

NEW MOLLUSCAN RECORDS AND PALAEOECOLOGY OF THE LATE PLEISTOCENE MARINE ASSEMBLAGE FROM LA CORONILLA (ROCHA, URUGUAY)

ALEJANDRA ROJAS^{1*}, JUAN CARLOS ZAFFARONI² AND SERGIO MARTÍNEZ¹

1 Universidad de la República, Instituto de Ciencias Geológicas, Facultad de Ciencias, Departamento de Paleontología, Montevideo, Uruguay

2 Sociedad Malacológica del Uruguay

* CORRESPONDING AUTHOR, alejandra@fcien.edu.uy

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Abstract

The Late Pleistocene marine molluscan assemblage from La Coronilla is one of the richest Quaternary marine deposit from Uruguay. This contribution represents an update of the bivalve and gastropod species composition of this deposit and includes a palaeoecological analysis of the molluscan fauna. The ecological preferences of the recorded species allowed the reconstruction of the palaeoenvironmental conditions of the eastern Uruguayan coast and the palaeobiogeographic scenario of the area during the Late Pleistocene. The fossil assemblage of La Coronilla contains 91 bivalve and gastropod taxa of which 28 are new to this deposit and 11 are first reported for the Uruguayan Quaternary marine assemblages. The latest are *Turbonilla abrupta*, *Turbonilla* cf. *farroupilha*, *Turbonilla brasiliensis*, *Turbonilla* cf. *deboeri*, *Turbonilla penistoni*, *Turbonilla turris*, *Olivella defiorei*,

Eurytellina angulosa, *Kellia* sp., *Paraleptopecten bavayi*, and *Pandora* sp. Almost all recorded species from the assemblage are marine and live in soft bottoms, although hard/consolidated substrate species and microgastropods that live in ecological interaction with other invertebrate taxa were also found. The high percentage of tropical-subtropical species, the absence of cold-water species, and the record of extralimital warm water northern species, adds new evidence for the inference of warmer than present conditions in the Uruguayan coast during the Late Pleistocene.

Keywords: Bivalves. Gastropods. Palaeoecology. Palaeobiogeography. MIS 5e. Southwestern Atlantic.

1. Introduction

The Pleistocene Epoch was characterized by the occurrence of global climatic oscillations and concomitant sea level changes that had strong effects on continental and marine life on Earth (e.g. Crowley and North, 1991; Pirazzoli, 1996; Petit et al., 1999; Lisiecki and Raymo, 2005; Medina-Elizalde, 2013; Murray-Wallace and Woodroffe, 2014). The study of the recent past is crucial for the understanding of the processes and events that shaped our modern biota; besides, Pleistocene records represent an important tool to predict the current and future biotic, environmental and climatic changes (Warwick and Turk, 2002; Oldfield, 2004; Meadows, 2012).

Several sources of information have been used for the reconstruction of the Pleistocene climatic changes, such as continental and marine geological and palaeontological records, ice cores, and climatic models (e.g., Emiliani, 1955; Kukla et al., 2002; Hearty et al., 2007; Jouzel et al., 2007; Van Meerbeek et al., 2009; Lang and Wolff, 2011). Historically, most of our knowledge on Pleistocene climates, sea level changes, and fossil assemblages came from Northern Hemisphere records (e.g. Anderson et al., 2013; Hearty et al., 2007; Lang and Wolff, 2011; Lowe and Walker, 2014; Bradley, 2015), meanwhile sources of information from the Southern Hemisphere are uneven. Despite Antarctic ice cores have been extensively analysed and much knowledge of southern climates derives from them (e.g., Petit et al.,

1999; EPICA, 2006; Jouzel et al., 2007; Sime et al., 2008, 2009), geological and palaeontological data from other southern areas, such as the Southwestern Atlantic Ocean, are relatively scarce. The analysis of Pleistocene marine assemblages from this biogeographically relevant region is essential for the reconstruction of the palaeoenvironmental conditions and evolution of this dynamic area of the Southern Hemisphere.

Pleistocene littoral fossiliferous deposits are frequent in coastal areas around the world. Their faunal composition, and palaeoecological and palaeobiogeographical analyses, may reveal changes in the geographical ranges of species as a response to shifting temperature regimes driven by oceanic currents (e.g. Valentine and Jablonski, 1993; Muhs et al., 2002; Garilli, 2011). South American marine assemblages are known from the Pacific littoral (e.g. Hsu et al., 1989; Ortlieb et al., 1990; Rivadeneira and Carmona, 2008), Beagle Channel (Rabassa et al., 2009; Gordillo et al., 2010; Gordillo and Isla, 2011), from the Atlantic coast; primarily from Argentina (e.g., Aguirre and Whatley, 1995; Isla et al., 2000; Aguirre, 2003; Aguirre and Fucks, 2004; Aguirre et al., 2011; Charó et al., 2013a, b, 2014, 2015; Martínez et al., 2016), from the southern coast of Brazil (Lopes and Simone, 2012; Lopes et al., 2013, 2014; Bettinelli et al., 2018), and from Venezuela in the Caribbean Sea (Macsoyay and Cáceres Hernández, 2005). In Uruguay, fossiliferous marine sediments deposited during Quaternary sea level fluctuations are exposed along a thin strip parallel to the present coastline, and yield an abundant molluscan content. Although the fossils have been long recognised since the work of Larrañaga (1819, published in 1894), d'Orbigny (1842) and Darwin (1846), until the 1970 decade few studies focused on their potential for palaeoenvironmental reconstructions, except from the pioneer research of Ihering (1907) and Teisseire (1928). Sprechmann (1978) and Martínez (1988, 1990) explicitly considered the ecologic requirements of the molluscan assemblages as an important factor to reconstruct palaeoenvironmental conditions. More recently, the incorporation of radiocarbon dating of shells from selected localities enabled a satisfactory discrimination between Pleistocene and Holocene deposits (e.g. Martínez et al., 2001, 2006; Rojas, 2002, 2007; Martínez and Ubilla, 2004; Martínez and Rojas, 2013; Rojas and Martínez, 2016).

