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**Taxonomical study on the Vetigastropoda (Mollusca) from Canopus Bank, NE Brazil,  
with further remarks on their distribution along the Western Atlantic**

São Paulo  
2017

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Dissertação apresentada ao Programa de Pós-Graduação em Sistemática, Taxonomia Animal e Biodiversidade do Museu de Zoologia da Universidade de São Paulo como pré-requisito para obtenção do título de Mestre.

Orientador: Prof. Dr. Luiz Ricardo Lopes de Simone

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*To my beloved wife,  
my parents, and family*

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## ABSTRACT

A taxonomic revision of 29 species distributed in 12 vetigastropod families collected in a 60-260 m depth range at Canopus Bank, a seamount off NE Brazil, is performed based on detailed shell morphology. Their distribution and bathymetric ranges are re-examined based on specimens from Canopus and the MZSP collection. Three possibly new species are revealed and tentatively described: *Arene* aff. *brareus* can be distinguished by a large shell for the genus; sculpture consisting of spiral cords ornamented by large, semi-hollow, scale-like spines; cords separated by equally wide, deep interspaces and thin axial growth lines more visible in the interspaces; protoconch sculptured by small, subsutural axial lamellae; and color ranging from white to intense reddish, darker on spiral cords, and lighter at the base, with a yellow apex. *Parviturbo* aff. *tuberculosis* can be told apart from local congeners by its slightly taller than wide shell, which is profusely sculptured by a reticulate pattern of equally strong axial ribs and spiral cords, with angular nodules at the intersections. *Calliostoma* sp.1 shows no close affinities with any other local congener and is characterized by a small shells with convex whorls and a large, rounded apex; ivory white ground color with honey yellow apex and spiral cords; sculpture consisting of 4-6 narrow, nodulous spiral cords per whorl; suture marked by a suprasutural cord; inflated and mostly smooth base; narrow, shallow, and axially sculptured umbilicus. Moreover, three species have their distributions expanded northward from SE to NE Brazilian waters: *Emarginula suspira* Simone & Cunha, 2014, *Hemimarginula hemitoma* Simone & Cunha, 2014, and *Homalopoma boffi* Marini, 1975. Three species have their northern range limit expanded from Bahia state to Ceará state: *Arene flexispina* Leal & Coelho, 1985 and *Turbo heisei* Prado, 1999; a single NE Brazilian species is newly reported from northern waters: *Haplocochlias risoneideneryae* Barros, Santos, Santos, Cabral & Acioli, 2002; and another species, previously known only from Pernambuco state, is newly reported from Ceará state, also in NE Brazil: *Solariella quinni* Barros & Pereira, 2008. Two Caribbean species are firstly reported in the SW Atlantic: *Dentistyla dentifera* (Dall, 1889) and *Gaza* cf. *fischeri* (Dall, 1889); and a species previously reported from the Venezuelan shelf is firstly recorded in Brazilian waters: *Parviturbo annejoffeae* Rubio, Rolán & Lee, 2015. The bathymetric ranges of 11 species are expanded. High-resolution photographs of the type specimens, SEM images, and comparisons with local congeners are also provided.

**Keywords:** Diversity; Gastropoda; Revision; Seamount; Zonation.

## RESUMO

Uma revisão taxonômica de 29 espécies distribuídas em 12 famílias de vetigastropodes coletadas a 60-260 m de profundidade no Banco de Canopus, uma montanha submarina do Nordeste do Brasil, é fornecida com base na morfologia detalhada da concha. Sua distribuição e intervalos batimétricos são reexaminados com base em espécimes de Canopus e da coleção do MZSP. Três espécies possivelmente novas são reveladas e tentativamente descritas: *Arene* aff. *briareus* pode ser distinguido por uma concha grande para o gênero; escultura constituída por cordas espirais ornamentadas por espinhos grandes, semi-ocos e escalares; cordas separadas por intervalos igualmente amplos e profundos e linhas de crescimento axiais finas mais visíveis nos inter-espacos; protoconcha esculpura por pequenas lamelas axiais subsuturais; e cor variando de branco a avermelhado intenso, mais escura nas costelas espirais, e mais clara na base, com um ápice amarelo. *Parviturbo* aff. *tuberculosis* pode ser distinguida dos congêneres locais pela sua concha mais alta do que larga, profusamente esculpura por um padrão reticulado de costelas axiais igualmente fortes e cordas espirais, com nódulos angulares nas intersecções. *Calliostoma* sp.1 não apresenta estreitas afinidades com qualquer outro congêner local e é caracterizado por uma concha pequena com voltas convexas e um grande ápice arredondado; cor branco-marfim com ápice e cordas espirais amarelo mel; escultura de 4-6 cordas espirais estreitas e nodulosas por volta; sutura marcada por um cordão suprasutural; base inflada e lisa; umbílico estreito, raso e axialmente esculpura. Três espécies têm suas distribuições expandidas para o norte, de águas do SE para o NE do Brasil: *Emarginula suspira* Simone & Cunha, 2014, *Hemimarginula hemitoma* Simone & Cunha, 2014, e *Homalopoma boffi* Marini, 1975. Três espécies têm seu limite de extensão norte expandido da Bahia para o Ceará: *Arene flexispina* Leal & Coelho, 1985 e *Turbo heisei* Prado, 1999; Uma única espécie brasileira do NE é relatada para águas do Norte: *Haplocochlias risoneideneryae* Barros, Santos, Santos, Cabral & Acioli, 2002; E uma outra espécie, anteriormente conhecida apenas do estado de Pernambuco, é reportada para o estado do Ceará: *Solariella quinni* Barros & Pereira, 2008. Duas espécies caribenhas são registradas pela primeira vez no Atlântico sudoeste: *Dentistyla dentifera* (Dall, 1889) e *Gaza* cf. *fischeri* (Dall, 1889); e uma espécie reportada previamente para a plataforma venezuelana é registrada pela primeira vez no Brasil: *Parviturbo annejoffeae* Rubio, Rolán & Lee, 2015. As distribuições batimétricas de 11 espécies são expandidas. Fotografias dos espécimes tipo, imagens MEV e comparações com congêneres locais são fornecidas.

