

A new species of *Plagiodontes* from Argentina, and new data on the anatomy of four other species in the genus (Gastropoda: Orthalicidae, Odontostominae)

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Plagiodontes weyrauchi sp. nov. is among the smallest species in the genus *Plagiodontes* (Doering, 1877). Statistical multivariate analyses confirmed its distinctiveness from other species, mostly because of its high number of whorls (8–9.75), relatively small width, and low proportions of last whorl and aperture length to shell length; multivariate discriminant analysis applied to this species and its most similar relative, *P. multiplicatus parvus*, correctly identified 100% of specimens. Pallial and genital anatomy supports *P. weyrauchi* as a different species, mainly because of the position of the ureteric pore, the small general size of the genital system, the presence of an accessory lobe alongside the verge, and the vaginal internal structure. Internal anatomy of four other small-sized taxa in the genus was studied. Two of them have a verge with no accessory lobe [*P. dentatus* (Wood, 1828) and *P. patagonicus* (d'Orbigny, 1835)], while the remaining two have an accessory lobe with different characteristics [*P. rocae* Doering, 1881 and *P. multiplicatus parvus* (Hylton-Scott, 1952)]. Internal structure of the vagina also shows specific differences among *Plagiodontes* species; their phylogenetic significance will be further investigated.

Keywords: land snails; Stylommatophora; shell variability; morphometry; pallial anatomy; genital anatomy; taxonomy

Introduction

Plagiodontes Doering, 1877 [“1875”] is a genus of terrestrial snails endemic to three disjunct areas of Argentina and Uruguay on and around three mountain systems (Pizá and Cazzaniga 2003). Currently, the genus is composed of seven nominal morphospecies, i.e. *P. dentatus* (Wood, 1928), the type species; *P. patagonicus* (d'Orbigny, 1835); *P. daedaleus* (Deshayes, 1851); *P. multiplicatus* (Doering, 1875); *P. brackebuschii* Doering, 1877; *P. weyenberghii* (Doering, 1877) and *P. rocae* Doering, 1881 (Parodiz 1939; Cazzaniga et al. 2005). Information about most of them is limited to shell characters, with descriptions of genital anatomy available only for some species (Hylton-Scott 1952; Breure and Schouten 1985; Cazzaniga and Fernández-Canigia 1985; Pizá et al. 2006). To date, no details that allow species delimitation have been provided or discussed.

While revising the small species of *Plagiodontes*, we identified a new shell morphology that, although resembling to some extent the subspecies *P. multiplicatus parvus* (Hylton-Scott 1952), differs from all known species.

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Plagiodontes multiplicatus (Doering, 1875 [“1874”]) was originally described as a slender shell conspicuously sculptured with regular axial ribs and with the aperture partially occluded by well-developed lamellae and folds. The type material (currently missing) included four specimens about 27 mm long and 10 mm wide (shell width/shell length, 0.37). Further publications and museum collections have labelled many specimens of different sizes and proportions as *P. multiplicatus*. Parodiz (1939) illustrated *P. multiplicatus* for the first time, stated its extreme variability, and included other more obese specimens with finer sculpture from Santiago del Estero and La Rioja.

Hylton-Scott (1948, 1952) described two new subspecies. *Plagiodontes multiplicatus crassus* (Hylton-Scott, 1948) from Cerro Colorado (Salta) has a much weaker teleoconch sculpture and an unusually thickened peristome. *Plagiodontes multiplicatus parvus* Hylton-Scott, 1952 from Negra Muerta (Santiago del Estero) is a “dwarf” variety, 17–21 mm long and 8–10 mm wide; the holotype is 19 × 9 mm (shell width/shell length, 0.47), i.e. proportionally wider than the typical form. *Plagiodontes multiplicatus parvus* is by far the most common and widely spread subspecies; it was morphometrically analysed and compared by Pizá and Cazzaniga (2003) and Pizá et al. (2006).

In the 1960s, Dr Wolfgang Weyrauch labelled some “dwarf” specimens either as “*Plagiodontes pusillus*” or as “*P. multiplicatus elongatus*” (nomina nuda) in the collection of Fundación Miguel Lillo (Tucumán, Argentina). Our recent study of these specimens, together with an assessment of shell morphometry and internal anatomy of recently collected specimens, revealed that these “dwarf” specimens are a different species. In recognition of Dr Weyrauch’s unpublished antecedent, we are naming it *Plagiodontes weyrauchi* sp. nov.

Genital anatomy was compared with the other four small-sized species in the genus (<25 mm long), i.e. *P. dentatus* (Wood, 1828), *P. multiplicatus parvus* Hylton-Scott, 1952, *P. rocae* Doering, 1881, and small adult specimens of *P. patagonicus* (d’Orbigny, 1835). Though some anatomical information has been published on the latter two species (Cazzaniga et al. 2005; Pizá et al. 2006), there were no records of the anatomy of *P. multiplicatus parvus* and *P. dentatus*. Our new data show that some of the five species studied have either a simple inner papilla (verge) in the penis, or a verge with an additional lobe, which may be as large as, or larger than, the verge itself. These features and the internal structure of the genital organs were not previously assessed for this genus and contribute new evidence for specific discrimination.

Material and methods

Study area

Live specimens of *Plagiodontes weyrauchi* sp. nov. were collected from Cuesta de la Chilca (Figure 1A), on the northern limit of the Ambato-Manchao mountain range, Catamarca province, Argentina. Ambato-Manchao is a sierra of north–south direction located from 27°50′ to 28°50′ S, at about 66°50′ W; its summits reach up to 4300 m above sea level (Cerro Manchao). General climate is temperate arid to semi-arid. Relief is a main factor affecting climate because it acts on the humid winds from the northeast causing scarce but torrential summer precipitations, which decrease to the west and create multiple microclimates in isolated valleys. From a phytogeographical



Figure 1. Cuesta de la Chilca, Catamarca province, Argentina. (A) Type locality of *Plagiodontes weyrauchi* sp. nov.; (B) Prepuna vegetation at Cuesta de la Chilca.

point of view, the studied area is part of the Prepuna province (Chaco Domain), though it has several elements of the Monte province (Cabrera and Willink 1973). Prepuna is the characteristic ecosystem of the dry slopes and ravines of the northwest mountains of Argentina, above the xerophytic woodlands of the Monte province. The latter are composed of a xerophytic shrub steppe with an abundance of Bromeliaceae and Cactaceae (*Trichocereus* spp. and *Opuntia* spp.) (Figure 1B).

Studied material

We have studied fresh collected material (shells and living snails) and museum specimens as detailed in Table 1. Figure 2 shows the collecting sites of the studied material.

Table 1. List of the studied material of *Plagiodontes weyrauchi* sp. nov., *P. multiplicatus parvus*, *P. dentatus*, *P. rocae* and *P. patagonicus*.

Set	M	A	Locality (Province): Lat., Long.	Collection data; collector, date of collection; number of specimens
<i>P. weyrauchi</i> sp. nov.				
1	M	A	Cuesta de la Chilca, 22 km far from Andalgalá, (Catamarca): 27°38'19" S, 66°10'27" W	45 living snails, of which 25 shells were used for morphometrical analysis and 6 specimens were dissected; 16 specimens were selected as the type series: MACN-In 37.465 [Holotype: alcohol-preserved specimen], MACN-In 37.466 [Paratypes: 3 shells and 2 alcohol-preserved specimens], MLP 12.673 [Paratypes: 3 shells] and 12.674 [Paratypes: 2 alcohol-preserved specimens], FML 15.145 [Paratypes: 3 shells] and FML 15.145A [Paratypes: 2 alcohol-preserved specimens]; J. Pizá and M. Carrizo, 2007. FML 1585; W. Weyrauch, 1968; 5 shells. Note: labelled as <i>Plagiodontes pusillus</i> (nomen nudum) by Dr Weyrauch.
2	M		Cuesta de la Chilca, 29 km from Andalgalá on the road to Concepción, (Catamarca)	FML 645; Schreiter, 1927; 3 shells. Note: labeled as <i>Plagiodontes multiplicatus elongatus</i> (nomen nudum) by Dr. Weyrauch.
3	M		Vipos, (Tucumán): 26°29' S, 65°20'60" W	MLP no number (formerly M.I. Hylton-Scott personal collection); Cichero, 1968; 7 shells. Note: this set also contains eight specimens of <i>Plagiodontes multiplicatus</i> Doering, 1875.
4	M		Cuesta de Andalgalá (Catamarca)	FML no number; C. Molineri, 2006; 2 alcohol-preserved specimens (one of them was dissected).
5	A		Margins of the Villavil river, close to the Mineraloduct, Andalgalá Department, (Catamarca)	
<i>P. multiplicatus parvus</i> Hylton-Scott 1952				
6	M	A	Negra Muerta, (Santiago del Estero): 28°58' S, 63°58' W	MLP 36082; 20 shells and 1 alcohol-preserved specimen.
7	M		Siján, Pie de Ambato (Catamarca): 28°15' S, 66°12' W	MLP no number (formerly M.I. Hylton-Scott personal collection); 20 shells.
	A		Chumbicha (Catamarca): 28°51'29" S, 66°16'44" W	Own material; J. Pizá and M. Carrizo, 2005; 3 alcohol-preserved specimens.
<i>Plagiodontes dentatus</i> (Wood, 1828)				
8	M		Montevideo, on the way to Artigas (Uruguay): 34°53' S, 56°11' W.	MACN-In 9345; 20 shells.
9	M		Victoria (Entre Ríos): 32°37' S, 60°10' W	MLP 36.084; 20 shells.
10	A		Victoria (Entre Ríos): 32°37' S, 60°10' W	Own material; J. Pizá, 2007; 5 alcohol-preserved specimens.

- P. rocae* Doering, 1881**
- 10 M Sierra de Curamalal, (Buenos Aires) MACN 14199; L. Hauman, 1924; 5 shells.
 11 M Sierra de Curamalal (Buenos Aires) MACN 11084; Kraglievich, 1892; 1 shell.
 12 M Ventania Mountain System MACN 9844; L. Hauman; 3 shells.
 13 M Curamalal Chico Mountain (Buenos Aires): 37°41' S, 62°18' W; 741. Own material; N Ghezzi, 2002; 10 shells.
- 14 M A Curamalal Grande Mountain (Buenos Aires): 37°43'19" S, 62°14'02" W Own material; J. Pizá, 2006; 21 shells and 5 alcohol-preserved specimens.
- P. patagonicus* (d'Orbigny 1835)**
- 15 M Estancia Las Mañanitas, National Road 33 km 8 (Buenos Aires); 38°41' S, 62°15' W Own material; P. Martín, 2002; 20 shells.
 16 M Cueva de los Leones, National Road 33 km 11 (Buenos Aires); 38°41' S, 62°15' W Own material; J Pizá, 2002; 20 shells.
 17 A Puente Canesa, Carrindanga way km 25; 38°35' S, 62°04' W (Buenos Aires) Own material; J Pizá, 2007; 5 alcohol-preserved specimens.

M: sets included in morphometric analyses; A: sets on which pallial and genital anatomy was studied.

