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Squamation of *Tetragonurus cuvieri* Risso, 1810 (Stromateoidei, Tetragonuridae)

Die Beschuppung von *Tetragonurus cuvieri* Risso, 1810 (Stromateoidei, Tetragonuridae)

Martin Licht[1]* & Peter Bartsch[2]

[1]Tannenweg 6, D-32105 Bad Salzuflen, Germany, martinlicht1@arcor.de

[2]Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, D-10115 Berlin, Germany, Peter.Bartsch@mfn-berlin.de

Summary: The pelagic perciform fish *Tetragonurus cuvieri* and the other two species of the Tetragonuridae ("squaretails") display a striking structure of the integument and especially the squamation is of particular interest. The spinoid scales present a rhomboidal external surface and are arranged in oblique lines, thus superficially resembling a ganoid squamation. For teleost fishes this is unusual and the scales have frequently been referred to in the literature. But the structure of its integument, especially the squamation, has never been described in detail. Here we describe and distinguish three different types of scales in *T. cuvieri*. Type I scales are the main trunk scales and are mainly characterized by the first two spines of the middle ridges, which are always elongate and flattened. Furthermore, the anterior part of the scale forms a kind of lip which lies in grooves of the skin and constitutes the skeletal bottom of an antrum or pocket underneath the preceding scale. Type II scales cover the caudal fin peduncle, are folded and bear higher spines on the external surface. Type III scales are found between the rays of the caudal fin as well as pectoral and pelvic fins. They are very small and their flanks are turned upwards without spine rows in the middle area of the scale. We suggest that the squamation of these fishes might be connected with the specific prey, several tissues of jellyfish they ingest. Trunk scales form an antrum probably filled with mucus that may decontaminate the cnides of this prey.

Key words: Actinopterygii, Perciformes, spinoid scales, scale arrangement, integument

Zusammenfassung: Eines der auffälligsten äußeren Merkmale von *Tetragonurus cuvieri* und der anderen beiden Arten der Familie Tetragonuridae ist ihre Beschuppung. Die Spinoidschuppen besitzen in ihrer exponierten Fläche eine rhombische Form und sind in Reihen angeordnet, die oberflächlich an eine Ganoidbeschuppung erinnern. Eine solche Anordnung der Schuppen ist für Vertreter der Teleostei sehr ungewöhnlich und wurde daher schon einige Male in der Literatur erwähnt. Allerdings wurde die Beschuppung niemals im Detail beschrieben. Wir beschreiben und unterscheiden bei *T. cuvieri* drei Schuppentypen. Typ I bedeckt den größten Teil des Körpers und wird hauptsächlich durch die beiden ersten Stacheln der beiden mittleren Reihen charakterisiert, welche stets verlängert und abgeflacht sind. Des Weiteren bildet der vordere Teil der Schuppe eine Art Lippe und formt unter der davor liegenden Schuppe in einer Hautfalte den knöchernen Boden einer Höhle. Typ II bedeckt den Schwanzstiel, ist gefaltet und besitzt größere Stacheln auf der Oberfläche. Typ III ist zwischen den Flossenstrahlen der Schwanz-, Brust- und Bauchflossen zu finden. Dieser Schuppentyp ist sehr klein; seine Seiten sind nach oben gebogen. Ferner besitzt dieser Schuppentyp keine Stachelreihen in der Mitte. Wir vermuten, dass die Beschuppung etwas mit der speziellen Beute dieser Fische (Gewebe von Cnidariern) zu tun hat. Jeweils mehrere Schuppen (Typ I) bilden eine Höhle, die sehr wahrscheinlich mit Schleim gefüllt ist, der die Cniden der Beute unschädlich macht.

Schlüsselwörter: Actinopterygii, Perciformes, Spinoidschuppen, Schuppenanordnung, Integument

1. Introduction

Members of the family Tetragonuridae are pelagic perciform fishes and belong to the suborder Stromateoidei. The family includes one genus with three extant oceanic species (*Tetragonurus cuvieri* Risso, 1810; *Tetragonurus atlanticus* Lowe, 1839; *Tetragonurus pacificus* Abe, 1953). Members of the genus and family are common in all oceans around the world (e.g. Berg 1940, Grey 1955, Haedrich 1986a, b). *T. cuvieri* is the best known and most prevalent species in collections and has a worldwide distribution in subtropical to temperate waters of 15 °C to 20 °C surface water temperature. It is found in the Mediterranean Sea, Pacific Ocean and Atlantic Ocean (Fitch 1951, 1952, Smith 1952, 1953, Grey 1955, Ahlstrom et al. 1976).

