

Identification of gut contents and microscopical observations of the gut epithelium of the macrophagous ascidian *Cibacapsa gulosa* Monniot and Monniot 1983 (Phlebobranchia, Octacnemidae)

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Received: 25 March 2010/Revised: 5 June 2010/Accepted: 15 June 2010/Published online: 1 July 2010
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Abstract Octacnemids represent a different pathway in the evolution of the typical filter-feeding ascidians. We examine and identify the prey items in the gut contents and describe the cell types that constitute the inner wall of different sections of the gut of the macrophagous octacnemid *Cibacapsa gulosa* collected in the South Sandwich Islands, Antarctica. A great variety of prey items were found: polychaetes, copepods, halacarids, amphipods, isopods and ophiuroids. The internal wall of the gut is lined with a monostratified, prismatic epithelium. Different cell types occur in the inner wall in different sections. The presence of zymogenic cells throughout the internal gut epithelium, as well as the presence of concretion cells in the stomach of *C. gulosa*, also present in the macrophagous tunicate group Sorberacea (= Hexacrobylidae), can be considered as an adaptation to the macrophagous diet.

Keywords Ascidian · *Cibacapsa gulosa* ·
Macrophagous · Prey items · Gut epithelium

Introduction

Antarctic benthic communities have been described as dense and taxonomically diverse, particularly on the shelf and the slope (Arntz et al. 1994; Mühlenhardt-Siegel 1988; Sahade et al. 1998; Lovell and Trego 2003; Teixido et al. 2007). Suspension feeders are one of the main components of these assemblages (Dayton et al. 1974; Arnaud 1977; Clarke 1996; Saiz-Salinas et al. 1998; Gili et al. 1999; Lovell and Trego 2003; Teixido et al. 2007). Different processes like vertical flux, resuspension (Graf 1992; Gili et al. 1999) and advection (Grebmeier and Barry 1991) fuel these communities by transporting particulate organic carbon (POC) to them. Nutritious particles are scarce in deeper ecosystems where little phytoplankton from seasonal shallow primary production reaches the bottom. Suspension-feeding organisms have to adapt themselves to a less plentiful supply of POC, and some become macrophagous (carnivorous) as an adaptive response (Monniot and Monniot 1975).

Ascidians are mostly filter feeders that utilize particulate matter, mainly phytoplankton, and consequently, play an important role in the coupling of pelagic and benthic systems (Sigsgaard et al. 2003). In the order Phlebobranchia, all species belonging to the family Octacnemidae are macrophagous (Monniot and Monniot 1975, 1991; Monniot 1984). They have an enlarged oral siphon, which is the main organ for prey capture, and have well-developed sense organs. The branchial sac is reduced and is a vestigial organ in *Cibacapsa*, the most specialized genus within this group (Monniot and Monniot 1983). However, the Antarctic species *Cibacapsa gulosa* presents a striking feature, even in the family, which is the replacement of suspension feeding with an exclusive macrophagous method of feeding (Monniot and Monniot 1983; Monniot 1984). Other

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genera of Octacnemidae have a mixed diet, composed both by zooplankton (crustaceans) and by phytoplankton, since diatom frustules were found in their gut contents (Okuyama et al. 2002). Some branchial structures engaged in filtration (e.g., oral tentacles, endostyle, dorsal line, stigmata) are absent in *Cibacapsa*, but are retained in other Octacnemidae genera like *Situla*, *Dicopia*, *Octacnemus* and *Megalodicopia*. Only four specimens of *C. gulosa* were previously collected in Antarctic areas such as the Ross Sea, South of the Kerguelen Islands and the Weddell Sea at depths ranging from 570 to 810 m (Monniot and Monniot 1994). More recently, the species was reported in the South Sandwich Islands (Tatián et al. 2005). Gut contents reported by Monniot and Monniot (1983, 1994) comprised polynoid polychaetes, serolid isopods and legs of crustaceans. Since copepods, ostracods and small amphipods were observed in the gut contents of other specimens within the Octacnemidae, it is probable that the diet of *C. gulosa* could also include these and other prey items (Monniot and Monniot 1983).

