

Form changes in *Amiantis purpurata* (Bivalvia, Veneridae) shells over the past 100,000 years in North Patagonia (Argentina)

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Amiantis purpurata shells from the San Matías Gulf (SMG) were analysed in order to compare both morphology and size throughout the late Quaternary in relation to environmental changes. Shells from modern beaches, Holocene marine assemblages (late Holocene, 3630 ± 100 years BP) and interglacial Pleistocene marine assemblages (MIS 5, 100 ka years BP) were studied by measuring the height and length, and using the elliptic Fourier analysis (EFA) to take an outline contour. The Pleistocene shells were smaller, more elliptical and with a deeper lunule than the Holocene and modern ones. No significant differences were recorded in the allometry index throughout the late Quaternary. The variation in size and shape of the *A. purpurata* shells could be related to the phenotypic plasticity of this species as a response to the environmental changes registered in the SMG during the Quaternary. These changes include variations in sea surface temperatures, salinities and substrates, and also water circulation changes, which would have modified nutrient availability. Morphological changes imply burrowing activity, mechanical stability, nutrient uptake and defence response to predation.

Keywords: *Amiantis purpurata*, bivalves, environmental changes, linear morphometrics, outline analysis, late Quaternary, Patagonia

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INTRODUCTION

Environmental factors can cause differences in the morphology of bivalves (Laudien *et al.*, 2003; Ubukata, 2003). Also, morphological characteristics reflect the phylogenetic history, functionality, behaviour and life habits of an individual (Stanley, 1975). Consequently, the size and shape of bivalve shells could be useful as environmental indicators for differentiating between phenotypic stocks and species (Stanley, 1970; Soares *et al.*, 1998; Crampton & Maxwell, 2000; Palmer *et al.*, 2004; Sousa *et al.*, 2007; Márquez *et al.*, 2010).

Some previous studies have registered morphological variations in modern and fossil specimens of the same species by analysing the size and shape of their preserved remains (Stanley & Yang, 1987; Crampton & Maxwell, 2000; Gordillo *et al.*, 2011; Boretto *et al.*, 2014).

In Northern Patagonia, Argentina, particularly in the San Matías Gulf (SMG) (Figure 1), the shells of the bivalve *Amiantis purpurata* are most abundant and well preserved as fossil (Pleistocene and Holocene) specimens in the marine coastal assemblages as well as in the modern beaches

(Bayer *et al.*, 2014). During the Patagonian Quaternary, glaciations and high-temperature interglacials produced palaeo-environmental and geomorphological changes in littoral areas (Schellmann, 1998; Schellmann & Radtke, 2003, 2010; Rabassa, 2008; Ponce *et al.*, 2011). One of the main global events registered in Patagonia was the Last Glacial Maximum at 24,000 cal. years BP (Rabassa, 2008), when temperature and sea level were distinctly lower than at present (Clapperton, 1993; Clark & Mix, 2002). The Argentine Atlantic coast would have changed considerably, with the exposure of a large portion of the Argentine Continental Shelf and the advance of ice (Ponce *et al.*, 2011). Most species, including *A. purpurata*, were able to survive these drastic environmental changes (Bayer *et al.*, 2014). However, other species, including at least three from the SMG – *Chama iudicai* (Pastorino, 1991), *Tegula atra* (Lesson, 1830) and *Glycymeris sanmatiensis* (Bayer & Gordillo, 2013) – became extinct, apparently during the glaciations, and were only found in the oldest Quaternary deposits surrounding this gulf (Pastorino, 1991; Bayer & Gordillo, 2013; Gordillo *et al.*, 2014; Charó *et al.*, 2014). A warmer period called the Hypsithermal occurred during the middle Holocene (between 6000 and 4500 years BP), in which temperatures were slightly higher (Schellmann & Radtke, 2010) than during the rest of the Holocene and the sea level transgression produced geomorphological changes along the Patagonian coastline (Kokot *et al.*, 2004; Favier-Dubois & Kokot, 2011).

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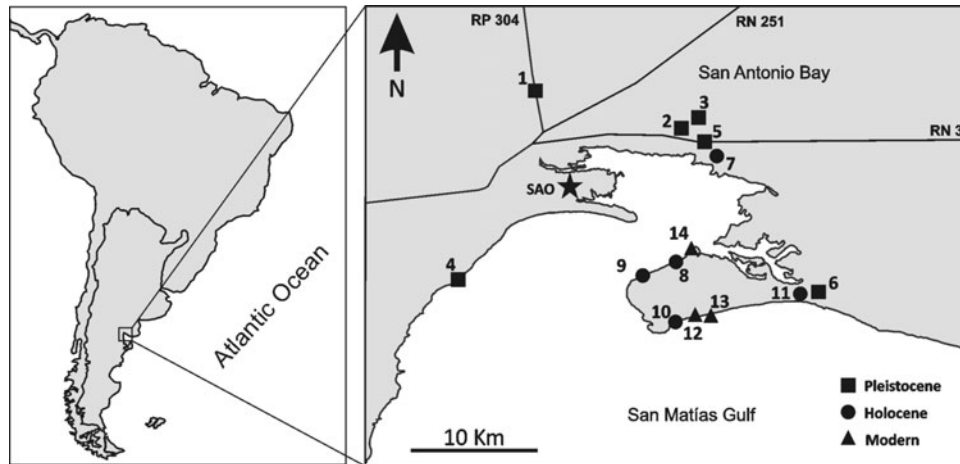


Fig. 1. Location map showing late Quaternary deposits in San Antonio Bay, San Matías Gulf (Argentina).

This global event is reflected in changing marine mollusc assemblages (Gordillo *et al.*, 2011; Charó *et al.*, 2013).

