

Secrets of a giant: anatomy and behavior of *Laternula elliptica*, a keystone species of the Antarctic benthos (Bivalvia: Anomalodesmata: Laternulidae) (#74171)

1

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I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

Secrets of a giant: anatomy and behavior of *Laternula elliptica*, a keystone species of the Antarctic benthos (Bivalvia: Anomalodesmata: Laternulidae)

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Laternula elliptica (P. P. King, 1832) is the sole representative of the anomalodesmatan family Laternulidae and the largest bivalve in the Arctic and Subantarctic. A keystone species of the regional benthic communities, it has reached model status by having been studied in hundreds of scientific works of many biological disciplines. In contrast, its anatomy has remained poorly known, with prior published data limited to partial descriptions based on chemically preserved specimens. Based on observations of aquarium-maintained living animals at the Brazilian Comandante Ferraz Antarctic Station, gross-morphological dissections, and histological sectioning, the comparative anatomy, functional morphology, and aspects of behavior of *L. elliptica* are described and discussed. Special focus is placed on the pallial organs (including elucidation of cleansing and feeding sorting mechanisms in the mantle cavity) and the musculature. Among the noteworthy findings are the presence of well developed siphons furnished with sensory tentacles at its tips, some of which bearing eyes; large, folded gills and labial palps capable of sorting the material entering the mantle cavity; an inter-chamber communication in the posterior region of the mantle cavity; and an ample ventral mantle fusion with an anterior pedal gape. This study reevaluates the available anatomical data in the literature, both supplementing and correcting previously published accounts.

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18 Abstract

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Commented [PRS1]: Certainly noteworthy as not previously detailed but certainly not unique among the laternulids.

labial palps capable of sorting the material entering the mantle cavity; an inter-chamber communication in the posterior region of the mantle cavity; and an ample ventral mantle fusion with an anterior pedal gape. This study reevaluates the available anatomical data in the literature, both supplementing and correcting previously published accounts.

Introduction

Laternula elliptica (P. P. King, 1832), the sole representative of the Laternulidae in Antarctic and subantarctic waters, is ubiquitous along its circumpolar distribution and [is](#) also known from the South Shetland, South Orkney, South Sandwich, South Georgia and Kerguelen Islands (Soot-Ryen, 1951; Dell, 1990). The species, which is known from the region since the Pliocene (Linse et al., 2006), is considered a sister taxon to other extant species of *Laternula* from Australia and the central Indo-West Pacific, with the species-level diversity of temperate and tropical members of the genus in need of investigation (Taylor et al., 2018; MolluscaBase eds., 2022).

The soft-substrate species has been collected from the intertidal to continental slope depth of about 700 m (Waller et al., 2016), but with almost all live-collected records from depths [s](#) shallower than 100 m (Dell, 1990; Engl, 2012). Nicol (1966), Morton (1976), and Narchi et al. (2002) described the shell valves in detail, ~~and it is here~~ (shown in Figure 1). Compared to its lower latitude relatives of the family, *L. elliptica* is larger and thicker-shelled (Watson et al., 2012; Prezant et al., 2015) and lacks the spinules on the shell surface recorded from other species of this group (Checa & Harper, 2010). *L. elliptica* is a simultaneous hermaphrodite, producing large eggs (about 200 µm in diameter), which develop as encapsulated lecithotrophic larvae (e.g., Ansell & Harvey, 1997; Kang et al., 2003).

Smith (1902: 210) already highlighted this species as "the giant of its genus" *Anatina* (then encompassing what is now the family Laternulidae). As the largest (>100 mm shell length) and very abundant bivalve, it dominates benthic communities (Stout & Shabica, 1970; Hardy, 1972; Momo et al., 2002; Urban & Mercuri, 1998; Zamorano et al., 1986), and is considered a keystone species of the Antarctic benthos (Harper et al., 2012). Its wide distribution in the Antarctic realm, high abundance, ease of collection, and ability to survive under experimental conditions have allowed it to reach model status, having been studied in hundreds of scientific articles (Waller et al., 2016) representing a broad spectrum of biological disciplines. Among

these are investigations focusing on metabolism and energy budget (e.g. Aguera et al., 2012; Ahn & Shim, 1998; Momo et al., 2002), biochemistry (Ahn, 2000; Gonzalez & Puntarulo, 2011), heavy metal concentrations and pollution (Ahn et al., 1996; Lister et al., 2015; Wing et al., 2020), shell composition and structure (Barrera et al., 1994; Nehrke et al., 2012; Sato-Okoshi & Okoshi, 2008), reproduction and larval development (Ansell & Harvey, 1997; Bigatti et al., 2001; Kang et al., 2003, 2008; Pearse et al., 1986, 1987; Powell et al., 2001), ageing (Peck et al., 2006; Philipp et al., 2005), ocean acidification and warming (Bylenga et al., 2015, 2017; Cummings et al., 2011), thermal stress and hypoxia (Kim et al., 2009; Morley et al., 2007, 2009a, b, 2012; Park et al., 2008; Peck et al., 2002, 2004; Portner et al., 2006), and iceberg scouring (Harper et al., 2012; Philipp et al., 2011). Numerous molecular studies have been applied to the species, from assembling the complete mitochondrial genome (Park & Ahn, 2015), transcriptomics (Clark et al., 2010), and studying heat shock proteins (Rams0e et al., 2020, Truebano et al., 2013), to treating it as the exemplar for its family in class-wide phylogenetic studies (Bieler et al., 2014a, b; Combosch et al., 2017).

However, none of the many published studies focusing on this otherwise well-known species has ever dealt in-depth with its anatomy. ~~For a long time, a~~Anatomical knowledge has remained limited to the work of Burne (1920), who provided an incomplete description based on a damaged individual specimen. During the Austral summers of 1996-1997 and 1997-1998, Professor Osmar Domaneschi had the opportunity to conduct aquarium-assisted observations of living animals over several weeks during research visits to the Brazilian Comandante Ferraz Antarctic Station, resulting in detailed drawings and associated notes toward a planned manuscript. Unfortunately, the research remained unpublished. The most comprehensive published treatment of *L. elliptica* appeared in the work by Bieler et al. (2014a, b), in which the species was analyzed, as the exemplar species of the family Laternulidae, in the context of a Bivalvia-wide phylogenetic study. Unaware of Domaneschi's field studies of living animals, Bieler et al. based their data on the analysis of preserved material (FMNH BivAToL-202), originally collected at the British Antarctic Survey's Rothera Research Station, Adelaide Island, Antarctic Peninsula. Other morpho-anatomical data were provided by Peck et al. (2004) on the anatomy of the organs concerned in the burrowing and surface movements and by Sartori et al. (2006) on the occurrence of arenophilic glands in both the mantle edge and surrounding the siphonal openings.

Before his untimely death in 2008, Domaneschi had entrusted his students (F.D.P. and A.S.) with his drawings and notes. The current publication utilizes many of the original illustrations and observations from that material. This paper reviews the comparative anatomy, functional morphology, and aspects of behavior of *L. elliptica*, with special focus on the pallial organs and musculature. Based on original information from living specimens, this study reevaluates literature data, both supplementing and correcting previously published accounts.

Material and methods

In the Austral summers of 1996-1997 and 1997-1998, living specimens of *Laternula elliptica* were collected from muddy and muddy-sand substrata at depths of 5 to 20 meters in the Admiralty Bay, King George Island, Antarctica (62°05'S - 58°23'W), both using a Van Veen grab and manually by SCUBA divers. Many living and intact specimens removed from undisturbed bottoms, as well as severely damaged specimens found unburied along new iceberg scours, were kept in aquaria with natural sediment and 330, circulating seawater at 0±1 °C at the Brazilian Comandante Ferraz Antarctic Station (EACF) on King George Island. In 1996-1997, twenty whole specimens with shell length ranging from 1.0 to 4.0 cm (n=10) and 5.0 to 9.6 cm (n=10) were allowed to bury in isolated aquaria, each containing circa 13 cm depth of natural muddy sediment, and their surface movements recorded over a four-week period. The morpho-functional analysis began at that time and continued in 1997-1998, through observations of both living and preserved specimens dissected under a stereomicroscope. Cleansing and feeding sorting mechanisms in the mantle cavity were elucidated using powdered carmine, graded mineral grains, and natural fine organic particles, which were precipitated over their epithelia.

