MORPHOLOGY OF *FASCIOLARIA TULIPA* FROM VENEZUELA (GASTROPODA: BUCCINOIDEA: FASCIOLARIIDAE)

DIOGO R. COUTO[1], LUIZ RICARDO L. SIMONE[1], ALEXANDRE D. PIMENTA[2]

[1]Laboratório de Malacologia, Museu de Zoologia da Universidade de São Paulo. Avenida Nazaré, 481, Ipiranga. CEP 04263–000 São Paulo, SP, Brazil

[2]Setor de Malacologia, Departamento de Invertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro. Quinta da Boa Vista s/n, São Cristóvão. CEP 20940–040 Rio de Janeiro, RJ, Brazil

Abstract *The morphology of* Fasciolaria tulipa*, type species for the genus, is described and illustrated. Features of the shell, head-foot, pallial organs, circulatory, excretory, digestive and reproductive systems are presented, along with comparisons of published descriptions of other members of Fasciolariidae. The anatomical features concord with previous characterizations of the family: proboscis retractor as a single and powerful muscle, lateral teeth of the radula wide and multicuspidate, ducts of the salivary glands immersed in the esophagus wall, and stomach without a posterior sorting area.* Fasciolaria tulipa *is notable for a large, thin walled auricle, a conspicuous nephridial gland, and a renal aperture sited close to the pericardium; also the odontophore cartilages are fused anteriorly in only 10% of their length, and the radula has the central side of the base of the lateral tooth rounded, a trait that is shared with other species of the subfamily Fasciolariinae. As the type of the genus, the soft-parts anatomy of* F. tulipa *is of great importance, especially because recent taxonomic revisions of the Fasciolariinae have not considered anatomical data.*

Key words *Fasciolariidae, Fasciolaria tulipa, anatomy, morphology*

INTRODUCTION

The Neogastropod family Fasciolariidae comprises more than 1300 living species distributed in the tropics and subtropics (Gofas, 2014). Members of the subfamily Fasciolariinae are usually easily recognized by their ample shell, sinuous columella, and oblique columellar folds. The genus *Fasciolaria* is restricted to the western Atlantic and its fossil record dates from the early Pliocene, which is relatively late in comparison with other fasciolariids (Snyder *et al*. 2012).

Two species of Fasciolariinae are recognized from Brazil: *Pleuroploca aurantiaca* (Lamarck, 1816) and *Fasciolaria tulipa* (Linnaeus, 1758) (Rosenberg, 2009). Although the former species was allocated to the new genus *Aurantilaria* by Snyder *et al*. (2012), no recent taxonomic rearrangement has been undertaken for the latter species, as it is the type for the genus *Fasciolaria*. Although *F. tulipa* occurs on virtually every Caribbean island, despite its non-planktotrophic mode of development, in Brazil this species is restricted to the northern border of Amapá state (Rosenberg, 2009; Snyder *et al*. 2012), implying the possible presence of a geographic barrier formed by the Amazon River mouth.

Contact author : diogoaut@gmail.com

Present knowledge on the anatomy of the Fasciolariidae is as described by Fraussen *et al*. (2007), with a combination of traits diagnostic for the family: multicuspidate lateral teeth and straight rachidian teeth, proboscis retractor muscle as a single or paired tuft of fibres, ducts of the salivary glands immersed in the esophagus wall, and the stomach without a posterior caecum. However, anatomical diagnoses of species within Fasciolariidae have not been developed.

In Brazil, few species of Fasciolariidae have undergone a thorough anatomical study. The anatomy of some species belonging to *Leucozonia* has been studied in detail: *L. nassa* (Gmelin, 1791) by Marcus & Marcus (1962), and *L. nassa* (Gmelin, 1791), *L. ocellata* (Gmelin, 1791) and *L. ponderosa* (Vermeij & Snyder, 1998) by Couto & Pimenta (2012). Recently, Simone *et al*. (2013) thoroughly described the anatomy of *Teralatirus roboreus* (Reeve, 1845). Matthews-Cascon *et al*. (1989) contributed a superficial characterization of *Aurantilaria aurantiaca*; however, no other member of Fasciolariinae from Brazil has had its anatomy studied. Kosyan *et al*. (2009) studied the anatomy of eight species of Fasciolariidae, including *Fasciolaria lignaria* (Linnaeus, 1758), although none of these occurs in Brazil.

The taxonomy of gastropod groups is based mainly on shell and radula features (*e.g*., Tryon,

1880; Thiele, 1929–1935; Snyder *et al*., 2012). Therefore, approaches using soft-part anatomy will prove useful in delimiting groups that have similar conchological features and/or those prone to polymorphisms and convergences. Also, morphological data will prove useful in validating phylogenetic relationships and resolve internal clades (Ponder & Lindberg, 2008; Simone, 2011). This study provides a thorough morphological description of the type species for the genus *Fasciolaria*, *F. tulipa*, from Venezuela, in order to provide supporting information for future comparative analyses.

Material and Methods

Material for this study is deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP).

The specimens collected were fixed in 70% ethanol. Shells were measured with a caliper, and photographs of individuals were taken with a digital camera. The anatomical dissections were made with the aid of a stereomicroscope. All drawings were done using a camera lucida. Radulae were extracted manually and prepared by immersion in KOH, followed by ultrasonic cleaning and rinsing in distilled water for SEM photography.

