HIGHSTANDS OF THE SEA LEVEL AND THE SPECIATION OF COASTAL COMMUNITIES: OPPORTUNITIES FOR THE NEW TERRITORIES IN SOUTHERN SOUTH AMERICA

Federico Ignacio Isla

Instituto de Geología de Costas y del Cuaternario, CONICET-UNMDP, casilla de correo 722, 7600 Mar del Plata, Argentina. Email: fisla@mdp.edu.ar

Abstract

The sea-level fluctuation during the Holocene has induced the emergence of new geographical extensions constrained by some conditioning factors as salinity regimes, habitats and substrates. At the coast of Argentina, some organisms have taken advantage of these factors. A genera of the rissoidean snail, *Heleobia australis* (D'Orbigny 1835), has colonised estuarine areas (mudflats, coastal lagoons, estuaries) with significant changes in regard to the salinity regime. The rodent *Ctenomys australis* (Rusconi 1934) has specialized to live on barrier dunes, environments significantly different from those occupied by the ancient lineages of this family. In Patagonia, embayments between headlands have changed in their sediment availability during the different highstands of the Quaternary. Benthic communities were therefore more related to the changes of the bottom composition of these marine terraces than to sea surface temperatures. The Holocene jumps of the sea level could have caused similar rapid effects when the sea surpassed certain levels causing the approximately-sudden flood of a former subaerial depression.

Keywords: sea level changes, new environments, speciation, Holocene.

Niveles altos del mar y la especiación de comunidades costeras: oportunidades para los nuevos territorios en el sur de Sudamérica

Resumen

La fluctuación del nivel durante el Holoceno indujo la emergencia de nuevas áreas geográficas limitadas a algunos factores condicionantes como el régimen de salinidad, hábitats y sustratos. En la costa argentina, algunos organismos han sido favorecidos por esos factores. El caracol risoideo, *Heleobia australis* (D'Orbigny 1835), colonizó áreas estuarinas (planicies de fango, lagunas costeras, estuarios) de cambios significativos en relación con el régimen salino. El roedor *Ctenomys australis* (Rusconi 1934) se ha especializado para vivir en barreras medanosas, ambientes significativamente diferentes a los que ocupaban los antecesores de esta familia. En Patagonia, las ensenadas entre cabos han cambiado en su disponibilidad de sedimento durante los estadíos altos del mar durante el Cuaternario. Las comunidades bentónicas estuvieron así más relacionadas a los cambios en la composición del fondo que a los de la temperatura superficial. Los saltos del nivel durante el Holoceno han causado similares efectos rápidos cuando el mar superó cierto nivel causando la inundación aproximadamente rápida de una depresión emergida previamente.

Palabras clave: cambios del nivel del mar, nuevos ambientes, especiación, Holoceno.

Introduction

Landscape controls the evolution of animals: The extended plains of South America have conditioned the evolution of running mammals (*Lama guanicoe, Hippidium* sp., *Dolichotis patagonum*) and running birds (*Hermosiornis, Rhea americana*). At the Argentine pampas, the Plio-Pleistocene interval, dominated by loessic plains, has permitted the survival of large mammals with high capacity to dig caves. Charles Darwin felt surprised that living armadillos seemed the smaller copies of the giant armadillos (gliptodontids). However, the processes of speciation have taken thousands of years and they are very difficult to discern along the geologic record (*"the missing pages of the book"*) although the Quaternary is particularly characterized by a more complete record, but dominated by rapid changes in climate and the sea level.

Evolution has milestones of geologic stable periods when species did not change separated by episodes of relatively abrupt changes ("coordinated stasis" in the sense of Brett *et al.*, 1996). Species associations are nearly constant with turnover events mostly associated to unconformities, sometimes associated to marine transgressions, although some apparent faunal turnovers can be related to the stratigraphic incompleteness of the record. Although the direct relationship between the geographical range size of species and their duration has been documented several times (with an inverse relation to species extinction), it is not clear the relationship between geographic ranges and the speciation rates (Jablonski & Roy, 2003). Spatial extensions imply a greater diversity of selective environments and so might drive greater adaptive opportunities for some populations. Although some authors assumed that larger areas are more subject to barrier constrains, the opposite can be also plausible: that larger areas make species insensible to these barriers and therefore can reduce the potential of speciation rates. In this sense, there are some examples where geographic ranges are inversely correlated, or without correlation to speciation rates (Jablonski & Roy, 2003). This reasoning extends beyond speciation rates towards the total number of species produced, increasing diversity (*i.e.* species richness) in direct relation to the territory involved.