After finding a wide opening between the supra- and infra-branchial chambers in the first dissected specimens, every specimen was checked to confirm the presence/absence of such opening. To ascertain that the opening was not an artifact of dissection, seven living, intact specimens (1.0 through 8.0 cm in shell length) were tested on their ability to quickly transfer water from the exhalant onto the inhalant chamber. These specimens had the exhalant siphon lumen injected with a highly concentrated carmine suspension and were immediately stimulated by forceps both to contract and tightly close the exhalant opening. One living, minute (1.0 mm in shell length) specimen was prepared for SEM analysis using the same methods applied in previous studies of other Antarctic bivalve species (Passos et al., 2005; Passos & Domaneschi,

Commented [PRS2]: Consider using either substrate/es or substratum/a consistently.

Commented [PRS3]: Not sure what this "330" is?

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Commented [PRS4]: Presumably in specimens with one valve removed. Do you know the sizes of specimens examined and how long they were already maintained in the aquaria?

2006; Passos et al., 2007; Passos & Domaneschi, 2009); its shell valves and mantle lobes were excised to observe this passage between the two chambers through a higher magnification.

For routine serial sectioning, a complete 1.7 cm-in-shell-length specimen and excised organs of larger specimens were ~~chemically~~-fixed in Bouin's fluid, embedded in paraffin, and sectioned at 7 μ m. Following the methodology by Passos et al. (2005), portions of the ctenidia were embedded with glycol methacrylate Leica Historesin and sectioned transversely and sagittally at 3 μ m. All histological sections were stained with haematoxylin and counterstained with eosin.

Voucher specimens of this study are deposited in the molluscan collection of the Museum of Zoology, UNICAMP, numbers ZUEC BIV 7570-7633, 8374-8390, and 8397-8399.

Results

Shell

The shell of *L. elliptica* from the Admiralty Bay population (Fig. 1) matches the general characterization given by Nicol (1966), Morton (1976), and Narchi et al. (2002).

Shells in the material examined (n=40) varied from 1.0 to 9.7 cm in length; some specimens exhibit evidence of injury in one or both shell valves, followed by regeneration of the nacreous layers only. The brownish periostracum is usually masked by loosely adhered particles from the surrounding sediment; particles attached to the shell surface by arenophilic threads as described for related species (Sartori et al., 2006) are not present. The valves are connected by an edentulous hinge, where there is a robust internal ligament attached to chondrophores (Fig. 1); a lithodesma was not observed in the material examined but, because hinge structure was not analyzed in every available specimen, it is possible that the presence of a lithodesma in specimens less than 1.5 cm in shell length, as reported by Sartori (2009) in specimens from Hangar Cove, Adelaide Island, might have been overlooked. Knife-like calcareous ridges support the chondrophores, functioning as strengthening buttresses or clavicles, and extend postero-ventrally from each of the valves' umbonal cavities; nearly anterior and parallel to each of these buttresses there is a long, periostracum-filled fissure (= dorsal crack) in the umbonal and disk regions visible from both the internal and external surfaces of the valves. The small, elliptical-elongated anterior and posterior adductor muscles scars are fused to the dorsally placed anterior

Commented [PRS5]: Is this sentence stating that the adherent sediment found were attached to/embedded within the periostracum? Is it possible the arenophilic mantle gland secretions are not forming threads but instead just an adhesive layer? Is there any alignment of location of attached sediments and the arenophilic mantle glands?

and posterior pedal retractors scars, respectively; right and left pedal protractor scars are ventrally fused to the anterior adductor scar. The well-marked, entire pallial line is slightly distanced from the anterior shell margin at the pedal gape; posteriorly it forms the wide, shallow pallial sinus.

Mode of life

Laternula elliptica lives completely buried in a vertical position within muddy and sandy substrata of the sea bottom (Fig. 2); underwater *in situ* photos showed that only few centimeters of the siphonal distal end in larger specimens are extended into the water column. All living specimens observed in aquaria (n=20) were able to rebury, the smallest ones performing such activities much faster. Thus, while nine individuals whose shell length range from 1.0 to 3.4 cm were found totally buried after six hours of being placed in aquaria with muddy sediment, the eleven larger specimens (shell length 4.0 to 9.6 cm) took up to three weeks to accomplish the same task. Only a few individuals in the latter group exhibited "jetting movements" (*sensu* Ansell & Harvey 1997) on the sediment surface (Figs. 2A, B); in contrast to the reported observations of Ansell & Harvey (1997) and Peck et al. (2004), these specimens did not try to burrow at the end of each cycle of movement. Likewise, additional "looping" and "levering" movements as described by these authors were not observed during the short research period of this project.

The siphons play an important role in the burrowing process. Individuals with their shells completely buried and with the reduced foot anchored in the substratum, force the wall of the siphons and the shell valves tightly against the sediment (Fig. 2C). This is accomplished by raising the hydrostatic pressure within both the pallial chamber and siphons through the closure of the pedal and siphonal openings, followed by a slow retraction of the siphons and concomitant relaxation of the orbital (pallial) and adductor muscles. Further vigorous retraction of the still-closed siphons, followed by contraction of the adductors and orbital muscles, and the opening of the pedal aperture force water to be powerfully expelled through the pedal aperture only. Jetting removes sediment from the depths of the burrow as the water exits through a narrow gap between the animal and the surrounding sediment (two asterisks in Fig. 2C). Subsequent contraction of the pedal retractor muscles pulls the cylindrical animal deeper into the hollow excavated below the animal. Disturbed (by using forceps), some of the largest (5 to 9.6 cm in shell length) and two small (± 2.0 cm in shell length) buried individuals kept the siphonal walls

182 so tightly pressed against the surrounding sediment that the water jet drilled a tunnel through the
183 substratum and escaped as a spring loaded with mud particles at a short distance from the bivalve
184 (one asterisk in Fig. 2C). The effect of such a muddy "spring" on the sediment surface can be
185 seen in Figure 2D, a photograph taken while SCUBA diving in the natural habitat.

186 Mantle

187 The mantle lobes are thin, translucent, except at their muscular border where the strong
188 pallial muscles are inserted to and unite both valves.

189 The mantle margins are extensively fused, except for the small, anteroventral pedal gape
190 and the posterior inhalant and exhalant siphonal openings (Figs. 1B, 1E-F, 3). From the mantle
191 isthmus, fusion extends forward up to the dorsal edge of the anterior adductor muscle, and
192 posteriorward up to the base of the exhalant siphon; it involves both the inner and middle mantle
193 folds, as well as the periostracal grooves (type C of Yonge, 1957). Fusion in these regions
194 accounts for the formation of an extensive secondary ligament that unites the shell valves
195 dorsally (Fig. 1D, 1G-H). From the dorsal edge of the anterior adductor muscle downward to the
196 dorsal edge of the pedal opening, mantle fusion involves the inner folds and the inner surfaces of
197 the middle folds only (type B of Yonge, 1957). This same type of fusion occurs along the entire
198 extent of the ventral margin between the pedal opening and the base of the inhalant siphon, and
199 accounts for the presence of a sheet of periostracum lining each side, except along the median
200 longitudinal line of fusion. The pallial muscles along this ventral margin extend from one to the
201 opposite valve and form the orbital muscles as termed by Morton (1976) in *Exolaternula*
202 *spengleri* (Gmelin, 1792) (as *Laternula truncata*). The orbital muscles in *L. elliptica* act as a
203 long, accessory ventral adductor as it was demonstrated experimentally: after having the orbital
204 muscles separated from one or both valves, living specimens (n=2) with the adductors muscles
205 and shell valves intact were unable to bring the ventral border of the valves in close contact.
206 Likewise, specimens collected along ice scours within the Admiralty Bay and with one or both of
207 their valves severely damaged (n=4) could tightly close the pieces of the shell adhering to the
208 orbital muscles, even though these fragments were not under the control of the adductors.

209 Siphons

210 The conjoined siphons of *L. elliptica* are formed by fusion of all three marginal mantle
211 folds including the periostracal groove (type C of Yonge, 1948, 1957, 1982), which accounts for

Commented [PRS6]: Since anatomical studies are few for this taxon, did the authors see any hint of a 4th pallial aperture? In preserved specimens these small opening might be missed.

the thick, corrugated, brownish periostracum that covers the siphonal walls (Fig. 3B). Fully extended siphons reach almost twice the shell length, as observed in a non-buried, 9cm-in-shell-length specimen that extended its siphons up to 14 cm; although their diameter equals that of the animal's body, they are capable of a slow, but complete retraction into the shell.