**Palavras-chave:** Diversidade; Gastropoda; Montanha submarina; Revisão; Zonação.



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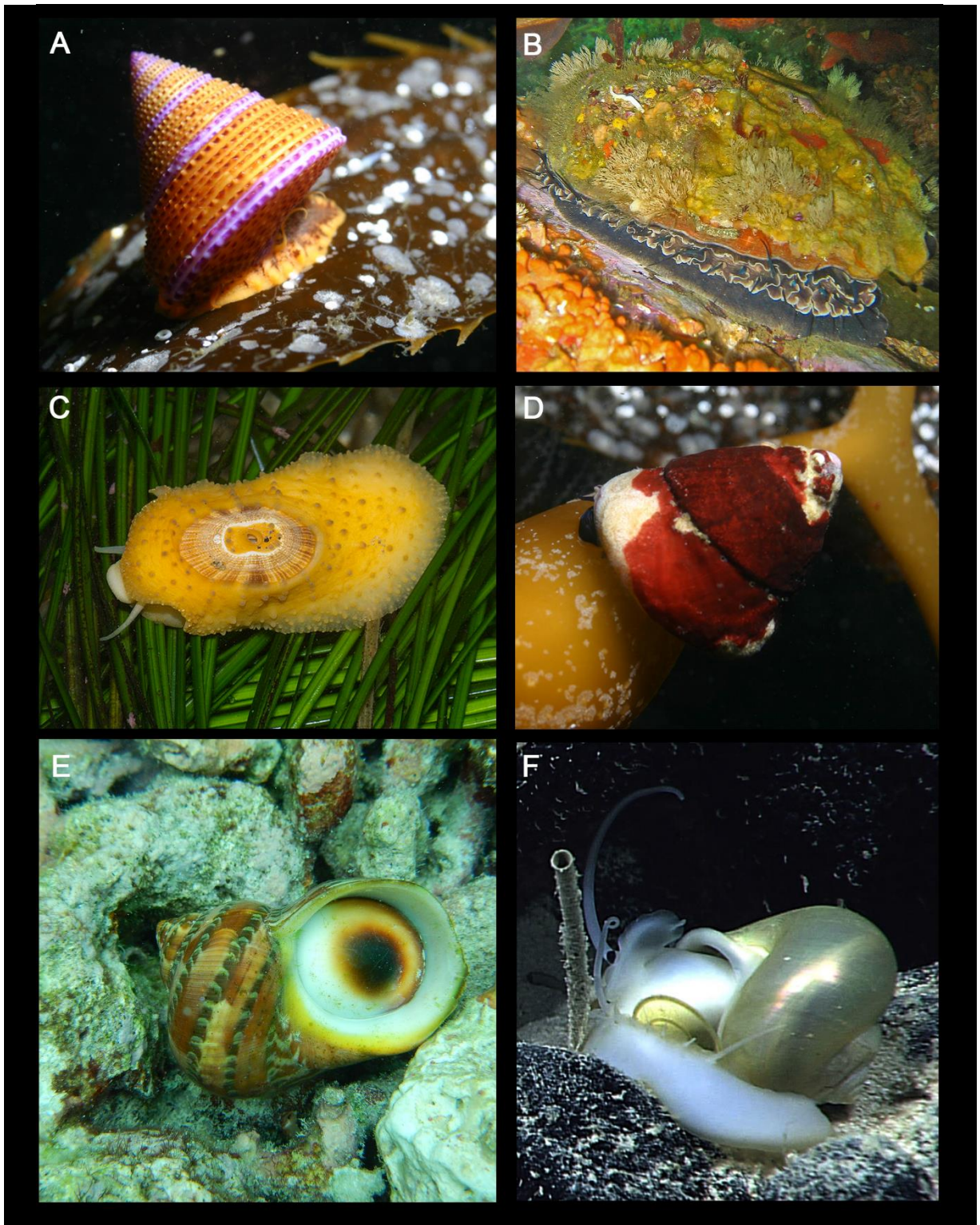
# 1. INTRODUCTION

## 1.1 Vetigastropoda

Vetigastropoda is a large and ancient gastropod clade comprising over 3,700 exclusively marine species. The group's shell morphology is incredibly diverse, encompassing limpet-like, calyptraeiform, neritiform, trochiform, biconical, and turbinoid shapes, and may bear forams, slits or other similar openings (Geiger et al., 2008). Some of the most familiar animals (Fig. 1) include turban shells (family Turbinidae), top-snails (Trochidae), abalones (Haliotidae), key-hole limpets (Fissurellidae), pheasant shells (Phasianellidae), and slit snails (Pleurotomariidae); their less-known kin are the deep-water seguenzioides (e.g., Seguenziidae, Calliotropidae), and hot-vent taxa (e.g., Lepetodrilidae, Sutilizonidae) (Geiger et al., 2008; Aktipis & Giribet, 2012).

An astounding adaptation to a wide assortment of marine environments from intertidal areas to abyssal depths, including harsher surroundings such as hydrothermal vents (Geiger et al., 2008; Aktipis & Giribet, 2012), made vetigastropod feeding habits correspondingly varied. While the majority of species are herbivores, feeding on periphyton, algae and marine angiosperms, there are filter feeders and species that feed on detritus and bacterial film. Some are even specialized carnivores, and their prey include foraminiferans, poriferans, and cnidarians (Hickman, 1988; Geiger et al., 2008). Likewise, reproductive strategies have become quite diverse in the Vetigastropoda, from broadcast spawners to species that lay eggs in gelatinous masses or in fewer numbers on particular substrata (Hickman, 1992; Geiger et al., 2008).

