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PLUTONIA (*CANARIVITRINA*), NEW SUBGENUS, FROM THE CANARY ISLANDS, AND THE PHYLOGENETIC RELATIONSHIPS OF THE SUBFAMILY PLUTONIINAE (GASTROPODA: LIMACOIDEA: VITRINIDAE)*

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ABSTRACT

Plutonia (*Canarivitrina*), n. subgen., and four new species of this subgenus are described from three islands of the mid-Atlantic Canarian archipelago. The genus *Plutonia* Morelet, in Stabile, 1864 (of which *Insulivitrina* Hesse, 1923, is a new synonym), restricted to the mid-Atlantic islands, is characterized by the autapomorphy of the special course of the penial retractor muscle, rounding the right optic nerve. *Canarivitrina,* n. subgen., has a penis with two easily distinguishable portions: a distal one, short and slightly widened, containing a globular to cylindrical and perforated penial papilla level with the opening of the vas deferens (far from the penial apex), and a proximal one, long and slender, with apical insertion of the penial retractor muscle and two parallel longitudinal inner structures: a torus (thick fold, with roundish cross section) and, opposite, a laminar crest (velum). Torus and penial papilla are coated by glandular tissue, the penial gland. The autapomorphic character state of this subgenus is the proximal portion of the penis, long and equipped with internal torus and velum.

New data are given about the sheath that surrounds the spout of the glandula amatoria in *Canarivitrina,* n. subgen., and in other supraspecific Plutoniinae taxa demonstrating the homology of the glandula amatoria and its spout sheath with the sarcobelum of the genus *Semilimax,* a basal branch of the Vitrinidae: the subfamily Plutoniinae has the "sarcobelum" fused with the proximal part of the vagina to form the glandula amatoria.

A phylogenetic scenario of the supraspecific taxa of the subfamily Plutoniinae is presented. The cladistic analysis shows the Plutoniinae as the sister group of *Semilimax,* and *Phenacolimax* as the sister group of the remaining Plutoniinae: the genera *Phenacolimax, Gallandia* (which is almost certainly a junior synonym of *Oligolimax*), *Arabivitrina* and *Plutonia;* but this analysis does not resolve for the other taxa because the data are still too few to apply to a cladistic study of the group.

The genus *Plutonia* includes the subgenera *Plutonia,* s. str., *Guerrina, Insulivitrina, Madeirovitrina* and *Canarivitrina,* n. subgen. The presence of this genus in the archipelagoes of the Azores, the Madeiras and the Canary Islands is probably as old as the humid "laurisilva" laurel-forest, a Tertiary relict that colonized these archipelagoes before the impact of the Pleistocene glaciations.

Key words: Gastropoda, Vitrinidae, Plutoniinae, *Canarivitrina*, phylogeny, biogeography.

INTRODUCTION

The Canarian Vitrinidae were studied only superficially between 1821-1954; eight species were described—one doubtful: *Vitrina fasciolata* A. Férussac, 1832; one of *Guerrina* Odhner, 1954: *Helix cuticula* Shuttleworth, 1852; and six grouped in *Insulivitrina: Helicolimax lamarckii* A. Férussac, 1821; *V. blauneri* Shuttleworth, 1852; *V. latebasis* Mousson, 1872; *V. canariensis* Mousson, 1872; *V. reticulata* Mousson, 1872; and *V. parryi* Gude, 1896. In the last years, ten additional species were described: *G. christinae* Groh, 1993; *I. eceroensis* Alonso & Ibáñez, 1987; *I. tuberculata* Ibáñez & Alonso, 1987; *I. gomerensis* Alonso & Ibáñez, 1988; *I. emmersoni* Morales, 1988; *I. oromii* Ibáñez & Alonso, 1988; *I. machadoi* Ibáñez & Alonso, 1990; *I. nogalesi* Alonso & Ibáñez, 1990; *I. tamaranensis* Valido, 1990; and *I. mascaensis* Morales, 1987 (Alonso et al., 1987; Ibáñez et al., 1987; Morales et al., 1988; Valido et al., 1990, 1993). The last species, from Tenerife Island, has a peculiar penis, with a very long and slender proximal portion having a remarkable distance

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between the vas deferens entrance to the penis and the insertion of the penial retractor.

We have recently found four additional new species with the same penial characteristics: three from La Gomera and one from La Palma (Fig. 5); these five species are assigned to a new subgenus, *Canarivitrina,* n. subgen. In this paper, we describe these taxa and attempt a phylogenetic study of the entire subfamily Plutoniinae.

METHODS

The introduction of *Canarivitrina,* n. subgen., is the consequence of our anatomical studies of the European *Phenacolimax major* (A. Férussac, 1807), *Arabivitrina jansseni* Neubert, 1988 (from the Asir province, Saudi Arabia), *Madeirovitrina nitida* (Gould, 1848) and *M. marcida* (Gould, 1848) from the Madeira Archipelago, and the Canarian species above mentioned. Moreover, bibliographic data on the Plutoniinae have been obtained from Forcart (1959), Hubendick (1953), Mermod (1930), Zilch (1979), and several additional papers (Table 1).

Calculation of number of shell whorls follows Kerney et al. (1979: 13). The terms "shell" and "specimen" in the enumerations of the material studied refer to empty shells and live specimens respectively, and "proximal" and "distal" refer to the position in relation to the gonad. The term "semislugs" refers to the classification of Tillier (1984), that is, the animal usually cannot withdraw completely into the shell, the posterior edge of the foot cavity is lower and further forward than the most posterior part of the digestive tract, and the stomach is retained in the upper visceral cavity.

The cladistic analysis involves the eight genus-group taxa of the Plutoniinae and was performed using PAUP 4.0 Beta 2 for Windows (Swofford, 1999) and the Treeview application (Page, 1996). Tree searches were performed using the exhaustive search command. Zerolegth branches were collapsed, MulTrees was activated and the accelerated transformation option (Acc Tran) was used. The characters and character states used are listed in Table 2 and the data matrix in Table 3 mainly based on the type species of the single supraspecific taxa. Character polarity was determined by outgroup comparison using *Semilimax* as outgroup for the reasons indicated in the comments after the family diagnosis. All characters have equal weight. Two out of nine characters

Abbreviations

a	atrium
A_1—A_5	stimulator portions; terminology based in Hausdorf (1988) and Schileyko (1984: 39, fig. 18)
ag	albumen gland
AIT	Alonso & Ibáñez collection, Department of Animal Biology, University of La Laguna, Tenerife, Canary Islands, Spain
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.
ar	atrial retractor muscles
Ara	*Arabivitrina*
bb	buccal bulb
bc	bursa copulatrix
Can	*Canarivitrina,* n. subgen.
CGH	K. Groh private collection, Hackenheim, Germany
CRD	T. Ripken private collection, Delft, The Netherlands
CRT	W. Rähle private collection, Tübingen, Germany
CGS	F. Giusti private collection, Siena, Italy
FMNH	Field Museum of Natural History, Chicago, Illinois, U.S.A.
ga	glandula amatoria inside proximal vagina
Gal	*Gallandia*
Gue	*Guerrina*
Ins	*Insulivitrina*
lc	laminar crest (velum)
Mad	*Madeirovitrina*
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHM	The Natural History Museum, London, England
NNM	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands
o	free oviduct
p	penis
pg	penial gland
Phe	*Phenacolimax*
pi	pilaster
Plu	*Plutonia*
pp	penial papilla
pr	penial retractor muscle
ps	penial sheath
ror	right ommatophore retractor muscle
s	sarcobelum
Sem	*Semilimax*
SMF	Natur-Museum Senckenberg, Frankfurt/Main, Germany
sp	spout
st	soft tissue
ST	supraspecific taxon grouping the five species herein described
t	torus
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain
v	distal vagina
vd	vas deferens
vf	vaginal fold
ZMH	Zoologisches Museum der Universität, Hamburg, Germany

TABLE 1. Genus-group taxa, type species and bibliographical sources of anatomical data.

Genus-group taxa	Type species	Sources
Arabivitrina Thiele, 1931	*Vitrina arabica* Thiele, 1910	Thiele, 1931; Forcart, 1957; Zilch, 1959; Neubert, 1998
Canarivitrina, n. subgen.	*P.* (*Canarivitrina*) *taburientensis* n. sp.	this paper
Oligolimax Fischer, in Paulucci, 1878	*Vitrina paulucciae* Fischer, in Paulucci, 1878	Manganelli et al., 1995
Gallandia Bourguignat, 1880 (= *Trochovitrina* O. Boettger, 1880)	*Vitrina conoidea, sensu* Bourguignat, 1880 [*non* Martens, 1874] = *Gallandia olympica* Hausdorf, 1995	Schileyko, 1986; Hausdorf, 1995, and personal communication
Guerrina Odhner, 1954	*Helix cuticula* Shuttleworth, 1852	Odhner, 1954; Ibáñez et al., 1987; Valido et al., 1993; personal unpublished data
Insulivitrina Hesse, 1923	*Helicolimax lamarckii* A. Férussac, 1821	Hesse, 1923; Odhner, 1937; Forcart, 1957; Ibáñez et al., 1987; Schileyko, 1986; personal unpublished data
Madeirovitrina Groh & Hemmen, 1986	*Vitrina nitida* Gould, 1848	Groh & Hemmen, 1986
Phenacolimax Stabile, 1859	*Helicolimax major* A. Férussac, 1807	Forcart, 1944, 1949, 1957; Hausdorf, personal communication; personal unpublished data
Plutonia Morelet, in Stabile, 1864	*Viquesnelia atlantica* Morelet, 1860	Wiktor & Backeljau, 1995; Mordan, personal communication
Semilimax Agassiz, 1845	*Helix semilimax* J. Férussac, 1802	Eckhardt, 1914; Forcart, 1944; Kerney et al., 1979; Grossu, 1983; Schileyko, 1986; Hausdorf, personal communication

(1, 7) had three character states that were treated as nonadditive; character 1 was treated as unordered, and 7 as ordered for the reasons indicated in the explanation of the cladistic analysis; four characters (3, 5, 8, 9) were autapomorphies with an additional autapomorphy in each multi-state character.

