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Histological Study of *Goniodoris castanea* Alder and Hancock, 1845 (Nudibranchia, Doridoidea, Goniodorididae)

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ABSTRACT The major organ systems of *Goniodoris castanea* were investigated by histological means, with an emphasis on those structures that are difficult to see by dissection. The species is characterized by some peculiar features that are unique or seldom within the Nudibranchia, such as the complete absence of specialized vacuolated cells, the presence of globular salivary glands, the presence of cuticular structures in the proximal intestine, a muscular sphincter around the distal vaginal duct, and the position of the blood gland closer to the pericardium than to the nervous system. Some of these characters are discussed in a phylogenetic context, although a thorough phylogenetic analysis is preliminary, due to lack of knowledge of probably related species. J. Morphol. 250:61–69, 2001. © 2001 Wiley-Liss, Inc.

KEY WORDS: *Goniodoris*; Doridoidea; Nudibranchia; systematics; anatomy; histology

The genus *Goniodoris* Forbes, 1840, is represented by about 25 species of nudibranch gastropods, although the anatomy has been studied in only two. *G. nodosa* (Montagu, 1808) with a distribution mainly restricted to the northeastern part of the Atlantic and the Mediterranean Sea (Thompson and Brown, 1984; Cattaneo-Vietta, 1984; Cervera et al., 1988; Picton and Morrow, 1994; Yonow, 1996), and *G. castanea* Alder and Hancock, 1845, with a probable worldwide distribution (Baba, 1955; Swennen, 1961; Schmekel and Portmann, 1982; Thompson and Brown, 1984; Gosliner, 1987; Rudman and Darvell, 1990; Cattaneo-Vietti et al., 1990; Picton and Morrow, 1994). Although we have a rough idea about the morphology and anatomy of these two species, extensive investigations on a comparative basis are missing. Especially some characters, which are of considerable interest for phylogenetic analyses (e.g., the presence of cuticular structures in the middle portion of the digestive tract) are not well known. Due to this lack of knowledge, Wägele and Willan (2000) did not include this highly interesting genus in their analysis of nudibranch phylogeny. Wollscheid and Wägele (1999), analyzing the phylogeny of the Nudibranchia with molecular markers, discussed the systematic position of *Goniodoris* as basal within the Doridoidea. In this article, the anatomy and histology of the organ systems of the common species, *G. castanea*, are presented to extend our knowledge on the morphology and anatomy of this species. The results are discussed in the light of the recent phylogenetic analyses of Wägele and Willan (2000) and Wollscheid and Wägele (1999).

MATERIALS AND METHODS

Two specimens of *Goniodoris castanea* (Montagu, 1808), collected by the second author from the intertidal at Playa de Santa María del Mar (Cádiz) and from El Portil (Huelva) (southwestern Spain) in October 1998 and November 1999, respectively, were preserved in 6% formaldehyde/seawater. After dehydration of one of the specimens, the whole animal was embedded in hydroxyethylmethacrylate for serial sectioning (2.5 mm). Sections were stained with toluidine blue. Notes on color refer to this staining. Photographs were taken with an Olympus camera (OM2) on an Olympus BX microscope. The other specimen was investigated macroscopically.

RESULTS

External Morphology

Figure 1A depicts a preserved animal (length 5 mm). The flattened oral veil bears two distinct oral tentacles, which have no grooves on the ventral side. The oral veil is not covered completely by the frontal notal edge. The rhinophores have about 10 to 12 lamellae. The eight bi- to tripinnate gills surround the anal papilla in a wide circle. The notal edge is

