

Some remarks on the gross anatomy of *Adelomelon ferussacii* (Donovan, 1824) (Gastropoda: Volutidae) from the coast of Patagonia, Argentina

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ABSTRACT

Specimens of the volutid *Adelomelon ferussacii* (Donovan, 1824) were dissected. These were collected during an extraordinary low tide on February, 2006, at Playa La Mina, Puerto San Julián, Santa Cruz Province, Argentina (49°09' S, 67°37' W). The gross anatomy, along with radulae and shell ultrastructure, are described for the first time. Analysis of these features suggests a close relationship with the other species of the genus *Adelomelon* Dall, 1906, and raises doubts about the validity of *Pachycymbiola* Ihering, 1907, a genus in which it has been included by recent authors.

Additional Keywords: Southwestern Atlantic, Mollusca, Patagonia

INTRODUCTION

The family Volutidae includes the most conspicuous species among all endemic mollusks of the Southwestern Atlantic. This is so not only because of their large size, but also because of their interesting reproductive biology (Penchaszadeh, 1976, 1999; Luzzatto, 2006). Volutes live in quite diverse environments (i.e., subtidal to deep water; soft, muddy, sandy, or mixed bottoms; cold, temperate, or warm waters). Several species are extremely rare, while others are quite common. At least two species, particularly in Uruguay, are the subject of extensive commercial fisheries. These are *Zidona dufresnei* (Donovan, 1823) and *Adelomelon brasiliiana* (Lamarck, 1811). Other species are likely to be exploited in the near future (Giménez and Penchaszadeh, 2002). In addition, volutids usually are top predators with great ecological importance in the marine realm. Species of volutes studied thus far generally have been found to be predators on other mollusks and/or scavengers.

About 30 names have been applied to Volutidae from the western Atlantic, from Venezuela to Argentina. Of these, 16 are living in Argentine waters. Most are poorly known, with data derived only from their original description, which generally included very little biological information. In addition, the taxonomic status of several names awaits clarification.

Adelomelon ferussacii (Donovan, 1824), a locally common volute similar to *A. brasiliiana*, is known only from its shell. Recent findings of egg capsules suggest a completely different reproductive biology (Penchaszadeh and Segade, submitted).

In this paper we provide new anatomical and ultrastructural data for *Adelomelon ferussacii* derived from a large ontogenetic series of live specimens, and compare them with other species of the same genus.

MATERIALS AND METHODS

Specimens used in this study were hand-collected during an extraordinary low tide on February 2006 at Playa La Mina, Puerto San Julián, Santa Cruz Province (49°09' S, 67°37' W) (Figure 1). The surface water temperature was 15°C. Animals were relaxed in freezing sea water, preserved in ethanol 70% and dissected under a stereoscopic microscope. Radulae were prepared according to the method described by Solem (1972). Photographs were taken using digital cameras and images were also digitally processed. Shell ultrastructure data were procured from freshly fractured colabral sections taken from the central portion of the lip on the last whorl of several individuals. MACN: Museo Argentino de Ciencias Naturales.

SYSTEMATICS

Family Volutidae Rafinesque, 1815

Subfamily Zidoninae H. Adams and A. Adams, 1853

Genus *Adelomelon* Dall, 1906

Adelomelon ferussacii (Donovan, 1824)

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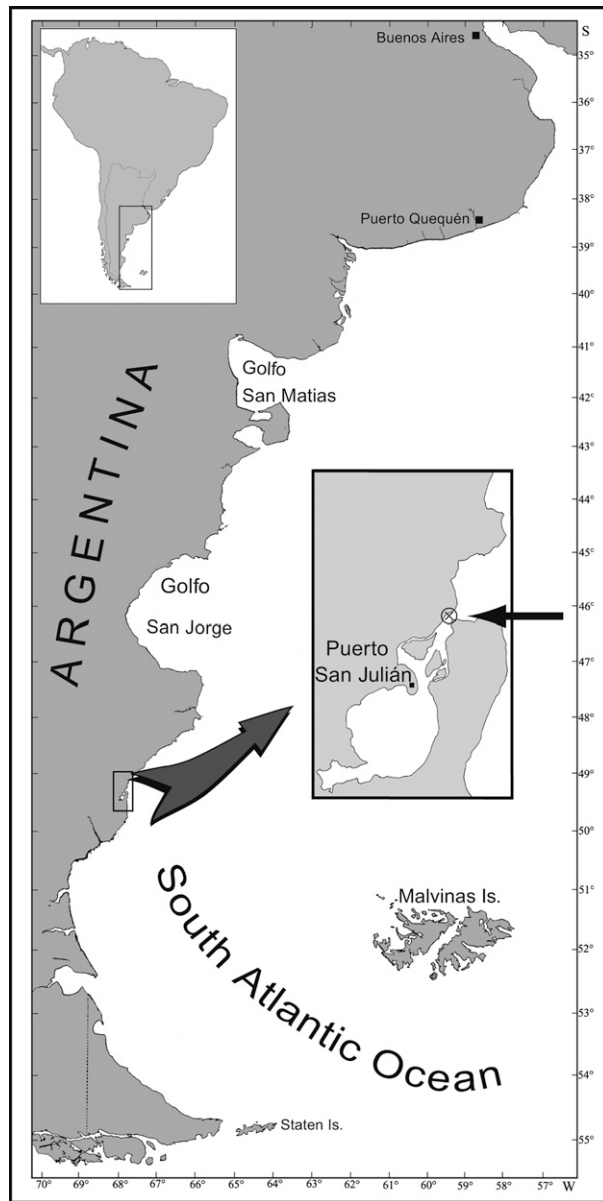


Figure 1. Map showing the study area of Playa La Mina, Santa Cruz, Argentina.

