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A unique Late Silurian *Thelodus* squamation from Saaremaa (Estonia) and its ontogenetic development

Tiiu Märss

Institute of Geology at Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia; Tiiu.Marss@gi.ee

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Abstract. A partly preserved squamation of *Thelodus laevis* (Pander) from the Himmiste outcrop (Saaremaa Island, Estonia) is described. Most of the trunk with a pectoral fin fragment and three fragments of posterior fins are present, while part of the head and the caudal fin are absent. Ontogenetic development of the scale cover of *T. laevis* is explained by comparing it with the squamation of *Lanarkia horrida* Traquair, *Loganellia scotica* (Traquair) and a modern fish. It is supposed that newly forming trunk scales of early juvenile *Thelodus* were smooth and rhomboidal. When the individual grew, ridged scales were added between smooth ones in irregular rows in the posterior part of the trunk. Adult individuals were covered with species-specific scales with particular morphology and sculpture of the crown. Co-occurrence of smooth and ridged scales on the trunk in the specimen studied corresponds to a young stage of ontogeny.

Key words: *Thelodus*, Thelodonti, squamation, ontogeny, Late Silurian, Estonia.

INTRODUCTION

During the study of Estonian Silurian osteostracans and the thelodont *Phlebolepis elegans* Pander in the Geological Museum at the University of Tartu, material found by Edmund Bölau at the time of the 2nd World War in the Himmiste Quarry, Saaremaa Island, caught my attention. This collection was recently added to the database of the university museum. The collection comprises over 1000 osteostracan specimens with different degrees of preservation, including shield fragments of *Tremataspis mammillata* Patten, one part and counterpart of its disintegrated tail, many shield pieces of *Dartmuthia gemmifera* Patten, four fragmentary *Saaremaaspis mickwitzi* (Rohon), a few *Tremataspis milleri* Patten, one *Procephalaspis oeselensis* (Robertson), a single *Witaaspis schrenkii* (Pander) shield and three incomplete squamations of the thelodont *Phlebolepis elegans* Pander. It contained also a rock with a patch of scales from *Thelodus laevis* (Pander), which is the focus of this paper.

E. Bölau excavated in Himmiste between 1942 and 1944, thus later than the main material of osteostracans, an anaspid and *Phlebolepis elegans* were collected. It is not exactly known which part of the quarry Bölau's specimens come from, but most possibly from its margins. Some of his material may originate from slabs which were quarried earlier. The rock with the *Thelodus* specimen discussed in this paper is somewhat different from that in which *Phlebolepis* or osteostracans were found: it is comparatively darker grey, argillaceous fine-grained, secondarily dolomitized dolostone, with indistinct horizontal microlamination. In origin, the sediment represents quiet-lagoonal dolomitic mudstone with the admixture of more clay material (Aaloe 1963; Märss et al. 2003).

Twenty-four thelodont species, represented by well-preserved squamations, and three species having smaller patches of scales, survived in the sedimentation processes, have been identified in the Silurian of Estonia, Scotland, northern Canada and Norway, and in the Lower Devonian of northern Canada and southern Britain (see for references Märss et al. 2007). *Thelodus* is very rare, with specimens of two species known so far. Fragments of squamations of *Thelodus macintoshi* Stetson and *Thelodus inauditus* Märss, Wilson & Thorsteinsson show some variations in scale morphology. *Thelodus macintoshi* was identified in the Long Reach Formation (Upper Llandovery, Lower Silurian) near Nerepis in New Brunswick, eastern Canada (Stetson 1928). The largest fragments measure 30 cm × 17 cm and 25 cm × 16 cm, which, according to Stetson's estimation, gives the total length of the animal up to 55 cm. Turner (1986) redescribed that material and showed that Stetson's taxon was a heterogeneous specimen comprising scales of two thelodonts, *Thelodus* and *Paralogania*. She (ibid.) synonymized *T. macintoshi* under *Thelodus parvidens* Agassiz. Nevertheless, the taxonomic affiliation of *T. parvidens* or its geological age (Late Llandovery) are not yet sure. According to Turner (1986), *T. macintoshi* reached the length of about 1 m, and has trilobatiform and bicostatiform scales in addition to smooth rhomboidal scales with numerous riblets on the lower neck.

Thelodus inauditus is preserved as a small patch of scattered scales in the rock from the Thorsteinsson Quarry in Cape Phillips (northeast Cornwallis Island, Canadian Arctic) in the Cape Phillips Formation (middle Sheinwoodian, lower Wenlock) (Märss et al. 2002, 2006). The size of the squamation fragment, which most probably comes from the anterior part of the body, is 6.3 cm × 3.0 cm. The scales are rhomboidal, with either a smoothly convex surface or with a few notches anteriorly and antero-laterally on both sides of the scale crown, and are thought to be of the transitional morphological scale type.

The *Thelodus* specimen from the Himmiste Quarry is preserved as an elongate cross-shaped patch of squamation. This specimen is not good for any anatomical study but is valuable for elucidation of scale variability of this taxon as well as other *Thelodus* species, and for comparative study of the ontogenetic growth of the exoskeleton.

