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DIGESTIVE SYSTEM AND FEEDING HABITS OF THE CUNNER, *TAUTOGOLABRUS ADSPERSUS*, A STOMACHLESS FISH^{1,2}

LABBISH NING CHAO³

ABSTRACT

The cunner, *Tautogolabrus adspersus*, completely lacks a morphologically or physiologically distinct stomach. The alimentary tract consists of the pharynx followed by a short esophagus with an esophageal-intestinal valve at the junction of esophagus and intestine. The intestine has three limbs and an S-loop. The intestinal bulb where the bile duct enters is present at the anterior end of the first limb. The border between the posterior end of S-loop and the rectum is marked by the intestinal-rectal valve. Histological and histochemical observations indicate that the rodlet cells, wandering cells, longitudinal muscle layers, and the rectal valve differ in minor ways from those of other stomachless fishes. Different forms of rodlet cells are found in the bile duct. An alkaline condition (pH values between 7.0 and 8.5) prevails throughout the alimentary tract. Alkaline phosphatase reaction was demonstrated only when food was present in the gut. Cunner are carnivorous, and the feeding habits change with growth. Juveniles feed mainly on planktonic crustacea and adults on sessile animals (mussels and barnacles). The time between ingestion and defecation of mussels (*Mytilidae*) by cunner is 10 to 14 hr. Intact mussels can pass through the alimentary tract of the fish undamaged and alive.

The most abundant labrid of the New England region, the cunner, *Tautogolabrus adspersus* (Walbaum), lacks a stomach. The absence of a stomach is here defined as the lack of an expansion of the alimentary tract between the end of the esophagus and the entrance of the bile duct into the intestine (Figure 1). The mucosa of this region lacks gastric epithelium and gastric glands. The alimentary tract is alkaline and lacks peptic digestion. Lack of a stomach appears to be a phylogenetic characteristic of the family rather than an adaptive one associated with feeding in this particular species.

The absence of a morphological stomach in teleostean fishes has been recorded in various species of several families, i.e., Atherinidae, Blenniidae, Callionymidae, Cobitidae, Cyprinidae, Cyprinodontidae, Gobiesocidae, Gobiidae,

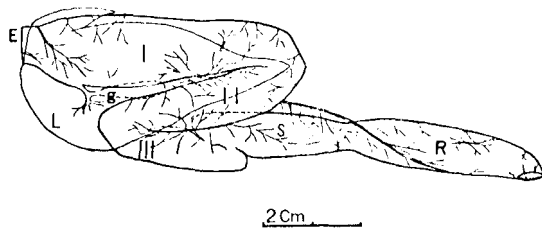


FIGURE 1.—Lateral view of the alimentary tract of a 280-mm SL cunner. E, esophagus; g, gallbladder; I, II, III, sections of intestine; S, S-loop of intestine; L, liver; R, rectum.

Labridae, Mugilidae, Poeciliidae, Scaridae, and Syngnathidae. These families have different feeding habits as noted by Ishida (1936), Barrington (1942), Suyehiro (1942), and Al-Hussaini (1947b) and are not closely related phylogenetically. Al-Hussaini (1949a) also recorded different feeding habits among three stomachless species of the family Cyprinidae: *Cyprinus carpio*, *Rutilus rutilus*, and *Gobio gobio*; they are herbivorous, omnivorous, and carnivorous, respectively. Physiological lack of stomach has been noted in various fishes: *Fundulus heteroclitus* by Babkin and Bowie

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(1928); Cyprinidae by Szarski (1956); *Spheroides niphobles* by Ishida (1936); Scaridae and Labridae by Gohar and Latif (1959). Both morphological and physiological characters of the stomachless fishes appear to be characteristic of the Labridae.

The morphology and histology of the entire alimentary tract in the cunner were described from the protrusible lip to the anal papillae. A histochemical study was made on the gut, i.e., the postpharyngeal portion of the alimentary tract. Also, feeding habits and habitat, gut contents, and the movement and digestion of food were investigated.

MATERIALS AND METHODS

The fish were collected at East Point, Nahant, Mass., from May to September 1970 and 1971. Larger specimens, over 100 mm SL (standard length), were taken by hook and line fishing along the shore, and smaller ones in plankton hauls, by bottom dredging, hand netting, and rotenone poisoning in tide pools. Some specimens were maintained in constant running seawater aquaria and fed with mussels (*Mytilidae*).

Histological and histochemical studies were made after starvation (7-10 days) and after feeding. Specimens less than 40 mm SL were killed in 10% Formalin,⁴ larger ones by severing the spinal cord and by intracoelomic injection of Dilantin (sodium diphenylhydantoin, USP) anesthetic (0.1 ml/10 g body weight). Tissues were fixed with absolute acetone, Baker's Formalin, Bouin's (also with seawater), Helly's, Hollande-Bouin's or Zenker's fixatives in order to demonstrate specific cell types. After fixation, dehydration was done in two ways: the standard method of ethyl alcohol or from water to Cellosolve (2-ethoxyethanol). Infiltration and embedding were carried out using Steedman polyester wax (1960); serial sections were cut at 1 to 8 μ . A variety of routine histological and histochemical stains were used, including hematoxylin (Ehrlich's, Galigher's, Heidenhain's Iron Alum, Groat's) counterstained with

eosin or fast green, Giemsa (Mallory, 1944, in Humason, 1967), Gomori's trichrome (1950, in Humason 1967), Heidenhain's azan (1938, in Humason, 1967), Masson's trichrome mixture (Gurr, 1956, in Humason, 1967). Histochemical methods included: alcian blue (Steedman, 1950; modified by Mowry, 1956, 1963, in Humason, 1967), periodic acid Schiff's technique (McMann's and Mowry, 1960, in Humason, 1967), toluidine blue (Lillie, 1929, in Humason, 1967). Acid and alkaline phosphatase tests were done by Gomori's modification according to Pearse (1960).

To determine the natural food and feeding habits, gut contents were examined immediately after capture, or specimens were frozen for subsequent examination. Also the feeding habitat was observed by SCUBA diving. Food movement and digestion rates were observed in specimens from 150 to 200 mm SL which were fed whole, small mussels less than 20 mm (shell length), or the visceral mass of larger mussels. Cunnners were either fed daily or were starved for 7 days prior to experimentation. Fish were allowed to feed voluntarily on a cluster of mussels during the ½- to 1-hr periods. Uneaten mussels and broken shells were removed after the feeding period. Carmine, Chinese ink, or ultramarine blue were injected into the visceral mass as indicators. Fishes were killed by severing the spinal cord at the base of the skull, at 1-hr intervals from 0 to 36 hr after feeding. Autopsy was done immediately after sacrificing the fish in order to locate the position of the food. All pH values of the gut lumen were determined from narrow range pH papers.

Ten adults (180-240 mm SL) and 6 juveniles (30-34 mm SL) were used for histological and histochemical studies, and 68 specimens (30-300 mm SL) for analyses of gut contents.

RESULT

Morphology and Histology of the Alimentary Tract

As reported by previous authors for other labrids (Barrington, 1942; Suyehiro, 1942; Al-Hussaini, 1947b; Gohar and Latif, 1959,

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1961), the alimentary tract of the cunner consists of neither a morphologically nor a physiologically differentiated stomach. The alimentary tract can be divided into several regions; the preesophageal cavities, esophagus and esophageal-intestinal valve, intestine, rectal valve and rectum, and associated organs.

Preesophageal Cavities

This region has three parts: the mouth, buccal cavity, and pharyngeal cavity (Figure 2).

MORPHOLOGY.—Cunners have large caninelike or incisorlike teeth on the premaxillary and dentary bones. The protrusible premaxillary bears three or four rows of conical teeth directed posteriorly, as are the two or three rows of dentary teeth. The most anterior rows of both premaxillary and dentary teeth are two to four times larger than the other rows. Also, the anterior most teeth are larger than the following ones on the same row. Teeth from 15 specimens (130-230 mm SL) numbered 32-66 on the premaxillary and 21-44 on the dentary. The number of teeth increases with the size of the fish. Developing teeth were found at the edges of the older teeth on all tooth bearing bones. Longitudinal ridges of mucous membrane extended from the vomer to the pharynx on the roof of the buccal cavity.

The buccal valve is located posterior to the buccal cavity (Figure 2). There are no teeth on the vomer and palatine bones. A large tongue covers the entire floor of the anterior pharyngeal cavity and forms a sublingual cavity. The pharyngeal cavity is bounded laterally by gill arches. A yellowish brown mucous layer, patchlike and thicker than that in the buccal cavity, covers the entire roof and posterior part of the floor. Strong mucous secreting activities occur in this area. Both the upper and lower pharyngeal teeth are surrounded partially by this mucus. The pharyngeal teeth (upper 41-59, lower 28-56) are multitubercular and molari-form. A pair of upper pharyngeal bones attach to the epibranchial bones and a triangular lower pharyngeal plate is attached to the basi-branchial bones.

