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A histological, histochemical and ultrastructural study of the digestive tract of *Dentex dentex* (Pisces, Sparidae)

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Summary. *Dentex dentex* has a short esophagus, a large caecal type stomach, three to six pyloric caeca and a short intestine. Light and electron microscope studies reveal that the esophageal mucosa displays primary and secondary folds, a stratified squamous epithelium with fingerprint-like microridges alternating with a few zones formed by a single layer of columnar cells with apical microvilli. Only primary folds are present in the stomach, which is rich in simple tubular glands, these being absent in the pyloric valve. Two cell types occur in the gastric glands, one with a well developed apical intracytoplasmic membrane system consisting of a vesicular network of smooth membranes, and the other with a supranuclear tubulovesicular system. Pyloric caeca and anterior and posterior intestine mucosae display the same pattern of folding, with primary and secondary folds, without following a definite pattern in their orientation. In the rectum, the folds are oriented longitudinally. Small dense particles containing chylomicrons appear in groups in the intercellular spaces of the caecal and anterior intestinal epithelia. Eosinophilic granular cells (mast cells) appear along the digestive tract mainly within the stratum compactum. Histochemical studies reveal no differences in the composition of goblet cell mucus along the digestive tract. No histochemical differences were detected between enterocytes of the intestine, pyloric caeca and rectum. Neutral mucosubstances dominate in the stomach epithelium and in the goblet cells of the esophagus, pyloric caeca and anterior intestine. Results of the present study are discussed in relation to descriptions of the digestive tract in other sparids.

Key words: *Dentex dentex*, Digestive tract, Histology, Ultrastructure, Histochemistry

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Introduction

The common dentex, *Dentex dentex* Linnaeus, 1758, is a carnivorous fish that inhabits the Mediterranean Sea, most commonly south of 40°, although rarely in the Black Sea. It also occurs in the Atlantic from the Bay of Biscay to Cape Blanc and Madeira and exceptionally to the British Isles (Bauchot and Hureau, 1986). It is a highly valued species in most of the Mediterranean countries, where it is marketed fresh, demanding a high market price. It is a promising species in marine aquaculture since its rapid growth and its high conversion rate make its culture economically valuable. Recent work by Koumoundouros et al. (2004) seems to demonstrate that the industrial exploitation of this species can start given presently established knowledge.

Until recently, studies on the biology of *Dentex dentex* and, especially, on its culture were rather scarce. Currently, data is available concerning its reproduction, development, nutrition, pathology and rearing (see reviews by Abellán, 2000; Rueda and Martínez, 2001). Histological (Santamaría et al., 2004) and histopathological (Crespo et al., 2001) studies on larval *D. dentex* digestive system have been carried out recently. However the digestive structures of adult fish have not been documented so far. Since knowledge of the morphology of the gut is necessary to the understanding of pathological or physiological alterations (either related to infectious and environmental diseases or artificial diets), the aim of the present work is to describe the digestive tract of *D. dentex* throughout a histological, histochemical and electron microscope (scanning and transmission) study.

Materials and methods

Eight specimens of *Dentex dentex* (body weight 860-1000 g; total length ranging from 30 to 40 cm) were collected from seacages in Port Andratx (Majorca,

Spain) mariculture facilities and killed by deep anaesthesia with MS-222. The specimens were sized (total length), dissected and stomach and intestine length was determined. The number of pyloric caeca was also recorded. Samples of esophagus, stomach, caeca, anterior and posterior intestine and rectum were immediately fixed in 10% buffered formalin, embedded in paraffin, sectioned at 4 µm and stained with Mayer's haematoxylin and eosin for routine light microscopic examination.

Samples for electron microscopy were fixed in 4% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.3) and dehydrated through ethanol series. Those for the scanning electron microscope (SEM) study, were critical-point dried with liquid CO_2, coated with gold, and viewed in a Hitachi S 570. Those for the transmission electron microscope (TEM) study were post fixed with OsO_4, stained "en bloc" with uranyl acetate and embedded in Spur. Ultrathin sections of 50 nm were viewed in a Hitachi H-7000.

Histochemical reactions (carbohydrates and proteins), summarized in Table 1, were carried out on unstained sections in paraffin, using also complementary techniques. Sections from the same region of different specimens were stained in the same lot and at the same time to reduce variability in stain intensities due to different staining runs. Since mucous cells in the digestive tract of different vertebrates including fish do not show mannose, glucose and fucose residues of the glycoproteins (Madrid et al., 1989), Con-A reaction permits to distinguish between mucins (Con-A -) and other glycoproteins (Con-A +) present throughout the whole digestive tract. The identification of sulphated and carboxylated glycoconjugates was made based on the characteristics of the sulphate and carboxyl groups. Sulphated groups have greater affinity to stain at Alcian Blue pH 1 and 0.5. Carboxyl groups are transformed into esters during esteriphication, recovering to carboxyl groups with saponification and being able to stain with Alcian Blue at pH 2.5, while sulphate groups cannot recover (sulphatolisis).

Results

General structure

The length of the alimentary tract is relatively short (intestine length and stomach length averaging 49.9% and 10.79% of the total body length, respectively). The short and wide esophagus is followed by a great caecal type stomach. Three to six (mainly four) pyloric caeca of variable length are visible between the stomach and the anterior intestine. This portion of the gut first runs dorsocaudally towards the distal part of the body cavity reaching up to 2/3 of its length and, after bending, runs cranially. After a second loop, it narrows to form the posterior intestine which finally widens to form a short rectum which ends in the anal sphincter. The ileorectal valve separates the posterior intestine from the rectum. An intense orange pigmentation is apparent throughout the whole length of the intestine, more evident in the pyloric caeca and the anterior part of the gut.

Histological and electron microscope observations

The wall of *D. dentex* digestive tract which consists of mucosa, submucosa, muscularis and serosa shows no muscularis mucosae between the lamina propia of the mucosa and the submucosa (Fig. 1). A thick layer of densely packed connective tissue fibres, the stratum compactum, separates the mucosa from the loose connective tissue (submucosa).

Esophagus

The mucosa is extremely folded. SEM observations

Table 1. Histochemical rections of carbohydrates and proteins

REACTIONS (AUTHORS)	FUNTIONS AND/OR COMPONENTS DEMOSTRATED
1. Schiff (1865)	Free aldehydes
2. Periodic acid_Schiff (PAS) (Mc Manus, 1948)	Neutral mucosubstances
3. Diastase_PAS (Lison, 1960)	Glycogen
4. Acetylation_PAS (Lillie, 1954)	Blockage of 1,2-glycol or amino-ol
5. Acetylation-saponification_PAS (Lillie, 1954)	Reactivation of 1,2-glycol or amino-ol
6. Alcian Blue (AB) (pH 2.5) (Lev & Spicer, 1959)	Acid glycoconjugates (sulphated or not)
7. Esterification-AB (pH 2.5) (Spicer & Lillie, 1959)	Blockage of acid groups of acid mucosubstances
8. Esterification-saponification_AB (pH 2.5) (Spicer & Lillie, 1959)	Reactivation of –COOH groups
9. AB pH 1 (Lev & Spicer, 1964)	Sulphated glycoconjugates
10. AB pH 0.5 (Lev & Spicer, 1964)	Very sulphated glycoconjugates
11. Concanavalin A (Kiernan, 1975)	Glycoproteins rich in α-D-Mannose and/or α-D-Glucose
12. Hg Bromophenol Blue (Chapman, 1971)	Proteins in general

References quoted in the table are taken from the monographs by Pearse (1985) and Bancroft and Stevens (1990).

show primary longitudinal folds of different sizes and many secondary ramifications, these being villiform in the anterior portion (Fig. 2A) and rounded in the posterior one (Fig. 2B). On the top of the secondary folds, a simple columnar epithelium with short microvilli alternates with a stratified squamous epithelium with fingerprint-like microridges (Fig. 2C,D, 3A), this being dominant at the base of the folds.

