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

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Abstract. Small to very small bones (ossicles) in one species each of the families Cyclopteridae and Liparidae (Cottiformes) of the Baltic Sea are described and for the first time illustrated with SEM images. These ossicles, mostly of dermal origin, include dermal platelets, scutes, tubercles, prickles and sensory line segments. This work was undertaken to reveal characteristics of the morphology, sculpture and ultrasculpture of these small ossicles that could be useful as additional features in taxonomy and systematics, in a manner similar to their use in fossil material. The scutes and tubercles of the cyclopterid *Cyclopterus lumpus* Linnaeus are built of small denticles, each having its own cavity viscerally. The thumbtack prickles of the liparid *Liparis liparis* (Linnaeus) have a tiny spinule on a porous basal plate; the small size of the prickles seems to be related to their occurrence in the exceptionally thin skin, to an adaptation for minimizing weight and/or metabolic cost and possibly to their evolution from isolated ctenii no longer attached to the scale plates of ctenoid scales. Nodular ultrasculpture was found on the tubercle denticles of *C. lumpus*, resembling some kinds of ultrasculpture seen in Palaeozoic vertebrates. Samples from the posterior part of the head of *C. lumpus* and the anterior part of the trunk of *L. liparis* each contained an ossified sensory line segment with distinct characteristics, as also reported in other cottoids.

Key words: morphology, sculpture, dermal units, Actinopterygii, Cottiformes, Cyclopteridae, Liparidae, lumpsucker, *Cyclopterus*, sea snail, *Liparis*, Baltic Sea.

INTRODUCTION

An Estonian Science Foundation project to investigate the fine structure of the small ossicles of recent fishes of the Baltic Sea is based on knowledge from palaeontology that the morphology, surface sculpture and ultrasculpture of microscopic dermal elements are often characteristic of particular fish taxa and can be used in taxonomy and systematics for identification and characterization of taxa. They can also be useful for phylogenetic analyses, for elucidating faunal migration routes and for biostratigraphy. Microremains including dermal ossicles of extant fishes are useful for studies of Holocene geology and, in addition to larger bones of fishes and seals (Lõugas 1997, 1999; Paaver & Lõugas 2003), in archaeology. Moreover, in modern fish biology, the remains obtained from stomach contents could prove useful for understanding food preferences of fishes and sea birds. The ossicles provide much of the same kind of taxonomic information as available from the study of fish otoliths (e.g. Assis 2003) but ossicles and otoliths can be recovered in different preservational situations. In a previous study (Märss et al. 2010) the small dermal ossicles of three Baltic Sea cottids were investigated, described and illustrated. The present contribution examines, illustrates and describes the tiny dermal ossicles and bony units in the representatives of the related families Cyclopteridae and Liparidae.

The families Cyclopteridae and Liparidae have sometimes been combined into the family Cyclopteridae, but currently are thought to be sister groups and together represent one of the more basal clades of Cottoidei (Ueno 1970; Jackson 2004; Knudsen et al. 2007). The family Cyclopteridae (common name ‘lumpfishes’) contains about 27 species in seven genera (Ueno 1970) and the family Liparidae (‘snailfishes’) embraces approximately 345 species in 29 genera (Chernova et al. 2004; Knudsen et al. 2007). The genus *Cyclopterus* is represented by just one species, the lumpsucker *Cyclopterus lumpus* Linnaeus, 1758, while the genus *Liparis* contains 71 species considered valid by Chernova (2008), including the one studied here, the sea snail *Liparis liparis* (Linnaeus, 1766). Publications on both groups are numerous, especially those on liparids.

Recent phylogenetic studies of Liparidae (Knudsen et al. 2007) suggest that *Liparis* is among the more basal clades in the family and that *L. liparis* is among the more derived species of *Liparis*. One of the most comprehensive early reviews on liparid fishes is that by Burke (1930), which includes nearly all the material in America at that time. Burke's historical account of these fishes embraces the period since 1892. In that publication he describes morphologies, discusses the distribution and relationships and analyses modifications of generic characters. Included in his evaluation of the taxonomic value of the characters of all treated species are teeth and (skin) prickles. According to Burke (*ibid*., p. 12), Liparidae have two types of prickles termed thumb-tack and cactus-like prickles, the former consisting of a short spine and a round, flat 'head' (= base by our terminology), and the latter consisting of groups of spines arising close together in the dermis, the number of spines varying from 4 to 10 or more. Some species of liparids (e.g. of *Careproctus*) may have both types (*ibid*., p. 101). Burke noted (1930, p. 49) that the real significance of prickles was unknown even if they were used by some authors for establishing a new genus (e.g. Jordan & Snyder 1904). The prickles could appear only on either males or females, or be occasionally present seasonally, and if present, were not distributed evenly over the body. In *Liparis liparis*, studied herein, he did not find prickles at all. Burke's (1930) descriptions are accompanied by abundant drawings of whole fishes, their prickles and teeth.

Later publications on Liparidae describing new taxa were illustrated with pictures of body morphology and usually accompanied by schematic drawings of teeth (e.g. Kaoru Kido 1983; Stein 2005). Only in rare cases were the prickles from the skin of the body illustrated (e.g. Balushkin & Voskoboinikova 2008).

Concerning Cyclopteridae, Ueno (1970) deals in his comprehensive review with 26 species and a subspecies in seven genera from the North Pacific, North Atlantic and Arctic oceans. The work is richly illustrated with drawings of different bones, sensory lines, pharyngeal bones and gill rakers. The distributional pattern of tubercles and tubercle rows on the body is also given where available; the terminology for fourteen tubercle rows has been elaborated (Ueno 1970, fig. 2).

The introduction of scanning electron microscopy allowed its use for detailed study of fish scales, such as that by Roberts (1993) on ctenoid scales of Teleostei, revealing their microstructure and variety. Roberts distinguished true ctenii, as found in ctenoid scales, as those that develop separately from the plate of the scale and become attached to it ontogenetically. The variety of scale morphologies seen among cottiforms is very wide. In his study of osteology and phylogeny of cottoids Jackson (2004) included drawings and character analyses of scale morphology and distribution on the body. He further suggested that the thumbtack prickles and cactus-like prickles of various cottoids are in fact (homologous with) isolated and clustered ctenii as found on the ctenoid scales of related fish taxa. However, these prickles closely resemble the teeth and denticles found in the jaws, oral cavity, branchial tooth plates and gill rakers of cottoid fishes, but have been little studied and illustrated (an exception is the work of Chernova 2008, fig. 2, who illustrated with SEM images the three lobed teeth of *L. bathyarcticus*). Distinguishing teeth and small denticles from ctenii and prickles found in dissolved samples or sediment residues requires careful comparison with examples taken from known body parts, as illustrated in the present work.

On an even finer scale than ctenii, sculptural elements measured only in tens of micrometres have been referred to as ultrasculpture. They have been illustrated during the last few decades using the SEM. Such a very fine pattern has been observed on the scales of both agnathans and gnathostome fishes (Märss 2006) in the Palaeozoic, and some details of the external surface of scales and tubercles have been illustrated in publications on histology (e.g. Sire et al. 1997; Meunier & Brito 2004). However, even today new taxa are usually described without any SEM pictures of microscopic dermal units.

This paper deals with the small ossicles such as bony platelets, scutes, tubercles, prickles, ossified sensory line segments, oral and branchial denticles and ossified gill raker tubercles of the cottoid families Cyclopteridae and Liparidae of the Baltic Sea. The results were first reported during the 13th European Congress of Ichthyology in Klaipeda in 2009. Short descriptions of the units were given in the abstract (Märss et al. 2009). Comparable ossicles of representative Cottidae of the same region are described by Märss et al. (2010).

During this study the work was divided between the authors as follows: terminology was corrected by T. M., M. V. H. W., H. Š. and T. S., chemical preparation and some SEM images were done by J. L. and T. M., the ossicles were described by T. M. and the material was discussed by all authors.

