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A scale atlas for common Mediterranean teleost fishes

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Abstract

Regular body scales of 80 species, belonging to 50 families and 16 orders of marine teleost fishes common in the Mediterranean Sea are described using morphological and morphometric characters. The morphological descriptions are based on the scale's type, shape, features of the anterior, posterior and lateral fields. Further characteristics of the focus, circuli, radii and spines or cteni, if present, are given. Morphometric indices are calculated for scales from the anterior dorsal flank area of each species. As scale shape varies along the body of a given specimen, respective images are provided generally from ten body areas. The current atlas also provides information that complements the characterization of certain taxa. In addition, it is to constitute a valuable instrument for species identification of scales collected from fossiliferous layers, from archaeological sites or from a variety of feeding remains of piscivorous marine predators.

Key words

Fish scales, cycloid, ctenoid, spinoid, crenate.

Introduction

The dermal skeleton of the body of gnathostomes shows considerable diversity in shape, such as various types of scales and body plates, as well as in histology including various types of bone, dentine, enamel, enameloid, and other derived tissues. In the literature on fish, the term "scale" is frequently used as a generalised term for any hard, flattened skeletal element in the skin. These include the scales of chondrichthyans (placoid scales), the scales of basal actinopterygians (ganoid scales), the bony scales of some actinopterygian taxa (dermal bony scales and scutes) and the scales of basal sarcopterygian taxa and most actinopterygian species (elasmoid scales) (Sire & Akimenko, 2004). Teleosts possess elasmoid scales, which consist of a thin bony plate without any additional distal hard layer. Like other elements of the dermal skeleton, elasmoid scales are formed in the dermis without any cartilaginous initium (Francillon-Vieillot *et al.*, 1990; Zylberberg *et al.*, 1992). They are ornamented, thin, lamellar, collagenous plates located within the upper region of the dermis, close to the epidermis (Sire & Akimenko, 2004). In their primitive condition, these scales are initiated as simple cycloid scales, i.e., more or less round with smooth margins and growth rings as their only ornamentation. Within the almost 30,000 teleost species, several modifications of this scale type have evolved: margins became dentated or repeatedly emarginated, various outgrowths formed, additional toothlike ossifications appeared or scales were greatly or completely reduced.

Agassiz (1833–1843) was the first to divide teleosts into two groups according to their scale types: the "Cycloides" and the "Cténoides". The nomenclature introduced by him has been fully incorporated into ichthyology. Few decades later, light microscope studies of scales by Williamson (1851), Baudelot (1873), Cockerell (1910, 1913, 1915), Chu (1935), Lagler (1947), and McCully (1961) contributed largely to our knowledge of scale morphology and demonstrated the scales' value for systematic studies. More recent investigations produced a rather complicated picture including several convergent evolutions. Nevertheless, scales bear valuable information for studies on different levels: on major groups (e.g., Coburn & Gaglione, 1992; Roberts, 1993; Schultze, 1996; Khemiri *et al*., 2001, Patterson *et al*., 2002), or on family level (e.g., Lagler 1947; Casteel, 1972, 1973; Lippitsch, 1990; Jawad, 2005), down to species level (e.g., Mosher, 1969; Kaur & Dua, 2004; Esmaeili *et al*., 2007; Jawad & Al-Jufaili, 2007; Esmaeili & Gholami, 2011; Yokogawa & Watanabe, 2011; Harabawy *et al*., 2012), and even within a species, e.g., to study sexual dimorphism (e.g., Dapar *et al.,* 2012; Ganzon *et al.*, 2012). Furthermore, geometric morphometric analysis of fish scales has provided a reliable tool for differentiating congeneric species, e.g., *Mugil* species by Ibáñez *et al*. (2007), and allowed identification of populations on a local and regional scale (e.g., Poulet *et al*., 2005; Staszny *et al*., 2012; Bräger *et al*., 2016a).

As thin bony structures, fish scales have only a poor chance to fossilize. Nonetheless, certain sediments deposited in quiet, anoxic bottom waters of contained basins archived a well-preserved record of bone and scale remains that still allow species identification. Some studies have used fish scales in lacustrine (e.g., Pennington & Frost, 1961; Davidson *et al.*, 2003) or marine (e.g., Soutar & Isaacs, 1969, 1974; Holmgren-Urba & Baumgartner, 1993; Patterson *et al.*, 2002; Díaz-Ochoa *et al.*, 2009) sediments to determine ancient or historic species compositions. Other researchers used fish scales to obtain information on alimentation habits of past human communities (e.g., Casteel, 1974; Hardy & Moncel, 2011). Although the necessary conditions to preserve fish scales are not common, in some remarkable deposits fish scales may even sum up to 16,000 fossils per square meter (Vallentyne, 1960).

Scales also provide information on the identity of prey species for a variety of piscivorous species. Morphological analysis of scales has been used, e.g., in several diet and feeding ecology studies and helped to identify prey by its scales from stomach contents in benthopelagic species by Mauchline & Gordon (1984), from regurgitated pellets in herring gull (*Larus argentatus*) by Ewins *et al.* (1994), and from faecal samples in harbour seal (*Phoca vitulina*) by Cottrell *et al.* (1996) or in Rickett's big-footed bat (*Myotis ricketti*) by Ma *et al.* (2003). Last but not least, scale analysis has proven to be a cost-effective way for prey determination in some foraging studies of odontocete species (e.g., Ford & Ellis, 2006; Bräger *et al.*, 2016b).

Growth of fish scales happens rhythmically allowing growth rings, the circuli, to appear on the external surface of the scales (Ottaway, 1978). Seasonal alterations of growth rates result in closer or wider spacing between the circuli thus providing information on the age of the fish (Casselman, 1987). This knowledge has been applied in several age determination studies (e.g., Jhingran, 1959; Johal & Tandon, 1992; Tandon & Johal, 1996; El-Haweet *et al.*, 2005). Growth rate alterations may also be caused by good and bad environmental conditions or good and bad health status (Casselman, 1987). Furthermore, heavy metals (Lake *et al.*, 2006) and some trace metals (Mugiya *et al.*, 1991) may accumulate in scales allowing studies on pollution using fish as bioindicators (Johal & Dua, 1994, 1995; Johal & Sawhney, 1999).

In summary, scales act as a useful tool in several scientific fields, such as systematics, palaeontology, phylogeny, life history, ecology and toxicology. Given this wide interdisciplinary applicability, well-elaborated atlases are necessary to provide references or examples of scale types, their morphology and variability. Here we present a scale atlas of 80 common Mediterranean teleost fish species. Highly specialized scales such as lateral line scales or ventral scutes were not included here. In this study, we focus on "regular" scales and their variability among different body parts within a specimen. The aim of this work was (1) to provide a useful guide for scale identification; (2) to describe a wide range of scale characteristics and morphometric parameters; and (3) to illustrate the inter-specific variability of scale shapes in the most common species of the Mediterranean Sea.

Material and Methods

Scales were sampled from 80 species, belonging to 50 families and 16 orders of teleost fishes occurring in the Mediterranean Sea. Few specimens that typically occur in the Mediterranean Sea, but were not available from that region, were sampled outside of the basin, i.e., in the adjacent Atlantic ocean. All scale samples are deposited in the Deutsches Meeresmuseum (DMM); for most samples also the voucher specimens are deposited in the respective collection. The standard length, place of origin and the accession numbers of all specimens are given in figure captions. For species names and family affiliation we followed Eschmeyer (2014); to order the species accounts we oriented on Nelson (2006).

Scale sampling and preparation. Scales were sampled from museum vouchers or fresh specimens purchased on fish markets. If fish were sampled alive, they were anaesthetised using benzocaine before fixation in 4% formalin-seawater. All museum specimens were finally transferred into 70% ethanol. Fishes purchased on fish markets were sampled shortly after the purchase. Each specimen was measured and rinsed with ethanol or freshwater before scale removal. The latter is an essential step to avoid sampling scales from foreign individuals. Scales were taken from 10 areas (Fig. 1) on the left side of each specimen. For flatfishes, scale sampling was separately performed for both sides. In some species, less than ten body areas are presented in this study due to the insufficient number of scales found within the given area on the available specimens. The lack of scales mainly occurred in open water and/or deep sea species that possess highly deciduous scales. This study focuses on 'regular' body scales and therefore specialized scales, like lateral line

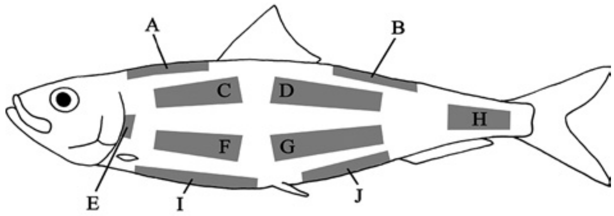

Fig. 1. Schematic drawing of the ten scale sampling areas; anterior, dorsal, rostral to dorsal fin (**A**); posterior, dorsal, caudal to dorsal fin (**B**); anterior, dorsal, above lateral line (**C**); posterior, dorsal, above lateral line (**D**); caudal to operculum (**E**); anterior, ventral, below lateral line (**F**); posterior, ventral, below lateral line (**G**); caudal peduncle (**H**); anterior, ventral, rostral to pelvic fin (**I**); posterior, ventral, caudal to pelvic fin (**J**).

scales, tiny scales on the base of fins or keel-scutes are not investigated herein.

Scale material was stored in 70% ethanol, gently brushed to remove loose tissue remains and stained with Alizarin Red S (ROTH, Germany). Images were taken either in ethanol or from mounted scales. For mounting scales were transferred into 100% ethanol, followed by acetone and embedded into MOUNTEX (MEDITE, Germany) on object slides. Imaging was performed using a LEICA MZ75, with mounted camera DFC-425 and dedicated software (LAS, LEICA, Germany). The imaging software provided all pictures with appropriate scale bars. Detailed measurements were subsequently taken in Photoshop CS6 (ADOBE, United States). Morphometric indices are exemplarily given for one scale only sampled in body area C (i.e., anterior part of the flank above lateral line). The same photo-editing program was used for composing the plates for each species. The scales are represented with the respective anterior (rostral) part to the top and the posterior (caudal) part to the bottom of each image.

Terminology of scale types. For definitions of scale types we oriented on Roberts (1993) with some changes and distinguished two main scale types (Fig. 2) with six subtypes (Fig. 4) as follows:

Cycloid scales. Scales without additional separate ossifications. Marginal indentations or spine-like projections might occur. Cycloid scale subtypes are:
True cycloid. Cycloid scale without any spine projections or marginal increments (Fig. 4A).
Crenate. Cycloid scale with marginal increments termed here as crenae (Fig. 4B).
Spinoid. Cycloid scale with spines that is continuous with the main body of the scale. Spines can be restricted to the posterior margin or scattered over the posterior field (Fig. 4C).

Ctenoid scales. Scales with additional separate ossifications, that form discrete spines called cteni (singular ctenus). Ctenoid scales can occur with three types of cteni:
Peripheral cteni. Ctenoid scale with separate ossifications that occur as whole spines in one row at the posterior margin (Fig. 4D); sometimes an alternating row of smaller secondary spines might be present.
Transforming cteni. Ctenoid scale with separate ossifications that arise as whole spines in two or more alternating rows marginally and transform into truncated spines sub-marginally (Fig. 4E).
Whole cteni. Ctenoid scale with separate ossifications that occur as whole spines marginally and sub-marginally (Fig. 4F).

Terminology of scale characteristics. The following scale characteristics were defined as main discriminative features to aid scale identification. The definitions of scale characteristics are based on Lagler (1947) to promote uniformity of criteria used in previous works by other scientists. Figures 2 to 4 illustrate the morphological characteristics, and Table 1 summarizes the discriminative features of these characteristics.

Field. An area of the scale surface, with the focus as centre and four “corners” of the scale four fields can be distinguished: anterior, posterior, dorsal and ventral, whereas the latter two are usually much similar and summarized as lateral fields (Fig. 2). For the purpose of better discrimination, the following characteristics of these fields were described: (1) the outer curvature of the anterior field: convex, concave or flattened; (2) the margin of the anterior field: smooth – without any in- or edentations; striate – with incisions usually caused by the distal parts of radii; waved – with rounded in- and edentations; scalloped – with rounded edentations and acute indentations; dentate – with regular acute in- and edentations; fluted – with irregular rounded in- and edentations (Fig. 3); (3) the outer curvature and extension of the lateral fields: convex, concave or flattened and extended in dorso-ventral axis or elongated in antero-posterior axis; (4) the posterior end: flattened, rounded, tapered or pointed, as well as the different characteristic features of the posterior margin, as follows: smooth, membranous, crenulated, spinous, ctenous.

Focus. Also named nucleus; the first part of the scale appearing in ontogeny, forming an area inside of the first circulus. The focus can be in the geometrical centre of the scale, but is often shifted posterior or anterior of this point (Fig. 2). Focal index (Fi) was calculated, as the distance from the outermost edge of the anterior field to the focus divided by the distance from the outermost edge of the anterior field to the outermost edge of the posterior field. The position of the focus was classified according to the focal index, as follows: < 0.20 – anterior; 0.21 – 0.40 – antero-central; 0.41 – 0.60 – central; 0.61 – 0.80 – postero-central; > 0.81 – posterior.

Circulus. Elevated marking on the outer surface usually appearing as line following more or less the outline shape of the scale; originating from batch-wise growth (Fig. 2). Circuli generally create continuous concentric

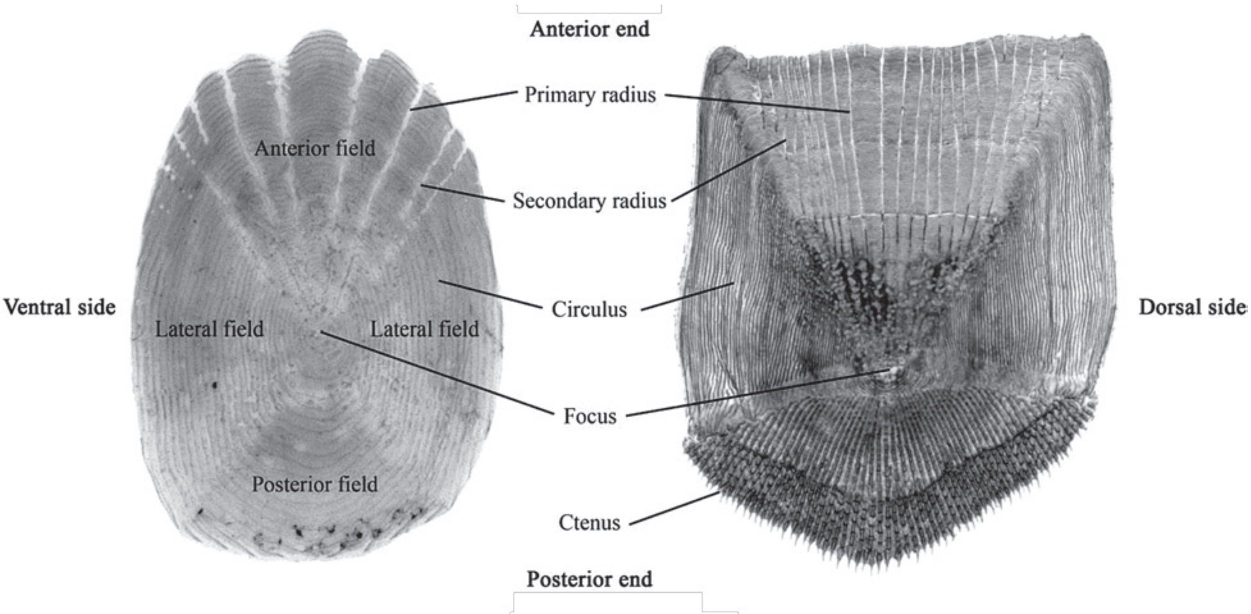

Fig. 2. Scale characteristics shown for a cycloid scale of *Seriola dumerili* (left) and a ctenoid scale of *Dicentrarchus labrax* (right).

lines, however, they can be interrupted by radii or other grooves (see below). In few cases, circuli can be ornamented by hyper-mineralization, or disconnected by unmineralized areas. These features are described in the respective species.

Radius. Groove with usually radial orientation. Commonly radii are restricted to the anterior field. They interrupt circuli. In general, a radius is rectilinear, positioned in the antero-posterior axis of the scale and pointing towards the focus. Primary radii reach the focus from the scale margin, while secondary radii start at the scale margin but do not reach the focus (Fig. 2). In some cases, radii are positioned between the focus and the scale margin. The latter are termed as tertiary radii.

Other forms of grooves (e.g., transverse, longitudinal, vertical or irregular) can also occur that do not necessarily have even rectilinear character neither radial orientation. The characteristics of these grooves are described within the particular species.

Ctenus. Tooth-like structure that ossifies separately and is more or less detached from the main body of the scale. Cteni appear in one or more rows marginally or sub-marginally at the posterior field (Fig. 4D–F).

Spine. Tooth-like ossification continuous with the main body of the scale. Spines appear at the posterior margin (Fig. 4C) or they are scattered within the posterior field (e.g., *Trachyrincus scabrus*, Fig. 22).

Terminology of scale shapes. Scales show a high level of diversity in their shapes with considerable intra- and inter-species variation. We categorized the observed scale shapes into 5 main types with in total 18 subtypes (Fig. 5). Transitions between these categories may be present and are noted in the respective descriptions, e.g., "circular to oval". Shape variability of scales was defined according to the number of different scale shapes that occurred within a specimen: uniform – 1 scale shape; low – 2 scale shapes; moderate – 3 scale shapes; high – 4 or more scale shapes.

The typical scale shapes are classified as follows:

Circular. A form of or similar to a circle with rounded outline, in which the diameter varies little between all directions.

Subtypes

True circular. Rounded outline with equal diameter in each direction.
Cordate. Rounded outline, more or less equal diameter, but slightly pointed posterior end and double (sometimes triple) rounded anterior field.
Discoidal. Circular with elongated lateral fields in dorso-ventral axis. The anterior field is rounded and slightly elevated.

Oval. A form of an elongated circle with rounded outline, in which the length of the diameter is not equal in all direction.

Subtypes

True oval. Rounded outline, elongated in antero-posterior axis with slightly wider (often flattened) anterior field with rounded edges and rounded, narrower posterior field.
Ovoid. Rounded outline, slightly elongated in antero-posterior axis, with narrower anterior field and wider posterior field.
Reversed ovoid. Rounded outline, slightly elongated in antero-posterior axis, with wider (never flattened) ante-

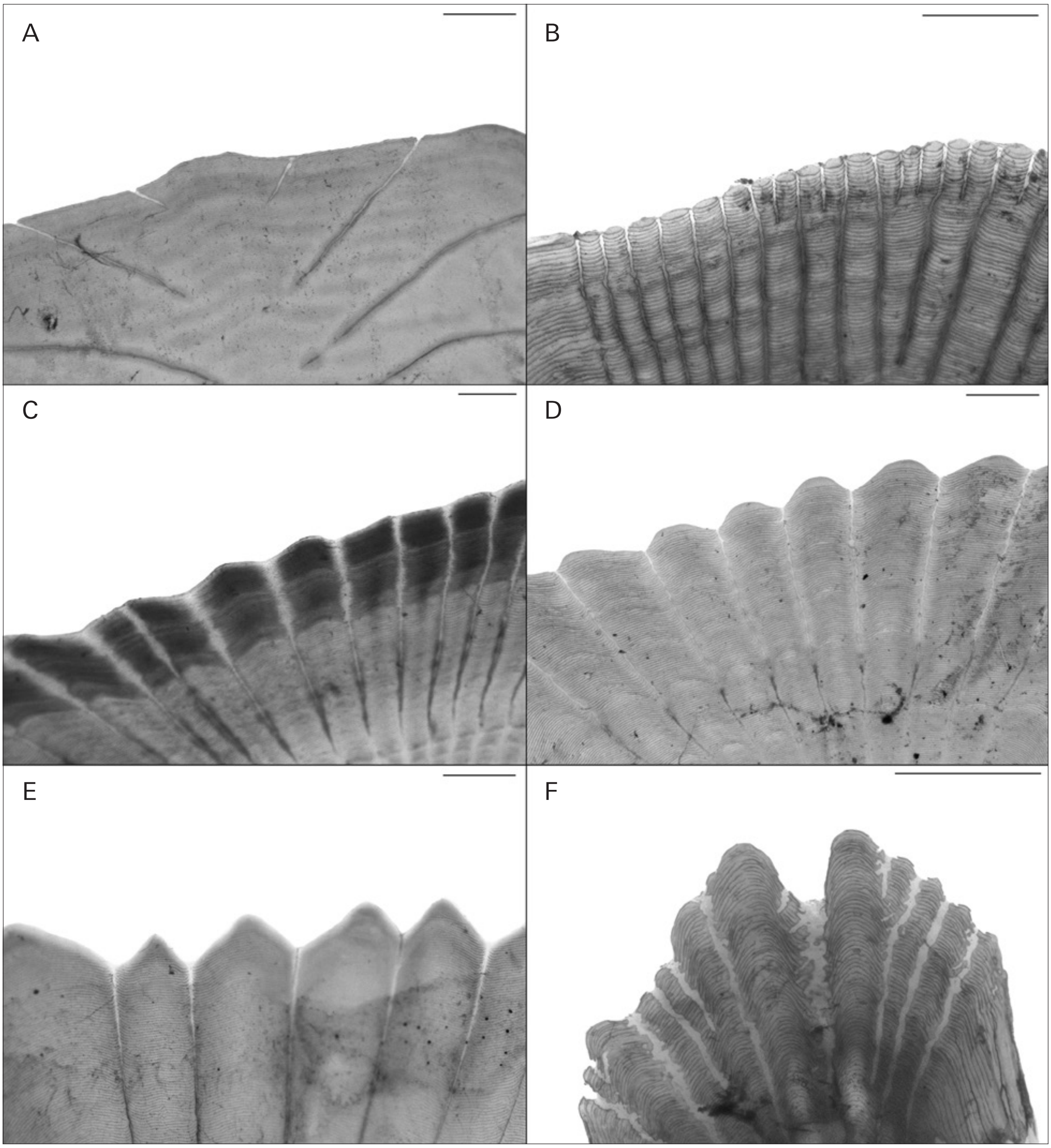

Fig. 3. Characteristic features of the anterior margin of different scale types. **A**: smooth (*Sardina pilchardus*); **B**: striate (*Dicentrarchus labrax*); **C**: waved (*Sparus aurata*); **D**: scalloped (*Diplodus vulgaris*); **E**: dentate (*Mullus surmuletus*); **F**: fluted (*Eutrigla gurnardus*). Scale bar = 500 µm.

rior field and narrower, slightly pointed posterior field.

Oblong. Rounded outline, largely elongated in antero-posterior axis with equally wide anterior and posterior field. The lateral fields are almost parallel.

Elliptical. Rounded outline, largely elongated lateral fields in dorso-ventral axis. The anterior or posterior field is slightly flattened.

Quadrilateral. A form of a four-sided polygon with more or less squared outline. Often the sides are parallel and the edges form right angles.

Subtypes

Square. Quadrilateral, having all sides equal in length forming more or less right angles.

Rectangular. Quadrilateral, that is elongated in antero-posterior axis with parallel lateral fields. The anterior and posterior fields are shorter than the lateral fields are long. The corners are not rounded but form more or less right angles.

Trapezoidal. Quadrilateral, where the length of its adjacent sides is unequal and its angles are oblique; has one pair of parallel sides.

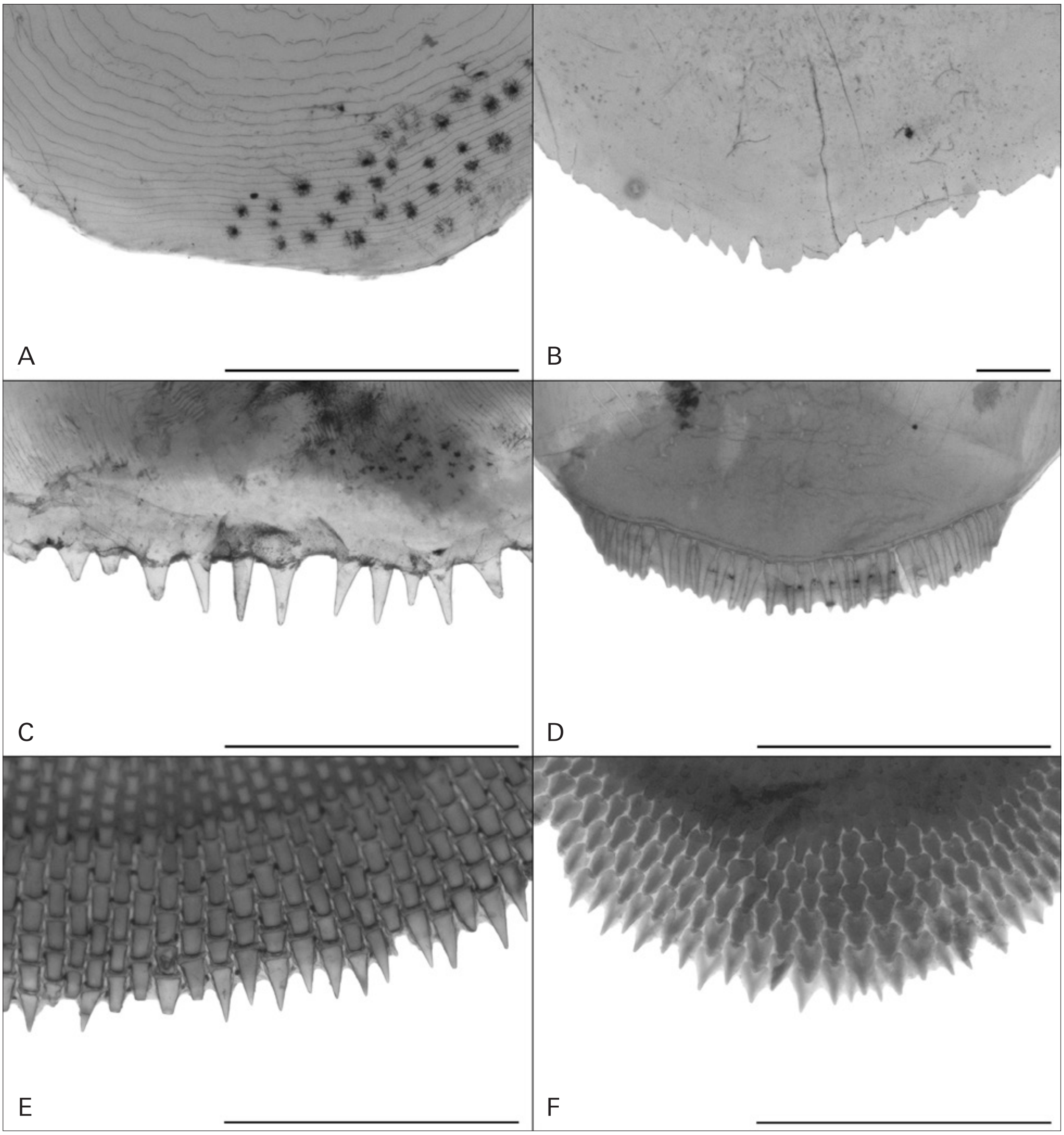

Fig. 4. Characteristic features of the posterior margin of different scale types. **A**: true cycloid (*Trachurus trachurus*); **B**: crenate (*Alosa fallax*); **C**: spinoid (*Lepidotrigla cavillone*); **D**: peripheral cteni (*Gobius bucchichi*); **E**: transforming cteni (*Chaetodon hoeferi*); **F**: whole cteni (*Chelon labrosus*). Scale bar = 1 mm.

Rhomboidal. Quadrilateral, where the length of its adjacent sides is unequal and its angles are oblique; has no pair of parallel sides.

Polygonal. Multi-sided forms with somehow square outline with angled corners.

Subtypes

Pentagonal. Five-sided polygon where each of the sides are about equal in length.

Hexagonal. Six-sided polygon where each of the sides are about equal in length.

Octagonal. Eight-sided polygon where each of the sides are more or less equal in length.

Intermediate. Typical shapes between quadrilateral, polygon and somewhat circular; corners may be square or round, i.e., not clearly defined.

Subtypes

Calyx. Resembles quadrilateral, but with wide anterior field that is extended in dorso-ventral axis and lateral fields that are bulged (convex) with one pair of rounded edges.

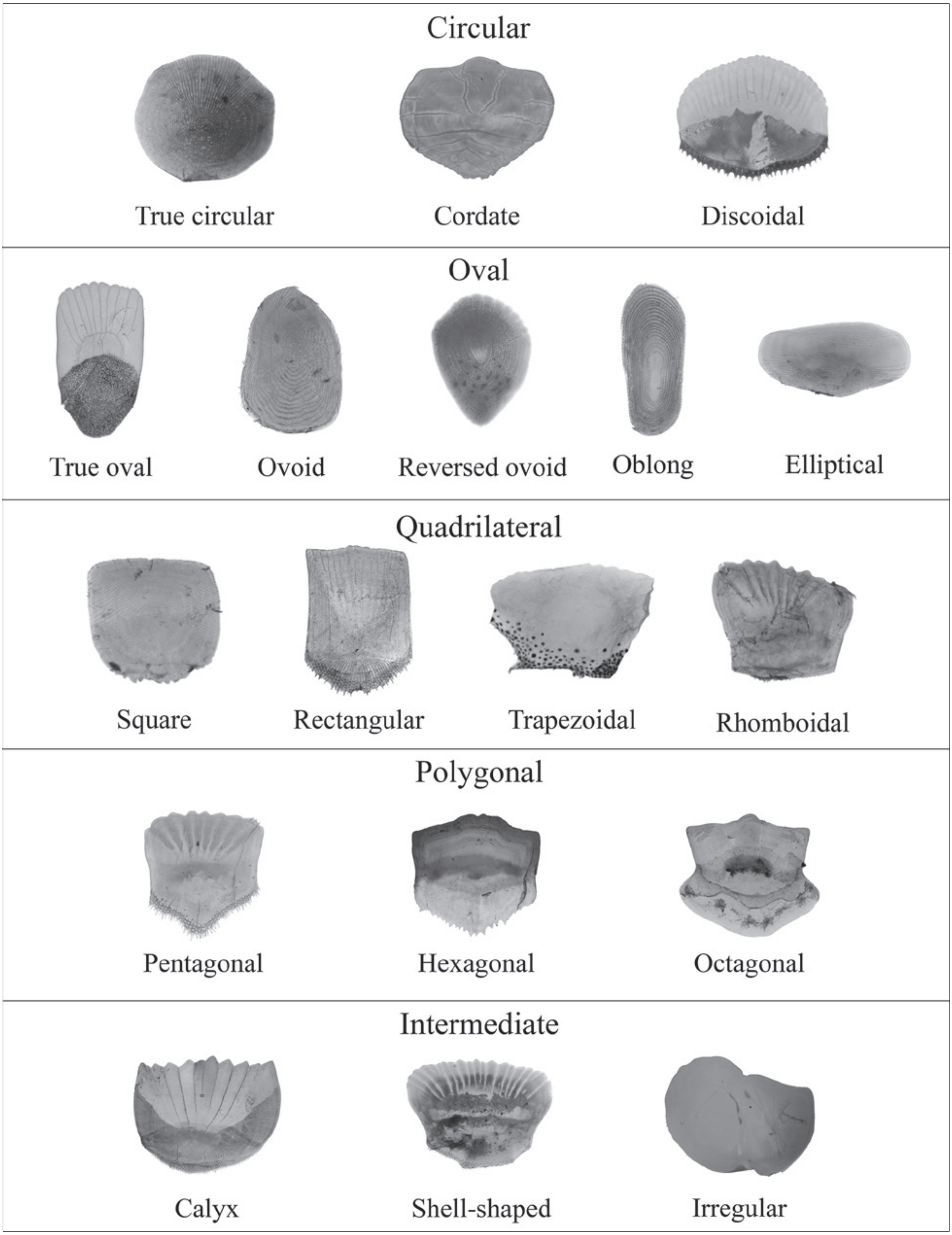

Fig. 5. Classification of scale shapes used in this study.

Shell-shaped. Usually resembles quadrilateral, but with wide anterior field that is extended in dorso-ventral axis and lateral fields that are concave with one pair of rounded edges.

Irregular. Without well-defined outline.

Terminology of scale morphometrics. Morphometric parameters of scales, derived from body area C, for each specimen were measured. In specimens, where scales were not available from body area C, the given body part is indicated from where the scale measurements were tak-

Table 1. Summary of the morphological characteristics and discriminative features used in fish scale identification.

Morphological characteristics	Discriminative features
Type	cycloid: true cycloid / crenate / spinoid ctenoid: peripheral cteni / transforming cteni / whole cteni
Shape	circular: true circular / cordate / discoidal oval: true oval / ovoid / reversed ovoid / oblong / elliptical quadrilateral: square / rectangular / trapezoidal / rhomboidal polygonal: pentagonal / hexagonal / octagonal intermediate: calyx / shell-shaped irregular: irregular
Shape variability	uniform / low / moderate / high
Anterior field	convex / concave / flattened
Anterior margin	smooth / striate / waved / scalloped / dentate / fluted
Lateral fields	convex / concave / flattened
Extension	extended in dorso-ventral axis / elongated in antero-posterior axis
Posterior field	flattened / rounded / tapered / pointed
Posterior margin	smooth / membranous / crenulated / spinous / ctenous
Focus position	anterior / antero-central / central / postero-central / posterior
Circuli	distinct / indistinct continuous / discontinuous
Radii	presence / absence primary / secondary / tertiary other grooves
Radii orientation	radial / parallel / transverse / longitudinal / vertical / irregular
Spines	marginal / scattered
Cteni	peripheral / transforming / whole

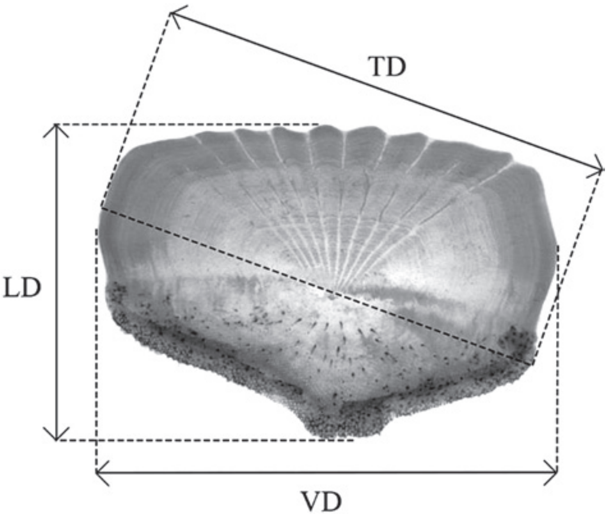

Fig. 6. Scale morphometric parameters for an exemplary scale of *Sparus aurata.*

en. In species, that belong to the order Pleuronectiformes, scales from both sides (i.e., ocular- and blind-side) were measured in body area C.

The following morphometric parameters were measured (Fig. 6):
Longitudinal diameter (LD).The maximal longitudinal diameter of the scale in antero-posterior axis.
Vertical diameter (VD). The maximal vertical diameter of the scale in dorso-ventral axis.
Transverse diameter (TD). The maximal transverse diameter of the scale.

To describe the shape of the scales, a shape index (**Si**) was calculated after BURDAK (1979), as the following: Si = TD / LD. The relative scale sizes (J-indices) for the scale length (**Jsl**) and scale width (**Jsw**) were calculated following ESMAEILI (2001): Jsl (Jsw) = length (width) of scale / fish standard length × 100. In species, where only total length is available, due to their morphology, standard length is substituted with the total length of the fish. Shape index, J-indices, focal index, as well as scale type for each species are summarized in Table 2.

Abbreviations

AF anterior field
Cr crenate scale
Cy cycloid scale
Fi focal index
Jsl relative scale length
Jsw relative scale width
LD scale longitudinal diameter
LF lateral field
Pe ctenoid scale with peripheral cteni
PF posterior field
Si shape index
SL standard length of the specimen
Sp spinoid scale
TD scale transverse diameter
TL total length of the specimen
Tr ctenoid scale with transforming cteni
VD scale vertical diameter
Wh ctenoid scale with whole cteni

Results

Morphological Descriptions

Order ALBULIFORMES

Family NOTACANTHIDAE

Notacanthus bonaparte **Risso, 1840**

Fig. 7

Type: cycloid: true cycloid. ***Shape***: circular: reversed ovoid to true circular. Shape variability: moderate. ***Anterior field***: convex with waved margin. ***Lateral fields***: convex and slightly extended in the antero-lateral section with rounded corners. These fields are gradually narrowing towards the posterior field. ***Posterior field***: tapered end with smooth margin. ***Focus***: antero-central. ***Circuli***: distinct and discontinuous. ***Radii***: primary, secondary and tertiary radii can occur in radial orientation in all four fields.

Order CLUPEIFORMES

Scales of Clupeiformes are easily distinguishable from other species, by having distinctive grooves (radii), and a membranous posterior field with crenulated margin. Grooves present on the scales of Clupeiformes were identified as "fracture lines" by Patterson *et al.* (2002), as "transverse striae (radii)" in the anterior field and as "longitudinal striae" in the posterior field by Roberts (1993). In this study, we classified these grooves as special form of radii and termed them according to their orientation (i.e., transverse, longitudinal, irregular).

Scales are highly variable in shape, and not only among the sampling areas, but also within a given area, hindering species identification. Scales of *Sardina pilchardus* and *Sardinella aurita* showed the highest similarity and a high level of plasticity in their scale characteristics.

Family ENGRAULIDAE

Engraulis encrasicolus **(Linnaeus, 1758)**

Fig. 8

Type: cycloid: crenate. ***Shape***: circular: true circular to cordate or discoidal. Shape variability: high. ***Anterior field***: convex to flattened with conical apex and smooth margin. ***Lateral fields***: convex and well-extended in dorso-ventral axis. ***Posterior field***: tapered end with crenulated margin that is subjected to fracturing. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: transverse, longitudinal and irregular grooves occur in all four fields. Grooves are radial, parallel or transverse in orientation and run across the scale in an irregular manner.

Family CLUPEIDAE

Alosa fallax **(Lacepède, 1803)**

Fig. 9

Type: cycloid: crenate. ***Shape***: circular to oval: true circular to true oval, or slightly polygonal. Shape variability: high. ***Anterior field***: convex to flattened with conical apex and smooth margin. ***Lateral fields***: flattened and only moderately extended in dorso-ventral axis. ***Posterior field***: rounded to tapered end with crenulated margin that is subjected to fracturing. Crenae form a teeth-like formation. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: transverse grooves are present in the anterior and lateral fields. In some cases (e.g., in body area B), longitudinal grooves can occur within the posterior field that run across the scale in an irregular manner.

Clupea harengus **Linnaeus, 1758**

Fig. 10

Type: cycloid: crenate. ***Shape***: circular to oval: cordate to discoidal, or true oval to reversed ovoid. Shape variability: high. ***Anterior field***: rather flattened than convex with conical apex and smooth margin. ***Lateral fields***: flattened to convex and extended in dorso-ventral axis. ***Posterior field***: tapered end with crenulated margin that is subjected to fracturing. Crenae show an irregular and membranous appearance. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: transverse grooves are present in the anterior and lateral fields. In body areas A, B, H, I, and J, longitudinal grooves can occur that run across the scale in an irregular manner.

Sardina pilchardus **(Walbaum, 1792)**

Fig. 11

Type: cycloid: crenate. ***Shape***: circular to oval: generally cordate to discoidal. Shape variability: high. ***Anterior field***: flattened with prominent conical apex and smooth margin. ***Lateral fields***: convex and extended in dorso-ventral axis. ***Posterior field***: rounded to tapered end with crenulated margin that is subjected to fracturing. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: transverse grooves are present in the anterior and lateral fields. Longitudinal grooves can occur, especially in body area A and B that run across the scale in an irregular manner.

***Sardinella aurita* (Valenciennes, 1847)**

Fig. 12

Type: cycloid: crenate. ***Shape***: circular to oval or slightly quadrilateral: generally cordate to discoidal. Shape variability: high. ***Anterior field***: flattened with low conical apex and smooth margin. ***Lateral fields***: flattened to convex and extended in dorso-ventral axis. ***Posterior field***: rounded to tapered end with crenulated margin that is subjected to fracturing. Crenae form a teeth-like formation. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: transverse grooves are present in the anterior and lateral fields. Longitudinal grooves can occur, especially in body area H that run across the scale in an irregular manner.

***Sprattus sprattus* (Linnaeus, 1758)**

Fig. 13

Type: cycloid: crenate. ***Shape***: circular to oval: true circular to true oval. Shape variability: high. ***Anterior field***: convex to flattened with smooth margin. The conical apex is virtually absent. ***Lateral fields***: convex to flattened and generally elongated in antero-posterior axis. ***Posterior field***: rounded end with crenulated margin. Crenae form a teeth-like formation. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: transverse grooves are present in the anterior and lateral fields. Longitudinal grooves rarely occur (e.g., in body area B) and are not typical.

Order ARGENTINIFORMES

Family ARGENTINIDAE

***Argentina sphyraena* Linnaeus, 1758**

Fig. 14

Type: cycloid: true cycloid. ***Shape***: irregular. Shape variability: high. ***Anterior field***: asymmetric, can be flattened or convex in shape with uneven but smooth margin. ***Lateral fields***: convex and generally extended in the antero-lateral section. ***Posterior field***: rounded, irregular or sometimes tapered end with smooth and membranous margin. ***Focus***: indistinct. ***Circuli***: distinct and continuous to indistinct in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent.

Family ALEPOCEPHALIDAE

***Alepocephalus rostratus* Risso, 1820**

Fig. 15

Scales are highly deciduous and it was not possible to obtain them from all body areas. Therefore, the description refers to scales found within body area A, B and C only.
Type: cycloid: true cycloid. Shape: oval: true oval. Shape variability: uniform. ***Anterior field***: flattened to slightly incline or concave end with smooth margin. Due to the dominance of the posterior field, this field is less prominent. ***Lateral fields***: flattened and elongated in antero-posterior axis. ***Posterior field***: convex with smooth margin. ***Focus***: anterior. ***Circuli***: distinct; continuous in the anterior and lateral fields, discontinuous in the posterior field. ***Radii***: primary and secondary radii are present in the posterior field in radial orientation.

Order STOMIIFORMES

Family STERNOPTYCHIDAE

***Maurolicus muelleri* (Gmelin, 1789)**

Fig. 16, 17

Scales are highly deciduous and it was not possible to obtain them from all body areas. Therefore, the description refers to scales found within body area B, F, I, J only. Morphometric parameters were measured on scale sampled in area F.
Type: cycloid: true cycloid. ***Shape***: circular to quadrilateral: true circular to square. Shape variability: moderate. ***Anterior field***: flattened or slightly convex with striate margin. ***Lateral fields***: flattened to convex and slightly extended in the dorso-ventral axis. ***Posterior field****:* flattened to rounded end with smooth margin. ***Focus****:* central. ***Circuli****:* distinct and discontinuous. Numerous elevated structures align among circuli that start as square-like structures and create uneven ridges in radial orientation towards the anterior margin. ***Radii****:* absent.

Order AULOPIFORMES

Family SYNODONTIDAE

***Synodus saurus* (Linnaeus, 1758)**

Fig. 18

Type: cycloid: true cycloid. ***Shape:*** intermediate: calyx to shell-shaped. Shape variability: low. ***Anterior field:*** flattened with deeply scalloped margin creating three to four lobes. ***Lateral fields***: convex and extended in dorso-ventral axis, except in body areas B and H, where these fields are rather flattened and elongated in antero-posterior axis. ***Posterior field***: rounded to tapered end with membranous margin that is subjected to fracturing. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation.

Order MYCTOPHIFORMES

Family MYCTOPHIDAE

***Myctophum punctatum* Rafinesque, 1810**

Fig. 19

Scales are deciduous and it was not possible to obtain them from all body areas. Therefore, the description refers to scales found within body area A, B, C, D, E, F, G, and H only. ***Type***: cycloid: true cycloid. ***Shape:*** intermediate to quadrilateral: calyx to shell-shaped or slightly trapezoidal. Shape variability: high. ***Anterior field:*** rather flattened than convex. The margin of this field is deeply scalloped creating a lobular appearance. ***Lateral fields***: flattened to convex and extended in dorso-ventral axis. ***Posterior field***: rounded or irregular end with smooth margin. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation.

Order GADIFORMES

Family MACROURIDAE

***Coelorinchus caelorhinchus* (Risso, 1810)**

Fig. 20

Type: cycloid: spinoid. Shape: circular to polygonal: cordate to hexagonal. Shape variability: low. ***Anterior field***: convex with pointed apex and smooth margin. The antero-lateral corners are extended and pointed. Lateral fields: convex and extended in dorso-ventral axis. ***Posterior field***: rounded to tapered end with smooth margin but spinous posterior field. ***Focus***: antero-central. ***Circuli***: distinct and continuous in the anterior and lateral fields, distinct and discontinuous in the posterior field. Radii: absent. ***Spines***: several large, thorn-shaped spines are scattered within the entire posterior field. The length of the longest spine on scale C is 21% of the total scale length.

***Nezumia sclerorhynchus* (Valenciennes, 1838)**

Fig. 21

Type: cycloid: spinoid. Shape: circular to intermediate: cordate to calyx. Shape variability: low. ***Anterior field***: convex with smooth margin. The antero-lateral corners are extended and pointed. ***Lateral fields***: convex and extended in dorso-ventral axis. ***Posterior field***: generally rounded end with smooth margin but spinous posterior field. Focus: central. ***Circuli***: distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent. ***Spines***: numerous small, leaf-shaped spines are scattered within the entire posterior field. The length of the longest spine on scale C is 13% of the total scale length.

***Trachyrincus scabrus* (Rafinesque, 1810)**

Fig. 22

Type: cycloid: spinoid. Shape: circular: true circular to discoidal. Shape variability: low. ***Anterior field***: convex or flattened with smooth but irregular margin. ***Lateral fields***: convex and extended in dorso-ventral axis, except in area H, where these fields are rather elongated in antero-posterior axis. ***Posterior field***: rounded end with smooth margin but spinous posterior field. ***Focus***: central. ***Circuli***: distinct and continuous in the anterior and lateral fields, distinct and discontinuous to indistinct in the posterior field. ***Radii***: absent. ***Spines***: few (2–5) robust, stout-shaped spines are scattered within the posterior field. The length of the longest spine on scale C is 44% of the total scale length.

Family MORIDAE

***Mora moro* (Risso, 1810)**

Fig. 23

Type: cycloid: true cycloid. ***Shape***: oval: ovoid to oblong. Shape variability: moderate. ***Anterior field***: strongly convex with prominent apex and smooth margin. The antero-lateral corners are slightly pointed. ***Lateral fields***: flattened and elongated in antero-posterior axis. ***Posterior field:*** mostly rounded, except in areas A, B and J, where the end of this field is rather pointed; in area H, it is concave. The posterior margin is smooth. ***Focus:*** postero-central. ***Circuli:*** distinct and continuous. ***Radii:*** absent.

Family MERLUCCIIDAE

Merluccius merluccius **(LINNAEUS, 1758)**

Fig. 24

Type: cycloid: true cycloid. ***Shape***: oval: ovoid to oblong. Shape variability: low. ***Anterior field***: strongly convex with rounded apex and smooth margin. ***Lateral fields***: flattened to convex and elongated in antero-posterior axis. ***Posterior field***: rounded end with smooth margin. ***Focus***: central. ***Circuli***: distinct and continuous. ***Radii***: absent.

Family GADIDAE

Molva molva **(LINNAEUS, 1758)**

Fig. 25, 26

Type: cycloid: true cycloid. ***Shape***: oval: oblong. Shape variability: uniform. ***Anterior field***: convex with smooth margin. ***Lateral fields***: flattened or concave and elongated in antero-posterior axis. These fields are slightly narrowing towards the posterior field. ***Posterior field:*** rounded end with smooth margin. ***Focus:*** central. ***Circuli:*** distinct and discontinuous. Circuli are densely ornamented by elevated, brick-like structures on the scale surface. ***Radii:*** absent.

Trisopterus luscus **(LINNAEUS, 1758)**

Fig. 27

Type: cycloid: true cycloid. ***Shape***: oval: ovoid to irregular. Shape variability: moderate. ***Anterior field***: convex with prominent apex and smooth to striate margin. ***Lateral fields***: flattened to inclined or convex and generally elongated in antero-posterior axis. ***Posterior field***: rounded end with smooth margin. ***Focus***: antero-central. ***Circuli***: distinct and discontinuous. ***Radii***: numerous primary, secondary and tertiary radii are present in radial orientation in all four fields.

Order MUGILIFORMES

Family MUGILIDAE

Scales from the herein investigated Mugilidae show a high level of morphological similarity. Therefore we present one description for the studied species. Scale images are provided for two species, as follows:

Chelon labrosus **(RISSO, 1827)**

Fig. 28

and

Liza aurata **(RISSO, 1810)**

Fig. 29

Type: ctenoid: whole cteni. ***Shape***: intermediate to quadrilateral: calyx to square or rectangular. Shape variability: moderate***.*** ***Anterior field:*** flattened with striate margin. ***Lateral fields:*** flattened to convex, and in general, equally extended in both axes. ***Posterior field:*** rounded end with ctenous margin. Within this field a distinct vertical cleavage often occurs in both species. ***Focus:*** postero-central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in parallel to radial orientation. ***Cteni***: whole cteni.

