

THREE UNDESCRIBED SPECIES OF *NAPAEUS* (GASTROPODA: PULMONATA: ENIDAE) FROM LA GOMERA (CANARY ISLANDS), THE RICHEST CENTRE OF SPECIES RADIATION FOR THE GENUS

JESÚS SANTANA¹, MIGUEL ARTILES², YURENA YANES³, FRANCISCO DENIZ¹, MARIA R. ALONSO⁴ & MIGUEL IBÁÑEZ⁴

¹Las Palmas de Gran Canaria, Gran Canaria, Canary Islands, Spain

²Arinaga, Gran Canaria, Canary Islands, Spain

³Department of Geology, University of Cincinnati, Cincinnati, OH 45221, USA

⁴Department of Animal Biology, La Laguna University, E-38206 La Laguna, Tenerife, Canary Islands, Spain

Abstract Three new species of the genus *Napaeus* (Albers 1850) are described from La Gomera (Canary Islands). This is one of the smaller islands of the archipelago but it has the highest number (26) of living species of the genus. Shells of *Napaeus* species on La Gomera include the shortest, the most slender, the longest and the widest in the genus and show significant diversity in shell colour. Moreover, the *Napaeus* species from La Gomera exhibit more different patterns of genital system anatomy (five) than the whole of the genus in all the other Canary islands together (four patterns, one of which is also present on La Gomera). Hesse's subgenera *Napaeus* and *Napaeinus* correspond to two of the eight anatomical patterns involved. At least adults of *N. doloresae* n. sp. and juveniles of the other new species described can disguise their shells with a cover of soil, apparently to reduce predation.

Key words *Napaeus*, taxonomy, species radiation, insular endemics, genital anatomy, shells, shell disguise

INTRODUCTION

Present knowledge of the Canary Islands archipelago (eastern mid-Atlantic) indicates that the small rounded island of La Gomera (378 km² and 1484 m altitude, 12 Mya old) is much the richest in living species of *Napaeus*, with 23 species (Mousson, 1872; Wollaston, 1878; Henríquez, Ibáñez *et al.*, 1993; Alonso *et al.*, 1995; Alonso, Goodacre *et al.*, 2006; Bank *et al.*, 2002; Yanes *et al.*, 2009; Yanes, Martín *et al.*, 2011; Holyoak *et al.*, 2011). Each of the Canarian species of *Napaeus* is typically restricted to a small area within a single island (i.e. they demonstrate "single island endemism"). The number of *Napaeus* species from La Gomera is clearly greater than that predicted by the most parsimonious species number–island age model for the richness of the main snail families of the Canarian Archipelago (Cameron *et al.*, 2013). Thus, it contrasts with that of the neighbouring Tenerife (8 Mya), which is five times more extensive and 2227 metres higher than La Gomera, but accommodates only 16 known living and one extinct *Napaeus* species described to date (Castillo *et al.*, 2006; Yanes *et al.*, 2009), and also with that of Gran Canaria Island (14.5 Mya), which is rounded like La

Gomera but four times more extensive and 466 metres higher, where only 13 known living and one possibly extinct species have been described to date (Webb & Berthelot, 1833; Mousson, 1872; Wollaston, 1878; Groh *et al.*, 1992; Alonso *et al.*, 1995; Yanes, Santana *et al.*, 2011).

In the present study three new *Napaeus* species are described from western, southern and eastern areas of La Gomera island. All of them occur outside the National Park of Garajonay, which occupies the centre of the island. As in previous papers, the new species are not assigned to the *Napaeus* subgenera (*Napaeus* and *Napaeinus*) described by Hesse (1933) because a phylogenetic analysis of the genus has not been carried out.

MATERIALS AND METHODS

Maps of geographical distribution (Fig. 1) were produced using MapViewer software (Golden Software Inc.). The photographic methodology was described by Ibáñez *et al.* (2006). Drawings of shell outlines (Fig. 2) were obtained semi-automatically, adopting the methods used by Yanes *et al.* (2009). Standardised measurements of the shells (Table 1, Fig. 2) were made following Alonso, Nogales *et al.* (2006), using the software

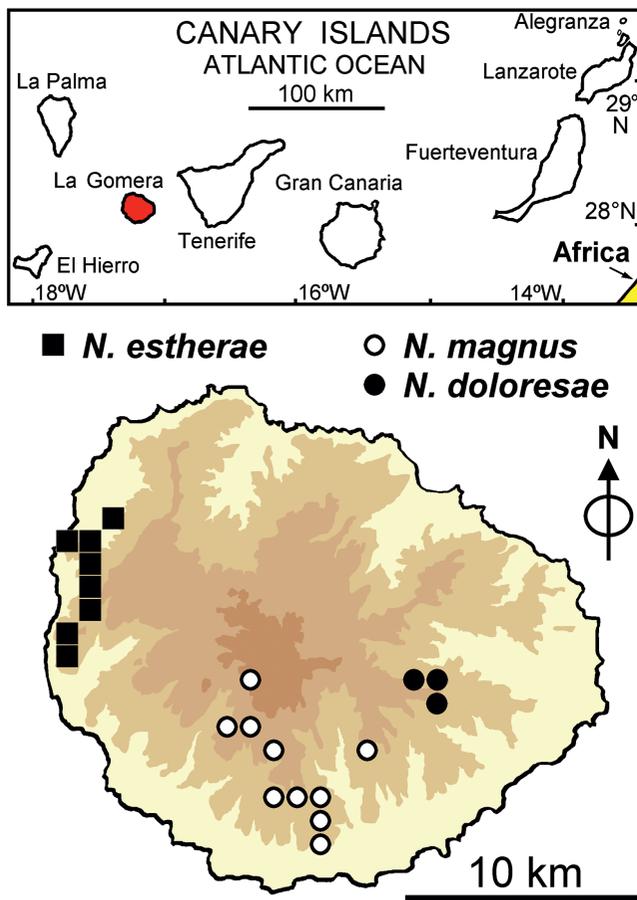


Figure 1 Geographical distribution of the three new species of *Napaeus*.

analySIS[®] (Soft Imaging System GmbH). The angle at the upper palatal corner between the columella and the upper palatal side of the aperture, as well as the lateral extension of the aperture beyond the penultimate whorl were also measured, following Yanes, Martin *et al.* (2011). Abbreviations for shell characters and measurements are shown in Fig. 2. The number of shell whorls was counted using the methodology described by Kerney & Cameron (1979: 13). Terminology for the shape and proportions of shells is based on the biometric data provided in Table 1, following Henríquez, Ibáñez *et al.* (1993; see also Table 2), and that of parts of the penial appendix follows Schileyko (1984: 39, fig. 18). “Proximal” and “distal” refer to the position in relation to the ovotestis. The distinction between “epiphallus” and “penis” is based on the internal anatomy of these organs, not the position of insertion of the penial retractor muscle which has been used by many early authors and some recent researchers.