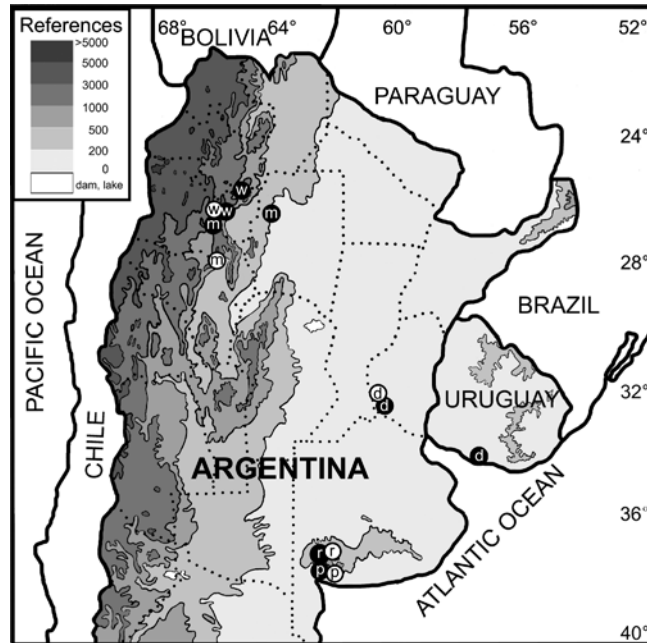


Figure 2. Map of the collecting localities of the studied material. Abbreviations: d, *Plagiodontes dentatus*; m, *P. multiplicatus parvus*; p, *P. patagonicus*; r, *P. rocae*; w, *P. weyrauchi* sp. nov. References: white circles, own material; black circles, museum collections.

Shell variability

Figure 3 shows some representative specimens of the five species that are compared in this paper. Shell variability was analysed for 200 shells, each species being represented by 40 shells as detailed in Table 1.

All shells showed fully developed apertural folds and lamellae, and they had a reflected outer aperture lip indicating adulthood. Six linear and two angular variables were measured on shell drawings made with a camera lucida device on a

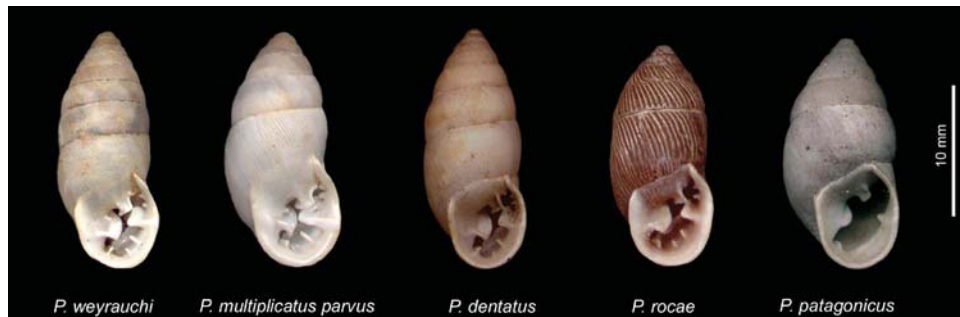


Figure 3. Representative shells of the five *Plagiodontes* species under comparison. Own material.

stereoscopic microscope: shell length (SL), shell width (SW), last whorl length (LWL), aperture major length (AML), aperture length (AL) and aperture width (AW); the major angle (MA) and the spiral angle (SA) were also determined as described in Pizá and Cazzaniga (2003).

Characteristics of the apertural folds and whorl numbers were determined by direct observation under a stereoscopic microscope. Protoconch and teleoconch sculpture of juvenile shells was analysed with a JEOL 35 CF scanning electronic microscope.

Quantitative data of the five species were analysed by multivariate principal component analysis to assess how the specimens of *P. weyrauchi* sp. nov. and those of the similar-sized species fit within the morphospace defined by the morphometric variables studied.

A multivariate discriminant analysis was then applied to *P. weyrauchi* sp. nov. and *P. multiplicatus parvus*, which are the only small forms living in central–north Argentina (Area 1 in Pizá and Cazzaniga 2003).

Multivariate analyses were performed using the SPSS statistical package, which also provided descriptive parameters (mean, standard deviation, coefficient of variation and range) and proportions of data. Significance of differences of linear measurements and their proportions between groups was checked through Bonferroni's corrected *t*-tests.

Internal anatomy

Table 1 indicates the collections on which anatomy of the pallial complex and genital system was studied.

Living specimens were drowned in previously boiled water, fixed and preserved in 70% ethanol. Dissections and illustrations were made using a stereoscopic microscope (Zeiss Stemi SV6) with a camera lucida device. Terminology used to describe the genital system follows Tompa (1984).

Results

Family **ORTHALICIDAE** Albers, 1860
Subfamily **Odontostominae** Pilsbry and Vanatta, 1898
Genus ***Plagiodontes*** Doering, 1877

Shell rimate, oblong, with 6.5 to 8 whorls compactly coiled, the protoconch having axial striae slightly decussated by minor spiral lines, last whorl large. Aperture subvertical, ovate, obstructed by three major lamellae, 0 to 5 small folds and a transverse barrier behind the lower palatal folds. Endemic from Uruguay and Argentina.

Type species: *Helix dentata* Wood, 1828 from Montevideo, Uruguay [subsequent designation by Pilsbry, 1898].

***Plagiodontes weyrauchi* sp. nov.**

Plagiodontes pusillus Weyrauch, ca. 1968, in schedula (nomen nudum).

Plagiodontes multiplicatus elongatus Weyrauch, ca. 1968, in schedula (nomen nudum).

Diagnosis

Shell greyish-brown, thin, quite translucent, elongate-cylindrical. Adults 16.7–22.3 mm long have a relatively smaller width (mean 40% of the shell length) and a higher number of whorls (8–9.75) than any other *Plagiodontes* species within its size range. Low proportion of the last whorl length (mean 57%) and aperture (mean 38%) to shell length. Aperture occluded by 10–12 teeth (lamellae + folds). Protoconch with axial costae crossed by straight spiral lines; teleoconch with straight, thin costae. Ureteric pore opening at the level of the upper third of the kidney. Genital system of proportionally small size (19–22 mm long). Penis papillae (verge) with a small accessory lobe. Inner surface of the vagina with parallel long lamellae that rarely show some weak anastomosis.

Type series

Holotype, MACN-In 37,465 (alcohol-preserved specimen) 19 mm long, 8.4 mm wide; 5 paratypes, MACN-In 37,466 (3 shells and 2 specimens in alcohol); 5 paratypes, MLP 12,673 (3 shells) and MLP 12,674 (2 specimens in alcohol); 5 paratypes, FML 15,145 (3 shells) and FML 15,145 A (2 specimens in alcohol).

Type locality

Cuesta de la Chilca, 22 km to the East of Andalgalá on the Provincial Route 48 (27°38'19" S, 66°10'27" W), 1455 m above sea level, Catamarca province, Argentina.

Other known localities

Villavil river, Andalgalá Department, Catamarca province, Argentina. Vipos (26°29' S, 65°22' W), Tucumán province, Argentina.

Etymology

Dedicated to the late Dr Wolfgang K. Weyrauch (1907–1970). A short biography and a list of his malacological contributions were recently compiled by Barbosa et al. (2008).

Description

Shell elongate-cylindrical, greyish brown, thin (pulmonary vein, kidney and pericardium are visible by transparency in live and alcohol-preserved specimens) (Figure 4). Spiral angle from 29° to 46°, major angle from 121° to 138°; 8–9.75 slightly convex whorls, the spire being about 40–46% the length of the shell, with a conical apex. Adult size ranging from 16.6 to 22.3 mm long, 7.1 to 9.0 mm wide. Narrowly perforated to rimate umbilicus (Figure 5). Shell variability is represented in Figure 6.

The protoconch has 2–2.5 whorls, with slightly undulated axial striae and some anastomoses in the first whorl (Figure 7A,D); protoconch ribs are decussated by straight spiral lines (Figure 7B). The limit between protoconch and teleoconch is well defined (Figure 7D). The teleoconch presents a regular striation of thin but conspicuous axial costae (Figure 7C,E).

Aperture 6.3–8.4 mm long, 5.3–7.4 mm wide, subvertical ovate with a thickened, expanded and slightly reflected adult peristome (Figure 8B), partially occluded by 10–12 teeth (lamellae + folds) (Figure 8A). The transverse lamella is long and



Figure 4. *Plagiodontes weyrauchi* sp. nov. Living snail.



Figure 5. *Plagiodontes weyrauchi* sp. nov. Holotype.

straight. A tongue-shaped columellar lamella is the largest piece occluding the aperture; its outer border is thick and slightly elevated. A minute supracolumellar knob appeared on the columellar lamella of most specimens (97.5%). The parietal lamella is dihedral, its faces forming an L-profile; it is seen as a quadrangular plate when viewed from the apertural plane and it is sometimes united to the angular fold. Two suprapalatal folds are present; the upper one is usually triangular and the lower one is always compressed. The upper palatal lamella is rectangular, with the outer border thickened and elevated; its lateral borders are curved upwards. The lower palatal folds were present in all specimens, with 41% of specimens showing one and 59% showing two; when two lower palatal folds were present, the most developed one was that located next to the upper palatal lamella (principal lower palatal). The basal fold is laterally compressed and generally larger than the principal lower palatal fold.

Pallial complex (Figure 9). The pallial complex is narrow and elongated, 30 mm long on average. A nearly triangular kidney is located proximally in the lung cavity alongside the periaortic intestinal bend. The kidney is twice as long as wide and occupied 24% of the length of the lung.



Figure 6. Shell variability of *Plagiodontes weyrauchi* sp. nov. from Cuesta de la Chilca, Argentina.

The primary ureter runs along the rectal side of the kidney up to the top of the lung cavity; it then turns down along the rectum and forms the secondary ureter, which opens in the ureteric pore at the level of the upper third of the kidney. From this point on, the open secondary ureter is delimited by two ridges forming a ureteric groove that ends at the pneumostome. The ad-rectal ridge is less developed than the ab-rectal one.

The pericardium, located in the upper columellar side of the pallial system, is 2.4–5.4 mm long. It is continuous with the prominent pulmonary vein that runs parallel to the rectum and reaches the mantle collar. The pulmonary vein is 15.0–24.4 mm long.

The afferent marginal vein branches out approximately from the distal third of the pulmonary vein, equalling about 41% of its length.

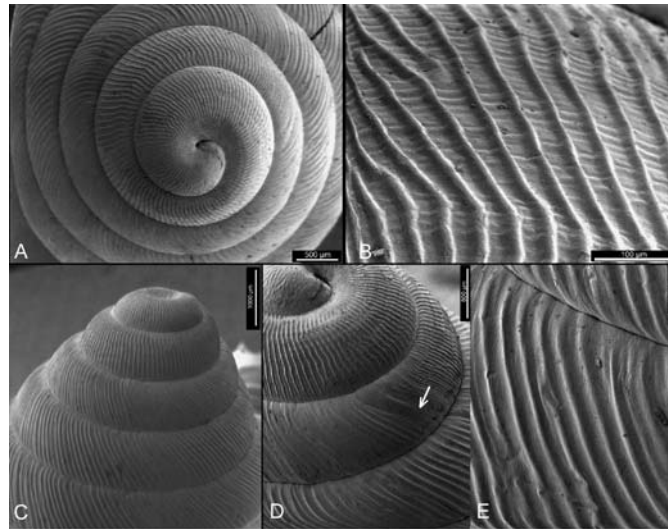


Figure 7. Scanning electron micrographs of the protoconch and teleoconch sculpture in *Plagiodontes weyrauchi* sp. nov. (A) Protoconch and first teleoconch whorls; (B) close-up of (A) showing the spiral lines crossing the axial striae; (C) protoconch and teleoconch sculpture; (D) protoconch–teleoconch limit (arrow); (E) close-up of (C) showing axial costae of the teleoconch.

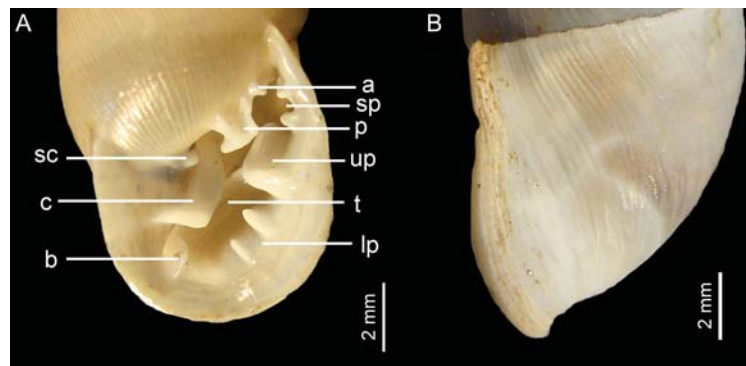


Figure 8. Apertural characteristics of *Plagiodontes weyrauchi* sp. nov. (A) Lamellae and folds nomenclature; (B) expanded and slightly reflected peristome. Abbreviations: a, angular fold; b, basal fold; c, columellar lamella; lp, lower palatal fold; p, parietal lamella; sc, supracolumellar knob; sp, suprapalatal folds; t, transverse lamella; up, upper palatal lamella.