The main objective of this study is to compare the size and shape of *Amiantis purpurata* shells from different stages of the late Quaternary (the last 100,000 years) in the SMG with respect to the environmental changes that took place during this interval in Northern Patagonia, Argentina.

Autoecology of *A. purpurata*

Amiantis purpurata is a suspension feeder which lives infaunally on fine sandy or silty-sand bottoms. This venerid is a warm-temperate water species, inhabiting the intertidal zone up to 15 m deep (Morsan, 2007). Its modern distribution extends from Espiritu Santo (Brazil) to the northern SMG in Argentina (Carcelles, 1944; Castellanos, 1967; Scarabino, 1977; Morsan & Kroeck, 2005). Its southernmost known living population is at Villarino Beach (San Antonio Este, SMG), where the population occurs in high densities which reach 10 kg m^{-2} at some sites (Morsan, 2003). The fossil record of *A. purpurata* extends back to the late Pleistocene in San Antonio Bay, located in the SMG (Figure 1; Feruglio, 1950; Angulo *et al.*, 1978; Rutter *et al.*, 1989; Morsan, 1997). A recent revision by Bayer *et al.* (2014) concluded that the species formed its richest southern population in the SMG throughout the whole Quaternary. The individuals from the SMG are slow-growing and can live for over 40 years (Morsan, 2000; Morsan & Kroeck, 2005).

The San Matías Gulf

This gulf exhibits a multiplicity of geomorphological features and littoral deposits assigned to two main Quaternary transgressive episodes which occurred during the late Pleistocene and Holocene (Angulo *et al.*, 1978; Martínez *et al.*, 2001; Fucks *et al.*, 2012).

San Antonio Bay is located in the north-western area of the SMG and is a tidal delta ($40^{\circ}42'140^{\circ}50' \text{ S}$ and $64^{\circ}43'165^{\circ}07' \text{ W}$) (Figure 1) that was flooded repeatedly by marine transgressions (Rutter *et al.*, 1989; Ponce *et al.*, 2011). This bay has a particular circulation pattern characterized by a low rate of water renewal (Mazio & Vara, 1983; Lanfredi & Pousa, 1988). This feature is also characteristic of the northern

SMG, and is the main cause of the increase in water temperature. Additionally, the lack of rain, the absence of natural freshwater input and the high evaporation rate all contribute to higher salinities, which contrast the colder and less saline waters from the southern sector of the gulf (Scasso & Piola, 1988; Rivas & Beier, 1990; Gagliardini & Rivas, 2004).

MATERIALS AND METHODS

Amiantis purpurata shells and study sites

Fossil and modern specimens of *Amiantis purpurata* (Figure 2) were collected at localities along the SMG, in the northern Argentine Patagonia (Figure 1). Fossil shells from the late Pleistocene (MIS5e, i.e. before the Last Glacial Maximum; 107,000–42,500 years BP; Rutter *et al.*, 1990) and the late Holocene (3730–2880 years BP), as well as from modern beaches were taken randomly from the exposed marine deposits. In total, 419 shells were used in the linear morphometric analyses, while 88 right valves were studied by elliptic Fourier analysis (EFA).

Linear morphometric analysis

Length and height measurements of shells from the different ages were compared with ANOVA. A Tukey test was conducted in order to identify which set of shells showed shell length and height differences.

In order to evaluate whether there were shape changes during ontogeny, differences in allometric relationships at the three sets of shells were assessed by the model $H_t = a L_t^b$ (Seed, 1980), where H_t is shell height and L_t is shell length. In order to estimate parameters of the model at each site, log-transformed shell height data were regressed against log-transformed shell length and significant departures from isometry were evaluated with *t*-tests (Zar, 2010).

Outline analysis (contour shape)

From the total number of shells ($N = 419$), 88 right valves (41 Pleistocene, 22 Holocene and 25 modern) were used for the outline analysis.

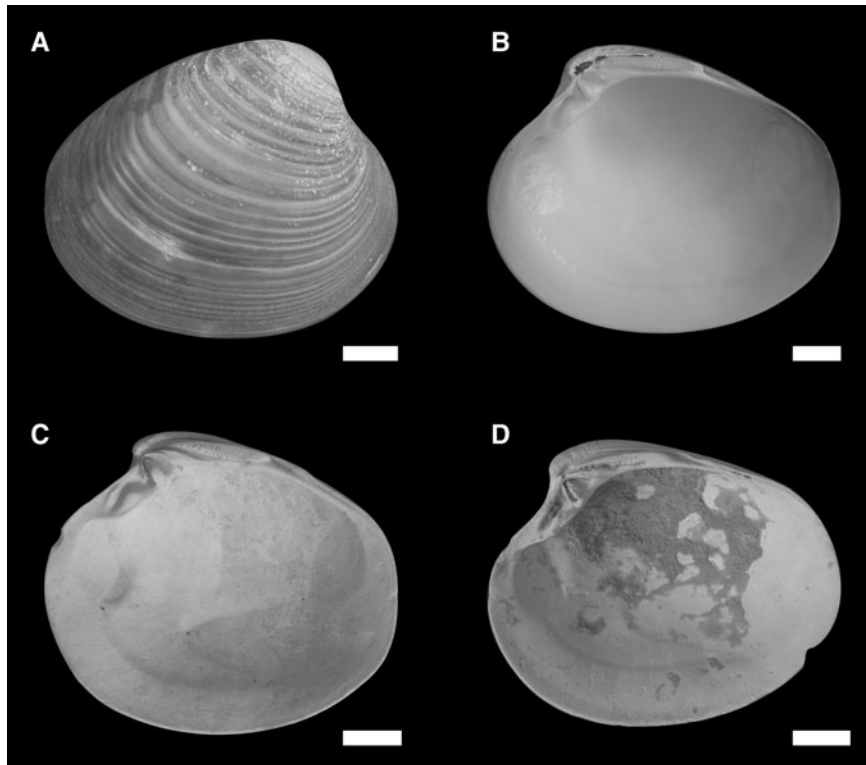


Fig. 2. Views of *Amiantis purpurata*. (A) external view of a modern shell; (B) internal view of a modern shell; (C) internal view of a Holocene shell; (D) internal view of a Pleistocene shell. Scale bars: 1 cm.

