ANATOMICAL DIFFERENCES AMONG SPECIMENS OF *Pinctada imbricata* RÖDING, 1798 FROM DIFFERENT SOUTH AMERICAN LOCALITIES*

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ABSTRACT

In the present study, we compared the internal and external anatomy of pearl oyster (*Pinctada imbricata* Röding, 1798) from some South American localities, including Venezuela and several regions of Brazil. The anatomical data shows non-geographical variations characterized by variable outline in adults, different degrees of posterior auricle shell development and mantle papillae ranging from normal to digitiform. The geographical variations can be divided into two major groups: the Venezuelan group presents a more folded mantle; pallial muscle grouped in anterior and median-posterior sets; poorly-developed perpendicular mantle groove; inner lamella not extended into the anterior mantle. Brazilian group specimens present a smoother mantle, with less clear separation between anterior and posterior mantle muscle groups; externally-developed perpendicular groove; inner lamella extension developed in anterior mantle. These differences may represent ecophenotypes or differences among isolated South American populations, which may be elucidated by subsequent phylogeographic studies.

Keywords: Bivalvia; Pteriomorphia; pearl oyster; anatomy; intraspecific variation

DIFERENÇAS ANATÔMICAS ENTRE ESPÉCIMES DE *Pinctada imbricata* RÖDING, 1798 DE DIFERENTES LOCALIDADES DA AMÉRICA DO SUL

RESUMO

No presente estudo comparou-se a anatomia da ostra perlífera (*Pinctada imbricata* Röding, 1798) de algumas localidades da América do Sul, incluindo a Venezuela e várias regiões do Brasil. Foram encontradas variações não geográficas e geográficas. As variações não geográficas foram caracterizadas por adultos com contorno bem variável, diferentes graus de desenvolvimento da aurícula posterior e papilas da lamela interna do manto variando de normal a digitiformes. Variações geográficas podem ser divididas em dois grandes grupos: o grupo venezuelano apresentou um manto mais pregueado; musculatura palial agrupada em dois conjuntos de feixes – um anterior e outro mediano-posterior; sulco perpendicular do manto pouco desenvolvido. Espécimes dos grupos brasileiros apresentaram um manto menos pregueado, com separação menos nítida entre os feixes musculares paliais anterior e posterior do manto; sulco perpendicular do manto bem desenvolvido; lamela interna do manto se estendendo externamente na região do manto anterior. Essas diferenças podem ser ecofenótipos ou diferenças entre as populações com certo grau de isolamento da América do Sul, que podem ser elucidados por estudos filogeográficos subsequentes.

Palavras chave: Bivalvia; Pteriomorphia; ostra perlífera; anatomia; variação intraespecífica

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INTRODUCTION

Species belonging to the pteroid genus *Pinctada* are traditionally known as pearl oysters, and have a long history in trading. They are a part of the epibyssate fauna along tropical and subtropical shallow seas, encompassing 17–19 species depending on the taxonomic authority (e.g. HUBER, 2010). *Pinctada imbricata* Röding, 1798 is a relatively common Western Atlantic species living on consolidate substrata, such as rocks, thalloid algae and corals, ranging from North Carolina, USA to Santa Catarina, Brazil. It has been historically associated with pearling activities on the Venezuelan coast, though it is considered less economically relevant than *P. fucata* (Gould, 1850) from Japan, or *P. margaritifera* (Linnaeus, 1758) from the Indo-Pacific (URBAN, 2000). More recently, the Fishery Institute of São Paulo (IPesca-SP) has studied the feasibility of *P. imbricata* as an edible species in southeastern Brazil.

Pinctada imbricata is externally characterized by a subquadrate shell with a thick ligament, showing a lamellose sculpture consisting of overlapping scales, generally more protruded in younger specimens. The external color ranges from black to reddish, going through yellow to creamy shades and may be radially stripped in a zigzag, patchy, or concentric pattern or a combination of all these. The general outline resembles *Pinctada radiata* (Leach, 1814) from the Red Sea and Mediterranean and the Indo-Pacific *P. fucata*. Overall similarities have led some authors to gather *P. imbricata* and several several Indo-Pacific species in a so called large species complex named *Pinctada fucata /martensii /radiata/ imbricata* complex by WADA and TËMKIN (2008). Alternatively, some authors consider them a single species with a cosmopolitan range (e.g. SHIRAI, 1994; HUBER, 2010). On the other hand, genetic distances indicate that Western Atlantic populations (i.e. *P. imbricata*) are different from their Indo-Pacific counterparts (MASAOKA and KOBAYASHI, 2002; 2005).