The studied material showed a moderate vascularization on the ad-rectal area between the rectum and the pulmonary vein, and between the pulmonary vein and the marginal afferent vein. A marginal vein of weak development branches out from the last portion of the pulmonary vein and runs along the mantle collar border.

The mantle collar includes a whitish spongy pallial gland and several indentations corresponding to the apertural teeth.

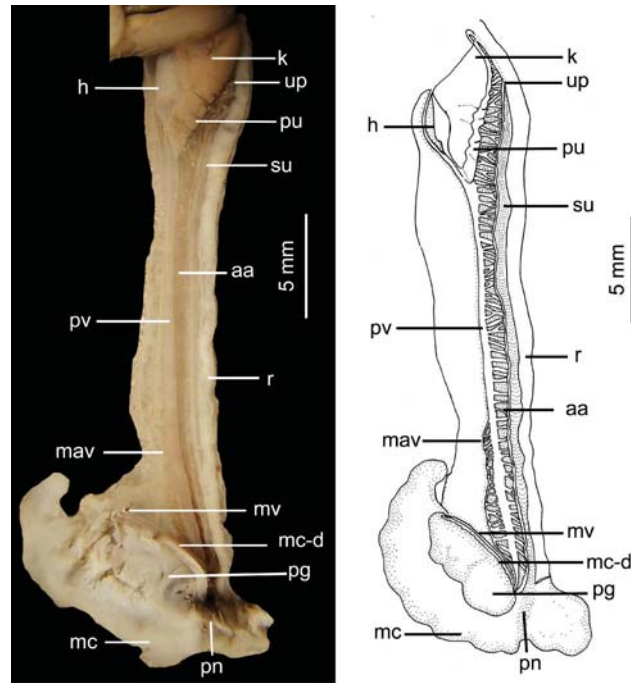


Figure 9. Pallial complex of *Plagiodontes weyrauchi* sp. nov. Abbreviations: aa, ad-rectal area; h, heart; k, kidney; mav, marginal afferent vein; mc, mantle collar; mb-d, mantle border and diaphragm junction; mv, marginal vein; pg, pallial gland; pn, pneumostome; pu, primary ureter; pv, pulmonary vein; r, rectum; su, secondary ureter; up, ureteric pore.

Reproductive system (Figures 10, 11). The ovotestis, embedded in the digestive gland, is composed of four to six groups of digitiform acini. The hermaphroditic duct is brown, markedly convoluted, and runs along the columellar side. The central portion of the duct is inflated to form the vesicula seminalis. The albumen gland is elongated, brownish orange, and lies against the anterior, concave surface of the digestive gland over the digestive pouch. The fertilization pouch–spermathecal complex is white, conspicuous and visible on the basal side of the albumen gland (Figure 10C,D). The fertilization pouch–spermathecal complex is proximally swollen, while the distal part is composed of a blind sac.

The spermoviduct is formed by a hyaline whitish-cream oviducal portion (uterus) and a white and glandular prostate. The uterus ends at the free oviduct, while the prostate is continuous with the vas deferens. The latter is a tubule of constant diameter that emerges just above the bifurcation of the vagina to the free oviduct and the bursa copulatrix duct; this bifurcation is marked by a notorious constriction. The vas deferens runs attached to the vagina and penis surface; it passes through the retractor muscle and ends in the epiphallus–flagellum boundary. It is shorter than the sum of the length of the penis and the epiphallus. The penis retractor muscle is attached to the penis–epiphallus boundary.

The bursa copulatrix or gametolytic gland is a round sac, 1.6 mm in diameter. The bursa copulatrix duct is about 18.3 mm long; internally it has straight folds or lamellae.

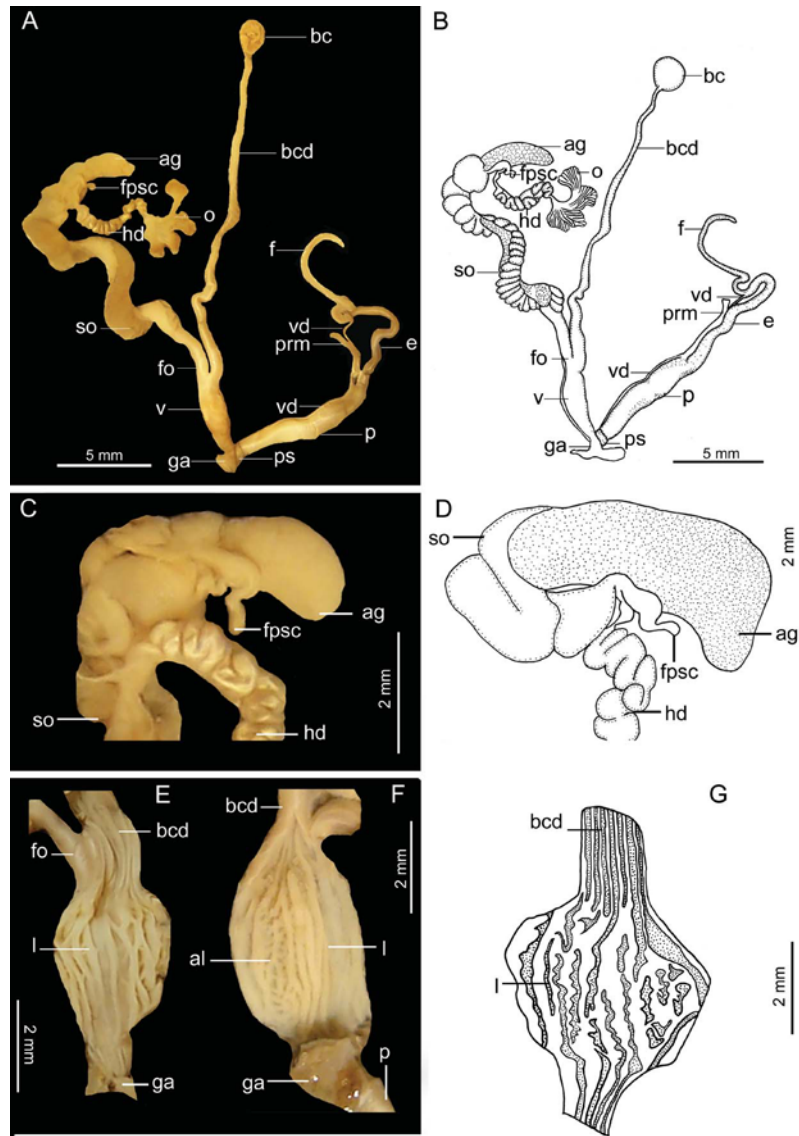


Figure 10. Genital system of *Plagiodontes weyrauchi* sp. nov. (A,B) Complete genital system; (C,D) proximal genitalia; (E–G) variability of the vaginal internal structure. Abbreviations: ag, albumen gland; al, anastomosed lamellae; bc, bursa copulatrix; bcd, bursa copulatrix duct; e, epiphallium; f, flagellum; fo, free oviduct; fp, fertilization pouch–spermathecal complex; ga, genital atrium; hd, hermaphroditic duct; l, straight lamellae; o, ovotestis; p, penis; pr, penis retractor muscle; ps, penial sheath; so, spermoviduct; v, vagina; vd, vas deferens.

The penial complex, 19.4–25.3 mm long, occupies a high proportion of the anterior portion of the visceral cavity. It is composed of the penis, epiphallium and flagellum (Figure 11). The penis, *c.* 7.8 mm long, is subcylindrical to club-shaped, with a slight proximal swelling 1.8–3.1 mm wide. The penial sheath is very short. Internally, the

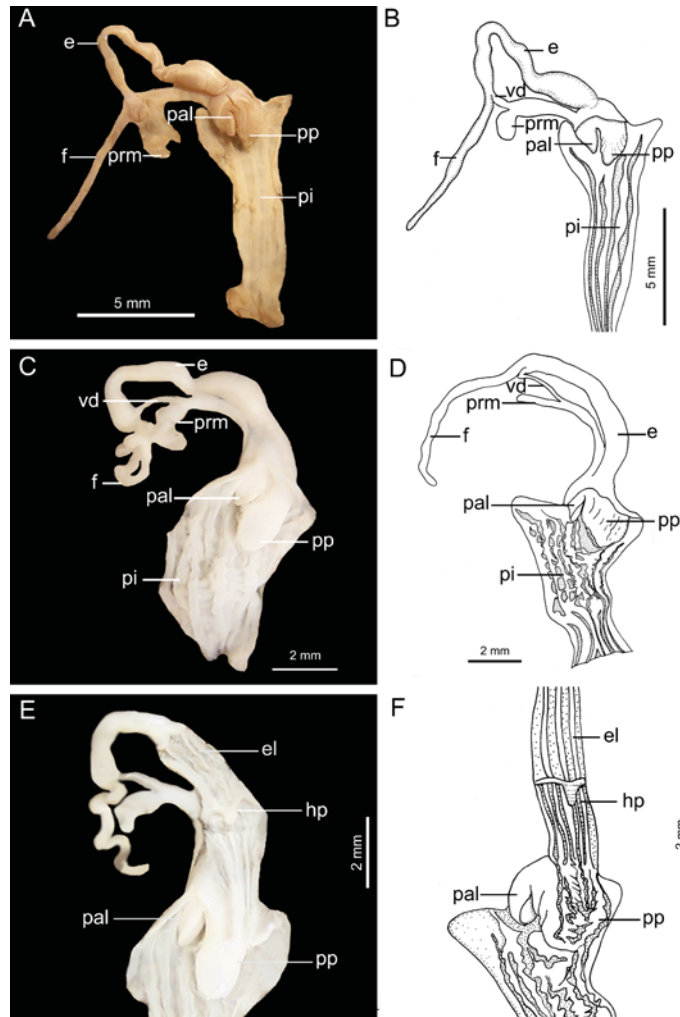


Figure 11. Terminal male genitalia of *Plagiodontes weyrauchi* sp. nov. (A–D) Variability of the penis internal structure; (E,F) internal structure of the epiphallus and penial papilla. Abbreviations: e, epiphallus; el, epiphallic lamellae; f, flagellum; prm, penis retractor muscle; hp, hollow papilla of the epiphallus; pal, penial papilla accessory lobe; pi, pilaster; pp, penial papilla; vd, vas deferens.

penis has a penial papilla or verge with a small accessory lobe about a third to half the size of the papilla; the papilla is continuous with the epiphallus (Figure 11E,F). The inner wall of the penis has four or five longitudinal folds or pilasters that are prominent, undulated, and can be to some extent anastomosed. The pilasters do not extend underneath the papilla. The epiphallus 6.5–10.0 mm long is cylindrical, and its transition to the penis is not clearly marked by a constriction. Internally, it has five straight folds and has a proximal partition at the point where the folds join to form a minute hollow papilla. The epiphallus continues in a cylindrical tube running into the fleshy penial papilla. This tube has an internal sculpture of elevated and branched, anastomosed folds (Figure 11E, F).

The vas deferens insertion demarcates the limit between epiphallus and flagellum. The flagellum, from 4.0 to 7.7 mm long, is cylindrical and has three straight folds that gradually merge to form one internal fold. It is as long as the epiphallus though markedly thinner.