RESULTS

TAXONOMIC DESCRIPTIONS

Family Vitrinidae Fitzinger, 1833
Type genus: *Vitrina* Draparnaud, 1801

Diagnosis

Limacoidea, *sensu stricto* (semislugs and slugs with vas deferens running along the inside of the penial sheath; without spermatophore, epiphallus and flagellum), with shell very thin, glossy, pale and translucent, usually with fewer than three rapidly expanding whorls. Protoconch generally spirally dotted with numerous pits, which sometimes are also present on the teleoconch. Animal with penial gland and without penial nerve passing through the cerebral ganglion (see Hausdorf, 1998).

Comments

Schileyko (1986) divided the Vitrinidae into three subfamilies – Vitrininae Fitzinger, 1833; Phenacolimacinae Schileyko, 1986; and Semilimacinae Schileyko, 1986. *Vitrina* Draparnaud, 1801, and Calidivitrina Pilsbry, 1919, were included in the subfamily Vitrininae (sarcobelum and glandula amatoria absent; vagina very reduced). Semilimacinae, characterized by the short vagina and by the presence of a distinct, atrial sarcobelum, included *Semilimax* Agassiz, 1845, *Oligolimax* Fischer, in Paulucci, 1878, *Vitrinobrachium* Künkel, 1929, and dubitatively *Eucobresia* Baker, 1929. This last genus lacks a sarcobelum and has a vaginal papilla near the atrium possibly

TABLE 2. Characters used on the phylogenetic analysis. The numeration refers to the explanations in the text.

(1) Shell
External, the animal cannot withdraw into it = 0
External, the animal can withdraw into it = 1
Internal, reduced = 2
(2) Teleoconch ornamentation
Glossy = 0
Entirely and very densely ribbed = 1
(3) Radular type
Dichoglossan = 0
Beloglossan = 1
(4) Location of the glandula amatoria—stimulator organ
Distinct from vagina (Sarcobelum) = 0
Fused with the proximal part of vagina = 1
(5) Proximal portion of penis long, equipped with torus and velum
Absent = 0
Present = 1
(6) Penial sheath
Strong = 0
Rudimentary or absent = 1
(7) Arrangement of the penial retractor muscle
Free of the right optic nerve = 0
Passing rounding the right optic nerve (Fig. 3G) = 1
Penial retractor absent = 2
(8) Vaginal retractor muscle
Absent = 0
Present = 1
(9) Oviducal retractor muscle
Absent = 0
Present = 1

homologous to the spout of the sarcobelum (Schileyko 1986: figs. 11, 12). Phenacolimacinae, characterized mainly by the long vagina and the presence of a glandula amatoria on the proximal vagina, includes *Guerrina* Odhner, 1954; *Arabivitrina* Thiele, 1931; *Insulivitrina* Hesse, 1923; *Phenacolimax* Stabile, 1859; *Trochovitrina* O. Boettger, 1880; and *Plutonia* Morelet, in Stabile, 1864.

Hausdorf (1998) regarded this system as unacceptable, the Vitrininae being polyphyletic, the Semilimacinae paraphyletic, and only the Phenacolimacinae monophyletic. Moreover, the name Phenacolimacinae is a junior synonym of Plutoniinae Cockerell (1893), established for *Plutonia.*

According to Schileyko (1986), the Vitrininae and the Phenacolimacinae evolved independently from an unknown common ancestor, while the Semilimacinae derived from the Phenacolimacinae by the transformation of the glandula amatoria ("vaginal gland") into a sarcobelum. We assume the contrasting theory, sketched by Simroth (1889) and supported by Hausdorf (1997, 1998), is the most probable: the Phenacolimacinae derived from a *Semilimax*-like ancestor by the fusion of the sarcobelum with the proximal vagina so as to give the glandula amatoria.

The sarcobelum of the type species of *Semilimax* (Fig. 1) consists of a voluminous oblong oval or club-shaped stimulator not covered by soft tissue, with a thick glandular layer wrapping a longitudinal duct, which opens distally into the atrium through a spout, the duct being upholstered (internally with respect to the glandular layer) by a thin layer of circular muscles and a horny tube, the latter missing in all the other Vitrinidae. The wall of the distal portion of the sarcobelum invaginates sheathing the spout; at the invagination edge, the sarcobelum wall is connected with the base of the spout by a very thin layer of connective tissue.

As Hausdorf (1998) has shown in his hypo-

TABLE 3. Original data matrix used for cladistic analysis. All characters with three character states are treated as nonadditive; the character '1' is treated as unordered and the character '7' as ordered. The keys and numeration refer to the explanations in the text. The variable or unapplicable character states were coded as a '?'.

Key	Taxa	1	2	3	4	5	6	7	8	9
A	Sem	0	0	0	0	0	0	0	0	0
B	Ara	0	?	0	1	0	1	0	0	0
C	'ST'	0	0	0	1	1	1	1	0	0
D	Gal	1	?	0	1	0	1	0	0	0
E	Gue	1	1	0	1	0	1	1	0	0
F	Ins	0	0	0	1	0	1	1	0	0
G	Mad	0	0	0	1	0	1	1	1	0
H	Phe	0	0	0	1	0	0	0	0	0
I	Plu	2	?	1	1	0	1	2	0	1

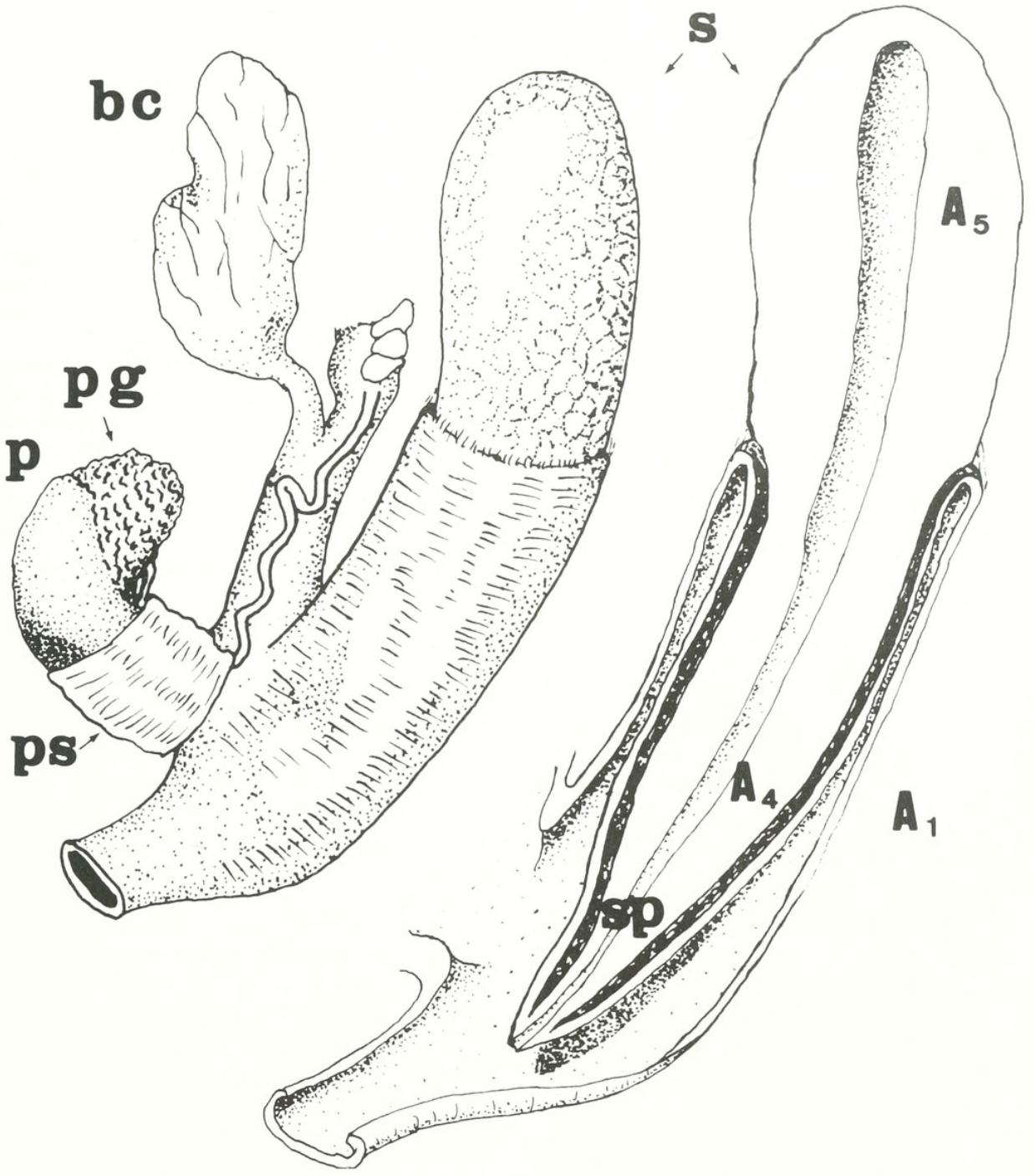


FIG. 1. Genital system of *Semilimax* showing the sarcobelum without the inner horny tube; redrawn from Schileyko (1986: figs. 6–7) without scale, as the original drawings.

thetical explanation of stimulator evolution in the Stylommatophora, the genus *Semilimax* may be seen as a basal branch of the Vitrinidae, the atrial sarcobelum possibly being homologous to the penial appendix of the Orthurethra, with portions A_3 and A_4 absent and A_2 and A_5 fused. But another explanation is also possible: the sarcobelum could be originated by the ancestral loss of portions A_2 and A_3, the shortening of the A_4 portion (the spout), and the invagination of A_4 into the A_1 portion (Giusti, pers. comm.). We assume the last theory because it explains favourably the presence of the spout sheath.

Subfamily Plutoniinae Cockerell, 1893

(junior synonym: Phenacolimacinae Schileyko, 1986)
Type genus: *Plutonia* Morelet, in Stabile, 1864

Diagnosis

Vitrinidae with a thin shell variable in shape, normally with a narrow basal periostracal fringe. Distinct atrial stimulator (sarcobelum) absent. Vagina long, its proximal portion housing a muscular glandula amatoria with a distal spout (see Schileyko, 1986).

The autapomorphic character state of this subfamily is the fusion of the sarcobelum with the proximal vagina to give the glandula amatoria (Hausdorf, 1995).

Comments

The name Plutoniinae was established by Cockerell (1893) for *Viquesnelia atlantica* Morelet, 1860, an Azorean carnivorous slug feeding on such animals as earthworms and slugs, and with an almost subterranean way of life, sheltered in moist places, in moss or under stones and detritus; due to its very specialized features for a predatory life style, Wiktor & Backeljau (1995) proposed to remove it from the family Vitrinidae and assign it to a separate family.