Order ATHERINIFORMES

Family ATHERINIDAE

Atherina hepsetus **LINNAEUS, 1758**

Fig. 30

Type: cycloid: true cycloid. ***Shape***: polygonal: octagonal. Shape variability: uniform. ***Anterior field***: flattened with pointed apex and smooth margin. The antero-lateral corners are extended and strongly pointed. ***Lateral fields***: strongly concave. ***Posterior field***: rounded end with smooth margin. ***Focus***: central. ***Circuli***: distinct and continuous in the anterior field, indistinct in the lateral and posterior fields. ***Radii***: absent.

Atherinomorus lacunosus **(FORSTER, 1801)**

Fig. 31

Type: cycloid: true cycloid. ***Shape***: circular: true circular to cordate or discoidal. Shape variability: moderate. ***Anterior field***: flattened to convex with smooth margin. The antero-lateral corners are extended and rounded. ***Lateral fields***: strongly convex and extended in the dorso-ventral axis. Scales are pierced by a varying number of small hollows that are arranged in line in the middle of the scale in dorso-ventral axis. ***Posterior field***: rounded to tapered end with smooth margin. ***Focus***: central.

Circuli: distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent.

Order BELONIFORMES

Family BELONIDAE

Belone belone **(Linnaeus, 1761)**

Fig. 32

Type**:* cycloid: true cycloid. ***Shape: circular to oval: true circular or discoidal to elliptical. Shape variability: high. **A*nterior field**:* flattened to slightly convex with smooth margin. ***Lateral fields**:* convex and extended in dorso-ventral axis. This extension is extreme in body areas E, F, and G. ***Posterior field**:* rounded end with smooth margin. ***Focus***: central. ***Circuli***: generally distinct and continuous; indistinct in the posterior field in areas A, B, C, and D; and indistinct in the lateral fields in areas E, F, G, and H. ***Radii***: absent.

Order BERYCIFORMES

Family BERYCIDAE

Beryx decadactylus **Cuvier, 1829**

Fig. 33

Type: cycloid: spinoid. ***Shape***: polygonal: pentagonal to hexagonal. Shape variability: low. ***Anterior field***: flattened to convex with waved margin. The antero-lateral corners are extended and pointed. ***Lateral fields***: flattened to concave. ***Posterior field***: tapered to pointed end with spinous margin. ***Focus***: central. ***Circuli***: distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent. ***Spines***: teeth-like spines emerge from the posterior margin and several tiny spines are scattered within the posterior field.

Family TRACHICHTHYIDAE

Hoplostethus mediterraneus **Cuvier, 1829**

Fig. 34

Within body area I, two distinct scale characters were found, thus here we present two scales within area I, i.e., Ia and Ib.

Type: cycloid: spinoid. ***Shape***: circular to polygonal: true circular to discoidal or pentagonal. Shape variability: high. ***Anterior field***: flattened or slightly convex with smooth margin. ***Lateral fields***: flattened to convex and generally extended in dorso-ventral axis. ***Posterior field***: rounded end with spinous margin. ***Focus***: central. ***Circuli***: distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent. ***Spines***: numerous, tiny spines are present marginally as well as scattered throughout the posterior field. In areas A and Ia (closer to the cranial part of the body), smaller scales have long spines that are both marginal and scattered.

Order ZEIFORMES

Family ZEIDAE

Zeus faber **Linnaeus, 1758**

Fig. 35

Type**:* cycloid: true cycloid. ***Shape: circular to oval: true circular to ovoid. Shape variability: low. **A*nterior field**:* slightly convex with smooth margin. This field is less extended in dorso-ventral axis than the posterior field. ***Lateral fields**:* convex or inclined, widening towards the posterior field. ***Posterior field**:* rounded end with smooth margin. ***Focus***: central. ***Circuli***: distinct and continuous. ***Radii***: absent.

Order GASTEROSTEIFORMES

Family MACRORAMPHOSIDAE

Macrorhamphosus scolopax **(Linnaeus, 1758)**

Fig. 36

Type: cycloid: spinoid. ***Shape***: circular to oval: cordate to reversed ovoid. Shape variability: moderate. ***Anterior field***: convex with smooth margin. A distinct diamond- or triangular-shaped structure emerging from the scale surface characterizes this field. ***Lateral fields***: convex and narrowing towards the posterior field. ***Posterior field***: strongly pointed end with spinous margin. ***Focus***: antero-central. ***Circuli***: indistinct. ***Radii***: absent. ***Spines***: long spines originate from the anterior field, forming longitudinal ridges that run across the entire scale surface and terminate as marginal spines.

Order SCORPAENIFORMES

Family SEBASTIDAE

Helicolenus dactylopterus **(DELAROCHE, 1809)**

Fig. 37

Type: ctenoid: transforming cteni. Shape: intermediate to oval: calyx to true oval. Shape variability: moderate. ***Anterior field***: flattened with scalloped margin. ***Lateral fields***: flattened to slightly convex and elongated in antero-posterior axis. ***Posterior field***: rounded end with ctenous margin. Focus: posterior. ***Circuli***: distinct; discontinuous in the anterior field, continuous in lateral fields, discontinuous in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation. ***Cteni***: transforming cteni.

Family SCORPAENIDAE

Scorpaena porcus **LINNAEUS, 1758**

Fig. 38

Type: cycloid: spinoid. ***Shape***: oval: true oval. Shape variability: low. ***Anterior field***: slightly convex with scalloped margin. ***Lateral fields***: flattened and elongated in antero-posterior axis. ***Posterior field***: rounded end with spinous margin. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation. ***Spines***: long, root-like spines originate within the posterior field, overstretching the entire field, and end in tiny spines on the posterior margin.

Family TRIGLIDAE

Eutrigla gurnardus **(LINNAEUS, 1758)**

Fig. 39

Type: cycloid: true cycloid in body areas I, J; and ctenoid: transforming cteni in areas A, B, C, D, E, F, G, H. ***Shape***: oval to quadrilateral: ovoid to square or trapezoidal. Shape variability: moderate. ***Anterior field***: flattened to convex with fluted margin. ***Lateral fields***: flattened to convex and elongated in antero-posterior axis. Slightly bulging towards the posterior field. ***Posterior field***: flattened to rounded end with smooth or ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation. ***Cteni***: transforming cteni.

Lepidotrigla cavillone **(LACEPÈDE, 1801)**

Fig. 40

Type: cycloid: spinoid. ***Shape***: quadrilateral: square or rectangular to rhomboidal. Shape variability: moderate. ***Anterior field***: flattened or inclined outline with fluted margin. ***Lateral fields***: flattened to convex or inclined and extended in dorso-ventral axis. ***Posterior field***: flattened end with spinous margin. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation. ***Spines***: thorn-like marginal spines are present, restricted to the posterior margin.

Order PERCIFORMES

Family MORONIDAE

Dicentrarchus labrax **(LINNAEUS, 1758)**

Fig. 41

Type: ctenoid: transforming cteni. ***Shape***: quadrilateral to polygonal: square or rectangular to pentagonal. Shape variability: moderate. ***Anterior field***: flattened with striate to slightly scalloped margin. The antero-lateral corners are slightly pointed. ***Lateral fields***: flattened and elongated in antero-posterior axis. ***Posterior field***: rounded to tapered end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation. ***Cteni***: transforming cteni.

Family SERRANIDAE

Anthias anthias **(LINNAEUS, 1758)**

Fig. 42

Type: ctenoid: peripheral cteni. ***Shape***: circular to intermediate: discoidal to calyx or shell-shaped. Shape variability: moderate. ***Anterior field:*** flattened to slightly convex with waved to scalloped margin. ***Lateral fields:*** vary from flattened to convex or concave. In general, these fields extend in dorso-ventral axis. ***Posterior field:*** rounded to tapered end with ctenous margin. ***Focus***: posterior. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, distinct to indistinct in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in the anterior field in radial orientation. ***Cteni***: peripheral cteni.

Epinephelus aeneus **(Geoffroy St. Hillaire, 1817)**

Fig. 43

Type: cycloid: true cycloid in body areas A, B, C, D, H, I, J; and ctenoid: transforming cteni in areas E, F, G. ***Shape***: oval to quadrilateral: true oval to rectangular. Shape variability: low. ***Anterior field***: flattened with scalloped margin. ***Lateral fields***: flattened to slightly convex and elongated in antero-posterior axis. ***Posterior field:*** rounded end with smooth or ctenous margin. ***Focus***: central. ***Circuli***: distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in the anterior field in radial orientation. ***Cteni***: transforming cteni.

Serranus cabrilla **(Linnaeus, 1758)**

Fig. 44

Type: ctenoid: transforming cteni. ***Shape***: intermediate to polygonal: calyx to pentagonal. Shape variability: moderate. ***Anterior field:*** flattened with scalloped margin. ***Lateral fields:*** flattened, and in general, equally extended in both axes. ***Posterior field:*** rounded to tapered end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior field, continuous to discontinuous in the lateral fields, discontinuous in the posterior field. ***Radii***: primary and secondary radii are present in the anterior and lateral fields in radial orientation. ***Cteni***: transforming cteni.

Serranus scriba **(Linnaeus, 1758)**

Fig. 45

Type: ctenoid: transforming cteni. ***Shape***: quadrilateral: square to rectangle. Shape variability: moderate. ***Anterior field:*** flattened with waved margin. ***Lateral fields***: flattened and elongated in antero-posterior axis. ***Posterior field:*** rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation. ***Cteni***: transforming cteni.

Family APOGONIDAE

Apogon imberbis **(Linnaeus, 1758)**

Fig. 46

Type: ctenoid: transforming cteni. ***Shape***: circular to intermediate: true circular, cordate, discoidal to shell-shaped. Shape variability: high. ***Anterior field***: slightly convex with scalloped margin. ***Lateral fields***: convex and extended in dorso-ventral axis. ***Posterior field***: rounded to slightly tapered end with ctenous margin. ***Focus***: posterior. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior and lateral fields in radial orientation. ***Cteni***: transforming cteni.

Family EPIGONIDAE

Epigonus denticulatus **Dieuzeide, 1950**

Fig. 47

Type: cycloid: true-cycloid. ***Shape***: circular to quadrilateral: cordate or discoidal to trapezoidal. Shape variability: moderate. ***Anterior field***: flattened with smooth to waved margin. It is extended in the antero-lateral sections. ***Lateral fields***: convex and extended in dorso-ventral axis, narrowing towards the posterior field. ***Posterior field***: rounded to tapered end with smooth and membranous margin. ***Focus***: indistinct. ***Circuli***: indistinct. ***Radii***: absent.

Family CORYPHAENIDAE

Coryphaena equiselis **Linnaeus, 1758**

Fig. 48

Type: cycloid: true cycloid. ***Shape***: oval to quadrilateral: ovoid to rectangular. Shape variability: moderate. In body area E, special thorn-like shaped scales are present. ***Anterior field***: highly variable: convex to strongly pointed or flattened to concave. Smooth margin. ***Lateral fields***: flattened to inclined and elongated in the antero-posterior axis. ***Posterior field***: flattened to tapered end with smooth or irregular margin. ***Focus***: central. ***Circuli***: distinct and continuous. ***Radii***: absent.

Family CARANGIDAE

Seriola dumerili **(Risso, 1810)**

Fig. 49

Type: cycloid: true cycloid. ***Shape***: circular to oval: true circular to true oval. Shape variability: moderate. ***Anterior field***: convex with scalloped margin. Lateral fields: convex, and in general, equally extended in both axes. ***Posterior field***: rounded end with smooth margin. ***Focus***: central. ***Circuli***: distinct; discontinuous in the anterior field, continuous to discontinuous in the lateral fields, continuous in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation.

Trachurus trachurus **(Linnaeus, 1758)**

Fig. 50

Type: cycloid: true cycloid. ***Shape***: circular to intermediate: true circular or discoidal to calyx. Shape variability: high. ***Anterior field***: generally flattened with waved to scalloped margin. ***Lateral fields***: convex and extended in dorso-ventral axis. ***Posterior field***: rounded end with smooth margin. ***Focus***: central. ***Circuli***: distinct; discontinuous in the anterior field, continuous in the lateral field, continuous to indistinct in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in the anterior field in radial orientation.

Family BRAMIDAE

Brama brama **(Bonnaterre, 1788)**

Fig. 51

Type: cycloid: spinoid. ***Shape***: polygonal: pentagonal to hexagonal. Shape variability: moderate. ***Anterior field***: flattened or convex with pointed apex and smooth margin. The antero-lateral corners are extended in dorso-ventral axis with a strongly pointed end resulting a bizarre thorn-like appearance of this field. ***Lateral fields***: flattened to concave and extended in dorso-ventral axis. ***Posterior field***: tapered end with more or less expressed spinous margin (see also discussion). ***Focus***: antero-central. ***Circuli***: distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent. ***Spines***: indistinct.

Family SPARIDAE

Scales from eight species of the family Sparidae were examined. All show a high level of similarity in their morphological characteristics. Therefore, here we provide a general description of their scale characteristics including further notes on species specific features. Scale images are displayed for the following species:

Boops boops **(Linnaeus, 1758)** · Fig. 52

Diplodus annularis **(Linnaeus, 1758)** · Fig. 53

Diplodus vulgaris **(Linnaeus, 1758)** · Fig. 54

Pagellus acarne **(Risso, 1827)** · Fig. 55

Pagellus erythrinus **(Linnaeus, 1758)** · Fig. 56

Sarpa salpa **(Linnaeus, 1758)** · Fig. 57

Sparus aurata **Linnaeus, 1758** · Fig. 58

Spondyliosoma cantharus **(Linnaeus, 1758)** · Fig. 59

Scale characteristics of the family Sparidae

Type: ctenoid: transforming cteni. ***Shape***: polygonal to intermediate: pentagonal to calyx or shell-shaped. Shape variability: moderate. ***Anterior field:*** flattened with generally waved margin. The margin varies among species: waved in *D. annularis*, *D. vulgaris*, *P. erythrinus*, and *S. aurata*; waved to scalloped in *S. salpa*; deeply waved to dentate in *B. boops* and *P. acarne*; irregularly waved in *S. cantharus*. ***Lateral fields:*** convex to concave, often bulge or extend in dorso-ventral axis. The position and extent of bulging varies between species; bulging in the antero-lateral section and being concave in the mid-lateral section in *B. boops*; bulging in the mid-lateral section in *D. annularis* and *D. vulgaris*, in the latter these fields are largely extended in dorso-ventral axis; bulging in the antero-lateral section and being concave in the postero-lateral section in *P. acarne*; bulging in the antero-lateral section without a major concavity in the postero-lateral section in *P. erythrinus*; bulging at mid-lateral section; bulging in the mid-lateral section or slightly in the antero-lateral section in *S. aurata*; bulging in the antero-lateral section with slight concavity in the postero-lateral section in *S. cantharus*. ***Posterior field:*** rounded to tapered end with ctenous margin. ***Focus***: central in *B. boops*, *P. acarne*, *P. erythrinus*, *S. salpa*, *S. aurata*, *S. cantharus*; postero-central in *D. annularis* and *D. vulgaris*. ***Circuli***: distinct and discontinuous in the anterior field, continuous to discontinuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in radial orientation. Radii usually remain within the anterior field in *D. annularis*, *D. vulgaris*, *P. erythrinus*, *S. aurata*, and partially in *S. salpa*. Radii occur both in the anterior, as well as in the lateral fields in *B. boops*, *P. acarne*, and *S. cantharus*. ***Cteni***: transforming cteni.

Family CENTRACANTHIDAE

Spicara maena **(Linnaeus, 1758)**

Fig. 60

Type: ctenoid: transforming cteni. ***Shape***: polygonal to intermediate: pentagonal to shell-shaped. Shape variability: moderate. ***Anterior field***: flattened with waved to scalloped margin. ***Lateral fields***: flattened to slightly concave and extended towards the antero-lateral section. ***Posterior field***: tapered to pointed end with ctenous margin. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior field, continuous to discontinuous in the lateral fields, indistinct in the posterior field. ***Radii:*** primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation. ***Cteni***: transforming cteni.

Spicara smaris **(Linnaeus, 1758)**

Fig. 61

Type: ctenoid: transforming cteni. ***Shape***: polygonal: heptagonal. Shape variability: moderate. ***Anterior field***:

flattened with waved to dentate margin. ***Lateral fields***: concave and extended towards the antero-lateral sections. ***Posterior field***: tapered to pointed end with ctenous margin. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior field, continuous to discontinuous in the lateral fields, indistinct in the posterior field. ***Radii:*** primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation. ***Cteni***: transforming cteni.

Family SCIAENIDAE

Sciaena umbra **Linnaeus, 1758**

Fig. 62

Type: ctenoid: transforming cteni. ***Shape***: quadrilateral to intermediate: square or rectangular to calyx. Shape variability: moderate. ***Anterior field:*** flattened with striate margin. ***Lateral fields:*** flattened to slightly convex, in general, elongated in the antero-posterior axis. ***Posterior field:*** rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior field, continuous in the lateral fields, continuous to discontinuous in the posterior field. ***Radii:*** primary, secondary and tertiary radii are present in the anterior field in parallel orientation. ***Cteni***: transforming cteni.

Family MULLIDAE

Two species of the family Mullidae were investigated, i.e., *M. barbatus* and *M. surmuletus.* The scales of the two species were found to be similar in their characteristic features, thus we provide a description that applies to both species. Scale images are displayed for both species.

Mullus barbatus **Linnaeus, 1758**

Fig. 63

Mullus surmuletus **Linnaeus, 1758**

Fig. 64

Type: ctenoid: transforming cteni. ***Shape***: intermediate to oval: calyx to true oval. Shape variability: low. ***Anterior field:*** flattened with dentate margin. ***Lateral fields:*** convex and elongated in the antero-posterior axis. ***Posterior field:*** rounded end with ctenous margin. ***Focus***: postero-central in *M. barbatus* and posterior in *M. surmuletus*. ***Circuli***: distinct and discontinuous in the anterior field, continuous lateral fields, indistinct in the posterior field. ***Radii:*** primary and secondary radii are present in the anterior field in radial orientation. In addition, few irregular grooves can occur in the posterior field in longitudinal orientation. ***Cteni***: transforming cteni.

Family CHAETODONTIDAE

Chaetodon hoefleri **Steindachner, 1881**

Fig. 65

Type: ctenoid: transforming cteni. ***Shape***: circular to oval or intermediate: true circular to ovoid or calyx. Shape variability: moderate. ***Anterior field***: flattened with scalloped margin. ***Lateral fields***: convex and extended in dorso-ventral axis. ***Posterior field***: rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior field, continuous to discontinuous in the lateral fields, discontinuous in the posterior field. ***Radii:*** primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation. ***Cteni***: transforming cteni.

Family CEPOLIDAE

Cepola macrophthalma **(Linnaeus, 1758)**

Fig. 66

Type: cycloid: true cycloid. ***Shape***: oval: ovoid. Shape variability: low. ***Anterior field***: convex with scalloped margin. ***Lateral fields***: flattened and elongated in antero-posterior axis. ***Posterior field***: rounded end with smooth margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior and posterior fields, continuous to discontinuous in the lateral fields. ***Radii***: primary, secondary and tertiary radii are present in the anterior, and partially in the lateral fields, in radial to parallel orientation.

Family POMACENTRIDAE

Chromis chromis **(Linnaeus, 1758)**

Fig. 67

Type: ctenoid: transforming cteni. ***Shape***: oval or quadrilateral to intermediate: true oval or rectangular to calyx. Shape variability: moderate. ***Anterior field:*** flattened with scalloped margin. ***Lateral fields:*** differ among body areas: in body areas A, B, C, D, H, and J they are rather flattened and elongated in antero-posterior axis; in areas E, F, G, and I they are convex and extended in dorso-ventral axis. ***Posterior field:*** rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii:*** primary, secondary and tertiary radii are present in the anterior field in parallel to radial orientation. ***Cteni***: transforming cteni.

Family LABRIDAE

Some species of the Labridae, analysed in this study, share a common characteristic feature, i.e., the membranous posterior field with longitudinal striae. Scales of the first three species (namely *Coris julis, Labrus viridis, Symphodus rostratus*) are remarkably similar, while the scale of *Thalassoma pavo* show higher similarity to the scales of *Sparisoma cretense* (Scaridae).

Coris julis (Linnaeus, 1758)

Fig. 68

Type: cycloid: true cycloid. ***Shape***: oval to polygonal: true oval to pentagonal. Shape variability: moderate. ***Anterior field****:* convex with scalloped margin. ***Lateral fields****:* flattened and elongated in antero-posterior axis. ***Posterior field****:* pointed end with membranous margin. ***Focus***: central. ***Circuli***: distinct and discontinuous. Within the posterior field, circuli join and create distinct longitudinal striae. ***Radii***: primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation.

Labrus viridis Linnaeus, 1758

Fig. 69

Type: cycloid: true cycloid. ***Shape***: oval to polygonal: true oval to pentagonal. Shape variability: moderate. ***Anterior field****:* flattened to slightly convex with scalloped margin. ***Lateral fields****:* flattened and moderately elongated in antero-posterior axis. ***Posterior field****:* pointed end with membranous margin and distinct longitudinal striae. ***Focus***: central. ***Circuli***: generally distinct and discontinuous; continuous only in a limited part of the lateral fields. Within the posterior field, circuli join and create distinct longitudinal striae. ***Radii***: primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation.

Symphodus rostratus (Bloch, 1791)

Fig. 70

Type: cycloid: true cycloid. ***Shape***: oval to circular: true oval to true circular. Shape variability: moderate. ***Anterior field****:* flattened to slightly convex with striate to scalloped margin. ***Lateral fields****:* flattened to convex and moderately elongated in antero-posterior axis. ***Posterior field****:* rounded to tapered end with membranous margin. ***Focus***: central. Instead of the presence of a clear focus, an expanded focal area is visible. Occasional grooves may be present within this area. No inner mosaic pattern, as in *Thalassoma pavo* (see below). ***Circuli***: distinct and discontinuous in the anterior field, continuous to discontinuous in the lateral fields, discontinuous in the posterior field. Within the posterior field, circuli join and create distinct longitudinal striae. ***Radii***: primary, secondary and tertiary radii are present in the anterior and lateral fields in radial orientation.

Thalassoma pavo (Linnaeus, 1758)

Fig. 71

Type: cycloid: true cycloid. ***Shape***: oval to polygonal: true oval or oblong to hexagonal. Shape variability: moderate. ***Anterior field****:* flattened with conical apex and striate margin. The antero-lateral corners are slightly extended and pointed. ***Lateral fields****:* flattened and elongated in antero-posterior axis. ***Posterior field****:* rounded to tapered end with membranous margin. ***Focus***: central. No clear focus point is visible. An expanded focal area is present, which is well-separated in the centre of the scale, with distinct mosaic pattern. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in all four fields in radial orientation. In addition, numerous, short, vertical grooves can occur in all four fields, with predominant occurrence within the focal area; these grooves are in contact with radii.

Family SCARIDAE

Sparisoma cretense (Linnaeus, 1758)

Fig. 72

Type: cycloid: true cycloid. ***Shape***: circular to oval: cordate to true oval. Shape variability: moderate. ***Anterior field***: flattened with prominent conical apex and smooth to striate margin. The antero-lateral corners are extended and pointed. ***Lateral fields***: flattened to convex, and in general, they are equally extended in both axes. ***Posterior field***: rounded end with smooth margin. ***Focus***: central. An expanded focal area with mosaic pattern rarely occurs (i.e., in area D). ***Circuli***: distinct and discontinuous in the anterior field, continuous to discontinuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary, secondary and tertiary radii are present in radial orientation, especially in the anterior and posterior fields. Only few radii are present in the lateral fields. In addition, few, short, vertical grooves can occur in all four fields; these grooves are in contact with radii.

Family AMMODYTIDAE

Gymnammodytes cicerelus (Raffinesque, 1810)

Fig. 73, 74

Gymnammodytes cicerelus indeed has scales only in some body areas; therefore the description refers to scales of body areas D, G, H and J only. Morphometric parameters were measured on scale Ga.

Type: cycloid: true cycloid. ***Shape***: circular: true circular to discoidal. Shape variability: moderate. ***Anterior field***: flattened to convex with smooth to waved margin. ***Lateral fields***: convex and slightly extended in dorso-ventral axis. ***Posterior field***: rounded end with smooth margin. Focus: central. ***Circuli***: distinct and discontinuous. Elevated circuli are separated by longitudinal depressions (i.e., unmineralized sections). ***Radii***: irregular wide grooves are present in all four fields in somewhat radial orientation.

Family TRACHINIDAE

Trachinus draco **Linnaeus, 1758**

Fig. 75

Type: cycloid: true cycloid. ***Shape***: quadrilateral: square to rhomboidal. Shape variability: moderate. ***Anterior field***: flattened and slightly inclined with striate margin. ***Lateral fields***: flattened or inclined and moderately elongated in antero-posterior axis. ***Posterior field***: rounded to tapered end with membranous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior and posterior fields, continuous in the lateral fields. ***Radii***: primary and secondary radii are present in the anterior field in parallel to radial orientation.

Family TRIPTERYGIIDAE

Tripterygion tripteronotum **(Risso, 1810)**

Fig. 76

Type: ctenoid: peripheral cteni. ***Shape***: circular: true circular to discoidal. Shape variability: moderate. ***Anterior field***: flattened to convex with scalloped margin. ***Lateral fields***: convex and extended in dorso-ventral axis. ***Posterior field***: flattened to rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior and lateral fields in parallel to radial orientation. ***Cteni***: peripheral cteni.

Family GOBIIDAE

Gobius bucchichi **Steindachner, 1870**

Fig. 77

Type: ctenoid: peripheral cteni. ***Shape***: circular to intermediate: true circular or discoidal to calyx. Shape variability: low. ***Anterior field***: flattened to convex with striate to scalloped margin. The antero-lateral corners are extended and slightly pointed. ***Lateral fields***: flattened to convex and moderately extended in dorso-ventral axis with a slightly bulging postero-lateral section. ***Posterior field***: rounded end with ctenous margin. ***Focus***: posterior. ***Circuli***: distinct and discontinuous; continuous only in the postero-lateral section. ***Radii***: primary, secondary and tertiary radii are present in the anterior and lateral fields in parallel to radial orientation. Radii often extend to the posterior field. ***Cteni***: peripheral cteni.

Gobius paganellus **Linnaeus, 1758**

Fig. 78

Type: ctenoid: peripheral cteni. ***Shape***: circular to oval: true circular to true oval. Shape variability: low. ***Anterior field***: convex with moderately scalloped margin. The antero-lateral corners are extended and slightly pointed. ***Lateral fields***: flattened to convex and moderately elongated in antero-posterior axis. ***Posterior field***: rounded end with ctenous margin. ***Focus***: posterior. ***Circuli***: distinct and discontinuous; continuous only in the postero-lateral section. ***Radii***: primary and secondary radii are present in the anterior and lateral fields in parallel to radial orientation. Radii often extend to the posterior field. ***Cteni***: peripheral cteni.

Family SPHYRAENIDAE

Sphyraena chrysotaenia **Kluzinger, 1884**

Fig. 79

Type: cycloid: true cycloid. ***Shape***: oval to quadrilateral or intermediate: true oval to square or calyx. Shape variability: moderate. ***Anterior field:*** flattened with striate margin. ***Lateral fields:*** flattened to slightly convex and moderately elongated in antero-posterior axis. ***Posterior field:*** rounded end with membranous margin. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior field, continuous in the lateral fields, indistinct in the posterior field. ***Radii***: primary and secondary radii are present in the anterior field in radial orientation.

Sphyraena sphyraena **(Linnaeus, 1758)**

Fig. 80, 81

Type: cycloid: spinoid. ***Shape***: circular: true circular to discoidal. Shape variability: low. ***Anterior field:*** convex with smooth to striate margin. ***Lateral fields:*** convex, and in general, extended in dorso-ventral axis, except in body areas A, B, and J, where these fields are rather elongated in the antero-posterior axis. ***Posterior field:*** rounded end with spinous margin. ***Focus***: central. ***Circuli***: distinct and discontinuous. Circuli are highly crested and elevated creating a network of branched ridges by longitudinal interconnection. Circuli are densely interrupted by spaces perforated by unmineralized square areas. These areas align among circuli and give a loosely similar appearance to radii. ***Radii***: absent. ***Spines***: small number (1–4) of tiny marginal spines.

Family SCOMBRIDAE

Scomber colias **Gmelin, 1789**

Fig. 82

Type: cycloid: crenate. ***Shape***: quadrilateral: square to rectangular or rhomboidal. Shape variability: high. ***Anterior field***: flattened with smooth margin. ***Lateral fields***: flattened or inclined and in general, extended in dorso-ventral axis, except in body areas A, B, I and J, where they are rather elongated in antero-posterior axis. ***Posterior field***: rounded end with crenulated margin. ***Focus***: central. ***Circuli***: distinct and continuous, however, frequently become indistinct in the posterior field. ***Radii***: absent.

Family TETRAGONURIDAE

Tetragonurus cuvieri **Risso, 1810**

Fig. 83

Type: cycloid: spinoid. ***Shape***: quadrilateral: square to rhomboidal. Shape variability: low. ***Anterior field***: flattened with smooth margin. ***Lateral fields***: flattened to inclined or convex, and in general, they are slightly extended in dorso-ventral axis. ***Posterior field***: rounded end with spinous margin. ***Focus***: antero-central. ***Circuli***: distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. ***Radii***: absent. Spines: long spines originate from the anterior field, forming longitudinal, parallel ridges that run across the entire posterior field and terminate as marginal spines.

Family CAPROIDAE

Capros aper **(Linnaeus, 1758)**

Fig. 84

Type: cycloid: spinoid. ***Shape***: circular to polygonal: true circular, cordate or discoidal to pentagonal. Shape variability: high. ***Anterior field***: generally convex with smooth margin. ***Lateral fields***: flattened to inclined or convex, and in general, extended in the dorso-ventral axis. ***Posterior field***: rounded end with smooth margin but spinous posterior field. ***Focus***: postero-central. ***Circuli***: distinct and continuous in the anterior and lateral fields, discontinuous to indistinct in the posterior field. ***Radii***: absent. Spines: numerous, long and thin spines are scattered within the entire posterior field; they overreach the posterior margin. The length of the longest spine on scale C is 19% of the total scale length.

Order PLEURONECTIFORMES

Family PSETTODIDAE

Scophthalmus maximus **(Linnaeus, 1758)**

Fig. 85

Typical scales are not present in adult *Scophthalmus maximus*. Skin appears rather smooth with some "stony structures". However, in early stage of development, cycloid scales can be distinguished on the ocular-side (left side) of the fish.
Type: cycloid: true cycloid. ***Shape***: oval: true oval to ovoid. Shape variability: uniform. ***Anterior field***: convex with moderately scalloped margin. ***Lateral fields***: slightly convex and elongated in antero-posterior axis. ***Posterior field***: rounded end with smooth margin. ***Focus***: central. ***Circuli***: distinct and discontinuous in the anterior and posterior fields, continuous in the lateral fields. ***Radii***: primary, secondary and tertiary radii occur in the anterior field in radial orientation.

Family BOTHIDAE

Bothus podas **(Delaroche, 1809)**

Fig. 86, 87

Type: ctenoid: transforming cteni on ocular-side (left side); and cycloid: true cycloid on blind-side (right side). ***Shape***: circular to oval: true circular to ovoid. Shape variability: low. ***Anterior field:*** convex with striated margin. ***Lateral fields:*** flattened to convex and moderately elongated in antero-posterior axis. ***Posterior field:*** rounded end with ctenous margin on ocular-side scales and smooth margin on blind-side scales. ***Focus***: postero-central. ***Circuli***: distinct and discontinuous. ***Radii***: primary, secondary and tertiary radii occur in the anterior and lateral fields in radial orientation. Radii often reach the posterior field. ***Cteni***: transforming cteni on the ocular-side; absent on the blind-side.

Family SOLEIDAE

Microchirus variegatus **(Donovan, 1808)**

Fig. 88, 89

Type: ctenoid: transforming cteni on both sides. ***Shape***: polygonal: hepta- to octagonal. Shape variability: low.

Anterior field: flattened with scalloped margin. ***Lateral fields***: flattened to concave and elongated in antero-posterior axis. The concavity of these fields is shifted slightly towards the posterior field. ***Posterior field***: tapered end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior and posterior fields, continuous in the lateral fields. ***Radii***: primary and secondary radii occur in the anterior field in radial orientation. ***Cteni***: transforming cteni on both sides.

Monochirus hispidus **Rafinesque, 1814**

Fig. 90, 91

Type: ctenoid: transforming cteni on both sides. ***Shape***: polygonal: hepta- to octagonal. Shape variability: low. ***Anterior field***: flattened with waved margin. ***Lateral fields***: flattened to concave and elongated in antero-posterior axis. The concavity of these fields is shifted slightly towards the posterior field. ***Posterior field***: tapered end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior and posterior fields, continuous in the lateral fields. ***Radii***: primary and secondary radii occur in the anterior field in radial orientation. ***Cteni***: transforming cteni on both sides.

Solea solea **(Linnaeus, 1758)**

Fig. 92, 93

Type: ctenoid: transforming cteni on both sides. ***Shape***: quadrilateral: rectangular. Shape variability: uniform. ***Anterior field***: flattened to concave with waved to scalloped margin. ***Lateral fields***: flattened and elongated in the antero-posterior axis. ***Posterior field***: rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior and posterior fields, continuous in the lateral fields. ***Radii***: primary and secondary radii occur in the anterior field in radial orientation. ***Cteni***: transforming cteni on both sides.

Family CYNOGLOSSIDAE

Symphurus nigrescens **Rafinesque, 1810**

Fig. 94, 95

Type: ctenoid: transforming cteni on both sides. ***Shape***: quadrilateral to oval: rectangular to true oval. Shape variability: low. ***Anterior field:*** flattened with scalloped margin. ***Lateral fields:*** flattened to slightly convex and elongated in antero-posterior axis. ***Posterior field:*** rounded end with ctenous margin. ***Focus***: postero-central. ***Circuli***: distinct; discontinuous in the anterior and posterior fields, continuous in the lateral fields. ***Radii***: primary and secondary radii occur in the anterior fields in radial orientation. Radii often extend to the lateral fields. ***Cteni***: transforming cteni on both sides.

Discussion

Classification of scale types. There is considerable variation in the literature concerning scale types (Roberts, 1993; Khemiri *et al*., 2001), shapes and related characters (Patterson *et al*., 2002; Jawad, 2005; Gholami *et al*., 2013). Nevertheless, some authors feel that grouping all scales with a spiny posterior margin under the term "ctenoid" is an oversimplification (Roberts, 1993; Khemiri *et al*., 2001). Our study proposes an improved classification for scale types. Regarding characters with an evolutionary background, instead of a purely phenological way, we see a major difference between scales made of a single bone and scales with additional ossifications. In contrast to other authors, we regard all crenate and spinoid scales as sub-types of cycloid scales, and consider ctenoid scales only those which possess separate ossifications from the main scale body. In the light of evolution, 'real' ctenoid scales likely developed only twice: in the characid family Distichodontidae and somewhere at the base or within the percomorphs (Roberts, 1993). Spined scales, on the other hand, certainly developed several times, as did crenate scales within the teleostei as variations of cycloid scales.

Besides these rather easily definable scale types, certain taxonomic groups developed special types of scales making a clear designation more difficult. Clupeiform fishes form such a taxon. The characteristic morphology of their scales previously gave rise to the term "clupeoid scales" distinct from cycloid and ctenoid (Timms, 1905). Clupeoid scales are rather thin, relatively large, more or less circular scales with numerous grooves and irregular crack marks, and possess a crenulated posterior margin. We termed the observed grooves in the anterior and lateral fields as "transverse grooves" and within the posterior field as "longitudinal or irregular grooves" according to the orientation of the groove (see Fig. 8 – Fig. 13). Broad range of names can be found in the literature for the same features, e.g., "transverse grooves" by Borodin (1924), "transverse striae (= radii)" and "longitudinal striae" by Roberts (1993), "fracture lines" by Patterson *et al*. (2002). Other unusual cycloid scales are equipped with a membranous flap on the posterior field. This can be seen in *Trachinus draco,* Trachinidae (Fig. 75), in *Sphyraena chrysotaenia,* Sphyraenidae (Fig. 79) and most prominent in the families Labridae and Scaridae (Figs. 68 – Fig. 72). Similar membranous flaps are also known from *Albula vulpes, Megalops atlanticus, Dussumieria acuta* and *Chirocentrus dorab* (Roberts, 1993). According to their radii on the posterior field, Labridae and Scaridae have rather unique scales. Nevertheless, we still regard clupeid scales or membranous scales as variations of cycloid scales without the need of introducing new classifying terms.

Similarly to cycloid scales, within spinoid scales unique shapes and ornamentations can occur. In this study, the most prominent features were found in *Brama brama* (Fig. 51), *Macrorhamphosus scolopax* (Fig. 36)

Table 2. List of fish species and their scale types with exemplary morphometric indices of scales derived from body area C (i.e., anterior part of the flank above lateral line). Scale type abbreviations based on Roberts (1993): **Cy** – true cycloid scale; **Cr** – crenate scale; **Sp** – spinoid scale; **Pe** – ctenoid scale with peripheral cteni; **Tr** – ctenoid scale with transforming cteni; **Wh** – ctenoid scale with whole cteni. Scale shape index after Burdak (1979): **Si** = TD/LD, where TD – maximal transverse diameter of the scale; LD – maximal longitudinal diameter of the scale. The relative scale sizes (J-indices) for the scale length (**Jsl**) and scale width (**Jsw**) were calculated following Esmaeili (2001): Jsl (Jsw) = length (width) of scale (in mm) / fish standard length (in mm) × 100. Focal index (**Fi**) is given as the distance (in mm) from the outermost edge of the anterior field to the focus / the distance (in mm) from the outermost edge of the anterior field to the outermost edge of the posterior field. Note: in some species, more than one scale type can occur, indicated with "/" mark. Notes: in Pleuronectiformes, information is provided on scales derived from both sides of the specimens (i.e., ocular/blind side). * n/a: not applicable. ** Scales of *Scophthalmus maximus* were sampled at early stage of development.

Teleostei	Scale type	Si	Jsl	Jsw	Fi
ALBULIFORMES					
Notacanthidae					
Notacanthus bonaparte	Cy	0.87	0.39	0.23	0.36
CLUPEIFORMES					
Engraulidae					
Engraulis encrasicolus	Cr	1.29	4.11	5.44	0.50
Clupeidae					
Alosa fallax	Cr	1.07	3.20	3.14	0.67
Clupea harengus	Cr	1.29	2.93	3.87	0.56
Sardina pilchardus	Cr	1.12	4.34	4.94	0.66
Sardinella aurita	Cr	1.22	3.78	4.76	0.61
Sprattus sprattus	Cr	1.09	3.37	3.45	0.62
ARGENTINIFORMES					
Argentinidae					
Argentina sphyraena	Cy	1.21	4.18	5.40	0.73
Alepocephalidae					
Alepocephalus rostratus	Cy	0.98	3.44	2.06	0.02
STOMIIFORMES					
Sternoptychidae					
Maurolicus muelleri	Cy	1.14	3.49	3.72	0.44
AULOPIFORMES					
Synodontidae					
Synodus saurus	Cy	1.14	3.49	3.75	0.64
MYCTOPHIFORMES					
Myctophidae					
Myctophum punctatum	Cy	1.40	4.90	6.15	0.58
GADIFORMES					
Macrouridae					
Coelorinchus caelorhinchus	Sp	1.22	1.37	1.67	0.40
Nezumia sclerorhynchus	Sp	1.27	1.43	1.75	0.60
Trachyrincus scabrus	Sp	1.31	0.98	1.36	0.48
Moridae					
Mora moro	Cy	1.04	2.16	1.79	0.70
Merlucciidae					
Merluccius merluccius	Cy	0.93	0.71	0.51	0.47
Gadidae					
Molva molva	Cy	0.88	0.37	0.13	0.59
Trisopterus luscus	Cy	0.93	1.47	1.13	0.30
MUGILIFORMES					
Mugilidae					
Chelon labrosus	Wh	1.21	3.71	3.85	0.72
Liza aurata	Wh	1.17	2.83	3.13	0.70
ATHERINIFORMES					
Atherinidae					
Atherina hepsetus	Cy	1.32	2.57	3.22	0.49
Atherinomorus lacunosus	Cy	1.06	1.93	2.06	0.44
BELONIFORMES					
Belonidae					
Belone belone	Cy	1.08	0.62	0.67	0.47

Table 2 continued.

Teleostei	Scale type	Si	Jsl	Jsw	Fi
BERYCIFORMES					
Berycidae					
Beryx decadactylus	Sp	1.17	2.07	2.37	0.44
Trachichthyidae					
Hoplostethus mediterraneus	Sp	1.72	1.54	2.89	0.47
ZEIFORMES					
Zeidae					
Zeus faber	Cy	0.95	1.03	0.87	0.44
GASTEROSTEIFORMES					
Macroramphosidae					
Macrorhamphosus scolopax	Sp	1.34	1.04	1.73	0.33
SCORPAENIFORMES					
Sebastidae					
Helicolenus dactylopterus	Tr	1.31	2.43	2.63	0.82
Scorpaenidae					
Scorpaena porcus	Sp	0.88	2.75	1.87	0.63
Triglidae					
Eutrigla gurnardus	Cy/Tr	1.09	1.01	0.78	0.75
Lepidotrigla cavillone	Sp	1.72	2.13	3.55	0.70
PERCIFORMES					
Moronidae					
Dicentrarchus labrax	Tr	1.15	1.85	1.74	0.64
Serranidae					
Anthias anthias	Pe	1.38	2.94	4.10	0.88
Epinephelus aeneus	Cy/Tr	0.97	1.43	0.87	0.57
Serranus cabrilla	Tr	1.13	1.80	1.79	0.77
Serranus scriba	Tr	1.11	2.03	1.75	0.72
Apogonidae					
Apogon imberbis	Tr	1.17	5.08	6.24	0.88
Epigonidae					
Epigonus denticulatus	Cy	1.29	1.88	2.88	n/a*
Coryphaenidae					
Coryphaena equiselis	Cy	1.01	0.90	0.61	0.45
Carangidae					
Seriola dumerili	Cy	1.02	0.91	0.73	0.60
Trachurus trachurus	Cy	1.17	1.04	1.38	0.59
Bramidae					
Brama brama	Sp	1.33	1.40	1.85	0.23
Sparidae					
Boops boops	Tr	1.21	2.13	2.45	0.45
Diplodus annularis	Tr	1.19	2.85	3.08	0.62
Diplodus vulgaris	Tr	1.50	3.51	5.40	0.80
Pagellus acarne	Tr	1.32	2.39	2.93	0.57
Pagellus erythrinus	Tr	1.39	2.22	2.96	0.60
Sarpa salpa	Tr	1.31	2.34	3.01	0.46
Sparus aurata	Tr	1.45	2.13	3.12	0.55
Spondyliosoma cantharus	Tr	1.40	2.10	2.77	0.52
Centracanthidae					
Spicara maena	Tr	1.47	2.14	2.93	0.58
Spicara smaris	Tr	1.44	1.53	2.08	0.49
Sciaenidae					
Sciaena umbra	Tr	1.23	2.33	2.36	0.63
Mullidae					
Mullus barbatus	Tr	1.33	4.86	5.60	0.73
Mullus surmuletus	Tr	1.16	5.17	5.11	0.81
Chaetodontidae					
Chaetodon hoefleri	Tr	1.04	5.31	5.24	0.76
Cepolidae					
Cepola macrophthalma	Cy	1.07	0.20	0.17	0.72

Table 2 continued.

Teleostei	Scale type	Si	Jsl	Jsw	Fi
Pomacentridae					
Chromis chromis	Tr	0.93	6.13	4.53	0.73
Labridae					
Coris julis	Cy	0.84	2.55	1.48	0.52
Labrus viridis	Cy	0.93	3.19	2.14	0.58
Symphodus rostratus	Cy	0.96	5.87	4.17	0.51
Thalassoma pavo	Cy	0.96	6.66	4.72	0.54
Scaridae					
Sparisoma cretense	Cy	0.97	8.02	6.65	0.54
Ammodytidae					
Gymnammodytes cicerelus	Cy	1.17	0.26	0.34	0.50
Trachinidae					
Trachinus draco	Cy	1.13	1.27	1.10	0.63
Tripterygiidae					
Tripterygion tripteronotum	Pe	1.27	2.70	3.90	0.67
Gobiidae					
Gobius bucchichi	Pe	1.15	2.72	2.77	0.90
Gobius paganellus	Pe	1.05	2.81	2.61	0.87
Sphyraenidae					
Sphyraena chrysotaenia	Cy	0.99	1.44	1.08	0.44
Sphyraena sphyraena	Sp	1.00	0.52	0.52	0.54
Scombridae					
Scomber colias	Cr	1.18	0.85	0.97	0.51
Tetragonuridae					
Tetragonurus cuvieri	Sp	1.24	1.15	1.29	0.28
Caproidae					
Capros aper	Sp	1.38	2.40	3.54	0.70
PLEURONECTIFORMES					
Psettodidae					
Scophthalmus maximus	Cy**/-	0.91/-	1.00/-	0.59/-	0.47/-
Bothidae					
Bothus podas	Tr/Cy	1.01/0.94	1.22/1.00	0.98/0.81	0.77/0.79
Soleidae					
Microchirus variegatus	Tr/Tr	0.96/0.91	2.27/1.82	1.46/1.18	0.65/0.61
Monochirus hispidus	Tr/Tr	0.92/0.90	2.33/1.93	1.40/1.22	0.62/0.63
Solea solea	Tr/Tr	0.95/0.95	1.36/1.17	0.72/0.62	0.73/0.70
Cynoglossidae					
Symphurus nigrescens	Tr/Tr	0.94/0.93	2.10/2.04	1.24/1.24	0.77/0.74

and *Tetragonurus cuvieri* (Fig. 83). The spines in the latter two form smooth continuous ridges terminating in an acute spine, along the entire posterior field in *T. cuvieri*, and across the whole scale in *M. scolopax*. The scales of *B. brama* and *M. scolopax* share another characteristic feature that is the presence of a spinous projection on the anterior field in dorso-ventral orientation. Roberts (1993) described for *B. brama* ridges along the posterior field ending in marginal acute spines. The specimen of the present study, however, showed virtually no ridges and there are no spines present. So far, specimen of *B. brama* seem to have either cycloid or spinoid scales. These differing observations cannot be satisfactorily explained in the current study and require further investigation.

We divided ctenoid scales into three sub-types based on Roberts (1993): peripheral, transforming and whole cteni. The latter is for cteni growing in several rows without any transformation of the cteni in the older rows. In our study, this condition was found only in members of the family Mugilidae. It may represent a precursor of the transforming cteni type, but further clarification of this issue is required.

Classification of scale shapes. Scales have very diverse outlines with considerable intra- and inter-specific variation. There is no obvious way for grouping these, and therefore, there is no standard classification of scale shapes (e.g., Patterson *et al.*, 2002; Jawad, 2005; Matondo *et al.*, 2010; Ganzon *et al.*, 2012; Gholami *et al.*, 2013). In this study, we sorted the scales by major geometric shape categories with several subcategories in the attempt to provide a generally usable scale shape classification system. Although a clear classification of scale shapes appears to be difficult in many cases, this is one of the most important characters in taxon identification. In some cases, a first glance of the scale shape provides useful identification clues: e.g., *Atherina* species have a unique octogonal scale shape (Fig. 30). To provide an objective measure for scale shapes, we used a set of morphometric parameters: the calculated shape index (Si), relative scale sizes (Jsl, Jsw) and focal index (Fi) serve as valuable tool in species differentiation.

Scale ornamentations. Some features of the observed scales do not fit into a simple classification scheme, especially the ones related to circuli. Instead of merging superficially similar structures, we described the observed ornamentations separately in the results section. In *Molva molva* (Fig. 25, 26) elevated brick-like structures are present. Comparable structures were reported from other Gadidae species by Patterson *et al*. (2002) referring to them as "intermarkings". The respective authors described intermarkings as "perpendicular or irregular lines/structures between the circuli that can align between circuli to give a loosely similar appearance to radii". In cases where surface ornamentations are arranged in an orderly pattern, it may become difficult to decide if "intermarkings" or the ornamentations of circuli are indeed present, or whether it is an occurrence of highly elevated circuli that are regularly divided by radii, like in *Trisopterus luscus* (Fig. 27). The comparative study of gadiform scales by Khemiri *et al*. (2001) revealed that the scale surface ornamentation, represented by the circuli, are variably developed but always present in this family. Whenever mineralization occurs only at the level of the circuli, the space between two adjacent circuli remains unmineralized. In this case, circuli can be recognized clearly as individual concentric lines on the scale surface. However, when the mineralization happens also in the space between the circuli, the surface becomes ornamented with a network of branched ridges, as in *Sphyraena sphyraena* (Fig. 80, 81). Similarly, in *Maurolicus muelleri* surface ornamentations occur in variable shape creating linear depressions (Fig. 17A) or unever ridges (Fig. 17B) in radial orientation.