METHODS

Drawings of small sets of the best-preserved scales were made from thirteen areas in the squamation. In a few cases a more anterior scale was removed to reveal a complete more posterior one. Small portions of scales were removed for thin-sectioning and SEM imaging. The scales were drawn with a drawing apparatus for stereomicroscope Leica M165C. Thin sections of the scales were photographed with a Nikon Digital Sight DS-Fi1 and the SEM images were taken with Zeiss EVO MA15.

The specimen is housed in the Geological Museum of the Natural History Museum, University of Tartu, under the collection number TUG 1025-1052 followed by the number of thin-sectioned and SEM-imaged scales.

DESCRIPTION

Squamation

The preserved squamation is about 3.4 cm long and 1.4 cm wide (Fig. 1A). Most of the trunk with a pectoral fin fragment and three fragments of posterior fins are present, while part of the head and the caudal fin are absent. It has almost no natural margins, except for a short undamaged portion of the left margin of the body (central lower part in Fig. 1A). The scales are small, with the measured length of 0.17–0.37 mm and width of 0.11–0.23 mm, yellowish to brown, very thin and fragile. Most scales are in crown view, and only a few in side or base view. Many scales have lost their crowns and only necks in cross section are exposed. Most of the scales are oriented in a certain direction, so the orientation of the fish body is distinct (Fig. 2). The scales are concentrated in some areas and scattered in others. In some places the squamation has cavities with dolomite crystals around the scales and inside the scale pulp cavities. In such places where the scale itself is destroyed the dolomitic infilling is still preserved.

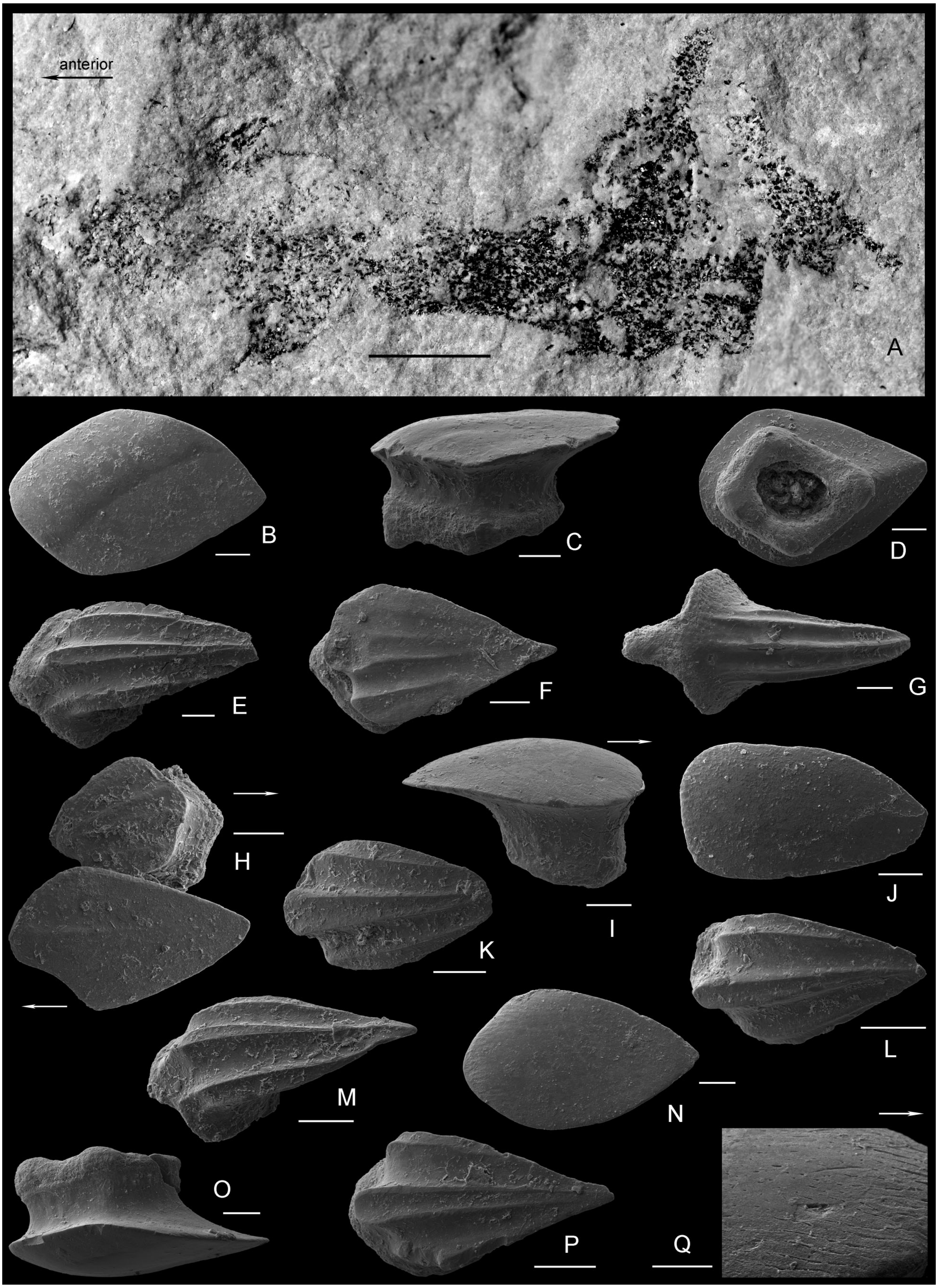
Morphology and sculpture of the scales

The scales were described from thirteen areas in the squamation. The trunk scales in this specimen are quite symmetrical. The crowns are rhomboidal in shape. The crown surface can be (a) entirely smooth and flat or with the anterior margin turned downwards, or (b) with longitudinal ridges and shallow furrows. The neck is wide and distinct, without any vertical riblets.

