

# MORELETINA, A NEW GENUS OF HYGROMIIDAE (PULMONATA: STYLOMMATOPHORA) FROM SANTA MARIA, AÇORES

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## ABSTRACT

*Moreletina*, gen. n. is proposed for *Helix obruta* Morelet, 1860, endemic to Santa Maria, Açores, and previously believed to occur only as a fossil. Characterized by possessing a single biramous mucous gland and a vestigial dart sac, a penial appendix, and a double-walled penial papilla, the new genus is related to the Madeiran hygromiid Geomitrinae, with which it shares a common continental European ancestor. The anatomy of *Moreletina obruta* is described in detail. The species shows two ecophenotypes: a light form, described by Morelet, living among grass on calcareous substrates, on the southern coast of the island, and a dark form, associated with the dark basaltic rock, living on the northern coast of Santa Maria. Besides body coloration, these two ecophenotypes differ in shell size, but do not show any detectable anatomical difference.

## INTRODUCTION

Arthur Morelet (1860) mentioned two species of fossil terrestrial molluscs from the island of Santa Maria, Açores: *Helix vetusta*, which he had described with H. Drouët in 1857 and Backhuys (1975) assigned to *Leptaxis*, and *Helix obruta*, which Morelet proceeded to describe. Morelet remarked that these species had probably become extinct not long ago, as a result of volcanic activity on the island. Backhuys (1975) tentatively assigned Morelet's species to *Ceriuella* and stated that, on account of the fairly fresh appearance of the shells he had found, it was possible that *Ceriuella ? obruta* could still be alive. Martins, Backeljau, Cunha & Brito (1991) found live specimens of Morelet's species and, on consideration of the bifid mucous gland, hypothesized that it could belong in the Ariantinae. A more detailed examination, however, indicates relationship with the predominantly Madeiran subfamily Geomitrinae. The new genus is herein described, its taxonomic relationships addressed, and a detailed anatomical description of *M. obruta* presented.

## MATERIALS AND METHODS

The type material of *Helix obruta* Morelet (1860), at the Natural History Museum, London, UK (NHM), was examined.

Live material was collected from four sites on the island of Santa Maria (Fig. 1):

- Sta 1. Figueiral. 14.06.1990. On a sea cliff of mostly calcareous substrate, about 100 m above sea level, among *Agave americana* plants and dense grass cover.
- Sta 2. W of Praia Formosa. 15.11.1995. Among grasses, on top of an escarpment about 10 m above sea level.
- Sta 3. E of Anjos. 17.07.1994. Under basaltic rocks, on a barren, rocky sea cliff, about 50 m above sea level.
- Sta 4. W of Anjos. 14.06.1990. Under basaltic stones covered with lichens and with some vegetation, at the base of a sea cliff, about 20 m above sea level.

Additional material of other species from Madeira was included for anatomical comparisons:

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- Caniço de Baixo, Madeira. October 1993. (*Actinella lenticinosa*, *Discula* sp.)
- São Lourenço, Madeira. R.A.D. Cameron leg. (*Actinella lenticinosa*)

The shells were measured and inspected for various parameters (Table 1) under a dissecting stereomicroscope (Wild M8) with aid of a camera lucida and simple statistical analyses were used to compare the morphometry of the four populations.

SEM (Jeol JSM 5410) was used to study the protoconch, jaw and radula, and with the aid of drying using hexamethyldisilane (10 min at each of the following steps: 95% alcohol; absolute alcohol; 1:1 absolute alcohol/acetone; acetone; hexamethyldisilane), also the internal morphology of the reproductive system. The samples were previously covered with gold/palladium 40/60 in a vacuum evaporator Jeol JEE 400.

## TAXONOMIC DESCRIPTIONS

Family Hygromiidae Tryon, 1866  
Subfamily Geomitrinae C. Boettger, 1909  
*Moreletina* gen. n.

Type species, by monotypy: *Moreletina obruta* (Morelet, 1860).

*Description:* Shell dextral, medium sized, subcarinate, marbled with transverse, irregularly interrupted, rib-like white spots; spire up to 5.7 whorls, moderately elevated; peristome sharp, slightly reflected over the small umbilicus.

Mandible odontognathous, with seven strong ribs. Radula with about 41 teeth per row.

Right ommatophore retractor not crossing between penis and vagina; bursa adhering to spermoviduct; one biramous mucous gland; dart sac vestigial; penial complex bifid proximally, with a short flagellum and a blunt appendix near it, distally wrapped in a sheath; penial papilla tubular, double walled, secured on one side by strong pilasters, tip wide, reflected. Penial nerve originating from right anterior tentacular nerve.

*Derivatio nominis:* The new genus is dedicated to the French malacologist Arthur Morelet, to whom we owe the first great comprehensive work on the terrestrial molluscs of the Açores.

**Moreletina obruta (Morelet, 1860)**

*Helix obruta* Morelet, 1860: 178, pl. v, fig. 13.  
*Helix obruta* Morelet et Drouët [sic]. Crosse, 1861: 73.  
*Helicella obruta* Morelet. Fischer-Piette, 1946: 259.  
*Cernuella? obruta* (Morelet, 1860). Backhuys, 1975: 203.  
*'Helix' obrupta* [sic] (Morelet). Martins *et al.*, 1991: 53 (mis-spelling).  
*Helicella* sp. Martins *et al.*, 1991: 54.

**Types** (Fig. 3A,B): Holotype NHM 93.2.4.1258 and 2 paratypes NHM 93.2.4.1259–60.

**Type locality:** Santa Maria, Açores, herein restricted to Figueiral.

**Description:** Shell (Figs 2–4) dextral, up to 9.1 mm in diameter and 6.3 mm in height (diameter to 8 mm and height to 5.6 mm in dark ecophenotype), moderately thick, translucent, sub-carinate, with very fine, irregular growth lines along which



**Figure 1.** Location of the four stations. See text for explanation.

**Table 1.** Measurements (mm) and counts of various shell parameters of specimens collected at the four stations. Hap, height of the aperture; Hlw, height of the last whorl; Hsp, height of the spire; Umb, width of the umbilicus; W, shell diameter; #, specimen number; #B, number of bands; #w, number of whorls.

#	#w	W	Hlw	Hsp	Hap	Umb	#B
<b>Sta. 1</b>							
01	5.5	8.2	4.2	1.1	2.9	0.8	2
02	5.5	7.9	3.8	1.1	2.9	0.9	0
03	5.3	8.0	3.8	1.0	2.8	0.8	2
04	5.2	8.2	3.9	0.6	3.2	0.6	0
05	5.0	7.6	3.3	0.7	2.8	0.8	2
06	5.1	7.2	3.7	0.8	2.8	0.7	0
07	4.7	7.1	3.3	0.6	2.6	0.7	1
08	5.3	9.0	4.0	0.9	2.9	0.8	1
09	5.0	7.4	3.8	0.8	2.8	0.7	2
10	5.4	8.4	4.4	1.2	2.9	1.0	0
11	5.2	7.8	3.3	1.0	2.9	0.8	1
12	5.2	8.2	3.8	0.8	2.6	1.0	2
13	5.3	7.8	4.0	1.1	2.8	0.8	0
14	5.3	8.4	4.2	1.2	3.0	0.8	2
15	5.3	8.3	3.8	1.1	2.6	1.0	0
16	5.5	8.3	4.1	1.2	2.7	0.8	0
17	5.2	7.6	3.8	1.2	2.9	0.7	2
18	5.2	7.8	3.7	0.8	2.8	0.6	0
19	5.1	7.7	3.6	0.6	2.8	0.6	1
20	5.3	7.5	3.8	1.0	2.7	0.5	2
21	5.2	7.6	3.7	1.2	2.8	0.8	2
22	5.1	7.2	4.0	0.8	2.9	0.6	2
23	5.0	7.5	3.8	1.0	2.9	0.8	2
24	5.2	7.8	3.8	0.8	2.7	0.7	2
25	5.2	7.0	3.4	1.0	2.5	0.7	2
26	4.9	7.5	3.2	0.9	2.5	0.7	0
27	5.0	7.1	4.0	0.9	2.9	0.6	2
28	5.0	7.3	3.5	0.8	2.5	0.5	2
29	4.9	7.1	3.3	0.8	2.5	0.7	2
30	5.1	7.5	3.6	0.8	2.7	0.8	2
31	5.5	8.0	4.1	1.3	2.9	0.9	2
32	5.5	8.7	4.2	1.4	3.1	0.9	2
33	5.7	7.7	4.4	1.4	2.9	0.7	2
34	5.5	7.9	4.1	1.1	3.0	0.7	2
35	5.2	7.5	3.6	1.1	2.8	0.7	2
36	5.5	7.8	4.0	1.2	2.8	0.5	2