MATERIAL AND METHODS

Dermal ossicles were examined in eleven specimens representing one species each of the families Cyclopteridae and Liparidae (see Table 1). The fishes were caught with the gillnet or pelagic trawl by fishermen

Table 1. Material studied

Fish	Collection No.	Male (M); female (F)	Total length (TL), cm	Date of catch	Location	Depth, m
Cyclopterus lumpus (L.)	GIT 584-7	Unidentified	16.7	29.04.08	Pärnu Bay	4–5
C. lumpus	GIT 584-9	M	14.5	28.04.08	East of Osmussaar Island	3
C. lumpus	GIT 584-54	F	12.0	29.01.09	West of Ainaži	35
C. lumpus	GIT 584-61	M	12.6	25.04.09	Vicinity of Krassi Island	10
C. lumpus	GIT 584-62	F	14.0	25.04.09	Vicinity of Krassi Island	10
C. lumpus	GIT 584-63	M	10.0	25.04.09	Vicinity of Krassi Island	10
Liparis liparis (L.)	GIT 584-11	F	10.0	27.04.08	East of Osmussaar Island	13
L. liparis	GIT 584-50	F	12.7	29.01.09	West of Ainaži	35
L. liparis	GIT 584-53	F	12.2	29.01.09	West of Ainaži	35
L. liparis	GIT 584-64	F	8.5	25.04.09	Vicinity of Krassi Island	10
L. liparis	GIT 584-65	F	8.1	25.04.09	Vicinity of Krassi Island	10

of the Estonian Marine Institute, University of Tartu, in the course of monitoring fish catches from the Baltic Sea (east of Osmussaar Island and in the vicinity of Krassi Island, Gulf of Finland; in Pärnu Bay and west of Ainaži, Gulf of Riga) (Fig. 1) between April 2008 and April 2009. Both male and female specimens of *Cyclopterus lumpus* were examined, along with one specimen of unidentified sex of *C. lumpus*; only females of *Liparis liparis* were available (Table 1). The 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 by the unit number of that specimen.

The following specimens of Liparidae, cleared and stained with alizarin red for bone and alcian blue for cartilage, were examined in the Museum of Zoology, University of Alberta, Edmonton, Alberta, Canada, to verify anatomical identification of the ossicles recovered from the chemically prepared specimens: *Liparis callyodon* (spotted snailfish): UAMZ2109 (four specimens); *L. florae* (tidepool snailfish): UAMZ2110 (two specimens); *L. herschelinus* (bartail snailfish): UAMZ6732 (three specimens), UAMZ5642 (three specimens). Additional examined material of cottoids was listed in Märss et al. (2010). The preparation methods used in this study are the same as those described in Märss et al. (2010).

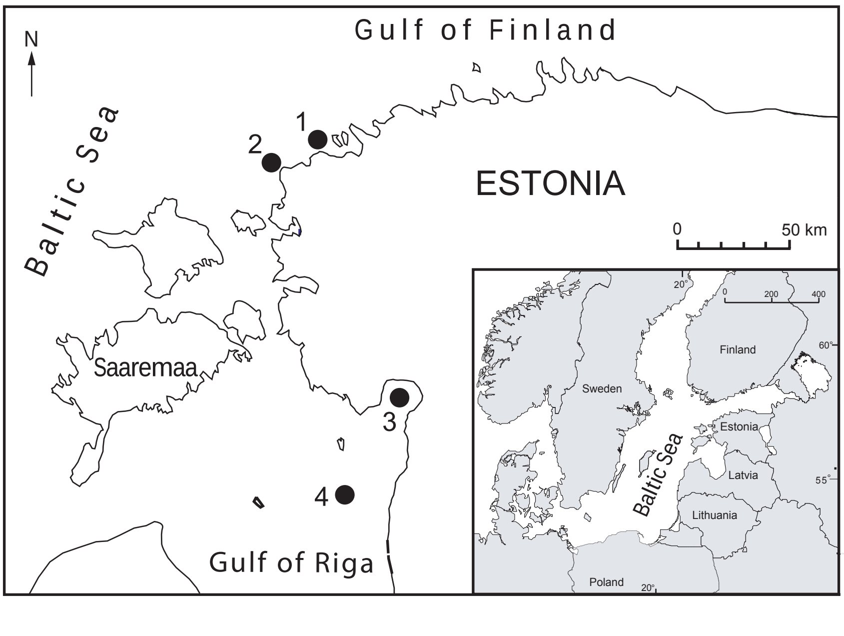


Fig. 1. Location of fishing grounds. 1, waters of Krassi Island; 2, east of Osmussaar Island; 3, Pärnu Bay; 4, west of Ainaži.

TERMINOLOGY

Representative types of ossicles of *Cyclopterus lumpus* and *Liparis liparis* are shown in Fig. 2. The terms used in descriptions are similar to those used by Märss et al. (2010) 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 and prickle; **basal rim**, free surface around the denticulated area of a tubercle; **base**, the lower, flat or conical part of a 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; **crown**, the top of a gill-raker tubercle bearing teeth and their sockets; **denticle**, a small, single, conical, tooth-like ossicle; **denticulate tubercles**, ossicles composed of a few to many denticles fused or grown together on a common base; **gill-raker tubercle**, smoothly convex to conical, superficially ossified tooth-bearing structure on the branchial arches that serves to retain food particles in the mouth; **scute**, a roof-like elongate or roundish conical denticulate ossicle with one or more upper spiny points; **sensory canal segment**, a single unit of the chain-like ossicles of the cephalic or trunk lateral line as illustrated in many cottoids by Jackson (2004); **swivel-joint platelets**, the paired perichondral ossifications of the ovoid or ball-shaped distal radial (pterygiophore) located between the proximal ends of the paired hemitrichs of the dorsal and anal fins, as illustrated for the carangid *Parastromateus* by Hilton et al. (2010); **thumbtack prickle**, a tiny ossicle with a sharp spinule on a circular basal plate (termed ‘skin spinules’ by Chernova 2008; interpreted as ‘isolated ctenii’ by Jackson 2004); **tubercle**, a general term for a small to medium-sized, usually convex platelet.

