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Morphological variability of *Brachidontes* Swainson (Bivalvia, Mytilidae) in the marine Quaternary of Argentina (SW Atlantic)

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Abstract

Morphometric analyses of abundant shells of *Brachidontes* from 27 localities (19 littoral deposits of Late Quaternary age and eight modern sites) in Argentina, where *Brachidontes rodriguezi* d'Orb., 1846, *Brachidontes darwinianus* d'Orb., 1846 and *Brachidontes purpuratus* Lamk., 1819 have been reported, show implications for palaeoenvironmental reconstructions. Only shell characters have been generally used for taxonomic discrimination of these taxa (i.e., general shape, size, external ornamentation, colour). Morphometric variation ranges from elongate, comparatively small shells (R), typical of coarse sandy substrates and warm or warm-temperate water masses in typically marine and polyhaline environments (dominant in the mid-Holocene), to bigger, more strongly ribbed and more globose shells (P), characteristic of pebbly or rocky substrates, and shallow, cold water masses in typically open marine habitats (dominant in the Magellanean province at present). Traditional and geometric morphometric techniques performed on large amounts of fossil and modern shells help to objectively define the morphometric variation of *Brachidontes* in the area. The coordinates for the shell outline (165 specimens) and five linear dimensions (485 specimens) were used for morphometric analyses of shell specimens of the three main morphs (D=*darwinianus*; R=*rodriguezi*; P=*purpuratus*) identified within the samples collected, for two main reasons: 1) They represent the most common features used for taxonomic discrimination at the species level; 2) comparative analysis of outer ornamentation and colour could produce deceiving results due to the varying preservation grades between fossil and modern shells. Results both by Relative Warps and Principal Component techniques show no difference among shell morphs, implying that *B. darwinianus* and *B. rodriguezi* (=*B. solisianus* d'Orb.=*B. exustus* Linn.) might have to be synonymized with *B. purpuratus* (P), which dominates in colder waters at higher latitudes. The morphotypes are extremes within a wide morphological range and can be linked together in a chain of transitional forms. They respond to different habitats (ecomorphs) controlled by temperature (geographical variation), substrate, energy and water-depth, and by salinity, and by competitive strategies for space (availability of food resources), all influencing growth. The morphometric variation of organisms in fossil strata could represent a valid tool to reconstruct palaeoenvironmental changes that occurred during high sea-level stands since ca. 300 ka (Pleistocene, MOIS 9) to ca. 7.6–4.5 ka (mid-Holocene Climatic Optimum, transgressive maximum of MOIS1) and up to present.

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Keywords: Brachidontes; Bivalvia; Morphometrics; Quaternary; Marine; Argentina

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1. Introduction

The mytilids, to which the genus *Brachidontes* Swainson, 1840 belongs, are well known from all modern oceans of the world and are very abundant in shallow littoral areas (supratidal, intertidal, upper infralittoral zones). As byssally attached benthic elements, usually on hard bottoms, they occur especially in intertidal highly energetic waters of normal marine salinity or in estuarine zones (polyhaline to euhaline gradients).

The fossil records range back to the Jurassic (Cox and Newell, 1969), although they have been most abundant probably since the Neogene. On a palaeoecological basis, they are useful indicators of depth and substrate

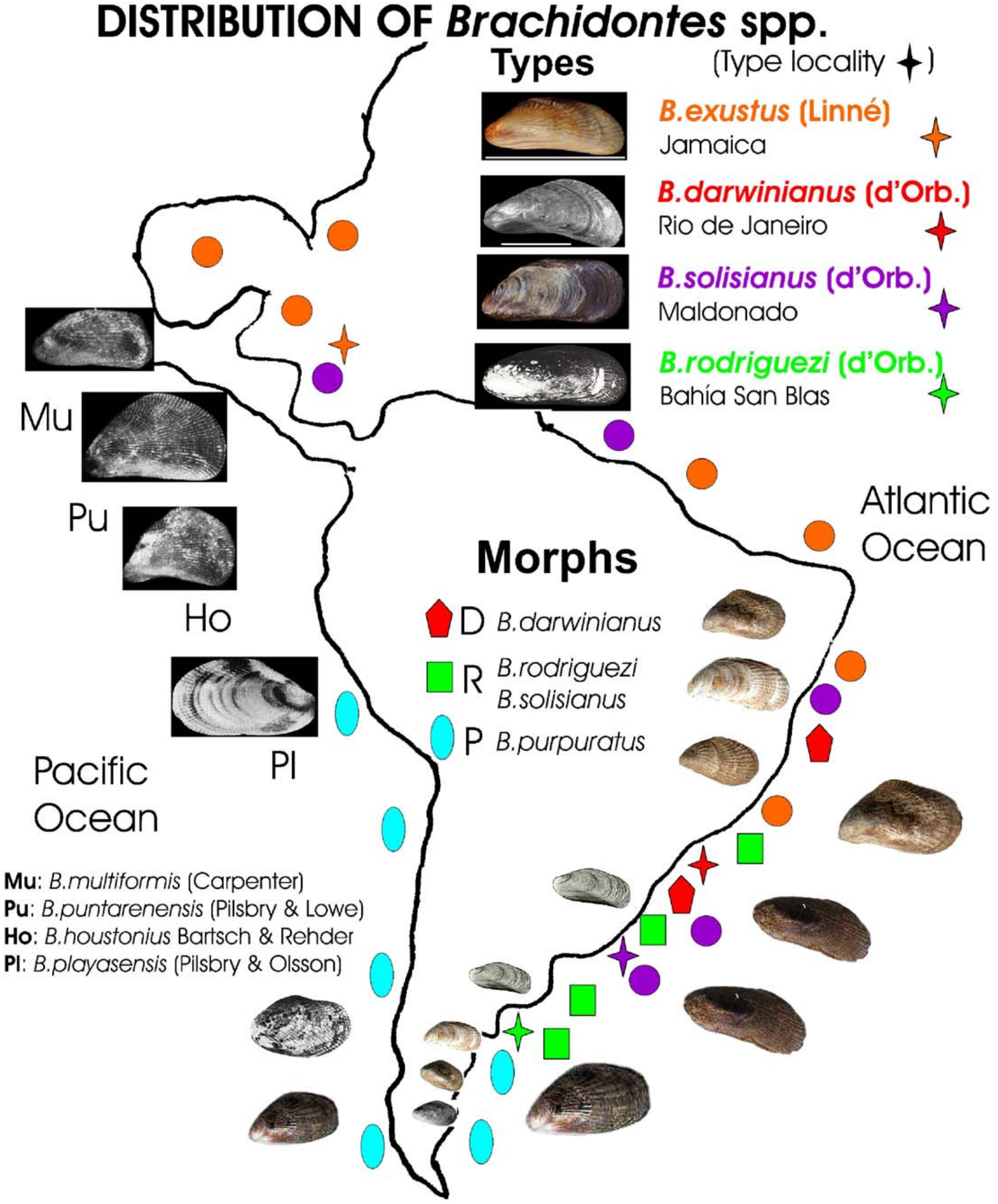


Fig. 1. Map showing the modern distribution of *Brachidontes* sp. in America along the western Atlantic Ocean and eastern Pacific Ocean, locality of type specimens of the species identified along the western Atlantic, and species identified along western America. Quaternary records along the coastal area of South America. Morphotypes recognized in Argentina.

Table 1
Morphological features of *Brachidontes* spp. from the western Atlantic and eastern Pacific littorals

Species		Range (group)	Shape	Size	Ornamentation	Teeth	Colour	Dorsal angle	Type locality	Modern distribution	Ecology (epibyssate; filter feeders)
exustus Linné, 1758	D	SW ATLANTIC (II)	moderately fan-shaped	18–38/40	numerous round radial ribs dividing near ventral margin	2 on anterior end; 5–6 behind	brownish	acute, well marked	Jamaica V	North Carolina, Gulf of Mexico, Florida, Antilles, Venezuela, Brazil: Pernambuco, F. Noronha, Bahía.	on mangroove roots, rocky shores; intertidal, surf zone
dominguensis Lamk., 1819	D	SW ATLANTIC (II)	oblong-trigonal, not gibbous dorsally; compressed	40	radial and concentric striae margin crenulated	not described	brownish	absent	Antilles V	Antilles to Brazil.	rocky shores; intertidal
purpuratus Lamk., 1819	P	SW ATLANTIC SE PACIFIC (IV)	oblong-elongate dorsal border not gibbous	40	coarsely ribbed; radial and concentric striae; radial, generally bifurcate	series of numerous small teeth	dark purple to black	absent	Unknown L	Atlantic from T. del Fuego to Golfo Nuevo; Pacific from Magellain Strait to Ecuador	intertidal among algae
darwinianus d'Orbigny, 1846	D	SW ATLANTIC (II)	oval oblong	30–46	strong radial ribs ventral margin and posterior border crenulated	various oblique	purple to black	strongly marked	Argentine coast, Río de Janeiro to Patagonia V	Río de Janeiro to Montevideo; Argentina?	rocky shores; intertidal
solisianus d'Orb., 1846	R	SW ATLANTIC (II)	oblong-elongate dorsal border not gibbous	12–17	exterior smooth; margin crenulated only posteriorly	not described	black	absent	Río de Janeiro, Maldonado V	E México, Campeche, Brazilian coast to Uruguay	on rocks and corals; intertidal, surf zone
rodriguezi d'Orb., 1846	R	SW ATLANTIC (III)	oblong-elongate dorsal border	16–30, 46–50	fine radial lines and growth striae, internal margin smooth, posterior crenulated	5–6 small; lacking behind the umbo	brown to purple	usually present	N of Patagonia; Río Negro-San Blas V	S Brazil to Golfo San José, Cubut (Patagonia)	on dead shells, submerged wrecks, rocky shores; intertidal to 25–100 m deep
multiformis Carpenter, 1855		E PACIFIC (II)	oblong-elongate	<14	smooth or with fine radiating ribs, generally absent ventrally	1 to 3, usually 2	dark purple to brown	absent	Mazatlán, México	Gulf of California to Ecuador (absent in tropical W America)	rocky shores; intertidal
puntarenensis P&Lowe, 1932	S	E PACIFIC (III)	oblong-elongate	17	radial sculpture	not described	brownish	marked	Puntarenas	Costa Rica	mud-flat dweller
playasensis P&Olsson, 1935	S	E PACIFIC (II)	oblong-elongate	21	fine radial sculpture concentric lines, ventral margin crenulated	not described	light brown	absent	Playas, Ecuador	Ecuador	hard substrates; intertidal
houstonius B & Rehder, 1939	S	E PACIFIC (IV)	oblong-elongate	10	very fine sculpture	not described	brownish	absent	Bahía de Sulivan	James Island, Galápagos Islands	on rocky shores; intertidal

References for morphological characters			Groups of species (Malacological Provinces)	
Linné, 1758	Castellanos (1967)	Camacho (1966)	I=pandemic	V=Type material examined and/or original illustrations compared
Lamarck (1835, 1819)	Keen (1971)	Feruglio (1933a,b)	II=warm waters (Antillean Malacological Province) IIII = warm-temperate (southern Argentina)	
d'Orbigny (1846)	Abbott and Dance (1991)	Del Río and Martínez (1998)	IV=cold waters (Magellanean)	L=lost
Philippi, 1893	Ríos (1994)	Aguirre and Farinati (2000)		
Ihering, 1907	Soot-Ryen, 1955	Klappenbach (1965)		

Only slight differences exist between species described for southern South America.

S=probably synonyms (local forms of one variable species); D, P, R=morphs; Sizes in mm.

