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Shell phenotypic variation in the south-western Atlantic gastropod *Olivancillaria carcellesi* (Mollusca: Olividae)

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Phenotypic variation on shell size and shape of Olivancillaria carcellesi *from four representative localities is confirmed using geometric morphometric techniques. This species lives along the entire range of the genus in subtidal soft bottoms from Rio de Janeiro (Brazil) to Punta Pardelas (Chubut, Argentina). Thickness of columellar callus, length and width are the main shell differences from specimens collected at several intermediate localities: Cassino (Brazil), La Paloma (Uruguay) and Mar del Plata (Argentina). All forms showed significant differences in shell size except* O. carcellesi *from La Paloma compared with those from Mar del Plata. The group with larger specimens was from Cassino.* Olivancillaria carcellesi *from Punta Pardelas, the southernmost population, was the smaller sized group and showed allometry between size and shape and this is responsible for their relatively higher spires. The possible ecological implications of the observed pattern are discussed. It is confirmed that* O. carcellesi *although variable, is a clearly defined species.*

Keywords: Argentina, intraspecific variation, molluscs, geometric morphometric analysis, *Olivancillaria*

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INTRODUCTION

The neogastropod genus *Olivancillaria* d'Orbigny, 1840 includes soft bottom species with oval–oblong and smooth shells. The spire is variable but usually low with the aperture narrow and always without operculum. The fasciolar band and columellar callus are both well defined. Radulae have an invariable tricuspidated rachidian tooth and two laterals. These species inhabit shallow waters to about 50 m depth at the Argentine Malacological Province, from Rio de Janeiro, Brazil, to Golfo Nuevo, Argentina (Pastorino, 1995; Scarabino *et al.*, 2006; Rios, 2009). Little is known about the predatory–prey interactions of these species. Marcus & Marcus (1959) and Rocha-Barreira (2002) mentioned the crustacean *Emerita brasiliensis* Schmitt, 1935 and the bivalves *Donax hanleyanus* Philippi, 1847 and *Mesodesma mactroides* Reeve, 1854 as main alimentary items of *Olivancillaria vesica vesica* (Gmelin, 1791) (as *Lintricula auricularia*) and *O. vesica auricularia* (Lamarck, 1811) from the coast of São Paulo and Cassino Beach (Brazil). In addition, Penchaszadeh *et al.* (2006) reported that *Olivancillaria deshayesiana* (Ducros de Saint Germain, 1857) and *O. urceus* (Röding, 1798) consumed *Amiantis purpurata* (Lamarck, 1818) and *Solen tehuelchus* (Hanley, 1842) in the subtidal community of Mar del Plata (Argentina) between 10 to 18 m depth.

The traditional south-western Atlantic malacological catalogues (i.e. Castellanos, 1970; Rios, 2009) recorded seven species belonging to the genus *Olivancillaria*: *O. carcellesi* Klappenbach, 1965, *O. contortuplicata* (Reeve, 1850), *O. deshayesiana*, *O. teaguei* Klappenbach, 1964, *O. uretai* Klappenbach, 1965, *O. urceus*, *O. vesica vesica* and *O. vesica auricularia*. The last two are commonly cited as subspecies by authors, although their real status remains obscure.

Olivancillaria species are based on conventional shell features i.e. protoconch, aperture and columella folds (Klappenbach, 1964, 1965; Borzone, 1995), probably because radulae and other anatomical features (such as penes) are remarkably similar and therefore not taxonomically informative. *Olivancillaria carcellesi* is the only species living along the entire range of the genus (Pastorino, 1995; Rios, 2009). This form shows considerable shell variation which has introduced taxonomic inconvenience. The nominal species *O. buckuporum* Thomé, 1966 was described as a new form from Brazilian waters. However, several authors considered this name a local variant of *O. carcellesi* (e.g. Rios, 1970; Thomé *et al.*, 2004).

