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COMPARATIVE ANATOMY OF CHIONINAE AND VENERINAE SPECIES (MOLLUSCA: BIVALVIA: VENERIDAE)

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ABSTRACT

Veneridae is the most diverse and largest family in Bivalvia, with more than 500 living species. We performed a comparative anatomical analysis between six Chioninae and one Venerinae species, plus four species whose classification in Chioninae remains underexploited. The Venerinae species *Chamelea gallina* and the Chioninae species *Anomalodiscus squamosus, Iliochione subrugosa, Leukoma thaca, Lirophora latillirata, Mercenaria campechiensis, Placamen berii, Placamen foliaceum*, and *Puberella intapurpurea* are anatomically very similar. This comparative study complement the description of these species, with information based on soft parts comparison of mantle, siphons, digestive and nervous systems. The work also pointed differences in some structures, such as the intestine loops and how the siphons are fused. A tabular identification key was provided that also includes other species based on literature data.

Key words: Veneroidea, Morphology, tabular key, taxonomy.

RESUMO

Veneridae é a maior e mais diversa família em Bivalvia, com mais de 500 espécies viventes. Nós realizamos uma análise anatômica comparativa entre seis espécies de Chioninae e uma espécie de Venerinae, além de quatro espécies cuja classificação em Chioninae permanece pouco estudada. A espécie de Venerinae *Chamelea gallina* e as espécies de Chioninae *Anomalodiscus squamosus, Iliochione subrugosa, Leukoma thaca, Lirophora latillirata, Mercenaria campechiensis, Placamen berii, Placamen foliaceum* e *Puberella intapurpurea* são anatomicamente muito similares.

Esse estudo comparativo complementa a descrição dessas espécies, com informações baseadas nas comparações de partes moles dos animais (manto, sifões e sistemas digestivo e nervoso). O presente trabalho também destaca diferenças em algumas estruturas, como as voltas do intestino e como os sifões estão fusionados. Uma chave de identificação tubular também foi fornecida, incluindo outras espécies com base em dados da literatura.
Palavras-chaves: Veneroidea, Morfologia, chave tabular, taxonomia.

INTRODUCTION

Veneridae Rafinesque, 1815 it is the most diverse and largest family in Bivalvia, with more than 500 living species, comprising about 12 subfamilies and 50 genera (Canapa *et al.*, 1996; Denadai *et a.l*, 2006; Mikkelsen *et al.*, 2006; Huber, 2010). Despite its diversity and economical importance, the studies have focused attention on certain species and, many times, they have not been placed into a phylogenetic context (Mikkelsen *et al.*, 2006; Cheng *et al.*, 2011).

Historically, Veneridae classification has been unstable in terms of taxon placement and subfamilies arrangement requiring more systematic studies and continual discussions (Frizzell, 1936; Canapa, 1996; Kappner & Bieler, 2006; Mikkelsen *et al.*, 2006; Bouchet *et al.*, 2010; Cheng *et al.*, 2011). Although the effort made it until now, gathering morphological and molecular data, the results remains controversial (Shimamoto, 1986; Canapa *et al.*, 1996, 1999, 2001, 2003; Adamkewicz, 1997; Roopnarine, 2001; Giribet & Wheeler, 2002; Roopnarine & Vermeij, 2000; Kappner & Bieler, 2006; Mikkelsen *et al*., 2006; Glover & Taylor, 2010; Roopnarine *et al.*, 2008; Cheng *et al.*, 2011; Ramos *et al.*, 2012).

Thus, the most Chioninae studies is less focused on phylogenetic approach and lay emphasis in others 'practicals' aspects like species reproduction or population dynamics. In Brazil, the most relevant Chioninae species – *Anomalocardia flexuosa* (Gmelin, 1971) – it is an example for this scenario, having many published papers focused on reproduction and ecology, besides few works about taxonomy (Narchi, 1972; Mouëza *et al.*, 1999; Denadai *et al.*, 2006; Mikkelsen *et al.*, 2006; JR & Boehs, 2011; Pezzuto *et al.*, 2010; Rodrigues *et al.*, 2010).

According to Keen (1969), a proposal widely used for many years, and Roopnarine (1996), Chioninae has about 141 species in 22 genera (except fossils). However, Kappner & Bieler (2006) pointed some genera commonly classified in Chioninae belonging to subfamily Venerinae (*Chamellea, Clausinella, Eurhomalea, Tawera*, and *Timoclea*). Morphological features as the anterior lateral tooth absent, crenulations in internal margin, and fused siphons are identified as distinguishing characters from Chioninae of Venerinae (Kappner & Bieler, 2006). Until now, there is no studies with more explanations about the genera *Anomalodiscus, Austrovenus, Bassina*, *Chioneryx*, *Chionopsis*, *Iliochione*, *Irursella, Panchione*, and *Placamen* (Chioninae sensu Keen, 1969). Therefore, Chioninae can be established like a monophyletic group counting on eight genera (*Anomalocardia, Chione, Chionista, Humilaria, Leukoma, Lirophora, Mercenaria*, and *Puberella*) (Kappner & Bieler, 2006), which comprise approximately 55 species (WoRMS, 2019).

The present study performs a comparative anatomical analysis between six Chioninae and one Venerinae species (sensu Kappner & Bieler, 2006), plus four species whose classification in Chioninae remains underexploited. To contribute with future taxonomic works, as well systematic and phylogenetic studies, this paper also aims to formulate a tabular identification key for the species.

