Journal of Natural History, 2005; 39(24): 2203–2216

Taylor & Francis
Taylor & Francis Group

Intraspecific clinal variation in *Plagiodontes patagonicus* (Gastropoda: Orthalicidae, Odontostominae), an endemic species from Argentina

NÉSTOR J. CAZZANIGA, JULIA PIZÁ, & NATALIA S. GHEZZI

Universidad Nacional del Sur, Laboratorio de Zoología de Invertebrados I, Bahía Blanca, Argentina

(Accepted 10 May 2004)

Abstract
Plagiodontes patagonicus (d'Orbigny, 1835) is a quite variable species endemic to southern Buenos Aires province (Argentina). Its taxonomic characterization did not include any quantitative analysis of variability for an accurate discrimination, and the extremes of its variation were described as different subspecies or species. In this paper, shell measurements and angles, and quantitative data on the terminal male genitalia were studied by Principal Component Analysis and Varimax multivariate analysis. Typical *Plagiodontes patagonicus* and the largest form known as *P. patagonicus magnus* Hylton-Scott, 1951 showed an almost continuous pattern of shell variation, which is positively correlated with the altitude gradient over their geographical range, which in turn is correlated with a rainfall gradient, i.e. they constitute a size-form cline that does not allow objective delimitation of different morphospecies. Data from the genital system were also arranged as a geographical gradient within the *P. patagonicus patagonicus–P. patagonicus magnus* continuum. The variability of protoconch sculpture and apertural teeth also indicate recognition of them as a single taxon.

Keywords: Plagiodontes patagonicus, *cline, genital anatomy, geographical variation, morphometry, taxonomy*

Introduction

Plagiodontes patagonicus (d'Orbigny, 1835) is an endemic species in southern Buenos Aires province, thriving over a land strip that ranges from the Atlantic coast to the Ventania Sierras ("area 3" according to Pizá and Cazzaniga 2003). This rather isolated region in the south of the Pampean realm was identified as a "faunal island", zoogeographically different from the rest of the province, mostly related to the Espinal realm (Ringuelet 1961; Cabrera and Willink 1972).

Earlier authors stated that *P. patagonicus* attains its largest size at the Ventania Mountains, some 100 km to the north of Bahía Blanca, which is the type locality. While Doering (1881) recognized two varieties, *major* and *minor*, Parodiz (1939) just mentioned

Correspondence: Néstor J. Cazzaniga, Universidad Nacional del Sur, Laboratorio de Zoología de Invertebrados I, San Juan 670, (8000) Bahía Blanca, Argentina. E-mail: ficazzan@criba.edu.ar

Published 28 June 2005.

ISSN 0022-2933 print/ISSN 1464-5262 online
DOI: 10.1080/00222930400004578

size differences with no attribution of a taxonomic level. Pilsbry and Vanatta (in Pilsbry 1898) described a small form of *P. patagonicus* as a separate species, *P. iheringi*, which was soon recognized as a synonym of typical *P. patagonicus* by Pilsbry (1902). Hylton-Scott (1951) described the largest shells from the Ventania Mountain System as a new subspecies, *P. patagonicus magnus*. Later, Cazzaniga and Fernández-Canigia (1985) considered them as two different species, separated by morphological and geographical gaps. Typical *P. patagonicus* have a smooth shell with a striated protoconch and weakly developed apertural teeth, the lack of a transverse lamella being its distinctive trait. *Plagiodontes magnus* was described as having colour polymorphism, smooth protoconch, some differences in its genital anatomy mostly related to size, and a transverse lamella often present. Quantitative variables allowing discrimination among species in this genus were not adequately analysed.

From a geomorphological viewpoint, the distribution area of these forms or species is included in the Subhumid South Pampean morphogenetic system, where the mountain systems and wide closed depressions interrupt the extensive grassland plains. González-Uriarte (2002) included this area in the geoenvironments called "Sierra relief" and "South Ventania plain". The main factor varying on a south–north gradient across the area is altitude, from sea level to about 1200 m on the highest peaks, with a correlative gradual change in humidity and soil composition. Mean rainfall is a linear function of the altitude, with a mean positive gradient of 3.73 mm km^{-1} (Paoloni et al. 1988). Coincidently, zonal soil distribution shows a succession of the aridic, ustic and udic edaphic regimes. In the north part of the range, there is a predominance of the Order Mollisol with different degrees of udic and ustic evolution (association of Hapludol and Argiudol in the north-west, and of Haplustol and Argiustol in the central west) (M. González-Uriarte, personal communication).

The discovery of new live material of *Plagiodontes* from places scattered between the previously known localities allows us to rectify the taxonomic status of these forms, after realizing that a continuous pattern of variation, correlated with a geographical gradient, is more realistic than splitting the edges of variation as different taxa.

The aim of this paper is to analyse qualitative and quantitative characters of the shell and genital anatomy relating to the identity of *P. patagonicus* and *P. magnus*, which are hereby interpreted as the extreme forms of a size-shape cline of a single morphospecies.

Material and methods

Shell variability was analysed on 342 adult shells from several localities in south-west Buenos Aires province (Table I). Adulthood was assumed for shells with a full development of the apertural teeth and presence of a reflected outer aperture lip. Seven linear and angular variables were measured on shell drawings that were made with a camera lucida device on a stereoscopic microscope: shell length (SL), shell width (SW), length of the last whorl (LWL), aperture length (AL) and aperture width (AW); major angle and spiral angle were also determined as described in Pizá and Cazzaniga (2003). Characteristics of the apertural teeth were determined through direct observation under a stereoscopic microscope. Special attention was paid to the presence of a transverse lamella, because this genus-diagnostic character was deemed to be absent in *P. patagonicus*.

Protoconch sculpture of juvenile shells and adult shells showing the effects of erosion and rebuilding was analysed with a stereoscopic and a scanning electronic microscope at CRIBABB (Centro Regional de Investigaciones Básicas y Aplicadas de Bahía Blanca, CONICET).