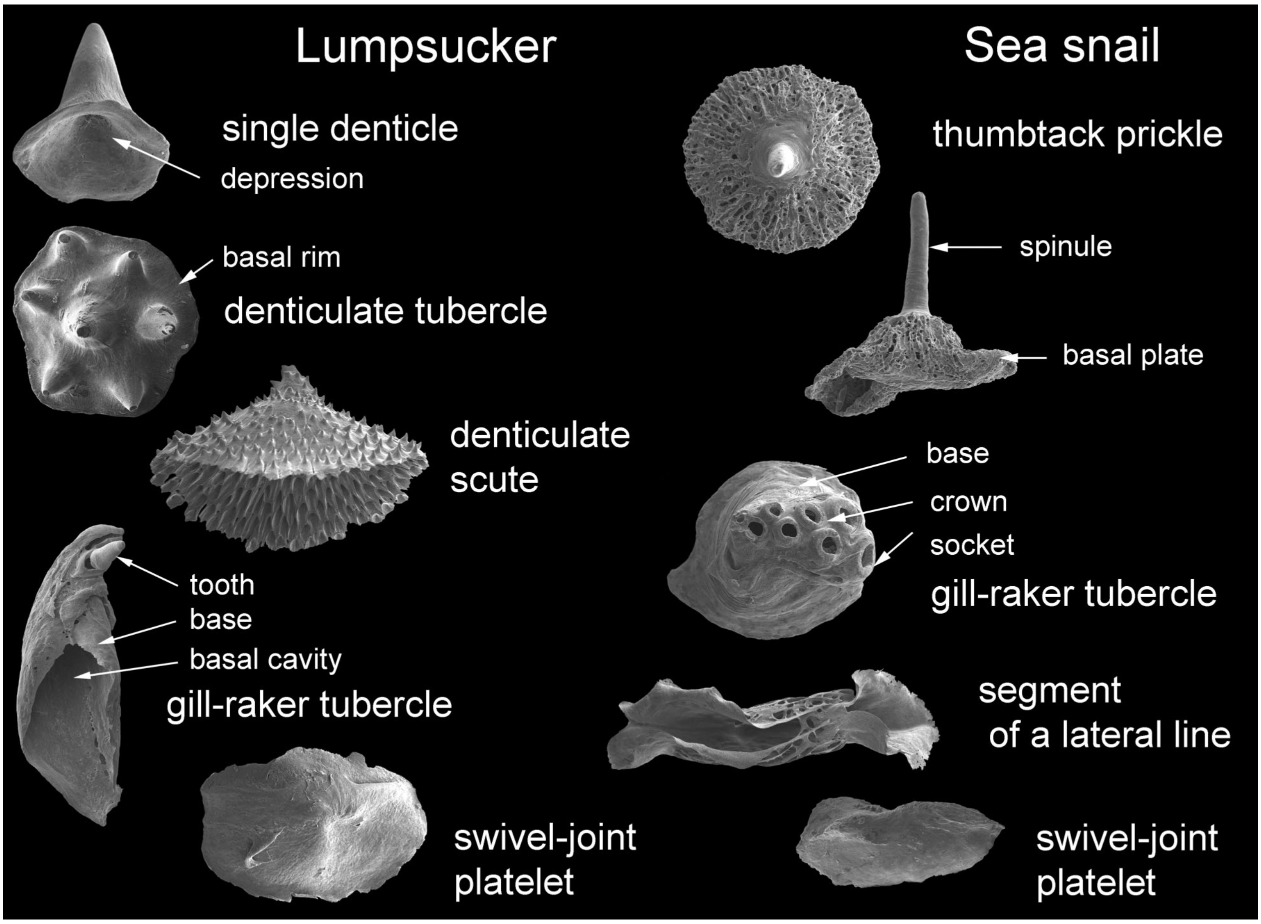


Fig. 2. Terminology of the small ossicles of *Cyclopterus lumpus* (lumpsucker) and *Liparis liparis* (sea snail) used in this paper; anterior is to the left for the ossicles of both species; the gill-raker tubercle is situated with its base directed towards gill filaments; the opening of the basal cavity is attached to the gill arch.

RESULTS

Order COTTIFORMES Regan, 1913 (as Cottoidei), sensu Wiley & Johnson, 2010
Family CYCLOPTERIDAE Bonaparte, 1832

Cyclopterus lumpus Linnaeus, 1758, lumpsucker
Figures 2, 3–5

Material. GIT 584-7, GIT 584-9, GIT 584-54, GIT 584-61, GIT 584-62, GIT 584-63 (for data on specimens see Table 1).

Description of ossicles. The thick skin is scaleless, except for tiny single bony denticles (Fig. 3A, O), denticulate tubercles (Fig. 3B–K) and denticulate scutes (Fig. 3L, M). The single denticles are very small (diameter of the base is 0.15–0.2 mm), conical and surrounded by a rather wide, smooth basal rim (Fig. 3A), the upper surface of which may have small pores (Fig. 3N). Each tiny conical denticle has its own depression viscerally (Fig. 3H, I, L, M, O, P).

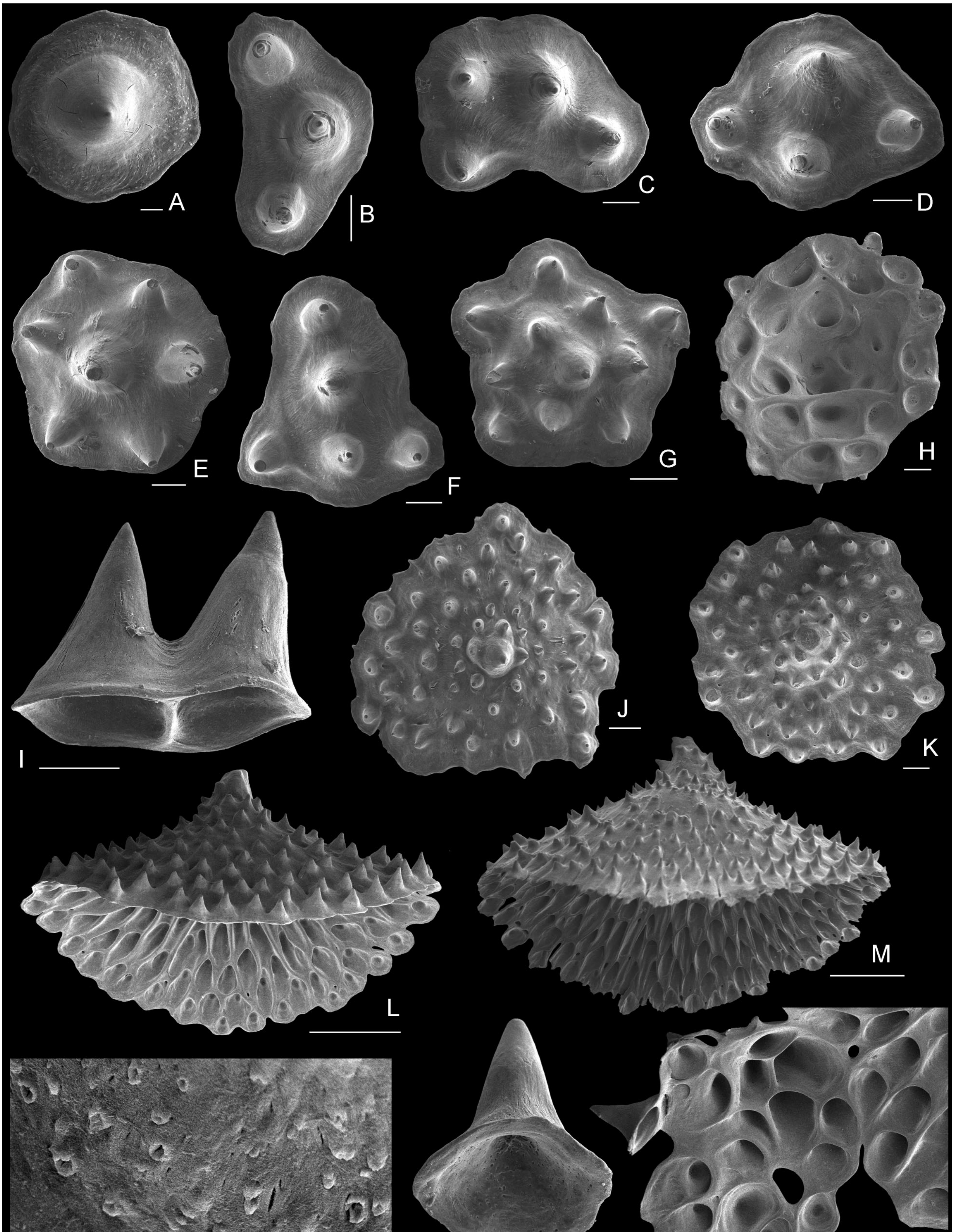
Transitional forms from a single denticle with a basal rim to larger denticulate tubercles having also the basal rim are common (see Fig. 3B–K). The number of denticles varies greatly and can be over 60 per tubercle. The scutes (Fig. 3L, M) are the largest ossicles in the skin; they are conical, may be somewhat compressed and are taller than tubercles. The conical scutes and roundish larger denticulate tubercles have their largest denticle in the middle (Fig. 3J, K). Each denticle, whether single or combined in a denticulate tubercle or scut, has a depression in its visceral side (Fig. 3H, L, M, P). These ossicles are distributed on the body, either scattered or in rows.

The scutes are arranged in longitudinal paired rows along the dorsolateral, lateral and ventrolateral sides of the body, and a single row is found along the dorsal midline (Fig. 4), on top of the first dorsal fin, which is hidden under the skin. A short dorsal row occurs anterior to the 2nd dorsal fin on both sides of the body. The number of scutes in the rows varies, as illustrated by the 12 cm long female specimen GIT 584-54. Its mediodorsal row has five large plates. The scutes of this row also have twin peaks, which are usually directed upwards or posteriorly; the peaks of the posteriormost two scutes are directed anteriorly. The scutes are large: a single one is 5.0 mm, a twin (the first and second scutes grown together) 10.0 mm long. The median dorsal row is caudally followed by four scutes on both sides, increasing in size posteriorly. The rows contain also triplets: a right-side triplet is 7.8 mm (a single scute 4.5 mm) and a left-side triplet 6 mm long. Dorsolateral rows, starting behind the nasal openings and running above the eyes, posteriorly as far as the caudal fin, have 24 scutes on the left side and 28 on the right side, and among these are some twins. Scutes on the left side (from anterior to posterior) are 2.5, 3.7, 4.0, 2.0 and 0.7 mm long. The largest scutes of this specimen are situated in the lateral row, which starts behind the head and reaches the caudal fin. The left lateral row has 20 and the right one 19 scutes. Seven scutes measured in this row (from anterior to posterior) are 6.5, 7.2, 9.0, 5.2, 2.8, 1.2 and 0.6 mm long. The scutes in the ventrolateral row are also large, with seven scutes on each side, the peaks of all scutes directed posteriorly. Scutes on the left side are 10.0 (a twin), 7.9, 5.8, 5.0, 4.0 and 1.0 mm long. A rather distinct mandibular row of tubercles, with larger tubercles occurring posteriorly and smaller anteriorly, passes along the edge of the lower jaw.