Area 1 (Figs 2, 3:1) is covered with small elongate scales, with the crown length of 0.29–0.33 mm and width 0.15–0.16 mm. The crown has a median ridge and one to two more ridges on both sides. The ridges are separated by furrows. The median ridge may have a short shallow furrow or be smooth and converge posteriorly into an apex. Lateral ridges, which are shorter, also form a small apex. Such scales have a trilobate appearance. The base is rhomboidal but may have a long horizontal or vertical spur anteriorly. The length of the horizontal spur is 0.11–0.16 mm; the width of the base is 0.14–0.18 mm.

The scales from area 2 (Figs 2, 3:2) are in base view. They are robust and solid, with the crown length of 0.32–0.37 mm and width 0.18–0.23 mm. The rhomboidal base is situated anteriorly on the scale; it is narrower than the crown. The large to medium-sized pulp opening is surrounded by a wall. A smooth ridge stretches from its posterior corner towards the posterior apex of the crown.

Fig. 1. *Thelodus laevis* (Pander), specimen TUG 1025-1052. **A**, Preserved squamation; **B–Q**, SEM images of extracted scales of the same specimen, from Himmiste Quarry, Saaremaa, Estonia; Himmiste Beds of the Paadla Stage, Ludlow, Upper Silurian. Scales B–G are from area A; scales H–M are from area B; scales N–P are from area C; Q is close-up of I showing ultrasculpture (anterior is on the right). Areas A–C are shown in Fig. 2. Arrows point to the anterior. Scale bar is 5 mm for the squamation, 50 μm for scales B–P, and 20 μm for the scale close-up in Q. B, TUG 1025-1052-28; C, TUG 1025-1052-29; D, TUG 1025-1052-26; E, TUG 1025-1052-19; F, TUG 1025-1052-30; G, TUG 1025-1052-14; H, TUG 1025-1052-9&10; I, TUG 1025-1052-3; J, TUG 1025-1052-5; K, TUG 1025-1052-12; L, TUG 1025-1052-8; M, TUG 1025-1052-7; N, TUG 1025-1052-21; O, TUG 1025-1052-22; P, TUG 1025-1052-20; Q, close-up of TUG 1025-1052-3.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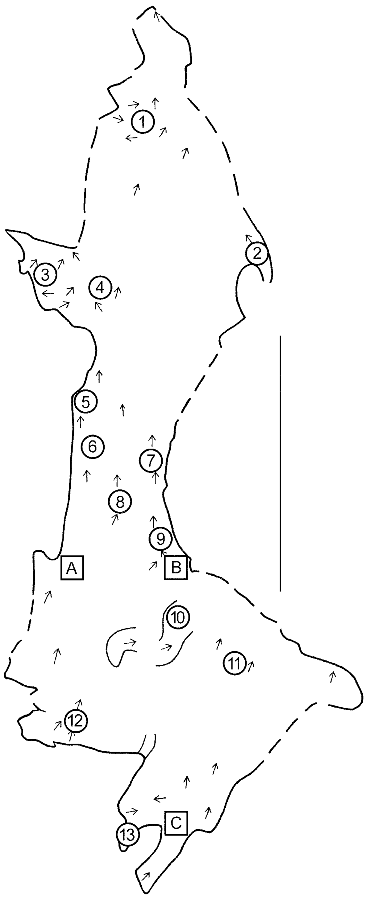

Fig. 2. *Thelodus laevis* (Pander), specimen TUG 1025-1052. Areas of scale samples drawn in Fig. 3 are indicated by numbers 1–13, those in SEM photos in Fig. 1 are shown by capital letters A–C. Arrows point to the anterior of scales. Scale bar 1 cm.

Area 3 (Figs 2, 3:3) exhibits so-called 'transitional scales'. They are small (0.17–0.30 mm long and 0.18–0.23 mm wide) and have a rather wide median ridge which can be smooth or with a shallow furrow. On either side of the median ridge there can be up to two ridges, all of which are separated from each other with furrows that are deep and steep anteriorly but shallow posteriorly. The furrows and ridges occur on the anterior 1/3–1/2 of the crown length, while the posterior part of the crown surface is smooth and the crown ends with a pointed apex.

Area 4 (Figs 2, 3:4) is covered with elongate scales with a crown that is 0.29–0.31 mm long and 0.13–0.18 mm wide. The base is narrower than the crown, and a few cuneiform scales have a short spur anteriorly. The division of the crown into three areas is distinct as the median ridge is wide, sometimes protruding anteriorly. The median ridge is smoothly rounded and separated from lateral ridges by wide and shallow furrows. The surface of the wide median ridge is smooth. Some scales have narrower median and lateral ridges and steeper furrows between them, while the ridges are narrower than the furrows. In such scales the median area stretches far back to form the posterior apex.