The vagina is shorter than the penis, about 2.4 times as long as wide, and centrally swollen. The inner vaginal surface bore about 10 longitudinal, parallel lamellae with some anastomoses that do not give it a general reticulated aspect (Figure 10E); two out of the seven dissected specimens showed some higher degree of reticulation (Figure 10F). A genital atrium is almost absent, because the vagina and penis merge together at the genital pore.

Comparative shell morphometry

Principal component analysis on shell parameters of the five compared species yielded two principal components with eigenvalues >1 accounting for 84.4% of the total variance (Table 2; Figure 12). Principal component 1 (PC1), a size and shape axis, was positively correlated with the linear variables and the spiral angle, while it was negatively correlated with the major angle. PC2 positively correlated with the shell length and the major angle, and negatively correlated with the spiral angle. The scatter plot in Figure 11 shows that *P. weyrauchi* sp. nov. mostly scored in the quadrant defined by negative values of PC1 and positive values of PC2, mainly because of its smaller general size and more acute shell (higher values of the major angle and lower values of the spiral angle and linear variables, except the shell length, which amply overlaps the range of other species; Table 3).

The remaining species were grouped at the intersection of the axes, though each one spread out towards a definite direction. While *P. patagonicus* from southern Buenos Aires province mainly scored on the quadrant defined by positive values of PC1 and negative values of PC2 because of its larger and more rounded shell, its sympatric species, *P. rocae*, scored towards positive values of both axes because of its slender and relatively large shell. Most scores of *P. dentatus* and *P. multiplicatus parvus* overlapped in intermediate values, but the former species tended to score in negative values of both components (small and slender shells) and the latter scored positively for PC1.

Multivariate discriminant analysis of the two forms inhabiting the Pampean Sierras in central Argentina, namely *P. weyrauchi* sp. nov. and *P. multiplicatus parvus*, yielded 100% correct classification, i.e. the discriminant scores of the two species did not overlap at all (Figure 13). *Plagiodontes weyrauchi* specimens scored towards

Table 2. Principal component analysis on adult shells of five species of genus *Plagiodontes* sharing a similar size range (*P. weyrauchi* sp. nov., *P. rocae*, *P. patagonicus*, *P. multiplicatus parvus* and *P. dentatus*): correlation of the original variables and the principal components PC1 and PC2.

Variable	SL	SW	LWL	AL	AW	AML	MA	SA
PC1	0.494	0.921	0.940	0.958	0.737	0.929	-0.422	0.514
PC2	0.830	-0.088	0.181	0.132	-0.002	0.122	0.807	-0.773

AL, aperture length; AML, aperture major length; AW, aperture width; LWL, length of the last whorl; MA, major angle; SA, spiral angle; SL, shell length; SW, shell width.

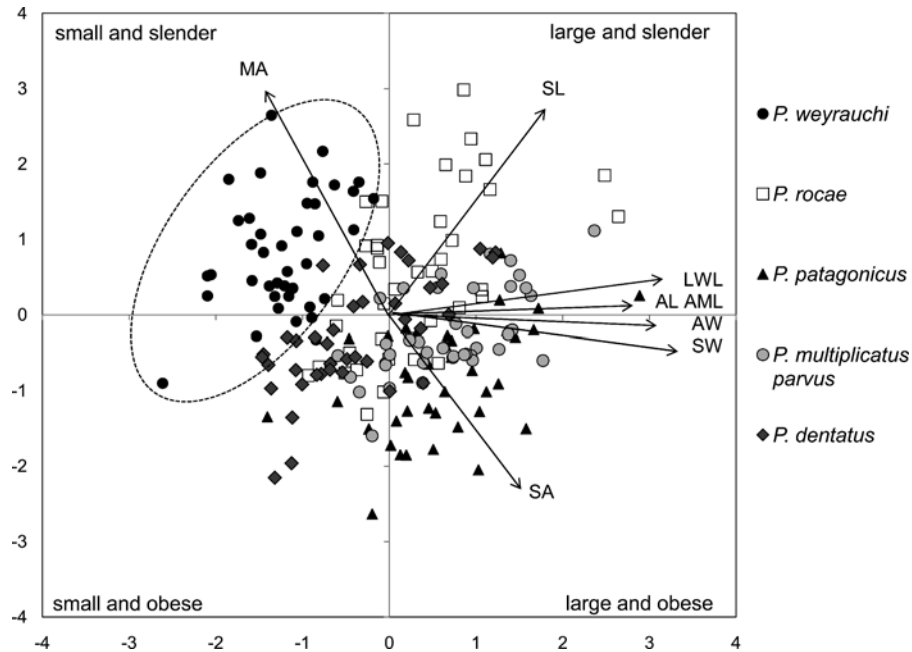


Figure 12. Scatter plot of the scores of the principal components 1 and 2 of the principal components analysis performed on shell measurements of *Plagiodontes weyrauchi*, *P. rocae*, *P. patagonicus*, *P. multiplicatus* and *P. dentatus*. Abbreviations: AL, aperture length; AML, aperture major length; AW, aperture width; LWL, length of the last whorl; MA, major angle; SA, spiral angle; SL, shell length; SW, shell width.

positive values of the discriminant function because of its smaller size and more slender shell, whereas *P. multiplicatus parvus* scored towards negative values, correlating with the spiral angle and lineal measurements (Table 4).

Bonferroni's comparisons between all pairs of species showed that *P. weyrauchi* significantly differs from the remaining species in its shell width, last whorl length, aperture length, major aperture length, spiral and major angles, and by the proportions SW/SL, LWL/SL and AL/SL (Table 3). Furthermore, the number of whorls partially overlaps only with *P. rocae* from the Sierra of Curamalal, Buenos Aires province.

Internal anatomy of similar species

Plagiodontes dentatus (Wood, 1828)

The pallial complex ranged from 20 to 27 mm (Figure 14A,B). It is whitish, translucent and poorly vascularized. The triangular kidney is nearly twice as long as wide and occupies 30% the length of the lung.

The ureteric pore is located slightly below the level of the midpoint of the kidney. From that point, the open secondary ureter is delimited by two ridges forming a ureteric groove ending in the pneumostome, the ad-rectal ridge being less developed than the ab-rectal one.

Table 3. Summary of shell variables and proportions of *Plagiodontes weyrauchi* sp. nov. and four species within a same size range.

	<i>P. weyrauchi</i>	<i>P. rocae</i>	<i>P. patagonicus</i>	<i>P. multiplicatus</i>	<i>P. dentatus</i>
SL	19.77 ± 1.22 [0.062] (16.65–22.34)	20.79 ± 2.13 [0.102] (17.66–25.06)	19.01 ± 1.41 [0.074] (16.30–22.01)	19.81 ± 1.28 [0.065] (17.20–23.03)	19.05 ± 1.54 [0.081] (16.02–22.16)
SW	7.96 ± 0.45 [0.057] (7.14–8.99)	9.39 ± 0.63 [0.068] (8.34–11.00)	9.75 ± 0.77 [0.079] (8.00–12.10)	9.42 ± 0.65 [0.069] (8.31–10.64)	8.64 ± 0.61 [0.071] (7.61–9.91)
LWL	11.21 ± 0.63 [0.056] (9.35–12.49)	13.25 ± 0.89 [0.067] (12.15–15.71)	13.03 ± 0.82 [0.063] (10.90–15.31)	13.54 ± 0.81 [0.060] (11.81–15.74)	12.17 ± 0.94 [0.077] (10.64–14.14)
AL	7.54 ± 0.50 [0.066] (6.28–8.42)	8.63 ± 0.71 [0.083] (7.35–10.57)	8.82 ± 0.65 [0.074] (7.10–10.64)	8.85 ± 0.59 [0.067] (7.73–10.20)	7.97 ± 0.65 [0.082] (7.00–9.48)
AW	6.44 ± 0.41 [0.064] (5.26–7.39)	6.81 ± 0.69 [0.102] (5.30–8.57)	6.84 ± 0.72 [0.105] (5.45–8.89)	7.20 ± 0.48 [0.066] (6.12–8.45)	6.72 ± 0.47 [0.069] (5.83–7.73)
AML	7.66 ± 0.48 [0.063] (6.43–8.57)	8.75 ± 1.02 [0.116] (4.38–11.00)	9.07 ± 0.63 [0.070] (7.50–10.64)	9.10 ± 0.57 [0.063] (8.02–10.35)	8.18 ± 0.67 [0.082] (7.00–9.77)
MA	128.83 ± 3.73 [0.029] (121–138)	125.03 ± 3.53 [0.028] (119–134)	117.40 ± 3.44 [0.029] (111–125)	120.85 ± 2.38 [0.020] (115–125)	122.1 ± 2.69 [0.022] (113–129)
SA	35.53 ± 3.75 [0.106] (29–46)	43.63 ± 5.46 [0.125] (33–54)	49.58 ± 5.16 [0.104] (40–58)	48.38 ± 3.39 [0.070] (43–60)	44.18 ± 3.27 [0.074] (37–53)
Whorl number	9.06 ± 0.39 [0.043] (8–9.75)	7.14 ± 0.51 [0.071] (6.25–8.25)	6.23 ± 0.58 [0.092] (5.00–7.25)	6.74 ± 0.29 [0.044] (6.00–7.25)	7.21 ± 0.26 [0.036] (6.50–7.75)

(Continued)

Table 3. (Continued)

	<i>P. weyrauchi</i>	<i>P. rocae</i>	<i>P. patagonicus</i>	<i>P. multiplicatus</i>	<i>P. dentatus</i>
Size (W+L)	27.73 ± 1.43 [0.051] (23.81–30.98)	30.18 ± 2.63 [0.087] (26.28–35.30)	28.76 ± 1.92 [0.067] (25–33.24)	29.23 ± 1.84 [0.063] (25.80–33.53)	27.69 ± 2.03 [0.073] (23.98–31.78)
W/L	0.40 ± 0.03 [0.069] (0.33–0.47)	0.45 ± 0.03 [0.069] (0.39–0.51)	0.51 ± 0.04 [0.077] (0.44–0.60)	0.48 ± 0.02 [0.043] (0.42–0.52)	0.45 ± 0.03 [0.058] (0.41–0.52)
LWL/L	0.57 ± 0.01 [0.025] (0.54–0.60)	0.64 ± 0.04 [0.057] (0.57–0.70)	0.69 ± 0.03 [0.042] (0.62–0.76)	0.68 ± 0.02 [0.032] (0.64–0.72)	0.64 ± 0.02 [0.032] (0.60–0.68)
AW/AL	0.86 ± 0.04 [0.050] (0.76–0.96)	0.79 ± 0.08 [0.106] (0.64–0.91)	0.78 ± 0.05 [0.069] (0.65–0.84)	0.81 ± 0.04 [0.051] (0.65–0.87)	0.85 ± 0.04 [0.050] (0.75–0.94)
AL/L	0.38 ± 0.02 [0.049] (0.34–0.43)	0.42 ± 0.03 [0.065] (0.36–0.48)	0.46 ± 0.03 [0.064] (0.42–0.54)	0.45 ± 0.02 [0.037] (0.41–0.48)	0.42 ± 0.02 [0.039] (0.38–0.45)
AW/L	0.33 ± 0.02 [0.064] (0.26–0.39)	0.33 ± 0.05 [0.142] (0.24–0.40)	0.36 ± 0.04 [0.100] (0.28–0.42)	0.36 ± 0.02 [0.064] (0.28–0.41)	0.35 ± 0.02 [0.059] (0.31–0.40)

Mean ± standard deviation [coefficient of variation] (minimum–maximum). Measurements in mm. Bonferroni's corrected *t*-test: different letters indicate significant differences (global α : 0.05, individual α : 0.005), $n = 40$ for each species.

AL, aperture length; AML, aperture major length; AW, aperture width; LWL, length of the last whorl; MA, major angle; SA, spiral angle; SL, shell length; SW, shell width.

