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Journal of South American Earth Sciences 20 (2005) 13–32

Journal of
South American
Earth Sciences

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Late Quaternary molluscan assemblages from the coastal area of Bahía Bustamante (Patagonia, Argentina): Paleoecology and paleoenvironments

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Received 1 April 2003; accepted 29 May 2005

Abstract

Variations in the composition, distribution, and diversity of molluscan assemblages from Patagonian marine terraces (MT) formed during the late Quaternary sea-level highstands and neotectonic events—between the late Pleistocene, mid-Holocene, and present—are discussed. Molluscs and associated macrofauna (balanids, brachiopods, polychaetes, bryozoans) from nine fossiliferous localities and three modern sites suggest paleoecological, paleobiogeographical, and paleoenvironmental implications for paleoclimatic interpretations of the coastal area of Bahia Bustamante–Caleta Malaspina (~44.9 and 45.3°S) since marine oxygen isotope stage (MOIS) 7. *Crepidula protea*, *Buccinanops paytensis*, and *Brachidontes rodriguezi* are first recorded for the late Pleistocene MTIV (MOIS5-7); *Nacella (Patinigera) deaurata*, *Epitonium magellanicum*, *B. paytensis*, *Aequipecten tehuelchus*, and *Clausinella gayi* are recorded for the mid-Holocene MTVI (MOIS1) in the area. These molluscs currently live in the SW Atlantic, but *Venericardia procera* represents a northward migration and *Tegula atra* a faunal extinction in response to climate change. Overall, they indicate hard substrates, shallow waters, and truly marine conditions, similar to the modern littoral. With respect to temperature, the qualitative, quantitative, morphological, and distributional variations suggest slightly higher SST during the mid-Holocene (MTVI, MOIS1, hypsithermal), colder for MTV (MOIS5c?, 5a?), and warmer or similar for MTIV (MOIS5e, 7?).
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Keywords: Bivalves; Gastropods; Late Pleistocene; Marine; Mid-Holocene; Paleoclimate variability; Patagonia

Resumen

Se discuten variaciones en la composición, distribución y diversidad de los agregados de moluscos de terrazas marinas (MT) de la Patagonia formadas durante episodios altos del nivel del mar y eventos neotectónicos, entre el Pleistoceno tardío, Holoceno medio y la actualidad. Los moluscos y la macrofauna asociada (balánidos, braquiópodos, poliquetos, briozoos) de 9 localidades fosilíferas y 3 modernas permitieron ampliar aspectos paleoecológicos, paleobiogeográficos y paleoambientales, con implicancias para las interpretaciones paleoclimáticasen el área de Bahía Bustamante–Caleta Malaspina (~44.9 and 45.3°S). *Crepidula protea*, *Buccinanops paytensis* y *Brachidontes rodriguezi* representan los primeros registros para la TMIV del Pleistoceno (MOIS5-7) y *Nacella (Patinigera) deaurata*, *Epitonium magellanicum*, *B. paytensis*, *Aequipecten tehuelchus,* y *Clausinella gayi* para la TMVI del Holocene medio (MOIS1) en esta área. Todos estos moluscos viven actualmente en el Atlántico sudoccidental, aunque *Venericardia procera* representa una migración hacia el norte y *Tegula atra* una extinción, ambas en respuesta al cambio climático. Conjuntamente los moluscos son indicativos de sustratos consolidados, aguas poco profundas y condiciones marinas típicas, similares a las del litoral moderno. Sobre la la base de la temperatura, variaciones cualitativas, cuantitativas, morfológicas y de distribución sugieren una temperatura oceánica superficial (SST) ligeramente más alta durante el Holoceno medio (MTVI, MOIS1, Hypsithermal), ligeramente más fría para la MTV (MOIS5c?, 5a?), y similar o ligeramente más cálida para la MTIV (MOIS5e, 7?).
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Palabras Clave: Bivalvos; Gastrópodos; Pleistoceno tardío; Holoceno medio; Patagonia; Variabilidad paleoclimática

1. Introduction

In Patagonia, littoral deposits (so-called 'marine terraces' [MT] in the local literature) known from classical contributions by d'Orbigny (1834–1847); Darwin (1846) accumulated during the late Quaternary sea-level episodes and neotectonic

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0895-9811/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jsames.2005.05.006

events (Feruglio, 1950; Codignotto, 1983; Cionchi, 1985; Codignotto et al., 1992; Peltier and Rostami, 2000; Rostami et al., 2000). They formed since at least >350 ka BP and represent episodes equivalent to the maximum sea-level highstands of the last interglacials recorded in South America (Martin et al., 1988; Martin and Suguio, 1992; Ortlieb et al., 1996a). Most contain highly fossiliferous marine strata, with abundant shell concentrations that exhibit excellent preservation and are useful as valid paleoenvironmental tools. MT have subsequently been studied in descriptive geological, geomorphological, and geochronological contributions (Cionchi, 1987, 1988; Codignotto, 1987; Rutter et al., 1990; Schellmann and Radtke, 2000; Schellmann et al., 2000). Feruglio (1950), however, was the first author to propose a pattern of MT (MTI–VI) that took into account their extension, altitude, and content of molluscs and other fossil invertebrates, including coastal evolution and variations linked to glacial cycles (Table 1).

General or preliminary conclusions based mainly on bibliographic data or systematic reviews of the gastropods are available for some of the MT (Aguirre and Codignotto, 1998; Gordillo, 1998; Pastorino, 2000), but paleoecological, paleobiogeographical, paleoenvironmental, and paleoclimatic approaches based on the whole molluscan fauna of geographically and stratigraphically well-constrained deposits need to be reviewed and updated.

This article presents a synthesis of the most characteristic bivalves and gastropods recorded from the late Quaternary MTIV, V, and VI preserved along the coastal area of Bahia Bustamante and Caleta Malaspina in northern Golfo San Jorge (Chubut province, Argentina, ~44.9 and 45.3°S) (Fig. 1). In this area, the molluscan assemblages represent a considerable proportion (80–90%) of the biogenic content and are preserved as parautochthonous concentrations of shells in the coarse sands. The aim of this study is to place the probable paleoenvironments on record in a suitable study area with modern chronological controls and for which present-day data are available. Our results complement recent work focused on the molluscs from Patagonian beach ridge systems preserved in southern Chubut and northern Santa Cruz provinces (Patagonia) and northward in Buenos Aires province (Aguirre and Whatley, 1995; Aguirre, 2002, 2003, and references therein) and integrate a major project attempting to speculate on the variations of littoral molluscan associations and climate conditions since the late Quaternary in Argentina.

Molluscs have proved valid indicators of ancient coastlines, paleoenvironmental parameters (substrate, depth, energetic conditions), and paleoclimatic changes (sea surface temperature [SST], rainfall seasonality, paleo-ENSO events) (Petersen, 1986; Rollins et al., 1987; Peacock, 1989; Aguirre, 1993a,b, 2001; Lutaenko, 1993; Perrier et al., 1994; Ortlieb et al., 1995, 1996a–c; Cohen and Tyson, 1995; Roy et al., 1996; Sandweiss et al., 1996; Murray-Wallace et al., 2000; Maasch et al., 2001; Aguirre et al., 2002).

Further studies are needed in Argentina to establish current molluscan variations, former environmental conditions, and climatic changes associated with sea-level highstands, especially along the coastal area of southern Chubut and in Santa Cruz province. For example, the composition and distribution of molluscan assemblages and the paleoceanographical implications must be compared with the modern littoral, paleoecological comparisons of highstands of the Last Interglacial Maximum (OIS5e) and the mid-Holocene (OIS1) transgression, as well as the possible effects of

Table 1
(a) Stratigraphical interpretation of the study area. (b) Available ages for the analyzed samples

Marine terraces	Altitude (+m a m.s.l.)	**Localities**	MOIS[a]	AGES[a]	Samples for molluscan studies
Holocene MTVI	+10–12		1 (4)	2880±90; 2030±85 (1, 2) ^{14}C **6758±75; 6894±87; 8090±113, 4473±40; 4420±80;5424±40; 5380±70 ^{14}C; 8–10±2 (U/Th) (5, 6)**	
		Pen. Gravina			**PA02Hol1**
		Ea. San Miguel			**PA02Hol2**
		Bahía Bustamante			PA02Hol3
		Zanjón El Pinter			PA02Hol4
Pleistocene MTV	+22–26		5e (4)	30,900+1100; 31,800MTV1400 as minimum ^{14}C (1)	
	+	S of Ea. La Ibérica	5e (6)	118–147 ESR (6)	PA02Q8
MTIV	+28–40		>5e, 7? (4)	36,000±2000; 37,000±2400; >4,30,000 as minimum ^{14}C (1)	
		S of Ea. San Miguel	7? (6)	211±27, 220±22, 227±30 ESR (6)	PA02Q4
		N of Ea. La Ibérica	5e (6)	111±19 ESR (6)	PA02Q5
		Cd. of Ea. La Ibérica	5e (6)		PA02Q6
		Ea. La Ibérica S	5e (6)	98–115 (ESR), 58–60 U/Th (6)	PA02Q7
		N of Ao.Marea	5e (6)	158±10; 147±14 ESR (6)	PA02Q9

References for dating available in the area: (1) Codignotto, 1983 (^{14}C, most in *Protothaca antiqua*); (2) Codignotto et al., 1988 (^{14}C); (3) Codignotto et al., 1992; (4) Rutter et al., 1989; 1990 (D/L, ESR, U/Th); (5) Schellmann and Radtke, 1997 (ESR) (no details about the species dated); (6) Schellmann and Radtke, 2000 (^{14}C, U/Th, ESR) (mostly on *P.antiqua* or unidentified taxa).

[a] Estimations for equivalent samples.

