

THE RELICTUAL POPULATION OF THE PURPLE CLAM *AMIAANTIS PURPURATA* (L.) IN NORTHERN PATAGONIA (ARGENTINA): THE HISTORY OF A WARM-TEMPERATE-WATER NEOGENE SURVIVOR



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Abstract. The purple clam *Amiantis purpurata* (Lamarck) is a warm-temperate species inhabiting shallow water along the coast from Espiritu Santo (Brazil) to northern Patagonia. It is one of the few survivors of the middle–late Miocene faunal turnover which was characterized by the appearance of new taxa, most of them living now along the Argentinean coast. In order to study the biogeographic history of *A. purpurata*, a detailed review of its records was carried out. The oldest record of this species is from late Miocene rocks in Uruguay, and it appears that *A. purpurata* survived because its wide thermal tolerance range allowed larvae to migrate southwards from Uruguay, settling on the southern coast of Buenos Aires Province and San Matías Gulf. The characteristics of this gulf would have favored the development and settlement of the larvae, thus giving rise to the most abundant southern population during the Pleistocene. At the end of the Pleistocene, *A. purpurata* also survived the Last Glacial Maximum. During the Holocene, the population of *A. purpurata* in San Matías Gulf became isolated, but also represented the most abundant southern population of this species. During its brief Neogene history, *Amiantis purpurata* followed main global, regional and local events; thus it can be considered as an environmental indicator for this period.

Key words. *Amiantis purpurata*. Neogene. Patagonia. Dispersion. Paleobiogeography.

Resumen. LA POBLACIÓN RELICTUAL DE LA ALMEJA PÚRPURA *AMIAANTIS PURPURATA* (L.) EN EL NORTE DE PATAGONIA (ARGENTINA): LA HISTORIA DE UN SOBREVIVIENTE DE AGUAS TEMPLADO-CÁLIDAS DEL NEÓGENO. La almeja púrpura *Amiantis purpurata* (Lamarck) es una especie de aguas templado-cálidas que habita en aguas poco profundas desde Espiritu Santo (Brasil) hasta el norte de Patagonia. Es uno de los pocos sobrevivientes del intercambio faunístico del Mioceno medio–tardío, que se caracterizó por la aparición de nuevos taxa, la mayoría de ellos vivientes en la actualidad a lo largo de la costa argentina. Con el fin de reconstruir su historia biogeográfica, se llevó a cabo una revisión detallada de los registros. El registro más antiguo de *A. purpurata* proviene del Mioceno tardío en Uruguay, y sobrevivió debido a su amplia tolerancia térmica lo que habría permitido que las larvas migren desde Uruguay hacia el sur, donde se establecieron en la costa sur de la Provincia de Buenos Aires y en el Golfo San Matías. Además, las características de este golfo han impulsado el desarrollo y asentamiento de las larvas, lo que daría lugar a la población más abundante situada más al sur durante el Pleistoceno. Al final del Pleistoceno, *A. purpurata* también sobrevivió al Último Máximo Glacial y, una vez en el Holoceno, la población de *A. purpurata* del Golfo San Matías quedó aislada, lo que representa la población más abundante y austral de esta especie. A lo largo de su breve historia geológica durante el Neógeno, *Amiantis purpurata* acompañó a los principales acontecimientos ocurridos a escala global, regional y local; por lo tanto, esta especie puede ser considerada como un indicador ambiental para este período.

Palabras clave. *Amiantis purpurata*. Neógeno. Patagonia. Dispersión. Paleobiogeografía.

THE purple clam *Amiantis purpurata* (Lamarck, 1818) is a warm-temperate species inhabiting intertidal and shallow subtidal soft bottoms from Espiritu Santo (Brazil) to northern Patagonia (Scarabino, 1977; Rios, 1994). It was also recorded as fossil in Cenozoic strata (e.g., Feruglio, 1950; del Rio and Martínez, 1998). The isolated beds with *A. purpurata* in San Matías Gulf (northern Patagonia, Argentina) exhibit high densities (Morsan, 2003) and represent the southernmost population of this species (Morsan and Kroeck, 2005).

Earth's climate experienced continuous change during the

Cenozoic (Zachos *et al.*, 2001). Rapid climatic modifications were accompanied by striking ecological shifts, extinctions and the emergence of new species (Valentine and Jablonski, 1985; Stanley, 1986; Jackson *et al.*, 1996; Jackson and Johnson, 2000). The South American fossil record is evidence for these changes, particularly in relation to mollusk species (Jablonski *et al.*, 2003; del Rio, 2004; Nielsen and Glodny, 2009; Kiel and Nielsen, 2010).

