TABLE OF CONTENTS

Abstract 161

Introduction 162

Materials and Methods 163

Discussion of Characters 175
- Shell (Characters 1-52) 175
- Head-foot (Characters 73-147) 177
- Operculum (Characters 53-72) 180
- Pallial organs (Characters 148-228) 181
- Circulatory system (Characters 240-261) 185
- Excretory system (Characters 262-290) 185
- Digestive system (Characters 291-539) 187
  - Foregut (Characters 291-302) 187
  - Buccal mass (Characters 303-326) 190
  - Odontophore (Characters 327-406) 190
  - Radula (Characters 407-444) 197
  - Salivary glands (Characters 445-461) 200
  - Esophagus (Characters 462-489) 200
  - Stomach (Characters 490-516) 203
  - Intestine (Characters 517-539) 206
- Reproductive system (Characters 540-648) 207
  - Male (Characters 540-582) 207
  - Female (Characters 583-648) 208
- Central nervous system (Characters 649-673) 210

Cladistic Analysis 212

Discussion of the Cladogram 212
- Extra characters, not utilized directly in the present study 217
- Analysis of the obtained cladogram and the taxonomy 219
- Paleontology 225
- Comparison with molecular studies 226

Conclusions 227

Resumo 227

Acknowledgments 228

References 228

Appendix 1 238

Appendix 2 267

Appendix 3 309

Appendix 4 318

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Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology

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ABSTRACT

The systematics, classification and phylogeny of the Caenogastropoda are revised based on an analysis of the morphology of representatives of all branches. The basis of this work is the detailed examination of the morphology of 305 species, most of which are reported on in detail elsewhere. Representatives of most caenogastropod families were included (comprising 270 species), and 35 outgroup taxa. A phylogenetic analysis based upon 676 morphological characters, with 2291 states (1915 of which are apomorphic states), is presented. The characters comprise every organ system and many are discussed in detail. The polarization is based on a pool of non-caenogastropods, comprising 27 representatives of Heterobranchia, Neritimorpha, Vetigastropoda, Cocculiniformia and Patellogastropoda. Additionally, eight representatives of other classes are also included. The root is based on the representative of Polyplacophora. A few characters were included in order to organize the outgroups, to find the position of Caenogastropoda among them, and to find the synapomorphies of Caenogastropoda. A strict consensus cladogram of the 48 most parsimonious trees (Fig. 20; length of 3036, CI = 51 and RI = 94) is presented, a synopsis of which is: ((((((Cyclophoroidea^{2} (Ampullarioidea^{5} (Viviparoidea^{15} (Cerithioidea^{19} (Rissooidea^{41} (Stromboidea^{47} (Calyptraeoidea^{67} (Naticoidea^{97} (Cypraeoidea^{118} (Tonnoidea^{149} (Conoidea^{179} (Cancellarioidea^{222} – Muricoidea^{212}))))))))))) Heterobranchia^{V}) Neritimorpha^{U}) Vetigastropoda^{L}) Cocculiniformia^{J}) Patellogastropoda) (superscripts indicating the nodes at Fig. 20). The monophyly of the Caenogastropoda is supported by 60 synapomorphies. Based on this cladogram, the systematics, evolution and paleontology of the group are discussed, as along with comparisons with other phylogenetic studies involving Caenogastropoda, including those obtained from molecular data. The list of characters is included in Appendix 1; the matrix of characters in Appendix 2; and the list of synapomorphies of each node are presented in Appendix 3 in form of symbols. As the phylogeny obtained in this analysis has a high degree of concordance with other recent phylogenetic studies, a number of new supra-superfamiliar taxa are introduced: Siphonogastropoda (Cypraeoidea + Peogastropoda); Adenogastropoda (Naticoidea + Siphonogastropoda); Rhynchogastropoda (Calyptraeoidea + Adenogastropoda); Strombogastropoda (Stromboidea + Rhynchogastropoda); Peogastropoda (Tonnoidea + Neogastropoda); Epiathroidea (Viviparoidea + Sorbeoconcha); Hydrogastropoda (Ampullarioidea + Epiathroidea); Adenogonogastropoda (Neritimorpha + Apogastropoda) (Appendix 4).

Key-Words: Gastropoda; Caenogastropoda; Phylogeny; Morphology; Anatomy; Systematics.

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INTRODUCTION

"Caenogastropoda – the field of success" (Haszprunar, 1988a: 415)

Despite some initial inconsistencies (*e.g.,* the inclusion of trochoids) when introduced by Cuvier (1814), the name Pectinibranchia generally encompassed most of the Meso- and all Neogastropoda as later defined by Thiele (1929) (the latter taxon was called Stenoglossa by that author). As the name suggests, the taxon is an assemblage of monopectinate gill bearing gastropods. The taxon most probably comprises more than half of all species of Mollusca (Ponder *et al.,* 2008), and has representatives in virtually all habitats suitable for a mollusk. They are found from abyssal depths to mountains; from thermal vents to glacial seas; are present in the marine, estuarine, freshwater, and terrestrial environments, as well as in the plankton, in caverns and soil interstices from phreatic basins (Hershler & Longley, 1986). Concordant with this ecological radiation, the group reached an enormous diversity of organic conformations and ecological niches (Colgan *et al.,* 2007, Ponder *et al.,* 2008). The size, for example, varies from more than 90 cm (*e.g., Syrynx* Röding, 1798; Melongenidae) to little more than 0.5 mm (*e.g.,* some species of *Amphithalamus* Carpenter, 1865; Anabathridae). Beyond the natural interest for shell collectors and biological research, several species have other applications, including food (*e.g.,* Strombidae – Muñoz *et al.,* 1987; Mulliken, 1996), and public health (*e.g.,* some Thiaridae, encephalitis transmitter – Abbott, 1948, 1952; Davis, 1971; Brandt, 1974; some Pomatiopsidae, transmission of Japanese schistossomiasis – Lima & Souza, 1990). At least 201 families are recognized, containing thousands of genera (Bouchet & Rocroi, 2005).

The name Pectinibranchia had a poor and confused definition in the early literature (Cuvier, 1814; Bouchet & Rocroi, 2005). It sometimes was utilized in apposition to the pulmonate (air breathing) gastropods by some authors (*e.g.,* Duméril, 1806, as *pectinibranches*). Though, it was of more restricted use by others (*e.g.,* Cuvier, 1817: *pectinibranches,* snail with spiral shell, sexes separate, gills pectinate in mantle cavity). The name Pectinibranchiata was, for example, utilized by Gray (1850) as one of the orders of the Ctenobranchiata. While the name Pectinibranchia was utilized by Goldfuss (1820), as a more restricted taxon than Cuvier's (1817), as it did not encompass the siphonate forms. The taxon Pectinibranchia is, however, credited to Blainville (1814) (as *pectinibranchés*), and Latinized by Goldfuss (1820) (Cox, 1960b; Bouchet, *personal communication*). Pectinibranchia has been also called Monotocardia in some classifications (*e.g.,* in Encyclopaedia Britannica; Marcus, 1958; Golikov & Starobogatov, 1987, 1988).

Probably because of above mentioned confusion and due to the informal tendency for erecting supra-familial taxa with the suffix – gastropoda (as the case of the Stenoglossa replaced for Neogastropoda), Cox (1960a) introduced the epithet Caenogastropoda for replacing the previous Pectinibranchia. The apparent objective of the author was to create a name in opposition to the Archaeogastropoda (the "old" forms), as the prefix *"caeno"* means "new" in Latin. Besides, the presence of monopectinate gills in other non-caenogastropods, as, *e.g.,* Cocculinimorpha and some basal Heterobranchia (some amathinids), may provide some additional motivation.

Cox (1960b: 152) defined the taxon Caenogastropoda as: "Proposed for the order of Prosobranchia formerly known by the name Pectinibranchia, as restricted by Gray in 1850. It combines the Mesogastropoda and the Stenoglossa or Neogastropoda."

The name Caenogastropoda was subsequently utilized (*e.g.,* Salvini-Plawén, 1980; Ponder & Warén, 1988). However, a secure definition by means of synapomorphy was only presented by Haszprunar (1985a). The author showed that the studied representatives possess special cell types on the osphradium, different from the remaining gastropods (three special cell types in constant mutual position), which could be regarded as synapomorphic. However, some authors considered Caenogastropoda a polyphyletic assemblage of unrelated groups (*e.g.,* Graham, 1985). Haszprunar, in his comprehensive phylogenetic approach of the Gastropoda (1988a), advocated the monophyly of the Caenogastropoda. Nevertheless, the organization of the taxon itself remained an enigma, and was represented by a question mark uniting the caenogastropod branches in his phylogram (Haszprunar, 1988a, fig. 5). The relationship of the caenogastropods with other affiliated taxa, such as Architaenioglossa and Campaniloidea also remained obscure as these taxa were represented outside the caenogastropod branch in Haszprunar's tree. Interestingly, Haszprunar (1988a) did not refer to the monopectinate condition of the gill; instead he gave as synapomorphies of the Caenogastropoda (excluding Architaenioglossa and Campanilidae), the osphradial cells, noted above, and the shared fine structure of eu- and parasperma (mostly based on Nishiwaki, 1964; and Healy, 1986, 1988). Haszprunar's classification and conclusions have received some criticism (*e.g.,*

Bieler, 1990; Haszprunar, 1990), mainly because of the lack of a formal treatment of the data through a cladistic methodology. A formal cladistic treatment was performed almost a decade later by Ponder & Lindberg (1996, 1997). In that study, 14 terminal taxa of the caenogastropods were included. Architaenioglossa and Campaniloidea emerged as branches of the Caenogastropoda where they had been placed earlier by Ponder & Warén (1988).

In an early molecular study (18S rDNA and cytochrome *c* oxidase I), which included some caenogastropods, Harasewych *et al.* (1997) also obtained a monophyletic Caenogastropoda, with the architaenioglossans as part of the ingroup. The 'higher' caenogastropods, or the Neomesogastropoda Bandel, 1991 plus Neogastropoda, were studied by Riedel (2000), based on 16S and 18S rDNA and morphology; he obtained a phylogenetic hypotheses consistent with the monophyly of the group, using an intuitive methodology. Barker (2001) performed a phylogeny of the terrestrial Gastropoda based on a set of 72 morphological characters. The author obtained a single cladogram having a branch with the caenogastropods divided into 2 basal branches, one of them includes the architaenioglossans and the Neritimorpha (as Neritopsina), and the other branch the remainding 13 caenogastropod taxa. The monophyly of the caenogastropods has not been fully supported by some molecular analyses (*e.g.,* Colgan *et al.,* 2000) while it has in others (*e.g.,* Winnepenninckx *et al.,* 1996; see section 5.4 of this paper). Controversially, molecular studies have been postulated as of limited use in higher systematics in gastropods (Dayrat & Tillier, 2003).

The present study has been developed over 14 years, as an attempt to improve the understanding of caenogastropod relationships, both its internal subdivisions and among the Gastropoda in general. Initially, about 24 superfamilies were included in the Caenogastropoda (*e.g.,* Vaught, 1989; Bouchet & Rocroi, 2005), despite most of these taxa being poorly defined. Although typical organisms are easily classifiable, some others have floated from one superfamily to another. One example is the Xenophoridae, which fluctuated amongst Stromboidea (*e.g.,* Wenz, 1938; Walls, 1980), Calyptraeoidea (*e.g.,* Morton, 1958), and Xenophoroidea (*e.g.,* Boss, 1982; Ponder, 1983; Rios, 1994).

During the time of development of this project, other important papers have been published attempting to determine the phylogenetic relationships within the Caenogastropoda at a higher level. Strong (2003) is one of the principal papers, including a set of 16 species, with a focus on the midgut. A single cladogram was obtained based on 64 characters of all systems. Colgan *et al.,* 2007 performed a multi-gene analysis of 29 species representing all of major lineages of Caenogastropoda. Ponder *et al.* (2008) summarized the knowledge of these and other studies, including parts of this one, and a strict consensus cladogram was presented (Ponder *et al.,* 2008; fig. 13.17), uniting morphological (including ultrastructure) and molecular data.

The knowledge on caenogastropods phylogeny is, then, based on sets of little more than 10, to a few tens of species. It is now possible to amplify the morphological dataset to some hundreds of species, considering a more holistic morphological approach, on a wider range of representatives of the main branches. This is the main contribution of the present paper, which is based on the examination of three hundred species at the same level of detail. Representatives of practically all families were studied; though, the main emphasis is at the superfamilial level.

Morphology is used as the main basis of the comparative analysis, with a wide range of characters being employed encompassing the shell, soft parts, and macro and micro-anatomy. However, it is important to emphasize that before the study commenced, many taxa and some structures lacked data or only scanty information was available. The attempts to complete the data set have resulted in almost a hundred papers which have been, or are in the process of being published (see below and Table 1). This paper is, also, the improved and actualized version of a Ph.D. dissertation (Simone, 2000b), transformed in an updated technical publication. This improvement has been also result of the mention of that dissertation in several papers (*e.g.,* Ponder *et al.,* 2008; Kocot *et al.,* 2011).

The main objective of the present paper is, as mentioned above, to analyze the taxon Caenogastropoda mainly at superfamily level, from a phylogenetic perspective, based on the morphology of representatives of practically all families. Secondary objectives are to propose a revision of the high-level systematics of the group, based on the results; and to provide a demonstration of the use of morphology in comparative analyses in mollusks.

MATERIALS AND METHODS

The ingroup and outgroup species included in the analyses are listed in **Table 1.** The list of characters used in analysis is given in **Appendix 1.** The data matrix is presented in **Appendix 2.** Each node of the

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material.

Superfamily	Family	Species	Geography	Main references
Ampullarioidea	Ampullariidae	*Pomacea crosseana* (Higalgo, 1871)	MS, Brazil	Simone, 2004a
		Pomacea curumim Simone, 2004a	PA, Brazil	
		Pomacea scalaris (Orbigny, 1835)	MS, Brazil	
		Pomacea bridgesi (Reeve, 1856)	AM, Brazil	
		Pomacea canaliculata Lamarck, 1804	MS, Brazil	
		Pomacea sordida (Swainson, 1823)	RJ, Brazil	
		Pomacea lineata (Spix, 1827)	BA, SP, Brazil	
		Asolene megastoma (Sowerby, 1825)	RS, Brazil	
		Felipponea neritiniformis Dall, 1919	PR, Brazil	
		Marisa planogyra Pilsbry, 1933	MT, MS, Brazil	
Cyclophoroidea	Cyclophoridae	*Neocyclotus prominulus* (Orbigny, 1840)	SP, Brazil	
		Incidostoma tupy Simone, 2004a	RO, Brazil	
		Aperostoma blanchetiana (Moricand, 1826)	MG, Brazil	
Viviparioidea	Viviparidae	*Viviparus acerosus* (Buirguignat, 1862)	Hungria	
		Viviparus contectus (Millet, 1813)	Hungria	
		Notopala ampullaroides (Reeve, 1863)	Australia	
		Notopala essingtonensis (Frauenfeld, 1862)	Australia	
		Larina cf. *strangei* (A. Adams, 1854)	Australia	
Cerithioidea	Thiaridae	*Aylacostoma exoplicata* Simone, 2001a	PA, Brazil	Simone, 2001a
		Aylacostoma ci Simone, 2001a	RO, Brazil	
		Aylacostoma tenuilabris (Reeve, 1860)	SP, Brazil	
		Melanoides tuberculatus (Müller, 1774)*	Eurasia, Brazil	
	Planaxidae	*Supplanaxis nucleus* (Bruguière, 1789)*	Venezuela	
	Pleuroceridae	*Doryssa ipupiara* Simone, 2001a	RO, Brazil	
		Doryssa atra (Bruguière, 1792)*	French Guiana	
		Doryssa macapa (Moricand, 1856)	AP, Brazil	
		Pachychilus sp.	Chiapas, Mexico	
	Turritellidae	*Turritella hookeri* Reeve, 1849	RJ, Brazil	
	Modulidae	*Modulus modulus* (Linné, 1758)*	Venezuela-Brazil	
	Cerithiidae	*Cerithium atratum* (Born, 1778)	Brazil	
	Diastomatidae	*Bittium varium* (Pfeiffer, 1840)	Brazil	
		Finella dubia (Orbigny, 1842)	Brazil	
	Litiopidae	*Alaba incerta* (Orbigny, 1842)	Brazil	
	Batillariidae	*Batillaria minima* (Gmelin, 1791)	Venezuela	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
	Cerithideidae	*Cerithidea costata* (da Costa, 1778)	Venezuela	
	Campanilidae	*Campanile symbolicum* Iredale, 1917	W Australia	
	Vermetidae	*Serpulorbis decussatus* (Gmelin, 1791)	ES, Brazil	
	Siliquariidae	*Stephopoma nucleogranosum* Verco, 1904	W Australia	Bieler & Simone, 2005
Stromboidea	Strombidae	*Strombus pugilis* Linné, 1758*	Brazil	Simone, 2005a
		Strombus alatus Gmelin, 1790	Florida, USA	
		Strombus gracilior Sowerby, 1825	W Panama	
		Eustrombus goliath (Schroter, 1805)	NE Brazil	
		Eustrombus gigas (Schröter, 1805)*	Caribbean	
		Aliger gallus (Linné, 1758)*	NE Brazil	
		Aliger costatus (Gmelin, 1791)	NE Brazil	
		Tricornis raninus (Gmelin, 1791)	Caribbean	
		Conomurex luhuanus (Linné, 1758)*	Australia	
		Canarium urceus (Linné, 1758)*	Australia	
		Lambis lambis (Linné, 1758)*	Australia	
		Terebellum terebellum (Linné, 1758)*	Australia	
		Tibia insulaechorab Röding, 1798	Pakistan	
	Struthiolariidae	*Struthiolaria papulosa* (Martyn, 1784)*	Australia	
		Tylospira scutulata (Gmelin, 1791)*	Australia	
	"Aporrhaidae"	*Cuphosolenus serresianus* (Michaud, 1828)	Europe	
		Aporrhais occidentalis Beck, 1836	E USA	
		Aporrhais pespelicani (Linné, 1758)*	Europe	
	Xenophoridae	*Onustus caribaeus* (Petit, 1856)	RJ, Brazil	
		Onustus indicus (Gmelin, 1971)*	Australia	
		Xenophora conchyliophora (Born, 1780)*	Caribbean – NE Brazil	
Calyptraeoidea	Calyptraeidae	*Bostrycapulus odites* Collin, 2005 as *B. aculeatus* (Gmelin, 1791)*	Brazil, Spain, Hawaii, Australia	Simone, 2002, 2006a
		Crepidula intratesta Say, 1822	SE Brazil	
		Crepidula plana Say, 1822	Florida, USA	
		Crepidula protea Orbigny, 1835	SE Brazil	
		C. argentina Simone, Pastorino & Penchaszadeh, 2000	Argentina	
		Crepidula glauca Say, 1822	Venezuela	
		Crepidula fornicata (Linné, 1758)*	Europe	
		Crepidula atrasolea Collin, 2000	Florida, USA	
		Crepidula depressa Say, 1822	Florida, USA	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Crepidula pyguaia Simone, 2006a	SC, Brazil	
		Crepidula carioca Simone, 2006a	RJ, Brazil	
		Crepidula glauca Say, 1822	Venezuela	
		C. cachimilla Cledón, Simone & Penchaszadeh, 2004	Argentina	
		Crepidula margarita Simone, 2006a	Venezuela	
		Calyptraea centralis (Conrad, 1841)	Brazil	
		Crucibulum auricula (Gmelin, 1791)*	Venezuela	
		Crucibulum quiriquinae (Lesson, 1830)	Chile	
		Trochita trochiformis (Born, 1778)*	Chile	
		Sigapatella calyptraeformis (Lamarck, 1822)	New Zealand	
	Hipponicidae	*Hipponix costellatus* Carpenter, 1856	NE Brazil	
		Hipponix subrufus (Lamarck, 1819)	NE Brazil	
		Hipponix incurvus (Gmelin, 1791)	NE Brazil	
		Hipponix grayanus Menke, 1853	Mexico-Ecuador	
		Hipponix leptus Simone, 2002	NE Brazil	
		Sabia conica (Schumacher, 1817)	Australia	
		Malluvium devotus (Hedley, 1904)	Australia	
		Cheilea equestris (Linné, 1758)*	NE Brazil	
	Capulidae	*Capulus sycophanta* Garrard, 1961	Australia	
	Trichotropidae	*Trichotropis cancellata* Hinds, 1843	W USA	
		Trichotropis borealis Broderip & Sowerby, 1829	N Atlantic	
		Trichotropis sp.	Alaska, USA	
	Vanikoridae	*Vanikoro* sp.	Australia	
Cypraeoidea	Cypraeidae	*Macrocypraea zebra* (Linné, 1758)*	Brazil	Simone, 2004b
		Macrocypraea cervinetta (Kiener, 1843)	W Panama	
		Erosaria acicularis (Gmelin, 1791)	NE Brazil	
		Erosaria spurca (Linné, 1758)	Mediterranean	
		Luria cinerea (Gmelin, 1791)	NE Brazil	
		Cypraea tigris Linné, 1758*	Pacific Is.	
		Lyncina lynx (Linné, 1758)*	Pacific Is.	
		Monetaria moneta (Linné, 1758)*	Micronesia-Japan	
		Monetaria annulus (Linné, 1758)	Micronesia	
		Ravitrona caputserpentis (Linné, 1758)*	Micronesia	
		Muracypraea mus	Venezuela	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Pseudozonaria arabicula (Linné, 1758)	Ecuador	
		Pseudozonaria robertsi (Hidalgo, 1906)	Ecuador	
	Ovulidae	*Cyphoma signatum* Pilsby & McGinty, 1939	Haiti – Brazil	
		Cyphoma gibbosum (Linné, 1758)*	Georgia, USA-Haiti	
		Pseudocyphoma intermedium (Sowerby, 1828)*	SE Brazil	
		Ovula ovum (Linné, 1758)*	Pacific Is.	
		Calpurnus verrucosus (Linné, 1758)*	Philippines	
		Simnialena uniplicata (Sowerby, 1848)	SE Brazil	
		Cymbula acicularis (Lamarck, 1810)*	Caribbean	
		Jenneria pustulata (Lightfoot, 1786)*	Panama	
	Triviidae	*Niveria pediculus* (Linné, 1758)	NE Brazil	
		Trivirostra oryza (Lamarck, 1810)*	Australia	
	Eratoidae	*Hespererato maugeriae* (Gray, 1832)	E USA	
	Velutinidae	*Velutina velutina* Müller, 1776	E USA	
		Velutina sp.	Massachusetts, USA	
	Pediculariidae	*Pedicularia* sp.1	Tonga	
		Pedicularia californica Newcomb, 1864	California, USA	
		Pedicularia decussata (Gould, 1855)	Bahamas	
		Pedicularia sp.2	Australia	
	Lamellariidae	*Lamellaria mopsicolor* Marcus, 1956	SE Brazil	
		Lamellaria banca Simone, 2004b	SE Brazil	
		Lamellaria patagonica Smith, 1881	Argentina	
Naticoidea	?	*"Amauropsis" rossiana* Smith, 1907	Antarctica	Simone *in prep.*
	Naticidae	*Amauropsis islandica* (Gmelin, 1791)*	Artic	
		Amauropsis andersoni (Strebel, 1906)	Antarctica	
		Naticarius cayenensis Récluz, 1850	Brazil	
		Natica n. sp.	Brazil	
		Natica cf. *sagrayana* Orbigny, 1850	Brazil	
		Naticarius canrenus (Linné, 1758)	Brazil	
		Natica cf. *marochiensis* (Gmelin, 1791)	Brazil	
		Natica livida Pfeiffer, 1840	Brazil	
		Natica vitellus Linné, 1758*	Pacific	
		Stigmaulax sulcatus (Born, 1778)*	Brazil	
		Polinices lacteus (Guilding, 1833)	Brazil	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Polinices hepaticus (Röding, 1798)	Brazil	
		Polinices uberinus (Orbigny, 1842)	Brazil	
		Polinices lewisii (Gould, 1847)	California, USA	
		Lunatia heros (Say, 1822)	E USA	
		Neverita duplicata (Say, 1822)	E USA	
		Eunaticina sp.	California, USA	
		Sinum n. sp.	Brazil	
		Sinum maculatum (Say, 1831)	Brazil	
		Sinum perspectivum (Say, 1831)	WE Atlantic	
		Conuber sordidus (Swainson, 1821)	Australia	
Rissooidea (Simone, 2006b)	Annulariidae	*Annularia* sp.	Yucatan, Mexico	
	Littorinidae	*Littorina flava* King & Broderip, 1832	Caribbean-Brazil	Simone, 1998b
	Barleeidae	*Amphithalamus glabrus* Simone, 1995c	SP, Brazil	Simone, 1995c
	Hydrobiidae	*Pothamolithus ribeirensis* Pilsbry, 1911	SP, Brazil	Simone & Moracchioli, 1994
		Pothamolithus troglobius Simone & Moracchioli, 1994	SP, Brazil	
		Pothamolithus karsticus Simone & Moracchioli, 1994	SP, Brazil	
Tonnoidea	Ficidae	*Ficus filosa* (Sowerby, 1892)	Australia	Simone *in prep.*
		Ficus ventricosa (Sowerby, 1852)	Costa Rica	
		Ficus carolae Clench, 1945	Gulf of Mexico	
		Ficus subintermedia (Orbigny, 1852)	Australia – Japan	
		Ficus ficus Linné, 1758*	South Africa	
	"Ficidae"	*Thalassocyon bonus* Barrard, 1960	Australia	
	"Ranellidae"	*Charonia laevigata* (Lamarck, 1816)	NE Brazil	
		Cymatium cynocephalum (Lamarck, 1816)	NE Brazil	
		Cymatium nicobaricum (Röding, 1798)	NE Brazil	
		Cymatium femorale (Linné, 1758)	NE Brazil	
		Cymatium parthenopeum (von Salis, 1793)	Brazil	
		Cymatium pileare (Linné, 1758)	NE Brazil	
		Sassia kamphyla (Watson, 1883)	Australia	
		Fusitriton retiolus (Hidley, 1914)	Australia	
		Fusitriton magellanicus (Röding, 1798)	S Brazil – Argentina	
	Bursidae	*Bursa corrugata* (Reeve, 1844)	NE Brazil	
		Bursa cubaniana (Orbigny, 1842)	NE Brazil	
		Bursa thomae (Orbigny, 1842)	NE Brazil	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Bursa tenuisculpta (Dautzenberg & Fisher, 1906)	SP, Brazil	
		Bufonaria bufo (Bruguière, 1792)	N Brazil	
	Cassidae	*Cypraecasis testiculus* (Linné, 1758)	NE Brazil	
		Cassis tuberosa (Linné, 1758)	NE Brazil	
		Phalium granulatum (Born, 1778)	SE Brazil	
		Phalium iheringi (Carcelles, 1953)	S Brazil	
		Palium labiatum (Perry, 1811)	Australia	
	Personiidae	*Distorsio clathrata* (Lamarck, 1816)	BA, Brazil	
		Distorsio anus Linné, 1758*	Oceania	
		Distorsio reticulata (Linné, 1758)	China, South Africa	
		Distorsio decipiens (Reeve, 1844)	New Caledonia	
		Personopsis purpurata Beu, 1998*	New Caledonia	
	Tonnidae	*Tonna galea* (Linné, 1758)*	Brazil	Simone, 1995a
		Tonna maculosa (Dillwyn, 1817)	NE Brazil	
Conoidea	Terebridae	*Hastula cinerea* (Born, 1778)	Caribbean-Brazil	Simone, 1999a,
		Hastula hastata (Gmelin, 1791)	BA-RJ, Brazil	2000
		Terebra brasiliensis (Smith, 1873)	RJ, Brazil	
		Terebra crassireticula Simone, 1999a	SE Brazil	Simone & Verissimo, 1995
		Terebra gemmulata Kiener, 1839	SP-RS, Brazil	
		Terebra leptapsis Simone, 1999a	RJ-SP, Brazil	
		Terebra taurina (Lightfoot, 1786)	BA-RJ, Brazil	
		Terebra spirosulcata Simone, 1999a	RJ, Brazil	
		Terebra sterigma n. sp.	ES, Brazil	
		Terebra dislocata Say, 1822	Florida, USA	
		Duplicaria crakei Burch, 1965	Australia	
	"Turridae"	*Cochlespira elongata* Simone, 1999c	SE Brazil	Simone, 1999c
		Cochlespira radiata Dall, 1889	Florida, USA	
		Pleurotomella aguayoi (Carcelles, 1953)	SP, Brazil	Simone, *in prep.*
		Carinodrilla braziliensis (Smith, 1915)	SP, Brazil	
		Gemmula mystica Simone, 2005c	SP, Brazil	
		Fenimorea sp.	FN, Brazil	
		Clathrodilla sp.	NE Brazil	
		Daphnella lymnaeiformis (Kiener, 1840)	FN, Brazil	
		Pilsbryspira albomaculata (Orbigny, 1842)	Brazil	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Glyphostoma sp.	SE Brazil	
		Polystira formosissima (E.A.Smith, 1915)	SE Brazil	
	Conidae	*Conus regius* Gmelin, 1791	NE Brazil	
		Conus mindanus Hwass, 1792	SE Brazil	
		Conus villepinii Fisher & Bernardi, 1867	SE Brazil	
		Conus clerii Reeve, 1844	SE Brazil	
		Conus archetipus Crosse, 1865	NE Brazil	
		Conus textile Linné, 1758	Indo-Pacific	
		Conus tulipa Linné, 1758	Japan	
		Conus selenae Van Mol *et al.,* 1967	NE Brazil	
		Conus ermineus Born, 1779	NE Brazil	
		Conus jaspideus Gmelin, 1791	NE Brazil	
		Conus bertarollae Costa & Simone, 1997	NE Brazil	
Muricoidea	Costellariidae	*Austromitra maculosa* Turner & Simone, 1998	South Africa	Turner & Simone, 1998
		Vexillum sp.	Saipan	*in prep.*
		Nodicostellaria crassa (Simone, 1995)	SE Brazil	Simone, 1995d
	Nassaridae	*Buccinanops monilifer* (Velenciennes, 1834)	SE + S Brazil	Simone, 1996a
		Buccinanops gradatus (Deshayes, 1844)	SE + S Brazil	
		Nassodonta dorri (Watteblet, 1886)	Vietnam	Simone, 2007a
	Columbellidae	*Amphissa acuminata* (Smith, 1915)	RJ, Brazil-Argentina	Simone & Leme, 2001
		Amphissa cancellata (Castellanos, 1979)	RJ, Brazil-Argentina	
	Muricidae	*Chicoreus spectrum* (Reeve, 1846)	NE, Brazil	
		Chicoreus brevifrons (Lamarck, 1822)	Caribbean	
		Chicoreus coltrorum (Vokes, 1991)	NE Brazil	
		Chicoreus carolinae (Vokes, 1990)	Caribbean-NE Brazil	
		Bolinus brandaris (Linné, 1758)	Mediterranean	
		Siratus senegalensis (Gmelin, 1791)	Brazil	
		Siratus tenuivaricosus (Dautzenberg, 1927)	Brazil	
		Siratus formosus (Sowerby, 1841)	Brazil	
		Siratus beauii (Fischer & Bernardi, 1857)	S Brazil	
		Phyllonotus pomum (Gmelin, 1791)	Brazil	
		Phyllonotus occulatus (Reeve, 1845)	Caribbean	
		Phyllonotus margaritensis (Abbott, 1958)	Venezuela	
		Murex trapa Röding, 1798	Thailand	

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Muricanthus radix (Gmelin, 1791)	W Panama	
		Eupleura sp.	W Panama	
		Trophon geversianus (Pallas, 1774)*	Argentina	
		Vitularia salebrosa (King & Broderip, 1832)	W Panama	Simone *et al.* 2009; Herbert *et al.* 2009
	Thaididae	*Thais biserialis* (Blainville, 1832)	W Panama	
		Nucella lapilus (Linné, 1758)*	Mediterranean	
		Acanthina bevidentata (Wood, 1828)	W Panama	
	Coralliophilidae	*Coralliophila nux* (Reeve, 1846)	W Panama	
	"Pseudolividae"	*Benthobia atafona* Simone, 2003	SE Brazil	Simone, 2003
		Benthobia compexirhina Simone, 2003	Tasmania Australia	
		Benthobia tornatilis Simone, 2003	Australia	
		Benthobia sima Simone, 2003	Madagascar	
		Zemira australis (Sowerby, 1833)	E Australia	Simone, 2007a
		Fulmentum ancilla (Hanley, 1859)	South Africa	
		Melapium lineatum (Lamarck, 1822)	South Africa	
	Olividae	*Olivancillaria urceus* (Röding, 1798)	SE Brazil	*in prep.*
	Marginellidae	*Prunum martini* (Petit, 1853)	SE Brazil	*in prep.*
	Buccinidae	*Cantharus aurithulus* (Link, 1807)	Caribbean – Brazil	*in prep.*
		Neobuccinum eatoni (Smith, 1875)	Antarctica	*in prep.*
Cancellarioidea	Cancellariidae	*Tritonoharpa lanceolata* (Menke, 1828)	NE Brazil	Simone, *in prep.*
		Cancellaria cancellata (Linné, 1758)	Florida, USA	
		Cancellaria petuchi Harasewych Petit & Vehecken, 1992	PI-ES, Brazil	
		Cancellaria reticulata (Linné, 1767)*	Caribbean	
		Cancellaria spirata Lamarck, 1822	Washington, USA	
		Trigonostoma tesselata Garrard, 1975	Australia	
		Trigonostoma tenerum (Philippi, 1848)	Florida, USA	
		Scalptia obliquata (Lamarck, 1822)	Solomon Is.	
		Scalptia contabulata (Sowerby, 1833)	Solomon Is.	
Ctenoglossa	Eulimidae	*Annulobalcis aurisflamma* Simone & Martins, 1995	SP, Brazil	Simone & Martins, 1995
		Balsis intermedia (Cantraine, 1835)	SP + PE	*in prep.*
OUTGROUPS				
Archaeogastropods				
Cocculiniformia	Addisoniidae	*Addisonia enodis* Simone, 1996c	SP, Brazil	Simone, 1996c
	Pseudococculinid	*Copulabyssia riosi* Leal & Simone, 2000	S Brazil	Leal & Simone, 2000

TABLE 1: Assembly of considered species, total 305 species. The indicated references are suggested for complementation of further details on the examined material (Continued).

Superfamily	Family	Species	Geography	Main references
		Pseudococculina rimula Simone & Cunha, 2003	SE Brazil	Simone & Cunha, 2003
Patellogastropoda	Lepetidae	*Propilidium curumim* Leal & Simone, 1998	S Brazil	Leal & Simone, 1998
Vetigastropoda	Haliotidae	*Haliotis aurantium* Simone, 1997a	SE-S Brazil	Simone, 1997a
		Haliotis poutalesii Dall, 1881	Caribbean	
	Pleurotomariidae	*Pleurotrochus atlanticus* Rios & Matthews, 1968	S Brazil	*in prep.*
		Pleurotrochus notialis Leme & Penna, 1969	S Brazil	
	Trochidae	*Calliostoma* sp.	Natal, RN	Simone & Cunha *in prep.*
		Falsimargarita stephaniae Rios & Simone, 2005	Falklands	Rios & Simone, 2005
		Gaza compta Simone & Cunha, 2006	RJ, Brazil	Simone & Cunha, 2006
		Gaxa superba (Dall, 1881)	Caribbean	2006
		Gaza cubana Clench & Aguayo, 1940	Gulf of Mexico	
	Fissurellidae	*Lucapina elisae* Costa & Simone, 2006	NE Brazil	Costa & Simone, 2006
		Fissurella mesoatlantica Simone, 2008a	Off N Brazil	Simone, 2008a
Neritimorpha	Neritidae	*Nerita ascencionis* Gmelin, 1971	Fernando de Noronha	*in prep.*
		Neritina zebra (Bruguière, 1792)	N-NE Brazil	*in prep.*
Heterobranchia	Amathinidae	*Cyclothyca pacei* Petuch, 1987	Florida, USA	Bieler & Simone, *in prep.*
	Omalogyridae	*Ammonicera plana* Simone, 1997b	SP, Brazil	Simone, 1997b
	Orbitestellidae	*Orbitestella patagonica* Simone & Zelaya, 2004	Argentina	Simone & Zelaya, 2004
	Rissoellidae	*Rissoella ornata* Simone, 1995b	SP, Brazil	Simone, 1995b
	Aeolidae	*Flabellina lucianae* DaCosta, Cunha, Simone & Schrödl, 2007	S Brazil	DaCosta *et al.,* 2007
	Aplysiidae	*Aplysia braziliana* Rang, 1828	SP, Brazil	*in prep.*
	Bulimulidae	*Anctus angiostomus* (Wagner, 1927)	BA, Brazil	Simone, 1998a
	Megalobulimidae	*Megalobulimus riopretensis* Simone & Leme, 1998	SP, Brazil	Simone & Leme, 1998
		Megalobulimus mogianensis Simone & Leme, 1998	SP, Brazil	
	Camaenidae	*Olympus nimbus* Simone, 2010	N Brazil	Simone, 2010
Cephalopoda	Nautilidae	*Nautilus pompilius* Linné, 1758	SW Pacific	Griffin, 1900; Sasaki *et al.* 2010
	Loliginidae	*Loliguncula brevis* (Blainville, 1823)	SE Brazil	Simone, 1997c
Bivalvia	Solemyidae	*Solemya occidentalis* Deshayes, 1857	Florida, USA	Mikkelsen & Bieler, 2008; Simone *et al., in prep.*
	Nuculidae	*Ennucula puelcha* (d'Orbigny, 1842)	Brazil-Uruguay	Simone, 2009
Scaphopoda				
	Dentaliidae	*Coccodentalium carduus* (Dall, 1889)	Brazil	Simone, 2009
	Gadilidae	*Gadila braziliensis* (Henderson, 1920)	SE Brazil	
Polyplacophora	Hanleyidae	*Hanleya brachyplax* Simone & Jardim, 2009	S Brazil	Simone & Jardim, *in press.*
Monoplacophora		*Neopilina galatheae* Lemche, 1957	Off Nicaragua, Pacific (9°23'N 8°32'W)	Lemche & Wingstrand, 1959

obtained consensus cladogram **(Figure 20)** has the synapomorphies that support it represented as symbols in **Appendix 3,** complementing Fig. 20. The suprafamilial taxa considered herein are described formally in **Appendix 4,** which also includes a checklist.

The present study is performed using standard phylogenetic methodology (*e.g.,* Pinna, 1996). The terminal taxa represent most of the morphological disparity seen in all superfamilies and almost all families of Caenogastropoda, representing superspecific taxa. Some secondary studies, which have used the same methodology, have been published (Simone, 1999a, 2000a, b, 2001a, 2002, 2004a, b, 2005a, 2006a, b, 2007a, 2009). Data presented here is referred to as *"personal observation" (pers. obs.)* for the taxa where data is currently unpublished. A large number of structures and organs have been found during the anatomical studies for which there is no formal terminology available or where the terminology is inconsistent. In those cases a topological terminology is used, or terminology to infer function is based on correlated taxa. In some cases, such as odontophore muscles, a simple numeration is provisionally applied.

Studies by other authors and methodologies (*e.g.,* molecular) are contrasted in the discussion. The principal papers used are as follows: Architaenioglossa (Bouvier, 1888; Berthold, 1989, 1990, 1991; Fretter & Graham, 1978; Bieler, 1993). Cerithioidea (Marcus & Marcus, 1964b; Houbrick, 1988; Ponder, 1991; Lydeard *et al.,* 2002). Stromboidea (Morton, 1958; Ponder, 1983). Rissooidea-Littorinoidea (Marcus Er & Marcus Ev, 1963, 1964a; Davis, 1967, 1969, 1971, 1979, 1981; Hershler & Davis, 1980; Reid, 1989; Ponder, 1988; Wilke *et al.,* 2001; Williams *et al.,* 2003; Hausdorf *et al.,* 2003; Winnepenninckx *et al.,* 2004). Calyptraeoidea (Bandel & Riedel, 1994; Collin, 2003). Naticoidea (Bandel, 1999). Cypraeoidea (Marcus, 1957; Marcus & Marcus, 1969b). Tonnoidea (Riedel, 1995, 2000). Muricoidea (Marcus & Marcus, 1959a, 1962b, 1968b; Ponder, 1974; Kantor, 1991, 1996, 2003; Kantor & Pavlinov, 1991; Kool, 1993; Coovert & Coovert, 1995; Harasewych *et al.,* 1997; deMaintenon, 1999; Haasl, 2000; Oliverio *et al.,* 2002; Pastorino, 2002; Hayashi, 2005). Conoidea (Marcus & Marcus, 1960b; Ponder, 1974; Kantor, 1988, Taylor, 1990; Kantor & Taylor, 1991, 2002; Taylor *et al.,* 1993; Rosenberg, 1998). Ptenoglossa (Taki, 1956, 1957; Kosuge, 1966; Robertson, 1985; Nützel, 1998). General features (Hyman, 1967; Voltzow, 1994; Lindberg & Ponder, 2001; Ponder *et al.,* 2008), and others presented below. In most cases, the author's examples or papers are evoked, however, the references listed above are also considered.

The specimens of the 305 species included in the study (Table 1), belong to institutional collections or were collected especially for this study (afterwards also deposited). The specimens were dissected in preservative, by standard techniques under a stereo-microscope. Some organs, such as oviduct and foregut, were serially sectioned using standard histological techniques; cut at 5 µm, and stained with Mallory tristain. Hard structures, such as shells, radulae and jaws were examined both in dissection and using standard SEM techniques at the "Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo" and at MZSP (Museu de Zoologia da Universidade de São Paulo). Some specimens were collected and examined alive in the laboratories of CEBIMar (Centro de Biologia Marinha, Universidade de São Paulo); The Bailey-Matthews Shell Museum, Sanibel, Florida; Keys Marine Laboratory, Long Key, Florida; Field Museum of Natural History, Chicago; Burapha University at Kungkraben Bay, Thailand; Smithsonian Tropical Research Institute, Panama; Smithsonian Marine Laboratory at Fort Myers, Florida. No descriptions are provided herein, since these are given in the complementary published studies or will be provided in papers that are in the process of being published.

The studied species are listed in Table 1, although 16 species included in that table are not included in the phylogenetic analysis because of a lack of some important data. The indicated papers should be consulted for further details on the examined material. Some material will be detailed in papers as yet unpublished, where additional explanation of the taxonomy and characters will be given. **Appendix 4** provides a revised classification of the Gastropoda based on the results of this study. Some new names for some taxa are also introduced and are formally described in Appendix 4, and, in some cases, the new taxa are also mentioned in the text.

The following section of comparative biology is organized in order to discuss main sets of characters, although all characters are presented in **Appendix 1.** In Appendix 1, the account of each character begins with an abbreviated descriptive sentence followed by the plesiomorphic and derived conditions(s) determined by the analysis; also included are the length (L), CI and RI (consistency and retention indices, respectively, expressed in percentages) values for the character under the most parsimonious hypothesis (Swofford & Maddison, 1987). Several additional characters and states were determined, based on the sampled taxa. Those that were autapomorphic, highly variable, or overlapping, were not included in this

analysis. The polarization is based on outgroup methodology (Maddison *et al.,* 1984; Nixon & Carpenter, 1993; Graham *et al.,* 2002).

The more distant outgroups belong to other molluscan classes; the bivalves (Simone, 1994, 1997d, 1998c, 1999b, 2001b; Simone & Chichvarkhin, 2004; Simone & Gonçalves, 2006), cephalopods (Simone, 1997c; Simone *et al.,* 2006; Sasaki *et al.,* 2010), scaphopods (Simone, 2009), monoplacophorans (Lemche & Wingstrand, 1959) and polyplacophorans (Jardim & Simone, 2010a, b). Within Gastropoda, 5 outgroups were selected, based on the references below and on samples examined and listed in Table 1: 1) Patellogastropoda (Lindberg, 1988; Sasaki *et al.,* 2006); 2) Vetigastropoda (Marcus & Marcus, 1960a; Leme, 1973; Salvini-Plawén & Haszprunar, 1987; Simone, 2005b; Simone & Birman, 2006b; Kano, 2007); 3) Neritimorpha (Ponder & Lindberg, 1997; Sasaki, 1998); 4) Heterobranchia (Marcus & Marcus, 1965, 1968a; Haszprunar, 1985a; Thollesson, 1999); 5) Cocculiniformia (Marshall, 1985; Haszprunar, 1988c; Strong *et al.,* 2003; Ardila & Harasewych, 2005). The root is based only on the polyplacophoran *Hanleya brachyplax* (Jardim & Simone, 2010b); all remaining outgroups were analyzed operationally as part of the ingroup.

Some of the more interesting characters, states, and polarizations are discussed in the following section. The discussion of each character is also based on the analysis of the obtained consensus tree (Fig. 20), although the matrix of characters **(Appendix 2)** and the succeeding cladogram (Fig. 20) are shown only in the subsequent section.

Some states in a single, multistate character are apparently not homologous. However, they were even though included in a single character because it is mathematically equivalent to erect the states as different characters (with possible change of indices) in the resolution of the matrix (Kitching *et al.,* 1998). This procedure decreases considerably the number of characters. All these multistate characters are considered as non-additive (unordered) (Meier, 1994; Pleijel, 1995). A few multistate characters were analyzed under an additive (ordered) optimization, following some previous approaches (*e.g.,* Giribet & Wheeler, 2005). In each case, the additive concept is justified in the discussion about that character and is always based on the ontogeny. This procedure was done only for basing some discussion, as the final analysis was performed with all states in an unordered optimization.

The cladistic analysis was performed with the aid of the computer programs Nexus (Maddison *et al.,* 1997), Winclada (Nixon, 1999), and TNT (Goloboff *et al.,* 2008) which generated the cladogram (Fig. 20). The cladogram illustrated is a strict consensus of 22 equally parsimonious trees by Winclada; and of 48 equally parsimonious cladograms in TNT with all character states unordered and with a basic algorithm of tree collapsing as minimum length equals to zero, and 1239 trees with algorithm maximum length equals to zero. The strict consensus cladogram is the same in all cases. The synapomorphies that support each node, and even some terminal taxa, are provided in Appendix 3; in case of ambiguity, the fast (ACCTRAN) optimization is shown (Agnarsson & Miller, 2008), with the few exceptions justified in the Discussion in section (3).

Details of the computer programs are: Nexus – A matrix containing 679 columns and 306 rows was created and fulfilled according to the taxa's characters. Parsimony is the basic criterion. Winclada – The matrix built in Nexus was opened in Winclada, with the change of the states to numeric mode, the analyses was performed under heuristic algorithm; the Nona search parameters was exhaustive, all numeric ones were added three zeros right; the strategy was multiple TBR = TBR (mult*max*). A number of eight cladograms were obtained. Afterwards, a strict consensus was generated, some branches collapsed. The states with non ambiguous optimization in each node were obtained directly at the consensus cladogram to generate the Appendix 3; additionally, the states that are ambiguously optimized in the support of any node were manually analyzed, and inserted in Appendix 3 in its respective numeric place. The matrix generated in Nexus was transformed into a text document, and processed in TNT under basic procedures of exhaustive searching of cladograms, with all multistate characters in unordered optimization; the change of minimum-maximum length of tree collapsing equals to zero was performed, the number of equally parsimonious cladograms, as above mentioned, increased, but the resulted strict consensus is the same.

In order to avoid redundancies of character or states, and its consequential augment of weight in the final analysis, the redundant characters had their overlapping states coded with dashes (–) in the matrix (Appendix 2) (Pleijel, 1995; Strong & Lipscomb, 1999; Sereno, 2007). The dash is interpreted as "inapplicable". For the other categories of questionable data, such as missing data, absence, etc., question marks (?) are applied. This has a didactical intention only, as dashes and question marks were treated the same by the computer programs.

Some well-known para- or polyphyletic names are utilized here without taxonomic significance, only

as an assemblage of organisms. They are used as shorthand to facilitate the discussion. Examples are "archaeogastropods", that means "the grade of taxa that precedes the apogastropods, *i.e.,* Patellogastropoda, Cocculiniformia, Vetigastropoda and Neritimorpha (Ponder & Lindberg, 1997)"; "mesogastropods", that means "the grade of caenogastropod taxa that precedes the Neogastropoda, as Cyclophoroidea, Ampullarioidea, Viviparoidea, Cerithioidea, Rissooidea, Stromboidea, Calyptraeoidea, Naticoidea, Cypraeoidea and Tonnoidea"; and "architaenioglossans" utilized to include the paraphyletic arrangement of Cyclophoroidea, Ampullarioidea and Viviparoidea (Simone, 2004a; Ponder *et al.,* 2008: 338). "Prosobranch" means the paraphyletic grade preceding Heterobranchia.

DISCUSSION OF CHARACTERS

For the following discussion, it is necessary to consult the consensus cladogram (Fig. 20), and the Appendices 1-4. For supporting the discussion, some items related actually to results are commented in this section.

Shell
(Characters 1-52)

Form: The form of the shell, summarized in Fig. 1, is of somewhat arbitrary categorization, since important details from a comparative point of view are overlooked. However, characters related to form are herein included for the purpose of testing them. Despite the form of the shell is widely utilized, as shown by the indices of the characters related to shape (*e.g.,* characters 1, 2, 4, etc.), the shell form appears to converge several times in caenogastropod evolution, even within each superfamily. An interesting state supporting an important node is the fusiform shape (character 1, state 4), supporting node 117, converging with the Stromboidea (node 47).

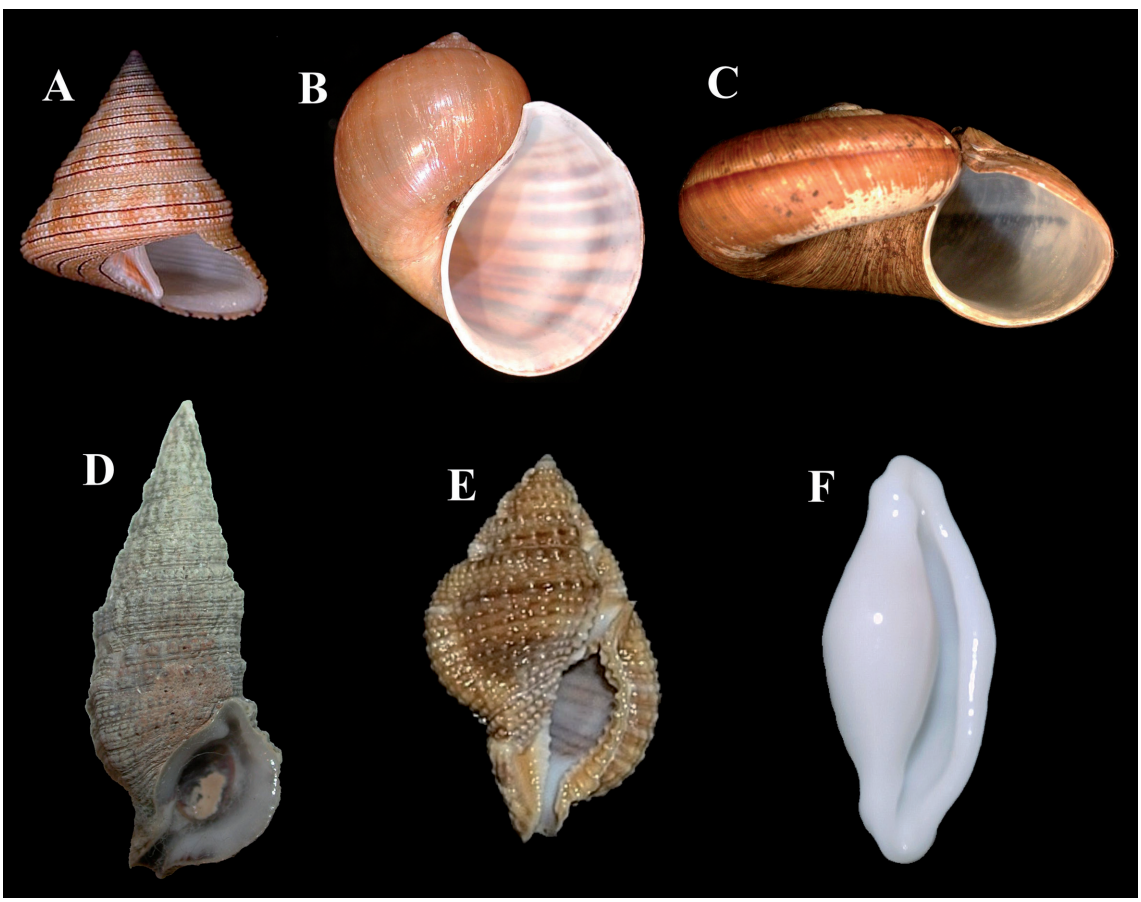

FIGURE 1: Shell form mentioned in character 1, some examples: **A)** trochiform (*Calliostoma gemmosum* – Trochidae); **B)** globose (*Pomacea crosseana* – Ampullariidae); **C)** discoid (*Incidostoma tupy* – Cyclophoridae). **D)** turriform (*Cerithium atratum* – Cerithiidae); **E)** fusiform (*Bufonaria bufo* – Bursidae); **F)** involute (*Pseudocyphoma intermedium* – Ovulidae). All of size around 30 mm.

Determinate growth (characters 26, 33) is the presence of a differentiated outer lip in the shell aperture, when the animal finishes, or has almost finished its development (Figs. 1D-F, 2B-E). It differs from the non-determinate growth, in which the outer lip of the shell aperture always remains undifferentiated with a sharp edge (Figs. 1A-C, 2A), as is the rule among the 'archaeogastropods'. Generally, the determination of the outer lip is by virtue of a deflection, thickness and/or appearance of teeth; while in the inner lip there is the appearance of a callus (see Vermeij & Signor, 1992). There is also **periodical** determinate growth, which is most probably a specialization of the simple determinate growth, characterized by the presence of several successive developed lips during the growth of the animal. In these cases, the older differentiated lips are impressed along the spire in form of axial ridges. The periodical determinate growth can be **inconstant,** in which the distance between the successive threads are somewhat randomized (*e.g.,* Cerithiidae; Fig. 1D); or **constant,** in which the distance between the successive threads is uniform. Examples of this type are approximately: 3/4 whorl (270°, as some ranellids), half whorl (180°, as most bursids; Fig. 2D), 1/3 whorl (120°, as most muricines, Muricidae; Fig. 2C), 1/6 whorl (60°, as some muricines; Fig. 2E), etc. These states are part of character 26. It is interesting to note that, in the case of periodic determinate growth, it is difficult to correlate it with maturity, since differentiated lips are formed even in immature specimens, and are apparently continue to be formed after the animal sexually matures.

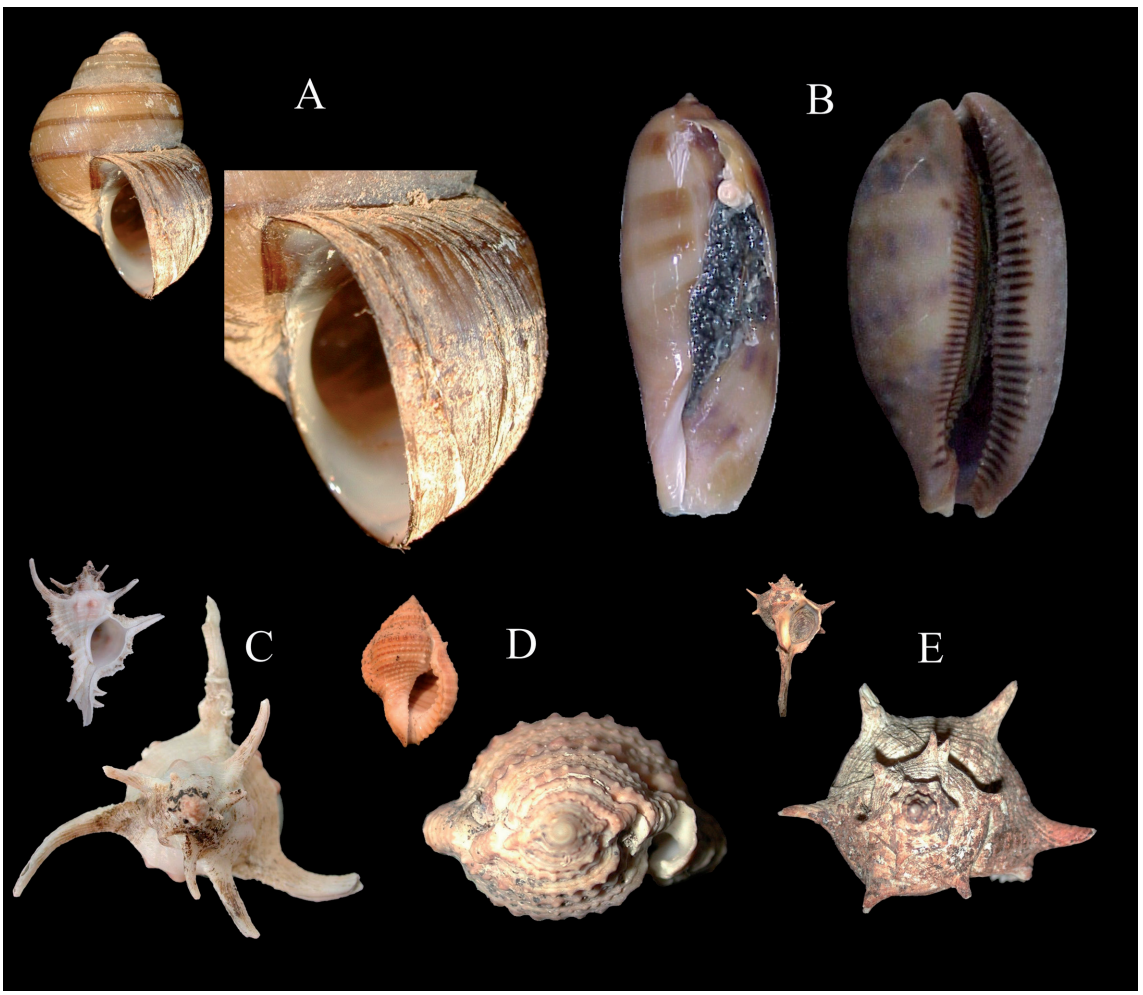

FIGURE 2: Examples of determinism of shell growth (character 3): **A)** *Notopala essingtonensis* (Viviparidae), non-determinate shell growth, note the cut-edged lip; **B)** *Macrocypraea zebra* (Cypraeidae), determinate shell growth, left a young specimen with cut-edged lip, right a mature specimen with formed lip; **C-E)** periodical determinate growth; **C)** *Siratus senegalensis* (Muricidae), a formed lip approximately each 120°; **D)** *Bufonaria bufo* (Bursidae), a formed lip approximately each 180°; **E)** *Bolinus brandaris* (Muricidae), a formed lip approximately each 60°. Sizes about 5 cm.

Siphonal (anterior) canal: An inhalant siphonal canal is found in several caenogastropods, and is developed apparently only by them, since the 'archaeogastropods' and heterobranchs characteristically lack an analogous structure. The canal (characters 34, 50) may or may not be associated with a differentiation of the adjacent mantle edge. Some groups, such as cerithioideans (node 19) and stromboideans (node 47), have a canal at the shell, but their mantles lack any apparent differentiation. On the other hand, the other caenogastropods that possess the structure have a differentiated siphon at the mantle border (see pallial structures below).

The **shell** is, undoubtedly, the most analyzed structure of mollusks and some entire higher taxa are only known by it. Of course the shell is the persistent part of the animal, and is the only part available in paleontology. Thus, it is important to transfer to the shell the conclusions resulting from the analysis of the whole animal. Despite this, and even though they have been extensively searched, it was not possible to use a lot of shell characters. Sometimes, the normal shape of the shell is totally disfiguring, as, *e.g.,* in the calyptraeoideans. The high plasticity of the shell may be a reflection on the many adaptations of the Caenogastropoda (Ponder *et al.,* 2008: fig. 13.2, where more information on shell characters can be obtained). As further discussed in the following chapters, apparently the shell can change greatly among the taxa, in contrast to the internal anatomy, which has not been modified to the same degree.

Head-foot
(Characters 73-147)

Head-foot siphons: The siphon found in the ampullariids and viviparids, also called "nuchal lobe" (Scott, 1957), is somewhat similar to the siphon found in the taxa located after node 66, although, it differs in having a cephalo-pedal origin, instead of pallial origin (Simone, 2004a, figs. 151, 174, 223, 276, 302: ll) (characters 77, 78). Another unusual feature of the architaenioglossan siphons is that they are paired (left-incurrent and right-excurrent siphons) (Simone, 2004a, same figs.: rl). The viviparid and ampullariid head-foot siphons are considered homologous. It appears in node 4 and reverses at node 18 (Fig. 20). Conversely, another optimization is possible: a convergence between Ampullarioidea (node 5) and Viviparoidea (node 15). This hypothesis may be valid, as the right siphon of the ampullariids differs in being simple, while that of the viviparids are divided by the food groove (Simone, 2004a, figs. 276, 302).

Eye: A lens in the eye (Simone & Martins, 1995, fig. 20: le) is one of the node K synapomorphies, supporting the taxon that encompasses Vetigastropoda, Neritimorpha and Apogastropoda. This was already pointed out by Ponder & Lindberg (1997) and Sasaki (1998), where a more extensive discussion can be found. The lens is an apomorphic structure that arises in the transformation of the eyes, which originally was an opened, photoreceptor vesicle (as in patellogastropods and basal vetigastropods). Afterwards, the eyes develop a lens that converges the light on the retina. According to the present analysis, the open eyes of Pleurotomariidae *(Perotrochus)* are a reversion. Lenses are also found, by convergence, in secondary eyes, as, *e.g.,* in the pallial eye of *Cerithidea costata* (Cerithioidea) (Simone, 2001a) and in bivalve mantle and siphonal eyes (Morton, 2000a, b). Based on the fact that lenses can appear in clearly non-related eye-bearing structures, it is possible that the lenses from Vetigastropoda and from Apogastropoda are convergences.

Eyes position: The presence of a pair of cephalic tentacles is a synapomorphy of the Gastropoda (Haszprunar, 1988a, b); Ponder & Lindberg, 1997; Sasaki, 1998) (node H). The present character is concernhed with their relationship with the eyes. In the Patellogastropoda and Cocculiniformia (node J), eyes are rarely found, and when present, they are simply structured structures. This, in part, precludes the analysis, which must be done only in the outgroups Vetigastropoda and Neritimorpha. In these taxa, in which the eyes generally are well developed, they are located at the tip of an ommatophore, situated just posterior to the base of tentacles (Fig. 3A) (Simone, 1998d, figs. 21, 39: om). This condition differs from that found in the caenogastropods, in such the eyes are situated on tentacular structures (Fig. 3B-E) (characters 128-133). This character was also utilized by Strong (2003), but with an inverted polarization.

In the heterobranchs, the interpretation of this character is very confused, since the homology of their tentacles with those of the 'prosobranchs' is unclear. There is the possibility of they are not related organs. Anyway, even in the heterobranchs, the eyes apparently are not related to the tentacles (*e.g.,* Marcus & Marcus, 1965).

Ommatophore in tentacles: Herein, the ommatophore is considered a stalk with an eye at its tip (Fig. 3). When present, the ommatophore of the archaeogastropods and heterobranchs has an origin close to the tentacles, but not derived from them (Fig. 3A). In the caenogastropods, the ommatophore

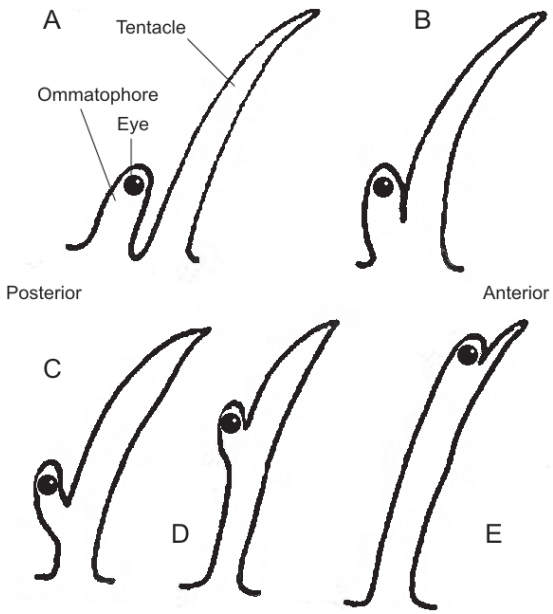

FIGURE 3: Schematic representation of relation between ommatophore and tentacle: **A)** Both located close from each other, but separated, *e.g.,* Vetigastropoda and Neritimorpha; **B)** Both with same origin, condition of node 1 of Caenogastropoda; **C)** Ommatophore originated from tentacle, slightly above its base, condition in node 3 of Caenogastropoda; **D)** Ommatophore originated approximately in middle level of tentacle, a tendency in most superfamilies; **E)** Ommatophore located close to tentacle tip, a condition found in Strombidae, Conidae and Terebridae.

or the eye (when an ommatophore is absent) is located on the tentacles. In the branches 2 and 5 of the cladogram (Cyclophoroidea and Ampullarioidea – Fig. 20) (Fig. 3B) the ommatophores are located close to the tentacle's base; in the remaining taxa, the structure has a tendency to be located between the basal and middle thirds of the tentacle. Additionally, inside some superfamilies, the ommatophore tends to be situated still closer to the apex of the tentacles (Fig. 3D-E); *e.g.,* strombids (node 55) (Simone, 2005a); terebrines (node 190) (Simone, 2000a).

Both, the eyes and the ommatophores, were lost several times inside each superfamily, mainly in those taxa with fossorial habits (*e.g., Olivancillaria, Buccinanops* – Muricoidea) (Simone, 1996a) or caverniculous (*e.g., Potamolithus troglobius* Simone & Moracchioli, 1994 – Risooidea). The analysis of some cladograms has shown that sometimes the loss of the eyes can be reverted, as in the Cancellarioidea (node 222) and Naticoidea (node 97).

Pedal glands: The pair of pedal glands is responsible for the mucus that flows along the foot sole, and allows to the animal to slide while crawling. It is well developed in most gastropods. Although, in the archaeogastropods and heterobranchs, the pedal glands are visible rising from the floor of the haemocoel during dissection, passing through the foot musculature. This condition does not occur in the caenogastropods, in which the glands are immersed inside the foot muscle, and do not encroach on the haemocoelic cavity. The single studied exception is *Serpulorbis decussatus* (here included in Cerithioidea – node 23 – see discussion on placement below) (Simone, 2001a), which, like all vermetids, has enormous glands that occupy about 1/4 of the haemocoel volume (Simone, 2001a, fig. 425: pd). They are responsible for the mucous net, utilized by the vermetids for capturing food. In these animals, the large size of the glands contrasts with the small size of the foot. Paradoxically, some taxa with a very large foot, utilized as a plow in the substrate, *e.g., Olivancillaria* (Muricoidea, node 220) and Naticidae (Naticoidea, node 97), have reduced pedal glands or have even lost them.

The ***cement gland*** is an unpaired glandular structure, present only in females, that is situated in median line of the anterior third of the foot sole. This gland is sometimes called the ventral pedal gland (Fretter & Graham, 1962; Strong, 2003) (character 641). Such a gland may aid in the attachment of egg capsules to the substrate (Ankel, 1936; Fretter, 1946) and in the final molding of the capsule (*e.g.,* as in volutids – Cledón *et al.,* 2005; Bigatti & Penchaszadeh, 2005). A single large branch [Cancellarioidea (node 222)] is supported by the cement gland. In the remaining branches after node 148 the character appears sparsely. Because of the similarity of attributes, the cement gland may be another character that defines node 148, although it has apparently been independently lost in several internal clades. However, such a hypothesis is only speculative. The presence of this gland, called a ventral pedal gland, has been utilized as an apomorphic character in coralliophinid neogastropods (Richter & Luque, 2002).

Although there are some species situated before node 148 that possess head-foot glands that aid in reproduction (Fretter, 1946; Ponder, 1965; Ponder & Yoo, 1980; Houbrick, 1988), because of their different localization, they are certainly not homologous. Additionally, it is possible that this gland has not been observed in some taxa because females were not reproductively mature. It may also be much less obviously developed in some – *e.g.,* those with lens shaped capsules.

A ***posterior pedal gland*** (character 110), is present in some minute sized caenogastropods, *e.g.,* some eulimids (Simone & Martins, 1995); node 32 (of cerithioideans) (Simone, 2001a, *e.g.,* fig. 345: pu); node 43 (some rissooideans) (Marcus Er & Marcus

Ev, 1963, fig. 71: io; Ponder, 1988; Simone, 2006b); etc. The posterior pedal gland has the function of anchoring the animal or aiding in the locomotion of minute snails. It is a totally different structure from the cement gland which has a reproductive function (see above). Some basal heterobranchs possessing minute size also present posterior pedal gland, *e.g.,* Rissoellidae (Fretter, 1948; Simone, 1995b); certainly convergences.

Aperture of the anterior pedal glands: In the caenogastropods, each anterior pedal gland opens in the central region of a furrow that, normally, reaches across the entire anterior edge of the foot sole (Fig. 4). This furrow is generally deep, and provides a uniform distribution of the mucus along the sole. In the outgroups, no similar furrow has been found, except, in some other gastropods there is a modest furrow at the anterior edge, close to median line, such as, *e.g.,* in *Aplysia brasiliana* (Marcus & Marcus, 1957; *pers. obs.*) or trochids (node M) (Simone & Cunha, 2006, fig. 67: pg).

The anterior pedal gland furrow was modified in several branches of the caenogastropod superfamilies. Sometimes it becomes ventral, due to the enlargement of the propodium (*e.g.,* Olividae – Muricoidea) (node 220) and, sometimes, it is lost. The lack of an anterior pedal gland is one of the synapomorphies of Naticoidea (node 97), although, the presence of these structures in the very young specimens, and the detection of a vestige in the basal taxa, suggest that the naticoidean possess a pedal gland. In some other taxa the furrow extends beyond the anterior pedal edge, extending laterally, as, *e.g.,* Ficidae (node 150), or lying along foot lateral edges, *e.g., Campanile* (node 21, Cerithioidea) (Houbrick, 1989; Simone, 2001a, fig. 406).

Distance between head base and furrow of anterior pedal gland: Normally, the distance between the ventral base of the head and the anterior edge of the foot (where the anterior pedal gland furrow lies) is short, *i.e.,* shorter than 1/10 of the total length of the foot. However, in the stromboideans (node 47) (Simone, 2005a) and tonnoideans (node 149) this distance is much greater (about half of the foot length) (character 161). This latter state is clearly convergent in the two groups.

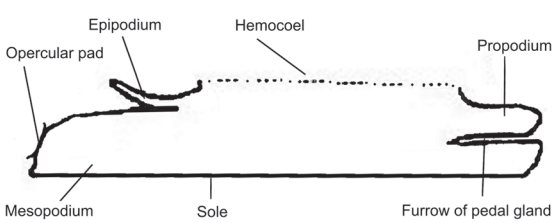

FIGURE 4: Schematic representation of a longitudinal, sagital section in a normal caenogastropod foot in crawling position, anterior region right, showing its main parts and their terminology adopted herein.

The ***foot*** is a very useful structure in comparative analyses. The high number of adaptations and respective morphological modifications of the organ are valuable for systematic and phylogenetic studies in all levels. Extremes of variations are easily found, as the complex, but small foot of the vermetids (node 23, Cerithioidea) (Simone, 2001a); the foot of the strombids, modified for working as a muscular and mobile stalk for the operculum (node 55, Stromboidea) (Simone, 2005a); and the enormously large feet of the several taxa that have representatives living in unconsolidated substrata, as, *e.g.,* Naticoidea (node 97).

The nomenclature shown in Fig. 4 is that normally utilized for the subdivisions of the foot (Ponder *et al.,* 2008). In the case of the **epipodium,** homology among the different branches possessing it is uncertain. It is relatively common among the vetigastropods (node L) (*e.g.,* Marcus & Marcus, 1960a, fig. 9; Fretter & Graham, 1962: 484; Simone, 1998d), but it is rare among caenogastropods (*e.g.,* Houbrick, 1988, fig. 2, a litiopid; 1993, fig. 4A a bittiine; *Annulobalcis aurisflamma* Simone & Martins, 1995 – Eulimoidea) (node 38). Something similar to an epipodium is found in the naticoideans (node 97); however, with particular features if compared with the other epipodia. Similar conceptual problem occurs with the **propodium.** This name has sometimes been utilized for any anterior projection of the foot, even though they have clear structural differences. The comparative analysis of the different "propodia" is facilitated by the presence of the pedal gland furrow, which shows homologous regions. In strombids (node 55) (Simone, 2005a) and hipponicids (node 72) (Simone, 2002, fig. 266: pr), there is a flat anterior projection of the foot, with a pedal gland furrow along the distal edge. This entire projection has been referred as "propodium" in the literature (*e.g.,* Walls, 1980); however, only its dorsal surface is homologous to the structure called propodium herein. Here, the structure is referred to as the "anterior projection of foot".

Number of columellar muscles: This is a character related to the organization of the outgroups. Their reduction to a single columellar muscle is one of the synapomorphies uniting the caenogastropods with its sister group, the heterobranchs (node W). Further discussion about this character is found in Ponder & Lindberg (1997: 106-108) and Sasaki (1998: 134-136). It is clear that, being an organ

directly connected to the shell, the columellar muscle presents an equal level of modification. The commonest is its transformation to a horseshoe shape (concavity anterior) in several branches with a limpet-like shell (*e.g.,* nodes S, 73). In these cases, the structure is called a "shell muscle". This kind of transformation was detected in distantly related groups, such as Patellogastropoda (node H) (Leal & Simone, 1998), Cocculiniformia (node J) (Simone, 1996c; Leal & Simone, 2000), Fissurellidae (node S) (Vetigastropoda), *Septaria* (Neritimorpha), Ancylidae and Umbraculidae (Heterobranchia) (Haszprunar, 1985a) and, among the Caenogastropoda, in Hipponicidae (node 73) (Simone, 2002). Details on the columellar muscle structure are found in Voltzow (1988), and the correlation between columellar muscle and columellar folds in Price (2003).

Snout/proboscis retractor muscles: A clear separation between snout and proboscis was not detected. According to the studied taxa, it is sometimes difficult to be sure which one is present. The main factor for the separation between the snout and the proboscis is the presence of retractor muscles. These muscles appear in node 46, which precedes Stromboidea, and become particularly more complex in the Tonnoidea (node 149). The multiplication of the retractor muscles happened independently, *e.g.,* Calyptraeoidea node 77 (Simone, 2002) and Conoidea (several branches after node 179). It is, however, part of a superfamily ground plan in the Tonnoidea (node 149). A more detailed discussion of the proboscis is provided under the foregut in the Digestive System below. A deeper analysis of the snout/proboscis retractor muscles, including a classification of the different pairs, with phylogenetic implications, is found in Golding *et al.* (2009b).

Septum separating haemocoel from visceral cavity: The presence of visceral organs inside the haemocoel, particularly an intestinal loop, is commonly found in basal gastropods (Sasaki, 1998: 151). In the present study, it was detected that no caenogastropod, including the architaenioglossans, has visceral structures inside the haemocoel. This separation is ensured by of the development of a transverse, membranous septum, situated at the posterior region of the haemocoelic cavity, almost at the boundary with the visceral region. Only the esophagus, the anterior aorta, and some nerves cross it. The septum may help in maintaining hydrostatic pressure in the head-foot. This interpretation explains the specialization of the septum as a thick muscular structure, like a diaphragm, in some stromboideans (node 62) (Simone, 2005a, figs. 118, 119) and tonnoideans (node 160), which encompass species of large size. No septum was found in outgroups, including heterobranchs. The septum is a noteworthy caenogastropod synapomorphy, with thickening occurring convergently in stromboideans and tonnoideans.

Operculum (Characters 53-72)

The presence of an **operculum,** which seals the shell aperture, is one of the synapomorphies of Gastropoda (Ponder & Lindberg, 1997: 105-106). All its representatives supposedly possess one, at least in larval or embryonic stage (although some direct developing heterobranch lack the structure). However, it may be reduced, or even lost, in the adult phase in several groups, including the basal gastropod branch Patellogastropoda. The opercular characters considered here refer to the adult phase.

In the more basal gastropod taxa, the operculum is generally circular; the outer surface is marked by spiral suture, originating from a nucleus situated in the central region. This fashion of operculum is here considered the basic standard for the other types of opercula. This proposed polarization is also based on the ontogeny, as larval or very young individuals have spiral opercula. The operculum underwent modification, according to the taxon, to a wide range of other opercular states (including loss). This scheme has also been proposed by other studies (*e.g.,* Checa & Jiménez-Jiménez, 1998). However, it is here proposed that concentric opercula, either with terminal nucleus or not, are derived from spiral ones. This is evidenced both by the allocation of the taxa on the cladogram, and by the development of the operculum from larva to young specimens (Kano, 2006, *pers. obs.*). An alternative proposal is that the concentric operculum with a terminal nucleus evolved from a paucispiral one, independently from the concentric operculum with a non-terminal nucleus (Checa & Jiménez-Jiménez, 1998, fig. 10).