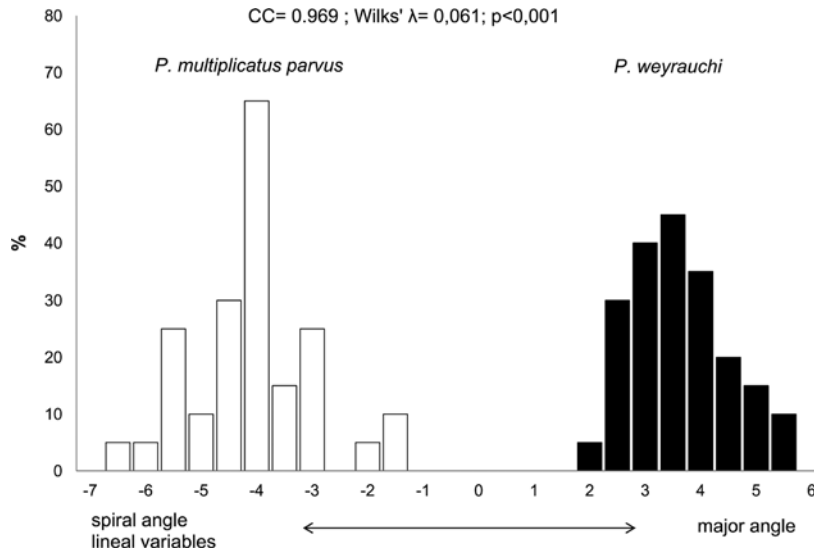


Figure 13. Frequency histogram of the discriminant function 1 scores of the multiple determinat analysis performed on shell measurements of *Plagiodontes weyrauchi* sp. nov. and *P. multiplicatus parvus*. Abbreviation: CC, canonical correlation.

Table 4. Structure matrix of the correlation coefficients among the original variables and the discriminant function (DF1) for *Plagiodontes weyrauchi* and *P. multiplicatus parvus*.

Variable	SA	LWL	AML	SW	MA	AL	AW	SL
DF1	-0.465	-0.414	-0.354	-0.336	0.330	-0.309	-0.219	-0.004

AL, aperture length; AML, aperture major length; AW, aperture width; LWL, length of the last whorl; MA, major angle; SA, spiral angle; SL, shell length; SW, shell width.

The pericardium is about 3.5 mm long and the pulmonary vein is 11.3–18.5 mm long. The afferent marginal vein branches out approximately from the distal third of the pulmonary vein, totalling about 50–60% of its length.

The vascularization was noticeable only from the point where the marginal afferent vein branches up to the pneumostome, both in the ad-rectal area and between the pulmonary vein and the marginal afferent vein. The marginal vein is weakly developed. The mantle collar includes a whitish spongy formation or pallial gland.

General arrangement of the genital system closely resembles other species of *Plagiodontes* (Figure 15A,B); the main general differences are its smaller size and a general whitish colour.

Ovotestis composed of four to six groups of digitiform acini. The fertilization pouch–spermathecal complex conspicuous, visible in the basal portion of the albumen gland, with the free portion long and curved. The albumen gland is whitish and triangular, very variable in size (Figure 16A,B).

The bursa copulatrix shape is variable, from spherical to ovoid (Figure 15A,B); its duct, from 13 to 18 mm long, is distally swollen and has internal longitudinal straight folds.

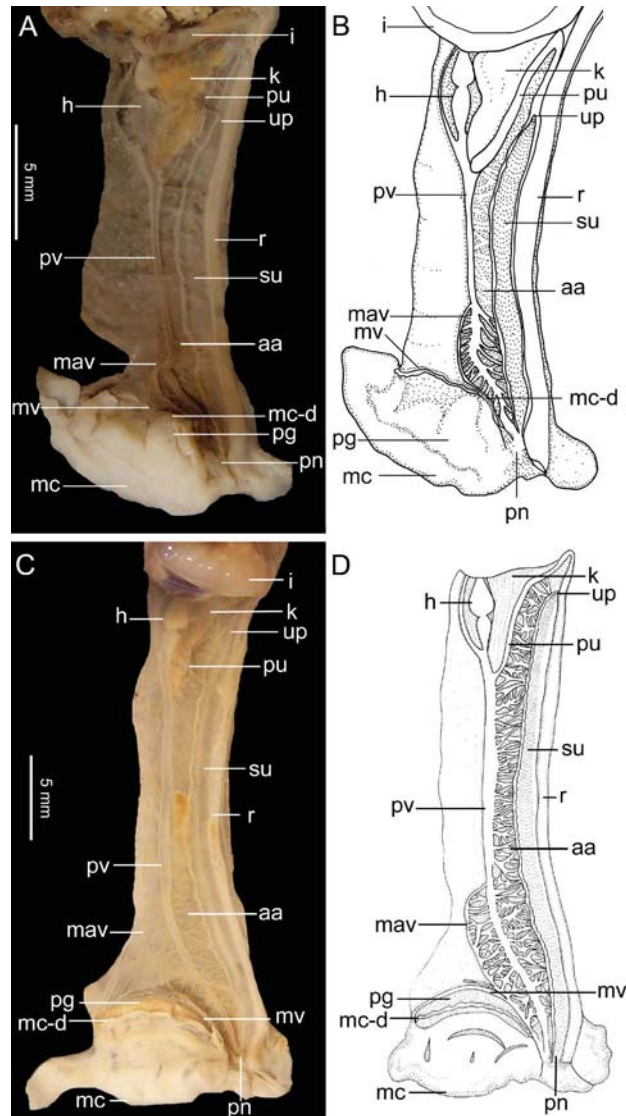


Figure 14. Pallial complex of *Plagiodontes dentatus* and *P. multiplicatus*. (A,B) Pallial complex of *P. dentatus*; (C,D) pallial complex of *P. multiplicatus*. Abbreviations: aa, ad-rectal area; h, heart; i, intestinal bend; k, kidney; mav, marginal afferent vein; mc, mantle collar; mc-d, mantle collar and diaphragm junction; mv, marginal vein; pg, pallial gland; pn, pneumostome; pu, primary ureter; pv, pulmonary vein; r, rectum; su, secondary ureter; up, ureteric pore.

The bifurcation of the vagina in the free oviduct and bursa copulatrix duct is symmetrical and has a constriction.

The vagina, shorter but wider than the penis, has internal longitudinal folds, with few signs of anastomosis, so it does not have the aspect of a reticulum (Figure 17D,E).

The penial complex is from 17 to 21 mm long. The penis is of variable shape (sub-cylindrical to club-shape), from twice to three times as long as wide and slightly

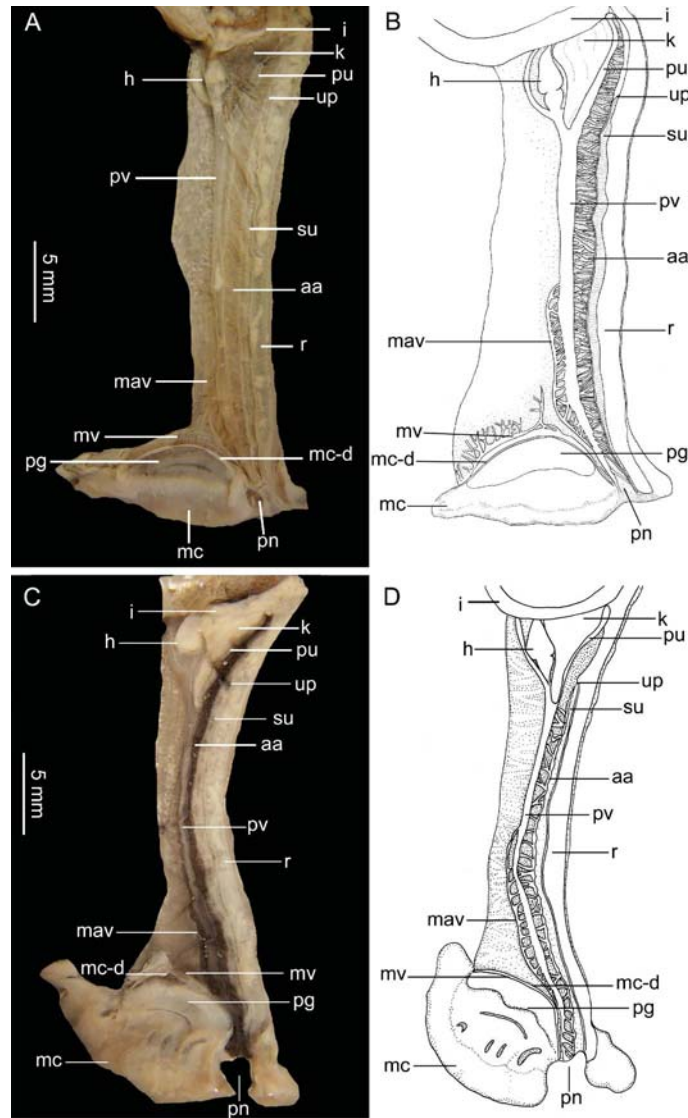


Figure 15. Pallial complex of *Plagiodontes patagonicus* and *P. rocae*. (A,B) Pallial complex of *P. patagonicus*; (C,D) pallial complex of *P. rocae*. Abbreviations: aa, ad-rectal area; h, heart; i, intestinal bend; k, kidney; mav, marginal afferent vein; mc, mantle collar; mc-d, mantle collar and diaphragm junction; mv, marginal vein; pg, pallial gland; pn, pneumostome; pu, primary ureter; pv, pulmonary vein; r, rectum; su, secondary ureter; up, ureteric pore.

shorter than the epiphallus. Internally, it has a simple penial papilla or verge, very short and lacking any additional lobe; the internal tube of the verge is sculptured with anastomosed folds (Figure 17A–C). The inner wall of the penis has longitudinal and undulated pilasters that become thin and straight in the area surrounded by the penis sheath and the genital atrium. The penis–epiphallus transition has a constriction. The epiphallus is cylindrical, with five to seven internal straight longitudinal lamellae. It has

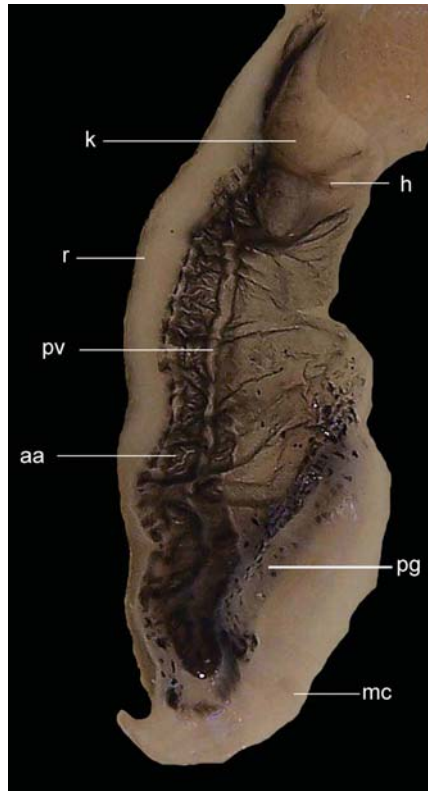


Figure 16. Dorsal view of the pallial complex of *Plagiodontes rocae* showing dark pigmentation. Abbreviations: ada, ad-rectal area; h, heart; k, kidney; mc, mantle collar; pg, pallial gland; pv, pulmonary vein; r, rectum.

a swollen distal portion separated from the cylindrical one by a partition bearing a hollow papilla, which is formed by the junction of the straight lamellae (Figure 17C).

The swollen area has internal undulated and anastomosed minor lamellae; it continues in a tubule running inside the penial papillae (Figure 17C).

The flagellum is cylindrical, slightly thinner than the epiphallus, and has an internal straight longitudinal fold.