Pteroids are a well studied bivalve group as far as anatomy is concerned, with numerous works since the nineteenth century (THURSTON, 1890; HERDMAN, 1903), though most were focused on specimens from restricted localities. In the present paper we describe anatomical variations of *P. imbricata* along the South American (Venezuela and Brazil) coast, and we test if there is a homogeneous morphology along the study area, or there is any recognizable regionalization. As the shell characteristic is widely variable, the anatomical data compiled here may be useful for understanding groups that are difficult to distinguish, such as the *Pinctada fucata/martensii/radiata/imbricata* complex.

MATERIAL AND METHODS

Regardless of the controversy involving the taxonomic status of *P. imbricata*, we consider it as a valid species restricted to the Western Atlantic. We surveyed the specimens previous housed on Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ) and Museu de Zoologia da Universidade de São Paulo (MZUSP) collections. For the soft parts anatomy, a total of 22 specimens from 10 localities (see Table 1) were dissected under stereomicroscopy, using standard techniques (see SIMONE and GONÇALVES, 2006).

Additionally, specifically for *Pinctada* the dissection following the sequential steps: 1) the right valve was removed, with subsequent exposure of the mantle; 2) the distal edge of the mantle was removed along with the radial pallial muscles; 3) the pericardium membrane was carefully removed so that the auricle and associated circulatory structures could be preserved; 4) an incision on the visceral sac was performed along the antero-posterior muscles; 5) gonads and distal portions of the digestive gland were removed to expose the stomach and intestine (partially); 6) an incision parallel to the direction of the style sac/proximal intestine towards the pearl pocket was performed to visualize the remaining intestine. This sequence should be met in order to reduce damage to internal organs.

The muscle system division follows the TRUEMAN *et al*. (1966), which is composed of extrinsic muscle (valve-to-valve muscles, as the adductor system) and intrisec muscle (valve-to-foot muscles, as the retractor and protractor systems).

Table 1. Ethanol fixed specimens utilized for dissections. MZSP = Museu de Zoologia da Universidade de São Paulo; MNRJ = Museu Nacional da Universidade Federal do Rio de Janeiro. n = number of specimens.

Localization	Coordinate data	n	Lot
Venezuela			
Isla Margarita	10°56'N, 63°51'W	1	MZSP 57975
		5	MZSP 61634
Brasil			
off Pará	0°01'S, 47°24'W	1	MZSP 94004
Acaraú, Ceará	2°53'S, 40°07'W	4	MZSP 115148
Maceió, Alagoas	9°40'S, 35°43'W	1	MZSP 80156
Mata de São João, Bahia	12°31'S, 38°17'W	1	MZSP 104784
Boipeba, Bahia	13°39'S, 38°53'W	1	MZSP 110076
Arraial do Cabo,	22°58'S, 42°01'W	2	MZSP 50350, MNRJ 19998
Ilha Grande, Rio de Janeiro	23°09'S, 44°14'W	2	MNRJ 31237
Caraguatatuba, SP	23°37'S, 45°24'W	1	MZSP 112091
Ilhabela, SP	23°46'S, 45°21'W	7	MZSP 89414; MZSP 104953; MZSP 105575; MZSP 117496
Pontal do Paraná, PR	25°40'S, 48°30'W	1	MZSP 115121

RESULTS

No latitude, clinal or grade-dependent variation was detected. The morphological variations observed here fall into two categories: non-geographical variations found in all localities, and geographical variations, which are restricted to certain ranges.

Non-geographical variations: *P. imbricata* presents high variation regarding external conchological characters, such as the periostracum extension and development of scales. The ornamentation on the anterior wing of the right valve may be composed of growth lines, scales or a combination of both, forming a cancellated pattern. The posterior and anterior wing ornamentation is variable (Figure 1: **pw** and **aw**). The posterior wing itself ranges from not developed (Figure 1a) to highly developed, extending beyond the posterior transverse line in some specimens (Figure 1b, c). However, the aragonitic shell presents a rounded ventral and middle margin, which is constant among all specimens. Teeth development is the most variable inner shell character. There may be one (Figure 2e-h) or two posterior teeth (**p1** and **p2**) on each valve. The posterior teeth generally forming a 45º or fewer angles with the dorsal margin. The anterior tooth is generally slightly developed anteriorly toward the byssal sinus line and umbo. There is a gradation in the development of the anterior teeth, ranging from bifid to a single elevation. If the left anterior tooth is bifid, the right is simple and vice versa (Figure 2a-d).