Except for the shell, the operculum has been the most analyzed structure in Gastropoda. However, just like the shell, the opercular characters are homoplastic, reflected by the indices in Appendix 1. Its loss is the commonest modification, and occurs in representatives of many superfamilies, both ingroup and outgroups (see, *e.g.,* Dayrat & Tillier, 2003: 172, on heterobranchs). Among the caenogastropods, the loss of the operculum is particularly common in all superfamilies after node 66, being a synapomorphy of the Cypraeoidea (node 118) (Simone, 2004b)

and Cancellarioidea (node 222) and of several inner branches of the remaining superfamilies (*e.g.,* nodes 71, 160). Another point of view, *i.e.,* the absence of an operculum in some gastropods being plesiomorphic, was advocated by Strong (2003: 487).

Pallial organs (Characters 148-228)

Mantle border length: The mantle border becomes particularly broad in the taxa situated after node 46, which may reflect a tendency towards increasing the width of the shell outer lip, and a specialization to assist in directing the flow of water towards the pallial cavity. This character is less clear in the naticoideans (node 97); in which some portions of the foot assist some functions of the mantle border. However, even in this taxon, it is clear that the mantle edge extends beyond head level when the animal is active. This tendency reaches its peak in the cypraeoideans (node 118), where the mantle extends to the dorsal surface of the shell, being functionally external (Simone, 2004b) and the shell is functionally internal, exposed only when the animal is disturbed. In a branch of the cypraeoideans (the lamellariids, node 119) (Simone, 2004b), the shell is permanently internal. Similar mantle covering in dorsal shell surface appeared convergently in other taxa, such as, *e.g.,* Volutidae, Marginellidae and Olividae (node 220, Muricoidea).

Appendices on mantle border: Being a structure exposed to the environment, it is to be expected that the mantle border bears special structures for reception of stimuli. Macroscopic structures were detected in several branches; some of them are superfamily synapomorphies, *e.g.,* papillae and tentacles in cerithioudeans and cypraeoideans (Simone, 2001a, 2005a). Several additional pallial structures are found, but were excluded because they were autapomorphic, as, *e.g.,* the pallial eye, with lens, of *Cerithidea costata* (Simone, 2001a, fig. 393: n1) (node 29) and the tentacle in front of the anus in strombids (Simone, 2005a) (node 55).

Distinct siphon in mantle border: There are 3 types of inhalant siphons in the caenogastropods: **1)** of cephalo-pedal origin, restricted to the ampullarioideans (node 5) and viviparoideans (node 15) (see above); **2)** present in the shell, but lacking in the adjacent region of the mantle border, as noted above, and found in Cerithioidea (node 19) and Stromboidea (node 47) (Simone, 2001a, 2005a); **3)** of pallial origin, arising from its anterior-left edge. Characters 149, 166, 174, 176, among others, refer to the type 3 of siphon. The siphon is separated from the mantle edge, which contours its base and, most probably, may be originated from its inner fold (*e.g.,* Simone, 1996a, fig. 12; Simone, 2004b, fig. 154: si). Further discussion on the mantle edge and siphon is found in Ponder *et al.* (2008: 346).

Although of pallial origin, part of the siphon musculature is connected to the left region of the cephalo-pedal mass (during the dissection, the siphon must be sectioned from the head to be extracted with the remaining pallial edge). The distinct siphon from the mantle edge is one of the synapomorphies of node 117. In this branch, the siphon has the form of a simple fold. It becomes long and outstandingly large in the taxa allocated after the node 148, becoming an important exploratory structure for the animal.

The ***number of gills and osphradia*** (character 158) are included herein for organization of the outgroups, being important issues for studies on the class as a whole. Ponder & Lindberg (1997) and Sasaki (1998), for example, explored the trend for gastropods loosing the right organs of the pallial cavity, reflected in the reno-pericardial structures. The loss of pallial structures is a probable consequence of the shell bending. A pair of gills and osphradia is the plesiomorphic condition in Gastropoda, if compared with the remaining classes. The loss of the right structures (left pre-torsional ones) is one of the synapomorphies of node T; although, this is also found, by convergence, in some internal branches of the taxa preceding this node, as, *e.g.,* node M (Trochidae – Vetigastropoda) (Marcus, 1957: fig. 6; Simone & Cunha, 2006), Acmaeidae (Patellogastropoda) (Sasaki *et al.,* 2006), and Addisoniidae (node J – Cocculiniformia) (Simone, 1996c).

Type of osphradium: The osphradium is a chemosensory organ. In the archaeogastropods and heterobranchs (Dayrat & Tillier, 2002, 2003), and even among the remaining classes of mollusks, the structure has the form of a ganglionar node (Fig. 5A), situated, generally, at the base of the gill (*e.g.,* Simone, 1998d, fig. 20; Simone & Cunha, 2006, fig. 71: os). Details of its structure have been utilized in gastropod comparative studies (Haszprunar, 1985b; Taylor & Miller, 1989). In caenogastropods, the osphradium characteristically becomes modified and more complex. The first modification is its elongation, becoming ridge-like (Fig. 5B) (*e.g.,* Simone, 2001a, fig. 172: os) (node 1). Another step is becoming pectinate (Fig. 5C) (*e.g.,* Simone, 2004b, fig. 485: os) (node 66).

As the osphradium is a sensory organ, the larger its surface area, the more efficient it becomes. The

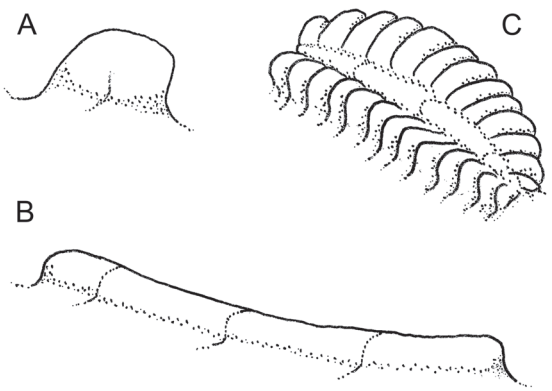

FIGURE 5: Schematic representation of the three main types of osphradia found in prosobranchs, ventral view; **A)** Nodular; **B)** Ridge-like; **C)** Bipectinate.

enlargement of the osphradium is a feature of caenogastropods (Haszprunar, 1985b; Ponder & Lindberg, 1997), with the organ initially modified from its nodular form to a long, ridge-like structure (node 1). Although, it is possible to increase its surface still more by: 1) further enlarging its length, resulting in an undulating, zigzag form; 2) or by enlarging its surface by folded edges. The first method was only found in a single taxon, Modulidae (node 19 – Cerithioidea) (Simone, 2001a, fig. 302). The second option is the most common among caenogastropods. The osphradium becomes bordered by a series of successive folds, or filaments, alternating on both sides of the ganglion, which lie along the center. This kind of osphradium is called pectinate if ridges are on one side or bipectinate if on both. The elongate form of the osphradial ganglion (excluding the filaments) suggests that the pectinate type may be derived from the ridge-like one. Also in the larvae and very young individuals, the osphradium has the ridge-like condition; the filaments are added afterwards (Pilkington, 1976; Parries & Page, 2003).

According to the distribution of this character on the cladogram, the pectinate condition evolved some times independently: in Ampullarioidea (node 5); in the nodes 21 and 31 of Cerithioidea (Cerithiidae *latu sensu* and *Campanile*) (Simone, 2001a, fig. 422); in the node 55 (Stromboidea) (Simone, 2005a); and in all branches allocated after node 66. Thus the bipectinate condition in these nodes is the result of convergences. However, they are classified in a same category – bipectinate osphradium, in some characters. However, in each higher taxon the osphradia possess other particularities that additionally suggest convergence, as discussed below.

Despite the obvious advantage of the pectinate condition, the result of the present study suggests that there was reversion to the ridge-like osphradium, *i.e.,* non-pectinate, in two taxa: in node 72 (Hipponicidae, Calyptraeoidea) (Simone, 2002) and node 98 (*Amauropsis,* Naticoidea). Although, the commonest modification is the **monopectinate** condition. This model is normally found in groups that present miniaturization. In those cases, it is possible to find members possessing a bipectinate condition in

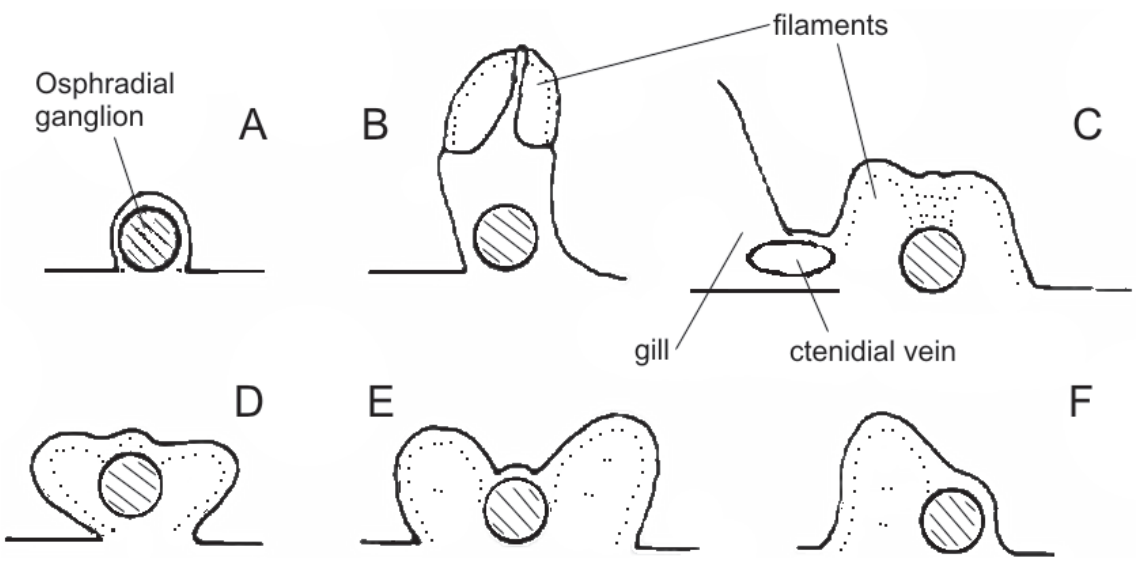

FIGURE 6: Schematic representation of a transverse section of a middle region of main types of osphradia; **A)** Ridge-like, simple; **B)** Bipectinate on a stalk (restricted to ampullarioideans); **C)** Bipectinate, with right filaments connected to ctenidial vein (exclusive of *Campanile*); **D)** Ridge-like, narrowly bipectinate (found in strombids and some cerithioideans); **E)** Bipectinate with elliptical outline (of higher caenogastropods); **F)** Monopectinate (common in miniaturized forms).

the posterior region and monopectinate anteriorly; as well as some related taxa with a totally monopectinate osphradium. Examples are node 123 (Pediculariidae, Cypraeoidea) (Simone, 2004b) and node 216 (Columbellidae, Muricoidea) (Simone & Leme, 2001, figs. 14, 25). In the monopectinate condition, it is always the right filaments that are retained (Fig. 6F).

Another common morphological adaptation of the osphradium is the presence of a **satellite fold.** This fold may be restricted to a side of the organ or surrounds it totally. Satellite folds are apparently glandular and much more common in the ridge-like osphradia than in the pectinate ones. Several clades have satellite folds as synapomorphies, *e.g.,* node 32 (in Cerithioidea) (Simone, 2001a, *e.g.,* fig. 335); node 98 (in Naticoidea); and node 72 (in Calyptraeoidea) (Simone, 2002, *e.g.,* fig. 319). In the last case, in *Cheilea equestris,* only the satellite fold is visible, instead of the osphradium (Simone, 2001, fig. 350: os).

Although, in character 179, all pectinate osphradia have been considered homologous, it is possible to observe, as shown in the Fig. 6, that they are the result of different kinds of modifications. This fact is taken into consideration in the characters 182, 183 and 195. The simple ridge-like osphradium (Fig. 6A) has the osphradial ganglion occupying most of its interior. In the node 5 – Ampullarioidea (Fig. 6B), the filaments are on the surface of a relatively tall fold, which functions as a stalk (Simone, 2004a, *e.g.,* fig. 156). After node 21, in *Campanile symbolicum* (Cerithioidea) (Simone, 2001a, fig. 422) (Fig. 6C), the filaments are widely connected to the mantle, and, additionally, they are connected to the ctenidial vein. The bipectinate osphradia of the node 31 (also Cerithioidea) (Simone, 2001a) and node 55 (in Stromboidea) (Simone, 2005a), are elongated, bearing minute filaments in both sides (Fig. 6D). These bipectinate osphradia of some branches of Cerithioidea (Simone, 2001a, *e.g.,* figs. 317-318) and Stromboidea (Simone, 2005a, *e.g.,* figs. 75-77) are similar to each other, despite in being, according to the obtained results, convergences.

In the taxa allocated after node 66, all superfamilies have the here called elliptic bipectinate osphradium (considering the outline, including the filaments) (Fig. 6E), being, then, an important synapomorphy of the clade. Some modifications of this fashion of osphradium are discussed above, inclusive the monopectinate condition (Fig. 6F).

The above mentioned range of different osphradium morphologies suggests that the different types of pectinate osphradia are probably the product of convergence, which corroborates the results here obtained. As coincidence, in all cases of bipectinate osphradia, the filaments are arranged alternately on both sides of the osphradial ganglion. In the osphradia of the cerithioidean-node 31 (Simone, 2001a) and stromboidean-node 55 (Simone, 2005a), the filaments are only visible by means of a microscope. For the remaining pectinate osphradia, the filaments are evident, forming the elliptical outline.

Being an important organ to the caenogastropods, a conclusion allowed by the wide range of adaptations described above, it is interesting to emphasize that, in several taxa of each superfamily, the osphradium still possesses additional modifications. In the Tonnoidea (node 149) and Conoidea (node 179), for example, the osphradium filaments become scalloped (*e.g.,* Marcus & Marcus, 1960b: fig. 3). However, probably the most peculiar transformation of the organ is found in the Ovulidae-Cypraeidae branch (node 129 – Cypraeoidea) (Simone, 2004b), the osphradium becomes trifid, *i.e.,* there are 3 equidistant bipectinate branches united at the center (Simone, 2004b, fig. 116).

The osphradium has aroused detailed and interesting studies on its ultrastructure and fine morphology. Haszprunar (1985b) pointed out that caenogastropods have, as a characteristic, the presence of 3 types of different cells, which mutually changes in position; this feature was used by Ponder *et al.* (2008, characters 54, 55). This pattern was utilized by the author as a synapomorphy of the taxon; however, he indicated that *Campanile symbolicum* and the architaenioglossans lack this feature. According to the present result, the character pointed out by Haszprunar (1985a, 1992) for Caenogastropoda, may, in fact, assists to support the node 18, with *Campanile* having additionally modified the feature (Simone, 2001a). However, Cyclophoroidea still lacks an examination at the same level of details (Simone, 2004a), and further studies may change the presented scenario. Taylor & Miller (1989) has also performed a study of the osphradium, with the aid of a scanning electron microscope, in species that in the present study belong to taxa situated after node 40. One of their conclusions is that, despite the high morphologic variation, all pectinate (called lamellar) osphradia appear to have arisen from a common plan, *i.e.,* they do not appear to be convergences. This is compatible with the proposition presented here.

Gill type: As stated in the Introduction, the name Caenogastropoda was introduced for replacing the name Pectinibranchia (Cox, 1960a, b). This name just mean "gill in form of comb", or monopectinate. This corroborates with the proposition

that the monopectinate gill is one of the long known characters uniting meso- and neogastropods. The monopectinate gill contrasts with the normal bipectinate pattern found in the archaeogastropods, and the absence of primary gills in the heterobranchs (Haszprunar, 1988a, b). The bipectinate gill is, characteristically, constituted by 2 series of alternated filaments, situated along opposite sides of a longitudinal axis (Fig. 7A), similar to those occurring in other classes (*e.g.,* Simone, 1994, 1997c, d, 1999b, 2001b). This axis has the efferent vessel (ef) running along its base, and the afferent vessel (af) along the distal edge. In the case of the Vetigastropoda (node L) (Simone, 1998d; Simone & Cunha, 2006) and Neritimorpha (node U) (Sasaki, 1998), the posterior portion of the gill with the longitudinal axis connected on both edges, forms a dorsal, supra-branchial chamber (cs), protecting the dorsal (right) filaments (Fig. 7B). These filaments are smaller than the ventral ("left") ones. By analyzing the position of the filaments and of the afferent and efferent vessels, it is possible to infer that the caenogastropod monopectinate gill arisen from the loss of the supra-branchial chamber, with the axis becoming part of the mantle roof that supports the gill; and the loss of the dorsal filaments (Fig. 7C).

Then, as schematized in Fig. 7, the evolutionary process suggested herein is that the monopectinate gill is only homologous to the ventral (left) filaments of the left gill, from a plesiomorphic Gastropoda (with a pair of bipectinate gills), by means of the loss of the dorsal branchial chamber. A somewhat intermediary condition is found in some vetigastropods and neritimorphs. In those, the anterior portion of the gill is free and symmetrically bipectinate. The gill gradually becomes asymmetrical posteriorly, as shown in Fig. 7B.

Although the monopectinate gill pattern is an important synapomorphy of the caenogastropods (but see remarks on the cyclophoroideans below), it is not exclusive. Some branches in the archaeogastropod grade also have monopectinate gill, surprisingly similar to that of Caenogastropoda, *e.g.,* Lirulariinae and Umboniinae (Trochidae), Larocheinae (Scissurellidae) in Vetigastropoda (Sasaki, 1998), as well as Addisoniidae in Cocculiniformia (Simone, 1996c, figs. 25-27) (node J).

Some characters (*e.g.,* 203-206) deal with gill details probably related to its enlargement amongst the caenogastropods. The loss of the gill was detected in some ingroup branches, as part of adaptations for terrestrial environment or miniaturization (some Hydrobiidae – Rissooidea) (Hershler & Holsinger, 1990; Hershler & Longley, 1986), *Annularia* (after node 41). In the case of invasion to the terrestrial habitat, the loss of the gill is accompanied by an augment in the pallial roof vessels between the rectum (adrectal sinus) and the left edge of the pallial cavity, in a

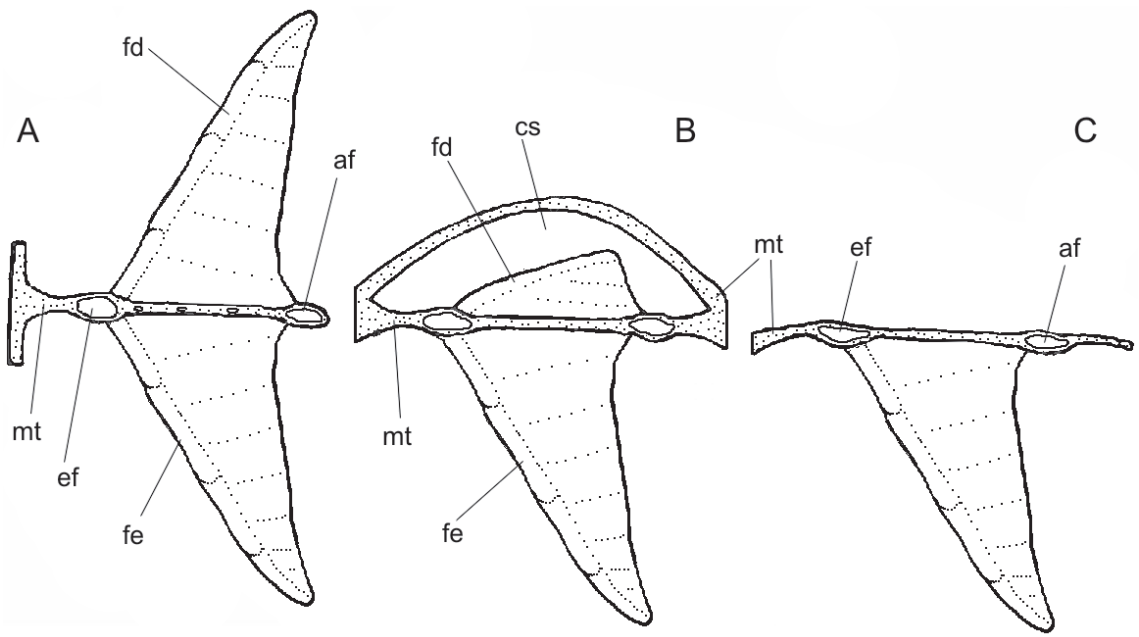

FIGURE 7: Schematic representation of transverse sections in three types of gills, in their middle level: **A)** Bipectinate, normal fashion (left gill); **B)** Bipectinate with asymmetrical filaments present in vetigastropods and neritimorphs; **C)** Monopectinate of caenogastropods. Lettering: af, afferent gill vessel; cs, suprabranchial chamber; ef, efferent gill vessel or ctenidial vein; fd, right or dorsal gill filament; fe, left or ventral gill filament; mt, mantle or connection to mantle.

region homologous to the ctenidial vein. This mantle area is normally called lung. The lung occurs in the cyclophoroideans (node 2) (Simone, 2004a), and in branches of other superfamilies, such as, *e.g.,* Annulariidae (after node 41 – Rissooidea) (Simone, 2004a, 2006b). However, the Ampullarioidea (node 5) have a peculiar lung, situated between the gill and the osphradium, isolated from the rest of the pallial cavity by a muscular and vascular membrane (Simone, 2004a, *e.g.,* fig. 153: lu). This condition is certainly not homologous to lungs of other gastropod.

Hypobranchial gland: The structure of the vetigastropods (node L) and neritimorphs (node U), generally, has well delimited edges, bearing transverse folds and mucous sub-chambers (*e.g.,* Simone, 1998d, fig. 20). Although, in the taxa situated after node W, the gland is normally a specialization of the mucosal epithelium of the mantle roof, in its area between the right edge of the gill (or left edge of the cavity when a gill is absent) and the rectum. It is rather possible that both kinds of glands are not homologous. An option is that the original hypobranchial gland was lost, and it had been replaced by the enlargement of the mucosa in the same mantle region. Regardless, this barely affect the phylogenetic aspect, since a change in the form of a homologous gland, or the replacement by analogous glands, is nevertheless a synapomorphy of node W. In the mean time, there are determined caenogastropod branches that have a more complex hypobranchial gland, despite in being dissimilar to those of the outgroups. An example is in muricids (node 232).

The ***anal gland*** in Neogastropoda revealed inconstant amongst the taxa (character 226). This gland has been considered a synapomorphy of Neogastropoda (Ponder, 1974; Strong, 2003), and normally is a small, pigmented, acinose gland connected by a narrow duct to a rectal region preceding the anal aperture (*e.g.,* Marcus & Marcus, 1960b: figs. 13, 14; Simone, 1999a, fig. 4B: al). It is immersed in the mantle, normally covered by the hypobranchial gland. Despite such a gland has not been found in several examined neogastropods, it could as well be a Neogastropoda synapomorphy, lost in several of its branches. Further comments on the anal gland characters and occurrence see Kantor (2002: 165).

Circulatory system (Characters 240-261)

Number of auricles: This character assists the organization of the outgroups. It is interesting that the basal Neritimorpha (node U) have a pair of auricles, contrasting with their complete loss of the pallial structures of the right side, including the gill, osphradium, and the kidney. After node W, all taxa possess a single auricle, homologous to the left auricle of basal gastropods. This character is the basis of the name Monotocardia (in contrast to Diotocardia) for that branch.

Another character linked to this issue is the liberation of the intestine. In the diotocardians, the intestine crosses through the pericardium and is encircled by the ventricle (*e.g.,* Marcus & Marcus, 1960a, fig. 12). This fashion is found in all basal taxa of the remaining mollusk classes, and must be plesiomorphic. In the monotocardians (Caenogastropoda + Heterobranchia – node W), the intestine is free from the ventricle and even from the pericardium, running only close to it (characters 243, 260). Convergently, there are archaeogastropods with the monotocardian condition, *e.g.,* Helicinidae (Neritimorpha) (Richling, 2004; *pers. obs.*), as well as most Patellogastropoda (after node H) (*e.g.,* Leal & Simone, 1998). Maybe for this reason, Ponder & Lindberg (1997) and Sasaki (1998) considered the polarization of this character inverted (ventricle encircling the intestine as apomorphic).

The appearance of the nephridial gland (discussed below) is a further modification of the connection between the renal cavity and the auricle, which normally is done by means of a narrow orifice of the auricular projection. Additionally, for the taxa situated after node 66, the auricle is attached to the inner surface of the anterior wall of the pericardium. This condition results in a triangular auricle when contracted (*e.g.,* Simone, 2004b, fig. 456), the anterior side has as vertices the ctenidial vein (at left) and the connection with nephridial gland (at right). This state appeared because of the increasing distance between the left margin of the renal chamber and the region where ctenidial vein runs.

Excretory system (Characters 262-290)

Number of kidneys: Although all basal gastropods already have a conspicuous asymmetry between the pair of kidneys (Haszprunar, 1988a; Ponder & Lindberg, 1997; Sasaki, 1998: 153), the loss of the right kidney is one of the synapomorphies of node T, and assists in the organization of the outgroups.

Relation between the kidney(s) and intestine: In all mollusks, there is a remarkable association between

the kidney(s) and intestine, being an adaptation for electrolytic balance (Hill, 1987). In gastropods, the kidney or kidneys are attached to the intestinal portion preceding the rectum, which runs through the pallial cavity. In caenogastropods, however, the intestine runs through the renal cavity, either attached to its inner surface or through its center. In the last case it may or may not be surrounded by a renal lobe. There are some caenogastropod groups that possess one or several intestinal loops inside the renal chamber [node 5 – Ampullarioidea (Simone, 2004a); after node 41 – Annulariidae, Rissooidea (Simone, 2004a); node 52 – Xenophoridae plus Strombidae, Stromboidea (Simone, 2005a)]. In these cases, the intestinal loop(s) always bear a conspicuous mesentery, connecting it with the dorsal inner surface of the renal cavity.

Kidney inner structure: The normal form of the (left or single) kidney of the outgroups (archaeogastropods and Heterobranchia) is of a gland, entirely filled by an apparently uniform solid tissue. In the caenogastropods, the kidney is a hollow cavity, having the renal tissue at the periphery. The renal tissue differentiates into two lobes, dorsal and ventral. These lobes generally fill the right region of the renal cavity (*e.g.,* Simone, 2003, fig. 9B).

In certain branches within some superfamilies, one of the kidney lobes is missing (*e.g.,* cypraeids, node 137), while in others the kidney becomes, secondarily, almost entirely solid (*e.g.,* aporrhaids, node 51). The former condition generally is a consequence of the miniaturization (*e.g.,* node 43) (Simone & Moracchioli, 1994). After node 96 there is a tendency for fusion of both lobes in their anterior region, surrounding the adjacent part of the intestine. The nature of the afferent renal vessel, which departs from the haemocoel, was addressed by Strong (2003: 524, character 50). The renal vessel bifurcates and supplies two differentiated renal lobes in the taxa allocated between nodes 40 and 96 of the present study, exhibiting a reversion to the plesiomorphic state (supplying a single lobe) in a branch of the Neogastropoda (node 210) (Marcus & Marcus, 1959a) excluding the cancellariids (node 222).

The afferent renal vessel is large in the taxa that have a bulky foot. The greater the foot, the larger the afferent renal vessel and its drainage to the renal lobes. It is here suppoded that his is a physiological adaptation to remove the liquid inside the foot, saving important substances like electrolytes and nutrients. This adaptation permits an animal that has an active foot 2-3 times larger than the shell volume, *e.g.,* naticids (node 97) and olivids (node 220), to retract the foot entirely inside the shell. Despite the recognition of this character, it is not utilized because of the difficulty in establishing standards.

Nephridial gland: The gland is one of the synapomorphies of node 40. This gland is narrow, triangular in section, and is situated inside the renal chamber, connected to the membrane that separates the kidney from the pericardium (*e.g.,* Simone, 2003, fig. 7B: ng). It possesses a connection, as a pore, to the auricle in its anterior-left end (*e.g.,* Simone, 2002, fig. 157). The nephridial gland processes the haemolymph that flows between the auricle and the renal chamber, as well as that haemolymph which exudes from the pericardial cavity to the renal cavity through the membrane separating them. Its constitution is glandular, with connective tissue and muscle fibers (Fretter & Graham, 1962; Strong, 2003). Investigations of the renal structures of the taxa positioned before node 40 have revealed no true nephridial gland (*e.g.,* Andrews, 1965, on ampullariids). On the other hand, some nephridial glands are found in other taxa preceding node 40 (*e.g.,* in *Viviparus,* Andrews, 1979), but most probably they do not represent homologous structures, since they are not placed in the same region of the kidney. The nephridial gland is reduced in some branches, and almost disappears in some, *e.g.,* in some hipponicids (node 73 – Calyptraeoidea) (Simone, 2002), and xenophorids (node 53 – Stromboidea) (Simone, 2005a). The contrary occurs in some branches, where the gland enlarged to the point of being the single visible renal gland, *e.g.,* aporrhaids (node 51 – Stromboidea) (Simone, 2005a).

Nephropore: This is the renal aperture by which the urine flows to the pallial cavity. In the outgroups, the nephrostome is, generally, a small papilla protected inside by renal tissue (*e.g.,* Fretter & Graham, 1962, figs. 53, 151; Simone & Cunha, 2006, fig. 71: ne). In the caenogastropods, however, it is an aperture free of inner structures (characters 283, 284). This forms a relatively large fissure, bordered by a sphincter (*e.g.,* Simone, 2005a, fig. 301: ne).

The renal characters are particularly modified in the non-marine taxa. In those, the additional effort for saving electrolytes (in the freshwater taxa) and water (in the terrestrial taxa) is reflected in their morphology. As can be observed in the cladogram, the caenogastropod mainland invasion occurred, independently, several times. In each case, peculiarities in the kidney are evident. There are non-marine groups in the Cerithioidea (nodes 26, 35), Rissooidea (node 44) and Muricoidea (after node 215) as well as the three basal taxa, Cyclophoroidea (node 2), Ampullarioidea (node 5) and Viviparoidea (node 15),

where the modifications are most obvious (Simone, 2004a). These include the development of a differentiated fold conducing urine in ampullarioideans (the taenia); the solid kidney of the cyclophorids, with a high vascular membrane exposed in the pallial cavity (Simone, 2004a); and the different wide renal aperture of the pleurocerids (Simone, 2001a).

The term "nephrostome" is used for the ciliated funnel-shaped inner opening of a nephridium into the coelom in some invertebrates and lower vertebrates. For this reason, the names "nephropore" or renal (or kidney) aperture are also is best utilized to designate this structure.

Digestive system (Characters 291-539)

Foregut (Characters 291-302)

The foregut characters refer to the digestive system, however, their analysis cannot be completely separated from the analysis of some regions of the head (cephalo-pedal mass) (characters 93-105). The literature is relatively confused with respect to the concept of snout and proboscis in various taxa, as well as with the classification of the different types of proboscides. However, they are consistently analyzed as part of the digestive system, an approach followed here.

The presence of a **snout** in the head-foot, in which the apex bears the mouth, is identified as one of the synapomorphies of Gastropoda (Ponder & Lindberg, 1997; Sasaki, 1998). However, any long structure in the anterior region of the head has sometimes been referred to as a proboscis (or trunk). This is the case, for example, with the proboscis of the palps of the protobranch bivalves, and even an elephant's trunk (order Proboscidea). As stated by Golding *et al.* (2009b), in gastropods, there is a clear difference between snout and proboscis. In Gastropoda, most representatives bear a projection forwards, between or just ventral to the cephalic tentacles. Such a projection has, naturally, the capacity of moving independently from the rest of the animal's body, and the ability of becoming shorter and longer. However, the point is the additional capacity of retraction inside the haemocoelic cavity.

Those snout elongations that have no capacity for retracting inside the haemocoel may be called as **snout** or muzzle. While those that have this capacity, may be called a **proboscis** (Golding *et al.,* 2009b: 2726). This definition is important, as there are some snouts labeled as proboscis in the literature, *e.g.,* Strombidae (node 55 – Stromboidea) (Walls, 1980) and Littorinidae (after node 42 – Rissooidea) (Ball *et al.,* 1997). However, this terminological confusion is indicative that the snout and proboscis are homologous structures.

In embryological studies [*e.g.,* Ball *et al.* (1997) on the development of the proboscis of the muricid *Nucella* (Muricoidea) (after node 234)], there is the designation for the first phases as snout. Only after the stage that the authors called "8" the structure progresses to a proboscis. Comparing the proboscis ontogeny of *Nucella* with a conid, Ball (2002: 72) found several characters in common and suggested that both proboscides are homologues.

With respect to the proboscis itself, there is a series of classifications found in the literature, aiming to organize the different types present inside or outside Caenogastropoda (*e.g.,* Miller, 1989; Ball *et al.,* 1997; Mendinskaya, 1992; Golding *et al.* 2009b). In general, most classifications have the following categories (in parenthesis are some taxa that supposedly possess it): 1) **pleurembolic** (Muricoidea, Tonnoidea); 2) **acrembolic** (Strombidae, Ptenoglossa, Cypraeoidea, Naticoidea, allogastropods); 3) **intraembolic** (most Conoidea); 4) **polyembolic** (Conoidea – some Terebridae); etc (*e.g.,* Ball *et al.,* 1997; Strong, 2003). Some propositions advocate that some proboscis types have evolved independently from proboscis-lacking gastropods (*e.g.,* Sheridan *et al.,* 1973; Shimek & Kohn, 1981; Kantor, 1990), and that the pleurembolic proboscis of the tonnoideans is unlike those of the neogastropods (*e.g.,* Ponder & Lindberg, 1997).

In the present study, both by the comparative analysis and by the position of the taxa at the cladogram (Fig. 20), it is possible to infer that all kinds of proboscises present in the caenogastropods are merely modifications of a single evolutionary ground plan. This proposition was in part published (Simone, 1999a: 243-245, fig. 27; Ponder *et al.,* 2008: 346). The following evolutionary scenario of the proboscis is schematized in the Fig. 8. Most outgroups (all archaeogastropods – nodes H-W; and most heterobranchs – node X), as well as the 5 first main branches of the caenogastropods, (nodes 1-65) have a snout (Fig. 8A). After node 40 (after Stromboidea), a pair of ventro-lateral retractor muscles in the snout appears, with their origin in the anterior region of the foot (its dorsal-inner surface), and their insertion close to the mouth (Simone, 2005a, *e.g.,* fig. 304: rm). This pair of muscles runs along the ventral surface of the haemocoelic cavity, snout included (Fig. 8B). Although the stromboideans, characteristically, have a pair of retractor muscles, they do have a snout, and do not

a proboscis. Moreover, in strombids (node 55), this pair of muscles was still lost, or was surrounded by the thick muscular layer of the snout wall (Simone, 2005a). In fact, the stromboidean snout has incapacity for introversion inside the haemocoel, which is an essential requirement to be considered proboscis. Even the struthiolariids (node 48), which have a long snout with high capacity of shortening, have no capacity of introversion. The retraction of the structure inside the haemocoel, beyond retractor muscles, also depends of the development of a cavity for accommodating it inside, when drawn back. This character arisen only in the taxa situated after node 66 (Calyptraeoidea + node 96), which possess a genuine proboscis.

In the calyptraeoideans (node 67) and naticoideans (node 97), the proboscis is short (*e.g.,* Simone, 2002, fig. 106). The region of the proboscis that remains protruded inside the rhynchocoel (the cavity formed when the proboscis is retracted) is small (Fig. 8C: α). This condition resembles the acrembolic one. When protracted, the proboscis (Fig. 8C) becomes similar to a stromboidean snout (Fig. 8B).

In the taxa represented after node 96, the proboscis becomes elongated. When retracted, almost half of

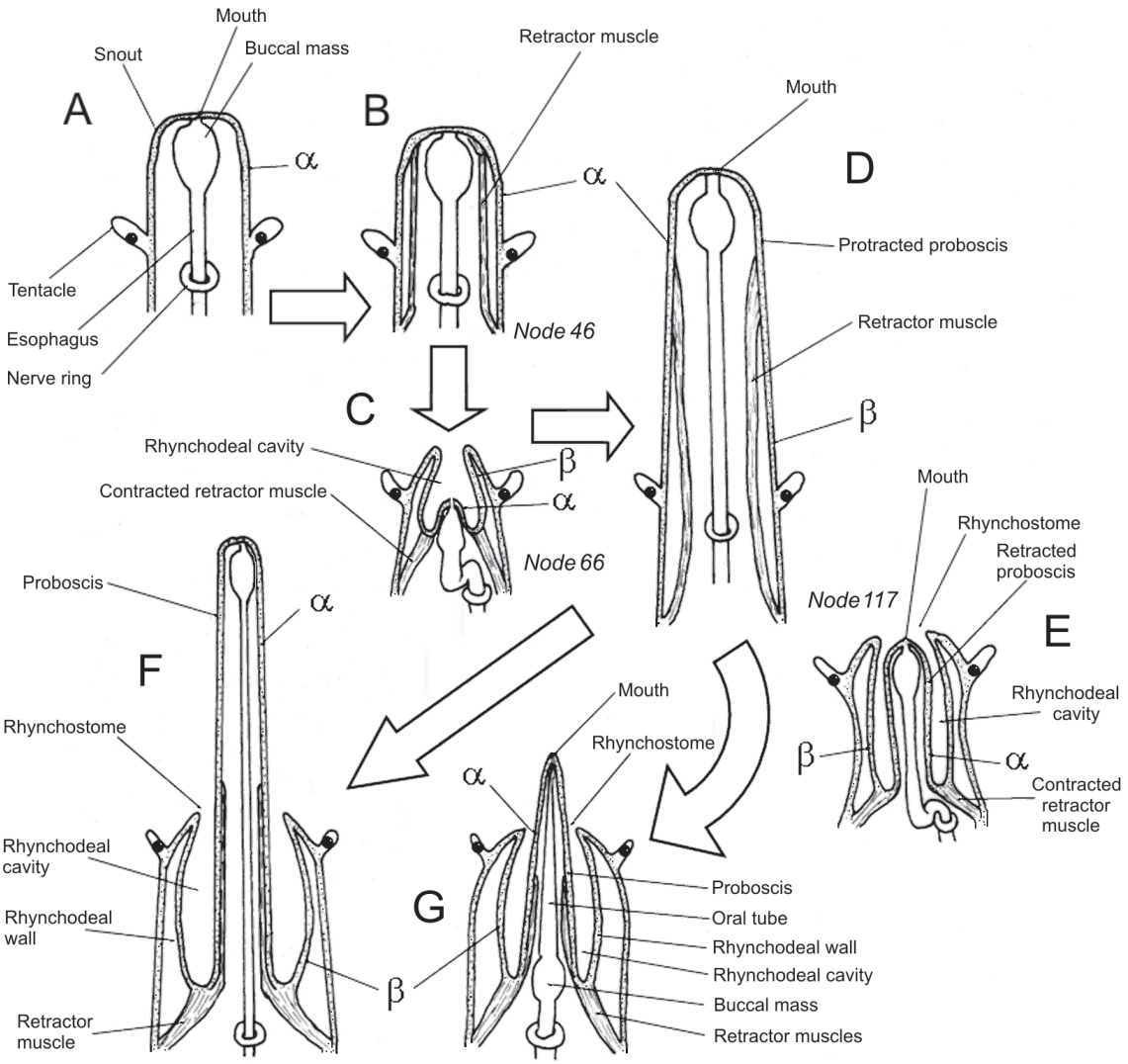

FIGURE 8: Scheme of the anterior region of head and digestive system in dorsal view, seen if longitudinally sectioned. No scales or proportions (the node numbers refer to Figure 20): **A)** Condition in outgroups and basal branches of ingroup, a truly snout; **B)** Condition in node 46, snout with retractor muscles; **C)** Condition in node 66, a true short proboscis; **D)** Condition in node 117, showing an extended long proboscis; **E)** Same, proboscis retracted inside haemocoel; **F)** Condition of Tonnoidea and some Muricoidea (*e.g.,* Buccinidae), with buccal portion of proboscis (α) excessively long; **G)** Condition of most Conoidea and some Muricoidea (*e.g.,* Marginellidae), with thin rhynchodeal wall that is rarely exteriorized, forming a permanent rhynchodeal chamber. Wide arrows show putative evolutionary pathway; α and β indicate probably homologue regions of proboscis.

its length remains protruded inside the rhynchocoel. This remaining portion (Figs. 8D, E) is called **buccal proboscis** or **proboscis buccal mass** (α), contrasting with the remaining portion, called **rhynchodeal wall** (ß) or rhynchothecium (Golding *et al.,* 2009b). This form is the typical pleurembolic proboscis, which is exclusive to the caenogastropods. It is represented extended in the Fig. 8D, and retracted in the Fig. 8E.

Although the elongated type of proboscis (typical pleurembolic) has arisen in node 96, which precedes Cypraeoidea (node 118) (Simone, 2004b, *e.g.,* fig. 419), this state was reversed inside this superfamily, in node 129 (Simone, 2004b, *e.g.,* fig. 121). Representatives of this clade possess a proboscis resembling those of the Calyptraeoidea and Naticoidea; and are not good representatives for illustrating the basic cypraeoideans proboscis.

The representation of the retracted proboscis (Fig. 8E) facilitates the appreciation of how the remaining proboscis categories probably evolved. In the case of the tonnoideans (node 149) and some muricoideans (*e.g.,* node 215 – Buccinidae and Nassaridae) (Fig. 8F), the buccal proboscis (α) increased to the point of no longer being retracted inside the rhynchodeal cavity (*e.g.,* Simone, 1995a, fig. 2; 1996a, fig. 15). In some particular taxa, the proboscis cannot be retracted completely by simple contraction, only by coiling (*e.g.,* node 150 – ficids; and node 173 – thalassocyonidae + personiids). In this kind of proboscis, the buccal mass (that precedes the esophagus and bears the odontophore) remains close to the mouth, connected to it by means of a short oral tube (*e.g.,* Simone, 1995d, fig. 7). Another character of this type of proboscis is that the rhynchodeal wall (rhynchothecium) is exteriorized when the animal totally protrudes the organ. Although the tonnoidean proboscis has been regarded as different from that of the neogastropods (Day, 1969, Ponder & Lindberg, 1997), no evidence to this separation has been found in the anatomy.

In the case of most conoideans (node 181) and some muricoideans (*e.g.,* node 219 – costellariids, marginellids) (Fig. 8G) (Turner & Simone, 1998; Simone, 1999a, c), the buccal proboscis (α) becomes the single protracted portion. The rhynchodeal wall (rhynchothecium) (ß) becomes a thin, scarcely muscular membrane, which remains inside the haemocoel even though the proboscis is totally protracted. The conoidean buccal proboscis is called simply "proboscis" in the specialized literature (*e.g.,* Taylor *et al.,* 1993). This condition allows a permanent rhynchodeal cavity, where the prey can be imprisoned for consuming. Another particularity of this kind of proboscis is that the buccal mass is generally situated at the proboscis base, far removed from the mouth. A long oral tube connects one another (Costa & Simone, 1997, fig. 16; Simone, 1999a). This type of proboscis has been called intraembolic (Miller, 1989). The position of the buccal mass relative to proboscis has been the main reason for the disparities of proboscis classification, but it is diminishing in importance (*e.g.,* Kantor, 2002: 166).

The evolutionary scheme of the proboscis referred above (Fig. 8) is only the base for the main categories of proboscises. However, there are several additional adaptations that originated several other types. For example, the Terebrinae (node 190 – Conoidea) possess a conspicuous **proboscis accessory structure,** a long, solid, muscular projection that can be protracted (Simone & Verissimo, 1995, fig. 7: lt). In other terebrids, the proboscis is greatly reduced, only the rhynchodeal wall is retained. This reduction is accompanied by the reduction of the entire buccal mass and of the venom apparatus, as well as the enlargement of the **introvert** (node 195). The introvert is a conical structure originating around the rhynchostome that can be exteriorized or retracted inside the rhynchodeal cavity, working as an extension of the rhynchostome (characters 104, 296). This described form of proboscis, with reduction of the proboscis and enlargement of the introvert, has been called polyembolic (Miller, 1989) (Simone, 1999a, *e.g.,* figs. 16B, 19A-E) and is found, beyond some terebrids, in some turrids (*e.g., Daphnella* – Conoidea after node 198). On the other hand, an introvert-like structure is found in the Conidae (node 199 – Conoidea), though, unlike that of the terebrids, the conid introvert cannot be retracted; it is a permanently outside cone (Costa & Simone, 1997) (character 295). Another noteworthy structure is the **epiproboscis,** with is present in Mitridae. The structure is a secondary protractile projection, moved by special muscles, used to exteriorize the ducts of the salivary glands (Ponder, 1972; Simone & Turner, 2010). It is located in the ventral region of the buccal cavity, and cen be extracted or retracted inside haemocoel.

Even if the current concept of proboscis classification is not highly rigorous, all proboscises of the ingroup are of the **pleurembolic** type, which, as noted above, is found only in the caenogastropods after node 66. However, there are proboscises in other gastropod taxa. A proboscis is found in some ptenoglossans (basal caenogastropods; after node 38) (Simone & Martins, 1995) and in basal heterobranchs; after node V) (*e.g.,* Bieler, 1988). Nevertheless, in those taxa, the type of proboscis is **acrembolic.**

The acrembolic proboscis is characterized by the absence of buccal proboscis, *i.e.,* it retracts entirely, up to the apex, an inside out fashion within the haemocoel. When retracted, this kind of proboscis possesses no portion projected inside the rhynchodeal chamber. Most probably the acrembolic proboscis has been developed independently in some branches, since both, ptenoglossans and allogastropods, are not monophyletic groups (Ponder *et al.,* 2008) and neither are they closely related to each other.

Despite the limited state of knowledge at the end of the 19th century, some of the points presented here are found in Amaudrut (1898), but they have not been subsequently taken into general consideration in the literature.

Buccal mass (Characters 303-326)

Oral tube: it is generally a cone, with thin walls and a smooth inner surface, which connects the mouth with the buccal mass. It is particularly well-developed in the proboscis-bearing taxa (*e.g.,* Simone, 2003, fig. 7G: ot). It becomes still longer in those groups in which the buccal mass is situated at the proboscis base (Fig. 8G) (*e.g.,* Simone, 1999a, fig. 5C: bt). In the short oral tube, some muscles can cover it entirely or at least its posterior regions. The muscles are the ventral buccal mass protractor (m10), the buccal sphincter (mc) and the jaw muscles (mj) (*e.g.,* Simone, 2004b, figs. 125, 126).

The buccal mass in gastropods generally can be divided into 2 portions: 1) a ventral, mostly solid, corresponding to odontophore, the organ that produces and moves the radula; and 2) a dorsal, mostly hollow cavity continuous to the esophagus, bearing muscular walls (*e.g.,* Simone, 2001a, fig. 179). The dorsal wall of the buccal mass touches intimately the exposed (in use) portion of the radula into buccal cavity, so, there are several mechanisms for avoiding auto-injury. Among these mechanisms are a series of muscular reflexes, as well as a reinforcement of the inner surface by means of a chitin or chitin-like cover.

The loss of the pair of **jaws** is problematic character. The presence of a pair of jaws is regarded as one of the synapomorphies of Conchifera (Wingstrand, 1985), and is present, generally, in the archaeogastropods (*e.g.,* Simone & Cunha, 2006, figs. 70, 74), heterobranchs (mostly fused with each other; *e.g.,* Simone, 1998a, fig. 13) (node V) and most caenogastropods (*e.g.,* Simone, 2004b, fig. 96) (node 1). A large range of jaw variation was detected, from their enlargement (*e.g., Campanile symbolicum* – Cerithioidea after node 21) (Simone, 2001a, figs. 81, 416), to their reduction (*e.g., Supplanaxis nucleus* – Cerithioidea after node 34) (Simone, 2001a, figs. 74, 201), or their absence (loss) (*e.g.,* Cypraeidae – Cypraeoidea node 20 – Simone, 2004b). The loss of jaws could be a conspicuous synapomorphy of node 178 (Neogastropoda), since it appears to be absent in its representatives. However, there are two problems: 1) the presence of vestiges of the structure in *Trophon gervesianus* (Muricoidea after node 236, as well as some other muricids; Simone, 1996b); and 2) the presence of a massive hyaline chitinous structure covering entirely the dorsal and lateral inner surface of the buccal cavity of the Cancellarioidea (node 222), forming an anterior conic tube. The homology of this structure with the jaws is intuitive, and even suggested in the literature (*e.g.,* Harasewych & Petit, 1982). However, the conformation is different, since the cancellarioidean structure has a long anterior tube, and an absence of muscular connections. Such differences makes it difficult to determine if the cancellarioidean structure is a extraordinary modification of the jaws, or is a product of the mere enlargement of the normal chitinous layer that protects the inner surface of the buccal mass (normally thin) of a jaw-lacking animal. Two characters related to jaws were utilized by Strong (2003), compounding 8 states. However, they do not support any important branch, except the partially bi-layered jaw composition, which supports the sorbeoconchs, with several reversions.

A pair of longitudinal, **dorsal folds,** generally tall and broad, is present in the caenogastropods, differentiating them from the outgroups (characters 310-312) (*e.g.,* Simone, 2001a, fig. 144: df). The appearance of this pair of folds is followed by the reduction of a dorsal chamber, situated along the medial region of the dorsal wall (*e.g.,* Simone, 2004a, fig. 195: dc) in the taxa situated after node 18. The caenogastropod pair of dorsal folds in the buccal mass, characteristically, has its origin in the pair of jaws (in those taxa that have them) and, normally, run along anterior esophagus. These folds generally bear the aperture of the salivary glands and can be very complex as, *e.g.,* in the cypraeoideans (node 118), in such the dorsal folds have a series of oblique furrows at the level of radula (*e.g.,* Simone, 2004b, figs. 162, 180: ff).

Odontophore (Characters 327-406)

The **mj** is a set of muscular pairs that forms the peribuccal region. It has at least 3 functions: 1) buccal

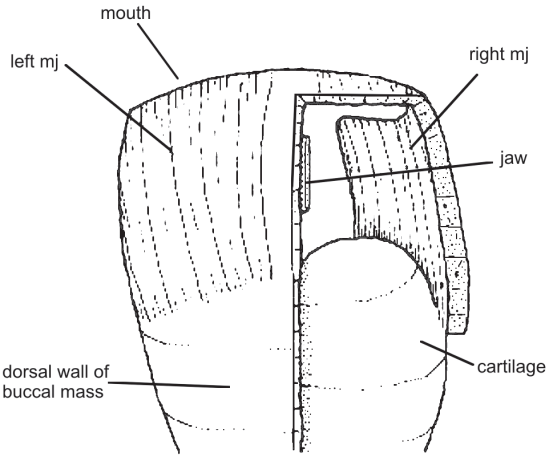

FIGURE 9: Scheme of buccal mass of a generalized caenogastropod, showing mainly mj, dorsal view; part of right region of dorsal wall removed; no other inner structure, except cartilage and a short portion of jaw, shown.

sphincter, closing the mouth, constituted by circular fibers that can or cannot entirely surround the mouth (in the case that they do not surround entirely, the region close to the median line lacks muscular fibers), when outstandingly large, it is designated separately as circular muscle **(mc);** 2) odontophore protractor, formed by antero-posterior fibers, reunited in a pair of bundles (Fig. 9), the origin is in the peri-buccal region, surrounding almost its entire circumference (except the region close to median line, both ventral and dorsal), running immersed in the buccal tube wall dorsally and ventrally, inserting in anterior and lateral edges of the odontophore cartilages, and also in the wall that externally surrounds the buccal mass; 3) muscles attached to the pair of jaws in those taxa that have it, whose movement is assisted, in some taxa (*e.g.,* node 5 – Ampullarioidea), by a pair of muscles called **ma** (*e.g.,* Simone, 2004a, fig. 161). This pair of muscles (ma) has their origin in the inner dorsal surface of the haemocoel, close to the mouth, runs ventrally, crossing through the mj fibers, inserting in the outer surface of the jaw plates. The set of muscles mj is weakly defined in the examined outgroups. In the caenogastropods, the portion working as protractor (function 2 above) is still separated into 2 bundles (*e.g.,* Simone, 2001a, fig. 416); this is the aim of character 330.

The **m2** is the pair of retractor muscles of the buccal mass, also referred to as retractor of the "pharynx". It is one of the most conspicuous synapomorphies of the taxa allocated after node 14 (Fig. 10B) (*e.g.,* Simone, 2001a, figs. 337, 400). The origin of the pair m2 is generally the floor and/or the lateral surface of the haemocoel, either in the foot or in the snout-proboscis (when they are longer than the buccal mass). The pair of muscles runs anteriorly, connected or not to the haemocoelic surface. The insertion is in the latero-ventral surface of the buccal mass, having, generally, a portion connected to the superficial membrane that surrounds the odontophore, and another portion connected to the adjacent deeper musculature. In some muricoideans (node 215) the pair of m2 is inserted in the odontophore cartilages (*e.g.,*

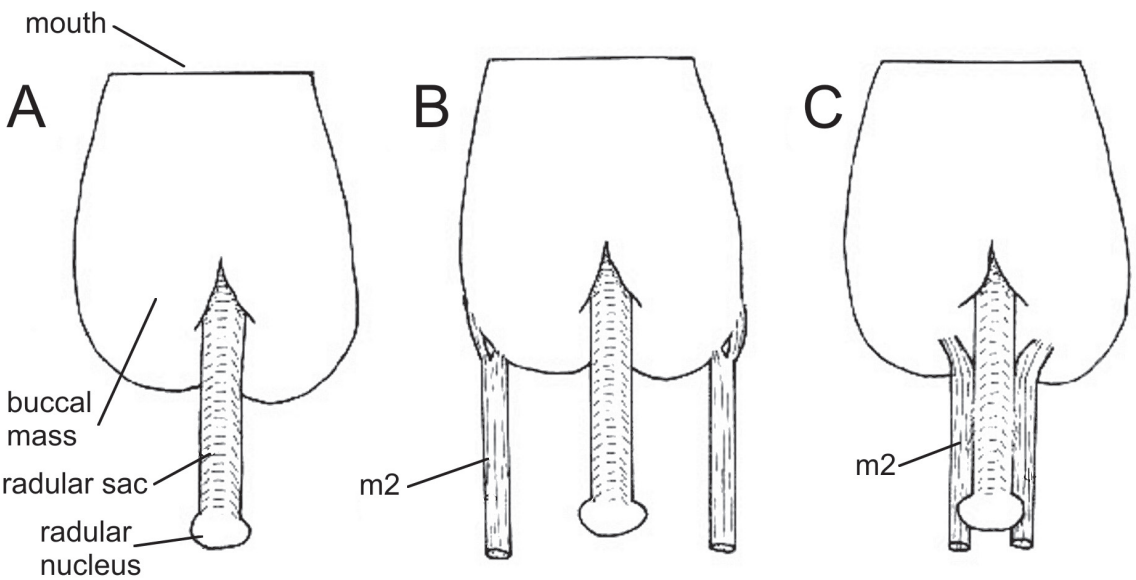

FIGURE 10: Scheme of buccal mass, ventral view, maily showing m2 pair (retractor muscle of buccal mass); **A)** Condition with m2 wanting; **B)** m2 laterally and ventrally inserted, found in node 14 (Fig. 20); **C)** m2 inserting closer to median line and, additionally, in radular sac, condition found in node 96 (Fig. 20).

Simone & Leme, 2001, fig. 19); while in some more basal groups, *e.g.,* pseudolivids, the m2 pair is inserted in m4-m5 pairs (Simone, 2007a) (nodes 210-214). In the taxa situated after node 96, the m2 insertion becomes closer to the median line, adjacent to the place where the radular sac penetrates the odontophore (Fig. 10C). In this case, there are also connections with both the superficial membrane and the adjacent deeper muscles. Additionally, the m2 connects with the radular sac, and can surround it totally, in the species in which it is very short (*e.g.,* Simone, 2003, fig. 8D).

No m2 was found in the examined outgroups (Fig. 10A), neither in the representatives of the 2 first branches of the ingroup. Moreover, some branches of the superfamilies represented after node 14, present a total reversion, losing the m2 completely. For example, node 21 (Campanilidae: Turritellidae: Vermetidae: Cerithioidea) (Simone, 2001a) and node 119 (Lamellariidae – Cypraeoidea) (Simone, 2004b).

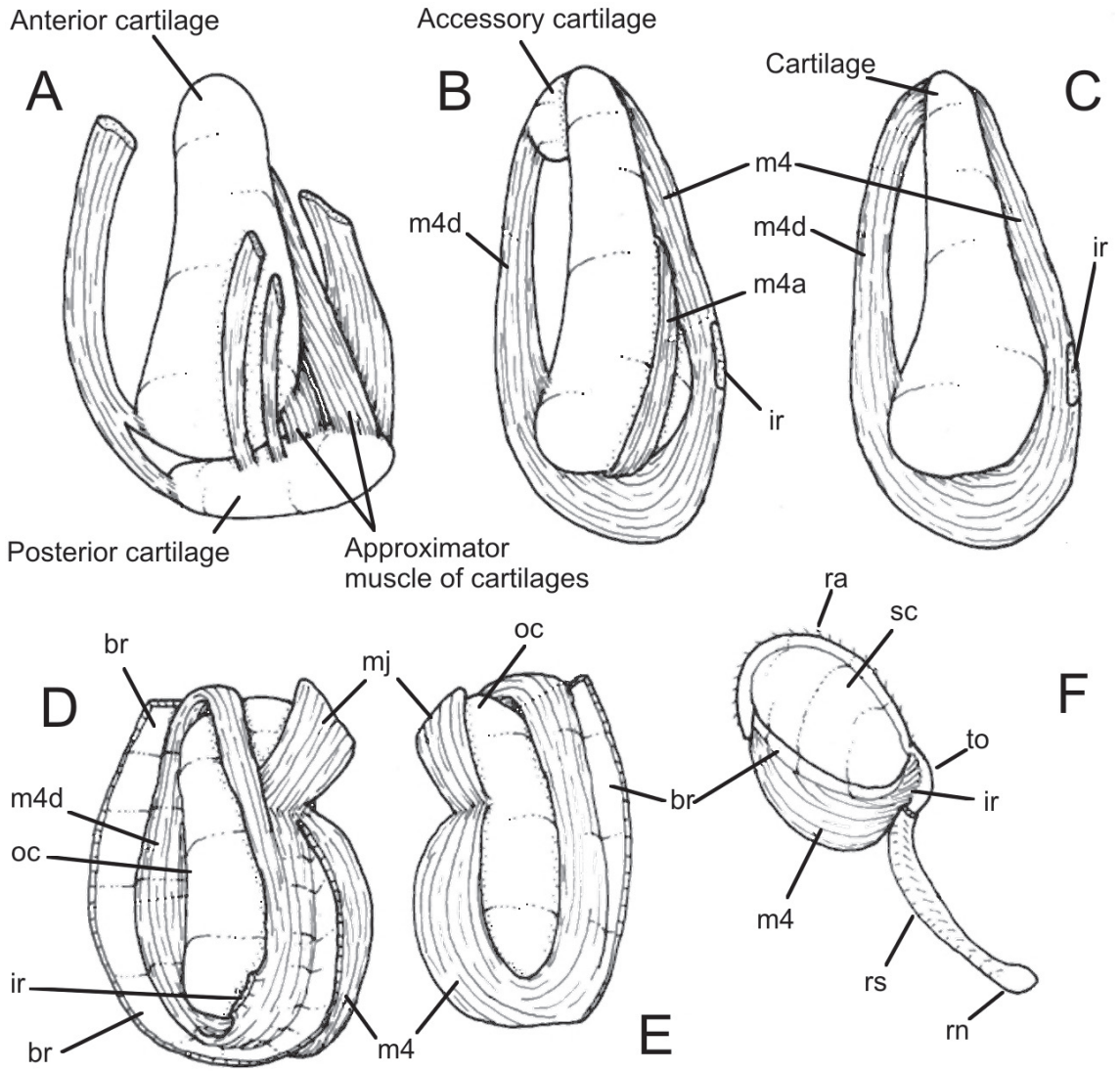

FIGURE 11: Schematic representation of odontophore, with main concern to m4 (main pair of dorsal tensor muscles of radula) (node numbers refer to Fig. 20): **A-C)** medial view of a right hemi-odontophore; **A)** Vetigastropoda and Neritimorpha, mainly showing the muscles that may originate m4; **B)** Condition in node 1, found only in the two first branches of ingroup (Ampullarioidea and Cyclophoroidea, although the last has no accessory cartilage); **C)** Typical m4 of the taxa after node 14, a simplification; **D-E)** Right hemi-odontophore with some adjacent structures also represented; **D)** Dorsal view; **E)** Ventral view; **F)** Pair m4 and its relation to radula and adjacent non-muscular structures, left lateral view, most structures artificially shown as transparent. Lettering: br, subradular membrane; ir insertion of m4 in tissue on radula (to); mj, peri-buccal and jaw muscles; oc, odontophore cartilage; rn, radular nucleus; rs, radular sac; sc, subradular cartilage; to, tissue on radula preceding exposed (in use) region.

The **m4** is the larger pair of muscles and may be the most important of the caenogastropod odontophore (Fig. 11B-F), working as main dorsal tensor of the radula. Characteristically, it surrounds both odontophore cartilages, originating in their outer and anterior regions, just posterior to the mj origin. Additionally, the m4 inserts in the subradular membrane, as well as in the tissue on the radula that precedes the exposed (in use) region in the buccal chamber (see character 346). The comparison with outgroups revealed that the m4, in the form described concisely above, is only found in the caenogastropods. The comparative analysis suggested that the pair m4 may originate from several pair of muscles present in the archaeogastropods (*e.g.,* Simone, 1998d, figs. 34, 35: da, oa; Simone & Cunha, 2006, fig. 77: m4, m8, m8a), associated with the loss of the posterior cartilages. As schematized in Fig. 11A, in the archaeogastropods, particularly in the examined cocculiniforms, vetigastropods and neritimorphs (nodes I-U), there are several pairs of muscles that connect the ventral, dorsal and medial surfaces of the cartilages with the subradular membrane, as well as 2 pair of muscles that connect the pair of anterior cartilages to the posterior ones (approximator muscles of the cartilages) (*e.g.,* Simone, 1996c, figs. 30-33: ap). It is a quite possible, and the scheme is suggested herein, that the pair of muscles m4 of the caenogastropods have arisen from the fusion of all those muscles, associated with the loss of the pair of posterior cartilages. Meanwhile, the archaeogastropod cartilage approximators and the remainder muscles that connect the cartilages to the subradular membrane, developed to surround the single pair of cartilages in the caenogastropods. Although in the 2 caenogastropod basal branches (nodes 2, 5) a pair of medial branches remains (Fig. 11B: m4a) (*e.g.,* Simone, 2004a, figs. 183, 252: m4, m4a), they disappear, or most probably become fused integrally with the remaining m4, in the taxa situated after the node 14 (Fig. 11C) (*e.g.,* Simone, 2001a, fig. 131).

Although in Fig. 11B an accessory cartilage is represented in the anterior region of m4, it is only present in the Ampullarioidea (node 5), which has been proved to be differential thickness of the subradular cartilage (Golding *et al.,* 2009a, fig. 6). The cyclophoroideans, which also possess a same m4 fashion, lack these accessory cartilages (character 345) (Simone, 2004a). The function of the m4 pair, suggested by analysis of their position and connections (Fig. 11D-F), is tensioning the subradular membrane. If these muscles do this, indirectly the subradular cartilage and the radula will be also tensioned, becoming rigid (Ponder *et al.,* 2008). For more details of the odontophoric cartilages see Golding *et al.* (2009a).

The **radular ribbon** can be divided into 2 regions: 1) anterior, exposed inside the buccal cavity, in use and with the radular teeth positioned to that; 2) posterior, confined inside the radular sac, storing the teeth that may migrate to the buccal cavity while the teeth have been lost. The radular portion inside the radular sac is coiled (when long enough to this) and its teeth are positioned inwards. The radular nucleus lies at the posterior end of the radular sac; it is where the teeth are formed. A solid conjunctive tissue marks the transition between the exposed and confined portions of the radular ribbon. This tissue (labeled **"to"** in the Figs.) (*e.g.,* Simone, 2005a, figs. 84, 86) is relatively strong, restricted inside the radular ribbon, and attaches firmly to its inner surface, inclusive to the teeth. The tissue length is equivalent to half of odontophore height, lying inside the radular sac (Fig. 11F: to). The pair of m4 muscles inserts both, in the subradular membrane, and in the above mentioned tissue (to). In the case of the ampullarioideans (node 5) and tonnoideans (node 149), this insertion is additionally done by means of muscular fibers (denominated m9) (*e.g.,* Simone, 2004a, fig. 163), while in the remaining caenogastropods represented after node 14 (except tonnoideans) this connection is done by means of ligaments only. According to the results, both taxa that possess m9 converged to that state.

The pair **m4:** As schematized in the Fig. 11A, the set of muscles that connect the odontophore cartilages with the subradular membrane in the archaeogastropods are not connected with each other in the odontophore anterior region. They are, however, indirectly connected via subradular membrane. With the probable transformation in those muscles in the m4 pair (character 345), its ventral and dorsal branches become closer with each other anteriorly in the cyclophoroideans (node 2), being still connected via a membrane as also occurs in the archaeogastropods (Simone, 2005a, fig. 253). In the ampullarioideans (node 5), a pair of accessory cartilages provides this connection (Simone, 2005a, fig. 167: oa); a synapomorphy of the taxon and most probably derived from the subradular membrane. In the remaining caenogastropods (node 14) the ventral branch (m4d) and dorsal branch (m4) are fused anteriorly, producing a pair of muscles that totally surround odontophore cartilages (Fig. 11C-E) (Simone, 2005a, fig. 314).

In the traditional schemes on the odontophore operation, as presented in the textbooks (*e.g.,* Barnes, 1984, figs. 10.2), the intrinsic musculature moves the radula in a backwards-and-forwards movement, sliding

it on the odontophore cartilages. The to-ing and fro-ing movement is mainly provided by alternate action of the pair of dorsal and ventral tensor muscles, as shown in the Fig. 12B. These muscles are antagonistic, and are inserted in both extremities of the radular ribbon.

Despite functional experiments have not been performed on the examined specimens, the analysis of the position of each pair of odontophore muscles, as well as the observation of the same working in live specimens, allow some conclusions, as that the sliding movement above described may be not a caenogastropod standard. The caenogastropod odontophore musculature appears to work in holding and tensioning firmly the radula, rather than to move it. The coming-and-going movement is performed by the odontophore as a whole, *i.e.,* the sliding movement between the radula and odontophore cartilages is weak (Ponder *et al.,* 2008). Then, if there is no sliding movement between the cartilages and the radula in the caenogastropods, the function of the tensors becomes scanty. In the case of the ventral tensors (m11), they become thin and narrow (character 383); and the dorsal tensors are substituted by the pair m4 (character 354). Another indirect indication that the radular ribbon does not slide in the cartilages is the presence of thicknesses in the subradular cartilage (Golding *et al.,* 2009a, as "subradular cartilage"). Those structures appear to preclude the sliding movement.

The pair of muscles called **m11** appears to be homologous to the archaeogastropod ventral tensor muscles. They originally insert in the distal edge of the radula, however, in the caenogastropods they become inserted more internally in the subradular membrane. The pair m11, characteristically, runs posteriorly along the subradular membrane connected to it, and, in the level of the entrance of the radular sac to the odontophore, they progress out to the haemocoelic cavity, one on each side of the radular sac (Fig. 14) (*e.g.,* Simone, 2001a, figs. 242, 243). The origin of the m11 pair, generally, is on the ventral surface of the haemocoel, just posterior to the buccal mass level.

The suggested functional working of the caenogastropod odontophore is somewhat modified in the muricoideans (node 210), that apparently reverted to the sliding movement. This possibility has been investigated and is part of another specific study on them (*e.g.,* Simone, 2007a). In muricoideans, then, a series of muscles has been lost or modified. The loss of the thickness of the subradular cartilages in this taxon (Golding *et al.,* 2009a) is another indication of the reversion to the sliding radular movement.

The pair **m5** is one of the main muscles of the odontophore, being only supplanted in size by the pairs mj and m4. Its function is assisting the main dorsal tensor muscles of the radula (m4). The insertion of the m5 pair is generally in the ventral surface of the subradular cartilage, just in the level, or slightly anterior to the tissue preceding its exposed region (to), and is situated on the opposite side of the m4 insertion on this tissue (to) (Fig. 13C). The insertion

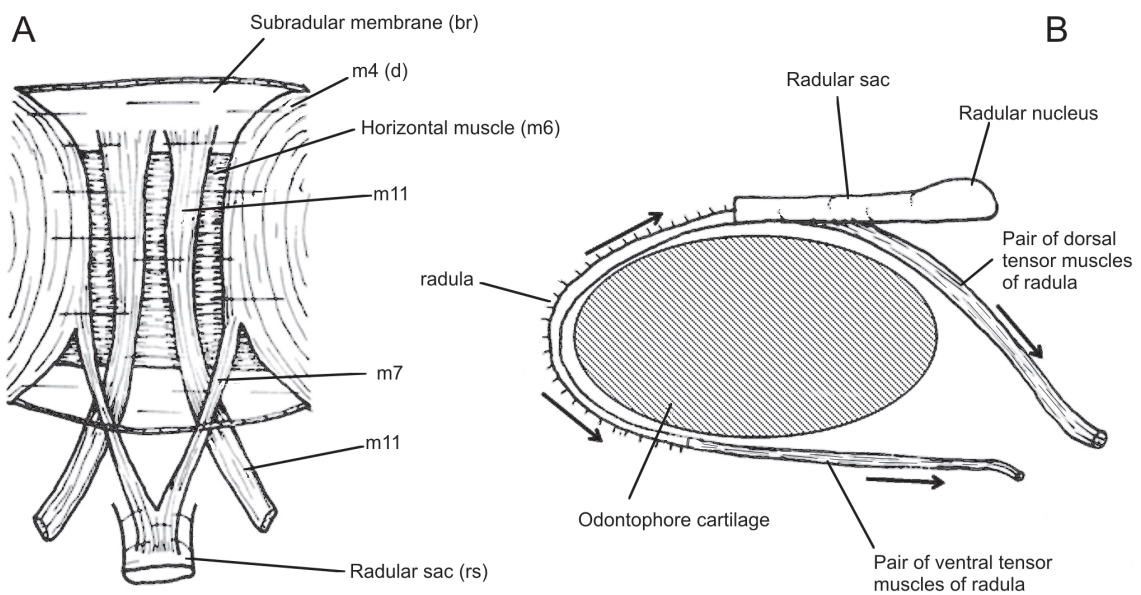

FIGURE 12: A) Scheme of antero-ventral region of odontophore, with radula and subradular cartilage removed, primarily showing pairs m7 and m11, subradular membrane (br) artificially shown as completely transparent; **B)** Scheme of longitudinal, medial section of odontophore of archaeogastropods, showing antagonist function of pairs of radular tensor muscles, indicated by arrows.

surface of m5 is ample and long in some caenogastropods, attaching along almost entire inner side correspondent to the radular exposed area in the buccal cavity, and a portion posterior to that (character 359). The origin of the pair m5 (character 356) is mainly in the posterior odontophore cartilages in the archaeogastropods (Fig. 13A), contouring medially and anteriorly the cartilages along the median line. However, in caenogastropods, which lost the odontophore posterior cartilages, the m5 origin is on the outer surface of m4 (*e.g.,* Simone, 2005a, fig. 224), the position, conversely, is comparable to that of the archaeogastropods (Fig. 13B). The m5 pair of the archaeogastropods works as an auxiliary dorsal tensor muscle, while in the caenogastropods it works as auxiliary muscle of the m4 in tensioning the radular ribbon. This functional difference can explain the distinct general aspect of this muscle pair, explored in character 359. On the other hand, the pair m5 of the muricoideans (node 210) have changed their origin, from m4 to direct to the cartilages. This is a synapomorphy.

The horizontal muscle, **m6,** is the easiest to compare among the taxa, due to its peculiar situation. It is single, with transverse fibers connecting the left and right odontophore cartilages (Fig. 10A) (*e.g.,* Simone, 2001a, fig. 222). In the patellogastropods, as well as in the remaining classes of Conchifera that bear an odontophore, the m6 is situated between the anterior cartilages, filling the space between them (character 55) (Leal & Simone, 1998, fig. 28). In the gastropods except patellogastropods, *i.e.,* the Orthogastropoda (node I), the m6 is positioned outside from the cartilages. In this taxon, the m6 connects both anterior cartilages (when there is more than 1 pair) along their outer dorsal surface. Furthermore, in the orthogastropods, the connection of the m6 in both cartilages is situated at some distance from their inner edges (character 367). The caenogastropod m6 differs from the homologous muscle of the outgroups in being shorter than the cartilages (character 360), and in generally being thicker and broader (character 361) (*e.g.,* Simone, 2005a, fig. 337).

It is interesting to emphasize that in some caenogastropod groups, neogastropods in particular (node 178), the m6 becomes thin (a reversion) (*e.g.,* Simone, 1996a, fig. 23: "m11"; Turner & Simone, 1998, fig. 20). On the other hand, in the cypraeoideans (node 118) it is divided it into 2 (m6 and m6a), situated sequentially or dorsal to one another (*e.g.,* Simone, 2004b, fig. 137).

The **m7** is a pair of muscles exclusive to the caenogastropods (character 368) (*e.g.,* Simone, 2001a, fig. 131). Its origin is in the medial region, attached to the inner-dorsal edge of the m4 pair (m4d) (Fig. 12A).

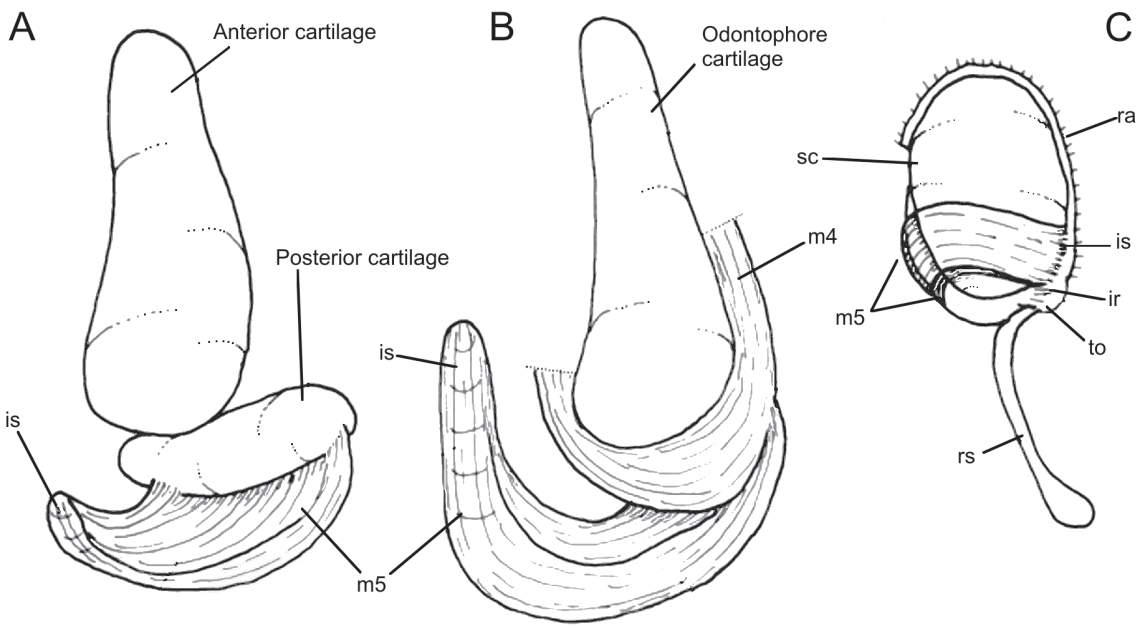

FIGURE 13: Schematic representation of odontophore mainly concerned to pair m5: **A)** Right hemi-odontophore, Vetigastropoda and Neritimorpha, medial view, no other muscle shown, cartilages positioned as *in situ;* **B)** The same to a Caenogastropoda, adjacent portion of m4 also shown; **C)** Whole odontophore, lateral-right view, structures except m5 pair artificially shown as transparent. Lettering: ir, insertion of m4 in "to"; is, insertion of m5 in subradular cartilage; ra, radular ribbon; rs, radular sac; sc, subradular cartilage; to, tissue preceding exposed (in use) portion of radula.

It runs posteriorly attached to the subradular membrane. Afterwards, it penetrates inside the radular sac, inserting in its inner surface a short distance from the radular nucleus. In the taxa represented after node 40, both m7 fuse and present a single insertion, like a fan (*e.g.,* Simone, 2004b, fig. 400). The homology of m7 with another muscle of the remaining gastropods is still unclear. Most probably, m7 is a new acquisition of the ingroup, resulted from the specialization of the inner surface of the subradular membrane. Each m7 generally is very thin and narrow, and in several taxa of the ingroup a reduction and even loss occurred. The function of the pair m7 is still unclear.