#	#w	W	Hlw	Hsp	Hap	Umb	#B
<b>Sta. 2</b>							
37	5.5	9.1	4.8	1.5	3.5	0.9	1
38	5.4	8.3	4.6	1.3	3.2	0.6	2
39	5.3	8.4	4.5	1.0	3.2	0.7	2
40	5.6	8.9	4.7	1.3	3.2	0.7	2
41	5.0	7.9	4.2	1.1	3.2	0.8	2
42	5.4	8.8	4.5	1.1	3.4	0.7	1
43	5.2	8.0	4.3	1.0	3.1	0.6	2
<b>Sta. 3</b>							
44	5.4	7.6	4.5	1.1	3.0	0.9	2
45	5.2	8.0	4.4	1.2	3.0	0.8	2
46	5.0	7.2	3.9	0.9	3.0	0.8	2
47	4.6	6.1	3.2	0.8	2.4	0.7	2
48	5.0	7.3	4.0	1.2	2.9	0.7	2
49	5.0	7.0	3.5	1.2	2.5	0.7	2
50	5.1	6.9	4.1	1.2	2.7	1.0	2
51	5.0	7.1	3.8	1.0	2.6	0.7	2
52	5.1	7.4	4.3	1.1	2.8	0.9	2
53	5.0	7.0	3.7	1.2	2.6	0.7	2
54	4.8	6.4	3.5	0.8	2.6	0.7	2
55	4.8	7.3	3.9	0.8	2.6	0.9	2
56	4.6	6.4	3.5	0.7	2.4	0.8	2
57	4.8	6.6	3.8	0.9	2.5	0.8	2
58	5.0	6.7	3.7	1.0	2.5	0.7	0
<b>Sta. 4</b>							
59	4.9	7.1	4.0	1.0	2.9	0.7	2
60	5.2	6.7	4.0	1.1	2.9	0.5	2
61	5.1	7.1	3.8	1.2	2.7	0.8	2
62	5.1	7.2	3.8	0.9	2.6	0.7	2
63	5.1	7.3	3.8	1.5	2.4	0.7	2
64	5.0	7.2	3.9	0.8	2.6	0.9	2
65	5.2	7.0	3.8	1.2	2.2	0.7	2
66	5.0	6.9	3.9	1.0	2.6	0.7	2
67	4.8	6.8	3.8	0.9	2.6	0.7	2
68	5.0	6.9	3.8	1.1	2.5	0.7	2
69	5.0	6.7	3.6	1.1	2.3	0.7	2
70	5.0	7.2	4.0	1.3	2.6	1.0	2

longitudinal, thickened, irregularly interrupted rib-like white spots are aligned; ground coloration whitish to light-brown, darker on the spire; two narrow, sometimes sharply marked dark-brown spiral bands, one above, the other below the last whorl equator, sometimes both bands or rarely the ventral band reduced to a faint marking; spire conical, depressed to somewhat raised, with 5–5.7 (5–5.4 in dark ecophenotype) convex whorls, regularly and slowly increasing; last whorl with a faint keel sometimes visible above aperture; umbilicus rather narrow, about 1/10 of shell diameter; aperture oval, peristome sharp, slightly reflected over the umbilicus. Protoconch (Fig. 3C) sculptured with fine, irregular, smooth transverse riblets not reaching the outer suture of the whorl, and with very fine spiral striae that disappear before the first marked growth line indicating the beginning of the teleoconch.

Animal of light ecophenotype pale straw-yellow to very light-brown, top of neck with same colour as sides of foot, tentacles

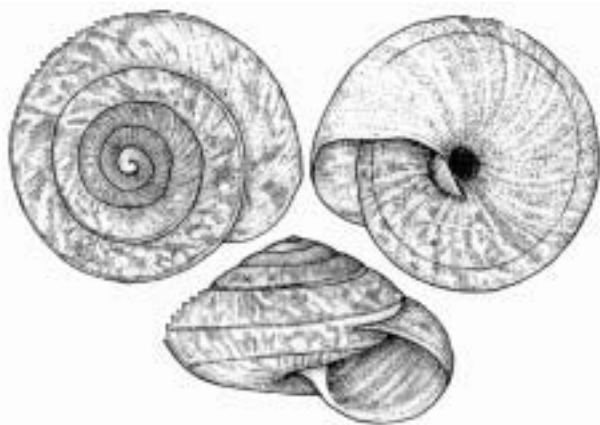


Figure 2. Shell of *Moreletina obruta*; W: 7.9 mm (Figueiral, specimen #1 in Table 1).

grayish, anterior ones darker, posterior ones (ommatophores) with black eye dots readily visible, mantle colour visible through translucent shell, sensibly the same colour as foot, border of mantle darker, speckled with brownish spots; distinctly visible anterior and posterior tentacular retractors of each side running separate until near the mantle border where they coalesce and faint somewhat before entering the visceral mass. The dark ecophenotype has the sides of the foot pinkish brown and the top of the neck dark gray; tentacles dark blue; mantle dark brown through translucent shell, border of mantle of a lighter brown speckled with the same colour as the foot.

Mantle collar (Fig. 5) with an extensive glandular patch on its inner left side; right lateral lobe developed, complex, with many rounded, fleshy protuberances; right dorsal lobe simple, with a shallow groove; subpneumostomal lobe well developed, flap-like, forming a short, rounded channel (anal slit) as it exits the pneumostome to the right and a longer, deep slit (urinary slit) to the left; left dorsal lobe barely visible as a shallow protuberance of the glandular field; left lateral lobe as long flap of the mantle edge reflected over the inner glandular portion.

Pallial cavity (Fig. 6) wide; pallial (anterior) lobe of kidney with narrow and elongate anterior tip squeezed between the heart and the ureter, secondary ureter continuing to the right, bordering posterior lobe of kidney, then bending anteriorly as it nears the rectum to open into a mucous groove (urinary tract), at the posterior right end of the lung; urinary tract following the rectum, exiting the pneumostome into the urinary slit.

Jaw (Fig. 7A) odontognathous, with seven strong ribs.

