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COMPARATIVE MORPHOLOGY AMONG REPRESENTATIVES OF MAIN TAXA OF SCAPHOPODA AND BASAL PROTOBRANCH BIVALVIA (MOLLUSCA)

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ABSTRACT

This study deals with detailed morphology and anatomy of 4 species of Scaphopoda and 5 species of protobranch Bivalvia. Both classes are traditionally grouped in the taxon Diasoma, which has been questioned by different methodologies, such as molecular and developmental. This study is developed under a phylogenetic methodology with the main concern in performing it in an intelligible and testable methodology. The analyzed Scaphopoda species came from the Brazilian coast and belong to the family Dentaliidae [(1) Coccodentalium carduus; (2) Paradentalium disparile] and Gadiliidae; [(3) Polyschides noronhensis, n. sp. from Fernando de Noronha Archipelago; (4) Gadila braziliensis]. These species represent the main branches of the class Scaphopoda. From protobranch bivalves, representatives of the families Solemyidae [(5) Solemya occidentalis, from Florida; S. notialis, n. sp. from S.E. Brazil], Nuculanidae [(6) Propeleda carpentieri from Florida], and Nuculidae [(7) Ennucula puelcha, from south Brazil] are included. These species represent the main branches of the basal Bivalvia. The descriptions on the anatomy of S. occidentalis and of P. carpentieri are published elsewhere. The remaining are included here, for which a complete taxonomical treatment is performed. Beyond these species, representatives of other taxa are operationally included as part of the ingroup (indices are then shared with them), as a procedure to test the morphological monophyly of Diasoma. These taxa are: two lamellibranch bivalves [(8) Barbatia – Arcidae; (9) Serratina – Tellinidae; both published elsewhere; and Propilidium (10) Patellogastropoda, and (11) Nautilus, basal Cephalopoda, based on basal taxa. The effective outgroups are (12) Neopilina (Monoplacophora) and (13) Hanleya (Polyplacophora). The phylogenetic analysis based on morphology revealed that the taxon Diasoma is supported by 14 synapomorphies, and is separated from Cyrtosoma (Gastropoda + Cephalopoda). Although they are not the main goal of this paper, the taxa Scaphopoda and Bivalvia are supported by 8 and by 7 synapomorphies respectively. The taxon Protobranchia resulted paraphyletic. Both scaphopod orders resulted monophyletic. The obtained cladogram is: (((((Coccodentalium carduus – Paradentalium disparile) (Polyschides noronhensis – Gadila brasiliensis)) (Solemya occidentalis – S. notialis) (Propeleda carpentieri (Ennucula puelcha (Barbatia cancellaria – Serratina capsoides)))))) (Propilidium curumim – Nautilus pompilius – Lolliguncula brevis)).

KEYWORDS: Scaphopoda; Bivalvia; Diasoma; Phylogeny; Morphology.

INTRODUCTION

As explained below, this paper is the result of a larger project related to a group of Bivalvia, of which some of the presently analyzed species are outgroups. As the information obtained with the comparative analyzes is interesting, and helps to answer some important questions on the Mollusca higher inter-relationship, it was organized as a separate paper. The main intention is to furnish a comparative and phylogenetic scenario with a theoretical background only based on morpho-anatomy. This is certainly interesting for further analysis, since analyses for the past, present or future have been produced using other equally important methodologies. The relationship of the Classes Scaphopoda and Bivalvia has been fluid, and even their monophyly has been questioned in some non-morphological approaches. Nevertheless, as also explained below, both classes were grouped in the presently controversial taxon called Diasoma.

Diasoma, also called Loboconcha, was coined by Runnegar & Pojeta (1974), reuniting the classes possibly derived from Rostroconchia, Scaphopoda and Bivalvia (Pojeta *et al.*, 1972; Runnegar, 1996) (Loboconcha was named by Salvini-Plawén, 1980). This molluscan branch is regarded to have diverged at the early Cambrian, bearing representatives with shells opening on both sides, and the digestive tube in a somewhat straight organization, *i.e.*, mouth and anus located on opposite sides. This somatic conformation is adapted to an infaunal mode of life, and to deposit feeding. Diasoma was, then, subsequently accepted and used in the current technical literature (*e.g.*, Pojeta & Runnegar, 1976, 1985; Salvini-Plawén, 1980 as Loboconcha; Haszprunar, 1988; Salvini-Plawén & Steiner, 1996; Wagner, 1997), which sometimes even complemented the concept of the taxon. One example is the taxon Ancrypoda (= Diasoma), meaning anchor foot (Hennig, 1979; Lauterbach, 1984).

In the early 1990s, the concept of Diasoma was relatively well established in every phylogenetic vision of the Mollusca. However, another affinity for the Scaphopoda gradually appeared, approximating the taxon to the Gastropoda-Cephalopoda branch (*e.g.*, Peel, 1991; Haszprunar, 2000; Wanninger & Haszprunar, 2001), collectively called Cyrtosoma Runnegar & Pojeta, 1974.

Two main approaches were responsible for this change of concepts: 1) microscopic and developmental studies (Wanninger & Haszprunar, 2002); 2) molecular studies (Steiner & Dreyer, 2003; Passamanek *et al.*, 2004). Both, which are explained in more detail below, gradually transferred Scaphopoda to Cyrtoso-

ma. The new point of view has persuaded more generic literature on Malacology (*e.g.*, Coan *et al.* 2000:13) and on Zoology (Brusca & Brusca, 2003).

Of course most of this controversial relationship of the Scaphopoda, whether it be related to the Bivalvia or Cyrtosoma classes, was stressed in early literature (*e.g.*, Lacaze-Duthiers, 1857-1858; Grobben, 1886; Plate, 1892; Simroth, 1894). However, with the introduction of phylogenetic methodologies, the discussion becomes more intelligible. This methodology has been applied mainly in the last three decades; conversely, and despite this, the scaphopod affinities are still inconclusive. A summary of this conceptual history is provided in the recent literature (*e.g.*, Steiner & Dreyer, 2003), details of which are not reported here. As the data of early literature was already explored by those papers, the present paper is, then, mainly concerned with argumentation of papers produced in the last three decades.

Some recent issues have directly or indirectly influenced analysis of the Scaphopoda relationship. For example, the appearance of a distinct pair of cephalic retractors during the development of a scaphopod species, which is also found in gastropods and cephalopods, was used as additional argumentation to consider Scaphopoda within Cyrtosoma (Wanninger & Haszprunar, 2002). Multiple cephalic appendages, scaphopod captacula, have been compared to cephalopod arms (Steiner & Dreyer, 2003). Molecular approaches, on the other hand, sometimes demonstrate scaphopod's affinity to Cephalopoda (Steiner & Dreyer, 2003 – 18S rDNA; Passamanek *et al.*, 2004: LSU + SSU rRNA), and sometimes to Bivalvia (Dreyer & Steiner, 2004 – mtDNA). In favor of the cyrtosome link, the scaphopod affinity to Bivalvia has even been considered as a mere consequence of homoplasies, resulting from the similar infaunal mode of life (Steiner & Dreyer, 2003). Some combined molecular approaches have even demonstrated that scaphopods are related to a set grouping cephalopods and non-conchiferan aplousobranchs, at the base of Mollusca (Giribet *et al.*, 2006).

This paper is actually part of a PEET project related to anatomy and systematics of bivalves from Florida (Mikkelsen & Bieler, 2000, 2008; Bieler *et al.*, 2001). Beyond samples from Florida, some species from other regions and other taxa were selected in order to provide scenarios and outgroups for comparative analyses. As stated above, the dataset in this paper revealed to be autonomous from the study on the Floridian taxa, and is worth publishing separately. Despite the consideration of some species from Florida, this study reached results important enough for individual publication.

Although the number of taxa studied here is equivalent to that found in most papers, above related, referent to molecular and ultrastructural aspects, the main objective is not to test the other methodologies, nor their importance for comparative approaches. The main goal, instead, is to furnish another point of view and further argumentation to the still inconclusive relationships of bivalves and tusk-shells. Another argument is that morphology is an autonomous science, and even if its importance in phylogeny and taxonomy has been proven to be weak, morpho-anatomy of the animals still must be studied. The final result, if only morphology is applied in the phylogeny at higher levels, must be exposed and debated.

The present study has, subsequently, the objective of testing the relationship of a set of Scaphopoda and Bivalvia, themselves and with remaining main branches of Mollusca, for the first time based on holistic morpho-anatomy. For this task, a set of species were selected and examined in the same sort of details. From Scaphopoda, two species of each main branch were chosen – *Dentaliida* and *Gadilida* (Scarabino, 1995; Steiner, 1999). From Bivalvia, one or two samples of the main branches of basal taxa, *i.e.*, the Protobranchia, were selected, as well as two representatives of the higher taxa, *i.e.*, Lamellibranchia (a filibranch and an eulamellibranch). From protobranchs, Nuculoidea (1 species), Nuculanoidea (1 species) and Solemyoidea (2 species) were chosen. Lamellibranchs include an Arcidae and a Tellinidae. Representatives of other molluscan classes were also selected as outgroups, however, some of them, as explained below, were operationally analyzed as part of the ingroup. This providence is a method for testing monophylies (Simone, 2006a). Further investigation on the phylogenies of Bivalvia and Scaphopoda was not performed, as they already exist in literature, such as in Bivalvia: Morton (1996), Giribet & Wheeler, (2005); and Scaphopoda: Steiner (1992a); of which data and concepts are hereby also applied.

Beyond the self-searched data, information from the literature was used to increase the dataset of characters. For Scaphopoda, the following papers, which dealt with anatomical aspects, are included: Deshayes (1825); Lacaze-Duthiers (1856-1857); Yonge (1937); Cotton & Godfrey (1940); Gainey (1972); Steiner (1991, 1992a, b, 1993, 1994, 1996, 1998, 1999); Palmer & Steiner (1998); Lamprell & Healy (1998); Reynolds (2002). For Bivalvia, the following general papers are considered: Yonge (1939); Allen (1978); Starobogatov (1992); Morton, 1996; Morton *et al.* (1998); Reid (1998); Villarroel & Stuardo (1998); Coan *et al.* (2000); Harper *et al.* (2000); and several

other more specific papers discussed in following sections. These papers also bring comprehensive history of the classification and evolution of both classes that are not reproduced here. Some points, however, are certainly broached in the discussion.

It is important to emphasize that some studies on the phylogeny of scaphopods and bivalves have been produced in the last decades, mostly or totally based on molecular biology. Although they are considered herein, all kinds of phylogenetic arrangements are found, which sometimes complicate comparisons (Giribet & Wheeler, 2002: 274-275). In those studies, morphology is not applied or is a secondary part of the dataset. This demonstrates that the morphology has not been properly evaluated, an impression that the present study has the objective of altering. Some interesting examples are Campbell (2000); Steiner & Hammer (2000); Steiner & Dreyer (2003); Dreyer & Steiner (2004).

As has been done for more general papers with phylogenetic approaches (Simone, 1999-2000, 2001, 2002, 2004a, b, 2005, 2006a, b, 2007), this paper initiates with the systematic part, containing taxonomical treatment and morphological descriptions. Afterwards, a phylogenetic treatment is given, with presentation and discussion of the characters. This paper ends with a discussion of the obtained cladogram in the light of present knowledge, with further implications mainly in taxonomy and phylogeny.

MATERIAL AND METHODS

A complete list of material examined follows each species description. The comparative parameter related to increased width along scaphopod length is provided by the formula: maximum (anterior) width/total length. This translates approximately to the rate of augment along the animal length, everything in mm. Dissections were made by standard techniques, with the specimens under a stereomicroscope, immersed in fixative or seawater. Digital photos of all steps of the dissection were taken. All drawings were obtained with the aid of a camera lucida. The presented measurements were obtained from selected specimens, normally dissected; these specimens are labeled at the collection. Description of the first species in each higher taxon is the most complete. For the other species, the description is comparative and more focused on distinctions, then called “distinctive description”. This measure is for decreasing the length of this volume and for optimizing the discussion. The same approach is taken in the figures.

The part of this paper related to comparative biology is performed under a phylogenetic (cladistic) methodology, which is the most practical and testable method. However, there is no intention to consider the analysis of this paper as “the phylogeny of Bivalvia” nor “of Scaphopoda”. Nevertheless, it is expected that the putative phylogenetic relationships among the species will remain even with the addition of more species, and that some taxonomical inferences can already be made. Analysis was performed with the aid of the program Tree-Gardener (Ramos, 1997) (under a few modifications for Windows XP and Vista), which basically is an interface for the program Hennig86 (Farris, 1988). The algorithm used was “ie”. As outgroups, two species are used to root the cladogram, Monoplacophora *Neopilina galathea* Lemche, 1957 (Lemche & Wingstrand, 1959) and Polyplacophora *Hanleya* sp. Another five species are outgroups, but they are operationally analyzed as part of the ingroup. The species are Cephalopoda *Nautilus pompilius* Linné, 1758 (Griffin, 1897) and *Loliguncula brevis* (Blainville, 1823) (Simone, 1997); Patellogastropoda *Propilidium curumim* Leal & Simone, 1998, Lamellibranchia *Barbatia cancellaria* (Lamarck, 1819) (Simone & Chichvarkhin, 2004 – Arcidae), and *Serratina capsoides* (Lamarck, 1818) (Simone & Wilkinson, 2008 – Tellinidae). This measure is for testing the monophyly of Diasoma; conversely, the indices are shared with these taxa. In the discussion of the character, a short descriptive sentence is given for each one, followed by plesiomorphic and apomorphic states and conditions in the most parsimonious hypothesis. The consistency index (CI) and the retention index (RI) are given last, expressed as %. Several other characters were selected but excluded from this analysis, because their states were overlapping or purely autapomorphic. However, some autapomorphic states were maintained; this measure is based on the interest of the state or to test its importance. Study on two of the protobranchs considered herein are published elsewhere: Nuculanidae *Propeleda carpenteri* (Dall, 1881) and a second Solemyidae *Solemya occidentalis* Deshayes, 1857. Partial anatomical descriptions and figures of these species are already published (Mikkelsen & Bieler, 2008: 31-33, 38-40).

Some characters were introduced in order to organize outgroups, *i.e.*, the representatives of other classes. However, the search for such characters was very superficial, sufficient only to this objective.

In the Discussion, some terms are used to designate a collective set of taxa, with no taxonomical purpose. Some of them are “protobranchs” in apposition to “lamellibranchs”; the former refers to the para-

phyletic bivalve taxon Protobranchia, the last to the remaining Bivalvia. The term “lamellibranch” sets the filibranchs and the eulamellibranchs (and possibly the septibranchs), *i.e.*, the filter-feeding taxa.

Abbreviations used in figures: **aa**, anterior aorta; **af**, afferent gill vessel; **am**, anterior adductor muscle; **an**, anus; **ap**, auxiliary protractor muscle of foot; **au**, auricle; **bg**, buccal ganglion; **br**, subradular membrane; **bs**, blood sinus; **cb**, captacula base; **ce**, cerebral ganglion; **cm**, cruciform-like muscle of bulged integument region anterior to kidney; **co**, cerebro-visceral connective; **cp**, captacula; **cv**, ctenidial vein or efferent gill vessel; **dd**, ducts to digestive diverticulae; **dg**, digestive diverticulae; **es**, esophagus; **fa**, anterior pedal retractor muscle; **fb**, median-anterior foot retractor muscle; **fe**, foot terminal expansion; **ff**, foot posterior flap; **fm**, posterior pedal retractor muscle; **fo**, outer fold of mantle border; **fp**, foot protractor muscle; **fr**, auxiliary middle pedal retractor muscle; **ft**, foot; **fv**, middle posterior foot retractor muscle; **gd**, gonoduct; **gf**, gastric fold; **gh**, gastric shield; **gi**, gill; **gm**, gill retractor muscle; **go**, gonad; **gs**, gill suspensory stalk; **he**, haemocoel; **hf**, hinge fold of mantle; **hg**, hypobranchial gland; **hi**, hinge; **if**, inner fold of mantle border; **in**, intestine; **io**, intestinal origin; **ki**, kidney; **li**, ligament; **lm**, longitudinal muscle; **m3**, transverse muscle of odontophore; **m4**, pair of ventral tensor muscles of radula; **m6**, horizontal muscle; **m7**, pair of internal muscle of radular sac; **ma**, mantle border papillae; **mb**, mantle border; **mc**, circular muscle fibers; **mf**, foot retractor muscle; **mi**, middle fold of mantle border; **mj**, protractor muscle of odontophore; **mo**, mouth; **mp**, mantle posterior aperture; **mt**, mantle; **ms**, mantle septum-like fold; **mu**, muscle of palp; **mv**, visceral muscle; **ne**, nephropore; **nv**, nerve; **oc**, odontophore cartilage; **od**, odontophore; **of**, inner fold of oral tube; **om**, oblique muscle of mantle border; **on**, odontophoral connection with esophagus; **ot**, oral tube; **pa**, posterior adductor muscle; **pb**, palp proboscis; **pc**, pericardium; **pd**, pedal aperture of mantle; **pe**, periostracum; **pf**, pallial folds; **pg**, pedal ganglion; **pj**, palp projections; **pl**, pallial gland; **pm**, pallial muscles; **po**, posterior origin of longitudinal muscles; **pp**, palp; **ra**, radula; **rm**, middle pedal retractor muscle; **rs**, radular sac; **rt**, rectum; **sc**, subradular cartilage; **se**, excurrent siphon; **sh**, shell; **si**, incurrent canal; **ss**, style sac; **st**, stomach; **sy**, statocyst; **tm**, transverse muscles of visceral sac; **um**, umbo; **un**, mantle border fusion; **ve**, ventricle; **vg**, visceral ganglia; **vl**, posterior visceral layer of muscles; **vm**, visceral mass.

Abbreviations of institutions: BMNH, The Natural History Museum, London, UK; IBUFRJ, Instituto de Biologia da Universidade Federal do Rio de Janeiro, Ilha do Fundão, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, USA; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

SYSTEMATICS

Family Dentaliidae

Genus *Coccodentalium* Sacco, 1896

(Type: *Dentalium radula* Schröter, 1784, OD)

Coccodentalium carduus (Dall, 1889)

(Figs. 1-9, 47-64)

Dentalium carduus Dall, 1889: 423 (pl. 27, fig. 3); Pilsbry & Sharp, 1897: 30 (pl. 7, fig. 6); Henderson, 1920: 33 (pl. 3, figs. 4, 5, 7); Steiner & Kabat, 2004: 573-574.

Dentalium (Fissidentalium) floridense Henderson, 1920: 64-65 (pl. 10, figs. 1, 2, 6, 7) [off Sand Key, Florida (Eolis sta. 301, 173 m depth); Penna-Neme, 1974: 113; Scarabino, 1975: 184 (pl. 59, fig. 902); Steiner & Kabat, 2004: 591.

Dentalium (Coccodentalium) carduus: Emerson, 1952: 2.

Dentalium (Dentalium) carduum: Turner, 1955: 311.

Dentalium (Coccodentalium) carduum: Abbott, 1974: 384 (fig. 4497).

Dentalium (Fissidentalium) amphialum: Penna-Neme, 1974: 113 (non Watson, 1879).

Fissidentalium floridense: Scarabino, 1985: 199 (pl. 72, fig. 1021); Emerson in Turgeon, 1988: 50; 1998: 54, 200; Sumida & Pires-Vanin, 1997: 781.

Fissidentalium carduum: Scarabino, 1994: 306 (pl. 106, fig. 1509); Steiner & Kabat, 2001: 444.

Coccodentalium carduum: Steiner, 1998: 81.

Fissidentalium carduus: Steiner & Kabat, 2004: 574.

Coccodentalium carduus: Caetano *et al.*, 2006: 18 (figs. 33-38); Caetano, 2007: 94-97 (figs. 73-83).

Types: lectotype MCZ 7692 (designed by Henderson, 1920: 30); paralectotypes: USNM 95321, 1 shell; USNM 95322, 1 shell; MCZ 7691, 1 shell. *D. floridense*: Holotype USNM 314457 (examined).

Type locality: Lesser Antilles, 13°50'N 61°03'W, off St. Lucia, 211 m depth (Blake sta. 220).

Description

Shell (Figs. 1-5): Size about 80 mm, walls thick, color white, weakly curved, section circular (Fig. 4). Color yellowish. Relatively abrupt widening (tax of increase about 0.145 mm/mm of length). Sculpture six longitudinal, equidistant primary ribs close to posterior aperture; gradually secondary ribs appearing between primary ribs towards anterior, about 30 similar-sized ribs close to anterior aperture (Figs. 2-3); each longitudinal rib spaced from neighboring ribs by space equivalent to its width, this space filled by transverse, uniform threads, located close to each other (space about half their width), each thread about three times smaller than longitudinal ribs, transversely aligned, producing uniform reticulate effect. Posterior aperture with narrow slit in ventral surface (Fig. 5), from 3 to 8% of shell length.

Main muscle system (Figs. 47-50): Pair of longitudinal muscles originated in ventral side of base of apical flap of posterior aperture (Fig. 49), occupying about half of this base. Both longitudinal muscles running straight towards anterior, gradually crossing from ventral to lateral, coming away from one another (Figs. 47, 48). Posterior half of each muscle incompletely divided longitudinally in two portions of equivalent sizes. Thinness of both longitudinal muscles equivalent to that of shell wall, gradually becoming slightly thicker anteriorly. Both longitudinal muscles bifurcating between middle and anterior thirds of animal's body; external branches splaying like a fan in anterior pallial wall up to anterior 1/6, where both muscles touch each other along medial line, thickness about half of that of shell wall, both muscles ending in anterior mantle edge; internal branches splaying in foot base as longitudinal layer of foot retractors, thickness equivalent to that of shell wall. Thin internal layer of circular muscles surrounding posterior half of foot, with thickness about half of external layer of longitudinal muscles. Longitudinal pedal muscles becoming thicker in anterior pedal half, forming two distinguishable thick layers, a dorsal layer covered by integument, another ventral layer running laterally, forming lateral walls of visceral mass, in direction of bifurcation of longitudinal muscles (Fig. 53). Posterior mantle flap with a very thin layer of longitudinal muscles inserted in a ring of entire flap base, just posterior to longitudinal muscles origin in ventral half.

Foot (Figs. 47, 52-54): Solid in anterior half, surrounding visceral mass in posterior half; total length approximately 1/3 of total shell length; width about 2/3 of

adjacent shell width. Proximal 3/4 somewhat cylindrical, abruptly expanding in distal tip as an umbrella, about 1/3 wider. This umbrella-like edge surrounding a central elevation, tall, with about half of foot width and 1/6 of its length; tip rounded. Foot edges producing a concavity turned anteriorly, uniform, except for a ventral notch becoming a longitudinal furrow, running along ventral side of central projection. Basal portion of foot divided by a pair of muscular bundles, one ventral and another dorsal to visceral mass, both gradually converging to longitudinal muscles.

Mantle (Figs. 47-49): Very thin, translucent, with anterior aperture about 4 times wider than posterior aperture. No pigment. Anterior edge very thick (Figs. 47, 48), a pair of folds; outer fold relatively narrow, thickness equivalent to that of shell wall; inner fold 5-6 times wider and taller than inner fold, positioned inward. Posterior mantle flap tall, about 1/7 of shell length; aperture with ventral notch very deep (Figs. 47, 49), almost reaching flap base; posterior region of aperture wider; edges simple and thin. Posterior aperture preceded by wide notch, occupying almost entire ventral length; edges thin, simple; length of notch about 1/7 of total shell length.

Pallial cavity: Compressed by pedal and visceral structures, with approximately 1/3 of internal shell space. Mantle with about 7-8 transverse folds present in basal level of foot, uniform, very narrow (width equivalent to mantle thickness), spaced by equivalent width (of folds); surrounding entire mantle; length about 1/20 of shell length (Fig. 47: pf). Glandular area located just posterior to folds, area about 3 times longer than folds, composed by irregular, yellow acini, very low, plane, close to each other (Fig. 47: pl).

Visceral mass (Figs. 47, 48, 52, 53, 55, 56): Elongated and conical as internal mould of shell. Anterior region (about 1/4 of shell length) located inside posterior half of foot; posterior region of foot bulged ventrally, containing almost exclusively digestive tubes (foregut and intestinal loops) (Figs. 53, 55). Middle region with about 1/8 of shell length containing reno-pericardial structures, with about same width of posterior region of foot. Posterior region almost as long as anterior region, containing stomach in anterior half and gonad in posterior half (Figs. 47, 52). All structures described below. Region preceding kidney and anus, continuous with foot, ventrally bulged; this form maintained by cruciform-like musculature of local wall of integument (Fig. 50: cm).

Circulatory and excretory systems (Figs. 47, 50, 51): Pericardium a simple hollow chamber located in center of reno-pericardial ventral surface (pc). Dorsal surface touching stomach centro-anterior region; ventral surface bulging inside pallial cavity; anterior and a portion of dorsal surface touching kidney. No detectable heart. Kidney solid, pale beige, triangular, occupying about 3/4 of reno-pericardial area. No detectable inner folds or chamber. Nephropore a pair of slits as lateral ends of kidney; apparently lacking sphincter, protected by pair of low flaps, one anterior and another posterior. Anterior third of kidney surrounding rectum.

