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Insights on the history of the scorched mussel *Brachidontes rodriguezii* (Bivalvia: Mytilidae) in the Southwest Atlantic: a geometric morphometrics perspective

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ABSTRACT

Some authors support the idea that an important part of the Miocene marine mollusc fauna is still represented in the Argentinean Province. The fossil mollusc *Brachidontes lepida* (Philippi) is considered a subspecies of the extant *B. rodriguezii* (d'Orbigny), a taxon currently present in the Argentinean Biogeographic Province. The aim of this study is to investigate the shell shape relationship between *B. lepida* and *B. rodriguezii* using geometric morphometrics. Samples of *B. rodriguezii* ($n = 63$) from four localities distributed in Uruguay and Argentina, of *B. lepida* from the Paraná Formation ($n = 26$) and of two other extant Brachidontinae present in the region were included in this study. Canonical variate analyses showed that extant species differed in shell shape, with the discriminant function properly allocating 93% of the individuals to their respective species. Using the extant discriminant function, approximate 92% of *B. lepida* individuals were allocated to *B. rodriguezii*. This result suggests that *B. lepida* is more similar in shell shape to *B. rodriguezii* than to the other extant species present in the region. Considering the material from the Pliocene of Cerro Laciár and from the Pleistocene deposits of Buenos Aires and Bustamante, the presence of *B. rodriguezii* from the Late Miocene in the warm temperate region is discussed.

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Introduction

Different biogeographic patterns are represented in the South American scorched mussels of the genus *Brachidontes* s.l. (Bivalvia: Mytilidae). Genetic evidence supports a close relationship of the southernmost species, *Perumytilus purpuratus*, with an Australian species, *Austromytilus rostratus*, and likely involving dispersion of a common ancestor through the Antarctic Circumpolar Current following the breakup of Australian, Antarctic and South American shelves (Trovant et al. 2015). *Brachidontes solisianus* (Brazil), exhibits instead a pattern of antitropicality with *B. exustus* I (sensu Lee & O'Foighil 2005) (Gulf of Mexico and the Caribbean), a pair of species distributed northwest and southeast to the combined plumes of the Amazonas and Orinoco Rivers (Trovant et al. 2016). Finally, the last pattern which is investigated herein corresponds to Regional Ancestry and is inferred for *B. rodriguezii*, a warm-temperate species of the Argentine Biogeographic Province and the Late Miocene taxa.

The marine transgression known as 'Entrerriense' or 'Paranense' took place during the Late Miocene and covered a large part of South America. The southernmost arm of this sea extended from northern Patagonia northwards to the Chaco-Paranense Region and along the Atlantic coast, from 50 km south of Puerto Madryn northwards to southern Brazil (Scasso & del

Río 1987). Its sedimentary deposits in Patagonia are known as Puerto Madryn Formation Haller 1978. The exposures on the left margin of the Paraná River were included in the Paraná Formation Yrigoyen (1969) and those outcrops in the southern coast of Uruguay in the Camacho Formation Goso and Bossi (1966). Based on the distribution of the genera and species found in these lithostratigraphic units, Martínez and del Río (2002a) recognized two Late Miocene Molluscan Provinces named as the Valdesian Province (extending from Península Valdés, Chubut Province (42° S) to the Salado Basin, Buenos Aires Province (37°–39° S)) and the Paranaian Province (extending northwards along the coast of Uruguay and southern Brazil). These two Provinces, comprising mainly cosmopolitan and Caribbean elements (del Río 1990) or paratropical warm-water genera (Martínez & del Río 2002a), coincide geographically with the region currently covered by the Argentinean Biogeographic Province.

Recent marine bivalve species may have evolved regionally as endemics from the Neogene faunas, which would particularly apply to the warm-temperate species related to the Late Miocene fossil taxa. Some authors (e.g. Aguirre & Farinati 1997; Aguirre et al. 2008) support the idea that an important part of the Miocene marine molluscs is still represented in the Argentinean Province, while others (del Río 1990, 2000; Martínez & del Río 2002b) suggest that only 8% of the Miocene species survived

in the Southwestern Atlantic Ocean (Argentine Biogeographic Province). This suggests that the Valdesian and Paranain Provinces could not have given rise to the present (geographically equivalent) Argentine Province. Moreover, the southern edge of the distribution of nearly 54% of the typical ‘Entrerriense’ genera contracted. Despite this general biogeographic pattern, some modern species inhabiting the region could be related to the Late Miocene fauna. A case in point is *B. rodriguezii* (d’Orbigny), which is distributed in the Argentinean Biogeographic Province (Scarabino 1977; Scarabino et al. 2006) and is possibly related to *Brachidontes lepida* (Philippi 1893), a fossil present in the Paranaian (Paraná Formation, del Río 1991), prompting the hypothesis that *B. rodriguezii* could have evolved from a Miocene taxon. The evaluation of this hypothesis requires an approach that uses both paleontological and morphological data.