HISTOLOGY.—The mouth is lined with a stratified epithelium of the transitional type without a cuticular surface. The mucosa is thrown into ridges which start at the inner side of the protrusible lips (Figure 3) and extend to the esophagus. Taste buds lie on the crest of the ridges, and basophilic mucous secreting cells occur at the sides and bases, but the large acidophilic mucous cells present in the skin are absent here (Figure 3). Polyhedral cells and low-columnar cells constitute the rest of the layer. The mucosal layer and

FIGURE 2.—Mouth (M), buccal cavity (B), and pharyngeal cavity (P) of a 40-mm SL juvenile cunner ($\times 40$; power of observation). bv, buccal valve; d, dentary teeth; p, premaxillary teeth; T, taste bud.

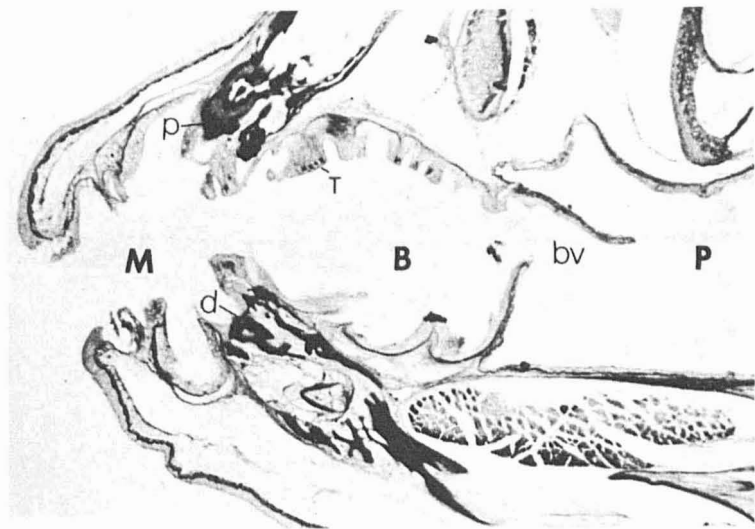
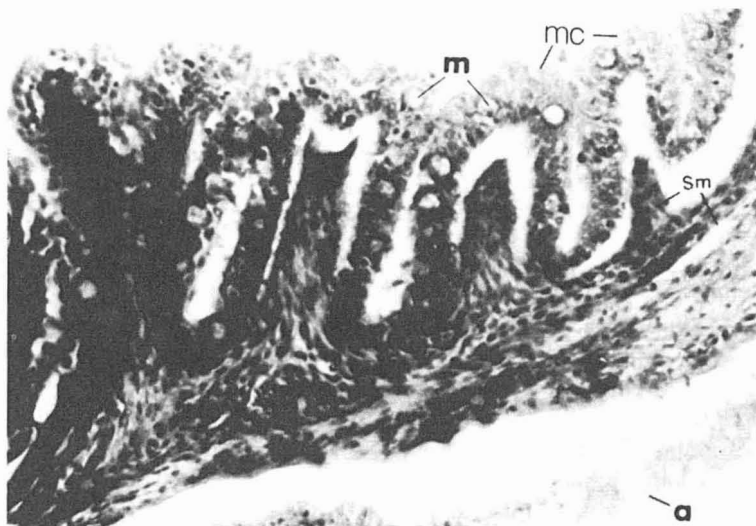


FIGURE 3.—Distribution of mucous secreting cells at sides and base of the mucosal ridges of protrusible lip in cunner ($\times 250$, x.s.). a, acidophilic mucous secreting cell; m, basophilic mucous secreting cell; mc, mucosal layer; Sm, submucosa.



the ridges are deepest in the region of the teeth where the mucosa may be over 10 cells thick. Elsewhere, the mucosa is four to six cells thick, except for the sublingual area and the lateral side of the buccal cavity where a thickness of only one or two cells may prevail. The lateral mucosa of the pharyngeal cavity (the internal epithelium of the opercle) is one cell thick and is entirely constructed of mucous secreting cells attached to the opercle by a thin layer of connective tissue (Figure 4). The ridges or mucosal folds are more prominent on the midlines of the roof and floor of the pre-

pharyngeal regions. There are no ridges on the surface of the sublingual cavity. The submucosa is a layer of fibrous connective tissue under the mucosa. It is continuous throughout this region, and the thickness is closely correlated with the depth of the mucosal folds.

Taste buds occur from the inside of the lips to the pharyngeal teeth (Figures 3 and 5) and occasionally are found on the gill arches. No taste buds were observed on the external side of lips, anterior sublingual cavity, or the lateral wall of the pharyngeal region. The aggregation of taste buds is closely related to the papillae

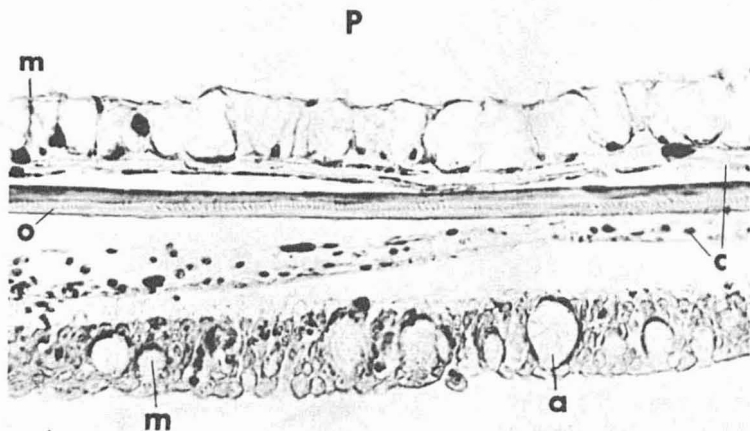


FIGURE 4.—Lateral mucosa of the pharyngeal cavity (P) entirely covered with mucous secreting cells in cunner ($\times 250$, x.s.). a, acidophilic mucous secreting cells; c, connective tissue; m, basophilic mucous secreting cell; o, opercle.

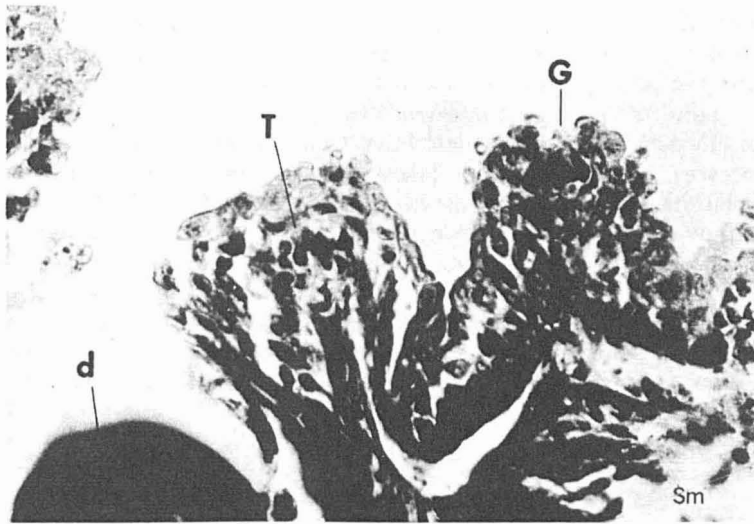


FIGURE 5.—Taste buds (T) on the mucosa of protrusible lip of cunner ($\times 400$). d, dentary tooth; G, gustatory pore; Sm, submucosa.

folds, i.e., to the middle lines of this region and to the teeth. The taste bud is an ovoid structure of epithelial cells (Figure 5). A gustatory pore is present at the tip of each taste bud. A thickening of the submucosal layer contains the nerve fiber and forms the base of the taste bud.

Basophilic mucous secreting cells continue from the external lips and appear throughout this region. Mucous cells increase in numbers posteriorly. The lateral surface of the pharyngeal cavity and the ridges among the teeth are covered by mucous secreting cells. Beneath

the basal membrane of the mucous layer, the submucosa is formed of a thick layer of collagen fibers toward the posterior part of the pharyngeal cavity. The areolar connective tissue of the tunica propria and submucosa are similar in this region. Lymphocytes and granulocytes are apparent in the submucosa of the ridges among the pharyngeal teeth. Circular muscles which connect to the head bones are external to the areolar connective tissue.

The epithelium and submucosa of the tongue are similar to that of the pharyngeal cavity but are much more compact (Figure 6). Posteriorly,

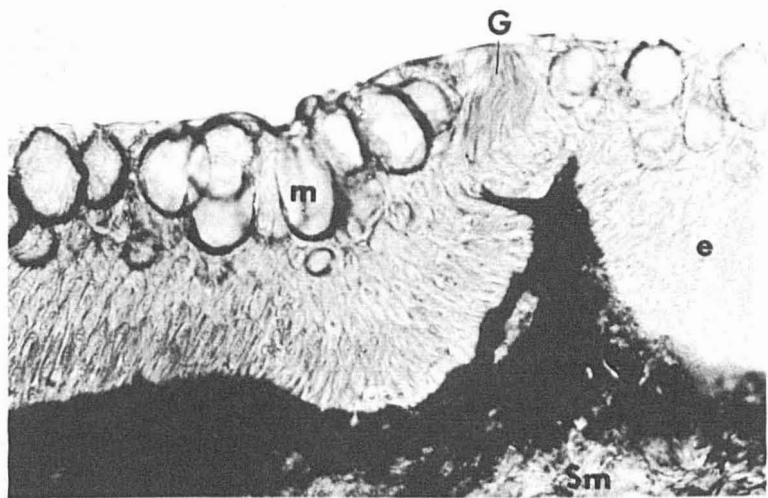


FIGURE 6.—Mucosa (e) and submucosa (Sm) of the tongue of cunner with hairlet sensory organ ($\times 400$). e, epithelium (mucosa); G, gustatory pore of hairlet sensory organ; m, basophilic mucous secreting cells.

the submucosa below the dorsal epithelial layer is thicker than beneath the ventral layer. A flaplike structure directed posteriorly was observed on the ventral side of the tongue. Sensory organs, consisting of numerous sensory cells provided with hairletlike processes, occur on the tongue (Figure 6) and open into the pharynx through a gustatory pore.