During siphoning, the tips of the siphons are the only parts kept in the water column. Not infrequently, freshly collected specimens had these parts of the siphons fouled (and thus camouflaged) by living hydrozoans, bryozoans, and filamentous algae attached to the periostracum. Such epizoans-epibionts and other extraneous elements from the surrounding sediment are firmly adhered to the surface of the periostracum by fine threads of a sticky secretion exuded from the apex of rounded papillae. These papillae form a continuous line adjacent to and internal to the periostracal groove surrounding the siphonal apertures (Fig. 4A). Each papilla corresponds to the discharging point of an arenophilic mantle gland, as shown by Sartori et al. (2006), who studied these glands in specimens of *L. elliptica* collected in the same field study.

The distal tips of both inhalant and exhalant siphons bear a crown of numerous digitiform tentacles; 4 to 9 tentacles on the inhalant, and 5 to 7 on the exhalant siphon, bear a complex eye at their distal end (optic tentacles) (Fig. 4A). The eyes have structure and complexity similar to those described by Morton (1973) and Adal & Morton (1973) for *Exolaternula spengleri* (as *L. truncata*). Neither regular number nor arrangement of the tentacles could be identified, but as a rule, they enlarge in size centrifugally, the optic tentacles being amongst the largest ones. Scarce tactile tentacles occupying an outer position in the crown bear a distal black spot that looks like an ill-defined eye.

In addition to the crown of tentacles at its periphery, the inhalant aperture has its free border indented by a series of digitiform tentacles of three different orders of size (Fig. 4A). As a general rule, four to six longer, first order tentacles alternate regularly with four to six medium-sized, second order tentacles. Inserted in between the first and second order tentacles lie 1 to 3 short, third order tentacles. Some first order tentacles are bifid.

The inhalant aperture contracts and expands quite uniformly, thus suggesting it is provided with a circular sphincter of muscular fibers. The tentacles associated with this aperture can be brought either closer or farther, as well as bent either centrifugally, allowing free intake of water and suspended material, or centripetally, creating a barely functional barrier against large particles and excess of material.

Commented [PRS7]: Interesting; earlier statements regarding extraneous materials adhering to the periostracum did not reflect, according to the authors, secretions from the arenophilic mantle glands (see my earlier comment). Can these accurately be described as separate processes?

Commented [PRS8]: It's a bit difficult to discern from figure 4A: you note that the arenophilic papillae actually line the siphons in one continuous and contiguous liner (as the drawing seems to indicate via a series of half-circles. If so, there are obviously an equal number of glands associated with each but the spacing on Fig. 4B suggests papillae would also be abutting. Are the papillae "inflated" to a diameter wider than the full cross section of the glands?

Commented [PRS9]: Does this sentence refer only to the optic tentacles (the Figure (4A) shows many tentacles but 4-5 optic tentacles – just need some clarity here.

Commented [PRS10]: These eyes are remarkable in *E. spengleri*; do you have histology sections that can be added as a figure here?

Commented [PRS11]: I think this answers my question above re number of tentacles.

Commented [PRS12]: Can you add some clarity here? Are these pigment spots or "an ill-defined eye"?

Commented [PRS13]: These movements, of course, demand circular, longitudinal and oblique muscle fibers...as shown in Fig. 4B.

243 The exhalant aperture lies at the summit of a thin, smooth, volcano-shaped valvular
244 membrane (Fig. 4A). Similar to what was described by Morton (1973) in *Exolaternula spengleri*
245 (as *L. truncata*), this aperture closes by contraction at two opposite lines of folding, one dorsal
246 and one ventral, thus forming two lateral valves. The fully expanded valvular membrane is
247 maneuvered around the siphon axis, driving the exhalant current with rejected material and
248 gametes far from the inhalant aperture.

249 Irregular bands of brown and yellowish-white pigment delicately pattern all tentacles and
250 the epithelium circumscribed by the periostracal groove. A homogeneously dispersed light-green
251 pigmentation, as well as patches of brown pigment that fade away onto the base of the siphons,
252 are also present all over the inner epithelium of both organs.

253 The wall of both siphons is provided with a thick musculature. This is arranged, from the
254 outer to the inner epithelium, in the following muscle layers (Fig. 4B): a narrow circular layer
255 (C1), intermingled with isolated bundles of longitudinal fibers (L1); a thick circular layer (C2); a
256 thick longitudinal layer (L2); two central circular layers (C3 and C4) separated by a haemocoel;
257 a massive longitudinal layer (L3) containing the nerve cords; a thick circular layer (C5); a
258 narrow band of isolated bundles of longitudinal fibers (L4); and a circular layer (C6) adjacent to
259 the inner epithelium. Radially arranged muscle strands run from one epithelium to the other,
260 splitting the longitudinal muscle layers "L2" and "L3" into a series of sharply defined bundles,
261 and the haemocoel lying between C3 and C4 into a linear series of compartments. Ubiquitous
262 oblique muscle strands arising from the circular muscle layers similarly cross the muscular
263 layers. Adjacent to each opposite margin of the intersiphonal septum lies a wide, longitudinal
264 haemocoelic compartment.

265 At the base of the siphons and inserted in the longitudinal layer "L3" there are fourteen
266 nerve cords, six in the exhalant and eight in the inhalant; these cords ramify as they extend
267 toward the tip of the siphons, where up to 24 nerves were identified.

268 The septum that divides the inhalant from the exhalant lumina is membranous, poor in
269 muscular fibers and extremely flexible at its basal portion near the posterior end of the ctenidia.
270 It thickens toward the distal end of the siphons, as the muscular layers C6, L4, C5, L3, and
271 oblique muscle strands participate in its constitution. Retraction of the siphons is accomplished
272 by vigorous contraction of the longitudinal muscles whereas protraction requires the modulation
273 of the radial and circular muscles acting on the haemal fluid.

Commented [PRS14]: This attends to my last comment on siphonal musculature so might want to fuse with previous paragraph on this topic.

Commented [PRS15]: Not sure what is meant by the word "vigorous" in this context?

274 Musculature and foot

275 The epithelium that lines both the distal and proximal (= visceral) portions of the foot
 276 bears 5 μm -long cilia; however, ciliary currents were detected on the visceral portion only. The
 277 distal, muscular portion of the foot is roughly hatch-shaped and small ($\pm 1/6$ of the shell length)
 278 when contracted; fully extended it reaches $\pm 1/4$ of the shell length. When protracted, the distal
 279 portion can extend to a reasonable distance beyond the shell margin and function as a digging
 280 tool, even in the largest specimens; juveniles possess a comparatively longer and more mobile
 281 foot ($\pm 1/2$ the shell length in 2.0-cm-long specimens) (Fig. 3C).

282 A shallow, vestigial byssal groove is easily noticed along the ventral edge of the
 283 contracted foot, but quite indiscernible in the well-protracted organ. At its rear end opens a single
 284 ciliated duct that bifurcates to join with the right and left components of a vestigial byssus gland
 285 immersed in the visceral portion of the foot.

286 The general muscular system of *L. elliptica* is shown in Figure 5. The anterior and
 287 posterior adductor muscles are reduced, with elliptical, subequal insertion areas. The extrinsic
 288 pedal musculature consists of bilateral pairs of much reduced, anterior and posterior pedal
 289 retractors, and one pair of anterior pedal protractors. Though both pairs of retractors have similar
 290 insertion area, the anterior pedal retractors are thicker than the posterior ones.

291 The anterior pedal retractors attach to the shell valves close to and behind the dorsum of
 292 the anterior adductor muscle; thence, both the right and left muscles pass downward almost
 293 vertically, flatten and twist as they converge to and unite at the sagittal plane just below the
 294 esophagus. At this point, their fibers spread out and penetrate both the proximal (visceral) and
 295 distal portions of the foot, where they form the innermost muscular layer of the organ.

296 The posterior pedal retractor muscles flatten and thin as they extend anteroventrally and
 297 unite under the kidneys; from here, their fiber bundles become well discernable as they spread
 298 fanwise at the ventrolateral sides of the visceral mass and form a muscular layer external to that
 299 of the anterior pedal retractors.

300 The pedal protractor muscles are the most developed among the extrinsic muscles. The
 301 main fiber bundle inserts on the shell valves juxtaposed ventrally to the anterior adductor muscle;
 302 thence, this bundle extends horizontally and posteriorward as it twists and spreads out on the
 303 dorsal half of the proximal (visceral) portion of the foot. The remaining, weaker portion of the

Commented [PRS16]: Relative density?

Commented [PRS17]: Was it not active at all in the smallest juveniles?

Commented [PRS18]: I presume you're using the term "weaker" as meaning less developed (as opposed to lesser strength...which was not measured here and would be a presumption).

