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A Morphological Study of the Pharyngeal Sac of Two Species of Stromateid Fishes: Perrilus triacanthus and P paru

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A Morphological Study of the Pharyngeal Sac of Two Species of Stromateid Fishes, *Peprilus triacanthus* and *P. paru*

A Thesis

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by

Thomas R. Sminkey

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This thesis is submitted in partial fulfillment of

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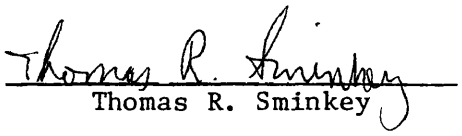

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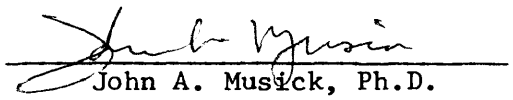

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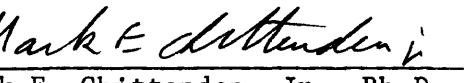

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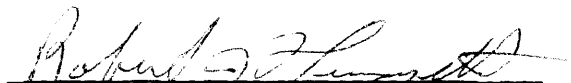

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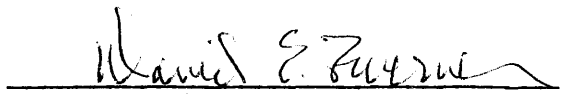

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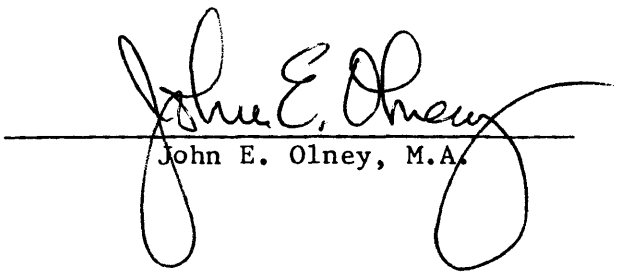

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Abstract

The butterfish and harvestfish are members of the sub-order Stromateoidei. This group of fishes is distinguished by the presence of an accessory organ in the gullet, the pharyngeal sac, and by the unusual diet of medusae during part or all of their lives. The structure and function of the pharyngeal sac is not well known. The structure of the sac was examined using histological and histochemical methods. Food of these two species is medusae, small crustaceans, and unidentified soft matter. The pharyngeal sac was muscular and contained esophageal teeth and many goblet cells, which principally secreted the glycoprotein group of sialomucins. Sphincters located at each end of the sac suggested a mechanism for control of passage of food through the sac. The muscles in the wall of the sac were striated indicating voluntary control of this structure. The thickened mucosal lining, heavy muscular walls, fine upturned esophageal teeth, numerous mucous secreting cells, and the appearance of the medusan remains in the stomach suggested a grinding and shredding function of the pharyngeal sac. The stomach may chemically alter the proteinaceous nematocyst toxin through acid denaturation, rendering the venom useful as a food item.

Introduction

The butterfish, Peprilus triacanthus (Peck), and harvestfish, P. paru (Linnaeus), are perciform fishes of the suborder Stromateoidei (Haedrich 1967). Members of this suborder are characterized by a unique, toothed, saccular outgrowth of the gullet located immediately posterior to the fourth gill arch (Willughby 1686; Gunther 1860; Gill 1862; Jordan and Evermann 1896; Regan 1902; Gilchrist 1922; Buhler 1930; Barnard 1948; Mansueti 1963; Isokawa et al. 1965; Haedrich 1967; Horn 1970). This structure has been referred to as an esophageal crop or pharyngeal sac. Although this organ is described in several studies, its function is not clearly understood.

The butterfish and harvestfish are sympatric, inhabiting coastal and oceanic waters in the Western North Atlantic. The butterfish ranges from Nova Scotia to Florida (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Liem and Scott 1966) and is commercially important throughout most of its range. The harvestfish is found from Massachusetts to Florida, throughout the Gulf of Mexico, and south to Argentina (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Hoese and Moore 1977). As adults these fishes are pelagic and migrate northward and inshore in spring in response to water temperature changes (Horn 1970).

Food habit studies of these fishes have been limited in descriptive scope because their food is often ground-up and unrecognizable. Hildebrand and Schroeder (1928) noted this

difficulty, but found a few fish with cycloid scales and what appeared to be strands of algae in their stomachs. Bigelow and Schroeder (1953) claimed that butterfish feed on small fish, squid, crustaceans, and annelid worms. They also reported that ctenophores had been found in a few stomachs at Woods Hole but that these were not a common dietary item. Liem and Scott (1966) reported that butterfish eat small fishes, amphipods, shrimp, and marine worms. Two other stomach content analyses of butterfish collected in the Northwest Atlantic reported a significant percentage of unidentifiable animal remains (Maurer and Bowman 1978; Bowman and Michaels 1984). In the first study of butterfish collected from 1969 to 1972 unidentifiable animal remains comprised 18.6% of contents, while the recognizable portion included tunicates and crustaceans. The latter study presented food data of butterfish collected from 1973 to 1976 from Nova Scotia south to Cape Hatteras. In the Mid-Atlantic region stomachs were found to contain 35.3% miscellaneous (unidentified material), and also included thaliaceans, polychaetes, and coelenterates. In the Southern New England region it was reported that 58.6% of stomach contents were miscellaneous, while polychaetes, crustaceans, and thaliaceans were included in the identifiable portion.

Food habits of harvestfish are less well known but Hildebrand and Schroeder (1928) indicated that stomach contents appeared to be identical to that of the butterfish: ground-up and often unrecognizable. Horn (1970) examined a few large (up to

150 mm SL) specimens of harvestfish and found them to contain medusan and ctenophore remains and small crustaceans.

Juvenile butterfish and harvestfish (up to 100 - 110 mm standard length) are often found in association with medusae or other floating objects (Pearson 1941; Dunnington and Mansueti 1955; Mansueti 1963; Schwartz 1964; Cargo and Schultz 1966; Haedrich 1967; Phillips et al. 1969; Horn 1970). Food of juveniles was reported to be coelenterate and ctenophore remains (Pearson 1941; Dunnington and Mansueti 1955; Mansueti 1963; Horn 1970; Oviatt and Kremer 1977). In Chesapeake Bay juvenile butterfish and harvestfish are often symbiotically associated with the scyphomedusa, Chrysaora quinquecirrha (Mansueti 1963). The interactions observed ranged from commensalism to parasitism or predation with young Peprilus utilizing the jellyfish as a refuge and older fishes actively feeding upon the nematocyst containing tentacles and manubria of the medusae. Mansueti (1963) hypothesized that the pharyngeal sac secretes a protective substance or somehow facilitates feeding on nematocyst containing tissues.

The sea nettle, Chrysaora quinquecirrha, is abundant in Chesapeake Bay from May to September (Cargo and Schultz 1966; Cargo and Schultz 1967; Calder 1977). The presence of cnidarian parts among the stomach contents of the butterfish and harvestfish indicates that these fishes consume nematocyst-containing tissue with no apparent harm. However, the stings have been observed to be lethal to young Peprilus when both the

jellyfish and the fish have been dip-netted together forcing the fish to contact the tentacles (Mansueti 1963).

The pharyngeal sac has received superficial descriptive treatment. A detailed examination of the cells and tissues lining the lumen of the pharyngeal sac, the possible secretory role of the sac, and the function of the sac in the digestive process has not been done. The presence of esophageal teeth, the muscular appearance of the sac, and the appearance of the stomach contents have led several authors to suggest that it may be used to grind food (Hildebrand and Schroeder 1928; Mansueti 1963; Horn 1970).

This study described in detail the morphology of the pharyngeal sac of Peprilus triacanthus and P. paru through the use of histological and histochemical methods and infered its functional role in the utilization of medusae as a food item.

Methods

Specimens of butterfish ranging from 18 mm - 174 mm standard length (SL) and harvestfish ranging from 20 mm - 125 mm SL were obtained from the Virginia Institute of Marine Science (VIMS) trawl surveys of the tributaries of the lower Chesapeake Bay and the National Marine Fisheries Service (NMFS) groundfish surveys of the coastal Atlantic Ocean. Fishes were collected by the VIMS surveys from May to October, 1983 and June to September, 1984. Specimens were collected by the NMFS surveys from Georges Banks and Cape May, NJ to Cape Fear, NC in March and September, 1984 (see Appendix A for collection and size data).

All fishes were fixed in 10% neutral buffered formalin and then transferred to 50% isopropyl alcohol for storage. Standard length, fork length and total length were recorded whenever possible. Pharyngeal sacs were removed and trimmed for histological examination. Stomachs were removed and stored in 50% isopropyl alcohol for later content analysis.

Pharyngeal Sac

Pharyngeal sacs from 39 harvestfish and 103 butterfish were examined. Their gross anatomy was studied under low-power magnification using a dissecting stereo-microscope. In preparation for histological examination the sacs were de-calcified in 0.1 N HCL for 18 - 36 hours then washed in tap water

for 4 hours. The tissue was then dehydrated through a graded alcohol series and processed for paraffin embedding following standard histological procedure. Cross sections were cut through the thickest portion of the sac at right angles to the anterior-posterior axis. Longitudinal sections were made dorso-ventrally along the plane of the anterior-posterior axis to bisect the central lumen of the sac. Semi-serial sections were cut at 6 um and stained with Harris' hematoxylin and eosin. Measurements of cells and structures of the pharyngeal sac were made with an ocular micrometer on a mono-objective microscope. Alcian blue-periodic acid - Schiff (AB-PAS) technique was used for identification of glycoproteins (Luna 1968). The AB-PAS was used at different pH, 2.5 and 1.0, to determine the particular conjugated protein in the goblet cell vacuole. With this method the goblet cells may stain either blue, red, or a combination of the two colors. Predominantly acid glycoproteins are found in those cells staining blue or blue-red after ABpH2.5-PAS, while those staining red or red-blue contain principally neutral glycoprotein. The acid glycoproteins may be either sialomucins or sulphomucins. Using ABpH1.0-PAS cells which contain sulphomucins stain positively with alcian blue, and those containing sialomcins stain PAS positive. This multiple AB-PAS protocol identified the type of glycoprotein present, and further characterizes the acid glycoprotein being produced by the goblet cells. Assessment of the method is described in more detail by Jones and Reid (1973).

Buccal Cavity

The buccal cavities of these fishes were examined for any structure that may aid in ingestion of nematocyst containing tissue. They were sectioned in cross and longitudinal planes and stained with Harris' hematoxylin and eosin in an attempt to study the entire epithelial lining.

Stomach

Stomach contents were analysed from 34 harvestfish ranging in size from 17 mm SL to 68 mm SL caught in the York and James Rivers in September, 1983 and 1984 when the sea nettle was abundant in these waters. Seventy-five butterfish were examined for stomach content analysis. They ranged in size from 23 mm SL to 174 mm SL and were collected from the coastal Atlantic Ocean. Contents from all fishes were identified using a stereoscopic dissecting microscope and the relative abundance of each food item was estimated for comparison with previous food habit studies. Smears were made of unidentifiable contents and examined under high power with a mono-objective microscope to determine if nematocysts from medusan food items were present. Estimates were made of relative proportions of discharged versus undischarged nematocyst capsules. Nematocyst capsules were considered to be discharged if either an empty capsule or a capsule with attached expelled thread was observed. Measurements

of nematocysts were made with an ocular micrometer on a mono-objective microscope. The stomach pH of butterfish and harvestfish was measured in freshly caught specimens using pH sticks (ColorpHast r , EM Reagents). Fishes for this purpose were caught in the York River, Virginia.

Results

Gross Anatomy of the Pharyngeal Sac

The pharyngeal sac in butterfish and harvestfish was located immediately posterior to the fourth gill arch and was followed by a short esophagus and the stomach (Fig. 1). The sacs of the two species were similar. They were globe-shaped with a shallow cleft running anterior to posterior along the dorsal mid-line and appeared muscular externally. Circular muscle bundles wrapped the sac (Fig. 2).

The pharyngeal sacs ranged in size from 4 mm diameter x 4 mm length in a harvestfish of 32 mm SL to 12 mm median diameter x 10 mm length in fish of 125 mm SL. In butterfish the sacs were smaller proportionately measuring 2.5 mm x 2 mm long in a 32 mm SL fish, and 12.5 mm x 11.5 mm long in a 152 mm SL fish. The sacs in all sizes examined were morphologically similar indicating complete development at an early age.

Two pairs of pharyngeobranchial plates were located dorsally at the entrance to the pharyngeal sac and extended partially into the sac (Fig. 3). The posterior pair of plates were elongated and tapered caudally. All four plates had large conical teeth covering them. Similar plates opposed them ventrally.

The interior of the sac was dominated by two distinct features. Along the dorsal and ventral mid-lines were two

central ridges protruding into the lumen. These ridges had numerous convolutions on the surface. In the harvestfish there were single rows of simple conical teeth between the folds on the ridges. These teeth were similar to those found on the pharyngeobranchial plates and extended partially into the lumen (Fig. 4). Between the similar folds in butterfish were the same simple teeth (Fig. 5). Both central ridges flattened toward the posterior of the sac. The second prominent feature of the sacs was the papillae lining the lateral walls (Fig. 6). These structures were densely packed and ranged from 1 to 2 mm in length and 0.2 to 0.65 mm in diameter. The largest papillae were found along the walls of the central portion of the sac with the distal papillae being reduced in size. They were erect and covered with the same lining as the rest of the interior of the sac. The support for a papilla was the esophageal tooth. It was a bulb shaped structure with a base of fine, tapered roots to anchor it in the underlying muscular layer. It was covered with many fine upturned teeth which protruded through the tissue covering it and was typical of teleost teeth in microstructure (Fig. 7 & 8). The esophageal teeth were morphologically similar in both species.

Underlying the ridges and papillae were two muscle layers (Fig. 6). A longitudinal layer extended over the length of the sac (anterior to posterior) and was thickest under the central ridges. A circular muscle layer was outermost.

