

Anatomy of *Olivella (Lamprodoma) volutella* (Lamarck, 1811) (Gastropoda, Olividae), a Panamanian Pacific species

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Abstract

Olivella (Lamprodoma) volutella (Lamarck, 1811), a common shallow water species from Central America is, by first time, anatomically described based on dissections and drawings at camera lucida. Its most remarkable characters are the presence of a long posterior tentacle of the mantle with a pleated laminar expansion on its proximal end, stomach oval to rectangular with a wide muscle ribbon surrounding it and without internal cuticular coating, a gastric caecum plentiful of sediment, penis cylindrical laterally compressed and without a flagellum, and a strong asymmetry of the central nervous system with left cerebral ganglion substantially larger than the right one.

Riassunto

Viene per la prima volta descritta l'anatomia di *Olivella (Lamprodoma) volutella* (Lamarck, 1811), una specie comune nelle acque basse del Centro America, sulla base di dissezioni e disegni alla camera lucida. I caratteri anatomici più notevoli di questa specie sono la presenza un lungo tentacolo posteriore del mantello, con una espansione laminare all'estremità prossimale, lo stomaco di forma da ovale a rettangolare, circondato da un'ampia fascia muscolare e privo di rivestimento cuticolare, un cieco gastrico pieno di sedimento, il pene cilindrico, compresso lateralmente e privo di flagello, ed una forte asimmetria del sistema nervoso centrale, con il ganglio cerebrale sinistro notevolmente più grande di quello destro.

Parole chiave

Olividae, *Olivella*, anatomy, Central America.

Introduction

The systematic of the family Olividae Latreille, 1825, like that of most other molluscan families, is fundamentally based on shell and to some extent on radular characters. To this day, the taxonomic basis of most genera is essentially the shell, and in *Olivella* is largely based on the work of Olsson (1956), who proposed and/or stabilized most currently accepted subgenera. Anatomical information on the family was first provided by Amaudrut (1896) and Kuttler (1913), although in a scattered manner. Marcus & Marcus (1959) were the first to present a complete anatomical study of a species of the genus *Olivella*, *O. verreauxi* (Duclos, 1857). However, their technique of anatomical reconstruction from serial histological sections led on the one hand to apparent simplification of some systems, and on the other to the revelation of details only perceptible through histology. Following these pioneering studies, only Kantor (1991, 1996) studied the anatomy of *Olivella* in detail, but still in a partial manner, concentrating on the anterior portion of the digestive system. Therefore, there is a pro-

found lack of anatomical information on members of this diverse genus. Still in relation to the family Olividae, Caetano & Absalão (2002) reported for the first time the occurrence of an impossex in a member of the family; and Simone (2003) revised the genus *Benthobia*, basing his study on anatomical data. Most lately, Absalão & Pimenta (2003) proposed the creation of a new subgenus in *Olivella* and described three new species from deep waters off Brazil.

The genus *Olivella* is especially rich in tropical species, being particularly well represented in the Atlantic Ocean (Olsson, 1956), though members of *Olivella* are present in all the oceans of the world. *Olivella (Lamprodoma) volutella* is one of the best known and most abundant species on the beaches of Central America, occurring from Mexico to Ecuador.

Nothing is known about the anatomy of *Olivella*. Therefore, accepting either the taxonomic proposition of Golikov & Starobogatov (1988) with the recognition of Olivellidae, or the more conservative scheme of Vaught (1989), the generation of anatomical information on the genus *Olivella* is essential for the elucidation of the phy-

logeny of the genus itself, which has over 15 subgenera, as well as to allow its correct positioning in the Muri-coidea (Simone, 2000).

Material and methods

The material used in this study was collected by the second author in the mangrove swamp of Santa Cruz, Islã de Coiba, Panama, on February 5th 1995, and was preserved in alcohol (70%). It is deposited in the malacological collection of the Zoology Department, Biology Institute, Federal University of Rio de Janeiro, Brazil.

The anatomical study of the soft parts was performed after the shells were dissolved in a solution of acetic acid. Prior to this procedure, all of the shells had their total length and width measured. Dissections were made with the use of ophthalmological scissors, fine-tipped tweezers, and entomological pins. Drawings were made with the aid of camera lucida. Ten individuals (six males and four females) were dissected.