Cockerell (1893) mentioned the possibility that *Plutonia* had also been used for a genus of trilobites, and Collinge (in Cockerell, 1893) proposed an eventual change of the name Plutoniinae to Vitriplutoniinae. However, as Backhuys (1975) indicated, the name *Plutonia* for a genus of the Trilobita was published later: *Plutonia* Hicks, 1871, Invalid Generic Name by homonymy (ICZN, 1997, Opinion 1880).

Shelley & Backeljau (1995) recognized a case of homonymy between Plutoniinae Bollman, 1893 (Arthropoda, Chilopoda, type-genus: *Plutonium* Cavanna, 1881) and Plutoniinae Cockerell, 1893, and proposed the emendation to Plutoniainae Cockerell, 1893. However, Backeljau & Shelley (1996) modified their original application and proposed to amend the myriapod name to Plutoniuminae and to retain the molluscan name unchanged as Plutoniinae; this proposition has been accepted by the ICZN (1997, Opinion 1880).

Taxa Belonging to Plutoniinae

Schileyko (1986: 147) referred *Guerrina, Arabivitrina, Insulivitrina, Phenacolimax, Trochovitrina,* and *Plutonia* to his Phenacolimacinae. The type species of *Trochovitrina, T. lederi* (O. Boettger, 1878) and *Phenacolimax annularis* (Studer, 1820), studied by Schileyko (1986) as examples of the respective genera, were later grouped with *Gallandia olympica* Hausdorf, 1995, in the genus *Gallandia* Bourguignat, 1880, by Hausdorf (1995). Hausdorf recognized this genus to be characterized by the following autapomorphies: shell conoid-globose, shell and mantle lobes reduced, free oviduct short, pedunculus [of the bursa copulatrix] short and penis short.

Ibáñez et al. (1987) grouped the taxa included by Forcart (1957) in *Phenacolimax, s. l. (Phenacolimax, s. str., Arabivitrina, Oligolimax, Insulivitrina, Plutonia,* and *Guerrina*) and Madeirovitrina in the Phenacolimacinae, mainly based on the same characters as Schileyko (1986).

The type species of *Oligolimax, Vitrina paulucciae* Fischer, in Paulucci, 1878, was considered by Forcart (1965) and Giusti (1971) to be a synonym of *V. bonelli* Targioni Tozzetti, 1873, which belongs to the genus *Semilimacella* Soós, 1917, anatomically not far from *Semilimax*. Recently, Manganelli et al. (1995) indicated that *V. paulucciae* is not a synonym of *Semilimacella bonelli* and that its genital system anatomy is so similar to that of the species grouped in *Insulivitrina* and *Gallandia,* that these last two names could be seen as junior synonyms of *Oligolimax*.

Gallandia is almost certainly a junior synonym of *Oligolimax,* but the complete description of *O. paulucciae* has not yet been published (Giusti et al., in prep.). We therefore continue to utilize the name *Gallandia*. On the other hand, *Insulivitrina* is clearly distinguishable from *Gallandia* (and *Oligolimax*) because of the peculiar course of its penial retractor.

Genus *Plutonia* Morelet, in Stabile, 1864

Type species by monotypy: *Viquesnelia atlantica* Morelet, 1860
(Junior synonym: *Insulivitrina* Hesse, 1923, n. syn.)

Diagnosis

Plutoniinae with the autapomorphic character state "penial retractor muscle (starting

from the penis) moving forward, forming loop around the optic nerve, passing below the right ommatophore retractor, then running backwards (left of the same right ommatophore retractor) to end on left side of diaphragm" (Fig. 3G).

Description

Slugs (*Plutonia atlantica*), semislugs (the "*Insulivitrina* group") or *Vitrina*-like helicoid snails (the "*Guerrina* group"). Mantle border with well-developed mantle and shell lobes (the "*Insulivitrina* group"), with lobes small to very small (the "*Guerrina* group"), or with shell lobes absent (*Plutonia atlantica,* with a vestigial shell entirely hidden in the mantle cavity). Right side of mantle generally with distinct darker coloured "lateral band" above pneumostome. Foot aulacopod. Sole tripartite, with distinct sole furrows, the lateral fused at short distance from tail end. Foot dorsally flattened beneath the shell, bordered by a pair of distinct lateral crests extending for about half the tail length; tail tip dorsally keeled.

Shell thin, greenish, translucent, glossy, with 2–4 whorls. Shell variable in shape, from slightly depressed, keeled, conical above and with small aperture, to auricular with lower side very little developed, very large aperture and with narrow periostracal fringe. Protoconch pitted, sometimes with radial ribs.

Jaw oxygnathous, smooth, with median rib and central denticle. Radula mainly dichoglossan (Jungbluth et al., 1985); central tooth little smaller than first lateral teeth, with long, slender mesocone having sharp pointed tip and two basal ectocones reaching half the mesocone length; lateral teeth with long, wide mesocone, one basal ectocone and one small laterodistal endocone; marginal teeth variable in shape.

System of retractor muscles basically as described by Odhner (1937) for *Insulivitrina:* right ommatophore retractor free of penis and vagina. Penial retractor, long and slender; soon after it leaves the penis wall, it moves forward passing below some nerves arising from the right pedal ganglion, then above the nerve and the retractor of the lower right tentacle; soon after, it forms loop around the optic nerve and, passing below the right ommatophore retractor, moves backwards (left of the same right ommatophore retractor) to end on left of diaphragm. This situation is secundarily lost in *Plutonia atlantica* and in at least one of the Azorean "*Insulivitrina*" due to reduction of the penial retractor (see Comments).

Nervous system as described by Tillier (1989: 64) for the family. Pallial complex as described by Wiktor & Backeljau (1995) in *Plutonia atlantica;* lung small, kidney sigmurethrous, bean-shaped, secondary ureter closed like a tube, renal opening near anus and pneumostome.

Genital atrium, penis and distal vagina become completely evaginated when protruded (in some preserved specimens and possibly also at mating; Fig. 2J). Genital atrium variable in length, connected with adjacent part of animal integument by short atrial muscles. Penial complex without epiphallus and flagellum. Penial sheath thin, inconspicuous, rudimentary or absent.

Bursa copulatrix duct and free oviduct insert side by side at proximal end of glandula amatoria. Glandula amatoria variable in dimensions, wider than distal vagina in which it opens through a spout. It can be partially to completely coated by a layer of soft tissue that can easily be stripped off and it is formed by thick outer muscular layer and inner glandular layer wrapping the longitudinal duct.

Distal vagina variably long, its wall invaginated to envelop the spout of the glandula amatoria, to its tip where it fuses with the same spout tip. Invaginated vaginal wall and spout wall entirely connected by thin connective fibres easily removable without destroying the vaginal wall (allowing the invagination to be eliminated in the laboratory); at the invagination edge, the vaginal wall is also connected with the base of the spout by a very thin layer of connective tissue (as found in the sarcobelum of *Semilimax;* Fig. 1).

Spermoviduct long, about one-quarter of total genital system length. Prostate poorly distinguishable. Albumen gland relatively small and oval in shape. Hermaphrodite duct long. Gonad follicular, located at apex of visceral sac.

Comments

The autapomorphic character state of the diagnosis was firstly evidenced in *Plutonia* (*Insulivitrina*) *lamarcki,* two other *Plutonia* (*Insulivitrina*) species and *Plutonia* (*Guerrina*) *cuticula* by Hoffmann (1929) and Odhner (1937, 1954). It is shared by all the Canarian and Madeiran Plutoniinae and was also evi-

denced in the Azorean Plutoniinae (those which retain a penial retractor; Mordan, pers. comm.). It is interesting to note that one Azorean species (different from *Plutonia atlantica*) has been recently discovered to have a very vestigial or perhaps missing retractor (Mordan & Frias Martins, in prep.), which hence has been interpreted as a possible synapomorphy of this species and *P. atlantica*. Thus, all the Macaronesian Plutoniinae would belong to the same genus, *Plutonia* Morelet, in Stabile, 1864, of which *Insulivitrina* Hesse, 1923, will become a subgenus. The relations of *P. atlantica* with the other Azorean Plutoniinae taxa is supported by the cladistic analysis given below.

The adult animal (with the exception of the *Guerrina* species), cannot withdraw completely into the shell. This may happen only after a long period of desiccation and (or) without feeding, a situation that has been verified in some probably senile adult specimens.

Forcart (1957) attributed a glandular function to the soft tissue coating the glandula amatoria. Other authors believe that despite it glandular appearance, it has a different function, as yet undetermined (Schileyko, 1986). The glandular function is feasible, but unproven since this tissue wraps the thick muscular layer of the glandula amatoria externally, and there is no evident communication with the central lumen of the glandula amatoria.

The *Plutonia* species are endemic to three mid-Atlantic archipelagoes located at the western fringe of the Palaearctic: Azores, Madeira and Canary Islands. The alpine *Vitrina glacialis* Forbes, 1837, once assigned to *Insulivitrina* (Forcart, 1944: 654), has been recently presumed as belonging to *Eucobresia* Baker, 1929 (H. Nordsieck, in Falkner, 1991: 103); data on the course of its penial retractor are nevertheless still pending.

Plutonia taburientensis
Groh & Valido, n. sp.

Diagnosis

Plutonia with penis as long as vagina (including its glandula amatoria portion), divided into two portions: proximal penis long, slender, with penial retractor muscle inserted at apex and two internal parallel longitudinal structures, a torus and, opposite, a wide velum. Distal penis short, slightly widened, containing a globular to cylindrical penial papilla level with the entrance of the vas deferens into the same penis (far from the penial apex). Penial papilla perforated, its central channel continuous with vas deferens. Penial papilla and torus coated by glandular tissue, the "penial gland". Distal portion of penis with two very thin penial folds, which join level with the penial papilla, a small pit remaining between them and the papilla itself. Thin vaginal fold sometimes present, ending before reaching genital atrium.

Type Material

Holotype (Fig. 2A): collected by K. Groh and M. Ibáñez (8-1-1988) in the Caldera de Taburiente (La Palma Island; UTM: 28RBS1879), at 750 m altitude; deposited in AIT. Paratypes: 144 specimens and 22 shells collected between January 1988 and February 1997, in various localities of the island and deposited in ANSP (A 18852/2), CGH (32 paratypes, 29 specimens and 3 shells), CRT (8 paratypes), CGS (1 paratype), SMF (311875/5), TFMC (MT 0314/2), ZMH (2745/2) and AIT.