Histology of the Pharyngeal Sac

The pharyngeal sac in both the butterfish and the harvestfish was composed of four tissue layers that are typical of the digestive tracts of vertebrates. These layers from the luminal lining outward were the mucosa (tunica mucosa), the submucosa (tela submucosa), the muscularis (tunica muscularis externa), and the serosa (tunica serosa). A pharyngeal sac measuring 6.7 mm x 6.1 mm from an 87 mm SL butterfish was the model for the following description.

The mucosa lined the entire lumen of the sac (Fig. 9). It was composed of epithelium and goblet cells on top of a thin acellular basement membrane and a lamina propria of connective tissue. Along the central lumen of the sac (dorsal and ventral ridges) the mucosa consisted of a squamous epithial layer 15 - 25 cells thick (50 -150 um). Luminally the squamous cells appeared keratinized. Goblet cells were scattered throughout the mucosa of the central lumen but were concentrated near the entrance of the central canal. These cells were round or oval shaped in section, are embedded among the squamous epithelial cells, and when stained with HHE had a blue cell membrane, a clear interior, and a dark flattened nucleus at the base of the cell (Fig. 10). Following Reifel and Travill (1977) I designated these goblet cells as Type A. On the lateral walls of the sac the mucosa was different from that found lining the central canal (Fig. 11). Cuboidal epithelium only one or two cells thick overlaid a

unicellular layer of goblet cells. They were 8 - 14 um x 19 - 29 um and contained a small, round, dark blue nucleus at the base. I designated these goblet cells as Type B (Reifel and Travill 1977) (Fig. 12). They were more numerous and were not deeply embedded in the mucosa as were Type A goblet cells. This layer of goblet cells was charactized as transitional epithelium, rather than columnar epithelium, because the goblet cells did not extend from the basement membrane to the lumen. A thin acellular basement membrane supported the epithelial mucosa. A lamina propria, composed of fibrous connective tissue from 20 to 50 um thick, supported the mucosa (Fig. 11).

There was no distinct boundary separating the submucosa and the lamina propria (Figure 11). In the pharyngeal sac the submucosa was composed of areolar connective tissue and longitudinal submucosal muscle. Arteries, veins, granular cells, and lymphocytes were scattered throughout the connective tissue layer. The longitudinal muscle was striated, loosely bundled, and very thick along the central ridges. This muscle should not be confused with a circular muscularis or a muscularis mucosae (Groman 1982), which was not present in the pharyngeal sacs of these fish. The esophageal teeth were anchored in this layer.

The muscularis was composed of densely packed striated muscle bundles wrapping the sac. Two muscular sphincters were present within this layer. They were located at the anterior and posterior openings of the central canal of the sac (Fig. 10 & 13).

The serosa was not well defined in the specimens I examined. There was a layer of loose, fibrous connective tissue surrounding the pharyngeal sacs, but epithelial cells were not present (Fig. 11).

The pharyngeal sac of the harvestfish was very similar to that of the butterfish. The two sacs were grossly virtually indistinguishable, but a few differences were apparent histologically. In the harvestfish's sac Type B goblet cells were located primarily at the bases of and between the papillae. These cells were clumped rather than distributed in a single cell layer, and were less numerous than in the butterfish's sac (Fig. 14). There did not appear to be any Type A goblet cells in the mucosa of the harvestfish. The squamous epithelial layer of the mucosa of the harvestfish was up to 20 cells and 119 um thick. These cells were also keratinized along the outer layer (Fig. 15).

All the goblet cells (Type A and Type B) found in the pharyngeal sacs of both fishes stained blue after ABpH2.5-PAS indicating acid glycoproteins were present (Fig. 16). Following staining with ABpH1.0-PAS all the cells were either red or magenta demonstrating the predominance of sialomucins (Fig. 17).

Buccal Cavity

The buccal cavity of the butterfish and harvestfish was lined with an oral mucosa and did not contain any specialized

secretory or accesory structures. The mucosa was comprised of squamous epithelium several cell layers thick and underlaid by an acellular basement membrane (Fig. 18). The oral mucosa was continuous with the mucosa layer of the pharyngeal sac.

Stomach Content Analysis

Thirty-four harvestfish stomachs were examined (Appendix B, Table 2); 25 were full and 9 were partially full. Except for one whole (0.5 mm long) and one partial crustacean and seven small teleost scales (0.8 x 1.3 mm) the contents were a white, transluscent material. Medusan remains were identified in 18 stomachs based on the presence of nematocysts, which were identified under magnification. In four of the eighteen less than 50 % of the nematocysts were discharged, and in nine 50 % or more were discharged. In the remaining samples there were very few nematocysts present and an estimate of discharged versus undischarged was not made. Two of the four types of nematocysts reported in the sea nettle were identified. They are the Type I, atrichous isorhizas, and Type III, euryteles (Burnett et al. 1968 - the Atrichous Haploneme `A' and Heterotrichous Microbasic euryteles, respectively, of Papenfuss 1936). The Type I nematocysts were oval and measured 15 x 20 - 25 um (Fig. 19). I noted the coiled meshwork interior but did not observe any of this type to be discharged. The Type III nematocysts were oval and measured 7 x 14 um (Fig. 20). This type of nematocyst was

much more numerous than Type I nematocysts. The proximal portion of the discharged thread was thickened and 10 um in length. The remainder of the thread was narrower, tapered, and up to 100 um in length. I observed both discharged and undischarged nematocysts of this type.

The contents in the remaining stomachs were not identifiable. No structures or recognizable cell types were observed.

Eighty butterfish stomachs were examined (Appendix B, Table 1). Two were empty. The remaining stomachs contained 68 % unidentified material and 32 % small crustaceans, crustacean remains, and a few teleost scales. A close examination of samples of the unidentified material using high-power magnification (mono-objective microscope) revealed no nematocysts. These results are consistent with other studies of stomach contents of butterfish collected in coastal Atlantic waters (Bowman, Maurer, and Murphey 1976; Maurer and Bowman 1978; Bowman and Michaels 1984),in which they found a high percentage of unidentified material and tunicates.

The pH of the gastric juices measured on seven butterfish and one harvestfish was found to average pH 3.

Discussion

Lacking in the literature is a comprehensive examination of the functional role of the pharyngeal sac and how its presence is related to the unusual diet (toxic medusan tissue) of these fishes. In the present study I have attempted to relate the two through morphological and histological examination and infer the functional role the sac plays in pre-digestion of food items. The pharyngeal sac was typical in composition of teleost upper alimentary canals. The distinguishing features were the thickened muscular walls and the papillae lining the sac. The function of these appeared to be to selectively grind and shred the food of the fish. From the ABPAS staining it was discovered that the goblet cells, which were typical esophageal mucoid cells, secreted sialomucins. References to the functional differences between the various mucoid glycoproteins, particularly those of fish, could not be found in the literature. In mammals a shift in the production of the type of predominant glyprotein within goblet cell populations has been shown to occur in response to infection (Jones et al. 1975) and to irritants (Lamb and Reid 1968; Jones et al. 1973). These studies describe an increase in numbers of goblet cells producing sulphomucins, suggesting that this glycoprotein may function to protect or ease the stress on the mucosa. Such a role may be possible for the sialomucins being secreted by the goblet cells of the pharyngeal sac of stromateoids. These cells were very numerous in the

fishes I studied and the diet of medusan tentacles is unusual among fishes and may be stressful to the internal tissues of the alimentary canal. I propose that it is the role of the sac to grind and trigger the nematocysts to discharge, releasing their toxic contents. The mucous from numerous goblet cells may help to protect the lining of the sac and ease passage of the contents to the stomach. The observation that not all stomach contents were ground beyond recognition, e.g. the small crustaceans found whole in stomachs of butterfish, is evidence for voluntary control of the crushing function. Passage of food items through the sac may be controlled by the sphincters at each end of it. The acid environment of the stomach is capable of breaking down the proteinaceous toxin into digestible elements, a possible role for the stomach during ingestion of medusan tissue.

The buccal cavity of these fish presented an enigma in that it was lined with a thin layer of mucosa, seemingly unprotected from the stinging of the nematocysts of the jellyfish as it is first bitten. Noteworthy was the lack of taste buds in this area. It is possible that during feeding the food items are not held in the mouth but are nipped off and simultaneously forcefully inhaled into the gullet, which would lead directly to the pharyngeal sac. Direct observation of the feeding behavior and mechanics was not possible during this study, but I suspect that it would be valuable in assessing the impact of the nematocysts on the buccal cavity.

Haedrich (1967) reviewed historical literature on the early

classification of stromateoids and noted many references to the presence of the pharyngeal sacs. Several studies superficially described these structures or merely noted their presence in families that are currently included in the sub-order Stromateoidei. John Ray's studies (Willughby 1686) noted pharyngeal sacs in Stromateus, which he mistakenly interpreted to be a second stomach. Cuvier and Valenciennes (1833) described the pharyngeal sacs in both "les Stromaties" and "les Centrolophes." Gunther (1860) examined the two genera Stromateus and Centrolophus and discovered " the gill-rakers of the upper segment of the last branchial arch enlarged and dentigerous or sacciform, and projecting backwards into the oesophagus." Jordan and Evermann (1896) and Regan (1902), while disagreeing on the classification of the group comprising the modern stromateoids, agreed on the presence of teeth in the esophagus of the genera. Gilchrist (1922) studied the esophageal teeth of several South African stromateoids and presented a detailed description of their structure and attachment within the sacs. Based on the support and attachment of the esophageal sacs in the gullet he suggested that they are not "strictly oesophageal, but are derived from an extension backwards of pharyngeal epithelium." He later commented that these teeth have "doubtless some connexion with the nature of their food" and "that some (of these fishes) feed on medusae." Barnard (1948) presented work he had done on the esophageal teeth of some stromateids. Correcting some of Gilchrist's errors he addressed the topic of

esophageal or pharyngeal derivation of the spiniferous lining of the sacs. Barnard stated "It seems rather doubtful to me whether detailed studies of the structures in question would confirm this view." Independent of Gilchrist's work and prior to Barnard's study Buhler (1930) closely examined the esophageal sacs of several stromateoids, including Peprilus triacanthus. He proposed the term "Rachensache" (pharyngeal sacs) to replace esophageal sacs to better indicate the origin of the structures. Buhler's work used serial micrographs primarily and is a substantial contribution to the understanding of the origin, morphology, and possible function of the teeth in the pharyngeal sacs. Isokawa et al. (1965) examined esophageal teeth of nine species of Pacific stromateoids noting the structure of the teeth and attachment bone. They suggested that the arrangement of the basal bones in the sacs of two species, Tetragonurus cuvieri and T. atlanticus, may have been well-suited for food storage in the sacs.

Grey (1955) reported on the digestive system of stromateoid fishes of the genus Tetragonurus (Risso). Her Figure 16 erroneously described the stomach, esophagus, and pharyngeal sac as the stomach divided into gastric and esophageal portions by a muscular constriction. She suggested that this digestive system may be an adaptation for the specialized diet of ctenophores and coelentrates, and further noted that the anterior esophageal portion with its prolonged pharyngeal bones extending into the muscular apparatus might be a method for moving food backwards

into the gastric part of the stomach. Haedrich (1967) considered Tetragonuridae to be the derived family of the second branch of the stromateoid sub-order with Nomeidae as the intermediate group. He reported that nomeids have smaller sacs and small papillae making it an efficient shredding organ. However, the diet of these fish is not well known but thought to include jellyfish.

All of these studies have noted the presence of a modified esophageal structure and several suggest food handling as a possible function. However, more detailed study of the pharyngeal sac has been confined to morphological studies of the esophageal teeth of various stromateoids. The present study has examined the histological structure of the sacs of two stromateoids in an attempt to further clarify structure and possible function of the sac as an accessory organ.

Haedrich (1967) included in his review and classification of stromateoids a study of the branchial assemblies of representatives of most of the genera recognized. He discussed the morphology of the papillae and esophageal teeth within the pharyngeal sacs and related it to the evolutionary gradient of 'primitive' to 'derived' members of the sub-order. He further correlated these changes in the sacs with the feeding habit shift from more or less omnivorousness to increased utilization of jellyfish for food. He considered Stromateidae to be a derived family in a branched lineage which includes Centrolophidae as an intermediate group between the ancestor of the stromateoids and

the present Stromateidae. The centrolophids are generalists in their food habits feeding on fish, squid, crustaceans, and sometimes garbage (Haedrich 1967). Stromateids, as reported by Haedrich and in this study, feed mainly on small crustaceans and medusans. It is interesting to note that in my stomach analysis of Peprilus most of the small crustaceans were whole, but there was a large percentage of unidentified material that appeared shredded or ground up. This observation coupled with the presence of striated muscle in the pharyngeal sac suggests that this organ is under voluntary control and need not crush all food items. In studying fishes of the genus Peprilus (Stromateidae) Horn (1970) noted that the phayngeal sac has muscular walls and appears to function as a shredding or grinding organ often causing stomach contents to be unrecognizable. Hildebrand and Schroeder (1928) also suggested that grinding the food is a possible function of the teeth found in the esophagus.

Based on the nematocysts present in stomachs examined in this study, and previous reports, it seems probable that the sea nettle is a major part of the diet of butterfish and harvestfish in Chesapeake Bay from May to September, even though contacting its tentacles is lethal to these fishes (Mansueti 1963). Burnett and his colleagues have extensively studied physical, chemical, and physiological properties of the nematocyst venom (Burnett et al. 1968; Burnett and Sutton 1969; Burnett and Goldner 1970; Burnett and Gould 1971; Burnett and Calton 1973; Burnett and Calton 1974; Burnett and Calton 1976; Warnick et al. 1981; Cobbs

et al. 1983; Calton and Burnett 1983; Kelman et al. 1984). Grinding and high-speed homogenization were the most effective physical means of discharging nematocysts for the purpose of collecting venom (Burnett et al. 1968). The soluble toxin has been characterized as proteinaceous with a molecular weight of 100,000 - 400,000 atomic units. It is neurotoxic, myotoxic, and cardiotoxic (reported in test animals - fiddler crabs and mice), as well as capable of producing dermonecrosis and hemolysis (reported in mice and humans) (Burnett and Gould 1971). The proteinaceous character of this toxin allows it to be denatured at low pH (< pH 6.8) rendering it harmless (Burnett and Goldner 1970). Thus, at the measured pH of 3.0 found in the stomachs of butterfish and harvestfish the toxin would be broken down. This denaturation may be part of a system whereby the pharyngeal sac grinds the jellyfish tentacles, triggering the nematocysts to discharge and release their toxin. Following acid denaturation of the toxin in the stomach the now harmless products could be absorbed in the intestine. Such a role seems consistent with the morphological and histological structure of the sac and the observed condition of the stomach contents of these fishes.

