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Some comparative histological aspects of the dendrodorid genera *Doriopsilla and Dendrodoris* (Opisthobranchia: Nudibranchia)

Gilianne D. Brodie

KEY WORDS: Histology, *Dendrodoris*, *Doriopsilla*, Nudibranchia, dendrodorid, radula-less dorids

ABSTRACT The nudibranch family Dendrodorididae O'Donoghue 1924 consists of two genera, *Dendrodoris* Ehrenberg 1831 and *Doriopsilla* Bergh 1880. These taxa are notable because they lack radula and possess highly modified digestive systems. At least one species of *Dendrodoris* is also novel, in possessing symbiotic bacteria within a vestibular gland of the female reproductive system. The digestive and reproductive systems of several dendrodorids were examined by methacrylate resin histology. This study was undertaken to search for new character sets to address the phylogenetic placement of dendrodorids within the radula-less dorids and to make a comparison between features of the two-dendrodorid genera. Methacrylate resin histology is particularly useful for investigation of glandular tissue at a cellular level. The position of glandular tissue is very relevant to the separation of *Doriopsilla* from its sister taxon *Dendrodoris*. Studies of gross morphology have indicated that the placement of glands within the digestive system of *Doriopsilla* is different from that of *Dendrodoris*, however, to date no comparison of these organ systems by histological means has been undertaken. The study found that in *Doriopsilla* the oral glands are an integral part of the oral tube and have a different cell structure to those found in *Dendrodoris* where the oral glands are clearly separated from the oral tube. In addition the extent of glandular and muscle tissue within the pharynx and oesophagus of the two genera is very different, suggesting that the function of the respective components of the anterior digestive system differ between the two genera. The investigation also found that the genera differ in the structural arrangement of their ovotestis, kidney and digestive gland tissue. This study provides basic information related to the function of digestive and reproductive systems in dendrodorid nudibranchs and will improve the phylogenetic resolution of these taxa particularly by indicating which glandular structures are likely to be homologous. These results also provide information vital to clarifying the phylogenetic relationship of dendrodorids to other radula-less dorids.

RIASSUNTO La famiglia Dendrodorididae O'Donoghue 1924 è costituita dai generi *Dendrodoris* Ehrenberg, 1831 e *Doriopsilla* Bergh, 1880. Questi due taxa presentano caratteristiche anatomiche particolari, mancano di radula e possiedono un sistema digestivo assai modificato. Almeno una specie di *Dendrodoris* inoltre è particolare in quanto presenta, all'interno della ghiandola vestibolare dell'apparato genitale femminile, batteri simbionti. I sistemi riproduttivi e digestivi di diverse specie di dendrodorididi sono stati esaminati dopo fissaggio in resina metacrilica, particolarmente adatta per studiare il tessuto ghiandolare a livello cellulare. Scopo di questo studio, oltre ad un confronto anatomico tra i due generi, è quello di definire nuovi caratteri utili a valutare la posizione filogenetica dei dendrodorididi nell'ambito dei doridacei senza radula. La posizione del tessuto ghiandolare è molto importante nella separazione tra i due generi: studi di morfologia di base indicano che la localizzazione delle ghiandole all'interno del sistema digestivo in *Doriopsilla* è differente rispetto a *Dendrodoris*, ma nessun confronto a livello istologico era mai stato condotto. I risultati di questo studio rivelano come le ghiandole orali in *Doriopsilla* siano parte integrante del tubo orale ed hanno una struttura cellulare differente da quella presente in *Dendrodoris*, dove le ghiandole orali sono nettamente separate dal tubo orale.
Inoltre lo sviluppo dei tessuti ghiandolari e muscolari all'interno della faringe e dell'esofago è diverso nei due generi, suggerendo che questi abbiano una funzione diversa nei sistemi digestivi anteriori dei due generi. La ricerca ha anche evidenziato come i due generi differiscano nell'organizzazione strutturale dell'ovotestis, del rene e della ghiandola digestiva. Questo studio, oltre a fornire indicazioni di base sul funzionamento dei sistemi ghiandolari e riproduttivi nei dendrodorididi, indica, a livello d'analisi filogenetica, quali strutture ghiandolari possano essere considerate omologhe, contribuendo dunque a chiarire i rapporti filogenetici tra i dendrodorididi e gli altri doridacei senza radula.