Esophagus and Esophageal-Intestinal Valve

Posterior to the pharyngeal teeth, the pharynx constricts markedly to form a short

muscular tube, the esophagus, which opens directly into the intestine through a muscular valve. Distinct longitudinal ridges (Figure 7) continue from the pharynx to the esophageal-intestinal valve and then diverge in the intestine. There are no transverse connecting cores between the longitudinal folds. These folds branch shortly anterior to the esophageal-intestinal valve (Figure 8). The mucous cells in the epithelium disappear in this region (transitional zone). This is more prominent in small specimens (less than 40 mm SL) than in larger specimens (200 and 210 mm SL).

FIGURE 7.—Longitudinal ridges of the anterior esophagus of a 40-mm SL juvenile cunner ($\times 40$, x.s.). ar, areolar connective tissue; cm, circular muscle layer; L, liver; m, mucous; Sk, skeletal muscle; sr, serosa; st, striated muscle.

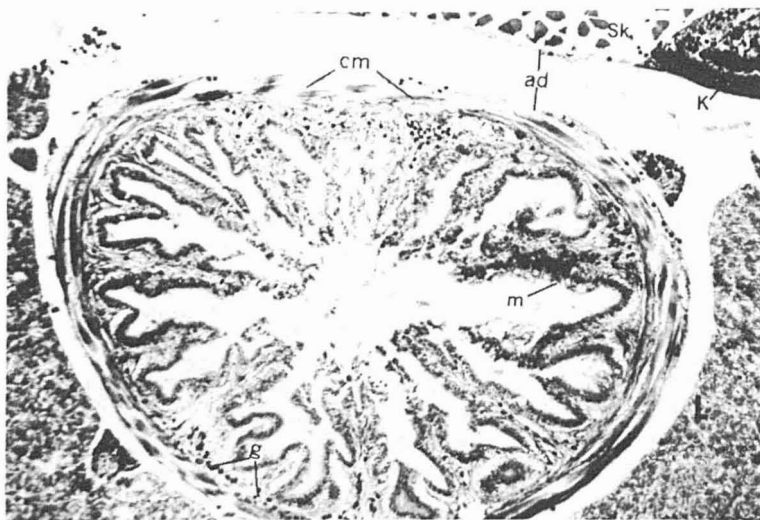


FIGURE 8.—Transitional zone anterior to the esophageal-intestinal valve in the esophagus of a 40-mm SL cunner ($\times 40$, x.s.). ad, adventitia; cm, circular muscle layer; g, granulocyte; K, kidney; L, liver; m, mucous secreting cell; Sk, skeletal muscle.

MUCOSA.—The epithelium of the anterior esophagus is a modified transitional type (Figure 9) with large mucous cells extending to various depths from the surface. While the esophagus proceeds posteriorly, the stratified epithelium gradually becomes simple columnar in the transitional zone between the esophagus and intestine. The flattened nucleus of each mucous cell is pressed against the base by the large vacuole. The mucous secreting cells do not narrow appreciably where they open into the lumen. They can occupy nearly the entire surface and thickness of the epithelium, and they decrease in numbers from anterior to posterior. Also, smaller mucous cells with large vacuoles filled with mucous were found among the basal cells in the anterior half of the esophagus (Figure 9). The columnar epithelium appears gradually while the mucous cells decrease toward the transitional zone. The large oval nuclei of columnar cells are located at the basal level under the level of the mucous cells in the transitional zone. The basal cell layer appears to maintain a uniform thickness throughout the esophagus. These cells are small with relatively large nuclei. Occasionally, taste bud like structures were found at the tip of major folds in the most anterior part of the esophagus. No cilia are present on the epithelium of the esophagus. The mucosal layer

of the esophageal-intestinal valve is similar to that of the transitional zone, except for an increased number of mucous secreting cells, especially, in the distal portion of the valve (Figure 10).

SUBMUCOSA.—The submucosal layer is an areolar connective tissue between the epithelium and the muscularis. The stratum compactum (Figure 9) is a layer of compacted fibrous connective tissue attached to the basal membrane of the epithelium. The rest of the areolar connective tissue is highly vascularized. Longitudinal bundles of striated muscles extend from the pharynx to the base of the esophageal-intestinal valve in the connective tissue. Also, in the anterior half of the esophagus, these longitudinal muscles are dispersed irregularly up to half of the depth of the folds in the submucosa (Figures 7, 9). Collagen fibers constitute the framework of the submucosal layer. The vascular system is scattered in this framework, and leucocytes, lymphocytes, fibrocytes, and granular cells are present. The granulocytes first appear in the posterior half of the esophagus (Figure 8). The submucosa becomes much thicker on both sides of the esophageal-intestinal valve. Increasing numbers of granulocytes appear in the submucosa of the intestinal side of the valve.

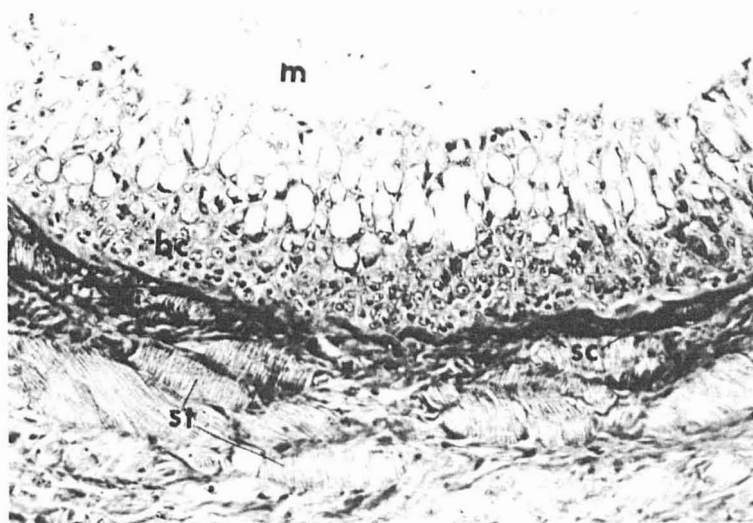
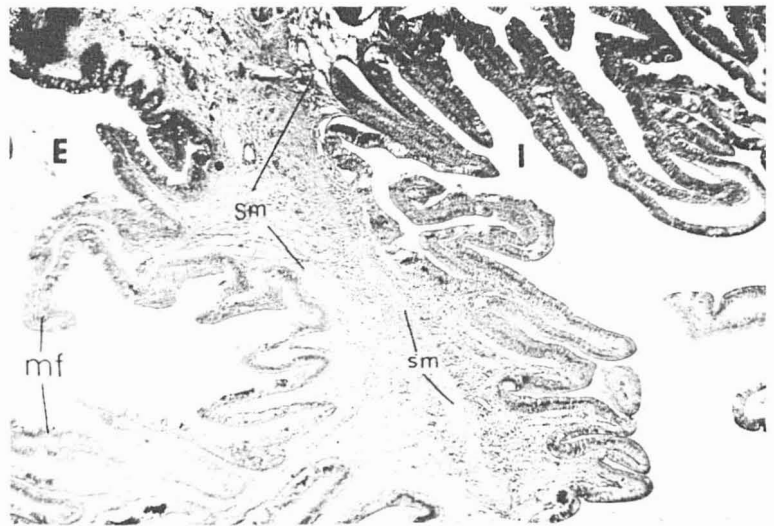


FIGURE 9.—Mucosa and submucosa of the anterior esophagus of a 200-mm SL cunner ($\times 400$, x.s.). m, mucous secreting cell; sc, stratum compactum; st, striated muscle.

FIGURE 10.—The esophageal-intestinal valve of a 240-mm SL cunner ($\times 40$). E, esophagus; I, intestine; mf, mucosal fold; sm, smooth muscle; Sm, submucosa.



MUSCULARIS AND SEROSA.—A very thick circular layer of striated muscles continues from the pharynx forming the external muscular layer of the esophagus (Figures 7, 8). It is invaded by elements of the vascular system accompanied by connective tissue; thus it is a loose rather than a compact layer. This muscularis appears to decrease in thickness posteriorly toward the esophageal-intestinal valve, where it forms a triangular, sphincterlike structure along the base of the valve fold. The basal muscularis of the valve is formed of smooth and striated muscles and retains significant connective tissue components. Leucocytes, fibroblasts, and a few granular cells also occur in this connective tissue. The distal portion of the valve contains a single undivided smooth muscle layer (Figure 10). This ring is continuous with the circular muscle layer of intestine.