The Late Pleistocene molluscan assemblages from Uruguay were firstly identified by Martínez et al. (2001) through the record of (minimum) radiocarbon ages in shells from Puerto de Nueva Palmira (western Uruguay, Colonia county) and La Coronilla (eastern Uruguay, Rocha county). Later, Rojas (2007) reached to similar results for the Zagarzazú fossil assemblage located in Colonia county. The ^{14}C ages from the three mentioned deposits range between 29500 and 35500 years BP, and were interpreted by the authors as minimum ages. In consequence, the assemblages were considered to be older than the numerical ages obtained and probably deposited during the Last Interglacial (see discussion in Rojas and Martínez, 2016).

The fossil content of the La Coronilla assemblage was studied by Martínez et al. (2001), where the molluscan taxonomic composition, and palaeoenvironmental information of the assemblage was presented. The authors recorded 22 molluscan taxa (11 bivalves and 11 gastropods) being the oyster *Ostrea equestris* (= *Ostrea stentina* according to Shilts, 2007) the most abundant species. Due to the tropical-subtropical affinities of the molluscs, including few extralimital northern species (*sensu* Roy et al. 1995), Martínez et al. (2001) inferred warmer temperatures during the Pleistocene than those recorded today in the Uruguayan coast. Rojas and Urteaga (2011) identified four chiton species in the assemblage, including the warm water *Ichnochiton striolatus*, which current southernmost distributional limit in Santa Catarina (Brazil), agree with the thermal inferences made by Martínez et al. (2001). Regarding salinity, the vast majority of the molluscs recorded by Martínez et al. (2001) support the development of marine conditions. Lorenzo and Verde (2004) dealt with the ichnofossil record from shells and reported three ichnotaxa in the assemblage: *Oicchnus paraboloides* and *Caulostrepsis taenicola* on *Ostrea stentina* and *Entobia* sp. on *Plicatula gibbosa*. Rojas et al. (2014) recorded the presence of *Oicchnus simplex* on a plate of the chiton *Chaetopleura angulata*, the first report of this ecological interaction in the fossil record. Recently, Rojas and Martínez (2016) updated the molluscan content and discussed the age of Pleistocene assemblages from Uruguay. Regarding the La Coronilla deposit, the authors listed 26 gastropod and 40 bivalve species derived from the review of the specimens studied in Martínez et al. (2001) and from the unpublished thesis by Rojas (2007). In summary, considering the previous works dealing with the La Coronilla fossil assemblage, 70 molluscan species represented by polyplacophorans, gastropods and bivalves have been reported.

During the summer of 2004, the La Coronilla outcrop became exposed enabling a sampling that provided new molluscan taxa for this assemblage and for the Quaternary marine deposits from Uruguay. The aim of this paper is to update the species composition of the La Coronilla deposit and to discuss its contribution for the reconstruction of the palaeoenvironmental and palaeobiogeographic scenarios of the Uruguayan coast during the Late Pleistocene.

2. Study area and geological setting

The Quaternary marine deposits from Uruguay are included in the Chuy and Villa Soriano formations (Goñi and Hoffstetter, 1964; Goso, 1972). These lithostratigraphic units include a similar lithologic composition, that varies from clays to coarse sands, and even conglomerates (Preciozzi et al., 1988; Goso, 2006; Ubilla and Martínez, 2016). For this reason, other criteria such as stratigraphic relationships or fossiliferous content have been invoked to distinguish between both units (see discussion in Martínez and Ubilla, 2004; Rojas and Martínez, 2016; Ubilla and

Martínez, 2016). In a recent review of the geology and palaeontology of the Uruguayan Quaternary strata, Ubilla and Martínez (2016) referred the La Coronilla deposit to the Chuy Formation.

The studied deposit crops out in the abrasion platform of the La Coronilla beach in Rocha county, Atlantic coast of Uruguay (Fig. 1). The degree of exposition of this fossiliferous horizon relies on littoral dynamic processes, and it may be covered by sand or temporarily remain under the water. The lithology corresponds to a greenish-greyish

muddy sandstone. Fossils are mostly well preserved and some of them can be found in life position. Articulated bivalve shells and unbroken specimens are common. Shell debris are also present, and abrasion is almost absent (Rojas et al. 2018).

A predominantly autochthonous–parautochthonous assemblage, and a proximal depositional environment protected from waves have been inferred (see Martínez et al., 2001; Rojas, 2007; Rojas and Martínez, 2016; Rojas et al. 2018).



Fig. 1. Geographic location of the La Coronilla Late Pleistocene molluscan assemblage.

3. Material and methods

The samples studied herein were collected by F. Scarabino and members of Karumbé (Centro de Tortugas Marinas) Team in January 2004 by a non-random sampling procedure. Specimens were preferentially collected by hand, and not in bulk samples, which precludes any statistical comparison with previous results, such as those presented by Martínez et al. (2001), and a quantitative analysis of the samples. Despite of this, a qualitative assessment of the taxonomic composition and ecological preferences is feasible. In the laboratory, samples were first dried and then sieved in water to facilitate the picking of specimens. The collected sediments were also inspected after sieving for the

record of micromolluscs. All specimens are housed at the Colección Paleontológica at Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (FCDPI).

Taxa were grouped according to salinity, temperature and substrate preferences. Following Martínez et al. (2006), two categories were considered for the salinity requirements: estuarine (taxa restricted to brackish waters), and marine, without considering the tolerance to salinity changes.

