

## On the relationships of the genus *Napaeus* (Gastropoda: Pulmonata: Enidae) with the descriptions of four new species from the Canary Islands

Yurena Yanes<sup>a</sup>, Javier Martín<sup>b</sup>, Leopoldo Moro<sup>c</sup>, María R. Alonso<sup>d</sup> and Miguel Ibáñez<sup>d\*</sup>

<sup>a</sup>Roy M. Huffington Department of Earth Sciences, Southern Methodist University, Dallas, TX 75275-0395 USA; <sup>b</sup>El Coromoto, La Laguna, 38206 Spain; <sup>c</sup>Centro de Planificación Ambiental (CEPLAM), La Laguna, 38206 Spain; <sup>d</sup>Department of Animal Biology, University of La Laguna, La Laguna, 38206 Spain

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Species of the *Napaeus* subgenera show incongruences between genital anatomy and molecular phylogenetic data. In this study, four new *Napaeus* species from the Canary Islands are described. Shell drawings of the 56 known *Napaeus* species were obtained from shell photographs for comparison. Differences between some genital system character-states of the species described here and those of the original subgenera descriptions are evident. Consequently, in the absence of phylogenetic analyses, the new species are not assigned to the *Napaeus* subgenera. In addition, the possible relationships among Macaronesian enids are preliminarily evaluated.

Within the Macaronesian region, enids are exclusively present in the Canaries and the Azores. The absence of enids from Madeira, combined with the differences in genital anatomy between the Canarian and Azorean enids and the relatively large distance between these archipelagos, may indicate different immigration pathways (Africa/Europe, respectively) and possibly different phylogenetic origins for the Canarian and Azorean enid populations.

**Keywords:** Macaronesian enids; taxonomic controversy; colonization pathways

### Introduction

Several volcanic and oceanic archipelagos, including the Azores, Madeira, Salvages, the Canaries and Cape Verde, are grouped in the Macaronesian biogeographic region (Webb and Berthelot 1845) of the northeast Atlantic Ocean. However, the biogeographic utility of this cluster of archipelagos has been questioned owing to several geophysical and biological dissimilarities among them (Beyhl et al. 1995; Borgen 1995).

The family Enidae is represented by a few species in the Azores and by numerous species in the Canaries (Martins 1989; Bank et al. 2002). Interestingly, this family is absent in Madeira, the archipelago situated between the Azores and the Canaries (Figure 1A) (Backhuys 1975; Waldén 1984); Salvages, located between Madeira and the Canaries; and Cape Verde, situated to the south of the Canaries. Reasons as to why enids successfully colonized two out of the five Macaronesian archipelagos are still unexplored. Possibly, a combination of several geographical (i.e., island age,

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\*Corresponding author. Email: mibanez@ull.es

area, location, etc.) and ecological (i.e., colonization patterns, range of habitats available, etc.) factors (Parent and Crespi 2006) may explain the observed distribution and richness of enids in the Macaronesian region.

Initial taxonomic surveys of the Canarian and Azorean enids were morphologically based. The Canarian enids have a penial appendix and were placed in the genus *Napaeus* Albers, 1850. In contrast, the Azorean enids lack the penial appendix (Backhuys 1975; Martins 1989) and were grouped in *Macaronapaeus* Kobelt, 1899 by Bank and Neubert (1998) who considered *Macaronapaeus* as a subgenus of *Napaeus*.

The genus *Napaeus* has experienced an outstanding radiation in the Canary Islands. In fact, *Napaeus* is the richest genus, with up to 51 living species (Ibáñez et al. 2007) and one extinct species (Castillo et al. 2006) described to date. *Napaeus* species generally display a distribution restricted to a small area within a single island (i.e., single insular endemism), a characteristic exhibited by the majority of the endemic Canarian land snail species. Paradoxically, the Enidae in the Azores have not radiated as remarkably as in the Canary Islands; only seven species are currently known (Bank et al. 2002).

The subgeneric location of new *Napaeus* species has been problematic because different modes of classification (i.e., genital anatomy and molecular phylogeny: Alonso, Goodacre, et al. 2006) have been controversial for this taxonomically complex genus. Hesse (1933) described two subgenera of *Napaeus* based on the genital system anatomy of some species, both subgenera being indistinguishable by shell morphology alone: (1) subgenus *Napaeus* Hesse, 1933: Bursa duct without diverticulum (albumen gland curved in its end; retractor muscle single on the diaphragm insertion, but later forked; epiphallus without caecum); and (2) subgenus *Napaeinus* Hesse, 1933: Bursa duct with a diverticulum (albumen gland not curved; retractor muscle forked on the diaphragm insertion; epiphallus with a caecum).

The genital system anatomy was initially known for only eight species: *N. helvolus* (Webb and Berthelot, 1833), *N. badius* (Webb and Berthelot, 1833), *N. variatus* (Webb and Berthelot, 1833), *N. bertheloti* (L. Pfeiffer, 1846), *N. baeticatus* (Webb and Berthelot, 1833), *N. tabidus* (Shuttleworth, 1852), *N. moquinianus* (Webb and Berthelot, 1833) and *N. nanodes* (Shuttleworth, 1852) (Krause 1895; Sturany and Wagner 1914; Wagner 1928; Odhner 1932; Hesse 1933). Since the majority of these species could not be catalogued in the appropriate subgenus solely based on genital system anatomy, three conchological groups were later established based on shell morphology to define a preliminary identification scheme and/or description of new *Napaeus* species: (1) the *N. nanodes* group, initially with six species (Henríquez et al. 1993b); (2) the *N. baeticatus* group, composed of three species (Henríquez 1993a); and (3) the *N. variatus* group, originally with 17 species (Alonso et al. 1995).

Henríquez et al. (1993a,b) have shown discrepancies between some details of the genital system anatomy of three *Napaeus* species and the original subgenera descriptions. Furthermore, Alonso, Goodacre, et al. (2006) found inconsistencies between anatomical and molecular data in the two subgenera; only the character-states “epiphallus with/without a caecum” of these subgenera appeared to coincide with the molecular study.

In the present study, four new *Napaeus* species from western La Gomera and northeastern Tenerife (Canary Islands) are described based on shell morphology and genital system anatomy. In addition, the taxonomic relationship between the new described species and the two Hesse (1933) subgenera, as well as the relationship between *Napaeus* (Canary Islands) and *Macaronapaeus* (Azores) are discussed.

## Methods

The geographic distribution map (Figure 1B) was produced using MapViewer software (Golden Software, Inc.). The photographic methodology was described by Ibáñez et al. (2006). The shell outline drawings of all species were obtained semi-automatically, directly from TIFF images of the shells, as follows: (1) the black background of the TIFF image was selected with the “magic wand” tool of the photographic software used (Paint Shop Pro, Jasc Software, Inc.); (2) a layer of some pixels were subtracted from the obtained selection; (3) the black colour of the selected area was changed to the white; (4) the suture lines and inner aperture lines of the shell were drawn (in black colour) directly upon the shell photograph image using the “pencil” tool, and, lastly; (5) the shell outline drawing was transferred to a white background and the colour depth was decreased to 1 bit (which renders only black and white colours). About half of the shell drawings (Figures 2–5) correspond to type material of the respective species.

Standardized measurements of the shells were taken as shown in Figure 2. The measurements (Table 1) were obtained following Alonso, Nogales, et al. (2006) using the software *analySIS*<sup>®</sup> (Soft Imaging System GmbH). All the shells were oriented to a Cartesian coordinate system with the shell axis (columella) aligned to the Y-axis and the maximum shell breadth represented accurately in plane view. The straight linear shell measurements were obtained from the projections of the respective structures on the X- and Y-axes. Unfortunately, the sample size available for many species was too small (see Table 1) to be statistically significant. Consequently, only comparative scatter-plots of the shell measurements were explored (Figure 6). Different combinations of shell measurements of the new species studied here and those of the species conchologically similar to them are shown in Figure 6. Some of the most commonly used straight linear measurements in the bibliography (shell height and shell breadth: Figure 6A, D, E) were evaluated together along with more specific discriminants, such as surface and perimeter measurements of diverse parts of the shell (Figure 6B, C, F–H).

The number of shell whorls was calculated following the Kerney and Cameron (1979: 13) methodology. The conchological terminology, based on the biometric data provided in Table 1, is the same as that of Henríquez et al. (1993b; see also Table 2). The terminology of parts of the penial appendix follows Schileyko (1984: 39, figure 18). “Proximal” and “distal” refer to the position of the respective structure (including the spermatophore prior to mating) in relation to the ovotestis. The distinction between “epiphallus” and “penis” is explained in Alonso and Ibáñez (2007): the insertion of the penial retractor is not the boundary between penis and epiphallus, but rather the internal anatomy of these organs. The taxonomic description of *N. bajamarensis* sp. nov. is given in full while only the main differential characteristics are presented for the remaining three species.

## Abbreviations

AIT	Alonso and Ibáñez collection, Department of Animal Biology, University of La Laguna, Tenerife, Canary Islands, Spain;
CGH	K. Groh private collection, Hackenheim, Germany;
CHB	R. Hutterer private collection, Bonn, Germany;

Table 1. Morphometric data (in mm or mm<sup>2</sup>) of the four new *Napaeus* species described.

Key	<i>N. bajamaricensis</i> sp. nov.				<i>N. tafadaensis</i> sp. nov.				<i>N. tafadaensis</i> irregular morphotype				<i>N. ornamentatus</i> sp. nov.				<i>N. teobaldoi</i> sp. nov.						
	Holo-type	Max	Min	Mean	SD	Holo-type	Max	Min	Mean	SD	Max	Min	Mean	SD	Holo-type	Max	Min	Mean	SD	Holo-type	Max	Min	Mean
SH	18.3	18.9	16.6	18.0	0.7	15.3	16.1	14.0	14.8	0.8	14.1	12.2	13.1	0.7	14.1	14.1	13.4	13.7	0.3	12.8	12.6	12.7	0.1
SB	8.9	9.2	8.3	8.9	0.3	7.8	7.8	6.9	7.3	0.3	6.9	6.4	6.6	0.2	6.0	6.0	5.4	5.8	0.3	6.2	5.7	5.9	0.2
SS	112.8	118.1	102.5	110.4	5.2	78.0	78.0	64.9	71.5	5.5	65.5	49.3	56.7	5.5	57.9	58.3	49.3	54.8	3.6	48.1	45.6	46.9	1.3
SP	44.1	45.2	41.3	43.6	1.3	37.5	38.0	33.8	35.8	1.7	34.3	30.2	32.1	1.5	33.6	33.6	31.6	32.6	0.9	31.4	30.4	30.7	0.5
BH	10.2	11.0	9.4	10.1	0.5	9.0	9.6	8.5	8.9	0.4	8.9	7.7	8.3	0.4	7.4	7.6	6.9	7.3	0.3	6.5	6.5	6.6	0.1
BS	69.8	75.5	61.7	68.5	4.5	53.1	53.1	46.1	49.4	2.9	47.5	36.5	41.8	3.7	35.0	36.8	28.7	34.0	3.1	29.6	29.6	29.0	0.5
BP	33.3	34.4	31.7	32.9	0.8	29.5	29.5	27.0	28.1	1.0	27.5	24.3	25.7	1.1	23.6	24.1	21.7	23.3	0.9	21.7	21.3	21.6	0.2
AH	7.3	8.0	6.8	7.3	0.4	6.5	6.5	5.8	6.1	0.3	6.0	5.5	5.7	0.2	4.9	5.0	4.5	4.8	0.2	4.6	4.4	4.5	0.1
AB	6.0	6.2	5.6	5.9	0.2	5.4	5.4	4.8	5.0	0.3	5.1	4.1	4.6	0.3	4.0	4.3	3.7	4.0	0.2	4.4	4.4	4.1	0.4
AS	30.5	34.3	26.1	30.2	2.5	25.6	25.6	20.3	22.0	2.3	21.8	17.4	19.3	1.8	14.0	14.4	11.6	13.5	1.1	14.1	11.9	13.4	1.3
AP	20.5	22.0	19.1	20.6	0.9	18.6	18.6	16.4	17.2	0.9	17.0	15.4	16.0	0.7	13.8	14.2	12.5	13.6	0.6	13.7	12.7	13.4	0.6
FH	4.9	5.6	4.1	4.8	0.4	3.4	3.7	2.8	3.3	0.3	3.0	2.3	2.7	0.3	4.2	4.2	3.8	4.0	0.2	4.1	3.9	4.0	0.2
FB	6.4	6.8	6.2	6.5	0.2	4.2	4.3	3.7	4.0	0.3	3.6	2.9	3.2	0.3	4.0	4.1	3.6	3.8	0.2	3.4	3.5	3.4	0.1
FS	19.9	22.7	15.5	19.5	2.1	9.2	9.7	6.7	8.5	1.1	7.0	4.4	5.7	1.1	11.1	11.1	9.3	10.1	0.7	9.5	8.6	9.1	0.5
FP	18.7	20.2	16.9	18.8	1.0	12.7	13.4	11.0	12.3	0.9	11.0	8.8	10.0	0.9	13.9	14.0	12.9	13.3	0.4	13.0	12.4	12.6	0.3