The anterior esophagus is attached to the associated skeletal muscles by a layer of adventitious tissue. After passing through the transverse septum, the esophagus separates from the visceral wall ventrally. The dorsal wall of the midesophagus is attached to the kidney and skeletal muscles by a thin layer of adventitia (Figures 7, 8). The ventral side is covered by the peritoneal lining (serosa) and is separated from the circular muscularis by a varying thickness of areolar connective tissue (Figure 7). Posteriorly, the serosa increases in

thickness in the vicinity of the esophageal-intestinal valve.

Intestine

The intestine starts posterior to the esophageal-intestinal valve and extends to the rectal valve. The intestine can be divided into four sections (Figure 1). The first section (I) begins dorsally and proceeds posteriorly and slightly to the left. It turns ventrally and extends anteriorly to the right as section II. The second loop curves abruptly posterior at about the level of the intestinal bulb. The third section (III) proceeds posteroventrally to an S-shaped loop which is connected by a short, straight portion of the intestine to the rectum. Intestinal veins from sections I, II, III, and the S-loop are associated with the anterior mesenteric vein and the posterior mesenteric vein from the rectum (Figure 1). The intestine has a consistent histological organization throughout its length with minor cytological variations. The mucosa is more complex in the intestine than in the esophagus and has zigzag folds as well as secondary and tertiary folds. The intestinal bulb is a dilation of the anterior portion of the intestine where the latter joins the esophagus. The mucosal folds of the intestinal bulb are deeper than in other portions of the intestine. There are four distinguishable layers

in the intestinal wall: mucosa, submucosa, muscularis, and serosa (Figure 11).

MUCOSA.—The epithelium of the mucosa consists mainly of columnar absorptive cells and goblet cells. The columnar absorptive cells of the cunner are similar to those of the stomachless cyprinids described by Al-Hus-saini (1949a). The epithelium can be divided into the same four regions: the free border, the subborder, the supranuclear, and the infra-nuclear zones (Figures 12, 13, 14). The free

border of the mucosa is sharply defined throughout the intestine. The striated border (or subborder) in the active digestive epithelium (Figure 14) is slightly thicker than in the inactive (Figure 13) epithelium. It stains intensively with periodic acid-Schiff (PAS) (Figure 15) and shows very prominent digestive effects in the active epithelium (Figure 14). In the resting cell of starved fish, the cytoplasm can be divided into a subcuticular zone and a layer of fine granules (Figures 12, 13). The sub-cuticular zone in starved fish is a compara-

FIGURE 11.—Mucosal folds of the posterior section I of the intestine of a 240-mm SL cunner ($\times 100$, x.s.). cm, circular muscle layer; lm, longitudinal muscle layer; mc, mucosa; ms, muscularis; Sm, submucosa; sr, serosa.

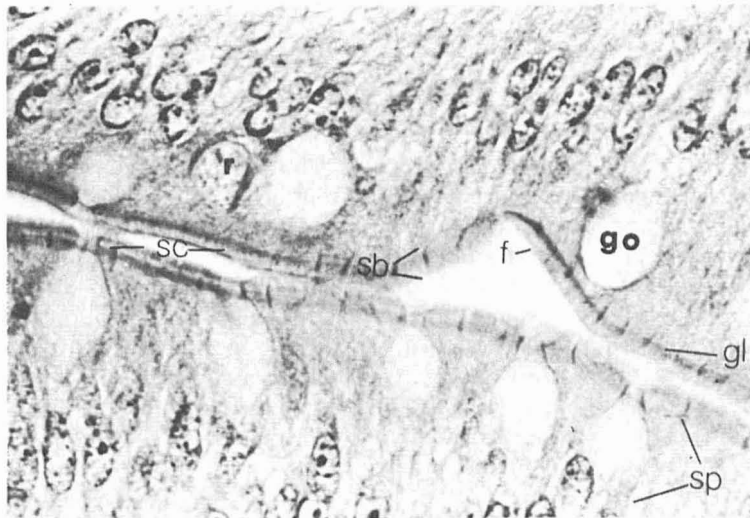


FIGURE 12.—Free border (f) of the columnar epithelium of the intestine (I) of cunner ($\times 1,000$). gl, granular layer; go, goblet cell; r, rodlet cell; sb, subborder; sc, subcuticular zone; sp, supranuclear zone.

FIGURE 13.—The mucosal epithelium of the intestine (II) of cunner ($\times 1,000$). am, ameobocyte; g, granulocyte; gl, granular layer; in, infranuclear zone; nz, nuclear zone; p, polymorpho-leucocyte; pr, parasite; sb, subborder; sc, subcuticular zone; sp, supranuclear zone.

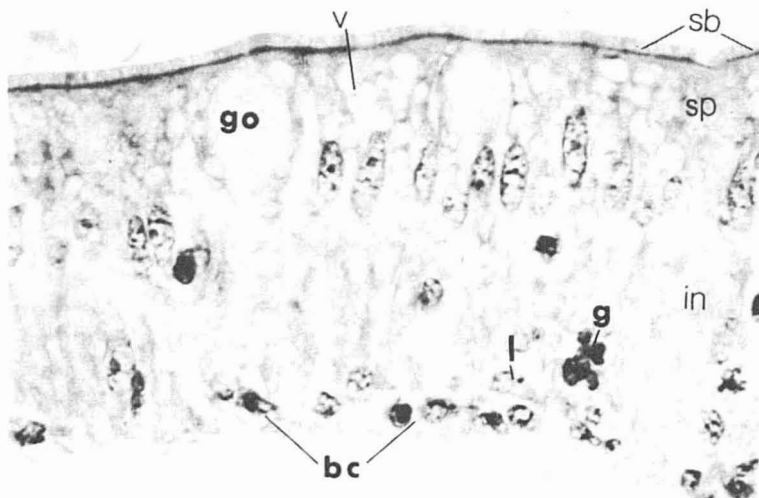
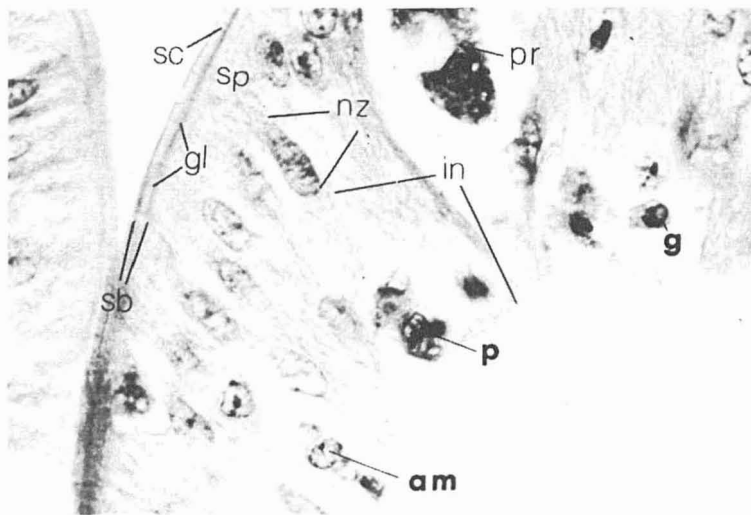


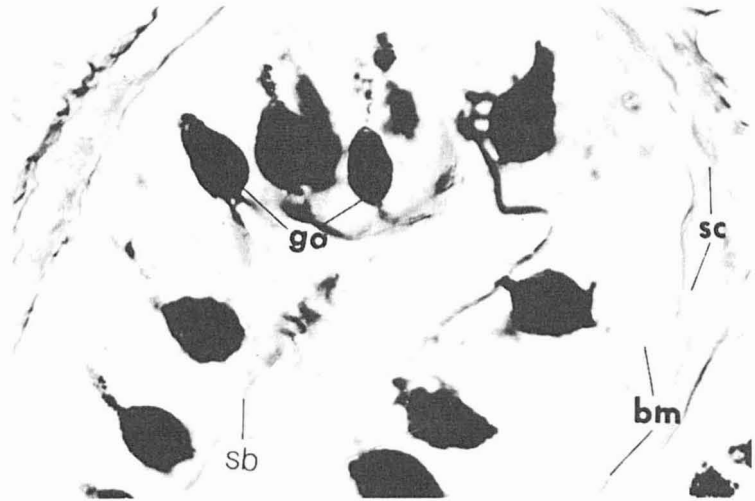
FIGURE 14.—The active absorption epithelium of the posterior intestine (III) of cunner ($\times 1,000$). bc, basal cells; g, granulocyte; go, goblet cell; in, infranuclear zone; l, lymphocytelike cell; sb, striated border (subborder); sp, supranuclear zone; v, vacuole.

tively clear region and has a higher affinity for eosin Y than the other regions. Cell membranes are indistinguishable or indistinct resulting in a homogeneous appearance. The granular layer (Figures 12, 13) continues to the supranuclear zone and is more basophilic than other parts of the nonnuclear zones. In well-fed specimens, the resting cells have the same appearance as in the starved ones. Numerous unstained vacuoles are present in the subborder and the supranuclear zone of the active cells of the absorptive epithelium (Figure 14). In many cases, vacuoles also appeared in the

infranuclear zone. The granular cytoplasm of the active cells forms a strong basophilic network around the vacuoles.

