

A SYSTEMATIC REVISION OF THE VITRINID SEMISLUGS OF THE AZORES (GASTROPODA:PULMONATA)

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(Received 19 November 2000; accepted 9 February 2001)

ABSTRACT

A total of six species, all endemic, are recognised in a comprehensive taxonomic revision of the vitrinid semi-slugs of the Azores. All are referred to the genus *Plutonia* on the basis of the disposition of the penial retractor muscle. One species, *P. brevispira*, is highly unusual in lacking a vaginal stimulator and having a large, elaborate penis which would appear to function as an intromittant organ during copulation.

INTRODUCTION

The principal island groups of the eastern north-Atlantic, the Azores, the Canaries and Madeira, provide an outstanding opportunity to study a rich variety of evolutionary radiations in areas relatively close to continental Europe. Together with the Cape Verdes and the Selvagens they form a region called Macaronesia, though the biogeographic utility of such a grouping has been questioned (Beyhl, Mies & Ohm, 1995). These archipelagos all exhibit very high levels of endemism, and their biotas have a relictual appearance, with those of Madeira and the Azores showing strong affinities with the Tertiary of western Europe and the Mediterranean (Waldén, 1963; 1983). The Canaries, on the other hand, show an obvious relationship with north-west Africa, and the Cape Verdes with tropical Africa (Waldén, 1983). Surprisingly, their affinities with North America are insignificant (Waldén, 1963; 1983).

The oldest of the nine islands which comprise the Azores, Santa Maria, is thought to be aged around 8 million years (Serralheiro & Madeira, 1993). As such, the Azores archipelago is younger than either the Canaries or Madeira, and this, together with its greater distance from the continent, have been suggested as reasons why species diversity there is relatively lower (Waldén, 1984). Nevertheless, there are over one hundred species of land mollusc recorded from the Azores, approximately half of which are endemic. Major endemic evolutionary radiations have taken place in the pulmonate families Helicidae, Vitrinidae, Buliminidae, Zonitidae and Vitrinidae.

Whilst there have been recent systematic revisions of the Vitrinidae of both the Canary Islands (Ibañez, Morales & Alonso, 1987; Alonso, Ibañez & Morales,

1987; Morales, Ibañez & Alonso, 1988; Valido, Alonso & Ibañez, 1990; Valido, Groh, Ibañez & Alonso, 1993) and Madeira (Groh & Hemmen, 1986), there is no comprehensive modern account of the Vitrinidae of the Azores. The present paper addresses this gap, and presents a revision of the vitrinid semi-slugs of the Azores based on extensive material collected over the last thirty years from throughout the archipelago.

THE HISTORY OF THE AZOREAN VITRINIDAE

The first description of vitrinids from the Azores was published by Morelet (1860) in his monumental *Histoire Naturelle des Açores*, following a trip in 1857 in which all the islands of the archipelago except São Jorge were visited. He described seven species in *Vitrina* Draparnaud, 1801, all new, from the islands of Santa Maria, São Miguel, Terceira and Flores: *pelagica* Morelet, 1860, *brumalis* Morelet, 1860, *laxata* Morelet, 1860, *brevispira* Morelet, 1860, *mollis* Morelet, 1860, *finitima* Morelet, 1860 and *angulosa* Morelet, 1860. Morelet's system for the Azorean *Vitrina* remained unchallenged until 1889 when Simroth (1889:5) grouped all seven Azorean species, together with a further three from Madeira (*ruivensis* Gould, 1848, *marcida* Gould, 1848, and *nitida* Gould, 1848) and five from the Canaries (*lamarcki* Férussac, 1821, *canariensis* Mousson, 1872, *reticulata* Mousson, 1872, *latebasis* Mousson, 1872 and *blaumeri* Shuttleworth, 1852), under the name *Vitrina pelagica*. He thus considered there to be a single species of vitrinid semislug throughout the Atlantic islands. Hesse (1923) included all the Atlantic vitrinid semislugs (together with the Arabian ones) in his new genus *Insulivitrina*, but recognised distinct

species for each of the three main archipelagos; the Azorean species were all synonymised under *pelagica*.

Six years later, Hoffmann (1929) revised the Atlantic-island vitrinids. His solution was to reduce Morelet's seven original Azorean species of *Vitrina* to three: *pelagica* (including *laxata*, as possibly a local form); *brumalis* (including *brevispira* and *finitima*, both thought to be juvenile forms); and *mollis* (including *angulosa*, which he also considered to be juvenile). Hoffmann's arrangement was subsequently taken up by Fischer-Piette (1946).

The most recent taxonomic treatment of the vitrinids of the Azores is that of Backhuys (1975). He reduced Morelet's seven species of *Vitrina* to two, one of which he considered to be a species complex, both placed within *Insulivitrina* Hesse, 1923, which he treated as a subgenus of *Phenacolimax* Stabile, 1859. His *pelagica* was restricted to Santa Maria and São Miguel, and included *laxata*. The *brumalis* species complex incorporated the remaining taxa, namely *mollis*, *finitima*, *brevispira*, and *angulosa*. He considered pigmentation to be a valuable diagnostic feature in separating these two taxa. Backhuys (1975:143), however emphasised that his conclusions were provisional, and stated that 'only future research can bring the problem to a definite solution'.

In addition to the seven *Vitrina* species, Morelet (1860) described a new species of vitrinid slug under the name *Viquesnelia atlantica* Morelet, 1960. *Viquesnelia* Deshayes, 1857 was based on a Romanian fossil shell. This attribution was shown to be erroneous by Stabile (1864) who erected a new monotypic genus, *Plutonia*, for *atlantica*. Zilch (1959) treated it as a subgenus of *Phenacolimax*. Shileyko (1986) included it as a full genus in his subfamily Phenacolimacinae, whereas Vaught (1989) placed it in its own subfamily Plutoniinae, both within the Vitrinidae.

Plutonia atlantica has recently been comprehensively redescribed by Wiktor & Backeljau (1995) who considered it to be sufficiently distinct from all other vitrinids to be placed in its own monotypic family Plutoniidae (formerly proposed as a subfamily of the Limacidae by Cockerell, 1893). Although its genital anatomy is remarkably similar to that of *Insulivitrina*, Wiktor and Backeljau believed the the lack of a penial retractor muscle, first noted by Simroth (1891:228), was sufficient to justify the new family. We will not attempt any further description of *P. atlantica*, which we believe to be a vitrinid.

The validity of Insulivitrina

Since Hesse (1923), the vitrinid semi-slugs of the Azores have been placed in *Insulivitrina*, usually as a subgenus

of *Phenacolimax* (e.g. Zilch, 1959; Backhuys, 1975). Indeed, excepting *Plutonia* and *Guerrina* Odhner, 1954, all the vitrinid semislugs of the northern Atlantic islands were originally united by Hesse (1923) in his new genus *Insulivitrina*, with *lamarcki* Férussac from the Canary Islands as the type species. Hesse also originally included the Arabian species *arabica* Thiele, 1910, but this was subsequently removed from *Insulivitrina* to a new genus, *Arabivitrina*, by Thiele (1931). However, there have been problems with the precise diagnosis of *Insulivitrina*, and definition of its taxonomic limits. Recently two cladistic studies have clarified this situation considerably (Alonso, Valido, Groh & Ibanez, 2000; Hausdorf, in press).

Alonso *et al.* (2000) addressed the problem of relationships within the vitrinid subfamily Phenacolimacinae of Shileyko (1986). They united the Macaronesian vitrinids in a single genus *Plutonia*, comprising five subgenera: *Plutonia sensu stricto*, *Guerrina*, *Insulivitrina*, *Madeirovitrina* Groh and Hemmen, 1986, and a new subgenus, *Canarivitrina*. *Plutonia sensu lato* was defined by the course of penial retractor muscle which, when present, 'loops round the optic nerve, passing below the right ommatophore retractor, then running backwards (left of the same right ommatophore retractor)' before inserting on the diaphragm. This is the condition in all those Azorean vitrinids having a penial retractor. In the analysis of Alonso *et al.* (2000) *Plutonia s.l.* appeared in an unresolved trichotomy with *Arabivitrina* and *Oligolimax* Fischer, 1878 (syn: *Gallandia* Bourguignat, 1880) which, together with *Phenacolimax*, comprised their subfamily Plutoniinae (syn: Phenacolimacinae).

Hausdorf (in press) undertook a phylogenetic analysis of the entire family Vitrinidae. He followed Alonso *et al.* (2000) in uniting all Macaronesian vitrinids under *Plutonia*. *Plutonia* was found to be the sister group of *Oligolimax* in his analysis, based on the course of the right ommatophoral retractor muscle, which 'does not pass between the penis and the female genitalia'. Hausdorf recommended against the use of subfamily groups in the Vitrinidae.

Thus it would appear that the Macaronesian vitrinids represent a monophyletic assemblage defined by the course of the penial retractor muscle, and should correctly be grouped together in the genus *Plutonia*. Alonso *et al.* (2000) included all the Azorean semislugs, and some from the Canaries, in the subgenus *Insulivitrina*. However, unlike *Madeirovitrina* and *Canarivitrina*, *Insulivitrina* does not appear to be supported by any autapomorphic characters in their analysis. Hausdorf (in press) considered *Insulivitrina* to be 'a paraphyletic group from which the other, more specialised

Macaronesian groups are derived'. Until the validity and relationships of these subgenera have been resolved, we prefer not to use subgeneric groupings within *Plutonia sensu lato*.

MATERIALS AND METHODS

Unless otherwise stated, all specimens listed are preserved in 70% ethanol following relaxation, and are housed in the collections of Prof. A. Frias Martins, University of the Azores, Ponta Delgada, São Miguel, Azores, Portugal. The abbreviation NHM refers to The Natural History Museum, London, U.K, where all Morelet's known Azorean vitrinid types are housed, and NMHM refers to the Museum National d'Histoire Naturelle, Paris.

Shell measurements are given to the nearest 0.1 mm as: maximum diameter × minimum diameter × maximum height; whorls are counted as described in Kerney and Cameron (1979). The abbreviations max.d./ht. and max.d./min.d. refer to the ratios 'maximum shell diameter:shell height' and 'maximum shell diameter: minimum shell diameter' respectively.

Distributional data are arranged by island, and then by site and date of collection. Key diagnostic characters in the descriptions are italicised.

SYSTEMATIC DESCRIPTIONS

Family VITRINIDAE Fitzinger, 1833

Genus *Plutonia* Stabile, 1864.

Type species by monotypy: *Viquesnelia atlantica* Morelet, 1860

Diagnosis: Vitrinidae in which the penial retractor muscle forms a loop around the optic nerve, passes below the right optic retractor, and then runs back left of the right optic retractor before inserting on the diaphragm.

Plutonia brevispira (Morelet, 1860)

Figs 1A–F, 2A, 3A–C, 4A–B.

Vitrina brevispira Morelet, 1860:148, pl.1, fig.6.

Vitrina brevispira Morelet. Drouët, 1861:146; Tristram, 1870:107; Pfeiffer, 1876:22;

Wollaston, 1878:15; d'Arruda Furtado, 1881:7; Milne-Edwards, 1885:316; Nobre, 1930:73.

Vitrina pelagica Morelet [part]. Simroth, 1889:5.

Insulivitrina pelagica Morelet [part]. Hesse, 1923:135.

Insulivitrina brumalis (Morelet) [part]. Hoffmann, 1929:231; Fischer-Piette, 1946:256.

Phenacolimax (Insulivitrina) brumalis (Morelet) [part]. Backhuys, 1975:144.

Types (Figs 1A–C): 3 syntypes NHM, 1893.2.4.1119–1121. [Santa Maria, Azores]. All ex Morelet Collection.

Other material: SANTA MARIA: Ribeira da Almagreira, 2.xi.1974; Cimo do Pico Alto, 12.x.1975; Pico Alto, 12.vi.1986; 21.x.1993; 21.vi.1994; 24.vi.1994; Vela, 12.vi.1990; 12.vi.1994; Calheta, 12.vi.1994; Cardal, 15.vi.1990; Base of Pico Alto, 16.vi.1990; 21.x.1993; Setadas, 21.vi.1994; Malbusca, 21.vi.1994; Alto Nascente, 22.vi.1994; Cavacas, 22.vi.1994; Road from Malbusca to Cavacas, 350m, 21.vi.1994.

External features: Body colour opaque-white 'opaline' in young animals, tending to become a more creamy brown in the adult. Mantle lobes covering almost the entire shell; heavily spotted with grey anteriorly, darker pigmentation extending posteriorly as an almost-black horseshoe-shaped mark on the left side, and as a line running through the pneumostome on the right. *A characteristic narrow dark line of pigment runs along a shallow groove obliquely across the right mantle lobe from above the pneumostome to near the posterior left margin of the lobe.* Sides of body deeply spotted with grey-black, becoming more intense dorsally.

Foot sole normally white or cream, but brown on some animals from Pico Alto, with pigmentation restricted to dark maculations on the inner margin of the lateral bands. Lack of spotting in the inner band characteristic, but a few weak spots noted on some individuals.

Shell (Figs 1A–F, 2A): Size range of dissected adult shell: 7.8–10.8 × 6.0–8.0 × 3.4–4.8mm; wh. 2.1–2.4 (largest syntype 7.2 × 5.0 × 3.2mm; wh. 2.3); max.d./ht 1.2–1.5; max.d./min.d. 2.0–2.4.

Entire shell smooth and shiny. Colour pale brown. When viewed from below, apertural membrane broad extending back as a spiral and reduced so as to virtually eliminate the columella, allowing the earlier whorls to be visible almost to the apex. Spire relatively flat, but shell profile more elevated than *P. finitima*, which shares the greatly reduced lower apertural margin.

Radula and jaw (Figs 3A–C): Central tooth with pointed mesocone and ectocones; laterals with strong, single-, rarely double-pointed ectocone and weak endoconal cusp about 1/3 down the edge; marginals long, sharp, pointed and slightly curved, lacking serrations or lateral cusps. Jaw of the oxygnath type, as in *P. brumalis* (Fig. 13A).

Reproductive system (Figs 4A–B): Atrium shorter than either penis or free oviduct, but longer than the vagina; spermatheca stalk equal to or slightly longer than head, which is elongate rather than rounded and opening into the vagina. Stimulator (vaginal gland) absent, internal vaginal wall smooth.

Penis somewhat longer than atrium and vagina combined; vas deferens inserting laterally; retractor muscle inserting subterminally on the penis, just below its apex; penial retractor passing under the right optic

retractor and anterior to then back over the optical retractor nerve prior to insertion on the lower lung wall.