- Voluta ferussacii* Donovan, 1824, 2, pl. 67; Sowerby, 1846 1: 203, pl. 46, fig. 7; Reeve, 1849 6, pl. 10, fig. 23, spec. 39; Dall, 1907: 362.
- Voluta rudis* Gray in Griffith and Pidgeon, 1834: 601, pl. 30, fig. 1.
- Voluta oviformis* Lahille, 1895: 20, pl. 1, figs. 1–2, pl. 2, figs. 53–56, pl. 7, figs. 121–138, pl. 10, figs. 4–9.
- Voluta oviformis typica* Lahille, 1895: 20.
- Voluta oviformis longiuscula* Lahille, 1895: 20.
- Voluta oviformis fratercula* Lahille, 1895: 20.
- Voluta (Cymbiola) ferussacii* Donovan.—Strebel, 1906: 100, pl. 9, figs. 46, 46a, 48–49.

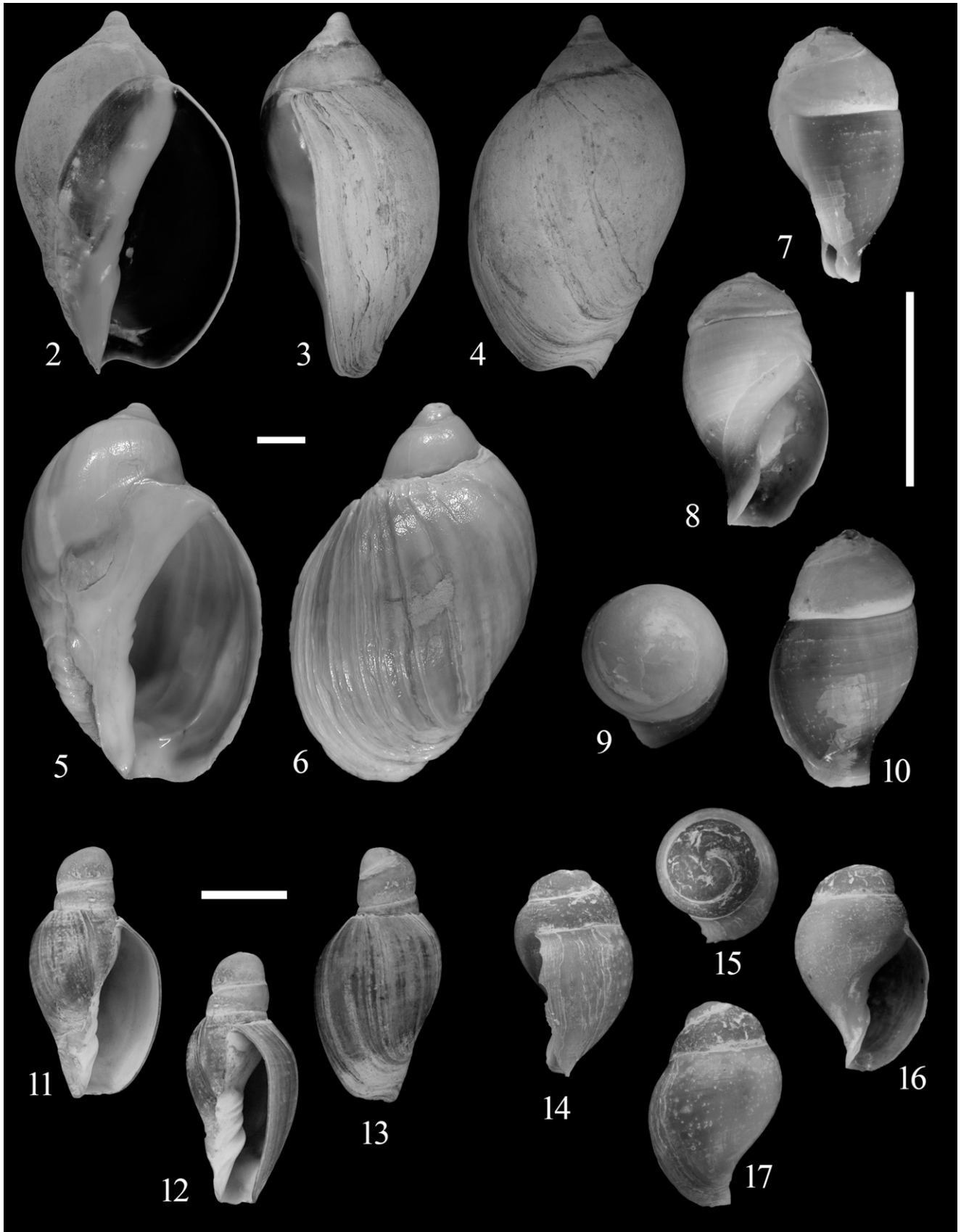
- Adelomelon* (?) *ferussacii* Donovan.—Clench and Turner, 1964: 157, Pl. 98, figs. 1–3.
- Adelomedon* (sic) *ferussacii* (Donovan).—Castellanos, 1970: 110, pl. 8, fig. 7.
- Adelomedon* (sic) *ferrussacii* [sic].—Castellanos, 1970b: 1, figs. 6, 9.
- Adelomelon (Pachycymbiola) ferussacii* (Donovan, 1824).—Weaver and DuPont, 1970: 108, pl. 45C, 45D.
- Adelomelon ferussacii* (Donovan, 1824).—Castellanos and Landoni, 1992: 12, Pl. 1, fig. 8.
- Pachycymbiola ferussacii* (Donovan, 1824).—Pope and Goto, 1992: 116, pl. 38, figs. 3–5.