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INTRODUCTION

The molluscan order Nudibranchia contains approximately 190 described genera (WÄGELE & WILLAN, 2000). Eleven of these genera (*Melibe, Tethys, Phyllidia, Fryeria, Phyllidiella, Phyllidiopsis, Ceratophyllidia, Reticulidia, Dendrodoris, Doriopsilla and Mandelia*) are notable because they have secondarily lost the characteristic molluscan radula. The latter nine genera are dorids, traditionally grouped together by radula absence and an adaptation to suctorial feeding. Controversy exists over this grouping, with results from the recent literature conflicting. VALDÉS (1996) and VALDÉS & GOSLINER (1999) support common ancestry while, BRUNCKHORST (1993) and RUDMAN (1998) oppose it. New phylogenetic character sets, with which to examine the taxa in more detail, are obviously required.

This study continues a search for new character sets by examining several members of the genera *Dendrodoris* and *Doriopsilla* by methacrylate resin histology. An extensive investigation of the Indo-Pacific dendrodorid *Dendrodoris nigra* (Stimpson), using this histological technique, revealed features contrary to those found in other cryptobranch dorids (WÄGELE *et al.*, 1999). These features include: the composition of the notal epithelium; the absence of "special" vacuolated cells; the cell structure of the salivary glands; the density of gland cells in the oesophagus; the muscle layers of the oesophagus; the size and structure of gill retractor muscles; the appearance of the oral glands; and the intermingled position of the gonad, digestive gland and kidney tissue.

In this current paper, data from the histological examination of the anterior digestive system and two features of the reproductive system (distal oviduct and gonad position) are presented for several species of dendrodorid i.e., *Dendrodoris fumata* (RÜPPELL & LEUCKART, 1828) (grey and orange/red form), *Dendrodoris albobrunnea* ALLAN, 1933, *Dendrodoris guttata* (ODHER, 1917), *Doriopsilla miniata* (ALDER & HANCOCK, 1864) and *Doriopsilla gemela* GOSLINER, SCHAEFER & MILLEN, 1999. This data reveals both considerable similarities and differences between the two-dendrodorid genera.

MATERIAL AND METHODS

Two specimens of *Doriopsilla miniata* (length of living specimens 25, 26 mm) from Hastings Point, New South Wales, Australia, collected in July 1991 and January 1998; one specimen of *Doriopsilla gemela* (length of preserved specimen 23 mm) from Bahia de Los Angeles, Baja California, Mexico collected in June 1996; one specimen of *Dendrodoris albobrunnea* (length of living specimen 49 mm) from Pioneer Bay, Orpheus Island, Palm Group, Great Barrier Reef, Australia, collected September 15 1993; 2 specimens of *Dendrodoris guttata* (both specimens 41 mm length alive) from Julian Rocks near Cape Byron, New South Wales, Australia, collected 30 January 1983; 1 specimen of *Dendrodoris fumata* [orange/red form] (length of living specimen 27 mm) from Bay Rock, off Magnetic Island, Great Barrier Reef, Australia, collected 14 August 1994; 1 specimen *Dendrodoris fumata* [grey form] (length of living specimen 37 mm) from Horseshoe Bay, Magnetic Island, Great Barrier Reef, Australia, collected 2 August 1997. All specimens, except *Doriopsilla gemela*, were preserved in formalin seawater for a minimum of 4 weeks; the specimen of *D. gemela* was preserved in Bouin's fixative before transfer to alcohol. All specimens were progressively dehydrated over a 9-hour period utilizing steadily increasing concentrations of ethanol. Whole dehydrated animals were embedded in hydroxyethylmethacrylate (Kulzer) before