In the Miocene, the sea covered a large portion of Argentina, Uruguay and Brazil. Evidence of this sea is seen in

the abundant and diverse mollusk fauna found in marine facies of the Paraná Formation, in the Puerto Madryn Formation, in subsurface strata in Buenos Aires Province, and in the Camacho Formation (del Rio, 2000; Martínez and del Rio, 2002a). The paleobiogeographic and paleoclimatic changes that took place during the middle–late Miocene included a faunal turnover; many new taxa appeared in the South Atlantic and diversity decreased when compared to that in the Paleogene Sea (del Rio, 2000). Evidence of this fact is that of the 143 Miocene species recorded for the area, only 25 species (17.5%) survive in the Recent fauna of the southwestern Atlantic (del Rio, 2000; del Rio *et al.*, 2010). Ten percent of the Miocene genera went extinct and 44% did not survive at higher latitudes, being currently restricted to the tropical areas of the Americas, the Caribbean, the Indo-Pacific and southwest Africa (del Rio, 2000). The geographic distribution reflects the current distribution of warm/temperate water (del Rio, 2000). One of the survivors of this faunal turnover was the purple clam *A. purpurata* (del Rio, 2000) (Fig. 1).

Glaciations and warmer interglacials produced paleoenvironmental and geomorphologic changes along littoral areas during the Quaternary (Schellmann, 1998; Schellmann and Radtke, 2003; Rabassa, 2008; Ponce *et al.*, 2011). A notable event known as the Last Glacial Maximum took place during the Pleistocene (24000 cal. years BP; Rabassa, 2008) when the global average temperature was 15°C below the current average temperature and sea level was 140 m lower than modern sea level (Clapperton, 1993; Clark and Mix, 2002). The southwestern Atlantic underwent important changes such as the exposure of a large portion of the Argentine Continental Shelf and the advance of ice, among others (Ponce *et al.*, 2011). Most species were able to survive these drastic environmental changes and *A. purpurata* was one of them (together with *Glycymeris longior*, *Crepidula onyx*, *Buccinanops globulosum*, among others; Aguirre and Farinati, 1999; Charó *et al.*, in press). But other species—at least three from San Matías Gulf—*i.e.*, *Chama iudicai* Pastorino, 1991; *Tegula atra* and *Glycymeris sanmatiensis* Bayer and Gordillo, 2013, became extinct apparently during the last glaciations and were found only in the oldest Quaternary deposits surrounding this gulf (Pastorino 1991; Bayer and Gordillo, 2013; Gordillo *et al.*, 2014; Charó *et al.*, in press).

The middle (and part of the early) Holocene coincided with a warmer period known as Hypsithermal (between 6000

and 4500 years BP), in which temperatures were slightly higher (Fucks *et al.*, 2005; Schellmann and Radtke, 2010) than during the rest of the Holocene. There were also coastline changes, as evidenced by the marine mollusk assemblages. Some warm-temperate water species such as *Mactra mactroides* and *G. longior* showed southward latitudinal changes during the Holocene when compared to their current distributions in Río Negro (*M. mactroides*) and Chubut (*G. longior*) (Boretto *et al.*, 2013; Charó *et al.*, in press).

The aim of this study is to reconstruct the paleobiogeography of *Amiantis purpurata* analyzing its fossil and living distribution in relation to climatic and environmental changes that took place during the Neogene in order to understand which were the strategies adopted by this species to address these changes.

Autoecology of *A. purpurata*

Amiantis purpurata is an infaunal suspension-feeder living buried in fine sandy or silty-sandy bottoms. A warm-temperate species, it inhabits the intertidal zone down to a depth of 15 m (Morsan, 2007). It currently ranges from Espírito Santo (Brazil) to the northern area of San Matías Gulf (Argentina) (Carcelles, 1944; Castellanos, 1967; Scarabino, 1977; Morsan and Kroeck, 2005). Its southernmost recorded living population is along Villarino Beach (San Antonio Este, San Matías Gulf), where the population occurs in high densities reaching 10 kg/m² at some sites (Morsan, 2003). This purple clam is a gonochoric species spawning during the summer, with external fecundation and planktonic larvae. Specimens from the San Matías Gulf are slow-growing and reportedly live for over 40 years (Morsan, 2003; Morsan and Kroeck, 2005).