TEM observations show that the epithelial cells (EC) of the squamous epithelium are cuboidal. They exhibit an ovoid centrally located euchromatinic nucleus (fig. 3B) and are joined, as most epithelial cell types found along the whole tract, by apical union complexes (Fig. 3C) and interdigitations of the lateral plasma membranes (Fig. 3B). Some mitochondria, profiles of endosplasmic reticulum, a well developed Golgi apparatus and Golgi-associated electron lucent vesicles can also be observed (Fig. 3B). Columnar cells exhibit an ovoid euchromatinic nucleus located in an intermediate basal portion (Fig. 3D), intercellular spaces being apparent between them.

Numerous goblet cells (GC) are found in the mucosa of stratified epithelium occupying the whole length of the esophagus. Only one type of globet cells can be distinguished on the basis of our morphological and histochemical data. TEM observations show that these have apical mucus granules and basal nuclei surrounded by rough endoplasmic reticulum (Fig. 4A). Rodlet cells (RC) are commonly found within both the columnar and stratified epithelial layers. They are formed by a distinctive cortex that separates them from adjacent EC. RC cytoplasm contains a peripheral basal nucleus and numerous cytoplasmic inclusions (Fig. 4B). Mitochondria are clustered in the apical cytoplasm.

Under the epithelium, there is a layer of connective tissue composed of densely-packed collagenous fibres. Cells with extremely electron-dense granules, termed eosinophilic granular cells (EGC), since they are strongly eosinophilic when stained with H&E, are dispersed amongst fibres (Fig. 4C). EGC contain an eccentric euchromatic nucleus and electron-dense granules.

Submucosa contains bundles of adipose tissue, blood vessels and many peripheral nervous elements. Two layers of striated muscle occur peripheral to connective tissue: an inner longitudinal layer, and a thicker outer circular layer (Fig. 4D). The serosa is a single layer of simple squamous epithelium, made up of mesothelial cells and loose connective tissue containing small blood vessels (Fig. 4E).

Stomach

SEM observations show that the mucosa forms a large number of primary longitudinal folds, the free surface exhibiting short microvilli. No secondary folds are apparent (Fig. 5A). The epithelium is constituted by simple columnar cells (Fig. 5A,B), with an oval euchromatinic nucleus with a large nucleolus located in

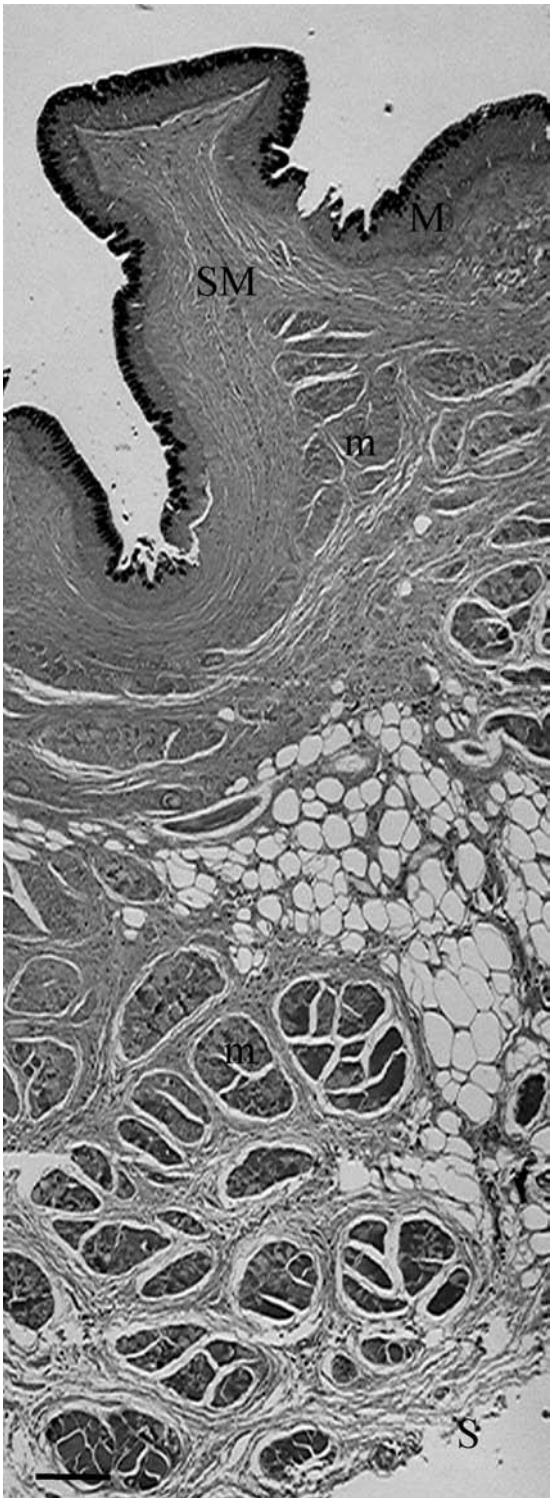


Fig. 1. Photomicrograph of *Dentex dentex* esophagus showing: mucosa (M); submucosa (SM); muscularis (m) and serosa (S) (H&E). Scale bar: 125 μm.

the basal third of the cell (Fig. 5B). Numerous apical spherical secretory granules containing a homogeneous material are particularly striking. No GC are observed and only a few RC are apparent. Some EGC can be observed scattered within the stratum compactum.

Simple gastric tubular glands open into gastric crypts in the cardiac, fundus and piloric regions of the stomach (Fig. 5C), but are completely missing in the pyloric valve. Two cell types are observed in the gastric glands (GG). Both are trapezoidal in shape with a large basal nucleus that sometimes shows an evident nucleolus. One of the two cell types encloses a well developed apical intracytoplasmic membrane system consisting of a vesicular network of smooth membranes