Geometric morphometrics (GM) allows to quantify the change in the form of individuals with respect to a reference shape (Rohlf & Marcus 1993) and the results can be displayed graphically, since the implicit nature of the geometric information form is not lost during the statistical analyses (Richtsmeier et al. 2002; Adams et al. 2004). GM is an appropriate method to distinguish among groups of bivalve molluscs (Rufino et al. 2007). Early studies of GM in bivalves generally used methods based on the shell shape outline by means of elliptic Fourier analysis (Ferson et al. 1985; Innes & Bates 1999; Krapivka et al. 2007; Márquez & Van Der Molen 2011), while most current studies use different types of landmarks or a combination of both approaches (Palmer et al. 2004; Rufino et al. 2007; Sousa et al. 2007; Márquez et al. 2010; Signorelli et al. 2013). Both techniques have been applied to differentiate species of the small mussels of the genus *Brachidontes* (Aguirre et al. 2006; Van der Molen et al. 2013). In the present study, we examine the shell shape relationship between *B. rodriguezii* and *B. lepida*, using geometric morphometrics. We hypothesize that *B. rodriguezii* is more similar in shell shape to *B. lepida* than to the other Brachidontinae species present in the region.

Material and methods

Samples

Extant taxa

Specimens of *B. rodriguezii* were collected from four localities along the southwest Atlantic coast: Punta Ballena (Uruguay), Santa Clara del Mar, Mar del Plata and Bahía San Blas (Argentina) ($n = 63$, Table 1, Figure 1), *Brachidontes darwinianus* from three localities in Brazil and Uruguay ($n = 42$, Table 1) and *P. purpuratus* from three localities along the coast of Argentina ($n = 58$, Table 1). In addition, images of the type material of *B. rodriguezii* and *B. darwinianus* d’Orbigny provided by the British Natural History Museum (NHMUK) were included (Figure 1). The type material of *P. purpuratus* Lamarck according to Soot-Ryen (1955) is missing.

Miocene records

The fossil material identified by del Río (1991) as *B. rodriguezii* *lepida* of the Late Paraná Formation is listed in Table 2. Based on the preservation of the material, 26 shells were selected and included in the analysis. According to del Río (1991) the original

Table 1. Sampling localities of extant mussel species used in this study.

Species	Locality	Latitude/longitude
<i>Brachidontes rodriguezii</i>	Punta Ballena, UY	34° 53’ S, 55° 02’ W
	Santa Clara del Mar, AR	37° 50’ S, 57° 30’ W
	Mar del Plata, AR	37° 58’ S, 57° 35’ W
<i>Brachidontes darwinianus</i>	Bahía San Blas, AR	40° 32’ S, 62° 15’ W
	Bahía de Ihleus, Bahía, BR	14° 47’ S, 39° 01’ W
	Montevideo, UY	34° 51’ S, 56° 09’ W
<i>Perumytilus purpuratus</i>	Punta Ballena, UY	34° 53’ S, 55° 02’ W
	Camarones, Chubut, AR	44° 47’ S, 65° 43’ W
	Puerto Deseado, Santa Cruz, AR	47° 44’ S, 65° 53’ W
	Bahía Ensenada, Tierra Del Fuego, AR	54° 49’ S, 68° 15’ W

description of the species (Philippi 1893) was based on material that came from the Bravard collection, but later the type material was lost in the Natural History Museum of Chile. Other related fossil materials of different geological ages were examined and are detailed below.

Other Paleogene-Neogene records

In addition, other fossil material older than *B. lepida* deposited at the Museo Argentino de Ciencias Naturales B. Rivadavia (MACN) has been examined: MACN 4271, ‘*Modiolus*’ sp. from the Salamanca Formation exposed at Río Chico, Chubut (Early Danian), two shells (one complete and the other broken) of the Wichmann Collection; MACN 313, ‘*Brachidontes*’ *andina* Ortmann 1900 from Lago Pueyrredón (Late Oligocene – Early Miocene), two internal casts of the von Ihering Collection. Also, the description and illustration of *B. ortmanni* (Chiesa et al. 1995) collected south to Lago Salitroso (Santa Cruz Province) were examined. Moreover, we obtained good quality images of two specimens identified as *Mytilus purpuratus* Lamarck (MACN-Pi 314, Figure 5) from the Pliocene horizons of Patagonia, collected by Carlos Ameghino in the surroundings of Cerro Laciár (Santa Cruz Province), described by von Ihering (1907) and later, included in a complete list compiled by Feruglio (1933a, 1933b, 1950).