The nuclei of absorptive cells are ellipsoidal with abundant basophilic granulation and a large centrally located nucleolus. The nuclei are located at the middle or the basal third of the columnar epithelium at the intestinal bulb and then gradually move to the upper third of the epithelium posteriorly. As a result, the depth of the supranuclear zone decreases slightly posteriorly. The nuclei of the developing absorptive cells, the goblet cells, and other non-

FIGURE 15.—PAS demonstration of goblet cells (go) in the intestinal epithelium (II) of cunner ($\times 1,000$). bm, basement membrane; sb, subborder; sc, stratum compactum.



absorptive cells are found always in the infranuclear zone. The mucous secreting cells in the intestine (Figures 12, 14, 15) differ morphologically from the mucous cells in the pre-esophagus (Figures 3, 4, 6, 9). They are elongate with a thin neck extending to the surface and a rodlike root extending straight down to the infranuclear region (Figures 12, 15). The ovoid nucleus of the mucous cell sits at the bottom of this root. Only the mucous secreting cells near the esophageal-intestinal valve of the intestinal bulb are the same shape as the mucous secreting cells of the esophagus. Mucous

cells also appear to develop in the infranuclear region and grow or extend gradually to the lumen.

A very distinct type of cell, the rodlet cell, a term introduced by Bullock (1963) for these cells in salmonids, was also found in the mucosa of the cunner (Figure 12). They are distributed throughout the intestine but are more abundant in sections II and III. They are most abundant in the bile duct (Figure 16) and inner epithelium of the gallbladder (Figure 17). The elongate, oval, rodlet cells are usually located in the supranuclear region of the mucosa and

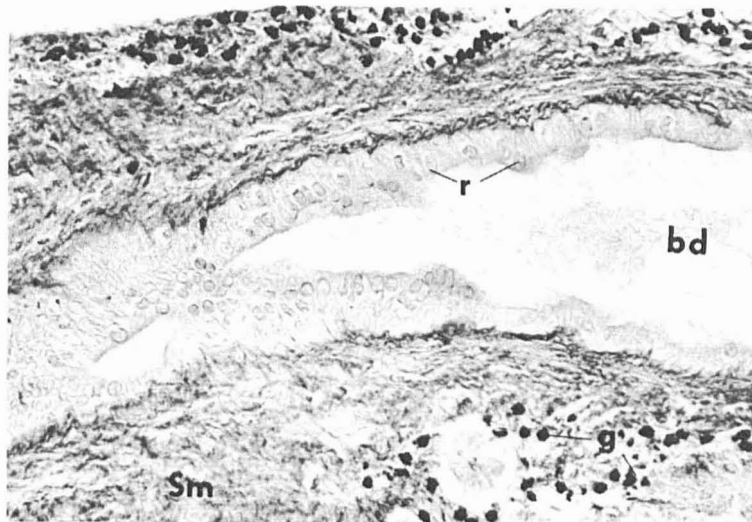
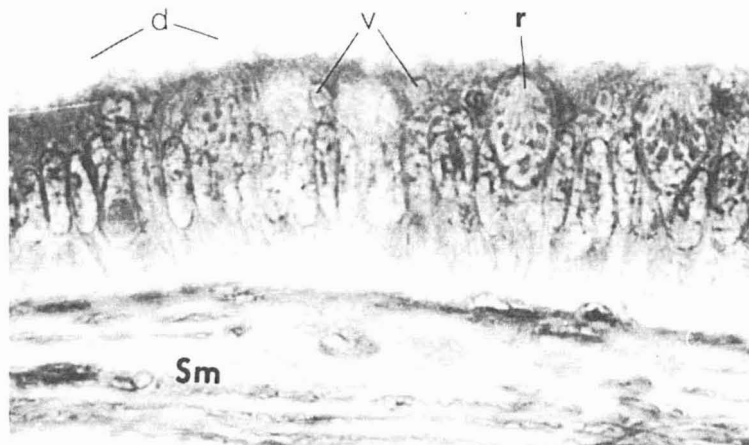


FIGURE 16.—The bile duct (bd) of cunner with abundant rodlet cells (r) ($\times 400$). g, granulocytes; Sm, submucosa.

FIGURE 17.—Epithelium in the gallbladder of cunner showing rodlet cells (r), vacuoles (v), and digitiform processes (d) ($\times 1,000$). n, nucleus of rodlet cell; Sm, submucosa.



are in direct contact with the lumen. The cytoplasm of the rodlet cells (Figure 17) consists of many granules with a threadlike structure extending from each granule to the distal end of the cell. These granules are acidophilic and stained deeply with PAS technique. A large nucleus is near the base of the cell. Various developmental stages of the rodlet cells can be observed in some of the bile duct preparations.

SUBMUCOSA.—The submucosa, which forms the core of the mucosal folds of the intestine, is a single homogeneous layer of fibrous connective tissue between the epithelium and

muscularis (Figure 11). The stratum compactum, a thin layer of dense connective tissue, can be identified just beneath the mucosa (Figure 15). The collagenous fibers in the submucosa are more dense at the posterior portions of the intestine and rectum. Several cell types are scattered in the collagenous tissue. The most abundant cells are fibroblast of different stages. The young fibroblast has an ovoid nucleus and basophilic astral cytoplasm (Figure 18). The fibrocytes (mature fibroblasts) are most easily seen in the submucosa of the top of the folds. It is very difficult to see any cytoplasm in these fusiform cells. The nuclei of fibrocyte is elongate or oval in shape with a

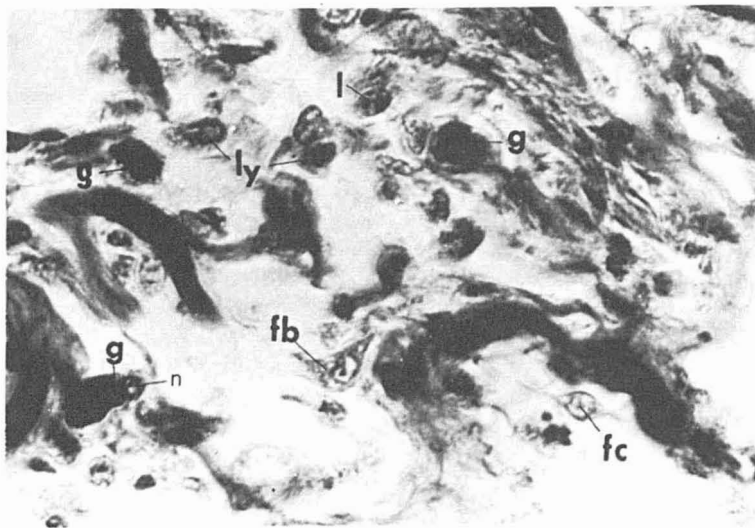


FIGURE 18.—The submucosa of the intestine of cunner ($\times 1,000$). fb, fibroblast; fc, fibrocyte; g, granulocyte; l, lymphocytelike cell; ly, lymphocyte; n, nucleus of granulocyte.

very dense eccentric nucleolus (Figure 18). Granular wandering cells occur in the mucosa, submucosa, and muscularis (Figures 13, 14, 18), and are most abundant in the submucosa at the base of the mucosal folds. In the mucosa they are found in both the supranuclear and infranuclear zones. These cells are packed with basophilic granules. The nuclei are always pushed to the cell margin by the large granules (Figure 18). Some of the granulocytes present in the mucosa have very large compact inclusion bodies (Figures 14, 18). The polymorphonuclear leucocytes represent one type of wandering cell (Figure 13). Its nucleus has two or three lobes, and there are very fine neutrophilic granules in the cytoplasm. These leucocytes were encountered only in the infranuclear zone and the submucosal layer of the fold. A lymphocytelike type of cell was encountered also in the infranuclear zone or the base of the epithelium. This type of cell has two nucleoli in the clublike nucleus and very little cytoplasm (Figures 14, 18). They also were encountered in the submucosa occasionally. The typical lymphocytes with large nuclei and thin basophilic cytoplasm were found in the submucosa (Figure 18). At least one type of amoebocyte (Figure 13) was found in the mucosa and submucosa. This type of amoebocyte has a round nucleus with karyosomes applied to the nuclear membrane and rays extending from the nucleolus which is often eccentric. Numerous

spherical granules and vacuoles occur in the cytoplasm. There are no significant differences in the distribution or types of wandering cells in the submucosa throughout the intestine.