Plagiodontes multiplicatus parvus (Hylton-Scott, 1952)

The pallial complex is about 26–31 mm long (Figure 14C,D). A triangular kidney occupies 20% of the lung length. The secondary ureter opens above the level corresponding to the midpoint of the kidney, and is delimited by two ridges of which the ad-rectal one is more developed. Within the pericardium the auricle is much wider than the ventricle.

The pulmonary vein is prominent. The afferent marginal vein branches out at its midpoint. There is a conspicuous vascularization in the ad-rectal area and between the two main veins. The marginal vein, with no branching, runs along the mantle

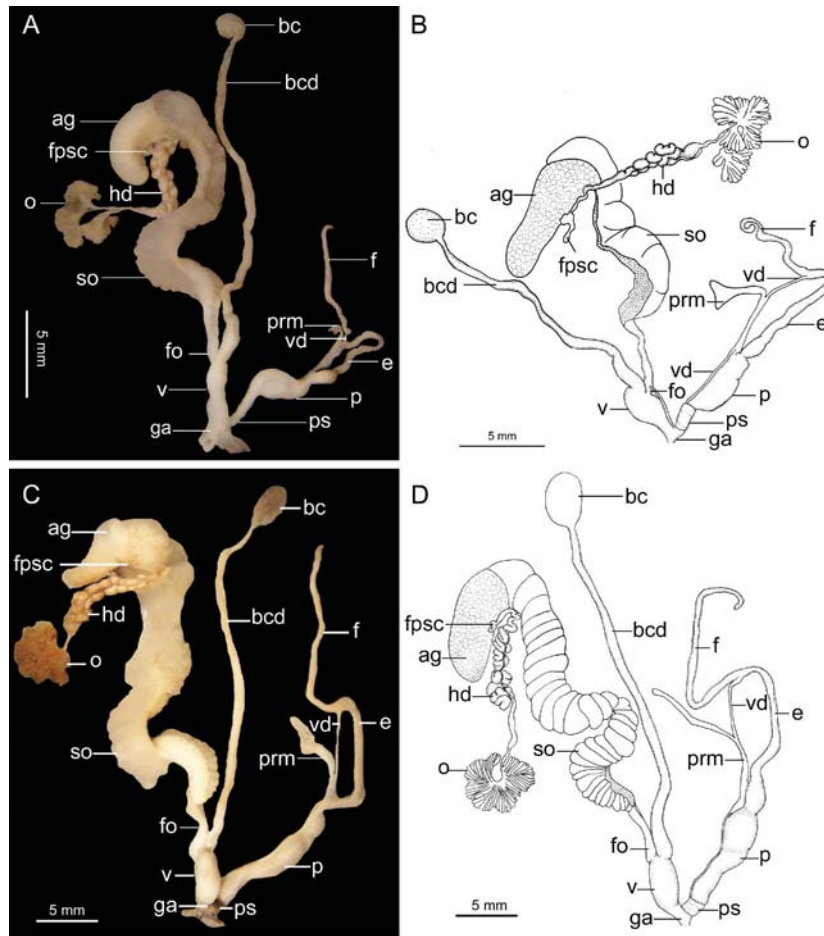


Figure 17. Genital system of *Plagiodontes dentatus* and *P. multiplicatus parvus*. (A,B) Genital system of *P. dentatus*; (C,D) genital system of *P. multiplicatus parvus*. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bcd, bursa copulatrix duct; e, epiphallum; f, flagellum; fo, free oviduct; fpsc, fertilization pouch-spermathecal complex; hd, hermaphroditic duct; o, ovotestis; p, penis; prm, penis retractor muscle; ps, penial sheath; so, spermoviduct; v, vagina; vd, vas deferens.

collar, which has a spongy pallial gland and several indentations that correspond to the position of the apertural teeth.

The genital system is relatively large (Figure 15C,D). The orange-brownish ovotestis is formed by six groups of digitiform acini. The hermaphroditic duct, cream to light-brown in colour, is convoluted and centrally swollen. The fertilization pouch-spermathecal complex, located in the inferior portion of the albumen gland, is white and proximally swollen; it is distally formed by a free L-shaped blind sac. The albumen gland is light brown to pale orange, elongated, of rectangular to triangular shape, and variable in size (Figure 16C,D).

The spermoviduct is a tubular and lobed organ formed by the hyaline white uterus and the opaque white prostatic portion, of glandular aspect. The vas deferens

emerging just above the bifurcation of the vagina has the same characteristics as in the remaining species.

The vagina is subcylindrical, short (the penis is from 1.5 times to twice as long), as wide as, or slightly wider than, the penis. Its internal surface is composed of thin anastomosed lamellae forming a reticulum (Figure 18E,F).

The bursa copulatrix is subspherical and its duct, of about 20–26 mm long, is internally provided with thin, straight lamellae that are intermingled with short undulated ones in the first portion of the duct.

The club-shaped penis is from 3.3 to 4.3 times as long as wide and about the same length as the epiphallus. The penial sheath is of medium length. The internal penis structure shows a verge with an accessory lobe. The verge, prolongation of the

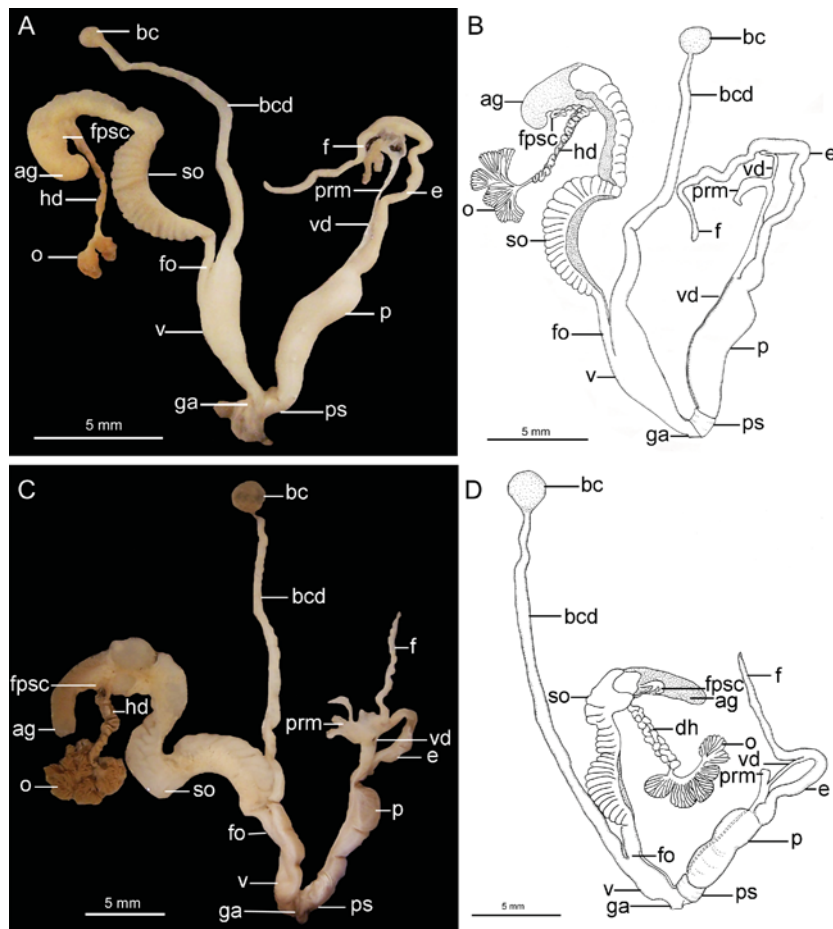


Figure 18. Genital system of *Plagiodontes patagonicus* and *P. rocae*. (A,B) Genital system of *P. patagonicus*; (C,D) genital system of *P. rocae*. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bcd, bursa copulatrix duct; e, epiphallus; f, flagellum; fo, free oviduct; fpsc, fertilization pouch–spermathecal complex; hd, hermaphroditic duct; o, ovotestis; p, penis; prm, penis retractor muscle; ps, penial sheath; so, spermoviduct; v, vagina; vd, vas deferens.

epiphallus, has an internal hollow tubule. The accessory lobe, proximally united to the papilla, is compact, of triangular shape and one-third the size of the papilla. The inner penis wall has a variable sculpture of protruding longitudinal and undulated pilasters with several branches and anastomoses. The pilasters become thin and straight in the area that is externally surrounded by the penial sheath; they are absent under the papilla (Figure 18A,B).

The transition from penis to epiphallus is marked by a constriction. The epiphallus is proximally swollen but otherwise cylindrical. Internally, the cylindrical portion bears five to seven straight thin folds or lamellae; it is separated from the swollen part by a small structure formed by the merging folds. This structure, of probable glandular function, was sometimes covered with a hard translucent cover. The swollen part has some internal longitudinal folds with lateral branches, and continues in a cylindrical tubule inside the verge. This tubule also bears internal longitudinal folds, which are more voluminous and have more branches and anastomoses (Figure 18E,F) than those in the swollen part. The flagellum, longer than the epiphallus, is cylindrical and has only one internal longitudinal fold. The epiphallus–flagellum transition is marked by the insertion of the vas deferens and a slight reduction of the diameter towards the flagellum.

Plagiodontes patagonicus (d'Orbigny, 1835)

The pallial complex (Figure 19A,B) was briefly described by Hylton-Scott (1952), so we add only some additional details.

It is about 30 mm long. The kidney is triangular and occupies less than 20% of the lung length. Although Hylton-Scott (1952) described the secondary ureter as closed, we determined that it is open, being the ureteric pore located at the level of the lower third of the kidney length. The conspicuous pulmonary vein branches in the afferent marginal vein that occupies 60–70% of its length. The vascularization in the ad-rectal area and in the area between the veins is conspicuous. The marginal vein, branching from the last portion of the pulmonary vein and bordering the pallial border, is branched in minor veins. The pallial border has a brown spongy area, the pallial gland.

Anatomy of the genital system and its morphometric variations were already described by Hylton-Scott (1952), Cazzaniga and Fernández-Canigia (1985) and Cazzaniga et al. (2005), but the inner anatomy of the penis and vagina has not been analysed until now. Figure 20A,B shows the general aspect of the genital system.

Internally, the penis bears a simple penial papilla or verge (Figure 18A,B), proximally rounded and swollen, with transverse slits bordering its opening; it is distally triangular, elongated and smooth. The penis inner wall has voluminous and undulated pilasters with only a few anastomoses. While the area surrounded by the penial sheath and the genital atrium has multiple straight, thin folds, the area below the penial papilla is smooth.