304 protractor penetrates shallowly into the posterior side of the anterior adductor muscle and inserts
305 on the shell valves with the adductor; its fibers forming a thin layer as they spread out ventral-
306 and posteriorward on the ventral half of the proximal (visceral) portion of the foot.

307 In addition to the extrinsic pedal muscles, the visceral and distal portions of the foot are
308 supplied with isolated, transverse muscle strands (intrinsic pedal musculature), which insert on the
309 cubical epithelium lining each side of the foot.

310 Ctenidia

311 The long, deeply plicate, eulamellibranch and heterorhabdic ctenidia of *L. elliptica*
312 extend from the labial palps deep into the siphons, well beyond the posterior limit of the shell in
313 specimens with protruded siphons (Fig. 3A). Each inner demibranch comprises descending and
314 ascending lamellae of near-equal height and a deep marginal food groove; the outer demibranch
315 consists solely of an upturned descending lamella (Fig. 6A).

316 The number of filaments per plica varies along the ctenidia of all specimens and increases
317 with age. Three (occasionally two) filaments at the apex of each plica (Figs 6B, E) are higher,
318 with a broader frontal surface and a larger number of mucocytes than the ordinary filaments on
319 the sides.

320 Subfilamentar tissue connects adjacent filaments, thus forming interfilamentar junctions.
321 At regular intervals, the interfilamentar junctions expand across the intraplical space and form
322 complete intraplical septa; these septa lie parallel to each other and compartmentalize the full
323 extent of the intraplical space in both demibranchs.

324 The principal filaments are remarkably-clearly differentiated, with a broad, shallow U-shaped
325 frontal surface (Fig. 6B). The abfrontal surface of every other pair of principal filaments in the
326 inner demibranchs fuses into a complete, high interlamellar septum that almost reaches the
327 ctenidial axis; these high septa alternate with low interlamellar septa that extend but a short
328 distance up from the free, ventral margin of the inner demibranchs.

329 The abfrontal portion of all principal filaments of the outer demibranchs forms a low-
330 extended septum that does not attach to the epithelium of the visceral mass. Thus, at each side of
331 the body the outer demibranch and the epithelium of the visceral mass limit a narrow
332 compartment that is continuous with the spacious suprabranchial chamber lying posterior to the
333 visceral mass.

Commented [PRS19]: Is subfilamentar the equivalent of interfilamentar and if so can't this sentence be lost?

334 The free ventral tips of the plicae that form the inner demibranchs give a deeply scalloped
335 appearance to the walls of the marginal food groove (Figs 6A, B), which can move toward and
336 away from one another, acting as a sorting device.

337 The frontal ciliary currents on both demibranchs are exclusively toward the ventral,
338 marginal food groove (Figs 6A, B) and the ctenidia can thus be ascribed to Atkins type E ~~of Atkins~~
339 (1937). Sorting mechanisms all over the outer and inner demibranchs are of the "*Pinna* type" of
340 Atkins (1937), i.e., fine particles traveling along the grooved frontal surface of the principal
341 filaments and on the frontal surface of their adjacent ordinary filaments are passed to an active
342 oralward current within the ventral marginal food groove, whereas coarse and excess particles
343 traveling on the remaining lateral and apical filaments are transferred to an oralward current
344 outside the marginal food groove and rejected. The ctenidia are highly muscular and very
345 sensitive; if stimulated, the plicae both shorten and flatten locally. By adjusting the distance both
346 among plicae and lateral walls of the marginal food groove, the animal can further regulate the
347 oralward uptake of particles. Coming near, the plicae and lateral walls of the food groove hide
348 the main acceptance tracts and expose unwanted and excess particles to an entirely rejectory
349 surface. Fine particles only and thin mucous strands protected inside the marginal food groove
350 are carried mouthward; this is the only oralward current along the ctenidia.

351 The dorsal margin of the ascending lamella of each inner demibranch forms a translucent
352 membrane that attaches to the visceral mass by cuticular fusion; posterior to the visceral mass the
353 ctenidial axes hang free and the membranous margins of both ascending lamellae unite each
354 other by tissue fusion, forming the floor of the spacious, posterior portion of the suprabranchial
355 chamber. The dorsal margin of the upturned outer demibranchs is also attached to the visceral
356 epithelium by cuticular fusion. Cuticular fusion in *L. elliptica* is not easily detached in living or
357 preserved specimens; it resists both displacement of the inner and outer demibranchs and strains
358 at the inner membranous margins of the inner demibranchs.

359 The posterior end of both ctenidial axes and inner demibranchs do not fuse with the inter-
360 siphonal septum, leaving a direct, permanent communication between the supra- and
361 infrabranchial chambers (Figs 3 and 6F) that was termed "inter-chamber aperture" by Sartori &
362 Domanechi (2005) in *Thracia meridionalis*. The free tips of the ctenidial axes form two
363 tentacular projections that bend either dorsalward into the suprabranchial chamber or retract
364 ventrally through the inter-chamber aperture. The membranous, basal portion of the inter-

Commented [PRS20]: More sensitive than other bivalves?

siphonal septum expands into a flat, trigonal lip that acts as an efficient valve allowing the animal to either retract and tightly close the inter-chambers ~~aperture, or aperture or~~ expand it widely. The aperture widens as the inter-chamber valve swells out ventralward into an igloo-shaped structure, with its free ciliated border (7.5 μm -long cilia; Fig. 6G) taking a U-shape outline. Conversely, flattening the domed valve up, its free, ciliated border is pushed forward and inserted in between the rear end of the ctenidia, thus isolating the infra- from the suprabranchial chamber completely. In its flattened state, the valve and inter-chambers aperture are easily overlooked; however, both are present from early juvenile stage as it could be confirmed by SEM of a minute, 1.0 mm-in-shell-length specimen (Figs. 6F, G), as well as by careful dissections of living and well-preserved specimens measuring 1.0 through 9.6 cm in shell length. The ability to detour water from the supra- to the infrabranchial chamber was tested in seven living specimens (1.0 through 8.0 cm in shell length). The animals had their exhalant siphon lumen injected with a concentrated carmine suspension and immediately stimulated with forceps both to contract and tightly close the exhalant opening. Water jets containing carmine particles were observed leaving forcibly through the pedal opening of 5 specimens and through both the pedal and inhalant openings of 2, thus corroborating data from the morphology.

381 Labial palps and lips

The labial palps are long (one fourth of the shell length), triangular, with the folded surfaces framed by a wide smooth area on both dorsal and adoral sides, and a narrow one along the ventral side of the organs (Fig. 6C). Very sensitive to mechanical stimuli, the palps may either roll up longitudinally into a hollow cone with the ventral and dorsal margins touching each other, or coil up spirally; in both cases the folded surface faces outward (Fig. 6C). The palps can also expand/contract moving their numerous low folds apart or closer; the folds can also either bend oralward or stand quite upright, thus hiding or exposing the troughs between them.

Figures 6C and D show the structure and ciliary sorting mechanisms on the palp surfaces (currents "a" through "i"). Transversely dorsalward current (a), on the smooth outer surface, conveys particles onto the smooth dorsal area of the folded surface. Thence, particles may be either thrown downward (b) toward the plicae or be captured and transported to the subdistal free end of the palp by a longitudinal ciliary tract (c); cilia on this portion transfer material to the folded area. Transversely directed currents (d) operating oralward across the crests of the folds

395 act as acceptance or rejection currents, depending on the size and/or total volume of particles.
 396 Cilia on the crests transfer (i) excess material and/or large particles onto a powerful rejection
 397 ciliary tract (e) along the narrow, smooth ventral margin of the organ; fine material trapped on
 398 the dorsal half of the plicae is preferably transferred to the mouth. Ciliary tracts (f) on the adoral
 399 surface of each plica deliver isolated particles either onto a rejection tract (g) on the floor of the
 400 groove between adjacent folds, or onto the aboral surface of its anterior, adjacent fold; here,
 401 ciliary tracts (h) transfer both large and minute mineral and organic material onto currents "d".
 402 Along the ventral third of the palps, particles traveling on currents "h" are intercepted by
 403 longitudinal ciliary tracts (i) on the aboral side of the crests and transferred to the main rejection
 404 tract "e" along the free ventral margin of the palp. Particles present on currents "g" also converge
 405 to this rejection tract "e".