Results

Fasciolaria tulipa (Linnaeus, 1758) (figs 1–30)

Murex tulipa Linnaeus, 1758: 754.
Colus achatinus Röding, 1798: 117.
Colus marmoratus Röding, 1798: 117.
Neptunea laevigata Link, 1807: 117–118.
Fasciolaria canaliculata Valenciennes, 1832: 286.
Fasciolaria tulipa var. concolor Kobelt, 1875: 362.
Fasciolaria tulipa var. rugosa Kobelt, 1875: 362.
Fasciolaria scheepmakeri Kobelt, 1875: 362.
Fasciolaria rugosa: Dall (1885:115).
Fasciolaria var. obsoleta Dall, 1890: 102.
Fasciolaria tulipa: Warmke & Abbott, 1961: 119 (pl. 2d); Rios, 1970: 96; 1975: 102 (pl. 29, fig. 431); 1985: 106 (pl. 36, fig. 465); 1994: 131(pl. 42, fig. 564); 2009: 248; Abbott, 1974: 227–228 (fig. 2500); (Vokes & Vokes, 1983: 26, (pl. 16, fig. 6); Bandel, 1984: 144, (pl. 17, figs 9, 10); Abbott & Morris, 1995: 233 (pl. 56, fig. 1); Redfern, 2001: 101, (pl. 46, fig. 428A–B); Snyder, 2003: 211, 235; Mallard & Robin, 2005: 8 (pl. 2); Jensen & Pearce, 2009: 143; Rosenberg, 2009; Tunnel *et al*., 2010: 221; Snyder *et al*., 2012: 40 (fig. 1).

Type locality Not given.

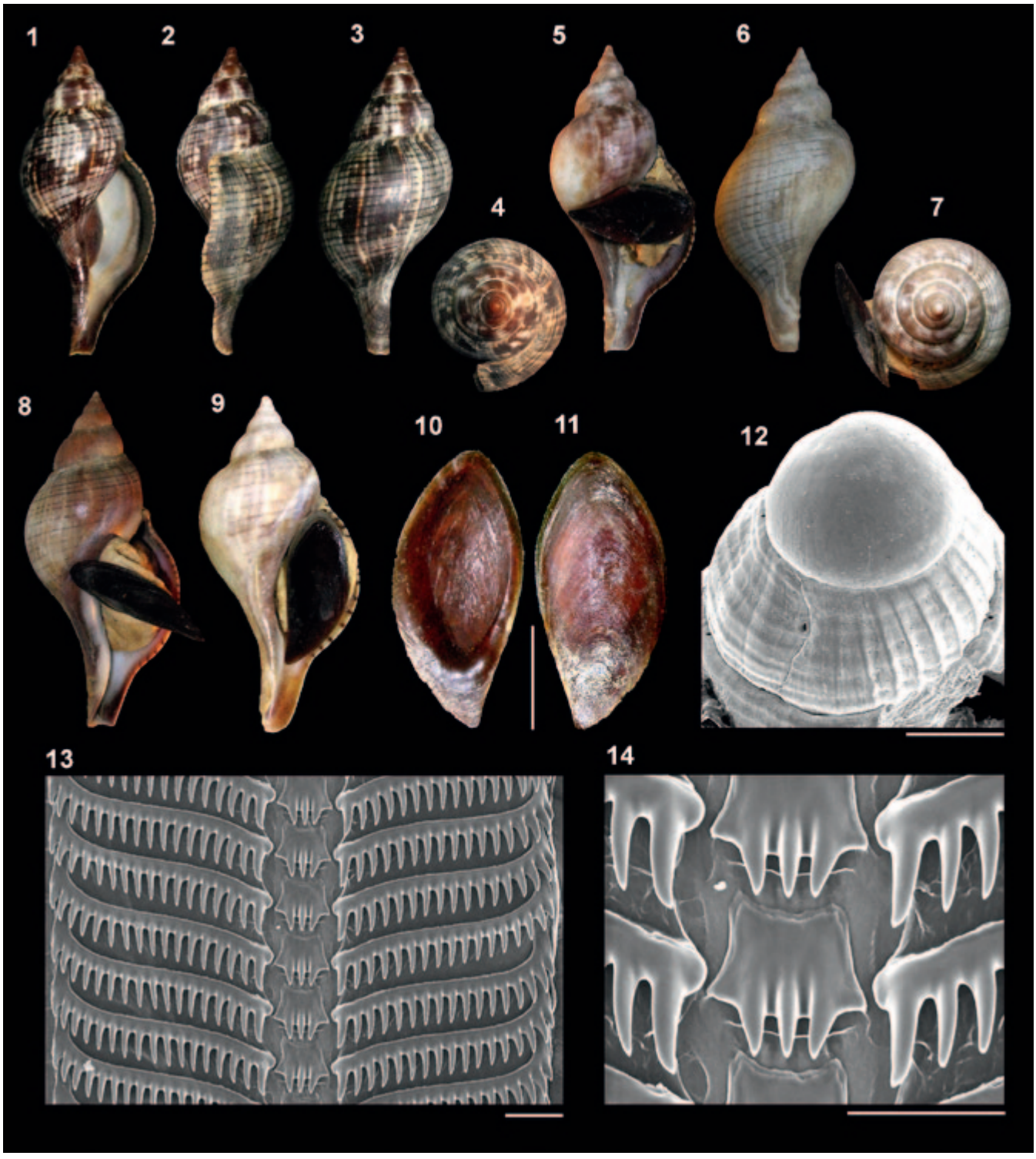
Type material Murex Tulipa P–Z 0010859. Linnean Society of London Collection, 3 specimens. Available online: http://linnean-online.org/17116/