Internally, penis with three longitudinal fold-like pilasters, the two largest lie one below the other, the third much shallower and broader, level with the lower of the other two. The upper of the two larger pilasters greatly expanded at its lower half and covers an extensive glandular patch into which vas deferens opens; this pilaster extends upwards into the thin-walled head of the penis. A

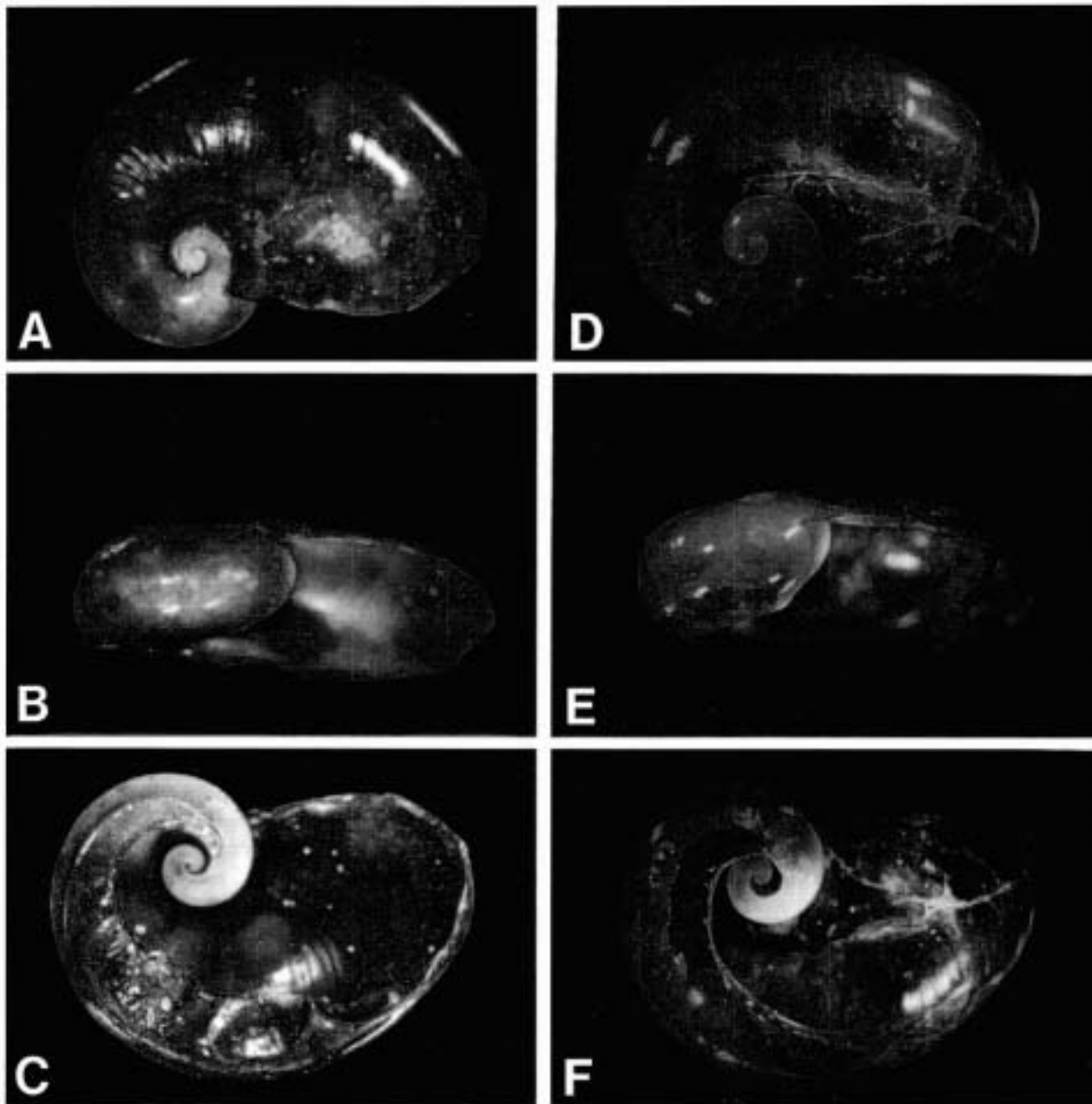


Figure 1. *Plutonia brevispira*. Shell. A–C. Syntype, Santa Maria, ex Morelet Collection (NHM 1893.2.4.1119). Shell width 7.4mm. D–F. Cimo do Pico Alto, Santa Maria, 9.x.1975. Shell width 9.2mm.

VITRINID SEMISLUGS OF THE AZORES

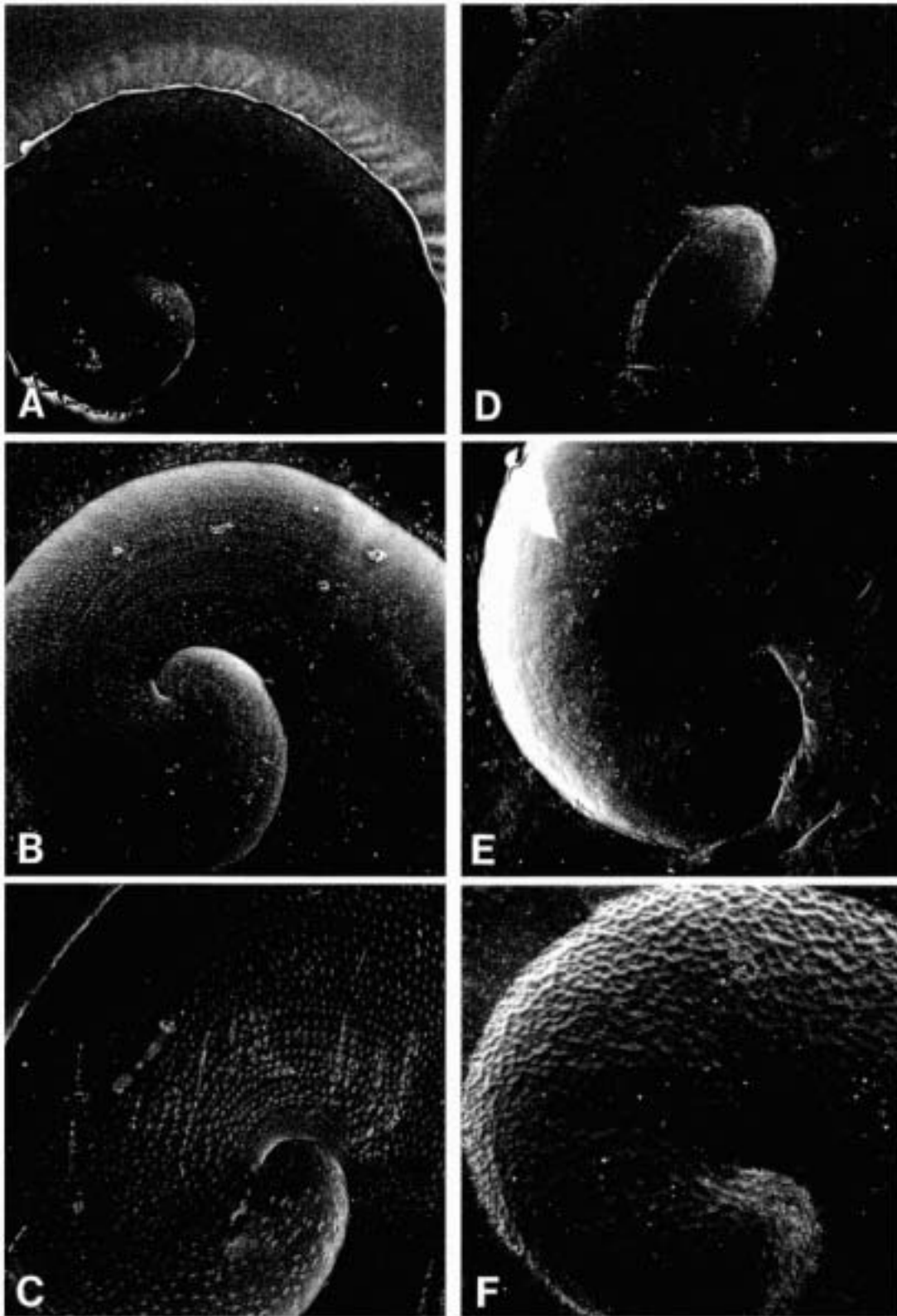


Figure 2. Protoconch sculpture. **A.** *Plutonia brevispira*. Ribeira da Almagreira, Santa Maria, 2.xi.1974. x100. **B.** *P. pelagica*. Pico Alto, Santa Maria, 21.x.1993. x100. **C.** *P. laxata*. Pico da Praia, Água Retorta, São Miguel, 24.x.1974. x150. **D.** *P. brumalis*. Arrasto, Água Retorta, São Miguel, 22.ii.1989. x150. **E.** *P. finitima*. Lomba, Corvo, 22.vii.1994. x150. **F.** *P. angulosa*. Pico Alto, Santa Maria, 480m. 21.x.1993. x150.

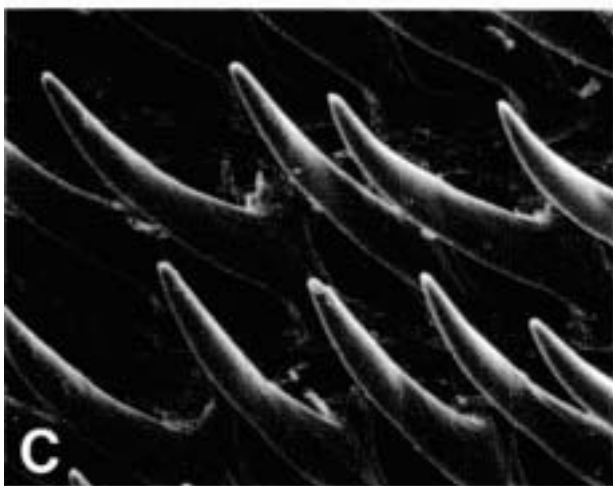
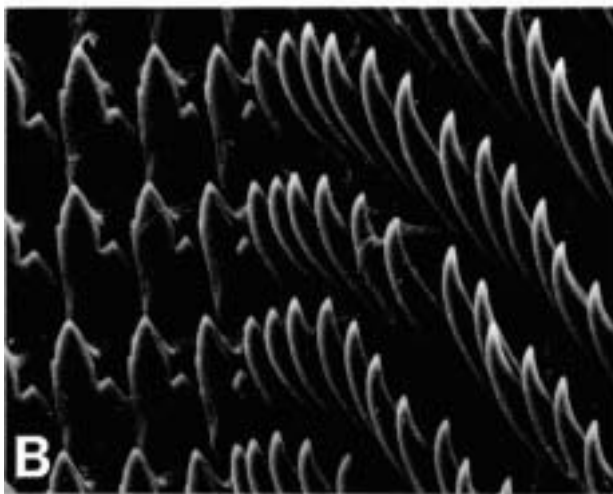
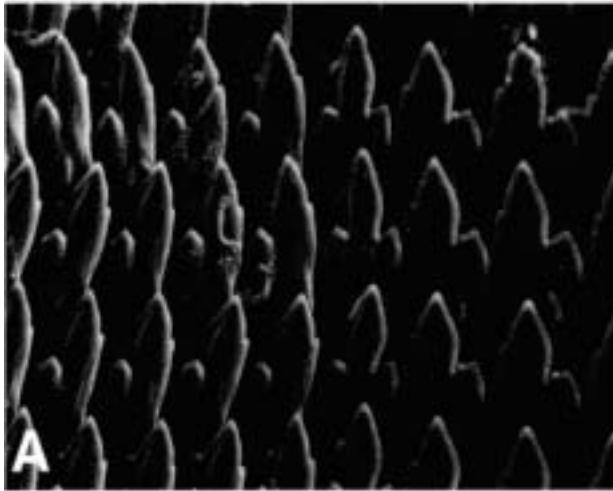


Figure 3. *Plutonia brevispira*. Radula. Ribeira da Almagreira, Santa Maria, 2.xi.1974. **A.** Central and lateral teeth, $\times 500$. **B.** Lateral and marginal teeth, $\times 500$. **C.** Marginal teeth, $\times 1000$.

large elongate patch covered with numerous small, conical structures runs down from base of glandular area, at the level of the two lower pilasters, and extends down into thin-walled pouch situated at the top of the atrium. Two additional weak ridge-like pilasters; one running from the lower penis wall up into vagina, the second extending most of the length of the atrium.

Distribution: This species is restricted to the Santa Maria, where it occurs on the wetter, more elevated parts of the island; we have found no material from São Miguel and presume this reference to have been an error on Morelet's part. It lives microsympatrically with both *P. angulosa* and *P. pelagica* on the top of Pico Alto at around 500m, and throughout the rest of its range (except at Vela) with *P. pelagica* alone.

Remarks: The reproductive system of *P. brevispira* differs fundamentally from that of any other Macaronesian vitrinid. In lacking any elaboration of the female genitalia it resembles *Vitrina media* Lowe from Madeira as described by Groh & Hemmen (1986), which was included in *Plutonia* by Hausdorf (in press).

