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ALLOPATRY AND ANATOMICAL DISTINCTIVENESS OF TWO PUZZLING LAND SNAILS IN GENUS *PLAGIODONTES*, FROM ARGENTINA (GASTROPODA: ORTHALICIDAE, ODONTOSTOMINAE)

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ABSTRACT

Plagiodontes daedaleus (Deshayes, 1851) is the most widespread species in the genus *Plagiodontes* Doering, 1877. Although some 19th century authors recorded some differences in shell shape between the populations living to the east or to the west of the Pampean Sierras, Argentina, such differences were ignored by later authors. A multivariate statistical analysis on 608 adult shells collected at 29 localities in and around these mountains was used to test if such narratively described shell differences were statistically significant, irrespectively of their taxonomic status. Shells classified as collected from the east or the west of the sierras were correctly identified in 91.9% of the cases by Multivariate Discriminant Analysis, leading to recognizition of two allopatric shell morphologies. These external divergences were found to correspond with anatomical differences in the reproductive system. We conclude that two different, allopatric species were merged under the name *Plagiodontes daedaleus* in the literature and raise the subspecies *Plagiodontes daedaleus strobelii* (Doering, 1877) to the specific level. Another subspecies living to west of the sierras, *Plagiodontes daedaleus salinicola* (Doering, 1877), also showed a simple penis papilla and a non-swollen vagina, which shows that *salinicola* is not a member of *P. daedaleus* but rather a population of *P. strobelii* that does not deserve subspecific status. The taxonomic significance of the presence of either a simple penial papilla or a papilla bearing an accessory lobe was also confirmed for these *Plagiodontes* species.

Key words: shell morphometry, pallial complex, reproductive system, *Plagiodontes strobelii*, taxonomy, Stylommatophora.

INTRODUCTION

Plagiodontes daedaleus (Deshayes, 1851) is known to be the most variable, widespread species in genus *Plagiodontes* Doering, 1877 (Parodiz, 1939; Fernández, 1973). Although some 19th century authors (Strobel, 1874; Doering, 1877, 1878) recorded noteworthy differences in shell shape between the populations found to the east or to west of the Pampean Sierras, Argentina, such differences were not taken into account by later authors. So, the literature merged under a single specific name many shells of variable obesity, the size of which ranges from medium to large, and which have either a blunt spire or a comparatively acute one.

After intensive sampling in and around these sierras, together with a detailed examination of samples stored in the principal museums of Argentina, we have found that those long-observed, subjectively detected shell differences were demonstrable by multivariate statistic analysis, and that they concurred with anatomical differences in the reproductive system that warrant recognition as two allopatric species.

The species living to the west of the sierras had already received the subspecific name *P. daedaleus major* (Strobel, 1874), which was replaced by *P. daedaleus strobelii* (Doering, 1877) to avoid homonymy with *P. daedaleus major* (Pfeiffer, 1853). The confusion of these two forms created long-lasting taxonomic confusion.

The aims of this paper are to test shell differences between populations of "*Plagiodontes daedaleus*" living over opposite slopes of the Pampean Sierras and to considerably enlarge

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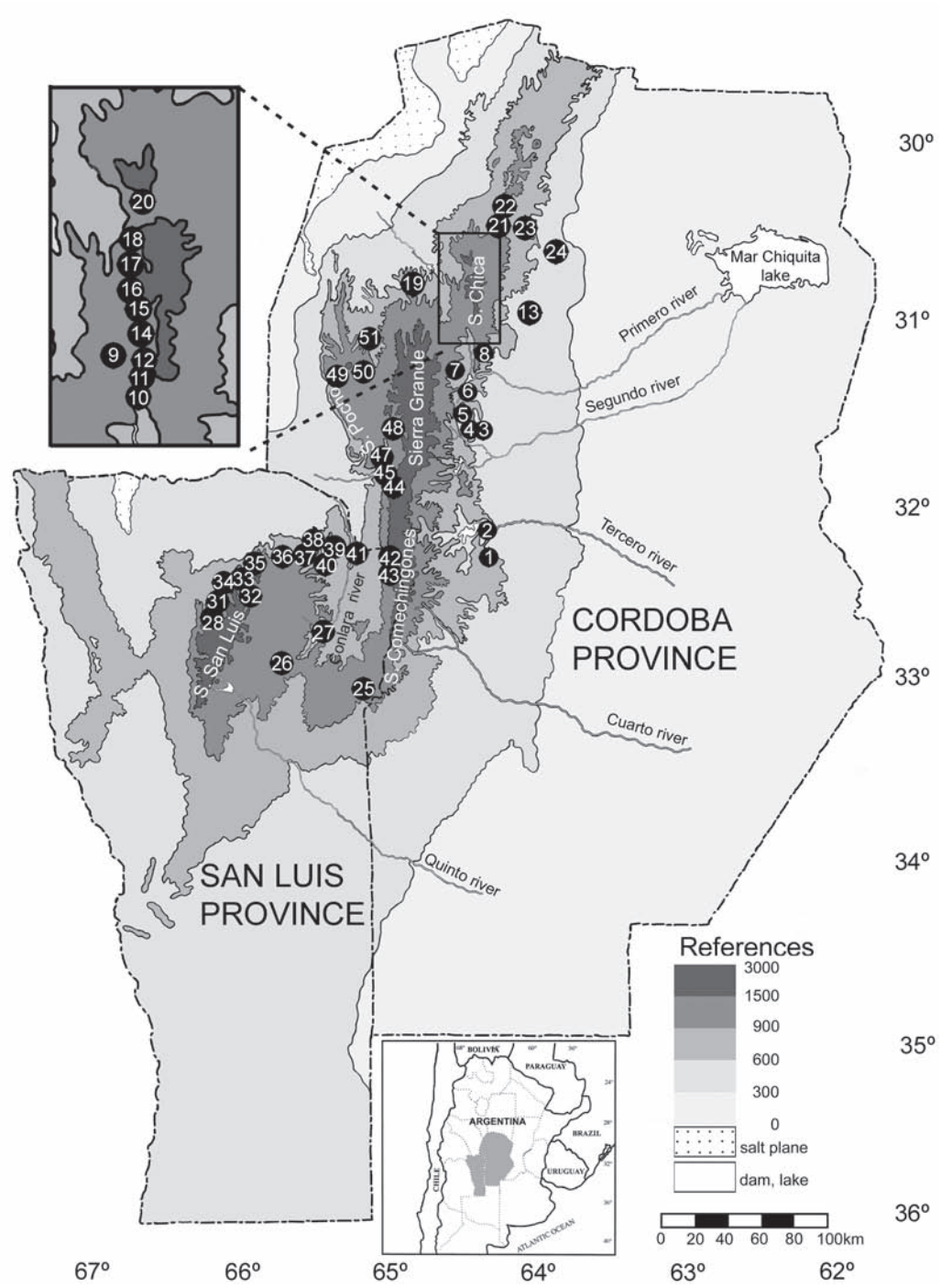


FIG. 1. Study area in the Pampean Sierras, Córdoba and San Luis provinces, Argentina. Localities indicated according to Appendix 1.

the description of the internal anatomy of the studied taxa, paying particular attention to the inner structure of penis and vagina, which are studied here for the first time.

According to our results, *Plagiodontes strobelii* (Doering, 1877) is raised to the species level and its distribution is described as allopatric with *P. daedaleus* (Deshayes, 1851).

MATERIAL AND METHODS

Study Area

The sampling area covered part of the Pampean Sierras and their surrounding areas in the provinces of Córdoba and San Luis, central Argentina (Fig. 1). They form a mountain complex 400 km long, of N-S direction from 33°30'S to 29°20'S and from 64°30'W to 66°30'W. This chain consists of parallel mountain ranges, the dominant of which is the central Sierra Grande and Sierra de Comechingones, highest summits of which are Champaquí (2,884 m) and Los Gigantes (2,880 m), respectively. The system of the Pampean Sierras constitutes an important geographic barrier that delimits a clear east-west climate differentiation.

The general climate is mountainous subhumid, with a marked temperature gradient due to altitude. Rainfall increases on the eastern slopes owing to the cooling and condensation of warm, humid winds from the Atlantic Ocean.

The studied area covers part of the phytogeographical provinces of Chaco and Espinal (Cabrera & Willink, 1973). Highest mountains are mainly characterized by mountain forest ("bosque serrano"), which gradually becomes a xerophytic forest in the piedmont; both kinds of woods are similar, but plant heights and species diversity are lower in the Espinal than in the Chaco province. The summits of the sierras are covered by mountain grasslands.

Allopatry and Shell Variability

Intensive fieldwork was carried out during January 2005, on the forests on both sides of Sierra Grande, Sierra de Comechingones and Sierra de San Luis. The material collected in the field was complemented by samples from the collections of Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Museo de La Plata (MLP), La Plata, and Fundación Miguel Lillo (FML), San Miguel de Tucumán (Appendix 1).

Shell variability was analyzed on 608 adult specimens from 29 localities. According to external features, most shells were identifiable either as *Plagiodontes daedaleus daedaleus* or *P. daedaleus strobelii,* though the identity of a few specimens was doubtful. Adulthood was assumed for shells that showed full development of the apertural folds and lamellae, together with a reflected outer aperture lip. Seven linear variables were measured on shell drawings made with the aid of a camera lucida device fitted to a stereoscopic microscope: shell length (SL), shell width (SW), length of the last whorl (LWL), width of the last whorl (LWW), aperture length (AL), major apertural length (MAL) and aperture width (AW); major and spiral angles were also determined as described in Pizá & Cazzaniga (2003).

Multivariate Principal Component Analysis (PCA) and Multivariate Discriminant Analysis (MDA) were applied to quantitative data using the SPSS statistical package.

Descriptors of measurements and proportions (mean, standard deviation, coefficient of variation and range) were calculated. The significance of differences in linear measurements and their proportions between groups was checked by t-tests using the SPSS statistical package.

Shell Morphology

Characteristics of apertural folds and lamellae and number of whorls were determined through direct observation under a stereoscopic microscope. Protoconch and teleoconch sculpture of juvenile and adult shells was analyzed with a JEOL 35 CF scanning electronic microscope.

Internal Anatomy

Pallial and genital systems were studied on 15 specimens of each form (*P. daedaleus daedaleus* and *P. daedaleus strobelii*), collected at the localities indicated in Appendix 1.

Living specimens were drowned in cold, previously boiled water, fixed and conserved in 70% ethanol. Dissections and illustrations were made with the aid of a Zeiss Stemi SV6 stereoscopic microscope fitted with a camera lucida device.

Terminology used to describe the genital system follows Tompa (1984) and Gómez (2001).

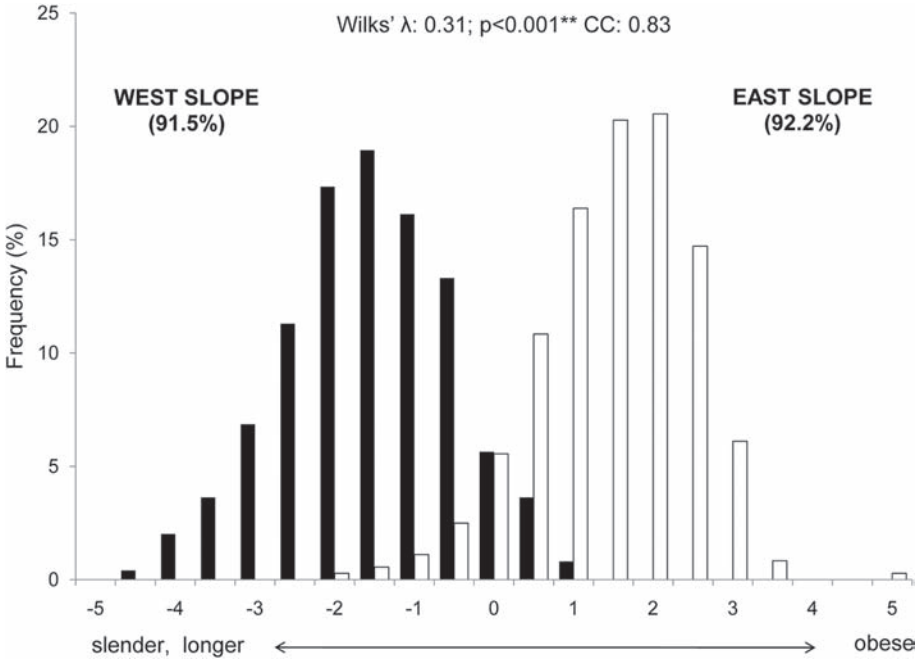


FIG. 2. Frequency histogram of the scores of discriminant function 1 of the MDA performed on shell measurements of *Plagiodontes* from the eastern and western slopes of the Pampean Sierras in Córdoba and San Luis provinces. Correct classification percentages, Wilks' λ, and canonical correlation (CC) are indicated.