Quaternary records

In regard to the Quaternary records of *B. rodriguezii* from Buenos Aires Province, we obtained good quality images from the Invertebrate Paleontology Collection of the Academy of Natural Sciences of Drexel University (ANSP 73,476, 30,907, 74,132; Richards & Craig 1963). One of the lots (ANSP 30,908) was given to Lamont Doherty Earth Observatory of Columbia University in 1963 (Curator John Sime pers. comm.) and it could not be examined. The Quaternary reference materials of this species cited by Rutter et al. (1990) from the terraces of Bahía Bustamante were lost (Rutter pers. comm.). We did not have access to the material cited by Aguirre et al. (2005). We thus collected new material of the molluscan assemblages from the Quaternary terraces of Bahía Bustamante (Chubut Province, Nov 2014). All collected scorched mussels are listed (Table 3).

Morphometric analysis

The interior side of the fossil shells was covered by sediment and the muscle scars were not visible, so we decided to use the

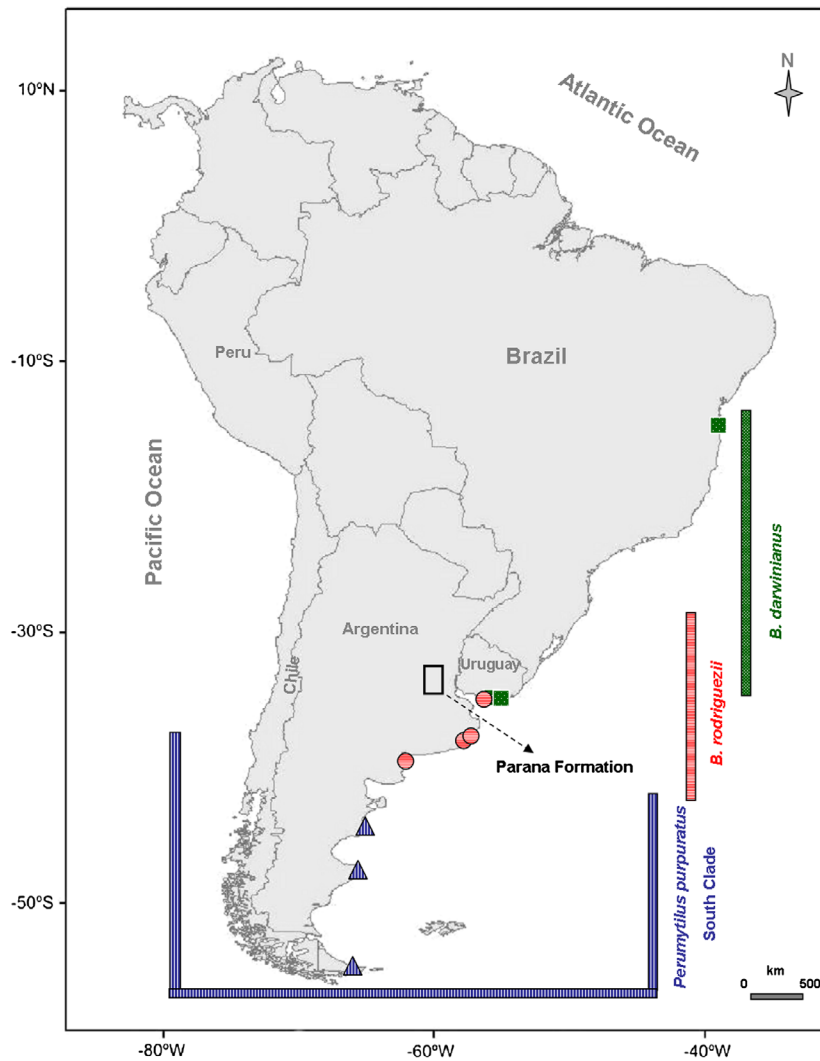


Figure 1. Distribution and sampling localities of the mussel species used in this study, green/square: *B. darwinianus*, red/circle: *B. rodriguezii* and blue/diamond: *P. purpuratus*.

Note: The rectangle indicates the origin region of the fossil material (Paraná Formation).

Table 2. Fossil materials identified as *B. lepida* from the Paraná Formation deposited at the 'Museo Argentino de Ciencias Naturales' (MACN).

Repository	Label	Specimens
4988	<i>Brachidontes (Brachidontes) rodriguezii lepida</i> (Philippi), Mioceno Form. Paraná Entre Rios, Paraná, Col Bravard	13 shells (6 complete + 6 with only one shell complete + 1 with the two shells broken) label #: 112, 4988
4992	<i>Brachidontes lepida</i> , Col Bravard	15 shells (6 complete + 9 broken), label #: 112, 121, 571, 577, 580, 583
4991	<i>Brachidontes lepida</i> , Col Bravard	9 shells (5 complete + 4 broken) label #: 112 + 579, 112 + 598, 112 + 587, 112 + 589, 112 + 598, 112
4990	<i>Brachidontes (Brachidontes) rodriguezii lepida</i> (Philippi), Col Bravard	6 shells (5 broken + 1 complete), label #: 112, 4990
4989	<i>Brachidontes (Brachidontes) rodriguezii lepida</i> (Philippi), Mioceno Form. Paraná, Entre Rios, Paraná, Col Bravard	7 broken shells, label #: 112, 4989

