

The morphology and sculpture of ossicles in the Cottidae (Teleostei) of the Baltic Sea

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Abstract. Small to very small ossified structures (ossicles) such as cephalic horns, dermal tubercles, fin-ray rods, lateral-line canal segments, branchial tooth plates and gill-raker tubercles of three species of the teleostean fish family Cottidae inhabiting the Baltic Sea are described and for the first time illustrated with SEM images, with emphasis on their microscopic external features. The morphology and sculpture of these small ossicles notably differ in the three genera, but differences can also occur between males and females, as documented here in *Myoxocephalus scorpius* (Linnaeus). The detailed features of such ossicles are potentially useful for taxonomic identification in sea-floor sediments or gut contents, in a manner similar to their use in many modern and fossil fishes, and may also prove useful as phylogenetically important characters at generic and familial levels.

Key words: dermal ossicles, Cottidae, Cottoidei, Cottiformes, Actinopterygii, Baltic Sea, *Myoxocephalus*, *Triglopsis*, *Taurulus*.

INTRODUCTION

Exoskeletal elements such as scales, tesseræ and bony plates of Palaeozoic jawless vertebrates (agnathans) and fishes with jaws (gnathostomes) have been shown to exhibit characteristic morphology, sculpture and microstructure, all of which have been useful for taxonomic identification, systematics and phylogenetic analyses of these fossils (Gross 1967; Karatajūtė-Talimaa 1978; Märss & Ritchie 1998; Wilson & Caldwell 1998; Wilson & Märss 2004, 2009; Märss et al. 2006, 2007). The shape and the sculpture pattern of the elements also vary, depending on their position on the body, the developmental age of the individual and the habitat of the species or group. The sizes of these microscopic sculpture elements differ greatly. For example, the width of ridges and grooves on agnathan thelodont scales is 20–200 µm, while the length may coincide with the length of the scale (up to 3.7 mm). Smaller sculptural elements, measured in tens of micrometres only and referred to as ultrasculpture by Märss & Gagnier (2001) and Märss (2006), have been illustrated during the last few decades, ever since the scanning electron microscope was available for use. Such a very fine pattern has been observed on agnathans (Gross 1967; Blicek 1982; Märss 1986; Long et al. 1988; Afanassieva 2004), early gnathostomes (e.g. Gross 1973; Schultze 1977; Derycke & Chancogne-Weber 1995;

Bezanosov 2001, 2005) and extant chondrichthyans (Reif 1985), and has been explained as imprints of epidermal cells (Gross 1973) or as a reflection of the composition of the underlying tissue (e.g. Schultze 1977; Gayet & Meunier 1986; Meunier & Gayet 1992). According to Afanassieva (2004), what she called microsculpture (= ultrasculpture of this paper) is a result of the mode of ossification or may have provided better attachment of the epidermis on the scale's surface. Märss (2006) distinguished seven main ultrasculpture types, including microtubercles and united micronodules. She showed that on the one hand similar main types of ultrasculpture occur on the scales of representatives of more than one higher taxonomic group (i.e. the same general type is found in two or more subclasses), but on the other hand, the finer details of the ultrasculpture are more specific and allow the subdivision, for example, of the subclass Thelodonti, into four orders. She also supposed that the different ultrasculpture types within Thelodonti may indicate the polyphyletic nature of this subclass. Nevertheless, the origin of most ultrasculpture types has remained unclear.

The work of Cockerell (1913) convinced ichthyologists of the great value of modern fish scales for identification and classification purposes. His investigations of the scales of Teleostomi were illustrated by many drawings of structural details and photographs.

Similar studies on the morphology of teleostean scales were continued by Taylor (1916), Haque (1955), Batts (1964) and many others.

The introduction of scanning electron microscopy (SEM) initiated a new approach in the study of fish scale morphology and surface ornamentation (DeLamater & Courtenay 1973, 1974; Hughes 1981; Bonwick et al. 1989; Sire & Meunier 1993) and ontogenic development of the ornamentation on scales (Sire 1986). The comprehensive work by Roberts (1993) gave descriptions, SEM investigations and comparison of spined scales of Teleostei, including representatives of the Scorpaeniformes in *Percomorpha sensu lato*. The sculpture characteristics of scales have occasionally been used as taxonomic criteria for cypriniform (Cyprinidae and Cobitidae) fish species (e.g. Kaur & Dua 2004; Jawad 2005; Johal et al. 2006; Jawad & Al-Jufaili 2007), but the fine details of the external surface of scales and tubercles have more often been illustrated in publications on histology (e.g. Sire et al. 1997; Meunier & Brito 2004). Usually, however, when a new fish was discovered, not much attention was paid to its smaller bony ossicles. The ultrasculpture of dermal tubercles becomes visible only at very high magnifications and is therefore even less investigated than the sculpture. An exception was the groundbreaking monograph of Reif (1985), who gave examples of ultrasculpture, including peculiar polygons on the scale surfaces of sharks.

To some extent the material under study in the present work (tiny ossified structures (ossicles), which have survived from chemical preparation of the fresh or preserved fish specimen) bears comparison with the material dealt with in palaeontology (fossilized microremains, which have escaped decay, sedimentation and the processes of fossilization and chemical preparation of the rocks). The main aim of the present study is to examine and describe the small ossicles of Cottiformes from the Baltic Sea, with particular emphasis on their fine surface structures, sculpture and ultrasculpture, at a level of detail that has proven useful in the study of fossil vertebrate microremains. This comparison can be informative for palaeontological work.

One potential benefit for fossil studies is that understanding the morphology and degree of variability of ossicles in living groups of fishes may contribute to our understanding of the possible sources of variation in Palaeozoic taxa. For example, in palaeoichthyology no differences have yet been recognized in scale shape, sculpture or ultrasculpture between male and female specimens, partly because assigning the fossils to male and female sexes usually has no objective basis, whereas such a basis exists for fresh and preserved specimens of recent fishes. Similarly, for ancient fossil species little is known about how characteristic features of scales may

change in different fish habitats and populations, whereas such effects can be observed in recent fishes (e.g. Poulet et al. 2004).

The results of this investigation might serve for several purposes in ichthyology: for analysis of feeding preferences of fishes (while studying their stomach content), for determination of fish migrations (e.g. Daniels & Peteet 1998), for taxonomic and systematic studies and for phylogenetic analyses. The microscopic ossicles studied here can provide much of the same kind of taxonomic information as available under ideal circumstances from the study of fish otoliths (e.g. Assis 2003), but ossicles and otoliths can be recovered in different preservational situations. Microremains obtained from drill cores of relatives of modern fishes can help elucidate the formation of the fish fauna of the Baltic Sea during different phases of its development. Such data can also show the content and abundance of fishes in the fresh water of the Baltic Ice Lake through the Preboreal brackish phase of the Yoldia Sea and freshwater *Ancylus* Lake stages, and the brackish-water *Litorina* Sea Stage. The results obtained can be utilized also in archaeology. Different fish and seal bones have been used in archaeological studies (Lõugas 1997, 1999; Paaver & Lõugas 2003), but these are never as numerous as microscopic external elements, denticles, tubercles, scales, etc. of fishes.

This paper deals with the dermal tubercles and other ossicles of representatives of three genera of the family Cottidae found in the Baltic Sea. The results of the study were first reported during the 13th European Congress of Ichthyology in Klaipeda in 2009. Short descriptions of the units (within Scorpaeniformes) are given in Märss et al. (2009).

Cottidae have at times been classified within the order Scorpaeniformes in the suborder Cottoidei, superfamily Cottoidea (e.g. Yabe 1985), but inclusion in Scorpaeniformes is controversial (Nelson 2006). Recent molecular studies suggest that cottoids are not close to Scorpaeniformes (e.g. Shinohara & Imamura 2007), and Wiley & Johnson (2010) most recently classified the former Cottoidei in a separate order Cottiformes. The families Cottidae (possibly not monophyletic; Smith & Wheeler 2004), Cyclopteridae, Liparidae, Psychrolutidae and Agonidae (also possibly not monophyletic), among others, are included within the suborder Cottoidei. Descriptions of comparable ossicles of selected species of Cyclopteridae and Liparidae are given in Märss et al. (accepted), and of other fish groups in two forthcoming papers, one treating the Gasterosteiformes and Syngnathiformes and the other, the Pleuronectiformes, in series. For the present study, the fish specimens were provided and terminology was corrected by H. Š. and T. S., the chemical preparation and some of the SEM

images were done by J. L. and T. M., the osteological and anatomical terminology and English text were revised by M. W. and the ossicles were described by T. M. The material was discussed by all authors.

MATERIAL AND METHODS

The detailed structure of small dermal and other ossicles including dermal tubercles, tooth plates and other very small elements was studied, described and compared in 19 specimens representing three species of the family Cottidae from the Baltic Sea (see Table 1). The three species, each the only representative of its genus in the Baltic Sea, are the fourhorn sculpin *Trigloopsis quadricornis* (Linnaeus, 1758), the shorthorn sculpin *Myoxocephalus scorpius* (Linnaeus, 1758) and the longspined bullhead *Taurulus bubalis* (Euphrasén, 1786). A fourth cottid in the Baltic Sea, the European bullhead *Cottus gobio* Linnaeus, 1758, was not included in the study because of insufficient material. The fishes were caught with the gillnet or pelagic trawl in the course of commercial trawl catches and monitoring of fish catches between April 2008 and April 2009. Geographically, the material originates from east of Osmussaar Island and the vicinity of Krassi and Pakri islands (Gulf of Finland), from Küdema Bay (northern Saaremaa), from the Väike Vain Strait (Väinameri), from the vicinity of Ruhnu Island and from the deeper waters of this island (the Ruhnu Deep, Gulf of Riga) (Fig. 1). Both male and female



Fig. 1. Location of fishing grounds. 1, vicinity of Krassi and Pakri islands; 2, east of Osmussaar Island; 3, Küdema Bay; 4, Väike Vain Strait; 5, vicinity of Ruhnu Island; 6, Ruhnu Deep southeast of Ruhnu Island.

specimens of *Trigloopsis quadricornis*, *M. scorpius* and *Taurulus bubalis* were represented; the sex of one specimen of both *Trigloopsis quadricornis* and *Taurulus bubalis* remained unidentified.