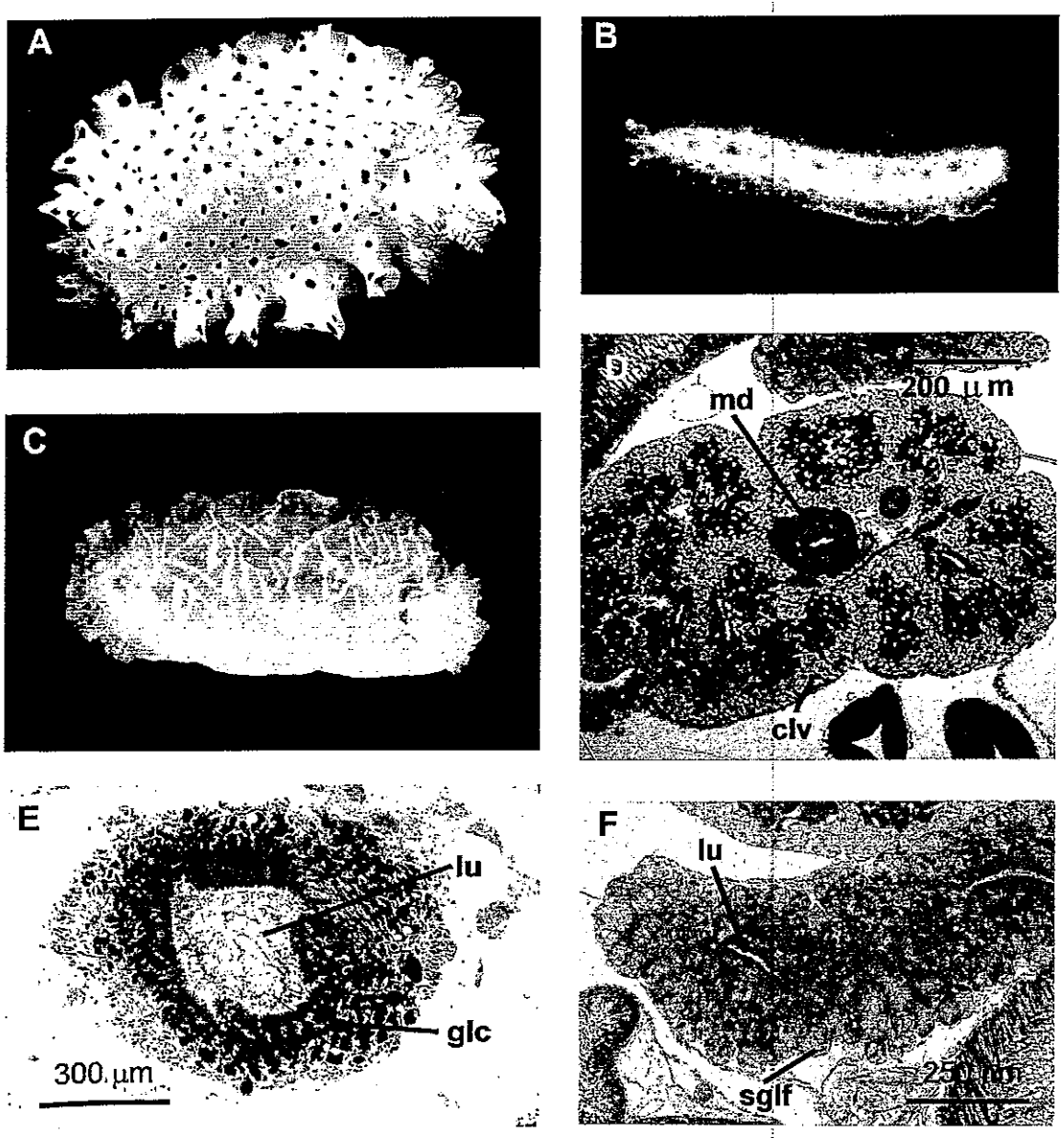

Figure 1. A. Photograph showing the external appearance of a living *Dendrodoris guttata* (length 41 mm) B. Photograph showing the external appearance of a living *Dendrodoris albobrunnea* (length 30 mm) C. Photograph showing the external appearance of a living *Doriopsilla miniata* (length 25mm) D. *A histological cross-section of the oral (ptyaline) glands in Dendrodoris albobrunnea* E. *A histological cross-section of the oral tube and associated oral glands in Doriopsilla miniata* F. A histological section of the salivary glands of *Dendrodoris fumata* (red form). Abbreviations: clv = cells with large vacuoles, glc = gland cell, lu = lumen, md = muscular duct, sglf = salivary gland follicle.