Due to its worldwide distribution and due to the fact that *T. cuvieri* has been repeatedly caught during scientific voyages, this species is generally a little better known than the other two species of the Tetragonuridae (fig. 1 A). In this study we concentrate on this species, but well preserved material is rare. Some previous studies deal with aspects of morphology, but most studies focus on the general biology and distribution (e.g. Grey 1955, Ahlstrom et al. 1976, Haedrich 1986b, Psomadakis et al. 2006).

Indeed, the Tetragonuridae do have a very interesting and remarkable lifestyle frequently observed and plausibly inferred from catches. Grown specimens of *T. cuvieri* are mostly found near the surface during the night and down to the mesopelagic realm during the day (Lowe 1843-60, Smith 1953). At juvenile stage the fish lives in salps and feeds on them (Janssen & Harbison 1981). Older juvenile and adult individuals are often found closely associated with several genera of Scyphozoa and Ctenophora (e.g. Mansueti 1963, Horn 1985, Castro et al. 2002). The grown juveniles as well as the adults apparently feed on jellyfish tissues, because the stomach content shows that they exclusively prey on it (Fitch 1952, Grey 1955). Furthermore, *T. cuvieri* and the other two tetragonurid

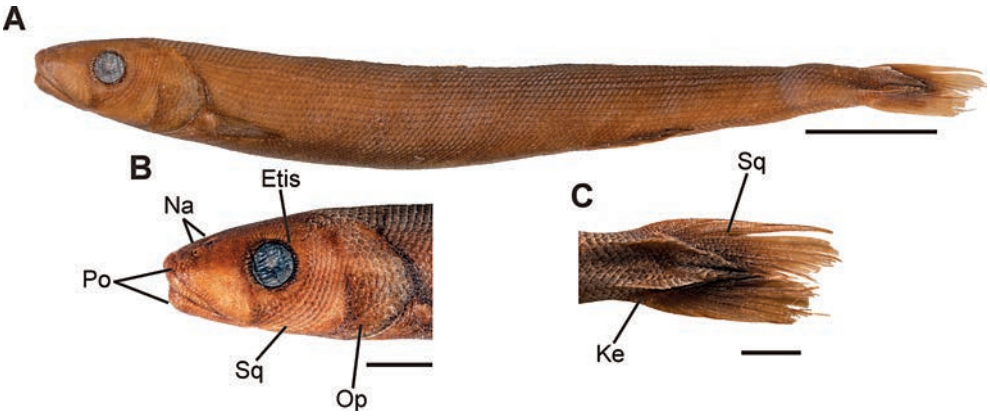


Fig. 1 A-C: A General shape of the body of *Tetragonurus cuvieri* (ZMB 33724) with the exceptional scale arrangement (scale bar 5 cm). **B** Magnification of the head to show the squamation of the opercular apparatus and cheek. Large numbers of pores of unknown function are visible on the lips and on the dorsal and lateral part of the head, between the nasal openings and the upper lip as well as around the eye. Around the eye a pronounced ridge of tissue is present. Scale bar 1 cm. **C** Detail of the peduncle and caudal fin to show the scales of the keels and the caudal fin. Scale bar 1 cm. Abbreviations see page 3.

Abb. 1 A-C: A Gesamtaufnahme von *Tetragonurus cuvieri* (ZMB 33724) mit der deutlichen Schuppenanordnung (Längenmaß 5 cm). **B** Vergrößerte Aufnahme des Kopfes, um die Beschuppung des Kiemendeckels und des Nackens zu zeigen. Eine große Anzahl von Poren mit unbekannter Funktion ist zwischen den Nasenöffnungen, der Oberlippe und um das Auge erkennbar. Längenmaß 1 cm. **C** Detailaufnahme der Kaudalflosse samt Flossenstiel mit ihrer Beschuppung. Längenmaß 1 cm. Abkürzungen siehe Seite 3.

species have large slicing teeth in the lower jaw and the general peculiar boxlike jaw seems to be optimally suited to prey on such a diet (Grey 1955, Haedrich 1967). Another morphological adaptation for such a diet is seen in the teeth of the pharyngeal sacs, which are a common character of all stromateoid fishes (Haedrich 1967).