Marine mollusks and water masses in the southwest Atlantic during the Neogene

The warm-water Brazil Current reached high latitudes during the late Miocene (Boltovskoy, 1979), fostering an association of mollusks representing the last tropical fauna at these latitudes. This fauna has been recorded in the Camacho Formation in Uruguay and the Paraná and Puerto Madryn formations in Argentina. It was used to identify, in part, two distinct malacological provinces, *i.e.*, Valdesiana and Paranaiana, characterized also by thermal differences (Martínez and del Rio, 2002a). The sea temperature in these bioprovinces

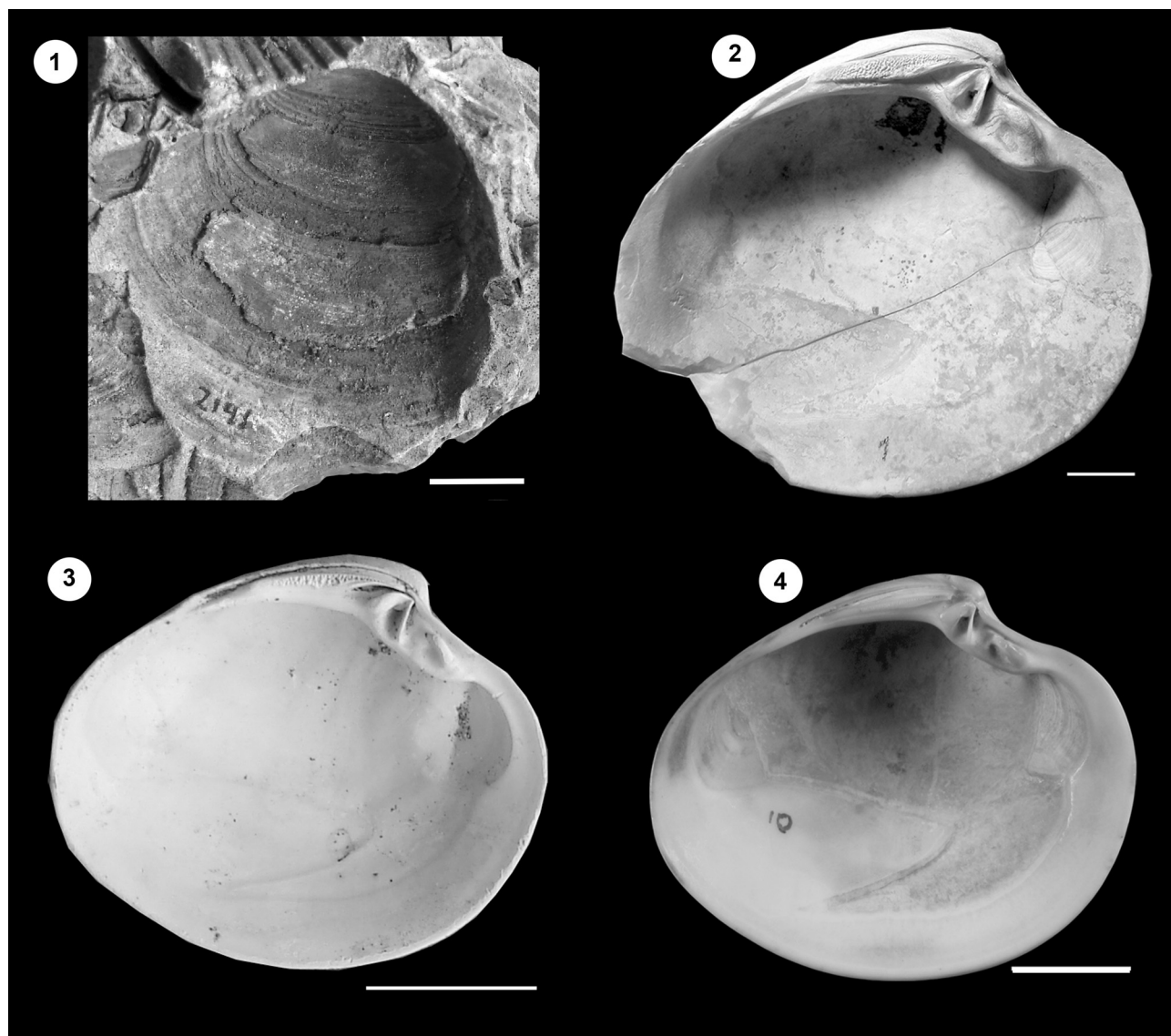


Figure 1. Specimens of *Amiantis purpurata* from different geological time and space. **1**, Miocene from San Pedro (FCDPI 2191, Uruguay); **2**, Pleistocene from Bahía San Antonio (CEGH-UNC 25198, Argentina); **3**, Holocene from La Coronilla (FCDPI 4711, Uruguay); **4**, Modern from Rio de Janeiro (GNS-WM 10, Brazil). Scale bar= 1cm.