Table 1. A comparative summary of the results of a histological investigation of the anterior digestive system, and parts of the reproductive system, of *Dendrodoris* and *Doriopsilla*.

	Dendrodoris	*Doriopsilla*
Anterior Digestive		
mouth	glandular cells present	glandular cells present
oral tube	uniform width, no glandular development	broad, extensive thick glandular layers
oral glands	distinctly separate ptyaline glands	integral part of oral tube
salivary glands	paired glands with compact follicles	absent
pharynx	Y-shaped lumen, 2 muscle layers, no glandular development, thin cuticle	Y-shaped lumen, thimer muscle layers glandular cells present, thin cuticle
oesophagus	extremely glandular development, 2 muscle layers, no cuticle	not glandular, considerable muscle development, no obvious gland cells
Reproductive System		
distal oviduct	vestibular gland present in some species	no glandular development
ovotestis	intermingled ovotestis, kidney & digestive gland tissue	layered arrangement of ovotestis, kidney and digestive tissue

serial sectioning at 2-4 um thickness. Sections were taken using a powered microtome equipped with a tungsten-carbide knife. The resulting sections were stained for 20 seconds with 1% toluidine blue which had 1% borax added.

Comparison is made with sections of *Dendrodoris nigra* and other dorids (WÄGELE *et al.*, 1999). For information related to the colour forms of *Dendrodoris fumata* the reader is referred to BRODIE *et al.* (1997). For anatomical drawings and a general description of the organ systems of dendrodorids the reader is further referred to VÁLDÉS *et al.* (1996), BRODIE *et al.* (1997), VALDÉS & ORTEA (1997) and GOSLINER *et al.* (1999).

RESULTS

The dendrodorid genera are dissimilar in external appearance (Figure 1A-C). However, the gross anatomy of their anterior digestive systems shows some similarity with respect to the relative position and size of components (Figure 2). Even at this level differences with respect to the form and position of the oral glands and the presence of salivary glands is obvious. Histological examination provided several additional similarities and differences that are detailed below and summarized in Table 1.

Anterior Digestive System

Mouth

All specimens examined of both genera possess similar glandular cells surrounding the mouth. The epithelium consists of high columnar cells. These cells contain large rounded basally positioned nuclei with bluish contents and clumps of small dark purple staining grana.

Oral Tube

In *Dendrodoris* the oral tube is relatively long and uniformly simple. However in *Doriopsilla* it is at first simple but then expands to become relatively broad. In *Doriopsilla* the oral tube also contains thick glandular layers within the tube wall. These glands first appear dorsally but soon surround the entire tube. Close to the mouth the lumen of the tube is small and round but in the broader section before the pharynx it becomes much larger and folded. Although the same extensive glandular development of the oral tube is present in both species of *Doriopsilla* examined, the extent of the exterior muscle layer is variable.

Oral glands

In *Dendrodoris* the paired oral glands (ptyaline glands) are distinctly separate organs connected to the distal oral tube by a thin very muscular duct (Figure 2). Many of the cells contain large pale-staining vacuoles (Figure 1D). In contrast, the oral glands of *Doriopsilla* are not only different in appearance but are an intregal part of the oral tube. The walls of the oral tube are extremely glandular in appearance with large dark-purple staining cells (Figure 1E). The build-up of glands in this section of the digestive system is similar in appearance to that found in the oesophagus of *Dendrodoris*.