The most striking external character of all extant and extinct *Tetragonurus* species are their rhomboid scales that superficially resemble a ganoid squamation by shape and general arrangement (e.g. Risso 1810, Cuvier & Valenciennes 1836, Mettenheimer 1854, Meunier & Saur 2007) (fig. 1 A). Cuvier & Valenciennes (1836), Mettenheimer (1854), Grey (1955), Ibanez (1975) and Meunier & Saur (2007) already described the shape as well as the mineralized and fibrous tissue components of the scales of *T. cuvieri*. The description of structure and arrangement, however, is not complete as differences in the scale anatomy of the trunk and fins appear to exist.

In the present study we supplement some histological data and characters of the scales and closely associated tissues and a description of different scale types and the topographical scale pattern and offer some speculations on their function.

2. Material and Methods

The scales of seven adult specimens of *Tetragonurus cuvieri* (ZMB 33655, 33724-33730) are studied and stored at the Museum für Naturkunde Berlin. The specimens were caught between August and September 1984 in the North Atlantic Ocean between 45.98° N, 15.78° W and 43.87° N, 26.97° W in 150 m down to 625 m depth, during an expedition of the Institut für Hochseefischerei Rostock with the ship RV Professor Siedlecki of the former German Democratic Republic. The size of the specimens ranges from 222 mm to 312 mm in standard length. The smallest specimen was treated by the clearing and staining method according to the protocol of Taylor & van Dyke (1985) for identification of scale types and topography of regional differentiation. Scales were sampled from the dorsal, middle and ventral part of the trunk and the pectoral fins, pelvic fins, and caudal fin of an adult specimen (ZMB 33655). Some trunk and caudal fin scales were cleaned and treated by ultrasound and sputtered with gold. A scanning electron microscope (SEM) of the type LEO 438 VP was used for inspection of the external structure of the mineralized scale investment. X-ray photos were produced with magnifying Feinfocus radiation-protected x-ray equipment at 25 kV and 6.5 seconds. Histological section series are based on paraffin embedded pieces of the integument close to the middle line. The scales with adjacent tissue of an adult individual were decalcified in 5 % nitric acid, were cut into 7 µm thick sections and stained according to the Heidenhain AZAN-protocol (Romeis 1968).

Abbreviations used in the figures: Ant = antrum; Ap = anterior part of the scale; De = dermis; Etis = pronounced tissue round the eye; Fs = flatted spine of the middle ridges; Fsv = flat spineless ventral area at the middle depression; Ke = keels; Mc = mucus cells; Myo = myomere; Na = nasal openings; Nl = lateral nerve; Op = opercular apparatus; Os = fin ray position overlapped by the scale side with higher number of spines; Po = pores; Pp = posterior part of the scale with spines; Sc = scale; Sp = spines of the scale arranged in ridges; Sq = squamation.