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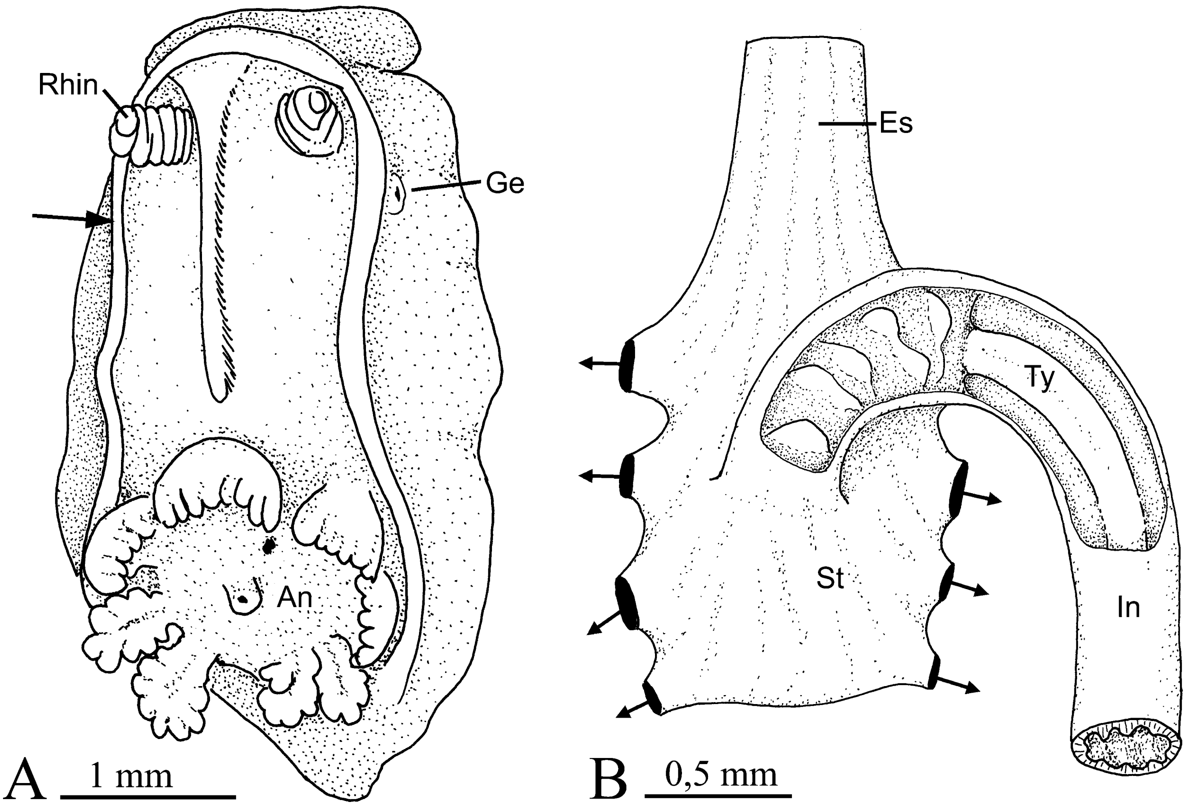

Fig. 1. *Gonidoris castanea*. **A**: Dorsal view of specimen; arrow, notal rim. **B**: General outline of the median part of the digestive system. The lateral entrances from the stomach into the digestive gland are indicated, but there are many more on the ventral side that are not shown here. The proximal part of the intestine is opened to show the cuticularized ribs in the ascending limb and typhlosole in the descending limb of the intestine. An, anus; Es, esophagus; Ge, genital opening; In, intestine; Rhin, rhinophore; St, stomach; Ty, typhlosole.

bent upwards as a distinct rim. Behind the gills, the notum does not form a distinct lobe, but merges with the foot. The foot is broad. Its anterior border is rounded and notched beneath the mouth and the posterior part is not covered by the notum.

Epithelia and Connective Tissue

The dorsal notal epithelium consists mainly of cuboidal to columnar cells, which have a characteristic large vacuole (Fig. 2A, arrows). These vacuoles do not stain, but appear empty. Between the cuboidal to columnar cells are interspersed cells containing brown to greenish stained grana. In some areas these cells dominate. Only a few glandular epithelial cells are present, which stain violet (acid mucopolysaccharides). In the notal margin (Fig. 2A), the same cells occur but they are more elongate than in the other epithelia (notum, rhinophores, gills) (Fig. 3A). No specialized vacuolated cells were detected.

The pedal epithelium is characterized by tall columnar, ciliated cells, with nearly no epithelial glandular cells between them. Subepithelial glandular follicles composed of several cells with violet contents form a nearly closed layer in the anterior part of the foot, but are less dense in the posterior part (Fig. 4E). Cells with brown to greenish grana are very rare here.

The epithelia of the rhinophores (Fig. 3A) and the oral veil consist of the same cell types as the epidermis. Only in the oral veil are subepithelial glandular follicles (stained violet), similar to those of the foot, present.

The epithelium of the gills is similar to that of the notum. Within the gills, only a few muscle fibers are present. At the bases of the gills and in the proximal third of the rachis, globular gill glands are present (Fig. 2B), which are composed of tall columnar cells with rather indistinct contents and a basally lying nucleus. In one of the medially lying gills a gill gland was also found in the tip of the gill branch.

The connective tissue in the notum is dense and stains rather homogeneously light blue, giving it the appearance of a hyaline tissue. The lumina of numerous mainly dissolved spicules are present in the tissue of the foot (Fig. 4D), the oral veil, the rhinophores, the basal parts of the gills, and the notal tissue (Fig. 3E), but not in the margin of the notum (Fig. 2A).

Digestive Tract

The epithelium of the short oral tube consists of tall columnar cells. No epithelial or subepithelial glandular cells were observed.