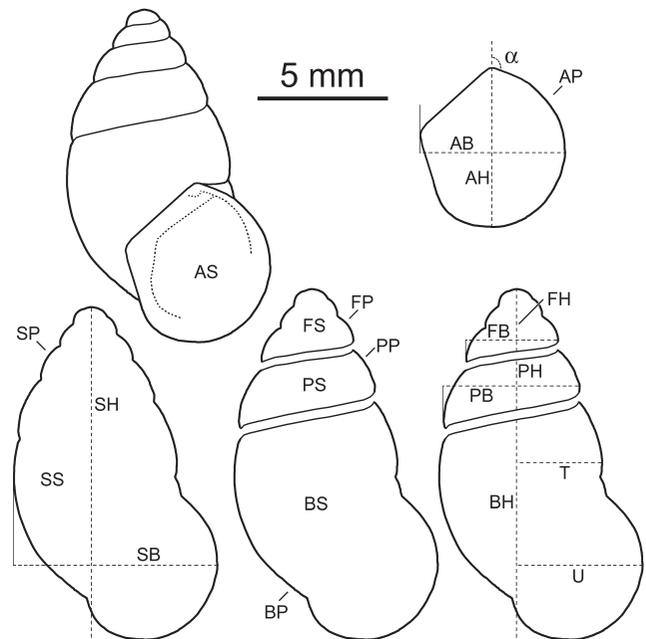


Figure 2 Drawings of the holotype shell of *N. doloresae* sp. nov. showing the placement of the measurements obtained (in mm or mm²): AB aperture breadth; AH aperture height; AP aperture perimeter; AS, aperture surface area (plane view); BH body whorl height (at columella level); BP body whorl perimeter; BS body whorl surface area (plane view); FB first whorls breadth; FH first whorls height; FP first whorls perimeter; FS first whorls surface area (plane view); PB penultimate whorl breadth; PH penultimate whorl height; PP penultimate whorl perimeter; PS penultimate whorl surface area (plane view); SB shell breadth; SH shell height; SP shell perimeter; SS shell surface area (plane view); T maximum distance from columella to start of body whorl; U maximum distance from columella to palatal aperture lip; α angle of columella-upper palatal side.

ABBREVIATIONS

AIT	Alonso and Ibáñez collection, Department of Animal Biology, University of La Laguna, Tenerife, Canary Islands, Spain
FDGC	F. Deniz private collection, Las Palmas de Gran Canaria, Spain
ICZN	International Commission on Zoological Nomenclature
JMHGC	J. M. Hernández private collection, Las Palmas de Gran Canaria, Spain
JSGC	J. Santana private collection, Las Palmas de Gran Canaria, Spain
MAGC	M. Artiles private collection, Arinaga, Gran Canaria, Spain

Table 1 Data for the shell characters measured (in mm or mm²) for *Napaeus* spp. sp1: *N. doloresae*; sp2: *N. estherae*; sp3: *N. magnus*; n, number of measured specimens; SD, standard deviation; Min., minimum; Max., maximum; other abbreviations as in Fig. 2.

Statistical parameter	Character/index	sp1	sp2	sp3	Character/index	sp1	sp2	sp3
Mean	SH	13,24	21,03	22,25	AP	18,20	24,52	31,17
SD		0,50	1,39	1,44		0,87	1,18	1,60
Min.		12,59	19,61	19,93		17,39	23,13	28,57
Max.		14,24	23,44	24,23		20,14	26,82	33,71
Mean	SB	7,69	10,11	13,00	FH	2,65	5,30	3,92
SD		0,28	0,51	0,67		0,30	0,64	0,74
Min.		7,21	9,59	11,97		2,14	4,27	2,87
Max.		8,27	11,25	14,09		3,20	6,49	5,06
Mean	SS	65,40	141,49	191,04	FB	3,61	6,49	6,59
SD		3,62	13,26	18,33		0,16	0,42	0,41
Min.		61,72	127,73	167,80		3,32	5,88	5,92
Max.		72,18	162,36	217,46		3,82	7,18	7,21
Mean	SP	33,32	50,77	56,46	FS	6,24	21,72	15,60
SD		1,03	2,91	3,14		0,90	4,03	3,84
Min.		32,14	48,17	51,62		4,73	16,09	11,29
Max.		35,46	55,44	60,69		8,01	29,13	21,73
Mean	BH	8,58	12,09	14,83	FP	10,58	19,58	17,86
SD		0,35	0,70	0,76		0,62	1,67	1,59
Min.		8,13	11,20	13,67		9,59	17,04	15,25
Max.		9,22	13,45	16,24		11,69	22,23	20,06
Mean	BS	49,28	91,78	145,01	PH	2,12	3,63	3,50
SD		3,06	6,64	13,20		0,35	0,30	0,36
Min.		45,90	83,80	131,09		1,68	3,27	2,99
Max.		55,73	102,06	167,40		3,14	4,25	3,96
Mean	BP	27,40	38,87	47,51	PB	5,29	8,00	9,58
SD		0,67	1,67	2,22		0,16	0,35	0,36
Min.		26,48	37,00	45,16		5,02	7,47	9,05
Max.		28,66	41,46	50,62		5,52	8,44	10,02
Mean	AH	6,34	8,47	10,91	PS	9,88	27,99	30,35
SD		0,36	0,50	0,49		1,07	3,49	4,51
Min.		5,97	7,74	10,21		7,86	23,33	24,79
Max.		7,05	9,33	11,64		11,57	33,87	36,43
Mean	AB	5,46	7,24	9,14	PP	13,81	22,48	24,72
SD		0,25	0,40	0,67		0,53	1,25	1,25
Min.		5,10	6,52	8,07		13,12	20,66	22,80
Max.		6,00	7,84	10,23		14,60	24,24	26,28
Mean	AS	24,76	45,04	72,21	SB/SH	0,58	0,48	0,58
SD		2,54	4,31	7,85		BH/SH	0,65	0,58
Min.		22,35	40,21	59,75	AH/SH	0,48	0,40	0,49
Max.		30,63	53,48	85,80	AB/SB	0,71	0,72	0,703
n		13	13	11	BS/SS	0,754	0,65	0,76

Mya millions of years ago
 NHMUK Natural History Museum, London, U.K.
 NMW National Museum Wales, Cardiff, U.K.
 sh shell
 TFMC Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain
 UTM Universal Transverse Mercator, cartographic projection system

Table 2 Terminology for shape and proportions of shells, based on the indices from 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	small	< 0.50	very short	< 0.30	narrow	< 0.60
slender	0.350–0.425	intermediate	0.50–0.60	short	0.30–0.38	wide	0.60–0.70
obese	0.425–0.500	large	0.60–0.66	long	> 0.38	very wide	> 0.70
very obese	> 0.50	very large	> 0.66				

RESULTS

Because of the high number of *Napaeus* species, we have plotted the average values of shell height and width (Fig. 3) of all known *Napaeus* species, using data from Alonso, Goodacre *et al.* (2006), Alonso, Henríquez *et al.* (1995), Castillo *et al.* (2006), Groh *et al.* (1992), Henríquez, Alonso *et al.* (1993), Henríquez, Ibáñez *et al.* (1993), Holyoak *et al.* (2011), Ibáñez *et al.* (2007), Mousson (1872), Wollaston (1878), Yanes, Martín *et al.* (2009), Yanes, Martín *et al.* (2011) and Yanes, Santana *et al.* (2011). Rectangles marked in Fig. 3 show the groups of species used for comparisons with the new species described in this paper, because they have similar shell dimensions.

SYSTEMATICS

Family Enidae B.B. Woodward 1903 (1880)
Woodward (1903: 354, 358); ICZN (2003,
Opinion 2018)

Genus *Napaeus* Albers 1850

Type species by subsequent designation of
Herrmannsen (1852): *Bulimus baeticatus* Webb &
Berthelot 1833

Napaeus doloresae sp. nov., Santana

Holotype 1 sh, TFMC (MT 0843); Leg. J. Santana,
23 July 2010 (Fig. 4A).

Paratypes 2 sh (AIT), 1 sh (FDGC), 18 sh (JSGC),
3 sh (MAGC), between November 2008 and
January 2012 from a small zone in the east of La
Gomera.

Type locality West side of Tagamiche mountain
(La Gomera; UTM: 28RBS8609; 879 m altitude).