Table 2
Stratigraphic and geographical distribution of *Brachidontes* sp. from southern South America. D, R, and P are the main morphotypes recognized

Localities	Stratigraphic occurrence of morphs			
	Tertiary (Mioc)	Pleistocene	Holocene	Modern
ANTILLES				D
BRAZIL				
Brazilian coasts				D–R
Fernando do Noronha				D
Pernambuco				D
Bahía				D
Río de Janeiro				D
Rio Grande do Sul				D–R
URUGUAY D–R				
Eastern coast			D	D–R
Carmelo			D	R
Río Uruguay			D	R
Montevideo			D	D–R
Punta Carretas			D	R
Cabo Santa María			D	R
Costa Azul			R	R
La Paloma			R	R
ARGENTINA				
Entre Ríos Province	R			NO
Buenos Aires Province				R
Plátanos		D	D	NO
Tolosa		D	D–R	NO
Punta Indio			R	R
Samborombon Bay	R		R	R
Punta Rasa				R
Las Toninas				R
Mar Chiquita				R
Mar del Plata P. Iglesias				R
Mar del Plata P. Grande				R
Puerto Quequén				R
Quequén Salado				R
Monte Hermoso				R
Sauce Grande				R
Bahía Blanca				R
S Buenos Aires Province				R
Patagonia	P			R–P
N Patagonia				R
San Antonio Oeste				R
Golfo San Matías				R
Punta Pardelas			P	R–P
Península de Valdés				R–P
Puerto Madryn	R		R–P	R–P
Puerto Lobos			P	P
Trelew-Bahía Bustamante				P
S of Bahía Vera-P.Pescadero				P
Cabo Raso			P	P
Camarones		R–P	R–P	P
Bahía Bustamante		P	R–P	P
Zanjón El Pinter				P
Península Gravina				P
Solano			P	P
Comodoro Rivadavia			R–P	P
Rada Tilly			P	P
Caleta Olivia			R–P	P
Golfo San Jorge			R–P	P
Puerto Deseado				P
Tierra del Fuego		P	P	P
Canal de Beagle			P	P
CHILE		P?	P	P
Magellain Strait				P
Pacific coast				P
PERÚ				P
Pacific coast				P
ECUADOR (*)				P

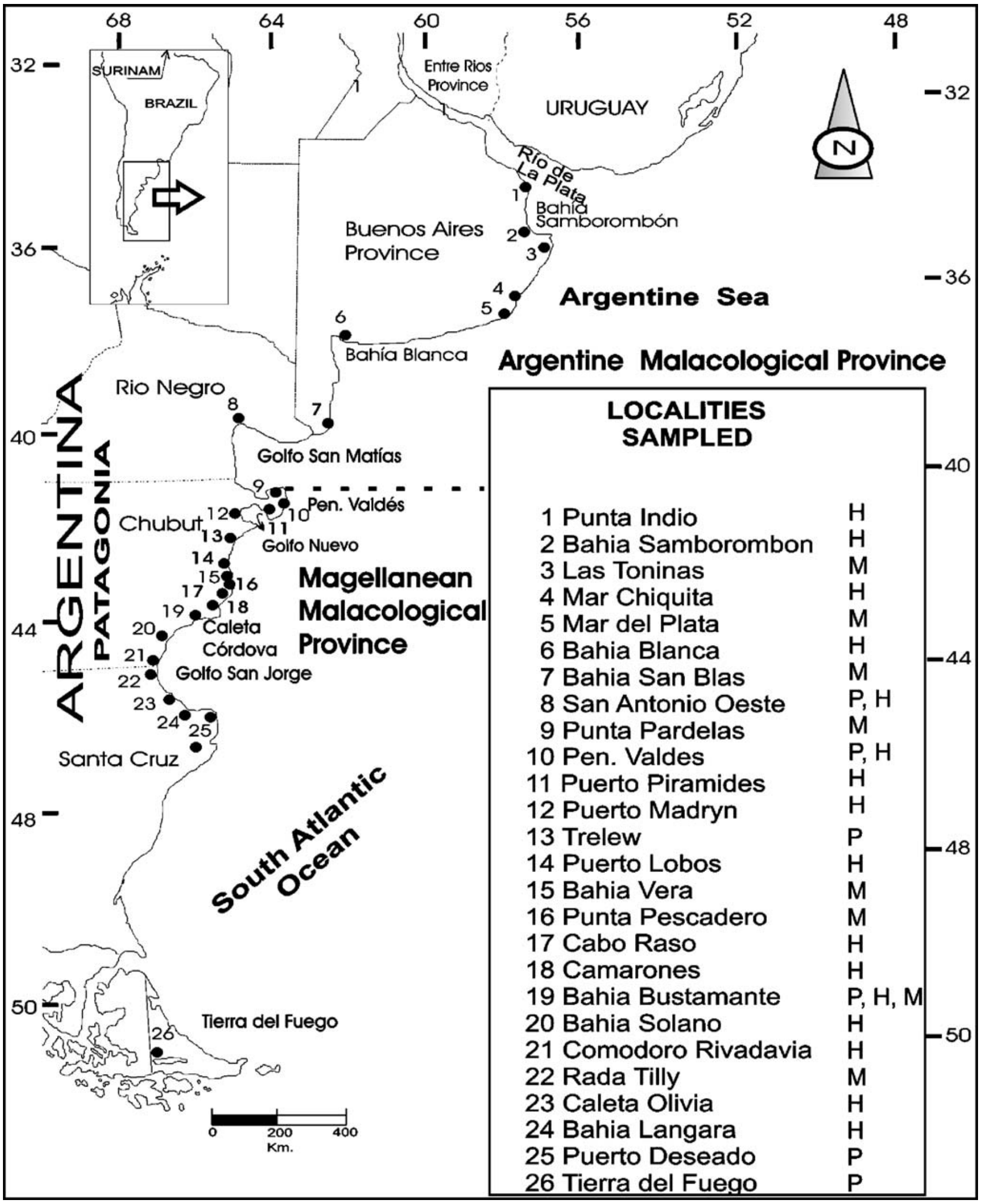
Horizontal bars indicate the geographical boundaries for each morphotype.
NO = absent at the locality.
*In this region, there is a transition zone along the Eastern Pacific coast between the Panamic (northwards, warm-water masses) and the Chilean-Peruvian (southwards, cold water masses) Malacological Province, defined by the influence of the cool Humboldt Current.

nature, i.e. of inner shelf environments and hard bottoms (rocky or sandy substrates with intercalated shell debris or pebbles).

Members of *Brachidontes* are characterized by small- to medium-sized shells. They are highly variable in shape (modioliform to elongate-ovate or cylindrical), size (10–49 mm long), outer ornamentation (comarginal growth striae and radial ribs of variable thicknesses), colour (light-brown to purple or black), degree of the inner margin crenulation, and number of hinge denticulations. A byssal sinus may be shallow or lacking, depending on the number of specimens clustered and on competition for space. All these features generally vary intraspecifically according to different habitats and geographical areas. The small dysodont hinge (anterior or posterior of the ligament) and the anysomiarian muscle scars may represent more stable characters at the family level, and sometimes the number of teeth and the shape and extension of the muscle scars (byssal retractor and posterior adductor) have been used for taxomic discriminations at the species level (Soot-Ryen, 1955; Castellanos, 1957; Klappenbach, 1965). However, when examining large numbers of specimens they appear to vary intraspecifically.

In addition to the intraspecific variability of shell characters, there are cases of strong interspecific morphological similarities, covering practically the same geographic areas (Fig. 1). This situation was already observed along the Brazilian coast by Klappenbach (1965) for *B. exustus* Linné, 1758, living from Florida to Pernambuco, and *B. dominguensis* Lamarck, 1819, living from Antilles to Brazil. He noticed that *B. dominguensis* replaces *B. exustus* southwards of Cabo Frío (Brazil) and that they may represent geographic variations of the same species.

Along the western Atlantic littoral of southern South America, both at present and in fossiliferous coastal deposits of Late Quaternary age, three species have been recorded. These are, in order of decreasing abundance, *B. rodriguezi* d'Orb., 1846, *B. purpuratus* Lamarck, 1819 and B. *darwinianus* Lamarck, 1819 (Tables 1, 2). Apparently they repeat a similar geographical pattern: *B. darwinianus* Lamarck, 1819, living from Río de Janeiro to Montevideo, is replaced southwards by *B. rodriguezi* d'Orb., 1846, living from southern Brazil to Golfo San Matías, and this species is replaced by *B. purpuratus* Lamarck, 1819, living from Golfo Nuevo down to Tierra del Fuego (Figs. 1, 2).



LOCALITIES SAMPLED

1 Punta Indio	H
2 Bahia Samborombon	H
3 Las Toninas	M
4 Mar Chiquita	H
5 Mar del Plata	M
6 Bahia Blanca	H
7 Bahia San Blas	M
8 San Antonio Oeste	P, H
9 Punta Pardelas	M
10 Pen. Valdes	P, H
11 Puerto Piramides	H
12 Puerto Madryn	H
13 Trelew	P
14 Puerto Lobos	H
15 Bahia Vera	M
16 Punta Pescadero	M
17 Cabo Raso	H
18 Camarones	H
19 Bahia Bustamante	P, H, M
20 Bahia Solano	H
21 Comodoro Rivadavia	H
22 Rada Tilly	M
23 Caleta Olivia	H
24 Bahia Langara	H
25 Puerto Deseado	P
26 Tierra del Fuego	P

Fig. 2. Localities sampled in Argentina. - - - : Modern boundary between the Argentine and Magellanean malacological provinces. P: Pleistocene; H: Holocene; M: modern.

This study aims at evaluating the potential implications that the analysis of shell form in *Brachidontes* have for palaeoenvironmental and palaeoclimate interpretations in the area of study. *Brachidontes* was selected for being a constant, abundant and well preserved component of the molluscan assemblages of Argentina with wide morphological variation. Precursor studies in this field are those by Imbrie (1956). A similar approach has been attempted with good results for other taxa from similar deposits in Buenos Aires Province (Argentina) (Aguirre, 1994; Aguirre and Urrutia, 2002), but not yet for taxa recovered from the whole Argentine coastal area including Patagonian marine terraces.

We attempt, by means of a preliminary multivariate morphometric study, to decipher whether the three taxa from the Argentine coast could represent environmental or geographical variations since the Late Quaternary, with implications linked to sea-level fluctuations and climate changes. It is assumed that they show a clinal variation if a gradual morphological change was revealed for one or more shell characters along a single environmental gradient (i.e., temperature, substrate) (Brown and Lomolino, 2000). This study aims to contribute to the analysis of changes in phenotype through space and time as a unique contribution of palaeontology to evolutionary biology.

Only a few species from a limited area are dealt with in this study and complementary decisive conclusions will probably result from ecological studies and comparative analyses of the soft parts performed on living specimens. Our results, based on the available data of the hard parts, could be used to reconstruct the general palaeoenvironmental conditions of the Argentine coastal area during the Quaternary. At the same time, they are relevant for presenting taxonomic lists and estimations of marine biodiversity, either from fossiliferous coastal deposits or from modern samples of the continental shelf and littoral, as in all cases only empty shells are generally preserved.

2. Area of study and geological setting

The area of study comprises the whole coastal area of Argentina between the Buenos Aires province and Santa Cruz province (Fig. 2). All along this area of southern South America molluscan assemblages were accumulated during different sea-level episodes in the Quaternary, at least since ca. 300 ka B.P. (MOIS9). They integrate beach ridges, raised marine terraces and estuarine facies where bivalve and gastropod taxa represent a major component of the whole biogenic composition.

The type sections of the marine Holocene from Argentina are located at Samborombon Bay (Las Escobas Formation; +5 m above msl, 7–2 ka B.P.), Mar Chiquita (Mar Chiquita Formation), and Bahía Blanca (Postglacial transgression) along the Bonaerensean area as described by Fidalgo (1979), Schnack et al. (1982), Aliotta and Farinati (1990), and Aguirre (1993a). In Patagonia, they are typically represented at Comodoro Rivadavia (Marine Terrace VI) as described by Feruglio (1950), and at Camarones and Bahía Bustamante as described by Cionchi (1987) and Schellmann and Radtke (2000), among others. The age of these landforms is ca. 9–2 ka B.P.^{14}C.