was warmer than in the modern southwestern Atlantic at the same latitude (Martínez and del Rio, 2002a). After the late Miocene the “Caribbean” association became extinct or moved northwards (Martínez and del Rio, 2002a), following paleoceanographic changes taking place during the Miocene that set the pattern that remains almost unchanged until today (Crame, 1999; Martínez and del Rio, 2002b; Livermore *et al.*, 2005; Lagabrielle *et al.*, 2009). These paleoceanographic changes resulted in the arrival of cold water masses deriving from the intensified Antarctic Circumpolar Current (15–6 Ma) (Crame, 1999; Lagabrielle *et al.*, 2009), a part of which branched off to the Atlantic Ocean as the Malvinas Current

(Shackleton and Kennett, 1975; Kennett, 1977; Boltovskoy, 1979). The Quaternary and current configuration of the southwestern Atlantic is therefore defined by two main currents: the Brazil Current, which is characterized by warm subtropical, high-salinity water, and the Malvinas Current, which is characterized by cold subantarctic, low-salinity water (Boltovskoy, 1979). The Malvinas Current is a determinant factor in the hydrology of the Argentine Sea because as a mass of subantarctic cold water invading the Argentinean shelf, it triggered a northwards shift of bioprovince boundaries (Boltovskoy, 1979; Isla and Lasta, 2006). The northern limit of the Malvinas Current is the Brazil Current. Thus, two

bioprovinces and a transitional area are recognized today: the Brazilian Province, which is clearly linked to the Brazil Current; the Magellanic Province, linked to the Malvinas Current; and the Argentinean Provincetone, which lies at the convergence area of the Brazil and the Malvinas currents (Martínez and del Rio, 2002a). The onset of the cold Malvinas Current thus led to a faunal extinction and the disintegration of the Valdesian and Paranian bioprovinces. All the Miocene “Caribbean” elements that dominated the assemblage became extinct in the Patagonian region and/ or moved northwards by the end of the Miocene (del Rio, 1990; Martínez and del Rio, 2002b).

MATERIALS AND METHODS

Material from several museum collections and collections assembled by ourselves was analyzed in detail (Fig. 1): FCDPI 3831, FCDPI 4711, Uruguay; CEGH-UNC 25198, CEGH-UNC 25199, Argentina; GNS-WM 10, Brazil. Collections and institutions housing the specimens include: **FCDPI**, Colección Paleontológica de la Facultad de Ciencias, Montevideo, Uruguay; **CEGH-UNC**, Cátedra de Estratigrafía y Geología Histórica de la Universidad Nacional de Córdoba, Córdoba, Argentina (material collected and inventoried by the authors); **GNS-WM**, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand (World Molluscan Collection, non-New Zealand Mollusca).

RESULTS

Dispersion clues for A. purpurata in the western Atlantic of South America

Miocene. The earliest findings of *A. purpurata* were in the late Miocene of the Camacho Formation along the coast of Uruguay (Figueiras and Broggi, 1973; del Rio and Martínez, 1998; Martínez and del Rio, 2005) (Fig. 2).

Pliocene. Undoubtedly Pliocene marine deposits are not known in northern Patagonia (Gelós *et al.*, 1992; Martínez and del Rio, 2002a). However, Pliocene sediments were reported in some areas surrounding San Matías Gulf, within the so-called Río Negro Formation (Andreis, 1965). These facies contain marine mollusks, most of them oysters and pectinids (Rossi de García and Levy, 1984; Farinati *et al.*, 2010), but *A. purpurata* has not been recorded. A different species of *Amiantis* –*A. laziarina* Ihering, 1907– is the only Pliocene record of the genus and was collected in Santa Cruz, Argentina

(Ihering, 1907; Parodiz, 1996). Del Rio (1994) mentioned this species as *Pitar laziarina* from the Miocene Puerto Madryn Formation in Chubut Province, Argentina.

The Quaternary records of A. purpurata

The record of *A. purpurata* spans the entire Quaternary to Recent along the Argentinean and Brazilian coasts (da Silva Forti, 1969; Weiler, 1993; Clavijo *et al.*, 2005). Feruglio (1950) mentioned *A. purpurata*, among other species, in his pioneering work on Quaternary mollusks from Argentinean Patagonia.

Pleistocene. In the early the Quaternary, *A. purpurata* appears in the Las Escobas Formation in Bahía Blanca in Buenos Aires Province, in the Baliza San Matías Formation in Río Negro Province (Weiler, 1993), in beach-ridges at Puerto Lobos in Chubut Province (Boretto *et al.*, 2013) and in the Continental Shelf off the Argentine coast (Richards and Craig, 1963), as well as in Uruguay (Clavijo *et al.*, 2005) and in Rio Grande do Sul, Brazil (Lopes and Buchmann, 2008) (Fig. 2).