METODOLOGY

It was analyzed six Chioninae species [*Leukoma thaca* (Molina, 1782)*, Leukoma staminea* (Conrad, 1837), *Lirophora latillirata* (Conrad, 1841)*, Mercenaria campechiensis* (Gmelin, 1791), and *Puberella intapurpurea* (Conrad, 1849)] and one Venerinae species [*Chamelea gallina* (Linnaeus, 1758)] (both sensu Kappner & Bieler, 2006). It was also analyzed four Chioninae species sensu Keen (1969) [*Anomalodiscus squamosus* (Linnaeus, 1758)*, Iliochione subrugosa* (W. Wood, 1828), *Placamen berii* (Wood, 1828)*,* and *Placamen foliaceum* (Philippi, 1846)]. Specialized bibliography was used for specimen's identification (Abbott, 1965; Abbott & Dance, 1982; Amaral *et al*. 2006; Coan *et al*. 2000; Denadai *et al*., 2006; Rios 1994, 2009; Huber, 2010).

For anatomical observation, the specimens were dissected without the shell, immersed in 70% ethyl alcohol. Schematic drawings were performed on stereoscopic microscope drawing tube. In each species were observed characteristics of labial palps, siphons, intestine, heart (ventricle), aortic bulb, and visceral ganglia.

All specimens are deposited in the Malacological Collection "Prof. Henry Ramos Matthews" (CMPHRM) – Series A and B of Universidade Federal do Ceará and the Malacological Collection of Florida Museum of Natural History (FLMNH). More information about the collection data available of each species (such as coordinates, depth, date, location, collector etc) can be accessed through collection's websites.

Key to abbreviation on figures: aa. anterior adductor muscle; **an.** anus; **au.** auricle; **b.** aortical bulb; **deo.** extension of outer demibranch; **di.** inner demibranch; **do.** outer demibranch; **es.** esophagus; **ft.** foot; **gci.** cerebral ganglia inside view; **gco.** cerebral ganglia outside view; **gvi.** visceral ganglia inside view; **gvo.** visceral ganglia outside view; **h.** heart; **in.** intestine; **lp.** labial palps; **m.** mouth; **mb.** mantle border; **mf1.** first mantle fold; **mf2.** second mantle fold; **mf3.** third mantle fold; **mf4.** fourth mantle fold; **pa.** posterior adductor muscle; **se.** excurrent siphon; **si.** incurrent siphon; **st.** stomach; **ve.** ventricle.

RESULTS

The main characteristics of the species examined are summarized in the tabular key for species identification of the Chioninae and Venerinae bivalves, based on observed characters and complemented with bibliography (Table 1).

All species have a similar shell and sometimes this similarity make identification at a specific level difficult. Shell symmetry (equivalve, inequilateral, and laterally inflated), umbo (subcentral anterior, prosogyrate, beak pointed, with conspicuous prodissoconch), internal surface (smooth and opaque) and dentition (heterodont hinge, with three cardinal teeth) were constant in all species analyzed.

The anatomy overview shows outer demibranch with a dorsal extension and pedal retractor muscles inserted into dorsal region of the adductor muscles (Figure 1:A). The siphons are fused, heart has an aortic bulb (Figure 1:B) and intestine exhibit several loops.

The alimentary groove on the inner demibranch is present in all species, except for *Iliochione subrugosa* and *Lirophora latillirata*, in which it was not visualized. The labial palps presented variations in folds type on its surface (Figure 1:C). *Lirophora latillirata*, *Mercenaria campechiensis*, *Placamen foliaceum*, and *Puberella intapurpurea* presented the labial palps with straight extremity and few folds, rough line type. *Anomalodiscus squamosus* and *Leukoma staminea* have curled ends and many delicate lines. *Leukoma thaca* and *Placamen berii* show straight extremity and no visible folds on external surface. *Iliochione subrugosa* present straight end, several folds, but delicate, and *Chamela gallina* long and flexible end with few delicate folds.

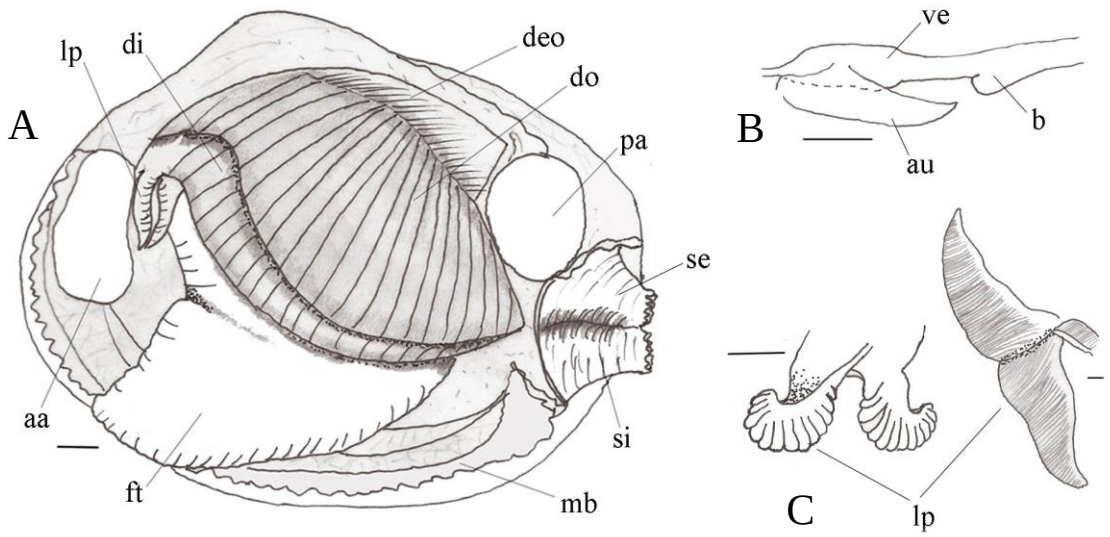

Figure 1. General anatomy of Chioninae spp., left view: **1.A -** Chioninae anatomy, left view, shell and mantle lobe removed; **1.B –** Heart (with ventricle and auricle) and aortic bulb, side view; **1.C -** Labial palps, frontal view of two different folds type. Scale bars = 5 mm.