outside of the shell. In the case of living taxa, all soft tissues were removed. The outside of the right shells from all the material (fossil and living taxa) was photographed with a Nikon D100 digital camera. The shell shape of specimens were captured by the Cartesian coordinates of a two dimensional configuration of four anatomical landmarks and 40 semi-landmarks, via TPSdig2 (Rohlf 1996) by one observer (F.M.). The landmarks and semi-landmarks configuration (Figure 2) used was as follows: (1) umbo (anterior end), (2) change of curvature on the ligament, (3) maximum posterior curvature, (4) projection at 90°

of the vector formed between the landmarks 1 and 2 on outline of shell, (5–14) semi-landmarks along the boundary between the landmarks 1 and 2, (15–24) semi-landmarks between landmarks 2 and 3, (25–34) semi-landmarks between landmarks 3 and 4, and (35–44) semi-landmarks between landmarks 4 and 1. To remove rotation, translation and scale effects landmark configurations were superimposed by generalized Procrustes analysis (Rohlf & Slice 1990; Slice et al. 1996) in the TPSRelw software. Also, this program offers an algorithm which allows relaxing the semi-landmarks along the contour tangents to minimize the

bending energy until they fit a reference configuration (Bookstein 1991). The Procrustes coordinates of the aligned individuals were then used as shape variables to perform the next multivariate statistical analyses. To assess and control putative allometric effects, we computed the multivariate regression of shape (dependent variable) on size (independent variable). The Centroid Size (CS) is used in GM as a proxy for size and is calculated applying the square root of the sum of the square distances from the landmarks to the centroid which they define (Zelditch et al. 2004). Klingenberg (2008) suggested that such regression is useful for the detection and removal the size effect, age or environmental factors before shape comparisons between groups. To evaluate the independence between the shape and size variables, we carried out a permutation test with 10,000 iterations.

The principal components of shape were calculated from a principal component (PC) analysis of the variance–covariance

matrix of the Procrustes coordinates of the aligned individuals to display the major features of shape variation along the axes. In order to capture axes of maximum discrimination among extant form groups, and calculate the discriminant function, a canonical variate analysis (CVA) on the first PCs was computed. Then, this previously defined discriminant function was used to assign the fossil individuals to the extant species, without group information. The same statistical analyses were used by Van der Molen et al. (2013) to assign individuals from the transition zone between *B. rodriguezii* and *P. purpuratus*. Only the first, most informative, PCs were used to accomplish the ‘rule of thumb’ of discriminant analysis which indicates that the sample size of the smallest group (*B. darwinianus*, $n = 42$) needs to exceed by large amounts the number of predictor variables (44 2D landmarks = 84 shape variables or PCs). We used a re-sampling procedure (the leave-one-out-cross-validation) to estimate the percentage of misclassification to each site (Johnson & Wichern 1998).

Table 3. Study material of *Brachidontes* spp. collected from the Pleistocene terraces in the area between Bahía Bustamante and Camarones (Chubut Province).

Terrace	Latitude	Longitude	MASL	Specimens	Remarks
IV	45° 08'	66° 36'	20	24 valves	Punta Malaspina
V	45° 08'	66° 36'	22	4 valves	Punta Malaspina
V	44° 48'	65° 44'	12–20	6 complete + 183 valves	Camarones
V	45° 07'	66° 35'	22	2 valves	Punta Malaspina
V	45° 03'	66° 28'	20	47 valves	North of Ea. La Ibérica

Results

The multivariate regression of shape on centroid size was statistically significant (permutation test with 10,000 random permutations, $p = 0.0019$) and accounted for the 2.4% of the total amount of shape variation indicating evidence of allometry in the samples. However, for subsequent analyses, we used the regression residuals as new allometric-free shell shape variables. In the principal component analysis, the first 3 PCs explained almost 87.76% of the total variation, the other PCs accounted for $\leq 5\%$ of the total variance and were ignored (Zelditch et al. 2004; Balzarini et al. 2008) (Figure 3). Shell shapes of the extant