RESULTS

Allopatry of Shell Morphologies

MDA on 608 shells classified according to their origin (west or east of the sierras) resulted in the following classification functions:

$Y_{west\ slope}$ = -7.84 SL + 66.04 SW - 21.52 LWL + 30.49 LWW + 31.64 AL - 15.98 AW - 43.12 AML + 20.23 MA + 3.16 SA - 1464.70

$Y_{east\ slope}$ = -8.29 SL + 65.52 SW - 24.48 LWL + 33.05 LWW + 34.12 AL - 13.16 AW - 44.66 AML + 20.16 MA + 3.26 SA - 1458.41

Cross validation results of this analysis (91.9% correct classifications) support the hypothesis that these two morphs are allopatric (Table 1, Fig. 2).

Shell Comparison of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*

Some representative specimens of the two taxa are shown in Figures 3 and 4. Morphometric information obtained from the studied shells is summarized in Table 2; means of all variables differed significantly ($p << 0.001$).

PCA of shell parameters revealed two Principal Components accounting for 85.9% of the total variance (Table 1). The scatter plot in Figure 5 shows that the specimens of *P. daedaleus strobelii* had predominantly negative PC2 scores. This is mainly due to its more slender shell, as evidenced by higher values of major angle and lower values of spiral angle. Conversely, the scores of P. *daedaleus daedaleus* form a cloud in the positive range of PC2 due to their obese shell.

The position of the samples on the PC1-PC2 plane was fully consistent with their geographical distribution.

Shell Morphology (Table 3)

Protoconch and Teleoconch Sculpture: The protoconch of *P. daedaleus daedaleus* has 2–2.25 whorls, with undulated axial striae and some anastomoses in the first half whorl (Fig. 6); it has straight ribs decussated by spiral lines in the two last protoconch whorls (Fig. 7). The limit between protoconch and teleoconch is well defined (Fig. 8). The teleoconch has a variable striation. Some

TABLE 1. Summary of the multivariate analyses performed on shell measurements of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*. MDA-Geo: Structure matrix of the MDA performed on *Plagiodontes* shells classified according to their origin from the east (N = 360) or west (N = 248) slope of the Pampean Sierras (Córdoba and San Luis provinces, Argentina). ACP-Taxa: Component matrix of the PCA performed on 608 shells of *Plagiodontes strobelii* and *P. daedaleus.* Abbreviations: AL, aperture length; AML, aperture major length; AW, aperture width; LWL, last whorl length; LWW, last whorl width; MA, major angle; NW, number of whorls; SA, spiral angle; SL, shell length; SW, shell width.

	MDA-Geo Structure Matrix	ACP-Taxa Component Matrix	
Variable	DF1	PC 1	PC 2
SL	-0.48	0.77	-0.57
SW	0.11	0.82	0.43
LWL	-0.31	0.91	-0.33
LWW	0.23	0.74	0.56
AL	-0.10	0.96	-0.04
AW	0.21	0.76	0.38
MAL	-0.09	0.96	0.00
MA	-0.57	0.08	-0.90
SA	0.63	-0.23	0.85

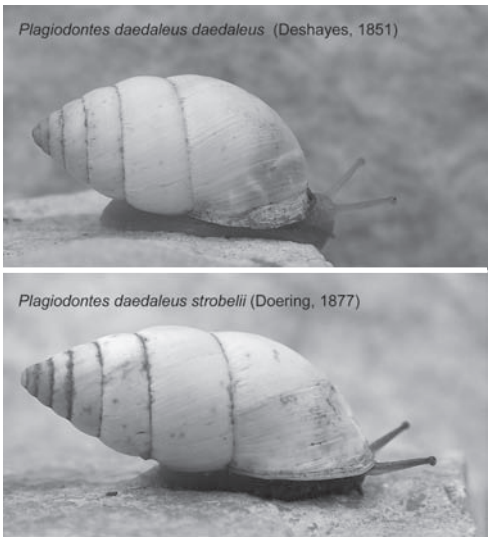


FIG. 3. Living specimens of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*.

shells that look almost smooth have a slight sculpture, which is visible at low magnification under a stereomicroscope. The shells usually have axial striae in the first post-nepionic whorls (Fig. 9), which are gradually replaced

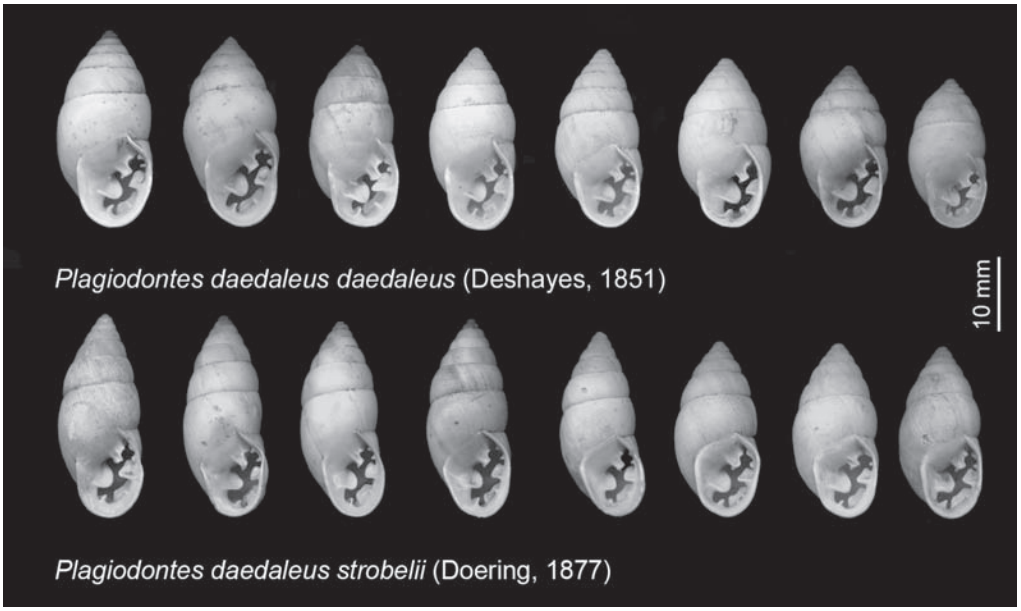


FIG. 4. Shell variability of the two species of *Plagiodontes* Doering, 1877, merged under the name *P. daedaleus* (Deshayes, 1851) in the literature.

TABLE 2. Summary of the shell variables (in mm) and proportions of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*. Mean ± standard deviation [coefficient of variation] (minimum-maximum). Independent samples t−test: all mean differences resulted in $p << 0.001$. Abbreviations as in Table 1.

Variable/ proportion	*P. daedaleus strobelii* (n = 248)	*P. daedaleus daedaleus* (n = 360)
SL	27.52 ± 2.110 [0.077] (21.70–33.53)	24.43 ± 2.124 [0.087] (17.46–30.90)
SW	12.46 ± 0.992 [0.08] (9.72–15.38)	12.83 ± 1.071 [0.084] (9.91–17.50)
LWL	18.24 ± 1.088 [0.06] (15.22–21.25)	17.04 ± 1.378 [0.081] (12.74–21.63)
LWW	11.58 ± 0.723 [0.062] (9.72–13.46)	12.16 ± 0.914 [0.075] (9.16–15.50)
AL	12.03 ± 0.829 [0.069] (9.86–14.63)	11.74 ± 1.030 [0.088] (9.12–15.50)
AW	9.21 ± 0.798 [0.087] (5.57–11.38)	9.75 ± 0.875 [0.090] (6.50–12.63)
AML	12.24 ± 0.830 [0.068] (10.00–14.88)	11.98 ± 1.030 [0.086] (8.89–16.13)
MA	124.38 ± 3.955 [0.032] (114.00–138.00)	117.71 ± 3.84 [0.033] (102.00–131.00)
SA	43.90 ± 5.083 [0.116] (27.00–57.00)	56.44 ± 5.24 [0.093] (42.00–76.00)
NW	7.36 ± 0.462 [0.063] (6.00–8.50)	7.25 ± 0.349 [0.048] (5.75–8.25)
Size (SL+SW)	39.99 ± 2.815 [0.070] (31.42–47.50)	37.26 ± 2.98 [0.080] (29.39–48.00)
SW/SL	0.45 ± 0.032 [0.070] (0.38–0.57)	0.53 ± 0.035 [0.066] (0.43–0.69)
LWL/SL	0.66 ± 0.028 [0.042] (0.56–0.73)	0.70 ± 0.025 [0.035] (0.61–0.76)
AL/SL	0.44 ± 0.024 [0.054] (0.36–0.50)	0.48 ± 0.024 [0.050] (0.42–0.56)
AW/AL	0.77 ± 0.049 [0.065] (0.54–0.86)	0.83 ± 0.043 [0.050] (0.69–1.01)

by growth lines on the remaining whorls; some shells have only growth lines (Figs. 3, 8).

The protoconch of *P. daedaleus strobelii* also has 2–2.5 whorls; the first half whorl has an irregular sculpture of spiral lines and fragments of axial components (Fig. 10), while the remaining two nepionic whorls are regularly sculptured with almost straight striae crossed by spiral lines (Fig. 11). The boundary with the teleoconch is a gradual transition to straight striae of variable thickness, with no spiral lines (Fig. 10). The teleoconch sculpture varies among different populations, exhibiting from weak growth lines to well-marked ribs (Figs. 12, 13).

Aperture Folds and Lamellae: All the studied shells of both subspecies had 9–14 apertural barriers (lamellae + folds) of similar distribution and shape (Figs. 14, 15).