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PH	3.1	3.3	2.8	3.1	0.2	2.9	2.9	2.3	2.6	0.2	2.3	1.9	2.1	0.2	2.5	2.2	2.4	0.1	2.2	2.2	2.1	2.2	0.1
PB	7.6	7.9	7.2	7.5	0.2	5.8	5.8	5.3	5.6	0.2	5.2	4.3	4.7	0.3	4.9	4.3	4.7	0.2	4.3	4.3	4.2	4.3	0.1
PS	23.0	24.5	20.1	22.5	1.2	15.7	15.7	11.3	13.6	1.7	11.3	7.7	9.3	1.5	11.8	9.8	10.8	0.9	8.9	9.1	8.3	8.8	0.4
PP	21.2	21.6	19.9	20.7	0.5	16.5	16.5	14.5	15.5	0.8	14.2	11.8	12.9	1.0	14.5	13.2	13.8	0.6	12.4	12.6	12.0	12.3	0.3
SB/SH				0.50				0.49					0.51				0.43						0.47
BH/SH				0.56				0.60					0.63				0.53						0.52
AH/SH				0.41				0.41					0.44				0.35						0.35
AB/SB				0.67				0.69					0.70				0.69						0.69
<i>n</i>				10				6					6				5						3

Notes: *SD*, standard deviation; Min, minimum; Max, maximum; *n*, number of measured specimens; SH, shell height; SB, shell breadth; SS, shell surface (plane view); SP, shell perimeter; BH, body whorl height (at columella level); BS, body whorl surface (plane view); BP, body whorl perimeter; AH, aperture height; AB, aperture breadth; AS, aperture surface (plane view); AP, aperture perimeter; FH, first whorls height; FB, first whorls breadth; FS, first whorls surface (plane view); FP, first whorls perimeter; PH, penultimate whorl height; PB, penultimate whorl breadth; PS, penultimate whorl surface (plane view); PP, penultimate whorl perimeter.

Table 2. Conchological terminology, based on the indices of Table 1.

Slenderness index (SB/SH)	Body whorl height index (BH/SH)	Aperture height index (AH/SH)	Aperture breadth index (AB/SB)
Very slender	< 0.350	Very short	Narrow
Slender	0.350–0.425	Short	Wide
Obese	0.425–0.500	Long	Very wide
Very obese	> 0.50		
	< 0.50	< 0.30	< 0.60
	0.50–0.60	0.30–0.38	0.60–0.70
	0.60–0.66	> 0.38	> 0.70
	> 0.66		

Notes: SB, shell breadth; SH, shell height; BH, body whorl height (at columella level); AH, aperture height; AB, aperture breadth.

CML	J. Martín private collection, La Laguna, Tenerife, Canary Islands, Spain;
FMNH	Field Museum of Natural History, Chicago, Illinois, USA;
ICZN	International Commission on Zoological Nomenclature;
NHM	Natural History Museum, London, UK;
NMW	National Museum of Wales, Cardiff, UK;
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain;
UTM	Universal Transverse Mercator, cartographic projection system;
ZMZ	Zoologisches Museum der Universität, Zürich, Switzerland.

## Results

The grouping of the *Napaeus* species according to their conchological similarities continues to be a useful method for initial taxonomic comparisons because of the great number of species of the genus. The placement of all the described *Napaeus* species in the three conchological groups previously mentioned is summarized in Table 3. The four new *Napaeus* species have been added to two of the three established conchological groups based on their shell shape and size as follows: *N. bajamarensis* sp. nov. (Figure 4B) and *N. tafadaensis* sp. nov. (Figure 3N, O) in the *N. baeticatus* group; and *N. ornamentatus* sp. nov. (Figure 4F) and *N. teobaldoi* sp. nov. (Figure 4S) in the *N. variatus* group.

## Systematics

### Family ENIDAE B.B. Woodward

Woodward (1903, p. 354, 358); ICZN (2003, Opinion 2018).

### Genus *Napaeus* Albers

Type species by subsequent designation of Herrmannsen (1852): *Bulimus baeticatus* Webb and Berthelot.

### *Napaeus bajamarensis* Ibáñez and Alonso sp. nov.

#### *Type material*

Holotype (Figures 2, 4B, 7A): TFMC (MT 0397). Type locality: Barranco de Vargas, Bajamar, Anaga massif (Tenerife; UTM coordinates: 28RCS7058; 300 m altitude); Leg. Manuel J. Valido and Fátima C. Henríquez, 1 December 1989.

Paratypes: 13 specimens and 160 shells, collected between 1982 and 2009, from the northeast of Tenerife (UTM coordinates: 28RCS6658, 28RCS6757, 28RCS6758, 28RCS6958, 28RCS6959, 28RCS7058, 28RCS7157, 28RCS7259, 28RCS7260, 28RCS7460 and 28RCS8160), deposited in AIT and the following collections: CGH (31 shells), CHB (24 shells), CML (2 shells), NHM (1992154/1), FMNH (158200/6), NMW (Z 1992.072.01/1) and TFMC (24 shells, in 5 lots: MT 0118, 0119, 0135, 0151 and 0152).

Table 3. Arrangement of all the *Napaeus* species described in the respective conchological groups. For synonymies, see Alonso, Goodacre, et al. (2006: 172).

Conchological group	Species name	Island/islet	Illustration
<i>N. baeticatus</i>	<i>N. badius</i> (Webb and Berthelot, 1833)	Tenerife	Figure 3P
<i>N. baeticatus</i>	<i>N. baeticatus</i> (Webb and Berthelot, 1833)	Tenerife	Figure 3G–J
<i>N. baeticatus</i>	<i>N. bajamarensis</i> sp. nov.	Tenerife	Figure 4B
<i>N. baeticatus</i>	<i>N. bertheloti</i> (L. Pfeiffer, 1846)	La Gomera	Figure 3B
<i>N. baeticatus</i>	<i>N. boucheti</i> Alonso and Ibáñez, 1993	La Palma	Figure 4C
<i>N. baeticatus</i>	<i>N. conseqoanus</i> (Mousson, 1872)	La Gomera	Figure 3A
<i>N. baeticatus</i>	<i>N. inflatiusculus</i> (Wollaston, 1878)	La Gomera	Figure 3E
<i>N. baeticatus</i>	<i>N. interpunctatus</i> (Wollaston, 1878)	Gran Canaria	Figure 3K
<i>N. baeticatus</i>	<i>N. obesatus</i> (Webb and Berthelot, 1833)	Gran Canaria	Figure 4D
<i>N. baeticatus</i>	<i>N. savinosa</i> (Wollaston, 1878)	El Hierro	Figure 3D
<i>N. baeticatus</i>	<i>N. servus</i> (Mousson, 1872)	La Gomera	Figure 3L
<i>N. baeticatus</i>	<i>N. severus</i> (J. Mabile, 1898)	La Gomera	Figure 3F
<i>N. baeticatus</i>	<i>N. subsimplex</i> (Wollaston, 1878)	El Hierro	Figure 3C
<i>N. baeticatus</i>	<i>N. tabidus</i> (Shuttleworth, 1852)	Tenerife	Figure 3M
<i>N. baeticatus</i>	<i>N. tafadaensis</i> sp. nov.	Tenerife	Figure 3N, O
<i>N. baeticatus</i>	<i>N. tenoensis</i> Henríquez, 1993	Tenerife	Figure 4A
<i>N. variatus</i>	<i>N. avaloensis</i> Groh, 2006	La Gomera	Figure 4K
<i>N. variatus</i>	<i>N. barquini</i> Alonso and Ibáñez, 2006	La Gomera	Figure 5O
<i>N. variatus</i>	<i>N. beguirae</i> Henríquez, 1995	La Gomera	Figure 5Q
<i>N. variatus</i>	<i>N. chrysaloides</i> (Wollaston, 1878)	Gran Canaria	Figure 5B
<i>N. variatus</i>	<i>N. elegans</i> Alonso and Ibáñez, 1995	Tenerife	Figure 5E
<i>N. variatus</i>	<i>N. encaustus</i> (Shuttleworth, 1852)	La Palma	Figure 4Q
<i>N. variatus</i>	<i>N. esbeltus</i> Ibáñez and Alonso, 1995	Tenerife	Figure 5F
<i>N. variatus</i>	<i>N. exilis</i> Henríquez, 1995	Gran Canaria	Figure 5G
<i>N. variatus</i>	<i>N. gruereanus</i> (Grasset, 1857)	El Hierro	Figure 5N
<i>N. variatus</i>	<i>N. helvolus</i> (Webb and Berthelot, 1833)	Tenerife	Figure 4M
<i>N. variatus</i>	<i>N. huttereri</i> Henríquez, 1991	Alegranza islet (Lanzarote)	Figure 5D
<i>N. variatus</i>	<i>N. indifferens</i> (Mousson, 1872)	Gran Canaria	Figure 5C
<i>N. variatus</i>	<i>N. isletae</i> Groh and Ibáñez, 1992	Gran Canaria	Figure 4O
<i>N. variatus</i>	<i>N. lajaensis</i> Castillo, Yanes, Alonso and Ibáñez, 2006 (fossil)	Tenerife	Figure 4T
<i>N. variatus</i>	<i>N. lichenicola</i> Alonso and Ibáñez, 2007	Fuerteventura	Figure 5M
<i>N. variatus</i>	<i>N. maculatus</i> Goodacre, 2006	La Gomera	Figure 4L
<i>N. variatus</i>	<i>N. maffioteanus</i> (Mousson, 1872)	Gran Canaria	Figure 5A
<i>N. variatus</i>	<i>N. moquinianus</i> (Webb and Berthelot, 1833)	Gran Canaria	Figure 4R
<i>N. variatus</i>	<i>N. myosotis</i> (Webb and Berthelot, 1833)	Gran Canaria	Figure 5L
<i>N. variatus</i>	<i>N. ocellatus</i> (Mousson, 1872)	El Hierro	Figure 4H
<i>N. variatus</i>	<i>N. orientalis</i> Henríquez, 1995	La Gomera	Figure 4G
<i>N. variatus</i>	<i>N. ornamentatus</i> sp. nov.	La Gomera	Figure 4F
<i>N. variatus</i>	<i>N. osoriensis</i> (Wollaston, 1878)	Gran Canaria	Figure 5J
<i>N. variatus</i>	<i>N. palmaensis</i> (Mousson, 1872)	La Palma	Figure 5K
<i>N. variatus</i>	<i>N. procerus</i> Emerson, 2006	La Gomera	Figure 4U
<i>N. variatus</i>	<i>N. propinquus</i> (Shuttleworth, 1852)	Tenerife	Figure 4E