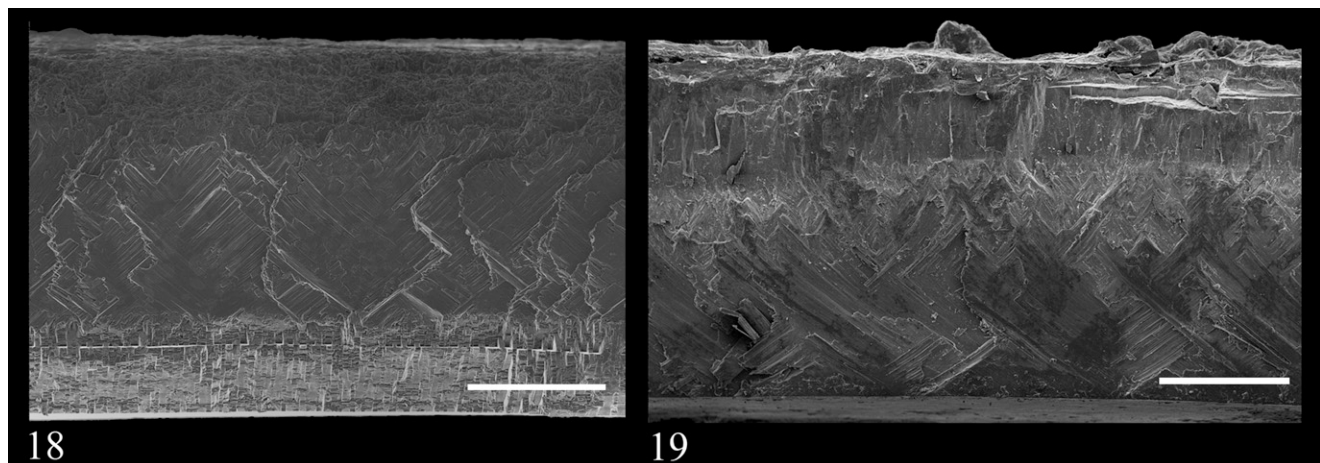
Description: Shell medium in size, up to 122 mm, solid, fusiform; color grayish-brown. Aperture semi-circular, dark-brown within. Protoconch of $1\frac{1}{2}$ smooth whorls; teleoconch of up to 4 slightly convex whorls; spire low, sometimes somewhat upturned; spire angle of 80° , suture well defined. Columella curved, orange, with three to six folds set obliquely to siphonal fasciole, regularly distributed except for the anteriormost one, which is separate from the others. Columellar callus usually weak, but sometimes thick. Siphonal canal fairly broad and shallow. Growth lines span the surface, sometimes producing irregular costae. Shell ultrastructure showing three layers: a crossed-lamellar aragonite layer in which the crystal planes are arranged perpendicularly to the growing edge of the shell, and also perpendicular to the middle layer (25% shell thickness); a middle layer (50% shell thickness) of colabrally aligned crossed-lamellar aragonite, and an outer layer (25% shell thickness) of amorphous calcite (Figure 18). The innermost layer varies in thickness according to the sector of the lip: along the most curved sector it appears thicker, while it is reduced or absent towards the ends of the lip. This arrangement is quite similar to that found in shells of *A. brasiliiana* (Figure 19) and *A. beckii* (Broderip, 1836).

Embryonic shells very thin (at hatching stage), whitish in the first whorls and dark brown in the last protoconch whorl. Surface covered by 8–10 regularly spaced spiral threads in the last whorl, no plaits visible. Calcarella reduced, weakly pronounced.

