The sculpture and morphology of postcranial dermal armor plates and associated bones in gasterosteiforms and syngnathiforms inhabiting Estonian coastal waters

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Abstract


Five fish species inhabiting Estonian coastal waters (Gasterosteus aculeatus L., Pungitius pungitius (L.), and Spinachia spinachia (L.) of the order Gasterosteiformes and Syngnathus typhle L. and Nerophis ophidion (L.) of the order Syngnathiformes) are described on the basis of the sculpture and morphology of their postcranial dermal armor plates, as revealed and illustrated by SEM images. This study shows that the shapes of these superficial skeletal elements vary by species as well as by their position on the body, whereas the sculpture on the bones is taxon specific. The detailed features allow the identification of isolated fossil and subfossil remains and show promise for future systematics studies.

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Introduction

Already at the beginning of the last century, Goodrich (1907) emphasized that the importance of scales in classification had been largely neglected. Several later researchers have tried to fill in this gap in respective studies. Cockerell (1913) described a broad range of differences in scale characters of representatives of bony fish. Similar studies were continued by Lagler (1947), Haque (1955) and many others. Besides classification, studies on the exoskeleton can offer useful material for identification of fishes, including analysis of the diet of piscivorous species (e.g. Britton and Shepherd 2005), determination of fish migrations (e.g. Daniels and Peteet 2004; Kristjánsson 2005). However, there are also several descriptive works. For example, Nelson (1971) compared pectoral and pelvic skeletons and some other bones in species of related families Aulorhynchidae and Gasterosteidae, including also G. aculeatus, Spinachia spinachia and Pungitius pungitius. Keivany and Nelson (2000) studied osteology in a taxonomic review of the genus Pungitius. But these studies...
focused on general morphology, not on sculptural elements. To some extent, the features of sculpture have been treated by Igarashi (1962, 1963, 1964, 1965, 1968, 1969, 1970a,b) in the discussion of the development and morphology of lateral plates in Japanese sticklebacks. A recent paper by Song et al. (2010) gave detailed ultrastructural and 3-D tomographic reconstructions of dermal armor plates in the single species G. aculeatus. The descriptions of sculptural elements on bones are lacking also in studies and taxonomic reviews of syngnathiforms (e.g. Dawson 1980; Kuiter 2001). An exception is the SEM study by Fedrigo et al. (1996). Treating the morphology and histology of scutes in three genera of Macroramphosidae, those authors drew attention to interspecies variations in sculpture.

Using the scanning electron microscope, the main objective of present study is to observe and record the main features of sculpture on the postcranial dermal armor and associated bones in gasterosteiforms and syngnathiforms of the Baltic Sea and to ascertain the occurrence or absence of ultrasculpture on the same bones. We not only describe the general morphology of the bones and their sculpture but also search for features of morphology and sculpture that distinguish the species found in this area from one another. In paleontology and archeology, it is common to find the assemblages of bones and scales that represent the fishes of a restricted region, such as the eastern Baltic Sea sampled in this study. For this paper, as a case study, we ask whether it is possible to identify and distinguish the dermal ossicles and scutes of gasterosteiform and syngnathiform species within that geographic area. If it is possible, then it might also be possible to distinguish and identify these or closely related species found in typical paleontological or archeological assemblages that contain a comparable diversity of species.

Instead of elasmoid scales, which are widespread among teleost species, the bodies of the studied species are covered by bony dermal plates to a greater or lesser extent. Unlike elasmoid scales, which are characterized by the presence of highly derived tissues (e.g. elasmodine), the dermal plates of gasterosteiforms and syngnathiforms are composed of bone tissue only (Sire and Huysseune 2003). Our initial observations showed that in young specimens, the pattern of the sculpture is still developing and has not reached its most distinctive form. As the main objectives of this study were to find diagnostic features for the species, we focused on adult individuals in which the features are best developed; the ontogenetic development of postcranial armor bones of studied species will be treated separately in the future. In addition, variations in the morphology and sculpture of the dermal armor in highly variable species such as G. aculeatus should be examined more fully in the future.

This is the third paper in a series describing dermal ossicles and associated bones in fishes of the Baltic Sea. The previous two papers dealt with the families Cottidae, Cyclopteridae, and Liparidae of the order Cottoiformes from the same region (Märs et al. 2010a,b).