The pair of **approximator** muscles of cartilages, which can be single or double, is present only in the taxa that possess 2 or more pairs of odontophore cartilages, *i.e.,* most archaeogastropods (nodes H-U) (*e.g.,* Simone, 1996c, fig. 29: ap; Simone & Cunha, 2006, fig. 77: m8, m8a). In Apogastropoda (Caenogastropoda and Heterobranchia) (node W), that possess a single pair of cartilages, such a muscle pair has no function. It possibly disappeared or, as suggested above, was incorporated in the pair m4 of the caenogastropods.

The pair **m10** originates in the ventral-inner region of the mouth, runs posteriorly along the ventral surface of the buccal mass, and inserts in the ventral surface of the odontophore (*e.g.,* Simone, 2001a, fig. 202). It works as a ventral protractor muscle of the buccal mass. In the archaeogastropods, the insertion of the pair m10 is more posterior, in the level of the posterior third part of the odontophore (character 378) (*e.g.,* Simone, 1998d, figs. 31-32: vb). However, in the caenogastropods, this muscle pair inserts in the anterior third part, just posterior to the mj insertion (Fig. 14).

The pair **m12** is constituted of very small muscles, with their origin close to the anterior-lateral edge of the m6 (horizontal muscle), one in each side, on the odontophore cartilages. They run laterally and insert shortly in the inner surface of the subradular membrane (*e.g.,* Simone, 2001a, fig. 222; Simone, 2004a, figs. 167, 287). Although the m12 found in the 3 superfamilies that posses it differ in some details, they are all suggestively considered homologous.

The pair **m14** is one of the node 96 synapomorphies. However, it appears to be absent in neogastropods (node 178), as a reversion. The caenogastropod m14 (Fig. 14) is very similar to the archaeogastropod m10. It differs in having a medial insertion (rather than lateral) in the posterior region of the odontophore, and in being deeper, penetrating into the superficial membrane that surrounds the odontophore, connecting to the m4. Besides, most caenogastropods that possess m14, also have the m10 (*e.g.,* Simone, 2004b, figs. 126-127). The origin of the pair m14 is close and slightly ventral to that of m10 (inner ventral surface of the mouth). Subsequently, each one runs parallel to m10 towards posterior.

The other pair of odontophore muscles, called m1 (differentiated jugal muscles), m3 (superficial dorsal muscles of odontophore), m8, m13-m16, are only found in some taxa. Comments and descriptions on them are present in the literature related to each superfamily.

Number of **cartilages:** As schematized in the Figs. 11A and 13A, the archaeogastropod basic pattern is 2 pairs of odontophoral cartilages, a pair anterior, generally larger, and a pair posterior (*e.g.,* Marcus, 1957: fig. 6; Simone, 1998d, fig. 35). This fashion of 4 cartilages is not present in the taxa represented after node W, where, characteristically, a single pair is present; it is homologous to the anterior cartilage. This conclusion is result of the comparative analysis of the muscles, mainly the horizontal (m6). On the other hand, among the archaeogastropods there are also taxa with a single pair of odontophore cartilages, such as, *e.g., Propilidium curumin* Leal & Simone, 1998 (Patellogastropoda) and most Cocculiniformia (node J) (Haszprunar, 1987, 1988c; Simone, 1996c; Simone & Cunha, 2003), certainly convergences. Additionally, it is important to emphasize that most patellogastropods (Sasaki, 1998) and a few neritimorphs (Salvini-Plawén, 1988; Strong, 2003) possess

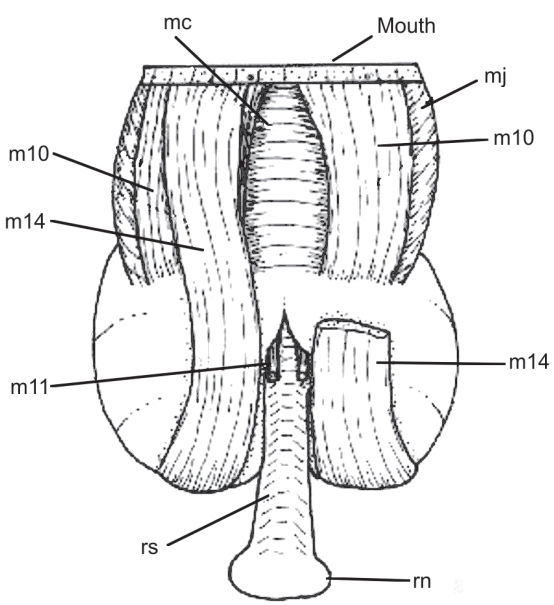

FIGURE 14: Scheme of odontophore of a Caenogastropoda having pairs m10 and m14, ventral view; left m14 (right in Fig.) sectioned (abbreviations in Fig. 13).

several pair of cartilages, possibly a derived condition of the groups. Another notable modification is the fusion of the cartilages in their anterior region, of some Muricoidea (*e.g.,* node 215 – Buccinidae, Nassaridae, Columbellidae) (Simone, 1996a, 2007a; Simone & Leme, 2001). Another important feature of the cartilages is the possibility of non-homology between the structure of the heterobranchs and other gastropods (Wingstrand, 1985; Mackenstedt & Märkel, 2001; Golding *et al.,* 2009a). However, respect to the morphology and origin of intrinsic musculature attached to the cartilages, there is nothing indicating that.

The **odontophore** characters show the great importance of the structure in comparative studies, being usable even in level of species. Although, detailed studies on the odontophore are surprisingly scarce in the literature, which rarely performs an extensive comparative analysis. This fact precludes the inclusion and discussion of those studies here, which mostly need to be based on self produced studies (*e.g.,* Simone, 2007b; Ponder *et al.,* 2008: figs. 13.9, 13.10). As referred in the "Material and Methods" section, the terminology of the odontophore muscles is still provisional, *i.e.,* it was preferred to designate each muscle (or pair of muscles) by a code (*e.g.,* m2) rather than a functional name (*e.g.,* buccal mass retractor muscle). This measure makes suggestion of homologies easier, without, necessarily, infer in the same functional action. The nomenclature of these muscles certainly deserves a deeper study in that sense, but is not the scope of the present one.

The **subradular organ** is a structure sometimes utilized in comparative studies (*e.g.,* Haszprunar, 1988a; Ponder & Lindberg, 1997; Strong, 2003), but it is not included in the present study because of the difficulty in defining it in the buccal cavity. The structure appears to be a synapomorphy of the Caenogastropoda, with a notable reversion (loss) in the taxa allocated here after the node 96 (Strong, 2003: character 14). However, more detailed studies are still necessary to determine the occurrence of the subradular organ amongst the considered taxa. More details are given in Ponder *et al.* (2008: 347-348, fig. 13.7).

Respect to the odontophoral cartilages, the simple dissection allows the observation of several important features, which resulted in the characters discussed above. However, there are a more complex structures on which to base comparative analyses (Guralnick & Smith, 1999; Katsuno & Sasaki, 2008; Golding *et al.,* 2009a), including, *e.g.,* additional pairs of cartilages, and special thickened portions of the subradular cartilage in non-carnivorous taxa. More detailed studies, using additional techniques, certainly will bring more revelations.

Radula
(Characters 407-444)

Mineralization of radular teeth: The main goal of the character (411) is the organization of the outgroups. It was inferred from the literature, since no investigation on the mineralization of the radular teeth has been done herein, although the mineralization can mostly be detected by dark spots at the radular teeth. The literature is relatively rich on the matter (*e.g.,* Cruz *et al.,* 1998). The mineralization of the radula, mainly by iron, is one of the characters of Mollusca (Fig. 15A), however, only the patellogastropods have mineralized teeth among the gastropods. For this reason, the loss of the mineralization, *i.e.,* the radula merely chitinous, is one of the synapomorphies of node I. Haszprunar (1988a) and Sasaki (1998) already had explored this character. However, Ponder & Lindberg (1997) did not utilize it, due to doubtful homology. One of the apparent reasons is the presence of non-mineralized radulae in some representatives of other classes, as, *e.g.,* the cephalopod *Nautilus* (Lowenstam *et al.,* 1984). This fact is here interpreted as convergence.

Radular type: The difference between the radula types explored in character 412 is not merely the teeth constitution, but also the position of the teeth in relation to each other. The type called docoglossate, also referred as stereoglossate (*e.g.,* Sasaki, 1998), bears successive rows of not aligned teeth, *i.e.,* some teeth stay in an intermediary level in relation to neighboring ones. This conformation generates a more rigid radular ribbon, precluding its looping and flexibility. The docoglossate kind of radula works and is stored in a straighter way. The docoglossate radula is the normal pattern of the Mollusca in general. The second type, flexoglossate, in contrast, possesses each row of teeth transversely aligned (perpendicular to the longitudinal axis of the ribbon). This fashion allows a higher flexibility and coiling of the radular ribbon; consequently, its functionality and storage have a wide variety of forms. Among the gastropods, only the patellogastropods have the docoglossate type of radula, while the remaining groups have the flexoglossate type. In the mean time, the flexoglossate radula is one of the node I synapomorphies, and helps in the outgroup organization. This character had been also utilized by Haszprunar (1988a), Sasaki (1998), and the coiling of radular sac by Ponder & Lindberg (1997: 144). In spite of the fact that most outgroups have flexoglossate radula, they have not the same intense coiling pattern present in the caenogastropods. This character, obviously, refers to the radular portion

inside the radular sac, and is clearer in the species in which the radula is sufficiently long for that.

Subradular cartilage: It is necessary to avoid some confusion between subradular **membrane (br)** and subradular **cartilage (sc).** The subradular membrane surrounds the ventral surface of the radular ribbon and is the structure in which most of the intrinsic odontophore muscles inserts. The muscles can not insert directly in the radula, a structure that is slowly moving for replacing the lost teeth. The subradular membrane also covers most of the dorsal, anterior and lateral inner surface of the odontophore and, in part, is continuous to the adjacent mucosa of buccal mass. It normally is part of the buccal cavity, in its ventral and posterior regions. The subradular cartilage, on the other hand, is a cover of chitinous appearance on the subradular membrane, and most probably is secreted by it (Figs. 11F, 13C). Subradular cartilage fits between the homonymous membrane and the radular teeth, wider than the ribbon in exposed (in use) portion at buccal cavity. In the buccal cavity, the subradular cartilage expands through lateral

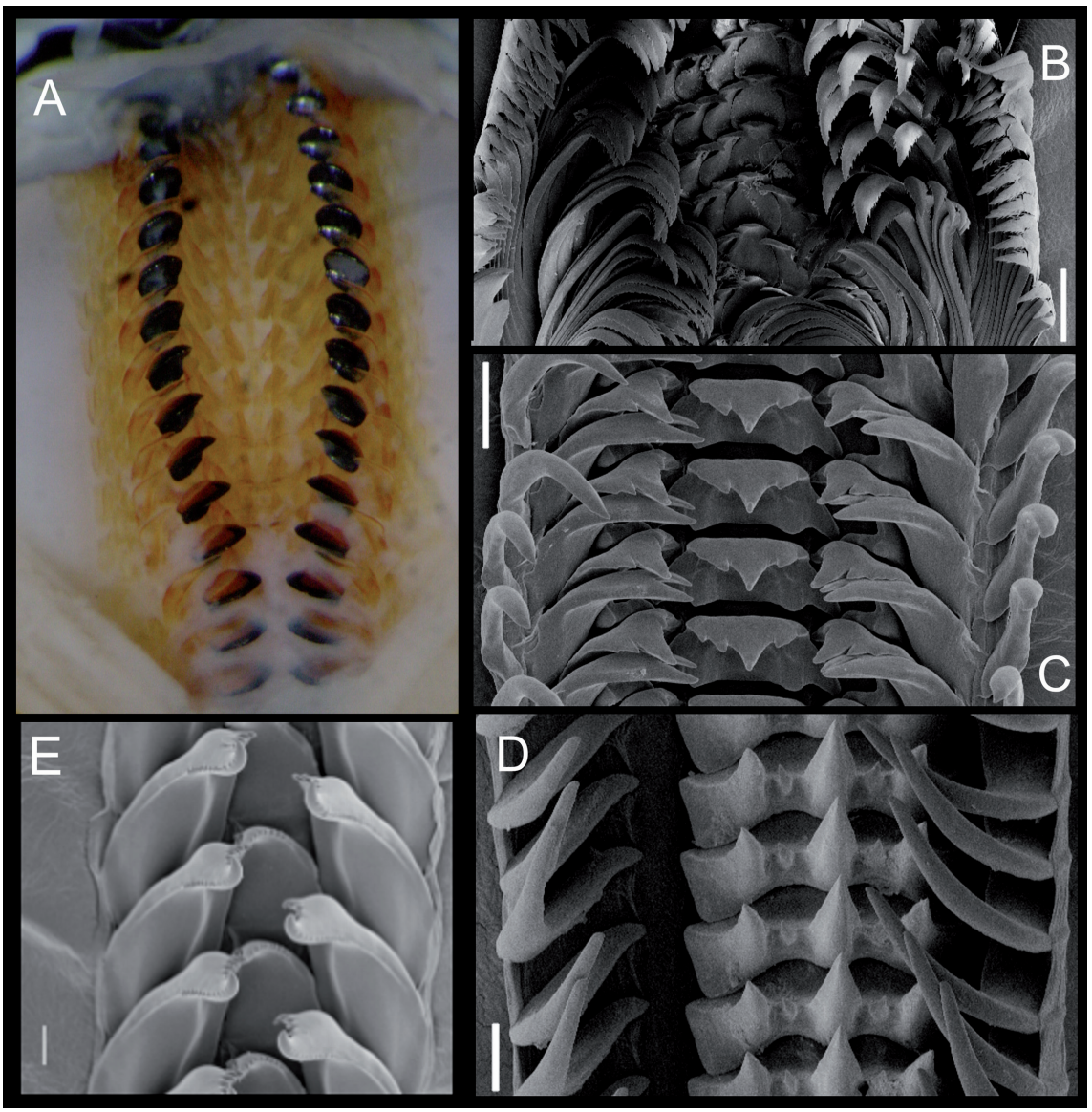

FIGURE 15: A) Portion of the radula in situ of the polyplacophoran *Acanthopleura* sp., from Thailand (MZSP) showing the mineralization of some teeth (dark spots); length of exposed area = 2 mm; **B)** Example of rhipidoglossate radula, trochid *Gaza superba* (USNM 94992), SEM; scale = 100 μm; **C)** Example of taenioglossate radula, naticid *Natica cayennensis* (MZSP), SEM; scale = 0 μm; **D)** Example of rachiglossate radula, muricid *Muricanthus radix* (MZSP 64195), SEM; scale = 50 μm; **E)** Special case of cypraeoidean *Lamellaria branca* (MZSP 30842) with a rhachiglossate-like radula, SEM; scale = 50 μm.

regions, beyond the radular ribbon, protecting the local subradular membrane and avoiding injuries in it. The subradular cartilage detaches relatively easily from the subradular membrane in the dead animal, being extracted connected to the radula in a form of a pair of lateral, elliptic, hyaline projections. However, functionally, the subradular membrane and subradular cartilage may be firmly attached to one another. The expanded portion of subradular cartilage in the buccal cavity is narrow in the archaeogastropods and heterobranchs. In those taxa, the structure expands little beyond the radular ribbon (although, there are more developed subradular cartilages in Pulmonata – node Z2). Further enlargement of subradular cartilage in the buccal cavity is one of the caenogastropod synapomorphies (node 1). It is, moreover, interesting to emphasize that subradular cartilage is a distinct structure from the odontophore cartilages. Thick regions of the subradular cartilage have been called as simply "subradular cartilages" (Golding *et al.,* 2009a, *e.g.,* fig. 15: sc), however the structure is wider, and, as stated above, entirely surrounds the radular sac and portion of odontophore exposed in the buccal cavity. Except for those thickened regions, the subradular cartilage is difficult to detect due to its thinness.

The **radula** has succeeded the shell and the operculum in importance in comparative studies on the gastropods. The literature on its attributes, even with a comparative base, is relatively abundant (*e.g.,* Bandel, 1984). Ponder & Lindberg (1997: 138-143); Sasaki (1998: 145-147), and Ponder *et al.* (2008: 346-347), for example, extensively analyzed the subject, a detailed discussion here is, then, unnecessary. On the other hand, Strong (2003) limited the radular analysis to the respective types (rhipidoglossate, the plesiomorphic state; taenioglossate, ptenoglossate, nematoglossate, uniserial, toxoglossate and rhachiglossate as derived states); the single state that resulted as non-autapomorphic in that analysis is the taenioglossate, as a caenogastropod synapomorphy. The study on the radula underwent a great advance with the widespread application of the scanning electron microscope (SEM), which was also utilized in the present study (Figs. 15B-E). The typical radula of the Caenogastropoda is the **taenioglossate** one, constituted by a **rachidian** (or central) tooth, flanked by 1 pair of **lateral** teeth (one in each side) and 2 pairs of **marginal** teeth, completing 7 teeth per row. Apparently, based on the data given in the above cited papers and in the present analysis, the taenioglossate radula (Fig. 15C) may have evolved from the rhipidoglossate one (Fig. 15B). The rhipidoglossate radula is present in archaeogastropods represented after node I (Simone, 1996c; Leal & Simone, 2000; Simone & Cunha, 2003). The rhipidoglossate radula differs from the taenioglossate one by the larger number of lateral teeth (about 5 pairs instead of 1) (character 422) and of marginal teeth (about 100 pairs instead 2) (character 430) (Figs. 15B-C). The taenioglossate radula appears to be exclusive for caenogastropods, although something similar occurs in some allogastropods (basal Heterobranchia), *e.g., Rissoella ornata* (node Z1).

The polarization of the radular characters is mainly based on the features of the rhipidoglossate radulae, although the analysis on the heterobranch radulae has also influenced. In the case of the neogastropods (node 178), in which radulae generally are modified, an origin from the taenioglossate radula is possible to be inferred. However, except for Conoidea, which encompasses basal taxa with a taenioglossate-like radula, the remaining neogastropods present homologies possibly with the rachidian and lateral teeth only. Although, five teeth per row has been also found in some non-examined Olivellinae (Olividae) and Nassaridae (Kantor, 2002). Some different pattern of radulae has been individually named, such as Toxoglossa (Conoidea), Rhachiglossa (Muricoidea) (Fig. 15D) and Nematoglossa (Cancellarioidea) (*e.g.,* Taylor & Morris, 1988; Harasewych & Petit, 1982; Strong, 2003).

The sharp pointed marginal tooth (character 73) is a notable synapomorphy aiding in the support of node 46. Although, according to obtained result, there are convergences with other inner branches of some superfamilies that precede it, *e.g.,* Cerithioidea nodes 21 and 32 (Simone, 2001a). The radula, like the shell, has a relatively high degree of plasticity, and can vary greatly in a single species, as has been demonstrated in littorinids (Reid & Mak, 1999). Among the sample presently examined, the most remarkable feature was found in the cypraeoideans (node 118). Normally they have an ordinary taenioglossate radula, however, the node 120 – *Lamellaria* spp. (Simone, 2004b, figs. 107-113) (Fig. 15E) have only 3 teeth per row, a notable convergence to rhachiglossate radula. While *Jenneria* (Cypraeoidea after node 130, figs. 93-95) developed an additional pair of teeth, completing 9 teeth per row. The tallness of the base of the lateral and marginal teeth of the mesogastropod taenioglossate radula has been claimed to be different from the neogastropod lateral (and marginal, when present) teeth (Bandel, 1984; Kantor, 2002). However, several taenioglossate taxa are exception, such as most cypraeoideans and tonnoideans. This character can be another one sustaining node 96, but the difficulty in establishing standards, and the uncertain

homology between the lateral and marginal teeth with those of the neogastropods, preclude the consideration of this character.

Salivary glands (Characters 445-461)

Salivary glands are found, normally, in all mollusks, including gastropods. However, the normal form of the gland is of glandular masses, fused with the buccal mass, lacking ducts or with very short ducts (Griffin, 1900; Fretter, 1937; Wingstrand, 1985; Sasaki, 1998). In the taxa allocated after node W, the pair of salivary glands possesses a well-developed pair of salivary ducts (*e.g.,* Simone, 2005a, fig. 361: sd). In relation to the form (characters 446-447), the separation of the salivary glands into 2 masses has not, apparently, any connection with their size, as it also occurs in both, very large and small glands (*e.g.,* Xenophoridae – Stromboidea node 53 – Simone, 2005; Tonnoidea – node 149). However, the separation in 2 is inevitable when the glands become minute, as is the case of the calyptraeoideans (node 67) (*e.g.,* Simone, 2002, fig. 174).

The salivary **ducts** passing outside from the nerve ring (character 450) is a long known character of the Neogastropoda (Ponder, 1974). This feature distinguishes them from the mesogastropods, in which, characteristically, the ducts pass through the nerve ring, flanking the local esophagus. This character has been utilized further (Bieler, 1992; Ponder & Lindberg, 1997; Strong, 2003). However, there are some mesogastropod taxa with salivary gland ducts free from the nerve ring, being a notable convergence. They are, for example, Pleuroceridae (node 26 – Cerithioidea) (Simone, 2001a), most Strombidae (node 55 – Stromboidea) (Simone, 2005a), all Calyptraeoidea (node 67) (Simone, 2002), and some Littorinidae (Reid, 1988). These features have brought some doubts for the importance of this character in higher systematics (Bieler & Mikkelsen, 1988; Strong, 2003). Besides, studies on neogastropod ontogeny (*e.g.,* Ball *et al.,* 1997) have shown that the salivary glands arise posteriorly to the nerve ring, migrating to the anterior region during development. This phenomenon may be typical for all taxa that lack relation between the salivary glands and nerve ring. Further analysis on the constitution of salivary gland tissue is found in Kantor (2002: 163).

The **aperture** of the salivary gland ducts is, generally, in the dorsal wall of buccal mass. In the case of the outgroups, this aperture is in the middle or even posterior region of the buccal mass (*e.g.,* Simone & Cunha, 2006, fig. 69), while in most ingroup taxa, the aperture is more interiorized, closer to the mouth (character 452). This state may be connected to the increasing size of the inner dorsal folds of the buccal mass (character 310). The final portion of the salivary gland ducts generally runs immerse in these dorsal folds (*e.g.,* Simone, 2005a, fig. 332) (character 451).

Accessory salivary glands are, supposedly, one of the characters of Neogastropoda **(node 178)** (Ponder, 1974; Ponder & Lindberg, 1997: 147; Kantor, 2002: 163). They are, in general, a pair of large glands in form of hollow vesicles, with a long and slender duct (Pastorino, 2002), inserted in the ventral surface of oral tube (anterior to the buccal mass) (*e.g.,* Simone, 2003, fig. 7F: ae). However, several neogastropods lack these structures (*e.g.,* Nassaridae – Simone, 1996a), while others have a single gland [*e.g.,* Marginellidae (Coovert & Coovert, 1995; *pers. obs.*); *Benthobia* (Kantor, 1991; Simone, 2003); *Babylonia* (Harasewych & Kantor, 2002)]. The same was observed in the Conoidea, with most representatives lacking accessory salivary glands; and the few ones that possess them, having a high degree of variation of constitution, number and insertion, bringing doubts on their homologies (Taylor *et al.,* 1993; Simone, 1999a). From the neogastropod main branches, only Cancellarioidea presented accessory salivary glands as a basal support (node 222). Taking into consideration the high degree of variation and the poor knowledge on the homology among the taxa that possess accessory salivary glands, the application of the character is relatively problematic. Ponder & Lindberg (1997) consider Cyclophoroidea and Ampullarioidea as having accessory salivary glands, however, none was found in the sampled species. Strong (2003) applied this character that resulted as a support to Neogastropoda plus epitoniid (ptenoglossan), with notable reversions in the conid and in the nassarid. The accessory salivary glands present in caenogastropods other than Neogastropoda, and allies, have been proposed to be homologous to them (*e.g.,* those of the ptenoglossans – Andrews, 1991; Strong, 2003) as well as non-homologous (*e.g.,* those of the neritids and tonnids – Ball *et al.,* 1997).

Esophagus (Characters 462-489)

In caenogastropods, a glandular longitudinal bundle running along the inner esophageal surface is found. The gland is mainly located along dorsal

region of esophagus as a strip, looking like a differentiated mucosa. This is different from the archaeogastropods, in such the main glandular portion of the foregut is in the laterally positioned pouches.

Esophageal origin: The buccal mass is constituted by the esophageal (dorsal) and the odontophoric (ventral) portions. For most basal gastropods, the separation between both portions is at middle level, producing a V-shaped buccal mass (*e.g.,* Simone & Cunha, 2006, fig. 69); the mouth stays in the vertex of the "V". In the caenogastropods and heterobranchs, in contrast, the esophagus separates from the odontophore posteriorly from buccal mass. In this fashion, the buccal mass looks like a bulged anterior portion of the anterior digestive tube (*e.g.,* Simone, 2005a, fig. 333). Although, it was detected that it has reverted in the muricoidean node 212, in which the representatives have a V-shaped buccal mass (*e.g.,* Simone, 1996a, fig. 15).

The esophagus in Gastropoda, generally, is not a simple connection between the mouth and stomach, as generally it is in the remaining mollusk classes (*e.g.,* Simone, 1997c, d). In the gastropod esophagus the food generally undergoes several digestive processes, as a result of the glands, cavities and muscles mostly found in it (Fretter & Graham, 1962; Salvini-Plawén & Haszprunar, 1987; Salvini-Plawén, 1988). In this way, the food reaches the stomach partially metabolized. The patellogastropods and cocculiniforms, following the style of the remaining mollusks, bear simple esophagi (Leal & Simone, 1998, 2000). However, Vetigastropoda, Neritimorpha, Cyclophoroidea and Ampullarioidea (nodes K to 13) have an esophageal pouch on each side, which have apertures situated just posterior to the buccal mass (Fig. 16A) (Sasaki, 1998; Simone, 1997a, 2004a, *e.g.,* fig. 195). The pair of esophageal pouches of these 4 taxa differs in morphological details from each other, as, *e.g.,* the presence of an inner cover of glandular papillae only in the vetigastropod pouches (Simone, 1997a; Sasaki, 1998); and the presence of a conspicuous blood vessel inserted in the median region of each pouch in the 2 basal caenogastropods branches (character 466) (Simone, 2004a, *e.g.,* fig. 159). Nevertheless, apparently,

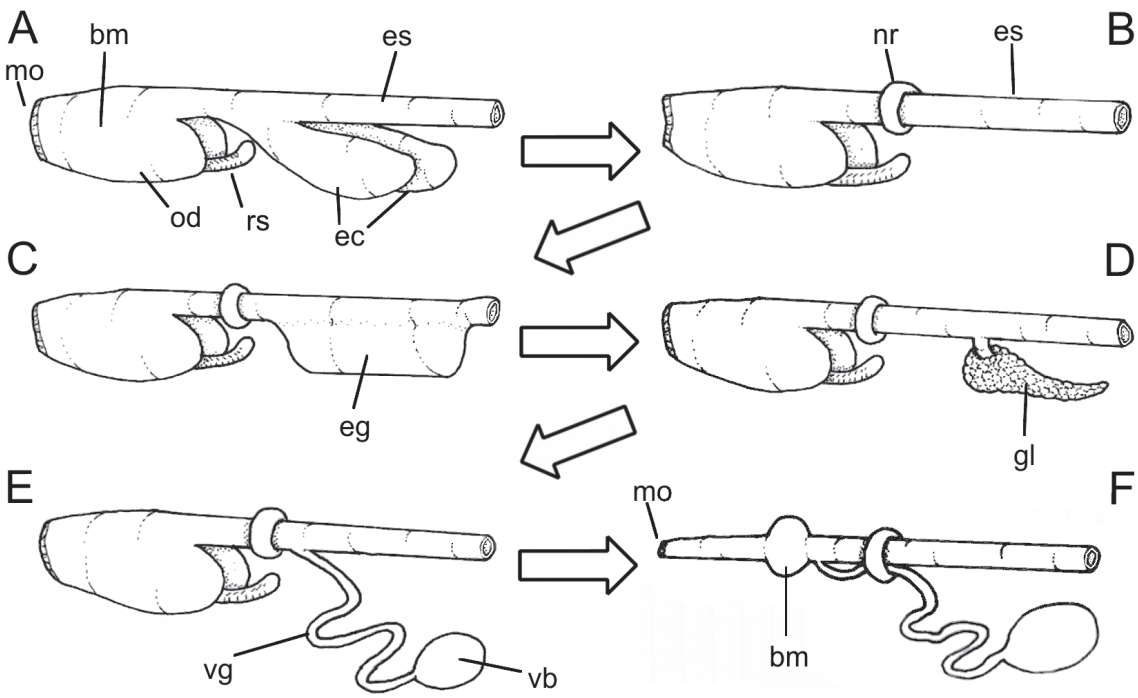

FIGURE 16: Schematic representation of esophagi found in Gastropoda and their possible evolution, indicated by wide arrows (node numbers refer to Fig. 20); **A)** Typical form of Vetigastropoda, Neritimorpha, Cyclophoroidea and Ampullarioidea, with a pair of esophageal pouches; **B)** Typical form lacking esophageal gland, found in node 14; **C)** Form with wide ventral esophageal gland, basing node 96; **D)** Form with gland of Leiblein, supporting node 178; **E)** Form with venom gland inserted posteriorly to nerve ring, found in basal Conoidea and some Marginellidae; **F)** Same, with venom gland passing through nerve ring, and loss of odontophore, state found in most Conoidea (node 181), , most Marginellidae and Volutidae. Lettering: bm, buccal mass; ec, esophageal pouch or glandular chamber; eg, esophageal gland; es, esophagus; gl, gland of Leiblein; mo, mouth; nr, nerve ring; of, odontophore; rs, radular sac; vb, venom muscular bulb; vg, venom gland.

such esophageal pouches may be homologous (character 464) (see Strong, 2003: 502, as buccal pouches). In the taxa allocated after the node 14, the esophagus lacks, secondarily (a loss?), any kind of attached pouches (Fig. 16B), only a gland that runs longitudinally along dorsal inner surface of esophagus is found. This esophageal gland, in some groups, gradually becomes ventral due to the torsion; it is located in the middle-posterior esophagus, and is present in most caenogastropods (character 80) (*e.g.,* Marcus, 1957: fig. 17 as "foliate stomach"; Simone, 1998b, fig. 22; 2001a, fig. 196). In the taxa situated after node 66, the middle region of the esophagus, denominated, generally, mid-esophagus, possesses a large ventral diverticulum (Fig. 16C: eg), which is filled by 1 (Naticoidea and Cypraeoidea; nodes 97, 118) or 2 (Tonnoidea; node 149) series of glandular transverse septa (*e.g.,* Simone, 2004b, fig. 162). This gland is very large in most species of these 3 superfamilies, and, sometimes, reaches most of the esophageal length. However, in some Pediculariidae (node 123 – Cypraeoidea) (Simone, 2004b, *e.g.,* fig. 450), the esophageal gland is reduced, and even lost in some species. In the neogastropods (node 178), a gland of different constitution appears just in the homologous region of the esophageal gland; it lacks septa, and has a uniform tissue; it is connected to the ventral surface of the esophagus by means of a duct (Fig. 16D-F). In the case of the muricoideans, including basal cancellarioideans (node 210), this gland is denominated "gland of Leiblein" (*e.g.,* Simone, 2003, fig. 7F). In the case of the conoideans (node 179), the gland has a very long, glandular, convolute tube called "venom gland" (*e.g.,* Costa & Simone, 1997, fig. 12), in which a massive muscular bulb lies at the distal end. Though, in some muricoideans (*e.g.,* Marginellidae and Volutidae; after node 220), the gland is very similar to that of the conoideans (Marcus & Marcus, 1968b: fig. 10; Coovert & Coovert, 1995; Leal & Harasewych, 1995). In the basal conoideans (node 180), the venom gland inserts close to the nerve ring (Fig. 16E) (Simone, 1999c, fig. 16), however, in most conoideans (node 181) and in the marginellids (Muricoidea after node 220), the gland passes through the nerve ring and inserts more anteriorly, close to the oral tube (Coovert & Coovert, 1995; *pers. obs.*). The terminal bulb of these neogastropods has been considered homologues by Strong (2003, as terminal ampulla).

Despite the differences among the distinct sorts of unpaired esophageal glands referred to above, the distribution of the taxa on the cladogram, and the equivalent topology (ventral side of the middle region of the esophagus), suggest that all them are homologous. Additionally, studies on ontogeny (Ball *et al.,* 1997; Ball, 2002) revealed that the development of the gland of Leiblein begins in stage 8, by means of a glandular evagination in the mid esophagus, closely similar to the esophageal gland of adult Naticoidea, Cypraeoidea and Tonnoidea. Only after stage 9 the duct begins its differentiation. Such an ontogenetic data demonstrate a single evolutionary trail for these esophageal glands. Besides, as another indicative of homology between the mesogastropod septate esophageal gland and the gland of Leiblein is a small glandular chamber with septa preceding the duct of the gland of Leiblein, found in some muricids (node 238; character 471). This septate small glandular chamber has been called "framboisse gland" in the literature (*e.g.,* Pastorino, 2002), although the septa were never reported. The comparative ontogeny of the glands of muricoideans and conoideans (Leiblein and venom glands) reveals very similar arrangement (Ball, 2002), further suggesting the homology between both structures.

The current literature advocates the homology of Leiblein and venom glands (Ponder, 1970, 1974; Kantor, 2002). Additionally, Strong (2003: 504) has also considered the gland of Leiblein as homologous to the esophageal glands of mesogastropods. Based in these data, the evolutionary scheme shown in the Fig. 16 is stated; where a connection among all type of unpaired esophageal glands of the caenogastropods is demonstrated in a single evolutionary trend. The usage or function of these kinds of esophageal glands is still subject of speculation, and it is possible that there is some variation of function or secretion. Secretor, storage, as well as absorptive functions have been suggested for the gland of Leiblein of nassariids and muricids (Andrews & Thorogood, 2005, in which a wide discussion of caenogastropod esophageal glands can be found).

The **valve of Leiblein** is one of the more notable synapomorphies of node 210, being characteristically present in the Muricoidea and Cancellarioidea (*e.g.,* Simone, 2003, fig. 7F: vl). The structure forms a bulge in the esophagus, and is situated just anterior to the nerve ring. Internally (Fig. 17), generally there is a valve composed by long and iridescent cilia situated in the anterior third portion, projected posteriorly; and a thick glandular chamber in the posterior 2/3. An oblique narrow furrow is generally present on one side (character 485), bypassing the esophageal region anterior to the valve with the region posterior to it (Graham, 1941, 1966; Ponder, 1974; Andrews & Thorogood, 2005, fig. 1). The outline of the valve of Leiblein, generally, is pyriform and divided into a

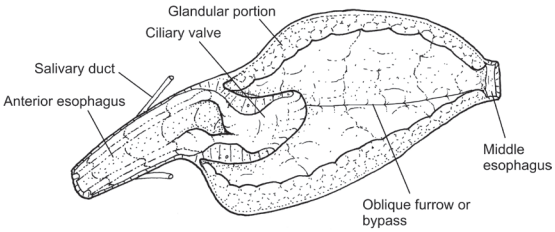

FIGURE 17: Valve of Leiblein of *Trophon geversianus,* sectioned longitudinally; short portion of adjacent regions of esophagus also shown. Whole length about 2 mm.

hyaline anterior area, and another whitish posterior, reflecting the inner structures described above. The oblique furrow is normally visible. The ducts of the salivary glands, usually, penetrate the esophageal wall just anterior to the valve (Fig. 17). On the other hand, this basic pattern is highly modified in some muricoideans, being somewhat reduced (*e.g.,* node 217 – *Buccinanops*) (Simone, 1996a), or totally absent (*e.g.,* node 219; *Marginella* spp., *Mitra* spp.) in some taxa. The valve was included in Strong's (2003) analysis, resulting as a convergence between the cancellariid and a branch bearing a nassariid and a muricid; it did not support the neogastropod branch as it is absent in the marginellid and in the conid included in that paper. More data on the structure, function and possible evolution of the valve is found in Kantor & Fedosov (2009) and Golding & Ponder (2010).

A structure similar to the valve of Leiblein has been found in two species of raphitomines Conoidea, *Paramontana rufozonata* (Angas, 1877) and *Kermia barnardi* (Brazier, 1876) (Kantor & Taylor, 2002, figs. 9-10). Kantor & Taylor (2002) called the structure only "valve" and, contentiously, did not include "of Leiblein"; although the authors called attention to the similarities of this conoidean structure with the true valve of Leiblein. There are several dissimilarities between both; some of them were explored by Kantor & Taylor (2002: 107), and Simone (2007a). The conoidean valve has not any of that inner complexity of the Leiblein's, including the high and pale colored fold as base of the cilia, and respective posterior gland. There is ciliated epithelium before and after the longer valvar cilia; this is very dissimilar to the normal valve of Leiblein, and indicates that the conoidean valvar cilia are merely a hypertrophy of a region of the ciliar epithelium. Moreover, the most significant argument of non-homology between the conoidean valve and the Leiblein's is its position. The conoidean valve is placed posterior to the venom gland (which is the homologue to the gland of Leiblein) (Kantor & Taylor, 2002, figs. 19A-B); it should be anterior to be comparable to the normal muricoidean and cancellarioidean valve. Despite these differences, the valve of those two conoideans has been considered subsequently as homologous to the valve of Leiblein (Kantor, 2002). Also, other peculiarities of the conoidean foreguts have also been proposed as a vestigial valve of Leiblein [*e.g.,* a sphincter between buccal cavity and esophagus in *Mangelia brachystoma* (Philippi, 1844): Robinson, 1960]. However, those structures can be as well considered new acquisitions (Smith, 1967). Based on these dissimilarities between the valves and other esophageal structures found in some conoideans, the valve of Leiblein has been here considered as an exclusivity of branch 210, *i.e.,* a synapomorphy of the neogastropods excluding the Conoidea. There are further reasons for excluding the conoideans as a valve-bearing group, as the more basal species of conoidean in esophageal aspects, *Cochlespira* (Simone, 1999c) (node 180), in which the venom gland inserts more posteriorly in the esophagus (in a fashion more similar to that of the muricoideans), has no vestige of a valve. Neither is any kind of valve found in ontogenetic studies on conoideans (Ball, 2002).

Despite some evidence of non homology of the neogastropod valve of Leiblein (Kantor & Fedosov, 2009), the detailed comparative study of the anterior esophagus of several caenogastropods revealed that the muricoidean valves are homologous (Golding & Ponder, 2010: 88), as also suggested by the present study.

Stomach
(Characters 490-516)

The **gastric caecum** is well developed in the vetigastropods (node L), in which several species have it very long, forming a spire. Less spectacular gastric caeca are found in the neritimorphs (node U) and are also present in other mollusk classes, such as the bivalves and cephalopods *(e.g., Nautilus)* (Griffin, 1900; Simone & Dougherty, 2004). Its presence, then, is regarded as plesiomorphic in Gastropoda, and its absence in the caenogastropods and heterobranchs as apomorphic. There are reports in the literature on the presence of a gastric caecum in caenogastropods (*e.g.,* Graham, 1949, Ponder & Lindberg, 1997; Strong, 2003); however, nothing similar to such a structure was found in the sampled specimens. In fact, the inference to any fortuitous inner fold, area of selection, or small chamber, which are reported as a vestigial caecum, is as explicative as the caecum disappearing in node W, and the other gastric details are new acquisitions of the inner surface of the organ. This

hypothesis, *i.e.,* the disappearance of the caecum and the putative caeca of caenogastropods are new acquisitions, is preferred in the present study. Strong (2003: 506) provided a long discussion of the gastric structures, considering the caecum as apomorphic. The presence of caecum in that study resulted in a convergence between the neritid and a caenogastropod branch bearing a calyptraeid and a bithyniid.

Crystalline style sac: The special chamber that shelters the crystalline style in the stomach, known as the style sac, may be present or absent in the different groups of Gastropoda, as well as in the remaining Mollusca. The polarization of the character is, then, dubious. The sense of crystalline styles in the literature is somewhat confused, since the single presence of a pair of typhlosoles in the region of intestinal origin is sometimes sufficient for considering the structure present (*e.g.,* Sasaki, 1998). In the present study, the style sac is interpreted as the conspicuous presence of a chamber, specialized for holding, production and movement of the crystalline style. However, it is recognized that the proximal portion (close to the origin) of the intestine, in all gastropods, is homologous to the style sac. The more sensate procedure would be to consider all stomachs that bear a style inside as having a gastric style sac; however, this is not trustworthy, since the style can be absorbed and/or lost during the preservation of the animal. This is what is observed in the dissection of different lots of the same species. Another indirect indication of the presence of a style sac is the presence of a chitinous gastric shield, against which it creates friction (Graham, 1949). However, the gastric shield seldom is conspicuous, and other inner structures of the stomach can, erroneously, be interpreted as that. The presence of the gastric shield was utilized by Strong (2003) as an apomorphy. The allocation of the character in the cladogram of that paper revealed a reversion, *i.e.,* its loss, at a branch that would be equivalent to a place between the node 46 and 96 of the present cladogram (with a further reversion in the nassariid). The style sac is virtually absent in the archaeogastropods and in the heterobranchs (Fig. 18A), and, based only on this fact, the structure would be a notable synapomorphy of the ingroup node 18. Although, a style sac with topology, function and action similar to those of the caenogastropods also commonly occurs in the Bivalvia (*e.g.,* Simone, 1999b, 2001b). Despite the fact that a style sac is not the rule among the other classes of mollusks, the similarity of the structure between the gastropods and bivalves permits consideration that its presence in the caenogastropods as plesiomorphic. However, it is necessary to keep in mind that the presence of style sacs in both groups could be an extraordinary convergence. The literature provides some basis for interpreting the presence of a style sac as plesiomorphic in Gastropoda (*e.g.,* Morton, 1952, 1953; Owen, 1966). However, Ponder & Lindberg (1997) and Sasaki (1998) consider the contrary. Among the basal heterobranchs, the Orbitestellidae (Ponder, 1990) and the Rissoellidae (Simone, 1995b, fig. 15: ss) (node X) appear to have a gastric style sac, corroborating with the plesiomorphic hypothesis accepted herein.

Among the superfamilies that possess the gastric style sac, in general a trend occurs – the propensity for its separation from the adjacent intestine. Normally, a gradation is notable in each taxon, from species having both structures (style sac and intestine) amply connected (Fig. 18B) towards their entire separation (Fig. 18C), with taxa in intermediary conditions. The so-called intermediary condition has the style sac physiologically separated from the intestine by means of a pair of tall folds (but both anatomically connected) as well as both incompletely separated anatomically. This evolutionary trend is detected in all superfamilies with representatives bearing style sac, such as Cerithioidea (node 19), Rissooidea (node 41), Stromboidea (node 47) and Calyptraeoidea (node 67) (Marcus & Marcus, 1964a; Ponder, 1983, 1988; Simone, 2001a, 2002, 2005a, 2006b). Similar trend also occur in the bivalves, in such some groups present style sac and intestine amply connected, *e.g.,* Mycetopodidae (Unionoidea – Simone, 1994, 1997d) up to those with total separation, *e.g.,* Lyonsiidae, Donacidae (Simone, 1999b; Simone & Dougherty, 2004). Another trend detected in the ingroup is the elongation of the style sac. Although the structure is very long in, *e.g.,* Cerithideidae (Cerithioidea after node 29 – Simone, 2001a), reaching 1 whorl in length, it was in the stromboideans that the tendency appeared exceptional. In the taxa allocated along the stromboidean cladogram, an increasing of the style sac is detected, reaching the apogee in the Strombidae (node 55 – Stromboidea) (Simone, 2005a), in which the structure runs along almost 2 whorls, lying through the kidney, pericardium, pallial cavity, reaching the mantle border (*e.g.,* Simone, 2005a, figs. 98, 100: ss).

The gastric characters show a general tendency for simplification in caenogastropods. In the basal branches, the stomach is, normally, voluminous and complex (Fig. 18D), having several inner structures, such as folds, chambers and select areas (*e.g.,* Simone, 2001a, figs. 279-280). In some taxa, such as cerithioideans (node 19) and rissooideans (node 41), most species have a very large stomach

that, practically, separates the visceral mass into 2 regions scarcely connected to one another (character 492) (Simone, 2001a, 2006b). In the ampullarioideans (node 5), the stomach, in general, has thick muscular walls, probably working as a gizzard (*e.g.,* Simone, 2004a, figs. 168-169); a state shared with pulmonate node Z3 (Marcus & Marcus, 1965). In the taxa allocated between nodes 96 and 117, as well as in the following nodes, the stomach gradually becomes a simpler structure, sometimes only detectable by the presence of the ducts to the digestive gland (characters 498, 509) (*e.g.,* Simone, 2004b, fig. 328). Such simplification (Fig. 18E) appears to be due to a dietary change, which has occurred during caenogastropod evolution. The basal clades are herbivorous or microphages, while the terminal branches are predatory carnivores. However, the cypraeoideans are supposedly grazing feeders (Gosliner & Liltved, 1985), contrasting with their simplified stomach (Simone, 2004b). Some taxa of the terminal branches, *i.e.,*

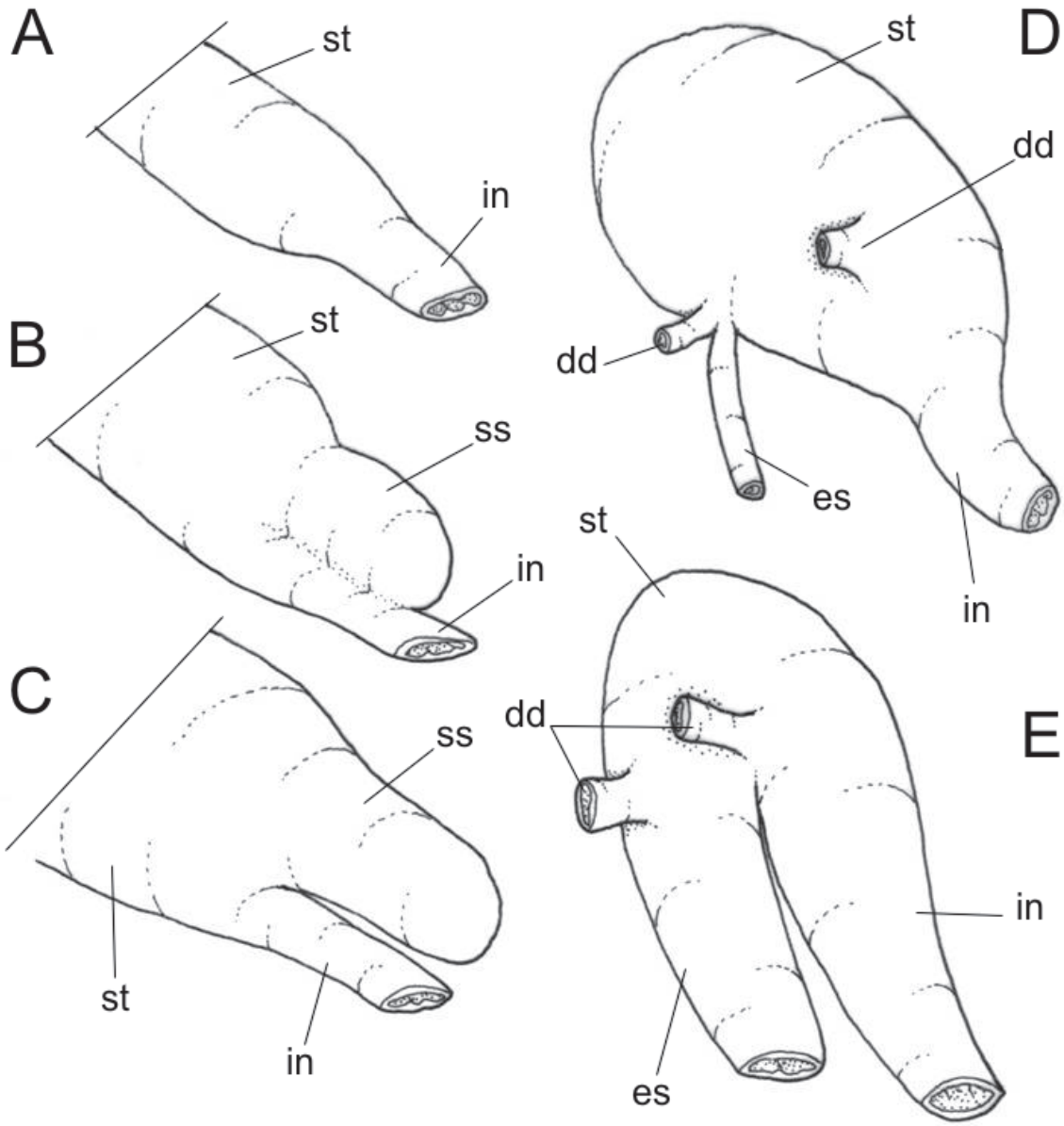

FIGURE 18: Schematic representations of main type of stomach in Gastropoda, ventral view: **A-C)** Pre-intestinal region of stomach; **A)** Style sac absent or inconspicuous; **B)** Style sac present and connected to adjacent intestine; **C)** Same, with total anatomical separation between style sac and adjacent intestine; **D)** Massive and globose type of stomach, a generalization; **E)** Stomach "U"-shaped, a generalization. Lettering: dd, duct to digestive gland; es, esophagus; in, intestine; ss, style sac; st, stomach.

neogastropods, also reverted to herbivore diet (*e.g.,* some columbellids – Marcus & Marcus, 1962b; de-Maintenon, 1999), with subsequent modifications in the buccal and gastric regions.

The **ducts** to the digestive gland are important point of reference, since they allow recognition of the homologous stomach region in those taxa in which it is barely evident. In the basal condition for the caenogastropods, the stomach bears a pair of ducts; one is closer to the esophagus and another to the intestine. However, the reduction to a single duct happened in several internal branches of the superfamilies, being a common case of convergence (character 498). Besides, according to the results obtained herein, a reversion to a pair of ducts happened in taxa likely evolved from a single-ducted ancestor. This is the case, *e.g.,* for the Campanilidae and Vermetidae (node 21 – Cerithioidea) (Simone, 2001a). The duplication of one or another duct also occur (*e.g.,* node 85 – *Crepidula,* Calyptraeoidea) (Simone *et al.,* 2000; Simone, 2002), as well as the change of their position in relation to esophagus and intestine.

The **digestive gland** is one of the larger organs of the gastropods, and is normally localized inside the first whorls and, together with the gonad, are practically the only structures situated posterior to the stomach. Despite the normal fashion is a pair of ducts to the digestive gland, the gland is normally a single uniform mass. This condition differs from that showed by heterobranchs (node V), in which the gland is separated into anterior and posterior lobes. However, some representatives of the ingroup also show the separation into 2 lobes, *e.g.,* node 23 (of Cerithioidea); Conidae (node 200 – Conoidea), with each lobe connected to a duct.

A more detailed description and discussion on the stomach and adjacent region of the midgut is provided by Strong (2003) (see also Ponder *et al.,* 2008: 348-349, fig. 13-8). Some of characters of that paper were not utilized here because they were not examined in all of the presently sampled species. An example is the ciliated esophageal fold in the gastric chamber (Strong, 2003: 510, character 30), which possibly aids in the support of node 96 (although it is convergent with neritids, node U). Another example is the intestinal groove sorting area (Strong, 2003: 518, character 36), it is a synapomorphy supporting a branch equivalent to node 18, reverting at node 96 (with a notable convergence in the neritid and a reversion in the nassariid in that paper). The clockwise rotation of the ciliary currents within the gastric chamber (Strong, 2003: 519, character 38) supports a branch equivalent to node 117, further modifying to a simple, linear fashion in the conid (node 200) and cancellariid (node 222). The main goal of Strong's paper is the examination of midgut characters. It is interesting to observe that her study and the present one, which were developed independently, greatly overlap and concord; this shows the importance of the midgut in comparative analyses.

Intestine (Characters 517-539)

The intestinal characters show a tendency for simplification among Caenogastropoda, even in microphages and herbivorous groups (Ponder & Lindberg, 1997). This pattern contrasts with the several-looped intestines (character 518), running immersed in the digestive gland (character 519), found in the archaeogastropods (Fretter & Graham, 1962; Simone, 1996c, 1997a; Strong, 2003; Simone & Cunha, 2003, *e.g.,* fig. 86) and many heterobranchs (Simone, 1998a, *e.g.,* fig. 2; Simone & Leme, 1998) (node V). The normal fashion of the caenogastropod intestine is running though the visceral mass, generally with only a single sigmoid loop (*e.g.,* Simone, 2004b, fig. 139). However, there are some taxa of the ingroup, such as, *e.g.,* Ovulidae (node 130 – Cypraeoidea) (Simone, 2004b) and Hipponicidae (node 72 – Calyptraeoidea) (Simone, 2002), which have an intestine with several loops. However, even in those cases, the loops are free from the visceral mass (and free from the digestive gland), running through the kidney and/or the roof of the pallial cavity.

The absence of a loop inside the haemocoel of caenogastropods is connected to the appearance of a transverse diaphragmatic septum separating the haemocoelic cavity from the visceral mass (character 143). Only the esophagus, anterior aorta and some nerves pass through this septum. In this situation, the haemocoel is free from visceral structures such as the intestine. In archaeogastropods, one to several intestinal loops are positioned at the side of the esophagus, even touching the buccal mass (*e.g.,* Simone, 1998d, fig. 26; Simone & Cunha, 2006, figs. 69, 71). The heterobranchs also mostly have intestinal loops in the haemocoel.

Formation of **fecal pellets:** Comparative analysis of the nature of the fecal matter in mollusks, and in the gastropods in particular, are presented in Moore (1931), Arakawa (1972 and others) and Ponder & Lindberg (1997: 154). Adding the data found in the literature with those found in the present study, it becomes clear that the formation of the fecal pellets is

one of the characters of Caenogastropoda (node 1). Nothing similar, practically, is found in the archaeogastropods and heterobranchs, in which generally there is a continuous fecal string. Although, fecal pellets appear to be present in the Amphibolidae (Pulmonata, Heterobranchia) and in some Polyplacophora (Ponder & Lindberg, 1997), they have been interpreted as convergences. The form and storage of the fecal pellets are important characters, in particular, for the cerithioideans (node 19) (Marcus & Marcus, 1964b; Simone, 2001a). Characteristically, they store the pellets in the rectum, positioning them successively in an oblique arrangement. Storage of fecal matther is also observed in some members of few other groups (*e.g.,* Hydrobiidae *sensu lato,* Hershler & Ponder, 1998. In the remaining caenogastropods the fecal pellets are stored aligned or randomly (character 527). The intestinal region where the fecal pellets are produced, *i.e.,* the region in which the fecal material changes from a continuous mass to a series of small ellipses, is, in general, possible to be marked. It is located in the portion preceding its penetration in the kidney. Of course the character suffered reversion in several branches of the ingroup, mainly in the carnivore ones, whose feces are made up of pieces of the prey (*e.g.,* marginellids).

Reproductive system (Characters 540-648)

Male (Characters 540-582)

The **seminal vesicle** is a differentiated portion of the vas deferens in the region preceding its access to the pallial cavity. The differentiation consists of an intense coiling in a convolute fashion, and, when full of sperm, iridescent. The seminal vesicle is a notable synapomorphy of node 18 and does not suffer reversion in any branch of the ingroup among the studied sample. Although, there are taxa that bear very small seminal vesicles, such as, *e.g.,* the Calyptraeoidea (node 67) (Simone, 2002). An equivalent result is obtained by Strong (2003). The normal localization of the seminal vesicle is in the ventral and medial region of the last whorl of the visceral mass. Sometimes it bulges inside the renal chamber, dislocating the renal lobes and the adjacent digestive gland portions (*e.g.,* Simone, 1995a, fig. 14). In some branches of the ingroup superfamilies, the seminal vesicle differentiates from its normal convolute fashion to a glandular form, in which coils are not clearly individualized, *e.g.,* node 179 – Conoidea (character 542). Although no seminal vesicle-bearing taxa have been examined in the sampled outgroups, there is, in the literature, a report respect to some neritimorphs bearing the structure (Sasaki, 1998), being a remarkable convergence.

Although some outgroups bear **prostate** glands, *e.g.,* Neritimorpha (node U) and Heterobranchia (node V), they differ in several aspects from that found in the caenogastropods. The prostate gland is, then, one of the characters supporting node 14. Among the differences, there are the high complexity of the neritimorphs prostates, possessing several divisions (Sasaki, 1998), and the haemocoelic position of the heterobranch prostates (Simone, 1995b, 1997b; Simone & Leme, 1998). Like the seminal vesicle, the prostate gland appears to be a differentiation of the vas deferens, in its region running along the pallial cavity, adjacent to the rectum. Its normal constitution is a glandular thickening, which can be open (cerithioideans) or closed (tubular) (most taxa situated after node 14). The prostate is missing (lost) in some branches of the ingroup, *e.g.,* Conidae (node 200 – Conoidea) and in some others (Fretter & Graham, 1962: 383).

Pallial **vas deferens:** The structure runs along the pallial cavity, differing from the vas deferens of the heterobranchs, which is haemocoelic. The pallial conduct is sometimes found in the archaeogastropod grade as only a furrow (*e.g.,* node J – Cocculiniformia) (Simone, 1996c; Simone & Cunha, 2003), while in the remaining branches it is closed, *e.g.,* most neritimorphs (Sasaki, 1998). Therefore, the open condition, *i.e.,* those with a glandular-furrow, is considered an intermediary step between the absence of pallial vas deferens and its closed (tubular) condition. However, the cladogram suggests that the closed type appeared in node 1, and reverted to the opened condition in node 18. After this node, only the rissooideans (node 41) possessed the closed pallial vas deferens as a basal character; despite in having some (basal?) representatives with opened penis duct [*Rissoina chesnelii* (Michaud, 1830) – Marcus & Marcus, 1964a]. Moreover, the (tertiary?) closure of the pallial vas deferens is convergent in some internal branches of all superfamilies, and, sometimes, it has occurred more than once (*e.g.,* Cypraeoidea, node 118) (see Marcus & Marcus, 1959a; Schileyko, 1977; Simone, 2001a, 2002, 2003, 2004b, 2005a). Possibly for this reason, Strong (2003) divided the character, jointly with the presence/absence of a prostate, into six states. As a result most were autapomorphic; except the closed vas deferens with a small posterior aperture, which supports Neogastropoda (with reversion in the nassarid).

The **exophalic penis,** or verge, is a copulatory structure that helps the transference of the sperm and/or spermatophore. It is characteristically positioned at the cephalo-pedal mass, close and posterior to the male right cephalic tentacle; and is innervated by the pedal ganglia (Fretter & Graham, 1962; Graham, 1985). The penis is one of the outstanding synapomorphies of node 38; with a surprising convergence with the cyclophoroideans (node 2). The presence of the exophalic penis did not suffer a reversion, however, a thorough study on the ptenoglossate taxa, which presents taxa with and without penis, is still lacking. The anatomical position of the exophalic penis is, normally, posterior to the right cephalic tentacle, however, in several representatives of the superfamilies the structure migrated to a medial dorsal region of the head, *e.g.,* some Rissooidea (node 43) (Simone, 2006b); and Conoidea (node 191), or to a medial region ventral of the head (node 73 – Calyptraeoidea) (Simone, 2002). The term "exophalic" means a long appendage, permanently exteriorized. It is easily seen in an active male. This fashion differs from the penes found in the (outgroup) heterobranchs. The basal heterobranch taxa lack a penis (*e.g.,* Architectonicidae – Bieler, 1988), and it is retractile in the remaining ones (node V), becoming invisible except during copulation (Marcus, 1972). However, in the ingroup branch node 109 – Naticoidea, the penis is retractile *(pers. obs.).*

Copulatory organs are present in the males of several archaeogastropods, even an exophalic penis, such as in some neritimorphs (Fretter, 1946; Sasaki, 1998). Nevertheless, the modification of the right tentacle appears to be the commonest adaptation (character 560). It is found in some members of almost all archaeogastropod taxa, although, it is remarkable in the Cocculiniformia (Sasaki, 1998; Simone, 1996c; Strong & Harasewych, 1999; Simone & Cunha, 2003) (node J), being cerebrally innervated (Strong, 2003). Copulatory organs are also present in the ingroup taxa preceding the penis-bearing node 38, except for cerithioideans (Houbrick, 1988; Simone, 2001a). The viviparoideans (node 15) possess a strong modification of the right cephalic tentacle; it has a closed inner duct running along its interior space, opening at the apex (Simone, 2004a, *e.g.,* fig. 291). In the ampullarioideans (node 5), the penis is of pallial origin, protected by a shield that appears to be a mantle border modification (Andrews, 1964; Schulte-Oehlmann *et al.,* 1994; Simone, 2004a, *e.g.,* fig. 171). The cyclophoroideans (node 2), as reported above, have an exophalic penis very similar to that of "higher" caenogastropods (Thompson, 1969; Simone, 2004a, *e.g.,* fig. 259), and appears to be a remarkable convergence. In favour to a convergence is the fact that some basal cyclophoroideans lack a penis (some Diplommatinidae – Tie Lecke, 1940). The presence of a penis was also included in Strong's (2003) analysis, being a caenogastropod synapomorphy, with reversions (loss) in the batillariid, vermetid and epitoniid. The penis **duct,** like the pallial vas deferens, also undergoes closure, *i.e.,* becomes a duct rather than a furrow (character 276), in several branches of the superfamilies that have a penis (node 38).

Female
(Characters 583-648)

The **pallial oviduct** is a remarkable synapomorphy that aids in the support of node T. In the first branches after this node, the pallial oviduct is closed, *i.e.,* tubular, with the major exception of the cerithioideans (node 19) (Marcus & Marcus, 1964b; Houbrick, 1988; Simone, 2001a). Despite this, the open condition of the cerithioidean oviduct, *i.e.,* the form of a glandular furrow (state 1), is considered as intermediate between the absence of a duct or the presence of a simple shallow furrow, lacking glands, as found, in some cocculinimorphs (node J), and the closed pallial oviduct condition. According to the result obtained in this analysis, and based on the above polarization, the cerithioideans suffered a reversion. The reversion of the oviduct from a closed state to an open one is rare among the caenogastropods. Beyond the cerithioideans, the reversion was detected only once more in this analysis, in the Strombidae (node 55 – Stromboidea) (Simone, 2005a). However, both taxa possess a short closed posterior portion of the pallial oviduct. Additionally, even within Cerithioidea, the oviduct closes in the Thiaridae (node 35) (Simone, 2001a). In several taxa the posterior portion of the pallial oviduct encroaches into the visceral mass, compressing adjacent structures, such as the kidney. This happens, *e.g.,* in stromboideans (node 47) (Simone, 2005a). This character was utilized by Strong (2003), with the albumen gland in the visceral mass, supporting the Sorbeoconcha (node 18) (despite some reversions).

The glands of the oviduct, responsible for the secretion of the albumen and of the capsule that protects the ova, are found from the neritimorphs (node T). However, in the basal taxa, only microanatomical studies reveal the separation between both glands. Those glands appear clearly separated from one another only in the taxa allocated after node 38, and, in several cases, they are even separated by a duct

(*e.g.,* Simone, 2005a, fig. 106). The presence of a capsule gland is obviously related to the building of a capsule, which has the function of protecting the ova and embryos from environmental factors (Marcus & Marcus, 1959b, 1963). Egg capsules first appear in the neritimorphs and may be another synapomorphy supporting node T. The study of capsule constitution and shape may be another important source of comparative data. However, these data were not obtained in the present study and there is not sufficient data in the literature. Although, as pointed out by Penchaszadeh (1988), it is a promising area for investigation.

The pallial oviduct is a very important source of data in comparative analyses; however it appears to be more useful in levels closer to species. At the level of superfamily, relatively few characters are useful. In several taxa, the oviduct is very simple, being little more than a uniformly tubular and glandular structure (*e.g.,* node 217, Nassariidae – Muricoidea) (Simone, 1996a), while in others it possesses a number of divisions and annexed structures (*e.g.,* Stromboidea – Simone, 2005a), difficult to identify at first instance. During this study, a large range of morphological conformations were observed, and a secure polarization and inferences of homology were difficult, mostly due to the absence of comparative structures in the outgroups. In the outgroups that possess pallial oviducts, *i.e.,* Neritimorpha (node U) and Heterobranchia (node V), the possibility of comparison with the same structure in the caenogastropods is weak. In the neritimorphs, the organ has high complexity, presenting, generally, more than one duct and pore. In the heterobranchs, in general the gonoducts run immersed in the pallial cavity floor or even free inside the haemocoel. However, in general terms, there are three basic patterns of pallial oviduct in caenogastropods and these form the basis of the characters used here (Fig. 19). In the first pattern (Fig. 19A), the bursa copulatrix is situated in the posterior region and mostly represents the condition found in the ingroup basal branches. The cerithioideans, in particular, represent a second pattern. They possess a pallial oviduct that appears to be derived from that shown in Fig. 19B – open, with a chamber situated in each lamina (a bursa copulatrix and a seminal receptacle) in the posterior region. The third pattern appears in the taxa after node 40; the bursa copulatrix lies in an anterior position, closer to the genital pore (Fig. 19C). These arrangements of the bursa are not considered homologous, which agrees with the data in the literature (*e.g.,* Ponder, 1988; Strong, 2003; Ponder *et al.,* 2008). Within each superfamily, however, there are many variations and modifications of these patterns. Nevertheless, as schematized in Fig. 19, they present approximately the basic plan of each superfamily. It is clear that the pallial glandular oviduct is a modification of the pallial mucosa. Further studies on the subject are necessary.

Some confusion with respect to the female structure for sperm storage is found in the literature. There are typically two structures which do that, the bursa copulatrix and the seminal receptacle. Normally, the interpretation of the animals that possess both is that the bursa copulatrix is the structure that receives the sperm, spermatophore, or equivalent, during copulation. The spermatozoa are afterwards transferred to the seminal receptacle via ciliated furrow, and sperm involved in fertilization are provided from that structure (*e.g.,* Lilly, 1953; Fretter & Graham, 1962; Reed,

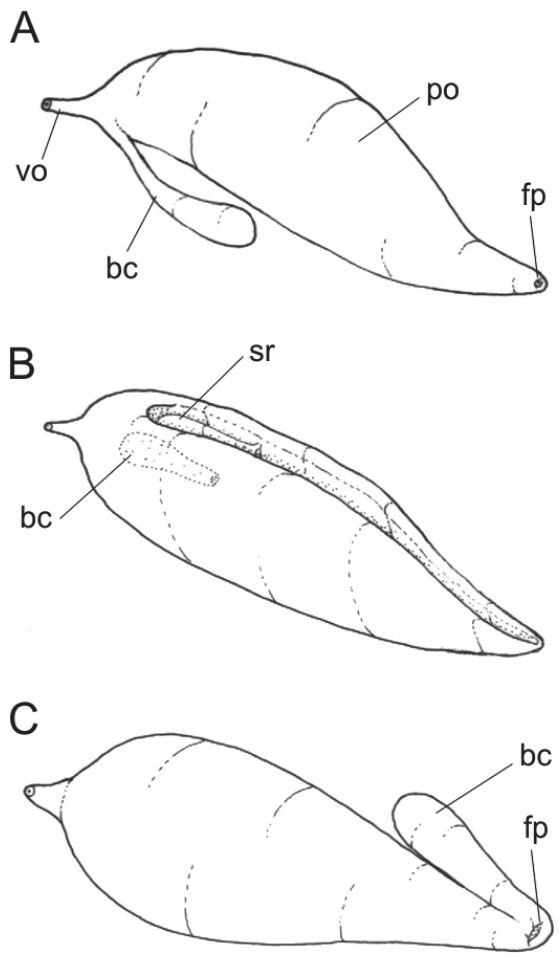

FIGURE 19: Schematic representations of main type of pallial oviduct, ventral view; **A)** Generalized pattern of node 1, present in more basal taxa, with posterior bursa copulatrix; **B)** Particular case of Cerithioidea; **C)** Generalized pattern of node 46 (Fig. 20), with anterior bursa copulatrix. Lettering: bc, bursa copulatrix; fp, female pore; po, pallial oviduct; sr, seminal receptacle; vo, visceral oviduct.

1995). However, further studies are necessary to confirm if all the structures so-called actually have those functions in the different groups. The posterior located bursa has been referred to as homologous to the neogastropod ingesting gland (Ponder & Lindberg, 1997); and the presence of this gland has supported the Neogastropoda branch in the analysis of Strong (2003), with a reversion in the conid in her analysis.

A furrow running along the right side of the female head-foot, which originates from the genital pore, is present in cerithioideans and stromboideans. It is shallow, and runs along the floor of the pallial cavity, on the right side ending on the right side of the foot. In the case of cerithioideans (node 19), the furrow finishes, generally, in an ovopositor, located on the dorsal-right region of the foot (*e.g.,* Houbrick, 1988; Simone, 2001a, fig. 265: rf). In stromboideans (node 47), this furrow ends close to the anterior groove of the pedal gland, where it gradually disappears (*e.g.,* Simone, 2005a, fig. 74: fo). Those differences, together with the location of the taxa on the cladogram, suggest that this groove is convergent in these two taxa.

Hermaphroditism is found in all heterobranchs (node V), but is rare among the 'prosobranchs'. They are mostly dioecious (gonochoric) animals. In the ingroup, protandric hermaphroditism is seen in Calyptraeoidea (node 67) (Simone, 2002), and is also common in the ptenoglossates (Warén, 1984) (*e.g., Annulobalcis aurisflamma,* Eulimidae – after node 38) (Simone & Martins, 1995). Simultaneous hermaphroditism is rare among the studied ingroup representatives, with only *Velutina velutina* (Cypraeoidea – after node 119) with this character (Simone, 2004b). Parthenogenesis is found in some Thiaridae (node 35 – Cerithioidea) (Simone, 2001a) and is known in a hydrobiid (*Potamopyrgus* – Wallace, 1992; Neiman, 2006).

The presence or absence of the gonopericarial duct is inconstant amongst the representatives of each superfamily (Krull, 1935; Lilly, 1953; Fretter & Graham, 1962; Marcus & Marcus, 1962b, 1964c) (character 584), perhaps in part as a result of the difficulty of detecting this structure in some species. As evidence of this, Strong (2003) has utilized this character which resulted in autapomorphic homoplasies.

Central nervous system (Characters 649-673)

Position of nerve ring: The central nervous system, or nerve ring, is located at the anterior end of the buccal mass in the examined outgroup taxa, both archaeogastropods (*e.g.,* Simone, 1998d, fig. 25) and heterobranchs (*e.g.,* Marcus & Marcus, 1969a; Simone, 1997b, fig. 9; DaCosta *et al.* 2007; Golding *et al.,* 2007). In most branches of the ingroup, however, it is situated posterior to the buccal mass, being an important synapomorphy of the taxa allocated after node 14. In Cyclophoroidea (node 2) and Ampullarioidea (node 5), the position of the nerve ring is intermediate, situated in the middle part of the buccal mass (*e.g.,* Simone, 2004a, fig. 159). This condition is interpreted as intermediate between the two extremes. Consequently this character is treated as three ordered states of a single character (653), with is corroborated with ontogeny (Ball, 2002). In this way, after node 1, the character shows a relocation of the nerve ring to the posterior position in the ingroup.

In some outgroups, heterobranchs in particular, the nerve ring is truly situated at the base of the buccal mass, but it is sufficiently large to permit the buccal mass to slide through it (*e.g.,* some Pulmonata – Simone, 1998a; Simone & Leme, 1998). This condition allows for the observation of some specimens with the nerve ring situated more posteriorly. This state differs from that of the caenogastropods allocated after node 14, in which the nerve ring is always posterior to buccal mass.

The central nervous system is hypoathroid in the archaeogastropods and epiathroid in the caenogastropods (Fretter & Graham, 1962; Haszprunar, 1988a: 394-396; Ponder & Lindberg, 1997). As commonly occurs in prosobranchs, the central nervous system presents three pairs of ganglia: cerebral, pleural and pedal (the triganglionate condition of Haszprunar, 1988a). The condition **hypoathroid** is so called due to the proximity between the pleural and pedal ganglia, which are far from the cerebral ganglia (*e.g.,* Marcus & Marcus, 1960a, fig. 13). The opposite situation occurs in the **epiathroid** type, in which the pair of pleural ganglia is located closer to the cerebral ganglia and far from the pedals (character 654). The nerve ring condition of the architaenioglossans is somewhat uncertain. Some authors (*e.g.,* Bouvier, 1888; Fretter & Graham, 1962: 308, fig. 601B; Haszprunar, 1988a) called hypoathroid the condition of the cyclophoroideans and ampullarioideans, and "dystenoid" that of the Viviparoideans (Bouvier, 1888; Annandale & Sewell, 1921: 236). This kind of nerve ring is, supposedly, hypoathroid on left side and epiathroid on right side. Having these facts in mind, the study on the architaenioglossans was carried out with special care in this aspect (Simone, 2004a). The result is that both Cyclophoroidea and Ampullarioidea actually have the

hypoathroid condition, in the archaeogastropod fashion (Simone, 2004a, *e.g.,* figs. 180, 237, 249, 263), as have been long know in the literature (*e.g.,* Bouvier, 1888). However, the Viviparoidea have the pair of pleural ganglia situated close to the cerebrals, being, then, epiathroid. This condition helps in the support of node 14. Although, the two pairs of connectives of viviparoideans, cerebro-pedal connectives and pleuro-pedal connectives, differ from the condition found in the remaining caenogastropods situated after node 18 in being separated from one another, forming a "V" (with the pedal ganglion at the point of the V) (characters 655, 656) (Simone, 2004a, figs. 348-352). In the taxa represented after node 18, both pairs of connectives run parallel and close to one another (*e.g.,* Simone, 2005a, fig. 94). This is a consequence of the approach of the dorsal ends of these connectives compared with the state seen in viviparoideans. On the other hand, the pedal ganglia of the Viviparoidea are very peculiar and, unlike other gastropods, they are quite diffuse, lacking clear boundaries with the pleuro-pedal connectives and with the anterior pedal nerves (Annandale & Sewell, 1921: figs. 8-9; Simone, 2004a).

Converging with caenogastropods, the condition of heterobranchs is also epiathroid (Ponder & Lindberg, 1997; Golding *et al.,* 2007). However, the nerve ring of this taxon is normally concentrated, and possesses, additionally, other ganglia (Pentaganglionata – 5 pairs of ganglia – Haszprunar, 1988a). These factors preclude an immediate interpretation. Apparently, assuming that the heterobranchs also have the epiathroid condition, it happened twice along the gastropod evolution, one in node 14 of the caenogastropods and another in the heterobranchs. However, further studies on the structure in the basal heterobranchs (allogastropods) may bring additional revelations, as they reveal to possess not concentrated, triganglionate nerve ring.

The **statocyst** is the molluscan organ of equilibrium and sense of position. The structure is one of the synapomorphies of Conchifera (Haszprunar, 1988a) (node A). Statocysts are a pair of hollow vesicles, covered internally by sensitive cells, and they have inside one or more free objects. These objects, due to gravity, tend to stay at the bottom of the vesicle, being, then, detected. Although innervated by the cerebral ganglia (Wingstrand, 1985), normally the statocysts are situated close to the pedal ganglia, immersed in the foot musculature adjacent to those, connected with the nerve ring by narrow nerves. In the caenogastropods there are two types of statocysts (Ponder & Lindberg, 1997): 1) with several small objects inside, generally sand grains, called **statoconia** (*e.g.,* Simone, 2001a, fig. 244: so); 2) with a single object inside, proportionally large, calcareous (being, then, secreted) and, most times, connected by a peduncle to a side of the inner surface (*e.g.,* Simone, 2002, fig. 128: sy); this single object is named **statolith** (*e.g.,* Simone & Birman, 2006a, fig. 7). The normal condition of the statocysts of archaeogastropods and heterobranchs is having statoconia and this condition is only found in the basal branches of the Caenogastropoda. The taxa allocated after node 38 have statoliths, one of the synapomorphies supporting the node. Although there are no exceptions, there are outgroup taxa that can also possess both kinds of statocysts (Ponder & Lindberg, 1997; Strong, 2003). This suggests that the phenomenon is more complicated and may also be susceptible to homoplasy. Moreover, Strong (2003) utilized this character with inverted polarization. The position occupied by the statocysts in relation to the pedal ganglia is also useful, as neritimorphs and vetigastropods have the statocysts situated dorsal to the pedal ganglia, while in the remaining taxa, including caenogastropods, they are situated laterally (Sasaki, 1998; Strong, 2003). However, some neogastropods appear to be exceptions (Strong, 2003: 530).