MUSCULARIS AND SEROSA.—The typical vertebrate muscularis of inner circular and outer longitudinal smooth muscle prevails in the intestine of the cunner (Figure 11). A very thin layer of smooth, longitudinal muscle fibers (no more than two cells thick) can often be seen inside the circular muscle layer. These fibers appear at random in the first three sections of the intestine and become more prominent (two to four cells thick) from the S-loop to the rectal valve. A nerve plexus usually can be found between the muscle layers. The serosa is of a more uniform thickness than that in the esophagus and abuts directly on the extended muscularis.

Rectal Valve and Rectum

A muscular flap valve is present at the juncture of the intestine and rectum. The rectal valve is formed by a folding of the circular muscle layer and is not a sphincter valve of thickened muscularis. The two layers of the fold are separated by connective tissue (Figure 19). This layer of connective tissue contains granular cells which are more abundant in the submucosa of the rectal side of the valve. The

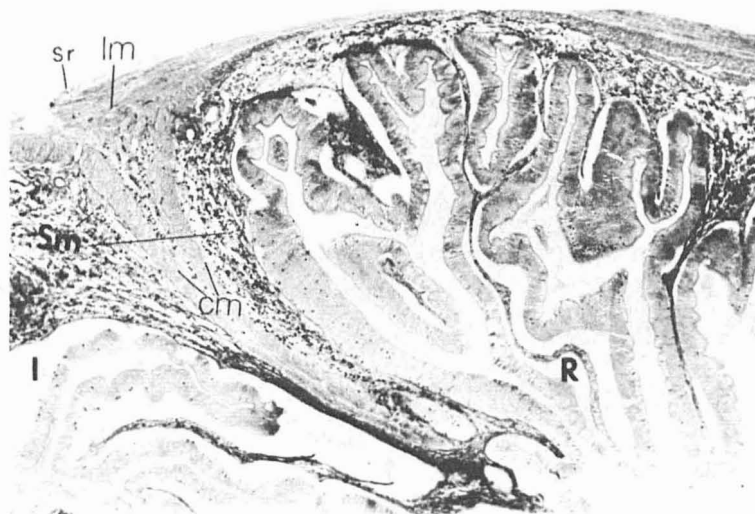


FIGURE 19.—Intestinal-rectal valve of a 210-mm SL cunner ($\times 40$, l.s.). cm, circular muscle; I, intestine; lm, longitudinal muscle; R, rectum; Sm, submucosa; sr, serosa.

nerve plexus, blood vessels, and longitudinal muscles merge in the connective tissue at the base of the rectal valve. Some bundles of the circular layer remain associated with the longitudinal layer at the base.

The rectum proceeds posteroventrally to the anus. In the anterior part of the rectum, the absorptive cells of the mucosa show more vacuoles in the supranuclear zone in well-fed specimens. The submucosal layer has more granulocytes than the intestine. The vascular system is also more prominent. The longitudinal muscle layer just inside the circular layer is distinct posterior to the rectal valve. Posteriorly in the rectum, the number of mucous cells decreases gradually and then increases around the anus. The epithelium of the rectum continues to the anal papillae (Figure 20). Granulocytes are the most abundant cell type in both the internal folds and external papillae of the anus. The circular muscle layer at the end of the rectum forms a sphincterlike structure. The longitudinal muscles and the nerve plexus radiate into the connective tissue around the anus. The serosa is replaced by an adventitia composed of an extensive development of fibrous connective tissue.

Associated Organs

GALLBLADDER—The gallbladder is half embedded into the liver and opens anteriorly

into the intestinal bulb via the common bile duct. The bile is usually dark green and has pH values between 7.5 and 8.5. The fullness of the gallbladder was usually inversely correlated to the fullness of the intestine. It is a highly elastic structure which becomes more elongate when full. The columnar epithelial cells of the mucosa have fingerlike projections extending toward the lumen (Figure 17); however, there are no mucosal folds. A small vacuolelike structure present in each columnar epithelial cell of the gallbladder at the supranuclear zone is stained intensively in fast green, aniline blue, and PAS preparations. Rodlet cells are present and are more concentrated in the bile duct than in the bladder itself (Figures 16, 17). The submucosa is a rather thin layer of very dense collagenous tissue in which a few granulocytes, fibrocytes, lymphocytes, and capillaries are present. Smooth muscle cells occur beneath the serosa, but their arrangement (spiral, random, etc.) could not be ascertained. The mucosa and submucosa of the bile duct are similar to those of the intestine; but mucous secreting cells are completely absent. The rodlet cells in the bile duct increase abruptly in number near its entrance into the intestine.

PANCREAS.—The pancreas is diffuse, forming small nodules, and consists of numerous small lobules scattered with fat and vascular

FIGURE 20.—External surface of the anal papillae of a 210-mm SL cunner ($\times 400$). a, acidophilic mucous secreting cell; g, granulocyte; m, basophilic mucous secreting cell; Sm, submucosa.



tissue in the mesentery (omentum). It is also dispersed into the liver in the vicinity of the bile duct. Granulocytes are very abundant around the pancreas and the hepatopancreatic complex. The pancreatic duct joins the bile duct near the entrance of the latter into the intestine. The mesenteric membranes are more prominent during late summer when fatty tissue accumulates after the active feeding season.

LIVER.—The liver is divided into three lobes. The central lobe, the largest one, is triangular in shape and the tip continues to the loop of sections I and II of the intestine (Figure 1). In large specimens this lobe elongates posteriorly and covers the spleen ventrally. Two smaller lobes extend lateral-dorsally to cover most parts of the esophagus and the intestine bulb.

Histochemistry

The PAS technique intensely stains the free border and subborder of the intestinal epithelium as well as the basal membrane and goblet cells (Figure 15). The goblet cells and the granules in the granulocytes and amoebocytes give the strongest PAS reaction. Alcian blue and toluidine blue methods stained only the mucoid contents of the goblet cells, indicating the presence of acid mucopolysaccharide

and mucin. None of the methods showed any secretory activity by the rodlet cells. There were no distinct differences in these reactions in the different portions of the intestine.

Throughout the alimentary tract the pH value ranged between 7.0 and 8.5. Acidic conditions were not found in either fed or starved specimens. Also, acid phosphatase tests were negative in all cases. Alkaline phosphatase can be demonstrated at the border of the epithelium throughout the gut except anterior to the esophageal-intestinal valve (Figure 21). No positive reaction for alkaline phosphatase was found in the epithelium of the gallbladder, bile duct, or pancreatic duct. Alkaline phosphatase activity was intense in the intestinal bulb and rectal valve, and it was most obvious on the distal surface of the intestinal folds in the presence of food particles.

Food and Feeding Habits

Cunners at East Point are abundant inshore during the summer and may feed intertidally during high tide. Cunner were observed swimming in the kelp beds and using the kelps *Agarum*, *Alaria*, *Laminaria*, etc. as shelter. Juveniles (less than 100 mm SL) moved intertidally or into tide pools where they use brown algae *Ascophyllum* and *Fucus* as shelter. The intestinal contents of 68 specimens (Table 1) show that the cunner is primarily carnivorous

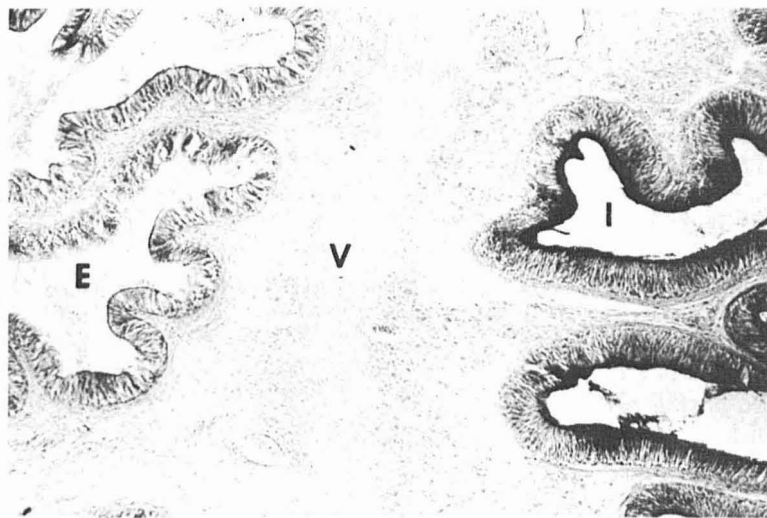


FIGURE 21.—Alkaline phosphatase test of the esophageal-intestinal valve (V) of a well-fed 180-mm SL cunner ($\times 100$, l.s.). E, esophagus; I, intestine.

TABLE 1.—Gut content of 68 cunners, *Tautoglabrus adspersus*, from Nahant, Mass.