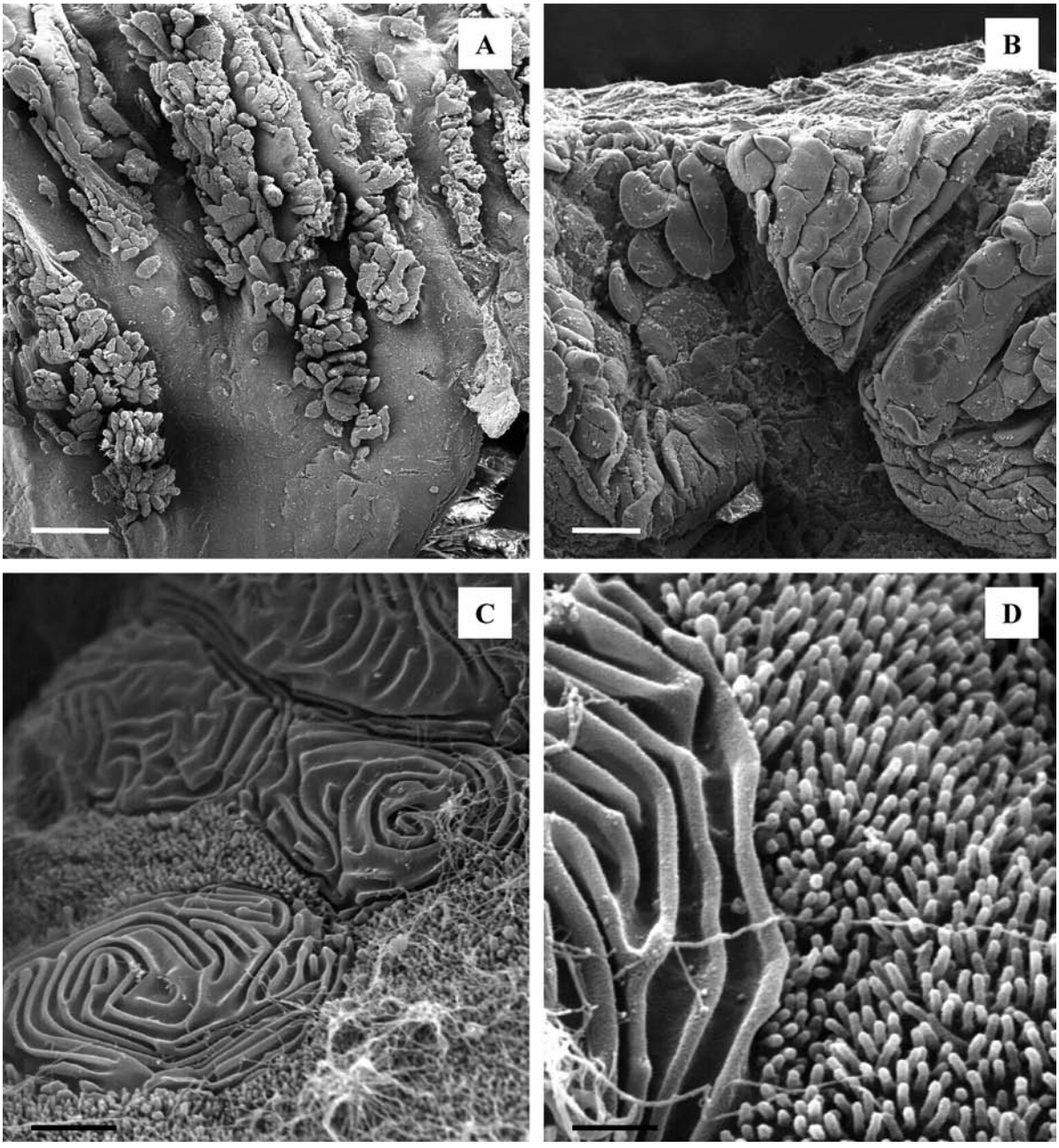


Fig. 2. SEM micrographs of superficial epithelial cells: **A** and **B** show the primary and secondary folds of the anterior and posterior region of esophagus, respectively. **C** and **D** show a detail of apical fingerprint-like microridges that alternates with short microvilli on the cell surface. Scale bars: A, 0.5 mm; B, 0.25 mm; C, 2.5 µm; D, 0.75 µm.

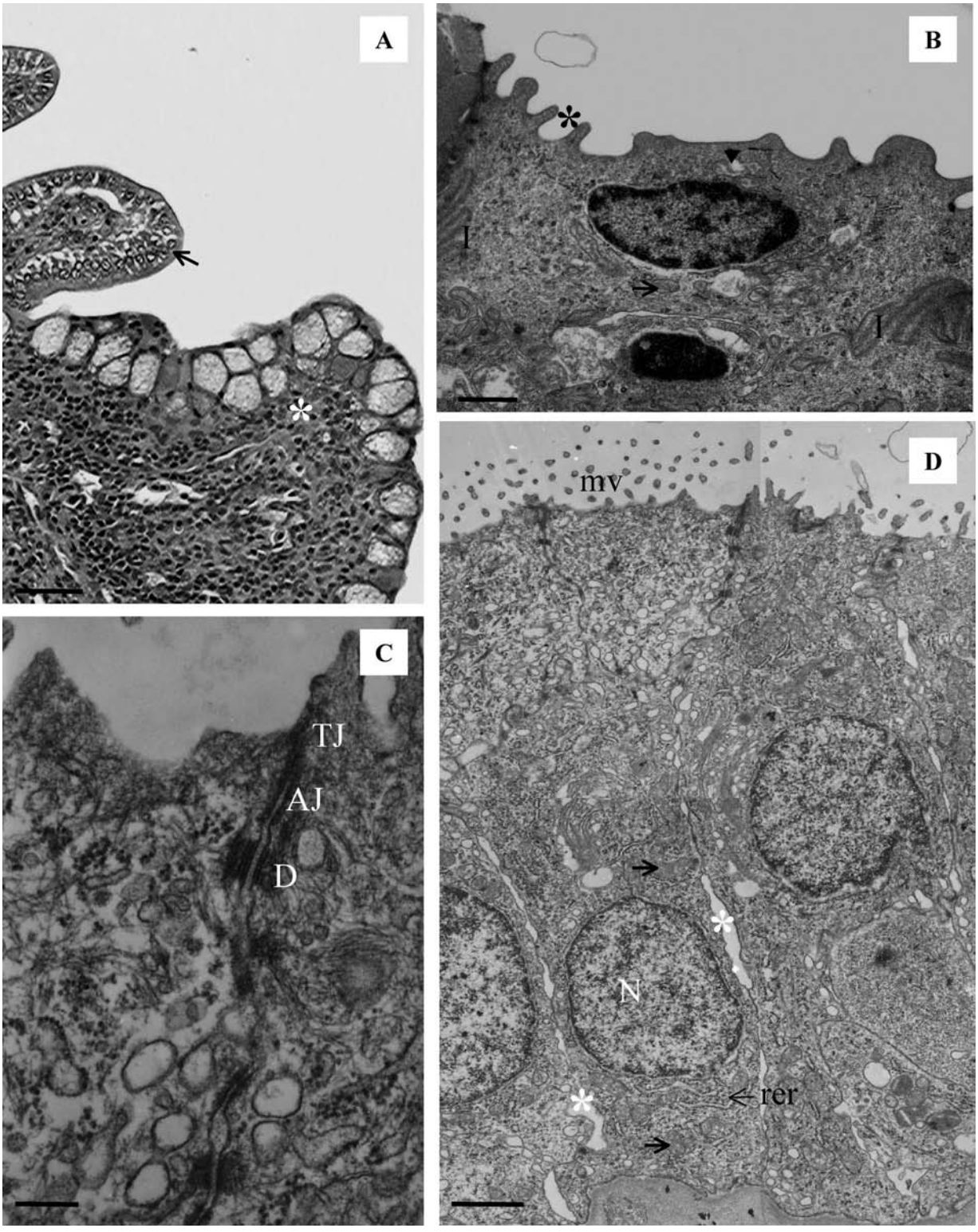


Fig. 3.A. Stratified (asterisk) and simple (arrow) epithelia of the esophagus (H&E). **B.** Epithelial cell from the squamous stratified epithelium with microridges (asterisk). Note interdigitations of the lateral plasma membranes (I), a few mitochondria (arrow) and electron lucent vesicles (arrowhead). **C.** Apical union complexes between epithelial cells: TJ: tight junction, AJ: adherens junction, D: desmosomes. **D.** Simple columnar epithelium. mv: microvilli, arrows: mitochondria, N: nucleus, rer: rough endoplasmic reticulum, asterisks: intercellular spaces throughout the columnar cells. Scale bars: A, 30 µm; B, 1 µm; C, 0.5 µm; D, 5 µm.