Type Locality

Caldera de Taburiente, La Palma Island.

Etymology

The specific name refers to the Caldera de Taburiente, a geological feature of La Palma.

Habitat and Distribution

A species endemic to La Palma, occurring in wide areas climatologically different, with pinewood and sometimes with lowland vegetation, at an altitude between 300 and 1,800 m (Fig. 5).

Animal

Body whitish-beige, with numerous small pale-beige spots, more dense in number at head. Mantle and tail with darker grey spots and a short blackish-grey lateral band. Foot sole sometimes with marginal grey spots.

Shell

Oblong, with about 2.5 whorls. Protoconch pitted; starting from beginning of second whorl, the pits are less deep and more scat-

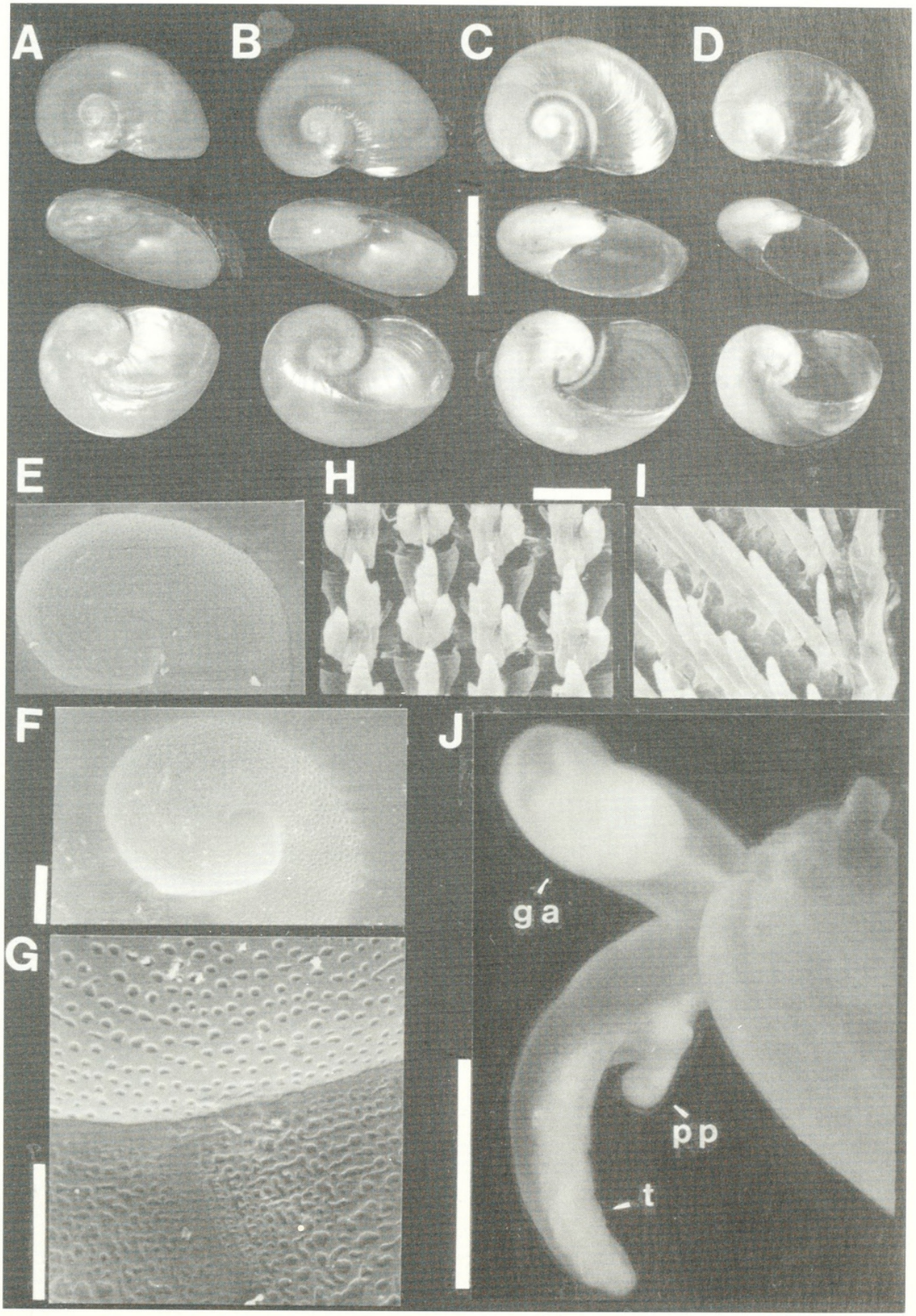
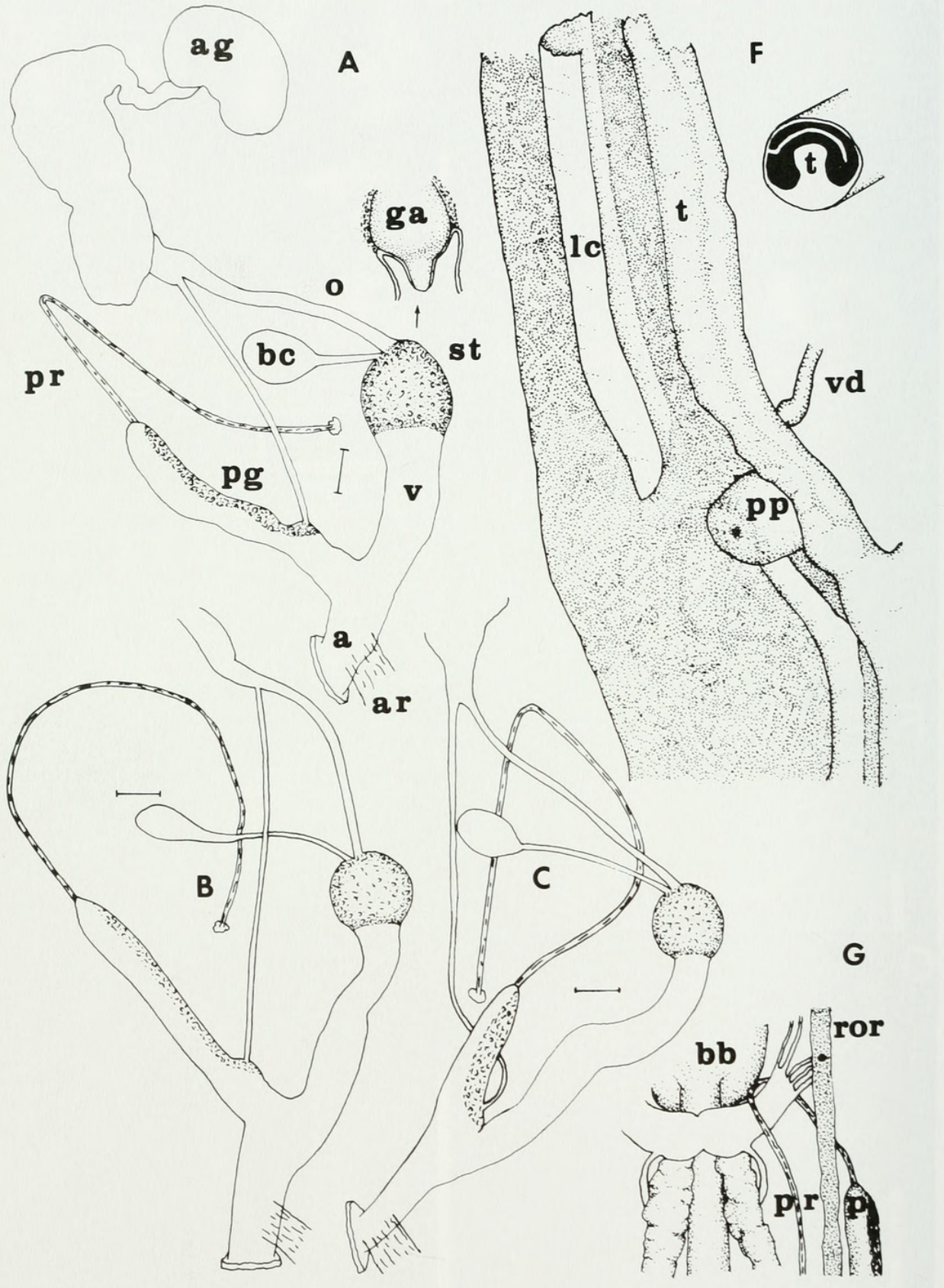


FIG. 2. A–D. Holotype shells. A. *P. taburientensis,* n. sp. B. *P. ripkeni,* n. sp. C. *P. dianae,* n. sp. D. *P. falcifera,* n. sp. E. Protoconch of *P. taburientensis,* n. sp. F–G. Protoconch and pits detail of *P. ripkeni,* n. sp. H–I. Radula of *P. ripkeni,* n. sp. H, central tooth and lateral teeth; I, marginal teeth. J. A specimen of *P. mascaensis* with the distal part of the genital system everted, showing the penis with the penial papilla and the vagina with the glandula amatoria (by transparency). Scale: A–D, J, 5 mm; E, F, 200 μm; G, 100 μm; H, I, 20 μm.



FIGS. 3, 4. Genital system and anatomical details. A. *P. taburientensis,* n. sp., paratype; Caldera de Taburiente. B. *P. ripkeni,* n. sp., paratype; Jerduñe. C. *P. dianae,* n. sp., paratype; Montaña Bejira. D. *P. falcifera,* n. sp., paratype; Tamolde. E. *P. mascaensis* (redrawn from Ibáñez et al., 1987, fig. 14). F. Internal penial details of *P. taburientensis,* n. sp. G. Arrangement of the Insulivitrina penial retractor muscle. Scale: A–E, 1 mm; F–G, without scale.