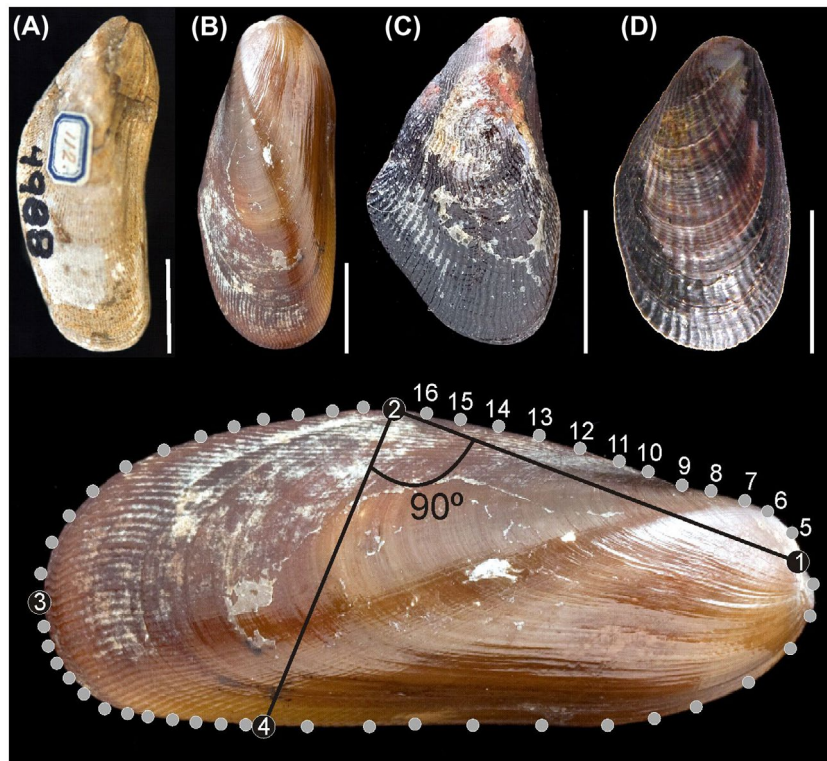


Figure 2. Miocene fossil material and extant mussels species used in this study. Top, external view of the shell of (A) *Brachidontes lepida*; (B) *B. rodriguezii* syntype; (C) *B. darwinianus* syntype and (D) *Perumytilus purpuratus* (South Clade). Below: configuration of landmarks and semi-landmarks on the outline of the shell.

Note: Bar: 1 cm.

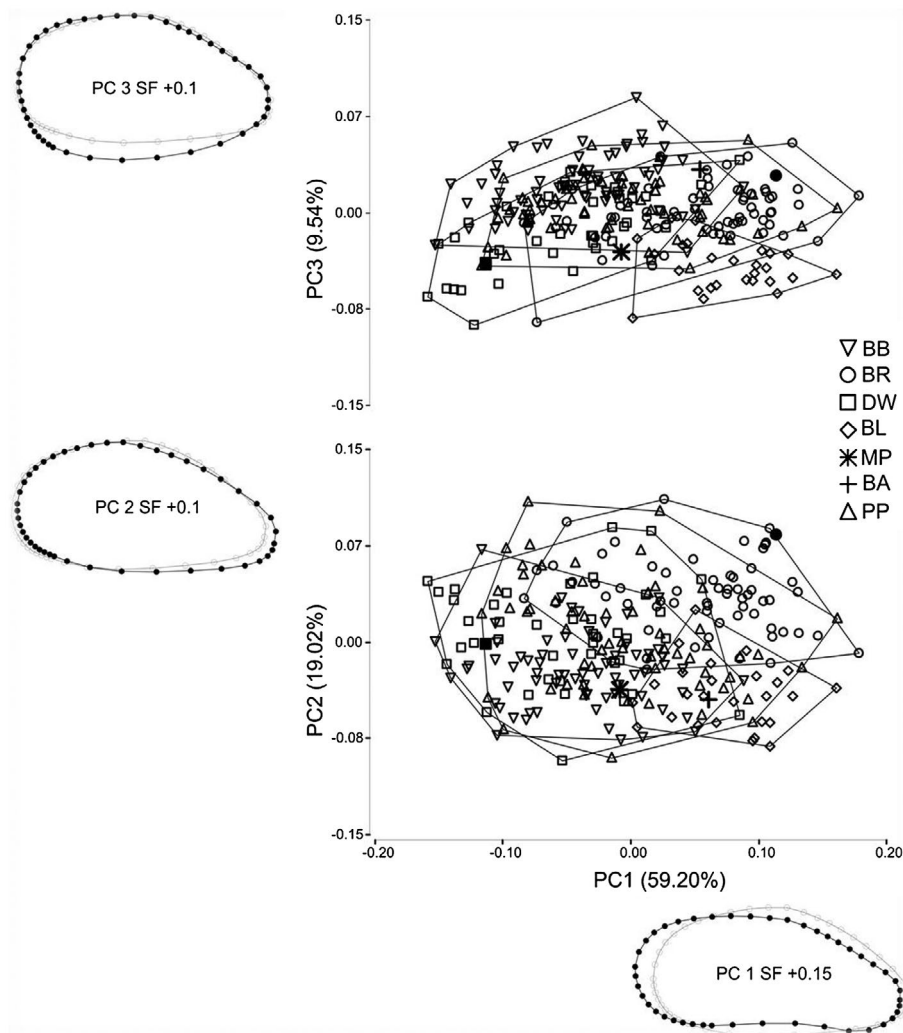


Figure 3. Plot of the principal components (PCs) based on allometric-free shell shape variables.