Digestive system: Enormous quantity of captacula (Figs. 47, 52). Conjunct of captacula about 4-5 times shell thickness. Base of captacula as curve flap located surrounding base of oral tube (Figs. 52, 54: cb), a distance equivalent to 1/5 of local visceral width from base of oral tube and restricted to ventral and lateral sides. Oral tube (Figs. 52-55: ot) wide, thin-translucent walled; length and width about 1/3 those of foot; base rounded, located somewhat equidistant from that of foot (dorsally) and of captacula (laterally and ventrally). Oral tube inner surface with pair of longitudinal folds (Fig. 55: of); each one U-shaped (opened anteriorly), located on each lateral side, dividing inner oral tube volume in three approximately equivalent chambers; tallness of each fold with about 1/4 of oral tube width; anterior ends of each fold gradual, distant from edge about 1/8 of oral tube length. Oral tube edge simple, undulating. Mouth located at base of oral tube (Figs. 53-55: mo), elliptic, simple, lacking apparent sphincter. Odontophore located on dorsal surface of esophagus, at about 1/20 of shell length posterior to mouth (Figs. 53, 55: od). Connection between esophagus and odontophore a small orifice with about half of local esophageal width, lacking sphincter (Figs. 57, 58: on). Odontophore spherical, with about 1/5 of visceral mass volume. Except for connection with esophagus, no other structure connecting odontophore with neighboring structures. Odontophore muscles (Figs. 57-62): mj, pair of thin protractor muscles (Figs. 57, 58), located immersed in halls connecting odontophore and esophagus, more concentrated laterally, becoming thinner ventrally (dorsal wall free from muscular tissue); originating in orifice with esophagus, inserting in odontophore cartilages lateral and ventral edges; m3, single muscle connecting dorsal edges of both odontophore cartilages (Figs. 59-62), about as wide as odontophore, with about 1/4 of odontophore thickness; m4, main pair of dorsal tensor muscles (Figs. 57-62), strong and

wide, originating on outer edge of anterior surface of odontophore cartilages, running posteriorly covering cartilages posterior edges, after running medially towards anterior, inserting in radular sac along its internal portion inside odontophore, origins almost as wide as cartilages, medial region with muscular fibers coming from each muscle imbricating, about half thick of m3; m6, single muscle of approximator of cartilages (Figs. 59-62), uniting medial-ventral edges of both odontophore cartilages, mainly in internal edges, with about half of cartilages length, posterior region with about 1/4 of each cartilage width, graduating becoming wider, anterior region with about double of posterior region, about half thick as m3; m7, pair of small muscles located inside radular sac lateral walls (Fig. 60); each with about 1/4 of radular sac wall width, originating in insertion of m4 pair, running towards posterior, gradually disappearing along radular sac lateral walls. Odontophore cartilages (oc) somewhat squared (with rounded vertices) (Figs. 61, 62), weakly curved and concave internally; thickness about 1/5 of that of odontophore; anterior edge about 85% shorter than posterior edge. Subradular cartilage expanding about 20% beyond radula in exposed (in use) region of odontophoral chamber connected to esophagus, performing a circular protective layer covering entire odontophore exposition inside this chamber (Figs. 6, 7). Radula relatively short, about 50% longer than odontophore length (Figs. 57, 58); color uniform pale brown; about half of radula located inside radular sac, possessing about same length of odontophore, positioned approximately in its center, and surrounded by pair of m4 muscles (Figs. 59, 60: rs); distal half of radula expanded, covering exposed portion of odontophore; about 20 rows of radular teeth along its length (Figs. 6, 7). Radular teeth (Figs. 6, 8, 9): rachidian (central) tooth almost rectangular, weakly curved; with about 1/4 of total radula width and about three times wider than long; no cusps or projections; distal edge shallowly concave and encased in preceding tooth, distal edge slightly thicker and shallowly convex. Pair of lateral tooth sigmoid, marginal half thinner and located at a position more distal than at medial half; width about 70% that of rachidian; medial half flattened, with rounded, relatively thick proximal edges, located approximately in same level of rachidian; lateral half with strong, subterminal concavity in proximal edge with about 1/3 of tooth's width, located approximately at level of following distal rachidian; proximal-marginal vertex marked by small cusp turned proximally. Pair of marginal teeth similarly shaped to rachidian, except in being flatter and obliquely positioned (approximate angle of

55° in relation to longitudinal axis of radula); medial edge thicker than lateral edge; medial edge articulating with lateral edge of lateral tooth. Esophagus running directly towards posterior (Figs. 53, 55, 56: es), flattened dorso-ventrally; length slightly longer than 1/3 of that of shell, width about 1/3 of local visceral width in anterior half, and gradually about half of that in posterior half. Esophageal insertion simple, on right side of stomach middle-dorsal region. Stomach (Figs. 47, 52, 53, 55: st) constituted by central chamber, with about 1/7 of total shell length, somewhat flattened dorso-ventrally, smooth, simple inner surface; and marginal digestive diverticles in lateral edges; about 20 pairs of similar-sized diverticles, each pair of diverticles performing lateral, flat expansions like wings, being slightly longer posteriorly (Figs. 50, 53, 55: dg); diverticles staying somewhat aligned in a virtual longitudinal line, directed externally, located immersed in lateral walls of visceral mass and part exposed in middle region of pallial cavity, each conjunct of diverticles with about 1/5 of shell length and about same width of stomach; surrounding animal walls towards ventral, performing, both conjunct of diverticles and ventral concavity. Each digestive diverticle with rounded tip; walls thin, translucent; performing an undulating cylinder with about 1/4 of local shell width; inner region hollow and continuous with stomach inner surface. Intestine originating in dorsal gastric wall just at left of esophageal insertion (Figs. 55, 56); both situated side by side and of equivalent size (about 1/4 of gastric main chamber). Intestine running direct towards anterior at a distance equivalent to 1/6 of shell length, up to visceral region just posterior to odontophore; in this region intestine performing a complex set of loops as shown in Fig. 55. Intestine with thin, translucent walls, with uniform width along its length, average width approximately 1/10 of local shell width. Rectum marked by gradual diminishment of width, crossing through kidney (Figs. 55, 56). Anus a small papilla, projected ventrally, edges somewhat expanded and thicker than preceding intestinal walls; located approximately at middle level of pallial cavity, on median line (Figs. 47, 50, 55: an).

Genital system: Gonad somewhat elliptical, with about 1/4 of shell length; about 4 times longer than wide (Figs. 47, 50); located in posterior limit of visceral mass, lying ventrally to posterior half of longitudinal muscles, and with ventral surface exposed in pallial cavity; color pale beige; gonad acini normally distributed in transverse rows connected in longitudinal furrow running along center. Anterior end of

gonad continuously connected to gonoduct, very thin walled (Figs. 56: gd), transparent. Gonoduct running towards anterior, between stomach and mantle, gradually running obliquely, from median line to right, crossing esophageal insertion; insertion on dorsal-right surface of kidney, just by side of local portion of esophagus.

Central nervous system (Figs. 53, 63, 64): Pair of cerebral ganglia located just dorsal to mouth (between bases of captacula and oral tube); each cerebral ganglion spherical, with approximate diameter equivalent to 1/15 that of anterior shell aperture; both ganglia located very close to one another and to median line; cerebral commissure very short, narrow, located in middle region of ganglia median surface; two pairs of large anterior nerves. Pair of pedal ganglia of equivalent size than cerebral ganglia, located on foot base at same level of cerebral ganglia, on opposite side of mouth; staying attached to ventral surface of pedal musculature; form of each ganglion roughly spherical, except for low expansions correspondent to each main nerve, being two anterior pairs and another pair postero-lateral. Pedal commissure short, very narrow, located in anterior region of medial surface of both ganglia. Pair of statocysts located just posterior to pedal ganglia, closer to median line; volume of each statocyst about 1/5 of each pedal ganglion; internally several statoconia. Visceral ganglia not seen. Pair of buccal ganglia very small (each ganglion about 1/100 of odontophore), located in ventral wall connecting odontophore to esophagus; distance between both buccal ganglia equivalent to 1/4 of odontophore width; a pair of anterior nerves and two pairs of posterior nerves.

Measurements (respectively antero-posterior length, dorso-ventral maximal lateral inflation in mm; finally tax of increase in mm/mm of length): MZUSP 32977: #1: 80.2 by 11.4, 0.142; #2: 74.5 by 11.0, 0.147; MZUSP 47189: 52.3 by 8.1, 0.154.

Distribution: From North Carolina, USA, to Rio Grande do Sul, Brazil.

Habitat: Sandy bottoms, from 40 to 1980 m depth; living specimens from 180 to 270 m depth (Steiner & Kabat, 2004; Caetano *et al.*, 2006). Content of buccal tube several foranmifer testa and rarely small mollusks.

Material examined: UNITED STATES. Florida. Dry Tortugas, Sand Key, 174 m depth, USNM 314457 (holotype of *Dentalium floridense*; Eolis sta. 301,

1915). BRAZIL. Rio de Janeiro. Off Cabo Frio, 350-400 m depth, MZUSP 32977, 21 specimens (o.t.; C. Cunha col iv/2001). São Paulo. Off Ubatuba, 320 m depth, MZUSP 47189, 17 specimens (R.V.W. Besnard sta. 5365; 07/xii/1988).

Genus *Paradentalium* Cotton & Godfrey, 1933
(Type: *Dentalium intercalatum* Gould, 1859, OD)

Paradentalium disparile (d'Orbigny, 1853)
(Figs. 10-15, 65-74)

Dentalium disparile d'Orbigny, 1853: 202 (pl. 25, figs. 14-17); Scarabino, 1973: 201 (fig. 8); Rios, 1970: 144; Matthews & Rios, 1974: 47; Steiner & Kabat, 2004: 584, 712.

Dentalium (Antalis) disparile: Pilsbry & Sharp, 1897: 56 (pl. 14, figs. 16-21); Henderson, 1920: 47 (pl. 6, figs. 4-8); Maury, 1922: 35; Haas, 1953: 203; Morretes, 1949: 53; Turner, 1955: 311; Penna, 1972: 230; 1974: 111; Abbott, 1974: 385 (fig. 4505); Almeida & Oliveira, 2000: 48, 54 (fig. 2).

Dentalium oerstedii: Jaekel, 1927: 130 (non Mörch, 1860).

Dentalium (Dentale) disparile: Rios, 1970: 144.

Dentalium (Heteroschimidoides) callinthrinx: Penna, 1972: 231; Almeida & Oliveira, 2000: 49 (fig. 3) (non Dall, 1889).

Antalis disparile: Scarabino, 1985: 198 (pl. 72, fig. 1012); 1994: 306 (pl. 106, fig. 1500); Díaz & Puyana, 1994: 256 (pl. 71, fig. 1040); García-Valencia & Díaz, 2000: 79; Steiner & Kabat, 2001: 440; 2004: 584.

Dentalium dispareli: Almeida & Oliveira, 2000: 48 (fig. 2) (err.).

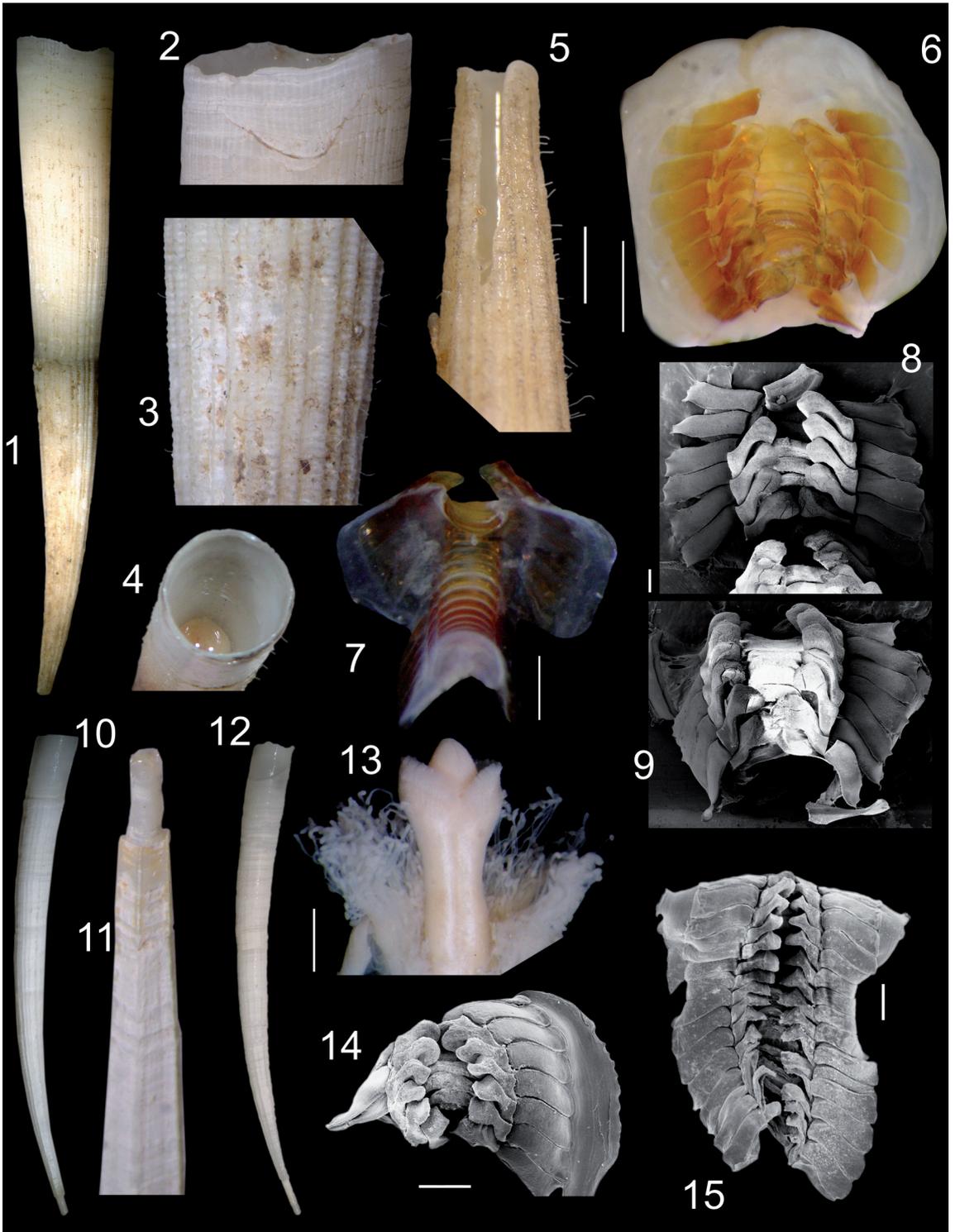
Paradentalium disparile: Caetano *et al.*, 2006: 11 (figs. 11-15); 2007: 797 (figs. 4-6); Caetano, 2007: 38-43 (figs. 19-25).

Types: BMNH 1854.10.4.465, 3 syntypes.

Type locality: Martinique.

Distinctive Description

Shell (Figs. 10-12): Size about 40 mm, walls thick, color white, weakly curved. Relatively abrupt widening (tax of increase about 0.087 mm/mm of length). Sculpture six longitudinal, primary ribs in posterior aperture area; secondary ribs gradually appearing towards anterior, extending up to anterior aperture; inter-rib



FIGURES 1-15: Shell, radular and anatomical aspects of Dentaliidae: 1-9) *Coccodentalium caduum*; 1) Shell, whole right view, MZUSP 32977, length = 74.0 mm; 2) Detail of anterior aperture, profile, right view; 3) Detail of sculpture of middle region. 4) Anterior aperture, anterior view, animal still inside; 5) detail of posterior aperture, dorsal view, scale = 2 mm; 6) Radula in situ, anterior view, scale = 1 mm; 7) Radula removed from odontophore, ventral view, scale = 1 mm; 8-9) Radulae of 2 specimens in SEM, scale = 200 μ m; 10-15) *Paradentalium disparile*; 10) Shell, whole left view, MZUSP 25589#1, length = 35.1 mm. 11) Same, detail of posterior aperture; 12) Shell, whole left view, MZUSP 25589#2, length = 31.5 mm; 13) Detail of dissected anterior region, central view, captacula deflected to show foot, scale = 2 mm. 14-15) Radulae of 2 specimens in SEM, scales = 100 μ m.

spaces smooth and somewhat irregular. Posterior pipe normally present. Posterior slit as in preceding species.

Main muscle system (Figs. 65, 66): Very similar in features to those of preceding species, except in being weakly thinner and narrower, and by pallial muscles in anterior region thinner.

Foot (Figs. 13, 68, 69): Character as described for preceding species, except in being somewhat narrower.

Mantle (Figs. 65-68): General features similar to those of preceding species. Main differences following. Anterior edge thick, feebly thicker than shell wall, length of thickness equivalent to 5% of total shell length; unclear separation in pair of edge folds. Pallial gland (Fig. 67: pl) a narrow transverse band located at short distance from, and weakly narrower than mantle anterior edge. Posterior mantle flap with narrower slit (Fig. 66).

Pallial cavity (Figs. 67, 68): Characters as described for preceding species. About 7-8 transverse folds also present in basal level of foot (Fig. 67: pf). Glandular area located just posterior to folds absent, presenting another located closer to mantle edge (Fig. 67: pl).

Visceral mass (Figs. 67, 68): Characters similar to those of preceding species, except in being somewhat narrower and with stomach proportionally shorter. Cruciform-like musculature of integument in postero-ventral region of foot absent.

Circulatory and excretory systems (Fig. 67): Pericardium and kidney with similar characters of previous species.

Digestive system (Fig. 68): Characters similar to *F. carduus*, except for the following features: Quantity of captacula apparently smaller (Fig. 13) but with similar remaining attributes; Oral tube edge straight; Odontophore muscles (Figs. 69-72): mj, pair of thin protractor muscles, slightly thicker; m3, shorter, about half of odontophore width (Fig. 71); m7, pair narrower and placed along median line (Fig. 69). Odontophore cartilages (oc) somewhat rectangular (with rounded vertices), about twice long as tall. Radula (Figs. 14, 15) with about 15 rows of radular teeth along its length. Radular teeth: rachidian (central) tooth with slightly more rounded cutting edge. Esophagus with glandular inner surface. Pair of lateral tooth with more irregular distal-medial tip, barely forming hooks. Stomach with about 1/9 of total shell length; marginal digestive diverticles in lateral edges; about 15 pairs of similar-sized diverticles. Intestine performing a complex set of loops as shown in Fig. 68.

Genital system: Characters somewhat similar to those of preceding species, except for more elongated and narrower gonad fashion (Fig. 67).

Central nervous system (Figs. 68): Main characters similar to those of *Coccodentalium carduus*, with the following remarkable features: Pair of cerebral ganglia more elongated laterally, possessing a single anterior nerve each (Fig. 74); Pair of pedal ganglia located in ventral surface of dorsal wall of foot base (Fig. 73); Each statocyst with volume approximately 1/3 of each pedal ganglion; Pair of buccal ganglia located more laterally in ventral wall connecting odontophore to esophagus (Figs. 70: bg); distance between both buccal ganglia equivalent to 3/4 of odontophore width.

Measurements (respectively antero-posterior length, dorso-ventral maximal lateral inflation in mm; finally tax of increase in mm/mm of length): MZUSP 25589: #1: 34.1 by 3.0, 0.088; #2: 30.6 by 2.8, 0.092.

Distribution: Florida, USA to Santa Catarina, Brazil.

Habitat: Sandy bottoms, from intertidal to 103 m depth, living species from 5 to 50 m depth. Content of buccal tube several foranmifer testa.

Material examined: BRAZIL. Rio de Janeiro. Angra dos Reis (iii/1969), MZUSP 25586, 19 specimens (sta. 345), MZUSP 25589, 2 specimens (sta. 334), MZUSP 25590, 1 specimen (sta. 341); Ilha Grande (R.V. Emilia), MZUSP 18135, 1 specimen (sta. 38, 12/xii/1965), 13 m depth, MZUSP 18137, 2 specimens (sta. 46, 10/xii/1965), MZUSP 25573, 1 specimen (sta. 30, 13/xii/1965). São Paulo. Ubatuba (Seção Bentos col.), Boqueirão, MZUSP 25645, 62 specimens (9/v/1962), Praia Sul, 16 m depth, MZUSP 25639, 2 specimens (23/iii/1962), Enseada do Flamengo, MZUSP 25627, 4 specimens (17/i/1962).

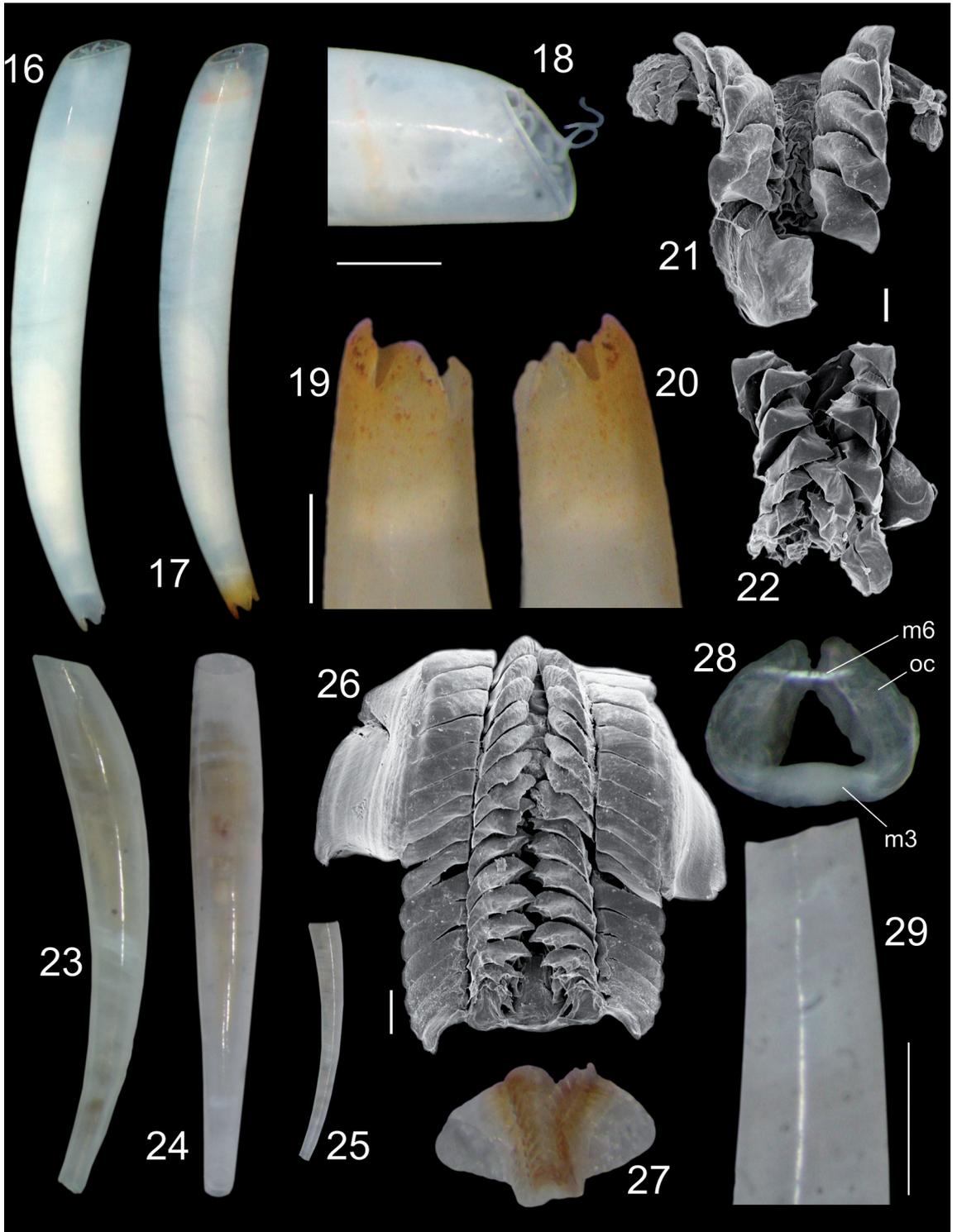
Family Gadilidae

Genus *Polyschides* Pilsbry & Sharp, 1898

(Type: *Siphodentalium tetraschistum*
Watson, 1879, OD)

Polyschides noronhensis new species (Figs. 16-22, 75-86)

Types: holotype MZUSP 88441. Paratypes: BRAZIL. Fernando de Noronha Archipelago. Porto Beach, 3°50'06.67"S 32°24'10.00"W, 6 m depth, MZUSP 32011, 3 specimens (Simone & Souza col. 20/viii/1999).



FIGURES 16-29: Shell and radular aspects of Gadilidae: 16-22) *Polyschides noronhensis*; 16) Holotype shell, left view, length = 8.6 mm; 17) same, paratype MZUSP 32011, length = 7.8 mm; 18) Paratype MZUSP 32011#1, left view, detail of anterior aperture in profile with some captacula, scale = 0.5 mm; 19-20) Paratype MZUSP 46736, detail of posterior aperture in profile, right and left views respectively, scale = 0.25 mm; 21-22) Radulae of 2 specimens in SEM, scale = 50 μ m; 23-29) *Gadila braziliensis* MZUSP 46736; 23) #3, right view, length = 7.5 mm; 24) #2, dorsal view, length = 7.9 mm; 25) #4, young specimen, length = 3.4 mm; 26) Radula in SEM, scale = 50 μ m; 27) Same in light microscopy; 28) Odontophore, radular ribbon removed, ventral view, maximum diameter = 0.7 mm; 29) #2, left view, detail of posterior aperture in profile, scale = 0.5 mm.

Distinctive Description

Shell (Figs. 16-20): Size about 8 mm, walls thin, color white, translucent; weakly curved; middle and anterior thirds almost straight, posterior third more curved (Figs. 16, 17). Softly widening (tax of increase about 0.125 mm/mm of length), general form almost cylindrical. Maximum width about half of shell length, located between middle and anterior thirds. Outer surface smooth, glossy. Anterior aperture oblique (ventral region slightly more posterior) (Figs. 16-18); weakly flattened dorso-ventrally; about 75% narrower than broader region of shell. Posterior aperture about half of anterior aperture size, rounded, weakly turned dorsally, normally pale-brown pigmented; four equidistant projections (Figs. 19, 20); dorsal and ventral projections about 50% wider than lateral projections; each projection with about 3% of total shell length.

Main muscle system (Figs. 75, 76): Pair of longitudinal muscles originating on ventral and lateral sides of base of apical flap, occupying about 3/4 of this base. Both longitudinal muscles running towards anterior, restricted to ventral side, touching one another along median line. Middle region of both muscles narrower than both ends (Fig. 76: lm). Both longitudinal muscles trifurcating in middle level of animal's body; external branches thin, splaying along anterior pallial wall; middle branches splaying in foot base as longitudinal layer of foot retractors (Fig. 79: mv); internal branches as pedal retractor muscles (Fig. 79: mf). Each pedal retractor muscle running anteriorly through haemocoel, flanking some intestinal loops (Fig. 80), connecting with its pair at middle level of haemocoel; after this, running as single bundle up to retracted pedal distal tip.

Foot (Figs. 78-80): Mostly hollow, looking like a retractile gastropod proboscis, with pair of above described pedal retractor muscles inserted in distal tip. Foot capable of enfolding along itself at about half its length (Figs. 79, 80). Foot with about 1/4 of animal's volume and approximately 1/3 of total shell length in retractile condition; width about half of adjacent shell width. Foot tip with central foramen corresponding to its enfolding portion. Transition between foot and insertion of pedal retractor muscles unclear; solid portion of foot about 1/6 its length; from this up to region of splaying longitudinal muscles of haemocoel (Fig. 79: mv) simple, thin walls.

Mantle (Figs. 75-78): Anterior edge thick, a pair of folds; outer fold relatively narrow, thickness equiva-

lent to that of shell wall; inner fold similarly thickened and 5-6 times longer than inner fold, positioned inwards (Figs. 75, 76, 78: mb). Posterior mantle flap tall, about 1/8 of shell length (Fig. 77). Low transverse septum present in base of posterior mantle edge (Fig. 78: ms).

Pallial cavity (Fig. 78): About 8-9 transverse folds present at posterior level of foot-visceral mass (Fig. 78: vm), uniform, very narrow (width equivalent adjacent to mantle thickness), spaced by equivalent width (of folds); only present in ventral half. Pallial gland with oblique folds (Fig. 78: pl) white, located approximately in middle region of mantle cavity, occupying about 1/6 of shell length; ventral folds slightly longer than dorsal folds and more anteriorly located; anterior edge of folds rounded and slightly taller, posterior end unclear. Transverse fold located close to mantle edge, with approximately same height of outer fold of mantle edge (Fig. 78: pf).

Visceral mass (Figs. 78-81): Middle region with about 1/10 of shell length containing renal structures. Posterior region of almost half of shell length containing practically only gonad (Figs. 78: go).

Circulatory and excretory systems (Fig. 78): Pericardium totally absent. Kidney solid, antero-posteriorly short, but with about same shell width.