Material and Methods

Postcranial dermal armor plates from 32 specimens of five species (G. aculeatus L., P. pungitius (L.), S. spinachia (L.), Syngnathus typhle L., N. ophidion (L.)) were used in this study. The fishes were caught with gillnets in the course of monitoring fish catches between March 2008 and June 2009. Geographically, the material originates from Eru Bay, the vicinity of Prangli Island, east of Osmussaar Island, the vicinity of Viilandi Island, Suur Väin Strait, and Pärnu Bay (Fig. 1). Sample sizes vary from 14 specimens for G. aculeatus to two specimens for S. typhle. The latter sample size was limited by availability of specimens caught during fisheries monitoring.

The collected specimens by location (GIT 584 – collection number; TL – total length, cm) are as follows: (1) Eru Bay: G. aculeatus (GIT 584-1, TL = 6.5), P. pungitius (GIT 584-2, TL = 5.1). (2) Vicinity of Prangli Island: S. spinacia (GIT 584-86, TL = 11.4; GIT 584-92, TL = 11.0). (3) east of Osmussaar Island: S. spinacia (GIT 584-13, TL = 14.5; GIT 584-14, TL = 14.5). (4) Vicinity of Viilandi Island: S. spinacia (GIT 584-73, TL = 11.9). (5) Suur Väin Strait: N. ophidion (GIT 584-37, TL = 13.5), S. typhle (GIT 584-36, TL = 18.0; GIT 584-39, TL = 17.0). (6) Pärnu Bay: G. aculeatus (GIT 584-21, TL = 5.6; GIT 584-22, TL = 6.5; GIT 584-23, TL = 7.5; GIT 584-28, TL = 5.8; GIT 584-29, TL = 6.3; GIT 584-30, TL = 6.8; GIT 584-66, TL = 7.0; GIT 584-67, TL = 6.2; GIT 584-68, TL = 4.0; GIT 584-76, TL = 6.6; GIT 584-77, TL = 6.0; GIT 584-85, TL = 6.2; GIT 584-87, TL = 6.8; GIT 584-91, TL = 6.3), P. pungitius (GIT 584-69, TL = 5.4; GIT 584-71, TL = 5.5; GIT 584-90, TL = 6.5), N. ophidion (GIT 584-35, TL = 20.2; GIT 584-70, TL = 21.3; GIT 584-74, TL = 10.3; GIT 584-75, TL = 17.0; and GIT 584-79, TL = 16.6).

The fishes caught were preserved in 70% ethanol. Fish bodies were washed to remove extraneous material such as loose scales of other taxa, sand grains and measured. Skin pieces were removed and put into a solution of 30% hydrogen peroxide (H2O2) and distilled water, buffered with 25% ammonia water (NH4OH) in the ratio of 4 : 2 : 1, respectively. The time for such a chemical treatment of samples varied, ranging from a day to 2–3 days, depending on the amount of organic material in the samples. After chemical treatment, the dermal units were washed with tap water in sieves with a mesh size of 0.01 mm and immersed in 65% ethanol. Before SEM studies, the units were kept in water for some time. Better-preserved specimens were semi-dried in open air, set on SEM stubs covered with double-sided sticky tape, dried, and then coated with gold. The specimens were scanned and photographed under scanning electron microscopes JEOL JSM-840A and Zeiss EVO MA15 at 10 kV.

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

Order Gasterosteiformes
Family Gasterosteidae
Gasterosteus aculeatus Linnaeus, 1758, three-spined stickleback
Figures 2 and 3