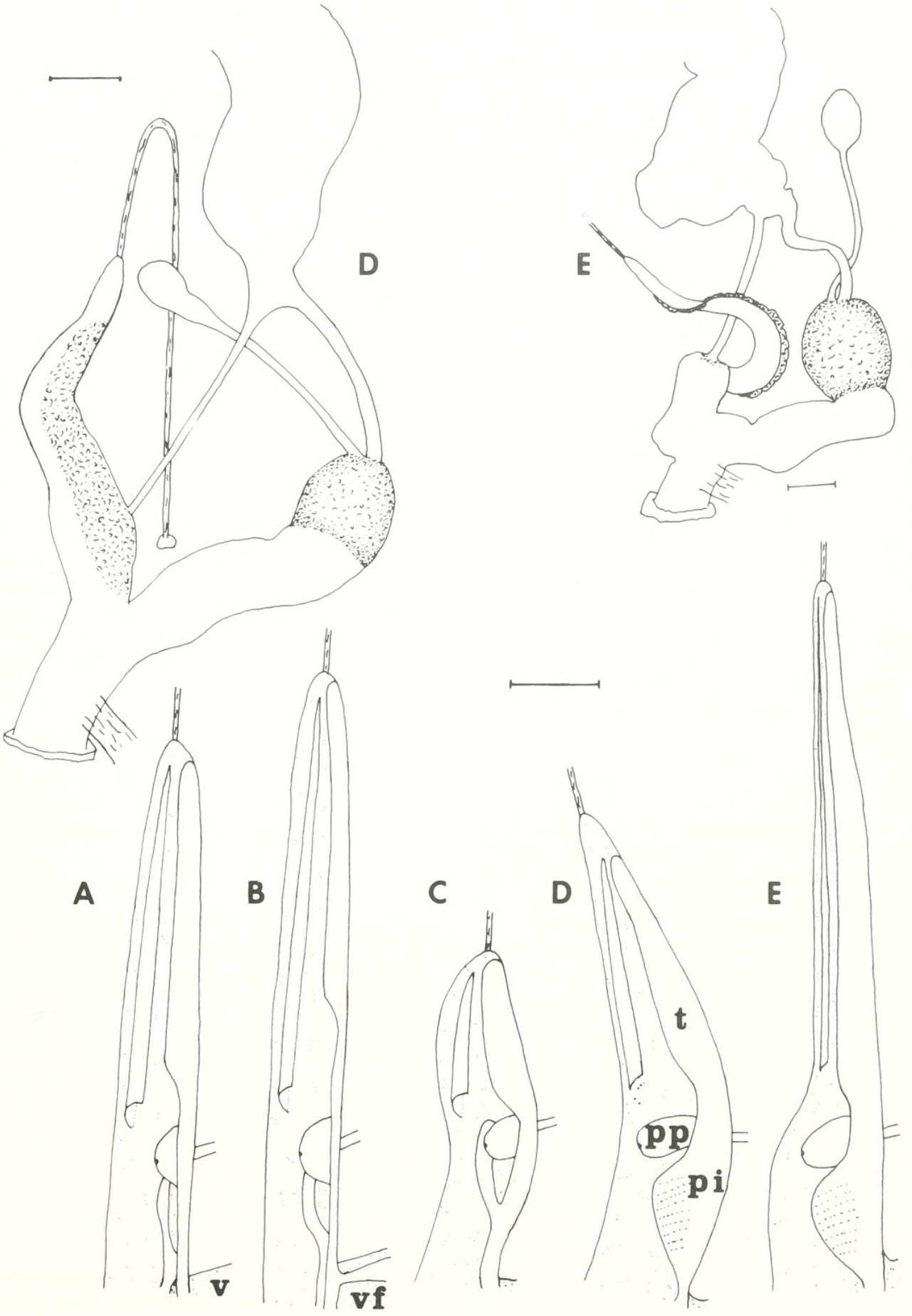


FIG. 4. See figure 3 for legend.

tered, disappearing after first half of second whorl (Fig. 2A, E).

Radula

Formula: 31–33M + 11–12L + C; marginal teeth with only one cusp.

Genital System

Shown in Figures 3A, F, 4A; 12 specimens dissected. Penis as long as vagina (including its glandula amatoria portion). Laminar crest inside the proximal portion of penis wide and same length as torus, the latter distally smaller and thinner, as a laminar fold, joins the penial papilla; this fold partially surrounds the penial papilla and extends into the distal portion of penis; opposite the papilla, another small laminar fold present inside distal penis; the two folds join level with the penial papilla, a small pit remaining between them and the papilla itself; finally, the folds extend separately into the atrium.

Distal vagina twice as long as the glandula amatoria portion, nearly one-third shorter than the free oviduct and 2–2.5 times longer than the bursa copulatrix duct; sometimes with one thin internal longitudinal fold ending before the atrium. Glandula amatoria with a protruding spout.

Comments

Of all the described *Plutonia* species, *P. taburientensis,* n. sp., shares only with *P. mascaensis* the presence of a proximal penis with the penial retractor muscle inserted at apex and internal torus and velum; the main differences between them are listed in the Diagnosis and Comments on the latter. The proximal penis is eversible (Fig. 2J) and it is not a flagellum. There is no spermatophore.

Plutonia ripkeni
Alonso & Ibáñez, n. sp.

Diagnosis

As for *P. taburientensis,* n. sp., but the vaginal fold, always present, extends to fuse with a penial fold into the atrium.

Type Material

Holotype (Fig. 2B): collected by K. Groh and M. Ibáñez (3-1-1988) from Tagamiche (La Gomera Island; UTM: 28RBS85 10), at 950 m altitude; deposited in AIT. Paratypes: 71 specimens collected between December 1985 and March 1997 in various localities of the island and deposited in ANSP (A 18853/2 and 400849/2), CGH (2 paratypes), CRD (2 paratypes), CRT (6 paratypes, 3 specimens + 3 shells), NNM (55868/1), SMF (311874/5 and 311876/2), TFMC (MT 0313/2), ZMH (2746/2) and AIT.

Type Locality

Tagamiche, La Gomera Island.

Etymology

The specific name derives from the family name of Mr. Theodor "Theo" E. J. Ripken, Delft, The Netherlands, to whom the species is dedicated.

Habitat and Distribution

A species endemic to La Gomera, occurring in wide areas with lowland vegetation, bordering the evergreen "laurisilva" forest of the National Park of Garajonay, at an altitude between 200 and 1,025 m (Fig. 5).

Animal

Body whitish-beige-grey, with numerous small darker grey spots, more dense on mantle and tail areas. Lateral band blackish-grey.

Shell

Oblong, with 2.25 whorls. Pits in spiral rows on protoconch and teleoconch; from beginning of second whorl, the pits of some rows or of adjacent rows frequently fuse forming an irregular drawing. Pits disappear after first half of second whorl (Fig. 2B, F, G).

Radula

Formula: 29M + 12L + C; first marginal teeth with very small ectocone and last marginal teeth with only one cusp (Fig. 2H, I).

Genital System

Shown in Figures 3B and 4B; 15 specimens dissected. Penis similar or little longer than vagina (including its glandula amatoria portion). Laminar crest inside proximal penis

wide and same length as torus, the latter distally thinner, as a fold, joins the penial papilla; this fold partially surrounds the penial papilla and extends into the distal portion of penis; opposite the papilla, another fold is present inside distal penis; the two folds join level with the penial papilla, a small pit remaining between them and the papilla itself; finally, the folds extend separately into the atrium, the fold deriving from torus fuses with the vaginal longitudinal fold.

Distal vagina nearly three times longer than the glandula amatoria portion, as long as free oviduct and 1.5–2 times as long as bursa copulatrix duct; with one internal longitudinal fold which fuses with the penial fold inside the atrium. Glandula amatoria with small spout.

Comments

Other than the characters listed in the diagnosis, *P. ripkeni,* n. sp., differs from *P. taburientensis,* n. sp., in vaginal folds more developed; distal portion of penis, penis and vagina longer; glandula amatoria smaller; and spout less protruding.

Plutonia dianae
Valido & Alonso, n. sp.

Diagnosis

As for *P. taburientensis,* n. sp., but the penis is approximately half as long as the vagina (including its glandula amatoria portion).

Type Material

Holotype (Fig. 2C): collected by R. Hutterer and M. Ibáñez (3-11-1994) from Montaña Bejira (La Gomera Island; UTM: 28RBS7320), at 530 m altitude; deposited in AIT. Paratypes: 10 specimens and 8 shells collected the same day in the type locality and the nearby Arguamul and deposited in ANSP (A 18854/1), CGH (1 paratype), TFMC (MT 0312/1) ZMH (2747/1, shell) and AIT.

Type Locality

Montaña Bejira, La Gomera Island.

Etymology

The specific name derives from that of the young daughter of the junior author, Diana Valido de Armas, to whom this species is dedicated.

Habitat and Distribution

A species endemic to northwest La Gomera, occurring in a small area with lowland vegetation, at an altitude between 350 and 530 m (Fig. 5).

Animal

Body whitish-beige, with numerous small pale-beige spots, more dense at head. Mantle and tail with darker grey spots. Lateral band short, blackish-grey, interrupted level with pneumostome. Foot sole sometimes paler than body.

Shell

Very oblong, with slightly more than 2.75 whorls. Pits in spiral rows on protoconch and teleoconch, disappearing at beginning of second whorl (Fig. 2C).

Genital System

Shown in Figures 3C and 4C; five specimens dissected. Penis approximately half as long as vagina (including its glandula amatoria portion), flattened, tongue-shaped. Proximal penis finger-like, with rounded tip. Laminar crest inside proximal penis wide and same length as torus; distal torus slightly smaller, partially surrounding the penial papilla and extending thicker into distal portion of penis; opposite the papilla, another similar fold present inside distal penis; the two folds join level with penial papilla, a deep pit remaining between them and papilla.

Distal vagina very long, up to four times longer than the glandula amatoria portion, little longer than free oviduct and 1.5–2 times longer than bursa copulatrix duct, with internal longitudinal fold that ends before reaching atrium. Glandula amatoria very short, with small spout.

Comments

Other than the characters listed in the diagnosis, *P. dianae,* n. sp., differs from *P. taburientensis,* n. sp., and *P. ripkeni,* n. sp., in the distal penis with deeper pit between penial papilla and the two thicker penial folds. *Plutonia dianae,* n. sp., differs from *P. taburienten-*

sis, n. sp., also in the spout less protruding and from *P. ripkeni,* n. sp., in the vaginal fold, which ends before genital atrium.

Plutonia falcifera
Ibáñez & Groh, n. sp.

Diagnosis

As for *P. taburientensis,* n. sp., but the laminar crest of the proximal portion of penis is narrow or even vestigial; distal portion of penis without pit near penial papilla; the pit is substituted by a pilaster connected proximally with the papilla and ending distally in a small slope with transversal furrows, reminiscent of a fingerprint.