Recently Carranza & Norbis (2005) documented the variation among the morphology of the shells of *O. urceus* from several south-western Atlantic localities using traditional morphometry. Chiu *et al.* (2002) and Carvajal-Rodríguez *et al.* (2005) worked with geometric morphometric methodology to report the phenotypic variation in shell morphology of several species of gastropods. Different environmental parameters like wave exposure (particularly on intertidal species), depth, or grain size, have been proposed to explain this variation (e.g. Olabarría & Thurston 2004; Conde-Padín *et al.*, 2007; Roopnarine *et al.*, 2008). Within this context the morphological shell variation of *O. carcellesi* observed along their distribution represents an interesting opportunity to study and quantify the specific constraints of this form. The size and shape variation of the shell of *O. carcellesi* from

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four representative localities was studied using geometric morphometric techniques. The possible ecological implications of the observed pattern are discussed.

MATERIALS AND METHODS

Specimens of *Olivancillaria carcellesi* were collected by bottom trawling from shallow subtidal zones off Mar del Plata (MdP) (38°02′S 57°37′W), Buenos Aires (Argentina) and, by SCUBA diving, around Punta Pardelas (PP) (42°37'S 64°15'W), Chubut (Argentina) (Figure 1). In addition, specimens from La Paloma (LP) (34°40'S 54°09′W), Rocha (Uruguay) and Cassino (C) (32°13'S 52°11'W), Rio Grande do Sul (Brazil) were analysed.

All specimens were collected alive and fixed in 70% ethanol. Specimens housed at Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHNM); Museu Oceanográfico 'Profesor Eliézer de Carvalho Rios' Rio Grande, Brazil (MORG) and Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (MACN) were also studied in order to compare an even number of specimens from each locality and species. For a more robust study the type specimens of *O. carcellesi* and *O. buckuporum* were also included in the analysis (Table 1).

Twenty specimens of each species were randomly selected and photographed with a Nikon D100 digital camera. Twelve landmarks (LM) representative of the shell (*sensu* Rohlf, 1996; Roopnarine & Vermeij, 2000) were chosen on apertural view (Figure 2). The location of the LM defines the category to which they belong. Bookstein (1991) classified the LM in three types (1, 2 and 3) where the type 1 is the optimal and defined in terms of specific local features (e.g. LM2). The type 2 lacks information from surrounding features in at least one direction (e.g. LM1). Finally the type 3 LM is defined as extremes of curvature or points along some structure (e.g. LM4, LM12) (Zelditch *et al.*, 2004). In this work landmarks are defined as follows: LM1 is located on the exact intersection of the sutural canal and the left border of the shell; LM2 is on the apex of the shell; LM3 is on the posterior edge of the outer lip; LM4 is on the widest point of the lip; LM5 is on the anterior edge of the outer lip; LM6 is on the concave centre of the siphonal canal; LM7 is on the anterior tip of the columella pillar; LM8 is on the posterior extreme of the basal fold; LM9 is the intersection of the fasciolar band and the columellar callus; LM10 is on the most internal part of the posterior fasciolar band; LM11 is on the most external part of the posterior fasciolar band; and LM12 is the widest point of the shell side. The landmark data were used to calculate the specimen size and to describe the shape variation between species. Size was calculated as the square root of the summed squared distances of a specimen's landmarks to their geometric centroid: $CS = [\Sigma\ (di)^2]^{1/2}$, where CS is centroid size and di is the distance of landmarks to their centroid. Particularly, the centroid size is the only size variable uncorrelated with shape in the absence of allometry (Bookstein, 1991). This absence of correlation is an advantage over other size measures used in morphometric analyses. Centroid size is the dimension measure used to scale a configuration of landmarks so they can be plotted as a point in Kendall's shape space. The denominator of the formula for the Procrustes distance between two sets of landmark configurations is the product of their centroid sizes. The description of shape was carried out using a relative warp analysis (Bookstein, 1991) performed with the tpsRelw (Rohlf, 2002). This method is comparable with the principal component analysis, which summarizes a specimen shape as a deformation from a common reference. The relative warps were computed with the scaling option $\alpha = 0$ which weights all landmarks equally, for studying differences in shell shape among samples (Rohlf *et al.*, 1996).