Salivary glands

The paired salivary glands of *Dendrodoris albobrunnea*, *D. guttata* and *D. fumata* are found close to the junction of the pharynx and oesophagus. The cells of this gland form compact follicles, which in turn contain small-round blue-staining vacuoles (Figure 1F). No epithelium layer can be seen surrounding the exterior of the gland, however a narrow lumen can be seen centrally. Sparsely scattered throughout the gland are several large cells with granular-looking pink-staining contents. No salivary glands appear to be present in either of the *Doriopsilla* avoid hyphens in generic names if possible examined.

Pharynx

A thick layer of muscle surrounds the pharynx of all *Dendrodoris* examined (Figure 3A). Another thinner muscle layer is found immediately inside the epithelial layer of the distinctly Y-shaped lumen. Glandular cells are lacking and the lumen possesses a thin but distinct cuticle. The cells of the pharynx contain large vacuoles that display an open spongy network-like structure.

Although the same basic external shape and characteristic Y-shaped lumen is repeated in *Doriopsilla*, the structure of cell layers is quite different (Figure 3B). Muscle layers are thimer and some glandular cells

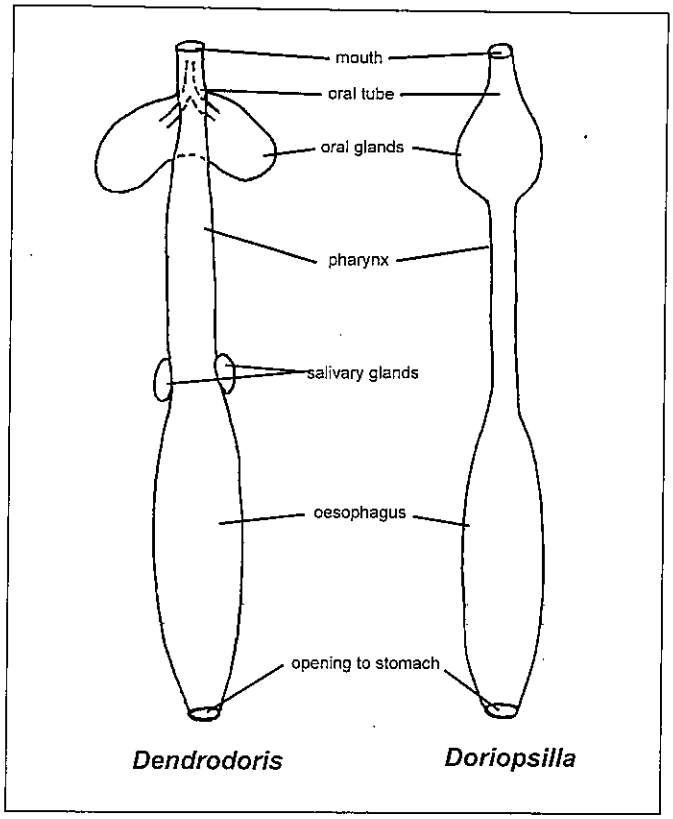

Figure 2. A schematic diagram comparing the anterior digestive system of *Dendrodoris* and *Doriopsilla*.

are present. Some cells with large non-staining vacuoles are present, as is a thin cuticle.

Oesophagus

The oesophagus of all *Dendrodoris* examined is extremely glandular in appearance (Figure 3C). A variable but distinct band of muscle surrounds the outer surface of the organ. There is no cuticle present in the lumen, and in many sections the dark purple glandular development is so extensive that the central lumen is difficult to locate.

The oesophagus of *Doriopsilla* has quite a different cell structure to that found in *Dendrodoris* (Figure 3D). Primarily the oesophagus is not glandular in *Doriopsilla,* but very muscular and the general histological appearance of the organ is quite different to that found in *Dendrodoris.* There are no obvious gland cells present but the muscle tissue is interspersed by cells with relatively large vacuoles containing pink-staining secretions. The oesophagus is surrounded by a very broad but loose layer of circular muscle followed by another broad layer of loose longitudinal muscle. In some areas of the oesophagus radial muscle is also distinctly present. The extent of this radial muscle is variable along the length of the organ. The oesophageal lumen is narrow distally but then widens. The epithelium of the lumen consists of uniform cells with large dark staining nuclei. No cuticle is present.