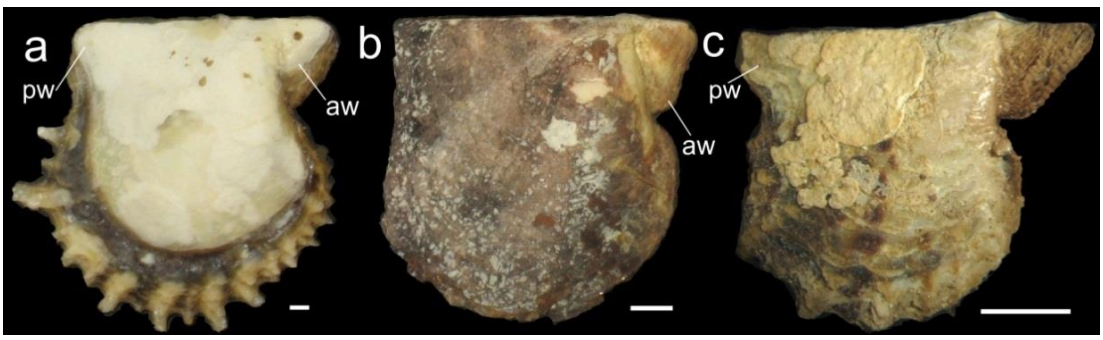

Figure 1. Right valve overall view. Isla Margarita, Venezuela (a); Itapagipe, Bahia State (b); and Cabo Frio, Rio de Janeiro State (c). aw = anterior wing; pw = posterior wing. Scale = 3 mm.

The four mantle regions are easily discernible (Figure 3), represented by: an isthmus zone (**iz**) present only dorsally, fused; a central zone (**cz**), without pallial muscles; a distal zone (**dz**) bearing pallial muscles; a three lobed marginal zone (**mz**). The external lamellae have extensions on the posterior region (Figure 4a). Marginal papillae are present on the inner and middle lamellae of the marginal area. They are well developed in the posterior region, becoming increasingly smaller towards the anterior region. In the posterior region, the papillae may similarly-sized or alternate between different sizes. This type of development is not related to body size or maturation. The papillae can be divided into two morphological types: simple, with smooth tips, (Figure 4b); digitiform with processes or buds on the papilla tip (Figure 4c, d). The anterior region of the mantle presents an extension of the internal lamellae (Figure 5b: **aem**). A perpendicular groove is present on the external lamellae in the anterior region (Figure 6: **pmg**), close to the internal lamellae extension, ranging from the space between the external and middle lamellae to the external mantle margin.

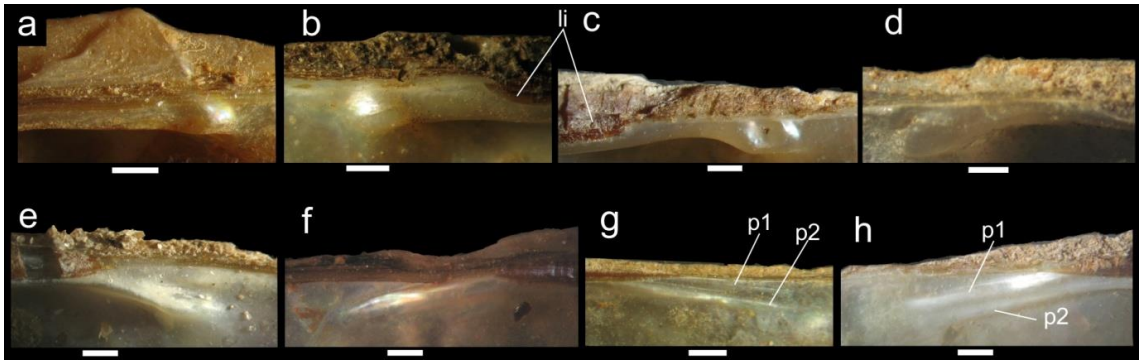

Figure 2. Detail of hinge teeth. Left (a) and right (b) not-bifid anterior tooth; left (c) and right (d) not-bifid anterior tooth; right (e) and left (f) posterior simple teeth; right (g) and left (h) posterior duplicated teeth. li = ligament; p1 = dorsal posterior tooth; p2 = ventral posterior tooth. Scale bar = 1 mm.

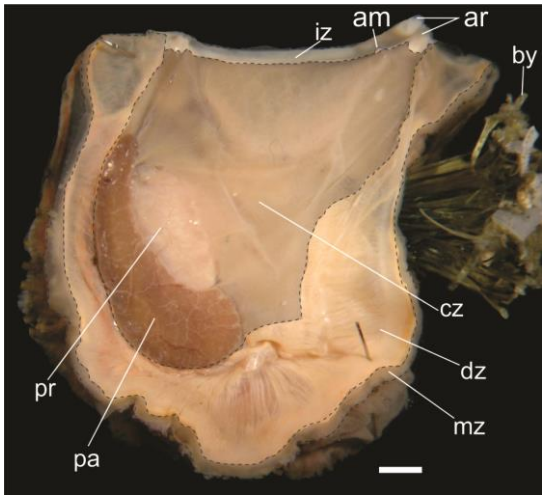

Figure 3. Right view with valves removed (based on Pontal do Paraná specimen); am = auxiliary pedo-byssal retractor muscle; ar = anterior pedo-byssal retractor muscle; by = byssus; cz = central zone; dz = distal zone; iz = isthmus zone; mz = marginal zone; pa = posterior adductor muscle; pr = posterior pedo-byssal retractor muscle. Scale: 5 mm.

