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Source: Copeia, 2004(2):391-396.
Published By: The American Society of Ichthyologists and Herpetologists
https://doi.org/10.1643/CG-03-126R2
URL: http://www.bioone.org/doi/full/10.1643/CG-03-126R2

Copeia, 2004(2), pp. 391–396

Ontogeny of Squamation in Swordfish, *Xiphias gladius*

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Spinoid scales appear early in the development of Swordfish, *Xiphias gladius*, and are first discernable in the larval stage. Scales vary in form between two principal types: small single and multispined scales and large multispined scales. Unlike the typical teleostean condition, *Xiphias* scales are attached along their base, not at their proximal end within scale pockets. Scales persist in juveniles and adults, that is, scales are not shed or resorbed. Scales become more deeply embedded within the dermis as the dermis thickens in ontogeny; consequently only the tips of spines protrude through the dermis of adults. A network of mucous canals with regularly spaced pores to the exterior develop in the dermis of adults, and the mucus produced further insulates scales from the surface of the integument. The ontogeny of the squamation of *Xiphias* differs from that of the related Istiophoridae.

XIPHIAS larvae are heavily armored with scales (Potthoff and Kelley, 1982). These scales have been thought to diminish (Collette et al., 1984; Webb, 1999) or disappear completely (Nakamura et al., 1951; Ovchinnikov, 1970; Nakamura, 1985) in adults. The purpose of this paper is to trace the ontogeny of scales in *Xiphias* and to determine whether scales disappear completely, decrease in size through resorption, or become buried under the epidermis or within the dermis.

The appearance of scales on and in the skin of fishes typically marks the beginning of metamorphosis or transformation (sensu Kendall et al., 1984; Fuiman et al., 1998). Some fish species, most notably the Scombroid fishes, are exceptions; scales appear on larvae well before metamorphosis and transformation (Webb, 1999). Whether scales appear early or late in development, squamation typically proceeds on the flanks in a posterior to anterior direction, then dorsally and ventrally (Helfman et al., 1997). Scales typically persist throughout juvenile and adult life and are regenerated if lost (Helfman et al., 1997).

The Billfishes, Istiophoridae, and *Xiphias* exhibit a peculiar condition. Not only do scales appear early in larval development, but the process of squamation, and the size and form of the scales, are exceptional. Scales on the larvae of Istiophorids and *Xiphias* have conspicuous and protrusive spines (Ovchinnikov, 1970). Spines on the scales of *Xiphias* are exaggerated, and on some scales, spines become multiple, as larvae and juveniles grow (Arata, 1954; Yabe et al., 1959). The ontogeny of squamation in *Xiphias* differs from that of the Billfishes (Istiophoridae). The scales of *Xiphias* are present in larvae, whereas the scales of the Billfishes develop later in their life history and remain conspicuous with their spines fully protrusive (Voss, 1953; Ovchinnikov, 1970; Nakamura, 1985; also present obs.).

Potthoff and Kelley (1982) characterized the gross morphology of scale development as follows. Scales first appear on the abdomen of larval *Xiphias* at ~6 mm standard length (SL). Thereafter, large scales with a single spine increase in number anteriorly and posteriorly in a row along the abdomen and ventral margin. By ~7 mm SL, another row of large single-spined scales forms on the dorsum and extends anteriorly and posteriorly. In addition, small, single-spined scales arise along the lateral flanks above the abdomen and extend anteriorly and posteriorly. At ~10 mm SL, large single-spined scales appear on the rostrum. Concomitantly, the large dorsal and ventral row scales begin to develop additional spines. Rostral and row scales begin to add spines at ~17 mm SL. Also at ~17 mm SL, two rows of single-spined scales of intermediate size arise along the lateral flanks of larvae, beginning above the abdomen and extending anteriorly and posteriorly. Scattered small scales on the flank remain single spined until ~48 mm SL and develop additional spines thereafter.

Xiphias as long as 192 mm total length have scales of varying size and spine number, some with as many as six spines (Arata, 1954). Rostral scales appear to diminish by ~48 mm SL and disappear by ~270 mm SL (Potthoff and Kelley, 1982). *Xiphias* retain many larval characters including the spinous row and rostral scales until they are at least 188 mm SL, which influenced Govoni et al. (2003) to refer to fish of this length as larvae and not juveniles.

Thus, there is some confusion about whether these scales become smaller or are replaced by a single scale type in adults and much confusion about the disappearance of scales altogether. *Xiphias* develop two types of scales as larvae and juveniles: large, multispined row and rostral scales; and small single-spined scales (Potthoff and Kelley, 1982). Scales are evident on the flanks of fish as large as ~700 mm in length (the measure of length was not reported [Collette, 2002]).