Reproductive System

Distal Oviduct

The presence of a vestibular gland associated with the distal oviduct varies between species. The gland is present within *Dendrodoris albobrunnea* and *Dendrodoris fumata* (both grey and orange/red forms) but absent in *Dendrodoris guttata*. The presence of microvilli is clearly seen in the gland of *Dendrodoris fumata* but is not so obvious within the gland of *Dendrodoris albobrunnea*. This could be the result of incomplete sexual maturity. In some species (e.g. *D. fumata*) this gland is not visible by dissection because of its position within the connective tissue of the body wall or oviduct. No vestibular gland or microvilli are present in association with the oviduct of either of the *Doriopsilla* examined in this study. The genital aperture and associated ducts are however, often distinctly folded and convoluted.

Ovotestis (Gonad)

In both genera the ovotestis (gonad) is locationally associated with the anterior digestive gland. The relative position of ovotestis, kidney and digestive gland tissue in all of the *Dendrodoris* examined is intermingled (Figure 3E). In contrast, in *Doriopsilla* it displays a more defined layered arrangement (Figure 3F). Thus in *Doriopsilla* the ovotestis forms a compact flattened layer which lies dorsally over the anterior of the digestive gland. In *Dendrodoris* however, the ovotestis forms branched projections, which sit above, below and between the digestive gland follicles and kidney tissue.

DISCUSSION

Anterior Digestive System

The anterior digestive system of the smooth bodied *Dendrodoris guttata*, *Dendrodoris albobrunnea* and *Dendrodoris fumata* is very similar to that already found by WÄGELE *et al.* (1999) for *Dendrodoris nigra*. Like *D. nigra* there is separate paired oral (ptyaline) glands, a network like pharynx, extremely glandular oesophagus and small compact salivary glands.

Oral tube and Oral glands

The oral glands, defined as glands associated with the oral tube, of all *Dendrodoris* examined are paired structures, distinctly separate from but connected to the oral tube by a single muscular duct. The oral glands of *Doriopsilla* on the other hand are found sub-epidermally within the walls of the oral tube itself. According to WÄGELE & WILLAN (2000) the latter arrangement is considered to be the plesiomorphic (primitive) state for nudibranchs.

Salivary glands

Suprisingly, the salivary glands of *Dendrodoris albobrunnea*, *D. guttata* avoid if possible and *D. fumata* are different from that reported by WÄGELE *et al.* (1999) for *Dendrodoris nigra*. Rather than containing large very pale staining cells, superficially similar in appearance to the cells of the ptyaline gland, the salivary glands cells in the *Dendrodoris* examined in this current study are different, being uniform blue in appearance and not containing any very-dark staining nuclei.

According to WÄGELE & WILLAN (2000) salivary glands are absent in only a few nudibranch genera. The presence of relatively compact salivary glands in all *Dendrodoris* examined confirms this character as an autapomorphy for the genus, however this character can no longer be extended to the Dendrodoridae since no salivary glands were found in *Doriopsilla*.

Pharynx

The pharynx (defined as the section of the digestive system between the oral tube and the oesophagus) is uniform in structure within the *Dendrodoris* examined. Histologically the pharynx displays a distinct network-like appearance as previously mentioned for *D. nigra* by WÄGELE *et al.* (1999) and described as homologous to the radula bearing cushions of other gastropods. Recent investigations of

Doriopsilla (GOSLINER *et al.*, 1999; VALDÉS & ORTEA, 1998; VALDÉS & GOSLINER 1999) have not acknowledged the presence of a pharynx, the area being interpreted as the first section of a two-part oesophagus. The similar appearance of this part of the digestive tube in both *Dendrodoris* and *Doriopsilla*, and its similarity to the radula-bearing cushions of other gastropods, is clearly shown by the histological results of this study.