The earliest vetigastropods appeared in the Paleozoic, most probably in the Cambrian/Ordovician boundary (~488 Ma), judging by a rich fossil record. Teleoconch features such as the outline, presence of a narrow sinus, slits, and selenizones are usually employed to typify fossilized basal vetigastropod shells (Frýda et al., 2008). Other features such as the presence of a nacreous layer or the absence of a second-stage protoconch associated with specific



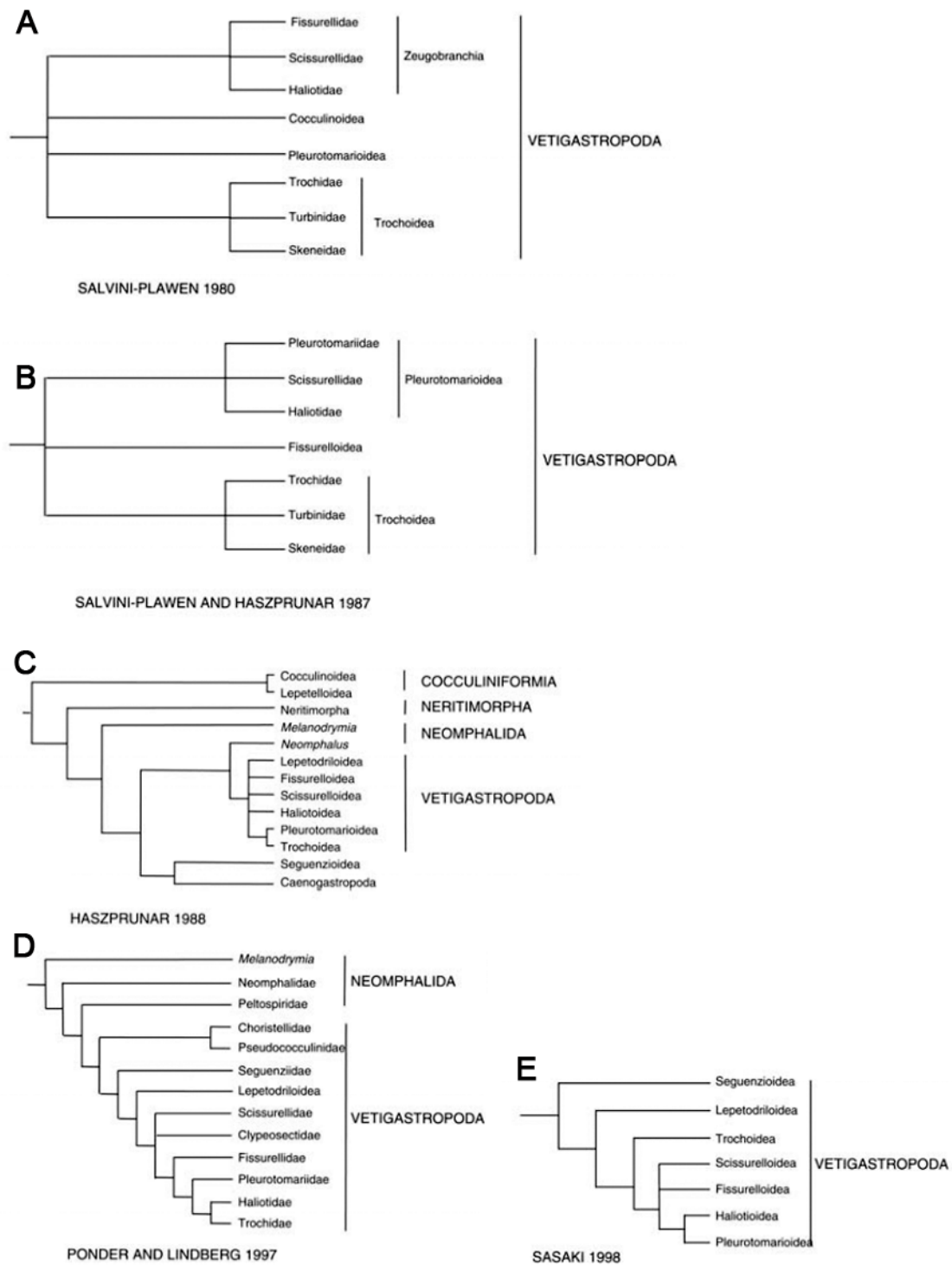
**Figure 1:** Vetigastropod diversity. **A.** *Calliostoma annulatum* (Lightfoot, 1786), family Calliostomatidae (public domain image); **B.** *Haliotis rufescens* Swainson, 1822, Haliotidae (public domain image); **C.** *Fissurellidea bimaculata* Dall, 1871, Fissurellidae (photo by Marlin Harms); **D.** *Tegula brunnea* (Philippi, 1848), Tegulidae (public domain image); **E.** *Turbo petholatus* Linnaeus, 1758, Turbinidae (photo by Frédéric Ducarme); **F.** *Gaza daedala* Watson, 1879 (public domain image).

larval development modes were often used as well (Bandel, 1997), but then again some of these features are shared with other mollusk groups, and their usage for such purpose is somewhat controversial (Frýda et al., 2008). Regardless, most of the specimens that can be safely associated with extant families date from the Mesozoic (Geiger et al., 2008). Vetigastropod diversity increased significantly in the Early Ordovician, reaching its peak in the Devonian and suffering great loss in the Permian-Triassic extinction event (252 Ma). A recovery followed in the Triassic, with the emergence of trochoideans and other smaller lineages. The group was yet again greatly affected by the Triassic-Jurassic mass extinction (201 Ma) but has since then remained stable in terms of family numbers (Sepkoski & Hulver, 1985; Erwin, 1990).