In order to perform temperature inferences, the recent geographic distribution of the involved taxa was taken into account. As the geographic range of marine species mostly reflects its thermal tolerance through latitudinal gradients

(e.g. Spalding et al., 2007; Belanger et al., 2012), studied taxa were grouped according to their biogeographic origin. The categories used were: tropical-subtropical for species shared with northern warmer areas with a distribution influenced by the warm Brazilian Current; cold, for taxa shared with the southern colder areas with a distribution controlled by the cold Malvinas Current; and endemic, for those species restricted to the Argentinean Province. The current percentage of each category in the Uruguayan coast was taken after Sicardi (1967), and considered in previous publications (Martínez et al., 2001, 2006).

Taxa were classified according to their substrate preferences as soft, hard, and consolidated ground dwellers, and an additional category was used for those species that develop an ecological interaction with other invertebrates (e.g. parasites).

Data on ecological preferences and geographic distribution was obtained from Figueiras and Sicardi (1972), Ríos (1994, 2009), Pimenta and Absalão (2002), Scarabino and Zaffaroni (2004), Demicheli and Scarabino (2006), Scarabino et al. (2006 a and b), Mikkelsen and Bieler (2007), Figueira and Pimenta (2008), Pimenta et al. (2009), Rosenberg (2009), Rosenberg et al. (2009), Turgeon et al. (2009), Huber (2010), Signorelli and Scarabino (2010), Pastorino and Bagur (2011), Forcelli and Narosky (2015) and Scarabino et al. (2015).

4. Results and discussion

4.1. Taxonomic composition and new records

The molluscs herein recorded in the La Coronilla assemblage comprises 91 taxa of gastropods (38 species) and bivalves (53 species) (Table 1 and Table 2).

The richness of this assemblage is higher than previously assessed, since Martínez et al. (2001) had reported only 22 taxa, and Rojas and Martínez (2016) summarised 66 species of bivalves and gastropods based on previous unpublished data of Rojas (2007). The present contribution adds 28 new records to the La Coronilla deposit, becoming this, one of the most diverse Quaternary assemblages from Uruguay, and by far, the richest of the Pleistocene ones. The 13 new recorded gastropods were *Buccinanops cochlidium*, *Bulla occidentalis*, *Calliostoma jucundum*, *Cerithiopsis* cf. *fusiformis*, *Epitonium* (*Asperiscala*) sp., *Olivella defiorei* (= *Olivella* sp. in Rojas and Martínez, 2016), *Turbonilla abrupta*, *T.* cf. *farroupilba*, *T. brasiliensis*, *T.* cf. *deboeri*, *T. penistoni*, *T. turris* (some of them included as *Turbonilla* spp. by Rojas and Martínez, 2016) and indetermined (indet.) Turridae. The specimens recorded herein as *Turbonilla* cf. *deboeri* are comparable to the specimen depicted in Fig.d by Pimenta and Absalão (2002). The 15 new bivalve records were *Amiantis purpurata*, *Anadara chemnitzii*, *Barnea lamellosa*, *Brachidontes rodriguezii* (as *Brachidontes* sp. in Rojas and Martínez, 2016), *Corbula hyni*, *C. patagonica*, *Eurytellina angulosa*, *Kellia* sp., *Mactra guidoi*, *Ostrea puelchana*, *Pandora* sp., *Paraleptopecten bavayi*, *Petricola* cf. *lapicida*, *Raeta plicatella* and

Transennella sp. (as *Clausinella gayi* in Martínez et al., 2001; as indet. Veneridae in Rojas and Martínez, 2016).

Taking into account recent compilations (Clavijo et al., 2005; Martínez et al., 2006; Rojas and Martínez, 2016), 11 taxa are recorded by the first time in the Quaternary of Uruguay. These are *Turbonilla abrupta*, *T.* cf. *farroupilba*, *T. brasiliensis*, *T.* cf. *deboeri*, *T. penistoni*, *T. turris*, *O. defiorei*, *Eurytellina angulosa*, *Kellia* sp., *Paraleptopecten bavayi*, and the genus *Pandora* (Fig. 2). It is noticeable that most of the new gastropod records are micromolluscs, highlighting the need of future collections and sample processing methods to increase the probability of finding small-sized species.

The studied samples allow to extend the chronologic range of nine taxa back to the Pleistocene since they were only previously known in Uruguay from Holocene or probable Holocene deposits. They are *Ostrea puelchana*, mentioned by Ihering (1907), and *Amiantis purpurata*, reported by Ihering (1923) for Punta Carretas and the latter also for Buceo (Montevideo); *Brachidontes rodriguezii*, known from Colonia del Sacramento (Teisseire, 1928); *Barnea lamellosa*, reported by Figueiras (1962) in Areneras de Carrasco; *Calliostoma jucundum*, *Corbula patagonica* and *Raeta plicatella* known from Arenales de Carrasco (de Mata, 1947); *Petricola lapicida*, known from Isla de Tala (Martínez, 1988) (although the specimens herein reported were determined as *Petricola* cf. *lapicida*); and *Mactra guidoi*, reported by Figueiras (1961) in the Areneras de Carrasco (as *Mactra patagonica*), and as *Mactra* sp. in a subsequent contribution (Figueiras, 1962), as commented by Signorelli and Scarabino (2010). All of them are currently living in the Uruguayan coast (Scarabino, 2003, 2004).

4.2. Palaeoecology

All recorded taxa are marine in a broad sense except for *Tagelus plebeius*, an estuarine species living today in the area of the Río de la Plata estuary, in coastal lagoons and in the mouth of the rivers of the Atlantic Uruguayan coast (Scarabino et al., 2006 b; 2015). Other species, such as the gastropods *Heleobia australis*, *Cylichnella bidentata* and *Buccinanops cochlidium*, and the bivalves *Barnea lamellosa*, *Brachidontes rodriguezii*, *Macoma uruguayensis*, *Mactra isabelleana*, *Ostrea puelchana* and *Pitar rostratus* are eurihaline. These species currently occupy a variety of sub environments in the Río de la Plata, and other low salinity habitats of the Uruguayan coast (Scarabino et al., 2006a, b, 2015).