The mantle is divided into four layers and all species analyzed had the fourth mantle fold short or very short (Figure 2). *Placamen foliaceum* shown muscles fibers disperse in the center of mantle (Figure 2:A).

Siphons showed different fusion degrees, whose some species (*Placamen berii* and *Leukoma thaca*) have siphons fused until the half part approximately (mainly in *Placamen berii)* (Figure 3:A and 3:B), near to the top (*Chamelea gallina*, *Leukoma staminea*, and *Lirophora latillirata*) (Figure 3:C to 3:E) or almost totally fused (*Anomalodiscus squamosus*, *Iliochione subrugosa*, *Mercenaria campechiensis*,

Puberella intapurpurea, and *Placamen foliaceum*) (Figure 3:F to 3:I). All siphons show a robust and well-developed musculature, except *Placamen foliaceum* that has more delicate musculature. It is also observed the outer ring of tentacles varying size (short or developed).

About the digestive system, all species exhibit a noticeable gut loops variation, having from simple configurations with just few loopings (*Placamen foliaceum, Placamen berii*, and *Chamelea gallina*) (Figure 4:A to 4:C) to some quite complex with several loopings (*Anomalodiscus squamosus, Iliochione subrugosa, Lirophora latillirata, Leukoma staminea, Leukoma thaca*, *Puberella intapurpurea*, and *Mercenaria campechiensis*) (Figure 4:D to 4:J). All species had a well-developed digestive gland.

The heart presented a ventricle usually developed with a robust musculature and a delicate auricle (Figure 1:B). Only *Leukoma staminea* shown delicate ventricle and it was the bigger. The aortic bulb was observed in all species, but varying in shape and relative size to the heart (Figure 4A to 4J).

The muscular system was very similar in all the species studied, which the anterior adductor muscle appeared oval or elliptic and the posterior adductor muscle commonly rounded. The only exception was *Leukoma staminea* that showed both muscles elliptical. It was also observed different conformations for the foot shape, mainly the anterior end (sometimes more elongated).

The cerebral and visceral ganglia were globular and elongated (mainly in *Puberella intapurpurea* and *Lirophora latillirata),* respectively (Figure 5:A to 5:H). The visceral ganglia in *Puberella intapurpurea* and *Lirophora latillirata* had a protuberance in the median region (Figure 5:B to 5:D). It was not possible to drawing the cerebral and visceral ganglia for *Leukoma thaca*, but its cerebral ganglia is similar to *Lirophora latillirata* (shape globular to triangular) (Figure 5:B) and its visceral ganglia is similar to *Placamen berii* (elongated) (Figure 5:C). The pedal ganglia of all species (located near to ventral foot margin) were not analyzed due to the difficulty of preserving such delicate structures during the dissection.

Material examined: *Anomalodiscus squamosus:* FLMNH 248030 (shell; Philippines, Luzon Id., Cavite Prov.); FLMNH 481552 (shell; Australia, Shark Bay,

Interdidally in sand); FLMNH 248034 (shell; Malaysia, Sabah, Jesselton, Liku); FLMNH 184871 (shell; Philippines, Cebu Id., Cebu city); FLMNH 298395 (shell; Australia, Western Australia, Shark Bay); FLMNH 248032 (shell; Japan); FLMNH 348690 (specimen; Australia, Western Australia, Little Lagoon, sand bottom, 4 meters depht). ***Chamelea gallina*****:** FLMNH 233810 (shell; Spain, Los Boliches); FLMNH 481478 (shell; Malta, Malta Island); FLMNH 44520 (shell; Mediterranean Sea); FLMNH 380800 (specimen; Spain, Beach in Malaga). ***Iliochione subrugosa***: FLMNH 458888 (specimen; Costa Rica, Gulf of Nicoya, W of Puntarenas, E of Hotel Jesusita). ***Leukoma thaca***: FLMNH 458951 (specimen; Chile, Antofagasta, Antofagasta, in Front of Hotel Antofagasta, rocky shore). ***Leukoma staminea:*** FLMNH 419969 (specimen; United States, Washington, Edmonds, intertidal sand flat with rubble, under rocks). ***Lirophora latillirata*****:** CMPHRM 426B (shell; Brazil, Maranhão); FLMNH 44641 (shell; Mexico, Campeche, Campeche Shrimp Beds); FLMNH 481405 (shell; United States, Florida, Cape Canaveral); FLMNH 369977 (shell; United States, Florida, Grassy Key, 150 fathoms depth); FLMNH 396920 (shell; Trinidad & Tobago, Tobago Island); FLMNH 263958 (shell; United States, Florida, 1.5 mi off Panama City, Texas Tower Stage 2, steel tower, 60 feet depth); FLMNH 427046 (specimen; United States, Florida, 70 km WSW of Tampa Bay, sand bottom, 40 meters depth). ***Mercenaria campechiensis*****:** FLMNH 340793 (shell; Mexico, Yucatan, San Felipe, beach and cienata); FLMNH 121313 (shell; United States, Florida, St. Petersburg Beach, near N Point at Mullet Key); FLMNH 343975 (shell; United States, Florida, Sanibel Island); FLMNH 457696 (specimen; United States, North Carolina, Core Creek, 14 feet depth). ***Placamen berii*****:** FLMNH 348695 (specimen; Australia, Little Lagoon, sand bottom, 4 meters depth); FLMNH 348694 (specimen; Australia, Monkey Mia). ***Placamen foliaceum*****:** FLMNH 286480 (specimen; Tanzania, Zanzibar, W of Stone Town, near Pange Reef, in sand, 60 feet depth). ***Puberella intapurpurea*****:** CMPHRM 3829A (shell; Brazil, Ceará); CMPHRM 3642B (shell; Brazil, Ceará, Pecém Beach); FLMNH 266620 (shell; United States, Florida, SW of Cape San Blas, 130 feet depth); FLMNH 369630 (shell; Panama, Canal Zone, Limon Bay); FLMNH 369458 (shell; Jamaica, Port Morant); FLMNH 457983 (specimen; United States, Florida, Gulf of Mexico, N of St. Petersburg, 82 feet depth).