(Continued)

Table 3. (Continued)

Conchological group	Species name	Island/islet	Illustration
<i>N. variatus</i>	<i>N. roccellicola</i> (Webb and Berthelot, 1833)	Tenerife	Figure 5P
<i>N. variatus</i>	<i>N. rufobrunneus</i> (Wollaston, 1878)	Lanzarote	Figure 4V
<i>N. variatus</i>	<i>N. rupicola</i> (Mousson, 1872)	La Gomera	Figure 4J
<i>N. variatus</i>	<i>N. subgracilior</i> (Wollaston, 1878)	La Palma	Figure 5H
<i>N. variatus</i>	<i>N. teobaldoi</i> sp. nov.	Tenerife	Figure 4S
<i>N. variatus</i>	<i>N. variatus</i> (Webb and Berthelot, 1833)	Tenerife	Figure 4P
<i>N. variatus</i>	<i>N. voggenreiteri</i> Hutterer, 2006	La Gomera	Figure 4N
<i>N. nanodes</i>	<i>N. bechi</i> Alonso and Ibáñez, 1993	Tenerife	Figure 5T
<i>N. nanodes</i>	<i>N. doliolum</i> Henríquez, 1993	Tenerife	Figure 5S
<i>N. nanodes</i>	<i>N. nanodes</i> (Shuttleworth, 1852)	Tenerife	Figure 5R
<i>N. nanodes</i>	<i>N. tagamichensis</i> Henríquez, 1993	La Gomera	Figure 5X
<i>N. nanodes</i>	<i>N. taguluchensis</i> Henríquez, 1993	La Gomera	Figure 5V
<i>N. nanodes</i>	<i>N. texturatus</i> (Mousson, 1872)	La Gomera	Figure 5U
<i>N. nanodes</i>	<i>N. pygmaeus</i> Ibáñez and Alonso, 1993	La Gomera	Figure 5Y

### Etymology

The specific name derives from Bajamar, the main area of the species distribution.

### Geographic range and habitat

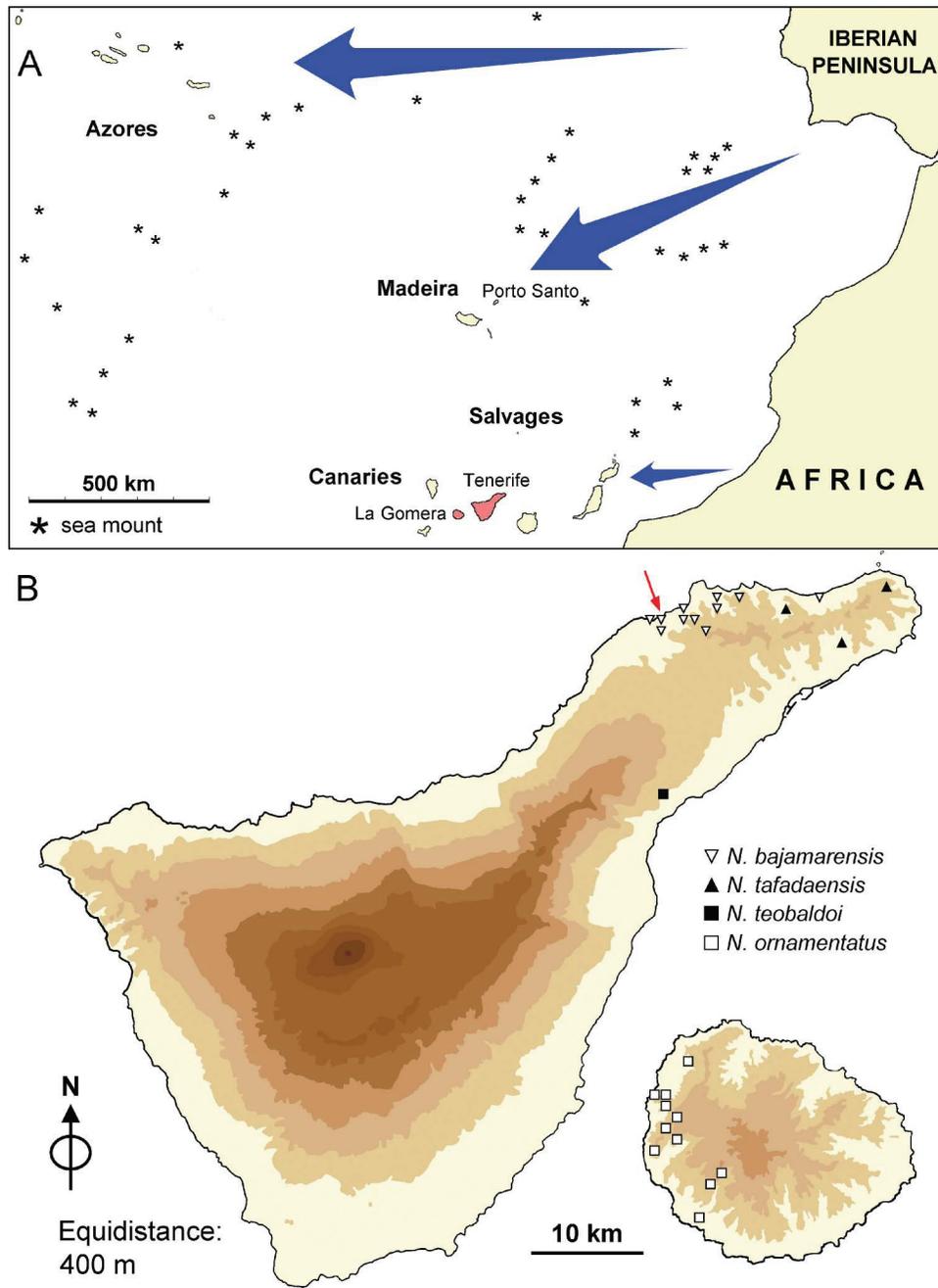
Endemic to Tenerife, occupying an area of about 20 km<sup>2</sup> along the north slope of the Anaga massif (northeast of the island), associated with lowland vegetation and humid subtropical scrub, within an altitudinal range between 20 and 750 m (Figure 1B). The highest locality includes a pine forest. This species is a ground dweller and is the only living *Napaeus* species found also in the Pleistocene Aeolian area of Mancha de La Laja, Bajamar (see arrow in Figure 1B), where the oldest species of this genus (>130 kyr BP) has been collected (Castillo et al. 2006).

### Diagnosis

Shell robust, ovate, pale brown to tan brown coloured, with first whorls darker than the rest. Teleoconch almost smooth. Epiphallus with epiphallar caecum. Bursa copulatrix duct exceptionally long, with a diverticulum.

### Description

Shell (Figure 7A) dextral, robust, obese (shell breadth (SB)/shell height (SH) index), ovate, cone-shaped above,  $6\frac{3}{4}$ – $7\frac{1}{2}$  convex whorls (almost flat), marked suture. Body whorl intermediate (body whorl height at columella level (BH)/SH index), protoconch smooth, shiny, with  $1\frac{1}{2}$ – $1\frac{3}{4}$  whorls. Aperture long, wide (aperture height (AH)/SH and aperture breadth (AB)/SB indices, respectively), with elliptical section at palatal side, slightly angular at union of columellar and palatal edges. Upper palatal side forms angle slightly less than 90° with parietal side, aperture juts out only slightly from body whorl beginning. Whitish discontinuous peristome expanded as



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Figure 1. (A) Geographical location of the Azores, Madeira and the Canaries; arrows indicate possible colonization patterns used by land snails; position of sea mounts comes from Van den Broeck et al. 2008; (B) geographical distribution of the *Napaesus* species; symbols represent 1×1 km Universal Transverse Mercator squares; arrow points to the Pleistocene deposit from Mancha de La Laja-Bajamar, where the oldest *Napaesus* species (*N. lajaensis*) has been collected (Castillo et al., 2006).

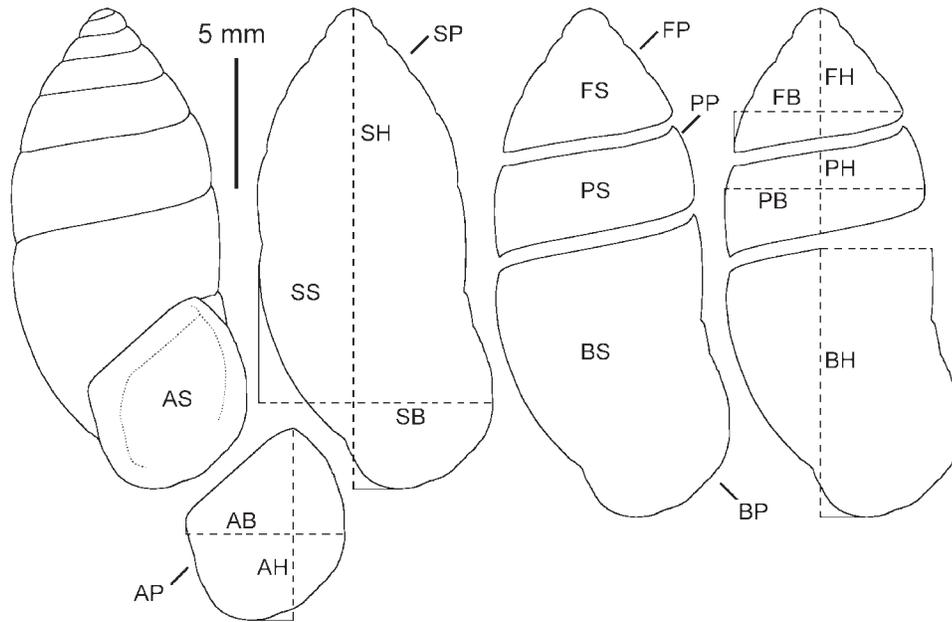


Figure 2. Drawings of the *N. bajamarensis* sp. nov. holotype shell, showing the placement of the measurements obtained. AB, aperture breadth; AH, aperture height; AP, aperture perimeter; AS, aperture surface (plane view); BH, body whorl height (at columella level); BP, body whorl perimeter; BS, body whorl surface (plane view); FB, first whorls breadth; FH, first whorls height; FP, first whorls perimeter; FS, first whorls surface (plane view); PB, penultimate whorl breadth; PH, penultimate whorl height; PP, penultimate whorl perimeter; PS, penultimate whorl surface (plane view); SB, shell breadth; SH, shell height; SP, shell perimeter; SS, shell surface (plane view).

small lip, more developed in lower part of palatal edge, reflected in columellar edge, where it partially covers umbilical slit. Older specimens with callosity between peristome edges, nodule at union of parietal–palatal area.

Shell colour pale brown to tan brown, with first whorls darker than rest. Ornamentation almost smooth, characterized by numerous weak, radial oblique ribs, regularly placed on almost entire shell (Figures 7A, 10A). Shell has some shine despite ribs.

Jaw aulacognathous, with numerous grooves, lateral extremities almost smooth. Radula (Figure 8) with 110–126 teeth rows, formula: C+14–15L+16–19M. Central tooth triangular–ovate, mesocone with rounded tip and two small basal ectocones. First lateral teeth bigger and stronger than central with rounded mesocone and sharp ectocone. Towards laterals, length and width of mesocone diminish as ectocone increases, last broader than mesocone. Marginal teeth with finger-shaped mesocone, much broader ectocone divided into four to six denticles of decreasing size with serrated appearance.