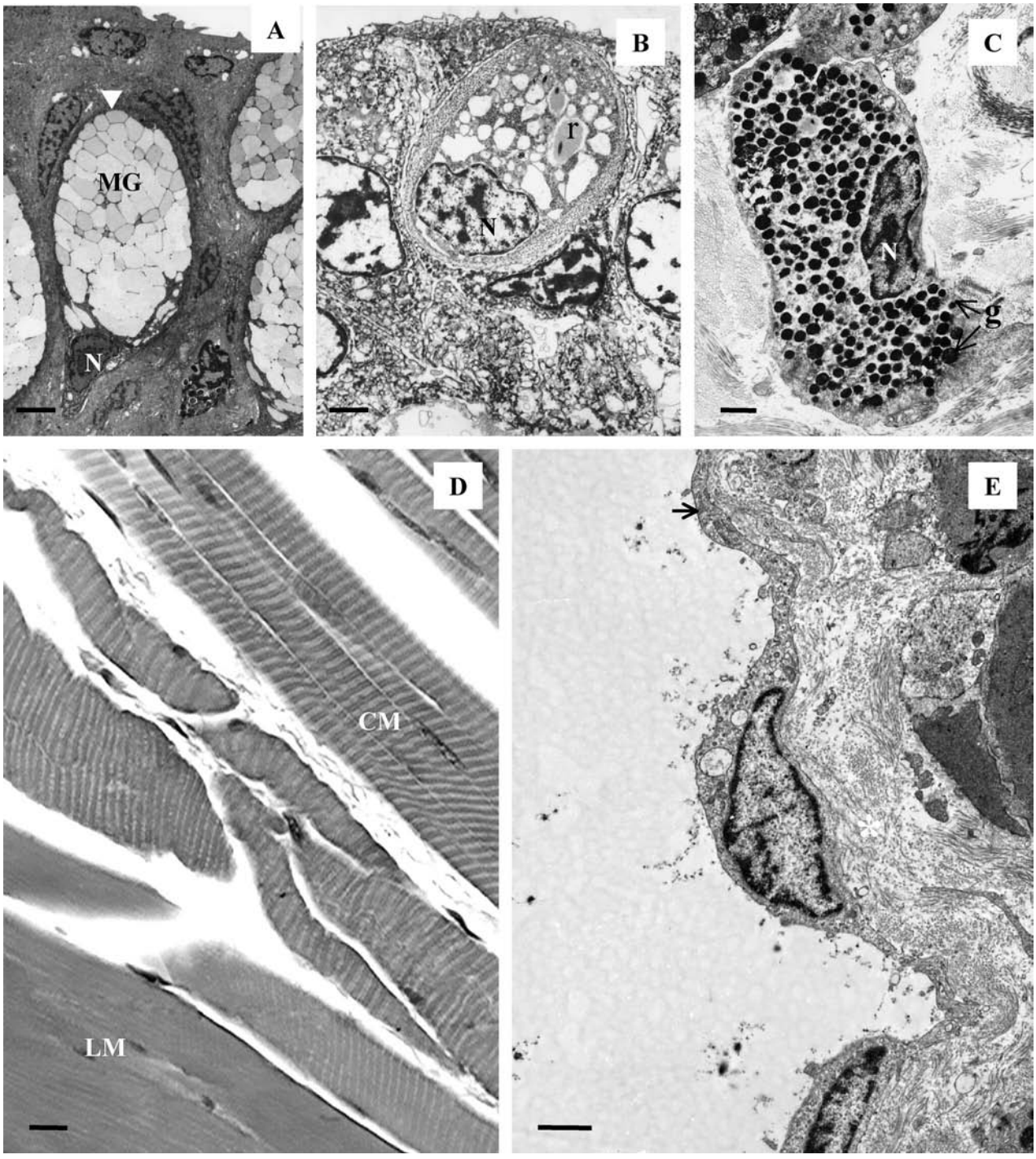


Fig. 4.A. Goblet cell (arrowhead). Note that mucus granules occupy almost the whole cytoplasm of the cell, the nucleus appearing basally. MG: Mucus granules of variable size and electron density, N: nucleus. **B.** Rodlet cell in the simple columnar epithelium showing a basal nucleus (N) and rodlets (r). **C.** Eosinophilic granular cell. N: nucleus, g: electron dense granules. **D.** Light micrograph showing two layers of striated muscle, an inner longitudinal layer (LM) and an outer circular layer (CM). **E.** Serosa showing a simple squamous epithelium (arrow) and connective fibres (asterisk). Scale bars: A, B, 1 µm; C, 2.5 µm; D, 8 µm; E, 5 µm.

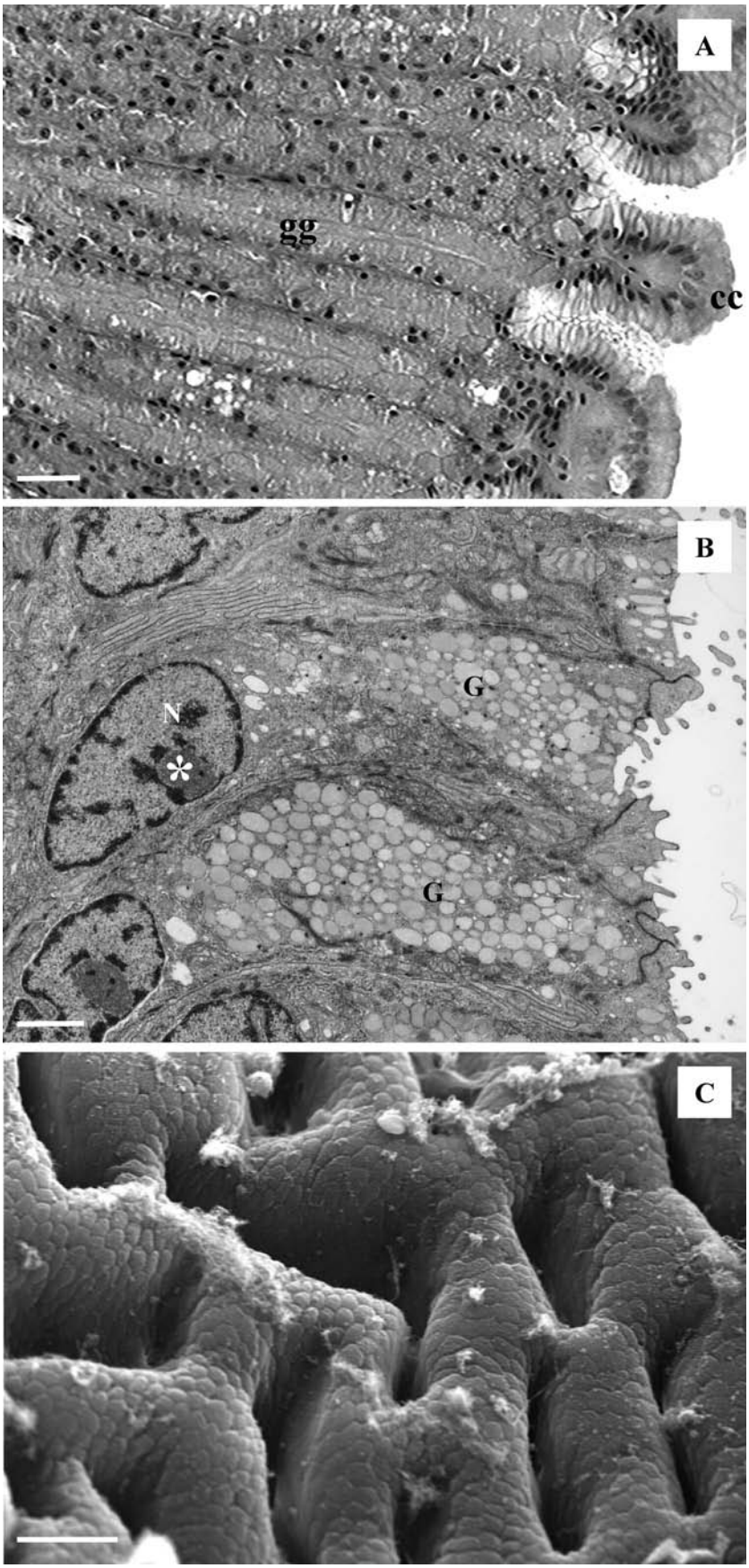


Fig. 5. Stomach: **A:** Section of the gastric mucosa showing the simple columnar cells (cc) and the simple gastric tubular glands (gg) (H&E). **B:** Micrograph of the simple columnar cells of the epithelium showing numerous granules (G). Note the basal position of the nucleus (N) with a prominent nucleolus (asterisk). **C:** SEM micrograph of the gastric epithelium; note the crypts of the gastric glands. Scale bars: A, C, 25 µm; B, 1 µm.

(Fig. 6A), an euchromatinic nucleus and a great number of mitochondria. The other cell type is characterized by a greater number of mitochondria and a supranuclear tubulovesicular system, its nucleus being heterochromatinic and irregular (Fig. 6B). The muscularis of the stomach is composed of two layers of smooth muscle, the inner circular and the outer longitudinal. The inner circular layer becomes enlarged at the pyloric valve to form a sphincter.