Buccal ganglia: The characters 658 to 662 refer to the pair of buccal ganglia. These are very conspicuous in Caenogastropoda. Normally they are situated in the region just posterior to the buccal mass (*e.g.,* Simone, 2001a, fig. 127: bg), and may coordinate the movement of that structure. The pair of buccal ganglia appears to be present in all gastropods with a buccal mass. Their general form is a pair of thickenings of the buccal nerves (Haszprunar, 1988a, fig. 4f: b). However, in the caenogastropods, the buccal ganglia become very distinct (character 110), *i.e.,* each one has a more-or-less spherical form linked by connectives (*e.g.,* Simone, 2005a, figs. 365-366: bg).

In the outgroups, the buccal ganglia are situated closer to the nerve ring, having a pair of short connectives to the cerebral ganglia. In the caenogastropods, these connectives become longer, probably due to the tendency of the buccal ganglia to be situated far from the nerve ring (character 661). However, the muricoideans have reverted to the plesiomorphic condition; possessing buccal ganglia closer to, or even incorporated into the nerve ring (Marcus & Marcus, 1962b). A thick commissure connects the pair of buccal ganglia with each other. In general, there are two conditions of this commissure in the ingroup: 1) ganglia close to one another, and situated near the median line with a short commissure (*e.g.,* Simone, 2002, fig. 125); 2) ganglia far apart, with a

long commissure and situated in the lateral-posterior region of the odontophore, generally encased in the insertion of the retractor of the buccal mass (m2), (*e.g.,* Simone, 2005a, fig. 286). The polarization of both states is problematic, since, as referred to above, there are no clear buccal ganglia in outgroups. Studying the position of the archaeogastropod thickening of the buccal nerves, which may be homologous to the caenogastropod buccal ganglia (*e.g.,* Sasaki, 1998: 159, figs. 102a-c), it is possible to observe that they are closer to the median line. In this way, such a state is considered plesiomorphic.

The **central nervous system** is an important source of characters, and very useful in comparative studies. Historical studies already revealed this (*e.g.,* Bouvier, 1887). The issue was explored by Ponder & Lindberg (1997), Sasaki (1998), and Strong (2003), analyzing different parameters from those presented herein; as well as Haszprunar (1988a), who performed an extensive comparative study (*e.g.,* fig. 3 of that paper). An attribute that has been pointed out by some authors is the degree of concentration of the nerve ring. A concentrated central nervous system differs from a non-concentrated one by the difficulty in distinguishing the ganglia, having the form of a single, amorphous mass surrounding the esophagus (Marcus & Marcus, 1962a). This occurs by the diminution of the connective length (*i.e.,* the ganglia become close to each other), as well as the proportional increase in size of each ganglion. This parameter could be utilized in the present study, since a tendency for concentration of the ganglia was observed, both in caenogastropods and the Gastropoda in general. The exclusion of this character, however, is based on the difficulty in establishing standards, since all range of variations exist. Another factor is that the degree of concentration of the nerve ring is associated with the degree of dilatation of the esophagus (which passes through it). Normally, in animals in which the esophagus expands greatly for the course of the food, the nerve ring is not concentrated, and vice-versa. For example, the calyptraeoideans (node 67), generally microphages and sedentary animals, have the nerve ring concentrated, since the esophagus has no necessity for considerable dilatation (*e.g.,* Simone, 2002, fig. 126). The contrary happens with the tonnoideans (node 149), they are predators that swallow large prey, and have large and weakly concentrated nerve rings (*e.g.,* Simone, 1995a, figs. 11, 23). Another feature that appears to influenciate the concentration of the nerve ring is the size. Very small species (*i.e.,* less than 3 mm) tend to have a concentrated nerve system as well as the juveniles (*e.g.,* Simone, 1995b, c, 1997b).

Among the non-utilized nervous system characters, because of the incompleteness of data, is the presence of the siphonal ganglion. It was utilized by Strong (2003), and supported Neogastropoda.

CLADISTIC ANALYSIS

The list of considered characters is in the **Appendix 1,** which resulted in the matrix of characters presented in the **Appendix 2.** Processing these data, 48 most parsimonious cladograms result, in such strict consensus is presented in the **Figure 20.**

Analyzing the resulted cladogram, under the light of the above discussions, it is possible to infer that the Caenogastropoda encompasses a set of, at least, 13 superfamilies, excluding the ptenoglossans (represented by the eulimid *Annulobalcis aurisflamma*), and the enigmatic *"Amauropsis" rossiana* (a supposed naticid that must be reallocated). The superfamilies are successively positioned along the tree, as follows: Cyclophoroidea (node 2), Ampullarioidea (node 5), Viviparoidea (node 15), Cerithioidea (node 19), Rissooidea (node 41), Stromboidea (node 47), Calyptraeoidea (node 67), Naticoidea (node 97), Cypraeoidea (node 118), Tonnoidea (node 149), Conoidea (node 179), and Muricoidea (node 210). This scheme is represented in the **Figure 21,** in such only the relationship of the superfamilies and the main outgroups is represented. This cladogram (Fig. 21) is essentially the same represented in Ponder *et al.* (2008, fig. 13.4B).

DISCUSSION OF THE CLADOGRAM

In the present section the obtained cladogram is discussed (Figs. 20, 21), based on the analysis, but also taking into consideration the literature data. Both the characters and the systematics are discussed, with the main focus at the superfamily level. The divisions and characters that revealed interesting in internal analysis inside superfamilies are explored in more detail in the secondary papers about them (Simone, 1999a, 2000, 2001a, 2002, 2004a, b, 2005a, 2006a, b, 2007a, and others in preparation).

During the completion of the study, a high degree of somatic plasticity was detected, revealing as an important feature of the mollusks. The degree of variation of homologous structures is impressive, homoplasies are abundant; the appearance of complex structures where, apparently, there was nothing in correlate taxa commonly occurs. This is the case,

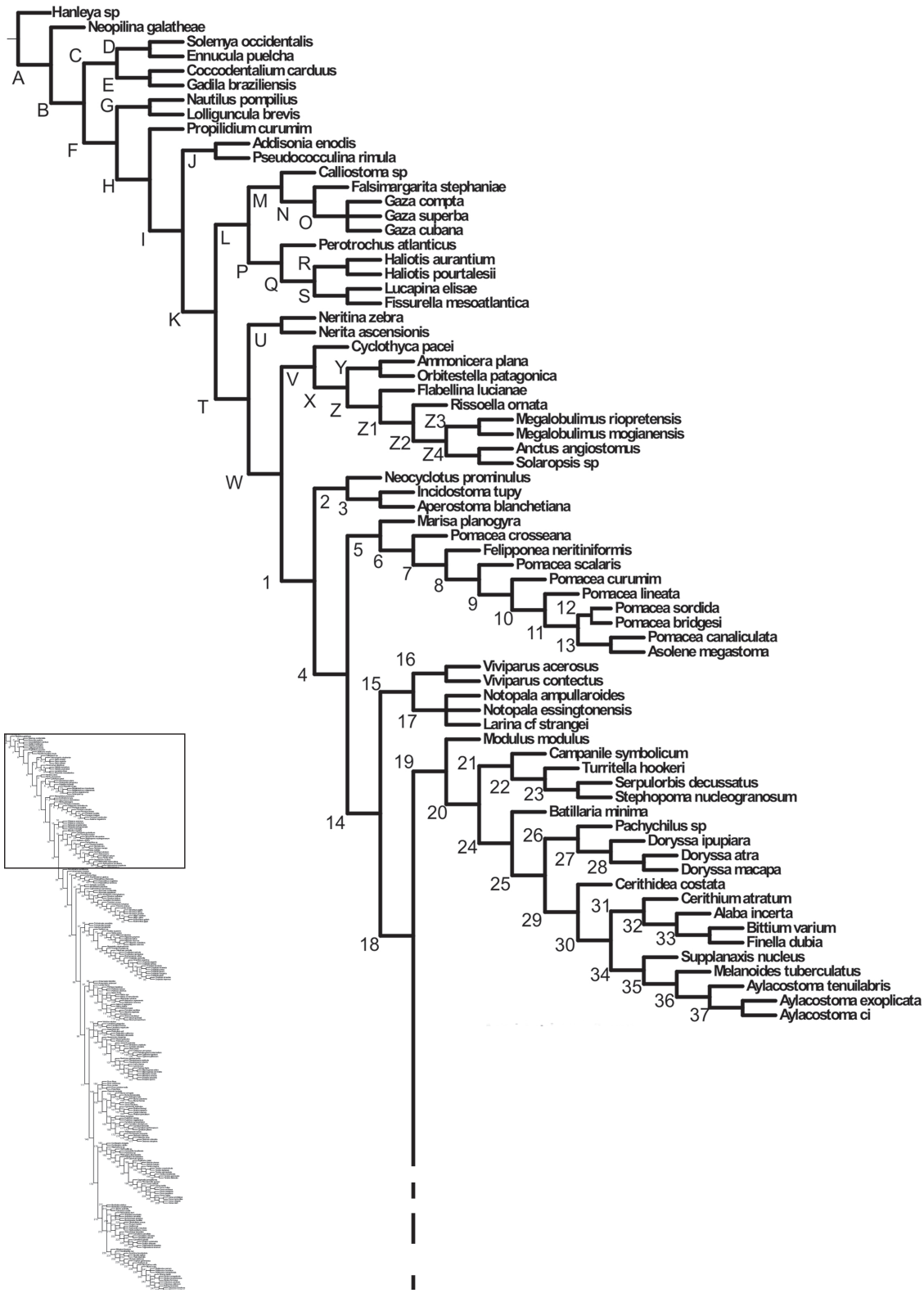

FIGURE 20: Strict consensus of most parsimonious cladograms with successively numbered nodes. Length = 3036; CI = 51; RI = 94. The cladogram shows the relationship of Caenogastropoda (node 1), its internal nodes and considered outgroups.

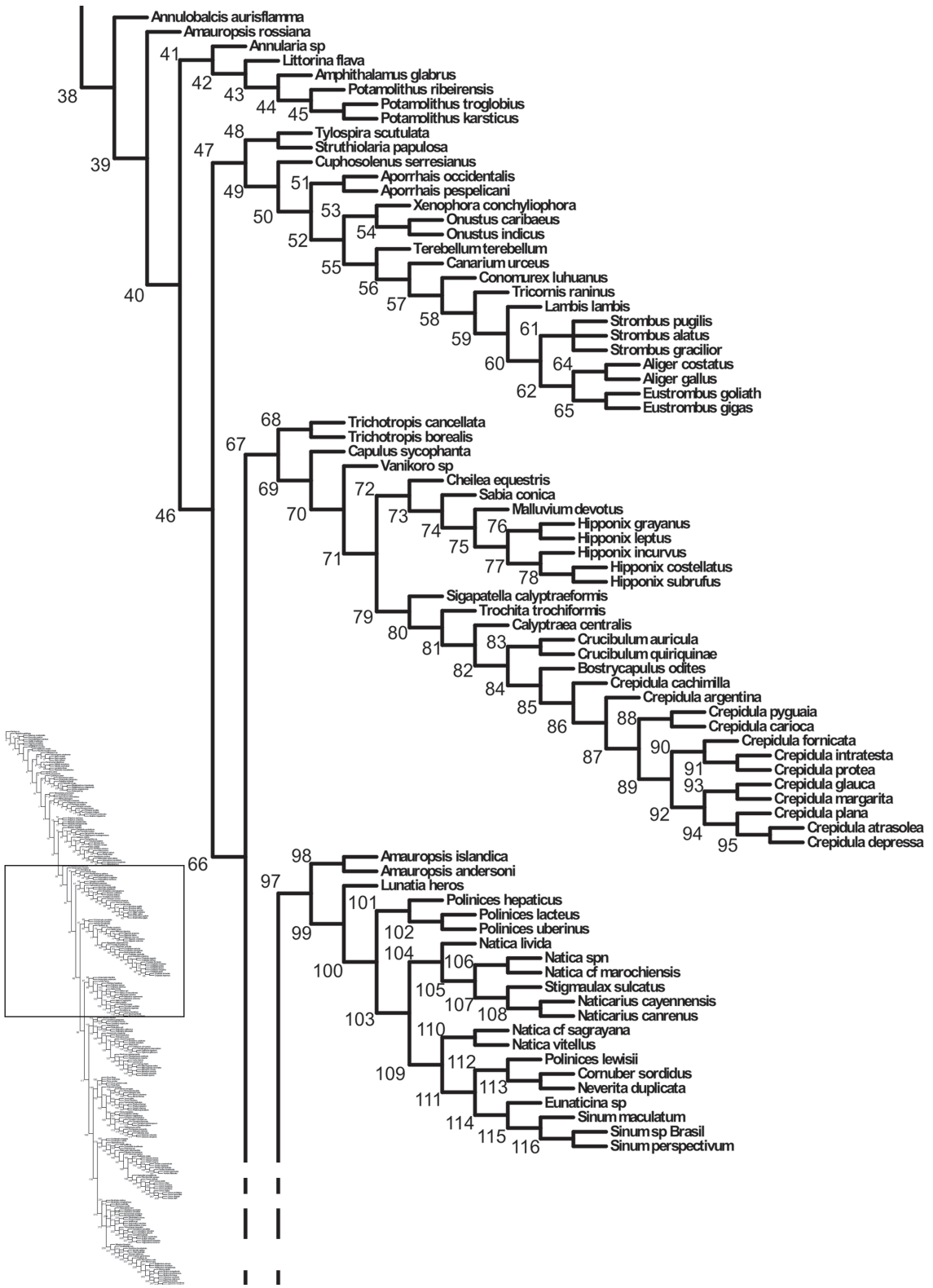

FIGURE 20 - CONTINUED: Strict consensus of most parsimonious cladograms with successively numbered nodes. Length = 3036; CI = 51; RI = 94. The cladogram shows the relationship of Caenogastropoda (node 1), its internal nodes and considered outgroups.

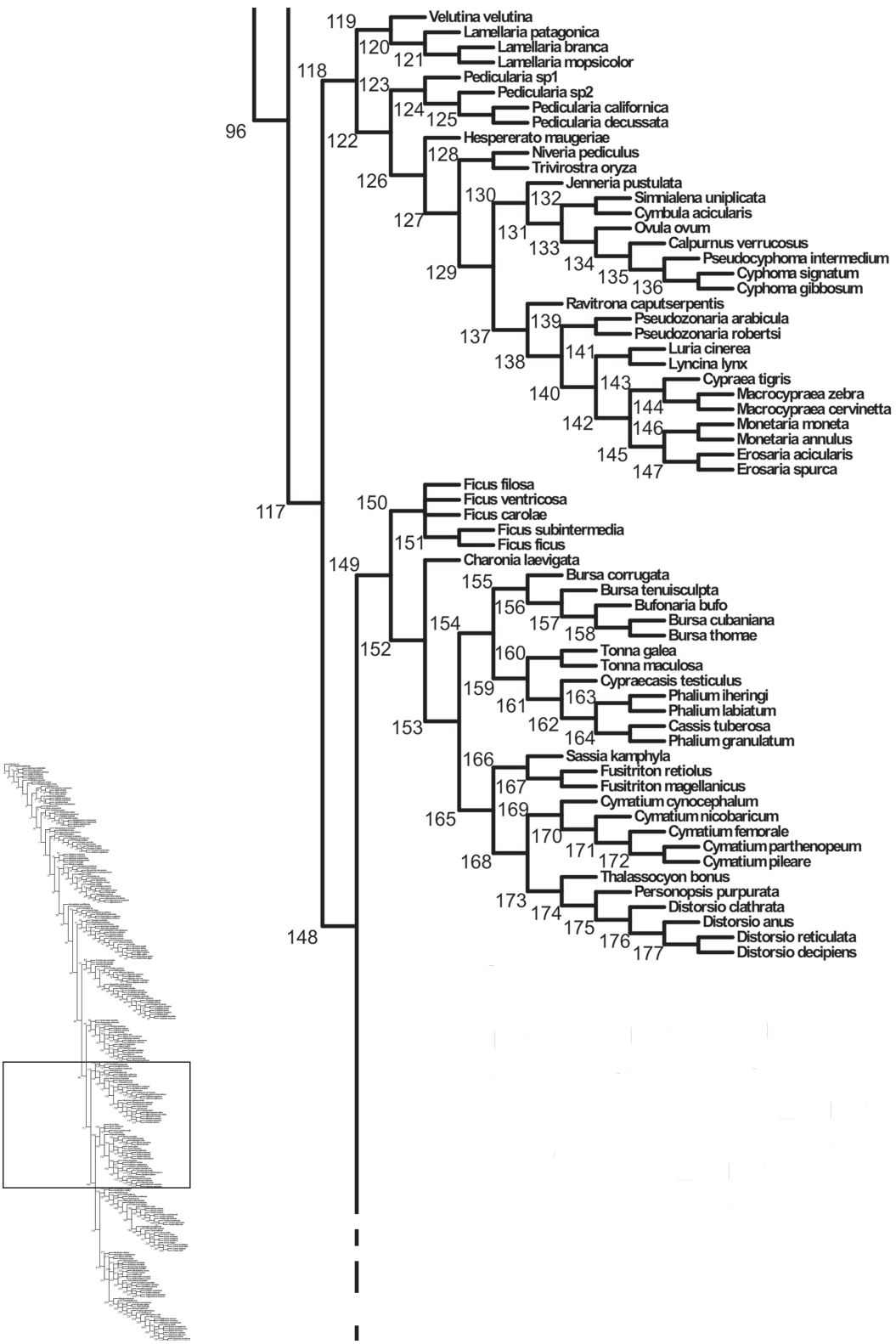

FIGURE 20 - CONTINUED: Strict consensus of most parsimonious cladograms with successively numbered nodes. Length = 3036; CI = 51; RI = 94. The cladogram shows the relationship of Caenogastropoda (node 1), its internal nodes and considered outgroups.

FIGURE 20 - CONTINUED: Strict consensus of most parsimonious cladograms with successively numbered nodes. Length = 3036; CI = 51; RI = 94. The cladogram shows the relationship of Caenogastropoda (node 1), its internal nodes and considered outgroups. This cladogram is based on some character with ordered optimization (see text for details). If all characters were analyzed under an unordered optimization the node 235 collapses.

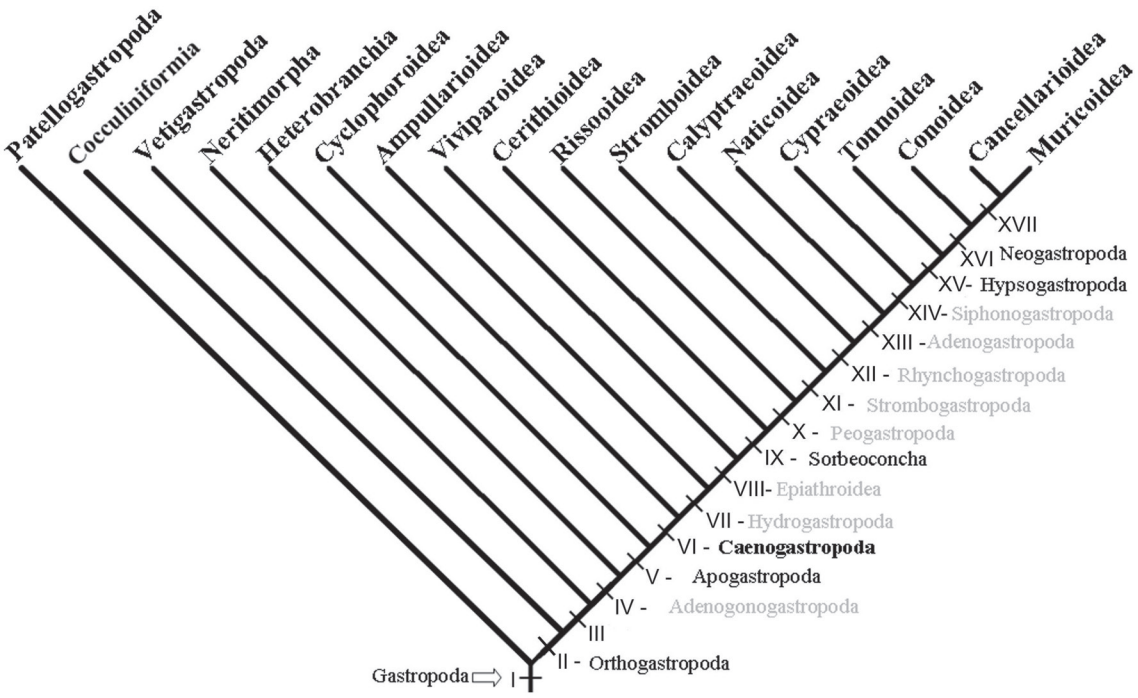

FIGURE 21: Schematic cladogram representing only the superfamilies of Caenogastropoda and other main branches, with named and numbered nodes (Roman numerals). Black names are already available in literature; grey names are introduced herein.

for example, for the massive glands connected to the oral tube of some Ovulidae (node 131 – Cypraeoidea) (Simone, 2004b, *e.g.,* fig. 326), the preceding branches represent species totally lacking any kind of glands in that body region.

Another remarkable example of homoplasy is the modifications of the pallial structures in filter-feeding organisms. The filter habit appeared, most probably independently, in Turritellidae (Cerithioidea after node 22) (Simone, 2001a), Struthiolariidae (node 48 – Stromboidea) (Simone, 2005a), Calyptraeidae (node 79 – Calyptraeoidea) (Simone, 2002), and Viviparoidea (node 15) (Simone, 2004a). Beyond the obvious increasing gill filaments, in all cases there is the appearance of an **endostyle** (characters 213, 214; Ponder *et al.,* 2008, character 47). This structure is a glandular fold that runs along the gill. Also there is the acquisition of a food groove that runs at the floor of the pallial cavity, along the region where the gill filaments tip touches it, and finishes in, or close to the mouth. The similarity of these modifications in apparently not closely related organisms is extraordinary, and is a picture of the immense difficulty in making comparative studies in mollusks. Such plasticity ensures that it is necessary to take extra care in analyzing data from other papers, and in electing single representatives in higher taxa (see below). Although applied in this study at several points, the data found in the literature, as explained below, was mostly excluded from the list of characters. The greatest reason, however, is the lack of data in representatives of all superfamilies. Notwithstanding, it is a quite possible that the utilization is only a question of time.

Extra characters, not utilized directly in the present study

In this paper, a total of 676 characters were searched, with 2291 states, being 1915 apomorphic states. Even though, an enormous quantity of extra characters was not possible to be utilized. The main reason is that they resulted autapomorphic, possessing overlapping states, or doubtfully scored states. In some considered characters, strange results happened, as some complex structure resulted convergences between several taxa; however, based on the complexity, similar organization and topology, the more logic possibility is that they appeared only once, and reduced several times along the related branches. An example is the presence of cement gland found in the Tonnoidea and in the Neogastropoda (node 148), commented above.

Studies of the ontogeny on the caenogastropod larva revealed that some groups possess a **larval mouth** and **larval esophagus,** which are reverted

and substituted by the normal mouth and esophagus after metamorphosis. The larval mouth and larval esophagus are derived conditions, already detected in the Naticoidea and Muricoidea and are absent in the Littorinidae (Rissooidea) (Page & Pedersen, 1998; Page, 2000). These structures may be other synapomorphies aiding the support of some branch between **nodes 46** to **96.** Another larval attribute is the presence of an **apical ganglion,** or apical cephalic sensitive organ. The structure appears to be one of the synapomorphies uniting the Heterobranchia and Caenogastropoda, *i.e.,* **node W** (Page & Parries, 2000), despite in being convergent with some polyplacophorans (Friedrich *et al.,* 2002). Moreover, it was detected that the caenogastropods (only taxa situated after node 40 herein have been examined) have, as a distinctive character, a different kind of sensory cell (modified ciliary axionems in ampulla cells) (Page & Parries, 2000). Such a character, certainly, may help the support of a basal node within Caenogastropoda.

Osphradium ultrastructural details also have shown potential for elucidation in comparative analyses, some of them were commented on in the discussion on osphradium (above). The osphradium characters of the Mollusca in general have been explored in several of Haszprunar's papers in the 1980's, being of particular interest that of 1985b, which focused the prosobranchs. According to that author, there are 3 kinds of different ultrastructural arrangements for the osphradium in the present ingroup: 1) of the Architaenioglossa, in particular Viviparidae and Ampullariidae; 2) of the Campanilidae; and 3) of the remaining caenogastropods. Because of the result of the present study, the type of osphradium here numbered as 3, which possess different kinds of cells interchangeable that Haszprunar designated *Si1, Si2* and *Si3,* can be another synapomorphy supporting **node 18.** Since the ultrastructurally peculiar osphradium of *Campanile* (here type 2) does not link it to other groups, it is possible to deduce that it is autapomorphic, resulted from modifications of the type 3. The type 1 is exclusive to the viviparids and ampullariids; although in both there are some differences, Haszprunar (1985a) erected a proper category to them. There is no knowledge on the osphradium ultrastructure of the Cyclophoroidea. Despite this, it is possible to infer that the type of osphradium here numbered 1 may be the basic pattern for the other 2 types. Probably, this character may be another synapomorphy helping in the support of the **node 4,** and, if confirmed in the cyclophoroideans, even of the node 1. Ponder & Lindberg (1997) explored another character of the osphradium, supported by the study of Haszprunar (1985b); related to the **satellite ciliated fields** of the osphradium. This feature appears to occur in all caenogastropods, in the form of dots or striae, and may be another synapomorphy supporting the **node 1** (although it should be confirmed in Cyclophoroidea).

Another valuable source of data for comparative studies has been the study of the sperm ultrastructure. Those studies have been developed by Healy (*e.g.,* 1988, 1996; Ponder *et al.,* 2008, figs. 13.11, 13.12). The data discovered by Healy gave rise to 17 sperm characters in Ponder & Lindberg (1997), some of which can be applied herein. Several of these characters help in the organization of outgroups of the present study. Those of main interest within Caenogastropoda are the following: (1) the presence of the **accessory membrane of the acrosome,** helps the support of **node 40;** (2) the presence of **mitochondrial cristae,** disposed in parallel plates, aids the support of the **node 1;** however, there is a reversion to a non-modified condition in node 40; (3) the **association** between the annulus (an annular, dense structure of the plasmatic membrane) and the nine satellite fibers disposed radially, it is apomorphically **absent** in the Caenogastropoda and Heterobranchia, and is another synapomorphy basing **node W;** (4) the presence of **parasperm** is another synapomorphy of the caenogastropods **(node 1),** although it is convergently present in some archaeogastropods (*e.g.,* some Vetigastropoda and Neritimorpha) (Ponder & Lindberg, 1997); (5) a special type of parasperm, of **vermiform** appearance, which appears to be present in the taxa allocated after **node 148.**

Ponder & Lindberg (1997) utilized also some ultrastructural characters of the kidney, mainly based on the synopsis of Andrews (1988). According to those studies, there are 2 characteristic types of histology in the present ingroup: (1) That of the ampullariids (node 5), possessing specialized epicardiac cells (instead of porocites), spread across the inner surface of the auricle, with extra-cellular channels in the form of slits; (2) That of the taxa allocated after **node 18,** in which porocites are restrict to special filter places, in the form of closed chambers. Despite the importance of these characters, those studies did not examine representatives of all caenogastropod superfamilies, mainly the basal ones, precluding the direct inclusion in this study.

Another character brought to bear by Ponder & Lindberg (1997: 162-164), which among the taxa obtained the same pattern described above for the kidney, is the enervation of some pallial organs. Ampullariidae, differing from the archaeogastropods, in which pallial structures are enervated by the gill ganglion,

characteristically present a gill enervated by the supraesophageal ganglion, and the osphradium by the left pleural ganglion. In the taxa here represented after **node 18,** the characteristic pattern is one or more nerves originated from the supraesophageal ganglion, enervating both gill and osphradium. The reason for discarding this character herein is also the same as for the above-mentioned kidney characters, *i.e.,* lack of data in the representatives of all superfamilies.

Other possible source of comparative data is the larvae characters. Unfortunately, the available data for the considered taxa are scanty, and mainly extracted from the pertinent literature. Textbooks (*e.g.,* Fretter & Graham, 1962; Barnes, 1984) relate 2 types of mollusk larvae, trochophoroid (or trochophore) and veliger. Veliger is considered derived, and absent in the basal taxa of each class. The complex conformation of the veliger larva is reasonably similar in the classes that possess it, *i.e.,* Gastropoda and Bivalvia. This fact promotes skepticism for independent origin (convergence) among both; however, this conclusion is yielded from the absence of veliger larva in their basal taxa. Besides, an additional complication is the fact that larval stages become embryological stages in the taxa with direct development. Among the gastropods, the **veliger** larva appears to have arisen in **node T.** However, a veliger-like stage (lacking a developed velum), has been described for *Haliotis tuberculatus* (Vetigastropoda) (Crofts, 1937; Fretter & Graham, 1962). Some authors, *e.g.,* Bandel (1988), Bandel *et al.* (1997), Riedel (2000), have also called attention to the importance of the larval characters in comparative analyses. An important character considered by them is the conformation of the embryologic shell (protoconch), which reveals the type of development (character 32). If the protoconch is paucispiral, the development is direct; if multispiral, the development is indirect (planktonic) (*e.g.,* Marcus & Marcus, 1964c; Leal, 1991). However, both kinds can occur in a same genus (*e.g.,* node 192 – *Terebra,* Conoidea) (Simone, 1999a, 2000), and even in a same species [poecilogony, *e.g.,* Ellingson & Krug, 2006; Krug, 2007; but see Hoagland & Robertson, 1988; Bouchet, 1989]. Ponder & Lindberg (1997) considered only 2 larval characters in their dataset, and both support Caenogastropoda **(node 1),** although there are still doubts about the basal taxa. They are (1) the presence of absorptive cells, associate to the protonephridium; and (2) the presence of polar lobes in the cleavage. Additionally, multispiral, orthostrophic larval shells have been considered characteristic for planktotrophic larvae, and are only present in Caenogastropoda (Ponder *et al.,* 2008: 344).

Analysis of the obtained cladogram and the taxonomy

The list of characters is in the Appendix 1. All taxa mentioned in this section are formally described in Appendix 4. The mentioned nodes in Arabic numerals are present in Fig. 20, while those in Roman numerals in Fig. 21. The list of synapomorphies of each node of the cladogram represented are shown in Fig. 20 is found in Appendix 3. Some comments on the obtained relationships of outgroups are present at the end of this section.

The arrangement of outgroups agrees with that obtained by Ponder & Lindberg (1996, 1997) and Ponder *et al.* (2008, fig. 13.16). On the other hand, it has some differences from the arrangement proposed by Haszprunar (1988a, b), by the inclusion of the Achitaenioglossa in the Caenogastropoda, and by the more basal situation of the Vetigastropoda. It differs, also, from the disposition of the taxa proposed by Sasaki (1998), by the paraphyly of his Rhipidoglossa (comprising Cocculinimorpha, Vetigastropoda and Neritimorpha). According to Sasaki (1998), Rhipidoglossa is redefined as monophyletic, and as sister group of the Apogastropoda (Heterobranchia + Caenogastropoda). The cladogram presented here is fairly similar to the final result of Strong (2003). The main differences are paraphyly of the architaenioglossans (which were monophyletic in that paper), and the paraphyly of the basal sorbeoconchs (in that paper, there is a branch uniting the sampled batillariid, vemetid, strombid, calyptraeid and bithyniid). The conid was more closely related to the muricoideans than the cancellarioidean in Strong's tree, an inverted position in relation to this study. There is considerable concordance with the cladogram presented by Ponder *et al.* (2008, fig. 13.16). The main differences are the junction of the cyclophorid and the ampullariid, taxa that resulted in paraphyletic arrangement here; the separation of the littorinid from the remaining higher caenogastropods, a taxon that as grouped with the rissooideans in the current analysis; the junction of the vermetid in a branch uniting xenophorid and strombid, while in the current analysis the vermetid is resolved as a basal cerithioidean; and the capulid and the ficid, taxa which respectively grouped with calyptraeoideans and tonnoideans while in the Ponder *et al.* (2008) analysis they were both isolated from those groups.

The Heterobranchia and the Caenogastropoda are sister taxa and this is in agreement with most of the results from recent in the literature (*e.g.,* Haszprunar, 1985a, 1988a, b); Ponder & Lindberg, 1997; Kaim,

2004). While the analysis of the relationship between the Caenogastropoda and the Heterobranchia is not the main goal of this study, it can be observed that both taxa share 20 synapomorphies **(node W).** Salvini-Plawén & Haszprunar (1987) and Ponder & Lindberg (1997) have named this taxon **Apogastropoda.**

The taxon Caenogastropoda (= Pectinibranchia) possesses a set of 70 synapomorphies that support it **(node 1)** (Appendix 3). Additionally, other possible synapomorphies, directly linked to the morphology or not, were pointed out in the preceding section (6.1).

From the synapomorphies that support the **node 1,** the more interesting are a pedal gland immersed in pedal musculature in a furrow restrict to anterior the margin (characters 109, 117, 122); an ommatophore attached to the cephalic tentacles (133); the diaphragm-like septal muscle in the posterior region of the haemocoel (143); the thick head muscles immersed in the integument (144); the ridge-like, long osphradial ganglion (177), running parallel to the gill (197); the single hypobranchial gland, which is thin and mucosa-like (225); the bilobed renal tissue (266), with the intestine passing through it (271); the nephrostome isolated in the central region of the membrane between the renal and pallial cavities, free from renal tissue (284); the broad pair of dorsal folds of the buccal mass (310); the jaw and peribuccal muscles organized in two bundles (328); diminishment of the ventral pair of radular tensor muscles (350); the pair of secondary ventral tensor muscles (m5) attached to the odontophoral cartilages (356); the thick horizontal muscle uniting outer surface of the cartilages (361); the pair m7 (368); the pair of buccal protractor muscles ventral positioned (m10) (378); the wide expansions of the subradular cartilage in the buccal cavity (407); the taenioglossan type of radula, *i.e.,* seven teeth per row (410, 430); the esophagus originating posteriorly to the buccal mass (462); visceral structures, *e.g.,* intestinal loops, not located into haemocoel (520); the fecal pellets (527); the pallial prostate (543); genital ducts running only in pallial roof (601); a short vaginal tube (617); the nerve ring positioned at the middle level of the buccal mass (653); and the buccal ganglia positioned far from the nerve ring (659).

The three first main branches of the cladogram are, to date, mostly considered a single taxon: Architaenioglossa. However, this taxon is represented by a paraphyletic arrangement, as also shown in a previous analysis (Simone, 2004a).

The first main branch, the Cyclophoroidea **(node 2),** encompasses land taxa, while the following two main branches, respectively Ampullarioidea **(node 5)** and Viviparoidea **(node 15),** encompass freshwater taxa. After these branches, *i.e.,* after node 18, the taxa are practically all marine. Secondary invasions to freshwater, and even to terrestrial environment, were detected in the Cerithioidea (nodes 26, 35) (Simone, 2001a), Rissooidea (node 44 and other taxa) (Simone, 2006b) and Muricoidea (2 branches, one of them *Nassodonta* – after node 215). Analyzing those data alone, the most parsimonious conclusion is that the caenogastropod **node 18** evolved from a non-marine ancestor. Inasmuch as node 18 is preceded by exclusively non-marine branches. Notwithstanding, an alternative evolutionary scenario is more likely. It is probable that the three first caenogastropod branches were survivors of ancient taxa that also had marine representatives, which are now extinct. The three surviving branches are those in more unusual environments, and, maybe, with less competition. On the other hand, Moore (1964) advocated the idea that the Meso- and the Neogastropoda had risen from a freshwater group, and returned to the sea secondarily. He did not reveal the reason for such an affirmation, but, apparently, this is based on an analysis of the ampullarioideans.

The affinity of the architaenioglossans to the Caenogastropoda is very strong and clear, which is in agreement with Ponder & Warrén's (1988) and Ponder & Lindberg's (1997) point of view.

Node 2 represents the superfamily Cyclophoroidea, supported by 26 synapomorphies, mainly related to adaptations to terrestrial environment, with further modifications in the pallial cavity, kidney, etc. Additional comments and analysis of this superfamily can be found in Simone (2004a).

Node 4 encompasses all Caenogastropoda except Cyclophoroidea. It is supported by 12 synapomorphies (Appendix 3). The main characters are the head-foot siphons (character 78); the odontophore pair m12 (388); the pair of esophageal pouches (464); the relation between albumen and capsule glands (642, 643), and the nerve ring positioned in middle level of odontophore (650, 652). In allusion to the predominant aquatic environment, the name **Hydrogastropoda** is suggested for this taxon (Fig. 21: node VII).

Node 5 represents the superfamily Ampullarioidea, supported by not less than 51 synapomorphies, some of them related to the development of additional lung by side of gill, and increase of complexity of the osphradium and reproductive system. More details in Simone (2004a).

Node 14 encompasses all Caenogastropoda except Cyclophoroidea and Ampullarioidea, and is supported by 19 synapomorphies (Appendix 3). It is interesting to observe that the Viviparoidea, the first branch of the subsequent taxon, is considered as part of the Ampullarioidea by some authors (*e.g.,* Haszprunar, 1985a, 1988a, b). The morphological similarity between ampullarioideans and viviparoideans come from the operculum (character 53 and others) and from the conformation of the head-foot nuchal siphons (characters 77, 78). These states are considered homologous herein; however, both taxa resulted separated. From the synapomorphies of node 14, the most remarkable is the epiathroid condition of the nerve ring (651, 654), and its situation posterior to buccal mass (653). Because of these features, the name **Epiathroidea** is erected for designating the taxon (Fig. 21: node VIII). In addition, there are other remarkable characters, the appearance of the pair m2 (retractor of the buccal mass) (334), the simplification of the pair m4 (345, 346), the prostate (559), and the lateral positioned buccal ganglia (659).

The Architaenioglossa has, then, resulted paraphyletic (three first main branches of Caenogastropoda). The paraphyly of this taxon has been proposed before (Simone, 2004a), corroborating with other studies (*e.g.,* Harasewych *et al.,* 1998; Colgan *et al.,* 2000, 2003, 2007; Strong, 2003; Ponder *et al.,* 2008).

The **node 15** represents the Viviparoidea, supported by 25 synapomorphies, some of them related to the filter feeding gill, and to the peculiar and complex reproductive system, possessing viviparity and copulation via right tentacle. All these and other features are discussed elsewhere (Simone, 2004a).

Node 18 comprises the predominantly marine groups, named **Sorbeoconcha** by Ponder & Lindberg (1997: 225-226) (Fig. 21: node IX). The node is supported by 17 synapomorphies, from which the more remarkable are the relation between tentacles and eyes (characters 128, 131); the pericardium positioned posteriorly to kidney (241); the appearance of a convolute male seminal vesicle (550); and the approach of the connectives between the pedal and remaining two pairs of ganglia of the nerve ring (649). The presence of a pair of aortic muscles appears to be another synapomorphy of this branch (Golding *et al.,* 2009b). Further comments on this taxon are found in Ponder *et al.* (2008: 340). Another name for this branch could be Neotaenioglossa (Haszprunar, 1988a; Ponder & Warén, 1988); however, the definition of that taxon excludes the Neogastropoda (Colgan *et al.,* 2007).

The **node 19** represents the superfamily Cerithioidea, which also included the representatives of the "Vermetoidea" (node 23) and "Campaniloidea" (after node 21). The node is supported by 33 synapomorphies, all them discussed in detail by Simone (2001a). In that paper, special attention was paid to the allocation of the Campanilidae. The taxon, which has a rich fossil record but has a single living representative (*Campanile symbolicum* from Australia), which has occupied several different places in gastropod phylogeny. It was considered non-caenogastropod by Haszprunar, 1988a (as sister group of Heterobranchia), but otherwise was considered caenogastropod, liked or not with cerithioideans (Healy, 1986; Harasewych *et al.,* 1998; Colgan *et al.,* 2000, 2003, 2007; McArthur & Harasewych, 2003). However, the taxonomical and phylogenetic positions of the Campanilidae have been more extensively discussed by Simone (2001a), who placed it in the second branch of Cerithioidea (after node 21; connected to Turritellidae and Vermetidae). The cerithioidean affinities of *Campanile* have been advocated in other studies (*e.g.,* Houbrick, 1981, 1989; Healy, 1996), but more recent studies (mentioned above) have included it in a separate superfamily.

Node 38, the ptenoglossans were not studied in detail as stated above. The single representative included herein is the eulimid *Annulobalcis aurisflamma.* It resulted in an isolated branch allocated after the cerithioideans, supported by 19 synapomorphies; from which the more important are odontophore pair free from radular sac (character 336); the loss of odontophore pair m12 (388); the diminishment of radular lateral teeth cusps (423); the loss of esophageal pouches (464); the exophalic penis (562-577); and the statolith in statocyst (657). This allocation of the Ptenoglossa has been suggested in the literature (*e.g.,* Kosuge, 1966; Kaim, 2004). The taxon is also known as Ctenoglossa, and may represent an artificial assembly of basal caenogastropods (Ponder *et al.,* 2008: 341) with coincident elongated and uniserial radula. Moreover, the name Ctenoglossa had also been used for cephalopods (*e.g.,* Robson, 1932). More details of the taxon in Haszprunar (1988a). (Fig. 21: node X). This taxon corresponds to the **Hypsogastropoda** Ponder & Lindberg (1997: 226).

Node 39. This node, supported by 14 synapomorphies, is the result of the inclusion of a supposed naticoidean, a sample identified *"Amauropsis" rossiana.* The study of the glacial material revealed that *A. rossiana* can not be allocated in Naticidae, in such the genus *Amauropsis* belongs, because of several features, in which the main is the absence of an accessory boring organ (ABO), and even of a proboscis. On the other hand, the shell and operculum absolutely fits in

the naticid definition, being, according to the present result, remarkable convergences. As the type species of *Amauropsis* is *A. islandica* (after node 98), the different allocation of *"A." rossiana* indicates that the latter species belongs to another genus. A full description and the formal taxonomic treatment of these taxa are under preparation. From the nodes that support this node, the more important are the pericardium more widely exposed in the pallial cavity (character 240); the appearance of two lobes in the kidney (268); the nephridial gland (285); the odontophore pair m14 (391); and the presence of a terminal female genital papilla (621).

Node 40 incorporates the predominantly marine taxa except Cerithioidea and the eulimid, being supported by 9 synapomorphies. From the synapomorphies the more important are the excentric nucleus of the operculum (character 56); and modifications of the style sac (503-507).

Node 41 represents Rissooidea, which also includes the representatives of the Littorinoidea (two first branches). The node is supported by 16 synapomorphies. The superfamily Rissooidea, as commented above, is still at an incipient level of phylogenetic knowledge (Ponder, 1988), and it can may represent a non-monophyletic taxon (Ponder *et al.* 2008). However, even if the risooidean taxa encompass more than one branch, they most probably occupy a position close to that suggested in the cladogram (node 41). Monophyly is advocated by Simone (2006b), but, as stated above, it is based on very limited taxon sampling.

Node 46 is supported by 13 synapomorphies, and includes the Stromboidea (node 47) and remaining "higher" caenogastropods. From the synapomorphies, the notable ones include the elliptical form of the operculum, with its nucleus closer to the inferior (anterior) end (characters 55, 57), the retractor muscle of the snout (98); the elongation of mantle border (175); the connection of auricle with the inner surface of pericardium (247); the further modification in the odontophore pair m7 (373); and the hook-shaped marginal teeth of the radula (432). As the first branch of the node is the Stromboidea, this still unnamed taxon can be called **Strombogastropoda** (Fig. 21: node XI).

Node 47 represents the superfamily Stromboidea, which also encompassed the representatives of the Xenophoroidea (node 53). The node is supported by 47 synapomorphies. Comments and discussion on this taxon are found in Simone (2005a).

Node 66 encompasses the remainder of the "higher" caenogastropods, being supported by 19 synapomorphies. Those more noteworthy are the pleurembolic proboscis (93, 98-100, 300); and the elliptical osphradium, of bipectinate type (179, 182). There are in the literature 2 names that could be attributed to this node, one of them is Neomesogastropoda Bandel (1991), however, for becoming a monophyletic taxon, it must encompass the Neogastropoda. Such inclusion disagrees with the original sense of the name, created just for opposing to the Neogastropoda, and this sense has been applied even in subsequent papers (*e.g.,* Riedel, 2000). The other name is Pleurembolica Riedel (2000); however, the author introduced the name excluding the Naticoidea and Cypraeoidea. They must be included in the sense of present work. The name Pleurembolica would be very adequate, since mentions the more outstanding character of the taxon, the presence of a pleurembolic proboscis. Due to the lack of available names, the **Rhynchogastropoda** is here proposed, referring to the presence of the proboscis (Fig. 21: node XII).

Node 67 represents the Calyptraeoidea, which resulted also encompassing Capuloidea (after node 69) and Hipponicoidea (node 72). A total of 21 synapomorphies support this node, in such discussion and taxonomical implications can be reached in Simone (2002).

Node 96, which comprises the main terminal branches including Naticoidea, is supported by 20 synapomorphies. Those more interesting are the connection of the pair m2 to the radular sac (character 336); the single gland in the ventral side of the esophagus (463, 469), with transverse septa (477); the secondary loss of the stomach style sac (503); the reduction of the stomach size and complexity (515); and the situation of the bursa copulatrix in the anterior region of the pallial oviduct (625). The simplification of the stomach and the modification of the foregut, probably, allow a tendency to the predatory behavior, so common in the grouped taxa. Respect to the esophageal gland, the taxon can be called **Adenogastropoda** (Fig. 21: node XIII).

Node 117 includes the Cypraeoidea and remaining 4 main taxa. It is supported by 16 synapomorphies, being the remarkable the fusiform shell (character 1) determinate growth of the shell (33); siphonal canal conspicuous (34) (being both convergent to other taxa, *e.g.,* Cerithioidea and Stromboidea); the further elongation of the pleurembolic proboscis (99); the development of a pallial siphon (166); the left position of visceral mass (232); the insertion of the retractor muscle of proboscis in its median region (302); and the additional simplification of the stomach (493, 511). Another feature that supports

this node is the presence of ventrolateral retractor muscles in the proboscis (Golding *et al.,* 2009b). This is another taxon that could be called as Pleurembolica; however, it must include the Calyptraeoidea for fitting in the original sense of Riedel (2000). Due to the appearance of the incurrent siphon, the taxon can be named as **Siphonogastropoda** (Fig. 21: node XIV).

Node 118 represents the superfamily Cypraeoidea, which also includes Lamellarioidea (node 119). It is supported by 41 synapomorphies deeply discussed, including a taxonomical treatment, by Simone (2004b).

Node 148 is supported by 18 synapomorphies, and encompasses Tonnoidea and Neogastropoda (Fig. 21: node XV). From the synapomorphies, those more eminent are the terminal localization of the opercular nucleus (53) (which converged with other branches, *e.g.,* Cerithioidea and Stromboidea); the growth of the incurrent siphon, becoming an exploratory structure (176); the ctenidial muscle (209); the further enlargement of the proboscis (319); the radular lateral teeth with sharp pointed tip (423); the anterior positioned bursa copulatrix (612); and the nerve ring encased in a chamber of ventral base of proboscis (672). This branch, in general, comprises voracious predators. The close relationship between Tonnoidea and Neogastropoda has been proposed before (*e.g.,* Amaudrut, 1898; Graham, 1941; Haszprunar, 1985b; Healy, 1988, 1996; Riedel, 1994, 1995, 2000, with the name Vermivora), in such further comments are provided by Ponder *et al.* (2008: 340). However, Kantor (2002: 170) rejected the close relationship between both taxa, exploring some differences between the proboscises. On the other hand, based on the arguments discussed above on proboscis, a common evolution of the structure of both groups is here advocated. Additional evidence from the histology of the anterior esophagus also shows a close relationship between tonnoideans and the neogastropods (Golding & Ponder, 2010: 90); as well as the presence of helical muscle layers in the proboscis (Golding *et al.,* 2009b). Because of the elongation of the proboscis, an appropriate name for the taxon is **Peogastropoda** (*peo* = elongation like a penis).

Another sister branch to neogastropods has been proposed by Strong (2003), Epitoniidae-Cypraeidae-Naticidae; however, no tonnoidean was included in that study.

Node 149 represents the superfamily Tonnoidea, which also bears the Ficoidea (node 150, plus *Thanassocyon* after node 173). It is supported by 41 synapomorphies, being the more important the decreasing operculum (character 60); the wide distance between anterior foot edge and head base (85); a series of proboscis retractor muscles (98); the scalloped osphradial filaments (183); hypobranchial gland with reinforcement of pallial septa (224); kidney tissue with successive broad folds converging to a central vessel (265); an intestinal loop in renal cavity containing mesentery (270); serrated pair of jaws (313); odontophore pair of jugal muscles m1a (332); muscles connecting odontophore pair m4 with tissue on radula (m9) (346); the pair m7 originated in inner-dorsal edge of anterior region of pair m4 (371), with pair m11 inserting dorsal to them (387); the hook-like radular outer marginal teeth (436); the large salivary gland separated in two masses (446); and the glandular convolute seminal vesicle (542).

Node 178 is the most traditional of the recognized taxa, the **Neogastropoda** (Fig. 21: node XVI). In the present analysis this node is supported by 28 synapomorphies, being the more interesting the middle positioned eyes on tentacles (character 128); the anal gland (226); the loss of jaws (315); the odontophore pair m2 passing thought the nerve ring (337); ducts of the salivary glands free from the nerve ring (449); and the modification of the esophageal gland to a uniform tissue, connected to the esophagus by a duct (469), *i.e.,* a gland of Leiblein (486); the buccal ganglia positioned closer to nerve ring (659); and concentration of the ganglia of the nerve ring (667). The monophyly of the neogastropods are found in several other studies, such as ontogenetic (Ball, 2002), molecular (Colgan *et al.,* 2007), and morphological (Ponder, 1974; Taylor & Morris, 1988; Ponder & Lindberg, 1996, 1997; Kantor, 1996, 2002; Strong, 2003). However, the monophyly is contested in few others (Sheridan *et al.,* 1973; Shimek & Kohn, 1981; Golikov & Starobogatov, 1988).

Node 179 represents the superfamily Conoidea, also known as Toxoglossa. It is supported by a set of 61 synapomorphies. The more interesting ones are the shell anal canal (character 41); the pointed proboscis tip (95); the small sized nephridial gland (286); the reduction of rhynchodeal wall musculature (292); rhynchostome with well-developed sphincter (297); reduction of the buccal mass (304), with long oral tube (306); buccal mass placed in proboscis base (320); the odontophore pair m4 connected with pair m2 forming a broad posterior muscular platform (352); the loss of pair m7 (371); the reduction of the radular rachidian tooth (415); the radular marginal teeth wishbone shaped in base, and tip sharp pointed (432); the pair of salivary gland as two semi-spherical masses (447); the gland of Leiblein modified in venom gland (469) positioned posterior to nerve ring

(480), with posterior venom muscular bulb (482); the male ejaculatory duct (552); penis with papilla in tip (563), protected by a preputial fold (580); and the female terminal pouch (627). The internal arrangement of the conoideans indicates monophyly of the families Conidae (node 200 – 21 synapomorphies) and Terebridae (node 189 – 13 synapomorphies); however, Turridae in traditional sense (remaining conoid nodes) revealed a total polyphyletic taxon. This possibility, although with some differences in some details, has been pointed out in the pertinent literature (Taylor *et al.,* 1993; Kantor & Taylor, 2000, 2002; Puillandre *et al.,* 2008; Holford *et al.,* 2009).

Node 210 encompasses the neogastropods excluding the Conoidea; this node is supported by 26 synapomorphies. From these, the more interesting are the modification of the odontophore pair mj (329); narrow and long pair m2 running attached to esophagus (335); the growth of odontophore pair of ventral tensors of radula (m11) (350); the modification of subradular cartilage at buccal cavity (407); the stenoglossan radular type (410); the hook-like lateral radular teeth (425); the loss of radular marginal teeth (430); the accessory salivary glands (458); the valve of Leiblein (484); and the supra-esophageal ganglion close to nerve ring (633). The valve of Leiblein, in particular, is a very complex structure and of special importance for the recognition of the clade (Golding & Ponder, 2010). The node 210 is still unnamed, but, as discussed below, it can simply be called Muricoidea (*sensu lato,* of Ponder, 1974) (Fig. 21, node XVII).

Node 211, supported by 16 synapomorphies, node 212, supported by 11 synapomorphies and node 213, supported by 12 synapomorphies, are the basal divisions of Muricoidea, which are deeply discussed in Simone (2007a). Node 212 bears a trichotomy, containing nodes 213 and 214, which represents the Buccinoidea (node 215), Volutoidea (node 219) and Cancellarioidea (node 222); and node 230 can be considered Muricidae in the wider sense.

The superfamily Cancellarioidea (node 222), supported by 47 synapomorphies, was a part of the Muricoidea *(sensu lato)* (node 210), a condition that has also been found in other studies (*e.g.,* Riedel, 2000), suggesting that the status of both groups may need to be reassessed.

The arrangement of the Neogastropoda found in this differs from some others found in the literature. For example, Kantor (1996), had Cancellarioidea as the first branch of Neogastropoda, being the sister group of both Muricoidea and Conoidea. Despite that study not being developed using computerized cladistic methods, Strong (2003, fig. 26), processed the data conventionally and obtained the same arrangement. The reason for this arrangement appears to be because (1) the gland of Leiblein of their examined marginellid and conid were coded as the same state (possessing a terminal bulb) and (2) the lack of the valve of Leiblein in these two taxa. If these two characters are removed, the neogastropod arrangement is the same obtained here (the conids at the base of the other neogastropods). On the other hand, and in favor of the interpretation of the result here exposed, is that some basal taxa in the marginellids possess a not bulged gland of Leiblein (Coovert & Coovert, 1995; *pers. obs.*); and that basal cancellariids bear a gland of Leiblein (*e.g., Tritonoharpa – pers. obs.*).

The nodes A to Z4 are related to the 32 representatives of outgroups, *i.e.,* non-caenogastropod gastropods, and even representatives of other classes. As asserted above, they are not the main goal of this study; subsequently, their characters were not extensively explored, except for a quantity sufficient to organize them. In the same way, the phylogenetic and taxonomical inferences are still provisional. The **node A** represents Conchifera, as *Hanleya* actually is an aculiferan. A single synapomorphy was selected to support the node (character 87 – loss of spicules), but a lot of others can be evoked, such as the development of a single, dorsal, wide shell, and the folded mantle border at the periphery; another is the presence of nacre or mother-of-pearl inner shell layer, which is present since the monoplacophorans (Robertson, 2008; Ponder *et al.,* 2008, character 8). The **node B** represents the remaining Conchifera except the monoplacophorans; it is supported by six synapomorphies, as the reduction of the number of foot retractor muscles of foot (character 29); the deep, postero-dorsal pallial cavity (159); and the gill with a longitudinal vascular axis connected directly to auricle (200, 223). The **node C** represents the Diasoma, linking the representatives of the Scaphopoda **(node D)** and those of the Bivalvia **(node E);** it is supported by seven synapomorphies, as the antero-posterior axis of retractor muscles (character 90) of the digging, embolus-like foot (106), directed anteriorly (121); the pallial cavity surrounding both sides of visceral mass (148); the pair of lateral expansions of mouth for food capture (303); and the hollow fashioned digestive gland acini (535). The taxon Diasoma is deeply studied in Simone (2009). The **node F** represents Cyrtosoma, a taxon that encompasses the Cephalopoda **(node G)** and the Gastropoda **(node H);** it is supported by 14 synapomorphies, as the protruded head with at least a pair of expansions (characters 74, 89); the pallial implantation of the gills (220); the U-shaped organization

of visceral mass (230); the increment of jaws (313) and of salivary glands (445). Further details on the cephalopod evolution and early development can be reached in Shigeno *et al.* (2008).

Node H represents the class Gastropoda. It is supported by 35 synapomorphies. From them, the more interesting are the operculum (characters 54-56); the torsion (88); the snout (93); the pair of pedal glands (117); the pair of cephalic tentacles (125); the columellar muscle (134); the reduction of right pallial structures (158); the enlargement of the osphradium (198); the loss of marginal radular plates (413); gonad single (541); the development of a pair of pleural ganglia (654) and buccal ganglia (658). Further comments on the Gastropoda phylogeny in, *e.g.,* Haszprunar (1988a), Ponder & Lindberg (1996, 1997), Sasaki (1998), and Ponder *et al.* (2008). The **node I** represents the remaining gastropods except the Patellogastropoda, symbolized by *Propilidium.* It is supported by 13 synapomorphies and can be called Orthogastropoda (Fig. 21, node II). From the synapomorphies, the more interesting are the asymmetry of kidneys (character 289); the dorsal chamber in buccal cavity (311); the rhipidoglossan type of radula (410) of flexiglossan condition (412); the loss of radular mineralization (411); and the pair of esophageal pouches (463). The node is divided in a branch representing the Cocculiniformia (**node J,** with 9 synapomorphies) and another representing the remaining gastropods in an unnamed taxon **(node K)** (Fig. 21, node III), supported by 12 synapomorphies. From these, the more remarkable are the globose, spiral shell fashion (characters 1, 2); the operculum in adult forms (57); the eyes (130); the reduction of visceral intestinal loops (239); and the odontophore horizontal muscle lying outside of cartilages (367). Because of the inconstancy of the taxon Cocculiniformia, no taxonomical inferences are provided here. The **node L** represents Vetigastropoda, being supported by 12 synapomorphies. The taxon resulted divided in two branches, each one separating the species possessing double pallial organs (node P) from those bearing single (node M). This possibly is inaccurate, as the node P possibly may be paraphyletic. More detailed studies on vetigastropods are current and this hypothesis will be tested. The presence of bursicles at mantle can be erected as an additional synapomorphy of this taxon (Ponder *et al.,* 2008, character 44).

The **node T** represents a taxon uniting Neritimorpha with Apogastropoda, here named Adenogonogastropoda (Fig. 21, node IV). It is supported by 13 synapomorphies, most related to modifications and development of pallial genital ducts, both, males and females, and the occurrence of a true veliger larva (character 648).

The taxa above, particularly the new named ones, here are formally described in the Appendix 4. Taking into consideration only the main branches, which can be considered in superfamily rank, a summary of the Caenogastropoda relationships can be represented in the Fig. 21.

Paleontology

The inclusion of fossils, for which usually only shell characters are available, aids in the calibration of the age of nodes in a phylogenetic analysis. In this study, however, only 5 to 10% of the characters are based on the shell, and they are mostly highly homoplastic. So, for this reason, fossil taxa were not included. Nevertheless, the minimum age of each branch can be calculated based on the oldest known fossil attributed to a particular taxon inside a given branch (Amorim, 1997). Under this methodology, the following result was obtained (Fig. 22).

The Fig. 22 shows, schematically, an attempt to correlate some nodes (Fig. 21) to geologic time. This correlation must be interpreted as **minimum age** only, obtained by searching the paleontologic catalogues (*e.g.,* Wenz, 1938, Tracey *et al.,* 1993; Simone & Mezzalira, 1994; Gründel, 1999; Bandel, 2002), the older members attributed to each superfamily. However, there are some discrepancies, as, *e.g.,* the Ampullarioidea, which is allocated between the Cyclophoroidea and the Viviparoidea, taxa already recognizable in the Carboniferous. Though, the oldest known ampullarioidean has Eocene age. Other remarkable discrepancy is the Stromboidea, the oldest fossil is from Jurassic, however, its sister taxon (node 66) has representatives in the Permian. The taxa allocated after the node 148, the Hypsogastropoda, were already widespread in the Cretaceous (Kollmann, 1982; Taylor & Morris, 1988; Tracey *et al.,* 1993; Bandel, 1993).

Distortions are expected in data based on fossil records; however, they may not be an impediment for analyzing them. It is possible to observe that Caenogastropoda is an ancient taxon, arisen at middle Paleozoic, perhaps in the Devonian. Most main branches were already present in the Cretaceous. Such antiquity, in part, shows the irradiative success of the taxon, as well as the enormous range of variation of somatic attributes found during the present study.

The estimation on the age of some caenogastropod branches referred above was also obtained by other authors, such as, *e.g.,* Fretter & Graham

(1962: 617) and Moore (1964). Additionally, further comments and data on paleontology can be reached in Ponder *et al.* (2008: 341-342, 344, 355-359; and references therein). The early appearance of most caenogastropod branches has been one of the factors for the difficulty in resolving their inter-relationships (Colgan *et al.,* 2007: 735). Furthermore, there are several erected taxa in superior levels than families that are totally extinct (*e.g.,* Bandel, 1991, 1993), which are not included in the present analysis. Conversely, a deeper analysis of the main branches of the Caenogastropoda and other molluscan taxa is found in Ponder & Lindberg (2008).

Comparison with molecular studies

Phylogenetic studies of gastropods based on molecular data (*e.g.,* cladograms by Tillier *et al.,* 1992; Rosenberg *et al.,* 1994, 1997; Harasewych *et al.,* 1997, 1998; Colgan *et al.,* 2000, 2003, 2007; Oliverio & Mariottini, 2001; Oliverio *et al.,* 2002; Lydeard *et al.,* 2002; Collin, 2003; McArthur & Harasewych, 2003) have yielded, in some instances, phylograms that show considerable discordance with trees based on morphology, including the present one. The causes of those incongruences have been debated in the literature (*e.g.,* Wheeler, 1991, 1995; Bang *et al.,* 2000; Giribet *et al.,* 2002; Janies & Wheeler, 2002; Carvalho & Ebach, 2009; Boero, 2010). An example are the partial trees shown by Riedel (2000), obtained by means of the analysis of 18S mtDNA and 16S rDNA. Practically, no branch obtained in the topology herein can be recognized in those. Another study evolving 18 rDNA, and more sampled species, Harasewych *et al.* (1997) demonstrated, at least, the monophyly of Caenogastropoda, which included Architaenioglossa. However, the analysis of the sequence of the Neogastropoda 591 bp citocrome c oxidase I, the taxon did not result monophyletic. Based on a given DNA sequence, Costellariidae are closer to a monophyletic Turridae than the other conoideans (Conidae and Terebridae) (Espiritu *et al.,* 2002). Monophyly of the Caenogastropoda and even Neogastropoda has been contradicted in other molecular approaches (Riedel, 2000; Colgan *et al.,* 2000, 2003, 2007; McArthur & Harasewych, 2003). Studies on some sequences have resulted in apparently displaced branches, as, *e.g.,* a costellariid placed among lower hypsogastropods, and a ficid and a Bursidae among the neogastropods

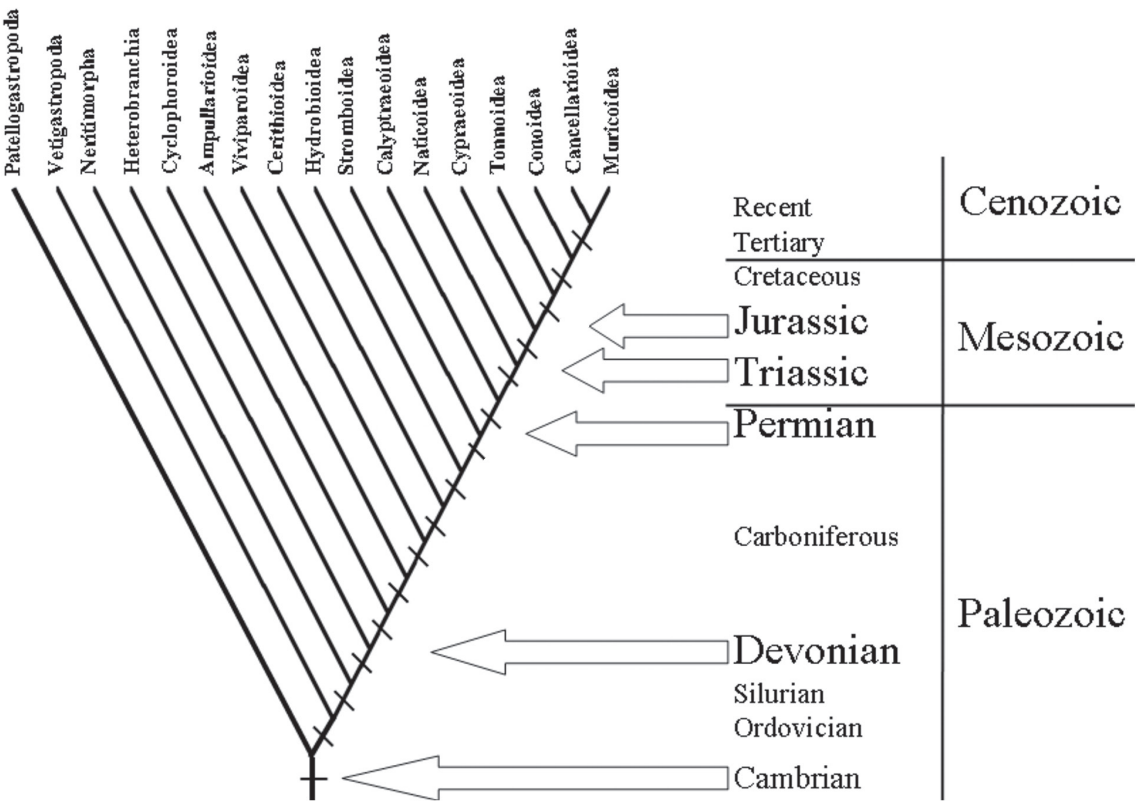

FIGURE 22: Minimum age of some nodes of the major nodes in the simplified cladogram, based on oldest known fossils.

(Riedel, 2000 in 18S rRNA dataset). Monophyly of Caenogastropoda has been pointed out by Colgan *et al.* (2003), but with the inclusion of a cephalopod *(Nautilus)* in it. As the main goal of this paper is not molecular, it is considered premature to analyze these incongruences, if they are of minor amount or if they evolve clearly misplaced taxa, reflecting some of the limitations of molecular or morphological data; or that the used algorithms (*e.g.,* Bayesian, maximum-linkelihood) can be considered phenetic (Mooi & Gill, 2010). Further analysis on this issue was displayed in Ponder *et al.* (2008: 359-361).

On the other hand, a recent paper based on phylogenomics shows a monophyletic Caenogastropoda (Kocot *et al.,* 2011: fig. 2), in such inner branches absolutely agrees with those from the present paper. However, only 5 taxa were included, in such arrangement (considering only the superfamily) is: (Cerithioidea (Rissooidea (Stromboidea (Muricoidea-Calyptraeoidea)))). Also in agreement, Heterobranchia branch (with 9 representatives) resulted as sister taxon of Caenogastropoda, as well as the arrangement of the remaining Gastropoda, showing the following arrangement (only considering the order): (Patellogastropoda (Vetigastropoda (Apogastropoda – Neritimorpha))). Then, the Gastropoda arrangement by Kocot *et al.* (2011) totally agrees with the result of the present paper. The discordances only appear in non-gastropod representatives, which are not the goal of the present paper.

CONCLUSIONS

Based on the results of the present study, it is concluded that:

1. The order Caenogastropoda is supported by 60 morphologic synapomorphies as a monophyletic group.
2. Thirteen monophyletic major groups, here treated as superfamilies, are found in Caenogastropoda, successively distributed along the cladogram.
3. The phylogeny obtained does not greatly differ from those in the current literature. It is as follows: (Cyclophoroidea (Ampullarioidea (Viviparoidea (Cerithioidea (Risooidea (Stromboidea (Calyptraeoidea (Naticoidea (Cypraeoidea (Tonnoidea (Conoidea (Cancellarioidea – Muricoidea))))))))))).
4. The taxon 'Architaenioglossa' (*sensu* Haszprunar, 1988a) is a paraphyletic arrangement of basal, non-marine Caenogastropoda, as shown also in some other recent studies.
5. Heterobranchia is the sister group of the Caenogastropoda.
6. From the higher classification found in the literature, the following taxa are also monophyletic: Neogastropoda, encompassing Muricoidea, Cancellarioidea and Conoidea (although Cancellarioidea resulted a branch of Muricoidea); Hypsogastropoda (exophalic penis bearing higher caenogastropods), Sorbeoconcha (Caenogastropoda except architaenioglossans) and Apogastropoda (Heterobranchia plus Caenogastropoda).
7. Characters from all systems, organs and structures were important in the analysis in somewhat equivalent levels.

RESUMO

A sistemática, classificação e filogenia de Caenogastropoda são revisadas baseando-se em uma análise da morfologia de representantes de todos os ramos. A base para este trabalho é o exame detalhado da morfologia de 305 espécies, em sua maioria descrita em artigos complementares. Representantes da maioria das famílias de cenogastrópodes são incluídos (compreendendo 270 espécies) e 35 grupos-externos. Uma análise filogenética baseada em 676 caracteres morfológicos, com 2291 estados (1915 estados apomórficos), é apresentada. Os caracteres abrangem todos os sistemas de órgãos que são discutidos em detalhes. A polarização é baseada em um pool de não-cenogastrópodes, compreendendo 27 representantes de Heterobranchia, Neritimorpha, Cocculiniformia e Patellogastropoda. Adicionalmente, 8 representantes de outras classes são também incluídos. O enraizamento é baseado no representante de Polyplacophora. Alguns poucos caracteres são considerados para organizar os grupos-externos, para encontrar a posição de Caenogastropoda entre eles, e para levantar as sinapomorfias do táxon. Um consenso estrito de 48 árvores mais parcimoniosas (Fig. 20; passos: 3036; IC = 51; IR = 94) é apresentado cuja sinopse é: ((((((Cyclophoroidea^{2} (Ampullarioidea^{5} (Viviparoidea^{15} (Cerithioidea^{19} (Rissooidea^{41} (Stromboidea^{47} (Calyptraeoidea^{67} (Naticoidea^{97} (Cypraeoidea^{118} (Tonnoidea^{149} (Conoidea^{179} (Cancellarioidea^{222} – Muricoidea^{212}))))))))))) Heterobranchia^{V}) Neritimorpha^{U}) Vetigastropoda^{L}) Cocculiniformia^{J}) Patellogastropoda) (sobrescritos indicam os nós na Fig. 20). A monofila de Caenogastropoda é suportada por 60 sinapomorfias. Baseado nesse cladogram, a sistemática, evolução e paleontologia do grupo são discutidas, dentro do contexto

de outros estudos que também abordam Caenogastropoda, incluindo estudos moleculares. A lista de caracteres é inclusa no Apêndice 1; a matriz de caracteres no Apêndice 2; e a lista de sinapomorfias de cada nó está apresentada no Apêndice 3 na forma de símbolos. Com a filogenia obtida neta análise tem um alto grau de concordância com outros estudos recentes, alguns táxons supra-familiares são criados: Siphonogastropoda (Cypraeoidea + Peogastropoda); Adenogastropoda (Naticoidea + Siphonogastropoda); Rhynchogastropoda (Calyptraeoidea + Adenogastropoda); Strombogastropoda (Stromboidea + Rhynchogastropoda); Peogastropoda (Tonnoidea + Neogastropoda); Epiathroidea (Viviparoidea + Sorbeoconcha); Hydrogastropoda (Ampullarioidea + Epiathroidea); Adenogonogastropoda (Neritimorpha + Apogastropoda) (Apêndice 4).

Palavras-Chave: Gastropoda; Caenogastropoda; Filogenia; Morfologia; Anatomia; Sistemática.

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APPENDIX 1

List of characters considered in present study.

In all character the matrix possesses question marks (?) in doubtful, innaplicable or non-seen states, and a dash (–) in the states that are redundant. This last measure is to avoint the increase the weight of a given state/charactes. More details in Material and Methods.

SHELL

General

1. Form: 0 = limpet; 1 = globose-trochiform; 2 = turriform; 3 = uncoiled; 4 = fusiform; 5 = patelliform-like, with a ventral calcareous plate; 6 = patelliform-like, with long, slight spiral; 7 = trochiform-like; 8 = naticiform (globose); 9 = auriculiform; 10(A) = coniform (L = 26; CI = 53; RI = 97).
2. Spire: 0 = absent; 1 = high (about 2 times aperture length); 2 = low; 3 = planispiral; 4 = weak; ? = fusiform shell (L = 27; CI = 14; RI = 79).
3. Size: 0 = medium/large; 1 = miniaturized (adult form smaller than 8 mm); 2 = extremely minute (smaller than 1 mm) (L = 9; CI = 22; RI = 46).
4. Fusiform shell relative height of spire: 0 = about similar length to aperture or aperture shorter than spire; 1 = spire shorter than half aperture length; 2 = spire less than 1/10 of spire length; ? = other kind of shell form (L = 10; CI = 20; RI = 87).
5. Periostracum: 0 = thin, simple; 1 = thick; 2 = pilose, *i.e.,* with hair; 3 = absent; 4 = with scales (L = 11; CI = 36; RI = 92).
6. Suture: 0 = absent; 1 = deep; 2 = shallow (plain) (L = 16; CI = 12; RI = 85) [– = avoids redundancy with character 2].
7. Relevant and non-autapomorphic teleoconch sculpture: 0 = absent (smooth-growth lines); 1 = axial ridges; 2 = spiral ribs; 3 = periodical nodes; 4 = radial; 5 = spiral furrow in inferior third at last whorl; 6 = cales on threads; 7 = glossy; 8 = carinate opened umbilicus (L = 27; CI = 29; RI = 84).
8. Inner chitinous layer (or inner hard organic layer): 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
9. Relevant and non-autapomorphic subsutural sculpture: 0 = absent; 1 = irregular nodes; 2 = somewhat regular nodes; 3 = strong shouldered; 4 = regular spines; 5 = spine on a varix; 6 = wide and blunt subsutural carina; 7 = series of holes – tremata (L = 9; CI = 77; RI = 95) [– = avoids redundancy with character 2].
10. Ventral calcareous plate form: 0 = absent or a true columella; 1 = a planar septum; 2 = a spiral septum; 3 = a cone; 4 = a semi-cone (L = 4; CI = 100; RI = 100) [– = avoids redundancy with character 1 – restrict to calyptraeoideans].
11. Unguiculate (*i.e.,* in form of human nail) shell color: 0 = non unguiculate; 1 = brownish; 2 = whitish; 3 = with narrow spiral bands (L = 6; CI = 50; RI = 72).
12. Unguiculate shell with spiral bands in early development: 0 = non unguiculate; 1 = weak or continuous; 2 = interrupted (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 11].
13. Unguiculate shell periostracum: 0 = non unguiculate; 1 = thick; 2 = deciduous (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 11].
14. Unguiculate shell septum left notch: 0 = non unguiculate; 1 = very shallow; 2 = well marked; 3 = deep; 4 = shallow, but associated to a very thin, transparent shell (L = 4; CI = 100; RI = 100) [– = avoids redundancy with character 11].
15. Umbilicus: 0 = lacking; 1 = simple (opened or closed); 2 = with a central, longitudinal, broad fold; 3 = covered by calcareous flap; 4 = helical growing (L = 8; CI = 50; RI = 89).
16. Spire in naticiform taxa: 0 = not naticiform; 1 = occupying about half of total shell length; 2 = occupying about 1/4 of shell length (L = 3; CI = 66; RI = 97).
17. Involution: 0 = weak/absent; 1 = involute shell, with apex visible; 2 = involute, with covered apex; 3 = with transverse external reinforcement at middle level (L = 4; CI = 75; RI = 96).
18. Situation: 0 = external; 1 = covered at least in part by retractable mantle; 2 = internal (L = 4; CI = 50; RI = 93).

19. Outer surface of involute shell: – = not involute shell; 0 = opaque smooth; 1 = glossy; 2 = opaque, sculptured (L = 6; CI = 50; RI = 90) [– = avoids redundancy with character 17].
20. Spire growth: 0 = regular or absent (*i.e.,* along a straight line); 1 = irregular (*i.e.,* somewhat randomic) (L = 3; CI = 33; RI = 60).
21. Flat central region of dorsal surface in involute shell; 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 17].
22. Periostracum type in fusiform shell: 0 = glabrous or not fusiform shell; 1 = simple hair; 2 = complex hair (L = 4; CI = 50; RI = 85) [– = avoids redundancy with character 1].
23. Pseudoumbilicus: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
24. Internal, inferior, V-shaped furrow in each whorl: 0 = absent; 1 = weak; 2 = present (L = 6; CI = 33; RI = 95) [– = avoids redundancy with character 1].
25. Spines on regular varices: 0 = absent, 1 = simple; 2 = branched (L = 4; CI = 50; RI = 88) [– = avoids redundancy with character 26].
26. Threads per whorl in regular periodical determinate growth: 0 = absent or periodical determinate growth absent; 1 = up to 2; 2 = 3; 3 = 4; 4 = 5 or more (L = 6; CI = 50; RI = 82) [– = inapplicable – *i.e.,* non periodical determinate grown].
27. Reabsorption of inner whorls or shell layers: 0 = absent, 1 = present (L = 1; CI = 100; RI = 100).
28. Type of shell: 0 = with eight valves and spicules; 1 = conic (simple or coiled), with closed tip; 2 = two valves connected by flexible region (ligament); 3 = conic, with aperture in both sides; 4 = shell with inner chambers; 5 = reduced/lost (L = 6; CI = 83; RI = 66).
29. Muscle scars: 0 = 7-10 pairs; 1 = less than 4 pairs (L = 1; CI = 100; RI = 100).