Genital system (Figure 9A–B; five specimens dissected). Atrium very short. Penis about three times shorter than epiphallus, with two portions. Distal portion tubular, located between atrium and insertion of penial retractor muscle. Proximal portion short and swollen, with well-developed penial papilla (Figure 9B). Epiphallus

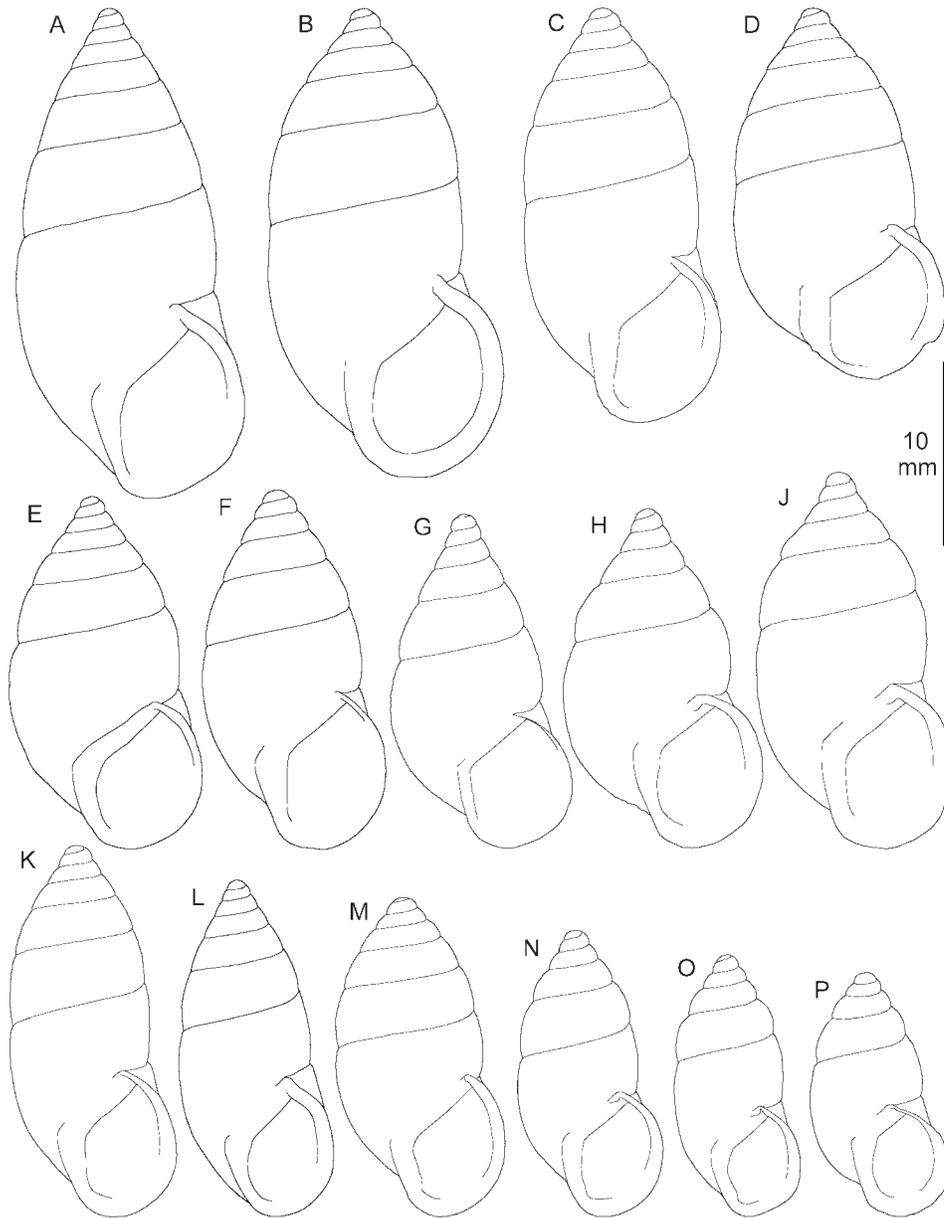


Figure 3. *Naepaeus* shell drawings. (A) *N. conseqoanus*; (B) *N. bertheloti*; (C) *N. subsimplex*; (D) *N. savinosa* (syntype, NHM 1895.2.2.223); (E) *N. inflatiusculus*; (F) *N. severus*; (G) *N. baeticatus*; (H) *N. baeticatus* morphotype *subbaeticatus*; (J) *N. baeticatus* morphotype *halmyris*; (K) *N. interpunctatus*; (L) *N. servus*; (M) *N. tabidus*; (N) *N. tafadaensis* sp. nov. (holotype, TFMC MT 0398); (O) *N. tafadaensis* sp. nov. morphotype “irregular” (*N. tafadaensis* paratype, AIT); (P) *N. badiusus*.

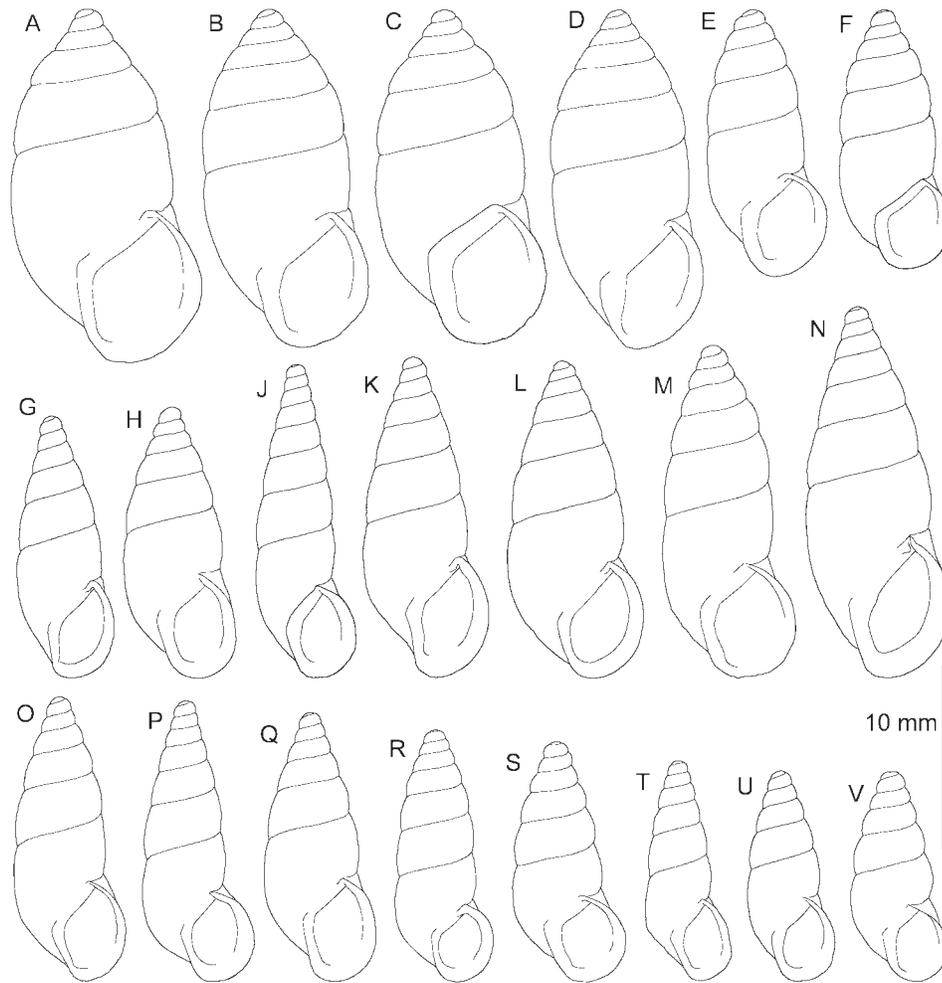


Figure 4. *Napaes* shell drawings. (A) *N. tenoensis* (holotype, AIT); (B) *N. bajamarensis* sp. nov. (holotype, TFMC MT 0397); (C) *N. boucheti* (holotype, AIT); (D) *N. obesatus*; (E) *N. propinquus*; (F) *N. ornamentatus* sp. nov. (holotype, TFMC MT 0400); (G) *N. orientalis* (holotype, AIT); (H) *N. ocellatus* (syntype, ZMZ 513767); (J) *N. rupicola*; (K) *N. avaloensis* (holotype, TFMC MT 0382); (L) *N. maculatus* (holotype, TFMC MT 0386); (M) *N. helvolus*; (N) *N. voggenreiteri* (holotype, TFMC MT 0384); (O) *N. isletae* (holotype, AIT); (P) *N. variatus*; (Q) *N. encaustus*; (R) *N. moquinianus*; (S) *N. teobaldoi* sp. nov. (holotype, TFMC MT 0399); (T) *N. lajaensis* (holotype, TFMC MT 0381); (U) *N. procerus* (holotype, TFMC MT 0385); (V) *N. rufobrunneus*.

tubular, opening distally on penis, two regions defined by presence of epiphallar caecum; proximal region widened, slightly longer than slender distal region. Flagellum very short. Vas deferens opens laterally on proximal end of epiphallus. Penial appendix arises in distal penis portion near retractor muscle insertion, similar in length or slightly longer than penis and epiphallus together. Part A<sub>1</sub> of penial appendix clearly differentiated from globular part A<sub>2</sub>, slightly longer than penis. Appendicular retractor

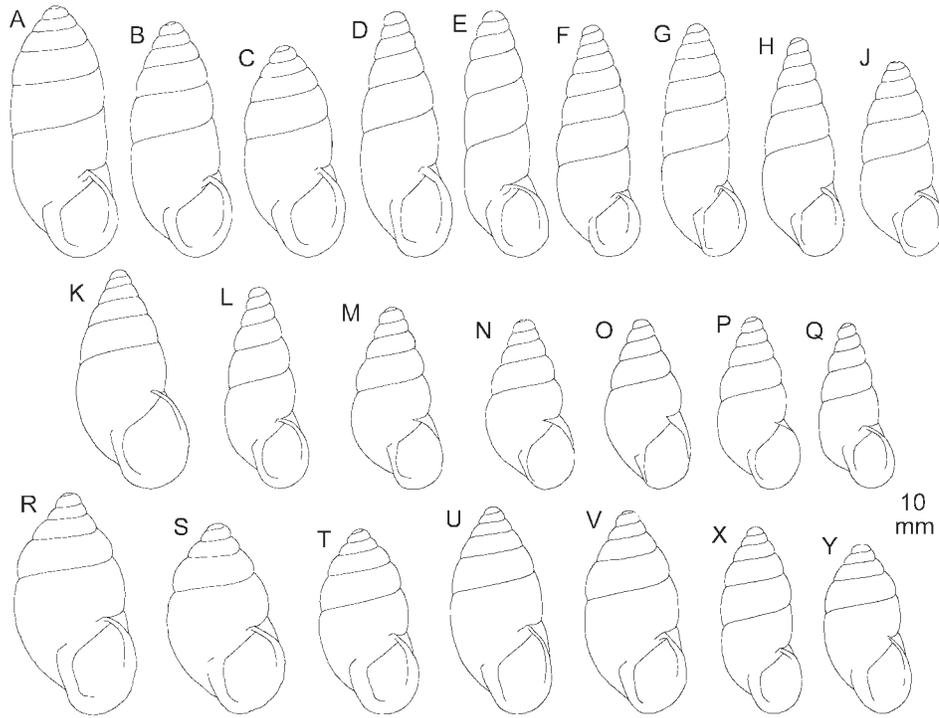


Figure 5. *Napaes* shell drawings. (A) *N. maffioteanus*; (B) *N. chrysaloides*; (C) *N. indifferens*; (D) *N. huttereri* (holotype, AIT); (E) *N. elegans* (holotype, AIT); (F) *N. esbeltus* (holotype, AIT); (G) *N. exilis* (holotype, AIT); (H) *N. subgracilior*; (J) *N. osoriensis*; (K) *N. palmaensis* (syntype, NHM 1895.2.2.219); (L) *N. myosotis*; (M) *N. lichenicola* (holotype, TFMC MT 389); (N) *N. gruereanus*; (O) *N. barquini* (holotype, TFMC MT 0383); (P) *N. roccellicola*; (Q) *N. beguirae* (holotype, AIT); (R) *N. nanodes*; (S) *N. doliolum* (paratype, AIT); (T) *N. bechi* (holotype, AIT); (U) *N. texturatus*; (V) *N. taguluchensis* (holotype, AIT); (X) *N. tagamichensis* (paratype, AIT); (Y) *N. pygmaeus* (holotype, AIT).

muscle inserts laterally, joined to penial retractor on diaphragm walls at certain distance of proximal  $A_1$  top; appendicular insertion delimits two  $A_1$  portions, proximal larger than distal. Part  $A_3$  more slender, shorter than proximal  $A_1$  portion. Parts  $A_3$  and  $A_4$  clearly separated from each other,  $A_4$  long, very thin distally, passing gradually into expanded  $A_5$ .

