

## Paleoecology and paleobiogeographic patterns of mid-Holocene mollusks from the Beagle Channel (southern Tierra del Fuego, Argentina)

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**ABSTRACT.** As the Beagle Channel lies between the Atlantic and the Pacific oceans, this is a critical region for the interpretation of faunal distributions in the Magellan Region. This work proposes a paleoenvironmental interpretation of the Holocene, inferred from malacological data. The development of different local benthic paleocommunities during the mid-Holocene is associated with the diversity of habitats inside this channel. The analysis of records of *Venus antiqua* and *Ensis macha* through time and their geographic links to ecological factors showed that these taxa are typical elements of the cold-temperate seas throughout the Magellan Region, showing a similar range of distribution and paleodistribution. The presence of these taxa in life position (AMS <sup>14</sup>C of 6,276±41 years BP) suggests that during the mid-Holocene the Beagle Channel was a path for dispersion of these taxa between the two oceans. Whether *Venus antiqua* and *Ensis macha* are Pleistocene survivors or Holocene migrants is herein discussed. In the future, integrated cross-disciplinary studies will be necessary for a better understanding of the biogeographic relationships among magellanic mollusks.

**Keywords:** Paleoecology, Mollusca, Holocene, Tierra del Fuego.

**RESUMEN.** Paleoecología y patrones paleobiogeográficos de moluscos del Holoceno medio del Canal Beagle (sur de Tierra del Fuego, Argentina). El Canal Beagle es una región crítica para la interpretación de las distribuciones faunísticas en la Región Magallánica, ya que representa una conexión entre los océanos Atlántico y Pacífico. Sobre la base de datos malacológicos, este trabajo propone una interpretación paleoambiental para el Holoceno. El desarrollo de diferentes paleocomunidades bentónicas locales durante el Holoceno medio se asocia a la diversidad de hábitats dentro del canal. El análisis de los registros de *Venus antiqua* y *Ensis macha* a través del tiempo, y sus vínculos geográficos con factores ecológicos, indicó que estos dos taxones son elementos típicos de los mares frío-templados de la Región Magallánica, exhibiendo un patrón similar de distribución y paleodistribución. La presencia de estos taxones en posición de vida (AMS <sup>14</sup>C de 6,276±41 años AP) sugiere que durante el Holoceno medio el Canal Beagle constituyó una vía de dispersión de taxones entre los dos océanos. Respecto a su procedencia, se discute la factibilidad de que estos taxones sean sobrevivientes del Pleistoceno o inmigrantes del Holoceno. En el futuro, serán necesarios más estudios interdisciplinarios integrados para lograr una mejor comprensión de las relaciones faunísticas de los moluscos magallánicos.

**Palabras claves:** Paleoecología, Mollusca, Holoceno, Tierra del Fuego.

## 1. Introduction

The Beagle Channel ( $54^{\circ}53'S$ ,  $67^{\circ}-68^{\circ}W$ ) is located at the southernmost extreme of South America (Fig. 1), being part of an 'austral archipelago region' which goes from the Chiloé Island ( $42^{\circ}S$ ) to Cape Horn ( $55^{\circ}S$ ). This long archipelago has historically experienced the combined effects of tectonic activity, glaciers and climatic processes. Considering the fact that the Beagle Channel lies between the Atlantic and the Pacific oceans, this is a critical region for the interpretation of faunal distributions in the Magellan Region.

During the Quaternary the southern tip of South America was affected by several glaciations which might have excluded much of the benthic marine fauna inhabiting this region, with the consequent interruption of the connection between the two oceans. In that context, fossil marine mollusks which have been recovered from interglacial and postglacial Quaternary deposits can be used to follow periods of interchange and colonization between the Atlantic and the Pacific oceans.

It is known that the survival of a species over time or in a given geographical area often depends upon its ability to disperse. On the other hand, Valdovinos *et al.* (2003) recognized the importance of regional processes (*i.e.*, geomorphological heterogeneity) in affecting global biogeographic patterns and increasing local diversity of mollusks.

Concerning glaciations, Crame (1996) suggests that one species could have survived repeated glacial advances over the past 40 million years by using some form of refugium. Thus, available data show that current biogeographic patterns are the result of a combination of biological factors, geomorphology and historical events which would have influenced the distribution of the species.

With regard to paleoecology, despite the bias in preservation (*i.e.*, the loss of soft body taxa, post burial taphonomic processes), Quaternary mollusk assemblages retain useful information about the life habits and habitats of the marine benthos from which they are derived (Aitken, 1990). Previous available information showed that mollusks from this region provide a key for the reconstruction of paleocommunities and the evaluation of changes in faunal composition during the Holocene (Gordillo *et al.*, 2005).