Holocene. Holocene records of *A. purpurata* are known from the state of Paraná in Brazil and along the coast of Uruguay (Ihering, 1907; Figueiras, 1961, 1962; Clavijo *et al.*, 2005; Martínez *et al.*, 2006; Angulo *et al.*, 2008; Lopes and Buchmann, 2008). Accumulations of shells of this clam were found in Buenos Aires Province, from the estuary of Bahía Blanca to the Mar Chiquita area, including the Quequén Salado (Fasano *et al.*, 1982; Schnack *et al.*, 1982; Farinati, 1984; Aliotta and Farinati, 1990; Farinati and Zavala, 1995; Gutierrez and Iribarne, 1999; Gutierrez and Valero, 2001).

Amiantis purpurata was recorded by Feruglio (1950) in Holocene sediments of Patagonia; he reported this species in terraces at San Antonio Oeste and Puerto Lobos. Boretto *et al.* (2013) also found this species at the latter locality. Pastorino (1989; 2000) reported *A. purpurata* at the two mentioned localities and also at Puerto Madryn. However, the material from Puerto Madryn locality (the southernmost record of *A. purpurata*) has been lost (G. Pastorino, pers. comm. to SB) and therefore could not be studied (Fig. 2).

Current distribution of A. purpurata

The geographic distribution of *A. purpurata* currently reaches from Espiritu Santo (Brazil) to northern San Matías Gulf (Argentina) (Scarabino, 1977; Denadai *et al.*, 2006; Pintor de Arruda and Rizzo, 2006; Penchaszadeh *et al.*, 2010) (Fig. 2).