The penis of *brevispira* is unique within the described Vitrinidae in its highly elaborate internal anatomy, incorporating two very large flap-like folds and a longitudinal pad, part of which is covered with sharply pointed, downwardly directed papillae, giving it an almost spiny appearance. This last structure resembles the internal penial structure of *Plutonia behnii* (Lowe) from Madeira, as described and illustrated by Odhner (1937:354, figs 1 and 2) under the name *Vitrina ruivensis* Gould, as follows: 'in one specimen, the ridges between the furrows bore, in the median large fold, a series of weak, conical papillae increasing in size towards the front and pointing forwards'. In this respect, *P. behnii* apparently differs from that of all other Madeiran vitrinids (Groh & Hemmen, 1986). The individual papillae in *P. brevispira* are over twice the size of the largest illustrated for *P. behnii*, even though *P. behnii* is a very much larger animal (Odhner gives a total length of 50mm, as compared with about 30mm for the largest *P. brevispira*). Nor are the papillae arranged in transverse rows as in *behnii*, and certainly there is no evidence of the furrows, or of the regular increase in size, to which Odhner refers. Finally, the papillae of *P. behnii* are figured as having rounded tips, whereas those of *brevispira* at the same magnification appear sharply pointed. Histologically the papillae of *brevispira* show no evidence of secretory activity, and the heavily thickened walls of the cells comprising the backwardly-directed tips of the papillae are compatible with having a function as spines

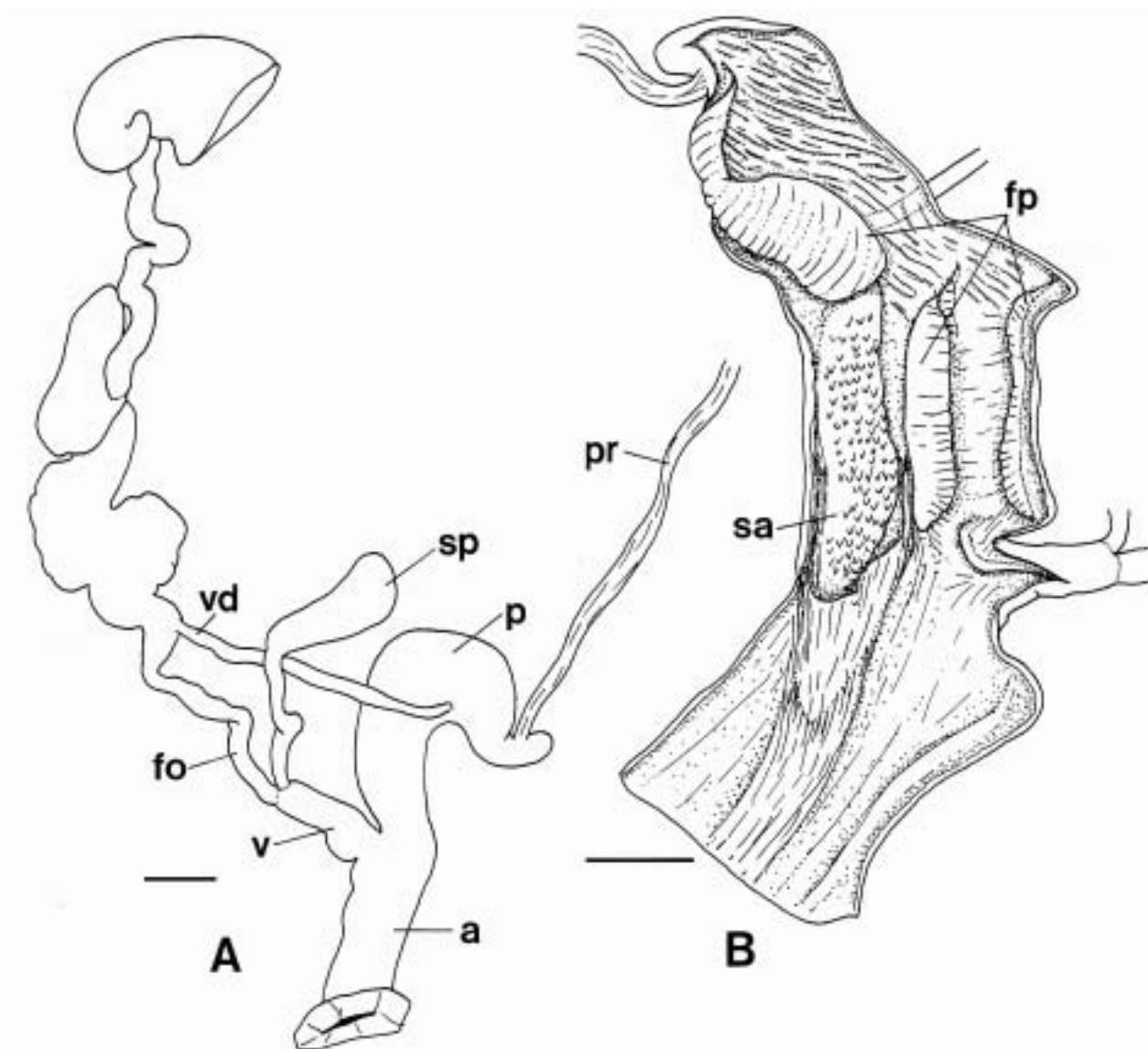


Figure 4. *Plutonia brevispira*. Ribeira da Almagreira, Santa Maria, 2.xi.1974. **A.** Reproductive system. **B.** Internal anatomy of the penis. Scale bars 2mm.

Abbreviations: a, atrium; fo, free oviduct; fp, fold-like pilaster; p, penis; pr, penial retractor muscle; sa, spiny area; sp, spermatheca; v, vagina; vd, vas deferens.

designed to retain the penis within the vagina during copulation. Furthermore, this putative function for the spines is in agreement with Forcart's (1949) hypothesis that all vitrinids lacking a stimulator have internal copulation, as opposed to groups like *Phenacolimax* and other *Plutonia sensu lato* in which sperm exchange is thought to be external. It therefore appears unlikely that these papillae could be homologous in the two species, even though their gross appearance and positioning are broadly similar.

Plutonia pelagica (Morelet, 1860)

Figs 2B, 5A–F, 6A–B.

Vitrina pelagica Morelet, 1860:143, pl.1, fig.2.

Vitrina pelagica Morelet. Drouët, 1861:143; Tristram, 1870:107; Pfeiffer, 1876:21; Wollaston, 1878:16; d'Arruda Furtado, 1881:7; Milne-Edwards, 1885:316. [part], Simroth, 1889:5; Nobre, 1930:73.

Insulivitrina pelagica (Morelet) [part]. Hesse, 1923:135; Hoffmann, 1929:231; Fischer-Piette, 1946:256.

Phenacolimax (Insulivitrina) pelagica (Morelet) [part].
Backhuys, 1975: 144.

Types: (Figs 5A–C) Neotype here selected, in accordance with Article 75.3 of the *International Code of Zoological Nomenclature*, in order to clarify the taxonomic status of *V. pelagica*; NHM, 1998184. From the type locality. Pico Alto, Santa Maria, Azores, 480m. Leg. A.M.F.Martins & P.B.Mordan, 21.x.1993. Type

material of this species cannot be located either in the Morelet collection in the NHM, or the collections of the MNHN. The specimen is in agreement with the original description and figure given by Morelet (1860).

Other material: SANTA MARIA: Ribeira da Almagreira, 2.xi.1974; Pico Alto, 480m., 21.x.1993; 21.vi.1994; 24.vi.1994; Calheta, 12.vi.1994; Cardal, 15.vi.1990; Chão do João Tomé, 15.vi.1990; Base of Pico Alto, 16.vi.1990;

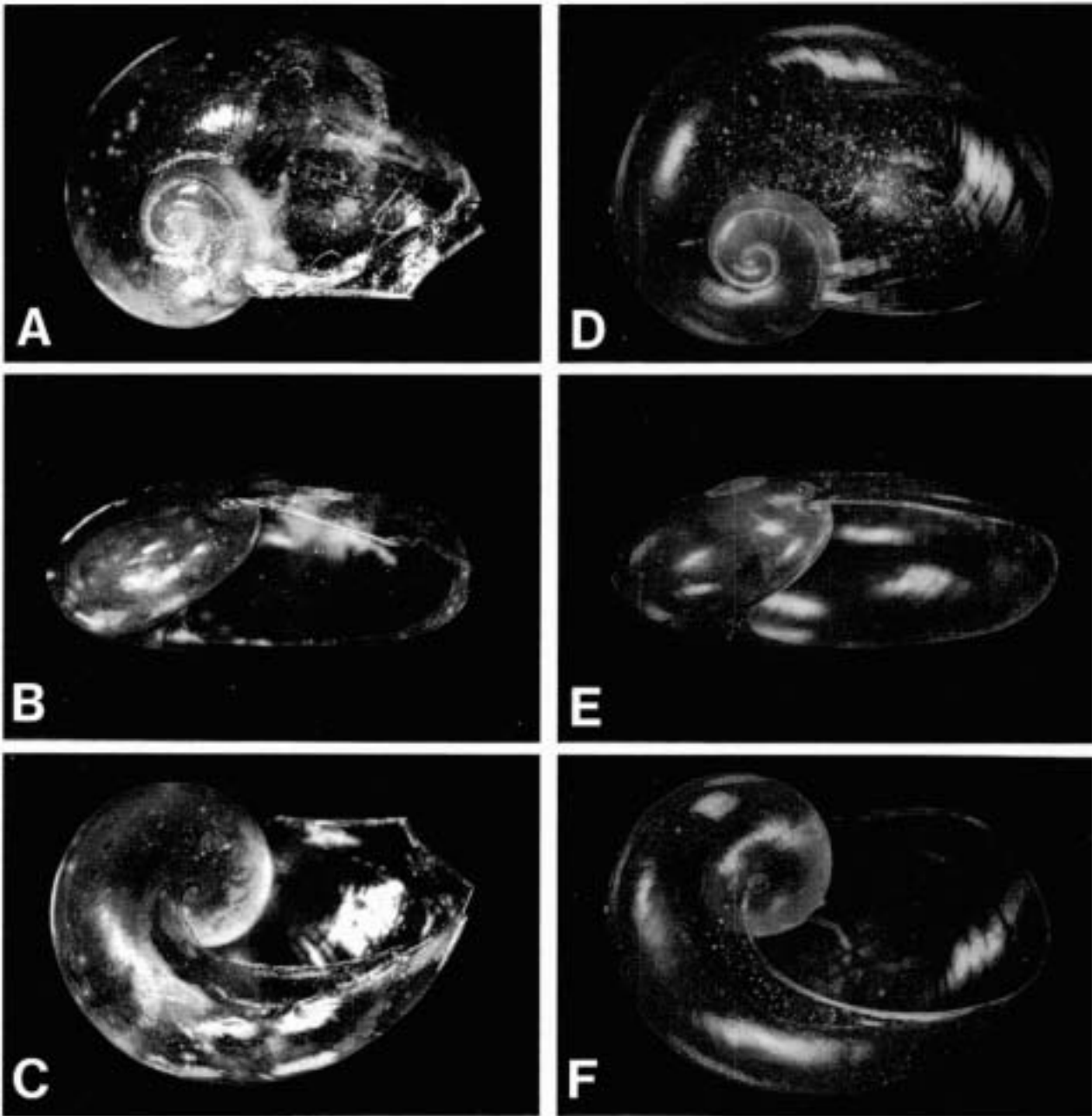


Figure 5. *Phytotia pelagica*. Shell. A–C. Neotype. Pico Alto, Santa Maria 21.x.1993. NHM 1998184. Shell width 7.1mm. D–F. Cimo do Pico Alto, Santa Maria, 9.10.1975. Shell width 7.1mm.

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21.x.1993; Setadas, 21.vi.1994; Malbusca, 21.vi.1994; Alto Nascente, 22.vi.1994; Cavacas, 22.vi.1994; Road from Malbusca to Cavacas, 350m.

External characters: Background body colour pale cream, but with distinct pinkish tinge. Rich-brown U-shaped kidney clearly visible under exposed area of shell. Left mantle lobe only covering the anterior part of shell; right lobe larger, but not as extensive as in *P. brevispira*, the two lobes covering most of shell in living animal. Mantle covered in black spotting, with a black line on the right side which runs through the pneumostome. Surface of mantle with diagonal groove extending backwards from top of pneumostome

Sides of body covered with irregular dark spots, as are the sides of the tail, which has a weak, unpigmented, shallow median longitudinal groove extending almost to its tip.

Sole of foot pinkish purple with widely spaced black spots all over, which are especially pronounced on the

median band; both spotting and background colour are densest towards the inner margin of lateral bands.

Shell (Figs 2B,5A–F): Size range of dissected adult shell: 7.1–9.5 × 5.0–6.8 × 3.1–4.2mm; wh. 2.4–2.5 (neotype 7.2'5.1 × 3.5; wh. 2.5); max.d./ht 1.2–1.5; max.d./min.d. 2.0–2.4.

Protoconch sculpture spiral rows of puncta; remainder of shell with smooth, shiny appearance; umbilicus slightly open. Colour pale brown. Spire gently rounded, giving the shell a smoothly oval profile.

Radula and jaw: Radula as in *laxata* and *finitima* (Fig. 18A,B), with marginals lacking an ectocone. Jaw as in *brumalis* (Fig. 13A).

Reproductive system (Figs 6A–B): Vagina considerably shorter than either atrium or free oviduct; spermathecal stalk approximately same length as its head.

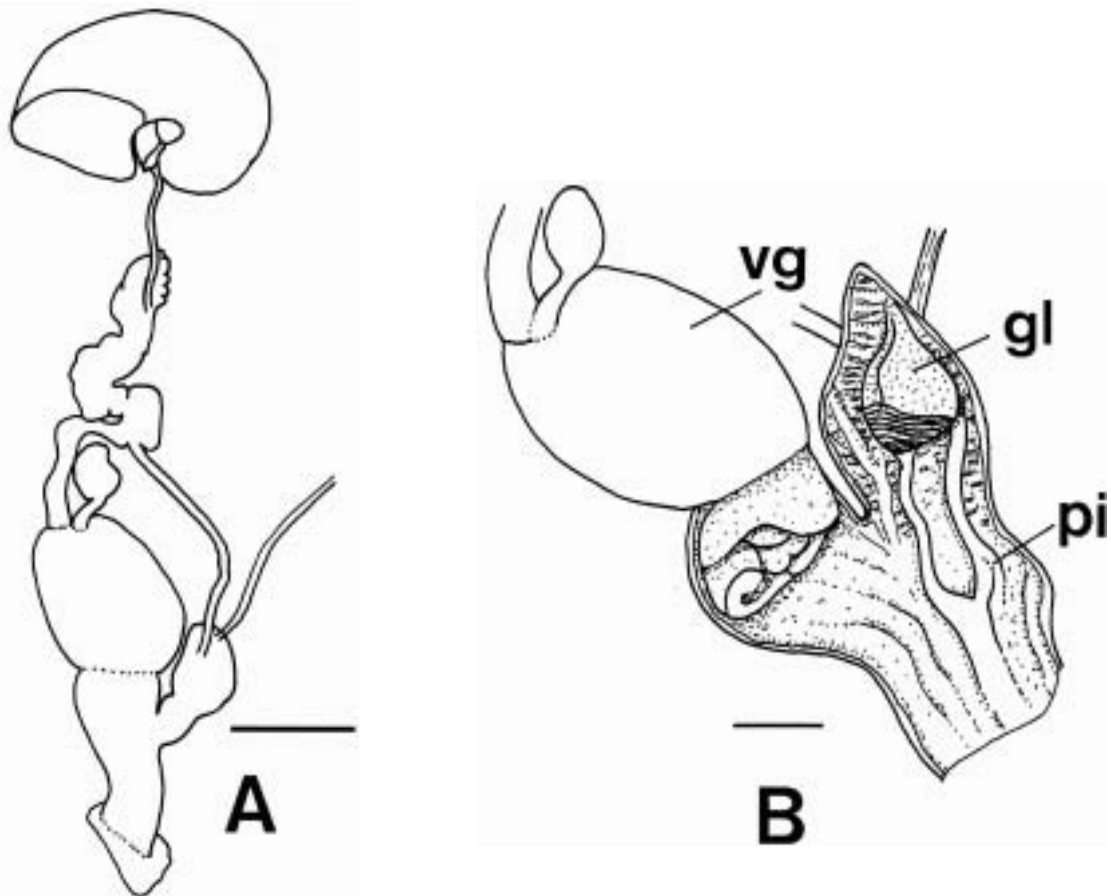


Figure 6. *Plutonía pelagica*. Pico Alto, Santa Maria, 21.x.1993. **A.** Reproductive system. Scale bar 2mm. **B.** Internal anatomy of basal reproductive system. Scale bar 1mm. Abbreviations: gl, glandular pad; pi, pilaster; vg, vaginal gland.