The fishes were preserved in 20% salt solution or in 70–96% ethanol, with the concentration depending on fish size. It was important to keep the salt solution concentration as low as possible to avoid the formation of salt crystals, which would break the bony material into pieces. Because of the formation of ice crystals the

Table 1. Material studied

Fish	Coll. No.	Male (M); female (F)	Total length, cm	Date of catch	Location	Depth, m
<i>Trigloopsis quadricornis</i>	GIT 584-15	F	30.0	07.05.08	Vicinity of Ruhnu Island	7.5
<i>T. quadricornis</i>	GIT 584-16	Unidentified	Not measured	04.04.08	Väike Vain Strait	3
<i>T. quadricornis</i>	GIT 584-31	F	22.0	06.11.08	Vicinity of Ruhnu Island	3
<i>T. quadricornis</i>	GIT 584-40	F	27.3	10.01.09	Ruhnu Deep	47
<i>T. quadricornis</i>	GIT 584-41	F	33.1	10.01.09	Ruhnu Deep	47
<i>T. quadricornis</i>	GIT 584-42	M	20.8	10.01.09	Ruhnu Deep	47
<i>T. quadricornis</i>	GIT 584-43	F	20.0	10.01.09	Ruhnu Deep	47
<i>T. quadricornis</i>	GIT 584-44	M	23.6	10.01.09	Ruhnu Deep	47
<i>T. quadricornis</i>	GIT 584-55	M	21.5	25.04.09	Vicinity of Krassi Island	10
<i>Myoxocephalus scorpius</i>	GIT 584-8	M	22.0	29.04.08	East of Osmussaar Island	20
<i>M. scorpius</i>	GIT 584-27	?F	19.7	11.10.08	Küdema Bay	17
<i>M. scorpius</i>	GIT 584-34	F	20.5	29.11.08	Küdema Bay	17
<i>M. scorpius</i>	GIT 584-56	F	18.0	25.04.09	Vicinity of Krassi Island	10
<i>M. scorpius</i>	GIT 584-57	M	14.5	25.04.09	Vicinity of Krassi Island	10
<i>M. scorpius</i>	GIT 584-72	F	28.8	28.04.09	Vicinity of Pakri Island	10
<i>Taurulus bubalis</i>	GIT 584-12	M	8.5	29.04.08	East of Osmussaar Island	3
<i>T. bubalis</i>	GIT 584-58	F	9.5	25.04.09	Vicinity of Krassi Island	10
<i>T. bubalis</i>	GIT 584-59	F	9.0	25.04.09	Vicinity of Krassi Island	10
<i>T. bubalis</i>	GIT 584-60	Unidentified	7.5	25.04.09	Vicinity of Krassi Island	10

fishes could not be kept in a freezer either. Fish bodies were washed to remove extraneous material such as loose scales of other taxa, sand grains, etc., and measured. At the beginning of this work, the very first specimens examined were skinned entirely, but later smaller skin pieces were taken for more detailed study. The positions of skin samples were marked, skin pieces were removed and put into a solution of 30% hydrogen peroxide (H₂O₂), distilled water and a buffer of 25% ammonia water (NH₄OH), in the ratio of 200:100:50 mL, respectively. The time for such a chemical treatment of samples varied, ranging from a day to two-three days, depending on the amount of organic remains in the samples. The methods using sodium hypochlorite were tested but not used because the reaction it caused was too strong and rapid, destroying the tested specimens. After chemical manipulation the dermal units were washed with tap water in sieves with a mesh size of 0.01 mm and stored in 65% ethanol. Chemically treated specimens gave a set of disarticulated and disoriented ossicles. It was somewhat difficult to distinguish the anterior and posterior ends of the roundish dermal tubercles in the fourhorn sculpin, but the length/height and direction of spinules helped to orient the tubercles because longer spinules were positioned posteriorly and directed posteriorly. Before SEM studies the ossicles were kept for some time in water. Better preserved specimens were semi-dried in open air, set on SEM stubs covered with double-sided sticky tape, dried and coated with gold. The specimens were scanned and photographed under scanning electron microscopes JEOL JSM-840A and Zeiss EVO MA15 at 10 kV. The mineralogical content of spiny dermal tubercles of shorthorn sculpin was analysed with a non-destructive INCAx-act EDS micro-analyser (Oxford Instruments Plc).

The illustrated specimens are housed in the Institute of Geology at Tallinn University of Technology and carry the collection number GIT 584, followed by the articulated specimen number and the unit number of that specimen.

The following cleared-and-stained (with alizarin red for bone and alcian blue for cartilage) specimens of related species in the Museum of Zoology, University of Alberta, Edmonton, Alberta, Canada, were examined to verify anatomical identification of the ossicles recovered from the chemically prepared specimens. Official common names are from Nelson et al. (2004):

Cottidae: *Myoxocephalus quadricornis* (fourhorn sculpin), UAMZ4645 (two specimens); *M. polyacanthocephalus* (great sculpin), UAMZ2106, UAMZ2328;
 Agonidae: *Xeneretmus latifrons* (blacktip poacher), UAMZ3196 (three specimens);
 Liparidae: *Liparis callyodon* (spotted snailfish), UAMZ2109 (four specimens); *L. florum* (tidepool snailfish),

UAMZ2110 (two specimens); *L. hershelinus* (bartail snailfish), UAMZ6732 (three specimens), UAMZ5642 (three specimens).

TERMINOLOGY

Dermal and other ossicles of the studied taxa differ from each other in overall morphology and sculpture details. Some of the described ossicles are thought to be modified scales, others are partially ossified cartilages and others are tooth plates from the oral and pharyngeal cavities. Their embryological origins vary and can often be controversial in various taxa. For example, bony plates bearing teeth and denticles are found in both the oral cavity and on the branchial arches. Teeth are usually assumed to be of ectodermal origin when found in the oral cavity, but of endodermal origin when found on the branchial arches, corresponding to the assumed embryonic origin of the epithelium in each location. However, recent work suggests that neural crest cells can initiate tooth formation in either ectoderm or endoderm (Soukup et al. 2008), so that the origin of the epithelium is not the determining factor. Sire & Huysseune (2003) investigated the detailed structure, histology and development of dermal skeletal and dental tissues in a variety of fishes. They found that, despite superficial similarities, the ctenial spines on the ctenoid scales of the cichlid *Cichlasoma* have a laminated construction and develop from the external layer of the elasmoid scale, whereas the dermal denticles on the head of the clupeomorph *Denticeps* have pulp cavities and develop like oral teeth.

The terms used in our descriptions are from Ojaveer et al. (2003), Froese & Pauly (2008), Sire & Meunier (1993) and Kapoor & Bhavna Khanna (2004) with some modifications herein (Fig. 2). The definitions of most terms follow Coad & McAllister (2009) and are given below in alphabetical order: **basal cavity**, cavity in the base of a gill-raker tubercle; **basal plate**, the disk forming the base of a tubercle; **base**, the lower, flat or conical part of a gill-raker tubercle – its anchoring structure; **branchial tooth plate**, a bony plate that is covered with tiny teeth and is attached to the branchial arches in the pharyngeal region (shown herein in *Trigloporus*; in cottoids, the tooth plates are usually on the 2nd and/or 3rd pharyngobranchial bones, and more rarely on the epibranchials; Yabe 1985); **crown**, the top of a gill-raker tubercle or tubercle bearing teeth and their sockets; **fin-ray rods**, partly unsegmented fin rays in the form of slender, usually spiny rods; **gill-raker tubercles**, smoothly convex to conical tooth-bearing structures, smaller than plates, probably with a cartilaginous core but ossified superficially, on the branchial arches (*Trigloporus*, *Myoxocephalus*, *Taurulus*; see Jakubowski 1996); **horn**,

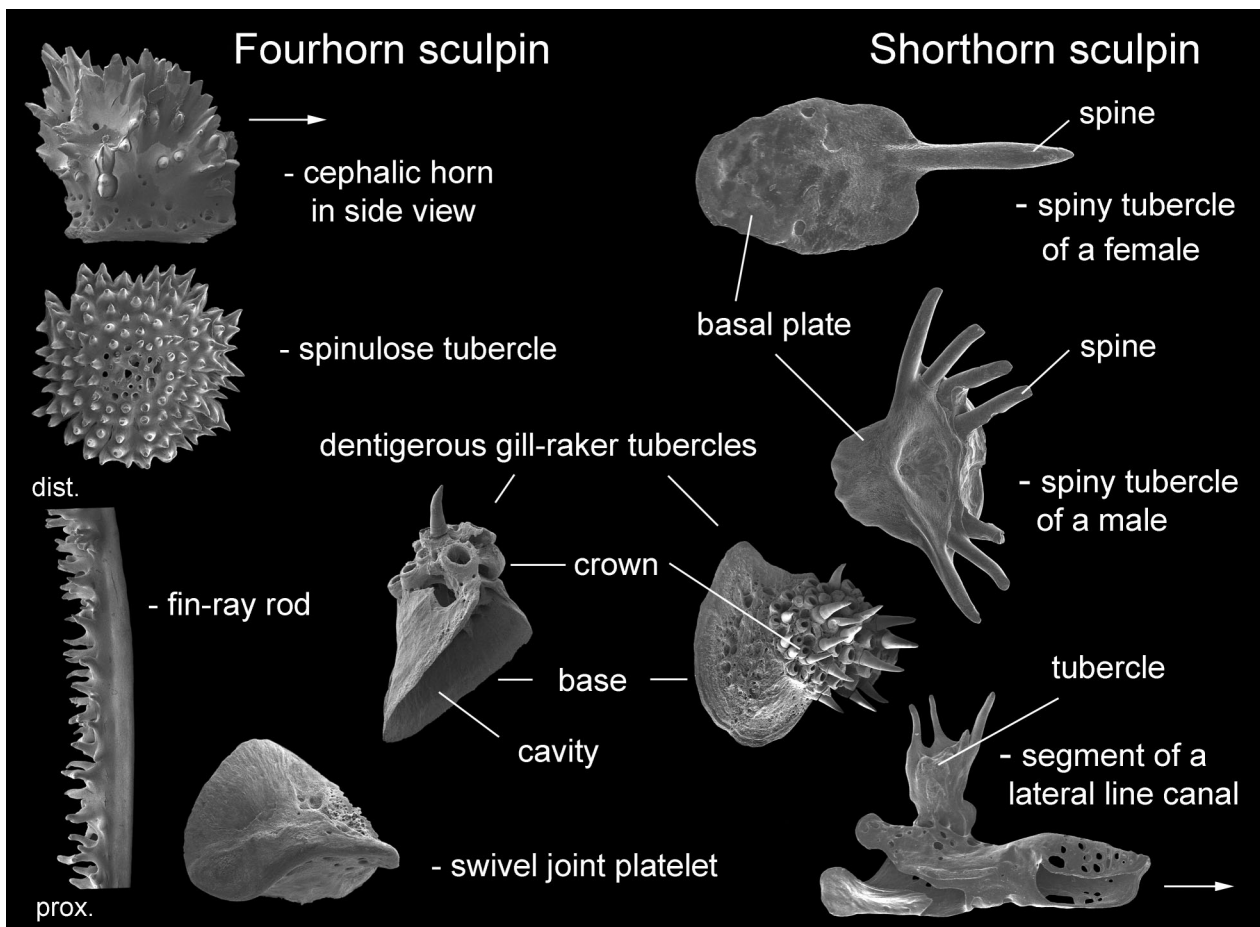


Fig. 2. Terminology of dermal units of fourhorn and shorthorn sculpins adopted in this work; anterior is to the left for the units of both body sides unless shown by an arrow, which points to anterior; the gill-raker tubercles on gill arches are situated with the base directed towards gill filaments; dist., distal; prox., proximal.