The macroscopical anatomy of the gut of *C. gulosa* is described by Monniot and Monniot (1983). However, the microscopic anatomy of the inner wall and epithelium has not been described. On the other hand, there are many studies on the microscopical anatomy of the gut of filter-feeding ascidians in a number of genera: *Ciona*, *Botryllus*, *Dendrodoa*, *Styela*, *Microcosmus* and *Pyura* (Thomas 1970a, b; Burighel and Milanese 1973, 1975, 1977; Thorndyke 1977; Buencuerpo 1991). In this study, we identify and quantify for the first time the prey items in the gut and describe the cell types of the inner wall of different sections of the gut of *C. gulosa*. From these results, we also discuss other aspects of the trophic ecology (i.e., capture and assimilation of prey) of this macrophagous ascidian.

Materials and methods

This study is based on the examination of three specimens of *Cibacapsa gulosa*. Samples were taken during the “LAMPOS” cruise (ANT XIX/5) of RV “Polarstern” in the central area of the South Sandwich Islands, at 590 m depth (St 207: 57° 33'91" S/26° 22'78" W), during April 2002. The specimens were collected by Agassiz (AGT) trawl. The area is characterized by restricted shallow water around volcano peaks and a swept slope; the substrate consists of volcanic stones, such as lava and pumices. Despite these inhospitable substrates, elements of the benthic fauna composed mostly by Brachipoda, Ophiuroidea, Asteroidea, Crinoidea and Holoturoidea were collected together with ascidians (see Arntz and Brey 2003). A specimen of *C. gulosa* was photographed in vivo to

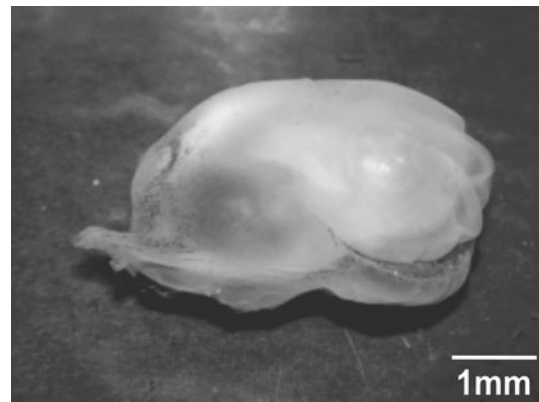


Fig. 1 *Cibacapsa gulosa*

document its appearance (Fig. 1). Two specimens were immediately fixed in buffered 2.5% formaldehyde in seawater and the other one in ethanol.

In the laboratory, specimens were dissected to separate the gut from the rest of the body. Gut contents were extracted with a Pasteur pipette. Prey items were identified using different keys and descriptions available (Smith 1977; Boltovskoy 1981; Sieg and Wägele 1990; Stanwell-Smith et al. 1997) and counted using a Bogorov 10-ml chamber under a stereomicroscope. In order to examine the microscopic anatomy of the epithelium, the gut was dissected into three sections: esophagus, stomach and intestine. Each section was dehydrated in a graded alcohol series and cleared in ethanol-xilol. They were then embedded in paraffin, sectioned at 5–7 μ m and stained with hematoxylin-eosin. The different gut sections were examined using a light microscope and photographed.

Results

Prey items

A variety of prey items were found in the gut contents of the three specimens of *Cibacapsa gulosa*. They belonged to six different phyla: Coelenterata, Annelida, Mollusca, Arthropoda, Echinodermata and Chordata (Table 1). Large quantities of orange-colored oil droplets were also observed in the gut. No phytoplankton components were found.

Although most prey items contained in the gut had a pelagic origin (82.9%), benthic preys were also present (8.5%). The food items had a wide size range: from 100 μ m for the small calanoid copepods, to 4 mm for amphipods and ophiuroids. Some items were partially digested, such as pelagic polychaetes, gastropods and crustacean parts (Fig. 2).