Foot, head, and siphon are finely mottled purple in color. The contact surface of the foot is whitish. Foot and shell length are similar. Operculum absent. Head broad and flattened, with two short tubular tentacles that separate the lateral lappets from the central one. Eyes are very small and located near the base of the tentacles. The penis emerges directly behind the right cephalic lappet (Figure 21). The siphon, also well pigmented, is muscular with paired and symmetrical siphonal appendages emerging from the base of the siphon and spanning half its length.

The bipectinate osphradium has approximately 100 equal leaflets. The ctenidium is $1\frac{1}{2}$ times as long as the osphradium. The hypobranchial gland is thin. The proboscis shows the same color pattern as the foot, head and siphon. Mouth opening is triangular.





Figures 18–19. Shell ultrastructure. **18.** *Adelomelon ferussacii* (Donovan, 1824). **19.** *Adelomelon brasiliana* (Lamarck, 1811). Scale bars = 500 μm .

Radular ribbon narrow, up to 17.4 mm in length ($n = 13$; $x = 11.7$; $DS = 1.97$), with 49–74 rows (proportional to shell length) with one tricuspid central tooth per row (Figure 22). The radulae increase the number of teeth with age (Figure 32). Central tooth thin and long, anterior profile concave with a ventral-posterior thickening (Figures 23 and 24). Lateral cusps of the rachidian tooth are similar in size to the central one. Each cusp with a dorsal shallow indentation or groove present, where the corresponding previous cusp imbricates (Figures 24–25). Embryonic radulae showing about 15 rows of teeth where lateral cusps are shorter than central cusps (Figure 26; Table 1).

Salivary glands (racemose glands) large and irregularly shaped. Accessory salivary glands (tubular glands) very long and extremely convoluted, distally expanded, overlying dorsal surface of salivary glands. The tubular glands can easily be separated from the racemose glands. Ducts of the accessory salivary glands descend laterally to oesophagus and are sub terminal with respect to the mouth. They never fused and end separately. Ducts of salivary glands become embedded in the

oesophagus anterior to small valve of Leiblein. The anterior oesophagus runs behind the proboscis, and passes through the nerve-ring where an externally inconspicuous valve of Leiblein is located. The gland of Leiblein is very long and extremely convoluted (Figure 20). The posterior oesophagus continues to the stomach.

Material Examined: (D = specimen was dead when sampled; A = alive) Punta Cavendish, Puerto Deseado, Santa Cruz province, 2 D, collected in 5 m depth (MACN-In 31354); Patagonian coast, 1 D (MACN-In 11385); Playa Cabo San Pablo, Tierra del Fuego, 4 D (MACN-In 12532); Punta Sinaia, Tierra del Fuego, Expedición Facultad, 5 D (MACN-In 12531); Ushuaia, Tierra del Fuego, 1 D (MACN-In 9441); Punta María, Río Grande, Tierra del Fuego, 9 D (MACN-In 35113); Bahía San Sebastián, Tierra del Fuego, 1 D (MACN-In 35393); San Sebastián south, Tierra del Fuego, 4 D, Exp. Facultad de Ciencias (MACN-In 12530); Playa del Río Grande, Santa Cruz province, 1 D, (MACN-In 6647); 52°20' S, 68°18' W, Station 28, Cabo Vírgenes.

Table 1. Dimensions (mm) of some adults of *Adelomelon ferussacii* from MACN collection.

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13
Sex	♂	♂	♀	♂	♀	♂	♂	♀	♀	♀	♀	♀	♀
Shell length (mm) (SL)	76.5	75	58	91	78	85	75	72	76	74.5	76	114	75
Aperture length (AL)	60	57	46	69	60	64	59	56	58	58	56	89	56.5
AL/SL	0.78	0.76	0.79	0.76	0.77	0.75	0.79	0.78	0.76	0.78	0.74	0.78	0.75
Spire angle (°)	80	78	77	83	82	84	89	80	83	78	81	85	82
Radula length (RL)	10.8	11.3	9.5	12.2	12.1	13.1	11.4	10.4	9.6	11.8	12.1	17.4	11.7
Number of radular teeth	56	50	49	53	61	58	56	52	50	60	58	74	57

Figures 2–17. Shells of *A. ferussacii* and *A. brasiliana*. **2–13.** *Adelomelon ferussacii* (Donovan, 1824). **2–4.** MACN-In 37013, Puerto San Julián, Santa Cruz. **5–6.** Holotype of *Voluta rudis* Griffith and Pidgeon, 1834, NHM 19920177. **7–10.** Embryo shells (at hatching stage) MACN-In 37014, Puerto San Julián, Santa Cruz. **11–13.** Juvenile shells MACN-In 37012, 3 km North of Puerto San Sebastián, Tierra del Fuego. **14–17.** *Adelomelon brasiliana* (Lamarck, 1811), embryo shells MACN-In 37015, off Mar del Plata, Buenos Aires. Scale bars = 10 mm.