The Holocene transgression signifies rapid environmental changes, with a sea level fluctuation that spanned only 6,000 years (Isla, 1989) and causing the emergence of several kilometres. It therefore offers an excellent interval to analyze the degree of change of coastal lineages. Human expansion by the Pacific Oceania was conditioned to the island habitability in response to the Late Holocene sea-level drop (Dickinson, 2003). Although predation and ecological interactions may explain some changes in the animal communities, they can not be related directly to speciation. Holocene fluctuations of the sea level, mostly those recorded in the Southern Hemisphere (Isla, 1989), implied significant changes in relation to the erosive action of rivers, waves or glaciers. At the same time, as the sediment availability causes significant changes in the environment, these changes control benthic communities. Dealing with estuaries, there are geological constrains as the geomorphological inheritance (paleoestuary configuration and river catchments dimensions) and the degree of sediment filling (estuary evolution-maturity) that conditioned the availability of ecological habitats (Roy *et al.*, 2001). The availability of sand induced coastal barriers as new territories for those organisms capable of getting advantage of these new habitats.
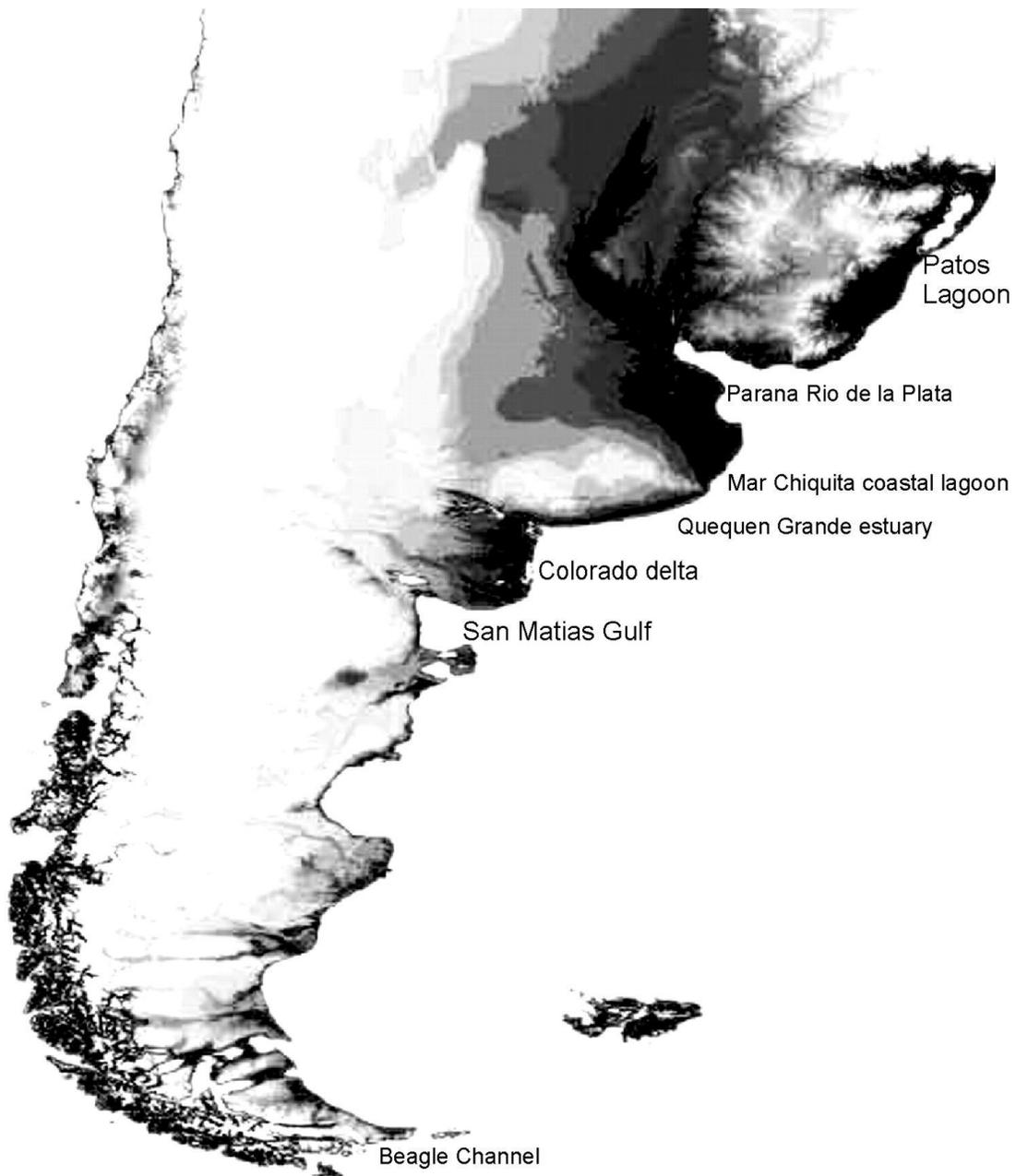
Figure 1. Digital terrain model of Eastern South America highlighting the costal plains below the 20 m altitude: Patos Lagoon, Paraná- de la Plata plain and Colorado delta (modified from Brooks *et al.,* 2006).

Figura 1. Modelo digital de superficie del Este de Sudamérica destacando las plancies costeras por debajo de los 20 m de altura: Laguna dos Patos, planicie del Paraná y Río de la Plata, y delta del Colorado (modificado de Brooks *et al.,* 2006).

Pleistocene faunistic changes were usually related to relatively-rapid climatic variations, being extinctions one of the most significant evidences (Grayson, 1984). While most of these extinctions were related to changes within the environment, little was searched about speciation phenomena related to areas that became emerged during the end of the highstands. In Patagonia there is a very good record of former highstands of the sea level with significant variations in the mollusc assemblages assigned mainly to climatic changes, sea-surface temperature, depth and substrate (Aguirre, 2003). Substrate effect is commonly referred to a simple dichotomy of hard or soft substrate. However, there are other significant conditioning factors related to the substrate; *e.g.* sediment transport, clogging effects, potential redox, bottom dynamics, predation, ecological interactions.

In the present review, several examples about the speciation of some taxa that took advantage of the Holocene sea-level fluctuation were described and analyzed. In particular, it was considered how hidrobid snails from Buenos Aires took advantage of extended tidal environments subject to different salinity dynamics (mudflats, coastal lagoons, estuaries). At coastal barriers, rodents of the genus *Ctenomys* evolved into new species with better conditions for digging into fine sand. The sediment composition of these barriers, beaches or nearshore facies are responsible for the composition, distribution and abundance of coastal mollusc communities.

The Holocene sea-level fluctuation in South America

The Eastern coast of South America is characterised by several Quaternary sea-level highstands, particularly where there are coastal plains below the 20 m height (Figure 1). However, the inherited topography conditioned the emplacement of these highstands. The Holocene is characterised by a sea-level fluctuation that occurred in the last 6000 years (Chappell, 1983; Isla, 1989, Angulo *et al.,* 2006). Conditioned to the slope of the coastal plain, this fluctuation provided significant extensions of land subject to tidal action or water-mixing effects (Isla *et al.,* 1996; Dillenburg *et al*. 2009). Plotting the maximum ages of the molluscs sampled in these Holocene estuarine deposits, progradation rates were maximum at the Patos coastal-lagoon, Paraná-De la Plata and Colorado Delta coastal plains (Figure 1).

At Rio Grande do Sul, several Quaternary highstands were recorded in response to a gentle coastal plain and a persistent sediment supply (Tomazelli *et al.,* 2000; Figure 2a). In Buenos Aires Province, the extension of coastal plains is conditioned to the inherited regional slope. The Eastern Barrier prograded on a very gentle dipping plain, while the Southern Barrier is attached to a hilly landscape between two ranges: Tandilia and Ventania (Isla *et al.,* 1996; Figure 2b).