406 In addition to the capacity of regulating the intake of particles by adjusting the steepness
 407 of the folds and/or the distance between them, *L. elliptica* can further regulate the amount of
 408 material being carried oralward by strengthening the rejection currents in two ways. The labial
 409 palps roll up longitudinally, bringing together both their dorsal and ventral margins and their
 410 respective longitudinal currents "c" and "e", which convert into a strong rejection current that
 411 sweeps away unwanted and excess material coming into contact with the folded surface (Fig. 6C,
 412 right inner palp). Alternatively, spiral coiling of the palp (Fig. 6C, both right and left outerpalps)
 413 brings the rejection ciliary tract "e" into intimate contact with the folded surface; being stronger,
 414 the rejection current "e" intercepts and gets rid of excess material being directed oralward on
 415 currents "d".

416 The long and wide dorsal and ventral lips deal with isolated particles that go deep into the
 417 anterior region of the mantle chamber. Both have the inner surface with a flat, distal margin,
 418 more conspicuous in the dorsal lip, and a cushion-like, often transversely corrugated basal
 419 portion. Corrugations may either mimic transverse folds or disappear as the lips contract and
 420 relax, respectively. Transversely directed cleansing currents on the flat, smooth outer surface of
 421 both lips convey particles onto their inner surfaces; thence, particles are passed transversely onto
 422 the oral groove; on the dorsal palp they may also be trapped by a ciliary tract that delivers
 423 unwanted material to the rejection current "e" along the free ventral margin of the palps.

Commented [PRS21]: Is there a high degree of confidence that the active movements ("coiling") of the palps is normal behavior or something that is seen when the covering shell/mantle is removed for behavioral observation?

424 Ciliary currents on the visceral mass and inner mantle surface

425 Weak ciliary cleansing currents on the visceral mass epithelium sweep particles ventral-
426 and posteriorward (Fig. 7A), except at its anterior portion overlapped by the proximal third of the
427 inner labial palps; in this anterior portion particles are carried dorsalward and caught by cilia on
428 the smooth outer surface of the palps and passed to the folded surface of this organ to be
429 resorted. Unwanted material about to reach the ventral limit of the visceral mass either falls onto
430 the rejection currents of the mantle or is removed by frontal cilia of the ctenidia and ultimately
431 discarded to and rejected by the mantle.

432 Cilia on the visceral mass epithelium, dorsal to the line of attachment of the reflected
433 outer demibranch, sweep particles dorsalward, toward the mantle lobe surface.

434 Ciliary activity all over the inner mantle surface transfers particles ventral- and
435 anteriorward onto the posterior end of the pedal opening predominantly (Fig. 7B). Here, a single,
436 strong rejection tract receives the bulk of pseudofeces coming also from the ctenidia, labial palps
437 and visceral mass epithelium and drives it posteriorward and concentrates in large mucous
438 masses at the base of the inhalant siphon. Unwanted material so collected is periodically ejected
439 through the inhalant siphon.

440 Discussion

441 The Anomalodesmata comprises a diverse group of bivalves, with the members of the
442 Laternulidae being well known as having a sedentary mode of life, living deeply borrowed
443 intertidally or sublittorally. Although comprising a relatively small number of species, the
444 taxonomy of the living species of Laternulidae has been much confused and discussed in the
445 literature (e.g., Huber, 2010; Huber 2015; Prezant, 2015). A preliminary revision by Taylor et al.
446 (2018), based on molecular data, museum specimens, and literature data, grouped the
447 approximately 15 extant taxa of the family into two genera, *Laternula* Roding, 1798 and
448 *Exolaternula* Habe, 1977, and pointed to several synonymies and misidentifications in prior
449 publications that have covered the members of the group. This is of relevance in the current
450 context as the few existing morpho-anatomical data in the literature were assigned, in part, to
451 incorrect nominal taxa.

452 *Exolaternula* differs from *Laternula* in having a lithodesma present in the adult, with
453 Taylor et al. (2018) recognizing three valid species in this genus, *E. spengleri* (Gmelin, 1792), *E.*

Commented [PRS22]: Very true!!

454 *liautaudi* (Mittre, 1844), and *E. erythraea* (Morris & Morris, 1993), and about a dozen species in
 455 *Laternula*. Habe (1977) stated the type species of *Exolaternula* to be *Anatina truncata* Lamarck,
 456 1818, which is a subjective synonym of *Cochlodesma praetenue* (Pulteney, 1799), a European
 457 anomalodesmatan species of the family Periplomatidae. However, Habe used it in the sense of
 458 *Exolaternula spengleri* (Gmelin, 1791); the name *Exolaternula* is thus based on a misidentified
 459 type species and a type species needs to be fixed under ICZN (1999) Art. 70.3. The available
 460 literature data on shell and anatomical characters of "*Anatina truncata*" or "*Laternula truncata*"
 461 (e.g., Ridewood, 1903; Burne, 1920; Morton, 1973, 1976; Adal & Morton, 1973; Sartori et al.,
 462 2006) are referable to *E. spengleri* (of which *E. rostrata* [G.B. Sowerby II, 1839] is another
 463 synonym) and thus fall under the current concept of *Exolaternula*.

464 Other early anatomical studies have been variously interpreted as referring to species of
 465 either genus. Woodward (1855: 26) figured and described the anatomy of "*Anatina subrostrata*"
 466 from the Philippines, which is a synonym of *L. anatina* (the type species of *Laternula*). Morton
 467 (1976: 263) claimed that Woodward reported on "*L. rostrata* (= *L. truncata*)", a synonym of the
 468 type species of *Exolaternula*. However, *Exolaternula* species retain a lithodesma throughout
 469 their ontogeny and this structure is not represented in Woodward's figure. Considering the shell
 470 shape of the figured specimen and the reported locality (Philippines), it seems more likely that
 471 Woodward studied *L. corrugata*. Pelseneer (1911: 71-73, pl. 24) provided a detailed anatomy of
 472 "*Anatina subrostrata*", which is a synonym of *L. anatina* (the type species of *Laternula*).
 473 However, Morton (1976: 263) stated this to be "(= *L. anserifera*)", which is a synonym of
 474 *Exolaternula spengleri* according to Taylor et al. (2018). Other studied species have also been
 475 synonymized or reidentified, such as *L. marilina* Reeve (1860) [examined, e.g., by Sartori et al.
 476 (2006) from Moreton Bay, Australia], now a synonym of *L. gracilis* (Reeve, 1860). The species
 477 recorded by Prezant et al. (2008, 2015) as *L. corrugata* or *L. anatina* from Kungkaben Bay,
 478 Thailand, has been recognized as a different species, *Laternula* sp., based on molecular analysis
 479 by Taylor et al. (2018).

480 ~~*Laternula elliptica*'s~~ The deep-burrowing habit of *Laternula elliptica*, with highly extendable
 siphons, has been
 481 interpreted as allowing it to avoid predation and ice scouring (e.g., Ahn 1994, Harper et al.
 482 2012).

483 The mode of operation of its valves and of other representatives of *Laternula* was
 484 described by Morton (1976) and Savazzi (1990). Morton (1976) claimed that in *L. truncata* and

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485 *L. boschasina* the lithodesma immobilizes the ligament. Sartori (2009) observed that in several
 486 anomalodesmatans a lithodesma is formed by the calcification of the sagittal portion of the early
 487 juvenile ligament (ligament 1 or L1). In many species L1 is retained as the sole **ligament**
 488 throughout ontogeny but, in many others, including *L. elliptica*, a second ligament (L2) forms
 489 behind L1. As ontogeny progresses and L2 grows, in *L. elliptica* the lithodesma is gradually
 490 absorbed and L1 resiliifers are overgrown. Hence, contrary to the observations made by Peck et
 491 al. (2004: 359), adult specimens of *L. elliptica* do not possess a lithodesma.

Commented [PRS23]: The calcified lithodesma would not have the flexibility to act as the “sole ligament”.

492 The siphons possess true tentacular eyes as in *E. spengleri* (Morton, 1973; Adal &
 493 Morton, 1973; as *L. truncata*), a possible adaptation to life in deep permanent burrows with little
 494 body movement, relying on siphonal retracting for defense. Also, arenophilic glands were
 495 described for the Laternulidae by Sartori et al. (2006), who pointed out in this family the glands
 496 are mostly restricted to the tip of the siphons. Sartori et al. (2006) suggested that the presence of
 497 arenophilic glands is a synapomorphy of the Anomalodesmata, and that in some of its families
 498 (Thraciidae, Cleidothaeriidae and Myochamidae) they have been **lost**. The presence of living
 499 hydrozoans, bryozoans and filamentous algae attached to the periostracum of the siphons
 500 suggests that these organs are not frequently disturbed.

Commented [PRS24]: There's a strong functional aspect to presence of these glands, even within a single (albeit small) family. Eg. Lyonsiidae – present in Lyonsia, Entodesma but not Mytilimeria. And lost with growth in Entodesma.