The type sections of the marine Pleistocene are located at Puente de Pascua (+6 m, minimum 40 ka B.P., MOIS 5e?; "Belgranense" in the local literature) in Buenos Aires Province, and in Patagonia at Camarones and Puerto Deseado as described by Feruglio (1950) and at Bahía Bustamante, Caleta Olivia and Bahía Lángara as described by Codignotto (1983, 1987), Cionchi (1987), and Codignotto et al. (1988, 1992). Their ages range from minimum of ca. 29 ka (^{14}C) to ca. 119–400 ka B.P. (Th/U, ESR).

In the Buenos Aires province, fossil molluscs were sampled from profiles along well stratified regressive beach ridges of the Cerro de la Gloria Member (Las Escobas Fm.; MOIS1) (complete data set in Aguirre and Whatley, 1995). Additional material from the whole Bonaerensian littoral was examined from museum collections (Appendix A, B).

In Patagonia, fossil molluscs were collected mostly atop beach ridges in regressive units at selected outcrops between Puerto Lobos and Puerto Deseado along Chubut and Santa Cruz provinces (Fig. 2). In this area, the coastal deposits are not as well stratified as those preserved in the Buenos Aires Province. The units belong to the so-called "Marine Terraces" (MT) IV, V and VI described by Feruglio (1950) and recently dated by Rutter et al. (1989, 1990) and Schellmann and Radtke (2000), allowing a provisional correlation with MOIS (Marine Oxygen Isotope Stages): MTVI (Holocene, Comodoro Rivadavia; +8–12 m a msl, MOIS1), MTV (Pleistocene, Puerto Mazarredo; +15–30 m; MOIS5e?), MTIV (Pleistocene, Puerto Deseado; +30–40 m; MOIS7/9?) and MTIII (Pleistocene, Camarones; +40–95 m; MOIS9/11?) (Table 3). The most easily recognized of all the Patagonian marine terraces is MTVI at +6–7 m, +8–9 m, +8–12 m a msl in Río Negro (San Antonio Fm.), Chubut (Zanjón El Pinter Fm.) and Santa Cruz provinces. It correlates with synchronous deposits

Table 3
Stratigraphic synthesis of the marine Quaternary along the coastal area sampled. MOIS: Marine Oxygen Isotope Stage or Substage (Feruglio, 1950; Fidalgo, 1979; Fasano et al., 1982; Farinati, 1985; Rabassa, 1987; Codignotto, 1987; Weiler et al., 1988; Ruttler et al., 1989, 1990; Aguirre, 1993a,b, 2003; Aguirre and Whatley, 1995; Aguirre and Codignotto, 1998; Martinez et al., 2001)

AREA	SURINAM	BRAZIL	URUGUAY	ARGENTINA			
				BUENOS AIRES PROVINCE			PATAGONIA
				BAHIA SAMBOROMBON	MAR CHIQUITA	BAHIA BLANCA	*" TERRAZAS MARINAS "*
				Fidalgo, 1979	Fasano *et al.*, 1982; Weiler *et al.*, 1988	Farinati, 1985	Feruglio, 1950
HOLOCENE	HOLOCENE TRANSGR. MOIS 1	HOLOCENE TRANSGR. MOIS 1	VILLA SORIANO FM. MOIS 1	LAS ESCOBAS FM. Cerro de la Gloria MOIS 1 Canal 18	MAR CHIQUITA FM. marine facies MOIS 1 estuarine facies	POSTGLACIAL TRANSGR. MOIS 1	**VI** **Comodoro Rivadavia** (+6-12 m) MOIS1
PLEISTOCENE		MARINE PLEISTOC. MOIS 3? MOIS 5e? (29.5-35.5ka)		D.RIO SALADO FM. PASCUA FM. (+3-10 m) MOIS 5e? (> 30-35ka)	SANGAMON INTERGL. MOIS 5e? ?	SANGAMON INTERGL. MOIS 5e? ? (+ 12-14 m)	**V** **Puerto Mazarredo** (+15-30 m) MOIS5e ?
	REFERENCES : Ka: 1,000 years B.P. MOIS: Isotopic Stage or Substage Partially modified from Aguirre (1993, 2003); Aguirre and Whatley (1995). Complete source of references: Feruglio (1950); Fidalgo (19 Codignotto (1987); Rabassa (1987);Weiler *et al.* (1988); Rutter *et al.* (1989, 1990); Aguirre and Codignotto (1998 Martinez*et al.* (2001).						**III** **Camarones** (+40-95 m) MOIS 9/11 ?

northwards in the Buenos Aires Province (+5 m a msl, Las Escobas Fm.) and with other areas of eastern South America, such as Surinam, Brazil (+0–1 m a msl) and Uruguay (Villa Soriano Fm., Vizcaíno Fm.) (Table 3).

The areas sampled in detail were selected because the rocks have been more precisely dated, providing a better chronological control for palaeoenvironmental interpretations. More complete data on the molluscan samples, geology, altitude, dating, and correlation of marine terraces can be obtained from Feruglio (1950), Codignotto et al. (1988, 1992), Schellmann and Radtke (2000), Rostami et al. (2000), Aguirre (2003), Aguirre et al., 2005, 2006, in press). Additional material was examined from localities between San Antonio Oeste down to Tierra del Fuego in museum collections.

2.1. Modern littoral area

The modern littoral area is characterized by open marine conditions in warm-temperate and cool subantarctic waters (Fig. 3). It corresponds to the Argentine Sea in the SW Atlantic Ocean and belongs to two malacological provinces: (1) the Argentine Province in

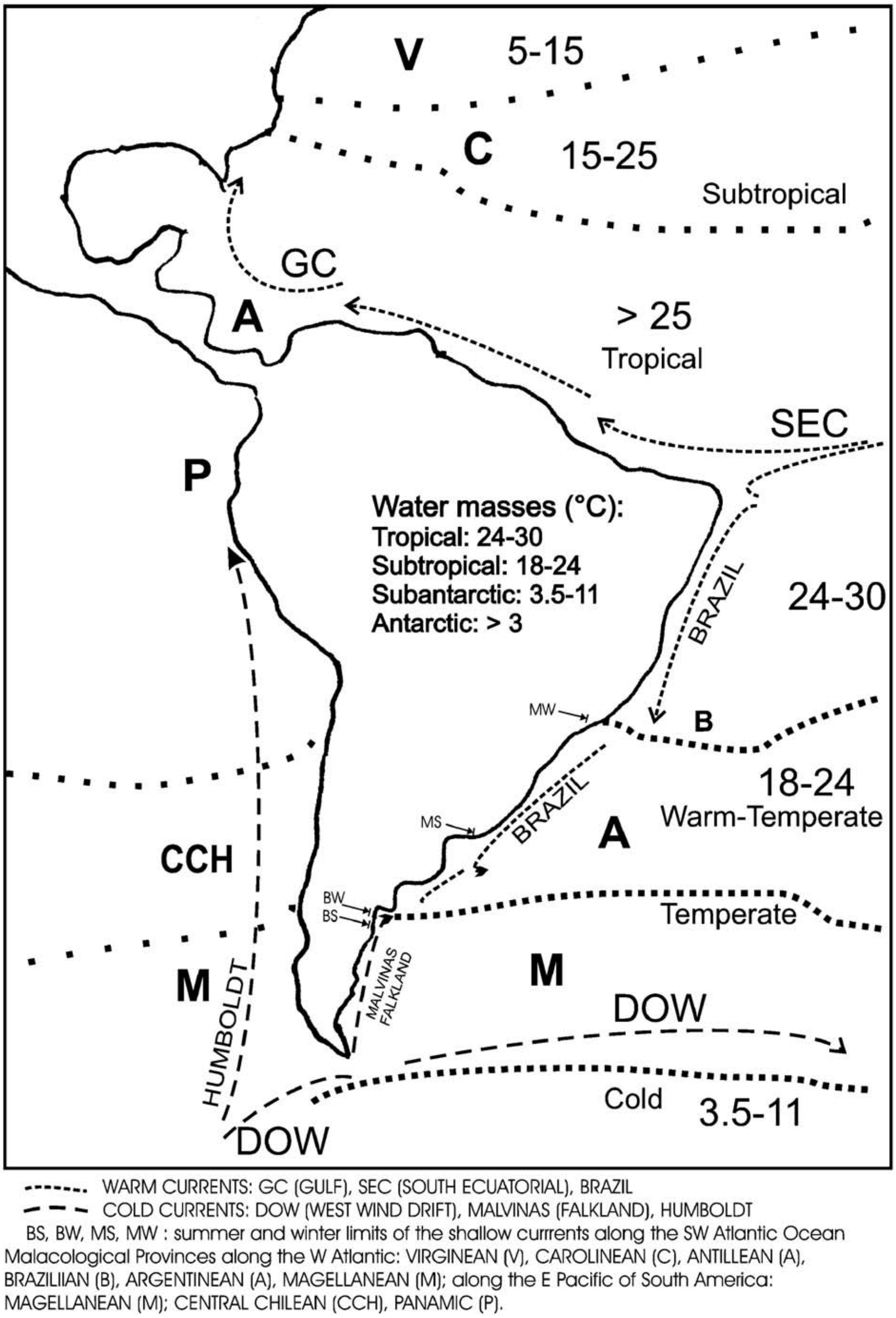


Fig. 3. Main shallow water masses and oceanic currents and malacological provinces of South America.

the north which extends from Río de Janeiro (Brazil) down to Golfo Nuevo (c. 43°S, Chubut Province, Argentina), and (2) the Magellanean Province in the south, which extends southwards along Atlantic Patagonia to Cabo Hornos (55°S, south of Tierra del Fuego) reaching the southern cone of eastern South America.

The boundaries of these provinces are defined by the seasonal extension of two shallow water currents: (1) the warm Brazilian Current (18–24 °C mean annual temperature, 34.5–36‰ mean salinity, a branch of the warm South Equatorial Current, flowing southwards, and (2) the cool Malvinas (Falkland) Current (4–11 °C mean annual temperature, 33.8–34‰ mean salinity, a branch of the West Wind Drift, flowing northwards. A third current of Subantarctic origin, the cool Patagonian Current (5–16 °C, 33–33.5‰), flows northwards between the coast and the Malvinas Current up to c. 38°S, affecting the coastal zone (Ekman, 1967; Knox, 1960; Briggs, 1974; Boltovskoy, 1979; Bastida et al., 1992; Guerrero and Piola, 1997; Piola and Rivas, 1997).

These currents are thought to have been active at least since the Late Miocene. During the Pleistocene climatic cycles they are expected to have suffered latitudinal shifts linked to the cold and warm (glacial–interglacial) stages and sea-level fluctuations.

The substrates along the Bonaerensian littoral consist mainly of fine sediments, sandy or silty (muddy along Samborombon Bay in the Río de La Plata), with scarce sectors of harder bottoms (Mar del Plata). In Patagonia, substrates consist mainly of coarse sediments, gravel and coarse sandy sediments characterizing most of the littoral area, while locally fine granulometric types are found along the Golfo San Matías (Río Negro Province), in Golfo Nuevo (Chubut Province) and in Golfo San Jorge (Chubut and Santa Cruz Provinces) (Bastida et al., 1992; Roux et al., 1995; Parker et al., 1997).