Vaginal gland present, and about same length as vagina and atrium combined. Internal walls of the vagina smooth. *Stimulatory papilla encircled by a large, irregularly convoluted fold, the surface of which is highly glandular.*

Penis appearing relatively large because of shortness of vagina and atrium; vas deferens inserting laterally; retractor muscle inserting laterally on the penis, just below its apex, and passing under the right optic retrac-

tor and anterior to then back over the optical retractor nerve prior to insertion on the lower lung wall. Internal penial wall with wavy transverse folds; containing a prominent glandular pad around pore of vas deferens, the lower part of which has distinct, lamellate structure. Two parallel pilasters, one continuous with base of glandular pad, run longitudinally in the penis and join outside penis to form a single thicker pilaster running down the atrium

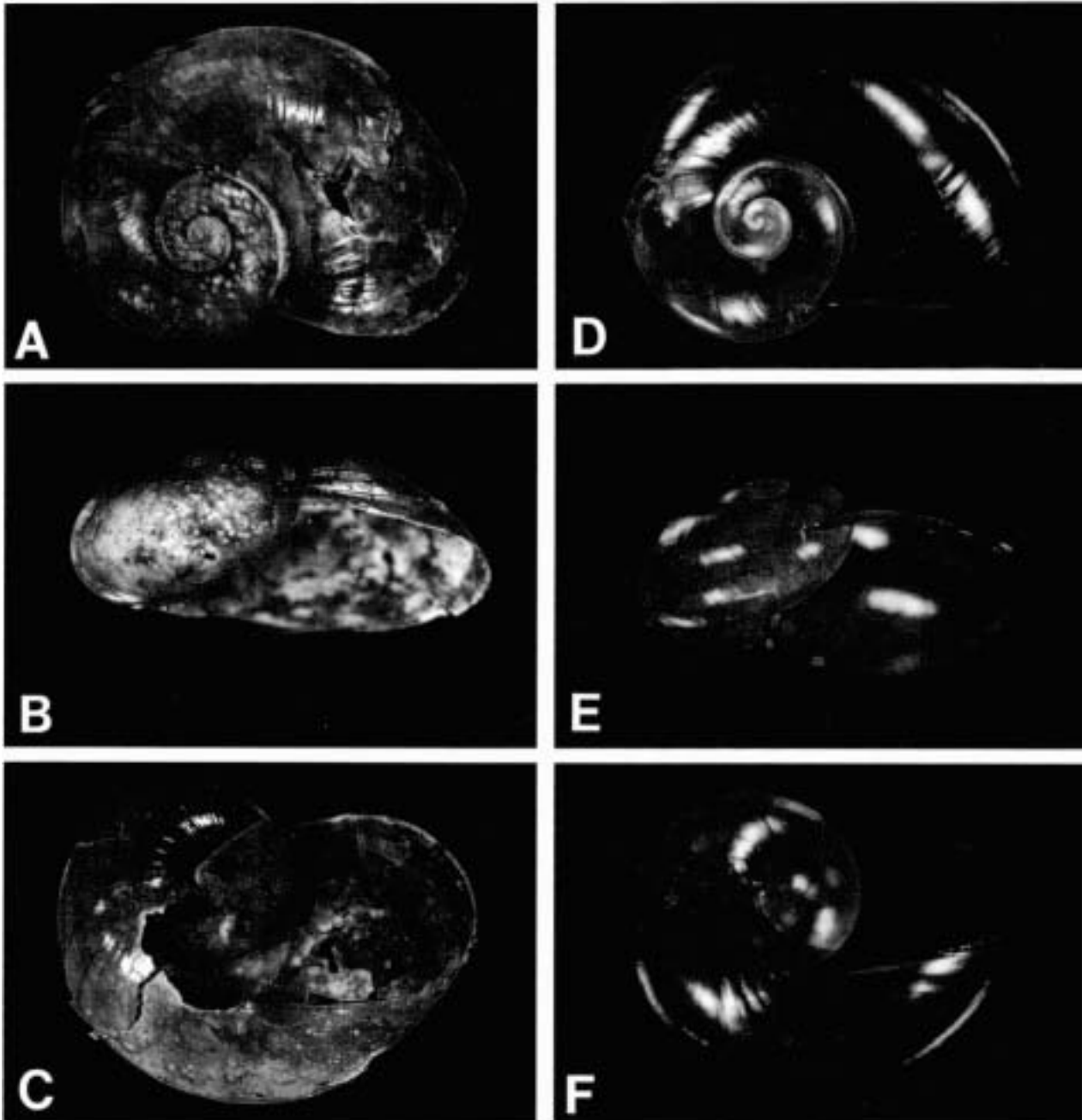


Figure 7. *Plutonia laxata*. Shell. A-C. Lectotype. São Miguel, Ex Morelet Collection, NHM 1993.2.4.1098. Shell width 11.7mm. D-F. Sete Cidades, São Miguel, 8.iii.1975. Shell width 8mm.

Distribution: Range as for *P. brevispira*; it is restricted to the Santa Maria where it occurs on the wetter, more elevated parts of the island. It lives microsympatrically with both *P. brevispira* and *P. angulosa* on the top of Pico Alto at around 500m, and throughout the rest of its range with *P. brevispira*.

***Plutonia laxata* (Morelet, 1860)**

Figs 2C, 7A–F, 8A, 9A–C.

Vitrina laxata Morelet, 1860:144, pl.1, fig.3.

Vitrina laxata Morelet. Drouët, 1861:142; Tristram, 1870:107; Pfeiffer, 1876:21; Wollaston, 1878:16; d'Arruda Furtado, 1881:7; Milne-Edwards, 1885:316; Nobre, 1930:73.

Vitrina pelagica Morelet [part]. Simroth, 1889:5.

Insulivitrina pelagica (Morelet) [part]. Hesse, 1923:135; Hoffmann, 1929:231; Fischer-Piette, 1946:256.

Phenacolimax (Insulivitrina) pelagica (Morelet) [part]. Backhuys, 1975: 144.

Types: (Figs 7A–C) Lectotype here selected in accordance with Article 74.7 of the *International Code of Zoological Nomenclature*, as the syntype series also contains *P. brumalis*. Lectotype NHM, 1893.2.4.1098 (largest specimen) and 4 paralectotypes NHM, 1893.2.4.1099–1102 (the smallest of which is *P. brumalis*). [São Miguel, Azores].

Other material: SÃO MIGUEL: Rosário, Vila Franco do Campo, 23.ix.1970; Pico da Praia, Água d'Alto, 25.ix.1970*; 24.x.1974; Sete Cidades, 8.iii.1975; Abelheira, Fajã de Baixo, 26.vii.1989; Arrasto, Água Retorta, 22.ii.1989*; Ribeira do Tosquiado, 3.viii.1989; 6.xii.1996*; Caminho de Penetração do Saragaço, Main road to Faial Terra, 27.x.1993; Canto dos

Carneiros, Sete Cidades, 17.vi.1994; Outeiro Açougues, 600m, 1.xii.1996+; Pico da Vara, 990m, 1.xii.1996* +; Above Algarvia, c. 400m, 17.ix.1998*+; Prainha do Lombo Gordo, 50m, 19.ix.1998.

* sympatric with *P. brumalis*; + protoconch not punctate.

External characters (Fig. 8A): Overall impression is of black spotting on a clear white background. Upper body whorls rather pale, combined with pale shell coloration giving a distinctly greyish appearance to occupied shell. Mantle with large black spots which coalesce to form prominent lateral stripe running antero-posteriorly on right side, which embraces pneumostome; typically also a broad dark spot or stripe in a more central position; right lobe more lateral, more obviously rounded, thicker and less extensive than in *P. brumalis*; diagonal groove running from top of pneumostome prominent and *darkly pigmented*. Sides of body with regular dark spots *which do not coalesce to form a lateral body stripe, or distinct solid black lateral tail stripes*; dark stripes behind optic tentacles remain interrupted.

Central foot band pale in juveniles, but may become as darkly spotted as the lateral bands of adult; lateral foot bands spotted with *large black maculations, which are not noticeably denser at inner margin*.

Shell (Figs 2C, 7A–F): Size range of dissected adult shell: 8.2–10.7 × 5.8–7.7 × 4.2–5.5mm; wh. 2.3–2.7 (lectotype 10.2 × 7.5 × 5.2mm; wh. 2.7); max.d./ht 1.4–1.4; max.d./min.d. 1.5–2.0.

Protoconch normally *finely punctate with pits arranged in spiral rows*; punctations very reduced or lacking in specimens from some of the western-most localities. Remainder of shell glossy, rather than shiny, in appearance owing to spiral thickenings and weak radial growth lines. Colour very pale grey-brown.



Figure 8. Living animals. Sete Cidades, São Miguel, 8.iii.1975. **A.** *Plutonia laxata* **B.** *P. brumalis*.

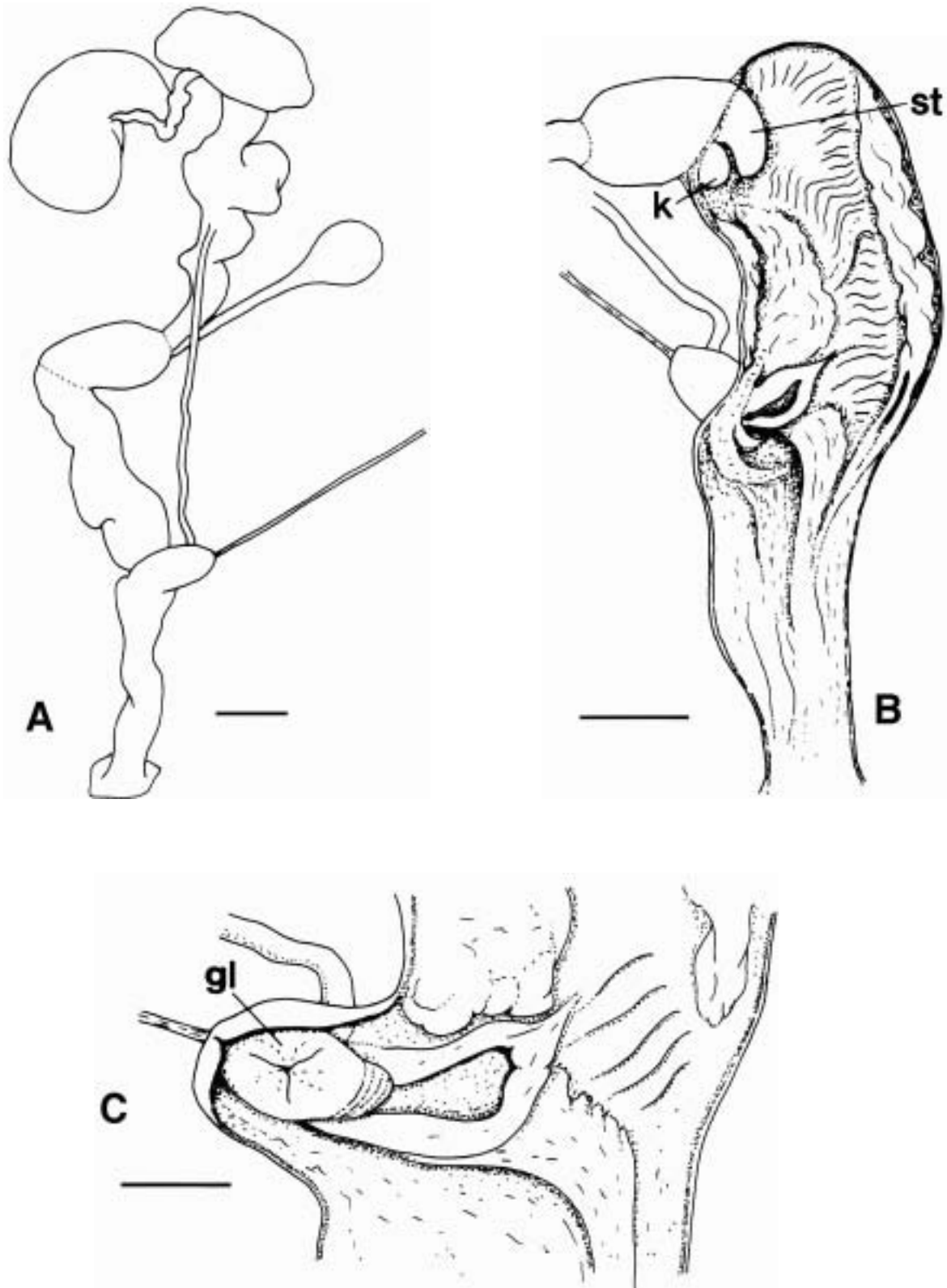


Figure 9. *Plutonia laxata*. Ribiera do Tosquiado, São Miguel, 6.xii.1996. **A.** Reproductive system. Scale bar 2mm. **B.** Internal anatomy of basal reproductive system. Scale bar 2mm. **C.** Detail of penis. Scale bar 1mm. Abbreviations: gl, glandular pad; k, knob; st, stimulatory papilla.

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Whorls expanding more regularly than *P. brumalis*, and aperture more downwardly deflected. Umbilicus only slightly open. Spire slightly more elevated than in *pelagica*, giving a rather less flattened profile.

Radula and jaw: As in *P. pelagica* and *P. finitima* (Fig. 18A,B), with radular marginals lacking an ectocone. Jaw as in *P. brumalis* (Fig. 13A).

Reproductive system (Figs 9A–C): Atrium similar in length to the vagina and free oviduct; spermathecal

stalk variable, between 1.5 and 5-times length of head. Vaginal gland with relatively weak stimulatory papilla. Vagina with well-developed, *greatly thickened, convoluted longitudinal pilaster*, more prominent than in *brumalis*, which terminates abruptly at about level of penial insertion; *knob-like structure present at top of pilaster*; wall opposite bears strong, regular transverse corrugations in older animals.