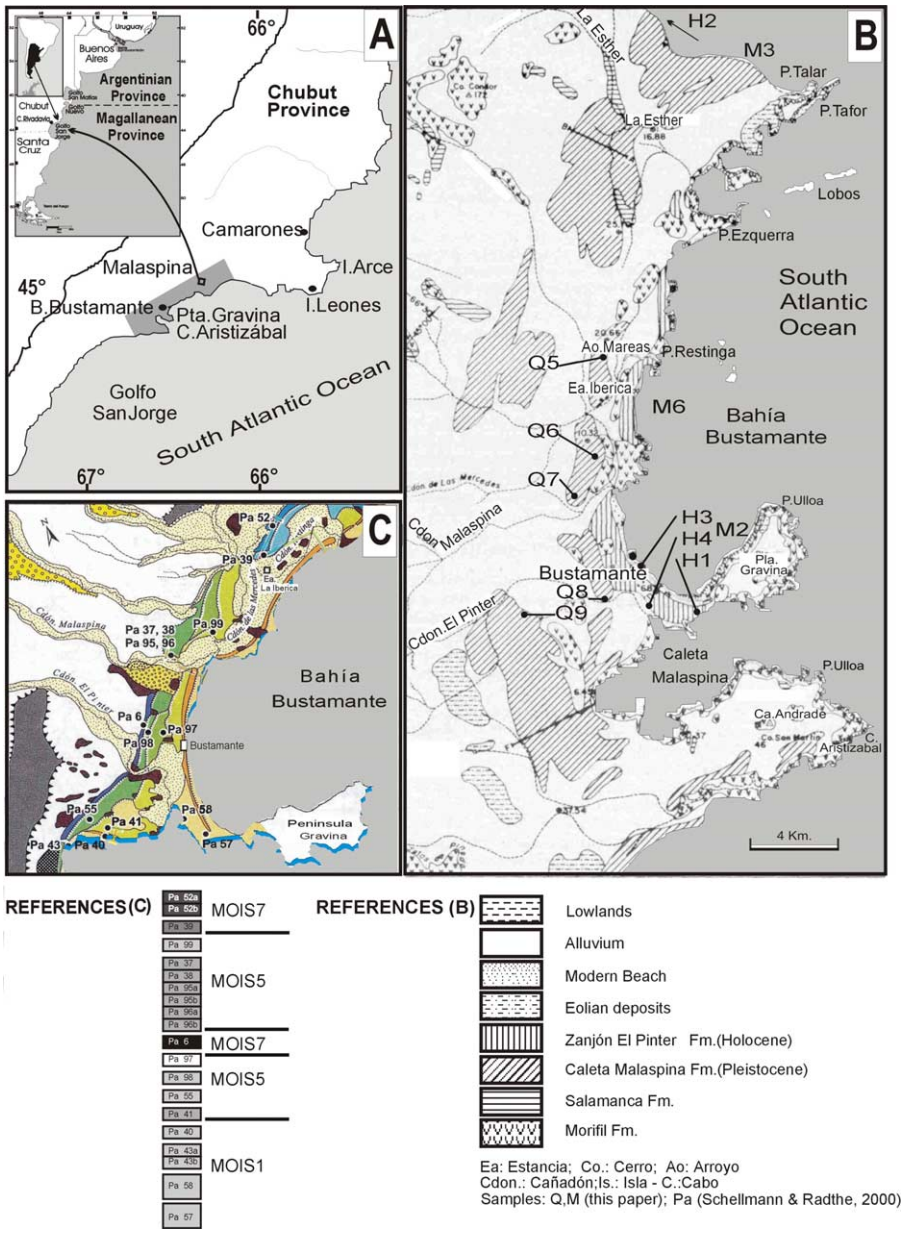

Fig. 1. Area of study. (A) General location in northern Golfo San Jorge (Patagonia, Argentina, SW Atlantic). Modern boundary for the Argentinean and Magellanean zoogeographical provinces. (B) Main geomorphological features along the coastal area of Bahía Bustamante and Caleta Malaspina. (C) Samples taken for modern dating of the ridge systems along the area. (A and B) Modified from Cionchi (1987), (C) from Schellmann and Radtke (2000). M, modern; H, Holocene; Q, Pleistocene samples.

the mid-Holocene hypsithermal on the littoral biotas. Our attempt to establish typical molluscan fauna and thereby characterize different marine episodes since at least the Last Interglacial (MOIS5) in the study area should help objective comparisons with the previous mid-Pleistocene terraces (MTIII) and late Tertiary deposits from the same area (MTI–II, Salamanca Formation) (*sensu* Feruglio, 1936-1937).

2. Geological and paleontological background

Since the classical precursor contributions by Feruglio (1932, 1933a,b, 1950) on the MT of Pliocene, Pleistocene, and Holocene ages from Patagonia, several authors have dealt with geological or paleontological aspects in selected localities. Although lacking modern dating techniques, Feruglio provided a full description and a virtually complete framework of six MT (I–VI), which he interpreted as follows: MTVI (+8–12 m) of Holocene age; MTV (+15–30 m), MTIV (+30–40 m), MTIII (+40–95 m), and MTII (+105–140 m) of Pleistocene age; and MTI (+170–186 m) of Pliocene age. In light of modern geochronological studies (Rutter et al., 1990), only four of these (MTIV–VI) are Quaternary; three are late Pleistocene (MTIII–V), and one is Holocene (MTVI).

In Chubut province, the Quaternary coastal deposits have been studied in the localities of Caleta Valdés, Camarones, Bahía Bustamante, Bahía Solano, and Comodoro Rivadavia by

Codignotto (1983, 1987), Codignotto et al. (1990a,b), Fasano et al. (1983), Cionchi (1987), Isla (1990), Schellmann and Radtke (2000), and Rostami et al. (2000). The Holocene accretionary landforms correlate with MTVI at Comodoro Rivadavia, are preserved between 6 and 12 m above mean sea level (m.s.l.) along the coastal margins of Chubut, and continue southward along the coast of Santa Cruz province. Some available ages include 2000–6300 ka (Bahía Solano) and 2030–8950 ka (Bahía Bustamante, 10–12 m above m.s.l.). At Bahía Bustamante, Cionchi (1987) defined the Zanjón El Pinter Formation (Holocene), represented by narrow (300–500 m) littoral ridges situated, at maximum, approximately 12 m above present m.s.l., that extends along the modern coast and follows a pattern similar to the present coastline (Table 1, Fig. 2). The Pleistocene landforms integrate two or three subparallel series of littoral ridges that correlate with MTIV and V. Cionchi (1987) proposed the Caleta Malaspina Formation (Last Interglacial) for these terraces at 25–41 m above m.s.l. According to the most modern studies (Rutter et al., 1990; Schellmann and Radtke, 2000), the coastal deposits sampled in this area most probably range from MOIS 7 (or older) to MOIS1 (Figs. 1 and 2).

Interpretations based on the molluscan assemblages are scarce and generally lack comparisons with the coastal deposits from other areas in Argentina or South America. From paleoecological and paleobiogeographical standpoints, the

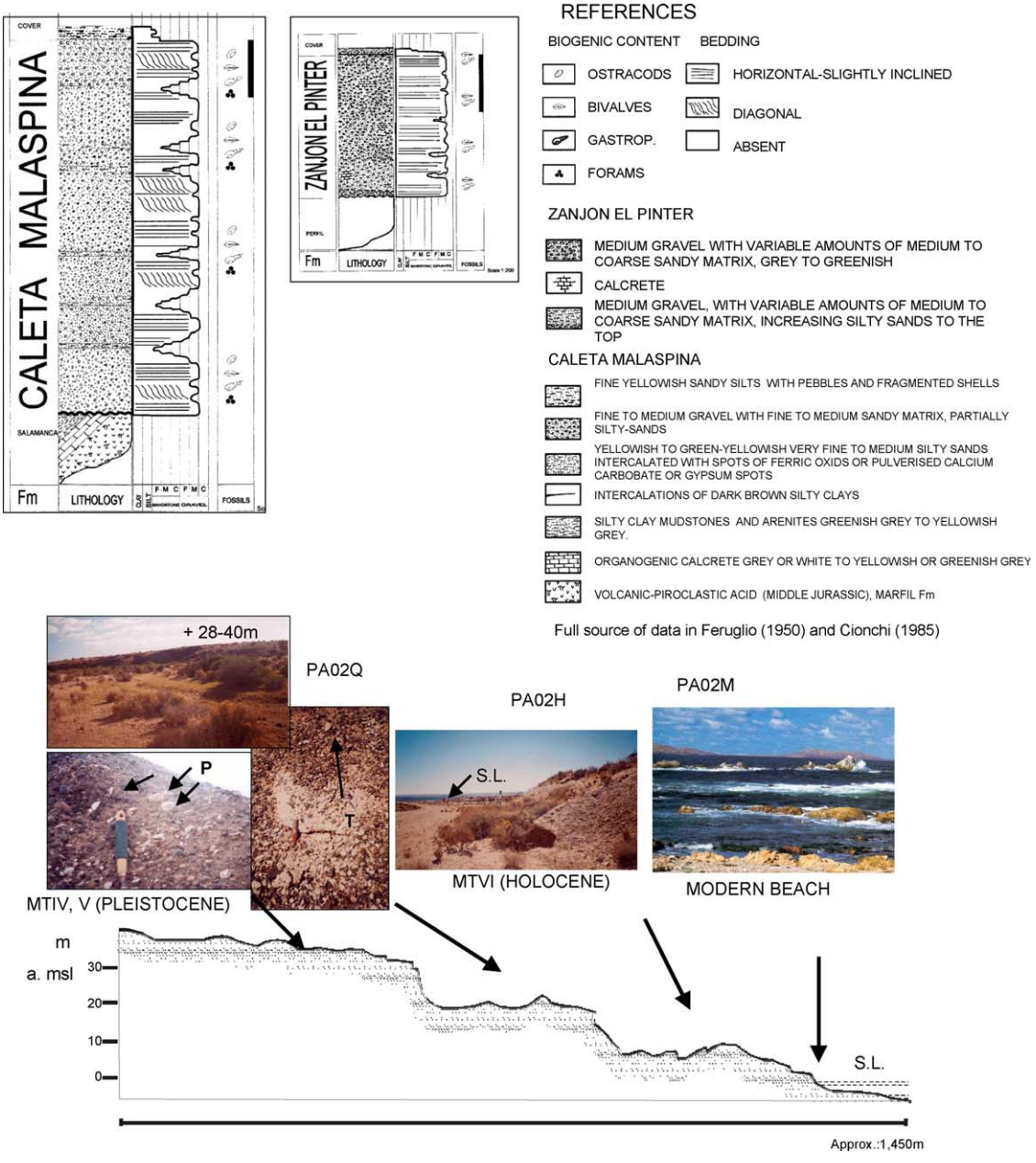

Fig. 2. (a) Schematic columns of Zanjón El Pinter (Pleistocene, MTIV and V) and Caleta Malaspina (Holocene, MTVI) formations, *sensu* Cionchi (1987); dark bars refer to the levels sampled. (b) Schematic profile of MTIV–VI, *sensu* Feruglio (1950); photographs of the modern beach at Bahía Bustamante and the MT sampled. In MTIV, complete shells of *P. antiqua* (P) with joined valves, some in living position, and large shells of *T. atra* (T).

molluscs are poorly understood; only in a few localities, they have been recently sampled or reviewed, and many coastal areas are known only through lists of taxa or illustrations of scarce specimens, isolated localities, or without modern dating.

