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Reading shell shape: implications for palaeoenvironmental reconstructions. A case study for bivalves from the marine Quaternary of Argentina (south-western Atlantic)

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Most research on bivalves from the south-western Atlantic used morphological (shell) characters for taxonomic discriminations. Dominant Veneroids from Argentinian Quaternary coastal deposits exhibit wide morphological variation – often making objective discriminations difficult/impossible, which could be objectively described and compared through geometric morphometrics techniques. This work focuses on comparison of geometric morphometrics methods applied to fossil and modern shells, to assess inter- and intra-generic variations. Three approaches were considered: landmarks (L), semi-landmarks (SL) and outlines. Shell shape analyses for different time spans (Pleistocene, fossil Holocene and modern) and areas (Patagonia and Bonaerensian) showed that Elliptic Fourier analysis (EFA), Landmarks and Landmarks plus Semilandmarks (L + SL) can discriminate at generic levels: *Mactra, Mulinia* (Mactridae) vs. *Pitar, Protothaca, Eurhomalea, Clausinella* (Veneridae). L and L + SL are powerful for inter/intraspecific distinctions of *Mactra*. Variability of *Mactra isabelleana* includes the remaining nominal 'species' (transitional morphs). Causal environmental factors of (phenotype) variation could be addressed for modern environments (substrate, salinity and energy). Subtrigonal-inflated shells predominate in muddy, quieter, shallow mixo-polyhaline waters; ovate-elongate-compressed in sandy, poly-euhaline, deeper habitats. Differential spatial distribution (and abundance) across time responds to Late Quaternary high sea-level stands: transgressive maxima allowed higher salinity in marginal-marine areas and optimal conditions for *Mactra isabelleana* contrasting with scarcer records in the Mar Argentino today.

Keywords: Molluscs; Holocene; Pleistocene; variability; geometric morphometrics; palaeoenvironments

1. Introduction

The study of form (shape and size) of organisms (Wagner 2001; McGhee 2007) has experienced a revitalised growing interest for several scientific fields, especially since the so called revolution in morphometrics and the morphometric synthesis (e.g. Reyment et al. 1984; Bookstein 1991, 1996; Rohlf & Marcus 1993; Wagner 2001; MacLeod & Forey 2002; Adams et al. 2004; Mitteroecker & Gunz 2009). This approach is meaningful for palaeontological as well as for evolutionary studies, biology, fishery, marginal marine and coastal research lines (e.g. Pimentel 1979; Videt & Néraudeau 2002; Palmer et al. 2004; Zelditch et al. 2004; Aragón-Noriega et al. 2007; McGhee 2007; Costa et al. 2008; Reolid et al. 2008; Roopnarine et al. 2008; Lawing & Polly 2010; Minton et al. 2011; Motz 2013; Echevarría 2014; Márquez et al. 2015). Overall, the latest advances provided by quantitative descriptions of morphology have shown implications for taxonomy and systematics, functional morphology and phenotypic plasticity, ecology, biogeography (including phylogeography), phylogeny, physical anthropology, archaeology and geological aspects dealing with palaeoenvironments (e.g. Roopnarine & Beussink 1999; Weill et al. 2001; MacLeod 2002, 2005; Klingenberg 2002; Ubukata 2003, 2005; Cardini et al. 2010; Cardini & Elton 2011; Polly et al. 2013).

In a worldwide context, morphometric studies have proved to represent powerful tools for descriptions and comparisons of fossil and modern shells of various taxonomic groups, to objectively discriminate between close taxa and to characterise intraspecific variation due to phenotypic plasticity (Lozano Francisco et al. 1995; Innes & Bates 1999; Aguirre, Perez, et al. 2006; MacLeod 2010; Pérez-Enriquez et al. 2011; Neubauer et al. 2013a, 2013b; Neubauer, Harzhauser, & Mandic 2013). In particular, for bivalve shells, problems encountered in characterisations and taxonomic discriminations have been successfully addressed by means of traditional linear and/or modern geometric morphometrics methods (e.g. Reyment et al. 1984; Crampton 1995; Rufino et al. 2006; Krapivka et al. 2007; Sousa et al. 2007; Bogan & Roe 2008; Wilk & Bieler 2009; Costa et al. 2010; Márquez et al. 2010; Valladares et al. 2010; Ocaña & Fernández 2011; Leyva-Valencia et al. 2012; Collins et al. 2013; Rufino et al. 2013;

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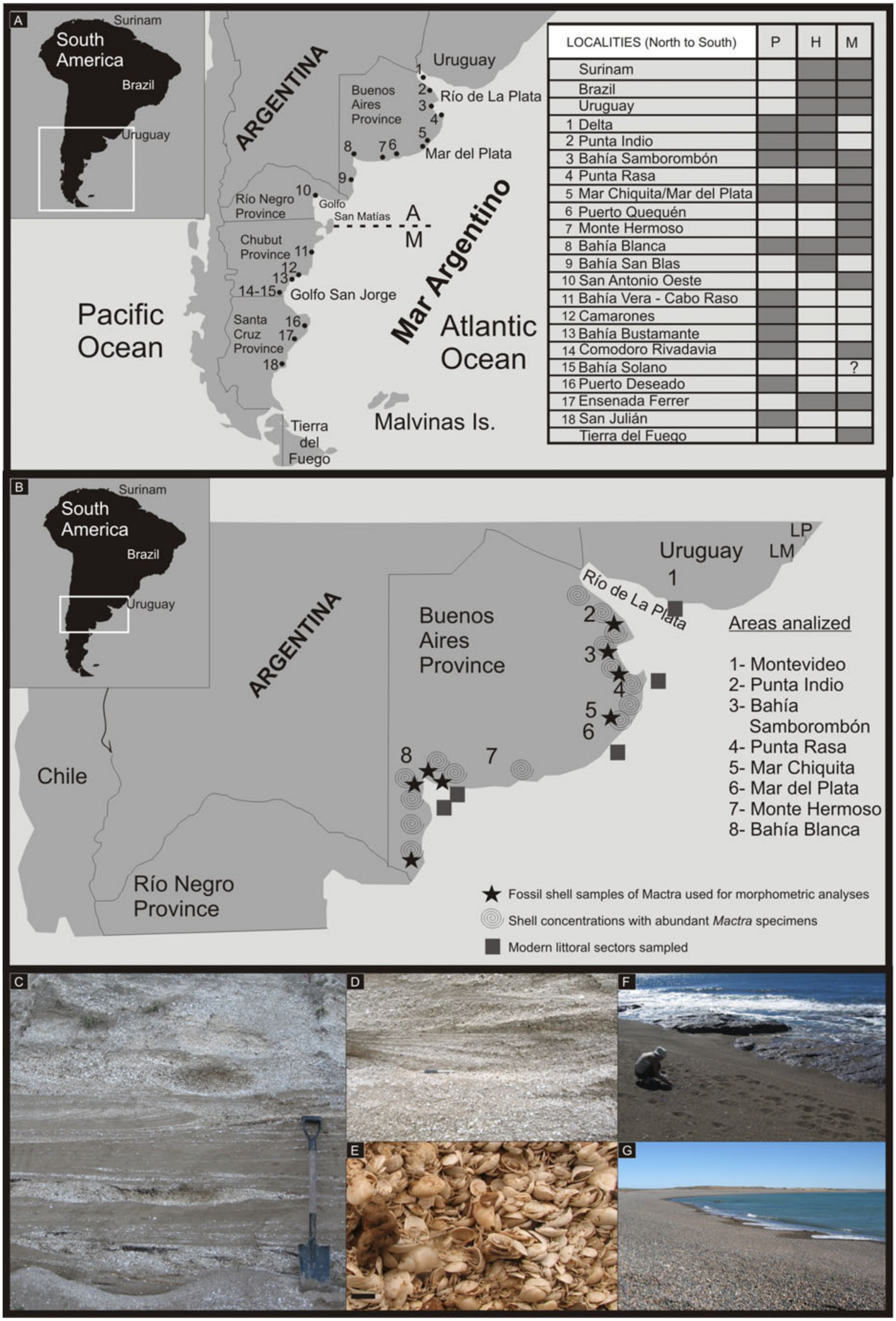


LOCALITIES (North to South)	P	H	M
Surinam		▨	▨
Brazil		▨	▨
Uruguay		▨	▨
1 Delta	▨	▨	
2 Punta Indio	▨	▨	
3 Bahía Samborombón	▨	▨	▨
4 Punta Rasa			▨
5 Mar Chiquita/Mar del Plata	▨	▨	▨
6 Puerto Quequén			▨
7 Monte Hermoso			▨
8 Bahía Blanca	▨	▨	▨
9 Bahía San Blas		▨	
10 San Antonio Oeste			▨
11 Bahía Vera - Cabo Raso	▨		
12 Camarones	▨		
13 Bahía Bustamante	▨		
14 Comodoro Rivadavia	▨		▨
15 Bahía Solano			?
16 Puerto Deseado	▨		
17 Ensenada Ferrer		▨	▨
18 San Julián	▨		
Tierra del Fuego			▨

Areas analized

1- Montevideo
2- Punta Indio
3- Bahía Samborombón
4- Punta Rasa
5- Mar Chiquita
6- Mar del Plata
7- Monte Hermoso
8- Bahía Blanca

★ Fossil shell samples of Mactra used for morphometric analyses
◎ Shell concentrations with abundant *Mactra* specimens
■ Modern littoral sectors sampled

Moneva et al. 2014; Morais et al. 2014; Rajaei et al. 2014). For Argentina, however, such studies attempting to read shell shape of fossil/subfossil Quaternary materials preserved along wide geographical areas – instead of isolated localities – represent a lag in our understanding of the effective usefulness of these techniques in order to assess objective identifications and interpretations linked to palaeoenvironmental changes through the most recent geological time slices.