Area 5 (Figs 2, 3:5) represents the scales from the marginal part of the squamation. The margin itself consists of a scale row in lateral view, but towards the middle of the body the scales are in crown view and exhibit two main sculpture types: (1) the crown surface is covered with a short median and two lateral longitudinal ridges with furrows between ridges anteriorly; (2) the scales have a flat and smooth main surface or indistinct shallow furrows. The crown length is 0.26–0.32 mm and width 0.19–0.23 mm.

The scales in area 6 (Figs 2, 3:6) have a ridged crown with a median and two rather wide and high lateral areas, all three extending far posteriorly. The length of the scales is 0.25–0.28 mm, the width 0.12–0.15 mm.

Area 7 (Figs 2, 3:7) and area 8 (Figs 2, 3:8) display scales similar in morphology and sculpture to the scales in areas 4 and 6. The length of the scales in area 7 is 0.26 mm, the width 0.14–0.16 mm. The length and width of the scales in area 8 are nearly the same as in areas 4 and 7, although in area 8 some scales are just slightly bigger (up to 0.32 mm long). Again, the scales exhibit two types of sculpture: (1) the surface is smooth and flat with the anterior margin smoothly curved downwards or (2) the crown surface is ridged with the median area protruding anteriorly. All scales have a pointed posterior apex.

Two different scale crowns are obvious in area 9 as well (Figs 2, 3:9). One scale is elongate and well ridged, about 0.37 mm long and 0.23 mm wide, the other is smooth and has weak furrows. The SEM-imaged scales from areas A, B and C (Figs 1B–Q, 2) are similar to those from areas 4 and 7–9; Fig. 1G is a cuneiform scale from area A.

The scales in area 10 (Figs 2, 3:10) have a smooth flat main surface and are turned down anteriorly. The crown shape is quadrangular to oval, and 0.24–0.35 mm long and 0.20 mm wide. Such scales are accompanied by ridged scales, which in this area seem to be arranged in a row.

The scales in area 11 (Figs 2, 3:11) are similar to those in areas 4 and 6–9 but smaller. The length of the scales is 0.25–0.30 mm and width 0.11–0.19 mm; the length of the base spur is 0.05 mm.

The scales in area 12 (Figs 2, 3:12) are similar in size and sculpture to the scales in area 10. Also here the ridged scales form indistinct rows. The scale marked with an 'X' has a vertical base and very narrow ridges on the crown surface. The ridges seem also to have an axial furrow.

