracanthodes* cf. *punctatus*, latero-posterior view, young (?) specimen, P 8823. Figure 29: *Poracanthodes* cf. *punctatus*, posterior view, P 8824. Figure 30: *Poracanthodes* cf. *punctatus*, same specimen, anterior view. Figure 31: Ischnacanthid tooth whorl, cf. '*Gomphodus*' sensu Gross 1957, new morphovariant 1, latero-anterior view, P 8825. Figure 32: Same specimen, anterior view. Figure 33: Ischnacanthid tooth whorl, new morphovariant 2, lateral view, P 8826. Figure 34: Same specimen, oral view. Figure 35: *Andreolepis hedei*, flank scale, crown view, P8827.