Materials and Methods

Specimens of larvae ranged from 4.8 to 180 mm SL; juveniles from 22 to 116.8 cm SL; and adults from 160 to 330 cm SL. Specimens and biopsies were obtained from various sources. Most specimens of larval *Xiphias* were obtained from plankton and neuston collections taken from the western North Atlantic ([recorded in Govoni et al. [2000]). An additional specimen was obtained from the University of Miami, Rosenstiel School of Marine and Atmospheric Sciences (RSMAS). A juvenile (MCZ 42155) was examined whole at the Museum of Comparative Zoology. A biopsy of the integument of a juvenile was obtained from fish collected in the central Pacific (taken from the stomach of a dolphinfish [*Coryphaena hippurus*] collected off the Hawaiian archipelago by the National Marine Fisheries Service (NMFS), Honolulu Laboratory and one housed at the U.S. National Museum [USNM 287996]). Biopsies of the integument of adult *Xiphias* were obtained from fish caught by commercial long-line fisheries off Australia, off New England (biopsied at the Fulton Fish Market, New York, and the Boston Fish Pier, Massachusetts), and in the Mediterranean (biopsied upon landing in Israel from local long-line fishers). A biopsy of an additional specimen was taken directly from a fish caught on long-line in the southeastern Atlantic (07°55′S/021°20′W). Because specimens were obtained from various sources and measurements taken for various body dimensions, standard lengths were approximated with the proportions given by Arata (1954).

Whole larvae, and some biopsies of juvenile and adult integument, were processed for histology with standard techniques. Some larval specimens were fixed in 95% ethanol and some in 10% neutral, phosphate buffered formalin (10% NBF). Ethanol fixed larvae were postfixed in 10% NBF. Larval specimens were decalcified in 14% EDTA (140 gm disodium ethylenediamine tetra-acetate plus 13 gm sodium hydroxide/1L deionized water) for 24 h. Biopsies from juvenile and adult fish were decalcified similarly, but for 48 h before processing for histology. Sections were cut at 5 μm and stained with hematoxylin and eosin Y (Luna, 1968). Scale dimensions were measured on histological sections through the apparent medial plane. Biopsies of the integument of the two juveniles and two adults from the Mediterranean were cleared and stained in whole mount for chondromucin and calcium with methods described by Potthoff (1984).

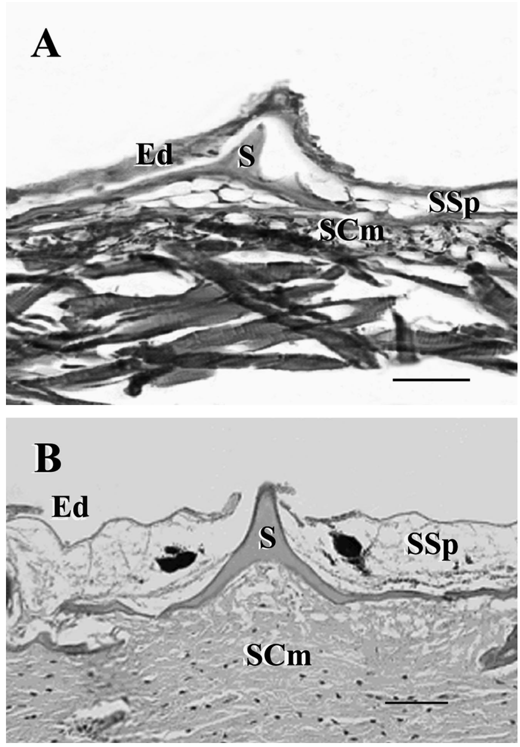

Fig. 1. Photomicrographs of the integument and scales of *Xiphias gladius.* (A) The integument with scale (S), epidermis (Ed), and dermis with stratum spongiosum (SSp), stratum compactum (SCm) of a 22.2 mm SL larvae (scale bar = 63 μm). (B) The integument of a ~330 cm SL adult (scale bar = 45 μm).

Results

The integument of *Xiphias* comprises of an external cuticle (sensu Groman, 1982), epidermis and a dermis (Fig. 1). Stratified squamous epithelium, with taste buds and mucous cells scattered on the peripheral surface, compose the epidermis. A basement membrane complex between the epidermis and dermis was not observed, probably because most sections were taken from the lateral flanks where developing scales consequently obscured this membrane (sensu Bullock and Roberts, 1974).