Head-foot mass (Fig. 1A, B)

Light grey with white edges. The head is quite reduced; oral flap small and laterally compressed. Rhynchostome a small horizontal slit, located below right oral flap. Foot large, approximately campanulate in shape, strongly compressed dorsoventrally in its lateral parts. Well-developed propodium, in the shape of an upside-down T with all of its borders free, laminar and fringed. Presence of a propodial sulcus separating it from the metapode. Located between the propodial lobes, there is a pedal gland defined by the elevation of the surrounding pedal tissue. Operculum thin, translucent and yellow. Penis cylindrical, laterally compressed, with a very slight decrease in caliber along its length, except near the tip where it tapers strongly, but without forming a flagellum. Vas deferens visibly zigzagging inside the penis. In some specimens, the penis is cylindrical and narrows sharply distally.

Mantle organs (Fig. 1C-E)

Pallial cavity broad, with mantle margin thin and relatively wide, anterior tentacle of the mantle with enlarged base dorsally enveloping the siphon and about 50% longer than it, posterior tentacle of the mantle long, in the shape of an open groove, and bordered by numerous deep indentations. At its proximal end, internally, there is a pleated laminar expansion which, due to its folds, generates the illusion of being several juxtaposed laminar expansions. Siphon of medium length, its distal end tapering, margin smooth, proximal muscular region of the siphon projecting slightly between the osphradium and the gill. Elliptical osphradium reaching about 1/3 of the length of the gill, its axis is only present in its distal half. Gill large, at least 3 times the width of the osphradium and occupying almost half the total area of the pallial cavity, strongly curved in its anterior region.

In females, the filaments on the distal _ of the gill extend almost to the anal region. Area between gill and gastric caecum concave, commonly used by males to accommodate the penis. Conspicuous darkened hypobranchial gland; in females it envelops the entire gill, in males it is dorso-distally enlarged and approaches the anal region. In females it is almost inconspicuously extended in its distal portion; anal gland well differentiated from the hypobranchial gland and positioned in the anterior region of the pallial cavity, in front of the anus and below the posterior lobe of the mantle, with the shape of folds projecting into the center of the pallial cavity. At least 1/3 of the area of the pallial cavity is occupied by the gastric caecum, which is positioned dorsally to the gill; externally to its internal face, part of the reproductive system is found, and, dorsally, a long narrow rectum which may have convolutions in its proximal and distal regions; anus small, without anal papilla.

Digestive system (Fig 2A-D)

Hemispherical buccal capsule, slightly wider than long, located in a proboscis to which it is connected by four narrow latero-ventral retractor muscles. There is a pair of narrow protractor muscles, positioned latero-dorsally above the retractor muscles. Esophagus forms a lateral fold, clearly indicating the protraction of the buccal capsule. There are three salivary glands, narrow and convoluted, positioned laterally to the point of union between esophagus and buccal capsule. Delicate odontophore bears medially, in its distal end, a protractor muscle which is inserted in the proboscis. Retractor muscles not observed.

Stomach oval to rectangular, pigmentation extremely dark, with a wide muscle ribbon surrounding it and without internal cuticular coating. Proximal region elongated stomach vestibule and connected to the esophagus, intestine, intestinal caecum, and receives ducts from the digestive gland. Internally the connection with the stomach is partially obstructed on the side of the intestine and gastric caecum by a fold of tissue. The ducts of the digestive gland are short, quickly ramifying and merging into the glandular tissue. Internal wall of the esophagus pleated on its entire surface, although this trait is particularly perceptible in its connection to the stomach vestibule. Intestine narrow, with convolutions of variable length but restricted to its proximal portion. Close to the anus it may once again show a few convolutions, but these are always smaller than those in its proximal portion. It is inserted in the interior of the gastric caecum, which begins in the stomach vestibule. The gastric caecum it is slightly compressed laterally and has a small bump dorsally that precedes its entrance into the pallial cavity. It is full of exogenous mineral granules of similar size. The interior wall of this caecum is completely covered by small pits/scars originating from the lodging of these granules in close contact with the animal's tissue. These pits/scars have the exact shape of the particles they housed, suggesting long-term, if not permanent, contact. The morphology