As a case study, Veneroid bivalves represent the most characteristic biogenic content preserved in marine Mid to Late Pleistocene and fossil Holocene landforms along the Patagonian and Bonaerensian coastal sectors of Argentina south-western Atlantic (SWA), exposed as beach ridges, marine terraces, tidal flat or lagoonal facies between the Río de La Plata margin and southern Santa Cruz province (Figure 1(A–G)) (see also Supplementary Appendix 1). Detailed examination of large amounts of shells collected during many years at such a macrogeographical scale (e.g. Aguirre, Donato, et al. 2011; Aguirre, Richiano, et al. 2011; Richiano, Varela, et al. 2012; Richiano, Aguirre, et al. 2012; Aguirre et al. 2013 and other references therein) allowed to recognise considerable large morphological variation (shape and size) for several taxa, for example, *Mactra* Linné and *Protothaca* Dall which are the most abundant and constantly present in the Bonaerensian and Patagonian sectors, respectively. Apart from being dominant, they exhibit excellent preservation and have thus been used by geologists and palaeontologists to perform most dating available for the Mid-Late Pleistocene and Holocene in Argentina. Also, with modern counterparts living in the adjacent littoral (Argentinean and Magellanean Malacological provinces), they have often been used for palaeoecological–palaeoenvironmental approaches focused on specimens from constrained local areas.

Variation in bivalve shell morphology has implications for palaeoenvironmental interpretations. Shell growth is controlled mainly by substrate nature and climatically driven environmental variables (e.g. sea surface temperature, salinity, productivity, food availability and quantity; Ansell 1968; Kennish & Olsson 1975; Witbaard et al. 1997; Schwartzmann et al. 2011; Schöne 2013). *Protothaca*, with only one species so far identified, *Protothaca antiqua* (King and Broderip, 1832), exhibits geographical and across-time differences of shell size and shape: bigger shells are mostly recorded southwards and within older Quaternary terraces along Patagonia (Aguirre 2003). Geographical/temporal morphological differences of one same species and for certain bivalve families have been linked to variations in habitat conditions (geochemical properties of the waters, temperature of shallow water masses, productivity, nutrients, food and latitude) (Nakaoka 1992; Carmichael et al. 2004; Berke et al. 2013). By contrast, interpretations of shell variation turn more problematic in the case of *Mactra*, with five species so far described for the Mar Argentino according to local catalogues and to biological studies focused on constrained geographical areas (Castellanos 1967; Rios 1994; also Supplementary Appendix 2). *Mactra* exhibits inter- and/or intraspecific differences (exterior and interior views) resulting in overlapping shell shapes (including the degree of elongation of the cardinal teeth and ligamental area), consequently preventing an objective discrimination of abundant shells, especially when collected at random along wide and continuous geographical areas.

Dealing with large amounts of empty shells (either fossil, subfossil or modern) of highly variable taxa, involving intermediate morphs very similar in shape to several nominal species described for the same geographical area can turn several issues problematic, e.g. defining objective criteria in order to establish clear boundaries between species, validity and implications of using typologic or morphologic species concepts, the chance of applying the biologic species concept. These are difficult matters still of controversy or at least of long open debate (e.g. Cronquist 1978; Mayr 2000a, 2000b; Wheeler & Meier 2000; Wiley & Mayden 2000a, 2000b; Cracraft

Figure 1. (A–G). Coastal sectors with molluscan assemblages recorded in marine Late Quaternary deposits along Argentina and northwards in other sectors of the SWA. (A), localities with records of Veneroida (Bivalvia) in marine Late Quaternary deposits and modern littoral of Argentina. 1–9: localities along the coastal area of Buenos Aires Province, here called ‘Bonaerensian’ sector; 10–18: localities along Patagonia (Río Negro, Chubut and Santa Cruz provinces) and Tierra del Fuego. Collections of Mactridae and Veneridae were performed in localities 1 to 18. Other materials examined from museum collections are from Surinam, Brazil, Uruguay and Tierra del Fuego. P, Pleistocene; H, fossil Holocene; M, modern. Stripped line: boundary for the Argentinean (A) and Magellanean (M) Malacological provinces in the Mar Argentino. (B), areas of collection for analyses of shell samples of *Mactra* (*) in the Bonaerensian coastal area. Material for morphometric analyses was selected from localities 1 to 8, where the fossiliferous deposits conform beach ridges or tidal flat and coastal lagoonal facies. Stratigraphical sections from where samples were collected are shown in Figure 2 of Supplementary Appendix 2. Other, scarcer, records of *Mactra* occur southwards at Bahía San Blas (Bonaerensian sector) and in Late Pleistocene deposits of Camarones and Bahía Bustamante areas (Chubut province, Patagonia) and southwards in the modern littoral of Ensenada Ferrer (Santa Cruz province, Patagonia) and in Tierra del Fuego. LM, Laguna Mirim (partially Uruguay and Brazil); LP, Lagoa dos Patos (Brazil). Note that the Rio de La Plata margin includes Punta Indio, Bahia Samborombon and extends eastwards to Punta Rasa in Argentina, and Montevideo in Uruguay. Note that the horizontal (East–West) zonation of the salinity gradient along this estuary was displaced several kilometres inwards during Pleistocene and Holocene high sea level episodes affecting the coastal area (Aguirre 1993). (C–G), field observations. C, general view of Holocene ridge facies from Bahía Samborombón coastal area (locality 3); D and E, detailed views of *Mactra* shell concentrations in Bahía Samborombón shell ridges; F, Cabo Raso, Chubut province (Patagonia); G, Camarones (Chubut province, Patagonia).

2000; Lee 2003; Bock 2004; Sites & Marshall 2004; Hey 2006; Futuyma 2006; Brakefield 2008; Zachos 2013; Schindel & Miller 2013). Moreover, palaeoenvironmental interpretations and selection of taxa for geochronological and isotopic comparisons can yield inaccurate results or rather difficult to interpret devoiding of accurate taxonomic identifications (for example, interpretations of amino acid racemization dating and stable isotope analyses are highly dependant on the species analysed). Similarly, phylogeographic hypotheses require strict knowledge of the taxonomic identity of the species analysed.

Following our previous research lines and problems, the aim of this study is to test different geometric morphometrics methods to objectively describe and compare shell shape variation of the most common Veneroid taxa preserved within marine Quaternary deposits between the Río de La Plata margin and Caleta Olivia, including their modern counterparts from the Mar Argentino (Figure 1(A),(B), Table 1a): Veneridae (*Protothaca* Dall*, Eurhomalea* Cossmann, *Pitar* Römer*, Clausinella* Gray) and Mactridae (*Mactra* Linné, *Mulinia* Gray). Also, to identify the most useful technique to discriminate between different taxa at the specific/intraspecific levels for *Mactra*, considering differences within and among samples from different geographical areas and time slices (Pleistocene, fossil Holocene, modern). A plausible result for *Mactra* spp could be that no significant sharp differences are apparent (our working hypothesis) or, alternatively, an objective distinction of morphological boundaries between the nominal species so-far described is possible. If the working hypothesis is valid, a link could be assumed between shape and external environmental parameters (phenotypic plasticity). It could then be assumed that differences observed on shell features respond to environmental adaptations and thus, shape characters traditionally used for taxonomic discriminations cannot be considered objective, but vary intraspecifically, reinforcing that a wide morphological variation of one species includes that of all the remaining morphs/nominal species (Aguirre 1994).

This provides information relevant for biological, phylogeographical, geochronological and palaeoenvironmental studies based on morphotypes – commonly identified in marine Quaternary landforms as well as in modern beaches – from the SWA (Argentina, Uruguay and Brazil) (Supplementary Appendix 1).

2. Area of study, deposits sampled and modern littoral

The area of study in Argentina comprises the Bonaerensian (Buenos Aires Province) and Patagonian (Río Negro, Chubut and Santa Cruz Provinces) coastal sectors (Figure 1(A)), where bulk samples (i.e. sediment and shells) from the fossiliferous deposits and adjacent modern beaches were collected. Veneroid shells (representing the families Veneridae and Mactridae) were recovered from a total of 18 localities. Specifically for *Mactra*, abundant shells of different ‘species’ were collected at eight localities from four Bonaerensian sectors (Figure 1(B)): Punta Indio, Bahía Samborombón, Mar Chiquita and Bahía Blanca. Stratigraphical and geographical ranges and the main ecological requirements of the bivalve taxa can be gathered from previous studies (Aguirre, Richiano, et al. 2006; Aguirre, Donato, et al. 2011; Aguirre, Richiano, et al. 2011) (full details are provided in Supplementary Appendixes 2–5).

The modern oceanic littoral of Argentina is influenced by two main shallow oceanic currents: the warm (subtropical) Brazilian Current and the cool (sub-Antarctic) Malvinas (= Falkland) Current (e.g. Piola et al. 2010 and other references therein). The so-called Mar Argentino is thus characterised by subtropical warm-temperate and cold sub-Antarctic water masses defining two malacological provinces: Argentine (or Argeninean) and Magellan (or Magellanean). Four salinity fronts and three thermal fronts have been described for the whole area (e.g. Bogazzi et al. 2005) (further information is shown in Supplementary Appendix 1). Physical parameters of the Rio de la Plata have been documented elsewhere (e.g. Giberto et al. 2004, 2007; Giberto 2008).