Protoconch

30. Autotomy of protoconch or any embryonic shell: 0 = absent; 1 = present (L = 5; CI = 20; RI = 55).
31. Protoconch position in dorsal view: 0 = central or near center; 1 = posterior (L = 6; CI = 16; RI = 72).
32. Number of protoconch whorls: 0 = paucispiral; 1 = multispiral; 2 = hyperstrophic (L = 9; CI = 22; RI = 93).

Aperture

33. Determinate growth: 0 = absent; 1 = present; 2 = periodical determinate growth; 3 = in same plain (a varix each half whorl) (L = 24; CI = 37; RI = 88).
34. Differentiated siphonal canal: 0 = absent; 1 = present; 2 = curved dorsally; 3 = long and slender; 4 = long, almost closed like a tube (L = 12; CI = 33; RI = 94).
35. Anterior notch in aperture (other than siphon): 0 = absent; 1 = present; 2 = forming anal slit (L = 4; CI = 50; RI = 94).
36. Aperture: 0 = orthocline; 1 = prosocline (L = 5; CI = 20; RI = 71) [– = avoids redundancy with character 2].
37. Outer lip: 0 = thin and simple or with varix; 1 = thick and expanded; 2 = with spines (L = 5; CI = 40; RI = 83) [– = avoids redundancy with character 36].
38. Tentacular notch in outer lip: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
39. Umbilical callus: 0 = absent; 1 = covering small superior portion of umbilicus; 2 = covering about 1/2 of umbilicus; 3 = covering most of umbilicus (L = 5; CI = 60; RI = 88).
40. Outer lip: 0 = thin, cutting-edged; 1 = thick, smooth; 2 = thick, with teeth; 3 = with long tooth in inferior third projected forwards; 4 = continuing with projected inner lip (L = 13; CI = 23; RI = 91) [– = avoids redundancy with character 37].
41. Anal canal: 0 = absent; 1 = present; 2 = a slit (continuous or cancellated); 3 = a simple apical hole (L = 8; CI = 37; RI = 91).
42. Anal canal fold; 0 = absent; 1 = present in columella; 2 = present as part of inner lip teeth (L = 3; CI = 66; RI = 80) [– = avoids redundancy with character 41].
43. Aperture localization: 0 = ventral or anterior-right; 1 = totally at right (L = 2; CI = 50; RI = 96).
44. Ventral, protruding calcareous band: 0 = absent; 1 = rounded; 2 = adult ventral region fitting in substrate; 3 = as calcareous flat platform covering right side of canal (L = 5; CI = 60; RI = 86).

45. Outer lip or shell edge: 0 = cutting edge or expanded; 1 = with a noded varix; 2 = with double varix (L = 5; CI = 40; RI = 94) [– = avoids redundancy with character 33].
46. Callus: 0 = smooth or absent; 1 = with folds; 2 = forming a flap covering umbilicus; 3 = deformed by columellar folds (L = 5; CI = 60; RI = 94) [– = avoids redundancy with character 39].
47. Aperture V-shaped due to teeth enlargement: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 36].
48. Aperture in coniform taxa: 0 = not coniform 1 = elliptical, long; 2 = very narrow (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 1, *i.e.,* non coniform].
49. Anal notch in fusiform taxa: 0 = absent; 1 = about in superior third of outer lip; 2 = close to suture (L = 5; CI = 40; RI = 89) [– = avoids redundancy with character 1].
50. Type of siphonal canal: 0 = short, wide; 1 = long, cylindrical, with preceding canals in same axis; 2 = left edge forming ventral platform; 3 = a ventral platform relatively wide, but with preceding canals at about 30° from preceding axis; 4 = preceding canals about 10° from final canal, long projecting along them (L = 5; CI = 80; RI = 90) [– = avoids redundancy with character 34].
51. Folds on inner lip continuous over columella: 0 = absent; 1 = present (L = 2; CI = 50; RI = 91).
52. Outer lip associated with involute shell: 0 = simple; 1 = thick, smooth; 2 = same, but with internal teeth (L = 4; CI = 50; RI = 94) [– = avoids redundancy with character 17].

OPERCULUM

In all opercular characters: ? = post torsional loss of operculum; – = avoids redundancy with non-gastropod taxa.

53. Outline: 0 = absent 1 = circular; 2 = with an upper-inner projection (sub-pyriform); 3 = sub-elliptical; 4 = elliptical; 5 = very long, pointed; 6 = somewhat triangular; 7 = with spine near nucleus; 8 = semi-circular; 9 = rectangular (L = 14; CI = 64; RI = 95).
54. Type: 0 = no operculum; 1 = corneous; 2 = calcareous (L = 6; CI = 33; RI = 80).
55. Outer surface: 0 = no operculum; 1 = spiral; 2 = concentric (L = 7; CI = 20; RI = 91).
56. Nucleus situation: 0 = no operculum; 1 = central; 2 = eccentric; 3 = subterminal; 4 = terminal; 5 = in middle region of inner edge; 6 = close to inferior and external edge; 7 = inferior to middle region of outer edge (L = 18; CI = 38; RI = 91).
57. Type of coiling: 0 = no operculum; 1 = multispiral; 2 = paucispiral; 3 = concentric (unguiculate); 4 = operculum lost after metamorphosis (L = 24; CI = 16; RI = 87).
58. Projects beyond foot: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
59. Opercular spines and projections at edge: 0 = absent; 1 = several along outer edge; 2 = single, close to nucleus; 3 = serrated in inner-superior edge (L = 4; CI = 75; RI = 91).
60. Occupies entire shell aperture: 0 = no operculum; 1 = yes; 2 = no (L = 9; CI = 22; RI = 90).
61. Opercular pad in foot: 0 = absent or in middle-dorsal region of foot posterior slope; 1 = sub-terminal (L = 1; CI = 100; RI = 100).
62. Opercular lobe: 0 = absent; 1 = present (L = 2; CI = 50; RI = 95).
63. Opercular pad surface on foot: 0 = absent; 1 = single elliptical connection; 2 = connection divided in middle by longitudinal band (L = 2; CI = 100; RI = 100).
64. Pair of transverse muscles between opercular connections; 0 = absent; 1 = present (L = 2; CI = 50; RI = 66).
65. A small, direct, single muscle between transverse pair of muscles: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
66. Special sculpture of outer surface: 0 = absent; 1 = few folds close to outer edge only; 2 = series of folds parallel to outer edge (L = 2; CI = 100; RI = 100).
67. Sand grains immersed in opercular wall: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
68. Pair of low projections inside scar at level of nucleus: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
69. Inner projections encased in foot; 0 = absent; 1 = inferior; 2 = in central region of inner edge (L = 2; CI = 100; RI = 100).
70. Projection in superior-inner corner in a circular, multispiral operculum: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
71. Operculum in larval phase: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

72. Opercular terminal nucleus associated with turriform shell: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 1].

HEAD-FOOT

General

73. Retractor muscles of shell: 0 = 7-10 pairs; 1 = less than 4 pairs (L = 1; CI = 100; RI = 100).
74. Head: 0 = plain, inconspicuous; 1 = protruded, with a pair or more of appendices (tentacles and similar) (L = 1; CI = 100; RI = 100).
75. Adductor muscles: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
76. Food groove: 0 = absent; 1 = present (L = 4; CI = 25; RI = 88).
77. Right siphon: 0 = absent; 1 = present; 2 = with a fold to mouth (L = 2; CI = 100; RI = 100).
78. Left siphon: 0 = absent; 1 = present; 2 = very long (L = 5; CI = 40; RI = 85).
79. Food groove in dorsal region of head-foot complex: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
80. Head-foot with distinct transverse, narrow color bands: 0 = absent; 1 = present over whole head-foot; 2 = banded pigment restricted to propodium (L = 2; CI = 100; RI = 100).
81. Connection between head-foot and visceral mass: 0 = posterior; 1 = turned towards left (L = 2; CI = 50; RI = 98).
82. Form: 0 = somewhat bulged; 1 = long antero-posteriorly (compressed laterally) (L = 3; CI = 33; RI = 94).
83. Anterior projection of nuchal region of head: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
84. Posterior projection in opposite side of anterior projection (character 83): 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
85. Distance between head base and anterior edge of foot: 0 = close; 1 = far (L = 1; CI = 100; RI = 100).
86. Special kind of pigmentation: 0 = irregular-coalescent spots; 1 = spots with different colors; 2 = albinism (lacking pigmentation) (L = 5; CI = 40; RI = 66).
87. Spicules: 0 = present; 1 = absent (L = 1; CI = 100; RI = 100).
88. Somatic torsion: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
89. Projections with complex muscular tissue located postero-dorsally in head: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
90. Foot-head retractor muscles: 0 = mostly running dorso-ventrally; 1 = running antero-posteriorly (L = 2; CI = 50; RI = 75).

Head

91. Head size: 0 = normal (about 1/2 of foot width); 1 = narrow (about 1/4 of foot width); 2 = broad (about same width as foot) (L = 8; CI = 25; RI = 85) [? = inapplicable].
92. Head form: 0 = inlay level or difficult to individualize; 1 = protruded without neck; 2 = a transverse flap; 3 = preceded by long neck region; 4 = very long projected; 5 = socket-like; 6 = conical, protruded; 7 = plain, inconspicuous; 8 = with tentacles located side by side; 9 = capable of retraction (L = 13; CI = 69; RI = 96).
93. Snout type: 0 = absent; 1 = cylindrical, deep ventral-anterior furrow; 2 = flattened, bilobed anterior mouth; 3 = conical, oval in section, with transverse furrows in retracted condition, capacity of great distention; 4 = long, circular in section, thickly muscular, distal tip broader; 5 = pleurembolic proboscis (L = 6; CI = 83; RI = 98).
94. Snout size: 0 = only a peri-oral fold; 1 = normal (about 1/4 whorl); 2 = large (~1 whorl) and flattened; 3 = small (~1/6 whorl) and flattened; 4 = large and cylindrical; 5 = proboscis (L = 7; CI = 71; RI = 97) [– = avoids redundancy with character 93].
95. Snout/proboscis anterior region: 0 = rounded; 1 = somewhat bifid; 2 = with lateral flaps; 3 = lateral projections long; 4 = long ventral projection; 5 = flat, with lateral projections; 6 = pointed; 7 = with papillae (L = 9; CI = 77; RI = 96) [– = avoids redundancy with character 93].
96. Outer peri-oral region: 0 = smooth; 1 = papillate; 2 = with pair of anterior flanges (L = 4; CI = 50; RI = 87).

97. Pair of snout tentacles: 0 = absent; 1 = present; 2 = pair of lateral projections (L = 2; CI = 100; RI = 100).
98. Retractor muscle of snout/proboscis: 0 = absent; 1 = two separated muscles in ventral inner region; 2 = immersed in the inner muscular layer of snout; 3 = a lateral pair; 4 = more than a pair; 5 = present mainly in ventral surface; 6 = a series contouring entire inner surface; 7 = almost atrophied (L = 7; CI = 100; RI = 100).
99. Pleurembolic proboscis: 0 = absent; 1 = short; 2 = long; 3 = very long and convolute (when retracted) (L = 6; CI = 50; RI = 98).
100. Proboscis retracted inside haemocoel by means of: 0 = no introversion; 1 = simple contraction of internal retractor muscles; 2 = shortening of longitudinal musculature by contraction and gliding of its wall; 3 = proboscis coiling; 4 = proboscis reduced to a muscular ring (L = 6; CI = 66; RI = 98).
101. Snout/proboscis retractor muscles: 0 = absent, weak or concentrated ventrally; 1 = concentrated dorsally (L = 1; CI = 100; RI = 100).
102. Planar neck ventral surface: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
103. Neck lateral flattened lappets: 0 = absent; 1 = present (L = 1; CI = 50; RI = 94).
104. Introvert: 0 = absent; 1 = present, contractile; 2 = present, retractile into rhynchodeal cavity (L = 2; CI = 100; RI = 100).
105. Snout longitudinal expansions: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

FOOT

106. Form of foot: 0 = flat for crawling; 1 = umbrella-like for digging; 2 = possessing several arms and siphon (L = 1; CI = 100; RI = 100).
107. Crawling foot size or form: 0 = normal (about 1/3 whorl); 1 = very large; 2 = small; 3 = cylindrical or sub-cylindrical; 4 = dorso-ventrally flattened; 5 = widely extensible (about 3 times shell size), with capability for total retraction; 6 = with well-developed lateral epipodium (L = 10; CI = 60; RI = 95) [– = avoids redundancy with character 106].
108. Foot size after extension: 0 = about same as or smaller than shell volume; 1 = about double of shell volume; 2 = more than 4 times shell volume (L = 2; CI = 100; RI = 100).
109. Anterior furrow of pedal glands: 0 = absent or only close to median line; 1 = anterior margin only; 2 = entire foot margin; 3 = also along sole, on median line; 4 = deep; 5 = edged by thick borders; 6 = extending by lateral projections of foot anterior edge (L = 12; CI = 50; RI = 91).
110. Extra pedal glands: 0 = absent; 1 = posterior pedal gland; 2 = only a posterior furrow; 3 = accessory boring organ (ABO) in anterior third of foot sole (L = 5; CI = 60; RI = 92).
111. Foot anterior margin: 0 = low, close to snout base; 1 = protruded, projected from snout base ("propodium"); 2 = covered by neck ventral surface; 3 = in distal margin of a tall and flat propodium; 4 = plough for digging; 5 = long anterior flap of sole; 6 = possessing 2 series of orifices (L = 10; CI = 60; RI = 96).
112. Foot sole: 0 = conspicuous, crawling; 1 = inconspicuous in a flattened foot; 2 = inconspicuous in a cylindrical foot; 3 = plain, flattened; 4 = conic, solid; 5 = dorsally concave (L = 8; CI = 62; RI = 91) [– = avoids redundancy with character 106].
113. Dorsal surface of foot: 0 = smooth; 1 = reticulate; 2 = possessing posterior epipodial tentacle; 3 = possessing lateral series of epipodial tentacles; 4 = with mosaic of furrows adapted to air exposing (L = 5; CI = 80; RI = 93).
114. Incurrent and excurrent canal formed by lateral edges of foot: 0 = absent; 1 = present (L = 2; CI = 50; RI = 95).
115. Mesopodium sole separated by a furrow from dorsal foot structures: 0 = absent; 1 = present; 2 = further separated by mesopodial flap (L = 4; CI = 50; RI = 93).
116. Posterior-dorsal edge of propodium covering part of shell: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
117. Pair of anterior pedal glands: 0 = absent; 1 = exposed inside haemocoel; 2 = immersed in anterior pedal musculature (L = 3; CI = 66; RI = 97).
118. Epipodium: 0 = absent; 1 = single; 2 = tentacular, with more than single layer (L = 4; CI = 50; RI = 81).
119. Foot retraction into shell: 0 = forming a median concavity; 1 = lateral positioning (L = 1; CI = 100; RI = 100).

120. Epipodial sense organs: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
121. Position of foot related to body main axis: 0 = ventral; 1 = anterior (L = 1; CI = 100; RI = 100).
122. Aperture of pedal glands: 0 = absent or a pore in the anterior region of sole; 1 = as a deep furrow along anterior foot sole (L = 2; CI = 50; RI = 96) [– = avoids redundancy with character 109].
123. Mosaic of furrows in dorsal surface of foot: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
124. Projected propodium possessing pedal gland furrow at distal edge, dorsally covered by base of snout or neck: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 111].

Tentacles

125. Tentacles type: 0 = tentacles absent; 1 = cylindrical and dorsal; 2 = flattened and dorsal; 3 = cylindrical and ventral; 4 = weakly bifid in retracted condition; 5 = flat, triangular, long; 6 = left tentacle bifid; 7 = as posterior ommatophore (L = 16; CI = 43; RI = 87).
126. Tentacle length in retracted condition: 0 = medium (equivalent to snout); 1 = short (about half of snout length); 2 = long (about 1.5 times the shout length); 3 = very short, almost vestigial (L = 6; CI = 66; RI = 90) [– = avoids redundancy with character 125].
127. Tentacles situation one with each other: 0 = about 1/3 of food width; 1 = widely spaced; 2 = closely spaced, plug-like (L = 7; CI = 28; RI = 92) [– = avoids redundancy with character 125].
128. Eye site in tentacles: 0 = absent or basal; 1 = sub-basal; 2 = middle; 3 = almost at tentacle tip; 4 = immersed in head flap, far from tentacles; 5 = in tentacle tips; ? = absent (L = 15; CI = 33; RI = 94) [– = avoids redundancy with character 125].
129. Ommatophore; 0 = absent; 1 = present (L = 7; CI = 14; RI = 90).
130. Eyes: 0 = absent; 1 = reduced; 2 = present (L = 16; CI = 12; RI = 64).
131. Ommatophore in tentacles: 0 = plain; 1 = peduncle-like; 2 = sessile; 3 = as main part of tentacles; 4 = producing two clearly different regions, a broader basal and a narrower distal (L = 12; CI = 33; RI = 94) [– = avoids redundancy with character 129].
132. Eye lens: 0 = absent; 1 = present (L = 2; CI = 40; RI = 72).
133. Ommatophore attached to tentacles: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 129].

Columellar muscle

134. Number of foot-shell retractor muscles: 0 = more than 2 pairs; 1 = a pair; 2 = single (L = 2; CI = 100; RI = 100).
135. Columellar muscle: 0 = absent; 1 = 1.5 whorls; 2 = 3/4 whorl; 3 = 1/3 whorl; 4 = more than 3 whorls; 5 = much reduced; 6 = a shell muscle (horseshoe shaped); 7 = separated into a pair (left and right shell muscles); 8 = lateral flap; 9 = little more than 2 whorls (L = 12; CI = 75; RI = 96).
136. Columellar muscle or equivalent: 0 = slightly narrow, haemocoel dorsal to it; 1 = very broad with a narrow haemocoel almost within it; 2 = bifid, possessing a siphonal branch projected backwards; 3 = with longitudinal furrows; 4 = a pair positioned divergently (L = 6; CI = 66; RI = 96).
137. Columellar muscle: 0 = well-developed, part attached to shell dorsal surface; 1 = very small, almost absent, only attached to shell septum edge; 2 = double posteriorly (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 135].
138. Lateral shell muscle on right: 0 = absent; 1 = present connected to a columellar muscle; 2 = as an isolated muscle (L = 2; CI = 100; RI = 100).
139. Dorsal shell muscle: 0 = absent; 1 = as a flat anterior expansion of a columellar muscle; 2 = distinct, close to columellar muscle; 3 = far from columellar muscle; 4 = thin, weak (L = 4; CI = 100; RI = 100).
140. Right accessory muscle of columellar muscle: 0 = absent; 1 = entirely connected to columellar muscle; 2: as an isolated muscle (L = 2; CI = 100; RI = 100).
141. Columellar muscle: 0 = absent; 1 = spiral or horseshoe-shaped; 2 = only one flap turned towards posterior, about half whorl; 3 = similar, but turned inwards (L = 4; CI = 75; RI = 97).
142. Siphonal muscle related to right side of columellar muscle: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

HAEMOCOEL

143. Diaphragm-like septal muscle in posterior region of haemocoel: 0 = absent; 1 = present; 2 = very developed, double layered (L = 2; CI = 100; RI = 100).
144. Head muscles: 0 = absent or inconspicuous; 1 = developed, immersed in integument; 2 = as a distinct muscle; 3 = of independent origin in relation to shell muscle; 4 = capable of retraction of head (L = 7; CI = 57; RI = 97).
145. Pair of crossing muscles anterior to head muscles: 0 = absent; 1 = incipient; 2 = large, well developed (L = 2; CI = 100; RI = 100).
146. Net of transverse muscles in haemocoel: 0 = absent or weak; 1 = greatly developed; 2 = greatly developed, passing through salivary glands (L = 2; CI = 100; RI = 100).
147. Haemocoel form: 0 = narrow; 1 = broad, somewhat triangular (L = 1; CI = 100; RI = 100).

PALLIAL CAVITY

GENERAL

148. Pallial cavity length: 0 = slightly thicker than foot edges; 1 = 1 whorl; 2 = 1.5 whorls; 3 = less than 1/2 whorl; 4 = more than 2/3 of animal length; 5 = less than 1/4 of animal length; 6 = surrounding both sides of visceral mass (L = 10; CI = 60; RI = 93).
149. Highly muscular mantle with mobile siphon at aperture: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
150. Lung sac: 0 = absent; 1 = present and short; 2 = present and very long; 3 = as main portion of pallial cavity, confined by pneumostome (lung) (L = 5; CI = 60; RI = 90).
151. Posterior region lacking gill: 0 = long; 1 = short (L = 4; CI = 25; RI = 94).
152. Differentiated vessels in aquatic forms: 0 = absent; 1 = between gill and rectum; 2 = near right margin of the pallial cavity; 3 = conspicuous transverse vessel from pallial cavity close to middle region of gill to anterior-right edge of kidney (L = 8; CI = 37; RI = 79).
153. Adrectal sinus type: 0 = inconspicuous; 1 = very broad, associated with the kidney lobe; 2 = very broad, associated with large nephrostome; 3 = differentiated vessel running near right margin of the pallial cavity; 4 = edged by secondary ureter (L = 5; CI = 80; RI = 96).
154. Mantle cavity anterior aperture: 0 = wide; 1 = narrow; 2 = closed by mantle fusion with head neck (L = 2; CI = 100; RI = 100).
155. Mantle fusion with posterior-dorsal surface of foot: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
156. Mantle cavity form: 0 = conic; 1 = almost a complete ring; 2 = divided by tall longitudinal septum (L = 2; CI = 100; RI = 100).
157. Approximate length of pallial cavity in relation to visceral mass in unguiculate forms: 0 = 60%; 1 = 75%; 2 = 90% (L = 4; CI = 50; RI = 84) [– = avoids redundancy with character 11].
158. Main pallial cavity structures: 0 = paired; 1 = single (L = 2; CI = 50; RI = 91).
159. Pallial cavity main location; 0 = a wide furrow surrounding foot; 1 = very deep in posterior (or anterior postorsional phase) region (L = 1; CI = 100; RI = 100).

MANTLE BORDER

160. Mantle edge appendages or form: 0 = none; 1 = several aligned papillae; 2 = tentacles; 3 = broad and thin; 4 = with a tentacle at right (anterior to anus); 5 = outer surface covered by papillae; 6 = satellite fold of siphon base; 7 = with projections for making spines; 8 = second flap in right side of mantle border; 9 = deep slit; 10 = fused with head (L = 24; CI = 37; RI = 81).
161. Mantle ventral insertion in head foot: 0 = close to mantle border; 1 = far from mantle border; 2 = very ample, as a lobe (L = 4; CI = 50; RI = 96).
162. Mantle border: 0 = narrow; 1 = wide and thick; 2 = restricting mantle cavity; 3 = extending beyond shell aperture; 4 = with wide thin area; 5 = almost totally fused with head neck; 6 = some differentiable tentacles in a slit; 7 = thick-muscular; 8 = with satellite basal fold of left edge of a siphon (L = 12; CI = 66; RI = 95).

163. Repugnatorial glands along mantle border: 0 = absent; 1 = present (L = 2; CI = 50; RI = 93).
164. Mantle border with special arrangement of folds between gill anterior extremity and osphradium: 0 = absent (smooth); 1 = present; 2 = extending towards left by mantle border (L = 2; CI = 100; RI = 100).
165. Anal siphon (separated from mantle border): 0 = absent; 1 = present (L = 21; CI = 50; RI = 95).
166. Developed anterior siphon (separated from mantle border): 0 = absent; 1 = present; 2 = with papillae in border (L = 4; CI = 50; RI = 98).
167. Coloration of inner surface mantle at some distance from edge: 0 = absent; 1 = clear or diffuse dark spots sometimes coalescent; 2 = alternate dark and pale bands; 3 = ample rings; 4 = small rings; 5 = dichotomic bands (L = 5; CI = 100; RI = 100).
168. Mantle border: 0 = simple; 1 = with two separate lobes; 2 = lobes with dorsal fusion (L = 2; CI = 100; RI = 100).
169. Papillae type in lobed mantle: 0 = absent; 1 = simple and short; 2 = simple and tall; 3 = some branched; 4 = simple, broad, base narrower (L = 6; CI = 62; RI = 88) [– = avoids redundancy with character 168].
170. Type of pallial papillae branches in lobed mantle: 0 = absent; 1 = alternate; 2 = brush-like (all branches in papilla apex); 3 = papilla resulted only by contraction of muscles, disappearing when mantle is retracted (L = 7; CI = 57; RI = 88) [– = avoids redundancy with character 168].
171. Uniform distribution of small and low papillae in lobed mantle: 0 = absent; 1 = present (L = 3; CI = 66; RI = 96) [– = avoids redundancy with character 168].
172. Outstandingly large papillae in lobed mantle: 0 = absent; 1 = closer to inner lobe region and far from outer edge; 2 = aligned transversely; 3 = randomly distributed throughout mantle, among smaller papillae (L = 4; CI = 100; RI = 100) [– = avoids redundancy with character 168].
173. Especial folds: 0 = absent; 1 = secondary, tall inner fold parallel to mantle border; 2 = inner fold extending greatly beyond mantle border; 3 = satellite basal fold of left edge of siphon; 4 = low septum in right base of siphon separating gill and osphradium anterior ends; 5 = high septum in right base of siphon separating gill and osphradium anterior ends; 6 = a pneumostome (L = 9; CI = 66; RI = 92).
174. Siphon: 0 = absent or with adjacent mantle surrounding its base; 1 = with adjacent mantle lying with it; 2 = similar, but with very short siphon (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 166].
175. Mantle border length: 0 = ending in head region during activity; 1 = extending beyond head during activity; 2 = covering externally shell (L = 4; CI = 50; RI = 98).
176. Distinct incurrent structure: 0 = absent, 1 = present, restrict to shell edge; 2 = further longer, with oblique muscles and working as exploratory structure (L = 2; CI = 100; RI = 100).

Osphradium

177. Osphradium ganglion form and type: 0 = small, circular; 1 = long, ridge-like; 2 = elliptical peduncle; 3 = elliptical button; ? = cyclophorids (L = 3; CI = 100; RI = 100).
178. Osphradium: 0 = sessile; 1 = on a stalk; 2 = on ctenidial vein; 3 = positioned in middle level of gill; 4 = narrow (somewhat pedunculated); 5 = with dark pigment in outer edge of right filaments (L = 7; CI = 71; RI = 85).
179. Osphradium type: 0 = spot; 1 = ridge-like and smooth; 2 = ridge-like and pectinate; 3 = elliptical and pectinate (L = 8; CI = 37; RI = 94).
180. Osphradium length: 0 = punctiform; 1 = about 2/3 of gill; 2 = shorter than 1/2 gill; 3 = equivalent to gill; 4 = small, less than 1/4 of aperture length (L = 32; CI = 12; RI = 83).
181. Osphradium anterior end shape or position: 0 = simple; 1 = strong zigzag; 2 = delicate zigzag; 3 = far from gill; 4 = with an anterior curve; 5 = with a strong, sigmoid region (L = 11; CI = 45; RI = 90).
182. Osphradium leaflets: 0 = absent; 1 = present; 2 = small projections on right side only; 3 = thick; 4 = triangular, in right side of osphradium ganglion, attached to mantle roof; 5 = somewhat separated; 6 = with dorsal-right edge on ctenidial vein; 7 = short anterior portion monopectinate (with only right filaments); 8 = possessing sharp pointed tip (L = 16; CI = 50; RI = 93).
183. Osphradium leaflets: 0 = absent; 1 = in both sides – bipectinate; 2 = left side only – monopectinate; 3 = monopectinate, with filaments on tip; 4 = monopectinate, with triangular filaments in right side; 5 = right filaments divided by a furrow; 6 = sharp projected tip; 7 = scalloped (L = 25; CI = 28; RI = 89) [– = avoids redundancy with character 182].

184. Osphradium satellite fold: 0 = absent; 1 = at left only; 2 = surrounding both sides (L = 6; CI = 33; RI = 75).
185. Osphradium anterior limit: 0 = far from mantle edge; 1 = close to mantle edge (L = 1; CI = 100; RI = 100).
186. Osphradium situation: 0 = restrict to a single point; 1 = very oblique, almost perpendicular to mantle border; 2 = slight oblique, but almost parallel to mantle border; 3 = parallel to mantle border (L = 3; CI = 100; RI = 100).
187. Siphonal fold: 0 = absent; 1 = protruding left; 2 = not protruding left (L = 2; CI = 100; RI = 100).
188. Osphradium length in unguiculate shell: 0 = more than half of pallial cavity aperture; 1 = about 15% of pallial cavity aperture; 2 = 5% of pallial cavity aperture (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 11].
189. Number of osphradium filaments in unguiculate forms: 0 = about 50; 1 = about 20; 2 = less than 10 (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 11].
190. Central fold of osphradium ganglion: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
191. Osphradium ganglion: 0 = a node; 1 = ridge-like; 2 = with three branches (L = 2; CI = 100; RI = 100).
192. Osphradium filaments: 0 = attached to mantle; 1 = projected from mantle; 2 = tall (3-4 times ganglion weight); 3 = reduction of number of left filaments (in relation of right filaments) (L = 6; CI = 50; RI = 92) [– = avoids redundancy with character 182].
193. Distance between osphradium and anterior region of gill: 0 = close; 1 = slightly separated (L = 1; CI = 100; RI = 100).
194. Distance between osphradium and posterior region of gill: 0 = close; 1 = slightly separated; 2 = very far (L = 4; CI = 50; RI = 81).
195. Sessile bipectinate osphradium symmetry: 0 = other kind of osphradium; 1 = symmetrical; 2 = right larger than left filaments (L = 9; CI = 22; RI = 95).
196. Width of osphradium in relation to gill: 0 = less than half; 1 = about as wide as (L = 1; CI = 100; RI = 100).
197. Osphradium location relative to gill: 0 = in gill axis; 1 = outside gill (L = 1; CI = 100; RI = 100).
198. Osphradium number of cells: 0 = microscopic; 1 = quantity sufficient to be easily visible (L = 3; CI = 33; RI = 85).
199. Osphradium location in pallial cavity: 0 = posterior; 1 = anterior (L = 1; CI = 100; RI = 100).

GILL

200. Gill longitudinal vascular axis: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
201. Gill number: 0 = a pair; 1 = single; 2 = absent (L = 4; CI = 50; RI = 84).
202. Gill outline: 0 = elliptical; 1 = narrow and curved inwards; 2 = curved forwards and left; 3 = broad, mainly in anterior third part; 4 = curved (concavity left) (L = 5; CI = 80; RI = 98).
203. Gill anterior end: 0 = posterior from mantle border; 1 = on mantle border; 2 = with short portion of ctenidial vein extending beyond anterior end of filaments; ? = no gill (L = 4; CI = 50; RI = 96).
204. Gill length: 0 = about 2/3 of the pallial cavity; 1 = almost same length as pallial cavity (L = 4; CI = 25; RI = 95).
205. Gill filaments form: 0 = triangular; 1 = rounded; 2 = flat; 3 = tall and thin; 4 = low, with a very long projection at left or on ctenidial vein; 5 = several times longer than wide, with hard rod; 6 = right edge strongly arched; 7 = sharply pointed; 8 = narrow and tall (L = 23; CI = 34; RI = 85).
206. Gill filament tip: 0 = central; 1 = at right; 2 = connected with each other at tip by cilia; 3 = clearly concentrated in their posterior region (L = 6; CI = 50; RI = 93).
207. Gill filaments: 0 = broad base; 1 = narrow base (three times taller than wide); 2 = elongated; 3 = clearly concentrated in their posterior region; 4 = absent (lost) (L = 9; CI = 44; RI = 91).
208. Ctenidial vein: 0 = simple; 1 = double; 2 = very broad (3-4 times broader than osphradium); 3 = compressed due a tall inner fold (L = 5; CI = 60; RI = 60).
209. Conspicuous longitudinal muscles in ventral wall of ctenidial vein: 0 = absent; 1 = present (L = 3; CI = 33; RI = 98).
210. Distance gill-rectum: 0 = broad (1 or 2 times broader than gill); 1 = very close; 2 = several times broader than gill, forming almost a chamber (L = 6; CI = 33; RI = 78).
211. Gill anterior septum-like region: 0 = absent; 1 = small, without filaments; 2 = a tall septum with filaments in its free border; 3 = only a short portion of ctenidial vein anterior to gill (L = 5; CI = 60; RI = 96).

212. Gill filament rods: 0 = same length of membranous part of filaments; 1 = extending little beyond membranous part of filaments; 2 = very long, two or three times longer than membranous part of filaments (L = 2; CI = 100; RI = 100).
213. Endostyle: 0 = absent; 1 = present at right of gill; 2 = present at left of gill; 3 = double in middle and posterior thirds (L = 4; CI = 75; RI = 95).
214. Endostyle along left side of gill: 0 = narrow; 1 = covering ctenidial vein; 2 = running in lateral surface of mantle (L = 5; CI = 60; RI = 90) [– = avoids redundancy with character 213].
215. Gill situation: 0 = longitudinal in pallial cavity; 1 = transverse, part parallel to mantle border (L = 1; CI = 100; RI = 100).
216. Gill width: 0 = less than 1/3 of that of pallial cavity; 1 = about 1/2 of that of pallial cavity (L = 3; CI = 33; RI = 86).
217. Left gill: 0 = bipectinate; 1 = monopectinate (L = 2; CI = 50; RI = 94).
218. Right gill: 0 = bipectinate; 1 = lost (L = 2; CI = 50; RI = 90).
219. Left gill longitudinal axis insertion in mantle; 0 = attached only by outer side; 1 = mostly attached in both sides; 2 = fused with mantle (L = 3; CI = 66; RI = 95).
220. Gill main attachment: 0 = visceral; 1 = pallial (L = 1; CI = 100; RI = 100).
221. Ciliary connection amongst tips of gill filaments: 0 = well developed; 1 = weak or absent (L = 2; CI = 50; RI = 95).
222. Respiratory, glandular and ciliary strings replacing gill loss: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
223. Gill (or its reminiscent) connection to auricle: 0 = indirect; 1 = direct (L = 1; CI = 100; RI = 100).

Hypobranchial gland

224. Pallial septa immersed in hypobranchial gland: 0 = absent; 1 = present; 2 = a transverse septa from mantle through hypobranchial gland (L = 8; CI = 25; RI = 90).
225. Hypobranchial gland: 0 = thick, with chambers; 1 = thin, inconspicuous; 2 = smooth, solid; 3 = white, transverse folded, hard (when in preservative); 4 = with purple lobe (L = 17; CI = 23; RI = 90).
226. Anal gland: 0 = absent; 1 = present (L = 5; CI = 20; RI = 93).
227. Hypobranchial gland: 0 = edged by pallial folds; 1 = splayed long mantle as mucosa (L = 1; CI = 100; RI = 100).
228. Hypobranchial gland: 0 = almost microscopic; 1 = easily detectable (L = 1; CI = 100; RI = 100).

VISCERAL MASS

229. Torsion: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
230. Alignment: 0 = antero-posterior; 1 = organized in U-shape (L = 1; CI = 100; RI = 100).
231. General shape: 0 = mixed with head-foot; 1 = as dorsal hump (L = 1; CI = 100; RI = 100).
232. Visceral mass at left of pallial cavity: 0 = absent; 1 = present (L = 5; CI = 20; RI = 95).
233. Location: 0 = posterior; 1 = along right side of pallial cavity (L = 2; CI = 50; RI = 97).
234. Size: 0 = of moderate size (about 1/3 of animal volume); 1 = small (L = 1; CI = 100; RI = 100).
235. Form: 0 = conic; 1 = spiral; 2 = triangular (turned posteriorly); 3 = long and fusiform; 4 = sac-like; 5 = triangular (turned forward); 6 = sac-like because of columellar re-absorption (L = 9; CI = 66; RI = 91).
236. Location: 0 = into shell only; 1 = part into foot (L = 1; CI = 100; RI = 100).
237. Haemocoel connection with visceral mass: 0 = posterior or dorsal; 1 = lateral-left (L = 1; CI = 100; RI = 100).
238. Digestive gland: 0 = a pair; 1 = single; 2 = single and separated into 2 lobes (L = 4; CI = 50; RI = 94).
239. Intestinal loops inside visceral mass: 0 = several; 1 = 1-2 only (L = 1; CI = 100; RI = 100).

CIRCULATORY SYSTEM

240. Pericardium: 0 = visceral and pallial; 1 = also connected to pallial floor; 2 = most exposed in pallial cavity roof; 3 = pericardium abbuptly narrowing in its left half (L = 5; CI = 60; RI = 92).

241. Pericardium location: 0 = anterior-left from kidney; 1 = posterior to kidney; 2 = exposed in pallial cavity roof, almost in its center; 3 = dorsal to posterior end of pallial cavity (L = 4; CI = 75; RI = 97).
242. Ampulla in anterior aorta: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
243. Aortas attachment: 0 = free from stomach; 1 = in style sac and adjacent intestine (L = 2; CI = 50; RI = 94).
244. Intestinal loop inside pericardium: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
245. Auricle end: 0 = in ventricle connection; 1 = with a portion beyond (at right) ventricle connection as a bind-sac (L = 1; CI = 100; RI = 100).
246. Auricle posterior form: 0 = somewhat spherical-triangular; 1 = short, attached to anterior inner surface of pericardium; 2 = same, but very long, tubular (L = 2; CI = 100; RI = 100).
247. Auricle: 0 = free from pericardium anterior wall; 1 = attached to inner surface of pericardium anterior wall (L = 1; CI = 100; RI = 100).
248. Posterior region of ctenidial vein between gill and auricle: 0 = long; 1 = very short (L = 1; CI = 100; RI = 100).
249. Ctenidial vein connection with auricle: 0 = in posterior end of gill; 1 = sub-terminal in gill, with a portion of the ctenidial vein beyond this connection as a blind sac; 2 = subterminal in auricle (L = 4; CI = 50; RI = 84).
250. Kidney and pericardium: 0 = occupying most of visceral anterior edge; 1 = occupying about half of visceral anterior edge (L = 3; CI = 33; RI = 93).
251. Anterior aorta; 0 = about 4 times broader than posterior aorta; 1 = several times broader than posterior aorta (L = 1; CI = 100; RI = 100).
252. Bulged portion of aorta posterior to common aorta; 0 = absent; 1 = present; 2 = present only in posterior aorta (L = 2; CI = 100; RI = 100).
253. Pericardium position: 0 = visceral, entirely posterior to gill; 1 = broad part dorsal to posterior region of gill; 2 = narrow part dorsal to posterior gill region (L = 2; CI = 100; RI = 100).
254. Auricle connection with ctenidial vein: 0 = posterior to gill, as an isolated vessel; 1 = anterior from posterior extremity of gill, with a short portion of ctenidial vein as a bind-tube; 2 = almost at middle level of gill (L = 2; CI = 100; RI = 100).
255. Auricle anterior form: 0 = obese-triangular; 1 = long, somewhat narrow, running through mantle up to ctenidial vein; 2 = triangular, with anterior edge attached to pericardium (L = 3; CI = 66; RI = 98).
256. Heart-pericardium range: 0 = about 1/4 of kidney volume; 1 = about 1/10 of kidney volume; 2 = about 1/8 of kidney volume; 3 = slightly more than 1/3 of kidney volume (L = 3; CI = 100; RI = 100).
257. Pericardium longer axis: 0 = antero-posterior (longitudinal); 1 = lateral (transverse) (L = 1; CI = 100; RI = 100).
258. Right auricle: 0 = present (diotocardian); 1 = lost (monotocardian) (L = 1; CI = 100; RI = 100).
259. Right pallial drainage to ventricle: 0 = present; 1 = absent (L = 1; CI = 100; RI = 100).
260. Ventricle and pericardium: 0 = surrounding intestine; 1 = running by site of intestine (L = 1; CI = 100; RI = 100).
261. Conspicuous vessel connecting ventral sinus of haemocoel with radular nucleus: 0 = present; 1 = absent (L = 1; CI = 100; RI = 100).

EXCRETORY SYSTEM

General

262. Number of kidneys: 0 = 2; 1 = 1 (L = 1; CI = 100; RI = 100).
263. Kidney length: 0 = less than 1/4 whorl or equivalent; 1 = more than 1/4 whorl, double lobed; 2 = more than 1/4 whorl, single lobed; 3 = more than 1/2 whorl (L = 6; CI = 50; RI = 92).
264. Kidney form: 0 = rhomboid; 1 = dorso-ventrally flattened; 2 = slender, curved and very long; 3 = oblique positioned; 4 = solid, flat and antero-posteriorly long (L = 4; CI = 100; RI = 100).

Renal tissue

265. Renal tissue: 0 = solid glandular mass in pallial cavity roof; 1 = solid glandular mass confined in a separated chamber; 2 = a thin layer of gland and vessels; 3 = hollow, with two chambers; 4 = hollow, with single

chamber; 5 = U-shaped lobe with dorsal branch large, surrounding intestine; 6 = thin, most exposed in pallial cavity; 7 = with successive broad folds converging to a central vessel; 8 = with ventral kidney lobe "U"-shaped; 9 = comprising a broad chamber limited by two lobes, one lobe septate attached to rectum and the other flattened dorso-ventral (L = 13; CI = 69; RI = 97).

266. Form of renal lobes: 0 = amorphous; 1 = 2 similar sized lobes; 2 = two lobes, dorsal lobe very smaller; 3 = single ventral lobe; 4 = single anterior lobe; 5 = a chamber between visceral mass and first intestine loops; 6 = single massive dorsal lobe; 7 = elongated and narrow; 8 = single flat dorsal lobe (L = 16; CI = 50; RI = 94).
267. Kidney isolated anterior lobe: 0 = absent; 1 = in mantle roof; 2 = two, anterior lobe attached to rectum, anterior lobe mostly solid; 3 = same, with anterior lobe mostly hollow (L = 4; CI = 75; RI = 85).
268. Number of kidney lobes: 0 = none, a single solid mass; 1 = two; 2 = 1 (dorsal); 3 = dorsal but with thin, with transverse folds (L = 3; CI = 100; RI = 100).
269. Anterior fusion between both renal lobes: 0 = absent (solid or lobes separated from each other); 1 = part connected to each other in anterior-right region, at least by a vessel; 2 = forming a single large mass (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 268].

Annexed structures

270. Intestinal loops in kidney chamber connected by mesentery: 0 = absent; 1 = one; 2 = two or more (L = 5; CI = 40; RI = 95).
271. Intestinal portion crossing through kidney: 0 = absent; 1 = longitudinal; 2 = transverse; 3 = only anterior 1/4 connected to renal tissue (L = 3; CI = 100; RI = 100).
272. Intestinal relation to renal tissue: 0 = connected to lobe or renal tissue; 1 = running almost free from lobes (connected only by a mesentery flap and sometimes in short anterior region); 2 = lobe away from intestine (L = 2; CI = 100; RI = 100).
273. Anterior septate chamber: 0 = absent; 1 = present, with two equal-sized series of septa; 2 = present, with two asymmetrical series of septa (L = 2; CI = 100; RI = 100).
274. Connection between longitudinal fold of renal anterior chamber with nephrostome edge: 0 = absent, 1 = present (L = 1; CI = 100; RI = 100).
275. Closed (tubular) ureter: 0 = absent; 1 = present; 2 = as primary and secondary ureter (L = 2; CI = 100; RI = 100).
276. Communication between kidney and ureter; 0 = absent; 1 = an open pore; 2 = a muscular papilla (L = 2; CI = 100; RI = 100).
277. Urinary gutter: 0 = absent; 1 = a furrow along right margin of pallial cavity and head; 2 = a fold along rectum and pallial gonoducts (L = 3; CI = 66; RI = 93).
278. Collar vessel: 0 = inserted in kidney; 1 = inserted in auricle (L = 1; CI = 100; RI = 100).
279. Vessel in pallial roof insertion in left margin of kidney: 0 = absent or inconspicuous; 1 = slightly perpendicular to kidney (L = 1; CI = 100; RI = 100).
280. Adrectal sinus: 0 = simple, separated from kidney by a membrane; 1 = continuous to kidney; 2 = possessing aperture close to anus (L = 2; CI = 100; RI = 100).
281. Connection of adrectal sinus with kidney: 0 = inconspicuous; 1 = surrounding intestine; 2 = separated from intestine; 3 = forming a pulmonary vein (L = 3; CI = 100; RI = 100).
282. Efferent renal vessel coming from head-foot: 0 = inconspicuous; 1 = very broad, inserted directly in dorsal lobe; 2 = possessing conspicuous branch vessel surrounding dorsal lobe of kidney (L = 3; CI = 66; RI = 96).

Nephrostome

283. Nephrostome allocation: 0 = in middle region of membrane between kidney and pallial cavity; 1 = close to posterior end of pallial cavity; 2 = inside ureter; 3 = connected by an anterior chamber; 4 = slit-like, situated close to rectum; 5 = wide opened, protected by a flap of gonoduct; 6 = far removed from renal chamber; 7 = lacking fold of renal lobe protecting internally; 8 = inner region protected at right by nephridial gland vessel (L = 9; CI = 88; RI = 98).

284. Nephrostome type: 0 = a papilla preceded by renal tissue; 1 = isolated in central region of the membrane between the renal and pallial cavities, free from renal tissue (L = 1; CI = 100; RI = 100).

Nephridial gland

285. Nephridial gland: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
286. Nephridial gland type: 0 = of medium size (about 1/2 of the membrane between the kidney and pericardium chambers); 1 = very large; 2 = very small; 3 = clearly broader anteriorly; 4 = thin and narrow (L = 11; CI = 45; RI = 96) [– = avoids redundancy with character 285].
287. Nephridial gland vessel: 0 = inconspicuous; 1 = large, anterior region septum-like, inserted at right of nephrostome (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 285].
288. Nephridial gland; 0 = absent; 1 = with transverse folds; 2 = irregular, mostly longitudinal folds; 3 = with a lobe slightly large, massive, with a well-developed vessel in its center (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 285].
289. Kidneys symmetry; 0 = symmetrical; 1 = right kidney smaller than left kidney; 2 = right kidney lost (L = 2; CI = 100; RI = 100).
290. Kidney inner papillate main chamber: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

DIGESTIVE SYSTEM

Anterior structures

291. Accessory boring organ (ABO) close to mouth: 0 = absent; 1 = present in proboscis ventral tip; 2 = same, trilobed (L = 2; CI = 100; RI = 100).
292. Rhynchodeal wall: 0 = absent or narrow; 1 = covering anterior 2/3 and dorsal region of haemocoel; 2 = never eversible; 3 = weakly muscular, barely eversible (L = 4; CI = 75; RI = 97).
293. Rhynchodeal wall forming a transverse membranous platform separating haemocoel into rhynchodeal and remaining foregut chambers: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 292].
294. Secondary muscular sac in posterior-dorsal region of rhynchostome: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
295. Non-retractile introvert: 0 = absent; 1 = present, conical; 2 = present as an inverted cone; 3 = same, with tentacles in edge (L = 3; CI = 100; RI = 100).
296. Retractile introvert: 0 = absent; 1 = with sphincter in distal edge; 2 = same, very long (L = 2; CI = 100; RI = 100).
297. Sphincter in rhynchostome: 0 = absent or weak; 1 = well-developed (L = 3; CI = 33; RI = 80).
298. Rhynchodeal wall musculature: 0 = no rhynchodeal wall; 1 = thick; 2 = weak; 3 = almost absent (a membrane) (L = 4; CI = 75; RI = 99) [– = avoids redundancy with character 292].
299. Rhynchodeal wall gland: 0 = absent, 1 = present at right; 2 = covering entire inner surface (L = 3; CI = 66; RI = 50).
300. Proboscis retractor muscles: 0 = absent; 1 = a ventro-lateral pair; 2 = several pairs surrounding proboscis base (L = 3; CI = 66; RI = 99).
301. Accessory proboscis structure: 0 = absent; 1 = present (L = 2; CI = 50; RI = 50).
302. Situation of distal end of retractor proboscis muscle: 0 = absent; 1 = close to apex; 2 = close to middle region (L = 2; CI = 100; RI = 100).

Buccal mass

303. Pair of lateral expansions of mouth for food capture: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
304. Buccal mass size: 0 = normal (larger than 1/4 of haemocoel); 1 = reduced (about 1/8 of haemocoel); 2 = absent (loss) (L = 9; CI = 22; RI = 85).
305. Oral tube: 0 = thin and conic; 1 = thick and cylindrical; 2 = relatively long; 3 = slender and narrow (L = 5; CI = 60; RI = 96) [– = avoids redundancy with character 309].

306. Oral tube connected with venom gland: 0 = short; 1 = medium (about half of proboscis length); 2 = long (about same proboscis length) (L = 2; CI = 100; RI = 100).
307. Sphincter in oral tube at some distance from mouth: 0 = absent; 1 = present; 2 = additionally more developed, almost free from wall (L = 4; CI = 50; RI = 88).
308. Secondary outer muscular oral tube layer: 0 = absent; 1 = some fibers only; 2 = very conspicuous (L = 2; CI = 100; RI = 100).
309. Oral tube (connects mouth with buccal mass): 0 = very short (almost absent); 1 = long (about half of the length of buccal mass or more) (L = 1; CI = 100; RI = 100).
310. Dorsal folds of buccal mass: 0 = absent to low, inconspicuous; 1 = broad, tall; 2 = with transverse furrows (L = 4; CI = 50; RI = 97).
311. Dorsal chamber of buccal mass: 0 = absent; 1 = deep; 2 = shallow (L = 3; CI = 66; RI = 97).
312. Dorsal folds of buccal mass inner surface: 0 = continuous in esophagus; 1 = finishing after odontophore level; 2 = originated from ventral positioned jaw plates (L = 3; CI = 66; RI = 75) [– = avoids redundancy with character 310].
313. Jaws: 0 = absent; 1 = pair of small plates; 2 = very large (most of dorsal surface of oral cavity); 3 = plates fused in median line; 4 = two plates connected with each other, with a median hook; 5 = a uniform chitinous thin plate; 6 = with a middle anterior spine; 7 = serrated; 8 = a single, large, tranparent, conical plate; 9 = single dorsal beak (L = 21; CI = 42; RI = 92) [– = avoids redundancy with character 314].
314. Jaw plates; 0 = absent; 1 = dorsal; 2 = dorsal and ventral (L = 2; CI = 100; RI = 100).
315. Jaw type: 0 = absent; 1 = thick; 2 = thin; 3 = pointed; 4 = thin curved plates; 5 = with strong hook; 6 = adapted for perforating; 7 = thick, with reinforcement protecting oral cavity lying posteriorly (L = 17; CI = 41; RI = 92) [– = avoids redundancy with character 314].
316. Buccal mass and esophagus connection with ventral-right surface of haemocoel: 0 = simple net of minute muscular fibers; 1 = additionally by a mesentery-like membrane; 2 = strong muscles connecting posterolateral surface of odontophore with adjacent region of proboscis inner surface (L = 3; CI = 66; RI = 95).
317. Buccal special glands opening in anterior-ventral region of oral tube: 0 = absent, 1 = single, solid; 2 = 2 pairs; 3 = unpaired accessory salivary gland (snout gland); 4 = accessory salivary glands; 5 = unpaired, balloon-like, hollow (L = 11; CI = 45; RI = 85).
318. Paired buccal glands: 0 = absent; 1 = larger hollow gland; 2 = larger solid-glandular gland (L = 2; CI = 100; RI = 100).
319. Buccal portion of proboscis: 0 = absent; 1 = about 1/3 of remainning proboscis length; 2 = about 2/3 longer than remaining proboscis length; 3 = 3-4 times longer than haemocoel (L = 7; CI = 42; RI = 98) [– = avoids redundancy with character 99].
320. Buccal mass situation: 0 = close to mouth; 1 = far from it, in base of proboscis (L = 1; CI = 100; RI = 100).
321. Buccal mass type: 0 = with a scarcely muscular dorsal wall; 1 = a somewhat muscular rounded cavity; 2 = same, with muscle thick and clearly separated from wall (L = 3; CI = 66; RI = 97).
322. Aperture of radular sac into buccal mass: 0 = in posterior region or via odontophore; 1 = in middle region; 2 = in anterior region (L = 6; CI = 33; RI = 90).
323. Muscular connection of buccal mass with proboscis base: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 99].
324. Ventral chitinous platform within the oral tube up to ventral region of odontophore: 0 = absent; 1 = present; 2 = additionally possessing spines in anterior half (L = 2; CI = 100; RI = 100).
325. Jaw tubular anterior region: 0 = absent; 1 = opened; 2 = closed (L = 2; CI = 100; RI = 100).
326. Muscular flap in oral tube for grasping radular tooth; 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

Odontophore

327. Odontophore: 0 = present; 1 = reduced; 2 = absent (L = 12; CI = 16; RI = 84).
328. Jaw and peri-buccal muscles – mj: 0 = diffuse; 1 = 2 broad bands; 2 = also forming a muscular plate in median-anterior region of odontophore, between its cartilages; 3 = two separate bands projected laterally; 4 = forming a circular band; 5 = forming a muscular plate projected anterior to cartilages (L = 5; CI = 100; RI = 100).
329. Mj insertion on cartilages: 0 = only in their outer surface; 1 = also in their inner surface; 2 = inserted along anterior-lateral region, running externally and anteriorly (L = 2; CI = 100; RI = 100).

330. Location of pair mj: 0 = in anterior wall of the buccal mass; 1 = in a form of 2 well defined bundles; 2 = also connected to m6 (L = 2; CI = 100; RI = 100).
331. Ma: 0 = absent; 1 = present and single; 2 = multiple; 3 = very wide and thick (L = 3; CI = 100; RI = 100).
332. M1a: 0 = absent; 1 = present; 2 = m1a (towards anterior); 3 = dorsal, close to median line; 4 = inserted in dorsal-middle region of buccal mass, running anteriorly originated from haemocoel (L = 9; CI = 44; RI = 94).
333. M1b: 0 = absent; 1 = double; 2 = single mass; 3 = laperal positioned, running ventrally; 4 = inserted in dorsal-middle region of buccal mass, running anteriorly attached to proboscis, covered by (m1c) (L = 4; CI = 100; RI = 100).
334. M2 as pair of retractor muscles of buccal mass: 0 = absent; 1 = present; 2 = narrow and long, inserting posteriorly (L = 11; CI = 18; RI = 89).
335. Insertion of pair m2: 0 = lacking; 1 = inserted in lateral-posterior side of odontophore; 2 = inserted in middle-ventral side of odontophore; 3 = narrow, running attached along esophagus; 4 = inserted in posterior region of cartilages and in medial region of posterior odontophore surface (L = 11; CI = 36; RI = 95).
336. Pair m2: 0 = free from radular sac; 1 = surrounding radular sac; 2 = with branch inserted in lateral surface of esophagus, in its region close to odontophore (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 334].
337. Pair m2: 0 = free from nerve ring; 1 = part passing through nerve ring; 2 = with a small branch passing through nerve ring (L = 5; CI = 40; RI = 95) [– = avoids redundancy with character 334].
338. Pair m2: 0 = absent; 1 = connected with each other posterior to odontophore; 2 = with branch inserted in lateral surface of esophagus, in its region close to odontophore; 3 = as radular muscle (L = 5; CI = 60; RI = 97) [– = avoids redundancy with character 334].
339. Abductor of jaw plates: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
340. Pair m2a (as continuation of m2): 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
341. Pair m2a connected to m4: 0 = absent; 1 = present, part inserted to m4; 2 = present, inserted mostly in tissue on radula (L = 2; CI = 100; RI = 100).
342. Pair m2a connected to m4, origin: 0 = absent; 1 = connected to inner surface of proboscis shortly posterior to buccal mass; 2 = running along esophagus (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 341].
343. M3a: 0 = absent; 1 = present as somewhat thick in region dorsal to radular sac; 2 = with additional transverse (dorso-ventral) fibers (L = 2; CI = 100; RI = 100).
344. M3b: 0 = absent; 1 = pair with dorso-ventral fibers; 2 = single, with transverse (latero-lateral) fibers; 3 = both (H-fashion); 4 = simple; 5 = thin, united with each other anterior to radular nucleus; 6 = thick, united with each other anterior to radular nucleus; 7 = thick, inserted in radular nucleus; 8 = dorsal, connecting posterior region of cartilages with dirsal region of subradular cartilage; 9 = well-developed layer immersed in ventral membrane evolving odontophore; 10(A) = transverse thin layer in odontophore region contacting esophagus; 11(B) = present, transverse, close to median line, surrounding radular sac (L = 16; CI = 75; RI = 92).
345. M4 pair: 0 = composed by several muscles; 1 = composed by 2 pairs of muscular layers surrounding odontophore cartilages; 2 = a single pair of large mass surrounding odontophore cartilages (L = 3; CI = 66; RI = 98).
346. M4 connection with tissue on middle region of radula ('to'): 0 = absent; 1 = via m9; 2 = present; 3 = also in subradular cartilage (L = 5; CI = 60; RI = 97).
347. Ventral and dorsal branches of m4 pair: 0 = not connected anteriorly; 1 = connected anteriorly; 2 = narrow, contouring cartilages posterior surface; 3 = originating in mj along median line; 4 = possessing insertion of m2a pair; 5 = as support of anterior muscular plate (L = 6; CI = 83; RI = 99).
348. Pair m4 posterior connection with subradular membrane: 0 = absent; 1 = present; 2 = connected directly splayed to subradular membrane (L = 3; CI = 66; RI = 97).
349. Pair m4 ventral branch: 0 = connected to dorsal branch; 1 = separated anteriorly; 2 = part originated in inner surface of cartilages; 3 = inserting along medial surface of cartilages (L = 3; CI = 100; RI = 100).
350. Ventral tensor muscle of radula: 0 = present; 1 = much reduced (m11) (L = 2; CI = 50; RI = 98).
351. Dorsal tensor muscle of radula: 0 = weak; 1 = strong (m4 + m5); 2 = additionally originating in opposed sides of posterior end of cartilages (L = 3; CI = 66; RI = 97).

352. Pair m4 connection with pair m2: 0 = narrow or absent; 1 = broad, forming a posterior muscular platform (L = 1; CI = 100; RI = 100).
353. Dorsal tensor muscles of radula m4 and m5: 0 = separated from each other; 1 = continuous with each other, surrounding cartilages edge (L = 1; CI = 100; RI = 100).
354. Pair m4, branch connected to posterior vertex of cartilages: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
355. Dorsal and ventral branches of m4: 0 = free from each other anteriorly; 1 = connected anteriorly by means of a cartilage pair; 2 = connected anteriorly (L = 2; CI = 100; RI = 100).
356. M5 pair: 0 = connected with odontophore cartilages; 1 = on m4; 2 = lateral-positioned (L = 2; CI = 100; RI = 100).
357. M5 pair form: 0 = short and broad; 1 = long and thin; 2 = very broad and slight short; 3 = weak and very small (L = 2; CI = 100; RI = 100).
358. Wide medial connection m5-m5: 0 = absent; 1 = present (L = 3; CI = 33; RI = 96).
359. Pair m5 insertion: 0 = only in dorsal side of radula; 1 = in lateral side of radula, encroaching both sides (dorsal and ventral); 2 = wide, along a considerable portion of radular sac (L = 4; CI = 50; RI = 97).
360. Horizontal muscle – m6: 0 = edging most of medial surface of odontophore cartilages; 1 = edging less than 2/3 of this surface (L = 2; CI = 50; RI = 98).
361. M6: 0 = narrow and thin; 1 = broad and thick; 2 = very thick; 3 = almost vestigial, only 1/10 of cartilages length; 4 = thin, restricted to anterior third of cartilages (L = 8; CI = 50; RI = 95).
362. Anterior thickness of m6: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
363. M6: 0 = single; 1 = double (m6 plus m6a); 2 = connected with inner-ventral surface of radular sac ('ih'); 3 = thin, connected in inner edge of cartilages (L = 3; CI = 100; RI = 100).
364. M6a type: 0 = similar sized to m6; 1 = m6 and m6a narrow; 2 = m6a dorsal to m6 (L = 4; CI = 75; RI = 96) [– = avoids redundancy with character 363].
365. M6a connection with adjacent ventral surface of mj platform: 0 = absent; 1 = present (L = 2; CI = 50; RI = 91) [– = avoids redundancy with character 363].
366. Ligament between ventral surface of m6 (horizontal muscle) and radular sac ('ih'): 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
367. Horizontal muscle (m6) position; 0 = between both cartilages; 1 = lying outside cartilages (L = 1; CI = 100; RI = 100).
368. Pair m7: 0 = absent; 1 = present; 2 = inserting in single fan-like shape (L = 5; CI = 40; RI = 96).
369. Pair m7a (inserted in m5): 0 = absent; 1 = present; 2 = connected to m4; 3 = a 'm7b' (in dorsal surface); 4 = originated among m4 fibers (L = 6; CI = 66; RI = 90).
370. Posterior connection m7-m11 with snout: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
371. Pair m7 origin: 0 = of middle region of m4 median-ventral surface; 1 = in anterior margin of m4; 2 = extremely narrow; 3 = in inner-dorsal edge of anterior region of pair m4 (L = 5; CI = 80; RI = 98) [– = avoids redundancy with character 368].
372. Pair m7: 0 = originating in median border of ventral m4 branch; 1 = originating in anterior border of ventral m4 branch (L = 7; CI = 28; RI = 94) [– = avoids redundancy with character 368].
373. Insertion of m7: 0 = 2 bundles; 1 = single bundle (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 368].
374. Approximator muscles of cartilages: 0 = present; 1 = absent or part of m4 (L = 1; CI = 100; RI = 100).
375. Radular muscle ('m8'): 0 = absent; 1 = short and broad; 2 = narrow and long; 3 = true pair m8 located in short portion of dorsal-outer edge of cartilages (L = 4; CI = 75; RI = 90).
376. Radular muscle ('m8a'): 0 = absent; 1 = connected to outer membrane around odontophore; 2 = free from any membrane; 3 = mair m8 on outer surface of cartilages (L = 4; CI = 75; RI = 95).
377. Pair m9: 0 = absent; 1 = connecting m4 with tissue on radula preceding oral cavity ('to'); 2 = similar, 'V' in section (L = 2; CI = 100; RI = 100).
378. Pair m10 insertion in odontophore ventral surface: 0 = lacking or posterior; 1 = anterior (L = 1; CI = 100; RI = 100).
379. Pair m10: 0 = absent; 1 = origin on m4; 2 = origin on m5 (L = 3; CI = 66; RI = 97).
380. Pair m10 fashion: 0 = absent; 1 = small; 2 = large (each about 1/3 odontophore width); 3 = immersed in mj; 4 = broad and thick; 5 = narrow and thin; 6 = double (L = 10; CI = 60; RI = 97) [– = avoids redundancy with character 379].

381. Pair m10a: 0 = absent; 1 = present; 2 = very thick, forming a single block (L = 2; CI = 100; RI = 100).
382. Pair m10c: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
383. Pair m11 (ventral tensor): 0 = broad, as ventral tensor muscle of radula; 1 = narrow; 2 = absent (L = 10; CI = 20; RI = 91).
384. Pair m11: 0 = origin in m4; 1 = free from m4; 2 = with muscular connection with dorsal branch of pair m4; 3 = secondarily lost (by ontogeny) (L = 3; CI = 100; RI = 100).
385. Pair m11a: 0 = absent, 1 = present (L = 3; CI = 33; RI = 0).
386. Pair m11 (not connected to ventral haemocoel = m4v): 0 = part of m4; 1 = attached to subradular membrane (L = 1; CI = 100; RI = 100).
387. Pair m11: 0 = free from m2; 1 = inserted in m2 in its region posterior to odontophore; 2 = with insertion surrounding ventral region of radular sac base; 3 = inserting dorsally to m7 (L = 5; CI = 60; RI = 95).
388. Pair m12 (annexed to m6): 0 = absent; 1 = present; 2 = elongated; 3 = covered by pair m4; 4 = running antero-posteriorly parallel to m6; 5 = short and with insertions in subradular membrane (L = 9; CI = 55; RI = 92).
389. Pair m13: 0 = absent; 1 = present, separated from m5; 2 = present, as part of m5 (L = 2; CI = 100; RI = 100).
390. Pair m13a (connecting lateral surface of odontophore with ventral surface of oral tube: 0 = absent; 1 = short; 2 = very long, with anterior region close to middle level of oral tube (L = 2; CI = 100; RI = 100).
391. Pair m14 (additional protractors): 0 = absent; 1 = present (L = 5; CI = 20; RI = 96).
392. Pair m14a: 0 = absent; 1 = lateral; 2 = ventral (L = 3; CI = 66; RI = 94).
393. Pair m15 (annex to m10): 0 = absent; 1 = as part of buccal walls (L = 1; CI = 100; RI = 100).
394. Pair m16: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
395. Pair mj (jaws and buccal muscles) insertion mixed with those of m6 (horizontal muscle): 0 = absent (both muscles separated); 1 = present (L = 1; CI = 100; RI = 100).
396. Mt: 0 = absent; 1 = present; 2 = as two bands ('mc') (L = 3; CI = 66; RI = 96).
397. Odontophore cartilages: 0 = separated pair; 1 = connected anteriorly; 2 = producing a very elongated, elliptical odontophore shape (L = 4; CI = 50; RI = 90).
398. Odontophore cartilages anterior portion clearly wider than posterior portion: 0 = absent (cartilages uniformly elongated); 1 = present; 2 = several times longer than wide (L = 2; CI = 100; RI = 100).
399. Odontophore tube connecting odontophore to the oral tube: 0 = absent or very short; 1 = long (L = 1; CI = 100; RI = 100).
400. Odontophore cartilage outline: 0 = elliptical; 1 = elongated (more than 3 times longer than wide); 2 = more than 10 times longer than wide (L = 2; CI = 100; RI = 100).
401. Bulged basal portion of radular sac for storing teeth: 0 = absent (odontophore present); 1 = present (L = 2; CI = 100; RI = 100).
402. Additional flap covering tissue preceding radular region exposed into buccal cavity "to": 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
403. Number of main cartilages: 0 = more than 1 pair; 1 = single pair; 2 = single pair fused anteriorly (L = 6; CI = 33; RI = 85).
404. Pair of anterior accessory cartilages: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
405. Pair mx: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
406. Posterior muscular flap covering part of odontophore separating it from esophageal aperture: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

RADULA

GERAL

407. Subradular cartilage in buccal cavity: 0 = narrow; 1 = broad; 2 = forming a deep cover covering anterior end (L = 2; CI = 100; RI = 100).
408. Radular sac length: 0 = long, more than 1.5 times odontophore; 1 = short (about same length of buccal mass); 2 = several times longer than buccal mass; 3 = two or three times odontophore length; 4 = lost (L = 22; CI = 18; RI = 84).

409. Radular nucleus form: 0 = simple; 1 = broad, almost bifid; 2 = entire sac Y-shaped; 3 = conspicuously bifid (L = 3; CI = 100; RI = 100).
410. Radular type: 0 = docoglossan or docoglossan-like (stereoglossan); 1 = rhipidoglossan; 2 = taenioglossan (7 teeth per row); 3 = stenoglossan or rachiglossan (3 teeth per row); 4 = toxoglossan; 5 = nematoglossan; 6 = with 9 teeth per row; 7 = only rachidian; 8 = several uniform teeth per row (L = 11; CI = 72; RI = 96).
411. Tooth mineralization: 0 = present; 1 = absent (L = 1; CI = 100; RI = 100).
412. Radular condition: 0 = rigidiglossan (docoglossan); 1 = flexiglossan (L = 1; CI = 100; RI = 100).
413. Marginal, cuspless pairs of low plates; 0 = present; 1 = absent (L = 1; CI = 100; RI = 100).
414. Teeth row transverse alignment: 0 = absent; 1 = weak; 2 = almost in same line (L = 2; CI = 100; RI = 100).

Rachidian

415. Rachidian form: 0 = narrow, simple; 1 = broad; 2 = tall and curved; 3 = with tall central cusp; 4 = almost a square; 5 = wide, comb-like; 6 = weak, narrow, with a median cusp; 7 = absent; 8 = very long, tall, brush-like (L = 16; CI = 50; RI = 94).
416. Rachidian cusps: 0 = few (1-2); 1 = multicuspid; 2 = secondary cusps large (about half than central cusp); 3 = cusps uniformly sized; 4 = with 3 cusps on tip; 5 = hook-like; 6 = inconspicuous or absent; 7 = boomerang-like, with 3 equidistant cusps in cutting edge (L = 18; CI = 33; RI = 92).
417. Rachidian basal cusps: 0 = absent; 1 = broad; 2 = more than 1 pair of small cusps; 3 = basal-lateral; 4 = pair of basal, cusp-like, reinforcements; 5 = simple, tall pair of cusps (L = 6; CI = 66; RI = 95).
418. Rachidian tip: 0 = broad; 1 = pointed; 2 = with central cusp outstandingly large; 3 = with special arrangement for perforation (L = 5; CI = 60; RI = 97).
419. Rachidian arched base with apical region close to cut edge: 0 = absent; 1 = present (L = 3; CI = 33; RI = 86).
420. Rachidian arched lateral edges: 0 = absent; 1 = present (L = 2; CI = 50; RI = 85).
421. Rachidian proximal edge: 0 = convex; 1 = concave (L = 3; CI = 33; RI = 71).

Lateral

422. Lateral teeth number: 0 = several (about 5) pairs; 1 = single pair; 2 = two pairs; 3 = none (L = 6; CI = 50; RI = 91).
423. Lateral teeth tip: 0 = multicuspid; 1 = 1-2 cusps; 2 = trifid; 3 = with 3 cusps; 4 = lacking cusps; 5 = sharp pointed (L = 13; CI = 38; RI = 92).
424. Lateral teeth shape: 0 = different from rachidian; 1 = tip tends to be similar shaped to rachidian; 2 = more than twice rachidian; 3 = with curved inwards, bifid tip (L = 4; CI = 75; RI = 98).
425. Lateral tooth tip: 0 = elongated, turned inwards; 1 = elongated, turned forwards; 2 = wide, comb-like; 3 = curved, low, multicupid; 4 = absent (loss); 5 = hook-like (L = 5; CI = 100; RI = 100).
426. Lateral tooth basal cusp well marked: 0 = present; 1 = absent; 2 = with basal-inner, cusp-like reinforcement (L = 4; CI = 50; RI = 92).
427. Lateral tooth outer edge cusps: 0 = 5-7; 1 = many; 2 = absent (L = 4; CI = 50; RI = 97).
428. Lateral tooth inner edge: 0 = many cusps; 1 = lacking cusps; 2 = a single, subterminal cusp (L = 7; CI = 28; RI = 92).
429. Lateral tooth reinforcement in lateral-distal edge articulating with neighbor tooth: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

Marginal

430. Marginal teeth number: 0 = none; 1 = many; 2 = 2 pairs (L = 6; CI = 33; RI = 94).
431. Marginal teeth shape: 0 = similar to each other; 1 = different from each other (L = 2; CI = 50; RI = 97).
432. Marginal teeth: 0 = absent; 1 = spoon shaped; 2 = hooked; 3 = pointed; 4 = bifid; 5 = 3 cusps; 6 = brush-like; 7 = wishbone shaped in base, sharp pointed tip; 8 = harpoon-like (L = 18; CI = 44; RI = 95) [– = avoids redundancy with character 430].

433. Inner and outer marginal teeth tip: 0 = with cusps; 1 = without cusps; 2 = with blunt pointed tip; 3 = similar shape of lateral tooth; 4 = outer edge of inner marginal tooth with many cusps; 5 = a series of elongated cusps aligned distally (L = 5; CI = 80; RI = 96) [– = avoids redundancy with character 430].
434. Inner and outer marginal teeth length: 0 = little more than rachidian width; 1 = more than twice rachidian width; 2 = more than 4 times rachidian width (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 430].
435. Inner and outer marginal teeth cusps: 0 = absent; 1 = in both sides of tip; 2 = only in tip inner margin; 3 = with 3 cusps; 4 = brush-like; 5 = lacking cusps; 6 = with 2 cusps; 7 = series of small cusps in harpoon-like tooth tip, edging its aperture (L = 12; CI = 58; RI = 95) [– = avoids redundancy with character 430].
436. Outer marginal tooth tip: 0 = with cusps; 1 = hook-like; 2 = clearly sigmoid; 3 = with subterminal cusps in inner edge; 4 = shorter and broader then inner marginal tooth; 5 = an elliptical aperture in distal orifice of harpoon-like tooth (L = 7; CI = 71; RI = 96).
437. Outer marginal tooth size: 0 = about same width as inner marginal (slightly narrower only); 1 = about half of inner marginal width (L = 3; CI = 33; RI = 77).
438. Outer marginal tooth base: 0 = simple, separated from inner marginal base; 1 = with a basal reinforcement and articulation with inner marginal tooth base; 2 = performing an S-shape (L = 2; CI = 100; RI = 100).
439. Inner marginal teeth inner edge: 0 = no cusp; 1 = middle single cusp; 2 = basal cusp (L = 4; CI = 50; RI = 81).
440. Inner marginal tooth apex: 0 = rounded; 1 = sharp pointed; 2 = with additional 3-4 subterminal cusps in inner edge (L = 4; CI = 50; RI = 97).
441. Hollow chitinous tube in marginal tooth base: 0 = absent; 1 = present (L = 2; CI = 50; RI = 91).
442. Single, bub-terminal barb in outer edge: 0 = absent or not harpoon like; 1 = present (L = 2; CI = 50; RI = 90).
443. Single, sub-terminal barb in inner edge: 0 = absent; 1 = present (L = 3; CI = 33; RI = 50).
444. Harpoon-like tooth form: 0 = not harpoon-like; 1 = short and conic; 2 = long and narrow (L = 3; CI = 66; RI = 94).

SALIVARY GLANDS

445. Salivary glands: 0 = absent; 1 = present (L = 7; CI = 14; RI = 45).
446. Salivary glands: 0 = present as 2 separated masses; 1 = a single fused mass; 2 = small mass in opposite side of buccal mass separated by loops of venom gland; 3 = clustering anterior to nerve ring (L = 17; CI = 23; RI = 91) [– = avoids redundancy with character 445].
447. Salivary glands size: 0 = large, occupying about 1/3 to half of haemocoel volume; 1 = very small; 2 = two semi-spherical masses; 3 = greatly modified in position (L = 14; CI = 28; RI = 92) [– = avoids redundancy with character 445].
448. Type: 0 = glandular; 1 = tubular; 2 = two separated masses of elliptical outline posterior to nerve ring; 3 = filiform, small; 4 = with glandular lobe additional, lying anterior to both proboscis gland, orange in color, with undulated anterior edge; 5 = right tissue divided forming two proboscis glands (L = 7; CI = 85; RI = 93) [– = avoids redundancy with character 445].
449. Location of glandular tissue: 0 = only posterior to nerve ring; 1 = anterior and posterior to nerve ring; 2 = only anterior to nerve ring (L = 8; CI = 25; RI = 95).
450. Salivary ducts: 0 = absent or narrow; 1 = wide, passing though nerve ring; 2 = running free from anterior esophagus (connected only by muscle fibers); 3 = very short, running immersed in dorsal folds of buccal mass; 4 = robust, free from nerve ring (L = 7; CI = 57; RI = 91).
451. Ducts anterior region: 0 = free from dorsal folds of buccal mass; 1 = passing immersed in these folds (L = 2; CI = 50; RI = 98) [– = avoids redundancy with character 450].
452. Aperture in dorsal wall of buccal mass: 0 = middle; 1 = anterior; 2 = posterior (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 450].
453. Right proboscis gland: 0 = absent; 1 = as part of salivary glands; 2 = separated from salivary glands; 3 = gland double (L = 3; CI = 100; RI = 100).
454. Left proboscis gland: 0 = absent; 1 = as part of salivary glands; 2 = separated from salivary glands (L = 2; CI = 100; RI = 100).