Table I. Studied collections of *Plagiodontes* shells from southern Buenos Aires province.

Set	Locality	Latitude	Longitude	Altitude (m)	*n*
1	Cordón Esmeralda, Ventania Mountain Range, PPET	38°03′21″S	61°55′03″W	375–500	20
2	Cerro de la Cruz, Ventania Mountain Range, PPET	38°05′19″S	61°55′07″W	450	12
3	Eastern neighbourhoods of Villa Ventana	38°05′24″S	61°52′44″W	375–425	12
4	Cerro Bahía Blanca (east slope), Ventania Mountains, PPET	38°04′28″S	61°58′54″W	600	21
5	Cerro Bahía Blanca (west slope), Ventania Mountains, PPET	38°04′13″S	61°59′08″W	675	18
6	Cerro Destierro, Ventania Mountain Range, PPET	38°01′40″S	62°01′53″W	550–950	33
7	Unnamed mountain, National Road 76, km 227	38°04′38″S	61°59′49″W	500–600	23
8	Cerro del Águila, Ventania Mountain Range	38°18′11″S	62°16′18″W	~400	13
9	Carrindanga Way, km 50	38°27′22″S	61°51′06″W	180	20
10	Carrindanga Way, km 40	38°30′01″S	62°02′53″W	156	19
11	Carrindanga Way, km 35	38°32′15″S	62°03′05″W	133	20
12	Carrindanga Way, km 30	38°32′55″S	62°03′15″W	131	15
13	Carrindanga Way, km 25: Canesa Bridge	38°35′15″S	62°05′18″W	128	20
14	National Road 33, km 34	38°34′S	62°15′W	166	14
15	National Road 33, km 30.5	38°35′S	62°15′W	156	20
16	Bahía Blanca city: Sarmiento Ave., 3300	38°41′38″S	62°14′15″W	60	17
17	Bahía Blanca city: Palihue University Campus	38°43′S	62°12′W	60	20
18	General Daniel Cerri	38°43′08″S	62°23′53″W	10	24

PPET, Provincial Park Ernesto Tornquist; *n*, number of shells in the sample.

Genital quantitative data were taken from 80 living specimens from four localities (20 snails from each): General Daniel Cerri; National Road 33 km 11 ("Cueva de Los Leones"); Cerro Bahía Blanca (a mountain in the Provincial Park Ernesto Tornquist); and Cerro Curamalal (Figure 1). The snails were sacrificed in hot water. The measured variables, taken with a micrometre eyepiece on a stereoscopic microscope, were: penis length, epiphallus length, length of the spermathecal stalk, and diameter of the spermatheca.

Quantitative data were analysed by multivariate Principal Component Analysis (PCA) using the SPSS statistical package. Scores on the first axis of a two-axis Varimax solution were plotted against altitude, and the Pearsonian correlation was calculated, to detect sample clinal distribution (Gould 1969). ANOVA, Bonferroni's and least significant difference tests were used to compare shell length means between pairs of samples.

Results

Table II summarizes the morphometric information on the studied shells arranged in three geographical intervals (mountains, intermediate locations, and vicinities of Bahía Blanca); some representative specimens are shown in Figure 2. PCA showed a wide overlap of the

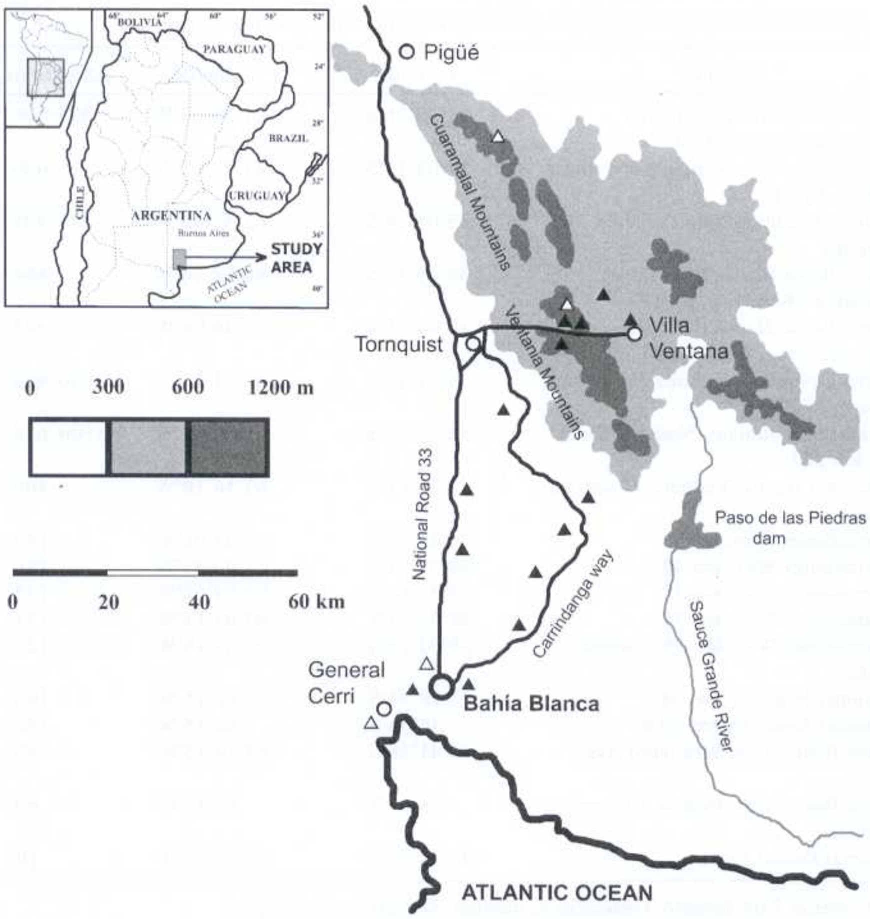


Figure 1. Sampling area. Black triangles: localities for shell morphometry; open triangles: localities for internal anatomy.

different samples. Even though shells from the type localities of *P. patagonicus patagonicus* (Bahía Blanca) and *P. patagonicus magnus* (Ventania Mountains) still appear separate in the graph, the intermediate localities are scattered in a way that does not allow any clear-cut boundary between the two alleged taxa (Figure 3). Evidence for a cline is unambiguous, since correlation between Varimax scores on axis 1 and ground altitude is highly significant ($P<0.001$; Figure 4).