Further research should be directed toward direct behavioral observation and physiological study of nematocyst venom detoxification. An appropriate experiment would be to feed the fish a known quantity of jellyfish tentacles with a known concentration of nematocysts. Following a series of time intervals the material could be removed from the pharyngeal sac

and stomach and bioassayed for toxicity. The results would serve to further clarify the role the sac plays, if any, in chemically altering the medusan food of these fish. Additionally, examination of the analogous organs found in the gullets of leatherback turtles and alepocephalid fishes, two other animals that feed on medusae, and the method that these creatures use to cope with their unusual food may aid in understanding how the stromateoids do so.

Conclusion

The butterfish and harvestfish are members of the sub-order Stromateoidei. This group of fishes is distinguished by the presence of an accessory organ in the gullet, the pharyngeal sac, and by having an unusual diet of medusae during part or all of their lives. The pharyngeal sac was muscular and contained esophageal teeth and many goblet cells, which principally secreted the glycoprotein group of sialomucins. Sphincters were located at the anterior and posterior openings of the sac. These muscles may control passage of food through the sac. Food of these two species was medusae, small crustaceans, and unidentified soft matter. Some crustaceans were passed through the pharyngeal sac whole. This observation and the presence of striated muscle in the pharyngeal sac's wall indicated voluntary control of this organ's muscle mass. The role the sac plays in pre-digestion of food is not clear. Evidence presented to indicate a grinding and shredding function of the pharyngeal sac was: the thickened mucosal lining, heavy muscular walls, fine upturned esophageal teeth in the papillae, numerous mucous secreting cells, and the appearance of the medusan remains in the stomach. The stomach secretions of these fishes are acidic (pH 3). The nematocyst toxin of the sea nettle can be denatured at this low pH.

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Appendix A

Table 1. Harvestfish

Specimen Number	Collection Location	Date	SL	TL	FL	Pharyngeal Sac Section
01	* Y-20	091483	35	41	46	cross
02	Y-20	091483	33	39	43	cross
03	Y-20	091483	37	43	49	cross
04	Y-20	091483	34	39	46	cross
05	Y-05	091483	32	38	43	cross
06	Y-05	091483	27	33	35	cross
07	Y-15	081883	38	45	49	cross
08	Y-15	081883	43	50	55	cross
09	Y-15	081883	50	57	64	cross
10	Y-15	081883	28	32	36	cross
11	Y-11	083183	70	81	94	cross
12	Y-11	083183	48	56	62	cross
13	Y-P	090783	31	37	41	cross
14	Y-P	090783	75	86	101	cross
15	Y-P	090783	49	57	65	cross
16	Y-07	092484	61	72	81	none
17	Y-07	092484	60	70	79	none
18	Y-07	092484	40	50	55	longitudinal
19	Y-07	092484	59	69	79	longitudinal
20	Y-07	092484	57	68	76	longitudinal
21	Y-07	092484	69	82	93	longitudinal
22	Y-07	092484	60	72	82	longitudinal
23	Y-07	092484	71	82	93	longitudinal
24	Y-07	092484	30	38	t	longitudinal
25	Y-07	092484	30	38	t	longitudinal
26	Y-07	092484	60	71	82	longitudinal
27	Y-07	092484	57	66	77	none
28	Y-07	092484	50	54	61	longitudinal
29	Y-07	092484	43	51	57	longitudinal
30	**	092484	46	55	61	longitudinal
31	**	092484	43	53	59	longitudinal
32	**	092484	30	37	42	longitudinal
33	**	092484	23	29	31	longitudinal
34	**	092484	33	39	45	longitudinal
35	**	092484	20	t	27	longitudinal
36	**	092484	27	34	38	longitudinal
37	**	092484	32	40	45	longitudinal
38	**	092484	26	t	37	longitudinal
39	JAM	050885	125	144	168	longitudinal

* Locations: Y - York River, Virginia (number indicates miles from mouth); Y-P - York River at mouth of Poropatank River; JAM- Collected offshore south of mouth of Chesapeake Bay.

** Lower Chesapeake Bay - Hampton Bar or mouth of Back River

t Length not available - damaged caudal fin

Table 2. Butterfish

Specimen Number	Cruise Number	* Station Number	Date	SL	FL	TL
01	84-02	43	030684	77	85	95
02	84-02	43	030684	65	74	83
03	84-02	43	030684	68	75	85
04	84-02	43	030684	71	78	88
05	84-02	48	030684	111	120	140
06	84-02	48	030684	115	122	145
07	84-02	48	030684	86	97	115
08	84-02	48	030684	110	120	140
09	84-02	48	030684	66	74	86
10	84-02	48	030684	83	92	100
11	84-02	48	030684	84	94	115
12	84-02	48	030684	74	85	99
13	84-02	45	030684	113	123	140
14	84-02	45	030684	84	96	105
15	84-02	45	030684	73	83	90
16	84-02	45	030684	74		
17	84-02	45	030684	71	80	90
18	84-02	45	030684	110	118	132
19	84-08	55	091784	97	110	126
20	84-08	55	091784	90	101	116
21	84-08	55	091784	92	105	117
22	84-08	55	091784	96	110	124
23	84-08	55	091784	84	95	110
24	84-08	55	091784	87	100	113
25	84-08	55	091784	87	99	112
26	84-08	55	091784	86	99	115
27	84-08	55	091784	91	103	118
28	84-08	55	091784	85	95	103
29	84-08	55	091784	90	103	117
30	84-08	55	091784	94	108	124
31	84-08	55	091784	92	104	120
32	84-08	55	091784	90	103	119
33	84-08	55	091784	87	101	117
34	84-08	55	091784	87	102	116
35	84-08	55	091784	87	99	113
36	84-08	55	091784	92	107	124
37	84-08	55	091784	93	106	122
38	84-08	55	091784	82	95	100
39	84-08	55	091784	92	106	120
40	84-08	55	091784	89	104	120
41	84-08	55	091784	86	100	116
42	84-08	55	091784	81	94	108
43	84-08	55	091784	82	96	111
44	84-08	09	09 84	170	191	220
45	84-08	09	09 84	152	171	200
46	84-08	09	09 84	150	169	198
47	84-08	09	09 84	147	167	191

Specimen Number	Cruise Number	Station Number	Date	SL	FL	TL
48	84-08	09	09 84	158	181	205
49	84-08	09	09 84	150	172	195
50	84-08	09	09 84	159	182	210
51	84-08	09	09 84	146	165	194
52	84-08	09	09 84	148	168	189
53	84-08	09	09 84	145	163	187
54	84-08	02	09 84	174	198	230
55	84-08	02	09 84	169	193	225
56	84-08	02	09 84	165	188	215
57	84-08	02	09 84	170	193	220
58	lower Ches. Bay		092484	43		58
59	84-08	87	092084	48		65
60	84-08	87	092084	31		42
61	84-08	87	092084	29		44
62	84-08	87	092084	36		50
63	84-08	96	092184	41		
64	84-08	96	092184	38		
65	84-08	96	092184	32		
66	84-08	96	092184	34		
67	84-08	96	092184	27		
68	84-08	96	092184	25		
69	84-08	96	092184	23		
70	84-08	96	092184	36		
71	84-08	96	092184	39		
72	84-08	96	092184	40		
73	84-08	96	092184	18		
74	84-08	96	092184	20		
75	84-08	121	092284	51		
76	84-08	121	092284	50		
77	84-08	121	092284	47		
78	84-08	121	092284	48		
79	84-08	121	092284	50		
80	84-08	121	092284	47		
81	84-08	121	092284	45		
82	84-08	121	092284	43		
83	84-08	121	092284	44		
84	84-08	121	092284	32		
85	84-08	121	092284	24		
86	84-08	166	092684	105	122	140
87	84-08	166	092684	127	146	170
88	84-08	166	092684	109	126	140
89	84-08	166	092684	109	126	144
90	84-08	166	092684	96	112	130
91	84-08	166	092684	129	150	169
92	84-08	166	092684	118	138	155
93	84-08	166	092684	130	148	171
94	84-08	166	092684	107	124	141
95	84-08	166	092684	103	120	140
96	84-08	166	092684	95	106	125

Specimen Number	Cruise Number	Station Number	Date	SL	FL	TL
97	84-08	166	092684	116	134	155
98	84-08	166	092684	93	110	130
99	84-08	166	092684	98	113	130
100	84-08	166	092684	112	130	147
101	84-08	166	092684	102	119	135
102	84-08	166	092684	124	137	166

Note: Missing FL or TL was the result of damaged caudal fin.

* Table 3 contains station location information.

Table 3. Butterfish Collection Station Locations

Cruise	Station	Latitude *	Longitude *	Depth (m)
84-02	43	34 11 N	77 45 W	16
84-02	45	34 22 N	77 23 W	12
84-02	48	34 30 N	77 05 W	21
84-08	2	**	**	**
84-08	87	35 46 N	75 28 W	18
84-08	96	36 37 N	75 42 W	17
84-08	121	38 34 N	74 51 W	24
84-08	166	39 40 N	72 04 W	149
84-08	55	38 29 N	73 38 W	68
84-08	9	**	**	**

* Latitude and longitude given in degrees and minutes.

** locations are on Georges Banks (lat. 41 29 - 42 07 N long. 65 47 - 66 50 W). Weather conditions prevented exact locations and depths being determined.

Appendix B

Table 1. Butterfish Stomach Contents

Specimen Number	Condition of Stomach	Crustaceans Whole	Crustaceans Remains	Crustaceans % total	Unidentifiable % total
19	full		x	50	50
20	full	x	x	85	* 15
21	full	x		95	5
22	partial	x		25	95
23	full	x		95	5
24	partial	x	x	100	
25	partial		x	95	5
26	partial		x	50	50
27	full		x	50	50
28	partial	x			75
29	partial		x	25	75
30	partial	x	x	85	15
31	partial	x	x	95	5
32	partial		x	10	90
33	partial	x	x	50	50
34	partial	x	x	50	50
35	partial		x	5	95
36	partial	x	x	50	50
37	full	x	x	100	
38	partial	x	x	75	25
39	full	x	x	100	
40	partial	x	x	60	40
41	partial	x	x	50	50
42	partial	x	x	50	50
43	partial	x	x	50	50
44	partial		x	25	75
45	partial		x	100	
46	partial				100
47	partial	x	x	90	10
48	partial	x	x	100	
49	partial				100
50	partial	x	x	1	99
51	partial	x	x	10	90
52	partial		x	1	99
53	partial	x		5	95
54	full	x		1	99
55	partial				100
56	partial				100
57	partial				100
58	partial				100
59	partial		x	50	50
60	empty				
61	empty				
62	partial				100
63	full	x		1	99
64	partial				100
65	full				100
66	partial				100
67	partial				100

Specimen Number	Condition of Stomach	Crustaceans Whole	Crustaceans Remains	Crustaceans % total	Unidentifiable % total
68	full				100
69	partial				100
70	partial				100
71	partial				100
72	partial				100
75	partial				100
76	full				100
77	full				100
78	full				100
79	full	x		10	90
80	full				100
81	full	x		1	99
82	full				100
83	partial	x		5	95
84	full				100
85	full	x	x	5	95
86	partial				100
87	partial				100
88	partial	x		5	95
89	partial	x	x	5	95
90	partial				100
91	partial				100
92	partial		x	10	90
93	partial	x		1	99
94	partial				100
95	partial				100
96	partial		x	25	75
97	partial	x	x	20	80
98	full	x	x	5	95
99	partial	x	x	50	50
100	partial				100
101	partial				100

* Includes 5 % teleost scales

Table 2. Harvestfish Stomach Contents

Specimen Number	Condition of Stomach	Medusan Remains % Total	Nematocysts % Released	Nematocysts % Not Released	Unidentifiable % Total
42	partial	100	**	**	
43	full				100
44	full	95	5	95	* 5
45	full	100	25	75	
46	full				100
47	partial	100	30	70	
48	partial	100	**	**	
49	full				100
51	full				100
52	full	100	**	**	
53	full				100
54	full	100	95	5	
55	full	100	50	50	
56	full	100	90	10	
57	full	100	50	50	
58	full	100	90	10	
59	full	1	**	**	99
60	full	1	**	**	99
61	full				100
62	full				100
63	full				100
64	full				100
65	full				100
66	full				100
67	full	100	50	50	
68	full				100
69	partial				100
70	partial	100	75	25	
71	partial	100	75	25	
72	partial				100
73	partial				100
74	partial	100	10	90	
75	full	97	95	5	t 3
76	full				100

** Not Determined

* Contained 5 % teleost scales

t Contained 3 % crustaceans

Figures

Figure 1. Butterfish cut open to show internal organs. ga, gill arches; ps, pharyngeal sac; e, esophagus; s, stomach.