Standard length (mm) Age group (years old) Specimens with food	30-50 0+ -1+		100-225 1+ -4+		230-300 4+ -6+	
	No.	%	No.	%	No.	%
Occurrences						
Mussels (<i>Mytilus</i> , <i>Modiolus</i>)			27	100.0	5	50
Bivalve larvae			5	18.5		
Gastropod (<i>Littorina</i> , <i>Thais</i> , etc.)			9	33.3	1	10
Barnacles (<i>Balanus</i>)			11	40.7	5	50
Sea urchin (<i>Strongylocentrotus</i>)			7	25.9	3	30
Crustaceans (amphipod, copepod, isopod, etc.)	8	100.0	3	11.1	1	10
Decapod (crabs)			1	3.7	3	30
Tunicate (<i>Amaroucium</i>)			2	7.4	2	20
Polychaete			1	3.7		
Seaweeds with epiphytic animals (Bryozoa, Hydrozoa, etc.)	1	12.5	9	33.1	3	30
Intestinal parasites						
Acanthocephala			3	11.1	3	30
Nematode					1	10

during the active feeding season (May to September). The foods were mainly mussels *Mytilus edulis* and *Modiolus modiolus*, barnacle *Balanus balanoides*, tunicate *Amaroucium* sp., and small specimens of the green sea urchin, *Strongylocentrotus drobachiensis*. Entire gut contents may consist entirely of one species mentioned above or, usually, of a mixture of these foods. Also some seaweeds, such as *Chondrus*, *Laminaria*, *Polysiphonia*, and *Porphyra*, were often associated with the animal foods. Occasionally, crabs, amphipods, and microcrustaceans (copepods, etc.) were found. In juvenile specimens (less than 40 mm SL), amphipods and microcrustaceans were the main food. The food was well triturated in most cases although entire mussels (less than 20 mm shell length) and, in one specimen, a crab leg longer than the first portion (I) of the intestine (Figure 1) was observed. In aquaria, cunners found their food by sight. They may pick up a whole mussel from the bottom or catch falling ones as they are introduced into the tank. Also, they removed small mussels one by one or as batches from clusters. Occasionally, the food, as well as mussel shell fragments, was spat out and reswallowed. Feeding activities greatly decreased during the winter when water temperature in the aquaria dropped below 4°-6°C. This was especially noticeable in the large individuals caught during the previous summer.

Movement and Digestion of Food Materials within the Gut

The gut in unfed cunner had little or no fluid in the lumen. The intestine and rectum were rather constricted with thick walls. During feeding, small mussels were picked up with the jaw teeth and triturated by the pharyngeal teeth before entering the esophagus. The crushed mussels were pushed back into the esophagus and intestine due to continuous food ingestion during the feeding period. Feeding continued until the food was packed up to the sigmoid loop (Figure 1) and occasionally even to the rectal valve or rectum. The intestinal lumen distends and the wall in turn becomes thinner when the gut is full. The shells of one feeding period always moved as a unit separate from the next feeding period. A period of 10-14 hr was required for mussel shells from a single feeding period (½-1 hr) to pass through the alimentary tract. The compact mass of shells moving along the intestine sometimes straightened the S-loop. Food storage in this stomachless fish was achieved mainly by the intestine anterior to the S-loop. The loop between sections I and II formed a saclike reservoir (Figure 1). Ingested foods remained in section III longer than in the other loops suggesting that this section may be responsible for more digestion and absorption than the other sections. Fluid developed in the lumen during and for a short while after the presence of shells. The amount of bile secretion depended on the quantity of food ingested. The volumes could not be estimated in the present study. In most fish with a full gut which were dissected immediately after capture, the gallbladders were shrunken or contained brownish fluid. The entire range of pH value found in all parts of the gut, both empty and full, was 7.0-8.5, thus suggesting alkaline digestion in the cunner gut.

DISCUSSION

Digestive System

The morphology of the mouth and buccal and pharyngeal cavities of the cunner is similar

to the labrids described by Al-Hussaini (1947b). The buccal valve (Figure 2) is similar to that of *Julis aygula* reported by Gohar and Latif (1961), except for the obvious thickening of the mucous layer of the anterior surface in juvenile cunners. The rather short relative length of the gut of the cunner, i.e., the post-pharyngeal portion of the alimentary tract, is about 0.8-1.0 of standard length. The extensive vascularization of the serosa and adventitia of the rectum and the strong alkaline phosphatase activity of the rectal mucosa indicate that this region is very active in absorption and/or secretion. The S-loop of the intestine may be unique because it was not described for other labrids by Suyehiro (1942) and Gohar and Latif (1959, 1961) nor in some other stomachless fishes reported by Babkin and Bowie (1928) and Al-Hussaini (1949a). Bullock (1967) recorded a similar flexure in the posterior portion of the intestine of *Gambusia affinis*. The S-loop was somewhat straightened by large amounts of food in the lumen. Alkaline phosphatase tests show weak positive reaction in the S-loop. The significance of the loop may be mechanical rather than physiological. There are no successive constrictions of the intestine in cunner as observed by Gohar and Latif (1961) in *Pseudoscarus harid* and credited by those authors to *Julis aygula*.

Epidermal mucous secreting cells in the epithelium of the alimentary tract of cunner are mostly concentrated in the postpharyngeal cavity and the esophagus and on the anal papillae. These cells have no stalklike elongation at the bottom of the globule nor a narrow necklike structure before the open end (Figures 3, 4, 6, 9, 20) as do those of the intestine and rectum (Figures 12, 14, 15). No precise histochemical differentiation of these mucous cells was obtained. These different types of mucous cells have been reported by Al-Hussaini (1947a), Gohar and Latif (1961), Mohsin (1962), Bullock (1967), Western (1969), and Bucke (1971) in various fishes. Al-Hussaini (1949b) and Bullock (1963), following the terminology of Baker (1942), described the free border of the absorptive columnar cells in the intestine as divided into a superficial layer, a canal layer (or microvilli region), and a granular

layer. These were also distinct in the cunner gut.

The rodlet cells are similar to those discussed by Bullock (1963) in the intestine of salmonid fishes and the pear-shaped cell of Al-Hussaini (1949b) recorded in *Gobio gobio*. These cells appeared throughout the gut except in the anterior intestinal bulb and the posterior rectum as in *Gambusia affinis* (Bullock, 1967). They are also found in the bile duct, gallbladder, and collecting duct of the kidney of the cunner. Bullock (1963) also described the appearance of rodlet cells in the kidney of *Catostomus* species. Al-Hussaini (1964) described the mitosis of the pear-shaped cell in *Cyprinus carpio*. He stated that experimental evidence indicated the pear-shaped cell may originate from goblet cells in *C. carpio* and *Gobio gobio* and from wandering blood or connective tissue cells in *Rutilus rutilus*. No comparable evidence of the division nor origin of the rodlet cells was found in this study. Bishop and Odense (1966) proposed that the pear-shaped cell may be a possible enzyme source in the intestine of the cod, *Gadus morhua*. But the negative phosphatase reactions of the rodlet cells in the cunner agree with Bullock's 1963 findings for salmonids. Different cytological or developmental stages of rodlet cells were observed in the mucosa of the bile duct, gallbladder, and intestine. The rodlet cells and their empty capsules, which have no distinct nuclei, were partially or entirely free from the mucosa of the bile duct. Occasionally, ejection of granules from the rodlet cells was seen. Rodlet cells have not been described in labrids prior to the present account. The question remains as to whether they are normal cells or coccidian parasites (Plehn, 1906).

The submucosal layer of the cunner gut is composed of a rather homogeneous fibrous connective tissue. There is neither muscularis mucosa nor lamina propria. The stratum compactum in various fishes has been discussed by Al-Hussaini (1947a), Burnstock (1959), Gohar and Latif (1961), Mohsin (1962), Bullock (1963), and Bucke (1971). In cunner it is a thin layer of regularly arranged fibers immediately beneath the mucosa. In oblique sections, fibrils can be seen passing from the

stratum compactum into the basement membrane.

Granulocytes in the submucosa of cunner can migrate to both the mucosa and the muscularis. According to Bolton (1933), basophilic granule cells occur in vast number in connective tissue throughout the gut of salmonid fishes. He suggested that they were histogenous cells developed from mesenchymal cells. Al-Hussaini (1949b) mentioned that two types of granulocytes also occurred in the intestine of a variety of fishes; some stained blue with Giemsa stain (*Trigla hirundo* and *Salmo trutta*), and others stained red with Giemsa (*Scarus sordidus*, *Rutilus rutilus*, *Gobio gobio*, *Atherina forskali*, *Cyprinus carpio*, *Crenilabrus melops*, and *Mulloidés auriflamma*). Bullock (1963, 1967) stated that the granulocytes had varying results in staining reaction according to the different pH value of the stain, which was also true in this study. Large granulocytes, densely packed with granules which appear purplish with Giemsa stain, were abundant in the mucosa of cunner (Figure 14); smaller granulocytes were present which have smaller red staining granules in Giemsa (Figure 18). In addition, a type of granulocyte was observed in which the granules were condensed against the nucleus (Figure 13). Bullock (1963) found cells intermediate between granulocytes and globule leucocytes in salmonids but not in *Gambusia affinis* (Bullock, 1967). This intermediate type cell was found in various levels of the epithelium and submucosa of cunner intestine. No precise cytochemical demonstration of the possible relationships between granulocytes and leucocytes was obtained in this study. The wandering nature of the granulocytes did not seem to correspond in any way with the food contents in the intestine of the cunner. Aggregations of granulocytes occurred in the submucosa of the bile duct, rectal valve, and anal papillae of the cunner (Figures 16, 19, 20). Granulocytes similar to those in the intestine were also very abundant in the pancreas and kidney. The function of granulocytes may differ from species to species (Al-Hussaini, 1949b). The fine granules of the granulocytes were stained with PAS in many specimens of cunner. No evidence that granulocytes help

in the absorption and transportation of digested foods was found in cunner as reported for other teleosts (Al-Hussaini, 1949b; Mohsin, 1962). Special aggregations of other types of wandering cells such as: polymorphonuclear leucocytes, lymphocytes, and amoebocytes were not found. The presence of amoebocytes (Figure 13) with large vacuoles and a large nucleus as observed in this study does not appear to have been previously recorded.