Oesophagus

The histological results indicate that the function of the oesophagus in *Dendrodoris* and *Doriopsilla* is quite different. In *Dendrodoris* this organ is extremely glandular indicating that its primary function lies with the production of digestive fluids. In *Doriopsilla* on the other hand this role is obviously performed by the extremely dense oral glands present in the walls of the oral tube. The notable muscle development of the oesophagus in *Doriopsilla* suggests a more mechanical role in the digestive process. The absence of a cuticle in the oesophagus of both *Dendrodoris* and *Doriopsilla* is expected. According to WÄGELE (1997) an oesophagus without a cuticle is an autapomorphy for the Doridoidea.

Reproductive System

Distal oviduct

The presence or absence of a vestibular gland in the reproductive system, as determined by dissection, has previously been used as a

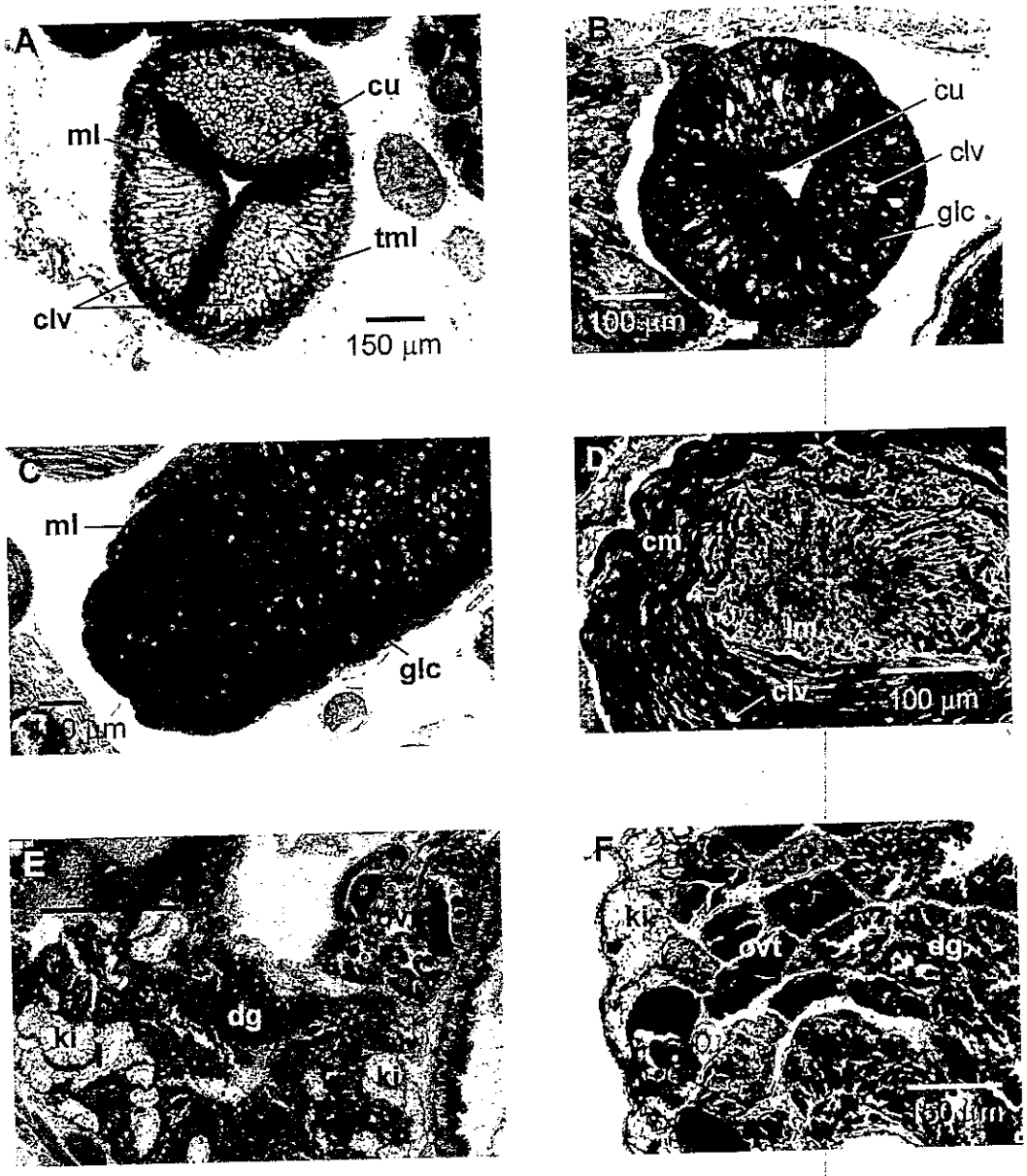

Figure 3. A. A histological cross-section of the pharynx in *Dendrodoris fumata* (grey form) B. A histological cross-section of the pharynx in *Doriopsilla miniata* C. A histological section of the oesophagus in *Dendrodoris fumata* (grey form) D. A histological section of the oesophagus in *Doriopsilla miniata* E. A histological section showing the intermingled arrangement of the ovotestis (gonad), kidney and digestive gland in *Dendrodoris fumata* (orange/red from) F. A histological section of the ovotestis (gonad), kidney and digestive gland in *Doriopsilla miniata* showing a layered arrangement.
Abbreviations: cu = cuticle, cm = circular muscle, dg = digestive gland, glc = gland cell, ki = kidney, lm = longitudial muscle, clv = cell with large vacuole, ml = muscle layer, ovt = ovotestis (gonad), tml = thick muscle layer.

species separating character for dendrodorids (BRODIE *et al.*, 1997). VALDÉS & GOSLINER (1999) in their phylogenetic analysis of radula-less dorids also utilized this character. However, the results of the present study clearly show the need for histological investigation of such characters, since positioning within the body wall or connective tissue can cause the presence of such glands to be consistently overlooked by dissective investigation alone. This is the case for *Dendrodoris fumata*, which until the present study had been thought to lack a vestibular gland.