Penis small, with lateral vas deferens insertion; retractor muscle inserting sublaterally, just below its apex, and passing under the right optic retractor and

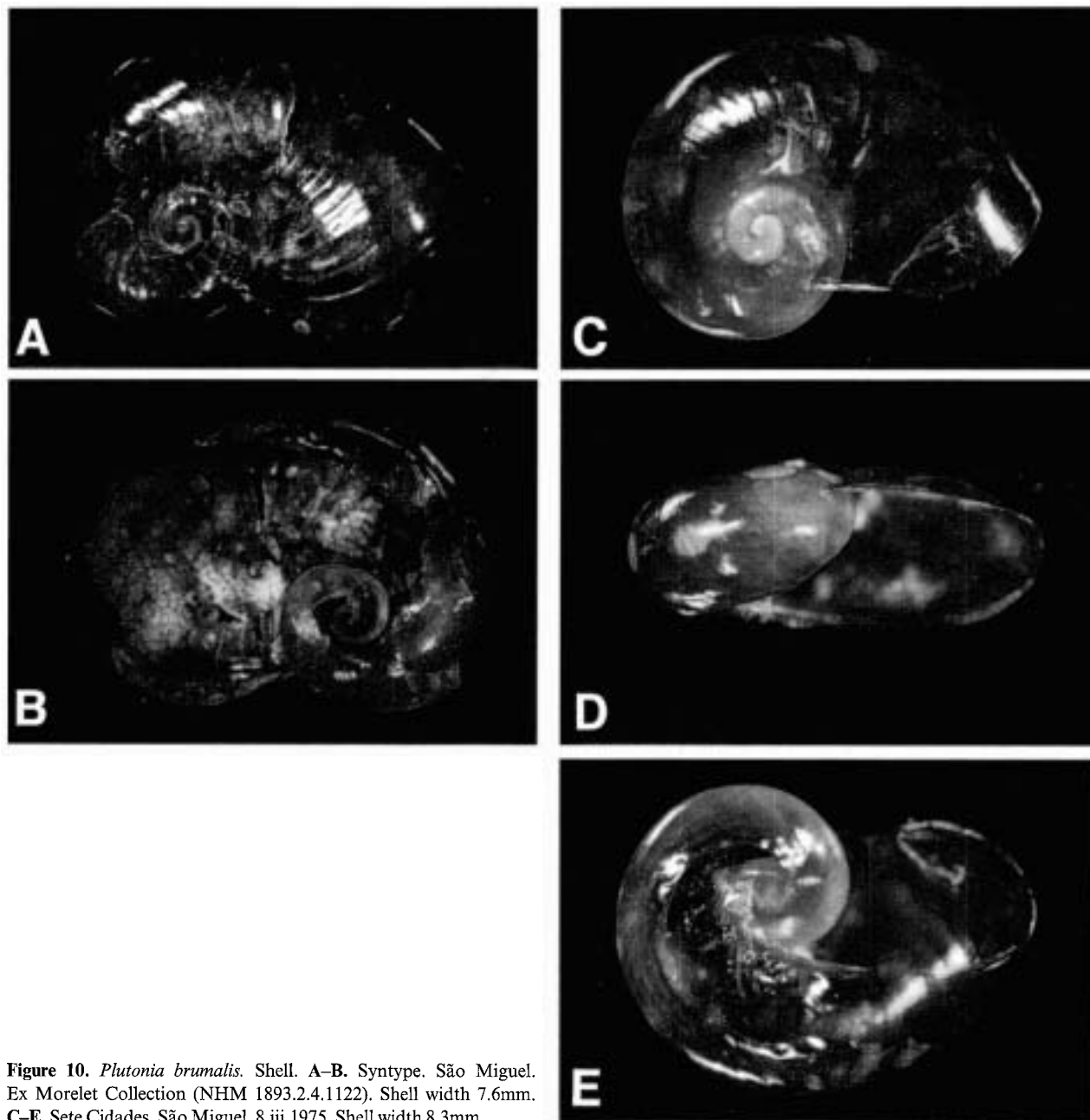


Figure 10. *Plutonia brumalis*. Shell. A–B. Syntype. São Miguel. Ex Morelet Collection (NHM 1893.2.4.1122). Shell width 7.6mm. C–E. Sete Cidades, São Miguel, 8.iii.1975. Shell width 8.3mm.

anterior to then back over the optical retractor nerve prior to insertion on the lower lung wall. Internally has large yellowish glandular pad which is broadly attached to penis wall rather than narrowly suspended, and has a well-defined, transversely lamellate basal region. This bounded by two short, thick muscular pilasters which meet but barely fuse. Weak atrial pilaster not an extension of penial pilasters.

Distribution: Restricted to the island of São Miguel, where it occurs throughout the altitudinal range almost to the top of Pico da Vara (c. 1000m). It is found in both the eastern and western parts of the island, often sympatrically with *P. brumalis* (see list of material). We have found no *P. laxata* on any other islands in the Archipelago and assume Morelet's record from Santa Maria to be an error; it may be that

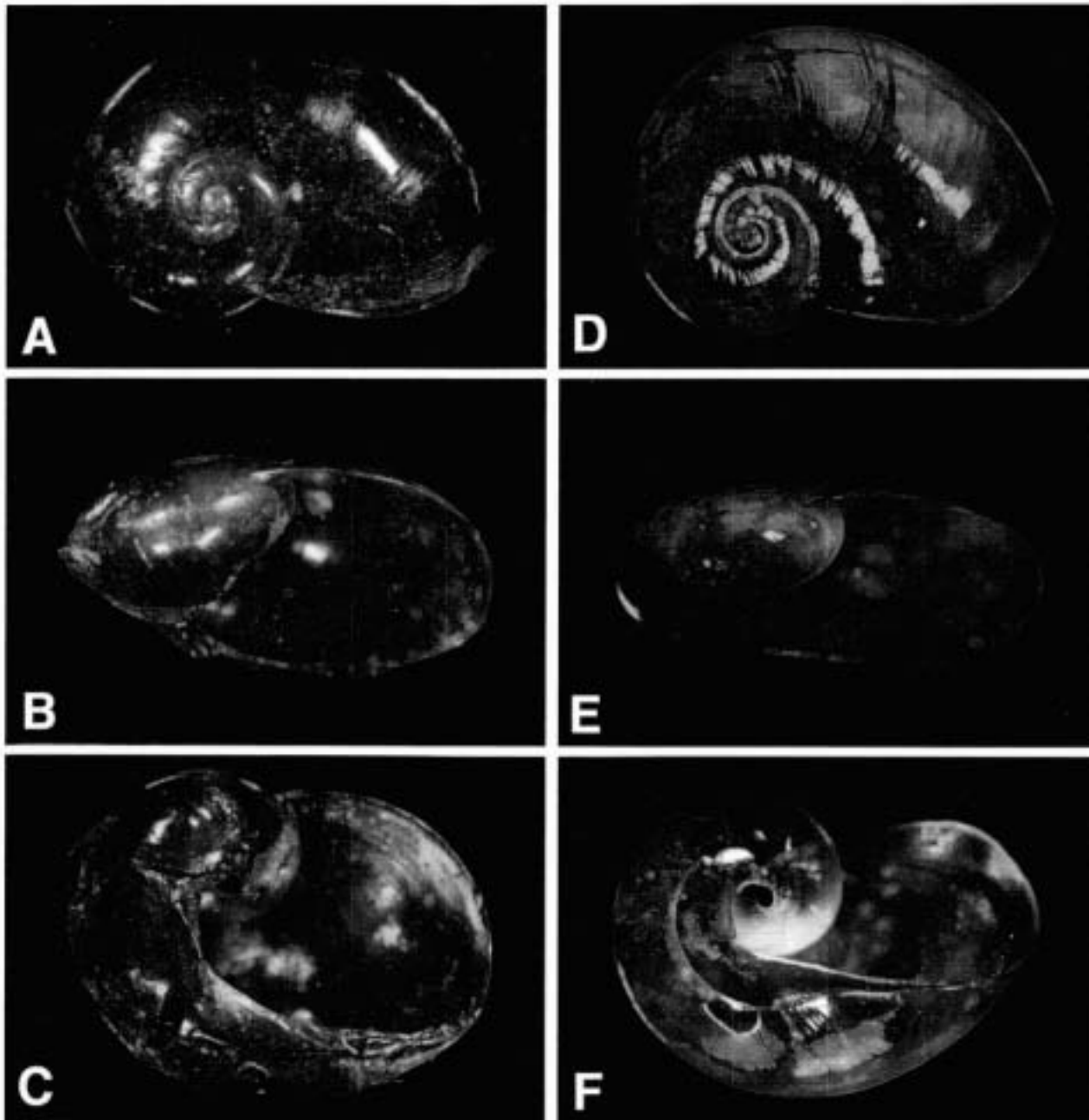


Figure 11. *Phutonia brumalis*. A–C. Syntype of *Vitrina mollis*, Terceira, Ex Morelet Collection (NHM 1893.2.4.1103). Shell width 8mm. D–F. Fajã de São João, São Jorge, 17.3.1996. Shell width 8.8mm.

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Morelet confused this species with *P. pelagica* from Santa Maria in which the columellar margin of the shell is not greatly reduced, and which also has a punctate protoconch (though the latter was not noted by Morelet).

Remarks: Specimens from two of the eastern sites, Pico da Vara and Algarvia, appear to lack punctations on the protoconch, whilst in those from nearby Ribeira

do Tosquiado these punctations are extremely faint (see list of material examined). In all other respects these samples resemble true *P. laxata*. Morelet's type series includes both punctate and non-punctate shells.

A transversely lamellate glandular area in the penis of the type found in *laxata* and *pelagica*, and referred to as a pilaster, has been described in two species of *Arabivitrina* from Arabia by Neubert (1998).

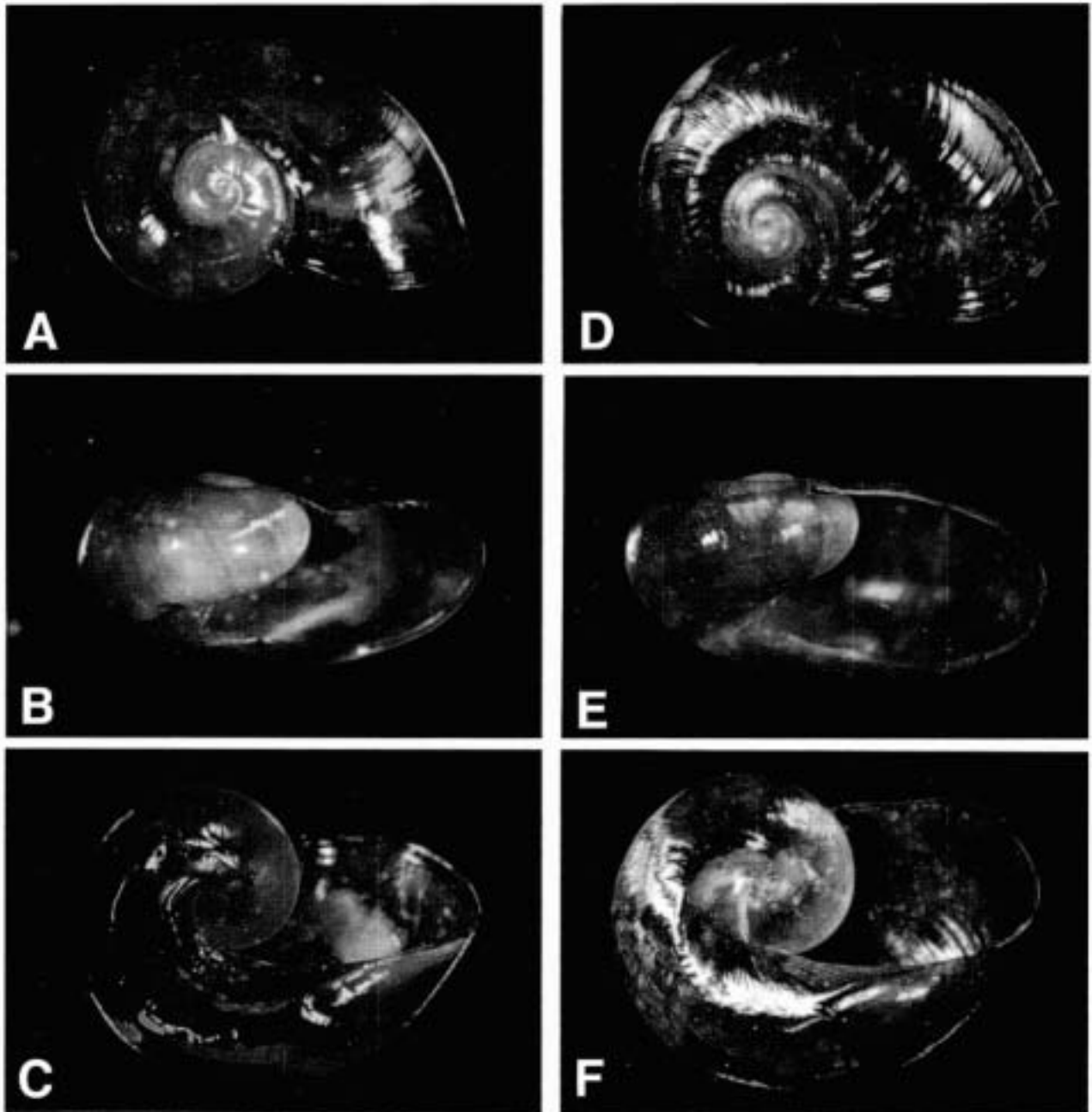


Figure 12. *Plutonia brumalis*. Shell. A–C. Corre Água, Pico, 28.vi.1991. Shell width 8mm. D–F. Ribeirinha, Faial, 6.ii.1990. Shell width 10mm.

Plutonia brumalis (Morelet, 1860)

Figs 2D, 8B, 10A–E, 11A–F, 12A–F, 13A–C, 14A–B, 15A–C, 16A–B.

Vitrina brumalis Morelet, 1860:146, pl.1, fig.4.
Vitrina mollis Morelet, 1860:147, pl.1, fig.5.
Vitrina brumalis Morelet. Drouët, 1861:146; Tristram, 1870:107; Pfeiffer, 1876:22; Wollaston, 1878:14; d'Arruda Furtado, 1881:7; Milne-Edwards, 1885:316; Nobre, 1930:73.
Vitrina mollis Morelet. Drouët, 1861:144; Tristram, 1870:107; Pfeiffer, 1876:22; Wollaston, 1878:14; d'Arruda Furtado, 1881:7; Milne-Edwards, 1885:316; Nobre, 1930:73.
 ? *Vitrina brumalis* Morelet. de Guerne, 1888:104 [Caldeira de Faial]. [Specimen from same locality has genitalia figured by Simroth, 1889, pl.2,fig.15.]
Vitrina pelagica Morelet [part]. Simroth, 1889:5.
Insulivitrina pelagica (Morelet) [part]. Hesse, 1923:135.
Insulivitrina brumalis (Morelet) [part]. Hoffmann, 1929:231; Fischer-Piette, 1946:256.
Insulivitrina mollis (Morelet) [part]. Hoffmann, 1929:231; Fischer-Piette, 1946:256.
Vitrina laxata Morelet. Nobre, 1930:73.
Phenacolimax (Insulivitrina) brumalis (Morelet) [part]. Backhuys, 1975: 144.

Types: Syntype of *Vitrina brumalis* (Figs 10A–B); NHM, 1893.2.4.1122 [São Miguel, Azores]; 3 syntypes of *Vitrina mollis* (Figs 11A–C); NHM, 1893.2.4.1103-1105 [Terceira, Azores].