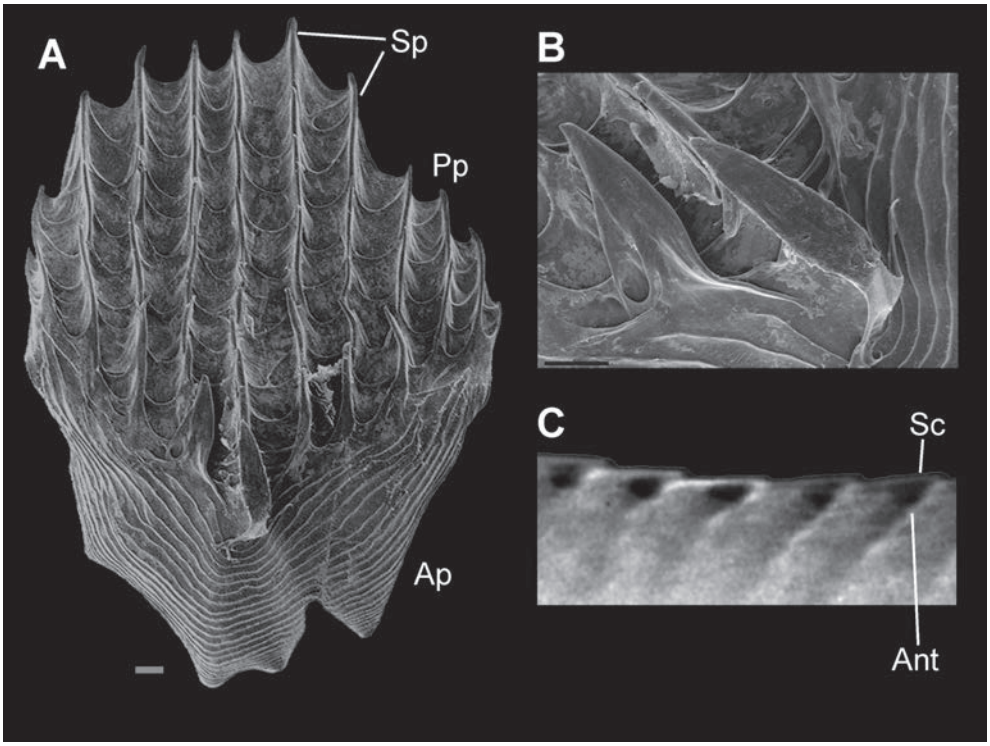
3. Results

Tetragonurus cuvieri shows a slender, elongate body with a complete squamation that reaches onto the fins, the cheek and frontal region of the head, well forward of the orbit (figs 1 A, B). A pronounced crest of connective tissue and underlain bony elements are present in ridges around the eye, especially at the posterior part (fig. 1 B). A double ridge is present on each side of the caudal peduncle which consists of unusually shaped scales (figs 1 A, C). Altogether three types of scales can be distinguished.

Type I is the trunk scale. Scales are arranged mostly in helical rows from ventrocranially to dorsocaudally (fig. 1 A). As usual for teleosts