Lateral plates of the dermal bony armor cover each side of the body in a single row. The number of lateral plates is morph specific (i.e. it depends on the degree of plate development in each individual and can vary by locality, environment, and selection pressures in a population, e.g. Bell 1981, 2001; Reimchen 1983, 1995), and the size and the shape of a plate depend on its position on the body. The size of lateral plates is larger in the middle of the trunk and decreases toward the head and caudally. The anteriormost lateral plates (Fig. 2A) on the trunk are small and roundish, without particular processes. The following plates (Fig. 2B–D) become bigger and elongate dorso-ventrally in shape. The anterior edge of these plates is smooth, but the posterior edge is serrated (Fig. 2L). At level of the lateral line appear bony processes. The processes are conspicuous on the anterior edge of plates, but slight processes may also occur in some plates at the posterior edge. The processes and lateral line divide the plates into dorsal and ventral wings. On lateral plates above the pelvic girdle, the anterior processes are especially large and ventral wings are much longer than dorsal ones. Lateral plates that are overlapped by the basal plate of the dorsal spine or by the ascending process of the pelvic girdle have traces of the overlapping bone in the plate edge contours (Fig. 2E). Toward the posterior part of the body, the size of lateral plates declines continuously, the processes are smaller or even absent, and the lengths of the ventral and dorsal wings equalize (Fig. 2F–H). On the caudal peduncle, the shape of lateral plates becomes more triangular. The posterior roof of the plate becomes stretched out and forms a thin, very high crest in the middle of the plate (Fig. 2I–K). These plates are also called keel plates (e.g. Bell 1981; Reimchen 1983).

The surfaces of lateral plates are covered with nodular ridges, which can form both linear and network patterns (Fig. 2L). However, sculpture is missing on the anterior border. As a rule, the ridges do not cross each other, but their separate segments are connected through nodules (Fig. 2M).
The distribution of nodules on lateral plates is variable. On the lateral plates with a long ventral wing, nodules are dense in the area of the lateral line and the dorsal wing. On the ventral wing, the density of nodules on ridges decreases toward the abdomen. Lateral plates with similar lengths of dorsal and ventral wings show a more uniform distribution of nodules. Nodules are visible even on the tips of the thin, high crests of keel plates (Fig. 2K). The surface of lateral plates is penetrated by openings of various sizes. The largest openings are located at the level of the lateral line.

Dorsal and ventral plates (median plates) are anteroposteriorly elongated plates, which may have tapering or diverging ends (Fig. 2N-Q). The plates are supported by pterygiophores (Fig. 2Q). The surfaces of median plates are penetrated by the openings of various sizes and covered with a network of nodular ridges in the non-overlapped region (Fig. 2R,S). The distribution of nodules in the pattern area is uniform.

Dorsal and anal spines have generally a sharpened tip and a wide base with two small processes on the proximal end forming the socket of the spine. Each spine articulates on a condyle (Fig. 3A), extending vertically from a basal plate (basal). The first two dorsal spines are long (Fig. 3B). The lateral edges of these spines are equipped with spinules, and the surface of the spines is covered with parallel nodular ridges (Fig. 3C). However, the tip area of the spines is smooth. Flanges on the lateral edges of associated basal plates (Fig. 3D) are wide, rounded in shape and descending. The surface of the basal is penetrated by numerous openings of various sizes and covered with nodular ridges, which radiate from the center (Fig. 3E). The distribution of nodules in the pattern area is uniform. Compared with the first two dorsal spines, the third dorsal spine, the anal spine, and their basal plates are modest in size. Lateral edges of these spines have only a few larger spinules (Fig. 3F,G). The basal of the third dorsal spine has a broad rounded anterior edge, which may have up to three processes (Fig. 3H). These spines and the basal are covered with rare nodules and ridges. The basal of the anal spine is small, with narrow short flanges and a condyle in the anterior end (Fig. 3I). Each basal is supported by a pterygiophore.

The pelvic plate (also called pelvic bone or pelvic girdle) has a V-shaped structure and consists of ascending, anterior and posterior processes (Fig. 3J). The ascending process is high, flat, and expands dorsally, with a rounded or bifurcate tip. It is covered with longitudinal ridges bearing a few modest nodules (Fig. 3K). The anterior process is short and rounded (Fig. 3L). Its ventral part is covered with a network of nodular ridges, whereas the dorsal part bears ridges that curve onto the ascending process. The posterior process is long, tapered toward the tip, and has a few nodular ridges. Unlike the other ridges, the one on the lateral edge of the posterior process is stronger and covered with conspicuous nodules (Fig. 3M). The ventral edge of the pelvic plate is strongly serrated. The condyle, to which the spine is attached, is located at the angle between the ascending and posterior processes.

The pelvic spine is long, with a sharpened tip and wide base having two small processes on the proximal end forming the socket of the spine (Fig. 3N). The width and serration on the dorsal lateral edge of the spine are much more distinct than on the ventral edge. The spine surface is covered with parallel nodular ridges. However, the tip area of the spine is smooth.