The muscular systems are homogenous among the studied specimens. Pallial muscle thickness depends on specimen size. Generally, the pallial muscle becomes thicker as the size increases, and the origin area becomes more protruded. The byssal groove reaches the distal end of the foot, sometimes reaching the foot dorsal surface (Figure 7a,b: **bg**) apart from larger specimens such as the Venezuelan ones. The byssus filaments are more greenish in juvenile specimens, becoming golden in older individuals. The pearl pocket is present as a hump, posterior to the byssal groove, ranging from creamy to black in color. The gill is pteriomorphian type (as defined by WADA and TËMKIN 2008), attached to the visceral mass by a "gill suspensory membrane" (*sensu* TËMKIN, 2006; Figure 8: **gm**). The gill suspensory membrane is partially translucent in most species. Internally, the renopericardial organs (ventricle, auricle, pericardium and kidneys) and the

asymmetric digestive system (always dislocated to the left) are constant, except for stomach thickness, which is greater in the larger specimens. The anterior intestinal loop ranges from pointed forward to ventrally (Figure 9). The palp, visceral sac and asymmetry of pedo-byssal retractor muscle are similar to the previously described for other *Pinctada* species (THIELE, 1886; FOUGEROUSE-TSING and HERBAUT, 1994; TËMKIN, 2006; FOUGEROUSE *et al*., 2008; MAMANGKEY, 2009). The gonads follow the same pattern for the genus (BUESTEL and POUVREAU, 2000; POUVREAU *et al*., 2000; YUKIHIRA *et al*., 2006).

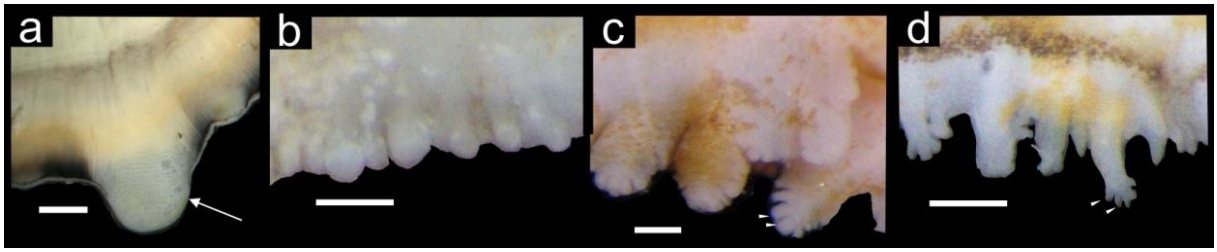

Figure 4. Mantle margin features. (a) extension of the external lamellae on posterior margin (long arrow). (b) simple papillae on internal lamellae; (c) retracted digitiform papillae with buds (short arrows); (d) non-retracted papillae, with extended buds (short arrows). Scale bar = 1 mm.

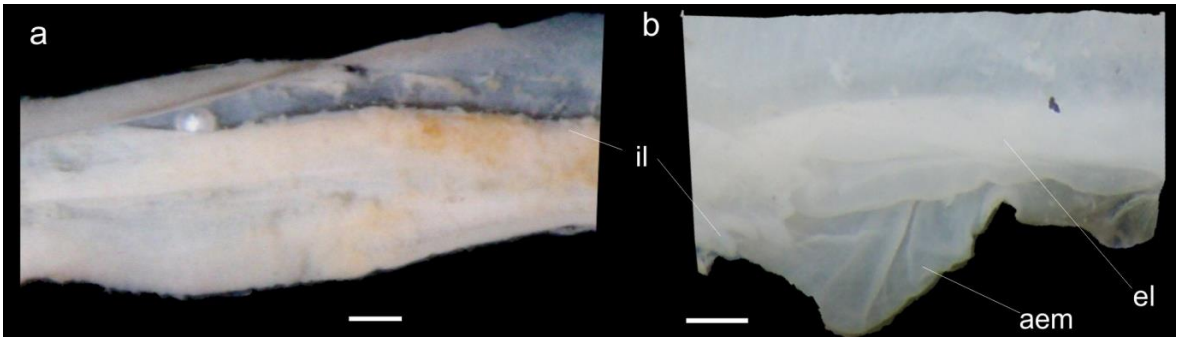

Figure 5. Detail of anterior mantle internal surface margin in of Venezuela specimen (a) and external surface of Brazilian specimen (b), showing the anterior extension of mantle (aem). el = outer lamellae; il = internal lamellae. Scale bar = 1 mm.