Scattered, flattened or slightly convex tubercles of different sizes and numbers of denticles occur on the rest of the body. The dorsal side of this specimen has more smaller tubercles than the ventral side. On the head, above the upper lip and behind the eyes, and on the sides of the 1st dorsal fin, the tubercles vary greatly in size and accordingly in the number of denticles (1–10, rarely over 10). Very many tiny single denticles are found on the sides of the trunk close to the 1st dorsal fin and posterior to it. Ventrally, between the left and right ventrolateral rows, scattered tubercles are more numerous immediately behind the modified pelvic fins that form a suction disk; many tiny single denticles also occur close to that area. Small areas, where the skin lacks denticles, are situated on the lower lip and in a short area below that, and between the lateral and ventrolateral rows up to the beginning of the anal fin.

The cephalic sensory canal is represented by a bony tubular ossicle on each side, each with a side branch. The illustrated example (Fig. 5C) is from the postorbital (temporal) canal on the left side of the head of specimen GIT 584-54-3. It is 3.95 mm long and has rare fine pores along with several large openings in the tubule walls. Another such unit comes from the left side of the same sensory canal of GIT 584-61. It is 6.15 mm long and the width of the tube is 0.7–1.3 mm; the tube of the side branch is 1.75 mm long and 0.4–0.6 mm wide.

The ossified parts of the gill rakers from the branchial arches of left and right sides are rather simple, cone-shaped and tapered upwards (Fig. 5A, B, E–H; see also Fig. 2, on the left side). The rakers are 0.7–1.2 mm high. In 14 cm long specimen GIT 584-62 the cape-like rakers have a split basal portion extending 2/3 of the entire height. The gill raker is attached with its slit side to the gill arch. There are up to two teeth in each raker, one of which is at the uppermost peak and the other just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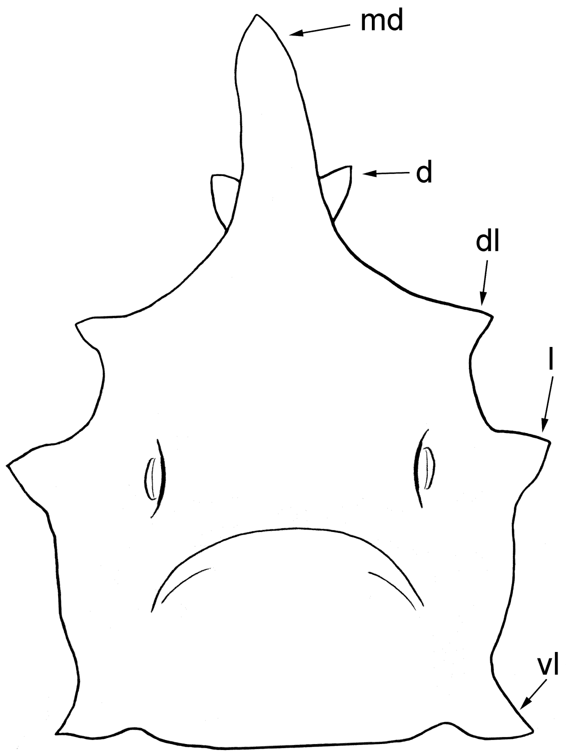


Fig. 4. *Cyclopterus lumpus* Linnaeus. Schematic drawing of fish in anterior view to show the placement of the rows of denticulate scutes. Abbreviations: d, dorsal; dl, dorsolateral; l, lateral; md, mediodorsal; vl, ventrolateral.

slightly below it. The teeth point in different directions, but still both extend up and to the side, towards the pharyngeal cavity and gill slit.

Very thin ossicles (Fig. 5I–K), here termed swivel-joint platelets, come from the base of the anal fin. They are the paired, outer ossified portions of the ovoidal distal pterygiophores that contribute to the swivel joints between themselves and the bases of the paired fin-ray hemitrichs. Each ossicle of a pair is rather small, 0.7–0.8 mm long, with a convex outer surface (Fig. 5I, J) and a smooth, concave inner surface (Fig. 5K). Its outer surface has a very weak cross-shaped ridge (Fig. 5I).

Nodular ultrasculpture occurs on the dermal denticles (Figs 3D, 5M–O). The denticle surface can be smoothly covered by these nodules (Fig. 5N) or new nodules, which cover older ones, form an uneven knobby surface (Fig. 5M, O). The teeth of both the upper and the lower jaws of specimen GIT 584-54 have a ring of nodules around their tips (Fig. 5D, L), at the place where the ‘acrodin cap’, which is characteristic of actinopterygian teeth (Ørvig 1978), meets the main shaft of the tooth.

Growth of tubercles. The dermal tubercles and scutes grow around their margins as each more distal row of denticles is added. In smaller tubercles with fewer denticles the tubercle margins are smooth, but scutes and larger tubercles composed of many denticles have scalloped margins.

Family LIPARIDAE Scopoli, 1777

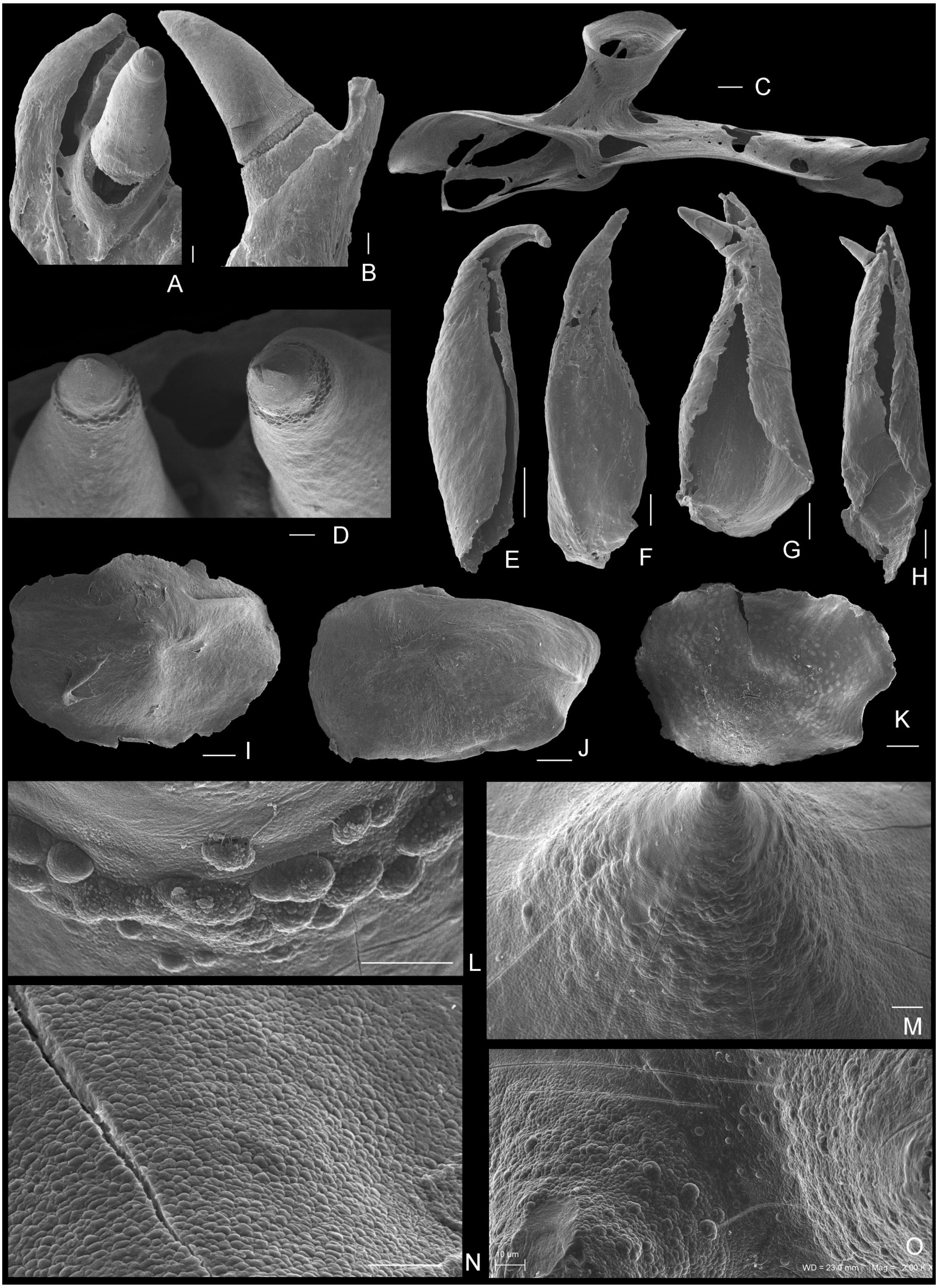
Liparis liparis (Linnaeus, 1766), sea snail
Figures 2, 6