The ectocoracoid is elongated anteroposteriorly and slightly warped in shape (Fig. 3O). The anterior end of this bony plate is somewhat sharp, but the width of the plate grows toward the posterior part, and it has a saddle-shaped end. The surface of the ectocoracoid is covered with nodular ridges (Fig. 3P). The arrangement of these ridges depends on their position with respect to the medial crest on the plate. Nodular ridges on the crest or above it run anteroposteriorly, but nodular ridges below radiate outward from the center.

The cleithrum consists of a triangular sculptured dorsal process, which has a posterior projection, and a narrow, vertically oriented ventral process (Fig. 3Q). The surface of the dorsal process is covered with nodular ridges. The ventral side of this triangular plate has a wide, thick edge where the density of nodules is higher than in the rest of the area (Fig. 3R).

_Pungitius pungitius_ (Linnaeus, 1758), nine-spined stickleback

Figure 4

Lateral plates are located on the anterior sides of the trunk and on the sides of the caudal peduncle. Lateral plates on the trunk are small, rhomboidal, or roundish (Fig. 4A,B). The edges of the plate are smooth. The lateral line canal runs anteroposteriorly in the middle of the plate. The lateral (keel) plates on the caudal peduncle are elongated to roundish (Fig. 4C,D). Some processes occur on the anterior and posterior ends of the plates, which supposedly help the adjacent plates get fixed with each other. A high crest runs anteroposteriorly in the middle of the plates above the lateral line canal.
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The surfaces of lateral plates are covered with a network pattern of smooth ridges (Fig. 4E), but also slight nodular sculpture is traceable on the crests of keel plates (Fig. 4C).

Dorsal and ventral plates (median plates) are anteroposteriorly elongated plates, which may have tapering or diverging ends (Fig. 4F–H). The plates are supported by a pterygiophore. The surfaces of median plates are penetrated by openings of various sizes and covered with a network of smooth ridges (Fig. 4I).

Dorsal and anal spines are quite of the same length, rounded, with sharpened tips and spines smoothly widening toward the base (Fig. 4J). The distal area of spines is smooth, but the proximal part may be covered with few grooves and openings inside them. The base of the spine has two small processes on the proximal end, forming the socket of the spine which articulates on a condyle extending vertically from the basal plate (basal) (Fig. 4K,L). Flanges of the basals are narrow and plane or slightly descending. The surfaces of flanges are penetrated by numerous openings which are separated by smooth ridges. Each basal is supported by a pterygiophore.

The pelvic plate, a V-shaped structure, consists of ascending, anterior and posterior processes (Fig. 4M). The ascending process is high, flat and expanding in the upper part and covered with branching smooth ridges (Fig. 4N). However, nodules are present on the high ridge located on the posterior edge of the ascending process. The anterior process is short, rounded, and covered with a network of smooth ridges (Fig. 4O). The posterior process is long, sharpens distally, and has a network of smooth ridges, whereas the lateral edge of the posterior process is strong and covered with nodules (Fig. 4P). The ventral edge of the pelvic plate is serrated. The condyle, to which the spine is attached, is located at the angle between the ascending and posterior processes.

The pelvic spine is long, with a sharpened tip and a wide base, which has two small processes on the proximal end forming the socket of the spine (Fig. 4Q). The dorsal lateral edge of the spine is wider than ventral edge. The spine surface is covered with parallel nodular ridges, but the frequency of nodules on them is uneven. The distal area of the spine is smooth.

The ectocoracoid is elongated anteroposteriorly and slightly warped in shape (Fig. 4R). The anterior end of this bony plate is sharper than the posterior end. The ventral edge is slightly concave, but the dorsal edge has two humps. The surface of the ectocoracoid is covered with a network of smooth ridges. Some nodules were observed only in the dorsal edge area (Fig. 4S).

The cleithrum consists of a triangular, sculptured dorsal process, which has a posterior projection, and a narrow vertically oriented ventral process (Fig. 4T). The surfaces of the dorsal process and the upper part of the ventral process are covered with smooth ridges. Nodular sculpture is only observed on the high crest on the ventral edge of the triangular dorsal process (Fig. 4U).