3. Systematic studies performed on *Brachidontes* from the southwestern atlantic margin

In South America at least ten living taxa of *Brachidontes* have been identified in the local literature (Soot-Ryen, 1955; Castellanos, 1957; Klappenbach, 1965; Castellanos, 1967; Keen, 1971; Ríos, 1994; Nuñez Cortés and Narosky, 1997; Forcelli, 2000). Along the southwestern Atlantic margin there are modern records of six taxa, i.e., ordered according to their geographical ranges from north to south, *B. exustus* Linnée, 1758, *B. dominguensis* Lamarck, 1819, *Brachidontes solisianus* d'Orbigny, 1846, *B. darwinianus* d'Orbigny, 1846, *B. rodriguezi* d'Orbigny, 1846, and *B. purpuratus* Lamarck, 1819 (Fig. 1, Table 1). Along the Pacific coast, five taxa are commonly recognized: *B. multiformis* Carpenter, 1855, *B. puntarenensis* Pilsbry and Lowe, 1932, *B. playasensis* Pilsbry and Olsson, 1935, *B. houstonius* Bartsch and Rehder, 1939, and *B. purpuratus* Lamarck which is the only species in common with the SW Atlantic group. Several authors have placed *B. purpuratus* under the genus *Perumytilus* Olsson, 1961.

From Argentina, three of these taxa have been mentioned: *B. darwinianus* along the coast of Buenos Aires Province and Northern Patagonia, *B. rodriguezi* almost exclusively in the Bonaerensian littoral and northern Patagonia, and *B. purpuratus* exclusively from Patagonia. However, a detailed review indicates that only *B. rodriguezi* and *B. purpuratus* are abundant and that at present the southernmost limit of *B. darwinianus* appears to be Montevideo (Uruguay) (Table 2).

The Argentine fossil records of *Brachidontes* spp. in Late Cenozoic sediments go back to the Miocene (ca. 10 Ma AP) (Puerto Madryn Formation in Chubut Province, also "Entrerriense" transgression or Paraná Formation in Entre Ríos Province) (Del Río and Martínez, 1998). They are especially abundant in marine Quaternary coastal deposits (beach ridges, marine terraces and estuarine facies), and mainly of Holocene age (ca. 7.6 to 3 ka B.P). The material recorded in Miocene sediments is assignable to *B. rodriguezi* while in the Quaternary, along the Bonaerensian and Patagonian coastal areas, both *B. rodriguezi* and *B. purpuratus* have been reported.

Although records of *Brachidontes* spp. from the modern littoral and from marine Quaternary molluscan assemblages are not uncommon in Argentina, comparative studies based on abundant material from a wide area and dealing with 'fossil populations' have as yet not been carried out. Most previous work includes descriptions and illustrations of only scarce fossil or modern specimens and from isolated localities (Feruglio, 1933a, b; d'Orbigny, 1834–1847; 1842–1844; Carcelles, 1944, 1950; Camacho, 1966; Castellanos, 1967; Forcelli, 2000; Nuñez Cortés and Narosky, 1997).

It is of primary importance to address, for the area of study, the advances and role that Late Quaternary bivalve shells have in the application of morphological variation analyses, and, in turn, the role they may play in palaeoclimate and biogeographical problems linked to sea-level and climate change. Of major importance is to decipher whether the morphometric characteristics of *Brachidontes* recognized within huge samples taken at random can be used as palaeoenvironmental and palaeoecological indicators.

3.1. Taxonomic status of Brachidontes spp.

The taxonomy of *Brachidontes* in Argentina has traditionally been based on the shell characters, e.g. hard parts only. As Klappenbach (1965) and Keen (1971) have shown, individuals of this genus like other mytilid bivalves, are very variable in form, sculpture and colour. Early in the 20th century Jukes-Browne (1905), in his detailed review of the mytilids, pointed out that the shell of *Brachidontes* is characterized by a finely ribbed, but sometimes wrinkled or even smooth outer surface, and a variable position of the beaks. In addition, the anterior margin shows several teeth and the posterior border is either crenulated throughout its length or only behind the ligament (see also Lamy, 1936–37). These features have led to the frequently attempted subdivision into two genera, *Brachidontes* Swainson, 1840 and *Hormomya* Mörch, 1853, which is very difficult to be made consistently. Soot-Ryen (1955) stated that nearly all species of littoral mytilids are variable in outline and colour and that, as many of them have been originally characterized by these features, they are often nearly impossible to recognize and must be considered synonyms, in particular as studies dealing with their potential hybridization are unavailable in most cases.

The same applies to the various species of *Brachidontes* recorded along the modern littoral of South America and to the material recorded from the Quaternary deposits studied (Figs. 1, 2). In fact, it is difficult for geologists and palaeontologists as well as for biologists dealing with the hard parts only, to define the limits between several of the taxa described. According to descriptions and illustrations available in the traditional catalogues, the three species reported from the modern littoral of Argentina and preserved in the marine late Quaternary (*B. darwninianus*, *B. rodriguezi* and *B. purpuratus*) are distinguished by their general shell shape (elongate to globose), shell margins (dorsal margin uniformly convex or angulate; ventral margin convex or sub-concave), outer ornamentation (comarginal growth lines and fine to coarse radial ribs, occasionally bifurcated), colour (brownish, purple or black), number of hinge teeth (a feature generally linked to the age of the specimen) and crenulations along the inner shell margin (in the dorsal margin alone or along the entire periphery) (this feature is related to the thickness of the outer ribs) (Table 1).

For the Atlantic species of *Brachidontes* living in southern South America, which show overlapping geographical ranges (Fig. 1), a detailed study of the ecology and soft parts, especially of the mantle margins, foot, byssal structures, of the retractor muscles of the foot and byssus (of higher systematic value), mtDNA, and nDNA, have not been carried out comparatively, and no information is available regarding a plausible hybridization.

Similar situations apply to close molluscan species with strong morphological similarity and overlapping modern ranges, also in the Cenozoic which have been sorted out by means of bivariate and multivariate biometric analyses of the shell form (e.g., Lozano Francisco et al., 1995, Pliocene; Aguirre, 1994; Aguirre and Urrutia, 2002, Quaternary).

4. Materials studied and methods

The review and update of *Brachidontes* from the marine Quaternary of Argentina is a result of previous studies performed at 36 localities containing molluscan assemblages consisting of more than 120 taxa (Aguirre, 1993a; Aguirre and Farinati, 2000; Aguirre, 2002, 2003) (Fig. 2).

Large samples (≥50 specimens) of fossil (Pleistocene and Holocene) and modern shells of *Brachidontes* collected from the coastal area and littoral zone of Argentina (Aguirre, 1993a,b; 2003; Aguirre et al., 2005, 2006, in press) confirm a wide range of morphological variation. This range includes morphologies assignable to several taxa as illustrated by different authors, of which some could be synonyms. When comparing large numbers of the empty shells (Fig. 4), three main morphs (so-called D, R, P in this paper; Fig. 5A) form a continuum, which includes several of the Atlantic species.

Among the numerous specimens collected (more than 2000) and those examined in museum collections (Appendix A, B), it is equally problematic to select specimens which are undoubtedly assignable to a given taxon. When dealing with material from different localities along wide areas, or even within abundant samples of a certain locality, to correctly and objectively make a conclusive taxonomic discrimination becomes problematic. When huge numbers of shells are compared, they allow specimens described previously as different "species" to be linked together in a chain of transitional forms. The boundaries between all the species described and between the main morphologies analyzed are as difficult to define for palaeontologists and geologists as for biologists which do not study soft parts in detail (i.e., only shells for inventories of oceanographic campaigns) or perform genetic studies

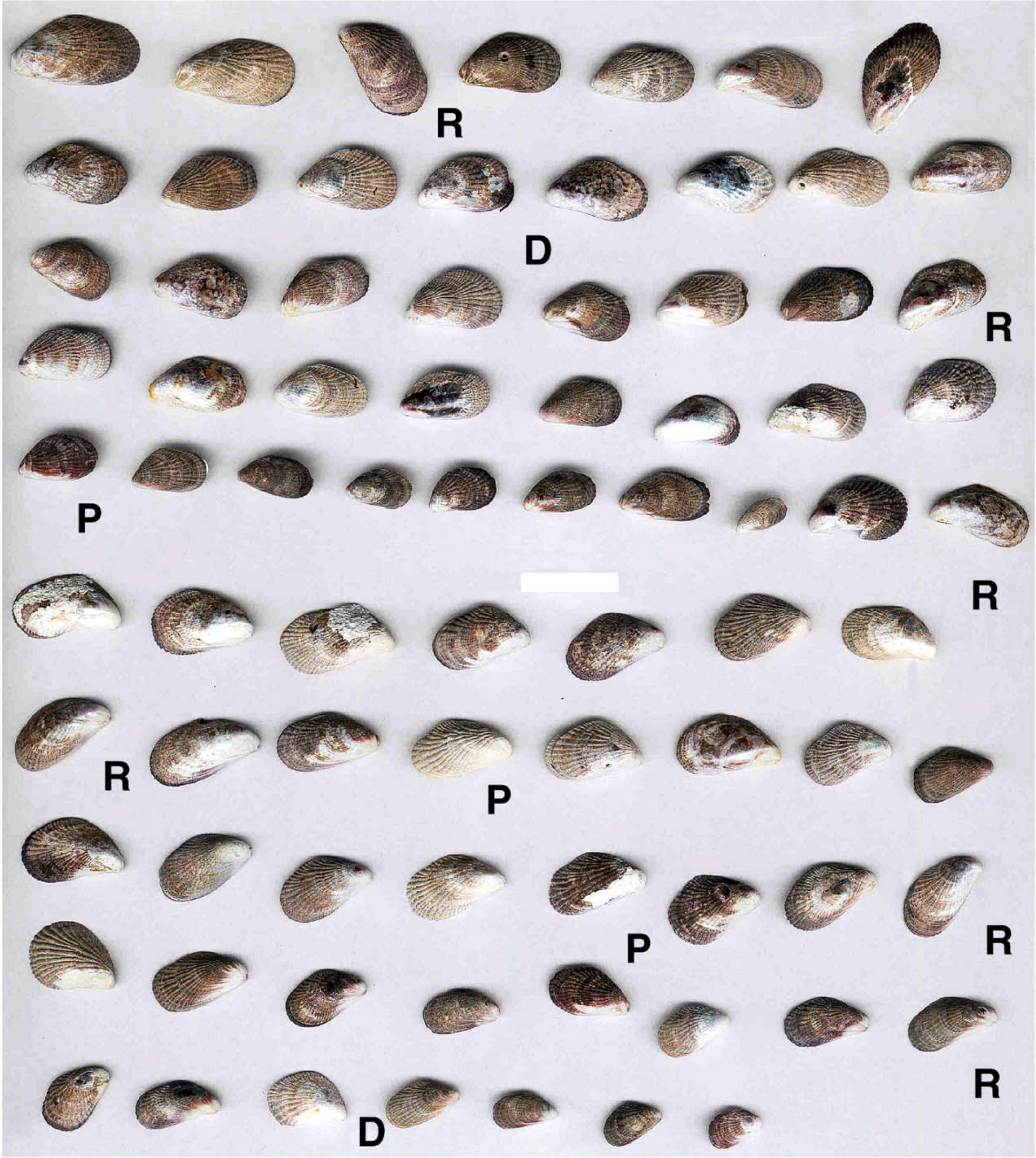


Fig. 4. Morphological variability exhibited by *Brachidontes* spp. from the Argentine littoral and from fossiliferous deposits along the coastal area. Bar = 20 mm. R, D and P are the main morphotypes recognized.

(DNA analyses). This points out the need to test the hypothesis that only a single taxon should be recognized.