Other material: SÃO MIGUEL: Lameiro, NHM, 1903.10.8.47 (shell); Pico da Praia, Água d'Alto, 25.ix,1970#; Sete Cidades, 8.iii,1975; Muro do Carvão, 5.ii.,1988; Pico do Canário, 9.iv.,1988; Arrasto, Água Retorta, 22.ii.,1989#; Grota da Fajã da Areia, Ribeira do Tosquiado, 3.viii.,1989; 19.ii.92; 2.xii.,1996; Ribeira do Canário, 6.viii.,1989; Salto do Cavalo, 9.x.,1991; Ponte despe-te-que-suas, 100m., 30.xi.,1996; 2.xii.,1996#; Tronqueira, Miradouro, 2.xii.,1996; 1.xii.1996; Pico da Vara, 990m, 1.xii.,1996#; Sete Cidades, 3km. Lagoa Verde, 20.vi.,1997; Above Algarvia, c. 400m, ix.,1998#. FAIAL: Above Horta, NHM, 1903.10.8.49-51; Ribeirinha, 6.ii.,1990; Fontenário, 190m, 12.x.,1993; Caldeira, 800m, 12.x.,1993; 500m east of lighthouse, Capelinhos, 90m, 12.x.,1993. PICO: Corre Água, 28.vi.,1991; Acima do Cais do Pico, 800m, 14.ii.,1995. TERCEIRA: Caldeira de Santa Barbara, 29.xii.,1975; 13.viii.,1987; 28.vi.,1994; Tombo Canada da Fronte Biscoitos, 12.viii.,1987; 27.vi.,1994; Caldeira Guilherme Moniz, 11.ii.,1976; Pico do Gaspar, 12.viii.,1987; 26.vi.94; Mata da Serreta, 29.vi.94; Pico Alto, 27.vi.94; 1.vii.94; SÃO JORGE: Above Calheta, NHM, 1903.10.8.80 (shell); Fajã da Ribeira da Areia, 16.iii.,1996..

sympatric with *laxata*.

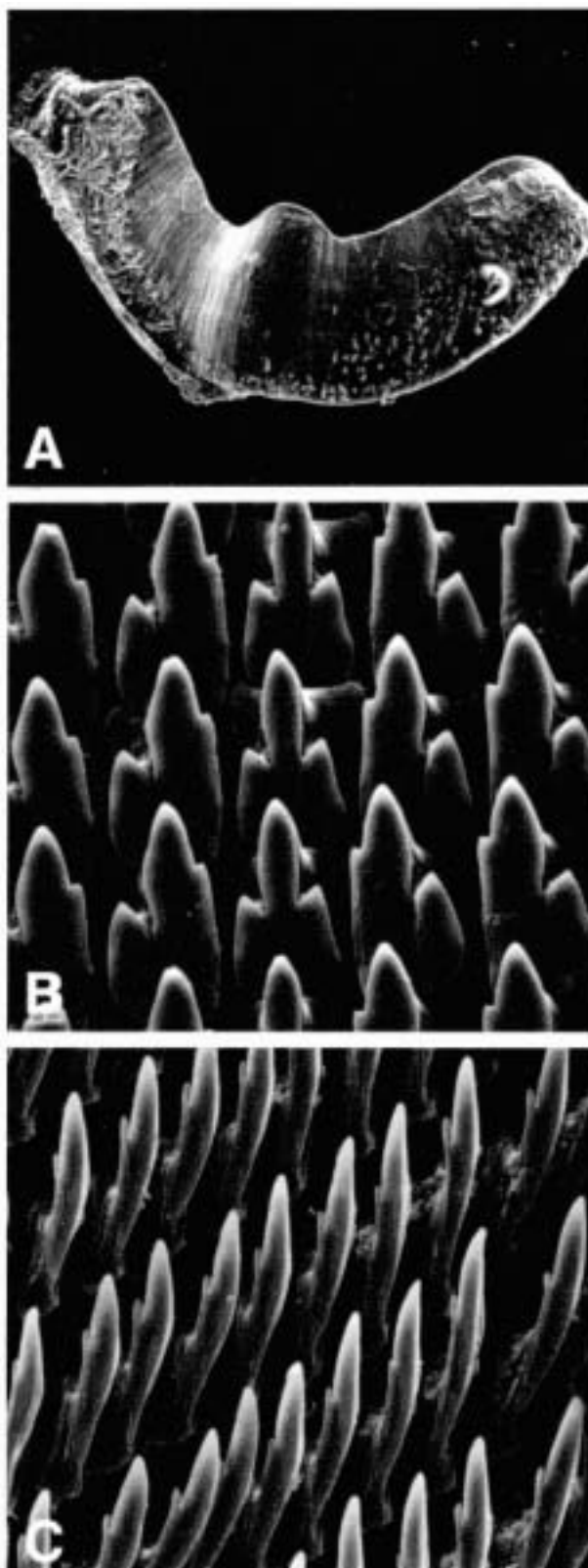


Figure 13. *Plutonia brumalis*, Salto do Cavalo, São Miguel, 9.x.1991. A. Jaw, x60. B. Central and lateral teeth of radula, x1000. C. Marginal teeth of radula, x1000.

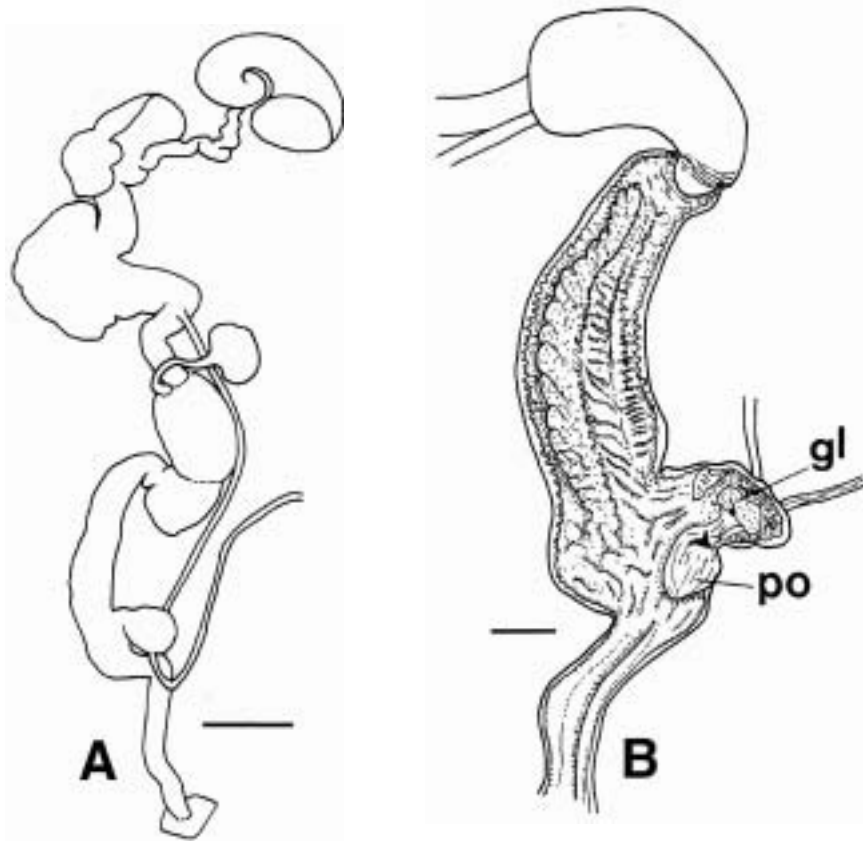


Figure 14. *Plutonia brumalis*. Muro do Carvão, São Miguel, 5.ii.1988. **A.** Reproductive system. Scale bar 2mm. **B.** Internal anatomy of basal reproductive system. Scale bar 1mm. Abbreviations: gl, glandular pad; po, pouch.

External features (Fig. 8B): Intensity of overall body pigmentation extremely variable, colour varying from cream through very pale brown to almost black (e.g. Caldeira da Santa Bárbara, Terceira). Except in the darkest forms, overall impression is of brown spotting on a cream background. Upper whorls of body typically brownish, which combined with the shell colour gives a distinctly brown appearance to the occupied shell. Mantle lobes cover more than half of shell, and principal lobe less obviously circular than in *P. laxata*; lobes strongly and darkly pigmented with brown blotches or stripe; dark lateral stripe on right-hand side embraces the pneumostome. Diagonal groove leading from the top of the pneumostome is only very faintly developed, if at all, and is not pigmented. Sides of body with numerous small brown spots, which form two obvious rather solid lateral body stripes, and prominent dark solid stripes on either side of the tail.

Spotting on sole of foot may be uniform throughout, but normally less intense in the median than in the lateral stripes; in the latter, spotting is noticeably stronger on the inner margin; entire foot uniformly dark in a few heavily pigmented individuals.

Shell (Figs 2D;10A–E;11A–F;12A–F): Size range of dissected adult shell: 6.7–10.3 × 5.2–7.8 × 3.4–5.4mm. Largest shells as follows: 10.3 × 7.8 × 5.4 (Pico); 9.6 × 7.2 × 4.5 (Faial); 9.4 × 6.8 × 5.0 (Terceira) 8.2 × 5.9 × 4.2 (São Miguel); total range of whorl number 2.0–2.4. (syntype of *brumalis* 9.2 × 6.9 × broken; wh. 2.3; largest syntype of *mollis* 7.9 × 5.9 × 4.0; wh. 2.4).

Entire shell, including protoconch, smooth and shiny with only faint striations. Colour light horn-brown. Profile noticeably flatter than *P. laxata*. Base of shell reduced, leaving umbilical area widely open; calcareous layers become thinner towards the columellar margin of the aperture leaving an extensive area of shell comprising just periostracum.

Shell ratios as follows:

	max.d./ht.	max.d./min. d.
São Miguel	1.8–3.0	1.3–1.4
Terceira	1.9–2.0	1.3–1.4
Faial	2.2–2.4	1.3–1.4
Pico	2.1–2.4	1.3–1.5

Radula and jaw (Figs. 13A–C): Central tooth with pointed mesocone and ectocones; laterals with strong,

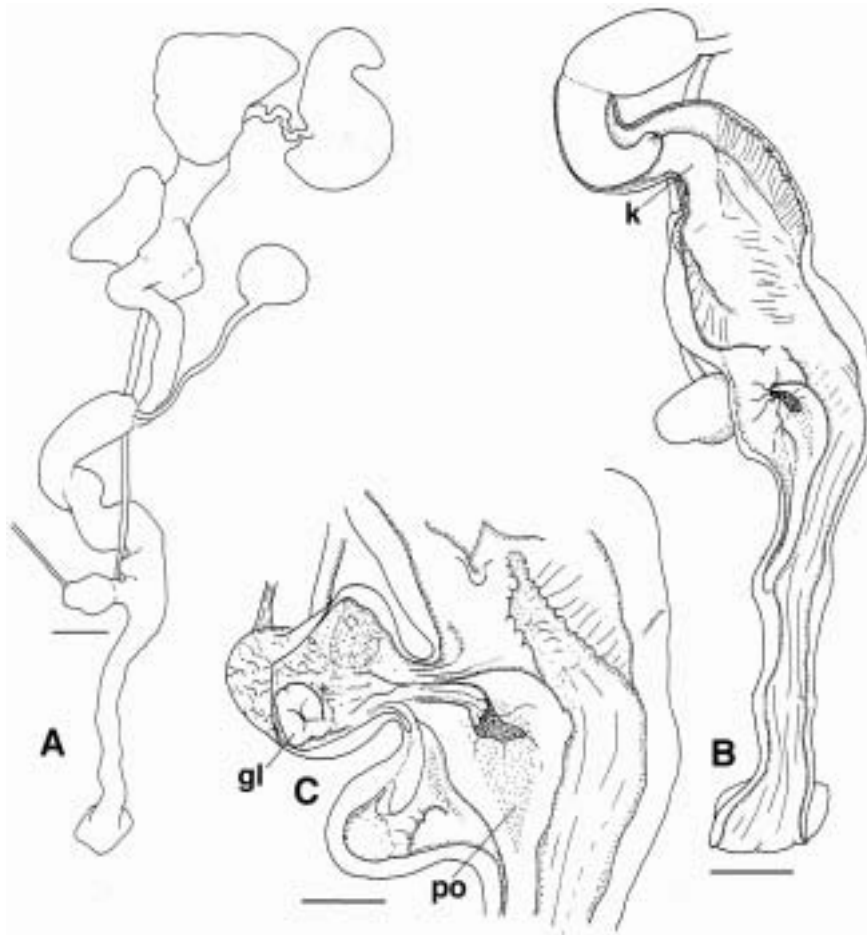


Figure 15. *Plutonia brumalis*. Caldeira de Santa Barbara, Terceira, 28.vi.94. **A.** Reproductive system. Scale bar 2mm. **B.** Internal anatomy of basal reproductive system. Scale bar 2mm. **C.** Internal anatomy of the penis. Scale bar 1mm. Abbreviations: gl, glandular pad; k, knob; po, pouch.

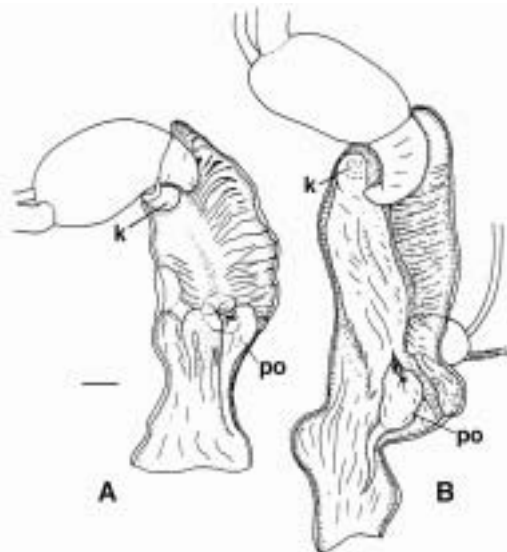


Figure 16. *Plutonia brumalis*. Internal anatomy of basal reproductive system. **A.** Caldeira, Faial, 800m, 12.x.1993. **B.** Corre Água, Pico 28.vi.1991. Scale bar 1mm. Abbreviations: k, knob; po, pouch.

pointed ectocone; marginals long, sharp, pointed and slightly curved, with a weak cusp about half way down outer edge. Jaw of the oxygnath type.

Reproductive system (Figs. 14A–B;15A–C;16A–B): Atrium and vagina more-or-less equal in length, or atrium slightly longer; spermathecal stalk varies from slightly longer than head to up to three-times longer. Free oviduct equal to vagina. Stimulatory papilla prominent. Internal walls of vagina with *strong longitudinal glandular pilaster in fully mature individuals, terminating in a prominent knob* situated alongside stimulatory papilla in fully mature specimens; opposite this pilaster, and above penial pore the vaginal walls are corrugated transversely. Two narrow, equal pilasters emerge from penial pore and rapidly unite to form a single pilaster which runs down the atrial wall almost as far as the genital opening; *at junction of these two pilasters a thin web develops which forms a pouch, typically with only a narrow opening at top, but which*

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in some specimens appears to be almost completely closed.

Penis small, with terminal retractor muscle and laterally inserting vas deferens; penial retractor passing under the right optic retractor and anterior to then back over the optical retractor nerve prior to insertion on the lower lung wall.. Internal walls of penis partly covered with areas of glandular tissue, a distinct circular papilla denotes opening of vas deferens.