The shell shape variation was studied by EFA, which consists of decomposing a curve into a sum of harmonically related ellipses (Lestrel, 1997). For each valve, images with the inner region upward were photographed using a Sony Cyber-shot (DSC-W610) digital camera. The closed contours of each valve outline were obtained as chain-coded data from the digital images (Freeman, 1974). The number of harmonics (n) was calculated following Crampton (1995). The Fourier series was truncated at $n = 10$ with an average cumulative power of 99.98% of the total average power. The orientation, size and starting point of the different outlines were standardized (Kuhl & Giardina, 1982) so that three of the four elliptic Fourier coefficients describing the first harmonic ellipse were constant for all outlines. The software Shape v.1.3 (Iwata & Ukai, 2002) was used for all the analyses. Principal component analysis (PCA) of the variance–covariance matrix (Rohlf & Archie, 1984; Crampton, 1995) was applied to summarize shape variation based on harmonic coefficients for each valve. Differences in the coefficients between ages (Pleistocene, Holocene and Modern) were tested using multivariate analysis of variance (MANOVA) and a Hotelling Bonferroni test ($P < 0.05$) in order to identify which assemblage was different. The average $+2$ standard deviation (SD) shape for each group was reconstructed from the mean values of Fourier coefficients using the inverse Fourier transformations (provided by SHAPE-PrinPrint).

An analysis of covariance (ANCOVA) was carried out in order to evaluate whether valve shape differs when valve size varies, using the sets of shells (Pleistocene, Holocene and modern beaches) as a classification factor, principal components as variables, and size (geometric mean, i.e. square root (length \times height); Kosnik *et al.*, 2006) as a covariable. Slope

homogeneity was also performed to identify which set of shells registered a different shape variation associated to shell size. Statistical analyses were processed using the software Infostat (Di Rienzo *et al.*, 2011).

RESULTS

Linear morphometry

Shell size variation from different geological sets of shells was significant in length (ANOVA, $F = 26.11$; $P < 0.0001$) and height (ANOVA, $F = 30.66$; $P < 0.0001$), where in both cases Pleistocene shells showed variations with respect to Holocene and modern ones in Tukey comparisons (Figure 3).

The shell size geometric means were significantly different (ANOVA, $F = 28.17$; $P < 0.0001$), with the Pleistocene shells smaller than Holocene and modern shells. Allometry indices of shells from different ages did not show significant differences (ANOVA, $F = 2.09$; $P = 0.1249$).

Each linear regression model between height and length showed a good fit ($R^2_{\text{Pleistocene}} = 0.982$; $R^2_{\text{Holocene}} = 0.968$; $R^2_{\text{Modern}} = 0.983$) (Figure 4). It was shown that valve length covaried with valve height with no differences between sets of shells (ANCOVA $F = 1.368$; $P = 0.255$).

The height–length relationships of the *A. purpurata* shells match close to linear. However, they were negatively allometric ($b < 1$) for all populations (t -tests: $P < 0.001$), thus indicating that this species grows slightly faster in length than in height, and a slight change of shape takes place during ontogeny. This pattern was the same in all analysed sets of shells.

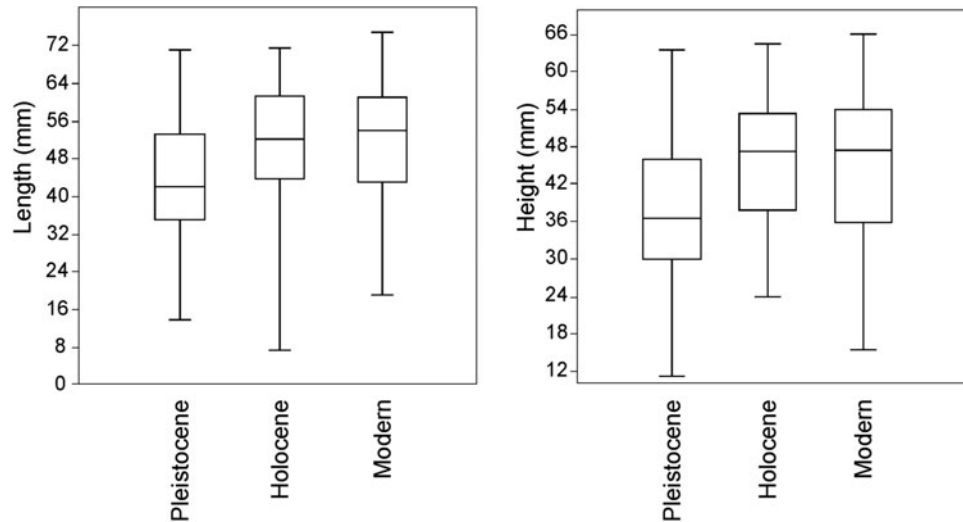


Fig. 3. Box plots for length and height of Pleistocene, Holocene and modern *A. purpurata* shells.