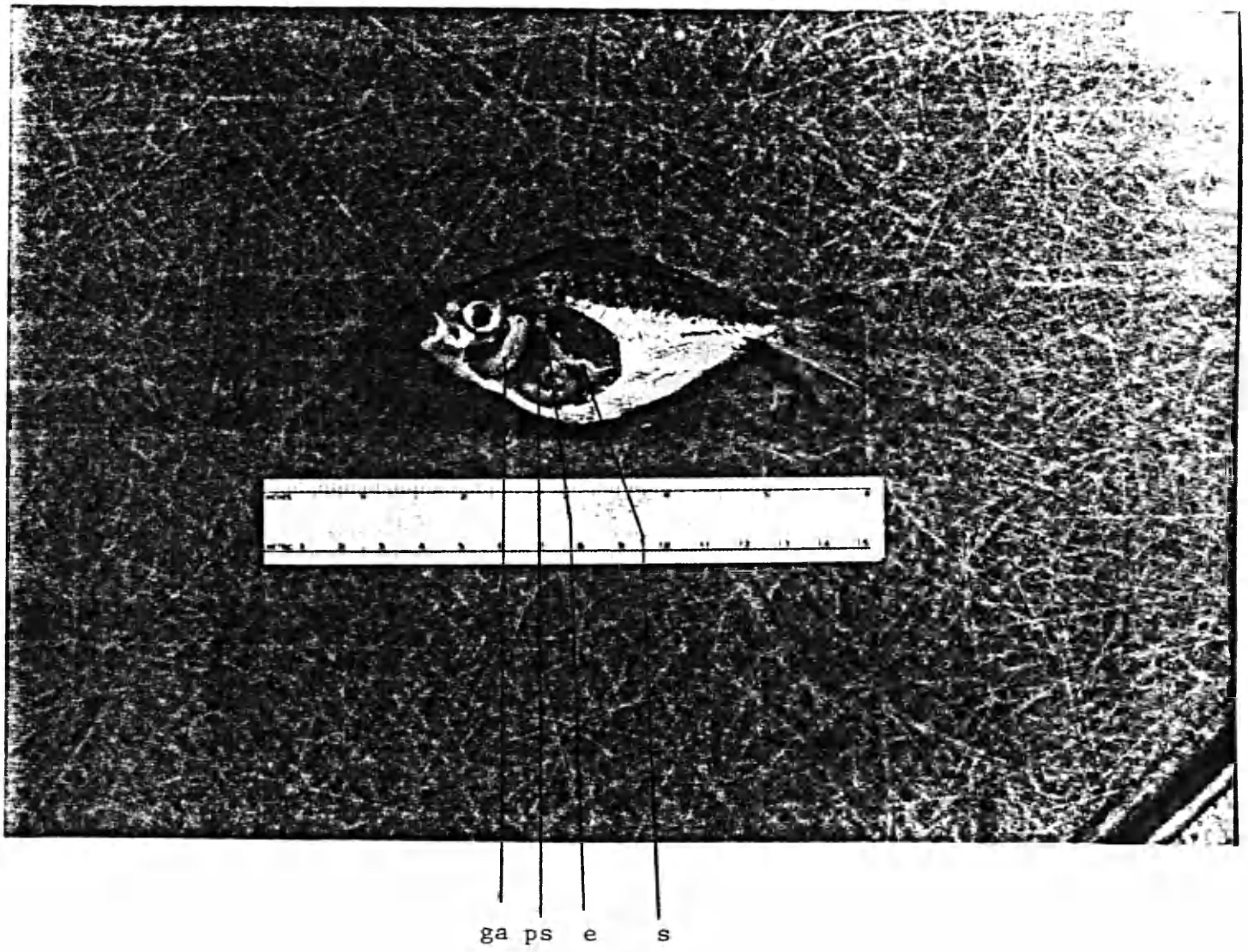

ga
ps
e
s

Figure 2. Branchial - gut assembly of a butterfish. ps, pharyngeal sac; ga, gill arches; cm, circular muscles; s, stomach.

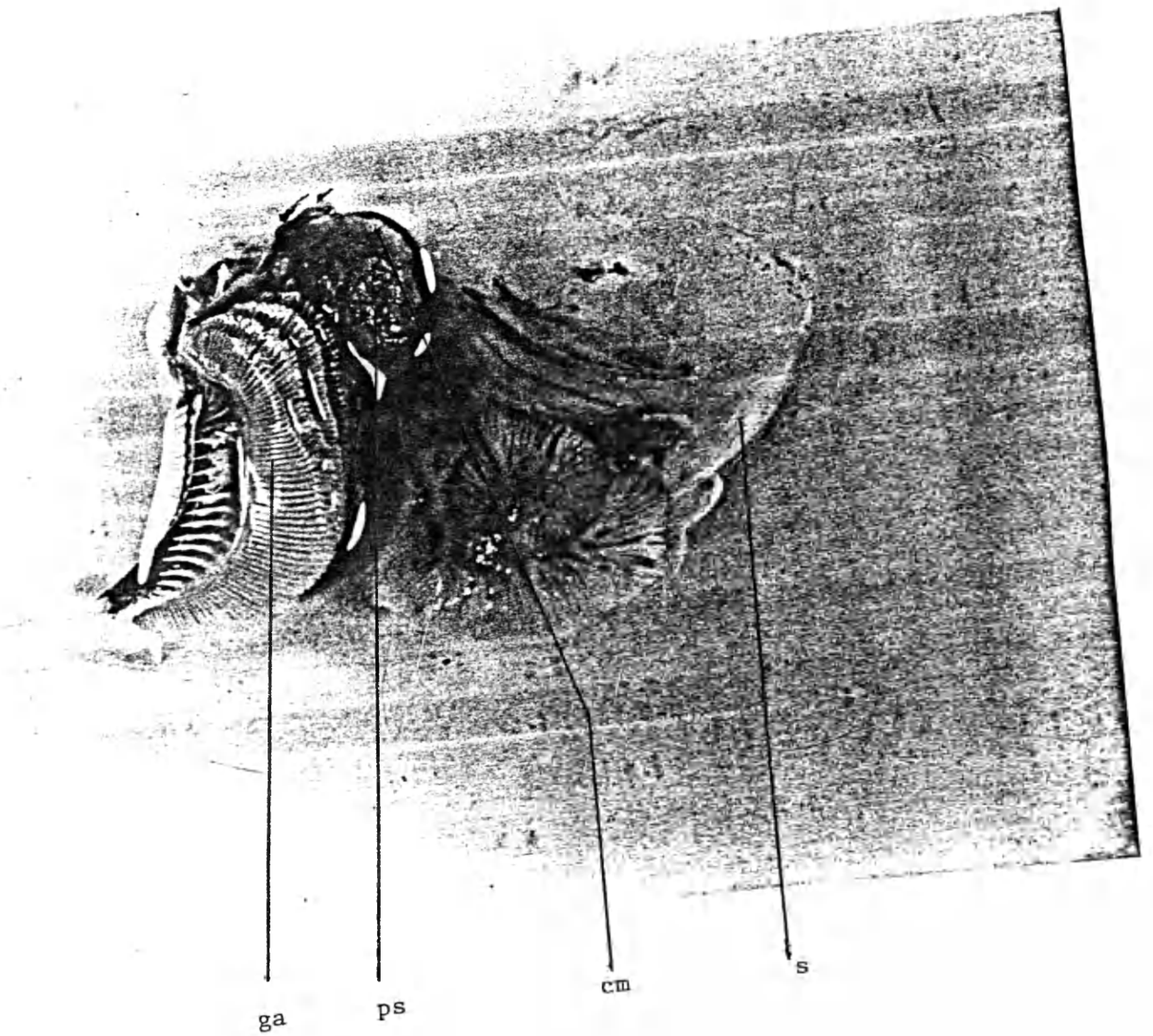
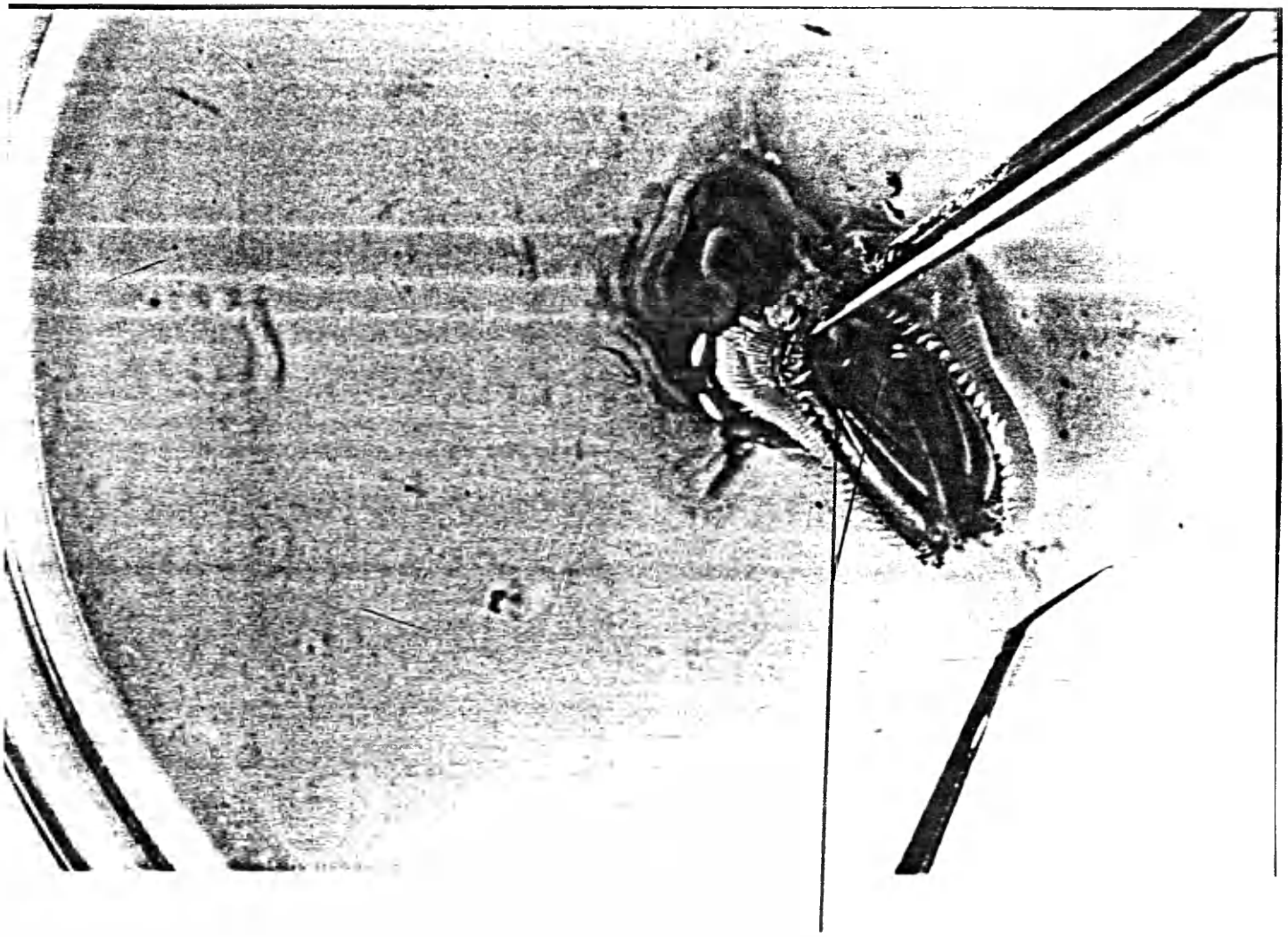

ga
ps
cm
s

Figure 3. Gullet of butterfish. pp, pharyngeobranchial plates.



PP

Figure 4. Central ridge of interior of pharyngeal sac of a harvestfish. mf, mucosal folds; ct, conical tooth.

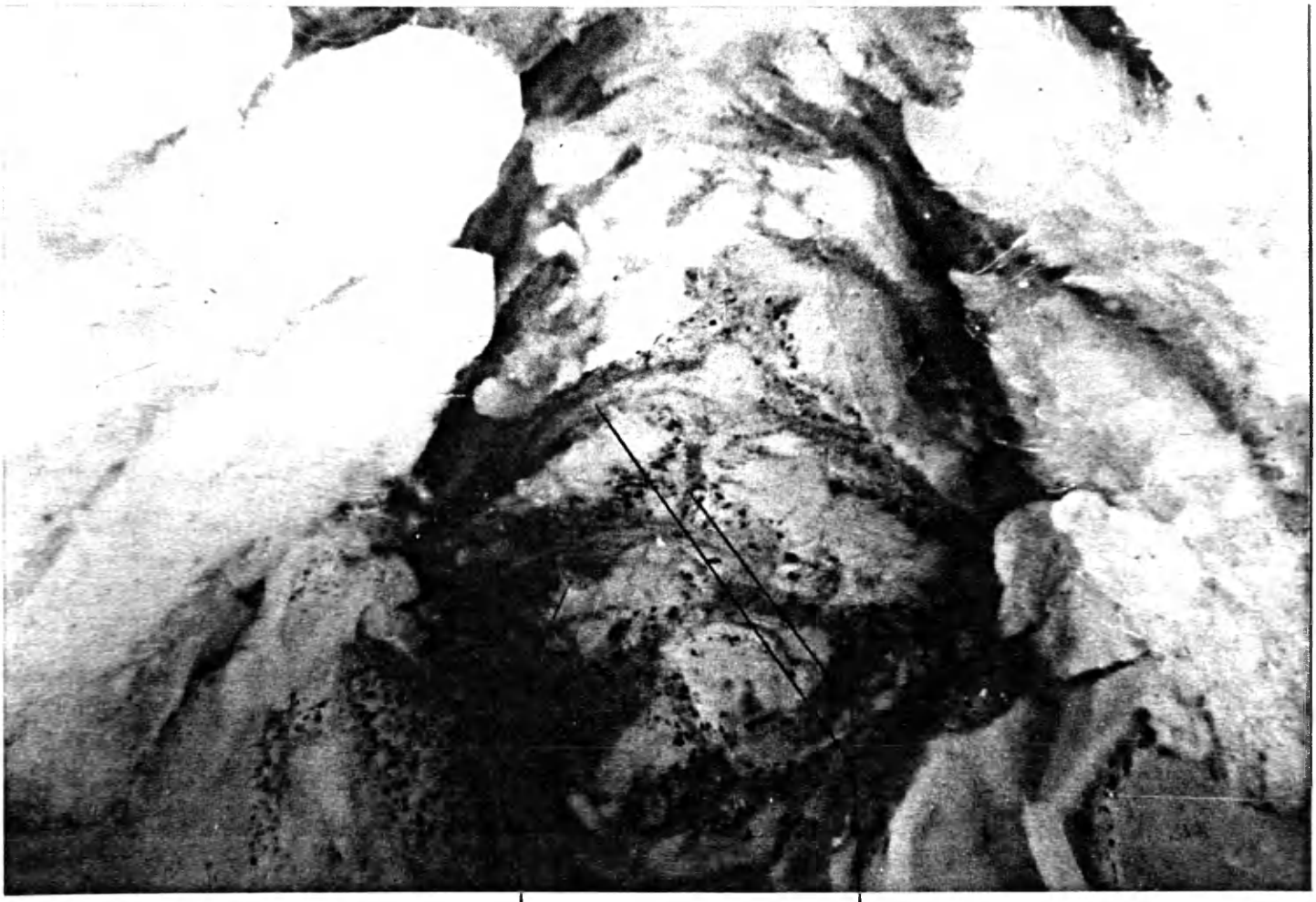

ct
mf

Figure 5. Central ridge of interior of pharyngeal sac of a butterfish. mf, mucosal folds; ct, conical tooth.