Digestive system (Figs. 80-85): Moderate quantity of captacula (Figs. 18, 80). Conjunct of captacula about 2-3 times shell thickness. Oral tube inner surface three equidistant longitudinal folds; each one low, narrow (about 1/10 of oral tube width). Oral tube edge with four equidistant projections (Fig. 81: ot), lateral and ventral projection corresponding to inner folds end. Odontophore muscles (Figs. 82-85): mj, pair of thin protractor muscles, only distinguishable in ventral side of tube connecting odontophore and esophagus (Fig. 83); m4, main pair of dorsal tensor muscles shorter, about 2/3 of odontophore cartilages height (Figs. 84, 85); m6, approximator of cartilages very narrow, about 1/6 of each odontophore cartilages thickness (Figs. 84, 85); m7, absent. Odontophore cartilages (oc) somewhat rectangular, dorsal edge rounded, ventral edge bluntly pointed (Fig. 85), about twice longer than tall. Radula with about 15 rows of radular teeth. Radular teeth (Figs. 21, 22): rachidian (central) thin, with about 1/8 of total radula width. Pair of lateral tooth thick, with serrated cutting edge (Fig. 22). Esophagus relatively wide (about half odontophore width) in its region close to mouth,

gradually narrowing; inner surface simple, smooth. No differentiated stomach, neither clear separation between esophagus and intestine. Intestine very narrow (about 1/8 odontophore thickness); performing 3-4 simple loops (Figs. 80, 81) of similar width, partially compressed between pedal retractor muscles (Fig. 80). Anus a relative wide papilla (Fig. 78: an).

Genital system (Figs. 78, 81): Gonad somewhat triangular, with almost half of shell length; anterior region as wide as kidney, gradually narrowing towards posterior, ending at base of posterior mantle border. Gonad constituted for relatively long digital acini forming transverse folds; each acinus with almost half of gonad width and bifid distal end; gonadal folds highly protruding inside posterior half of pallial cavity, surrounding almost completely adjacent animal's diameter. Gonoduct running towards anterior and right, crossing rectum (Fig. 81).

Central nervous system (Figs. 79-81, 86): Located surrounding esophageal connection to mouth, edging base of oral tube as a nerve ring. Pair of cerebral ganglia located just dorsal to mouth; each cerebral ganglion spherical, with approximate diameter equivalent to 1/10 of that of anterior shell aperture. Pair of pedal ganglia of equivalent size to cerebral ganglia, located in opposite side of cerebral ganglia, ventrally to mouth; form of each ganglion roughly spherical. Pedal commissure with about half each ganglion length (Fig. 86). Cerebro-pedal connectives of similar length, lying on esophageal wall. Pair of statocysts located just posterior to pedal ganglia; volume of each statocyst about 1/3 of each pedal ganglion. Pair of buccal ganglia absent.

Measurements (respectively antero-posterior length, dorso-ventral maximal lateral inflation in mm; finally tax of increase in mm/mm of length): MZUSP 32011: #1: 8.0 by 1.1, 0.137; #2: 7.4 by 0.9, 0.122.

Distribution: Endemic to Fernando de Noronha Archipelago, Brazil.

Habitat: Sandy bottoms, about 6 m depth. Content of buccal tube several foranmifer testa.

Material examined: Types.

Discussion: *Polyschides noronhensis* possesses the shell character arrangement typical of the genus, as the maximum diameter located in the anterior third, and wide posterior aperture bearing four lobes. The

new species differs from the other co-generic species from the region (Caetano *et al.*, 2006; Caetano, 2007) mainly by the shape of the shell. *P. noronhensis* is wider than *P. tetraschistus* (Watson, 1879), and than *P. xavante* Caetano & Absalão, 2005, from which it also differs by a straighter shape. The other two species have a more arched shell, *P. noronhensis* still differs from *P. portoricensis* (Henderson, 1920) and from *P. tetradon* (Pilsbry & Sharp, 1897) in being narrower, particularly close to the anterior aperture, and in having a more uniform width along its length; *P. noronhensis* has the wider portion of the shell closer to the anterior aperture than the other two species, as it is in the anterior third in *P. portoricensis* and almost in the middle in *P. tetradon*.

Genus *Gadila* Gray, 1847

(Type: *Dentalium gadus* Montagu, 1803, OD)

Gadila braziliensis (Henderson, 1920)

(Figs. 23-29, 87-94)

Cadulus (Platyschides) braziliensis Henderson, 1920: 124 (pl. 19, fig. 16); Turner, 1955: 316; Scarabino, 1970: 41 (pl. 1, fig. 1); 1973, 198-199 (fig. 6); 1975: 182 (pl. 58, fig. 887); 1985: 201 (pl. 73, fig. 1032); 1994: 309 (pl. 107, fig. 1520); Penna-Neme, 1974: 115; Steiner & Kabat, 2004: 570, 715.

Cadulus (Platyschides) brasiliensis: Rios, 1966: 7; 1970: 143; 1975: 182 (pl. 58, fig. 887) (err).

Platyschides braziliensis: Scarabino, 1980: 113 (pl. 1, fig. 9).

Gadilabraziliensis: Steiner & Kabat, 2001: 445; 2004: 570; Caetano, 2007: 150-153 (figs. 141-142).

Cadulus braziliensis: Absalão *et al.*, 2005: 175-178 (fig. 2); 2006: 67.

Type: holotype and paratype USNM 96113.

Type locality: BRAZIL, off Rio de Janeiro, 23°08'S 41°34'W, 108 m depth (USBF).

Distinctive Description

Shell (Figs. 23-25, 29): Size about 8 mm, walls thin, color white-translucent, regularly curved; outer surface smooth, glossy. Relatively abrupt widening (tax of increase about 0.133 mm/mm of length). Wider portion weak, located approximately in anterior 1/5 of shell. Weakly dorso-ventrally compressed. Anterior aperture oblique, elliptical. Posterior aperture about

half of anterior aperture, circular. Other details in above given references.

Main muscle system (Fig. 88): Components similar to those described for *Polyschides noronhensis*.

Foot (Figs. 87, 88): Mostly similar in features to that of preceding species. Tip clearly rounded, stubby.

Mantle (Figs. 87, 88): General features as described for *Polyschides noronhensis*.

Pallial cavity (Fig. 87): Characters similar to those described for *Polyschides noronhensis*, except in lacking transverse folds in posterior level of foot-visceral mass, pallial gland, and transverse fold located close to mantle edge.

Visceral mass (Figs. 88): Similar organization of preceding species.

Digestive system (Figs. 88-92): Mostly similar to *Polyschides noronhensis* characters, distinctive features following: Odontophore muscles (Figs. 28, 89-92): mj, inconspicuous; m4, pair slightly narrower (Figs. 90, 91); m6, narrower 1/8 of each odontophore cartilages thickness (Figs. 28, 91, 92). Odontophore cartilages (oc) with ventral edge with wide furrow in middle level (Fig. 92). Radular teeth (Figs. 26, 27): pair of lateral teeth with three sub-terminal cusps in median third, being that more lateral approximately twice larger than remaining (Fig. 26). Intestine slightly broader; performing 3-4 simple loops (Fig. 88: in). Anus a relative wide papilla (Fig. 87: an).

Genital system (Figs. 87): Features similar to those of preceding species.

Central nervous system (Figs. 88, 94, 95): Features similar to those described for *Polyschides noronhensis*. Nerve connected to each cerebral ganglion wider in vicinity of these ganglia, forming almost a ganglion.

Measurements (respectively antero-posterior length, dorso-ventral maximal lateral inflation in mm; finally tax of increase in mm/mm of length): MZUSP 46736: #1: 7.8 by 1.3, 0.166; #2: 7.4 by 1.1, 0.149.

Distribution: Rio de Janeiro, Brazil, to La Plata river, Argentina.

Habitat: Sandy bottoms, from 23 to 220 m depth. Content of buccal tube several foranmifer testa.

Material examined: Types. BRAZIL (R.V.W. Besnard). Rio de Janeiro. Angra dos Reis; 23°13'S 44°24'W, 36 m depth, MZUSP 18761, 2 specimens (R.V.W. Besnard sta. 340, 19/iii/1969). São Paulo. Ubatuba; 23°47'S 44°58'W, 47 m depth, MZUSP 46736, 11 specimens (P.I. sta. 4854, 17/xii/1985).

Class Bivalvia

Family Nuculidae

Genus *Ennucula* Iredale, 1931

(Type: *Nucula obliqua* Lamarck, 1819, OD)

Ennucula puelcha (d'Orbigny, 1842)

(Figs. 30-38, 95-105)

Nucula puelcha d'Orbigny, 1842: 162; 1846: 624 (pl. 84, figs. 24-26); Schenck, 1939: 30; Carcelles, 1944: 268; Ihering, 1907: 371; Castellanos, 1967: 189 (pl. 14, fig. 5); Figueiras, 1976: 73; Roux *et al.*, 1995: 295, 301-303; Bremec & Roux, 1997: 157; Paiva, 2001: 428; Soares-Gomes & Pires-Vanin, 2003: 721; Acha *et al.*, 2004: 93; Absalão *et al.*, 2006: 67; Gilberto *et al.*, 2006: 5; Vinuesa & Varisco, 2007: 29.

Nucula puelchana d'Orbigny, 1842 (pl. 84, fig. 24-26); Borchert, 1901: 32 (pl. 3) [error].

Nucula uruguayensis E.A. Smith, 1880: 320-321 [loc: 36°47'S, 55°17'W, 51.2 m depth, off Rio de la Plata mouth].

Nucula savatieri Mabile & Rochebrune in Rochebrune & Mabile, 1889: 112 (pl. 8, fig. 2) [loc: Canal du Beagle; Baie Orange, Tierra del Fuego].

Ennucula puelcha: Dell, 1964: 141; Camacho, 1966: 53 (pl. 8, fig. 6); Scarabino, 2003: 229; Rosenberg, 2005; Clavijo *et al.*, 2005: 391.

Nucula (*Ennucula*) *puelcha*: Rios, 1970: 146 (pl. 50); 1975: 188 (pl. 60, fig. 918); Figueiras & Broggi, 1973: 203.

Nucula (*Leionucula*) *puelcha*: Abbott, 1974: 411; Del Rio, 1991: 27 (pl. 27, fig. 1); Rios, 1985: 203 (pl. 74, fig. 1040); 1994: 225 (pl. 78, fig. 1111).

Nucula (*Nucula*) *semiornata*: Del Rio, 1992: 12 (pl. 1, fig. 11).

Leionucula puelcha: Del Rio, 1998: 14, 48 (pl. 4, figs. 10, 11; pl. 16, fig. 5; pl. 24, fig. 10).

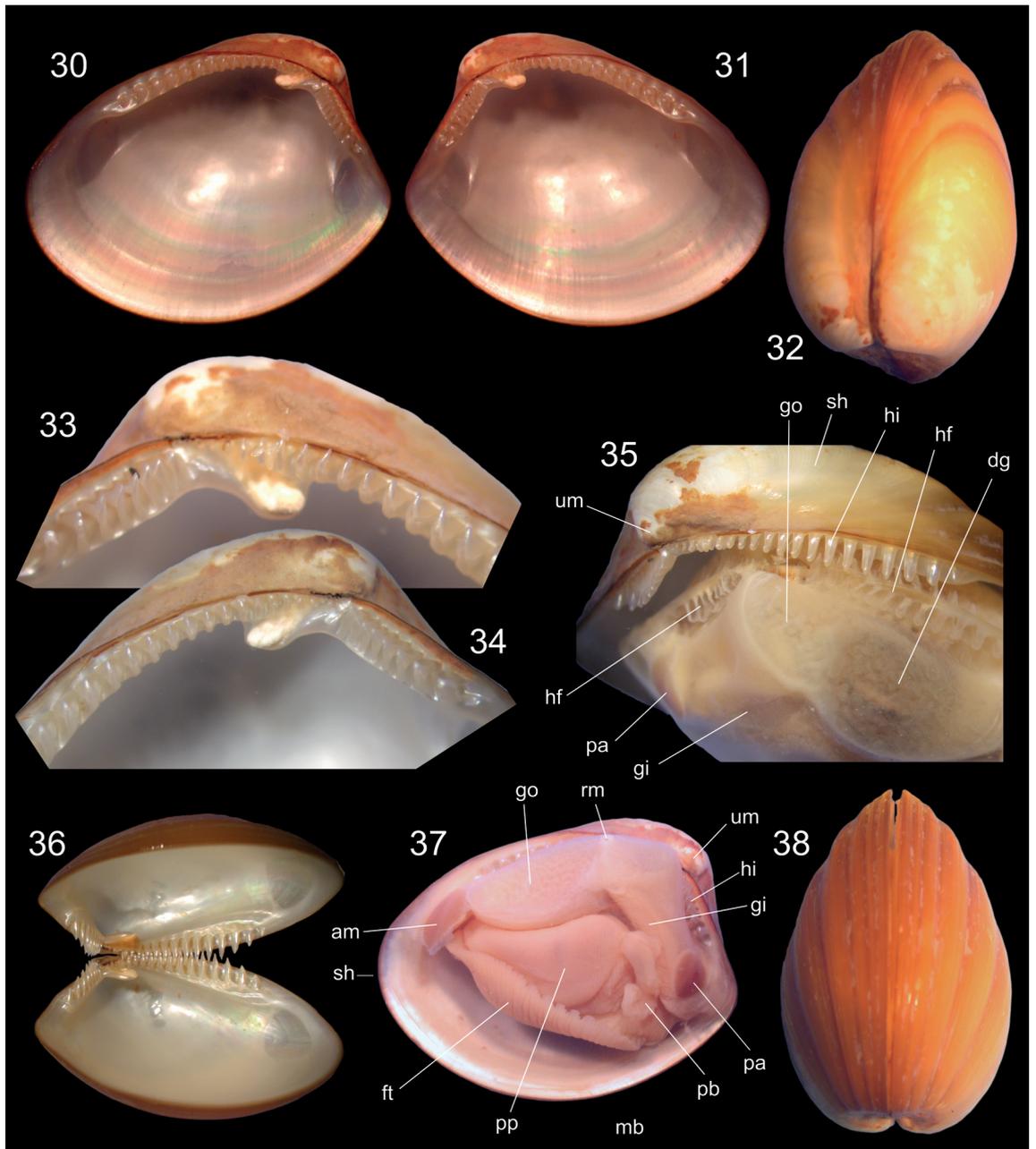
Types: lectotype BMNH 1854.12.4.774/1 (single valve; designation Aguirre, 1994). Paralectotypes BMNH 1854.12.4.774/2-3 (possibly of another species, see below).

Type locality: Riacho del Ingles, au fond de la Bahia de San-Blas, Patagonia (fossil).

Redescription

Shell (Figs. 30-38): Size about 15 mm, color pale to dark brown. Height about 80% of length; width about 60% of length. Periostracum glossy, smooth, relatively thick. Sculpture lacking except for growth

lines (Figs. 32, 38). Umbos tall, rounded, located close to each other (Fig. 31) approximate angle 110°, located about 20% of total length from posterior margin, extending about 10% of total height dorsal from hinge (Figs. 30, 31). Resilium internal, conic (wider region posterior), located approximately between pos-



FIGURES 30-38: Shell and anatomical aspects of *Ennucula puelcha* (MZUSP 19101; length = 13.0 mm): 30) Right valve, inner view; 31) Same, left valve; 32) Dorsal-slightly right view; 33) Left valve, detail of hinge, inner view; 34) Same, right valve; 35) Dorsal region with left valve somewhat still in situ, dorsal-slightly right partial view; 36) Whole shell, ventral view, valves somewhat deflected; 37) Whole left view, left mantle lobe partially removed; 38) Anterior-slightly ventral view.

terior and middle thirds of hinge (Figs. 33, 34). Ligament length about 10% of shell length and height about 5% of shell height. Inner surface glossy, silver-nacred, including hinge. Hinge with approximately 18 teeth anterior and 8 posterior to ligament; teeth increasing height from umbonal region towards both (anterior and posterior) ends (Figs. 35, 36); anterior set of teeth becoming dorso-ventrally wider towards anterior (Figs. 30, 31, 33-35); posterior set of teeth of similar width. Scar of anterior adductor muscle elliptical, about twice tall than long, located in middle level of anterior edge, about 15% of shell length away from anterior margin; occupying about 4% of inner surface of valve (Figs. 30, 31, 36). Scar of posterior adductor muscle with similar characters than anterior adductor scar, located in opposed side and with about 75% anterior scar size. Pallial line simple, located edging ventral edge a distance equivalent to 17% of shell height.

Main muscle system (Figs. 37, 95, 99): Anterior adductor muscle elliptical in section; about twice high than wide; occupying approximately 4% of valve; located between middle and ventral thirds of animal's height, and about 15% of shell length posterior to anterior edge; anterior region about half of posterior region (Fig. 35). Posterior adductor muscle approximately 75% anterior adductor muscle size, and positioned slightly in opposite region; remaining characters, including horizontal level, similar; clearly divided into two equally sized portions (quick and slow components) along dorso-ventral axis (Figs. 95, 98-100; pa). Pair of auxiliary protractor muscle of foot (Fig. 99: ap) very narrow and long; each one originating in dorso-posterior region of anterior adductor muscle in area approximately 1/150 of that of this adductor; running posteriorly and ventrally between integument and anterior foot musculature, splaying superficially along anterior foot base. Pair of foot protractor muscle (Fig. 99: fp), relatively thick and long; each one originating dorsally to anterior adductor muscle in area equivalent to 1/30 of this adductor; running towards posterior and slightly ventral a distance equivalent to half shell length, gradually broadening; inserting along lateral walls of visceral sac and middle pedal base. Pair of anterior pedal retractor muscle, very broad and thick (Fig. 99: fa); each one originating just dorsal and slightly posterior to origin of anterior protractor muscle in area equivalent to half of anterior adductor muscle; running towards ventral and slightly posterior, close to median plane, broadening weakly along their length; inserting along anterior foot base, fulfilling almost entire anterior volume

of visceral sac. Pair of middle pedal retractor muscle, broad and thick (Figs. 95, 98, 99: rm); each one originating in umbonal cavity, between posterior and middle thirds of distance between umbo and anterior shell margin, close to dorsal medial line, in area equivalent to 1/5 that of anterior adductor muscle; running towards ventral and slightly posterior, weakly curved (concavity anterior), widening gradually, positioning closer to medial plane; insertion in middle-posterior region of foot base, fulfilling most of middle-ventral volume of visceral sac. Pair of auxiliary middle pedal retractor muscle, narrow and long (Fig. 99: fr); each one originating just ventral to origin of middle pedal retractor muscle; running almost vertically towards ventral (slightly posteriorly), somewhat away from middle retractor muscle; inserting in middle region of foot base, flanked externally by middle pedal retractor muscles. Pair of posterior pedal retractor muscles, very broad and thick (Figs. 95, 98, 99: fm); each one originating at some distance dorsal and slightly anterior to posterior adductor muscle, in area slightly larger than half that of anterior adductor muscle, antero-posteriorly long (about three times longer than wide); running close to median plane towards ventral, almost vertically (slightly anterior); inserting along posterior pedal base.

Foot (Figs. 45, 95, 101): Laterally flattened, about 1/3 of shell volume. Distal region with expanded edges, umbrella-like, extending about twice foot width beyond lateral edges. Posterior vertical posterior flap (Fig. 101: ff) rounded, extending about 1/6 of entire foot length towards posterior, occupying ventral half of posterior foot surface, along medial plane.

Mantle (Figs. 35, 95): Mantle lobes symmetrical, thin, translucent, colorless. Mantle border trifolded (Fig. 96); outer fold tall and thin (about 1/3 of shell thickness), about 15 times taller than thick; middle fold with about same thickness of outer fold and about half its height; inner fold about double thick than remaining folds, only 1/5 of middle fold height. Periostracum positioned between outer and middle folds. Mantle border slightly thicker in base of folds. Inner fold differentiated in about 12 small pairs of papillae in ventro-posterior region (Fig. 95: ma); each papilla about as tall and as wide as middle fold, tip rounded, separated between neighboring papillae by space equivalent to width of each papilla. Mantle lobes totally separated from each other along entire ventral edges; connection between both lobes only in hinge region. Hinge dorsal fold of mantle (Fig. 35: hf), relatively tall, closely related to every shell tooth.

Pallial cavity (Figs. 37, 95, 101): Occupying about half of inner shell volume. Palps with about 1/3 of valves size; main (broader) region oval, slightly longer than half shell length and height (Figs. 101: pp); inner surface entirely covered by narrow transverse folds; each fold very narrow and close to each other, ventral end rounded, dorsal end connected with its pair of other hemipalp; inner palp folds diminishing in both ends, posterior folds situated slightly more separated from each other and in oblique, curved way (Figs. 101). Palp inner folds end before palp ventral edges, producing smooth, uniform margin. Proboscis of palps about as long as main portion of palps, and about 1/6 its width; located as posterior continuation of furrow between both hemipalps; inner surface as wide groove, smooth; proboscis tapering gradually, tip slightly rounded; edges undulating. Two pairs of small projections located only in inner hemipalps, by side and internally from proboscis; similar in characters to proboscis but about 1/10 its length and half its width; more ventral projection weakly smaller than dorsal projection (Fig. 101: pj). Palps inner folds reaching region close to mouth. Pair of small palp muscles located in postero-dorsal corner between both hemipalps (Figs. 95, 99: mu), running immersed in adjacent integument up to posterior region carving base of both posterior pedal retractor muscles. Gills bipectinate and proportionally small (about 1/15 of shell volume), about 6 times longer than tall; located obliquely from pericardial area to region ventral to posterior adductor muscle; anterior end rounded, gradually narrowing up to pointed posterior end. Gills posterior end supported by pair of suspensory stalks (Figs. 98, 100: gs), as thick membranes connected to ventral surface of posterior adductor muscle, close to median line. Suspensory membrane becoming shorter and wider towards anterior, supporting entire gills (Figs. 97, 98); in anterior region bearing some muscular fibers, and thin hypobranchial gland in both sides (Fig. 97: hg). Gills periphery connected to mantle and to visceral sac by cilia. Gill filaments symmetrical in both sides (Fig. 97), edges somewhat thicker, rounded ventrally and bluntly angled dorsally; afferent and efferent gill vessels (Fig. 97: af, cv) narrow, located in opposed sides of central rod, efferent vessel slightly broader than afferent vessel. Supra-branchial chamber about 1/6 of infra-branchial chamber.

Visceral mass (Figs. 35, 37, 98, 99, 102): With about half shell volume, placed as dorsal continuation of foot; strongly compressed by pedal musculature (Fig. 99). Stomach as central structure, positioned vertically from umbonal cavity up to region close to

ventral foot surface. Digestive diverticula pale green, located surrounding dorsal half of stomach, occupying about 1/4 of inner visceral volume. Gonad fulfilling remaining regions, mainly umbonal cavities, color cream to white. Digestive tubes mainly positioned at right from stomach, looping through digestive diverticula and gonad. Pericardium occupying about 1/5 of visceral volume, located posteriorly to umbos, flanking posterior pedal retractor muscles (Fig. 98); about twice wider than long. Transverse muscles well developed in region surrounding stomach (Fig. 102: tm), crossing through gonad, connecting both sides of pedal base integument; generally four anterior and five posterior to stomach.

Circulatory and excretory systems (Fig. 98): Located compressed between pair of posterior pedal retractor muscles and middle pedal retractor muscles. Pair of auricles elongated, connected to efferent gill vessel in ventral region of gills anterior end; crossing perpendicularly towards medial a distance equivalent to 1/4 shell width. Ventricle relatively small, located in middle region of pericardium, on median line, surrounding intestinal portion crossing pericardium. Kidneys solid, small (about 1/8 of pericardial volume), pale brown; located in both sides of pericardium, covering anterior region of gill.

Digestive system (Figs. 99, 102): Palps and digestive diverticula described above. Mouth small, located terminally between both palps (Fig. 101: mo). Esophagus located relatively far from anterior adductor muscle, passing between both anterior pedal retractor muscles, running a distance equivalent to 1/4 shell length on dorsal region of visceral sac; width about 1/6 that of anterior adductor muscle. Esophagus inner surface smooth (Fig. 103). Stomach large (about 1/4 visceral volume), broader and irregular dorsally, tapering ventrally (Fig. 102: st). Pair of ducts to digestive diverticula located ventral to esophageal insertion (Figs. 102, 103: dd). Inner surface of stomach (Fig. 103), mostly smooth; distinct thickness located on dorsal-right region, occupying about 1/3 of gastric inner area, supposedly gastric shield (gh); middle transverse gastric fold dividing horizontally entire circumference (middle gf) into two similar-sized halves. Pair of longitudinal folds located on left side of intestinal origin, separating style sac (ss) from intestinal portion of that region of stomach (inferior gf). This region corresponding to style sac equivalent to 1/8 of entire gastric volume. Intestine region after style sac forming strongly angled loop ventral to stomach (Figs. 99, 102); after this, running ventro-dorsally

between posterior series of transverse muscles and middle pedal retractor muscles (Figs. 99, 102); after this, performing complex series of loops (Fig. 99) at right from stomach; finally crossing from anterior to posterior in dorsal region of visceral mass along medial line, crossing through origins of middle and posterior retractor pedal muscles (Fig. 99) and pericardium. Entire intestine narrow (about 3/4 esophageal width), uniform width along its length. Rectum crossing along median line attached to dorsal and posterior surface of posterior adductor muscle. Anus simple, sessile (Figs. 98, 100).

Genital system: Gonad above described. No gonoducts detected.

Central nervous system (Fig. 99): Pair of cerebral ganglia located close to origins of foot protractor muscle (Fig. 99; ce); each one rounded, size equivalent to half esophageal transverse section. Cerebral commissure with about half shell maximum width. Pair of pedal ganglia (Figs. 99, 102; pg) 6-7 times larger than cerebral ganglia, about three times longer than wide; located close to median plane, flanking posterior surface of base of anterior pedal retractor muscle; each pedal ganglion with single main connective in both ends. Pair of visceral ganglia of similar size than cerebral ganglia (Figs. 98, 99; vg), located in space between pair of posterior pedal retractor muscle and ventro-posterior region of posterior adductor muscle. Cerebro-visceral connectives crossing gonad close to lateral regions of integument of visceral sac.

Measurements (respectively length, height and maximum inflation in mm): MZUSP 19101 #1: 13.0 by 10.0 by 7.6.

Distribution: From south Bahia, Brazil, to north Argentina (Pacific records contested, see below).

Habitat: Muddy bottoms, from infratidal to ~ 100 m depth.