Outline analysis

Elliptic Fourier analysis of *A. purpurata* shells revealed contour differences between shells of different ages, although there were considerable overlaps. The first four PCs (Figure 4)

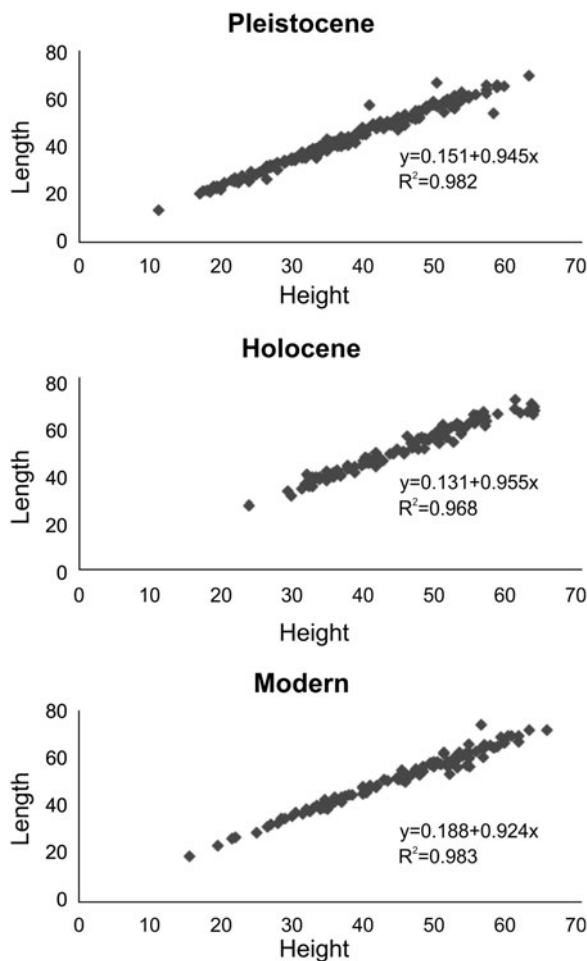


Fig. 4. Height and length (mm) relationship on shells from Pleistocene, Holocene and modern beaches.

explained around 87% of the total variation. Of the four principal components, PC1 (ANOVA, $P = 0.0118$) and PC4 (ANOVA, $P < 0.0001$) showed variation between the different sets of shells, and in both cases Pleistocene shells were significantly different in a Hotelling Bonferroni test (Figure 5). However, PC2 and PC3 did not show significant differences between the three sets of shells. When the four coefficients were tested together (MANOVA, $F_{Wilks} = 7.46$; $P < 0.0001$), Pleistocene shells showed significant differences using the Hotelling Bonferroni test. Using the extreme shapes of these figures it was possible to assign morphological meaning to the PC axes. The first PC (50.43%) could be explained by the degree of roundness. Although high variation was observed, the average shape of Holocene and modern shells were more closely related than the Pleistocene shells. The last ones exhibit a more elliptical and elongated shape than the Holocene/ modern ones, which were more rounded. The second PC (27.18%) represented the position of the umbo. Pleistocene and modern shells had a more prosogyrous umbo than the Holocene ones. The third PC (7.17%) did not follow any pattern which permitted a differentiation between assemblages. Although the fourth PC (6.05%) represented a low variation, it was related to the depth of the lunule, and showed that average Holocene and modern shells had deeper lunules than the Pleistocene shells.

In Pleistocene, Holocene and modern shells, shape variation was not independent from size changes (ANCOVA, $F = 2.52$; $P = 0.0866$). Additionally, the relationship between the shape variation and the size changes showed no significant differences in an F-test on the Pleistocene, Holocene and modern shells slopes (Homogeneity of slopes, $F = 0.9915$; $P = 0.3755$).

DISCUSSION

The relationship between the length and height of the *A. purpurata* shell is almost linear. However, b was weakly but significantly less than 1 in all assemblages, indicating weak allometry. Shape variation was observed throughout the late Quaternary, although differences in allometric indices from

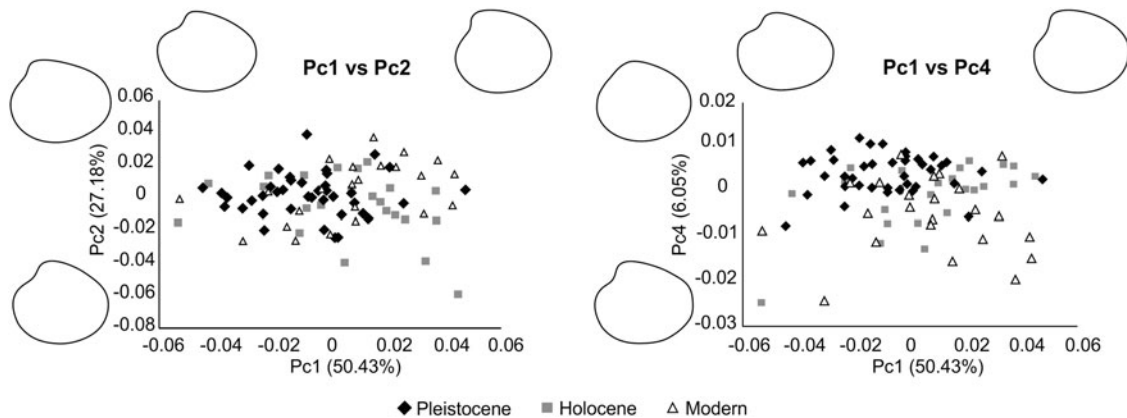


Fig. 5. Principal component plots from the elliptic Fourier analysis of *A. purpurata* from Quaternary assemblages, with indication of reconstructed extreme configurations.

different sets of shells were not detected. Shells were negatively allometric, which indicates that during ontogeny the individual growth is expressed more in terms of their length than in terms of their height (Seed & Richardson, 1999; Gaspar *et al.*, 2002a; Barón *et al.*, 2004). Hence, this elongated shape may be an adaptive strategy that allows improving the efficiency of the burrowing process within substrate (Gaspar *et al.*, 2002b; Barón *et al.*, 2004).

