



Oxychilus (Drouetia) viridescens (Gastropoda: Pulmonata: Oxychilidae), a new species from Santa Maria, Açores, and a review of the subgenus

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Abstract

Oxychilus (Drouetia) viridescens n.sp. is described from Santa Maria Island, Açores. It is conchologically similar to the sympatric *Oxychilus (Drouetia) brincki* Riedel, 1964, from which it is distinguished by the greenish coloration, the flatter spire and the slightly smaller number of whorls. Anatomically, the new species differs from all consubgenerics by the genital morphology: the penis is very thin, the distal half is wrapped in a very thick penial sheath; the epiphallus has two distinct portions, the proximal one attached to the edge of the penial sheath, the distal one attached to a constriction near mid-length of the penis; the atrial end of the vagina has a spongy, glandular appearance.

A detailed morphological and anatomical comparison of the new species with the non-umbilicated *Oxychilus* species of Santa Maria is presented. The species of *Drouetia* are reviewed and an identification key is provided.

Key words: morphology, anatomy, endemics, Azores

Introduction

Santa Maria, the southernmost and oldest island of the Açores (Féraud *et al.* 1984; Serralheiro & Madeira 1993), harbours a rich endemic terrestrial malacofauna (Morelet 1860; Backhuys 1975; Martins *et al.* 1991; Martins 1999, 2002; Cunha *et al.* 2010). The Azorean Oxychilidae provide a good example of this endemism for they show a remarkable conchological, anatomical and allozymic diversity (Riedel 1964; Martins 1981, 1989, 1991, 1999, 2005; Martins & Ripken 1991; Brito 1992). In this context, the present study aims at describing *Oxychilus (Drouetia) viridescens* n.sp. as a new non-umbilicated endemic oxychilid species from the island of Santa Maria and, in the process, a comparative morphological and anatomical account of the sympatric non-umbilicated *Oxychilus* is presented. A review of the species of the subgenera *Drouetia* and *Atlantoxychilus* is initiated, patterns of their morphological and anatomical variation and differentiation are compared, and an identification key to the Azorean non-umbilicated *Oxychilus* is provided.

Materials and methods

Materials

Specimens of *Oxychilus (Drouetia) viridescens* n.sp. were collected at the stations shown in Table 1 and Figure 1. The remaining oxychilid species used for comparisons were collected throughout the islands, their locations being mentioned *ad casum*.

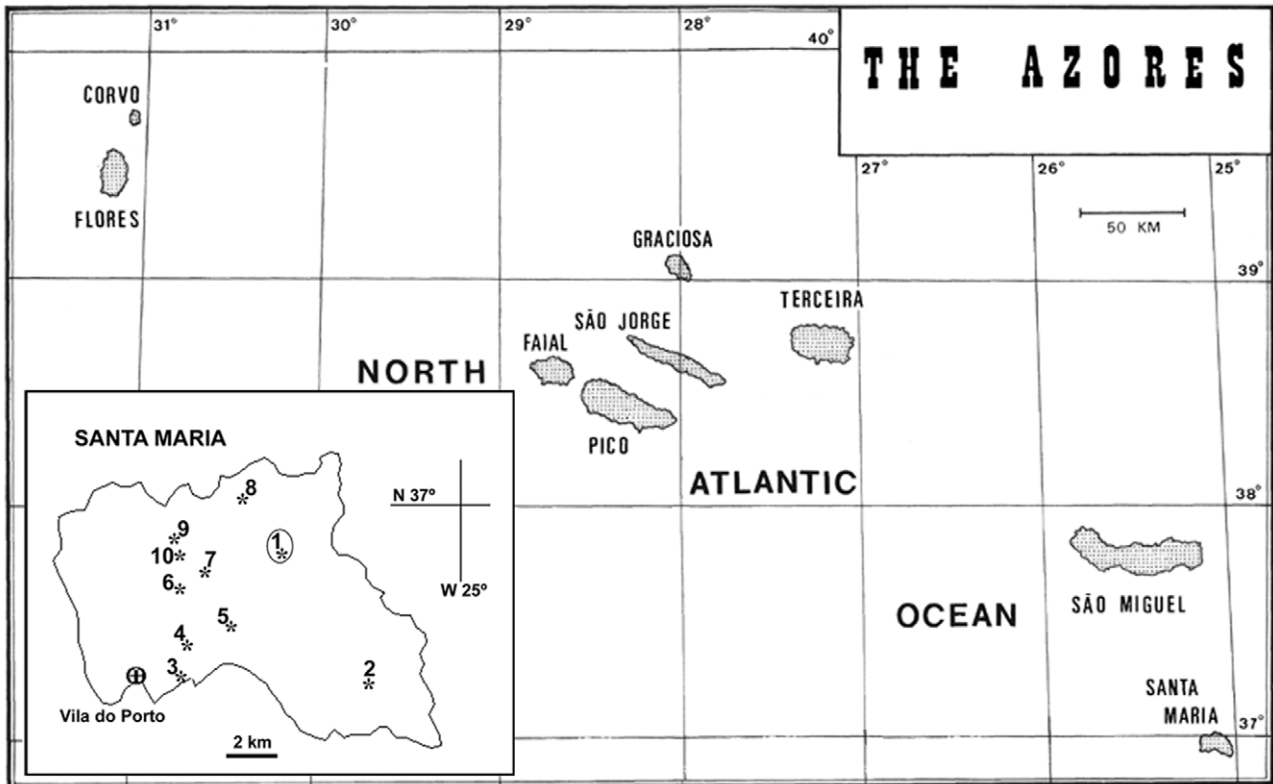


FIGURE 1. The Azores. Insert: location of the stations where specimens of *Oxychilus (Drouetia) viridescens* n.sp. were collected. Type locality encircled. See Table 1 for explanation.

Methods

Specimens were killed by drowning overnight and then preserved in 70% ethanol. The soft parts were prepared for SEM observation either by critical point drying with CO₂ or by running the dissection through pure ethanol, acetone/ethanol (1:1), pure acetone, and hexamethyldisilazane (10 minutes/step). SEM material was coated in a Denton DV-502 vacuum evaporator with two layers of gold/palladium (60:40) over a single layer of carbon, and observed in a JEOL 4500 SEM. Anatomical orientation of the reproductive system considers proximal those structures closest to the ovotestis.

Taxonomy

Family Oxychilidae P. Hesse, 1927 (1879)

Genus *Oxychilus* Fitzinger, 1833

Subgenus *Drouetia* Gude, 1911

Original description. Shell hyaline, very finely striated, and covered with excessively fine spirals, imperforate, the reflexed columella slightly twisted.

Type species. *Helix atlantica*, Morelet & Drouët, 1857, from the Azores [São Miguel Island (Riedel 1964)].

Remarks. Gude (1911) proposed *Drouetia* as a monotypic genus for the endemic *Helix atlantica*, which according to Morelet (1860) occurred in most islands of the Azores. Zilch (1959) relegated the name to subgeneric status, and since then it has been generally accepted in this category. After Riedel's (1964) anatomical research, several new species of *Drouetia* have been recognized (Martins 1981, 1989) and the group was recorded in all Azorean islands (Martins *et al.* 1989, 1990).

TABLE 1. List of stations where material of *Oxychilus (Drouetia) viridescens* n.sp. was collected.

sta #	locality	co-ordinates	altitude (m)	characterization	date	specimens	
1	Ribeira Funda, Feteiras de Santa Bárbara (type locality)	N 36° 59' 57" W 25° 05' 03"	140	Secondary forest of <i>Pittosporum undulatum</i> , undergrowth of <i>Tradescantia fluminensis</i>	22-10-1993 28-03-1996 12-12-2008	10 live 5 live + 4 shells 1 live	
	Calheta, Terras do Raposo	N 36° 56' 30" W 25° 01' 30"		200	Forest of <i>Cryptomeria japonica</i> and <i>Pittosporum undulatum</i> , undergrowth of <i>Hedychium gardneranum</i> and <i>Pteridium aquilinum</i>	13-06-1990	10 live
	E of Pico do Facho	N 36° 57' 10" W 25° 07' 10"		150	<i>Pittosporum undulatum</i> , sparse undergrowth of Gramineae	23-10-1993	1 live
4	Cavacas, slope W	N 36° 57' 15" W 25° 04' 50"	330	Forest of <i>Pittosporum undulatum</i> and <i>Myrica faya</i>	22-06-1994 29-03-1996	4 live + 4 shells 1 live + 2 shells	
5	Cruz dos Picos	N 36° 58' 10" W 25° 04' 55"	400	Forest of <i>Cryptomeria japonica</i> and <i>Pittosporum undulatum</i>	30-03-1996	2 live + 12 shells	
6	Ribeiro, Almagreira, at the foot of Pico Alto	N 36° 58' 12" W 25° 06' 10"	200	Forest of <i>Pittosporum undulatum</i> , undergrowth of <i>Hedychium gardneranum</i>	02-11-1974 16-06-1990 21-10-1993	13 live 2 live 15 live	
	Top of Pico Alto	N 36° 59' 10" W 25° 05' 27"		480	Primary forest with thick patches of <i>Hedychium gardneranum</i>	09-10-1975 12-06-1986 30-03-1996 12-12-2008	1 shell 2 live + 2 shells 3 shells 1 live
8	Fátima	N 37° 00' 05" W 25° 06' 30"	200	Forest of <i>Laurus azorica</i> and <i>Pittosporum undulatum</i>	17-06-1990	3 live + 3 shells	
9	Boundary Chã do João Tomé/ Feteiras de São Pedro	N 36° 59' 46" W 25° 06' 27"	200	Forest of <i>Pittosporum undulatum</i> , <i>Acacia melanoxylo</i> n and <i>Platanus</i> , undergrowth of <i>Hedychium gardneranum</i>	28-01-2009	37 live	
	Alto Nascente, at the N foot of Pico Alto	N 36° 59' 03" W 25° 05' 52"		340	Forest of <i>Pittosporum undulatum</i> , undergrowth of <i>Hedychium gardneranum</i>	13-12-2008	30 live

***Oxychilus (Drouetia) viridescens* n.sp.**

Helix atlantica Morelet & Drouët, 1857: 149 (*partim*); Morelet, 1860: 167 (*partim*).

Types. Holotype (Figs. 2A, 4A, C; Table 2, Ov1): Natural History Museum, London (NHMUK 20100658). Paratypes: Natural History Museum, London (2 specimens NHMUK 20100659); Muséum National d'Histoire Naturelle, Paris (1 specimen MNHN 24265); National Museum of Natural History, Washington (2 specimens USNM 1155712 and 1155713); Museum of Comparative Zoology, Harvard University, Cambridge (1 specimen MCZ 373862); Royal Belgian Institute of Natural Sciences, Brussels (1 specimen IG 31765 (MT 2329)); Museum of Natural History, Wrocław University, Poland (1 specimen MP 1011); Department of Biology, University of the Azores, Portugal (7 specimens DB/UAç-MT 1423 and 1424).

Type locality. Ribeira Funda, Feteiras de Santa Bárbara, Santa Maria, Açores (N 36° 59' 57", W 25° 05' 03") (Figure 1 and Table 1, Sta 1)

Etymology. The name refers to the characteristic greenish color of the shell.

TABLE 2. Measurements (mm) and counts of various shell characters of specimens of *Oxychilus (D.) viridescens* (Ov) and *Oxychilus (D.) brincki* (Ob). di, shell diameter; he, height of the shell; sp, height of the spire; sta/date, station number/date of collection; spc.#, specimen number; #w, number of whorls. For museum abbreviations, see text under “Types”.

spc.#	#w	di	he	sp	sta/date	Observations
Ov1	5.75	7.12	3.83	0.65	1/(12-12-2008)	holotype (NHMUK 20100658)
Ov2	5.70	7.20	3.79	0.60	1/(22-10-1993)	paratype (NHMUK 20100659a)
Ov3	5.75	6.30	3.78	0.81	1/(22-10-1993)	paratype (NHMUK 20100659b)
Ov4	5.80	7.05	3.89	0.72	1/(22-10-1993)	paratype (MNHN 24265)
Ov5	6.00	7.10	3.98	0.87	1/(22-10-1993)	paratype (USNM 1155712)
Ov6	6.00	7.22	4.43	0.79	1/(22-10-1993)	paratype (MCZ 373862)
Ov7	6.00	7.80	4.00	0.61	1/(22-10-1993)	paratype (IG31765 (MT 2329))
Ov8	5.70	6.89	3.72	0.51	1/(22-10-1993)	paratype (MP 1011)
Ov9	5.70	7.10	3.93	0.65	1/(22-10-1993)	paratype (DB/UAç-MT 1423)
Ov10	6.00	7.90	4.52	0.99	1/(22-10-1993)	paratype (DB/UAç-MT 1423)
Ov11	5.80	7.41	4.07	0.70	1/(28-03-1996)	paratype (DB/UAç-MT 1424)
Ov12	5.80	7.31	4.30	0.72	1/(28-03-1996)	paratype (DB/UAç-MT 1424)
Ov13	6.00	7.28	3.89	0.65	1/(28-03-1996)	paratype (DB/UAç-MT 1424)
Ov14	6.00	7.05	4.25	0.97	1/(28-03-1996)	paratype (DB/UAç-MT 1424)
Ov15	6.00	7.32	4.42	0.78	6/(02-11-1974)	(DB/UAç-MT 1425)
Ov16	5.75	7.02	3.88	0.55	6/(02-11-1974)	(DB/UAç-MT 1425)
Ov17	5.80	7.00	3.76	0.62	6/(02-11-1974)	(DB/UAç-MT 1425)
Ov18	6.00	7.40	4.20	0.95	6/(02-11-1974)	(DB/UAç-MT 1425)
Ov19	5.75	6.92	3.91	0.64	6/(02-11-1974)	(DB/UAç-MT 1425)
Ov20	6.20	7.10	4.28	0.72	6/(02-11-1974)	(DB/UAç-MT 1425)
Ov21	6.00	7.10	4.18	0.70	6/(21-10-1993)	(DB/UAç-MT 1426)
Ov22	5.90	7.22	4.22	0.71	2/(13-06-1990)	(DB/UAç-MT 1427)
Ov23	6.00	8.18	4.86	0.74	5/(30-03-1996)	(DB/UAç-MT 1428)
Ov24	6.00	7.60	3.85	0.61	1/(22-10-1993)	paratype (DB/UAç-MT 1423)
Ov25	5.75	7.33	4.07	0.89	1/(28-03-1996)	paratype (DB/UAç-MT 1448)
Ob1	6.40	7.60	4.65	0.95	2/(13-06-1990)	(DB/UAç-MT 1442)
Ob2	6.35	7.90	4.53	0.95	2/(13-06-1990)	(DB/UAç-MT 1442)
Ob3	6.70	7.80	4.85	1.04	10/(13-06-1990)	(DB/UAç-MT 1443)
Ob4	6.60	9.18	5.50	1.11	5/(30-03-1996)	(DB/UAç-MT 1444)
Ob5	6.80	8.70	5.59	1.32	5/(13-06-1986)	(DB/UAç-MT 1445)
Ob6	6.80	8.50	5.00	0.90	7/(12-06-1986)	(DB/UAç-MT 1446)
Ob7	6.75	8.25	5.19	0.95	7/(21-06-1994)	(DB/UAç-MT 1447)
Ob8	7.00	8.41	5.10	1.15	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob9	6.60	7.75	4.98	1.31	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob10	6.40	8.72	4.76	0.98	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob11	7.00	7.98	5.11	1.48	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob12	6.50	7.90	4.80	0.92	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob13	6.30	7.77	4.57	1.03	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob14	6.35	7.42	4.65	0.81	1/(28-03-1996)	(DB/UAç-MT 1448)
Ob15	6.40	7.50	4.60	0.99	1/(28-03-1996)	(DB/UAç-MT 1448)