Examined material HONDURAS; Roatan Island, 16°22'49.2"N, 86°24'39.6"W (80–100m depth, Femorale col. iii/2006), MZSP 69277, 1 specimen. VENEZUELA; Marguerite Island, 10°56'38.9"N, 64°01'31.1"W, (L. R. Simone col.), MZSP 35530, 2 specimens; 10°53'51.3"N, 63°58'11.9"W, (El Yaque, 2m depth, Simone col. 28/i/1998), MZSP 56870, 2 specimens.

Geographic distribution North Carolina, USA; Caribbean islands; west coast of central America to Amapá state, Brazil.

Description Shell (figs 1–9) Elliptical and moderately fusiform, height up to 106mm, width usually less than 1/2 of height. Colour chestnut to brown, with darker blotches. Spire moderately high, angle 55°-65°, ~2/5 of total shell height. Protoconch small with 1 1/2 whorls, sculptured with axial ribs in last 1/2 whorl, terminal varix low. Teleoconch with 5–7 rounded whorls; suture slightly raised. Spiral sculpture of 17–27 main spiral cords, color dark brown, usually grouped in pairs, along entire teleoconch but usually obsolete in siphonal canal. Axial sculpture indistinct. Aperture elliptical, ample, height ~3x width. Columella bearing 3 folds medially, close to siphonal canal. Outer lip thin, marked internally by 45–50 discontinuous lirae, crenulated by spiral sculpture and forming brownish sharp protuberances. Siphonal canal short, length ~1/3 of length of aperture. Siphonal fasciole indistinct. Pseudoumbilicus indistinct.

Head-foot (figs 15, 16) Colour cream in fixed species. Head prominent, of medium size, width ~1/3 of adjacent width of head-foot; cephalic tentacles blunt and medium-sized, length ~2/3 of anterior width of head, situated very close to each other; bases lying side by side. Eyes dark, small, rounded, situated in middle region of outer edge of tentacles. Foot short, rounded, anterior region



Figures 1–14 *Fasciolaria tulipa*. 1–4: 69,5mm (MZSP 69277); 5–7: 92,3mm (MZSP 56870); 8: 77,5mm (MZSP 35530); 9: 107,9mm (MZSP 35530); 10: operculum, internal view; 11: operculum, external view; 12: detail of protoconch, lateral view; 13: radula; 14: detail of rachidian tooth of radula. Scale bars: 10–11: 10mm; 12: 1mm; 13–14: 100µm.

bifid. Pedal gland as a shallow median anterior slit, with anterior furrow extending along entire anterior edge. Columellar muscle thick, ~1 1/2 whorls in length.