501 In the adults of *L. elliptica*, a nonfunctional byssal groove was observed in the ventral
 502 part of the foot. The byssus likely is present in the larval stages of the species, and the byssal
 503 gland becomes reduced after metamorphosis. When the animal is displaced from its natural
 504 position in the substratum, the foot is used in burrowing, but this repositioning in the sediment
 505 takes hours, in contrast to the more rapid burying by juveniles, who possess a comparatively
 506 longer and more mobile distal portion of the foot. **As** discussed by Moreley et al. (2007b), *L.*
 507 *elliptica* has 25-30% longer relative foot length than tropical congeners of the same size, which
 508 could be a morphological adaptation compensating for reduced burrowing speeds in a colder
 509 environment.

Commented [PRS25]: Similar to *L. truncata*, a tropical species, where smaller specimens more readily/rapidly burrowed.

510 *L. elliptica* may be regarded as a specialized detritus **suspension** feeder, collecting
 511 material in suspension near the sediment surface. Within the mantle cavity, the organs concerned
 512 with the collection, sorting and either acceptance or rejection of this material are well developed.
 513 The ctenidia are plicate, passing food material into the ventral marginal food groove of the inner
 514 demibranch only. The labial palps and the rejectory tracts of the mantle and visceral mass are
 515 efficient, this being probably related to a large amount of material that enters the mantle cavity.

Commented [PRS26]: Were stomach contents examined in histological sections? If not can this be supported via a relevant citation.

Sartori (2009) examined the anatomy of numerous anomalodesmatans and noted that an inter-chamber aperture appears to be present in all members of the group bearing ctenidia. In *L. elliptica*, this aperture plays a role in its burrowing process. To move deeper into the stiff, muddy substratum, completely buried individuals of *L. elliptica* profit from hydraulic burrowing mechanisms, powered by extra-water previously retained within the capacious lumina of both suprabranchial chamber and exhalant siphon. Forcibly transferred via the inter-chamber aperture onto the infrabranchial chamber, such extra water allows an extended jetting that lasts more than one would expect in a typical siphonate bivalve lacking such inter-chamber communication. The function of the cilia present along the free border of the inter-chamber valve and of the free, tentacle-like tips of the ctenidial axes still deserve investigation.

Conclusions

Prior observations on the anatomy of *Laternula elliptica* were based on limited, preserved, and partly damaged material. The current work greatly expands on, and corrects, earlier observations. Among them were the foundational reports by Burne (1920), who missed anatomical features such as the presence of optical tentacles and interpreted a connection of the gill axis to the body wall by a "membranous sheet" (the latter likely was an artifact because of contortion of the single, damaged, specimen at his disposal; Burne's figure 20, plate IV). Among the noteworthy findings of the present study are the presence of well-developed siphons furnished with sensory tentacles at its tips, some of which are bearing eyes; large, folded gills and labial palps capable of sorting the material entering the mantle cavity; an inter-chamber communication in the posterior region of the mantle cavity; and an ample ventral mantle fusion with an anterior pedal gape. Benefiting from the careful dissections and live-animal observations during field studies conducted by the late Osmar Domaneschi, details could be explored that reveal the anatomical and behavioral 'secrets' of this giant and important Antarctic keystone bivalve species.

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Figure 1

Shell of *Laternula elliptica*

A to G from the same specimen (ZUEC BIV 8397): (A) Outer left view. (B) Anterior view. (C) Dorsal view. (D) Ventral view with valves partially opened. (E) Posterior view, with preserved soft parts. (F) Same, without soft parts. (G) Inner view of the left valve. (H) Sketch of inner surface of a right valve. B, E, F and C, D, G are at the same scales, respectively.

Abbreviations: aas, anterior adductor muscle scar; ars, anterior pedal retractor muscle scar; b, buttress; cr, crack filled with periostracum; l, ligament attached to the chondrophore; pas, posterior adductor muscle scar; pg, pedal gape; pl, pallial line; prs, posterior pedal retractor muscle scar; ps, pallial sinus; s, siphons; sg, siphonal gape; sl, secondary ligament.

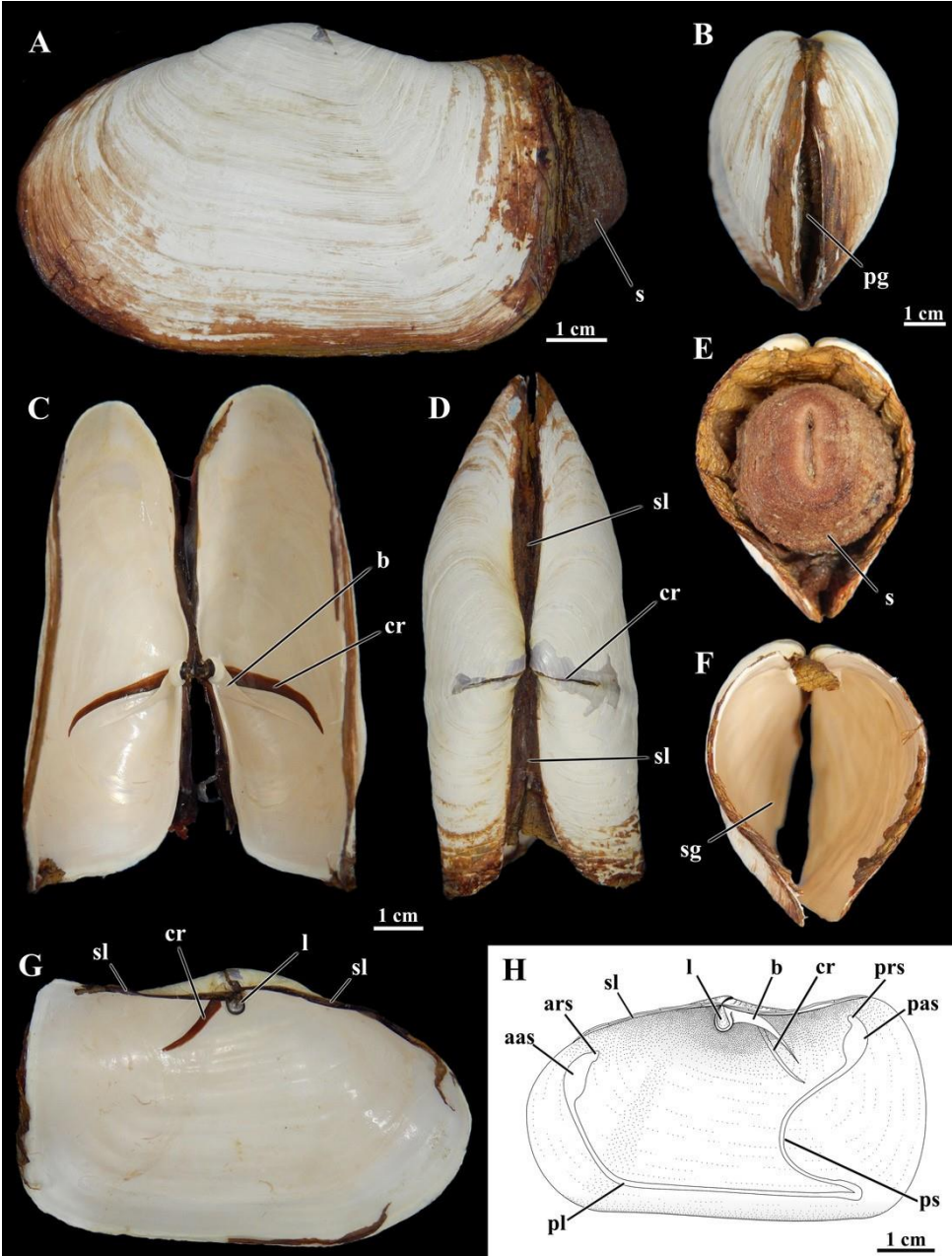


Figure 2

Observed behavior of *Laternula elliptica*

(A-B) Surface movement (<jetting= cycle): (A) viewed from sidewall of the aquarium. (B) Same, viewed from water surface. In <t1= the animal is lying on the sediment surface, dorsal side down. The initial phase of the cycle is preceded by the closure of the pedal gape, valves opening, and swelling of both siphons that bend their tips onto the sediment surface. In <t2= the adductors and orbital muscles contract and the diameter of the siphons reduces, generating a strong jetting (arrow); only the posterior half of the shell and siphons are lifted above the sediment surface, while the body rotates around its antero-posterior axis. In <t3= the cycle completes with the animal lying on one shell valve, after a clockwise/anticlockwise translocation (arrow in B) of the animal. (C) Burrowing behavior: (C1) Ventral view of the animal in its natural position, with the arrows indicating inhalant and exhalant currents. (C2) Protective reaction against predators, with the animal closing pedal and siphonal openings, relaxing pallial and adductor muscles, and retracting siphons; positive hydrostatic pressure generated on the water in the pallial chamber and siphons forces the valves and siphonal walls tightly against the sediment, also preventing collapse of the surrounding soft, plastic sediment. (C3) Burrowing within the substratum: to move deeper into the substratum, the animal contracts the siphons and expels water vigorously through the pedal opening (black arrow), revolving and removing sediment from the depths of the gallery. White arrows indicating the two escape routes for the water: running through the narrow space between the shell and sediment (indicated by two asterisks in C); and drilling a tunnel throughout the sediment to emerge a short distance from the bivalve (indicated by one asterisk in C and D). Under gravitational forces or by contraction of the pedal retractor muscles, the heavy and cylindrical body <drops= into the hollow excavated below the animal. (D) Underwater photograph taken just after complete precipitation of the blackish mud removed from the