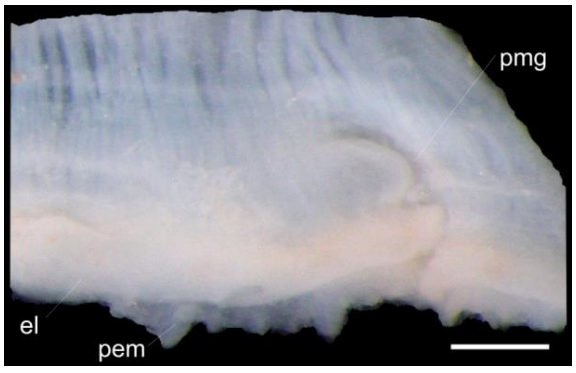

Figure 6. Detail of anterior mantle external surface of a Brazilian specimen, showing the perpendicular mantle groove (pmg). Other abbreviations as in Figure 5. Scale bar = 1 mm.

The extrinsic muscular system is composed of the adductor muscle, with origin area occupying about 1/8 of mantle surface (Figures 8, 9). The intrtinsec muscular system is composed of: a pair of pedo-byssal retractor muscles, with origin area equivalent to 1/10 of adductor muscle area, connected to the foot and visceral mass; a pair of accessory pedo-byssal retractor muscles, with origin area ~2/3 of pedo-byssal retractor area. The proportion of the extrinsic muscle origin areas is constant along the studied region, regardless of overall size. The right pedo-byssal retractor muscle is thicker and broader, mainly when spreading on the visceral mass. The ctenidial muscle (Figure 10: **cm**) ranging along

ctenidial axis, originating in conjunction with the pedo-byssal retractor muscle. The intrinsic muscular system is composed of transverse and longitudinal muscles of the visceral mass, pallial muscle, umbonal muscle and minor muscle distributed in the visceral cavity (Figures 10, 11).

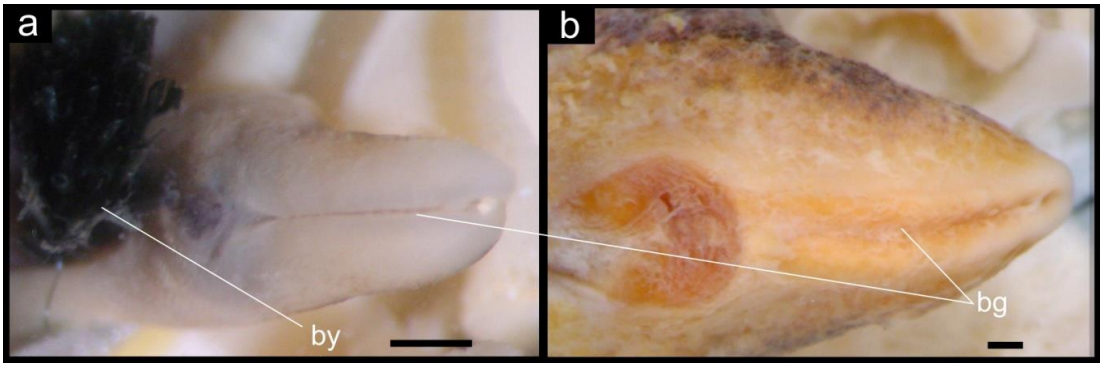

Figure 7. Ventral view of foot and byssal groove in: a) São Paulo specimen Venezuela specimen bg, byssal groove; by, byssus. Scale bar = 2 mm.

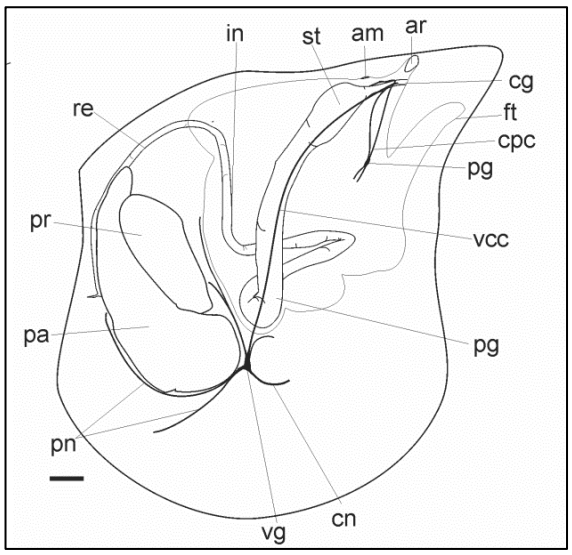

Figure 8. Detail of pallial organs; right mantle partially removed. an = anus; de = external demibranch; di = internal demibranch; gm = suspensory membrane of the gill; ki = kidney (seen by transparency); pp = palps; um = umbonal muscles. Other abbreviations as in Figure 3. Scale bar = 4 mm.