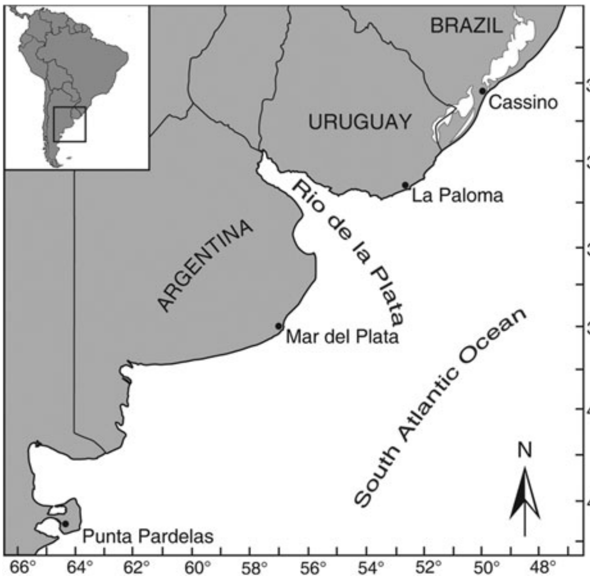

Fig. 1. Map showing the sampled localities.

In addition, the intraspecific variations found in *O. carcellesi* were tested with a multivariate analysis of variance (MANOVA) of partial warp scores. The following categorization was revealed by canonical variates analysis (CVA). Allometric variation was tested with a multiple regression model with the relationships between RWs and CS. Differences in centroid size distributions among groups were tested with the one-way analysis of variance (ANOVA) test and *post-hoc* Tukey HSD test (Sokal & Rohlf, 1995). Statistical analysis was carried out with the software Statistic v. 6.0. When homogeneity of variances could not be achieved by transformation, data were analysed nonetheless, since analysis of variance is robust for departure from this assumption when sizes of samples are equal (Underwood, 1997). Results were, however, interpreted with caution by judging significance more conservatively ($\alpha = 0.01$).

RESULTS

The intraspecific analysis of *O. carcellesi* performed with the MANOVA and subsequent CVA showed significant differences among groups in the first three axes of the analysis (Axis 1: Wilks' $\lambda = 0.0122$, $\chi 2 = 295.0285$, $P < 2.22045$ exp-16; Axis 2: Wilks' $\lambda = 0.0731$, $\chi 2 = 175.2362$, $P < 2.22045$ exp-16; Axis 3: Wilks' $\lambda = 0.3428$, $\chi 2 = 71.7313$, $P = 2.29703$ exp-8) (Figure 3). The study revealed four morphotypes (Figure 4). We found that 97.5% of the original cases were cross-validated correctly into their species groups based on the Mahalanobis distance in the space defined by the significant CVA axes (100% *O. carcellesi* MdP, 100% *O. carcellesi* C, 100% *O. carcellesi* LP and 90% *O. carcellesi* PP).

Table 1. Localities and museum specimens of *Olivancillaria* used for the analysis. Punta Pardelas (PP), La Paloma (LP), Cassino (C) and Mar del Plata (MdP).

Species	Localities	Museum lots	N
O. carcellesi	PP	MACN-In 37506	20
O. carcellesi	LP	MNHNM 638, 1298, 737 (paratypes); 3866, 4520, 4402	20
O. carcellesi	C	MORG 3715, 2606, 9525, 7949 (*O. buckuporum* paratypes); 24755, 27603, 29765, 31346, 42701;MNHNM 15048	20
O. carcellesi	MdP	MACN-In 25366, 37505	20

All forms showed significant differences in centroid size distribution (ANOVA, F = 55.2 $P < 0.01$) except *O. carcellesi* from LP compared with those from MdP (Tukey tests $P > 0.05$). The smaller group was *O. carcellesi* from PP and the larger group was *O. carcellesi* from C (Table 2).