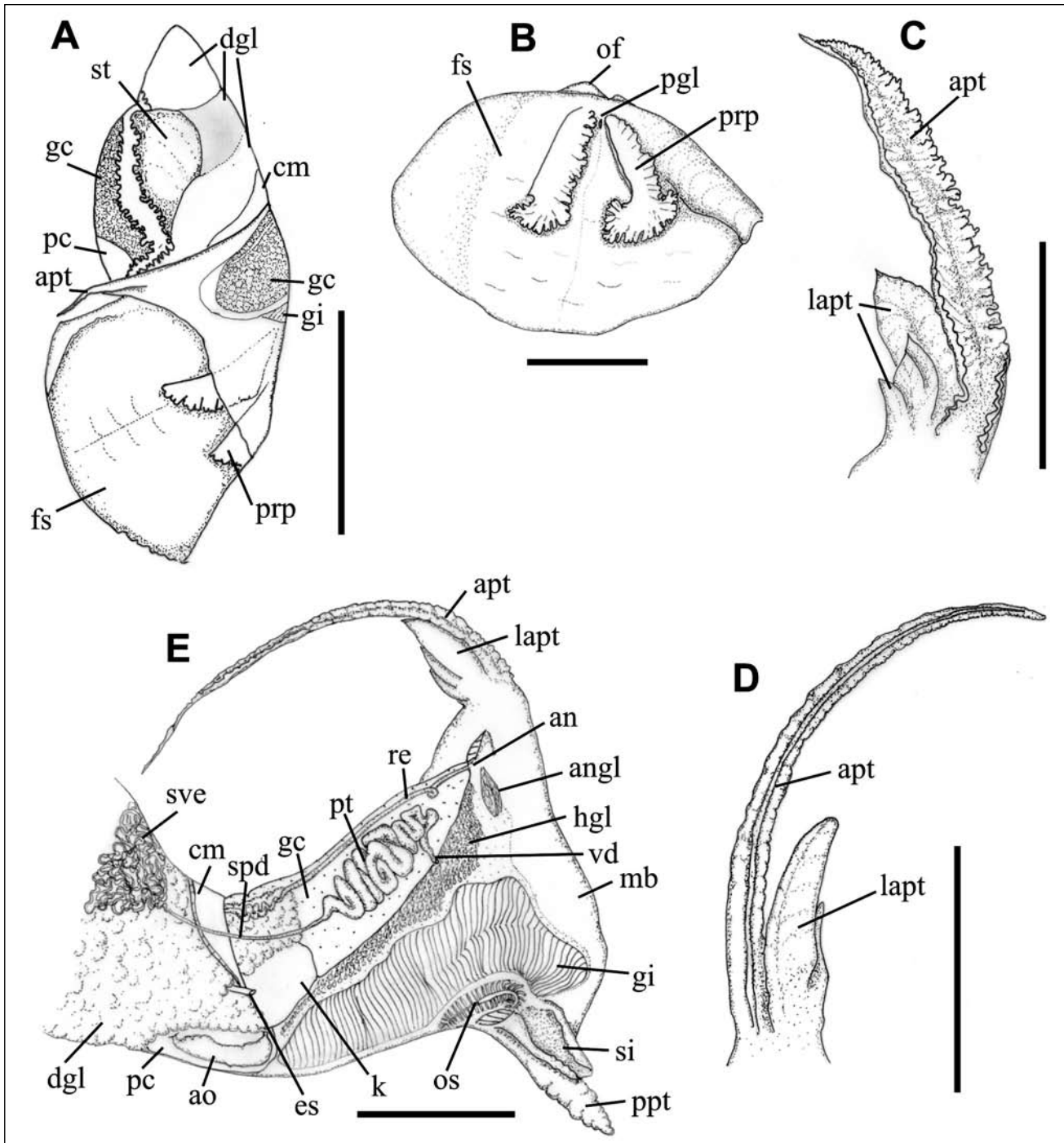


Fig. 1. **A.** Hole animal; **B.** Foot sole, ventral view; **C.** Posterior palial tentacle, dorsal view; **D.** Posterior palial tentacle, ventral view; **E.** Open palial cavity and anterior region of visceral mass, male, ventral view. Scale bars: A = 5 mm, B-E = 2 mm. Abbreviations: (an) anus, (angl) anal glands, (apt) anterior palial tentacle, (ao) aorta, (cm) columellar muscle, (dgl) digestive gland, (es) esophagus, (fs) foot sole, (gc) gastric caecum, (gi) gill, (hgl) hypo-branchial glands, (k) kidney, (lapt) lobes of anterior palial tentacle, (mb) mantle border, (of) oral flap, (os) osphradium, (ppt) posterior palial tentacle, (pc) pericardium, (pgl) pedal glands, (prop) propodia, (pt) prostate, (si) siphon, (spd) spermoduct, (sve) seminal vesicle, (vd) vas deferens.

Fig. 1. **A.** Intero animale; **B.** Suola, vista ventrale; **C.** Tentacolo palleale posteriore, vista dorsale; **D.** Tentacolo palleale posteriore, vista ventrale; **E.