Radula (Figs. 7B–D): formula  $(12 + 8 + 1 + 8 + 12) \times 95$ . Central tooth with wide base, crown with a strong, pointed mesocone, and two small, sharp ectocones; lateral teeth slightly larger than central, without endocone, with one sharp ectocone becoming slightly wider on the outer teeth; marginal teeth with one faint endocone progressively becoming stronger, mesocone gradually decreasing in the teeth located towards the edges of the radula, one strong ectocone soon splitting into

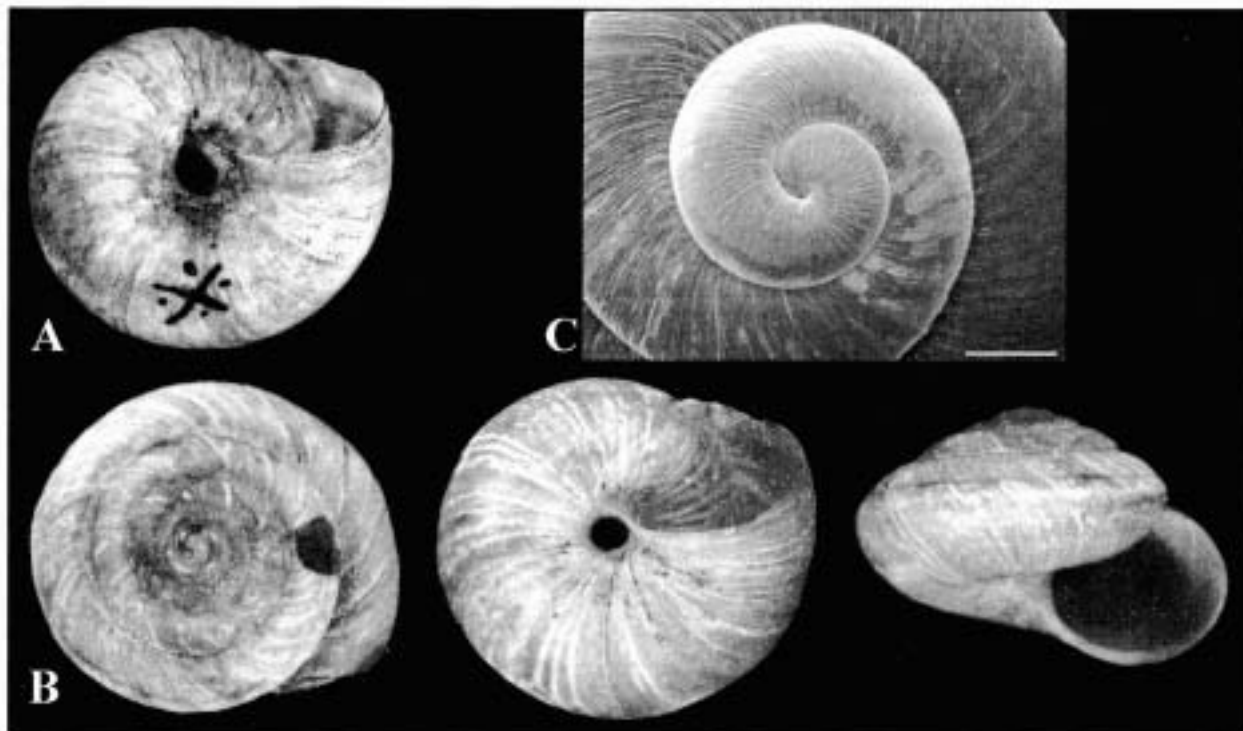


Figure 3. Shells of *Moreletina obruta*. (A) Holotype, ventral view (NHM 93.2.4.1258, marked Type x), W: 8.0 mm. (B) Paratype (NHM 93.2.4.1259), W: 7.8 mm. (C) First whorls (Figueiral, specimen #7 in Table 1), scale bar: 0.5 mm.

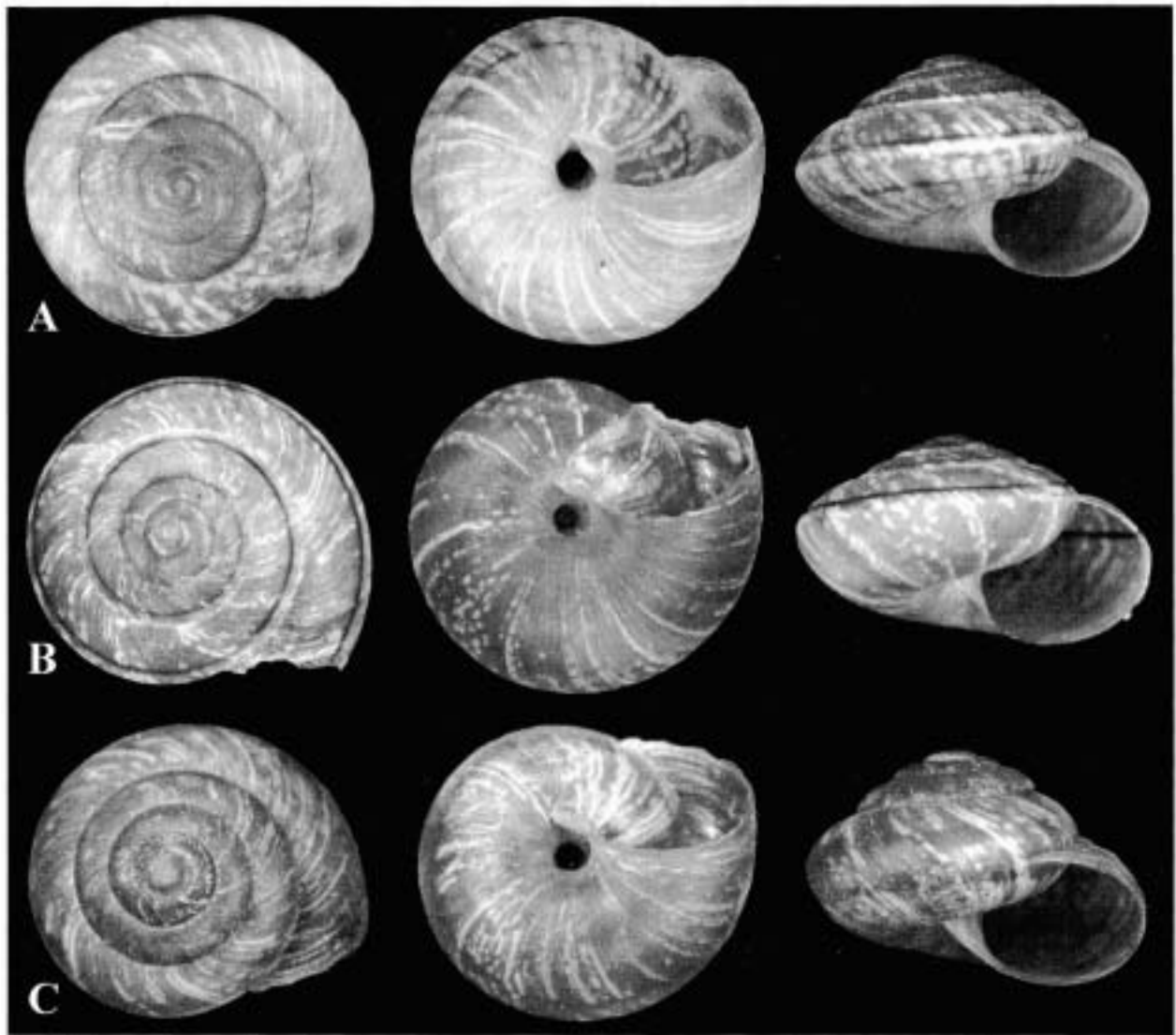


Figure 4. Shells of *Moreletina obruta*. (A) Figueiral (specimen #1 in Table 1), W: 8.2 mm. (B) W of Praia Formosa (specimen #37 in Table 1), W: 9.1 mm. (C) E of Anjos (specimen #45 in Table 1), W: 6.7 mm.