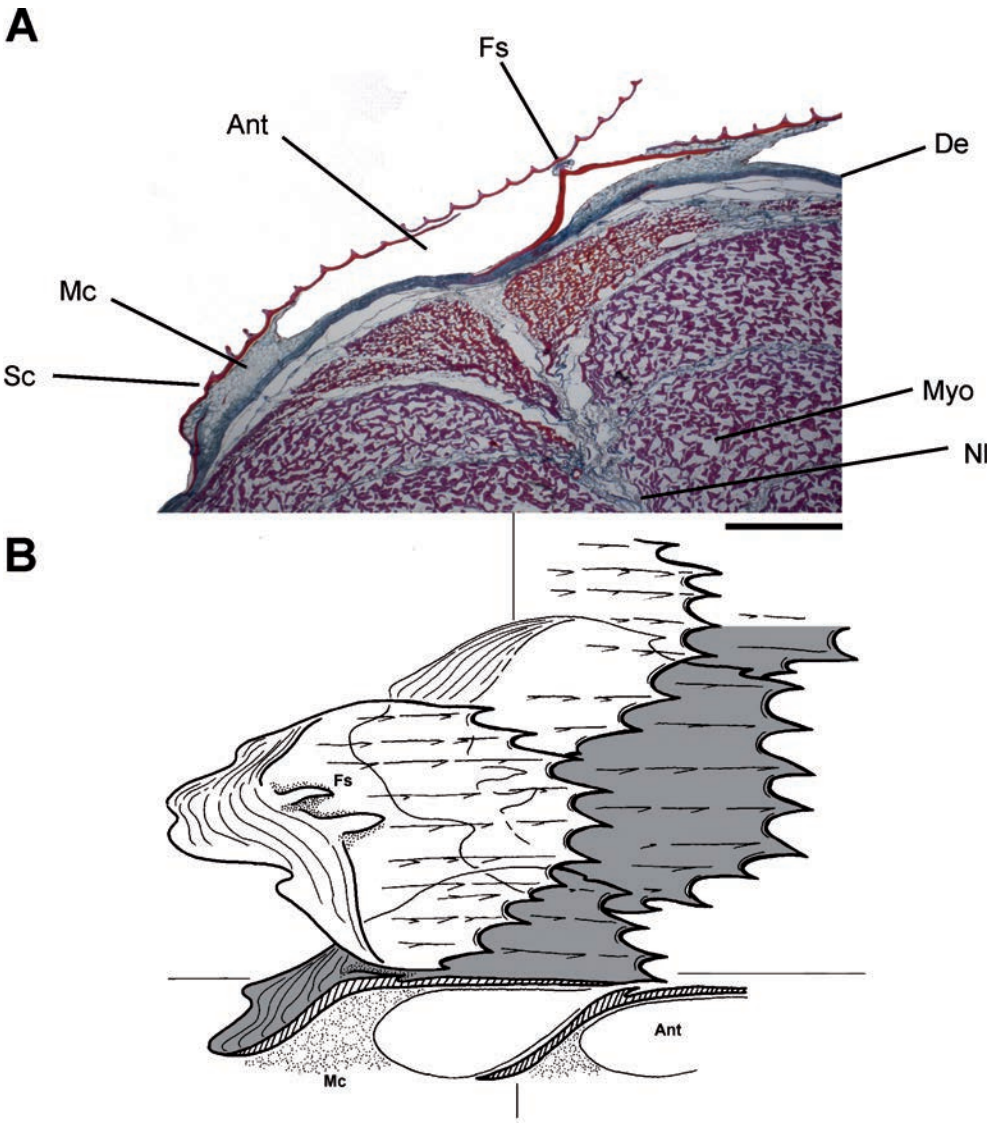
each scale overlaps the (caudally) following one (figs 1, 3). However, in some body regions and depending on individual variability reversions of this pattern to a dorsocranial-ventrocaudal direction may occur. About two-thirds of the scale surface are covered with bony spines (fig. 2 A). The spines are directed backwards and form a lengthwise oriented series of ridges or keels. The number of those ridges (about nine to twelve) and spines (about four to eleven) differs depending on body region and size of the specimen. The first two spines of the middle ridges are always elongate and flattened (figs 2 A, B, 3). These spines mark the area, where the anterior scale is in touch with the posterior one (figs 2 C, 3). Neighbouring spinous ridges are separated by depressions that form continuous grooves also oriented lengthwise. These show a wavy bottom or low ridges interconnecting two neighboring spines (fig. 2 A).

The anterior part of the scale forms a kind of lip which lies in grooves of the skin and constitutes the skeletal bottom of an antrum or pocket underneath the preceding scale (figs 2 C, 3). In horizontal or transverse section, the dermis forms tubercles or hillocks out of mucus cells where the scales are pegged (figs 2 C, 3). This arrangement minimizes the area, where the posterior part of the scale has direct contact with the skin. This arrangement also brings the spinous surface area of the scale outward and thus produces the antrum underneath. The



Figs 2 A-C: A Scanning electronic microscopic picture of a trunk scale (type I) of an adult specimen of *Tetragonurus cuvieri* (ZMB 33655). Scale bar 100 µm. **B** Magnification of the first two spines of the middle ridges from the same scale, which are elongate and flattened. Scale bar 100 µm. **C** X-ray photo of the arrangement of the trunk scales in *T. cuvieri* (ZMB 33655). Abbreviations see page 3.

Abb. 2 A-C: A Elektronenmikroskopische Aufnahme einer Körperschuppe (Typ I) eines adulten Individuums (ZMB 33655). Längenmaß 100 µm. **B** Vergrößerte Aufnahme der beiden ersten Stachel der mittleren Stachelreihen. Diese beiden Stachel sind verlängert und abgeflacht. Längenmaß 100 µm. **C** Röntgenaufnahme von *T. cuvieri* (ZMB 33655), die die Anordnung der Schuppen in der Haut zeigt. Abkürzungen siehe Seite 3.