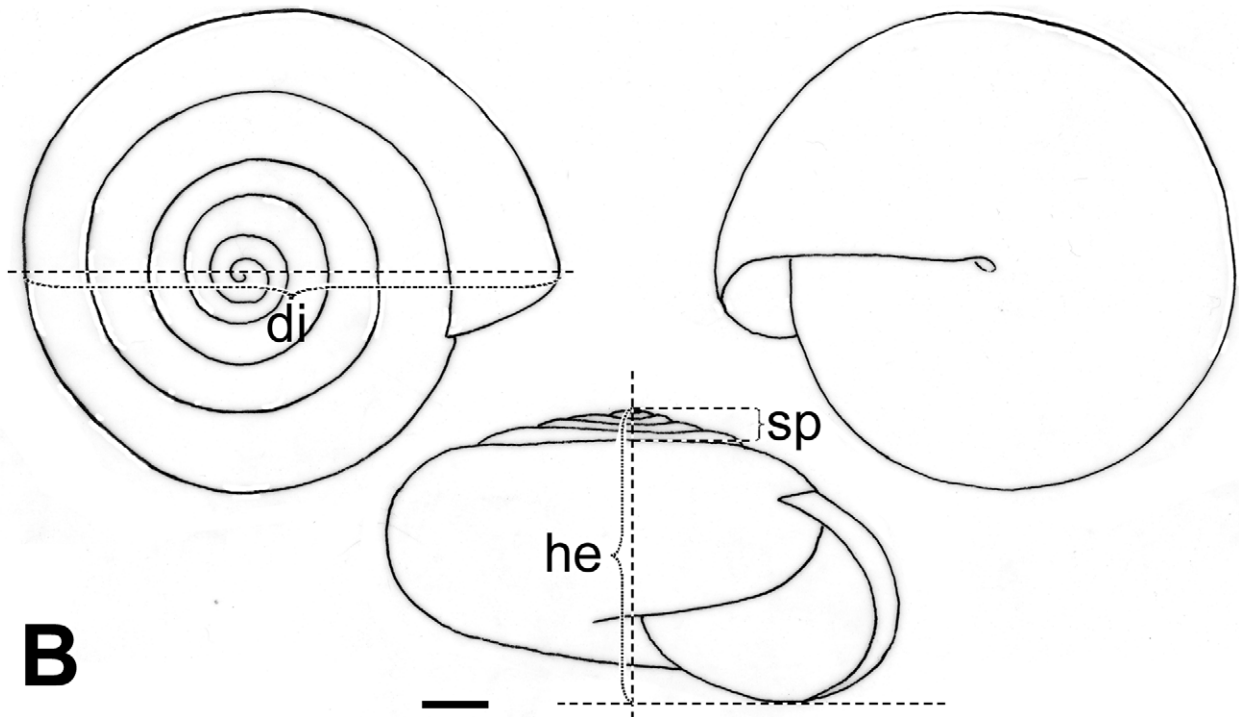
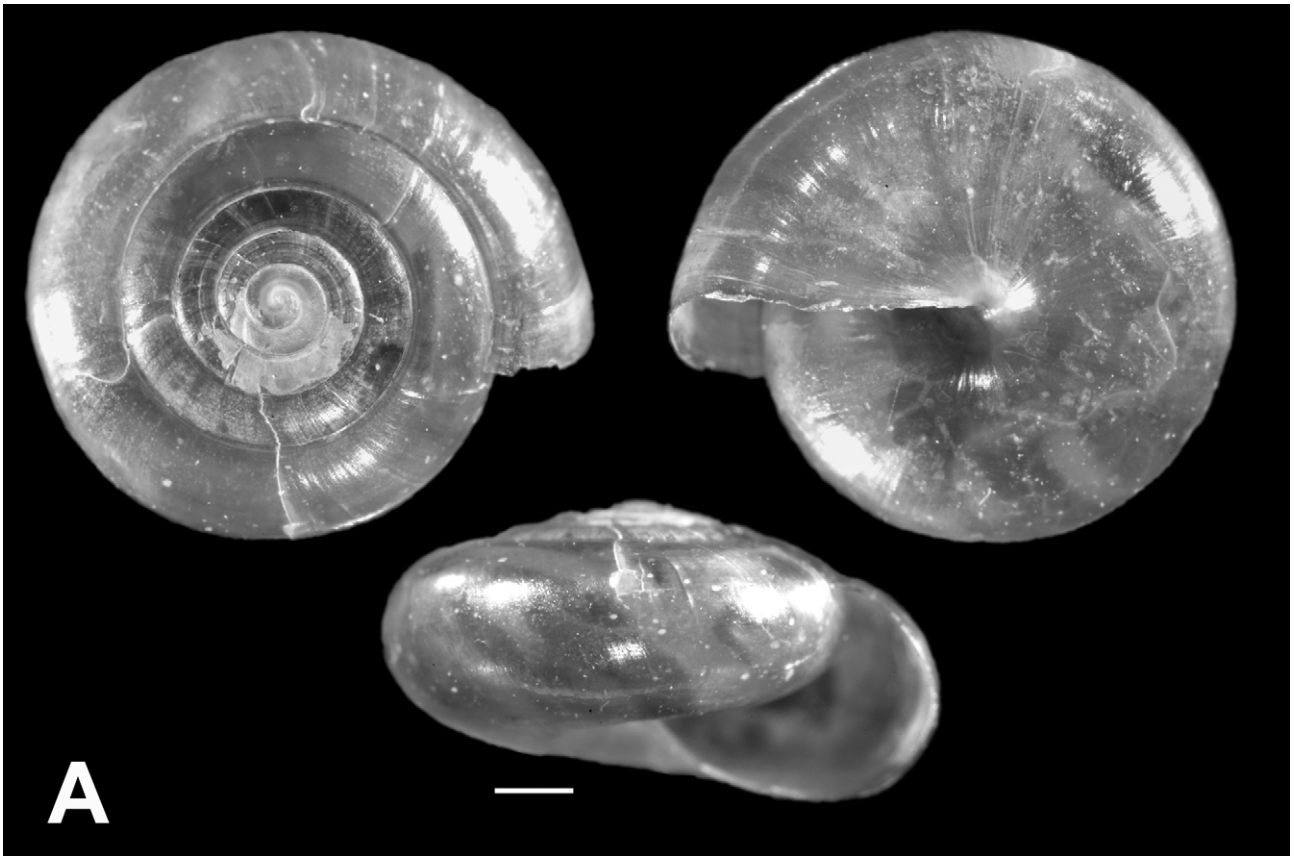


FIGURE 2. Shell of *Oxychilus (Drouetia) viridescens* n.sp. **A.** Holotype (NHMUK 20100658). **B.** Outline showing the morphometric characters used in the analysis. Abbreviations: di, shell diameter; he, height of the shell; sp, height of the spire. Scale bars = 1 mm.

Diagnosis. Shell diameter 8 mm, greenish, umbilical region grayish, columellar lip and parietal lip almost at the same plane; penis very thin, penial caecum long; epiphallus with two distinct swellings, proximal one attached to penial sheath, distal one attached to penial constriction; distal vagina glandular.

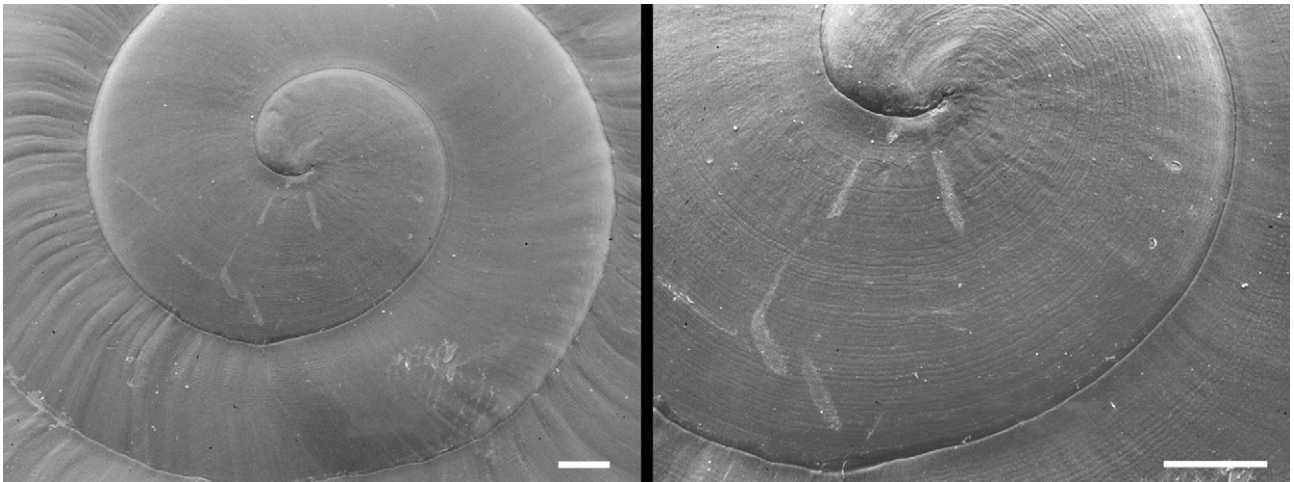


FIGURE 3. First whorls of the shell of *Oxychilus (Drouetia) viridescens* n.sp. (Sta 1). Scale bar: 100 μ m.

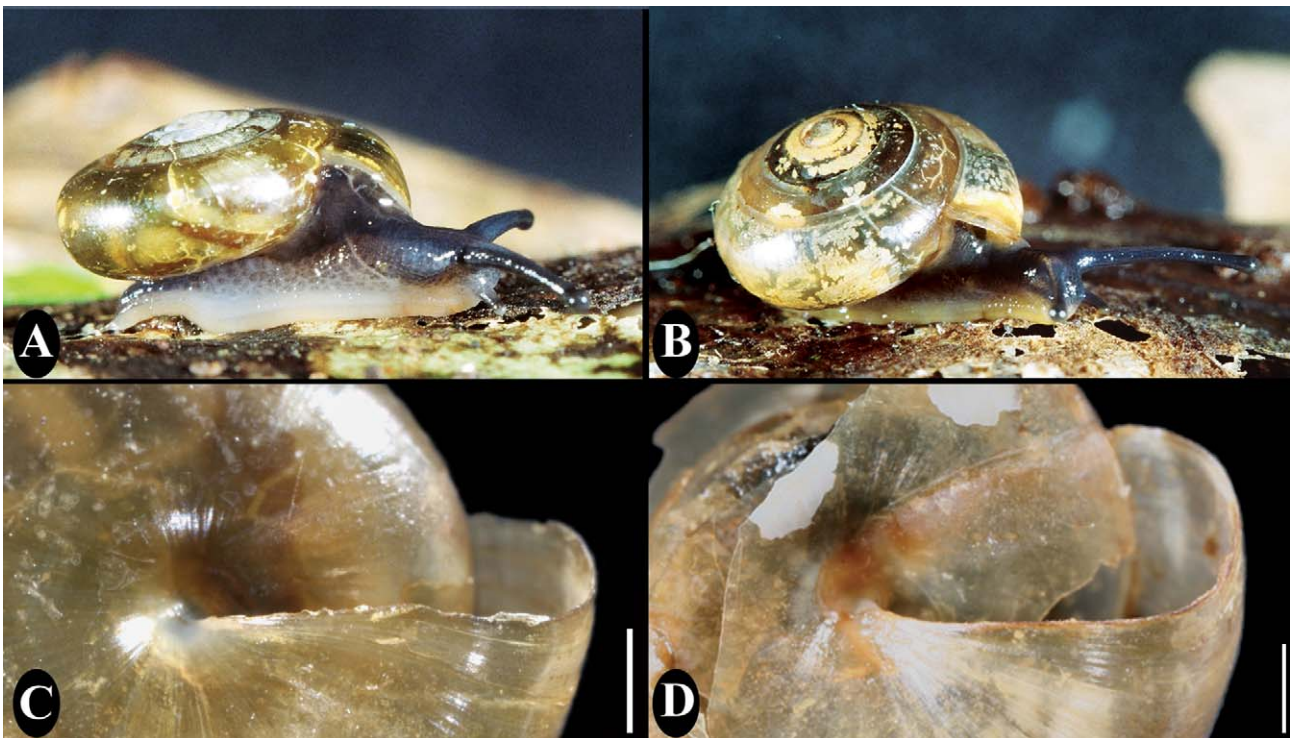


FIGURE 4. Animals and bottom view of shells of *Drouetia*. **A, C.** *Oxychilus (Drouetia) viridescens* n.sp, holotype. **B, D.** *Oxychilus (Drouetia) brincki*. (Sta 9).

Description. *Shell* (Figs. 2, 3, 4C; Table 2) up to 8.2 mm in diameter and 4.8 mm in height, non-umbilicate, somewhat solid, translucent, glossy, conspicuously golden green, with very fine, microscopic spiral striae crossing dense and regular growth lines; spire low, with up to 6.2 flattened whorls, last whorl with a squarish profile. Aperture oblique, the columellar lip running almost at the same plane as the parietal lip (see Fig. 4C); outer lip sharp, columellar lip slightly reflected over the umbilical region which is grayish and covered by a tenuous, whitish callus. Protoconch not well defined, with very faint, fine spiral striae continuing more markedly on the teleoconch.