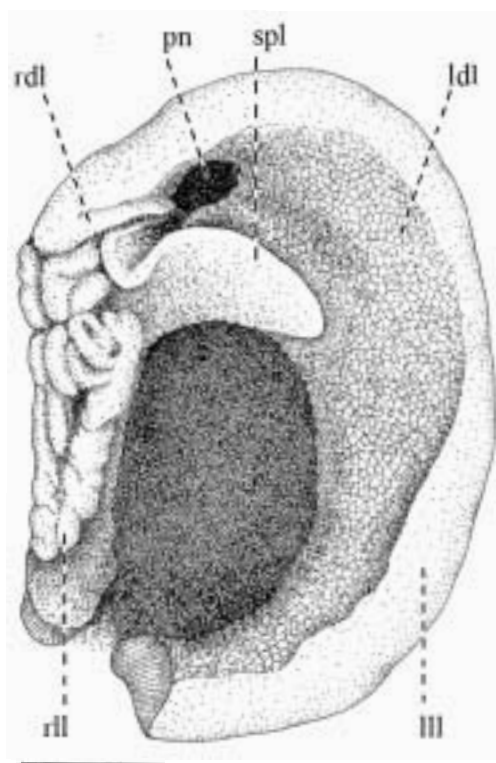
several (as many as five) irregular denticles, a pattern not consistent, however, from row to row.

Salivary glands attached to crop, left one larger, expanding posteriorly and to the right to fuse with posterior portion of right gland; anterior half of both glands separated, gradually tapering anteriorly to the glandular ducts, which enter buccal bulb anterodorsally to buccal ganglion.

Genitalia (Figs 8–10): right ommatophore retractor not crossing between penis and vagina; genital atrium very short, wide. Penial complex short, distal portion about as long as epiphallus and enveloped in a penial sheath; the moderately sized penial retractor muscle inserts at the proximal border of the sheath and attaches to the floor of the mantle just underneath the collar attachment; flagellum about as long as epiphallus, conical, with a short, blunt appendix at its base. Penial papilla tubular, double walled, resulting from the invagination of the epiphallus into the proximal portion of the penis; strong pilasters secure the wall of the papilla on one side, the opposite side remaining free; tip wide, flaring. Anterior vas deferens enters epiphallus protected inside by an oblong pad, the sinuous pore facing distally; remaining of the internal surface of epiphallus shows two wide grooves, one entering to the

appendix, the other to the flagellum; the former presents an irregular thickening inside, the latter shows a strong, conical pilaster in all its length. Vagina short, about half the length of the oviduct, widening toward the atrium, wrapped with muscular tissue proximally. A single, biramous, digitiform mucous gland, rarely with a third branch, opens at the proximal end of the vagina, opposite to the confluence of oviduct with bursa duct, with a vestigial dart sac at its base, distally. Bursa oval, adhering to prostate side of spermoviduct; bursa duct reaching in length the middle of the spermoviduct, with base thicker than oviduct and continuous with the vagina. Oviduct about as long as vagina and atrium combined, inserting laterally in the bursa duct/vagina; anterior vas deferens exiting about midway the length of the oviduct, which has a conspicuous prostate groove lining the corresponding proximal half of its lumen.

Central nervous system (Fig. 11) typical of helicids, showing great ganglionic concentration of the visceral nerve ring; left parietal ganglion and visceral ganglion fused; penial nerve branching off right anterior tentacle nerve, dividing in two branches, the thinner branch enters the penial side of the atrium, the thicker follows the anterior vas deferens and

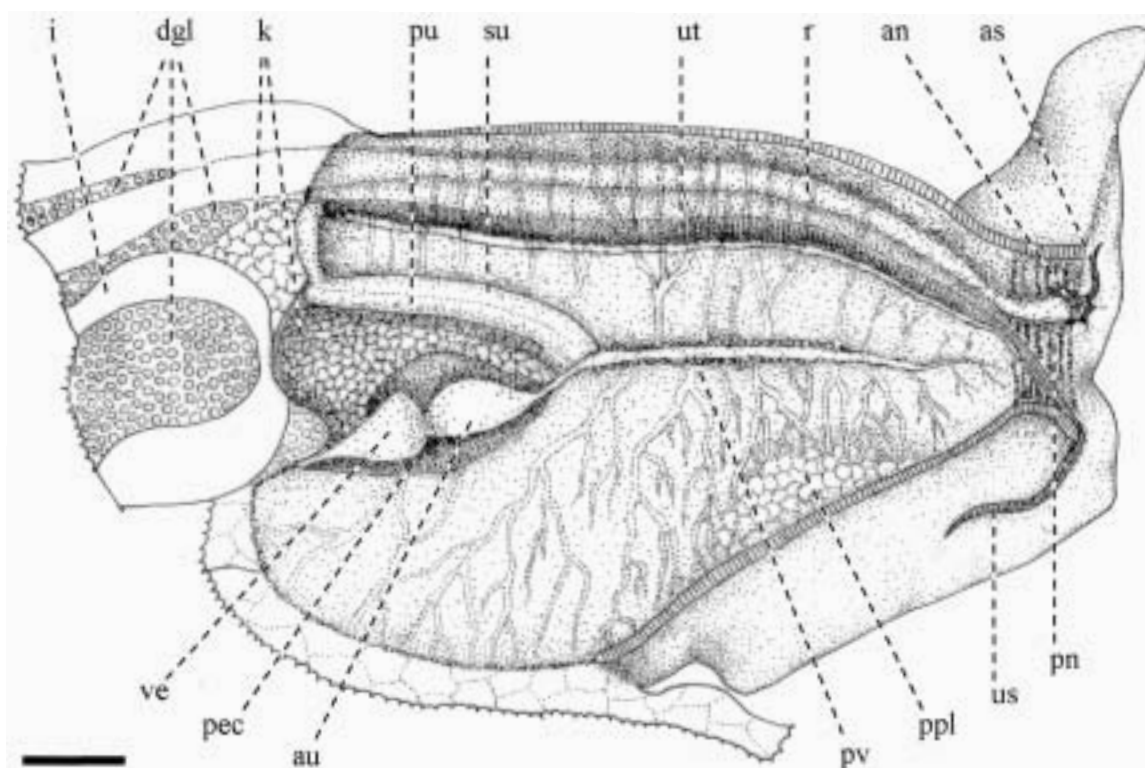


**Figure 5.** Mantle collar of *Moreletina obruta* (Praia Formosa, specimen #40 in Table 1); scale bar = 1 mm. Abbreviations: ldl, left dorsal lobe; lll, left lateral lobe; pn, pneumostome; rdl, right dorsal lobe; rll, right lateral lobe; spl, subpneumostomal lobe.

branches near the base of the flagellum, one branch entering the epiphallus near the confluence of vas deferens, the other branch entering the epiphallus about opposite to such confluence.

*Habitat and distribution:* *Moreletina obruta* is endemic to the Azorean island of Santa Maria. Morelet (1860) found shells of this species in a fossil or subfossil state, and Backhuys (1975) noted the freshness of some of the specimens he had collected, thus arguing for the possibility of it still being extant. Martins *et al.* (1991) found live specimens at Figueiral (Sta. 1) and nearby (Sta. 2), in the south coast of the island where Morelet and Backhuys had found dead shells, and also at the north coast, near Anjos. The Figueiral populations lived among agave plants and dense grass cover, on a calcareous substrate, from about 10 m above sea level (near Praia Formosa beach) up to 100 m at the type locality. The animals at this habitat are light coloured, thus blending in perfectly with the straw of the dead gramineae. The specimens found at Anjos are much darker, the mantle, seen through the translucent shell, is dark brown and the sides of the neck deep blue, their shells somewhat smaller in average than the southern ones (Table 2).