The transverse lamella was centrally depressed in all the studied specimens, and

TABLE 3. Summary of shell and anatomical differences between *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii.*

	P. daedaleus daedaleus	*P. daedaleus strobelii*
Shell shape	ovate-elongate, obese	elongate-ovate, slender
Spire	blunt	acute
Protoconch-teleoconch boundary	well defined	gradual
Teleoconch sculpture	variable, generally smooth	variable, generally with strong axial ribs
Vagina shape	distally swollen	centrally swollen
Vaginal internal surface	reticulated	variable, generally principal longitudinal lamellae with few anastomoses to reticulated
Penis shape	club shaped	subcylindrical
Accessory lobe of the penial papilla	present	absent

generally longer in *P. daedaleus daedaleus* than in *P. daedaleus strobelii*. The tongue-shaped columellar lamella, the outer border of which is thick and slightly elevated, is the largest piece occluding the aperture in the two species. In *P. daedaleus daedaleus*, the columellar lamella is concave, with a rounded outline; its size is positively correlated to the

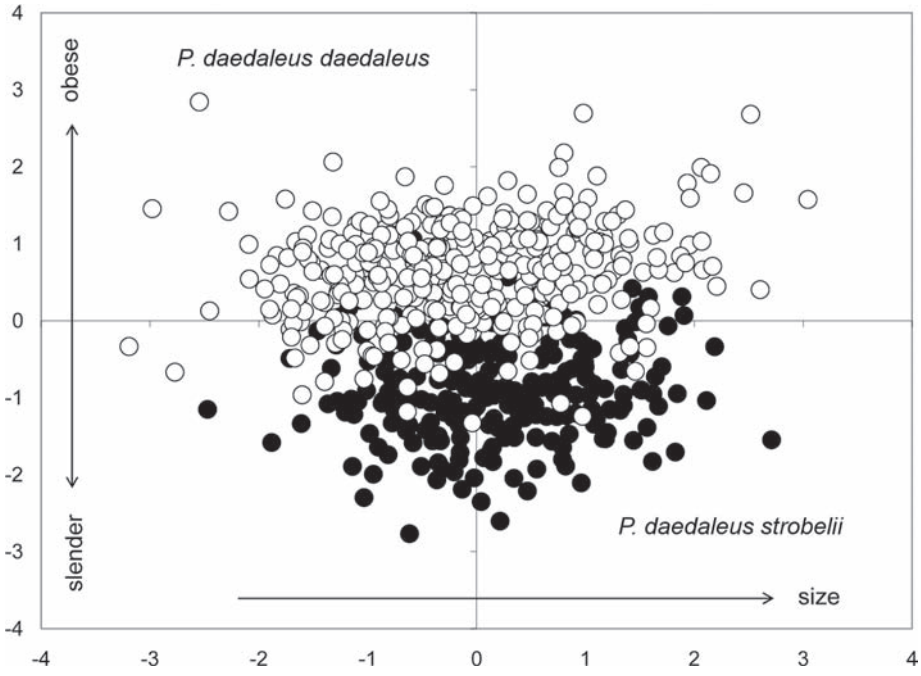
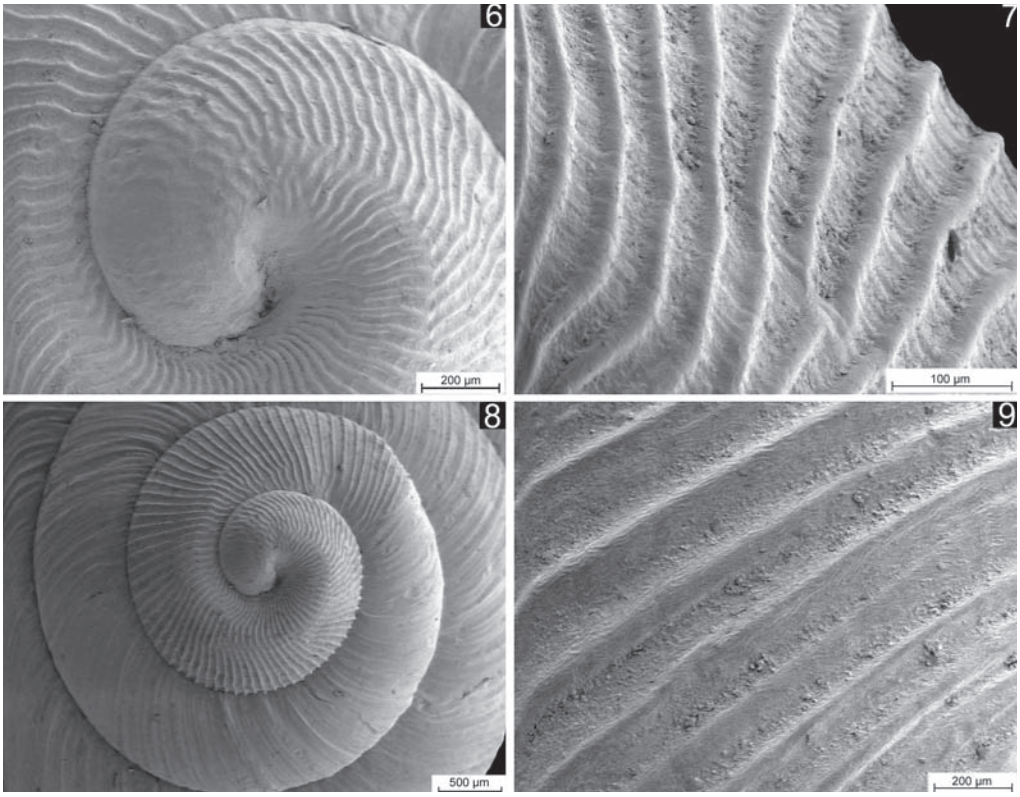


FIG. 5. Scatter plot of the scores of the first (PC1) and second (PC2) principal components performed on shell measurements of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*.

aperture width (r = 0.650; n = 229, p < 0.01); such a correlation was lower, but still significant in *P. daedaleus strobelii* (r = 0.385; n = 95, p < 0.01), the columellar lamella of which is relatively more straight and less concave than in *P. daedaleus daedaleus*. A minute supracolumellar knob or denticle of variable development may appear on the columellar lamella (Fig. 15). It was equally present in both *P. daedaleus daedaleus* (14.56% of the specimens; n = 360), and *P. daedaleus strobelii* (14.85% of the specimens; n = 248). The parietal lamella is dihedral, its faces forming a C to L profile; it is seen as a quadrangular plate when viewed from the apertural plane and it was united to the angular fold in all the studied specimens. The externally visible part of the parietal lamella is longer in *P. daedaleus daedaleus* than in *P. daedaleus strobelii*. Two suprapalatal folds were present in all the studied material; the upper one is usually triangular, though it is compressed in some specimens of *P. daedaleus daedaleus;* the lower one is always compressed. The upper-palatal lamella is constant in size and shape for both species. It is rectangular, with the outer border thickened and elevated; the lateral borders are curved downwards. The lower-palatal folds were present in most specimens, in numbers ranging from one to three or four, as shown in Figure 16. The lower-palatal fold located next to the upper-palatal lamella is usually the most developed one (principal lower-palatal). There was a very highly significant difference in the frequency distribution of the number of lower-palatal folds between *P. daedaleus daedaleus* and *P. daedaleus strobelii* (χ^2 = 23.90; df =



FIGS. 6–9. SEM micrographs of the protoconch sculpture in *Plagiodontes daedaleus daedaleus*. FIG. 6: Axial undulated and anastomosed ribs of the first protoconch whorl; FIG. 7: Close-up of (6) showing spiral lines crossing axial striae; FIG. 8: Protoconch and first teleoconch whorls of *P. daedaleus daedaleus* (limit indicated by an arrow); FIG. 9: Teleoconch sculpture of *P. daedaleus daedaleus*.

4; p = 0.001). The number of lower-palatal folds was not correlated to size in either species (Fig. 17). The basal fold is laterally compressed and generally has the same size as the principal lower-palatal fold; it may be larger than the principal lower-palatal fold in *P. daedaleus strobelii*.

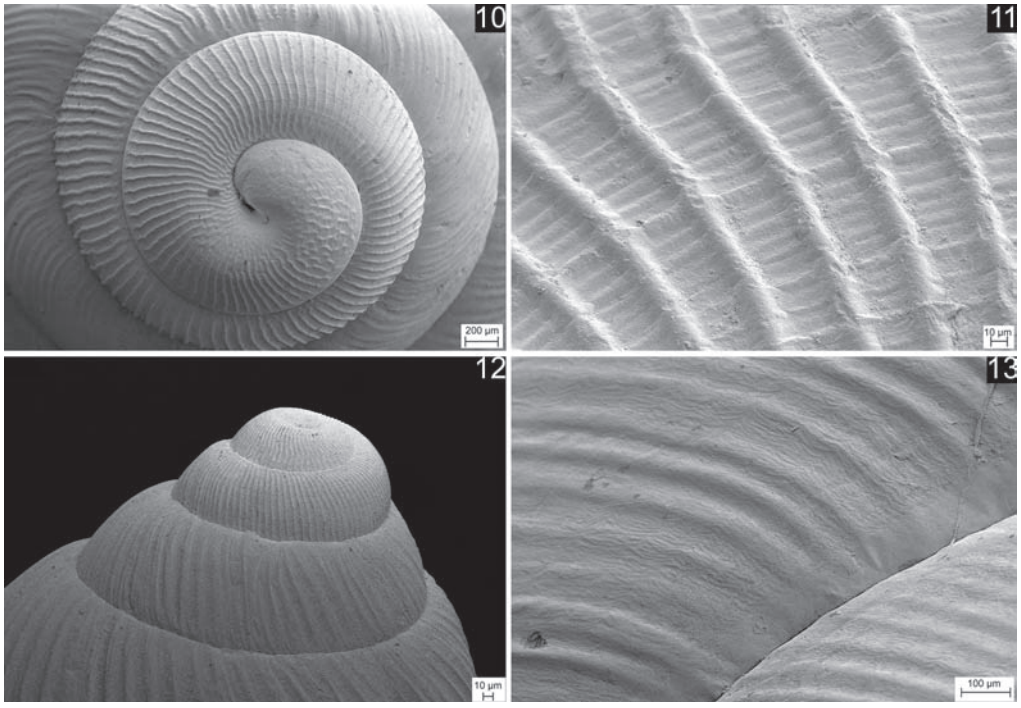
Comparative Anatomy (Table 3)

Pallial Complex: The length of the pallial complex of *P. daedaleus daedaleus* ranged between 19.5 mm and 39.5 mm long (29.8 mm on average) (Figs. 18, 19). The pallial complex of *P. daedaleus strobelii* (Figs. 20, 21) was within the same range, from 20.3 to 38.1 mm long (30.1 mm on average).

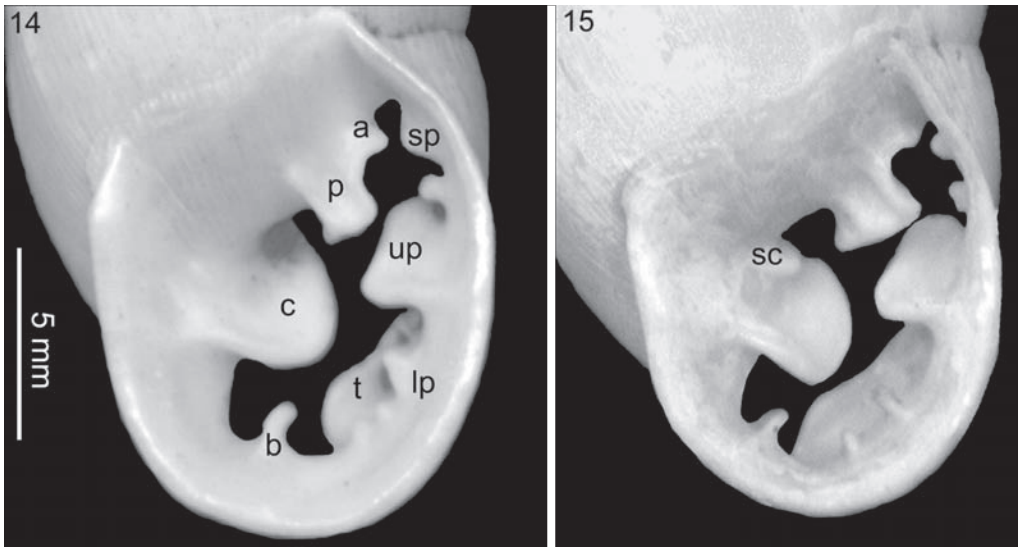
The nearly triangular kidney was always located in the proximal part of the lung cavity alongside the periaortic intestinal bend. The kidney of *P. daedaleus daedaleus* is twice as long as it is wide and occupies between 20% and 50% of the length of the lung; the kidney of *P. daedaleus strobelii* is usually shorter, only 1.6 times as long as it is wide, and it never occupied more than 25% of the length of the lung.