Animal (Fig. 4): neck blue with purplish hues changing gradually to light orange toward the foot, the darkly pigmented posterior tentacle retractors conspicuous through the dorsal neck skin; four dorsal white grooves run forward from the border of the mantle on the dorsal neck, the central ones to the posterior tentacles and front, the two lateral ones descending obliquely, on each side, to underneath the anterior tentacles; head and front with dark blue longitudinal streaks on a pinkish background; posterior tentacles long, dark grayish blue, clearer near base, anterior tentacles faintly blue with sparse brownish dots near the tips; posterior dorsal tip of foot dark blue; sole of the foot longitudinally tripartite, whitish green to dark yellow.

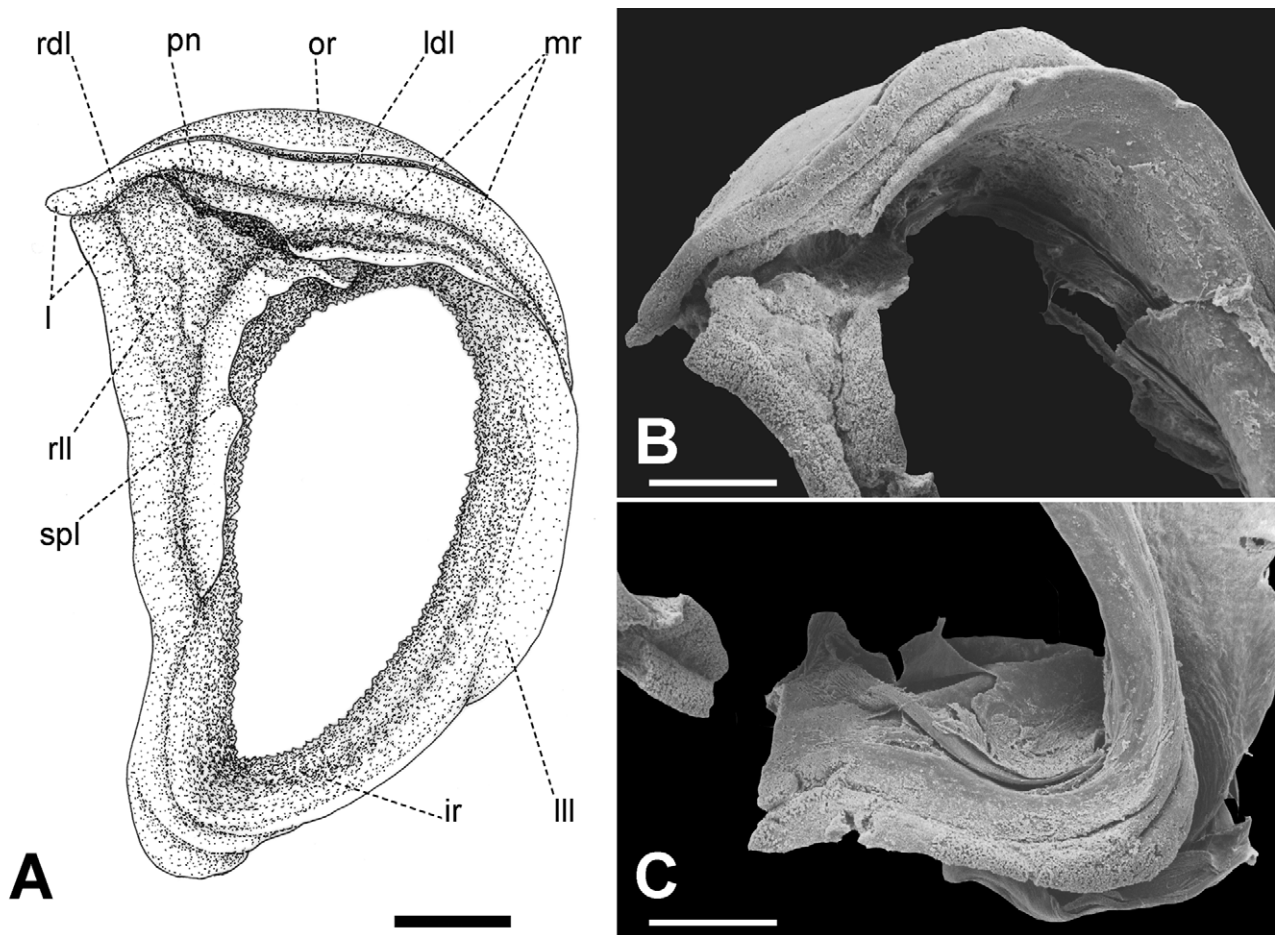


FIGURE 5. Mantle collar of *Oxychilus (Drouetia) viridescens* n.sp. (Ov22 of Table 2). **A.** Total view. **B.** Detail of pneumostomal region. **C.** Detail of posterior (foot) angle. Abbreviations: ir, inner ring; l, lappet; ldl, left dorsal lobe; ll, left lateral lobe; mr, middle ring; or, outer ring; pn, pneumostome; rdl, right dorsal lobe; rll, right lateral lobe; spl, subpneumostomal lobe. Scale bars: = 500 μ m.

Mantle collar (Figs. 4, 5) dark blue, darker around the pneumostome and lappet, becoming lighter toward the left side of the animal. The three basic lobes of the mantle border (secretory, sensory and muscular) are present and are here referred to as rings, the term “lobe” being reserved to follow the current terminology for the description of this structure in helicids (e.g., Martins 2002). Outer, secretory ring, responsible for the secretion of the shell, thin, somewhat retracted behind the next ring, surrounding the entire border of the mantle. The middle, thick, originally sensory ring is bilobed and appears to be primarily of a glandular nature as indicated by its spongy appearance, and it is separated on its right side by the deep pneumostomal slit; right lateral lobe triangular, gently narrowing posteriorly from the lappet; right dorsal lobe forming the dorsal tip of the lappet and extending continuously outside the innermost, left dorsal lobe. Inner, muscular ring expanding to each side of the pneumostome in two wide and thin flaps, the subpneumostomal lobe and the left lateral lobe. The three rings compress posteriorly into a narrow, rounded canal.

The blotched coloration of the visceral mass is seen through the translucent, greenish shell; conspicuous dark spot just behind the pneumostomal area, the remaining few spots, of various sizes, yellowish, sparsely distributed over a brownish green to golden green background.

Pallial cavity (Fig. 6) elongated, deep; kidney bilobed, completely located in the pallial cavity, roughly triangular, with narrow and elongate anterior lobe squeezed between the heart and the primary ureter; sigmoid, secondary ureter bordering posterior lobe of kidney, then bending anteriorly as it approaches the rectum and following forward to open in a cloacal atrium, side-by-side with the rectum, near the pneumostome; a valve-like papilla, the pneumostomal valve, isolates the cloacal atrium from the pneumostomal aperture, thus separating the excretory slit from the pneumostomal canal. A thick, glandular body lies between the secondary ureter and the rectum, to the right of the kidney. Various white, possibly calcareous bodies aggregate in blotches irregularly dispersed throughout the roof of the pallial cavity.

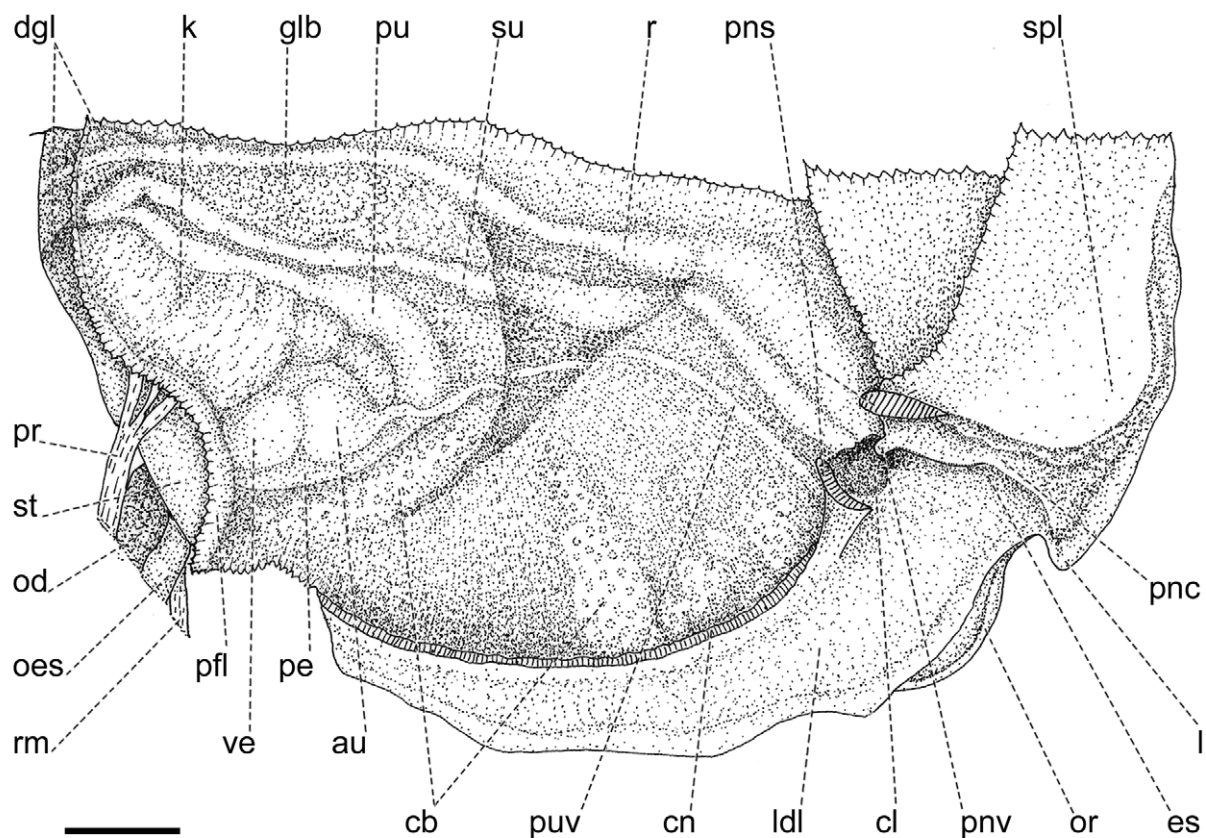


FIGURE 6. Pallial cavity and associated organs of *Oxychilus (Drouetia) viridescens* n.sp. (Sta 2). Abbreviations: au, auricle; cb, 'calcareous' bodies; cl, cloacal atrium; cn, connection to neck (cut); dgl, digestive gland; es, excretory slit; glb, glandular body; k, kidney; l, lappet; ldl, left dorsal lobe; od, oviduct; oes, oesophagus; or, outer ring; pe, pericardium; pr, penial retractor; pfl, posterior floor of lung (cut); pnc, pneumostomal canal; pns, pneumostomal sphincter (cut); pnv, pneumostomal valve; pu, primary ureter; puv, pulmonary vein; r, rectum; spl, subpneumostomal lobe; st, stomach; su, secondary ureter; ve, ventricle. Scale bar = 1 mm.

Mandible (Fig. 7) oxygnathous, moderately long, strong, smooth, half-moon shaped, with convex median prominence on its free edge.

Radula (Fig. 8) $[21+(1+2)+1+(2+1)+21] \times 50$. Central tooth shorter and narrower than laterals, tricuspid; mesocone long, about half the length of the tooth, narrow, sharply pointed; ectocones small, sharp; base narrowing towards the crown, base line receding medially until at about the tip of the mesocone. First lateral tooth about twice as long as the central, tricuspid, endocone moderately long and merging medially into a basal tooth, receding laterally along with the base, with which it forms a pointed, long mesocone, the tip of which extends up to the arms of the base of the central tooth, ectocone short, triangular, wide, located far back in the crown; second lateral tooth similar to the first, but larger; a third lateral tooth of the transitional (intermediate) type is also tricuspid but much narrower than the other two, the shape resembling a marginal tooth, with both endocone and ectocone very small, sharp, mesocone long, curved and pointed. Marginal teeth falciform, retaining only the mesocone which is long, curved and pointed; first marginal teeth about the size of the transitional tooth, decreasing in size towards the outer edge of the row.

Reproductive system (Figs. 9–11). Ototestis acinose, four acini embedded in last whorls of posterior lobe of digestive gland; hermaphroditic duct long, with a median convoluted seminal vesicle, connecting to base of albumen gland through a small, pouch-like fertilization chamber; spermoviduct morphologically divided into three portions: (1) a proximal whitish, globular, glandular portion into which the fertilization chamber opens distally, (2) a narrow, weakly convoluted channel, and (3) a wide, strongly convoluted and internally folded portion to which the elongate prostate gland adheres; after the separation of the prostate duct into a vas deferens, a free oviduct

funnels into the confluence with the bursa duct, both ducts opening into a wider vagina, the extremities of the three ducts covered with a spongy perivaginal gland; vagina adhering to neck wall, the proximal half muscular, smooth outside and ridged inside, the distal portion spongy, apparently glandular, opening into a small, internally smooth genital atrium. Penis almost entirely covered with a thick penial sheath, long and very thin, divided by a constriction into two equally long chambers, with a conspicuous penial caecum proximally, and the distal half internally ridged with pilasters; epiphallus at least twice as thick as the penis where it inserts laterally through a narrow duct; the epiphallus is composed of two distinct long swellings, the proximal portion attached by muscular strands to the edge of the penial sheath (primary epiphallic attachment), the distal portion attached to the penial constriction (secondary epiphallic attachment), thus causing the distal swelling to be almost entirely wrapped by the penial sheath; penial retractor muscle long and thin, inserting on back of the mantle cavity, near the heart region. Spermatophore (Fig. 12) moderately long, thin, anterior portion hooked, with four high, longitudinal ridges, remainder of spermatophore laterally flattened.