Consideration of the significance of the shell differences (Table 3, Fig. 12) should take into account the small sample size of Sta. 2, which specimens are clearly separated from those of the remaining stations, including the equally white form of Sta. 1. Such differences among specimens from the southern localities are indicative of considerable morphological variability of the species and, *per se*, should not hinder the inclusion of the northern, dark form within the same taxon. The dark form lives under basaltic stones, on the barren cliff or with lichens and sparse vegetation, from 20 to 50 m above sea level. The animals, aside from the colour, exhibit no noticeable



**Figure 6.** Pallial cavity and associated organs of *Moreletina obruta* (E of Anjos, specimen #45 in Table 1); scale bar: 1 mm. Abbreviations: an, anus; as, anal slit; au, auricle; dgl, digestive gland; i, intestine; k, kidney; pec, pericardium; pn, pneumostome; ppl, pulmonary plexus; pu, primary ureter; pv, pulmonary vein; r, rectum; su, secondary ureter; us, urinary slit; ut, urinary tract; ve, ventricle.

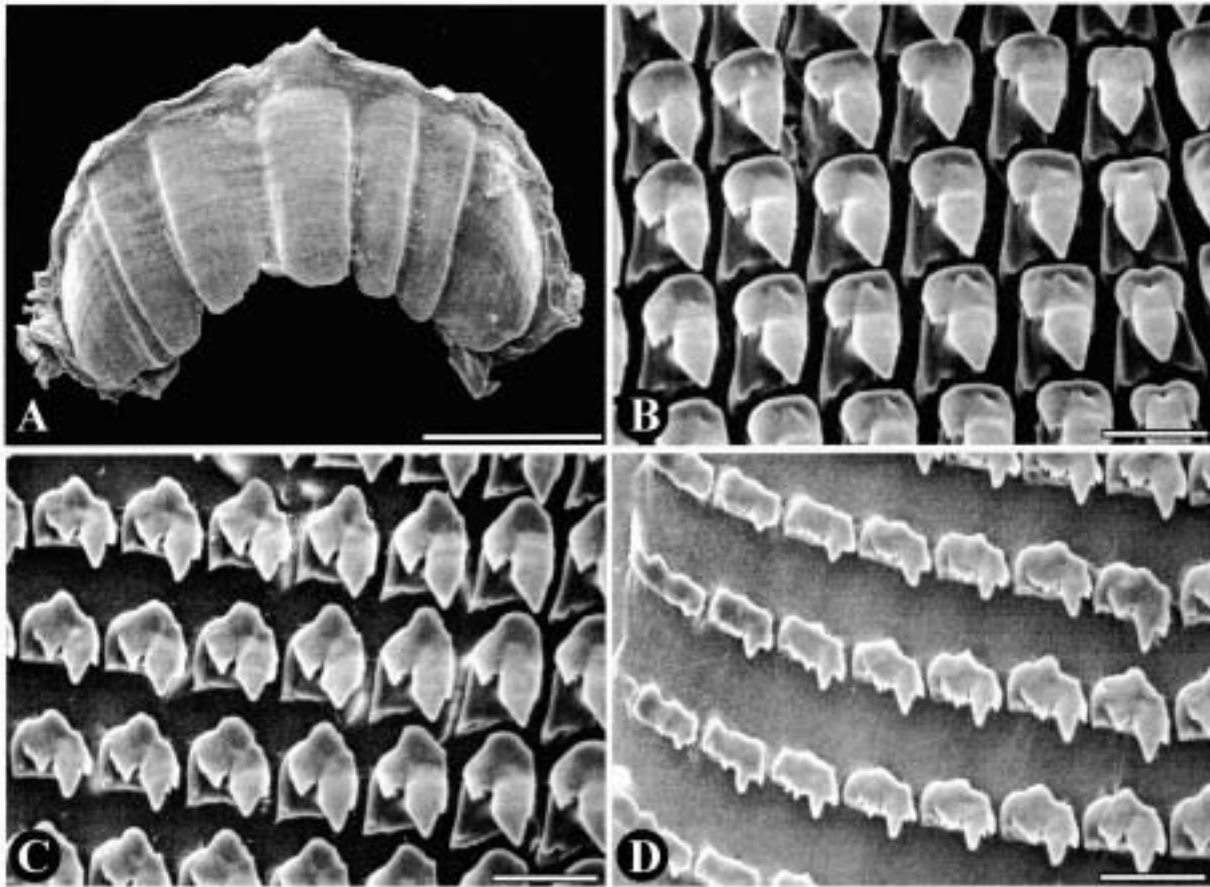


Figure 7. *Moreletina obruta* (Figueiral, specimen #5 in Table 1). (A) Jaw; scale bar = 200 µm. (B–D) Radula; scale bar = 20 µm.

Table 2. Average and standard deviations (SD) of morphometric measurements of specimens (*n*) from Stations 1–4. Different letters (a–c) following SD's indicate significant differences between stations (Scheffé test,  $\alpha = 0.05$ ). Symbols as in Table 1.

	Sta. 1	Sta. 2	Sta. 3	Sta. 4
<i>n</i>	36	7	15	12
Characters				
#W	5.23	5.34	4.96	5.03
SD	0.22 (a)	0.20 (a)	0.21 (b)	0.12 (b)
W	7.77	8.49	7.00	7.01
SD	0.47 (a)	0.46 (b)	0.50 (c)	0.21 (c)
H	4.80	5.70	4.86	4.94
SD	0.48	0.38	0.49	0.21
HLW	3.81	4.51	3.85	3.85
SD	0.31 (a)	0.21 (b)	0.36 (a)	0.12 (a)
HSP	0.98	1.19	1.01	1.09
SD	0.22	0.19	0.18	0.19
HAP	2.80	3.26	2.67	2.58
SD	0.17 (a)	0.14 (c)	0.22 (ab)	0.21 (b)
UMB	0.74	0.17	0.79	0.73
SD	0.13	0.11	0.10	0.12

anatomical difference from their southern counterparts (Figs 8–9). I have, thus, interpreted the abovementioned differences as due to adaptation to different habitat conditions, and northern and southern populations should be considered as ecophenotypes of a single species. However, in view of the striking

Table 3. Analysis of variance for the morphometric characters.

Character	<i>df</i> effect	<i>df</i> error	<i>F</i>	<i>P</i>
#w	3	66	9,699137	2,18E-05
W	3	66	26,62421	2,11E-11
Hlw	3	66	11,63721	3,26E-06
Hsp	3	66	2,506219	0,066569 NS
Hap	3	66	22,73747	3,19E-10
Umb	3	66	0,771227	0,514224 NS

NS, non-significant value. Symbols as in Table 1.