Well-preserved shells of *Brachidontes*, exhibiting the intact outline, ornamentation and hinge teeth, from well constrained (geographically and stratigraphically) samples were used for the analyses. Samples were collected at localities of the Argentine provinces of Buenos Aires, Río Negro, Chubut, and Santa Cruz (Fig. 2, Appendix A, B). Fossil shells from the Bonaerensian

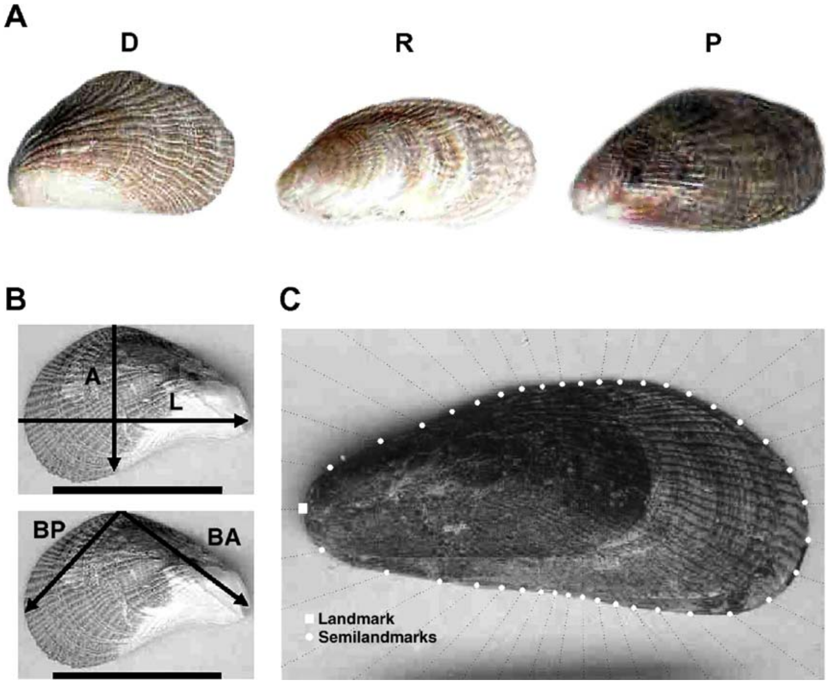


Fig. 5. Material studied, morphotypes recognized, dimensions and images analyzed. A. Main morphotypes recognized within the shell samples studied: D (*B. darwinianus*), P (*B. purpuratus*) and R (*B. rodriguezi*). Not to scale. B. Linear dimensions analyzed. A: dorso-ventral height, L: antero-posterior length, BA: anterior end, PB: posterior end. C. Landmark (■, beak) and semilandmarks (●, shell margin) records.

area are from marginal marine environments. The material studied from Patagonia is entirely from open-ocean environments.

The fossil and modern shells were collected as bulk samples in the field, from beach ridge deposits and estuarine sediments (Bonaerensian area), marine terraces (Patagonian area), and along the modern supratidal, intertidal and upper infralittoral zones.

The fossiliferous deposits were selected on the basis of the best stratigraphic framework available, because they have previously been studied from geological or geochronological standpoints and because they show excellent preservation appropriate for palaeoenvironmental interpretations.

The modern samples were taken from the littoral zone adjacent to the fossiliferous localities and some of them (samples from Mar del Plata and Punta Pardelas) were provided by Dr. R. Bastida and Dr. J. P. Martín, who are carrying out a detailed ecological study of *B. rodriguezi*.

The main reasons to select *Brachidontes* to carry out the morphometric analyses are as follows:

(1) It is a characteristic molluscan component in Quaternary sediments along the coastal area of Argentina and in the modern littoral communities along the Argentine and Magellanean Malacological provinces.
(2) It shows a wide range of morphological variation.
(3) It is generally well preserved, so that various shell characters and their properties can be accurately measured.
(4) It is a valuable palaeoecological indicator, being characteristic of the shallow littoral zone (supratidal to shallow infralittoral), of hard substrates, turbulent waters and normal marine salinity (sometimes polyhaline habitats).
(5) It occurs in Late Pleistocene and Holocene deposits of the Buenos Aires Province and in Patagonia, offering the opportunity to test its use for palaeoenvironmental and palaeoclimatic reconstructions of the different littoral scenarios during former high sea-level episodes.

Subsamples of each morph consist of well preserved shells taken at random, all probably adult specimens (allometric growth affects data, therefore small and large shells were not lumped for the analyses) from the fossil and modern field samples.

The specimens examined, illustrated or measured for this study are housed in the Museo de Ciencias Naturales, La Plata (MLP), Museo de Ciencias

Naturales Bernardino Rivadavia, Buenos Aires (MACN). The type specimens are deposited with the Linnean Society (London), with the Department of Zoology of the Natural History Museum (London), and with the Invertebrate Zoology Department of the Museum of Evolution at Uppsala (Sweden).

As *Brachidontes* is a highly variable genus, which includes species that often vary intraspecifically only in response to environmental conditions (ecophenotypic plasticity; Miner et al., 2005), the hypothesis can be put forth that the morphological sequence is composed of ecomorphs which respond to different environmental controls, for example to latitude (temperature), substrate type, depth, and water energy.

Several authors have explained similar variations (general shell shape, growth, width, proportions of the morphometric parameters, form of the ligament) in bivalve taxa as a response to different environmental conditions (Allen, 1954; Carter, 1967; Thomas, 1975, 1976, 1978; Aguirre, 1994; Trucco, 2001). For example, within the same species, the shells are bigger and thicker in shallow waters and in varied substrates (sand and gravel or pebbles), while more fragile shells are adapted to muddy substrates and deeper waters. Even the relative abundance can depend on the substrate type.

The morphometric characterization of fossil and modern shells applied to highly correlated attributes which best define shell shape (length, height, width, thickness and outline) is useful to improve an objective evaluation of the variability and taxonomic status of *Brachidontes rodriguezi* in the deposits and area studied.

The hypothesis is:

- only one polymorphic species occurred in the Late Quaternary;
- the morphological variation is due to environmental conditions (ecomorphs), not to different taxa.

The alternative hypothesis is

- at least two or more highly variable species occurred;
- stable characters of the shells vary interspecifically and do not correlate with different or local environmental controls.

We acknowledge that the problem concerning the morphospecies recognized by palaeontologists against sibling molluscan species recognized on the basis of modern genetic techniques cannot be discerned by the shell form only.

We also acknowledge that a complementary study should be performed on the soft parts, including the genetic differentiation by modern techniques. These have been applied in the case of the *Mytilus edulis* complex from the SW Atlantic (Trucco, 2001). Modern DNA techniques in combination with classic morphometric studies have been performed in taxa such as *Mytilus edulis*, *Mytilus galloprovincialis* and *Mytilus trossulus*. Several of these studies have shown that, in some cases, morphological differentiation is not evident, hybridization can occur, local adaptation plays a role for maintaining species boundaries, and that some authors still consider them as valid species or subspecies depending on the species concept used (e.g. Beaumont et al., 1989; Seed, 1992; Geller et al., 1993; Comesaña and Sanjuan, 1997; Suchaneck et al., 1997; Borsa et al., 1999; Innes and Bates, 1999; Hayhurst, 2001; Martínez-Lage et al., 2002; Gardner, 2004; Riginos and Cunningham, 2005; Lee and Ó Foighil, 2005; and other references therein). For most evolutionary biologists, however, species of sexually reproducing organisms exist by virtue of reproductive isolation, not phenotypic distinctiveness (Futuyma, 2005).

However, this approach exceeds the possibility faced by palaeontologists and geologists or even for marine biologists dealing with macroevolution problems. Tracing phenotypes through space and time represents a unique contribution of palaeontology to evolutionary biology.

The criteria used in the taxonomic discrimination of *Brachidontes* spp. are based on the morphology of the shell only, within the framework of the palaeontological species concept. Analysis of outer ornamentation and colour is difficult in our material as their preservation differs among samples of different age and occasionally within modern samples from different habitats.

In order to provide objective evidence on how much morphologic variation exists within and among samples of the three main morphs recognized (here called D, R and P), as well as on temporal–geographical groups (age and latitude of the samples), two different approaches were used: traditional morphometrics (Marcus 1990) or multivariate morphometrics (Blackith and Reyment, 1971) and geometric morphometric analysis (Bookstein, 1991; Rohlf and Marcus, 1993; Adams et al., 2004).

The analysis of variation in shell form was performed by breaking down the total variability in size and shape based on the Mosimann proposal (Mosimann and James, 1979; Darroch and Mosimann, 1985; Mosimann, 1988; Bookstein, 1989a), where size is defined as an attribute of a specimen (e.g. geometric mean, centroid size) and the shape analysis (understood as "geometric similarity", implying that shape is preserved among specimens of different size) focuses on shape differences (Bookstein, 1989a; Jungers et al., 1995).

4.1. Traditional morphometrics

From a total of more than 2000 shells collected in the field, a total of 485 very well preserved, whole specimens were measured with a digital calliper in mm.

As a first step, five linear variables (L = maximum antero-posterior length; A = maximum dorsal–ventral height; H = lateral inflation; BA = antero-dorsal length; BP postero-dorsal length) were recorded (Fig. 5b) on all specimens. The geometric mean (GM) of all variables for each individual was used as size indicator (Jungers et al., 1995). The GM is computed as the *n*th root of the product of all *n* variables (Jungers et al., 1995). To obtain the shape variables, the raw variables were transformed in ratios formed by dividing each variable by the geometric mean (GM) of all variables for each individual (i.e., Y/GM; Darroch and Mosimann, 1985; Jungers et al., 1995). A principal component analysis (Hotelling, 1933; Pearson, 1901) was performed to find the linear combinations of the shape variables that have the greatest variance in the data (Marcus, 1990).

4.2. Geometric morphometrics

Digital images of 165 specimens (left valve) were obtained with a scanner Hewlett Packard scanjet 4670 of the external lateral view. Coordinates for one landmark (■, beaks) and thirty-nine semi-landmarks (●, shell margin) were recorded (Fig. 5c). The digital images of the specimens were processed with the MakeFan6 software (Sheets, 2003). MakeFan6 is a tool that places alignment "fans" at equal angular displacements along a curve, to ensure a consistent placement of semi-landmarks coordinates. The coordinates of landmarks and semi-landmarks were registered by means of the tpsDIG 1.40 software (Rohlf, 2004a).

In landmark-based analysis, the shape can be defined as the information left in a figure after location, scale and orientation data are removed (Bookstein, 1991, 1996). Generally, this is done by generalized least square (GLS) Procrustes superposition (Gower, 1975; Rohlf, 1990; Rohlf and Slice, 1990). When the outline coordinates are included in the landmark-based analysis the points in the curves are not claimed to be homologous from subject to subject. Consequently, the variability along tangent directions is not informative and only the coordinate normal to the outline carries information about differences between specimens or groups (Bookstein, 1997; Bookstein et al., 2002). The coordinates of semi-landmarks of the external lateral view of the shell were aligned by means of the sliding semi-landmark method proposed by Bookstein and Green (Green, 1996; Bookstein, 1997). This operation extends the generalized least square (GLS) Procrustes superposition (Gower, 1975; Rohlf, 1990; Rohlf and Slice, 1990): in addition to optimally translating, scaling, and rotating landmarks, the semi-landmark points are slid along the outline curve until they match as much as possible the positions of corresponding points along an outline in a reference specimen (Bookstein, 1997; Bookstein et al., 2002; Adams et al., 2004). In this study the perpendicular projection or minimum Procrustes distance criterion was used to align the semi-landmarks along their respective curves. In this case the coordinates of the outlines are sliding along it, in order to minimize the Procrustes distance between the subject and a reference (view Sampson et al., 1996; Sheets et al., 2004). The centroid size (s_i) of all coordinates for each individual was used as size indicator or scale factor (Bookstein, 1989a, 1991).