Free oviduct longer than vagina. Vagina firmly fixed to the body tegument by short connective fibres. Bursa copulatrix complex with a well-developed diverticulum. Bursa duct exceptionally long. Two spermatophores found in diverticulum and basal stalk of bursa copulatrix complex of one specimen.

Spermatophore rigid, long, narrow, twisted, with two parts delimited by strong, spur-like hook curved towards distal tip, moulded in internal pit of epiphallar caecum. Proximal area compressed near tip with semilunar section; proximal tip probably moulded into flagellum, with oval orifice for sperm transfer; proximal edge reflected as collar in ellipsoidal lip with notch on one side. Remainder proximal area tubular, with two well-developed, non-striated

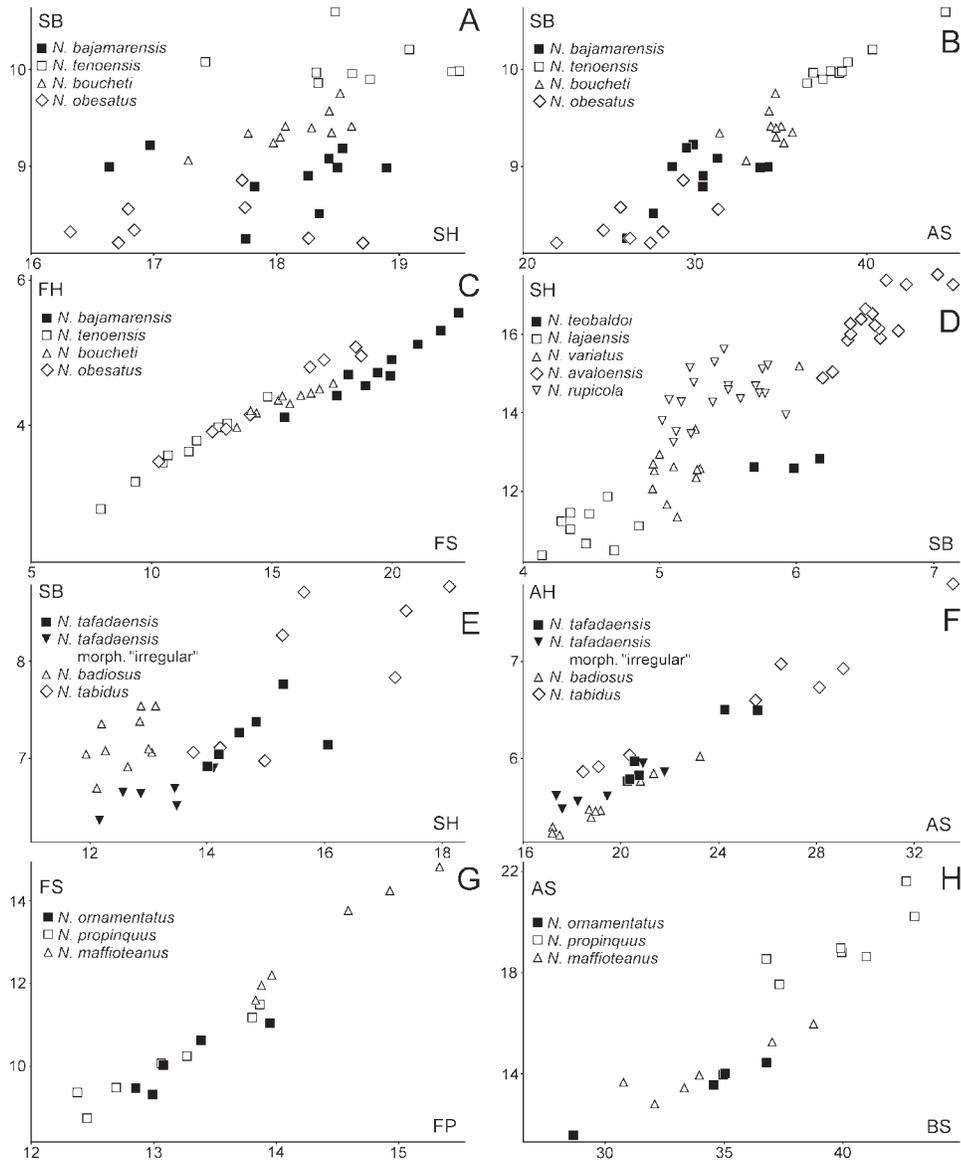


Figure 6. Scatter plots of some shell measurements for the new species and the nearest species of their respective conchological group. AH, aperture height; AS, aperture surface (plane view); FH, first whorls height; FP, first whorls perimeter; FS, first whorls surface (plane view); SB, shell breadth; SH, shell height.

longitudinal lamellae running from proximities of the lip up to near the hook. Distal area tubular, narrowing gradually towards tip (first part to be inserted in other specimen during mating), ending in rounded point. Spermatophore similar to that of *N. moquinianus* (Webb and Berthelot) from Gran Canaria, photographed in Alonso et al. (1995: 311, figures 22–24).

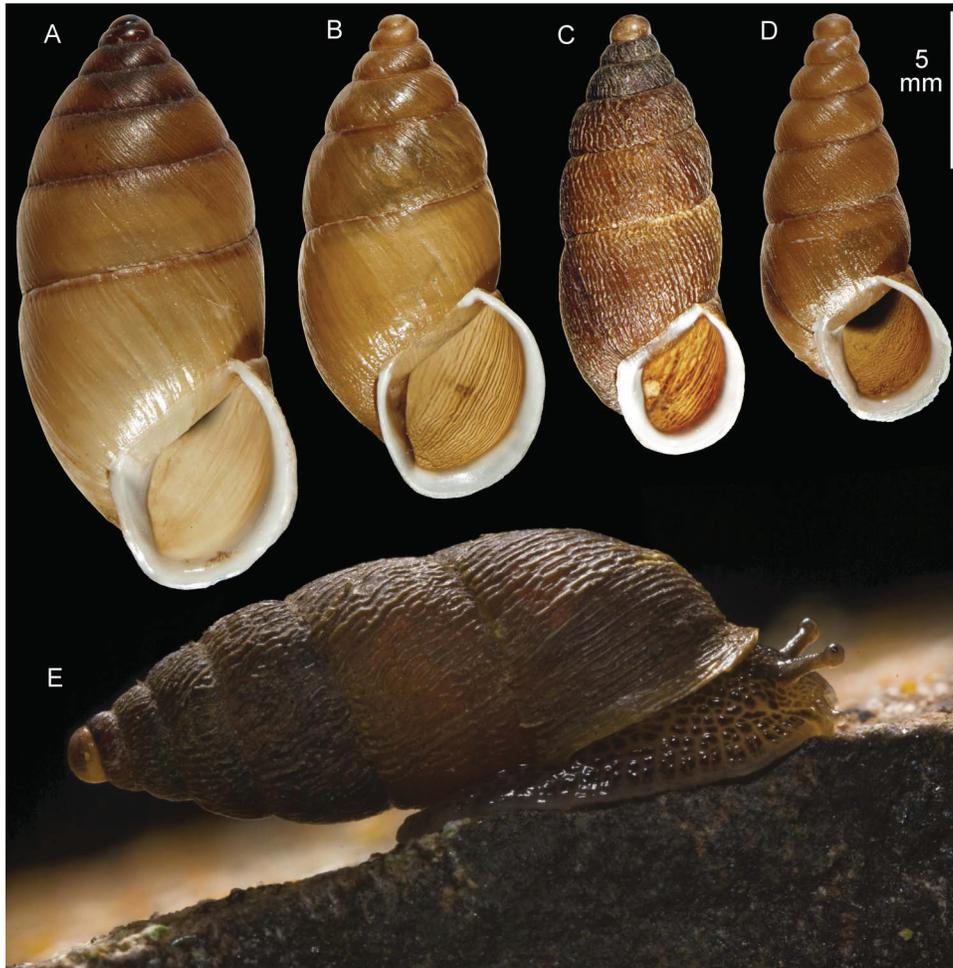


Figure 7. Holotype shells (A–D) and a specimen (E). (A) *N. bajamarensis* sp. nov.; (B) *N. tafaldaensis* sp. nov.; (C) *N. ornamentatus* sp. nov.; (D) *N. teobaldoi* sp. nov.; (E) *N. ornamentatus*, paratype from Mirador de Taguluche (L. Moro photograph).

#### Remarks

*Shell morphology.* Within the conchological group of *N. baeticatus*, the shell of *N. bajamarensis* sp. nov. (Figure 4B) is comparable in shape and size mainly with those of *N. boucheti* (Figure 4C), *N. obesatus* (Figure 4D) and *N. tenoensis* (Figure 4A).

The shell of *N. bajamarensis* is more slender than that of *N. tenoensis* and *N. boucheti* and is slightly more obese than that of *N. obesatus* (Figure 6A). The first whorls of *N. bajamarensis* are similar but slightly more obese than those of *N. obesatus* and bigger than those of *N. tenoensis* and *N. boucheti* (Figure 6C). The shell aperture of *N. bajamarensis* is bigger than that of *N. obesatus* and smaller than those of *N. tenoensis* and *N. boucheti* (Figure 6B). The shell ornamentation is almost smooth in *N. bajamarensis* (Figure 10A) and well-developed in the other species (Figure 12 A–C).

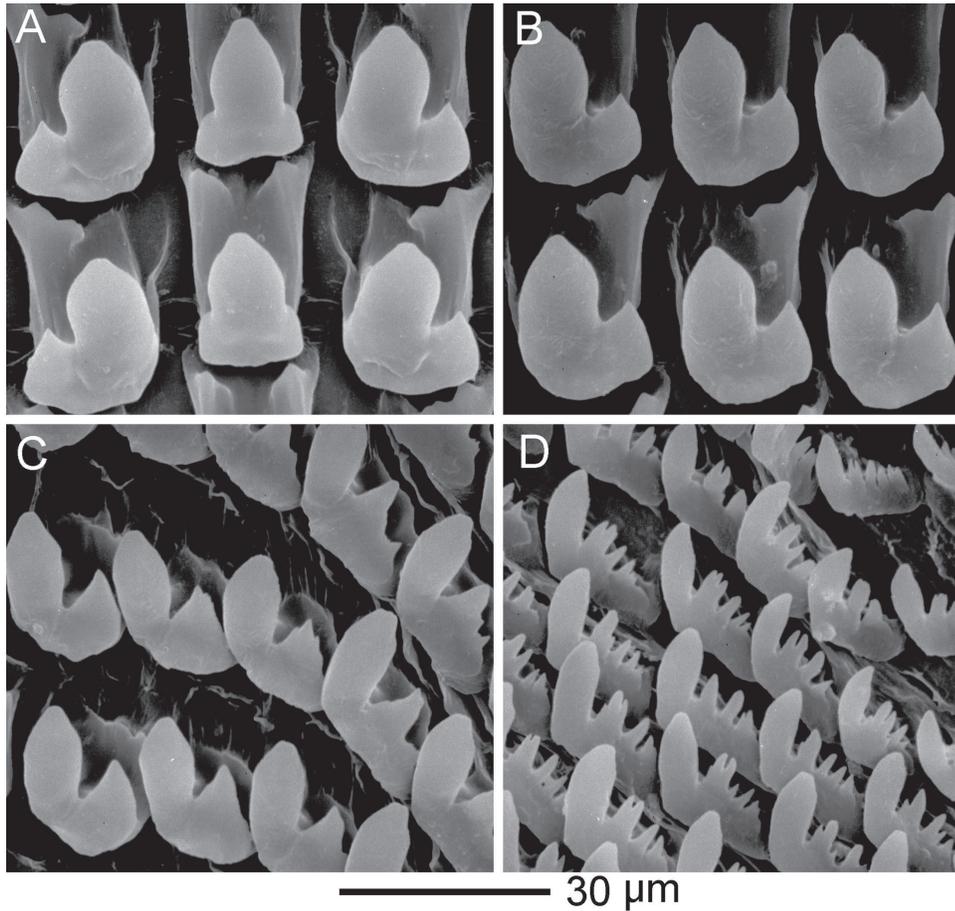


Figure 8. Radula of *N. bajamarensis* sp. nov. (A) Central tooth and first lateral teeth; (B) lateral teeth; (C) outermost lateral teeth and first marginal teeth; (D) outermost marginal teeth.