Material examined: BRAZIL. Bahia. Alcobaça; Parcel de Paredes, 2-3 m depth, MZUSP 46333, 7 valves (Souza & Gonçalves col., 2005). Espírito Santo. Guarapari; MZUSP 77268, 6 specimens (Coltro col., 2006). Rio de Janeiro. off Campos, 22°34'S 40°29'W, 213 m depth, MZUSP 18793, 1 specimen (R.V.W. Besnard sta. 9, 11/iii/1969, laminarias); Angra dos Reis; MZUSP 56232, 1 shell (IOUSP sta. 327, iii/1969); Ilha Grande Bay (R.V. Emilia); MZUSP 18287, 1 specimen (sta. 5B, 1968) MZUSP 18284,

45 shells (sta. 132, 12/v/1966), 25.5 m depth, MZUSP 18289, 2 shells (sta. 7B, v/1965), 17.5 m depth, MZUSP 18276, 1 shell (sta. 31, 13/xii/1965), MZUSP 18281, 1 shell (sta. 65, 18/v/1966), MZUSP 18277, 4 specimens, (sta. 40, 12/xii/1965), MZUSP 18288, 1 specimen (sta. 6B), MZUSP 18278, 1 specimen (sta. 43, 11/xii/1965), MZUSP 18283, 1 specimen (sta. 118, 2/vii/1966), MZUSP 18286, 1 specimen (sta. 137, 4/vii/1966), MZUSP 18282, 1 specimen (sta. 104, 1/vii/1966), MZUSP 18280, 2 specimens (sta. 99, 1/vii/1966), MZUSP 18285, 6 specimens (sta. 134, 12/v/1966), 50-60 m depth, MZUSP 38458, 1 specimen (o.t., Magenta leg. vii/2003), (R.V.W. Besnard) 22 m depth, MZUSP 23658, 1 specimen (sta. 331, 21/iii/1969), MZUSP 23660, 1 specimen (sta. 341, 14/iii/1969), 30 m depth, MZUSP 23659 m, 2 specimens (sta. 339, 19/iii/1969). São Paulo. Ubatuba (Projeto Integrado; R.V. Veliger II); 23°37'24"S 45°03'48"W, 35 m depth, MZUSP 86366, 25 valves (sta. 2, 26/x/1985), 23°50'S 45°10'W, MZUSP 83141, 1 shell (sta. 22, 16/iv/1986); off Queimada Grande Island, 40-50 m depth (o.t., Coltro leg.), MZUSP 65891, 2 specimens (vii/2002), MZUSP 65892, 2 specimens (vii/2000), 50-60 m depth (Magenta leg., viii/2002), MZUSP 35717, 20 specimens, MZUSP 35753, 12 specimens. Paraná. off Paranaguá, MZUSP 35371, 8 specimens (o.t., Magenta leg. xi/1999) Santa Catarina. Bombinhas; Zimbros Bay, 5-8 m depth, MZUSP 32079, 1 specimen, MZUSP 32080, 1 specimen (in starfish stomach, o.t., Tarasconi leg. vii/1993); off Gaivotas, 29°33'S 48°57'W, 91 m depth, MZUSP 18787, 13 specimens (R.V.W. Besnard sta. 1706, 6/iv/1972). Rio Grande do Sul (R.V.W. Besnard). Off Tramandai, 30°12'S 50°11'W, 90 m depth, MZUSP 18788, 37 specimens (sta. 1723, 10/iv/1972); off Mostardas, 30°50'S 50°06'W, 79 m depth, MZUSP 18790, 10 specimens (sta. 1860, 6/vii/1972); Off Rio Grande, 32°48'S 50°27'W, 197 m depth, MZUSP 18789, 2 specimens (sta. 1758, 22/iv/1972). URUGUAY. Off Maldonado, 35°00'S 54°50'W, 23 m depth, MZUSP 19101, 62 specimens (GEDIP-RS sta. 1866; R.V.W. Besnard col., 11/viii/1972). Rocha (R.V.W. Besnard). Off Punta del Diablo, 34°05'S 53°30'W, 20 m depth, MZUSP 18792, 2 specimens (sta. 1877, 14/viii/1972); off La Paloma, 35°51'S 53°06'W, 206 m depth, MZUSP 18791, 1 specimen (sta. 1870, 12/viii/1972).

Discussion

Some reports of *Ennucula puelcha* have referred the species to the Pacific coast of South

America [Bernard, 1983: 10; Villarroel & Stuardo, 1998: 134-136 (figs. 29-32, 72, 110-112); Osorio & Reid, 2004: 78-79 (fig. 2J)]. However, the shells of the Pacific samples have more pointed umbones. This shell difference, allied to a relatively wide geographic distance and the glacial separation between that region and the south Atlantic coast of South America, are indicative of the reports from Chile and Peru that the species actually belongs to another, possible new species. This shell difference has also been pointed out in the literature (Osorio & Reid, 2004: 79). However, remarkably, the papers on the Pacific samples are those that changed the species from *Nucula* (Lamarck, 1799) to the genus *Ennucula*.

The type specimens of *Ennucula puelcha* were examined at BMNH (Figs. 104-110). The lectotype (Figs. 104, 105) matches with the specimens examined herein. On the other hand, the paralectotypes (Figs. 106-110) do not; in the meantime, they are somewhat similar to *Nucula semiornata* d'Orbigny, 1846, of which they can possibly be the types. The paralectotypes (Figs. 106-110) have taller umbones, the apical angle is narrower, the outer concentric sculpture is more evident (Figs. 106, 107, 110), the resilium is more projected and the hinge is narrower and possesses slightly more teeth (Figs. 108, 109). These characters fit the description of *N. semiornata* and differentiates it from that of *E. puelcha*. With the above mentioned possibility that the Pacific and Atlantic specimens belong to separate species, some species supposedly synonymous to *E. puelcha* were not included in the present synonymic list. These species are: *Nucula agujana* Dall, 1908 (described from Aguja, Peru; 1895 m depth). *N. pigafettae* Dall, 1908 (described from Magellan Strait; 494 m depth); and possibly *N. feliiponei* Marshall, 1928 (Bernard, 1983); as well as some Pacific citations of *E. puelcha*, such as Villarroel & Stuardo (1998) and Osorio & Reid (2004). Accounts on the anatomy of Pacific samples identified as *E. puelcha* are provided by Villarroel & Stuardo (1998, figs. 29-31, 72, 110-112). The stomach of the Atlantic specimens has a shorter style sac, about 20% in contrast to 60% of the Pacific species, and less developed dorsal sorting area and dorsal hood. Additionally, the gills are proportionally smaller, and the papillae in mantle edge are restricted to the posterior region in Atlantic species, while papillae occur in most mantle edges in Pacific samples.

Another *Ennucula* has accounts written on its anatomy, *E. tenuis* (Montagu, 1818) (Kuznetsov *et al.* 1983). In such *E. puelcha* differs in having proportionally larger palps and respective proboscises, as well as larger adductor muscles.

Family Solemyidae

Genus *Solemya* Lamarck, 1818

(Type: *Solemya mediterranea* Lamarck, 1818, SD Children, 1823)

Solemya notialis new species

(Figs. 39-46, 111-117)

Solemya patagonica: Rios, 1975: 186 (pl. 60, fig. 912-left) (part) (non E.A. Smith, 1885).

Solemya occidentalis: Rios, 1985: 207 (pl. 75, fig. 1058); 1994: 224 (pl. 78, fig. 1105) (non Deshayes, 1857).

Types: Holotype MZUSP 88440. Paratypes: BRAZIL. Rio de Janeiro. Cabo Frio, MZUSP 35257, 1 specimen (Paulo Gonçalves col.; v/2002); Off Maricá, 23°08'S 42°47'W, IBUFRJ 2172. 1 specimen (NOAS sta. CF-VII-6165); off Saquarema, 22°59'S 42°19'W, IBUFRJ 1335, 1 specimen (Geocosta Rio II sta. B3, 20/iii/1986); Angra dos Reis, 31 m depth, MZUSP 20396, 2 specimens (R.V. Emilia sta. 53; 29/vi/1966), 27 m depth, MZUSP 20397, 1 specimen (R.V. Emilia sta. 54; 29/vi/1966). São Paulo. Off Ubatuba, 33.5 m depth, MZUSP 20395, 1 specimen (R.V. Emilia sta. 12; 17/xii/1965).

Type locality: BRAZIL. São Paulo. Off Ubatuba, 23°25'S 44°43'W, 33.5 m depth (R.V. Emilia sta. 12, 17/xii/1965).

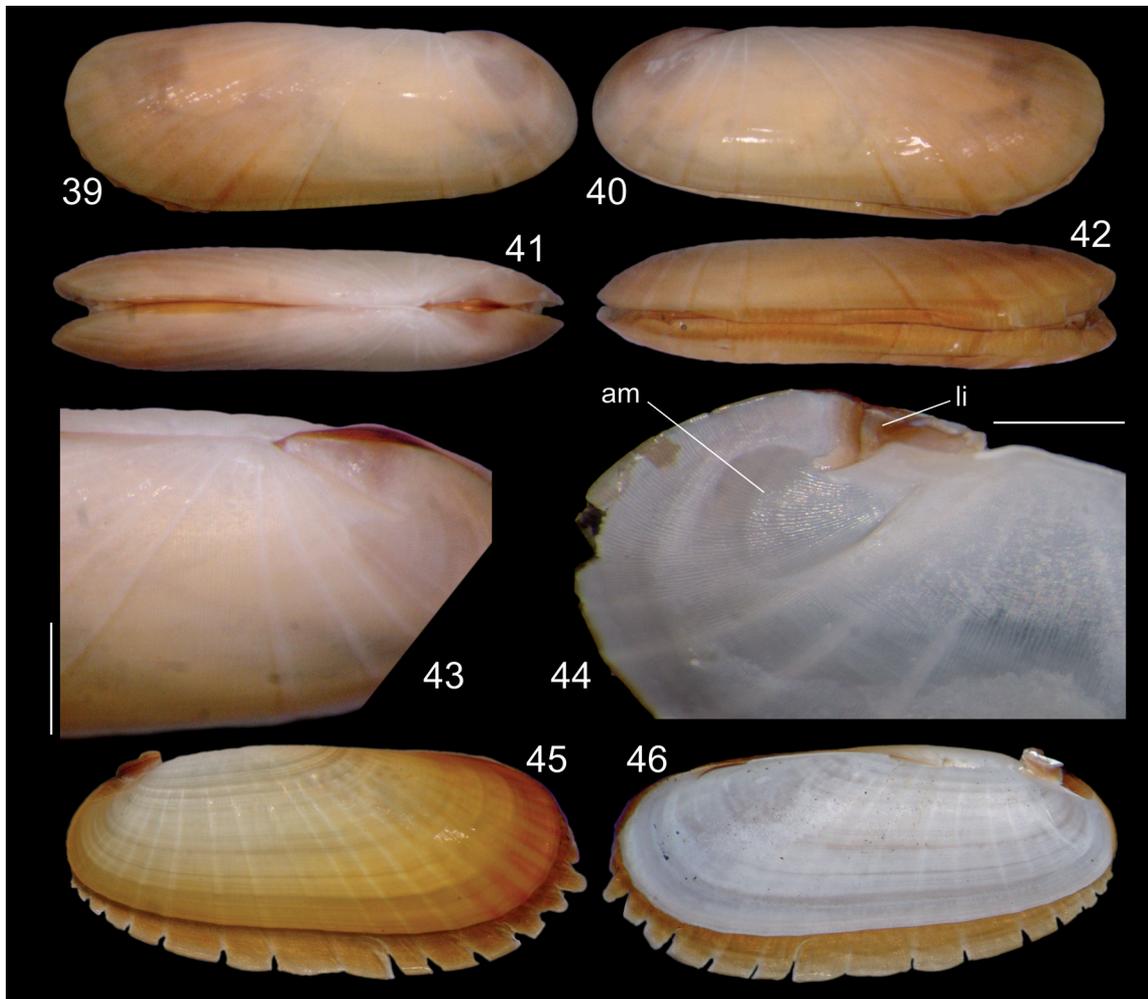
Description

Shell (Figs. 39-46): Thin, translucent, fragile, slightly rectangular; about 2.7 times longer than tall. Anterior and posterior ends rounded, similar-sized (anterior end slightly wider). Periostracum thin, translucent, glossy, beige-brown with radial, pale-beige bands, slightly more concentrated anteriorly (Figs. 39, 40, 45); clearer close to umbones; extending about 1/4 beyond calcareous portion of shell (Figs. 42, 45, 46), attached to ventral connection between both lobes of mantle (Fig. 114: pe). Umbones located preceding anterior quarter of shell length, not-protruded, flattened. Pair of oblique, shallow and narrow furrows, running gradually anteriorly to umbones towards posterior and ventral (Figs. 41, 43). Ligament simple, restricted to posterior region of mantle, being abruptly wider posteriorly, reaching about 1/6 of dorso-ventral shell height (Figs. 43, 44: li, 46). Hinge edentulous. Inner surface white, bearing transverse, fine striation (Fig. 44), gradually becoming oblique in anterior and posterior ends. Scar of adductor muscles approxi-

mately equal-sized; each one equivalent to 15% of calcareous portion of each valve (Figs. 44, 46); anterior adductor scar located close to dorsal edge, just posterior to anterior quarter of valve's length; posterior adductor scar located at short distance from posterior end (Figs. 46, 111). Pallial line simple, thick, located between middle and ventral thirds of shell height.

Main muscle system (Figs. 111, 113, 116): Anterior adductor muscle elliptical (with longer axis parallel to adjacent shell border) in section, attached in area equivalent to 15% of each valve area. Posterior adductor muscle similar in characters to anterior muscle, section slightly more rounded (for position of adductor muscles, see shell description). Pedal protractor

muscle of foot (Fig. 116: fp) broad and thin; originating surrounding ventral edge of anterior adductor muscle on both sides; running immersed in ventro-anterior wall of visceral mass, disappearing along foot dorsal base. Pair of anterior pedal retractor muscles (Figs. 111, 116: fa) narrow and long; originating just dorsal and posterior to anterior adductor muscle, in area equivalent to 1/15 of adductor muscle, antero-posteriorly elongated; running ventral and posteriorly with uniform width along its length; inserting splaying along wall between visceral mass and antero-dorsal foot base. Pair of median-anterior foot retractor muscles (Fig. 116: fb) very narrow and long, filiform; originating at small points approximately in middle of distance between umbones and anterior adductor



FIGURES 39-46: Shell aspects of *Solemya notialis* n. sp: 39) Holotype, left view, length = 10.6 mm; 40) Same, right view; 41) Same, dorsal view; 42) Same, ventral view; 43) Same, detail of peri-umbonal region, left-slightly dorsal view, scale = 1 mm; 44) Same, right valve, inner view, detail of hinge and anterior region, scale = 1 mm; 45-46) Paratype MZUSP 20397, right valve with extended periostracum, outer and inner views respectively, length = 12.9 mm.

muscles in area equivalent to 1/5 that of origin of anterior pedal retractor muscle; running towards ventral; inserting along ventro-anterior region of visceral mass, close to median line. Pair of auxiliary middle pedal retractor muscles (Figs. 111, 116: fr) broad and thick; originating in umbonal cavity close to median line, antero-posteriorly long (about 4 times longer than wide); running towards ventral, narrowing gradually; inserting just internally to insertion of anterior pedal retractor muscles. Middle posterior foot retractor muscle (Figs. 116, 117: fv) a single muscular layer covering posterior wall of visceral mass anterior to pericardium; originating as wide, transverse horseshoe (concavity anterior) located between anterior and middle thirds of distance between umbones and posterior end, anterior region thicker (almost as thick as auxiliary middle pedal muscles), directed internally, remaining regions about half thinned, performing an arc; running ventrally separating reno-pericardial structures from gonad; inserting along postero-ventral walls of foot. Pair of posterior pedal retractor muscles (Figs. 111, 116: fm), long and thick; originating just posterior and dorsal to posterior adductor muscle in approximately same area as adductors, slightly antero-posteriorly long (about twice longer than wide); running towards ventral and anterior almost half shell length, with uniform width along their length; inserting covering insertion of middle posterior foot retractor muscle in postero-ventral region of foot base. Large transverse muscle (Fig. 117: tm) located just ventral to pericardium, connecting both sides of middle posterior foot retractor muscle, approximately in its central region; size about 1/8 that of anterior adductor muscle. Pallial muscles see below (mantle).

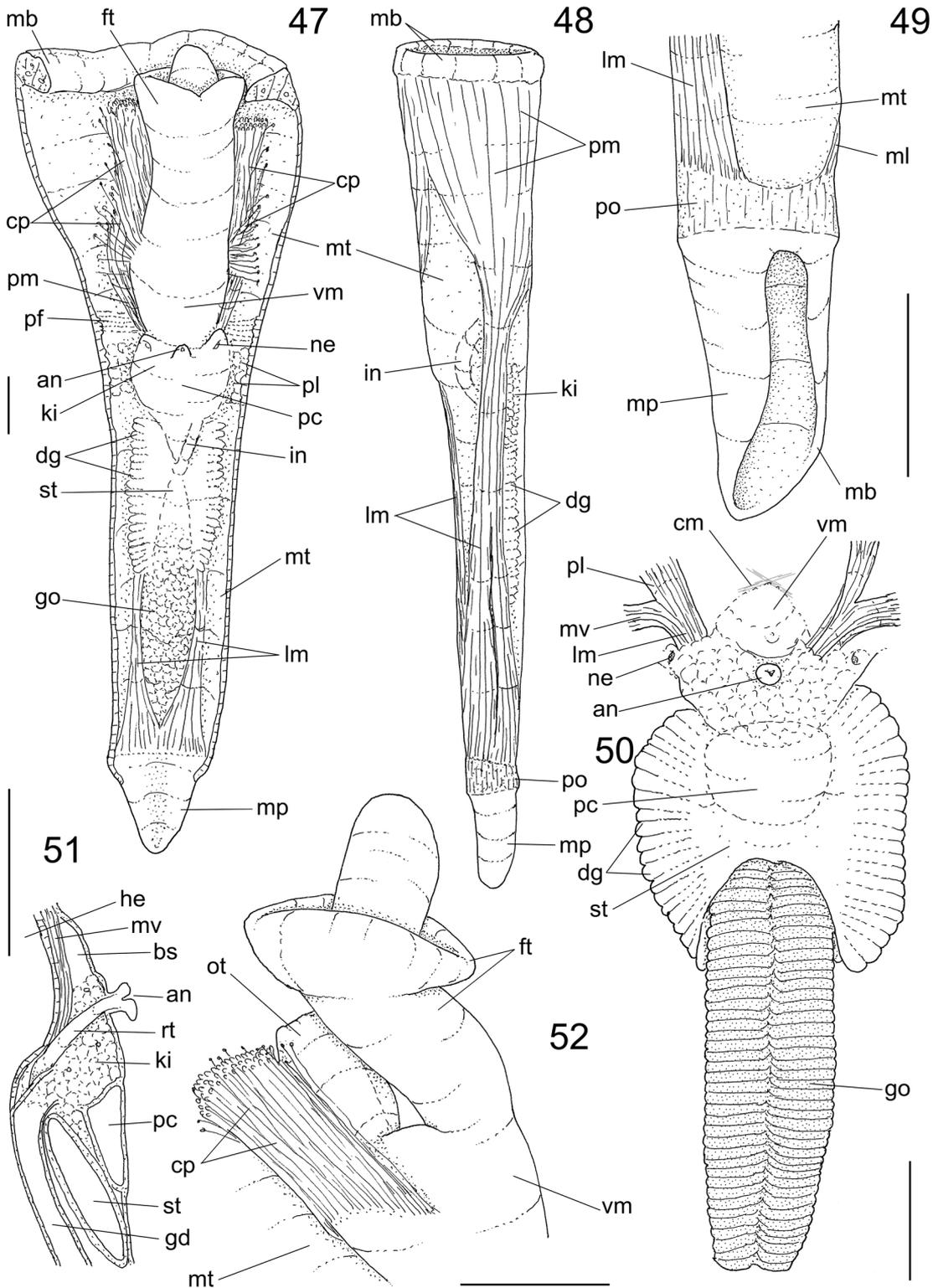
Foot and byssus (Figs. 111, 116): Foot with about 1/3 of inner shell volume, position directed anteriorly and ventrally. Foot cylindrical, with half to a third shell length in retracted condition. Foot distal tip umbrella-like, edges thinner, undulating and with short, stubby papillae; expanding externally about double the foot base width. No byssus.

Mantle (Figs. 111, 113-115): Mantle lobes about 25% larger than calcified portion of valves. Border of mantle lobes widely fused and thick, muscular. Pedal aperture anterior length about 1/3 that of shell. Excurrent aperture (Figs. 113, 115: se) located at middle level of posterior border about 8 times smaller than pedal aperture; edges simple; a series of papillae flanking excurrent aperture located at midway between inner edges and periostracum insertion (Fig. 115: ma); a larger dorsal papilla with approximately same length

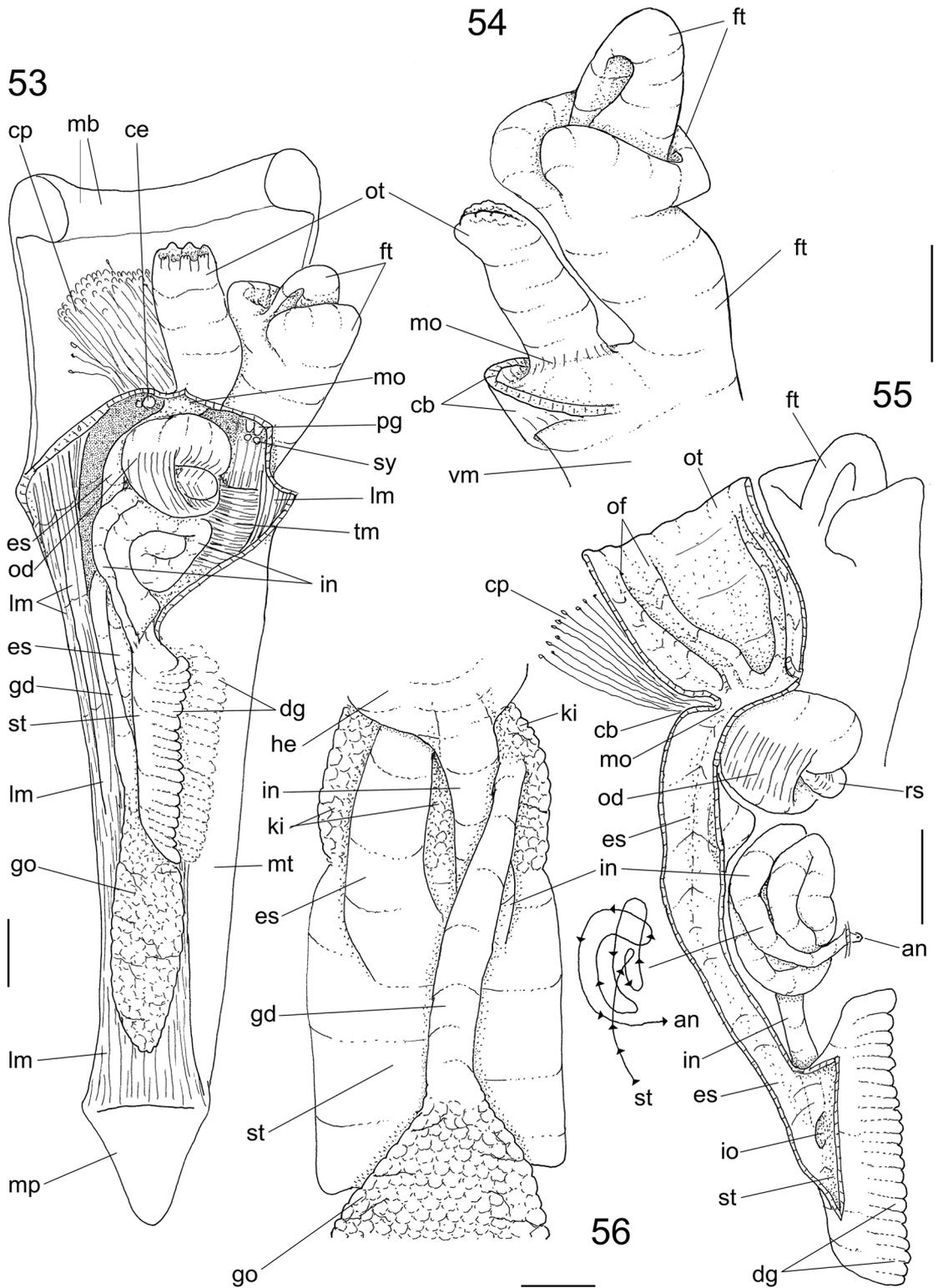
of excurrent aperture and width about 1/3 of adjacent mantle width, separated from excurrent aperture a distance equivalent to half its length; 2 pairs of papillae positioned between dorsal papilla and dorsal edge of excurrent siphon, outer pair with about half of dorsal papilla size, median pair with a quarter dorsal papilla size; 9 papillae surrounding ventral half of excurrent aperture, each one similarly sized to each other and with about 1/3 of dorsal papilla size. Pallial muscles mostly obliquely disposed (Figs. 113, 114: pm), with about double shell thickness; inserted in thick pallial line positioned between middle and ventral thirds of calcareous part of shell (Figs. 44, 46, 111, 114); about 2/3 of portion of mantle containing pallial muscles covered only by periostracum (Fig. 114). Pallial longitudinal muscle running along ventral pallial fusion (Fig. 114: lm) from pedal to excurrent apertures; slightly wider than shell's calcareous thickness; immersed dorsally by oblique muscles and ventrally by pallial tissue. Mantle edge located beyond calcareous portion of shell about 1/4 of its width (Fig. 114), possessing two folds, outer folds with tip rounded, about as tall and calcareous shell thickness, periostracum attached to their inner surface; inner fold thin (about 1/4 of outer fold), tall and fused to its pair.

Pallial cavity (Fig. 111): Occupying about 75% of each valve surface and more than half of shell volume. Pair of palps narrow and long (pp), about 5 times longer than tall, length approximately half of shell height; located about midway between anterior adductor muscle and gills' anterior end. Palps inner surface smooth. Gills bipectinate, with about half shell length and height; located in posterior half of shell. Dorsal gill filaments slightly larger, more obliquely positioned and possessing more rounded tip than ventral filaments; ventral filaments with pointed tip and positioned vertically. Gill filaments with skeletal rod lying at external edge, occupying about 1/3 of filament width (Fig. 112). Gill central, horizontal axis with efferent gill vessel externally and afferent gill vessel internally; gill longitudinal muscle lying along outer region of efferent gill vessel (Fig. 112: gm). Suprabranchial chamber small, mostly compressed by posterior foot retractor and adductor muscles and by kidneys (Figs. 116-117).