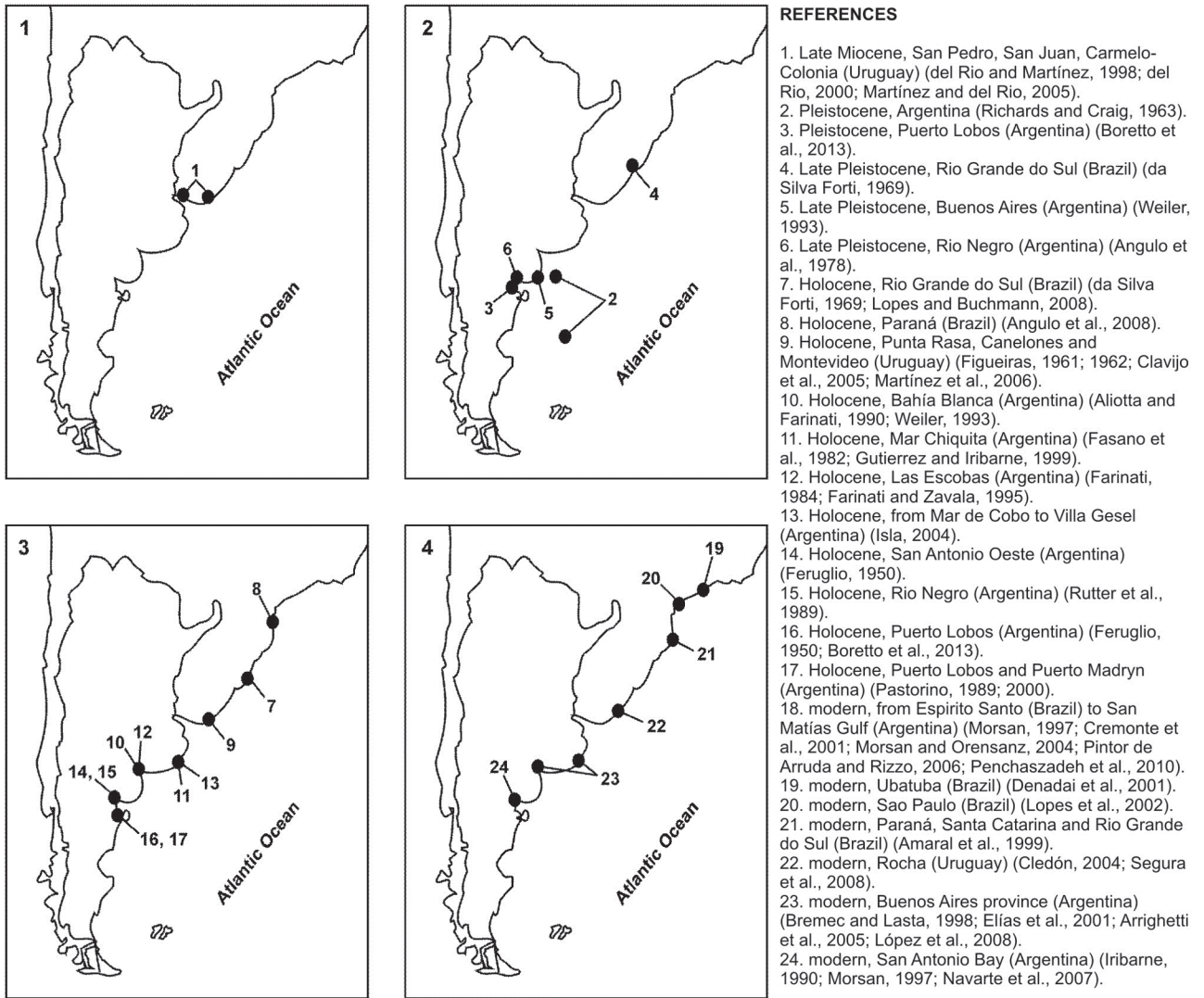


Figure 2. Records of *Amiantis purpurata* along the east coast of South America through geological time. **1**, Miocene records; **2**, Pleistocene records; **3**, Holocene records; **4**, Modern records. Maps based on PALEOMAP Project by Scotese (2003). References listed below.

These coasts are characterized by long sandy beaches (between Torres, Rio Grande do Sul, in Brazil and La Coronilla, in Uruguay), and then further south for 620 km between Cabo San Antonio and Bahía Blanca, Buenos Aires, Argentina. This last stretch is only interrupted by a few rocky points and consolidated Pleistocene sediment shoals between Mar Chiquita and Necochea (Escofet *et al.*, 1980). Along the coast of Buenos Aires Province, substrates are largely fine sandy sediments along Bahía Samborombón, with a few areas of hard substrates (Mar del Plata; from Mar del Plata to Bahía Blanca the coast consists of low cliffs and a narrow beach; from south of Bahía Blanca to the Colorado River mouth, beaches are extremely wide. The substrates of San Matías Gulf coast

consist of fine-grained sediment (Bastida *et al.*, 1992; Roux *et al.*, 1995; Parker *et al.*, 1997; Morsan, 2003; Schwartz, 2005) (Fig. 2).

As mentioned above, *Amiantis purpurata* was recorded in Brazil, in Buenos Aires Province and in San Matías Gulf. Based on Pastorino (1989; 2000), it seems that during the Holocene this species expanded its distribution southwards to the southern part of Península Valdés (Golfo Nuevo). Subsequently, there were no records in Península Valdés by the end of the Hypsithermal, thus evidencing a northwards shift of their southernmost range; the San Matías Gupopulation is therefore the most southernmost extant population.

DISCUSSION

The reasons behind the isolation of A. purpurata in San Matías Gulf

The southernmost population of *A. purpurata* is confined to the northwestern sector of San Matías Gulf, forming a densely packed bed at Villarino Beach (Morsan and Kroeck, 2005). This population seems to be a closed, self-sustaining unit, which has low or null larval connection to other populations and depends on very sporadic pulses of recruitment (Morsan and Kroeck, 2005). The isolation of the population seems to be linked to a set of hydrological, geomorphological and climatic conditions (restricted water circulation, high air temperature during the summer, high rates of evaporation, low slope of the beach and high tidal amplitude; Piola and Scasso, 1988; Morsan and Kroeck, 2005) that may retain larval patches (Morsan, 2000). This area is isolated because water circulation there behaves as a clockwise coastal eddy predominantly influenced by tidal currents, with limited interaction with the general circulation in the gulf (Lanfredi and Pousa, 1988; Tonini and Palma, 2011), thus generating a stagnant zone (Palma *et al.*, 2008; Tonini and Palma, 2011). Moreover, the mean sea surface temperature is high since it is less exposed to the effects of the cold Malvinas Current (Rivas, 2010), and heat transferred from the atmosphere is more efficiently used by shelf water to increase their sea surface temperature (Rivas and Pisoni, 2010). This combination is convenient for the success of the reproductive process and the survival of critical life stages (Morsan, 2000).

One of the few survivors: suitable settlement sites, thermal tolerance and eddies

Amiantis purpurata lives in warmer waters at the convergence of the Brazil and Malvinas currents (35°–40°S and 50°–60°W) (Francisco and Silveira, 2004). This clam was one of the surviving species from the late Miocene faunal turnover (del Rio, 2000). Prior to the opening of Drake Passage the surface water temperature of the Southern Ocean was warm in high- to mid-latitudes of the Southern Hemisphere (Zachos *et al.*, 2001). The oldest sea-bed in Drake Passage dates from 34–30 Ma (Livermore *et al.*, 2005), and its widening dates from 32.8–29.5 Ma (Pfuhl and McCave, 2005). This led to the formation of a cold water proto Antarctic Circumpolar Current (Livermore *et al.*, 2005; Lagabrielle *et al.*, 2009). At the onset of this current, a branch headed toward the Atlantic

Ocean and produced the so-called Malvinas Current, along with colder water (Shackleton and Kennett, 1975; Kennett, 1977; Boltovskoy, 1979; Isla and Lasta, 2006). After the late Miocene, a large percentage of taxa became extinct (del Rio, 2000, 2008).