Diagnosis Shell fragile, weakly calcified, very
obese, conic-ovate, with about 6 convex whorls

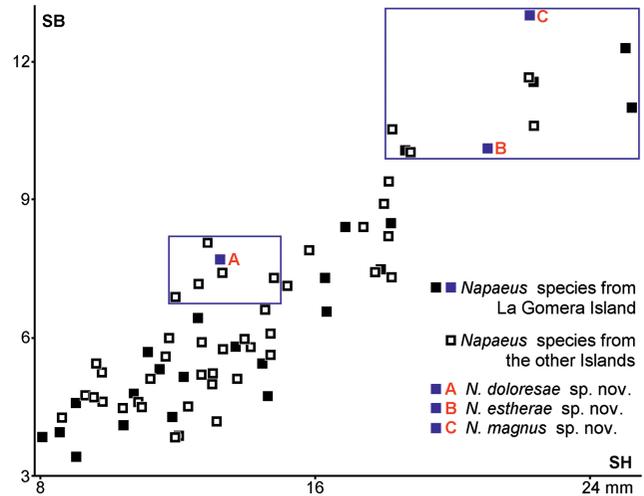


Figure 3 Scatter plot of mean shell breadth (SB) and mean shell height (SH) of all the known *Napaeus* species.

increasing regularly in size, distinct suture and slightly wrinkled ornamentation. Body whorl large. Aperture rounded, long and very wide, with a slightly reflected peristomial lip. Penis with two parts, the distal being tubular and the proximal globular; the penial retractor muscle inserts near the proximal end of the distal part. Bursa copulatrix subspherical; bursa duct without diverticulum, slightly swollen distally.

Description Body dark greyish blue (Fig. 5 B), with a reddish hue. Shell (Fig. 4 A) fragile, weakly calcified, dextral, very obese (Table 2, SB/SH index), conic-ovate, with about 6 convex whorls increasing regularly in size and a distinct suture. Body whorl large (BH/SH index), comprising slightly more than 3/4 of the shell surface area (BS/SS index). Protoconch smooth, shiny, with 1½ whorls, generally partly deteriorated. Aperture rounded, long and very wide (AH/SH and AB/SB indices). Angle (Fig. 2) between columella and start of upper palatal margin

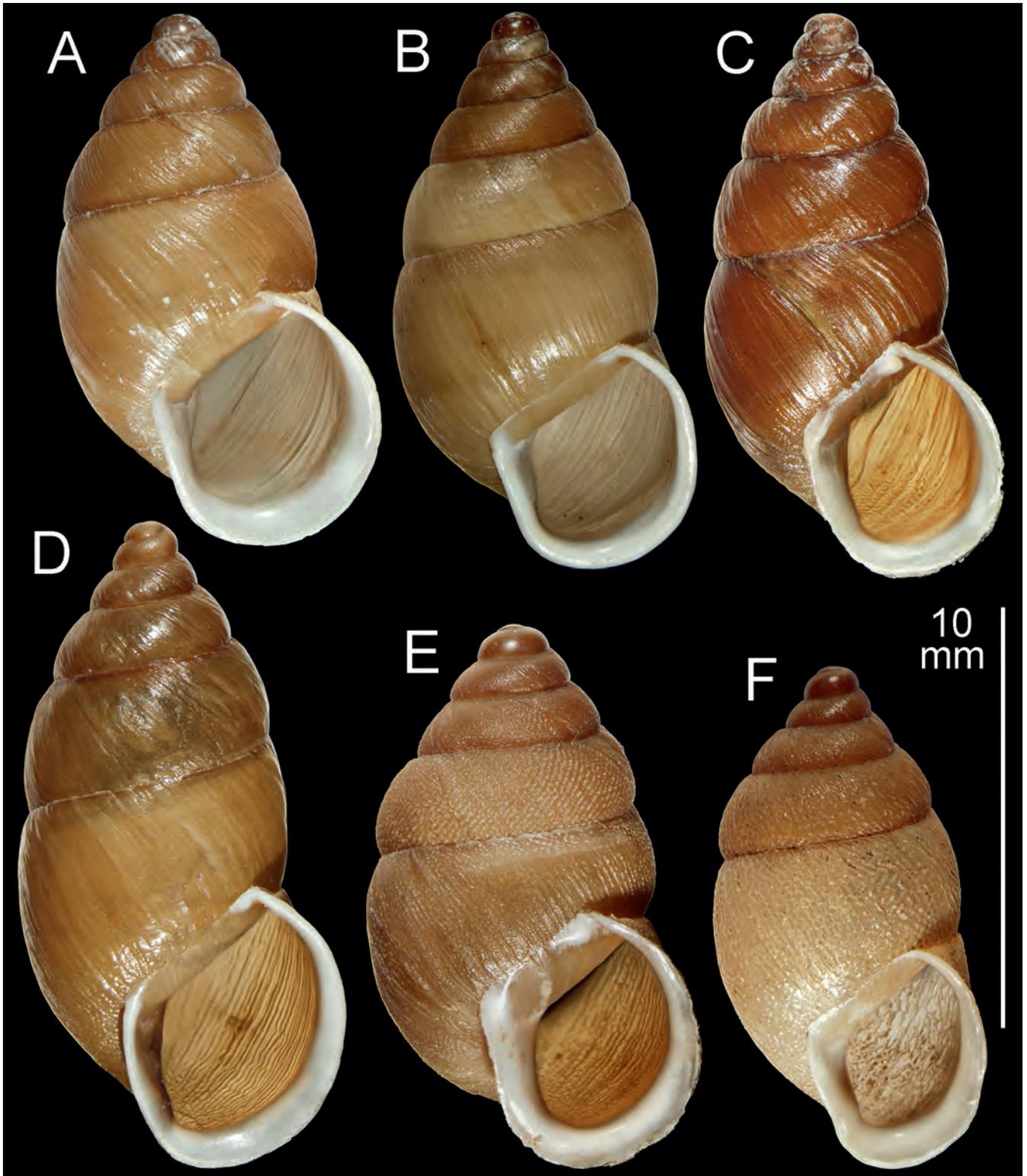


Figure 4 *Napaeus* shells: A holotype of *N. doloresae* sp. nov., from Tagamiche, La Gomera; B holotype of *N. grohi* Alonso, Ibáñez & Santana in Yanes *et al.* 2011, from Pista del Derrabado, El Hierro; C *N. badiusus* (Webb & Berthelot 1833), from Barranco de Valle Seco, Tenerife; D holotype of *N. tafadaensis* Yanes in Yanes *et al.* 2009, from Montaña Tafada, Tenerife; E holotype of *N. josei* Santana, Alonso & Ibáñez in Yanes *et al.* 2011, from Barranco del Lechugal, Gran Canaria; F *N. nanodes* (Shuttleworth 1852), from Barranco del Agua, Tenerife. The figures 4B, 4C, 4E and 4F were first published in Yanes, Santana *et al.* (2011, figs 3J, 3C, 3A and 3B, respectively); Fig. 4D was first published in Yanes, Martín *et al.* (2009, fig. 7B).