3. Studies on bivalve morphology in the marine Quaternary of Argentina

Studies dealing with the morphological variation of bivalves from marine Quaternary deposits of Argentina are scarce. Previous research on Holocene *Mactra* spp. from the Bonaerensian sector was based on biometric analyses using traditional statistical methods (e.g. regression and covariance analysis) applied to sets of measures (e.g. length and width) and the morphological variation quantified was interpreted in terms of phenotypic plasticity (Aguirre 1994), in contrast to traditional taxonomic criteria assigning different shell morphologies to different species (i.e. Camacho 1966; Castellanos 1967; Rios 1994). Geometric morphometric techniques (e.g. landmarks (L) and semilandmarks (SL)) applied to dominant taxa preserved in fossiliferous deposits along the Bonaerensian and Patagonian areas and in the adjacent modern beaches were used to discriminate different taxonomic groups (Aguirre, Perez, et al. 2006; Aguirre, Perez, & Farinati 2010; Aguirre, Perez, Charó, et al. 2010; Perez & Aguirre 2006).

Research on modern bivalves, however, is more recent: materials of *Mactras* were studied (mainly shells from museum collections) through conventional and geometric morphometrics (Signorelli & Scarabino 2010; Signorelli et al. 2013), discriminating different living nominal species; analyses of *Protothaca antiqua* shells (assigned to *Ameghynomya* by other authors, e.g. Pérez

Table 1a. Veneroid taxa analysed.

Distribution and ecological requirements	Distribution						Argentina		Malacolo gical provinces				Bathymetry		Subs	Life mode		Trophic	
Class bivalvia	Miocene	Pleistocene	Holocene	Surinam	Brazil	Uruguay	Bonaerensian	Patagonia	Ant	Bra	Arg	Mag	Intertidal	Infralittoral	Soft	Shallow infaunal	Deep INF.	Susp.	Detrit.
Subclass HETERODONTA																			
Order VENEROIDA																			
Superfamily MACTRACEA																			
Mactra (*M.*) *isabelleana* d'Orbigny					H	H	PL-H												
Mactra aff. *isabelleana* d'Orbigny				H	H	H	PL-H	PL											
Mactra "*patagonica*" d' Orbigny							H												
Mactra "*petiti*" d'Orbigny							H												
Mactra "*marplatensis*" Doello-Jurado							H												
Mactra "*janeiroensis*" Smith							H												
Mulinia edulis (King & Broderip)								PL-H											
Superfamily VENERACEA																			
Pitar (*P.*) *rostratus* (Koch)				H	H	H	PL-H	PL											
Eurhomalea exhalbida (Dilwyn)								PL-H											
Protothaca antiqua (King)					H			PL-H											
Clausinella gayi (Hupé)								PL-H											

Note: Spatial distribution and ecological requirements (additional information and full references in Supplementary Appendixes 2, 5). ANT, Antillean province; ARG, Argentinian; BRA, Brazilian; MAG, Magellanean; SUBS, substrate type; INF, infaunal; TROPHIC, trophic type; SUSP, supensivorous; DETRIT, detritivorous.

et al. 2013) were performed with outline and landmarks techniques focused on stocks from different fishing grounds at constrained local geographical scales (Golfo San José, northern Patagonia) (Márquez et al. 2010); Mytiloids (*Brachidontes* spp) were analysed through contour geometric analyses (EFA) by Van Der Molen et al. (2013) based on three extreme sites of Patagonia (200 specimens), revisiting the scientific problems addressed by Aguirre, Perez, et al. (2006) who used L and SLs of over 2000 specimens, fossil and modern shells, from more than 26 localities of a latitudinal range along the SWA, including the type materials from the type localities and obtaining different results.

By contrast, the novelty of this study is to compare different geometric morphometrics techniques (outline vs. landmarks) applied to fossil (Pleistocene, Holocene) and modern shells of Veneridae and Mactridae. For the case of *Mactra*, we consider a wider geographical area of Argentina including other coastal areas of the SWA, in order to revisit and update the taxonomic problems pointed out earlier on the basis of Holocene records (Aguirre 1994; Aguirre, Perez, & Farinati 2010). The morphological features originally and/or traditionally used to discriminate between the Argentinian species of *Mactra* consist mainly of shell characters only. On top of that, there are close similarities between them in terms of type specimens, shape, dimensions and type localities (see Figures 3–6 and Tables 4, 5 of Supplementary Appendix 2). Moreover, they have been reported from the same geographical ranges in non-fully marine conditions, i.e. marginal marine areas between Rio de Janeiro (Brazil) and Golfo San Matías (Patagonia) (Argentine Malacological Province (Balech & Ehrlich 2008).

Table 1b. Shell samples, provenance and age of the genera analysed.

Veneroid Taxa	Localities	Age
Clausinella	Punta Pescadero, Chubut, Patagonia	Modern
Eurhomalea	Puerto Lobos, Chubut, Patagonia	Pleistocene
Mactra	Mar Chiquita, Bonaerensian area	Holocene
Mactra	Montevideo, Uruguay	Modern
Mactra	Puente de Pascua, Bonaerensian area	Pleistocene
Mulinia	North of Caleta Olivia, Sante Cruz, Patagonia	Pleistocene
Pitar	Punta Rasa, Bonaerensian area	Modern
Protothaca	Bahía Bustamante, Chubut, Patagonia	Holocene

4. Material studied and methods applied

Veneroid bivalve shells were collected from 18 localities (Figure 1(A)) along Argentina coasts, and additional materials were examined from museum collections. Geometric morphometrics analyses were focused on *Mactra, Mulinia, Pitar, Protothaca, Eurhomalea* and *Clausinella* (Table 1a–c). A comparison of methods (L, SL and outlines) was performed by means of inter- and intra-genera analyses. We followed two methodological approaches: (1) comparison of results obtained by techniques based on L + SL vs. outline analyses (elliptic Fourier analysis (EFA) of shape), applied to fossil and modern shells of all six Veneroid genera; (2) identification of the most powerful method for discrimination of *Mactra* spp. using fossil and modern shell samples. The second approach put emphasis on *Mactra* for several reasons: (a) it is constant and dominant in the Late Pleistocene and mid-Holocene Bonaerensian deposits;

Table 1c. Shell samples, provenance and age of *Mactra* spp analysed.

			IS		aff IS		MARP		PAT LIT		PE		cf MARP		cf JAN		cf PAT LIT	
Bonaerensian area (AGE)	Total N	Total M	M	N	M	N	M	N	M	N	M	N	M	N	M	N	M	N
Bahía Samborombon (MODERN)	11	125	5	97	3	17	2	10			1	1						
Bahía Blanca (MODERN)	5	25	2	4			1	11	1	9					1	1		
Punta Indio (MODERN)	8	44	4	27			2	13	1	1	1	3						
Bahía Samborombon (HOLOCENE)	37	681	30	625	2	38	3	12	1	1	3	7						
Mar Chiquita (HOLOCENE)	11	122	2	11	1	5	6	89			1	6	1	11				
Bahía Blanca (HOLOCENE)	3	9					2	8									1	1
B.Samborombon (PLEISTOCENE)	5	118	5	118														
TOTAL	80	1124	48	882	6	60	16	143	3	11	6	17	1	11	1	1	1	1

Note: IS, aff. IS, MARP, PAT LIT, PE, cf. MARP, cf. JAN, cf. PAT LIT: different morphs according to the nominal species known for the area of study.

(b) it shows excellent preservation, therefore, various shell characters and their properties (i.e. dentition, hinge area, adductor and pallial sinus scars) can be accurately marked in different specimens; (c) it is recorded by high number of specimens of all dimensions ('fossil populations') and can thus be interpreted as an autochthonous element of the original benthic communities; (d) it shows a wide range of morphological variation (intra- and interspecific); (e) modern records of known environmental constraints are available for comparison; (f) its occurrence is associated with marginal marine, unstable environments, consequently allowing to check our hypothesis that shape variation could respond to phenotypic plasticity (Aguirre 1994; Aguirre, Perez, & Farinati 2010) or if, alternatively, an objective distinction of several species is possible (complete information on the systematic review is available in Supplementary Appendixes 2 and 3).