a large, protruding bony tubercle (sometimes also called protuberance) found on the head of many cottoid fishes (e.g. *Trigloporus*); **sensory canal segment**, a single unit of the chain-like ossicles of the cephalic or trunk lateral line (*Trigloporus*, *Myoxocephalus*, *Taurulus*), as illustrated in the cottoid *Neophrynichthys* (Psychrolutidae) by Jackson & Nelson (2000, fig. 4) and in other cottoids by Jackson (2004); **spine**, a sharp needle-shaped bony structure on a dermal tubercle or other ossicle (*Taurulus*); **spinule**, a tiny spine projecting from a larger spine or horn; **spinulose tubercle**, a tubercle covered with many tiny spinules (*Trigloporus*); **spiny rod**, a spine-bearing fin ray of the paired fins (e.g. *Trigloporus*); **spiny tubercle**, a tubercle with a few long spines emerging from a basal plate (*Myoxocephalus*); **swivel-joint platelets**, the paired perichondral ossifications of the ovoid or ball-shaped distal radials (pterygiophores) located between the proximal ends of the paired hemitrichs of the dorsal and anal fins (*Trigloporus*, *Myoxocephalus*, *Taurulus*);

tubercle, a general term for a small to medium-sized, usually convex platelet, such as those in the skin of many cottoids.

RESULTS

Order COTTIFORMES Regan, 1913 (as Cottoidei),
sensu Wiley & Johnson, 2010
 Family COTTIDAE Richardson, 1836

Trigloporus quadricornis (Linnaeus, 1758), fourhorn sculpin
 Figures 3, 4

Remarks. For *Trigloporus quadricornis* (Linnaeus, 1758), the common names fourhorn sculpin and four-horned sculpin (fourhorned sculpin) have been used by Estonian and Russian ichthyologists. On the basis of the valid common name given in Nelson et al. (2004), we employ the name fourhorn sculpin.

Material. GIT 584-15, GIT 584-16, GIT 584-31, GIT 584-40, GIT 584-41, GIT 584-42, GIT 584-43, GIT 584-44, GIT 584-55 (for data on specimens see Table 1).

Description of ossicles. The head bears four large, characteristic bony horns of various shapes and some smaller horns (Fig. 3A) between them. As a rule, the horns are smaller in females and juveniles and absent in freshwater forms; in Baltic populations the anterior pair of horns is better developed than posterior ones (Ojaveer 2003a). The upper part of each horn is built of bony, sheet-like, serrated and folded structures, the lower part of outwardly pointed spinules.

Posterior to the head, rows of bony spinulose tubercles are arranged along the dorsolateral flank between the dorsal fins and lateral line. The tubercles are usually arranged in two rows, but locally in one to three rows; the pattern of rows on the left and right sides of the body is not identical. Both the pattern of these rows and the size of tubercles in rows change with the age/length of a fish; the diameter of tubercles in our material was 1 to 5 mm. The tubercles in rows tend to be roundish (Fig. 3B, E, F, J, K) or quadrangular (Fig. 3C, D). Beyond the rows sparsely scattered tubercles (Fig. 3G, H, L) on the flanks between the 2nd dorsal fin and the anal fin and on the caudal peduncle are crescent-shaped. Sample GIT 584-44 also had many crescent-shaped tubercles behind the head. The crescent-shaped configuration of tubercles is not always distinct because in older specimens the slit anteriorly may be overgrown (Fig. 3G, Q, R). Some tubercles are oval and high (Fig. 3I). The base of each tubercle has an internal surface that is radially structured, smoother and more porous in younger tubercles (Fig. 3J, K) than in older tubercles, which have an uneven, knobby internal surface (Fig. 3Q, R).

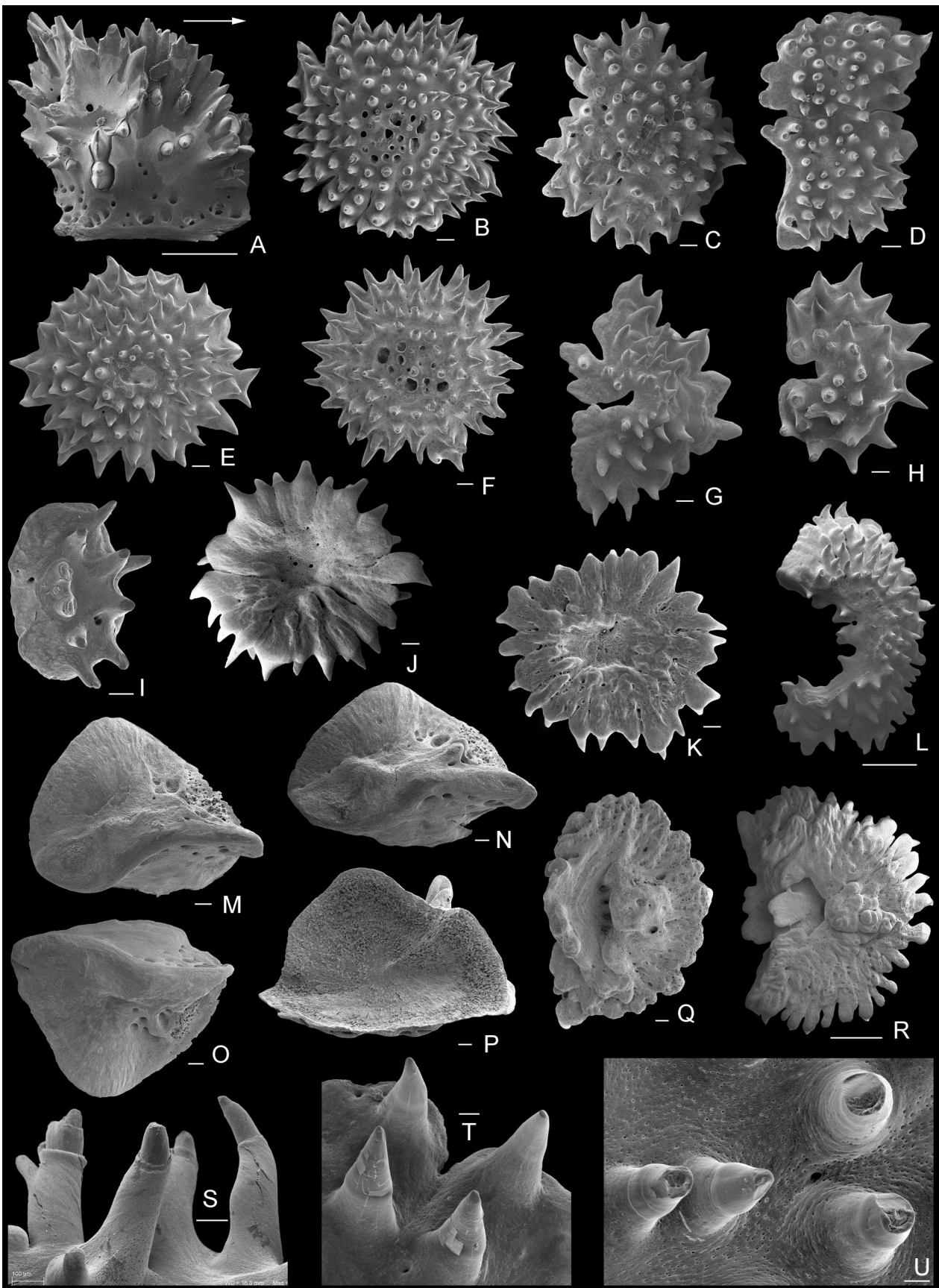
Tubercles are covered with numerous fine spinules arranged concentrically. Spinules are placed rather close to each other; they are smaller in the middle of each tubercle and become bigger at the margins, especially towards their posterior margins. The spinules lying anteriorly on the tubercles are directed upwards (at right angles to the plane of the tubercle), while posterior ones point obliquely posteriorly. In twinned tubercles (Fig. 3D) the size of spinules follows the same rule: the spinules in the middle are smaller than at the margins of both individual units; at the junction of the two tubercles, the spinules are directed towards the neighbouring individual unit. Sometimes the spinules may be lost in the centre of tubercles where only openings are left (Fig. 3B, F). Each spinule is approximately conical, but with a slight thickening at about half its height, followed by tapering to a point (Fig. 3T, U). The cap of each spinule is translucent, resembling the acrodin or enameloid caps of

the teeth and oral denticles in most actinopterygian fishes (Ørvig 1978; Sasagawa et al. 2009).

Specific swivel-joint platelets (Fig. 3M–P) from between the bases of the 2nd dorsal and anal fin rays (the 1st dorsal fin was not studied) cover the ovoidal distal radials (Hilton et al. 2010, fig. 10D, E for perciform *Parastromateus niger*) situated between the paired bases of the fin rays. These platelets are convex and occur in symmetrical pairs (Fig. 3M, O), are 1.2–1.8 mm long (measured along the external ridge) in the 23.6 cm long specimen GIT 584-44. The external ridge is slightly curved; it starts at the anterior corner as a low, moderately wide ridge and rises diagonally posteriorly, where it is narrower and higher and protrudes slightly above the platelet, ending there with a free point (Fig. 3M–O). A few smaller projections can occur posteriorly on the sides of this ridge. The platelet is porous posteriorly (Fig. 3M–O). The internal side of the platelet is concave, with a narrow groove beneath the ridge, but otherwise its surface is rather smooth (Fig. 3P).