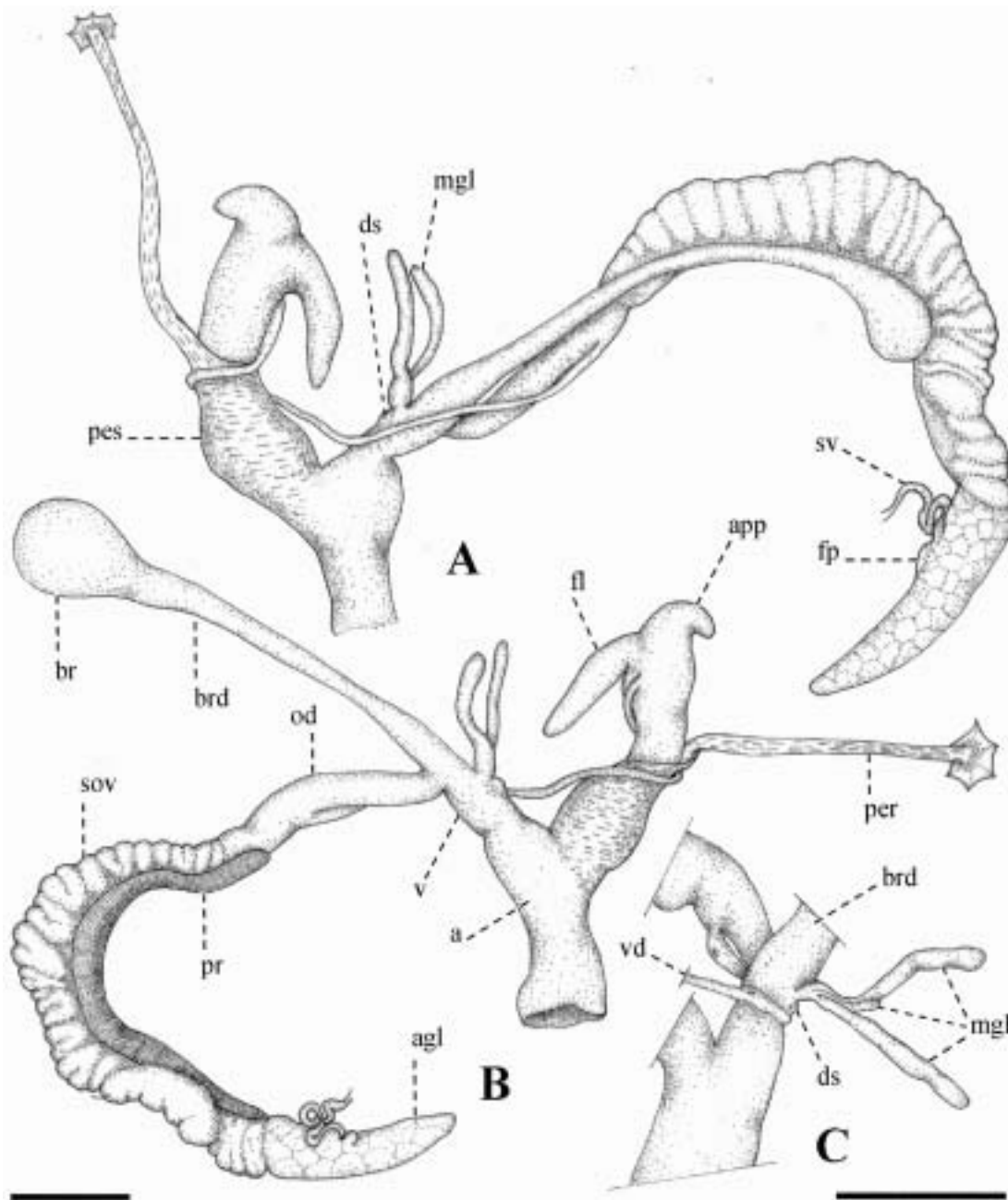
colour difference, I found it advisable to restrict the type locality to that area in the island where Morelet (1860) first found the shells.

## DISCUSSION

### *The taxonomic position of Moreletina*

Previous generic classifications of *Moreletina obruta* were based on shell characters. Morelet (1860) found the shells in a fossil bed and attributed them to the then all encompassing genus *Helix* Linnaeus, 1758, noting the similarities with *Helix armillata* Lowe, 1852. Wollaston (1878), following Morelet, included *H. obruta* within the § *Xerophila*, Held, 1837, together with *H. armillata* and *H. apicina* Lamarck, 1822. Fischer-Piette (1946), on his study on the colonization of the Macaronesian Archipelagos, considered it under *Helicella* Férussac, 1821. Backhuys (1975), who reported the species as subfossil and





**Figure 8.** Reproductive organs of *Moreletina obruta*. (A,B) Overall view (Figueiral, specimen #1 in Table 1). (C) Detail of proximal vaginal region (Figueiral, specimen #4 in Table 1). Scale bars = 1 mm. Abbreviations: a, atrium; agl, albumen gland; app, penial appendage; br, bursa; brd, bursa duct; ds, dart sac; fl, flagellum; fp, fertilization pouch; mgl, mucous gland; od, oviduct; pe, penial papilla; per, penial retractor muscle; pes, penial sheath; pr, prostate gland; sov, spermatheca; sv, seminal vesicle; v, vagina; vd, vas deferens.

found fairly fresh shells, hinting the possibility of it being still alive, placed *H. obruta* tentatively under *Cernuella* Schlüter, 1838, acknowledging the impossibility of determining with certainty the generic affiliation without anatomical information. Martins *et al.* (1991) found the species alive and, based on the anatomy of the reproductive system, raised the possibility of it belonging in a new genus, herein described.

Martins *et al.* (1991) considered '*Helix*' *obruta* (therein misspelled *obrupta*) as belonging in the Ariantinae Mörch, 1864, a subfamily of the Helicidae Rafinesque, 1815. Although *Moreletina* has only one bifid mucous gland, as in the Ariantinae, the dart sac in the new genus is vestigial, without any

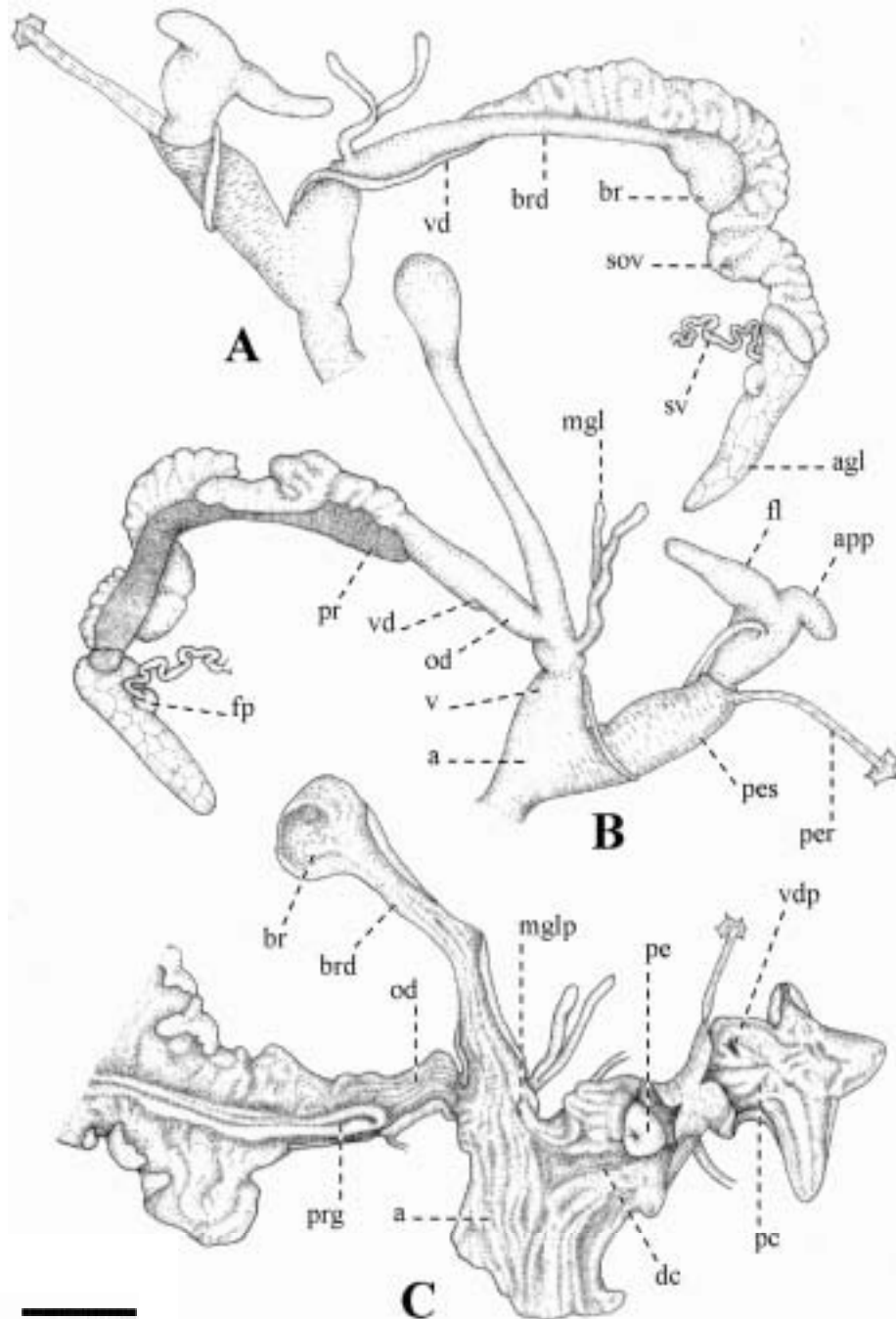
trace of dart, and the diverticulum of the bursa is wanting, thus precluding the proposed association.