The objective of this work is to analyze the paleobiogeographical patterns of distribution of the bivalves *Venus antiqua* and *Ensis macha* in southern South America, and to examine the mid-Holocene records from the Beagle Channel in a paleoecological and paleoenvironmental context. This contribution is part of a cooperative research project between the Centro de Investigaciones Paleobiológicas (CIPAL, Universidad Nacional de Córdoba) and the Laboratorio de Geología del Cuaternario (CADIC-CONICET, Ushuaia), in Argentina.

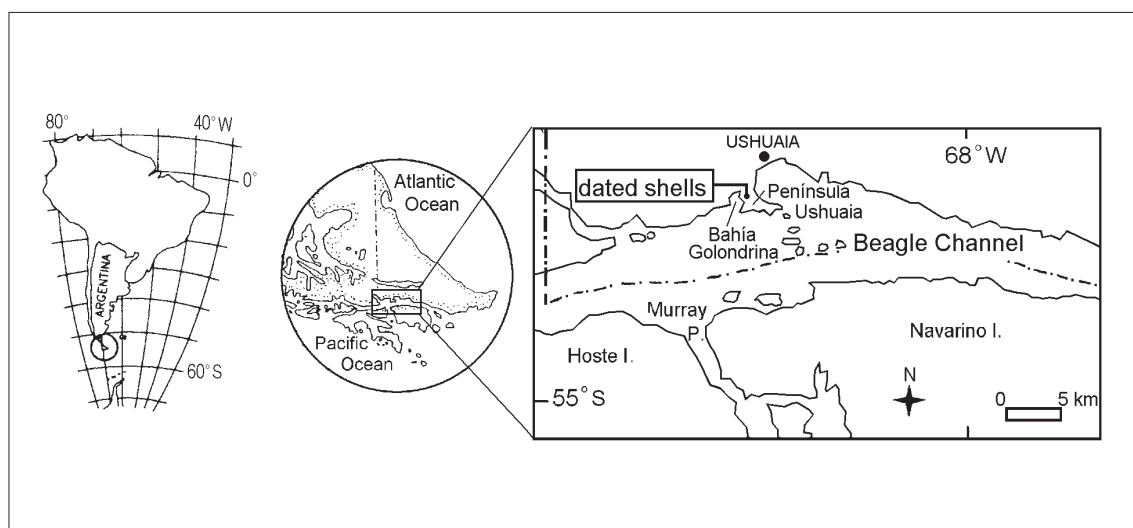


FIG. 1. Map of the studied region showing the Beagle Channel area and the location of Bahía Golondrina.

## 2. Geological Setting and the Main Quaternary Events

The Beagle Channel is a drowned glacial valley 5 km wide and 180 km long in a western-eastern trend located in the seismotectonically active area of the Fuegian Andes, which was glaciated in at least two major episodes during the middle and late Pleistocene (Rabassa *et al.*, 2000). The Last Glacial Maximum (LGM) was attained sometime around 25-24 ka BP (Kaplan *et al.*, 2004) and the ice recession of the Beagle Glacier began sometime before 14.7 ka BP (Heusser, 1998). After these episodes, geomorphologic and stratigraphic evidence shows that the area was occupied by glaciolacustrine and glaciofluvial environments (Heusser, 1989; Rabassa *et al.*, 2000). Freshwater was gradually replaced by seawater in the early Holocene, and the marine environment was then fully established in the Beagle Channel around 8,000-7,000 years ago, with a transgressive episode peaking around 6,000 years ago leaving scattered marine deposits in both northern and southern Beagle Channel coasts (Porter *et al.*, 1984; Rabassa *et al.*, 1986; Gordillo *et al.*, 1992).

## 3. Water Masses

The Beagle Channel is a semi-closed basin with relatively shallow and constrained entrances (Antezana, 1999) and estuarine dynamics (Isla *et al.*, 1999).

The large-scale oceanic surface circulation is controlled by the Antarctic Circumpolar Current (ACC), which transports cold, subantarctic water towards Chile. Off southern Chile (at around 43°S) the ACC sends a branch, the Cape Horn Current, southwards. It passes around the continent through the Drake Passage and joins the Malvinas (Falkland) Current on the Atlantic side of South America, influencing both the eastern and western coasts.

A medium-scale hydrographic feature joining the subantarctic water of the Fuegian Archipelago is the input of a high fresh water supply originating from the melting of resident glaciers, high precipitation and river runoff.

## 4. Material and Methods

The Bahía Golondrina site is located on Península Ushuaia (Fig. 1) and is characterized by

marine deposits at different elevations from +2 to +10 m (Urien, 1968; Gordillo, 1990a). Shells were collected from this site when they became exposed during the construction of a road to the Ushuaia international airport. A 125 dm<sup>3</sup> bulk sediment sample containing mollusks was obtained from a grey silty-sand section at +2 meters above sea level (Gordillo, 1999). In the field, the specimens were counted and a sub-sample (n=20) was randomly collected from the entire sample. Some specimens are housed in the Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba (Argentina) under prefix CEGH-UNC 22209 to 22210.