Studies performed on similar deposits of the SW Atlantic margin are available for the Bonaerensian littoral (Aguirre, 1993a,b, 1996), some areas along the Patagonian coasts (Feruglio, 1932; Aguirre and Codignotto, 1998; Gordillo, 1998; Pastorino, 2000; Aguirre, 2002, 2003), and other coastal deposits in South America, such as Guyana (Altena, 1971, 1975), Uruguay (Martínez et al., 2001), and Brazil (Forti Esteves, 1974). Along the Pacific South American coast, most detailed work has been devoted to Peru (e.g. Ortlieb et al., 1990, 1996a,b) and northern Chile (Ortlieb et al., 1995, 1996a). The modern SW Atlantic molluscan fauna is known from the lists of taxa or catalog illustrations (Carcelles, 1944; Carcelles and Williamson, 1951; Bastida et al., 1992; Castellanos and Landoni, 1988–1993; Roux and Fernández, 1997; Forcelli, 2000).

3. Area and deposits studied

The area of this study (Fig. 1) is located in the southern Chubut province (central Patagonia, Argentina), approximately 100 km NE of Comodoro Rivadavia. It extends 25 km along Bahía Bustamante between Punta Tafor (north of Punta Ezquerra) and Punta Ulloa (Península Gravina). The area is dominated by tablelands with thin, scanty vegetation adapted to sporadic rainfall, typical of arid climates such as Patagonia. Sand dunes are widely distributed, and ancient beach ridges complete the landscape. All coastal areas have rocky shores and beaches with volcanic rocks and coarse to fine gravels.

Three series of well-preserved, regressive, pebbly beach ridge systems (MTIV–VI of Feruglio's local pattern) lie parallel to the shoreline and are adequate for paleontological studies. They extend several kilometers subparallel to one another, following the shape of the modern coastline, reach 2–8 km wide, and are separated approximately 3–4 km from the sea. Their altitude ranges between 41–32 and 10–8 m above m.s.l. Two late Pleistocene terraces occur at +28–32 (inner ridge, MTIV) and +20–26 m (intermediate ridge, MTV); the youngest, of Holocene age, lies at +10–12 m (exterior ridge, MTVI) (Fig. 2), occupies a narrower fringe approximately 300–500 m wide along the coastal area, and shows scarce erosive signatures. They form isolated landforms among which coastal lagoons, porphyritic bodies, and alluvial deposits extend. All fossiliferous beds are composed of gravel, coarse sand, and molluscan shells (mainly gastropods and bivalves) in varying amounts, generally abundantly and well preserved.

These ridges are similar to the MT preserved in Patagonia along the provinces of Rio Negro (San Antonio, Baliza San Matías formations) and Santa Cruz (MTVI from Comodoro Rivadavia, MTV from Puerto Mazarredo, MTIV from Puerto Deseado) and the littoral of Buenos Aires province (Las Escobas and Pascua formations and equivalent units) (Table 1a). Further details of the geomorphology can be obtained from Cionchi (1987).

Three main series of ridges sampled, proposed as part of the Caleta Malaspina (Pleistocene = MTIV + MTV) and Zanjón El Pinter (Holocene, MTVI) formations by Cionchi (1987, 1988), correlate with similar deposits preserved at Caleta Olivia and Puerto Deseado in Santa Cruz province (Table 1b).

The first radiocarbon dates based on molluscan shells from these deposits were supplied by Codignotto (1983) and Codignotto et al. (1988). Rutter et al. (1990) and Schellmann and Radtke (1997, 2000) added more modern dating: amino acid razemization, U/Th, and ESR. According to Rutter et al. (1990), the ages obtained at various locations of the Patagonian littoral suggest that the MT corresponds to three episodes of high sea-level stands: (1) the oldest event (Pre- or Penultimate Interglacial, MOIS 7 or 9) with deposits lying at +24–45 m, for which molluscan shells give 0.64–0.81 D/L ratios of aspartic acid and an ERS age estimation of 72,700–242,000; (2) an intermediate event (Last Interglacial, MOIS5e), +12–25 m, 0.43–0.65 D/L ratios, and ERS age estimation of 81,400–450,000; and (3) the youngest (Holocene, MOIS1), +8–12 m, 0.15–0.34 D/L ratios, and ERS age estimation of 9520 for Puerto Deseado. Bahía Bustamante was assumed to represent the area in which this pattern fits most clearly. The ESR dates are not always entirely in agreement with the ages suggested by the D/L ratios, but as a whole, the results demonstrate that the highest marine terraces belong to interglacials older than 5 e.

According to the most modern and detailed survey performed in the area (Schellmann and Radtke, 2000), the ages of the deposits sampled (Fig. 1C) are ESR 211–227 ka (inner ridge, MTIV), ESR 98–155 ka (intermediate ridge, MTV), and ^{14}C 6894–8090 ka (exterior ridge, MTVI). On this basis, they have been assigned to MOIS 7 or older?, MOIS5 (5e, 5a or 5c), and MOIS1 (Penultimate Interglacial, Last Interglacial, and Middle Holocene Interglacial, respectively) (Table 1b; note that the correlation is not coincident with Cuadros 1, 2 by Pastorino, 2000, MTV Holocene in age).

4. Modern littoral

The littoral area at Golfo San Jorge is characterized by open marine conditions in sub-Antarctic cold temperate waters. Salinity is 34–34.5‰, and the temperatures reach 3–11 °C in winter and 5.5–14.5 °C in summer (Knox, 1960; Boltovskoy, 1979).

In the study area at the northern end of the gulf, the substrate is characterized by gravel–sandy sediments. Roux et al. (1995) performed a detailed granulometrical analysis of geographically well-constrained biosedimentological samples, including data on the bottom temperatures and salinity gradients. At Bahía Bustamante, the substrate is coarser, and the environment is characterized by higher energy than along Caleta Malaspina. Swamps can be observed near the Cañadón Zanjón El Pinter outlet.

The Golfo San Jorge currently is strongly influenced by the Falkland (Malvinas) cool current, which flows northward along the SW Atlantic to the Río de La Plata in summer and southern Brazil (~28°S, Santa Catarina) in winter. It belongs to the Magellanean province (cool–temperate and cold sub-Antarctic

waters). This marine biogeographical area extends from Golfo Nuevo (Chubut, ~43°S) southward to Cabo de Hornos (55°S). Mean temperatures range yearly from 4 to 11 °C, and salinity ranges yearly from 33.8 to 34.4‰. The Patagonian current, a relatively stable water mass of sub-Antarctic origin, influences the coastal zone and flows northward to 38°S, with the mean temperature ranging annually from 5 to 16 °C and salinity from 33 to 33.5‰ (Boltovskoy, 1979; Bastida et al., 1992). North of the study area, from Golfo Nuevo to 28°S, the Argentine zoogeographic province extends, a transitional area influenced by the cool Falkland and the warm Brazilian currents (mainly subtropical shallow water masses of 34.5–38.85‰ and 18–24 °C), which flows southward to Golfo Nuevo in summer (Bastida et al., 1992).

5. Samples and methods

Fossil and modern bulk samples (sediment and mollusc shells) were collected in 12 localities (Fig. 1, Appendix 1). Fossils were taken from exposures of natural cuttings, abandoned quarries, and well-preserved outcrops; six samples are considered late Pleistocene (TMIV, PAO2Q4-7, 9; TMV, PA02Q8), and three undoubtedly are Holocene (TMVI, PA02HOL1-4) in age (Table 1b) (schematic illustrations of the most representative stratigraphical sections are shown in Fig. 2). To determine species composition, selective manual collecting was performed on the upper 40 cm of the coastal deposits, and faunal lists were drawn up; additional information on previous collections and faunal lists also was taken into account (Appendices 2 and 3).

The samples of modern molluscs and other invertebrates were collected at three localities along the Atlantic littoral (Magellanean province). Additional information on the living molluscs was obtained through examination of collections housed at museum collections (Natural History Museum, London; Bernardino Rivadavia Museum, Buenos Aires; Museo de La Plata, Argentina) and collected during oceanographic cruises (Richards and Craig, 1963; Bastida et al., 1992).

For a rough idea of the quantitative data, 400 cm^3 of complete samples (sediment and biogenic content) were taken from each fossiliferous level. At modern sites, collection was made of all the material within a 1×1 m surface in supratidal and intertidal zones. Subsamples were selected for different approaches (taxonomic, taphonomic, morphological variability, qualitative and quantitative comparisons) and future stable isotopic studies.

Special emphasis was placed on the bivalves to reconstruct the physical parameters of the original communities. In general, they provide better and more accurate paleoenvironmental information than do gastropods in littoral and nearshore assemblages. Observations on the preservation and paleoecology within and between different terraces in comparison with the present were complemented by estimations of substrate preferences and the warm- or cold-water affinity of the species recovered, abundance and distribution of the most characteristic taxa, and qualitative and semiquantitative indexes (species richness, Margaleff's diversity index (d), Shannon–Weaver's diversity index (H'')).

The paleoecological analysis aimed at reconstructing the original paleoenvironments in terms mainly of substrate, SST, salinity, and depth to compare reconstructions of the nearshore environment during the late Pleistocene (MTIV, V) and mid-Holocene (MTVI) highstands with older terraces and the modern Magellanean region at Golfo San Jorge. Sea levels are not discussed herein. General paleoclimatic trends were sought, with an emphasis on the local evidence for higher SST (climatic optima), which has been accepted worldwide during the maximum of the Last Interglacial (MOIS5e) and during the mid-Holocene hypsithermal. (MOIS1).

There are three main reasons for these approaches. (1) It is important to compare the faunal composition between different MT and the modern coastline along the area of study, where detailed geomorphological, sedimentological, and dating studies have been previously performed, to provide evidence of the environmental change during sea-level highstands as recorded by molluscan variations; (2) our knowledge about the fluctuations through time of paleobiogeographical boundaries in response to climate variability must be improved; and (3) the results should provide useful information for paleoceanographic and paleoclimatic reconstructions, such as those in previous works on other marine terraces of late Quaternary age in South America (Ortlieb et al., 1990; Guzmán et al., 1995), and aid in the interpretation of the unresolved problem about the origin of modern molluscan fauna in the SW Atlantic and especially the Magellanean province.

Earlier Pleistocene deposits from this and surrounding areas were not sampled because they are not adequate for reliable paleoecological analyses. Molluscs from older deposits were compared through bibliographic lists and illustrations (Feruglio, 1932, 1936-1937, 1950).

6. Faunal composition

The macroinvertebrate faunal composition in nine fossiliferous localities, between Estancia San Miguel (north of P. Tafor) and Caleta Malaspina, consists mostly of molluscan shells and associated barnacles, bryozoans, brachiopods, polychaetes as epizoic encrustations, and accompanying microfauna (ostracods and forams). A total of 30 characteristic molluscan taxa were noted among these deposits: 16 gastropods (more than 900 specimens) and 11 bivalves (more than 1700 specimens). The complete taxonomic composition appears in Table 2, and the species mentioned in the available systematic lists (Feruglio, 1933a, b, 1950; Cionchi, 1985) are in Appendices 2 and 3.