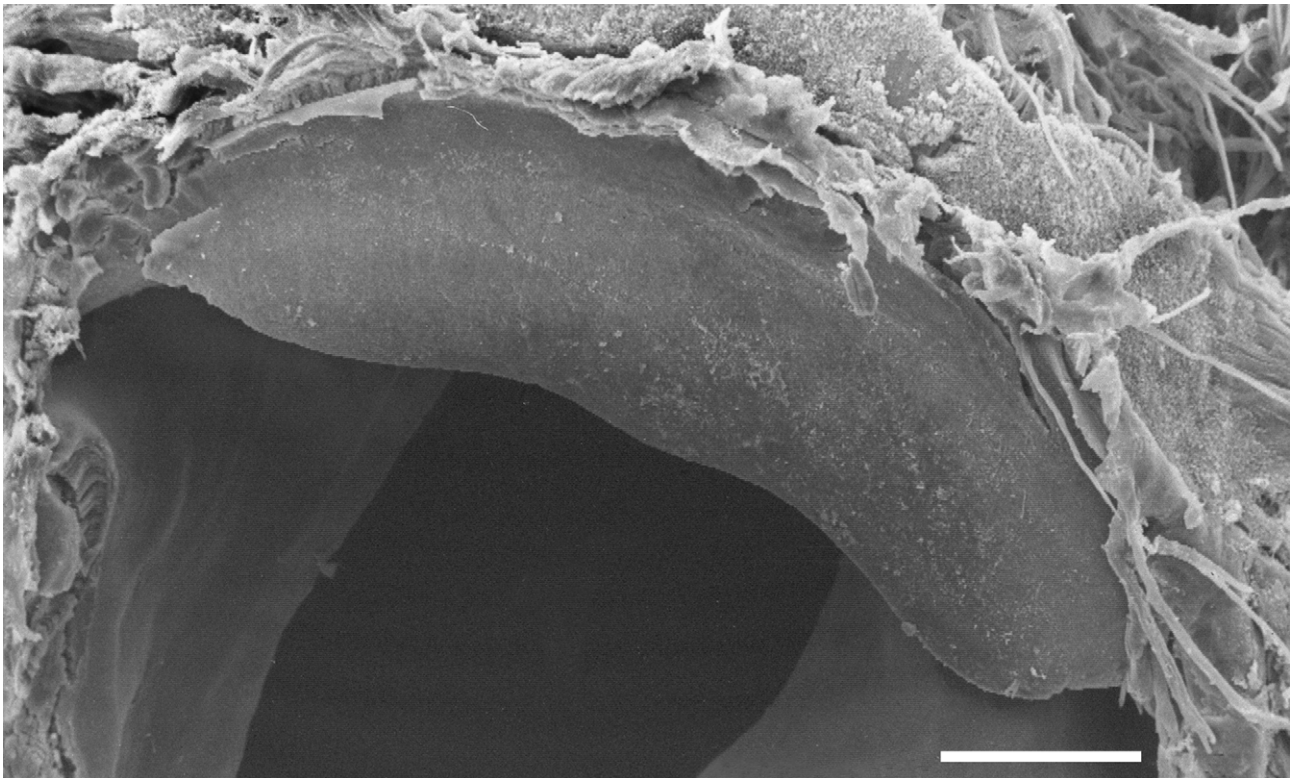


FIGURE 7. Mandible of *Oxychilus (Drouetia) viridescens* n.sp (Sta 1). Scale bar = 100 μ m.

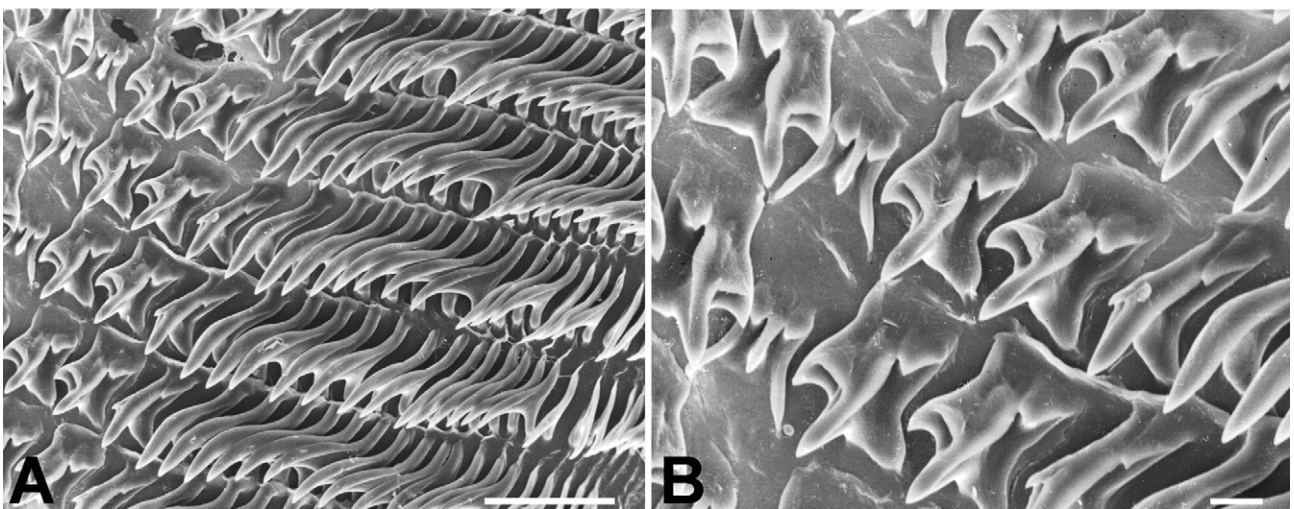


FIGURE 8. Radula of *Oxychilus (Drouetia) viridescens* n.sp. (Sta 1). Scale bars: **A** = 50 μ m; **B** = 10 μ m.

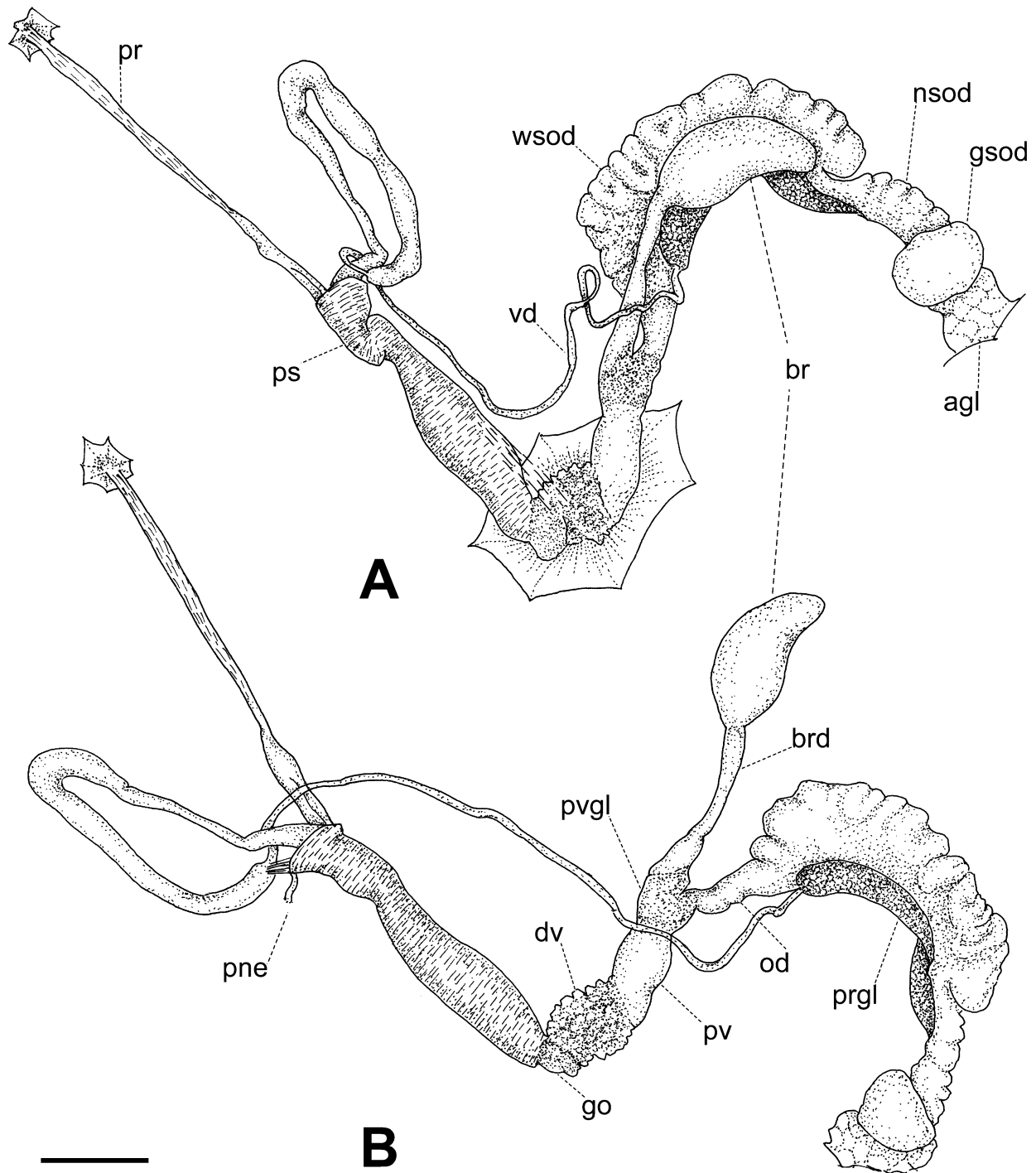


FIGURE 9. External morphology of the reproductive organs of *Oxychilus (Drouetia) viridescens* n.sp. (Sta 1). **A**, with bursa in place; **B**, structures separated. Abbreviations: agl, albumen gland; br, bursa; brd, bursa duct; dv, distal vagina; gsod, glandular spermoviduct; go, genital opening; nsod, narrow spermoviduct; od, oviduct; pne, penial nerve; pr, penial retractor muscle; prgl, prostate gland; ps, penial sheath; pv, proximal vagina; pvgl, perivaginal gland; vd, vas deferens; wsod, wide spermoviduct. Scale bar = 1 mm.

Nervous system (Fig. 13) of the zonitoid type (Bargmann 1930), the cerebral ganglia large, pleural ganglia triangular, left parietal ganglion conspicuous, distinct from visceral ganglion which is fused to right parietal ganglion; right cerebropleural connective very short causing the visceral nerve ring to be lopsided to the right; pedal ganglia nearly fused, slightly smaller than the cerebral ganglia. Right tentacular nerve crossing between male and female organs; penial nerve branching off the right internal lip nerve.

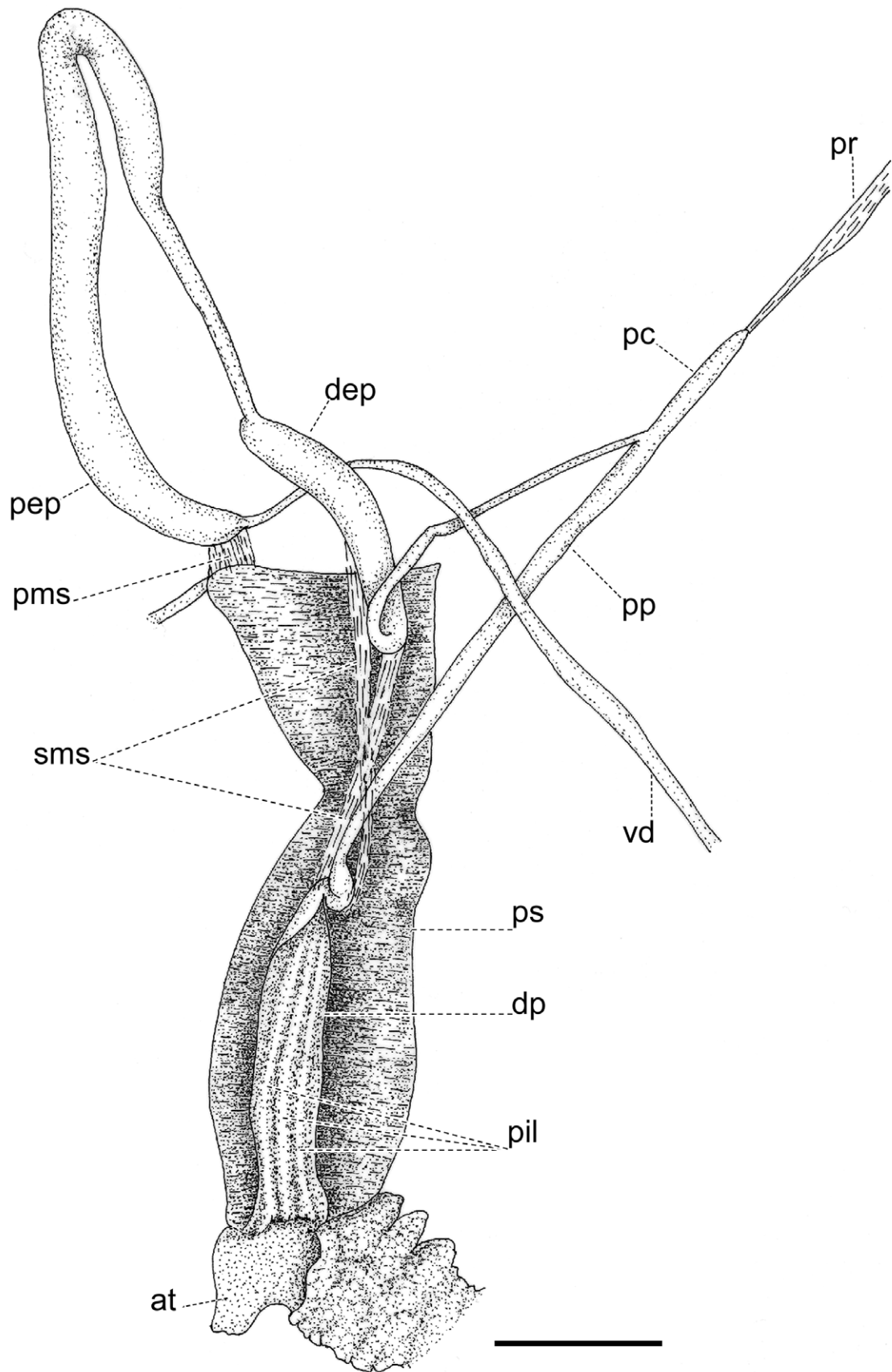


FIGURE 10. Internal morphology of the penial complex of *Oxychilus (Drouetia) viridescens* n.sp. (Sta 1). The penial sheath and distal penis were opened and reflected. Abbreviations: at, atrium; dep, distal epiphallus; dp, distal penis; pc, penial caecum; pep, proximal epiphallus; pms, primary epiphallic muscle strands; pp, proximal penis; pr, penial retractor muscle; ps, penial sheath; sms, secondary epiphallic muscle strands; vd, vas deferens. Scale bar = 1 mm.