Figure 5 shows the variation of mean shell size along the geographic gradient from the coastal plain (General Daniel Cerri, 10 m above sea level) to the highest sampling sites (Cerro Bahía Blanca, 900 m high; Cerro Destierro, 1100 m high). Even though a great variability was found in each region, there was a clear tendency to increasing shell size as land altitude increases; the smallest adult shells from the Ventania Mountains did not have a significant shell size difference from the largest shells from areas around Bahía Blanca (Figure 5). Factors other than altitude may influence local shell size, e.g. shells in set 6, showing a relatively small size, were collected from Cerro Destierro, at 900 m above sea level, in an area exposed to strong winds and deprived of sheltering vegetation, while sample 5 showing the largest shell lengths was mostly gathered from rock fissures occupied

Table II. Summary of the variables and proportions measured on *Plagiodontes* shells from southern Buenos Aires province.

Variable	Mountains	Intermediate locations	Bahía Blanca surrounding areas
n	152	129	61
Shell length (SL)	24.49 SD 2.33 (20.45–30.34)	21.03 SD 2.16 (16.96–27.69)	20.87 SD 1.71 (18.08–24.64)
Shell width (SW)	11.88 SD 1.08 (10.11–15.23)	10.43 SD 0.78 (8.92–12.46)	10.52 SD 0.61 (9.55–11.95)
Last whorl length (LWL)	16.3 SD 1.33 (14.09–20.23)	14.14 SD 1.22 (11.84–17.69)	14.14 SD 1.04 (12.24–16.33)
Aperture length (AL)	11.15 SD 1.06 (9.2–14.2)	9.62 SD 0.85 (7.75–12.15)	9.69 SD 0.74 (8.31–11.37)
Aperture width (AW)	8.92 SD 0.75 (7.39–11.36)	7.89 SD 0.63 (6.56–9.54)	8 SD 0.47 (7.05–9.04)
Major angle	120.86 SD 3.93 (102–129)	120.11 SD 3.35 (111–127)	119.79 SD 2.76 (112–125)
Spiral angle	48.74 SD 4.45 (37–60)	48.98 SD 4.72 (38–60)	49.64 SD 3.95 (42–61)
SW/SL	0.49 SD 0.03 (0.39–0.54)	0.5 SD 0.04 (0.4–0.6)	0.51 SD 0.03 (0.46–0.57)
LWL/SL	0.67 SD 0.02 (0.59–0.72)	0.67 SD 0.04 (0.55–0.77)	0.68 SD 0.02 (0.64–0.72)
AL/SL	0.46 SD 0.02 (0.37–0.53)	0.46 SD 0.03 (0.37– 0.53)	0.47 SD 0.02 (0.41–0.5)
AW/SL	0.37 SD 0.03 (0.28–0.43)	0.38 SD 0.03 (0.31–1.47)	0.38 SD 0.02 (0.34–0.44)
AW/AL	0.8 SD 0.05 (0.65–0.93)	0.82 SD 0.04 (0.71–0.96)	0.83 SD 0.04 (0.75–0.92)

Values are given as mean SD (minimum–maximum). Mountains=sets 1–8; intermediate locations=sets 9–15; Bahía Blanca surrounding areas=sets 16–18.

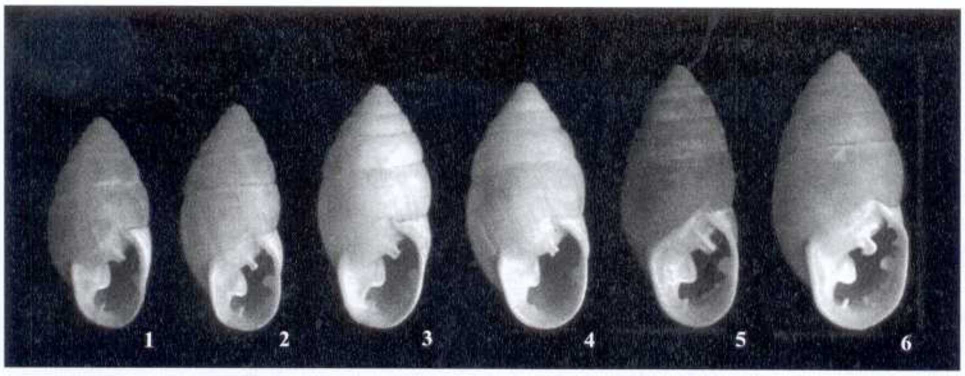


Figure 2. *Plagiodontes* shells from three localities in southern Buenos Aires province. (1, 2) Shells from Bahía Blanca vicinities (i.e. typical *P. patagonicus*); (3, 4) shells from Carrindanga way, km 50 (i.e. an intermediate place between the type localities of *P. patagonicus* and *P. magnus*); (5, 6) shells from the Ventania Mountain System (i.e. typical *P. magnus*).

by mosses and ferns, gaining advantage of the retained humidity, at 600–675 m on Cerro Bahía Blanca.