** Cavità palleale aperta e regione anteriore della massa viscerale, maschio, vista ventrale. Scale: A = 5 mm, B-E = 2 mm. Abbreviazioni: (an) ano, (angl) ghiandola anale, (apt) tentacolo palleale anteriore, (ao) aorta, (cm) muscolo columellare, (dgl) ghiandola digestiva, (es) esofago, (fs) suola, (gc) cieco gastrico, (gi) branchia, (hgl) ghiandole ipobranchiali, (k) rene, (lapt) lobi del tentacolo palleale anteriore, (mb) bordo del mantello, (of) lembo orale, (os) osfradio, (ppt) tentacolo palleale posteriore, (pc) pericardio, (pgl) ghiandole del piede, (prop) propodia, (pt) prostata, (si) sifone, (spd) dotto spermatico, (sve) vescicola seminale, (vd) dotto deferente.

of the radula will not be discussed here, but in another report on that specific subject.

Circulatory and excretory systems (Fig. 2E)

Ample pericardium, smaller than the renal cavity. Medium-sized auricle, convex with thick walls, partially

adhered to the interior wall of the pericardial cavity which has a cartilaginous texture; large ventricle, trilobate, with thick walls, rounded posteriorly and more acuminate anteriorly (shaped like a bell pepper). Aorta longer than the ventricle and of about the same width, with a slight lateral compression; the external border with some convexities and in contact with the pericar-