Radii are characterized by the absence of superficial mineralized layers (Khemiri *et al*., 2001). As a result, they appear as even grooves often in radial orientation on the surface interrupting circuli. Radii are most common on the anterior field, but also can be distributed over the whole scale surface, as in *T. luscus* and in *Bothus podas* (Figs. 86, 87) where scales have highly elevated circuli that are densely carved by radii. The same seems to be true for *Gymnammodytes cicerelus* (Figs. 73, 74), but with much more broadened radii becoming more irregular in the posterior field.

Scales from different body areas. Even though this study focused on regular body scales, excluding for example lateral line scales, ventral scutes, scales on fin bases or cheeks, there is still notable variability within single specimens. Only in few cases, such as in flatfishes, the scales from the sampled body areas A to J appear almost identical. For most species, scale shape and size varies significantly along the body.

In general, scales found in areas A, B, H, and most of the scales in I and J are smaller in size compared to scales from areas C, D, E, F and G. Most of the time, scales found in area E and F were the biggest, whereas scales in H were the smallest in size, and scales in area C appeared to be most consistent in size.

In few species, there are different types of scales present on a single specimen, e.g., *Epinephelus aeneus* (Fig. 43) and *Eutrigla gurnardus* (Fig. 39) possess both cycloid and ctenoid scales. However, for other species changes in shape may also occur among body areas. As a general pattern, we observed that scales in areas A, B, I and J are rather elongated along the antero-posterior axis, whereas in areas C, D, F and G they extend in dorso-ventral axis. Scales in area H are either square-shaped, circular or slightly elongated. In area E, directly behind the operculum, scale shape differs in most cases from the "typical" shape for a given species. The least variability in scale shape was again found in area C. For morphometric analyses, e.g., when comparing species or populations, scales from this area should provide the most reliable results. In morphometric studies, scales from a area comparable or identical to our area C are already commonly used (e.g., Richards & Esteves, 1997; Poulet *et al*., 2005; Ibañez *et al*., 2007; Staszny *et al*., 2012; Gholami *et al.*, 2013). Shape, relative size and/or characteristics of scales may change during ontogeny (Jacot, 1920; Sire, 1986; Sire & Arnulf, 2000), which is why morphometric studies have to take also the developmental stage into account before comparing taxa or groups.

Use of the atlas for species identification. The results presented herein show an amazing variety of scale types, shapes and ornamentations. Morphological features of relevance are mostly the shape and the pattern of the surface of a scale. A single scale often bears enough information to assign it clearly to a taxon, often to species level. In this study, optimal features are displayed, for instance, within the family Macrouridae (Figs. 20–22). The scales of the family are easily recognizable, and at the same time, the number and shape of the spines differ among the species, thus allowing a clear species differentiation. Even for additional marcourid species described by Khemiri *et al.* (2001), spine shape and pattern still seems to be species-specific. In other cases, species identification may be much more difficult, e.g., in *Spicara* species (Figs. 60, 61) or in gobies (Figs. 77, 78). Especially of the latter group, only two of many species have been studied here. In such cases, a simple identification by consulting an atlas does not appear feasible. If the respective information is available, however, morphometric analyses may still allow for species identification (e.g., Jawad, 2005).

There are at least three notable shortcomings of our study: (1) the selection of only the most common species, (2) the disregard of intra-specific scale variability, and (3) the lack of ontogenetic information of scale growth in the different species. A study taking all species and their ontogenetic stages into account, however, hardly appears to be feasible and future investigations are necessary to supplement the information of this atlas. Nevertheless, we trust this study will provide helpful orientation for the identification of fish scales from the Mediterranean area.

Phylogenetic information inferred from scales. Since our study was designed to produce a descriptive atlas and not as a phylogenetic study, the base for statements in a phylogenetic context is limited. Nevertheless, the potential of studying scales in an evolutionary setting becomes visible already by the species selection presented herein. The distribution of the grooves, for example, on the scales of the clupeiform fishes, appears to allow some phylogenetic grouping. In some species, such as *Alosa fallax* (Fig. 9) and *Clupea harengus* (Fig. 10), grooves run quite regular in dorso-ventral orientation, and are usually restricted to the anterior and lateral fields. This pattern is best visible in the larger body scales. In *Sardina pilchardus* (Fig. 11), *Sardinella aurita* (Fig. 12) and *Sprattus sprattus* (Fig. 13), however, grooves are usually interrupted in the middle and especially in the latter species less regularly distributed. In *Engraulis encrasicolus* (Fig. 8), the grooves are more irregular, running radially, and transverse grooves are present in the posterior field as well. Whether these different types of groove groupings allow statements on the evolutionary history and phylogenetic relationships, it needs to be proven by future studies. Nonetheless, it seems very likely that the type of grooves in clupeiform fishes bear valuable information on their relationships.

It may not be surprising that closely related species have similar scales (Patterson *et al*., 2002; Jawad, 2005; Yokogawa & Watanabe, 2011), but life history, habitat characteristics and other factors could have also a strong influence on the scale morphology of a fish species (Johal & Dua, 1994, 1995; Dapar *et al*., 2012; Ganzon *et al*., 2012; Ibáñez *et al*., 2012). Since the effect of the habitat might be manifested in scale morphology, scales of species that share similar or identical living conditions may look alike, for instance scales of *Thalassoma pavo* (Labridae, Fig. 71) and *Sparisoma cretense* (Scaridae, Fig. 72). Scales of *T. pavo* resemble more the scales of *S. cretense* than those of other labrid species investigated in this study (i.e., *Coris julis*, Fig. 68, *Labrus viridis*, Fig. 69 and *Symphodus rostratus*, Fig. 70). Labrid and scarid scales are truly cycloid with membranous posterior fields. In contrast to the above mentioned three labrid species, the scales of *T. pavo* and *S. cretense* have a rather smooth posterior margin, radii in all fields and web-like ornamentation of radii in the centre of the scale. Although belonging to different families, both species share similar ecological habitats. Both species are found mostly on rocky shores, whereas the other three labrid species prefer different habitats close to seagrass meadows and/or among mixtures of sandy and rocky ground (Quignard & Pras, 1986). Whether or not the similarity of scale shape or characteristic features and habitat are causally related, warrants further investigation.

The results of this study show that much information provided by teleost scales is not yet fully understood in its biological context. We suggest that scale characters could be incorporated to a morphological matrix to attempt to investigate relationships among teleost families. Further decryption of scale information will significantly widen our knowledge about life history, ecology and phylogenetic relationships of fishes.

Conclusions

In a phylogenetic context, our classification varies from traditional views by assigning crenate and spinoid scales as subtypes of cycloid instead of ctenoid scales.

Regular body scales may significantly differ within a single specimen depending on body area.

Type, shape and ornamentation of single scales allow designation to certain taxa; in many cases to species-level.

Scales likely bear information for phylogenetic or ecological studies, so far used only to a small degree.

Future studies should (1) complete the species account for Mediterranean species; (2) investigate scale variability within species during ontogeny; (3) take other scale types, such as lateral line scales and scutes, into account; (4) produce atlases for other seas, and (5) mine the phylogenetic information stored in scale morphology.

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Appendix

Fig. 7. *Notacanthus bonaparte*; 190 mm TL, Costa Brava, Spain, DMM IE/4609. Scale bar = 500 µm.

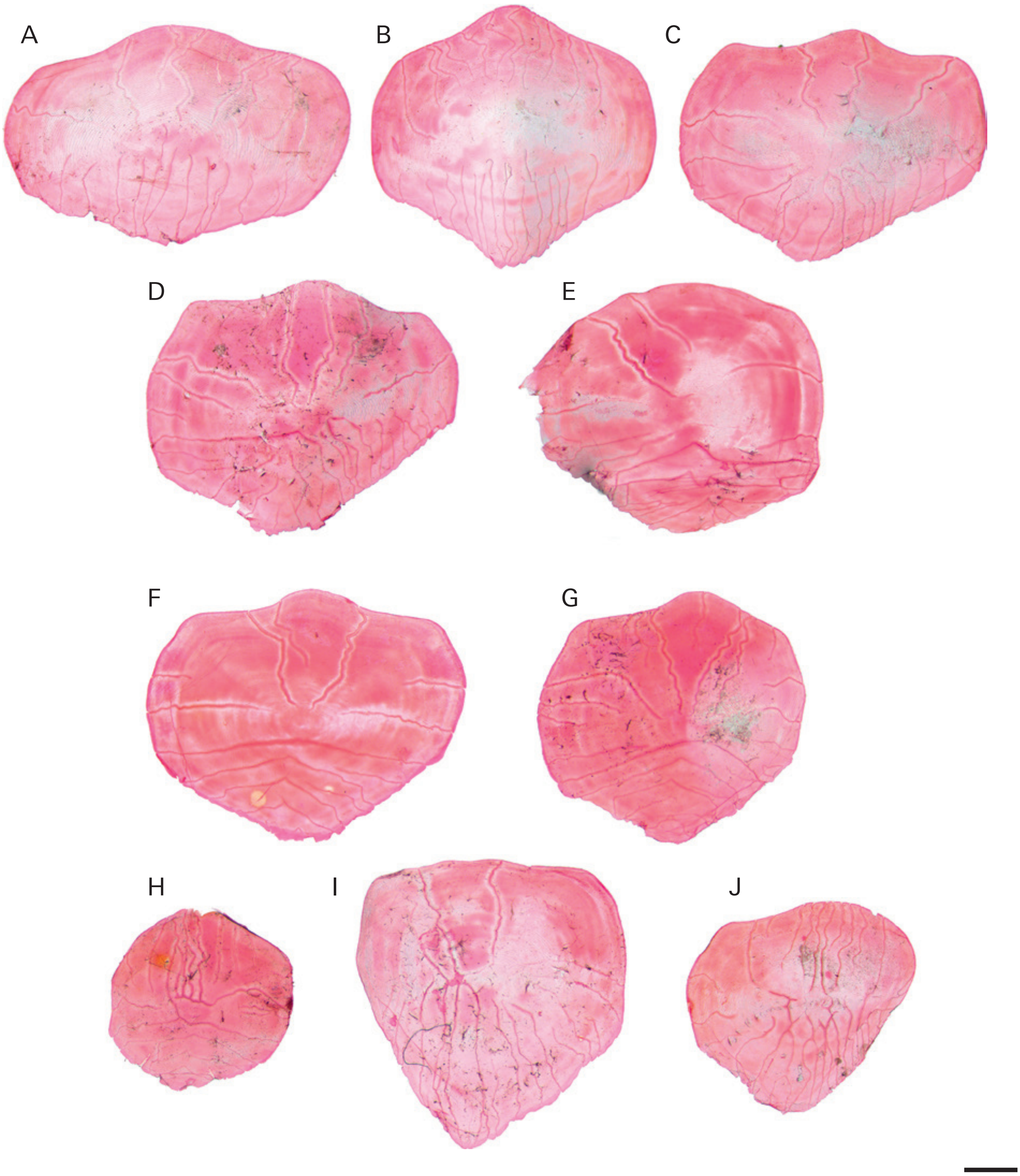

Fig. 8. *Engraulis encrasicolus*; 108 mm SL, Mali Lošinj, Croatia, DMM IE/9008. Scale bar = 1 mm.

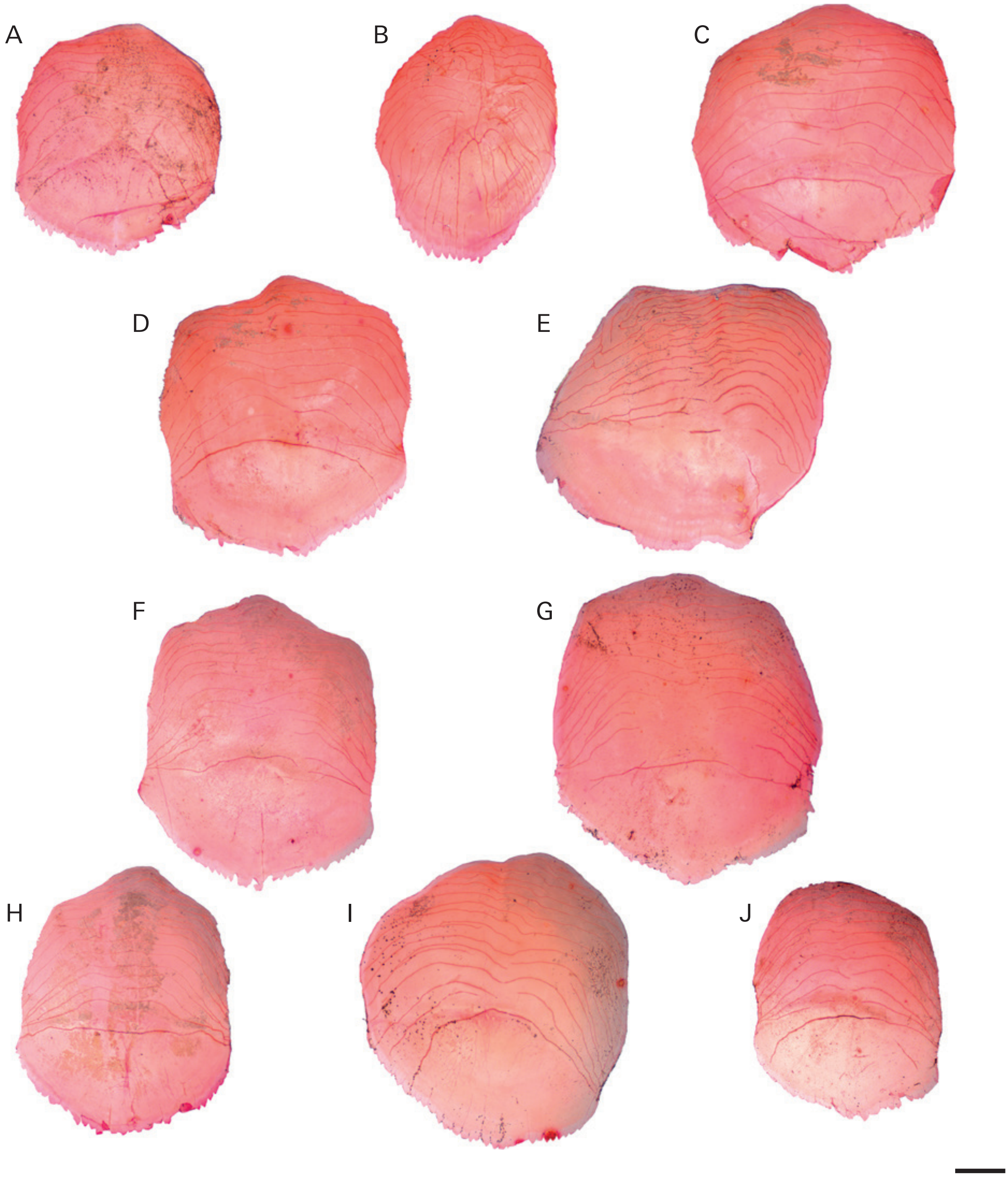

Fig. 9. *Alosa fallax*; 330 mm SL, Baltic Sea, Germany, DMM IE/4361. Scale bar = 2 mm.

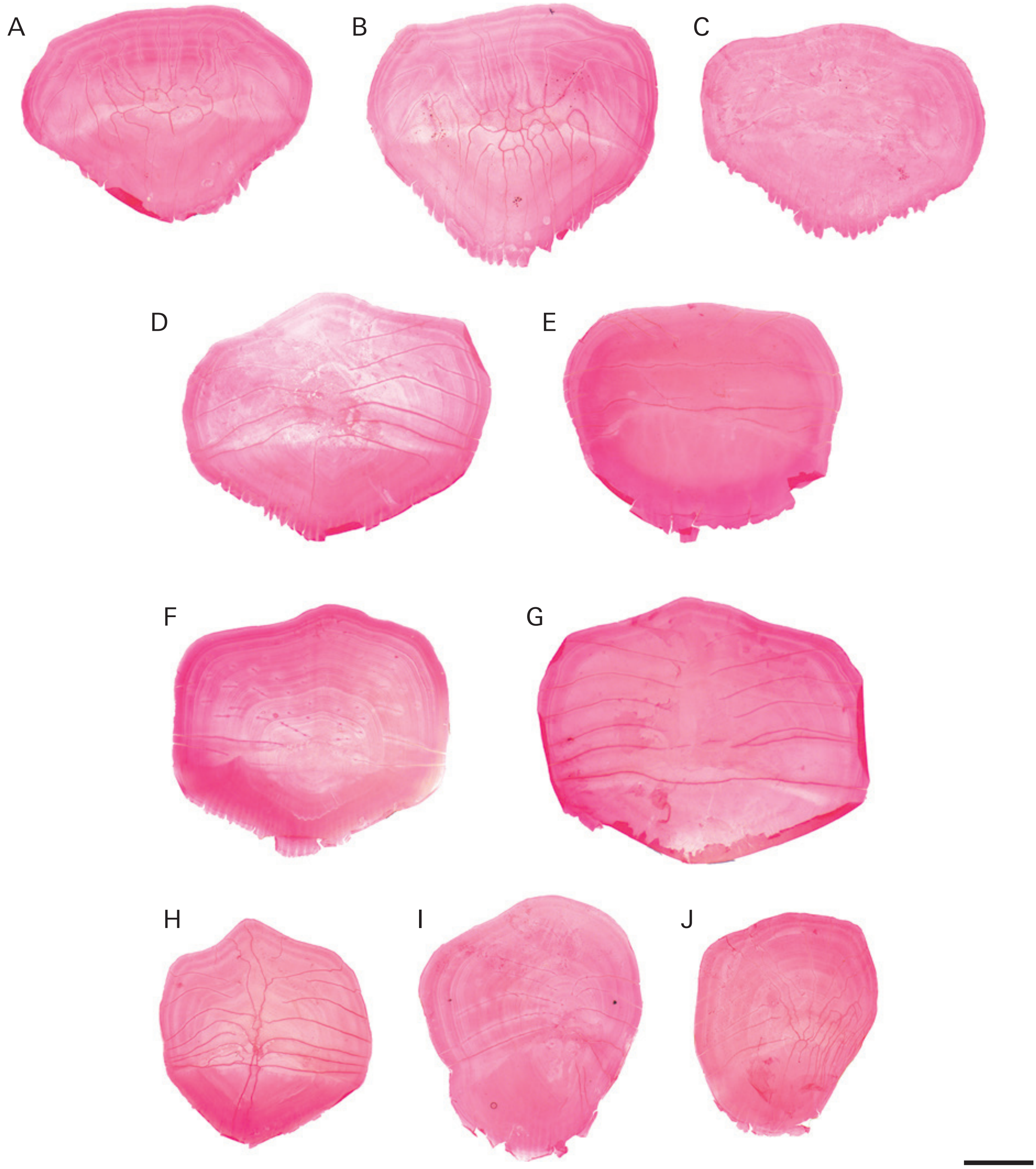

Fig. 10. *Clupea harengus*; 210 mm SL, Costa Brava, Spain, DMM IE/4611. Scale bar = 2 mm.

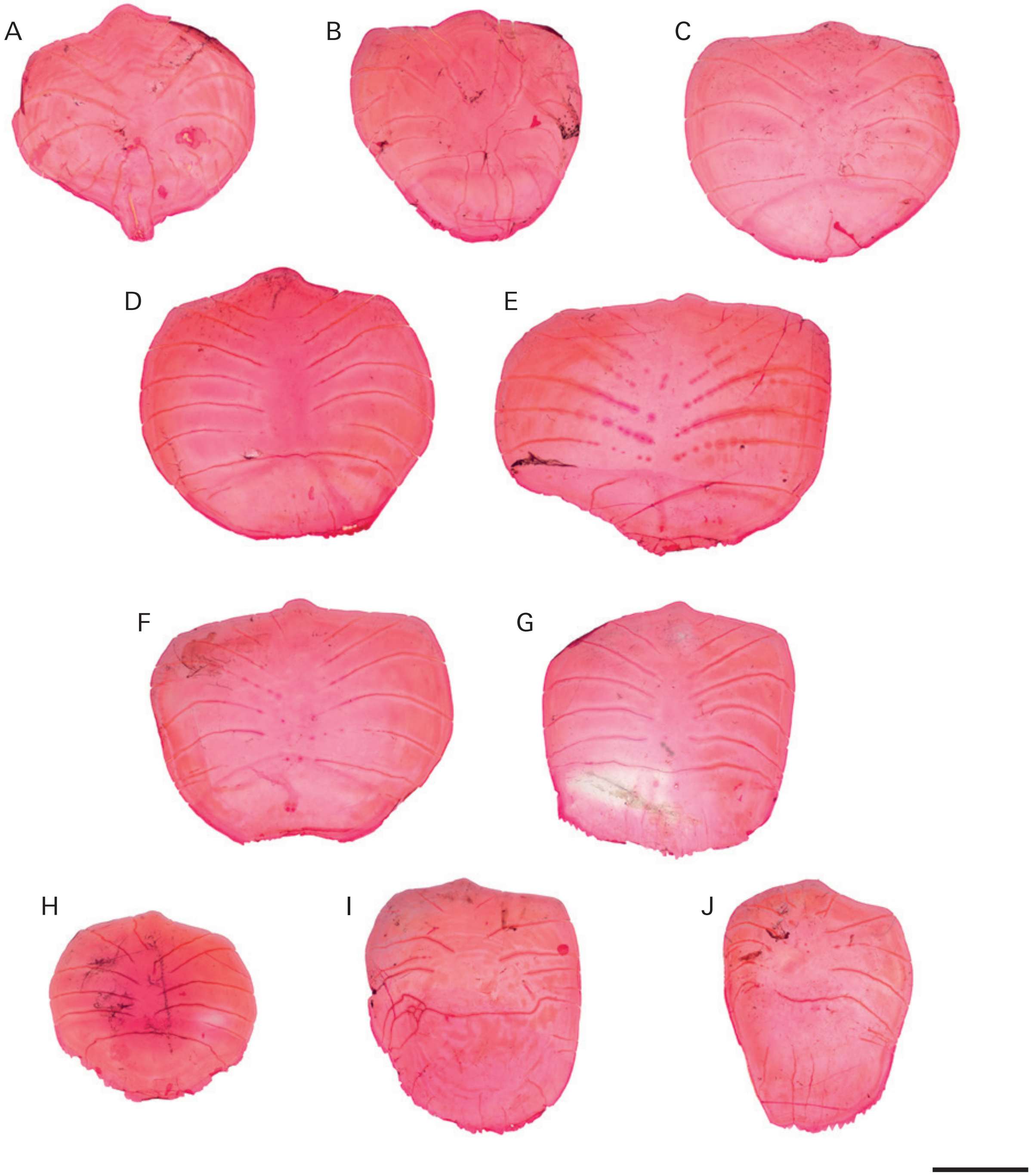

Fig. 11. *Sardina pilchardus*; 115 mm SL, Mali Lošinj, Croatia, DMM IE/9009. Scale bar = 2 mm.

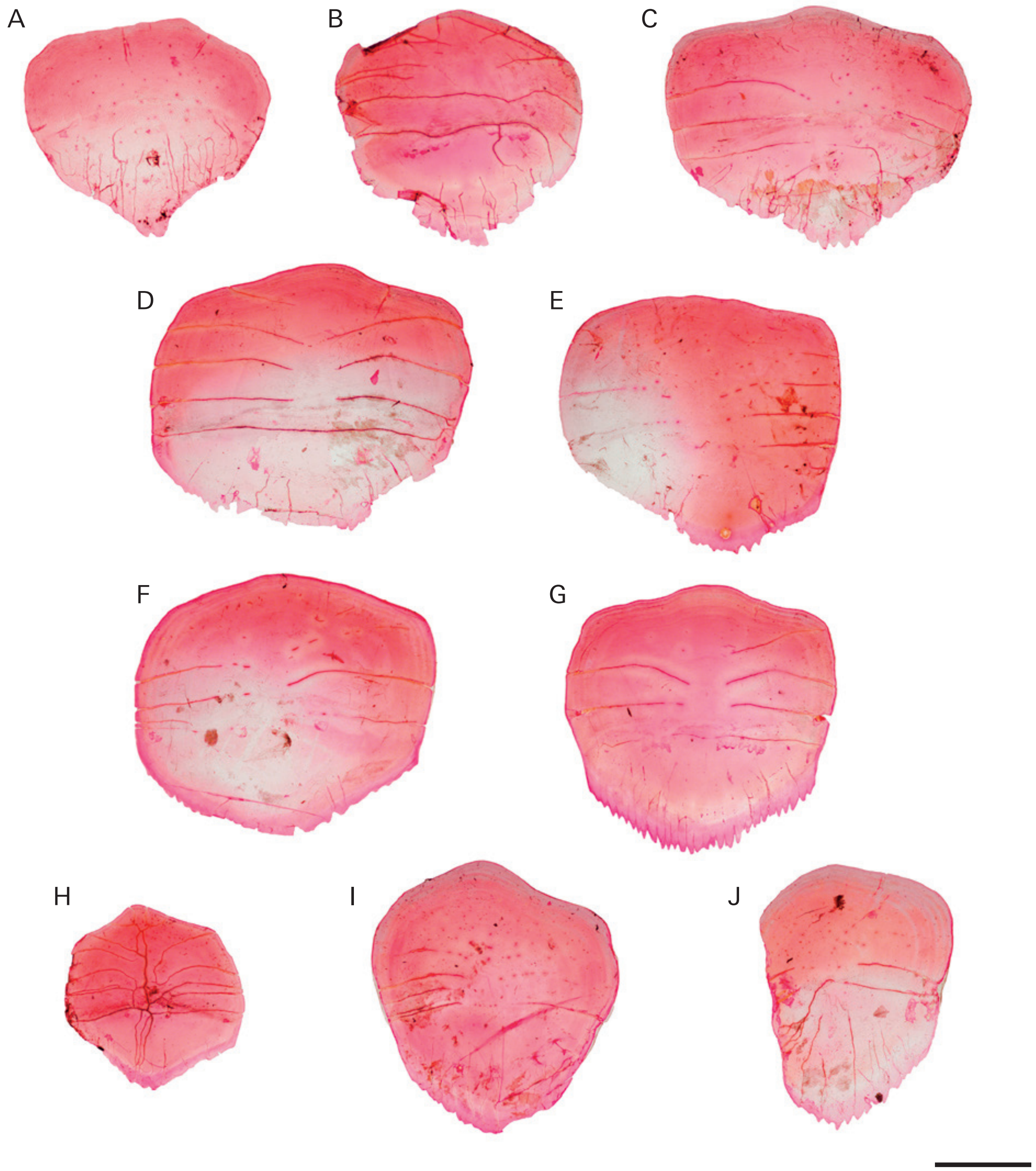

Fig. 12. *Sardinella aurita*; 132 mm SL, Costa Brava, Spain, DM IE/5843. Scale bar = 2 mm.

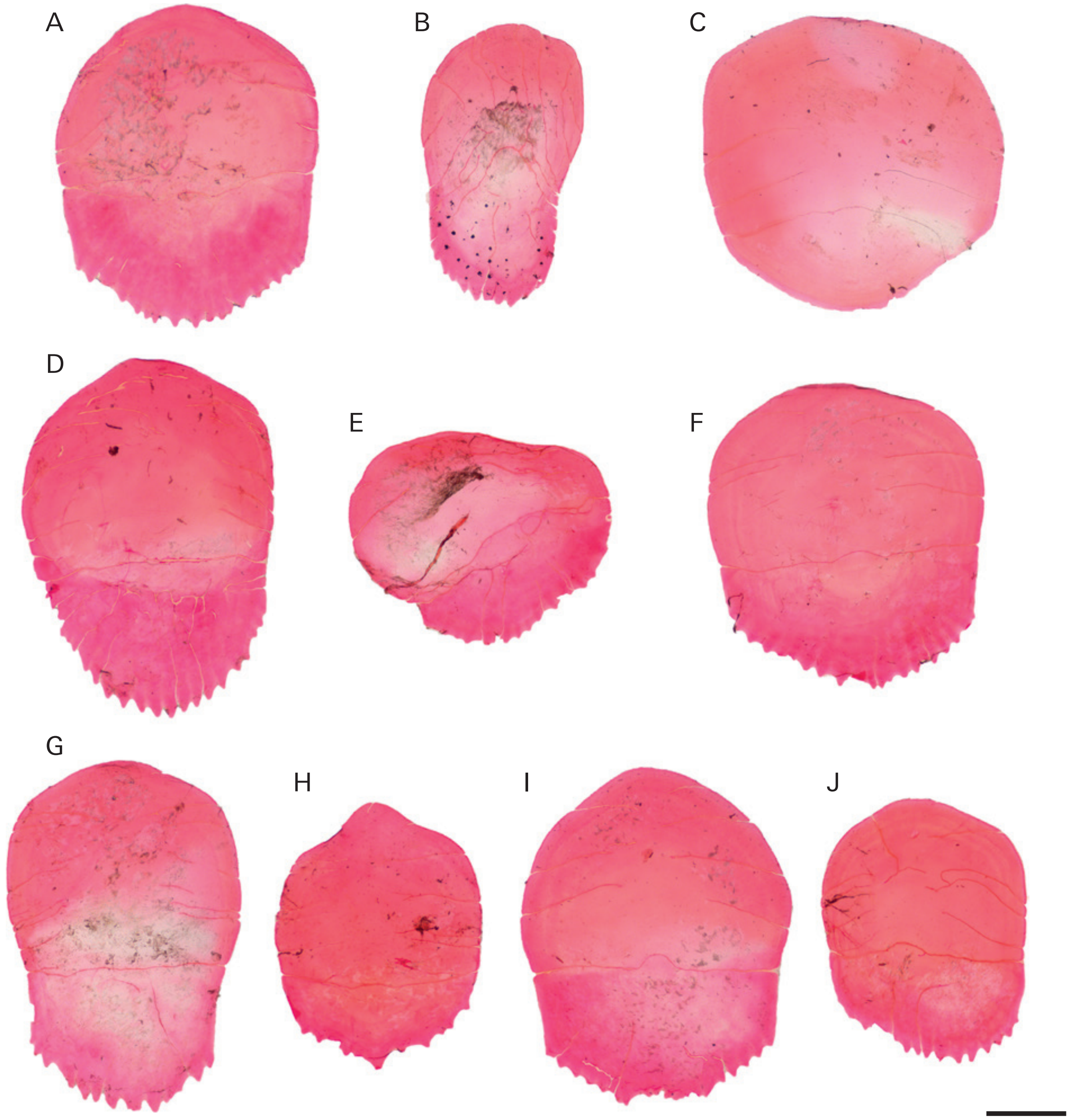

Fig. 13. *Sprattus sprattus*; 108 mm SL, North Sea, DM IE/6726. Scale bar = 1 mm.

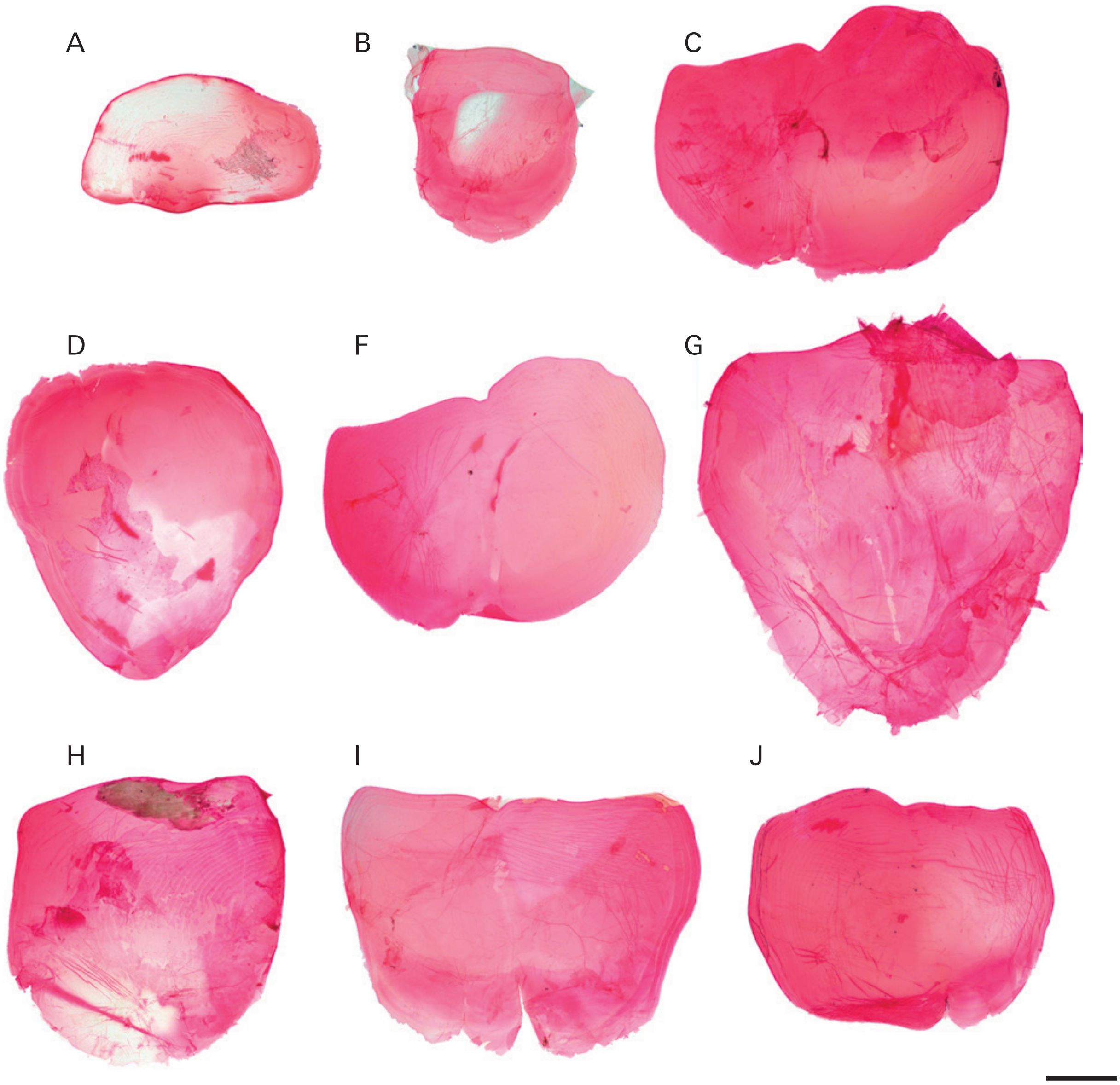

Fig. 14. *Argentina sphyraena*; 185 mm SL, Costa Brava, Spain, DMM IE/5003. Scale bar = 2 mm.

Fig. 15. *Alepocephalus rostratus*; 250 mm SL, Costa Brava, Spain, DMM IE/5805. Scale bar = 2 mm.

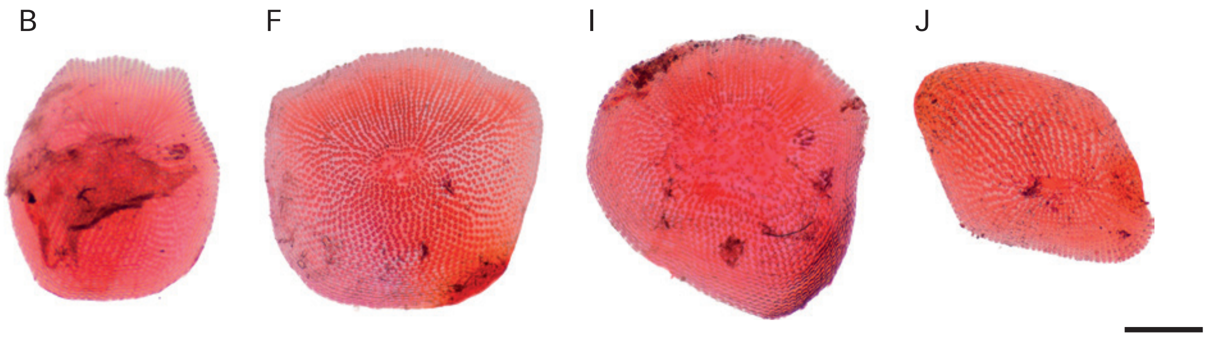

Fig. 16. *Maurolicus muelleri*; 4 specimens, 42–51 mm SL, Costa Brava, Spain, DMM IE/5048. Scale bar = 500 µm.

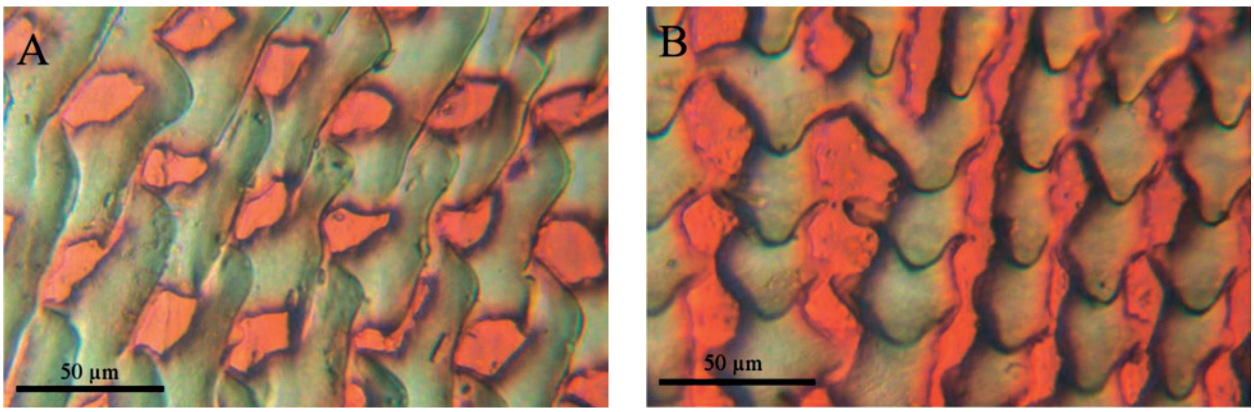

Fig. 17. Surface ornamentations of the scale of *Maurolicus muelleri* in sampling area F. **A**: individual scale ornamentations; **B**: scale ornamentations forming ridges.

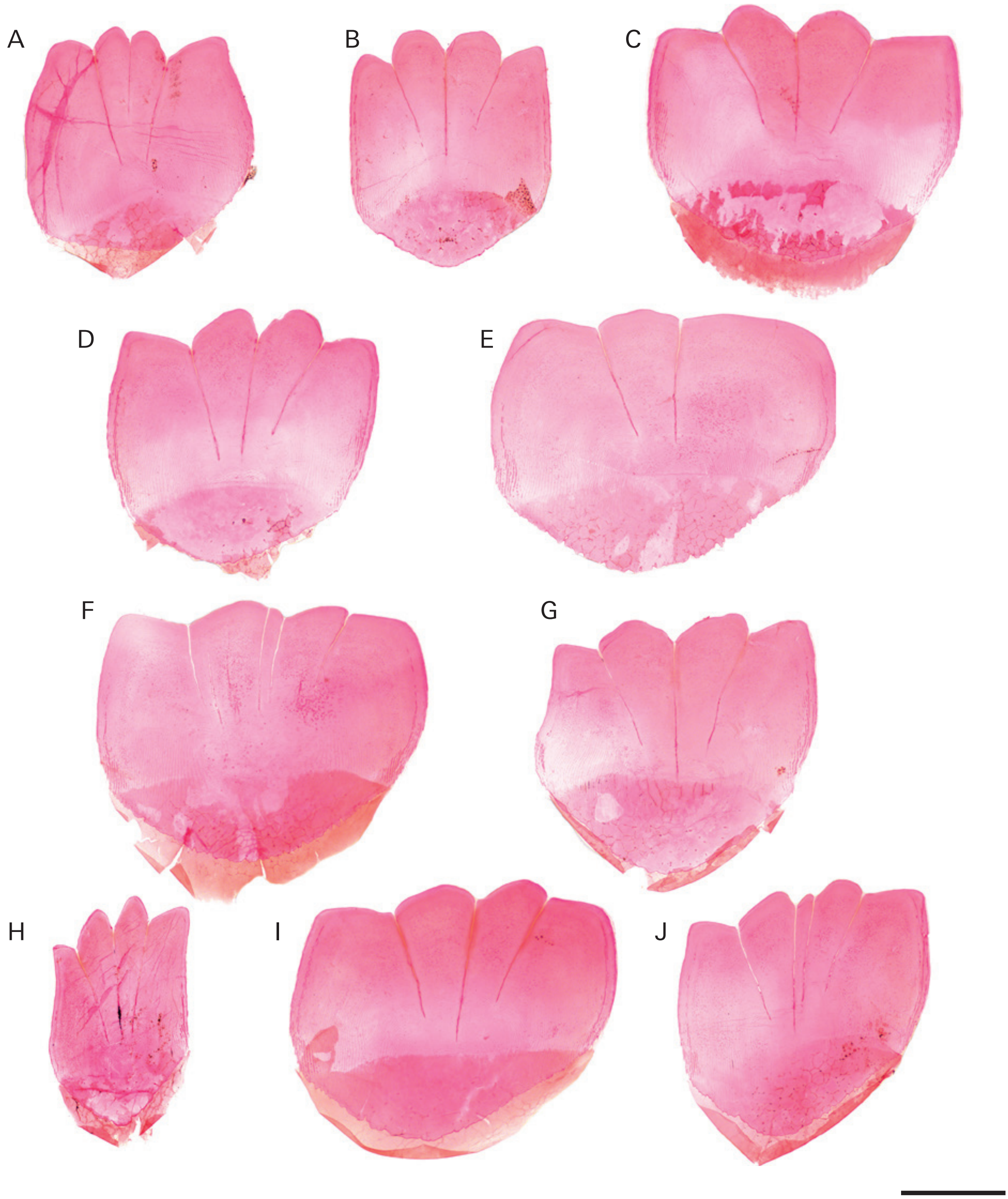

Fig. 18. *Synodus saurus*; 164 mm SL, Costa Brava, Spain, DMM IE/5026. Scale bar = 2 mm.

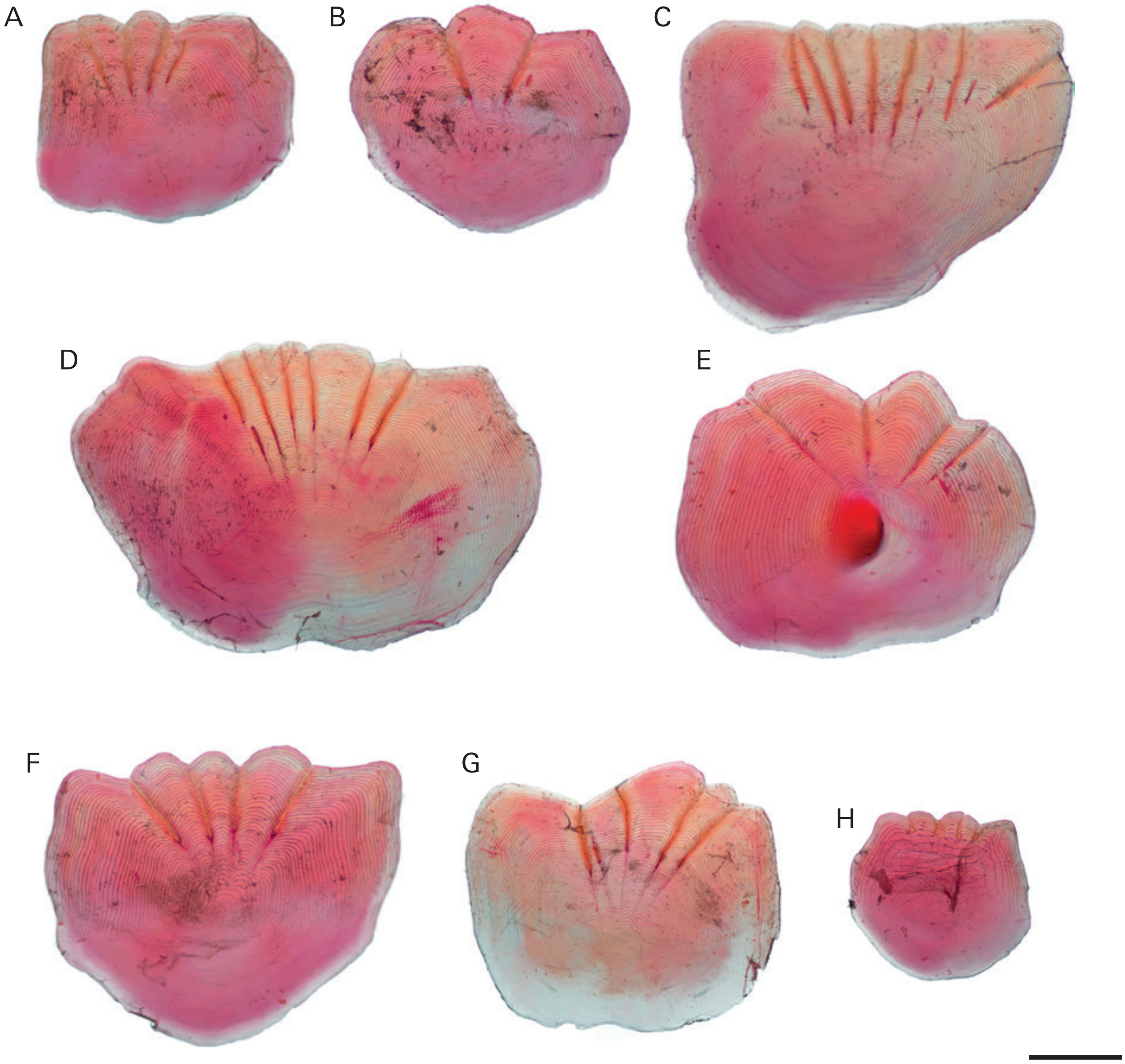

Fig. 19. *Myctophum punctatum*; 68 mm SL, Costa Brava, Spain, DMM IE/5114. Scale bar = 1 mm.

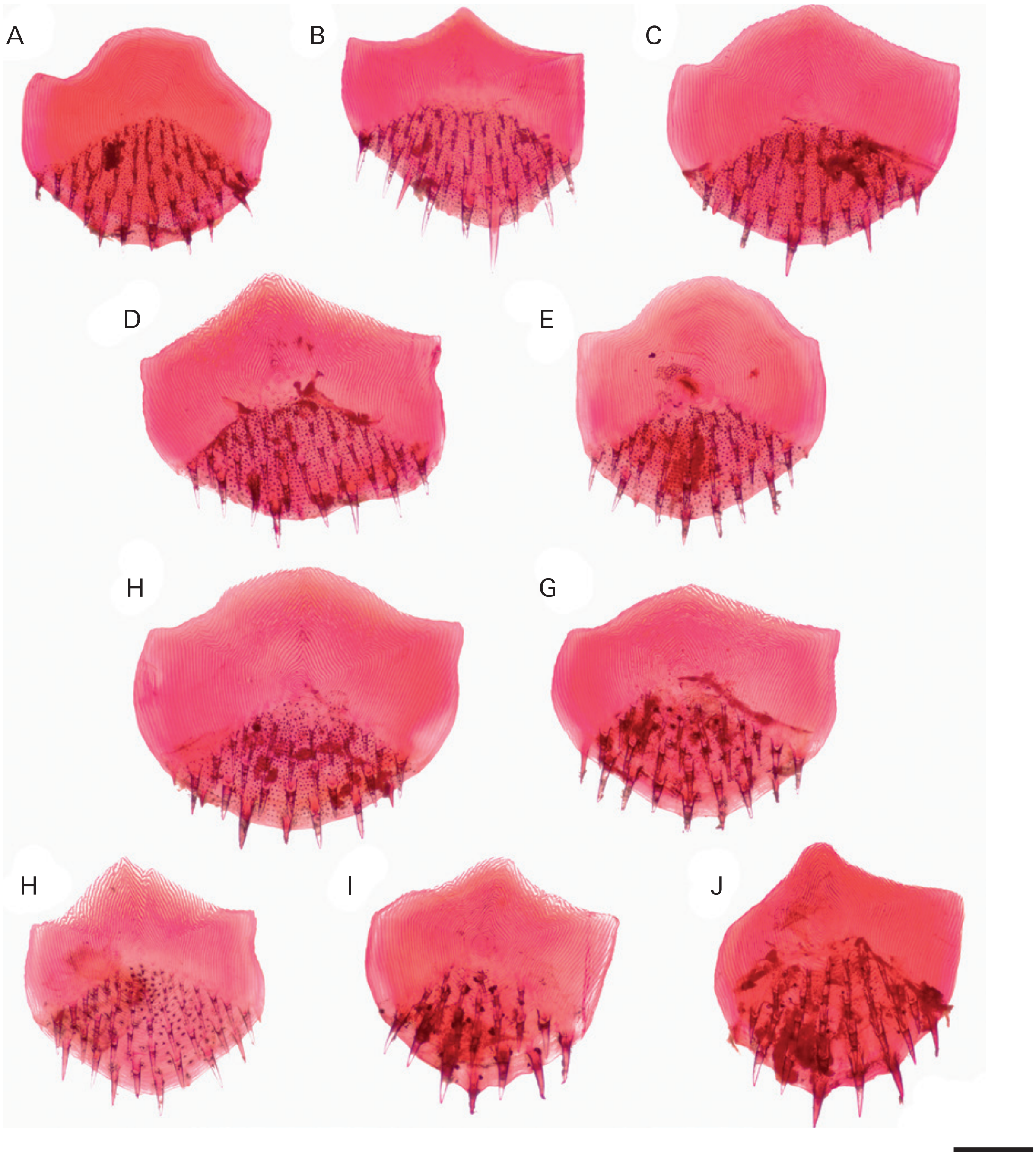

Fig. 20. *Coelorinchus caelorhinchus*; 219 mm SL, Costa Brava, Spain, DMM IE/5899. Scale bar = 1 mm.