On the basis of the anatomical evidence herein presented, and following the comprehensive classification systems of Nordsieck (1987) and Shyleiko (1991), *Moreletina* n. gen. belongs in the Hygromiidae Tryon, 1866. Although in both systems the subfamilial division is based on the arrangement of the vaginal stimulatory apparatus, that is, the combination of glandular and dart sac components, precise taxonomic placement of the new genus within this complex family is not coincident within the abovementioned systems. The present study, however, does not carry information sufficient to clarify the dis-

agreements between the two classification schemes and, for geographical reasons, I have opted to follow Nordsieck's (1987) revision, which recognizes the peculiarity of the Madeiran Geomitrinae.

Within the Hygromiidae, *Moreletina* shows anatomical affinities with Nordsieck's Geomitrinae C. Boettger, 1909, an assemblage to which Shyleiko attributes tribal status under the name Trochoideini Nordsieck, 1987. The presence of a rudimentary,

non-functional dart sac, and the fact that the right ommatophore retractor does not cross between penis and vagina justify this taxonomic allocation of the new genus. Aside from the continental *Trochoidea* Brown, 1827, all other related genera are Madeiran endemics, gathered by Pilsbry (1894) under the genus *Geomitra* Swainson, 1840. The presence of a single, bifid mucous gland and of a vestigial dart sac just distal to the latter approaches *Moreletina* from *Discula* Lowe, 1852. However, as



**Figure 9.** Reproductive organs of *Moreletina obruta* (E of Anjos, specimen #44 in Table 1). (A,B) External morphology. (C) Organs cut open to show internal morphology. Scale bar = 1 mm. Abbreviations: a, atrium; agl, albumen gland; app, penial appendage; br, bursa; brd, bursa duct; dc, distal chamber of penis; ds, dart sac; fl, flagellum; fp, fertilization pouch; mgl, mucous gland; mglp, mucous gland pore; od, oviduct; pc, proximal chamber of penis; pe, penial papilla; per, penial retractor muscle; pes, penial sheath; pr, prostate gland; prg, prostate groove; sov, spermooviduct; sv, seminal vesicle; v, vagina; vd, vas deferens; vdp, vas deferens pore.

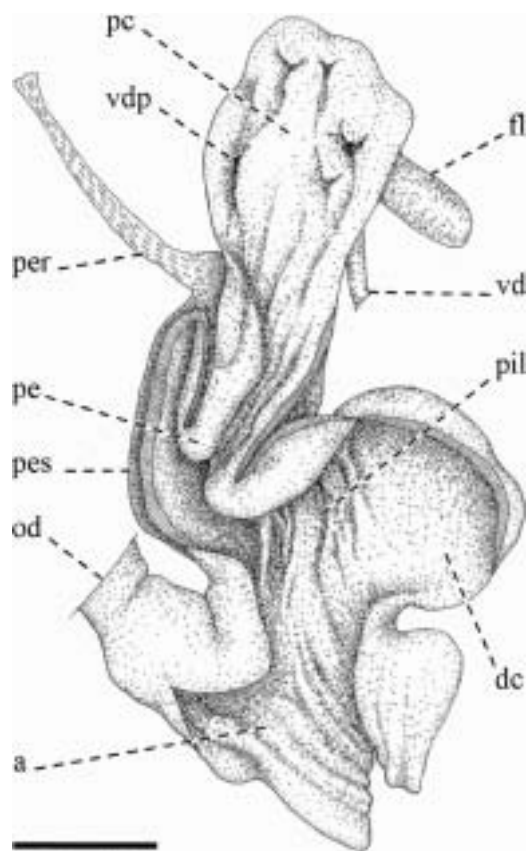


shown by Mandahl-Barth (1937, 1943), the species of this taxon have a reduced but not vestigial dart sac. Mandahl-Barth (1937) represents *Geomitra (Actinella) arcta* Lowe, 1852, another Madeiran endemic, without dart sac, but I have found a vestigial structure, much like the one in *Moreletina*, in *Actinella lentiginosa* Lowe, 1852. However, this Madeiran species possesses various short, digitiform mucous glands with paired elements opposite one another ordered in two successive groups, at the proximal end of the vagina. At the base of the bursa duct there is a rudimentary structure, much like a small mucous gland; however, its location appears to be more consistent with that of a rudimentary diverticulum, a structure that characterizes the Helicidae. Also, the penial papilla of *A. lentiginosa* is a muscular structure free all around its base, with a conspicuous sub-papilla at its tip, whereas the penial papilla in *Moreletina* is an invagination of the wall of the epiphallus, with strong pilasters attaching to one side and with a wide, reflected tip (Fig. 10). A similar type of penial structure is found in the Canarian endemic *Candidula ultima* (Mousson, 1872) (Alonso, Ibáñez & Henríquez, 1996), but the dart sac arrangement precludes any close relationship with *Moreletina*. The radula of the Azorean *Moreletina* and that of the Madeiran geomitrid snails is very similar, having a low number of teeth per row (Mandahl-Barth 1937, 1943).