In addition to being a food source for humans, vetigastropods and their shells are often sought for their nacre (mother of pearl), used as decoration or in handicraft. Either fished by tons or even farmed, animals such as abalones (family Haliotidae, Fig. 1B) constitute a relevant part of the economy in many countries (Freeman, 2001). These facts also help explain why these animals have been extensively investigated by science, and are, in fact, one of the most frequently studied mollusk groups (Geiger et al., 2008).

### **1.1.1 Taxonomy and phylogeny**

Vetigastropoda was broadly investigated and redefined since being first introduced in the 1980s (Salvini-Plawén, 1980). Despite the fact that its monophyly has been recognized by a plethora of morphological and molecular studies (e.g., Ponder & Lindberg, 1997; Sasaki, 1998; Geiger & Thacker, 2005; Kano, 2008; Williams et al., 2008; Uribe et al., 2015), the group's taxonomic rank changed a few times over the years. Since its introduction, Vetigastropoda was traditionally ranked as a suborder of the Archaeogastropoda Thiele, 1925, a group now widely recognized as paraphyletic (Lindberg, 2008; Gofas, 2009c). Ponder & Lindberg (1997) considered it as a superorder belonging to their subclass Orthogastropoda (also non-monophyletic by recent standards; Zapata et al., 2014). In their wide-ranging nomenclatural revision, Bouchet et al. (2005) rebutted Ponder & Lindberg's (1997) classification, referring to Vetigastropoda as an unranked clade. It has been treated as such in recent



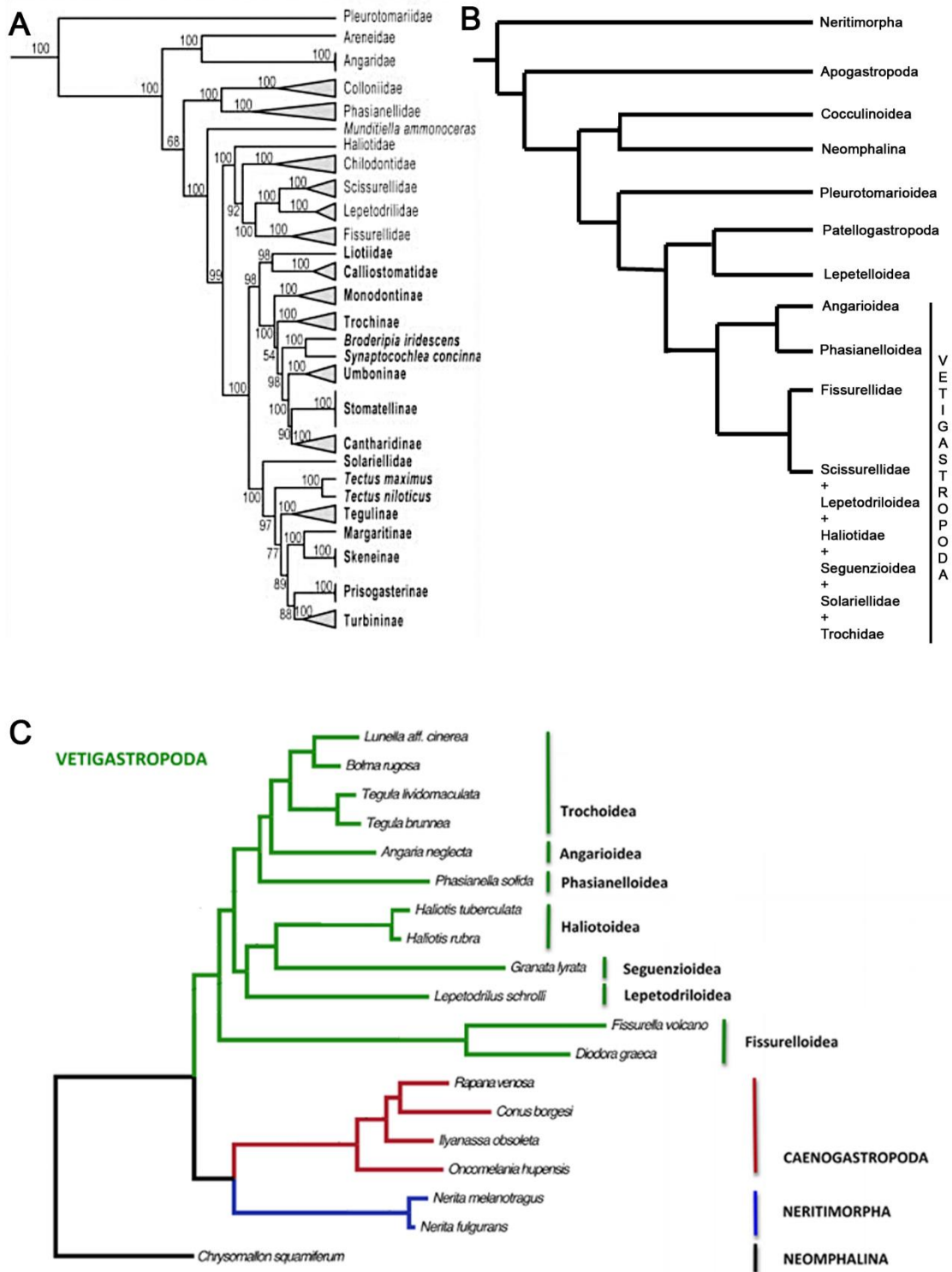
**Figure 2:** Morphology-based phylogenetic hypotheses of Vetigastropoda. **A.** After Salvini-Plawen (1980); **B.** After Salvini-Plawen & Haszprunar (1987) **C.** After Haszprunar (1988); **D.** After Ponder & Lindberg (1997). **E.** After Sasaki (1998). Extracted and modified from Aktipis & Giribet (2012).

systematics works (e.g., Williams, 2012; Uribe, 2015) and the matter is unresolved, even though the World Register of Marine Species database currently ranks it as a subclass of Gastropoda, without any support of published material.