Material. GIT 584-11, GIT 584-50, GIT 584-53, GIT 584-64, GIT 584-65 (for data on specimens see Table 1).

Description of ossicles. The marginal teeth of the jaws are mostly tricuspid, as noted by Ueno (1970). The tricuspid teeth are small, with a slightly bent median tip (Fig. 6A–C); all three cusps are sharp-edged. Lining the oral and pharyngeal cavities are gill-raker tubercles and branchial tooth plates. The ossified parts of the gill rakers are rather simple and small (the length along the longer axis is 0.35–0.47 mm), roundish to elongate, convex and widely open ossicles, with one or two rows of teeth near one edge (Fig. 6G–K). Branchial tooth plates are larger (1.25 + 1.8 is the base + crown length along the longer axis of the unit), more complex, suboval ossicles that bear many teeth on a very porous basal plate (Fig. 6M). Branchial tooth plates and gill-raker tubercles bear simple, slender, conical teeth (Fig. 6D, E). The teeth on tooth plates and tubercles were lost during chemical treatment of samples and only sockets with circular bases surrounding circular openings were left (Fig. 6G, J–L).

The skin on the body is thin, loose and bears sparse, minute thumbtack prickles (Ojaveer 2003). Thumbtack prickles are more numerous dorsally on the head. Samples from the left side of specimen GIT 584-50 had

Fig. 3. *Cyclopterus lumpus* Linnaeus. Bony denticulate tubercles and scutes. **A–G**, **J**, **K** and **N** (close-up of A) are in external view; **H** and **P** are in base view; **I**, **L**, **M**, **O** are in oblique base view. A = N, GIT 584-54-6; B, GIT 584-9-10; C, GIT 584-9-12; D, GIT 584-9-11; E, GIT 584-9-14; F, GIT 584-9-13; G, GIT 584-9-15; H, GIT 584-54-27; I, GIT 584-54-14; J, GIT 584-9-6; K, GIT 584-7-2; L, GIT 584-7-3; M, GIT 584-9-7; O, GIT 584-54-6; P, GIT 584-54-16. The specimens were caught from west of Ainaži, from Pärnu Bay and east of Osmussaar Island. Scale bar for A and O is 20 µm, for B–F, H, I, L, M, P 100 µm, for N 10 µm and for G, J, K 200 µm.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altogether 27 prickles: 12 from the head, a few of them broken, 10 from just behind the head to the end of the 1st dorsal fin and 5 from between the end of the 1st dorsal fin and the beginning of the caudal fin. Thumbtack prickles are all very small (diameter of the basal plate 0.27–0.35 mm) and of the same overall morphology (Fig. 6L, N–R). They have a porous, roundish basal plate and a single spinule arising from the centre of that plate. The spinule and a small area around it on the surface of the basal plate are smooth. The spinule is 0.2 mm high and of the same width nearly along its whole height, becoming pointed just at the peak. The prickle base is spongy, with elongate pores, cavities and canals running radially from the spinule towards the basal plate margin. The lower side of the plate is also porous (Fig. 6P) but less so than the upper surface, and concave.

A skin sample from GIT 584-53, extending from the left side of the head to the end of the 1st dorsal fin, contained, in addition to prickles, one sensory canal segment. A sensory canal segment from the lateral line was also found in a sample taken from the anterior part of the trunk just behind the head of GIT 584-50 (Fig. 6S). It is 2.22 mm long, slightly curved and its wall is porous, with roundish openings in deeper layers and quadrangular ones in outer layers. Both anterior and posterior canal openings are somewhat rounded, the posterior opening with a longitudinal slit. Vertical, rather high septae occur between the pores to strengthen the segment wall. These ossicles likely correspond to the suprabrachial sensory pore of *Liparis* noted by Chernova (2008, fig. 1a).

Swivel-joint platelets from the fin base (Fig. 6T, U) are very thin, small (0.4–0.7 mm long) and have a relatively high and strong longitudinal ridge with a raised and pointed tip (Fig. 6U). The basal plate is slightly convex, compact and lacks pores.

DISCUSSION

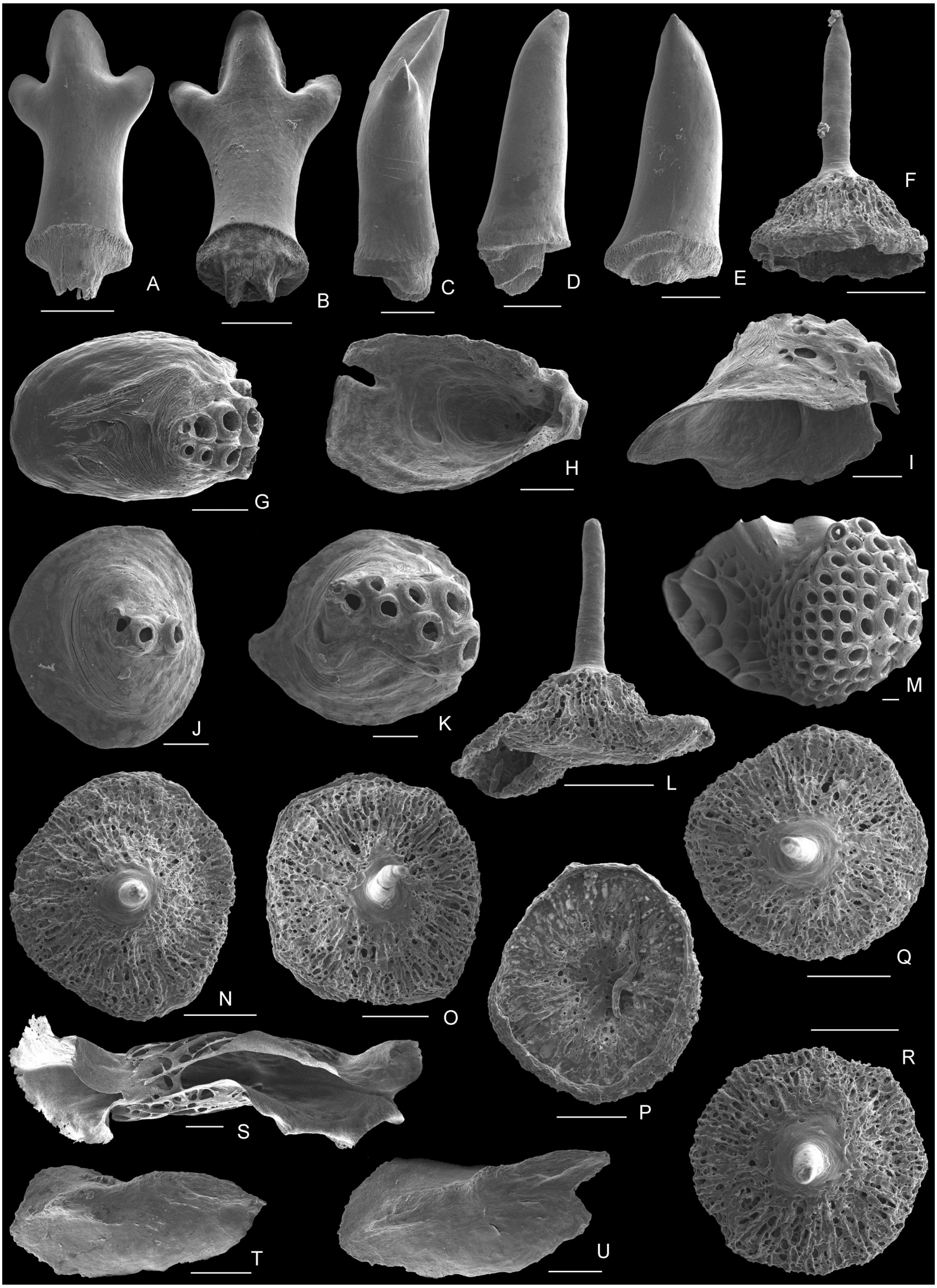
The morphology, variability, ultrasculpture and inferred growth of small dermal and other ossicles of *Cyclopterus lumpus* (lumpsucker) and *Liparis liparis* (sea snail) from the Baltic Sea can be compared with those seen in three genera and species (*Triglopsis quadricornis* – fourhorn sculpin, *Myoxocephalus scorpius* – shorthorn sculpin, *Taurulus bubalis* – longspined bullhead) of the related cottoid family Cottidae (sculpins) as described by Märss et al. (2010).