Shells were thick, uniformly greyish white at all localities along the plain (localities 9–18); occasionally some shells showed a slight pink hue. Shell colour was polymorphic at the mountains, where greyish specimens may co-occur with either pinkish, rufous brown or wine-coloured shells. Most live specimens were intensely wine-coloured at Cerro Bahía

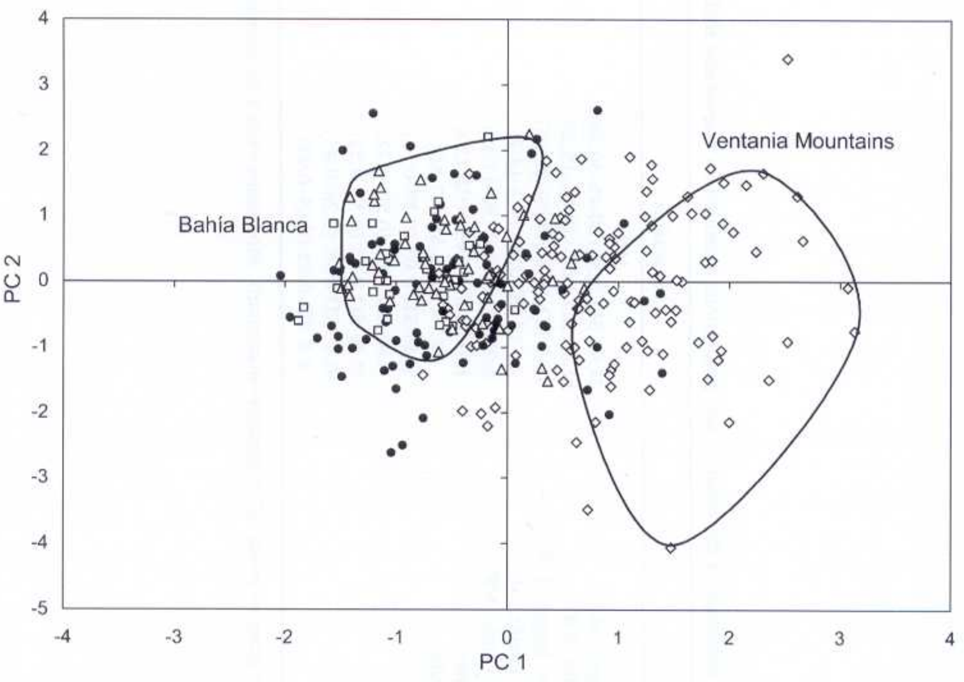


Figure 3. Scatter plot of the scores of the first (PC1) and second (PC2) principal components for shells of *Plagiodontes* snails from southern Buenos Aires province. Bahía Blanca and Ventania Mountains are the typical localities of *P. patagonicus* and *P. magnus*, respectively.

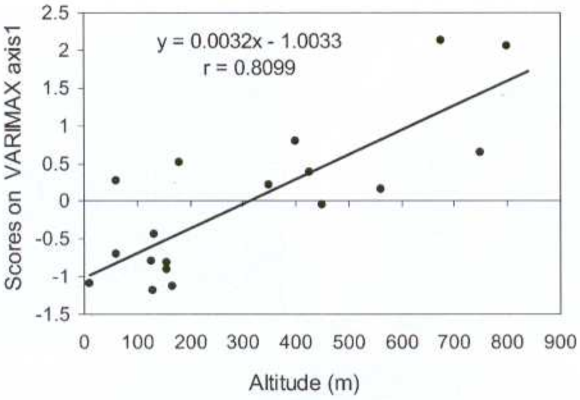


Figure 4. Scatter plot of the scores on the first axis of a two-axis Varimax solution against the altitude of the sampling localities, and regression line. *r*, Pearson correlation coefficient.

Blanca (Ventania Mountains, localities 4 and 5). Coloured shells are slightly shiny, smoother and thinner than the greyish white ones.

Differences were also found in the protoconch and apertural teeth of snails from different locations. The protoconchs of specimen areas around Bahía Blanca (typical *Plagiodontes patagonicus*) showed diverse levels of striation, from irregularly waved striae crossed by tiny thread lines giving the aspect of a stair (Figure 6), to weakened striae on which spiral lines are seldom or not visible (Figure 7). Young animals from the Ventania Mountains (typical *P. patagonicus magnus*) showed the same striation pattern as *P. patagonicus* (Figure 8). However, young adult shells had weaker striae, and most full-sized snails showed a