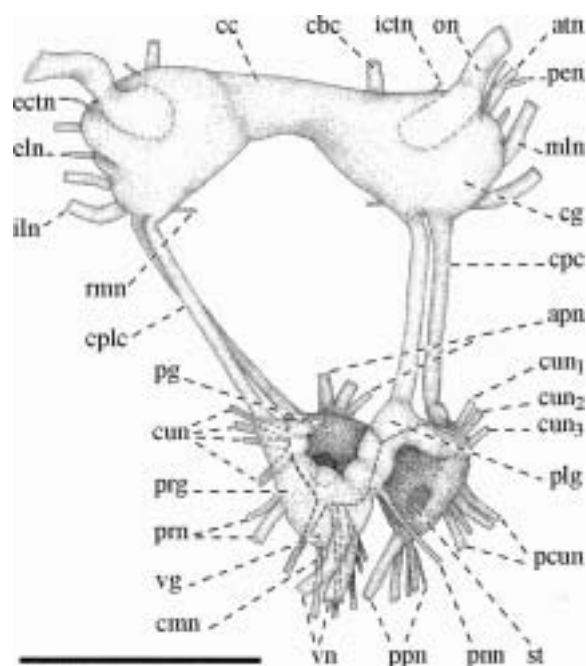
Fischer-Piette (1946) treated *Helix obruta* as *Helicella*, as did Martins *et al.* (1991) for the dark ecophenotype from Anjos. Backhuys (1975) considered tentatively that it could belong in the genus *Cerutuella*, adding that only anatomical evidence

would substantiate his hypothesis. The composition of these two European genera has fluctuated greatly. Hesse (1934), who studied their anatomy, gave *Helicella* a wide range, including *Cerutuella* as a subgenus; Nordsieck (1987) considered both genera to be separate, but included them under the Helicellini Ihering, 1909, of the subfamily Trichiinae Lozek, 1956; Shyleiko (1991), on the other hand, although maintaining *Helicella* in the Helicellini, considered *Cerutuella* to belong to the subfamily Hygromiinae on account of the relative position of the stylophores. Manganelli & Giusti (1987), Giusti & Manganelli (1989), and Manganelli, Favilli & Giusti (1996) addressed the anatomy of *Cerutuella*, *Helicella* and other closely related genera. The presence of a well-developed stimulatory apparatus with two active dart sacs, the many mucous glands crowning the vagina and, in *Cerutuella*, a penial papilla secured with frenula and the origin of the penial nerve from the pedal ganglia preclude the proposed associations (Manganelli & Giusti, 1987; Manganelli *et al.*, 1996).

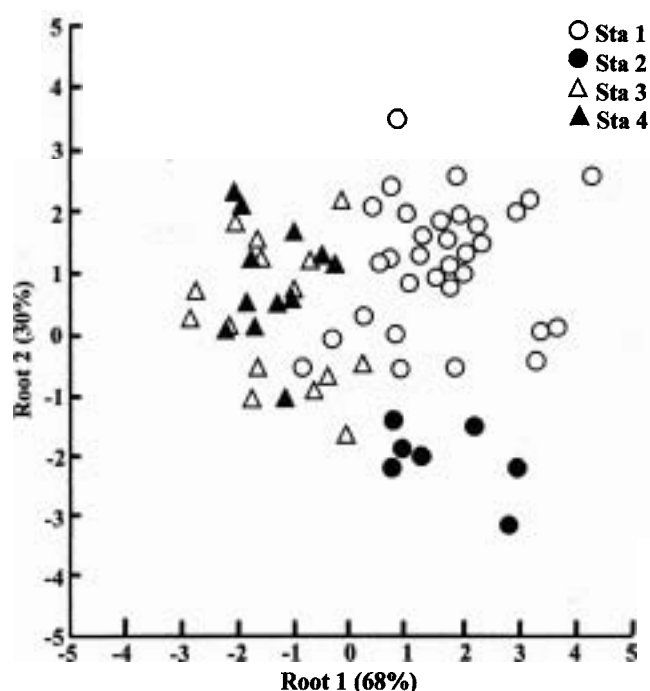
In *Helicella*, as in *Cerutuella*, the right ommatophore does not cross between penis and vagina, a situation found also in *Moreletina*. However, Shyleiko (1991) dismisses the importance of this character for it has appeared independently in various unrelated taxa, or appears differently in otherwise related groups (e.g. in the Trichiinae). It is said that this situation has bearing on the copulatory behaviour of xerophilous snails, which can thus copulate without exiting the shell. Considering the habitat of *Moreletina*, one can understand why the non-crossing situation exists.



**Figure 10.** Internal morphology of the penial complex of *Moreletina obruta* (Praia Formosa, specimen #39 in Table 1). Scale bar = 1 mm. Abbreviations: a, atrium; dc, distal chamber of penis; fl, flagellum; od, oviduct; pc, proximal chamber of penis; pe, penial papilla; per, penial retractor muscle; pes, penial sheath; pil, pilaster; vd, vas deferens; vdp, vas deferens pore.



**Figure 11.** Central nervous system of *Moreletina obruta* (E of Anjos, specimen #45 in Table 1); scale bar = 1 mm. Abbreviations: apn, anterior pedal nerve; atn, anterior tentacle nerve; cbc, cerebro-buccal connective; cc, cerebral commissure; cg, cerebral ganglion; cmn, columellar nerve; cpc, cerebro-pleural connective; cplc, cerebro-pleural connective; cun, cutaneous nerves; ectn, external circumtentacular nerve; eln, external lip nerve; ictn, internal circumtentacular nerve; iln, internal lip nerve; mln, median lip nerve; on, ocular nerve; pcun, posterior cutaneous nerves; pen, penial nerve; pg, pedal ganglion; plg, pleural ganglion; pnn, pneumostomal nerve; ppn, posterior pedal nerve; prg, parietal ganglion; prn, parietal nerves; vg, visceral ganglion; vn, visceral nerves



**Figure 12.** Canonical analysis of the significantly different morphometric characters (see Table 3). Projection of individuals from the four stations according to two canonical roots with an accumulated explained variance of 98%.

*Canariella* Hesse, 1918, a genus endemic to the Canary Islands, which lacks dart sac and has a penial sheath, could also be compared with *Moreletina*. However, in the Canarian genus the right ommatophore crosses between penis and vagina, the penial papilla appears as a modified pilaster, and the mucous glands, usually digitiform, vary in number (Ibañez, Ponte-Lira & Alonso, 1995); in *Canariella (Alvaradoa)* Groh, Ponte-Lira, Alonso & Ibañez, 1994, there is only one vaginal gland which can be digitiform, with two or with three unequal branches (Groh *et al.*, 1994). *Moreletina*, in addition, has a very low number of radular teeth per row (41), as opposed to the Canarian endemics, which have in excess of 81.

An additional feature that separates *Moreletina* from the abovementioned groups is the penial appendage, which gives the proximal end of the penial structure a conspicuous bifid appearance.

#### Zoogeographic remarks

The Geomitrinae were previously mentioned with respect to the Azores through the names *Actinella* and *Lemniscia* Lowe, 1852 (Backhuys, 1975). However, the anatomy of the Azorean taxa referred by Backhuys to these genera does not conform to that of the corresponding Madeiran taxa and they are to be awarded appropriate designation (Prieto & Martins, in prep.). *Moreletina obruta* should, then, be considered the first confirmed record of the group outside the Madeiran archipelago.

The Macaronesian relationships of the new genus, although more closely associated with Madeira and Porto Santo through some resemblance with *Discula*, clearly departs from it in some aspects of the reproductive anatomy shown above, namely the bifid proximal penis, the structure of the penial papilla and the vestigial dart sac. Such differences, reinforced by the fact that the Madeiran Geomitrinae are, themselves, apomorphic relative to the very diverse European Hygromiidae (Nordsieck, 1987; Shyleiko, 1991), lead us to propose that the Azorean

taxon could have arrived from Europe, as it did to the Madeiran Archipelago. Allied to the above mentioned apomorphies, the presence of *Moreletina* in Santa Maria, the oldest Azorean island, dating from the Lower Miocene (Serralheiro & Madeira, 1993), and its fossilized condition can also be thought as corroborating the hypothesis of common European ancestry for the Macaronesian Geomitrinae, instead of an ancestor/descendant relationship.

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