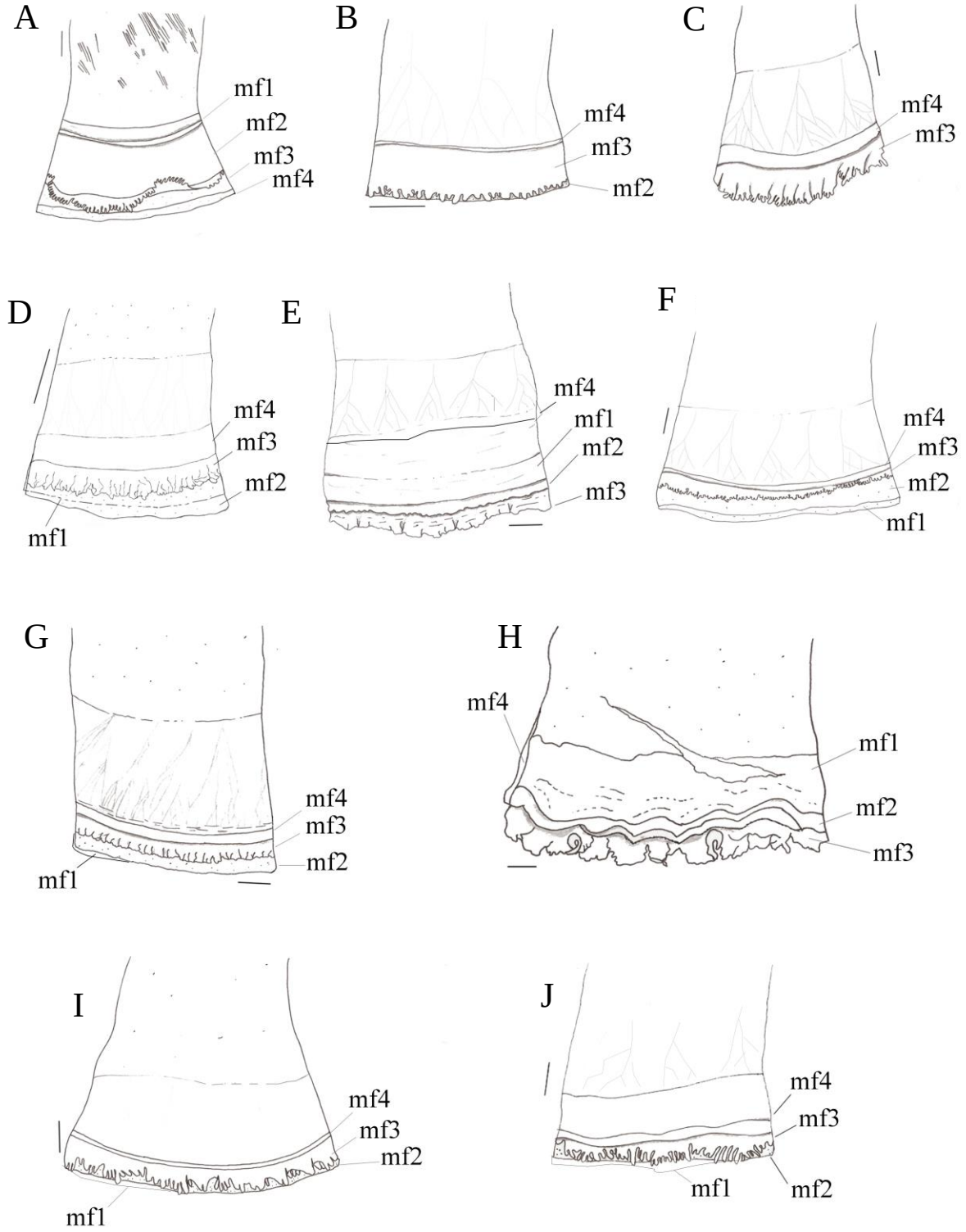

Figure 2. Mantle overview showing the four layers of Chioninae spp.: **A -** *Placamen foliaceum*; **B -** *Placamen berii*; **C -** *Leukoma thaca*; **D -** *Chamelea gallina*; **E -** *Leukoma staminea*; **F -** *Lirophora latillirata*; **G -** *Iliochione subrugosa*; **H -** *Mercenaria campechiensis*; **I -** *Puberella intapurpurea*; **J -** *Anomalodiscus squamosus*.