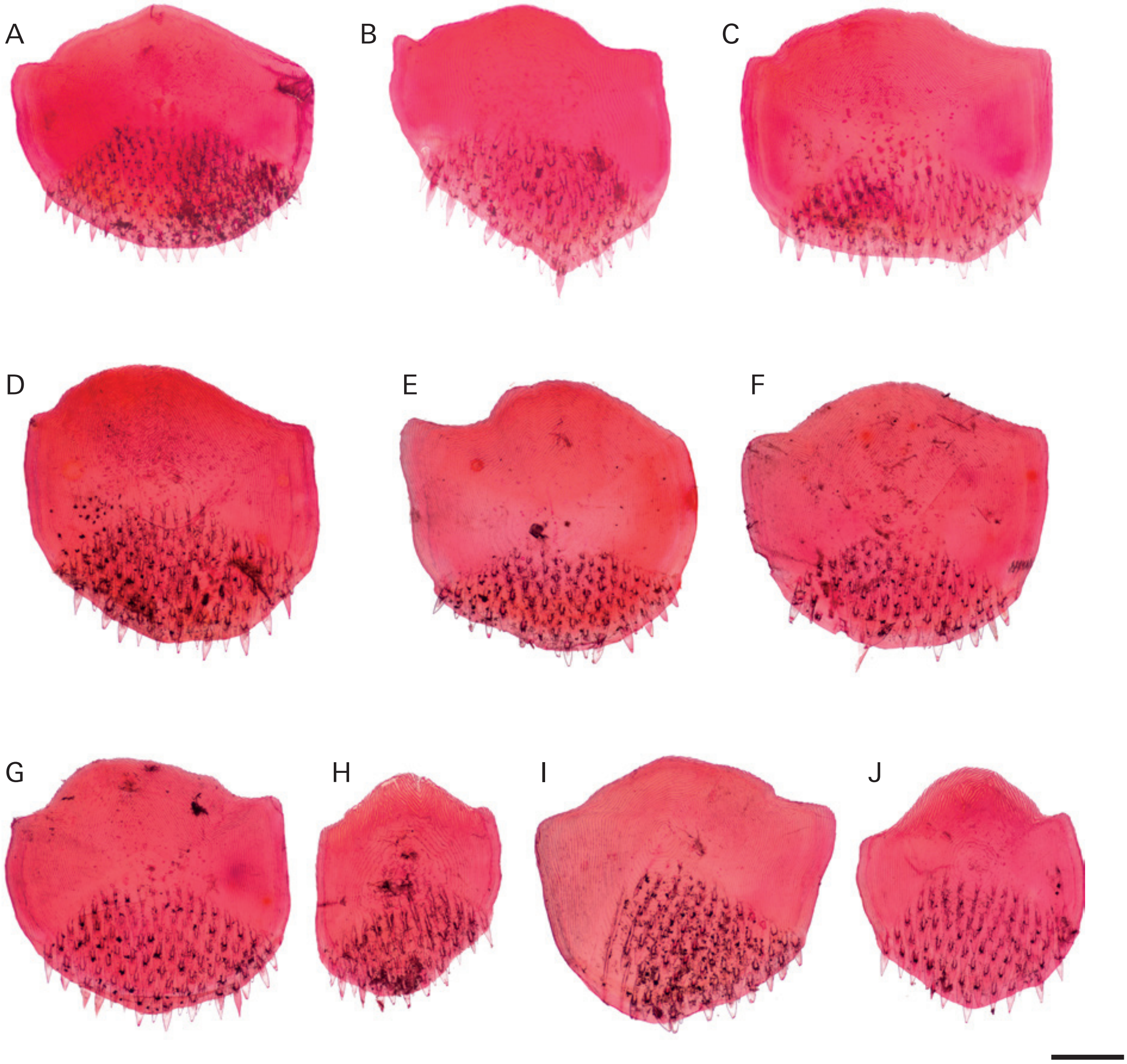

Fig. 21. *Nezumia sclerorhynchus*; 232 mm TL, Costa Brava, Spain, DMM IE/5902. Scale bar = 1 mm.

Fig. 22. *Trachyrincus scabrus*; 300 mm SL, Costa Brava, Spain, DMM IE/5103. Scale bar = 1 mm.

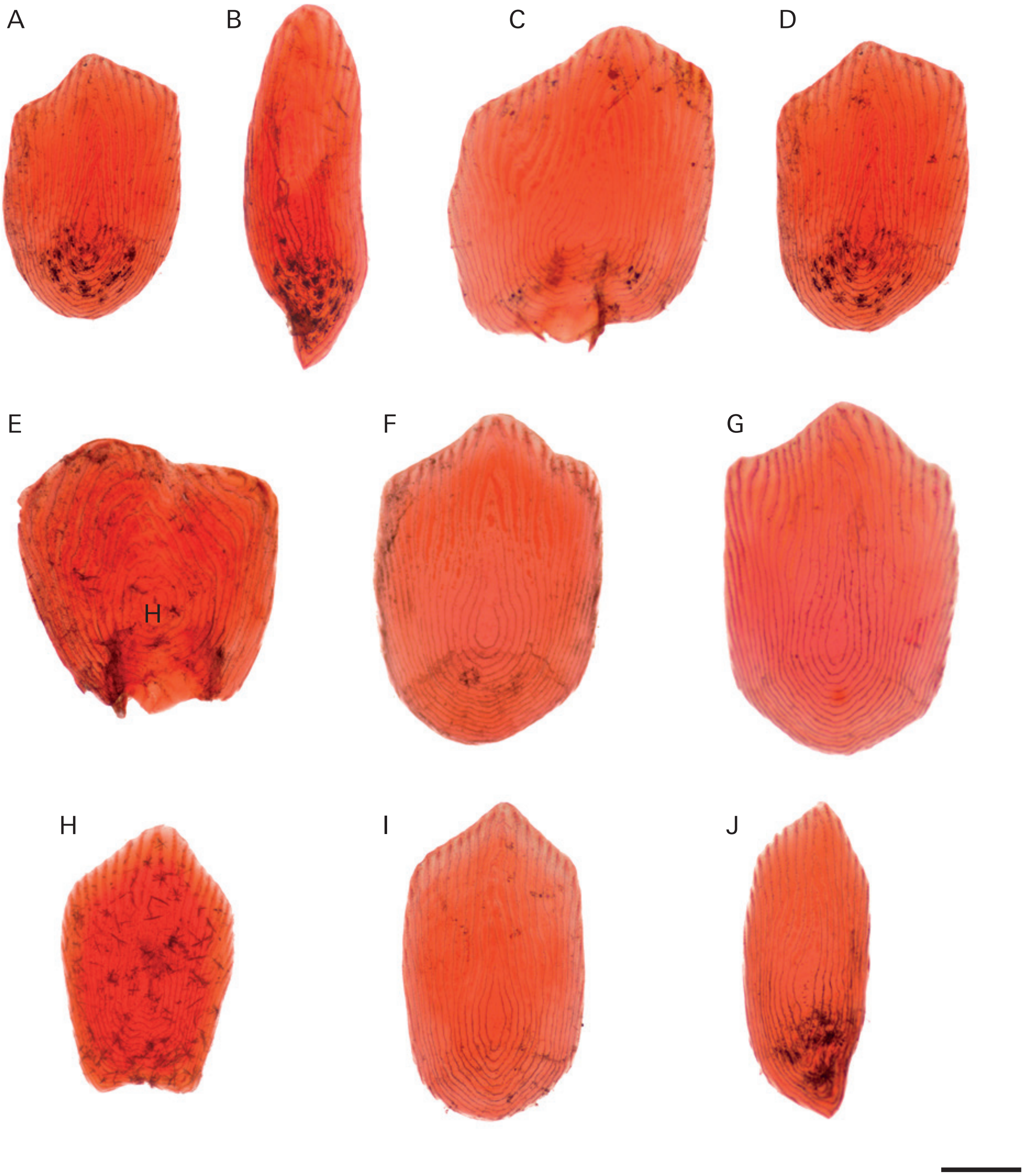

Fig. 23. *Mora moro*; 3 specimens, 86–99 mm SL, Costa Brava, Spain, DMM IE/5900. Scale bar = 500 µm.

Fig. 24. *Merluccius merluccius*; 323 mm SL, Mali Lošinj, Croatia, DMM IE/9010. Scale bar = 500 µm.

Fig. 25. *Molva molva*; 340 mm SL, North Atlantic, Norway, DMM IE/5642. Scale bar = 500 µm.

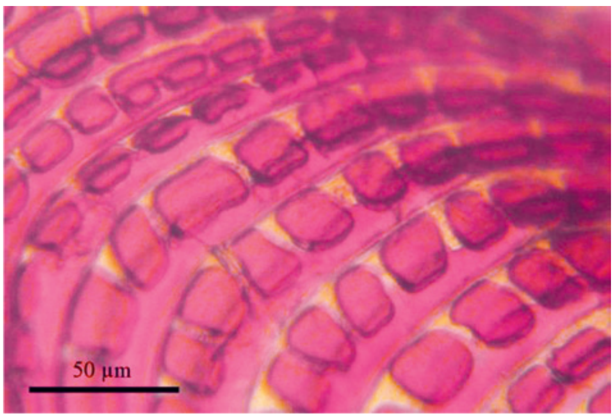

Fig. 26. Surface ornamentations of the scale of *Molva molva* in sampling area C.

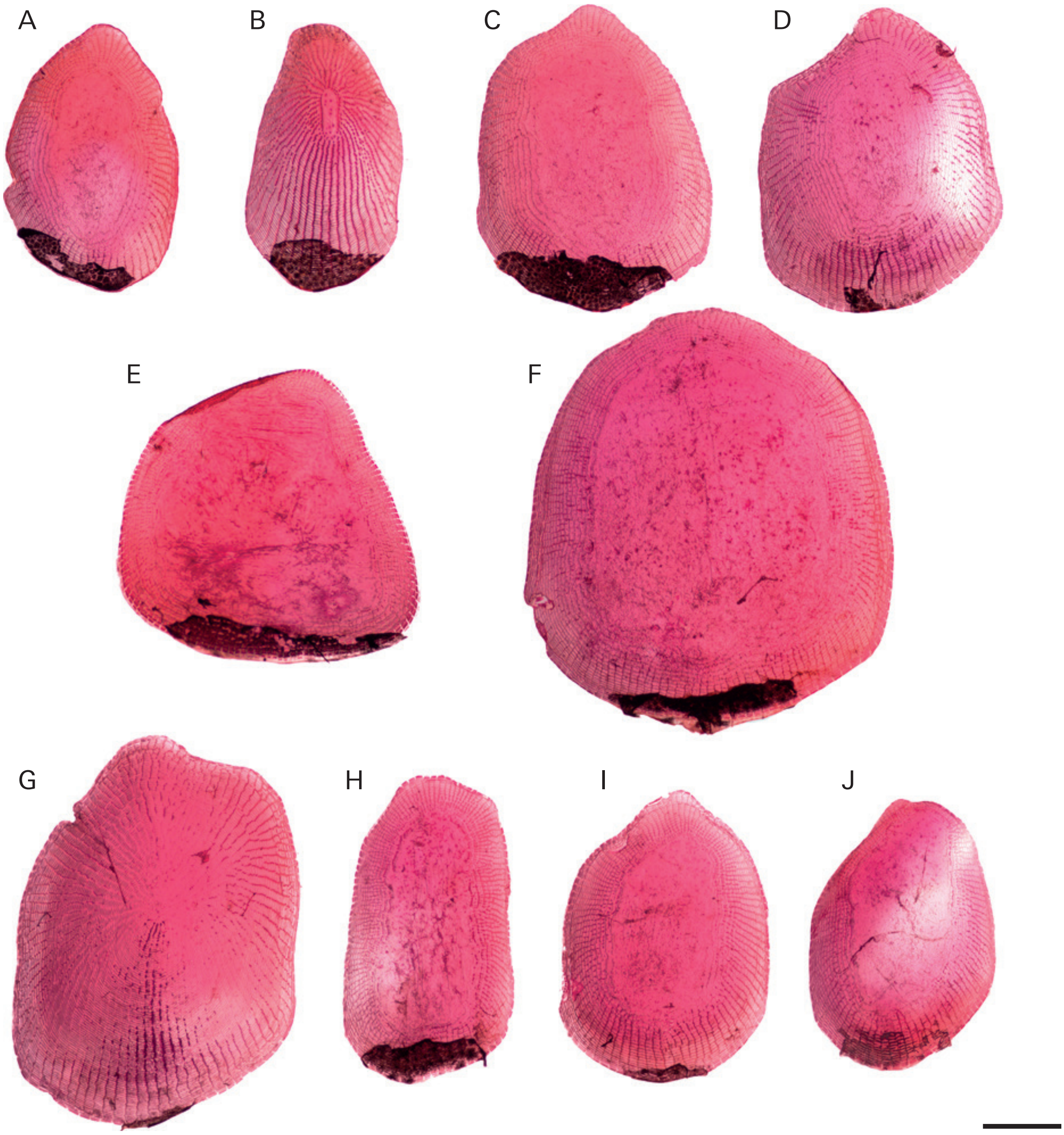

Fig. 27. *Trisopterus luscus*; 278 mm SL, North Atlantic, United Kingdom, DMM IE/9011. Scale bar = 1 mm.

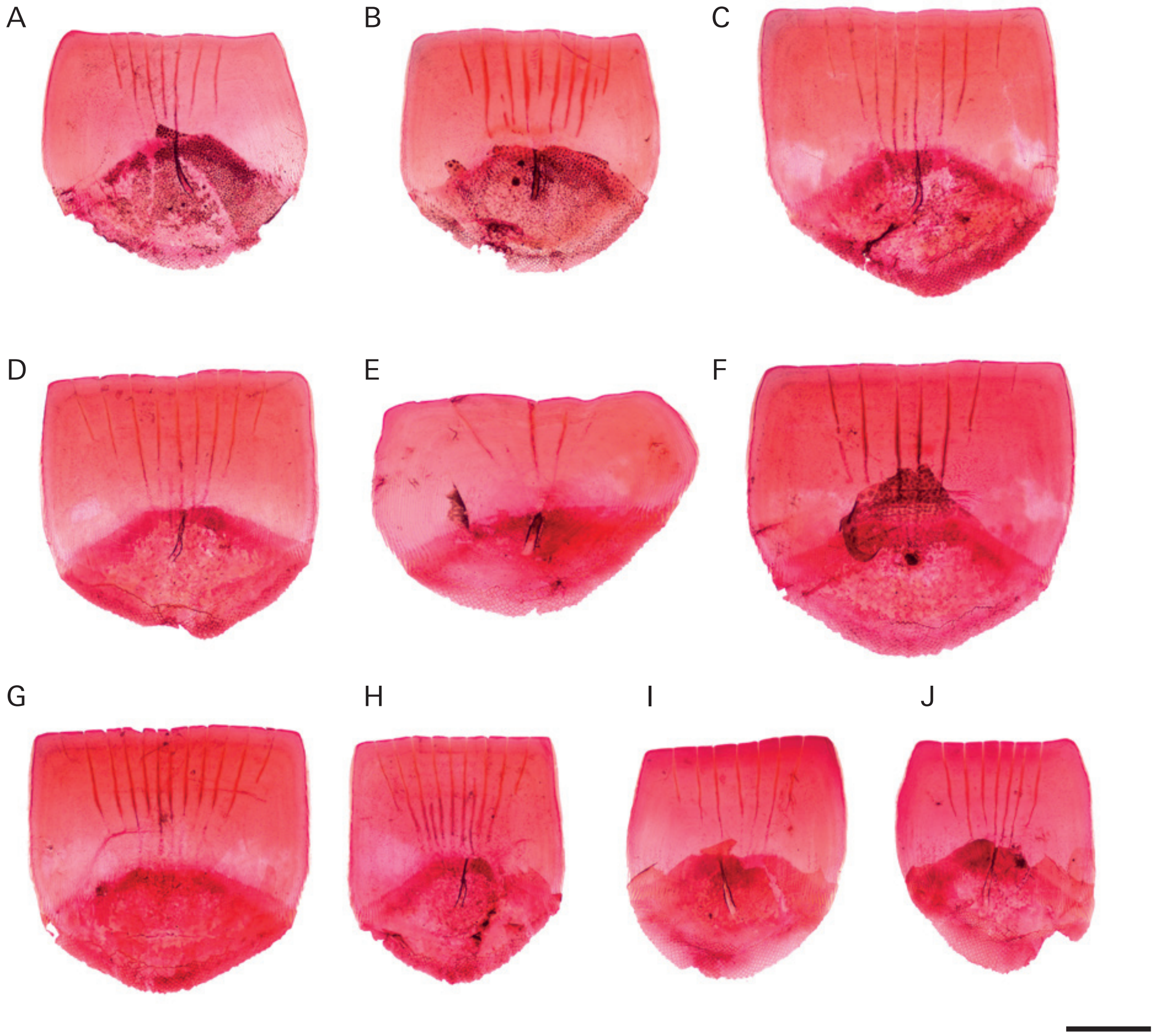

Fig. 28. *Chelon labrosus*; 181 mm SL, Elba, Italy, DMM IE/6188. Scale bar = 2 mm.

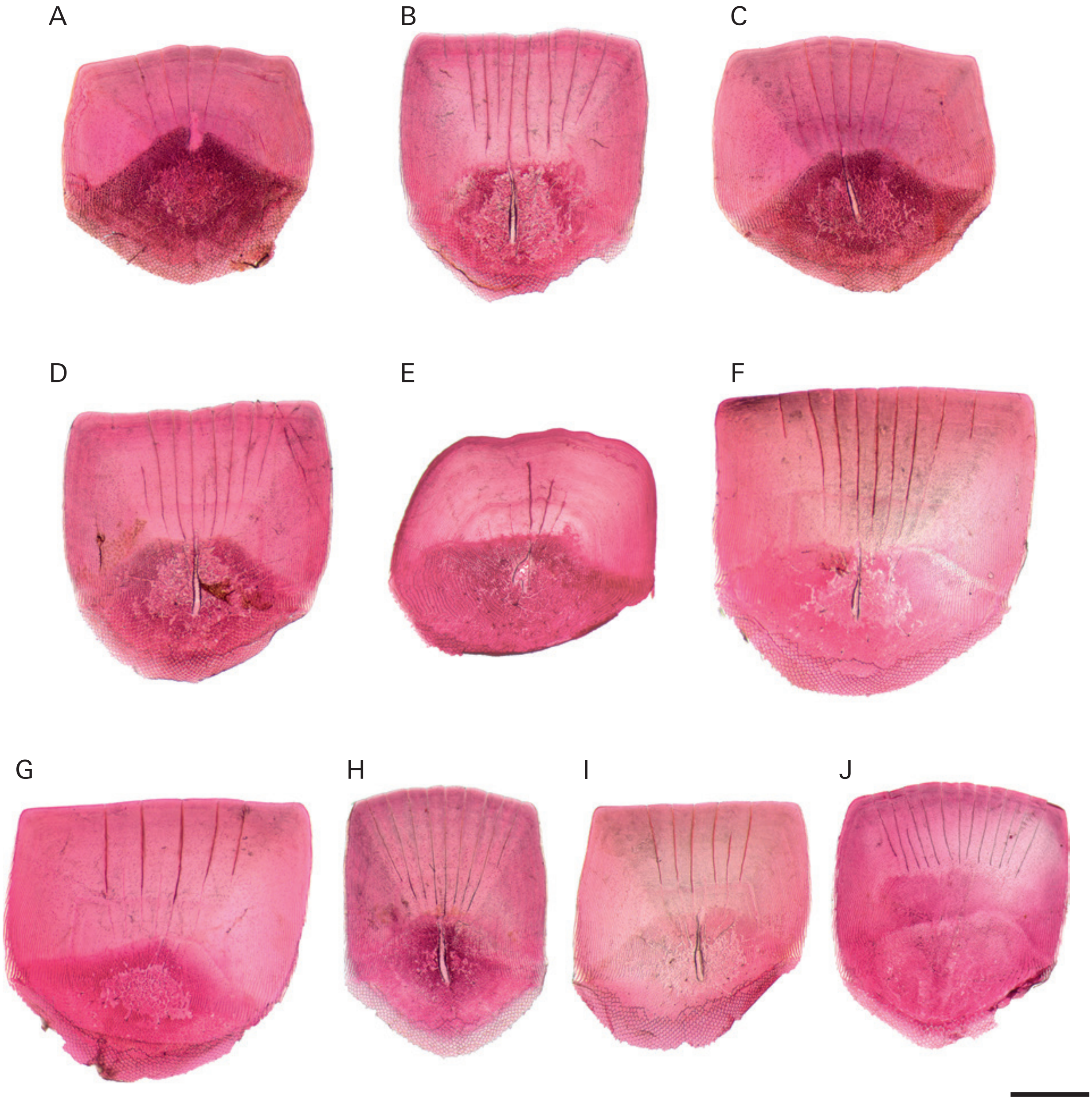

Fig. 29. *Liza aurata*; 207 mm SL, Gulf of Ambracia, Greece, DMM IE/9012. Scale bar = 2 mm.

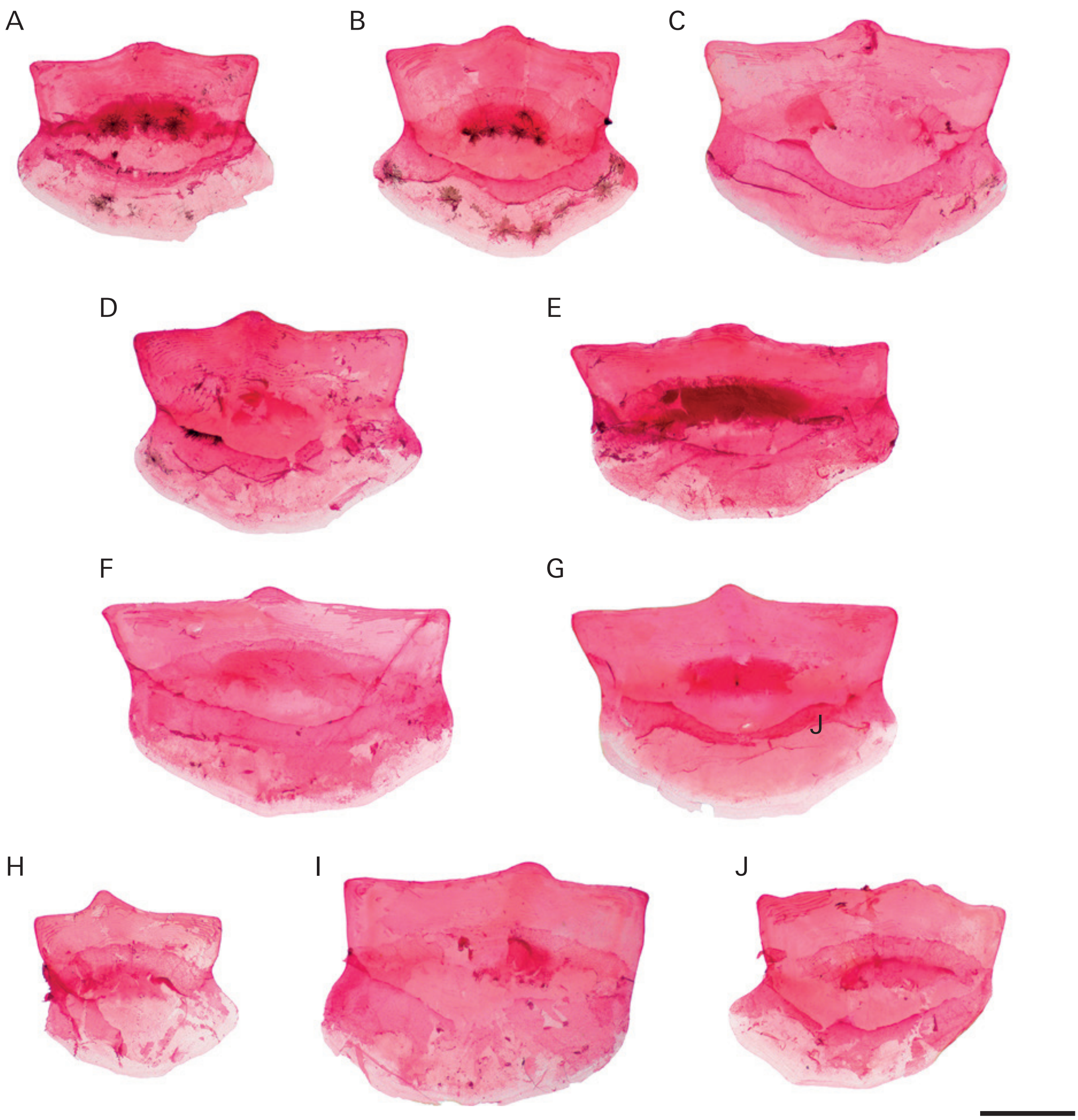

Fig. 30. *Atherina hepsetus*; 101 mm SL, Costa Brava, Spain, DMM IE/5080. Scale bar = 1 mm.

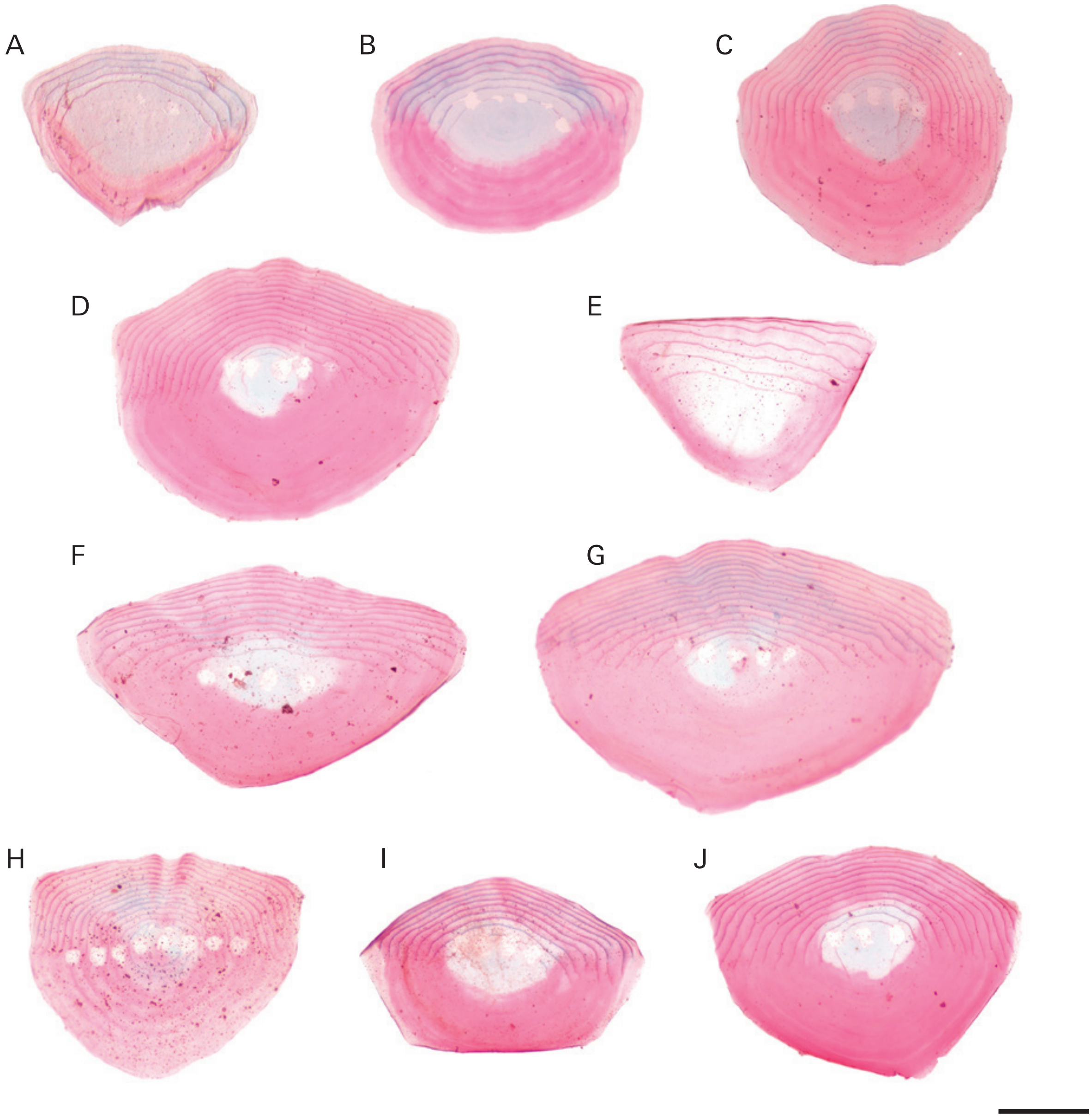

Fig. 31. *Atherinomorus lacunosus*; 72 mm SL, Turkey, DMM IE/9013. Scale bar = 500 µm.

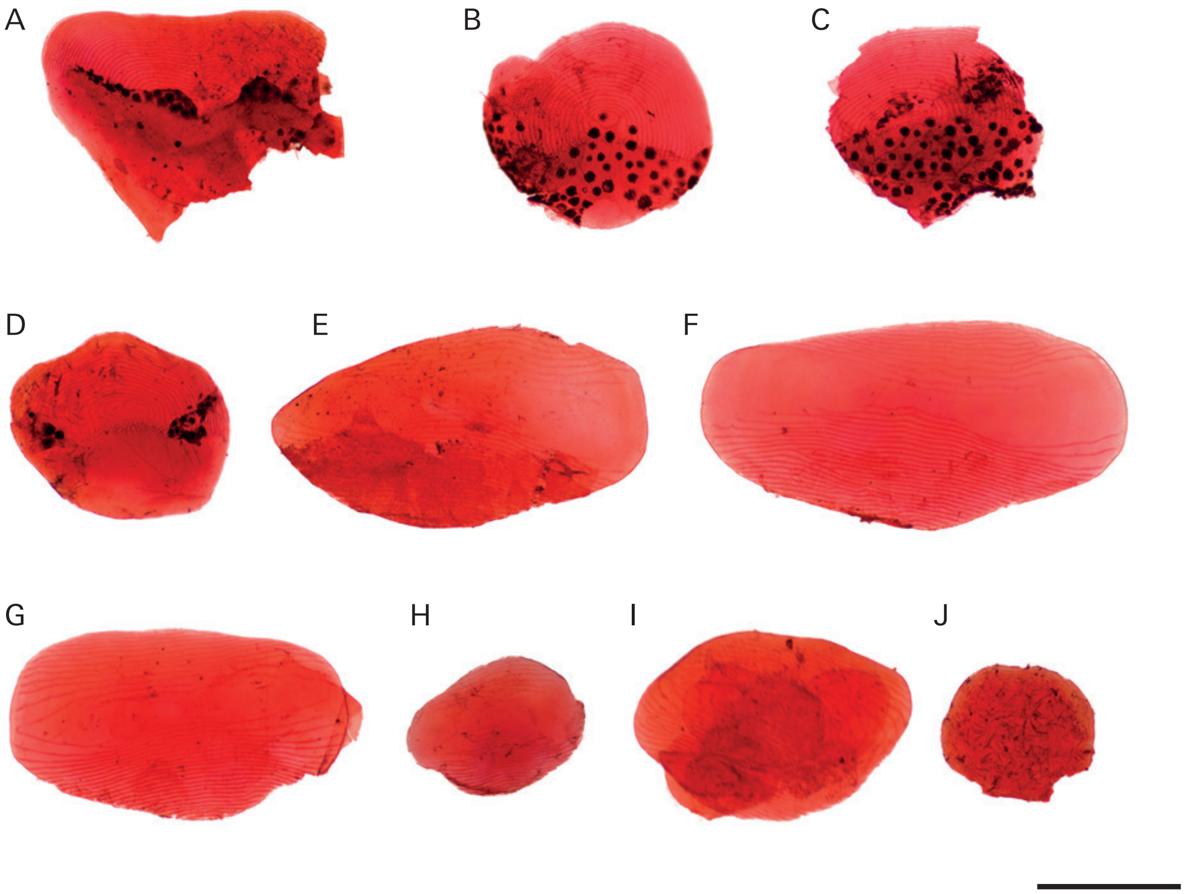

Fig. 32. *Belone belone*; 222 mm SL, Elba, Italy, DMM IE/6175. Scale bar = 1 mm.

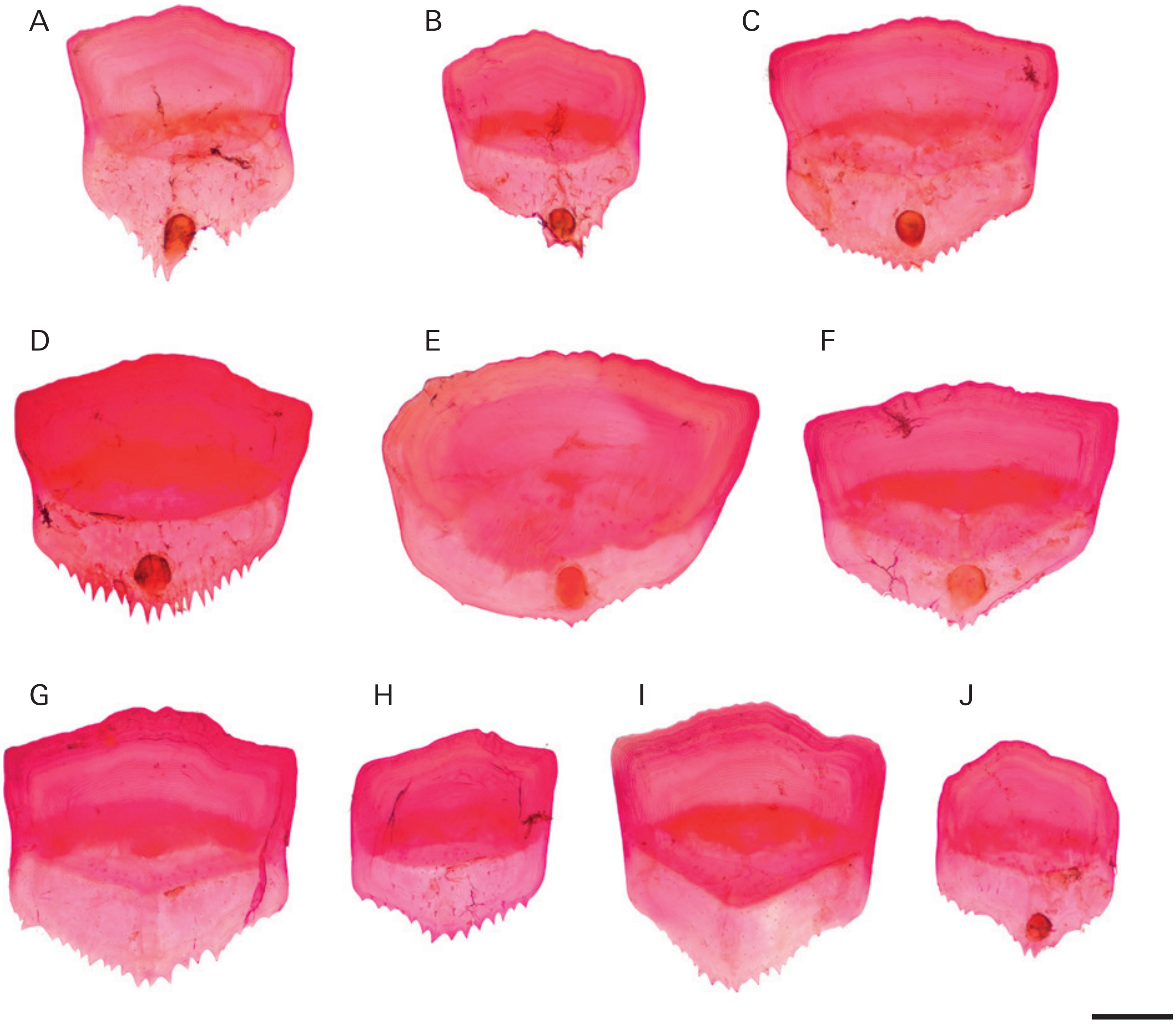

Fig. 33. *Beryx decadactylus*; 313 mm SL, Central Atlantic, Azores, DMM IE/6718. Scale bar = 2 mm.

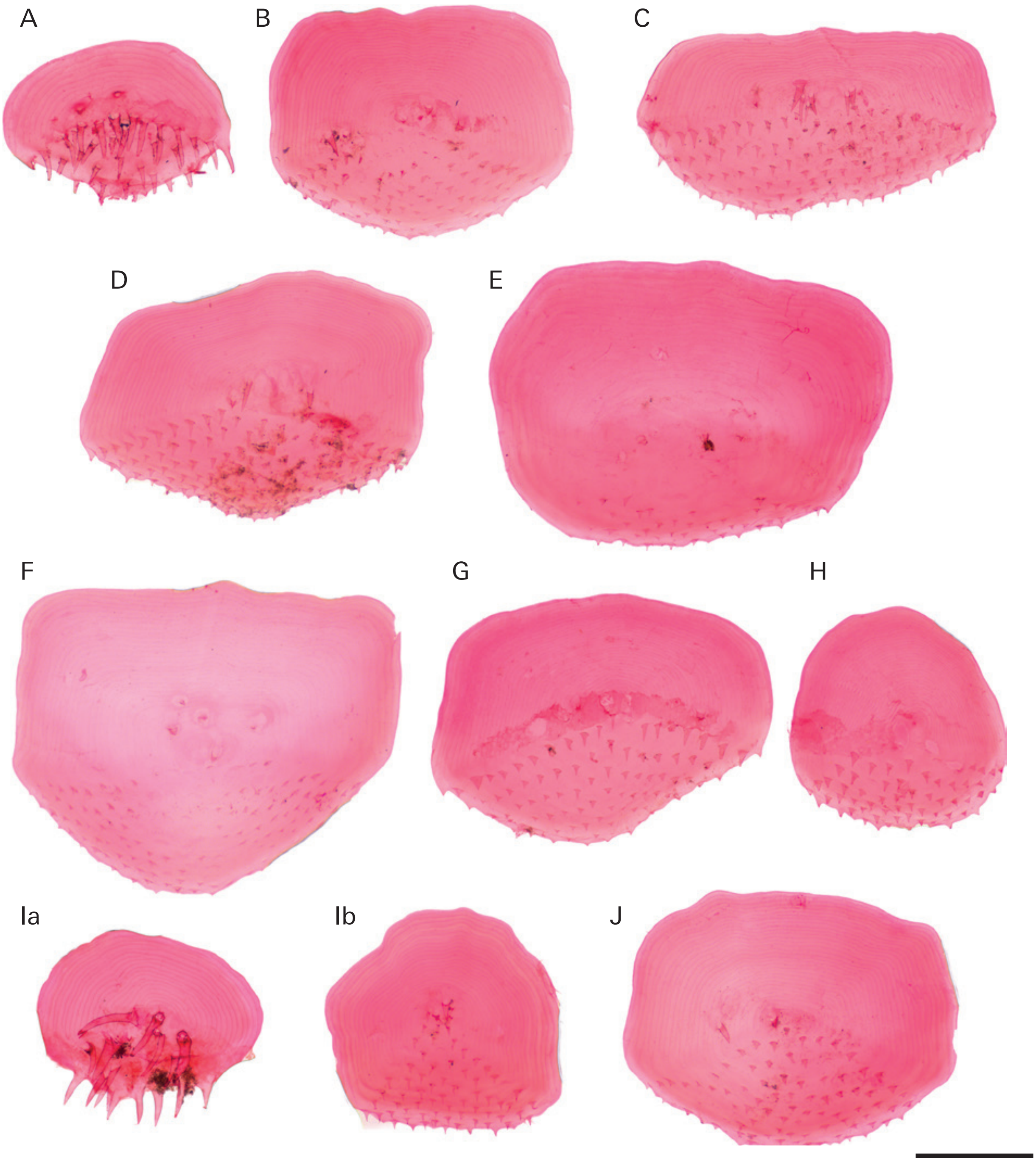

Fig. 34. *Hoplostethus mediterraneus*; 109 mm SL, Costa Brava, Spain, DMM IE/5896. Scale bar = 1 mm.

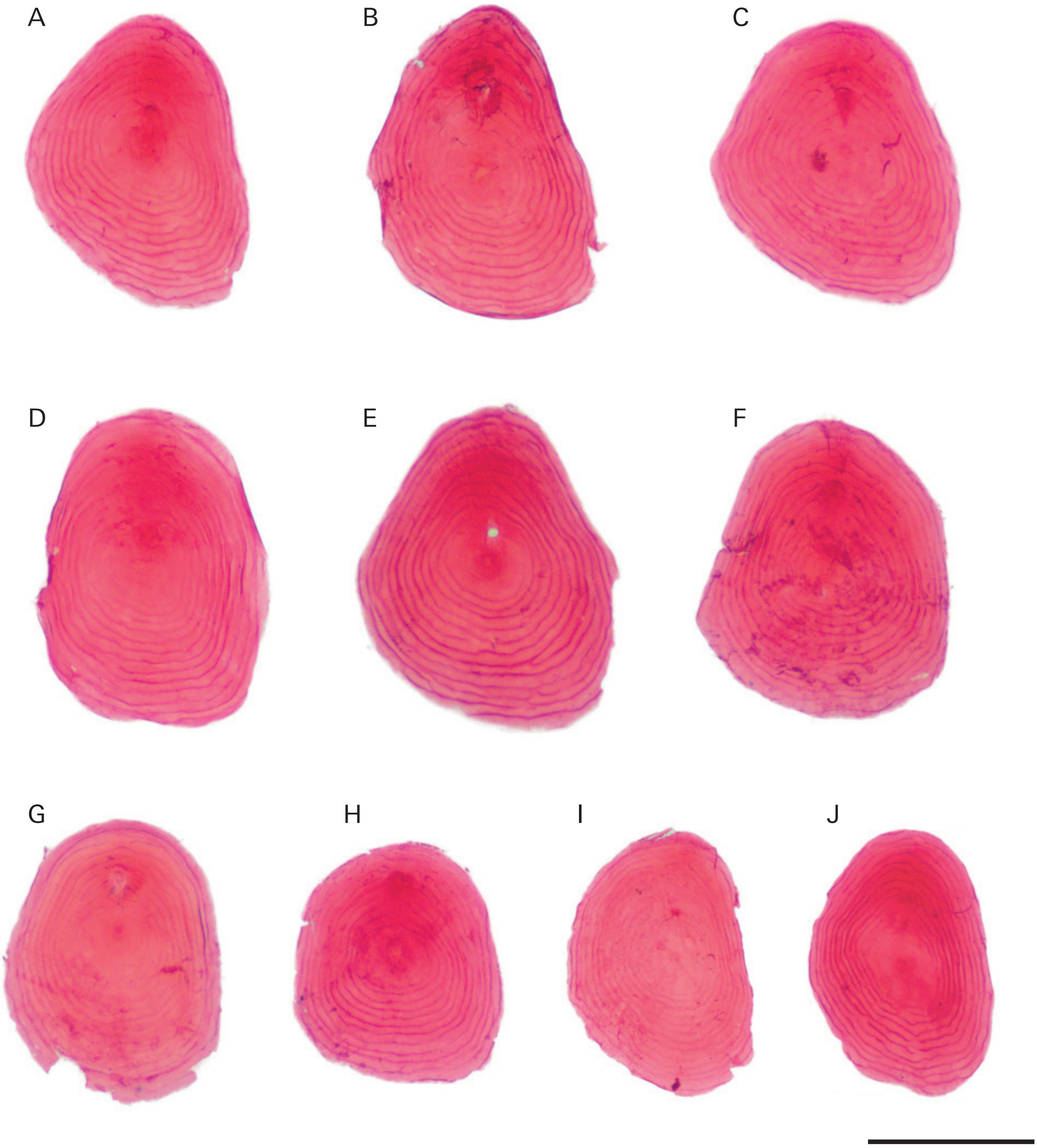

Fig. 35. *Zeus faber*; 82 mm SL, Costa Brava, Spain, DMM IE/5039. Scale bar = 500 µm.

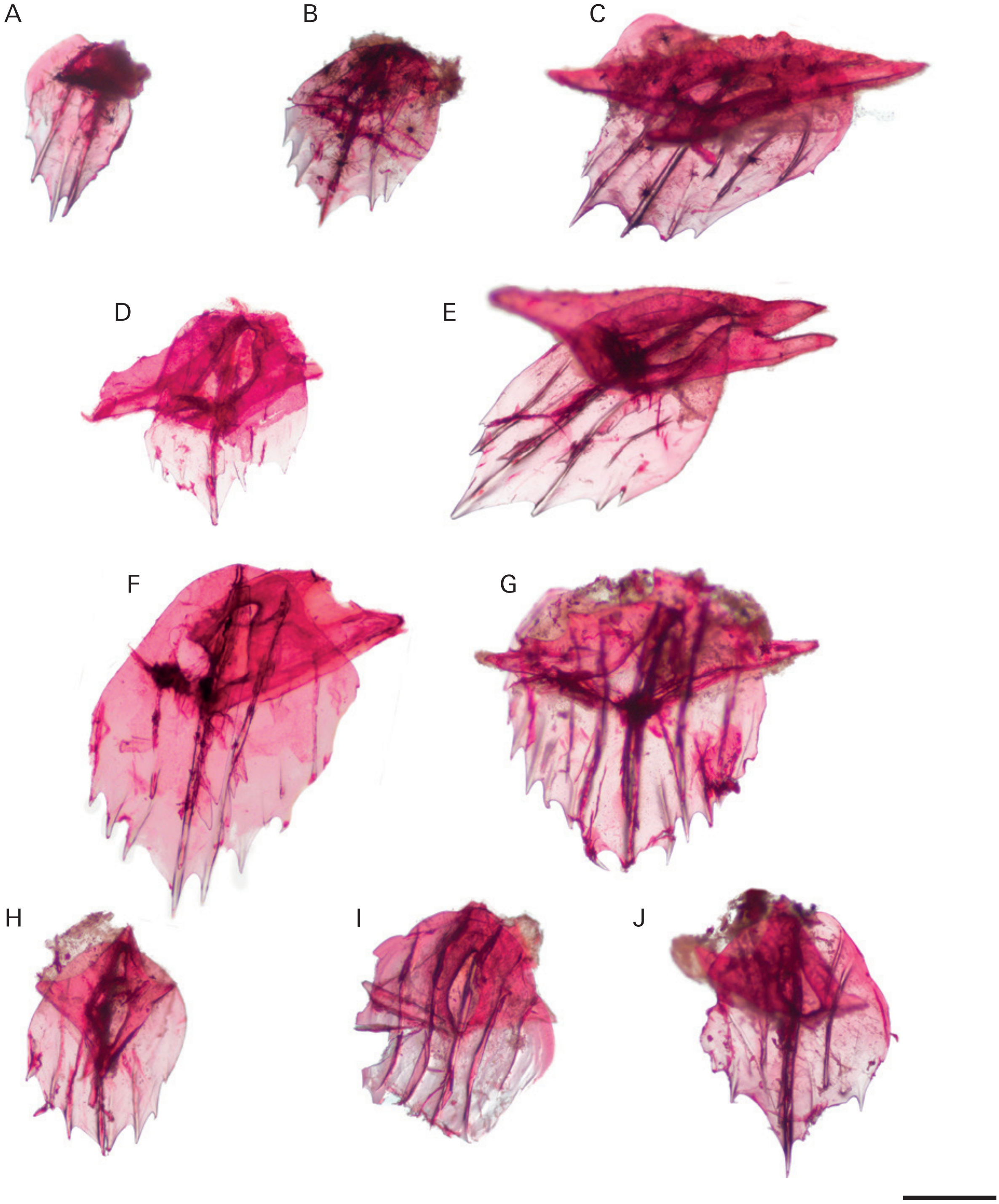

Fig. 36. *Macrorhamphosus scolopax*; 114 mm SL, Central Atlantic, Azores, DMM IE/6520. Scale bar = 500 µm.