No other anatomical differences were found between the pallial complex of the two taxa. The internal structure of the kidney was similar in all the studied material, with two layers of longitudinal lamellae, the upper layer of which showed short, thin straight lamellae, while the lower one was formed by long and thicker undulating lamellae. The primary ureter runs along the rectal side of the kidney up to the top of the lung cavity; then it turns down along the rectum and forms the secondary ureter, which opens at the ureteric pore, at the level of the midpoint of the kidney. From that point onwards, the open secondary ureter is delimited by two ridges that form a ureteric groove ending in the pneumostome. The rectal ridge is the less developed one in both species.

The pericardium, located in the proximal side of the pallial complex, was variable in



FIGS. 10–13. SEM micrographs of the protoconch sculpture in *Plagiodontes daedaleus strobelii*. FIG. 10: Axial undulated and anastomosed ribs of the first protoconch whorl; FIG. 11: Close-up of (10) showing spiral lines crossing axial striae; FIG. 12: Protoconch and first teleoconch whorls; FIG. 13: Teleoconch sculpture.



FIGS. 14–15. Aperture and apertural lamellae and folds. FIG. 14: *Plagiodontes daedaleus strobelii*; FIG. 15: *P. daedaleus daedaleus*. Abbreviations: a, angular fold; b, basal fold; c, columellar lamella; lp, lower-palatal fold; p, parietal lamella; up, upper-palatal lamella; sc, supracolumellar knob; sp, supra-palatal folds; t, transverse lamella.

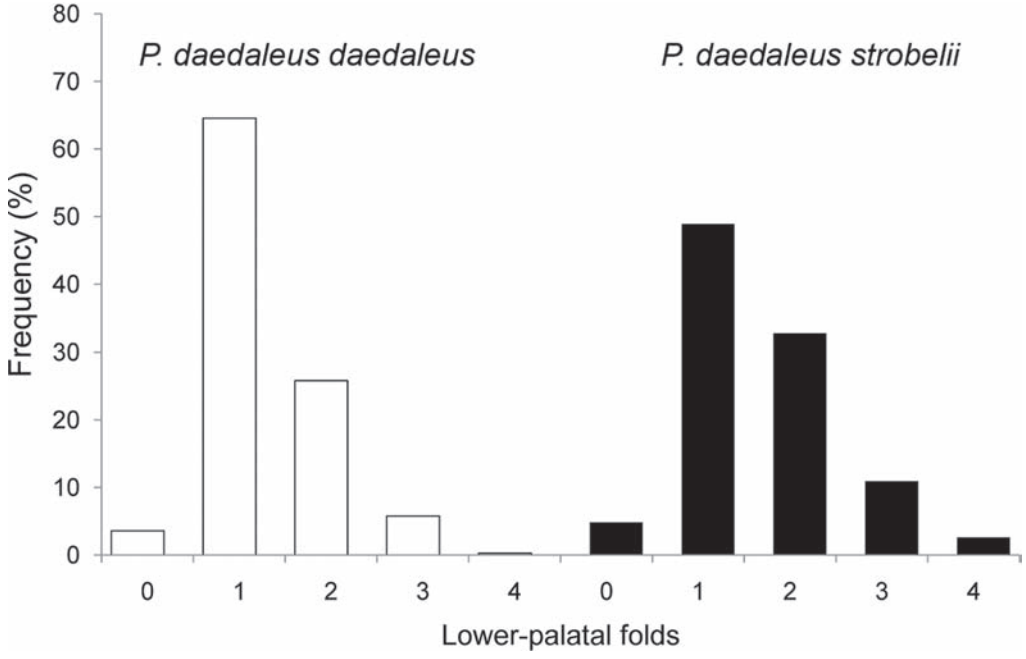


FIG. 16. Frequency distribution of the number of lower-palatal folds in *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*.

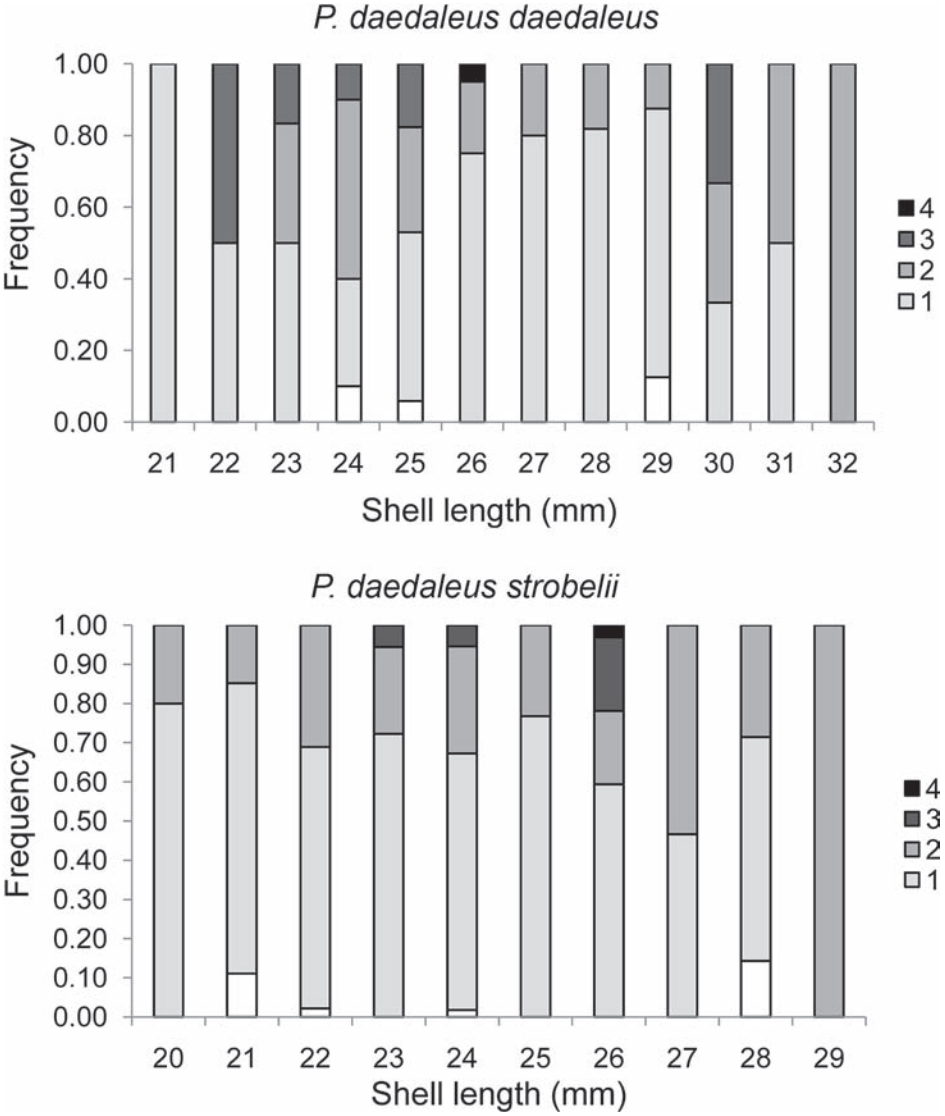


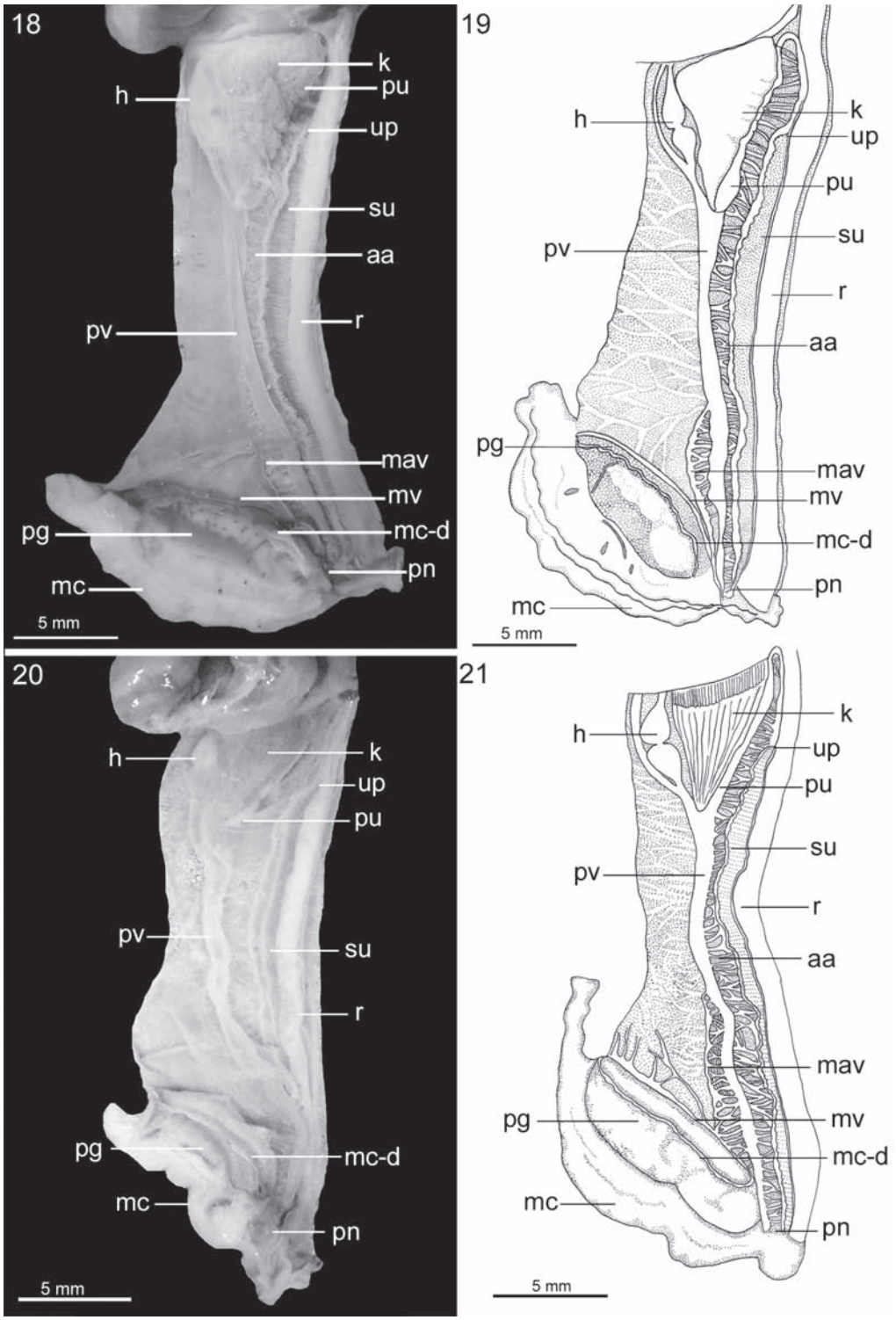
FIG. 17. Frequency of shells of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii* showing either 0, 1, 2, 3 or 4 lower palatal teeth plotted against shell length.

length, though of similar size in both species (3.0–5.4 mm in *P. daedaleus daedaleus*; 3.5–6.0 mm in *P. daedaleus strobelii*); it is equivalent to 50–60% of the kidney length.

A prominent pulmonary vein runs parallel to the rectum and reaches the mantle collar. The pulmonary vein was 18–29 mm long in *P. daedaleus daedaleus*, and 14–30 mm long in *P. daedaleus strobelii*.

The afferent marginal vein of *P. daedaleus strobelii* branches near the midpoint of the pulmonary vein, thus equaling from 40% to 62% of the length of the latter; this position is quite variable in *P. daedaleus daedaleus,* where the afferent marginal vein was 39% to 75% of the pulmonary vein length.