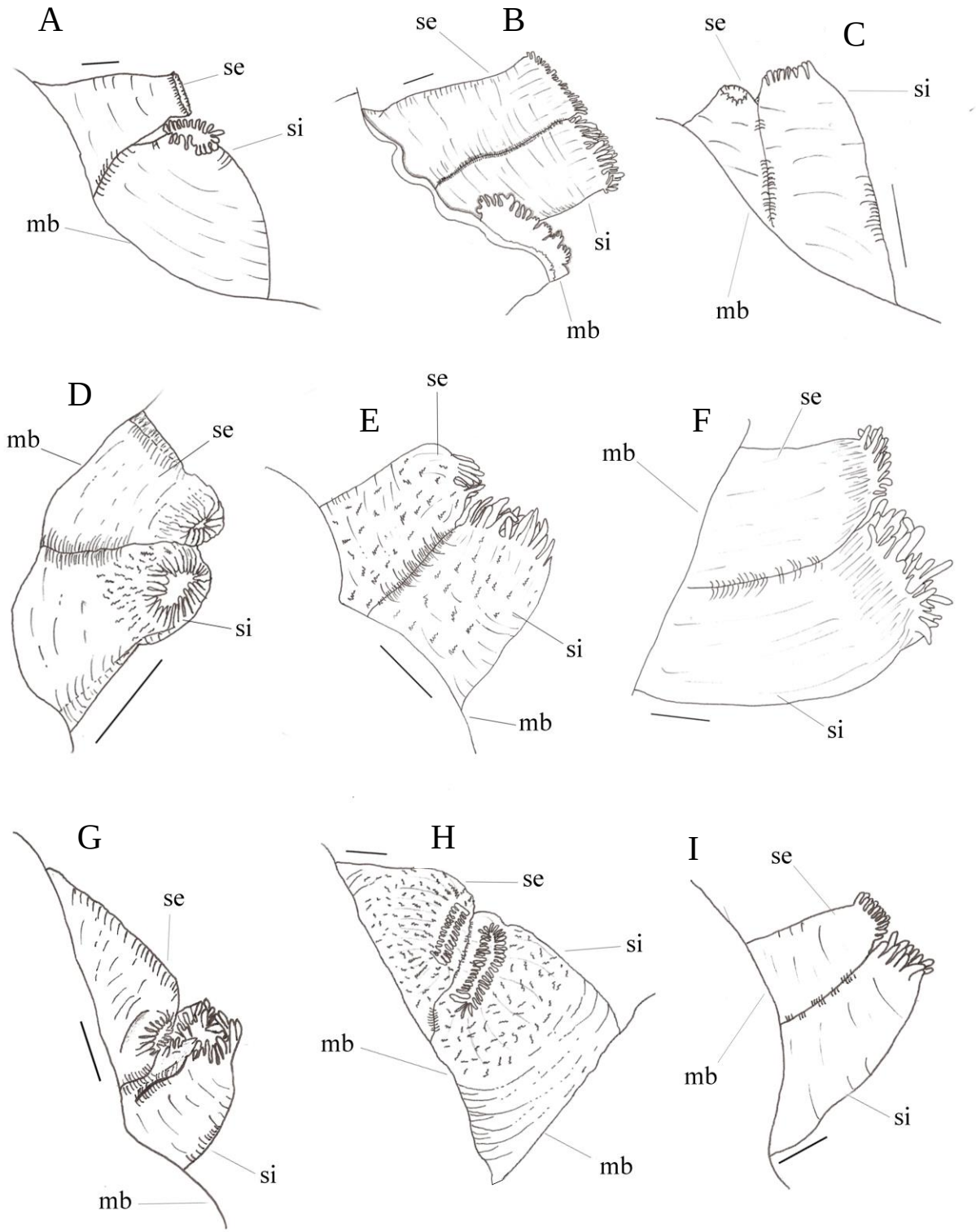

Figure 3. Siphons of Chioninae spp, left view. **A -** *Placamen berii*; **B -** *Leukoma thaca*; **C -** *Chamelea gallina*; **D -** *Leukoma staminea*; **E -** *Lirophora latillirata*; **F -** *Iliochione subrugosa*; **G -** *Mercenaria campechiensis*; **H -** *Puberella intapurpurea*; **I -** *Placamen foliaceum*.