The RWA of all groups demonstrates that 70.5% ($\alpha = 0$) of total variations are expressed by the first three axes (RW1 = 32.3%, RW2 = 21.1% and RW3 = 17.1%). The scores obtained after this analysis revealed significant regression between shape and centroid size ($P < 0.0001$). Two groups discriminated by the CVA, exhibited significant allometry between RW1 and CS (linear regression: *O. carcellesi* LP $r^2 = 0.53$, $P < 0.0001$; *O. carcellesi* PP $r^2 = 0.83$, $P < 0.0001$) (Figure 5). The two allometric relationships differed significantly (ANCOVA, F = 37.05, $P < 0.0001$). Allometry does not account for shape differences between *O. carcellesi* C and *O. carcellesi* MdP. Allometry in *O. carcellesi* PP is responsible for the relatively higher spires. The main differences among specimens of *O. carcellesi* from C, LP and MdP lay in width and length of the shells; and thickness of the columellar callus. This is observed in Figure 4.

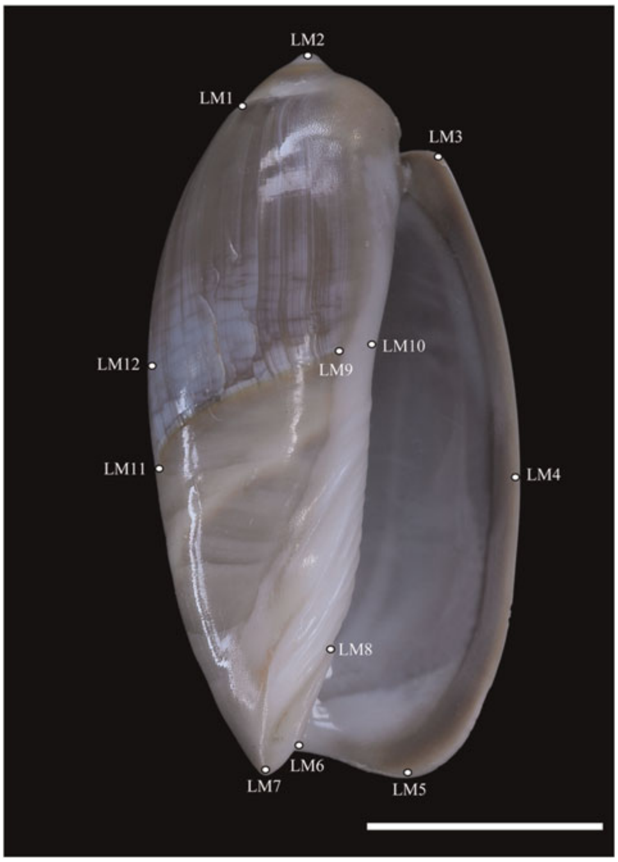

Fig. 2. Apertural view of *Olivancillaria carcellesi* (MACN-In 37505) showing the homologous landmarks. Scale bar = 1 cm.

DISCUSSION

The geometric morphometric method analyses the data obtained from digitized landmarks that would be later used for the calculation of size, as a centroid size, and reveals the shape of the specimens. It allows identifying groups and/or individual differences, or variation between samples and other results based on the original shape of the studied species (Zelditch *et al.*, 2004). Bookstein (1991) described the shape using the relative warp analysis. This method summarizes the specimen's shape as a transformation to a common reference form. The specimen coordinates (partial warp scores) from axes of major shape dimensions in a Kendall shape space, can be used as ordinary variables in parametric statistical analyses.

Phenotypic variation on shell size and shape of *O. carcellesi* from different localities was here detected using geometric morphometric methods. Previously, Carranza & Norbis (2005), using traditional morphometric, reported shell variation of *O. urceus* among specimens from several localities from the south-western Atlantic coast. Chiu *et al.* (2002), Conde-Padín *et al.* (2007) and Olabarría & Thurston (2004) among others, showed external factors such as environmental conditions to induce variations on shell shape. Trussell & Etter (2001) suggested that latitudinal differences in water temperature contribute to biogeographical variation in gastropod shell form. In the area studied, the range of surface seawater temperatures vary among localities, with the higher values at Cassino beach (C), 14°C to 26°C (Das Neves *et al.*, 2008)