It was therefore necessary to investigate the relationship between the shape and size of *A. purpurata* shells, and to understand how shape varied when size was modified. In our samples, shell shape from Pleistocene, Holocene and modern beaches was dependent on shell size, and this relationship did not differ between these sets of shells, thus indicating that shape variation is associated with shell size changes. This was constant throughout the late Quaternary.

Environmental changes

Through the late Quaternary the coastal environment of the SMG forced sudden changes in the faunal communities (Ponce *et al.*, 2011; Fucks *et al.*, 2012) due to modifications in substrates, water exchange with the open sea (Ponce *et al.*, 2011; Fucks *et al.*, 2012), sea surface temperatures, palaeocirculation and productivity, as seen on a preliminary analysis of isotopes (see Bayer *et al.*, 2013).

PHYSICAL ENVIRONMENT

It has been proposed that the presence of a deep lunule gives stability to the burrowing process (Ansell, 1962; Stanley, 1975; Camacho, 2007). Indeed, more elliptical and elongated shells with deeper lunules and smaller sizes lessen the resistance to sediment and allow faster and/or easier burrowing for infaunal bivalves (Stanley, 1970, 1975; Seilacher, 1984; McLachlan *et al.*, 1995).

During the Pleistocene, the environment of the SMG area was an open sea affected by tidal regimes (Fucks *et al.*, 2012). Pleistocene shells were more exposed to wave action and the influence of tides (compare Neubauer *et al.*, 2013) than the modern shells and more stability was needed (Stanley, 1970). Consequently, physiological responses to environmental factors has probably led to slightly different contours in Pleistocene shells when compared with Holocene and modern ones. Pleistocene shells tended to be

slightly more elliptical and elongated with a deeper lunule than younger Holocene and modern shells, which had more rounded shapes with a shallower lunule. Interestingly, Charó *et al.* (2014) found that throughout the late Quaternary the proportion of taxa adapted to sandy-rocky environments has decreased in favour of taxa preferably colonizing rocky environments. A rounder shell with a shallow lunule, as observed in Holocene and modern shells, is more suitable in environments with a higher proportion of hard substrates and areas more protected from water energy where stability and/or easier burrowing would not be needed. Furthermore, this species attained its largest size in Holocene/modern assemblages compared with the Pleistocene. The larger individuals experienced higher sediment resistance during burrowing (Trueman *et al.*, 1966; Stanley, 1970), but had higher mechanical stability in environments with a high proportion of rocky patches in connection with higher water energy (Neubauer *et al.*, 2013).

NUTRIENT AVAILABILITY

The size of the studied shells could be a consequence of multiple variables such as growth rate and age structure of the death assemblages. The growth rate of *A. purpurata* was studied and modelled on several beaches from Uruguay to the SMG (Morsan, 2000). A latitudinal gradient from north to south in the estimated growth rate was observed, suggesting an influence of temperature on growth. Differences were pronounced between the SMG and the other populations. Slow growth of the SMG population was linked to a food-mediated density-dependence, which was further studied by Morsan *et al.* (2011), using 30 years of data. Growth curves were indicative of a density-dependent effect: individuals at low-density sites grew faster than individuals at high-density sites. Differences were stronger between sites than between cohorts. The *A. purpurata* size is therefore strongly affected by local environmental conditions, probably more influenced by availability or quality of nutrients than temperature (Vermeij, 1978, 1980; Wikelski & Thom, 2000; Regehr *et al.*, 2006; Zaluzniak *et al.*, 2006; Schneider *et al.*, 2010; Kefford *et al.*, 2011).

Throughout the Holocene the coastal environment of the SMG would have forced sudden changes, such as modifications in water exchange with the open sea (Ponce *et al.*, 2011; Fucks *et al.*, 2012), sea surface temperature changes,

palaeocirculation and productivity (see Bayer *et al.*, 2013). Thus, the larger size of Holocene *A. purpurata* compared with the Pleistocene might be due to increased nutrient uptake following the higher productivity during the Holocene and up to the present time as reported by Ponce *et al.* (2011) and Fucks *et al.* (2012).

PREDATION

Another factor that could possibly have triggered the modifications in shell size and shape is predation, since more efficient burrowing ensures a rapid escape from predators (Stanley, 1970; Seilacher, 1984). For example, the burrowing gastropod *Adelomelon brasiliana* (Lamarck, 1811) produces high predatory pressure on living *A. purpurata* from northern Argentine coasts (Cledón, 2004; Penchaszadeh *et al.*, 2006). This gastropod was also found in Pleistocene assemblages in the SMG (Charó *et al.*, 2014), suggesting a comparable pressure on *A. purpurata*. Consequently, the bivalves may have developed a suitable shell form that allowed it to burrow deeply and thus escape from *A. brasiliana*.

During the Holocene the proportion of carnivores increased (Charó *et al.*, 2014). *Amiantis purpurata* shells tended to have a rounded shape with a shallow lunule, so they were likely not able to burrow as fast and easily as Pleistocene representatives. Thus, the larger size of Holocene *A. purpurata* compared with the Pleistocene could be a defence response to possible predators (Hone & Benton, 2005; Schneider *et al.*, 2010).

FINAL REMARKS AND CONCLUSIONS

The environmental changes taking place during the late Quaternary, such as variations in sea level, substrate, water circulation and nutrient availability, as well as interspecific competition, likely affected the morphology and size of *A. purpurata*.

Amiantis purpurata shell size (length and height, and geometric mean) was smaller in Pleistocene shells than Holocene/modern ones, probably due to variations in productivity.

The Pleistocene shell contours of *A. purpurata* were slightly different from the Holocene and modern ones. This contour variation was expressed as a more elliptical shape and a deeper lunule, which enabled the bivalves to burrow more easily and efficiently than the Holocene and modern ones.