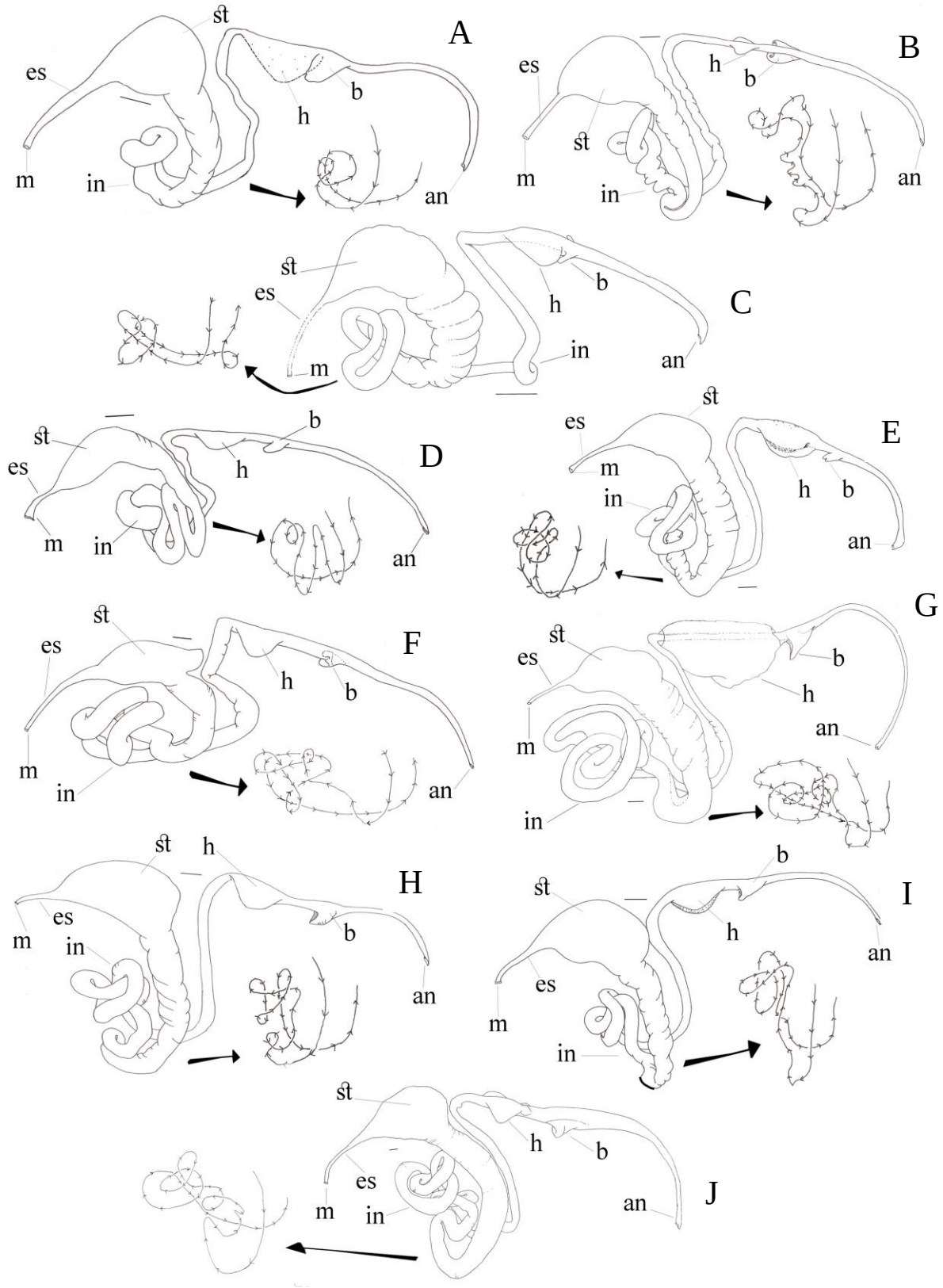

Figure 4. Digestive system of Chioninae spp., left view. **A -** *Placamen foliaceum*; **B -** *Placamen berii*; **C -** *Chamelea gallina*; **D -** *Anomalodiscus squamosus*; **E -** *Iliochione subrugosa*; **F -** *Lirophora latillirata*; **G -** *Leukoma staminea*; **H -** *Leukoma thaca*; **I -** *Puberella intapurpurea*; **J -** *Mercenaria campechiensis*.