Pyloric caeca and intestine

The structure of the pyloric caeca does not differ greatly from that of the intestine, both regions consisting of serosa, both circular and longitudinal smooth muscle layers, submucosa and mucosa (Fig. 7A). The submucosa and the two layers of muscle are relatively thin. A very thin band of connective fibres is visible between the serosa and the muscularis in some places.

The highly folded mucosa extends and branches along the entire length of the intestinal tract and the pyloric caeca. Primary folds can be observed projecting into the lumen without following a definite pattern in their orientation. Secondary folds are also apparent (Fig. 7B). No differences in the folding patterns of the mucosa can be observed between pyloric caeca and the different regions of the intestine, except in the rectum where the orientation of the mucosal folds becomes longitudinal (Fig. 7C).

The epithelium consists of simple columnar cells that are interspersed with GC, RC and migratory lymphocytes (Fig. 8A,B). EGC dominate in the submucosa but can also be found in the mucosa. The absorptive columnar cells exhibit long microvilli and a basal nucleus with a large nucleolus (Fig. 8C). Mitochondria are present throughout the whole cell but show a tendency to cluster either in the apical region (pyloric caeca) or in the middle and basal regions (intestine). Numerous free ribosomes, dispersed long cisternae of rough endoplasmic reticulum, lysosomes of varying sizes are seen in the enterocytes (Fig. 8D). Some lamellar structures are observed in the infranuclear

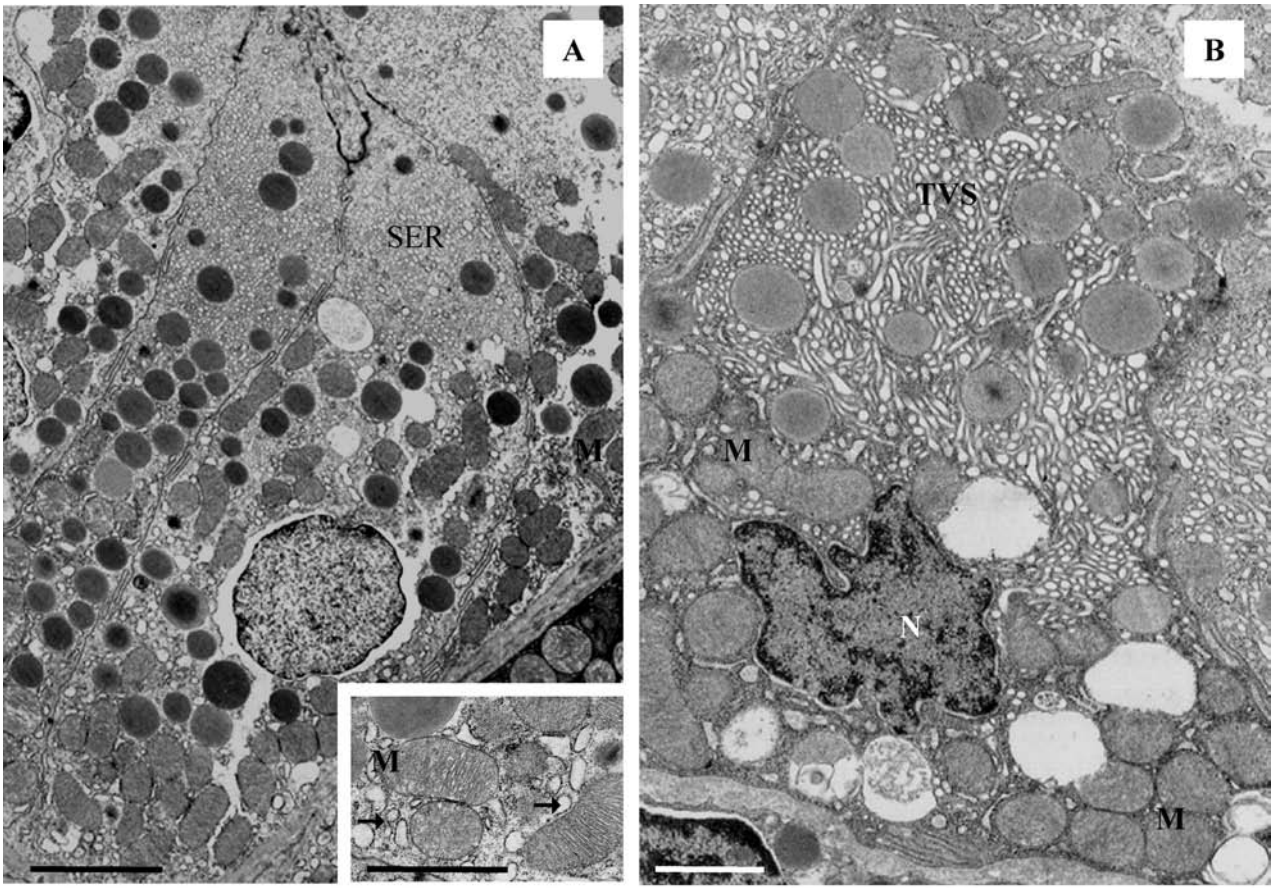


Fig. 6.A. A cell of the gastric glands with abundant smooth endoplasmic reticulum (SER), mitochondria (M) and rough endoplasmic reticulum (arrows) (scale bar: 5 µm). Inset: scale bar: 4 µm. **B.** A cell of the gastric glands showing the tubulo-vesicular system (TVS), heterochromatinic nucleus (N) and numerous mitochondria (M) (scale bar: 1 µm).