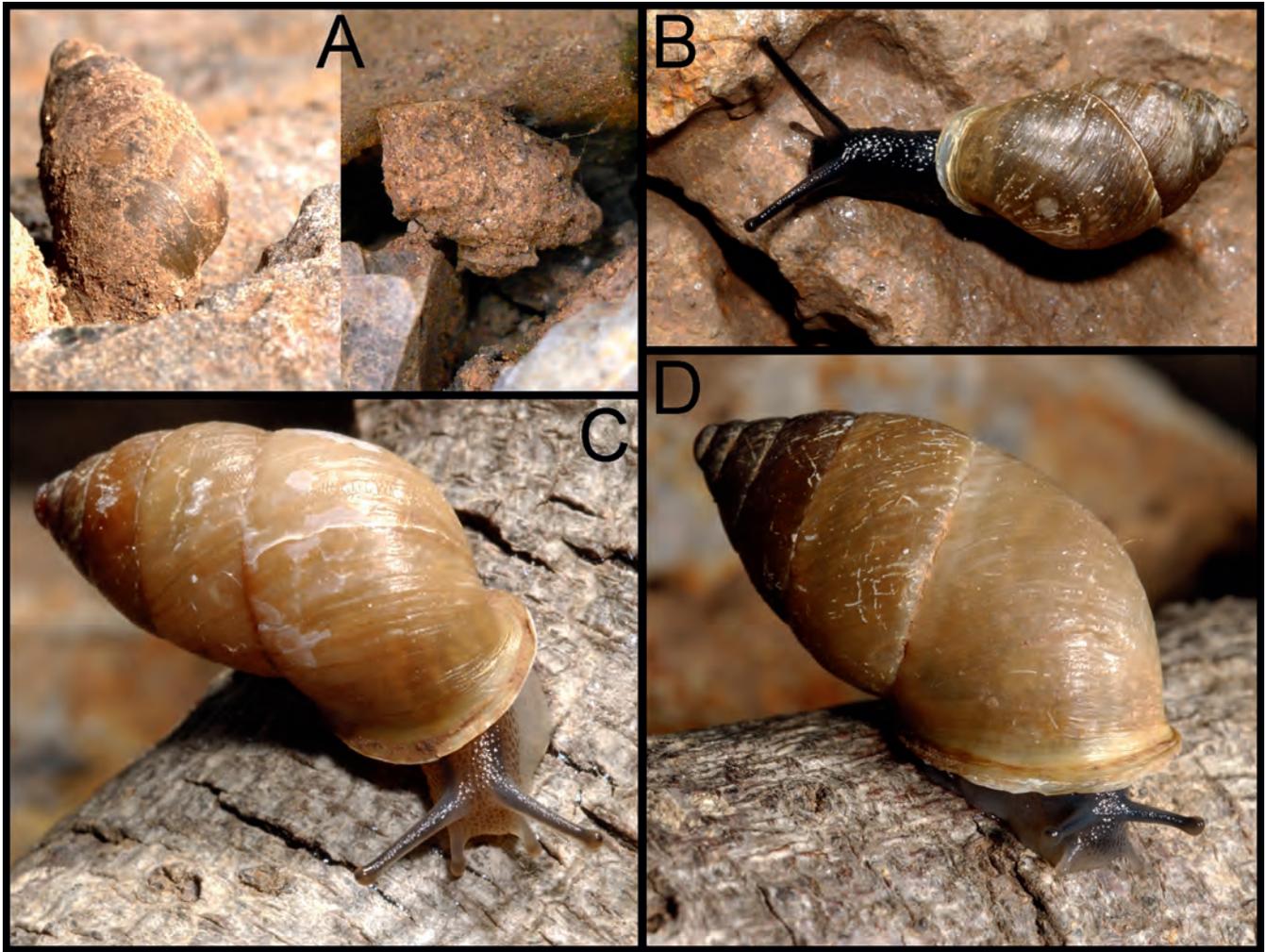


Figure 5 *Napaeus* animals: A, B *N. doloresae* sp. nov., from Tagamiche, La Gomera; A disguised adult and juvenile specimens; B undisguised adult specimen; C *N. estherae* sp. nov., from Alojera, La Gomera; D *N. magnus* sp. nov., from Monte Calvario, La Gomera.

about 114° . Edge of aperture projects about 46% (1.5 mm) from start of body whorl (see Fig. 2, ratio T:U, due to combination of upper palatal angle and projection of peristomial lip). Peristome discontinuous, expanded as a whitish, slightly reflected lip, which partly covers the umbilical slit. Older specimens have a very small callosity between peristome edges and a small nodule at the junction of parietal and palatal margins. Shell colour uniform, brown. Shell ornamentation slightly wrinkled, with numerous weak, sometimes irregular, undulating, radial oblique ribs (Fig. 6A). Shell with some gloss despite ribs.

Genital system (Fig. 7A; six specimens dissected) Atrium very short, penis and vagina meet at level of the genital orifice. Penis about one-third the length of epiphallus, with two

parts, the distal part tubular and the proximal part globular; the penial retractor muscle inserts near the proximal end of the distal part; the distal side of this distal part (between the atrium and the insertion of the penial appendix) is thicker than the proximal side only in the genital system of the specimen figured, both sides have a similar diameter in the other specimens dissected. Penial papilla absent and a small sphincter is present between epiphallus and the proximal part of the penis; penial cavity wide, with a small, longitudinal fold in the proximal part. Epiphallus tubular, without caecum and not subdivided into sections, opening distally into penis. Flagellum very short, located at the proximal end of the epiphallus. Vas deferens opens laterally into proximal end of epiphallus. Penial appendix similar in length to penis and epiphallus combined, arising from

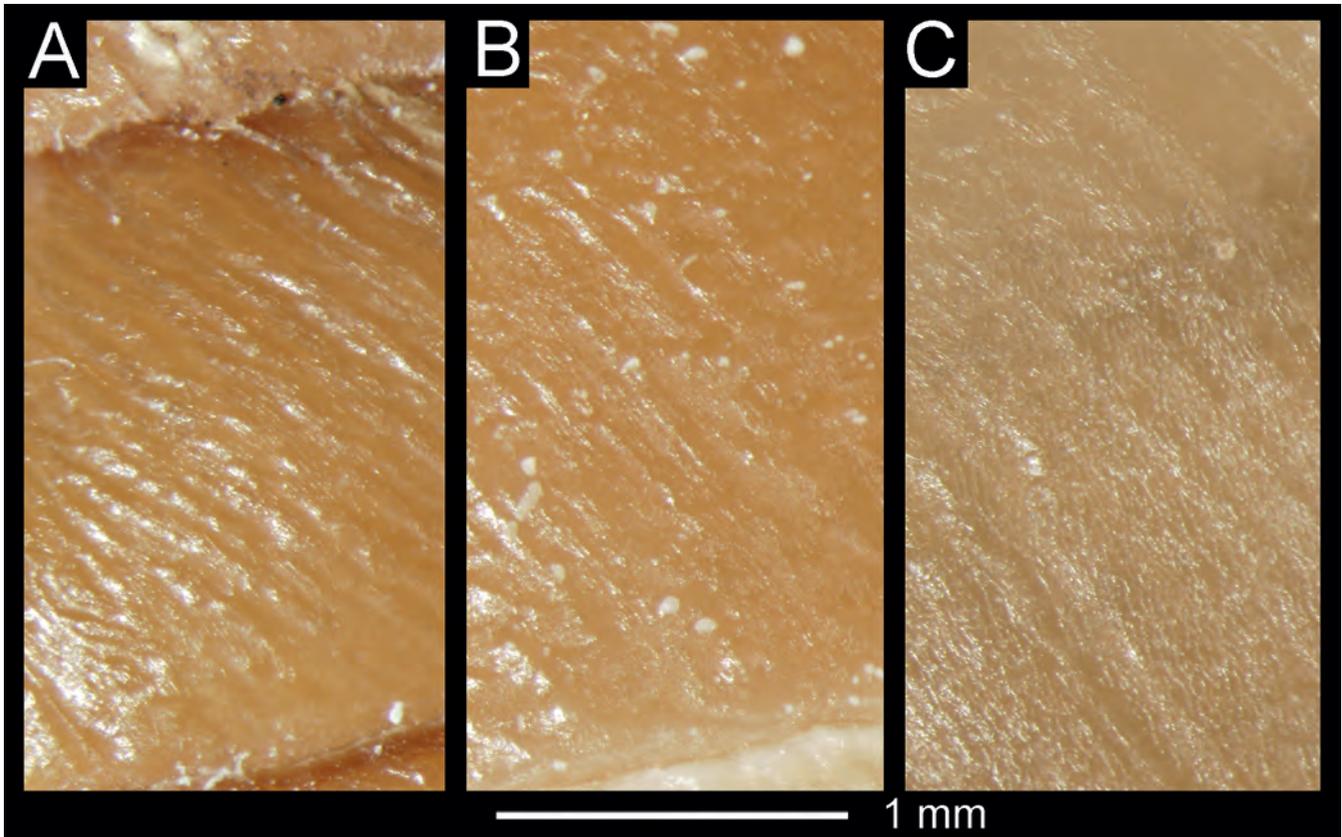


Figure 6 *Napaeus* shell microsculpture: A *N. doloresae* sp. nov., from Tagamiche, La Gomera; B *N. estherae* sp. nov., from La Mérica, La Gomera; C *N. magnus* sp. nov., from Monte Calvario, La Gomera.

distal part of penis; its penial opening is nearer to the atrium than the penial retractor insertion. Part A_1 of penial appendix tubular, apparently undifferentiated from part A_2 . Appendicular retractor muscle short, joined to penial retractor on diaphragm walls. Part A_4 slightly thinner than part A_3 , slender, passing gradually into expanded and longer A_5 . Free oviduct slightly longer than vagina. Vagina firmly attached to body tegument by short connective fibres. Bursa copulatrix slightly subspherical; bursa duct without diverticulum, slightly swollen distally, near its connection with the female duct.