The transition between penis and epiphallus is constricted, the epiphallus being proximally swollen and distally cylindrical. This cylindrical portion has five to seven straight thin folds (Figure 21C). It is separated from the swollen part by the same structure found in the remaining *Plagiodontes* species. The flagellum, cylindrical and

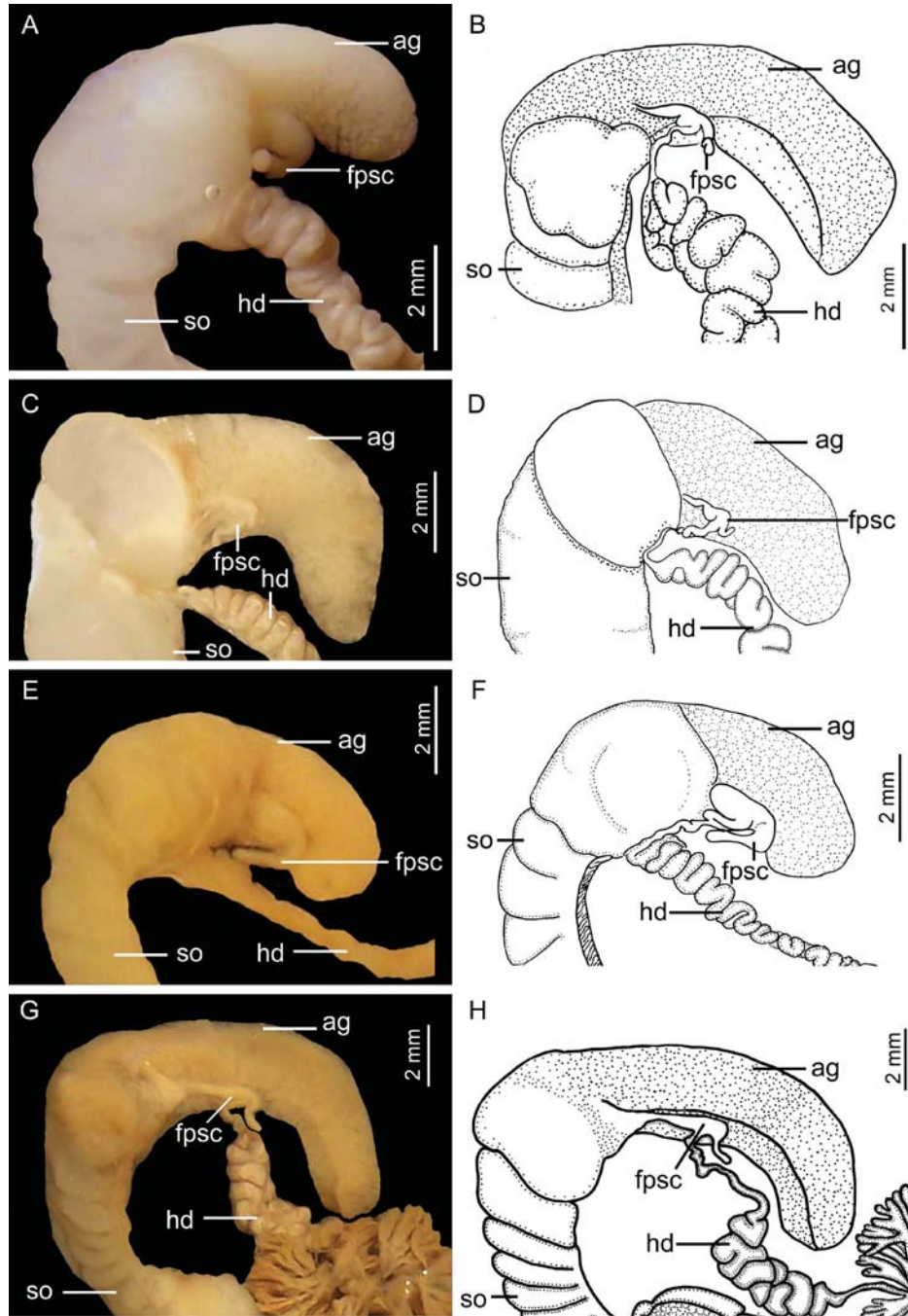


Figure 19. Proximal genitalia of *Plagiodontes dentatus* (A,B), *P. multiplicatus parvus* (C,D), *P. patagonicus* (E,F), and *P. rocae* (G,H). Abbreviations: ag, albumen gland; fpsc, fertilization pouch-spermathecal complex; hd, hermaphroditic duct; so, spermoviduct.

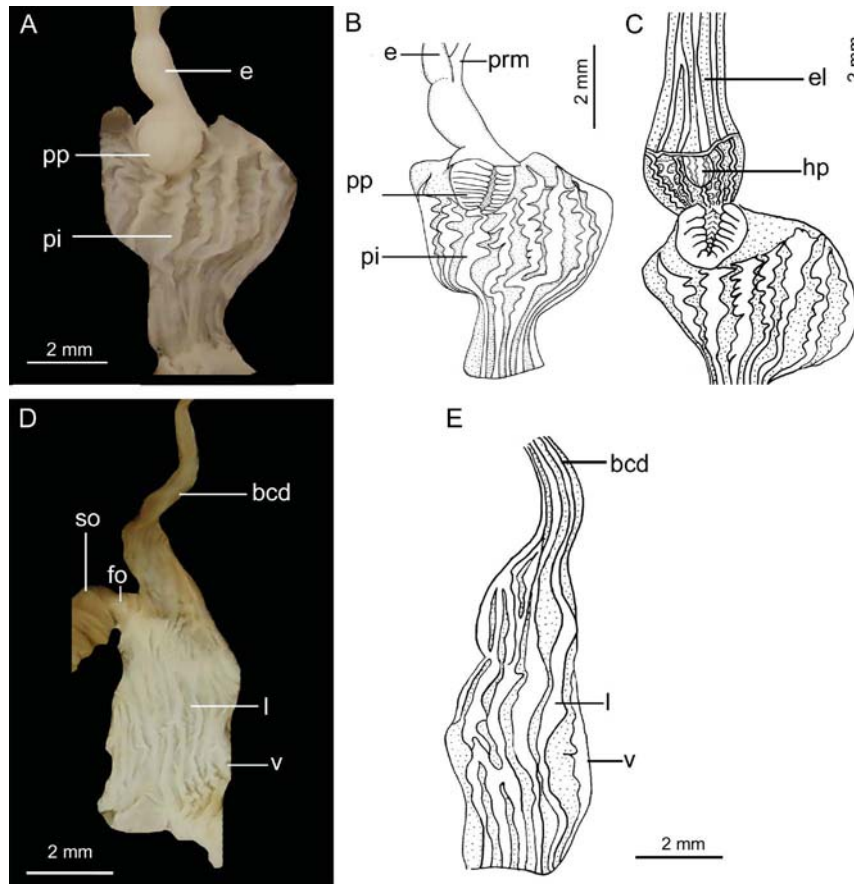


Figure 20. Terminal genitalia of *Plagiodontes dentatus*. (A,B) Internal structure of the penis; (C) internal structure of the epiphallus and penial papilla; (D,E) internal structure of the vagina. Abbreviations: bcd, bursa copulatrix duct; e, epiphallus; el, epiphallic lamellae; fo, free oviduct; hp, hollow papilla of the epiphallus; l, straight lamellae; pi, pilaster; pp, penial papilla; prm, penis retractor muscle; so, spermooviduct; v, vagina.

shorter than the epiphallus, has a straight fold in its inner wall. There is a noticeable change of diameter between the epiphallus and the flagellum. The vagina, shorter than the penis and twice as long as it is wide, has its inner surface longitudinally folded, with minor anastomoses that give it a reticulate aspect (Figure 21D,E). The bursa copulatrix duct is distally swollen and has internal longitudinal straight folds (Figure 21D,E).

Plagiodontes rocae Doering, 1881

The pallial complex (Figure 19C,D), 31–33 mm long, has a noticeably dark pigmentation, mainly in the vascularized area (Figure 22). The triangular kidney occupies 20% of the lung length. The ureteric pore is located at a point corresponding to the inferior third of the kidney. From that point on, the secondary

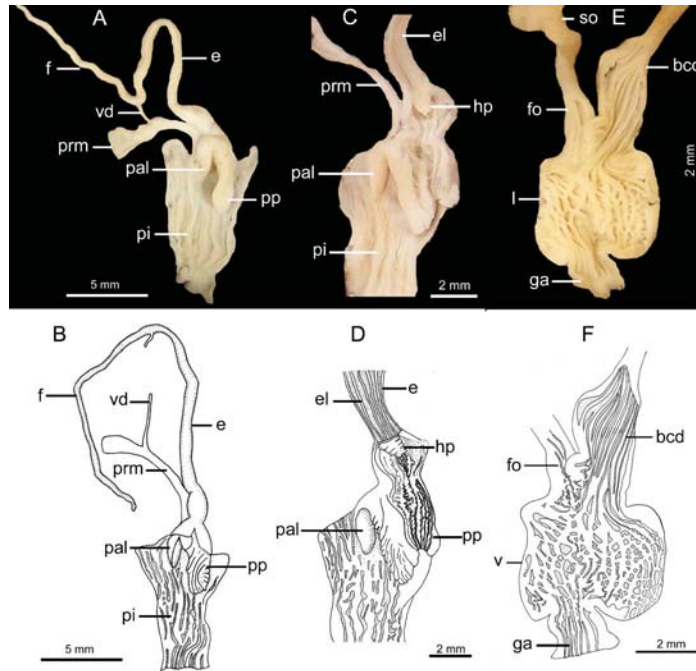


Figure 21. Terminal genitalia of *Plagiodontes multiplicatus parvus*. (A,B) Internal structure of the penis; (C,D) internal structure of the epiphallus and penial papilla; (E,F) internal structure of the vagina. Abbreviations: al, anastomosed lamellae; bcd, bursa copulatrix duct; e, epiphallus; el, epiphallic lamellae; f, flagellum; fo, free oviduct; hp, hollow papilla of the epiphallus; pi, pilaster; pp, penial papilla; pal, penial papilla accessory lobe; prm, penis retractor muscle; so, spermoviduct; v, vagina; vd, vas deferens.

ureter is a ureteric groove delimited by two ridges. The pulmonary vein is conspicuous and branches in a marginal afferent vein of variable extent (it ranges from 40% to 80% of the pulmonary vein length). There is an important vascularization in the ad-rectal area and between the pulmonary vein and the marginal afferent vein. The marginal vein, adjoining the mantle collar, is not branched. The mantle collar has a spongy pallial gland and several indentations caused by the apertural lamellae and folds.

Genital anatomy and morphometric variations were already described by Pizá et al. (2006), but the inner anatomy of the penis has not been previously analysed. Figure 20C,D show the general aspect of the genital system. It shows a penial papilla with an accessory lobe that is up to twice as long as the true verge (Figure 23A–D). The shorter and wider verge has a medial slit (fissure) where the epiphallus opens. The accessory lobe is laterally attached to the penis wall; it is smooth and triangular in section. The internal sculpture of the penis is composed of longitudinal pilasters with some branches and anastomoses (Figure 23C,D). The internal structure of the vagina is unique because it has two different areas; one of them, externally identifiable, is markedly thick, with undulated and branched folds, while the other is thin and smooth, although it may have minor longitudinal thread lines.

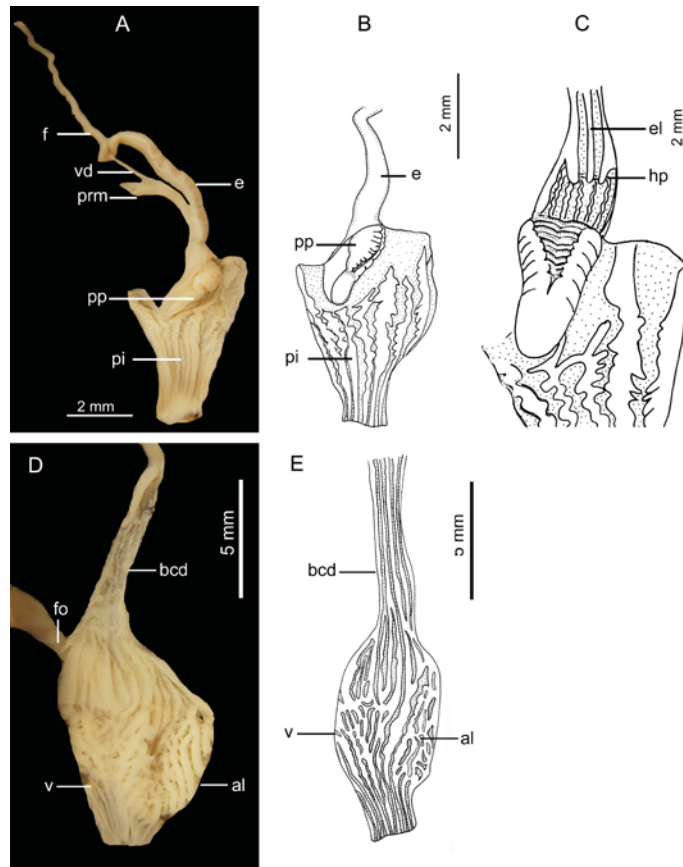


Figure 22. Terminal genitalia of *Plagiodontes patagonicus*. (A,B) Internal structure of the penis; (C) internal structure of the epiphallus and penial papilla; (D,E) internal structure of the vagina. Abbreviations: al, anastomosed lamellae; bcd, bursa copulatrix duct; e, epiphallus; el, epiphallic lamellae; f, flagellum; fo, free oviduct; hp, hollow papilla of the epiphallus; pi, pilaster; pp, penial papilla; prm, penis retractor muscle; v, vagina; vd, vas deferens.