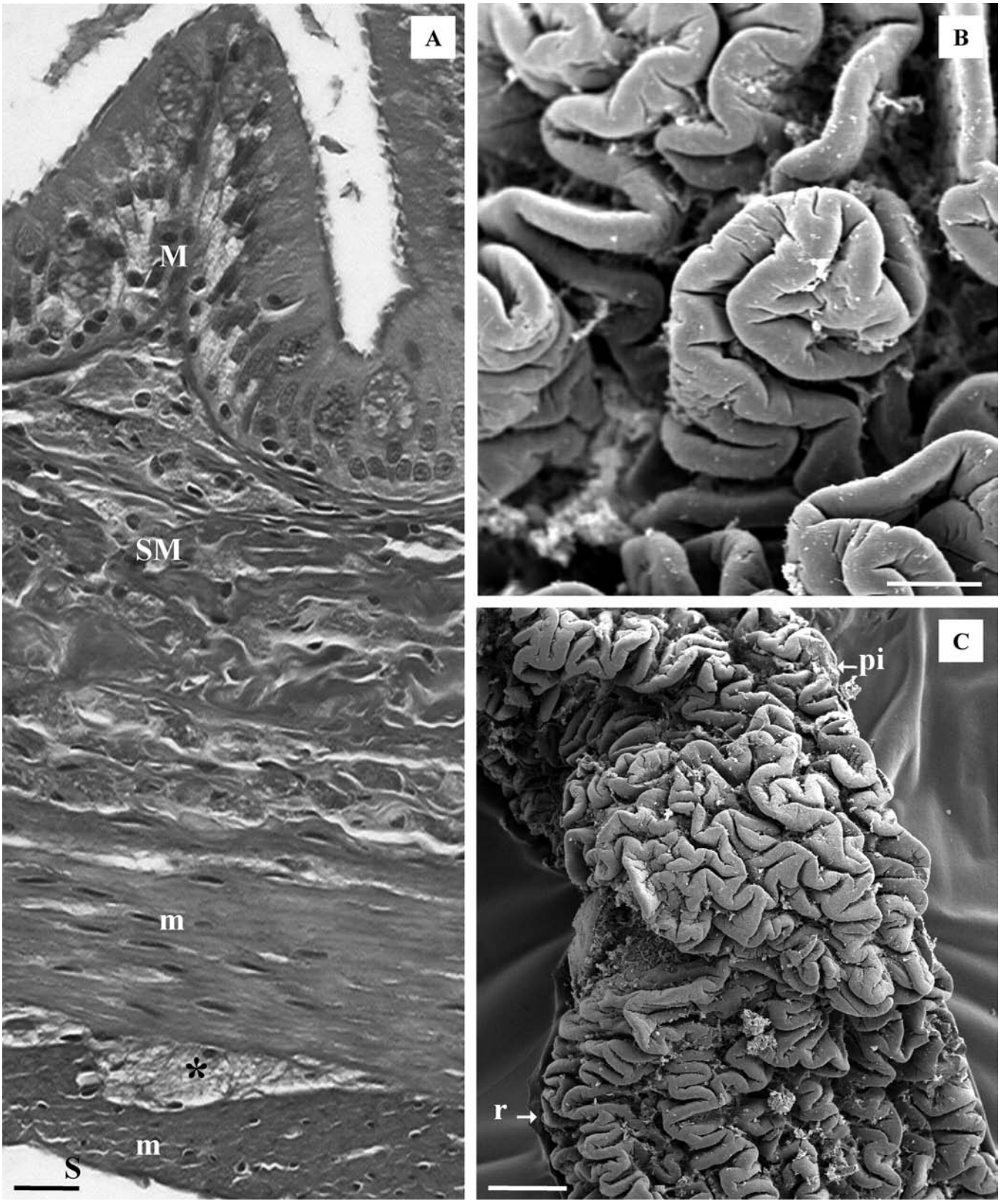


Fig. 7. Intestine and pyloric caeca. **A.** Intestinal wall: mucosa (M), submucosa (SM), muscularis (m) and serosa (S); note that longitudinal muscle is separated from the circular layer by connective tissue supporting blood vessels and the nervous elements (asterisk). **B.** primary and secondary folds of the mucosa. **C.** A funnel-like valve separates the posterior intestine (pi) from the rectum (r); note that in the rectum the orientation of the mucosa folds becomes longitudinal. Scale bars: A, 15 µm; B, 0.15 µm; C, 0.43 µm.

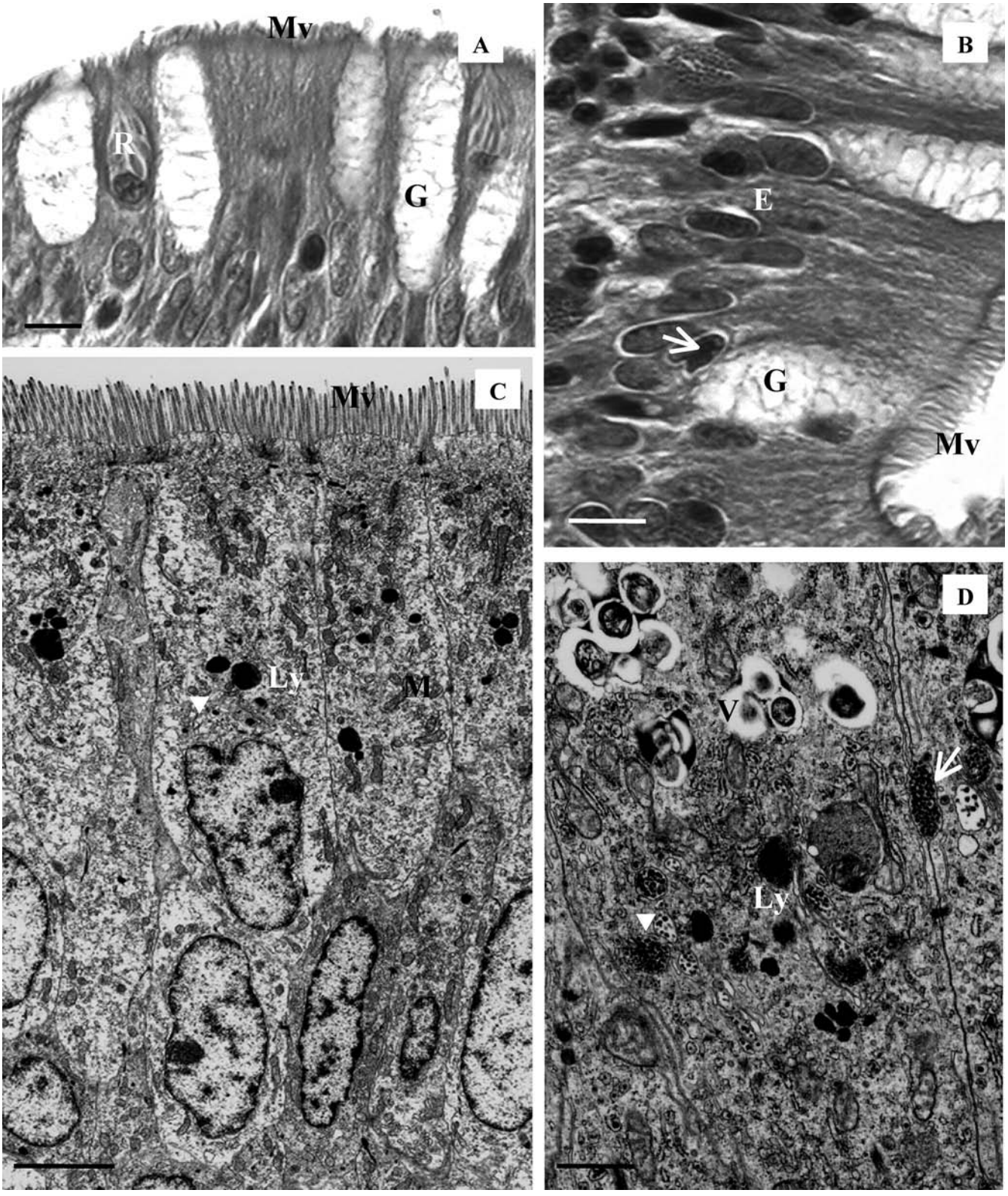
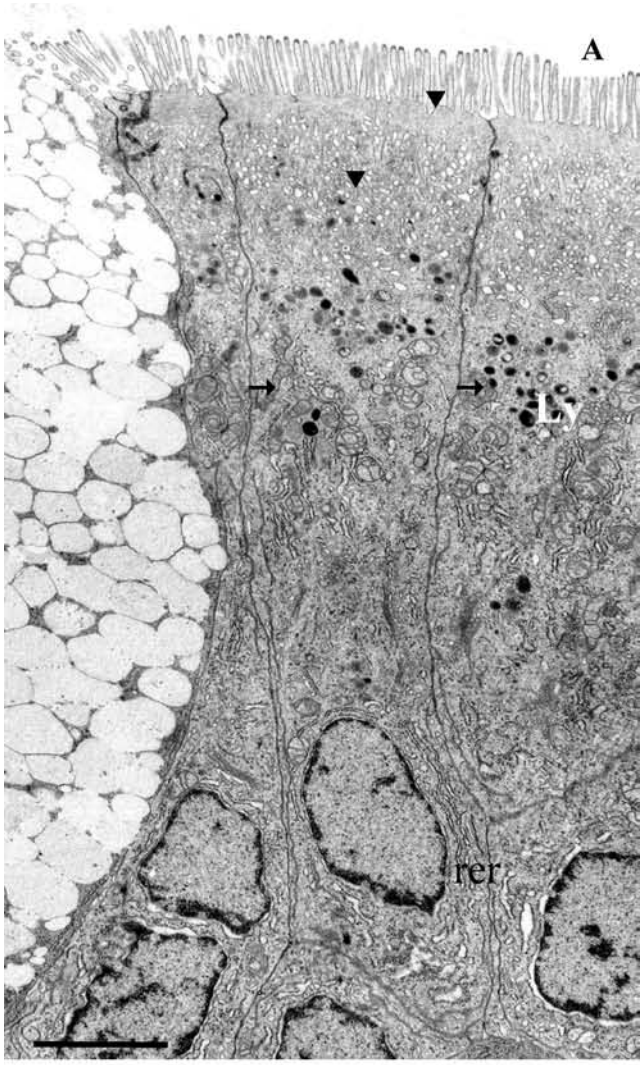
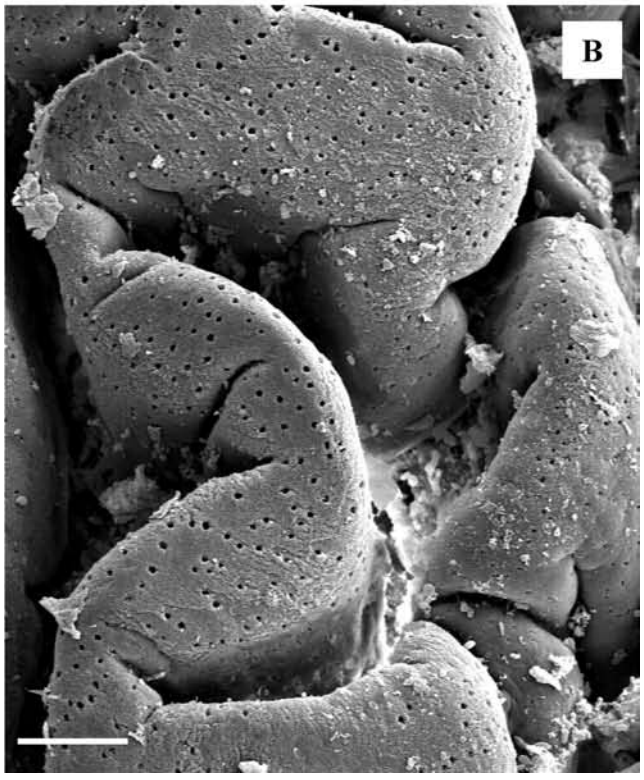