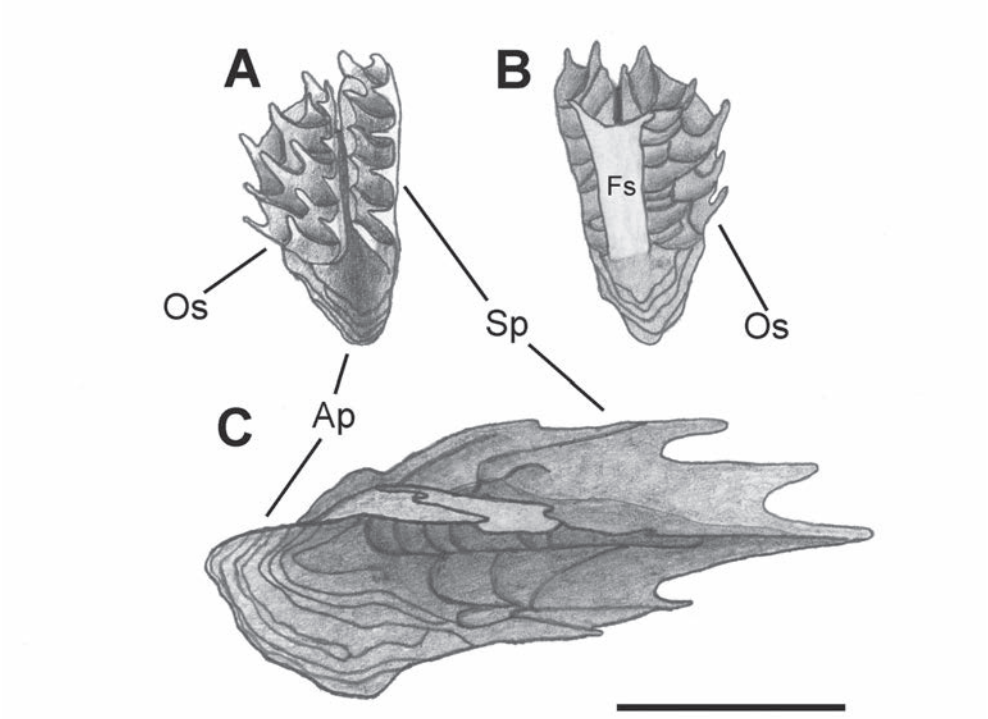
Figs 3 A-B: A Histological transverse sections through the scales with the underlying dermis of *Tetragonurus cuvieri* (ZMB 33655). Scale bar 1 mm. **B** Simplified schematic drawing of 3A without underlaying muscle tissue but with lateral overlapping scales. Drawing not scaled with 3A. Abbreviations see page 3.
Abb. 3 A-B: A Histologischer Schnitt durch die Schuppen mit unterliegenden Gewebsschichten von *Tetragonurus cuvieri* (ZMB 33655). Längenmaß 1 mm. **B** Vereinfachte schematische Zeichnung von 3A ohne unterliegende Muskelschichten, aber mit lateral überlappende Schuppen. Die Zeichnung entspricht nicht der Vergrößerung von 3A. Abkürzungen siehe Seite 3.

hillocks by themselves consist mostly of mucus cells which fill the antrum with mucus (fig. 3). There is no thick protective mucus layer on top of the exposed scale area preserved and it cannot be stated here, if such a layer is also missing in life specimens. But if such a mucus layer is also missing in life specimen, here the anterior overlies the posterior scale with the mucus cells sandwiched in between. The scales of the head also belong to the very similar

trunk scale type. This scale type is found on the opercle and preopercle region where it is arranged in semicircular rows and in the front and neck region where it forms transverse rows (fig. 1 B).

Type II are the scales of the keels at the caudal fin peduncle. These scales are folded, arranged in arched longitudinal rows and bear higher spines on the external surface, thus forming a crest (figs 1 C, 4 C). The keels are drawn out towards the middle of the caudal fin between the lobes. These keels are underlain by soft connective cushion tissue and mucus pouches.

