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Molluscan assemblages from the marine Holocene of Uruguay: composition, geochronology, and paleoenvironmental signals

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Abstract. Dates of marine Holocene molluscs from Uruguay (Villa Soriano Formation) range from 6849 to 1858 cal. years BP. There are no significative gaps among the different ages obtained, with the exception of the interval 2276-2830 calculated years BP. Two kinds of concentrations are distinguished: autochthonous, for which a low energy depositional environment is inferred, and parautochthonous, deposited in foreshore and nearshore high-energy environments. Results of different types of multivariate analyses on presence-absence and abundance data show that only three localities are clearly differentiated from the others. The discrimination of two of them (Arazatí, Las Cañas) is explained by the presence of only one or two species, but the third (Punta Rasa) is the only one where characteristic species of rocky or hard substrates are undoubtedly represented . Analyses of salinity and temperature ranges of the various mollusc assemblages suggest a displacement of the Rio de la Plata estuary about 300 km westwards along the Uruguayan coast from its present position, and the presence of warmer waters than those found today at the same latitude. With the exception of the currently northwards displaced *Anomalocardia brasiliana* (Gmelin), *Marshallora nigrocincta* (C.B. Adams), *Nioche subrostrata* (Lamarck), *Bulla striata* Bruguìere and *Miralda* sp., all species are present today at the Uruguayan coast.

Resumen. ASOCIACIONES DE MOLUSCOS DEL HOLOCENO MARINO DE URUGUAY: COMPOSICIÓN, GEOCRONOLOGÍA E INDICADORES PALEOAMBIENTALES. Las asociaciones de moluscos marinos holocenos contenidos en la Formación Villa Soriano (Uruguay) presentan un rango máximo de 6849-1858 años cal. AP. No existen discontinuidades significativas entre las diversas edades obtenidas, con la excepción del intervalo 2276-2830 años calculados AP. Se distinguen dos tipos de concentraciones: autóctonas, propias de un ambiente de baja energía, y parautóctonas, depositadas en ambientes de alta energía del *foreshore* y *nearshore*. Los resultados de diferentes técnicas de análisis multivariado sobre datos de presencia-ausencia y abundancia de especies muestran que solamente tres se distinguen claramente de las demás localidades. La separación de dos de ellas (Arazatí, Las Cañas) se explica porque presentan una o dos especies solamente, en tanto que la tercera (Punta Rasa) es la única donde están claramente representados elementos propios de fondos duros. Sobre la base de las asociaciones estudiadas, se infiere un desplazamiento del frente estuárico del Río de la Plata de aproximadamente 300 km sobre la costa uruguaya, y una temperatura del agua mayor que la actual para la latitud considerada. Con la excepción de *Anomalocardia brasiliana* (Gmelin), *Marshallora nigrocincta* (C.B. Adams), *Nioche subrostrata* (Lamarck), *Bulla striata* Bruguìere y *Miralda* sp., cuyo límite de distribución meridional presente se encuentra más al norte, todas las especies viven hoy día en la costa de Uruguay.

Key words. Uruguay. Holocene. Paleoecology. Shell-beds. Mollusca. Bivalvia. Gastropoda.

Palabras clave. Uruguay. Holoceno. Peleoecología. Concentraciones fosilíferas. Mollusca. Bivalvia. Gastropoda.

Introduction

Quaternary shelly marine deposits are widespread along the Atlantic coast of South America (Clappertton, 1993; Aguirre and Whatley, 1995; Suguio, 1999; Pastorino, 2000; Martínez *et al.*, 2001, and references therein). Although poorly known, the geographic location of the Uruguayan deposits in the Río de la Plata area constitute an interesting case for studying fluctuations in biological and environmental parameters, including faunal distributions, temperature and salinity.

The earliest published papers on Quaternary marine fossiliferous deposits from Uruguay are those by d'Orbigny (1842) and Darwin (1846). However, the first reference belongs to Larrañaga, who recognised shell-beds in 1819, but whose observations were not published until 1894. Since then, several studies have been carried out on those deposits, focalizing on their geology, paleontology and cartography, but many questions about the marine Quaternary of Uruguay remain unanswered. In this paper we focus on widespread Holocene molluscan

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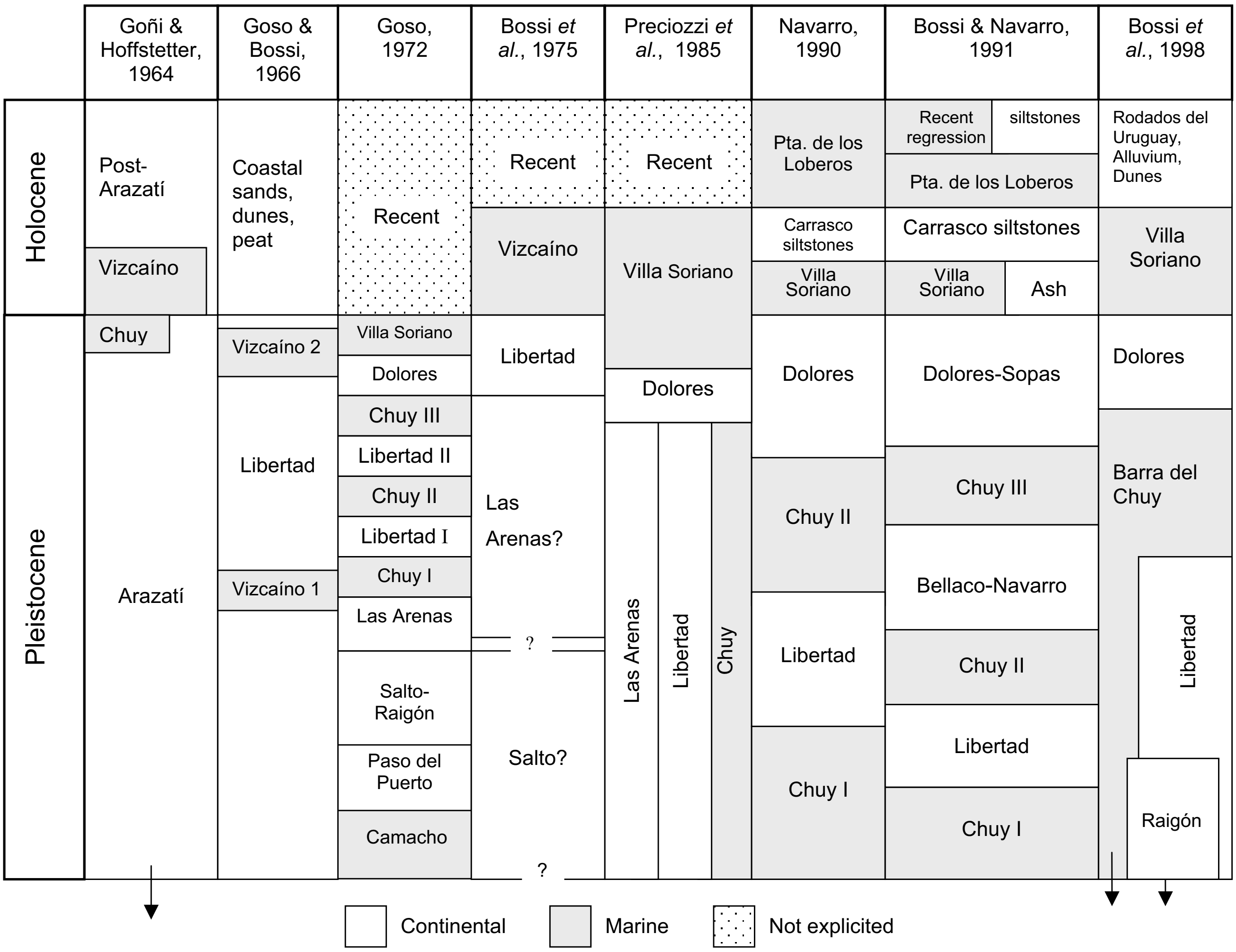