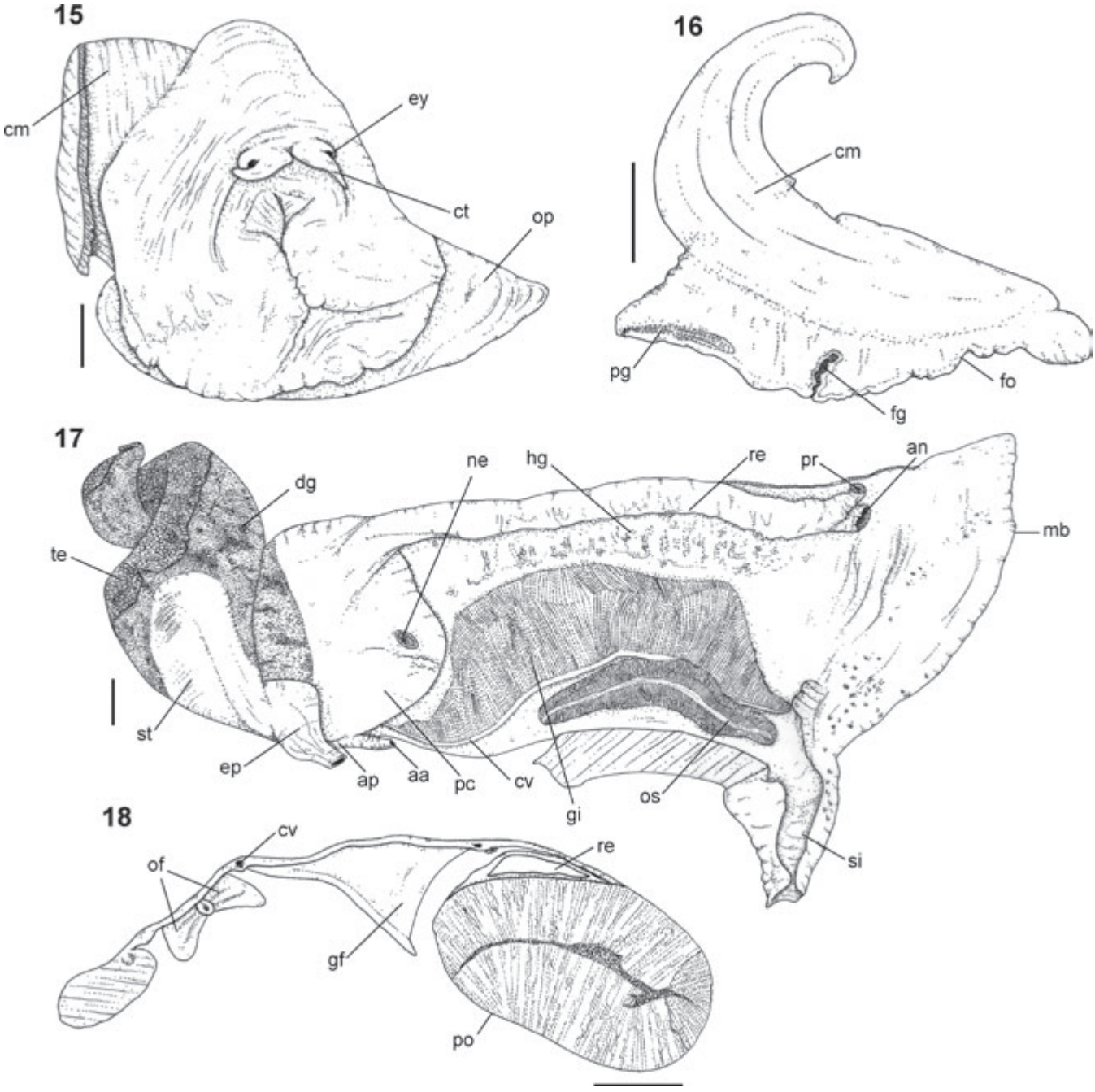
Operculum (figs 10, 11) Corneous, unguiculated (width ~2/3 of length), filling entire aperture; outer surface opaque, with anterior nucleus; inner surface with attachment scar elongated,

elliptical, situated posteriorly, occupying ~2/3 of inner area.

Pallial complex (figs 17, 18) Pallial cavity wide than longer, of 1/2 whorl. Mantle border simple, thickened. Siphon short (length ~1/4 of free portion of mantle edge), its margin smooth; right fold of siphon base extending into pallial cavity, ending as a thickened transversal flap, close to anterior end of ctenidium and osphradium. Osphradium elongated, tapering posteriorly; length ~2/3 of ctenidium; almost symmetrical longitudinally; osphradium leaflets rounded, short (height ~1/2 of ctenidial filament height at middle region of pallial cavity), ~equal in size. Ctenidium curved, ~1/3 of total pallial cavity area, width ~twice than osphradium; anterior and posterior region pointed, posterior end situated close to pericardium; filaments triangular; ctenidial vein (efferent branchial vessel) uniformly narrow along its length. Hypobranchial gland thin, loosely fixed, situated in all the area between gill and rectum. Rectum elongated. Anus elliptical, situated at ~1/3 of mantle edge.