Santa Cruz province, A.R.A. Bahía Blanca, 1 D, in 11 m (MACN-In 24080); Bahía Laura, Puerto Deseado, Santa Cruz province, 1 D (MACN-In 9199-16); Bahía San Sebastián, Tierra del Fuego, 1 D (MACN-In 21154); Estancia "Viamonte", Río Grande, Tierra del Fuego, 2 D (MACN-In 27219); Isla Quiroga, Puerto Deseado, Santa Cruz province, 1 D (MACN-In 26199); Punta Arenas, Chile, 1 D (MACN-In 9040-27); Río Grande, Tierra del Fuego, 24 D (MACN-In 12529); Playa La Mina, Puerto San Julián, Santa Cruz Province (67° 37' W, 49° 09' S), 10 A in low tide (MACN-In 37487).

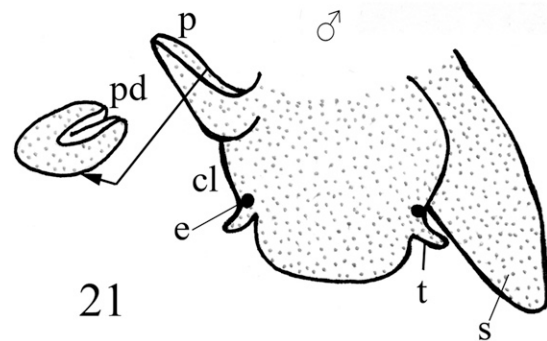
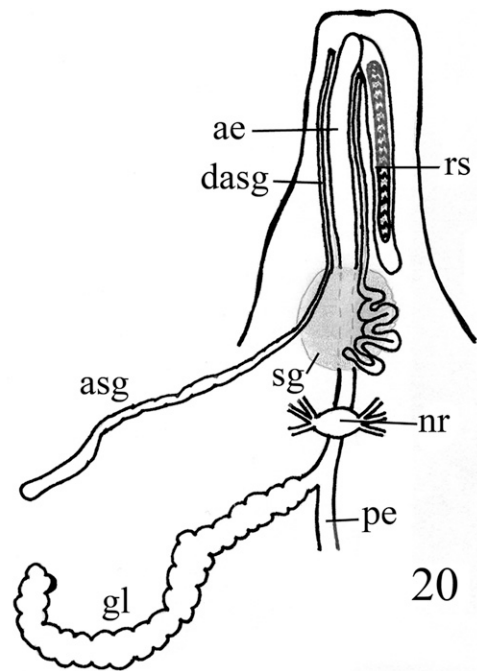
Distribution: *Adelomelon ferussacii* is a typical component of the Magellanic province, ranging from the province of Santa Cruz to Southern Chile. More northern citations of the species (e.g., Clench and Turner, 1964; Castellanos and Landoni, 1992), are here referred to *A. brasiliiana*. No specimens of *A. ferussacii* from revised collections (MLP and MACN) were found outside of this range.

Distribution According to Previous Records in the Literature: Puerto Gallegos, Punta Arenas, (Strebler, 1906); Santa Cruz coast, (Lahille, 1895); Southern Patagonia and Magellanic region (Carcelles and Williamson, 1951); Golfo San Matías to Straits of Magellan (Clench and Turner, 1964), however they only examined specimens from the localities of Puerto Deseado, Cabo Buen Tiempo, Río Gallegos, Bahía de la Posesión and San Gregorio in Chile; Golfo San Matías to Magellan Straits (Weaver and DuPont, 1970); Santa Cruz (Castellanos, 1970b); Southern coast of Buenos Aires province to Magellan Straits (Castellanos and Landoni, 1992); Southeastern coast of Argentina, south to the Magellan Straits (Poppe and Goto, 1992).

DISCUSSION

Clench and Turner (1964) suggested the inclusion of *Voluta ferussacii* in the genus *Adelomelon* Dall, 1906, because of shell similarity with *A. brasiliiana*. However, at that time they examined no complete specimens to confirm such generic placement. Weaver and Du Pont (1970) mentioned that no live specimens were collected. Later, Castellanos (1970) illustrated the radula confirming the generic placement suggested by Clench and Turner (1964). However, data on the gross anatomy had not previously been reported.

The last comprehensive taxonomic revision of the family Volutidae from the southwestern Atlantic was prepared by Clench and Turner (1964, 1970). They described the new subfamily Odontocymbiolinae and the new genus *Odontocymbiola*, and finally resolved the confusion of previous authors (e.g., Pilsbry and Olsson, 1954) between *Adelomelon ancilla* (Lightfoot, 1786) and *Odontocymbiola magellanica* (Gmelin, 1791). These authors also described two new species: *O. pescalia* and *A. riosi* (Clench and Turner, 1964). The latter was included in the new subgenus *Weaveria*. After their work,