All the studied material showed a conspicuous vascularization between the secondary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ureter and the pulmonary vein (ad-rectal area), and between the pulmonary vein and the marginal afferent vein. A marginal vein branching from the distal portion of the pulmonary vein and running along the mantle collar was always present. The region of the lung delimited by the pericardium, the columellar side and the above mentioned vessels (pulmonary, marginal afferent and marginal vein) was translucent and exhibited slight vascularization.

The mantle collar includes a brown, spongy pallial gland and some indentations corresponding to the position of the apertural lamellae and folds.

Reproductive System: The genital organs of *P. daedaleus daedaleus* are illustrated in Figures 22–24. The ovotestis, embedded in the digestive gland, is composed of 6–7 groups of digitiform acini (most often six) that converge to form the collector duct. The studied specimens of *P. daedaleus strobelii* (Figs. 25–27) had six groups of acini.

Ovotestis color is variable (white, orange or light brown) in *P. daedaleus daedaleus*, sometimes with black spots*;* it is orange to light or reddish-brown in *P. daedaleus strobelii*.

The hermaphroditic duct was similar in all the studied material. It is brown, markedly convoluted, and runs along the columellar side of the visceral mass. The diameter of the duct varied among specimens, but its central portion always became dilated to form the vesicula seminalis.

The albumen gland is elongated, highly variable in size and color (white or pale orange in *P. daedaleus daedaleus;* white, cream or pale orange in *P. daedaleus strobelii*), and located against the anterior, concave surface of the digestive gland over the digestive pouch. The fertilization pouch-spermathecal complex (FPSC) is white, conspicuously visible on the basal side of the albumen gland. FPSC is proximally swollen, while its distal part consists of a free blind sac.

The spermoviduct is composed of a hyaline pale-orange oviduct portion (uterus) and a white and glandular prostatic portion. The uterus continues into the free oviduct that ends at the vagina, while the prostatic portion extends to the vas deferens.

The hermaphroditic duct, the albumen gland and the uterine part of the spermoviduct are highly variable in size. The penis retractor muscle is always attached to the penis-epiphallus boundary.

The bursa copulatrix of *P. daedaleus daedaleus* is generally a round sac, 1.20 to 3.10 mm in diameter, though it was slightly ovoid in some specimens; it is a round to ovoid sac in *P. daedaleus strobelii,* 1.76 to 2.84 mm in diameter. The color of the bursa varies, in both species, depending on the eventual presence of sperm, that is, it is white or cream color in virgin snails, and brown in the individuals that have already copulated.

The duct of the bursa copulatrix was 13 to 27 mm long in *P. daedaleus daedaleus,* and 17 to 27 mm long in *P. daedaleus strobelii*. Internally, it exhibits straight folds or lamellae in both species.

The penial complex, consisting of penis, epiphallus and flagellum, is long and occupies a high proportion of the anterior portion of the visceral cavity, with a total length of 26.2–47.6 mm in *P. daedaleus daedaleus* (Figs. 28–31), and of 26.2–39.2 mm in *P. daedaleus strobelii* (Figs. 32–35).

The main internal differences between *P. daedaleus daedaleus* and *P. daedaleus strobelii* were found in the anatomy of penis and vagina. The penis is club-shaped in *P. daedaleus daedaleus* (Figs. 22, 23), due to a significant swelling of its proximal portion, which was 2.6 to 4.2 mm wide; the distal part is much narrower and of variable length, and therefore the high variability of penis length (4.8 to 14.7 mm long) was mostly due to variations in the length of the narrow part. By contrast, in *P. daedaleus strobelii* the penis has only a slight swelling towards the epiphallus (Figs. 25, 26); as a result, the organ is almost cylindrical in shape and significantly thinner than in *P. daedaleus daedaleus* (1.89 to 2.62 mm wide). Penis length was also highly variable in *P. daedaleus strobelii,* 3.50 to 14.29 mm long, that is, in the same range of shell

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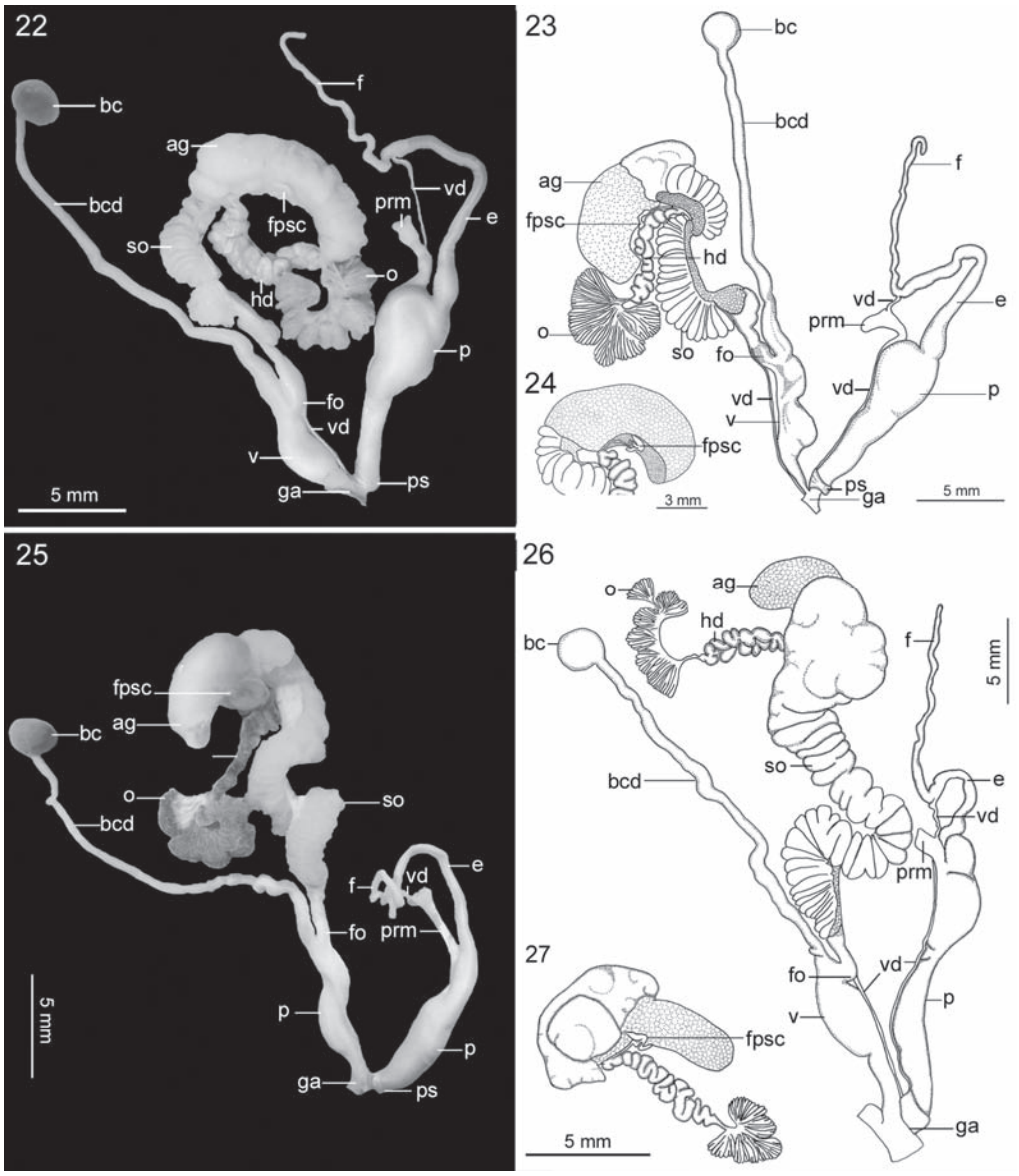
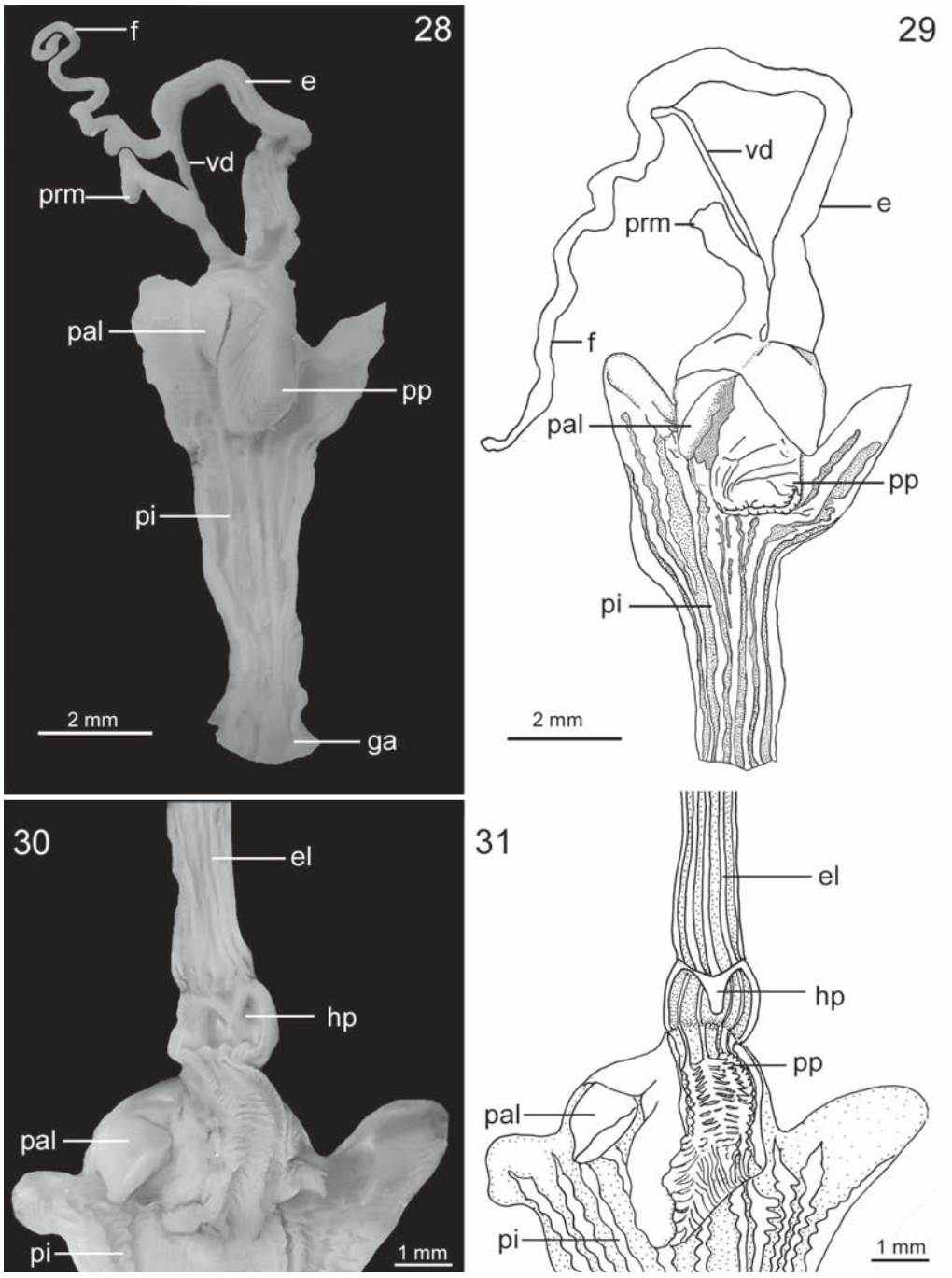
FIGS. 18–21. Pallial complex of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*. FIGS. 18, 19: Pallial complex of *P. daedaleus daedaleus*; FIGS. 20, 21: Pallial complex of *P. daedaleus strobelii.* Abbreviations: aa, adrectal area; h, heart; k, kidney; mav, marginal afferent vein; mc, 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.