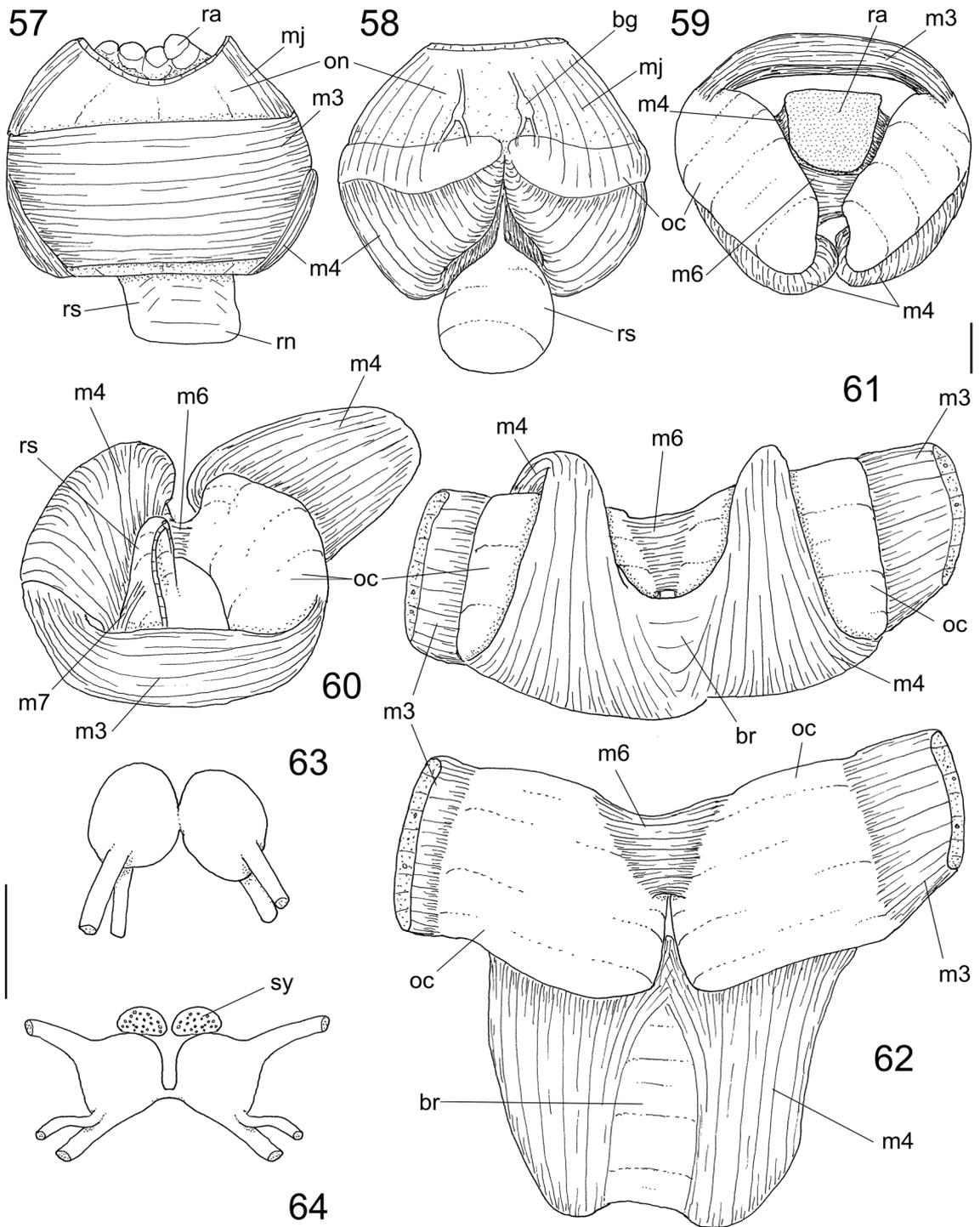
Visceral mass (Figs. 116, 117): Volume about 1/4 that of shell, located in central region of dorsal half. Mostly compressed by pedal and adductor musculature, divided almost completely in two halves by middle posterior foot retractor muscle (fv) (described above). Anterior half bent on dorsal surface of foot. Region anterior to middle pos-



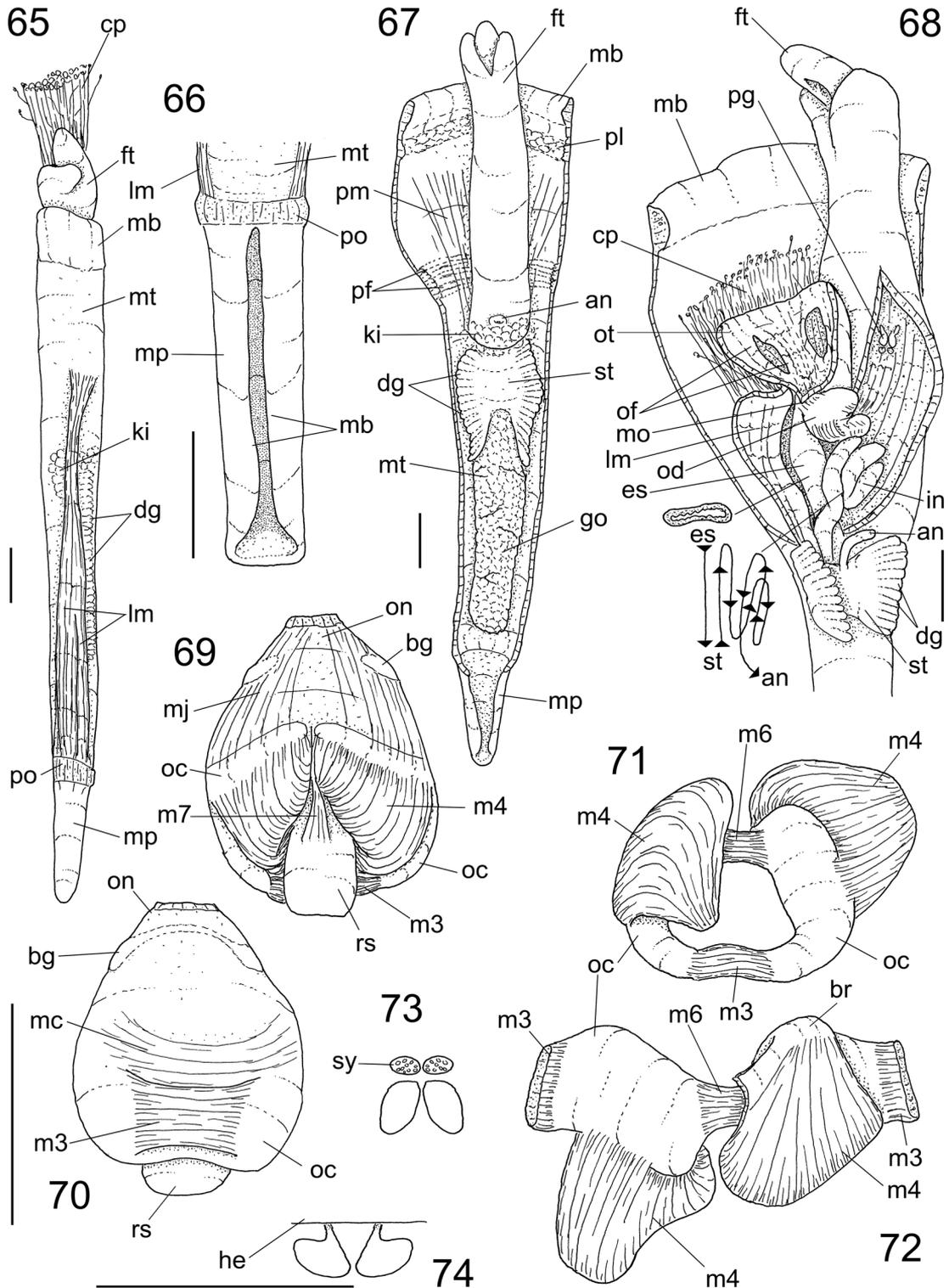
FIGURES 47-52: *Coccodentalium caduum* anatomy: 47) Whole ventral view, mantle opened longitudinally along median line and deflected; 48) Whole left view; 49) Detail of posterior region, dorsal-slightly right view; 50) Detail of middle and posterior region of pallial cavity roof, ventral view; 51) Anterior region of visceral mass, just posterior to haemocoel, transverse, semi-schematic section; 52) Foot and anterior region of haemocoel, left view. Scales = 2 mm.



FIGURES 53-56: *Coccodentalium caduum* anatomy: 53) Whole ventral-slightly right view, haemocoel opened longitudinally exposing internal organs, stomach partially deflected, topology of some other structures also shown; 54) Detail of foot and anterior region of haemocoel, left view, captacula mostly extracted, except their base; 55) Digestive tubes, left view, foregut opened longitudinally, topology of some adjacent structures also shown, trajectory of intestine indicated in schematic representation at left; 56) Middle region of visceral mass, dorsal view, outer layer of structures, main mantle and longitudinal muscles, removed. Scales = 2 mm.



FIGURES 57-64: *Coccodentalium caduum* anatomy: 57) Odontophore, dorsal view; 58) Same, ventral view; 59) Odontophore, anterior view, superficial layer of muscles and membranes removed, part of radula also removed (except portion inside radular sac); 60) Same, posterior view, radula completely removed, left portion of radular sac shown in situ, right m4 deflected; 61) Same, dorsal view, m3 transversally sectioned, both cartilages deflected; 62) Same, both m4 deflected downwards; 63) Cerebral ganglia, ventral view; 64) Pedal ganglia and statocysts, dorsal view. Scales = 0.5 mm.

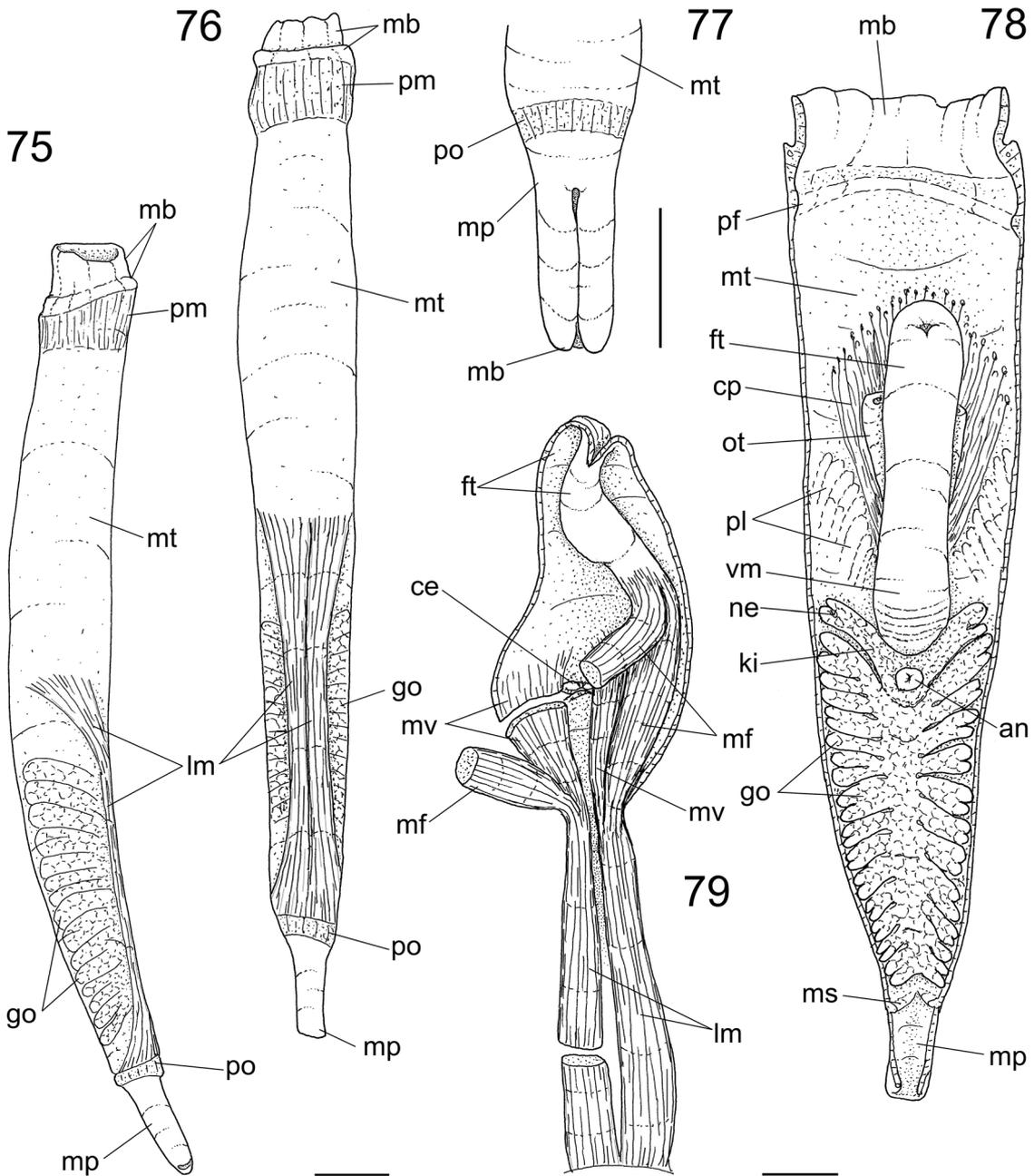


FIGURES 65-74: *Paradentalium disparile* anatomy: 65) Whole right view; 66) Detail of posterior region, dorsal view; 67) Whole ventral view, mantle opened longitudinally along median line and deflected; 68) Anterior region, mainly showing digestive tubes, right view, foregut opened longitudinally, topology of some adjacent structures also shown, trajectory of intestine indicated in indicated schematic representation at left, a transverse section of esophagus in indicated level also shown; 69) Odontophore, ventral view; 70) Same, dorsal view; 71) Odontophore, posterior view, radula completely removed, right m4 deflected; 72) Same, m3 sectioned transversally, both cartilages and left m4 deflected; 73) Pedal ganglia and statocysts, ventral view; 74) Cerebral ganglia, ventral view. Scales = 1 mm.

terior foot retractor muscle mostly filled by pale-cream gonad; region posterior to that muscle mostly filled by reno-pericardial structures, being pericardium dorsal and kidneys ventral, somewhat equivalently sized.

foot retractor muscle and posterior pedal retractor muscle; occupying about 1/4 of visceral volume. Pericardium oval, dorso-ventrally flattened; with about 90% of shell width. Pair of auricles lateral, positioned horizontally and transversally at middle pericardial region; connecting posterior end of gill efferent vessel with antero-lateral regions of ventricle. Ventricle oval,

Circulatory and excretory systems (Figs. 116, 117): Located in triangular space between middle posterior

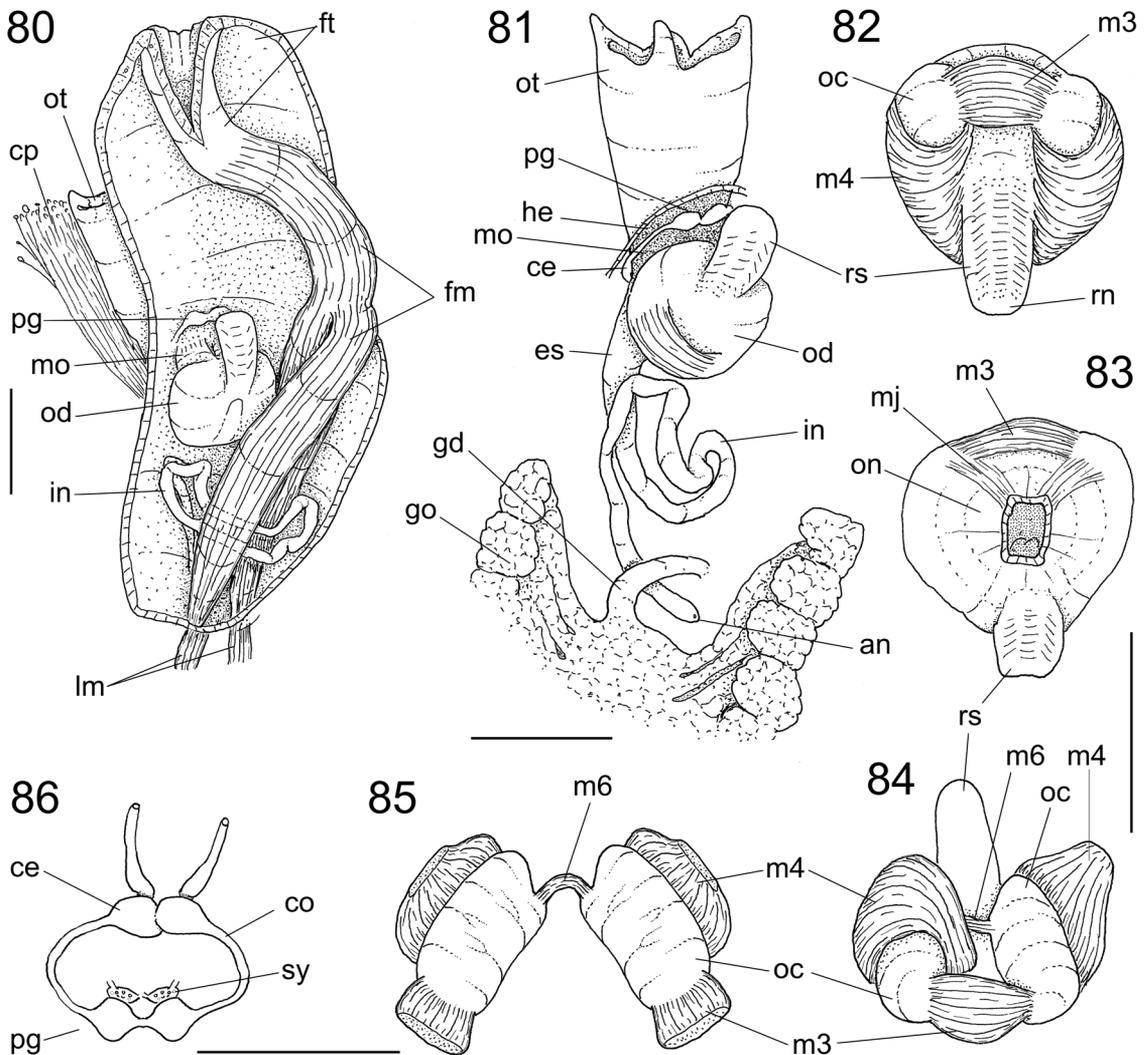


FIGURES 75-79: *Polyschides noronhensis* anatomy: 75) Whole left view; 76) Whole dorsal view; 77) Detail of posterior region, dorsal view; 78) Whole ventral view, mantle opened longitudinally along median line; 79) Haemocoel, dorsal view, mainly showing pedal musculature, foot and visceral sac opened longitudinally. Scales = 0.5 mm.

tapering posteriorly, with equivalent size of auricles and with about 1/5 of pericardial volume; surrounding 80% of intestinal loop crossing through pericardium. Kidneys solid, white, fulfilling ventral region of pericardium and dorsal surface of posterior pedal retractor muscle.

Digestive system (Figs. 116, 117): Pair of palps described above (pallial cavity) (Fig. 111). Mouth very small, located at central region between both palps, compressed between foot and anterior portion of visceral mass. Esophagus filiform, running between both auxiliary middle pedal retractor muscles up to

their middle level; suddenly running posteriorly, gradually expanding and forming stomach; lacking clear limit between esophagus and stomach. Stomach with about 1/10 of shell length, about three times longer than wide; inner surface smooth, simple; pair of ducts to digestive diverticula in anterior third of gastric lateral walls. Digestive diverticula small, mixed with gonad. Intestine also filiform, possessing single loop anterior to middle posterior foot retractor muscle, along median plane; crossing dorsal edge of this muscle, running along median line almost straight, edging hinge, passing between origins of both posterior pedal retractor muscles

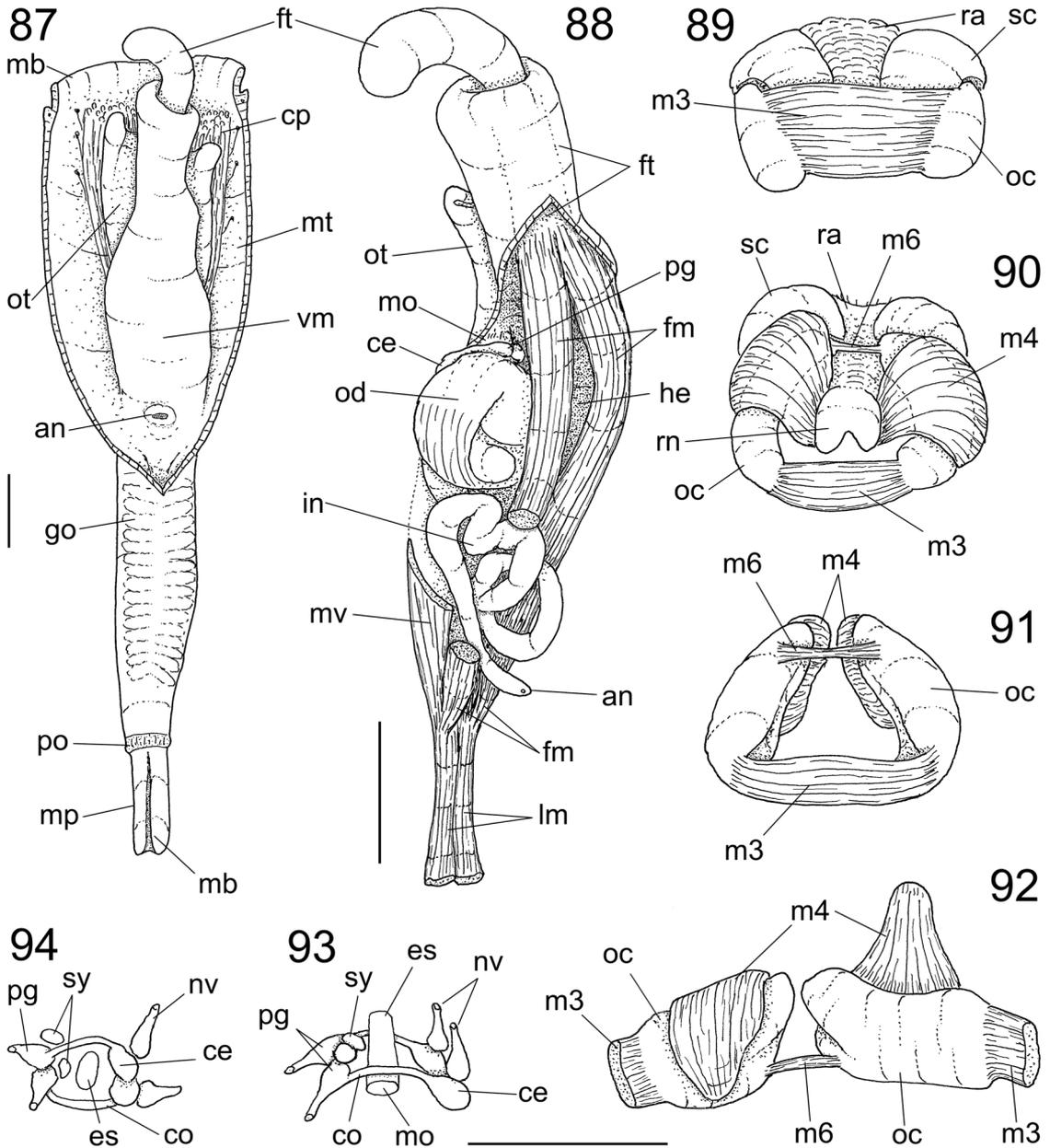


FIGURES 80-86: *Polyschides noronhensis* anatomy: 80) Haemocoel, dorsal view, mainly showing pedal musculature, digestive tubes and part of nerve ring, foot and visceral sac opened longitudinally; 81) Digestive tubes, dorsal view, topology of some adjacent structures also shown; 82) Odontophore, ventral view, superficial layer of membranes removed; 83) Same, whole ventral view; 84) Odontophore, dorsal view, radula removed (only radular sac topology indicated), right m4 deflected; 85) Same, m3 sectioned transversally, both cartilages and m4 deflected; 86) Nerve ring, anterior view. Scales = 0.5 mm.

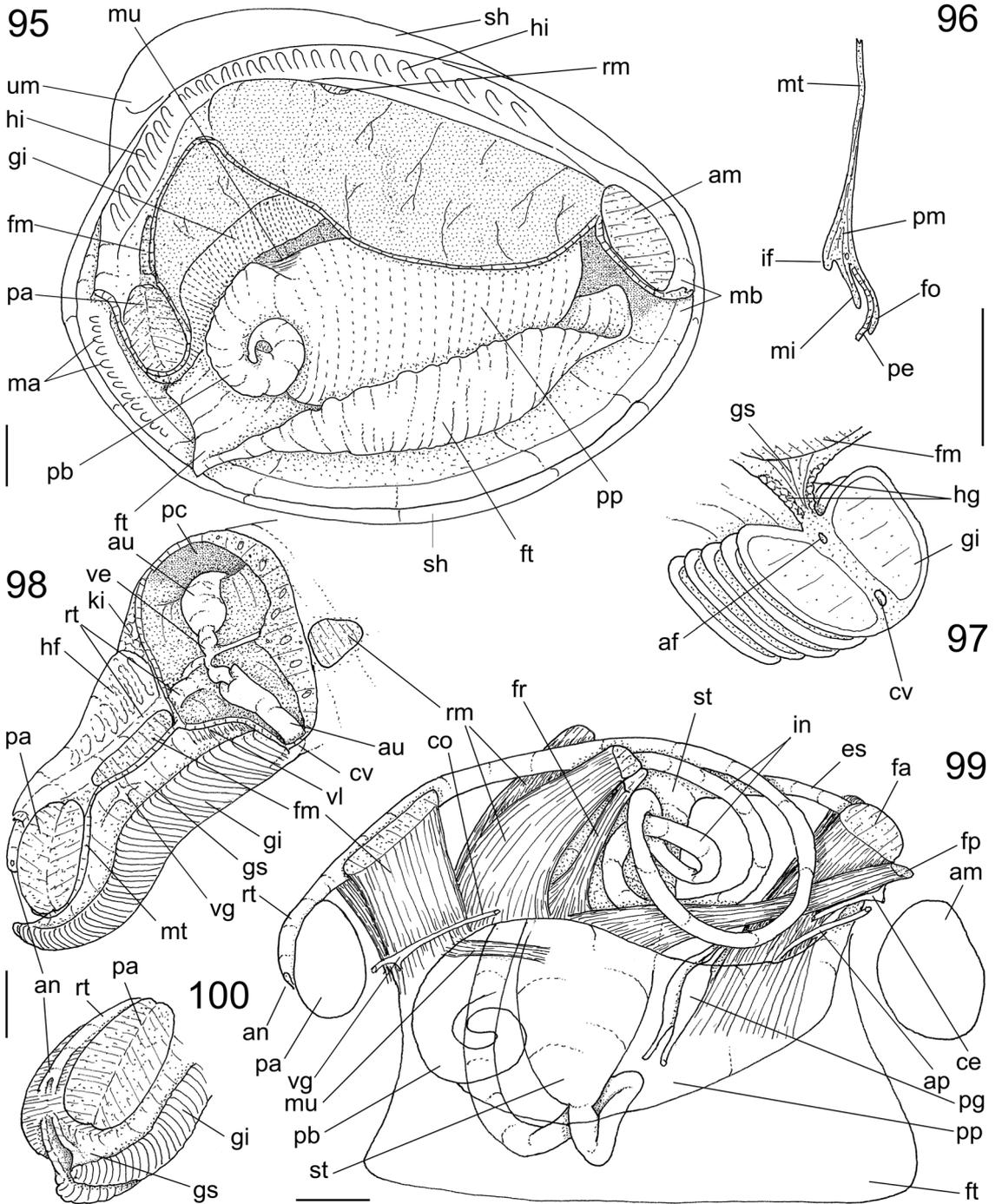
and along dorsal and posterior surface of posterior adductor muscle. Anus simple, sessile, located in middle level of posterior surface of posterior adductor muscle.

Genital system: Gonad described above (visceral mass). No detected genital duct or pore.

Central nervous system (Fig. 116): Cerebral ganglion a single, curved mass anterior to middle portion of esophagus, surrounding middle level of auxiliary middle pedal retractor muscle (fr); about 1/10 thickness of anterior adductor muscle in wider (anterior) region. Cerebral ganglion running along both sides horizontally towards posterior, through gonad, gradu-



FIGURES 87-94: *Gadila brasiliensis* anatomy: 87) Whole ventral view, anterior half of pallial cavity opened longitudinally along median line; 88) Foot and haemocoel, right view, more superficial structures, mantle and integument extracted, a portion of left retractor muscle of foot extracted to show intestine; 89) Odontophore, ventral view, superficial layer of membranes removed; 90) Same, posterior view; 91) Odontophore, radular ribbon removed, ventral view; 92) Same, both cartilages deflected, m3 transversally sectioned, right m4 deflected; 93) Central nervous system, left view, topology of adjacent esophagus also shown; 94) Same, anterior view. Scales = 0.5 mm.