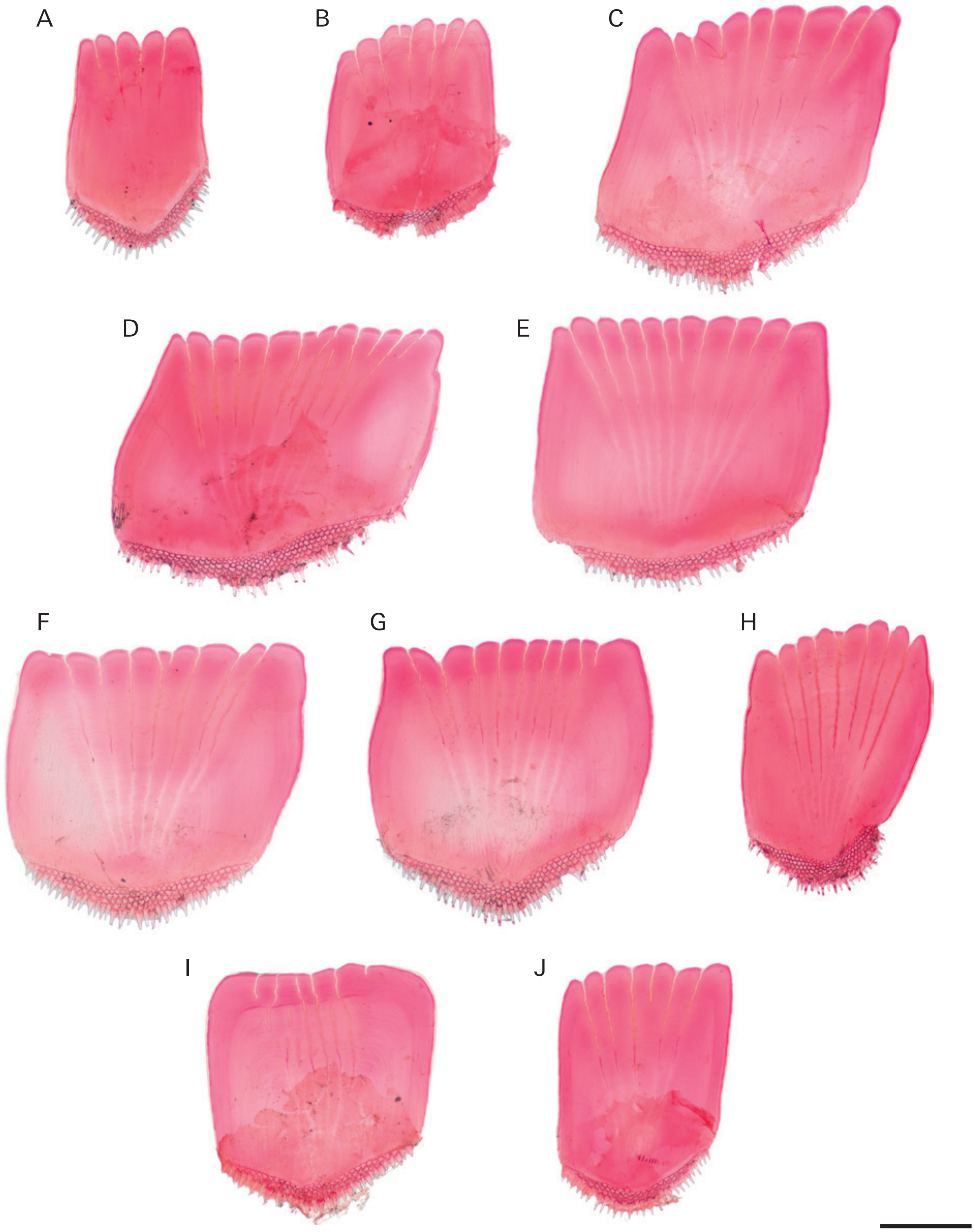

Fig. 37. *Helicolenus dactylopterus*; 131 mm SL, Costa Brava, Spain, DMM IE/5818. Scale bar = 1 mm.

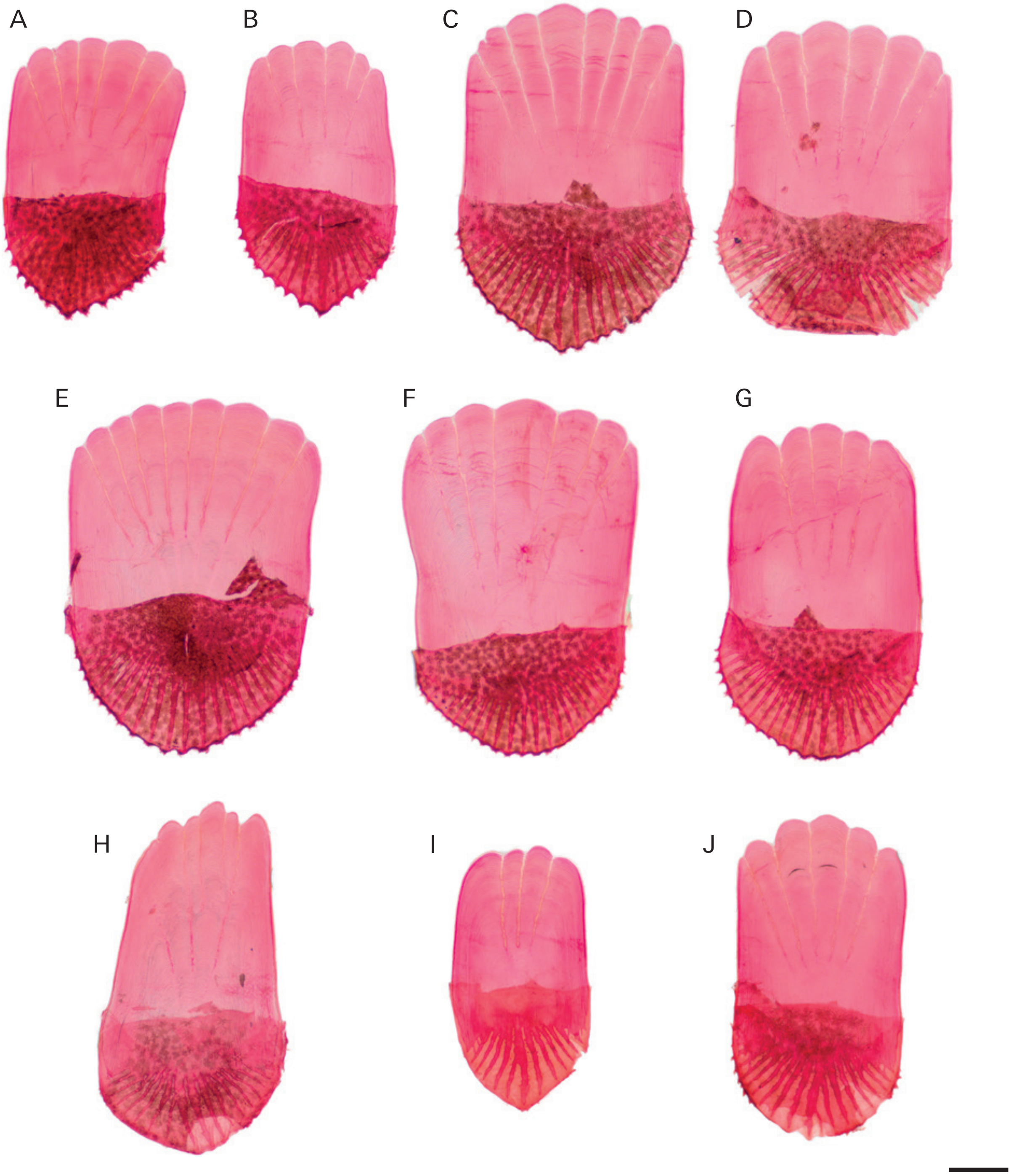

Fig. 38. *Scorpaena porcus*; 114 mm SL, Costa Brava, Spain, DMM IE/4571. Scale bar = 500 µm.

Fig. 39. *Eutrigla gurnardus*; 220 mm SL, Costa Brava, Spain, DMM IE/5089. Scale bar = 500 µm.

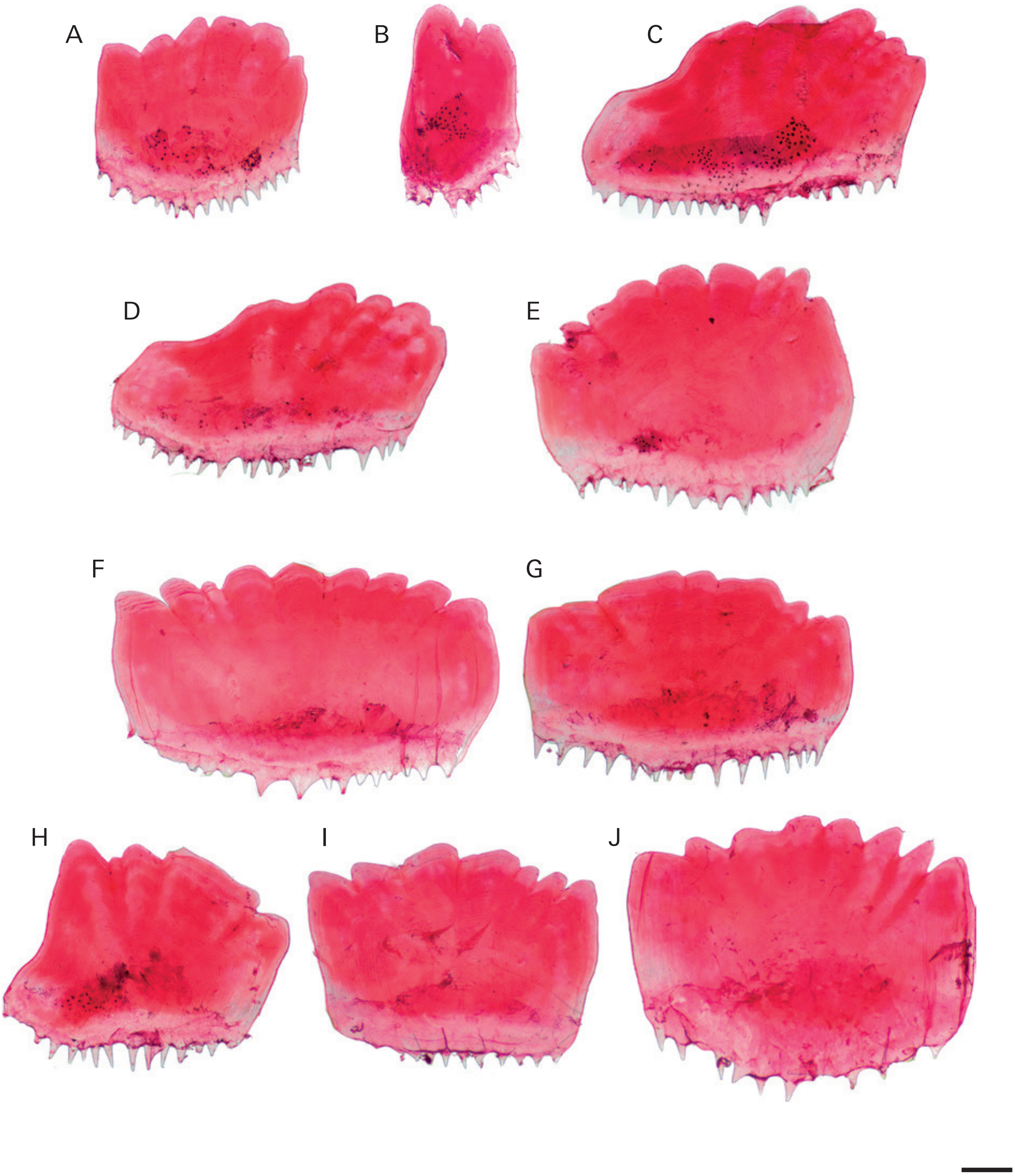

Fig. 40. *Lepidotrigla cavillone*; 87 mm SL, Costa Brava, Spain, DMM IE/4993. Scale bar = 500 µm.

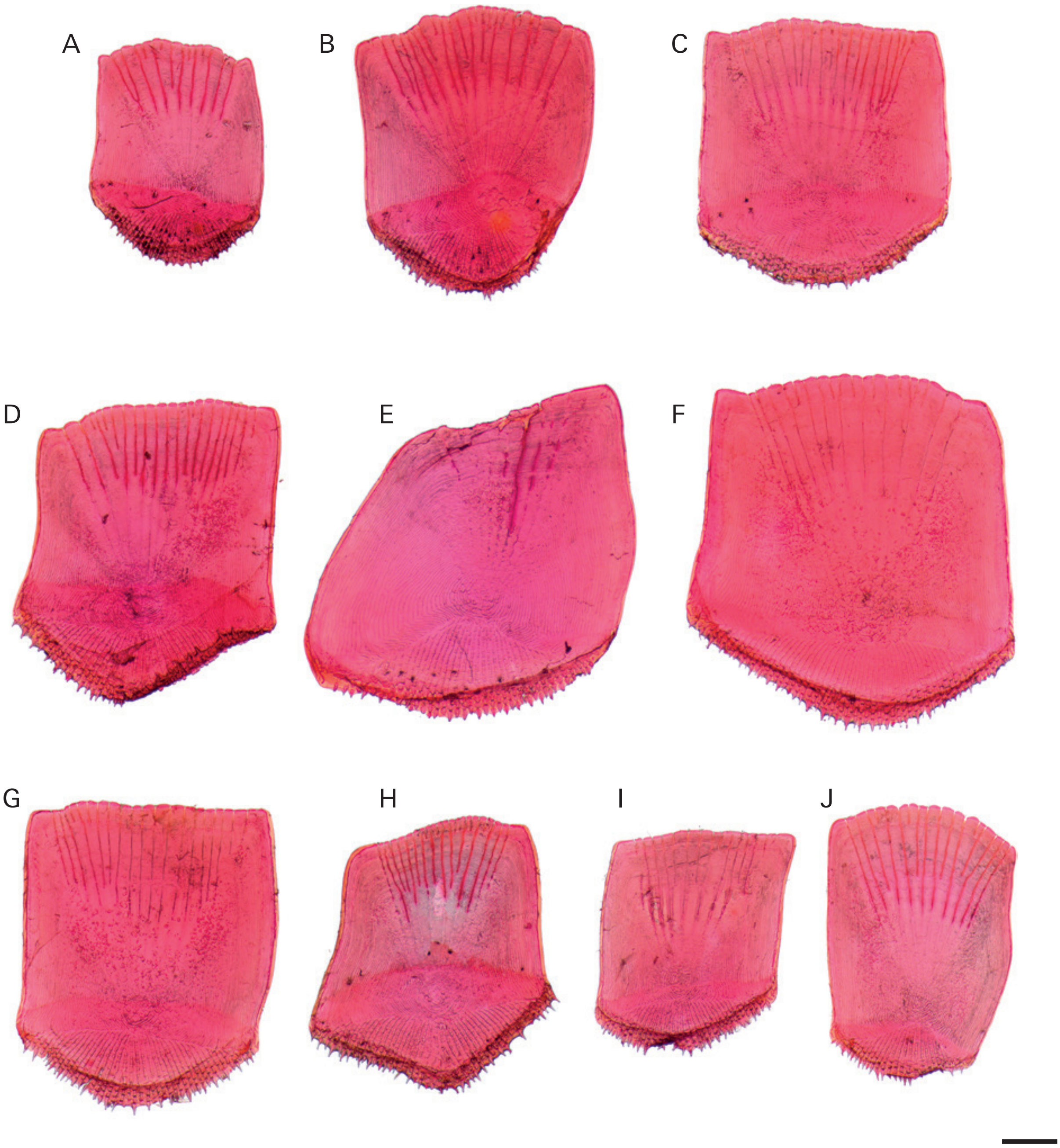

Fig. 41. *Dicentrarchus labrax*; 264 mm SL, Mali Lošinj, Croatia, DMM IE/9014. Scale bar = 1 mm.

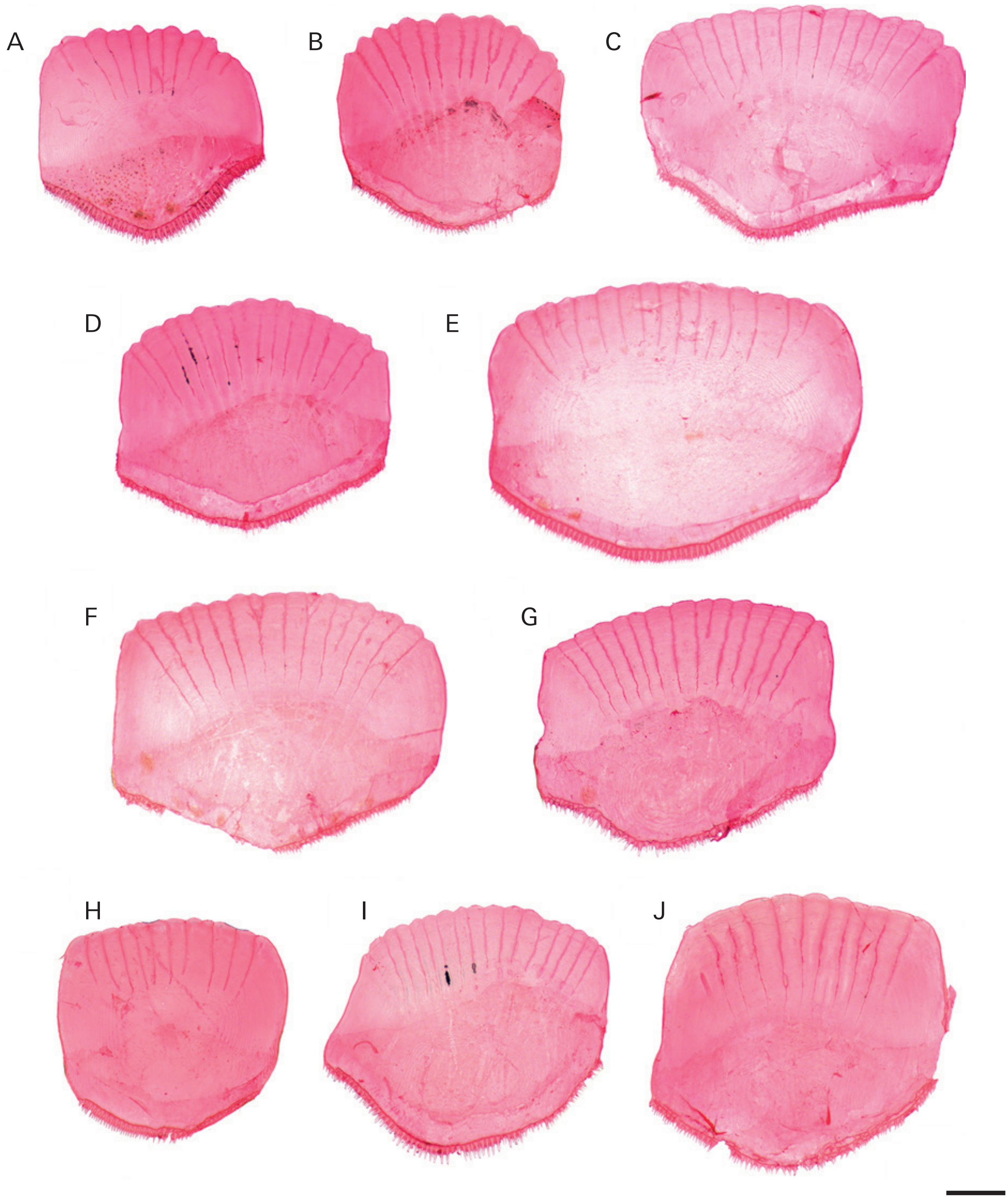

Fig. 42. *Anthias anthias*; 134 mm SL, Costa Brava, Spain, DMM IE/4594. Scale bar = 1 mm.

Fig. 43. *Epinephelus aeneus*; 264 mm SL, Central East Atlantic, Morocco, DMM IE/1233. Scale bar = 1 mm.

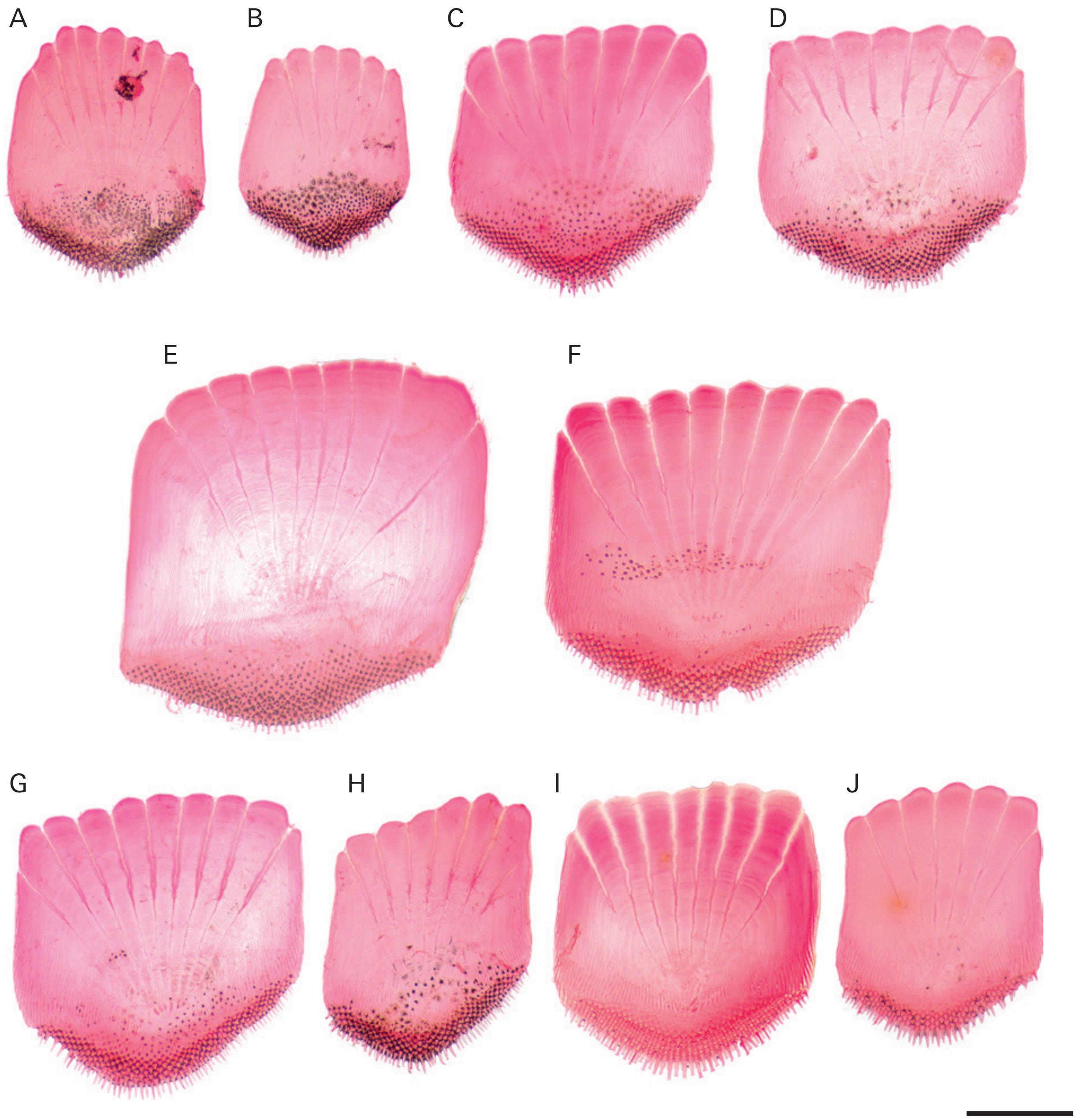

Fig. 44. *Serranus cabrilla*; 137 mm SL, aquarium specimen, Spain, DMM IE/5942. Scale bar = 1 mm.

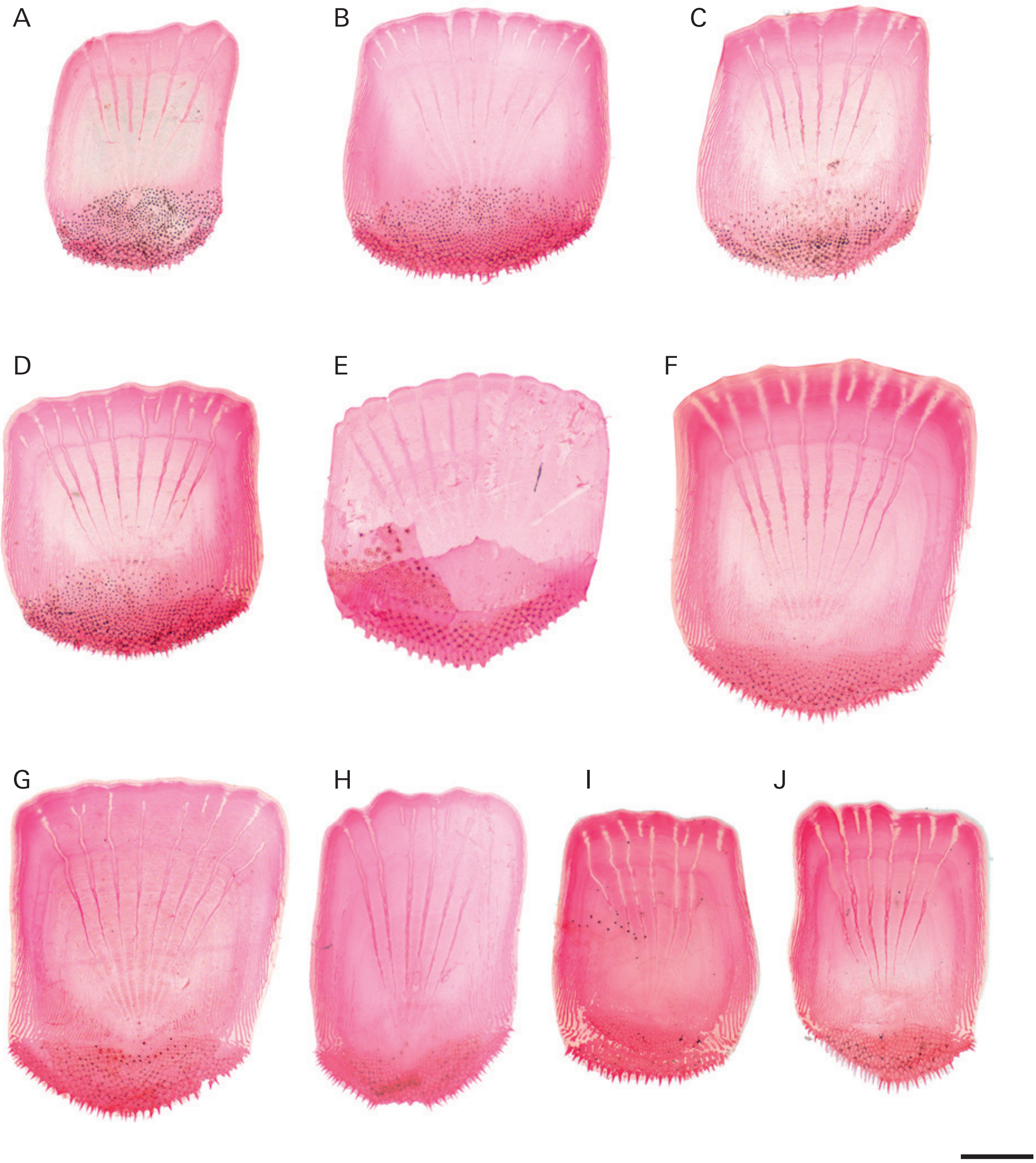

Fig. 45. *Serranus scriba*; 183 mm SL, Costa Brava, Spain, DMM IE/5024. Scale bar = 1 mm.

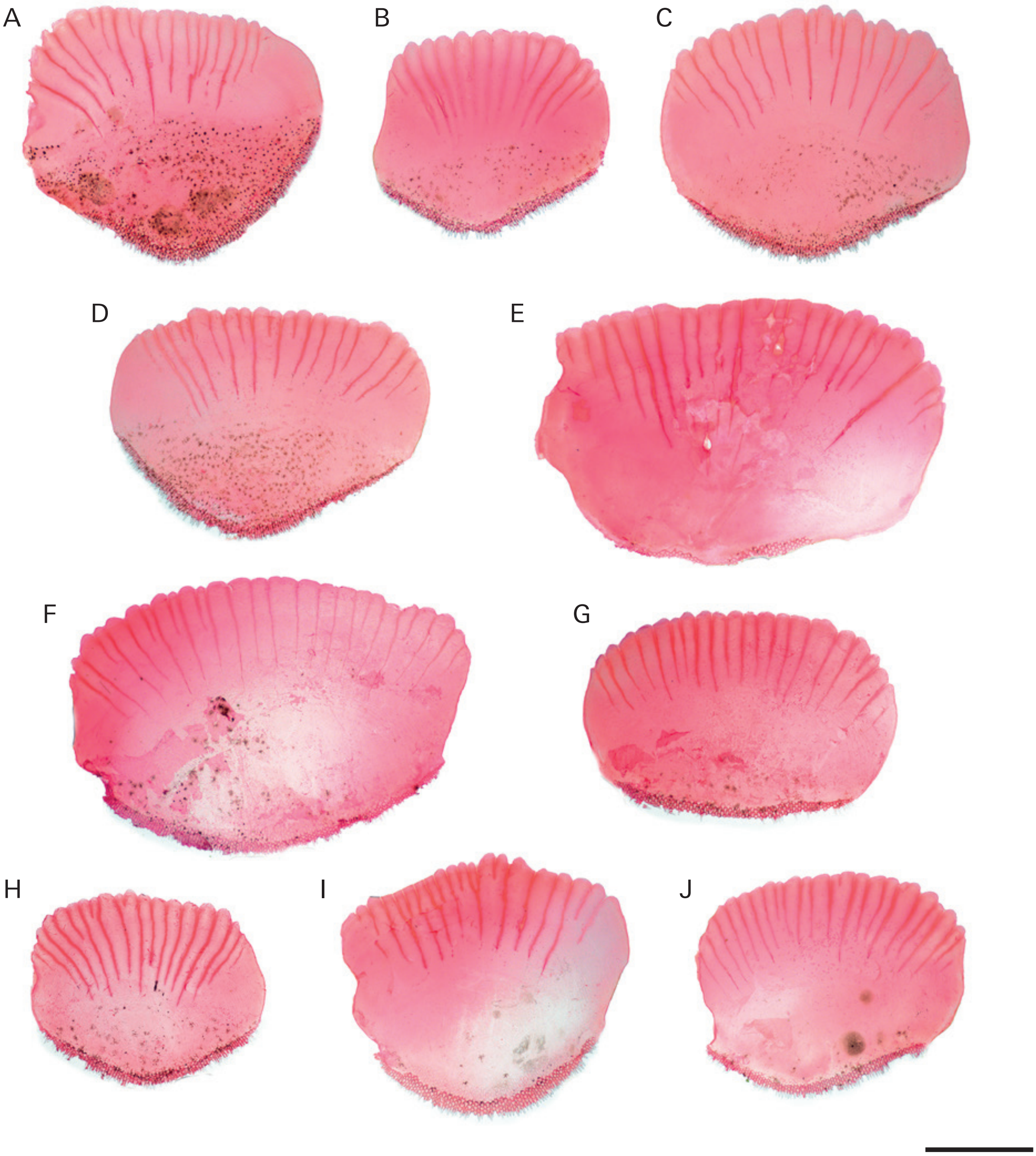

Fig. 46. *Apogon imberbis*; 89 mm SL, aquarium specimen, DMM IE/5593. Scale bar = 2 mm.

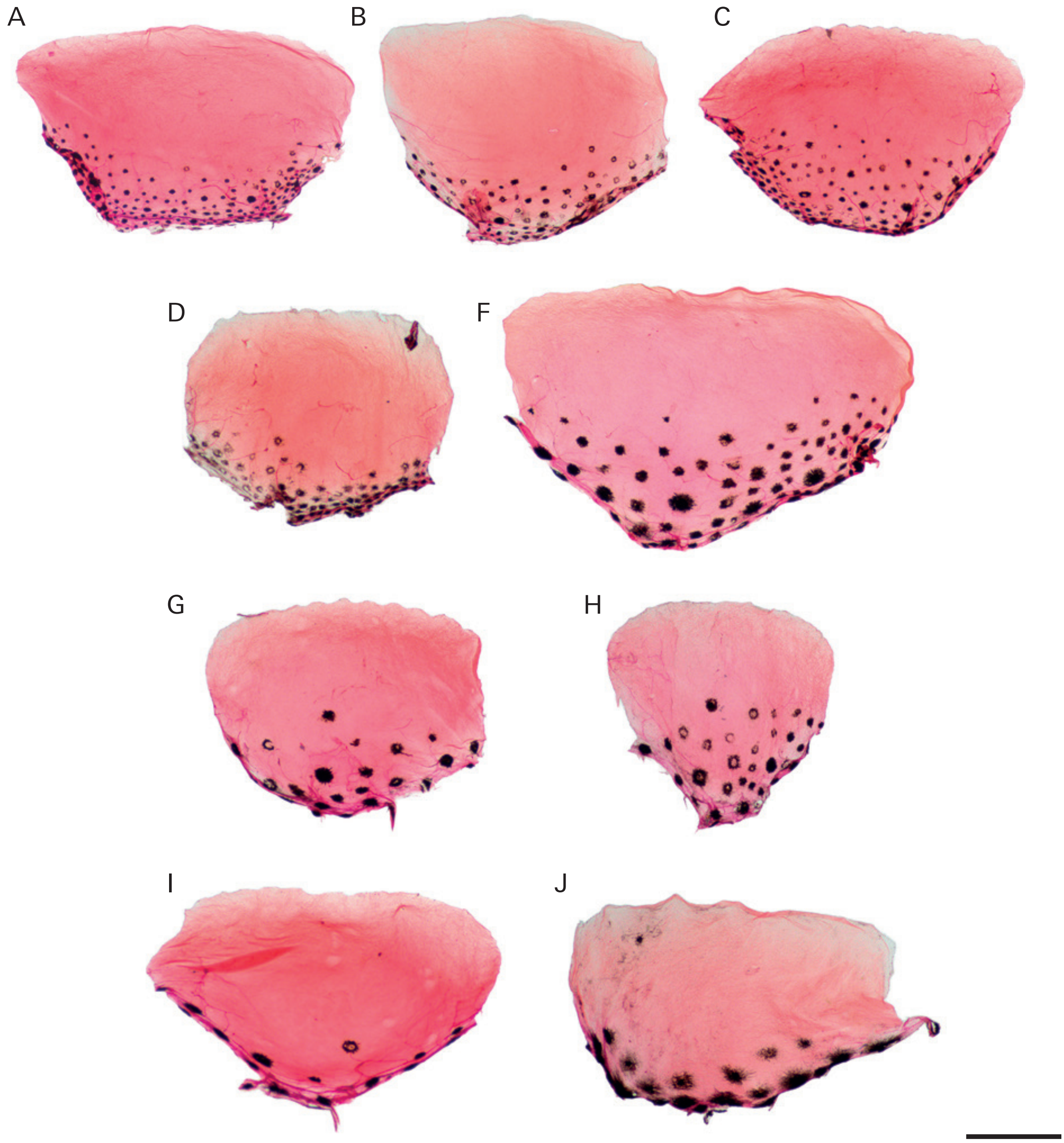

Fig. 47. *Epigonus denticulatus*; 117 mm SL, Costa Brava, Spain, DMM IE/4642. Scale bar = 1 mm.

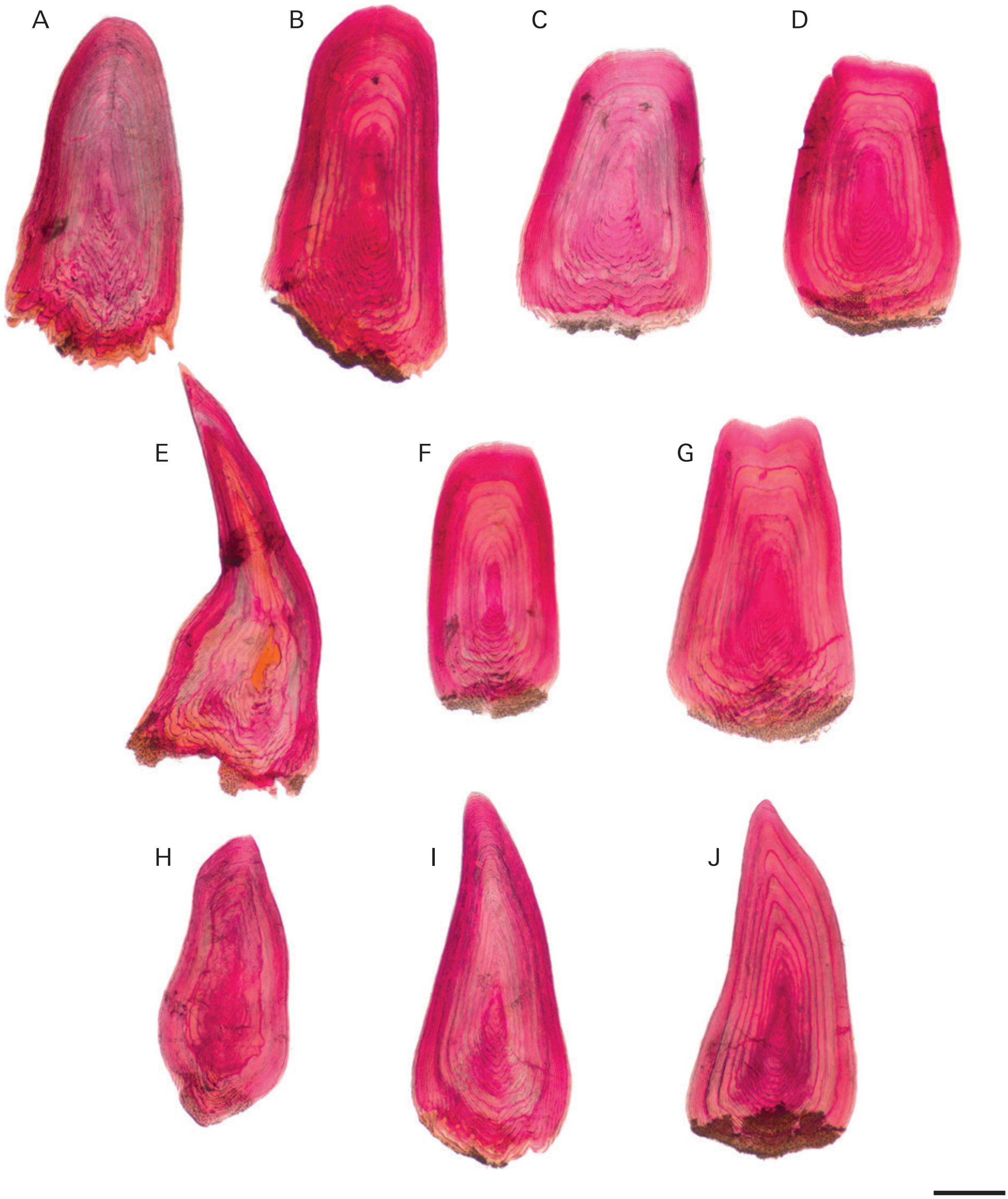

Fig. 48. *Coryphaena equiselis*; 434 mm SL, Algarve, Portugal, DMM IE/5566. Scale bar = 1 mm.

Fig. 49. *Seriola dumerili*; 233 mm SL, Costa Brava, Spain, DMM IE/5000. Scale bar = 500 µm.

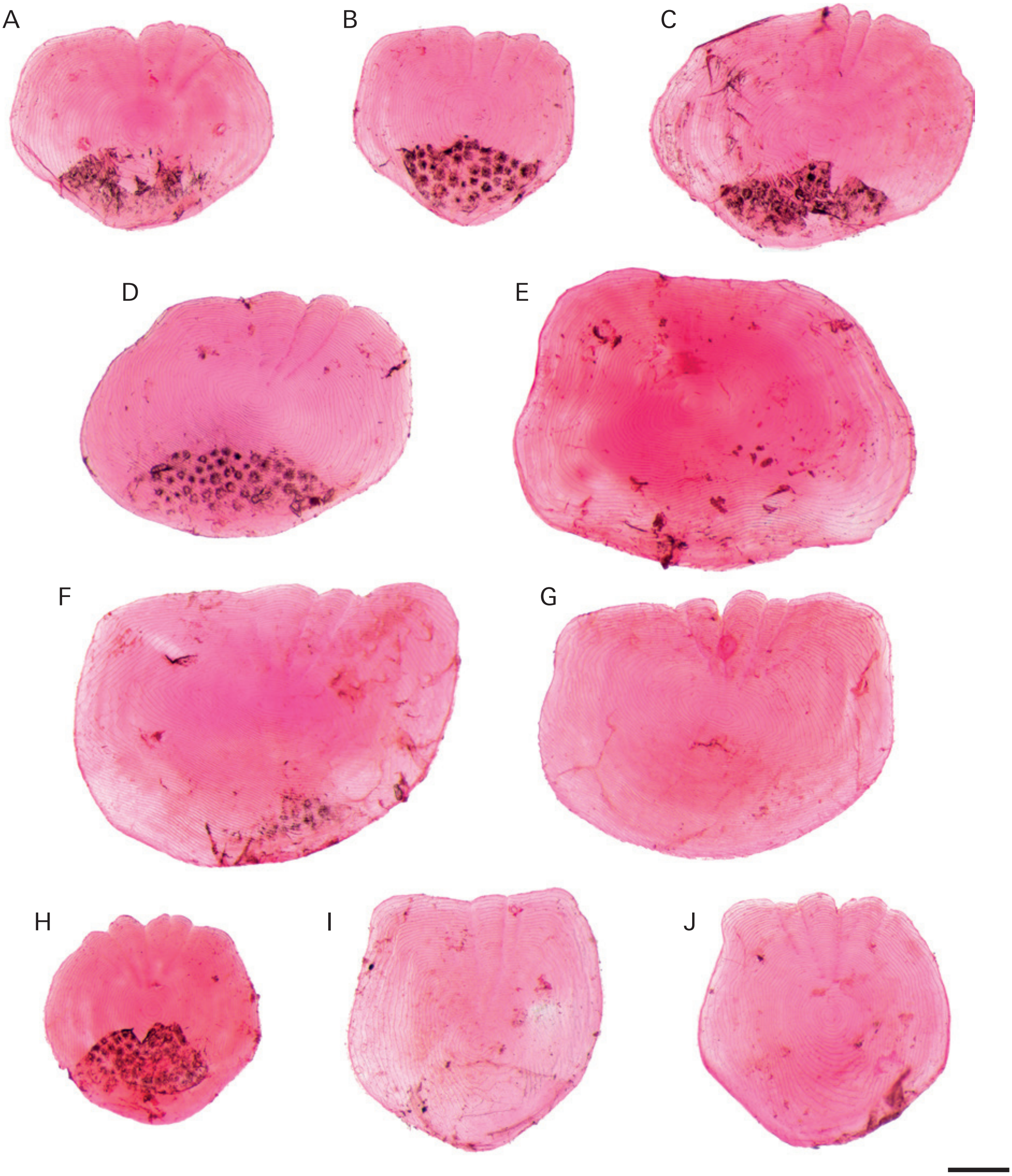

Fig. 50. *Trachurus trachurus*; 199 mm SL, Mali Lošinj, Croatia, DMM IE/9015. Scale bar = 500 µm.

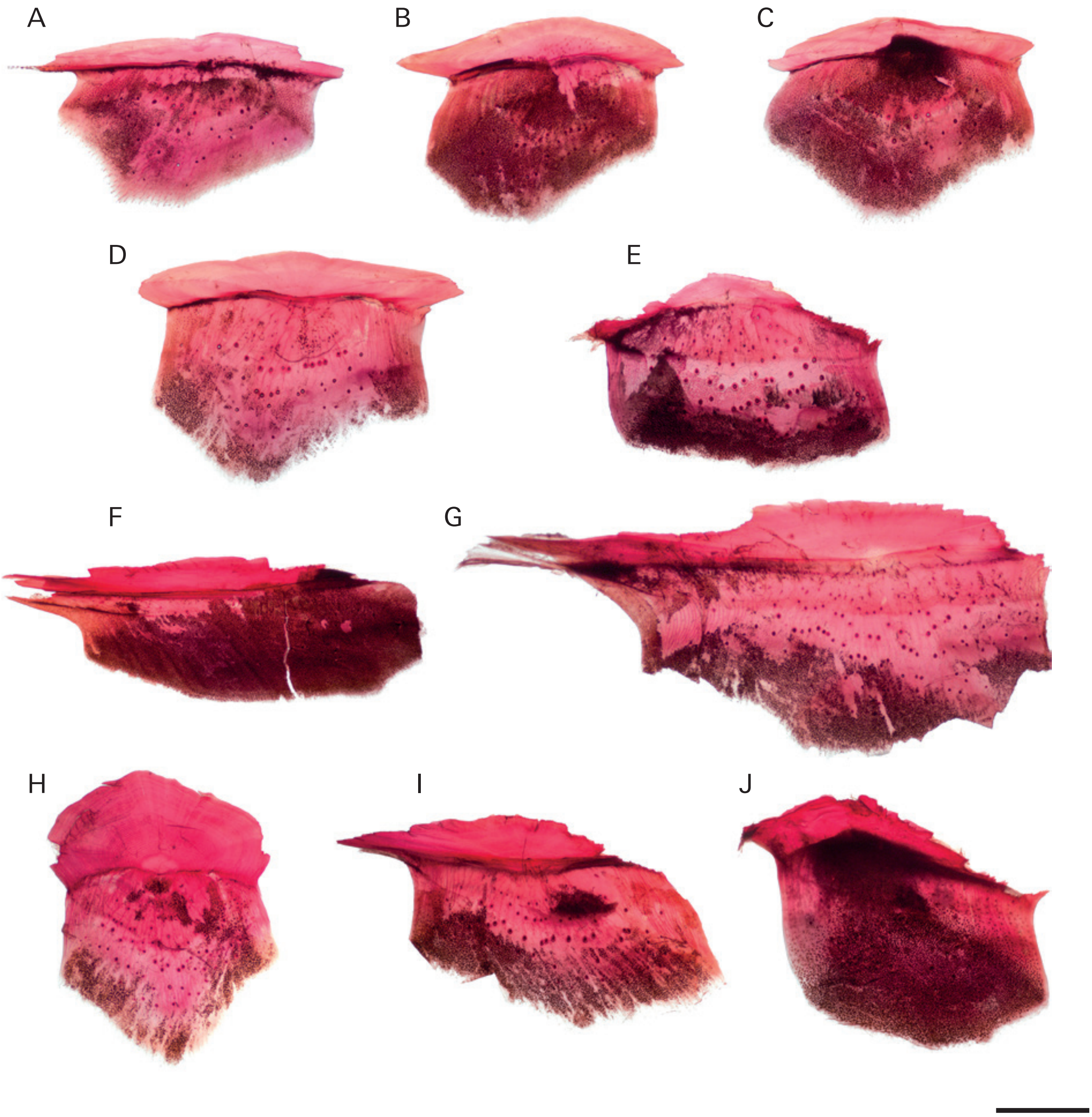

Fig. 51. *Brama brama*; 325 mm SL, Central East Atlantic, Morocco, DMM IE/0451. Scale bar = 2 mm.

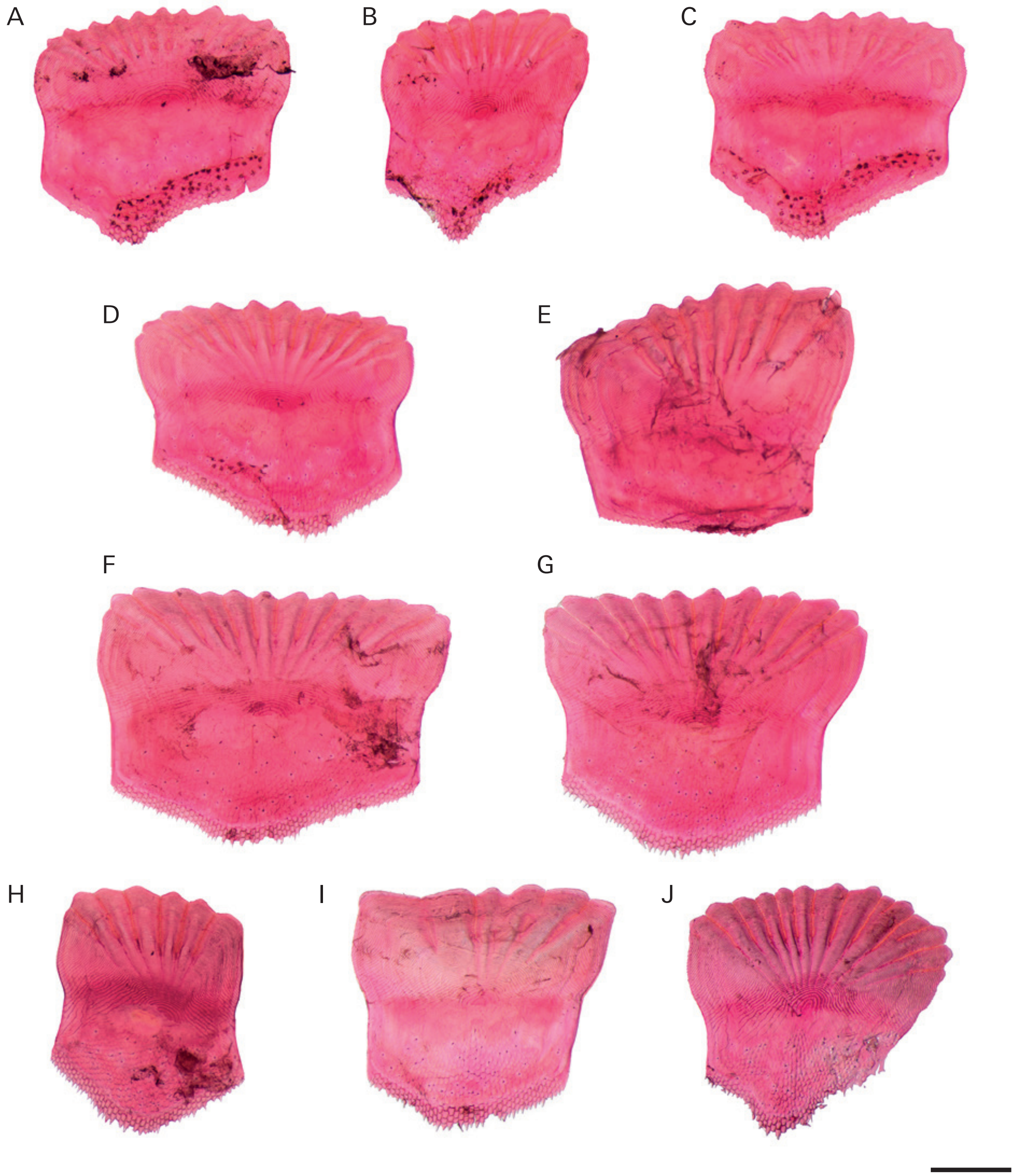

Fig. 52. *Boops boops*; 128 mm SL, Gulf of Ambracia, Greece, DMM IE/9016. Scale bar = 1 mm.