455. Salivary glands insertion: 0 = in dorsal wall of buccal mass; 1 = in buccal mass close to radular sac; 2 = in radular sac (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 450].
456. Aperture of ducts of salivary glands: 0 = in median side of dorsal folds; 1 = in lateral side of dorsal folds; 2 = in ventral side of buccal cavity (L = 5; CI = 40; RI = 92) [– = avoids redundancy with character 450].
457. Accessory salivary glands: 0 = absent; 1 = a pair of hollow sacs; 2 = pair of solid glands; 3 = single; 4 = very long, narrow, convolute, inserting in oral tube (L = 9; CI = 44; RI = 82).
458. Size of accessory salivary glands: 0 = large; 1 = very small; 2 = very large; 3 = glands becoming narrow suddenly in level of buccal mass (L = 6; CI = 66; RI = 91) [– = avoids redundancy with character 457].
459. T-shaped duct of accessory salivary glands: 0 = absent; 1 = present (L = 2; CI = 50; RI = 66).
460. Salivary glands: 0 = clustering close to nerve ring; 1 = 2 small and long masses just posterior to buccal mass; 2 = very narrow and long (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 450].
461. Ducts of salivary glands running immersed in esophageal latero-dorsal wall: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

Esophagus

462. Position of esophagus origin: 0 = in lateral-dorsal region of odontophore; 1 = in its posterior region (L = 2; CI = 50; RI = 98).
463. Anterior esophagus: 0 = a simple tube; 1 = with a pair of pouches; 2 = one pouch; 3 = several narrow longitudinal folds; 4 = few (2-4) broad longitudinal folds; 5 = narrow and long; 6 = thickly muscular, with most muscles originated from proboscis base; 7 = with continuous thick muscular walls of anterior and posterior esophagus; 8 = reduced (very short); 9 = a wide crop (L = 19; CI = 47; RI = 94).
464. Esophageal pouches: 0 = absent; 1 = simple diverticulum; 2 = covered with papillae; 3 = with a dorsal fold; 4 = single pouch papillate; 5 = single and long; 6 = a pair (L = 13; CI = 46; RI = 89) [– = avoids redundancy with character 463].
465. Anterior esophagus inner surface: 0 = smooth or with low folds; 1 = with a pair of tall longitudinal folds; 2 = with gland between both folds (L = 2; CI = 100; RI = 100).
466. Special pair of blood vessels connected to esophageal pouches: 0 = absent; 1 = present (L = 2; CI = 50; RI = 91).
467. Middle esophagus: 0 = narrow; 1 = bulging; 2 = extremely narrow; 3 = with splayed glandular tissue, mucose; 4 = gland confined in a ventral diverticle; 5 = thick muscular; 6 = differentiated whitish gland (L = 17; CI = 35; RI = 93).
468. Aligned multiple muscles inserting in lateral region of esophagus, originated from adjacent region of proboscis inner surface: 0 = absent; 1 = present (L = 2; CI = 50; RI = 66).
469. Middle esophagus ventral gland: 0 = absent; 1 = purely glandular; 2 = with transverse folds; 3 = isolated by a duct (gland of Leiblein); 4 = duct very long and glandular (venom gland) (L = 13; CI = 30; RI = 97).
470. Relation anterior aorta and middle esophagus: 0 = absent; 1 = tangent; 2 = dividing transversely middle level of a gland (L = 5; CI = 40; RI = 96).
471. Middle esophagus ventral gland: 0 = absent; 1 = with low longitudinal folds; 2 = with 2 series of septa; 3 = with a deep blind sac; 4 = some transverse septa restrict to duct of gland of Leiblein as vestige of esophageal gland (gland framboese); 5 = replaced by thick muscular walls (L = 10; CI = 50; RI = 95) [– = avoids redundancy with character 463].
472. Right series of septa in middle esophagus: 0 = absent; 1 = with same length of left series; 2 = longer than left series (L = 5; CI = 40; RI = 91).
473. Right series of septa in middle esophagus: 0 = absent; 1 = symmetrical with left series; 2 = broader than left series (L = 3; CI = 66; RI = 96) [– = avoids redundancy with character 472].
474. Esophageal inner folds: 0 = a pair or several low folds; 1 = none; 2 = forming a central canal and other secondary folds; 3 = with a tall inner flap in esophageal gland aperture (L = 8; CI = 37; RI = 95).
475. Esophageal insertion in stomach: 0 = in posterior region; 1 = in middle region; 2 = anterior level (L = 10; CI = 20; RI = 94).
476. Dorsal inner folds of buccal mass and esophagus: 0 = simple or absent; 1 = with oblique secondary furrows in their anterior, broader region; 2 = with oblique glandular folds (L = 4; CI = 50; RI = 91).

477. Esophageal gland transverse septa: 0 = absent; 1 = present, with some transverse septa (about 10); 2 = present, with much transverse septa (L = 6; CI = 33; RI = 96).
478. Esophagus: 0 = narrow, slightly thick walled; 1 = broad, very thin walled; 2 = very narrow and convolute (L = 2; CI = 100; RI = 100).
479. Venom gland form: 0 = absent; 1 = short and broad; 2 = long, narrow and convolute (L = 3; CI = 66; RI = 97).
480. Venom gland situation: 0 = entirely at right from esophagus; 1 = about 1/3 at right from it (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 479].
481. Venom gland insertion: 0 = posterior to nerve ring; 1 = anterior to it, close to buccal mass; 2 = secondarily lost (L = 5; CI = 60; RI = 96) [– = avoids redundancy with character 479].
482. Muscular venom bulb: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
483. Two muscular layers of venom bulb: 0 = equally thick; 1 = inner about half of outer; 2 = inner about 1/4 of outer; 3 = inner about twice outer (L = 10; CI = 40; RI = 75) [– = avoids redundancy with character 482].
484. Valve of Leiblein: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
485. Valve of Leiblein oblique furrow (bypass): 0 = valve lacking furrow; 1 = valve with furrow; 2 = with elevated edges; 3 = additionally with anterior septum attached to elevated edges (L = 6; CI = 66; RI = 97) [– = avoids redundancy with character 484].
486. Gland of Leiblein: 0 = absent; 1 = present; 2 = elongated; 3 = bulbar at tip (L = 5; CI = 60; RI = 96).
487. Gland of Leiblein duct: 0 = short; 1 = long (about half the length of the middle esophagus) (L = 5; CI = 40; RI = 92) [– = avoids redundancy with character 479].
488. Gland of Leiblein duct: 0 = absent; 1 = with transversal septa; 2 = glandular; 3 = simple (L = 4; CI = 75; RI = 96) [– = avoids redundancy with character 479].
489. Pair of longitudinal folds in middle esophagus: 0 = absent; 1 = present; 2 = gland framboise (L = 3; CI = 66; RI = 98).

STOMACH

490. Stomach walls: 0 = thin; 1 = dorsal half muscular; 2 = almost entirely muscular (L = 4; CI = 50; RI = 88).
491. Gastric caecum: 0 = absent; 1 = small, only internal; 2 = developed (L = 2; CI = 100; RI = 100).
492. Width: 0 = narrow, about half local width of visceral mass; 1 = broad, almost completely separating visceral mass; 2 = small, flat; 3 = narrow, "U"-shaped, covered innerally by longitudinal folds; 4 = broad, rounded (L = 14; CI = 28; RI = 93).
493. Gastric general form: 0 = wide blind sac; 1 = narrow "U" or "V" shape (L = 1; CI = 100; RI = 100).
494. Anterior chamber of stomach, delimited posteriorly by a constriction: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
495. Stomach transverse muscular septum: 0 = absent; 1 = present; 2 = bending inwards (L = 2; CI = 100; RI = 100).
496. Esophageal insertion: 0 = anterior; 1 = middle; 2 = posterior (L = 6; CI = 33; RI = 96).
497. Gastric muscle originated in columella: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
498. Ducts to digestive gland: 0 = a pair; 1 = single; 2 = several; 3 = 2, posterior very reduced; 4 = 2 close from each other; 5 = with conspicuous furrow connecting both ducts to digestive gland (L = 27; CI = 18; RI = 78).
499. Gastric central pad: 0 = absent; 1 = flap-like; 2 = broad fold; 3 = with acinose lobe (L = 5; CI = 60; RI = 97).
500. Central pad as broad fold: 0 = long; 1 = short (L = 3; CI = 66; RI = 95) [– = avoids redundancy with character 499].
501. Gastric crescentic ridge: 0 = absent; 1 = part of central; 2 = broad (L = 2; CI = 100; RI = 100).
502. Inner curved fold: 0 = absent; 1 = double pre-intestinal fold; 2 = single pre-intestinal fold; 3 = transverse fold in inner curve adjacent to anterior duct to digestive gland (L = 5; CI = 60; RI = 93).
503. Style sac: 0 = absent; 1 = present (L = 6; CI = 16; RI = 93).
504. Style sac and intestine: 0 = entirely fused; 1 = separated by a constriction; 2 = entirely separated with each other (L = 16; CI = 18; RI = 82) [– = avoids redundancy with character 503].

505. Style sac length: 0 = about 1/2 stomach length (or 1/4 whorl); 1 = long (about than 1 whorl); 2 = up to anterior extremity of kidney; 3 = up to anterior region of pallial cavity (more than 2 whorls) (L = 11; CI = 36; RI = 94) [– = avoids redundancy with character 503].
506. Style sac position in anterior region of visceral mass: 0 = ventral; 1 = dorsal (L = 4; CI = 50; RI = 97) [– = avoids redundancy with character 503].
507. Style sac location: 0 = very short; 1 = entirely immersed in digestive gland; 2 = part exposed within kidney chamber (L = 4; CI = 50; RI = 97) [– = avoids redundancy with character 503].
508. Digestive gland anterior limit: 0 = anterior to stomach; 1 = middle; 2 = posterior to stomach (L = 3; CI = 66; RI = 94).
509. Stomach posterior duct to digestive gland: 0 = absent or bifurcating shortly; 1 = long, narrow simple in base; 2 = originated just between esophageal insertion and intestine origin; 3 = about as large as intestine (L = 7; CI = 42; RI = 86).
510. Esophageal (anterior) duct to digestive gland: 0 = absent or inside stomach; 1 = present, preceding its insertion in stomach (L = 1; CI = 100; RI = 100).
511. Stomach: 0 = with inner folds and sorting areas; 1 = with smooth inner surface; 2 = with conspicuous furrow connecting both ducts to digestive gland; 3 = with weak longitudinal folds; 4 = with a dilated chamber posterior to esophageal insertion; 5 = narrow, a single curve edging kidney (L = 8; CI = 62; RI = 97).
512. Inner surface of anterior duct to digestive gland: 0 = simple; 1 = several transverse septa (L = 3; CI = 33; RI = 50).
513. Gastric shape: 0 = broad or wide; 1 = narrow, ample "U"-shaped; 2 = "U"-shaped, but with esophagus and intestine attached to each other (L = 7; CI = 28; RI = 97).
514. Transverse gastric septum separating duct to digestive gland from esophageal insertion: 0 = absent; 1 = present (L = 2; CI = 50; RI = 90).
515. Stomach size: 0 = occupying from almost entire visceral mass space where it is located to half of it; 1 = less than 1/3 of that region (L = 3; CI = 33; RI = 98).
516. Stomach transverse section: 0 = flat; 1 = approximately cylindrical, having almost same width of adjacent esophagus and intestine regions (L = 1; CI = 100; RI = 100).

Intestine

517. Intestinal loop close to kidney-pericardium region, in left part of visceral mass: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
518. Intestinal loops in visceral mass: 0 = several wide; 1 = few (1-2), sigmoid (L = 2; CI = 50; RI = 96).
519. Intestinal loops localization: 0 = immersed in digestive gland; 1 = free from digestive gland (L = 1; CI = 100; RI = 100).
520. Intestinal loop in haemocoel: 0 = present; 1 = absent (L = 1; CI = 100; RI = 100).
521. Dorsal chamber of intestinal region close to pericardium: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
522. Ventral chamber of intestinal region close to pericardium: 0 = absent; 1 = simple; 2 = complex (L = 2; CI = 100; RI = 100).
523. Intestinal region passing through kidney: 0 = none (passing adjacent); 1 = with single or two loops; 2 = several looped (L = 3; CI = 66; RI = 97).
524. Intestinal loops: 0 = several; 1 = up to two adjacent to postero-ventral region of stomach; 2 = most in renal chamber (L = 8; CI = 25; RI = 92).
525. Especial intestinal loops: 0 = absent; 1 = closely contouring style sac; 2 = loop U-shaped, preceding rectum, exposed in pallial cavity roof; 3 = surrounding anterior lobe of digestive gland (L = 3; CI = 100; RI = 100).
526. Intestinal typhlosole: 0 = absent; 1 = present (L = 2; CI = 50; RI = 75).
527. Fecal pellets: 0 = absent; 1 = present; 2 = obliquely compacted; 3 = aligned; 4 = several pellets, with elliptical outline, chaotically compacted (L = 7; CI = 57; RI = 95).
528. Fold at left, posterior to those folds which precede intestine: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
529. Rectum width in pallial cavity: 0 = medium (about 1/8 of pallial cavity width); 1 = wide (about 1/4 of pallial width); 2 = narrow (about 1/16 of pallial width) (L = 5; CI = 40; RI = 95).

530. Rectum position in pallial cavity: 0 = running almost in its center; 1 = running in its right margin (L = 2; CI = 50; RI = 96).
531. Intestinal loop anterior to kidney: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
532. Intestinal U-shaped portion exposed in pallial cavity: 0 = absent 1 = short (far from stomach anterior end); 2 = long (close to stomach anterior end) (L = 4; CI = 50; RI = 92).
533. Intestine: 0 = narrow (at least in region near its origin); 1 = wholly broad (L = 3; CI = 33; RI = 90).
534. Intestinal loops in pallial roof region: 0 = none, *i.e.,* almost straight; 1 = a sigmoid loop; 2 = several (L = 3; CI = 66; RI = 88).
535. Digestive gland: 0 = glandular (solid acini); 1 = diverticle (hollow branches) (L = 1; CI = 100; RI = 100).

Anus

536. Anus site: 0 = near mantle border; 1 = far from mantle border; 2 = close to an anal siphon; 3 = situated about in middle level between mantle border and posterior end of pallial cavity (L = 9; CI = 33; RI = 92).
537. Anal annexed papillae: 0 = absent; 1 = only three; 2 = several; 3 = a single ventral pointing forwards (L = 5; CI = 60; RI = 94).
538. Anus position in females: 0 = close to genital pore or equivalent; 1 = far from it (L = 2; CI = 50; RI = 87).
539. Anus form: 0 = sessile or shortly siphoned; 1 = very long siphoned; 2 = a sessile rounded papilla; 3 = on a small septum (L = 6; CI = 50; RI = 81).

GENITAL SYSTEM

Male

Testis

540. Testis: 0 = along visceral mass; 1 = restrict to posterior region of visceral mass; 2 = at right from digestive gland (L = 2; CI = 100; RI = 100).
541. Testis: 0 = a pair; 1 = single (L = 1; CI = 100; RI = 100).

Vas deferens

542. Convoluted seminal vesicle: 0 = absent; 1 = present; 2 = glandular; 3 = with additional secondary ramifications and glands (L = 9; CI = 33; RI = 96).
543. Pallial prostate: 0 = absent; 1 = present in pallial region; 2 = further inflated (L = 4; CI = 50; RI = 96).
544. Pallial vas deferens: 0 = absent; 1 = a furrow; 2 = partially closed; 3 = entirely closed (tubular) (L = 25; CI = 12; RI = 90).
545. Vas deferens aperture: 0 = in posterior end of pallial cavity; 1 = in dorsal end of right cephalic tentacle; 2 = in penis tip; 3 = in penis base; 4 = preceded by a triangular attachment of mantle in head-foot surface; 5 = in tip of retractible penis (L = 9; CI = 66; RI = 97) [– = avoids redundancy with character 544].
546. Ejaculatory tube as a long muscular portion of vas deferens immersed in integument, and protruding into pallial floor and haemocoel: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
547. Pallial prostate situation relative to rectum: 0 = ventral; 1 = dorsal (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 543].
548. Seminal vesicle location: 0 = ventral to digestive gland, edging kidney; 1 = bulging into ventral surface of kidney chamber; 2 = in right-anterior extremity of visceral mass; 3 = lateral-left, terminal; 4 = T-shaped, contouring kidney and pericardium; 5 = running along right edge of pallial cavity; 6 = close to albumen gland (L = 12; CI = 58; RI = 95) [– = avoids redundancy with character 542].
549. Prostate tissue in pallial sperm groove: 0 = not detectable; 1 = reunited in posterior region of pallial sperm groove; 2 = along entire pallial sperm groove (L = 2; CI = 100; RI = 100); ? = closed spemduct. [– = avoids redundancy with character 544].
550. Coiling of seminal vesicle: 0 = absent; 1 = intense (about 1/10 of visceral mass); 2 = weak (about 1/20 of visceral mass) (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 542].

551. Region of sperm groove close to penis base performing acute angle: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 544].
552. Penis duct: 0 = simple; 1 = coiled, with thick walls (L = 9; CI = 11; RI = 69) [– = avoids redundancy with character 544].
553. Ejaculatory duct situation: 0 = immersed in integument; 1 = protruded into haemocoel; 2 = a duct with a loop free in haemocoel close to penis base; 3 = thick muscular, convolute; 4 = bulged into rhynchodeal cavity (L = 8; CI = 50; RI = 73) [– = avoids redundancy with character 544].
554. Vas deferens region anterior to seminal vesicle or to visceral mass: 0 = short, turned forward, terminal (in relation to seminal vesicle mass); 1 = long, oblique, sub-terminal (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 544].
555. Closed pallial prostate: 0 = absent; 1 = present; 2 = inside triangular sinus; 3 = with additional sperm sac preceding pallial spermduct (L = 10; CI = 30; RI = 94) [– = avoids redundancy with character 543].
556. Anterior male genital duct location: 0 = absent; 1 = pallial; 2 = haemocoelic (L = 2; CI = 100; RI = 100).
557. Spermatophoric sac: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
558. Component of genital structures: 0 = gonads and single ducts only; 1 = addition of pallial components at right from rectum; 2 = addition of components running in haemocoel; 3 = isolated structures in right side of visceral mass (L = 3; CI = 100; RI = 100).
559. Prostatic tissue in pallial vas deferens, even microscopic: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 543].

Copulatory organ

560. Right cephalic tentacle modified as copulatory organ, with vas deferens running along it: 0 = absent; 1 = present (L = 2; CI = 50; RI = 83).
561. Special cavity for retraction of right cephalic tentacle tip: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 560].
562. Exophalic penis (behind right tentacle): 0 = absent; 1 = present (L = 2; CI = 50; RI = 98).
563. Papilla on exophalic penis tip: 0 = absent; 1 = simple; 2 = double; 3 = with a somewhat broad chamber; 4 = present in a curved penis; 5 = a pair of whole papillated folds (L = 21; CI = 23; RI = 72) [– = avoids redundancy with character 562].
564. Pallial penis sac: 0 = absent; 1 = present, with a broad and short penis; 2 = present, with a very long, convolute penis (L = 3; CI = 66; RI = 90).
565. Pallial penis duct highly convolute: 0 = absent; 1 = present (L = 2; CI = 50; RI = 80).
566. Pallial penis shield: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
567. Penis shield tip: 0 = simple; 1 = glandular (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 566].
568. Penis shield middle-right gland: 0 = absent; 1 = present (L = 4; CI = 25; RI = 50) [– = avoids redundancy with character 566].
569. Penis shield gland in tip: 0 = no gland; 1 = far from middle flap, 2 = close to flap (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 566].
570. Penis shield base: 0 = without gill; 1 = with gill (L = 5; CI = 40; RI = 76) [– = avoids redundancy with character 566].
571. Pallial sperm groove type: 0 = non-glandular or non-pallial; 1 = glandular grove; 2 = which a chamber in inner lamina; 3 = closed (L = 6; CI = 50; RI = 95).
572. Exophalic penis situation: 0 = just posterior to right tentacle; 1 = far removed towards posterior; 2 = at right from right tentacle; 3 = ventral to right tentacle; 4 = by side of right tentacle, on head flap; 5 = near median line (L = 9; CI = 66; RI = 97) [– = avoids redundancy with character 562].
573. Penis kind of appendages in distal region associated with thick expanded shelled species: 0 = lacking appendages; 1 = an ample, flat, longitudinal projection in a side, and a lateral papilla in other side; 2 = semicircular in section, with a pair of longitudinal undulating folds along middle region; 3 = a pair of whole papillated folds; 4 = papilla long in opposite side of penis groove; 5 = with retractile terminal broad papilla (L = 7; CI = 71; RI = 71) [– = avoids redundancy with character 562].

574. Dorsal longitudinal flap of penis tip: 0 = absent; 1 = only a low, bilateral fold; 2 = a tall fold, covering part of penis tip, presenting apical projection; 3 = flap broad, rounded (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 562].
575. Distal end of penis sperm groove: 0 = extends to distal tip of penis; 1 = slight far from penis tip; 2 = edged by undulating membrane (L = 5; CI = 60; RI = 97) [– = avoids redundancy with character 562].
576. Exophalic penis duct; 0 = a groove (opened); 1 = a duct (closed) (L = 19; CI = 10; RI = 89) [– = avoids redundancy with character 562].
577. Head-foot penis type: 0 = simple; 1 = retractile; 2 = with spermatic sac of penis base protruding into haemocoel (L = 4; CI = 75; RI = 98) [– = avoids redundancy with character 562].
578. Differentiated broad and flat basal region of penis: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 562].
579. Exophalic penis: 0 = with simple fashion; 1 = with tip pointed; 2 = with small nodes along dorsal edge; 3 = flat tip; 4 = with papilla in tip; 5 = tip narrow, long and sinuous; 6 = a papilla with closed duct; 7 = papilla with closed duct protected within a concavity; 8 = broad, rounded tip; 9 = twisting in middle region (L = 19; CI = 47; RI = 83) [– = avoids redundancy with character 562].
580. Preputial-like protection to papilla: 0 = absent; 1 = present; 2 = very complex (L = 6; CI = 33; RI = 75) [– = avoids redundancy with character 562].
581. Exophalic penis distal end: 0 = blunt or rounded; 1 = sharply pointed (L = 2; CI = 50; RI = 92) [– = avoids redundancy with character 562].
582. Anatomical copulation strategy: 0 = absent; 1 = via exophalic penis; 2 = via tentacle; 3 = transfer of spermatophore; 4 = vial pallial penis; 5 = via retractile penis (L = 7; CI = 71; RI = 96).

FEMALE

VISCERAL STRUCTURES

583. Gonad site: 0 = around digestive gland; 1 = superior region of digestive gland only; 2 = concentrated in anterior and ventral regions; 3 = somewhat in center of ventral region; 4 = surrounded by digestive gland posterior lobe (L = 4; CI = 100; RI = 100).
584. Gonopericardial duct: 0 = present; 1 = absent (L = 8; CI = 12; RI = 90).
585. Ovary anterior limit: 0 = posterior to isolated visceral oviduct; 1 = anterior to it; 2 = tapering gradually (L = 2; CI = 100; RI = 100).
586. Glandular loop of pallial oviduct preceding its main chamber: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
587. Narrow part of anterior visceral gonoduct (adjacent to kidney): 0 = absent. 1 = short; 2 = long (about half whorl) (L = 3; CI = 66; RI = 98).
588. Nidimental gland: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).

PALLIAL OVIDUCT

589. Pallial oviduct: 0 = absent; 1 = present and opened (a glandular furrow); 2 = posterior half closed (a half tube); 3 = closed (a glandular tube) (L = 10; CI = 30; RI = 93).
590. Pallial oviduct localization: 0 = renal pore; 1 = in pallial floor; 2 = entirely at right of rectum; 3 = in haemocoel (L = 3; CI = 100; RI = 100).
591. Albumen gland: 0 = absent; 1 = loop of visceral oviduct; 2 = a compact mass; 3 = a posterior glandular sac; 4 = along pallial oviduct; 5 = sac-like, separated from capsule gland; 6 = as loops; 7 = isolated gland with hilum (L = 12; CI = 58; RI = 93).
592. Bursa copulatrix in pallial oviduct base: 0 = absent; 1 = present, connected to visceral oviduct; 2 = present, opening in pallial cavity (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 589].
593. Capsule gland: 0 = absent; 1 = present; 2 = with a complex, barely spiral inner duct; 3 = separated by a narrow portion; 4 = with aperture by side of that of bursa; 5 = with aperture in bursa wall; 6 = with secondary projections in mantle roof (L = 8; CI = 75; RI = 96).
594. Inner blind-sac glandular chamber in capsule gland: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 593].

595. Female pore: 0 = not developed (pallial oviduct opened); 1 = a slit; 2 = a papilla; 3 = broad, short, muscular papilla; 4 = a large, long, muscular, projected papilla; 5 = a broad papilla in bursa copulatrix anterior end; 6 = in an eversible vaginal tube (L = 15; CI = 40; RI = 93) [– = avoids redundancy with character 593].
596. Sessile vaginal tube: 0 = absent or very short; 1 = origin in anterior end of pallial oviduct; 2 = origin in middle level of pallial oviduct (L = 4; CI = 50; RI = 83).
597. Chamber in outer lamina of pallial oviduct: 0 = none; 1 = single (L = 5; CI = 20; RI = 66) [– = avoids redundancy with character 589].
598. Chamber in inner lamina of pallial oviduct: 0 = none; 1 = single; 2 = double (L = 9; CI = 22; RI = 0) [– = avoids redundancy with character 589].
599. Posterior situated seminal receptacle: 0 = absent; 1 = present (L = 2; CI = 50; RI = 80) [– = avoids redundancy with character 589].
600. Posterior situated bursa copulatrix: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 589].
601. Pallial genital ducts: 0 = running only in pallial roof; 1 = anterior region running in pallial floor (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 589].
602. Pallial oviduct position: 0 = antero-ventral to kidney; 1 = bulging in anterior-dorsal region of kidney (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 589].
603. Capsule gland: 0 = in continuation from oviduct; 1 = separated from oviduct, as a sinuous duct most dorsal to rectum; 2 = presenting secondary expansions (L = 4; CI = 75; RI = 97) [– = avoids redundancy with character 593].
604. Seminal receptacle positioned outside of pallial capsule gland: 0 = absent; 1 = a closed sac posterior to aperture of pallial oviduct; 2 = same, with folded dorsal wall (L = 4; CI = 50; RI = 83) [– = avoids redundancy with character 593].
605. Glandular brood pouch in a sac-like form: 0 = absent; 1 = terminal; 2 = immersed in capsule gland (L = 2; CI = 100; RI = 100).
606. Bursa copulatrix located parallel to pallial oviduct: 0 = absent; 1 = as separated structure anterior to anus, with an own aperture; 2 = a sac connected to anterior extremity of pallial oviduct (before it crosses to pallial floor) (L = 2; CI = 100; RI = 100).
607. Intermediary middle fold in anterior region of pallial oviduct before it crosses to pallial floor: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 589].
608. Seminal receptacles connected to albumen gland: 0 = absent; 1 = present; 2 = united in a single region (L = 7; CI = 28; RI = 81) [– = avoids redundancy with character 593].
609. Seminal receptacle: 0 = absent or simple; 1 = several acina in a single sac; 2 = long and narrow (single or multiple); 3 = connected to bursa copulatrix; 4 = several along albumen gland; 5 = a series of several small vesicles (L = 11; CI = 45; RI = 53) [– = avoids redundancy with character 589].
610. Albumen gland location: 0 = in pallial cavity, posterior to capsule gland; 1 = edging visceral mass, at side of capsule gland; 2 = a single mixed, barely spiral, glandular mass with capsule gland; 3 = difficulty distinct from capsule gland; 4 = in base of duct connecting gonad and capsule gland (L = 5; CI = 100; RI = 100) [– = avoids redundancy with character 593].
611. Capsule gland: 0 = absent; 1 = continuation of pallial oviduct; 2 = a blind; 3 = similar, but with vaginal tube in its base (L = 3; CI = 100; RI = 100) [– = avoids redundancy with character 593].
612. Anterior positioned bursa copulatrix: 0 = missing; 1 = present; 2 = with a flat concavity; 3 = terminal, as continuation of oviduct (L = 15; CI = 20; RI = 87).
613. Bursa copulatrix glandular wall: 0 = simple; 1 = attached to capsule gland; 2 = posterior, to capsule gland; 3 = bursa copulatrix large, muscular, attached by a duct directly to capsule gland; 4 = wide, originated from or close to genital pore; 5 = immersed in capsule gland walls (L = 9; CI = 55; RI = 92) [– = avoids redundancy with character 612].
614. Scanty glandular bursa copulatrix form: 0 = absent; 1 = a simple sac; 2 = "U"-shaped, with inner folds; 3 = with dorsal duct; 4 = constituting main part of genital pore (L = 16; CI = 25; RI = 85) [– = avoids redundancy with character 612].
615. Bursa copulatrix position in pallial oviduct: 0 = anterior; 1 = middle; 2 = posterior; 3 = as part of its dorsal (outer) wall; 4 = as part of its ventral (inner) wall (L = 10; CI = 40; RI = 80) [– = avoids redundancy with character 612].

616. Bursa copulatrix posterior-dorsal located, connected to capsule gland by a duct: 0 = absent; 1 = present (L = 4; CI = 25; RI = 50) [– = avoids redundancy with character 612].
617. Vaginal tube: 0 = absent or simple; 1 = very short (extending little beyond capsule gland); 2 = very long; 3 = arched towards posterior; 4 = with subterminal spiral portion of pallial oviduct; 5 = with some longitudinal folds, separated from capsule gland by a differentiated fold; 6 = forming an anterior atrium preceding pore; 7 = connected to pallial oviduct far from rectum (L = 13; CI = 53; RI = 95).
618. Genital pore in pallial roof: 0 = absent; 1 = a slit; 2 = a small papilla; 3 = a tall papilla (L = 5; CI = 60; RI = 98).
619. Genital papilla pair of longitudinal folds at posterior surface: 0 = absent; 1 = present (L = 3; CI = 33; RI = 77) [– = avoids redundancy with character 618].
620. Genital papilla dorsal fold: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 612].
621. Genital papilla: 0 = absent; 1 = simple, at end of capsule gland; 2 = tall, erected, at end of vaginal tube (L = 5; CI = 40; RI = 97) [– = avoids redundancy with character 612].
622. Anterior chamber close to female pore: 0 = absent; 1 = present (L = 2; CI = 50; RI = 50).
623. Female genital pore: 0 = simple; 1 = preceded by a tubular region attached to pallial floor; 2 = elevated; 3 = a slit in anterior region of pallial oviduct protected by a pallial flap; 4 = a broad and low papilla; 5 = surrounded by muscular atrium; 6 = eversible (L = 12; CI = 50; RI = 87) [– = avoids redundancy with character 618].
624. Bursa copulatrix form and location associated with fusiform shelled taxa: 0 = absent or other kind of shell; 1 = long, running posteriorly at left from pallial oviduct; 2 = short, running forwards; 3 = short, running obliquely towards posterior-right; 4 = short, running backwards (L = 9; CI = 44; RI = 94) [– = avoids redundancy with characters 1 and 612].
625. Bursa copulatrix: 0 = absent; 1 = situated in posterior region of pallial oviduct; 2 = situated in anterior region of pallial oviduct, originating from genital pore (L = 4; CI = 50; RI = 98) [– = avoids redundancy with character 612].
626. Inner tall, glandular fold separating capsule gland almost into 2 chambers, pleated when mature: 0 = absent; 1 = present (L = 2; CI = 50; RI = 66) [– = avoids redundancy with character 611].
627. Ingesting gland: 0 = hollow or absent; 1 = solid; 2 = an isolated sac; 3 = located posterior to albumen gland (L = 6; CI = 50; RI = 91).
628. Muscular, thick-walled duct of pallial bursa copulatrix: 0 = absent; 1 = present (L = 5; CI = 20; RI = 60) [– = avoids redundancy with character 612].
629. Glandular tissue of capsule gland: 0 = absent or not related to bursa; 1 = covering bursa; 1 = does not cover bursa (L = 2; CI = 100; RI = 100) [– = avoids redundancy with character 611].
630. Septum connecting rectum in mantle in females: 0 = absent; 1 = present (L = 2; CI = 20; RI = 75).
631. Terminal pouch: 0 = absent; 1 = present (L = 2; CI = 50; RI = 96).
632. Pallial oviduct albumen and capsule glands associated with valve of Leiblein: 0 = separated from each other by a constriction; 1 = widely connected (L = 6; CI = 33; RI = 90) [– = avoids redundancy with character 484].
633. Copulation strategies: 0 = absent (external fecundation); 1 = present (L = 2; CI = 50; RI = 94).

HEAD-FOOT STRUCTURES

634. Brood pouch: 0 = absent; 1 = present as part of oviduct; 2 = dorsal and single in haemocoel; 3 = ventral and double in haemocoel; 4 = present in foot with an aperture in sole; 5 = present as a hole in anterior region of pedal sole, running transversely towards dorso-ventral, with a broad posterior region in pallial floor bulging into haemocoel; 6 = brood into pallial cavity (L = 7; CI = 85; RI = 95).
635. Ovopositor: 0 = absent; 1 = present; 2 = transverse lateral-right furrow ending at some distance from foot sole (L = 8; CI = 25; RI = 25).
636. Ciliated furrow in right side of female head: 0 = absent; 1 = present (L = 3; CI = 33; RI = 95).
637. Aperture on right side connected to an inner brood pouch: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 634].
638. Development of an epithelial chamber within haemocoel-foot muscles: 0 = absent; 1 = present (L = 3; CI = 33; RI = 88).

639. Number of embryos in brood pouch: 0 = brood pouch absent; 1 = up to 20; 2 = about 100; 3 = about 1000 (L = 6; CI = 50; RI = 85) [– = avoids redundancy with character 634].
640. Glandular concavity in propodium base for capsules attachment: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
641. Cement gland (a glandular orifice in anterior region of foot sole): 0 = absent; 1 = present (L = 8; CI = 12; RI = 88).
642. Albumen and capsule glands anatomically related with each other by glandular tissue: 0 = absent; 1 = present (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 589].
643. Capsule gland: 0 = with single, flat lumen; 1 = with double lumen; 2 = paired; 3 = as blind sac; 4 = connected to prostate (L = 5; CI = 100; RI = 100) [– = avoids redundancy with character 593].

Development

644. Brood strategy: 0 = absent (eggs free); 1 = inside pallial oviduct; 2 = a jelly mass laid out of water; 3 = in shell cavity, protected by neck ventral surface; 4 = in shell cavity protected by and connected to propodium; 5 = capsules united in a semi-circular, sandy ribbon; 6 = capsules attached to substrate (L = 11; CI = 54; RI = 95).
645. Parthenogenesis. 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
646. Reproduction type: 0 = gonochoristic; 1 = protandric hermaphroditism; 2 = simultaneous hermaphroditism (L = 5; CI = 40; RI = 92).
647. Echinospira larva: 0 = absent; 1 = present (L = 2; CI = 50; RI = 50).
648. Veliger larva: 0 = absent; 1 = present (at least intra-capsular) (L = 1; CI = 100; RI = 100).

CENTRAL NERVOUS SYSTEM

649. Connectives between pair of pleural and pedal ganglia: 0 = very short or absent; 1 = long, but separated from the connectives between cerebral and pedal; 2 = long, running parallel and close to cerebro-pedal connective (L = 2; CI = 100; RI = 100).
650. Right pedal and pleural ganglion: 0 = very closely located from each other; 1 = separated from each other by distance equivalent to ganglion width or more; ? = highly concentrated nerver rings (L = 1; CI = 100; RI = 100).
651. Position of left pleural ganglion: 0 = pleural ganglion indistinct; 1 = close to pedal ganglia (hypoathroid); 2 = close to cerebral ganglia (epiathroid) (L = 2; CI = 100; RI = 100).
652. Left pedal and pleural ganglion: 0 = very closely located from each other; 1 = separated from each other by distance equivalent to ganglion width or more; ? = highly concentrated nerver rings (L = 1; CI = 100; RI = 100).
653. Nerve ring position: 0 = surrounding mouth; 1 = in middle level of buccal mass; 2 = posterior to buccal mass; 3 = very posterior, far removed from buccal mass (L = 4; CI = 75; RI = 99).
654. Position of right pleural ganglion: 0 = no pleural ganglion; 1 = close to pedal ganglia (hypoathroid); 2 = close to cerebral ganglia (epiathroid) (L = 2; CI = 100; RI = 100).
655. Connective of right pedal-pleural ganglion: 0 = absent; 1 = very short; 2 = long, separated from pedal-cerebral connective; 3 = long, running close to pedal-cerebral connective (L = 3; CI = 100; RI = 100).
656. Connective left pedal-pleural ganglion: 0 = absent; 1 = very short; 2 = long, separated from pedal-cerebral connective; 3 = long, running close to pedal-cerebral connective (L = 3; CI = 100; RI = 100).
657. Statocysts: 0 = with several statoconia; 1 = with single statolith (L = 1; CI = 100; RI = 100).
658. Buccal ganglia: 0 = absent (undifferentiated); 1 = close to nerve ring; 2 = separated, far from nerve ring (L = 4; CI = 50; RI = 96).
659. Buccal ganglia position: 0 = weakly formed; 1 = close to median line; 2 = lateral; 3 = in middle region between lateral and median line; 4 = positioned closer to nerve ring and far from buccal mass; 5 = practically as part of nerve ring (L = 20; CI = 25; RI = 92) [– = avoids redundancy with character 658].
660. Buccal ganglia: 0 = absent to medium sized, unpigmented; 1 = large, pigmented with brown spots (L = 1; CI = 100; RI = 100) [– = avoids redundancy with character 658].

661. Shape of buccal ganglia: 0 = diffuse, only a fusiform thickness of buccal nerves; 1 = well defined ganglia (L = 1; CI = 100; RI = 100).
662. Buccal ganglia: 0 = undifferentiated or one close to another, near median line; 1 = far from one another, situated in lateral region of buccal mass (L = 3; CI = 33; RI = 96) [– = avoids redundancy with character 658].
663. Supra-esophageal ganglion location: 0 = absent or far from nerve ring; 1 = close to nerve ring (L = 5; CI = 20; RI = 93).
664. Several parallel pair of nerves running from cerebral ganglion to anterior region of snout: 0 = absent (one or two large pairs only); 1 = present (L = 1; CI = 100; RI = 100).
665. Nerve ring shape: 0 = well separated ganglia; 1 = ganglia large, close with each other, but still individualized; 2 = complex brain (L = 4; CI = 50; RI = 97).
666. Connective between pedal and remaining 2 pairs of ganglia: 0 = narrow, 1 = broad (almost as broad than pleural ganglia) (L = 1; CI = 100; RI = 100).
667. Ganglia delimitation: 0 = pairs clearly distinct; 1 = concentrated, without clear distinction of pairs (L = 4; CI = 25; RI = 97).
668. Cerebral and pleural ganglia pairs: 0 = no pleural ganglia; 1 = separated from each other; 2 = forming a single mass (L = 3; CI = 66; RI = 99).
669. Connectives among pedal pair of ganglia and remaining pairs of ganglia in non-concentrated nerver rings: 0 = long; 1 = short (L = 3; CI = 33; RI = 86). (? = concentrated nerve ring).
670. Statocyst location: 0 = close to pedal ganglion: 1 = slightly far from it (L = 2; CI = 50; RI = 98).
671. Sub-esophageal ganglion: 0 = far from nerve ring; 1 = close to it (L = 4; CI = 25; RI = 95).
672. Nerve ring positioned encased in a chamber at ventral base of proboscis/snout; 0 = absent; 1 = present (L = 1; CI = 100; RI = 100).
673. Nerve ring relative size: 0 = about 1/10 of haemocoel volume; 1 = about 1/4 of haemocoel volume (L = 1; CI = 100; RI = 100).

ENVIRONMENT

674. Habit of unguiculate forms: 0 = rocky; 1 = on or inside gastropod shells; 2 = on bivalve shells (L = 5; CI = 60; RI = 80) [– = avoids redundancy with character 11].
675. Environment: 0 = marine; 1 = freshwater; 2 = terrestrial (L = 8; CI = 25; RI = 81).
676. Feeding habits: 0 = microphagy or herbivory; 1 = carnivore or predator; 2 = parasitic; 3 = filter-feeding (L = 9; CI = 33; RI = 96).

APPENDIX 2

Matrix of characters considered in the present study

Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890											
Pomacea crosseana	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Pomacea curumim	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Pomacea scalaris	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Pomacea canaliculata	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Pomacea lineata	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Pomacea sordida	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Pomacea bridgesi	120?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Asolene megastoma	120?0200000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100110000000011100111001000000000001000000002000											
Felipponea neritiniformis	120?0200000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100110000000011100111001000000000001000000002000											
Marisa planogyra	130?0100000---1000-0--00-0011000000000000-000-0---0-2121300000100000001-1100120000000011100111001000000000001000000002000											
Neocyclotus prominulus	120?0110000---1000-0--00-0011000000000000-000-0---0-1221200000100000001-1100000000000011100111000000000000020000000002000											
Incidostoma tupy	120?0110000---1000-0--00-0011000000000000-000-0---0-1221200000100000001-1100000000000011100111000000000000001000000002000											
Aperostoma blanchetiana	120?0110000---1000-0--00-0011000000000000-000-0---0-1221200000100000001-1100000000000011100111000000000000001000000002000											
Viviparus acerosus	110?1100000---1000-0--00-0011000000000000-000-0---0-2121200000100000001-1101210000000011100111000000000000001000000002000											
Viviparus contectus	110?1100000---1000-0--00-0011000000000000-000-0---0-2121200000100000001-1101210000000011100111000000000000001000000002000											
Notopala ampullaroides	110?1100000---1000-0--00-0011000000100000-000-0---0-2121200000100000001-1101210000000011100111000000000000001000000002000											
Notopala essingtonensis	110?1100000---1000-0--00-0011000000100000-000-0---0-2121200000100000001-1101210000000011100111000000000000001000000002000											
Larina cf. *strangei*	120?1100000---1000-0--00-0011000000100000-000-0---0-2121200000100000001-1101210000000011100111000000000000001000000002000											
Annularia sp.	210?0110000---1000-0--0000011100100000000-000-0---0-1212200000100000001011000000000000111001112000000000000300000002000											
Aylacostoma exoplicata	210?0100000---1000-0--0000011100111000000-000-0--00-4123300000100000001111000000000000111001210000000000100010000002000											
Aylacostoma ci	210?0100000---1000-0--0000011100111000000-000-0--00-4123300000100000001111000000000000111001210000000000100010000002000											
Aylacostoma tenuilabris	210?0100000---1000-0--0000011100111000000-000-0--00-4123300000100000001111000000000000111001210000000000100010000002000											
Melanoides tuberculatus	210?0110000---1000-0--0000011000111000000-000-0--00-4123300000100000001111000000000000111001210000000000100010000002000											
Supplanaxis nucleus	210?0100000---1000-0--0000011000111000000-000-0--00-4123300000100000001111000000000000111001210000000000100010000002000											
Doryssa ipupiara	210?0100000---1000-0--0000011100111000000-000-0--00-1111100000100000001011000000000000111001210000000000100010000002000											
Doryssa atra	210?0100000---1000-0--0000011100111000000-000-0--00-1111100000100000001011000000000000111021210000000000100010000002000											
Doryssa macapa	210?0100000---1000-0--0000011100111000000-000-0--00-1111100000100000001011000000000000111021210000000000100010000002000											
Pachychilus sp.	210?0200000---1000-0--0000011000111000000-000-0--00-1111100000100000001011000000000000111001210000000000100010000002000											
Turritella hookeri	210?0110000---1000-0--0000011000000000000-000-0---0-1111100000100000001011010010000000111011110000000000001010000002100											
Modulus modulus	120?0100000---1000-0--0000011000001000000-000-0---0-1111100000100000001-1100000000000011100111000000000000001000000002000											
Cerithium atratum	210?0110000---1000-0--0000011000211000000-000-0--00-4123200000100000001111000000000000111021220000000000100010000002000											
Bittium varium	211?0111000---1000-0--0000011000211000000-000-0--00-4123200000100000001111000000000000111001230000000000101011000000200											
Finella dubia	211?0111000---1000-0--0000011000211000000-000-0--00-4123200000100000001111000000000000111001230000000000100011000000200											
Alaba incerta	211?0100000---1000-0--0000011000211000000-000-0--00-4123200000100000001111000000000000111001230000000000100011000000200											
Batillaria minima	210?0100000---1000-0--0000011000111000000-000-0--00-1111100000100000001011000000000000111001210000000000100010000002000											
Cerithidea costata	210?0110000---1000-0--0000011000211000000-000-0--00-1121100000100000001011000000000000111001210000000000100010000002000											
Campanile symbolicum	210?0200000---1000-0--0000011000000000000-000-0---0-1111100000100000001011000000000000111001110000000000001020000002000											
Serpulorbis decussatus	310?0100000---?000-1--0000011?0000000000-000-0---0-???140???0?00000001-1101001000000011102114000000000000020100?00001100											

Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890											
Stephopoma nucleogranosum	3?0?0100000---?000-1--00-00110?0000000000-000-0---0-11111000001000000001-1101001000000011101114000000000000020100000001100											
Amphithalamus glaber	121?0120000---1000-0--00-0011000000000000-000-0---0-11122000001000000001-1100000000000011100111100000000000010310000002000											
Littorina flava	120?0120000---1000-0--00-0011000000000000-000-0---0-11122000001000000001-1100000000000011100111000000000000010100000002000											
Potamolithus ribeirensis	121?0100000---1000-0--00-0011000000100000-000-0---0-11122000001000000001-1100000000000011100111100000000000010310000002000											
Potamolithus troglobius	121?0100000---1000-0--00-0011000000100000-000-0---0-11122000001000000001-1100000000000211100111100000000000010310000002000											
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Strombus alatus	4?010130200---1000-0-0000001100011101101 0-000-0-000-5124311110100000001-1100000000000011101144010200000000030101200002000											
Strombus gracilior	4?000130200---1000-0-0000001100011101101 0-000-0-000-5124311110100000001-1100000000000011101144010200000000030101200002000											
Eustrombus goliath	4?010130200---1000-0-0000001100011101101 0-000-0-000-5124310110100000001-1100000000000011101144000200000000030101210002000											
Eustrombus gigas	4?010130200---1000-0-0000001100011101101 0-000-0-000-5124310110100000001-1100000000000011101144000200000000030101210002000											
Aliger costatus	4?010130100---1000-0-0000001100011101101 0-000-0-000-5124311110100000001-1100000000000011101144000200000000030101210002000											
Aliger gallus	4?010130100---1000-0-0000001100011101101 0-000-0-000-5124311110100000001-1100000000000011101144000200000000030101210002000											
Tricornis raninus	4?010130100---1000-0-0000001100011101101 0-000-0-000-5124311110100000001-1100000000000011101144000200000000030101200002000											
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Lambis lambis	4?010130100---1000-0-0000001100011102101 0-000-0-000-5124311110100000001-1100000000000011101144000200000000030101200002000											
Terebellum terebellum	4?000130000---1000-0-0000001100011101001 0-000-0-000-5124311110100000001-1100000000000011101144000200000000030101100002000											
Tylospira scutulata	4?000130200---1000-0-0000001100011101001 0-000-0-000-7124312110100000001-1101000000000011100132000200000000030101000002000											
Struthiolaria papulosa	4?000130200---1000-0-0000001100011101001 0-000-0-000-7124312110100000001-1101000000000011100132000200000000030101000002000											
Cuphosolenus serresianus	4?000130000---1000-0-0000001100011102001 0-000-0-000-4124310110100000001-1100000000000011100112000200000000030101000002000											
Aporrhais occidentalis	4?000130000---1000-0-0000001100011101001 0-000-0-000-4124310110100000001-1100000000000011100112000100000000030101000002000											
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Onustus caribaeus	12000200000---1000-0--00-0011000001000010-000-0---0-6124310010100000001-1100000000000011101112000200000000030101000002000											
Onustus indicus	12000200000---1000-0--00-0011000001000010-000-0---0-6124310010100000001-1100000000000011101112000200000000030101000002000											
Xenophora conchyliophora	12000200000---1000-0--00-0011000001000010-000-0---0-6124310010100000001-1100000000000011101112000200000000030101000002000											
Bostrycapulus odites	500?2200011111?000-0--00-0011010000000000-000-0---0-????400??0?00000001-1101000010000011100155000311011000401023000002000											
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Crepidula cachimilla	540?2200011112?000-0--00-0011010000000000-000-0---0-????400??0?00000001-1101000010000011100155000311011000401023000002000											
Calyptraea centralis	501?2200020000?000-0--00-0011000000000000-000-0---0-????400??0?00000001-1101000010000011100155000311011000401023000002000											
Crucibulum auricula	500?2200030000?000-0--00-0011000000000000-000-0---0-????400??0?00000001-1101000010000011100155000311011000401024000002000											
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Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
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Trochita trochiformis	740?22000000001000-0--00-0011000000000000-000-0---0-????400??0?00000001-1101000010000011100155000311011000401020000002000											
Sigapatella calyptraeformis	740?22000000001000-0--00-0011000000000000-000-0---0-????400??0?00000001-1101000010000011100155000311011000401023000002000											
Hipponix costellatus	000?20400000000000-0--00-0011000000000000-000-0---0-????400??0?00000001-1100000010000011100155300411000000401035000002000											
Hipponix subrufus	600?20400000000000-0--00-0011000000000000-000-0---0-????400??0?00000001-1100000010000011100155300411000000401035000002000											
Hipponix incurvus	000?20400000000000-0--00-0011010000000000-000-0---0-????400??0?00000001-1100000010000011100155300411000000401035000002000											
Hipponix grayanus	000?20400000000000-0--00-0011000000000000-000-0---0-????400??0?00000001-1100000010000011100155300311000000401035000002000											
Hipponix leptus	000?20400000000000-0--00-0011000000000000-000-0---0-????400??0?00000001-1100000010000011100155300311000000401035000002000											
Sabia conica	000?20400000000000-0--00-0011000000000000-000-0---0-????400??0?00000001-1100000010000011100155300311000000401035000002000											
Malluvium devotus	600?20400000000000-0--00-0011010000000000-000-0---0-????400??0?00000001-1100000010000011100155300311000000401035000002000											
Cheilea equestris	500?2000040000?000-0--00-0011000000000000-000-0---0-????400??0?00000001-1100000010000011100155000311000000401030000002000											
Capulus sycophanta	000?2000000000?000-0--00-0011010000000000-000-0---0-????400??0?00000001-1100000000000011100155400311000000001005000002000											
Trichotropis cancellata	120?21000000001000-0--00-0011000000000000-000-0---0-1122300000100000001-1100000000000011100155400311000000001000000002000											
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Vanikoro sp.	120?21200000001000-0--00-0011000000000000-000-0---0-1122300000100000001-1100000000000011100155000311001000001030000002000											
Naticarius cayennensis	820?0100000---2200-0--00-0011000000000100-00000---0-8212203001201210001-1100000100000011100255000311000000510040011112000											
Naticarius canrenus	820?0100000---2200-0--00-0011000000000100-00000---0-8212203001201210001-1100000100000011100255000311000000510040011112000											
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Natica cf. *marochiensis*	820?0100000---2200-0--00-0011000000000100-00000---0-8212200001211210001-1100000000000011100255000311000000510040011112000											
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Neverita duplicata	820?0100000---2200-0--00-0011000000000300-00000---0-8112200001100001001-1100000000000011100255000311000000510040011112000											
Lunatia heros	820?0100000---1100-0--00-0011000000000000-000-0---0-8112200001100000001-1100000000000011100255000311000000510040011112000											
Eunaticina sp.	820?0100000---1200-0--00-0011000000000000-000-0---0-8112200001100000001-1100000000000011100255000311000000520040011112000											
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Amauropsis islandica	820?0100000---1100-0--00-0011000000000000-000-0---0-8112200001100000001-1100000000000011100255000311000000510040011112000											
Amauropsis andersoni	820?0100000---1100-0--00-0011000000000000-000-0---0-8112200001100000001-1100000000000011100255000311000000510040011112000											
"Amauropsis" rossiana	820?0100000---1100-0--00-0011000000000000-000-0---0-1111200001100000001-1100000000000011100111000000000000304001002000											
Macrocypraea zebra	44023270000---1011100000000011001110000021010 0-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Macrocypraea cervinetta	44023270000---1011100000000011001110000021010 0-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Erosaria acicularis	44023270000---1011100000000011001110000021211 0-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Erosaria spurca	44023270000---1011100000000011001110000021211 0-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Luria cinerea	44023270000---1011100000000011001110000021010 0-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Cypraea tigris	44023270000---1011100000000011001110000021010 0-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											

Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
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Lyncina lynx	44023270000---1011100000000011001110000021010O-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Monetaria moneta	44023270000---1011101000000011001110000021211O-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Monetaria annulus	44023270000---1011101000000011001110000021211O-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Ravitrona caputserpentis	44023270000---1011100000000011001110000021011O-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Pseudozonaria arabicula	44023270000---1011100000000011001110000021010O-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
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Cyphoma signatum	43023270000---1031100000000011001110000011010O-0-0001????400??0?00?00001-1100000211100011100155000511000000001000000002000											
Cyphoma gibbosum	43023270000---1031100000000011001110000011010O-0-0001????400??0?00?00001-1100000211100011100155000511000000001000000002000											
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Ovula ovum	43023270000---1021100000000011001110000021110O-0-0002????400??0?00?00001-1100000011100011100155000511000000001000000002000											
Calpurnus verrucosus	43023270000---1021100000000011001110000021110O-0-0002????400??0?00?00001-1100000211100011100155000511000000001000000002000											
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Lamellaria branca	42023270000---1012000000-0011001100000000-000-0-0-00????400??0?00?00001-1100000010000011100155000521000000001000000002000											
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Ficus carolae	4?020120000---1000-0-0010001100101000000O-000-0-000-????4??????00?00001-1100000000001011100455000632100000006010000002000											
Ficus subintermedia	4?020120000---1000-0-0010001100101000000O-000-0-000-????4??????00?00001-1100000000001011100455000632100000006010000002000											
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Thalassocyon bonus	4?020130000---1000-0-0120001100121000000O-000-0-000-????4??????00?00001-1100000000001011100155000633100000005010000002000											
Charonia laevigata	4?000100000---4000-0-0120001100121000002O-001-0-000-3122300100100000001-1100000000001011100155000621100000001010000002000											
Cymatium cynocephalum	4?022130000---1000-0-2120001100121000002O-00110-000-3125300100100000001-1100000000001011100155000621100000001010000002000											
Cymatium nicobaricum	4?002130000---1000-0-1120001100121000002O-00110-000-3126300100100000001-1100000000001111100155000621100000001010000002000											
Cymatium femorale	4?002130000---1000-1-1120001100121000002O-00110-000-3126300100100000001-1100000000001111100155000621100000001010000002000											
Cymatium parthenopeum	4?002130000---1000-0-1120001100121000002O-00110-000-3126300100100000001-1100000000001111100155000621100000001010000002000											
Cymatium pileare	4?002130000---1000-0-1120001100121000002O-00110-000-3126300100100000001-1100000000001111100155000621100000001010000002000											
Sassia kamphyla	4?002130000---1000-0-1120001100122000002O-00110-000-3126300100100000001-1100000000001011100155000621100000001010000002000											
Fusitriton retiolus	4?002130000---1000-0-1120001100122000002O-00110-000-3126300100100000001-1100000000001011100155000621100000001010000002000											
Fusitriton magellanicus	4?002130000---1000-0-1120001100122000002O-00110-000-3126300100100000001-1100000000001011100155000621100000001010000002000											
Bursa corrugata	4?000130000---1000-0-0120101100131000002100021O-000-3126300100100000001-1100000000001011100155000621100000001010000002000											
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Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
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Bursa thomae	4?000130000---1000-0-0120101100131000002100021 0-000-3126300100100000001-1100000000001011100155502621100000001010000002000											
Bursa tenuisculpta	4?000130000---1000-0-0120101100121000002100021 0-000-3126300100100000001-1100000000001011100155000621100000001010000002000											
Bufonaria bufo	4?000130000---1000-0-0120101100131000002100021 0-000-3126300100100000001-1100000000001011100155502621100000001010000002000											
Cypraecasis testiculus	4?020130000---4000-0-0120001100121000002 0-00110-000-????4??????00?00001-1100000000001011100155000621100000004010000002000											
Cassis tuberosa	4?020130000---4000-0-0120001100121000002 0-03110-000-4125300100100000001-1100000000001011100155000621100000004010000002000											
Phalium granulatum	4?020130000---4000-0-0120001100121000002 0-03110-000-4125300100100000001-1100000000001011100155000621100000004010000002000											
Phalium iheringi	4?020130000---4000-0-0120001100121000002 0-03110-000-4125300100100000001-1100000000001011100155000621100000004010000002000											
Phalium labiatum	4?020130000---4000-0-0120001100121000002 0-03110-000-4125300100100000001-1100000000001011100155000621100000004010000002000											
Distorsio clathrata	4?002130000---1000-1-1120001100122000002 0-03111-000-3127300100100000001-1100000000001011100155000633100000005010000002000											
Distorsioanus	4?002130000---1000-1-1120001100122000002 0-03111-000-3127300100100000001-1100000000001011100155000633100000005010000002000											
Distorsio reticulata	4?002130000---1000-1-1120001100122000002 0-03111-000-3127300100100000001-1100000000001011100155000633100000005010000002000											
Distorsio decipiens	4?002130000---1000-1-1120001100122000002 0-03111-000-3127300100100000001-1100000000001011100155000633100000005010000002000											
Personopsis purpurata	4?002130000---1000-0-1120001100121000002 0-03111-000-3126300100100000001-1100000000001011100155000633100000005010000002000											
Tonna galea	4?024130000---1000-0-0120001100111000002 0-001-0-000-????4??????00?00001-1100000000001011100155000621100000001010000002000											
Tonna maculosa	4?024130000---1000-0-0120001100111000002 0-001-0-000-????4??????00?00001-1100000000001011100155000621100000001010000002000											
Cochlespira elongata	4?000100400---1000-0-0000001100013000000 10000-00100-3124300000100000001-1100000000000011100555600322000000001050000002000											
Cochlespira radiata	4?000100400---1000-0-0000001100013000000 10000-00100-3124300000100000001-1100000000000011100555600322000000001050000002000											
Pleurotomella aguayoi	4?002100000---1000-0-0000001100001000000 10000-00200-3124300000100000001-1100000000000011100555600322000100001050000002010											
Carinodrilla braziliensis	21000100000---1000-0--0000011000110000001 0000-00100-3124300000100000001011000000000000111005556003220000000010500000 2000											
Gemmula mystica	4?000100000---1000-0-0000001100013000000 10000-00100-3124300000100000001-1100000000000011100555600322000000001050000002000											
Fenimorea sp.	21000100000---1000-0--0000011000110000001 0000-00100-3124300000100000001011000000000000111005556003220000000010500000 2000											
Clathrodilla sp.	21000100000---1000-0--0000011000110000001 0000-00100-3124300000100000001011000000000000111005556003220000000010500000 2000											
Daphnella lymnaeiformis	4?000100000---1000-0-0000001100001000000 10000-00200-????400??0?00000001-1100000000000011100555600????002000010500000 2010											
Pilsbryspira albomaculata	41000100000---1000-0-0000001100011000000 10000-00100-3124300000100000001-1100000000000011100555600322000000001050000002000											
Glyphostoma sp.	4?000100000---1000-0-0000001100011000000 10000-00100-3124300000100000001-1100000000000011100555600322000000001050000002000											
Polystira formosissima	4?000100000---1000-0-0000001100013000000 10000-00100-3124300000100000001-1100000000000011100555600322000000001050000002000											
Conus regius	A2020200300---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus mindanus	A2020200300---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus villepinii	A2022200300---1000-0-1000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus clerii	A2022200300---1000-0-1000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus archetipus	A2022200300---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus bertarollae	A2022200300---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus textile	A2020200000---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus tulipa	A2020200000---1000-0-0000001100001000000 10000-01200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus selenae	A2020200000---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000000000011100655600322000100001050000002010											
Conus ermineus	A2020200000---1000-0-0000001100001000000 10000-01200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Conus jaspideus	A2020200300---1000-0-0000001100001000000 10000-02200-9124300100100000001-1100000001000011100655600322000100001050000002010											
Duplicaria crakei	21000200000---1000-0--0000011000010000000 -000-00-00-3124300000100000001011000000000000111007556 00????002000010000000 2000											
Hastula cinerea	210?0200000---1000-0--0000011001010000000 -000-00-00-3124300100100000001011000000000000111017556003220002001000000000 2000											
Hastula hastata	210?0200000---1000-0--0000011001010000000 -000-00-00-3124300000100000001011000000000000111017556003220002000000000000 2000											
Terebra gemmulata	210?0100000---1000-0--0000011000010000000 -000-00-00-3124300000100000001011000000000000111017556007?400020000100000000 2000											
Terebra crassireticula	210?0100000---1000-0--0000011000010000000 -000-00-00-3124300000100000001011000000000000111017556003220002000010000000 2000											

Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890											
Terebra leptapsis	210?0100000---1000-0--0000011000010000000-000-00-00-3124300000100000001011000000000000111017556003220002000010000000002000											
Terebra brasiliensis	210?0100000---1000-0--0000011000010000000-000-00-00-3124300000100000001011000000000000111017556007?4000200001000000002000											
Terebra spirosulcata	210?0100000---1000-0--0000011000010000000-000-00-00-3124300000100000001011000000000000111017556003220002000010000000002000											
Terebra taurina	210?0100000---1000-0--0000011000010000000-000-00-00-3124300000100000001011000000000000111017556003220002000010000000002000											
Terebra dislocata	210?0100000---1000-0--0000011000010000000-000-00-00-3124300000100000001011000000000000111017556007?4000200001000000002000											
Zemira australis	4?000150000---1000-0-0000001100011000030-000-0-000-3123300000100000001-110000000000001110075500032100000000100000002000											
Fulmentum ancilla	4?000150000---1000-0-0000001100011000030-000-0-000-3124300000100000001-110000000000001110075500032100000000100000002000											
Melapium lineatum	4?000100000---1000-0-0010001100111000000-000-0-000-????400100?00000001-110000000000001110075500032100000000100000002000											
Benthobia atafona	4?000150000---1000-0-0000001100001000000-000-0-000-3124300000100000001-110000000000021110015500031100000000120000002000											
Benthobia complexirhyna	4?000150000---1000-0-0000001100001000000-000-0-000-3124300000100000001-110000000000021110015500031100000000120000002000											
Nassodonta dorri	4?000150000---1000-0-0000001110011000000-000-0-200-3124300100100000001-110000000000001110055500032100000000100020002000											
Siratus senegalensis	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Siratus tenuivaricosus	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Siratus formosus	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Sirarus beauii	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Phyllonotus pomum	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Phyllonotus occulatus	4?000160500---1000-0-0021401100124000020-001-0-020-3123300000100000001-110000000000001110085500032100000000130000002000											
Phyllonotus margaritensis	4?000160500---1000-0-0021401100124000020-001-0-020-3123300000100000001-110000000000001110085500032100000000130000002000											
Chicoreus brevifrons	4?000160500---1000-0-0022301100124000020-001-0-030-3122300000100000001-110000000000001110085500032100000000130000002000											
Chicoreus spectrum	4?000160500---1000-0-0022301100124000020-001-0-030-3122300000100000001-110000000000001110085500032100000000130000002000											
Chicoreus carolinae	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Chicoreus coltrorum	4?000160500---1000-0-0021301100124000020-001-0-040-3123300000100000001-110000000000001110085500032100000000130000002000											
Murex trapa	4?000100500---1000-0-0021301100124000020-001-0-010-3123300000100000001-110000000000001110085500032100000000130000002000											
Trophon geversianus	4?000160500---1000-0-0010001100121000020-001-0-000-3123300000100000001-110000000000001110085500032100000000130000002000											
Bolinus brandaris	4?000100500---1000-0-0021401100124000020-001-0-010-3123300000100000001-110000000000001110085500032100000000130000002000											
Nucella lapillus	4?000100500---1000-0-0010001100101010002100 01-0-200-3125300000100000001-110000000000001110085500032100000000130000002000											
Thais biserialis	4?000100500---1000-0-0010001100101010002100 01-0-200-3125300000100000001-110000000000001110085500032100000000130000002000											
Coralliophila nux	4?000100500---1000-0-0010001100101000020-001-0-000-3125300000100000001-110000000000001110085500032100000000100000002000											
Eupleura sp.	4?000160500---1000-0-0021101100124000020-001-0-000-3122300000100000001-110000000000001110085500032100000000130000002000											
Acanthina brevidentata	4?000100500---1000-0-0010001100101000002100 01-0-200-3125300000100000001-110000000000001110085500032100000000130000002000											
Muricanthus radix	4?000160500---1000-0-0022401100124000020-001-0-020-3122300000100000001-110000000000001110085500032100000000130000002000											
Vitularia salebrosa	4?000160500---1000-0-0021001100124000020-001-0-000-3125300000100000001-110000000000001110085500032100000000130000002000											
Olivancillaria urceus	4?023170000---1000-0-0000001100111000010-10030-001-????4?0100?????2001-110000000000001110075500032100000010004000002000											
Vexillum sp.	4?000100000---1000-0-0000001100111000010-00030-001-????4?0100?????2001-110000000000001110075500032100000000100000002000											
Austromitra maculosa	4?000100000---1000-0-0000001100111000010-00030-001-????4?0100?????2001-110000000000001110055500032100000000100000002000											
Buccinanops gradatus	4?000100000---1000-0-0000001100111000010-00000-200-3124300100100000001-110000000000021110075500032100000000100020002000											
Buccinanops monilifer	4?000100000---1000-0-0000001100111000010-00000-200-3124300100100000001-110000000000021110075500032100000000100020002000											
Nodicostellaria crassa	4?000100000---1000-0-0000001100111000010-00030-001-????4?0100?????2001-110000000000001110075500032100000000100000002000											
Prunum martini	4?023?70000---1010-0-0000001100111000010-10030-0010????4?0100?????2001-110000000000001110075500032100000000100000002000											
Amphissa acuminata	4?000100000---1000-0-0000001100111000001100 0000-200-3124300100100000001-110000000000001110055500032100000000100100002000											
Amphissa cancellata	4?000100000---1000-0-0000001100111000001100 0000-200-3124300100100000001-110000000000001110055500032100000000100100002000											
Tritonoharpa lanceolata	4?000100000---1000-0-0000001100111000010-00030-000-????4??????????2001-110000000000001110075500032300000000100000002000											

Taxon\character	1	2	3	4	5	6	7	8	9	10	11	12
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890											
Cancellaria reticulata	4?000100000---1000-0-00000011001110000010-00030-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Cancellaria petuchi	4?000100000---1000-0-00000011001110000010-00030-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Cancellaria cancellata	4?000100000---1000-0-00000011001110000010-00030-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Cancellaria spirata	4?000100000---1000-0-00000011001110000010-00030-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Trigonostoma tesselata	4?000180600---1000-0-00000011001110000010-00130-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Trigonostoma tenerum	4?000180600---1000-0-00000011001110000010-00130-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Scalpia contabulata	4?000180600---1000-0-00000011001110000010-00130-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Scalpia obliquata	4?000180600---1000-0-00000011001110000010-00130-001-????4???????????001-11000000000000111007550003230000000010000000002000											
Annulobalcis aurisflamma	210?0100000---1000-0--00-00110010000000000-000-0---0-31132000001000000010110000000000000111001??000?000000000010000020210											
Perotrochus atlanticus	120?0100000---1000-0--01-00110000020000020000-0---0-11111000001000000001-11000000000000111021110000000000006000000000001001											
Lucapina elisae	040?0040000---0000-0--00-00111000020000030000-0---0-????400?00?00000001-11000000000000111021117100000000000600000302012 01											
Fissurella mesoatlantica	040?0040000---0000-0--00-00111000020000030000-0---0-????400?00?00000001-11000000000000111021117100000000000600000302012 01											
Haliotis aurantium	940?0100700---1000-0--00-00110100021000020000-0---0-????400?00?00000001-11000000000000111021117100000000000600000302012 01											
Haliotis pourtalesii	940?0100700---1000-0--00-00110100021000020000-0---0-????400?00?00000001-11000000000000111021117100000000000600000302012 01											
Falsimargarita stephaniae	120?0100000---1000-0--00-00110000000100000-000-0---0-11111000001000000011-11000000000000111021117100000000000600006302011 01											
Calliostoma sp.	120?0100000---1000-0--00-00110000000100000-000-0---0-11111000001000000011-11000000000000111021117100000000000600000302011 01											
Gaza compta	120?3170000---3000-0--00-00110001001000010-00020---0-11111000001000000011-11000000000000111021117100000000000600006302011 01											
Gaza superba	120?3170000---3000-0--00-00110001001000010-00020---0-11111000001000000011-11000000000000111021117100000000000600006302011 01											
Gaza cubana	120?3170000---3000-0--00-00110001001000010-00020---0-11111000001000000011-11000000000000111021117100000000000600006302011 01											
Addisonia enodis	040?0000000---0000-0--00-00110000000000000-000-0---0-????400?00?00000001-11000000000000111001110000000000000000000000001000											
Pseudococculina rimula	041?0000000---0000-0--00-00110000000000000-000-0---0-????400?00?00000001-11000000000000111001110000000000000000000000001000											
Neritina zebra	120?0200000---1000-0--00-01110000000000000-000-0---0-82122000001000001 01-11000000000000111001110000000000000000000000001000											
Nerita ascensionis	120?0200000---1000-0--00-01110000000000000-000-0---0-82122000001000001 01-11000000000000111001110000000000000000000000001000											
Cyclothyca pacei	640?0140002---1000-0--00-00110100000000000-000-0---0-????400?00?00000001-11000000000000111001110000000000000000000000001000											
Rissoella ornata	212?0100000---1000-0--00-00110020000000000-000-0---0-11253000001000002010110000000000000111001 0?020000000000000000000001000											
Ammonicera plana	132?0100000---1000-0--00-00110020000000000-000-0---0-11112000001000000 01-11000000000002111001 0?000000000000000100000001000											
Orbitestella patagonica	132?0100000---1000-0--00-00110020000000000-000-0---0-11112000001000000 01-11000000000002111001 0?000000000000000100000001000											
Flabellina lucianae	?00???00000---?00--0--0--?051???2?00??0???0-?0???---0-????400?00?00000001-11000000000000111001 0?020000000000-000000001 0?0											
Anctus angiostomus	110?0100000---1000-0--00-00110001000000 10-000-0---0-????400?00?00000001-11000000000000111009 0?020000000000000000400001000											
Megalobulimus riopretensis	110?0100000---1000-0--00-00110001000000 10-000-0---0-????400?00?00000001-11000000000000111009 0?020000000000000000400001000											
Megalobulimus mogianensis	110?0100000---1000-0--00-00110001000000 10-000-0---0-????400?00?00000001-11000000000000111009 0?020000000000000000400001000											
Olympus nimbus	120?0100000---1000-0--00-00110001000000 10-000-0---0-????400?00?00000001-11000000000000111009 0?020000000000000000400001000											
Propilidium curumim	001?0000000---0000-0--00-00110000000000000-000-0---0-????400?00?00000001-11000000000000111001110000000000000000000000001000											
Nautilus pompilius	?00?0-00--0---0000-0--0--00410000000000000-000-0---0-00--------0-------0-11000000000000101001 0---0000000002-0000-00000000											
Lolliguncula brevis	?00??-00--0---0001-0--0--00510??000--00-0-?0?-----0-00--------0-------0-11000000000000101101 0---0000000002-?000-000000-0											
Coccodentalium carduus	?00?0000--0---0000-0--0--00310000000--00-0-?00-----0-00--------0-------0-10000000000000100110 0---0000000001-000?-000000-0											
Gadila braziliensis	?01?0000--0---0000-0--0--00310000000--00-0-?00-----0-00--------0-------0-10000000000000100110 0---0000000001-000?-000000-0											
Solemya occidentalis	?00?1-00--0---0000-0--0--00210000000--00-0-?00-----0-00--------0-------0-10100000010000100110 0---0000000001-000?-000000-0											
Ennucula puelcha	?00?1-00--0---0000-0--0--00210000000--00-0-?00-----0-00--------0-------0-10100000010000100110 0---0000000001-000?-000000-0											
Neopilina galatheae	000?0000-00---0000-0--0--00100000000000000-000-0---0-00--------0-------0-00000000000000100000000-000000000000000000000000											
Hanleya sp.	000?0-00--0---0000-0--0--00000000000--00-0-000-----0--0--------0-------0-00000000000000000000000-0000000000000000-00000000											

APPENDIX 2 - Continued

Matrix of characters considered in the present study

Taxon\character	12	13	14	15	16	17	18	19	20	21	22	23	24
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
Pomacea crosseana	0100101012011230000010110003010000000-11000000000----0-0021320100010--0100000111111000000001000-0011211010101111100010011												
Pomacea curumim	0100101012011230000010110003010000000-11000000000----0-0020320100010--0100000111110001100010000-0011211010101111100010011												
Pomacea scalaris	0100101012011230000010110003010000000-11000000000----0-0020320100010--0100000111111000100010000-0011211010101111100010011												
Pomacea canaliculata	0100101012011230000010110003010000000-11000000000----0-0021320100010--0100000111111000101010000-0011211010101111100010011												
Pomacea lineata	0100101012011230000010110003010000000-11000000000----0-0020320100010--0100000111111000101010000-0011211010101111100010011												
Pomacea sordida	0100101012011230000010110003010000000-11000000000----0-0021320100010--0100000111111000001010000-0011211010101111100010011												
Pomacea bridgesi	0100101012011230000010110003010000000-11000000000----0-0021320100010--0100000111111000000001000-0011211010101111100010011												
Asolene megastoma	0100101012011230000010110003010000000-11000000000----0-0021320100010--0100000111111000100010000-0011211010101111100010011												
Felipponea neritiniformis	0100101012011230000010110003010000000-11000000000----0-0020320100010--0100000111111000100010000-0011211010101111100010011												
Marisa planogyra	0100101012011210000010110001020000000-11000000000----0-0020320100010--0100000111111000000000000-0011211010101111100010011												
Neocyclotus prominulus	0100101012011220000010110001000000000-11000000000----0-00?01??0-00?0--01-000010112??0???0000000-00?1?1?010101?111000100110												
Incidostoma tupy	0100101012011220000010110001000000000-11000000000----0-00?01??0-00?0--01-000010112??0???0000000-00?1?1?010101?111000100110												
Aperostoma blanchetiana	0100101012011220000010110001000000000-11000000000----0-00?01??0-00?0--01-000010112??0???0000000-00?1?1?010101?111000100110												
Viviparus acerosus	0100101012011210000010110002000000000-11000000000----0-00101100-0010--01-000011111010010000001-0011211010001111100010011												
Viviparus contectus	0100101012011210000010110002000000000-11000000000----0-00101100-0010--01-000011111010010000001-0011211010001111100010011												
Notopala ampullaroides	0100101012011210000010110002000000000-11000000000----0-00121102-0010--01000001111101000000001-0011211010101111100010011												
Notopala essingtonensis	0100101012011210000010110002000000000-11000000000----0-00121102-0010--01000001111101000000001-0011211010101111100010011												
Larina cf. strangei	0100101012011210000010110002000000000-11000000000----0-00121102-0010--01000001111101000000001-0011211010101111100010011												
Annularia sp.	0100101112011210000010110001?0000-11000000000----0-00101100-0010--01-000011112??0?0000000-0011211010101111100010012												
Aylacostoma exoplicata	0100101112011210000010110001001110000-11200000000----0-00101300-1010--01-000011111000010000000-0011211010201111100010011												
Aylacostoma ci	0100101112011210000010110001001010000-11200000000----0-00101200-0010--01-000011111000010000000-0011211010201111100010011												
Aylacostoma tenuilabris	0100101112011210000010110001001110000-11200000000----0-00101100-0010--01-000011111000010000000-0011211010201111100010011												
Melanoides tuberculatus	0100101112011210000010110001001010000-11200000000----0-00101200-0010--01-000011111000010000000-0011211010201111100010011												
Supplanaxis nucleus	0100101112111210000010110001001000000-11000000000----0-00101300-0010--01-000011111000010000000-0011211010201111100010011												
Doryssa ipupiara	0100101112211210000010110001001020000-11000000000----0-00101200-0010--01-000011111000111200000-0011211010201111100010011												
Doryssa atra	0100101112211210000010110001001120000-11000000000----0-00101220-0010--01-000011111000111200000-0011211010201111100010011												
Doryssa macapa	0100101112211210000010110001001120000-11000000000----0-00101220-0010--01-000011111000111200000-0011211010201111100010011												
Pachychilus sp.	0100101112211210000010110001001020000-11000000000----0-00101200-0010--01-000011111000111000000-0011211010201111100010011												
Turritella hookeri	0100101112011240000010110002000000000-11110000000----0-00101300-0010--01-000011111001311000000000112110102011111000100110												
Modulus modulus	0100101212111210000010110001000000000-11100000000----0-00101310-0010--01-000011111000011000000-0011211010001111100010011												
Cerithium atratum	0100111112111210000010110001001000000-11100000000----0-0010230100010--0100000111110000010000000-0011211010201111100010011												
Bittium varium	0100121112011210000010110001001000000-11100000000----0-0010230112010--0100000111110000010001000-0011211010201111100010011												
Finella dubia	0100121112011210000010110001001000000-11100000000----0-0010230112010--0100000111110000210001000-0011211010201111100010011												
Alaba incerta	0100121112011210000010110001001000000-11100000000----0-0010210112010--0100000111110000010001000-0011211010201111100010011												
Batillaria minima	0100101212111210000010110001000000000-11100000000----0-00101100-0010--01-000011111000010001000-0011211010201111100010011												
Cerithidea costata	0100101112011210000010110001001000000-11110000000----0-00101200-0010--01-000011111000010001000-0011211010201111100010011												
Campanile symbolicum	0100201212111240000010110001000100000-11110000000----0-0010320100010--0100000111110010100000000-0011211010201111100010011												
Serpulorbis decussatus	0000311112011240000010110002000000000-11110000000----0-00101100-0010--01-000011111001311001000000112110102011111000100210												