Materials and methods

Most of the methods of this review were explained in previous papers or doctoral thesis (De Francesco, 2002; Mora, 2008; Godillo & Isla, 2010; Isla, 2011). Samplings of specimens of the *Heleobia* genus were collected at the same time that salinity and temperature were measured by the mean of a Horiba U10 water-quality checker (De Francesco & Isla, 2003). DNA haplotypes were compared from tissues of *Ctenomys talarum* and *C. australis* (Mora *et al.,* 2007). The isolation of the population of *C. australis* associated to habitat fragmentation was analyzed from ancient

photographs and modern images (Mora *et al.*, 2010).The ages of the different highstands were obtained from absolute datings (Uranium series, ESR and radiocarbon decayment methods) of different highstands (Gordillo & Isla, 2010). A radiocarbon dating on wood fragments was performed by the traditional "bulk sample" method. Distribution maps of molluscs were drafted using GIS procedures.
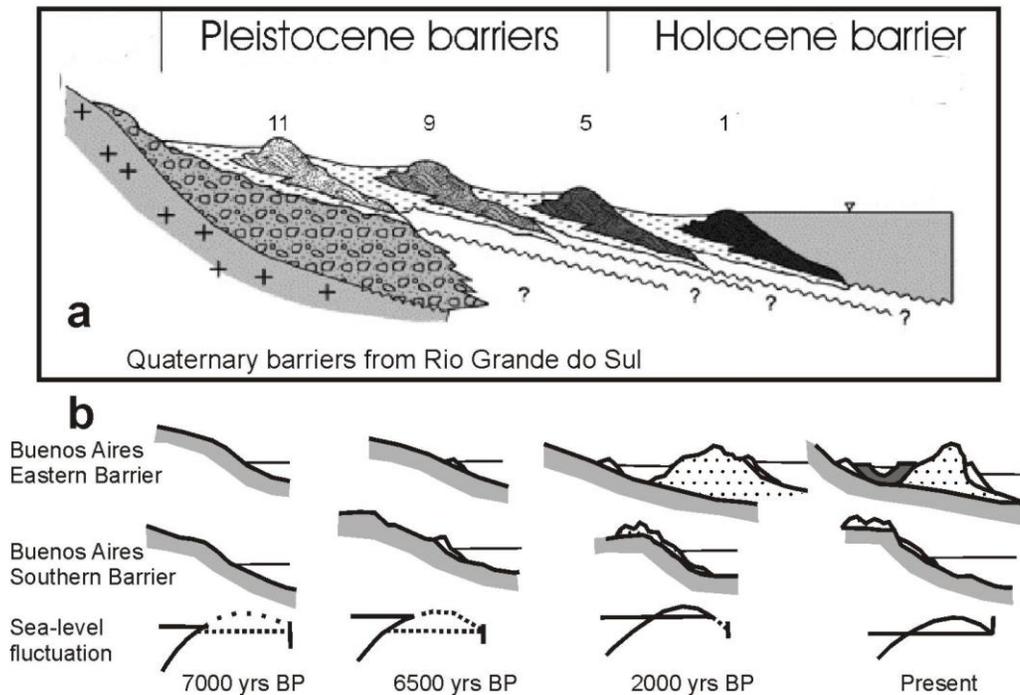

Figure 2. a) Progradation of Quaternary coastal plains of Rio Grande do Sul. Numbers correspond to Oxygen isotopic stages (modified from Tomazelli *et al.*, 2000). b) Inherited morphology conditions the emplacement of the Eastern and Southern barriers of Buenos Aires (modified from Isla *et al.*, 1996).

Figura 2. a) Porgradación de las planicies costeras cuaternarias de Rio Grande do Sul. Los números corresponde n a los estadíos isotópicos del oxígeno (modificado de Tomazelli *et al.*, 2000). b) La morfología heredada condiciona el emplazamiento de las barreras Oriental y Austral de Buenos Aires (modificado de Isla *et al.*, 1996).

Results

Estuarine dynamics: the speciation of estuarine snails

The Holocene record of Mar Chiquita coastal lagoon (Figure 1) is dominated by shells of rissoidean snails belonging to the genus *Heleobia*, also called *Littoridina* (De Francesco, 2002; De Francesco & Isla, 2003). Three species are living along this coastal lagoon: *Heleobia australis*, *H. conexa and H. parchappii*. The former is restricted to the inlet areas subject to tidal effects. *Heleobia conexa* occupies most of the extended area of the coastal lagoon while *H. parchappii* is restricted to the creeks and channels flowing to the lagoon (De Francesco & Isla, 2004). From the 16 living

species of *Heleobia*, these three belonging to the "*parchappii* group" (*sensu* Gaillard 1973) are the only mentioned for the Holocene (De Francesco, 2002). In this sense, it is thought that many recent specimens must have been collected and classified by the generic name of "*parachappi*" (De Francesco, 2002).

Along the Quequén Grande River (Figure 1) similar patterns of distribution were assigned to salinity effects. *H. australis* (D'Orbigny, 1835) and *H. conexa* (Gaillard, 1974) are varying along the estuarine gradient while *H. parchappii* distributes at the freshwater courses, far from the tidal excursion. (De Francesco & Isla, 2003). Significant differences in the average densities of hidrobids (specimens sampled under stones at areas of 100 cm^2) were recorded (Figure 3). Although the tidal excursion is completely different same pattern of distribution was also found along the Mar Chiquita coastal lagoon.

In regard to fossil specimens, it has been accepted that the estuarine sediments assigned to the Holocene transgression was dominated by *H. australis* (Aguirre & Farinati, 2000; De Francesco, 2007) and that this species is today scarce and restricted to shallow marginal marine habitats spanning from latitudes of 5°N to 42°S (Aguirre & Farinati, 2000; Aguirre & Urrutia, 2002). Although there are some references about specimens of *H. australis* collected from Pleistocene sediments (see Aguirre & Urrutia, 2002) much of these specimens were collected from sediments comprising the "*Querandinense Stage*" (Aguirre & Whatley, 1995), today assigned to the Holocene transgressive phase of the sea-level fluctuation.