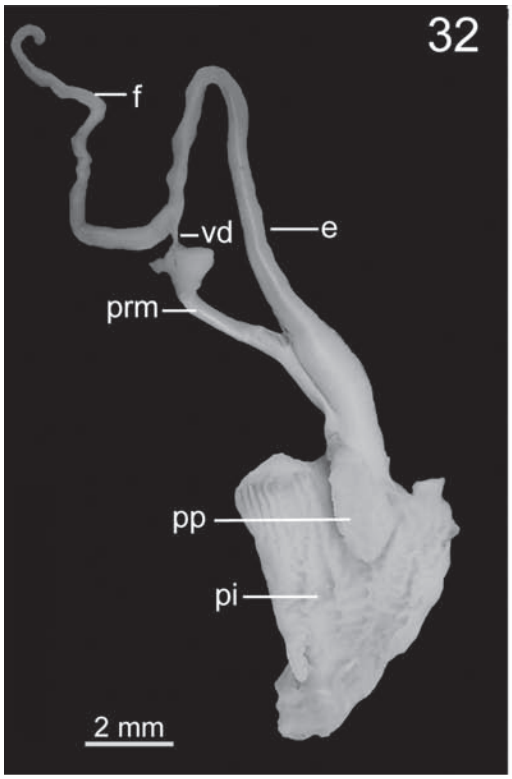


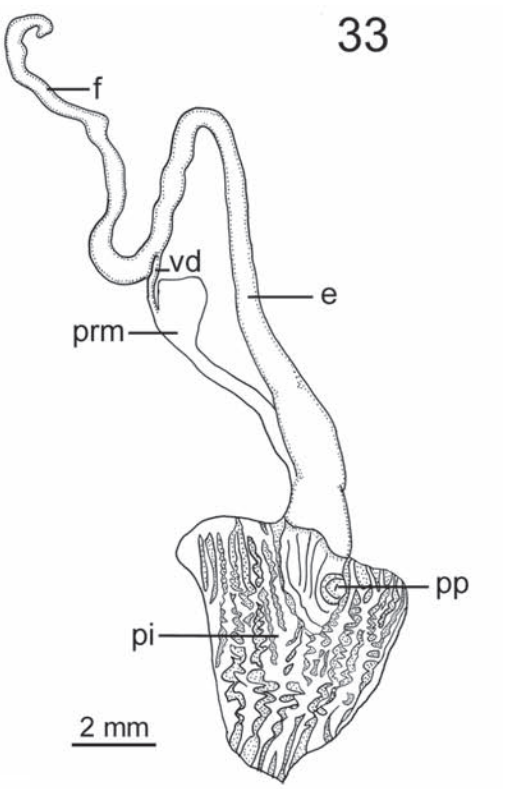
FIGS. 22–27. Genital system of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii.* FIGS. 22, 23: Genital system of *Plagiodontes daedaleus daedaleus*; FIG. 24: Proximal genitalia of *P. daedaleus daedaleus*; FIGS. 25, 26: Genital system of *Plagiodontes daedaleus strobelii*; FIG. 27: Proximal genitalia of *P. daedaleus strobelii*. 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.

length values of *P. daedaleus daedaleus*. The proportion penis-length/penis-width was 1.60 to 4.32 in *P. daedaleus daedaleus* (2.76 on average), whereas the penis was 2.75 to 6.00 times as long as it is wide in *P. daedaleus strobelii* (4.67 on average).



FIGS. 28–31. Terminal male genitalia of *Plagiodontes daedaleus daedaleus*. FIGS. 28, 29: Internal structure of penis; FIGS. 30, 31: Internal structure of epiphallus and penial papilla. Abbreviations: e, epiphallus; el, epiphallic lamellae; f, flagellum, ga, genital atrium; hp, hollow papilla of the epiphallus; pi, pilaster; pp, penial papilla; pal, penial papilla accessory lobe; prm, penis retractor muscle; vd, vas deferens.


32
f
vd
e
prm
pp
pi
2 mm


33
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vd
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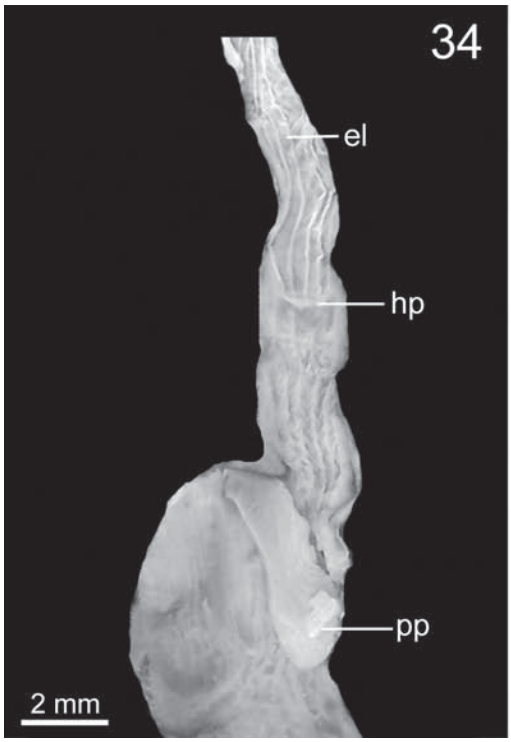
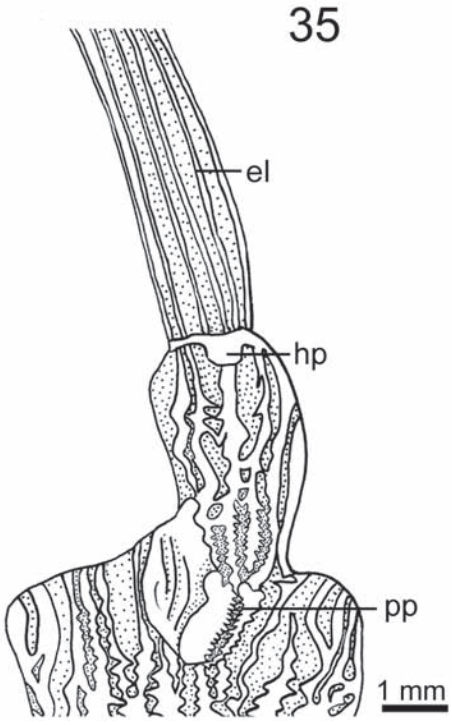

34
el
hp
pp
2 mm


35
el
hp
pp
1 mm

The external swelling of the penis is correlated with its inner anatomy. The verge exhibited an accessory lobe in *P. daedaleus daedaleus* (Figs. 28, 29), with an internal tube sculptured with anastomosing folds (Figs. 30, 31). In *P. daedaleus strobelii,* the penial papilla was quadrangular, elongated and simple, with no accessory lobe (Figs. 32, 33) but also with internal anastomosing folds (Figs. 34, 35).

The inner wall of the penis of *P. daedaleus daedaleus* exhibits longitudinal folds or pilasters of variable development, ranging from thin and straight to prominent and undulated folds. The pilasters always become thin and straight in the area surrounded by the penis sheath, and are absent underneath the papilla (Figs. 28, 29). In *P. daedaleus strobelii,* the internal surface of the penis is composed of pilasters with a variable degree of anastomosis, which become distally thin and straight (Figs. 32, 33).

The penis sheath is short in both species. The epiphallus is cylindrical, except for a swelling in the transition to the penis, which is marked by a constriction; it was 10.12–17.86 mm long (13.25 mm on average) in *P. daedaleus daedaleus,* and 8.93–18.94 mm long (12.38 mm long on average) in *P. daedaleus strobelii*. Internally, the cylindrical part exhibits five to seven straight folds in both species (Figs. 30, 31 and 34, 35), and it is separated from the swollen part by a septum-like structure at a point where the folds join to form a minute hollow papilla. The swollen part continues into a cylindrical tube that runs into the fleshy penial papilla. This tube has an internal sculpture of elevated, branching and anastomosing folds.

The vas deferens is a tubule of constant diameter that emerges exactly above the point where the vagina bifurcates to form the free oviduct and the bursa copulatrix duct. It is shorter than the sum of the lengths of the penis and the epiphallus. The vas deferens runs attached to the vagina, passes through the penis sheath, and continues along the penis, attached to its surface, to end finally in the epiphallus-flagellum boundary, after crossing the retractor muscle (Figs. 25, 26). The flagellum is cylindrical, as long as the epiphallus, and has one straight internal fold in both species; it was 10.12 to 17.86 mm long (13.25 mm on average) in *P. daedaleus daedaleus,* and 8.06 to 13.69 mm long (11.1 mm on average) in *P. daedaleus strobelii*.

The vagina of *P. daedaleus daedaleus* is generally slightly shorter than the penis, swollen and two to four times as long as it is wide; it was 4.74 to 10.82 mm long, 1.55 to 3.45 mm wide in the studied material. The inner vaginal surface is covered by anastomosing thin folds which give it a reticulated aspect (Figs. 36, 37).

The vagina of *P. daedaleus strobelii* has similar characteristics, except that it is centrally swollen; it was 6.30 to 8.33 mm long, 1.35 to 3.00 mm wide, and 2.4 to 5.0 times as long as it is wide. It exhibited a remarkable intra- and interpopulational variation (Figs. 38–40), with a sculpture of main longitudinal folds that may show from some minor transverse folds up to a true reticulation.

A genital atrium was almost absent in all the studied material, since vagina and penis join together at the genital pore.

TAXONOMY

On the basis of the anatomical differences detected between the snails living to the east and west of the Pampean Sierras, we have compiled a new synonymy for *P. strobelii*, as a species characterized by the following diagnosis.

ORTHALICIDAE Albers, 1860
Odontostominae Pilsbry & Vanatta, 1898

Plagiodontes Doering, 1877
Type species: *Helix dentata* W. Wood, 1828, from Montevideo, Uruguay [subsequent designation by Pilsbry, 1898].