Tooth plates occur in the oral and pharyngeal cavities. The vomerine tooth patch is situated anteriorly in the roof of the mouth. In the pharyngeal region two large roundish upper branchial tooth plates (Fig. 4A, and close-up in I) and two large, elongate lower branchial tooth plates carry tiny teeth. Anterior and lateral to the lower plates the gill rakers (Fig. 4B, C, G, H) occur on branchial arches and also carry tiny teeth on bony tubercles (Fig. 4B; Hilton et al. 2010, fig. 20A–F on perciforms). As a rule, jaw, vomerine and branchial tooth plate teeth are directed towards the centre of the oral or pharyngeal cavity. On the lower and upper jaw teeth are curved rather strongly, whereas on tooth plates the teeth stand more-or-less perpendicularly. The curvature and direction of teeth on the gill-raker tubercles change. The upper teeth are curved towards the middle of the pharynx, but the lower teeth project at right angles to the surface of the branchial arch, across the flow of water. The gill-raker tubercles are conical, with a wide base and numerous tooth sockets in their crown. The teeth on tooth plates (Fig. 4D, E) are thicker than those on gill-raker tubercles (Fig. 4F, J). The teeth of tooth plates and gill-raker tubercles were usually lost during chemical treatment of samples, leaving open, ring-shaped sockets (one tooth in Fig. 4B and some replacement teeth in Fig. 4A, I survived). Smaller openings of vascular canals are arranged in rings around the sockets on the branchial tooth plates (Fig. 4I).

The lateral-line canal posterior to the head extends along the trunk to the end of the caudal peduncle. It is enclosed in a chain of ossified lateral-line canal segments of rather variable shape (Fig. 4K–P) and length, which



can differ 2.5-fold (3–8 mm long). The lateral-line canal on the left side in the 23.6 cm long specimen GIT 584-44 had 22 well-preserved but very porous segments plus four more segments broken during preparation. The segments have an oval cut anteriorly of the tubule wall, which opens outwards (Fig. 4K–O), and another cut posteriorly, in the basal part of the tubule wall (Fig. 4L, M) to fit with adjacent anterior and posterior segments. The upper (external) posterior part has a sometimes shorter, sometimes longer incision along the midline (Fig. 4L, M, O). An elongate oval opening, the canal pore, is present on both sides of each segment (Fig. 4L–O). A few segments (one taken from between the 2nd dorsal and anal fins and shown in Fig. 4P) are plate-like, with a ring-shaped pore wall on both sides. The external posterior sides of segments usually bear a tubercle covered with fine spinules similar to those on the trunk tubercles (Fig. 4L, N, O). The tubercles are usually on one side of the external surface of the segment but in older specimens they can be on both sides (Fig. 4L). The tubercle size and spinule number vary, but size is always smaller and spinule number always fewer than those of the trunk tubercles. The lateral-line segments are pierced by fine pores of variable density and diameter. Perforation occurs nearly everywhere in the walls except in the posterior external part. The size and thickness of lateral-line segments increase with the age of the fish and growth lines can be seen anteriorly on the tube (Fig. 4N–P).

The fin web is supported by fin rays in the form of bony, spiny rods (Figs 3S, 4Q–U). The number of fin-rays is different in different fins. Small spines on rods are more pointed in smaller/younger specimens than in larger/older ones. In some rods of the pectoral fin the spines are worn away (compare Fig. 4Q, R and S, which all come from the left pectoral fin). Figure 4T shows a damaged right pectoral fin rod that was later repaired and covered with irregularly distributed spines. The broken (or worn?) peaks of spines are repaired (Fig. 4S, and close-up of the peaks in Fig. 3S). In the caudal fin-

ray rod (Fig. 4U) the distribution of spines is discontinuous. The segmentation of fin-ray rods is seen in the upper part of Fig. 4Q, T.

Myoxocephalus scorpius (Linnaeus, 1758),
shorthorn sculpin
Figures 5, 6

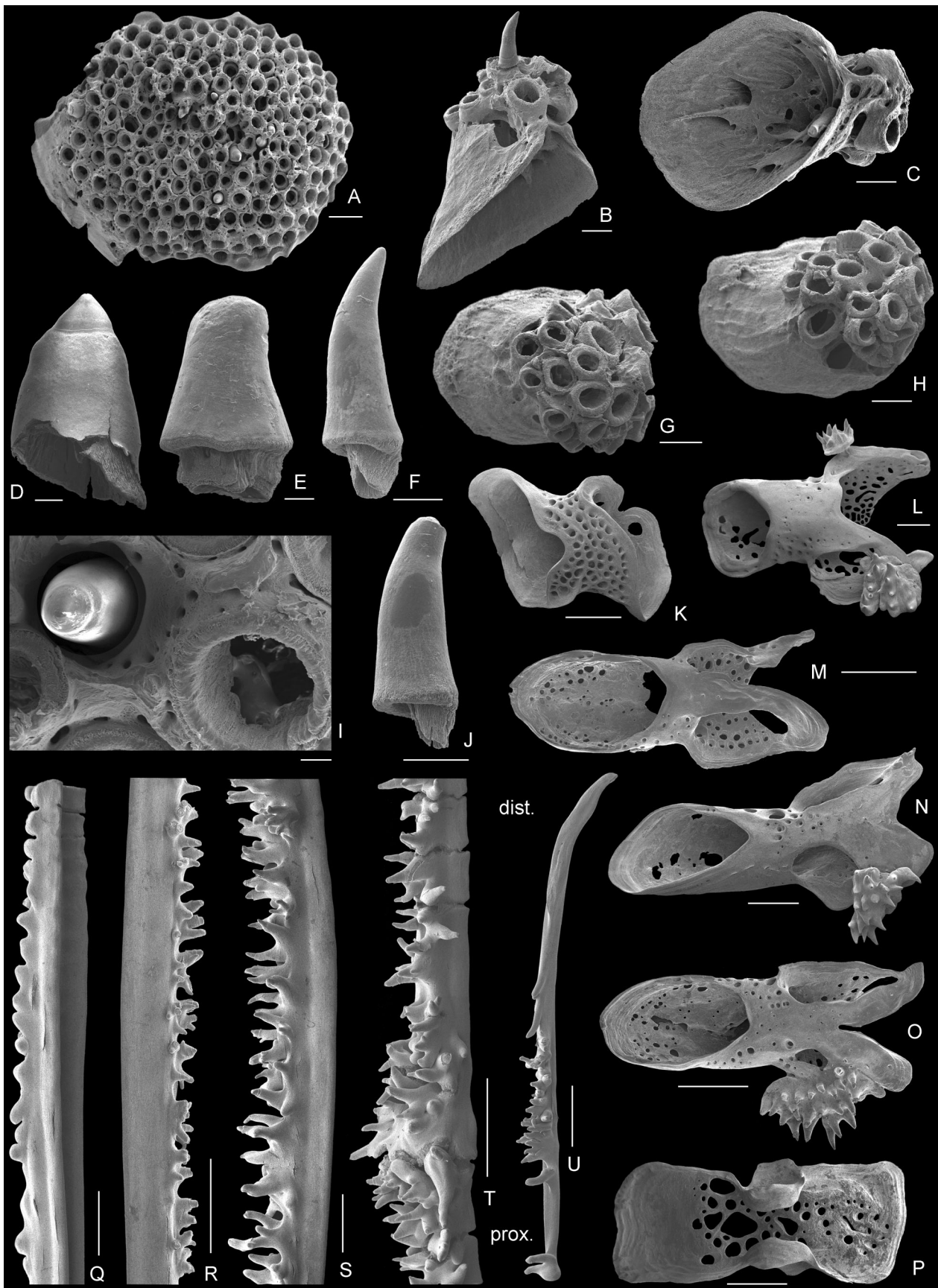
Material. GIT 584-8, GIT 584-27, GIT 584-34, GIT 584-56, GIT 584-57, GIT 584-72 (for data on specimens see Table 1).

Description of ossicles. The skin contains small spiny tubercles, which are better developed in males (Ojaveer 2003b) (measurements of some tubercles are given in Table 2) than in females. Below, a male example is described first, followed by a female example.

Spiny tubercles of male specimen GIT 584-8 are palmate in shape but have a rather changeable configuration of the basal plate, variable features of the upper surface and variable numbers and arrangement of spines (Fig. 5A–K). The configuration of the basal plate is irregularly quadrangular, oval or roundish. The lower surface of the basal plate is smooth (Fig. 5D) or with a shallow depression. Anteriorly the basal plate can have a wide medial projection with smooth margins and surface (Fig. 5B, G, I), or it can have knobs anteriorly on that projection (Fig. 5C, F). The medial part of the upper surface of the basal plate is flat (Fig. 5A, B) or more frequently with a depression (Fig. 5C, E, F, H, I, K). Many spiny tubercles carry small knobs on the flat surface of the medial projection (Fig. 5A, B) or remnants of earlier generations of spines posterolaterally behind the depression (Fig. 5C, E, F, I).

Spines in the male tubercles are roundish in cross section (Fig. 5C, F, I, K); sometimes a fine ridge runs along the spine (Fig. 5C, H, the lowest spine). The basal plate bends on each side to form the most lateral spines (Fig. 5B–K); the intermediate spines may occur as posterior outgrowths of the basal plate (Fig. 5A–C, G)

Fig. 3. Fourhorn sculpin, *Triglopsis quadricornis* (Linnaeus, 1758). Bony units from the head, trunk and left pectoral fin. **A**, cephalic horn; **B–F**, **J**, **K**, spinulose tubercles from tubercle rows on the body; **G**, **H**, **L**, **Q**, **R**, crescent-shaped tubercles from trunk sides beneath tubercle rows; **I**, small tubercle from the trunk (scattered material); **M–P**, swivel-joint platelets from the bases of the 2nd dorsal and/or anal fins; **S**, detail of the fin-ray rod of the left pectoral fin. **S–U**, close-ups of Figs 4S, 3D and 3B, respectively. All figures are in external view except **A** and **S**, which are in side view, and **J**, **K**, **P–R**, which are in internal view; anterior is to the left for the units of both sides of the body unless shown by an arrow, which points anteriorly; for **S**, proximal is to the left. **A**, GIT 584-42-10; **B** = **U**, GIT 584-16-5; **C**, GIT 584-16-8; **D** = **T**, GIT 584-16-4; **E**, GIT 584-15-2; **F**, GIT 584-16-14; **G**, GIT 584-41-5; **H**, GIT 584-15-3; **I**, GIT 584-16-10; **J**, GIT 584-16-9; **K**, GIT 584-16-6; **L**, GIT 584-41-7; **M**, GIT 584-44-3; **N**, GIT 584-44-5; **O**, GIT 584-44-2; **P**, GIT 584-44-4; **Q**, GIT 584-41-8; **R**, GIT 584-41-12; **S**, GIT 584-44-9. Specimen GIT 584-15 comes from the vicinity of Ruhnu Island, GIT 584-16 from the Väike Väin Strait, GIT 584-41, GIT 584-42 and GIT 584-44 were caught from the deeper waters east of Ruhnu Island, Gulf of Riga. Scale bar for **A**, **L**, **R** is 1 mm, for **B–K** 200 µm, for **M–Q**, **S** 100 µm, for **T–U** 10 µm.



or, more commonly, may emerge from the surface of the basal plate (Fig. 5E, F, H, I, K). There is no change, boundary or gap in the transition from basal plate to lateral spine. Often also the intermediate spines arise in a similar way (Fig. 5A, B, G), but frequently some intermediate spines appear to arise from a depression or cleft (Fig. 5H–J). One interpretation is that the spine is in the process of development or replacement, and another is that the base of the spine has been overgrown by a new layer of the basal plate. The total number of spines varies from four (Fig. 5G) to twelve (Fig. 5E). The posterior spines are arranged in one distinct row (Fig. 5A, B, G), or in two to three indistinct rows (Fig. 5C, E, F, H, I, K) representing the generations of spines. The space between the spines is sometimes rather even (Fig. 5A, G, H), but irregularly spaced spines are more common (Fig. 5B, C, K).