Taxon\character	12	13	14	15	16	17	18	19	20	21	22	23	24
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
Stephopoma nucleogranosum	0100311112111240000010110002000000-11110000000----0-00101310-0010--01-0000111110013110010000-0011211010201111100010011												
Amphithalamus glaber	0100101102-1121000001011000300100000-11300000000----0-00301100-0010--01-0000111110001000000000-0011211010101111100010011												
Littorina flava	0100101112011210000010110003001000-11000000000----0-00101100-0010--01-0000111110000000000000-0011211010101111100010011												
Potamolithus ribeirensis	0100101102-1121000001011000300100000-11300000000----0-00331100-0010--01-0000111110001000000000-0011211010101111100010011												
Potamolithus troglobius	0100101102-?1210000010110003001000-11300000000----0-00331100-0010--01-0000111110001000000000-0011211010101111100010011												
Potamolithus karsticus	0100101102-1121000001011000300100000-11300000000----0-00331100-0010--01-0000111110001000000000-0011211010101111100010011												
Strombus pugilis	0100101312311211000010110001001230-00-11011000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Strombus alatus	0100101312311211000010110001001230-00-11011000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Strombus gracilior	0100101312311211000010110001001230-00-11011000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Eustrombus goliath	0110101312311211000010210001001230-00-11011000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Eustrombus gigas	0110101312311211000010210001001230-00-11011000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Aliger costatus	0110101312311211000010110001001230-00-11411000000----0-1010235100110--0100000111110013010101000-0011211010001111110010011												
Aliger gallus	0110101312311211000010110001001230-00-11411000000----0-1010235100110--0100000111110013010101000-0011211010001111110010011												
Tricornis raninus	0100101312311211000010110001001230-00-11411000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Conomurex luhuanus	0100101312311211000010110001001230-00-11411000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
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Lambis lambis	0100101312311211000010110001001230-00-11011000000----0-1010233100110--0100000111110013010101000-0011211010001111110010011												
Terebellum terebellum	0100101312311211000010110001001230-00-11411000000----0-1010233100010--0100000111110013010101000-0011211010001111110010011												
Tylospira scutulata	0100101112011211000010110001001000-00-11411000000----0-10101330-1010--01-0000111110010000000020001121101000111110010011												
Struthiolaria papulosa	0100101112011211000010110001001000-00-11411000000----0-10101330-1010--01-0000111110010000000020001121101000111110010011												
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Aporrhais occidentalis	0100101212011211000010110001001230-00-11411000000----0-10101330-1010--01-0000111110013003001000-0011211010001111110010011												
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Xenophora conchyliophora	0100101212011211000010110001001231-00-11111000000----0-10101300-0010--01-0000111110014010002000-0011211010101111100010011												
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Crepidula intratesta	0101401202-1125012401011010400100010211002120000----0-1010340320032110100000111112115220000220101121001010111110112000110												
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Calyptraea centralis	0101101212011210013010110104001000100110021100 00----0-1010310320031--0100010111112115220000220101121001020111110115000110												
Crucibulum auricula	0101101212011250023010110104001000110110021100 00----0-1010310300031--0100010111112115220000220101121001020111110113000110												
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Taxon\character	12	13	14	15	16	17	18	19	20	21	22	23	24
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Naticarius canrenus	0100502400-1121000001010000100100000-11000000000----0-1010330600010--0100010111113000000000000-0011211010101111110001000110												
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Natica cf. *marochiensis*	0100502401-1121000001010000100100000-11000000000----0-1015334640010--0100010111113000000000000-0011211010101111110001000110												
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Eunaticina sp.	0100502400-1121000001010000100100000-11000000000----0-1014324100010--1100010111113000000000000-0011211010101111110001000110												
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Amauropsis islandica	0100501102-1121000001010000100100000-11000000000----0-10101300-2010--01-0010111110006000000000-0011211010201111110001000110												
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"Amauropsis" rossiana	0100101102-1121000001011000100100000-11000000000----0-00101200-0010--01-0000111110000000000000-0011211010201111110001001 12												
Macrocypraea zebra	0100301212111280000221100001001000 00-1152300121140010021103108500 10--0211101111140000000000-0011211011201111110010 1110												
Macrocypraea cervinetta	0100301212111280000221100001001000 00-1152300121140010021103108500 10--0211101111140000000000-0011211011201111110010 1110												
Erosaria acicularis	0100301212111280000221100001001000 00-1152300121131010021103108500 10--0211010111140000000000-0011211011201111110010 1110												
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Taxon\character	12	13	14	15	16	17	18	19	20	21	22	23	24
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Lyncina lynx	0100301212111280000221100001001000000-1152300121132020021103108500l0--021111011111400000000000-00112110112011111100101110												
Monetaria moneta	0100301212111280000221100001001000000-1152300122131010021103108500l0--021101011111400000000000-00112110112011111100101110												
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Ravitrona caputserpentis	0100301212111280000120100001001000000-1152300121131010021103101000l0--021101011111400000000000-00112110112011111100101110												
Pseudozonaria arabicula	0100301212111280000221100001001000000-1152300121130130021103108500l0--021101011111400000000000-00112110112011111100101110												
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Cyphoma signatum	0100301212111280000030100001001000000-1152300125100000021103101000l0--021111011111400000000000-00112110112011111100101110												
Cyphoma gibbosum	0100301212111280000030100001001000000-1152300123100000021103101000l0--021111011111400000000000-00112110112011111100101110												
Pseudocyphoma intermedium	0100301212111280000030100001001000000-1152300115100000021103101000l0--021111011111400000000000-00112110112011111100101110												
Ovula ovum	0100301212111280000030100001001000000-1152300111110000021103101000l0--021111011111400000000000-00112110112011111100101110												
Calpurnus verrucosus	0100301212111280000030100001001000000-1102300114100000021103101000l0--021111011111400000000000-00112110112011111100101110												
Simnialena uniplicata	0100301212111280000030100001001000000-1152300111120000021103101000l0--021101011111400000000000-00112110112011111100101110												
Cymbula acicularis	0100301212111280000030100001001000000-1152300111110000021103101000l0--021101011111400000000000-00112110112011111100101110												
Jenneria pustulata	0100301212111280000020100001001000000-1152300111132000021103101500l0--021101011111400000000000-00112110112011111100101110												
Niveria pediculus	0100101212111280000020100001001000000-1102300011103000021103101600l0--011101011111400000000000-00112110102011111100101110												
Trivirostra oryza	0100101212111280000020100001001000000-1102300011103000021103101600l0--011101011111400000000000-00112110102011111100101110												
Hespererato maugeriae	0100101212111280000020100001001000000-1102300011100000021103101000l0--011101011111400000000000-00112110102011111100101110												
Pedicularia sp.1	0100101102-1128000002010000100100000-1102000011100000011103101100l0--011121011111400000000000-00112110102011111100101110												
Pedicularia californica	0100101102-1128000002010000100100000-1102000011100000011103101100l0--011121011111400000000000-00112110102011111100101110												
Pedicularia decussata	0100101102-1128000002010000100100000-1102000011100000011103101100l0--011121011111400000000000-00112110102011111100101110												
Pedicularia sp.2	0100101102-1128000002010000100100000-1102000011100000011103101100l0--011121011111400000000000-00112110102011111100101110												
Lamellaria branca	0100101112111270000010100001001000000-1102300011200000021103101500l0--011001011111000000000000-00112110102011111100100110												
Lamellaria mopsicolor	0100101112111270000010100001001000000-1152300011210000021103101000l0--011001011111000000000000-00112110102011111100100110												
Lamellaria patagonica	0100101112111270000010100001001000000-1102300011200000021103101600l0--011001011111000000000000-00112110102011111100100110												
Velutina velutina	0100101112111260000010100001001000000-1102300011100000021103101600l0--011001011111000000000000-00112110102011111100100110												
Ficus filosa	0100101112111210000010100001001000000-11000000100----201210323160010--010002011111001000010300-01112110113011111100100110												
Ficus ventricosa	0100101112111210000010100001001000000-11000000100----201210323160010--010002011111001000010300-01112110113011111100100110												
Ficus carolae	0100101112111210000010100001001000000-11000000100----201210323160010--010002011111001000010300-01112110113011111100100110												
Ficus subintermedia	0100101112111210000010100001001000000-11000000100----201210323160010--010002011111001000010300-01112110113011111100100110												
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Thalassocyon bonus	0100101l?211121000001010000100100000-11000000100----001210323160010--010002011111021000010300-00112110103011111100100110												
Charonia laevigata	0100101112111210000010100001001000000-11000000100----001210343160010--010002011111001000010300-01112110113011111100100110												
Cymatium cynocephalum	0100101112111210000010100001001000000-11104000100----101210323160010--010002011111021000010300-00112110113011111100100110												
Cymatium nicobaricum	0100101112111210000010100001001000000-11104000100----101210343160010--010002011111021200010300-00112110113011111100100110												
Cymatium femorale	0100101112111210000010100001001000000-11104000100----101210343160010--010002011111021200010300-00112110113011111100100110												
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Cymatium pileare	0100101112111210000010100001001000000-11104000100----101210343160010--010002011111021200010300-00112110113011111100100110												
Sassia kamphyla	0100101112111210000010100001001000000-11004000100----001210343760010--010002011111021200010300-01112110103011111100100110												
Fusitriton retiolus	0100101112111210000010100001001000000-11004000100----001210343760010--010002011111021700010300-01112110113011111100100110												
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Bursa corrugata	0100101112111210000010100001001000000-11000001100----001210323160010--010002011111021800010300-00112110113011111100100110												
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Bursa thomae	0100101112111210000010100001001000000-11000001100----001210323160010--0100020111110218000103000-0011211011301111111001001100												
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Bufonaria bufo	0100101112111210000010100001001000000-11000001100----001210323160010--0100020111110218000103000-0011211011301111111001001100												
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Phalium granulatum	0100101112111210000010100001001010000-11600000100----001210323160010--0100020111110210000103000-0111211011301111111001001100												
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Distorsio clathrata	0100101112111210000010100001001000000-11104000100----001210323160010--0100020111110217000123000-0011211011301111111001001100												
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Distorsio decipiens	0100101112111210000010100001001000000-11104000100----001210323160010--0100020111110217000123000-0011211011301111111001001100												
Personopsis purpurata	0100101112111210000010100001001000000-11104000100----001210323160010--0100020111110217000123000-0011211011301111111001001100												
Tonna galea	0100101112111210000010100001001010000-11000000100----001210323160010--0100010111110210000103000-0111211010301111111001001100												
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Cochlespira elongata	0100101212111210000010110001001000000-11000000100----001210310100010--0100020111110008000100000-0011211010211111111000100110												
Cochlespira radiata	0100101212111210000010110001001000000-11000000100----001210310100010--0100020111110008000100000-0011211010211111111000100110												
Pleurotomella aguayoi	0100101212111210000010110001001000000-11000000100----001210330100010--0100010111110000000100000-0011211010211111110101001100												
Carinodrilla braziliensis	0100101312111210000010110001001000000-11000000100----001210310100010--0100020111110000000100000-0011211010211111110001001100												
Gemmula mystica	0100101?10?1121000001011000100100000-11000000100----001210310100010--0100020111110008000100000-0011211010211111110001001100												
Fenimorea sp.	0100101312111210000010110001001000000-11000000100----001210310100010--0100020111110008000100000-0011211010211111110001001100												
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Daphnella lymnaeiformis	0100101212111210000010110001001000000-11000000100----001210330100010--0100020111110008000100000-0011211010211111110101001100												
Pilsbryspira albomaculata	0100101312111210000010110001001000000-11008000100----301210310100010--0100020111110008000100000-0011211010211111110001001100												
Glyphostoma sp.	0100101212111210000010110001001000000-11000000100----001210310100010--0100020111110008000100000-0011211010211111110001001100												
Polystira formosissima	0100101312111210000010110001001000000-11000000100----001210320100010--0100020111110008000100000-0011211010211111110001001100												
Conus regius	0100101312111210000010110011001000000-11000000100----301210320160010--0100010111110002000100000-0011211010201111110101002100												
Conus mindanus	0100101312111210000010110011001000000-11000000100----301210310160010--0100010111110002000100000-0011211010201111110101002100												
Conus villepinii	0100101312111210000010110011001000000-11000000100----301210320160010--0100010111110002000100000-0011211010201111110101002100												
Conus clerii	0100101312111210000010110011001000000-11000000100----301210320160010--0100010111110002000100000-0011211010201111110101002100												
Conus archetipus	0100101312111210000010110011001000000-11000000100----301210320160010--0100010111110000000100000-0011211010201111110101002100												
Conus bertarollae	0100101312111210000010110011001000000-11000000100----301210320160010--0100010111110000000100000-0011211010201111110101002100												
Conus textile	0100101312111210000010110011001000000-11000000100----301210320160010--0120010111110000000100000-0011211010201111110101002100												
Conus tulipa	0100101312111210000010110011001000000-11000000100----301210320160010--0120010111110002000100000-0011211010201111110101002100												
Conus selenae	0100101312111210000010110011001000000-11000000100----001210320100010--0100010111110008000100000-0011211010201111110101002100												
Conus ermineus	0100101312111210000010110011001000000-11000000100----301210320160010--0120010111110002000100000-0011211010201111110101002100												
Conus jaspideus	0100101312111210000010110011001000000-11000000100----301210310160010--0100010111110002000100000-0011211010201111110101002100												
Duplicaria crakei	0100111?10?1129000001011000200100000-11000000100----001210310100010--0100020111110002000102000-0011211010211111110001001100												
Hastula cinerea	0100132112111290000010110002001000000-11000000200----001210310160010--0100020111110008000002000-0011211010211111110001001100												
Hastula hastata	0100131112111290000010110002001000000-11000000200----001210310160010--0100020111110008000002000-0011211010211111110001001100												
Terebra gemmulata	0100132511?1129000001011000200000000-11000000100----001210320100010--0130020111110008000002000-0011211010211111110001001100												
Terebra crassireticula	0100131512111290000010110002001000000-11000000100----001210330100010--0130020111110008330002000-0011211010201111110001001100												

Taxon\character	12	13	14	15	16	17	18	19	20	21	22	23	24
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Terebra brasiliensis	0100131512111290000010110002000000 00-11000000100----001210320100010--0130020111110008000002 00-0011211010201111100010 0110												
Terebra spirosulcata	0100131512111290000010110002000000 00-11000000100----001210320100010--0130020111110008000002 00-0011211010211111100010 0110												
Terebra taurina	0100131512111290000010110002000000 00-11000000100----001210310100010--0100020111110008000002 00-0011211010201111100010 0110												
Terebra dislocata	0100132512111290000010110002000000 00-11000000100----001210320100010--0130020111110008000002 00-0011211010211111100010 0110												
Zemira australis	0100102212111210000010100001001000 00-11000000100----001210330100010--0100010111110000000010000-0011211010211111100010 0110												
Fulmentum ancilla	0100102212111210000010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Melapium lineatum	0100101212111212200010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Benthobia atafona	0100101??0?1?2100000101000010010000 0-11000000100----001210330700010--0130010111110000000010000-0011211010211111100010 0110												
Benthobia complexirhyna	0100101??0?1?2100000101000010010000 0-11000000100----001210330700010--0130010111110000000010000-0011211010211111100010 0110												
Nassodonta dorri	0100102212111210000010100001001000 00-11000000100----001210310100010--0130010111110000000010000-0011211010211111100010 0110												
Siratus senegalensis	0100102212411212200010100001001000 00-11700000100----511210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Siratus tenuivaricosus	0100102212411212200010100001001000 00-11700000100----511210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Siratus formosus	0100102212411212200010100001001000 00-11700000100----511210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Sirarus beauii	0100102212411212200010100001001000 00-11700000100----511210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Phyllonotus pomum	0100102212411212200010100001001000 00-11700000100----411210310160010--0100010111110007000100 00-0011211010411111100010 0110												
Phyllonotus occulatus	0100102212411212200010100001001000 00-11700000100----411210310160010--0100010111110007000100 00-0011211010411111100010 0110												
Phyllonotus margaritensis	0100102212411212200010100001001000 00-11700000100----411210310160010--0100010111110007000100 00-0011211010411111100010 0110												
Chicoreus brevifrons	0100102212411212200010100001001000 00-11700000100----411210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Chicoreus spectrum	0100102212411212200010100001001000 00-11700000100----411210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Chicoreus carolinae	0100102212411212200010100001001000 00-11700000100----411210310100010--0130021111110007000100 00-0011211010411111100010 0110												
Chicoreus coltrorum	0100102212411212200010100001001000 00-11700000100----411210310100010--0130021111110007000100 00-0011211010411111100010 0110												
Murex trapa	0100102212411212200010100001001000 00-11700000100----411210310100010--0100010111110007000100 00-0011211010411111100010 0110												
Trophon geversianus	0100102212411212200010100001001000 00-11000000100----411210310100010--0100010111110000000010000-0011211010411111100010 0110												
Bolinus brandaris	0100102212411212200010100001001000 00-11700000100----411210310100010--0100011111110007000100 00-0011211010411111100010 0110												
Nucella lapillus	0100102212411212200010100001001000 00-11000000100----411210310100010--0100010111110000000010000-0011211010411111100010 0110												
Thais biserialis	0100102212411212200010100001001000 00-11000000100----411210310100010--0100010111110000000010000-0011211010411111100010 0110												
Coralliophila nux	0100102212111212200010100001001000 00-11000000100----411210310100010--0100010111110000000010000-0011211010411111100010 0110												
Eupleura sp.	0100102212411212200010100001001000 00-11700000100----411210310100010--0100010111110007000100 00-0011211010411111100010 0110												
Acanthina brevidentata	0100102212411212200010100001001000 00-11000000100----411210310100010--0100010111110000000010000-0011211010411111100010 0110												
Muricanthus radix	0100102212411212200010100001001000 00-11700000100----411210310100010--0100010111110000000010000-0011211010411111100010 0110												
Vitularia salebrosa	0100102212411212200010100001001000 00-11000000100----511210310100010--0100010111110000000010000-0011211010411111100010 0110												
Olivancillaria urceus	0100002??0?1121000001010000100100000-11000000100----001210310100010--0100010111110000000010000-0011211010211111100100 0110												
Vexillum sp.	0100102212111213000010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Austromitra maculosa	0100102212111213000010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Buccinanops gradatus	0100102?10???2100000101000010010000 0-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Buccinanops monilifer	0100102?10???2100000101000010010000 0-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Nodicostellaria crassa	0100102212111213000010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Prunum martini	0100102212111213000010100001001000 00-11003000100----001210310100010--0100010111110000000010000-0011211010211111100100 0110												
Amphissa acuminata	0100102212111210000010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Amphissa cancellata	0100102212111210000010100001001000 00-11000000100----001210310100010--0100010111110000000010000-0011211010211111100010 0110												
Tritonoharpa lanceolata	0100002212111210000010100001001000 00-11000000100----001210320100010--0100020111110000000010300-0011211010211111100010 0110												

Taxon\character	12	13	14	15	16	17	18	19	20	21	22	23	24
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Cancellaria reticulata	0100602212111213000010100001001000000-11000000100----001210320100010--0100020111110200000103000-0011211010211111100010011												
Cancellaria petuchi	0100602212111213000010100001001000000-11800000100----001210320100010--0100020111110200000103000-0011211010211111100010011												
Cancellaria cancellata	0100002212111213000010100001001000000-11800000100----001210320100010--0100020111110200000103000-0011211010211111100010011												
Cancellaria spirata	0100602212111213000010100001001000000-11000000100----021210320100010--0100020111110000000103000-0011211010211111100010011												
Trigonostoma tesselata	0100002212111213000010100001001000000-11000000100----021210320100010--0100020111110000000103000-0011211012211111100010011												
Trigonostoma tenerum	0100002212111213000010100001001000000-11000000100----021210320100010--0100020111110000000103000-0011211012211111100010011												
Scalpia contabulata	0100002212111213000010100001001000000-11000000100----021210320100010--0100020111110000000103000-0011211012211111100010011												
Scalpia obliquata	0100002212111213000010100001001000000-11800000100----021210320100010--0100020111110000000103000-0011211012211111100010011												
Annulobalcis aurisflamma	0100102112111210000010110001001000000-11000000000----0-10101200-0010--01-0000111110000000000000-0011211010201111100010011												
Perotrochus atlanticus	0000101002-0011000001000000100000000-01900000000----0-00000000-0000--00-0000011100000000000000-0000111011000111100010010												
Lucapina elisae	0000101002-1011000001000000100000000-01900000000----0-00000000-0000--00-0000011100000000000000-0000111011000111100000010												
Fissurella mesoatlantica	0000101002-1011000001000000100000000-01900000000----0-00000000-0000--00-0000011100000000000000-0000111011000111100000010												
Haliotis aurantium	0000101002-0011000001000000100000000-01906000000----0-00000000-0000--00-0000011100000000000000-0000111011000111100010010												
Haliotis pourtalesii	0000101002-0011000001000000100000000-01906000000----0-00000000-0000--00-0000011100000000000000-0000111011000111100010010												
Falsimargarita stephaniae	0000101002-1011000001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111011000111100010010												
Calliostoma sp.	0000101002-1011000001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111011000111100010010												
Gaza compta	0000101002-1011000001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111011000111100010010												
Gaza superba	0000101002-1011000001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111011000111100010010												
Gaza cubana	0000101002-1011000001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111011000111100010010												
Addisonia enodis	0000101?00-?0110000010000001000000000-11000000000----0-00000000-0000--00-0000011110000000000000-0011211010100111110000000000												
Pseudococculina rimula	0000101?00-?0110000010000001000000000-11000000000----0-00000000-0000--00-0000011110000000000000-0011211010100111110000000000												
Neritina zebra	0000101002-1011400001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111010000111110006000010												
Nerita ascensionis	0000101002-1011400001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0001111010000111110006000010												
Cyclothyca pacei	0000101002-1021000001000000100000000-11000000000----0-00000000-0000--00-0000011110000000000000-0011211010201111100010011												
Rissoella ornata	00007??002-1021000001004000100?00200-11?05000000----6-00??0000-0000--00-0000011110000??4????0?0-??1121?110?011111000100212												
Ammonicera plana	00000??002-1021000001000000100000000-11300000000----0-00000000-0000--00-000001111?????4????0?0-????1?1?110?011111000100112												
Orbitestella patagonica	00000??002-1021000001000000100000000-11300000000----0-00000000-0000--00-000001111?????4????0?0-????1?1?110?011111000100112												
Flabellina lucianae	00000??002-1021000001004000?00?0000?-??00000000?----0-00000000-0000--00-0000011???????4????0?0-????1?1?110?0?1111000??0112												
Anctus angiostomus	00007??002-1021000001004000103?04200-11A05000000----6-00??0000-0000--00-0000?011???????4????0?0-????1?1??10?0??1110001002l2												
Megalobulimus riopretensis	00007??002-1021000001004000103?00202-11A05000000----6-00??0000-0000--00-0000?011???????4????0?0-????1?1??10?0??1110001002l2												
Megalobulimus mogianensis	00007??002-1021000001004000103?00202-11A05000000----6-00??0000-0000--00-0000?011???????4????0?0-????1?1??10?0??1110001002l2												
Solaropsis sp.	00007??002-1021000001004000103?04200-11A05000000----6-00??0000-0000--00-0000?011???????4????0?0-????1?1??10?0??1110001002l2												
Propilidium curumim	0-00101?00-?0110000010000001000000000-?1000000000----0-00000000-0000--00-0000011???????????0?0-?????11010?001111100000000												
Nautilus pompilius	0-000---02-0-00?-0000000000310000000-01007000000----0-00000000-0000--00-0000000100000000000000-000001101O?0?0011000100000												
Lolliguncula brevis	0-000---02-1-00?-000000000?10000000-01007000000----0-00000000-0000--00-0000000100000000000000-000001101O?0?00110000?0000												
Coccodentalium carduus	1-000---00-?-00?-0000000000600000000-01000000000----0-00000000-0000--00-0000000???????4????0?0-??????0?010?0?0000000000000												
Gadila braziliensis	1-000---00-?-00?-0000000000600000000-01000000000----0-00000000-0000--00-0000000???????4????0?0-??????0?010?0?0000000000000												
Solemya occidentalis	1-000---00-?-00?-00000000006000000?-010?0000000----0-00000000-0000--00-0000000100000000000000-000000001O?0?0000000000000												
Ennucula puelcha	1-000---00-?-00?-00000000006000000?-010?0000000----0-00000000-0000--00-0000000100000000000000-000000001O?0?0000000000000												
Neopilina galatheae	00000---00-?-000-000100000000000000-00000000000----0-00000000-0000--00-0000000000000000000000-?000000000?0000000000000												
Hanleya sp.	00000---00-?-000-0000000000000000000-00000000000----0-00000000-0000--00-0000000000000000000000-0000000000000000000000000												

APPENDIX 2 - Continued

Matrix of characters considered in the present study

Taxon\character	24	25	26	27	28	29	30	31	32	33	34	35	36
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
Pomacea crosseana	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-031100011000111001												
Pomacea curumim	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-021100011000111001												
Pomacea scalaris	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-021100011000111001												
Pomacea canaliculata	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-031100011000111001												
Pomacea lineata	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-021100011000111001												
Pomacea sordida	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-021100011000111001												
Pomacea bridgesi	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-021100011000111001												
Asolene megastoma	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-031100011000111001												
Felipponea neritiniformis	0100000000000000001110100110001102100200000310---2000-000000000000-000210211000-000-000010120000---100-031100011000111001												
Marisa planogyra	0100000000000000001110100110001101000200000310---2000-000000000000-000210211000-000-000010120000---100-031100011000111001												
Neocyclotus prominulus	0000000000000000001110100010000100000110000110---2000-000000000000-000110311000-000-000010111100---000-011000011000011001												
Incidostoma tupy	0000000000000000001110100010000100000110000110---2000-000000000000-000110311000-000-000010111200---000-001000011000011001												
Aperostoma blanchetiana	0000000000000000001110100010000100000110000110---2000-000000000000-000110311000-000-000010111200---000-001000011000011001												
Viviparus acerosus	0000000000000000001110100210000100011000000210---2000-000000000000-000110111000-000-000010100010---000-002210011000211001												
Viviparus contectus	0000000000000000001110100210000100011000000210---2000-000000000000-000110111000-000-000010100010---000-002210011000211001												
Notopala ampullaroides	0001000000000000001110100210000100012000000210---2000-000000000000-000110111000-000-000010100010---000-002210011000211001												
Notopala essingtonensis	0001000000000000001110100210000100012000000210---2000-000000000000-000110111000-000-000010100010---000-002210011000211001												
Larina cf. *strangei*	0001000000000000001110100210000100012000000210---2000-000000000000-000110111000-000-000010100010---000-002210011000211001												
Annularia sp.	0000000000000000001110100010101100000000000011000 2000-000000000000-000020010000000-000010100011000000-022210011000211001												
Aylacostoma exoplicata	1010000000000000001111110313000100000000000410---2000-000000000001-000120111000-000-000010100010---000-042210011000221121												
Aylacostoma ci	1010000000000000001111110313000100000000000410---2000-000000000001-000120111000-000-000010100010---000-042210011000221121												
Aylacostoma tenuilabris	1010000000000000001111110312000100000000000410---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Melanoides tuberculatus	1010000000000000001111110311000100000000000410---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Supplanaxis nucleus	1010000000000000001111100310000100000000000010---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Doryssa ipupiara	1010000000000000001110120410000100000000000510---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Doryssa atra	1010000000000000001110120410000100000000000510---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Doryssa macapa	1010000000000000001110120410000100000000000510---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Pachychilus sp.	1010000000000000001110120410000100000000000510---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Turritella hookeri	1010000000000000001110130010000100000000000010---2000-000000000000-000120111000-000-000010100000---000-002210011000221121												
Modulus modulus	1010000000000000001110100010000100000000000010---2000-000000000000-000120111000-000-000010100010---000-002210011000221001												
Cerithium atratum	1010000000000000001111100010000100000000000010---2000-000000000001-000120111000-000-000010100020---000-002210011000221121												
Bittium varium	1010000000000000001111100010000100000000000010---2000-000000000001-000120111000-000-000010100020---000-002210011000221121												
Finella dubia	1010000000000000001111100010000100000000000010---2000-000000000001-000120111000-000-000010100020---000-002210011000221121												
Alaba incerta	1010000000000000001111100010000100000000000010---2000-000000000001-000120111000-000-000010100020---000-002210011000221121												
Batillaria minima	1010000000000000001110100010000100000000000010---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Cerithidea costata	1010000000000000001111100010000100000000000010---2000-000000000001-000120111000-000-000010100010---000-002210011000221121												
Campanile symbolicum	1000000000000000001110130010000100000000000010---2000-000000000000-000120111000-000-000010100000---000-002210011000221121												
Serpulorbis decussatus	1010000000000000001110130010000100000000000010---2000-000000000000-000120111000-000-000010100000---000-002210011000221121												

Taxon\character	24	25	26	27	28	29	30	31	32	33	34	35	36
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Stephopoma nucleogranosum	1010000000000000001110130010000100000000000010---2000-000000000000-000120112000-000-000010100000-00000-002210011000221121												
Amphithalamus glaber	0000000000000000001110100610100100000000000000110002000-000000000002-0000?0111000-000-000010100011000000-002210011000211001												
Littorina flava	0000000000000000001110100010100100000000000000110002000-000000000000-000020010000-000-000010100001000000-002210011000211001												
Potamolithus ribeirensis	0000000000000000001110100610100100000000000000110002000-000000000002-000020111000-000-000010100011000000-002210011000211001												
Potamolithus troglobius	0000000000000000001110100610100100000000000000110002000-000000000002-000020111000-000-000010100011000000-002210011000211001												
Potamolithus karsticus	0000000000000000001110100610100100000000000000110002000-000000000002-000020111000-000-000010100011000000-002210011000211001												
Strombus pugilis	0000001000000000001110130430101100000000000000110102000-000000000000-000120111000000-000010131301000000-062210011000211101												
Strombus alatus	0000001000000000001110130430101100000000000000110102000-000000000000-000120111000000-000010131301000000-062210011000211101												
Strombus gracilior	0000001000000000001110130430101100000000000000110102000-000000000000-000120111000000-000010131301000000-062210011000211101												
Eustrombus goliath	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-072210011000211101												
Eustrombus gigas	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-072210011000211101												
Aliger costatus	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-072210011000211101												
Aliger gallus	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-072210011000211101												
Tricornis raninus	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-072210011000211101												
Conomurex luhuanus	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-062210011000211101												
Canarium urceus	0000001000000000001110130420101100000000000000110102000-000000000000-000120111000000-000010131301000000-062210011000211101												
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Terebellum terebellum	0000001000000000001110130440101100000000000000110102000-000000000000-000120111000000-000010131301000000-052210011000211101												
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Cuphosolenus serresianus	0000001000000000001110130430101100000000000000111102000-000000000010-000120111000000-000010100311000000-002210011000211001												
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Hipponix subrufus	30000111110000000011101010101001000000000006112002000000001010100-0011201110001000000001010001100000-00220001100021100 1												
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Ficus carolae	0000001000000020011101007601211100000000000113002000010001010200 0-0011207110003000000001010141110000111021400110002110 01												
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Gemmula mystica	0000001000000001011101008301110300000000000011400200200001302020102111020 0?0000212210002??1000??-??000-00????0????002??0??												
Fenimorea sp.	0000001000000001011101008301110300000000000011400200200001302020101011020 0?0000211110001101000131110 00-0022100111002110 01												
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Glyphostoma sp.	0000001000000001011101008101110300000000000011400200200001202020101011020 0?0000211210001101000131110 00-0022100111002110 01												
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Conus ermineus	0000001000000001011101008301110300000000000011400200200200302020102221020 0?0000212210002???000?????000-00????0????00???0??												
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Duplicaria crakei	0000001000000001011101008301110300000000000011400200200010300?02010???1020 0?0000??2210001101000131110 00-0022100111002110 01												
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Taxon\character	24	25	26	27	28	29	30	31	32	33	34	35	36
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Terebra spirosulcata	0000001000000001011101009301103000000000000114002002000 2?3020201021210200?004021221000 2???000?????000 0-00???0????00???0??												
Terebra taurina	0000001000000001011101009301103000000000000114002002000 1?3020201021210200?000021221000 2???000?????000 0-00???0????00???0??												
Terebra dislocata	0000001000000001011101009301103000000000000114002002000 2030?02010?1210200?00400???1000 2???000?????000 0-00???0????00???0??												
Zemira australis	0000001000000000011101005101101000000000000110002000000001010200000011200?000020000100032100013111000-0A2210201010211000												
Fulmentum ancilla	0000001000000000011101005101101000000000000110002000000001010200000011200?005020000100032100013111000-0A2212201010211000												
Melapium lineatum	0000001000000000011101005101101000000000001011000200000000101020000011200?004020000100032100013121000-0A2210201010211000												
Benthobia atafona	0000001000000000011101005101101000000000000110002000000001010200000011200?005020000000012100013111000-0A2210001000211001												
Benthobia complexirhyna	0000001000000000011101005101101000000000000110002000000001010200000011200?005020000000012100013111000-0A2210001000211001												
Nassodonta dorri	0000001000000010011101305101101000000000000110002000000001010200000011200?000020000000032100013111000-0A2212201011211001												
Siratus senegalensis	0000001000000000011101005101101000000000002011000200000000101020000011205100402000020004210001412 1000-0A2210201010211000												
Siratus tenuivaricosus	0000001000000000011101005101101000000000002011000200000000101020000011205100402000020004210001412 1000-0A2210201010211000												
Siratus formosus	0000001000000000011101005101101000000000002011000200000000101020000011205100402000020004210001412 1000-0A2210201010211000												
Sirarus beauii	0000001000000000011101005101101000000000002011000200000000101020000011205100402000020004210001412 1000-0A2210201010211000												
Phyllonotus pomum	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014121000-0A2210201010211000												
Phyllonotus occulatus	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014121000-0A2210201010211000												
Phyllonotus margaritensis	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014121000-0A2210201010211000												
Chicoreus brevifrons	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014222000-0A2210201010211000												
Chicoreus spectrum	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014222000-0A2210201010211000												
Chicoreus carolinae	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014222000-0A2210201010211000												
Chicoreus coltrorum	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014222000-0A2210201010211000												
Murex trapa	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014121000-0A2210201010211000												
Trophon geversianus	0000001000000000011101005101101000000000000110002000000001010200000011205100402000010004210001412 1000-0A2210201010211000												
Bolinus brandaris	0000001000000000011101005101101000000000002011000200000000101020000011200?004020000200042100014222000-0A2210201010211000												
Nucella lapillus	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000100042100013121000-0A2210201010211000												
Thais biserialis	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000100042100013121000-0A2210201010211000												
Coralliophila nux	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000?002?21000????1000-0A???0?????02??0??												
Eupleura sp.	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000100042100014121000-0A2210201010211000												
Acanthina brevidentata	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000100042100013121000-0A2210201010211000												
Muricanthus radix	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000200042100014121000-0A2210201010211000												
Vitularia salebrosa	0000001000000000011101005101101000000000000110002000000001010200000011200?004020000100042100013121000-0A2210201010211000												
Olivancillaria urceus	0000001000000000011101305101101000000000000110002000000001010200000011200?004020000000032100013121000-0A2212202010211001												
Vexillum sp.	0000001001000000011101305101101000000000000110002003000001010200000011200?004020000000032100013121000-0A2212202010211001												
Austromitra maculosa	0000001001000000011101305101101000000000000110002003000001010200000011200?004020000000032100013121000-0A2212202010211001												
Buccinanops gradatus	0000001000000010011101305101101000000000000110002000000001010200000011200?000020000000032100013121000-0A2212202011211001												
Buccinanops monilifer	0000001000000010011101305101101000000000000110002000000001010200000011200?000020000000032100013121000-0A2212202011211001												
Nodicostellaria crassa	0000001001000000011101305101101000000000000110002003000001010200000011200?004020000000032100013121000-0A2212202010211001												
Prunum martini	0000001001000000011101305101101000000000000110002003000002010200000011200?004020000000032100013121000-0A2212202010211001												
Amphissa acuminata	0000001000000010011101305101101000000000000110002000000001010200000011200?000020000000032100013121000-0A2212202011211001												
Amphissa cancellata	0000001000000010011101305101101000000000000110002000000001010200000011200?000020000000032100013121000-0A2212202011211001												
Tritonoharpa lanceolata	0000001000020003011101005801101000000000000110002000000001010201300011208160003000001005210000?-00000-0A2252302010211001												

Taxon\character	24	25	26	27	28	29	30	31	32	33	34	35	36
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
Cancellaria reticulata	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Cancellaria petuchi	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Cancellaria cancellata	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Cancellaria spirata	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Trigonostoma tesselata	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Trigonostoma tenerum	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Scalpia contabulata	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Scalpia obliquata	0000001000020003011101005803101200000000000110002000000001010201300011208160003000002105210000?-00000-0B2252302010211001												
Annulobalcis aurisflamma	1000000000000000011101000110001000000000000010---2000-00000010?021-00?1200?00000???-0002???000??-0?000-00?????????0??????												
Perotrochus atlanticus	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000-00000-0000000000000000												
Lucapina elisae	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Fissurella mesoatlantica	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Haliotis aurantium	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Haliotis pourtalesii	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Falsimargarita stephaniae	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Calliostoma sp.	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Gaza compta	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Gaza superba	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Gaza cubana	0000000000000000000000000000000000000000000000---1100-000000000000-000010911000-000-000000000000---000-0000000000000000												
Addisonia enodis	0000000000000000000000000000000000000000000000---1000-000000000000-000010911000-000-000000000000---000-0000000000000000												
Pseudococculina rimula	0000000000000000000000000000000000000000000000---1000-000000000000-000010911000-000-000000000000---000-0000000000000000												
Neritina zebra	0000000000000000000000000000000000000000000000---1000-000000000000-000010911000-000-000000000000---000-0000000000000000												
Nerita ascensionis	0000000000000000000000000000000000000000000000---1000-000000000000-000010911000-000-000000000000---000-0000000000000000												
Cyclothyca pacei	0000000000000000011101000000000000000000000000---2000-000000000020-00?0000?00000???-0002???00000--?000-00?????????0??????												
Rissoella ornata	000000000000?0000111010400000000000000000000000---2000-000000000000-000000112000000-000000000000--3000-0020000010000000												
Ammonicera plana	00000000?000??000111010000000000000000000000---2000-000000000020-000000010000000-000100000000---000-00?????????00?????												
Orbitestella patagonica	00000000?000??000111010000000000000000000000---2000-000000000000-000000010000000-000000000000---000-0020000010000000												
Flabellina lucianae	00000000?000??000111010400000000000000000000---2000-000000000000-000000917000000-000000000000--3000-0020000010000000												
Anctus angiostomus	00000000?000??000111010400000000002010003000---2000-000000000000-000000917000000-000000000000--3000-0020000010000000												
Megalobulimus riopretensis	00000000?000??000111010400000000000010003000---2000-000000000000-000000917000000-000000000000--3000-0020000010000000												
Megalobulimus mogianensis	00000000?000??000111010400000000000010003000---2000-000000000000-000000917000000-000000000000--3000-0020000010000000												
Olympus nymbus	00000000?000??000111010400000000002010003000---2000-000000000000-000000917000000-000000000000--3000-0020000010000000												
Propilidium curumim	0000000000000000000000000000000000000000000000---0000-000000000000-000000912000-000-000000000000---000-0000000000000000												
Nautilus pompilius	0000000000000000000000000000-000000000000000---0000-0000-000000--00000-221000-000-000000000000---000-0000000000000000												
Lolliguncula brevis	0000000000000000000000000000-000000000000000---0000-0000-000000--00000-221000-000-000000000000---000-0000000000000000												
Coccodentalium carduus	00000?????????0???0??000000000-000000000000000---0000-0000-000010--00000--0-000-000-000000000000---000-0000000000000000												
Gadila braziliensis	00000?????????0???0???00000000-000000000000000---0000-0000-000010--00000--0-000-000-000000000000---000-0000000000000000												
Solemya occidentalis	0000000000000000000000000000-000000000000000---0000-0000-000012--00?00--0-000-???-0002??000000---000-000??0?????0???0??												
Ennucula puelcha	0000000000000000000000000000-000000000000000---0000-0000-000012--00?00--0-000-???-0002??000000---000-000??0?????0???0??												
Neopilina galatheae	0000000000000000000000000000-000000000000000---0000-0000-000000--00000--0-000-000-000000000000---000-0000000000000000												
Hanleya sp.	0000000000000000000000000000-000000000000000---0000-0000-000000--00000--0-000-000-000000000000---000-0000000000000000												

APPENDIX 2 - Continued

Matrix of characters considered in the present study

Taxon\character	36	37	38	39	40	41	42	43	44	45	46	47	48
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
Pomacea crosseana	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Pomacea curumim	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Pomacea scalaris	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Pomacea canaliculata	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Pomacea lineata	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Pomacea sordida	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Pomacea bridgesi	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113011000-0-000000-												
Asolene megastoma	100-0011000001001111001001010000000000000011001102111211100001110000021000000000000011000000000000-001113011000-0-000000-												
Felipponea neritiniformis	100-0011000001001111001001010000000000000011001102111211100001110000021000000000000011000000000000-001113011000-0-000000-												
Marisa planogyra	100-0011000001001111001001010000000000000011001102111211100001010000021000000000000011000000000000-001113010000-0-000000-												
Neocyclotus prominulus	100-0011000001000111011001000000000000000010001002111200000001110000021000000000000001000000000000-001112010000-0-010000-												
Incidostoma tupy	100-0011000001000111011001000000000000000010001002111200010001110000021000000000000001000000000000-001112010000-0-010000-												
Aperostoma blanchetiana	100-0011000001000111011001000000000000000010001002111200010001110000021000000000000001000000000000-001112010000-0-010000-												
Viviparus acerosus	100-0011100001000111010010100000000000000010001002111221000001010000021000000000000010000001000000-001101000000-0-000000-												
Viviparus contectus	100-0011100001000111010010100000000000000010001002111221000001010000021000000000000010000001000000-001101000000-0-000000-												
Notopala ampullaroides	100-0011000001000111010010100000000000000010001002111221000001010000021000000000000010001000100000-001101002000-0-000000-												
Notopala essingtonensis	100-0011000001000111010010100000000000000010001002111221000001010000021000000000000010001000100000-001101002000-0-000000-												
Larina cf. strangei	100-0011000001000111101001010000000000000010001002111221000001010000021000000000000010010001000000-001101002000-0-000000-												
Annularia sp.	100-0011000001000111002001000010000000000010001202111230110001110000021000000000000011000001000000-001101000000-0-010000-												
Aylacostoma exoplicata	100-0011200001000121001101020000000000000010001102111201000001010000021000000000000010000001000000-001131003010-0-010000-												
Aylacostoma ci	100-0011200001000121001101020000000000000010001102111201000001010000021000000000000010000001000000-001131003010-0-010000-												
Aylacostoma tenuilabris	100-0011200001000121001101010000000000000010001102111201000001010000021000000000000010000001000000-001131003010-0-010000-												
Melanoides tuberculatus	100-0011200001000121001101010000000000000010001102111201000001010000021000000000000010000001000000-001131003010-0-010000-												
Supplanaxis nucleus	100-0011200001000121001111010000000000000010001102111201000001010000021000000000000010001001000000-001111003010-0-010000-												
Doryssa ipupiara	110-0011210001220111001111010000110000000010001002111201000001010000021000000000000010001001000000-001124003010-0-010000-												
Doryssa atra	110-0011210001220111001111010000110000000010001002111201000001010000021000000000000010002001000000-001124003010-0-010000-												
Doryssa macapa	110-0011210001220111001101010000110000000010001002111201000001010000021000000000000010001001000000-001124003010-0-010000-												
Pachychilus sp.	110-0011010001220111001101010000010000000010001002111201000001010000021000000000000010001001000000-001124003010-0-010000-												
Turritella hookeri	100-0011000001110121201101010000000000000010001102111201000001010000021100000000000010000001000000-001111003010-0-010000-												
Modulus modulus	100-0011000001000111001101010000000000000010001102111201000001010000021000000000000010001001000000-001111000010-0-010000-												
Cerithium atratum	100-0011200001000121001101010000000000000010001102111201000001010000021000000000000010000001000000-001111003010-0-010000-												
Bittium varium	100-0011200001000121001101010000000000000010001102111201000001010000021100000000000010000001000000-001141003010-0-010000-												
Finella dubia	100-0011200001000121001101010000000000000010001102111201000001010000021100000000000010000001000000-001141003010-0-010000-												
Alaba incerta	100-0011200001000121001101010000000000000010001102111201000001010000021100000000000010000001000000-001111003010-0-010000-												
Batillaria minima	100-0011000001220121001101010000000000000010001002111201000001010000021000000000000010000001000000-001111003010-0-010000-												
Cerithidea costata	100-0011000001000121001101010000000000000010001102111201000001010000021000000000000010000001000000-001141003010-0-010000-												
Campanile symbolicum	200-0011200001110121001101010000000000000010001102111201000001010000021100000000000010001001000000-001111003010-0-010000-												
Stephopoma nucleogranosum	100-0011000001110121201101010000000000000010001102111201000001010000021100000000000010000001000000-001111003010?0-010000-												

Taxon\character	36	37	38	39	40	41	42	43	44	45	46	47	48
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Serpulorbis decussatus	100-0011000001110121201101010000000000000010001102111201000001010000021100000000000010000001000000-001111003010-0-010000-												
Amphithalamus glaber	100-0011000001000111002001000010000000000010001102111230110001110000021000000000000010000001000000-001101003000-0-010000-												
Littorina flava	100-0011000001000111002001000010000000000010001202111230110001110000021000000000000011000001000000-001101004021000-010100-												
Potamolithus ribeirensis	100-0011000001000111002001000010000000000010001102111231110001110000021000000000000010000001000000-001101003000-0-010000-												
Potamolithus troglobius	100-0011000001000111002001000010000000000010001102111231110001110000021000000000000010000001000000-001101003000-0-010000-												
Potamolithus karsticus	100-0011000001000111002001000010000000000010001102111231110001110000021000000000000010000001000000-001101003000-0-010000-												
Strombus pugilis	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Strombus alatus	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Strombus gracilior	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Eustrombus goliath	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Eustrombus gigas	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Aliger costatus	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Aliger gallus	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Tricornis raninus	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Conomurex luhuanus	200-0112000011000111001001000000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-200000-												
Canarium urceus	200-0112000011000111001001000000001000000010001102111200000001010000021100000000000011000011000000-001100000000-0-200000-												
Lambis lambis	200-0112000011000111001001030000001000000010001102111200000001010000021100000000000013002411000000-001100000000-0-210000-												
Terebellum terebellum	200-0112000011000111001001000000001000000010001102111200000001010000021100000000000000???????00000-00?100000000-0-210000-												
Tylospira scutulata	200-0012000011000111001001000000000000000010001102111200000001010000021100000000000011000001000000-001100000000-0-120000-												
Struthiolaria papulosa	200-0012000011000111001001000000000000000010001102111200000001010000021100000000000011000001000000-001100000000-0-120000-												
Cuphosolenus serresianus	200-0012000011000111001001000000000000000010001102111200000001010000021100000000000011000001000000-001100000000-0-100000-												
Aporrhais occidentalis	200-0112000011000111001001002000000000000010001102111201000001010000021100000000000011000101000000-001100000000-0-000000-												
Aporrhais pespelicani	200-0112000011000111001001002000000000000010001102111201000001010000021100000000000011000101000000-001100000000-0-000000-												
Onustus caribaeus	200-0112000011000111001001001000001000000010001102111201000001010000021100000000000010020111000000-001100000000-0-120000-												
Onustus indicus	200-0112000011000111001001001000001000000010001102111201000001010000021100000000000010020111000000-001100000000-0-120000-												
Xenophora conchyliophora	200-0112000011000111001001001000001000000010001102111201000001010000021100000000000011020111000000-001100000000-0-020000-												
Bostrycapulus odites	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001000200100000-001140000000-0-010000-												
Crepidula intratesta	000-0011000011032l1?002301040012000100000001000100211120000000102000002122110000000001010200100000-001140000000-0-010000-												
Crepidula protea	000-0011000011032l1?002301040012000100000001000100211120000000102000002122110000000001010200100000-001140000000-0-010000-												
Crepidula argentina	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												
Crepidula glauca	000-0011000011032l1?002301000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												
Crepidula fornicata	000-0011000011032l1?002301000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												
Crepidula margarita	000-0011000011032l1?002301000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												
Crepidula plana	000-0011000011032l1?002301000012000100000001000100211120000000102010002120110000000001010200100000-001140000000-0-010000-												
Crepidula atrasolea	000-0011000011032l1?001301000012000100000001000100211120000000102010002120110000000001013200100000-001140000000-0-010000-												
Crepidula depressa	000-0011000011032l1?002301000012000100000001000100211120000000102010002120110000000001013200100000-001140000000-0-010000-												
Crepidula pyguaia	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001000200100000-001140000000-0-010000-												
Crepidula carioca	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												
Crepidula cachimilla	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001000200100000-001140000000-0-010000-												
Calyptraea centralis	000-0011000011032l1?001001000012000100000001000100211203000001020000021201100000000001010200100000-001140000000-0-010000-												
Crucibulum auricula	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												
Crucibulum quiriquinae	000-0011000011032l1?001001000012000100000001000100211120000000102000002120110000000001010200100000-001140000000-0-010000-												

Taxon\character	36	37	38	39	40	41	42	43	44	45	46	47	48
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
Trochita trochiformis	000-0011000011032l1?0010010000110001000000100010021112000000010200000212011000000000101020010000-00114000000-0-010000-												
Sigapatella calyptraeformis	000-0011000011032112001001040011000100000010001002111200000001020000021201000000000101020010000-00114000000-0-010000-												
Hipponix costellatus	100-0011001011000110001001000010000000000010001002111213300001021000021202000000000011102001000-00110000000-0-010000-												
Hipponix subrufus	100-0011001011000110001001000010000000000010001002111213300001021000021202000000000010102001000-00114000000-0-010000-												
Hipponix incurvus	100-0011001011000111001001000010000000000010001002111213300001021000021202000000000010102001000-00114000000-0-010000-												
Hipponix grayanus	100-0011001011000110001001000010000000000010001002111213300001021000021202000000000011102001000-00114000000-0-010000-												
Hipponix leptus	100-0011001011000110001001000010000000000010001002111213300001021000021202000000000010102001000-00114000000-0-010000-												
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Malluvium devotus	100-0011001011000110001001000010000100000010001002111210000001021000021202000000000101020010000-00114000000-0-010000-												
Cheilea equestris	100-0011000011000110001001000012000100000010001002111210000001020000021201000000000101020010000-00110000000-0-010000-												
Capulus sycophanta	100-0011000011000112001001000010000100000010001002111210000001010000021200000000000101020010000-00114000000-0-010000-												
Trichotropis cancellata	100-0011302011000112001001000010000100000010001002111240000001010000021210000000000101020010000-00111000000-0-010000-												
Trichotropis borealis	100-0011302011000112001001000010000100000010001002111240000001010000021210000000000101020010000-00111000000-0-010000-												
Vanikoro sp.	100-0011000011000112001001000010000100000010001002111210000001020000021201000000000101020010000-00114000000-0-010000-												
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Erosaria acicularis	1011101?000?1100011300120105001000000000001000130211120401000131000002023022020000001100000100000-00112000402100-012210-												
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Cypraea tigris	1011101?000?1100011300120105001000000000001000130211120401000131000002023022020000001100000100000-00112100402100-011210-												

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Pleurotomella aguayoi	?0?-001?00-?1?000???00??0??000?000000000?0?000??04111276?00?????4???????7???0???11001?2020?200200											-0011800050404?-1000021	
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Conus jaspideus	?0?-00??00-???000???00??0??000?00000000?10?000??04111?760?00????4???????7???5???1110112220202?200200											-0011800050404?-1000021	
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Fulmentum ancilla	103-00110000110001100000010000100000001100100020031112540000015050210???????????0??0111020110000000010000403												0?0-100000-
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Benthobia atafona	103-00110000110001100000010000100000001000100020031112540000015050210???????????0??0111020110000300010000403												0?0-100000-
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Chicoreus carolinae	103-00110000110001100000010000100000001110010002003111257000001505021??????????0??0111020110001?00100000403												030-100100-
Chicoreus coltrorum	103-00110000110001100000010000100000001110010002003111257000001505021??????????0??0111020110001?00100000403												030-100100-
Murex trapa	103-00110000110001100000010000100000001110010002303111257000001505021??????????0??0111020110001110010000403												030-100100-
Trophon geversianus	103-00110000110001100000010000100000001110010002303111257000001505021??????????0??0111020110001?00100000403												030-100000-
Bolinus brandaris	103-00110000110001100000010000100000001110010002303111257000001505021??????????0??0111020110001?00100000403												030-100100-
Nucella lapillus	103-00110000110001100000010000100000001100100023031112570000015050210???????????0??0111020110002221010000403												0?0-100000-
Thais biserialis	103-00110000110001100000010000100000001100100023031112570000015050210???????????0??0111020110002221010000403												030-100000-
Coralliophila nux	?0?-00??00??1?000???00??0??000?00000000???0?000?????112??0?????????????0?????????0??0111020110001?001?000403												0?0-100000-
Eupleura sp.	103-00110000110001100000010000100000001110010002303111257000001505021??????????0??0111020110002121010000403												0?0-100000-
Acanthina brevidentata	103-00110000110001100000010000100000001100100023031112570000015050210???????????0??0111020110001211010000403												0?0-100000-
Muricanthus radix	103-00110000110001100000010000100000001110010002303111257000001505021??????????0??0111020110001110010000403												030-100100-
Vitularia salebrosa	103-00110000110001100000010000100000001100100023031112570000015050210???????????0??0111020110002?001000004030												?0-100000-
Olivancillaria urceus	003-00110000110001100000010000100000001100100020031112510000015050210???????????0??0111020110001010010000000												030?0-100000-
Vexillum sp.	003-00110000110001100000010000100000001011001000200311125100000150502100???????????0??0111020110001010010000060												030?0-100000-
Austromitra maculosa	003-00110000110001100000010000100000001011001000200311125100000150502100???????????0??0111020110001110010000060												030?0-100000-
Buccinanops gradatus	003-00110000113001100000010000100000012120020002003111251000001505021??????????0??0111020110001?001000000030												?0-100000-
Buccinanops monilifer	003-00110000113001100000010000100000012120020002003111251000001505021??????????0??0111020110001?001000000030												?0-100000-
Nodicostellaria crassa	003-00110000110001100000010000100000001011001000200311125100000150502100???????????0??0111020110001110010000060												030?0-100000-
Prunum martini	003-00110000110001100000010000100000001011001000200711125100000								3???02?00??????????0??0111020110001110010000000				030?0-100000-
Amphissa acuminata	003-00110000113001100000010000100000012120020002003111256000001535021??????????0??0111020110001?001000000030												?0-100000-
Amphissa cancellata	003-00110000113001100000010000100000012120020002003111256000001535021??????????0??0111020110001?001000000030												?0-100000-
Tritonoharpa lanceolata	403-00100???1100011000?2?0??000100000201100200120051112810300030???????0??????????0??00????????00??4?001000000												030?0-100000-

Taxon\character	36	37	38	39	40	41	42	43	44	45	46	47	48
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Cancellaria reticulata	403-00100????1000110002?0??00110000020110020012005111281030003????????0???????????0??0101023110001 4?0110000000000?0-100020-												
Cancellaria petuchi	403-00100????1000110002?0??00110000020110020012005111281030003????????0???????????0??0101023110001 4?0110000000000?0-100020-												
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Cancellaria spirata	403-00100????1000110002?0??00110000020110020012005111281030003????????0???????????0??0101023110001 43011000000000?0-100020-												
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Trigonostoma tenerum	403-00100????1000110002?0??00110000020110020012005111281030003????????0???????????0??0101023110001 4?0210000000000?0-100020-												
Scalpia contabulata	403-00100????1000110002?0??00210000020110020012005111281030003????????0???????????0??0101023110001 43011000000000?0-100020-												
Scalpia obliquata	403-00100????1000110002?0??00210000020110020012005111281030003????????0???????????0??0101023110001 43011000000000?0-100020-												
Annulobalcis aurisflamma	?0?-00???0-???000????0??0????0?0000?0??0?00?00????????1?????????????????????????????00000???????00000-00??000200?0-100000-												
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Lucapina elisae	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Fissurella mesoatlantica	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Haliotis aurantium	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Haliotis pourtalesii	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Falsimargarita stephaniae	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Calliostoma sp.	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Gaza compta	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Gaza superba	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Gaza cubana	000-001000---000000-000000000000000000000000000311112000000000000001000?000000000010100000000-000012001000-0-000000-												
Addisonia enodis	000-000000---000000-000000000000000000000010000011112000000000000001000?000000000010100000000-000010000000-0-000000-												
Pseudococculina rimula	000-000000---000000-000000000000000000000010000011112000000000000001000?000000000010100000000-000010000000-0-000000-												
Neritina zebra	000-001000---000000-000000000000000000000000000011112000000000000001000?000000000010100000000-000012001000-0-000000-												
Nerita ascensionis	000-001000---000000-000000000000000000000000000011112000000000000001000?000000000010100000000-000012001000-0-000000-												
Cyclothyca pacei	?0?-00???0---?000??-?0??0??00?0000?0??0?00?00????????1?????????????????----?????00000-??????00000-00??00000000-0-100000-												
Rissoella ornata	000-001000---100000-000000000000000000000001000010211120000000100000020----?????000010000000000-001000000000-0-000000-												
Ammonicera plana	?0?-00???0---?000??-?0??0??00?0000?0??0?00?00????????1?????????????????----?????000010100000000-001000000000-0-000000-												
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Flabellina lucianae	000-001000---100000-000000000000000000000001000010811120000000000000102--200000000010000000000-001000000000-0-000000-												
Anctus angiostomus	000-001000---100000-000000000000000010000010000108111200000000000000102--200000000010000000000-001090001000-0-000000-												
Megalobulimus riopretensis	000-001000---100000-000000000000000010000010000108111200000000000000102--200000000010000000000-001090001000-0-000000-												
Megalobulimus mogianensis	000-001000---100000-000000000000000010000010000108111200000000000000102--200000000010000000000-001090001000-0-000000-												
Olympus nimbus	000-001000---100000-000000000000000010000010000108111200000000000000102--200000000010000000000-001090001000-0-000000-												
Propilidium curumim	000-000000---000000-000000000000000000000000000010000000000000000----?????00000??000000000-000000000000-0-000000-												
Nautilus pompilius	000--00000---000000-000000000000000000000010000000000000000000000----????????01010?00000000-00000-000000-0-000000-												
Lolliguncula brevis	000--00000---000000-000000000000000000000010000000000000000000000----????????01010?00000000-00000-000000-0-000000-												
Coccodentalium carduus	100--00000---?00000-000000000000000000000010000100000100000004000???00----????????00----0--00--0-0-000-000000-0-000000-												
Gadila braziliensis	100--00000---?00000-000000000000000000000010000100000100000004000???00----????????00----0--00--0-0-000-000000-0-000000-												
Solemya occidentalis	?0?--0?000---?000?0-00??0??000000000?00????000??????????0?????????????----????????00----0--00--0-0-0?0-000000-0-000000-												
Ennucula puelcha	?0?--0?000---?000?0-00??0??000000000?00????000??????????0?????????????----????????00----0--00--0-0-0?0-000000-0-000000-												
Neopilina galatheae	000--00000---000000-000000000000000000000000000000000000000000000----????????00----0--00--0-0-000-000000-0-000000-												
Hanleya sp.	000--00000---000000-000000000000000000000000000000000000000000000----0000000000----0--00--0-0-000-000000-0-000000-												

APPENDIX 2 - Continued

Matrix of characters considered in the present study

Taxon\character	48	49	50	51	52	53	54	55	56	57	58	59	60
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890												
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Pomacea curumim	-0-0-0--02000010120-000----0000000001111112000100100000000001013200-?-0000010100-0-10111113----------4010010322020210000												
Pomacea scalaris	-0-0-0--01000010120-000----0000000001111112000100100000000001013200-?-0000010100-0-10100003----------4010010322020210000												
Pomacea canaliculata	-0-0-0--02000020120-000----0000000001111122000100100000000001013200-?-0000010100-0-21111203----------4010010322020210000												
Pomacea lineata	-0-0-0--02000020120-000----0000000001111122000100100000000001013200-?-0000010100-0-11111113----------4010010322020210000												
Pomacea sordida	-0-0-0--02000020120-000----0000000001111122000100100000000001013200-?-0000010100-0-11111203----------4010010322020220000												
Pomacea bridgesi	-0-0-0--02000020120-000----0000000001111122000100100000000001013200-?-0000010100-0-11111213----------4010010322020220000												
Asolene megastoma	-0-0-0--02000020120-000----0000000001111122000100100000000001013200-?-0000010100-0-21110213----------4010010322020220000												
Felipponea neritiniformis	-0-0-0--01000010120-000----0000000001111111000100100000000001013200-?-0000010100-0-10101003----------4010010322020220000												
Marisa planogyra	-0-0-0--01000010120-000----0000000001111112000100100000000001013200-?-0000010100-0-10101013----------4010010322020210000												
Neocyclotus prominulus	-0-0-0--00000000010-000----0000000000001001000100100000000011012300-?-0000010100-11000----300000?0000100001032111110000												
Incidostoma tupy	-0-0-0--00000000010-000----0000000000001001000100100000000011012300-?-0000010100-12000----300000?0000100001032121110000												
Aperostoma blanchetiana	-0-0-0--00000000010-000----0000000000001001000100100000000011012300-?-0000010100-12000----300000?0000100001032121110000												
Viviparus acerosus	-0-0-0--10100000000-000----0000000000111001000100100000000001013110-?-000001011110-000----3----------2000010320010200000												
Viviparus contectus	-0-0-0--10100000000-000----0000000000111001000100100000000001013110-?-000001011110-000----3----------2000010320010200000												
Notopala ampullaroides	-0-0-0--10000000010-000----0000000000111001000100100000000001013110-?-000001011100-000----3----------2000010323010200000												
Notopala essingtonensis	-0-0-0--10000000010-000----0000000000111001000100100000000001013110-?-000001011100-000----3----------2000010323010200000												
Larina cf. *strangei*	-0-0-0--10000000000-000----0000000000111001000100100000000001013110-?-000001011100-000----3----------2000010323010200000												
Annularia sp.	-0-0-0--10000001011000100010000000000111001000100100000000001232000?10000110110-10000----3000010000010100103250101000000												
Aylacostoma exoplicata	-0-0-0--10010101012011120011000000000111001101211100000000001111000001000001011 0-0-000----?----0-----3100010224010001000												
Aylacostoma ci	-0-0-0--10010101012011120011000000000111001101211100000000001111000001000001011 0-0-000----?----0-----3100010224010001000												
Aylacostoma tenuilabris	-0-0-0--10010101012011120011000000000111001101211100000000001111000001000001011 0-0-000----?----0-----3100010224010001100												
Melanoides tuberculatus	-0-0-0--10010101012011120011000000000111001101201100000000001111000001000001011 0-0-000----?----0-----3100010324010001000												
Supplanaxis nucleus	-0-0-0--10010101012011110011000000000111001100201100000100001111000001000001011 0-0-000----1----0-----3100010124010001200												
Doryssa ipupiara	-0-0-0--10010101012010110011000000000111001100201100000000001111000001000001011 0-0-000----2----0-----3100010124010000000												
Doryssa atra	-0-0-0--10010101013012110011000000000111001100201100000000001111000001000001011 0-0-000----2----0-----3100010124010000000												
Doryssa macapa	-0-0-0--10010101013012110011000000000111001100201100000000001111000001000001011 0-0-000----2----0-----3100010124010000000												
Pachychilus sp.	-0-0-0--10010101012010110011000000000111001100201100000000001111000001000001011 0-0-000----2----0-----3100010124010000000												
Turritella hookeri	-0-0-0--10010101011000110010000000000111001000201100000100001111000001000001011 0-0-000----1----0-----3100010124010001100												
Modulus modulus	-0-0-0--10010101011000120010000000000111001000201100000100001111000001000001011 0-0-000----1----0-----3100010124010001100												
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Bittium varium	-0-0-0--10010101012120110011000000000111001100202100000100001111000001000001011 0-0-000----1----0-----3100010124010001200												
Finella dubia	-0-0-0--10010101012120110011000000000111001100202100000100001111000001000001011 0-0-000----1----0-----3100010124010001000												
Alaba incerta	-0-0-0--10010100012120110011000000000111001100202100000100001111000001000001011 0-0-000----1----0-----3100010124010001100												
Batillaria minima	-0-0-0--10010100011000110011000000000111001000201100000100001111000001000001011 0-0-000----1----0-----3100010124010001100												
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Campanile symbolicum	-0-0-0--10010101001001100010000000000111001001101100000100001111000001000001011 0-0-000----1----0-----3100010124010000000												
Serpulorbis decussatus	-0-0-0--10010102001000100010000000000111001000201100000100001111000001000001011 0-0-000----1----0-----3100010124010001000												

Taxon\character	48	49	50	51	52	53	54	55	56	57	58	59	60
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Littorina flava	-0-0-0--1000000100100010001100000000011100110010010000000000011232000?10000110110-10000----3200010000010000102250102000010												
Potamolithus ribeirensis	-0-0-0--1001000101100012001200000000011100111030010000000000011232000?10000110110-10000----3100010000010100102240102000011												
Potamolithus troglobius	-0-0-0--1001000101100012001200000000011100111030010000000000011232010?10000110110-10000----3100010000010100102250102000011												
Potamolithus karsticus	-0-0-0--1001000101100012001200000000011100111030010000000000011232010?10000110110-10000----3100010000010100102250102000011												
Strombus pugilis	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1012200000001010010226060100000												
Strombus alatus	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1012200000001010010226060100000												
Strombus gracilior	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1012200000001010010226060100000												
Eustrombus goliath	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1022200000001010010226060100000												
Eustrombus gigas	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1022200000001010010226060100000												
Aliger costatus	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-15000----1032200000001010010226060100000												
Aliger gallus	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-15000----1032200000001010010226060100000												
Tricornis raninus	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1000000000001010010226010100000												
Conomurex luhuanus	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100000100000101 10-10000----1040000000001010010226010100000												
Canarium urceus	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100000100000101 10-10000----1040000000001010010226010100000												
Lambis lambis	-0-0-0--1000000100 1-0012312000000000011100120040110000002002111100002100000101 10-10000----1001000000001010010226060100000												
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Tylospira scutulata	-0-0-0--1000000100 1-0012011000000000011100100040010000011000111100000100000101 10-10000----1000000000001010010226010200000												
Struthiolaria papulosa	-0-0-0--1000000100 1-0010011000000000011100100040010000001000111100000100000101 10-10000----1000000000001010010226010200000												
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Aporrhais occidentalis	-0-0-0--1000000100 1-0010111000000000011100120040110000012000111100000100000101 10-10000----1000000000001010010326010200000												
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Onustus indicus	-0-0-0--1000000101 1-0012212000000000011100120040100000012000111100010100000101 10-10000----1000000000001010010326010200000												
Xenophora conchyliophora	-0-0-0--1000000101 1-0012212000000000011100120040100000012000111100010100000101 10-10000----1000000000001010010326010200000												
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Crucibulum quiriquinae	-0-0-0--1000000101 1-0010001000000000011100112010011100000000011122002?10000110110-10000----3000000000001200010324010200000												

Taxon\character	48	49	50	51	52	53	54	55	56	57	58	59	60
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Sigapatella calyptraeformis	-0-0-0--10000001001-0010001000000000011100110010011100000100111220021?10000110110-10000----3000000000012000103240102000000												
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Hipponix subrufus	-0-0-0--10000001011-0012001000000000011100110010011000000100111220021?10000110110-11000----3300100000013100103240102000000												
Hipponix incurvus	-0-0-0--10000001011-0012001000000000011100100010011000000100111220021?10000110110-10000----3300000000013100103240102000000												
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Malluvium devotus	-0-0-0--10000001031-0012001000000000011100100010011000000100111220021?10000110110-10000----3300000000013100103240102000000												
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Lunatia heros	-0-0-0--10020001000-000---0001000010011100110010010000000000111120000100000010110-10000----3400000000010100103220102000000												
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Sinum maculatum	-0-0-0--10020001000-000---0001000010011100110010010000000010110320-0010110010110-10000----3400011000010100103220102000000												
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Amauropsis andersoni	-0-0-0--10020001000-000---0001000010011100110010010000000000111120000100000010110-10000----3400000000010100103220102000000												
"Amauropsis" rossiana	-0-0-0--10020001000-000---0000000000011100110010010000000000111120000100000110110-10000----3200000000010100103250104000010												
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Cymbula acicularis	-0-0-0--10001001000-000---0020100011011100110010010001020000111340 03?10001010110-11000----3000010000010110103240101000 00												
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Phalium granulatum	-0-0-0--10001000000-030---0000102011011100110010010000000000131100007100001101107-10000----10000000100101001032401010000												
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Tonna galea	-0-0-0--10001000040-000---0000101011011100110010010000000000131100007100001101107-10000----10000000400101001032401010000												
Tonna maculosa	-0-0-0--10001000040-000---0000101011011100110010010000000000131100007100001101107-10000----10000000300101001032401010000												
Cochlespira elongata	0130-3--10031000000-000---0000302011011100110010210000030010111320007101301101107-11000----30000100120101001032404020000												
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Daphnella lymnaeiformis	2??0-?--?0031000000-000---0000302011011100110010210000030000120320-0?10000110110-10000----30000100100101001032405020000												
Pilsbryspira albomaculata	1110-3--10031000000-000---0000302011011100110010210000030000110320-0?10030110110-11000----30000100110101001032405020000												
Glyphostoma sp.	1100-3--10031000000-000---0000302011011100110010210000030000111320007101001101107-11000----30000100110101001032404020000												
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Conus tulipa	1120-3--?0031000000-000---0000302011011100110010210000030000120320-0?10000110110-10000----30000100100101001032404020000												
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Duplicaria crakei	2??0-?--10031000000-000---0000302011011100110010210000030000120320-0?10000110110-10000----30000100100101001032404020000												
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Terebra gemmulata	2??0-?--?0031000000-000---0000302011011100110010210000030020120320-0?10100110110-11000----35000100110101202032404020000												
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Melapium lineatum	-0-1121210041000000-000---0000402011011100110010010000003000121320 00?10000110110-10000----3000000090010100003240101000000												
Benthobia atafona	-0-1010210031000010-000---0000102011011100110010010000000000011132000?10000110110-10000----3050010090010100003240101000000												
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Nassodonta dorri	-0-1110210031000?0-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Siratus senegalensis	-0-1210020041000010-000---0000402111011100110010010000003000121220 00?10000110110-11000----3000000000110100003240102000000												
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Siratus formosus	-0-1210020041000010-000---0000402111011100110010010000003000121220 00?10000110110-11000----3000000000110100003240102000000												
Sirarus beauii	-0-1210020041000010-000---0000402111011100110010010000003000121220 00?10000110110-10000----3000000000110100003240102000000												
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Chicoreus coltrorum	-0-1310020041000010-000---0030402011011100110010010000003000121220 00?10000110110-10000----3000010090110100003240102000000												
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Trophon geversianus	-0-1110020031000010-000---0000402011011100110010010000003000121320 00?10000110110-11000----3000010090010100003240102000000												
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Nucella lapillus	-0-1110?10031000010-000---0000402011011100110010010000003000111220 00?10000110110-11000----3000010000010100003240102000000												
Thais biserialis	-0-1110?10041000000-000---0000402011011100110010010000000000011122000?10000110110-10000----3000010000010100003240102000000												
Coralliophila nux	-0-1110?10031000000-000---0000402011011100110010010000000000012132000?10000110110-10000----3000010000010100003240102000000												
Eupleura sp.	-0-1110010031000010-000---0000402011011100110010010000003000121320 00?10000110110-10000----3000010000010100003240102000000												
Acanthina brevidentata	-0-1110?10041000010-000---0000402011011100110010010000000000012132000?10000110110-10000----3000010000110100003240102000000												
Muricanthus radix	-0-1210020041000010-000---0000402111011100110010010000003000121320 00?10000110110-11000----3000010000110100003240102000000												
Vitularia salebrosa	-0-1110?10031000000-000---0000402011011100110010010000000000012132000?10000110110-11000----3000010000010100003240102000000												
Olivancillaria urceus	-0-1110210031000000-000---0000102011011100110010010000000000011122000?10000110110-10000----3000000000010000003240102000000												
Vexillum sp.	-0-1110210031000000-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010090010100003240102000000												
Austromitra maculosa	-0-1110210031000000-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Buccinanops gradatus	-0-1010210031000000-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Buccinanops monilifer	-0-1010210031000000-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Nodicostellaria crassa	-0-1110210031000010-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010090010100003240102000000												
Prunum martini	-0-1111210031000010-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Amphissa acuminata	-0-1110210031000000-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Amphissa cancellata	-0-1110210031000000-000---0000102011011100110010010000000000011132000?10000110110-10000----3000010000010100003240102000000												
Tritonoharpa lanceolata	-0-1010210031000010-000---0000502011011100110010010000000000011132000?10000110110-10000----3000010000010100003240105000000												

Taxon\character	48	49	50	51	52	53	54	55	56	57	58	59	60
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Cancellaria petuchi	-0-100??10031000010-000---0000502011011100110010010000000030111132005?10000110110-14000----3000010000010100003240105000000												
Cancellaria cancellata	-0-100??10031000010-000---0000502011011100110010010000000030111132000?10000110110-10000----3000010000010100003240105000000												
Cancellaria spirata	-0-100??10031000010-000---0000502011011100110010010000000030121132000?10000110110-10000----3000010000010100003240105000000												
Trigonostoma tesselata	-0-100??10031000010-000---0000502011011100110010010000000030121132000?10000110110-10000----3000010000010100003240105000000												
Trigonostoma tenerum	-0-100??10031000010-000---0000502011011100110010010000000030121132000?10000110110-10000----3000010000010100003240105000000												
Scalpia contabulata	-0-100??10031000010-000---0000502011011100110010010000000000012132005?10000110110-10000----3000010000010100003240105000000												
Scalpia obliquata	-0-100??10031000010-000---0000502011011100110010010000000000012132005?10000110110-10000----3000010000010100003240105000000												
Annulobalcis aurisflamma	-0-0-0--10030000010-000---0000101010011100110000210000010000111220?110000110110-14000----1000000040010100103240101000000												
Perotrochus atlanticus	-0-0-0--00210000000-000----0000000000000000000000000000000?001000-0-?-0-----000-0-0-000----0----------0000000000-0-00----												
Lucapina elisae	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Fissurella mesoatlantica	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Haliotis aurantium	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Haliotis pourtalesii	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Falsimargarita stephaniae	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Calliostoma sp.	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Gaza compta	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Gaza superba	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Gaza cubana	-0-0-0--00210000000-000----0000000000000000000000000000010000?001000-0---0-----000-0-0-000----0----------0000000000-0-00----												
Addisonia enodis	-0-0-0--00010000000-000----0000000000000000000000000000000000?001000-0---0-----000-100-000----0----------2000000000-0-00----												
Pseudococculina rimula	-0-0-0--00010000000-000----0000000000000000000000000000000000?001000-0---0-----000-100-000----0----------2000000000-0-00----												
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Nerita ascensionis	-0-0-0--00010000000-000----0000000000000000000000000000000000?001000-0---0-----101-0-0-000----0----------000000021401-10--0-												
Cyclothyca pacei	-0-0-0--00030000000-000----0000010100100000000000100000000000100050-6-0-----101-0-0-000----0----------541000032401-10----												
Rissoella ornata	-0-0-0--00010000000-00120?0000000000000000003000010000000000100050-6-0-----202-0-0-000----0----------541000033401-60----												
Ammonicera plana	-0-0-0--00010000010-00100?0000000000000000000000010000000000100050-6-0-----202-0-0-000----0----------541000033401-10----												
Orbitestella patagonica	-0-0-0--00010000010-00100?0000000000000000000000010000000000100050-6-0-----202-0-0-000----0----------541000033401-10----												
Flabellina lucianae	-0-0-0--00010000000-000----0000000000000000000000010000000000100050-6-0-----202-0-0-000----0----------541000033701-60----												
Anctus angiostomus	-0-0-0--00010000000-000----0000000000000000003000010000000000100050-6-0-----202-0-0-000----0-----1----541000033701-60----												
Megalobulimus riopretensis	-0-0-0--02010000000-000----0000000000000000003000010000000000100050-6-0-----202-0-0-000----0-----1----541000033701-60----												
Megalobulimus mogianensis	-0-0-0--02010000000-000----0000000000000000003000010000000000100050-6-0-----202-0-0-000----0-----1----541000033701-60----												
Olympus nimbus	-0-0-0--00010000000-000----0000000000000000003000010000000000100050-6-0-----202-0-0-000----0-----1----541000033701-60----												
Propilidium curumim	-0-0-0--00000000000-000----0000000000000000000000000000000000?001000-0---0-----000-0-0-000----0----------000000000000-00----												
Nautilus pompilius	-0-0-0--00000000000-000----0000000000?0000000000000000000?000000-0---------?13-0-0-000----0----------20?0001100?-?-?0----												
Lolliguncula brevis	-0-0-0--00000000000-000----0000000000?0000000000000000000?000000-0---------?13-0-0-000----0----------20?0001100?-?-?0----												
Coccodentalium carduus	-0-0-0--00000000000-000----000?0000000?0000000000?000001100?000000-0---------000-0-0-000----0----------0000000000-0-00----												
Gadila braziliensis	-0-0-0--00000000000-000----000?0000000?0000000000?000001100?000000-0---------000-0-0-000----0----------0000000000-0-00----												
Solemya occidentalis	-0-0-0--000?0000000-000----000?0000000000000000000000000100?000000-0---------000-0-0-000----0----------0000000000-0-00----												
Ennucula puelcha	-0-0-0--000?0000000-001-1--0000000000000000000000000000100?000000-0---------000-0-0-000----0----------0000000000-0-00----												
Neopilina galatheae	-0-0-0--00000000000-000----0000000000000000000000000000000?000000-0---------000-0-0-000----0----------0000000000-0-00----												
Hanleya sp.	-0-0-0--00000000000-000----0000000000000000000000000000000000000-0---------000-0-0-000----0----------0000000000-0-00----												