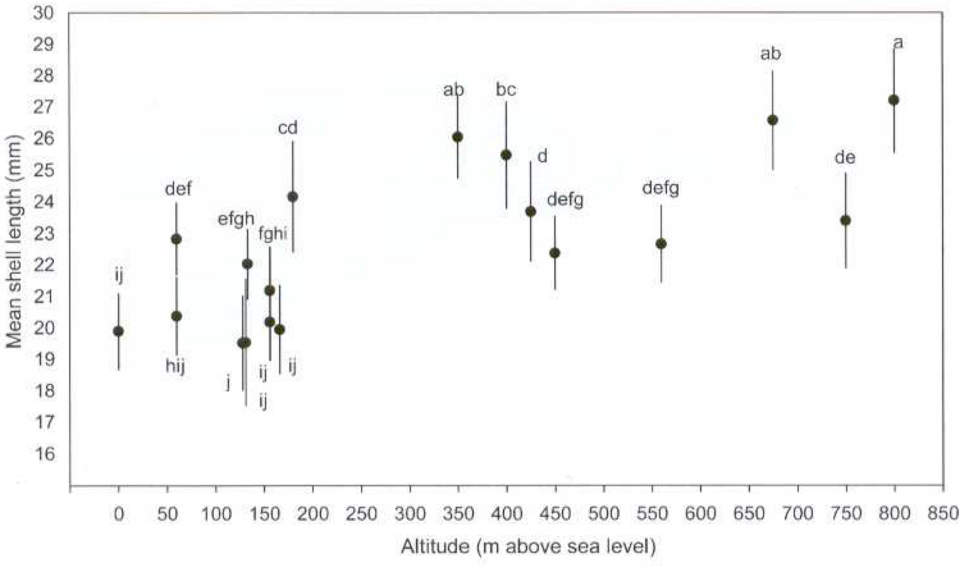
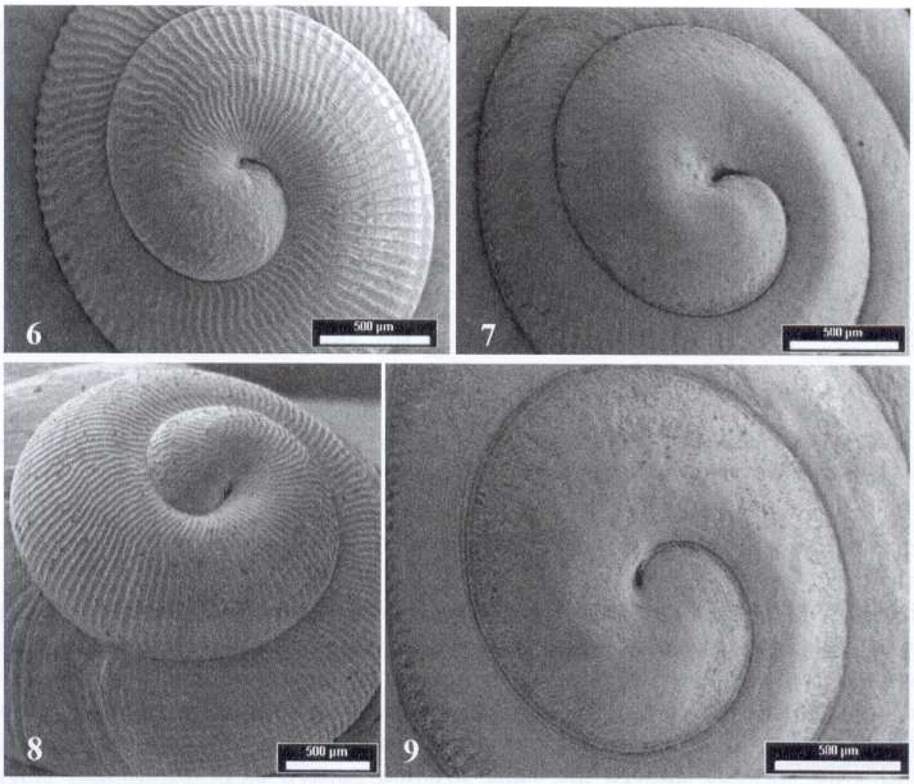


Figure 5. Scatter plot showing the mean shell size and standard deviation of *Plagiodontes patagonicus* as a function of land altitude. Values showing the same lower-case letter are not significantly different from each other (least significant difference and Bonferroni's tests).



Figures 6–9. Scanning electron micrographs of protoconchs of *Plagiodontes patagonicus* from southern Buenos Aires province, Argentina. (6) Young typical specimen from Bahía Blanca (i.e. typical *P. patagonicus*). (7) Adult, eroded shell from Bahía Blanca. (8) Young specimen from the Ventania Mountains (i.e. *P. magnus*). (9) Adult shell from the Ventania Mountains.

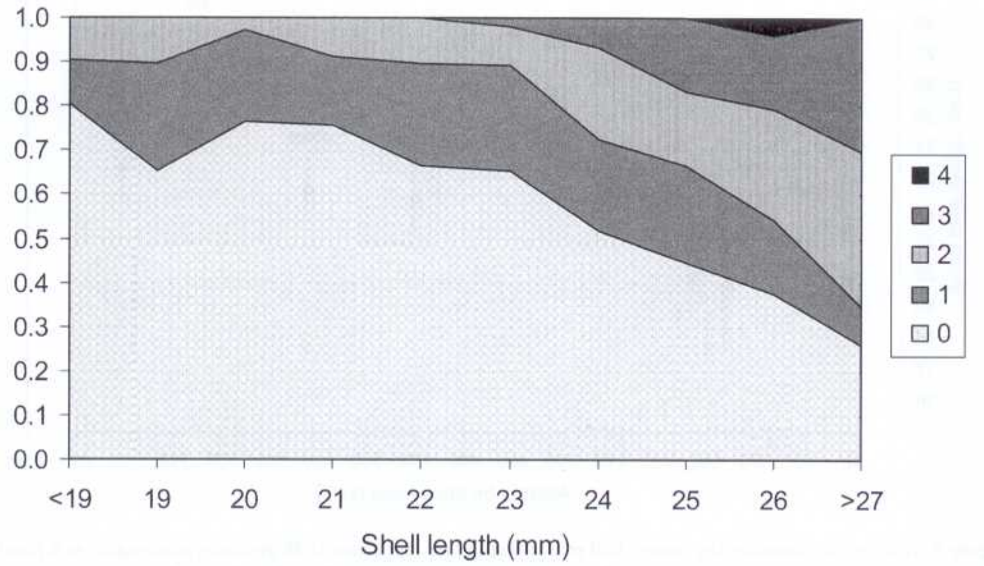


Figure 10. Proportions of shells showing 0, 1, 2, 3, or 4 lower palatal teeth as a function of shell length.

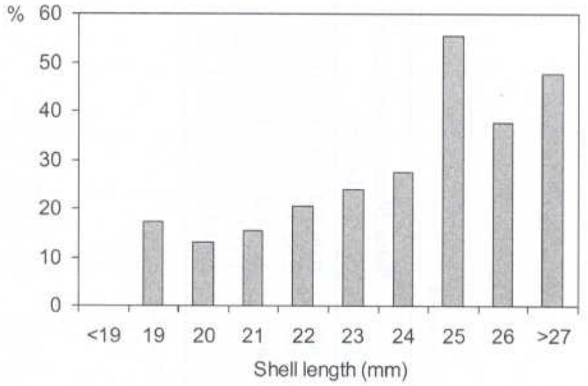


Figure 11. Relative frequencies of shells showing a rudimentary or developed transverse lamella as a function of shell length.

completely smooth protoconch, with a spiral cord or thread bordering the suture (Figure 9). This spiral thread was never observed in typical *P. patagonicus*.