However, a controversy still remains about the taxonomic position of *H. australis*. Some authors proposed a single species that originated about 7500 years BP, with several morphs related to salinity tolerances: for oligo-mesohaline condition the morph A (*H. conexa*) dominates; for mesohaline conditions the morph B comprises the *species H. australis* and *H. crassa*; and for poly-euhaline conditions (morph C) *H. isabelleana* dominates (Aguirre & Farinati, 2000; Aguirre & Urrutia 2002). On the other hand, De Francesco (2007) holds that the morphometric parameters (length-width relationship) lacks of a biological base. In his sense, fossil determinations should follow the taxonomic and environmental significance of living specimens; although this way of reasoning, based on the assumption that modern specimens distribute similarly to fossil specimens, should be carefully applied to times older than Holocene. At the same time, the puzzle about the origin of *H. australis* from the original "parchappii Group" remains unsolved. The Pleistocene record has plenty of references for the genus *Heleobia.* However, the only species determined was dominantly assigned to the living *H. parachappii*, a species that today lives on submerged vegetation, silt or hard substrates (Darrigran, 1995). Although it is today easily recognized in freshwater environments, it can also be sampled from tidal channels of Mar Chiquita coastal lagoon at salinities ranging between 17 and 23‰ (De Francesco & Isla, 2003). In the geologic record, it has been sampled in fluvial-swamp sequences extending from Upper Pleistocene to Holocene: Quequén Grande River (Zárate *et al.,* 1995), Chasicó Creek (Bonadonna *et al.,* 1999), Punta Hermengo shallow lake (Figini *et al.,* 1999) and Luján River (Prieto *et al.,* 2004). DNA studies of the living specimens will solve the puzzle about the relationships between these estuarine species: either their parental relationship between *H. parachappii* and *H. australis*, or if it is a single species (*H. australis*) whose morphometry depends on salinity.
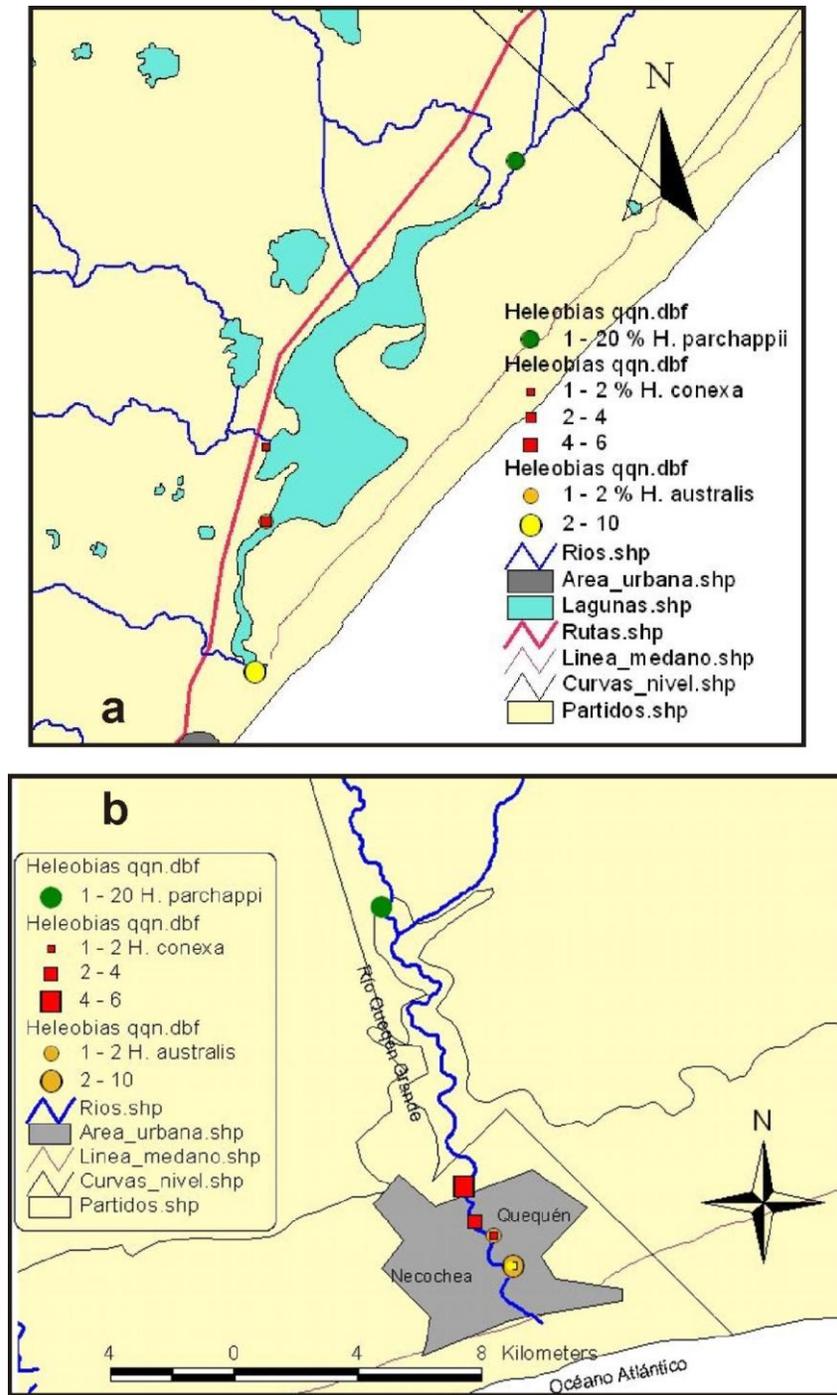
Figure 3. a) Distribution of different species of the genus *Heleobia* along the Mar Chiquita coastal lagoon b) Distribution of the same genus along the Quequén Grande River estuary (modified from De Francesco & Isla, 2003).

Figura 3. a) Distribución de diferentes especies del género *Heleobia* a lo largo de la laguna costera Mar Chiquita. b) Distribución del mismo género a lo largo del estuario del Río Quequén Grande (modificado de De Francesco & Isla, 2003).