*Genital system anatomy.* *N. bajamarensis* has an exceptionally long bursa copulatrix duct; it is clearly shorter in the other three species. *N. bajamarensis* and *N. obesatus* have a well-developed diverticulum, which is lacking in *N. tenoensis* and *N. boucheti*.

*Napaeus tafadaensis* Yanes sp. nov.

*Type material*

Holotype (Figures 3N, 7B): TFMC (MT 0398). Type locality: Montaña Tafada, Anaga massif (Tenerife; UTM coordinates: 28RCS8761; 600 m altitude). Leg. M. Ibáñez, 6 April 1991.

Paratypes: 8 specimens and 11 shells, collected between 1991 and 2008, from the northeast of Tenerife (UTM coordinates: 28RCS7859, 28RCS8356 and 28RCS8761), deposited in CML (one shell), TFMC (MT 0134/2) and AIT.

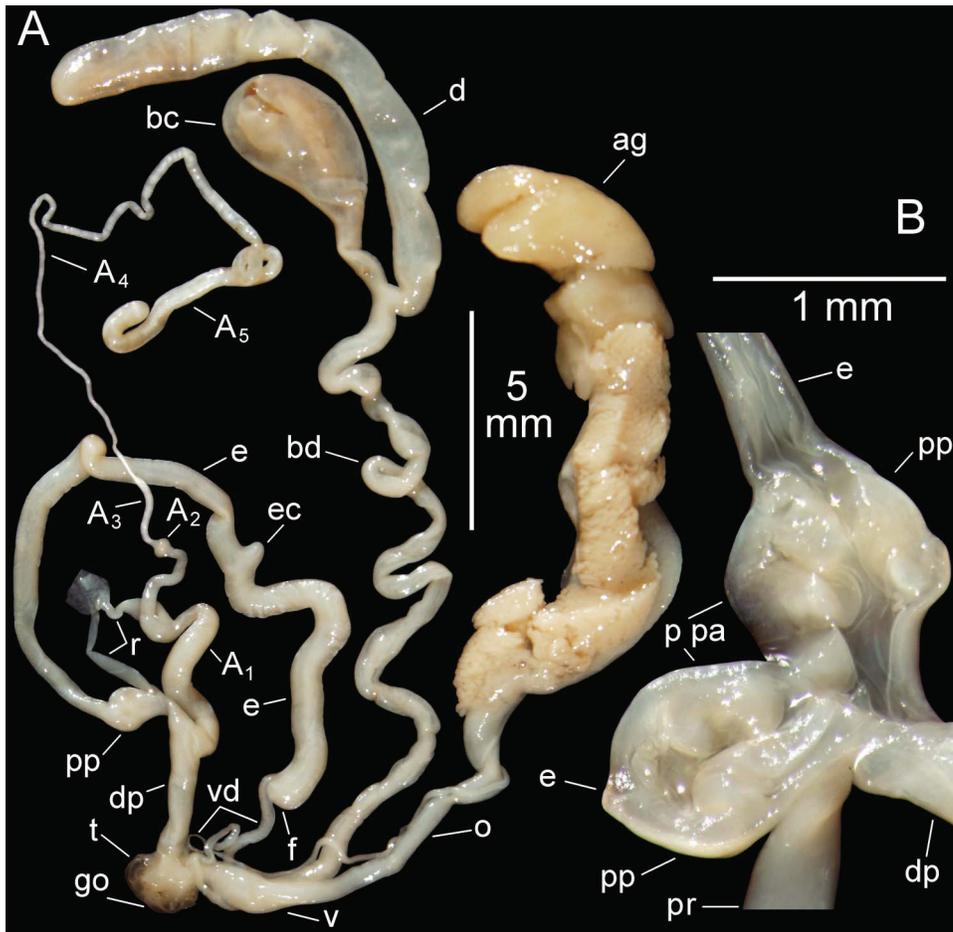


Figure 9. *N. bajamarensis* sp. nov., paratypes from Barranco de Vargas, Bajamar. (A) Genital system; (B) inner anatomy of distal epiphallus and proximal penis, showing the penial papilla. A<sub>1</sub>–A<sub>5</sub>, parts of the penial appendix; ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; d, diverticulum; dp, distal penis; e, epiphallus; ec, epiphallar caecum; f, flagellum; go, genital orifice; o, free oviduct; p pa, penial papilla; pp, proximal penis; pr, penis retractor; r, retractor muscles; t, body tegument; v, vagina; vd, vas deferens.

#### *Etymology*

The specific name derives from that of the type locality.

#### *Geographic range and habitat*

Ground dweller endemic to Tenerife, present in about 25 km<sup>2</sup> area along the north and south facing slopes of the Anaga massif (northeast of the island), associated with lowland vegetation and some subtropical scrub, ranging in altitude between 140 and 600 m (Figure 1B).

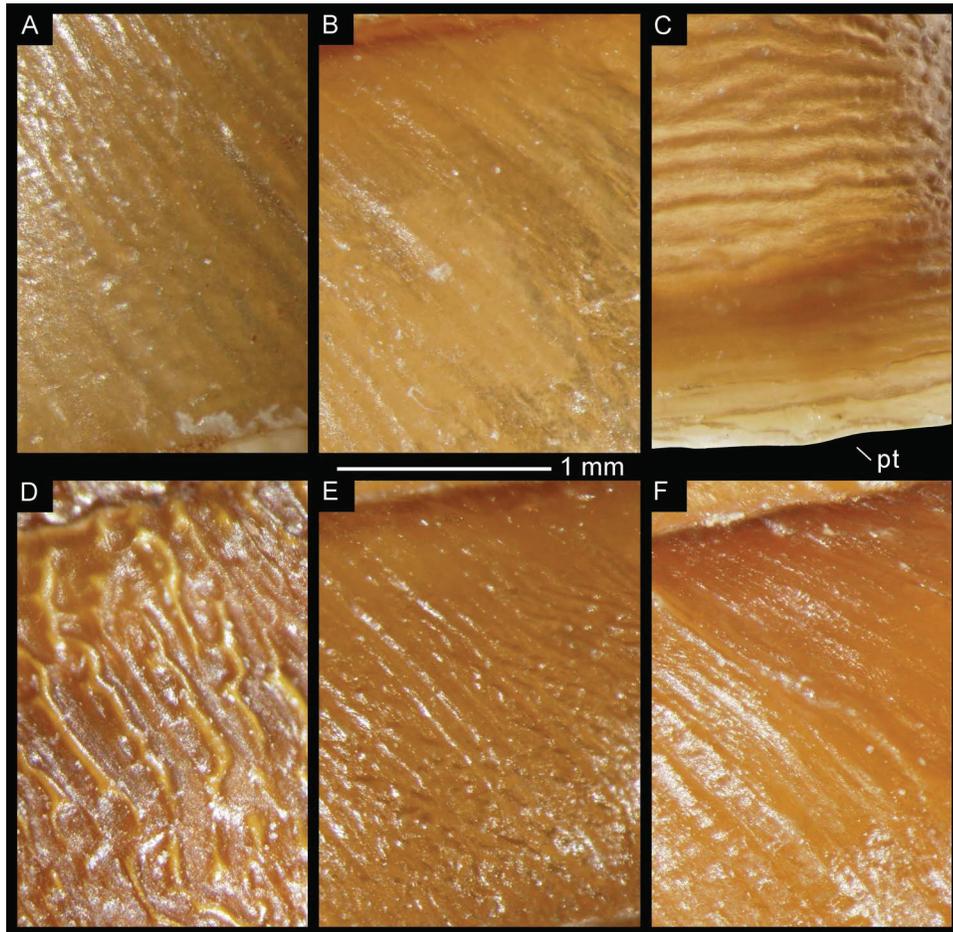


Figure 10. Holotype shell ornamentation details of the penultimate whorl (A, B, D, E) and that of the body whorl columellar zone, near the peristome (C). (A) *N. bajamarensis* sp. nov.; (B–C) *N. tafadaensis* sp. nov.; (D) *N. ornamentatus* sp. nov.; (E) *N. teobaldoi* sp. nov.; (F) shell ornamentation detail of the penultimate whorl of *N. badiusus*, from Barranco de Valle Seco (Tenerife); pt, peristome.

#### Diagnosis

Shell elongated oval, weakly ornamented, sometimes with an irregular growth mode, tan brown coloured, with first whorls slightly darker than the rest. Epiphallus with a well-developed epiphallar caecum. Bursa copulatrix duct without diverticulum.

#### Description

Two morphotypes of the species displayed small but clear conchological differences while the genital system remained the same.

Typical form (Figure 3N): shell obese (SB/SH index), elongated oval, cone-shaped above,  $6\frac{1}{4}$ – $6\frac{1}{2}$  convex whorls, deeply marked suture (Figure 7B). Body whorl

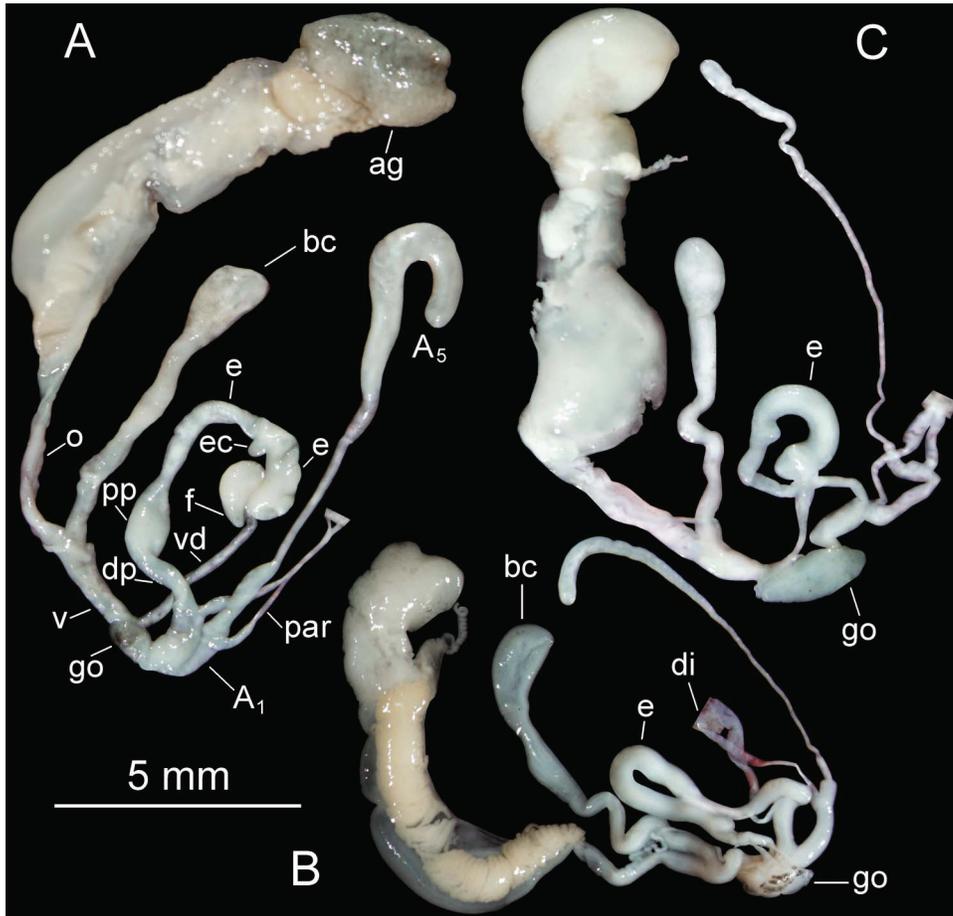


Figure 11. Genital system. (A) *N. tafadaensis* sp. nov., paratype from Montaña Tafada; (B) *N. ornamentatus* sp. nov., paratype from Mirador de Taguluche; (C) *N. teobaldoi* sp. nov., paratype from Barranco Hondo. A<sub>1</sub>, A<sub>5</sub>, parts of the penial appendix; ag, albumen gland; bc, bursa copulatrix; di, diaphragm; dp, distal penis; e, epiphallus; ec, epiphallar caecum; f, flagellum; go, genital orifice; o, free oviduct; par, penial appendix retractor; pp, proximal penis; v, vagina; vd, vas deferens.