Upper palatal, columellar and parietal teeth were present in all specimens from any locality. Lower palatal teeth showed a variation from zero to four teeth, with a tendency to an increasing number of lower palatal teeth with larger shell size (Figure 10). More than 70% of the small adults from Bahía Blanca and its vicinities, i.e. typical *P. patagonicus*, were devoid of lower palatal teeth; approximately 70% of the large, >26 mm long adults from the Ventania Mountains, i.e. typical *P. patagonicus magnus*, had one to three lower palatal teeth.

Most of the studied specimens from all sites lacked a transverse lamella. Sometimes a small denticle was present in its place; the transverse lamella was occasionally formed by two or three linearly arranged teeth, and even a well-developed lamella was also seen in some shells (Figure 2). The frequency of shells with a rudimentary or developed transverse lamella increases with size (Figure 11). So, adult snails from Bahía Blanca, 18–24 mm long, lacked in most cases a transverse lamella, but some populations (e.g. General Cerri) that were typical *P. patagonicus* in every other respect, showed up to 17% of shells with this fold; conversely, 67% of the snails from Cerro Bahía Blanca (in the Ventania Mountains), reaching 30 mm long (i.e. typical *P. magnus*), showed a transverse lamella, although only one out of 33 shells from Cerro Destierro had this structure.

Table III shows the results of genital morphometry. PCA of genital anatomy showed that no difference can be traced among populations other than a general size factor; the only remarkable arrangement occurred on the first principal component, which accounts for 73.4% of the variation (Figure 12).

Discussion

Land snails usually show shell polymorphism due to the effect of environmental changes, food and calcium availability, differential predation, and other factors. Habitat fragmentation, which isolates groups of populations, contributes to the inaccurate assessment of specific variability, since the morphologically different snails collected from remnant patches of native vegetation may look as if they were of different species. The pampas are the most modified eco-region in Argentina and, since *Plagiodontes* snails are mostly

Table III. Summary of the genital variables measured on *Plagiodontes patagonicus* from four localities in southern Buenos Aires province.

	Cerro Bahía Blanca (PPET)	Cerro Curamalal	General Daniel Cerri	Bahía Blanca (Cueva de los Leones)
Penis length (mm)	1.15 SD 0.12 (1.31–0.83)	1.22 SD 0.09 (1.43–0.89)	0.83 SD 0.08 (1.01–0.65)	0.99 SD 0.14 (1.31–0.77)
Spermatheca duct length (mm)	3.23 SD 0.34 (4.17–2.74)	2.89 SD 0.67 (4.46–1.25)	2.06 SD 0.36 (2.50–1.19)	2.51 SD 0.29 (3.21–2.02)
Flagellum length (mm)	1.61 SD 0.19 (2.02–1.37)	1.43 SD 0.17 (1.79–1.13)	1.09 SD 0.11 (1.43–0.89)	1.34 SD 0.16 (1.67–1.01)
Epiphallum length (mm)	1.35 SD 0.16 (1.67–1.13)	1.25 SD 0.15 (1.73–0.95)	0.94 SD 0.11 (1.13–0.71)	1.21 SD 0.17 (1.55–0.95)
Spermatheca diameter (mm)	2.20 SD 0.44 (3.42–1.44)	1.97 SD 0.35 (3.16–1.32)	1.34 SD 0.32 (1.97–0.79)	1.64 SD 0.30 (2.50–1.32)

Values are given as mean SD (minimum–maximum); $n=20$ specimens from each locality. PPET, Provincial Park Ernesto Tornquist.

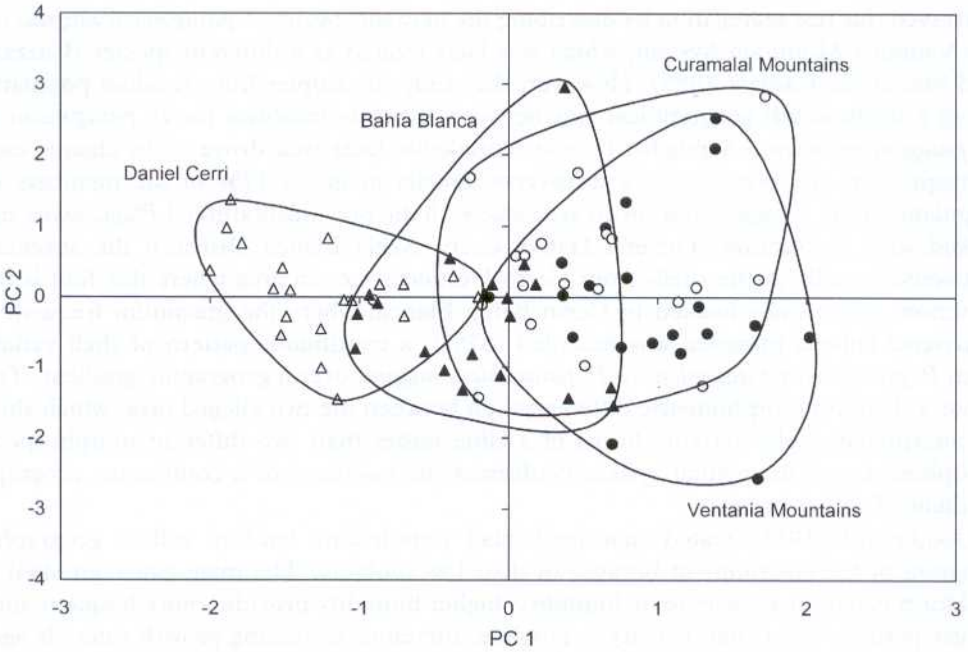


Figure 12. Scatter plot of the scores of the first (PC1) and second (PC2) principal components for genital anatomy data of *Plagiodontes* snails from southern Buenos Aires province. Specimens from Bahía Blanca and Daniel Cerri (10–60 m above sea level) were recognizable as typical *Plagiodontes patagonicus*, while those from Curamalal and Ventania Mountains fitted the description of *P. magnus*.

associated with relatively pristine areas, they are at present scattered in places showing suboptimal conditions for agriculture, especially fields with scarps or wide outcrops (Cazzaniga and Delhey 2002). Therefore, intermediate shell forms ranging between the extremes of the size-form cline are infrequently seen.