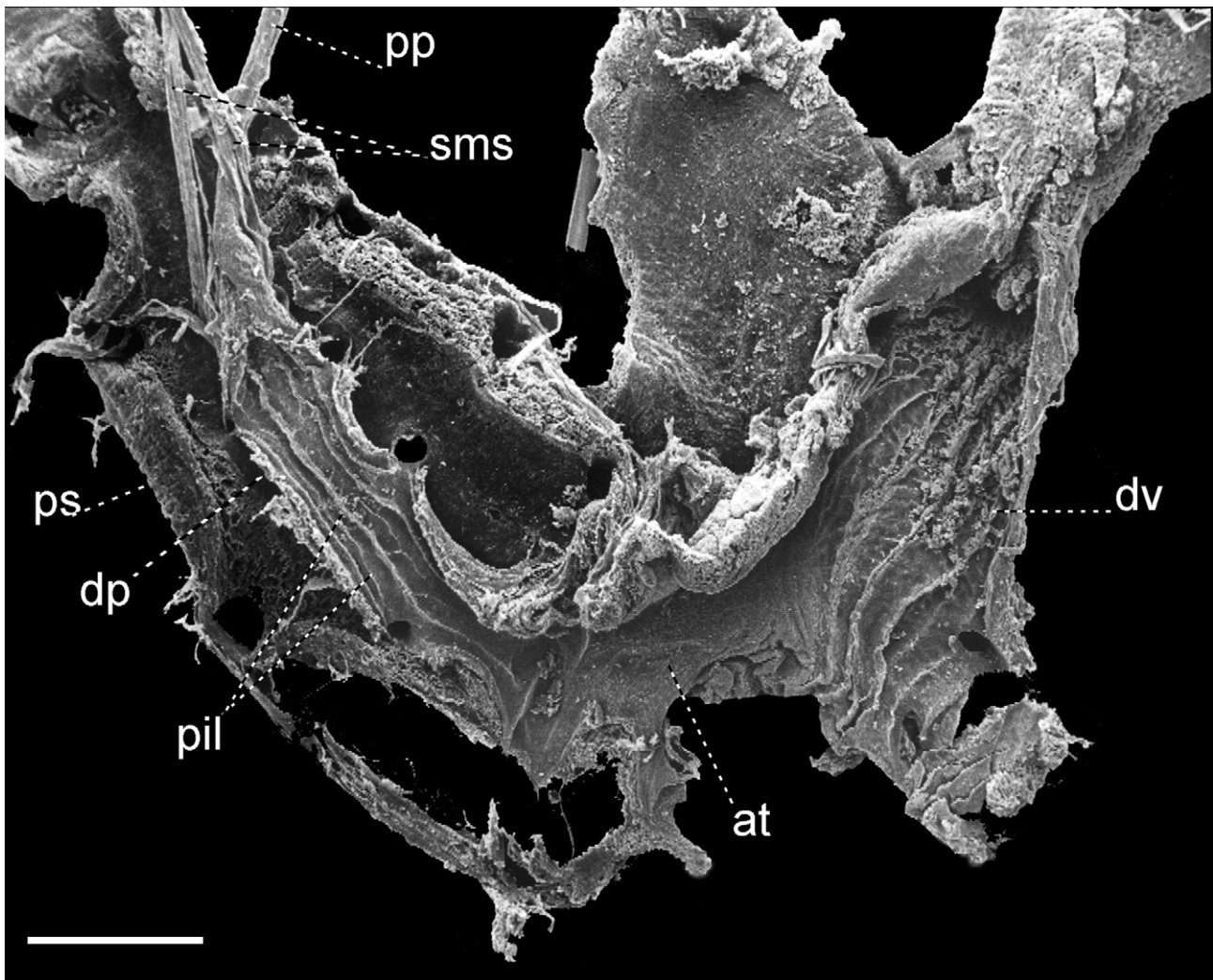


FIGURE 11. Internal morphology of penial complex and distal vagina of *Oxychilus (Drouetia) viridescens* n.sp. (Sta 1). Abbreviations: at, atrium; dp, distal penis; dv, distal vagina; pil, pilasters; pp, proximal penis; ps, penial sheath; sms, secondary epiphallic muscle strands. Scale bar = 500 μ m.

Habitat. Like most consubgenerics, *Oxychilus (Drouetia) viridescens* lives in shady, moist environments of primary forests, and of secondary forests of *Pittosporum*, *Acacia* or *Cryptomeria* with undergrowth of *Tradescantia*, preferentially gathering under piles of rocks, fallen logs and dead leaves of *Hedychium*.

Distribution. The new species is distributed throughout the mountainous region of the island of Santa Maria. Although not common, it was most abundantly collected at the type locality, near Santa Bárbara, and also on the northern and western slopes of Pico Alto.

Remarks. In their first publication, Morelet & Drouët (1857) described most of the new records from their expedition to the Azores without precise locality data. Subsequently, Morelet (1860) provided these data while Drouët (1861) further completed them with his own notes. Morelet (1860) vaguely stated that *Helix atlantica* lived in most Azorean islands but, apparently, the species description was based on material from São Miguel, for Morelet (1860: 168–169) remarked that it was abundant mainly in this island, while referring to peculiar varieties in Santa Maria and Faial. However, no type locality was assigned to the species. Morelet's (1860) variety “ γ var. *spectabilis*” from Santa Maria was elevated to specific rank by Milne-Edwards (1885) (Fig. 14), and Riedel (1964) awarded subspecific rank to Morelet's (1860) “ β minor” from Faial and described *Oxychilus atlanticus brincki* from material collected in 1957 by the Lund expedition from which he selected a holotype (Fig. 15A). Riedel (1964) also restricted the type locality of *Helix atlantica* to the island of São Miguel. Later Riedel (1980) raised the taxa from Santa Maria and Faial to species level. However, three specimens from Santa Maria are marked as syntypes of *H. atlantica* in the Natural History Museum, London; two of them belong in fact to the new species

herein described, the other being Riedel's (1964) *O. (D.) brincki*. Hence, due to Riedel's (1964) taxonomic decisions, the type material for the name *Helix atlantica* is from a locality where this species does not occur. Therefore, a petition was submitted to the ICZN (Case 3553; Martins *et al.* 2011) to render those specimens unavailable for nomenclatural purposes. However, the recent discovery of Henri Drouët's collection and syntypes at the Muséum Jardin des Sciences de Dijon (MJSD) (Cédric Audibert, *in litt.*), has allowed us to select a lectotype of *H. atlantica* from São Miguel island, thereby rectifying the anomalous situation created by Riedel (1964).

The imperforate *Oxychilus* are represented in the Açores by two endemic subgenera: *Drouetia*, present throughout the archipelago, and the monotypic *Atlantoxychilus* Riedel, 1964, only recorded from Santa Maria [*O. (A.) spectabilis* (Milne-Edwards, 1885)]. Three species of *Drouetia* live in Santa Maria: *Oxychilus (D.) brincki*, *O. (D.) agostinhoi* Martins, 1981 and *O. (D.) viridescens* n.sp (Figs. 15, 16). *Oxychilus (D.) viridescens* and *O. (D.) brincki* are conchologically similar but can be readily distinguished from *Oxychilus (D.) agostinhoi*, which has a very small, paucispiral, flat shell and from *O. (A.) spectabilis* which bears a distinct furrow along the suture; the microsculpture of the first whorls is more marked in the new species and in *O. (D.) brincki*, somewhat fainter in *O. (D.) agostinhoi* and absent in *O. (A.) spectabilis*. A more detailed comparison is shown in Table 3.

At first sight *Oxychilus (Drouetia) viridescens* n.sp. could be confused with the sympatric *O. (D.) brincki* because both species have similar shells. However, a brief survey of simple morphometric characters (Fig. 2; Table 2) showed that, although with some overlap, the new species has about half a whorl less and is more depressed than *O. (D.) brincki* (Fig. 17). Because the palatal lip and the columellar lip of the shell run almost at the same plane, the aperture, seen from the bottom, is very narrow in the new species whereas it is extended in *O. (D.) brincki*. Moreover, fresh shells of the new species exhibit a conspicuous greenish colour whereas the shell of *O. (D.) brincki* has a more golden-brown pigmentation; the coloration around the umbilical area is grayish in the new species, but it is pinkish in *O. (D.) brincki* (Figs. 4C, D). The colour pattern of the animal in both species shows also some differentiation, with greenish tones and smaller, sparser and whitish blotches on the mantle, as well as a whitish foot predominating in the new species (Figs. 4A; 18A), whereas yellowish blotches predominate in the mantle of *O. (D.) brincki*, and its foot is typically yellowish to orange (Fig. 4B). The mantle of *O. (D.) agostinhoi* may sometimes exhibit a greenish colour, but it is usually redish-brown with some small, whitish spots around the spire and large, black spots restricted to the apertural area, a feature common in the genus; the border of the mantle is black, the neck dark-blue with lighter-blue transverse stripes anteriorly, changing posteriorly to a lighter-blue background strewn with darker spots; foot light-blue, bordered by a dark-blue rim (Fig. 18B).

The reproductive system remains the most important source of characters by which the new species can be differentiated; however, care must be exercised when comparing structures, for the degree of relaxation at the time of death may affect the shape and the proportions of the various organs or parts thereof (Martins 1991). Also the degree of development may render some structures more evident at certain times of the year (Rodrigues *et al.* 1998; Cunha *et al.* 2001). In this work, only organs that do not depend entirely on the degree of maturation were used (e.g. penis *vs.* albumen gland) or structures that, although variable in other taxa, were observed to maintain a relatively constant pattern across different preserving situations.

The reproductive system, and in particular the morphology of the penial complex, is very diverse in the four species from Santa Maria. The distal glandular vagina, the epiphallus with double swellings, and the very thin penis of *O. (D.) viridescens* n.sp. (Figs. 10, 11) are unique features in the Azorean oxychilids; the muscle strands attaching the distal portion of the epiphallus to the penial constriction are also seen in *O. (D.) atlanticus* (Fig. 19A) and *O. (D.) furtadoi* Martins, 1989 (Fig. 20B), although not as developed as in the new species.

Some variability was found in the morphology of the male organ of *O. (D.) brincki*. The typical form, from Pico Alto, shows a stout, bulging penial complex and a short, thick epiphallus connected to the penial sheath through a very long, thin muscle, whereas the specimens from Santa Bárbara have a much thinner penis and epiphallus and a shorter muscular attachment of the latter structure. The internal morphology of the penis, however, with many long, homogeneous furrows running from the epiphallic pore, is a reliable indicator of the conspecificity of both populations; this morphology is also unique among *Drouetia* (Fig. 17A, B).

The penis of *O. (D.) viridescens* n.sp. and that of *O. (D.) agostinhoi* may exhibit a mid-length constriction (see Martins 1981), whose presence may depend on the degree of relaxation at the time of death. This constriction was never observed in the two other species. *Oxychilus (D.) viridescens* n.sp. and *O. (D.) agostinhoi* are also similar in the presence of a few strong pilasters inside the penis (Figs. 10; 11; 16B); this resemblance, however, is probably misleading, for it can be attributed to the narrow penis of the former and to the small size of the latter species.

TABLE 3. Comparison of the morphological and anatomical characters of *Oxychilus (Drouetia) viridescens*, n.sp. with the related species living in Santa Maria, O. (D.) *brincki*, O. (D.) *agostinhoi* and O. (*Atlantoxychilus*) *spectabilis*.

Characters	<i>O. (D.) viridescens</i>	<i>O. (D.) brincki</i>	<i>O. (D.) agostinhoi</i>	<i>O. (A.) spectabilis</i>
Animal coloration				
Neck color	dark blue	dark blue	deep dark blue, transverse light streaks running down toward foot	light pink, darker in front, faint gray blotches posteriorly
Anterior tentacles	faint blue	dark blue	dark blue, tips lighter	light blue
Posterior tentacles	dark blue	dark blue	deep dark blue	dark blue
Posterior tentacle retractors	entirely blackish	entirely blackish	entirely blackish	dark blue, fading back until half neck
Foot rim	dark blue posteriorly only	same color as foot sole	almost continuously dark blue	brownish, interrupted all along foot
Foot sole	Whitish green to dark yellow	yellowish green to orange	whitish	pinkish
Collar	blackish near pneumostome, fading to pinkish on left side	blackish near pneumostome, fading to pinkish on left side	blackish all around	pinkish all around
Pneumostomal area	all blackish	pinkish above, dark blue underneath	all blackish	pink, faint bluish blotch underneath
Mantle color	brown	pale brown	dark yellow to brick red	golden yellow
Front blotch	black, only on right side	black, only on right side	black, across front	black, only on right side
Mantle blotches	light yellow, small, sparse	whitish, large, abundant	dark yellow, very small, very sparse	whitish, large, abundant
Shell				
Maximum diameter (mm)	9.0	8.9	5.1	5.5
Number of whorls	6.2	6.8	4.2	5
Spire	moderate	high	flat	moderate
Aperture, basal view	narrow	very extended	extended	moderately extended
General coloration	greenish	golden brown	greenish	golden brown
Umbilical region	grayish	pinkish	whitish	golden brown
Sculpture	finely grooved spirally	finely grooved spirally	very finely grooved spirally	smooth, w/ furrow
Radula				
marginal teeth/half row	21	19	13	19
cusps of central tooth	central cusp much longer	central cusp much longer	cusps small, equal	central cusp much longer
Mandible	slender and curved	slender and less curved	slender and less curved	very slender and straight
Mantle collar				
Right lateral lobe	elongate	elongate	truncate	elongate
Posterior canal	round, rings tightly compressed	round, rings tightly compressed	sharply acute, rings convoluted	moderately acute, rings tightly compressed
Hermaphroditic Reproductive Organs				
Prostate	long	long	short	short
Free oviduct	somewhat shorter than vagina	much longer than vagina	about as long as vagina	much shorter than vagina
Base of bursa duct	as wide as free oviduct	much wider than free oviduct	about as wide as free oviduct	about as wide as free oviduct
Relative width of bursa	much wider than duct	about as wide as duct	much narrower than duct	about as wide as duct
Perivaginal gland	covering bursa duct and oviduct	covering oviduct	covering bursa duct and oviduct	covering oviduct
Distal vagina glandular (yes/no)	yes	no	no	no
Penial complex				
General shape	thinner than vagina	much thicker than vagina	about as thick as vagina	about as thick as vagina
Penial sheath	very long	very short	moderately short	moderately short
Penial caecum	small	very small	long	small
Shape of epiphallus	double	single	single	single
Primary epiphallic attachment	short	long	short	short
Secondary epiphallic attachment	present	absent	absent	absent
Penial constriction	present	absent	present	absent
Interior sculpture	few furrows	many furrows	few furrows	furrows and papillae



FIGURE 12. Spermatophore of *Oxychilus (Drouetia) viridescens* n.sp. (Ov22 in Table 2). Scale bar = 100 μ m.