Table 1 Different prey items found in the gut contents of *Cibacapsa gulosa*

	Habitat	Frequency (mean \pm SD)
Crustacean parts		
Crustacean cuticula type I ("ring-shaped")		94.7 \pm 56.4
Crustacean cuticula type II ("tube-shaped")		4.7 \pm 4.5
Crustaceans (mandible parts)		32.7 \pm 14
<i>Eusirus antarcticus</i> (gnathopod)	Pelagic/Benthic	4.3 \pm 7.5
Hyperiid amphipods (head)	Benthic	0.3 \pm 0.6
Calanoid copepods (part of prosome and urosome)	Pelagic	0.3 \pm 0.6
Halacaroida (leg)	Benthic	0.3 \pm 0.6
Crustacea (complete animals)		
Calanoid copepod	Pelagic	16 \pm 4.4
Harpacticoid copepod	Benthic	0.3 \pm 0.6
Gammarid amphipod	Benthic	0.3 \pm 0.6
Echinodermata		
Ophiuroid	Benthic	0.3 \pm 0.6
Annelida		
Lumbrinerid polychaete	Benthic	0.7 \pm 1.2
Polychaete Type I	Pelagic	20.3 \pm 33.5
Polychaete Type II	Pelagic	1.3 \pm 1.2
Mollusca		
Gastropod	Benthic	2.3 \pm 4
Coelenterata		
Medusa (<i>Euphysora</i>)	Pelagic	1.3 \pm 1.2
Other		
Fecal pellet		1.3 \pm 1.2
Fish scale		3.3 \pm 5.8

Histology

The internal wall of the gut of *Cibacapsa gulosa* was lined with a prismatic epithelium overlying a mesenchyme with blood cells.

The internal epithelial cells of the esophagus (Fig. 3) showed an intense basophilia in the apical region. Two cell types were present: the most abundant cell type was ciliated mucous cells (CMC). The other cell type was zymogenic cells (ZC), scattered throughout the epithelium. The CMC had a large, round nucleus; the cytoplasm contained basophilia in the apical third region. The ZC had a round nucleus, located in the basal third of the cell; the cytoplasm contained vacuoles and numerous basophilic granules.

The stomach (Fig. 4) was characterized by an epithelium with dense microvilli. This epithelium consisted of several cell types: CMC, ZC, undifferentiated cells (UC) and concretion cells (CC). The CMC showed abundant

microvilli, a round nucleus located in the basal third of the cell and big supranuclear vacuoles. The ZC were smaller than the CMC but similar to the ZC described for the esophagus. Throughout the epithelium, there were stratified zones with small cells with a round central nucleus, the UC. The CC had a large vacuole containing heterogeneous inclusions, and the nucleus was located close to the outer portion of the cell.

The epithelium of the intestine (Fig. 5) consisted mainly of CMC. These cells showed a round basal nucleus, supranuclear vacuoles and some cilia; the cytoplasm of the apical cells showed a light basophilia. The ZC showed an intense basophilia. The UC in the intestine were similar to those in the stomach.

Discussion

Sessile organisms living in deep benthic systems are adapted to a scarce food supply, since little of the planktonic primary production in surface waters reaches such depths. These conditions can be harsher in some areas, such as Antarctica and specifically the South Sandwich Islands, described as "extremely depauperate" because their remote position and lava bottoms (Arntz et al. 2005).

The ascidian *Cibacapsa gulosa* is clearly a macrophagous species adapted to capture occasional food items, some of which are often energy-rich organisms. The large quantity of oil droplets in the gut of *C. gulosa* can be explained by the capture of zooplanktonic prey. In high latitudes, zooplankton organisms store lipids (especially wax esters) as energy supplements to be used during the long periods of food scarcity (Graeve et al. 1994). Thus, these organisms constitute an important supply of energy for other trophic levels. The daily vertical displacement of the zooplankton (Shulenberger et al. 1984) as well as the winter migration of some species to deep waters (Cassareto and Nemoto 1986; Smith and Schnack-Schiel 1990) increases their availability for benthic organisms living within the deep benthos.