Shell variability of Argentine land snails was usually described in a narrative style, with hardly any morphometric data. Parodiz (1962) authored a pioneering work on the variation of *Spixia doellojuradoi* (Parodiz, 1941) (Odontostominae), which was not followed by further similar contributions. Pizá and Cazzaniga (2003) have recently analysed the variability of *Plagiodontes dentatus* (Wood, 1828) and its morphologic discrimination from its closer species, among which *P. patagonicus* is found.

Identifying the latter species has always been a simple task because it is the one that has the smaller number of apertural teeth within the genus and, especially, because it lacks the transverse lamella so characteristic of the genus. Although d'Orbigny (1840) and other authors considered it at first sight as a variety of *P. dentatus*, its specific status was definitively clarified by Doering (1881) and Parodiz (1939), who recognized *P. patagonicus* as a different, endemic species from southern Buenos Aires province. The reference to its presence in Uruguay (d'Orbigny 1840) was based upon a misidentification of *P. dentatus*, as was discussed by Klappenbach and Olazarri (1973). Pizá and Cazzaniga (2003) demonstrated that, beyond differences in the number of teeth and other binary characters, shells of *P. patagonicus* and *P. dentatus* of the same size also have significant differences in their morphometric proportions.

Doering (1876) stated that attaining larger sizes in the mountains and smaller sizes in the plains was a general characteristic of species in the genus *Plagiodontes*. Hylton-Scott (1951) portrayed this size segregation by describing the new subspecies *P. patagonicus magnus* from the Ventania Mountain System, which was later treated as a different species (Cazzaniga and Fernández-Canigia 1985). However, the study of samples from residual populations along a north–south geographical axis between the type localities for *P. patagonicus* and *P. patagonicus magnus* highlighted some remarkable facts that drove us to change earlier concepts, e.g. the presence of a transverse lamella in up to 17% of the members of a population of *P. patagonicus* from an area where all the previously studied *Plagiodontes* snails lacked such a structure (General Daniel Cerri, Bahía Blanca District); the absence of transverse lamella in the shells from Cerro Destierro, i.e. an area where this fold is fairly common, very closely located to Cerro Bahía Blanca, where the maximum frequency of transverse lamella presence was recorded (67%); a continuous pattern of shell variation from *P. patagonicus patagonicus* to *P. patagonicus magnus* over a geographic gradient. There is not a clear-cut morphometric differentiation between the two alleged taxa, which should be interpreted as the extreme forms of a cline rather than two different morphospecies. Morphometry of the genital system confirmed the existence of a continuous geographic gradient of variation too.

Goodfriend (1986) stated that land snail populations tend to reflect geographical variation of the environment because of their low mobility. The main cause for shell size and form variation appears to be humidity; higher humidity provides more frequent and/or longer periods when snail activity is possible, therefore increasing growth rates. If age at maturation is not negatively correlated with growth rate, then faster-growing snails would attain a larger adult size. This seems to be the case with *P. patagonicus*. Climate is semi-arid at Bahía Blanca, with approximately 500 mm of annual rainfall, and 300 mm of water deficit; conditions get progressively wetter towards the north, rainfall amounting to 900 mm, with only 100 mm of water deficit, at the Ventania Mountains (Glave 1975). Moreover, the snails living in the mountains generally inhabit rock cracks where lichens and ferns provide shelter and suitable microclimatic conditions.

Age at maturation was estimated at 4 years for *P. patagonicus* (Delhey and Cazzaniga 2002a), a reflection of the apertural outer lip marking the end of growth. Our hypothesis is that snails in the mountains are larger because they have a higher growth rate rather than because they are older; attaining a larger shell size would be the simple direct cause for a greater number of teeth, including a higher frequency of presence of transverse lamella, with no taxonomic consequence. It is worth noting that the specimens collected at Cerro Destierro, which did not have a transverse lamella, were also relatively small for the area.

It is not only altitude and humidity that influence snail size. The small adults collected from Cerro Destierro formed a very dense population, an inverse relationship between shell size and population density having already been described for another population of *P. patagonicus* (Delhey and Cazzaniga 2002b).

Colour polymorphism in land snails is usually explained as an adaptive response to selective predation on the less cryptic morphs (Sheppard 1951), and/or by means of thermoregulatory constraints on dark shells in open habitats (Burla and Gosteli 1993); the interaction between these two selective forces would account for maintenance of a balanced polymorphism (Jones et al. 1977; Goodhart 1987). However, Slotow et al. (1993) reported a case in which neither selective predation nor thermal advantages could explain the colour variation of a polymorphic desert snail; rather, inequality in individual access to calcium carbonate among habitats seems to result in the observed differences of shell-colour frequencies, with whiter, thick-shelled snails present at sites with greater availability of calcium carbonate, and weaker, dark-coloured ones collected in low calcium carbonate sites (Slotow and Ward 1997). This hypothesis should be tested for *P. patagonicus* on account of the evidence that all specimens are thick and white over the loess plains, related to geologically younger terrains (Tertiary and Quaternary), with calcareous tufa outcrops, while dark-coloured shells are frequent at the rocky habitats in the Ventania Mountains, where Palaeozoic rocks of metamorphic origin constitute the main substratum. The rocks are quartziferous sandstones and schists associated with scarce conglomerate argillaceous material (Harrington 1947).

Acknowledgements

We are very grateful to Viviana Sorrivas for her help in obtaining the micrographs; to Valdemar Delhey for the photographs; to the Ventania Project Group for some material from PPET; to Magdalena González-Uriarte and Edgardo Navarro for helping with geological-related aspects; to Lea Cazzaniga for revising English grammar. J.P. is a fellow of Universidad Nacional del Sur, and N.J.C. is a staff researcher in the Comisión de Investigaciones Científicas de la provincia de Buenos Aires (Argentina). This work was totally supported by the Universidad Nacional del Sur, Bahía Blanca, Argentina.