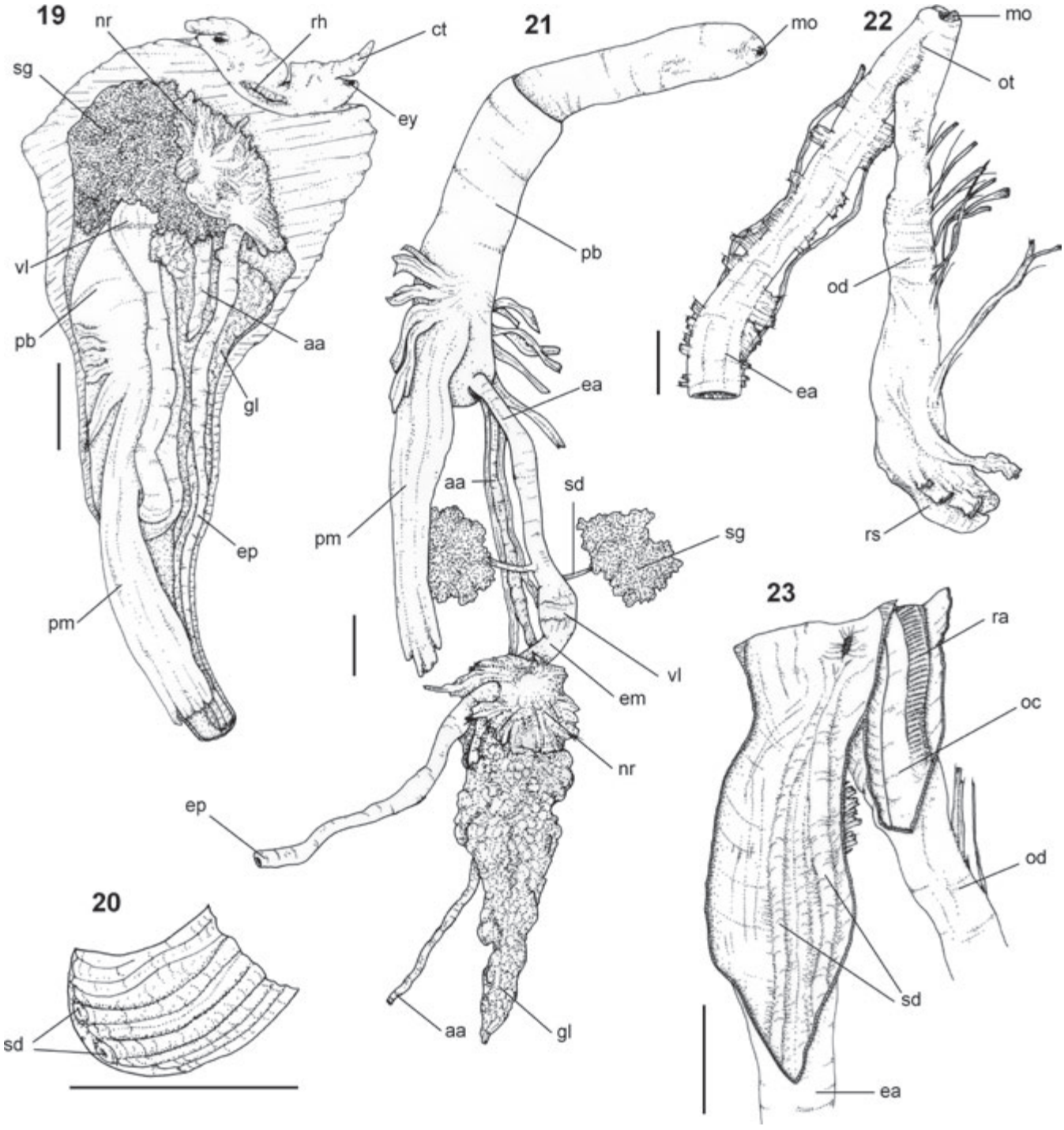
Circulatory and excretory systems (fig. 30) Pericardium ample, spanning ~1/3 of total renal cavity area. Auricle large, translucent, walls thin, posterior wall elongated ending close to renal aperture; ventricle large and rounded (~larger than auricle), rounded, with thick walls. Aorta bifurcating immediately after ventricle; posterior aorta following visceral mass close to stomach; anterior aorta crossing diaphragmatic septum anteriorly. Kidney small, ~1/4 whorl, bearing ventral and dorsal lamellar lobes similar in shape; nephridial gland prominent, situated on dorsal side of membrane between renal cavity and pericardium; renal aperture sub-circular, situated in membrane closer to pericardium, flanked by thick folds, longitudinal to roof of pallial cavity. Part of intestine running longitudinally on inner side of kidney, ventrally adhered to its membrane.

Digestive system (figs 19–28) Rhynchostome as ample transversal slit, located between and below cephalic tentacles, flanked by lip-like folds bearing longitudinal lamellae. Proboscis straight, of moderate length (~2/3 of haemocoel length), with thick muscular walls bearing 2 lateral grooves; a single proboscis retractor muscles originating in ventral posterior wall of the proboscis; series of short lateral muscles fibers connected to inner walls of haemocoel. Mouth small, circular. Odontophore long, slender, ~same length as proboscis; pair of odontophore cartilages dorsally concave, fused anteriorly at ~1/10 of total cartilage length; series of transversal muscle fibers connecting odontophore tube with anterior esophagus; superficial circular muscles (m^3) enveloping entirely odontophore, except for most posterior end; horizontal muscle (m^6), originating on ventral surface of odontophore cartilages, except for most posterior region, ~1/6 of total odontophore length; pair of odontophore retractor muscles (m^2) originating from posterior end of odontophore cartilages, near to radular sac, inserted in inner wall of proboscis; pair of accessory odontophore retractor muscles (m^2a), originating from inner surface of proboscis, near origin of m^2, enveloping radular sac, a long branch of m^2a accompanies anterior aorta posteriorly to nerve ring; pair of dorsal tensor muscles of radula (m^4) originating from posterior dorsal end of odontophore, covering its dorsal surface, inserting m^2a; pair of auxiliary dorsal tensor muscles of radula (m^5) originating from posterior end of odontophore, covering its ventral surface, inserting in m^2a; pair of ventral tensor muscles of radula (m^{11}), inserting anteriorly in sub-radular membrane, running, ventrally adhered (~2/3 of total odontophore length), its origin bifid: main branch originating in ventral posterior cartilage of odontophore near origin of m^2, secondary branch originating ventrally in m^2a, crossing m^6 dorsally , connecting in main branch, at ~2/3 of total m^{11} length. Radula long and thin; radular sac extending to posterior end of odontophore; Radular teeth (figs 13, 14): rachidian tooth straight, trapezoidal, its base with concave outline, cusped margin convex, bearing 3 sharp cusps of ~equal size; lateral tooth wider than long, bearing 17–18 prominent, slightly centrally recurved cusps of approximately same size, central side of base rounded. Anterior esophagus moderately long and broad (~2x proboscis length), dorsally-ventrally compressed, originating in oral tube. Valve of Leiblein pyriform, forming orange ring around esophagus, ~of same width. Salivary glands just anterior to valve of Leiblein, forming pair of branching and amorphous masses; free portion of salivary ducts short, extending along esophagus, anteriorly to valve of Leiblein, becoming merged with esophageal wall, running