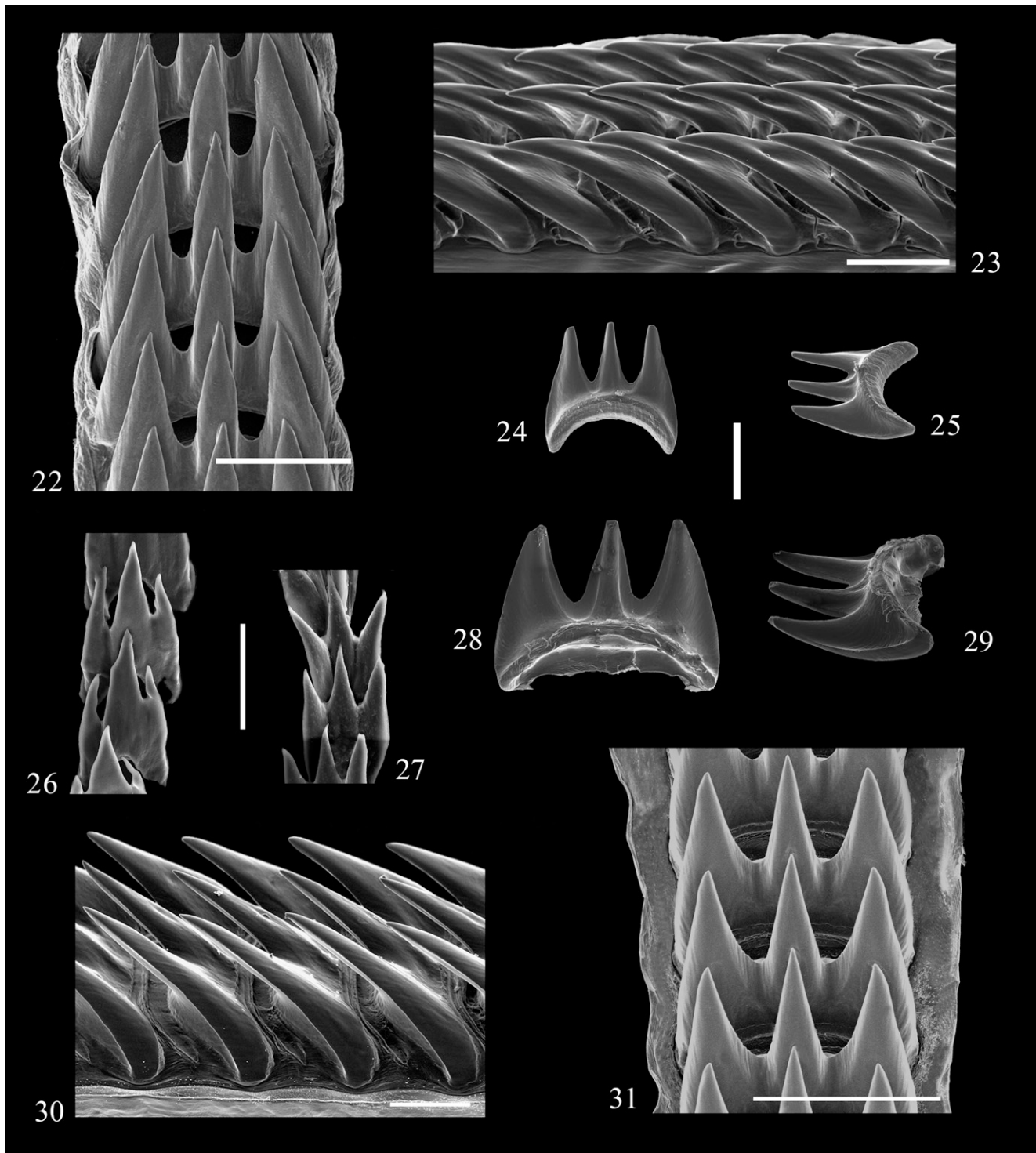


Figures 20–21. *Adelomelon ferussacii* (Donovan, 1824). **20.** Anterior alimentary system. **21.** Dorsal view of head, siphon, and penis of a male specimen. **ae**, anterior esophagus; **asg**, accessory salivary gland; **cl**, cephalic lappet; **dasg**, duct accessory salivary gland; **e**, eye; **gl**, gland of Leiblein; **nr**, nerve ring; **p**, penis; **pd**, penial duct; **pe**, posterior esophagus; **rs**, radular sac; **s**, siphon; **sg**, salivary gland; **t**, tentacle.

several additional new species were described, in particular from Brazil (e.g., Leal and Bouchet, 1989; Leal and Rios, 1990).

Most of the literature dealing with southwestern Atlantic volutids is primarily taxonomic. Anatomical data are scarce and usually drawn from one or relatively few specimens, sometimes incomplete. Exceptions are the papers by Novelli and Novelli (1982) and Ayçaguer (2002), particularly the latter, in which the authors described in some detail the anatomy of *Zidona dufresnei*.

Clench and Turner (1964) and Ayçaguer (2002) mentioned that *Adelomelon beckii*, *A. ancilla*, *A. brasiliiana*, and *Zidona dufresnei* all have characteristic racemose salivary glands loosely intertwined in the tubular



Figures 22–31. Radulae of *Adelomelon* species. **22–26.** *Adelomelon ferussacii* (Donovan, 1824). **22.** Frontal view. Scale bar = 250 μm . **23.** Lateral view. Scale bar = 200 μm . **24–25.** Rachidian teeth. Scale bar = 200 μm . **26.** Radula of an embryo. Scale bar = 50 μm . **27–31.** *Adelomelon brasiliiana* (Lamarck, 1811). **27.** Radula of an embryo. Scale bar = 50 μm . **28–29.** Rachidian teeth. Scale bar = 200 μm . **30.** Lateral view. Scale bar = 200 μm . **31.** Frontal view. Scale bar = 250 μm .