Plagiodontes strobelii (Doering, 1877)

Bulimus (Odontostomus) daedaleus var. major Strobel, 1874: 16–17 [subspecific name; junior homonym of *B. daedaleus major* Pfeiffer,

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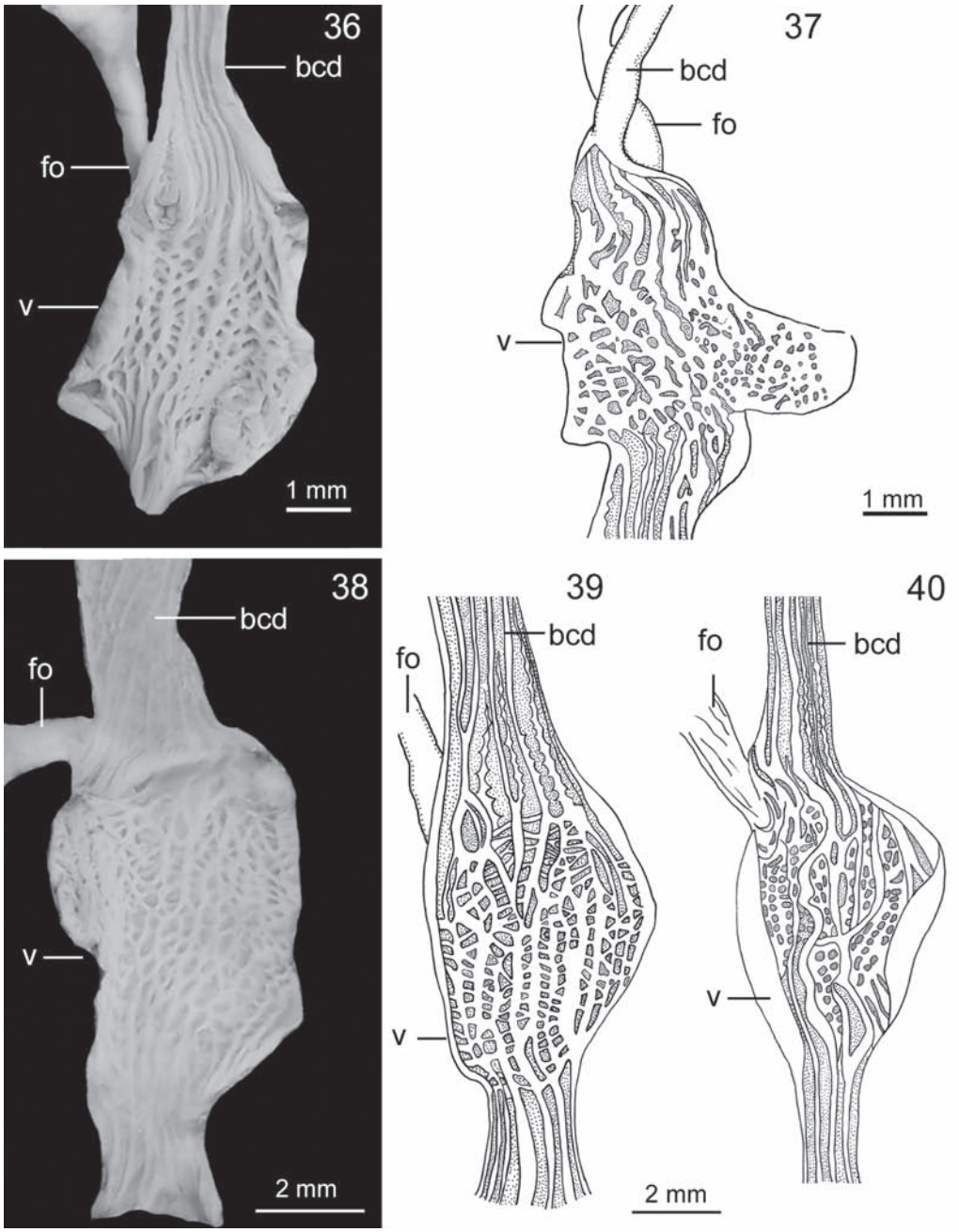
FIGS. 32–35. Terminal male genitalia of *Plagiodontes daedaleus strobelii*. FIGS. 32, 33: Internal structure of penis; FIGS. 34, 35: Internal structure of epiphallus and penial papilla. Abbreviations: e, epiphallus; el, epiphallic lamellae; f, flagellum, hp, hollow papilla of the epiphallus; pi, pilaster; pp, penial papilla; prm, penis retractor muscle; vd, vas deferens.



FIGS. 36–40. Terminal female genitalia of *Plagiodontes daedaleus daedaleus* and *P. daedaleus strobelii*. FIGS. 36, 37: Vaginal internal structure of *P. daedaleus daedaleus*; FIGS. 38–40: Vaginal internal structure of *P. daedaleus strobelli*. Abbreviations: bcd, bursa copulatrix duct; fo, free oviduct; v, vagina.

1853]; Pilsbry, 1901: 98–99 [partim].

Bulimus (Plagiodontes) daedaleus var. strobelii Doering, 1877: 239–240 [replacement name for *var. major* Strobel, 1874; subspecific name]; Doering, 1878: 320–321; Kobelt, 1878: 133.

Bulimus (Plagiodontes) daedaleus var. salinicola Doering, 1877: 240 [subspecific name]; Doering, 1878: 321.

Odontostomus (Plagiodontes) daedaleus var. salinicola – Kobelt, 1878: 133; Pilsbry, 1901: 99.

Cyclodontina (Plagiodontes) daedalea major – Parodiz, 1939: 721 [partim]; 1957: 28 [partim].

Cyclodontina (Plagiodontes) daedalea minor – Parodiz, 1939: 721 [partim]; 1957: 28 [partim].

Scalarinella (Plagiodontes) daedaleus strobelii – Zilch, 1971: 199.

Bulimus (Odontostomus) daedaleus major – Breure, 1974: 118 (catalogue) [partim].

Plagiodontes daedaleus major – Fernández, 1973: 147 [partim]; Richardson, 1993: 54 [partim].

Diagnosis: Elongate-ovate shell, with a conic spire and an acute apex; protoconch and teleoconch sculptures not sharply limited. Penis subcylindrical; penial papilla quadrangular elongated, simple, with no accessory lobe. Vagina subcylindrical, centrally swollen. A comparison to *P. daedaleus daedaleus* is summarized in Table 3.

Type Series: Lectotype, SMF 25351 (Fig. 41) from "Sierra de Aconjigasta, Argentina", as designed by Zilch (1971).

Type locality: Sierra de Aconjigasta [Sierra de Pocho], Córdoba Province, Argentina.

Distribution: Central and northern San Luis province, west slope of Sierra Grande and Sierra de Comechingones, Córdoba province, Argentina.

Status of *Plagiodontes daedaleus salinicola* (Doering, 1877)

Forty one living specimens were found near the type locality of this nominal subspecies ("salty margins of the Laguna de Pocho"; Doering, 1877: 240; 1878: 321), at Provincial Road 28, close to Las Palmas (about 6 km from Laguna de Pocho). Their shells were not different to the 20 specimens collected at Chancaní (29 km far from the type locality).

As described by Doering (1877: 200; 1878: 321), some of these adult shells were smaller than typical *P. strobelii* (range: from 21.70 to 30.05 mm), and somehow similar to *P. daedaleus,* so five shells scored in the overlapping area of the MDA histogram (8.19% of incorrect classifications, that is, fitting the general model of variation found for the whole data set).

Eight additional dissections were made on snails from Las Palmas, confirming that all specimens had a simple penis papilla and a non-swollen vagina that warrant *salinicola* not being a member of *P. daedaleus* but rather a population of *P. strobelii* that does not deserve any subspecific status.

DISCUSSION

A subspecies is "an aggregate of local populations of a species inhabiting a geographical subdivision of the range of the species and differing taxonomically from other populations of the species" (Mayr & Ashlock, 1991). However, formal tests of morphometric discrimination and degree of allopatry were seldom performed for most available trinomina.

Six nominal subspecific names were recorded for *Plagiodontes daedaleus*:

(1) *Plagiodontes daedaleus daedaleus* (Deshayes, 1851): The locality "Brazil" given by Deshayes (1851, in: Férussac & Deshayes, 1851) was erroneous (Pilsbry, 1901; Parodiz, 1939). This form is very common in the Sierras de Córdoba, central Argentina. Doering (1875) described *P. daedaleus minor,* which is a junior synonym of the typical *P. daedaleus daedaleus* (Pilsbry, 1901; Parodiz, 1939).

(2) *Plagiodontes daedaleus major* (Pfeiffer, 1853: 370): It was characterized as a larger, more ventrose variety of *P. daedaleus* ("β. Major, ventrosior") with no geographical restriction. Richardson (1993: 54) recognized Pfeiffer (1853) as the author of *Plagiodontes daedaleus major* as an available name.

(3) *Plagiodontes daedaleus strobelii* (Doering, 1877): Strobel (1874: 16–17) misidentified the largest variety, and described a var. *major* as a shell with a produced, acute

conic spire, from Cerro del Morro, San Luis province, that is, a slender shell, less ventrose than any *daedaleus* form, and with a considerably different spire shape. The name was explicitly intended to be subspecific, since in the same work the author stated that varieties were equivalent to subspecies ("sottospecie" in the Italian original text), or the entities that Darwin called *"specie incipienti"* (Strobel, 1874: 15), and employed the term *mutationes* to describe some infrasubspecific variations.

Doering (1877: 239; 1878: 320) acknowledged that the name *daedaleus* included two main configurations separated by the Sierra de Córdoba*:* the snails on the east slope have ventrose shells of variable size, with a short, blunt spire, like typical *daedaleus*; the snails over the west slope have more elongated, less ventrose shells, with a longer conic spire (i.e., *B. daedaleus major* Strobel, 1874, non Pfeiffer, 1853). Because of this difference, Doering was reluctant to keep Strobel's variety in the same species, and unambiguously stated that he did so only in a provisional way ("provisoriamente la reunimos con el *P. daedalens*" [sic; lapsus calami]: Doering, 1877: 239; 1878: 320). To avoid homonymy, he explicitly replaced the name *major* Strobel, 1874, by *strobelii.*

(4) *Plagiodontes daedaleus multidentatus* (Doering, 1875): Described as similar to *P. daedaleus daedaleus* but with a stronger dentition in the shell aperture. Parodiz (1939) considered it to be a junior synonym of *P. daedaleus daedaleus* (= *P. daedaleus minor*).

(5) *Plagiodontes daedaleus salinicola* (Doering, 1877): It was described as smaller and less slender than *P. daedaleus strobelii,* from Laguna de Pocho in San Luis province.

(6) *Plagiodontes daedaleus costatus* Hylton-Scott, 1952: It was characterized as obese shells, with a blunt apex, like typical *daedaleus,* but with strong axial ribs in the teleoconch. The only documented locality is Copacabana, Córdoba province.

Four out of these six subspecies have obese shells, a blunt apex, a well-defined boundary between the protoconch and the teleoconch, and live to the east of the Pampean Sierras: *P. d. daedaleus, P. d. major, P. d. multidentatus,* and *P. d. costatus.* The remaining two subspecies, *P. d. strobelii* and *P. d. salinicola,* have slender shells with a conical acute apex and live to the west of the sierras.

Our results confirmed the existence of significant morphological gaps between the two groups. Pilsbry (1901) and Parodiz (1939) failed to recognize the shell differences between the two largest varieties, included the misleading statement that *major* Strobel was apparently identical to *major* Doering, and listed the objective synonyms *major* Strobel and *strobelii* Doering as if they had been proposed for different entities. This opinion is rejected here because *P. strobelii* is recognizable as a significantly different morph.

A morphometric discrimination that correctly classifies more than 90% of the shells collected to the east or the west of the sierras should have been a good argument for subspecific recognition, but the existence of definite differences in the genital anatomy between the two groups (especially the presence of either a simple penial papilla or a papilla with an additional lobe) supports the specific status of both forms.

The internal anatomy of *Plagiodontes daedaleus* was still poorly known. Only Breure & Schouten (1985) outlined the genital anatomy of some specimens from Cerro del Morro, San Luis (i.e., the locality mentioned by Strobel, 1874, for his *P. daedaleus major;* now: *P. strobelii*), and Alta Gracia, Córdoba (i.e., from an area within the range of *P. daedaleus*), and Tillier (1989) sketched the pallial complex of a specimen from Cerro del Morro, San Luis, indicating the position of the ureteric pore and the open condition of the secondary ureter.

In this study, all specimens from the east slope of the Pampean Sierras (i.e., *P. daedaleus*) had a papilla with an accessory lobe. By contrast, all specimens from the west slope of the sierras (i.e., *P. strobelii,* including *salinicola*) exhibited a simple penial papilla.

Figure 9 in Breure & Schouten (1985: 18) illustrated the genital system of a specimen from Cerro del Morro. It was labelled as *Plagiodontes dealdalea* [lapsus calami for *daedaleus*], but it shows a subcylindrical penis and a non-swollen vagina, which according to our results allow inferring that the specimen had a simple penial papilla and actually was *P. strobelii*. Conversely, the drawing for *Plagiodontes* sp. from Alta Gracia, Córdoba, in figure 12 of Breure & Schouten (1985: 21) shows a club-

shaped penis and a centrally swollen vagina that correspond to typical *P. daedaleus,* as a consequence of having an accessory lobe to the penial papilla.