A few species from the Paranian bioprovince, such as *A. purpurata*, could survive (del Rio and Martínez, 1998; del Rio, 2000; Martínez and del Rio, 2005) and were recorded in Argentinean and Uruguayan Holocene deposits and modern beaches: *Adrana electa*, *Mactra isabelleana*, *Raeta plicatella*, *Diplodonta vilardeboena*, *Tellina gibber* and *Cyrtopleura lanceolata*. Their geographic distribution from Espirito Santo to the San Matías Gulf (Aguirre, 1990; Gordillo, 1998; Absalão *et al.*, 1999; Scarabino *et al.*, 2006; Signorelli and Pastorino, 2012) is similar to that of *A. purpurata*. These appear to have survived the faunal turnover because they were probably tolerant to wider temperature ranges than the rest of the “Caribbean elements”.

As many authors have proposed, planktonic larvae are transported over long distances by water circulation and swimming abilities (Mileikovskiy, 1968; Scheltema, 1971, 1989; Roughgarden *et al.*, 1988; Possingham and Roughgarden, 1990; Gaines and Bertness, 1992; Cowen *et al.*, 2000; Largier, 2003). There are processes and factors that influence their dispersal and settlement behavior, as well as the distribution of suitable settlement sites and refuge availability (Largier, 2003). Moreover, there are retention zones along coastlines that may have an impact on the transport and recruitment success of larvae (Largier, 2004; Levin, 2005).

The convergence zone between the Brazil Current and the Malvinas Current is a dynamic region with the presence of eddies and filaments that constitute an important biogeographic boundary between assemblages of subtropical and sub-Antarctic origin (Gordon, 1989; Gayoso and Podestá, 1996; Bogazzi *et al.*, 2005; Souza, 2005).

Based on the literature reviewed in this study and the presence of a planktonic larval stage, we propose that in the area where the waters of the Brazil and the Malvinas currents mix *A. purpurata* larvae could have migrated southwards from Uruguay and/ or northern Buenos Aires Province, settling in the southern coast of the Buenos Aires Province and San Matías Gulf. The characteristics of the gulf, such as high summer temperatures, poor water circulation and the predominance of tidal currents, would have favored the de-

velopment and settlement of larvae (Lanfredi and Pousa, 1988; Piola and Scasso, 1988; Tonini *et al.*, 2007), thus giving rise to the most abundant southern population during the Pleistocene.

During the Last Glacial Maximum (24000 cal. years BP; Rabassa, 2008) the southwestern Atlantic coast would have experienced significant changes, as commented above. One of the main scenarios that explains how species could survive glaciations was retreatment to shelf slope and deep-sea habitats (Frasier *et al.*, 2012). A strategy of individualistic response of species to climate changes was probably employed by *A. purpurata* and other marine taxa which survived the last glaciations. Examples of this kind of strategy were previously pointed out by other authors (*e.g.*, Stewart, 2008; Stewart *et al.*, 2010). The survival of species to climate change depends on their adaptations and environmental tolerance (Stewart *et al.*, 2010), such as changing their geographical distribution, developing phenotypic plasticity and/ or pre-existing physical conditions required for these species (Lister, 1996). Some populations are likely to have responded differently to the same environmental change, even within the same species. These refuge populations are viable and can subsequently expand when optimal conditions return (Stewart, 2008). There are also other taxa in continental Patagonia that survived the Last Glacial Maximum (Vianna *et al.*, 2010; Zemplak *et al.*, 2010). Records of *A. purpurata* in the Continental Shelf of Argentina (Richards and Craig, 1963) match the inferred coastline for the Last Glacial Maximum (Rostami *et al.*, 2000; Ponce *et al.*, 2011), suggesting that this species survived by tracking its preferred environments during climatic changes.

The San Matías, San José and Nuevo gulfs are sensitive to environmental changes because they would have been affected by climate variations and sea level changes in the Pleistocene and Holocene (Mouzo, 2005; Bernasconi and Cusminsky, 2009; Ponce *et al.*, 2011; Isla, *in press*). In fact, these gulfs have the same origin at the end of the late Pleistocene (Ponce *et al.*, 2011). Particularly, the formation of the San Matías Gulf would have favored variations in substrate type, water circulation, productivity, among others (Ponce *et al.*, 2011; Bayer *et al.*, 2013a,b). These new environmental characteristics brought about by the final configuration of San Matías Gulf did not disturb or were not disadvantageous for *A. purpurata* and did not affect its survival.