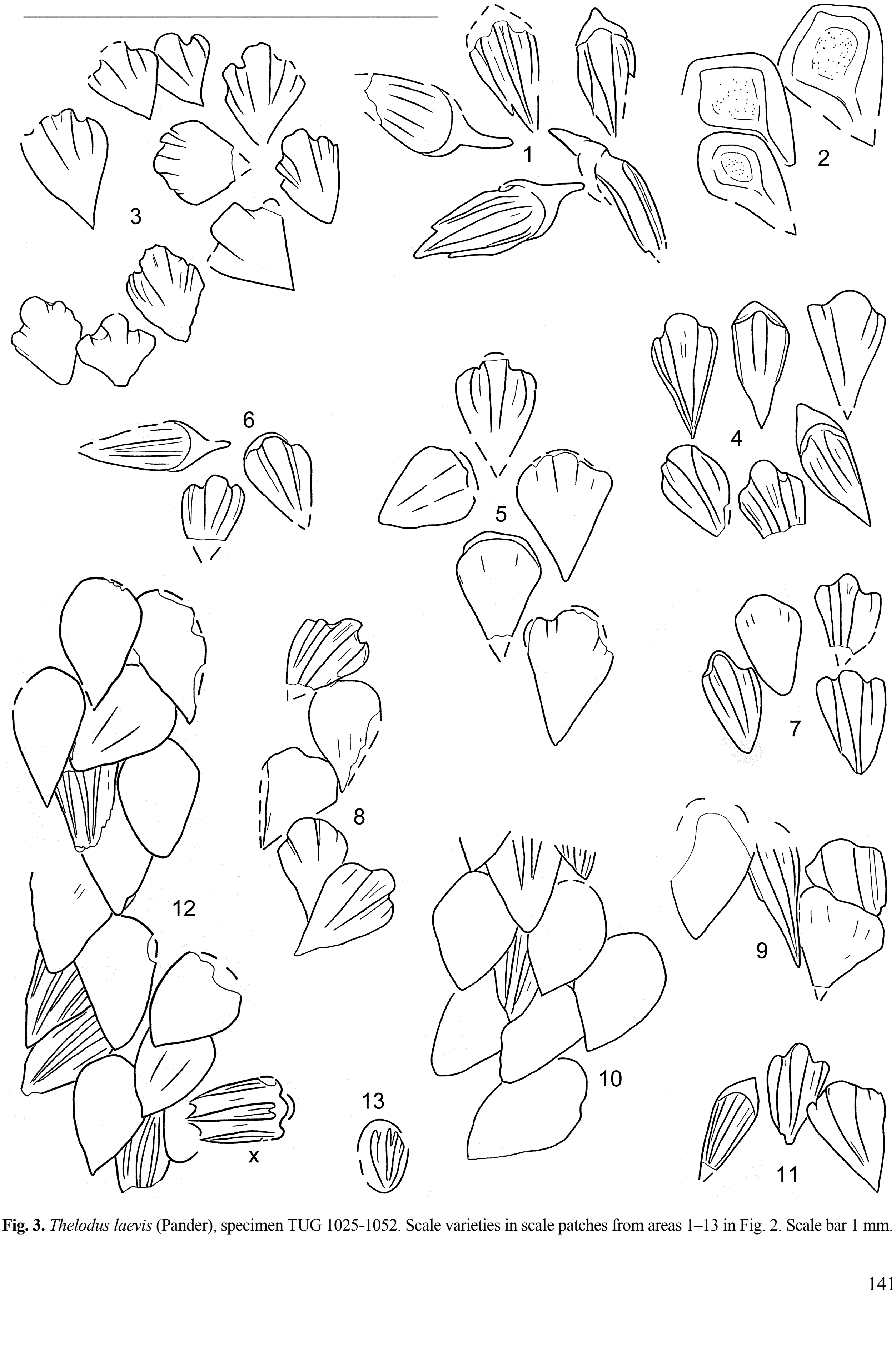

Fig. 3. *Thelodus laevis* (Pander), specimen TUG 1025-1052. Scale varieties in scale patches from areas 1–13 in Fig. 2. Scale bar 1 mm.

Area 13 (Figs 2, 3:13) exhibits at least one oval bicostatiform scale with two long ridges and one short ridge on the crown. The length of the scale is 0.17 mm, the width 0.11 mm.

Ultrasculpture

The ultrasculpture (Fig. 1Q) is preserved on the anterior part of scale crowns and is formed of longitudinal regular short microscopic furrows, subparallel to each other. Such furrows occur posteriorly of the crown as well, but here they have a more irregular arrangement. Microscopic small pores are also observed in the superficial crown layer.

Microstructure

The microstructure is characterized by the wide pulp cavity of the scales, growth layers, dentine tubules and the enameloid layer in the crown, dentine tubules in the neck and criss-cross and Sharpey fibre tubules in the base (Fig. 4A–F). The dentine tubules are sinuous in vertical longitudinal cross section, especially in the central part of the crown (Fig. 4A, B). There, very soon after emerging from the pulp cavity, dentine tubules curve first to the anterior and then to the posterior of the scales, ending as straight, fine tubules under or in the enameloid layer (Fig. 4A, B). The dentine tubules branch in 5–8 levels in the middle of the crown; the number of dark growth lines there is about the same. The dentine tubules are fairly wide and straight in the posterior part of the crown in horizontal scale view (Fig. 4D–F). In the neck the dentine tubules are sparse and irregular (Fig. 4A, B). Tubules for the Sharpey fibres in the base are weak. Strong criss-cross fibre tubules in the base are seen in some horizontal thin sections (Fig. 4C).

DISCUSSION

Identification of the specimen TUG 1025-1052 required detailed comparison of scale morphology and histology. Three thelodontiforms, *Thelodus laevis* (Pander), *T. carinatus* (Pander) and *Oeselia mosaica* Märss, have all been identified from isolated scales occurring in the same Himmiste Quarry. The scales of *Thelodus* species here are variously ridged and mostly bigger than those in TUG 1025-1052: up to 1.4 mm in *T. laevis* and up to 1.5 mm in *T. carinatus*. Small scales similar to our material are definitely present in many acetic acid treated rock residues, but they are easily overlooked due to their very small size and because they occur together with much coarser and more conspicuous scales and other bony fragments, which may preoccupy all the researcher's attention.

The scales of *O. mosaica*, figured in Märss (2005), are very small; the length of the scales is between 0.20 and 0.45 mm. Another *Thelodus* species, *T. calvus*, with very small scales, has been described from the Wenlock of the Severnaya Zemlya Archipelago (Märss & Karatajūtė-Talimaa 2002). Its scales are up to 0.4 mm long, but an extremely high neck makes it different from TUG 1025-1052. Furcacaudids from the Silurian and Devonian of the Mackenzie Mountains, northern Canada, have also tiny scales but their sculpture is not comparable with scales of our specimen (Wilson & Caldwell 1998, fig. 3). The scales of three *Barlowodus* species from the Canadian Arctic are also very small, but again, their crown morphologies are completely different (see Märss et al. 2006, pls 25, 26). According to the scale size range, the specimen could belong to *Oeselia* but their scale bases are different: in *Oeselia* the base is wider than long, while in TUG 1025-1052 it is usually more longitudinally stretched. The microstructure of these two taxa is different as well. In TUG 1025-1052 the perpendicular fibre tubules are weak and the scales have intrinsic and extrinsic fibre tubules (criss-cross lattice tubules), which are not noticed in *Oeselia* but are known in three *Barlowodus* species. The dentine tubules in TUG 1025-1052 are bent in the middle of the crown like in *T. laevis* and *T. carinatus*. *Thelodus carinatus*, however, has much weaker bending of tubules than *T. laevis*. The crown surface sculpture of *T. carinatus* is composed of anterior gentle ridges and downstepped margins, while *T. laevis* has longitudinal flat-topped ridges. The ultrasculpture in TUG 1025-1052 consists of short furrows and pores in the superficial layer of the crown. In Thelodonti such pores are found in *T. laevis* and not in *T. carinatus*, *T. calvus* and *O. mosaica*. *Oeselia mosaica* has ultrasculpture of honeycomb-like pattern. On the basis of such features as longitudinally ridged scales, bending dentine tubules and pores in ultrasculpture, the specimen TUG 1025-1052 is identified as *Thelodus laevis* (Pander).