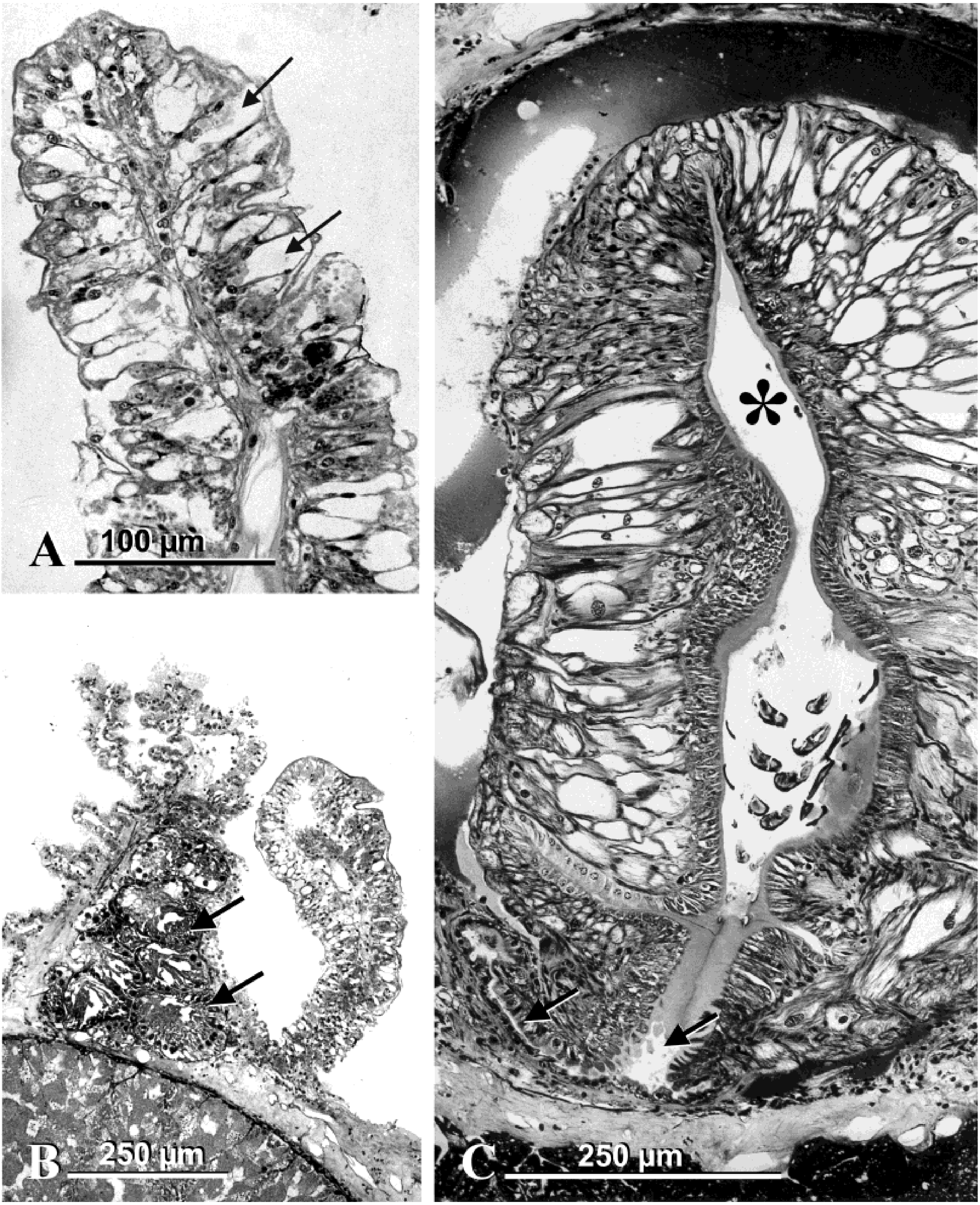

Fig. 2. *Goniodoris castanea*. **A**: Cross section of notal rim; arrows, large vacuole. **B**: Cross section of gill and adjacent notal rim; arrows, gill glands. **C**: Cross section through pharynx and buccal pump (asterisk). Both are lined by the homogeneously light-staining cuticle. Note the darkly stained hemolymph in the visceral cavity above the buccal pump. Arrows at bottom of figure, labial disc (left arrow) and jaws with rodlets (right arrow).