Distribution: This species has been found on São Miguel, and all the islands comprising the Central Group except Graciosa, from which no vitrinid has been recorded. On São Miguel it reaches the top of Pico da Vara.(c1000m), and has been recorded at elevations of 800m on Fayal and 1500m on Pico in the Central Group. At numerous sites throughout São Miguel, but especially in the east of the island, it lives micro-sympatrically with *P. laxata*.

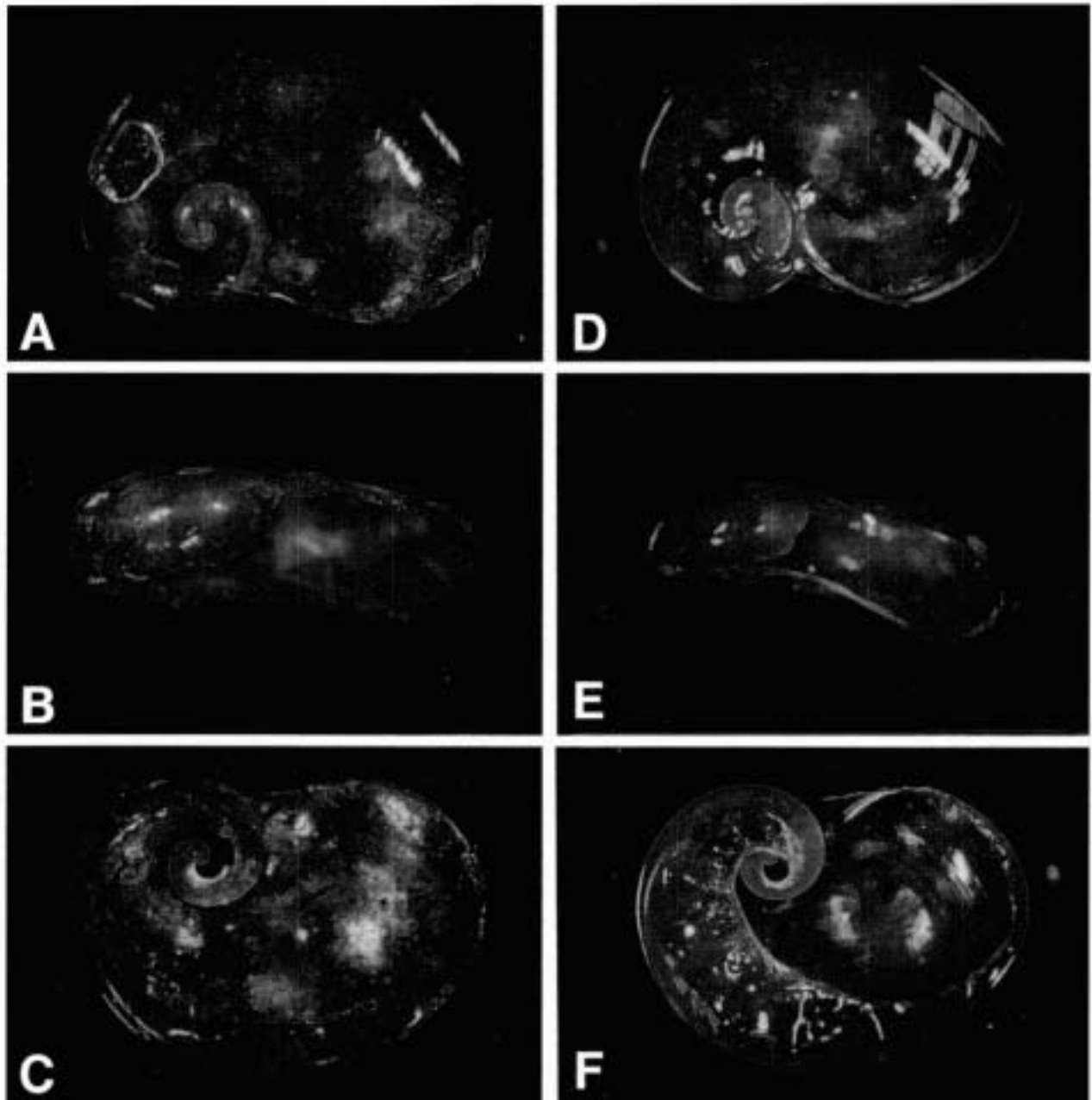


Figure 17. *Phutonia finitima*. A–C. Syntype. Flores, Ex Morelet Collection (NHM 1893.2.4.1124). Shell width 8.0mm. D–F. Lomba, Corvo. 22.vii.1994. Shell width 9.8mm.

Plutonia finitima (Morelet, 1860)

Figs 2E, 17A–F, 18A–B, 19A–D.

Vitrina finitima Morelet, 1860:150, pl.1, fig.7.

Vitrina finitima Morelet. Drouët, 1861:145; Tristram, 1870:107; Pfeiffer, 1876:22; Wollaston, 1878:15; d'Arruda Furtado, 1881:7; Milne-Edwards, 1885:316; Nobre, 1930:73.

Vitrina pelagica Morelet [part]. Simroth, 1889:5.

Insulivitrina pelagica (Morelet) [part]. Hesse, 1923:135.

Insulivitrina brumalis (Morelet) [part]. Hoffmann, 1929:231; Fischer-Piette, 1946:256.

Phenacolimax (Insulivitrina) brumalis (Morelet) [part]. Backhuys, 1975: 144.

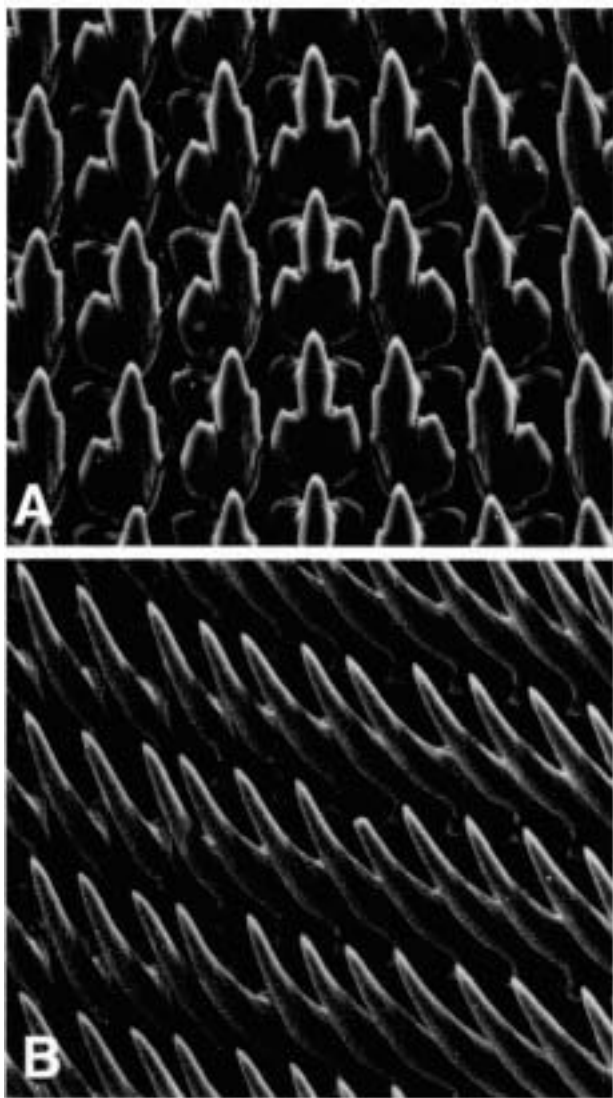


Figure 18. *Plutonia finitima*. Radula. Ribera de Santa Cruz da Fazenda, Flores, 15.x.1993. A. Central and lateral teeth, $\times 500$. B. Marginal teeth, $\times 500$.

Types: Two syntypes (Figs 17A–C); NMH, 1893.2.4.1124-1125. [Flores].

Other material: FLORES: Fajãzinha (Laranjeiro), 6.vii.1989; 17.x.1993; Ponta Delgada, 7.vii.1989; Terra Nova, 9.vii.1989; Lagoas, 9.vii.1989; Juncal, 9.vii.1989; Pico do Padre. Alfredo, 9.vii.1989; Ribera de Santa Cruz da Fazenda, 140m 15.x.1993; Ponte da Ribeira da Silva, 350m, 15.x.1993; Ribera Funda, 130m 15.x.1993; Lajedo, 380m, 5.x.1993; Alagoa 30m, 16.x.1993; Ribeira do Cascalho, 130m, 16.x.1993; Tapada da Forcada, 510m, 16.x.1993; Vertente do Facho, Ponta Delgada, 200m, 16.x.1993; Lagoa Seca, 580m, 18.x.1993. CORVO: Caldeirão, 8.vii.89; Lomba, 22.vii.94; Caldeira, 15.x.1997.

External features: Intensity of colour in pigmented areas extremely variable from very pale brown to black. Mantle folds relatively extensive, covering more than half of the shell; bearing prominent dark grey/brown stripes, one on right side running through pneumostome, and an equivalent on left mantle margin. Broad double stripe, sometimes partly fused, running lengthwise on top of the mantle, slightly to the left of centre, and a characteristic thin line of pigmentation running obliquely from just above the pneumostome to the left posterior mantle edge along a shallow groove. Darker individuals have additional mantle spotting and marbling which in extreme forms can become uniformly black on right of mantle fold.

Sides of body may be almost clear or weakly to strongly spotted, coalescing into distinct dark bands running back from base of optic tentacles. Dark elongate triangular patch on dorsum of tail in groove anterior to tail crest. Spotting on sides of tail becomes denser dorsally giving the appearance of weak lateral stripes.

Marginal bands on foot sole with dark spots, dense towards the centre, becoming weaker towards the outer edge; median band clear or weakly speckled.

Shell (Figs 2E;17A–F): Size range of dissected adult shell: $6.2-10.5 \times 4.8-8.2 \times 2.7-5.2$ mm; wh. 1.8–2.0 (largest syntype of *Vitrina finitima* $7.8 \times 5.4 \times 2.9$ mm; wh. 1.8). Range max.d./ht 1.2–1.4; max.d./min.d. 1.8–2.7. Protoconch with a very finely granular appearance under microscope; remainder of shell smooth and shiny. Colour pale to mid-brown; base of shell greatly reduced allowing all previous whorls to be visible when viewed from below.

Radula and jaw (Figs 18A–B): Radular marginals lacking an ectocone. Jaw as for *P. brumalis* (Fig. 13A).

Reproductive system (Figs 19A–D): Atrium rather longer than entire vagina; vaginal lumen in particular

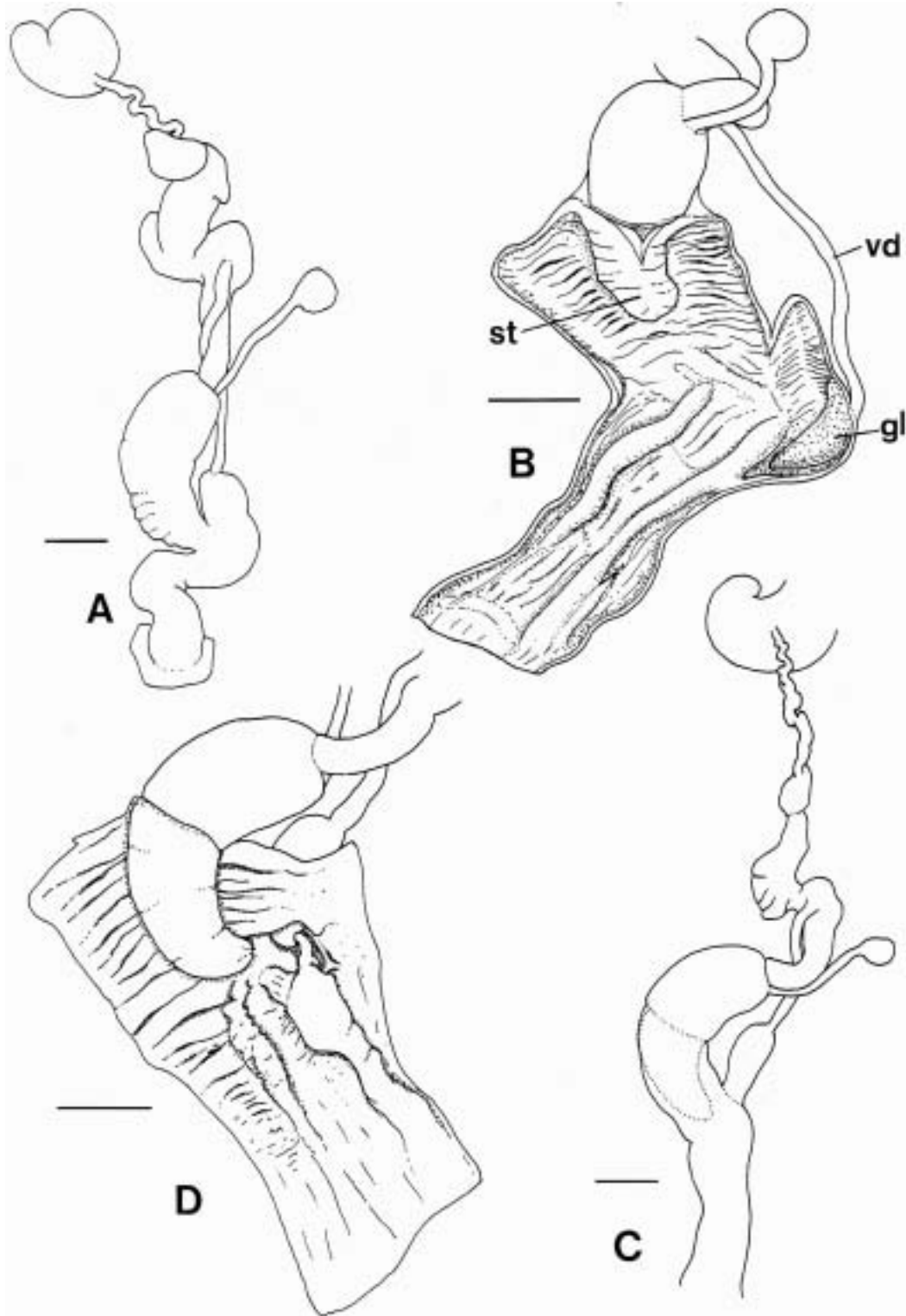


Figure 19. *Phutonia finitima*. **A.** Reproductive system. **B.** Internal anatomy of basal reproductive system. Ribera de Santa Cruz da Fazenda, Flores, 15.x.1993. **C.** Reproductive system. **D.** Internal anatomy of basal reproductive system. Lomba, Corvo, 22.vii.1994. Scale bars 2mm. Abbreviations: gl, glandular pad; st, stimulatory papilla; vd, vas deferens.