The remaining and majority of species are mostly regarded as marine and therefore, the molluscan assemblage is considered to represent a coastal marine environment.

In reference to the substrate, the molluscs from La Coronilla show a wide range of preferences (Fig. 3), being most of them soft-substrate inhabitants. Some prefer sandy substrates (e.g. *Amiantis purpurata*, *Corbula hyni*, *Crassinella lunulata*, *Cylichnella tenuis*, *Gouldia cerina*, and the *Anadara* and *Olivella* species recorded), and a few inhabit muddy bottoms (*Corbula patagonica*, *Macoma uruguayensis*).

However, the majority can live in sandy-muddy substrates (e.g. *Anomalocardia flexuosa*, *Corbula caribaea*, *Macra isabelleana*, *Semele* aff. *proficua*, *Tellina gibber*, *Acteocina candei*, *Bulla occidentalis*, *Cylichnella bidentata*, *Zidona dufresnei*). These preferences are consistent with the lithology of

the deposit and it can be assumed that the muddy fine sand was the original substrate where the community settled. Moreover, the shells good preservation indicates that the species lived in or near of their burial emplacement (see Rojas et al., 2018).

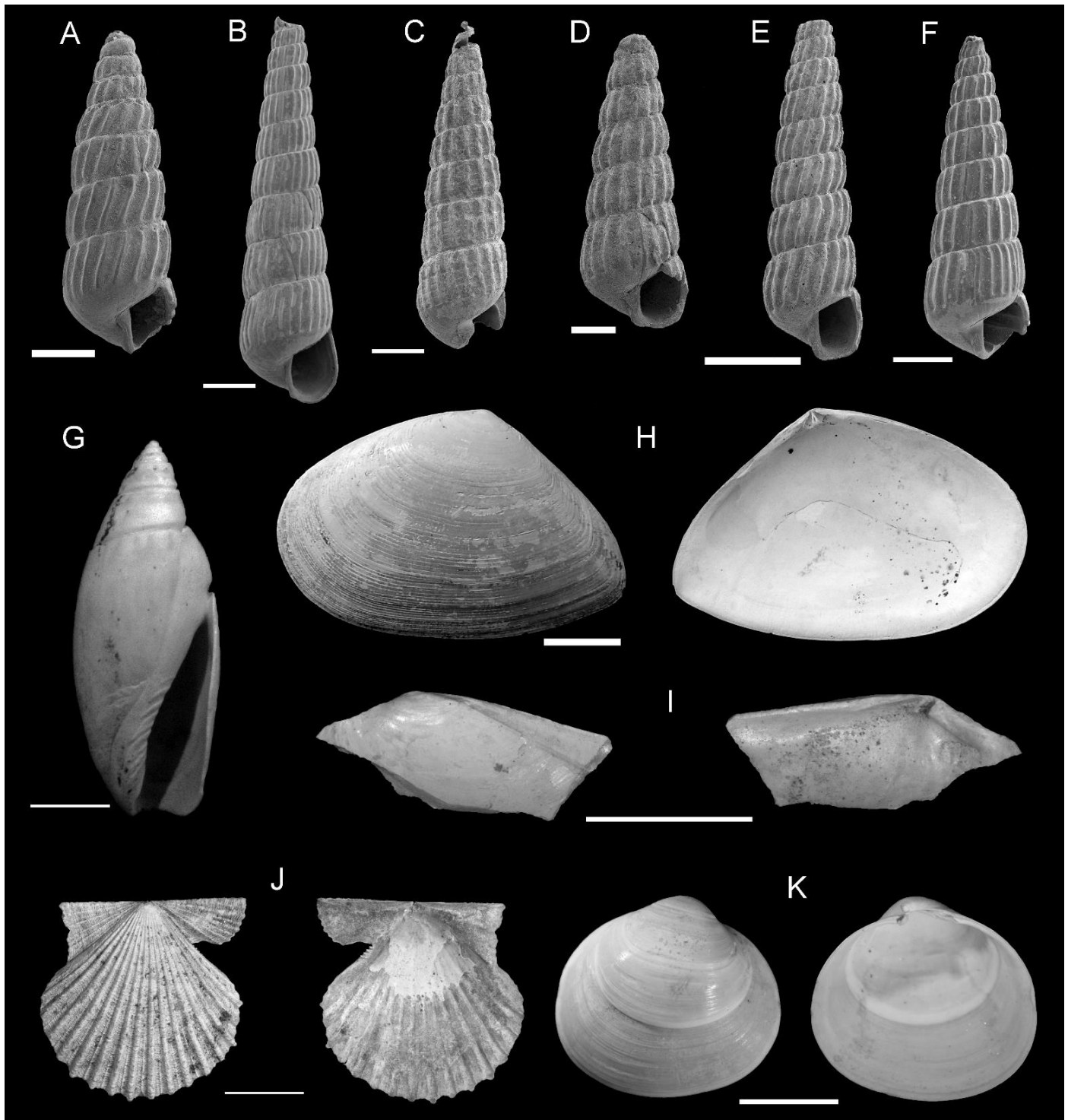


Fig. 2. Mollusks recorded for the first time in the Quaternary marine assemblages from Uruguay. (A) *Turbonilla abrupta*, scale bar = 500 μ m. (B) *Turbonilla* cf. *farroupilha*, scale bar = 1 mm. (C) *Turbonilla brasiliensis*, scale bar = 1mm. (D) *Turbonilla* cf. *deboeri*, scale bar = 500 μ m. (E) *Turbonilla penistoni*, scale bar = 1 mm. (F) *Turbonilla turris*, scale bar = 1 mm. (G) *Olivella defiorei*, scale bar = 2 mm. (H) *Eurytellina angulosa*, scale bar = 10 mm. (I) *Pandora* sp., scale bar = 5 mm. (J) *Paraleptopecten bavayi*, scale bar = 5 mm. (K) *Kellia* sp., scale bar = 5mm.