Type III scales are positioned between the rays of the caudal fin as well as pectoral and pelvic fins at least reaching to two thirds of the extension of the fin-fold (figs 1 C, 4 A, B). There are no such scales visible on the dorsal or anal fin, which might also be due to the bad state of preservation of the interradial fin web and delicate, easily shed scale cover of the fins. At the level of the first, spinous part of the dorsal fin, *T. cuvieri* shows paired middle ridges forming a groove in which this fin is completely retracted in depressed state. The fin scales are very small, about half the size of the trunk scales and have four to six spine rows (figs 1 C, 4 A, B). The flanks of these scales are turned upwards without spine rows in the middle area of the scale. Thus the marginal spine rows are separated by a flat spineless area of the middle depression of the scale (figs 4 A, B). The inner series of spines of both margins is directed upwards and inwards but do not connect. This flat middle area is extended anteriorly and forms the connecting point between two consecutive



Figs 4 A-C: Detailed drawings of the fin scales and peduncle keel scales. **A** Dorsal view of a scale from the caudal fin of *Tetragonurus cuvieri* (ZMB A06333). **B** Same scale in ventral view. **C** Scale of the peduncle keel of the same specimen in ventro-lateral view. Scale bar 1 cm. Abbreviations see page 3.

Abb. 4 A-C: Zeichnungen der Flossenschuppen und des Schwanzflossenstiels. **A** Dorsalansicht einer Schuppe von der Schwanzflosse von *Tetragonurus cuvieri* (ZMB A06333). **B** Ventralansicht der gleichen Schuppe. **C** Schuppe vom Schwanzstiel desselben Individuums in ventro-lateral Ansicht. Längenmaß 1 cm. Abkürzungen siehe Seite 3.

scales. The anterior, spineless part of the fin scales is directed forward and fits into the clearance underneath the anterior scale. In this way the scales are arranged in one row covering the fin web tissue. One side of these scales is more expanded than the other side and overlaps a neighboring fin ray. The side which overlaps the neighboring fin rays shows some variation depending on its position on the caudal fin. On the dorsal lobe it is the lower part and on the ventral lobe it is the upper side. On the pectoral and pelvic fins it is the proximal side of a scale, oriented towards the body, which is expanded and overlaps the neighboring fin ray.

4. Discussion

The structure and arrangement of scales in *Tetragonurus cuvieri* is very unusual in several respects. Usually, scales are arranged like tiles and lie in scale pockets rather flat on the dermis, surrounded by the epidermis and several consecutive scales overlapping (e.g. Hase 1907, 1911, Rosén 1915a, b, Whitear 1986), thus doubling or multiplying thickness of squamation or bony layers of the integument while maintaining flexibility at the same time. In *T. cuvieri* the scales are not really arranged like tiles flat on the dermis and the integument is considerably thickened by an antrum under the posterior part of the scale.

Exoskeletal elements, like scales, are to protect the individual against external influences, as poisonous cnides of jellyfishes, which are the favorite prey of *T. cuvieri*. The squamation of *T. cuvieri* possibly provides mechanical protection to certain soft tissues, i.e. musculature, vascular system, fin rays and innervation of the trunk in two ways. First, the contact between the scales and the underlying soft tissue is minimized and second, the scales form an antrum which is probably filled with mucus by large epidermal mucus cells. Another possible consequence of this unusual combination of scale arrangement and mucus cell concentration is that cnides of the prey, which get stuck in the mucous mass, can be decontaminated with the extruded mucus when the antrum is open, while the body curves convex during swimming movements. The scales are well movable against each other, despite the spines because the first two elongate and flatted spines of the middle ridges form a sliding support. The next scale in front lies on them and is able to slide forward and backward to a certain degree during flexion.

The fin scales are perfectly aligned and form a kind of plating with their shoehorn like connection and broadening at the side which overlies the neighboring fin ray. It can be assumed that they protect the tissue between the fin rays. The shoehorn like connection ensures that the underlying tissue is protected by doubling the thickness of the scale as for the hillocks at the trunk.

Admittedly, these are still speculations, but we think that the unusual structure and arrangement of the scales in *T. cuvieri* primarily is connected with the feeding biology of this fish and its intimate association with gelatinous macroplancton. The type of this association, however, is not really well defined by observations or experiments. The type of life-style seems risky, since fishes of that size range do belong to the usual prey of some cnidarian medusa or are at least subject to stunning or infliction of severe and lethal wounds. However, there is still nothing known about the traumatogenic effect of poisonous cnides on the tissues of *T. cuvieri* and whether there are kinds of chemical immunity or protective inhibitor substances involved in this species.

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