substrate during burrowing activity. The distal end of the siphons is exposed above the sediment surface; arrows indicating inhalant and exhalant currents.

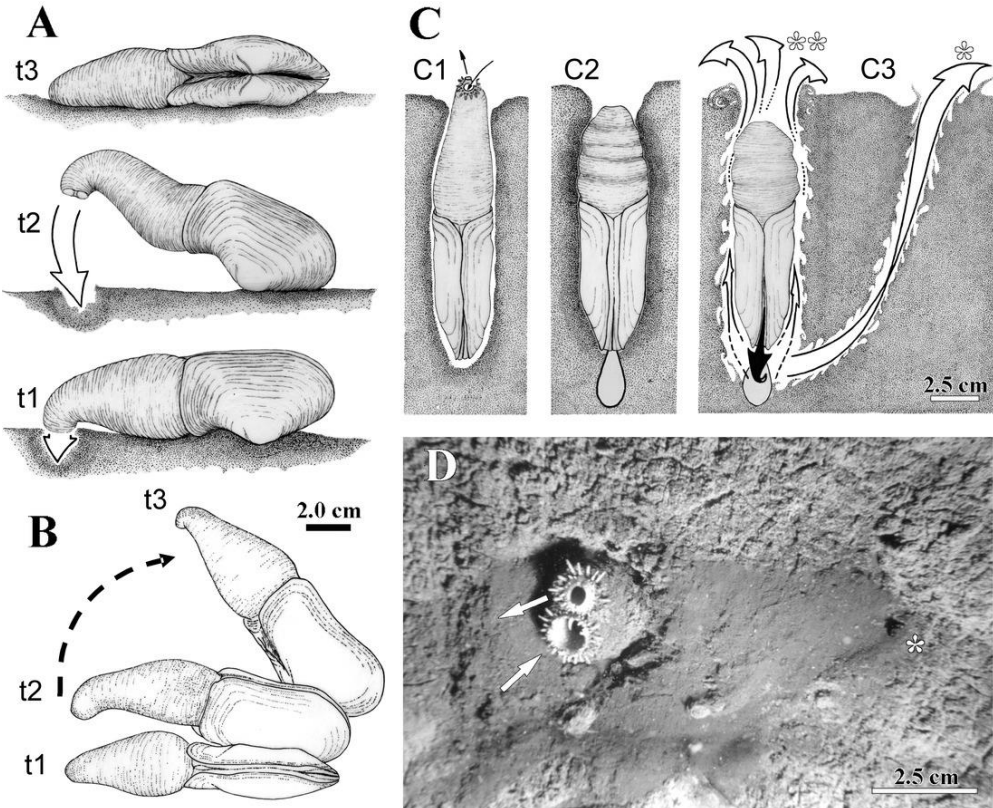


Figure 3

Laternula elliptica 3 Anatomy, with focus on the pallial cavity (A), and external morphology (B, C)

(A) Organs of the pallial cavity viewed from the left side, after removal of the left shell valve and partial section of the left mantle lobe, outer demibranch and siphons. [Details of the ctenidial and labial palp folds and ciliary currents are shown in Figure 6.] (B) Photograph of a living specimen from the left side. (C) Sketch of a juvenile. Abbreviations: aa, anterior adductor muscle; apr, anterior pedal retractor muscle; es, exhalant siphon; f, distal portion of the foot; ia, inter-chamber aperture; id, inner demibranch; ilp, inner labial palp; imf, inner marginal mantle fold; is, inhalant siphon; lod, left outer demibranch; mmf, middle marginal mantle fold; olp, outer labial palp; omf, outer marginal mantle fold; orm, orbital muscle; pa, posterior adductor muscle; ppr, posterior pedal retractor muscle; re, rectum; rod, right outer demibranch; se, inter-siphonal septum; sml, sectioned mantle lobe.

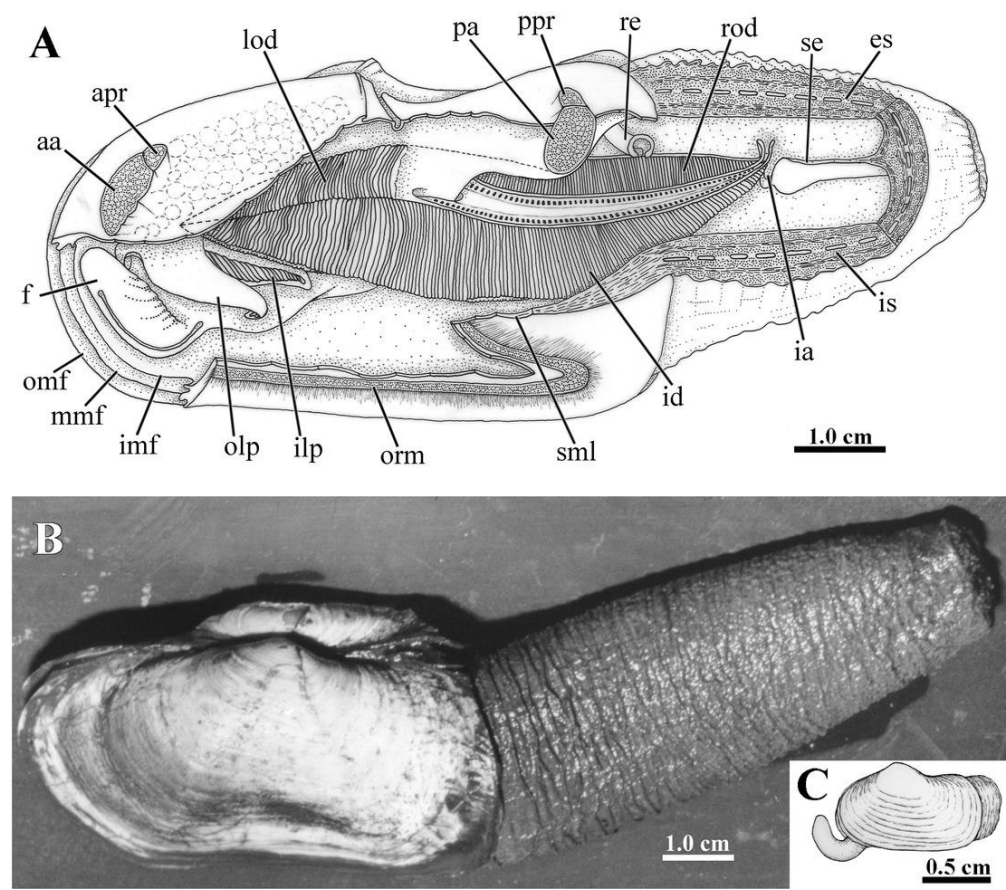


Figure 4

Laternula elliptica 3 Siphons

(A) Frontal view of the siphonal tips (the lines of arenophilic threads with adhered particles in the siphonal walls here omitted for simplification). (B) Diagrammatic transverse section through the wall of the conjoined siphons near their tips, showing the musculature, arenophilic mantle glands, and thick periostracal covering. Abbreviations: amg, arenophilic mantle gland; ap, arenophilic papilla; C1 to C6, circular muscle layers; dt, digitiform tentacle of the inhalant aperture; ee, external epithelium; eo, exhalant opening; h, haemocoel; ie, internal epithelium; io, inhalant opening; L1 to L4, longitudinal muscle layers; nc, nerve cords; om, oblique muscle strands; ot, optic tentacle; p, periostracum; pg, periostracal groove; rdm, radial muscle strands; tt, tactile tentacle; vm, valvular membrane.