A lateral line canal segment from the male specimen (Fig. 5L; arrow points to anterior) is 4.25 mm long; the width of the intact tubule is 1.2 mm. The segment has a porous tubule wall, a rather large pore on both sides of the tubule and a wide opening at its anterior and posterior ends. The segment bears a palmate tubercle, similar to the trunk spiny tubercles, with three rather large spines, one shorter spine and a knobby medial surface; height of the tubercle is 1.55 mm.

Spiny tubercles of three female specimens GIT 584-34, GIT 584-56 and GIT 584-72 were studied (for measurements of some spiny tubercles see Table 3); a fourth specimen, GIT 584-27 was a fish 19.7 cm long whose sex was not defined, but its spiny tubercles were simple and similar to those of female GIT 584-34; therefore, GIT 584-27 is identified also as a female. This specimen was notable because it also yielded four small, very thin, smooth and flat platelets (0.75–1.0 mm long and 0.55–0.75 mm wide) without posterior spines (Fig. 6A–C), which possibly are the basal plates of an early developmental stage of spiny tubercles. The configuration of these basal plates is irregularly oval or quadrangular. The posterior 1/3 of these plates is finely porous while

the anterior 2/3 is translucent (Fig. 6A); the posterior lower side also contains fine pores (Fig. 6B). A single small knob (initial spine?) arises slightly posterior to the midpoint of a small plate, which otherwise lacks posterior spines (Fig. 6C).

Spiny tubercles have a flattened basal plate with variable posterior outgrowths and with up to three somewhat radially placed rows of spines, which extend either nearly parallel to the skin of the fish (Fig. 6D–F, H, L–N) or rise slightly posteriorly (Fig. 6I–K). Spines may also emerge from the outgrowths of the basal plate (Fig. 6M, N), although sometimes there is no spine on such outgrowths (e.g. uppermost protrusions in Fig. 6K, N). The basal plates of some smaller tubercles have a somewhat convex external surface, sometimes with a short blunt spine in the middle (Fig. 6K). Anteriorly most tubercles have a wide medial projection. Specimen GIT 584-72 has radially placed spines or knobs interpreted as remnants from the earlier spine generations (Fig. 6D, I, J, O). In the same specimen some spines arise from depressions like sockets and it appears as though they were replacement spines (Fig. 6I, possibly also G, J), although another explanation is overgrowth of the base of a spine by a new layer deposited on the basal plate. The posterior ends of spines may have a surface covered with compound nodules, whereby the older nodules are partly hidden under younger ones (Fig. 6E, N, S); the diameter of nodules varies from 3.1 to 7.7 μm . On the anterior flat surface of the basal plate there are several (two to seven in our material) very small, oval or roundish, low depressions, situated in the transitional zone from the translucent area anteriorly to the finely porous area posteriorly (Figs 2 right top, 6E, H, L).

Distinctive ossicles representing gill-raker tubercles of large female specimen GIT 584-72 differ strongly in size (Fig. 5M–Q). The length of the base (measured lengthwise the branchial arch) is 0.8–5.9 mm, the latter number being the length of a twin. The number of teeth varies markedly from four to at least 73. The smallest

Fig. 4. Fourhorn sculpin, *Trigloporus quadricornis* (Linnaeus, 1758). Ossicles from the head and fins. **A**, large, upper, roundish branchial tooth plate; **B, C, G, H**, tooth-bearing gill-raker tubercles; **D, E**, teeth from tooth plates; **F, J**, teeth from gill-raker tubercles; **I**, close-up of the tooth plate in Fig. 4A. The teeth in A–C, G and H were lost during the chemical treatment of samples except the one in B and a few replacement teeth in A = I. **K–P**, lateral-line canal segments; **Q–U**, spine-bearing fin-ray rods; Q–S, from the left pectoral fin; T, repaired fin-ray rod of the right pectoral fin; U, from the caudal fin. A, G–I, K–P, in external view; D–F, J, Q–U, in side view; B, in oblique side view; C, in base view; anterior for K–P is to the left; dist., distal; prox., proximal. A, I, GIT 584-16-1; B, GIT 584-42-6; C, GIT 584-42-8; D, GIT 584-42-4; E, GIT 584-42-5; F, GIT 584-42-2; G, GIT 584-42-7; H, GIT 584-42-9; J, GIT 584-42-1; K, GIT 584-42-11; L, GIT 584-41-9; M, GIT 584-16-7; N, GIT 584-15-1; O, GIT 584-16-12; P, GIT 584-41-4; Q, GIT 584-44-7; R, GIT 584-44-8; S, GIT 584-44-9; T, GIT 584-44-10; U, GIT 584-44-6. Specimen GIT 584-16 was caught from the Väike Väin Strait, specimens GIT 584-41, GIT 584-42 and GIT 584-44 come from the deeper waters east of Ruhnu Island, Gulf of Riga. Scale bar for A, K–U is 1 mm, for B, C, G, H 200 μm , for D–F, I, J 100 μm .



and the largest gill-raker tubercles are relatively flat, while the medium-sized ones are conical. The base is vascularized (Fig. 5M, O–Q) as is the crown beneath the teeth (Fig. 5N). Both the external and internal surfaces of the gill-raker tubercles bear concentric growth rings (Fig. 5M, N, P).

Altogether fifty lateral-line canal segments were picked out of the sample from specimen GIT 584-27. They vary in size: the largest is 5 mm long with the width of the tube 1 mm, and the smallest is 2 mm long with the width of the tube 0.55 mm. The segments are slender, the side openings being situated in the middle of segments. The tubule walls are pierced by fine to medium pores (Fig. 6Q, T); very many segments have rather compact tubule walls with sparse pores (Fig. 6P, R) which may be arranged in rows. One segment (Fig. 6P) has a closed inner and an open outer arch (roof). Segments from the studied females do not bear tubercles on their posterior flanks. The segment in Fig. 6Q shows up to four layers in its tubule wall development (close-up in Fig. 6T).

Swivel-joint platelets from the anal fin of female specimen GIT 584-72 are rather large (1.3–2.6 mm long) and have a relatively high ridge and one large pore and a number of smaller pores on either side of that ridge (Fig. 6U–W); the depression on the internal surface is deep beneath the ridge. Platelets in Fig. 6W survived the oxidation process and are still articulated to each other.

Mineralogical content. The mineralogical content of a few ossicles was studied. There were no marked differences in the quantitative content of carbon (C), phosphorus (P) and calcium (Ca) in the translucent and porous parts of basal plates and spines of three measured tubercles (GIT 584-8-12, GIT 584-27-16 and GIT 584-27-17). In the translucent area the content in weight% of C was 25.15–37.47, that of P was 7.61–11.71 and that of Ca was 17.42–28.59. In the porous area of basal plates and spines the content in weight% of C was 31.11–37.45, that of P was 8.65–10.10 and that of Ca was 17.57–21.45.

Taurulus bubalis (Euphrasén, 1786), longspined bullhead
Figure 7

Material. GIT 584-12, GIT 584-58, GIT 584-59, GIT 584-60 (for data on specimens see Table 1).

Description of ossicles. According to Hayward & Ryland (1995), the skin of longspined bullhead is loose, with minute spinules, but according to Ojaveer (2003c), their skin lacks spinules. No separate minute spinules were found in our material. Fine spinules occur on dermal skull bones (Fig. 7A, B) and on lateral-line canal segments.

Male specimen GIT 584-12 has altogether 46 lateral-line canal segments, eight of which are shown in Fig. 7C–K. The largest segment was 2.12 mm long and 1.5 mm wide, measured at the large lateral openings; the smallest segment was 1.25 mm long and 0.4 mm wide. A relatively short but wide lateral-line canal segment (Fig. 7F) comes from just behind the head. Larger segments coming from the anterior part of the body have a rather smooth and flat base with a narrow rim around the segment (Fig. 7D, E). If this basal rim is not developed, the lateral-line canal segments are much slender (Fig. 7G, J, K). They are pierced by rows of pores; the pores are rather large compared to those of lateral-line segments of the other examined species (Fig. 7D, E, G). The rim of the anterior aperture of the segment is oblique anteriorly (Fig. 7H, I) and is overlapped by the segment next anteriorly. Almost all segments, except the smallest ones (Fig. 7K), carry fine spinules along the external, dorsal side; spinules are similar to those on the dermal skull bones shown here for comparison (Fig. 7A, B). All spinules are translucent. A large opening occurs on the dorsal and ventral sides of each segment (Fig. 7D, E, G–I, K). The medial surface of each segment is smooth, with a large pore in the middle (Fig. 7J). About 11 growth layers in the base are seen through the anterior canal opening (Fig. 7D, E, G) and six layers in the segment wall (Fig. 7C).

Swivel-joint platelets from the dorsal and anal fins have a strong longitudinal ridge and a few medium-

Fig. 5. Shorthorn sculpin, *Myoxocephalus scorpius* (Linnaeus, 1758). A–L, spiny tubercles and a lateral-line canal segment from the whole skin sample of male specimen GIT 584-8; A–C, E–J, K, spiny tubercles in external view; J is close-up of H to show emerged secondary spines; D, tubercle in internal view; L, lateral line segment, slightly turned around its longitudinal axis. M–Q, tooth-bearing, gill-raker tubercles of female specimen GIT 584-72; M, O–Q, gill-raker tubercles in external view; N, gill-raker tubercle in internal view. Anterior is to the left for the ossicles of both sides of the body unless shown by an arrow, which points anteriorly; M–Q are oriented with base towards the gill filaments. A, GIT 584-8-8; B, GIT 584-8-4; C, GIT 584-8-5; D, GIT 584-8-1; E, GIT 584-8-10; F, GIT 584-8-6; G, GIT 584-8-7; H = J, GIT 584-8-2; I, GIT 584-8-3; K, GIT 584-8-9; L, GIT 584-8-11; M, GIT 584-72-22; N, GIT 584-72-21; O, GIT 584-72-27; P, GIT 584-72-28; Q, GIT 584-72-25. Specimen GIT 584-8 was caught east of Osmussaar Island, and GIT 584-72 in the vicinity of Pakri Island. Scale bar for A–C, F, H, M–P is 200 µm, for D, E, G, I–K 100 µm, for L and Q 1 mm.