Landscape: the speciation of the sand-dune tuco-tuco

Two ctenomids are characteristic of the southern area of Buenos Aires province: *Ctenomys talarum* and *C. australis.* The former occupies areas dominated by grass between dunes or fixed dunes with soils with a certain moisture content and vegetation cover (Malizia *et al.,* 1991; Vasallo, 1993; Mora *et al.*, 2003). On the other hand, *C. australis* lives only at coastal sandy dunes with a very sparse vegetation cover (Mora, 2008). This species is solitary, highly territorial with restrictions for digging ability (Mora *et al.*, 2010), and belongs exclusively to the southern barrier of Buenos Aires that originated about 6000 years ago (Isla *et al.*, 1996). Today this "tuco tuco" of the dunes has problems of habitat fragmentation originated by small rivers dissecting the barrier, and more recently by forestation and urbanization of this coastal barrier (Mora, 2008). It was already accepted that *C. australis* belongs to the ctenomid group related to sandy soils of Quaternary dunes (Mora, 2008). In terms of age, *C. talarum* was living at least during the Upper Pleistocene while *C. australis* originated by the consequences of the sea-level fluctuation. On the other hand, *C. talarum* specimens have occupied a wider range of microhabitats, and therefore have been less affected by the sea-level fluctuation that could have triggered habitat changes and consequently genetic isolation by distance.
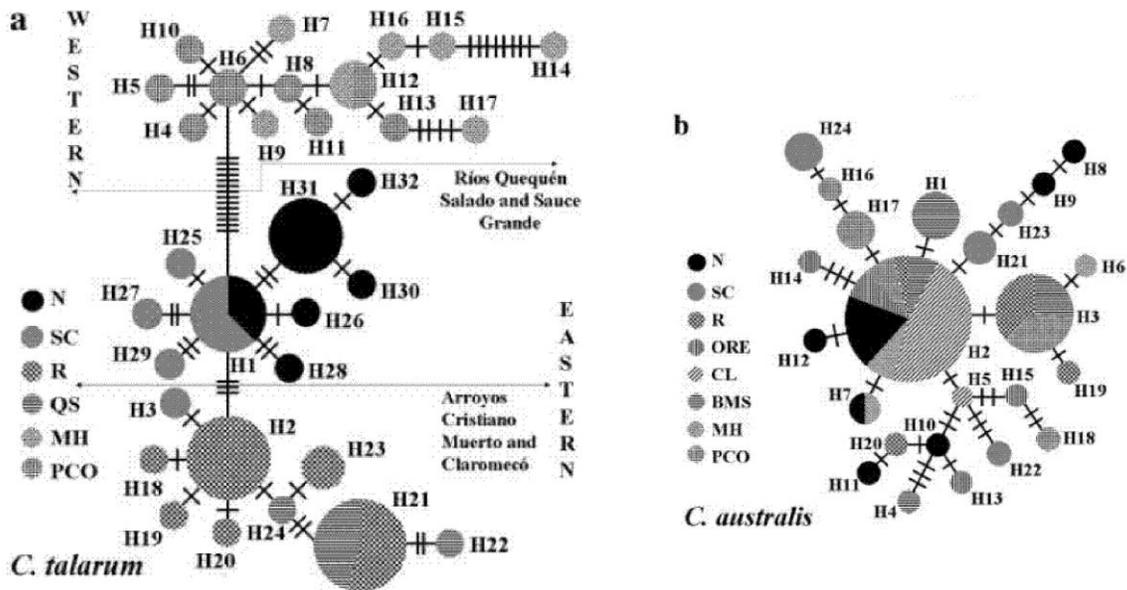

Figure 4. Comparison of minimum spanning trees for mitochondrial DNA haplotypes of the two ctenomids from southern Buenos Aires. a) *Ctenomys talarum*. b) *Ctenomys australis* (modified from Mora *et al.*, 2007).

Figura 4. Comparación de los *minimum spanning trees* de haplotipos de ADN mitocondrial de dos ctenómidos del sur de Buenos Aires. a) *Ctenomys talarum*. b) *Ctenomys australis* (modificado de Mora *et al.*, 2007).

Comparing their mitochondrial DNA, the differences of *C. talarum* (the "tuco tuco of the talas" *Celtis tala*) were conditioned to geographical barriers like the rivers flowing within gorges (Quequén Salado - Sauce Grande, and Cristiano Muerto – Claromecó). Instead, the haplotype tree of *C. australis* has a star shape meaning a low genetic drift (Mora *et al.*, 2007). It was concluded that *C. australis* has not occupied this sandy barrier during much time as there are not many differences within this population regarding their mitochondrial DNA (Mora, 2008). Assuming a recent expansion of the populations of *C. australis*, it could have derived from an ancestral species in a new vacant habitat (Mora *et al.,* 2007). Although it is clear that landscape controls the distribution of these species, and causing very modern variations that can be explained by habitat discontinuities, sex and age are also conditioning factors of their present dispersal (Mora *et al.*, 2010). Comparing genetically their demographic history, it has been concluded that *C. talarum* has experienced a stable history while the *C. australis* is dominated by an expansion pattern (Figure 4; Cutrera *et al.,* 2010).

Habitat: coastal mollusc changes during Patagonian highstands

In the Beagle Channel (Figure 1), the climatic deterioration that occurred during the Pliocene-Pleistocene glaciations produced significant environmental changes followed by a repopulation by migrants from other areas (Gordillo *et al.*, 2009). On the other hand, it is well known that regarding benthic coastal communities, it is the substrate the most important variable that controls their distribution. Highstands comprise particular environments (beaches, barriers, coastal lagoons, estuaries, tidal flats) with different potential of preservation. At the same time, benthic communities from these environments are subject to differential erosion, burial or destruction of their skeletons, and the highstands are only a minimum gap of the transgressive-regressive cycles they are representing (Valentine, 1989). Dealing with the mollusc distribution of the Atlantic beaches of Tierra del Fuego, Pleistocene assemblages are characterized by infaunal specimens, dominated by the venerid *Retrotapes* sp., Del Río 1997. On the other hand, Holocene assemblages are dominated by epifaunal communities (Isla *et al.*, 2005; Gordillo & Isla, 2010). In this sense, it is the sediment availability the factor that controls the habitat-type of the communities that colonise each bay during each highstand (Figure 5). Along the different pocket beaches or bays of the Eastern coast of Tierra del Fuego, there are significant variations between the habitat preferences of the benthic communities.

Flooded depressions and sea-level jumps

In the same way that the mid-Holocene was characterised by a rapid sea-level fluctuation that caused the emergence of low-lying coastal plains, during the transgressions there were two sea-level jumps that could caused rapid floods of some specific depressions.

Northern Patagonia is today characterised by large depressions below the sea level. They remain emerged below the sea level due to the low Precipitation rates and high evaporation (exacerbated by the strong Westerly winds). Several non-flooded depressions below Present sea level are localised in Bajo del Gualicho (72 m below sea level; Figure 6), Gran Bajo Valdés (4 m