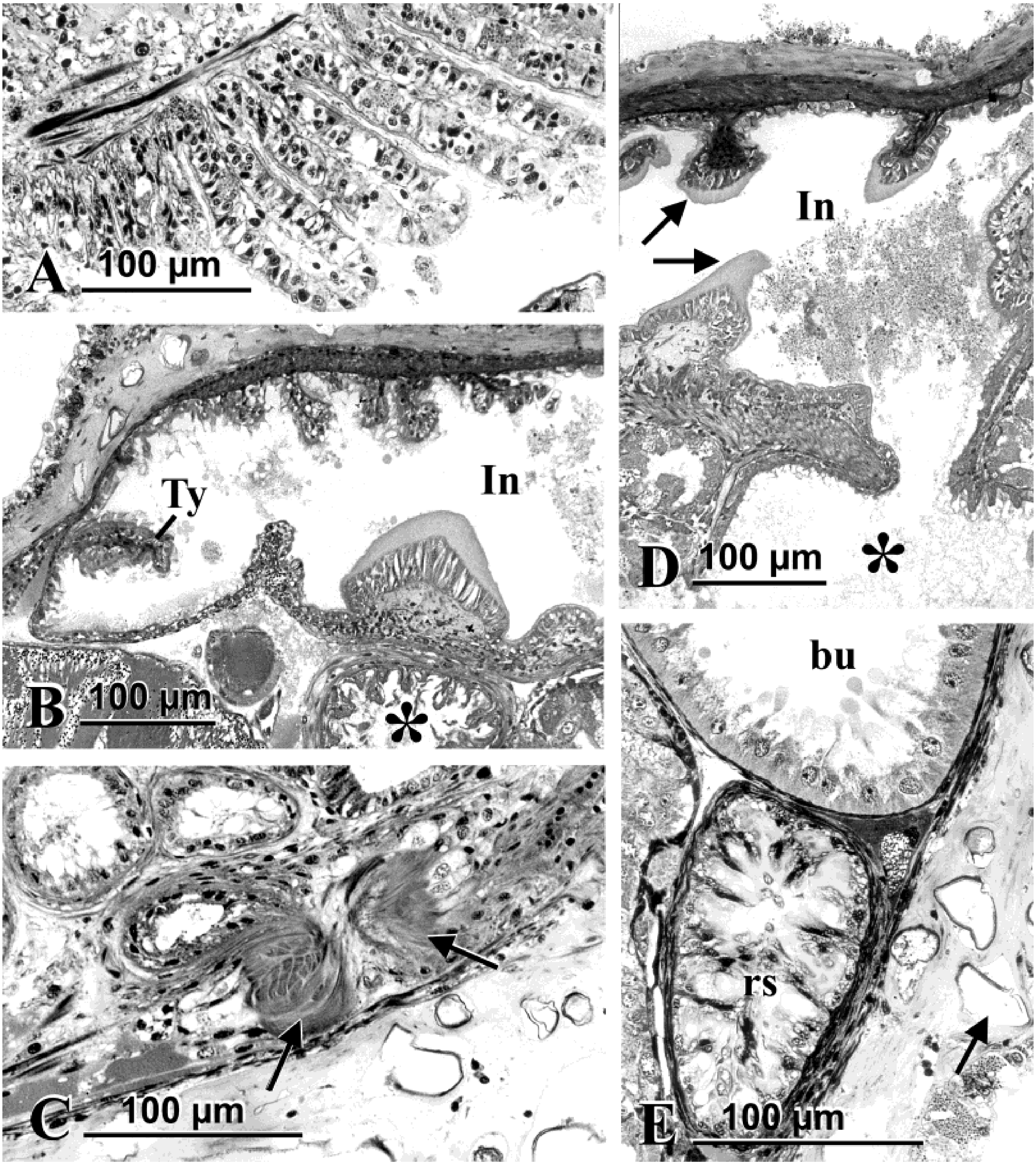

Fig. 3. *Goniodoris castanea*. **A**: Longitudinal section through rhinophoral lamellae. **B**: Cross section through esophagus/stomach (asterisk) and intestinal loop. Left part shows the intestine with the typhlosole and the right part the intestine with the cuticular structures. **C**: Muscle sphincter (arrows) in the distal part of the vaginal duct. **D**: Cross section through transition of stomach (asterisk) into intestine. Note the cuticular plates on the dorsal and ventral part of the proximal intestine (arrows). **E**: Cross section of bursa copulatrix and receptaculum seminis. Arrow, lumen of dissolved spicule; bu, bursa copulatrix; In, intestine; rs, receptaculum seminis; Ty, typhlosole.

The pharynx is lined by a cuticle, which is composed of rodlets in the most anterior part (labial disc). In gross anatomy the pharynx appears as a network of muscle fibers, which are arranged radially, circularly, and longitudinally (Fig. 2C).

The buccal pump is connected to the pharynx by a broad base. It is lined by a cuticle (Fig. 2C, top) and