The bursa copulatrix duct has straight longitudinal folds as in the remaining species (Figure 24A–D).

Discussion

Plagiodontes weyrauchi sp. nov. significantly differs by shell characters from the other species in the genus, four of which share the same size range; a higher number of whorls, a relatively small width and the low proportions of the last whorl length and aperture length to shell length make its shape unique.

Multivariate statistical analysis demonstrated that these shells are definitely distinct from the remaining forms in the genus, supporting the hypothesis that this is a different morphospecies.

The new species is similar to *P. multiplicatus parvus* in the acute form of the apex and the protoconch and teleoconch sculpture. However, on equal shell

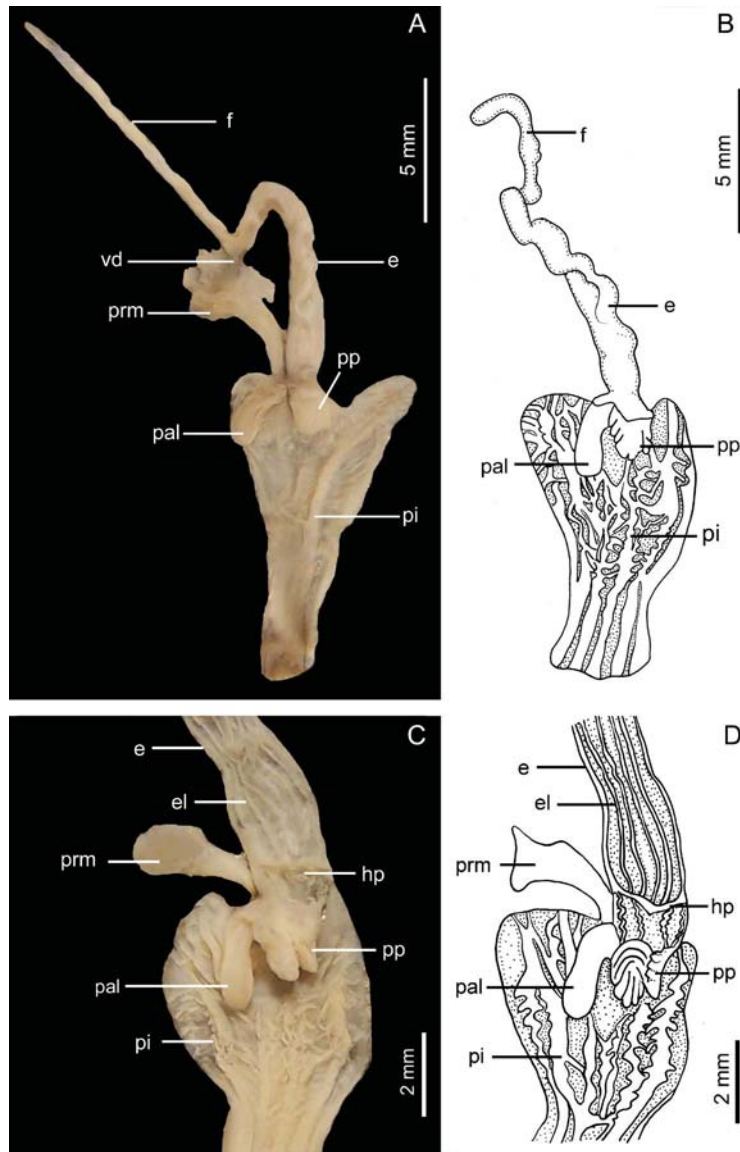


Figure 23. Terminal male genitalia of *Plagiodontes rocae*. (A,B) Internal structure of the penis; (C,D) internal structure of the epiphallus and penial papilla. Abbreviations: e, epiphallus; el, epiphallic lamellae; f, flagellum; hp, hollow papilla of the epiphallus; pi, pilaster; pp, penial papilla; pal, penial papilla accessory lobe; prm, penis retractor muscle; vd, vas deferens.

lengths *P. weyrauchi*, reaches a higher number of whorls (8 to 9.75) than any specimen of *P. multiplicatus* (6 to 7.25). The 100% correct classification of these species in a multivariate discriminant analysis and their statistically significant differences in most measurements confirm that their shells are morphologically separate.

On equal shell lengths, the genital system of *P. weyrauchi* was also significantly smaller (penial complex 19–22 mm long) than that of *P. multiplicatus parvus* (31–35 mm).

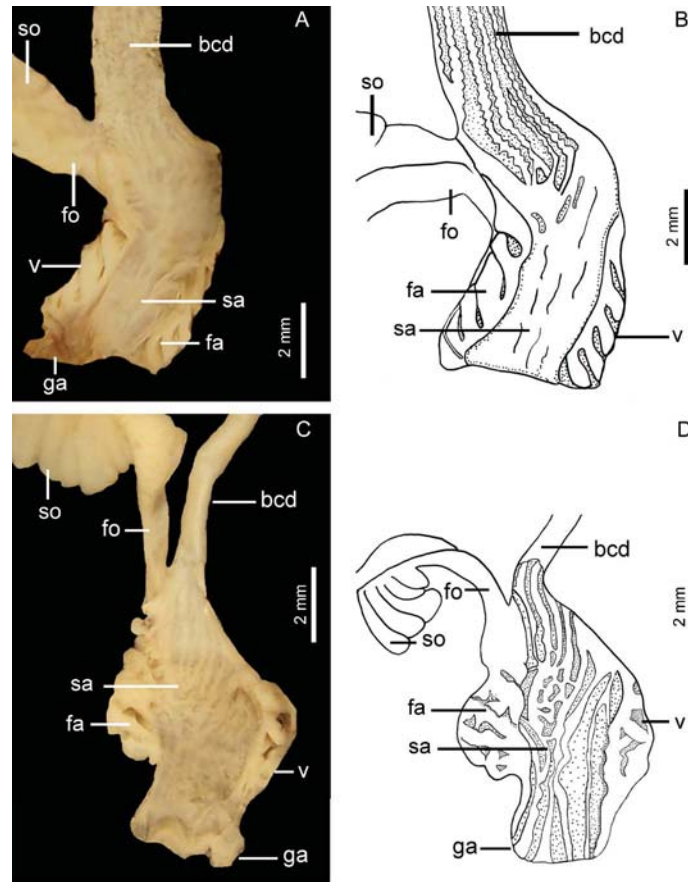


Figure 24. Terminal female genitalia of *Plagiodontes rocae* showing the internal structure of the vagina. Abbreviations: bcd, bursa copulatrix duct; fa, folded area of the inner vaginal surface; fo, free oviduct; ga, genital atrium; sa, smooth area of the inner vaginal surface; so, spermooviduct; v, vagina.

The penis verge is of similar appearance in both species, with a small accessory lobe, and a subcylindrical or club-shaped penis. In turn, the inner texture of the vagina differs between them, as it is always strongly reticulated in *P. multiplicatus*, whereas in *P. weyrauchi* it generally has longitudinal parallel lamellae, with a low degree of anastomosis.

These two species might not be strictly sympatric because all living specimens of *P. weyrauchi* were collected from rock cracks or attached under stones whereas *P. multiplicatus* was normally found associated with the vegetation, under shrubs and among roots (J. Pizá and M. Carrizo, personal observation). However, a quantitative comparison based on extensive sampling from more localities is needed to confirm this. The penial papilla of *P. rocae* also has an accessory lobe in the verge but, in contrast to *P. weyrauchi* and *P. multiplicatus parvus*, the papilla is notably longer than the verge itself. The ureteric pore of *P. rocae* opens at the height of the inferior third of the kidney, i.e. the lowest level among the five species studied. The strongly

Table 5. Summary of shell and anatomical characteristics of the five studied taxa of *Plagiodontes*.

	<i>P. weyrauchi</i> sp. nov.	<i>P. multiplicatus parvus</i>	<i>P. dentatus</i>	<i>P. patagonicus</i>	<i>P. rocae</i>
Teeth number	9–13	9–13	9–14	3–10	9–11
Protoconch sculpture	straight axial ribs that never branch, decussated by spiral lines	straight axial ribs that never branch, decussated by spiral lines	waved axial ribs that usually branch, decussated by spiral lines	waved axial ribs that seldom branch, decussated by spiral lines	slightly waved axial ribs that seldom branch, decussated by spiral lines
Protoconch–teleoconch boundary	defined	not defined	defined	defined	not defined
Teleoconch sculpture	axial ribs	axial ribs	almost smooth (growth lines only)	almost smooth (growth lines only)	strong axial ribs
Pallial complex	not pigmented	not pigmented	not pigmented	not pigmented	dark pigmented
Ureteric pore (relative to kidney)	proximal third	proximal third	distal third	distal third	distal third
Vascularization	moderate, distal third of the ad-rectal area and between pulmonary and marginal afferent vein	well-developed, along ad-rectal area and between pulmonary and marginal afferent vein	weak, distal third of the ad-rectal area and between pulmonary and marginal afferent vein	well-developed, along ad-rectal area and between pulmonary and marginal afferent vein	well-developed, along ad-rectal area and between pulmonary and marginal afferent vein
Penis shape	subcylindrical	club-shaped or subcylindrical	subcylindrical	subcylindrical	club-shaped

Accessory lobe of the penial papilla	present	present	absent	absent	present
Relative size of penial papilla and accessory lobe	papilla larger than the accessory lobe	papilla larger than the accessory lobe	—	—	papilla shorter than the accessory lobe
Size and shape of the penial papilla	large, longer than wide, quadrangular	large, longer than wide, quadrangular	small, as long as wide, rounded	large, longer than wide, triangular	small, slightly longer than wide, quadrangular
Vaginal internal surface	principal longitudinal lamellae with few anastomoses	reticulated; anastomosed lamellae	principal longitudinal lamellae with few anastomoses	reticulated; anastomosed lamellae	divided into two areas; one of them smooth, the other with thick folds
Bursa copulatrix duct	uniform diameter	uniform diameter	uniform diameter	distally swollen	distally swollen

pigmented pallial complex and the inner relief of the vaginal wall further reinforce the morphological uniqueness of *P. rocae*.

The genital anatomy groups *P. dentatus* and *P. patagonicus*, which have a simple penis verge with no accessory lobe, separately. This is a major distinctive feature separating them from *P. weyrauchi*, *P. multiplicatus* and *P. rocae*, in addition to the remaining morphometric and anatomical differences described by Pizá and Cazzaniga (2003), Cazzaniga et al. (2005) and Pizá et al. (2006). The new results reinforce the taxonomic conclusions of these previous papers.

The verge of *P. dentatus* is very short and round, while that of *P. patagonicus* is proximally rounded and distally it is elongated and triangular. This makes the verge an outstanding character to further separate the commonest two species from eastern Argentina (Pizá and Cazzaniga 2003).

The internal anatomy of the penis and vagina provided some good characters to improve discrimination among the five small species of *Plagiodontes*, and they are probably of phylogenetic bearing. Table 5 summarizes the main characteristics of these species.

Three other species have been described within this genus, all of >25 mm adult length; the genital anatomy was only sketched for *P. daedaleus* (Deshayes, 1851) and *P. weyenberghii* (Doering, 1877) by Breure and Schouten (1985), though the inner structure of the organs is not known. Nothing has been published on the internal anatomy of *P. brackebuschii* (Doering, 1877). Anatomical research of these species is now in progress.

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