below sea level), Salinas Grandes (-40 m) and Salina Chica de Valdés (-31 m). Constant arid to semiarid conditions persisted during the last 5,500 years. During Late Holocene there was a slight change to present semiarid conditions (Schäbitz, 1994). As these climate conditions did not change significantly, it was expected that present gulfs (San Matías, San José and Nuevo) had been subaerial depressions with minimum areas covered by hipersaline water or saltpans. The San Matías Gulf is the largest flooded depression of 18,000 km^2 (Gagliarindi & Rivas 2004). Shrub fragments in living position at the bottom of the gulf (70 m depth) were dredged from the western slope of this gulf. The wood was dated in 11,310 +/- 150 years (LP-2384), probing that the depression was not yet flooded during that age. Considering the sea-level rise proposed for the Argentine Shelf (Guilderson *et al,*. 1998), 11,000 years ago the sea level had not reached the level of the present sill of the San Matías and San Jose gulfs (Figure 6). About 10,000 years ago, these depressions were rapidly flooded (Isla 2011), transformed into gulfs (San Matías, San José and Nuevo) and therefore subject to colonisation by marine species. A ramp with a sand wave field has been mapped at the southern portion of this sill (Gagliardini *et al.*, 2005).
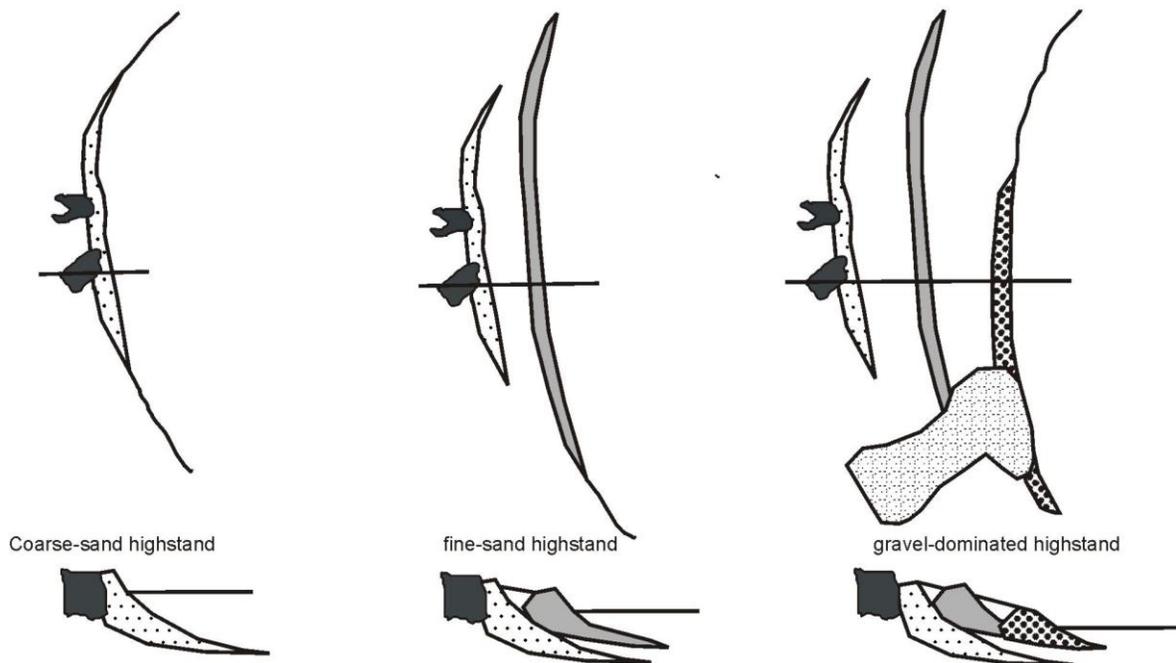

Figure 5. Variations of substrate conditions (sediment availability) during different highstands (modified after Isla & Bujalesky, 2008).

Figura 5. Variaciones de las condiciones de sustrato (disponibilidad de sedimento) durante diferentes niveles altos del mar (modificado de Isla & Bujalesky, 2008).
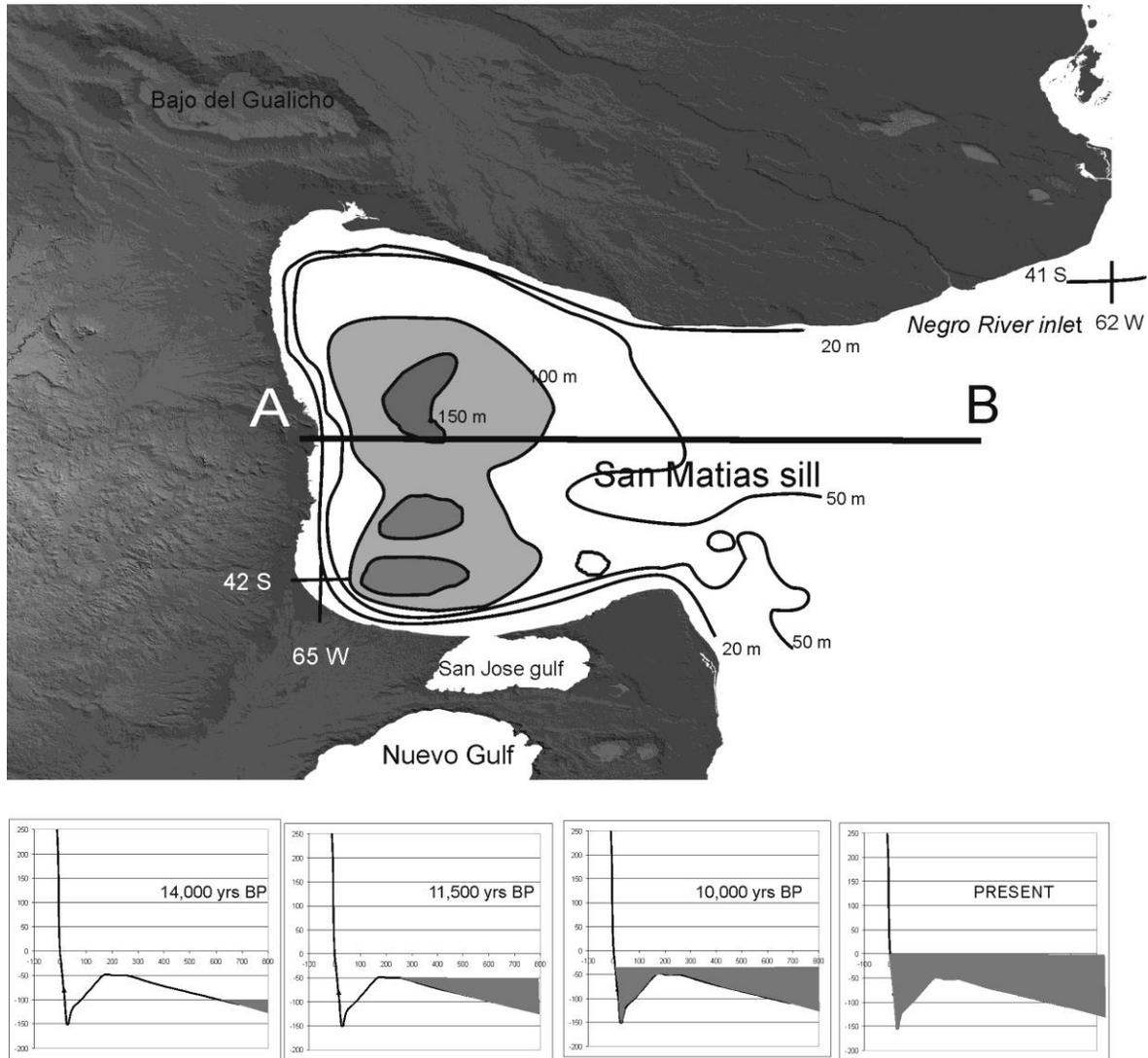
Figure 6. (top) Digital terrain model of the region of San Matías Gulf with emerged depressions below sea level and the bathymetry of the gulf. (bottom) Evolution of the sea level in relation to the flooding of the tectonic depression of the San Matías Gulf 14,000, 11,000, and 10,000 years ago, and present level (modified from Isla, 2011).