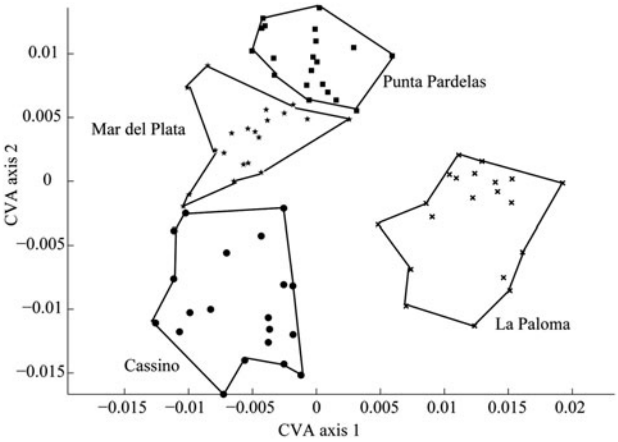

Fig. 3. Results of canonical variates analysis of *Olivancillaria carcellesi* from four localities.

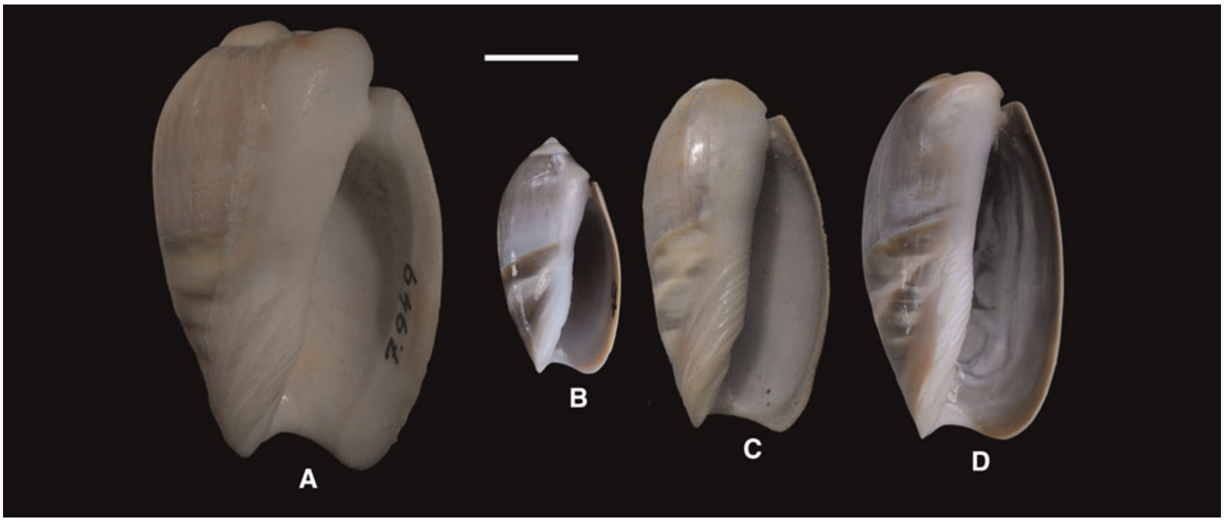

Fig. 4. Different morphs of *Olivancillaria carcellesi* (Klappenbach, 1965) analysed morphometrically. (A) Cassino (MORG 7949) (paratype of *O. buckuporum* Thomé, 1966); (B) Punta Pardelas (MACN-In 37506); (C) La Paloma (MNHNM 4520); (D) Mar del Plata (MACN-In 37505). Scale bar =1 cm.

and the lower at Punta Pardelas (PP), 10.5°C to 17°C (Rivas & Ripa, 1989). In agreement with the latter conditions, specimens of *O. carcellesi* from PP are significantly smaller than the others, whereas those from C are the largest.

It is a fact that natural variation of $CaCO_3$ saturation in seawater decreases from the Tropics to the Poles (mostly as a function of the effect of temperature on the CO_2 solubility) (Marubini *et al.*, 2003). This could be an explanation of the smaller sizes from PP and the larger sizes from C. A similar pattern was observed in the thickness of the callus at low temperatures in *Cypraea annulus* Linnaeus, 1758 from the Indian and West Pacific Oceans (Irie, 2006), and in the shell thickness of *Littorina obtusata* (Linnaeus, 1758) from northern and southern areas of the Gulf of Maine, USA (Trussell & Etter, 2001). No differences in CS were found among populations of LP and MdP, which could be due to the similarity of environmental factors between those localities (Martos & Piccolo 1988; Guerrero *et al.*, 1997).