For the comparison of the configurations of landmarks and semi-landmarks the relative warps method was used (Bookstein, 1991; Rohlf, 1993). The relative warps are principal component vectors of the partial warps – variables generated for thin-plate spline transformations (Bookstein, 1989b) – and were used to describe the major trends in shape variation among specimens within the sample (for a review on this subject see Rohlf, 1993, 1996). An important aspect of

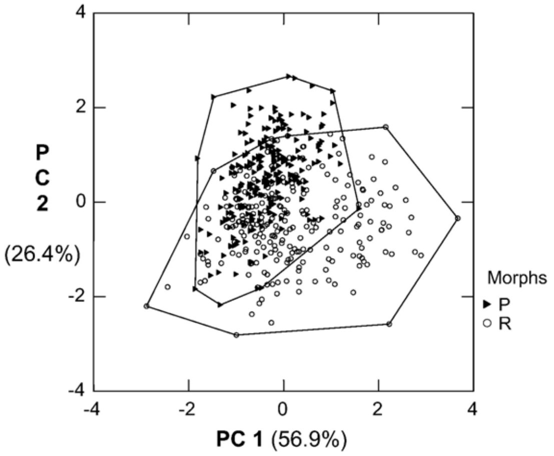


Fig. 6. Scatterplot of the first two principal component axes (analysis based on proportions - shape -) for morphs P (*B. purpuratus*) and R (*B. rodriguezi*). Five linear variables, adult specimens. *N* = 485.

Table 4
Component loadings of principal component analysis of five lineal variables by morphs

Variables	PC 1	PC 2
L	0.061	−0.098
A	0.011	0.024
BA	0.122	0.011
BP	−0.099	−0.051
H	−0.029	0.027

this analysis is that the results of statistical analysis can be expressed as a deformation of each case over the mean form or reference (Bookstein, 1989b, 1991; Rohlf, 1993, 1996). The analyses were performed by means of the Relative warps 1.39 software (Rohlf, 2004b). The uniform and no-uniform component of variation (global and localized change among landmarks and semi-landmarks, respectively) were analyzed in this study (Rohlf, 1993, 1996). The alpha parameter was used with a 0 value, including all scales of variations (view revision in Rohlf, 1993).

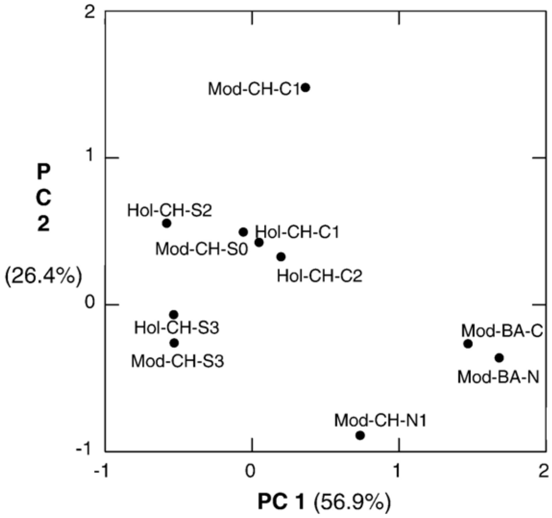


Fig. 8. Scatterplot of scores means, based on geographic–temporal samples, of the first two principal component axes. Five linear variables, adult specimens. Negative values for PC1 correspond to higher latitude. Mod=modern; Hol=Holocene. BA=Buenos Aires; CH=Chubut; N=north; C=central; S=south.

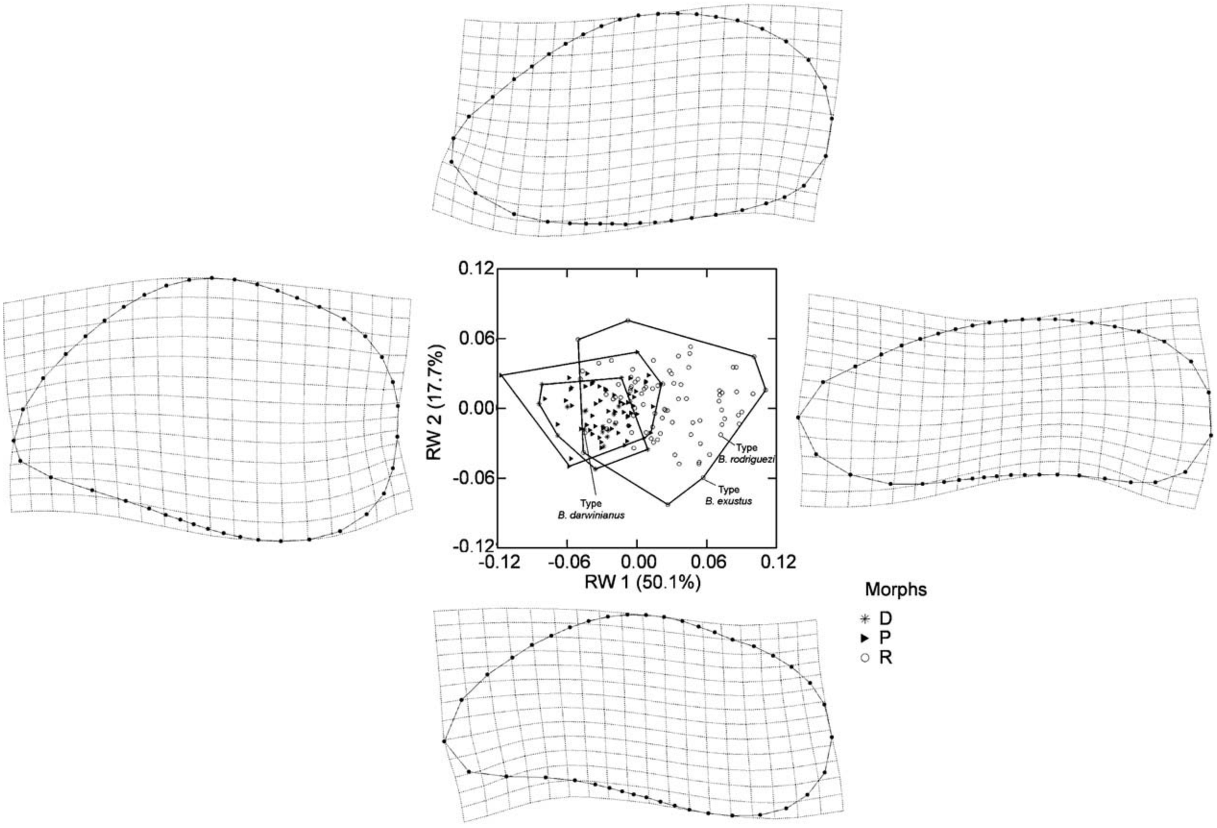


Fig. 7. Scatterplot of the first two relative warps axes for morphs D (*B. darwinianus*), P (*B. purpuratus*) and R (*B. rodriguezi*) and the deformation grids for each axis. Outline co-ordinates, adult specimens. *N*= 165.

Finally, a Pearson correlation and linear regression analysis of the mean first principal component scores and first relative warps scores, as well as a Spearman correlation analysis of the mean centroid size and geometric mean from temporal–geographic groups, were carried out on the latitude variable.

5. Results

Fig. 6 shows the two first principal components axes of the principal component analysis carried out on the ratio variables (linear shape variables), with the cases grouped as traditional "morphotypes" (*R*, *P*). In this figure, morphs greatly overlap and *R* shows greater morphometric variation than *P*. Table 4 presents the component loading for the two components in Fig. 6. *BA* and *BP* are the most related variables with the principal component 1 scores, whereas *L* and *BP* are more closely related with the scores of principal component 2.

Fig. 7 displays the two first relative warps of the analysis performed on landmarks and semi-landmarks, with the cases also grouped by traditional morphs. In this figure, too, the three morphs greatly overlap. In addition, the variation of morph *R*, with the greatest morphometric variation, includes most of the variability of the other morph. The type specimens of *Brachidontes rodriguezi* (d'Orb.), *B. darwinianus* (d'Orb.), and *B. exustus* (Linné) were also included in the analysis for comparison (Fig. 7). They represent extreme morphologies but within the range of variation of the abundant shells analyzed in this study. This figure also exhibits the deformation grids of the negative and positive extreme values of relative warps scores 1 and 2. The grid corresponding to the positive value of score 1 presents compression in both dorsal and ventral margins, as well as an expansion in the anterior and posterior areas. The score 1 grid for negative values exhibits an anterior–posterior compression and dorsal–ventral expansion. Additionally, a local change in the morphology of the dorsal slope and ventral inflexion are observed. The score 1 grid for negative values shows a more globose dorsal slope and a more convex ventral region than the score 1 grid for positive values. Finally, the positive values for score 2 grid shows a positive inflexion in the anterior–basal area, while the grid corresponding to the negative values of score 2 presents a negative inflexion in this area.

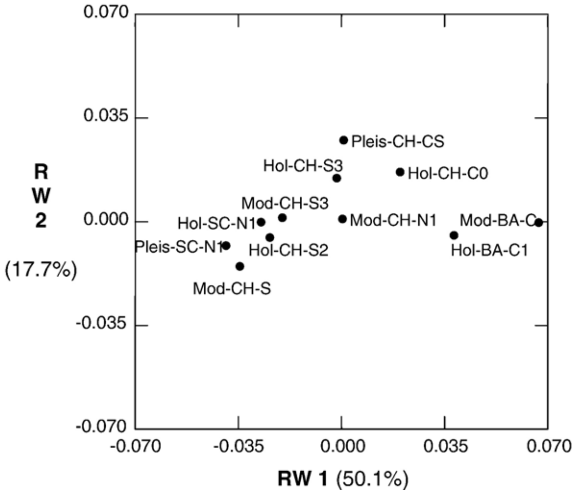


Fig. 9. Scatterplot of scores means, based on geographic–temporal samples, of the first two relative warps axes. Outline coordinates, adult specimens. Negative values for RW1 correspond to higher latitude. Mod=modern; Hol=Holocene; Pleis=Pleistocene. BA=Buenos Aires; CH=Chubut; N=north; C=central; S=south.

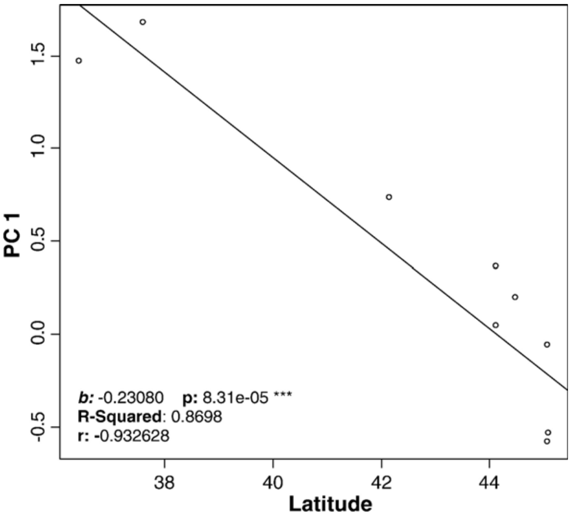


Fig. 10. Linear regression of scores means, based on geographic–temporal samples, of the first principal component axis against latitude and Pearson correlation analysis.

Figs. 8 and 9 illustrate the means for samples grouped by geographic position and temporal period (Pleistocene, Holocene, modern) of the two first principal components and relative warps, respectively. In these figures a latitudinal ordination of the samples can be observed, with little temporal differences. Figs. 10 and 11 show the latitude against the principal component score 1 and relative warp score 1, respectively. A great linear relationship of these shape scores – which explain the main variation axis (approximately 50% of the overall variation) – relative to latitude, as well as a strong correlation (*r*: −0.93) can be observed. The other scores do not show a relationship with the latitude. Figs. 12 and 13 illustrate the latitude against the

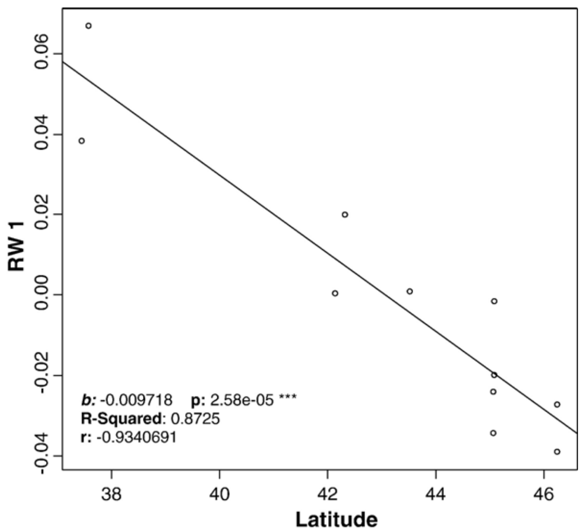


Fig. 11. Linear regression of scores means, based on geographic–temporal samples, of the first relative warps axis against latitude and Pearson correlation analysis.