Parodiz (1939) and Fernández (1973) supplied long lists of localities in Argentina for *P. daedaleus* that included information on the distribution of the overlooked *P. strobelii*. Our listing of studied material (Appendix 1) supports the hypothesis that *P. strobelii* is restricted to western Córdoba and San Luis province, whereas *P. daedaleus* is widely distributed in eastern Córdoba; they are separated by the central sierras and they would not have any degree of sympatry.

Mountain grasslands in the summits seem to be an effective barrier that prevents the expansion of these species towards the opposite side of the sierras. It is suggestive that also *P. patagonicus* appears to be similarly limited, since it only extends southwards, from the summits of the sierras in southern Buenos Aires province to the plains, and was never reported from localities over the northern slope (Cazzaniga et al., 2005).

The presence of either a simple penial papilla or a papilla with an additional lobe, which is correlated with a characteristic widening of penis and vagina, was recently argued by Pizá & Cazzaniga (2009) as a reliable character for distinguishing some species in genus *Plagiodontes,* which is currently composed by nine species.

Other than in *P. strobelii,* a simple penis papilla is only found in *P. dentatus* from Uruguay and eastern Argentina, and *P. patagonicus* from southern Buenos Aires, but its shape is different in these three species: it is short and round in *P. dentatus;* it is proximally swollen and distally triangular and elongated in *P. patagonicus* (Pizá & Cazzaniga, 2009), and it is quadrangular elongated in *P. strobelii.*

All the remaining species in the genus have an accessory lobe that derives in a club-shaped penis. The accessory lobe was described by Pizá & Cazzaniga (2009) as smaller than the penial papilla in *P. multiplicatus parvus* Hylton-Scott, 1952, and *Plagiodontes weyrauchi* Pizá & Cazzaniga, 2009. *Plagiodontes daedaleus* also has a papilla larger than the accessory lobe (this paper). The penial papilla of *P. brackebuschii* and *P. weyenberghii* also has a small accessory lobe, which is similar to that of *P. daedaleus* (Pizá, MS). Also, *P. rocae* Doering, 1881, has an accessory lobe but in this species the lobe is larger than the papilla itself.

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APPENDIX 1

Studied collections of *Plagiodontes daedaleus* and *P. strobelii*. S: species (D: *P. daedaleus;* S: *P. strobelii*)*;* M: sets included in morphometric analyses of shells; A: sets on which pallial and genital anatomy was studied*.* Altitude in m a.s.l. Province abbreviations: C, Córdoba; SL, San Luis.

Set	S	M	A	Locality (Province): Lat., Long.; Altitude (m a.s.l.)	Collection data; collector [previous museum label]; Note
1	*P. d.*	X	X	Embalse−Berrotarán (C): 32°20'00.6"S, 64°21'41.9"W; 628	Own material; J. Pizá & M. Carrizo, 2005.
2	*P. d.*	X		Embalse (C): 32°14'29.1"S, 64°21'43"W; 630	FML 1277/6; W. Weyrauch [*P. daedaleus*].
3	*P. d.*	X	X	Alta Gracia (C): 31°39'01.5"S, 64°27'56.6"W; 651	Own material; J. Pizá & M. Carrizo, 2005.
4	*P. d.*			La Granja. Alta Gracia (C): ~31°40'S, ~64°26'W	MACN-In 14204; Bruch.
5	*P. d.*	X	X	Observatorio (C): 31°35'46.5"S, 64°32'39.4"W; 1,455	Own material; J. Pizá & M. Carrizo, 2005.
6	*P. d.*	X		Carlos Paz (C): ~31°25'S, ~64°28'W	MACN-In 26589; A. Castellanos.
7	*P. d.*	X		Tanti (C): 31°21'33.9"S, 64°35'17.3"W; 921	Own material; J. Pizá & M. Carrizo, 2005.

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Set	S	M	A	Locality (Province): Lat., Long.; Altitude (m a.s.l.)	Collection data; collector [previous museum label]; Note
8	*P. d.*	X		Pan de Azúcar (Cosquín) (C): ~31°14'S, ~64°25'W; 800	Own material; Pablo Martín.
9	*P. d.*			Pampa de Olaen (C) : ~31°10'S, ~64°36'W; ~1,120	MLP 9736.
10	*P. d.*	X	X	Valle Hermoso (C): 31°06'49.5"S, 64°28'09.3"W; 999	Own material; J. Pizá & M. Carrizo, 2005.
11	*P. d.*			La Falda (C): ~31°05'S, ~64°30'W	MACN-In 23555; Haedo [*P. daedaleus major*].
12	*P. d.*	X		Huerta Grande (C): ~31°04'S, ~64°30'W; 963	Own material; Pablo Martín.
13	*P. d.*	X	X	Jesús María (C): 30°58'58.6"S, 64°06'43.1"W; 531	Own material; J. Pizá & M. Carrizo, 2005.
14	*P. d.*	X		La Cumbre (C): 30°58'36.6"S, 64°28'52.6"W; 1,221	Own material; Pablo Martín.
15	*P. d.*	X	X	Los Cocos−La Cumbre (C): 30°57'16.4"S, 64°31'23"W; 1,107	Own material; J. Pizá & M. Carrizo, 2005.
16	*P. d.*	X		San Esteban (C): ~30°55'S, ~64°32'60"W; 1,007	MLP no number; M. I. Hylton-Scott.
17	*P. d.*	X		Dolores (C): ~30°54'S, ~64°32'W; 1,026	MLP 36015.
18	*P. d.*	X	X	Los Cocos−Capilla del Monte (C): 30°53'37.6"S, 64°32'01.7"W; 1,014	Own material; J. Pizá & M. Carrizo, 2005.
19	*P. d.*			Soto (C), ~30°51'S, ~65°01'W	MLP 6693 [*Plagiodontes daedaleus*].
20	*P. d.*	X	X	Ongamira (C): 30°46'08.1"S, 64°29'07.8"W; 1,076	Own material; J. Pizá & M. Carrizo, 2005.
21	*P. d.*	X	X	Ischilín (C): 30°36'06.336"S, 64°20'52.908"W; 913	Own material; J. Pizá & M. Carrizo, 2007.
22	*P. d.*	X	X	Deán Funes−Ischilín (C): 30°29'24.9"S, 64°22'19.2362"W; 822	Own material; J. Pizá & M. Carrizo, 2007.
23	*P. d.*	X		Avellaneda (C): 30°34'S, 64°12'W; 675	FML 24; W. Weyrauch, 1969 [*Plagiodontes daedaleus*].
24	*P. d.*	X		Villa Totoral (C): 30°40'58.1"S, 64°00'59.9"W; 523	Own material; J. Pizá & M. Carrizo, 2005.
25	*P. s.*			Cerro del Morro (SL): ~33°08'S, ~65°26'W	MACN-In 30680; F. Pastore [*P. daedaleus major*].
26	*P. s.*	X		Cerro Rosario (SL): 32°57'0"S, 65°42'14.8"W; 1,110	FML 1304; W. Weyrauch [*P. brakkebuschii attenuatus* Weyrauch (*nomen nudum*)].
27	*P. s.*			To the West of Renca (SL): ~32°45'S, ~65°22'W	MACN-In 16226; A. Castellanos [*Odontostomus*].
28	*P. s.*			San Francisco del Monte de Oro (SL), Quebrada del río Gomez: 32°37'02"S, 66°04'17.3"W; 805	Own material; J. Pizá & M. Carrizo, 2009.
29	*P. s.*	X	X	San Francisco del Monte de Oro (SL): 32°37'30"S, 66°08'49.5"W; 896	Own material; J. Pizá & M. Carrizo, 2005.
30	*P. s.*			Sierra de San Francisco (SL): ~32°37'S, ~66°08'W	MACN-In 15130; A. Castellanos y Serié [*Odontostomus (Plagiodontes) daedaleus* var. *major*].

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Set	S	M	A	Locality (Province): Lat., Long.; Altitude (m a.s.l.)	Collection data; collector [previous museum label]; Note
31	*P. s.*			San Francisco del Monte de Oro (SL): ~32°37'S, 66°08'W	MACN-In 16750; [*Odontostomus* sp.].
32	*P. s.*			Dique La Huertita (SL): 32°24'11.4"S, 65°43'28.5"W; 1,004	Own material; J. Pizá & M. Carrizo, 2009.
33	*P. s.*		X	Provincial Road # 2, San Martín-Quines (SL): 32°19'32.8"S, 65°41'39.3"W; 808	Own material; J. Pizá & M. Carrizo, 2009.
34	*P. s.*			Sierras de Luján (SL): ~32°22'S, ~65°57'W	MACN-In 15135; A. Castellanos y Serié [*Odontostomus (Plagiodontes) daedaleus major*].
35	*P. s.*			Sierras de Quines (SL): ~32°13'S, ~65°47'W	MACN-In 15126; A. Castellanos y Serié [*Odontostomus (Plagiodontes) daedaleus* var. *major*].
36	*P. s.*			La Quebrada, Santa Rosa−Quines (SL)	MACN-In 1639; C. Vega [*Odontostomus (Plagiodontes) daedaleus major*].
37	*P. s.*	X		Quebrada de Cautana (SL): ~32°17'S, ~65°30'W; ~600	MACN-In 31616; R. Bidart [*Plagiodontes* sp.].
38	*P. s.*			Quebrada de Cautana (SL): 32°12'45.3"S, 65°21'37.3"W; 683	Own material; J. Pizá & M. Carrizo, 2009.
39	*P. s.*	X		Bajo de Veliz (SL): ~32°19'S, ~65°20'W; ~600	MLP no number; A. Castellanos [*P. daedaleus mayor* (Strobel)].
40	*P. s.*			Bajo de Veliz (SL): 32°19'18.5"S, 65°24'28.5"O; 659	Own material; J. Pizá & M. Carrizo, 2009.
41	*P. s.*	X		Santa Rosa de Conlara (SL): 32°19'55.8"S, 65°14'51.9"W; 619	Own material; J. Pizá & M. Carrizo, 2005.
42	*P. s.*			Rincón. Depto. Junín (SL): ~32°26'S, ~65°28'W	MACN-In 18313; Yepes [*Odontostomus* sp.].
43	*P. s.*			Cortaderas, near Rodríguez Saa station (SL): ~32°30'S, ~65°12'W	MACN-In 23550; C. Vega 1938 [*Odontostomus (Plagiodontes) daedaleus major*].
44	*P. s.*			San Javier (C): ~32°02'S, ~65°03'W	MACN-In 1653; A. Castellanos.
45	*P. s.*	X		Dique La Viña (C): ~31°53'S, ~65°01'W; 885	MACN-In 3241; J. Jurado [*Plagiodontes* sp.].
46	*P. s.*			Dique La Viña (C): ~31°53'S, ~65°01'W; 885	MACN-In no number; Gancedo [*P. brackebuschi*].
47	*P. s.*	X		Dique La Viña (C): 31°53'19"S, 65°01'50"W; 885	Own material; J. Pizá & M. Carrizo, 2005.
48	*P. s.*			Mina Clavero (C): ~31°42'S, ~65°00'W	MACN-In 9245; C. de Villalobos [*Odontostomus*].
49	*P. s.*	X	X	Chancaní Provincial Park (C): 31°20'12.72"S, 65°29'5.82"W; 330	Own material; S. Burela & N. Pelegrin.
50	*P. s.*	X	X	Provincial Road # 28 near Las Palmas (C): 31°21'49.3"S, 65°12'17.3"W; 1,083	MACN-In 37086; J. Pizá & M. Carrizo, 2005 [*P. daedaleus*].
51	*P. s.*	X		Taninga−Salsacate (C): ~31°12'S, ~65°08'W; 840	FML 914; W. Weyrauch [*P. daedaleus*].