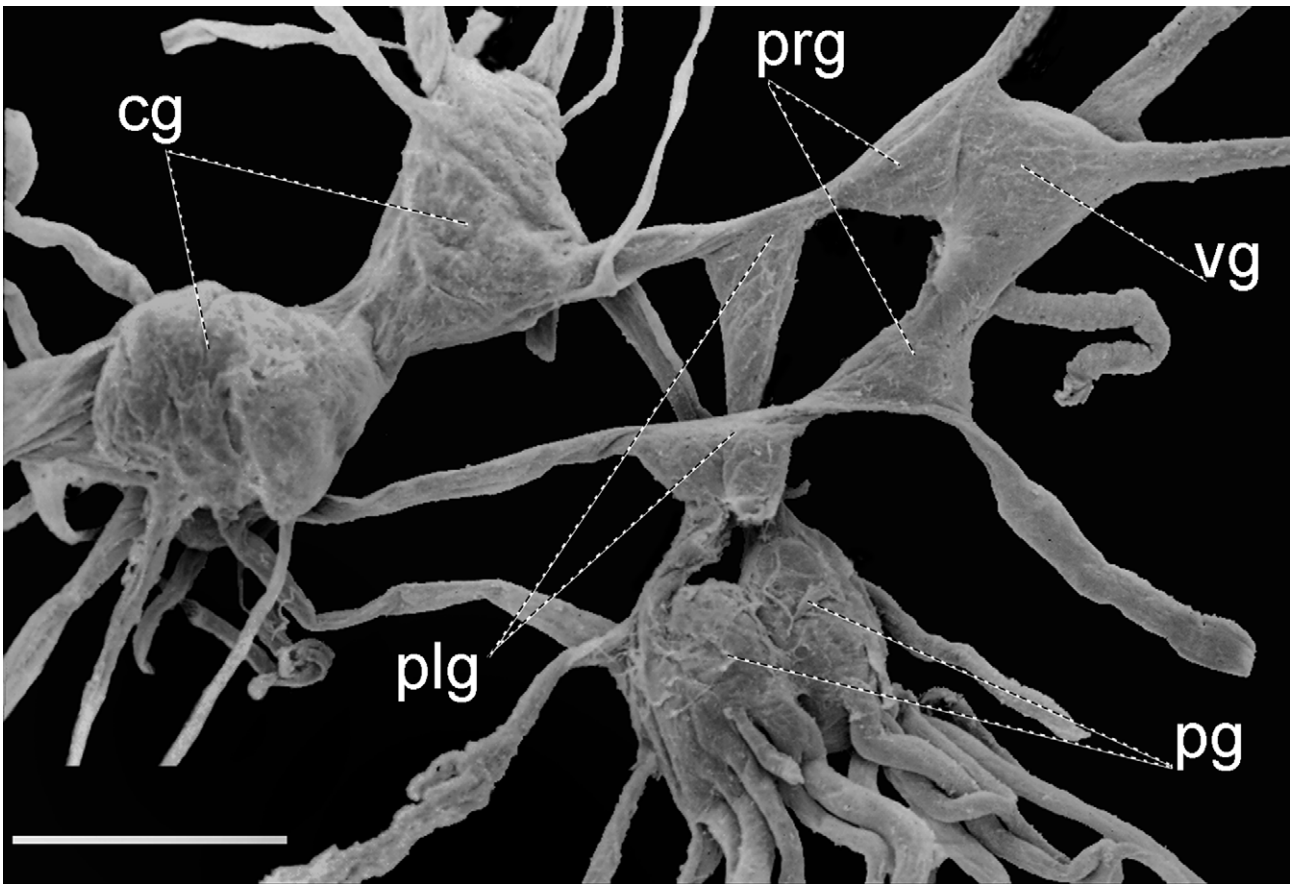


FIGURE 13. Central nervous system of *Oxychilus (Drouetia) viridescens* n.sp (Ov21 in Table 2). Abbreviations: cg, cerebral ganglia; pg, pedal ganglia; plg, pleural ganglia; prg, parietal ganglia; vg, visceral ganglion. Scale bar = 500 μ m.

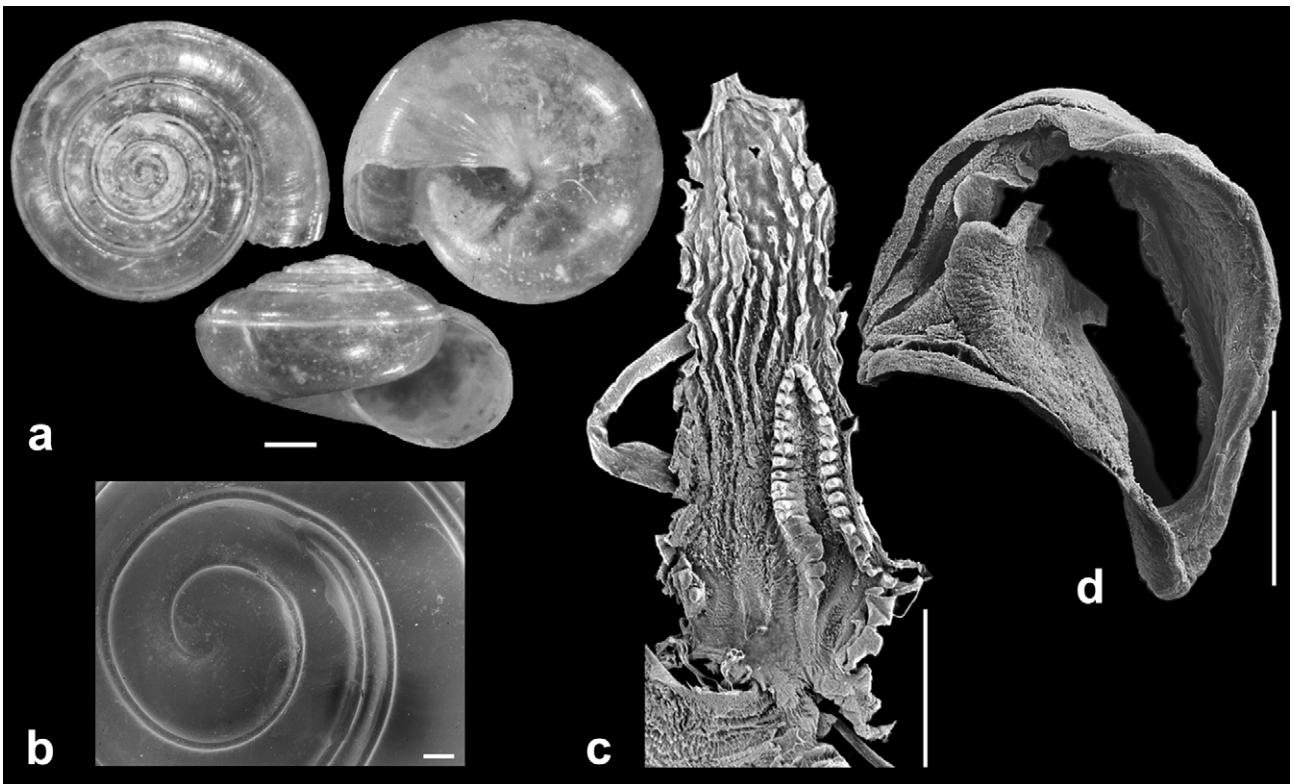


FIGURE 14. *Oxychilus (Atlantoxychilus) spectabilis*. **a**, shell, syntype (NHMUK 93.2.4.1003), Santa Maria; **b**, first whorls; **c**, internal penis morphology; **d**, mantle collar. Scale bars: **b** = 100 μ m; all others = 1 mm.

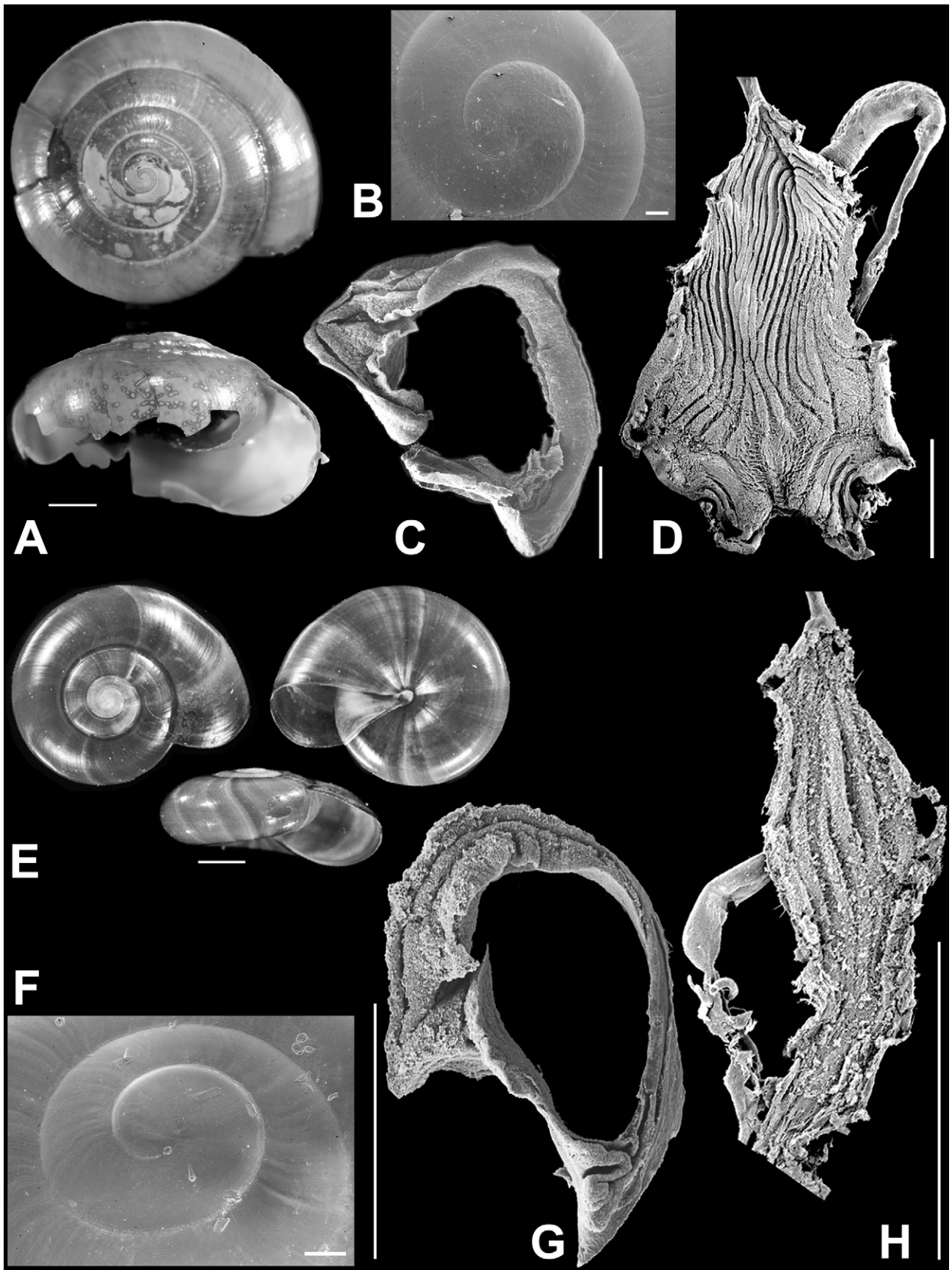


FIGURE 15. Shells, first whorls, internal penis morphology and mantle collar of species of *Drouetia* from Santa Maria related to *Oxychilus (Drouetia) viridescens* n.sp. **A–D**, *Oxychilus (Drouetia) brincki*: **A**, holotype (Museum of Natural History, Lund University, Sweden), Pico Alto, Santa Maria. **E–H**, *Oxychilus (Drouetia) agostinhoi*: **E**, holotype (MCZ 288926), Fontinhas, Perímetro Florestal, Santa Maria. Scale bars: **B, F** = 100 µm; all others = 1 mm.

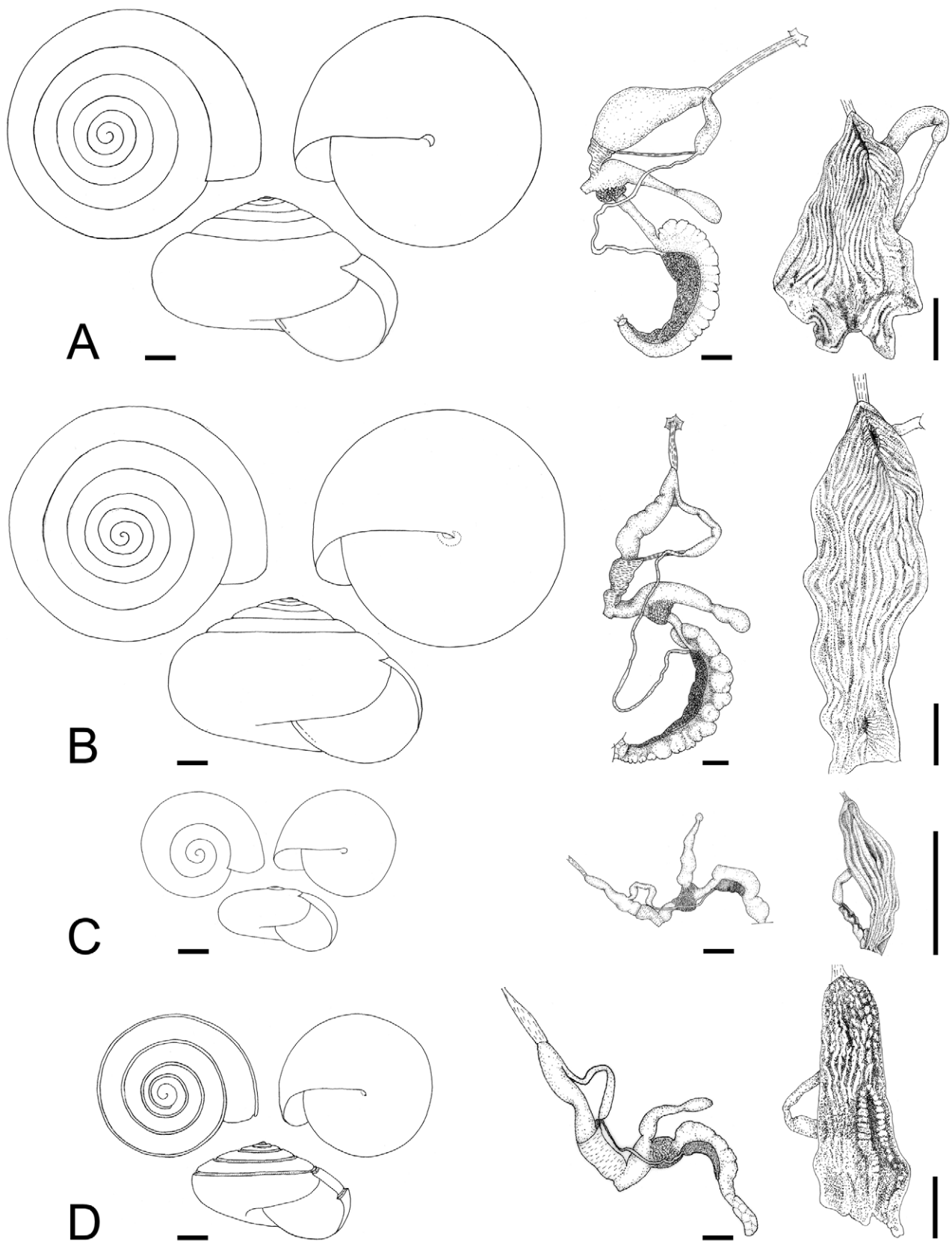


FIGURE 16. Shells and reproductive anatomy of oxychilid species related to *Oxychilus (Drouetia) viridescens* n.sp. **A, B.** *Oxychilus (Drouetia) brincki*; **A**, Sta 2, **B**, Sta 1. **C.** *Oxychilus (Drouetia) agostinhoi*, Sta 7. **D.** *Oxychilus (Atlantoxychilus) spectabilis*, Panasco, Santa Maria. Scale bars = 1 mm.