Type Material

Holotype (Fig. 2D): collected by R. Hutterer and M. Ibáñez (31-1-1994) from Tamolde (La Gomera Island; UTM: 28RBS9112), at 200 m altitude; deposited in AIT. Paratypes: 23 specimens collected between January 1988 and March 1997 in various localities from the island and deposited in ANSP (A 18855/1), CGH (7 paratypes), SMF (311979/1) TFMC (MT 0311/2), ZMH (2748/1) and AIT.

Type Locality

Tamolde, La Gomera Island.

Etymology

The specific name derives from the Latin *falcifer* ("sickle carrier"), due to the shape of penis.

Habitat and Distribution

A species endemic to east La Gomera, occurring in a small area with lowland vegetation and pinewood, at an altitude between 200 and 600 m (Fig. 5).

Animal

Body whitish-beige, with numerous small beige spots, more dense at head. Mantle and tail with darker grey spots. Lateral band short, blackish-grey. Foot sole sometimes with marginal grey spots.

Shell

Oblong, with 2.75 whorls. Pits in spiral rows on protoconch and up to the end of second whorl where they become smaller to disappear at the beginning of third whorl (Fig. 2D).

Genital System

Shown in Figure 4D; eight specimens dissected. Penis as long as vagina (including its glandula amatoria portion), with proximal portion curved, entire penis being sickle shaped when extended after dissection; proximal penis with an empty zone at its beginning, which is narrower than the rest. Laminar crest narrow, vestigial in some specimens. Torus big, starting after the empty zone at the beginning of proximal penis. Distal torus thin, partially surrounding the penial papilla and extending into the distal penis as a thick pilaster, which ends in a small slope with transversal furrows, reminiscent of a fingerprint.

Distal vagina with thin internal longitudinal fold, nearly twice as long as glandula amatoria portion and little longer than both free oviduct and bursa copulatrix duct. Glandula amatoria with spout well protruding.

Comments

Other than the characters listed in the diagnosis, *P. falcifera,* n. sp., differs from all the other species herein described for: penis sickle shaped when extended after dissection; at its beginning the proximal penis has an empty zone. The vagina has a thin internal longitudinal fold.

Plutonia mascaensis
(Morales, 1987)

Insulivitrina mascaensis Morales, 1987, in Ibáñez et al.: 133–135, 139, figs. 7, 14, 26–28, 36, 47, 48, 51 [loc. typ.: Barranco de Masca, Tenerife].

Diagnosis

As for *P. falcifera,* n. sp., but the proximal penis ends pointed and lacking an empty zone.

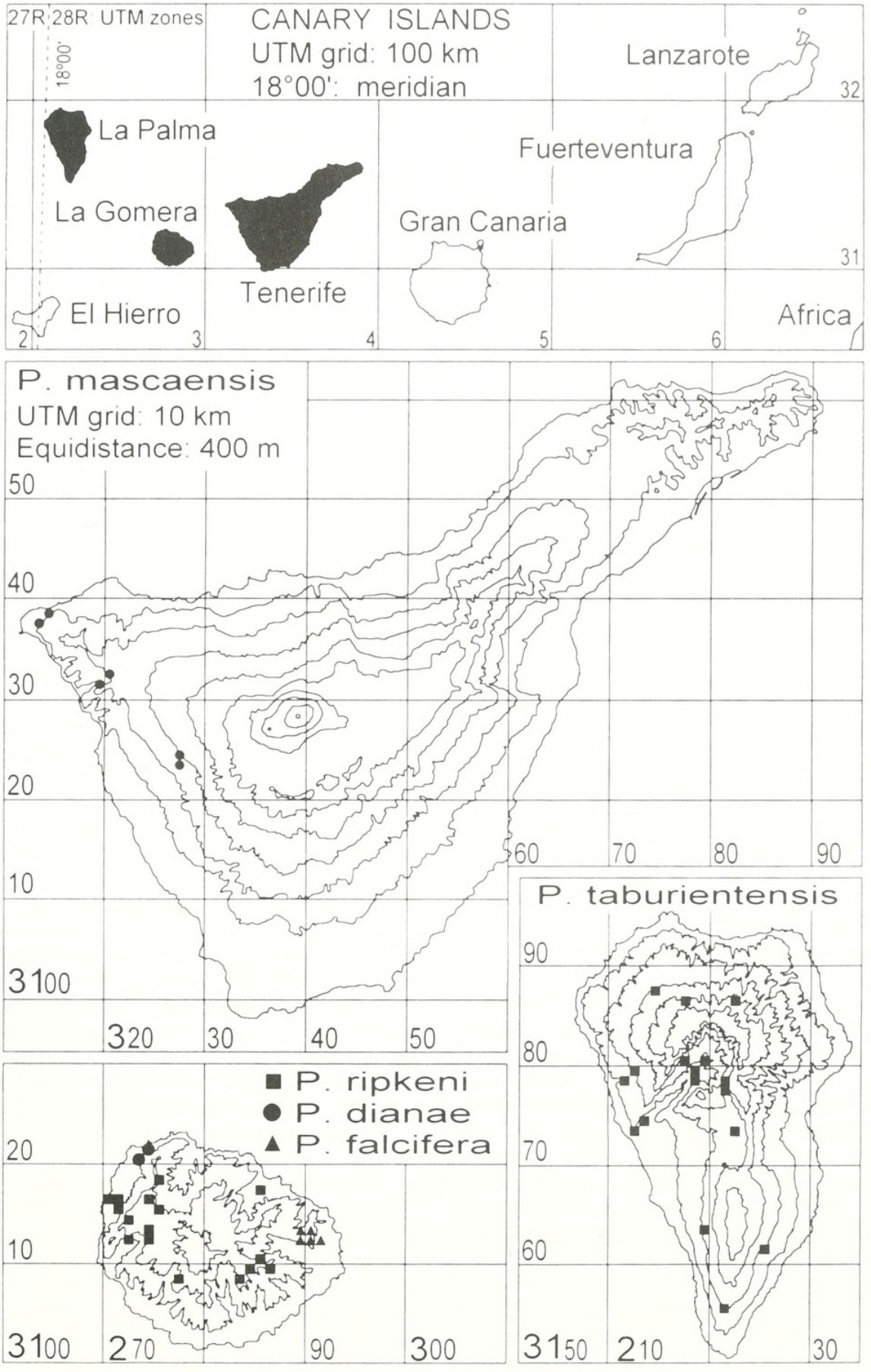


FIG. 5. Geographical distribution of the *Canarivitrina*, n. subgen, species; the symbols represent 1 × 1 km squares.

Type Material

Holotype (AIT) and 114 paratypes, deposited in ANSP (A18856/2), CGH (2 paratypes), FMNH (205917/1), MHNG (984647), MNHN, NHM (1986130/2), NNM (55862/1), SMF (305945/2), TFMC (MT 0310/2), ZMH (2749/2) and AIT.

Habitat and Distribution

A species endemic to west Tenerife, occurring in areas with lowland vegetation or pinewood, at an altitude between 90 and 1,100 m (Fig. 5).

Animal

Body whitish-grey, with numerous small darker grey spots, more dense on mantle, head and tail areas. Lateral band grey, blurred. Some specimens have foot sole uniformly whitish.

Shell

Slightly oblong, with 2.5 whorls. Pits in spiral rows on protoconch and teleoconch, becoming smaller after first whorl to disappear at end of second whorl.

Radula

Formula: 29M + 10L + C (Ibáñez et al., 1987: figs. 26–28); marginal teeth with very small ectocone.

Genital System

Shown in Figures 2J, 4E; 18 specimens dissected. Penis longer than vagina (including its glandula amatoria portion), generally coiled in natural position, fringed on one side. Proximal penis very long, proximally pointed. Distal penis short, slightly widened. Laminar crest narrow, sometimes vestigial. Distal torus thin, partially surrounding penial papilla and extending into distal penis as a thick pilaster, which ends in a small distal slope with transversal furrows, reminiscent of a fingerprint.

Vagina twice as long as the glandula amatoria portion, one-third longer than free oviduct and little longer than bursa copulatrix duct, with two thick internal longitudinal folds which converge near the atrium. Glandula amatoria with small spout, almost blunt.

Comments

Other than the characters listed in the diagnosis, *P. mascaensis* differs from the other species described herein because the penis, coiled in natural position, is fringed on one side; from P. falcifera, n. sp., it also differs in not having a sickle-shaped penis, its penis instead having a shorter distal portion and a longer proximal portion.

DISCUSSION

The five species are cohesive and probably represent a distinct supraspecific taxon, ST, due to the following synapomorphies: genital system with long penis divided into two portions; proximal penis long and slender, with penial retractor muscle inserted at apex and with two internal parallel longitudinal structures, a torus and, opposite, a velum; distal penis short and slightly widened, containing a globular to cylindrical and perforated penial papilla level with the entrance of the vas deferens into the same penis (far from the penial apex); penial papilla and torus coated by glandular tissue (the "penial gland").

ST differs from all the other Plutoniinae in the following autapomorphy: proximal penis long and equipped with two internal parallel longitudinal structures, torus and velum. Following the praxis of traditional taxonomy, this autapomorphy is sufficient to support inclusion of ST in a distinct supraspecific taxon closely related to the other Macaronesian Plutoniinae.

The structure of the glandula amatoria in ST and in the other Plutoniinae supports the hypothesis of a homology with the sarcobelum of *Semilimax,* even if the latter is distinct from the proximal vagina. The homology was advanced by Simroth (1886, 1889), rejected by Wiegmann (1886), and later accepted by several authors, such as Hesse (1923), Schileyko (1986), and Hausdorf (1995).

To verify the status (genus/subgenus) of ST, that of the other Macaronesian Plutoniinae and their relationships we applied a cladistic approach.

Plutoniinae Phylogenetic Relationships

Explanations of the characters used in the phylogenetic analysis; the numeration refers to Table 2 and 3 and the cladogram (Fig. 6). In

these explanations and Table 3, we utilize the name *Plutonia* in the old sense, that is, only for *P. atlantica.*

(1) Shell. *Semilimax,* as well as ST, *Arabivitrina, Insulivitrina, Phenacolimax,* and Madeirovitrina have an external shell with more than 1.5 whorls, into which the animal cannot withdraw.

Gallandia and *Guerrina* have a conical-depressed shell, keeled in *Guerrina* and *Gallandia lederi,* with a small aperture through which the animal can withdraw entirely.