The La Coronilla assemblage also includes more than 20% of species that prefer hard substrates, where they live freely or attached by different strategies (e.g. *Brachidontes rodriguezii*, *Ostrea stentina* and *O. puelchana*, *Plicatula gibbosa*, *Bostrycapulus odites*, *Diodora patagonica*, *Urosalpinx haneti*). These hard substrates were probably provided by the accumulation of shells on the sea bottom (Rojas et al., 2018). Almost all of the recorded microgastropods are known to live in association with other invertebrates (e.g. sponges, cnidarians) through parasitism or epibiosis. Within this group, pyramidellids are the more diverse, and are mostly represented by the genus *Turbonilla*. The presence of their hosts must be inferred to have lived in the La Coronilla community, probably facilitated by the development of the shelly hard substrate. Few species bore into hard or consolidated substrates, such as *Barnea lamellosa*, *Lamychaena* sp. and *Petricola* cf. *lapicida*. Scarabino et al. (2015) found that the bivalve communities that currently live in the coastal and platform areas of the Uruguayan coast are more diverse when mud is present in a sandy bottom. Thus, those all evidences lead us to conclude that an appropriate substrate availability was probably one of the factors that played an important role in the high species richness of the La Coronilla assemblage.

4.3. Palaeobiogeography

Compared to the biogeographic composition of the molluscs that currently inhabit the Uruguayan coast, the La Coronilla deposit includes a higher percentage of molluscs with tropical-subtropical affinities, and a slightly lower proportion of endemic species (Fig. 4). Similar proportions of endemic and warm water taxa were obtained by Martínez et al. (2001) despite the lower number of recorded species. Regarding the cold-water species, almost 20% of magellanic taxa reach nowadays the Uruguayan coast (Sicardi, 1967) meanwhile none of them were present in the La Coronilla assemblage.

As stated by Rojas and Martínez (2016), the only putative cold-water species reported by Martínez et al. (2001) for this deposit was *Clausinella gayi* (= *Tawera elliptica*), specimens which in fact correspond to *Transennella* sp., and not to a cold-water species. Thus, the results indicate that the Pleistocene molluscan fauna of La Coronilla lived during warmer conditions than today, as previously suggested (Martínez et al., 2001; Rojas, 2007; Rojas and Martínez, 2016). In addition to the global analysis of thermal preferences, it must be stressed that some of the warm water recorded molluscs, live currently northwards from the Uruguayan coast, with a southern geographic range boundary in Brazilian waters. Some of these warm extralimital species, such as *Fargoa bushiana* (as *Chrysalida gemmulosa*), *Laevicardium* sp. and *Limaria* sp. were recorded by Martínez et al. (2001). Later, Rojas and Urteaga (2011) added the chiton *Ischnochiton striolatus* to these warm water species. More recently, Rojas and Martínez (2016) summarised the record of 14 northern extralimital species for the La

Coronilla assemblage by the incorporation of the gastropod *Bittolum varium* and the bivalves *Anatina anatina*, *A. flexuosa*, *C. tenuis*, *Ervilia concentrica*, *G. cerina*, *Chione subrostrata*, *Pitar palmeri*, *Anadara brasiliana* and *Merisca martinicensis*.

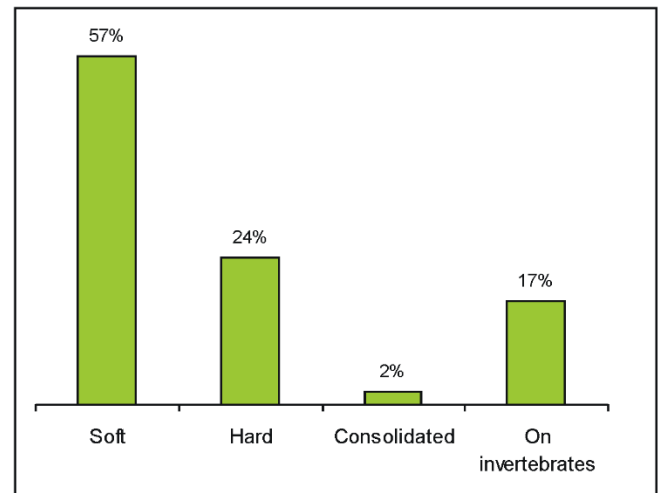


Fig. 3. Substrate preferences (in percentages) of the molluscan species recorded in the La Coronilla assemblage.

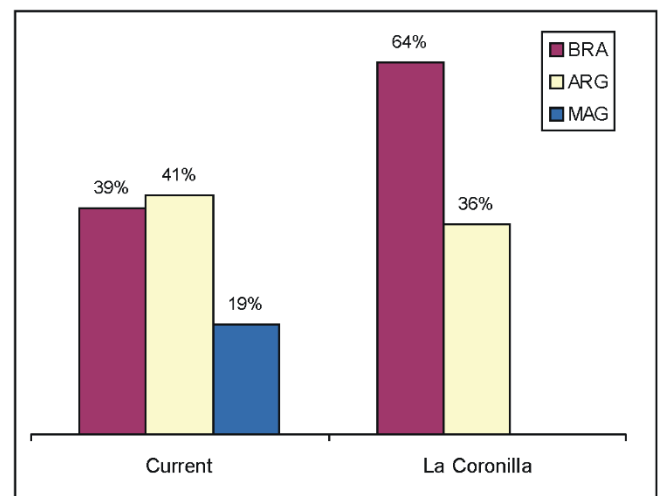


Fig. 4. Temperature ranges (in percentages) of the molluscan species currently living on the Uruguayan coast (according to Sicardi, 1967) compared to those of the La Coronilla assemblage. BRA: warm-water taxa; ARG: endemic taxa; MAG: cold-water taxa.