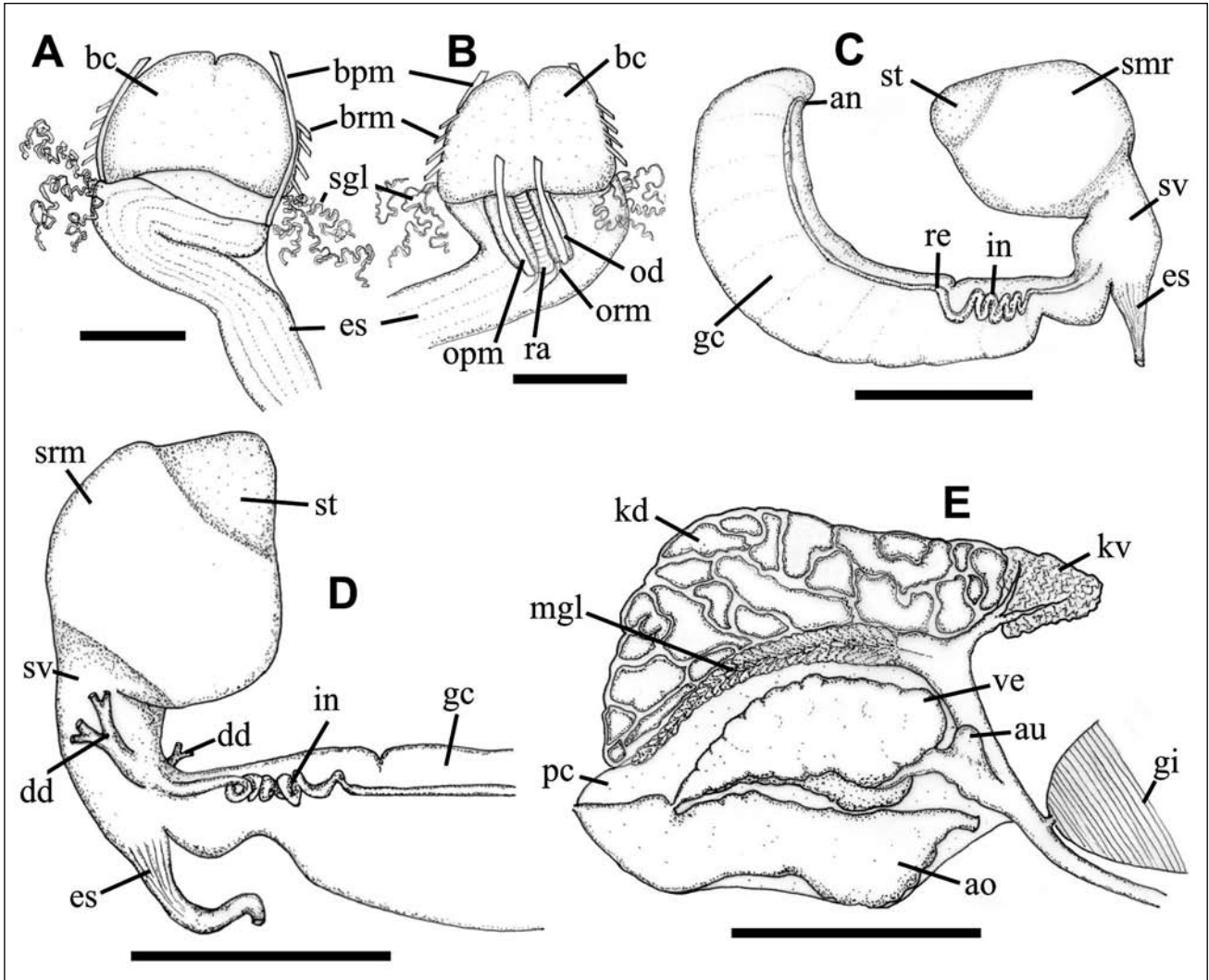


Fig. 2. **A.** Foregut, dorsal view; **B.** Foregut, ventral view; **C.** Digestive system, dorsal view; **D.** Detail of digestive system, ventral view; **E.** Excretory and circulatory systems, ventral view. Scale bars: A, B = 0.5 mm; C, D = 2 mm; E = 1 mm.

Fig. 2. **A.** Parte anteriore del tratto digerente, vista dorsale; **B.** Parte anteriore del tratto digerente, vista ventrale; **C.** Apparato digerente, vista dorsale; **D.** Dettaglio dell'apparato digerente, vista ventrale; **E.** Apparato escretorio e circolatorio, vista ventrale. Scale: A, B = 0.5 mm; C, D = 2 mm; E = 1 mm.

dium. Whitish kidney formed by two glandular lobes, adjacent and asymmetrical, presence of supporting tissue of cartilaginous appearance, particularly visible dorso-anteriorly to the pericardium, dorsal lobe four times wider than adjacent anterior lobe, appearing as a long solid mass composed of segments of various sizes, ventral lobe distinctly less voluminous, composed by a structure of narrow branching tubules that drain into two wider branches which are prolonged into the seemingly cartilaginous support of the kidney; nephridial gland narrow, located in an elongated triangular chamber positioned dorsally to the ventricle and formed from the supporting tissue with cartilaginous appearance. The nephridial gland itself is formed by elongated drop-shaped vesicles; renal aperture appears as a narrow longitudinal gap. Intestine runs posterior and dorsally to the external surface of the kidney.

Reproductive system (Fig. 3A-C)

Female (Fig. 3A)

Apical gonad, partially pigmented in black externally,

oviduct translucent and difficult to see, except in its pallial portion where it connects to the glandular complex, which is positioned dorsally to the pallial complex. From the proximal to the distal end, the glandular complex is composed of internal vesicle, albumen gland, vestibule, seminal receptacle and capsule gland. Genital pore as a vertical cleft in the distal end of the capsule gland. Vestibule positioned ventrally between the seminal receptacle and the albumen gland. Oviduct is usually connected to the glandular complex, approximately in its middle region, right after the vestibule; alternatively it may be connected posteriorly, near the internal vesicle. The direct connection between the vestibule and the internal vesicle suggest that this latter structure can, maybe, act as a fertilization chamber.