The morphology of dermal ossicles varies among the examined cottoids of the Baltic Sea. Both *Triglopsis quadricornis* (Märss et al. 2010) and *Cyclopterus lumpus* have a few rows of dermal ossicles along with scattered ones. *Cyclopterus lumpus* has scutes and tubercles composed of numerous small, cone-shaped denticles. Each denticle is surrounded by a smooth rim and has its own deep cavity viscerally. The largest denticles occur in the middle of the scutes and tubercles, with smaller ones towards the margins; in the fourhorn sculpin, however, the largest denticles occur at the margins. There are no hollows or cavities corresponding to the spinules in the visceral sides of the basal plates of the tubercles in the fourhorn sculpin. The spinules and denticles in both *T. quadricornis* and *C. lumpus* form integrated structures with basal plates, although in the latter this integration is weaker than in the former. The dermal units of both taxa grew at the margins, but the spinules and denticles, having different features, may have been added in different ways.

Young specimens of Baltic *C. lumpus* lack bony scutes (Ojaveer & Ojaveer 2003). Larink & Westheide (2006, fig. 2) illustrated *C. lumpus* of unidentified age with indistinct rows of plates (= scutes). According to Ueno (1970, p. 152), sometimes the skin is entirely free from small tubercles and the prickles on the large tubercles are only weakly developed. He presumed that low temperature and low salinity may influence the development of tubercles as well as body form. In our material the abundance and development of tubercles certainly depend on the age of an individual specimen.

Dermal ossicles of *Liparis liparis* differ radically from those of the other Baltic Sea cottoids (Märss et al. 2010, and this work). The compound units occurring in *T. quadricornis* and *Cyclopterus lumpus* are lacking in *L. liparis*. Instead, its skin bears very tiny thumbtack

Fig. 5. *Cyclopterus lumpus* Linnaeus. **A**, **B**, **E–H**, gill-raker tubercles; A, B, G, H from the left side and E, F from the right side of the head (A is close-up of the gill-raker tubercle in Fig. 2; B is close-up of H); **C**, temporal sensory canal segment from the left side of the head; **D**, a part of the jaw with teeth; **I–K**, platelets from the swivel joints of fins; **L**, close-up of the left tooth with 'pearls' in D; **M–O**, nodular surface of denticles. A, GIT 584-62-11; B = H, GIT 584-62-8; C, GIT 584-54-3; D = L, GIT 584-54-5; E, GIT 584-62-5; F, GIT 584-62-3; G, GIT 584-62-9; I, GIT 584-54-18; J, GIT 584-54-25; K, GIT 584-54-24; M, GIT 584-9-11; N, GIT 584-7-4; O, GIT 584-9-4. Specimen GIT 584-7 was caught from Pärnu Bay, GIT 584-9 from east of Osmussaar Island, GIT 584-54 from west of Ainaži, Gulf of Riga, and GIT 584-62 from the vicinity of Krassi Island. Scale bar for A, B, D is 20 µm, for C 200 µm, for E–K 100 µm and for L–O 10 µm.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prickles, each with a nearly round, porous basal plate and a single high vertical spinule. The number of prickles in the skin is low. Interestingly, the skin of *L. liparis* oxidated ('dissolved') in H_2O_2 much more slowly than the skin of other taxa of this order. The skin of another species of Liparidae, *Paraliparis devriesi* Andriashev, is nearly scaleless, having only a few 35–45 μm long thumbtack prickles embedded in the superficial epidermis (Eastman et al. 1994). *Paraliparis* has a light skeleton with a low mineral content to lighten the body (*ibid*.). The small size of the prickles and the porosity of their basal plates in the Baltic Sea *L. liparis* must have a similar effect; the small size of the prickles may also minimize expenditure of metabolic resources and is obviously also related to their being carried in the exceptionally thin skin of this species.

At least one pair of ossified sensory line segments is SEM documented in both *C. lumpus* and *L. liparis*. *Cyclopterus lumpus* has a three-branched, porous ossicle in its cephalic postorbital sensory canal; more posterior lateral line ossicles are lacking, as the lateral line is absent in this species (Ojaveer & Ojaveer 2003). The same ossicle seen in two fish specimens, which are of nearly the same length, differs greatly in size: in one specimen it is 6.15 mm long and in the other only 3.95 mm long.

The sensory line segment of *L. liparis* is porous, with quadrangular pore openings in the upper layer and vertical thin septae arising from the surface; the pores become roundish inside the segment wall. The quadrangular shape of the openings differs from the shapes in all other Baltic Sea cottoids (*C. lumpus*, *Triglopsis quadricornis*, *M. scorpius* and *Taurulus bubalis*), which all have roundish pores (Märss et al. 2010). The vertical, rather high septae of the sensory canal segment probably strengthen the wall while contributing little weight. The sensory line segment of *L. liparis* was found in the anterior part of the trunk, but no such unit was present in more posterior skin samples of this particular specimen. According to Chernova (2008, fig. 1a), in *Liparis* there is on each side a single sensory pore called the suprabranchial pore, dorsal to the external gill slit, at the posterior end of the temporal sensory line, opening from a short ossified tube. In *Paraliparis devriesi* the cephalic lateral line and anterior lateral line nerve are well developed, while the trunk lateral line is similarly reduced to a single suprabranchial pore innervated by a small posterior lateral line nerve (Eastman & Lannoo 1998). The ossified sensory line segment of *L. liparis* undoubtedly corresponds to this suprabranchial pore.

The ossified swivel-joint platelets (paired ossicles of the distal pterygiophores) in the anal fin region of both *C. lumpus* and *L. liparis* occur also in the cottids *Triglopsis quadricornis*, *Myoxocephalus scorpius* and *Taurulus bubalis* (Märss et al. 2010). In the cottids the platelets are small, slightly convex, paired and each pair together is symmetrical, with a ridge on the convex external surface and with a smoothly concave internal side. In *T. quadricornis* the ridge and vascularization are strongest, while in *C. lumpus* the ridge is weakest; homologous platelets of *L. liparis* and *C. lumpus* have a rather compact, non-porous construction.

Ueno (1970, fig. 64D) illustrated gill rakers of *C. lumpus* as much simpler than found and illustrated by SEM in our material. Ueno (1970) said that plankton feeders have numerous, crowded, elongate and fine rakers while predators have few, separated, short and stubby rakers, as is common in other fish taxa. In his work the gill rakers have no visible tooth, while we discovered one to two teeth attached to each. Gill rakers of Baltic cottiforms differ in complexity (Märss et al. 2010, and this work). Those of *L. liparis* have multiple teeth in rows but the number is smaller than in other treated taxa. Gill-raker tubercles of *Taurulus bubalis* also have teeth in rows but the teeth are much more numerous; in *Triglopsis quadricornis* and *M. scorpius* the teeth are roughly in rings, except for a few strongly elongated rakers (Märss et al. 2010).