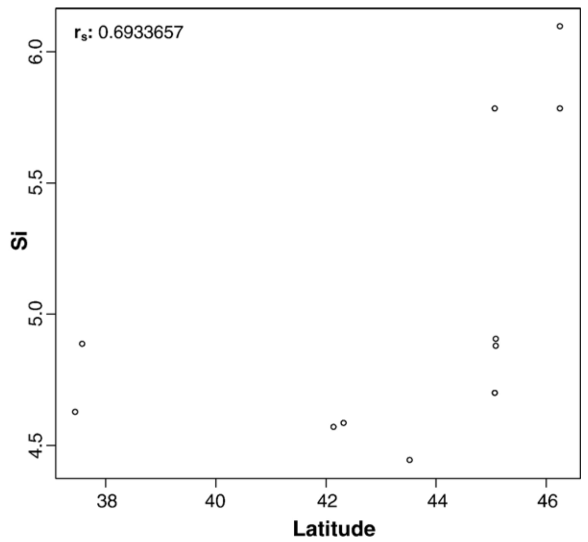


Fig. 13. Scatterplot of centroid size, based on geographic–temporal samples, versus the latitude and Spearman correlation analysis.

geometric media and centroid size, respectively. Only the centroid size shows a strong correlation with latitude ($r_s = 0.69$).

Overall, the results obtained seem to be linked to environmental and/or geographical variations of shell shape. The wide morphological variation of *Brachidontes* shells appears to be strongly related to environmental characteristics of their habitats. For example, Stanley (1970) showed that small shells (less than 20mm in length) of *B. exustus* (Linné) from Puerto Rico, thin, fairly compressed and hooked anteriorly, and ornamented with fine radial ribs, correspond to byssally attached forms living on intertidal rocky substrata. While shells of *B. citrinus* (Röding) from the same area, of similar size (less than 30mm), thin, more elongate and cylindrical in outline, with a straight umbonal ridge and the dorsal margin flared, and ornamented with radial ribs coarsening posteriorly to form serrated valve margins, are most common on subtidal grass flats, living byssally attached to coarse sand, rocks, or coral debris. *B. darwinianus* is very close to *B. exustus*, and *B. rodriguezi* to *B. citrinus*.

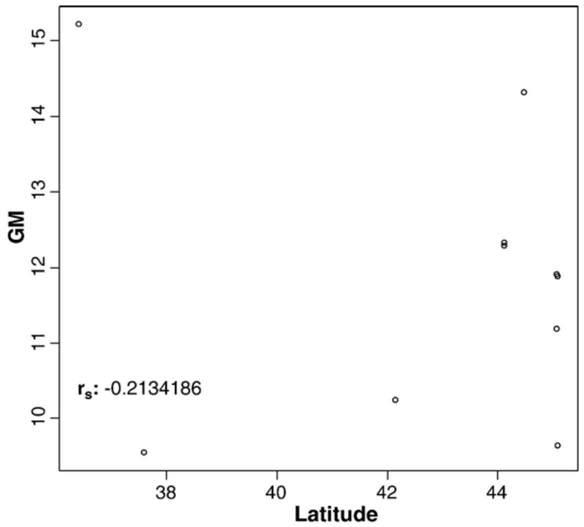


Fig. 12. Scatterplot of geometric mean, based on geographic–temporal samples, versus the latitude and Spearman correlation analysis.

Interpretation of our data must take into account information about the ecology, shell growth, and distribution of *Brachidontes* along the Atlantic coastal area studied.

6. Ecology and shell growth of *Brachidontes* from the SW Atlantic

Brachidontes is a very common epibenthic molluscan component of the shallow littoral communities in the Argentine Malacological Province and in the Magellanean Province. It lives in clusters covering the supratidal zone in the restingas (or sandy zones of marine coastal areas, with small hard elevations and with constant width for long distances, or similar sandy zones between lagoons and the ocean), forming compact shell masses exposed to wave action. *Brachidontes* also lives in the upper and middle intertidal zones, where it can resist extreme exposure intervals.

The biology of *B. rodriguezi*, *B. purpuratus* and *B. darwinianus* in the Argentine littoral is not known in detail, probably due to their low economic value compared to other mytilids of the SW Atlantic (i.e., *Mytilus edulis* Linné, *Aulacomya atra* (Molina)). According to Stanley (1970, 1972), individuals of a closely related species, *B. exustus* Linné, attach themselves by strong byssal threads to hard substrata in crowded clusters, or partially imbed themselves in crevices or cavities, the posterior portions of the shells being exposed, animals generally wedged tightly together, and the posterior end of the shells directed upwards.

Brachidontes rodriguezi is the dominant organism on intertidal rocky substrata in warm-temperate shores of Buenos Aires Province (Argentina) (Penchaszadeh, 1973; López Gappa et al., 1990; Adami et al., 2004). It is a typical epifaunal marine species but may also be found in areas influenced by estuarine waters. Apart from marine habitats, it also inhabits the polyhaline zone of estuaries (Carcelles, 1944; Barattini and Ureta, 1960; Castellanos, 1967; Olivier et al., 1966, 1968, 1972a,b; Scarabino, 1977; Aguirre, 1988; Nugent Rincón, 1989) and brackish waters (at Quequén and Necochea, between Mar del Plata and Bahía Blanca; Fig. 2) (Adami et al., 2004). Generally, it forms large clusters, also with other species (*Mytilus edulis*, *Siphonaria lessoni*, *Diodora* spp, *Fissurella* spp., cirripeds, among others). *B. rodriguezi* is a shallow water indicator; it has not been recovered by oceanographic campaigns off Mar del Plata (Olivier et al., 1968) or along the Argentine continental shelf (Bastida et al., 1992).

B. rodriguezi is known to live byssally attached to hard bottoms, but it can also occur on soft substrates (sand or silt) attached to pebbles, calcareous aggregates or shell debris or any submerged object whereby all specimens of a cluster are attached to each other. In areas where top predators are absent, it has the ability to build up secondary substratum, allowing the development of a rich infaunal assemblage of taxa associated with *B. rodriguezi* (Adami et al., 2004).

Exceptionally the species also occurs partially buried. It exhibits competitive strategies in the occupation of substrates and is highly variable depending on the environmental conditions. Most frequently it is found in the supratidal and intertidal zones and, less abundantly, in the upper infralittoral. It is a suspension-feeder, feeding basically on flagellates and organic detritus in the water column.

In Argentina, *B. rodriguezi* has been discussed in synecological studies performed in Mar Chiquita (Olivier et al., 1968) and its ecology was later studied by Nugent Rincón (1989) for populations from Mar del Plata, where it characterizes the intertidal rocky shore. The vertical zonation of the populations is controlled mainly by two factors, exposure level and topography (water energy). The relative abundance is controlled by wave action.

Topography affects the distribution of the populations and determines locally altered patches of specimens. There is a high correlation between variations in the structure of the (patchy) populations and particular environmental conditions. When competitive exclusion occurs, a spatial escape allows subsistence of forms tolerant of stress and to the most exigent levels of the environment. Among the factors controlling competition are the activity of consumers (predators or herbivores), episodic physical disturbance (i.e., storms) and degree of availability of spatial resources. Competition for space is the main mechanism controlling the structure of these and other intertidal communities.

The relative growth in specimens of *B. rodriguezi* from the intertidal zone at Santa Clara del Mar (ca. 20 km north of Mar del Plata, Buenos Aires Province) was studied by Blanco et al. (1988). According to them, the species is characterized by allometric shell growth, showing a marked trend towards an increase in length and width over height and towards enlarging shell weight. This allometry was shown to be controlled by the general environmental and biogenic conditions (stress by the pressure that close specimens exert on each other) and by substrate. Secondarily, it responds to instability of the intertidal habitat (wave action). Length and width grow isometrically. The greatest variability of the shell dimensions was found to be in width (the stress caused by close specimens on growth in shell width is not uniform). Therefore, crowding strongly affects shell shape.

A greater growth in shell length leads to elongate, subcylindrical shell outline. In turn, a subcylindrical shell form facilitates a burrowing life habit in dense clusters. Another environmental factors controlling the shell proportions is the protection offered by rocks or hard substrates, which influences the lateral growth and most probably serves as a protection mechanism of the shell against abrasion by wave action. A similar allometric pattern has been shown for other mytilids typical of unstable habitats, i.e., *Mytilus edulis* Linné and *Modiolus modiolus* Linné, which modify their dimensions during shell growth according to their proximity to other specimens of the cluster and to the kind of substrate (Seed, 1973; Brown et al., 1976).

7. Distribution of *Brachidontes* in the SW Atlantic

According to their modern geographical ranges the most common taxa from the Quaternary molluscan assemblages in Argentina have been gathered into four groups (Aguirre, 2001): (I), eurythermal or cosmopolitan, (II), warm and warm-temperate species (typical of tropical, subtropical or warm-temperate water masses); (III) taxa of cool-temperate and cold waters (the predominant group, which typically lives in the Argentine or northern Magellanean provinces), and (IV) species exclusive of the Magellanean Province (cold waters).

7.1. Modern records

The traditional Argentine malacological bibliography (i.e., Castellanos, 1967; Ríos, 1994; Nuñez Cortés and Narosky, 1997) indicates that *B. rodriguezi* lives along the SW Atlantic from southern Brazil down to Golfo San Matías and Golfo Nuevo. In contrast, *B. purpuratus* has modern records in cool-temperate and cool waters of the Magellanean Province at both sides of South America (Carcelles and Williamson, 1951; Soot-Ryen, 1955; Guzmán et al., 1998).

These data and synecological studies performed by Bastida et al. (1992) on the Argentine continental shelf, by Nugent Rincón (1989) on the benthic communities of Mar del Plata, at Mar Chiquita by Olivier et al. (1968) and at Puerto Deseado by Bastida and Martín (in prep.), indicate that *B. rodriguezi* and *B. purpuratus* can be considered typical elements of groups II–III and IV, respectively.

Nugent Rincón (1989) considered *B. purpuratus* as a Patagonian vicariant of *B. rodriguezi*. However, in modern samples of *Brachidontes* from Patagonia, collected in the central and southern Chubut Province (Bustamante, Camarones), Santa Cruz Province (Puerto Deseado) (this study), and at Golfo San Jorge (Aguirre, 2003), it is not uncommon to recognize specimens assignable to *B. rodriguezi*. In these same samples, other specimens are intermediate forms between *rodriguezi* and *purpuratus*. In addition, no geographic barrier is apparent along the SW Atlantic southwards of the Río de La Plata. Apart from this, the syntype of *darwinianus* shows close similarity to some of the specimens from Patagonia (*purpuratus*), while the living specimens of *Brachidontes* from Brazil referred to *darwinianus* are closer to *exustus* (Fig. 1).

Altogether, these observations culminate on the main problem: where are the boundaries between the morphotypes? This is crucial for establishing biodiversity patterns and biogeographic ranges of *Brachidontes* spp. along the SW Atlantic.