Male (Figs 1E, 3B, C)

Apical gonad, partially pigmented in black externally, with an imperceptible vas deferens, seminal vesicle triangular and flat, formed by the curling of thin tubules positioned behind the columellar muscle. From these originates a narrow but visible vas deferens that enters

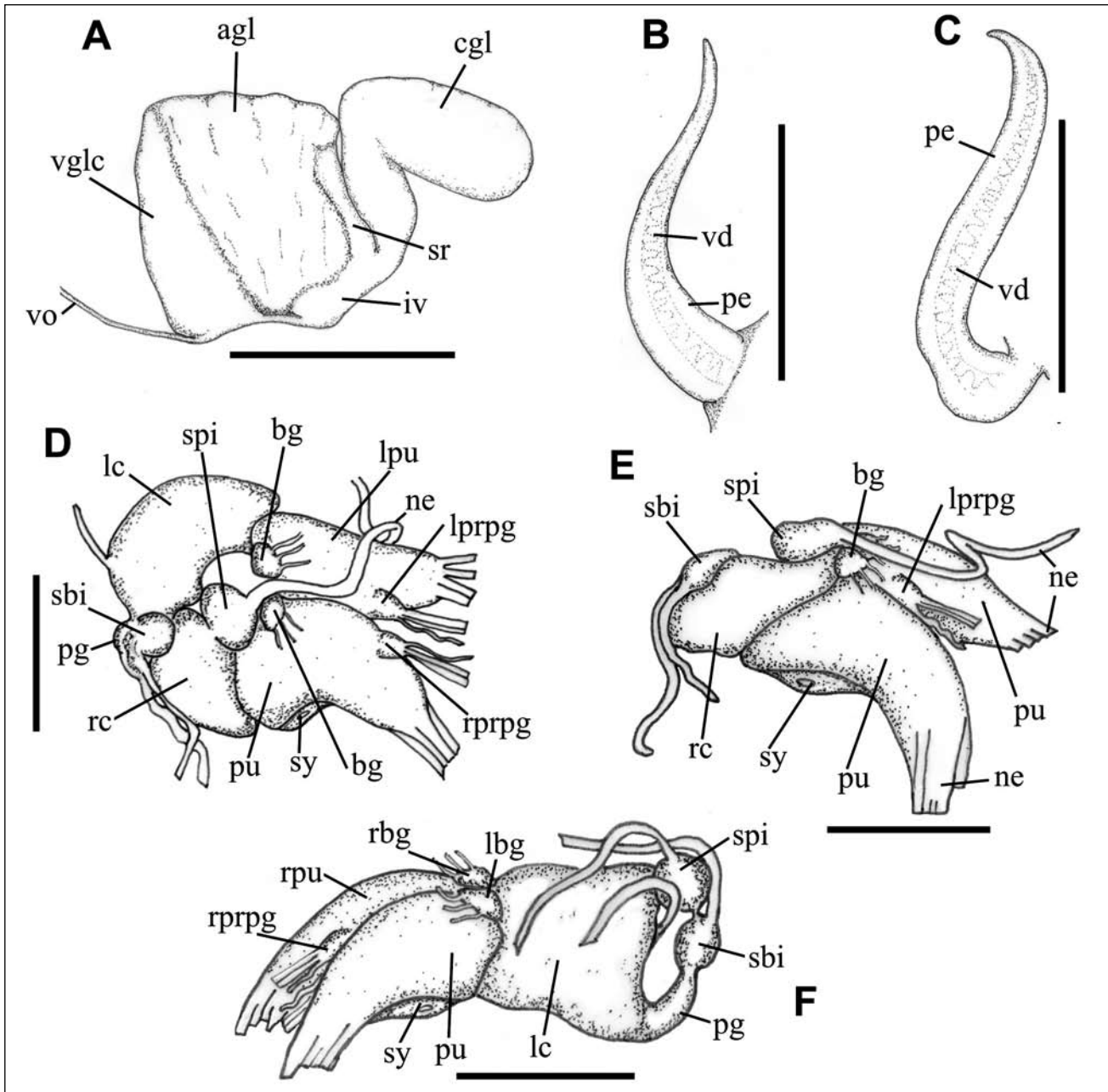


Fig. 3. **A.** Female pallial reproductive system, ventral view; **B, C.** Male reproductive system, penis; **D.** Central nervous system, dorsal view; **E.** Central nervous system, right lateral view; **F.** Central nervous system, left lateral view. Scale bars: A = 1 mm; B, C = 2 mm; D-F = 0.5 mm. Abbreviations: (agl.) albumen gland, (iv) vestibule, (sr) seminal receptacle, (cgl) capsule gland, (vglc) internal vesicle, (vo) oviduct, (pe) penis, (vd) deferens duct, (pg) parietal ganglion, (rpu) right pedal ganglion, (lbg) left buccal ganglion, (rbg) right buccal ganglion, (sbi) subintestinal ganglion, (spi) supraintestinal ganglion, (pu) pedal ganglion, (sy) statocyst, (ne) nerve, (rprpg) right propodial ganglion, (lprpg) left propodial ganglion, (lpu) left pedal ganglion, (bg) buccal ganglion, (rc) right cerebral ganglion, (lc) left cerebral ganglion.

Fig. 3. **A.** Apparato riproduttivo palleale femminile, vista ventrale; **B, C.** Apparato riproduttivo maschile, pene; **D.** Sistema nervoso centrale, vista dorsale; **E.** Sistema nervoso centrale, vista laterale destra; **F.** Sistema nervoso centrale, vista laterale sinistra. Scale: A = 1 mm; B, C = 2 mm; D-F = 0.5 mm. Abbreviazioni: (agl) ghiandola dell'albume, (iv) vestibolo, (sr) ricettacolo seminale, (cgl) ghiandola della capsula, (vglc) vescicola interna, (vo) ovidotto, (pe) pene, (vd) dotto deferente, (pg) ganglio