According to Pastorino (1989; 2000), there is one record

of *A. purpurata* from the Holocene of southern Península Valdés (Nuevo Gulf), south of its modern southern limit of distribution. Although this record was not verified in this study, this expansion to the south would have been associated to the Hypsithermal interval (between 6000 and 4500 years BP) (Holocene Thermal Maximum), in which sea-surface temperatures were slightly higher than modern ones, and salinity was lower in the coastal area of Buenos Aires and Patagonia (González *et al.*, 1983; Aguirre, 1993; Aguirre and Whatley, 1995; Fucks *et al.*, 2005; Schnack *et al.*, 2005). These conditions caused an increase in precipitation that occurred in the vicinity of the Nuevo Gulf, and a rise in sea level caused by weather improvement. In turn, geomorphology and oceanological characteristics caused San José Gulf to function as an ecosystem subordinate to San Matías Gulf (Escofet *et al.*, 1980). In this scenario, *A. purpurata* larvae migrated from San Matías Gulf to Nuevo Gulf (southern Península Valdés), expanding its area of distribution *ca.* 100 km. At the end of the Hypsithermal, *A. purpurata* retracted its range due to a drop in temperature, leaving the relictual San Matías Gulf population isolated.

Another southward expansion of *A. purpurata* is recorded in the late Holocene, probably in response to environmental conditions. This species was found by Boretto *et al.* (2013) in the youngest beach ridge of Puerto Lobos in Chubut Province, the southern boundary of the Argentinean Province. The authors concluded that these records correspond to a warmer period than nowadays and would be associated with the last Holocene marine transgression, before the Maunder Minimum of the Little Ice Age.

In conclusion, larvae can be transported by their swimming ability and by water circulation such as eddies (Mileikovsky, 1968; Scheltema, 1971, 1989; Roughgarden *et al.*, 1988; Possingham and Roughgarden, 1990; Gaines and Bertness, 1992; Cowen *et al.*, 2000; Lagier, 2003). At the convergence of the Brazil and Malvinas currents, a dynamic area with the influence of eddies (Gordon, 1989; Gayoso and Podestá, 1996; Bogazzi *et al.*, 2005; Souza, 2005), *A. purpurata* larvae could be transported from Uruguay to the coasts of Buenos Aires Province and San Matías Gulf. These larvae need to settle in an appropriate environment, and the coastline from Uruguay to the San Matías Gulf seems to have been a suitable place, as evidenced by the fossil record. The latter location shows dispersal isolation because of its restricted water

circulation, high sea surface temperature, low slope of the beach and high tidal amplitude, factors that may retain larval patches (Piola and Scasso, 1988; Morsan, 2000; Morsan and Kroeck, 2005). The characteristics of San Matías Gulf favor the development of the species, resulting in the isolated, southernmost population of *A. purpurata*, which would be a relict through time. *Amiantis purpurata* could therefore be considered an environmental proxy of warm to temperate, low energy coastal environments of fine-grained substrate, based on the characteristics of the locations where this species lives.

This species exhibits enough plasticity to adapt and/ or to survive global (*e.g.*, the Last Glacial Maximum, the Hypsithermal and the Little Ice Age), regional (*e.g.*, the Miocene faunal turnover) and local (final configuration of San Matías Gulf) events that took place during the Neogene.

FINAL REMARKS

The survival of *Amiantis purpurata* to the middle–late Miocene faunal turnover is here attributed to an individualistic response caused by its wide thermal tolerance to warm-temperate waters, coupled with the persistence of soft substrates.

In this mixing area, larvae of *A. purpurata* migrated southwards from Uruguay and Buenos Aires Province, settling in the southern coast of Buenos Aires Province and San Matías Gulf. The characteristics of this gulf would have favored the development and settlement of the larvae, giving rise to the southern and most abundant population during the Pleistocene. At the end of the Pleistocene, *A. purpurata* also survived the Last Glacial Maximum. During the Holocene, *A. purpurata* apparently extended its area of distribution from San Matías Gulf to southern Península Valdés, probably associated to the Hypsithermal, but at the end of this event water temperature dropped and the San Matías Gulf population became isolated. Today, this relictual record from San Matías Gulf is the southernmost population of *A. purpurata*.

Amiantis purpurata is a useful proxy to environmental changes recorded at global (the Last Glacial Maximum, the Hypsithermal and the Little Ice Age), regional (the Miocene faunal turnover) and local (final configuration of the San Matías Gulf) scale through its biogeographic history.

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