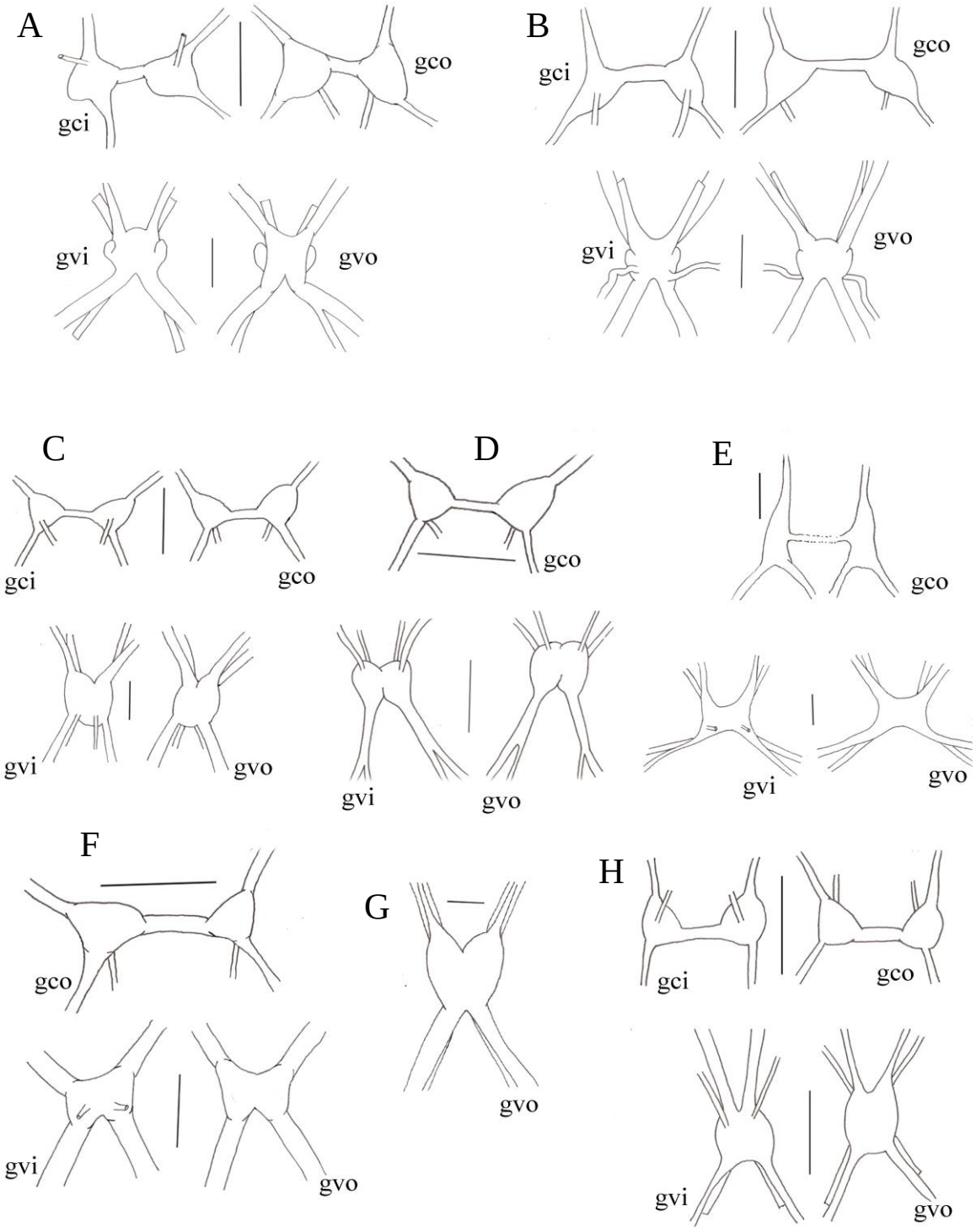

Figure 5. Cerebral and/or visceral ganglia of Chioninae spp., dorsal view. **A -** *Puberella intapurpurea*; **B -** *Lirophora latillirata*; **C -** *Placamen berii*; **D -** *Placamen foliaceum*; **E -** *Leukoma staminea*; **F -** *Iliochione subrugosa*; **G -** *Mercenaria campechiensis*; **H -** *Anomalodiscus squamosus*. Scale bars = 1 mm.

DISCUSSION

This anatomy overview study corroborates with previous information of Chioninae and Venerinae (Narchi, 1972; Jones, 1979; Narchi & Gabrieli, 1980; Guéron & Narchi, 2000; Ebel, 2001; Bieler *et al*., 2004).

Generally, bivalve molluscs have a ventral groove in their inner demibranch, responsible for carrying food from the lamellae to labial palps (Atkins, 1937; Guéron & Narchi, 2000) and sometimes this channel may not be observed or is inconspicuous. Species that do not present ventral sulcus in inner demibranch (dissection view), probably, still have the food movement towards the palps, but without the groove aid (Marques, 2012). Such flow can only be observed in the living animal and the morphological evidence in the fixed animal is absent. This fact may explain that sulcus absent in some species in this study.

The present work observed different conformations in palps extremities as well as the roughness present, corroborating observations made by Jones (1979). Labial palps are structures that select and carry particles to the mouth. Differences in such structure could be related to species adaptations to their environment (turbid waters, for example), where filter feeder animals tend to have more specialized palps to select particles (large size, roughness type, and number) (Ansell, 1961; Pohlo, 1982; Marques, 2012). Hence, it is justified the different features observed on palps among the studied species, still sometimes similar for sharing comparable environments.

In this study, the fourth mantle fold indicates species from more calm and protected environments, once its size may vary according to habitat conditions, being less prominent in less turbid environments and/or the substrate with less silt (Hillman & Shuster, 1966; Hillman, 1969; Eble, 2001). The fourth mantle fold probably secreting mucus to remove foreign particles and discarded particles in the mantle.

Two functions could explain the variance in size and shape of tentacles present in an outer ring in the siphons: select particles (especially the inhalant siphon) and sensory function (Owen, 1953; Young, 1957; Narchi, & Gabrieli, 1980). Besides, the way that the animal is fixed could be caused a muscle retraction and modifying the siphon and tentacles conformation. This study also corroborates the information that

fused siphons have been present in all Chioninae species (Narchi, 1972; Jones, 1979; Narchi & Gabrieli, 1980; Bieler *et al.*, 2004; Mikkelsen *et al*., 2006).

Ansell (1961) considered that species having siphons unfused on the top would be adapted to shallower and turbulent waters. However, *Iliochione subrugosa* and *Anomalodiscus squamosus* are typical of shallow usually turbulent waters and have fully fused siphons. Consequently, other structures must be present in the siphon, associated to the water flow and particles control [as membranes in basal region, observed by Jones (1979) and Guerón & Narchi (2000)].

The digestive and muscular systems presented similar pattern in Chioninae species (Narchi, 1972; Jones, 1979; Nachi & Gabrieli, 1980; Guerón & Narchi, 2000; Eble, 2001). However, small variances observed among the species indicate possible adaptations to their environments.

The several intestine loops and complex turns designs observed on this study suggested that those conformation is linked to digestion process, requiring a larger path to increase nutrient absorption efficiency (the greater intestine complexity, the greater the absorption). Studies demonstrate the intestine also participating in digestion and absorption processes, mainly in rectum anterior portions (Purchon, 1983).

The heart showed the same way of others venerids and rubout ventricle, together with two auricles (lateral and delicate) acting as valves, preventing the return blood flow (Narchi, 1972; Jones, 1979; Nachi & Gabrieli, 1980; Guerón & Narchi, 2000; Eble, 2001). Just *Leukoma staminea* presented a dilated and delicate ventricle. An abrupt valve close (and rapidly retracted muscles) during the fixation step could be caused this alteration. Others specimens of *L. staminea* should be observed to verify (or confirm) this heart conformation.