Nodular ultrasculpture was discovered in *Cyclopterus lumpus*, surrounding the denticles on dermal tubercles and forming a ring around the base of the presumed acrodin cap of jaw teeth. The nodular ultrasculpture covers most of the surface of denticles, while the acrodin caps occupy just their tips.

Somewhat similar nodular ultrasculpture has been recognized on the dermal elements of Palaeozoic mongolepid ?chondrichthyans from China (Sansom et al. 2000). Some other fossil fishes also have a nodular ultrasculpture on their scales but it differs strongly in

Fig. 6. *Liparis liparis* (Linnaeus). **A–C**, separate teeth; **D**, **E**, teeth from the tubercles; **F**, **L**, **N–R**, thumbtack prickles; **G–K**, gill-raker tubercles; **M**, tooth plate; **S**, suprabranchial sensory canal segment; **T**, **U**, swivel-joint platelets. A–F, L, units in anterior? and/or side view; G, J, K, M–O, Q–S, units in external view; H, P, units in base view; I, T, U, units in oblique side view. A, GIT 584-50-2; B, GIT 584-50-6; C, GIT 584-50-3; D, GIT 584-50-4; E, GIT 584-50-5; F, GIT 584-50-16; G, GIT 584-11-2; H, GIT 584-50-13; I, GIT 584-50-12; J, GIT 584-50-8; K, GIT 584-50-11; L, GIT 584-50-20; M, GIT 584-50-23; N, GIT 584-50-14; O, GIT 584-50-21; P, GIT 584-50-18; Q, GIT 584-50-15; R, GIT 584-50-19; S, GIT 584-50-22; T, GIT 584-65-4; U, GIT 584-65-5. Specimen GIT 584-50 was caught from west of Ainaži, Gulf of Riga, and specimen GIT 584-65 from the vicinity of Krassi Island. Scale bar for A–L, N–R, T, U is 100 μm, for M and S 200 μm.

measurements (the nodes being very fine: 1–2 µm in Acanthodii, see Beznosov 2001; 2.75–9.07 µm in Actinopterygii, see Gayet & Meunier 1986). The ultrasculpture described on Palaeozoic fish scales has been said to have diverse origins. It has been considered as imprints of epidermal cells (Gross 1973; Schultze 1977), a reflection of the probable mode of ossification or as a mechanism for better attachment of the epidermis on the scale surface (Afanassieva 2004).

Overall, the morphology, ultrasculpture and inferred growth patterns of the small dermal and other ossicles of both *Cyclopterus lumpus* and *Liparis liparis* differ significantly from those of each other and even moreso in structure and variety from the corresponding ossicles of the Cottidae studied by Märss et al. (2010). Further comparative work is necessary to learn whether these differences extend to the level of different species within a genus, but the present study suggests that there are strong differences between genera and families that may be of value in phylogenetic and faunal studies.

CONCLUSIONS

- The dermal and other small ossicles of the cottoids *Cyclopterus lumpus* (Cyclopteridae) and *Liparis liparis* (Liparidae) from the Baltic Sea were studied and described for the first time by using SEM imagery.
- The morphology and sculpture of units of these species differ noticeably, suggesting that such details may be useful in the taxonomic and systematic studies, allowing identification of taxa from small ossicles found in sediment residues or gut contents. These data may be useful for biostratigraphic and biogeographic studies such as those on the evolution of the Baltic Sea or on fish migrations and community structure.
- The skin of *L. liparis* is very thin and bears extremely tiny prickles. Their reduced mineral content may serve to consume fewer metabolic resources. The small size may be a function of the thinness of the skin and lighten the body, as has been suggested also for *Paraliparis devriesi* (Eastman et al. 1994). It has been opined by other workers (e.g. Jackson 2004) that prickles are homologous with isolated ctenii of ctenoid scales in other Acanthopterygii. Comparison of prickles in diverse liparid species might reveal variation that would test this hypothesis.
- Dermal tubercles of *C. lumpus* are compound structures, formed of one to many denticles each with its own basal plate and depression in it. The tubercles and larger scutes grow by addition of denticles to their external margins. During early growth of the tubercle, its margin is smooth, but later the margins of tubercles become indented or scalloped.
- Fine nodular structure, which can be treated as ultrasculpture, was found surrounding the denticles of tubercles of *C. lumpus*, as well as in a ring below the acrodin cap of its jaw teeth. Ultrasculpture may correspond to the type of scale surface structure known already in Palaeozoic (Early Silurian) vertebrates, namely mongolepid ?chondrichthyans from China (Sansom et al. 2000, fig. 14d).
- Samples from the head of *C. lumpus* and from the anterior part of the trunk of *L. liparis* contained ossified sensory line segments not illustrated earlier by SEM. The detailed structure of these ossicles differs greatly among Cottidae, Cyclopteridae and Liparidae and is potentially of taxonomic value.
- Both *C. lumpus* and *L. liparis* have thin, paired, symmetrical platelets in the swivel joints of dorsal and anal fin rays, enclosing their distal pterygiophores and located between the proximal ends of the fin-ray hemitrichs. These ossicles have only weak sculpture on their external surface. Such platelets have not been discovered in fossil material, but the described platelets may be recognized in the future if investigators are aware of their possible existence.
- Samples obtained from archaeological sites, gut contents or from sea-floor sediments will contain mixtures of ossicles from different parts of the body and from different species. The present work contributes to the illustration and description of the kinds of tiny ossicles to be expected in such samples. By sampling skin and associated structures from specific parts of the body of the fishes studied here, it was possible to identify most of the ossicles and place them in their correct anatomical position.
- Additional similar work is planned for other fish taxa whose ossicles would be anticipated in samples from the Baltic Sea. The same work can be extended to related fish taxa from elsewhere in the world. Identification of fishes by their small ossicles should allow reconstruction of past and present fish communities, in much the same way as otoliths have been used for many decades in species identification and community reconstruction. However, ossicles and otoliths will be successfully recovered from different preservational situations and thus their usefulness should be complementary.

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REFERENCES

Afanassieva, O. B. 2004. Microrelief on the exoskeleton of some early osteostracans (Agnatha): preliminary analysis of its significance. In *The Gross Symposium 2: Advances in Palaeoichthyology* (Lukševičs, E., ed.), *Acta Universitatis Latviensis, Earth and Environmental Sciences*, **679**, 14–21.

Assis, C. A. 2003. The lagenar otoliths of teleosts: their morphology and its application in species identification, phylogeny and systematics. *Journal of Fish Biology*, **62**, 1268–1295.

Balushkin, A. V. & Voskoboinikova, O. S. 2008. Revision of the genus *Genioliparis* Andriashev et Neelov (Liparidae, Scorpaeniformes) with description of a new species *G. kafanovi* sp. n. from the Ross Sea (Antarctica). *Journal of Ichthyology*, **48**, 201–208.

Beznosov, P. 2001. The scales of '*Acanthodes*' sp. from the Lower Kraipol Subformation (Upper Devonian, Frasnian) of Middle Timan. In *Struktura, veshchestvo, istoriya litosfery Timano-severoural'skogo segmenta* [*The Structure, Composition, History of Lithosphaere of the Timan-North Urals Segment*] (Burtsev, I. N. et al., eds), pp. 23–27. Institute of Geology of KSC, Syktyvkar [in Russian].

Bonaparte, C. L. 1832. *Iconografia della fauna Italica per le quattro classidegli animali vertebrati, tomo 3. Pesci*. Roma, Salviucci, without pagination, in 30 fasc, 78 pls. (1832: Fasc. 1, 2 pls.).

Burke, V. 1930. Revision of the fishes of the family Liparidae. *Bulletin of the United States National Museum*, **150**, 1–204.

Chernova, N. V. 2008. Systematics and phylogeny of fish of the genus *Liparis* (Liparidae, Scorpaeniformes). *Journal of Ichthyology*, **48**, 831–852.

Chernova, N. V., Stein, D. L. & Andriashev, A. P. 2004. Family Liparidae Scopoli 1777 – snailfishes. *California Academy of Sciences. Annotated Checklists of Fishes*, **31**, 1–72.