Gastropods (16 taxa) outnumber bivalves (10 taxa) in most fossil samples. The main species identified are as follows: *Fissurella oriens* Sowerby, *Fissurella radiosa* Lesson, *Nacella (Patinigera) magallanica* (Gmelin), *Nacella (Patinigera) deaurata* (Gmelin), *Tegula patagonica* (d'Orbigny), *Tegula atra* (Lesson), *Crepidula protea* d'Orbigny (also specimens of *Crepidula cf. aculeata* (Gmelin), *Crepidula cf. unguiformis* Lamarck, *Trophon varians* (d'Orbigny), *Trophon geversianus*

Table 2
General biogenic composition of the beach ridge systems sampled (see also Appendices 2 and 3)

MOLLUSCS	PLEISTOCENE			HOLOCENE		
GASTROPOD TAXA	Feruglio, 1933, 1950	Cionchi, 1985	this paper	Feruglio, 1933, 1950	Cionchi, 1987	this paper
Fissurella oriens Sowerby	X		X	X		
Fissurella radiosa Lesson	X		X	X		X
Nacella (P.) magellanica (Gmelin)	X	X	X	X	X	X
Nacella (P.) deaurata (Gmelin)	X		X			X
Nacella delicatissima (Strebel)	X					
Tegula (A.) patagonica (d´orb.)	X		X			
Tegula (C.) atra (Lesson)	X	X	X	X	X	
Crepidula aculeata (Gmelin)						
Crepidula protea d´Orb.			X			X
Crepidula cf. onyx Sowerby						
Crepidula dilatata Lamarck	X		X	X		X
Epitonium (B.) magellanicum (Phil.)						X
Ataxocerithium pullum (Philippi)	X		X			X
Trophon varians (d´Orb.)	X		X	X		X
Trophon geversianus (Pallas)	X	X	X	X	X	X
Acanthina monodon (Pallas)						X
Adelomelon ferrussacii (Donovan)	X					
Odontocymbiola magellanica (Gm.)	X	X	X	X	X	X
Buccinanops globulosus (Kiener)		X	X	X	X	X
Buccinanops paytensis (Kiener)			X			X
Pareuthria plumbea (Phil.)	X			X		X
Siphonaria lessoni (Blainville)	X	X		X	X	X
Fissurella picta (Gmelin)	X			X		
Diodora patagonica d´Orb.)		X		X	X	
Crepidula dilatata patagonica (d´Orb.)	X	X		X	X	
Photinula caerulescens (King)				X		
Ximenopsis muriciformis (King & Broderip)	X			X		
Colisella ceciliana (d´Orb.)	X					
Trophon elongatus Str.	X					
Pareuthria rosea	X					
Pareuthria cerealis (Roch. & Mab.)	X					
Acanthina calcar Mart.	X					
Adelomelon ancilla (Lightf.)		X			X	
Olivella tehuelcha (Duclos)	X					
Buccinanops cochlidium ((Dillwyn)	X					
Morula necocheana (Pilsbry)	X			X		
Siphonaria tristensis (Leach)						
BIVALVE TAXA						
Mytilus (M.) edulis chilensis (Hupé)	X	X	X	X	X	X
Brachidontes (B.) rodriguezi (d´Orb.)			X			X
Brachidontes (B.) purpuratus (Lamk.)	X	X	X	X	X	X
Aulacomya atra (Molina)	X	X		X	X	X
Aequipecten tehuelchus (d´Orb.)						X
Ostrea sp.						
Pitar (P.) rostratus (Koch)			X			
Venericardia procera (Gould)	X		X			
Eurhomalea exalbida (Dillwyn)	X					
Protothaca antiqua (King)	X	X	X	X	X	X
Clausinella gayi (Hupé)	X			X		X
Hiatella arctica (Linné)						
Mactra isabelleana d´Orb.	X					
Mactra patagonica d´Orb.	X					
Kellia suborbicularis Mont.						
Chlamys patagonicus (King & Broderip)	X	X			X	
Ensis macha (Molina)	x					
Bushia rushi (Pilsbry)		X			X	
Chione sp.		X			X	
OTHER INVERTEBRATE TAXA						
Balanus laevis Brug.	X					
Balanus psittacus Brug.	X			X		
Magellania venosa (Sol.)	X					
Toxocidaris albus (Mol.)	X			X		

Table 2 (*continued*)

PLEISTOCENE (Caleta Malaspina Fm.) (Cionchi, 1985)
FORAMS
Elphidium macellum (Fitchel & Moll, 1798)
Elphidium cf. discoidale (d´Orbigny, 1839)
Nonion depressulus (Walker & Jacob, 1798)
Buliminella elegantissima (d´Orbigny, 1839)
Bulimina cf. affinis d´Orbigny, 1839
Bolivina cf. variabilis (Williamson, 1858)
Bolivina danvillensis Howe & Wallace, 1932
Bolivina compacta Sidebottom, 1905
Cibicides aknerianus (d´Orbigny, 1846)
Epistominella exigua (Brady, 1884)
Buccela frigida (Cushman, 1921)
Buccela peruviana (d´Orbigny, 1839)
Elphidium lessoni (d´Orbigny, 1826)
Bolivina variabilis (Williamson, 1858)
Bolivina translucens Phleger & Parker, 1950
Bolivina doniezi Cushman, 1922
Bolivina cf. difformis (Williamson, 1858)
Bolivina ordinaria Phleger & Parker, 1950
Bolivina striatula Cushman, 1922
Quinqueloculina seminulum (Linné, 1767)
Discorbis williamsoni Chapman & Parr, 1932
OSTRACODS
Leptocythere patagonica Hartmann, 1962
Callistocythere dispersocostata Hartmann, 1962
Cytherura portmonttensis Hartmann, 1962
Pterigocythereis sp.
Krite sp.
Semicytherura sp.
Hemitheria sp.
Quadracythere sp.
Urocythereis sp.
Cytherura sp.

(Pallas), *Odontocymbiola magallanica* (Gmelin), *Ataxocerithium pullum* (Philippi), and *Epitonium magellanicum* Philippi), *Buccinanops globulosus* (Kiener), *Buccinanops paytensis* (Kiener), and *Siphonaria lessoni* (Blainville). Of these, the most characteristic gastropods are *Fissurella* spp., *Nacella* spp., *Tegula* spp., *Crepidula* spp., *Trophon* spp., *Buccinanops* spp., and *S. lessoni*.

The bivalve species include *Mytilus edulis chilensis* (Hupé), *Aulacomya atra* (Molina), *Brachidontes purpuratus* (Lamarck), *Brachidontes rodriguezi* (d'Orbigny), *Aequipecten tehuelchus* (d'Orbigny), *Ostrea sp., Protothaca antiqua* (King), *Clausinella gayi* (Hupé), *Venericardia procera* (Gould), and *Pitar rostratus* (Koch). The most typical in the ridge systems are *P. antiqua* and *B. purpuratus*.

In the modern adjacent nearshore, the most typical taxa identified are the gastropods *C. dilatata*, *N. deaurata*, *T. geversianus, T. patagonica*, and *B. globulosum* and the bivalves *B. purpuratus* and *A. atra* (Molina).

Microfossils have not been recovered from Holocene but only from Pleistocene terraces in the study area, all of which are well preserved and without abrasion or dissolution signatures. A complete list of the forams and ostracods recovered in the sediments of Caleta Malaspina Formation appears in Appendix 3. Paleoecological interpretations based on the forams indicate brackish to mixohaline conditions and temperate waters, not unlike those of the modern Malvinensean and Patagonian foraminiferal subprovinces along the South Atlantic, whereas the ostracods suggest brackish littoral waters (Boltovskoy, 1967 in Cionchi, 1985; Whatley et al., 1997, 1998).

7. Analysis of results: Comparison with shell concentrations from older terraces and other coastal areas

In the late Quaternary MT of central Patagonia along the Chubut and Santa Cruz provinces, the most constant and abundant mollucs are pateliform, trochid, buccinid, and volutid gastropods (*Fissurella* spp., *Nacella* spp., *Tegula* spp., *Buccinanops* spp., *Adelomelon* spp., *Odontocymbiola* spp.) and mytilids, mactraceans, and mainly veneracean bivalves (*Mytilus* spp., *Brachidontes* spp., *A. atra*, *Mulinia edulis*,

P. antiqua, *Eurhomalea exalbida*, *C. gayi*)—as a whole, a fauna qualitatively similar to that currently living nearby and generally in agreement with the results from the study area.

At Bahía Bustamante, most taxa preserved in the late Pleistocene are common with those of the Holocene (Table 2, Appendix 2; Feruglio, 1933; a, 1950; Cionchi, 1985). Within MTIV and V (Caleta Malaspina), the most characteristic taxa are *T. atra*, *C. protea*, and *P. antiqua*. In the Holocene (MTVI, Zanjón El Pinter), the most characteristic taxa are *Nacella* spp., *Acanthina monodon*, *Odontocymbiola magellanica*, *Buccinanops cochlidium*, *B. globulosum*, *S. lessoni*, *Colisella ceciliana*, *A. pullum*, *Ximenopsis muriciformis*, *M. edulis*, *Corbula patagonica*, *Petricola patagonica,* and *Chlamys patagonica*. Of these, *C. protea*, *B. paytensis*, and *B. rodriguezi* are first recorded for the late Pleistocene MTIV and *P. deaurata*, *E. magallanicum*, *B. paytensis*, *A. tehuelchus*, and *Cl. gayi* for the Holocene MTVI.

Most of these taxa also occur in synchronous deposits north (Camarones) and south along Golfo San Jorge (Aguirre, 2003). In contrast, compositional differences are evident with assemblages of the same age preserved in Rio Negro province, where other gastropods such as *Littoridina australis* d'Orbigny, *Adelomelon brasiliana* (Lamarck), *Zidona dufresnei* (Donovan), *Olivancillaria urceus* (Röding), and *Olivella tehuelcha* (Duclos) and the bivalves *Glycymeris longior* Sow., *Darina solenoides* (King), *Ostrea equestris* Say, *Solen tehuelchus* d'Orbigny, and *Amiantis purpuratus* (Lamarck) are abundant.