The dermis is divided into two strata, an outer layer, the stratum spongiosum, and an inner layer, the stratum compactum. A network of collagen fibers and an array of scales with osteoblasts compose the stratum spongiosum. A dense layer of collagen bundles and fibroblasts, which is the only cellular component of this layer, compose the stratum compactum. The stratum compactum rests on the hypodermis, which consists of a wide layer of adipose tissue, with bundles of striated muscle interspersed. *Xiphias* exhibit a condition that is typical of most teleosts; melanophores occur throughout the stratum spongiosum and the hypodermis. The network of mucous canals, described by Ovchinnikov (1970) for Istiophorids and suggested for *Xiphias*, become apparent in adults and open through pores either directly through the epidermis to the exterior or through adult scales.

The thickness of the epidermis and the dermis, increases as *Xiphias* grow. The epidermis of larvae is 2.5 μm thick with two cell layers. The number of cell layers increase and the epidermis thickens as larvae grow. The number of cell layers and epidermal thickness is variable in adults depending upon the region of the body. The stratum spongiosum of the dermis is present in young larvae (4.8 mm SL), but the stratum compactum does not develop until larvae are > 20 mm SL. The stratum spongiosum and stratum compactum thicken as larvae grow in greater proportion than does the epidermis. The thickness of the dermis as a whole increases curvilinearly (regression equation: dermis thickness = (13.05)(standard length$^{0.52}$); R^2 = 0.8578).

Scales of *Xiphias* are highly modified; larval, juvenile, and adult scales conform best with the description of Type 4 spinoid scales within the classification of Roberts (1993). Scales are not rooted in scale pockets (sensu Groman, 1982) within the dermis, the typical condition in fishes. Rather than having attachment at the proximal end within scale pockets, *Xiphias* scales are closely applied along their base to the dermis (Fig. 1). Scales persist in adults but become deeper in the dermis as the stratum spongiosum increases in thickness above the scale (Fig. 1). Scales do not recede; the thickness of the dermis above the basal attachment increases. The result is that scales remain only partially protuberant in adults. In most fishes, scales emerge through the dermis obliquely, but in *Xiphias*, the scale base does not emerge and is parallel to the plane of the dermis; scale spines emerge perpendicular to the base of the scale with the crown curving caudad (Fig. 2). Scales of larvae, juveniles, and adults interdigitate, although some overlap along their margins (Fig. 2). The mode of attachment of overlapping margins remains the same as it is with interdigitating

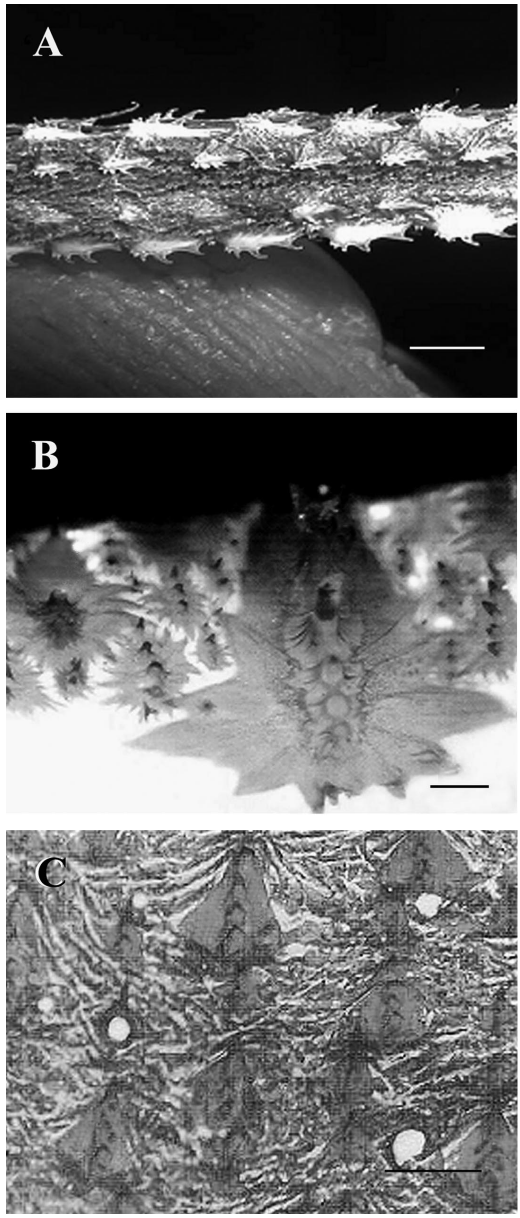

Fig. 2. Gross morphology of the scales of *Xiphias gladius*. (A) Photograph of the ventral aspect of a preserved larvae 114 mm SL (scale bar = 1.5 mm). (B) Photograph of a cleared and stained biopsy of the lateral flank of a ~150 mm SL larvae (scale bar = 0.3 mm). (C) Photograph of a cleared and stained biopsy of the lateral flank of a ~102 cm SL juvenile (scale bar = 0.6 mm).