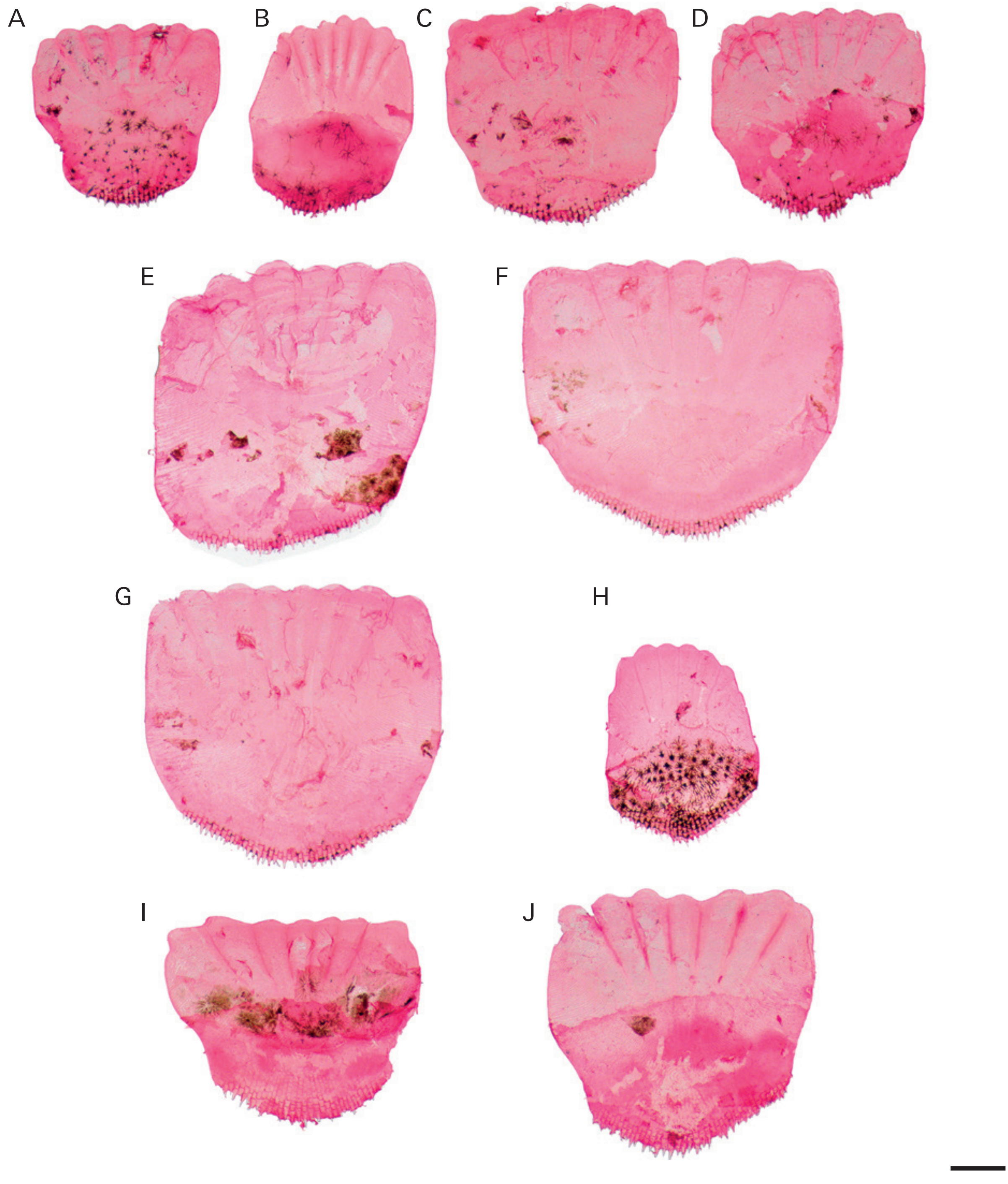

Fig. 53. *Diplodus annularis*; 73 mm SL, Costa Brava, Spain, DMM IE/5033. Scale bar = 500 µm.

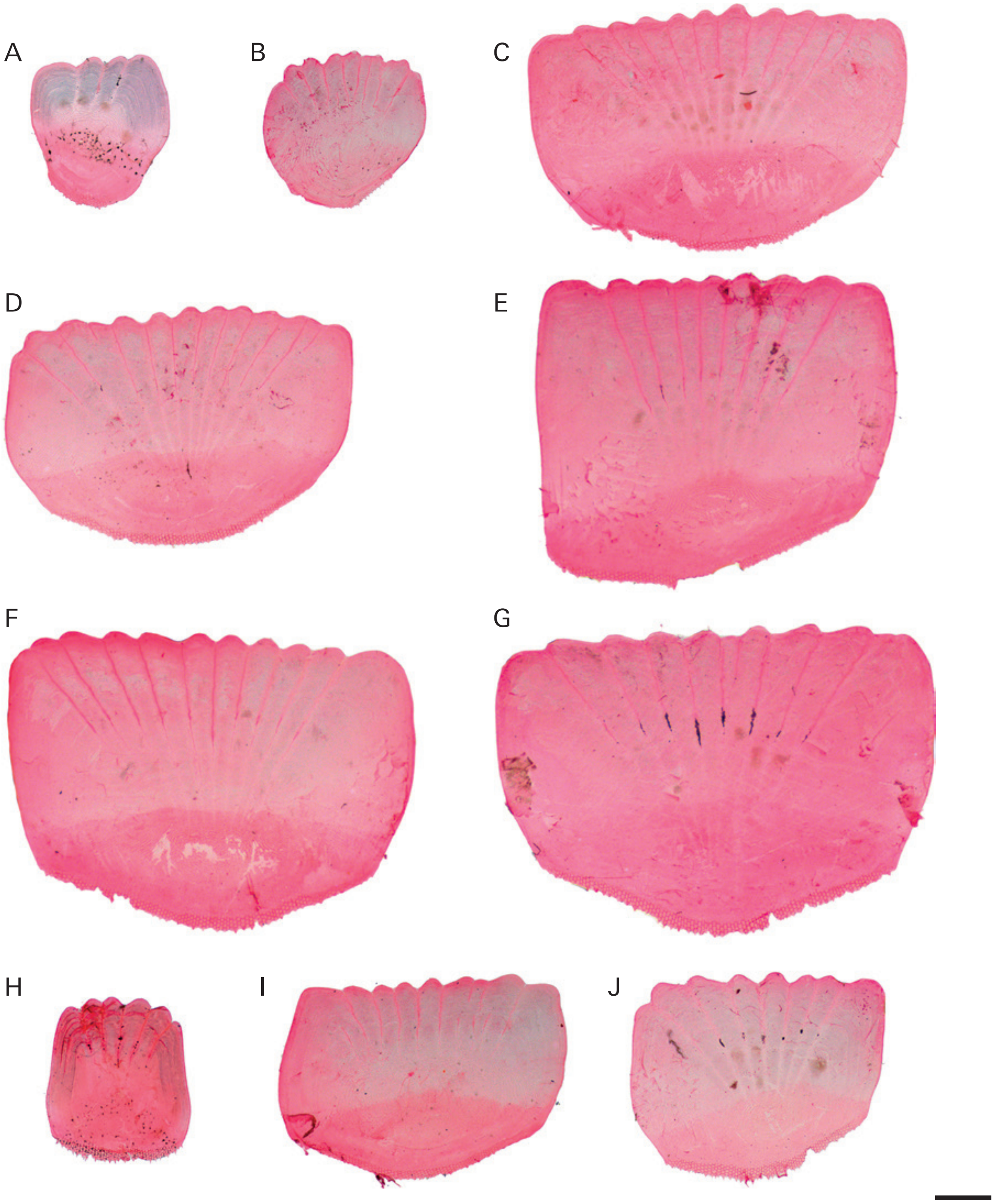

Fig. 54. *Diplodus vulgaris*; 128 mm SL, Costa Brava, Spain, DMM IE/5030. Scale bar = 1 mm.

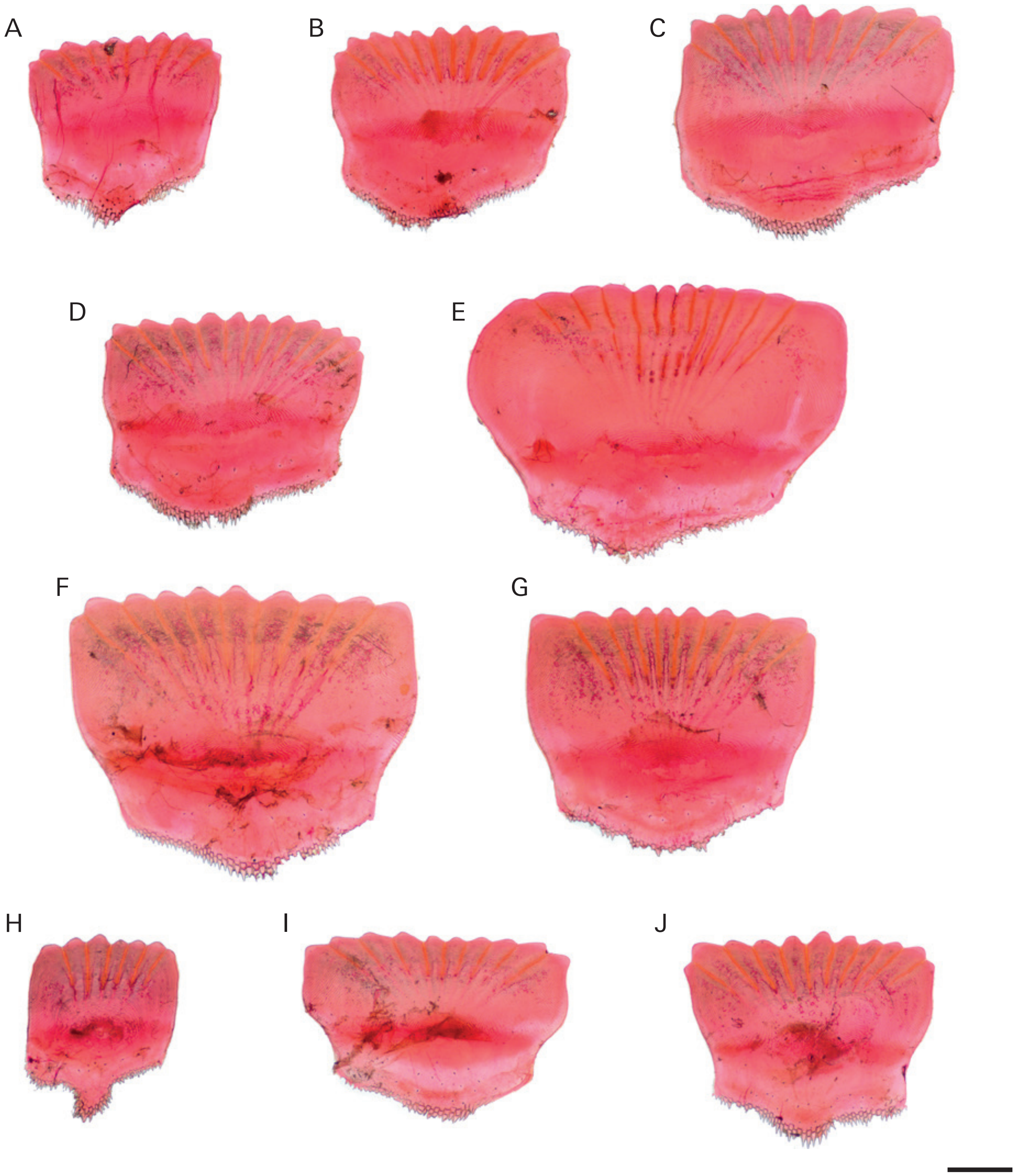

Fig. 55. *Pagellus acarne*; 153 mm SL, Cote Vermeille, France, DMM IE/6095. Scale bar = 1 mm.

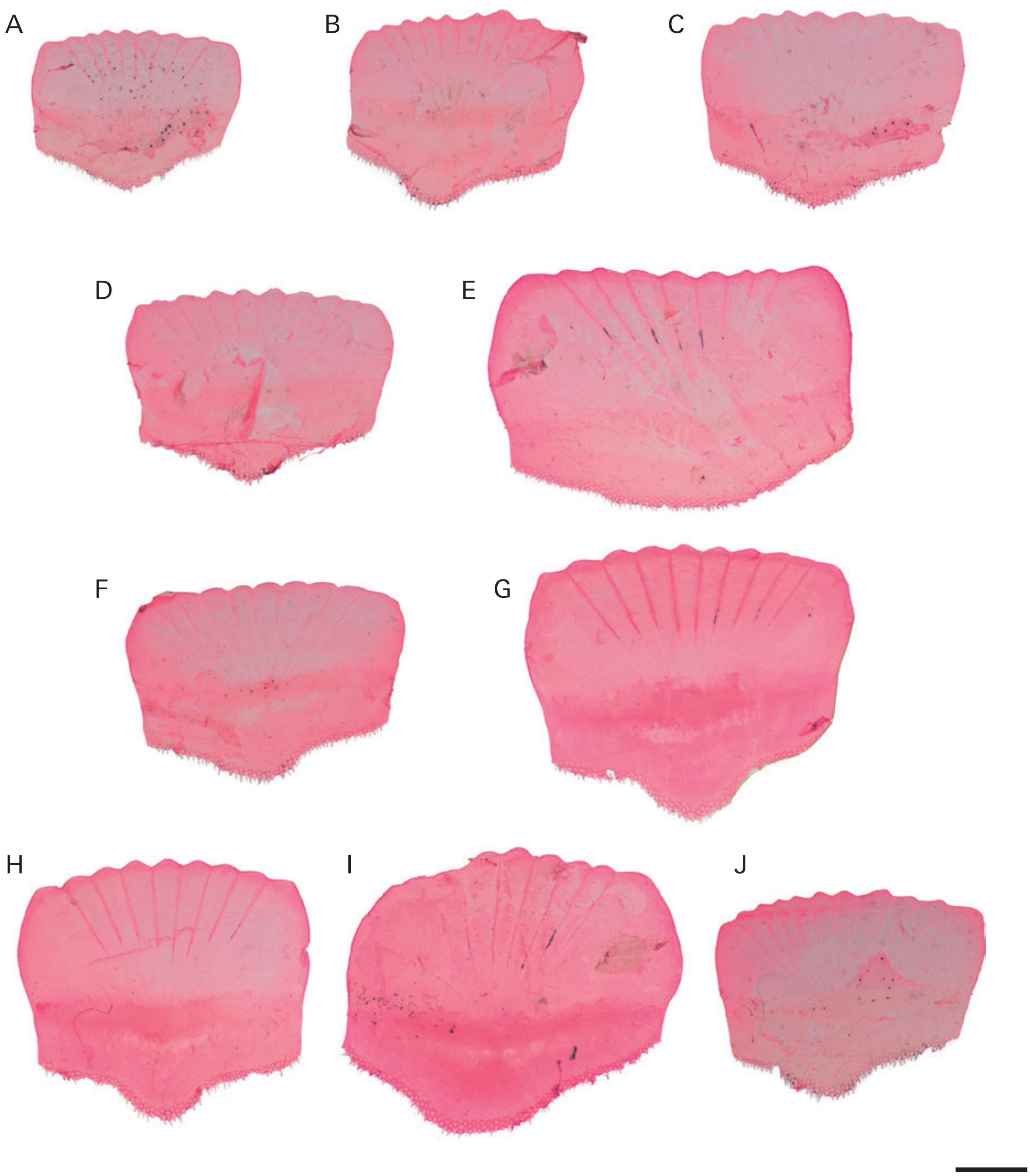

Fig. 56. *Pagellus erythrinus*; 130 mm SL, Costa Brava, Spain, DMM IE/5064. Scale bar = 1 mm.

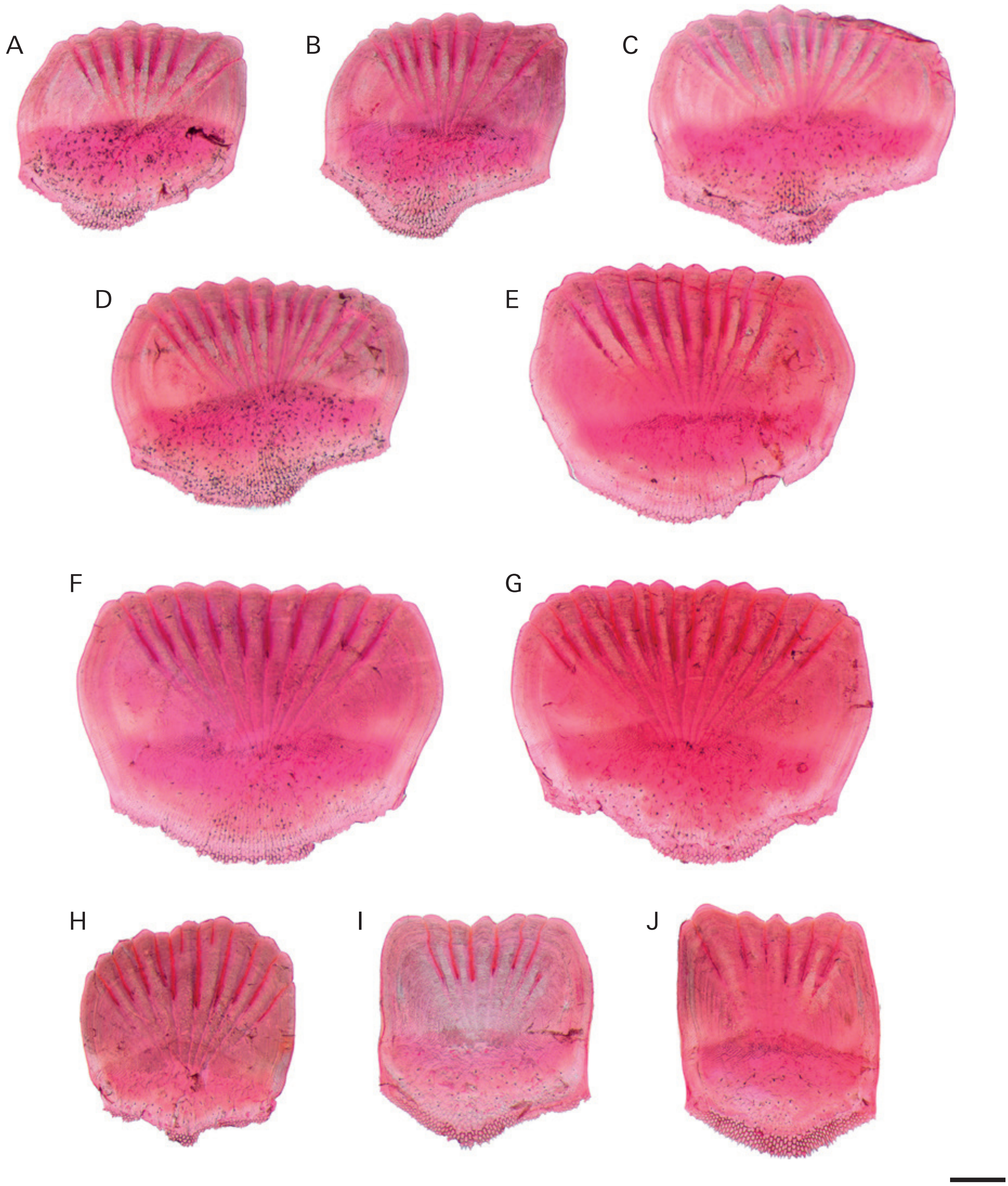

Fig. 57. *Sarpa salpa*; 174 mm SL, Mali Lošinj, Croatia, DMM IE/9017. Scale bar = 1 mm.

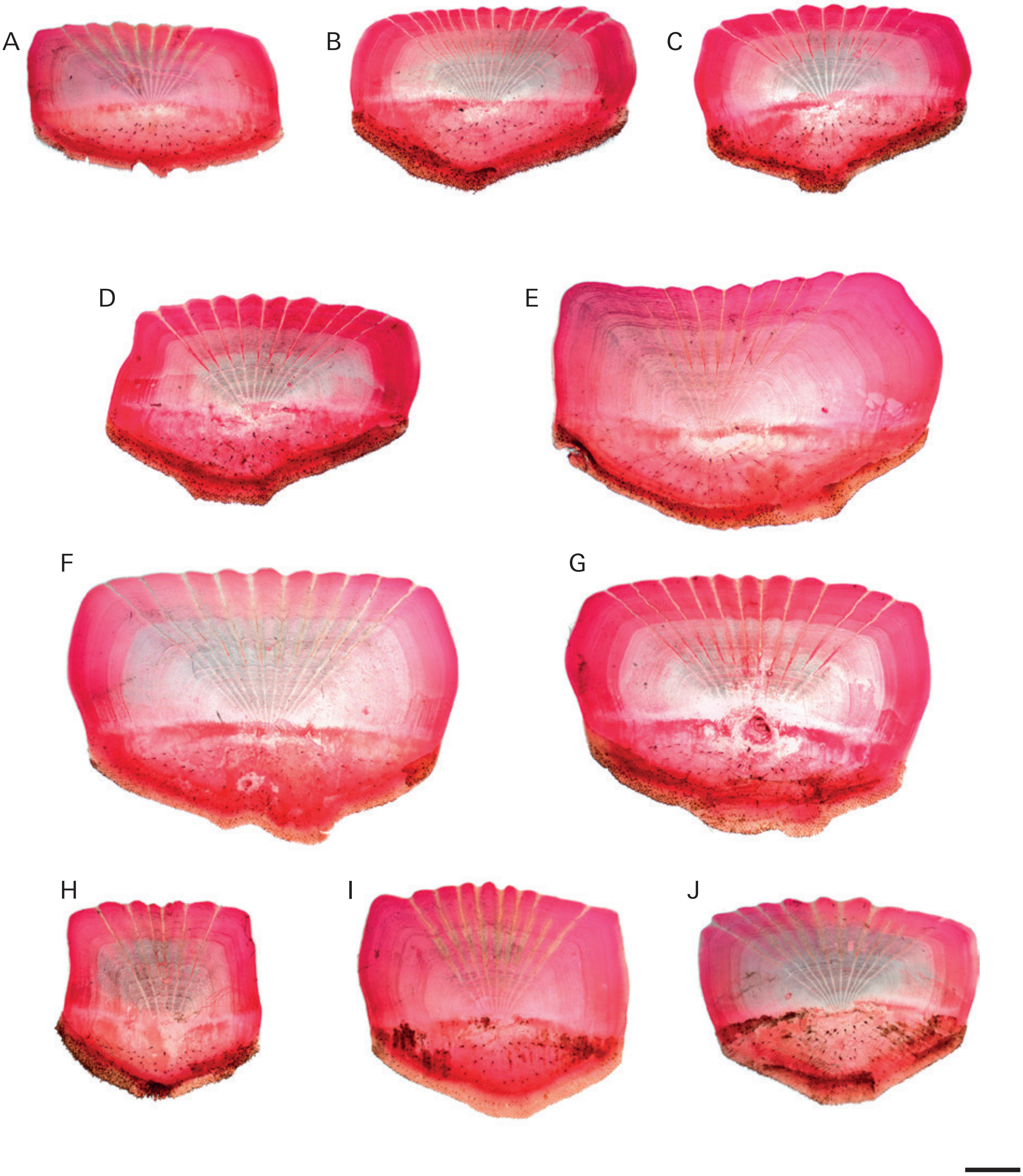

Fig. 58. *Sparus aurata*; 318 mm SL, aquarium specimen, DMM IE/9023. Scale bar = 2 mm.

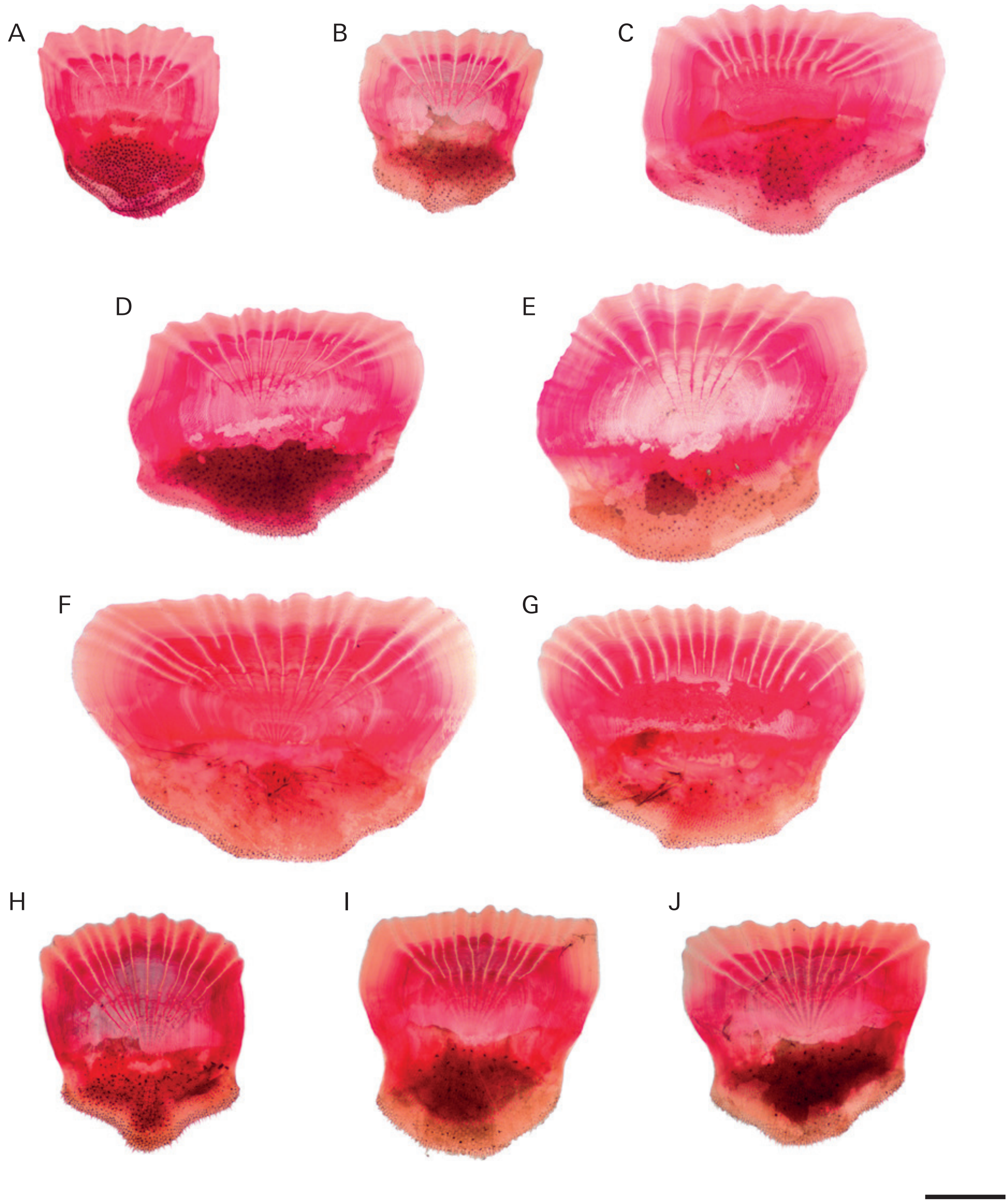

Fig. 59. *Spondyliosoma cantharus*; 264 mm SL, aquarium specimen, DMM IE/9024. Scale bar = 2 mm.

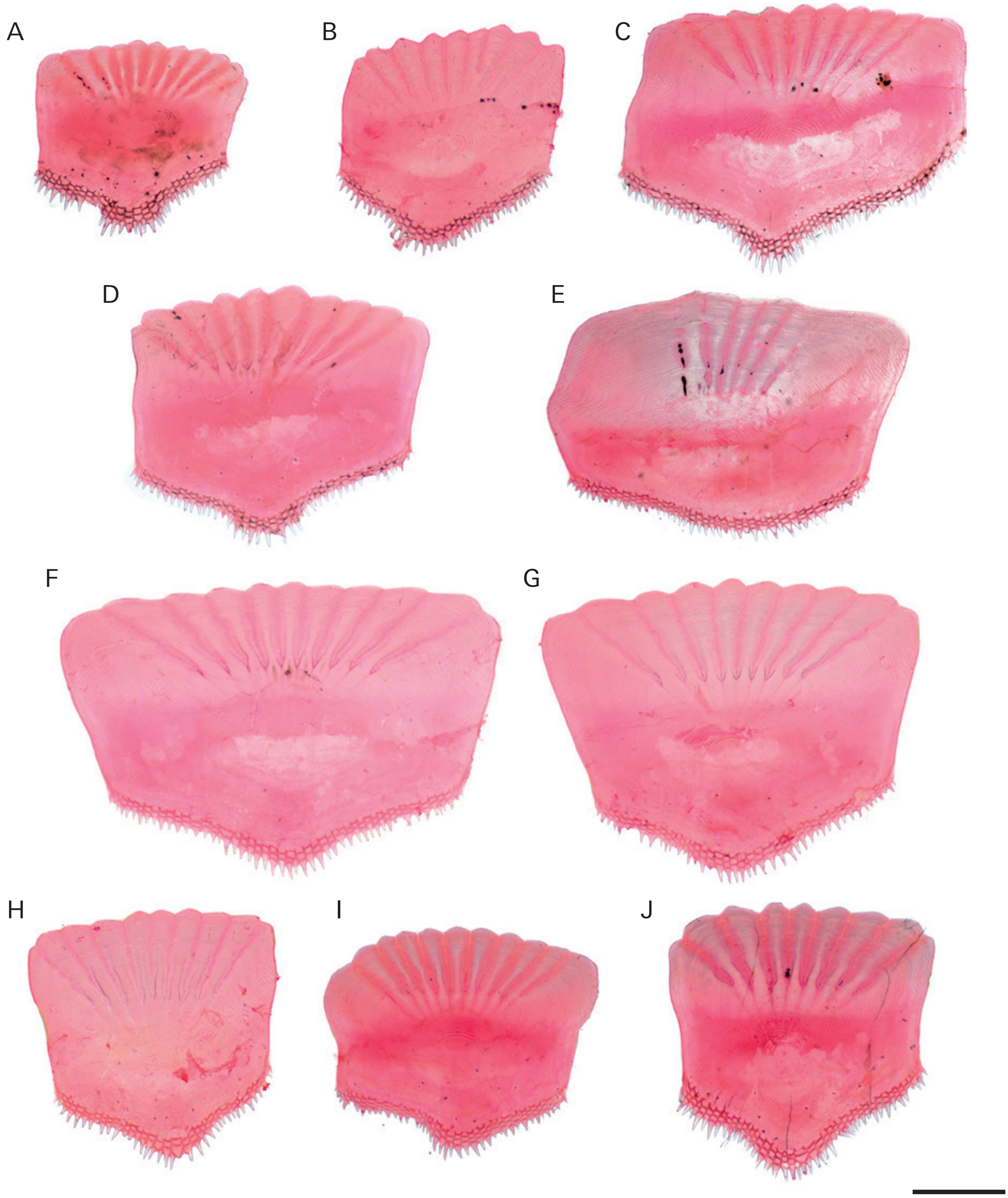

Fig. 60. *Spicara maena*; 123 mm SL, Costa Brava, Spain, DMM IE/5056. Scale bar = 1 mm.

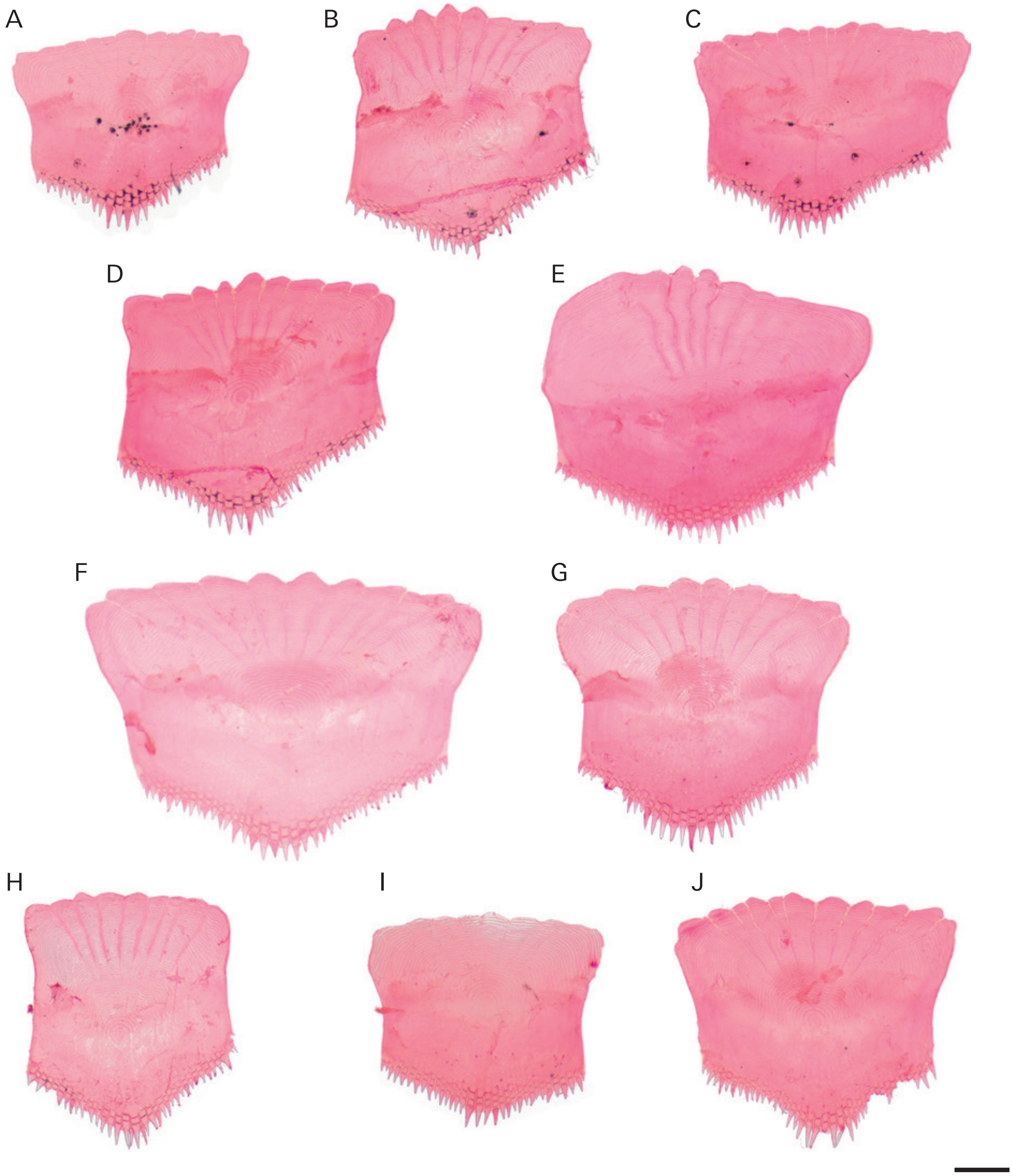

Fig. 61. *Spicara smaris*; 113 mm SL, Costa Brava, Spain, DMM IE/5058. Scale bar = 500 µm.

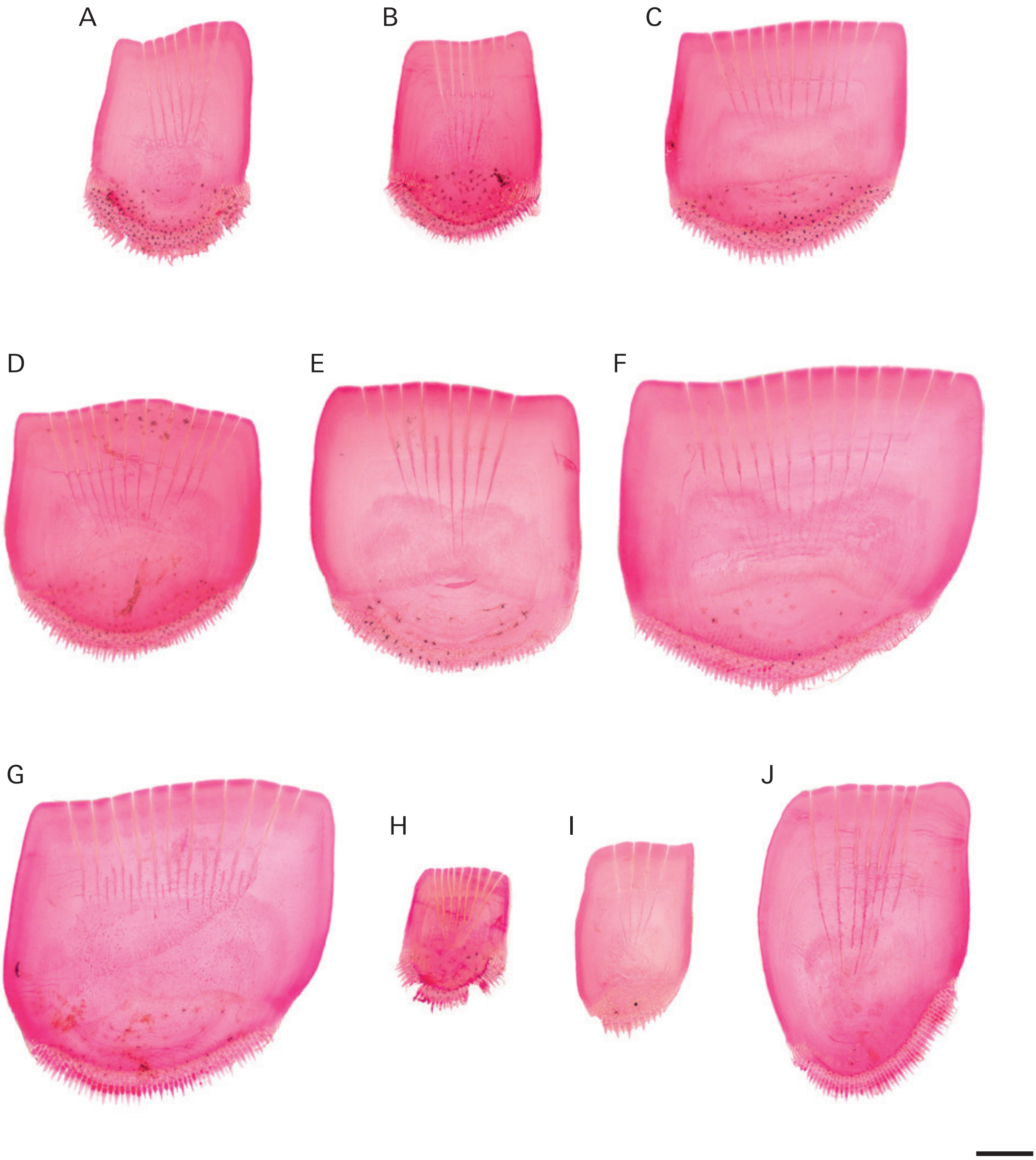

Fig. 62. *Sciena umbra*; 179 mm SL, Costa Brava, Spain, DMM IE/4588. Scale bar = 1 mm.

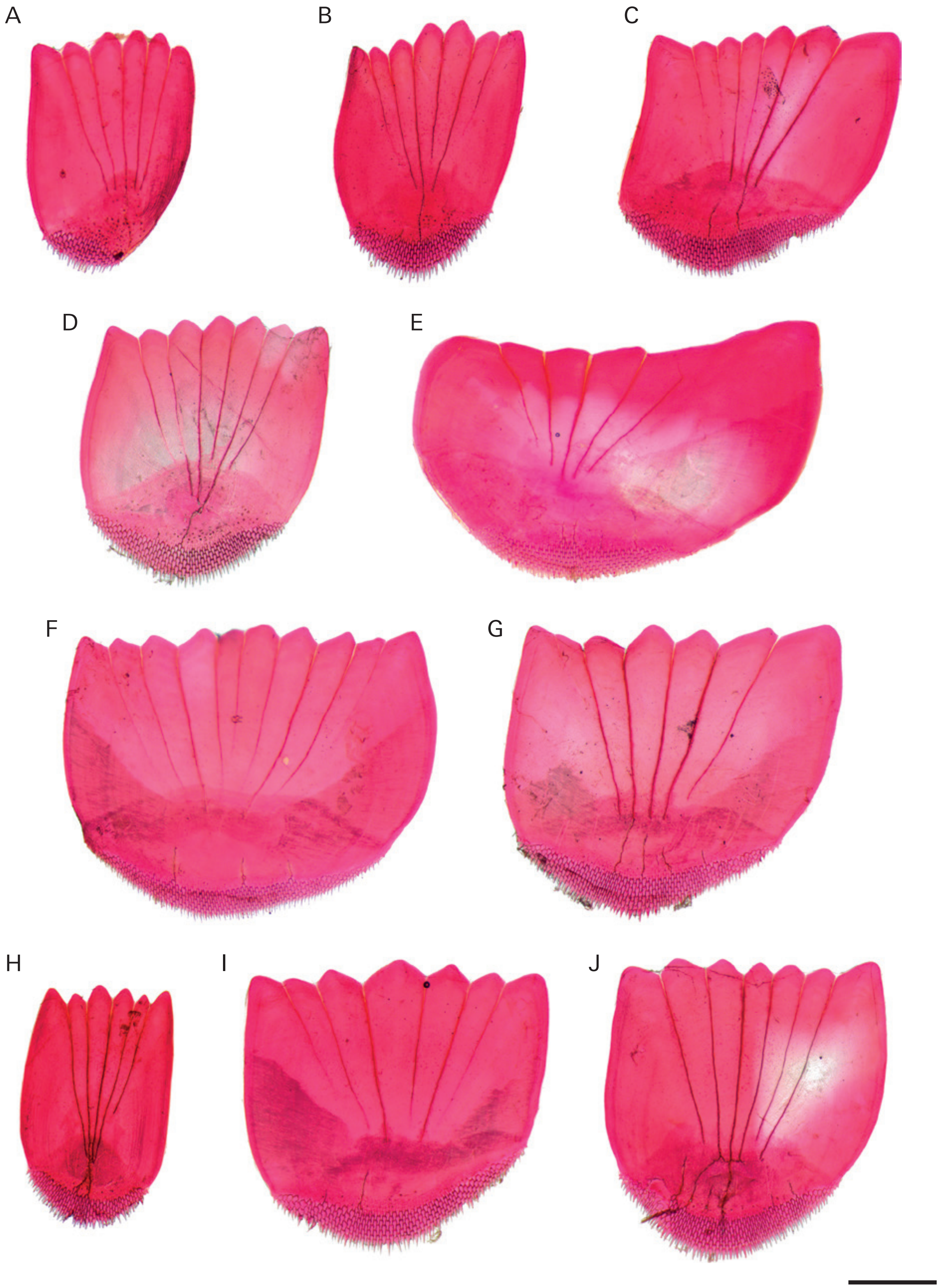

Fig. 63. *Mullus barbatus*; 114 mm SL, Gulf of Ambracia, Greece, DMM IE/9018. Scale bar = 2 mm.

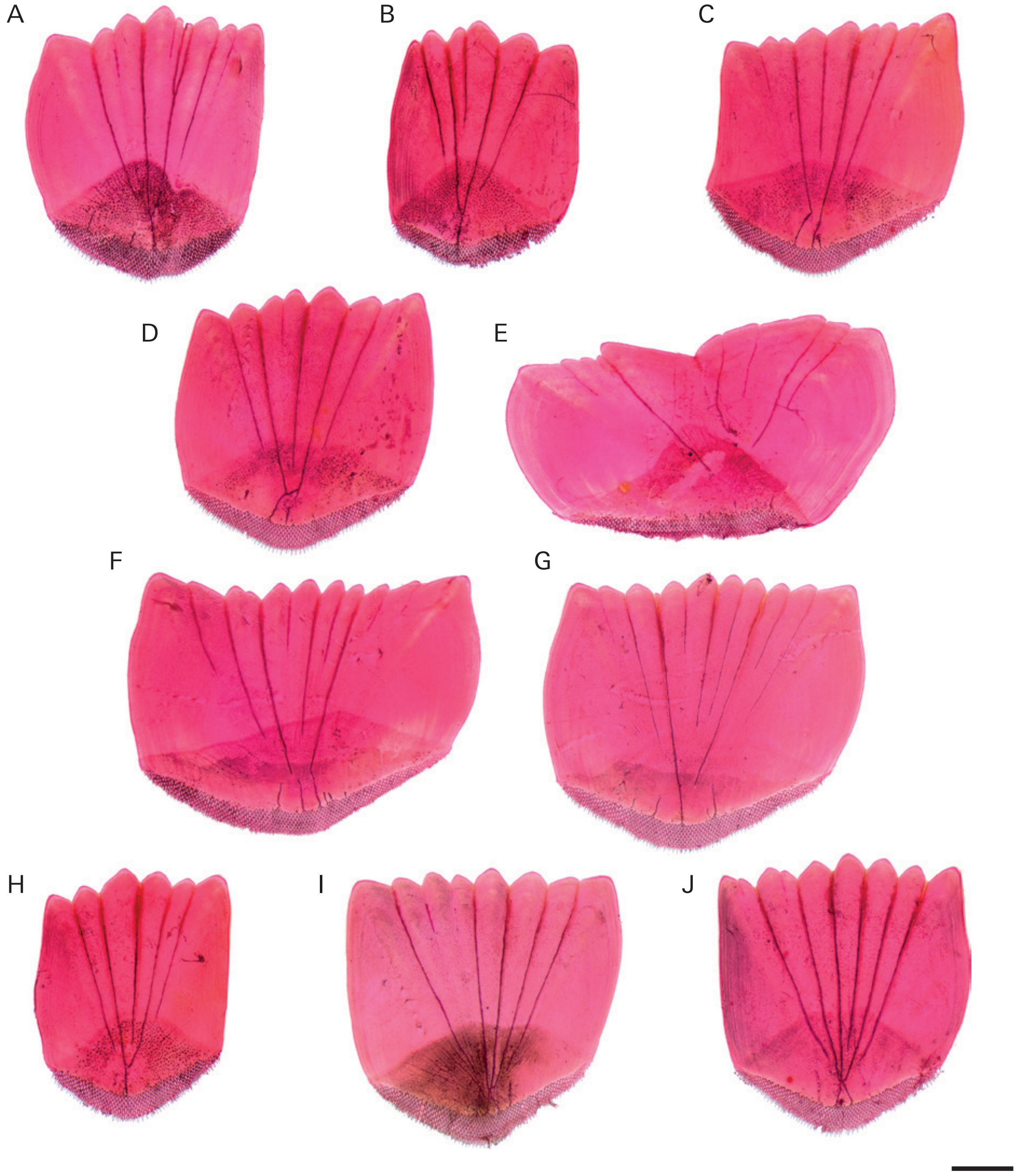

Fig. 64. *Mullus surmuletus*; 164 mm SL, Mali Lošinj, Croatia, DMM IE/9019. Scale bar = 2 mm.