The present study further confirms that *C. gulosa* is a macrophagous, non-specialized species able to capture pelagic and benthic prey. Previous records revealed only crustaceans and polychaetes in the gut contents of this species (Monniot and Monniot 1994). The zooplankton organisms observed, such as medusae, calanoid copepods and hyperiid amphipods, are active swimmers. Also, the benthic organisms captured, such as ophiuroids and halacarids, move actively on the substrate. The mobility of these preys supposes a special behavior of *C. gulosa*. The strategy that allows *C. gulosa* to capture mobile preys seems to be the same as previously reported for octacnemid species: passively waiting for the forthcoming

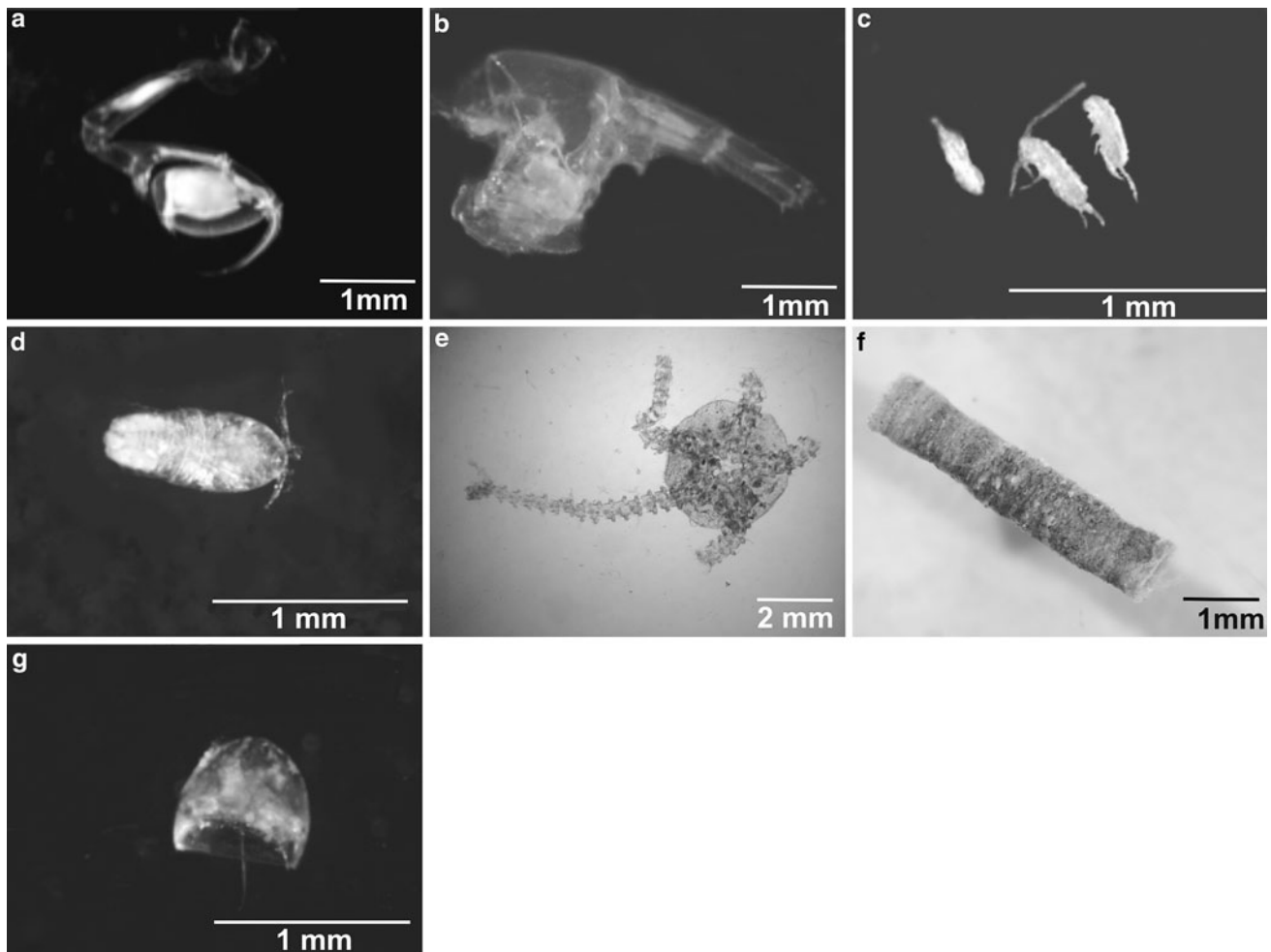


Fig. 2 **a** Gnathopod; **b** Hyperiid amphipod (head); **c** Calanoid copepods; **d** Harpacticoid copepod; **e** Ophiuroid; **f** Lumbrinerid polychaete; **g** Medusa (*Euphisora*)

prey and trapping it in some way (Okuyama et al. 2002; Havenhand et al. 2006). In situ observations of *Megalodicopia hians* revealed that most individuals oriented their large oral apertures in the counter direction of the presumed upwelling currents, suggesting the utilization of water currents for feeding (Okuyama et al. 2002). Different is the case of other macrophagous tunicates such as Hexacrobrylidae, which are also able to capture a wide variety of prey items but catching these prey actively, using their lobed oral siphon: analyses in the rectum of individuals of the species *Asajirus indicus* revealed foraminifers, polychaetes, ostracods, cladocerans, isopods, gastropods and what appeared to be particles of an ophiuroid (Kott 1992).