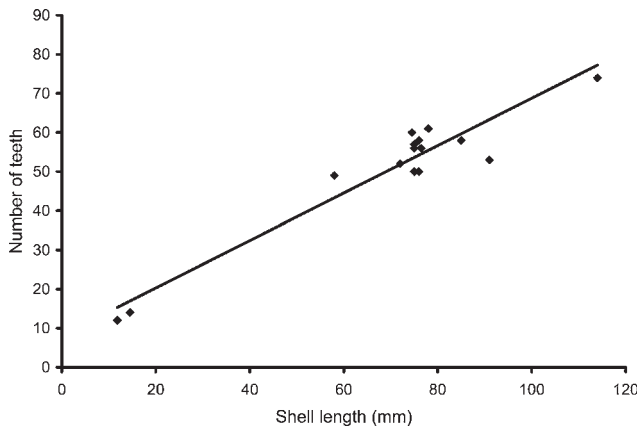


Figure 32. Relationship between radular and shell length ($R = 0.9178$).

accessory glands. The radula in these species is also rachiglossate with a unique central tricuspoid tooth. These characters, together with several shell similarities placed *A. ferussacii* in the Zidoninae subfamily.

Radulae of the species *A. ferussacii* and *A. brasiliiana* are quite similar (Figures 22 and 31). However, *A. brasiliiana* has a wider and more convex base of the rachidian teeth than *A. ferussacii* (Figures 24 and 28). Lateral cusps of the rachidian teeth are shorter and wider in *A. brasiliiana* than in *A. ferussacii*. These differences are probably specific characters and are also present in the embryos of both species (Figures 26 and 27).

The name *Pachycymbiola* was proposed by Ihering (1907: 209) as a subgenus of *Adelomelon* for *A. brasiliiana*, which is actually the type species. Pilsbry and Olsson (1954) and later Scarabino et al. (2004) promoted *Pachycymbiola* to generic rank, and mentioned as main characters an ovate shell with a short spire, a free oval egg capsule, and a protoconch without calcarella. Del Río and Martínez (2006) also treated *Pachycymbiola* at the generic rank following the latter authors. They described five Tertiary species, three new, under this genus, pointing out as main differences from *Adelomelon* the ovate shape of the shell, the short spire and the protoconch without calcarella, in agreement with Scarabino et al. (2004). *Adelomelon brasiliiana* has all these features and a large free ovoid ovicapsule, with 9 to 33 embryos per capsule (Penchaszadeh and de Mahieu, 1976; Luzzatto, 2006). On the other hand, *A. beckii* and *A. ancilla*, which belong in the subgenus *Adelomelon*, have smaller egg capsules, always attached to hard substrates (Penchaszadeh et al., 1999). *Adelomelon ferussacii* presents egg capsules similar to those of *A. beckii*, which are globose hemispherical and flexible, with a white opaque color and a leathery texture, attached to a hard substrate such as stones or rocky substrates (Penchaszadeh and Segade, in preparation).

The inclusion of *A. ferussacii* in the subgenus *Pachycymbiola* was first suggested based on some external similarity to *A. brasiliiana*. However, the egg capsules do

not match those of *A. ferussacii*. In fact they look more similar to those of other species of *Adelomelon*. Also, the gross anatomy revised here does not show conclusive features to include *A. ferussacii* in a different group as suggested previously. The only character that could stand as a difference are those of shell morphology. Pilsbry and Olsson (1954), Scarabino et al. (2004) and Del Río and Martínez (2006) concede that shell shape place *A. ferussacii* close to *Pachycymbiola*. They do not mention that a calcarella is reduced, present in the young of *A. ferussacii* (Figures 7–13), but absent in those of *A. brasiliiana*. At a closer look even the shell shape is substantially different, since *A. brasiliiana* has a more flattened spire and pronounced shoulder tubercles more similar to *A. beckii* than *A. ferussacii*. Further detailed anatomical studies will confirm the relationships of these Southwestern Atlantic endemic volutids.