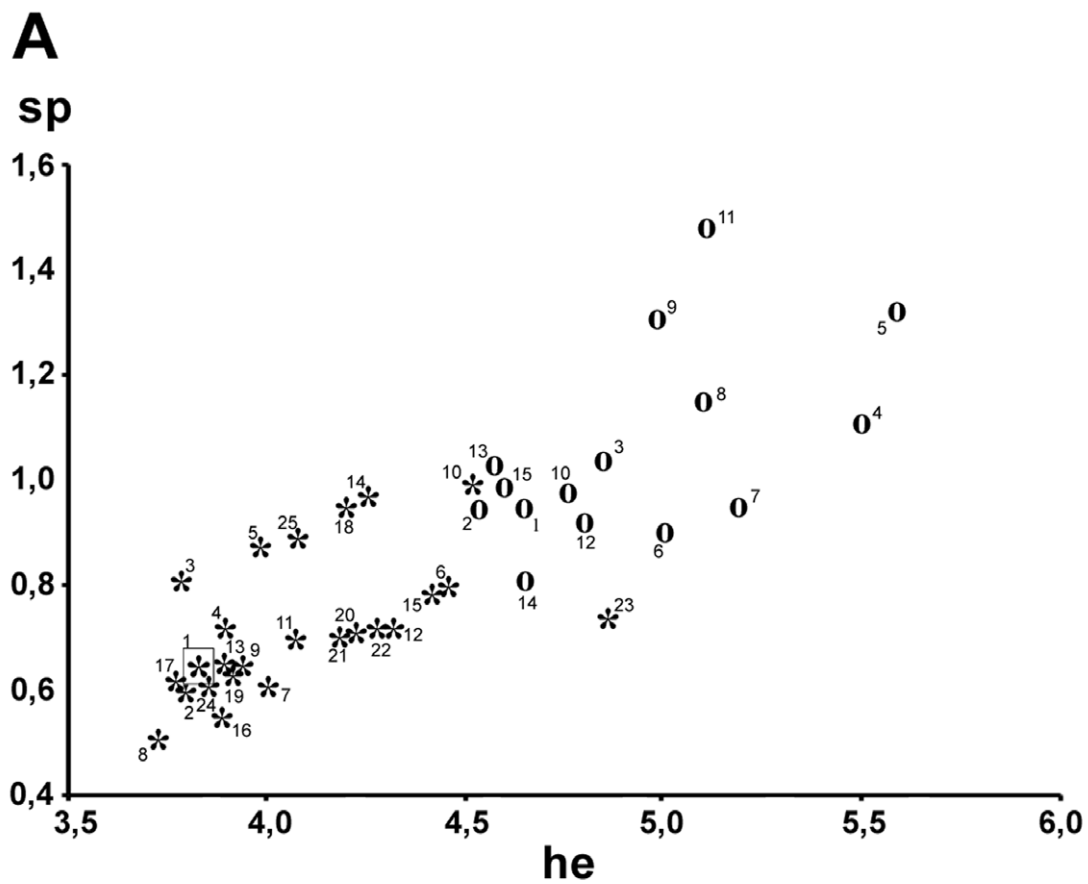
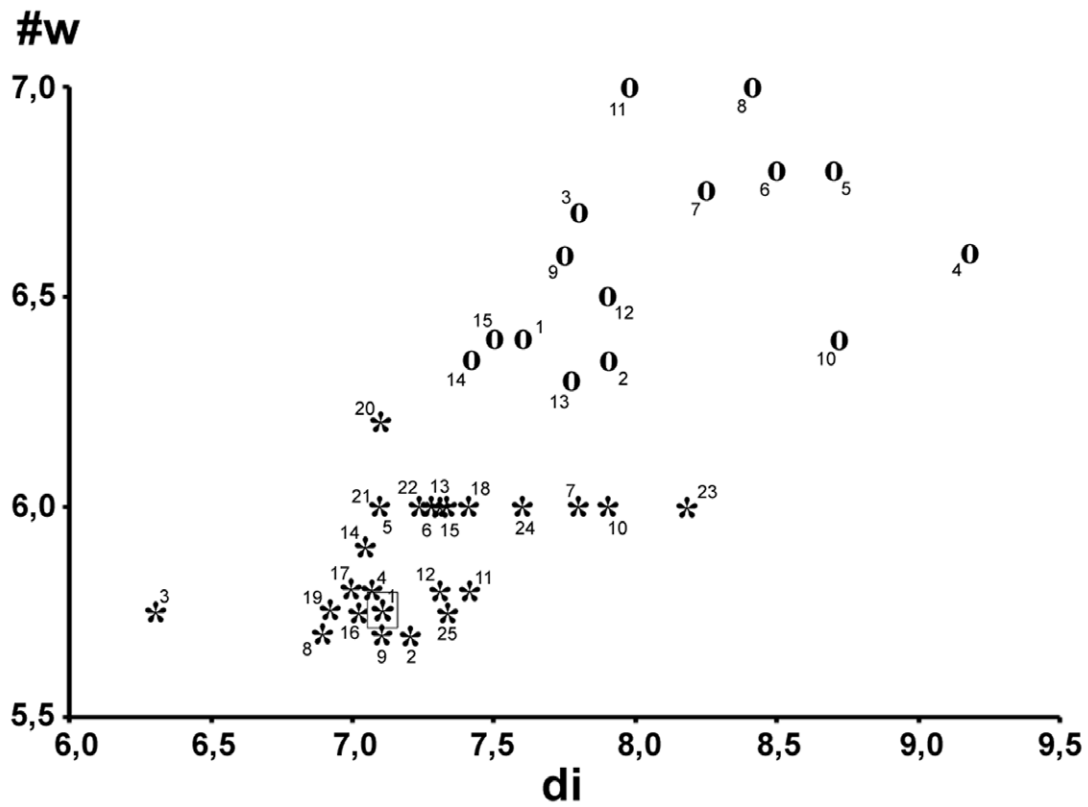
Oxychilus (*A.*) *spectabilis* has a rather peculiar internal penial morphology: it resembles *O. (O.) cellarius* (Müller, 1774) by the presence of rows of papillae which coalesce into weak pilasters (Giusti & Manganelli 1997), but it also shows an arch of conspicuous conical papillae (Figs. 14; 16D). In fact, the rows of papillae inside the penis, coalescing into weak pilasters, reminded Riedel (1964) of the situation in *Oxychilus* s.s. Yet, he dismissed such a relationship because in *Atlantoxychilus* the papillae are conical, whereas in *Oxychilus* s.s. they are squamiform. Riedel (1964), however, did not mention the peculiar arch of prominent papillae in *Atlantoxychilus*. On the other hand, Riedel (1980) did show that the Caucasian *O. (Conulopolita) raddei* (Boettger, 1879) has a somewhat similar, but more complex structure as that found in *O. (A.) spectabilis* even though the remaining internal penial surface appeared to be smooth in the Caucasian species. However, the relationships of these two taxa cannot be ascertained on that peculiarity alone.

Reviewing *Drouetia* Gude, 1911 and *Atlantoxychilus* Riedel, 1964

The genus with the highest number of endemic taxa in the Azorean biota is the molluscan *Oxychilus*, of which the subgenus *Drouetia* accounts for 8 of the 15 hitherto described endemic species of that genus. However, *Drouetia* was first monotypic (Gude 1911), for its type species, *Helix atlantica*, was considered to live throughout most islands of the Azores (Morelet 1860). It was only through Riedel's (1964) anatomical research that the diversity of *Drouetia* started to be noticed, and Martins (2005) has provided evidence that the number of known species remains understated. Besides the three species from Santa Maria sufficiently dealt with above, five more species are known: two from São Miguel, *O. (D.) atlanticus* and *O. (D.) batalhanus* de Winter, 1989; two from Terceira, *O. (D.) miceui* Martins, 1989 and *O. (D.) furtadoi*; one from Faial, *O.(D.) minor* Riedel, 1964. *Atlantoxychilus* is represented by one, already mentioned species: *O. (A.) spectabilis*.

Oxychilus (Drouetia) atlanticus (Fig. 18C, 19, 20A). The history of this taxon has been dealt with above (see *Remarks*). Martins (1991) first reported the anatomical variability of *O. (D.) atlanticus* throughout São Miguel and, although calling attention to variability as an artifact of preservation, recognized the possibility of additional species, namely Riedel's (1964) "small form" and the population of Sete Cidades. Nevertheless, Martins' (2005) extended analysis interpreted those differences as allotopic, demic variability. However, further anatomical and morphometric research has revealed syntopic variability, with different shell and genitalia patterns existing sympatrically, thus suggesting the existence of various taxonomic units in São Miguel (Martins *et al.* 2010), the description of which is presently under way. *Oxychilus (D.) atlanticus* needed, thus, to be unequivocally characterized. To this end, a neotype was proposed so to restrict *O. (D.) atlanticus* to the large shell phenotype living in Sete Cidades, São Miguel (ICZN Case 3553; Martins *et al.* 2011). However, this proposal is no longer needed, since the recent discovery of Drouët's collection of Azorean material, with specimens from São Miguel, provided a suitable lectotype for *Helix atlantica* (MJSD.2012.CO.68 a; Fig. 19). The specimen selected is the largest of a lot of 48 (diameter 7.8 mm; height, 4.8 mm; number of whorls, 6) and conforms with the measurements given in the original description (maximum diameter, 8 mm; height, 5 mm; Morelet & Drouët 1857). Due to the taxonomic and morphological complexity of *Drouetia* in São Miguel and the importance of anatomy and locality for species identification (Martins 1991, 2005), the type locality for *Helix atlantica* Morelet & Drouët is herein restricted to Caldeira das Sete Cidades. Indistinguishable from the following species on the basis of shell morphology alone, *O. (D.) atlanticus* has a darker border of the mantle and the foot sole is yellowish; however, it is readily identified anatomically, namely by the long epiphallus, the long and narrow bursa duct and large bursa, and, inside the penis, the reticulate ornamentation on the penial caecum and around the epiphallic pore.

Oxychilus (D.) batalhanus de Winter, 1989 (Fig. 18D, 20B). Conchologically indistinguishable from the previous species, *O. (D.) batalhanus* was proposed on the basis of the morphology of the penial complex (de Winter 1989). Martins (1991) showed that the proportions of various structures of the penial complex, namely the penial caecum, can change as an artefact of preservation methods and, therefore, are by themselves unreliable diagnostic characters. For that reason *O. (D.) batalhanus* was considered a junior synonym of *O. (D.) atlanticus* (Martins 2005). Recent research based mostly on the internal morphology of the penis (Martins *et al.* 2010) has provided evidence for the existence of various taxonomic units in São Miguel; restriction of *O. (D.) atlanticus* to the anatomically different Sete Cidades population restores the validity of *O. (D.) batalhanus*. Although very variable, when compared with the previous species *O. (D.) batalhanus* shows a lighter blue border of the mantle and the foot is pinkish to orange, sometimes greenish; it is diagnosed by the short vagina, the membranous proximal penis with weak crests radiating from the epiphallic pore, the strongly muscular distal penis with strong pilasters inside. *Oxychilus (D.) batalhanus* is distributed throughout the entire island of São Miguel.



B

FIGURE 17. Shell morphometry in *Oxychilus (Drouetia) viridescens* n.sp. (*) and *Oxychilus (Drouetia) brincki* (o). **A.** Relationship di/#w. **B.** Relationship he/sp. Abbreviations: di, shell diameter; he, height of the shell; sp, height of the spire; #w, number of whorls. Holotype within square.



FIGURE 18. Animals of species of *Drouetia* and *Atlantoxychilus*. **A**, *Oxychilus (Drouetia) viridescens*, Sta 7. **B**, *Oxychilus (Drouetia) agostinhoi*, Sta 7. **C**, *Oxychilus (Drouetia) atlanticus* (NHMUK 20100653), Sete Cidades, São Miguel. **D**, *Oxychilus (Drouetia) batalhanus*, Batalha, São Miguel (type locality). **E**, *Oxychilus (Drouetia) miceui*, paratype, Caldeira de Santa Bárbara, Terceira. **F**, *Oxychilus (Drouetia) furtadoi*: paratype, Fonte da Telha, Posto Santo, Terceira. **G**, *Oxychilus (Drouetia) minor*, Ribeirinha, Faial. **H**, *Oxychilus (Atlantoxychilus) spectabilis*, Sta 7.

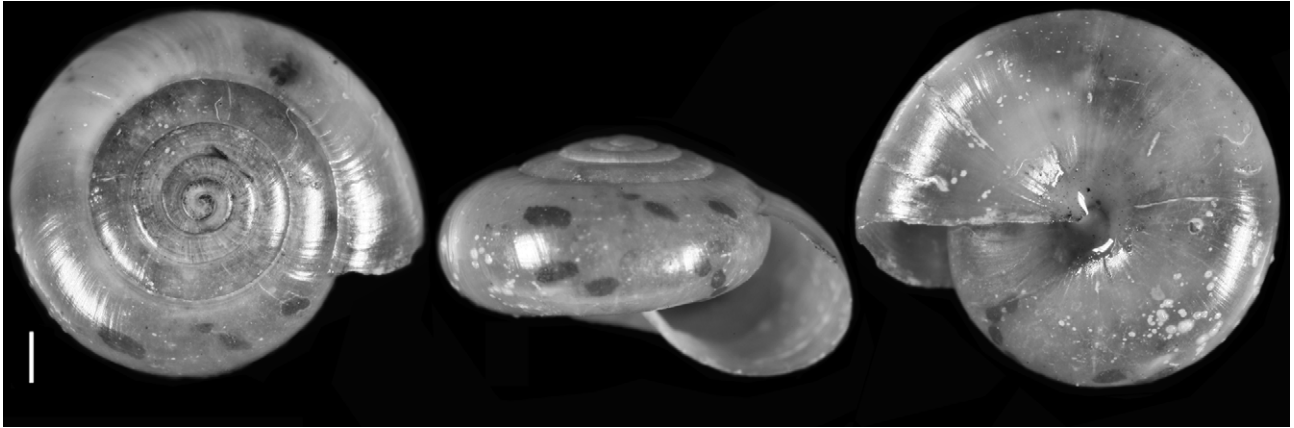


FIGURE 19. Lectotype of *Helix atlantica* Morelet & Drouët, Muséum Jardin des Sciences de Dijon, France (MJS.D.2012.CO.68 a), São Miguel. Scale bar = 1 mm.