Plutonia has a reduced, capuliform, internal oval shell, with about half a whorl.

(2) Teleoconch ornamentation. ST, *Insulivitrina, Madeirovitrina,* and *Phenacolimax* have a glossy teleoconch, like *Semilimax.*

The *Arabivitrina* teleoconch ornamentation is variable (see Appendix).

Gallandia lederi and *G. olympica* have an entirely ribbed teleoconch, with the ribs ramified and interconnected in *G. olympica; G. annularis* has a glossy teleoconch. Therefore the character state is variable within the genus.

Guerrina has an entirely and very densely ribbed teleoconch, with a pattern different from that of *Gallandia lederi* and *Gallandia olympica.*

Plutonia has the teleoconch with concentric growth lines but the shell is internal and its ornamentation is not comparable with that of the other Plutoniinae.

(3) Radula. *Semilimax,* as well as almost all the Vitrinidae, has the radula of the dichoglossan type.

The radula of *Plutonia* belongs to the beloglossan type.

(4) Location of the glandula amatoria. In *Semilimax,* this is a club-like atrial diverticulum distinct from vagina.

All the Plutoniinae have a glandula amatoria fused with proximal vagina.

(5) Penis. *Semilimax,* as well as *Arabivitrina, Gallandia, Guerrina, Insulivitrina, Madeirovitrina, Phenacolimax,* and *Plutonia,* have a penis without a long proximal portion equipped with torus and velum.

ST has a penis with a long proximal portion equipped with torus and velum.

(6) Penial sheath. *Semilimax* and *Phenacolimax* have a strong penial sheath.

In the other Plutoniinae, the penial sheath is rudimentary or absent.

(7) Penial retractor muscle. *Semilimax,* as well as *Arabivitrina, Gallandia,* and *Phenacolimax,* have the penial retractor muscle with a normal course between its insertions, free from the right optic nerve.

In ST, *Guerrina, Insulivitrina,* and *Madeirovitrina* the penial retractor muscle has a peculiar course, rounding the right optic nerve (Fig. 3G).

Plutonia has no penial retractor muscle, probably due to a secondary reduction originating independently from that of *S. semilimax.*

(8) Vaginal retractor muscle. ST, *Arabivitrina, Gallandia, Guerrina, Insulivitrina, Phenacolimax,* and *Plutonia* have no vaginal retractor muscle, like *Semilimax.*

Madeirovitrina, with the exception of *M. albopalliatus* (see above), has a vaginal retractor muscle.

(9) Oviducal retractor muscle. ST, *Arabivitrina, Gallandia, Guerrina, Insulivitrina, Madeirovitrina,* and *Phenacolimax* have no oviducal retractor muscle, like *Semilimax.*

Plutonia has a short oviducal retractor with a branch inserting at the bursa copulatrix duct.

Cladistic Analysis

The Plutoniinae phylogenetic relationships are not easy to establish, because it is not yet possible to determine the state of several characters which initially appear to be taxonomically interesting, due to insufficient knowledge, intrageneric variability or redundancy (see Appendix).

Character 7 was treated as ordered by the possible synapomorphy of one Azorean *Insulivitrina* species and *Plutonia atlantica,* referred to the absence of the penial retractor muscle (as indicated in the Comments after the description of the genus *Plutonia*); a similar scenario was found also in the outgroup. (*Semilimax semilimax* does not have a penial retractor muscle but one is present in *S. kotulae,* free from the right optic nerve: see Appendix.)

Character 4 justifies the monophyly of the Plutoniinae with respect to the outgroup. Unfortunately, only three other characters (1, 6 and 7) are phylogenetically informative; the remaining characters (2, 3, 5, 8, and 9) are only found in one taxon.

Eight informative (but not resolutive) trees from the matrix (Table 3) were found. However, the strict consensus of these trees shows the Plutoniinae as the sister group of

Semilimax (character 4) and *Phenacolimax* as the sister group of the remaining Plutoniinae (character 6). Moreover, the eight trees show ST (key C), *Insulivitrina* (key F), and *Madeirovitrina* (key G) grouped together at the same level. The trees are as follows:

tree 1 = (A((B(CFG)(D(EI)))H))
tree 2 = (A((B(C(DEI)FG))H))
tree 3 = (A((B(CDEFGI))H))
tree 4 = (A((B(CEFGI)D)H))
tree 5 = (A((B(CFGI)(DE)H))
tree 6 = (A((BC(DEI)FG)H))
tree 7 = (A((B(C(DE)FGI))H))
tree 8 = (A((BC(DE)FGI)H))
Strict consensus tree = (A((BCDEFGI)H))

Figure 6 represents tree number 4 of the analysis, with a consistency index (CI) of 0.917, a retention index (RI) of 0.800 and a rescaled CI index (RC) of 0.733. This tree shows a probable phylogenetic scenario with the Macaronesian taxa included in the genus *Plutonia* (of which *Insulivitrina* is a new synonymy), with a single conflict: the character state 1.1 ('shell external, the animal can withdraw into it') appears in *Gallandia* and *Guerrina,* but it could be homoplasic. This supposition is based on:

(A) *Guerrina* clearly differs from *Gallandia* and belongs to the genus *Plutonia.* This is demonstrated by the fact that it shares the same synapomorphy (the peculiar course of the penial retractor) which links all the other taxa of the *Plutonia* group.

(B) The capacity of the animal to withdraw into the shell is related to the respective dimensions and the shell form; the suitable relation could be acquired independently in *Gallandia* and *Guerrina.*

(C) The independent action of the Vitrinidae limacization process, found in *Semilimax, Insulivitrina,* and *Madeirovitrina,* as well as in other Vitrinidae; these taxa have some species with the ventral side of the shell well developed and other species with the shell auricular with very wide aperture and very reduced ventral side (see Appendix). The Guerrina shell form could have originated as a phase opposite to the auricular form in the limacization process of the genus *Plutonia.*

(D) *Gallandia* and *Guerrina* live at opposite ends of the geographical range of the Plutoniinae.

After excluding character 1 of the analysis, only one tree was found: the same one represented in Figure 6, with a consistency index (CI) of 1.0000.

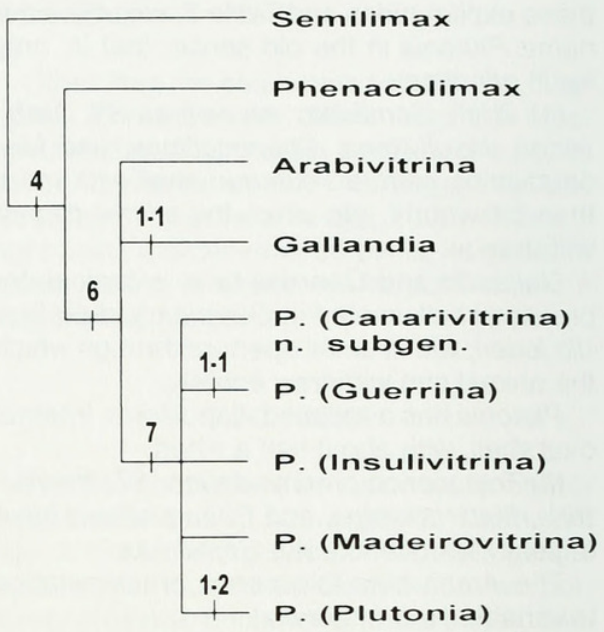


FIG. 6. Hypothesis of phylogeny of Plutoniinae. Numbers refer to characters listed within the Table 2.

CONCLUSIONS

(1) The subfamily Plutoniinae includes the genera *Phenacolimax, Gallandia* (which is almost certainly a junior synonym of *Oligolimax,*) *Arabivitrina,* and *Plutonia.*

(2) The genus *Phenacolimax* is the sister group of the remaining Plutoniinae.

(3) The supraspecific taxon ST has a subgeneric category in the genus *Plutonia,* which also includes the subgenera *Plutonia,* s. str., *Guerrina, Insulivitrina,* and *Madeirovitrina.*

(4) We describe the supraspecific taxon ST as follows:

Subgenus ***Canarivitrina***
Valido & Alonso, n. subgen.

Type species: *P.* (*C.*) *taburientensis* Groh & Valido, n. sp.

Diagnosis

Plutonia with a long penis divided into two portions. Proximal portion long, slender, with penial retractor muscle inserted at apex and two internal parallel longitudinal structures: torus and, opposite, velum. Distal portion short, slightly widened, containing a globular to cylindrical and perforated penial papilla level with entrance of the vas deferens into penis (far from proximal apex). Penial papilla

and torus coated by glandular tissue, the "penial gland".

BIOGEOGRAPHY

The monophyly of the Macaronesian Plutoniinae has biogeographical implications. The three archipelagoes housing these Plutoniinae, plus the Cape Verde Islands (which also house a vitrinid, probably a Plutoniinae: Groh, 1983) are often considered to form a biogeographic unit called Macaronesia (= "fortunate islands"), located in the north-eastern Atlantic at the western fringe of the Palaearctic. The Azores are the most remote from continental land, nearly in the centre of the Atlantic, and are situated at about 850 km NW of Madeira, the latter lying about 650 km from Morocco.

The Canary Islands lie about 450 km south of Madeira, about 500 km north of the Tropic of Cancer, and their easternmost island is only 100 km distant from Morocco. Land bridges with Morocco have been hypothesized in the past but today the oceanic origin of all the Canary Islands is currently attributed to the activity of a hotspot in the Earth's mantle (Holik et al., 1991; Carracedo et al., 1998).

The oldest island of the Azores dates back nearly 5.5 Ma (Nunn, 1994), the oldest part of the Madeiran archipelago has an age between 13–20 Ma (Mitchell-Thomé, 1976) and that of the Canaries, 22.5 Ma (Ancochea et al., 1993).

The present subtropical flora of the three northern archipelagoes, which includes the evergreen laurel-forest or "laurisilva," is closely related and also with that of the Miocene and Pliocene of the Mediterranean region. Nevertheless, the fauna is different, although it is predominantly of a Palaeartic origin (the Azores have also Neartic affinities; Eason & Ashmole, 1992). The flora and fauna of the Cape Verde Islands show a remarkably strong Ethiopian influence, especially of the region called Saharo-Sindian, (Lobin, 1982), but it also include some relicts of the laurel-forest. With respect to the malacofauna there is a mixture of Palaeartic, Ethiopian and Macaronesian elements in equal portions (Groh, 1983). As Baez (1993) indicated, most of the Madeiran faunal groups present more affinities with those of Central Europe than with those of the Mediterranean area. The contrary is true for the neighbouring Canary Islands. Waldén (1984) concluded that "the most conspicuous difference between the mollusc faunas of Madeira and the Canary Islands is the complete absence of taxa with NW African affinities on Madeira".