Added to the wide variety of shell shapes, the internal morphology of Vetigastropoda is correspondingly quite diverse, and, naturally, reaching a consensus on a general characterization of the group is a problematic task at best. This becomes evident when observing the dissimilar topologies resulting from morphological analyses (Fig. 2), which differ expressively among themselves. Furthermore, such studies have pointed different characters as synapomorphies of Vetigastropoda over the course of time. For instance, Salvini-Plawen & Haszprunar (1987) listed the ctenidial sense organs (or bursicles), esophageal structures (specialized tissues and papillae), epipodial sensory organs, position and structure of the osphradia, and chromosomal arrangement as synapomorphic characters. Ponder & Lindberg (1997) cited the position of the renal organs on either side of the pericardium, absence of a nephridial gland, ctenidial bursicles, sensory papillae, multiple statoconia; and Sasaki (1998) enumerated the epipodial sensory organs, expanded esophageal pouches, fimbriate anterior edge of the jaw, papillate esophageal glands, and paired kidneys on either side of the pericardium as synapomorphies, also citing micropapillae on the tentacles, posterior depressor muscles, five pairs of lateral teeth, paired auricles and the transverse pallial vein as possible synapomorphies depending on character optimization. Although there is little apparent consensus, the ctenidial bursicles and epipodial sensory structures appear as synapomorphies in most cases. A summary of these and additional characters from the phylogenies was presented by Geiger et al. (2008; tab. 12.2), and brief discussions on several characters were provided by Simone (2011) in a broader context.

As molecular techniques emerged, several molecular phylogenies of Vetigastropoda were published. Unsurprisingly, earliest published topologies agreed very little, displaying widely different relationship hypotheses (e.g., Geiger & Thacker, 2005; Williams & Ozawa, 2006; Kano, 2007). This dissimilarity was initially attributed to insufficient taxon sampling, and a low number of analyzed genes or base pairs (Geiger et al., 2008). Consequently, subsequent approaches (Fig. 3) sought to remediate these issues by including more analyzed loci and widening taxon sampling, e.g., Williams et al. (2008) sampled 162 terminals; Aktipis & Giribet (2010) analyzed 7 different loci and sampled 31 ingroup taxa; Aktipis & Giribet (2012) analyzed 6 kb from 5 different loci, and sampled 69 terminals. Alternatively, more recent methods





**Figure 3:** Molecular-based phylogenetic hypotheses of vetigastropod relationships. **A.** Simplified topology after Williams et al. (2008); **B.** Redrawn and simplified topology after Aktipis & Giribet (2012); **C.** Extracted and simplified topology after Uribe (2015).

such as mitogenomics, have begun to be employed to produce hypotheses for Vetigastropoda (Uribe et al., 2015). Nevertheless, the resulting topologies are still very discrepant. Wort et al. (2016), while examining the use of mitochondrial markers in phylogenetic studies on Vetigastropoda, cautioned against the careless use of these markers, as diverse marker combinations produced drastically different topologies in their own analysis. This may at least partially explain the different topologies obtained by the studies published so far, and it is clear that more work is necessary in order to resolve vetigastropod relationships.

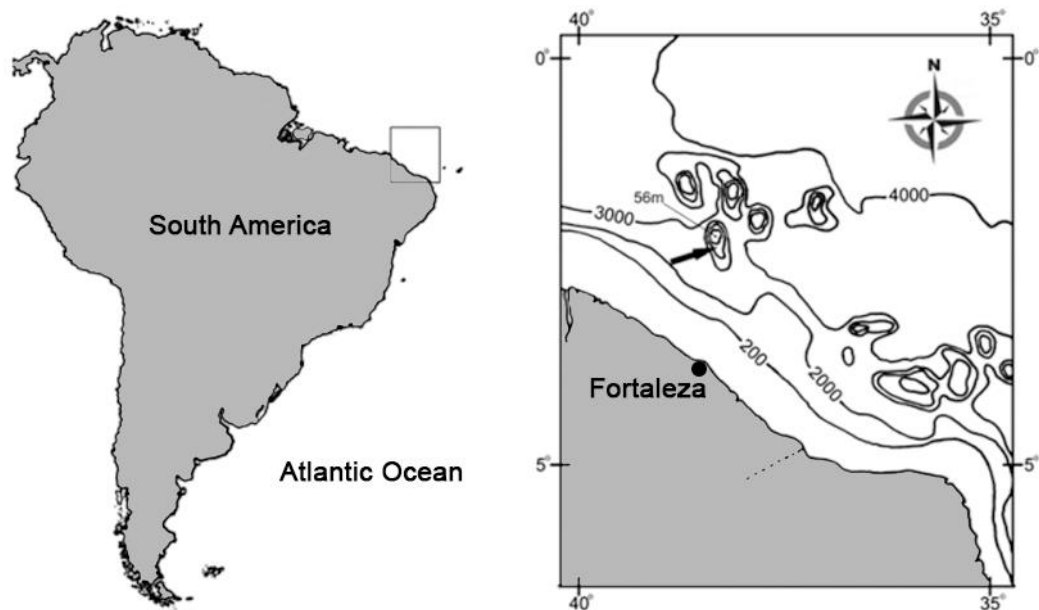
## **1.2 Brazilian seamounts and mollusk diversity**

Seamounts are undersea elevations rising from the seabed to waters below sea level, having a relatively restrict summit area. These topographic features often reach over a thousand meters bottom to top and may present particular and intricate surface structures such as calderas, terraces, pit craters, canyons, etc., which provide rich, complex habitats (Vieira et al., 2010). In fact, seamounts are a common feature in the world's oceans and harbor a richly diverse and often highly endemic part of the marine biota (Stocks, 2004). They often suffer greatly from the intense commercial fishery, which causes severe impact on local species (Morato et al., 2004; 2006). Despite that, and even though there are thousands of seamounts around the globe, few (~300) have been thoroughly sampled and studied, and many questions regarding these interesting environments are still beginning to be answered (Santana & Tavares, 2008; Schlacher et al., 2010).