Figure 1. Units and ages proposed for the Uruguayan Quaternary (from Martínez *et al.*, 2001) / *unidades y edades propuestas para el Cuaternario de Uruguay (tomado de Martínez* et al.*, 2001).*

associations, their radiocarbon ages, and the information that these associations imply about temperature and salinity, using a uniform sampling strategy and a taxonomic approach.

Geological setting and study area

The deposits bearing the mollucs presently known as Villa Soriano Formation have been cited with different names along the years. Some of the terms arose from Argentine stratigraphy (e.g. "Querandinense", "Platense", or Querandina Formation), or are local expressions ("Arcillas grises de Vizcaíno", Vizcaíno Formation, Villa Soriano Formation). A summary of the nomenclature of Uruguayan Quaternary is presented in figure 1.

The highly fossiliferous Villa Soriano Formation crops out patchily along a narrow strip parallel to the present coast line, spreading from the mouth of the Negro river to the Merín lagoon margins. According to most authors (e.g. Preciozzi *et al.*, 1985), this unit comprises claystones, medium sandstones and conglomerates of up to 9 meters of thickness. However, due to its wide lithologic definition the best criteria to define the litostratigraphic unit are the abundant shell content and the stratigraphic relationships, taking into consideration that the Villa Soriano Formation is not overlaid by any unit (Martínez and Ubilla, 2004).

The published radiocarbon ages appear either in abstracts or papers lacking information about taphonomic/diagenetic conditions or proper taxonomic identification (e.g. Cortelezzi and Lerman, 1971, Bracco *et al.*, 1994, García *et al.*, 2002).

The Villa Soriano Formation has often been correlated with units from Argentina (e.g. "Platense", "Querandinense", Las Escobas Formation) (Goñi and

Hoffstetter, 1964; Aguirre and Whatley, 1995). Forti-Esteves (1974) and Martínez (1990) correlated it with the Patos Group of Rio Grande do Sul, Brazil.

It has been extensively discussed whether these sediments have been originated in one or more transgressive events (e.g. Figueiras, 1961, 1962; Goso and Bossi, 1966; Sprechmann, 1978; Preciozzi *et al*., 1985), but no conclusive data has been presented yet.

Molluscan content has been mentioned by several authors, such as Ihering (1907) Teisseire (1928), De Mata (1947) Figueiras (1961, 1962, 1967), but mostly limited to species identification. Sprechmann (1978) intended to reconstruct past depositional environments on the basis of foraminifers and molluscs, but some information about the latter group was compiled from very heterogeneous data (of sampling effort or taxonomic criteria), and Pleistocene and Holocene deposits still had not been discriminated, and were treated as contemporaneous.

The area of study comprises the Uruguayan coastline in the zones where the shell-bearing deposits of Villa Soriano Formation outcrop. Localities where collection took place are shown in figure 2.

Taphonomy and depositional environment

According to our own observations, two kinds of shell-beds have been found: 1) autochthonous assemblages, and 2) parautochthonous shell concentrations.

Autochthonous associations (La Caballada, Arazatí and Playa Pascual, see figure 3) are defined by the predominance of articulated valves in life position found in frequently bioturbated mudstones, which are very rich in organic content. Shells are unsorted by size. A low energy regime is clear, and the depositional environment is interpreted as coastal lagoons.

Parautochthonous shell concentrations (the remaining localities) are composed of accumulations of disarticulated, sometimes broken and abraded, mostly chaotically arranged (although sometimes nested) shells, in a coarse to medium sandy matrix, showing parallel or cross-bedded stratification. They are interpreted as littoral bars deposited in foreshore to near shore high-energy environments, strongly influenced by waves and currents.

Material and methods

After making taphonomic and stratigraphic observations, bulk sample units of about 3 dm^3 of the mollusc bearing levels were collected at the localities shown in figure 2. Stratigraphic sections for each locality studied are shown in figure 3.

Data on the present distribution, temperature and salinity tolerance of the molluscs (Appendix 1) were taken from Figueiras and Sicardi (1968-1974, 1979, 1980), Sprechmann (1978), Layerle and Scarabino (1984), Di Persia and Olazarri (1986), Mansur *et al.*

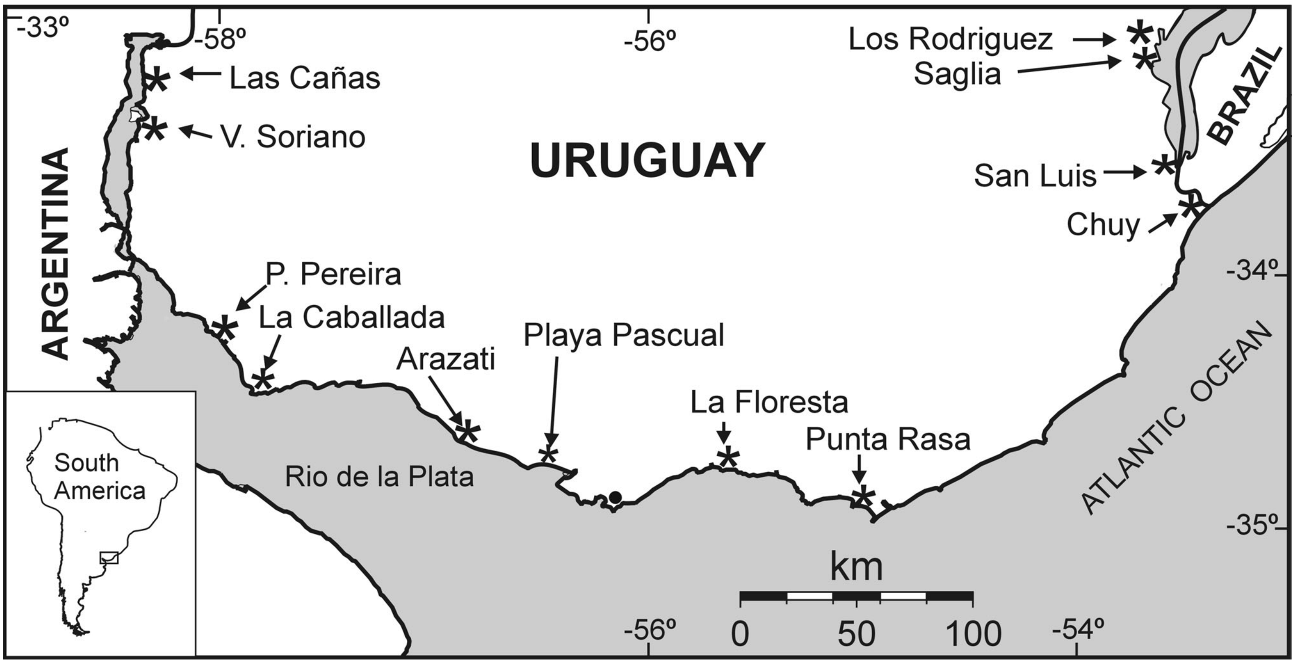


Figure 2. Localities mentioned in the text / *localidades mencionadas en el texto.*