Comparisons The shell of *N. doloresae* (Figs 3A, 4A) is comparable in size with those of *N. grohi* Alonso, Ibáñez & Santana in Yanes, Santana *et al.* 2011 (Fig. 4B), from El Hierro island, *N. josei* Santana, Alonso & Ibáñez in Yanes, Santana *et al.* 2011 (Fig. 4E), from Gran Canaria island and three species from Tenerife island: *N. badiusus* (Webb & Berthelot 1833) (Fig. 4C), *N. tafadaensis* Yanes in Yanes *et al.* 2009 (Fig. 4D) and *N. nanodes* (Shuttleworth 1852) (Fig. 4F). *Napaeus*

doloresae has the largest and most rounded aperture of the six species and differs clearly from *N. josei* and *N. nanodes* by the shell ornamentation; it is also more obese than shells of *N. badiusus* and *N. tafadaensis*. The species that is most similar conchologically is *N. grohi*, but the latter has the penis globose, without sections, with eight longitudinal, wrinkled folds, a sphincter between epiphallus and penis, and the penial retractor muscle inserting on distal end of penis, near the genital orifice (Yanes, Santana *et al.*, 2011: fig. 10A). *N. tafadaensis* has an epiphallar caecum (Yanes *et al.*, 2009: fig. 11A) and *N. nanodes* and *N. josei* also have a diverticulum in the bursa copulatrix complex (Henríquez, Ibáñez *et al.*, 1993: fig. 6A; Yanes, Santana *et al.*, 2011: fig. 6A). The genital system of *N. badiusus* has not yet been described.

Derivation of name The specific name is dedicated to Dolores Benitez, the mother of J. Santana.

Distribution and habitat A species endemic to La Gomera, where it was collected between 880

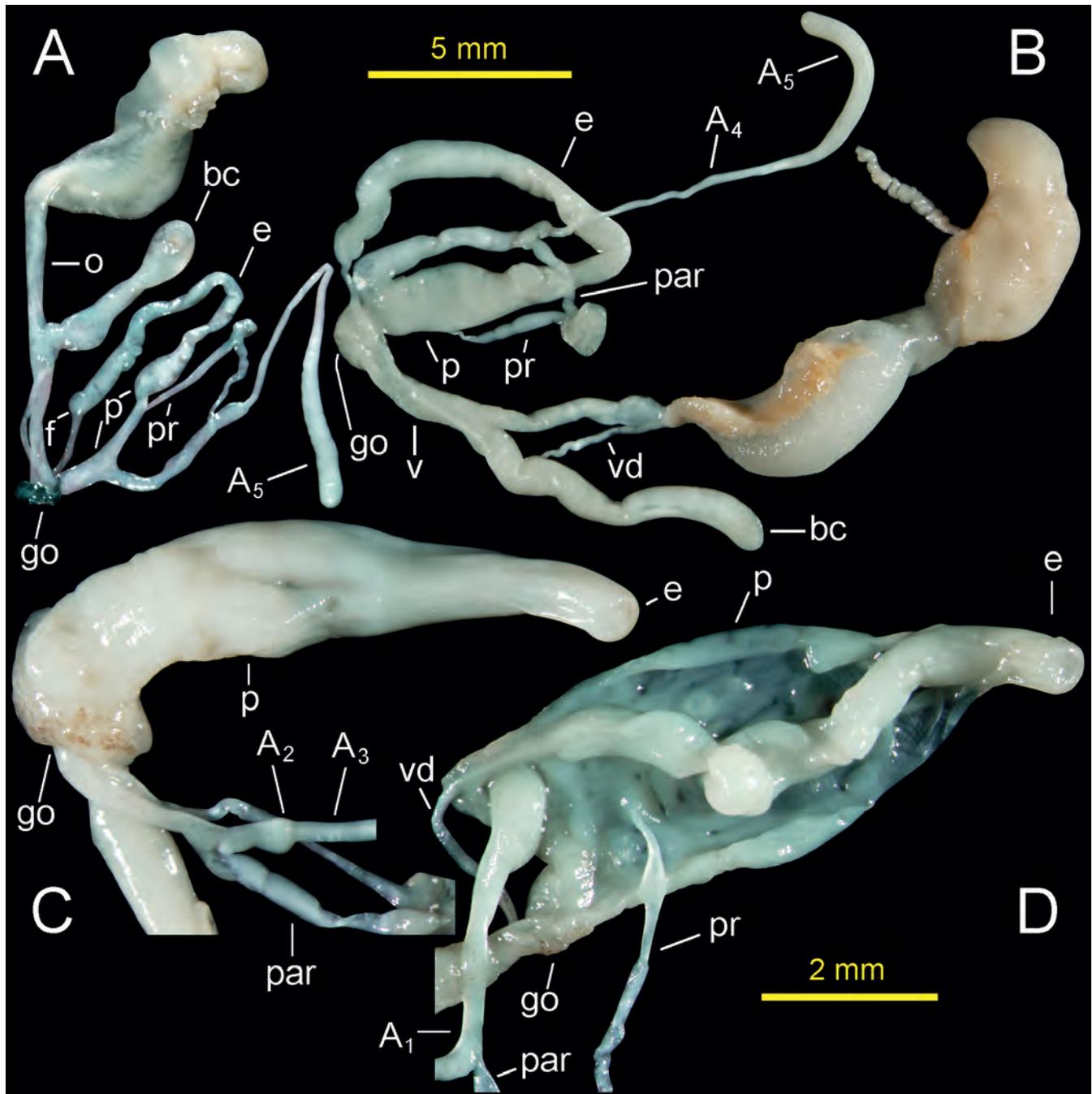


Figure 7 *Napaeus* genital systems: A *N. doloresae* sp. nov., from Tagamiche, La Gomera; B *N. estherae* sp. nov., from La Mérica, La Gomera; C, D *N. estherae* sp. nov., from Alojera, La Gomera, detail and dissection of the evaginated distal genital system of a specimen. A₁–A₅ parts of the penial appendix, bc bursa copulatrix, e epiphallus, f flagellum, go genital orifice, par penial appendix retractor, pr penial retractor, o free oviduct, v vagina, vd vas deferens.

and 920 m altitude in the east of the island (Fig. 1), co-habiting with *N. barquini* Alonso & Ibáñez in Alonso *et al.* 2006, on north-facing open, partially lichen-covered rocky slopes exposed to the humid trade winds, with succulent and sparse low vegetation (*Aeonium saundersii* Bolle, *A. viscatum* Bolle, *A. diplocyclum* Webb ex Bolle,

Monanthes laxiflora (DC.) Bolle, *M. amygdros* Svent. and *Argyranthemum* sp.). The shells were disguised with a muddy soil covering, more complete in the juveniles (Fig. 5 A). They were mostly found on the rock of crags, some on open, vertical surfaces, others hidden in crevices or behind *Aeonium* rosettes.