The different faunistic composition of these archipelagoes is probably due, at least partially, to the different origin of the colonizers that landed on them after the Pleistocene glaciations. The Azorean fauna and flora are much less diverse than those of the other archipelagoes (Ashmole et al., 1996).

A conspicuous example of the different faunistic composition is offered by the Buliminidae, a taxon present with different subfamilies on the Azores and the Canaries (Hesse, 1933; Henriquez et al., 1993). The Madeiran archipelago lacks Buliminidae, their niches occupied by the Clausiliidae, a group absent from the Azores and the Canaries (Neubert & Groh, 1998).

Eason & Ashmole (1992) evidenced isolation of the Azores to be severe and that it depends not only on their distance from continents, but also on meteorological and oceanographic conditions, which are not conducive to the arrival of animals or plants by sea from western Europe or Africa. Surface currents are, in fact, basically from the west throughout the year. The same authors also pointed out that water circulation in the North Atlantic was in a highly dynamic state around the end of the last glaciation and earlier in the Pleistocene, and that colonization by the ancestors of the modern Azorean forms might have occurred during a relatively short phase in one of the glaciation cycles during which oceanic currents were more conducive to colonization than they are at present.

As for the Madeiran fauna, Baez (1993) suggested it must have been originated mainly by anemochore or idrochore transoceanic colonization. Nevertheless, the seamounts along the Madeira-Iberian crest may have provided stepping stone islands in early times.

Finally, the Canary Islands colonization has probably taken place from northwest Africa, which in the past was covered by dense forests and had mighty rivers (Baez et al., 1983). In the Miocene-Pliocene, the Atlantic Moroccan rivers would drag vegetation islets, floating rafts, that would be transported to the nearby coasts of the Canarian archipelago by the trade winds and the marine streams. The wadi Drâa was the most probable colonizing source because its mouth is located opposite

to Lanzarote and Fuerteventura, the easternmost Canarian Islands.

We consider that the presence of *Plutonia* on the three (or four) archipelagoes is not recent, but probably as old as the humid laurel-forest, that is, existing long before the Pleistocene glaciations, as Waldén (1984) suggested, and that the evolution of the genus took place in all archipelagoes in a period preceding the Pleistocene glaciations. The *Plutonia* species survived the glaciations probably associated to the Tertiary relict forest and later on they conquered some others of their present biotopes, whereas their extinction in the continental lands may also be associated to the extinction of the laurel-forest.

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APPENDIX. TAXONOMIC COMPARISON OF THE GENUS-GROUP TAXA

Semilimax (anatomical data taken mainly from Schileyko, 1986). Shell variable in shape: auricular with very wide aperture and reduced ventral side (*S. semilimax*) or with ventral side well developed (*Vitrina carniolica* O. Boettger, 1884: Grossu, 1983). Animal cannot withdraw into shell. Teleoconch glossy. Right shell lobe rather narrow, twisted backwards to cover shell apex. Radula dichoglossan (Jungbluth et al., 1985). Genital atrium short (Fig. 1). Penis short, without long proximal portion (torus and velum consequently absent). The presence of a perforated penial papilla needs verification. *Semilimax semilimax* does not have a penial retractor muscle, but one is present in *S. kotulae* (Westerlund, 1883), free from the right optic nerve. "Glandula amatoria" voluminous, oblong oval or club-shaped, not covered by soft tissue, located in atrial sarcobelum, which wall invaginates sheathing the spout (no data available about connection between invaginated sarcobelum wall and spout wall). Vagina short.

Arabivitrina (anatomical data taken mainly from Neubert, 1998). Shell medium to large, auricular to subglobose, with 3–3.5 whorls. Animal cannot withdraw completely into shell (at least in *A. jansseni*). Teleoconch ornamentation variable, almost smooth, sometimes with blunt axial riblets in several species (as in type species, *Vitrina arabica* Thiele, 1910), or without blunt axial riblets. Aperture bordered by a small periostracal fringe. Right shell lobe rather narrow, twisted backwards to cover shell apex. Radula dichoglossan. Genital atrium long. Penis as a broad tube, about as long as vagina, without long proximal portion (torus and velum are consequently absent); with a longitudinal pilaster consisting at least of an apical glandular part followed by a narrow to broadened part with transverse lamellae. Typical penial papilla missing.

Penial retractor free from right optic nerve. Vas deferens entering penis subapically, then turning towards retractor insertion area to run inside glandular tissue of apical organ and open at apex. Distal vagina and glandula amatoria similar in length. Glandula amatoria covered with soft tissue, large, club-shaped to oblong oval, but *A. darnaudi* has a short glandula amatoria. Invaginated vaginal wall and spout wall entirely connected by strong connective fibres in *A. jansseni.*

Gallandia (anatomical data taken mainly from Hausdorf, 1995). Shell conoid-globose, with 2.5–3.25 whorls and small aperture. Teleoconch entirely ribbed or glossy. Animal can withdraw more-or-less entirely into shell. Shell and mantle lobes reduced (as Hausdorf, 1995, stated, this reduction is connected with the fact specimens can withdraw completely into the shell). Radula dichoglossan. Genital atrium long. Penis short, without long proximal portion (torus and velum consequently absent). Vas deferens entering subapically at penis, under penial gland. Penial retractor free from right optic nerve. Glandula amatoria small, club-shaped to oblong-oval, sometimes partially covered by soft tissue, arranged like a flower calyx (no data available about connection between invaginated vaginal wall and spout wall).

Guerrina (anatomical data taken mainly from Ibáñez et al., 1987, and Valido et al., 1993). Shell slightly depressed, keeled, conical above, with 3.25–3.75 whorls and small aperture. Teleoconch entirely and densely ribbed. Animal can withdraw entirely into shell. Shell lobes and right body lobe of mantle very small, not evident in live specimens; left body lobe small. Radula dichoglossan. Penis short, with perforated penial papilla and two small portions, the homologies of which are unclear because of different location of insertion of penial retractor in *G. cuticula* and *G. christinae;* without long proximal portion (torus and velum consequently absent). Vas deferens entering penis laterally, between the two portions. Penial retractor rounding right optic nerve. Glandula amatoria small, spheroidal, with proximal end covered with soft tissue, arranged like a flower calyx. Distal vagina very long, up to four times longer than glandula amatoria portion. Invaginated vaginal wall and spout wall entirely connected by thin connective fibres.

Insulivitrina (anatomical data taken mainly from Ibáñez et al., 1987). Shell variable in shape, as in *Semilimax.* Teleoconch glossy. Animal cannot withdraw into shell. Right shell lobe well developed, covering almost entire shell in undisturbed conditions, but disturbed specimens (Ibáñez et al., 1987: figs. 6, 8) show this lobe similar to those published for *Semilimax semilimax, S. pyrenaicus* (A. Férussac, 1821), and *Phenacolimax major* (Falkner, 1989: 173; 1992: 270–271; Kerney et al., 1979, pls. 6, 7). Radula dichoglossan with variable marginal teeth (finger-shaped with or without ectocones, or multicuspid). Genital atrium variable in length. Penis short, without long proximal portion (torus and velum consequently absent) and with perforated penial papilla. Vas deferens entering penis apically to subapically. Penial retractor rounding right optic nerve. Glandula amatoria covered with soft tissue, usually voluminous, club-shaped to oblong-oval, but *Insulivitrina canariensis* (Mousson, 1872) has a small glandula amatoria. Distal vagina similar in length or even shorter than glandula amatoria portion. Invaginated vaginal wall and spout wall entirely connected by thin connective fibres.

Madeirovitrina (anatomical data taken mainly from Groh & Hemmen, 1986). Shell variable in shape, as in *Semilimax.* Teleoconch glossy. Animal cannot withdraw into shell. Right shell lobe well developed, covering almost entire shell in undisturbed conditions. Radula dichoglossan. Genital atrium medium to long. Penis large and proximally globe-shaped, with perforated penial papilla subapical and without long proximal portion (torus and velum consequently absent). Vas deferens entering penis subapically. Penial retractor rounding right optic nerve. Glandula amatoria voluminous, club-shaped to oblong-oval, covered with soft tissue. Invaginated vaginal wall and spout wall entirely connected by thin connective fibres. Distal vagina wide and shorter than glandula amatoria portion, with a strong vaginal retractor muscle. (*Madeirovitrina albopalliatus* Groh & Hemmen, 1986, differs from the other species in its tubular penis and the absence of a vaginal retractor muscle; this species should there-

fore be referred to another genus, possibly *Insulivitrina*).

Phenacolimax (anatomical data taken mainly from Forcart, 1957; Hausdorf, pers. comm., and our own unpublished data). Shell globose-depressed, with 2.5–3.25 whorls and small aperture. Teleoconch glossy. Animal cannot withdraw into shell. Right shell lobe rather narrow, twisted backwards to cover shell apex. Radula dichoglossan. Genital atrium very short. Penis long, tubular, with a clear constriction wrapped by a short but strong penial sheath (similar to those shown by Schileyko, 1986: figs. 11–12, in *Eucobresia*); without long proximal portion (torus and velum consequently absent) and with perforated penial papilla. Vas deferens running inside penial sheath and entering penis subapically. Penial retractor free from right optic nerve. Glandula amatoria small, not completely covered by soft tissue (no data available about connection between invaginated vaginal wall and spout wall). Distal vagina and glandula amatoria similar in length.

Plutonia (referred to *P. atlantica;* anatomical data taken mainly from Wiktor & Backeljau, 1995). Shell entirely hidden by the mantle (shell lobes absent), oval, vestigial, whitish, transparent, with about half a whorl and a wide aperture. Teleoconch with growth lines. Radula beloglossan, with dagger-shaped teeth. Vas deferens entering penis apically. Penis short, without long proximal portion (torus and velum consequently absent), penial papilla and penial retractor. Glandula amatoria voluminous, club-shaped to oblong-oval (no data available about connection between invaginated vaginal wall and spout wall). Distal vagina similar in length or even longer than glandula amatoria portion. Short oviducal retractor with one branch inserted into bursa copulatrix duct.