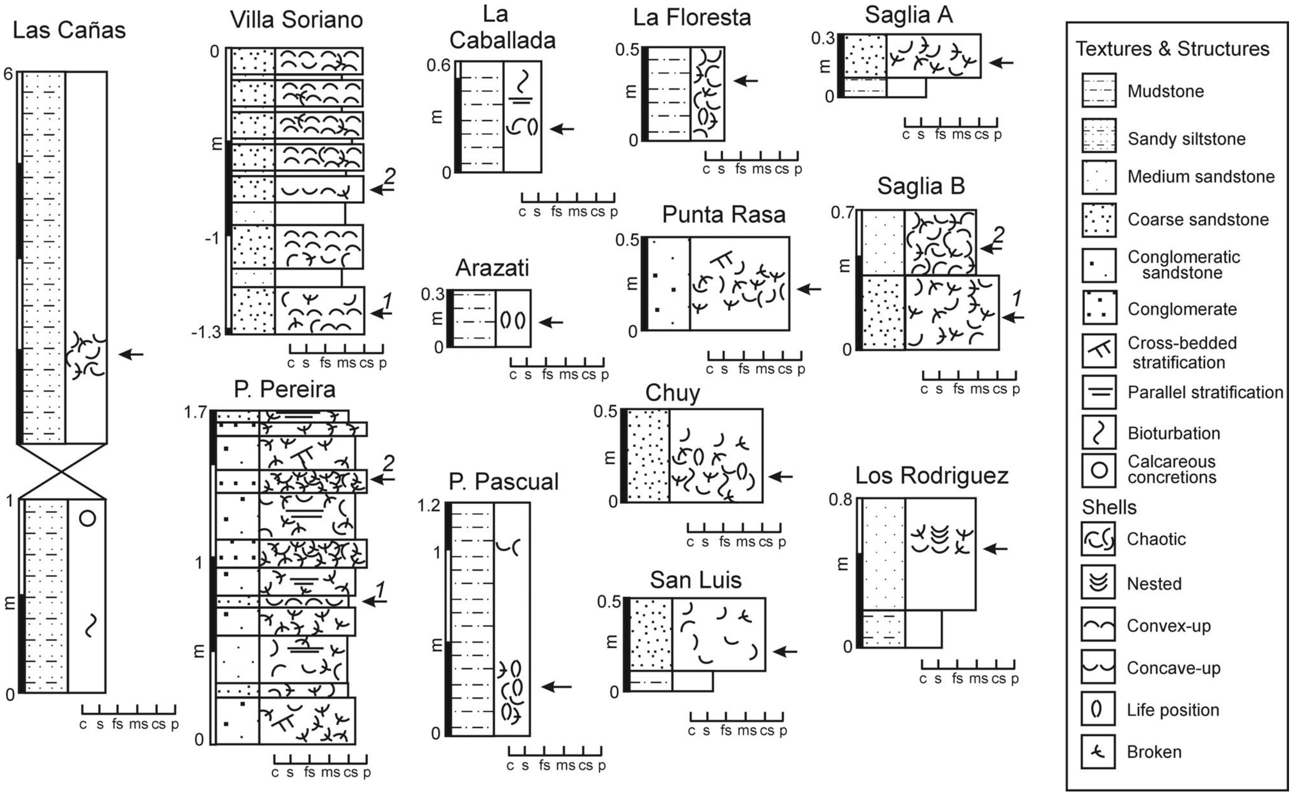


Figure 3. Stratigraphic sections of the localities studied. Samples were taken from levels shown by the arrows. c = clay, s = silt, fs = fine sand, ms = medium sand, cs = coarse sand, p = pebble. 0 = local base of stratigraphic section / *secciones estratigráficas de las localidades estudiadas. Las muestras fueron tomadas de los niveles señalados con las flechas. c = arcilla, s = limo, fs = arena fina, ms = arena media, cs = arena gruesa, p = grava. 0 = base local de la sección estratigráfica.*

(1991), Rios (1994), and Scarabino (2003, 2004). Regarding salinity, species were classified into two categories: estuarine and marine (no limnic species were found). The first one comprises species considered true estuarine, that is, those that only live in brackish water. Since this was the delimiting criterion, the remaining species were considered to be marine, regardless their tolerance to salinity changes. To be euryhaline implies a potential attribute, not a true environmental restriction. In relation to temperature, species were grouped according to their origin: tropical-subtropical, those that are shared with northern warmer areas (Brazilian Province); cold, those shared with the southern colder areas (Magallanic Province); and endemic, those present only in the Argentinean Province.

Specimens were counted (right and left valves of bivalves were counted separately, taking into account the maximum number), and relative abundance of species was expressed as (i) percentages (see appendix 1), and (ii) intervals: 1 (>50%), 2 (50%-25%), 3 (25%-5%), 4 (<5%).

Similarity-dissimilarity in mollusc species content among the localities (presence-absence) was asserted using both Dice association Coefficient and Raup and Crick (1979) Index. (Dice Coefficient= 2a/(2a+b+c), where "a" is the number of taxa shared by the samples; "b" and "c" are the taxa present in one sample and absent from the other; RC Index= the probability that kerl will be less than or equal to kobs, being kerl theoretically possible values of k generated by Monte Carlo simulations; kobs the number of taxa actually shared by assemblages, and k the number of taxa common to both assemblages). Although Dice Coefficient provides a minimum distortion in binary data (Archer and Maples, 1987; Maples and Archer, 1988), the Raup and Crick Index was also calculated because it uses a randomization of Monte Carlo procedure. Non Metric Multidimensional Scaling, minimum spawning tree, and Q and R modes (UPGMA) Cluster Analysis were carried out. Correspondence analyses were performed for abundance data. It is an ordination method that uses eigenanalysis of the Chi-squared distances between all data, very appropiated for counted data. (Kent and Coker, 1994; Hammer *et al.*, 2001). PAST 1.34 (Hammer *et al.*, 2001) was the computer program used.