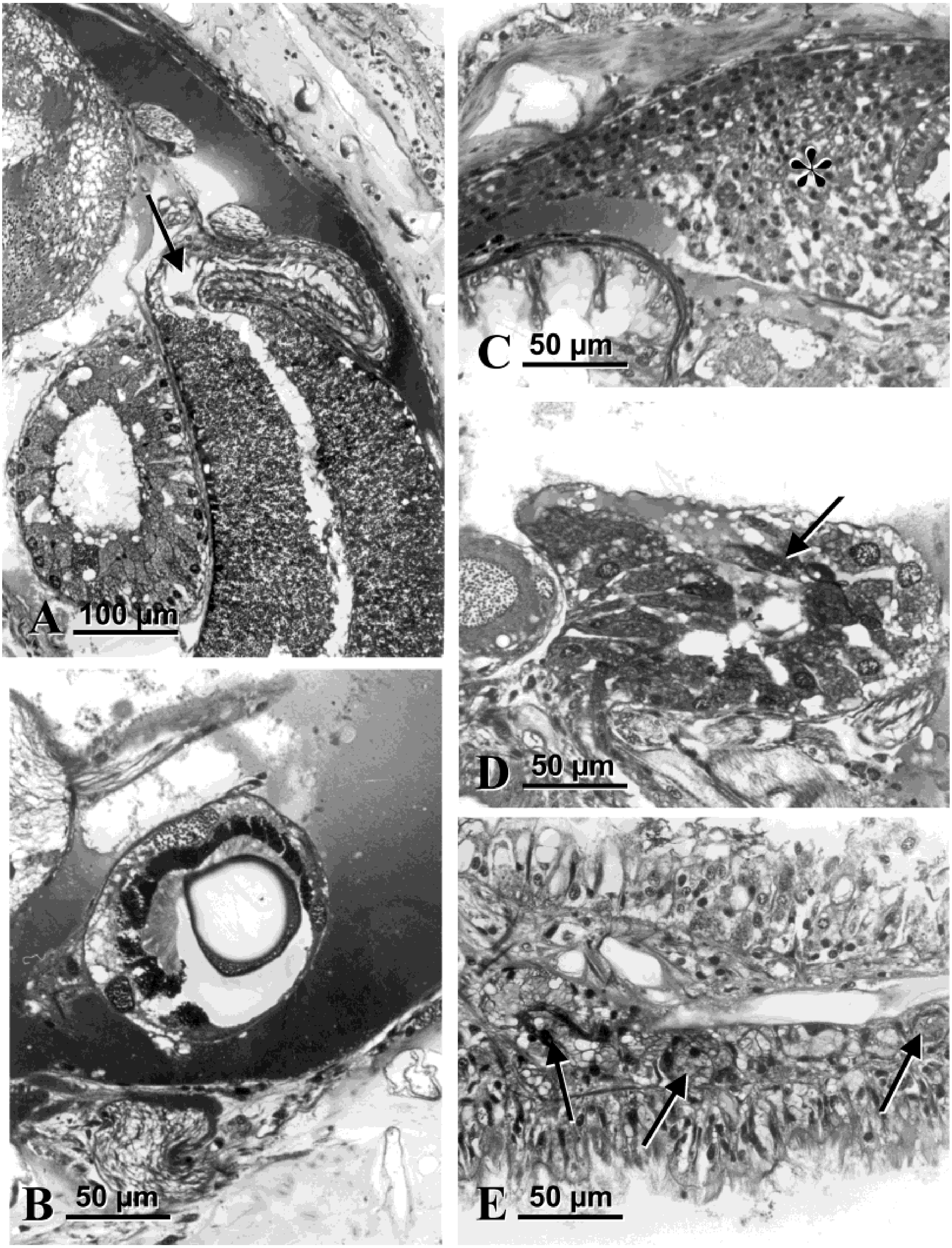

Fig. 4. *Goniodoris castanea*. **A**: Transition from distal prostatic part (right side) into the narrow distal vas deferens (arrow). Tube on left side depicts proximal prostatic part. **B**: Cross section of eye with lens and pigment cells. Note the dark coloration of the hemolymph, which surrounds the eye in the visceral cavity. **C**: Blood gland (asterisk) on top of receptaculum seminis. **D**: Globular salivary glands, with darkly stained cells (arrow), indicating secretion of acid mucopolysaccharides. **E**: Foot epithelium with few, not very prominent underlying glandular follicles (arrows).

its lumen has the shape of a triangle in cross section. The muscle fibers, which are mainly arranged radially, show the same arrangement as the network that can be seen in the pharynx (Fig. 2C, bottom).

The salivary glands are two small ball-like structures (Fig. 4D), lying on either side of the pharynx and lacking ducts. They are composed of glandular cells that stain dark violet, indicating the secretion of acid mucopolysaccharides. The epithelium of the esophagus, composed of prismatic undifferentiated cells, is highly folded and surrounded by a thin muscle layer. No glandular cells were observed. The transition of the esophagus into the stomach is not distinct (Fig. 1B).

The stomach is completely surrounded by the digestive gland and is only recognizable by the prismatic, ciliated cells. In the anterior portion of the stomach are two large openings into the right and left parts of the holohepatic digestive gland. In the posterior portion of the stomach, several openings in the lateral and ventral components of the digestive gland can be observed (Fig. 1B). The transition into the intestine is distinct (Fig. 3D, asterisk). A caecum is not present. The intestine is divided into two parts. The first part, leaving the stomach on the dorsal side and forming the main part of the intestinal loop, is characterized by a thin cuticular lining and thick cuticularized ridges lying dorsally as well as laterally and ventrally (Figs. 1B, 3B,D). This part is underlain by a thick layer of connective tissue that stains reddish. When turning caudad, the intestine is no longer cuticular. It has several ciliated ridges and a very distinct typhlosole (Figs. 1B, 3B). Its ciliated inner epithelium is underlain by red-stained connective tissue. This second part is therefore clearly separated from the first. There are no glandular cells present in the whole intestine. In the posterior part, neither the typhlosole nor the folds are present. The interior lining is composed of columnar ciliated cells.