FIGURES 95-100: *Ennucula puelcha* anatomy: 95) Whole right view, right valve and part of mantle right lobe removed; 96) Mantle edge, transverse section in middle portion of its ventral region; 97) Gill, transverse section in its middle region along 5 filaments; 98) Posterior half of visceral mass, dorsal-slightly right view, right mantle lobe and dorsal portion of pericardium removed; 99) Digestive tubes, main musculature and central nervous system in situ, right view, semi-diagrammatic representation artificially transparent; 100) Region of posterior adductor muscle, right-slightly posterior view, pallial lobes fully removed. Scales = 1 mm.

ally narrowing and becoming connectives with visceral ganglion; no clear separation between ganglion and connective. Cerebro-visceral connective crossing laterally in dorsal region of middle posterior foot retractor muscle (fv) (Fig. 117); crossing through dorsal muscular posterior wall of visceral mass (Fig. 117: mv), after this, running between gills base and dorsal region of posterior pedal retractor muscles (fm). Visceral ganglion a single transverse mass, slightly wider than preceding connective and with about 1/5 of cerebral ganglion size; located in middle level of dorsal third of posterior pedal retractor muscles. Two pairs of conspicuous lateral nerves running from each ganglion, running straight towards anterior in case of cerebral ganglion and on opposite side in visceral ganglion. No detectable pedal ganglion.

Measurements (in mm): Holotype: 10.9 by 4.1 by 2.3; paratypes 20395: 10.3 by 3.4 by 2.2.

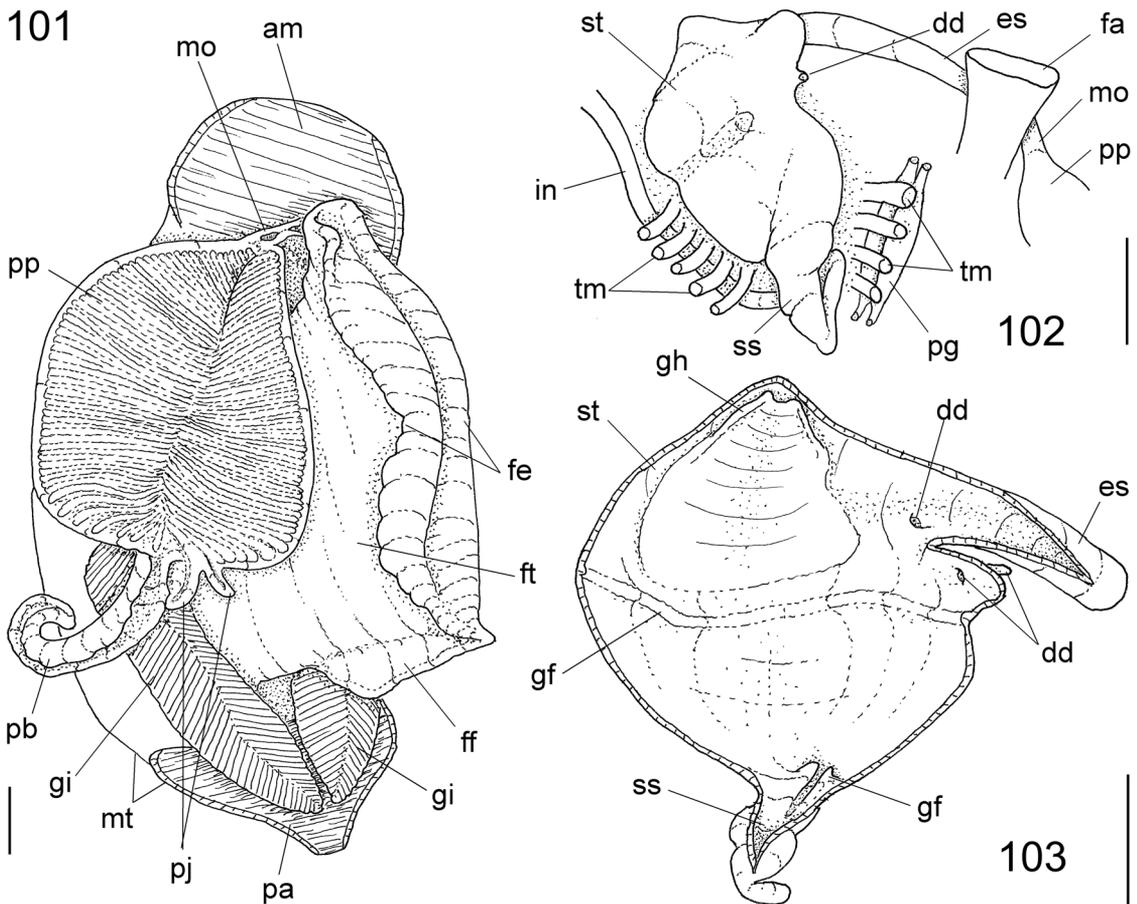
Distribution: Brazil, from Rio de Janeiro to Northern São Paulo.

Habitat: Unconsolidated substrate, about 30 m depth.

Material examined: Types.

Discussion

Solemya notialis has a shell very similar to *S. occidentalis*, and has thus far been identified as such. Nevertheless, important anatomical differences reveal the specific separation. *S. notialis* has much longer palps than *S. occidentalis* (Mikkelsen & Bieler, 2008), which has a comparable palp size to *S. cf. australis* (Reid, 1998, fig. 5-8E). On the other hand, there are some species lacking palps and entire digestive tubes (Reid, 1980). Those species that still bear digestive systems, even slightly re-



FIGURES 101-103: *Ennucula puelcha* anatomy: 101) Whole ventral-slightly right view, right hemipalps deflected, pallial lobes removed; 102) Midgut and adjacent structures in situ, right view; 103) Stomach and adjacent digestive tubes, right view, mostly opened longitudinally. Scales = 1 mm.

duced, still maintain suspension feeding (Krueger *et al.*, 1992). *S. notialis* differs from the western American species *S. reidi* Bernard, 1980, in having shallower pre-umbonal concavity, and from *S. valvulus* (Carpenter, 1864) in having a wider anterior region. *S. notialis* still differs from *S. patagonica* E.A. Smith, 1885, which has northern register in south of Rio Grande do Sul coast, in having shorter shell length (length/height tax of *S. notialis* is about 2.8; while that of *S. patagonica* is about 3.2), clearer color and less developed radial sculpture.

Discussion of Characters

Shell

1. *Portion of shell weakly calcified between two calcified portions (ligament):* 0 = absent; 1 = present (Bivalvia) (CI = 100; RI = 100).

The ligament of the bivalve shell is one of the conspicuous synapomorphies of the class. The structure, however, is part of the shell and is produced by a portion of the dorsal fold between both mantle lobes (Fig. 35: hf). The ligament, different from the re-

maining shell regions, is only or mainly constituted by conchiolin and is weakly calcified (Trueman, 1952; Owen, 1959), providing the abduction movement of the valves, antagonistic of the adductor muscles.

2. *Hinge:* 0 = absent; 1 = present (Bivalvia); 2 = taxodont (*Propeleda carpentieri*, *Ennucula puelcha*, *Barbatia cancellaria*) (CI = 66; RI = 85).

The hinge is the interlocking region between both valves of the bivalve shell, which is connected by the ligament. This region of the shell is produced by the lateral surfaces of the dorsal fold between both mantle lobes (Fig. 35: hf), and as such fulfill the space between a tooth and respective socket. In the case of the taxodont type of hinge, a series of somewhat uniform teeth are present. These appear in the basal bivalve branches, and raise the other types of hinges.

3. *Slit in posterior shell aperture:* 0 = absent; 1 = present (*Coccodentalium carduus*, *Paradentalium disparile*) (CI = 100; RI = 100).

Although a slit is present in the posterior mantle border of all examined scaphopods, a slit at the shell's



FIGURES 104-110: *Ennucula puelcha* BMNH type lot (1854-12-4-774): 104-105) Lectotype single (left) valve, outer and inner views, length = 13.0 mm; 106-107) Paralectotype #2, outer views of both valves, length = 6.8 mm; 108-110) Paralectotype #3, inner view of both valves and outer view of left valve, length = 7.8 mm; Paralectotypes 2-3 appear to be *Nucula semiornata* d'Orbigny, 1846.

posterior aperture is only found in the above mentioned species. Besides this character, no others are hereby applied to scaphopods because of polarization problems; however, further exploration of shell characters can be found in previous comparative analyses (*e.g.*, Emerson, 1952; Scarabino, 1995; Steiner, 1996).

4. *Periostracum*: 0 = ending with or short beyond calcified shell region; 1 = extending long beyond it (*Solemya* spp) (CI = 100; RI = 100).

The normal fashion of the periostracum is to extend little beyond the calcified portion of the shell. This free periostracum surrounds the calcified edge and encases in the inner surface of the outer mantle edge fold (Bottjer & Carter, 1980). In the case of solemyids, however, this free portion of the periostracum is much longer, extending about a quarter of the calcified portion beyond its edges (Figs. 45, 46).

5. *Umbos*: 0 = absent; 1 = opisthogyre (*Solemya* spp, *Propeleda carpentieri*, *Ennucula puelcha*); 2 = prosogyre (*Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

A portion of the shell called umbos is the part which is oldest. This portion, exclusive of the bivalves, is a pair, *i.e.*, an umbo in each valve. In the case of the protobranchs, the structures are opisthogyre, meaning they are turned backwards (Fig. 37). This feature is particularly clearer in the nuculids, as their umbos are protruded. In the remaining protobranchs, however, the umbos are flat and difficultly individualized (Figs. 39, 40, 45). On the other hand, the other bivalves have prosogyre umbos, *i.e.*, turned forwards, being a notorious lamellibranch synapomorphy. Despite the fact that the states of this character are not considered additive, the result shows that they possibly are. Analyzing the cladogram, the opisthogyre umbos appear to be a bivalve synapomorphy, becoming prosogyre at node 9, which represents the lamellibranchs.

Several other shell features were researched, but were not utilized here due to an autapomorphic nature in the present sample, or because of difficulty in polarizing. One of them is the nacre, inner aragonite layer of the shell. This layer is present in basal taxa of most conchiferan classes, notoriously in Gastropoda, Cephalopoda and Bivalvia; and mostly lost in higher taxa (Watabe, 1988). However, the nacreous layer is absent in Scaphopoda, in bivalve Solemyidae and in several lamellibranchs, including both sampled here. Considering nacre in this analysis, it assists in support

of node A (Conchifera minus monophacophorans), with remarkable reversions in nodes 2, 6 and 9. On the other hand, nacreous structure was considered apomorphic in bivalves (Giribet & Wheeler, 2002).

Another example is the shell sculpture. The feature is very difficult to polarize, as all kinds of sculptures are found both in ingroups and outgroups. Longitudinal striae are, however, found as basal stock, having smooth and annulated forms as derived states in scaphopod analyses (*e.g.*, Reynolds, 1997; Steiner, 1998; Reynolds & Okusu, 1999). Similar difficulty in polarizing exists for other scaphopod shell attributes, such as curvature, placement of wider region, etc., which certainly are worthy of a longer analysis of the class.

Mantle

6. *Mantle*: 0 = conic; 1 = divided into two lobes (*Bivalvia*, Scaphopoda) (CI = 100; RI = 100).

The conic state is found in those classes that possess a shell practically restricted to the dorsal region of the body; the cone can be flattened, as in monoplacophores, or deep (a bind-sac) as in gastropods and cephalopods. The lobed state is something like a horse saddle that mostly covers the dorsal and lateral regions of the animal's body. In the case of bivalves, this bilobed condition persists from the larval phase to adulthood, and each lobe secretes each shell valve. A hinge fold of the mantle (Fig. 35: hf) lies on the intersection of both lobes, building the hinge and the ligament. While in the case of scaphopods, the bilobed condition is restricted to the larval phase. The ventral edges of these lobes fuse ventrally, producing a tubular conformation, which secretes the tubular shell.

Lateral mantle lobes have been used to base *Diasoma* upon some previous phylogenetic analyses (Steiner, 1996; as *Loboconcha*; Giribet & Wheeler, 2002, characters 50, 51).

7. *Lobes free ventrally in adult phase*: 0 = absent; 1 = present (*Bivalvia* except *Solemya*) (CI = 100; RI = 100).

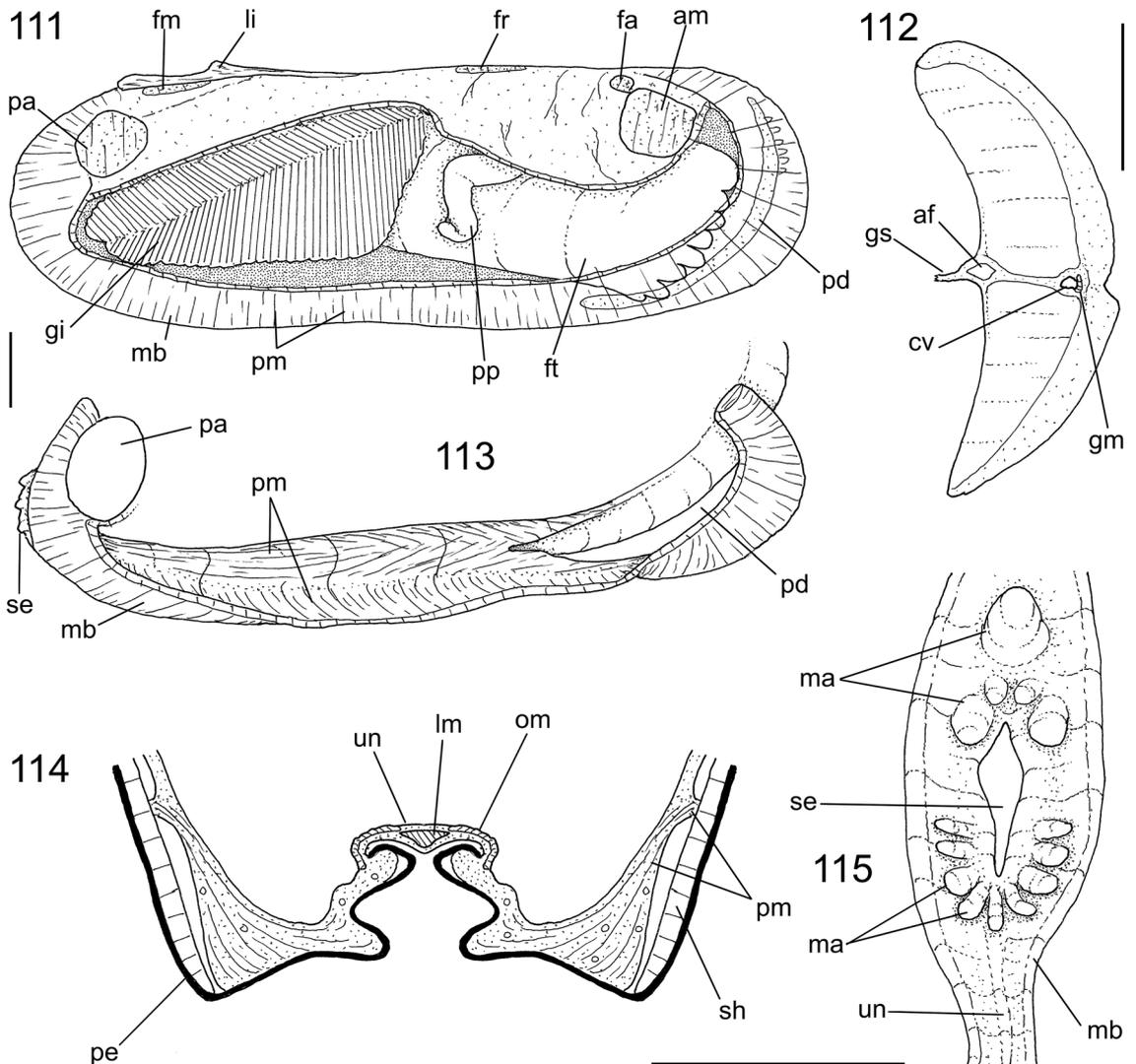
As explained in the previous character, the characteristic state of scaphopods is to have a fusion of the mantle lobes during metamorphosis. However, a similar process happens in solemyids, which possess mantle lobes that are totally fused ventrally (Figs. 42, 113-115) (Beedham & Owen, 1965). In fact, the solemyid mantle is fashioned in a very similar way to those of scaphopods. Analyzing the allocation of the character on the cladogram, the fusion of mantle lobes

in metamorphosis appears to be a basal *Diasoma* feature; freedom of the ventral edge of the mantle lobes is only based on node 7.

Different degrees of mantle fusion are, on the other hand, observed in lamellibranchs (e.g., hiatellids – Simone & Penchaszadeh, 2008). However, those cases are convergences or, in the light of the present study, possibly reversions.

- 8. *Mantle edge*: 0 = mono- or bifolded; 1 = trifolded (*Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

The mantle edge of shelled mollusks is particularly an important structure, as it secretes most of the shell and bears some receptors to interact with the environment. The mantle edge has one or two lobes in most molluscan classes, including the basal taxa of the ingroup (Figs. 47, 49, 67, 114). Protobranch nuculids (Fig. 96) and lamellibranchs are those which have a trifolded mantle edge condition, revealing to be a conspicuous node 8 synapomorphy. In the embryology, the middle fold in higher bivalves appears later (Morton *et al.*, 1998, fig. 4.8A), which also indicate via ontogeny the apomorphic state of the trifolded mantle edge.



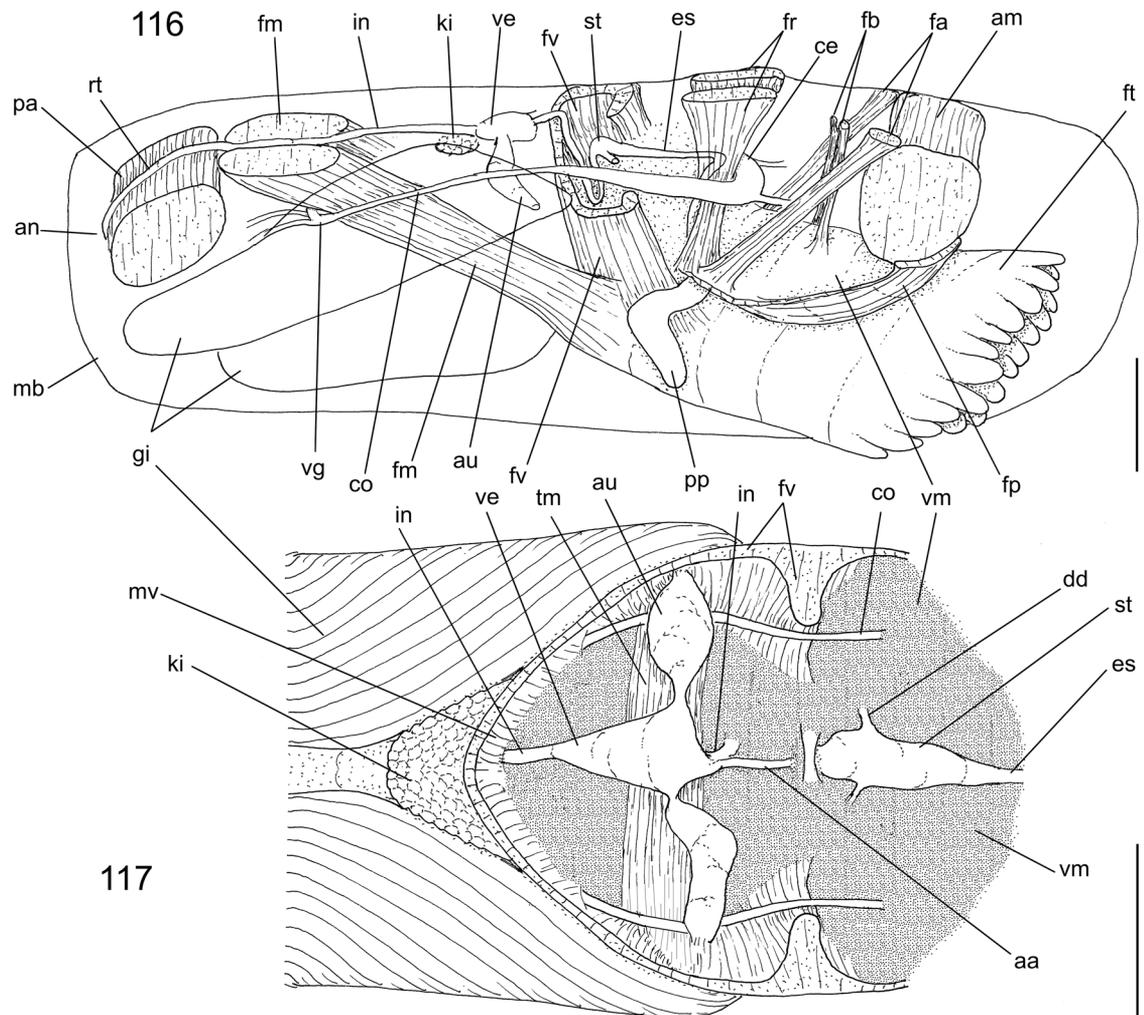
FIGURES 111-115: *Solemya notialis* anatomy: 111) Whole right view, part of right mantle lobe removed, some structures show by artificial transparency; 112) Gill, transverse section in its middle region; 113) Mantle border, right-slightly dorsal view, remaining portion of mantle lobes removed, topology of some adjacent structures also shown; 114) Same, transverse section in middle level of ventral region; 115) Mantle border in region of excurrent siphon, posterior-outer view. Scales = 1 mm.

Additional features can be found in the epithelium of scaphopod anterior mantle edge, which can differentiate both orders (Steiner, 1992a, 1996: 331).

- 9. *Pallial cavity*: 0 = opened ventrally; 1 = opening antero-posteriorly (Bivalvia, Scaphopoda); 2 = a blind-sac (*Propilidium curumim*, *Nautilus pompilius*) (CI = 100; RI = 100).

The pallial cavity is one of the outstanding features of Mollusca, protecting important and delicate structures such as gills, osphradia, etc. The organization and the placement of this cavity are, however, differently structured in the molluscan classes. In the

presently considered outgroups monoplacophores and polyplacophores, the pallial cavity is merely a furrow which surrounds the foot. This condition also appears in very basal, Cambrian mollusk-like forms [e.g., *Odontogriphus omalus* Morris, 1976 (Caron *et al.*, 2006); *Wiwaxia corrugata* (Matthew, 1899) (Morris, 1985; Eibye-Jacobsen, 2004)]. In Conchifera, this condition is modified, except for monoplacophores. In the case of *Cyrtosoma* (node B), the pallial cavity is deeper, resembling a profound blind-sac. In the case of the *Diasoma*, the pallial cavity is arranged in an antero-posterior manner, flanking laterally the visceral sac, with a flow of water from anterior or antero-ventral to posterior. This condition (state 1) is an important synapomorphy of node 1.



FIGURES 116-117: *Solemya notialis* anatomy: 116) Digestive tubes, main musculature and central nervous system in situ, right view, semi-diagrammatic representation artificially transparent, topology of some adjacent structures also shown; 117) Posterior region of visceral mass, dorsal view, dorsal wall of pericardium and adjacent mantle removed. Scales = 1 mm.

Head and Foot

10. *Head and appendages*: 0 = absent; 1 = present (*Propilidium curumim*, *Nautilus pompilius*) (CI = 100; RI = 100).

This character was inserted in order to organize the pair of cyrtosome outgroups. It is important, however, to emphasize that no further research on this issue was performed, as *Cyrtosoma* is beyond the scope of this paper.

11. *Foot position*: 0 = ventral; 1 = mostly turned forwards (anterior) (*Bivalvia*, *Scaphopoda*) (CI = 100; RI = 100).

A crawling foot is the normal fashion of Mollusca, lying along the ventral surface of the animal's body. This attribute is found in all classes except those above mentioned, in which the foot instead is directed forward or, at least, in an antero-ventral manner (Figs. 119, 120). The foot, in these cases, and as another indicative of homology, separates the mouth and respective appendages (palps or captacula) from the remaining pallial cavity.

The infaunal mode of life is not the only explanation for this feature, as with several other digging molluscs, such as some aplacophorans and gastropods (*e.g.*, olivids and volutids), do not possess the same form.

As the foot of the Cephalopoda is highly modified, the state is not clear. However, the structures possibly derived from the foot, such as the siphon and ventral part of the arms, are ventrally positioned (Shigeno *et al.*, 2007).

12. *Foot retractor muscles*: 0 = 7-8 pairs; 1 = 4 pairs (*Bivalvia*, *Scaphopoda*) 2 = 2 pairs (*Propilidium curumim*, *Nautilus pompilius*) (CI = 100; RI = 100).

Several pairs of foot retractors are the normal state in basal mollusk branches, including the conchiferan Monoplacophora (Lemche & Wingstrand, 1959). A reduction of the number of pedal retractors is one of the synapomorphies that substantiates a branch of the Conchifera that excludes Monoplacophora, and groups *Cyrtosoma* and *Diasoma*. This taxon (node A) is still not named.

Despite the fact that this character appears divided into two apomorphic states that support *Diasoma* and *Cyrtosoma* respectively (Fig. 122, nodes 1 and B), it most probably is part of a single evolution-

ary tendency towards the simplification of the number of foot retractor muscles.

13. *Foot main form of operation*: 0 = peristaltic contractions; 1 = hydraulic inflation (*Bivalvia*, *Scaphopoda*) (CI = 100; RI = 100).

14. *Foot function*: 0 = crawling; 1 = digging (*Bivalvia*, *Scaphopoda*) (CI = 100; RI = 100).

The characters 13 and 14 refer to adaptations for digging. In these cases, there is a normal mode of working; the foot is introduced in the soft sediment, it inflates the tip, and, by means of foot retractor muscles, it pulls the remaining of the animal's body inside the sediment. The constituents of the other classes, even those that are active diggers and have an infaunal mode of life, do not possess such modifications, and peristalsis is still present.

The typical *Diasoma* foot is, then, a somewhat hollow cylinder, in which fluid content contributes to its inflation. The inflation is wider in the foot's tip.

Of course the basic form of the foot in *Bivalvia* and *Scaphopoda* was modified several times along their evolution. In the former, this structure even disappeared in several taxa. However, in these cases, the modifications appear to be derived from the basic plan described above.

A "Burrowing foot with anterior enlargement" was used as a character uniting scaphopods and bivalves in a morphological study by Giribet & Wheeler (2001: 303, character 109).

15. *Foot distal region*: 0 = simple; 1 = umbrella-like (*Coccolentalium carduus*, *Paradentalium disparile*, *Solemya* spp., *Propeleda carpentieri*, *Ennucula puelcha*) (CI = 33; RI = 60).