The muscularis of the esophageal-intestinal valve (Figure 10) and rectal valve (Figure 19) are formed of circular muscles. Gohar and Latif (1959, 1961) mentioned only one layer of muscle fibers in both the esophageal-intestinal valve and the rectal valve of the labrid *Julis aygula*. This is true in the esophageal-intestinal valve of the cunner, but in the rectal valve of the cunner, the circular muscle layer is folded and the two folds are separated by fibrous connective tissue. Al-Hussaini (1947a, 1947b) indicated two separate muscle layers in the ileo-rectal valve of the stomachless *Atherina forskali*, and Western (1969) described the same arrangement in *Cottus gobio*. It would appear that a more careful analysis of the intestinal-rectal (ileo-rectal) valve is required.

The differentiation of duodenum and ileum reported to occur in stomachless labrids (Gohar and Latif, 1961) was not found in the intestine of the cunner. Histological differentiation of the intestine was not mentioned by Curry (1939), Al-Hussaini (1947b), Khanna (1961), nor Bullock (1967) in other stomachless fishes. Thickening of the circular muscle layer at the anterior end of the rectum in cunner was similar to that in other species of stomachless fishes (Dawes, 1929; Al-Hussaini, 1947a, 1947b; Khanna, 1961; Gohar and Latif, 1961; Mohsin, 1962; Bullock, 1967). However, the additional thin layer of longitudinal muscle fibers present inside the muscularis in the rectum of the cunner was not reported by these investigators.

Al-Hussaini (1949b) reported that alkaline phosphatase was most abundant in the free border of the absorptive cell of three species of stomachless minnows—*Cyprinus carpio*, *Gobio gobio*, and *Rutilus rutilus*. Similar results were found along the free border of the

intestinal epithelium of the cunner in cells which are in direct contact with the food. An extremely strong alkaline phosphatase reaction was found in the intestinal bulb and anterior half of the rectum in the cunner. This reaction seems to be restricted to the free border of the epithelial layer of the intestine and rectum. Evidence of active rectal digestion also has been reported by Babkin and Bowie (1928), Ishida (1936), Al-Hussaini (1949b), Bullock (1967), and Western (1971) in other stomachless fishes.

The close association of the pancreas and bile duct in cunner observed in this study agrees with the observations of Gohar and Latif (1959) for another labrid, *Julis aygula*. Vacuoles (which stained intensively with fast green or with aniline blue) were observed in the supranuclear zone of the columnar epithelium of the gallbladder (Figure 17). No reference to this situation was found in the literature, and no data were acquired in this study to determine the function of these vacuoles.

Feeding Habits

Cunners are most active in daytime both in aquaria and in the field. Their activity decreased sharply during the night, the fish lying against objects on the bottom or hiding in crevices. Torpid behavior was observed during the day when the water temperature in the aquarium fell below 4°C. Bigelow and Schroeder (1953) and Green and Farwell (1971) also noticed that cunners become torpid during winter.

Cunner reach their greatest inshore abundance in summer (July- August). They were absent from the summer habitat from early November to late April. Observations made by SCUBA diving indicate that the offshore movements began as the water temperature dropped below 11°C (September 1971). A slight migration of cunner during the winter was postulated by Johansen (1925) and also reported by Bigelow and Schroeder (1953) and Green and Farwell (1971). Local fishermen reported the species to be present in deeper (more isothermal) waters in the winter. Juveniles tended to move

into shallow water in early spring as reported by Johansen (1925). Some juveniles were collected during this season in brackish water at the Jackson Laboratory of the University of New Hampshire on Great Bay, N.H. This is in accordance with the statements of Johansen (1925) but is contrary to those of Bigelow and Schroeder (1953).

Cunners fed on both sessile (*Mytilus edulis* and *Modiolus modiolus*) and moving animals (*Fundulus heteroclitus*, *Gammarus oceanicus*, *Nephtys buccera*, *Nereis virens*, and *Cerabratulus lacteus*) in the laboratory and also acted as scavengers. Gut content analyses (Table 1) indicate that cunner are carnivorous rather than omnivorous in contrast to statements by Johansen (1925) and Bigelow and Schroeder (1953). There was no evidence that cunner actively consume algae in the aquarium even when starved. Algae found in the gut of cunner are always small and undigested and are frequently associated with digested epiphytic animals (bryozoans, hydrozoans, and larval molluscs). A change of prey was noted between juvenile and adult cunner (Table 1). Juveniles feed mainly on motile crustaceans in the water column, adults on sessile or sedentary animals. A few large, offshore specimens showed a further change in feeding habits.

In this study almost every adult specimen had mussel shells in the gut. Mussels *Mytilus edulis* and *Modiolus modiolus* cover the rock faces in the feeding habitat from which the cunner were taken. Most of the mussels eaten by cunner were less than 2 years old. Many other labrids are also mollusk feeders (Suyehiro, 1942; Al-Hussaini 1947b; Gohar and Latif, 1959). Randall (1967) recorded the food habits of 11 species of western Atlantic wrasses—all of which, except for the plankton feeding *Clepticus parrai*—tended to feed on hard-shelled invertebrates such as mollusks, crustaceans, and echinoderms. No algae were mentioned by these authors except that 5 out of 50 specimens of *Halichoeres poecilopterus* had seaweeds (*Ulva*, etc.) present (Suyehiro, 1942).

Feeding habits of cunner are related to their jaws, teeth, pharyngeal mill, and also the length of the intestine as reported for other stomachless fishes (Suyehiro, 1942; Al-Hussaini,

1949a; Gohar and Latif, 1961; Mohsin, 1962; Weatherley, 1963). The protrusible jaws of the cunner have sharp caninlike teeth which are adapted to catching, picking, and scraping animal foods. The strong muscles (hypobranchial and branchiomic muscles) associated with the mouth can keep the jaws closed tightly, and quick movements of the body could help in detaching sessile organisms from the rocks. The molariform pharyngeal teeth of the cunner serve as a mill to grind up the hard shells of the ingested foods. The probability that well-developed pharyngeal teeth have taken over the mechanical function of the stomach among the stomachless fishes had been suggested previously by Barrington (1942, 1957), Suyehiro (1942), Al-Hussaini (1947b), and Gohar and Latif (1961).

Ingested foods passed rapidly through the buccal cavity and pharynx in the cunner as in most bony fishes. In the present study, the movement of mussels through the intestine of cunners fed in the laboratory, required 10 to 14 hr. Intact and alive mussels were found in all parts of the gut of freshly killed specimens both in the field and aquarium. Some of these mussels (less than 16 mm shell length) still were able to resetttle. Field observations indicated that the largest individual mussels (over 100 mm shell length) were scattered on the surface of bare rocks 5 to 10 m below the tidal zone. However, the major population of the mussels formed patches or clusters in the intertidal zone. Perhaps cunner play a role in the vertical distribution of mussels.

No specific area of food storage was found in the cunner; the gut of fish which had been fed all they desired was completely packed with food, and it appeared that the entire intestine can serve as a storage organ while digestion is being completed. The intestinal bulb of stomachless fishes may substitute as a storage organ (Babkin and Bowie, 1928; Barrington, 1942; Al-Hussaini, 1947a; Khanna, 1961; Mohsin, 1962; Bullock, 1967).

Alkaline conditions (pH 7.0-8.5) prevailed throughout the gut in all specimens of cunners examined. In starved controls, there was little variation in pH value observed among regions

of the intestine. However, in feeding fishes, the pH varied in a random fashion from region to region and showed no significant gradient. Phosphatase tests show a positive reaction for alkaline phosphatase, but negative for acid phosphatase. Intercellular digestion per se in the cunner is exclusively alkaline. Among other stomachless fishes, alkaline digestion was observed throughout the gut by Babkin and Bowie (1928), Ishida (1936), Barrington (1942, 1957), Al-Hussaini (1947a), Gohar and Latif (1959, 1961), and Bullock (1967).

Szarski (1956) discussed the advantages of alkaline digestion in stomachless freshwater fishes. He referred to the high biological value in retention of essential ions, which could also apply to the present species. Cunners feed mainly on shelled animals and the incidence of tooth damage is high. As is evident from having developing teeth along the edge of the old ones on the premaxillary, dentary, and pharyngeal bones. The apparent continuous regeneration and growth of teeth needs large amounts of calcium. The calcium supply cannot be obtained from the calcium carbonate of the animal shells due to the alkaline condition in the gut. Presumably, the calcium source is from the calcium pool of the viscera of the ingested animals.

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