Reproductive System

The gonad extends over the digestive gland, forming follicles, which mainly lie on the dorsal side, but also on the lateral and ventral sides. Very often they intermingle with the digestive gland. They do not form a compact and complete layer on top of the digestive gland. In the follicles only spermatogonia have been observed. The ampulla is very prominent and filled with autosperm. Its epithelium is composed of flat cells.

Figure 5 depicts a general outline of the distal genital system. The vas deferens has a huge, sausage-shaped prostate gland, with tall columnar cells filled with small, violet-stained grana (Fig. 4A, right side). The transition from the prostate into the muscular distal vas deferens is distinct (Fig. 4A, arrow). The epithelium consists of ciliated cells. A short distance from this transition, the vas deferens forms a muscular sheath in which the muscular penis lies completely intruded. About half of the invaginated penis has tiny spines.

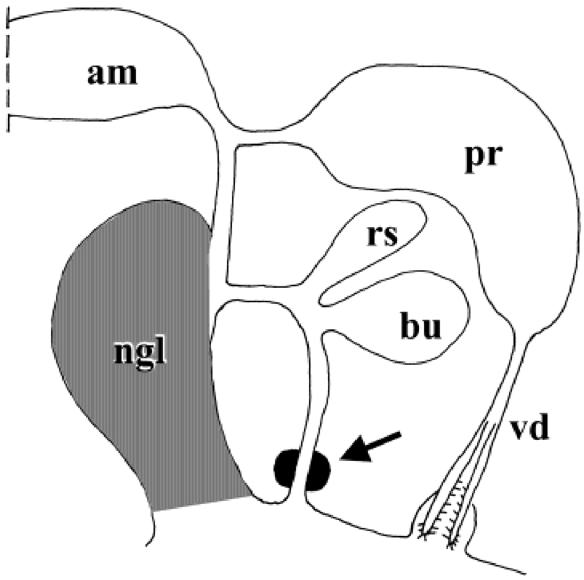

Fig. 5. *Goniodoris castanea*. Schematic outline of reproductive system. Note the muscular sphincter at the distal vaginal duct (arrow). Am, ampulla; bu, bursa copulatrix; ngl nidamental glands; pr, prostate; vd, vas deferens.

The vaginal duct, starting as a small ciliated duct, bears a thick muscular ring that functions as a sphincter (Fig. 3C). The bursa copulatrix, an elongate structure filled with disintegrating sperm is lined by an apocrine-secreting epithelium (Fig. 3E). The muscular receptaculum seminis is empty. Its epithelium is folded and composed of small cells (Fig. 3E). A distinction between capsule gland, membrane gland, and mucous gland in the nidamental glands is already possible, although the cells do not have the typical features of mature specimens functioning as females (Klussmann-Kolb, in press). No further glands could be detected next to the genital opening.

Nervous System

The connective tissue sheath surrounding the ganglia is very thin. The eyes, which are very large (125 μm, Fig. 4B), are close to the cerebropleural complex. They are composed of a globular lens and a thick surrounding pigment layer. The statocyst contains several otoconia of different sizes, but none of them is considerably larger than the others.

Circulatory System

The pericardial complex is very compressed; therefore, an investigation of this organ system was not possible. The blood gland lies a short distance in front of the heart and stretches just above the genital system. It is very flat and composed of tiny cells with tiny nuclei. The hemolymph floating in the visceral cavity is stained dark blue (Figs. 2C, 4A,B).

Excretory System

The elongate syrinx is lined by an epithelium with long cilia. The tissue of the kidney forms a flat layer on top of the gonad or digestive gland. It does not intermingle with gonadal or digestive gland tissue. The ureter is very short and has no glands. Cells with the typical appearance of rhogocytes were not observed.

DISCUSSION

Anatomical details of *Goniodoris castanea* are scattered throughout the literature. Many of the results mentioned by different authors can be confirmed. Descriptions of the histology of organ systems are rare for the Gonodorididae as well as for other members of the Doridoidea or even Nudibranchia in general. Therefore, these results can only be compared in a rather sketchy way at the moment.

Although Schmekel (1985), Wägele (1997), and Wägele and Willan (2000) stated the presence of specialized vacuolated cells in the notal epithelia as an autapomorphy of the Nudibranchia, no cells of this kind could be detected in the specimen investigated. The complete absence of the specialized vacuolated epithelium can also be observed in *Dendrodoris* species, *Phyllidia flava, Limacia clavigera* (Wägele, 1997), and *Corambe lucea* (Schrödl and Wägele, in press). Its significance for phylogenetic analysis on a higher taxa level is not clear yet; many more species have to be investigated.

The glandular cells with the brown to greenish grana usually found in the ectodermal epithelia of notum, rhinophores, and gills in *Goniodoris castanea* are unusual and we do not know the function of them. Perhaps they produce repellents for possible enemies, as this has been suggested for other doridoidean members with glandular cells in the notum (Avila, 1995). Marcus (1955:161) described “cyanophil mucus glands” in the epidermis of *G. mimula*. Whether these glands are the same as the ones we describe has to be investigated.