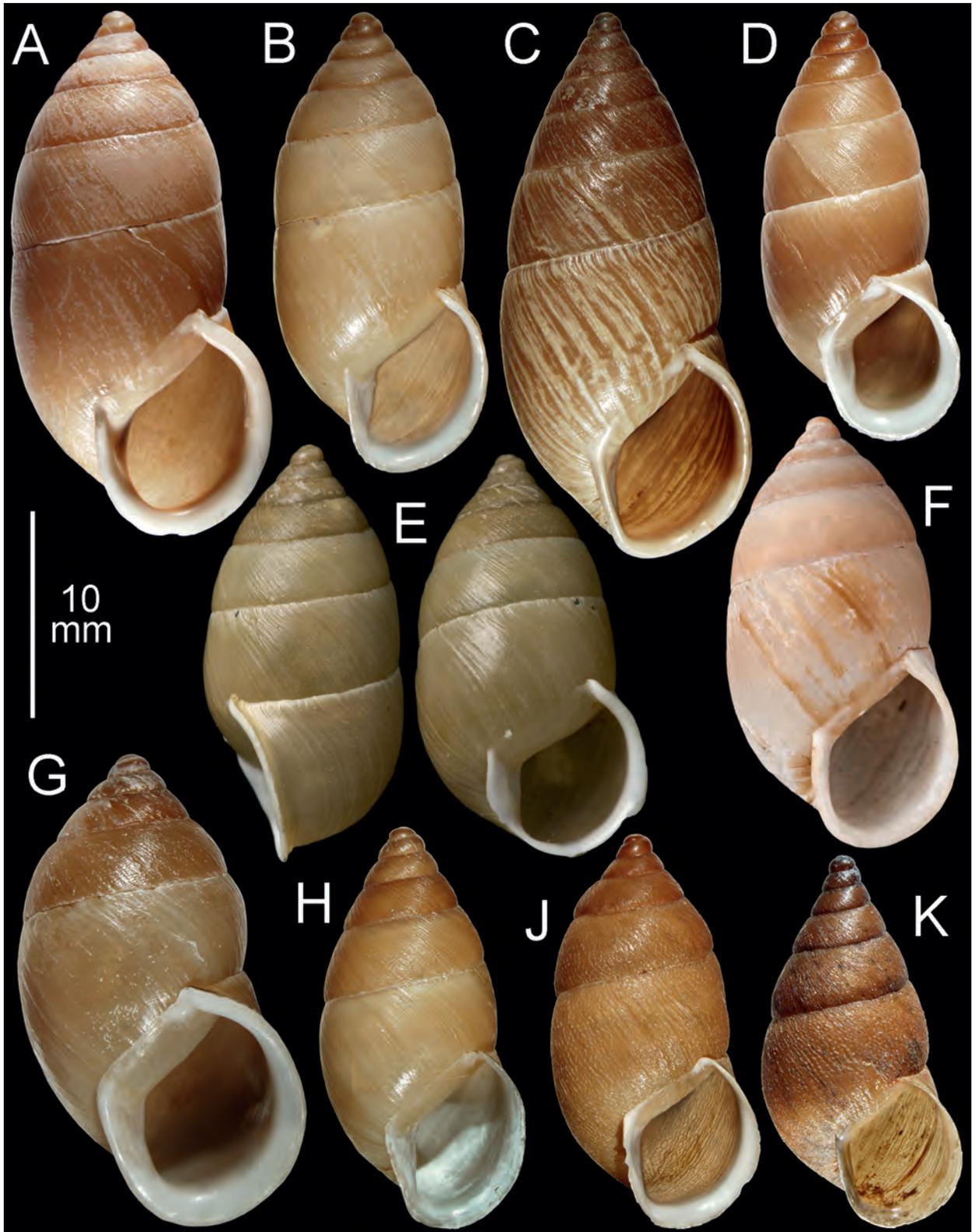


Figure 8 *Napaeus* shells: A *N. bertheloti* (L. Pfeiffer 1846), from Jerduñe, La Gomera; B *N. subsimplex* (Wollaston 1878), from Valle del Cabrito, El Hierro; C *N. conseqoanus* (Mousson 1872), from Túnel de Agulo, La Gomera; D holotype of *N. estherae* sp. nov., from La Mérica, La Gomera; E syntype of *Bulimus savinosa* Wollaston 1878 (NHMUK 1895.2.2.223; photo by Jonathan Ablett); F holotype of *Bulimus savinosa* var. *inflatiuscula* Wollaston 1878, from the Melvill-Tomlin collection (NMW.1955.158.25066; photo by James Turner); G holotype of *N. magnus* sp. nov., from Monte Calvario, La Gomera; H *N. severus* (J. Mabile 1898), from Hurona, La Gomera; J holotype of *N. tenoensis* Henríquez 1993, from Las Tablas, Tenerife; K, *N. baeticatus* (Webb & Berthelot 1833), from Casas de Afur, Tenerife.