Notes: The figures represent the transformation and displacement vectors from the overall mean shape (light grey outline and grey dot) to the positive extreme shape (black outline and dot) for each PC. (Lower) PC1 versus PC2 and, (Upper) PC1 versus PC3. Percentages of explained variance for each axis are in parentheses. Circle (BR): *Brachidontes rodriguezii*, square (DW): *B. darwinianus*, diamond (BL): *B. lepida*, triangle (PP): *Perumytilus purpuratus*, star (MP): *Mytilus purpuratus* (Pliocene), inverted triangle (BB): Bustamante materials (Pleistocene) and cross (BA): Buenos Aires materials (Pleistocene). The species syntypes are represented by the symbol of the corresponding species but solid.

and fossil species were generally overlapping (Figure 3). The geometrical interpretation of the positive extreme of the PC1 (59.20% of the total variation) was associated to elongated shells with subterminal umbos. The positive extremes of the second PC2 (19.02% of the total variation) and third PC3 (9.54% of the total variation) axes were related to the elongation of the umbo and to a more globular shell shape, respectively.

Only the first 10 PCs, which accounted for 98.2% of the total variance, were used to compute a CVA. The shell shape variations among the three extant species were successfully discriminated using CVA (Figure 4). The geometric interpretation of canonical axis 1 (CV1) was associated with umbo position and the amplitude of the shell (similar to the relationship between height/length). In the positive extreme of the axis, *B. darwinianus* shows a terminal umbo and a compression in anterior-dorsal and ventral direction, generating a sub-triangular shell with a anterior-ventral curve slightly inward, while in the negative extreme values, *B. rodriguezii* exhibits a sub-terminal umbo and a compression in dorsal-ventral direction, generating an elongated shell with a anterior-ventral convex curve (Figure 4). The

CV1, which explains most of the variance (67.52%), separates *B. rodriguezii* from *B. darwinianus* leaving *P. purpuratus* at an intermediate position. The CV2 (32.48%) was associated with the curvature of the dorsal region of the shell; on the positive values are *B. darwinianus* and *B. rodriguezii* with a straight anterior dorsal and a rounded dorsal posterior regions, while on the negative values is *P. purpuratus* exhibiting a rounded dorsal anterior and a straight posterior dorsal regions (Figure 4). The syntype of *B. rodriguezii* was within the variation of the species and the same happened with the syntype of *B. darwinianus* (Figure 4).

On average, the discriminant function correctly allocated 90.18% of the extant form individuals. While approximate 92% of *B. lepida* individuals were allocated to *B. rodriguezii*, only 8% was assigned to both *B. darwinianus* and *P. purpuratus* (Table 4). The Pliocene material identified as *M. purpuratus* (Figure 5) from Cerro Laciari, was assigned to *P. purpuratus* and the Pleistocene material from Buenos Aires was assigned to *B. rodriguezii*. Almost 90% (88.06%, $n = 59$) of the Quaternary material of Bahía Bustamante (Chubut) was allocated to *P. purpuratus*, and only 11.94% to *B. darwinianus*.

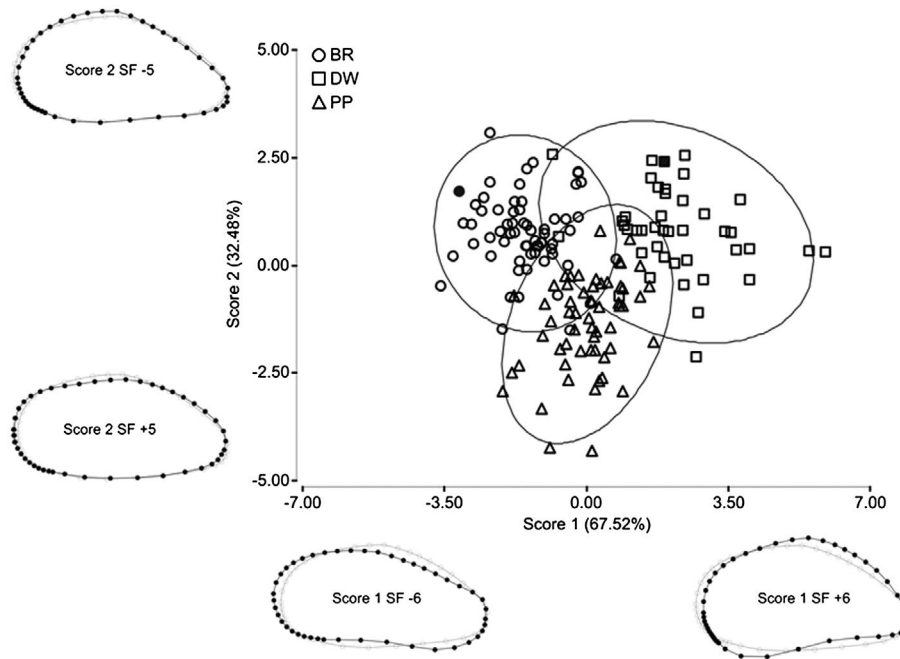


Figure 4. Canonical Variate Analysis of the maximum overall shell shape variation of extant form small mussel species along the first two canonical axes.