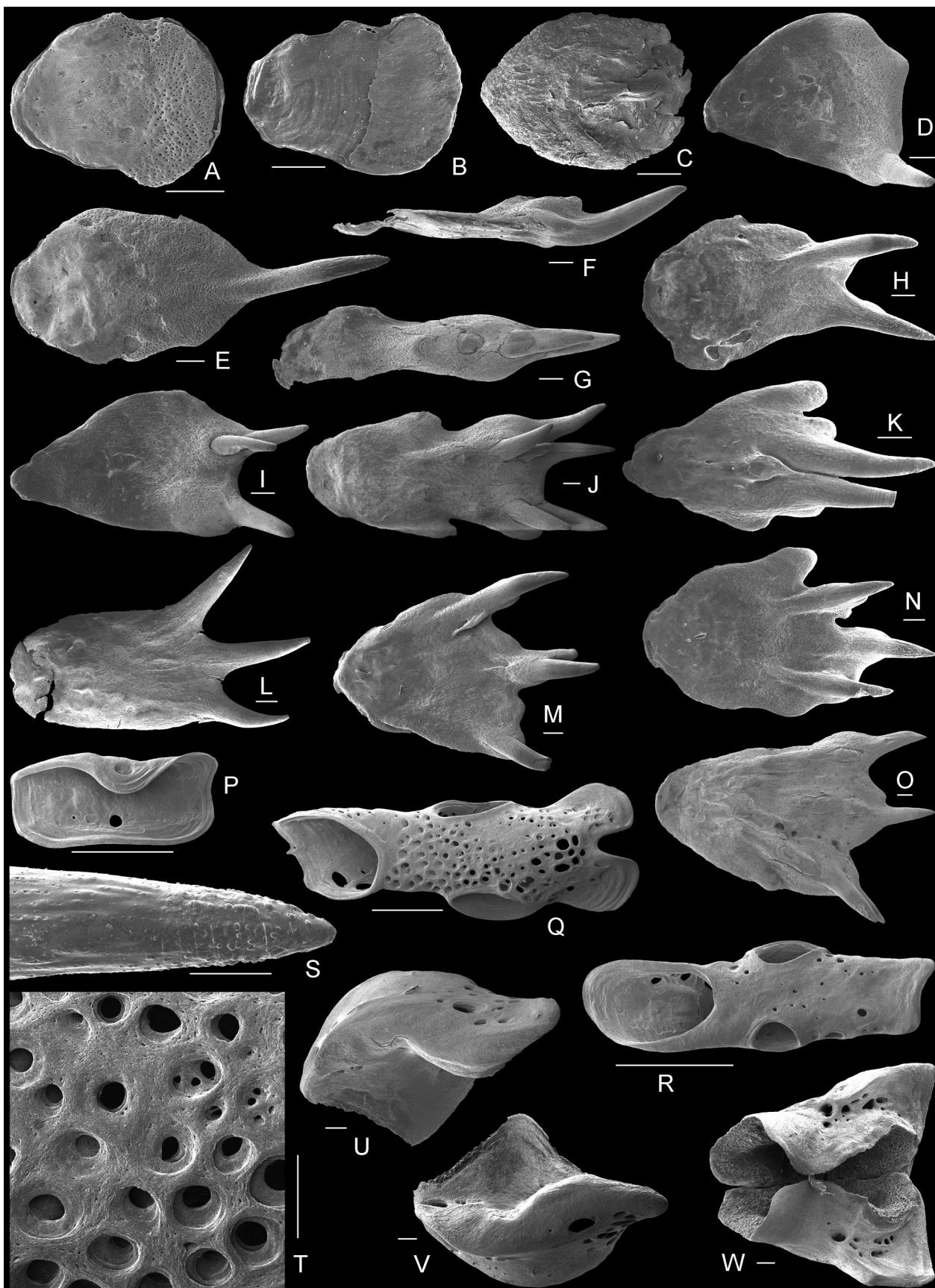


Table 2. The measurements of spiny tubercles in male *Myoxocephalus scorpius* (sample GIT 584-8)

Tubercle	Basal plate length, mm	Basal plate width, mm	Max length of spines, mm
GIT 584-8-1	1.0	1.2	0.5–0.6
GIT 584-8-2	1.0	1.15	0.6
GIT 584-8-5	1.25	1.25	0.5
GIT 584-8-8	1.75	2.5	0.5

Table 3. The measurements of spiny tubercles in female *Myoxocephalus scorpius* (sample GIT 584-27)

Tubercle	Basal plate length, mm	Basal plate width, mm	Max length of spines, mm
GIT 584-27-2	1.4	0.87	1.2
GIT 584-27-3	1.85	1.5	1.25
GIT 584-27-4	1.65	1.3	0.9
GIT 584-27-5	0.75	0.45	0.7
GIT 584-27-6	0.75	0.55	0.7

sized pores on the external surface (Fig. 7L). The depression on the internal surface becomes deeper towards the posterior point of the ridge (Fig. 7M). The length of platelets is 0.6–1.3 mm, measured along the ridge in the 9.5 cm long specimen GIT 584-58.

The tooth-bearing gill-raker tubercles (Fig. 7N–U) on the branchial arches are oriented with the base towards the gill filaments. The orientation of teeth changes along these gill-raker tubercles, being curved towards the middle of the pharyngeal cavity in the upper part of the crown and directed at right angles to the surface of the branchial arch closer to the base. Ring-shaped tooth bases are arranged in rows (Fig. 7O, P, R) or irregularly (Fig. 7N, S, U) with openings on different heights (Fig. 7Q).

The gill-raker tubercle may be simple (Fig. 7O–Q, S, U) or compound, incorporating two to three units grown together. The base of each gill-raker tubercle is either flattened (Fig. 7N–P) or convex (Fig. 7Q, S–U). The base has a rather smooth surface on its external and visceral sides; beneath the tooth bases the tubercles are vascularized.

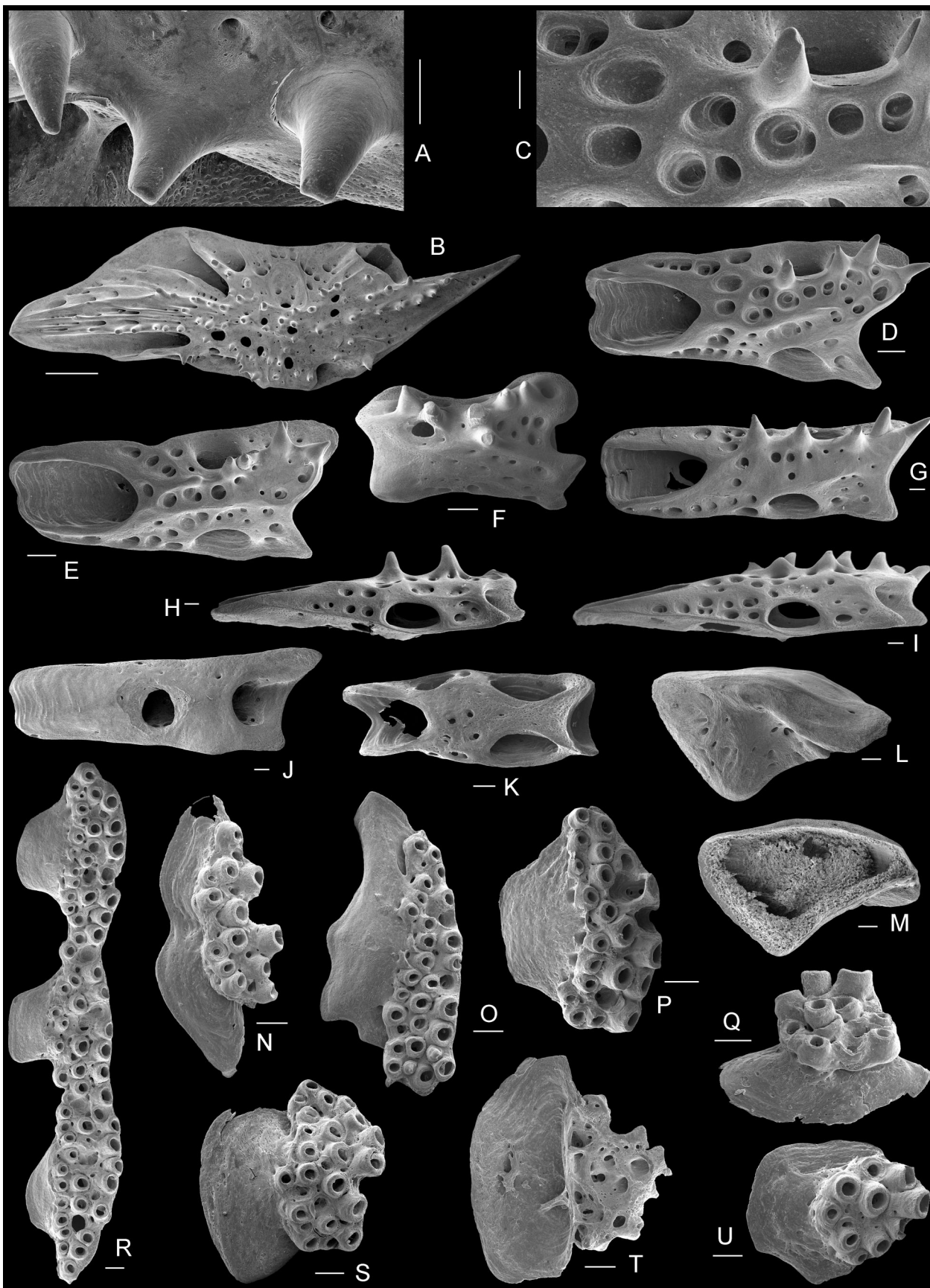
DISCUSSION

This study is the first detailed account of the small dermal tubercles and other ossicles of members of the teleostean order Cottiformes, suborder Cottoidei, of the Baltic Sea. The research was divided into two parts, the present one dealing with the taxa of the family Cottidae (except *Cottus*), and a subsequent one dealing with the families Cyclopteridae and Liparidae (Märss et al. accepted). Each genus of Cottidae inhabiting the Baltic Sea is represented by one species only. Even within this single family found in a single geographic region there exists a great deal of distinctive variation among species and between sexes in the presence or absence of and detailed morphology, sculpture and ultrasculpture of the studied ossicles.