The lack of glandular development on the distal oviduct of *Doriopsilla* and *Dendrodoris guttata* is noteworthy considering the unique findings of this area in *Dendrodoris nigra*, where thousands of symbiotic bacteria were found in a vestibular gland annexed to the distal oviduct (KLUSSMAN-KOLB & BRODIE, 1999). Results to date indicate that sexual maturity may influence the presence of microvilli and/or bacteria.

Ovotestis (Gonad)

The unusual intermingled position of ovotestis, kidney and digestive gland reported by WÄGELE *et al.* (1999) for *Dendrodoris nigra,* is also found in all other members of *Dendrodoris* examined in this present study. Such an arrangement appears to be unique to the genus. The layered arrangement found in both *Doriopsilla* species examined is more typical of other dorids. These results are in direct conflict with the findings of VALDÉS & GOSLINER (1999) who determined (without histological investigation) that in the majority of *Dendrodoris* species the hermaphrodite gland (ovotestis) was clearly separate from the digestive gland, and that in *Doriopsilla* the two glands were interdigitated.

CONCLUSIONS

The function of the respective components of the anterior digestive system would appear to differ substantially between the two-dendrodorid genera. All *Dendrodoris* characters considered by this study, except salivary gland structure and vestibular gland development, appear consistent across the genus. The study indicates that the continued use of methacrylate resin histology will provide the additional character sets required to adequately address the question of how closely related the radula-less dorid nudibranchs are. Moreover, it highlights the importance of information derived from histological investigations, to both taxonomic and phylogenetic analyses. A very clear example of this is the discovery of a vestibular gland within the reproductive system of *Dendrodoris fumata* that is not visible by dissection. Further studies of dendrodorids are required to investigate all organs systems, examine tuberculate dendrodorids (such as *Dendrodoris tuberculosa* (QUOY & GAIMARD, 1832) and compare (using the same techniques) other radula-less nudibranch families, particularly Phyllidiidae and Tethydidae.

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