The present study adds the record of other nine new warm water extralimital species for the La Coronilla assemblage: *Bulla occidentalis*, which was previously reported in the Pleistocene assemblage of Puerto de Nueva Palmira (Rojas and Martínez, 2016) and in the Arroyo Chuy Holocene deposit (Martínez et al., 2006); *Cerithiopsis* cf. *fusiformis* that was reported as *Cerithiopsis* aff. *C. emersoni* (Piñeiro et al., 1992) and as *Cerithiopsis greeni* (Martínez et al., 2006) for Saglia, and *Anadara chemnitzii* that was mentioned by Figueiras and Sicardi (1968) for the Uruguayan Holocene but that record was not precise or confirmed later (see Clavijo et al., 2005).

Tab. 1. Gastropod species recorded in the La Coronilla assemblage, Collection number (FCDPI), ecological preferences, and current presence in the Uruguayan coast. Bra: influenced by the warm Brazilian Current; Arg: endemic to the Argentinian Province.

Gastropods	FCDPI	Substrate	Temperature	Uruguayan coast
<i>Acteocina candei</i> (d'Orbigny, 1841)	4236; 4730	sand-mud	Bra	yes
<i>Bittium varium</i> (Pfeiffer, 1840)	4856; 4761	soft	Bra	no
<i>Boonea jadisi</i> (Olsson & McGinty, 1958)	4275; 4740	on invert.	Bra	yes
<i>Boonea seminuda</i> (C. B. Adams, 1839)	6115; 6120	on invert.	Bra	yes
<i>Bostrycapulus odites</i> R. Collin, 2005	4197; 4703	hard	Bra	yes
<i>Buccinanops cochlidium</i> (Dillwyn, 1817)	4762	sand-mud	Arg	yes
<i>Buccinanops globulosus</i> (Kiener, 1834)	4696	sand	Arg	yes
<i>Bulla occidentalis</i> A. Adams, 1850	4693	sand-mud	Bra	no
<i>Calliostoma jucundum</i> (Gould, 1849)	4736	hard	Arg	yes
<i>Cerithiopsis</i> cf. <i>fusiformis</i> (C. B. Adams, 1850)	4745	on invert.	Bra	no
<i>Costoanachis sertulariarum</i> (d'Orbigny, 1839)	4276; 4698	hard	Arg	yes
<i>Crepidula plana</i> Say, 1822	4218; 4759	hard	Bra	yes
<i>Crepidula protea</i> (d'Orbigny, 1841)	4219	hard	Arg	yes
<i>Cylichnella bidentata</i> (d'Orbigny, 1841)	4234; 4729	sand-mud	Bra	yes
<i>Diodora patagonica</i> (d'Orbigny, 1839)	4212; 4721	hard	Bra	yes
<i>Epitonium (Asperiscala)</i> sp.	4749	on invert.		
Eulimidae indet.	4283	on invert.		
<i>Fargoa bushiana</i> (Bartsch, 1909)	4274; 4733	on invert.	Bra	no
<i>Finella dubia</i> (d'Orbigny, 1840)	4272; 4741	sand-mud	Bra	not confirmed
<i>Heleobia</i> cf. <i>australis</i> (d'Orbigny, 1835)	4237; 4728	sand-mud	Arg	yes
<i>Iselica globosa</i> (H. C. Lea, 1843)	4238; 4731	on invert.	Bra	yes
<i>Lucapinella henseli</i> (Martens, 1900)	4214; 4751	hard	Arg	yes
<i>Olivella defioerei</i> Klappenbach, 1964	6125; 4792	sand	Bra	no
<i>Olivella tebuelcha</i> (Duclos, 1835)	4277; 4722	sand -shells	Arg	yes
<i>Parvanachis</i> sp.	4235; 4724	sand-mud		
<i>Tegula patagonica</i> (d'Orbigny, 1835)	4211; 4690	hard	Arg	yes
<i>Turbonilla abrupta</i> Bush, 1899	6123; 6117	on invert.	Bra	yes
<i>Turbonilla brasiliensis</i> Clessin, 1902	6114	on invert.	Bra	no
<i>Turbonilla</i> cf. <i>deboeri</i> Jong & Coomans, 1988	6121	on invert.	Bra	no
<i>Turbonilla</i> cf. <i>farronpilba</i> Pimenta & Absalão, 2004	6119	on invert.	Bra	yes
<i>Turbonilla multicostata</i> (C. B. Adams, 1850)	4273; 4742	on invert.	Bra	yes
<i>Turbonilla penistoni</i> Bush, 1899	6124	on invert.	Bra	no
<i>Turbonilla turris</i> (d'Orbigny, 1840)	4271	on invert.	Bra	no
<i>Turbonilla uruguayensis</i> Pilsbry, 1897	4732	on invert.	Arg	yes
Turridae indet.	4758			
<i>Urosalpinx haneti</i> (Petit, 1856)	4209; 4726	hard	Arg	yes
Vitrinellidae indet.	4284; 4747	soft		
<i>Zidona dufresnei</i> (Donovan, 1823)	4240; 4700	sand-mud	Arg	yes

Tab. 2. Bivalve species recorded in the La Coronilla assemblage, Collection number (FCDPI), ecological preferences, and current presence in the Uruguayan coast. Bra: influenced by the warm Brazilian Current; Arg: endemic to the Argentinian Province.