Comparison of ossicles

The skin of Baltic cottids is bare or bears different small ossicles. In the fourhorn sculpin *Triglopsis quadricornis* horns are borne on the head and spinulose tubercles on the trunk; rays of some fins contain spiny rods which are repaired when injured. The fourhorn sculpin has the largest spinulose tubercles, arranged in a row on each side of the trunk; the remaining part of its body carries scattered crescent-shaped spinulose tubercles of variable size. The completeness of tubercle rows as well as the size of tubercles in the rows vary with the age/length of

Fig. 6. Shorthorn sculpin, *Myoxocephalus scorpius* (Linnaeus, 1758). **A, B**, very thin basal plates of spineless tubercles, with translucent anterior and porous posterior portions. **C, L**, tubercles of a female specimen GIT 584-34; note a spine which is emerging from the basal plate in **C**. **D, F, G, I, J, O**, tubercles and their details of female specimen GIT 584-72. **E = S, H, K, M, N**, tubercles; **S**, close-up of spine to show the nodular ultrasculpture. **P, Q = T, R**, lateral line segments of specimen GIT 584-27, whose sex was originally not identified; because of the simple morphology of tubercles and similarity with those of GIT 584-34 and GIT 584-72, the specimen is identified as a female; **Q** is the anteriormost and **P** is from between the 2nd dorsal and anal fins (compare with Fig. 3S); **T** is close-up of **Q** showing at least four levels of development of the wall. **U–W**, swivel-joint platelets of the base of the anal fin of GIT 584-72. The units are in external view except **B**, which is in internal view, and **F**, which is in side view; anterior is to the left for the units of both body sides. **A**, GIT 584-27-6; **B**, GIT 584-27-8; **C**, GIT 584-34-1; **D**, GIT 584-72-1; **E = S**, GIT 584-27-9; **F**, GIT 584-72-5; **G**, GIT 584-72-6; **H**, GIT 584-27-4; **I**, GIT 584-72-2; **J**, GIT 584-72-12; **K**, GIT 584-27-1; **L**, GIT 584-34-4; **M**, GIT 584-27-10; **N**, GIT 584-27-3; **O**, GIT 584-72-11; **P**, GIT 584-27-11; **Q = T**, GIT 584-27-14; **R**, GIT 584-27-13; **U**, GIT 584-72-17; **V**, GIT 584-72-16; **W**, GIT 584-72-15. Specimens GIT 584-27 and GIT 584-34 were caught in Küdema Bay north of Saaremaa Island and GIT 584-72 was caught in the vicinity of Pakri islands. Scale bar for **A–O, T–W** is 200 μ m, for **P–R** 1 mm, for **S** 100 μ m.



the fish. New tubercles are added when the fish grows. The configuration of spinulose tubercles is roundish, crescent-shaped or quadrangular. Each tubercle is covered with closely packed spinules on the common basal plate, which is thin in young and thicker in older tubercles. On roundish tubercles the spinules occur concentrically, being smaller in the middle and larger towards the margin, especially towards the posterior margin. Apparently, these large, roundish tubercles grew by thickening of the basal plate and by addition of new spinules at the external margin. In the crescent-shaped tubercles the addition of spinules proceeded posteriorly and laterally. In young specimens the basal plates of crescent-shaped tubercles have a more widely open slit anteriorly, whereas in older specimens the slit becomes overgrown. In the latter stages of growth root-like outgrowths (knobs) appear at the margins of both types of spinulose tubercles.

The shorthorn sculpin *Myoxocephalus scorpius* differs from the fourhorn sculpin in having tubercles with relatively few rather long spines posterolateral or posterior to the oval to quadrangular basal plate. These spiny tubercles are not arranged in distinct rows on the fish's body. Tubercles of male and female specimens differ in the configuration of the basal plate and in the number and arrangement of spines. Males have more spines (4–12), which occur in one to two somewhat irregular rows along the posterior margin, while females have fewer spines (maximum 6) in up to three radial rows. The growth of tubercles in both males and females proceeds by either the addition of new generations of spines as extensions from the posterolateral margin of the basal plate, or by spines arising as extensions from outgrowths of the basal plate, each next generation more distally. The older spines become worn or broken. Some spines appear to emerge from a hole left from the previous spine, which might mean that these are secondary spines. Such replacement of broken spines by new ones takes place in posterior rows, while in the anterior ones they were not replaced.

The dramatic sexual dimorphism in the dermal tubercles of *M. scorpius* is a cautionary tale for palae-

ontologists who study microfossils of primitive fishes and early vertebrates, where there is seldom any objective basis for distinguishing sexes in the fossil material. The difference between dermal tubercles of males and females in the present example would be enough to suggest taxonomic differences in the absence of direct evidence of sexual dimorphism.

The longspined bullhead *Taurulus bubalis* has spinulose dermal bones on the head and, according to Hayward & Ryland (1995), minute spinules on the trunk. We were not able to find trunk spinules; the spinules on the head plates and on the lateral line segments are very tiny and arranged in rows.

The swivel-joint platelets (paired ossifications of distal radials) of dorsal and anal fins were available from all three studied taxa, and even these simple elements display differences among the taxa. The platelets are paired, symmetrical and convex, with a curved antero-posterior ridge on the external surface and with a concave, rather smooth internal side. The size of platelets depends on the taxon, being largest in fourhorn sculpin, and also on the age/size of the specimen. The ridge is very strong and high in all three species. The external surface of the platelets in the fourhorn sculpin is more vascularized than in shorthorn sculpin and longspined bullhead; the platelets in the bullhead have the fewest pores.

Lateral line canal segments were documented in all three species. In different genera these segments differ in size (larger in larger species, but also strongly dependent on the age of the specimen), shape of tubercles attached to the posterolateral sides in some cases, porosity of walls and the position of the openings in the sides of the segments. The tubercles attached to the posterior external sides of the segments copy the features of dermal tubercles from the trunk. The segments of the studied female shorthorn sculpin lack tubercles. Its segments are slender and the side openings are situated in the middle, more anteriorly than in the two other taxa. The large lateral line segments of the longspined bullhead, placed anteriorly of the body, have a rim extending from the basal plate, a long anterior opening

Fig. 7. Longspined bullhead, *Taurulus bubalis* (Euphrasén, 1786). **A, B**, dermal skull bone showing tiny spines situated in somewhat irregular lines; A is close-up of B. **C–K**, lateral-line canal segments; C is close-up of D. **L, M**, swivel-joint platelets. **N–U**, tooth-bearing gill-raker tubercles. **A–G, K, L, N–P, R, S, U**, units in external view; **H, I, Q**, units in side view; **J, M, T**, units in base or internal view; **C–M**, anterior is to the left for the units of both sides of the body; the base of gill-raker tubercles is directed downwards towards the gill filaments and the teeth and sockets of the crown are directed towards the middle of the pharyngeal cavity. **A = B**, GIT 584-12-1; **C = D**, GIT 584-12-3; **E**, GIT 584-12-2; **F**, GIT 584-12-5; **G**, GIT 584-12-7; **H**, GIT 584-12-9; **I**, GIT 584-12-6; **J**, GIT 584-12-8; **K**, GIT 584-12-10; **L**, GIT 584-58-17; **M**, GIT 584-58-16; **N**, GIT 584-58-5; **O**, GIT 584-58-9; **P**, GIT 584-58-3; **Q**, GIT 584-58-12; **R**, GIT 584-58-2; **S**, GIT 584-58-13; **T**, GIT 584-58-8; **U**, GIT 584-58-6. Specimen GIT 584-12 was caught east of Osmussaar Island and GIT 584-58 in the vicinity of Krassi Island. Scale bar for **A, C, G–U** is 100 µm, for **B** 1 mm, for **D–F** 200 µm.

and pores arranged in rows. The basal rim is not found in the other studied taxa. Both the fourhorn and shorthorn sculpin also have a few lateral line segments with an open roof. The study of the lateral line of *Hexagrammos stelleri* by Wonsetter & Webb (1997) showed that the development of scales along a lateral-line canal is not sequential, and they distinguished six stages of scale development (*ibid.*, fig. 9A–F). The developmental stage of the segment in Fig. 4P corresponds to their stage III.

Ontogenetic classification of ossicles

Sire & Huysseune (2003) investigated the development and histology of a variety of tooth-like dermal bony structures in actinopterygians and distinguished between two categories of dermal ossifications. One develops similarly to teeth at the boundary between the epithelium and dermis (or mesenchyme) and has a polarized development, its denticles exhibiting a pulp cavity and, in actinopterygians, an acrodin cap (enameloid tip) (Ørvig 1978; Sasagawa et al. 2009), among other features. The second category of Sire & Huysseune (2003) develops remotely from and is unpolarized relative to the epithelium, tissues being laid down equally on inner and outer surfaces. These ossifications typically lack both pulp cavities and acrodin caps. In the former category Sire & Huysseune (2003) included jaw and branchial teeth as well as denticles found on the head in a few teleost lineages (e.g. the clupeomorph *Denticeps*). In the latter category they included the dermal ‘plates’ found in the skin on the body of fishes such as gasterosteiforms. They further suggested that elasmoid scales of teleosts (including ctenoid scales of many acanthopterygians) are more similar in some ways to the first, dental type of ossification, despite the evident absence of pulp cavities in scales and the absence of both pulp cavities and acrodin caps in their ctenii, but the clues to this relationship are not obvious from their detailed morphology.

The dermal tubercles of cottids in our study are usually assumed to be modified scales (e.g. Roberts 1993). They differ from the presumably more primitive elasmoid scales in being much thicker, lacking division into fields and in not overlapping, i.e., not being imbricated. In one species, *Trigloopsis quadricornis*, tubercles are spinulose and two different types are developed, the crescent-shaped spinulose tubercles, which grew posterolaterally but not anteriorly, and the sub-circular or quadrangular spinulose tubercles from the rows, which grew more or less centrifugally; both are completely covered with spinules on the common basal plate. The spinules differ from tooth-like elements of

the same species (e.g. branchial tooth plate teeth, gill-raker teeth; see below) in shape, attachment (usually not becoming detached during processing) and in lacking both the pulp cavity and well-developed, distinct acrodin cap (spinule tips can be translucent, but this appearance is confined to a small region near the tip).