The present study is the first one to histologically examine the inner wall of a macrophagous ascidian. The gut epithelium of *C. gulosa* is simpler than that of filter-feeding ascidians (Table 2). The mesenchyme is thinner, and the epithelium has fewer cell types than filter-feeding species. Thus, epithelial cells of macrophagous tunicates

may be involved in multiple functions, such as movement and progress of the food, secretion, absorption and osmoregulation. The most abundant cell type in the esophagus of *C. gulosa*, as in filter-feeding ascidians (Burighel and Milanese 1975; Buencuerpo 1991), is a ciliated mucous cell. Therefore, the main function of the esophagus is the transportation of the food string toward the stomach while it is being mixed with mucous. These cells provide mechanical and chemical protection to the epithelial surface and contribute to the formation of the food cord (Relini Orsi 1969). Undifferentiated cells were not observed in the esophagus as occurs in other ascidians (Relini Orsi 1968, 1969; Ermak 1975). In several filter-feeding ascidians the stomach presents a deeply folded surface. The internal wall of stomach of *C. gulosa* is smooth, and undifferentiated cells (UC) are scattered throughout the epithelium. The CMC are very abundant in the stomach of *C. gulosa* and we believe that these cell types in this section have diverse functions, i.e., secretion, transport and absorption. The main role played by CMC in

Fig. 3 Transverse section of the esophagus. **a** General view; **b** Close-up of ciliated mucous cells (CMC) and mucous secretion into the lumen

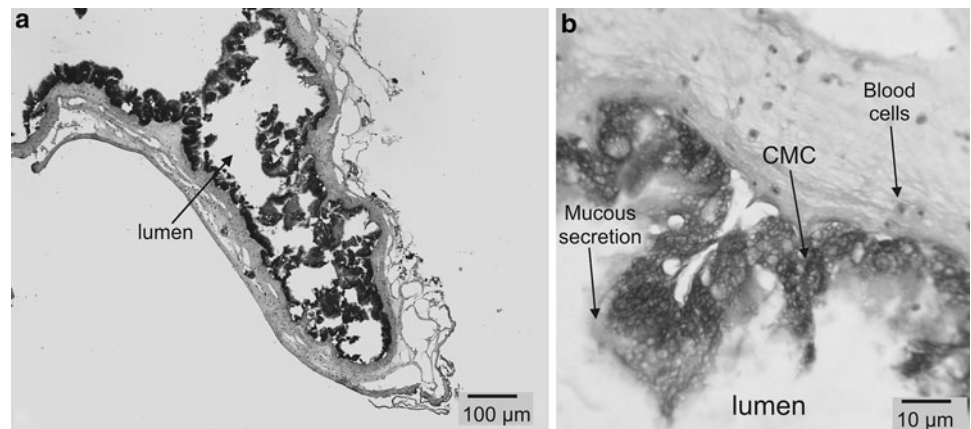


Fig. 4 Internal wall of the stomach. **a** General view; **b** Close-up of concretion cell (CC) and their heterogeneous inclusions (arrows)