large (BH/SH index), protoconch weakly striated with  $1\frac{1}{2}$ – $1\frac{3}{4}$  whorls. Aperture long, wide (AH/SH and AB/SB indices, respectively), elliptical section at palatal side, slightly angular at union of columellar and palatal edges. Upper palatal side forms angle slightly greater than  $90^\circ$  with parietal side, aperture juts out considerably from body whorl beginning. Whitish discontinuous peristome expanded as lip, more developed in lower part of palatal edge, reflected in columellar edge, where it partially covers umbilical slit. Older specimens with callosity between peristome edges, nodule at union of parietal–palatal area.

Second morphotype, “irregular” (Figure 30): shell with irregular growth mode, body whorl and palatal side of aperture flatter, shell smaller (with about six whorls only). Morphotype found in two lower localities (140 and 350 m altitude, respectively).

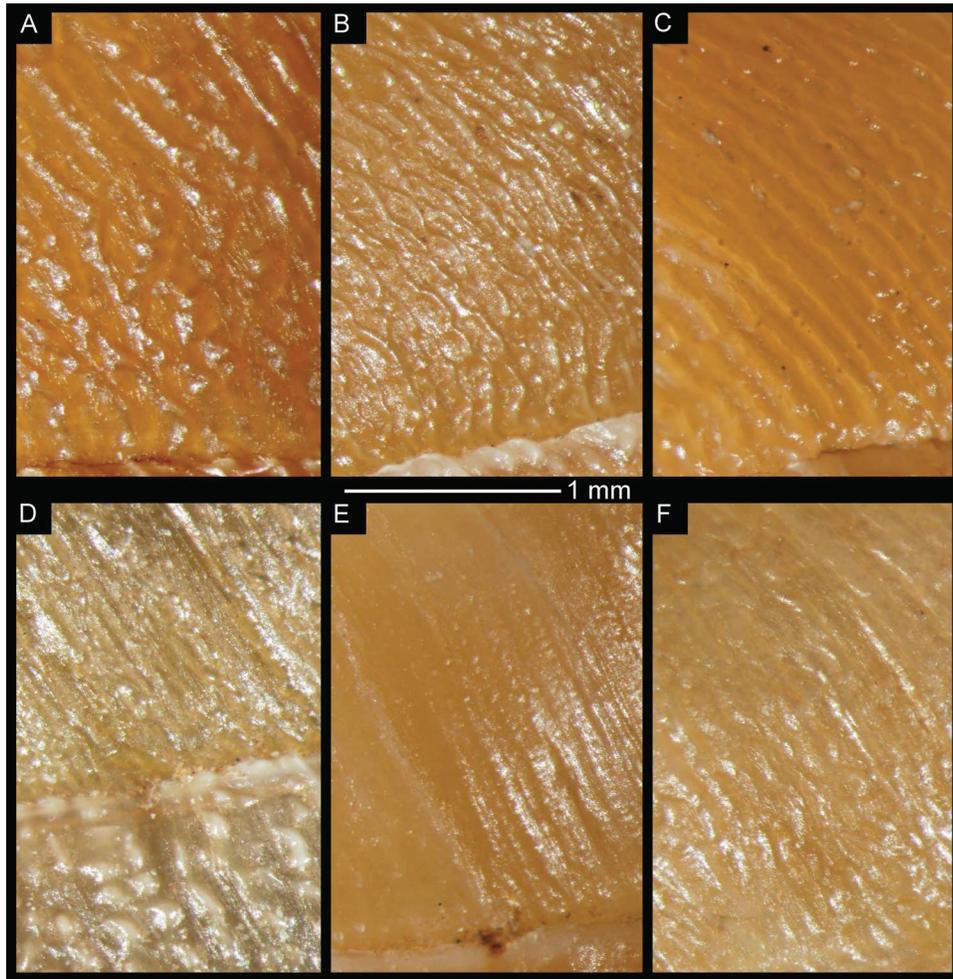


Figure 12. Shell ornamentation details of the penultimate whorl (A–C, E, F) and that of the two last whorls (D). (A) *N. tenoensis* holotype, from Tamargo (Tenerife); (B) *N. boucheti* holotype, from Llano del Lance (La Palma); (C) *N. obesatus*, from La Milagrosa (Gran Canaria); (D) *N. tabidus*, from La Laguna (Tenerife); (E) *N. maffioteanus*, from Barranco de La Aldea (Gran Canaria); (F) *N. propinquus*, from Barranco de Las Galgas (Tenerife).

Shell colour tan brown, first whorls slightly darker than rest. Ornamentation characterized by weak, radial oblique ribs, more-or-less regular on almost all shell (Figures 7B, 10B). Shell shiny despite ribs. At columellar zone of body whorl, ribs sinuous, irregularly undulating, several ribs interrupted forming granules (Figure 10C).

Genital system (Figure 11A; four specimens dissected of typical form, three of “irregular” morphotype). Atrium very short. Penis mainly tubular, similar in length to epiphallus, four times longer than  $A_1$  portion of penial appendix. Penis with three portions; distal portion located between atrium and insertion of penial retractor muscle; slender, tubular, intermediate portion slightly longer than each of the others; swollen, proximal portion with small penial papilla and inner thick, ring-shaped

folds. Epiphallus tubular, opening distally on penis, with two regions defined by presence of well-developed caecum, for moulding and initial accommodation of spermatophoral spur-like hook. Proximal region widened, slender distally, tubular. Flagellum very short. Vas deferens opens laterally on proximal end of epiphallus. Penial appendix arising near distal end of penis, slightly longer than penis and epiphallus together, and shorter than that of other *Napaeus* species. Male genital system with two slender retractor muscles, penial and appendicular, inserting closely, but not fused, on diaphragm walls. Penial muscle inserts between distal and intermediate penis portions, appendicular muscle inserts laterally near proximal top of penial appendix part A<sub>1</sub>.

Free oviduct longer than vagina. Bursa copulatrix duct without diverticulum. Bursa duct short, less than half of penial appendix length.

#### Remarks

*Shell morphology.* The shell of *N. tafadaensis* sp. nov. (Figure 3N, O) is comparable in dimensions with those of *N. tabidus* (Figure 3M) and *N. badius* (Figure 3P), but clearly more slender than that of *N. badius* (Figure 6E). *N. tafadaensis* has similar ornamentation to *N. badius* (Figures 10B and 10F, respectively) while the radial oblique ribs of the body whorl are discontinuous and granulated in *N. tabidus* (Figure 12D). *N. tabidus* shows variability in shell dimensions but normally has a bigger aperture than *N. tafadaensis* (Figure 6F). The other species of the *N. baeticatus* group are clearly bigger, while the species of the *N. nanodes* group are smaller and have prominent radial oblique striation. Lastly, the species of the *N. variatus* group are evidently more slender.

*Genital system anatomy.* The epiphallar caecum is present in *N. tabidus* (Odhner 1932: 62, figure 21) and *N. tafadaensis*, and lacking in *N. badius* (Krause 1895: pl. 1, figure 9). The bursa duct of *N. tafadaensis* and *N. badius* lacks a diverticulum; this is present in *N. tabidus*.

### *Napaeus ornamentatus* Moro sp. nov.

#### Type material

Holotype (Figures 4F, 7C): TFMC (MT 0400). Type locality: Mirador de Taguluche (La Gomera; UTM coordinates: 28RBS7113; 800 m altitude). Leg. Javier Martín and Leopoldo Moro, 5 March 2008.

Paratypes: 15 specimens and 26 shells, collected between 1981 and 2009, from western La Gomera (UTM coordinates: 28RBS7011, 28RBS7016, 28RBS7113, 28RBS7115, 28RBS7116, 28RBS7212, 28RBS7214, 28RBS7319, 28RBS7405, 28RBS7508 and 28RBS7609), deposited in TFMC (MT 0136/1), CML (six shells) and AIT.

#### Etymology

The specific name derives from the distinctive shell ornamentation.

#### Geographic range and habitat

Ground dweller endemic to La Gomera, with a distribution area of about 60 km<sup>2</sup> on the western side of the island, mainly related to lowland vegetation and semi-arid subtropical scrub and palm grove, ranging in altitude from 175 to 1000 m (Figure 1B).

*Diagnosis*

Shell elongated ovate–cylindrical, cone-shaped above. Protoconch very fragile. Teleoconch heavily ornamented with strong, laminar, prominent and irregularly undulating radial oblique ribs. Shell colour tan brown, with first whorls slightly darker than the rest. Epiphallus without epiphallar caecum. Bursa copulatrix duct without diverticulum.

*Description*

Shell (Figures 7C, E) obese (SB/SH index), elongated ovate–cylindrical, cone-shaped above, 7–7½ convex whorls, deeply marked suture. Body whorl intermediate (BH/SH index), protoconch smooth, shiny, with 1½–1¾ whorls. Protoconch very fragile, broken in many shells and living specimens. Aperture short, wide (AH/SH and AB/SB indices, respectively), with elliptical section at palatal side, rounded at union of columellar and palatal edges. Upper palatal side forms angle slightly less than 90° with parietal side, aperture juts out only slightly from body whorl beginning. Whitish discontinuous peristome expanded as lip, more developed in lower part of palatal edge, reflected in columellar edge, where it partially covers umbilical slit. Older specimens with callosity between peristome edges, nodule at union of parietal–palatal area.

Shell colour dark brown, first teleoconch whorls slightly darker than rest. Heavily ornamented teleoconch characterized by strong, laminar, prominent, irregularly undulating, sometimes interrupted radial oblique ribs (Figures 7C, E, 10D). Ribs of body whorl more regularly located.

Genital system (Figure 11B; five specimens dissected). Atrium very short. Penis mainly tubular, slightly longer than A<sub>1</sub> portion of penial appendix. Penis with three portions, distal portion located between atrium and insertion of the penial retractor muscle; proximal portion small, slightly widened, with incipient penial papilla; intermediate portion slender, tubular, slightly longer than distal portion. Epiphallus long, tubular, without epiphallar caecum, opening distally on penis. Flagellum short. Vas deferens opens laterally on proximal end of epiphallus. Penial appendix arises near distal end of penis, is longer than penis and epiphallus together. A<sub>1</sub> penial appendix portion similar in length to penis. Appendicular retractor muscle inserted laterally, at certain distance of proximal top of A<sub>1</sub> portion; insertion on diaphragm walls very close, but not fused to penial retractor. Free oviduct slightly longer than vagina. Bursa copulatrix complex without diverticulum.