Mineralogical alteration of the shells used for the radiocarbon dating was evaluated by analysing their

Table 1. Radiocarbon and calculated ages for molluscs and additional data / *edades radiocarbónicas y calculadas de los moluscos y datos complementarios.*

Locality	HPMSL estimated	species	^{14}C yr BP	95.4 % (2σ) cal age (BP)	lab. Nr.
Las Cañas	5 m	*E. mactroides*	4550+/-60	4445 - 4816	LP-913
V. Soriano 1	1m	*E. mactroides*	5530+/-80	5598 - 5996	LP-744
V.Soriano 2	2m	*E. mactroides*	5840+/-70	5946 - 6313	LP-740
P.Pereira 1	1.5m	*E. mactroides*	3590+/-60	3209 - 3565	LP-775
P.Pereira2	3m	*E. mactroides*	3300+/-60	2830 - 3235	LP-753
La Caballada	0.5m	*M. isabelleana**	6020+/-85	6163 - 6580	LP-806
Arazatí	0.4m	*O. equestris**	6260+/-90	6388 - 6849	LP-747
Playa Pascual	0.4m	*M. isabelleana**	5870+/-90	5953 - 6393	LP-815
La Floresta	0.4m	*M. isabelleana*	4790+/-80	4772 - 5258	LP-904
Punta Rasa	0.4m	*T. patagonica*	2490+/-70	1858 - 2276	LP-817
Chuy	1m	*M. isabelleana*	5070+/-70	5073 - 5541	LP-821
San Luis	2m	*E. mactroides*	5150+/-80	5279 - 5577	LP-829
Saglia A	3m	*E. mactroides*	3530+/-50	3148 - 3468	LP-907
Saglia B 1	2m	*E. mactroides*	4800+/-70	4798 - 5241	LP-901
Saglia B 2	2.5m	*E. mactroides*	4460+/-70	4312 - 4786	LP-893
Los Rodríguez	3m	*E. mactroides*	4000+/-70	3673 - 4124	LP-887

* = life position.
HPSML: height above present mean sea level
* = posición de vida
HPSML: altura sobre el nivel medio del mar actual.

mineralogical composition using X-ray diffraction. Four samples showed some degree of mineralogical alteration (La Caballada, San Luis, Chuy, Saglia 2B), however, their results do not disagree with the range of ages obtained by the other samples.

Radiocarbon and X-ray diffraction analyses were performed at the Laboratorio de Tritio y Radiocarbono (LATYR) at the Museo de La Plata (Argentina). Ages were calibrated using the program CALIB 4.4.1 (Stuiver and Reimer, 1993), with the Stuiver *et al.* (1998) calibration dataset, assumed 15+ -2 per mil delta ^{13}C, and 82+ -46 delta R.

Samples used for dating in La Caballada, Arazati, and Playa Pascual were articulated valves found in life position (autochthonous). but the others were isolated valves recovered from parautochthonous assemblages that presumably represent time-averaged accumulations (single or multiple events). Flessa *et al.* (1993), Flessa and Kowalewski (1994), Wehmiller *et al.* (1995), Schellmann and Radtke (1997), and Kowalewski *et al.* (1998), have demonstrated time averaging from hundreds (usually) up to three thousands years, for recent and near shore Quaternary shell-beds. Estimations of the exact extent of this time averaging are strongly dependent on several variables for each shell-bed. In our case, for example, and due to reworking (although alteration may be playing a role), we found in Villa Soriano a stratigraphical lower sample with a radiocarbon age around 300 years younger than the upper sample. Although it gives some uncertainty, both are within the range of ages presented here.

Specimens are deposited in the collection of invertebrate fossils, Facultad de Ciencias, Montevideo, Uruguay (FCDPI).

Results and discussion

Age

Radiocarbon ages and related data are shown in table 1. According to our results, mollusc-bearing Holocene deposits of Uruguay would have a maximum range of 6849-1858 cal. years B.P. These results are similar to the radiocarbon ages obtained for the Argentinean (Buenos Aires province) Las Escobas Formation, with ranges from 7600 to 1400 ^{14}C yr B.P. (Aguirre and Whatley, 1995; Aguirre and Urrutia, 2002). However, Rojas (2002) has reported in a brief communication an age of 9830 +/- 90 ^{14}C yr B.P. for a Uruguayan locality (Sauce creek, near Nueva Palmira city) a datum that must be confirmed.

As is shown in figure 4, age-ranges make a rather compact group, with a pair of exceptions, that would be Los Rodríguez and Punta Rasa. The range of the former does not overlap with others in general, but just for a brief period of time (*ca.* 100 years), and it can be safely included into the group. On the other hand, Punta Rasa is clearly disconnected from the other ages, being the youngest of all. According to our data, if the age hiatus between Punta Rasa and the other lo-

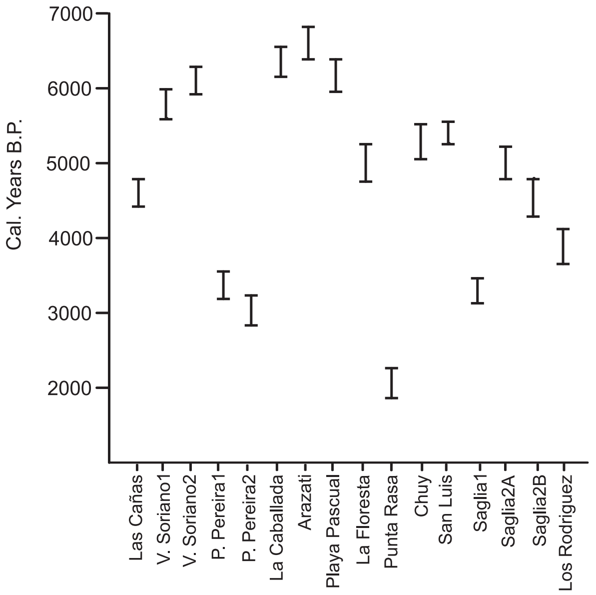


Figure 4. Age ranges (bars) for the studied localities / *rangos de edades (barras) de las localidades estudiadas.*

calities is consequence of a lowering of sea level and represents a true absence of a marine record, it would be the only relevant oscillation registered.