APPENDIX 2 - Continued

Matrix of characters considered in the present study

Taxon\character	60	61	62	63	64	65	66	67
	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456							
Pomacea crosseana	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Pomacea curumim	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Pomacea scalaris	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Pomacea canaliculata	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Pomacea lineata	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Pomacea sordida	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Pomacea bridgesi	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Asolene megastoma	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Felipponea neritiniformis	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Marisa planogyra	00000000001000001000000-0000000-1000-0-00102000101111111021010000000100000-10							
Neocyclotus prominulus	00000000001000001000000-1000000-1000-0-00010000100101111021010000000100000-20							
Incidostoma tupy	00000000001000001000000-1000000-1000-0-00010000100101111021010000000100000-20							
Aperostoma blanchetiana	00000000001000001000000-1000000-1000-0-00010000100101111021010000000100000-20							
Viviparus acerosus	00000000001000001000000-0000000-1100001001010001112122220220110000010000-10							
Viviparus contectus	00000000001000001000000-0000000-1100001001010001112122220220110000010000-10							
Notopala ampullaroides	00000000001000001000000-0000000-1100001001010001112122220220110000010000-10							
Notopala essingtonensis	00000000001000001000000-0000000-1100001001010001112122220220110000010000-10							
Larina cf. *strangei*	00000000001001001000000-0000000-1100001001010001112122220220110000010000-10							
Annularia sp.	00000000001000001100100-1000000-1000000001000001212122331220110000010000-20							
Aylacostoma exoplicata	00000000001000001000000-1000000-1201111001001001212122330220110000010000-10							
Aylacostoma ci	00000000001000001000000-1000000-1201111001001001212122330220110000010000-10							
Aylacostoma tenuilabris	00000000001000001000000-1000000-1201111001001001212122330220110000010000-10							
Melanoides tuberculatus	00000000001000001000000-1000000-1201112001001001212122330220110000010000-10							
Supplanaxis nucleus	00000000001000001000000-1000000-1301113001000001212122330220110000010000-00							
Doryssa ipupiara	00000000001000001000000-1000000-1001-0-00100000121212233022011000010000-10							
Doryssa atra	00000000001000001000000-1000000-1001-0-00100000121212233022011000010000-10							
Doryssa macapa	00000000001000001000000-1000000-1011-0-00100000121212233022011000010000-10							
Pachychilus sp.	00000000001000001000000-1000000-1011-0-00100000121212233022011000010000-10							
Turritella hookeri	00000000001000001000000-1000000-1611000001000001212122330210110000010000-00							
Modulus modulus	00000000001000001000000-1000000-1011-0-00100000121212233021011000010000-00							
Cerithium atratum	00000000001000001000000-1000000-1011-0-00100000121212233022011000010000-00							
Bittium varium	00000000001000001000000-1000000-1011-0-00100000121212233022011000010000-00							
Finella dubia	00000000001000001000000-1000000-1001-0-00100000121212233022011000010000-00							
Alaba incerta	00000000001000001000000-1000000-1011-0-00100000121212233022011000010000-00							
Batillaria minima	00000000001000001000000-1000000-1001-0-00100000121212233022011000010000-00							
Cerithidea costata	00000000001000001000000-1000000-1011-0-00100000121212233022011000010000-00							
Campanile symbolicum	00000000001000001000000-1000000-1001-0-00100000121212233021011000010000-00							
Serpulorbis decussatus	00000000001000001000000-1000000-1601000001000001212122330210110000010000-00							

Taxon\character	60	61	62	63	64	65	66	67
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Stephopoma nucleogranosum	00000000001000001000000001000000-1601000001000001212122330210110000010000-00							
Amphithalamus glaber	00000000001001001100100-1000000-1000-0-0010000012121223312201100000100000-00							
Littorina flava	00000000001001001100100-1000000-1000-0-0010000012121223312201100000100000-00							
Potamolithus ribeirensis	00000000001001001100100-1000000-1000-0-0010000012121223312201100000100000-10							
Potamolithus troglobius	00000000001001001100100-1000000-1000-0-0010000012121223312201100000100000-10							
Potamolithus karsticus	00000000001001001100100-1000000-1000-0-0010000012121223312201100000100000-10							
Strombus pugilis	11210210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Strombus alatus	11210210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Strombus gracilior	11110210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Eustrombus goliath	11210210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Eustrombus gigas	11210210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Aliger costatus	11220210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Aliger gallus	11210210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Tricornis raninus	11110210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Conomurex luhuanus	11120210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Canarium urceus	11110210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Lambis lambis	11220210001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Terebellum terebellum	11000200001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Tylospira scutulata	11000100001001001000100020000000-1001-0-0010000012121223312201100000100000-00							
Struthiolaria papulosa	11000100001001001000100020000000-1001-0-0010000012121223312201100000100000-00							
Cuphosolenus serresianus	11000000001001001000100020000000-1001-0-0010000012121223312201101000100000-00							
Aporrhais occidentalis	11000000001001001000100020000000-1001-0-0010000012121223312211101000100000-00							
Aporrhais pespelicani	11000000001001001000100020000000-1001-0-0010000012121223312211101000100000-00							
Onustus caribaeus	11001000001001001000100-2000000-1001-0-0010000012121223312201111000100000-00							
Onustus indicus	11001000001001001000100-2000000-1001-0-0010000012121223312201111000100000-00							
Xenophora conchyliophora	11002000001001001000100-2000000-1001-0-0010000012121223312201111000100000-00							
Bostrycapulus odites	00000001012001001200100-1000000-1000-0-0010301012121323312101000100100000003							
Crepidula intratesta	00000001013001002311200-1000000-1000-0-0010301012121323312101000100100000103							
Crepidula protea	00000001013001002311200-1000000-1000-0-0010300012121323312101000100100000103							
Crepidula argentina	00000001013001002210200-1000000-1000-0-0010301012121323312101000100100000203							
Crepidula glauca	00000002013001002301200-1000000-1000-0-0010301012121323312101000100100000003							
Crepidula fornicata	00000002013001002311200-1000000-1000-0-0010301012121323312101000100100000003							
Crepidula margarita	00000002013001002311200-1000000-1000-0-0010301012121323312101000100100000003							
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Crepidula depressa	00000001013001002311200-1000000-1000-0-0010301012121323312101000100100000103							
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Calyptraea centralis	00000001002001001200100-1000000-1000-0-0010301012121323312101000100100000?03							
Crucibulum auricula	00000001012001001200100-1000000-1000-0-0010301012121323312101000100100000?03							
Crucibulum quiriquinae	00000001012101002200100-1000000-1000-0-0010301012121323312101000100100000?03							

Taxon\character	60	61	62	63	64	65	66	67
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Sigapatella calyptraeformis	0000000100100100310010-1000000-1000-0-0010301012121323312101000100100000?03							
Hipponix costellatus	0000000000100100110010-1000000-1000-0-1010401012121323312201000100100000?00							
Hipponix subrufus	0000000100100100110010-1000000-1000-0-1010401012121323312201000100100000?00							
Hipponix incurvus	0000000100100100110010-1000000-1000-0-1010401012121323312201000100100000?00							
Hipponix grayanus	0000000000100100110010-1000000-1000-0-1010401012121323312201000100100000?00							
Hipponix leptus	0000000000100100110010-1000000-1000-0-1010401012121323312101000100100000?00							
Sabia conica	0000000100100100110010-1000000-1000-0-1010401012121323312201000100100000?00							
Malluvium devotus	0000000100110100110010-1000000-1000-0-1010401012121323312201000100100000?00							
Cheilea equestris	0000000000100100110010-1000000-1000-0-0010601012121323312101000100100000?00							
Capulus sycophanta	0000000100110100110010-1000000-1000-0-0010601112121323312101000000100000?00							
Trichotropis cancellata	0000000000100100110010-1000000-1000-0-0010601112121223312201000000100000?00							
Trichotropis borealis	0000000000110100110010-1000000-1000-0-0010601112121223312201000000100000?00							
Vanikoro sp.	0000000100100100110010-1000000-1000-0-0010601012121323312201000000100000?00							
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Naticarius canrenus	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Natica sp. n.	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Natica cf. *marochiensis*	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Natica livida	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Natica cf. *sagrayana*	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Stigmaulax sulcatus	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Natica vitellus	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Polinices lacteus	0000000002100100110010-2000000-1000-0-0010500012121223312101000001200000-01							
Polinices uberinus	0000000002100100110010-2000000-1000-0-0010500012121223312101000001200000-01							
Polinices hepaticus	0000000002100100110010-2000000-1000-0-0010500012121223312101000001200000-01							
Polinices lewisii	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Cornuber sordidus	0000000002100100410010-2000000-1000-0-0010500012121223312101000011200000-01							
Neverita duplicata	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Lunatia heros	0000000002100100110010-2000000-1000-0-0010500012121223312101000001200000-01							
Eunaticina sp.	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Sinum sp. Brasil	0000000002100100410010-2000000-1000-0-0010500012121223312101000011200000-01							
Sinum perspectivum	0000000002100100410010-2000000-1000-0-0010500012121223312101000011200000-01							
Sinum maculatum	0000000002100100110010-2000000-1000-0-0010500012121223312101000011200000-01							
Amauropsis islandica	0000000002100100110010-2000000-1000-0-0010500012121223312101000001200000-01							
Amauropsis andersoni	0000000002100100110010-2000000-1000-0-0010500012121223312101000001200000-01							
"Amauropsis" rossiana	0000000000100100110010-1000000-1000-0-0010100012121223312201100000100000-00							
Macrocypraea zebra	0000000000100211010010102000000-1000-0-0010600012121223312201010000200000-00							
Macrocypraea cervinetta	0000000000100211010010102000000-1000-0-0010600012121223312201010000200000-00							
Erosaria acicularis	0000000000100120010010102000000-1000-0-0010600012121223312201010000200000-00							
Erosaria spurca	0000000000100100010010102000000-1000-0-0010600012121223312201010000200000-00							
Luria cinerea	0000000000100121010011102000000-1000-0-0010600012121223312201010000200000-00							
Cypraea tigris	0000000000100121010011102000000-1000-0-0010600012121223312201010000200000-00							

Taxon\character	60	61	62	63	64	65	66	67
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Monetaria moneta	00000000001003215100101020000000-1000-0-00106000121212233122010100002000000-00							
Monetaria annulus	00000000101003205100101020000000-1000-0-00106000121212233122010100002000000-00							
Ravitrona caputserpentis	00000000001001200100101020000000-1000-0-00106000121212233122010100002000000-00							
Pseudozonaria arabicula	00000000001001000100101020000000-1000-0-00106000121212233122010100002000000-00							
Pseudozonaria robertsi	00000000001001010100101020000000-1000-0-00106000121212233122010100002000000-00							
Cyphoma signatum	00000000301011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Cyphoma gibbosum	00000000301011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Pseudocyphoma intermedium	00000000301011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Ovula ovum	00000000001011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Calpurnus verrucosus	00000000001011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Simnialena uniplicata	00000000001011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Cymbula acicularis	00000000001011200100101020000000-1000-0-00106000121212233122010100002000000-00							
Jenneria pustulata	00000000001021200100101020000000-1000-0-00106000121212233122010100002000000-00							
Niveria pediculus	00000000201001000100001020000000-1000-0-00106000121212233122010100002000000-00							
Trivirostra oryza	00000000201001200100001020000000-1000-0-00106000121212233122010100002000000-00							
Hespererato maugeriae	00000000001001000100001020000000-1000-0-00106000121212233122010100002000000-00							
Pedicularia sp.1	00000000001001000100101020000000-14000110010?000121212233122010100002000000-02							
Pedicularia californica	00000000001031000100101020000000-14000110010?000121212233122010100002000000-02							
Pedicularia decussata	00000000001031200100101020000000-14000110010?000121212233122010100002000000-02							
Pedicularia sp.2	00000000001001000100101020000000-14000110010?000121212233122010100002000000-02							
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Lamellaria mopsicolor	00000000001001000100100020000000-1000-0-00106000121212233122010100002000000-00							
Lamellaria patagonica	00000000401001000100100020000000-1000-0-00106000121212233122010100002000000-00							
Velutina velutina	00000000001001000100100020000000-1000-0-00106020121212233122010100002000000-00							
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Ficus carolae	0????00??????????0??00?0???2?00000-10?0-0-0?106000121212233123010000002100010-01							
Ficus subintermedia	00000000001144000100104321000000-1000-0-00106000121212233123010000002100010-01							
Ficus ficus	00000000001144000100104321000000-1000-0-00106000121212233123010000002100010-01							
Thalassocyon bonus	00000000501100006100103020000000-1000-0-00106000121212233123010000002100010-01							
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Cymatium cynocephalum	00000000501100006100103020000000-1000-0-01106000121212233123010000002000010-01							
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Cymatium femorale	00000000001141006100103120000000-1000-0-00106000121212233123010000002000010-01							
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Cymatium pileare	00000000501141006100103120000000-1000-0-01106000121212233123010000002000010-01							
Sassia kamphyla	00000000501100006100100020000000-1000-0-00106000121212233123010000002000010-01							
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Fusitriton magellanicus	00000000001100006100100020000000-1020-0-00106000121212233123010000002000010-01							
Bursa corrugata	00000000001144000100100220000000-1000-0-00106000121212233121010000002100010-01							
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Taxon\character	60	61	62	63	64	65	66	67
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Bursa tenuisculpta	0???00?????????0??00?0???2?00000-10?0-0-0?10600012121223312201000000210010-01							
Bufonaria bufo	0000000000011410001001002200000 0-1000-0-0010600012121223312301000000210010-01							
Cypraecasis testiculus	0000000050114400010010012000000-1000-0-0110600012121223312301000000200010-01							
Cassis tuberosa	0000000050114100010010312000000-1000-0-0110600012121223312101000000200010-01							
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Phalium labiatum	0000000050114400010010012000000-1000-0-0010600012121223312301000000200010-01							
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Distorsioanus	0000000000110000610010212000000-1000-0-0010600012121223312301000000210010-01							
Distorsio reticulata	0000000050114100610010212000000-1000-0-0010600012121223312301000000210010-01							
Distorsio decipiens	0000000000114400010010212000000-1000-0-0010600012121223312301000000210010-01							
Personopsis purpurata	0???00?????????0??00?0???2?00000-10?0-0-0?10600012121223312301000000210010-01							
Tonna galea	0000000050114400010010012000000-1000-0-0010600012121223312101000000200010-01							
Tonna maculosa	0000000050114400010010012000000-1000-0-0010600012121223312101000000200010-01							
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Cochlespira radiata	0000000000120100010000042010001-1000-0-0010600012121323312401000001201110-01							
Pleurotomella aguayoi	0000000000125140010000042011001-1000-0-0010600012121323312401000001201110-01							
Carinodrilla braziliensis	0000000000125100010000042000001-1000-0-0010600012121323312401000001201110-01							
Gemmula mystica	0000000000125140010000042010001-1000-0-0110600012121323312401000001201110-01							
Fenimorea sp.	0000000000120100010000042000001-1000-0-0010600012121323312401000001201110-01							
Clathrodilla sp.	0000000000110130010000042010001-1000-0-0010600012121323312401000001201110-01							
Daphnella lymnaeiformis	0000000000115140010000042011001-1000-0-0010600012121323312401000001201110-01							
Pilsbryspira albomaculata	0000000000115140010000042011001-1000-0-0010600012121323312401000001201110-01							
Glyphostoma sp.	0000000000011010001000042010001-1000-0-0010600012121323312401000001201110-01							
Polystira formosissima	000000000001151?00100000420??001-1000-0-0010600012121323312401000001201110-01							
Conus regius	0000000000115130010000042011201-1000-0-0110600012121323312401000001201010-01							
Conus mindanus	0000000000115130010000042010201-1000-0-0110600012121323312401000001201010-01							
Conus villepinii	0000000000115130010000042011201-1000-0-0110600012121323312401000001201010-01							
Conus clerii	0000000000115130010000042011201-1000-0-0110600012121323312401000001201010-01							
Conus archetipus	0000000000115130010000042011201-1000-0-0110600012121323312401000001201010-01							
Conus bertarollae	0000000000115130010000042011201-1000-0-0110600012121323312401000001201010-01							
Conus textile	0000000000115130010000042011101-1000-0-0110600012121323312401000001201010-01							
Conus tulipa	0000000000115130010000042010101-1000-0-0110600012121323312401000001201010-01							
Conus selenae	0000000000115130010000042010201-1000-0-0110600012121323312401000001201010-01							
Conus ermineus	0000000000115130010000042011101-1000-0-0110600012121323312401000001201010-01							
Conus jaspideus	0000000000115130010000042011201-1000-0-0110600012121323312401000001201010-01							
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Hastula cinerea	0000000000125100010000042010001-1000-0-0010600012121323312401000001201110-01							
Hastula hastata	0000000000125100010000042010001-1000-0-0010600012121323312401000001201110-01							
Terebra gemmulata	0000000000125100710000042010011-1000-0-0010600012121323312401000001201110-01							
Terebra crassireticula	0000000000125100010000042010011-1000-0-0010600012121323312401000001201110-01							

Taxon\character	60	61	62	63	64	65	66	67
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Terebra brasiliensis	0000000000012510001000004203000 0-1000-0-0010600012121323312401000001201110-01							
Terebra spirosulcata	0000000000012510001000004201001 1-1000-0-0010600012121323312401000001201110-01							
Terebra taurina	0000000000012510071000004201000 1-1000-0-0010600012121323312401000001201110-01							
Terebra dislocata	0000000000012510071000004203001 1-1000-0-0010600012121323312401000001201110-01							
Zemira australis	0000000000013010001000004200000011000-0-0110600012121323311401010101200010-01							
Fulmentum ancilla	0000000000013010001000004200000011000-0-0110600012121323311501010101200010-01							
Melapium lineatum	0000000000011010001000054200000011000-0-0110600012121323311401010101200010-01							
Benthobia atafona	0000000000013010001000004200000011000-0-0010600012121323311401010101200010-01							
Benthobia complexirhyna	0000000000013010001000004200000011000-0-0010600012121323311401010101200010-01							
Nassodonta dorri	0000000003110100010000042000000 11000-0-0110600012121323311501010101200110-01							
Siratus senegalensis	000000000010?000100000420000001 1000-0-0110600012121323311401000101201110-01							
Siratus tenuivaricosus	000000000010?000100000420000001 1000-0-0110600012121323311401000101201110-01							
Siratus formosus	000000000010?000100000420000001 1000-0-0110600012121323311401000101201110-01							
Sirarus beauii	000000000010?000100000420000000 1000-0-0110600012121323311401000101201110-01							
Phyllonotus pomum	0000000000011010001000004200000001000-0-0110600012121323311401000101201110-01							
Phyllonotus occulatus	0000000000011010001000004200000001000-0-0110600012121323311401000101201110-01							
Phyllonotus margaritensis	0000000000011010001000004200000001000-0-0110600012121323311401000101201110-01							
Chicoreus brevifrons	0000000000011010001000004200000001000-0-0110600012121323311401000101201110-01							
Chicoreus spectrum	0000000000011010001000004200000001000-0-0110600012121323311401000101201110-01							
Chicoreus carolinae	0000000000011010001000004200000011000-0-0110600012121323311401010101201110-01							
Chicoreus coltrorum	0000000000011010001000004200000001000-0-0110600012121323311401010101201110-01							
Murex trapa	0000000000011010001000004200000011000-0-0110600012121323311401000101201110-01							
Trophon geversianus	0000000000011010001000054200000011000-0-0110600012121323311401010101201110-01							
Bolinus brandaris	0000000000011010001000004200000001000-0-0110600012121323311401000101201110-01							
Nucella lapillus	0000000000011010001000054200000011000-0-0110600012121323311401010101201110-01							
Thais biserialis	0000000000011010001000004200000001000-0-0110600012121323311401010101201110-01							
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Eupleura sp.	0000000000011010001000004200000011000-0-0110600012121323311401000101201110-01							
Acanthina brevidentata	0000000000011010001000054200000011000-0-0110600012121323311401010101201110-01							
Muricanthus radix	0000000000011010001000004200000?1000-0-0110600012121323311401000101201110-01							
Vitularia salebrosa	0000000000011010001000054200000011000-0-0110600012121323311401010101201110-01							
Olivancillaria urceus	000000000010?000100000020000001 1000-0-0110600012121323311501010101200110-01							
Vexillum sp.	0000000000011010001000004200000011000-0-0110600012121323311501010101200110-01							
Austromitra maculosa	0000000000011010001000004200000011000-0-0110600012121323311501010101200110-01							
Buccinanops gradatus	000000000310?000100000020000001 1000-0-0110600012121323311501010101200110-01							
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Prunum martini	0000000000011010001000004200000011000-0-0110600012121323311501010101200110-01							
Amphissa acuminata	0000000003110100010000042000000 11000-0-0110600012121323311501010101200110-01							
Amphissa cancellata	0000000003110100010000042000000 11000-0-0110600012121323311501010101200110-01							
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Taxon\character	60	61	62	63	64	65	66	67
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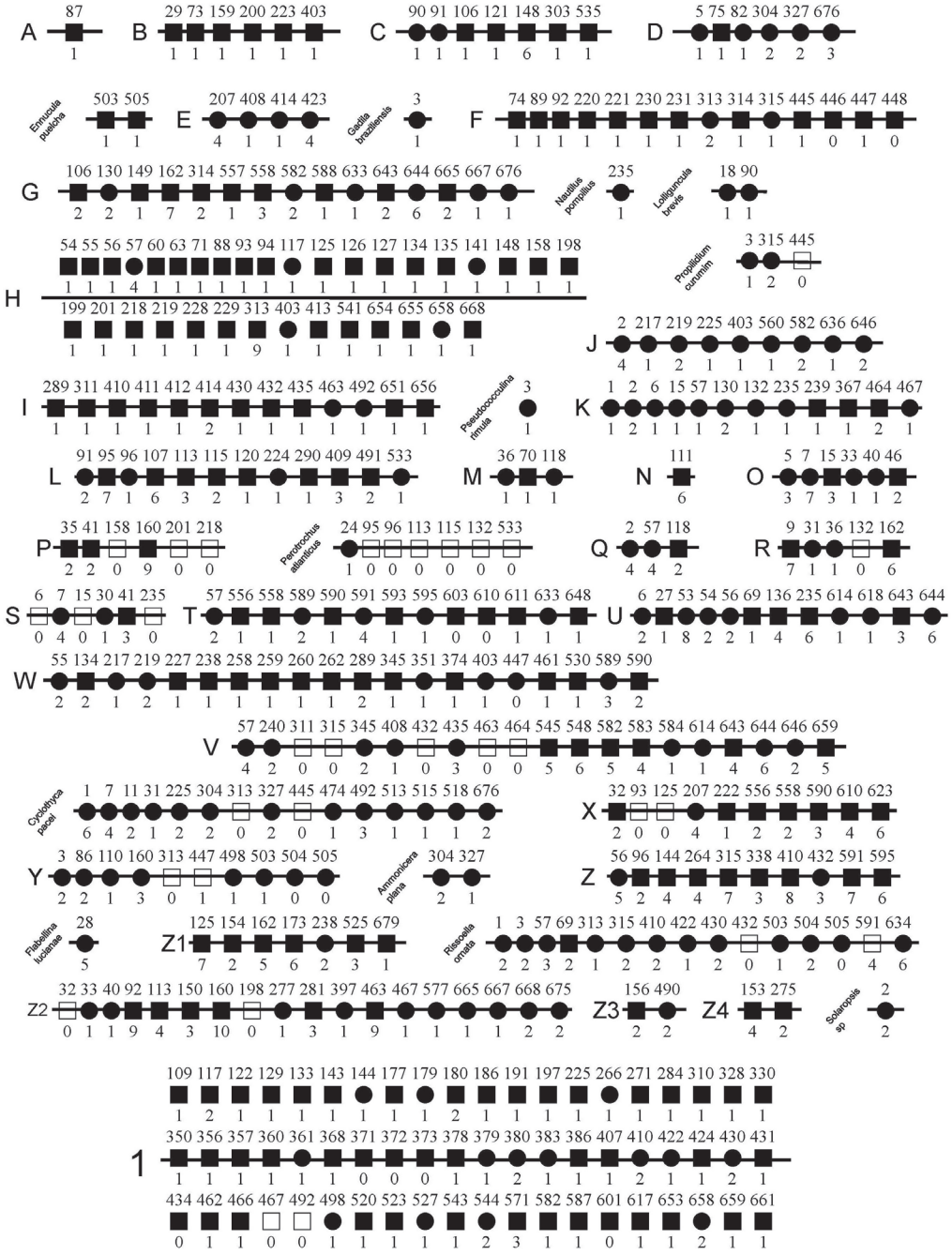
Cancellaria petuchi	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Cancellaria cancellata	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Cancellaria spirata	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Trigonostoma tesselata	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Trigonostoma tenerum	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Scalpia contabulata	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Scalpia obliquata	0000000000011010001000004201000001500013011060001212132331210101010120011 1-02							
Annulobalcis aurisflamma	0000000000010000001000000 1000000-1000-0-00106000121212233 12??1000000100000-02							
Perotrochus atlanticus	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Lucapina elisae	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Fissurella mesoatlantica	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Haliotis aurantium	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Haliotis pourtalesii	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Falsimargarita stephaniae	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Calliostoma sp.	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Gaza compta	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Gaza superba	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Gaza cubana	----00-----0----00---0--0-0--00-0000-0-00--0000000100111010000000000100000-00							
Addisonia enodis	----00-----0----00---0--0-0--00-0001-0-00--0020000100111010000000000100000-00							
Pseudococculina rimula	----00-----0----00---0--0-0--00-0001-0-00--0020000100111010000000000100000-00							
Neritina zebra	-00-0000-010-1000100000-0000000-1000-0-0003600010010011101000000000100000-00							
Nerita ascensionis	-00-0000-010-1000100000-0000000-1000-0-0003600010010011101000000000100000-00							
Cyclothyca pacei	--0-00---010-1000000000-0000000-1000-0-0004602010010 0?1101500000000100000-02							
Rissoella ornata	--0-00---410-1000000006-0000000-160000000046020100100?11?1500000000100000-00							
Ammonicera plana	--0-00---410-1000000006-0000000-1000-0-0004602010010 0?11?1500000000100000-00							
Orbitestella patagonica	--0-00---410-1000000006-0000000-1000-0-0004602010010 0?11?1500000000100000-00							
Flabellina lucianae	--0-00---410-1000000006-0000000-1000-0-000460201????0?1??1500000000100000-00							
Anctus angiostomus	--0-00---410-1000000006-0000000-1000-0-000460201????0?1??1500000101 2?0000-20							
Megalobulimus riopretensis	--0-00---410-1000000006-0000000-1000-0-000460201????0?1??1500000101 2?0000-20							
Megalobulimus mogianensis	--0-00---410-1000000006-0000000-1000-0-000460201????0?1??1500000101 2?0000-20							
Olympus nimbus	--0-00---410-10000---06-0000000-1000-0-000460201????0?1??1500000101 2?0000-20							
Propilidium curumim	----00-----0----00---0--000--00-0000-0-00--0000000000110010000000000100000-00							
Nautilus pompilius	----00----?0----00---0----0--00-1000-0-00-260000????????00--0-002010?0000-01							
Lolliguncula brevis	----00----?0----00---0----0--00-1000-0-00-260000????????00--0-002010?0000-01							
Coccodentalium carduus	----00-----0----00---0----0--00-0000-0-00--000000000000000--0-00000000000-00							
Gadila braziliensis	----00-----0----00---0----0--00-0000-0-00--000000000000000--0-00000000000-00							
Solemya occidentalis	----00-----0----00---0----0--00-0000-0-00--000000000000000--0-00000000000-03							
Ennucula puelcha	----00-----0----00---0----0--00-0000-0-00--000000000000000--0-00000000000-03							
Neopilina galatheae	----00-----0----00---0----0--00-0000-0-00--000000000000000--0-00000000000-00							
Hanleya sp.	----00-----0----00---0----0--00-0000-0-00--000000000000000--0-00000000000-00							

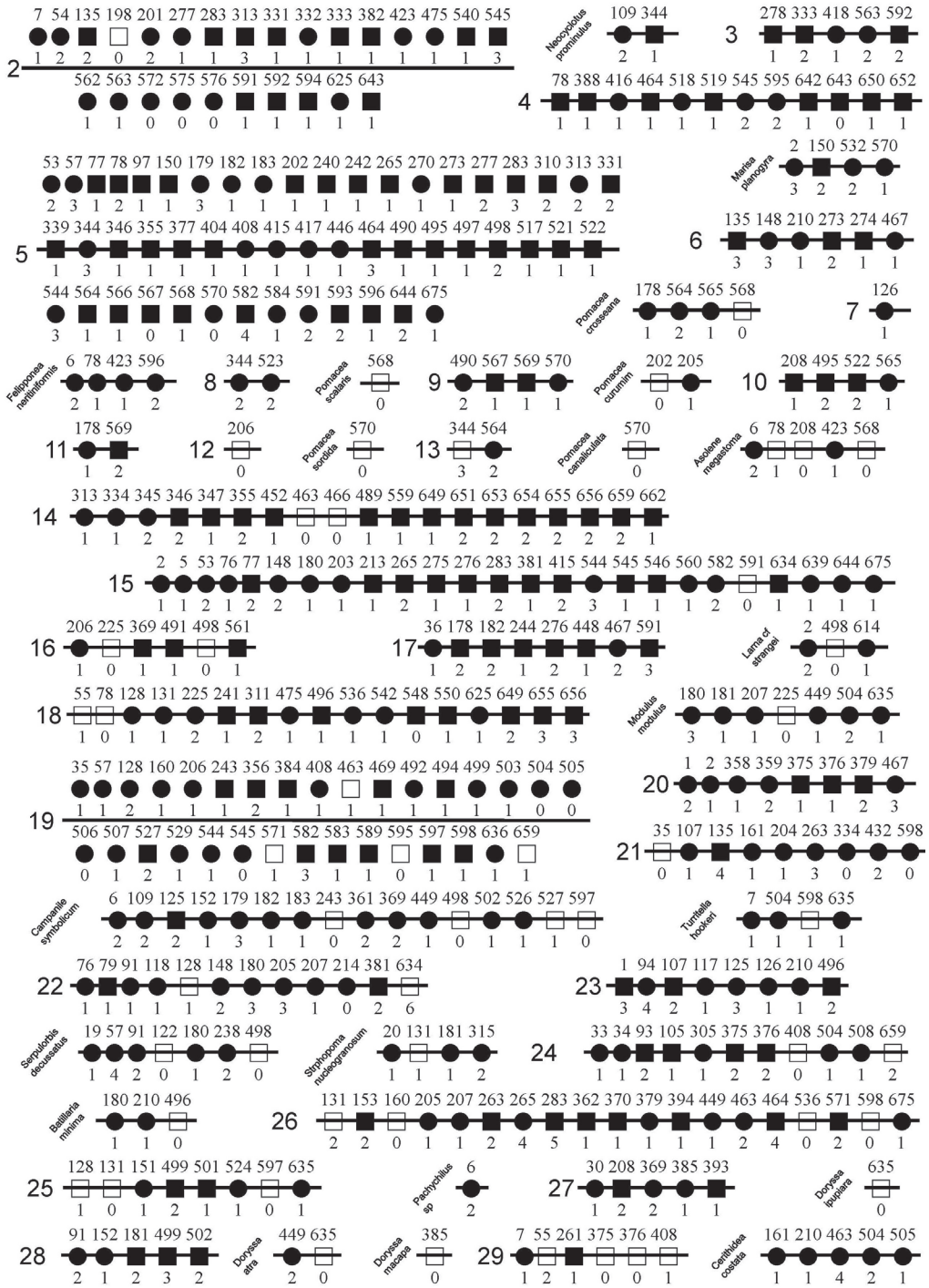
APPENDIX 3

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



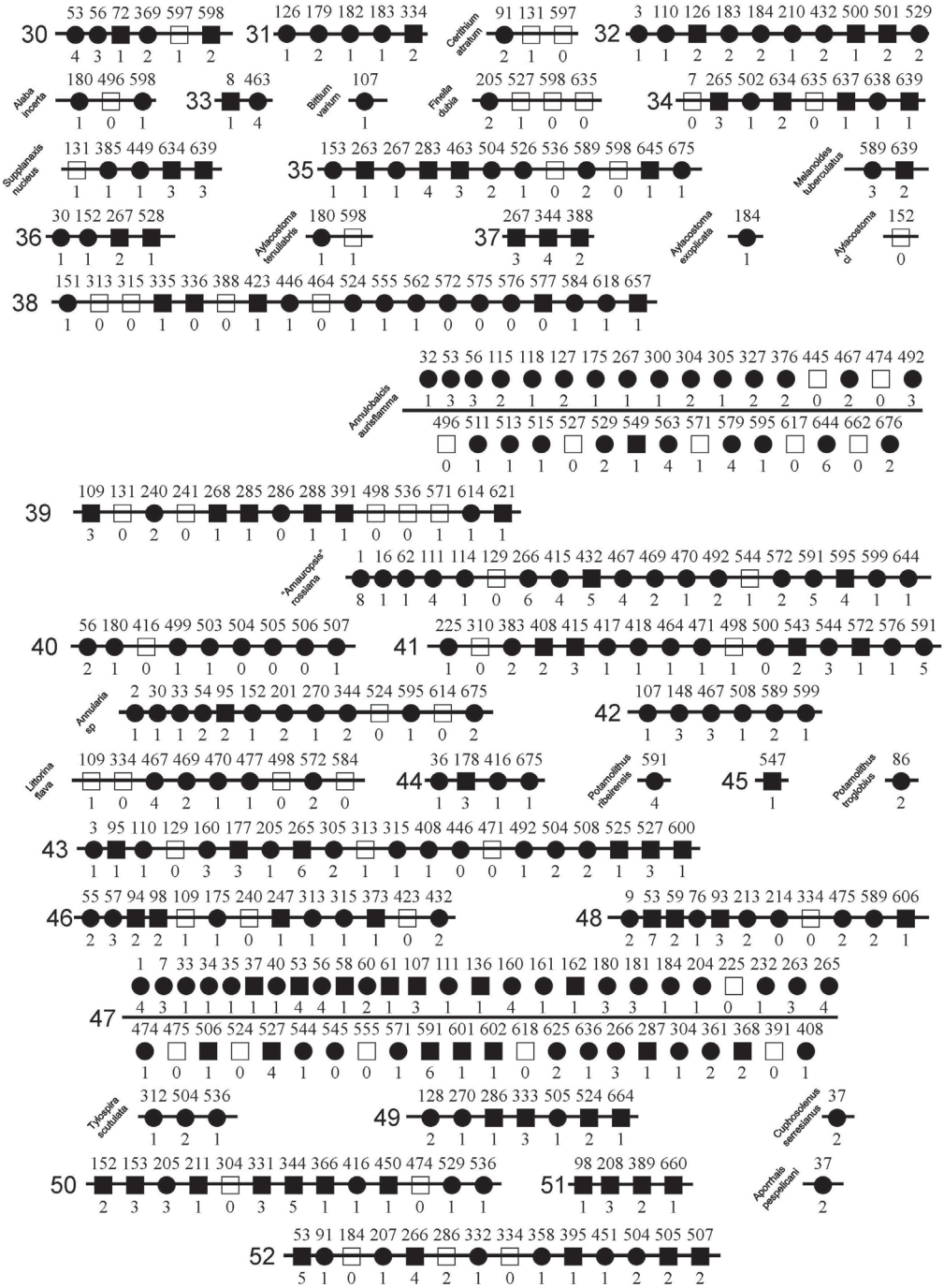
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



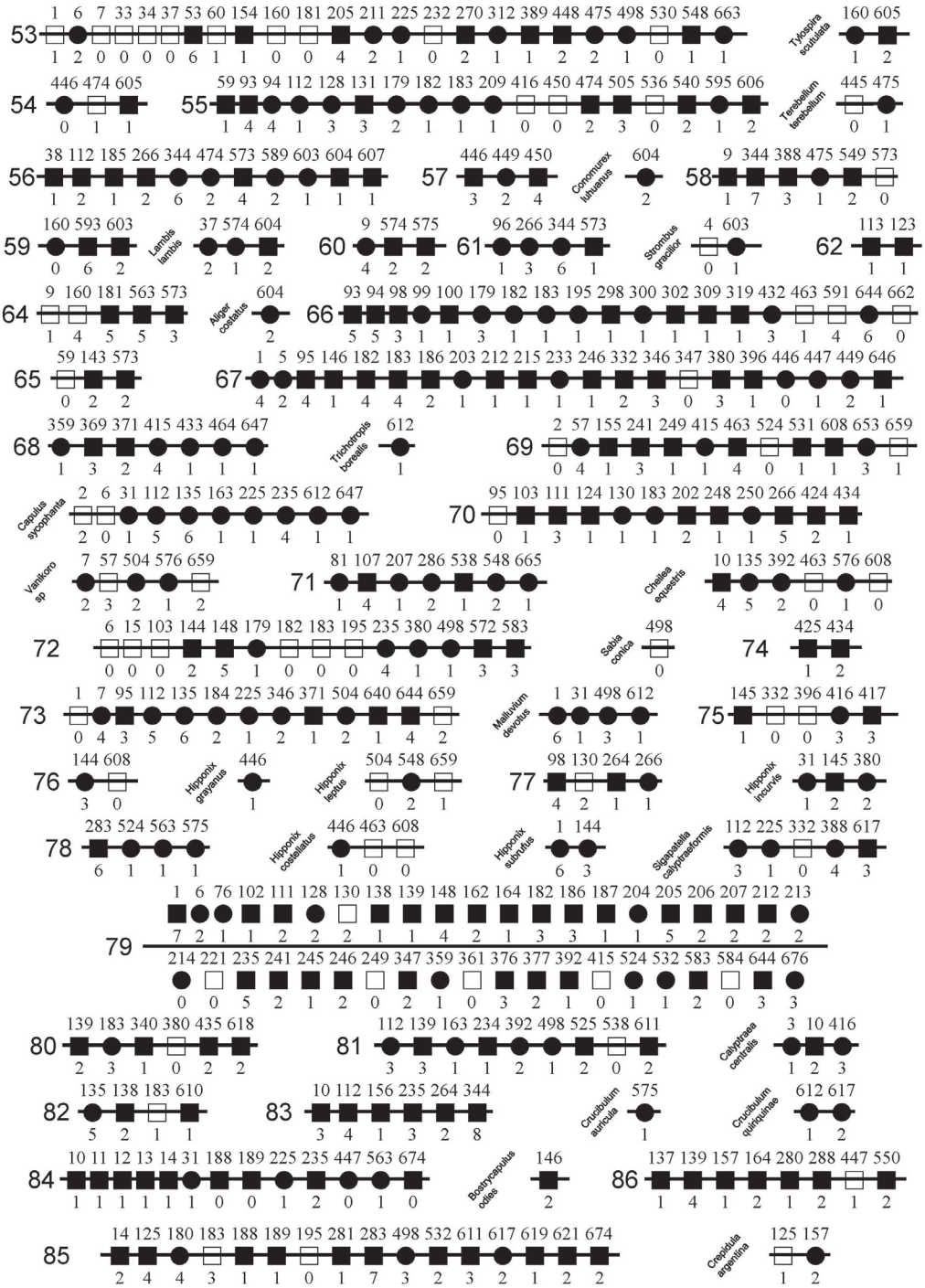
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



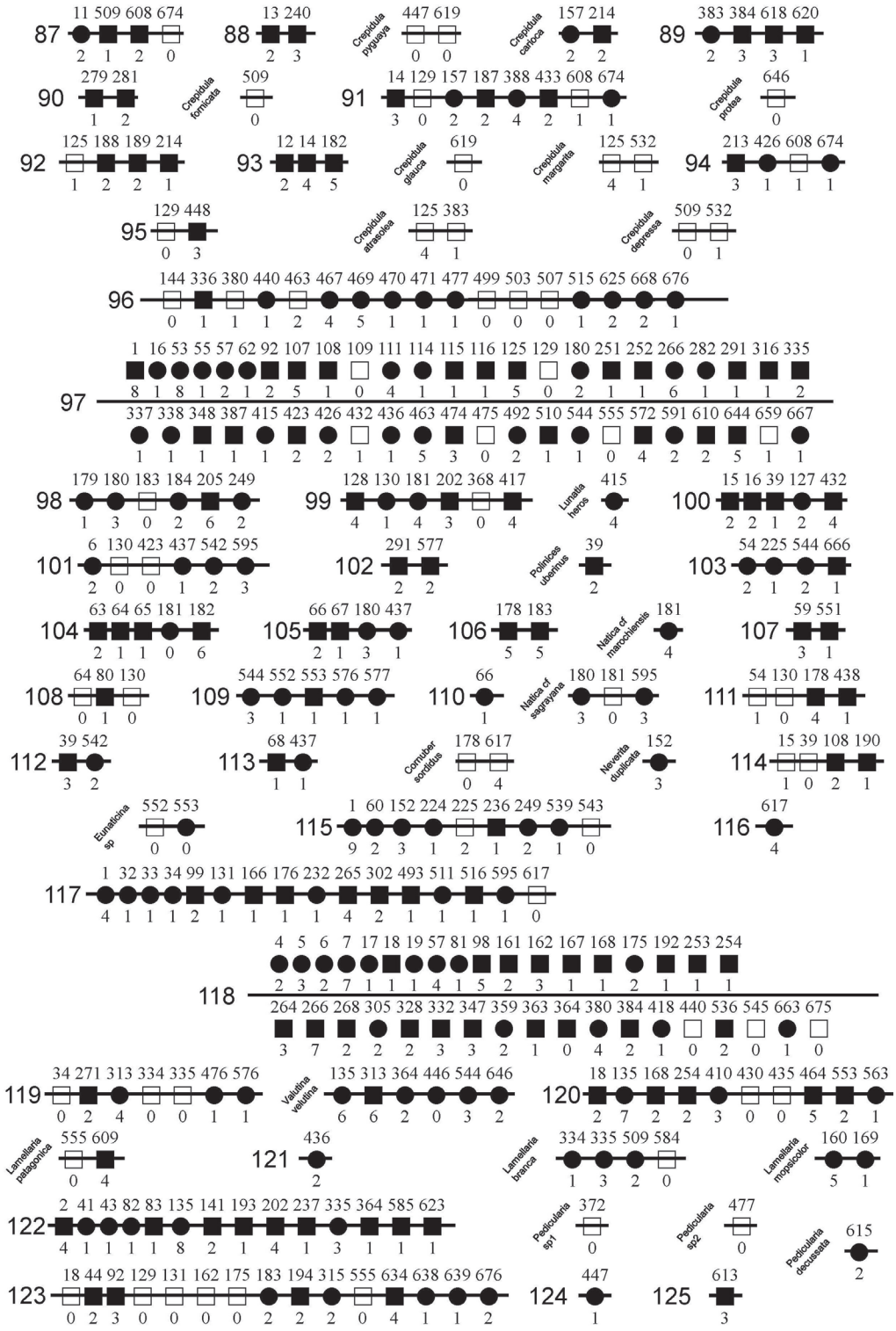
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



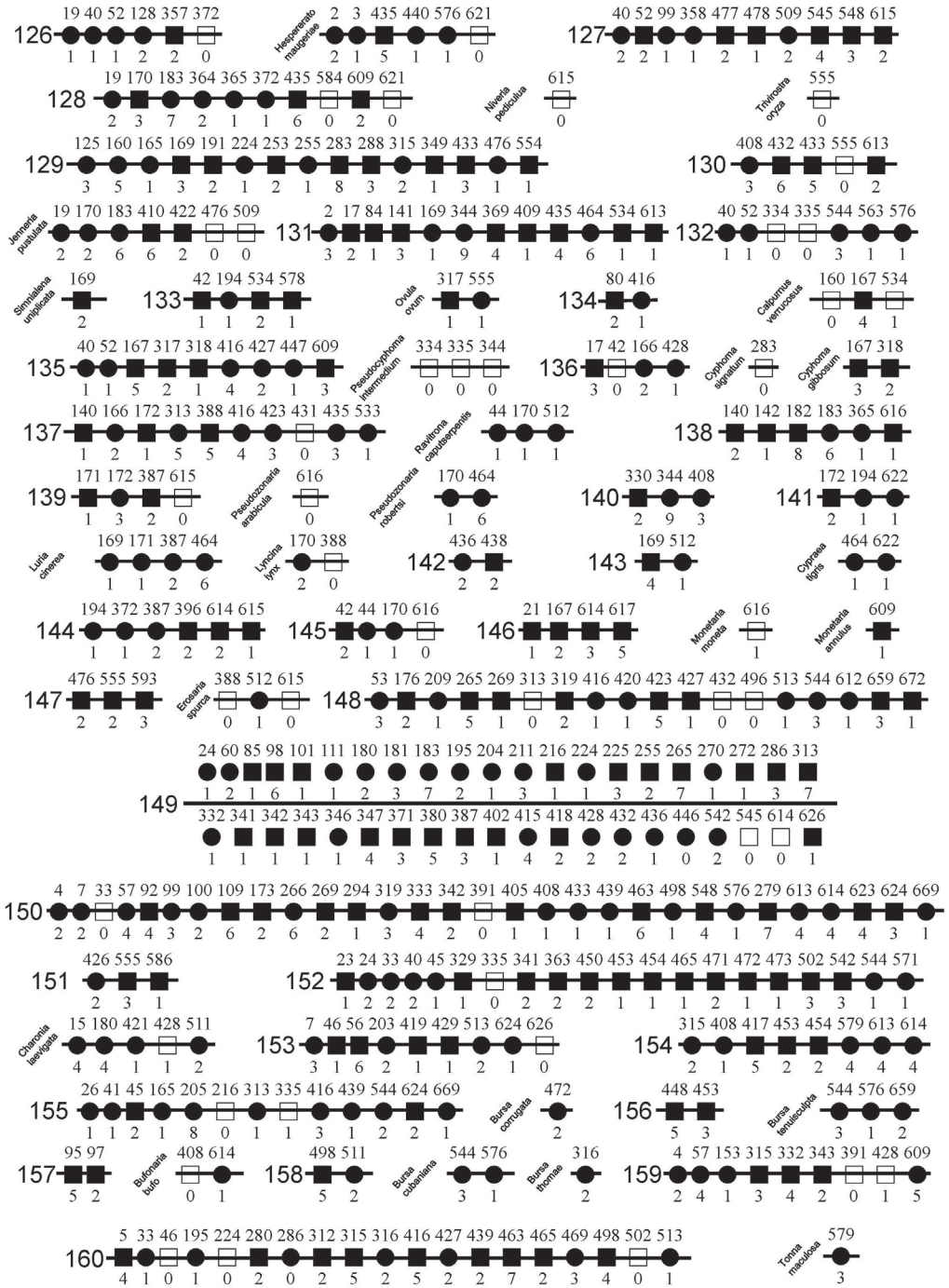
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



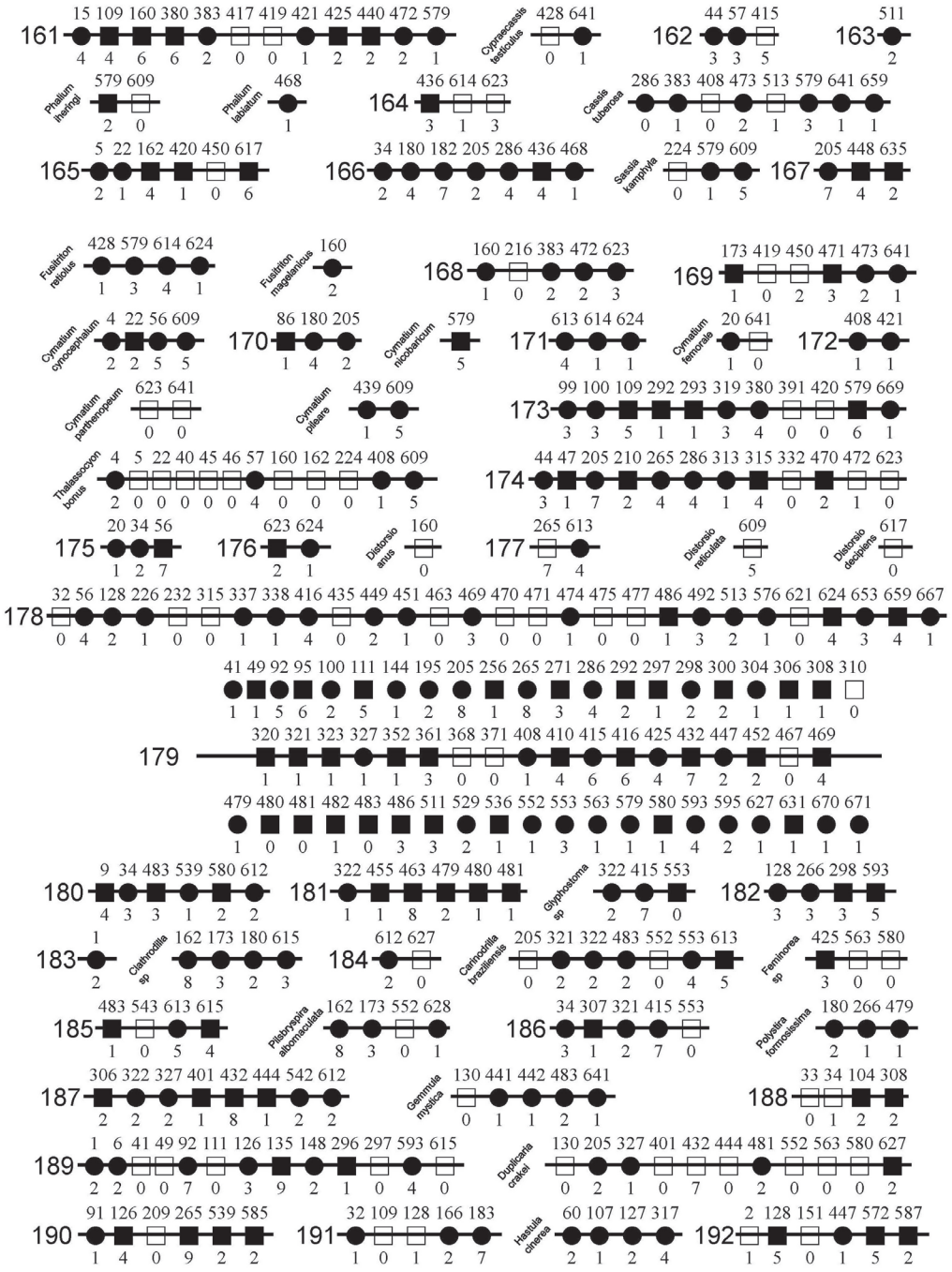
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



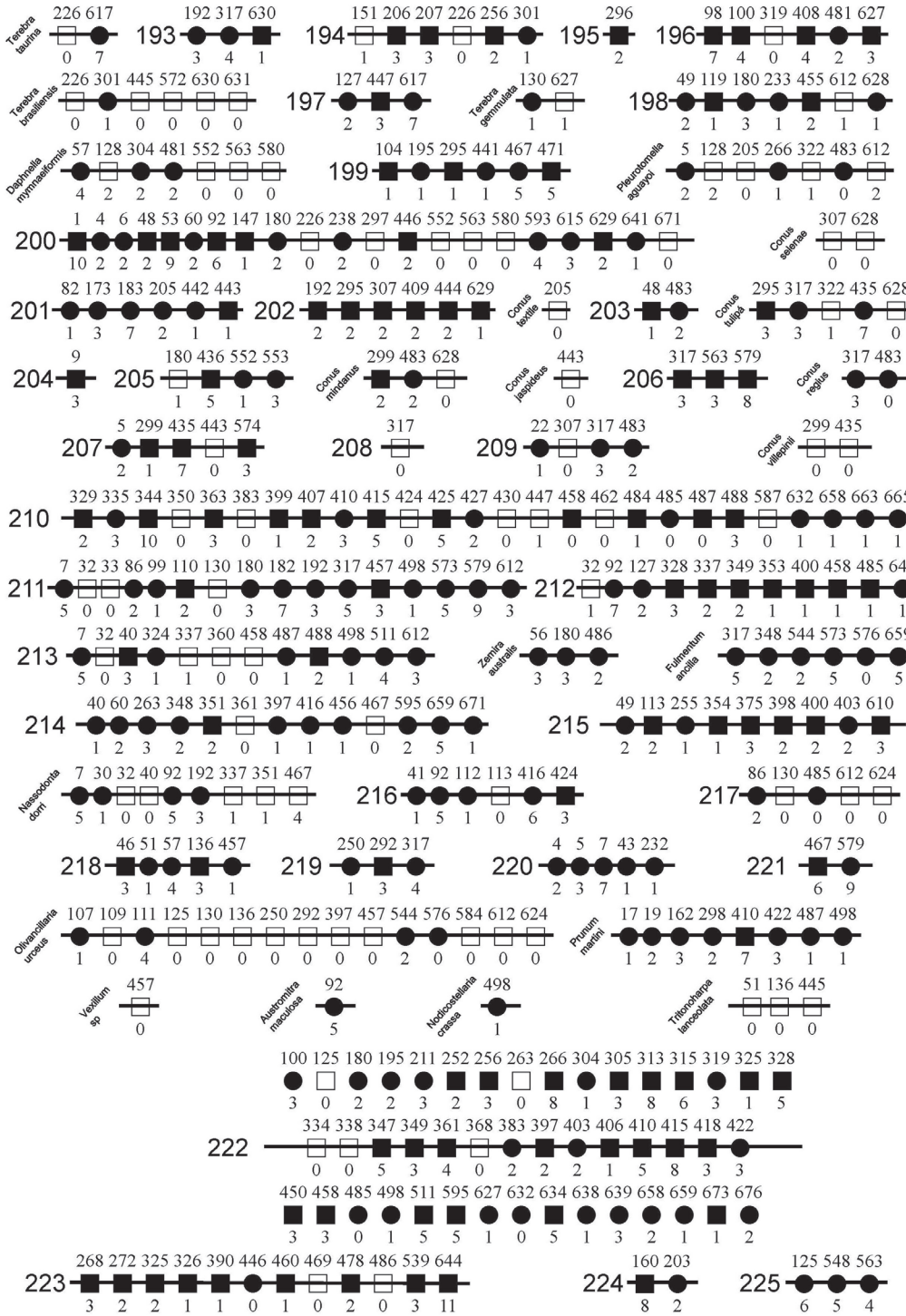
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



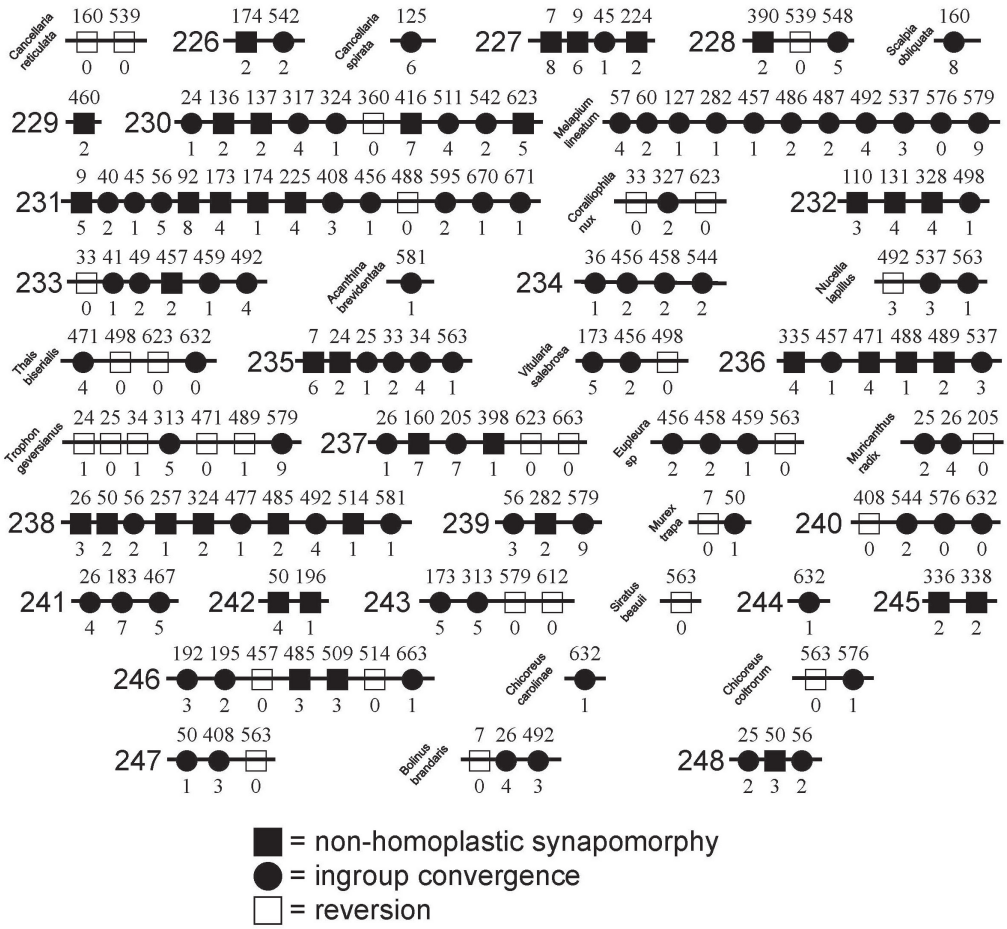
APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



APPENDIX 3 - Continued

The nodes of obtained cladogram (Fig. 20) with representation of the synapomorphies that support them; some terminal taxa also shown. The number above each symbol means the character, the number below means the state. Symbols: dark square = nom-homoplastic synapomorphy; empty square = reversion; circle = convergence.



APPENDIX 4

Formal description of the taxa and taxonomical checklist

N.B.: the categories upper than Caenogastropoda are not the main concern of this present study, then their diagnosis are not complete. The scenario is Bouchet & Rocroi (2005), check that paper for authorities and further synonymy. Other details in section 5.2 (node numbers as in Fig. 20).

1. Class Gastropoda (node H)

Diagnosis: torsion and operculum (at least in larval phase).

1.1. Patellogastropoda

Diagnosis: different kind of nacre, reduction of at least one gill.

1.2. Orthogastropoda (node I)

Diagnosis: shell coiled. Horizontal muscle (m6) located externally to odontophore cartilages. Loss of radular teeth mineralization. Flexiglossate condition of the radula.

1.3. *Incertae sedis:* Cocculiniformia (node J)

1.2.1. Vetigastropoda (node L)

Diagnosis: epipodial tentacles with special receptors.

1.2.2. Adenogonogastropoda (new) (node T)

Diagnosis: Eyes with lens. Loss of right pallial structures, such as gill, osphradium and hypobranchial gland. Loss of right kidney. Pallial oviduct glandular, producing a protective capsule to eggs.
Etymology: the epithet refers to the glandular oviduct at pallial region, from Greek *adenos* meaning gland, and *gono,* genital structure.
List of included taxa: Neritimorpha + Apogastropoda.

1.2.2.1. Neritimorpha (node U)

Diagnosis: shell with absorption of inner whorls in spire. Columellar muscle inserted divergently in both sides of aperture. Calcareous operculum.

1.2.2.2. Apogastropoda (node W)

Diagnosis: shell coiled compressing right side of head-foot and mantle cavity. Columellar muscle single. Hypobranchial gland simple, as glandular layer. Loss of right auricle. Loss of posterior pair of odontophore cartilage and their approximator muscle of cartilages. Salivary glands with conspicuous ducts. Origin of esophagus at posterior end of buccal mass. Loss of gastric caecum. No intestinal loop inside haemocoel.
List of included taxa: Heterobranchia + Caenogastropoda.

1.2.2.2.1. Heterobranchia (node V)

Diagnosis: protoconch shell heterotrophic. Loss of gill, replaced by ciliary folds. Loss of esophageal lateral pouches. Genital ducts running along haemocoel. Hermaphroditism.

1.2.2.2.2. Caenogastropoda Cox, 1960a (node 1)

Synonymy: Pectinibranchia Cuvier, 1814.
Diagnosis: eyes located at tentacle base, normally on ommatophore. Pedal gland immerse in foot musculature with corresponding furrow along entire anterior foot sole. Septum separating haemocoelic chamber from visceral mass. Operculum with concentric sculpture. Osphradium elongated, ridge-like. Kidney with hollow space, having pair of lobes, one of them surrounding intestinal portion. Nephrostome isolated in membrane separating renal chamber and pallial cavity. Wide pair of longitudinal folds in dorsal wall of buccal cavity. Peribuccal musculature (mj) reunited into two bundles. Reduction of number of dorsal tensor muscles of radula (m4) to two pairs. Reduction of size of ventral pair of tensor muscles of radula (m11). Accessory pair of tensor muscles of radula (m5) long and thin, originated from main dorsal tensor (m4) instead of cartilages. Reduction of length of horizontal muscle (m6) related to odontophore cartilages length, with form broad and thick. Pair of muscles running inside radular sac (m7). Pair of protractor muscles of odontophore (m10) inserted in its anterior region. Subradular cartilage very broad in buccal cavity, covering its entire ventral wall. Radular sac normally coiled. A single pair of lateral teeth on radula, similar shaped to rachidian. Two pairs of lateral teeth on radula. Loss of longitudinal bundle of inner surface of esophagus, and appearance of longitudinal pair of folds. Reduction of intestinal loops, mainly in visceral mass. Formation of fecal pellets. Development of pallial vas deferens. Nerve ring positioned posteriorly, at middle level of buccal mass. Buccal ganglia well-defined, located close to buccal mass.

1a. Cyclophoroidea Gray, 1847 (node 2)

Diagnosis: shell discoid, umbilicus ample. Operculum calcareous, rounded. Salivary glands separated from each other. Esophageal insertion in middle level of stomach. Exophalic penis with opened furrow. Pallial oviduct with bursa copulatrix located in its posterior region. Terrestrial environment (Simone, 2004a).
List of included taxa: Cyclophoridae s.l. *OR* Cyclophoridae s.s., Poteriidae, Megalomastomidae, Maizaniidae, Diplommatinidae, Pupinidae.

1b. Hydrogastropoda (new) (node 4)

Diagnosis: left and right (incurrent and excurrent respectively) siphons of head origin. Monopectinate gill (which can be a Caenogastropoda synapomorphy), of about same length of pallial cavity, and filament tips turned to right. Main dorsal pair of radular tensor (m4) connected to a tissue on radular ribbon (to), and to its pair. Pair of accessory muscles of horizontal muscle (m12).
Etymology: the epithet refers to the predominant aquatic environment of occurrence, from Greek *hydros.*
List of included taxa: Ampullarioidea + Epiathroidea.

2a. Ampullarioidea Gray, 1824 (node 5)

Diagnosis: shell globose. Operculum with an upper projection. Osphradium pectinate located on a folded stalk. Lung located between gill and osphradium. Heart with ampulla at anterior aorta. Freshwater environment (Simone, 2004a).
List of included taxa: Ampullariidae.

2b. Epiathroidea (new) (node 14)

Diagnosis: shell somewhat turriform. Osphradium ridge-like with about same length of gill. Pair of retractor muscles of buccal mass (m2). Further simplification of pair of main dorsal tensor muscles of radula (m4) to a single bundle each; connected to tissue in radular ribbon via ligaments and a direct connection with its pair. Pair of salivary glands opening in anterior region of buccal mass. Middle esophagus with a conspicuous pair of folds. Loss of esophageal lateral pouches and respective vessels. Prostate in pallial spermoduct. Nerve ring positioned totally posterior to buccal mass. Pair of pleural ganglia positioned close to cerebral ganglia, *i.e.,* epiathroid condition. Pair of buccal ganglia situated far from each other.

Etymology: the epithet refers to the epiathroid condition of the central nervous system, *i.e.,* the closure between the pair of pleural ganglia to the cerebral ganglia.
List of included taxa: Viviparoidea + Sorbeoconcha.

3a. Viviparoidea Gray, 1847 (node 15)

Diagnosis: Shell multispiral, with tall spire, deep suture. Operculum with an upper-inner projection. Gill filaments long for filter-feeding. Endostyle in right side of gill. Salivary gland as two separated masses Right tentacle as copulatory organ and closed (tubular) vas deferens (Simone, 2004a).
List of included taxa: Viviparidae.

3b. Sorbeoconcha Ponder & Lindberg, 1997 (node 18)

Diagnosis: Loss of head-foot inhalant siphons. Dorsal chamber of buccal mass reduced (shallow). Insertion of esophagus in middle level of stomach. Reappearance of stomach style sac. Males with convoluted seminal vesicle. Reversion to an opened pallial vas deferens. Bursa copulatrix located at posterior level of pallial oviduct. Approximation between cerebro-pedal and pleuro-pedal connectives.
List of included taxa: Cerithioidea + Hypsogastropoda.

4a. Cerithioidea Flemming, 1822 (node 19)

Synonymy: Campaniloidea Douvillé, 1904; Vermetoidea Rafinesque, 1815.
Diagnosis: Shell normally turriform with determinated growth; with anterior canal. Reversion to a spiral sculptured operculum. Mantle border with a series of papillae. Reversion to a hypobranchial gland thick, with sub-chambers. Reduction to an opened condition of pallial oviduct. Presence of a head-foot furrow running along right side, from female genital pore to right side of foot. Marine environment (Simone, 2001a).
List of included taxa: Cerithiidae, Batillariidae, Cerithideidae, Litiopidae, Modulidae, Pachychilidae, Planaxidae, Pleuroceridae, Potamididae, Siliquariidae, Thiaridae, Turritellidae, Campanilidae, Vermetidae and others.

4b. Hypsogastropoda Ponder & Lindberg, 1997 (node 38)

Diagnosis: nephridial gland. Loss of pair of auxiliary muscle (m12) of horizontal muscle (m6). Exophalic penis situated behind and at right from right cephalic tentacle, with respetive duct. Development of albumen and capsule glands at pallial oviduct. Each statocysts with single statolith.
Etymology: the epithet refers to the exophalic penis (peo = penis).
List of included taxa: Rissooidea + Strombogastropoda; some Ptenoglossa.

5a Rissooidea Gray, 1847 (node 41)

Synonymy: Littorinoidea Children, 1834.
Diagnosis: Shell normally globose. Reversion to a spiral sculptured operculum. Ommatophore. Short pallial cavity. Osphradium shortened to less than half of gill length. Reduction of dorsal folds of buccal mass. Total loss of ventral tensor muscles (m11). Very long radular sac. Rachidian basal cusps. Broad central pad in stomach. Wide pallial prostate (equivalent to oviduct). Pallial vas deferens and penis duct closed (tubular), located relatively far from right tentacle (Simone, 2004a, 2006b).
List of included taxa: Rissoinidae, Rissoidae, Hydrobiidae, Littorinidae, Annulariidae, Anabathridae, Barleeidae and others.

5b Strombogastropoda (new) (node 46)

Synonymy: Neomesogastropoda Bandel, 1991 (in part, if includes Neogastropoda); Pleurembolica Bandel, 2000 (in part, if includes Naticoidea and Cypraeoidea).

Diagnosis: Pair of retractor muscles of snout. Operculum ovoid or elliptic with eccentric nucleus, smaller than shell aperture. Enlargement of mantle border, covering head during activity. Auricle attached to inner surface of anterior wall of pericardium. Odontophore muscle pair m7 inserting as a single bundle. Radula with sharp pointed apex of marginal teeth (Simone, 2005a).
Etymology: the epithet refers to the first branch of the taxon, the Stromboidea.
List of included taxa: Stromboidea + Rhynchogastropoda.

5c *Incertae sedis:* Some Ptenoglossa (Eulimidae); *"Amauropsis" rossiana*

N.B.: Despite the clear allocation of *Annulobalcis aurisflamma* (Eulimidae, a Ptenoglossa) and *"Amauropsis" rossiana* at the cladogram, the study on the higher taxa that they belong is still in progress. Then, no taxonomic treatment is given to these branches.

6a. Stromboidea Rafinesque, 1815 (node 47)

Synonymy: Xenophoroidea Troschel, 1852.
Diagnosis: Shell fusiform with determinated growth. Incurrent shell canal. Englarmement of distance between head base and furrow of pedal gland. Septum separating haemocoel from visceral cavity muscular constituted. Terminal nucleus of operculum. Pallial tentacle in front of anus. Reversion to a thick hypobranchial glans. Loss of pair of longitudinal folds in middle esophagus. Bursa copulatrix of females situated in anterior region of pallial oviduct, originating from genital pore. Females with furrow running in the right side of the head-foot, originating from genital pore.
List of included taxa: Strombidae, Xenophoridae, Aporrhaidae, Struthiolariidae.

6b. Rhynchogastropoda (new) (node 66)

Diagnosis: Osphradium of bipectinate type, with filaments connected directly by side of osphradial ganglion of elliptical outline. Osphradium length shorter than half of that of gill. Proboscis of pleurembolic type, with retractor muscles well-developed. Oral tube long. Both buccal ganglia situated close to one another.
Etymology: the epithet refers to the proboscis, from the Greek *rhynchos,* meaning snout.
List of included taxa: Calyptraeoidea + Adenogastropoda.

7a. Calyptraeoidea Lamarck, 1809 (node 67)

Synonymy: Capuloidea Fleming, 1822; Vanikoroidea Gray, 1840; Hipponicoidea Troschel, 1861.
Diagnosis: Hairy periostracum. Nuchal flaps in both sides of head. Salivary ducts relatively long and free from nerve ring. Loss of pair of longitudinal folds in middle esophagus. Protandrous hermaphroditism (Simone, 2002).
List of included taxa: Calyptraeidae, Capulidae, Hipponicidae, Trichotropidae, Vanikoridae.

7b. Adenogastropoda (new) (node 96)

Diagnosis: Shell with spire normally shorter than half of aperture length. Enlargement of hypobranchial gland. Pair of retractor muscles of buccal mass inserting close to radular sac. Accessory pair of ventral protractor muscles of buccal mass (m14). Middle esophageal gland isolated in a large ventral diverticle, constituted by transverse septa. Reversion to a posterior inserted esophagus in stomach. Loss of crystalline style sac. Stomach narrow. Females with bursa copulatrix positioned in anterior region of pallial oviduct.
Etymology: the epithet refers to the esophageal gland, from Greek *adenos* (gland).
List of included taxa: Naticoidea + Siphonogastropoda.

8a. Naticoidea (Guilding, 1834) (node 97)

Diagnosis: Shell globose. Reversion to spiral sculptured operculum, occupying entire shell aperture. Reduction of pallial siphon. Accessory boring organ located at ventral region of proboscis tip.

List of included taxa: Naticidae.

8b. Siphonogastropoda (new) (node 117)

Diagnosis: Shell with determinate growth and anterior siphonal canal. Development of a pallial siphon. Insertion of pair of proboscis retractor muscle approximately in middle level of proboscis. Stomach approximately cylindrical, with almost same width of adjacent regions of esophagus and intestine, and "U" shaped.
Etymology: the epithet refers to the development of the pallial siphon.
List of included taxa: Cypraeoidea + Peogastropoda.

9a. Cypraeoidea Rafinesque, 1815 (node 118)

Synonymy: Velutinoidea Gray, 1840; Lamellarioidea d'Orbigny, 1841.
Diagnosis: Shell involute. Loss of adult operculum. Mantle lobe covering most of outer surface of shell. Part of pericardium lying dorsal to gill. Auricle connecting subterminally to ctenidial vein. Duplication of horizontal muscle (m6) of odontophore (Simone, 2004b).
List of included taxa: Cypraeidae, Eratoidae, Lamellariidae, Ovulidae, Pediculariidae, Triviidae, Velutinidae.

9b. Peogastropoda (node 148)

Diagnosis: Shell fusiform. Operculum with terminal nucleus. Elongation of pallial siphon, becoming exploratory. Elongation of pleurembolic proboscis. Salivary gland as two separated masses. Predatory behavior.
List of included taxa: Tonnoidea + Neogastropoda.

10a. Tonnoidea Suter, 1913 (node 149)

Synonymy: Ficoidea Meek, 1864.
Diagnosis: Long distance between head base and furrow of pedal gland. Septum separating haemocoel from visceral cavity muscular. Insertion of m4 in the tissue on the radula preceding its exposed (in use) portion in buccal cavity muscular. Enlargement of salivary glands.
List of included taxa: Tonnidae, Bursidae, Cassidae, Ficidae, Personiidae, Ranellidae, Cymatiidae.

10b. Neogastropoda Wenz, 1938 (node 178)

Synonymy: Stenoglossa Bouvier, 1887.
Diagnosis: Shell with spire normally tall. Loss of accessory pair of protractor muscles of odontophore (m14). Lateral radular teeth different shaped from rachidian. Salivary glands free from nerve ring. Gland of middle esophagus acinar, connected to esophagus via duct.
List of included taxa: Conoidea + Muricoidea-Cancellarioidea.

11a. Conoidea Fleming, 1822 (node 179)

Diagnosis: Shell normally thick walled. Reduction of odontophore and midesophagus. Esophageal gland elongated (venom gland), with muscular bulb at distal end, inserted close to nerve ring. Rinchodeal wall weakly muscular and not exteriorized.
List of included taxa: Conidae, Terebridae, "Turridae" s.l.

11b. Muricoidea Rafinesque, 1815 – **Cancellarioidea** Forbes & Hanley, 1851 (node 210)

Diagnosis: Loss of radular marginal teeth. Valve of Leiblein.
List of included taxa: Muricoidea l.s. (*sensu* Ponder, 1974), *i.e.,* Buccinidae, Colubrariidae, Columbellidae, Fasciolariidae, Nassariidae, Melongenidae, Muricidae, Babyloniide, Costellariidae, Cysticidae, Harpidae, Marginellidae, Mitridae, Turbinellidae, Volutidae, Volutomitridae, Olividae, "Pseudolividae"; Cancellariidae.

Synopsis:

1. Class Gastropoda (node H)
  1.1. Patellogastropoda
  1.2. Orthogastropoda (node I)
  1.3. *Incertae sedis:* **Cocculiniformia** (node J)
    1.2.1. Vetigastropoda (node L)
    1.2.2. Adenogonogastropoda (new) (node T)
      1.2.2.1. Neritimorpha (node U)
      1.2.2.2. Apogastropoda (node W)
        1.2.2.2.1. Heterobranchia (node V)
        1.2.2.2.2. Caenogastropoda Cox, 1960a (node 1)
1a. Cyclophoroidea Gray, 1847 (node 2)
1b. Hydrogastropoda (new) (node 4)
  2a. Ampullarioidea Gray, 1824 (node 5)
  2b. Epiathroidea (new) (node 14)
    3a. Viviparoidea Gray, 1847 (node 15)
    3b. Sorbeoconcha Ponder & Lindberg, 1997 (node 18)
      4a. Cerithioidea Flemming, 1822 (node 19)
      4b. Hypsogastropoda Ponder & Lindberg, 1997 (node 38)
        5a Rissooidea Gray, 1847 (node 41)
        5b Strombogastropoda (new) (node 46)
        5c *Incertae sedis:* **Some Ptenoglossa**
          6a. Stromboidea Rafinesque, 1815 (node 47)
          6b. Rhynchogastropoda (new) (node 66)
            7a. Calyptraeoidea Lamarck, 1809 (node 67)
            7b. Adenogastropoda (new) (node 96)
              8a. Naticoidea *Incertae sedis:* (Guilding, 1834) (node 97)
              8b. Siphonogastropoda (new) (node 117)
                9a. Cypraeoidea Rafinesque, 1815 (node 118)
                9b. Peogastropoda (new) (node 148)
                  10a. Tonnoidea Suter, 1913 (node 149)
                  10b. Neogastropoda Wenz, 1938 (node 178)
                    11a. Conoidea Fleming, 1822 (node 179)
                    11b. Muricoidea Rafinesque, 1815 – **Cancellarioidea** Forbes & Hanley, 1851 (node 210)