Spinachia spinachia (Linnaeus, 1758), boltnose

Figure 5

Lateral plates cover each side of the body in a single row. The plates on the trunk are oval or roundish. A robust medial crest runs anteroposteriorly in the middle of the plates, rises from front to rear and forms processes beyond the edges (Fig. 5A–C). On the caudal peduncle, the lateral plates become narrow and their dorsal and ventral wings forming an acute angle. There are many processes on the plate’s ends which supposedly help fix the adjacent plates with each other (Fig. 5D). The surfaces of lateral plates are penetrated by openings of various sizes and are covered with nodular ridges. Nodules in the crest area are much larger and more close by together than on the wings (Fig. 5E). A large opening of the lateral line canal is located below the crest in the anterior part of the lateral plates on the body.

Dorsal and ventral plates (median plates) are oval or slightly triangular in shape (Fig. 5F–J). A medial crest or separate higher ridges proceed anteroposteriorly in the middle of the plates. The plates may have many processes on plate ends and also on the edges of wings. The surfaces of median plates are penetrated by openings of various sizes and are covered with nodular ridges. The nodules in the crest area or on higher ridges are larger than those on the wings, where the nodules have quite modest dimensions (Fig. 5K). However, median plates become narrow near the tip of the tail and the crest or higher ridges disappear, as well as nodules. Median plates are supported by a pterygiophore.

Dorsal and anal spines are relatively short and slightly warped (Fig. 5L,M). They are roundish, with a sharpened tip and wide base. The surfaces of spines are covered with longitudinally nodular ridges, but the frequency of nodules on them is uneven. The tip area of the spine is smooth. The bases of spines have two small processes on proximal ends, which...
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articulate on a condyle extending vertically from the basal plates (basals). Dorsal basals are quadrangular, having processes on anterior and posterior ends and flanges on sides (Fig. 5L,M). The basal of the anal spine is small, triangular, and has a condyle in the anterior end (Fig. 5N). Flanges of the basals are of medium width; they are descending and have a slightly rounded outer edge. The surfaces of flanges are covered with longitudinally arranged high nodular ridges on the inner edges and lateral to them a network of ridges bearing rare modest nodules (Fig. 5O). Each basal plate is supported by a pterygiophore.

The pelvic plate consists of ascending, anterior and posterior processes (Fig. 5P). The ascending and anterior processes are long and taper to a point. The ascending process extends posteriorly rather than dorsally (as referred by Mural 1973). The posterior process is short and extends ventrally. The surface of the pelvic plate is penetrated by numerous openings and covered with a network of ridges bearing modest nodules. However, ridges with conspicuous nodules are present on the robust crest located in the middle of the anterior process and on the ventral edge of the ascending process (Fig. 5Q). The ventrally extending body of the plate and the posterior process have serration. The condyle, to which the spine is attached, lies at the angle between the ascending and posterior processes.

The pelvic spine is relatively short, with a wide base and a sharpened tip (Fig. 5R). The base has two small processes on the proximal end, forming the socket of the spine. The spine surface is covered with longitudinal nodular ridges and openings between them. The frequency of nodules on ridges is uneven. The tip area of the spine is smooth.

The ectocoracoid is anteroposteriorly elongated, and its anterior part is slightly warped (Fig. 5S). The posterior end of this bony plate is sharper than the anterior end. Two high crests run longitudinally on the plate. The middle crest is robust, but the crest on the upper side edge is quite narrow (Fig. 5T). The surface of the ectocoracoid is penetrated by numerous openings and covered with longitudinal nodular ridges. The size of the openings and nodules is variable. The density of nodules is higher in the middle crest area.

The cleithrum consists of a triangular sculptured dorsal process, which has a posterior projection, and a narrow vertically oriented ventral process (Fig. 5U). The surface of the dorsal process is covered with nearly smooth ridges, where only a few modest nodules may occur. However, conspicuous nodular ridges are observed on the high crest on the ventral edge of the dorsal process (Fig. 5V).

Order Syngnathiformes
Family Syngnathidae

*Nerophis ophidion* (Linnaeus, 1758), straight-nosed pipefish

Bony plates cover the whole body of *N. ophidion*. There are two basic types of plates – large elongated plates (Fig. 6A–D), which form rows on the body, and small roundish ones (Fig. 6F), occurring like patches between large plates. The large plates have processes that help to fix the adjacent plates with each other. Such processes are missing on the small plates.