The nervous ganglia system is composed of: a pair of a triangular cerebral ganglia; an antero-posteriorly elongated pair of visceral ganglia; an asymmetrically positioned pair of pedal ganglia (Figures 9, 11). Each pair of ganglia is connected by a respective connective nerve – the cerebro visceral connective (Figure 11: **vcc**) (visceral-cerebral) and cerebropedal connective (Figure 11: **cpc**) (cerebral-pedal). Each cerebral ganglion is located between the esophagus and the region near the branching portion of the pedo-byssal and accessory pedo-byssal retractor muscles, small-sized, with dimensions equivalent to 1/2 of anterior pedo-byssal muscle origin area, connected by a cerebral commissure nerve. The cerebral commissure nerve crosses over the esophagus. The pedal ganglia are almost fused, with dimension about 3X of cerebral ganglion. This pair of ganglia is positioned beneath a thin transverse muscle layer on the middle right side of the visceral sac almost touching the right visceral mass wall, with the left cerebrovisceral nerve longer than the right (Figure 11). The visceral ganglia are positioned below the posterior adductor muscle, close to the suspensory membrane of gill, and connected by a visceral commissure nerve (Figures 9, 11). In addition to the mentioned nerves, the following are also apparent during macroscopic examination: the anterior pallial nerves (Figure 11: **apn**) , ranging parallel to the anterior pedo-byssal retractor muscle from each cerebral ganglia to the anterior mantle; pair of pedal posterior nerve emerging from pedal ganglia to posterior side of visceral mass (Figure 11: **ppn**). From each pair of visceral ganglia emerges the ctenidial nerve (Figure 9: **cn**), extending to the gill; the posterior pallial nerve (Figure 9: **pn**), running to posterior mantle, beneath posterior adductor muscle and dorsal pallial

mantle, branching to the posterior and middle mantle margin, umbonal and pericardial regions.

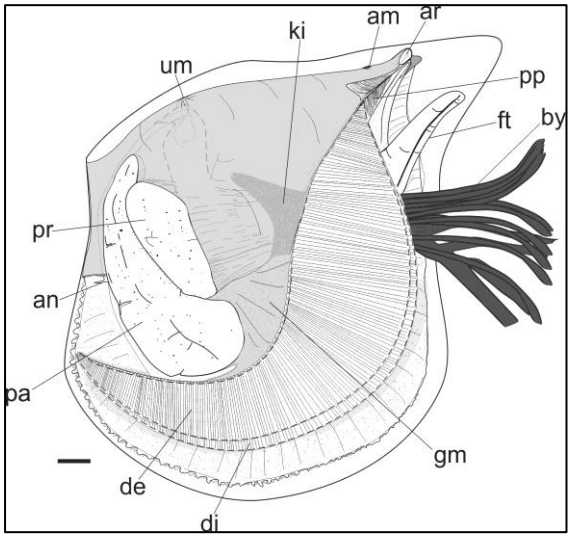

Figure 9. Schematic drawing showing the topography of the digestive system and nervous system. ar = anterior pedo-byssal retractor muscle; cn = ctenidial nerve; cpc = cerebropedal connective nerve; ft = foot; in = intestine; pg = pedal ganglia; pn = posterior pallial nerves; re = rectum; ss = style sac; st = stomach; vcc = cerebrovisceral connective nerve; vg = visceral ganglion. Other abbreviation as in Figure 3. Scale bar = 4 mm.

Geographical variations: There are two regional variation groups: specimens from Venezuela and from the Brazilian coast, ranging from Pará to Paraná. The geographical variations are related to mantle border features. The Venezuelan group presents the pallial muscles separated into two sets, with one set being formed by fibers that originate from the ventral posterior adductor muscle, and the other originating from a sequence of areas near the anterior margin of the mantle (Figure 12a); perpendicular mantle groove poorly developed; extension of the inner lamella of the anterior mantle reduced (Figure 5a). The Brazilian group presents the pallial muscle with fibers originating from the posterior adductor margin, the anterior region and from the area between the anterior and posterior regions, running perpendicular to the mantle margin (Figure 12b); the perpendicular mantle groove is well developed on the anterior margin, reaching the outer surface of the distal area (Figure 6); the extension of the inner lamellae is well developed, sometimes with a frilled margin (Figure 5b).