The dating of this deposit was carried out on paired valves of the fragile shells of *Ensis macha* found in life position, an atypical situation with respect to other fossil mollusk assemblages along the Beagle Channel, which normally consist of transported mollusk assemblages (Gordillo *et al.*, 1992). A radiocarbon date on this sample was obtained with AMS <sup>14</sup>C techniques at the NSF-Arizona AMS Laboratory (University of Arizona).

The ecological characterization of these taxa and their patterns of distribution are based on their equivalent living counterparts. A correlation of the Bahía Golondrina site with other previously studied sections of similar age (*i.e.*, the Río Varela and Lago Roca sites; see references in Gordillo *et al.*, 1993, 2005 and Coronato *et al.*, 1999) contributed to the understanding of the environmental conditions during the Holocene transgression.

In addition, previous paleontological data for each species was compiled from different authors (*i.e.*, Carcelles, 1944; Feruglio, 1950; Richards and Craig, 1963; Figueiras, 1967; Herm in Osorio *et al.*, 1983; Cionchi, 1987; Pastorino, 1989, 2000; Gordillo, 1992; Ortlieb *et al.*, 1991, 1994; Valdovinos, 1996; Frassinetti, 1997; del Río *et al.*, 1998; Guzmán *et al.*, 2000; Ortlieb *et al.*, 2003; Aguirre, 2003; Aguirre *et al.*, 2005, 2006; Cárdenas-Mancilla and Gordillo, 2006).

## 5. Remarks on Systematics of *Venus Antiqua*

The generic and subfamiliar assignment of *Venus antiqua* has been debated for a long time and is still under discussion. Some authors place it in *Protothaca*, or in *Ameghinomya*. However, on the basis of shell characters, it differs from species of *Protothaca* in its shape and in the prominence of its external sculpture (Beu, 2004); and it differentiates

from species of *Ameghinomya* in having a nodular anterior lateral tooth in the left valve (Osorio *et al.*, 1983). Beu (2004) also noted that *Venus antiqua* shell resembles that of *Austrovenus stutchburyi* from New Zealand. Nonetheless, the use of traditional shell-based characters alone appears to be questionable for resolving phylogenetic relationships of this group. In a recent molecular analysis within the family Veneridae, Kappner and Bieler (2006) found that this morphotype (*i.e.*, with a lateral tooth) falls into the Venerinae *s. novo clade*. Therefore, these authors concluded that a revision of this enigmatic species is necessary. In the meantime, and taking into account the subfamilial assignment by Kappner and Bieler (2006), we follow Osorio *et al.* (1983) and we refer to this species as *Venus*.

## 6. Autoecology

Two taxa in life position were recovered from the studied site: the razor clam *Ensis macha* (Molina, 1782) and the striped clam *Venus antiqua* (King and Broderip, 1832). These two species are dominant members of the shallow-water, soft-bottom communities of the Chilean coast zone (Urban, 1996), and they are within the 10 commercially most important species in Chile (Reid and Osorio, 2000).

*Ensis macha* (Fig. 2A) inhabits shallow subtidal soft bottoms along its area of distribution. This is a filter feeder which lives deeply buried in the sediment, favored by its shape and large foot (Urban, 1994a). It can be found on coarse sandy sediments or silty sands between 2 and 50 m depth (Ramorino, 1968; Urban, 1994a; Guzmán *et al.*, 1998). In relation to the reproductive cycle, *Ensis macha* is a planktotrophic species which spawns either in the cold or the warm seasons (Avellanal *et al.*, 2002; Barón *et al.*, 2004).

The other bivalve, *Venus antiqua* (Fig. 2B) is a filter feeder which lives semi-infaunally or infaunally on silty-sand to stony bottoms from the intertidal zone to 40 m depth (Ramorino, 1968; Clasing *et al.*, 1994; Urban, 1994a; Urban and Tesch, 1996; Reid and Osorio, 2000). *Venus antiqua* feeds on plankton and organic detritus, and also exhibits annual reproductive cycles with long spawning (Verdinelli and Schuldt, 1976; Lozada and Bustos, 1984).

Both species display variations in their reproductive cycles, which may be associated with changes in salinity and temperature affecting the

coastal areas. They are able to develop under normal to lower salinity (of 21–27‰; Reid and Osorio, 2000) and tolerate a temperature range from 4° to 20°C (Urban, 1994b).