The tip of the foot of the species above listed has an additional modification for digging. There is an expansion surrounding the tip that assists the animal in anchoring into sediment (Drew, 1900). This expansion is hereby called "umbrella-like" because of a similarity in appearance to an opened umbrella. This feature is found in an animal that is actively exploring a new environment. Analyzing the result, it is possible to infer that the umbrella-like foot appeared at the base of *Diasoma* (node 1), suffering a simplification in scaphopod node 4 and in lamellibranchs (node 9). This last taxon is also designated Pelecypoda, *i.e.*, axe-like foot.

The lateral expansions of the foot in scaphopods have been named crenulated fringe and anchoring organ (Steiner, 1992a, b, 1998). They are defined as a

pair of epipodial flaps with rippled surfaces and crenellated edges, forming a dorsally interrupted collar (Steiner, 1992b: 186).

It is equally parsimonious to consider state 1 as a *Diasoma* synapomorphy (node 1), with a reversion in *Gadilidae* (node 4), or a convergence between *Dentalliidae* and *Bivalvia* (nodes 3 and 5). The first optimization is shown in Fig. 122, as the *gadilids* still remain a terminal disk when the foot is totally extended (Steiner, 1992b, figs. 17, 18). As the homology between the *gadilid* terminal disk and the *dentaliid* umbrella-like foot tip is unclear, the *gadilid* state is coded as absent here. Despite this conservative approach, this concept is subject to change with further studies. In this case, the umbrella-like foot is maintained as a *Diasoma* synapomorphy, with a single reversion in *lamellibranchs* (node 9).

Pedal features are one of more clear similarities between bivalves and scaphopods, and were explored in previous phylogenetic proposals. Steiner (1996), for example, stated "contractile, burrowing foot, with longitudinal muscles associated with pedal wall, transverse muscles present, lateral epipodial lobes as anchoring organ" as synapomorphies of *Diasoma* (as *Loboconcha*).

16. *Proboscis form of foot*: 0 = absent; 1 = present (*Gadila braziliensis*, *Polyschides noronhensis*) (CI = 100; RI = 100).

The inversible foot of *Gadilida* representatives (node 4) resembles the proboscis of some gastropods in its organization (Figs. 79, 80, 88). There is a pair of retractor muscles (fm) that can be used to retract and enfold the distal half of the foot. These disappear inside the more basal portion of the foot-visceral mass axis (Steiner, 1992b; this study); only a small apical orifice remains in the fully retracted position (Figs. 78, 80). This is a notorious synapomorphy of the taxon and is responsible for the name *Siphodentaliidae* (a siphon-bearing tusk-shell, an allusion to the strange foot), a synonym of *Gadilidae*. The "proboscis" form is based on structural similarities between the *gadilid* foot and the gastropod proboscis. However, a comparison with nemertean proboscis is also found in the literature (Steiner, 1992b, Palmer & Steiner, 1998). A More detailed study on the pedal musculature has been used for phylogeny overtures (Steiner, 1996, 1998; Reynolds & Okusu, 1999). In such, a correlation between the internal layer of the longitudinal pedal muscles of *Dentaliida* and the *Gadilida* pedal inner retractor muscles is demonstrated. Additionally, transverse muscles appear to be reduced in *Gadilida*, amplifying the pedal sinus.

17. *Retraction of postero-dorsal foot base*: 0 = muscular integument; 1 = pair of conspicuous retractor muscles (*Bivalvia*, *Scaphopoda*) (CI = 100; RI = 100).

The posterior region of the foot of most molluscan classes is retracted normally by a muscular integument, rather than a developed pair of muscles. This condition is not the case with bivalves and scaphopods. A conspicuous pair of posterior retractor muscles is present in both taxa which supposedly appear to be homologues. In the case of scaphopods, this pair of muscles surrounds the visceral mass and is positioned dorso-laterally as longitudinal muscles (Figs. 48, 53, 65, 76, 88: lm), while in bivalves, the pair is positioned more ventrally (Figs. 99, 116: fm).

Suggestions on the homology of some muscular structures are represented in Figs. 118-120, in which directly related structures are indicated, and some others are suggested with grey marks. Two of them, the scaphopod longitudinal muscles (lm) and the bivalve posterior pedal retractor muscles (fm), are mentioned above. Along the same point of view, the posterior origin of the longitudinal muscle (po) may be homologous to that of the bivalve retractor muscle. The scaphopod visceral muscle (vm) appears to be homologous to the bivalve middle posterior foot retractor muscle (fv). The difference in position is due to the more dorsal position of the scaphopod longitudinal muscles and the more ventral position of the bivalve retractor muscle. Both can be derived from laterally positioned muscles in rostroconchs (Fig. 118), by opposite migration (dotted arrows). Further information on the similarities of pedal musculature between scaphopods and bivalves is found in Steiner (1992b, 1996) and in scaphopod inner branches in Steiner (1998).

18. *Byssal gland*: 0 = absent; 1 = present (*Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

A gland that secretes byssus is not present in protobranch bivalves. However, it being a remarkable lamellibranch synapomorphy. Most possess that gland only in early development (Yonge, 1962), as is the case of *Serratina*. On the other hand, some pedal glands in nuculids have been referred to as possible byssal glands (Rhind & Allen, 1992), an issue that merits further evaluation. This character was divided in three ordered states by Giribet & Wheeler (2001, character 105): absent, present in larvae and adults, and lost in adults.

19. *Adductor muscles*: 0 = absent; 1 = present (Bivalvia); 2 = with two components (*Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

A possible homologous muscle to the bivalve's anterior adductor muscle is the buccal muscle ring of scaphopod larva (Wanninger & Haszprunar, 2002, fig. 2D-E: bm), which occupies a similar position in front of the esophagus and bears transverse muscle fibers. Despite the fact that the states of this character are not considered additive, the present result demonstrates that they can be regarded as such. The simple pair of adductor muscles is one of the Bivalvia synapomorphy, but a clear division between quick and slow components of each muscle (Villarroel & Stuardo, 1998) is only detected in node 8.

20. *Pallial component of main retractor muscle of foot*: 0 = absent; 1 = present (Scaphopoda) (CI = 100; RI = 100).

The pallial component originated from each longitudinal muscle is notable in the examined scaphopods (Figs. 48, 67, 119: pm). Although this pair of muscles is very thin in Gadilida.

Visceral Mass

21. *Transverse muscles through surrounding visceral sac*: 0 = absent; 1 = present (Bivalvia, Scaphopoda) (CI = 100; RI = 100).

22. *Visceral sac*: 0 = filling dorsal region of shell; 1 = exposed in pallial cavity (Bivalvia, Scaphopoda) (CI = 100; RI = 100).

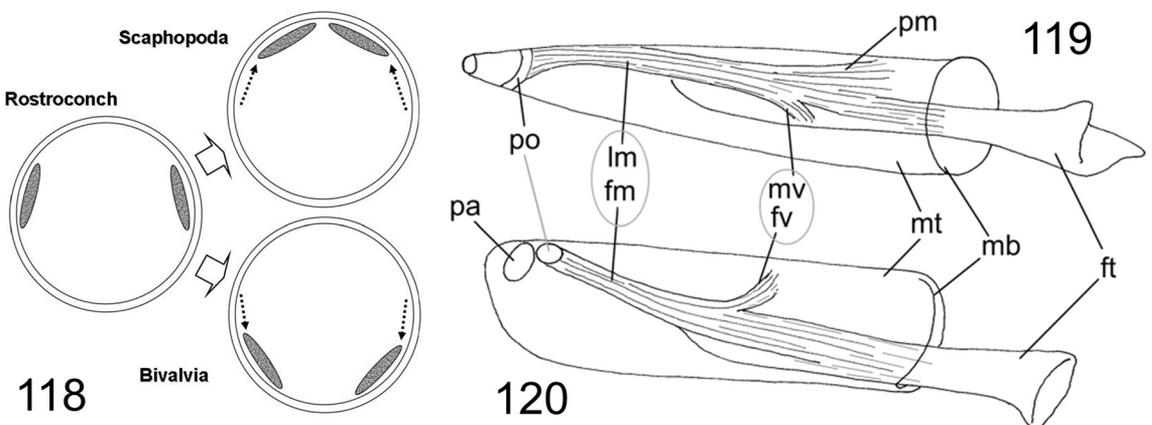
In mollusks, the visceral mass, or visceral sac or hump, is normally a dorsal continuation of the foot. Rarely there is a clear separation between foot and viscera. Yet characters 21 and 22 explore special features of the Diasoma classes, which are absent in the remaining ones. In both scaphopods and bivalves, the visceral sac protrudes into the pallial cavity, forming a bulged sac at the ventral base of the foot. Additionally, transverse muscles are present, crossing from one side to another, through visceral glands (gonad and digestive) and the intestinal loops. These transverse muscles are possibly an adaptation to improve the hydrostatic high pressure necessary to project the foot forward.

In cephalopods, which have a visceral sac somewhat similar to the above mentioned features, important differences are present (Simone, 1997c). The visceral organs are not protected by a muscular integument, and neither transverse muscles are present.

Pallial Organs

23. *Pair of gills*: 0 = present; 1 = absent (Scaphopoda) (CI = 100; RI = 100).

Total loss of the gills is a long known synapomorphy of Scaphopoda. Some pallial structures have been described as additional respiratory structures, as secondary gills (e.g., Boss, 1982). Nothing like that



FIGURES 118-120: Schematic representation of main retractor muscles of foot with indication of possible homologous structures. The grey marks are suggestions of homologies; 118) scheme of a transverse section in middle level of foot-visceral axis in a rostroconch, with putative intermediary lateral position of pair of longitudinal muscles, and generic basal scaphopod and bivalve, in which that pair of muscles migrated respectively towards dorsal and ventral (dotted arrows), originating from the longitudinal muscles and the posterior adductor pedal muscles (lm, fm). 119) A generic scaphopod; 120) A protobranch bivalve. Not to scales. Some structures seen by transparency.

was found in the examined species, except for some series of low folds (Figs. 47, 67: pf; 78: pl), which look more like glands than pallial folds. These folds are interesting differences amongst the species and appear to hold possible importance for scaphopod taxonomy.

The gonad of the Gadilida is intensely folded, and is separated from the posterior region of the pallial cavity by a very thin integument (Figs. 78, 81, 87: go). This special conformation certainly assists in blood oxygenation, as also do the gastric folds (digestive diverticula) of the Dentaliida (Figs. 47, 67: dg).

24. *Gills modified for filtering*: 0 = absent; 1 = present (*Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

The formal taxon Lamellibranchia is named in order to appraise this important structure for non-protobranch (and non-septibranch) bivalves (node 9). The increase in pairs of gills, each one forming a pair of demibranchs, is one of the necessary modifications for filter feeding, which is so characteristic of most bivalves.

25. *Gills modified to support symbiotic bacteria*: 0 = absent; 1 = present (*Solemya* spp) (CI = 100; RI = 100).

The thick gills filaments of solemyids are one of the more interesting features of this protobranch family. The large sized gills possibly raised some confusion in early literature, as protobranchs supposedly should possess only small, merely respiratory gills. However, increased solemyid gills appear to be a convergence, which, instead of being used for filtration, are used for symbiotic purposes (Cavanaugh, 1983; Conway & Capuzzo, 1991; Coan *et al.*, 2000). A parallel condition is also found in lamellibranch Lucinidae (Reid & Brand, 1986; Glover & Taylor, 2001).

26. *Gills positioned separating infrabranchial from suprabranchial chambers*: 0 = absent; 1 = present (*Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

In most protobranch bivalves, gills serve merely a respiratory purpose, as in other mollusks. For this propose, gills are relatively free in the pallial cavity. In nuculids and in lamellibranchs, however, each gill is arranged in order to separate an infra- from a suprabranchial chamber. Ciliary connections attach the

gills to neighboring structures, such as mantle lobes and visceral sac (Figs. 95, 101), which, in some eulamellibranchs, are substituted by tissue connections. In this arrangement, the flow of water necessarily must pass through gill filaments to be exteriorized. Some nuculids, additionally, have also facultative capacity to collect suspended particulate material, passing it anteriorly to the palp (Stasek, 1961; Reid, 1998: 237), showing that the arrangement of gills in nuculids is a step towards the lamellibranch condition.

27. *Gill suspensory stalk connected to ventral surface of posterior adductor muscle*: 0 = absent; 1 = present (*Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

The gill suspensory stalk is a reinforced rod located between both demibranchs that support the posterior region of the gills. Its origin is on ventral surface of the posterior adductor muscle and is usually reduced, membrane-like in some eulamellibranchs, as the gills are connected to adjacent structures. However, it is muscular and retractile in nuculids and in filibranchs.

Reno-Pericardial Structures

28. *Pericardium*: 0 = surrounding heart; 1 = empty (*Coccardentalium carduus*, *Paradentalium disparile*); 2 = absent (*Gadila braziliensis*, *Polyschides noronhensis*) (CI = 100; RI = 100; non additive).

The loss of the heart is a well known scaphopod feature (Reynolds, 1990a, b, 2002). However, dentaliids still retain a pericardial chamber (Figs. 50, 51: pc). This is totally absent in Gadilida. Although states were treated in a non additive optimization, an arrangement of the vestigial pericardium as an intermediary step towards its total loss is intuitive, and is represented in Fig. 122.

29. *Auricle connection to ctenidial vein*: 0 = terminal; 1 = subterminal (*Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100) (? in Scaphopoda).

This character, exclusive of the lamellibranchs, is related to the increase of gills. A portion of the gill augmented forward and the connection to auricles emerge approximately at mid-level. The anterior portion of gills has an antero-posterior flow, while the posterior one has a contrary course.

30. *Kidney*: 0 = narrow; 1 = thick-glandular (Bivalvia, Scaphopoda, *Propilidium curumim*, *Nautilus pompilius*) (CI = 100; RI = 100).

Most basal mollusks, including the monoplacophorans, has narrow kidneys somewhat splayed along the haemocoel. The remaining Conchifera have kidneys concentrated in the sub-pericardial region forming a solid triangular chamber, which appears as a notable synapomorphy. For additional discussion on the molluscan kidney see Morse & Reynolds (1996), Ruthensteiner *et al.* (2001).

Digestive System

31. *Mouth sphincter*: 0 = developed; 1 = weak or absent (Bivalvia, Scaphopoda) (CI = 100; RI = 100).

The occurrence of a mouth sphincter is the rule in most molluscan classes. However, in scaphopods and bivalves this muscle is reduced or absent. The mouth, then, remains as a permanently opened orifice.

As explained in character 36, the scaphopod mouth is in the base of the conic oral tube (Figs. 53-55, 68, 81: mo), instead of in its distal tip.

32. *Pair of lateral folds of mouth for food capture*: 0 = absent; 1 = present (Bivalvia, Scaphopoda) (CI = 100; RI = 100).
33. *Captacula*: 0 = absent; 1 = present (Scaphopoda) (CI = 100; RI = 100).
34. *Pair of palps*: 0 = absent; 1 = present (Bivalvia) (CI = 100; RI = 100).

The homology between bivalve palps and the scaphopod captacula has been suggestively proposed in previous phylogenetic analyses (Steiner, 1996) as large labial appendages, as it is here corroborated (Fig. 121). This proposition is based on several factors explained as follows:

The captacula clearly appear as lateral expansions of the mouth during early development of the scaphopods (Wanninger & Haszprunar, 2002, fig. 1C). Afterwards the slender expansions grow. This is exactly the way that the bivalve palps appear and remain during the course of a lifetime. Additionally, the captacula are certainly separated from the foot since early development (Shimek & Steiner, 1997) and, as in palps, do not appear to constitute a pedal structure.

Considering that the scaphopod mouth is at the base of the oral tube (see character 36), both captacula

and palps are lateral expansions of this structure, being located in the same region.

The captacula originate from a double folded base that surrounds the mouth dorsally and laterally (Figs. 52, 54). A double folded flap also raises the palps (Fig. 121).

Originally, both structures are designed to work in the same way. They are inserted into the surrounding sediment in search of food, which is then captured and conducted to the mouth. In filter-feeding lamelibranchs, however, the palps are modified to collect food from the proper pair of gills.

Another piece of evidence for the homology between palps and captacula is their innervations. In both structures, anterior nerves from the cerebral ganglia are responsible for sensorial and locomotive features (Steiner, 1991, 1992a).

Supposed homologous structures are indicated schematically in Fig. 121 (in grey), which represents the above discussion.

Scaphopod captacula have been proposed to be homologous to cephalopod arms. However, dorsal arms of cephalopods, which occupy an equivalent location to the captacula base, are much more complexly organized as expansions of the muscular head-foot portion. It therefore more closely resembles gastropod cephalic tentacles rather than the thin, muscle-less scaphopod structure.

In relation to basal bivalves, nuculid palps have another character in common with those of lamelibranchs in that they are suspension-feeding organs (Reid & Brand, 1986; Reid, 1998).

35. *Proboscis of palps*: 0 = absent; 1 = present (*Propeleda carpentieri*, *Ennucula puelcha*) (CI = 50; RI = 0).

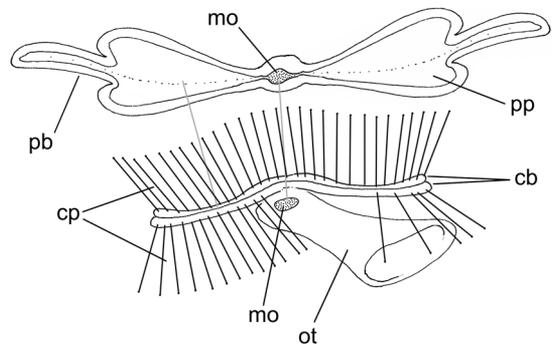


FIGURE 121: Schematic representation of structures annexed to mouth of a protobranch bivalve (above) and a scaphopod (below), frontal-slightly right view. Captacula (cp) only partially represented. Oral tube (ot) represented as if it were transparent with mouth at base instead of its tip. Not to scale. Suggestions of homology of mouth position are based on topology and on location of nerve ring, just posterior to it in more basal taxa of both classes.

The proboscis component of labial palps is a remarkable feature of most protobranchs (Stasek, 1965). It is absent in the palps of the solemyids. However, the structure is almost useless, as most nutrients comes from the symbiotic mode of life in gills. Palps are almost atrophied in Solemyidae and even absent in some species.

It is equally parsimonious to consider that state 1 is a synapomorphy of node 7 with a reversion in eulamellibranchs (node 9), or a mere convergence between both above species. The former optimization is shown in Fig. 122, as the proboscis is widely present in most protobranchs.

Regarding palps, Giribet & Wheeler (2002) considered two characters that resulted in relation to nukulids and nukulianids: a hypertrophied palp and palp appendages (= proboscis) (characters 80, 81 of that paper).

36. *Conic oral tube*: 0 = absent; 1 = present (Scaphopoda) (CI = 100; RI = 100).

As suggested in the characters above related to the mouth, the oral tube appears to be a structure located in front of the mouth, homologous to the remaining mollusks, and is located at the base of the oral tube (Figs. 53-55, 68, 81, 121: mo). The oral tube is a flexible and muscular cone projected forwards, normally full of prey, such as foraminifers and more rarely, small mollusks and other organisms.

The homology of the mouth at the base of the oral tube, instead of its tip, is mainly based on the position of the nerve ring and odontophore. These structures are always located close to the mouth in Mollusca. In the case of the nerve ring, those of the Gadilida are considered (Figs. 80, 81, 88). As in Dentaliida, the structure is decentralized.

The oral tube is also called proboscis, and the mouth is considered to be its tip (Steiner, 1992a, Palmer & Steiner, 1998). This concept is explained above, but is not applied here.

37. *Oral tube arrangement*: 0 = absent; 1 = three internal chambers (*Coccodentalium carduus*, *Paradentalium disparile*); 2 = four equidistant projections at edge (*Polyschides noronhensis*, *Gadila braziliensis*) (CI = 100; RI = 100).

The important structure for scaphopods additionally includes the above mentioned differences that, so far, have upheld the two traditional orders (nodes 3 and 4).

38. *Odontophore*: 0 = as part of buccal mass; 1 = as appendix of esophagus (Scaphopoda); 2 = absent (Bivalvia) (CI = 100; RI = 100).

39. *Radula*: 0 = present; 1 = absent (Bivalvia) (CI = 100; RI = 100).

40. *Horizontal muscle (m6)*: 0 = wide; 1 = narrow (*Polyschides noronhensis*, *Gadila braziliensis*) (CI = 100; RI = 100).

41. *Pair of ventral tensor muscles of radula (m11)*: 0 = present; 1 = absent (Scaphopoda) (CI = 100; RI = 100; ? in Bivalvia).

42. *Transverse muscle of odontophore (m3)*: 0 = absent; 1 = present (Scaphopoda) (CI = 100; RI = 100; ? in Bivalvia).

The odontophore and radular features explored here (characters 38-42) demonstrate some peculiarities of a highly modified structure. All bivalves lack any trace of odontophore, and such a structure is not indicated in embryological studies (e.g., Reverol *et al.*, 2004; Costa *et al.*, 2008). The odontophore loss is, then, a remarkable Bivalvia synapomorphy. On the other hand, nothing with respect to this structure can be inferred, and for this reason, a question mark represents the above character in the given matrix (Table 1).

The odontophore of Scaphopoda is different from the normal pattern of the structure in other mollusks. It is positioned away from the esophageal axis, outside the buccal cavity. A short odontophoral tube (Figs. 27, 28: on) separates it from the remaining digestive tube. There is no clear ventral tensor muscles of the radula, although the pair of dorsal tensor muscles is very thick (Figs. 59-62, 71, 72, 82-85, 90-92: m4). Therefore, the antagonistic muscle of the dorsal tensors is absent, and the radular return action, usually done by the ventral tensor, is a mystery. In the Dentaliida, there are two muscles that connect both sides of both odontophore cartilages, forming a strong ring (Figs. 59, 60, 71: m3 and m6). One of them, however, is very narrow in the Gadilida (Figs. 84, 85, 91, 92: m6). Observing the muscular and radular arrangement, it is possible to deduce that the scaphopod radula is not used to scratch the food, but to crush it. As the oral tube is full of foraminifer tests, which are not found after the odontophore level, *i.e.*, in the stomach and intestinal loops, it is possible to infer that each prey is brought inside the odontophore to be squeezed.

Further comparison amongst the scaphopod radulae is found in the literature (Morton, 1959; Steiner, 1996, 1998; Reynolds & Okusu, 1999). However, no applicable character was found to be considered here. The more important difference is in the rachidian, which is rectangular and smooth in the Dentaliida (Figs. 8, 9, 14, 15), while the Gadilida is thin, narrow and somewhat irregular (Figs. 21, 22, 26). This feature was explored phylogenetically at the ordinal level (Steiner, 1996: 330).

- 43. *Stomach*: 0 = wide; 1 = inconspicuous (a simple curve) (*Polyschides noronhensis*, *Gadila brazilien-sis*, *Solemya* spp) (CI = 50; RI = 66).

Scaphopods above mentioned, and possibly every Gadilida, lack any clear gastric region. A simple, several-looped intestine follows the esophagus (Figs. 80, 81, 88). This feature is convergently found in solemyids, which possess a reduced digestive tube because of the symbiotic mode of life; some species have even lost their digestive tubes (Reid, 1980).

- 44. *Stomach sorting areas*: 0 = absent; 1 = present (*Propeleda carpentieri*, *Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).
- 45. *Style sac and crystalline style*: 0 = absent; 1 = present (*Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

A large and complex stomach is a possible consequence of the simplification of the buccal mass in bi-

valves, and as such some characters are explored above (44, 45). Internal gastric folds and sub-chambers are found in bivalves after the node 7. A clear style sac, which forms a crystalline style, is found after node 8 (Graham, 1949; Purchon, 1956; Halton & Owen, 1968; Villarroel & Stuardo, 1998; personal obs.).

- 46. *Structure annexed to stomach*: 0 = digestive gland; 1 = hollow digestive diverticula (*Bivalvia*, *Scaphopoda*) (CI = 100; RI = 100).

Different from the solid digestive gland of most mollusks, the above taxa possess hollow diverticula directly connected to the stomach. This is a further modification for nutrient absorption that possibly characterizes Diasoma. However, in some classes that were not included in this study, Solenogastres and Caudofoveata, a single and large hollow chamber appears to work as a digestive gland (Scheltema, 1993).

Certainly, the digestive gland and diverticula merit further studies with respect at least to their homology. Few studies have so far being realized related to protobranchs and scaphopods. An example reveals extracellular digestion postulated for nuculids (Owen, 1959, 1972), and dentaliids (Taib, 1981; Palmer & Steiner, 1998).

Central Nervous System

- 47. *Central nervous system*: 0 = surrounding esophagus/mouth; 1 = ganglia except cerebral removed from esophagus (*Coccodentalium carduus*, *Paradentalium disparile*, *Propeleda carpentieri*, *Solemya* spp, *Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 50; RI = 80).

TABLE 1: Matrix of characters of the ingroup and three outgroups (bottom rows)

Character/Taxa	1				2				3				4				5			
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12			
<i>Coccodentalium</i>	00100	10010	11111	01001	11100	001?1	11100	11100	11000	11100	00									
<i>Paradentalium</i>	00100	10010	11111	01001	11100	001?1	11100	11100	11000	11100	00									
<i>Polyschides</i>	00000	10010	11110	11001	11100	002?1	11100	12101	11100	10000	00									
<i>Gadila</i>	00000	10010	11110	11001	11100	002?1	11100	12101	11100	10000	00									
<i>Solemya occid.</i>	11011	10010	11111	01010	11001	00001	11010	00210	??100	11001	00									
<i>Solemya notialis</i>	11011	10010	11111	01010	11001	00001	11010	00210	??100	11001	00									
<i>Propeleda</i>	12001	11010	11111	01010	11000	00001	11011	00210	??010	11001	00									
<i>Ennucula</i>	12001	11110	11111	01020	11000	11001	11011	00210	??011	11111	00									
<i>Barbatia</i>	12002	11110	11110	01120	11010	11011	11010	00210	??011	11111	10									
<i>Serratina</i>	11002	11110	11110	01120	11010	11011	11010	00210	??011	11111	10									
<i>Propilidium</i>	00000	00021	02000	00000	00000	00001	00000	00000	00000	00000	00									
<i>Nautilus</i>	00000	00021	02000	00000	00000	00001	00000	00000	00000	00000	00									
<i>Lolliguncula</i>	00000	00021	02000	00000	00000	00001	00000	00000	00000	00000	00									
<i>Neopilina</i>	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00									

There is a clear tendency for the position of the ganglia of the central nervous system to be distant from the esophagus in most Diasoma, although some basal taxa still maintain a nerve ring surrounding it (Figs. 80, 81, 86, 93, 94, 116).

It is equally parsimonious to consider state 1 as a Diasoma synapomorphy (node 1), with a reversion in Gadilidae (node 4), or a convergence between Dentaliidae (node 3) and Bivalvia (node 5). The first optimization was applied in Fig. 122.

- 48. *Well-differentiated ganglia*: 0 = absent; 1 = present (*Coccodentalium carduus*, *Paradentalium disparile*, *Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 50; RI = 75).
- 49. *Cerebral ganglia location*: 0 = central, far from anterior adductor muscle; 1 = lateral, close to anterior adductor muscle (*Ennucula puelcha*, *Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

- 50. *Visceral ganglia*: 0 = inconspicuous; 1 = large (Bivalvia) (CI = 100; RI = 100).
- 51. *Position of visceral ganglia*: 0 = between posterior adductor muscle and posterior pair of foot retractors; 1 = ventral to posterior adductor muscle (*Barbatia cancellaria*, *Serratina capsoides*) (CI = 100; RI = 100).