The high predatory pressure on *A. purpurata* probably produced a development of elliptical and elongated shells with deep lunules that allowed it to burrow fast and deeply during the Pleistocene. The large size of *A. purpurata* shells could be also a defence response to possible predators since the Holocene.

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REFERENCES

- Angulo R., Fidalgo F., Gomez Peral M. and Schnack E. (1978) Las ingresiones marinas Cuaternarias en la Bahía de San Antonio y sus vecindades, Prov. de Rio Negro. 7° Congreso Geológico Argentino Neuquén, *Proceeding* 1, 271–283.
- Ansell A.D. (1962) Observations on burrowing in the Veneridae (Eulamellibranchia). *Biological Bulletin* 123, 521–530.
- Bayer M.S. and Gordillo S. (2013) A new Pleistocene species of *Glycymeris* (Bivalvia, Glycymerididae) from northern Patagonia, Argentina. *Ameghiniana* 50, 265–268.
- Bayer M.S., Brey T., Beierlein L. and Gordillo S. (2013) Late Quaternary climatic variability in northern Patagonia Argentina – information from modern and fossil shells of *Amiantis purpurata* (Bivalvia, Veneridae). *Third International Sclerochronology Conference. Caernarfon, Wales. 18–22 May 2013*, pp. 85.
- Bayer S., Gordillo S. and Morsan E. (2014) The relictual population of the purple clam *Amiantis purpurata* (L.) in northern Patagonia: the history of a warm-temperate Neogene survivor. *Ameghiniana* 51, 333–343.
- Barón P.J., Real L.E., Ciocco N.F. and Ré M.E. (2004) Morphometry, growth and reproduction of an Atlantic population of the razor clam *Ensis macha*. *Scientia Marina* 68, 211–217.
- Boretto G., Baranzelli M., Gordillo S., Consolini I., Zanchetta G., and Moran A.G. (2014) Shell morphometric variations in a Patagonian clam (*Ameghinomya antiqua*) from southern Argentina along the Mid-Pleistocene to the present. *Quaternary International* 352, 48–58. doi: 10.1016/j.quaint.2014.09.033
- Camacho H. (2007) *Los invertebrados fósiles*, 1st edn. Buenos Aires: Fundación de Historia Natural Félix de Azara. Universidad Maimónides.
- Carcelles A. (1944) Catálogo de los moluscos marinos de Puerto Quequén. *Revista del Museo de La Plata* 3, 233–309.
- Castellanos Z.A. (1967) Catálogo de moluscos marinos bonaerenses. *Anales de la Comisión de Investigaciones Científicas de la provincia de Buenos Aires* 8, 365.
- Charó M.P., Gordillo S. and Fucks E.E. (2013) Paleocological significance of Late Quaternary molluscan faunas of the Bahía San Blas area, Argentina. *Quaternary International* 301, 135–149.
- Charó M.P., Gordillo S., Fucks E.E. and Giacconi L.M. (2014) Late Quaternary molluscs from the northern San Matías Gulf (Northern Patagonia, Argentina), southwestern Atlantic: faunistic changes and paleoenvironmental interpretation. *Quaternary International* 352, 26–47. doi: 10.1016/j.quaint.2013.12.044.
- Clapperton C. (1993) Nature and environmental changes in South America at the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101, 189–208.
- Clark P.U. and Mix A.C. (2002) Ice sheets and sea level of the Last Glacial Maximum. *Quaternary Science Reviews* 21, 1–7.
- Cledón M. (2004) *Reproductive biology and ecology of Adelomelon brasiliana (Mollusca: Gastropoda) off Buenos Aires, Argentina*. PhD thesis. University of Bremen, Bremen, Germany.
- Crampton J.S. (1995) Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia* 28, 179–186.
- Crampton J.S. and Maxwell P.A. (2000) Size: all it's shaped up to be? Evolution of shape through the lifespan of the Cenozoic bivalve *Spissatella* (Crassatellidae). In Harper E.M., Taylor J.D. and Crame J.A. (eds) *Evolutionary biology of the Bivalvia*. Geological Society of London Special Publication 177, 399–423.

- Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M. and Robledo C.W.** (2011) *InfoStat* v.2011. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. <http://www.infostat.com.ar>
- Favier-Dubois C.M. and Kokot R.** (2011) Changing scenarios in the Bajo de la Quinta San Matías Gulf, Northern Patagonia, Argentina: impact of geomorphologic processes in the human use of coastal habitats. *Quaternary International* 245, 103–110.
- Feruglio E.** (1950) Descripción geológica de la Patagonia. *Yacimientos Petrolíferos Fiscales*. Technical report No. 3, pp. 74–196.
- Freeman H.** (1974) Computer processing of line drawing image. *Surveys* 6, 57–97.
- Fucks E.E., Schnak E.J. and Charó M.** (2012) Aspectos geológicos y geomorfológicos del sector N del Golfo San Matías, Río Negro, Argentina. *Revista de la Sociedad Geológica de España* 25, 95–105.
- Gagliardini D.A. and Rivas A.L.** (2004) Environmental characteristics of San Matías Gulf obtained from LANDSAT-TM and ETM+ data. *Gayana* 68, 186–193.
- Gaspar M.B., Chícharo L.M., Vasconcelos P., García P., Santos A.R. and Monteiro C.C.** (2002a) Depth segregation phenomenon in *Donax trunculus* (Bivalvia: Donacidae) populations of the Algarve coast (southern Portugal). *Scientia Marina* 66, 111–121.
- Gaspar M.B., Santos M.N., Vasconcelos P. and Monteiro C.C.** (2002b) Shell morphometric relationships of the most common bivalve species (Mollusc: Bivalvia) of the Algarve coast (southern Portugal). *Hydrobiologia* 477, 73–80.
- Gordillo S., Márquez F., Cárdenas J. and Zubimendi M.A.** (2011) Shell variability in *Tawera gayi* (Veneridae) from southern South America: a morphometric approach based on contour analysis. *Journal of the Marine Biological Association of the United Kingdom* 91, 815–822.
- Gordillo S., Bayer M.S., Boretto G. and Charó M.** (2014) *Mollusk shells as bio-geo-archives. Evaluating environmental changes during the Quaternary*. London: Springer.
- Hone D.W.E. and Benton M.J.** (2005) The evolution of large size: how does Cope's Rule work? *Trends in Ecology and Evolution* 20, 4–6.
- Iwata H. and Ukai Y.** (2002) Shape: a computer program package for quantitative evaluation of biological shapes based on elliptical Fourier descriptors. *Journal of Heredity* 93, 321.
- Kefford B.J., Marchant R., Schäfer R.B., Metzeling L., Dunlop J.E., Choy S.C. and Goonan P.** (2011) The definition of species richness used by species sensitivity distributions approximates observed effects of salinity on stream macroinvertebrates. *Environmental Pollution* 159, 302–310.
- Kokot R.R., Codignotto J.O. and Elissondo M.** (2004) Vulnerabilidad de la Costa de la Provincia de Río Negro al Ascenso del Nivel del Mar. *Revista de la Asociación Geológica Argentina* 59, 477–487.
- Kosnik M.A., Jablonski D., Lockwood R. and Novack-Gottshall P.M.** (2006) Quantifying molluscan body size in evolutionary and ecological analyses: maximizing the return on data-collection efforts. *Palaio* 21, 588–597.
- Kuhl F.P. and Giardina C.R.** (1982) Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* 18, 236–258.
- Lanfredi N.W. and Pousa J.L.** (1988) *Mediciones de corrientes, San Antonio Oeste, Provincia de Río Negro*. San Antonio Oeste: Informe Inédito, Instituto de Biología Marina y Pesquera Almirante Storni, 13 pp.
- Laudien J., Flint N.S., van der Bank F.H. and Brey T.** (2003) Genetic and morphological variation in four populations of the surf clam *Donax serra* (Röding) from southern African sandy beaches. *Biochemical Systematics and Ecology* 31, 751–772.
- Lestrel P.E.** (1997) *Fourier descriptors and their applications in biology*. New York, NY: Cambridge University Press.
- Márquez F., Robledo J., Escati Peñaloza G. and Van der Molen S.** (2010) Use of different geometric morphometrics tools for the discrimination of phenotypic stocks of the striped clam *Ameghinomya antiqua* (Veneridae) in north Patagonia, Argentina. *Fisheries Research* 101, 127–131.
- Martínez H., Nañes C., Lizuain A., Dal Molin C. and Turel A.** (2001) Hoja geológica de San Antonio Oeste, Provincia de Río Negro. SEGEMAR. Technical report No 4166-II, 32 pp.
- Mazio C. and Vara D.** (1983) *Las mareas del Golfo San Matías*. Technical report No 13, 83 pp.
- McLachlan A., Jaramillo E., Defeo O., Dugan J., de Ruyck A. and Coetzee P.** (1995) Adaptations of bivalves to different beach types. *Journal of Experimental Marine Biology and Ecology* 187, 147–160.
- Morsan E.M.** (1997) Extracción intermareal de almeja púrpura (*Amiantis purpurata*) en la costa norte del Golfo San Matías. *Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica (Puerto Madryn, Argentina)*. Technical report No. 33, 15 pp.
- Morsan E.M.** (2000) *Dinámica poblacional y explotación de la almeja púrpura, Amiantis purpurata L.* PhD thesis. Universidad Nacional del Sur, Bahía Blanca.
- Morsan E.M.** (2003) Spatial analysis and abundance estimation of the southernmost population of purple clam, *Amiantis purpurata* in Patagonia (Argentina). *Journal of the Marine Biological Association of the United Kingdom* 83, 4241–4251.
- Morsan E.M.** (2007) Spatial pattern, harvesting and management of the artisanal fishery for purple clam (*Amiantis purpurata*) in Patagonia (Argentina). *Ocean and Coastal Management* 50, 481–497.
- Morsan E.M. and Kroeck M.A.** (2005) Reproductive cycle of purple clam, *Amiantis purpurata* (Bivalvia: Veneridae) in northern Patagonia (Argentina). *Journal of the Marine Biological Association of the United Kingdom* 85, 367–373.
- Morsan E.M., Pappalardo P. and Doldan M.S.** (2011) Growth compensation as a regulatory mechanism of purple clam *Amiantis purpurata* population dynamics in Patagonia. *Marine Ecology Progress Series* 443, 207–216.
- Neubauer T.A., Harzhauser M. and Mandic O.** (2013) Phenotypic evolution in a venerid bivalve species lineage from the late Middle Miocene Central Paratethys Sea: a multi-approach morphometric analysis. *Biological Journal of the Linnean Society* 110, 320–334.
- Palmer M., Pons G.X. and Linde M.** (2004) Discriminating between geographical groups of a Mediterranean commercial clam (*Chamelea gallina* (L.): Veneridae) by shape analysis. *Fisheries Research* 67, 93–98.
- Pastorino G.** (1991) The genus *Chama* Linné (Bivalvia) in the marine Quaternary of northern Patagonia, Argentina. *Journal of Paleontology* 65, 756–760.
- Penchaszadeh P.E., Arrighetti F., Cledón M., Livore J.P., Botto F. and Iribarne O.O.** (2006) Bivalve contribution to shallow sandy bottom food web off Mar del Plata (Argentina): inference from stomach content and stable isotope analysis. *Journal of Shellfish Research* 25, 51–54.
- Ponce J.F., Rabassa J., Coronato A. and Borromei A.M.** (2011) Paleogeographical evolution of the Atlantic coast of Pampa and Patagonia from the last glacial maximum to the Middle Holocene. *Biological Journal of the Linnean Society* 103, 363–379.
- Rabassa J.** (2008) Late Cenozoic glaciations of Patagonia and Tierra del Fuego. In Rabassa J. (ed.) *Late Cenozoic of Patagonia and Tierra del Fuego, Developments in Quaternary Science*. Amsterdam: Elsevier, pp. 151–204.