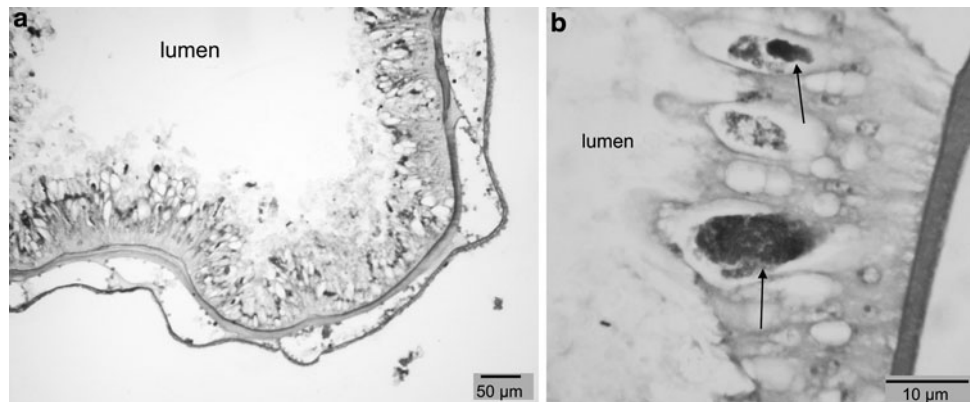
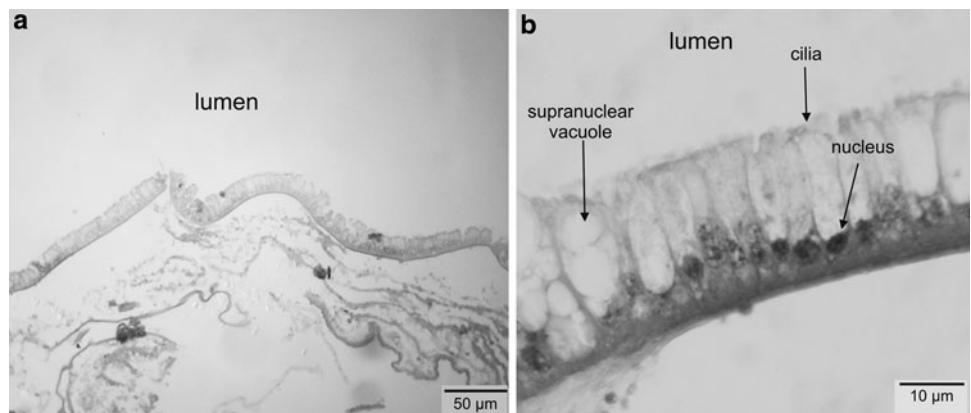


Fig. 5 Internal epithelium of the intestine. **a** General view; **b** Close-up of ciliated mucous cells (CMC)



the stomach appears to be the absorption of the extracellularly digested food. Many authors (Burighel and Milanesi 1973; Burighel 1979; Buencuerpo 1991) have reported the presence of zymogenic cells (ZC) in the internal walls of ascidians and considered that these cells are responsible for production of most of the digestive enzymes in the gut. In the stomach of *C. gulosa*, ZC are present and probably with this function. Nevertheless, a physiological study to determine whether these cells are secreting different types of digestive enzymes is needed.

In the inner intestinal epithelium, the most common cell type was the CMC, which show big supranuclear vacuoles, some cilia and apical cell basophilia. These cells may perform absorption and mucous secretion functions as well as transportation of the remaining non-digested material, as was previously suggested (Goodbody 1974; Relini Orsi 1968, 1969; Buencuerpo 1991).