In both Diasoma classes a clear tendency for ganglia to become distant from each other appears. In scaphopods, Gadilida still remain circum-buccal ganglia, which is also found in some protobranchs such as nuculanids and partially in solemyids. In the remaining taxa of both classes, the ganglia are positioned far, such as in Dentaliida (Plate, 1892; Palmer & Steiner, 1998: fig. 10.11), and in bivalves after node 8 (Burne, 1904; this study). The epiatroid condition of the nervous system, *i.e.*, the cerebral and pleural ganglia closed or fused, was used to support Diasoma in previous phylogenetic analyses (Steiner, 1996).

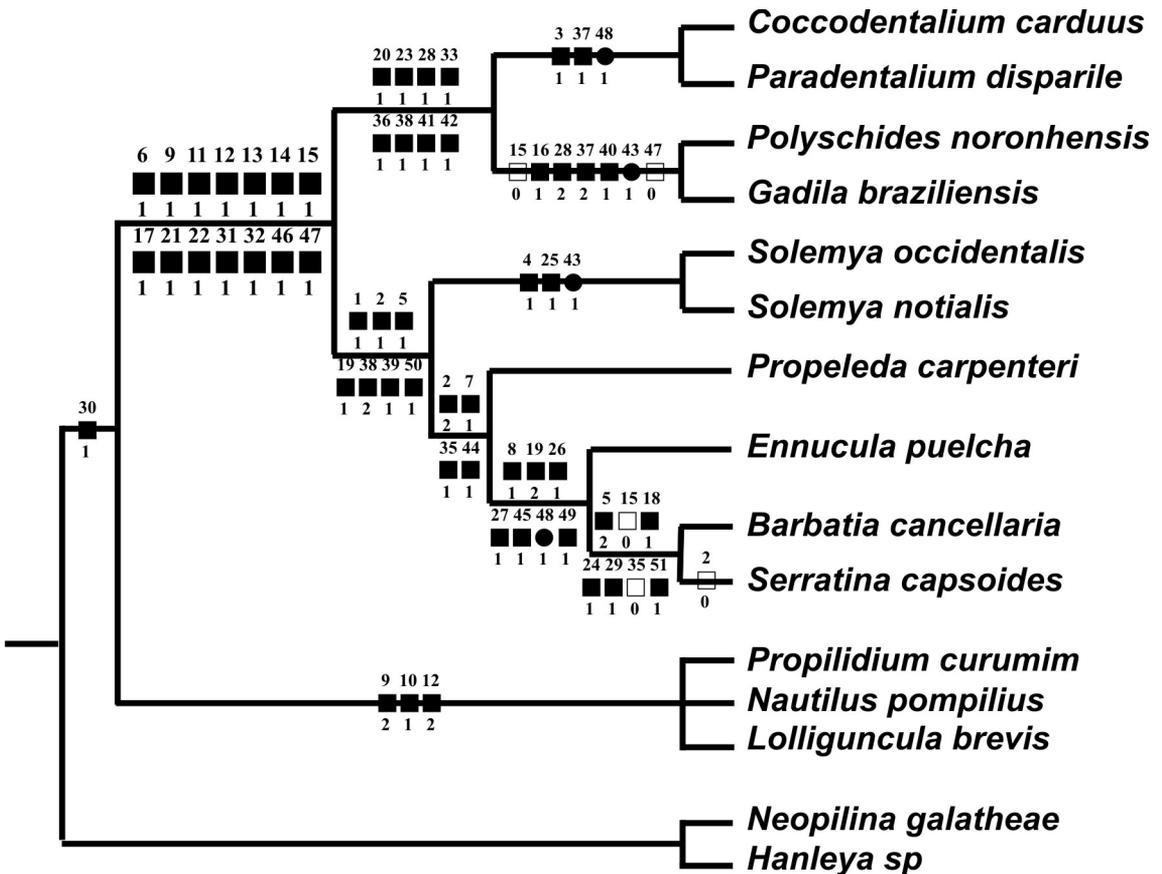


FIGURE 122: Most parsimonious cladogram with synapomorphies of each node represented by symbols (black square: non-homoplasic synapomorphy; white square: reversion; circle: convergence). The number above indicates the character, the number below indicates its state. Four outgroups also shown in the bottom. Length: 65; CI: 89; RI: 95.

Discussion of the Cladogram

General Aspects and Paleontology

In this section systematics and characters are discussed under light of the obtained cladogram (Figs. 122, 123), taking also into consideration the results of previous analyses of other authors. As stated above, comparative molecular studies have produced low resolution cladograms (Steiner & Dreyer, 2003). However, the scaphopod relationship with bivalves is common (Dreyer & Steiner, 2004). In paleontologic and evolutionary scenarios, inferences are also found in literature; evolution of the class Bivalvia has been debated, and even ancestors or early forms have been proposed (e.g., Morton *et al.*, 1998, fig. 4.5).

Taking into consideration Paleontology, the Cambrian genus *Heraultia* has been indicated as the stem group of Diasoma, raising scaphopods, rostroconchs and bivalves (Pojeta *et al.*, 1972; Runnegar & Pojeta, 1974). Other less precise scaphopod stem groups have also been erected, such as Paleozoic Xenonconchia (Starobogatov, 1974; Chistikov, 1979), a

shell-less ancestor (Yochelson (1978), and monoplacophoran stocks (Edlinger, 1991; Carter *et al.*, 2000). Also, Rostroconchia has been indicated as stem group of both classes (Runnegar & Pojeta, 1974; Salvini-Plawén, 1980; Steiner, 1992a).

Despite some controversies with respect to the early fossil records of scaphopods (Engeser & Riedel, 1996; Yochelson, 1999; Yochelson & Goodison, 1999; Palmer, 2001), the oldest recognizable scaphopod is Ordovician *Rhytidentalium kentuckyensis* Pojeta & Runnegar, 1979. On the other hand, recognizable bivalves have been found since the early Cambrian (Runnegar & Bentley, 1983; Pojeta & Runnegar, 1985; Bengston *et al.*, 1990; Runnegar & Pojeta, 1992).

Naming Rostroconchia as stem group of Diasoma (Scaphopoda plus Bivalvia) presents a dilemma in consideration of the following: 1) the univalve, pseudobivalved shell, and 2) the early appearance of the Bivalvia. Paleo-larval studies of rostroconchs (Pojeta & Runnegar, 1985) revealed that the larva is univalved, becoming bivalve-like during metamorphosis. This shell is compressed laterally and possesses a pair

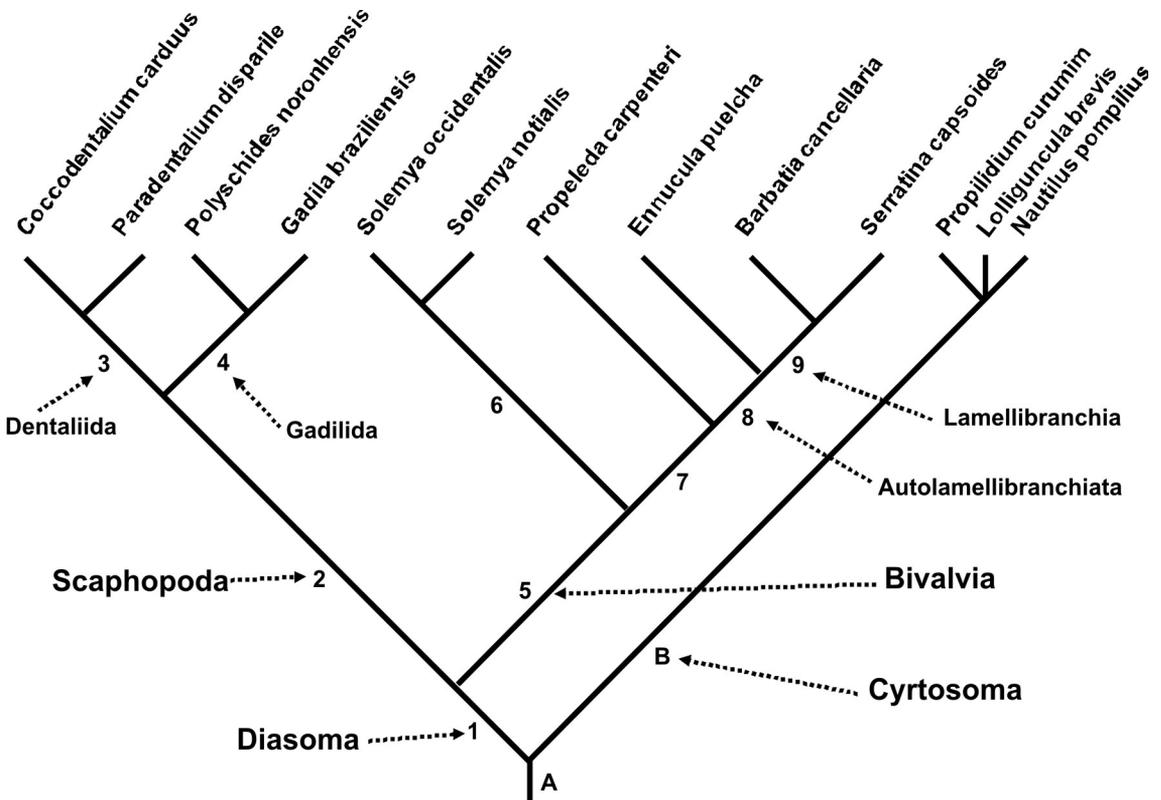


FIGURE 123: Most parsimonious cladogram with each node numbered (ingroup) or named by letters (outgroups at right). Some supra-familiar taxa already acknowledged indicated by dotted arrows. Length: 65; CI: 89; RI: 95.

of inseparable valves, united by continuous shell layers in dorsal margin. Inferred internal anatomy shows similarities with early bivalves (Pojeta & Runnegar, 1985), except that rostroconchs bear a radular apparatus. The life history of these groups shows that rostroconchs are highly diverse in the lower Paleozoic, mainly in the Ordovician, being gradually replaced by bivalves (Pojeta, 1978). Both occupied similar niches, an infaunal position anchored by foot in the sediment. Possibly the transition from rostroconchs to bivalves may be preceded by a phase lacking a ligament, but possessing adductor muscles (Runnegar & Pojeta, 1985). The dorsal shell layer between valves could be flexible enough to permit some adduction and abduction. Parallel evolution to closure of the shell aperture only by means of shell flexibility is found in some other groups of molluscs, such as the gastropod sacoglossans *Ascobulla* Marcus, 1972 and *Cylindrobulla* Fisher, 1857 (Volvatellidae). In these taxa an adductor-like muscle works in the shell aperture/closure, pressing the outer lip towards the inner lip (Marcus, 1972; Mikkelsen, 1998), functioning only on the calcified shell wall. Even in the bivalve-like crustacean Conchostraca, in which the rostroconchs were previously classified (*e.g.*, Nicholson & Etheridge, 1880; Kobayashi, 1933), a calcified dorsal layer functions with the valve movement (Eriksen & Brown, 1980). The same occurs in the bivalved crustacean Ostracoda (Kornicker & Sohn, 1976). Both crustacean groups have a pair of adductor muscles. On the other hand, the fact that in early development the scaphopod shell is univalve has been used as an argument for contradicting the monophyly of the Diasoma (Wanninger & Haszprunar, 2001).

Observing only the mantle, bivalves still retain a single piece that expands on both sides, forming the mantle lobes, each one producing a valve. The mantle is still continuous dorsally, showing no clear clue of valve separation except for a fold that builds the hinge (Fig. 35: hf). This fold stays introduced between each hinge tooth and its respective socket at the opposed valve. Its distal edge secretes the ligament. The mantle of bivalves, if the shell is extracted, is identical to the conformation of the mantle of scaphopods in early development (Wanninger & Haszprunar, 2002, figs. 1A-B: pro).

The Ordovician ribeiroid rostroconch *Pinnocaris* Etheridge, 1878 have been erected as the stem group of scaphopods (Runnegar & Pojeta, 1974; Pojeta & Runnegar, 1976, 1979). However, based on a different kind of protoconch, this possibility has been rejected (Peel, 2004). A conocarioid rostroconchs has been, then, proposed to originate the class (Yochel-

son, 1978; Peel, 2004). On the other hand, the theory of *Pinnocaris*, or *Pinocaris*-like basic stock for scaphopods does not seem strange, despite the argumentation regarding the protoconch position (Peel, 2004) and body axis (Steiner, 1992). A scaphopod-like creature can be extracted from *Pinnocaris*, by means of a greater and curved development mainly from the anterior region. This modification could explain the posteriorization of protoconch (Sasaki, 2007) and the rather oblique longitudinal axis in Scaphopoda.

Discussion of Each Branch of the Cladogram (Fig. 123)

Node 1: This branch represents a monophyletic relationship between Bivalvia (node 5) and Scaphopoda (node 2), which can be called Diasoma as originally introduced (Runnegar & Pojeta, 1974), Ancrypoda (Hennig, 1979), or Loboconcha (Salvini-Plawén, 1980). This branch is the main focus of the present paper and is supported by 14 morphological synapomorphies as follows: the mantle divided into two lobes (at least in a phase of development) (character 6); an antero-posteriorly opened pallial cavity (9); the foot turned forward (11), with four pairs of retractor muscles (12), working mainly by hydraulic inflation for digging (13, 14), with an umbrella-like distal tip (15); the presence of transverse muscles in visceral mass (21); visceral sac exposed in the pallial cavity (22); mouth lacking sphincter (31); a pair of lateral expansions for food capture (32); the hollow digestive diverticula (46); and a tendency for ventral ganglia of nerve ring to be positioned far from esophagus (47).

On the other hand, molecular studies have sometimes revealed support of a Scaphopoda-Cephalopoda relationship, such as 18S rDNA (Steiner & Dreyer, 2003). However, according to this same method, Bivalvia and Gastropoda are not supported (Steiner & Müller, 1996; Steiner & Hammer, 2000). In a total-evidence approach, monophyly of Scaphopoda + Bivalvia is supported by morphological data, with Bremer index of 3 (Giribet & Wheeler, 2002, fig. 2); however, this relationship disappears with the addition of molecular data, transferring scaphopods to a place closer to cephalopods (Giribet & Wheeler, 2002, fig. 6).

The common morphological characters between Bivalvia and Scaphopoda have been considered mere convergences induced by the burrowing characters, such as enclosure of the body by the mantle and shell, and the burrowing foot innervated by concentrated pedal ganglia (Steiner & Dreyer, 2003: 352). How-

ever, as commented above, such kind of modifications are not found in other burrowing mollusks, as, *e.g.*, neogastropods Olividae and Volutidae, vetigastropod Umbraculinae, stromboidean Aporrhaidae, and many others. This leads to an interpretation that infaunal habits appear as insufficient explanations to justify the common organization between bivalves and scaphopods.

Another interesting argument in favor of the inclusion of Scaphopoda in Cyrtosoma, *i.e.*, closer to Cephalopoda and Gastropoda instead of Bivalvia, is the appearance of cephalic retractors (Wanninger & Haszprunar, 2002). However, such a character looks rather like a plesiomorphy. Bivalves have a totally reduced head and buccal apparatus. The absence of muscles that retract an atrophied region comprises a synapomorphy, *i.e.*, the loss of cephalic retractors in bivalves that are present in scaphopods and cyrtosomes, and even in other mollusks.

In Summary, in the literature (*e.g.*, Engeser & Riedel, 1996) there are propositions that Scaphopoda is considered a branch of Rostroconchia. This is hereby corroborated. However, Bivalvia must be included as well. Consequently, in the point of view of the present result, Rostroconchia is not an isolated extinct class, and two rostroconch branches are still living today – Bivalvia and Scaphopoda. In other words, bivalves and scaphopod are existent, modified, special rostroconchs. A parallel concept is applied in relation to birds, which are considered to be modified, existent dinosaurs (Currie *et al.*, 2004).

Node 2: This branch represents the class Scaphopoda, being well-supported by 8 synapomorphies, despite this not being the main goal of the present study. Among them and worthy of remark are: a branch of the longitudinal muscle coming from the mantle (character 20); loss of gills and heart (23, 28); the captacula (33); a conic oral tube (36); the odontophore as an appendix of the esophageal axis (38); loss of the ventral tensor muscle of the radula (m11) (41); and a great development of an auxiliary, single muscle from horizontal muscle, the m3 (42). The class is also well-supported by molecular approaches (Steiner & Dreyer, 2003).

Nodes 3-4: The division of scaphopods obtained here agrees with the current classification, which divides the class into two orders: Dentaliida (node 3) and Gadilida (node 4) (*e.g.*, Steiner & Kabat, 2001; Steiner & Dreyer, 2003). Dentaliida (node 3) is supported by 3 synapomorphies: the slit at posterior shell aperture (character 3); the tree internal divisions of

the oral tube (37); and the differentiation of ganglia of the central nervous system (48). Gadilida (node 4) is supported by 7 synapomorphies, of which the more important are: the proboscis-fashion of the foot (character 16); the total reduction of the pericardium (28); the four equidistant projections at oral tube edge (37); the narrow odontophore horizontal muscle (m6) (40); and reduction of the stomach (43).

Node 5: This branch represents the class Bivalvia, supported by seven synapomorphies despite the fact that the investigation of the monophyly of this taxon is not the main goal of this study. From the synapomorphies, the interesting ones are: the shell having ligament, hinge and umbos (characters 1, 2, 5); the pair of adductor muscles (19); the loss of buccal mass structures (38, 39); and enlargement of the pair of visceral ganglia (50).

The first three branches of bivalves on the cladogram (Figs. 122, 123, nodes 6-9) demonstrate that the taxon Protobranchia is a paraphyletic arrangement of basal Bivalvia. However, the monophyly has been postulated, based on shared features of endoderm reorganization and organogenesis during and after metamorphosis (Gustafson & Reid, 1986, 1988; Reid, 1998). Some classifications still divide the Protobranchia into two orders: Nuculoida and Solemyoidea (*e.g.*, Sanders & Allen, 1973), based mainly on the contrast between a taxodont (former) and a cryptodont (last) hinge. Besides, even independent origin of protobranchs and lamellibranchs has been advocated in the literature (Reid, 1998), based on different ligaments (Waller, 1990; Cope, 2000), particularities of the stomach (Graham, 1949; Purchon, 1956, 1987), and dissimilar form of larva – pericalymma versus veliger (Gustafson & Reid, 1986, 1988; Cragg, 1996). On the other hand, paraphyly of protobranchs is the result of other phylogenetic analyses (*e.g.*, Giribet & Wheeler, 2002).

Solemyidae, the first bivalve branch (node 6) appears to be quite ancient, with records since the Silurian, such as *Janeia silurica* Liljedahl, 1984. However, it has been postulated that the family had originated from nuculoids (Allen & Sanders, 1969; Kuznetsov & Sileiko, 1984; Reid, 1998; Carter *et al.*, 2000). Additionally, some members of solemyids from Ordovician to the Carboniferous possess a taxodont hinge (Reid, 1998; Cope, 2000), suggesting that the edentulous hinge of modern forms may be derived from it. This is an indicator that the taxodont kind of hinge (character 2, state 2) may be at the base of Bivalvia, *i.e.*, in node 5 (Fig. 123). Its appearance in node 7 is

actually an artifact due to further modification of the modern examined solemyids.

Node 6: The node represents the family Solemyidae, supported by three synapomorphies such as: the extension of the periostracum longer beyond the calcified shell edge (character 4); the modifications of the gill to support symbiotic bacteria (25); and the reduction of the stomach (46). Solemyids have been, nevertheless, considered at the base of a monophyletic Protobranchia in some phylogenetic approaches (e.g., Purchon, 1987, Cope, 1996, 1997). However, they are sometimes considered to be derived taxon (Waller, 1990, 1998; Salvini-Plawén & Steiner, 1996). This approach is possibly based on a set of highly derived characters that modern solemyids have, which, when analyzed alone, suggest they could not be placed at the base of protobranchs. Those characters are: the lack of nacre, the edentulous hinge, the large gill (especially for a protobranch), the high degree of fusion of the mantle lobes, and the excurrent siphon. Conversely, under light of the present result, those derivations can be interpreted as remarkable convergences with other higher branches of Bivalvia, and that modern solemyids are highly modified animals. This is expressed, for example, by the well-developed foot of *Solemya* that even helps the animal to swim (Reid, 1980; 1998: fig. 5.9).

Node 7: This branch reunites bivalves except Solemyidae, and is supported by four synapomorphies. They are: the taxodont hinge (character 2, but see observation above, in last paragraph of the discussion on node 5); the freedom of mantle lobes (7); the proboscis on palps (35 – which can also be transferred to the base of Bivalvia with further studies on the symbiotic solemyids); and the presence of sorting areas in stomach (44).

Node 8: This branch groups nuculids and lamellibranchs, supported by seven synapomorphies. The more important are: the trifolded mantle edge (character 8); the presence of two (quick and slow) components in the adductor muscles (19); the anatomical position of the gill separating an infra- from a supra-branchial chamber (26); the development and position of gill suspensory stalks (27); the gastric style sac (45); and differentiation of the central nervous system in differentiated ganglia placed away from each other (48, 49).

Some phylogenetic approaches have shown the Nuculoida as stem group of the lamellibranchs

(e.g., Cope, 2000; as Autolamellibranchiata Grobben, 1894). However, the molecular data reveals Nuculanidae at the base of Autolamellibranchiata (Giribet & Wheeler, 2002, fig. 11). Another feature that could support this node is pedal feeding in early juveniles; this feature is common to nuculids and most lamellibranchs (Reid *et al.*, 1992). Nuculidae appeared in the Ordovician (Keen, 1969; Reid, 1998).

The lamellibranchs are represented in node 9 by a filibranch and an eulamellibranch. Although, as mentioned above, no exhaustive research for lamellibranch synapomorphies was performed herein, the main characters from the seven that support this branch are: prosogyre umbos (character 5); loss of the umbrella-like foot distal end (15); the byssal gland (18); further gill modification for filter feeding (24), which is a character that could be dismembered in several others, such as the presence of demibranchs, food groves, etc.; the sub-terminal connection of auricles in the gills (29); loss of proboscis of palps (35); and the position of the visceral ganglia ventral to posterior adductor muscle (51).

Beyond these morphological characters, the absence of haemocyanin of the lamellibranch blood, a common feature in protobranchs and other mollusks (Morse *et al.*, 1986), can be another synapomorphy.

The argumentation on independent origin between protobranchs and lamellibranchs (beginning of this section), can be used to further base the lamellibranch set of synapomorphies. Those characters erected as differences between both groups can perfectly be considered lamellibranch modifications.

Most phylogenies based mainly on morphology have shown monophyly of lamellibranchs, although normally protobranchs are not always properly tested (Starobogatov, 1992; Cope, 1996; Morton, 1996; Waller, 1998; Steiner & Hammer, 2000). The age of appearance of the filibranch branch is late Cambrian or early Ordovician (Cope, 1996, 2000), showing a very ancient path of evolution. The Cardiolarioidea appears to be the basic stock of the taxon (Cope, 2000).

Node B: This branch is part of the outgroups, which, as explained above, do not have an exhaustive search for synapomorphies. Two synapomorphies support this node, although many others can be evoked. One of them is the derived position of the visceral connectives median to the dorso-ventral muscles (Haszprunar & Wanninger, 2000).

CONCLUSIONS

1. The taxon *Diasoma* is monophyletic, supported at least by 14 morphological synapomorphies, and encompasses both classes, Bivalvia and Scaphopoda.
2. In a certain point of view, Bivalvia and Scaphopoda can be regarded as modern branches, modified Rostroconchia.
3. Despite not being the main goal of the present paper, both diasome classes, Bivalvia and Scaphopoda, are monophyletic, supported at least by 7 and 8 morphological synapomorphies respectively.
4. Both traditional Scaphopoda divisions, Dentalida and Gadilida, are monophyletic, supported respectively at least by 3 and 7 morphological synapomorphies.
5. The taxon Protobranchia is paraphyletic, an arrangement of at least three branches of basal bivalves.
6. The bivalve Solemyidae appears to be the more basal bivalve, and includes species with similar organization to scaphopods.

RESUMO

*Este estudo analisa a morfologia e anatomia detalhadas de 4 espécies de Scaphopoda e 5 espécies de bivalves protobrânquios. Ambas as classes são tradicionalmente agrupadas no táxon Diasoma, o qual vem sendo questionado por diferentes metodologias, tais como molecular e de desenvolvimento. Este estudo é desenvolvido sob uma metodologia filogenética, a qual a maior preocupação é fornecer um procedimento inteligível e testável. As espécies de Scaphopoda analisadas provieram da costa brasileira e pertencem à família Dentaliidae [(1) *Coccodentalium carduus*; (2) *Paradentalium disparile*] e Gadilidae [(3) *Polyschides noronhensis*, n. sp. do Arquipélago de Fernando de Noronha; (4) *Gadila braziliensis*]. Estas espécies representam os ramos principais da classe Scaphopoda. Dos bivalves protobrânquios, representantes das famílias Solemyidae [(5) *Solemya occidentalis*, da Flórida; *S. notialis*, n. sp. do S.E. Brasil], Nuculanidae [(6) *Propeleda carpentieri*, da Flórida] e Nuculidae [(7) *Ennucula puelcha*, do sul do Brasil] são incluídos. Estas espécies representam os principais ramos dos bivalves basais. As descrições anatômicas de *S. occidentalis* e de *P. carpentieri* estão sendo publicadas em outro artigo, as das demais espécies estão incluídas neste, o qual também inclui um completo tratamento taxonômico. Além dessas espécies, representantes de outros táxons são*

*operacionalmente incluídos como parte do ingroup (então os índices são compartilhados com eles), um procedimento visando testar a monofilia morfológica de *Diasoma*. Esses táxons são 2 bivalves lamelibrânquios [(8) *Barbatia* – *Arcidae*; (9) *Serratina* – *Tellinidae*; ambos publicados em artigos a parte]; Propilidium (10) *Patellogastropoda* e (11) *Nautilus*, *Cephalopoda* basal, baseados em táxons basais. Os outgroups efetivos são (12) *Neopilina* (*Monoplacophora*) e (13) *Hanleya* (*Polyplacophora*). A análise filogenética baseada na morfologia revelou que o táxon *Diasoma* é suportado por 14 sinapomorfias, sendo separada de *Cyrtosoma* (*Gastropoda* + *Cephalopoda*). Embora não sendo o principal enfoque do presente artigo, os táxons *Scaphopoda* e *Bivalvia* são suportados por 8 e por 7 sinapomorfias respectivamente. O táxon *Protobranchia* resultou parafilético. O cladograma obtido é: (((((*Coccodentalium carduus* – *Paradentalium disparile*) (*Polyschides noronhensis* – *Gadila braziliensis*)) (*Solemya occidentalis* – *S. notialis*) (*Propeleda carpentieri* (*Ennucula puelcha* (*Barbatia cancellaria* – *Serratina capsoides*)))))) (*Propilidium curumim* – *Nautilus pompilius* – *Lolliguncula brevis*)).*

PALAVRAS-CHAVE: Scaphopoda; Bivalvia; *Diasoma*; Filogenia; Morfologia.

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