Fig. 8. Intestine and pyloric caeca. **A and B.** Light micrographs showing the enterocytes (E) with microvilli (Mv), goblet cell (G), rodlet cell (R) and migratory lymphocytes (arrow) (H&E). **C.** TEM micrograph of the cells of the pyloric caeca showing microvilli (Mv), abundant elongated mitochondria (M), many elements (vesicles and saccules) of the smooth endoplasmic reticulum (arrowhead) and lysosomes (Ly). **D.** Anterior intestine. Note the presence of vacuoles (V), Lysosomes (Ly) and chylomicrons enclosed by a membrane (arrowhead). Some chylomicrons are observed between adjacent cells (arrow). Scale bars: A, B, 7.6 µm; C, 5 µm; D, 0.5 µm.





cytoplasm. Small dense particles containing chylomicrons are seen within Golgi saccules and appear in groups in the intercellular spaces of the caecal and anterior intestinal epithelium (Fig. 8D). Pinocytotic vesicles are also frequent in the apical portion of enterocytes of the posterior intestine (Fig. 9A).

A funnel-like valve separates the posterior intestine from the rectum (Fig. 7C), numerous GC being found in this region (Fig. 9B). The cytoplasm of enterocytes exhibits multivesicular bodies. A large number of pinocytotic vesicles are observed in the apical portion.

Histochemical observations

Tables 2-3 show the histochemical reactions (carbohydrates and proteins) of the EC, GC and GG of the digestive tract of *D. dentex*. No histochemical

Table 2. Carbohydrates and proteins in epithelia of the digestive tract of *Dentex dentex*.

	Oesophagus	Stomach	Caeca	Intestine	Rectum
NM	1	3	2	2	2
CM	1	1	1	1	1
SM	0	1	1	1	1
GP	2	2/3	1/2	1/2	1/2
P	1	1/2	1/2	1/2	1/2

0: negative; 1: weak; 2: moderate and 3: intense; NM: neutral mucosubstances; CM: carboxylated mucosubstances; SM: sulphated mucosubstances; GP: glycoproteins; P: proteins in general

Table 3. Carbohydrates and proteins in the goblet cells of the oesophagus, intestine, caeca, and rectum and the gastric glands of the stomach of *Dentex dentex*.

	Oesophagus	Stomach	Caeca	Anterior Intestine	Posterior Intestine	Rectum
NM	3	1	3	3	1	1
CM	3	0	3	3	3	3
SM	3	0	2	2	2	2
GP	0	1	0	0	0	0
P	0	2	0	0	0	0

0: negative; 1: weak; 2: moderate and 3: intense; NM: neutral mucosubstances; CM: carboxylated mucosubstances; SM: sulphated mucosubstances; GP: glycoproteins; P: proteins in general

Fig. 9.A. Enterocytes of posterior intestine showing mitochondria (arrows), rough endoplasmic reticulum (rer), lysosomes (Ly) and abundant pynocitotic invaginations (arrowheads). **B.** SEM micrograph of the mucosal surface of the rectum showing the crypts of many goblet cells. Scale bars: A, 1 µm; B, 50 µm.

differences are detected between intestine (either anterior or posterior), pyloric caeca and rectum mucosae (Table 2). The epithelium of the stomach is rich in neutral mucosubstances. These are also present, although with a weaker intensity, in the GG and the esophagus mucosa. No histochemical differences are found between neck cells of the GG and the columnar EC of the stomach.

GC of the esophagus, caeca and anterior intestine are rich in neutral mucosubstances, which exhibit much weaker intensity in the posterior intestine and rectum. Levels of carboxylated and sulphated mucosubstances are also high in GC located throughout the whole length of the digestive tract. Using an Alcian Blue pH 2.5 PAS double staining, some GC are only stained in magenta (PAS-positive reaction, neutral glycoconjugates), whereas other cells are stained in purple (neutral and acid glycoconjugates). Proteins are absent from most GC, whilst they are dominant in the GG (Table 3). They are also present, although with a weaker intensity, in the whole tract mucosa, glycoproteins being dominant in the esophagus and stomach (Table 2).

Connective and muscular layers contain mainly proteins and neutral mucosubstances. Sulphomucines and acid mucosubstances are also present in the connective tissue and the serosa of the whole tract. Neutral mucosubstances and glycoproteins are dominant in the serosa and the connective layer is particularly rich in neutral mucosubstances. The granules of EGC contain mainly proteins and are glycogen-free.

Discussion

The digestive tract of the *D. dentex* is relatively short although it exhibits a large stomach. The intestine is shorter than that of other members of the family Sparidae such as the gilthead sea bream *Sparus aurat*a and the sharpsnout sea bream *Diplodus puntazzo* (intestinal lengths of 57 % and 63% of the total body length, respectively; Grau, unpublished data), whereas the stomach is bigger. This might be related to the fact that dentex is a strictly carnivorous (mainly ichtiophagous) fish (Morales-Nin and Moranta, 1997) whereas the other two species are omnivorous (Kapoor et al., 1975). Dentex stomach is a caecal-type organ with a highly distensible caecum which, in fish with predatory habits and irregular intake of large quantities of food, might be used as a reservoir (Martin and Blaber, 1984). Dentex exhibits a low number of pyloric caeca (3-6). The number of caeca is not always constant within a teleost species (Kapoor et al., 1975; Carrassón and Matallanas, 1994). This is noticed, as in dentex, in other sparids such as *S. aurata* (3-5) or *D. puntazzo* (5-9) (pers. observ.). An increase of the number of pyloric caeca has been correlated with bulk of food (De Groot, 1969). Nevertheless, dentex with habits more predatory than those of *S. aurata* and *D. puntazzo* has similar or inferior number of caeca. It would seem that the number and shape of pyloric caeca is a character related to phylogeny rather than a character associated to diet, as previously pointed out by Geistdoerfer (1981) and Carrassón and Matallanas (1994).

In dentex oesophageal mucosa, a stratified squamous epithelium with fingerprint-like microridges alternates with some regions formed by a single layer of columnar cells with apical microvilli, without showing any definite pattern. The columnar epithelium has been described in the posterior esophagus as a differentiated region in other teleosts (*Scomberomorus maculatus*: Mota-Alves, 1969; *Seriola dumerili*: Grau et al., 1992). However, in dentex, as well as in larval (Elbal et al., 2004) and juvenile (pers. observ.) sea bream, two different regions in the esophagus mucosa (cranial and caudal) cannot be distinguished.