4.1 Materials

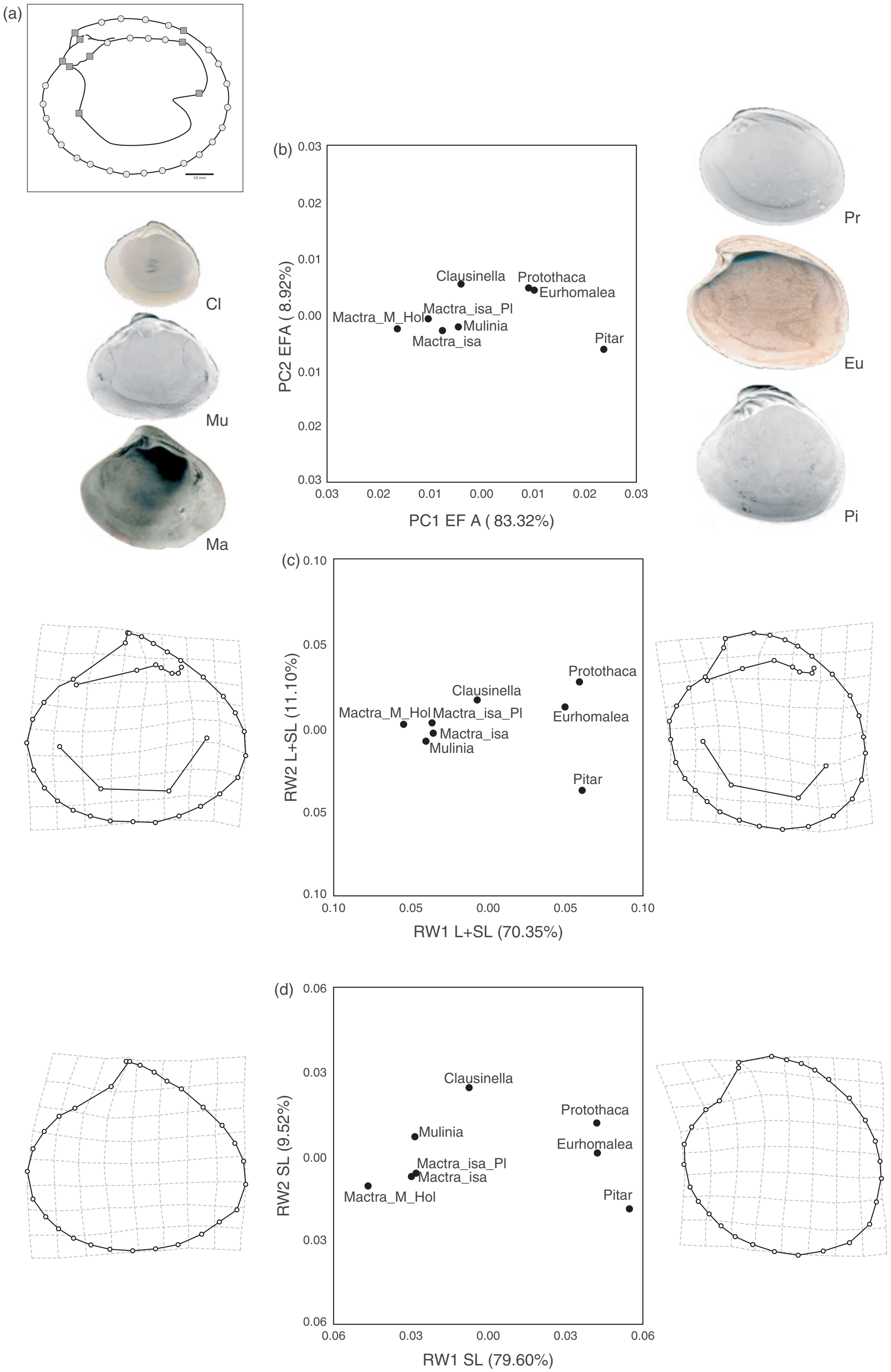
Samples of *Mulinia, Pitar, Protothaca, Eurhomalea, Clausinella* and *Mactra* were taken at random from fossil and modern field samples and examined from museum collections (institutional numbers, provenance and age in Appendix 4). Subsamples of *Mactra* consist of shells of six morphs (nominal species according to the literature): *Mactra isabelleana, Mactra petiti*, *Mactra marplatensis, Mactra patagonica, Mactra janeiroensis, M.* cf. *patagonica*). The specimens examined, illustrated and analysed in this study are housed at the Museo de La Plata (MLP), Museo de Ciencias Naturales 'Bernardino Rivadavia' (Buenos Aires, MACN), Instituto Nacional de Investigación y Desarrollo Pesquero (Mar del Plata, INIDEP) and BMNH (Mollusca Section, Natural History Museum, London) (see Supplementary Appendix 4).

4.2 Methods

For the first approach, i.e. inter-generic analyses, a total of 76 Cartesian coordinates of 9 L (umbonal area, cardinal teeth and internal muscle scars) plus 29 SL (geometrical points around the inner margin and hinge area) (Figure 2 (A)) were recorded on 2D digital images of the interior view of the right valve for 50 shells (10 shells per genera) scanned with a Hewlett Packard scanjet 4670. The software tpsDig (Rohlf 2009) was employed for the digitalisation. Cartesian coordinates of the L and SL were aligned through a generalised Procrustes analysis (Bookstein 1991). SL were slid along vectors tangent to represented curves (i.e. inner outlines of shells) using the Minimum Procrustes criterion (Bookstein 1997). We carried out two separate analyses, the first including both L + SL, and a second that included only the SL. Finally, the same Cartesian coordinates which describe the shell contour were used for EFA (Rohlf 1990). The three analyses were performed on the consensus configuration of each genus. The shape variables (i.e. aligned Procrustes coordinates and Fourier coefficients) obtained by the three procedures were then analysed using principal component (PC) analyses [i.e. relative warp (RW) for L + SL analyses] in order to define the axes of greater variation in shape between the samples considered. PCs describe the major trends in shape variation among specimens and samples (Rohlf & Marcus 1993; Rohlf 1993, 1996). Differences in shape among genera were described by means of deformation grids (Bookstein 1991). Morphometric analyses based on L and SL were carried out with *tpsRelw* 1.46 (Rohlf 2009).

For the second approach (Figure 3(A), (B)), i.e. the analysis of shape variation among and within *Mactras* was based on a data-set including coordinates of 20 L (anatomical points marked on the umbonal area, hinge features, internal muscle scars, pallial line and sinus) and 21 SL (regularly spaced along the inner shell surface) that were registered on 2D digital images of 1200 shell specimens. The same procedures described above were performed on these coordinates in order to summarise and visualise shape variation. To analyse the association between shape variation and geographical/environmental parameters, we performed an ordinary least squares regression analysis. Shape was represented by the first three RWs of the analysis of the shape variation of the mean configurations corresponding to selected samples/localities (Table 2). The selected explanatory variables were salinity, temperature, type of substratum, energy and depth of the localities (modern environmental data and inferred for fossiliferous sites) (Table 3). A PC analysis was applied to reduce the number of variables and avoid multicollinearity; the first three PCs were included in the analysis. We also included the location represented by the first PC of a PC analysis which included both latitude and longitude of the 38 localities. Further information about morphological differences, ecological requirements and habitat could be found in Appendixes 2–4.

It is acknowledged that the number of L and SL is different for the two approaches performed and in comparison with those used for other bivalve studies (e.g. Rufino et al. 2013; Moneva et al. 2014; Morais et al. 2014) as we analysed taxa which belong to different taxonomic categories and thus with different shell characters. For the first approach, between genera/inter-generic analyses (comparison between *Mactra, Mulinia, Protothaca, Clausinella*, *Eurhomalea*, and *Pitar*), the landmarks selected (9) are anatomical points common for all of them, the 29 SL are geometric points around the contour of each shell, other internal structures/points were not common to all of them. For the second approach, the intra-generic analysis of *Mactra*, the use of a higher number of


(a)
10 mm
Cl
Mu
Ma
(b)
PC2 EFA (8.92%)
PC1 EF A (83.32%)
0.03
0.02
0.01
0.00
0.01
0.02
0.03
Clausinella
Protothaca
Eurhomalea
Mactra_isa_Pl
Mactra_M_Hol
Mulinia
Mactra_isa
Pitar
Pr
Eu
Pi
(c)
RW2 L+SL (11.10%)
RW1 L+SL (70.35%)
0.10
0.05
0.00
0.05
0.10
Protothaca
Clausinella
Mactra_M_Hol
Mactra_isa_Pl
Eurhomalea
Mactra_isa
Mulinia
Pitar
(d)
RW2 SL (9.52%)
RW1 SL (79.60%)
0.06
0.03
0.00
0.03
0.06
Clausinella
Protothaca
Mulinia
Eurhomalea
Mactra_isa_Pl
Mactra_isa
Mactra_M_Hol
Pitar

landmarks (20) was possible as they are all available in the different 'species' compared; 21 SL are geometric points around the inner margin, adductor muscle scars and pallial line.

The material studied was washed by means of an ultrasonic cleaner (Lilis 3.8). The shell specimens used for geometric morphometric analyses were scanned and additional material from museum collections (Figures 4 and 5 of Supplementary Appendix 2; Supplementary Appendix 4) was photographed using a digital camera (Nikon D3100) and a digital camera (Nikon Colpix S10 VR) attached to a binocular loop (Nikon SMZ1000).

5. Results

5.1 Comparison of different techniques for inter-generic and interspecific differentiation

The three geometric morphometric techniques, L + SL, SL and EFA, gave congruent results when applied to fossil and modern shells of different Veneroid genera. As expected, *Mactra* and *Mulinia* were clearly discriminated from *Pitar, Protothaca, Eurhomalea* and *Clausinella* (Figure 2(B)–(D)). Specifically, the inter-generic shell variation showed shells of subtrigonal contour with better defined cardinal teeth (*Protothaca, Eurhomalea, Pitar*, Veneridae) discriminated from more subovate to more elongate shells with less defined teeth (*Mulinia* and the *Mactra* group, Mactridae), intermediate shells were represented by *Clausinella* (see PC1 of EFA, RW1 L + SL and RW1 SL in Figure 2; L + S and SL showed this discrimination more clearly).

By contrast, when applied to an interspecific/intraspecific level for shells of *Mactra* spp. from different localities, EFA did not allow any objective discrimination. As explained beneath, only L + SL allowed to visualise shell shapes and a rough discrimination of morphs according to a geographical (latitudinal) pattern (Figures 3(B), and 4): samples from the southern Bonaerensian sector (areas 6, 7, 32, 33, Bahía Blanca, Table 2) yielded apart from the northern samples (i.e. specimens from Rio de la Plata sites: Montevideo, Punta Indio, Bahía Samborombón area, Punta Rasa).