Crothers (1998) and Plejdrup *et al.* (2006) among others reported that exposure to tributyltin (TBT) could cause changes in shell size and shape. Recently, Teso & Penchaszadeh (2009) described shell size variation produced by TBT in two populations of *O. deshayesiana* from Argentina. However, this was not tested here as Mar del Plata is the only locality that qualifies for TBT contamination.

Roopnarine *et al.* (2008) found phenotypic variation in the bivalve *Anomalocardia squamosa* (Linnaeus, 1758) from Thailand and attributed this variation to differences in sediment type and water energy. However, in our study the samples were obtained in very homogeneous sediment (medium sand). Carranza & Norbis (2005) reported that wider specimens of *O. urceus* with shorter spires are found in high-energy habitats and elongated forms occur in protected localities. We did not find those differences in the analysed shells, despite that sandy beaches of C, LP and MdP are exposed and have a strong wave action in contrast with those of PP. The main shell differences of *O. carcellesi* specimens from C, LP and MdP, found by means of the morphometric analysis, are width, length and thickness of the columellar callus. Specimens from PP showed allometry between size and shape and this is apparently responsible for their relatively higher spires.

As a general proposition, higher rates of metabolism should make possible higher potential rates of growth, or expansion. Available evidence indicates that shell form is greatly affected by food availability and other factors that influence growth (Vermeij, 2002). Kemp & Bertness (1984) found that in dense populations of *Littorina littorea* (Linnaeus, 1758) individuals have relatively elongate shells in comparison to individuals in sparse populations, which have rounder, globose shells. They demonstrated that shell variation is a function of snail growth rate which depends on food supply; with rapidly growing snails developing thin, globose shells and slower growing snails with elongate, cone-shaped shells. However, no data are available on densities and food availability of *O. carcellesi* to corroborate this hypothesis.

In accordance with our results *O. buckuporum* is a local variation of *O. carcellesi* as was previously suggested by many authors (e.g. Rios, 1970; Thomé *et al.*, 2004). When compared to the whole dataset of *O. carcellesi*, a correlation between size and shape is detected. This suggests that the phenotypic variation is due to allometric differences with a

Table 2. Tukey test and centroid sizes (average ± SD) of each morphotype of *Olivancillaria carcellesi*. Numbers in bold are cases that were significant at $P < 0.01$.

	***O. carcellesi* C** **56.8 ± 10.5**	***O. carcellesi* LP** **44.3 ± 13.6**	***O. carcellesi* MdP** **44.3 ± 6.8**	***O. carcellesi* PP** **19.2 ± 4.1**
O. carcellesi C		**0.000609**	**0.000568**	**0.000148**
O. carcellesi LP	**0.000609**		0.999995	**0.000148**
O. carcellesi MdP	**0.000568**	0.999995		**0.000148**
O. carcellesi PP	**0.000148**	**0.000148**	**0.000148**	

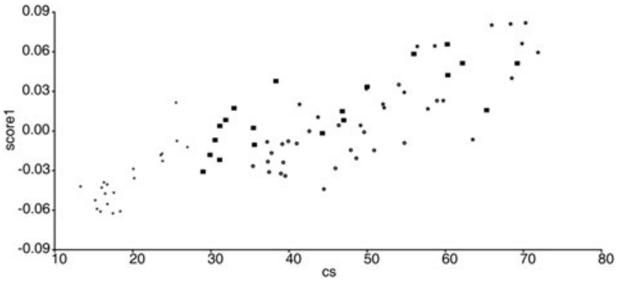

Fig. 5. Multivariate regression between shape and centroid size of *Olivancillaria carcellesi* from four localities showing allometry. Punta Pardelas, filled grey circle; La Paloma, black square; Mar del Plata, empty black circle; Cassino, black star.

progressive relative shortening of the spire and increasing expansion of the inner lip. However, a genetic study on the population structure of this species would be necessary to confirm this hypothesis.

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