Even stronger differences can be recognized with the assemblages that have been studied in Buenos Aires province, with exclusive taxa such as *Lucapinella henseli*, *Puncturella conica*, *Calliostoma coppingeri*, *Calliostoma carcellesi*, *Calliostoma nordenskjoldi*, *Epitonium tenuistriatum*, *Urosalpinx rushi**, *Urosalpinx cala*, *Morula necocheana*, *Olivancillaria uretai*, *Anachis avara**, *Marginella martini*, *Terebra gemmulata*, *Dorsanum moniliferum*, *Turbonilla uruguayensis* (Gastropoda), *Nucula nucleus*, *Nucula obliqua*, *Nuculana whitensis*, *Adrana electa*, *Noetia bisulcata**, *Crassostrea rhizophorae**, *Musculus viator*, *Plicatula gibbosa*, *Diplodonta patagonica*, *Phlyctiderma semiaspera*, *Carditamera guppyi*, *Mulinia lateralis*, *Raeta plicatella*, *Anomalocardia brasiliana**, *Macoma uruguayensis*, *Tellina petitiana*, *Strigilla carnaria, Semele proficua*, *Abra aequalis*, *Tagelus plebeius*, *Donax hanleyanus*, *Tivella isabelleana*, *Petricola lapicida*, *Petricola pholadiformis*, *Sphenia hatcheri*, *Corbula lyoni*, *Cyrtopleura lanceolata*, *Barnea lamellosa*, *Nettastomella darwini*, *Lyonsia alvarezii*, *Entodesma patagonicum*, *Periploma ovatum*, *Thracia similes*, and *Bushia rushi* (*extinct in the adjacent littoral; Aguirre, 2001; for details of authors and a systematic review of the species, see Farinati, 1985; Aguirre and Farinati, 2000).

Of the other Patagonian deposits, our fauna shows the closest similarity with MTV (+12–25 m) at Camarones, north of Bahía Bustamante, where 16 of the 21 taxa are common but exhibit clear differences with the older Pleistocene assemblages typical of MTIII at +40–95 m (MOIS 9?) in the same area (18 of 30 taxa in common).

Less similarity is observed with pre-Pleistocene Patagonian terraces (MTII and I, *sensu* Feruglio, 1950), which contain extinct taxa (e.g. *Ostrea* spp.). Only few molluscs (five gastropods and six bivalves; Table 3) are shared with the marine molluscan faunas of the late Miocene age (Aguirre and Farinati, 1999) and virtually none with older Tertiary assemblages (Salamanca Formation) (Feruglio, 1936-1937).

A comparison of the assemblages sampled with the modern associations from the Bahía Bustamante area shows no marked qualitative differences, except for two species, *T. atra* and *V. procera,* that do not live in the area today and probably were extinguished after a late Pleistocene highstand prior to the Last Glacial Maximum (Fray and Ewing, 1963; Richards and Craig, 1963) (MOIS5?). Some indications, however, point to quantitative variations of several taxa (*P. antiqua*, mytilids, *Crepidula* spp.) and differences in size through time (*T. atra* and *P. antiqua* were considerably larger during the Pleistocene sea-level episodes). In addition, modern fauna collected along the SW Atlantic margin (Magellanean province) (Fig. 1) and known from illustrations by other authors is much richer in typically or exclusively cold-water taxa (Carcelles, 1950; Castellanos and Landoni, 1988–1993).

8. Preservation

The deposits, which consist of coarse sand grains and shell debris with rounded pebbles, contain a large proportion of whole, well-preserved shells and some scattered angular pieces of shells or rocks. The shells exhibit variable degrees of preservation; as expected, better taphonomic grades occur with the decreasing age of the ridge systems or less energetic final depositional environments.

The bivalve shells are oriented either horizontally or, more commonly, at random in the strata. Many shells of *P. antiqua* retain their original unaltered sculpture. Although in Pleistocene samples (PA02Q8, 9) they often occur as whole joined valves—some in apparent lifelike positions—most shells in other samples have moved from their original inclination within the sediment. The remaining bivalves are preserved as single entire or fragmented valves.

The gastropod species identified within the Holocene deposits (MTVI) exhibits good preservation, whereas those from the Pleistocene MTIV and V show high levels of fragmentation or abrasion or have lost their original color and luster, though dissolution is not often observed. *Tegula atra*, despite its considerable thickness and maximum sizes within the Pleistocene samples PA02Q5–7 (MTIV), exhibits the lowest taphonomic grade, often with a very abraded external surface even in scales, a chalky appearance, fragmented margins, and poorly preserved original color or luster (except for the nacreous inner layer that generally is intact). Epifaunal gastropods have probably moved longer distances from their original life positions and thus offer less precise environmental data.

9. Paleoecology and distribution

A synthesis of the ecological requirements (substrate and zonation), modern distribution, and stratigraphical ranges of the species identified appears in Table 3. Bivalves are excellent

Table 3
Ecological requirements and distribution in time and space of characteristic taxa recovered

Paleoecological data	Distribution								Bathymetry			Substrate		Life mode			
	Stratigraphical			Geographical													
Bivalves	M	PL	HOL	PAND	ANT	BRAZ	ARG	MAG	Supral.	Intert	Sublit	Soft	Hard	Epibys	Cement	Sh. Inf	Deep in
Aequipecten tehuelchus	X	X	X			X	X				X	X	X	X			
Aulacomya atra		X	X			X	X	X		X	X		X	X			
Brachidontes purpuratus	X	X	X					X	X	X	X		X	X			
Brachidontes rodriguezi	X	X	X			X	X	X	X	X	X		X	X			
Ostrea sp.	X	X	X		X	X	X	X			X		X		X		
Protothaca antiqua	X	X	X			X	X	X			X	X				X	
Clausinella gayi			X			X	X	X			X	X				X	
Mytilus edulis	X	X	X	X						X	X		X	X			
Venericardia procera		X	X			X										X	
Pitar rostratus		X	X			X	X	X			X	X				X	

Paleoecological data	Distribution								Bathymetry			Substrate		Life mode				
	Stratigraphical			Geographical														
Gastropods	M	PL	HOL	PAND	ANT	BRAZ	ARG	MAG	Supral.	Intert	Sublit	Soft	Hard	F	S	Carniv	Herb	Filtr
Fissurella oriens		X						X	X	X	X		X		X		X	
Fissurella radiosa		X	X				X	X	X	X	X		X		X		X	
Nacella (P.)magellanica			X				X	X		X	X		X		X		X	
Patinigera deaurata		X	X				X	X	X	X	X		X		X		X	
Tegula patagonica	X	X	X				X			X	X		X	X			X	
Tegula (C.) atra		X					X	X		X	X		X	X			X	
Crepidula protea	X	X	X		X	X	X			X	X		X		X			X
Crepidula dilatata	X	X	X	X	X	X	X	X			X		X		X			X
Trophon varians	X	X	X				X			X	X	X	X	X		X		
Trophon geversianus	X	X	X				X	X		X	X		X	X		X		
Pareuthria plumbea		X	X				X	X		X	X		X	X		X		
Odontoc.magellanica		X	X				X	X		X		X		X		X		
Buccinanops globulosus		X	X				X	X		X	X	X		X		X		
Buccinanops paytensis		X	X					X		X	X	X		X		X		
Epitonium sp.			X				X			X	X	X		X			X	
Ataxocerithium pullum		X	X					X		X		X	X	X			X	
Siphonaria lessoni			X	X			X	X	X	X	X		X	X			?	

paleoecological indicators and, mainly on the basis of systematic revisions of the dominant taxa (Aguirre and Farinati, 2000), offer important data about the original depositional environments for each MT. The most abundant gastropods (*Nacella* spp., *Tegula* spp., *Buccinanops* sp., *Crepidula* spp.) are epifaunal and more exposed to postmortem transport than are the infaunal bivalves (*P. antiqua*, *C. gayi, Pitar* sp.), but they can offer general information on the substrate and energy levels of the littoral environment.

All the species are recorded live in the SW Atlantic, along the Antillean, Brazilian, Argentinean, or Magellanean malacological provinces; only few are pandemic (rarely cosmopolitan). The updated paleobiogeographical analysis recognizes four groups of species (I–IV) according to their modern geographical ranges: (I) wide or pandemic; (II) typical of warm–temperate or tropical water masses (Antillean, Brazilian, northern part of the Argentinean); (III) temperate or cool–temperate waters (Argentinean and Magellanean); and (IV) exclusively cold-water species (Magellanean).

10. Paleoenvironments

The compositional variations among different MT, though not as strong as records from other coastal areas in South America (Ortlieb et al., 1996a–c), could be linked to environmental and climatic variations, similar to some of the early observations of Feruglio (1950).

As a whole, the molluscs indicate truly marine conditions, shallow waters, and hard substrates, essentially similar to the modern littoral at the same latitude. Temperature, however, was slightly higher during the deposition of MTVI and probably during the accumulation of assemblage sampled at PA02Q5 (MTIV) but slightly colder for the remaining Pleistocene samples (MTIV and V).

Qualitative and semiquantitative estimations are informative and useful for paleoenvironmental interpretations. Although complete, accurate quantitative data are not available at this stage, some approximations are helpful (Figs. 3 and 4).

10.1. Salinity, depth, substrate

All gastropods and bivalves recovered are typically euhaline marine species (Table 3). The most characteristic are supralittoral, intertidal, or upper infralittoral and of high energy environments, such as that in Golfo San Jorge. No precise information is known about their depth ranges, and detailed ecological studies are available only for those species that have known economic value, such as *A. tehuelchus*, *P. antiqua*, *O. magallanica*, and buccinid, patellid and fissurellid gastropods (Lasta et al., 1995).

The predominance of hard bottoms (rocky or coarse sands with pebbles) is assumed from the ecological requirements and life habits of most species (Fig. 3a). No strong changes in the type or distribution of substrates can be inferred during the late Pleistocene or Holocene highstands. In the mid-Holocene, the mytilid bivalves and pateliform gastropods dominate, providing a similar environmental framework to that of the present day (Bastida et al., 1992; Roux and Fernández, 1997).