- Regehr E.V., Amstrup S.C. and Stirling I.** (2006) *Polar bear population status in the southern Beaufort Sea*. Reston, VA: U.S. Geological Survey, 20 pp.
- Rivas A.L. and Beier E.J.** (1990) Temperature and salinity fields in the North Patagonic Gulfs. *Oceanologica Acta* 13, 15–20.
- Rohlf F.J. and Archie J.W.** (1984) A comparison of Fourier methods for description of wing shape in mosquitos (Diptera: Culicidae). *Systematic Zoology* 33, 302–317.
- Rutter N., Schnack E.J., del Rio J., Fasano J.L., Isla F.I. and Radtke U.** (1989) Correlation and dating of Quaternary littoral zones along the Patagonian coast, Argentina. *Quaternary Science Reviews* 8, 213–234.
- Rutter N., Radtke U. and Schnack E.J.** (1990) Comparison of ESR and amino acid data in correlating and dating Quaternary shorelines along the Patagonian Coast, Argentina. *Journal of Coastal Research* 6, 391–411.
- Scarabino V.** (1977) Moluscos del Golfo San Matías (Provincia de Rio Negro, República Argentina). Inventario y claves para su identificación. *Comunicaciones de la Sociedad Malacológica de Uruguay* 4, 177–285.
- Scasso L.M. and Piola A.R.** (1988) Intercambio neto de agua entre el mar y la atmósfera en el Golfo San Matías. *Geoacta* 15, 13–31.
- Schellmann G.** (1998) Coastal development in Southern South America (Patagonia and Chile) since the Younger Middle Pleistocene. Sea-level changes and neotectonics. In Kelletat D. (ed.) *German Geographical Coastal Research: The Last Decade*. Tübingen: Institute for Scientific Co-operation, pp. 289–304.
- Schellmann G. and Radtke U.** (2003) Coastal terraces and Holocene sea-level changes along the Patagonian Atlantic coast. *Journal of Coastal Research* 103, 983–996.
- Schellmann G. and Radtke U.** (2010) Timing and magnitude of Holocene sea-level changes along the middle and south Patagonian Atlantic coast derived from beach ridge systems, littoral terraces and valley-mouth terraces. *Earth-Science Reviews* 103, 1–30.
- Schneider S., Fürsich F.T., Schulz-Mirbach T. and Werner W.** (2010) Ecophenotypic plasticity versus evolutionary trends – morphological variability in Upper Jurassic bivalve shells from Portugal. *Acta Palaeontologica Polonica* 55, 701–732.
- Seed R.** (1980) Shell growth and form in the Bivalvia. In Rhoads D.C. and Lutz R.A. (eds) *Skeletal growth of aquatic organisms*. New York, NY: Plenum Press, pp. 23–67.
- Seed R. and Richardson C.A.** (1999) Evolutionary traits in *Perna viridis* (Linnaeus) and *Septifer virgatus* (Wiegmann) (Bivalvia: Mytilidae). *Journal of Experimental Marine Biology and Ecology* 239, 273–287.
- Seilacher A.** (1984) Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology* 27, 207–237.
- Soares A.G., Callahan R.K. and De Ruyck A.M.C.** (1998) Microevolution and phenotypic plasticity in *Donax serra* Röding (Bivalvia: Donacidae) on high energy sandy beaches. *Journal of Molluscan Studies* 64, 407–421.
- Sousa R., Freire R., Rufino M., Méndez J., Gaspar M., Antunes C. and Guilhermino L.** (2007) Genetic and shell morphological variability of the invasive bivalve *Corbicula fluminea* (Müller, 1774) in two Portuguese estuaries. *Estuarine, Coastal and Shelf Science* 74, 166–174.
- Stanley S.M.** (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America, Inc. Memoir* 125, 296.
- Stanley S.M.** (1975) Adaptative themes in the evolution of the Bivalvia (Mollusca). *Annual Review of Earth and Planetary Sciences* 3, 361–385.
- Stanley S.M. and Yang X.** (1987) Approximate evolutionary stasis for bivalve morphology over millions of years: a multilineage study. *Paleobiology* 13, 113–139.
- Trueman E.R., Brand A.R. and Davis P.** (1966) The dynamics of burrowing of some common littoral bivalves. *Journal of Experimental Biology* 44, 469–492.
- Ubukata T.** (2003) A morphometric study on morphological plasticity of shell form in crevice-dwelling Pterioidea (Bivalvia). *Biological Journal of the Linnean Society* 79, 285–297.
- Vermeij G.J.** (1978) *Biogeography and adaptation: patterns of marine life*. Cambridge, MA: Harvard University Press.
- Vermeij G.J.** (1980) Gastropod growth rate, allometry, and adult size: environmental implications. In Rhoads D.C. and Lutz R.A. (eds) *Skeletal growth of aquatic organisms*. New York, NY: Plenum Press, pp. 379–394.
- Wikelski M. and Thom C.** (2000) Marine iguanas shrink to survive El Niño. *Nature* 403, 37–38.
- Zalizniak L., Kefford B.J. and Nugegoda D.** (2006) Is all salinity the same? I. The effect of ionic compositions on the salinity tolerance of five species of freshwater invertebrates. *Marine and Freshwater Research* 57, 75–82.
- and
- Zar J.H.** (2010) *Biostatistical analysis*, 5th edn. Englewood Cliffs, NJ: Prentice Hall.

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