7.2. Fossil records

The fossil record of *B. rodriguezi* and its synonyms go back at least to the Miocene of Argentina (Borchert, 1901; Del Río, 1991). In the Quaternary of the Argentine coastal area (Aguirre, 2001, 2003), it occurs in Pleistocene and Holocene sediments of the Buenos Aires Province and in Patagonia along Río Negro, Chubut and Santa Cruz provinces. The Pleistocene records are along the Bonaerensian littoral at Punta Indio, Faro Querandí, Arroyo Las Gallinas (Aguirre and Farinati, 2000; Aguirre, 2001); along Patagonia at San Antonio Oeste (Río Negro), Puerto lobos, Camarones, Bahía Bustamante (Chubut). The Holocene records are along the Bonaerensian littoral at Punta Indio, Samborombon Bay, Mar Chiquita, Bahía Blanca, and along Patagonia, at San Antonio Oeste, Puerto Madryn, Puerto Lobos, Camarones, Comodoro Rivadavia, and at Puerto Mazarredo.

The Pleistocene records for *B. purpuratus* are from Bahía Bustamante, Caleta Olivia, Camarones; the Holocene records are from San Antonio Oeste, Puerto Lobos, Puerto Madryn, Cabo Raso, Camarones, Bahía Bustamante, Solano, Comodoro Rivadavia, Rada Tilly, Caleta Olivia, Bahía Lángara, Puerto Mazarredo, Puerto Deseado, Bahía Laura, San Julián, and Tierra del Fuego.

In summary, *rodriguezi* is the predominant morphotype along the Bonaerensian and northern Patagonian modern littoral zone (Argentine province). It was also dominant in this area during the mid-Holocene, but extended as far as about 47–48°S. The morphotype of *purpuratus* characterizes the modern Magellanean Malacological Province (south of 42°S), but was dominant during the mid-Holocene along Patagonia southwards of 47°S. This shows a geographic displacement in comparison with the present biogeographic ranges.

8. Discussion

Our results show that, from a morphometric point of view, the three morphs analyzed cannot be differentiated. The variation observed among the type specimens of *B. rodriguezi*, *B. darwinianus*, and *B. exustus* can be explained by the fact that these represent extreme morphotypes within the whole morphological range as shown in Fig. 7. The major variation in the samples is related to geography (Figs. 8–11). However, the available data do not allow to establish essential chronological differences between most samples from different collection areas (Figs. 8, 9). These results support our working hypothesis. In summary, regardless whether dealing with Quaternary or modern shells of *Brachidontes* from Argentina, it seems more correct to interpret them as intraspecifc variability. The variability pattern could be related to local environmental variations (temperature, substrate, water energy, and depth, secondarily salinity) (ecomorphs).

Although we plotted latitude (x axis) against various form variables (y axis) (Figs. 10–13), probably other factors linked to latitude can stand for the independent variable. Factors such as temperature or bottom type or water energy, which vary latitudinally along the Argentine coast, can be the variables which control the shell morphology. At present, the more globose and bigger morphologies, traditionally assigned to *B. purpuratus* (P), dominate southwards in high energy, euhaline, cold waters of the Magellanean province, on a variety of hard substrates. The more elongate and smaller shells, traditionally assigned to *B. rodriguezi* (R), are most abundant northwards in euhaline and polyhaline warm or warm-temperate waters of the Argentine province, on sandy bottoms with shell debris or dispersed pebbles or rocks. This in turn must be a response to ideal (optimum) space, substrate and feeding resources. As living *Brachidontes* generally wedge tightly together in clusters with the posterior end of the shells directed upwards (Stanley, 1970), a more elongate posterior outline may be related to higher competition for space.

We obtained a strong correlation between shell shape and size (r_s: -0.682) for the same samples arranged geographically. Moreover, these two components of the shell form vary latitudinally (Figs. 10–13). Altogether, the environmental variables interact to define shell form, as supported by studies mentioned above performed on modern *B. rodriguezi* (Blanco et al., 1988) and on other mytilids (Seed, 1968; Brown et al., 1976), in which shape variation depends on habitat conditions, such as the pressure exerted by neighbouring specimens within crowded clusters, substrate type, and wave action.

Apart from these general comments, it is interesting that Fig. 9 displays a temporal difference in the distribution of these morphotypes (elongate or globose) at present versus during the mid-Holocene and the late Pleistocene. Samples PleisCH-CS (Pleistocene specimens from the area between Trelew and Bahía Bustamante) and Hol–CH–CO (Holocene specimens from Península Valdés) show a slight latitudinal shift, southwards of their modern occurrence, suggesting warmer sea surface temperatures than at present. Climate change in the area of study must have been a major factor controlling oceanic circulation and the geographic ranges of *Brachidontes*. Shallow oceanic water currents depend on the seasonal position of the South Atlantic anticyclonic centre, which must have been displaced from the modern pattern several times during sea-level and climate changes of the recent past, for example during the Last Interglacial (ca. 125 ka B.P.) and during the Last Glacial Maximum (ca. 20–18 ka B.P.) (Clapperton, 1993).

The displaced geographic pattern for the mid-Holocene probably shows a biotic response of the littoral biota to the Climatic Optimum (7.6–4.5 ka B.P.) followed by a cooling trend, which determined the modern distribution of shell morphology. The prevailing shell morphology of *Brachidontes* traditionally assigned to morphotype R must have reached as far south as 47°S ca. 5–6 ka B.P. during warmer SST than presently at the same latitude, where shell morphology traditionally assigned to morphotype P is dominant or exclusive. A similar trend in palaeobiodiversity is an independent source of evidence which supports this interpretation, with the highest peak in the north (Bahía Blanca, Mar Chiquita) ca. 8–5 ka B.P. and minimum values after ca. 4.5 ka B.P. and southwards in Patagonia (Santa Cruz Province) (Aguirre et al., in prep.). For the Pleistocene samples, assigned to highstands of MOIS9, 7, and 5 (Table 2), the still scarce chronological control prevents accurate comparisons with the Holocene and modern assemblages. However, records of *B. rodriguezi* in the Pleistocene of Trelew-Bahía Bustamante and at Puerto Deseado (MTV, MOIS7?) could be linked with warmer than present interglacial waters.

Substrate nature, a factor directly linked to water energy and depth within the littoral zone, strongly influences shell form, constraining the number of specimens that are byssally attached in clusters to hard substrates. The more turbulent the environment, the less elongate modern shells are. This applies to fossil specimens as well.

As Trucco (2001) has pointed out regarding latitudinal trends of morphological variation in *Mytilus edulis* Linné along the SW Atlantic, the Río de La Plata could have operated as a drastic salinity barrier for several molluscan taxa of the Argentine province. This barrier probably originated after the Holocene transgressive maximum, when a change in the salinity gradient during a falling sea-level trend along the Río de La Plata outlet led to the present estuarine zonation. At present, at this latitude, euhaline waters (35‰) of the South Atlantic Ocean mix with oligohaline waters from the river and produce an estuarine zone with a polyhaline (18–30‰) gradient. Several molluscan taxa, which live northwards in water masses of similar temperature as the Bonaerensian littoral, could not cross this barrier southwards (Castellanos, 1967). Probably salinity changes may explain the modern distribution of typical R morphotypes, found mostly along littoral marginal marine areas (Punta Rasa, Mar Chiquita, Puerto Quequén, Bahía Blanca, south of Río Colorado in Río Negro Province), and of similar morphotypes of modern *Brachidontes* from the Brazilian coasts (D), while shells of morphotype P inhabit typically euhaline waters southwards along Patagonia.

In summary, the morphological evidence supports the idea that the samples analyzed form a single species. Similar analyses were performed on the *Mytilus edulis* complex. Many authors have considered the common mussels in temperate waters of the northern and southern Hemispheres to be a single cosmopolitan species, *Mytilus edulis* Linné. Others have divided these mussels into several subspecies or species (McDonald et al., 1991). Mussels within the *Mytilus edulis* complex have been divided into three species (*M. edulis*, *M. galloprovincialis*, *M. trossulus*) based on genetic and morphological differences (Koehn, 1991; McDonald et al., 1991). In some of these studies, there was no evidence for interbreeding among genetically distinct individuals in mixed populations, suggesting the possibility that populations may consist of distinct species. However, other, more recent studies have shown that the species within this complex appear to hybridize whenever they come into contact (Skibinski et al., 1978; Costau et al., 1991; Sanjuan et al., 1994; Rawson et al., 1996; Suchaneck et al., 1997; Wilhelm and Hilbish, 1998; Hilbish et al., 2002; Gardner, 2004; other references therein). The hybridization occurs between *M. edulis* and *M. trossulus* (Comesaña et al., 1999), morphological differences between individuals are pure *M. edulis* and *M. trossulus* (homozygous for species-specific alleles at the Pgm and Est loci), while hybrids were small (Innes and Bates, 99).

However, whether or not one interprets the *Mytilus* taxa under consideration to be valid species, *M. trossulus*, *M. edulis*, and *M. galloprovincialis* each maintains unique genetic cohesiveness throughout much of its range and has distinct evolutionary histories (e.g. Mallet, 1995). In several papers authors refer to these taxa as species for convenience, but it is generally recognizing that they could also be considered as subspecies depending on ones' preferred definition of species boundaries (Riginos and Cunningham, 2005).

A similar interpretation could be applicable to *Brachidontes* spp. from the area of this study. A final conclusion on this group should be based on similar studies.

9. Conclusions

The causal factors of phenotype variation within and among species with fossil records can be addressed by morphometric analyses. This study attempts to show the morphological variability of Argentine *Brachidontes* as probable environmental tools, and of the geographical and chronological distribution of the morphotypes identified, mainly through comparisons with the Pleistocene, Holocene and present sea-levels.

This contribution shows once more the great value of studying populations to describe species properly. In most cases lumping of all different taxa in one species is convenient in terms of the palaeontologic species concept and of the implications for palaeobiodiversity and palaeobiogeographic studies.

(1) There is not enough morphometric differentiation among *Brachidontes* spp. of the Argentine marine Quaternary and the modern littoral to recognize different taxa. Most likely, the morphological variation results from spatial environmental heterogeneity.
(2) Differences in form reflect conditions of the local habitats, mainly substrate, temperature, water energy, and salinity.
(3) Our results help to analyze changes in phenotype through space and time as a unique contribution of palaeontology to evolutionary biology. The occurrence and relative abundance of the different morphotypes can be used as palaeoenvironmental tools for the late Quaternary, with implications for interpretations of palaeoclimatic changes, especially since ca. 7.6 ka in the area.
(4) The modern distribution of these morphotypes is a consequence of the last sea-level fall after the mid-Holocene Climatic Optimum. This event, global in extent, caused the present configuration of the atmospheric and oceanic circulation patterns (winds, currents, water masses, which define malacological provinces) and the modern biogeographic pattern of *Brachidontes* spp. in the SW Atlantic.

It is acknowledged that only a few species from a limited area are dealt with in this paper and that final conclusions can only be obtained by increasing the number of samples from the northern Argentine coastal area (where *Brachidontes* is scarcer) and including samples from northern South America (Surinam, Brazil). The validity of their taxonomic status should be based on results of similar multivariate analyses of the soft parts and on an objective genetic differentiation of living specimens. However, our data can be used as valuable tools for quantifying the occurrence of average morphologies in abundant samples of empty shells to reconstruct palaeoenvironments. Clearly, a detailed ecological study of *Brachidontes* spp. from Argentina (Bastida and Martin, in progress) will show in more detail how environmental parameters influence the general shape and other characters of the shell.

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Appendix A

Material examined and studied: A, localities and samples analyzed; B, other collections. MACN: Museo Argentino de Ciencias Naturales “ Bernardino Rivadavia”, Buenos Aires, Argentina. MLP: Museo de La Plata, Argentina.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2006.01.019.

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