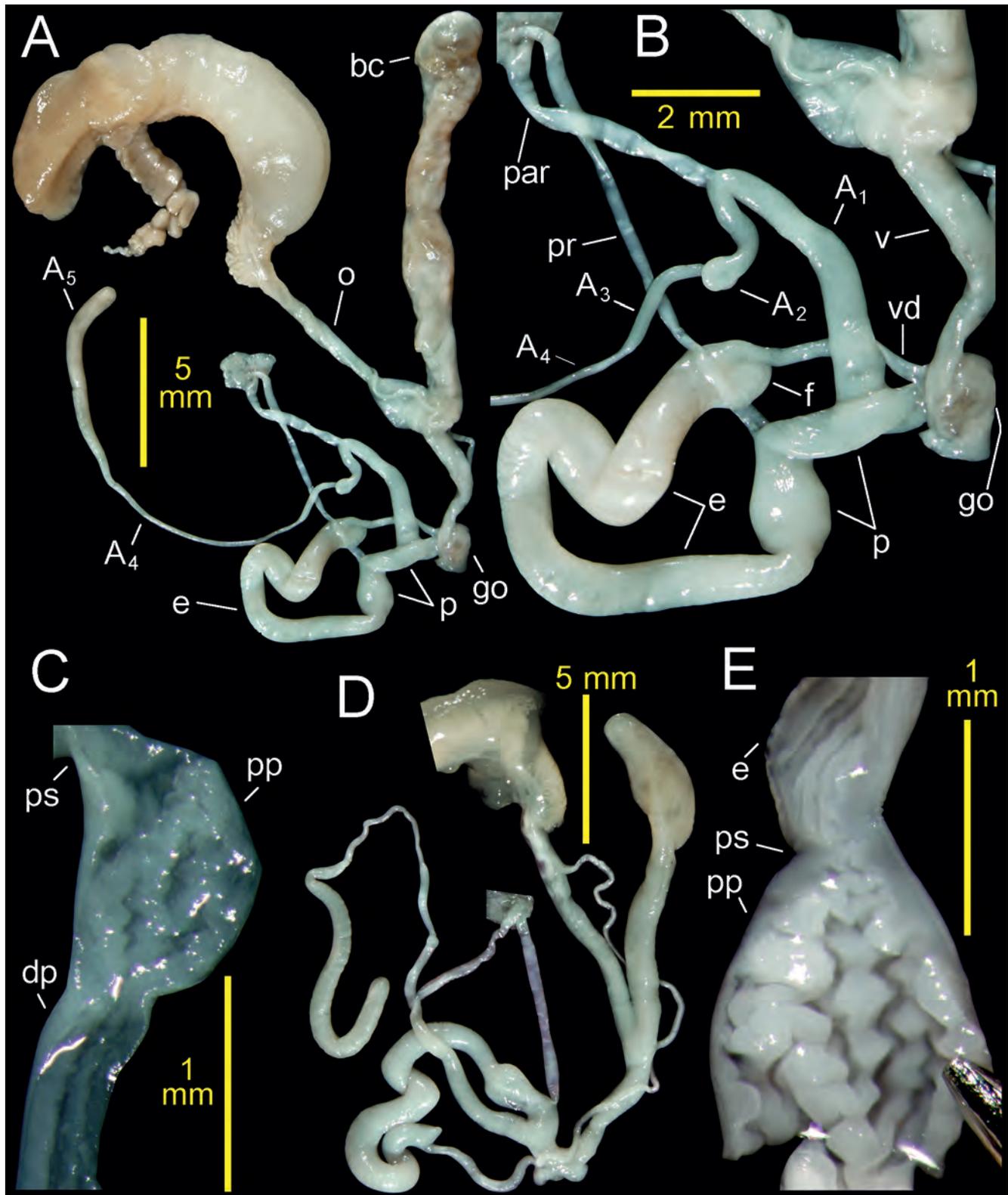


Figure 9 Comparisons between the genital systems of *N. magnus* sp. nov. and *N. bertheloti*: A–C *N. magnus* sp. nov., from Monte Calvario, La Gomera; D–E *N. bertheloti* (L. Pfeiffer 1848), from Enchereda, La Gomera; A, D genital system; B detail of the distal region; C detail of the penis internal anatomy; E detail of the internal anatomy of the epiphallus distal part and the penis proximal part. A₁–A₅ parts of the penial appendix, bc bursa copulatrix, dp distal penis, e epiphallus, f flagellum, go genital orifice, par penial appendix retractor, pr penial retractor, ps penial sphincter, pp proximal penis, o free oviduct, v vagina, vd vas deferens. Fig. 9 D was first published in Yanes, Martín *et al.* (2011, fig. 6C).

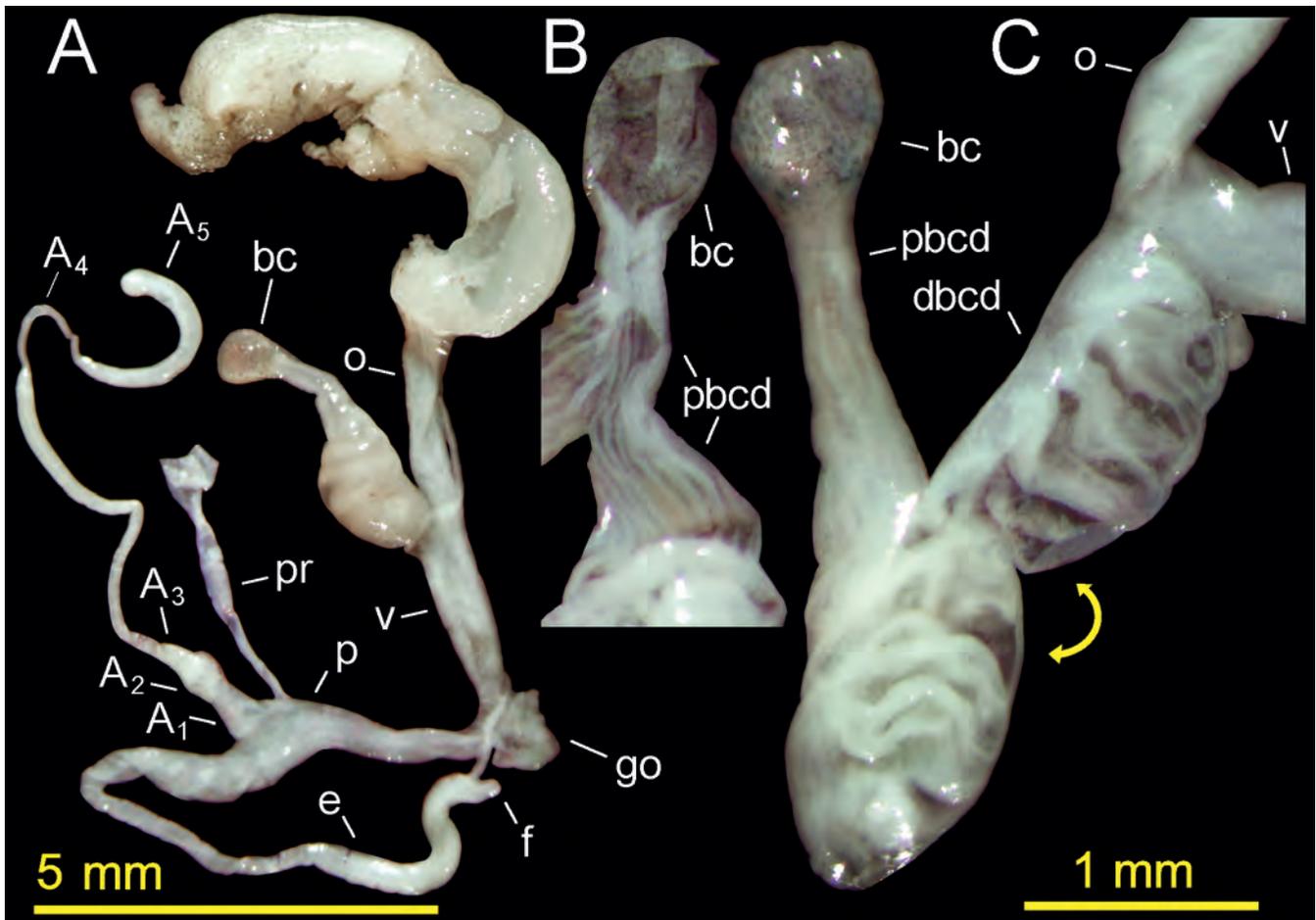


Figure 10 Genital system of *Napaeus gruereanus* (Grasset, 1857), from Valverde, El Hierro, which corresponds to the pattern “H” of the *Napaeus* genital system anatomy described in the “remarks” chapter. A₁–A₅ parts of the penial appendix, bc bursa copulatrix, dbcd distal part of bursa copulatrix duct, e epiphallus, f flagellum, go genital orifice, o free oviduct, p penis, pbcd proximal part of bursa copulatrix duct, pr penial retractor, v vagina.

Napaeus estherae sp. nov., Artiles

Holotype 1 sh, TFMC (MT 0842); Leg. J. Santana, 7 December 2010 (Fig. 8D).

Paratypes 2 sh (AIT), 13 sh (FDGC), 12 sh (JSGC), 28 sh (MAGC), collected between 1989 and 2012 from the west of La Gomera.

Type locality La Mérica, north slope (La Gomera; UTM: 28RBS7012; 820 m altitude).

Diagnosis Shell well calcified, obese, conic-cylindrical, with the first 6 whorls increasing regularly in size and the body whorl nearly cylindrical; with a distinct suture and weak ornamentation. Aperture rounded, long and very wide, with a well developed peristomial lip, reflected mainly on the parietal-palatal sides. Penis without sections but broadened distally, the penial retractor

muscle inserted towards the broader half. Bursa copulatrix elongated; bursa duct thick, without diverticulum.

Description Body (Fig. 5C) pale brown with numerous dark brown spots. Shell (Fig. 8D) well calcified, obese (Table 2, SB/SH index), conic-cylindrical, with 6½ to 7¼ whorls and a distinct suture; the first six whorls increase regularly in size and the body whorl is nearly cylindrical and intermediate (BH/SH index), occupying nearly ¾ of the shell surface area (BS/SS index). Protoconch smooth, shiny, with 1½ whorls. Aperture rounded, long and very wide (AH/SH and AB/SB indices), with a well developed peristomial lip, reflected mainly on the parietal-palatal sides, which partly covers the umbilical slit. Older specimens have a small callosity between peristome edges and a

nodule at the junction of parietal and palatal margins. Angle of columella-upper palatal side about 112°. Edge of aperture projects about 45% (1.9 mm) from start of body whorl (see Fig. 2, ratio T:U, due to combination of upper palatal angle and projection of peristomial lip). Shell colour pale brown, slightly darker in the first whorls (Figs 5C, 8D). Shell ornamentation with numerous weak, radial oblique ribs, more or less regularly interrupted forming small granulations (Fig. 6B). Shell with some gloss despite ribs.