The few muscle fibers in the rhinophores and the gills confirm the observations on preserved animals and statements of Eliot (1908) that these organs are not retractile, but only contractile to a certain extent. The presence of spicules in the notum is also described for *Goniodoris joubini* (Risbec, 1953) and *G. mimula* (Marcus, 1955).

Although Eliot (1908) and Forrest (1953) mentioned the absence of rodlets in the jaws, Bergh (1905) as well as Schmekel and Portmann (1982) observed them in *Goniodoris castanea*. This is confirmed here in histological sections. Rodlets occur in several species of the genus, e.g., *G. punctata* or *G. mimula* (Bergh, 1905; Marcus, 1955), but some of them, e.g., *G. glabra* or *G. modesta,* lack these structures (Eliot, 1905; Baba, 1937). The structure of the pharynx and buccal pump, with a muscular network, is observed only in a few nudibranchs. It is described in the same way for the tubular pharynx of *Dendrodoris nigra* (Wägele et al., 1999) and was observed also in *Phyllidia coelestis, P. flava* and *Polycera quadrilineata* (personal observations). In *Acanthodoris pilosa* and *Onchidoris bilamellata*, a similar structure occurs, although the network formed by the muscle fibers seems much denser than in the species mentioned above (personal observations).

Small, globular salivary glands, as observed in *Goniodoris castanea* (Bergh, 1905; Forrest, 1953; this article), are rather rare in dorids, which usually have tube-like glands stretching more or less over or along the esophagus. Globular salivary glands are described for members of the genus *Dendrodoris* (Valdés et al., 1996; Brodie et al., 1997), but in this genus the salivary glands are composed of cells which do not produce acid mucopolysaccharides and are composed of cells with large vacuoles containing light bluish-stained grana (Wägele et al., 1999). According to the staining properties and the fine structure, the secretion of acid mucopolysaccharides seems quite probable in *Goniodoris*, as is observed in other dorids.

A nonglandular esophagus is found in several other dorid species (*Phyllidia coelestis, P. flava, Trapania maculata*), whereas chromodorids, *Jorunna tomentosa*, *Polycera quadrilineata* and especially *Dendrodoris* have a highly glandular esophageal epithelium (Wägele et al., 1999; personal observations). The absence of a caecum, and the stomach completely covered by the digestive gland, mentioned by Bergh (1905) and Forrest (1953), have also been observed in our specimen. Forrest (1953) described the cuticular ridges, but he assigned them to the stomach, which according to his description is divided into a ventral ciliated part and a dorsal cuticularized part. Following the terms used by Wägele and Willan (2000), we consider the stomach to be the portion of the digestive tract where the esophagus enters and where the digestive glandular ducts and the intestine leave. Since the cuticularized portion of the posterior digestive tract lies on top of the ciliated stomach, and since this part first runs anteriorly and then bends backwards (identical to the intestinal loop of other doridoidean members), we consider this part a specialized proximal part of the intestine. Cuticularized structures in the digestive system (except jaws and radula) are known from few doridoidean species. Marcus (1955) described and figured similar ridges to those of *Goniodoris castanea* for *G. mimula*. Following Forrest (1953), he called the stomach that part that “is directed forward” (Marcus, 1955:162). Cuticularized lamellae in the stomach are also mentioned for *G. joubini* (Risbec, 1953). Marcus (1957:428) described a cuticularized “posterior gizzard” in *Thecacera pennigera*, which he compared to those of *Corambella carambola* and *Goniodoris*. Unpublished observations of the senior author confirm the presence of a thick cuticle in *Thecacera pennigera*. Similar to the observations for *G. castanea*, this cuticle lies in the proximal part of the intestine. Although Forrest (1953) speculated about the function of the cuticle (trituration of food, functioning as a sieve), it is unclear what effect the prominent cuticularized ridges or a simple cuticle may have in the beginning of the intestine. Forrest (1953) described the intestinal epithelium as ciliated and glandular in *G. castanea*, whereas it is nonglandular in *G. nodosa*. Our findings do not confirm his observations on *G. castanea*. Glandular cells are absent throughout the intestine.

The genital arrangement of the specimen investigated here corresponds to the description given by Schmekel and Portmann (1982) for *Goniodoris castanea*. No additional glands were found next to the genital opening. In this study a muscular sphincter in the distal part of the vaginal duct is depicted in *G. castanea*. Marcus (1955) also indicated a sphincter around the vaginal duct of *G. mimula*. In accordance with several authors, the specimen investigated here exhibited penial spines along the invaginated penis and quite a long way further up in the vas deferens (Vayssière, 1901; Bergh, 1905; Schmekel and Portmann, 1982). Penial spines are also recorded for *G. mercurialis* (Macnae, 1957), *G. punctata* (Bergh, 1905), and *G. violacea* (Risbec, 1953). Marcus (1955) mentioned the absence of a prostate in *G. mimula*. The prostate of *G. castanea* is very thick and sausage-shaped (Schmekel and Portmann 1982, present article).