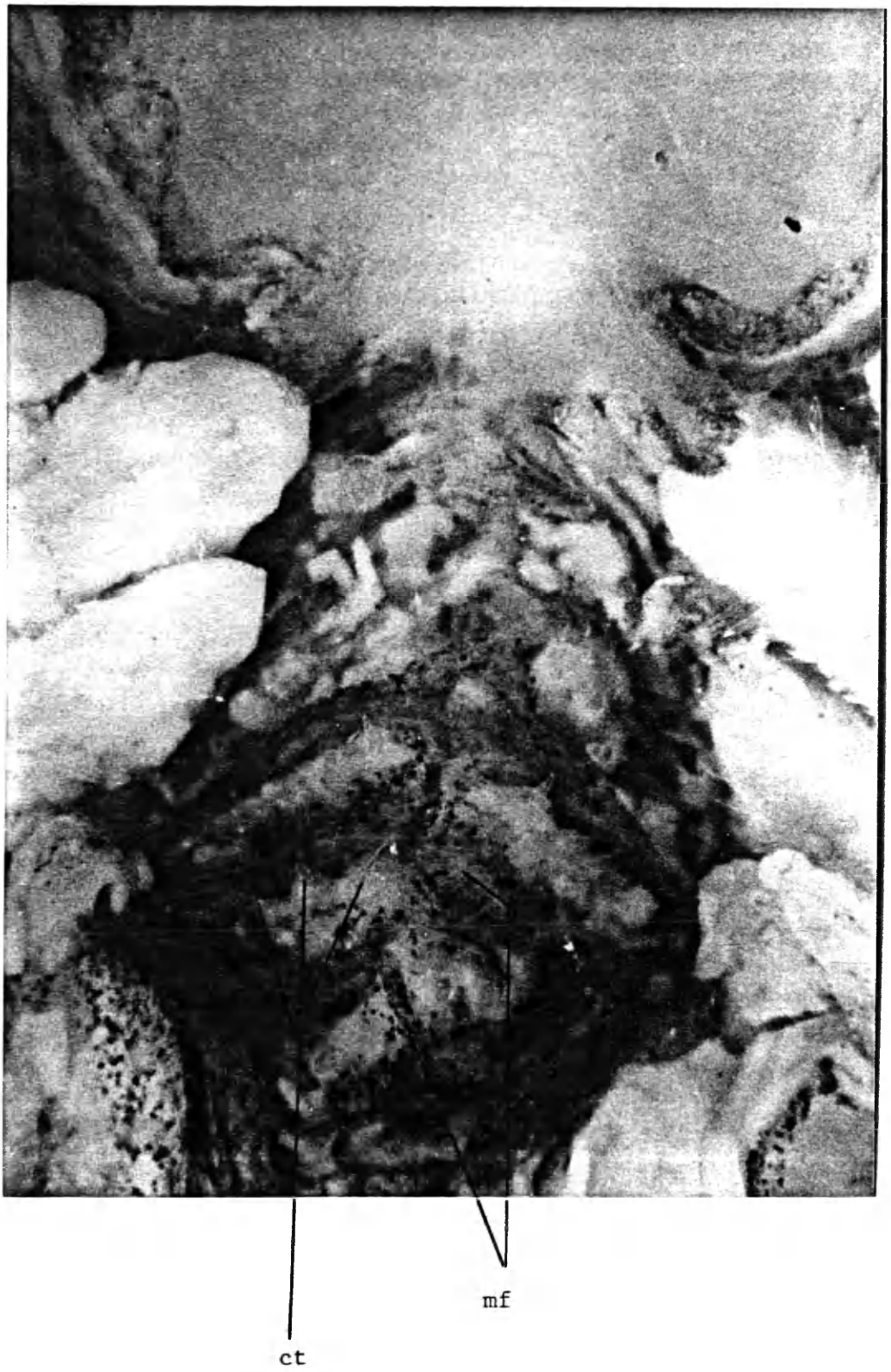

mf
ct

Figure 6. Interior of pharyngeal sac of a butterfish. p, papilla; lm, longitudinal muscle; cm, circular muscle.

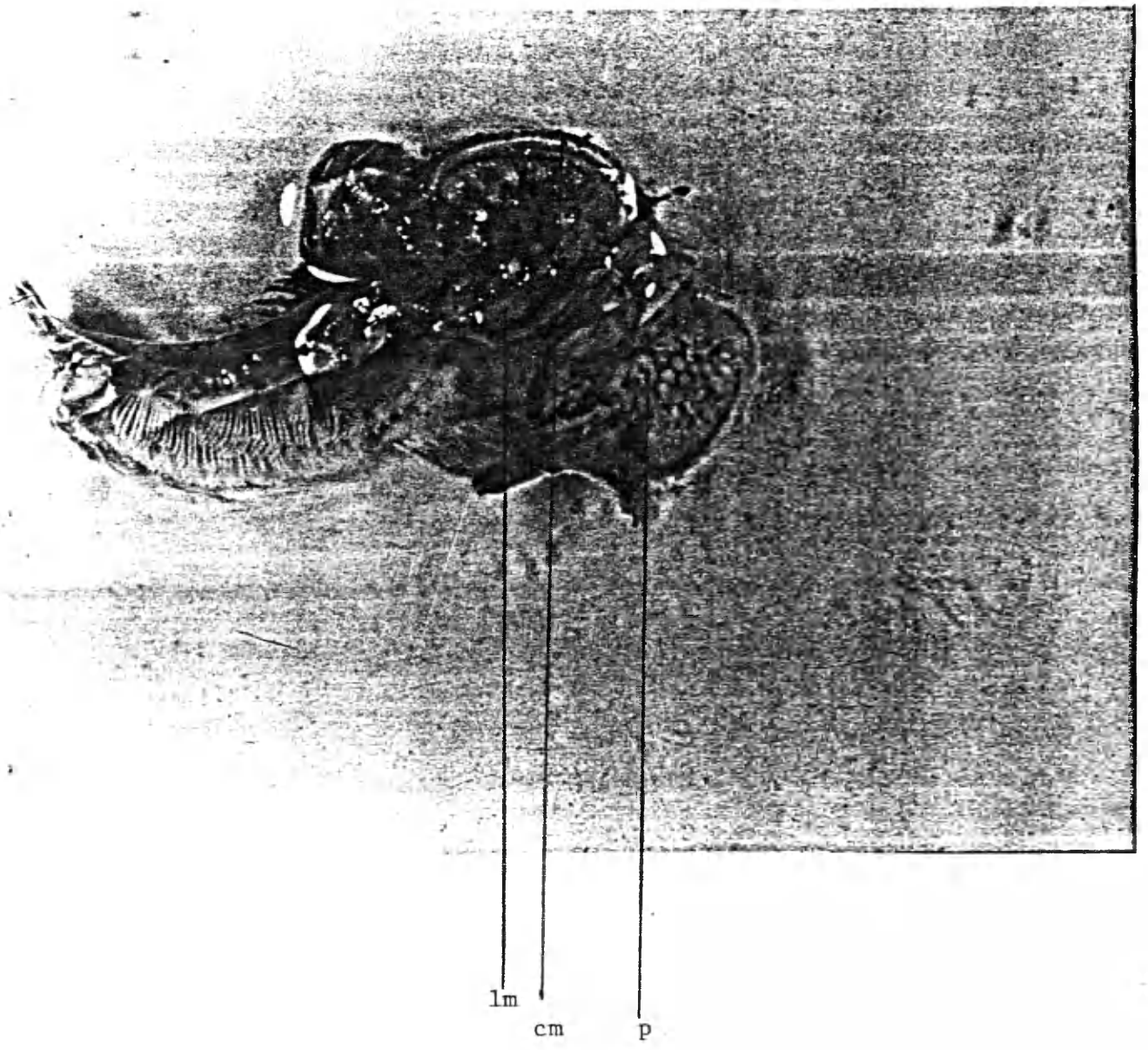

lm
cm
p

Figure 7. Esophageal tooth of a butterfish.

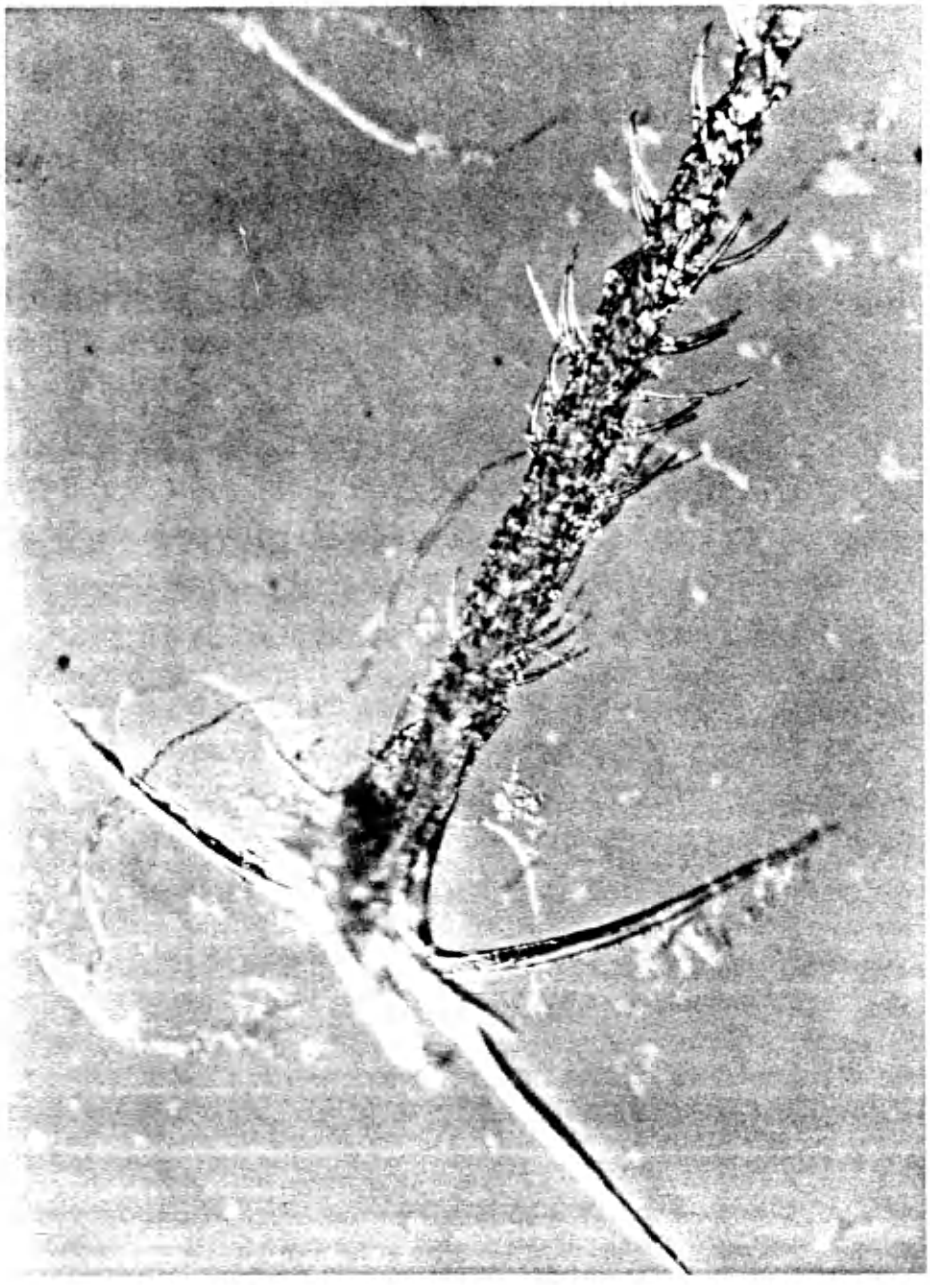


Figure 8. Lateral wall of pharyngeal sac of a butterfish. et, esophageal tooth (in section). HHE stain.