Note: Circle (BR): *Brachidontes rodriguezii*, square (DW): *B. darwinianus*, and triangle (PP): *Perumytilus purpuratus*. The species syntypes are represented by the symbol of the corresponding species but solid.

Table 4. Cross classification table, showing number of individuals successfully assigned to each extant form species and error percentages.

Group	Extant species				Error (%)	Fossil materials			
	<i>B. rodriguezii</i>	<i>B. darwinianus</i>	<i>P. purpuratus</i>	Total		Pliocene <i>M. purpurata</i>	Miocene <i>B. lepida</i>	Pleistocene (Buenos Aires)	Pleistocene (Bustamante)
<i>B. rodriguezii</i>	58	1	4	63	7.94	–	24	1	0
<i>B. darwinianus</i>	2	38	2	42	9.52	–	1	–	8
<i>P. purpuratus</i>	2	5	51	58	12.07	1	1	–	59
Total	62	44	57	163	9.82	1	26	1	67

Note: The classification from discriminant function of the fossil individuals are showed in the last column.

Discussion

The geometric morphometric analysis differentiated the three extant species included in this study, *B. rodriguezii*, *B. darwinianus* and *P. purpuratus*, assigning nearly all individuals correctly.

Aguirre et al. (2006), using a different landmark and semi-landmark configuration, found no differences between *B. rodriguezii*, *B. darwinianus* and *P. purpuratus*. They suggested that *B. rodriguezii* and *B. darwinianus* could be considered synonyms of *P. purpuratus*. However, the findings of the current study do not support the previous research. Coincidentally, quantitative observations from an outline analysis (Fourier analysis) by Van der Molen et al. (2013), qualitative observations of morphological characters by Adami et al. (2013); and molecular analysis by Trovant et al. (2013) provided independent evidence that *B. rodriguezii* and *P. purpuratus* are different species.

Miocene records

The majority of *B. lepida* individuals (92.30%, $n = 24$) were assigned to *Brachidontes rodriguezii*. This shell shape evidence supports the conclusion that *B. lepida* is more similar to *B. rodriguezii* than to the other extant species present in the region. *B. rodriguezii* and *B. lepida* are also similar in some qualitative

characters considered to be symplesiomorphic among taxonomists. A shared phenotypic character between *B. lepida* and *B. rodriguezii*, upon which these species were considered related, is the expansion of the front edge of the shell, ventral with respect to the umbo, which provides them a ‘modioliform’ aspect. This character is present in very few living Brachidontinae, including *Geukensia*, which prior to the availability of molecular sequences (Distel 2000) was traditionally considered a member of the Modiolinae, and in at least two living species of *Brachidontes*: in *B. rodriguezii* as previously noted and in *B. modiolus* (Linnaeus 1767). There is molecular evidence showing that this last species, from the Northwest Atlantic and the Caribbean region, is not closely related to *B. rodriguezii* (Trovant et al. 2016). Notwithstanding the results, it would be interesting to investigate the relationship between *B. lepida* and *B. modiolus* by the strong resemblance of their shell shapes, previously highlighted by Genta Iturrería (2014). On the other hand, the more parsimonious hypothesis would be that *B. lepida* is related to some of the extant species present in the South-western Atlantic region. This relationship is unlikely in the case of *P. purpuratus* with a distribution pattern associated with a Trans-Pacific connection (Trovant et al. 2015) or *B. darwinianus*, an estuarine species, which does not share with *B. lepida* the modioliform aspect or the quantitative characters analyzed in this study.



Figure 5. Pliocene Fossil Material identified as *Mytilus purpuratus* Lamarck (MACN-Pi 314 (Santa Cruz Province).

Other Paleogene-Neogene records

Interestingly, there are several, though fragmentary, fossil records of scorched mussels from Patagonia older than *B. lepidoides*, with a modioliform aspect, which apparently correspond to Brachidoninae: *B. ortmanni* Chiesa, Parma and Camacho 1995 (Santa Cruz Province) and ‘*Brachidontes*’ *andina* Ortmann 1900 (Lago Pueyrredón), both from the Centinela Formation (Late Oligocene-Early Miocene) and material identified as ‘*Modiolus*’ sp. from the Salamanca Formation, exposed at Río Chico (Chubut Province) (Early Danian, Late Paleocene). Later, ‘*Brachidontes*’ *andina* was placed in *Gregariella* by Griffin and Nielsen (2008). We examined the material of this last species but its identification is difficult. The material identified as *Modiolus* sp. strongly resembles *B. lepidoides*. Nonetheless, the comparative study of this series of records and their possible relationships are beyond the scope of this study.