The Brazilian seamounts are mainly clustered off the coast of Ceará state, the Fernando de Noronha Chain, and off Bahia state in northeastern waters, the Vitória-Trindade Chain in the southeast, and the Rio Grande Rise in the south (Vieira et al., 2010). They are no exception to the “general rules” of being poorly known and overfished. The faunal diversity of Brazilian seamounts is mostly known from isolated surveys carried out in the 19<sup>th</sup> and 20<sup>th</sup> centuries (e.g., Challenger, Calypso, and Branner-Agassiz expeditions), and, more recently, from the REVIZEE project, which was not focused on seamounts (Coelho-Filho, 2006). Fortunately, however, scientific attention has been increasingly drawn to these sites. Recent studies on species

from Brazilian seamounts have been published, mostly describing new invertebrates (e.g., Santana & Tavares, 2008; Vieira et al., 2010).

Deep-sea and shelf-dwelling mollusks have received particular attention in Brazil as of late, and many new species have emerged from recent studies (e.g., Simone & Cunha, 2008; Fernandes et al., 2013; Cavallari et al., 2014; Simone, 2014; Simone & Cunha, 2014). A notable case is a Brazilian-French expedition, Marion Dufresne MD55, which conducted an extensive sampling along the Vitória-Trindade Chain in SE Brazil (see Tavares, 1999, for details). This sampling resulted in several papers on mollusks (some cited above), with dozens of new species, and much of this material is still being studied. Nevertheless, apart from the MD55, the Brazilian mollusk fauna from seamounts along the coast remains largely unknown, except perhaps for a small point outside of the curve: Canopus Bank.



**Figure 4:** Seamount cluster off Ceará state; arrow indicates the location of Canopus Bank, the site studied in the present work. Extracted and modified from Andrade et al. (2011).

Canopus Bank is a seamount located ~190 km off the capital city of Fortaleza (Fig. 4), Ceará state, in NE Brazilian waters ( $02^{\circ}14'25''\text{S}$ ,  $38^{\circ}22'50''\text{W}$ ), which is known to harbor a highly diverse mollusk fauna. The study of relatively limited sediment samples collected in

2005 by a team of fishermen, naturalists and malacologists has resulted in an impressive amount of published material describing new gastropod species (e.g., Simone, 2005; Simone & abate, 2005; Cossignani, 2006; Costa & Simone, 2006; Simone, 2006; Pimenta et al., 2008; Cunha, 2011; Andrade et al., 2011; Costa & Pastorino, 2012; Costa & Pimenta, 2012; Abbate & Cavallari, 2013; Simone & Cunha, 2014; Fernandes et al., 2015). To date, 17 new gastropod species belonging to 12 different families have been described from Canopus, four of which are vetigastropods (Tab. 1).

Even though many new species from Canopus were described since 2005, more comprehensive studies on the local fauna are still lacking. While the local species diversity appears to be very high based on the sheer amount of published material, no checklists or large taxonomical studies focused on Canopus have been published to date. It is clear that studies dedicated to entire mollusk groups are needed to better understand, and thoroughly describe the local diversity. Such studies would allow for effective comparisons with faunas from the Caribbean and especially the remaining Brazilian seamounts. In that regard, according to Spalding's (2007) biogeographical hypothesis, Canopus is close to the Northeastern Brazil Ecoregion, within the Tropical Southwestern Atlantic province. Nearby Oceanic Islands (and surrounding seamounts) such as Fernando de Noronha and Trindade & Martim Vaz were placed in homonymous isolated ecoregions, based on a wide understanding of the local biodiversity (among many other characteristics). The numerous studies published to date have shown that Canopus may harbor many endemic species. Consequently, the faunal composition may as well be very distinct from the nearest coastal-shelf fauna from off Ceará, and other seamounts, which reinforces the necessity of broader studies.

**Table 1:** Gastropod species described from Canopus Bank, organized by year of description (2005-2015), with indications to clades and families.

<b>Taxa</b>	<b>Clade</b>	<b>Family</b>
<i>Diptychophlia hubrechtii</i> Cunha, 2005	Neogastropoda	Turridae
<i>Hipponix climax</i> Simone, 2005	Caenogastropoda	Hipponicidae
<i>Pedicularia tibia</i> Simone, 2005	Caenogastropoda	Pediculariidae
<i>Fasciolaria agatha</i> Simone & Abbate, 2005	Neogastropoda	Fasciolariidae
<i>Pedicularia bonfigliolii</i> Cossignani, 2006	Caenogastropoda	Pediculariidae
<i>Lucapina elisae</i> Costa & Simone, 2006	Vetigastropoda	Fissurellidae
<i>Inella unicornium</i> Simone, 2006	Caenogastropoda	Triphoridae
<i>Leptotrophon atlanticus</i> Pimenta, Couto & Costa, 2008	Neogastropoda	Muricidae
<i>Acteon mirim</i> Cunha, 2011	Heterobranchia	Acteonidae
<i>Opaliopsis cearense</i> Andrade, Costa & Pimenta, 2011	Caenogastropoda	Epitoniidae
<i>Notocochlis laurae</i> Costa & Pastorino, 2012	Caenogastropoda	Naticidae
<i>Pazinotus gili</i> Costa & Pimenta, 2012	Neogastropoda	Muricidae
<i>Nassarius levis</i> Abbate & Cavallari, 2013	Neogastropoda	Nassariidae
<i>Cranopsis canopa</i> Simone & Cunha, 2014	Vetigastropoda	Fissurellidae
<i>Cranopsis cearensis</i> Simone & Cunha, 2014	Vetigastropoda	Fissurellidae
<i>Cranopsis columbaris</i> Simone & Cunha, 2014	Vetigastropoda	Fissurellidae
<i>Trituba anubis</i> Fernandes, Garofalo & Pimenta, 2015	Caenogastropoda	Newtoniellidae