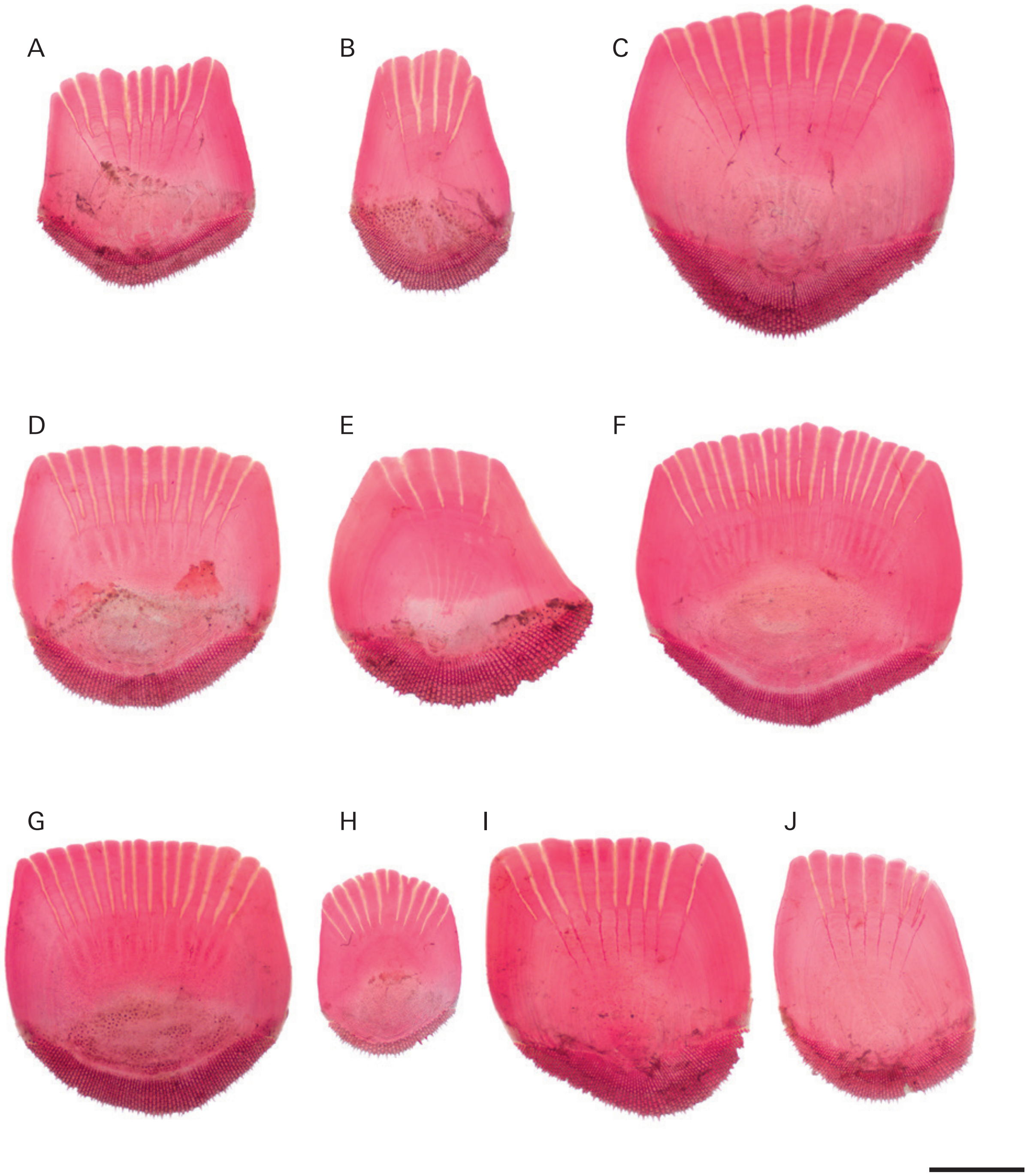

Fig. 65. *Chaetodon hoefleri*; 132 mm SL, Central East Atlantic, Morocco, DMM IE/2267. Scale bar = 2 mm.

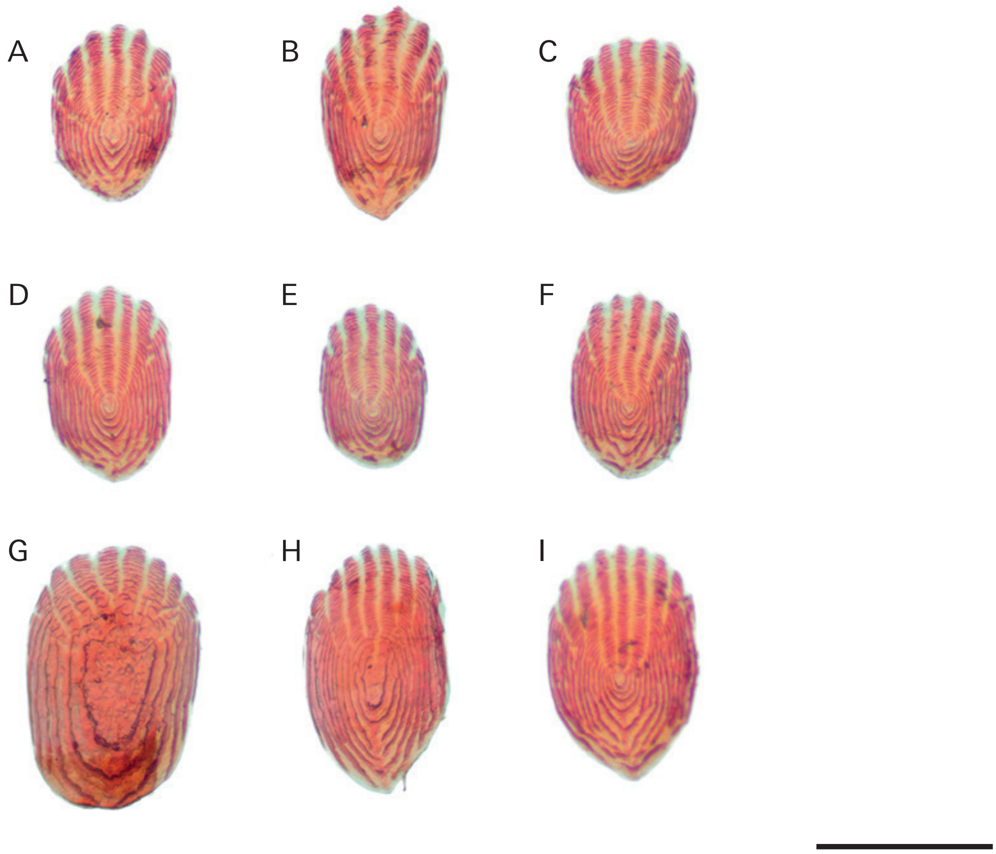

Fig. 66. *Cepola macrophthalma*; 218 mm TL, Costa Brava, Spain, DMM IE/4992. Scale bar = 500 µm.

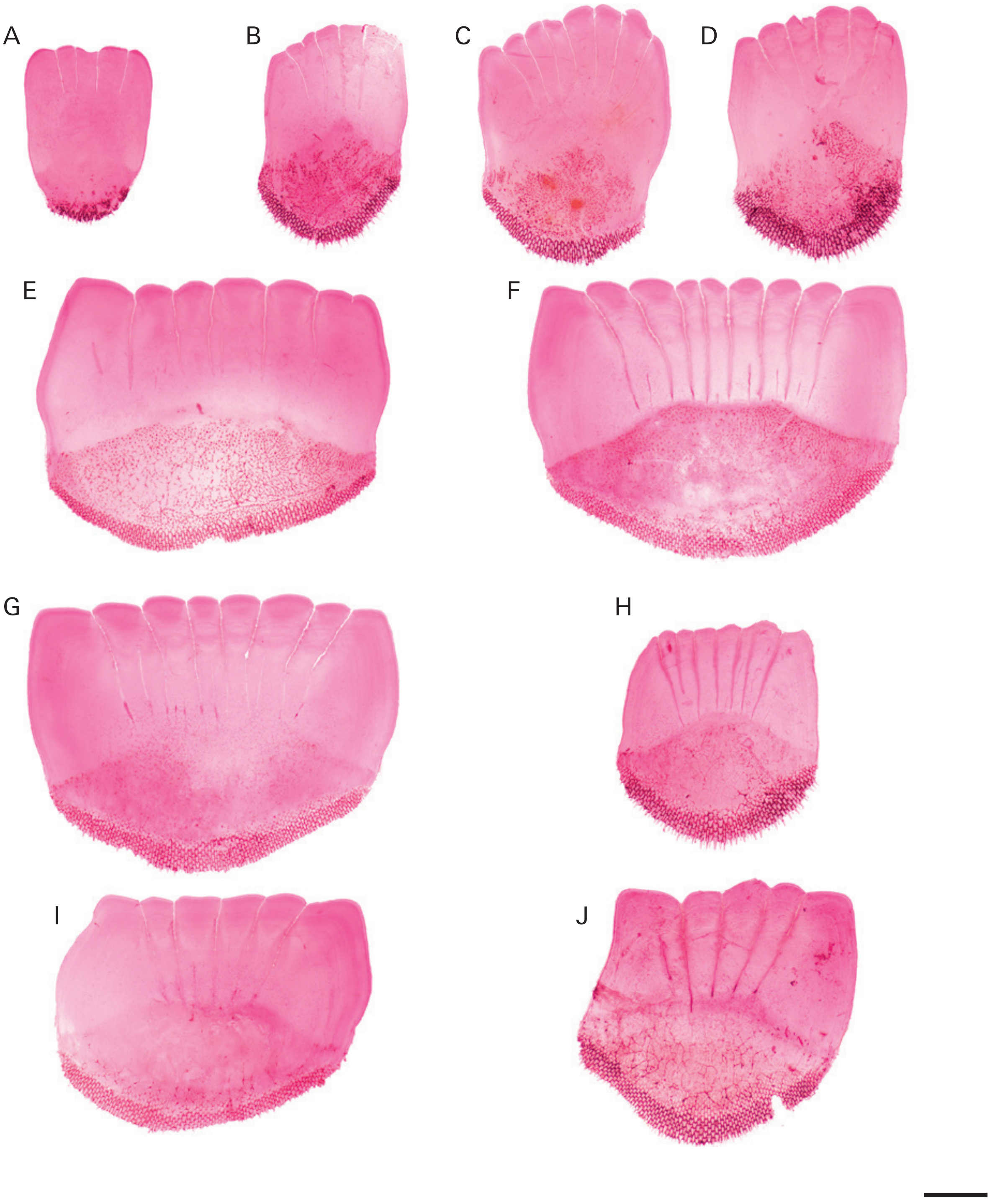

Fig. 67. *Chromis chromis*; 68 mm SL, aquarium specimen, Spain, DMM IE/5943. Scale bar = 1 mm.

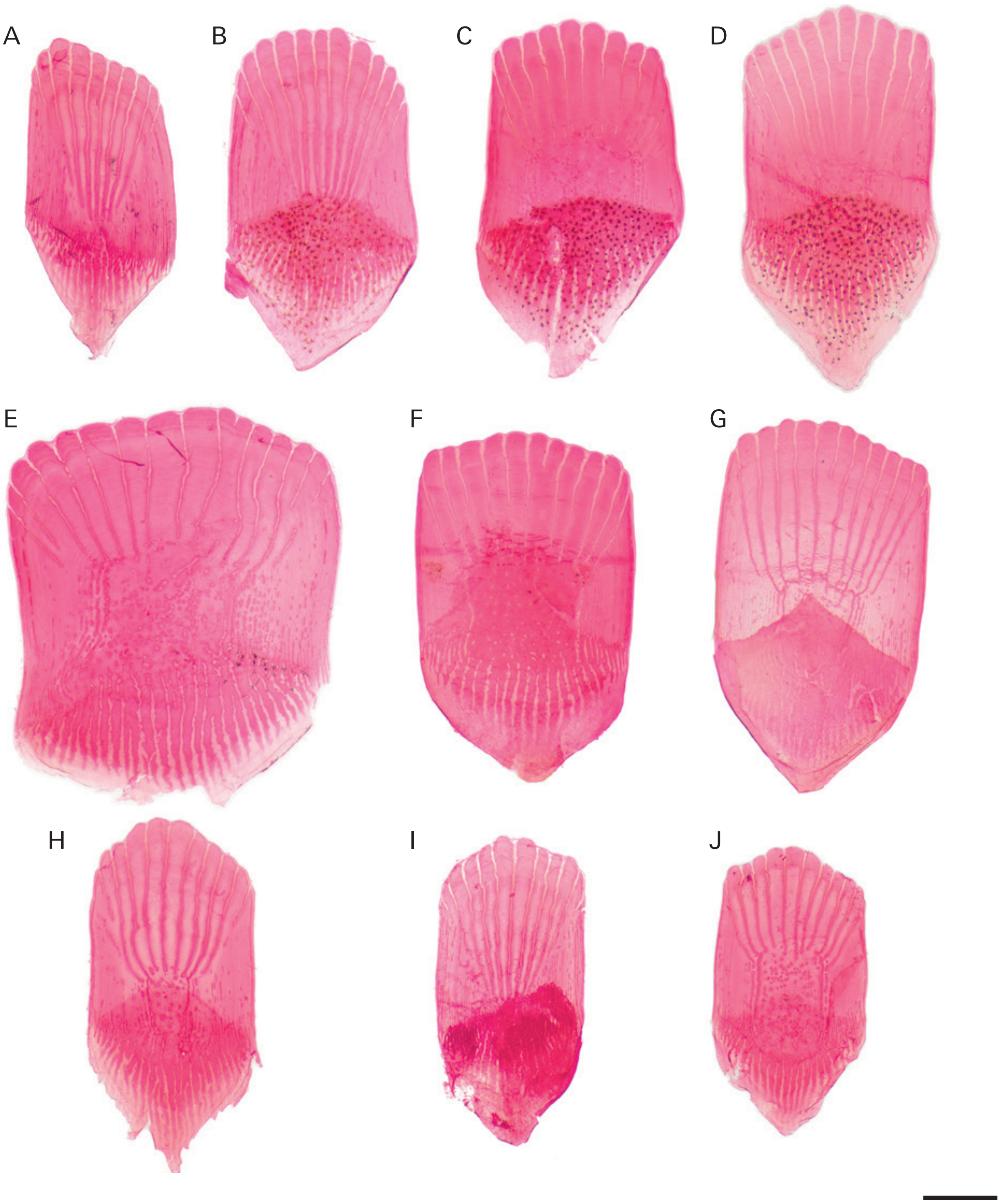

Fig. 68. *Coris julis*; 96 mm SL, Costa Brava, Spain, DMM IE/5020. Scale bar = 500 µm.

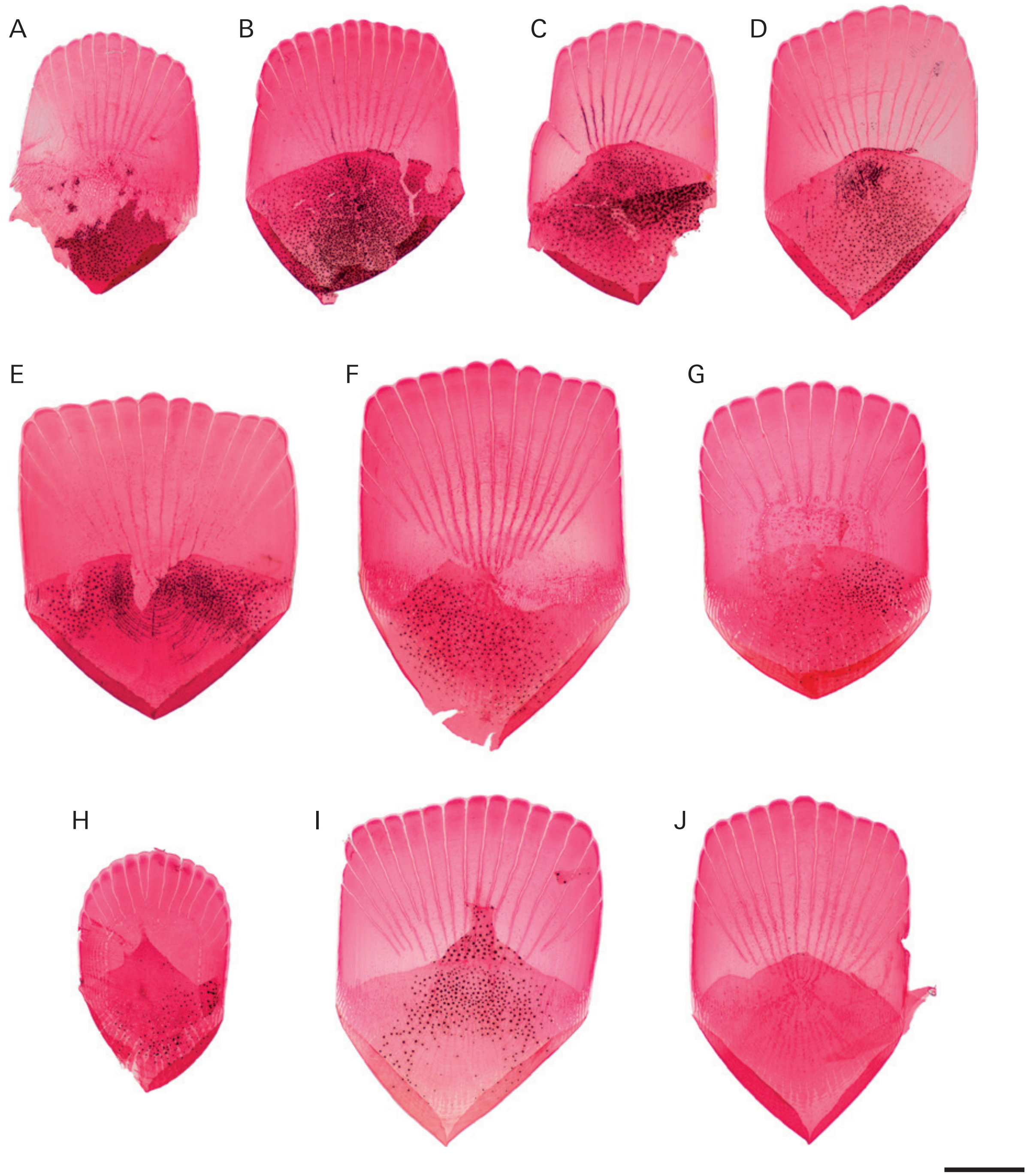

Fig. 69. *Labrus viridis*; 106 mm SL, Costa Brava, Spain, DMM IE/5886. Scale bar = 1 mm.

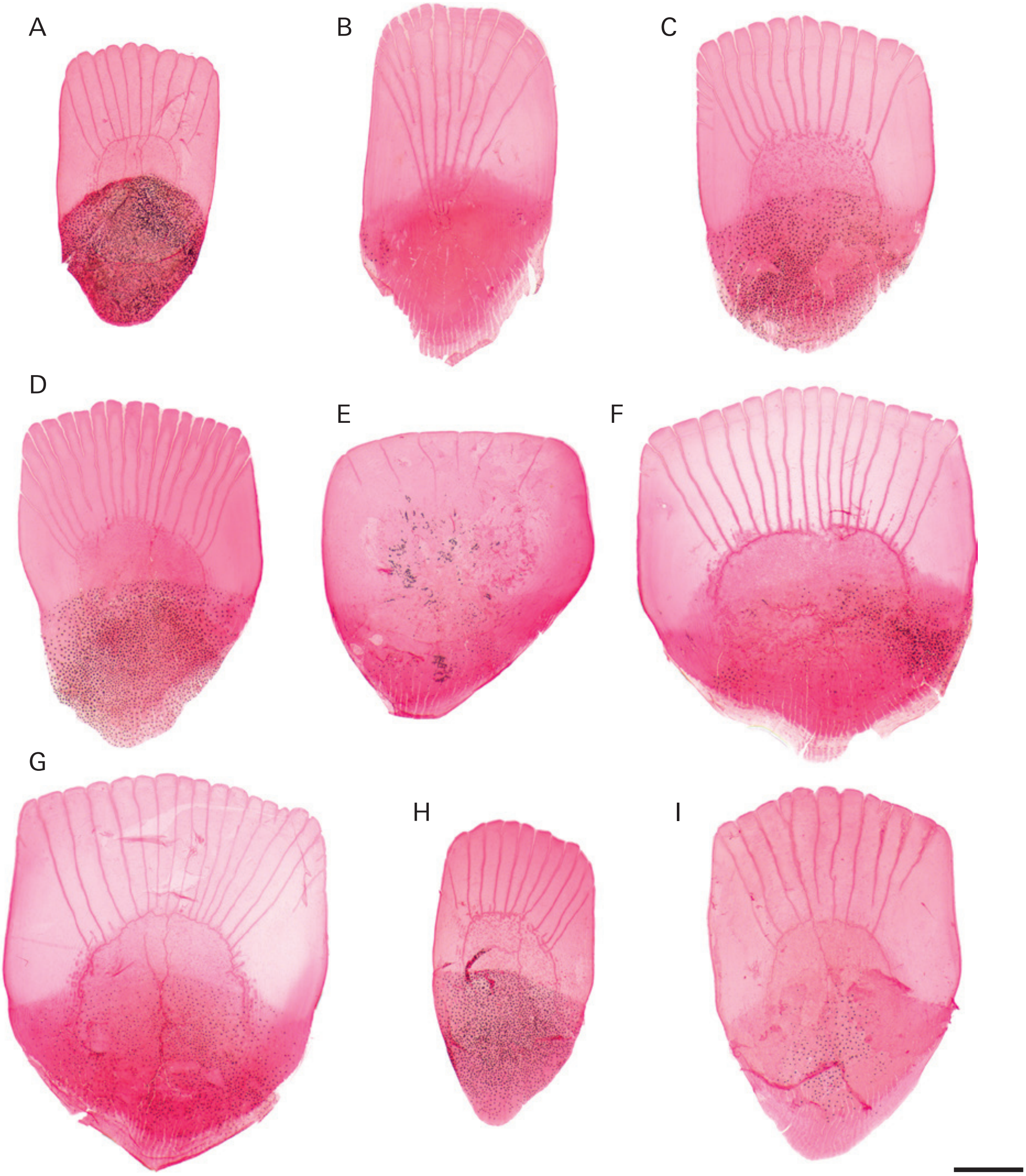

Fig. 70. *Symphodus rostratus*; 84 mm SL, aquarium specimen, Spain, DMM IE/5945. Scale bar = 1 mm.

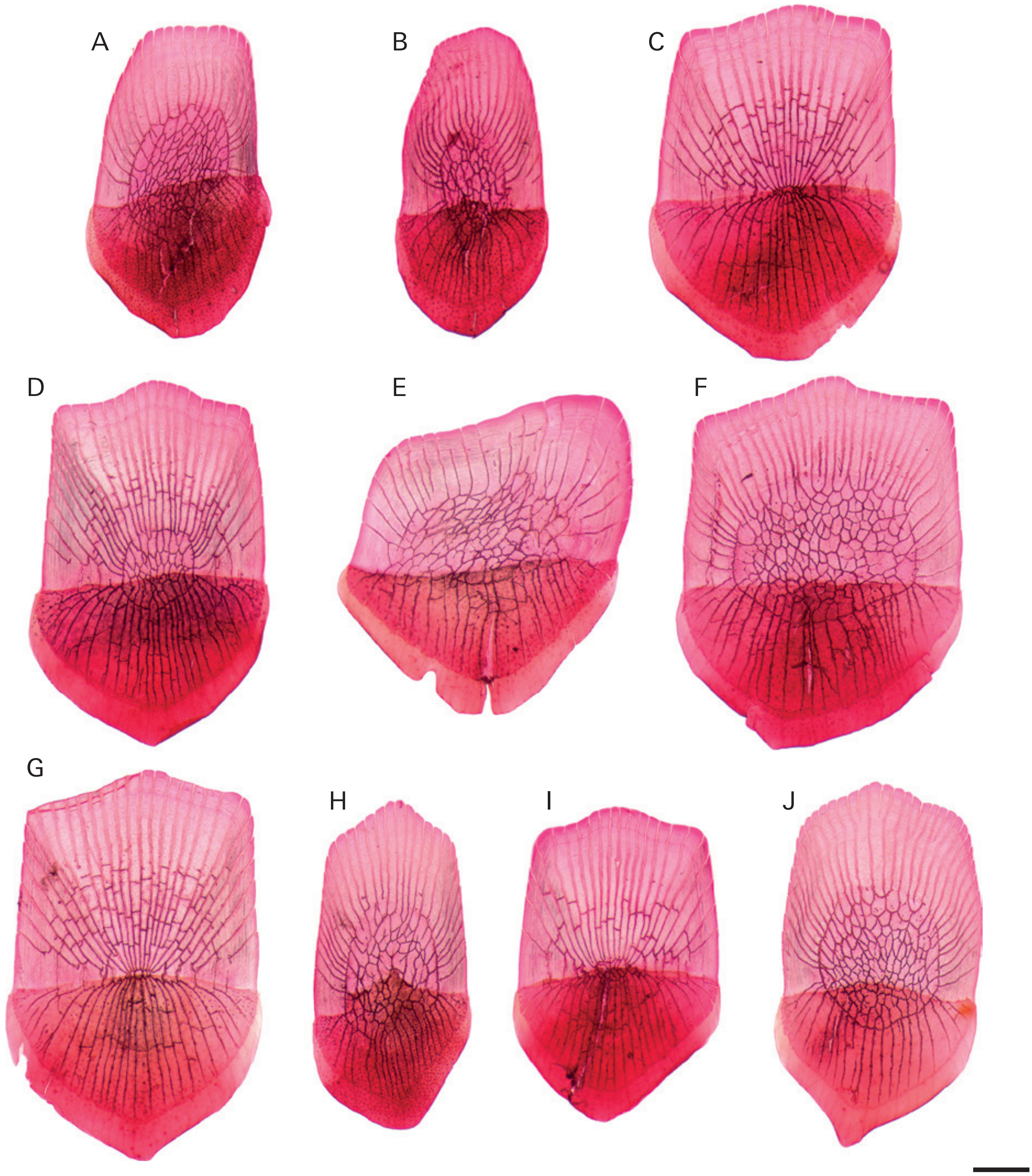

Fig. 71. *Thalassoma pavo*; 95 mm SL, Central Atlantic, Azores, DMM IE/6113. Scale bar = 1 mm.

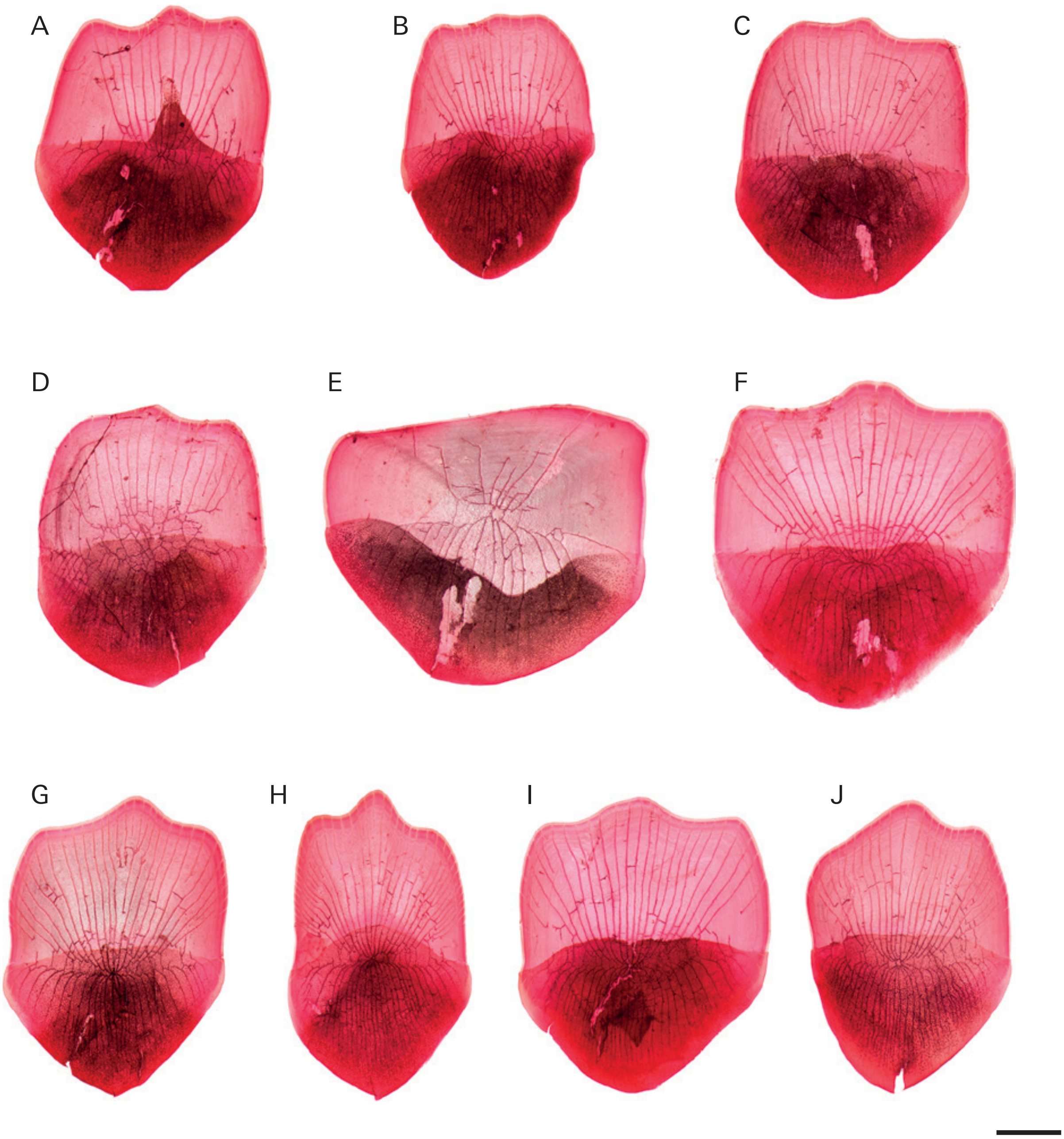

Fig. 72. *Sparisoma cretense*; 110 mm SL, Central Atlantic, Azores, DMM IE/6115. Scale bar = 2 mm.

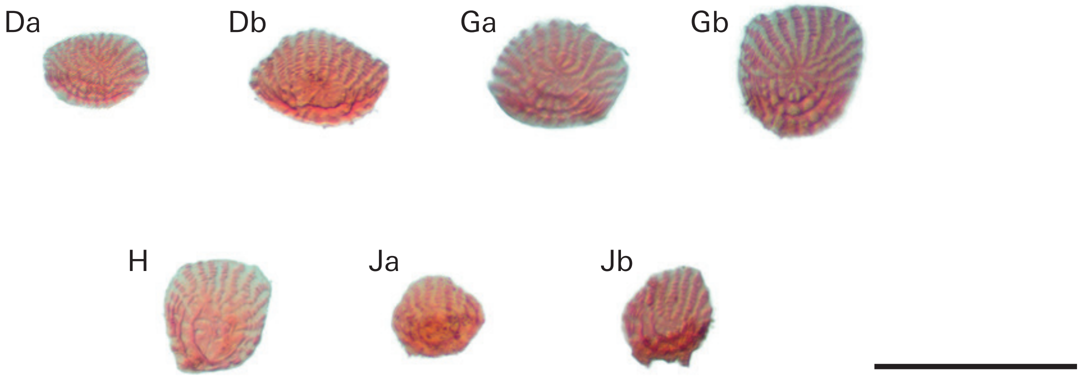

Fig. 73. *Gymnammodytes cicerelus*; 102 mm SL, Costa Brava, Spain, DMM IE/5840. Scale bar = 500 µm.

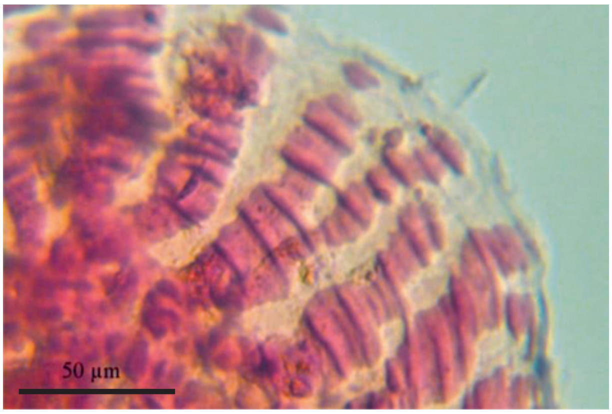

Fig. 74. Scale surface of *Gymnammodytes cicerelus* in sampling area D.

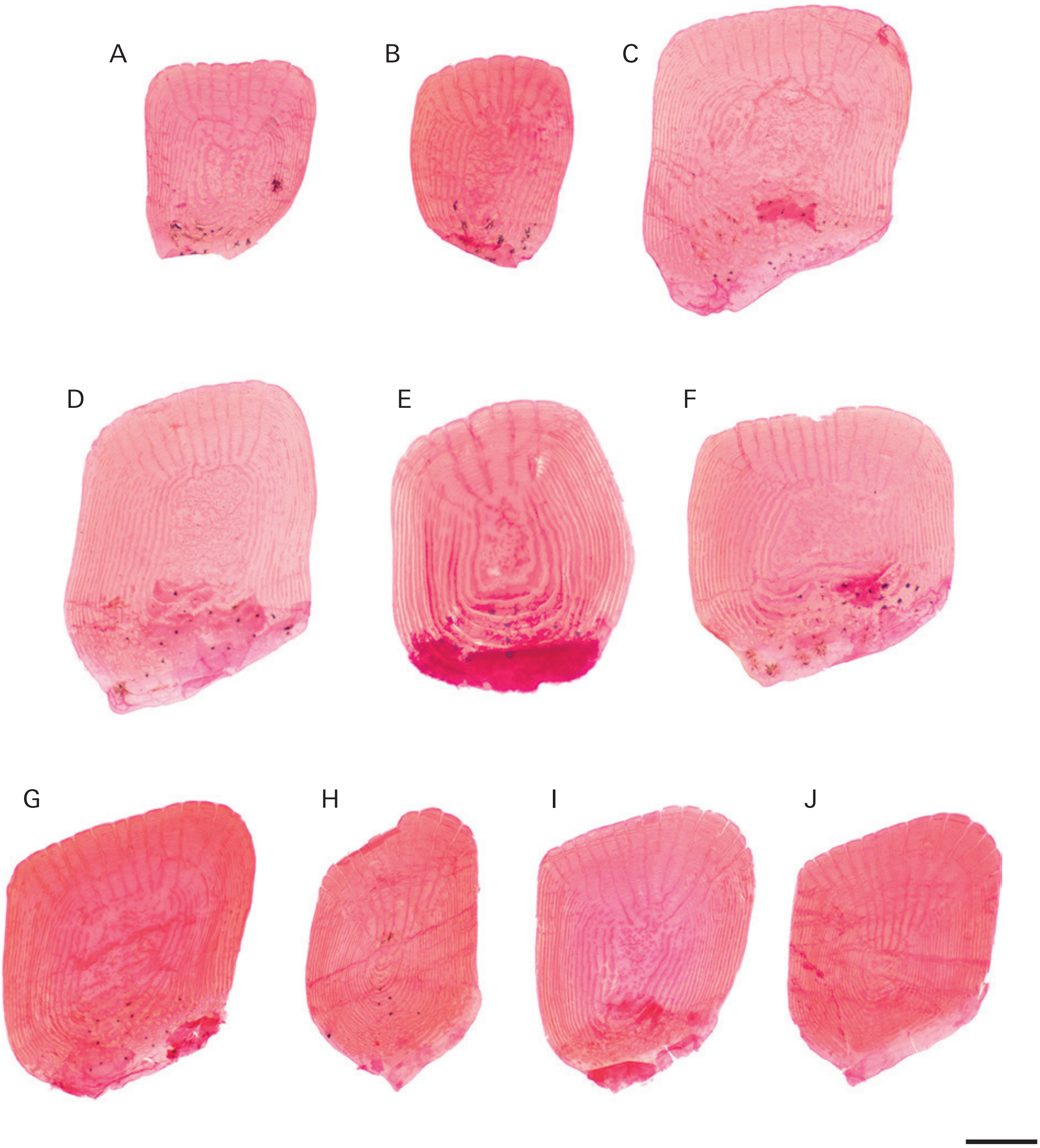

Fig. 75. *Trachinus draco*; 179 mm SL, Wismar Bay, Germany, DMM IE/4561. Scale bar = 500 µm.

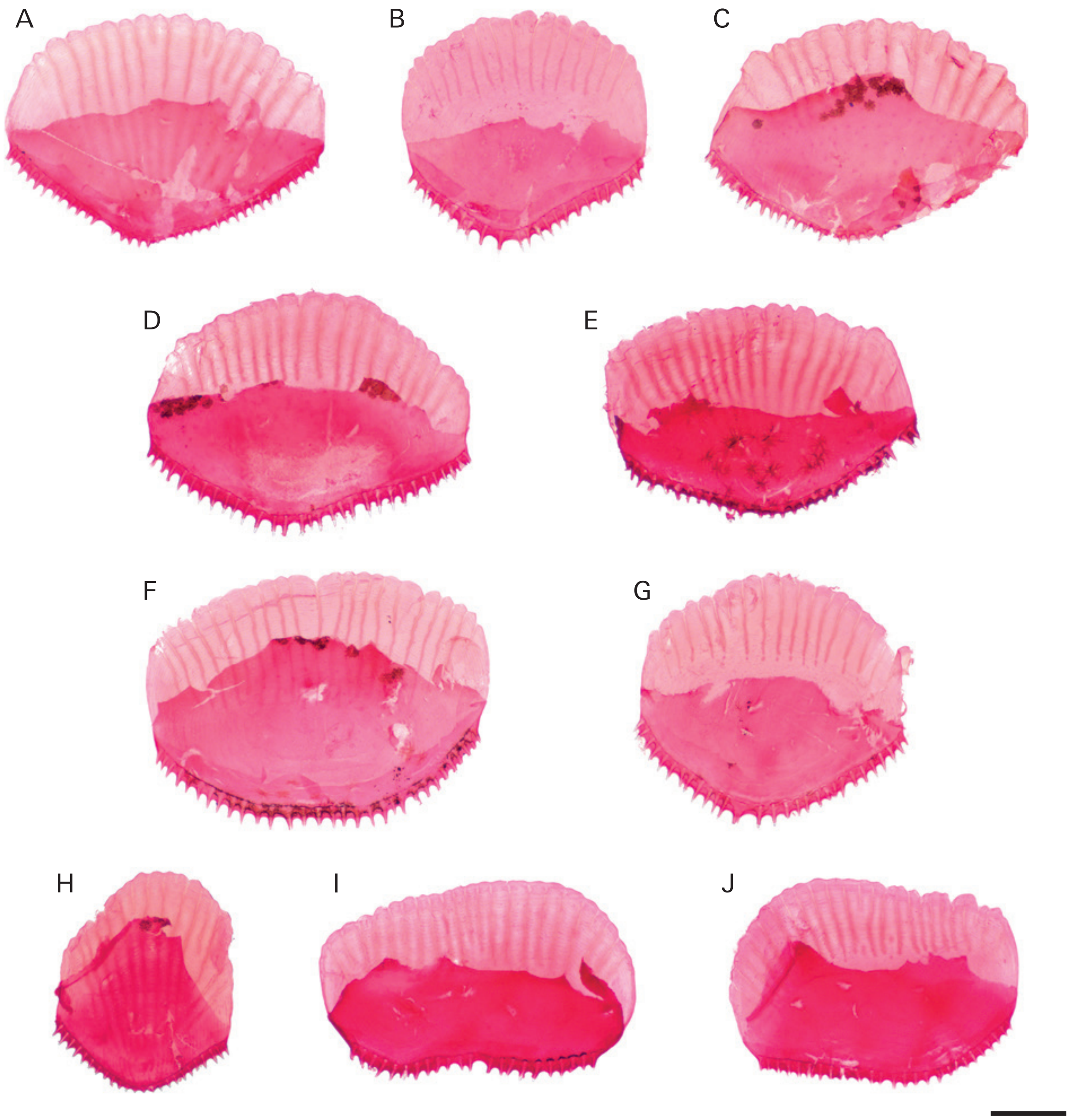

Fig. 76. *Tripterygion tripteronotum*; 53 mm SL, Costa Brava, Spain, DMM IE/4570. Scale bar = 500 µm.

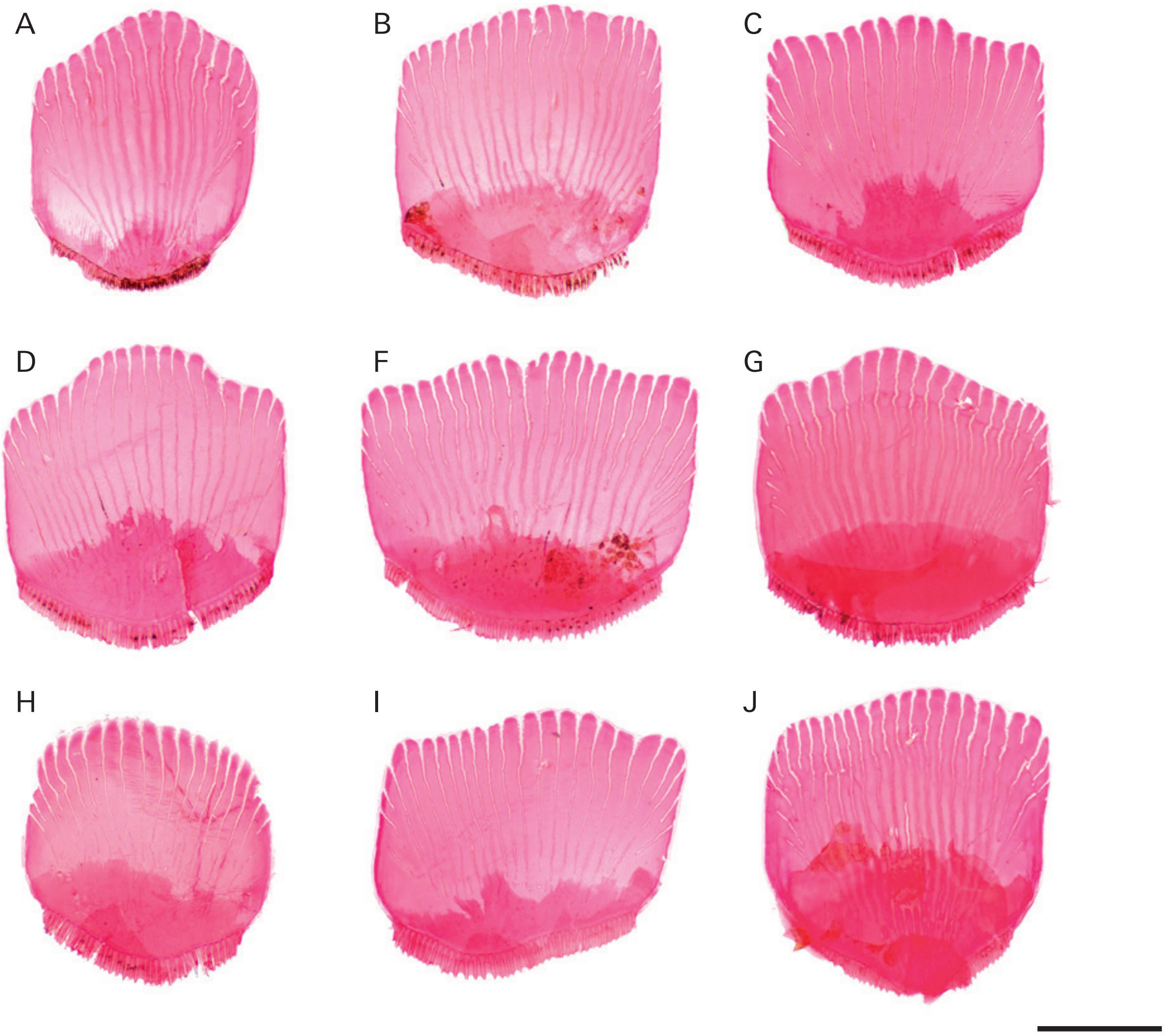

Fig. 77. *Gobius bucchichi*; 81 mm SL, Costa Brava, Spain, DMM IE/5861. Scale bar = 1 mm.

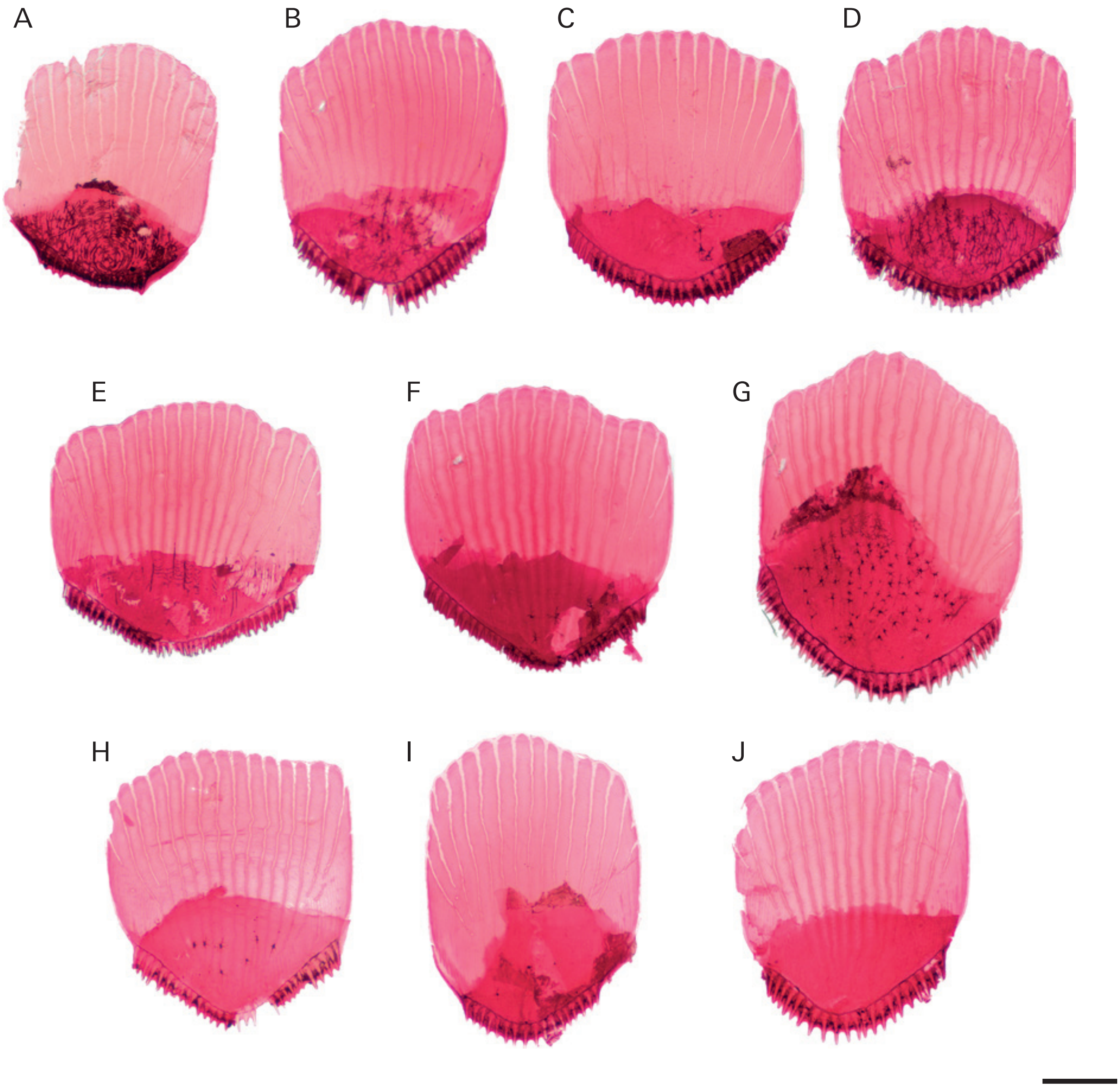

Fig. 78. *Gobius paganellus*; 61 mm SL, Costa Brava, Spain, DMM IE/5870. Scale bar = 500 µm.

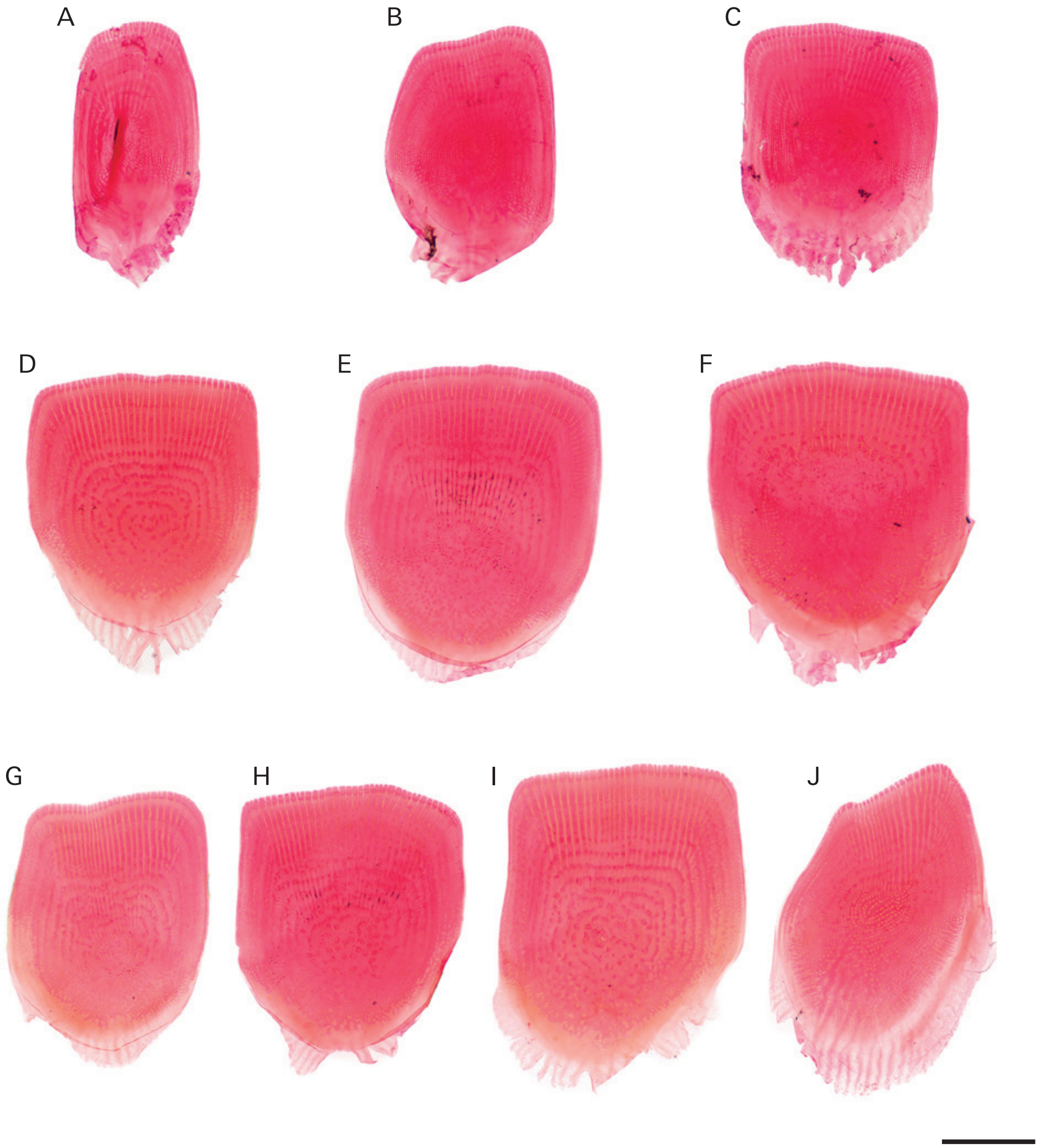

Fig. 79. *Sphyraena chrysotaenia*; 194 mm SL, Cilician Sea, Turkey, DMM IE/3864. Scale bar = 1 mm.