Paleoecology

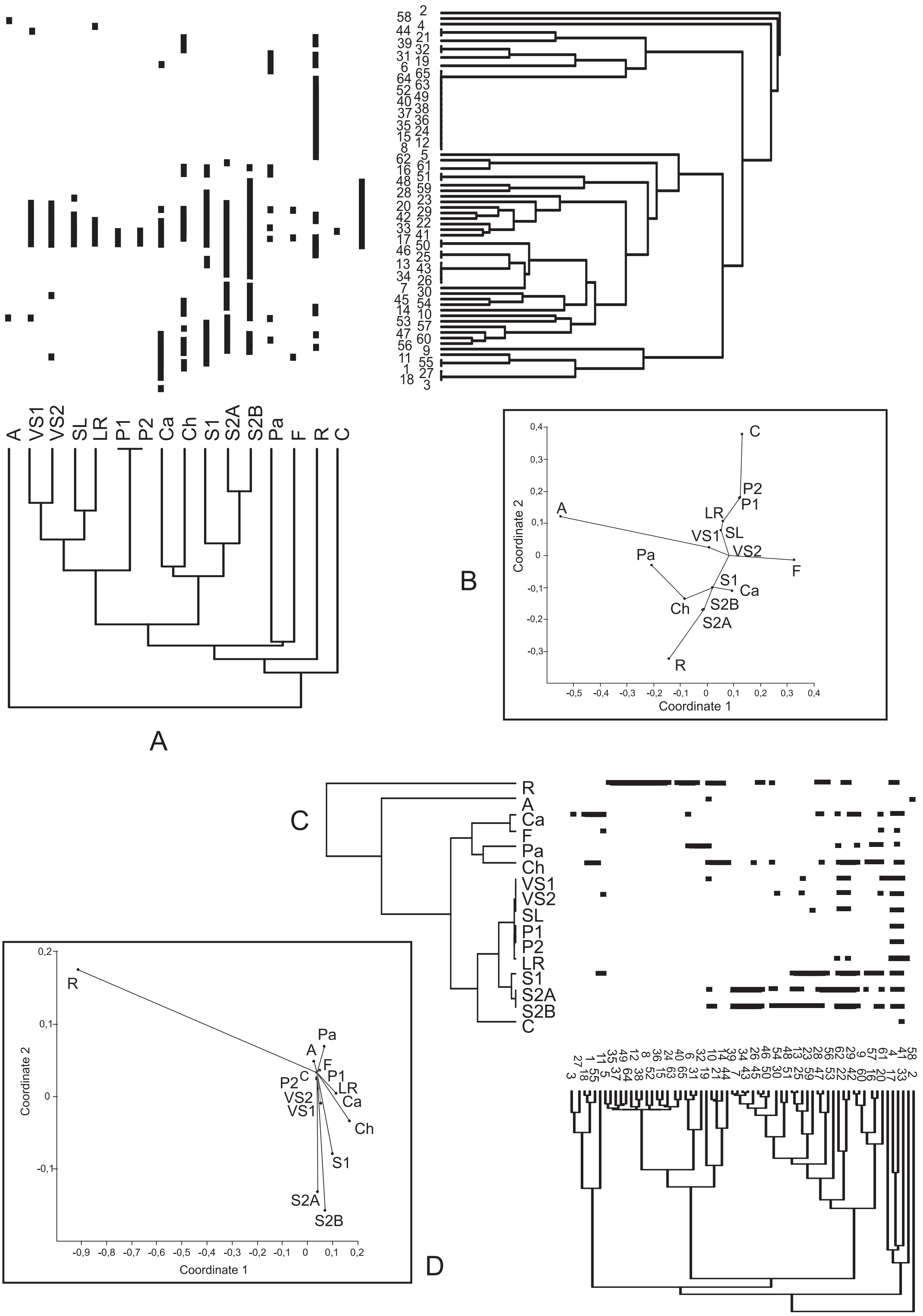
Remarks on faunal composition. Recorded taxa are listed by locality in Appendix 1. With the exceptions of *Anomalocardia brasiliana* (Gmelin), *Marshallora nigrocincta* (C.B. Adams), *Nioche subrostrata* (Lamarck), *Bulla striata* Bruguìere, and *Miralda* sp., all species are present today along the Uruguayan coast. The geographic distribution of *Anomalocardia brasiliana* and *Bulla striata* ranges from the Caribbean region to Rio Grande do Sul (Brazil), *Marshallora nigrocincta* from North Carolina (USA) to Santa Catarina (Brazil), and *Nioche subrostrata* from Florida (USA) to São Paulo (Brazil). The genus *Miralda* is present from Florida to northern Brazil (Rios, 1994).

Some taxa are recorded for the Uruguayan Quaternary for the first time: *Nuculana janeiroensis* E. A. Smith, *Crepidula plana* Say, *Miralda* sp., and a representative of the Family Ellobidae, not determined yet.

Results of Cluster analysis and NMDS (figure 5) show that three localities are discriminated from the others: Punta Rasa in all cases, and Arazatí and Las Cañas in some (both in dendrograms applying Dice coefficient, and Arazatí in the result of cluster analysis applying Raup and Crick coefficient). The two latter differ from the other localities in being monospecific or almost [Las Cañas: *Erodona mactroides* Daudin; Arazatí: *Ostrea equestris* Say, and *Ennucula puelcha* (d'Orbigny)], but Punta Rasa is the richest in number of species. It includes some species that are not shared with any other site. These are: *Glycymeris longior* (G. B. Sowerby I), *Brachidontes darwinianus* (d´Orbigny), *Plicatula gibbosa* Lamarck, *Crassinella maldonadoensis* (Pilsbry), *Amiantis purpuratus* (Lamarck), *Lottia subrugosa* (d´Orbigny), *Diodora patagonica* (d´Orbigny), *Tegula patagonica* (d´Orbigny), *Calliostoma jucundum* (Gould), *Nodiottorina lineolata* (d'Orbigny), *Seila adamsi* (H.C. Lea), *Urosalpinx cala* (Pilsbry), *Hanetia haneti* (Petit de la Saussaye), *Siphonaria lessoni* (Blainville), Ellobidae indet. It is suggestive the high proportion of species that inhabit rocky or hard substrates (*B. darwinianus*, *P. gibbosa*, *L. subrugosa*, *D. patagonica*, *H. haneti*, *U. cala*, *S. lessoni*, see Appendix 1), the maximum among the samples studied.

When analyzing abundance (figure 6, Correspondence analysis), Arazatí and Punta Rasa are also differentiated from the rest of the localities, but Las Cañas is grouped with others (especially Punta Pereira 1 and 2) where *Erodona mactroides* largely predominates. Arazatí is distinguished either by the presence of *Ennucula puelcha*, when taking into account abundance intervals, or *Ostrea equestris*, when using percentages. Considering abundance intervals, Punta Rasa is related with *Mytilus edulis* Linné, and following percentages with *Glycymeris longior*, *Brachidontes darwinianus*, *Plicatula gibbosa*, *Crassinella maldonadoensis*, *Amiantis purpuratus*, *Lottia subrugosa*, *Diodora patagonica*, *Tegula patagonica*, *Seila adamsi*, *Urosalpinx cala*, *Siphonaria lessoni*, Ellobidae indet., *Corbula lyoni* Pilsbry, *Corbula* sp. and *Tawera gayi* (Hupé). This species list is very similar to the resultant of the presence-absence data, with the addition of the two species of *Corbula* and *T. gayi*, and the elimina-