**Table 2:** Range and bathymetric expansion of the vetigastropods studied herein.

Taxon	Range exp.?	From-to	Bathym. exp.?	From-to
<b>Fissurellidae</b>				
<i>Cranopsis canopa</i>	No		Yes	250-260m
<i>Cranopsis cearensis</i>	No		Yes	250-260 m
<i>Diodora mirifica</i>	No		Yes	63-260 m
<i>Diodora sayi</i>	No		No	
<i>Emarginula suspira</i>	Yes	SE to NE Brazil	No	
<i>Hemimarginula hemitoma</i>	Yes	SE to NE Brazil	No	
<i>Lucapina aegis</i>	No		Yes	55-260 m
<i>Lucapina elisae</i>	No		No	
<i>Lucapinella limatula</i>	No		Yes	146-260 m
<b>Areneidae</b>				
<i>Arene brasiliana</i>	No		Yes	81-120 m
<i>Arene flexispina</i>	Yes	S Bahia to Ceará	No	
<i>Arene</i> aff. <i>briareus</i>				
<b>Colloniidae</b>				
<i>Homalopoma boffi</i>	Yes	SE to NE Brazil	No	
<i>Homalopoma linnei</i>	No		No	
<b>Phasianellidae</b>				
<i>Eulithidium affine</i>	No		No	
<b>Calliostomatidae</b>				
<i>Calliostoma hassler</i>	No		No	
<i>Calliostoma</i> sp. 1				
<b>Liotiidae</b>				
<i>Macrarene digitata</i>	No		Yes	146-260 m
<b>Margaritidae</b>				
<i>Callogaza watsoni</i>	No		No	
<i>Gaza</i> cf. <i>fischeri</i>	Yes	Caribbean to NE Brazil	No	
<b>Skeneidae</b>				
<i>Haplocochlias risoneideneryae</i>	Yes	NE to N Brazil	Yes	20-200 m
<i>Parviturbo rehderi</i>	No		No	
<i>Parviturbo annejoffeae</i>	Yes	Venezuela to Brazil	Yes	0-260 m
<i>Parviturbo</i> aff. <i>tuberculosis</i>				
<b>Turbinidae</b>				
<i>Turbo heisei</i>	Yes	S Bahia to Ceará	Yes	92-620 m
<b>Solariellidae</b>				
<i>Solariella carvalhoi</i>	No		No	
<i>Solariella quinni</i>	Yes	Pernambuco to Ceará	Yes	71-350 m
<b>Seguenziidae</b>				
<i>Ancistrobasis costulata</i>	No		No	
<b>Chilodontidae</b>				
<i>Dentistyla dentifera</i>	Yes	Barbados to NE Brazil	No	

**Table 3:** Minimum and maximum depths of species studied herein.

Taxon	Min depth	Live?	Max depth	Live?
<b>Fissurellidae</b>				
<i>Cranopsis canopa</i>	60	no	260	no
<i>Cranopsis cearensis</i>	60	no	260	no
<i>Diodora mirifica</i>	240	no	260	no
<i>Diodora sayi</i>	60	no	70	no
<i>Emarginula suspira</i>	240	no	260	no
<i>Hemimarginula hemitoma</i>	240	no	260	no
<i>Lucapina aegis</i>	240	no	260	no
<i>Lucapina elisae</i>	260	yes	260	yes
<i>Lucapinella limatula</i>	240	no	260	no
<b>Areneidae</b>				
<i>Arene brasiliana</i>	60	operc	260	no
<i>Arene flexispina</i>	240	no	260	no
<i>Arene aff. briareus</i>	200	no	260	no
<b>Colloniidae</b>				
<i>Homalopoma boffii</i>	60	no	260	no
<i>Homalopoma linnei</i>	60	no	260	yes
<b>Phasianellidae</b>				
<i>Eulithidium affine</i>	260	no	260	no
<b>Calliostomatidae</b>				
<i>Calliostoma hassler</i>	60	no	60	no
<i>Calliostoma sp. 1</i>	60	yes	260	no
<b>Liotiidae</b>				
<i>Macrarenne digitata</i>	240	no	260	no
<b>Margaritidae</b>				
<i>Callogaza watsoni</i>	260	no	260	no
<i>Gaza cf. fischeri</i>	260	no	260	no
<b>Skeneidae</b>				
<i>Haplocochlias risoneideneryae</i>	200	no	200	no
<i>Parviturbo rehderi</i>	240	no	260	no
<i>Parviturbo annejoffeae</i>	240	no	260	no
<i>Parviturbo aff. tuberculosus</i>	240	no	260	no
<b>Solariellidae</b>				
<i>Solariella carvalhoi</i>	240	no	260	no
<i>Solariella quinni</i>	240	no	260	no
<b>Turbinidae</b>				
<i>Turbo heisei</i>	60	no	260	no
<b>Seguenziidae</b>				
<i>Ancistrobasis costulata</i>	200	no	260	no
<b>Chilodontidae</b>				
<i>Dentistyla dentifera</i>	60	no	260	operc