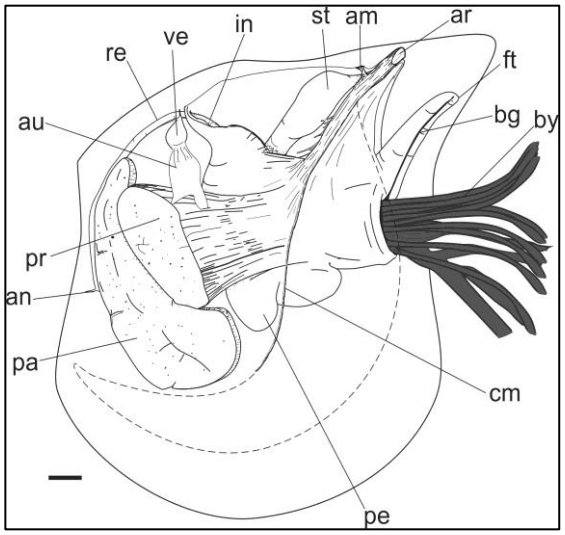

Figure 10. Detail of muscular system and the pericardial cavity. au = auricle; bg = byssal groove; cm = ctenidial muscle; pe = pearl pocket; st = stomach; ve = ventricle. Other abbreviations as in Figures 3, 6 and 7. Dashed line represents the gill. Scale bar = 4 mm.

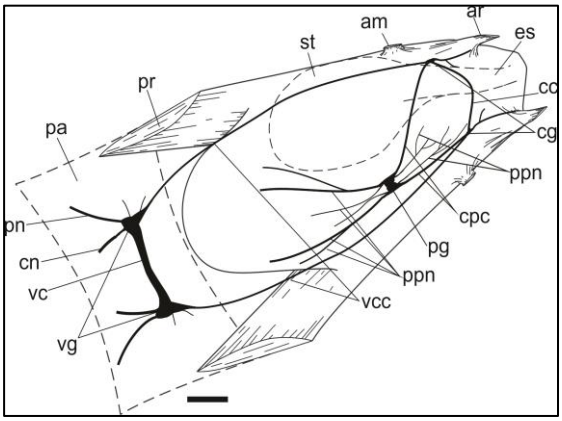

Figure 11. Schematic drawing of the main structures of nervous system (dorsal view). The posterior muscle is represented by dashed line. apn = anterior pedal nerves; cc = cerebral commissure; cg = cerebral ganglia; cn = ctenidial nerve; cpc = cerebropedal connective nerve; es = esophagus; ppn = posterior pedal nerves; vcc = visceral commissure. Other abbreviations as in Figures 3 and 6. Scale bar = 3 mm.

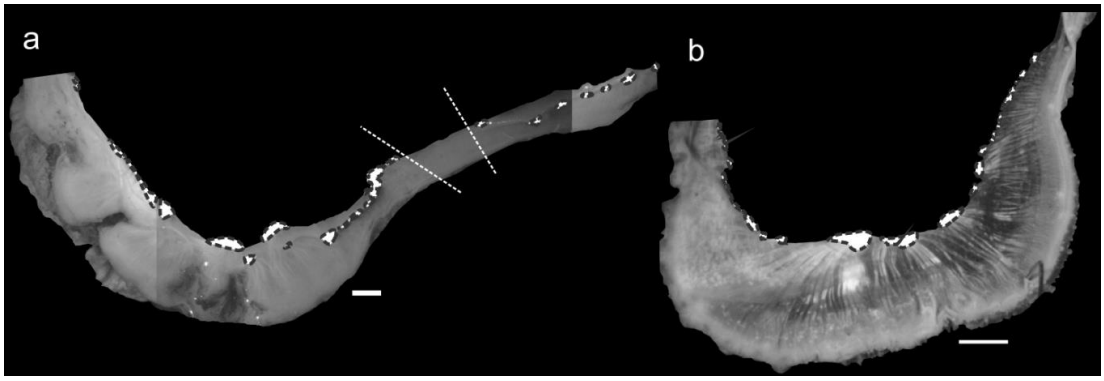

Figure 12. Origin areas of pallial muscles along distal zone in Venezuelan specimens (a) and Brazilian specimen (b). White areas are the origin area of pallial muscles. Dashed lines delimits a region without origin areas in Venezuelan specimens. Scale bar = 2 mm.

DISCUSSION

Being an important commercial taxon, *Pinctada* is a genus with a long history of studies on reproduction, growth and regional viability that can be traced to the earliest reports on pearl oyster farming from the Gulf of Manaar (THURSTON, 1890; HERDMAN, 1903; 1904). There are several references to organs and internal structures, including the mantle, muscles, circulatory, reproductive (e.g. RANSON, 1961; GERVIS and SIMS, 1992; FOUGEROUSE-TSING and HERBAUT, 1994; WADA and TËMKIN, 2008) pericardial and digestive systems. However, as mentioned by WADA and TËMKIN (2008), these data are scattered, hindering comparisons and the consequent visualization of species-level morphological variations.