Figura 6. (arriba) Modelo digital de superficie de la región del Golfo San Matías con depresiones emergidas debajo del nivel del mar y la batimetría del golfo. (abajo) Evolución del nivel del mar en relación a la inundación de la depresión tectónica del Golfo San Matías hace 14.000, 11.000 y 10.000 años, y el presente (modificado de Isla, 2011).

The success of different species to distribute, adapt or even interact within these gulfs would explain some changes between the benthic communities of the different highstands. Holocene sea-level curves have been compiled from different coasts in order to minimize the biases induced by tectonic effects. Two important sea level jumps were detected at 14,000 and 11,500-11,000 years BP, and called MWP1A and MWP1B. These jumps were related to melt-water pulses simultaneously detected at Barbados, Tahiti and New Guinea, and were correlated to the oxygen isotopic variations measured at GRIP ice core and forams sampled cores collected at the sea bottom (Bard *et al.*, 1996). The impacts of these sea level jumps would explain much of the changes recorded at the beaches and sea bottoms at these large depressions. Although ecological interactions can explain changes in the distribution, abundance and even extinctions, they cannot explain other variations assigned to physical constraints in short determined periods (as a sea level fluctuation, or a rapid flooding) in large areas.

Conclusions

Sea-level highstands comprised enough time to originate new conditions and different coastal territories. Changes in salinity dynamics, landscape and habitats can induce changes in the distribution, isolation and therefore the speciation of some taxa. The jumps of the sea level can also produced significant changes, flooding in short periods former emerged depressions.

Acknowledgements

References

Aguirre, M. L., 2003. Late Pleistocene and Holocene palaeoenvironments in Golfo San Jorge, Patagonia: molluscan evidence. *Marine Geology*, 194: 3-30.

Aguirre, M. L. & E. A Farinati, 2000. Aspectos sistemáticos, de distribución y paleoambientales de *Littoridina australis* (D'Orbigny, 1835) (Mesogastropoda) en el Cuaternario marino de Argentina (Sudamérica). *Geobios*, 33: 569-597.

Aguirre, M. L. & M. I. Urrutia, 2002. Morphological variability of *Littoridina australis* (d'Orbigny, 1835) (Hydrobiidae) in the Bonaerensian marine Holocene (Argentina). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183: 1-23.

Aguirre, M. L. & R. C. Whatley, 1995. Late Quaternary marginal marine deposits from north-eastern Buenos Aires Province, Argentina: A review. *Quaternary Science Reviews*, 14: 223-254.

Angulo, R. J., G. C. Lessa & M. C. de Souza, 2006. A critical review of mid- to late-Holocene sea-level fluctuations on the eastern Brazilian coastline. *Quaternary Science Reviews* 25: 486-506. doi:10.1016/j.quascirev.2005.03.008.

Bard, E., B. Hamelin, M. Arnold, L. Montaggioni., G. Cabioch, G. Faure & F. Rougerie, 1996. Deglacial sea-level record from Tahiti corals and the timing of global meltwater discharge. *Nature,* 382: 241-244.

Bonadonna, F. P., G. Leone & G. Zanchetta 1999. Stable isotope analyses on the last 30 ka molluscan fauna from pampa grassland, Bonaerense region, Argentina. *Palaeogeography, Palaeclimatology, Palaeecology,* 153: 289-308.

Brett, C. E., L. C. Ivany & K. M. Schopf, 1996. Coordinated stasis: An overview. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 127: 1-20.

Brooks, N., J. Hall, & R. Nichols, 2006. Sea-Level Rise: Coastal Impacts and Responses. Die zunkuft der mere: zu warm, zu hoch, zu sauer. Externe expertise für das WBGU, Berlin, 49 pp.

Cutrera, A. P., E. A. Lacey, M. S., Mora & E. P Lessa, 2010. Effects of contrasting demographic histories on selection at major histocompatibility complex loci in two sympatric species of tuco-tucos (Rodentia: Ctenomyidae). *Biological Journal of the Linnean Society,* 99: 260-277.

Chappell, J., 1983. Evidence for smoothly falling sea levels relative to North Queensland, Australia during the past 6,000 years. *Nature,* 302: 406-408.

Darrigran, G., 1995. Distribución de tres especies del género *Heleobia* Stimpson, 1865 (Gastropoda: Hydrobiidae) en el litoral argentino del Río de La Plata y arroyos afluentes. *Iheringia, Serie Zoologia,* 78: 3–8.

De Francesco, C. G., 2002. *Significado paleobiológico y paleoambiental de las concentraciones holocenas de Heleobia (Gastropoda) presentes en el sudeste de la Provincia de Buenos Aires.* Unpublished thesis University of Mar del Plata, Mar del Plata, 109 pp.

De Francesco, C. G., 2007. Las limitaciones a la identificación de especies de *Heleobia* Stimpson, 1865 (Gastropoda: Rissooidea) en el registro fósil del Cuaternario tardío y sus implicancias paleoambientales. *Ameghiniana,* 44: 631-635.

De Francesco, C. G. & F. I. Isla, 2003. Distribution and abundance of hydrobiid snails in a mixed estuary and a coastal lagoon, Argentina. *Estuarine Research Federation, Estuaries,* 26: 790-797.

De Francesco, C. G. & F. I. Isla, 2004. The life cycle and growth of *Heleobia australis* (d'Orbigny, 1835) and *Heleobia conexa* (Gaillard, 1974) (Gastropoda: Rissooidea) in Mar Chiquita coastal lagoon (Argentina). *Journal of Molluscan Studies,* 70: 173-178.

Dickinson, W. R., 2003. Impact of Mid-Holocene hydro-isostatic highstand in regional sea level on habitability of islands in Pacific Oceania. *Journal of Coastal Research,* 18(3): 589-502.