5.2 Mactra spp

The results obtained using L + SL applied to *Mactra* (Figure 3(B)) show that all the morphs are largely superimposed, reinforcing that the wide morphological variation of *Mactra isabelleana* includes all the remaining morphs. The RW analysis includes the cases (specimens) grouped as traditional 'morphotypes' according to their similarity with the type material of the species described, i.e. *Mactra isabelleana* (ISA), *petiti* (PE), *marplatensis* (MARP), *janeiroensis* (JA) and *patagonica* (PA), apart from the remaining 'intermediate' morphs. Figure 3(B), displaying the two first RWs, explains a low percentage (ca. 30%) of the total variation. The morphs ISA (similar to the lectotype of *Mactra isabelleana*) and MARP (similar to the holotype of *Mactra marplatensis*) represent extreme morphologies within the whole range of variation. The degree of antero-posterior elongation is the most related variable with RW1 scores: more elongate (longer than high) shells – referable to *marplatensis* – are on the left side, whereas more trigonal (height nearly equal to length) shells – identical to the type of *isabelleana* – are on the opposite extreme. In addition, shells with anterior-posterior expansion (negative values on RW1) have less conspicuous dentition and ligamental features, bigger posterior adductor scars and deeper pallial sinus. Shells with dorsal-ventral expansion leading to a more subtrigonal and inflated shape (positive scores on RW1) also show more conspicuous hinge features, shorter posterior adductor and pallial sinus. On the other hand, positive values for RW2 grid show a marked inflation in the umbonal area and more developed hinge features, while the grid corresponding to the negative values of RW2 presents a negative inflation in this area. Overall, the degree of umbonal inflation is a variable mostly related to RW2 scores: more convex trigonal shells (*isabelleana, petiti*) (positive scores on this axis) contrast with less inflated shells (opposite scores) (*marplatensis, janeiroensis* and *patagonica*). The variation observed could be synthesised in a sequence of transitional morphs, decreasing umbonal inflation and increasing elongation, with consequent changes in size and elongation of the pallial sinus and hinge features (cardinal and lateral teeth): *petiti, isabelleana, marplatensis, janeiroensis, patagonica* and cf. *patagonica*.

Second, the comparison of the mean shapes for 38 selected shells, grouped by geographical area and temporal period (Pleistocene, fossil Holocene, modern) (Figure 4, Table 2) shows that no discrimination is apparent according to age, while a general latitudinal ordination of samples was possible: northern (N) and southern (S). Shells from the southern Bonaerensian sector (Bahía Blanca area; fossil Holocene and modern; elongate morphotype) keep apart from those collected in the remaining coastal sectors

◄

Figure 2. Comparison of shape variation through different morphometric techniques between Veneroid bivalves predominant in the marine Quaternary of Argentina (Bonaerensian and Patagonian coastal areas): *Mactra*, *Mulinia*, *Pitar, Protothaca, Eurhomalea*, *Clausinella*. Pl, Pleistocene; Hol, fossil Holocene; M, modern shells; isa: *Mactra isabellana*. (A), two-dimensional landmarks (L, squares) and semilandmarks (LS, circles) used in these analyses. (B), Scatterplot of the first two PC axes of an outline analysis (EFA). (C), Scatterplot of the first two RWs of the L + SL analysis. Deformation grids show main shape changes along first axis. (2D), Scatterplot of the first two RWs axes of the SL analysis. Deformation grids show main shape changes along first axis.

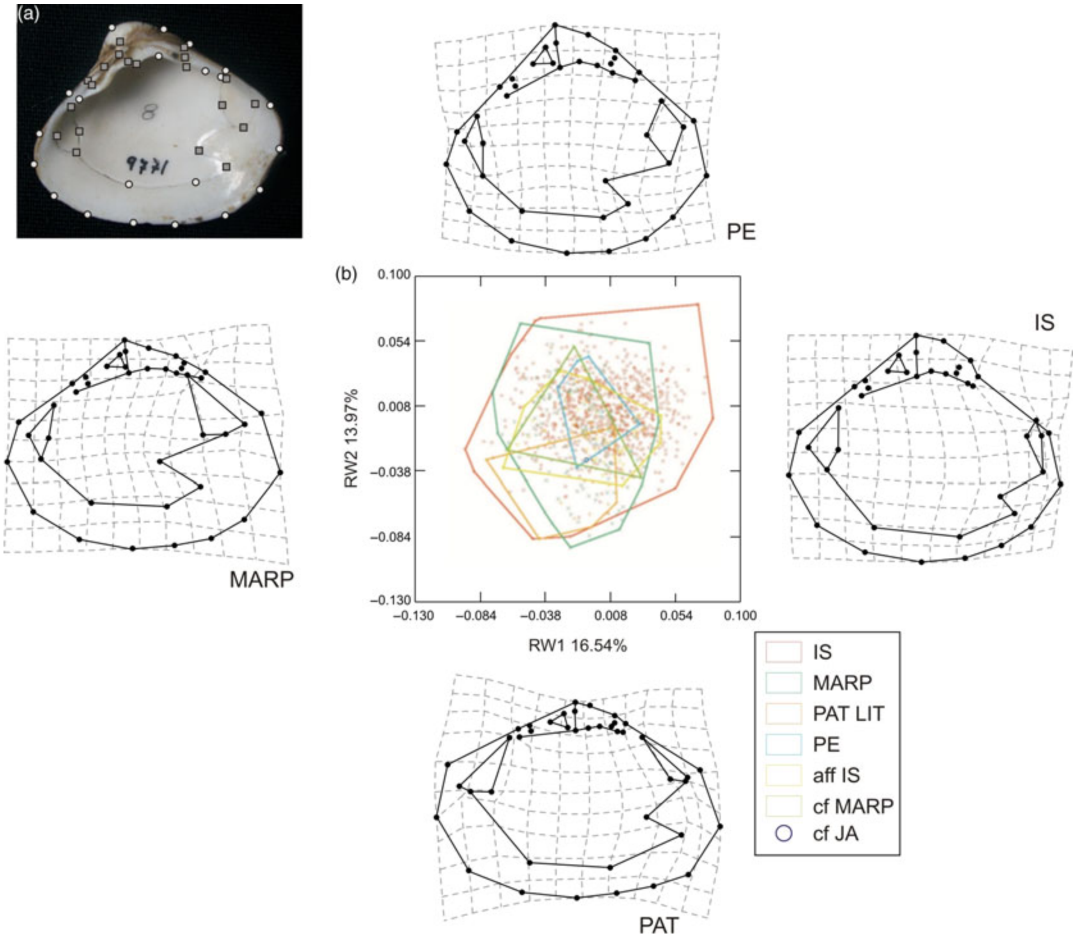


Figure 3. Analyses on *Mactra*. RWs analysis to study shell shape relationships between morphs (nominal species) of *Mactra* from the Bonaerensian littoral. (A), diagram showing the 20 landmarks (L squares) and 21 semilandmarks (SL circles) recorded on digital images along the internal view of the right valve. (B), scatterplot of the first two RWs. Deformation grids show main shape changes along both axes. MARP: shells similar to the holotype of *marplatensis*; IS: similar to the holotype of *isabelleana*; PE: shells similar to the holotype of *petiti*; PAT: shells similar to *patagonica* of the literature; JA: *janeroensis*; LIT: *patagonica* according to the literature (traditional local catalogues), not to the type specimen (the holotype as illustrated by Aguirre 1994).

(Pleistocene, Holocene, modern; Rio de La Plata margins; subtrigonal morphotype), pointing to an environmental control. The regression analysis carried out between shape variation and environmental and geographical variables yielded a significant result ($r^2 = 0.73$, F 4,33 = 25.56, P-value < 0.000). Partial coefficients obtained indicated that the environmental PC3 has a significant effect on shape variation. This PC3 was mainly correlated with the type of substrate.

6. Discussion

Our results show the potential of combining different morphometric techniques to interpret shell variation of typical bivalve taxa abundantly preserved in coastal Quaternary settings and with modern counterparts in the adjacent littoral area. They allow assessing the number of taxa that can be objectively discriminated, with implications for estimations of palaeobiodiversity and for interpretations of palaeonvironmental changes to present.

6.1 Usufullness of the morphometric techniques applied

According to the results reported, we show that the three geometric morphometric procedures applied are useful to discriminate between supraspecific taxonomic levels. However, only L + SL proved to be powerful to visualise shell shape differences between closely related 'species', in contrast with EFA (but see results by Van Der Molen et al. 2013 for other bivalve taxa from South America, Rajaei et al. 2014 for Pteriomorphia bivalves from the northern hemisphere). In the case of *Mactra*, analyses of L and L + SL on the interior view of the right valve (Figure 3(B)) are more powerful procedures than EFA techniques (Figure 2(B)), since these do not allow to

Table 2. Geographic-temporal samples of *Mactra* spp from the Bonaerensian coastal area.