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LITERATURE CITED

- Ayçaguer, C. 2002. Anatomía de Volutas del Atlántico sudoccidental, I: Anatomía general y del sistema reproductor de *Zidona dufresnei* (Donovan, 1823) (Neogastropoda: Volutidae). Comunicaciones de la Sociedad Malacológica del Uruguay 8(76–77): 159–180.
- Carcelles, A. and S. Williamson. 1951. Catálogo de los moluscos marinos de la provincia magallánica. Revista del Instituto Nacional de Investigación de las Ciencias Naturales 2, Ciencias Zoológicas: 225–383.
- Castellanos, Z. J. A. de. 1970. Reubicación de algunas especies de Volutidae del Mar Argentino. Neotropica 16: 1–4.
- Castellanos, Z. J. A. de and N. Landoni. 1992. Catálogo descriptivo de la malacofauna marina magallánica 10. Neogastropoda, Volutidae, Volutomitridae, Cancellariidae, Olividae y Marginellidae. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, La Plata, 37 pp.
- Clench, W. J. and R. D. Turner. 1964. The subfamilies Volutinae, Zidoninae, Odontocymbiolinae and Calliotectinae in the Western Atlantic. *Johnsonia*, 4(43): 129–180.
- Clench, W. J. and R. D. Turner. 1970. The family Volutidae in the Western Atlantic. *Johnsonia* 4: 369–372.
- Dall, W. H. 1907. A review of the American Volutidae. Smithsonian Miscellaneous Collections 48(3): 341–373.
- del Río, C. J. and S. A. Martínez. 2006. The family Volutidae (Mollusca-Gastropoda) in the Tertiary of Patagonia (Argentina). *Journal of Paleontology* 80: 919–945.
- Donovan, E. 1824. The naturalist's repository or miscellany of exotic natural history, exhibiting specimens of

- foreign birds, insects, shells. Sheet EE, FF, pp. 214–216, Plate 67.
- Giménez, J. and P. E. Penchaszadeh. 2002. Reproductive cycle of *Zidona dufresnei* (Caenogastropoda: Volutidae) from the southwestern Atlantic Ocean. *Marine Biology* 140: 755–761.
- Griffith, E. and E. Pidgeon. 1834. The animal kingdom arranged in conformity with its organization by the baron Cuvier. The Mollusca and Radiata. London, Whittaker & Co., 601 pp.
- Ihering, H. von. 1907. Les Mollusques fossiles du Tertiaire et du Cretace superieur de l'Argentine. *Anales del Museo Nacional de Buenos Aires* (3)7: 1–611.
- Lahille, F. 1895. Contribución al estudio de las volutas argentinas I. Morfología externa. *Revista del Museo de La Plata* 6: 293–333.
- Leal, J. H. and P. Bouchet. 1989. New deep-water Volutidae from off southeastern Brazil (Mollusca: Gastropoda). *The Nautilus* 103: 1–12.
- Leal, J. H. and E. de C. Rios. 1990. *Nanomelon cossi*, a new deep-water Zidoninae from off southern Brazil (Gastropoda: Volutidae). *The Veliger* 33: 317–320.
- Luzzatto, D. C. 2006. The biology and ecology of the giant free egg capsules of *Adelomelon brasiliiana* Lamarck, 1811 (Gastropoda: Volutidae). *Malacologia* 49: 107–119.
- Novelli, R. and A. U. G. Novelli. 1982. Algumas considerações sobre a subfamília Zidoninae e notas sobre a anatomia de *Adelomelon brasiliiana* (Lamarck, 1811), Mollusca, Gastropoda, Volutidae. *Atlântica* 5: 23–34.
- Penchaszadeh, P. and G. C. De Mahieu. 1976. Reproducción de gasterópodos Prosobranquios del Atlántico suroccidental. Volutidae. *Physis A*, 35(91): 145–153.
- Penchaszadeh, P. E., P. Miloslavich, M. Lasta, and P. M. S. Costa. 1999. Egg capsules in the genus *Adelomelon* (Caenogastropoda: Volutidae) from the Atlantic coast of South America. *The Nautilus*, 113(2): 56–63.
- Pilsbry, H. A. and A. A. Olsson. 1954. Systems of the Volutidae. *Bulletins of American Paleontology*, 35(152): 5–36.
- Poppe, G. T. and Y. Goto. 1992. Volutes. *Mostra Mondiale Malacologia Cupra Marittima (AP-Italy)*. L'Informatore Piceno Ed., Ancona, 348 pp.
- Reeve, L. 1849. *Conchologia Iconica: or, illustrations of the shells of moluscous animals*. London.
- Scarabino, F., S. Martinez, C. J. del Río, A. E. Oleinik, H. H. Camacho, and W. J. Zinsmeister. 2004. Two new species of *Adelomelon* Dall, 1906 (Gastropoda: Volutidae) from the Tertiary of Patagonia (Argentina). *Journal of Paleontology* 78: 914–919.
- Sowerby, G. B. II. 1846. Descriptions of Tertiary fossil shells from South America. In: Darwin, C. *Geological Observations on South America*. Smith Elder Co., London, 249–267.
- Solem, A. 1972. Malacological application of Scanning Electron Microscopy, II. Radular structure and functioning. *The Veliger*, 14: 327–336.
- Strebel, H. 1906. Beiträge zur Kenntnis der Molluskenfauna der Magalhaen-Provinz. 4. *Zoologischen Jahrbuchern. Abteilung für Systematik, Geographie und Biologie der Tiere*, 24: 91–174.
- Weaver, C. S. and J. E. Dupont. 1970. Living volutes. A monograph of the Recent Volutidae of the world. Delaware museum of Natural History. Monograph Series No. 1, Delaware, xv + 375 pp.