## 7. Living Distribution and Fossil Occurrences

*Ensis macha* and *Venus antiqua* are typical elements of the Magellan Province, exhibiting a wide area of distribution within the Pacific and the Atlantic oceans (Fig. 3, Table 1). The Magellan Province is a U-shaped, wide, cold-temperate region, comprising both sides of southern South America between 56°S to about 40°–42°S. *Ensis macha* lives from 55°S to 40°S along the Atlantic, but along the Pacific it penetrates into the peruvian waters to about 23° (Osorio *et al.*, 1979; Guzmán *et al.*, 1998; Lasta *et al.*, 1998; Barón *et al.*, 2004). *Venus antiqua* also inhabits the Beagle Channel, and extends its range of distribution along the Pacific coast to Callao, in Peru, but also along the Atlantic coast to southern Brazil, penetrating the Argentinean Province (Ríos, 1994; Urban and Tesch, 1996; Reid and Osorio, 2000).

Brattström and Johanssen (1983) discuss the factors that favor and impede distribution in Chilean waters. They consider that both, the direction and the great extension of the oceanic currents from south to north or north to south, parallel to the coast, favor passive distribution over long distances. The direction of the Cape Horn Current and the similar hydrographic conditions on both sides of the tip of South America make it likely that ‘Pacific or Chilean’ species will be found on the Atlantic side. Currents of different depths and directions may also play a role in larval distribution, since many larvae migrate vertically. Where currents meet, larvae can also be transferred passively from one current system to another by vertical and horizontal eddies; tidal currents and waves may facilitate spreading, both with and against the main ocean currents (Brattström and Johanssen, 1983). Thus, theoretically, larvae from the Pacific may be transported by the Cape Horn Current, farther south than the Beagle Channel, some even into the Atlantic.

At present, both taxa are extant species in the Beagle Channel and this region appears to be their southernmost geographical distribution. However, it is noted that both of them are apparently scarce in modern communities of Tierra del Fuego. For example, in the Magellan Strait, *Venus antiqua* and

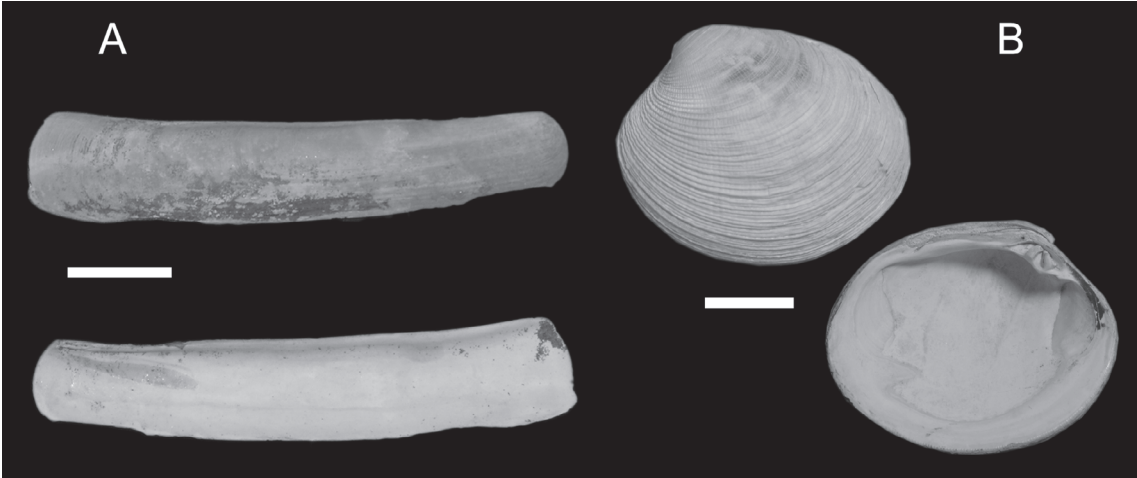


FIG. 2. A. *Ensis macha* (Molina), external and internal lateral views of right valve, CEGH-22209, Bahía Golondrina site, Beagle Channel; B. *Venus antiqua* (King and Broderip), external and internal lateral views of left valve, CEGH-22210, Bahía Golondrina site, Beagle Channel. Scale bar=20 mm.

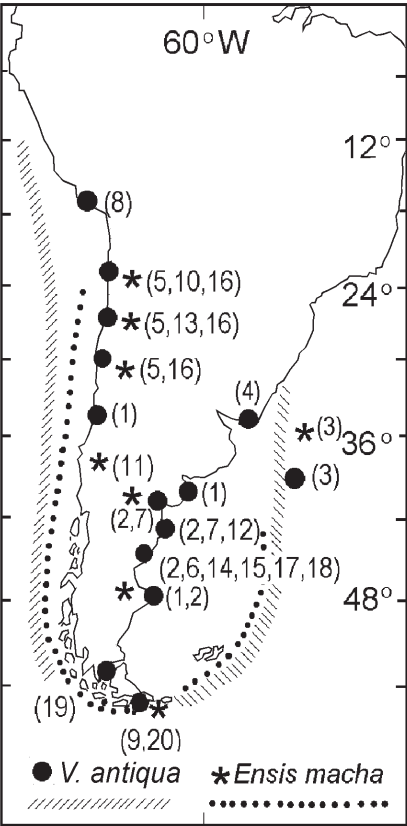


FIG. 3. South American map showing areas of present distribution of *Ensis macha* (dotted line) and *Venus antiqua* (slashed line) and locations of their fossil records (references of numbers in table 1).