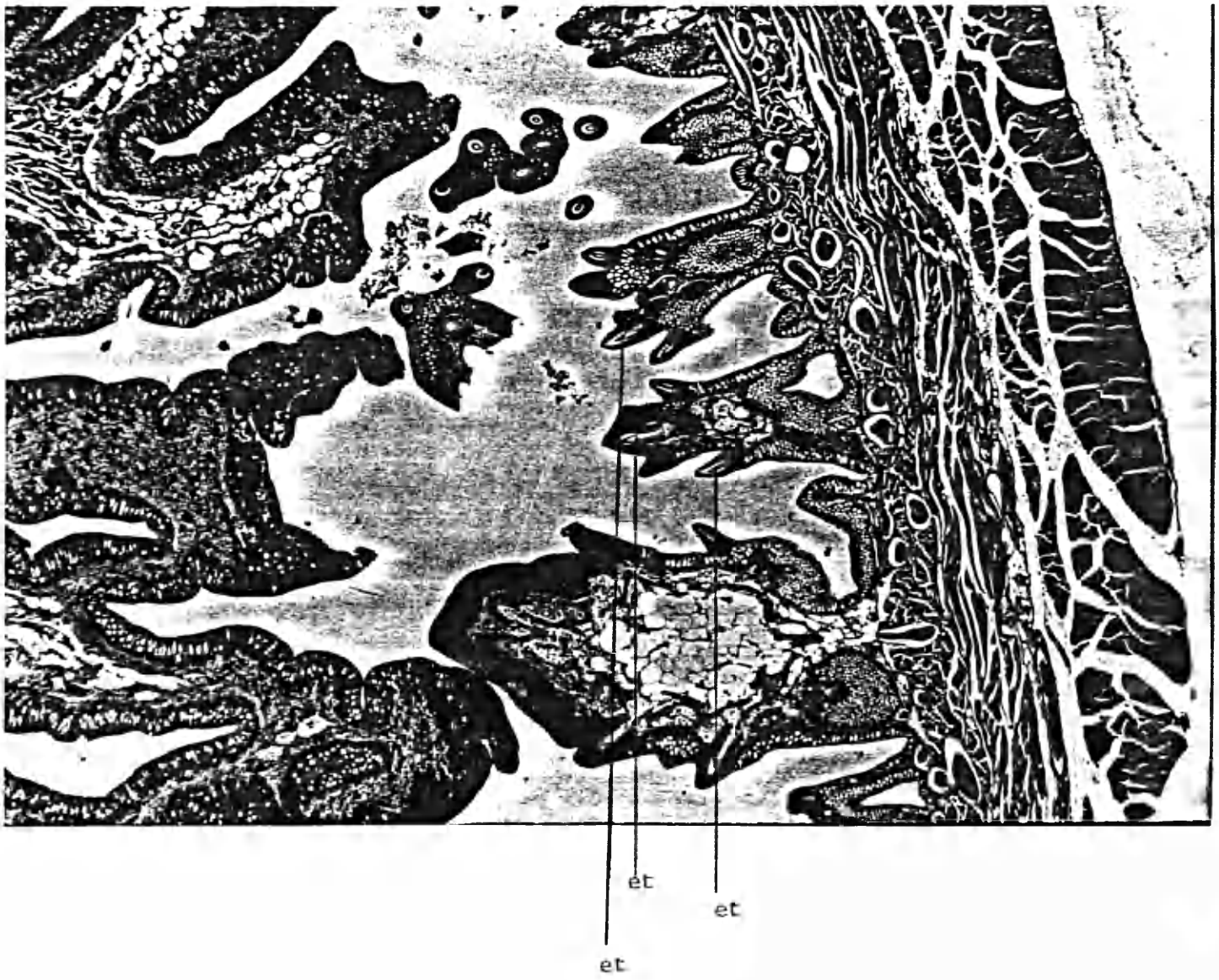

et
et
et

Figure 9. Central lumen of the pharyngeal sac of a 32 mm SL butterfish. m, mucosa; sse, stratified squamous epithelium; lp, lamina propria; gA, Type A goblet cell (longitudinal section-HHE stain).

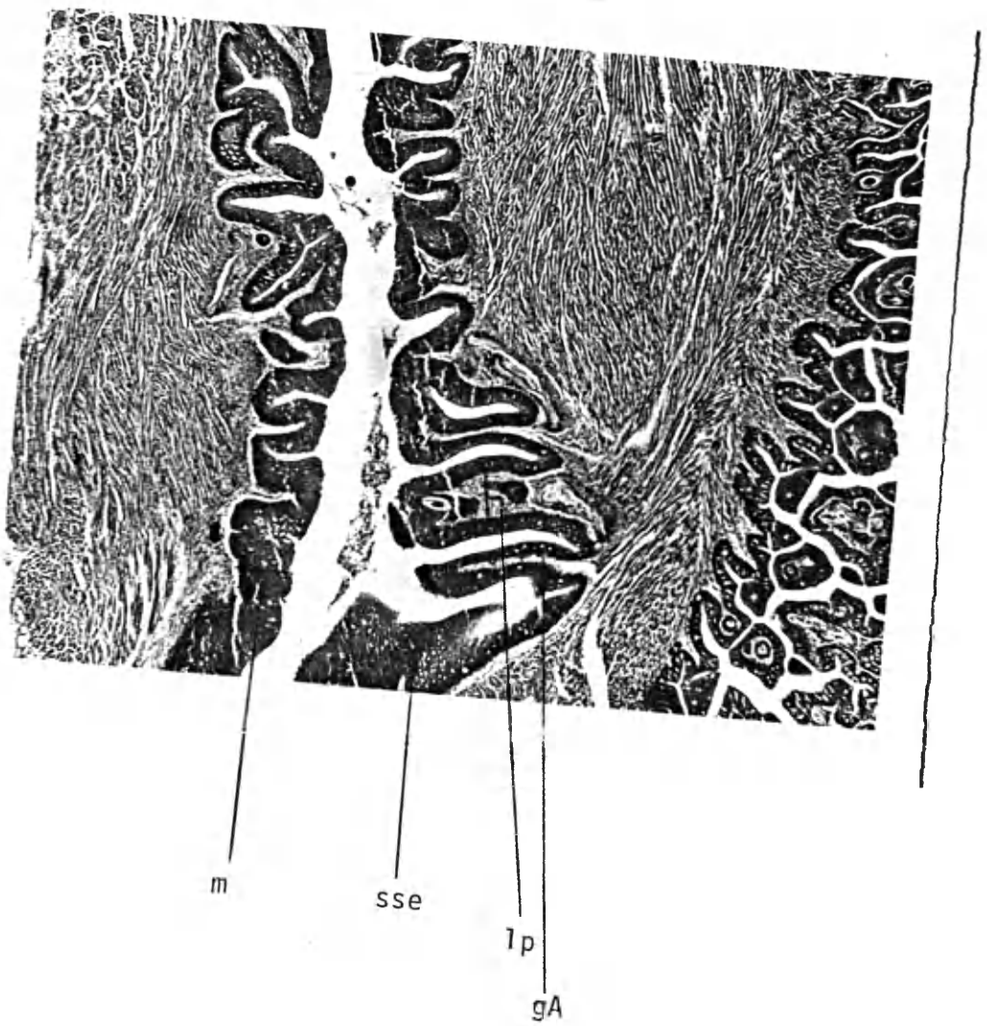

m
sse
lp
gA

Figure 10. Central lumen of anterior portion of the pharyngeal sac of an 87 mm SL butterfish. m, mucosa; sse, stratified squamous epithelium; gA, Type A goblet cell; lp, lamina propria; sph, sphincter - circular muscle bundle (longitudinal section-HHE stain).

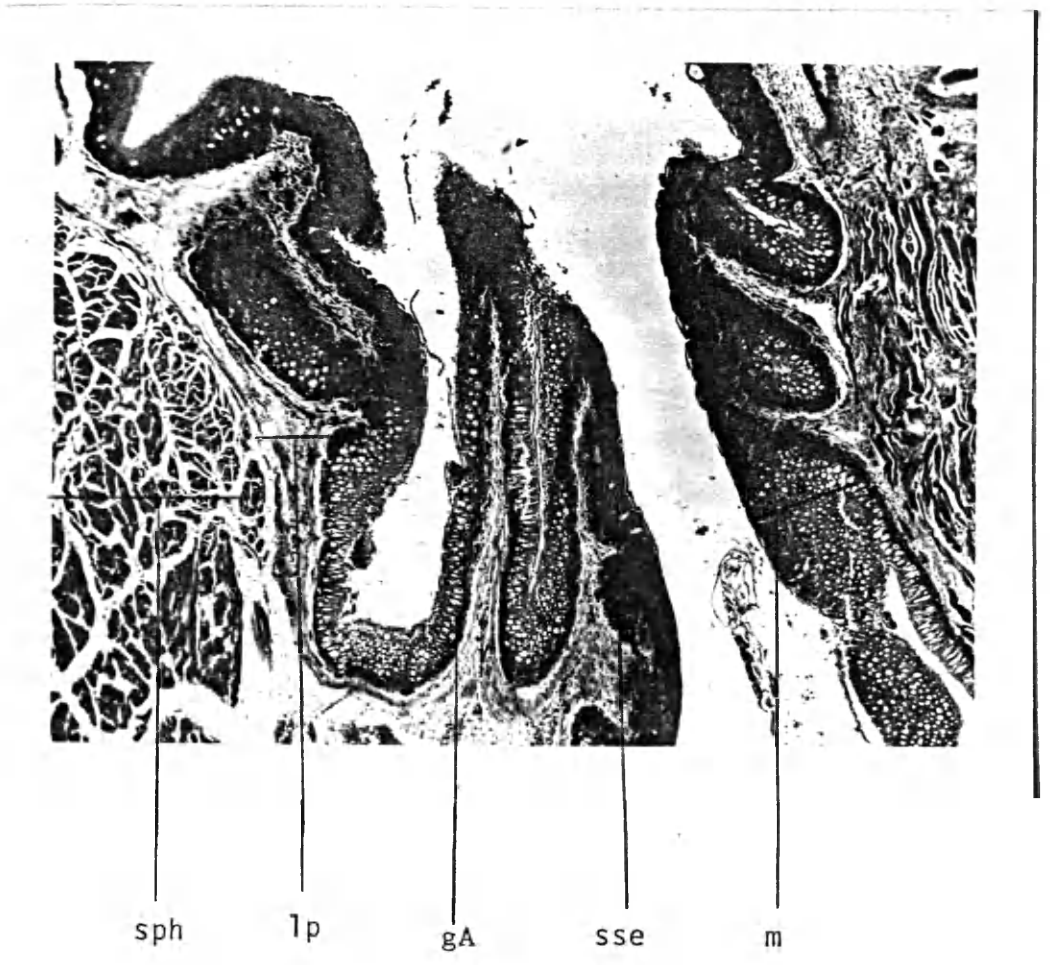

sph
lp
gA
sse
m

Figure 11. Lateral wall of the pharyngeal sac of a 152 mm SL butterfish. m, mucosa; sm, submucosa; tse, transitional epithelium; ce, cuboidal epithelium; gB, Type B goblet cells; lp, lamina propria; et, esophageal tooth - in section; sr, serosa (longitudinal section - HHE stain).

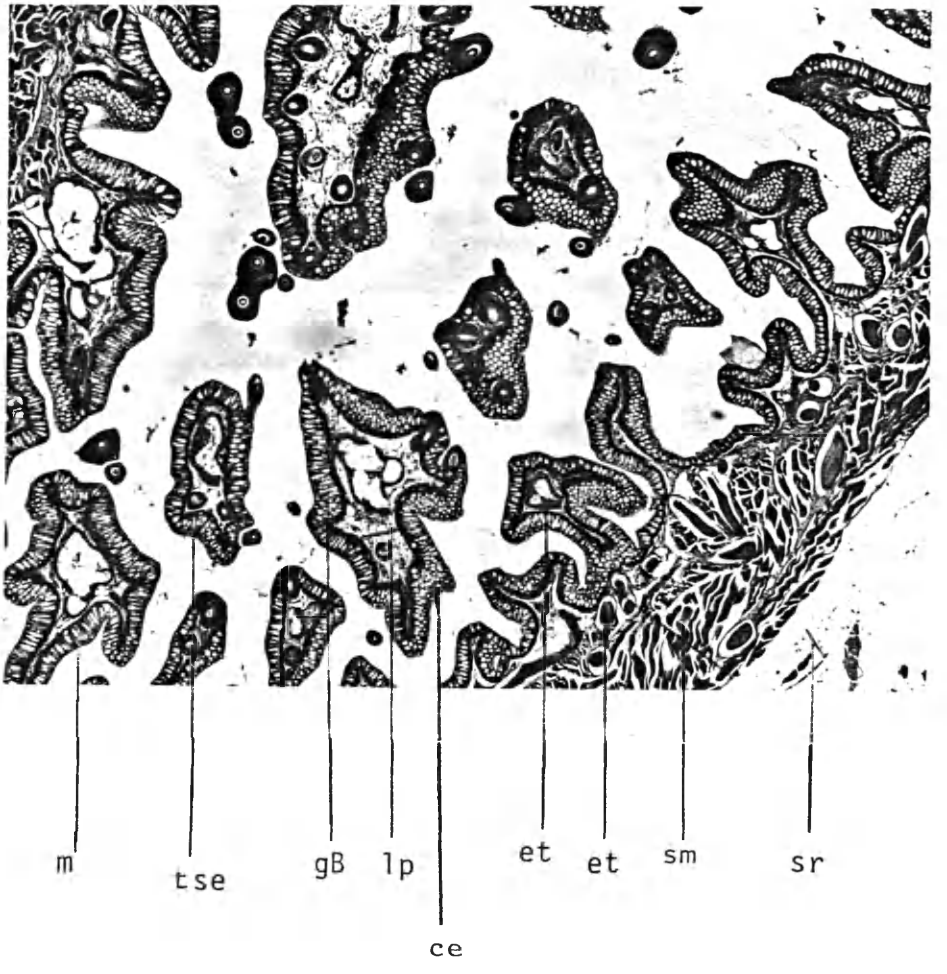

m
tse
gB
lp
ce
et
et
sm
sr

Figure 12. Mucosa of the pharyngeal sac of a 152 mm SL butterfish. gB, Type B goblet cell; n, nucleus of goblet cell; et, esophageal tooth - in section; ce, cuboidal epithelium; lp, lamina propria (longitudinal section - HHE stain).