Figure 5. A, Two-way cluster analysis, Dice coefficient. **B,** NMDS with superimposed minimum spawning tree, Dice coefficient. **C,** Two-way cluster analysis, Raup-Crick coefficient. **D,** NMDS with superimposed minimum spawning tree, Raup-Crick coefficient. Codes of localities and species as in Appendix 1 / ***A,*** *Análisis de agrupamiento de dos vías, coeficiente de Dice.* ***B,*** *NMDS con árbol de distancias mínimas sobreimpuesto, coeficiente de Dice.* ***C,*** *Análisis de agrupamiento de dos vías, coeficiente de Raup y Crick.* ***D,*** *NMDS con árbol de distancias mínimas sobreimpuesto, coeficiente de Raup y Crick. Las codificaciones de las localidades son las mismas del Apéndice 1.*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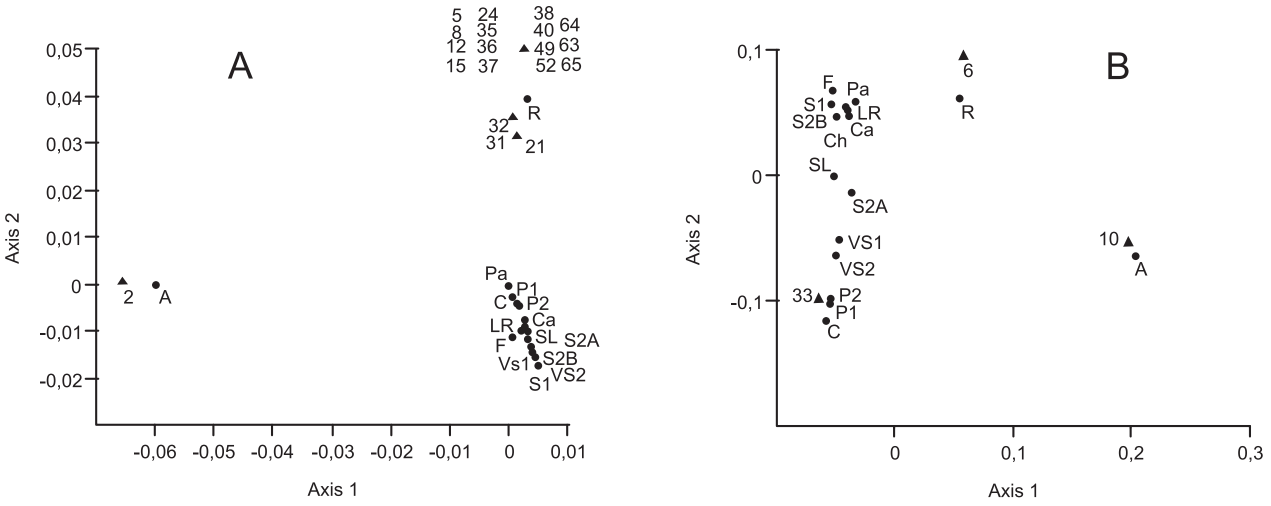

Figure 6. A, Correspondence analysis, abundance of species expressed as intervals (see text). Only the species close to Punta Rasa and Arazatí are included, since the others are too crowded in the remaining localities. **B,** Correspondence analysis, abundance of species expressed as percentages. Only the species close to Punta Rasa, Arazatí and Las Cañas are included, since the others are too crowded in the remaining localities. Codes of localities and species as in Appendix 1 / ***A,*** *Análisis de Correspondencia, la abundancia de las especies tomada en intervalos (ver texto). Solamente las especies cercanas a Punta Rasa y Arazatí se han incluido, ya que las demás forman un grupo muy compacto junto con las restantes localidades.* ***B,*** *Análisis de Correspondencia, la abundancia de las especies tomada como porcentajes. Solamente las especies cercanas a Punta Rasa, Arazatí y Las Cañas se han incluido, ya que las demás forman un grupo muy compacto junto con las restantes localidades.*

tion of *Calliostoma jucundum*, *Nodilittorina lineolata* and *Hanetia haneti*.

Salinity

Species were classified according to their salinity range (see Appendix 1), and the relative frequency of salinity groups was calculated for each sample. This information is summarized in figure 7, altogether with the current distribution of mollusc salinity ranges.

We then propose that the marine front during the Holocene was further to the northwest than at

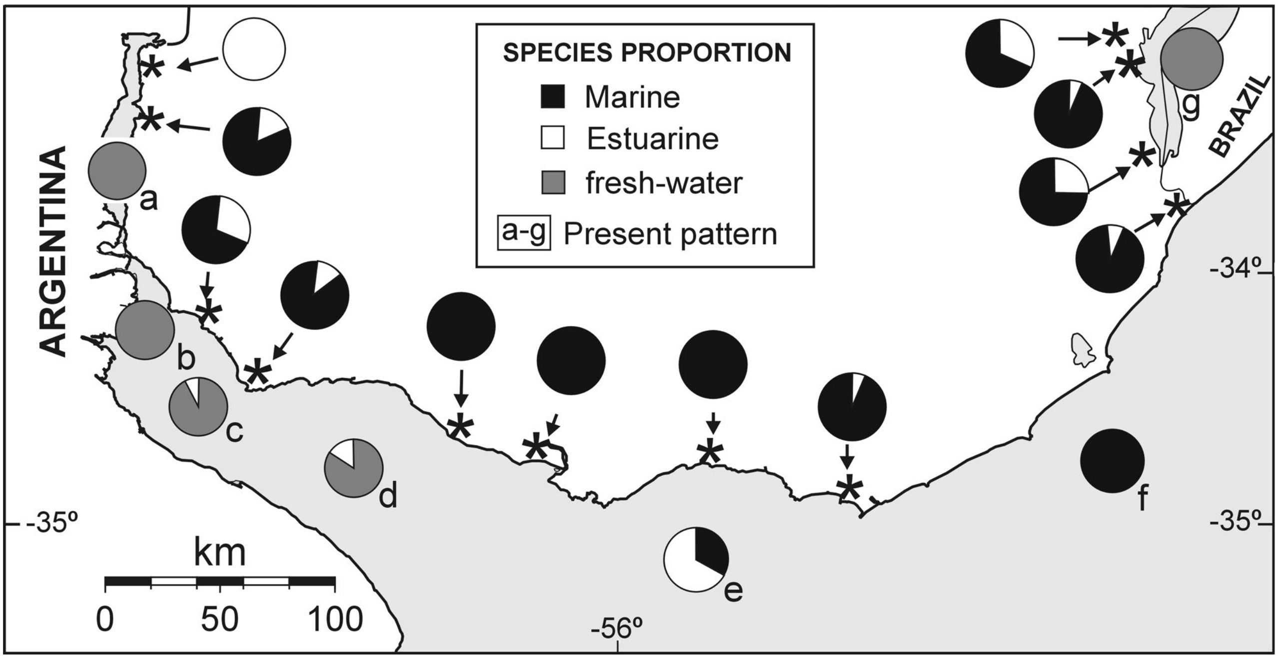

Figure 7. Proportion (by locality) of molluscan species according to their salinity range / *proporciones por localidad de las especies de moluscos según su rango de salinidad.*

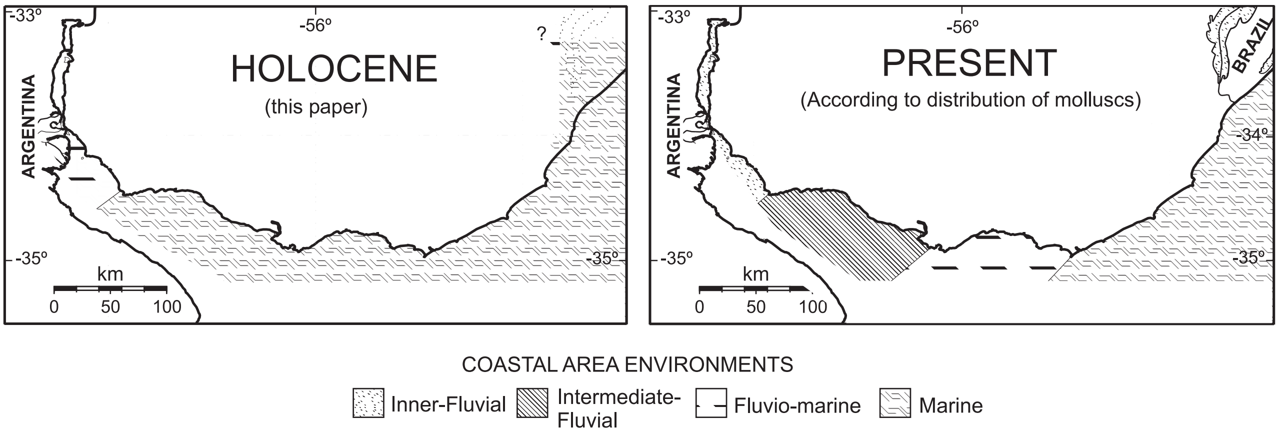

Figure 8. Holocene and Present Uruguayan coastal area environments according to mollusc content / *ambientes del Holoceno y Actual de la costa Uruguaya de acuerdo a sus moluscos.*

present times (about 300 km farther) (figure 8), beyond the limits proposed by Sprechmann (1978). This conclusion must be interpreted as a general trend throughout the estimated age range of the deposits (taking into account the shell-beds time averaging).