parietale, (rpu) ganglio destro del piede, (lbg) ganglio buccale sinistro, (rbg) ganglio buccale destro, (sbi) ganglio subintestinale, (spi) ganglio supraintestinale, (pu) ganglio del piede, (sy) statocisti, (ne) nervo, (rprpg) ganglio destro del propodio, (lprpg).

the pallial cavity and will originate the prostate. The latter is positioned dorsally to the pallial complex and consists of a large involuted tube. From its distal end a new segment of the vas deferens originates and penetrates the head-foot mass posteriorly to the cephalic region.

Central nervous system (Fig. 3D-F)

Asymmetrical. Left cerebral ganglion substantially larger than the right one. Supra-intestinal ganglion connect-

ed to the right cerebral ganglion by a commissure, sub-intestinal ganglion connected to the pleural ganglion, which is a prolongation of the left cerebral ganglion to which it is partially fused. Right pleural ganglion not discernible. Each intestinal ganglion originates one large nerve, the largest of which originates from the nerve ring. Pedal ganglia larger than the cerebro-pleural ganglia and positioned almost perpendicularly to them, apparently connected to the cerebral ganglia by a wide commissure. Distal extremity ending in four large nerves. Propodial ganglia partially fused to the pedal

ganglia and positioned in their lower (ventral) half in its internal portion. Each of them originates three nerves, the external ones being larger. Buccal ganglia small, almost triangular, and partially flattened dorso-ventrally, each ganglion originating three nerves, connected to the cerebral ganglia by a thin commissure. Statocyst immersed in a translucent matrix, positioned latero-dorsally to the pedal ganglia.