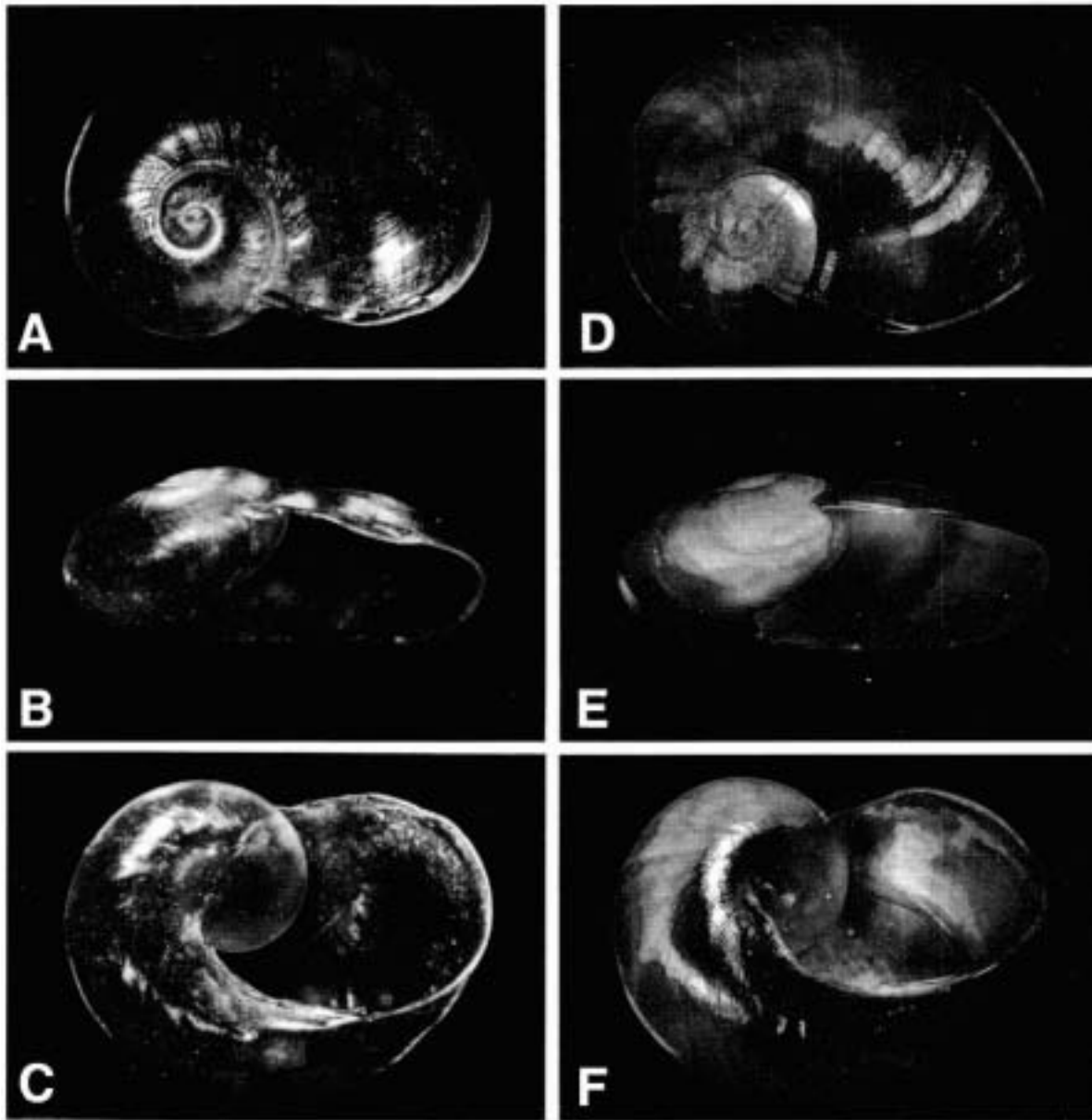


Figure 20. *Plutonia angulosa*. Shell. A–C. Neotype. Pico Alto, Santa Maria, 480m. 21.x.1993. NHM 1998183. Shell width 6.4mm. D–F. Pico Alto, Santa Maria, 12.vi.1986. Shell width 6.1mm.

variable in length but always relatively short (in specimens from Corvo the vaginal lumen is noticeably shorter in than in those from Flores, but this distinction alone was not considered sufficient to separate these two groups taxonomically); spermathecal stalk two to three-times longer than head. Free oviduct about equal in length to the vagina. Stimulatory papilla prominent, sometimes extending into atrium. *Internal walls of vagina without ornamentation* other than transverse corrugations.

Penis small, *lacking (or with a vestigial) retractor*

muscle and with terminally inserting vas deferens. Internally walls glandular, weakly ridged transversely, bearing a prominent, pointed, glandular pad. There are two distinct pilasters in the atrium: one free and rather shorter, the second opposite it and originating in penis. Where the latter leaves the penis a shallow pouch with a large opening develops.

Distribution. Restricted to the two islands of the western-most group: widely distributed on Flores but more restricted on Corvo.

Remarks: *P. finitima* is unusual in having a penial retractor muscle that is vestigial or, more usually, absent, a character which within the Vitrinidae is shared only with the slug *P. atlantica*.

***Plutonia angulosa* (Morelet, 1860)**

Figs 2F, 20A–F, 21A–B, 22A–B.

Vitrina angulosa Morelet, 1860:151, pl.2, fig.1 [as *angulata*].

Vitrina angulosa Morelet. Drouët, 1861:144; Tristram, 1870:107; Pfeiffer, 1876:23; Wollaston, 1878:16; d'Ar-ruda Furtado, 1881:7; Milne-Edwards, 1885:316; Nobre, 1930:73.

Vitrina pelagica Morelet [part]. Simroth, 1889:5.

Insulivitrina pelagica (Morelet) [part]. Hesse, 1923:135.

Insulivitrina mollis (Morelet). Hoffmann, 1929:231; Fischer-Piette, 1946:256.

Phenacolimax (Insulivitrina) brumalis (Morelet) [part]. Backhuys, 1975: 144.

Type: (Figs 20A–C) Neotype here selected, in accordance with Article 75.3 of the *International Code of Zoological Nomenclature*, in order to clarify the taxonomic status of *V. angulosa*; NHM, 1998183. From the type locality: Pico Alto, Santa Maria, Azores, 480m. Leg. A.M.F. Martins & P.B. Mordan, 21.x.1993. Type material of this species cannot be located either in the Morelet collection in the NHM, or the collections of the MNHN. The specimen is in agreement with the original description and figure given by Morelet (1860).

Other material: SANTA MARIA: Pico Alto, 480m, 21.x.1993; 21.vi.1994; 24.vi.1994. N do Pico Alto, 480m, 21.x.1993.

External features: Background coloration orange-pink, with deep-brown to black patterning. Right lobe of mantle narrow but with expanded, rounded tip, covering only a small part of lower left posterior side of shell; mantle with black mottling and wide dark-brown band on left side, arching over and embracing pneumostome. Sides of body speckled with pale brown or black, colour becoming intense and almost solid below mantle region. Mantle groove runs diagonally backwards from above the pneumostome. Dark, backwardly pointed, arrow-shaped mark in groove on dorsum of tail, extending forward just under shell.

Background colouration of foot sole as for body; intensity may be stronger in the median band, which is weakly speckled. Lateral bands strongly speckled on inner edge, more weakly towards outer edge.

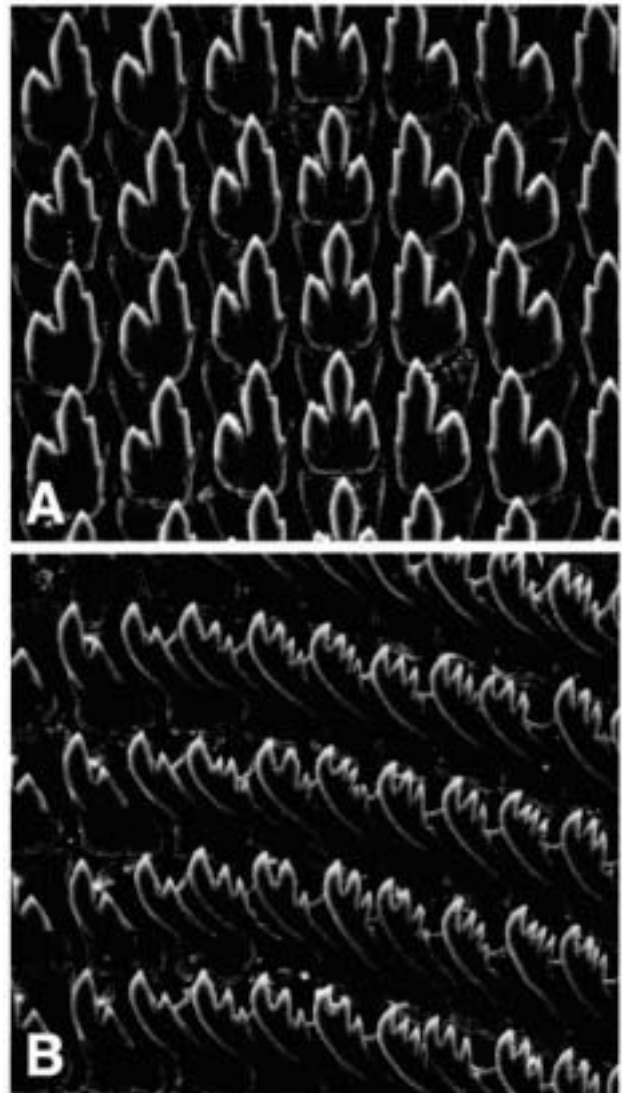


Figure 21. *Plutonia angulosa*. Radula. Pico Alto, Santa Maria, 21.x.1993. A. Central and lateral teeth, $\times 1000$. B. Marginal teeth, $\times 1000$.

Shell (Figs 2F; 20A–F): Size range of dissected adult shells: $6.1\text{--}6.3 \times 4.6 \times 5.1 \times 2.7\text{--}3.0\text{mm}$, wh $2.3\text{--}2.5$ (neotype $6.2 \times 4.7 \times 2.9\text{mm}$; wh 2.5). max.d./ht $1.2\text{--}1.4$; max.d./min.d. $2.0\text{--}2.2$.

Protoconch strongly malleated; malleations extending in a much weaker form to the rest of the shell, giving it a glossy appearance. Colour mid-brown; whorls not greatly expanded. *Periphery of shell with a weak but noticeable carination or angulation on the body whorl, from which species name derives.* Umbilicus weakly exposed by reduction of basal and columellar apertural wall.

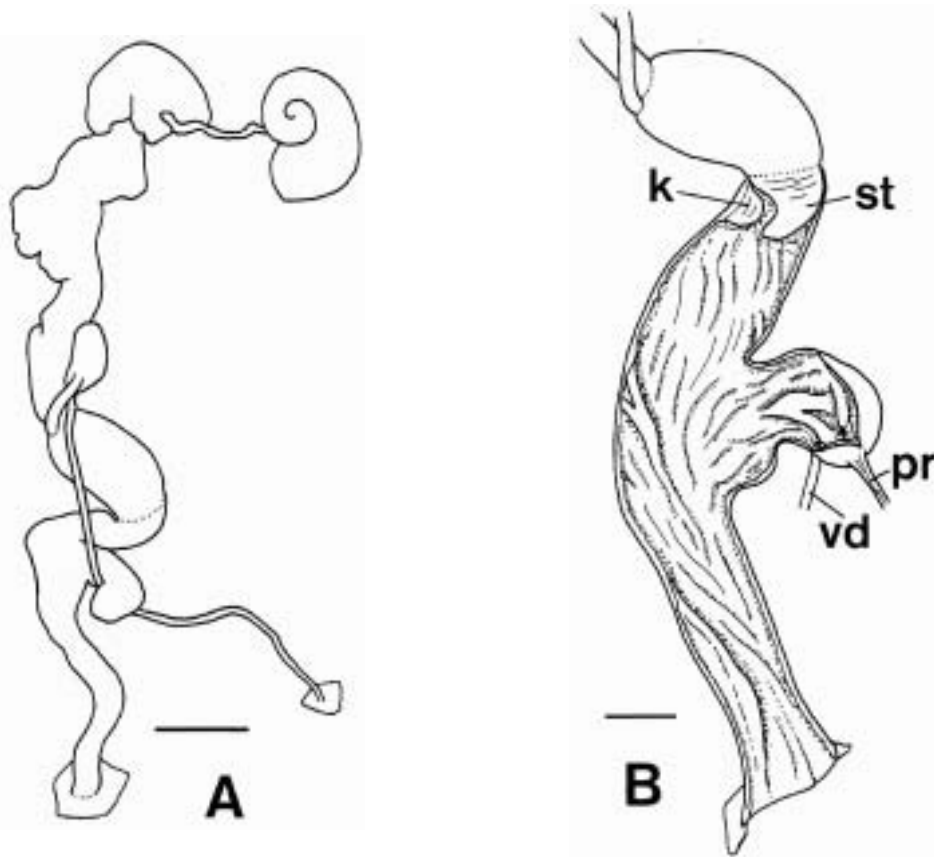


Figure 22. *Plutonia angulosa*. Pico Alto, Santa Maria, 480m, 21.x.1993. **A.** Reproductive system. Scale bar 2mm. **B.** Internal anatomy of basal reproductive system. Scale bar 1mm. Abbreviations: k, knob; pr, penial retractor muscle; st, stimulatory papilla; vd, vas deferens.

Radula and jaw (Figs 21A–B): Central and lateral teeth similar to *P. brumalis*, but *marginals relatively short, broad and multicusped*. Jaw as for *P. brumalis* (Fig. 13A).

Reproductive system (Figs 22A–B): Atrium rather longer than vagina; spermathecal stalk more-or-less equal in length to head. Free oviduct longer than vagina. Stimulatory papilla small. Internal walls of vagina with weak longitudinal band of glandular tissue but lacking a strong pilaster; prominent knob at top of lumen.

Penis small; retractor muscle and vas deferens inserting subterminally; penial retractor passing under the right optic retractor and anterior to then back over the optical retractor nerve prior to insertion on the lower lung wall. Walls of penis glandular, with Y-shaped pilaster emanating from penial pore and running down the atrial wall towards genital opening.

Distribution: This species appears to be restricted to its type locality, Pico Alto on Santa Maria at around

500m., where it lives microsympatrically with *P. pelagica* and *P. brevispira*.

ACKNOWLEDGEMENTS

This research was undertaken as part of the projects STRIDE/CEN/508/92 and PRAXIS/2/2.1/BIA/169/94-Biodiversidade. We are grateful to our colleagues in both programmes for their company and assistance in the field: Keppa Altonaga, Sérgio Ávila, Thierry Backeljau, Carlos Brito, Regina Cunha, Paula Lourenço, Roberto Madeiros, Carlos Prieto and Armindo Rodrigues.

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