*Ensis macha* were not mentioned alive between the Primera and Segunda Angostura sector (Ríos *et al.*, 2003). Di Gerónimo *et al.* (1991) did not find these taxa when they sampled other Magellan Strait stations between 80 and 630 m, and only Urban and Tesch (1996) collected *Venus antiqua* during low tide from San Juan (53°40'S), a bay located about 60 km south of Punta Arenas. This scarcity may be attributed to a variety of factors: patchy distribution, sampling bias, preservation potential and/or accumulation of shells on the marine seafloor.

Although the Atlantic entrance to the Magellan Strait seems to be a natural barrier to the distribution of many species (Stuardo, 1964), the Beagle Channel probably does allow the dispersal of many species which have been recorded within or near it, and environmental constraints within this channel, such as low depths and low salinities, do not appear to represent barriers.

The occurrence of these taxa in the fossil record is presented in figure 3. Both taxa exhibit widespread Quaternary distribution along the Atlantic and the Pacific coasts of southern South America. Tertiary records appear more isolated and in some cases they should be treated with caution. For example, Frassinetti (1997) mentioned the finding of *Ensis* specimens from Pliocene strata in Guafo Island (43°37'S), southern Chile, but their preservation state prevents their assignment as *Ensis macha*. This lack of accurate data makes it difficult

TABLE 1. THE FOSSIL RECORD OF *ENSIS MACHA* AND *VENUS ANTIQUA* INDICATED IN THE MAP (FIG. 3).

| Ref. | Fossil record                                | Geological age  | Locality, Region  | Source  |
|------|--|---|---|---|
| 1    | <i>Venus antiqua</i>                         | Cenozoic (Araucaniano, Belgranense, Querandinense, Prequequense, Navidense) | Puerto Belgrano (38°53'S) / Puerto Deseado (48°S), Argentina. Navidad (34°S), Central Chile | Carcelles (1944)                                  |
| 2    | <i>Ensis macha</i> ,<br><i>Venus antiqua</i> | Quaternary  | Patagonia (40 to 46°S), Argentina   | Feruglio (1950)                                   |
| 3    | <i>Ensis macha</i> ,<br><i>Venus antiqua</i> | Pleistocene<br>Pleistocene  | Off Uruguay (34°47'S); 55 m depth. Atlantic Ocean (37°38'S, 38°38'S; 39°02'S)               | Richards and Craig (1963)                         |
| 4    | <i>Venus antiqua</i>                         | Quaternary  | Punta Carretas, Montevideo, Uruguay   | Figueiras (1967)                                  |
| 5    | <i>Venus antiqua</i>                         | Pliocene<br>Pleistocene, Holocene   | Chañaral de Azeitunas (30°S) Hornito, Mejillones, Caldera, La Serena, Tongoy (23 to 30°S)   | Herm (1969) <i>in</i> Osorio <i>et al.</i> , 1983 |
| 6    | <i>Venus antiqua</i>                         | Pleistocene, Holocene   | Bahía Bustamante and Caleta Malaspina (45°S), Patagonia                                     | Cionchi (1987)                                    |
| 7    | <i>Venus antiqua</i>                         | Holocene  | San Antonio O., Pla. Valdés, Madryn (40° to 42°S), Patagonia                                | Pastorino (1989)                                  |
| 8    | <i>Venus antiqua</i>                         | Late Pleistocene  | San Juan-Marcona (15° 30'S), Perú   | Ortlieb <i>et al.</i> (1991)                      |
| 9    | <i>Venus antiqua</i>                         | Holocene  | Archipiélago Cormoranes, Beagle Channel   | Gordillo (1992)                                   |
| 10   | <i>Ensis macha</i> ,<br><i>Venus antiqua</i> | Late Pleistocene  | Antofagasta area (22°47'to 23° 47'S)  | Ortlieb <i>et al.</i> (1994)                      |
| 11   | <i>Ensis macha</i>                           | Plio-Pleistocene  | Tubul (36°S), central Chile   | Valdovinos (1996)                                 |
| 12   | <i>Venus antiqua</i>                         | Miocene   | Puerto Pirámide (42°S), in Pla. Valdés, Patagonia.  | Del Río <i>et al.</i> (1998)                      |
| 13   | <i>Ensis macha</i> ,<br><i>Venus antiqua</i> | Pleistocene<br>Pliocene to Recent   | Caldera (27°-28°S), northern Chile  | Guzmán <i>et al.</i> (2000)                       |
| 14   | <i>Venus antiqua</i>                         | Holocene  | Camarones (45°S), Patagonia   | Pastorino (2000)                                  |
| 15   | <i>Venus antiqua</i>                         | Pleistocene, Holocene   | Golfo San Jorge, Patagonia  | Aguirre (2003)                                    |
| 16   | <i>Ensis macha</i>                           | Early Pleistocene   | Mejillones (23°S), Caldera (27°-28°S) and La Serena (30°S), northern Chile                  | Ortlieb <i>et al.</i> (2003)                      |