A statocyst with a few smaller otoconia and one larger otolith is described for *Goniodoris joubini* (Risbec, 1953) and *G. nodosa* (Pelseneer, 1894). Although in our specimen we observed otoconia of different sizes, we do not consider the larger ones to be otoliths. Wägele and Willan (2000) demonstrated the presence of only one huge otolith and no otoconia in the aeolidoidean taxon Tergipedidae, a situation that is clearly different from the otoconia of different sizes observed in *G. castanea*.

Pelseneer (1894) recognized that the blood gland in *Goniodoris nodosa* is not situated in the head, contrary to the situation in many other doridoidean species. We could demonstrate for *G. castanea* that it lies closer to the pericardium than to the nervous system. The presence of hemolymph which stains with toluidine blue is unusual and not known yet from other nudibranch species. It can be assumed that stainable substances are present here, which are lacking in other nudibranchs.

Although we can confirm some of the peculiar features of *Goniodoris castanea,* it is impossible yet to conclude that these characters are typical of the genus. The following characters appear unusual in *G. castanea*: 1) complete absence of specialized vacuolated cells, 2) presence of globular salivary glands, 3) presence of cuticular structures in the proximal intestine, 4) muscular sphincter next to the vaginal opening, 5) the position of the blood gland more close to the pericardium than to the nervous system, and 6) presence of staining hemolymph.

More investigations on *Goniodoris* species and especially other members of the Phanerobranchia are needed to gain a better understanding of the evolution of this peculiar nudibranch group. Nevertheless, some of the previously observed characters and some described and discussed here throw a light on possible relationships of the genus. Due to the presence of a sucking bulb and the differentiated teeth into a huge first lateral and usually only one small second lateral, the affinity of *Goniodoris* to the suctorial Phanerobranchia (Goniodorididae, Corambidae, Onchidorididae) is quite obvious (see Millen and Nybakken, 1991). Millen and Nybakken (1991) discuss a sister-taxa relationship of the Goniodorididae with the Onchidorididae on the basis of the following synapomorphies: anus and gills lie dorsally and the cerebropleural ganglia are fused. These characters are plesiomorphic (see Wägele and Willan, 2000) and have to be reconsidered when analyzing the phanerobranch groups within the Doridoidea. On the basis of musculature and complexity of the buccal pump, Martynov (1995) discussed the Goniodorididae as having evolved separately from the Onchidorididae and Corambidae, with a convergent evolution of the buccal pump. The possibility of transformation from one system into the other is not discussed.

Observations on the cuticularized structures in the proximal intestine not only in *Goniodoris castanea* but also in *Thecacera pennigera* (Polyceridae, nonsuctorial Phanerobranchia) suggest a closer relationship of these two taxa. Observations on other phanerobranchs with a cuticularized stomach/intestine (e.g., *Okenia evelinae*; see Marcus, 1957) are scarce, and do not allow further conclusions yet. Nevertheless, the presence of spines on the vas deferens in these two latter taxa additionally strengthens this possible relationship, although Millen and Nybakken (1991) consider this coincidence as a convergency, and spines are also present in several other doridoidean taxa. Spines are absent in the suctorial Onchidorididae and Corambidae.

Schrödl and Wägele (in press) mentioned a peculiar position of the receptaculum seminis at the proximal oviduct for *Corambe lucea*, *Onchidoris neapolitana,* and *Adalaria jannae*. In *G. castanea*, the receptaculum seminis is attached to the vaginal duct, as is usual for many members of the Doridoidea. Therefore, a general statement in favor of the clade Suctoria is preliminary.

Goniodoris castanea shows some features that are discussed as plesiomorphic for the Doridoidea (Wägele and Willan, 2000). The notum in front of the rhinophores does not extend very much and therefore does not cover the oral veil completely, a situation which can be interpreted as the beginning of the overgrowth of the notum over the head (autapomorphy of the Anthobranchia; Wägele and Willan, 2000). The blood gland is situated near to the heart and not on top of the cerebropleural complex. This character state can be found in the Pleurobranchoidea (sistergroup of the Nudibranchia), the Bathydoridoidea (sistergroup of the Doridoidea), a few members of the Doridoidea (e.g., *Aegires*) (Wägele and Willan, 2000) and *Doridoxa* (Schrödl et al., in press). Wollscheid and Wägele (1999) analyzed the DNA sequences of the 18SrDNA with different cladistic algorithms. According to their results, the systematic position of *Goniodoris nodosa* is basal within the Nudibranchia. It usually represents the sister-taxon to all other Doridoidea, rendering the Phanerobranchia paraphyletic.

A thorough phylogenetic analysis based on morphological and histological data that includes related species of *Goniodoris* (members of the Onchidorididae, Corambidae, and Polyceridae) as well as other doridoidean species is desirable but not possible yet, due to a lack of information on the taxa mentioned above, but also on doridoidean taxa in general.

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