***Oxychilus (D.) miceui* Martins, 1989** (Figs. 18E, 21A). This species lives on the mountains of Terceira and is characterized by the yellow to whitish mantle spotted with small brown to blackish patches, contrasting with the dark-blue mantle border and neck, fading to light-blue toward the foot. The shell has a depressed spire, the last whorl a quadrangular profile, the aperture is slightly wider than that of the following species. Anatomically this species is characterized by a long, convoluted oviduct and moderately long vagina, a membranous proximal penis and penial caecum cumulatively as long as the muscular distal penis, both units usually separated by a constriction.

***Oxychilus (D.) furtadoi* Martins, 1989** (Figs. 18F, 21B). This species lives at lower altitude around the town of Angra do Heroísmo, Terceira. Conchologically similar to *O. (D.) miceui*, it has a slightly narrower aperture. The mantle has a greenish-brown background spotted with sparse, small whitish patches, the mantle border and neck light-blue, turning pinkish toward the foot. The reproductive anatomy is characterized by a long, narrow vagina, a short, membranous proximal penis and penial caecum, a long, narrow, muscular distal penis and an equally long penial sheath; the epiphallus is long, the distal third connected to the distal penis by muscular strands.

***Oxychilus (D.) minor* Riedel, 1964** (Figs. 18G, 21C). This species was first referred by Morelet (1860) as variety “ β minor”, and it was Riedel (1964) who considered it a discrete taxon, attributing authorship and date to Morelet (1860). Bank *et al.* (2002), however, interpreted Morelet’s word “minor” not as a name but as part of the description, thus attributing authorship and date to Riedel (1964). The animal of *O. (D.) minor* is characteristically pink, the mantle mottled with white patches and rare dark spots, posterior tentacles dark-blue becoming lighter toward the base. The shell has a depressed spire and the aperture is somewhat wide. The most peculiar anatomic feature is the stout, strongly muscular penis without noticeable constriction, with strong pilasters running back to the penial caecum.

***Oxychilus (Atlantoxychilus) spectabilis* (Milne-Edwards, 1885)** (Fig. 18H). Hausdorf (1993) considered *Helix atlantica* var. *spectabilis* Morelet, 1860 to be a primary homonym of *Helix spectabilis* Pfeiffer, 1844, and introduced accordingly the new name *Oxchilus (Atlantoxychilus) riedeli*. However, Bank *et al.* (2002) considered Hausdorf’s (1993) nomenclatorial action invalid, for Morelet’s (1860) indication of a “ γ var. *spectabilis*” did not constitute attribution of a name to the variety, the word “*spectabilis*” instead being part of the description of variety γ . The name was validly introduced by Milne-Edwards (1885) as *Hyalinia spectabilis*, which is not preoccupied. Some aspects of this species were already dealt with, and only a brief morphological characterization will be added. The mantle is brown, crossed by elongated, irregular golden-brown blotches; border of mantle light-brown; neck dark-brown, sharply separated from the golden-brown foot which is surrounded by an intermittent brown rim.

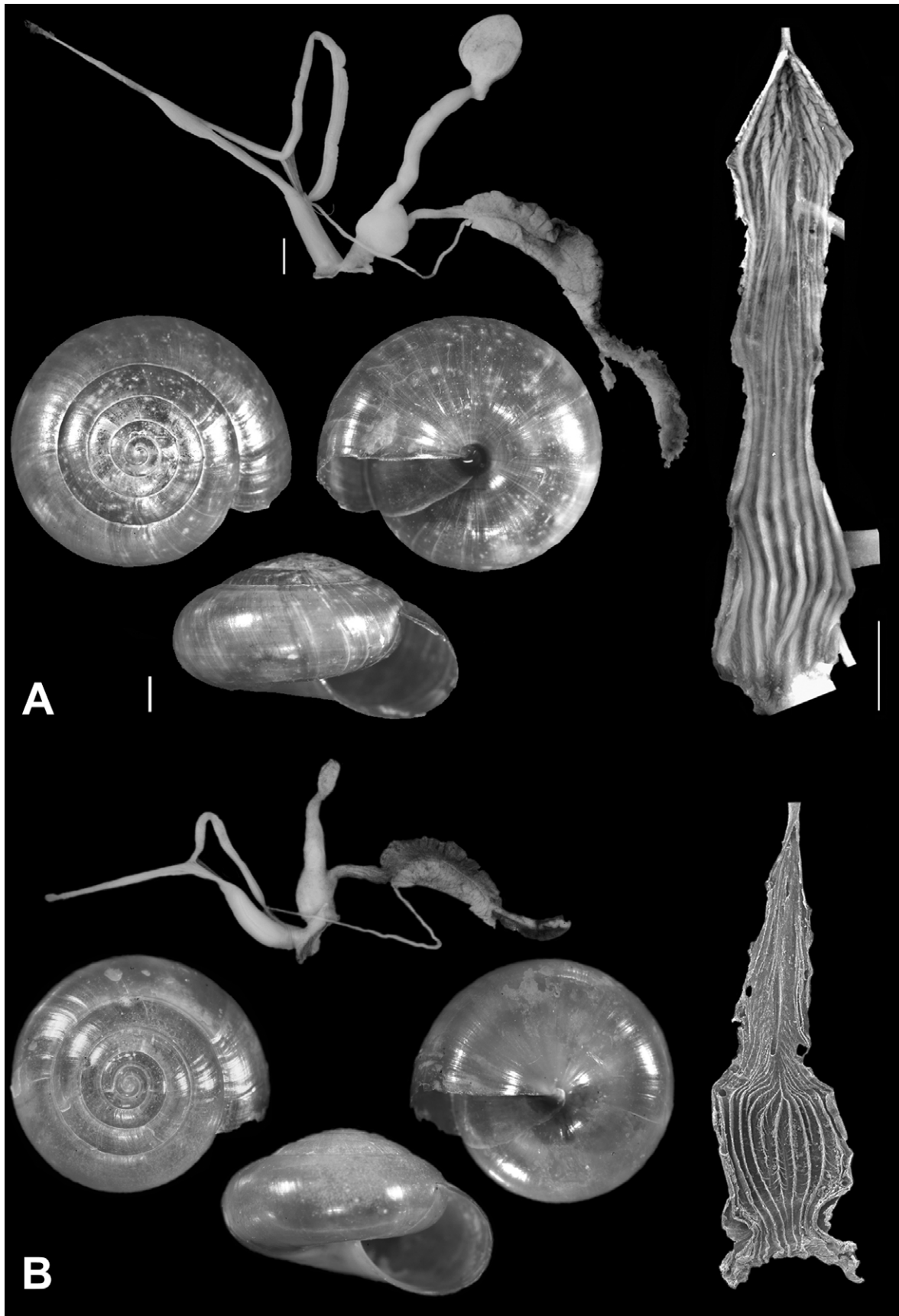


FIGURE 20. Shells, genitalia and internal penis morphology of species of *Drouetia*. **A**, *Oxychilus (Drouetia) atlanticus*, Sete Cidades, São Miguel (type locality) (NHMUK 20100653; see Martins *et al.*, 2011). **B**, *Oxychilus (Drouetia) batalhanus*, Batalha, São Miguel (type locality). Scale bars = 1 mm.

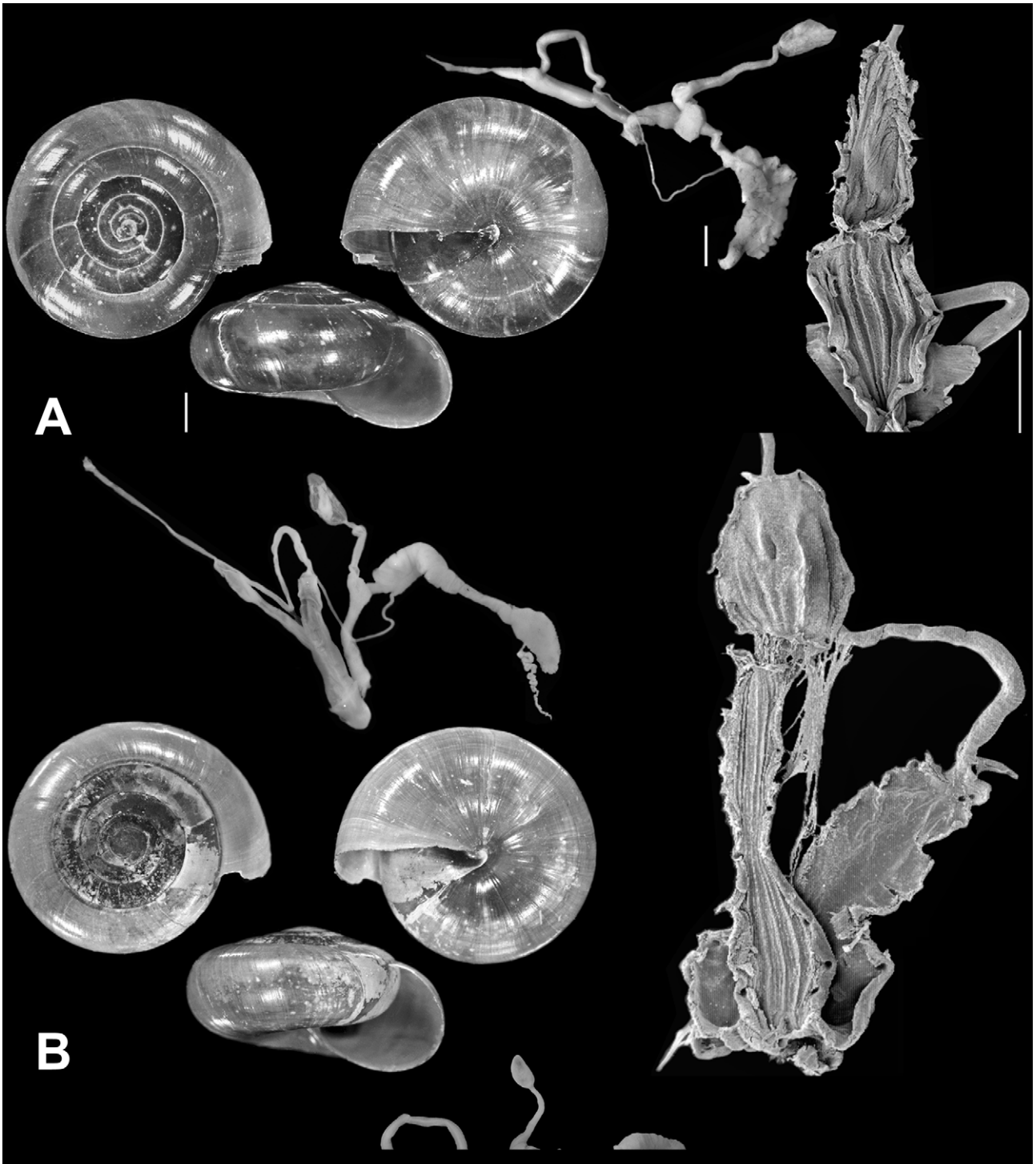


FIGURE 21. Shells, genitalia and internal penis morphology of species of *Drouetia*. **A**, *Oxychilus (Drouetia) miceui*: shell, holotype (NHMUK 1989162); genitalia and penis, paratype, Caldeira de Santa Bárbara, Terceira. **B**, *Oxychilus (Drouetia) furtadoi*: shell, holotype (NHMUK 1989156); genitalia and penis, paratype, Fonte da Telha, Posto Santo, Terceira; the penial sheath was slit longitudinally to expose the muscle strands attaching the epiphallus to the distal penis. **C**, *Oxychilus (Drouetia) minor*: shell and genitalia, Ribeirinha, Faial; penis, Flamengos, Faial. Scale bars = 1 mm.

A key to the non-umbilicate Azorean *Oxychilus*

Shell with furrow
 Shell without furrow

O. (A.) spectabilis
 1

1.	Spire elevated (height of spire/height of shell ≥ 0.1)	2
	Spire depressed (height of spire/height of shell ≤ 0.1)	5
2.	Epiphallus with discrete swellings	<i>O. (D.) viridescens</i>
	Epiphallus without discrete swellings	3
3.	Separation proximal/distal penis marked, pilasters not running to penial caecum	<i>O. (D.) batalhanus</i>
	Separation proximal/distal penis not marked, pilasters running to penial caecum	4
4.	Crests inside proximal penis reticulate around epiphallic pore	<i>O. (D.) atlanticus</i>
	Crests inside proximal penis radiating from epiphallic pore	<i>O. (D.) brincki</i>
5.	Spire flat	<i>O. (D.) agostinhoi</i>
	Spire somewhat raised	6
6.	Separation proximal/distal penis not marked, pilasters running to penial caecum	<i>O. (D.) minor</i>
	Separation proximal/distal penis marked, pilasters not running to penial caecum	7
7.	Distal penis as long as proximal penis+penial caecum, penial sheath not covering entire distal penis	<i>O. (D.) miceui</i>
	Distal penis much longer than proximal penis+penial caecum, penial sheath covering entire distal penis	<i>O. (D.) furtadoi</i>

Conclusion

Martins (2005) and Martins *et al.* (2010) have provided evidence that the diversity of *Drouetia* in the Azores is much greater than what the described taxa show. This work, besides adding a new species to the Azorean oxychilids, is intended to be an updated baseline for the continuing description of the new taxa. Although important in a holistic study of the evolutionary processes, morphological and anatomical characters alone do not carry enough power to unravel the relationships of the Azorean *Drouetia*. Molecular analyses are currently under way, and will surely yield a phylogenetic framework capable of explaining the fantastic evolutive radiation of the *Oxychilus* in the Azores archipelago.

Acknowledgements

We are grateful to our colleagues Regina Cunha, Armindo Rodrigues and Peter Mordan for their assistance in the field work. Jorge Medeiros (CIRN – Universidade dos Açores) assisted with the SEM photography. I am also thankful to Cédric Audibert for calling attention to the Drouët collection in the MJSD, and for his and Monique Prost's precious help in the consultation of that collection. This research is part of the project "Speciation in *Drouetia*: evidence of punctuated equilibrium?" – (PTDC/BIA-BDE/73467/2006), financed by the Fundação para a Ciência e a Tecnologia (FCT), Portugal. TB was supported by BELSPO Action 1 MO/36/017.

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