Locality number	Area	Sample – Age M: modern; H: fossil Holocene; P: Pleistocene
1	Punta Rasa	A186 - M
2	Punta Rasa	A186 otra - M
3	Punta Rasa	A186 otra bis - M
4	Punta Rasa	A186 otra bisa - M
5	Punta Rasa	A186 otra bisb - M
6	Bahía Blanca	San Antonio - M
7	Bahía Blanca	Monte Hermoso - M
8	Punta Indio	Locality 2 - H
9	Bahía Samborombón	Locality 5 - H
10	Bahía Samborombón	Locality 6 - H
11	Bahía Samborombón	Locality bet. 5 & 6 - H
12	Bahía Samborombón	Locality bet. 5 & 6 South - H
13	Bahía Samborombón	Locality 7 Ea.R.López - H
14	Bahía Samborombón	Locality 7 WA4 - H
15	Bahía Samborombón	Locality 7 WA5 - H
16	Bahía Samborombón	Locality 7 A25 A26 - H
17	Bahía Samborombón	Locality DRS - H
18	Bahía Samborombón	Locality 10 - H
19	Bahía Samborombón	Locality 10 -BSM2- H
20	Bahía Samborombón	Locality 10 -BSM3- H
21	Bahía Samborombón	Locality 10 -BSM4- H
22	Bahía Samborombón	Locality 10 -BSM5- H
23	Bahía Samborombón	Locality 10 -BSM6- H
24	Bahía Samborombón	Locality 10 -BSM7- H
25	Bahía Samborombón	Locality 10 -BSM8- H
26	Bahía Samborombón	Locality 10 -BSM9- H
27	Bahía Samborombón	Locality 12- H
28	Bahía Samborombón	Locality 13- H
29	Mar Chiquita	Locality 22- H
30	Mar Chiquita	Locality 23- H
31	Mar Chiquita	Locality 24- H
32	Bahía Blanca	Cantera Biac- H
33	Bahía Blanca	Ebytem- H
34	Bahía Samborombón	Pascua- P
35	Bahía Samborombón	Pascua- P
36	Bahía Samborombón	Pascua- P
37	Bahía Samborombón	Pascua- P
38	Bahía Samborombón	Pascua- P

Note: Locality numbers and provenance of shells used for RWs analysis of geographic-temporal samples of *Mactra* spp from the Bonaerensian coastal area (see Results and Figure 4; additional information in Appendixes 2, 5).

register relevant information contained in the hinge structure or adductor muscle scars and pallial line.

6.2 How many species of Mactra can we recognise in the area?

Overall, the results of L and L + SL for *Mactra* (Figures 3(A),(B) and 4), together with the habitat conditions and ecological requirements of the five nominal species compared (see further detailed information provided in Table 5 and Figure 6 of Supplementary Appendix 2), brought light into the unresolved problem of an objective description, comparison and discrimination of huge number of very similar shells. From these results it is clear that (1) a considerable superposition of morphs is evident; (2) the 'interspecific' differences are not sufficiently strong to objectively discriminate between several species on the basis of shell characters (which preserve both traces of the whole shell outline and of the internal anatomy, e.g. Collins et al. 2013); (3) the largest variation belongs to *Mactra isabelleana* and includes all that of the remaining morphs/species, reinforcing previous research lines and our working hypothesis. The different morphs/'species' of *Mactra* resulted indistinguishable and the variation observed within and between different 'species' (including their type specimens) can be explained by the fact that they represent extremes within a wide morphological range, in agreement with interpretations based on conventional morphometrics (Aguirre 1994). Our results do not agree with those of Signorelli and Pastorino (2007) who distinguished two different species, *isabelleana* and *marplatensis*, for restricted areas of the Bonaerensian area. Based on a considerably higher number of shells, from a wider coastal area and larger number of localities, of different ages (Late Pleistocene, fossil Holocene and modern), we can independently test and confirm our hypothesis as plausible: only one (polymorphic) species, *Mactra isabellena*, with phenotypic plasticity linked mainly to substrate variations. According to salinity gradients along the distribution range in the northern and southern Bonaerensian coastal areas, salinity is another important control factor.

In support of this statement, if the morphologic species concept is applied, a discrimination of different species would imply a clear distinction of separate, independent, groups/morphs within an RW scatter plot diagram such as that depicted in Figure 3(B). On the contrary, our results allowed a clear immediate visualisation of very similar relationships between them all. Consequently, the nature of the observed shape variation must be explained by local physical controls reinforcing our working hypothesis (Aguirre 1994). Phenotypic plasticity of *Mactra isabelleana* was later also observed by Signorelli et al. (2013) based on 15 modern shell specimens (see other well-documented studies dealing with phenotypic plasticity in space and time, e.g. Miner et al. 2005; Roopnarine et al. 2008; Neubauer, Harzhauser, & Mandic 2013; Moneva et al. 2014).

6.3 What can explain Mactra shell shape variation in the area?

The discrimination of two groups of *Mactra* (North, South; Figure 4) is linked to the main local environmental conditions. Substrate nature is the main factor involved in the regression analysis, although other parameters of the coastal area involved were previously considered (salinity, water temperature (SST) and energetic level) (Aguirre, Richiano, et al. 2011; see Supplementary Appendixes 1, 2). The northern samples (mostly Punta Indio-Mar

Table 3. Location and environmental variables (salinity gradient, substrate nature, water energy, water temperature) of the sampled sites along the Bonaerensian coastal sector for geometric morphometric analyses of *Mactra*.

	AREA	LOCALITY/ SAMPLE	AGE	S LATITUDE	W LONGITUDE	SALINITY	RANK	SUBSTRATE	RANK	TEMPERATURE	RANK	ENERGY	RANK	DEPTH	RANK
1	PUNTA INDIO	Loc. 2	HOLOCENE	35 11	57 26	POLY-EUHALINE	3	HARDER	5	HIGHEST	5	HIGH	5	VERY LOW	1
2	Ba.SAMB. NORTH	Loc.5	HOLOCENE	35 39 30	57 19 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
3	Ba.SAMB. NORTH	Loc.6-Cantera Spaletti	HOLOCENE	35 40 30	57 20 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
4	Ba.SAMB. NORTH	between Loc.5 & 6	HOLOCENE	35 41 30	57 21 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
5	Ba.SAMB. NORTH	between Loc.5 & 6 S	HOLOCENE	35 41 30	57 21 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
6	Ba.SAMB. NORTH	Loc. 7 Ea.R.L	HOLOCENE	35 46 20	57 24 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
7	Ba.SAMB. NORTH	Loc. 7 -WA4	HOLOCENE	35 46 20	57 24 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
8	Ba.SAMB. NORTH	Loc. 7 -WA5	HOLOCENE	35 46 20	57 24 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
9	Ba.SAMB. NORTH	Loc. 7- A25-A26	HOLOCENE	35 46 20	57 24 30	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
10	Ba.SAMB. CENTRAL	Loc. 10 - A88 + A82-WA7	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
11	Ba.SAMB. CENTRAL	Loc. 10 -BSM2	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
12	Ba.SAMB. CENTRAL	Loc. 10 -BSM3	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
13	Ba.SAMB. CENTRAL	Loc. 10 -BSM4	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
14	Ba.SAMB. CENTRAL	Loc. 10 -BSM5	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
15	Ba.SAMB. CENTRAL	Loc. 10 -BSM6	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
16	Ba.SAMB. CENTRAL	Loc. 10 -BSM7	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
17	Ba.SAMB. CENTRAL	Loc. 10 -BSM8	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
18	Ba.SAMB. CENTRAL	Loc. 10 -BSM9	HOLOCENE	35 58 20	57 27	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
19	Ba.SAMB. CENTRAL	Loc. DRS	HOLOCENE	35 58 20	57 27	MIXO-POLYHALINE	1	SOFT SILTY CLAY	1	MEDIUM	4	MUY BAJA	1	LOW	4
20	Ba.SAMB. CENTRAL	Loc. Pascua Fm -BS1P	PLEISTOCENE	35 55 35.99	57 43 16.78	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	MEDIUM	3
21	Ba.SAMB. CENTRAL	Loc. Pascua Fm -BS3 P	PLEISTOCENE	35 55 35.99	57 43 16.78	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	MEDIUM	3
22	Ba.SAMB. CENTRAL	Loc. Pascua Fm - BS4 P	PLEISTOCENE	35 55 35.99	57 43 16.78	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	MEDIUM	3
23	Ba.SAMB. CENTRAL	Loc. Pascua Fm - BS7 P	PLEISTOCENE	35 55 35.99	57 43 16.78	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	MEDIUM	3
24	Ba.SAMB. CENTRAL	Loc. Pascua Fm- Pascua P	PLEISTOCENE	35 55 35.99	57 43 16.78	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	MEDIUM	3

(*Continued*)

25	Ba.SAMB. SOUTH	Loc. 12-Ao.La Huella	HOLOCENE	36	22	40	57	21	35	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
26	Ba.SAMB. SOUTH	Loc. 13-N Canal 1	HOLOCENE	36	26	30	57	21	00	POLYHALINE	2	SOFT SAND	3	MEDIUM	4	MODERATE-HIGH	3	LOW	2
27	PUNTA RASA	Punta Rasa-A186	MODERN	36	17	32.25	56	46	35.67	POLYHALINE	2	SOFT FINE SAND	2	MEDIUM SOUTH	3	HIGH	4	LOW	2
28	PUNTA RASA	Punta Rasa-A186	MODERN	36	17	32.25	56	46	35.67	POLYHALINE	2	SOFT FINE SAND	2	MEDIUM SOUTH	3	HIGH	4	LOW	2
29	PUNTA RASA	Punta Rasa-A186	MODERN	36	17	32.25	56	46	35.67	POLYHALINE	2	SOFT FINE SAND	2	MEDIUM SOUTH	3	HIGH	4	LOW	2
30	PUNTA RASA	Punta Rasa-A186	MODERN	36	17	32.25	56	46	35.67	POLYHALINE	2	SOFT FINE SAND	2	MEDIUM SOUTH	3	HIGH	4	LOW	2
31	PUNTA RASA	Punta Rasa-A186	MODERN	36	17	32.25	56	46	35.67	POLYHALINE	2	SOFT FINE SAND	2	MEDIUM SOUTH	3	HIGH	4	LOW	2
32	MAR CHIQUITA	Loc. 22	HOLOCENE	37	33	30	57	21	0.5	MIXO-POLYHALINE	1	COARSE SAND	4	LOW	2	MODERATE-LOW	2	LOW	2
33	MAR CHIQUITA	Loc. 23	HOLOCENE	37	34	20	57	22	40	MIXO-OLYHALINE	1	COARSE SAND	3	LOW	2	MODERATE-LOW	2	LOW	2
34	MAR CHIQUITA	Loc. 24	HOLOCENE	37	44	0.5	57	26	35	POLYHALINE	3	COARSE SAND	3	LOW	2	HIGH	4	VERY LOW	1
35	BAHÍA BLANCA	Bahía Blanca BIAC	HOLOCENE	38	51	03.69	62	09	54.65	POLYHALINE	3	COARSE SAND	4	LOW SOUTH	1	HIGH	4	LOW	2
36	BAHÍA BLANCA	Bahía Blanca EBYTEM	HOLOCENE	38	51	03.69	62	09	54.65	POLYHALINE	3	COARSE SAND	4	LOW SOUTH	1	HIGH	4	LOW	2
37	BAHÍA BLANCA	Bahía Blanca San Antonio	MODERN	38	51	03.69	62	09	54.65	POLYHALINE	3	COARSE SAND	4	LOW SOUTH	1	HIGH	4	LOW	2
38	BAHÍA BLANCA	Monte Hermoso	MODERN	39	0.1	53.18	61	33	29.31	EUHALINE	4	COARSE SAND	4	LOW SOUTH	1	HIGHEST	5	VERY LOW	1