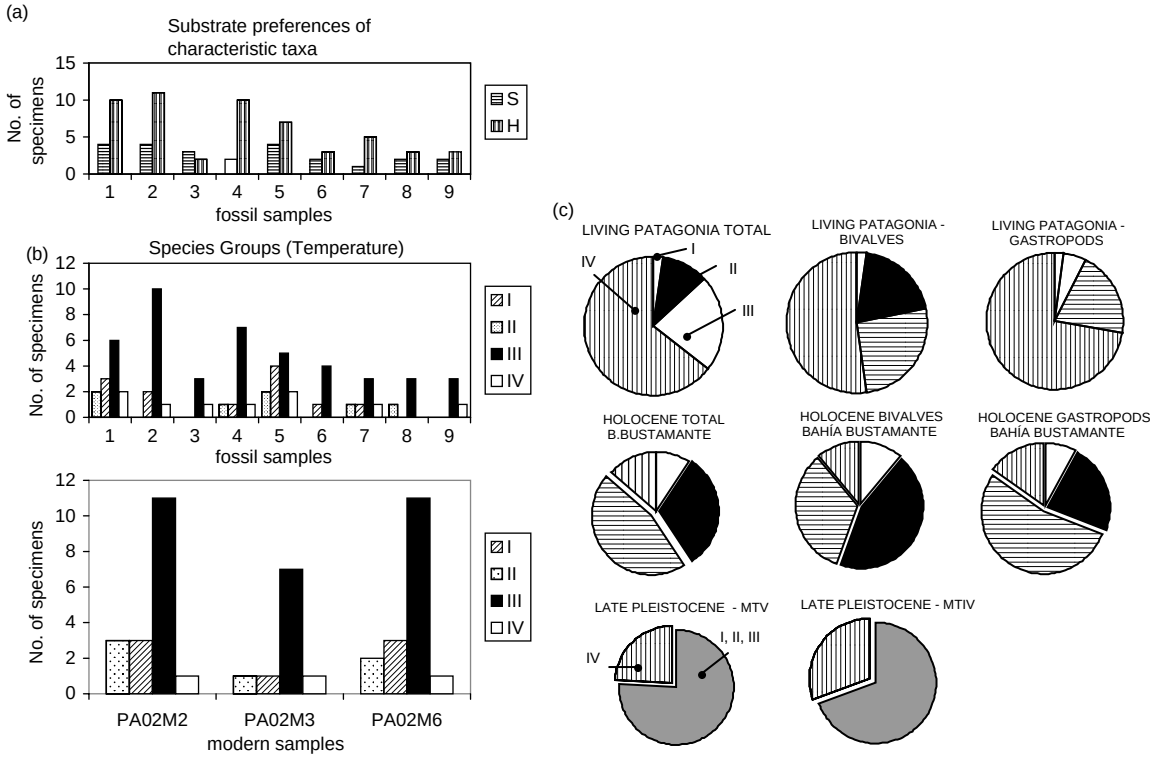

Fig. 3. (a) Substrate preferences of most characteristic taxa: S, soft; H, hard. (b) Distribution of species groups in modern and fossil samples. Samples 1–4, Holocene (PA02Hol1–4); 5–9, Pleistocene (PA02Q5–9). (c) Relative abundance of the species groups collected in the Holocene (MTVI) and currently (Bahía Bustamante area and Patagonia in general). I–IV, species groups according to their distribution in shallow water masses.

The abundance of the infaunal *P. antiqua* and epifaunal *T. atra* in the late Pleistocene, both with larger sizes than the present, may indicate more varied bottoms, but their main controlling factor could have been a colder SST.

To judge from the qualitative faunal composition, there is no evidence of strong changes in terms of salinity, depth, or substrate conditions since deposition of the late Pleistocene terraces.

10.2. Temperature

The distribution and abundance of four groups of species (I–IV) provide a measure of SST conditions and climate variability in the area. In all the Pleistocene and mid-Holocene samples, Group III (Argentinean province) is dominant (Fig. 3b); no marked abundance of Groups II (Antillean) or IV (Magellanean) is evident. In contrast, currently there is a greater proportion of Group IV and other taxa typical of or exclusive to cold-water masses (Fig. 3c), which are absent in MT.

Measuring the amount of variation in temperature per unit of time is more difficult at this stage, because no precision about the MOI substages in the late Pleistocene deposits is possible, but special emphasis can be placed on the mid-Holocene (MOIS1) assemblages, which offer more precise dating.

Groups II and III are more abundant than during either the late Pleistocene or the present, especially in the samples H2 and H4 (6750–8090 ^{14}C BP). The SST preferences of the

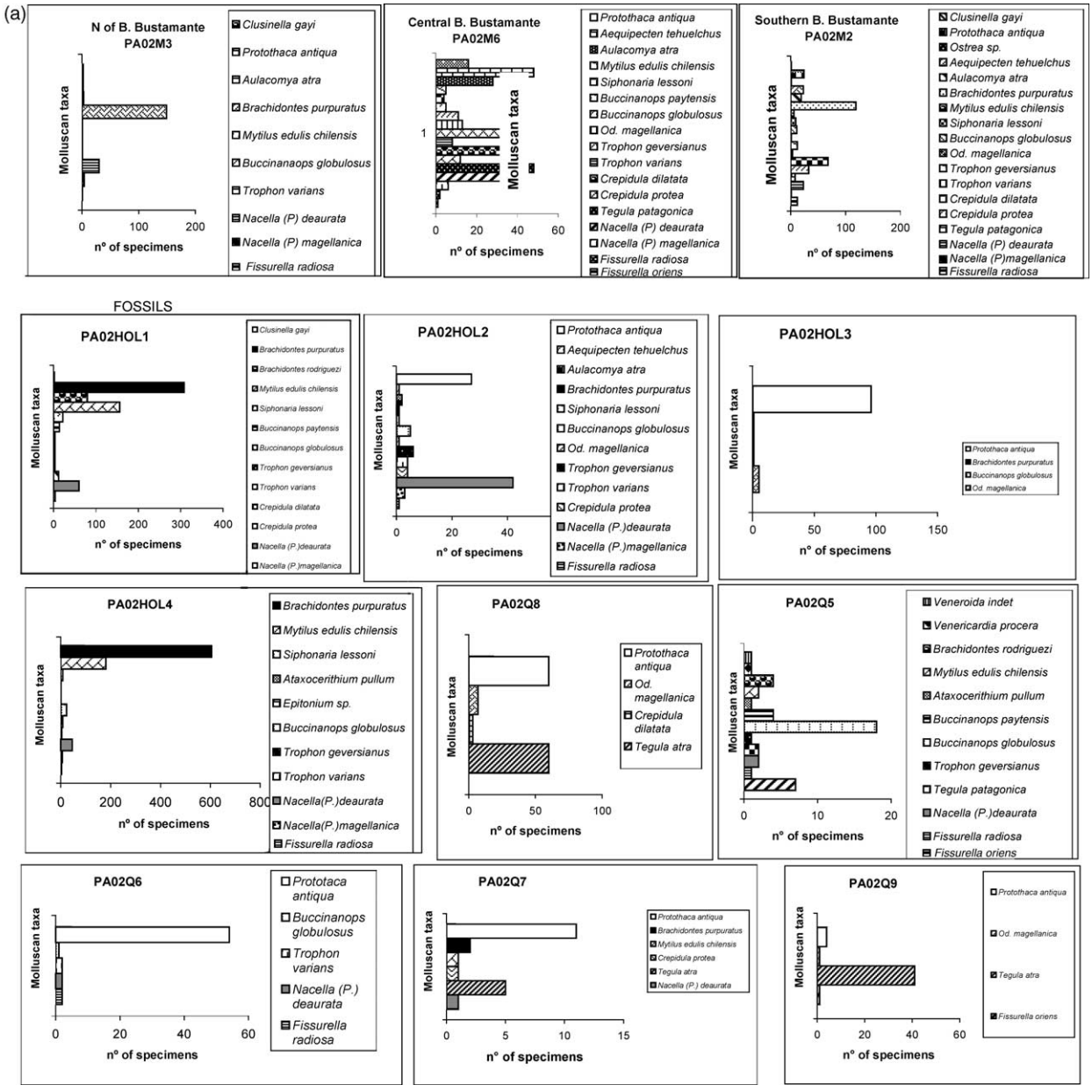

Fig. 4. (a) Abundance of most characteristic molluscan species (M, modern; Hol, Holocene; Q, Pleistocene). (b) Species richness (*D*, %), 1-–3, modern; 4–7, Holocene; 8–12, Pleistocene. (c) Margaleff (d) and Shannon–Weaver (H'') diversity indices.

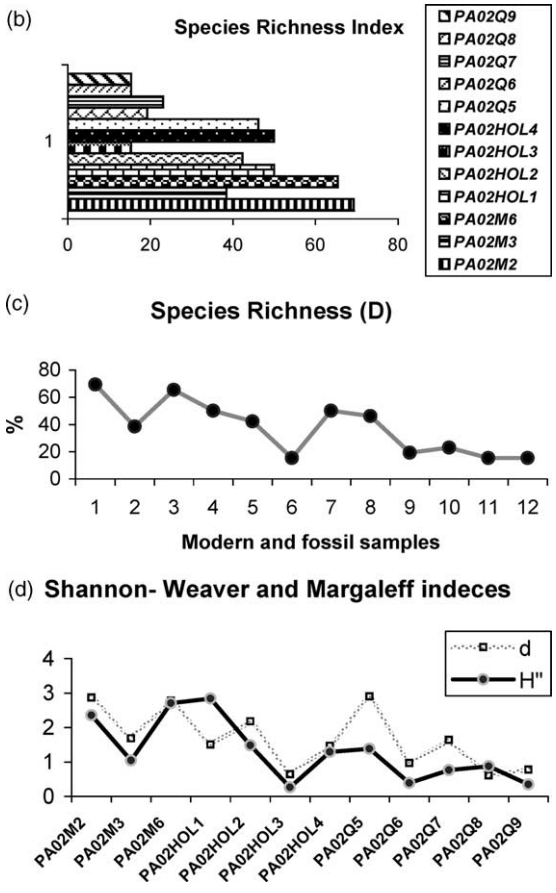

Fig. 4 (*continued*)

species recorded in the mid-Holocene suggest that original communities lived in shallow water, similar to the present, but the scarcity or absence of typical cold-water elements common today along the Magellanean province at the same latitude suggests slightly warmer waters. This theory implies the paleobiogeographical response of the littoral biotas that affected the hypsithermal (climatic optimum) south of the Río de La Plata, at least to 43–44°S.

In Argentina, a southward decreasing trend of Groups II and III and increasing trend of Group IV occur during both the mid-Holocene and currently (Aguirre, 2002), but the highest percentages of Groups II and III characterize the mid-Holocene (8–4.5 ka BP) from southern Brazil to Santa Cruz. The most probable process that led to this pattern is climate change (hypsithermal effect), which is in partial disagreement with the bibliographic compilations by Gordillo (1998); Pastorino (2000).

No such evidence is documented for the Pleistocene ridges; MTV (PA02Q8) and MTIV, which were correlated with the Last Interglacial Maximum (MOIS5e); or previous interglacials (MOIS7 or 9) (samples PA02Q5–7 and 9, respectively) (Fig. 1, Table 1). Groups III and II are abundant only in PA02Q5 (118–147 ESR ka), which could belong to MOIS5e, in agreement with the previous results for equivalent samples (Pa99–97 dated by Schellmann and Radtke, 2000).

It is widely accepted that the SST was higher than it is currently worldwide during both MOIS1 and especially MOIS5e, as has been documented by the global isotope curve (Haq et al., 1987). The primary effect of climate change must be expected on the levels of extinctions or migrations of warm- and cold-water taxa, as well as on the diversity patterns and origination of new species in the area and quantitative variations over time. However, only *T. atra* and *V. procera* are extinct forms at the same latitude. *T. atra* is a typically cold-water species (Group IV) and characterizes MTIV in considerable quantities, where other cold-water invertebrates (*Magellania*, *Balanus* spp.; Table 2, Appendix 2) are also present. *Venericardia procera* currently lives in SW Atlantic, with records in Brazil as the southernmost limit (Ríos, 1994), and is represented by only one specimen in sample PA02Q5 (MTIV), which is also the unique sample in which *T. patagonica* (typical of the Argentinean province, Group III) occurs.