Temperature

Species were also classified according to their thermal ranges (see Appendix 1), and the relative frequencies of these classes compared with the modern ones, according to the data of Sicardi (1967). The results (figure 9) indicate that for the time interval considered, a greater proportion of warm-water species and a smaller proportion of cold-water species characterized the fossil mollusc assemblages. Furthermore, there are in the Holocene assemblages five warm water species that do not live today along the Uruguayan coast, having their southern distribution limit displaced northwards. Stronger south-

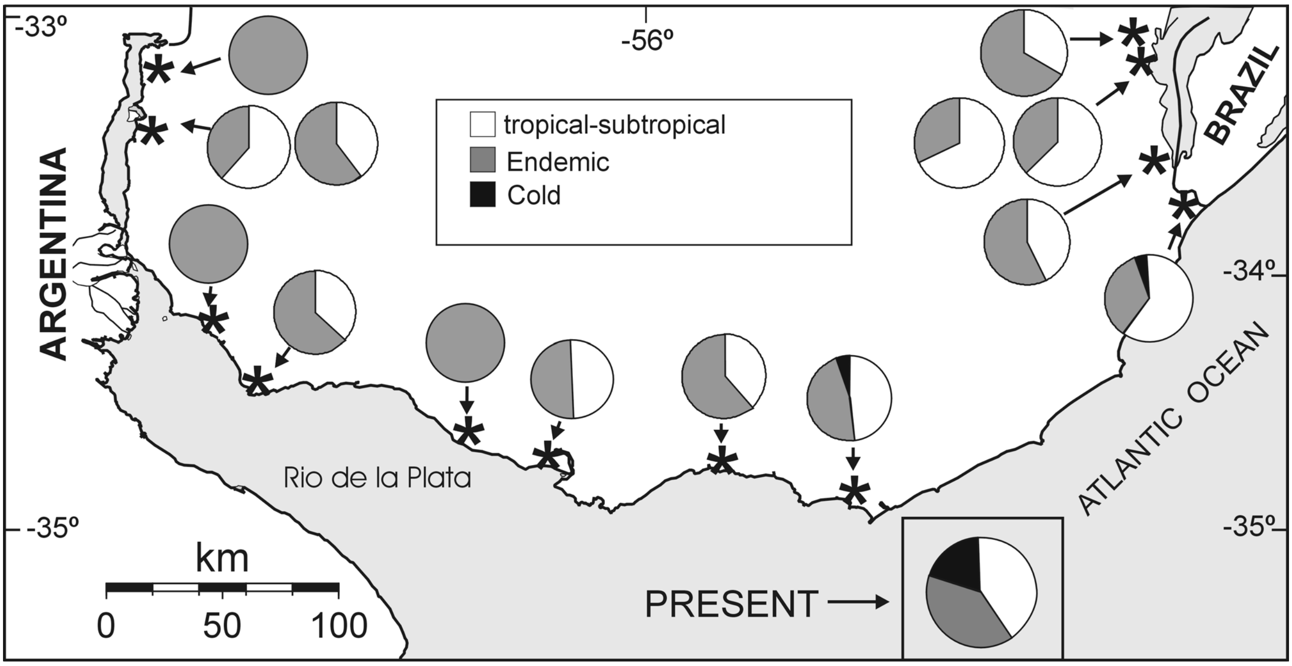

Figure 9. Proportion (by locality) of molluscan species according to their thermal range / *proporciones por localidad de las especies de moluscos según su rango térmico.*

ward-flowing warm Brazil currents could be postulated as a mechanism to explain warmer temperatures in the Quaternary (Martínez, 1990; Martínez *et al.*, 2001). This would be reinforced by the shift of the estuarine and marine fronts of the Río de la Plata towards the West, given that today the decrease in salinity caused by the discharge of fresh water from the Rio de la Plata is a significant barrier for many subtropical species (Scarabino, 1977; Piola *et al.*, 2000).

Conclusions

The age of Holocene shell-beds from Uruguay range from 6849-1858 cal. years B.P. and indicate almost continuously a higher sea level than that present today.

The only possible gap could be between 2276 and 2830 cal. years B.P. (oldest and youngest calculated ages of Punta Rasa and Punta Pereira).

The salinity front of the Rio de la Plata estuary was displaced in the Uruguayan coast about 300 km westwards during the Holocene transgression.

For the time interval considered, temperature was warmer than at present.

Nearly all the recorded species are present today along the Uruguayan coast.

Exceptions to the condition stated above are *Anomalocardia brasiliana*, *Marshallora nigrocincta*, *Nioche subrostrata*, *Bulla striata* and *Miralda* sp., whose present geographical ranges do not reach as far south as Uruguay.

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Appendix 1. Recorded species by locality (percentages) and classification according to temperature and salinity ranges / *especies registradas en cada localidad (abundancia expresada en porcentajes), y clasificación de acuerdo a sus rangos térmicos y de salinidad.* * = less than 0.1 / *menor que 0,1.*

C: Las Cañas, VS1: Villa Soriano 1, VS2: Villa Soriano 2, P1: Punta Pereira 1, P2: Punta Pereira 2, Ca: La Caballada, A: Arazatí, Pa: Playa Pascual, F: La Floresta, R: Punta Rasa, C: Arroyo Chuy, SL: Arroyo San Luis, S1: Saglia 1, S2A: Saglia 2A, S2B: Saglia 2B, LR: Los Rodríguez.

TS: tropical-subtropical, AR: endemic to Argentinean Province, CO: cold, MA: marine, ES: estuarine. See Material and Methods for details. TS: tropical-subtropical, AR: endémica de la Provincia Argentina, CO: fría, MA: marina, ES: estuarina. Ver Material y Métodos por detalles.