## 4.2 Concluding remarks

The specimens studied herein reveal that the vetigastropod fauna from Canopus is quite diverse, adding up to 29 species distributed in 12 different families, three of which are possibly new. In number of species, this represents nearly 0.8% of the global extant vetigastropods, and 20% of the species recorded in Brazil (Geiger et al., 2008; Rios, 2009). These findings are apparently in line with the theoretically high diversity expected of seamounts, although any assertions on endemism depend on more samplings, especially in the surrounding seamounts of the Ceará cluster. Nonetheless, compared to the Vitória-Trindade Chain, which harbors the most well-studied vetigastropod fauna from seamounts in Brazil, Canopus seems to be somewhat similarly diverse. Leal (1991; appendix C), while analyzing material from the Vitória-Trindade seamounts Jaseur, Columbia, Montague, Davis, and Dogoressa, reported 25 vetigastropod species belonging to 11 families. The author reported 8 fissurellid species (vs. 9 herein); 1 anatomid (vs. none); 3 calliostomatids (vs. 2); 1 solariellid (vs. 2); 2 chilodontids (vs. 1); 1 trochid (vs. none); 1 skeneid (vs. 4); 1 turbinid (same); 4 areneid (vs. 3); 2 colloniids (vs. 2); 1 phasianellid (same). Subsequent studies on further specimens from the MD55 expedition revealed more species from the same locations: Salvador et al. (2014) revealed two additional seguenziids from Dogoressa and Montague, even though Simone & Cunha (2014) did not reveal any other fissurellids coming specifically from the seamounts.

It is noteworthy that the MD55 expedition collected large amounts of material using several different methods at variable depths (Tavares, 1999), while the present study is based on a limited sampling collected in a relatively restricted location at the shallowest portions of Canopus (50-260 m). Hence, additional diversity may yet be revealed by further samplings, especially at deeper portions (~600 m) of the seamount where deep-water species (e.g., several seguenzioids) are usually more frequent (e.g., Salvador et al., 2014). Vetigastropoda aside, gastropod families belonging to other clades were present in large numbers in the samples analyzed herein, e.g., Turridae (l.s.), Muricidae, Columbelloidea, several heterobranch families, and many others. The high diversity in seamounts has been attributed to the action of Taylor columns, which imprisons larvae, eggs, and nutrients in the water flowing over the seamount peaks (Norse et al., 2005). Nevertheless, although the present findings constitute an important



step towards better understanding the Brazilian seamount fauna, the complete spectrum of reasons behind the astounding diversity present in Canopus, as is the case in most seamounts around the globe, are yet to be studied in detail.

Benthic depth zonation is a common phenomenon in continental shelves and slopes, where vertical gradients and stratification generates pelagic zones with diverse conditions for life. In such environments, the distribution of organisms is thus limited or rather defined by said conditions, and zones with distinct faunal composition and abundance can be observed along the depth range (Norse et al., 2005; Thresher et al., 2014). This phenomenon also happens in seamounts, but, compared to shelves and slopes, is dictated by distinct factors such as lower sediment load, the effect of the mountains on the ocean currents and water flow, oxygen concentration, etc (Wishner et al., 1990; Norse et al., 2005). The distribution of some species from Canopus seems to be restricted to certain depths. Some species were only found at the seamount's peak (60 m depth), e.g., *Calliostoma hassler*, *Diodora sayi*, while others seem to occur only at the deepest range (200-260 m), e.g., most fissurellids except for *Cranopsis* spp. and *Diodora sayi*, *Arene flexispina* and *Arene* aff. *briareus*, *Macrarenne digitata*, the margaritids, skeneids, and solariellids. At first glance, there is an obvious difference between the faunas depending on the analyzed depth, with the greatest diversity occurring at the deepest range studied herein. This seems to be congruent with the general understanding that species richness tends to peak at intermediate depths, but declines with increasing depths (Rex et al., 2006). Then again, the diversity of the deepest parts (~600 m) of Canopus has not yet been surveyed, and further observations depend on more samplings.

Some of the Canopus species have very interesting distribution patterns. In fact, Canopus seems to be the north/northwestern range limit for species exclusively occurring in the SW Atlantic, e.g., *Emarginula suspira*, *Hemimarginula hemitoma*, *Arene flexispina*, *Homalopoma boffii*, *Solariella quinni*, and *Turbo heisei*. On the other hand, a few openly Caribbean species have their southernmost range limit set herein to Canopus, e.g., *Dentistyla dentifera*, and *Gaza* cf. *fischeri*, and some species studied herein occur in the Caribbean and along the Brazilian coast as well, e.g., *Ancistrobasis costulata*, *Diodora sayi*, *Parviturbo rehderi*, *Homalopoma linnei*, *Lucapina aegis*. A similar situation has been verified for other invertebrates collected in Canopus, such as brachiopods (see Marques, 2016). Several authors consider the fauna of the northern Brazilian coast as an “impoverished” extension of the Caribbean counterpart, with a continuous decrease in diversity towards the south (e.g., Mathews & Rios, 1974; Palacio, 1982).

If mollusks are concerned, recent studies have systematically contradicted this point of view, showing a rich, highly characteristic SW Atlantic/Brazilian fauna that is, in fact, poorly understood. This is the case in most studies on the MD55 material. The Canopus assemblage, in truth, illustrates this contradiction very well, showing a very rich fauna with several possibly endemic species, and a complex mixture of Caribbean-SW Atlantic faunas.

The present discoveries, though restricted to limited samplings and focused on a single mollusk group, are a testimony to the importance of thoroughly studying seamount habitats. Even as many species were described in the ten years that followed the 2005 samplings, an exhaustive analysis of a single (though very diverse) group revealed several novelties. It is clearly essential that other mollusk groups that are very abundant in Canopus be meticulously studied in the future, e.g., neogastropods or heterobranchs. Other similar discoveries are likely to happen, adding more pieces in the complex puzzle of seamount biology.

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## APPENDIX