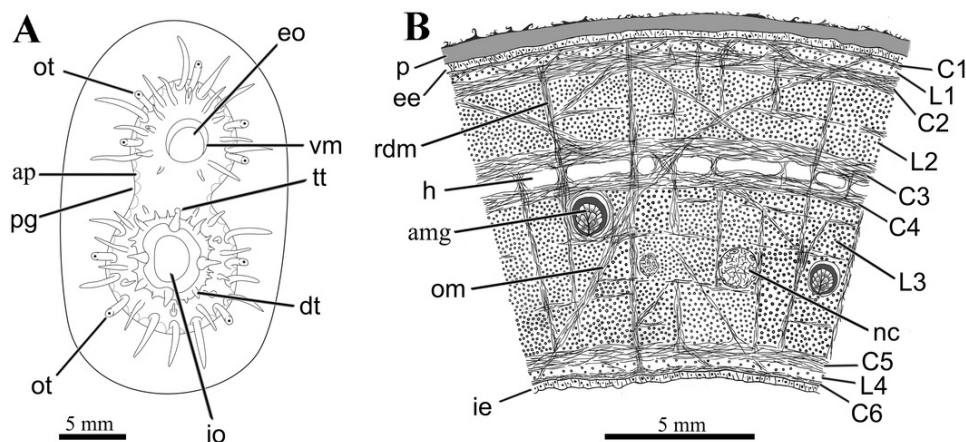


Figure 5

Laternula elliptica 3 Musculature, as viewed on the leftside

Abbreviations: aa, anterior adductor muscle; apr, anterior pedal retractor muscle; bg, byssal groove; f, distal portion of the foot; pa, posterior adductor muscle; ppm, pedal protractor muscle; ppr, posterior pedal retractor muscle.

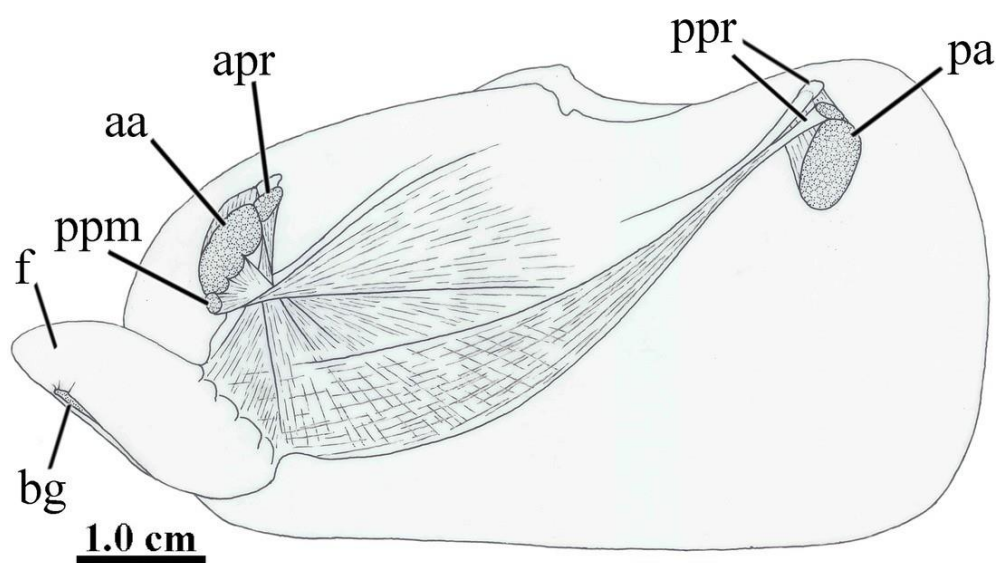


Figure 6

Laternula elliptica 3 Ctenidia and palps

(A) Transverse section, diagrammatic view of the ctenidial ciliary currents. (B) Detailed sketch of the ctenidial ûlaments, with one fold turned out to expose principal and ordinary ûlaments. (C) Semi-diagrammatic anterior view of the oral region, summarizing the functioning of the labial palps. Outer palps shown coiled spirally; the right inner one bent longitudinally, while the inner left one is extended. (D) Diagrammatic section through three folds, showing ciliary currents. (E) Scanning electron micrograph of a plica. (F) Scanning electron micrograph of inter-chamber aperture of a juvenile (1.0 mm long) specimen. (G) Detailed view of the cilia bordering the aperture in (F). Abbreviations: a through i, ciliary currents (see text for details); ad(id) and dl(id), respectively, ascending and descending lamella of the inner demibranch; bg, byssal groove; cf, apical ûlament of plica; dl, dorsal lip; f, foot; ia, inter-chamber aperture; id, inner demibranch; ilp(r) and ilp(l), inner right and left labial palp, respectively; mo, mouth; mfg, marginal food groove; ncf, newly formed ctenidial ûlaments; ocf, older ctenidial ûlaments; od, outer demibranch; olp(r) and olp(l), outer right and left labial palp, respectively; pf, principal ûlament; vl, ventral lip; vm, visceral mass.

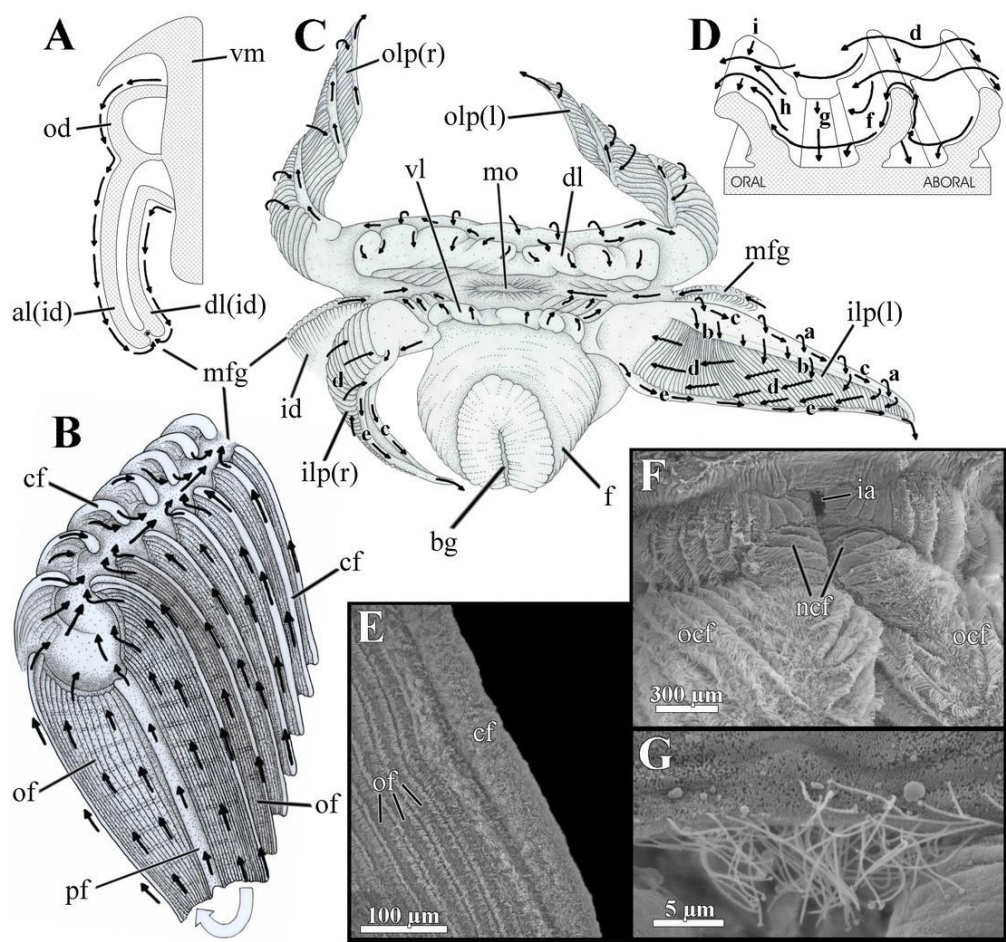


Figure 7

Laternula elliptica 3 Cleansing ciliary currents, indicated by arrows

(A) Currents on surface of the visceral mass. (B) Currents on inner surface of right mantle lobe. Abbreviations: f, foot; idil and odil, lines of insertion of the inner and outer demibranchs with the visceral mass, respectively; psf, pseudofaeces; ume, upper mantle edge (roof of the pallial cavity).