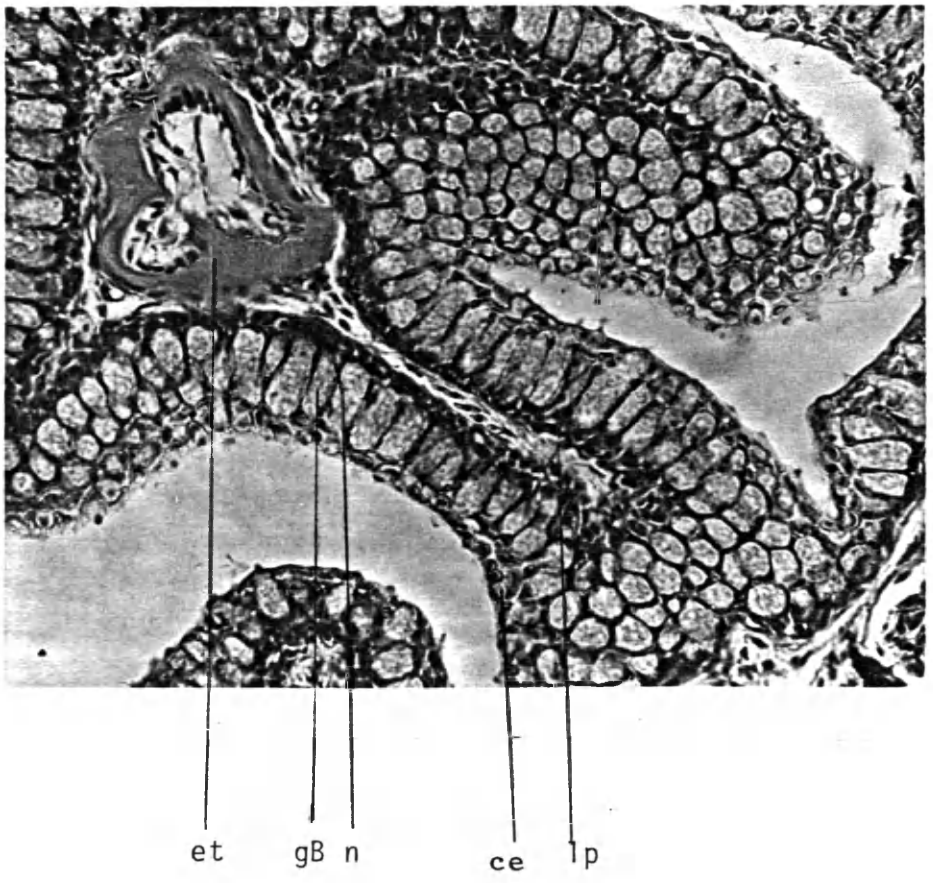

et
gB
n
ce
lp

Figure 13. Central lumen of posterior portion of pharyngeal sac of an 87 mm SL butterfish. sse, stratified squamous epithelium; gA, Type A goblet cell; sph, sphincter - circular muscle bundle; lp, lamina propria (longitudinal section - HHE stain).

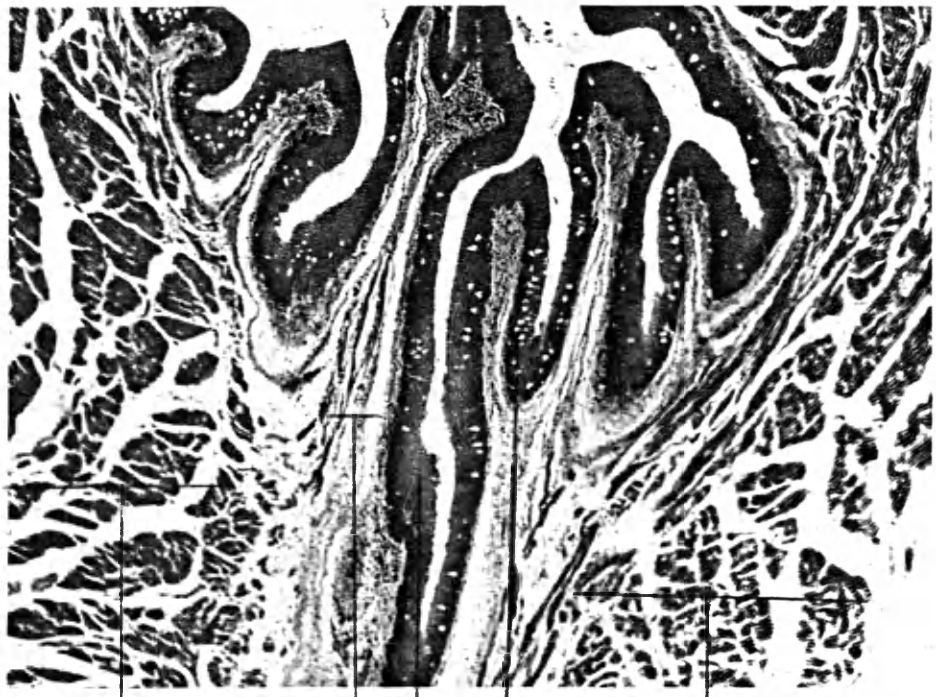

sph
lp
sse
gA
sph

Figure 14. Lateral wall of the pharyngeal sac of a 34 mm SL harvestfish. m, mucosa; sse, stratified squamous epithelium; tse, transitional squamous epithelium; gB, Type B goblet cell; et, esophageal tooth - in section; lp, lamina propria (longitudinal section - HHE stain).

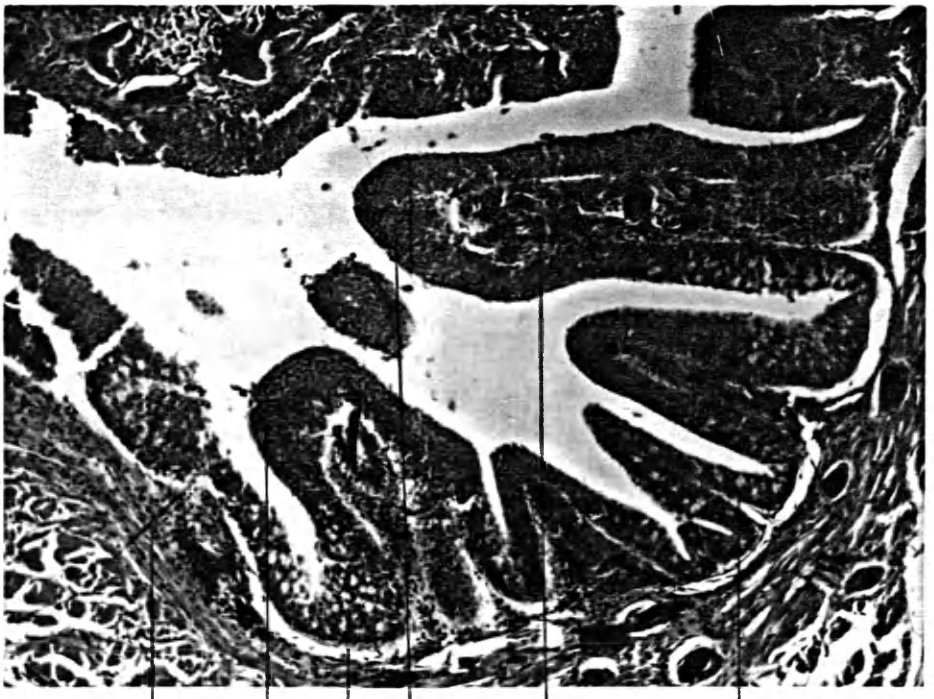

lp
sse
tse
m
et
gB

Figure 15. Central lumen of posterior portion of the pharyngeal sac of a 40 mm SL harvestfish. m, mucosa; sse, stratified squamous epithelium; lp, lamina propria (longitudinal section-HHE stain).

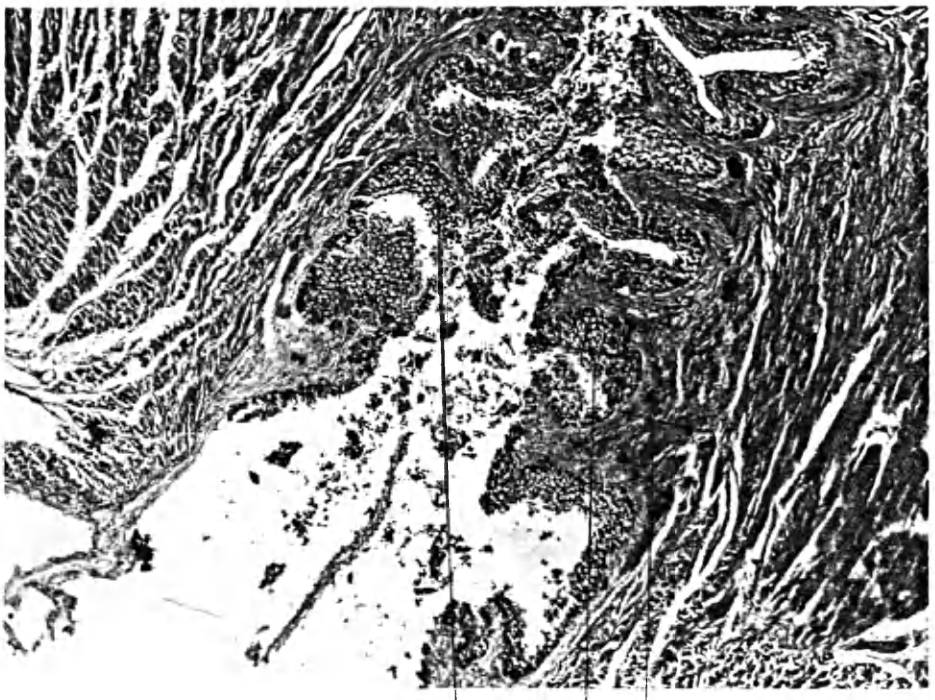

sse
m
lp

Figure 16. Mucosa of the pharyngeal sac of a 90 mm SL butterfish. ABpH2.5-PAS stain. gB, Type B goblet cell - AB positive (blue) (longitudinal section).

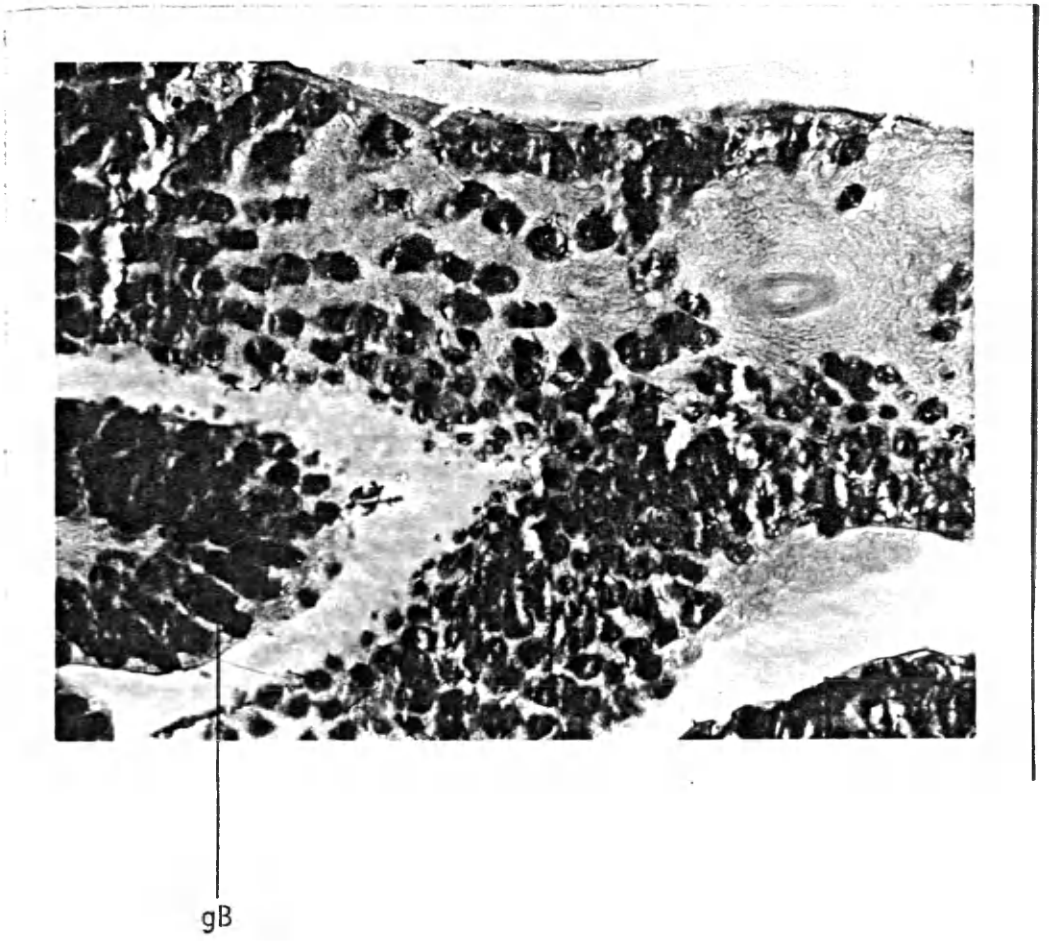

gB

Figure 17. Mucosa of the pharyngeal sac of an 87 mm SL butterfish. ABpH1.0-PAS stain. gB, Type B goblet cell - PAS positive (magenta) (longitudinal section).