Figures 15–18 *Fasciolaria tulipa*. 15: head-foot mass in dorsal view; 16: longitudinal section of foot, female; 17: roof of pallial cavity in ventral view, male 18: transversal section of roof of pallial cavity, female. Abbreviations: **aa,** anterior aorta; **an,** anus; **cm,** columellar muscle; **ct,** cephalic tentacle; **cv**, ctenidial vein; **dg,** digestive gland; **ep**, posterior esophagus; **ey,** eye; **fg**, female cement gland; **fo**, foot; **gf**, gill filament; **gi,** gill; **hg,** hypobranchial gland; **ki,** kidney; **mb,** mantle border; **ne,** nephrostome; **of**, osphradium filament; **op,** operculum; **os,** osphradium; **pc**, pericardium; **pe,** penis; **pg**, pedal gland; **po**, pallial oviduct; **pr,** prostate; **re,** rectum; **si,** siphon; **st,** stomach; **sv,** seminal vesicle; **te**; testis. Scale bars: 4mm.

immersed anteriorly, opening in oral lumen, immediately before oral tube. Accessory salivary glands absent. Middle esophagus short. Duct of gland of Leiblein short and narrow, inserted posterior to nerve ring. Gland of Leiblein brownish, long, of ~same length as posterior esophagus, posterior end acute. Posterior and anterior esophagus of ~same width. Inner wall of anterior esophagus bearing many longitudinal folds, salivary ducts immersed in marked lateral folds.



Figures 19–23 *Fasciolaria tulipa*. 19: hemocoel in ventral view; 20: longitudinal section of anterior esophagus; 21: anterior digestive system; 22: buccal mass in lateral view; 23: buccal mass in lateral view opened longitudinally. Abbreviations: **aa,** anterior aorta; **ct,** cephalic tentacle; **ea**, anterior esophagus; **ep**, posterior esophagus; **ey,** eye; **gl,** gland of leiblein; **mo,** mouth opening; **nr,** nerve ring; **oc**, odontophore cartilage; **od**, odontophore tube; **ot,** oral tube; **ra,** radula; **rh,** rhynchostoma; **rs,** radular sac; **sd,** salivary gland duct; **sg,** salivary gland; **vl,** valve of leiblein. Scale bars: 19–20: 4mm; 21–23: 2mm.

Sudden broadening of posterior esophagus anteriorly to stomach. Stomach wide, walls thin, bearing many internal folds. Digestive gland dark-brown, occupying all whorls of visceral mass, from apex to kidney/pericardium area, surrounding stomach, emitting two narrow, branching ducts discharging near esophagus and intestine apertures. Intestine ~same width

of posterior esophagus and rectum, with smooth lumen.

Male genital system (fig. 29) Testis cream colored, occupying all whorls of visceral mass; surrounding apically entire length of digestive gland. Visceral vas deferens running along testis. Seminal vesicle indistinct; vas deferens narrow, simple, running along ventral wall of kidney. Prostate thin and long, tubular, located along right side of roof of pallial cavity, next to rectum and of its ~equal width. Penis medium-sized, close to head-foot, ~circular in transverse section; penis becoming narrower at mid of its length, terminating in tip-like extension; duct of penis sinuous.

Female genital system (fig. 18) Ovaries brownish, with same texture and length as testis. Cement gland opening centrally on foot, forming somewhat elongated and deep sac of depth of ~2/3 of foot thickness. Pallial oviduct ample, occupying ~1/2 of total pallial cavity area, covering part of ctenidium and renal aperture. Pallial oviduct glands not analyzed due to poor preservation.