Thelodus laevis (Pander) has so far been known only as disarticulated scale material. It is widely distributed in the outcrop and drill core material of the Baltic (Upper Wenlock–Lower Ludlow, Lower–Upper Silurian of Estonia, Latvia, Lithuania and Gotland Island) and elsewhere. A wide variety of scales of *T. laevis* and *T. carinatus* has been illustrated in publications of Pander (1856), Rohon (1893), Hoppe (1931), Gross (1947, 1967), Karatajūtė-Talimaa (1978), Märss (1986a) and Fredholm (1988) (note that Gross and Karatajūtė-Talimaa did not recognize *T. carinatus*). Data on *T. laevis* and *T. carinatus* are summarized in Märss et al. (2007).

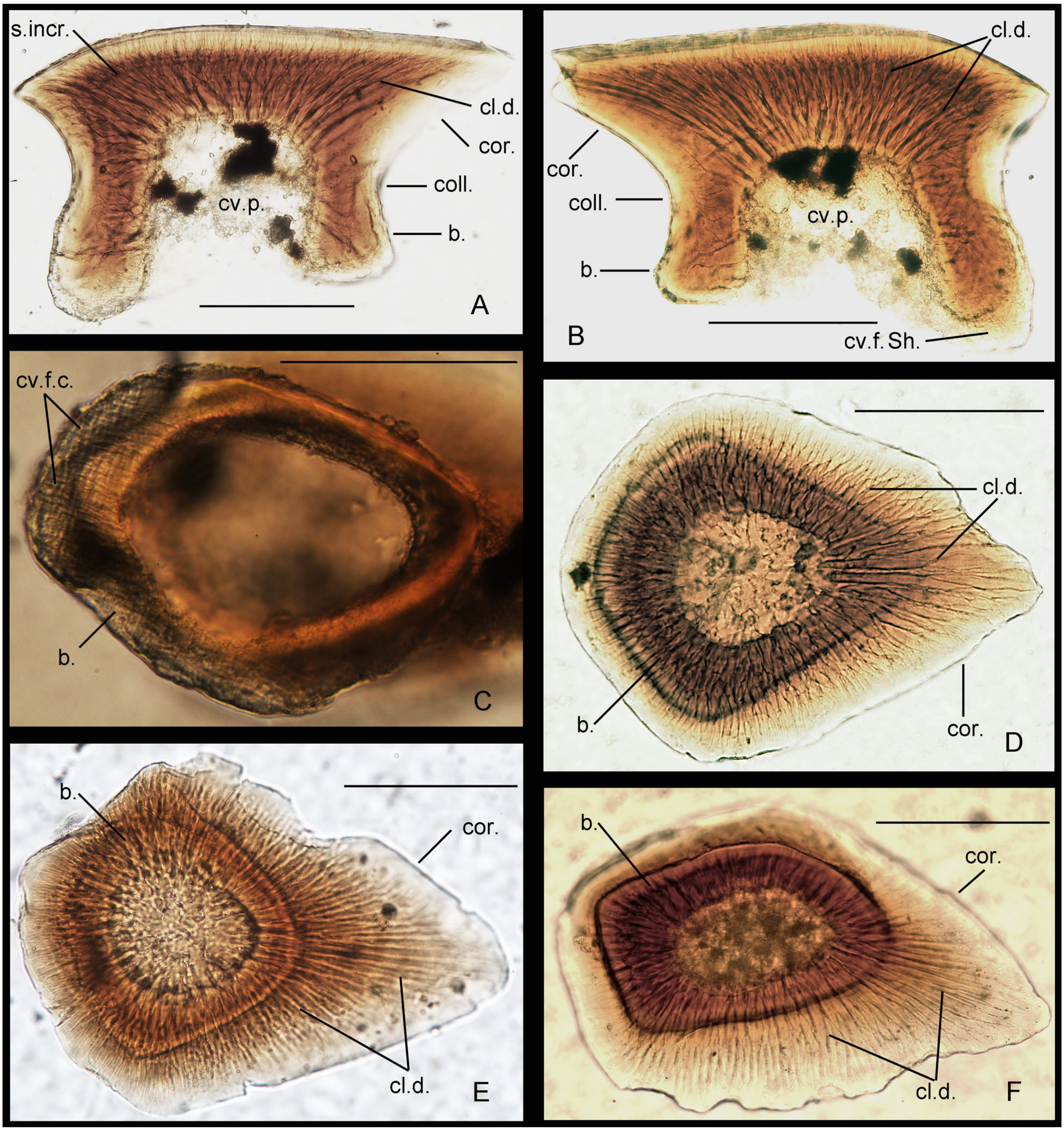

Fig. 4. *Thelodus laevis* (Pander), specimen TUG 1025-1052. Microstructure of scales with a smooth crown surface. **A**, **B**, scales in vertical longitudinal section; **C–F**, scales in horizontal section (C is on the level of the base). Scale bars 100 µm. A, TUG 1025-1052-36; B, TUG 1025-1052-37; C, TUG 1025-1052-38; D, TUG 1025-1052-39; E, TUG 1025-1052-40; F, TUG 1025-1052-41. Abbreviations: cor., crown; coll., neck; b., base; cl.d., dentine tubule; cv.p., pulp cavity; s.incr., growth lines; cv.f.Sh., tubules for Sharpey fibres; cv.f.c., tubules for lattice fibres.

The most surprising find in articulated TUG 1025-1052 was the co-occurrence of scales with ridged and smooth crown surfaces in the same body areas (Figs 1B–P, 3:4, 7–12), which suggested that this specimen represents an unknown taxon with a specific pattern of scale morphological types and arrangement. Based on current thought, the body of each conventional thelodont taxon is covered by particular types (morphotypes) of the scales: rostral, cephalo-pectoral, postpectoral, precaudal and pinnal scales. Smooth scales cover the head and leading edges of fins, while ridged scales cover the more flexible body parts, posteriorly of the fins and trunk (with some variations in Gross 1967; Karatajūtė-Talimaa 1978; Turner 1984; Märss 1986a, 1986b; Märss & Ritchie 1998; Blom 1999; Märss et al. 2007). In furcacaudids the scale morphotypes are different because of their different body form (Wilson & Caldwell 1998). The scale morphotypes have characteristic features but transitional forms from one type to another are also found. A mixture of scale morphotypes, co-occurrence of smooth scales with ridged ones in one area, is not observed in most of the known adult thelodont taxa (except *Lanarkia horrida*). Such scale combination in our specimen requires explanation.

The development of the squamation in the ontogeny of two thelodonts, *Lanarkia horrida* Traquair and *Loganellia scotica* (Traquair), is well known (Turner 1991; Märss & Ritchie 1998). According to theory, the formation of the squamation started in an early juvenile stage (in *Lanarkia* the smallest specimen available for study was 33 mm and the largest 162 mm long; Märss & Ritchie 1998). Its body surface was first covered with relatively large (in comparison with the whole body), vertical, smooth and conical, trumpet-shaped scales, which were of nearly equal size anterior to the trunk but laterally compressed, posteriorly pointed and finely striated behind the pectoral fins. In 45–50 mm long specimens these ‘trumpets’ appear to form weak rostro-caudally directed rows. Small ridged scales occur irregularly between them. On the caudal peduncle small scales occupy most of the space. In 153 to 162 mm long adult specimens, smaller scales are placed in a well-packed pattern, which may form indistinct rows between the obvious rows of ‘trumpets’. Also in *Loganellia* (with the body length 85–228 mm) the squamation grows by addition of new scales in indistinct longitudinal rows (Märss & Ritchie 1998).