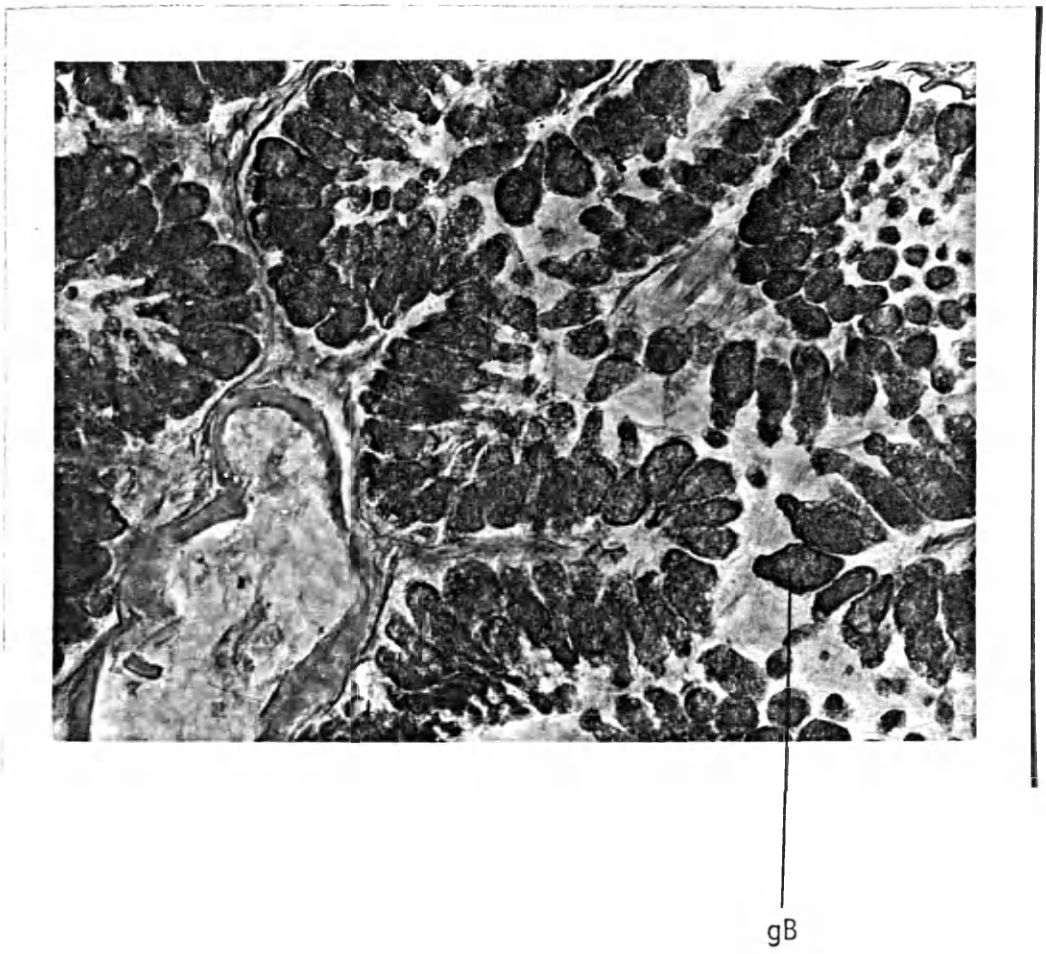

gB

Figure 18. Buccal cavity of a butterfish. m, mucosa; se, squamous epithelium; bm, basement membrane.

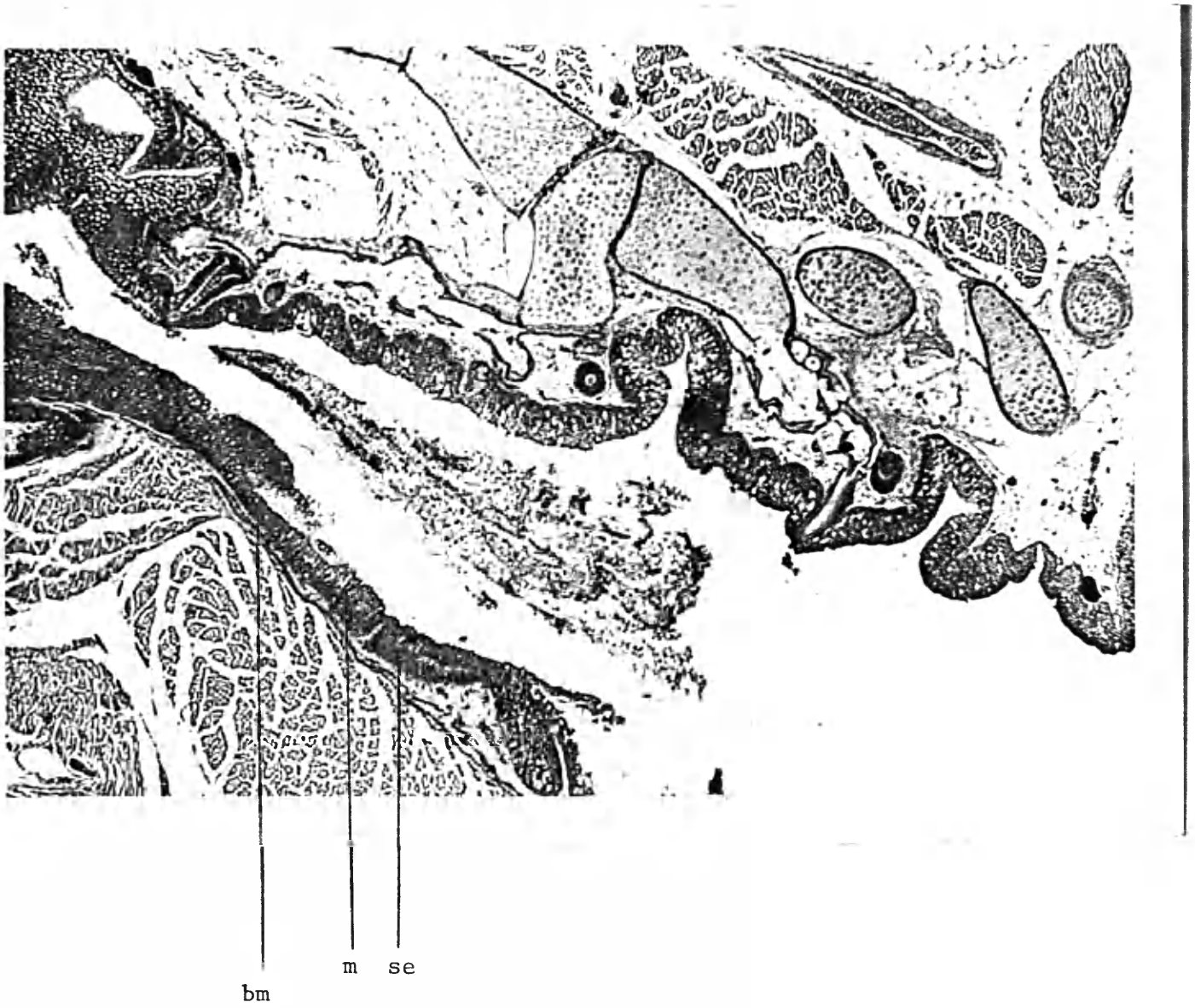
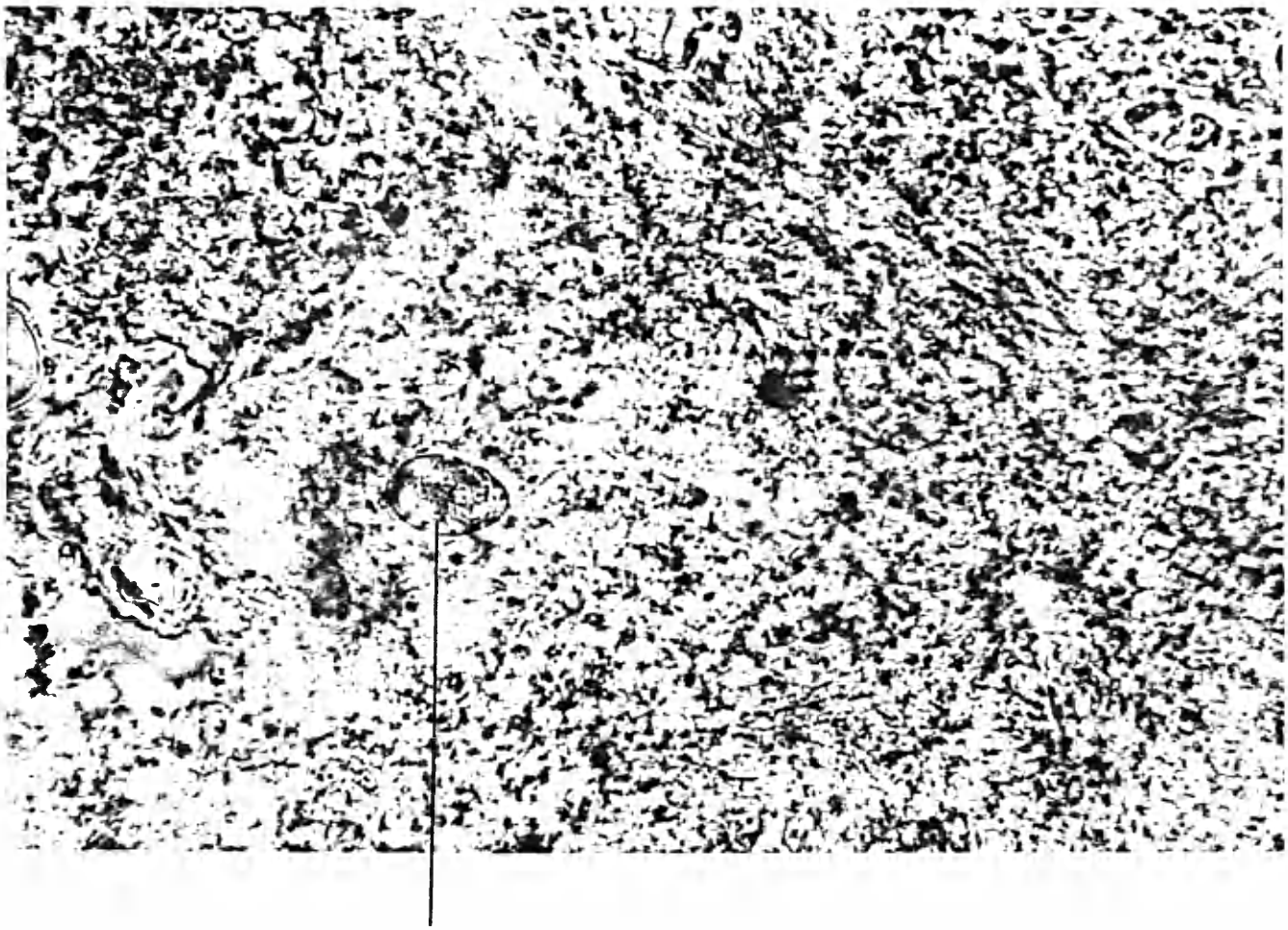
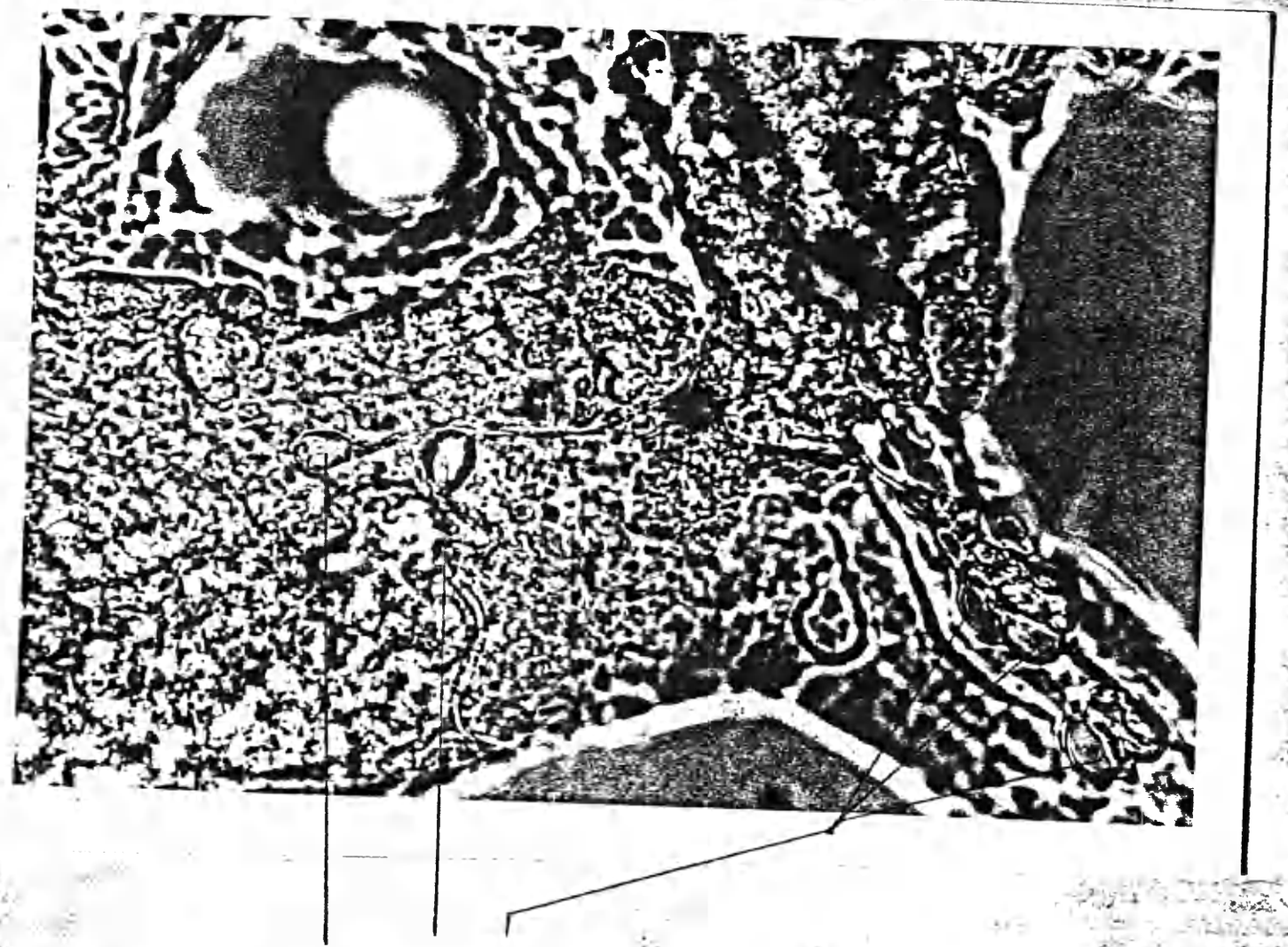

bm
m
se

Figure 19. Type I nematocyst of sea nettle (from stomach content sample of harvestfish).



nematocyst

Figure 20. Type III nematocyst of sea nettle (from stomach content sample of harvestfish).



nematocysts