DISCUSSION

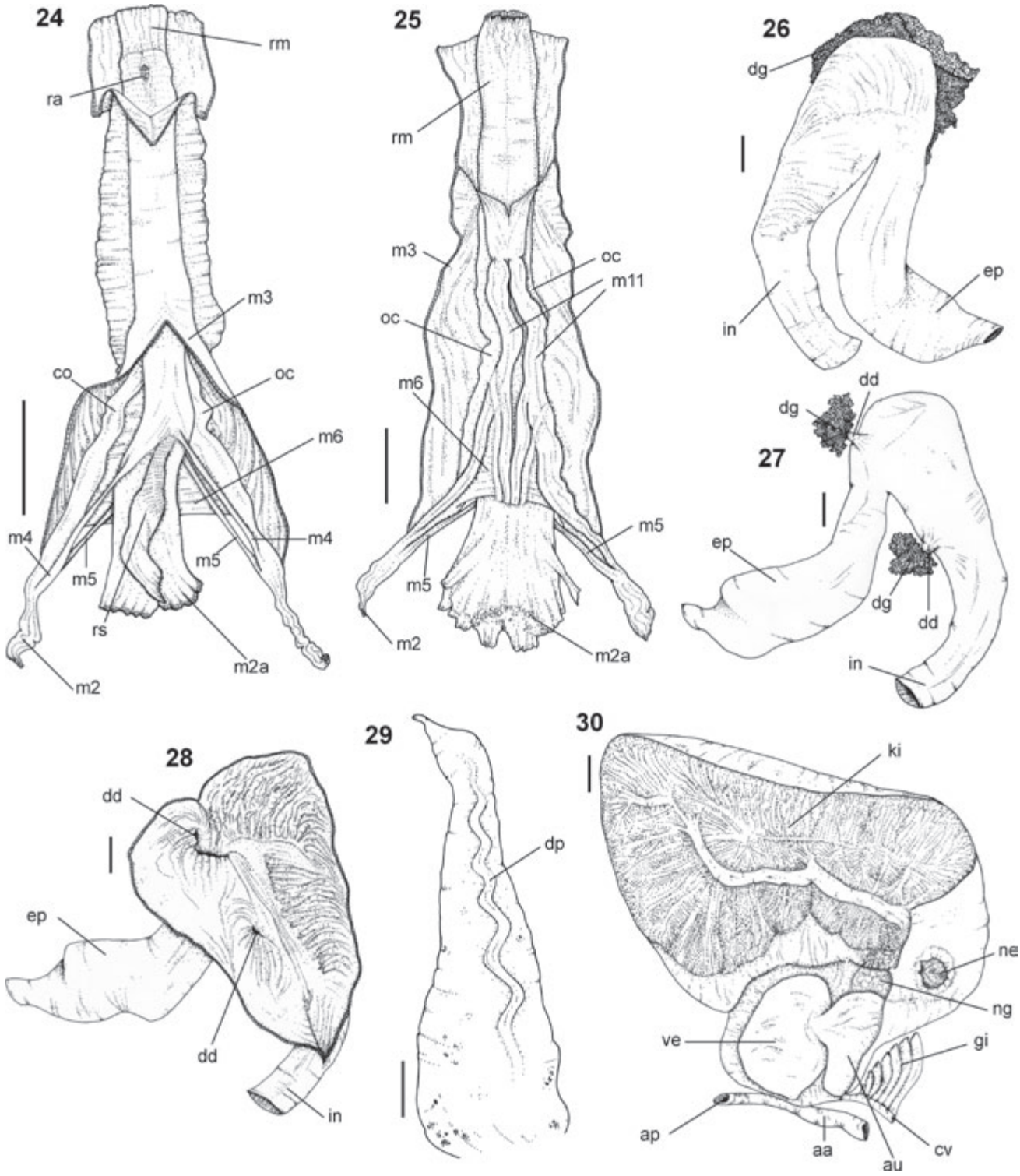
The anatomy of the fasciolariid *Fasciolaria tulipa* is consistent with the framework within the Neogastropoda, as well as Buccinoidea, in lacking accessory salivary glands and an anal gland. The proboscis retractor as a single and powerful muscle, the multicuspidate lateral teeth of the radula, the stomach without a posterior sorting area (caecum), and the ducts of the salivary glands immersed in the esophagus wall confirm the species as a member of the Fasciolariidae in the context of Buccinoidea as diagnosed by Fraussen *et al*. (2007).

Snyder *et al*. (2012) noted that the distributions of both species of Fasciolariinae (*F. tulipa* and *Aurantilaria aurantiaca*) overlap in northern Brazil. Fasciolariinae have a free-swimming larval stage of up to six days, allowing some species to occur over a wide range, supposedly because the veligers gain access to floating objects and disperse to areas inaccessible to crawlers (Snyder *et al*., 2012). Juveniles of *A. aurantiaca* hatch from egg capsules attached to the bottom and crawl directly onto the surrounding substrate (Meirelles & Matthews-Cascon, 2005); the protoconch morphology also indicates a direct mode of development. However, *F. tulipa* has a wide distribution and probably has a free-swimming larva during its development, albeit briefly (Leal, 1991), and its protoconch indicates this. The distinction of the *Fasciolaria* species from the West Atlantic is problematic (Lyons, 1972); Rosenberg (2009) argued for the occurrence of at least seven distinct species occurring in sympatry in the Caribbean Sea: *Fasciolaria tulipa* (Linnaeus, 1758); *F. bullisi* Lyons, 1972; *F. hollisteri* Weisbord, 1962; *F. tephrina* de Souza, 2002; *F. branhamae* Rehder & Abbott, 1951; *F. hunteria* (G. Perry, 1811) and *F. lilium* G. Fischer, 1807. However, Snyder *et al*. (2012) recognized only the first four of these as belonging to this genus.

Shells of members of Fasciolariinae are morphologically similar to those of Peristerniinae: both groups are characterized by the presence of folds in the columella, with one fold marking the entrance to the siphonal canal, and an outer lip with lirae internally. The folds in Fasciolariinae, however, are orientated obliquely, whereas in Peristerniinae they are transverse (Snyder *et al*. 2012).

The central side of the base of the lateral tooth with a rounded outline is unique for Fasciolariinae. Bandel (1984) illustrated many fasciolariid radulae, with three species of *Fasciolaria*, including *F. tulipa*; all the radulae that he described agree with this pattern. All the cusps of the laterals are more or less equal in size, and the number of these is generally larger than in other fasciolariids (see Bandel, 1984, figs 257–268, for examples of radulae of Peristerniinae and Fusininae). The radula of *Fasciolaria lignaria* (Küster & Kobelt, 1876; Kosyan *et al*., 2009) resembles that of many *Latirus*-like species in having a minute cusp on the inner side of the base of the lateral tooth, as well as fewer, shorter and more strongly curved cusps. Snyder *et al*. (2012) tentatively placed the species in the genus *Tarantinae* Monterosato (1917) (see also Gofas & Bouchet, 2014), previously a subgenus of *Fasciolaria*, due to the presence of an adapical sinus on the outer lip. Moreover, this species was considered a member of Peristerniinae "pending molecular confirmation" by these same authors.