References

Burla H, Gosteli M. 1993. Thermal advantage of pale coloured morphs of snail *Arianta arbustorum* (Helicidae, Pulmonata) in alpine habitats. Ecogeography 16:345–350.

Cabrera AL, Willink A. 1972. Biogeografía de América Latina. Washington, DC: Organización de los Estados Americanos. 120 p. (Monografías, Serie Biología; 13).

Cazzaniga NJ, Delhey VK. 2002. Some observations on habitat and feeding of *Plagiodontes patagonicus* (Gastropoda: Odontostominae). In: V CLAMA, Congreso Latinoamericano de Malacología, Resúmenes; 2002 June; São Paulo. p 94.

Cazzaniga NJ, Fernández-Canigia MV. 1985. Aporte al conocimiento de *Plagiodontes patagonicus* (d'Orbigny) y *P. magnus* Hylton-Scott (Gastropoda: Odontostomidae). Spheniscus 1:35–51.

Delhey VK, Cazzaniga NJ. 2002a. Population dynamics of *Plagiodontes patagonicus* (Gastropoda: Odontostominae). In: V CLAMA, Congreso Latinoamericano de Malacología, Resúmenes; 2002 June; São Paulo. p 91.

Delhey VK, Cazzaniga NJ. 2002b. Inverse relationship between shell size and population density in *Plagiodontes patagonicus* (Gastropoda: Odontostominae). In: V CLAIM, Congreso Latinoamericano de Malacología, Anales; 2002 June; São Paulo. p 223–224.

d'Orbigny AD. 1840. Voyage dans l'Amérique Méridionale. Volume 5, Mollusques. Paris.

Doering A. 1876. Apuntes sobre la fauna de moluscos de la República Argentina. Tercera Parte. Boletín de la Academia Nacional de Ciencias Exactas, Córdoba 2:300–400.

Doering A. 1881. Moluscos. In: Informe Oficial de la Comisión Científica de la Expedición al Río Negro bajo las órdenes del General D. Julio A. Roca. Buenos Aires. p 61–75, Plate 1.

Glave AE. 1975. Caracterización física y económica de la región semiárida bonaerense. Informes de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires 9:1–22, 9 plates.

González-Uriarte M. 2002. Geoambientes del suroeste bonaerense. In: Vaquero MC, editor. Territorio, Economía, Medio Ambiente en el Sudoeste Bonaerense. Bahía Blanca: EDIUNS. p 463–483.

Goodfriend GA. 1986. Variation in land-snail shell form and size and its causes: a review. Systematic Zoology 35:204–223.

Goodhart CB. 1987. Why are some snails visibly polymorphic, and others not. Biological Journal of the Linnean Society 31:35–58.

Gould SJ. 1969. Character variation in two land snails from the Dutch Leeward Islands: geography, environment and evolution. Systematic Zoology 18:185–200.

Harrington HJ. 1947. Explicación de las hojas geológicas 33m y 34m. Sierras de Curamalal y de la Ventana, Prov. de Buenos Aires. Boletín de la Secretaría de Industria Comercio, Dirección de Minas y Geología 61:1–43.

Hylton-Scott MI. 1951. Nuevos moluscos terrestres del norte argentino. Acta Zoologica Lilloana 10:5–29.

Jones JS, Leith BH, Rawlings P. 1977. Polymorphism in *Cepaea*: a problem with too many solutions? Annual Review of Ecology and Systematics 8:109–143.

Klappenbach MA, Olazarri J. 1973. El género *Scalarinella* Dohrn, 1874 (Moll. Gastropoda) en el Uruguay. In: Congreso Latinoamericano de Zoología, 5; 1971 Oct 18–23; Montevideo. Trabajos 1:111–116.

Paoloni JD, Vázquez R, Fiorentino EC. 1988. La topografía y la variación de las precipitaciones y los escurrimientos en el sistema de Ventania. In: Jornadas Geológicas Bonaerenses, 2. Bahía Blanca. Actas 651–661.

Parodiz JJ. 1939. Revisión de *Plagiodontes* y *Scalarinella* (Odontostominae). Physis 17:711–734.

Parodiz JJ. 1962. Variabilidad en *Cyclodontina (Spixia) doello-juradoi* Par. (Gastropoda Pulmonata). Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciencias Zoológicas 8:69–80, 1 plate.

Pilsbry HA. 1898. New species of *Odontostomus* from Brazil and Argentina. Proceedings of the Academy of Natural Sciences of Philadelphia 50:471–474.

Pilsbry HA. 1902. Manual of conchology, 2nd series: Pulmonata. Volume 14, Oriental Bulimoid Helicidae; Odontostominae, Cerionidae. Philadelphia: Academy of Natural Sciences. 302 p, 62 plates.

Pizá J, Cazzaniga NJ. 2003. Redescription, shell variability and geographical distribution of *Plagiodontes dentatus* (Wood, 1828) (Gastropoda: Odontostomidae) from Uruguay and Argentina. Zootaxa 154:1–23.

Ringuelet RA. 1961. Rasgos fundamentales de la zoogeografía de la Argentina. Physis 22:151–170.

Sheppard PM. 1951. Fluctuations in the selective value of certain phenotypes in the polymorphic landsnail *Cepaea nemoralis* (L.). Heredity 5:125–134.

Slotow R, Goodfriend W, Ward D. 1993. Shell colour polymorphism of the Negev desert landsnail, *Trochoidea seetzeni:* the importance of temperature and predation. Journal of Arid Environments 24:47–61.

Slotow R, Ward D. 1997. Habitat constraints on shell-colour variation of a desert landsnail, *Trochoidea simulata*. Journal of Molluscan Studies 63:197–205.