																	Temperature			Salinity	
	C	VS1	VS2	P1	P2	Ca	A	Pa	F	R	Ch	SL	S1	S2A	S2B	LR	TS	AR	CO	MA	ES
1 *Nucula semiornata*	0	0	0	0	0	0.2	0	0	0	0	1.14	0	0	0	0	0	x			x	
2 *Ennucula puelcha*	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0		x		x	
3 *Nuculana janeiroensis*	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0		x		x	
4 *Anadara ovalis*	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x			x	
5 *Glycymeris longior*	0	0	0	0	0	0	0	0	0	0.8	0	0	0	0	0	0	x			x	
6 *Mytilus edulis*	0	0	0	0	0	3.89	0	5.4	0	50.2	0	0	0	0	0	0		x		x	
7 Mytilidae indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	*	0					
8 *Brachidontes darwinianus*	0	0	0	0	0	0	0	0	0	0.8	0	0	0	0	0	0		x		x	
9 *Brachidontes* sp.	0	0	0	0	0	1.7	0	0	0	0	0.1	0	*	0.1	*	0					
10 *Ostrea equestris*	0	1.2	0	0	0	0	98	0.7	0	10.8	0.1	0	0	2.2	0.3	0	x			x	
11 *Ostrea* sp.	0	0	1.6	0	0	0.37	0	0	1	0	0	0	*	0	0	0					
12 *Plicatula gibbosa*	0	0	0	0	0	0	0	0	0	2.03	0	0	0	0	0	0	x			x	
13 *Phlyctiderma semiaspera*	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.2	*	0	x			x	
14 *Carditamera plata*	0	0	0	0	0	0	0	0	0	0.1	1.2	0	0	0	*	0	x			x	
15 *Crassinella maldonadoensis*	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0		x		x	
16 *Mactra* sp.	0	0	0	0	0	0	0	4.7	0	0	*	0	*	0	0	0					
17 *Mactra isabelleana*	0	10.1	6	11.5	14.7	7.2	0	0	0	2.4	0	0.5	1.8	19.9	2.8	*		x		x	
18 *Tellina gibber*	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0		x		x	
19 *Macoma uruguayensis*	0	0	0	0	0	0	0	0.7	0	0	0	0	0	0	0	0		x		x	
20 *Tagelus plebeius*	0	0.4	1.3	0	0	1.7	0	8.8	1	0	0.4	0	*	0.2	0.2	0		x		x	
21 *Tawera gayi*	0	0	0	0	0	0	0	0	0	0.6	4.3	0	0	0	0	0			x	x	
22 *Anomalocardia brasiliana*	0	4.3	5.1	0	0	0.9	0	3.4	0	0	15.1	0.2	*	0.1	*	*	x			x	
23 *Pitar rostratus*	0	0.8	0.9	0	0	0	0	0	0	0	0	0	*	0.3	0.1	0	x			x	
24 *Amiantis purpuratus*	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	x			x	
25 *Nioche subrostrata*	0	0	0	0	0	0	0	0	0	0	0	0	0.1	1.9	0.3	0	x			x	
26 *Petricola lapicida*	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	x			x	
27 *Petricola stellae*	0	0	0	0	0	0.6	0	0	0	0	*	0	0	0	0	0	x			x	
28 *Sphenia fragilis*	0	0	0	0	0	0	0	0	0	0	0	*	0.1	0	0.1	0	x			x	
29 *Corbula caribaea*	0	1.2	0.6	0	0	0	0	0	0	0.2	1.4	0.2	0.4	3.1	1.3	0	x			x	
30 *Corbula patagonica*	0	0	0,3	0	0	0	0	0	0	0	0	0	0	0,1	*	0		x		x	
31 *Corbula lyoni*	0	0	0	0	0	0	0	0.7	0	0.1	0	0	0	0	0	0		x		x	
32 *Corbula* sp.	0	0	0	0	0	0	0	0.7	0	0.1	0	0	0	0	0	0					
33 *Erodona mactroides*	100	55.4	65.8	88.2	85.1	0.2	0	0	0	0	0.7	37	4.4	30	6.1	1		x			x
34 *Cyrtopleura* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.1	0					

Appendix 1. (cont.)

																	Temperature			Salinity	
	C	VS1	VS2	P1	P2	Ca	A	Pa	F	R	Ch	SL	S1	S2A	S2B	LR	TS	AR	CO	MA	ES
35 *Lottia subrugosa*	0	0	0	0	0	0	0	0	0	4.6	0	0	0	0	0	0	x			x	
36 *Diodora patagonica*	0	0	0	0	0	0	0	0	0	0.6	0	0	0	0	0	0	x			x	
37 *Tegula patagonica*	0	0	0	0	0	0	0	0	0	4.6	0	0	0	0	0	0		x		x	
38 *Calliostoma jucundum*	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0		x		x	
39 *Finella dubia*	0	0	0	0	0	0	0	0	0	0	1.51	0	0	0	0	0	x			x	
40 *Nodiolittorina lineolata*	0	0	0	0	0	0	0	0	0	1.9	0	0	0	0	0	0	x			x	
41 *Heleobia australis*	0	19.8	14.6	0.3	0.2	74.1	0	71.6	98	3.72	71.	61	92.6	37.2	83.6	70.7		x		x	
42 *Heleobia charruana*	0	6.6	3.8	0	0	1.3	0	0	0	2	0.6	1.2	0.1	1.5	2.8	28.2		x			x
43 *Crepidula plana*	0	0	0	0	0	0	0	0	0	0	0	0	0	*	*	0	x			x	
44 *Crepidula protea*	0	0	0	0	0	0	0	0	0	0	0.1	0	0	*	*	0	x			x	
45 *Bostrycapulus aculeata*	0	0	0	0	0	0	0	0	0	7.1	0.1	0	0	0	0	0	x			x	
46 *Marshallora nigrocincta*	0	0	0	0	0	0	0	0	0	0.6	0	0	0	*	0.2	0					
47 “*Triphora*” *medinae*	0	0	0	0	0	0.2	0	0	0	0.1	0	0	*	0.1	0.1	0	x			x	
48 *Cerithiopsis greeni*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	x			x	
49 *Seila adamsi*	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	x			x	
50 *Epitonium albidum*	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0.1	0.1	0	x			x	
51 *Epitonium georgettinum*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0		x		x	
52 *Urosalpinx cala*	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0		x		x	
53 *Hanetia haneti*	0	0	0	0	0	0	0	0	0	1.1	0	0	0	0	0	0		x		x	
54 *Costoanachis sertulariarum*	0	0	0	0	0	0	0	0	0	2.6	0	0	*	*	0	0		x		x	
55 *Paravanachis paessleri*	0	0	0	0	0	0	0	0	0	0.1	0.4	0	0	0.1	0.3	0		x		x	
56 *Buccinanops globulosus*	0	0	0	0	0	2.4	0	0	0	0	*	0	*	0	0	0		x		x	
57 *Olivella tehuelcha*	0	0	0	0	0	0.2	0	0	0	0.1	0.3	0	*	1.1	0.3	0		x		x	
58 *Turbonilla uruguayensis*	0	0	0	0	0	0	0	0	0	0	0.1	0	*	*		0		x		x	
59 *Miralda* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	x			x	
60 *Boonea jadisi*	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0.2	0	x			x	
61 *Cylichna bidentata*	0	0	0	0	0	2.6	0	0.7	0	0	0.8	0	0.1	0.1	0.4	0	x			x	
62 *Acteocina candei*	0	0	0	0	0	0	0	0.7	0	0	0.6	0	*	0	0.1	0	x			x	
63 *Bulla striata*	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	x			x	
64 *Siphonaria lessoni*	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0			x	x	
65 Ellobidae indet.	0	0	0	0	0	0	0	0	0	1.2	0	0	0	0	0	0	x			x	