Note: See map of Figure 1 (also physical parameters shown in Figure 1 of Supplementary Appendix 1; and sites and variables shown in Figures 2 and 6 and Table 5 of Supplementary Appendix 2). Rank order of variables according to physical parameters from bibliographic sources (Figure 1 of Appendix 1, Figure 6 of Appendix 2, and references therein).

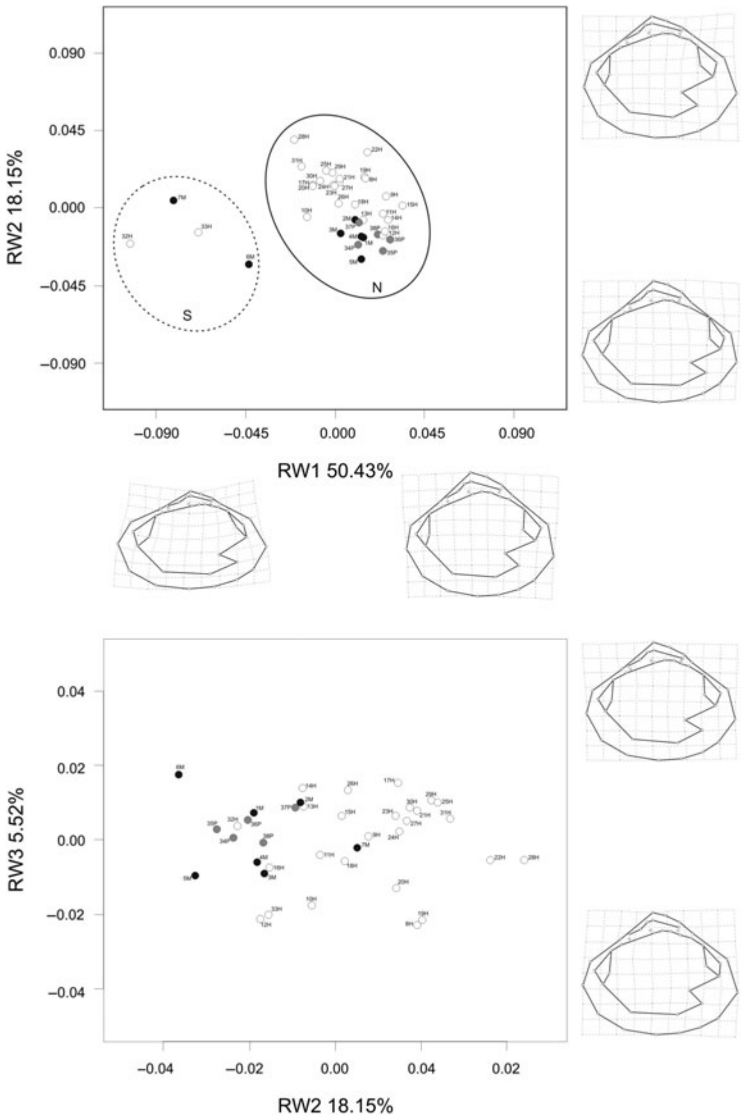


Figure 4. Three first axes of the RWs analysis for geographical–temporal samples of *Mactra* (mean scores per sampled locality). The samples of *Mactra* are discriminated by age and location (South, S, and North, N; numbers 1–38 indicate the number of samples as in Table 2). P, Pleistocene (grey circles); H, Holocene (white circles); M, modern (black circles). North: Bonaerensian localities along the northern littoral area, between the Río de La Plata margin and Mar del Plata; South: southern Bonaerensian area including Bahía Blanca surroundings.

Chiquita area; Figure 1(B)) contain subtrigonal shells from mud-fine sands, mixo to poly-euhaline warmer waters. The southern group (samples from Monte Hermoso-Bahía Blanca area) includes more elongate shells typical of sandy substrates in euryhaline environments of higher salinity and less warm waters (supplementary data on environmental conditions are provided in Supplementary Appendix 1 and Table 5 and Figure 6 of Supplementary Appendix 2).

Due to the lack of studies dealing with the functional morphology of modern *Mactras* along the SWA (and worldwide), which could objectively test their correlation to abiotic or ecological processes, no empirical data are available to explain patterns and mechanisms of their morphological responses to environmental changes. It is widely known, however, that in mixed, estuarine, unstable environments, benthic taxa suffer strong physical stress through seasonal and daily influence of wave tides and winds. Thus, low taxonomic diversity and strong phenotypic plasticity are not uncommon conditions in these habitats (Cadée 1968; Flessa & Fürsich 1991).

Looking at their modern spatial distribution, subtrigonal shells (morphs *isabelleana, petiti*) have their modern optima in muddy substrates, poly to polyeuhaline and warmer waters along the Rio de La Plata margin (i.e. Montevideo, Bahía Samborombón, Punta Rasa), where burrowing mechanisms can be easier, and not necessarily deep in order to avoid burial. Elongate, less convex shells (*marplatenses, janeiroensis, patagonica* of the literature) are typical of sandy bottoms, in contact with more energetic open oceanic conditions (i.e. Mar Chiquita surroundings, Puerto Quequén, Bahía Blanca, Bahía San Blas) or in open marine conditions (off Mar del Plata), where they require a more intense burrowing activity to avoid burial. Very thin, compressed and fragile shells are typical of mixohaline, low energetic, shallow conditions (very fine sediments in the outlet of coastal lagoonal settings).

In addition, data about the distribution and ecological requirements (Tables 1a, 3; systematic review in Supplementary Appendix 3) point to salinity as a strong abiotic factor linked to shell shape. Moreover, salinity is acknowledged as the main controlling factor on diversity in estuarine macroinvertebrate benthic assemblages (i.e. Josefson et al. 2013). The modern range of *Mactra isabelleana* in the SWA, between Laguna de Los Patos (southern Brazil) and Bahía San Blas and Río Negro outlet (Argentina), is restricted to marginal marine coastal settings (not fully marine as traditionally and erroneously pointed out, see for example Castellanos 1967; Rios 1994; Giberto et al. 2007). This area, characterised by three major basins (Río de la Plata; El Rincón at Bahía San Blas area; Golfo San Matías), is influenced by three large river discharge effects (Paraná-Río de la Plata, Río Colorado and Río Negro). The northern and southern areas also match with two salinity fronts, the Río de La Plata estuarine Front and the El Rincón Estuarine Front (additional information is in Figure 1 of Supplementary Appendix 1).

Interestingly, records of modern *Mactra isabelleana* well documented by illustrations and/or collections – not just bibliographic lists – are available for Laguna de los Patos in Brazil (i.e. Bemvenuti et al. 1978; Bemvenuti & Netto 1998; Seeliger et al. 1998), Montevideo and Punta del Este in Uruguay, the Río de La Plata (i.e. Giberto et al. 2004; Giberto 2008) and Bahía Blanca, all areas located within the so-called *Temperate Estuarine Zone*. By contrast, at present *Mactra isabelleana* is absent from the oceanic Bonaerensian littoral and from the Patagonian coasts where open marine conditions prevail. (Carcelles 1950; Carcelles & Williamson 1951; Castellanos 1971, 1982; Castellanos & Landoni 1988–1993) (see Supplementary Appendixes 2 and 3).

Moreover, in spite of the fact that *Mactra isabelleana*, together with the remaining close ‘species’ (Figure 3(B)), has originally and traditionally been considered typically marine, no records of *Mactra* spp from oceanographic expeditions are available for the Mar Argentino. Exceptions are a few mentions off Mar del Plata surroundings (i.e. MACN 9771, MACN 10916, MACN11580 and MACN14152; Supplementary Appendix 4). According to Castellanos (1971), the ‘*Goyena*’ expedition supplied shells from the Bonaerensian coasts, between 37° 56′07″S, 57° 29′02″W (station 4) and 38° 01′S, 57° 26′07″W (station 8): two shells of *Mactra isabelleana* recorded on fine sands at ca. 13.50 m deep off Mar Chiquita, seven specimens of *Mactra marplatensis* and three of *Mactra patagonica* on muddy sands at ca. 20 m deep off Mar del Plata. However, at this latitude, the littoral area is still influenced in summer by the freshwater discharge of the Río the La Plata plume (Piola et al. 2005, 2008) (see map provided in Appendix 1). Other records mentioned by Signorelli and Pastorino (2007) off Mar del Plata are approximately at the same location as that reported by Castellanos (1971) for *Mactra marplatensis*. In fact, fresh (modern) shells of this species are not abundant along Bonaerensian beaches as a product of strong wave action, except for Punta Rasa area, which represents the boundary between the Río de La Plata (Bahía Samborombón) and the oceanic littoral (Mar Argentino). On the other hand, other modern Mactras from Argentina like *Mactra fueguensis*, very close to ‘*Mactra marplatensis*’, are known for Tierra del Fuego and southern Santa Cruz province (i.e. Ensenada Ferrer, see Figure 1), areas of influence of the *Patagonian cold estuarine zone*. This large-scale biogeographical pattern for *Mactra* along Argentina reinforces a strong link between its distribution with constrained salinity gradients.