On the other hand, the poor representation of the Pliocene deposits in the Southwest Atlantic coast (del Río et al. 2013) makes the study of the connections between the well represented Late Miocene marine fauna and the extant biota difficult. The only Pliocene material available of Brachidoninae comprises two valves described by von Ihering (1907) as *Mytilus purpuratus* (Figure 5) and collected by C. Ameghino in the area surrounding Cerro Laciari. While the geometric morphometrics assigned them to *P. purpuratus*, the inspection of species-specific characters from photographic images suggests these specimens do not correspond to *B. rodriguezii* or *P. purpuratus*, while the geometric morphometric analysis assigned them to *P. purpuratus*.

Quaternary records

Quaternary of Bahía Bustamante, Chubut Province

Brachidontes rodriguezii has been mentioned in the Quaternary fossil record with a rudimentary illustration (Rutter et al. 1990; Aguirre et al. 2005, 2006) in Terrace IV (according Feruglio 1950; ‘terminology’) exposed at Bahía Bustamante coastal area (MIS 7 or even older, >190–240 Ky Pleistocene, according to these authors),



Figure 6. *Perumytilus purpuratus* from the Pleistocene of Bahía Bustamante (Punta Malaspina, Chubut province; see Table 4 for more information).

Note: The arrows indicate some of the diagnostic characters of *Perumytilus purpuratus*: in the external view, the terminal umbo and the thick ribs; and in the internal view, the calcareous tube-shaped structure, in this specimen is broken.

but, unfortunately, supporting materials have been lost (N. Rutter, pers. comm.) and this assertion cannot be verified. A careful sampling of molluscan assemblages performed in the Quaternary terraces of Bahía Bustamante by our team, provided specimens to demonstrate that the phenotype of this scorched mussel corresponds instead to *Perumytilus purpuratus* (Table 4; Figure 6). The material presented assorted sizes and shapes, although all specimens share the following diagnostic characters identified by Olsson (1961) and Adami et al. (2013): in each valve, an expansion of the inner shell layer continuous with the hinge plate, which becomes encased in a quasi-tubular calcareous structure that extends forward underneath the hinge plate. The posterior end of this calcareous wrapping often was broken, giving the visual impression of a truncated stump. The scar of the insertion area of the anterior adductor muscle is thickened in some specimens, and in others the scar forms a prominent tubercle. The ventral margin is weakly crenulated (Figure 6). Coincidentally, in the geometric morphometrics analysis, almost 90% of the Quaternary material of Bahía Bustamante (Chubut) was allocated to *P. purpuratus* (Table 4). The presence of *B. rodriguezii* in the Pleistocene of Bahía Bustamante (Chubut) is not supported by these results.

Quaternary of Buenos Aires Province

Brachidontes rodriguezii has also been mentioned for the Pleistocene deposits of Buenos Aires Province by Aguirre and Farinati (1997) and for the adjacent platform by Richards and Craig (1963). Aguirre and Farinati (*op. cit.*) provided a rudimentary illustration of the material, however, the presence of a sub-terminal umbo and the elongated shell suggest that it corresponds to *B. rodriguezii*. We obtained good quality images of the Richards and Craig (*op. cit.*) material (one complete specimen, two broken valves) from the Academy of Natural Sciences of Drexel University (Figure 7) and the specimens also correspond to a typical *B. rodriguezii* form, sharing the following diagnostic characters identified by Adami et al. (2013): the sub-terminal umbo, thin ribs and insertion area of the anterior adductor muscle without scar. Coincidentally, in the geometric morphometrics



Figure 7. *Brachidontes rodriguezii* (ANSP 30907, Richards & Craig 1963) from the Pleistocene of Buenos Aires province.

Note: The arrows indicate some of the diagnostic characters of *Brachidontes rodriguezii*: in the external view, the sub-terminal umbo and the thin ribs.

analysis the material was assigned to *B. rodriguezii* (Table 4), providing support to the presence of this species on the Pleistocene of Buenos Aires.

Conclusions

This study examines the shell shape relationship between the extant scorched mussel *B. rodriguezii* and the fossil *B. lepida*. Although, the poor representation of the Pliocene deposits in the Southwest Atlantic coast make the study of the connections between the well represented Late Miocene marine fauna and the extant biota very difficult, we found shell shape evidence to support that *B. lepida* is more similar to *B. rodriguezii* than to the other extant species present in the region. Additionally, while there is evidence to support the presence of *B. rodriguezii* in the Pleistocene of Buenos Aires Province, there is none for its presence in the Pleistocene exposures of the Bustamante area (Chubut Province). Based on these results, *Brachidontes rodriguezii* seems to have a long history of presence in the warm-temperate region going back to the Late Miocene, being *B. rodriguezii lepida* the oldest record for the genus. This biogeographic pattern that we refer as 'Regional Ancestry', is part of a collage of patterns (dispersion via West Wind Drift and antitropicality) exhibited by the South American scorched mussels of the genus *Brachidontes* s.l. (Bivalvia: Mytilidae). This collage indicates that the apparent uniformity of intertidal communities dominated by mussels hides very different evolutionary histories.

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Disclosure statement

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