Discussion

The limited amount of anatomical information on the genus makes it difficult to formulate any kind of comparison. However, even considering information not formally published (Pimenta, 2005), *O. volutella* has a stomach-intestinal caecum (herein named gastric caecum) that is unique among the Olividae. The only species of the genus which had their digestive systems anatomically studied were *O. verreauxi* (Duclos, 1857) [= *O. minuta* (Link, 1807)] and *O. borealis* Golikov, 1967, respectively by Marcus & Marcus (1959) and Kantor (1991); in both cases no similar structure was reported. Examination of the internal wall of this structure reveals that it is covered by scars caused by the prolonged contact of mineral particles with the wall. Similar scars are found in the gizzard of species of the genus *Aplysia* (Marcus & Marcus, 1957); however the walls of the stomach-intestinal caecum are not thickened, and nothing else suggests that it functions as a grinding organ. Unfortunately all of the dissected individuals had their stomachs empty, and therefore no inference could be made concerning the diet of this species. The stomach in *O. verreauxi* and *O. borealis* has an internal cuticular coating, which is absent in *O. volutella*. This structure is usually associated with a strong muscle band surrounding the stomach wall, which would suggest a grinding or mixing action for this organ. However, although the stomach in *O. volutella* has the same external muscular ribbon, it does not have the characteristic internal cuticular coating. This fact, together with the presence of the gastric caecum, makes the exact *modus operandi* of the digestive system a mystery.

Our preliminary observations support the interpretation of the posterior pallial tentacle as a synapomorphy of the clade *Olivella+Oliva+Olivancillaria+Agaronia* (Pimenta, 2005). Its morphology may have taxonomic value at the species level within the genus *Olivella*. Marcus & Marcus (1959) reported this same morphological structure, but represented it in an overly schematic way, which does not permit a valid comparison. Considering that the head is quite reduced and therefore does not have sensory organs, and that even when the animal is entirely retracted inside the shell the pallial tentacle remains exposed to the exterior (though partially protected by the channeled suture), it seems reasonable to suppose that it has a sensory function.

The nervous system, in general terms, is similar to that described by Marcus & Marcus (1959) for *O. verreauxi*; however, there are also several differences. Perhaps the

most obvious difference is the asymmetry seen in *O. volutella*, in which the cerebro-pleural ganglia are completely fused and the left ganglia are significantly larger than the right ganglia. In *O. verreauxi*, the ganglia, besides being partially fused, are also equal in size. Marcus & Marcus (1959: pl. 4, fig. 19) clearly showed the innervation of the statocysts from the cerebral ganglia, but in our case this was not observed and the statocysts were in close contact with the pedal ganglia. The number and arrangement of the nerves that originate from the pedal ganglia also help differentiate the two species. While the four nerves originate very close to each other and to the distal region of the pedal ganglia in *O. volutella*, in *O. verreauxi* there are five nerves equidistant from each other and distributed over the entire external surface of the pedal ganglia. The propodial ganglia are fused to the pedal ganglia by an ample base, which suggests a partial fusion between them in both species. However, in *O. volutella* there are three nerves, the internal nerve clearly narrower than the others; on the other hand, in *O. verreauxi*, there are four nerves originating from each propodial ganglion, and the second nerve (from the inside) is substantially larger than the others. Also, there are differences in the buccal ganglia of the two species: in *O. volutella*, besides being dorso-ventrally flattened, each ganglion originates three nerves; in *O. verreauxi* the ganglia are more spherical, and each originates only two nerves. The large commissures represented in the figures of Marcus & Marcus (1959: pl. 4, fig. 19) were impossible to observe in *O. volutella*.

Clear differences were also observed in the reproductive system. For example, the presence of an albumen gland as an external covering to the capsule gland and of an external sac on the capsule gland in the female reproductive system; a simple pallial sperm duct, without convolutions; and the connection between the sperm duct and the pallial cavity in the male reproductive system in *O. verreauxi*; while in *O. volutella* the same structures are, respectively, a compact mass integrating a real glandular complex for the albumen gland, absence of an external sac on the capsule gland, sperm duct with convolutions, formation of a prostate, and absence of communication between the sperm duct and the pallial cavity.

While some of these differences may be attributed to intrinsic traits of each species, and in the future they may be useful in studies of comparative morphology for phylogenetic analysis, it is difficult to distinguish between these differences and those caused by the use of different techniques. Marcus and Marcus (1959) frequently used morphological reconstruction from serial histological sections. In our opinion, this difference in technique may be particularly critical for the discussion of the nervous and reproductive systems. In the future, morpho-anatomical analysis of *O. verreauxi* will resolve many questions, and will contribute to establishing a solid morphological background that will permit the development of an evolutionary hypothesis for the group.

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