Table 1 (continued).

| Ref. | Fossil record                                | Geological age        | Locality, Region                               | Source                                |
|------|--|-----------------------|--|---------------------------------------|
| 17   | <i>Venus antiqua</i>                         | Pleistocene, Holocene | Bahía Bustamante, Patagonia                    | Aguirre <i>et al.</i> (2005)          |
| 18   | <i>Venus antiqua</i>                         | Pleistocene, Holocene | Vera-Camarones, Patagonia                      | Aguirre <i>et al.</i> (2006)          |
| 19   | <i>Venus antiqua</i>                         | Holocene              | Strait of Magellan (52°S-53°S), southern Chile | Cárdenas-Mancilla and Gordillo (2006) |
| 20   | <i>Ensis macha</i> ,<br><i>Venus antiqua</i> | Holocene              | Beagle Channel (54°49'S), Argentina            | This work                             |

to determine the migration direction. However, their age and pattern of distribution show that both taxa are Tertiary elements that participated in the interchange between the Atlantic and the Pacific oceans via southern South American seas. In the Beagle Channel there is also a second group of taxa (the Quaternary elements), mostly composed of micromollusks, which exhibit Antarctic affinities (Gordillo *et al.*, 2005). Coming back to *Ensis macha* and *Venus antiqua*, when comparing their fossil distribution with the distribution of their living counterparts, they maintain a similar pattern along both sides of the South American coasts. It can be interpreted that these taxa evolved during the Plio-Pleistocene and migrated and extended their areas of distribution as connecting seaways formed. They may have crossed into southern waters during the Plio-Pleistocene, and much later during the Pleistocene and/or the Holocene. During migration, they probably occupied newly vacant areas formed during deglaciation. These new habitats were colonized by new communities formed by immigration of species living in any location with geographic access to these sites.

As fossils, their maximum northward extension corresponds to a middle Pleistocene interglacial episode (Marine Isotopic Stage 11; Ortlieb *et al.*, 2003), recorded in northern Chile (23°S). The new records on the northern coast of the Beagle Channel constitute the southernmost fossil record for both taxa.

The poor representation of *Ensis macha* in the fossil record (in comparison with *Venus antiqua*) may be due to ecological reasons (*i.e.*, patchy distribution), but it is also plausible that it is due

to low preservation potential of this taxon; the *Ensis macha* shell is thin and fragile; while, *Venus antiqua* is a thick-shelled species, which favors its preservation as a fossil.

## 8. Paleoecology and Paleoenvironment Reconstruction

A combination of neontological, paleontological and sedimentological data was used to reconstruct the paleoecology of the macrofossil assemblage from the Bahía Golondrina site.

Macrofossils from this site were found in life position (autochthonous assemblage). The *Ensis* sample used for dating gave a radiocarbon age of 6,276±41 years BP (AA 62801) by AMS <sup>14</sup>C. Life position specimens and the absence of sedimentary structures could be explained by a rapid accumulation process, probably caused by regional storms at the age of deposition. Figure 4 represents one hypothetical benthic macrofaunal paleocommunity characterized by the presence of green algae and macroinvertebrates such as Annelida (Polychaeta), Anthozoa (ceriantharia), Mollusca (bivalves) and Crustacea (Decapoda), among others. This reconstruction is based on both our fossil findings at the Bahía Golondrina site and additional ecological information; *i.e.*, observations on benthic communities living in the Beagle Channel and data provided by Escofet *et al.* (1978), who described a similar modern macrofaunal *Venus-Ensis* assemblage at 41°S in Patagonia.

To improve understanding of the relationship between this site at +2 m a.s.l. and the environmental conditions during the Holocene transgression, an

analysis with two other sites of similar age, the Río Varela site, located 50 km east, and the Lago Roca site, 20 km west (Table 2), was carried out.

Difference in altitude among these sites would be explained by seismotectonic activity (Scotia Plate domain) and glacioeustatic processes affecting the whole Fuegian Andes region. Along the Beagle Channel, the Holocene tectonic uplifting reached its maximum level on the western sector of this channel, decreasing toward the east.

Taphonomic analysis and taxonomy of these assemblages support the distinction of different local mollusk assemblages. The fossil assemblages from the Río Varela and Lago Roca sites were transported after their death (allochthonous assemblages). This resulted in more diverse assemblages dominated by infaunal taxa (e.g., *Retrotapes*, *Tawera*, *Mulinia*) intermixed with some epifaunal elements (e.g., mytilidae, *Nacella*, *Trophon*, *Xymenopsis*). As it happens today in the Beagle Channel, the development of different local paleocommunities appears to be associated with a complex mosaic of microhabitats. The presence of hard (e.g., rocky intertidal) and soft areas (e.g., sandy beaches) are

common features on the Beagle Channel seafloor. Variations in faunal composition would mainly be related to differences in substrate types, water depth and sedimentation rates.