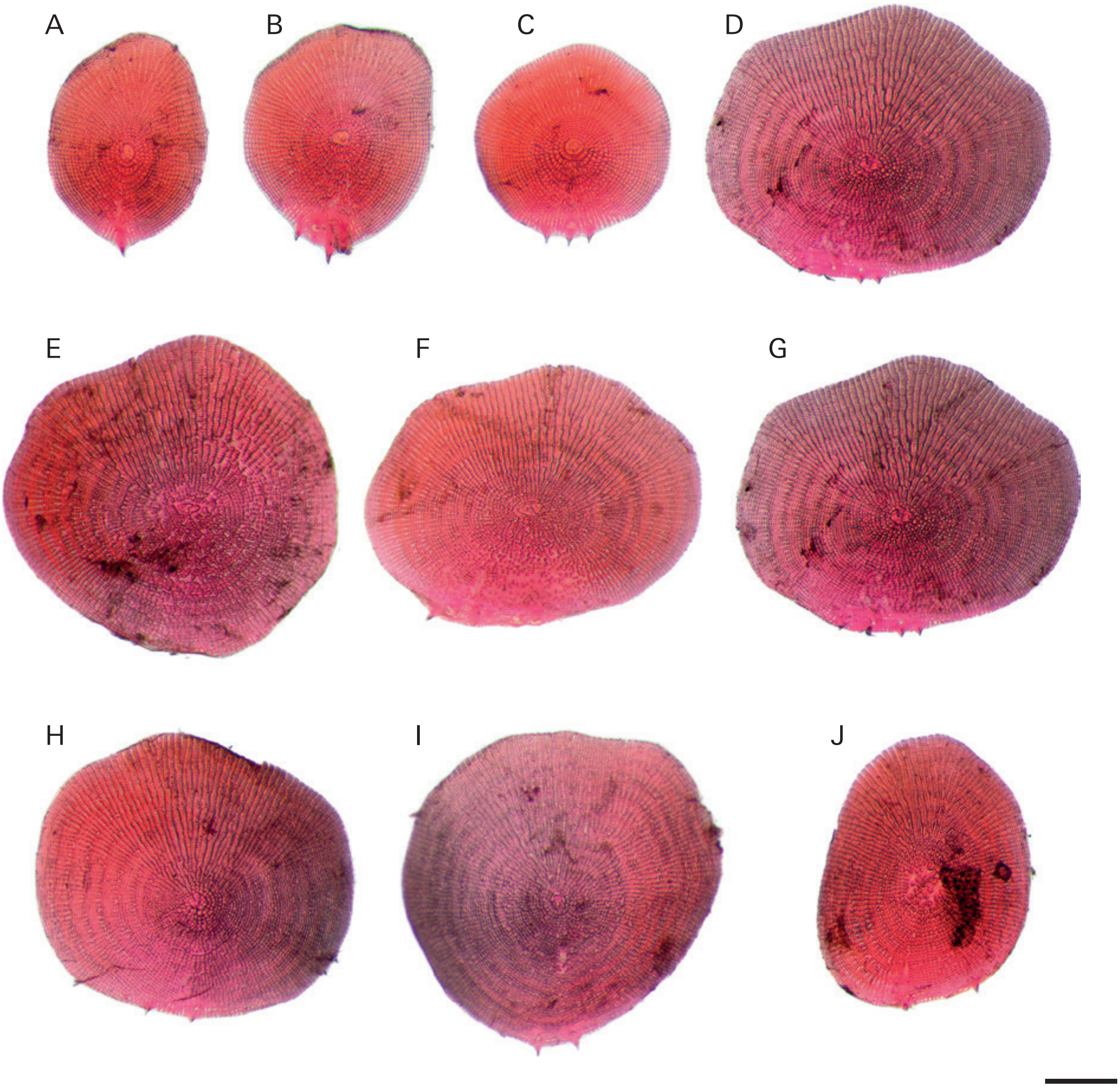

Fig. 80. *Sphyraena sphyraena*; 268 mm SL, Gulf of Ambracia, Greece, DMM IE/9020. Scale bar = 500 µm.

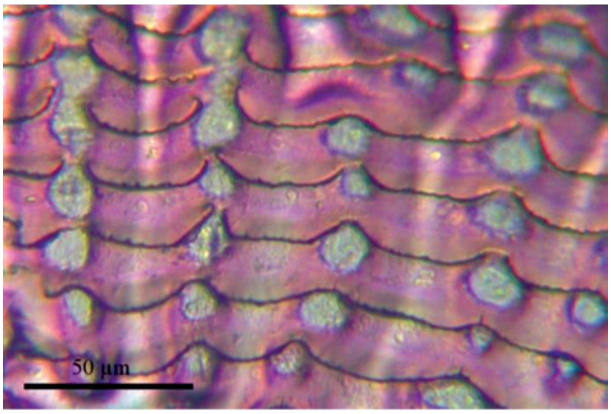

Fig. 81. Surface ornamentations of the scale of *Sphyraena sphyraena* in sampling area H.

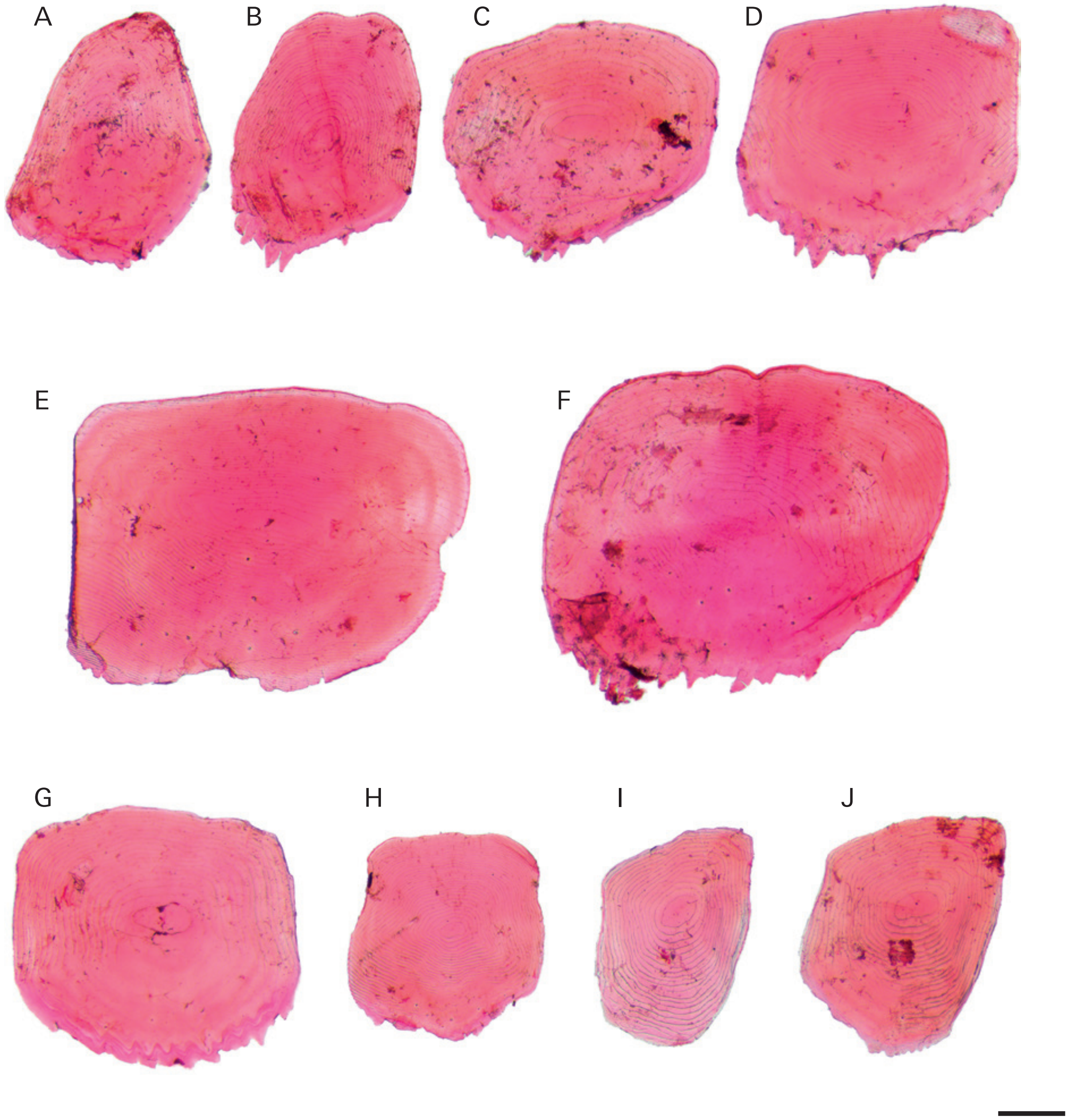

Fig. 82. *Scomber colias*; 215 mm SL, Mali Lošinj, Croatia, DMM IE/9021. Scale bar = 500 μm.

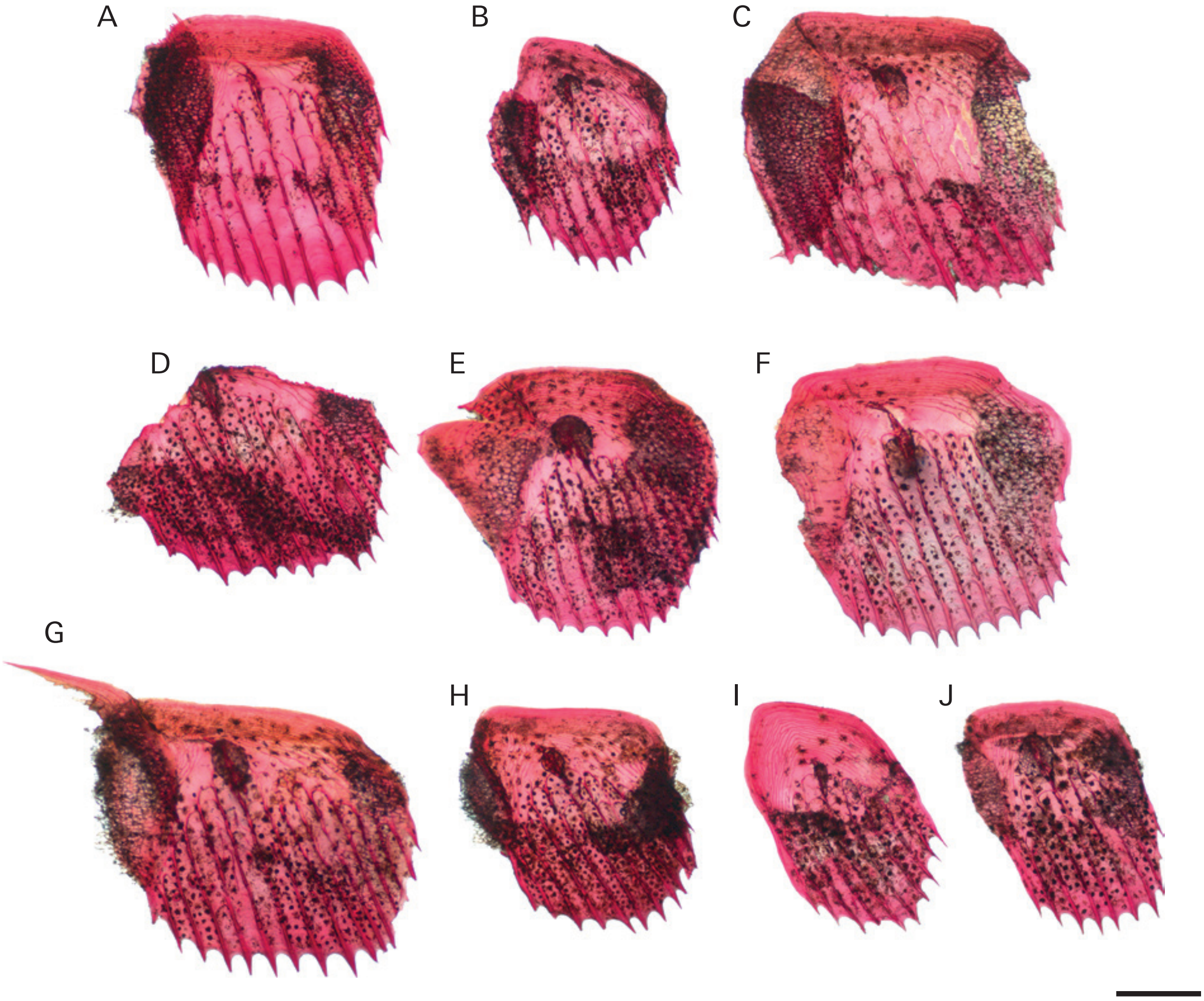

Fig. 83. *Tetragonurus cuvieri*; 298 mm SL, South East Atlantic, Namibia, DMM IE/3469. Scale bar = 1 mm.

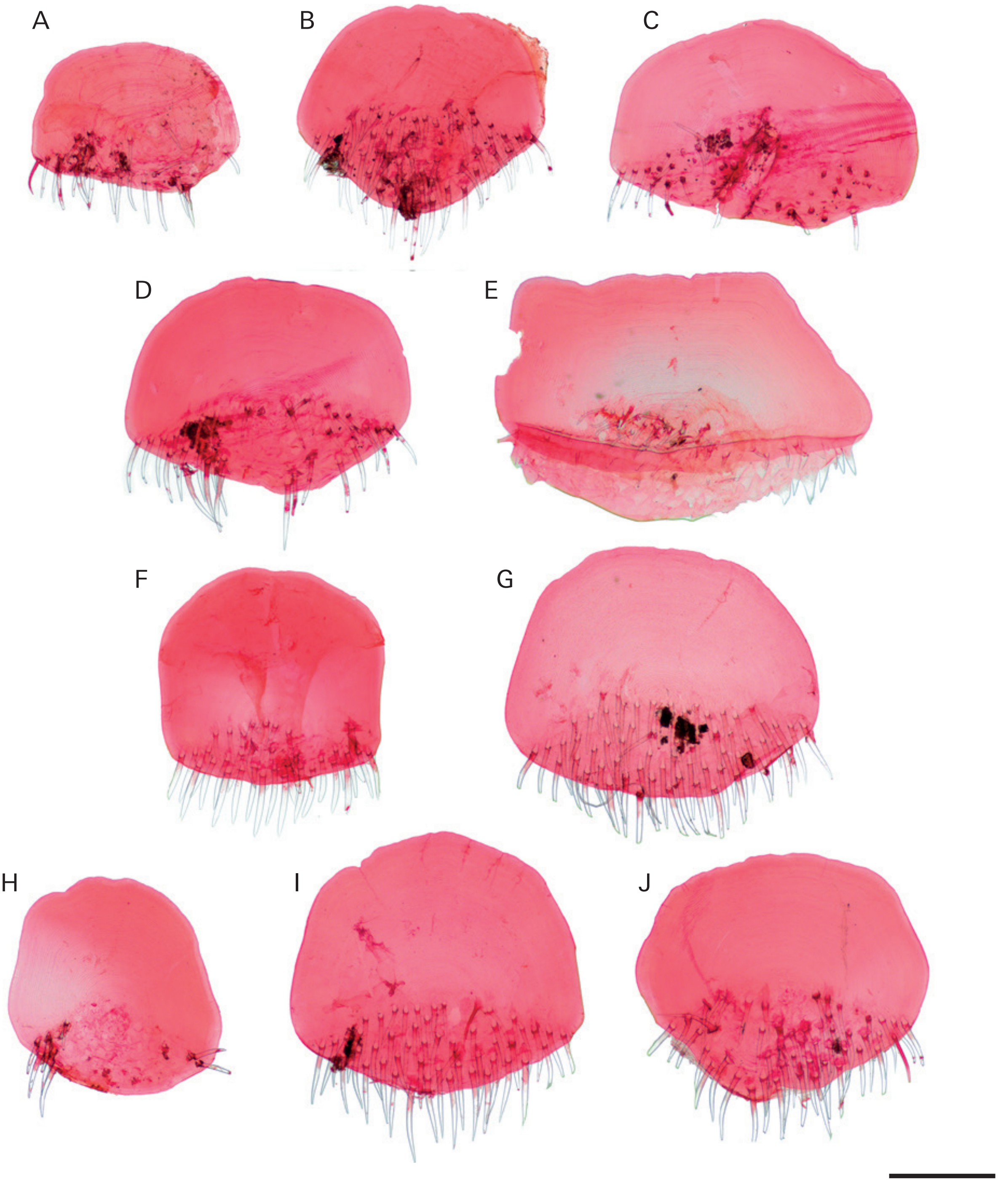

Fig. 84. *Capros aper*; 81 mm SL, Costa Brava, Spain, DMM IE/5038. Scale bar = 1 mm.

Fig. 85. *Scophthalmus maximus*, ocular-side (left side); 45 mm SL, Baltic Sea, Germany, DMM IE/9022. Scale bar = 100 µm.

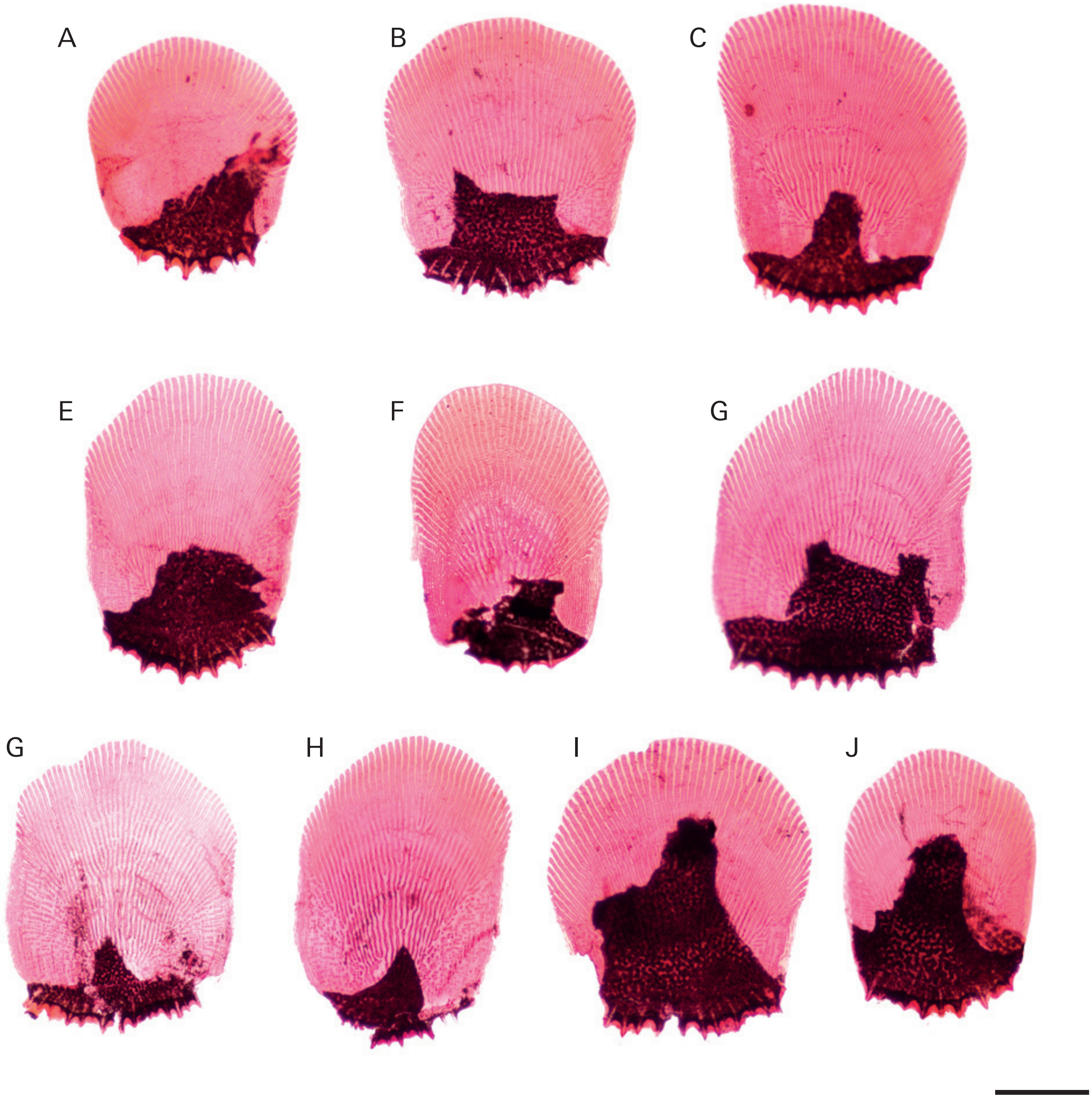

Fig. 86. *Bothus podas*, ocular-side (left side); 132 mm SL, Central Atlantic, Azores, DMM IE/6627. Scale bar = 500 µm.

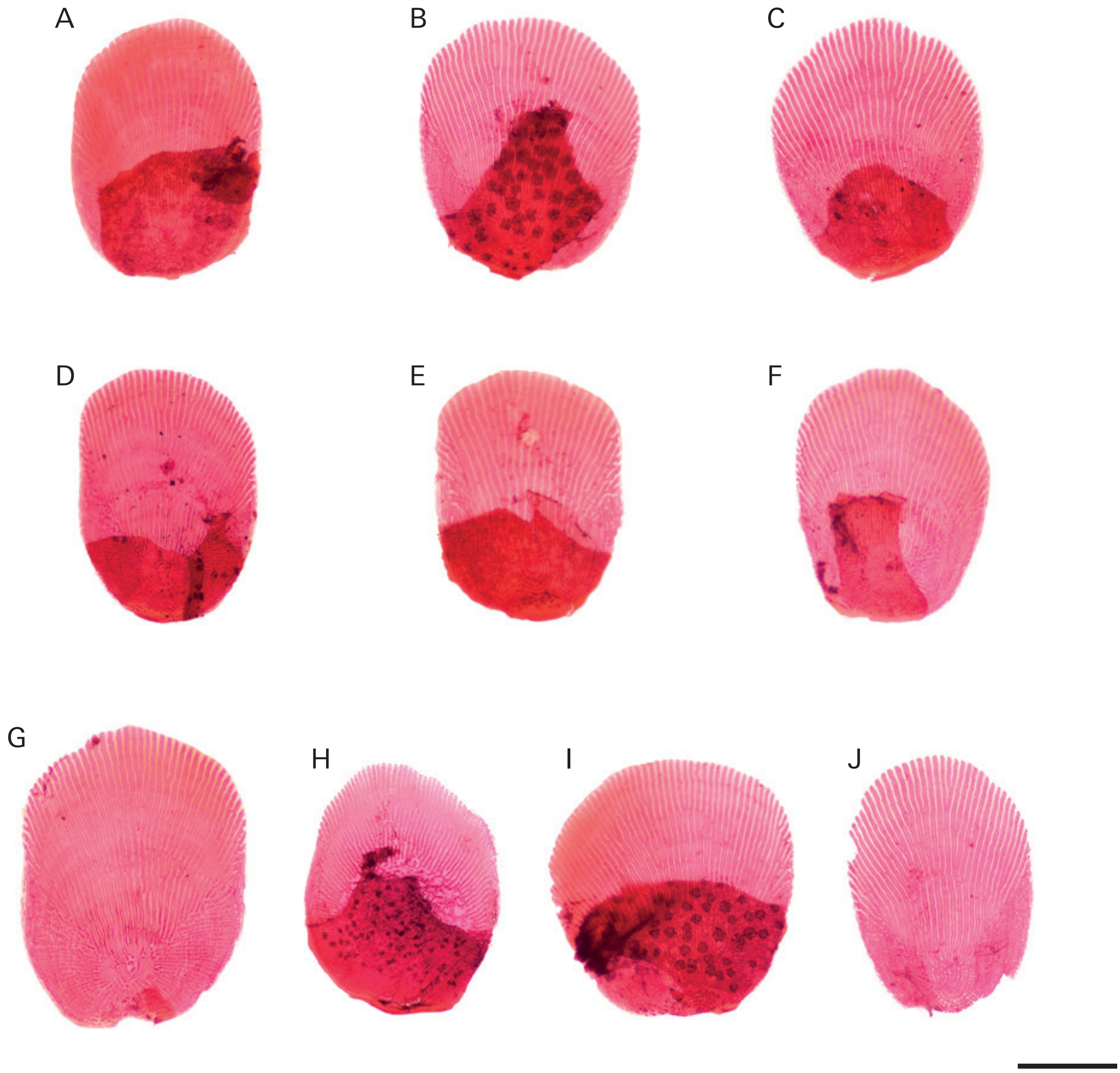

Fig. 87. *Bothus podas*, blind-side (right side); 132 mm SL, Central Atlantic, Azores, DMM IE/6627. Scale bar = 500 µm.

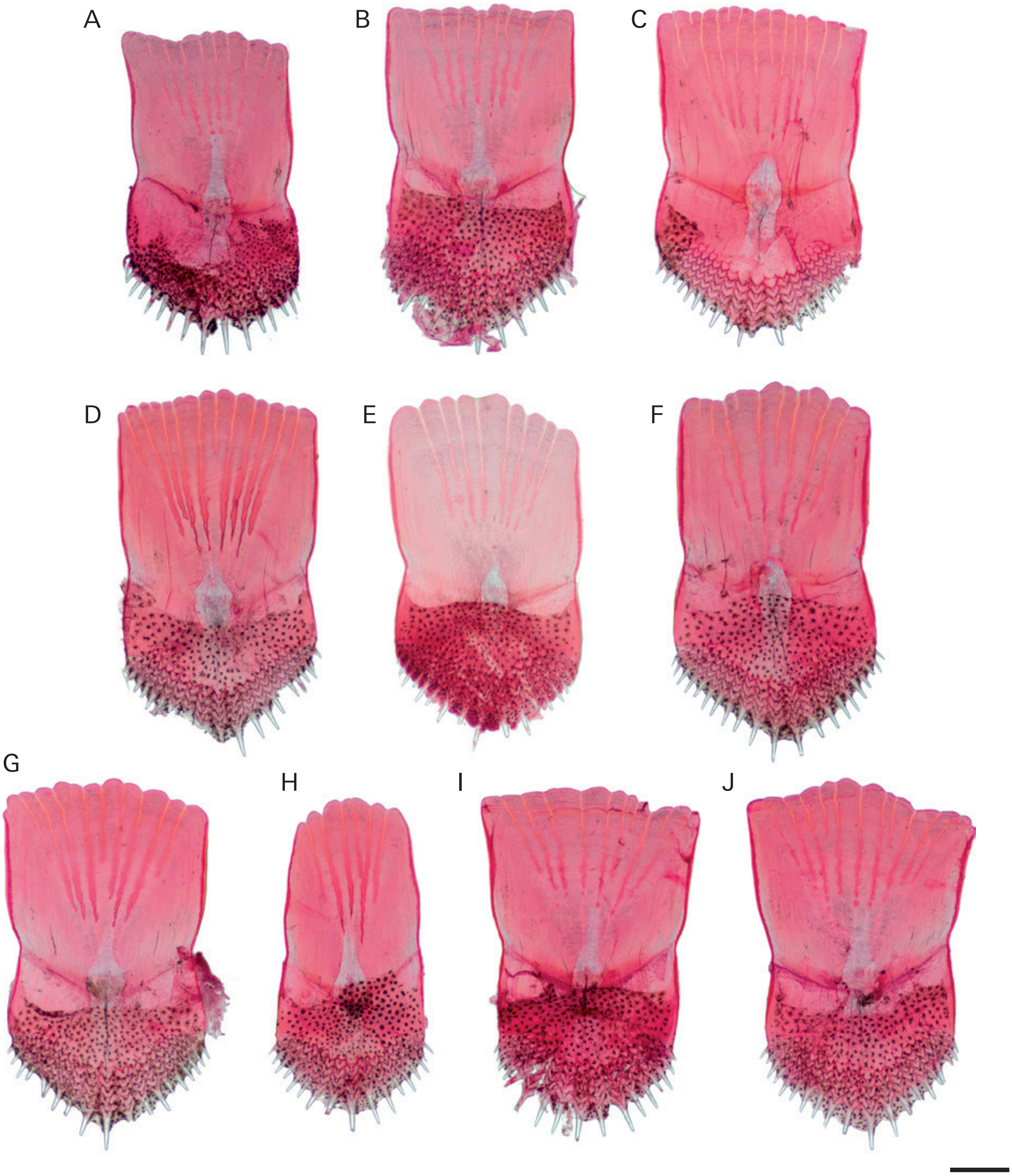

Fig. 88. *Microchirus variegatus*, ocular-side (right side); 129 mm SL, Costa Brava, Spain, DMM IE/5101. Scale bar = 500 µm.

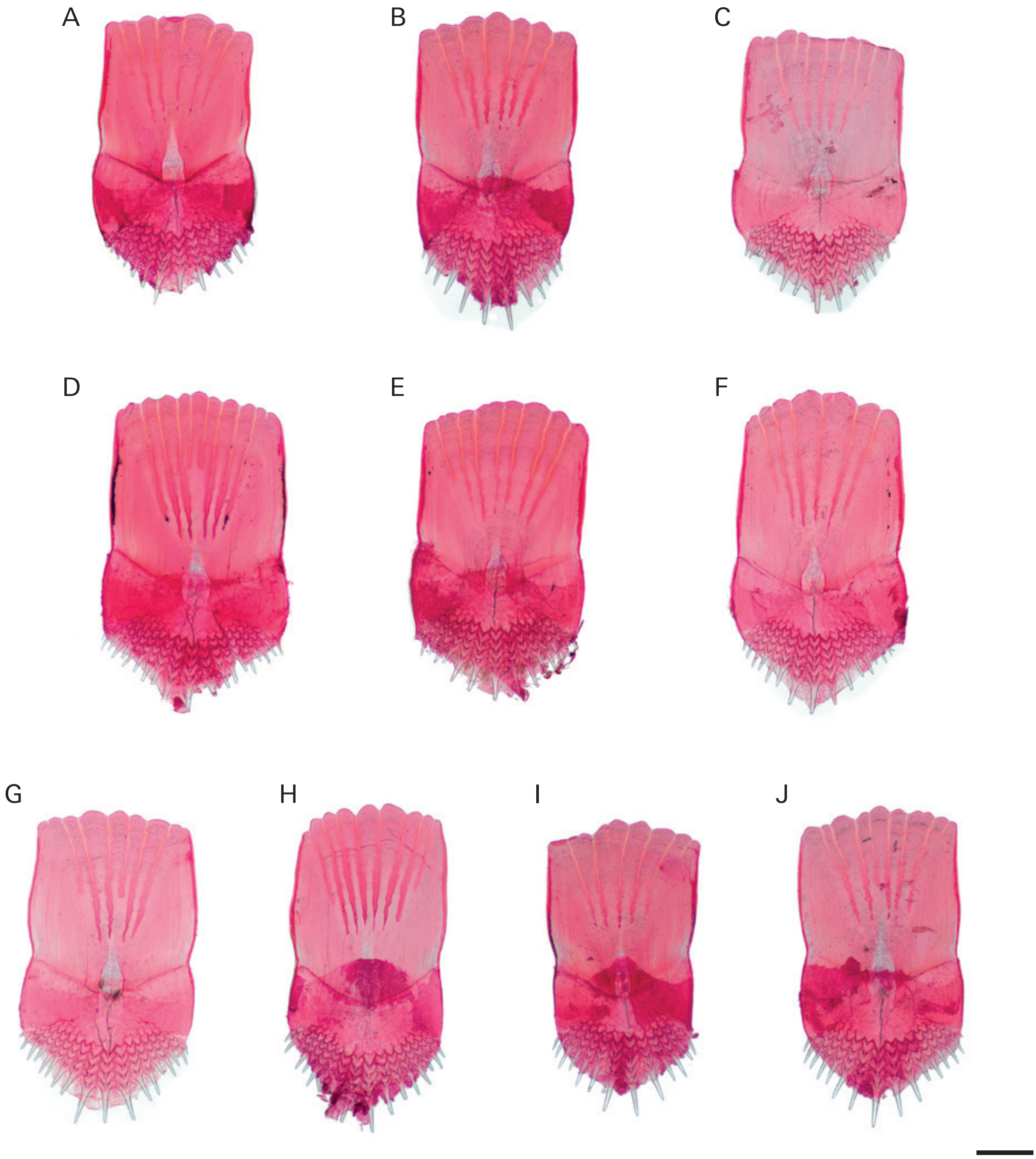

Fig. 89. *Microchirus variegatus*, blind-side (left side); 129 mm SL, Costa Brava, Spain, DMM IE/5101. Scale bar = 500 µm.

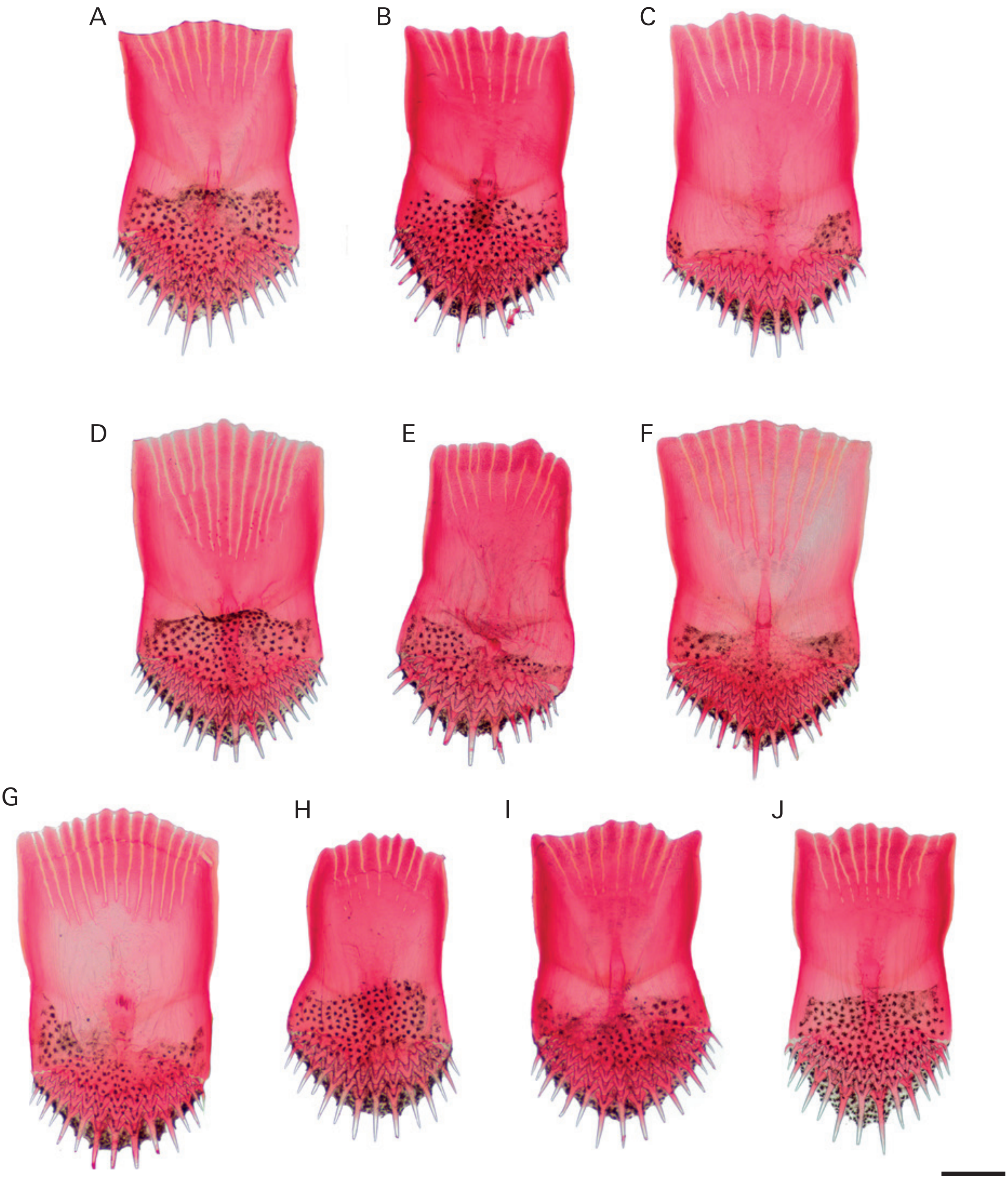

Fig. 90. *Monochirus hispidus*, ocular-side (right side); 104 mm SL, Costa Brava, Spain, DMM IE/4600. Scale bar = 500 µm.

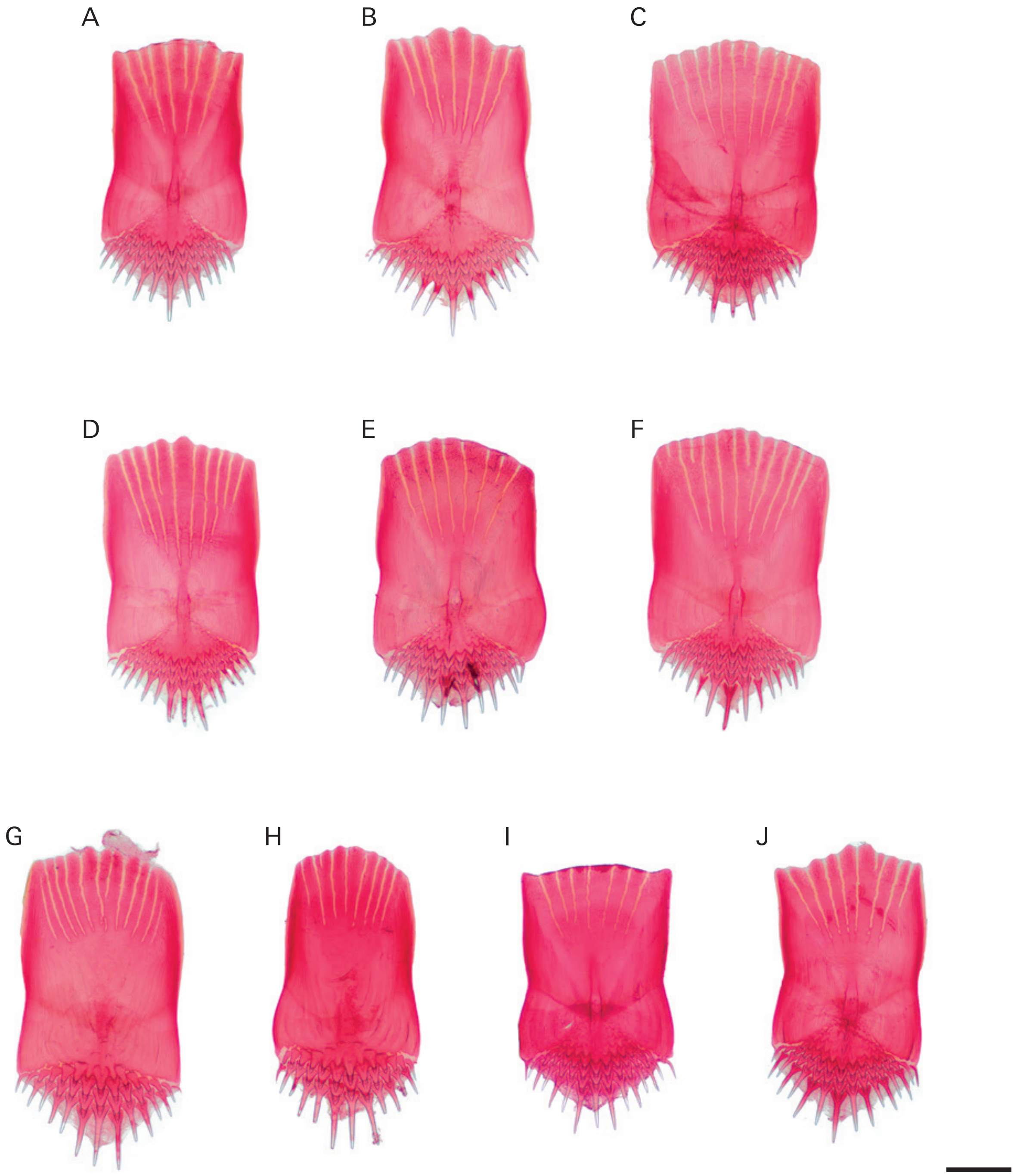

Fig. 91. *Monochirus hispidus*, blind-side (left side); 104 mm SL, Costa Brava, Spain, DMM IE/4600. Scale bar = 500 µm.

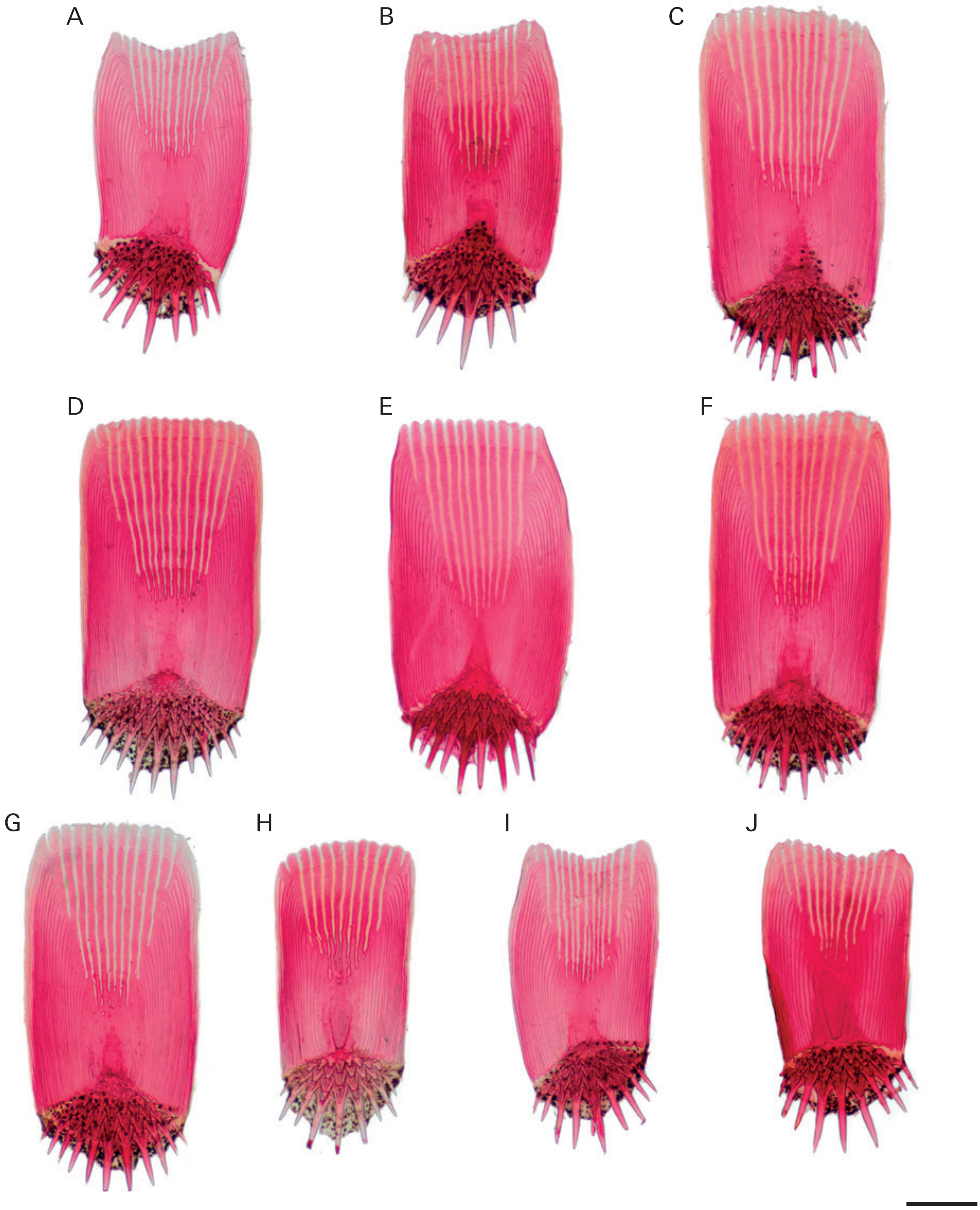

Fig. 92. *Solea solea*, ocular-side (right side); 187 mm SL, Elbe estuary, Germany, DMM IE/4782. Scale bar = 500 µm.

Fig. 93. *Solea solea*, blind-side (left side); 187 mm SL, Elbe estuary, Germany, DMM IE/4782. Scale bar = 500 µm.

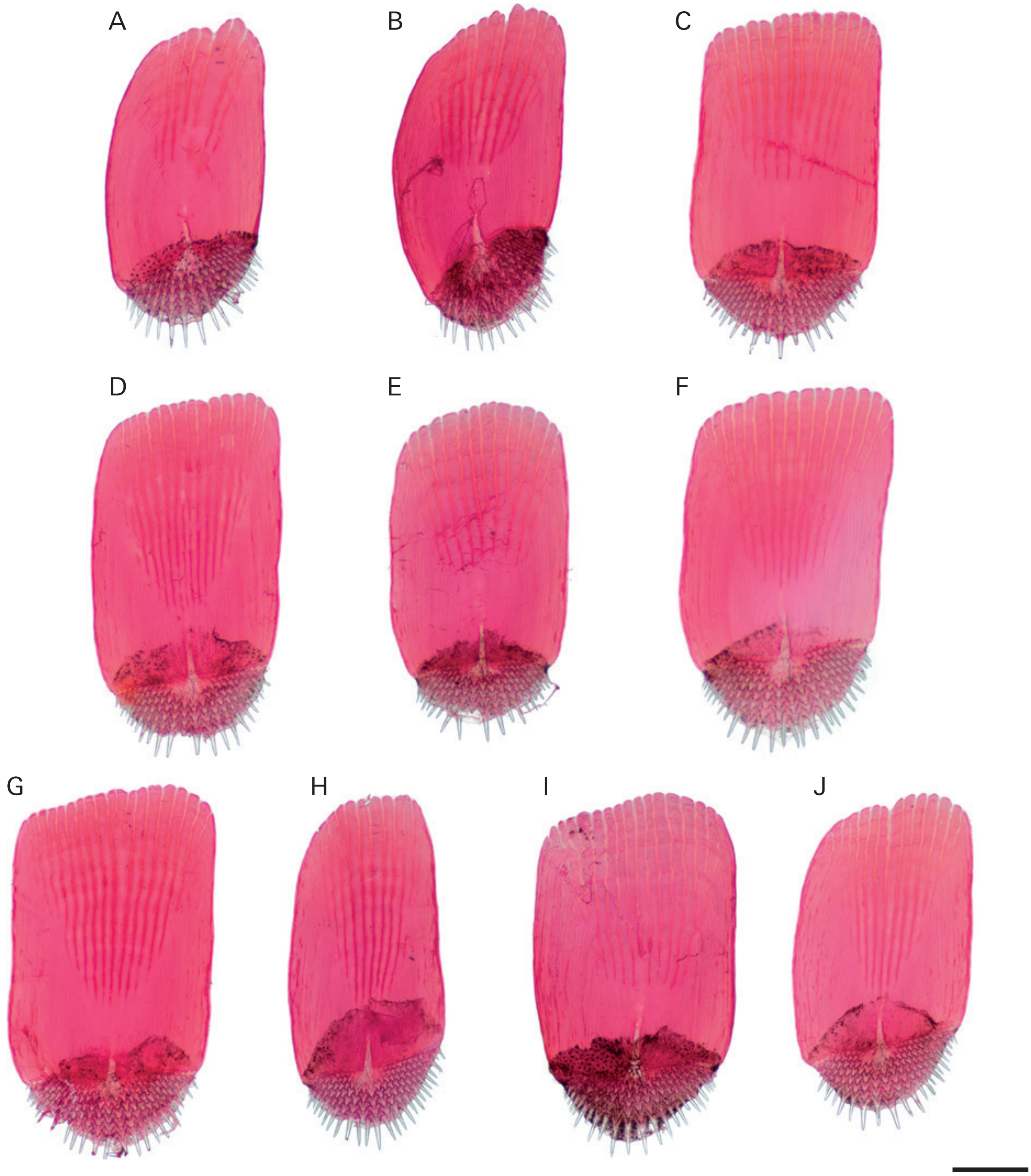

Fig. 94. *Symphurus nigrescens*, ocular-side (left side); 104 mm SL, Costa Brava, Spain, DMM IE/5100. Scale bar = 500 μm.

Fig. 95. *Symphurus nigrescens*, blind-side (right side); 104 mm SL, Costa Brava, Spain, DMM IE/5100. Scale bar = 500 µm.