In all species, the aortic bulb, a typical organ for Veneridae, was detected. This structure works to prevent heart rupture when the siphons and foot are retracted rapidly and the fluids need to return to posterior aorta (Eble, 2001; Mikkelsen *et al.*, 2006), and could be a possible regulator of the hemolymph flow from the anterior and posterior aorta to the ventricle in normal situations (Deaton *et al.*, 2001). In *Leukoma staminea*, the aortic bulb probably protected heart to disrupt, besides its distension.

The ganglia observed in the present study corroborate data from previous studies (Jones, 1979; Eble, 2001; Bieler *et al.*, 2004; Mikkelsen *et al*., 2006). The Veneridae nervous system is mainly formed by three pairs of ganglia: cerebral, usually next to the anterior pedal retractor muscle; visceral, located in the anterior region of the posterior adductor muscle; and pedal, in the anteroventral region distal to the intestine middle portion, enervating the foot (Jones, 1979; Mikkelsen *et al*., 2006). However, it was observed a lateral protuberance in the visceral ganglia of two species: *Lirophora latillirata* and *Puberella intapurpurea*. A similar structure, often more developed, has also been detected in other bivalves, such as Tellinidae and Spondylidae species (Simone & Wilkinson, 2008; Marques, 2012; Simone *et al*., 2015) and it is probably feature of a more complex system.

The present study filled some gaps in knowledge of Veneridae. Supplementary investigations on functional anatomy, as well as histology studies, should be performed for further elucidation on all differences observed in some organs and in nervous system.

ACKNOWLEDGEMENTS

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Table 1- Tabular identification key for identification of Chioninae and *Chamelea gallina* species analyzed in this study. Species with description observed in the literature are marked with an asterisk (*****) followed by the reference. Legends: **1.** Shell shape: T (triangular), O (ovate or suborbicular) or R (rostrated); **2.** Lunule: S (smooth) or O (ornated); **3.** Escutcheon: A (absent), U (undeveloped) or D (developed); **4.** Anterior cardinal teeth (left valve): S (smooth) or B (bifid); **5.** Central cardinal teeth (left valve): S (smooth) or B (bifid); **6.** Posterior cardinal teeth (left valve): S (smooth) or B (bifid); **7.** Anterior cardinal teeth (right valve): S (smooth) or B (bifid); **8.** Central cardinal teeth (rigth valve): S (smooth) or B (bifid); **9.** Posterior cardinal teeth (right valve): S (smooth) or B (bifid); **10.** Nymph: S (smooth) ou R (rugose); **11.** Shell ornamentation (outer): A (concentric and radial elements co-dominant) ou B (concentric elements dominant); **12.** Labial palps rugosity: D (delicated), R (rough) or S (smooth); **13.** Labial palps end: S (straight) or R (rolled); **14.** Siphons fusion: T (totally fused), AT (fused almost until the end – about 2/3) ou M (fused up to half – about the middle); 15. Intestine loops: C (complex, two or more loops) ou S (simple); **16.** Heart size (ventricle) in relation to the aortic bulb: S (similar or slightly smaller) or L (larger); **17.** Visceral ganglia protuberance: A (absent) ou P (present).

Species	Features																
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
**Anomalocardia flexuosa* – Narchi, 1972; Marques, 2012	T	S	D	S	S	S	S	S	S	S	B	D	S	M	C	S	A
Anomalodiscus squamosus	R	O	D	S	B	S	S	S	B	R	A	D	R	T	C	S	A
**Austrovenus stutchburyi* - Jones, 1979	T	O	U	B	B	S	B	B	S	R	B	D	R	AT	C	L	A
Chamelea gallina	T	S	D	S	S	S	S	B	S	R	B	R	R	AT	C	L	A
**Chione cancellata* - Jones, 1979	T	O	D	S	B	S	S	S	B	S	A	R	R	M	C	L	A
Iliochione subrugosa	T	O	D	S	S	S	S	S	S	R	B	D	S	T	C	L	A
**Chione undatella* - Jones, 1979	T	O	D	S	S	S	S	S	S	R	A	R	R	T	C	S	A
**Leukoma pectorina* – Narchi, 1972	O	O	U	S	B	S	S	S	B	S	A	D	R	T	C	L	?
Leukoma staminea	O	O	A	S	B	S	S	B	B	R	A	D	R	T	C	L	A
**Leukoma subrostrata* – Narchi & Grabrieli, 1980	T	O	D	S	S	S	S	S	S	S	A	D	S	T	C	?	A
Leukoma thaca	O	O	A	S	B	S	S	B	B	R	B	S	S	M	C	L	A
Lirophora latillirata	T	S	U	S	S	S	S	S	S	R	B	R	S	AT	C	L	P
**Lirophora paphia* - Jones, 1979	T	S	D	S	S	S	S	S	S	R	B	R	R	AT	C	L	A
Mercenaria campechiensis	T	O	D	S	B	S	S	B	B	R	B	D	R	T	C	L	A
**Mercenaria mercenaria* – Jones, 1979; Eble, 2001	T	O	D	S	B	S	S	B	S	R	B	D	S	T	C	L	A
Placamen berii	T	O	D	S	S	S	S	S	B	R	B	S	S	M	C	S	A
Placamen foliaceum	T	O	D	S	S	B	S	S	B	R	B	R	S	AT	S	L	A
Puberella intapurpurea	T	O	D	S	S	S	S	S	S	S	B	R	R	AT	C	L	P

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