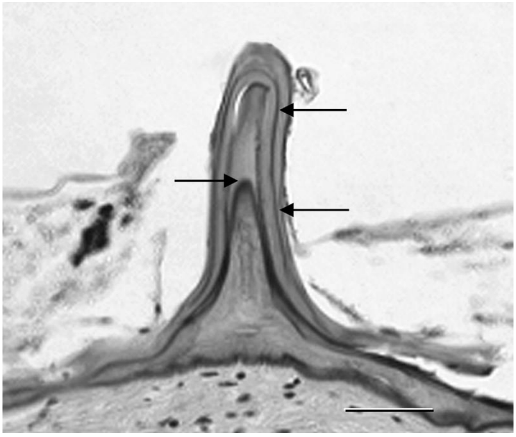

Fig. 3. Photomicrograph of a scale of a ~330 cm SL adult *Xiphias gladius* with growth increments (arrows) (scale bar = 27 μm).

scales. Scales of juveniles and adults appear in rows; both small single and multispined scales and large multispined scales are interspersed within rows (Fig. 2).

Scales grow after formation and are not replaced by an adult form. Scales measured on histological sections exhibited an increase in their base width, as well as their spine height, with larval growth until fish reach ~22.0 cm SL. The average scale-base width and spine height decreased in fish > 22.0 cm SL, because the range of the size of scales, and the number of spines and height of spines increased and became highly variable on juveniles and adults (Fig. 2).

Xiphias scales grow and are not resorbed. Numerous osteoblasts along the basal attachment of scales indicate scale growth. There is no evidence of wide-scale osteoclasis along the base of scales (sensu Bigler, 1989; Persson et al., 1999). Osteoclasts were scattered in the dermis but not aggregated in proximity of scale attachment. In addition, adult scales have layers, probably the manifestation of incremental, annually periodic scale growth (Fig. 3). The age of *Xiphias* has been determined from layers on fin spines and otoliths (Ehrhardt, 1992; Megalofonou et al., 1995; Govoni et al., 2003) but not on scales. *Xiphias* acquire adult squamation, rows of scales of variable size, and spine height, in the interval between ~100 and 200 mm SL, an interval within which *Xiphias* loose other larval characters: cranial spines, spinoid scales on the rostrum, and extended lower jaw (Govoni et al., 2003).

Discussion

The scales of *Xiphias* are unusual in their formation, form, and mode of attachment; different from typical teleostean ctenoid and cycloid scales. Scales form in larvae (Potthoff and Kelley, 1982), persist in adults as a highly modified spinous type (Roberts, 1993), and are attached not at the proximal margin within scale pockets (Groman, 1982) but along the base. The confusion in the literature about the presence or absence of scales on adult *Xiphias* owes to the thickening of the dermis above the scale as larval and juvenile *Xiphias* grow. The result is that only the tips of the scale spines protrude in adults. Scales are often fractured and abraded when fish are caught and processed by the fishery. The cuticular layer of the integument is also covered with a thick layer of mucus, secreted by a network of mucous canals within the epidermis. This mucus lubricates the integument and renders scale spines less conspicuous. More complex adult scales do not replace scales of larval *Xiphias*. Scales may be replaced if lost, but they apparently are not deciduous as suggested by Nakamura et al. (1951); no scales appeared on the surface of the epidermis where they might be sloughed off (Roberts et al., 1971, 1973).

Scales do not become reduced in size by resorption. Most evidence for partial resorption of scales indicates that resorption typically occurs at the focus of the scale (Schoenboerner, 1981), not at the periphery although Payne (1976) suggests that peripheral resorption may play a role in annulus formation. Scale resorption in fishes is typically associated with calcium demand owing to physiological stress (Persson et al., 1995) or reproduction (Ouchi et al., 1972; Mugiya and Watabe, 1977; Persson et al., 1997) not with scale replacement. There was no evidence of wide spread osteoclasis anywhere along the basal attachment of scales in *Xiphias*.

Acknowledgments

We thank T. Capo and R. Humphreys for donating specimens; S. Goldhor for procuring biopsies; L. Willis for processing some biopsies as whole mounts, O. Sonin, O. Goffman, and D. Barak for providing whole fish from the Mediterranean fishery and J. Regenstein for examining specimens landed by the New England fishery. We thank J. Hare, J. Merriner, M. Prager, W. Richards, and D. Johnson for their reviews of the manuscript.

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