These three assemblages were deposited during the 7,000-6,000 yr BP. In the Beagle Channel, measurements of paleotemperatures show a fall in values between 6,500 and 5,000 BP (Obelich *et al.*, 1998). At the Río Varela site, marine waters flooded the present mouth area at ca. 6,200 BP ( $6,240 \pm 70$  yr BP; Coronato *et al.*, 1999), thus forming a shallow, low-energy, nearshore environment, strongly influenced by the river input and seasonal ice melt-water (Grill *et al.*, 2002).

It therefore seems that these assemblages were formed during a phase of climatic 'deterioration' which took place during the interval 7,000-6,000 BP, prior to ca. 5,500 BP, when paleotemperatures and paleosalinities reached their maximum values for the last 8,000 years (Lamy *et al.*, 2002).

## 9. Provenance of mid-Holocene Bivalves

Pleistocene beaches are not very common in the inner portion of the Beagle Channel due to the erosive effect of the last glaciations (Rabassa *et al.*, 2000). However, fossil records would indicate that the Beagle Channel was occupied by sea water at least once during the Pleistocene (Rabassa *et al.*, 1986; Gordillo, 1990b).

In regard to the provenance of mid-Holocene *Venus antiqua* and *Ensis macha* specimens in the Beagle Channel, two alternatives are considered: **1.** as survivors, they might have evolved from stocks that remained in the region within unglaciated marine refuges during Pleistocene glaciations; or **2.** as migrants, they might derive from specimens from northern regions with geographic access to the new habitats formed after the last deglaciation. Although the two alternatives are theoretically possible (see Crame, 1996), the mid-Holocene age of these taxa and their mode of life (i.e., infaunal suspension feeders) make it more plausible that they migrated and colonized the new vacant areas after the first stages of the deglaciation period, in which rapid rates of sedimentation made the environment unsuitable for them. Bathymetrical analysis suggests that these taxa entered the Beagle Channel through constricted waterways which have connections with the open Pacific (Antezana, 1999). Rabassa *et al.* (1986) suggested that the Holocene sea trans-

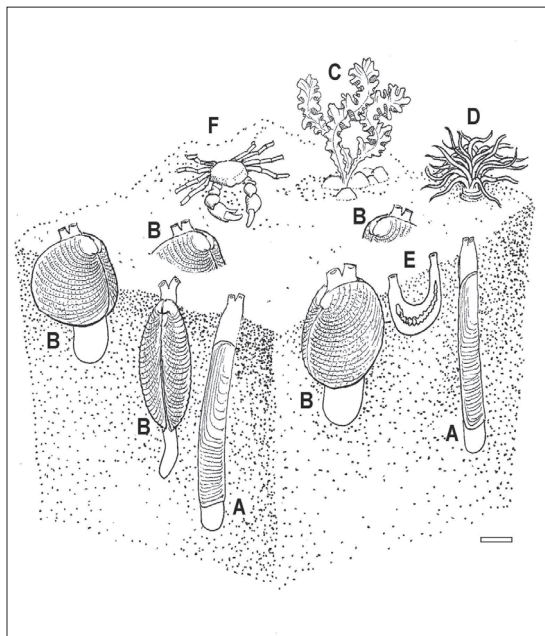


FIG. 4. Reconstruction of the *Venus-Ensis* paleocommunity based on the fossil record and soft bottom modern communities in the area. A. *Ensis macha*; B. *Venus antiqua*; C. green alga; D. tube-dwelling anemone; E. polychaete tube worm; F. crab. Scale bar=20 mm.

TABLE 2. CHRONOLOGICAL DATA AND PALEONTOLOGICAL CHARACTERIZATION OF 3 HOLOCENE MOLLUSK ASSEMBLAGES COLLECTED FROM THE BEAGLE CHANNEL.