Secondly, other factors, such as substrate nature and water energy, are connected to shape variation. According to Stanley (1970), energetic conditions determine the burrowing rate and depth of burial that a bivalve must reach to avoid being removed from the sediment–water interface. Indeed, it is not unlikely that subtrigonal specimens of *Mactra* match with muddy and quieter environments (northern samples) with an easier burrowing activity, within habitat conditions where the organism needs not to burrow deeply to avoid being buried. While less trigonal shells match with coarser sediments (southwards), more energetic environments, where burrowing is more difficult and the organism needs to dig deeper to avoid being buried, consequently show greater foot development, adductor scars and siphons, resulting in a more elongate shell shape. The same applies to shells from very shallow environments which need to burrow deeper to avoid burial. Stanley (1970) also showed that substrate type affects the behaviour and burrowing mechanisms in most Mactridae. Similarly, many studies have shown that grain size and total organic matter are the most important controlling factors for the distribution, abundance and shell shape variation in intertidal and infralittoral soft-bottom molluscan faunas (among others, Cacabelos et al. 2008). Also, several authors earlier explained, for various bivalve taxa, similar shell variations (general shape, growth, thickness, morphometric parameters, hinge shape and development) in response to different substrate and depth conditions. For example, for a given species, thicker shells occur in shallow waters of gravel and coarse sand bottoms while they are thinner and more fragile in muddy substrates, and their relative abundance can vary according to the sediment. In *Nucula*, morphologic differences also vary according to the substrate type (among others Allen 1954; Carter 1967; Stanley 1970; Thomas 1975, 1976, 1978); the sculpture of different bivalves can correlate with their burrowing activities (Savazzi 1987, 1991).

Regarding the shells of *Mactra* from Quaternary facies, similar constraints are valid. Differential shell shape, general size and other intrinsic features such as thickness and the depth of the pallial sinus may respond to habitat and life mode conditions. Large, thicker, subtrigonal inflated shells, with shorter pallial sinus, predominate along the Río de La Plata margin (Punta Indio-Bahía Samborombón) in Late Pleistocene (Last Interglacial, ca. 125 ka B.P.) and Mid-Holocene deposits. Larger, more elongate shells, with deeper pallial sinus, are most common in the Holocene sand shell ridges from Mar Chiquita (localities 22 and 24) and Bahía Blanca (localities 28 and 29). In Holocene tidal flat and coastal lagoonal facies (Destacamento Río Salado at locality 10; Canal 18 Mb. at locality 11) (map showing locality details in Figure 2 of Supplementary Appendix 2), where muddy bottoms, less energetic and very shallow waters, in lower salinity conditions were inferred from independent sedimentological and geological background (Richiano, Varela, et al. 2012), the shells are smaller, thinner, more fragile, provided of a postumbonal 'posterior line'. (detailed morphological differences are given in Table 4 of Supplementary Appendix 2).

Overall, due to the fact that (1) modern records of *Mactra isabelleana* can be found in restricted areas (Río de La Plata, Punta Rasa, surroundings of Mar Chiquita-Mar del Plata, Puerto Quequén, Bahía Blanca; polyeuhaline) but are clearly absent or very scarce in the Mar Argentino and (2) a lower relative abundance at present sets off in contrast to the dominance in Late Quaternary deposits, we interpret the differential distribution and abundance of the morphs since the Last Interglacial (ca. 125 ka B.P.) as an evolutionary response to local abiotic changes to present. Substrates along the Bonaerensian littoral have been probably rather similar across time. However, cyclic changes of salinity occurred during high sea-level maxima when the coastline was placed several kilometres westwards relative to its modern position (Aguirre, Donato, et al. 2011, 2013), accounting for the high abundance of *Mactra isabelleana* in areas which today are characterised by oligohaline waters (Río de la Plata margin) and for the modern scarcer numbers if compared especially to Mid-Holocene times. Also, it is acknowledged that during the Mid-Holocene transgressive maximum, SST was higher than present, in coincidence with the so-called *Mid-Holocene Climatic Optimum* (*Thermal Maximum*; Briner et al. 2006; ca. 7–5 ka B.P). A ca. 1–2°C increase is thought to have caused a southern shift of warm water masses as postulated previously for this coastal area (Aguirre 1993; Aguirre, Donato, et al. 2011; Aguirre et al. 2013). After that, during the regressive trend, progressively changing and unstable conditions restricted the availability of optimum niches for *Mactra isabelleana* in the area, allowing subtrigonal ecomorphs in northern warmer waters, and elongate in the southern (less warm) water masses. Phenotypic changes through time as a result of functional adaptations to varying habitat conditions have also been well documented for other Cenozoic Venerid bivalves (e.g. Neubauer, Harzhauser, & Mandic 2013) (see also Pigliucci 2001). Our interpretation is based on the association between shape variation–geographical/environmental parameters taking into account the location, salinity, type of substrate, energy, secondary depth and water temperature of the localities selected (modern environmental data and inferred for fossiliferous sites).

The level of detail for palaeoenvironmental reconstructions obviously varies according to the ecological requirements of the taxa implied. It is generally argued that eurytypic species bring undesirable variability, whereas stenotypic species are preferred as they provide accurate information (Rizzo & Wetzel 1985). The results show that Quaternary shells from marginal marine environments can provide relatively long-term records of environmental variations, at least since ca. 125 ka B.P. in the area. Being so abundant and easy to collect, they can be used prior to any other biological proxy, as a first step into reconstructions of Holocene and Pleistocene coastal environments (see Poirier et al. 2009).

In spite of the unavoidable criticism and discussions regarding the use of a morphologic species concept against a better (more complete) biologic species concept (not applicable for fossil materials although suggested by authors, e.g. De Francesco 2007), most biological research performed on bivalves from the SWA margin has so far used solely hard (shell) characters for taxonomic discriminations. Recently, full descriptions of soft (endosomatic) parts (again morphological characters) were considered (i.e. Signorelli & Scarabino 2010). However, even when soft parts are missing and if the morphological species concept is applied (instead of the biological), the Quaternary fossil and subfossil shells can be useful tools for indirect information about substrate, salinity and SST conditions within the original littoral habitats. Also, the biological species concept is seldom really applied by most biologists worldwide and regarding any taxonomic unit dealt with. Species of sexually reproducing organisms are real and exist by virtue of reproductive isolation rather than of phenotypic distinctiveness (i.e. Futuyma 2006), but no such studies are available so far for most of the molluscan bivalves from the Mar Argentino. The results of our study are descriptive and need further multivariate analyses including soft parts and molecular data, the geographical distribution of genetic lineages could provide additional fundamental basis to test whether the differences between ecomorphs prevent interbreeding or not (Avise 2000). Up to now, however, there is no fundamental ‘biological’ evidence to discriminate species of *Mactra* from the area of study. On the other hand, defining phenotypes through space and time represents a unique contribution of palaeontology to evolutionary biology. Systematics is a rigorous multidimensional scientific discipline (Crisci 2006), and in future, more detailed studies are expected to integrate palaeontological, biological, ecological, genetic and statistical approaches of these molluscan assemblages from multidisciplinary standpoints.

7. Conclusions

This study confirms the advantage of examining large number of shell specimens, from different time slices and at macrogeographical scales, in order to objectively characterise and interpret the morphological variability of dominant taxa provided with modern counterparts, leading to the following conclusions:

1. Combining different morphometric techniques has a high potential to assess how many taxa can be objectively discriminated, a problem equally faced by palaeontologists, geologists, archaeologists and even biologists and phylogeographers and with implications for estimations of biodiversity and environmental changes.
2. The three morphometric procedures applied (EFA, L and L + SL) are useful to discriminate between familiar/generic levels for dominant Veneroid bivalves from the marine Quaternary of Argentina, and living in the Mar Argentino.
3. Only L + SL is powerful to discriminate between closely related taxa with scarce recent evolutionary divergence (e.g. ‘species’ of *Mactra*).
4. For *Mactra*, a unique polymorphic species, *Mactra isabelleana*, can be objectively discriminated within the Bonaerensian marine Quaternary, with ecomorphs potentially useful as palaeoenvironmental markers (mainly substrate; salinity).
5. Rapid palaeoclimatic/palaeoenvironmental changes linked to the last eustatic episodes are the most plausible explanations for the morphological and spatial trends observed since the Last Interglacial to present. Late Quaternary high sea-level stands had strong influence in the physical parameters of the coastal area, availability of optimum habitats for *Mactra isabelleana* and, consequently, on shell geometry and geographical distribution of its various phenotypes. The history of its distribution and abundance until the present responds mostly to salinity changes, which allowed its dominance in optimum conditions during transgressive maxima, contrasting with the scarcer modern records, which were featured after the regressive phases altered the coastal geomorphology, moving the coastline (and salinity gradients) some kilometres eastwards relative to previous positions.

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Supplementary material

Supplemental data for this article are available online.

Notes

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