The finding of concretion cells (CC) in the stomach of *C. gulosa* is unique among the ascidians. So far, intracellular concretions have only been observed in the stomach

Table 2 Different cell types observed in the inner wall of the gut of microphagous ascidians and *Cibacapsa gulosa*

Cell types	Microphagous ascidians	<i>Cibacapsa gulosa</i>
Esophagus		
Undifferentiated	X ^f	
Ciliated mucous	X ^a	X
Endocrine	X ^{g,e}	
Zymogenic		X
Stomach		
Undifferentiated	X ^{a,j,i}	X
Ciliated mucous	X ^{e,k}	X
Zymogenic	X ^{b,d,k}	X
Vacuolated	X ^{c,k}	
Endocrine	X ^{e,h}	
Plicated	X ^e	
Concretion		X
Intestine		
Undifferentiated	X ^b	X
Ciliated mucous	X ^{b,d}	X
Zymogenic		X
Endocrine	X ^{b,h}	

The letter X indicates the presence of the cell type

^a *Ciona* (Thomas 1970b); ^b *Styela* (Relini Orsi and Pestarino 1971); ^c *Styela* (Thorndyke 1977); ^d *Brotryllus* (Burighel and Milanese 1973); ^e *Brotryllus* (Burighel and Milanese 1975); ^f *Styela* (Ermak 1975); ^g *Styela* (Bevis and Thorndyke 1978); ^h *Styela* (Thorndyke and Bevis 1978); ⁱ *Microcosmus* (Pestarino and Staffieri 1980); ^j *Styela* (Ermak 1981); ^k *Dendrodoa* (Buencuerpo 1991)

of Sorberacea (Gaill 1979), a macrophagous benthic tunicate group whose classification remains unclear. Their presence of concretion cells in Sorberacea, and now in *C. gulosa*, may be interpreted as a result of a macrophagous-feeding habit.

The reduction in the branchial sac, the organ where enzymatic digestion is initiated in tunicates (Fiala-Médioni and Pequignat 1980), leaves this important function to be developed exclusively in other gut sections. Besides the pyloric gland, in some species (Pyruids, Molgulids), there is a “liver” which produces digestive enzymes (Berrill 1929; Fouque 1959). When these structures are absent, the digestive enzymes are produced in the gastric mucosa as demonstrated by Relini Orsi (1968). In our study, the cells which produce digestive enzymes, the zymogenic cells (ZC), were found in the stomach and scattered throughout the esophagus and intestinal epithelium. The wide distribution of ZC along the gut could be considered as an adaptation to the macrophagous diet, because the breakdown of exoskeletal hard parts present in some prey supposes a high enzymatic activity.

The absence of endocrine and plicated cells in our observations could be attributed to the methods employed

in this study. Staining with hematoxylin-eosin and observations under light microscope does not allow the differentiation of these cell types, which are present in the digestive tract of ascidians (Burighel and Cloney 1997) and were detected by immunofluorescence and immunocytochemistry in their study. However, it is likely that *C. gulosa* has these cells in the internal gut epithelium, considering their important role in some tunicates. Endocrine cells probably take part in the regulation of the digestion (Thorndyke and Georges 1988) and plicated cells participate in fluid regulation in the absence of typical excretory organs (Burighel et al. 1985).

The capture and assimilation of a wide variety of prey coming from both the pelagic and the benthic systems allow *C. gulosa* to grow in a critical environment. The present results contribute to the better understanding of deep-sea biology and the interaction between these ascidians and their environment.

Acknowledgments This study was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto Antártico Argentino (IAA), Alfred Wegener Institute (AWI) and the Universidad Nacional de Córdoba (UNC). This work was partially funded by PICTO ANPCyT-DNA N° 36326 and SECyT (05/I602), Universidad Nacional de Córdoba. We also express our gratitude to the members of the “Polarstern” crew, especially to the Spanish team (Pablo López-González, Estefanía Rodríguez and Neus Vert) and Prof. Dr. Wolf Arntz for their permanent support. We thank Dr. Mirian Bulfon, Dr. Gabriela Pirk, Dr. Howard Feder and two anonymous reviewers whose suggestions greatly improved the manuscript.

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