With respect to temperature, the available data demonstrate a slightly warmer SST for MTIV south of Estancia La Esther (north of Estancia la Ibérica, PA02Q5) and during the mid-Holocene (MTVI, PA02H) but not for the remaining Pleistocene ridges. These deposits could be correlated partly with late Pleistocene sediments of the Belgranense and Pascua Formation from Buenos Aires (Isla et al., 2000; Fucks et al., 2006) and the Chuy Formation from Uruguay (Martínez et al.,

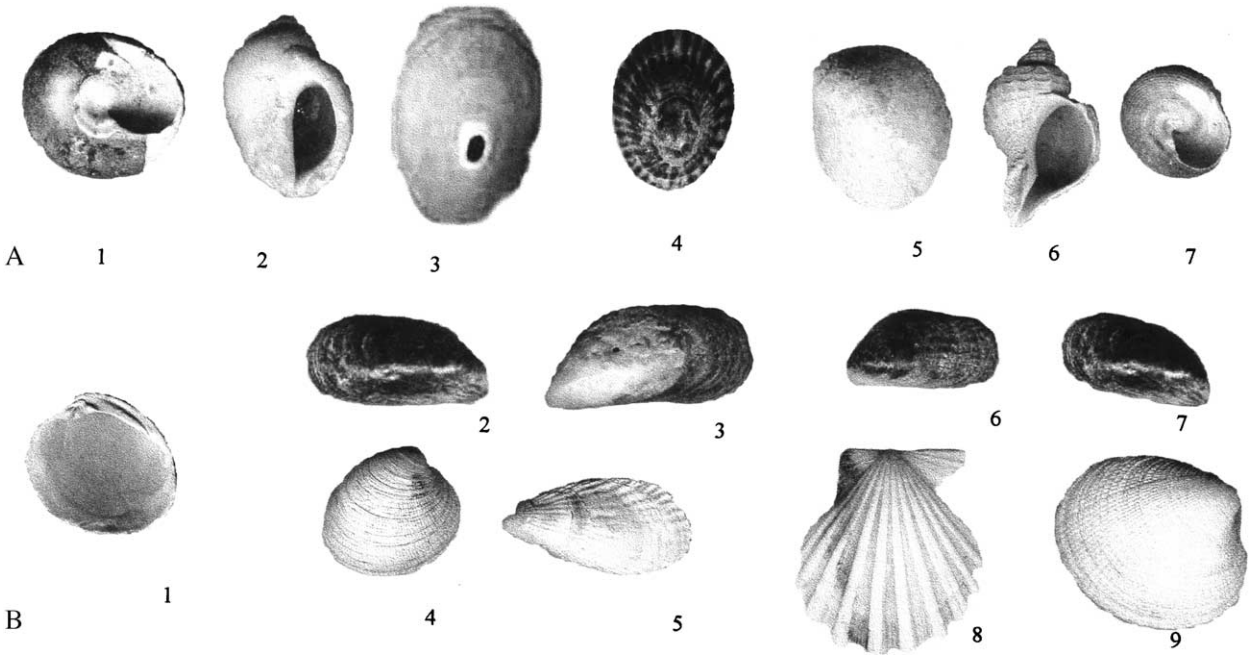

Fig. 5. Most characteristic molluscan species recovered in the late Pleistocene (MTIV and V), mid-Holocene (MTVI), and modern adjacent littoral. (A) Gastropods: 1, *Tegula atra* ($W=20$), PA02Q7; 2, *Fissurella radiosa* ($H=67$), PA02Q6; 3, *Buccinanops globulosum* ($H=31$), PA02Q6; 4, *Nacella (P.) deaurata* ($H=28$), PA02Hol2 ($L=26$); 5, *Crepidula dilatata* ($H=35$), PA02M2 ($H=23$ mm); 6, *Trophon geversianus* ($H=4.3$), PA02M6; 7, *Tegula patagonica* ($W=17$), PA02M6. (B) Bivalves: 1, *Protothaca antiqua* ($H=91$), PA02Q8; 2, *Brachidontes purpuratus* ($L=18$), PA02Hol1; 3, *Mytilus edulis chilensis* ($L=70$), PA02Hol1; 4, *P. antiqua* ($H=65$), PA02Hol2; 5, *Aulacomya atra* ($L=42$), PA0Hol2; 6, *B. purpuratus* ($L=20$), PA02M2 ($L=28$); 7, *B. purpuratus* ($L=58$), PA02M2 ($L=19$); 8, *Aequipecten tehuelchus* ($L=58$), PA02M6; 9, *P. antiqua* ($H=43$), PA02M3. (A1–3, B1) Late Pleistocene; (A4, B2–5) Holocene; (A5–7, B6–9) modern. Dimensions (in mm): *H*, height; *W*, maximum width; *L*, length.

2001), which has been assigned to the Last Interglacial. Future stable isotope analyses of paleoecologically important species should provide more accurate clues.

10.3. Characteristic species, species richness, and diversity

Along the modern littoral in the northern, central, and southern Bahía Bustamante area (Fig. 1), between P. Tafor and Pen. Gravina, the most typical molluscan taxa are *B. purpuratus*, *N. (P.) deaurata*, *N. (P.) magallanica*, *C. dilatata*, *C. protea*, *A. atra*, and *T. geversianus* (Fig. 4a). In the Holocene samples, *N. (P.) deaurata* and *B. purpuratus* are very abundant, followed by *M. edulis chilensis*, *A. atra,* and *P. antique*; during the late Pleistocene, *P. antiqua* and *T. atra* are practically dominant. Along the modern littoral, *C. dilatata*, *T. geversianus*, *T. patagonica, B. purpuratus*, *A. tehuelchus*, and *P. antiqua* (Fig. 5) are the most characteristic.

The timing and patterns of diversity changes and extinctions are responses of faunas to climate change (Prado et al., 2001). The highest diversity patterns of molluscan species in different littoral areas generally are associated with optimum habitats for the taxa or conditions typical of climatic optima. No drastic extinction of species occurred after the deposition of the MTIV and V since at least MOIS7 in this area, apart from the migrations already mentioned—*T. atra* (cold species) and *V. procera* (warm species). However, several indices can be used to attempt an objective comparison of the fossil assemblages with modern conditions (Fig. 4b).

The species richness index (D, %) shows that, as expected, the highest percentages are observed in modern samples that represent complete populations, when taphonomic loss is disregarded, followed by greater values in the Holocene ridges (maximum in H1 and H4) than in the late Pleistocene. Within MTIV, the greatest richness belongs to PA02Q5, the unique Pleistocene sample from which the warmer SST was inferred. The lowest richness corresponds to the Pleistocene MTV.

The Margaleff (d) and Shannon–Weaver (H'') diversity indices find that maximum diversity values belong to the mid-Holocene (H1) and modern (M6) samples and minimum to the late Pleistocene, except for PA02Q5. The highest mid-Holocene diversity coincides with the highest sea-level peak ($\sim$6 ka), which was followed by a fluctuating climatic condition during decreasing trends in sea level and temperature.

If the 'age of the tropics hypothesis' (tropical climates are older, dominant clades evolve in the tropics from which they expand their geographical ranges; Leighton, 2001), which is based on the highest diversity patterns, is correct, our molluscs should show increasing geographical ranges through time. However, the molluscan evidence suggests that the highest diversity does not correspond to the oldest terraces in the area of study (MTIV) and that species do not seem to have expanded their latitudinal ranges over time. The general diversity is also lower than in equivalent and synchronous Bonaerensian coastal

deposits. Our results reinforce the finding that climate, not time, may have driven biodiversity and latitudinal displacements of the littoral taxa.

Other than qualitative and quantitative variations through time, the wide morphological variability apparent in several abundant taxa (i.e. *Brachidontes*, *Nacella*, *Crepidula*, *Tegula*) likely represent phenotypic changes linked to changes in space (environmental) and time (climate), as documented for the northern ridges of Buenos Aires province (Aguirre and Urrutia, 2002).

11. Discussion

An outstanding observation is that within the mid-Holocene, the proportion of exclusively cold taxa is lower than at present at the same latitude and that species richness and diversity are higher. This observation confirms the Patagonian occurrence of the hypsithermal and its paleobiogeographical effect, though obviously less markedly than in the lower latitudes of Patagonia (Rio Negro province).

The climatic optimum (hypsithermal) can be placed approximately at the 9–6 ka interval in this area and should be synchronous with atmospheric and oceanographic changes, such as a southward shift of the warm Brazilian current and the intensification and southward displacement of the South Atlantic anticyclonic center. The paleozoogeographical effect on the littoral molluscan fauna, however, is less evident than it is farther north along the Bonaerensian coastal area, where apart from quantitative differences with the modern molluscan associations, geographical shifts have been linked to SST differences of 1–2 °C (Aguirre, 1993b, 2002).

Regarding the preserved late Pleistocene highstands, the peak of the Last Interglacial (MOIS5e) has been interpreted worldwide as warmer than at present (2 °C?) (Stanley, 1989; Murray-Wallace and Belperio, 1991; Williams et al., 1994; Brown and Lomolino, 1995; Zazo, 1999; Martínez et al., 2001). In other parts of South America, such as northern Chile (Ortlieb et al., 1996a), it has been postulated as cooler than the present and previous interglacials (e.g. MOIS11 is significantly warmer than MOIS5e).

Schellmann and Radtke (2000) favor an interpretation of some late Pleistocene deposits in this area (our PA02Q5–7, 9; MTIV and V of Feruligo, 1950; Systems I and II of Cionchi, 1987) as of Last Interglacial age (MOIS5, some MOIS5e), though they acknowledge that ESR dating of molluscan shells provides insufficient accuracy for chronostratigraphical distinctions between substages within MOIS5 (5e, 5c, and 5a).

Only one Pleistocene sample previously dated as MOIS5e (PA02Q5) contains a higher abundance of warm temperate fauna and higher diversity and probably accumulated during higher SST than that of the present. Other taxa mentioned previously (i.e. *Mactra* spp., *C. patagonica*, *T. patagonica*; Appendix 2) are bound on the south by Golfo Nuevo (Chubut), north of the beach systems studied, which suggests only slight climatic differences with the present. The remaining samples (MOIS5, MOIS7?) do not provide evidence of a higher SST. On the contrary, MTIII (MOIS9, 11?), with its higher percentages of species that are either extinct or displaced to the north, must have been deposited during highstands with a higher SST.