The large plates are covered with a network of ribbon-like flattened ridges, but also parallel ridges may occur on the lateral edges (Fig. 6G,H). The median crest on the large plates runs anteroposteriorly and is flat and smooth. However, the crest is high on the posterior process. The small roundish plates are covered only with a network of ribbon-like flattened ridges and lack the median crest (Fig. 6F,I). In addition, a fine striped ultrasculpture is found on the edges of the small plates, forming linear and network patterns.

*Syngnathus typhle* Linnaeus, 1758, broad-nosed pipefish

Bony plates cover the whole body of *S. typhle*. Two basic types of plates are found – large elongated or roundish plates (Fig. 6J–M), forming rows on the body, and small roundish plates (Fig. 6N) situated between large plates. The large plates have processes fixing the adjacent plates with each other. The small plates lack such processes.

The large plates are covered with long subparallel smooth ridges arising from the medial crest (Fig. 6O). These subparallel ridges may be connected by smaller ridges forming a network. The network sculpture is more widespread near the crest (Fig. 6P). The median crest, which runs anteroposteriorly, is conspicuously high and may bear a row of nodules on the top (Fig. 6O). The small roundish plates are covered with linear smooth ridges, but there is one ridge among them that seems slightly stronger than the others (Fig. 6N).

A fine striped ultrasculpture was revealed at a higher magnification on both types of plates. The fine stripes on the large

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**Fig. 5**—Boltmose, *Spinachia spinachia* (Linnaeus, 1758). Postcranial bone units. —**A–D.** Lateral plates. —**E.** Nodular ridges on lateral plate surface, close-up of **B.** —**F–J.** Median plates. —**K.** Sculpture on median plate surface, close-up of **I.** —**L, M.** Dorsal spine on basal. —**N.** Basal of anal spine, front view. —**O.** Sculpture on flanges surface of spine basal. —**P.** Pelvic plate with spine. —**Q.** Sculpture on pelvic plate, close-up of **P.** —**R.** Pelvic spine, close-up of **P.** —**S.** Ectocoracoid. —**T.** Sculpture on ectocoracoid, close-up of **S.** —**U.** Cleithrum with first lateral plate. —**V.** Sculpture on triangular dorsal process of cleithrum, close-up of **U.** N is in front view; anterior of the other bone units is to the left unless shown by an arrow, which points anteriorly. A, GIT 584-73-9; B = E, GIT 584-73-12; C, GIT 584-73-10; D, GIT 584-92-11; F, GIT 584-92-2; G, GIT 584-73-19; H, GIT 584-73-3; I = K, GIT 584-73-18; J, GIT 584-73-2; L, GIT 584-73-31; M, GIT 584-73-33; N, GIT 584-92-10; O, GIT 584-92-8; P = Q = R, GIT 584-86-2; S = T, GIT 584-86-3; U, GIT 584-92-14; V, GIT 584-92-4. Scale bar for **A–C, F, G, I, L, N, T** is 400 µm; for **D, H, J, M, P, R, S, U, 1 mm**; for **E, K, V, 200 µm**; for **O and Q, 100 µm**.

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plates are rather short and linear, located between the ridges and run outward from the median crest (Fig. 6Q). However, the small plates are covered with fine worm-like stripes, which visually extend outward from the center (Fig. 6R).

Discussion

This study is the first detailed overview of the sculpture on the postcranial armor bones of five fish species: three-spined stickleback *G. aculeatus*, nine-spined stickleback *P. pungitius* and boltmose *S. spinachia* of the order Gasterosteiformes and broad-nosed pipefish *S. typhle* and straight-nosed pipefish *N. ophidion* of the order Syngnathiformes. In addition, the general morphology of these bones is discussed.

The diversity of different armor bones in the members of the two studied orders is very different. The body of the syngnathiforms is completely enclosed by rather homogeneous dermal bony plates. Armor bones of the gasterosteiforms are highly variable. Besides dermal lateral plates, the superficial defense structure in gasterosteiforms includes median plates, pelvic girdle, spines, spine basals, ectocoracoids, and cleithra.

A very significant difference can be observed in the direction of the coverage of body plates. In the gasterosteiforms, the following lateral plate is covered by the previous plate, but in the studied syngnathiforms, this relationship is reversed.