Fingerprint-like microridges of the squamous EC of the esophagus mucosa like those shown in dentex have been described in other teleosts (*S. aurata*: Elbal and Agulleiro, 1986; Cataldi et al., 1987; *Gadus morhua*: Morrison, 1987; *S. dumerili:* Grau et al., 1992). These structures may act as devices protecting the mucosa from mechanical trauma and chaining mucous secretions, therefore forming an optimally lubrificated surface for the passage of food (Humbert et al., 1984; Grau et al., 1992; Murray et al., 1994).

The layer of columnar cells with apical microvilli, numerous mitochondria and prominent intercellular spaces has been proposed to play a role in ion transport (Kirsch et al., 1984, 1985; Elbal and Agulleiro, 1986). Replacement of a stratified epithelium by a monocellular layer with similar intercellular spaces and changes in the mucous sheet, have been reported in the eel *Anguilla japonica* during sea water adaptation (Yamamoto and Hirano, 1978), supporting this osmoregulatory function.

The existence of electron-lucent Golgi associated granules in the EC of dentex could suggest that a secondary mucin of surface epithelial origin may combine with GC mucus to provide a digestive function for the esophagus. The occurrence of positive histochemical reactions to glycoconjugates and glycoproteins in the EC of the esophagus suggests that the secretory product is glycoprotein based. The histochemical differences observed in the oesophageal mucus of different teleosts would indicate functional differences for the mucus beyond lubrication, including digestion (Reifel and Travill, 1977).

RC were frequently observed in the gut epithelium of adult dentex (present work), as well as in dentex larvae (Santamaría et al., 2004). In freshwater and marine fish, these cells have been described in different sites throughout the body (Leino, 1996; Iger and Abraham, 1997; Dezfuli et al., 1998; Koponen and Myers, 2000; Arellano et al., 2002). Although RC functions still remain enigmatic, the strong staining reaction of their granules (rodlets) for proteins and certain enzymes suggests that one of the main components of the RC granules is enzymatic (Leino, 1982; Iger and Abraham, 1997).

The gastric mucosa of dentex is similar to that of

most teleosts (Elbal and Agulleiro, 1986; Osman and Caceci, 1991; Takashima and Hibiya, 1995).

The existence of a PAS+ brush border formed by numerous short microvilli may indicate nutrient absorption occurring in the stomach (Ezeasor and Stokoe, 1980; Grau et al., 1992; Ortiz-Delgado et al., 2003). On the other hand, the neutral mucous secretion of the gastric EC may serve to protect the stomach epithelium from auto-digestion processes caused by hydrochloric acid and the enzymes secreted by GG (Ferraris et al., 1987). These epithelial cells contain sulphated mucopolisaccharides, as in gilthead sea bream and other teleosts (Elbal and Agulleiro, 1986; Grau et al, 1992, Reifel and Travill, 1978), but not in other fish species including some members of the Sparidae (Sarasquete et al., 2001; Ortiz-Delgado et al., 2003). Spicer and Schulte (1992) speculated that sulphomucins may be able to form a complex with pepsin, thereby stabilizing or buffering the enzyme, due to their known anti-peptic activity.

It is generally accepted, as pointed out by other authors, that only the GG of mammals have distinct acid –producing parietal cells (oxyntic cells) and zymogenic chief cells. In fish, amphibians and birds, both hydrochloric acid and pepsinogen are assumed to be secreted by one cell type (Rebolledo and Vial, 1979). The two cell types of the gastric glands observed in common dentex may correspond to the light and dark cells described for *S. aurata* (Elbal and Agulleiro, 1986). These cells presumably perform the functions of both the chief and oxyntic cells of mammals (Reifel and Travill, 1978; Morrison, 1987), the cells with the vesicular network of smooth membranes producing mainly pepsinogen and the cells with the tubulovesicular system producing mainly acid (Kierszenbaum, 2002). Alarcon et al. (1998) found important differences in total activity of digestive proteases between *D. dentex* and *S. aurata*. However, from the present study, it is apparent that dentex does not differ either ultrastructurally or histochemically from seabream.

It is well established that enterocytes of the anterior intestine and the pyloric caeca of fish are involved in lipid absorption (Bergot et al., 1975; Ezeasor and Stokoe, 1981; Deplano et al., 1989, 1991; Grau et al., 1992; Murray et al., 1996; Houssain and Dutta, 1998). Elements of smooth membranes containing chylomicrons were detected in the cytoplasm of enterocytes in the anterior portion of dentex intestine, which would indicate that intestinal EC are the site of active lipid absorption (Morrison, 1987).

Lamellar structures observed in the infranuclear enterocyte cytoplasm of dentex intestine were also described in other fish species (Elbal and Agulleiro, 1986; Deplano et al., 1991; Calzada et al., 1998; Arellano et al., 2002). The involvement of these membrane infoldings in the transport of lipoproteins has been suggested by Deplano et al. (1991), although other authors (Morris, 1972; Arellano et al., 2002) have also pointed out their possible role in osmoregulation.

The large multivesicular bodies and numerous pinocytotic vesicles in the apical cytoplasm of the intestinal and rectal cells of dentex support the view of a pinocytotic function of these cells, as indicated in *S. aurata* (Elbal and Agulleiro, 1986). The higher abundance of these structures in the rectal cells, also observed in some pleuronectids (Murray et al., 1996), would suggest that the rectal epithelium of fish is specialized in pinocytotic activity and intracellular digestion.

Common dentex, as other teleosts (Grau et al., 1992; Sarasquete et al., 1995; Murray et al. 1996; Radaelli et al., 2000; Arellano et al. 2002), exhibited GC in the postgastric mucosa. An increased number of GC was observed in the rectum of this species as well as in that of other teleosts (Grau et al., 1992; Murray et al., 1996), which might be related to the need, in this part of the tract, for increased mucosa protection and lubrication for faecal expulsion.

Histochemical differences were observed in GC mucus along adult dentex digestive tract, and the affinity to neutral and acid mucosubstances differs from that observed during dentex larval development (Santamaría et al., 2004). This might reflect a chemical division of labour between each region, as has been pointed out in pleuronectids (Murray et al., 1996) and could indicate differences in functionality between digestive sections of larvae and adult dentex. On the other hand, in adult dentex, some GC stained positive for both acid and neutral mucins. Generally, teleost GC have been reported to contain at least two combinations of nonsulphated mucins, sulphated acid mucins and neutral mucins (Morrison and Wright, 1999; Sarasquete et al., 2001; Ortiz-Delgado et al., 2003). According to Harrison et al. (1987) variability in staining within a given goblet cell could be attributed to a temporal sequence in the mucus biosynthesis. Thus, the presence of two types of mucins in a cell may be a function of the level of mucus maturity (Elbal and Agulleiro, 1986; Murray et al., 1996; Sarasquete et al., 2001).

Different mucosubstances have been correlated with a variety of digestive functions. The existence of long microvilli and the presence of neutral mucosubstances on the enterocytes might be related to the absorptive function of these cells (Grau et al., 1992). Neutral mucosubstances combined with alkaline phosphatase assist in digestion and emulsification of food into chyme (Clarke and Witcomb, 1980). Also, mucosubstances may provide cofactors required for the enzymatic breakdown of food (Anderson, 1986). In vertebrates (Rhodes et al., 1985), acid mucins have been proposed to protect the intestinal epithelium against the degradative action of glycosidases. Moreover, sialitation and sulphation of the glycoproteins may be important for increasing the resistance of mucus to bacterial degradation (Rhodes et al., 1985). According to Madrid et al. (1989), the presence of Con-A+ granules could indicate the absorption of carbohydrates in the digestive epithelium. In *Dentex dentex*, Con-A reaction is positive along the

whole digestive tract, which would indicate that carbohydrate absorption would occur in all the different parts of the tract of this species.

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