Dillenburg, S. R., E. G. Barboza, L. J. Tomazelli, P. A. Hesp, L. C. P. Clerot & R. N. Ayup-Zouain, 2009. Holocene Coastal Barriers of Rio Grande do Sul. In Dillenburg, S. R. & P. A Hesp (eds.) *Geology and geomorphology of Holocene coastal barriers of Brazil.* Lecture notes in Earth Sciences 107, Springer, Ch. 3: 53-91.

Figini, A. J., J. E. Carbonari., R. A. Huarte & E. Tonni, 1999. Cronología radiocarbónica del Holoceno de Punta Hermengo, Buenos Aires. *XIV Congreso Geológico Argentino, Salta,* II: 63-66.

Gagliardini, D., S. Aliotta, A. Dogliotti & P. Clemente-Colón, 2005. Identification of bed forms through ERS SAR images in San Matías gulf, Argentina. *Journal of Coastal Research,* 21: 193-201.

Gagliardini, D. A. & A. L. Rivas, 2004. Environmental characteristics of San Matías Gulf obtained from Landsat – TM and ETM+ data. *Gayana* 68: 186–193.

Gaillard, M. C., 1973. *Contribución al conocimiento del género Littoridina Souleyet, 1852 en Argentina.* Unpublished Thesis 320, Universidad Nacional de La Plata, La Plata.

Gordillo, S., G. Cusminsky, E. Bernasconi, J. F. Ponce, J. O. Rabassa & M. Pino, 2009. Pleistocene marine calcareous macro-and-microfossils of Navarino Island (Chile) as environmental proxies during the last interglacial in southern South America. *Quaternary International,* 74: 1-16.

Gordillo, S. & F. I. Isla, 2010. Faunistic changes between the Middle/Late Pleistocene and the Holocene on the north coast of Tierra del Fuego: Molluscan evidence. *Quaternary International,* doi:10.1016/j.quaint.2010.06.006

Grayson, D. K., 1984. *Explaining Pleistocene extinctions. Thoughts on the structure of a debate.* In Martin, P. S. & R. G. Klein (eds.) Quaternary extinctions.: a prehistoric revolution. The University of Arizona Press, 807-823.

Guilderson, T. P., L. Burckle, S. Hemming & W. R. Peltier, 2000. Late Pleistocene sea level variations derived from the Argentine Shelf. *Geochemistry, Geophysics, Geosystems* 1, 2000G000098.

Isla, F. I., 1989. The Southern Hemisphere sea-level fluctuation. *Quaternary Science Reviews,* 8: 359-368.

Isla, F. I., 2011. Submerged woods of Upper Pleistocene age at San Matías Gulf: a sea level Curve for Northern Patagonia. *XIII ABEQUA Congress - The South American Quaternary: Challenges and Perspectives*. Buzios, Brasil, 5 pp.

Isla, F. I. & G. G. Bujalesky, 2008. *Coastal Geology and morphology of Patagonia and Fueguian Archipielago.* En Rabassa, J. R. (ed.) The Late Cenozoic of Patagonia and Tierra Del Fuego**.** Elsevier Sci. Publ., Ch. 10: 227-240**.**

Isla, F. I., L. C. Cortizo & E. J. Schnack, 1996. Pleistocene and Holocene beaches and estuaries along the Southern Barrier of Buenos Aires. *Quaternary Science Reviews* 15(8-9): 833-841.

Isla, F. I., G. G. Bujalesky, M. L. Galasso & C. G. De Francesco, 2005. Morphology, grain-size and faunistic composition of the macrotidal beaches of Tierra del Fuego, Argentina. *Revista de la Asociación Geológica Argentina,* 60: 433-445.

Jablonski, D. & K. Roy, 2003. Geographical range and speciation in fossil and living molluscs. *Proceedings Royal Society of London B*, 270: 401–406.

Malizia, A. I., A. I Vassallo & C. Busch, 1991. Population and habitat characteristics of two sympatric species of *Ctenomys* (Rodentia: Octodontidae). *Acta Theriologica,* 36: 87-94.

Mora, M. S., 2008. *Metapopulation biology of the sand dune tuco-tucos (Ctenomys australis): Effects of habitat spatial structure on population genetics and ecology.* Ph. D. Thesis, National University of Mar del Plata, 185 pp.

Mora, M. S., I. Olivares & A. I. Vassallo, 2003. Size, shape and structural versatility of the subterranean rodent *Ctenomys* (Rodentia, Caviomorpha): Functional and morphological analysis. *Biological Journal of the Linnean Society*, 78: 85-96.

Mora, M. S., E. P Lessa, A. P. Cutrera, A. I. Vassallo & M. Kittlein, 2007. Phylogeographical structure in the subterranean tuco-tuco *Ctenomys talarum* (Rodentia: Ctenomyidae): contrasting the demographic consequences of regional and habitat-specific histories. *Molecular Ecology,* 16: 3453–3465.

Mora, M. S., F. J. Mapelli, O. E. Gaggiotti, M. J. Kittlein & E. P. Lessa, 2010. Dispersal and population structure at different spatial scales in the subterranean rodent *Ctenomys australis. BMC Genetics 11*, 9: doi:10.1186/1471-2156-11-9

Prieto, A. R., A. M. Blasi, C. G De Francesco & C. Fernández, 2004. Environmental history since 11,000 [14]Cyr B.P. of the northeastern Pampas, Argentina, from alluvial sequences of the Luján River. *Quaternary Research,* 62: 146-161.

Roy, P. S., R. J. Williams, A. R. Jones, O. Yassini, P. J. Gibbs, B. Coates, R. J. West, P. R. Scanes, J. P. Hudson & S. Nichol, 2001. Structure and function of South-east Australian estuaries. *Estuarine, Coastal and Shelf Science,* 53: 351–384.

Schäbitz, F., 1994. Holocene climatic variations in Northern Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 109: 287-294.

Tomazelli, L. J., S. R Dillenburg & J. A. Vilwock, 2000. Late Quaternary geologic History of Rio Grande do Sul coastal plain, Southern Brazil. *Revista Brasileira de Geociéncias*, 30(3): 470-472.

Valentine, J. W., 1989. How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology,* 15: 83-94.

Vassallo, A. I., 1993. Habitat shift after experimental removal of the bigger species in sympatric *Ctenomys talarum* and *Ctenomys australis* (Rodentia:Octodontidae). *Behaviour,* 127: 247-263.

Zárate, M. A., M. A. Espinosa & L. Ferrero, 1998. Paleoenvironmental implications of the Holocene diatomite, Pampa Interserrana, Argentina. *Quaternary of South America and Antarctic Peninsula,* 11: 135-152.