The development of the squamation in the ontogeny of different recent fishes has been considered by many authors. For example, Reif (1985) investigated the morphogenesis and function of the squamation of sharks, Hill (1971) the appearance of scales and patterns of squamation on an actinopterygian, the spring cavefish (*Forbesichthys agassizii* (Putnam)), Sire & Akimenko (2004) scale development and squamation pattern in another actinopterygian zebra danio (*Danio rerio* (Hamilton)). Burdak (1979) discussed the dynamics of cycloid and ctenoid scales in squamations of the leaping mullet *Liza* (= *Mugil*) *saliens* (Risso). The development of the squamation of this actinopterygian fish begins on the body sides when the fish is less than 1 cm long, and soon, when it reaches 1 cm, the entire body is covered with cycloid scales. Ctenoid scales start to appear on the lower side of the caudal peduncle when the body is 1.40–1.42 cm long, and then appear more anteriorly, first ventrally then dorsally. When the fish is 10 cm long, it has cycloid scales dorsally on the head only; all other body parts are covered with ctenoid scales. Burdak (ibid. p. 125) distinguished stages in the development of the dermal covering as follows: scaleless, primary cycloid, ctenoid, and secondary cycloid stages. The cycloid and ctenoid scales form different stages, which in ontogeny replace each other according to the swimming velocities of each fish.

Our specimen shows some similarities with the squamation pattern development of some actinopterygians, characterizing actively swimming fishes. During thelodont ontogeny the swimming velocity change and the squamation pattern change were possibly related. The scales of *Thelodus laevis* appear to be added in the same way as in *Lanarkia horrida* and *Loganellia scotica*. Smooth scales probably covered the whole body of an early juvenile fish (larvae might have been scaleless). Then ridged scales, the functional-morphologically analogous forms of ctenoid scales, appeared on the posterior trunk, and eventually the smooth scales were replaced by ridged, species-specific scales, except on the head and leading edges of fins, where smooth scales persist; the posterior part of the head carried scales of transitional type. At the same time the scales gradually became larger, i.e. the replacement scales are larger. The criss-cross appearance of fibres in the base may have been characteristic of juvenile scales but also of all taxa which had small scales (e.g. *Barlowodus* species), providing firm attachment of such scales in the skin. During the growth of the scale the criss-cross distribution of attachment fibres in the base of *Thelodus* was replaced by perpendicular fibres. This process is not well studied in thelodonts and needs additional investigation.