Bivalves	FCDPI	Substrate	Temperature	Uruguayan coast
<i>Abra</i> cf. <i>uruguayensis</i> (Pilsbry, 1847)	4226; 4718	sand-mud	Arg	yes
<i>Aequipecten tehuelchus</i> (d'Orbigny, 1842)	4199; 4701	sand-mud	Arg	yes
<i>Amiantis purpurata</i> (Lamarck, 1818)	4711	sand	Arg	yes
<i>Anadara brasiliiana</i> (Lamarck, 1819)	4702	sand	Bra	no
<i>Anadara chemnitzii</i> (Philippi, 1851)	4210; 6126	sand	Bra	no
<i>Anatina anatina</i> (Spengler, 1802)	4192	sand	Bra	no
<i>Anomalocardia brasiliiana</i> (Gmelin, 1791)	4205; 4705	sand-mud	Bra	no
<i>Atrina seminuda</i> (Lamarck, 1819)	4239; 4694	sand-mud	Bra	yes
<i>Barnea lamellosa</i> (d'Orbigny, 1841)	4709	consolidated	Arg	yes
<i>Brachidontes rodriguezii</i> (d'Orbigny, 1842)	4233; 4725	hard	Arg	yes
<i>Bushia rushii</i> (Pilsbry, 1897)	4225; 4727	sand-mud	Bra	yes
<i>Cardiomya</i> sp.	4230	sand-mud		
<i>Chione subrostrata</i> (Lamarck, 1818)	4206; 4692	sand-mud	Bra	no
<i>Corbula caribaea</i> (d'Orbigny, 1853)	4200; 4697	sand-mud	Bra	yes
<i>Corbula lyoni</i> Pilsbry, 1897	4712	coarse sand, shells	Arg	yes
<i>Corbula patagonica</i> d'Orbigny, 1846	4752	sand-mud	Arg	yes
<i>Crassinella lunulata</i> (Conrad, 1834)	4228; 4723	sand	Bra	yes
<i>Cyclinella tenuis</i> (Récluz, 1852)	4221; 4707	sand	Bra	no
<i>Ennucula puelcha</i> (d'Orbigny, 1842)	4207; 4720	sand-mud, shells	Arg	yes
<i>Ennucula uruguayensis</i> (E. A. Smith, 1880)	4224; 4755	mud	Arg	yes
<i>Ervilia concentrica</i> (Holmes, 1858)	4217; 4715	sand	Bra	no
<i>Eurytellina angulosa</i> (Gmelin, 1791)	4753	sand	Bra	no
<i>Gouldia cerina</i> (C. B. Adams, 1845)	4220; 4713	sand	Bra	no
<i>Kellia</i> sp.	4750	sand		
<i>Laevicardium</i> sp.	4204; 4691	sand	Bra	no
<i>Lamychaena</i> sp.	4231; 4737	hard		
<i>Limaria</i> sp.	4738		Bra	not confirmed
<i>Lanarca ovalis</i> (Bruguière, 1789)	4739	hard	Bra	yes
<i>Macoma uruguayensis</i> (E. A. Smith, 1885)	4232; 4756	mud	Arg	yes
<i>Mactra guidoi</i> Signorelli & Scarabino, 2010	4743	sand-mud	Arg	yes
<i>Mactra isabelleana</i> d'Orbigny, 1846	4201; 4699	sand-mud	Arg	yes
<i>Merisca martinicensis</i> (d'Orbigny, 1853)	4223; 4717	sand	Bra	no
<i>Musculus</i> sp.	4285	hard		
Mytilidae indet.	4282	hard		
<i>Noetia bisulcata</i> (Lamarck, 1819)	4208; 4710	hard	Bra	yes
<i>Nucula semiornata</i> d'Orbigny, 1842	4215; 4754	sand	Arg	yes
<i>Nuculana decora</i> (A. Adams, 1856)	4216; 4714	sand-mud	Arg	yes
<i>Ostrea puelchana</i> d'Orbigny, 1842	4744	hard	Arg	yes
<i>Ostrea stentina</i> Payraudeau, 1826	4194; 4689	hard	Bra	yes
<i>Pandora</i> sp.	4748	sand-mud		

Tab. 2. (cont.). Bivalve species recorded in the La Coronilla assemblage, Collection number (FCDPI), ecological preferences, and current presence in the Uruguayan coast. Bra: influenced by the warm Brazilian Current; Arg: endemic to the Argentinian Province.

Bivalves	FCDPI	Substrate	Temperature	Uruguayan coast
<i>Paraleptopecten bavayi</i> (Dautzenberg, 1900)	4763	hard	Bra	yes
<i>Petricola</i> cf. <i>lapicida</i> (Gmelin, 1791)	4213; 4734	consolidated	Bra	yes
<i>Phlyctiderma semiaspera</i> (Philippi, 1836)	4222	sand-mud, hard	Bra	yes
<i>Pitar</i> cf. <i>palmeri</i> Fischer-Piette & Testud, 1967	4193	sand	Bra	no
<i>Pitar rostratus</i> (Philippi, 1844)	4195; 4695	sand-mud	Arg	yes
<i>Plicatula gibbosa</i> Lamarck, 1801	4704	hard	Bra	yes
<i>Raeta plicatella</i> (Lamarck, 1818)	4202; 4735	sand-mud	Bra	yes
<i>Semele</i> aff. <i>proficua</i> (Pulteney, 1799)	4227; 4708	sand-mud	Bra	yes
<i>Sphenia fragilis</i> (H. & A. Adams, 1854)	4203; 4746	hard, shells	Bra	yes
<i>Tagelus plebeius</i> (Lightfoot, 1786)	4198; 4716	sand-mud	Arg	yes
<i>Tellina gibber</i> Ihering, 1907	4196; 4706	sand-mud	Bra	yes
<i>Trachycardium muricatum</i> (Linnaeus, 1758)	4229; 4688	sand-mud	Bra	yes
<i>Transennella</i> sp.	4757	soft		

The remaining extralimital northern species, such as *O. defiorei*, *T. brasiliensis*, *Turbonilla* cf. *deboeri*, *Turbonilla penistoni*, *T. turris* and *E. angulosa* are reported by the first time for the Uruguayan Quaternary marine deposits as was previously stated. Moreover, the living status of certain species in the Uruguayan coast must be confirmed, such as *Finella dubia*, which was reported by Figueiras and Sicardi (1980) in Rocha and Maldonado County and by Layerle and Scarabino (1984).