Eastman, J. T. & Lannoo, M. J. 1998. Morphology of the brain and sense organs in the snailfish *Paraliparis devriesi*: neural convergence and sensory compensation on the Arctic Shelf. *Journal of Morphology*, **237**, 213–236.

Eastman, J. T., Hikida, R. S. & DeVries, A. L. 1994. Buoyancy studies and microscopy of skin and subtermal extracellular matrix of the Antarctic snailfish, *Paraliparis devriesi*. *Journal of Morphology*, **220**, 85–101.

Gayet, M. & Meunier, F. J. 1986. Apport de l'étude de l' ornementation microscopique de la ganoïne dans la détermination de l'appartenance générique et/ou spécifique des écailles isolées. *Compte-Rendu de l'Académie des Sciences, Paris, Série II*, **303**, 1259–1262.

Gross, W. 1973. Kleinschuppen, Flossenstacheln und Zähne von Fischen aus Europäischen und Nordamerikanischen Bonebeds des Devons. *Palaeontographica*, **A142**, 51–155.

Hilton, E. J., Johnson, G. D. & Smith-Vaniz, W. F. 2010. Osteology and systematics of *Parastromateus niger* (Perciformes: Carangidae), with comments on the carangid dorsal gill-arch skeleton. *Copeia*, **2010**, 312–333.

Jackson, K. Y. 2004. *Contributions to the Systematics of the Cottoid Fishes (Teleostei: Scorpaeniformes)*. Ph. D. thesis, Department of Biological Sciences, University of Alberta, Edmonton, 181 pp.

Jordan, D. S. & Snyder, J. O. 1904. On a collection of fishes made by Mr. Alan Owston in the deep waters of Japan. *Smithsonian Miscellaneous Collections*, **45**, p. 230.

Kaoru Kido. 1983. New and rare liparidid species from the Okhotsk and Bering Seas and their adjacent waters. *Japanese Journal of Ichthyology*, **29**, 374–384.

Knudsen, S. W., Møller, P. R. & Gravlund, P. 2007. Phylogeny of the snailfishes (Teleostei: Liparidae) based on molecular and morphological data. *Molecular Phylogenetics and Evolution*, **44**, 649–666.

Larink, O. & Westheide, W. 2006. *Coastal Plankton*. Photo guide for European Seas. Verlag Dr. Friedrich Pfeil. München, 143 pp.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordinus, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Impensis Direct. Laurentii Salvii, Holmiae, 824 pp.

Linnaeus, C. 1766. *Systema naturae per regna tria naturae, secundum classes, ordinus, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio duodecima, reformata. Impensis Direct. Laurentii Salvii, Holmiae, 532 pp.

Lõugas, L. 1997. *Postglacial Development of Vertebrate Fauna in Estonian Water Bodies: a Paleozoological Study*. Dissertationes Biologicae Universitatis Tartuensis, **32**, Tartu, 184 pp.

Lõugas, L. 1999. Postglacial development of fish and seal faunas in the Eastern Baltic water systems. In *The Holocene History of the European Vertebrate Fauna. Modern Aspects of Research* (Benecke, N., ed.), pp. 185–200. Verlag Marie Leidorf, Rahden/Westfahlen.

Märss, T. 2006. Exoskeletal ultrasculpture of Early Vertebrates. *Journal of Vertebrate Paleontology*, **26**, 235–252.

Märss, T., Lees, J., Saat, T. & Špilev, H. 2009. The morphology and sculpture of dermal units of Scorpaeniformes of the Baltic Sea. In *13th European Congress of Ichthyology, 6th–12th September, Klaipeda, Lithuania. Abstract Book*, p. 35. Klaipeda University, Klaipeda.

Märss, T., Lees, J., Wilson, M. V. H., Saat, T. & Špilev, H. 2010. The morphology and sculpture of ossicles in the

Cottidae (Teleostei) of the Baltic Sea. *Estonian Journal of Earth Sciences*, **59**, 216–237.

Meunier, F. J. & Brito, P. M. 2004. Histology and morphology of the scales in some extinct and extant teleosts. *Cybium*, **28**, 225–236.

Ojaveer, E. 2003. Sea snail, *Liparis liparis* (L.). In *Fishes of Estonia* (Ojaveer, E., Pihu, E. & Saat, T., eds), pp. 357–358. Estonian Academy Publishers, Tallinn.

Ojaveer, E. & Ojaveer, H. 2003. Lumpsucker, *Cyclopterus lumpus* L. In *Fishes of Estonia* (Ojaveer, E., Pihu, E. & Saat, T., eds), pp. 354–356. Estonian Academy Publishers, Tallinn.

Ørvig, T. 1978. Microstructure and growth of the dermal skeleton in fossil actinopterygian fishes: *Birgeria* and *Scanilepis*. *Zoologica Scripta*, **7**, 33–56.

Paaver, T. & Lõugas, L. 2003. Origin and history of the fish fauna in Estonia. In *Fishes of Estonia* (Ojaveer, E., Pihu, E. & Saat, T., eds), pp. 28–46. Estonian Academy Publishers, Tallinn.

Regan, C. T. 1913. The osteology and classification of the teleostean fishes of the order Scleroparei. *Annals and Magazine of Natural History*, **11**, 169–184.

Roberts, C. D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. *Bulletin of Marine Science*, **52**, 60–113.

Sansom, I. R., Aldridge, R. J. & Smith, M. M. 2000. A micro-vertebrate fauna from the Llandovery of South China. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **90**, 255–272.

Schultze, H.-P. 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläontologische Zeitschrift*, **51**, 152–168.

Scopoli, G. A. 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae*. Prague. Introd. Hist. Nat. i-x + 506 pp.

Sire, J.-Y., Quilhac, A., Bourguignon, J. & Allizard, F. 1997. Evidence for participation of the epidermis in the deposition of superficial layer of scales in zebrafish (*Danio rerio*): a SEM and TEM study. *Journal of Morphology*, **231**, 161–174.

Stein, D. L. 2005. Descriptions of four new species, redescription of *Paraliparis membranaceus*, and additional data on species of the fish family Liparidae (Pisces, Scorpaeniformes) from the west coast of South America and the Indian Ocean. *Zootaxa*, **1019**, 1–25.

Ueno, T. 1970. *Fauna Japonica: Cyclopteridae (Pisces)*. Tokyo, Academic Press of Japan, 233 pp.

Wiley, E. O. & Johnson, G. D. 2010. A teleost classification based on monophyletic groups. In *Origin and Phylogenetic Interrelationships of Teleosts* (Nelson, J. S., Schultze, H.-P. & Wilson, M. V. H., eds), pp. 123–182. Verlag Dr. Friedrich Pfeil, München.

Läänemere kahe võldaselise (Teleostei, Cottiformes, Cyclopteridae ja Liparidae) väikeste luuliste elementide morfoloogia ning skulptuur

Tiiu Märss, Janek Lees, Mark V. H. Wilson, Toomas Saat ja Heli Špilev

Artiklis on kirjeldatud ja esimest korda SEM-piltidega illustreeritud Läänemere kahe võldaselise, merivarblase *Cyclopterus lumpus* Linnaeus, 1758, ning pullukala *Liparis liparis* (Linnaeus, 1766), mitmesugused luulised elemendid, luuplaadikesed, tuberklid, ogad, küljejoonekanalite lülid ja hambad. Nende kahe taksoni luuliste elementide kuju ja skulptuuri saab edukalt kasutada perekondade eristamisel.

Nahaproovid *C. lumpus*'e peast ja *L. liparis*'e kere esiosast sisaldasid sensoorsete kanalite lülisid, mida seni ei ole täpsemalt kirjeldatud. Peenekühmuline ultraskulptuur leiti *C. lumpus*'e dermaalsetel tuberklitel ja hammastel. Selliseid pinnastruktuure on leitud ka paleosoiliste oletatavate kõhrkalade dermaalsetel elementidel. Mõlemal liigil leiti luustunud sümmeetrilised paarilised plaadikesed selja- ja anaaluime liigenditelt. Nende kahe taksoni puhul on need plaadikesed eriti õhukesed, *L. liparis*'el väiksemad kui Cottidae esindajatel.