In another species (*Myoxocephalus scorpius*) males and females have tubercles exhibiting different degrees of complexity, but bearing longer spines that also show no evidence of pulp cavities or well-developed acrodin caps. Their spines have ultrasculpture on the surface. The third species (*Taurulus bubalis*) lacks tubercles or spinules on its trunk, but the dermal skull bones and lateral-line segments bear spinules that, like those of the spinulose tubercles of *Trigloopsis quadricornis*, similarly resisted separation during processing and show no evidence of pulp cavities or distinct acrodin caps.

In contrast to the spiny and spinulose tubercles, along with the spinules and tubercles of the lateral-line segments, all of which fit better within the non-tooth-like category of Sire & Huysseune (2003), the branchial tooth plates, gill-raker tubercles and associated teeth of the studied cottids, along with their jaw and vomerine teeth, conform better with the tooth-like development and structure of the first category of Sire & Huysseune (2003). These teeth exhibit loose attachment and are easily separated from their circular bases; both bases and tooth shafts have a hollow pulp cavity (Fig. 4). Most of these teeth have well-developed, smooth caps interpreted as acrodin caps, as have the jaw teeth. Tooth replacement appears to have begun within the hollow tooth bases of the branchial tooth plates in *Trigloopsis quadricornis* (Fig. 4A, I), rather than as an outgrowth of the plate. All of these features suggest that these tooth-like structures are true teeth.

The case of the spines on the fin-ray rods of *Trigloopsis quadricornis* is more equivocal. These tooth-like projections appear to be extensions of the rod-like fin-ray; when abraded they are worn down or broken, rather than being separated at their base. There is no evidence of a hollow pulp cavity. On the other hand, each spine has a tip resembling a tiny acrodin cap. On balance, it seems better to classify these tiny projections with spines and spinules of dermal tubercles, rather than with teeth.

Roberts (1993) divided spiny scales of teleosts into three main types: the crenate with simple marginal indentations and projections, the spinoid with spines continuous with the main body of the scale and the ctenoid with spines formed separately from the main body of the scale. The last type, in turn, was divided into the transforming or peripheral ctenoid and the whole ctenoid.

The closest morphological comparison between the scale types of Roberts (1993) and scales of cottids can be perhaps with the second, spinoid type, and with the third, ctenoid type, especially its subtype, the whole ctenoid type. The growth of spiny tubercles of female *Myoxocephalus scorpius* started with a single spine in the middle of the tubercle as also shown for basal percomorphs by Roberts (1993), Hase (1911) and Rosén (1915, in Roberts 1993). *Myoxocephalus scorpius* has up to three radial spine rows in females or one to several row(s) along the posterior margin in males, which is a rather strong difference even between the sexes. The ontogenetic development in examined cottids differs from transforming ctenoid scales in that in the latter the new generations of ctenii appear in between the older ones (Roberts 1993, fig. 28) while, according to our material, in female *M. scorpius* they followed one after another in line. There is only limited evidence for separate development of the spines from the scale plate in our material, as would be expected under the ctenoid type of Roberts (1993). When some separation is suggested (e.g. Fig. 6I), it appears more likely to be a process of separation or overgrowth of a spine rather than initial development of new spines. Therefore, the spiny tubercles of male and female *M. scorpius* can possibly be classified better in the spinoid scale type of Roberts.

Ultrasculpture on the dermal ossicles

Ultrasculpture on the dermal ossicles is represented by compound nodular ultrasculpture found on the tubercle spines of *M. scorpius*, with the nodule diameter of 3.1–7.7 µm, the older nodules partly covered by younger ones. Somewhat similar nodules (roundish, with diameter less than 10 µm) were discovered on scutes of lower Silurian mongolepid ?chondrichthyans from China (Sansom et al. 2000, fig. 14b–d). Several other Palaeozoic and Mesozoic fishes also have a nodular ultrasculpture, yet with differences in shape (elongate or roundish), distribution (regular or irregular; simple and separate or compound), spacing (dense or sparse), underlying tissue (enameloid or enamel) and measurements of nodes. The nodes are much finer (1–2 µm) in Acanthodii from the Upper Devonian of Timan (Beznosov 2001) and 1.7–4.7 µm in an acanthodian from Belgium (Derycke & Chancogne-Weber 1995). Among the Actinopterygii, the size of nodules for polypterids varies from 2.6–3 µm (African living polypterid) to 5.3 µm in a polypteriform from the Late Cretaceous and middle Palaeocene of South America; the diameter of nodes for three lepisosteiform taxa is given as 3.79–9.07 µm (Meunier & Gayet 1996, p. 97). The nodules of *M. scorpius* are rather similar in size to those of these other actinopterygians but the

underlying tissue is different, as the teleost scales consist of laminated bone, while the polypteriform and lepisosteiform fishes have ganoid scales with hard, multilayered, enamel-like ganoine in their upper part.

Adaptive value of ossicles

Large horns and spines on the head and trunk, spine-bearing fin-ray rods in the fins and spiny or spinulose trunk tubercles, along with spinules on lateral-line segments or small tubercles attached to lateral-line segments, attract speculation as to their adaptive value to the organisms. The trunk tubercles have wide morphological variety but are rather small in size and sparsely dispositioned on the body. They may be of little help in protecting the fish physically from predation, but can play some other significant role, for instance, in improving camouflage.

The cottid fishes of the Baltic Sea are bottom-dwellers. The shorthorn sculpin and bullhead live in areas with sandy, gravelly or stony seafloor (Järvekülg & Turovski 2003; Ojaveer 2003b) and the longspined bullhead has been found in areas with a steep and stony coastal slope (Ojaveer 2003c). Fourhorn sculpin usually inhabits the bottom waters, but some specimens have been caught by pelagic trawl at 50–65 m depth above deeper parts of the sea (Ojaveer 2003a). In benthic forms exoskeletal elements often have a cryptic function, making the fish's exterior resemble the environmental background (Burdak 1979, p. 70). The tuberculation on the body surface of fourhorn sculpin appears to resemble sand and gravel grains, and spiny tubercles of shorthorn sculpin might have a similar effect. The body surface of all three taxa is mottled. We agree with Burdak (1979) that the tuberculation of these bottom-dwelling fishes likely improves their camouflage and thus their ability to avoid being detected by predators.

CONCLUSIONS

- The small dermal tubercles and other ossicles of *Trigloopsis quadricornis*, *Myoxocephalus scorpius* and *Taurulus bubalis* of the family Cottidae, originating from the Baltic Sea have been studied, compared and SEM imaged for the first time. The features of morphology and sculpture of ossicles differ noticeably in different genera. This phenomenon can be used in the taxonomic, systematic and phylogenetic studies of cottids.
- The morphology of dermal tubercles in *M. scorpius* exhibits strong sexual dimorphism in the studied specimens. Future studies of geographic variation in

- this species and of related species may reveal how widespread such strong sexual differences are.
- The growth of tubercles in tubercle rows and scattered tubercles on the remaining part of the body differs greatly among *Trigloporus quadricornis*, and males and females of *Myoxocephalus scorpius*. Roundish dermal spinulose tubercles of *Trigloporus quadricornis* grew extensively by addition of spinules evenly around their external margin; in crescent-shaped spinulose tubercles of the same species new spinules are added mainly laterally and posteriorly; in later stages of growth the margins of tubercles become indented. Growth of spiny tubercles of *M. scorpius* was achieved by addition of new generations of spines posterolaterally, spines arranged in radial rows in females and along the posterior margin in males; broken spines of older generations were replaced by new ones.
 - The dermal ossicles in the skin of cottids, the spiny and spinulose tubercles, differ from tooth plates in the same species because their spines and spinules lack open pulp cavities and acrodin caps, both of which would be expected in tooth-like structures (Sire & Huysseune 2003). Tubercles appear to be modified scales with several specific characteristics (being much thicker, lacking division into fields and not overlapping) distinguishing them from typical elasmoid scales. In the classification of Roberts (1993) they resemble the spinoid type rather than the ctenoid type because the spines develop not separately from, but as extensions from, and remain firmly attached to, the basal plate.
 - Paired symmetrical platelets, which occur bilaterally in the swivel joints situated between the dorsal and anal fin rays and pterygiophores in *Trigloporus quadricornis*, *Myoxocephalus scorpius* and *Taurulus bubalis* have not been described previously, but their morphologies reveal common features and taxon-specific features.
 - A type of ultrasculpture, a compound fine nodular structure was found on the spines of tubercles of *M. scorpius*. It is similar to ultrasculpture described earlier on Palaeozoic mongolepid ?chondrichthyan fish scales. Some Actinopterygii, e.g., polypterids and lepisosteids, have simple separate nodules on scale surface. Radical difference between these groups and *M. scorpius* is in different underlying tissues.
 - The illustrated and described morphologies and microstructure may be helpful for identification of species from microremains. Such data may contribute to future studies of faunal change in the Baltic Sea or identification of species in fish or sea birds' gut contents or archaeological sites.

- This study was instructive for palaeoichthyological works for understanding the morphology and extent of variability of ossicles of species and for realizing differences in ossicles of male and female specimens.

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Läänemere kolme võldaseliste (Teleostei) perekonna luuliste elementide morfoloogia ning skulptuur

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Detailselt on kirjeldatud ja kujutatud Läänemere võldaseliste hulka kuuluvate võldaslaste *Trigloopsis quadricornis* (Linnaeus, 1758), *Myoxocephalus scorpius* (Linnaeus, 1758) ning *Taurulus bubalis* (Euphrasén, 1786) mitmesugused luuplaadikesed, tuberklid ja küljejoonekanalite lülid. Elementide kuju ja skulptuur erinevad perekonniti ning seda saab edukalt kasutada võldaseliste taksonoomilis-süsteemaatilistes uuringutes. Luuelemendid võivad siiski erineda ka emas- ja isaskaladel (*M. scorpius*). Esmakordselt on kirjeldatud distaalsete radiaalide (pterügiofooride) perikondraalsel luustumisel tekkinud paarilisi pöördteljega plaadikesi, mis paiknevad selja- ja pärakuuimede paariliste hemitrihhide proksimaalse osa vahel. Selliseid plaadikesi ei ole seni kirjeldatud ei tänapäevastel ega leitud paleosoilistel kiir-uimsetel kaladel ja antud kirjeldus võib kaasa aidata vastavate elementide äratundmisele fossiilses materjalis. Peenkühmline ultraskulptuur leiti *M. scorpius*'e tuberklitel.