The muscular arrangement, gill, palps, as well as internal structures such as the renopericardial, circulatory and digestive systems of South American *P. imbricata* are similar to other *Pinctada* (*fucata/martensii/radiata/imbricata*) species. However, the asymmetry of the pedal nervous system is a noteworthy feature that has not been reported to the genus so far (Figure 11). DUVERNOY (1853) remarked on the asymmetry in the positioning of the peripheral nerves (i.e.: mantle nerves) in *Anomia.* However the ganglia arrangement in *Anomia* is symmetrical with respect to the midline. The pedal ganglia in *P. margaritifera* are described as a "single mass" at the base of the foot (FOUGEROUSE *et al*., 2008) and in *P. fucata* from India as "single ganglion" at the base of the foot (VELAYUDHAN and GANDHI, 1987). In *P. imbricata* from the South American coast, each pedal ganglia, although medially fused, can be recognized as an individualized structure. The asymmetry in such structures is well known among Pteriidae, as is the case in the abdominal sense organ position (HASZPRUNAR, 1983; TËMKIN, 2006), stomach position lying on the left visceral wall, intestine and ventricle turned to the left (PELSENEER, 1911), different sizes of anterior pedo-byssal retractor muscle (HERDMAN, 1904; pointed as a synapomorphy of genus *Pinctada* by TËMKIN, 2006), and the well known different width of valves. The right position of the pedal ganglia, much like other organs, may be a consequence of differential development in epibyssate pleurothetic bivalves (YONGE, 1962).

Morphological variation is well reported among several bivalve clades (e.g. STANLEY, 1970; THOMAS, 1976). These variations (i.e. ecophenotypes) may be influenced by substrate type, energy flow regime or other local environment variables (e.g. HORNBACH *et al*., 1980; FASSATOUI *et al*., 2014). The intraspecific variation of soft part anatomy is less known but not less important (YONGE, 1979). *Pinctada imbricata* described here shows a range of variations in outline and external shell structures. This pattern is common to other Indo-Pacific species (HERDMAN, 1904; HYND, 1955; 1960) and the close *P. radiata* (LODOLA *et al*., 2013; RAJAEI *et al*., 2014; DEIDUN *et al*., 2014). This variation was expected among Pteriomorphia, pointed out as one of the most plastic Bivalvia groups regarding shell features (UBUKATA,

2003). Although the shell outline may obliterate diagnostic taxonomic characters, the internal nacreous layer outline presents a consistent morphology. *Pinctada margaritifera* presents a variable morphology among periostracal structures, but the nacre and fibrous layers have a common outline pattern (DAUPHIN *et al*., 2008). Thus, analyzing the internal nacreous layer outline is recommendable. The posterior wing ("ear" or "auricle") show a significant variation in all sampled locations. This structure is commonly associated with shell stabilization in pleurothetic species (STANLEY, 1970), presenting a correlation with the substrate.

Geographical variation of *Pinctada* species has been reported to *P. albina* based on color and shell size (HYND, 1960). The author recognized each variation group as a separate subspecies. Recently RAJAEI *et al*. (2014) recognized regional variations on *P. radiata* in different sites of the Persian Gulf, mainly based on the dorso-ventral elongation of the shell. However, no study has shown variations based on internal gross morphology. The intraspecific geographic variations in *P. imbricata* are related to pallial muscles and the anterior mantle margin lamellae. The pallial muscle bundles in bivalves are commonly attached to a uniform area corresponding to the pallial line scar on the internal surface of the valve (OWEN, 1958). However, some Pteriomorpha species show a convergence of attachment areas of pallial muscle on specific sites (KÜHNELT, 1938; YONGE, 1968; TËMKIN, 2006), which can be distinguished as small muscle scars on the internal surface of the valve. *Pinctada imbricata* from the Brazilian coast presents a group of pallial muscle attachment areas equally distributed along the distal area of the mantle (Figure 12a). The Venezuelan specimens present an area along the antero-median region of distal portion lacking pallial attachment scars. Thus, the median-posterior bundles are attached below the posterior adductor muscle, while the anterior bundles are attached to the anterior region of the mantle edge (at the same level of the retractor pedo-byssal muscle). The extension of the outer lamellae of the mantle is first described here, as well as the perpendicular groove ranging from the region between the outer and median lamellae to the outer lamellae tip. In the Venezuelan specimens this groove area is formed by a fold of the outer lamellae, whereas in Brazilian specimens the groove presents as channel-like aspect without folds (Figure 6). There is no obvious role to this structure. The extensions of the inner lamellae are frilled in Venezuelan specimens, which may indicate movement in vivo.

CONCLUSION

Here we describe for the first time the existence of two geographical variations of *P. imbricata* in South America. Both groups may actually represent two populations isolated by a geographic barrier (e.g. the Amazon River mouth), thus representing two possible cryptic species. On the other hand, these variations may indicate ecophenotypes, which could be associated with different environments. However, due to taxonomic problems concerning the *Pinctada* group and the regional limitations (not all Caribbean specimens were sampled), this question remains open. An increase of data associated with phylogeography techniques may further elucidate these taxonomic issues.

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