From the faunal content of the ridge systems, the interpretation of whether MOIS5 conditions in the area belong to substage 5e, 5c, or 5a and if the SST was warmer, similar, or slightly colder than present day requires further study. More detailed work, including dating and isotopic measures of unaltered shells of selected molluscs, especially characteristic taxa that have paleoenvironmental value for the area and the deposits studied (i.e. *Protothaca*, *Brachidontes*, *Aulacomya*, *Tegula*, *Patinigera*), should help to better explain climatic variations.

12. Conclusions

A collection of molluscs and associated macrofauna (bryozoans, balanids, polychaetes, brachiopods) preserved in 12 localities (late Quaternary marine terraces and modern beaches) along the Bahía Bustamante coastal area in northern Golfo San Jorge (Chubut) enables updating of paleoecological, paleoebiogeographical, and paleoenvironmental data and provides some implications for paleoclimatic interpretations of the littoral area during the last sea-level highstands.

The species *C. protea*, *B. paytensis*, and *B. rodriguezi* are first recorded for the Pleistocene (MTIV), along with *N. (P). deaurata*, *E. magallanicum*, *B. paytensis*, *A. tehuelchus*, and *Cl. gayi* for the Holocene (MTVI) in the area.

The general conditions of the littoral environment (substrate, depth, water energy conditions) during the late Pleistocene (MOIS7, 5) and mid-Holocene (MOIS1) highstands were similar to the modern nearshore.

Only climatic conditions (SST) of the littoral environment changed, though not dramatically, since at least MOIS7. In addition, the molluscs recovered still live in SW Atlantic littoral. No drastic variations or extinctions of species occurred during sea-level highstands since at least MOIS7. The main examples of considerable migrations are shown by *T. atra* (cold species) and *V. procera* (warm species), which live far from the area of study.

Some of the late Pleistocene deposits assumed to represent MOIS5e (MTIV at PA02Q5) probably were characterized by slightly warmer shallow waters than those of the present, as revealed by the highest richness, diversity, and occurrence of species typical of the Argentinean and Antillean provinces and one currently displaced northward (*V. procera*).

The dominance of the association *T. atra–P. antiqua* can be considered a valid biostratigraphical tool for deposits of MTIV (MOIS7?), in which both taxa reach their maximum abundance and sizes.

The molluscan assemblage from MTV (MOIS5c or 5a?) is characterized by *P. antiqua* in scarce quantities and low diversity. It is not indicative of the warmer SST typical of an interglacial climatic optimum but rather of an SST colder than the mid-Holocene and similar to the present, probably not during MOIS5e. If deposited during MOIS5, they probably

Table B1

Molluscs	Pleistocene			Holocene		
	Feruglio (1933, 1950)	Cionchi (1985)	Feruglio (1933, 1950)	Feruglio (1933, 1950)	Cionchi (1987)	This paper
Gastropod taxa						
Fissurella oriens Sowerby	X		X	X		
Fissurella radiosa Lesson	X		X	X		X
Nacella (P.) magellanica (Gmelin)	X	X	X	X	X	X
Nacella (P.) deaurata (Gmelin)	X		X			X
Nacella delicatissima (Strebel)	X					
Tegula (A.) patagonica (d'orb.)	X		X			
Tegula (C.) atra (Lesson)	X	X	X	X	X	
Crepidula aculeata (Gmelin)						
Crepidula protea d'Orb.			X			X
Crepidula cf. onyx Sowerby						
Crepidula dilatata Lamarck	X		X	X		X
Epitonium (B.) magellanicum (Phil.)						X
Ataxocerithium pullum (Philippi)	X		X			X
Trophon varians (d'Orb.)	X		X	X		X
Trophon geversianus (Pallas)	X	X	X	X	X	X
Acanthina monodon (Pallas)						X
Adelomelon ferrussacii (Donovan)	X					
Odontocymbiola magellanica (Gm.)	X	X	X	X	X	X
Buccinanops globulosus (Kiener)		X	X	X	X	X
Buccinanops paytensis (Kiener)			X			X
Pareuthria plumbea (Phil.)	X			X		X
Siphonaria lessoni (Blainville)	X	X		X	X	X
Fissurella picta (Gmelin)	X			X		
Diodora patagonica d'Orb.)		X		X	X	
Crepidula dilatata patagonica (d'Orb.)	X	X		X	X	
Photinula caerulescens (King)				X		
Ximenopsis muriciformis (King & Broderip)	X			X		
Colisella ceciliana (d'Orb.)	X					
Trophon elongatus Str.	X					
Pareuthria rosea	X					
Pareuthria cerealis (Roch. & Mab.)	X					
Acanthina calcar Mart.	X					
Adelomelon ancilla (Lightf.)		X			X	
Olivella tehuelcha (Duclos)	X					
Buccinanops cochlidium ((Dillwyn)	X					
Morula necocheana (Pilsbry)	X			X		
Siphonaria tristensis (Leach)						
Bivalve taxa						
Mytilus (M.) edulis chilensis (Hupé)	X	X	X	X	X	X
Brachidontes (B.) rodriguezi (d'Orb.)			X			X
Brachidontes (B.) purpuratus (Lamk.)	X	X	X	X	X	X
Aulacomya atra (Molina)	X	X		X	X	X
Aequipecten tehuelchus (d'Orb.)						X
Ostrea sp.						
Pitar (P.) rostratus (Koch)			X			
Venericardia procera (Gould)	X		X			
Eurhomalea exalbida (Dillwyn)	X					
Protothaca antiqua (King)	X	X	X	X	X	X
Clausinella gayi (Hupé)	X			X		X
Hiatella arctica (Linné)						
Mactra isabelleana d'Orb.	X					
Mactra patagonica d'Orb.	X					
Kellia suborbicularis Mont.						
Chlamys patagonicus (King & Broderip)	X	X			X	
Ensis macha (Molina)	X					
Bushia rushi (Pilsbry)		X			X	
Chione sp.		X			X	
Other invertebrate taxa						
Balanus laevis Brug.	X					
Balanus psittacus Brug.	X			X		
Magellania venosa (Sol.)	X					
Toxocidaris albus (Mol.)	X			X		

belong to the substages 5c or 5a. This claim supports Feruglio's framework of colder waters and a post-Last Interglacial maximum episode.

Assemblages of MTVI (mid-Holocene, MOIS1) are characterized by the dominance of *N. (P.) deaurata* and mitylid bivalves (*B. purpuratus*, *A. atra*), as well as the highest diversity in the MT sampled. Paleobiogeographical evidence and quantitative compositional variations support the influence of climatic optimum during 6–9 ka interval.

These results widen the effect of the hypsithermal on the SW Atlantic littoral biota, down to at least 44°S. The influence of warm Brazilian current must have reached south of Golfo Nuevo in the summer, which provoked a southward displacement of the Argentinean province.

From the faunal content of the ridge systems, deciphering with more precision whether MOIS5 conditions in the area belong to substages 5e, 5c, or 5a needs further isotopic studies of unaltered shells of selected taxa.

Acknowledgements

The authors thank J. Hlebszebitch, J. Codignotto, and R. Kokot for assistance in the field. Discussions with and suggestions by Luc Ortlieb improved the study. Laura Ferrero provided helpful information for Appendix 3. M.I. Trucco, E. Fucks, and C. Deschamps helped in several stages of this study. Special thanks are due to Prof. R.C. Whatley (Aberystwyth) and an anonymous referee for their comments and corrections on the first version of this manuscript. This contribution benefited from a grant by Conicet (PEI 126/98, PICT) to partially cover fieldwork. This article is a contribution to IGCP 437, 'Coastal environmental change during sea-level highstands: A global synthesis with implications for management of future coastal change.'

Appendix A. List of samples

PA02M2: Pen. Gravina. Abrasion platform (see Fig. 2b); PA02M3: area of Estancia San Miguel (north of P. Tafor); PA02M6: Estancia La Ibérica; PA02HOL1: Pen. Gravina, abandoned quarry (see Fig. 2b); PA02HOL2: Estancia San Miguel (out of the area shown in Fig. 1B); PA02HOL3: exterior ridge at Bahía Bustamante; PA02HOL4: type locality of Zanjón El Pinter Formation; PA02Q5: north of Estancia la Ibérica, south of Estancia La Esther, abandoned quarry (MTIV); PA02Q6: ridge 'Estancia La Ibérica' of Feruglio (MTIV); PA02Q7: Estancia la Ibérica, south of Q6 (MTIV); PA02Q8: south of Q7 (MTV); PA02Q9: 200 m north of Ao. Marea (MTIV) (see Fig. 2b). Q7, 8, 9 coincide with Feruglio's description (1950, p. 101). Additional samples were taken south of Estancia San Miguel (PA02Q4, abandoned quarry = ridge with *M. isabelleana* and *M. patagonica* of Feruglio, 1950) and in the Caleta Malaspina area (PA02Q1, TMIV; PA02Q2 and PA02Q3, TMV) but were not included in this analysis because of the badly preserved material. The general faunal composition seems similar to that observed in the remaining terraces of equivalent ages at Bahía Bustamante.

Table C1

Pleistocene (Caleta Malaspina Fm.) (Cionchi, 1985)
Forams
Elphidium macellum (Fitchel and Moll, 1798)
Elphidium cf. discoidale (d'Orbigny, 1839)
Nonion depressulus (Walker and Jacob, 1798)
Buliminella elegantissima (d'Orbigny, 1839)
Bulimina cf. affinis (d'Orbigny, 1839)
Bolivina cf. variabilis (Williamson, 1858)
Bolivina danvillensis (Howe and Wallace, 1932)
Bolivina compacta (Sidebottom, 1905)
Cibicides aknerianus (d'Orbigny, 1846)
Epistominella exigua (Brady, 1884)
Buccela frigida (Cushman, 1921)
Buccela peruviana (d'Orbigny, 1839)
Elphidium lessoni (d'Orbigny, 1826)
Bolivina variabilis (Williamson, 1858)
Bolivina translucens (Phleger and Parker, 1950)
Bolivina doniezi (Cushman, 1922)
Bolivina cf. difformis (Williamson, 1858)
Bolivina ordinaria (Phleger and Parker, 1950)
Bolivina striatula (Cushman, 1922)
Quinqueloculina seminulum (Linné, 1767)
Discorbis williamsoni (Chapman and Parr, 1932)
Ostracods
Leptocythere patagonica (Hartmann, 1962)
Callistocythere dispersocostata (Hartmann, 1962)
Cytherura portmonttensis (Hartmann, 1962)
Pterigocythereis sp.
Krite sp.
Semicytherura sp.
Hemitheria sp.
Quadracythere sp.
Urocythereis sp.
Cytherura sp.

Appendix B. List of molluscan species and other invertebrates known from the deposits sampled

Table B1

Appendix C. List of microfossils recovered from the Late Pleistocene Caleta Malaspina Formation (MTV + MTIV) (Cionchi, 1985).

Table C1

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