Empty and abraded shells of this species have been mentioned by Scarabino et al. (2006a) and for this reason the authors cast doubt on the living status of *F. dubia*. Also, Forcelli and Narosky (2015) excluded the Uruguayan coast from the southern boundary of distribution of this species. Regarding another taxon, specimens of the genus *Limaria* were recently collected alive in the Uruguayan coast and housed in the personal collection of one of the authors of the present study (JCZ). The status of the recorded specimens assigned to *Limaria* sp. in Martínez et al. (2001), should be further analysed in order to establish if the fossil and the living record of *Limaria* correspond to the same species. Therefore, the extralimital status of this taxon remains uncertain.

The 22 warm extralimital species found represent 24% of the bivalve and gastropod species recorded from La Coronilla. This is a great increase in the percentage of molluscan species that show this biogeographical pattern from the initial report of a few warm water species by Martínez et al. (2001). Therefore, a strong environmental signal for the reconstruction of the thermal conditions during the Pleistocene in the area is suggested. The southernmost limit of the majority of extralimital species is located in the coasts of Santa Catarina and Rio Grande do

Sul. Thus, it can be inferred that the temperature regime in the Uruguayan coast during the Late Pleistocene was warmer than today and similar to the current thermal conditions found in the southern region of the Brazilian coast (at least 600 km northwards). However, some of them, such as *T. deboeri* and *T. penistoni* currently live at even lower latitudes, northwards from Rio de Janeiro.

As proposed by Martínez et al. (2001) and further discussed by Rojas and Martínez (2016), the more likely temporal framework for the development of the warm water molluscan fauna preserved in La Coronilla is the Last Interglacial, or Marine Isotope Stage 5e (MIS 5e). This interval, around 126,000 years BP, is globally regarded as having had higher temperatures than today from different sources of information (e.g. Masson-Delmotte et al., 2006; Otto-Bliesner et al., 2006; Jouzel et al., 2007; Turney and Jones, 2010; Miller et al., 2013). In addition, worldwide MIS 5e molluscan assemblages record warm water extralimital species, such as in La Coronilla (e.g. Meco et al., 2002; Garilli, 2011; Zazo et al., 2013; Muhs et al., 2014; Ávila et al., 2015). Many studies invoke changes in ocean currents to account for the biogeographic range modifications of the stenothermal species. The presence of 22 extralimital molluscs in the Uruguayan coast (Southwestern Atlantic Ocean) during the Last Interglacial can be explained by a southwards influence of the warm Brazilian Current.

The Confluence Zone between this oceanic current and the cold Malvinas (Falkland) Current might have been located at a higher latitude than today during MIS 5e. This mechanism has been previously invoked by Martínez et al. (2001), Rojas (2007) and Rojas and Martínez (2016), and the present study provides further supporting evidence of this assumption. Moreover, Martínez et al. (2016) considered the

presence of a MIS 5e stronger than the Recent Brazilian Current as the cause of the biogeographical range changes verified for seven molluscan species from the Ezeiza assemblage in Argentina, all of them shared with the La Coronilla assemblage. A southwards displacement of the Brazilian Current has also been considered for other intervals during the Quaternary. Lopes and Simone (2012) and Lopes et al. (2013) proposed this mechanism for the presence of northern extralimital molluscan species in Middle Pleistocene deposits of the southern coastal plain of Rio Grande do Sul, Brazil. Additionally, Holocene molluscan assemblages from Argentina (especially from the Buenos Aires Province) and Uruguay also record out of range warm water species, which presence was explained by shifting ocean current regimes (e.g., Sprechmann, 1978; Aguirre, 1991; Aguirre and Farinati, 2000; Aguirre et al., 2005; Martínez et al., 2006; Rojas, 2007).

5. Conclusion

The La Coronilla fossiliferous deposit contains a highly diverse molluscan fauna, being this, one of the richest Quaternary marine assemblages of Uruguay. It is composed by 91 bivalve and gastropod taxa, of which 28 are herein reported by the first time and 11 consist of new records for the Uruguayan Quaternary marine deposits. It is noticeable that the majority of those new records correspond to micromolluscs. Most of the taxa are marine species inhabiting soft substrates. The development of shell bottoms must have been important for the settlement of the hard substrate dwellers, and of other invertebrate taxa that allowed the presence of most recorded microgastropods. The high proportion of tropical- subtropical species, the lack of cold-water taxa, and the new records of extralimital northern species, add further evidence for Late Pleistocene warmer conditions than those developed today in the Uruguayan coast, reinforcing a probable MIS 5e age for the studied assemblage.

The molluscan assemblage from La Coronilla represents an important source of information to disentangle the palaeobiogeography of the molluscan faunas and palaeoenvironmental evolution of the Uruguayan coast and the Southwestern Atlantic Ocean during the Late Pleistocene. The new records of molluscan species and the palaeoecological analysis of the fauna highlight the need of focusing in future standardised sampling efforts to enable a quantitative diversity analysis, in order to allow the comparison with similar molluscan rich assemblages from Uruguay and the SW Atlantic region.

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