*Remarks*

*Shell morphology.* Within the conchological group of *N. variatus*, the shell of *N. ornamentatus* sp. nov. (Figure 4F) is quite similar in form and size to that of *N. propinquus* (Figure 4E), and also comparable with that of *N. maffioteanus* (Figure 5A), although the latter species is more cylindrical. The first whorls of *N. ornamentatus* and *N. propinquus* are smaller than those of *N. maffioteanus* (Figure 6G). The body whorl and the aperture of *N. ornamentatus* and *N. maffioteanus* are similar in form and size but smaller than those of *N. propinquus* (Figure 6H). The main difference between *N. ornamentatus* and the other two species is in the shell ornamentation, which is smooth and not strongly developed in *N. maffioteanus* and *N. propinquus* (Figures 12E and 12F, respectively), in contrast to that of *N. ornamentatus* (Figure 10D). Besides, *N. ornamentatus* has a high protoconch.

*Genital system anatomy.* The genital systems of *N. ornamentatus* and *N. propinquus* are similar in shape and dimensions but *N. propinquus* has an epiphallar caecum that is absent in *N. ornamentatus*. The genital system of *N. maffioteanus* has an epiphallar caecum and also a well-developed diverticulum in the bursa copulatrix complex, whereas *N. ornamentatus* lacks both structures.

*Napaeus teobaldoi* Martín sp. nov.

*Type material*

Holotype (Figures 4S, 7D): TFMC (MT 0399). Type locality: Barranco Hondo, in the southeastern slope of La Culata mountain (Tenerife; UTM coordinates: 28RCS6742; 270 m altitude). Leg. Javier Martín, 7 May 2008

Paratypes: two specimens and four shells, collected in 2008 from the type locality and deposited in CML (four shells) and AIT.

*Etymology*

The specific name derives from Teobaldo, the name of Javier Martín's father, to whom this species is dedicated.

*Geographic range and habitat*

Endemic to Tenerife, only present in the type locality, associated with lowland vegetation (Figure 1B). It is a ground dweller; living specimens were found buried to some cm deep.

*Diagnosis*

Shell elongated, cone-shaped, with a very regular growth, uniform brown coloured. Teleoconch with very numerous radial oblique ribs, regularly spaced in the first whorls and frequently interrupted, irregularly undulating, giving the appearance of granulation in the rest. Epiphallus with an epiphallar caecum. Bursa copulatrix duct without diverticulum.

*Description*

Shell (Figure 7D) obese (SB/SH index), elongated cone-shaped, about  $6\frac{3}{4}$ –7 convex whorls, deeply marked suture. Body whorl intermediate (BH/SH index) and protoconch smooth, with two whorls. Aperture short, wide (AH/SH and AB/SB indices, respectively), elliptical section at the palatal side, slightly angular at union of columellar and palatal edges. Upper palatal side forms angle greater than  $90^\circ$  with parietal side, aperture juts out considerably from body whorl beginning. Whitish discontinuous peristome expanded as lip, more developed in lower part of palatal edge and reflected in columellar edge, where it partially covers umbilical slit. Older specimens display callosity between peristome edges, nodule at union of parietal–palatal area.

Shell uniform brown coloured. Ornamentation characterized by very numerous radial oblique ribs, regularly disposed in first whorls. From third/fourth whorls, some shell ribs sinuous, many shell ribs interrupted, irregularly undulating (Figures 7D, 10E) giving appearance of granulation. At columellar zone of body whorl, all ribs sinuous, irregularly undulating.

Genital system (Figure 11 C). Genital system not fully developed in three live specimens collected (holotype and two paratypes). Atrium very short. Penis and epiphallus tubular, without clear delimitation between both in three specimens. Only distal penis portion clearly distinguishable, located between atrium and insertion of penial retractor muscle. Epiphallus with epiphallar caecum and widened proximal region. Flagellum very short. Vas deferens opens laterally on proximal epiphallar end. Penial appendix about twice length of penis and epiphallus together, arising near proximal end of distal penis portion.  $A_1$  appendix penial portion about twice length of distal penis portion. Appendicular retractor muscle inserts very close to penial retractor on diaphragm walls and, laterally, about midpoint of  $A_1$  portion. Free oviduct longer than vagina. Bursa copulatrix complex without diverticulum.

#### Remarks

*Shell morphology.* The shell of *N. teobaldoi* sp. nov. (Figure 4S) has very regular growth, being cone-shaped. Few other *Napaeus* species have such regular growth. These include *N. variatus* (Figure 4P), *N. rupicola* (Figure 4J), *N. avaloensis* (Figure 4K) and the Pleistocene extinct *N. lajaensis* (Figure 4T), but they are more slender and their dimensions differ from *N. teobaldoi* (Figure 6D).

*Genital system anatomy.* The genital system of *N. teobaldoi* has an epiphallar caecum which is lacking in *N. variatus*, *N. rupicola* and *N. avaloensis*.

### Taxonomic complexity and relationships of *Napaeus*

#### *The Canarian enid species*

Study of the genital system of *N. baeticatus*, *N. tenoensis*, *N. boucheti* (Henríquez et al. 1993a,b) and *N. propinquus* (unpublished data), together with that of *N. tafadaensis* (Figure 11A) and *N. teobaldoi* (Figure 11C) described here, reveals contradictions with the original Hesse (1933) subgenera descriptions. These six species share two important character-states of both Hesse subgenera: the presence/absence of a diverticulum in the bursa copulatrix duct and/or an epiphallar caecum. The absence of a diverticulum is the main character-state of *Napaeus* (*Napaeus*) and the presence of an epiphallar caecum is a character-state of *Napaeus* (*Napaeinus*). The six species cited earlier lack a diverticulum in the bursa copulatrix duct as in *Napaeus* (*Napaeus*), but possess an epiphallar caecum as in *Napaeus* (*Napaeinus*). These dissimilarities were also highlighted by Alonso, Goodacre, et al. (2006), who correlated anatomical and molecular data in only one of the characters used by Hesse (1933) in the original description of the *Napaeus* subgenera, the character-states “epiphallus with/without a caecum”. As Bank and Neubert (1998) state, the systematic significance of the presence or absence of a diverticulum is probably irrelevant and its presence or absence does not reflect natural affinities. Thus, the new species are not assigned to the Hesse *Napaeus* subgenera until a phylogenetic analysis of the genus is conducted.

Moreover, Henríquez et al. (1993b) showed two different patterns of spermatophore: with/without a spur-like hook. They also found a positive correlation between the presence of the epiphallar caecum and the spur-like hook of the spermatophore, a relationship confirmed here with the new species *N. bajamarensis*. Several spermatophoral architectures have been described previously (Henríquez et al. 1993b; Alonso

et al. 1995). These architectures relate to the internal anatomy of the epiphallus (Ibáñez et al. 2007) and the flagellum, a fact which validates the utility of these characters within taxa classification and description. Therefore, the study of the spermatophore appears to be a useful, complementary method for understanding the taxonomic relationships among *Napaeus* species.

### *The Macaronesian enids*

The relationships among Macaronesian enids are unknown due to the absence of phylogenetic analyses. However, it is possible to hypothesize potential relationships based on the available taxonomic data.

There is a clear, anatomical difference between *Napaeus* and *Macaronapaeus* based on the penial appendix. The presence of the penial appendix is a symplesiomorphy of the Canarian *Napaeus* shared by several other enids. This character was used by Forcart (1940) for the division of the Enidae into two subfamilies, Eninae (with a penial appendix) and Chondrulinae (without it). However, Bank and Neubert (1998), utilizing the data of Gittenberger (1978, 1983) and Bank (1985), pointed out that the penial appendix has been independently lost in at least six Enidae groups, including the group containing *Macaronapaeus*. Bank and Neubert (1998) considered the treatment of *Napaeus* and *Macaronapaeus* as genera or subgenera a matter of opinion and subsequently placed *Macaronapaeus* as a subgenus of *Napaeus*. However, the absence of enids in the Madeira archipelago together with the respective absence/presence of the penial appendix in the Azorean/Canarian enids and the large distance separating those two populations suggest not only a different immigration pathways (Figure 1A: arrows) but also potentially different phylogenetic origins.

Several authors have noted a lack of homogeneity within and between the different plant communities of the Macaronesian archipelagos (Azores, Madeira, Salvages, Canary Islands and Cape Verde) and suggested that the observed heterogeneity may be the result of independent colonizations events from different mainland sources (Beyhl et al. 1995; Borgen 1995). Waldén (1984) indicated that “the most conspicuous difference between the mollusc faunas of Madeira and the Canary Islands is the complete absence of taxa with northwest African affinities on Madeira, despite the fact that they hold a similar position relative to the African continent. “Porto Santo, the oldest island of the Madeiran archipelago, was susceptible to colonization for a period of 10 million years without major volcanic activity. Colonizers arrived by island-hopping from Europe (specifically, from the southwest Iberian Peninsula) through the chain now remaining as sea mounts (Cook 2008). The western and northernmost Azorean islands – its oldest island, Santa Maria, is estimated to have a maximum age of 8.12 million years, with S. Miguel following with an age of 4.01 million years (Borges et al. forthcoming 2009) – were probably colonized directly from Europe. By this mode of expansion, Arnedo et al. (2001) showed that the spider dysderid species of the Azores Islands are certainly the result of independent colonization from Europe, unrelated to those of the Madeiran and Canarian archipelagos.

Alonso et al. (2000) and Arnedo et al. (2001) suggested that the Canary Islands were colonized from neighbouring northwest Africa. This hypothesis is also supported by the presence of several species of the genera *Obelus* Hartmann, 1842 (Ibáñez et al. 2003) and *Theba* Risso, 1826 (Gittenberger and Ripken 1985, 1987; Gittenberger et al. 1992) in both regions.

The eastern Canary Islands (Lanzarote and Fuerteventura) are the oldest islands (15–20 million years; Carracedo et al. 2005) only about 115 km distant from the northwest African coast. Sea level fluctuations during recent glacial events decreased that distance to as little as ~70 km (García-Talavera 1997, 1999). During the Miocene–Pliocene, northwest Africa was wetter, supporting abundant vegetation (see recent review in Swezey (2009)) and mighty river systems including the Drâa, which is located opposite Lanzarote and Fuerteventura. The Drâa currently has a wide valley (4–5 km) and a relatively short course, both of which are compatible with high flow and torrential currents. Moroccan rivers would drag vegetation islets (floating rafts) to the Atlantic Ocean where the material would be transported to the nearby coasts of the Canarian archipelago by the trade winds and the marine currents (Alonso et al. 2000), a process which may be primarily responsible for snail dispersion from Africa to the Canaries.

Thus, *Napaeus* is almost certainly a genus with northwest African natural affinities while *Macaronapaeus* most likely displays European natural affinities. *Napaeus* could be related to *Merdigera* Held, 1837, from northwest Africa and southern Europe, or *Mauronapaeus* Kobelt, 1899, from the north African countries of Algeria and Tunisia, because both genera are geographically close to *Napaeus* and all three share a similar type of genital system, including the presence of a penial appendix (Schileyko 1998, figures 266 and 287, respectively).

*Macaronapaeus*, which lacks a penial appendix, could have derived from a European population of a penial appendix-bearing, ancestor of genera such as *Merdigera* or *Zebrina* Held, 1837 (present in the Iberian Peninsula). Alternatively, *Macaronapaeus* could also be related to a penial appendix-absent genus present in the Iberian Peninsula, such as *Chondrula* Beck, 1837.

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