Two other features of the anterior digestive system are noteworthy for *F. tulipa.* The odontophore cartilages are fused anteriorly along only 10% of their length, less than in other fasciolariids: 30–40% in *Leucozonia* (Couto & Pimenta, 2012) and 25% in *Polygona*. The posterior esophagus



Figures 24–30 *Fasciolaria tulipa*. 24: odontophore in dorsal view; 25: odontophore in ventral view; 26: stomach in dorsal view; 27: stomach in ventral view; 28: stomach opened longitudinally; 29: penis in dorsal view; 30: renal cavity and pericardium opened ventrally. Abbreviations: **aa,** anterior aorta; **ap**, posterior aorta; **au,** auricle; **cv**, ctenidial vein; **dd,** duct of digestve gland; **dg,** digestive gland; **dp,** duct of penis; **ep**, posterior esophagus; **in,** intestine; **ki,** kidney; $\mathbf{m^{11}}$, ventral tensor muscles of radula; $\mathbf{m^2}$, odontophore retractor muscles; $\mathbf{m^2a}$, accessory odontophore retractor muscles; $\mathbf{m^3}$, superficial circular muscles; $\mathbf{m^4}$, dorsal tensor muscles of radula; $\mathbf{m^5}$, auxiliary dorsal tensor muscles of radula; $\mathbf{m^6}$, horizontal muscle; **ne,** nephrostome; **ng,** nephridial gland; **oc**, odontophore cartilage; **pc,** pericardium; **ra,** radula; **re,** rectum; **rm**, sub-radular membrane; **rs,** radular sac; **ve,** ventricle. Scale bars: 2mm.

broadens anteriorly to the entrance of the stomach; this suggests a premature digestion in this part of the esophagus, although histological procedures are required to verify this statement.

As in many groups, the morphology of the anterior digestive and male reproductive systems is more informative for species-level taxonomy, and this is also true for Fasciolariidae (Fraussen *et al*. 2007; Kosyan *et al*. 2009; Couto & Pimenta, 2012; Couto *et al*. 2015). The radula is especially important, as an easily preserved structure that distinguishes fairly well the families of Neogastropoda (Fraussen *et al*. 2007).

A renal aperture of *F. tulipa* is situated very close to the pericardium, instead of being located centrally in the membrane; this is not seen in any other fasciolariid (*e.g.,* Marcus & Marcus, 1962; Couto & Pimenta 2012, Couto *et al*. submitted). This occurs together with two other unique features: a large auricle with thin, translucent walls, its posterior end elongated and terminating close to the renal aperture; and a very conspicuous nephridial gland. The posterior end of the auricle seems to be attached to the roof of the pericardium wall, hence the elongation of its wall; the nephridial gland is conspicuous, visible through the transparent wall between the pericardium and renal cavity. No other member of Fasciolariidae is so far known to present these features (Marcus & Marcus, 1962; Couto & Pimenta, 2012), whereas both occur in *A auruntiaca* (Couto, pers. obs.).

Fraussen *et al*. (2007) defined a diagnostic character for *F. tulipa*: the ducts of the salivary gland do not run free alongside the anterior esophagus, as they do in other fasciolariids (Marcus & Marcus, 1962; Couto & Pimenta, 2012; Fedosov & Kantor, 2012), but are merged in its wall anteriorly to the valve of Leiblein. This feature was reported only for *Latirus polygonus*, among the fasciolariids examined by Kosyan *et al*. (2009).

An important diagnostic feature for the family *sensu* Fraussen *et al*. (2007) is the proboscis retractor as a single ventral-lateral muscle. All fasciolariids except *Latirus polygonus* and *Fusinus tenerifensis* have a single muscle, while in the buccinids, multiple fibers occur posteriorly to the proboscis, distinguishing the Fasciolariidae from the Buccinidae (Kosyan *et al*., 2009). Other studies that mention the proboscis retractor for Fasciolariidae agree on this (Marcus & Marcus, 1962; Couto & Pimenta, 2012; Fedosov & Kantor, 2012; Couto *et al*., submitted).

Fasciolaria tulipa is the type species of the genus, so the study of its anatomy is fundamental in resolving species-level taxonomy, particularly because the subfamily Fasciolariinae has undergone a thorough taxonomic revision in recent years, albeit only conchologically (Snyder *et al*. 2012). A more detailed understanding of the morphology of soft-parts will be able to provide further data, and possibly help to define groups that are currently doubtful, as is the case for many *Latirus*- and *Fusinus*-like species. Moreover, knowledge of anatomical characters is imperative for phylogenetic analysis, as the relationships of most groups within the Buccinoidea, including family and genus level are still unknown. This analysis is in effect a permanent work in progress, of which the present study is a part.

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