Although we can distinguish similar armor bones in representatives of the same order, the shape of bones varies by species. In *G. aculeatus*, lateral plates are elongated dorsoventrally in shape. In the other two studied gasterosteiforms, however, the lateral plates are elongated anteroposteriorly.

The pelvic plate of *G. aculeatus* and *P. pungitius* has a V-shaped structure, but that of *S. spinachia* is an anteroposteriorly elongated bone because the ascending process extends posteriorly rather than dorsally. Basals of dorsal spines are very useful bones for identification. In *G. aculeatus*, the flanges on the lateral edges of the basals are wide, rounded in shape and descending; in *S. spinachia*, the flanges of the basals are of rather medium width, descending, with a slightly rounded outer edge; in *P. pungitius*, the flanges are narrow and straight.

The shapes of some superficial bones may vary greatly also in a specimen, depending on the position of the bone on the body. It is understandable that the size of lateral and median plates must follow the shape of the body, and the shape variations are mainly related to function; for example, the processes on edges likely ensure better linkage between adjacent plates and the keel on the plate may assist in swimming in some way.

The present study shows that although the shapes of superficial bones may vary substantially within an individual, the sculpture on these bones is similar in an individual and moreover is taxon specific within the geographic area studied. The pattern of the sculpture is alike in fishes that were caught from different locations. It is clear that the sculpture and morphology of armor bones can somewhat vary within the species. For example, such differences occurred in the size of the sculpture elements, but the overall plan remains the same in the studied examples. However, the pattern of the sculpture in young fishes is still acquiring species-specific characteristics. It is not as complicated as that in older fishes and is therefore more difficult to identify species.

The body plates of *N. ophidion* are mainly covered with a network of ribbon-like flattened ridges, whereas the body plates of *S. typhle* carry long, subparallel, and smooth ridges, arising from the median crest. The plates of *S. typhle* have also a much stronger crest than those of *N. ophidion*. In *G. aculeatus* and *S. spinachia*, the surfaces of armor bones are covered with nodular ridges. These ridges can form both linear and network patterns. The distribution and size of the nodules on these bones in *G. aculeatus* are more uniform than in *S. spinachia*, whose nodules are concentrated in the crest area. Unlike the above-mentioned gasterosteiforms, *P. pungitius* has external bones bearing mainly ridges without nodules. Nodular sculpture is observed only in a few places — mainly on the top of higher ridges such as on the crests of keel plates, on some edges on certain bones, and on the pelvic spine.

One aim of this study was to ascertain the occurrence or absence of ultrasculpture. A fine, striped ultrasculpture was found on the body plates of both studied syngnathiforms. This ultrasculpture is different from that described in our previous works concerning cottoids, where the fine nodular sculpture surrounded the denticles on tubercles of *Cyclopterus lumpus* and the spines on tubercles of *Myoxocephalus scorpius* (Märrs et al. 2010a, b).

Summary

1. The postcranial armor bones of the gasterosteiforms *G. aculeatus*, *P. pungitius*, and *S. spinachia* and the syngnathiforms *S. typhle* and *N. ophidion* from Estonian...
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2 The surface of postcranial armor bones is covered with sculpture.

3 The morphology and sculpture of postcranial armor bones in the studied species are different. Although the shape of these superficial bones may vary substantially even in an individual, the general feature of sculpture on these bones is similar within individuals and within the studied taxa.

4 Young fishes are still in the process of developing the distinctive features of morphology and sculpture of their dermal armor, and it is more difficult to identify species than their older conspecifics.

5 The main sculptural elements on postcranial armor bones of the gasterosteiforms 

6 The main sculptural elements on postcranial armor bones of the syngnathiforms 

7 A fine striped ultrasculpture was found on the body plates of both studied syngnathiforms.

8 The gasterosteiform and syngnathiform species and genera found in the eastern Baltic Sea can be distinguished by many features of morphology and sculpture of their dermal armor and associated bones.

9 We suggest that the distinguishing features may have taxonomic and phylogenetic value with further study of related species in other areas.

10 The diagnostic features found in this study offer the hope that samples of similar bones from gut contents, fossil samples, and archaeological sites can also be identified to species.

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References