The ultrasculpture on scales of our specimen consists of short subparallel microscopic furrows anteriorly on the crown, irregular longitudinal short furrows more posteriorly, and randomly distributed fine pores. The ultrasculpture is not exactly the same as the fine regular longitudinal striation of other thelodont scales. Fine pores do occur in *T. laevis*. In *Oeselia* the ultrasculpture is composed of very different multiangular polygons (honeycomb-like pattern).

The scale varieties in this *T. laevis* squamation help us test the validity of morphological sets established in other thelodonts. The thin nature of all scales points to an ontogenetically young stage of development of this individual. The area of the body preserved is most of the trunk with a pectoral fin fragment and three fragments of posterior fins (dorsal or anal), while part of the head and the caudal fin are absent. The scales from area 2 are definitely the leading edge scales of the pectoral fin. Two portions of a fin in or close to area 10 are not displaced very far from their original position (a small portion of a fin is between areas 12 and 13). The transitional scales in area 3 are from the cephalo-pectoral body part. Trilobatiform and cuneiform scales in area 1 are displaced; these cannot be the anteriormost scales in the squamation of thelodonts and instead should belong either to the more posterior part of the body or fins. A cuneiform scale in area 6 and a bicostatiform scale in area 13 may also be displaced from their original sites. The scales in area 11 are smaller and correctly positioned posteriorly on the body. In summary, in the squamation of TUG 1025-1052 the following morphological scale varieties (or morphological scale types or morphotypes) are present, which are not all in situ: (1) rhomboidal crown and base, smooth crown surface (bigger scales anteriorly on fins, smaller scales on the trunk); (2) rhomboidal, longitudinally ridged crown surface, base directed downwards anteriorly; (3) transitional scale form, notched anteriorly; (4) almost trilobatiform scales; (5) cuneiform scales; (6) bicostatiform scales. On the basis of the occurrence of scale types and comparison of proportions of other articulated thelodonts, we suggest that the total length of the body of our specimen is about 4–5 cm.

CONCLUSIONS

The patch of the scale cover studied belongs to a young *Thelodus laevis* (Pander) specimen. The co-occurrence of smooth and ridged scales in the same scale patch is the result of the ontogenetic development of the squamation. We suppose that the scale morphotypes on the body change during ontogeny, i.e. one type is replaced by another until the individual matures and the squamation obtains the taxon-specific pattern. In juvenile individuals the scales are of one (two) morphotype(s) over the trunk surface, as well exemplified by the Palaeozoic thelodont *Lanarkia horrida* Traquair. The juvenile scales over the trunk were trumpet-shaped in *L. horrida* but most probably the scales were smooth and rhomboidal in *T. laevis*. As the individual grew, new scales, i.e. the ridged scales in *T. laevis*, were added between the smooth ones in irregular rows in the squamation as exemplified by TUG 1025-1052. The ridged scales started to grow on the posterior part of the body (possibly on the caudal peduncle), while at that stage the cephalothorax was still covered with smoother scales. Adult individuals have all area- and taxon-specific types of scales with a wide variety of morphologies and sculptures of the crown as revealed by earlier studies.

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Haruldane *Thelodus*'e soomuskate Hilis-Silurist Saaremaalt ja tema ontogeneetiline arenemine

Tiiu Märss

On kirjeldatud suur soomuskattetükk, mis kuulub noorele isendile *Thelodus laevis* (Pander). On säilinud suur osa kerest koos rinnauime ja tagumiste uimede fragmentidega, kusjuures pea ning sabauim on puudu. Iseäralik on uuritud eksemplari säilinud kereosal siledate ja ribitatud soomuste koosesinemine, mida artiklis on seletatud kui soomuskatte arenemise tulemust ontogeneesi teatud etapil. Juveniilsete kalade keha katab üks või kaks soomuse morfotüüpi, nii nagu see oli võrdluseks toodud Paleosoikumi telodondil *Lanarkia horrida* Traquair (Märss & Ritchie 1998) või ka tänapäevasel kiiruimsel *Liza* (= *Mugil*) *saliens* (Risso) (Burdak 1979). Ka varajuveniilse *T. laevis*'e soomused võisid arvatavasti olla üle keha rombja kuju ja krooni sileda pealispinnaga. Isendi kasvades uued, ribitatud soomused lisandusid soomuskattes siledate vahele ebakorrapäraste ridadena alates keha tagaosast, samal ajal kui pea ja kere esiosa olid endiselt siledamate soomustega kaetud. Sellises arengustaadiumis on meie kirjeldatud eksemplar. Täiskasvanud isendite soomused (ka asendussoomused) on asukoha- ja liigispetsiifilised oma variatsioonidega nii soomuste kujus kui ka skulptuuris, aga ka mikrostruktuuris.