| Characterization   | Bahía Golondrina                           | Río Varela  | Lago Roca  |
|--|--|---|--|
| Lat., long.  | 54°49'S, 68°19'W                           | 54°52'S, 67°11'W  | 54°48'S, 68°36'W   |
| Elevation (a.s.l.)   | 2,0 m                                      | 3,0 m   | 6,4 m  |
| Dating method  | AMS method                                 | Conventional method   | Conventional method  |
| Uncorrected radiocarbon age and C <sup>14</sup> laboratory sample code | 6,276±41 yr BP<br>(AA 62801; this work)    | 6,240±70 yr BP<br>(Pta. 7581;<br>Coronato <i>et al.</i> , 1999)   | 5,920±90 yr BP<br>(AC 1060;<br>Rabassa <i>et al.</i> , 1986)   |
| Calibrated age<br>(Calib 5.0*)   | 6,473±73 yr BP                             | 6,433±96 yr BP  | 6,097±112 yr BP  |
| Assemblage type  | Authochthonous assemblage                  | Allochthonous assemblage  | Allochthonous assemblage   |
| Faunal composition   | <i>Venus antiqua</i><br><i>Ensis macha</i> | <i>Venus antiqua</i><br><i>Retrotapes exalbidus</i><br><i>Trophon geversianus</i><br><i>Xymenopsis muriciformis</i> | <i>Tawera gayi</i><br><i>Retrotapes exalbidus</i><br><i>Mulinia edulis</i><br><i>Mytilus chilensis</i><br><i>Aulacomya atra</i><br><i>Perumytilus purpuratus</i><br><i>Venus antiqua</i><br><i>Hiatella solida</i><br><i>Trophon geversianus</i><br><i>Xymenopsis muriciformis</i><br><i>Pareuthria plumbea</i><br><i>Nacella deaurata</i> |

\* Radiocarbon Calibration Program; version 5.0 ([www.calib.org](http://www.calib.org)) in conjunction with: Stuiver, M.; Reimer, P.J. 1993. Radiocarbon 35: 215-230.  
Calibration dataset: marine04.14c. One sigma set. Delta R= 221±40 (additional shift in regional <sup>14</sup>C age).

gression in the Beagle Channel took place through the Murray passage (Fig. 1), a narrow entrance to the Beagle Channel between Navarino and Hoste islands, or perhaps somewhere in another more western position.  
At the moment, the two alternatives (Pleistocene survivors or Holocene migrants) are possible since available information cannot be used to discard either of these two hypotheses.

10. Discussion

Concerning paleobiogeographic patterns of distribution, the presence of *Ensis macha* and *Venus antiqua* in life position suggests that during the mid-Holocene, the Beagle Channel acted as a path for dispersion of these taxa between the Atlantic

and the Pacific oceans. As both taxa produce planktonic larvae, this served as their primary agent of dispersal. Such larvae are important because they provide a chance for wide geographic distribution and, as a result, they do not always settle or survive in areas better suited for adult growth; other means of dispersal (*i.e.*, drifting of juveniles or small adults) are therefore likely to be important. However, it is unknown yet if these two taxa can drift.  
The opportunity for the larvae of these two taxa to settle in the Beagle Channel during the Holocene could be due to the fact that this channel is a more protected area in comparison with the open sea. On the other hand, Brattström and Johanssen (1983) stated that this kind of environment offers the chance of finding suitable biotopes everywhere, because all kinds of bottom types are found on the shore and in

deeper water, and there is no reason to believe that species will not find suitable bottoms somewhere within the spreading range of the larvae.

Evidence also suggests that both *Ensis macha* and *Venus antiqua* probably migrated to the Beagle Channel from northern adjacent areas or deeper waters after deglaciation, entering the channel from the Pacific Ocean via restricted waterways. However, the possibility that these taxa survived the glacial advances within Pleistocene refuges cannot be ruled out.

The analysis of records of *Ensis macha* and *Venus antiqua* through time and their geographic links to ecological factors such as their reproductive strategies, showed that both taxa are typical elements of the cold-temperate seas throughout the Magellan Region, exhibiting a similar range of distribution and paleodistribution.

A considerable number of mollusk taxa share the same area of distribution with *Ensis macha* and *Venus antiqua* in both oceans. This results in a similar taxa composition in both the Atlantic and the Pacific coasts. A reason for this similarity might be the existence of marine pass-ways during Pleistocene interglacial periods.

Scherer *et al.* (1998) also mentioned that similar richness and taxa composition between the Ross and Weddell seas might be due to the existence of marine pass-ways during Pleistocene ice sheet collapses that enabled biotic interchange between these disjunct Antarctic seas. Based on the fossil records compiled here, it seems that during the Plio-Pleistocene a great exchange of cold-temperate mollusks took place between the Pacific and the Atlantic basins.

Whether the Magellan Strait represents a second migration route for these taxa between the two oceans is still unknown. Available data proves that during the Quaternary period, the Atlantic entrance was opened just after the first Pleistocene glaciation, whereas communication between the Atlantic and the Pacific oceans occurred after the last glaciation (Brambati *et al.*, 1998).

The faunal and climatic changes during the Holocene are just beginning to be understood. For a more complete understanding of Holocene marine paleoenvironments in the Magellan Region, we need to determine whether these local changes can be correlated over a broader regional scale. Regarding glaciations and faunal exclusion in the Beagle Channel, the origin of the Holocene fauna of

this critical geographic area is still under discussion. Only on the basis of an integrated cross-disciplinary approach, a better knowledge of the Holocene history of the Beagle Channel will be achieved.

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