Genital system (Fig. 7B-D; five specimens dissected) Atrium very short, penis and vagina meet at level of the genital orifice. Penis without division into sections, shorter and broader than epiphallus, slender proximally; the penial retractor muscle inserts towards the broader distal half. The penis lacks penial papilla and has a small sphincter between it and the epiphallus; penial cavity wide, with several small, irregular folds. Epiphallus tubular, without caecum and not subdivided into sections, opening distally into penis. Flagellum very short, located at the proximal end of the epiphallus. Vas deferens opens sub-terminally into proximal end of epiphallus. Penial appendix arising from distal portion of penis, close to atrium, slightly longer than penis and epiphallus combined. Part A₁ of penial appendix tubular, differentiated from part A₂. Part A₄ slightly thinner than part A₃, which is slender, passing gradually into expanded part A₅. Appendicular retractor muscle inserted near the proximal top of part A₁ and joined to penial retractor muscle on diaphragm walls. Free oviduct similar in length to vagina. Vagina firmly attached to body tegument by short connective fibres. Bursa copulatrix elongated; bursa duct thick, without diverticulum. Two specimens everted the distal genitalia during their relaxation phase previous to the fixation process; one of them everted the entire penis and the distal end of the epiphallus (Fig. 7C, D) and the other specimen also partly everted part A₁ of the penial appendix.

Derivation of name The specific name is dedicated to Esther Sosa, the wife of M. Artiles.

Distribution and habitat A species endemic to La Gomera, where it was collected on the western side of the island, within an altitudinal

range between 250 and 830 m (Fig. 1). It is a ground-dweller in north-west facing, open, partly lichen covered rocky slopes exposed to the humid trade winds, with succulent and sparse low vegetation (*Aeonium* sp., *Monanthes* sp. and *Argyranthemum* sp.), as well as under stones in lowland areas living associated with large *Euphorbia* species (*E. balsamifera* Aiton and *E. berthelotti* Bolle ex Boiss.). The shells of juvenile specimens collected at higher altitude were disguised by a fine soil cover and mostly found on the rock of crags, partly hidden in crevices, while the adults were detected in deep crevices or under stones. Other *Napaeus* species found cohabiting were *N. minimus* D. Holyoak & G. Holyoak in Holyoak *et al.* 2011 at higher altitude, as well as *N. ornamentatus* Moro in Yanes *et al.* 2009 and *N. taguluchensis* Henríquez 1993 in the drier lowland areas.

Comparisons. The shell of *Napaeus estherae* (Figs 3B, 8D) is comparable in size to those of *N. subsimplex* (Wollaston 1878) (Fig. 8B), from El Hierro island, *N. severus* (J. Mabile 1898) (Fig. 8H), from La Gomera island and two species from Tenerife island, *N. tenoensis* Henríquez 1993 (Fig. 8J) and *N. baeticatus* (Webb & Berthelot 1833) (Fig. 8K). *N. estherae*, *N. subsimplex* and *N. severus* have similar shell ornamentation but the latter two species have the aperture ovate, larger than that of *N. estherae*, in which it is also more rounded. The shell of *N. estherae* is the most slender and it is slightly larger than that of *N. severus*, whereas the shell of *N. subsimplex* is the largest and most cylindrical of the three. *N. tenoensis* and *N. baeticatus* have the shell ornamentation rough and a different shell shape, that of *N. tenoensis* being more cylindrical, whereas that of *N. baeticatus* is more triangular.

The genital system is known from only two of these species, *N. tenoensis* and *N. baeticatus* (Henríquez, Alonso *et al.*, 1993: plate 4; figs 19–20). The genital system of *N. estherae* differs by the absence of an epiphallar caecum, which is present in *N. tenoensis* and *N. baeticatus*. The distal part of the penis of *N. estherae* is also clearly broader than in those two species.

Napaeus magnus sp. nov. Yanes, Deniz, Alonso & Ibáñez

Holotype 1 sh, TFMC (MT 0844); Leg. M. Ibáñez, January 1999 (Fig. 8G).

Paratypes 2 sh (AIT), 24 sh (FDGC), 5 sh (JMHGC), 46 sh (JSGC), 23 sh (MAGC), collected between September 1988 and December 2012 from the south of La Gomera.

Type locality Monte Calvario (La Gomera; UTM: 28RBS7012; 750 m altitude).

Diagnosis Shell strong, well calcified, very obese, with 6 to 6½ whorls, the first 5 whorls increasing regularly in size whereas the body whorl is very large; with a distinct suture and weak ornamentation. Aperture rounded, long and very wide, with a well developed peristomial lip, reflected mainly on the parietal-palatal sides. Genital atrium very short. Penis with two parts, delimited by retractor muscle insertion; without penial papilla but with a small sphincter between epiphallus and proximal part of penis. Bursa copulatrix elongated, bursa duct long and thick, without diverticulum.

Description Body grey (Fig. 5D), darker on the dorsal side. Shell (Fig. 8G) strong, well calcified, very obese (Table 2, SB/SH index), with 6 to 6½ whorls and a distinct suture; the first five whorls increase regularly in size; body whorl very large (BH/SH index), occupying slightly more than 3/4 of the shell surface area (BS/SS index). Protoconch smooth, with 1¼ to 1½ whorls, sometimes partly deteriorated. Aperture rounded, long and very wide (AH/SH and AB/SB indices), with a very well developed peristomial lip, reflected mainly on the parietal-palatal sides, which partly covers the umbilical slit. Older specimens have a callosity between peristome edges and a nodule at the junction of parietal and palatal margins. Angle of columella-upper palatal side about 113°. Edge of aperture projects about 42% (2.3 mm) from start of body whorl (see Fig. 2, ratio T:U; due to combination of upper palatal angle and projection of peristomial lip). Shell colour pale brown, darker in the first whorls. The shell is almost smooth, shiny (Fig. 8G), but with high magnification a delicate ornamentation is observed on the body whorl (Fig. 6 C), with weak, radial oblique ribs; many specimens, as in the figure, have tiny cracks in the periostracum.

Genital system (Fig. 9A-C; five specimens dissected) Atrium very short. Penis with two parts, delimited by the retractor muscle insertion; distal part tubular, slender; proximal part swollen,

with several small, irregularly pleated longitudinal folds inside. Penial papilla absent, but a small sphincter is present between epiphallus and proximal penis portion. Epiphallus tubular, without caecum, with thickness intermediate between those of the two penis parts. Flagellum very short. Penial appendix inserts laterally in the distal part of penis, near the atrium. Part A₁ of penial appendix slightly longer than penis and with similar thickness to distal part of penis. Part A₂ small, globular. Part A₃ short and slightly thicker than part A₄, which is similar in length to the epiphallus. Part A₅ swollen and slightly shorter than part A₄. Appendicular retractor muscle inserts laterally near the proximal top of part A₁ and inserts on the lower lung wall together with penis retractor. Free oviduct about 1.5 times longer than vagina. Bursa copulatrix elongated, bursa duct without diverticulum, thick and nearly twice as long as oviduct.

Derivation of name The specific epithet refers to the large size and characteristic obese outline of its shell.

Distribution and habitat A species endemic to La Gomera, where it was found as a ground-dweller, under stones in lowland areas, with large *Euphorbia* species (*E. canariensis*, *E. balsamifera* and *E. berthelotii*), *Agave salmiana* Otto and other lowland shrubs within an altitudinal range between 300 and 1325 m (Fig. 1). Shells of this huge species generally lack any disguise in the adult specimens, although in the juvenile and some adult animals a fine soil cover may be evident when they are found in crevices in rocky slopes.

Comparisons The shell of *Napaeus magnus* (Figs 3C, 8G) is comparable in size to those of *N. bertheloti* (L. Pfeiffer 1848) (Fig. 8 A), *N. conseqoanus* (Mousson 1872) (Fig. 8C) and *N. inflatusculus* (Wollaston 1878) (Fig. 8F), from La Gomera island, as well as with *N. subsimplex* (Wollaston 1878) (Fig. 8B) and *N. savinosa* (Wollaston 1878) (Fig. 8E), from El Hierro island. The shell of *N. magnus* has the smallest first whorls of these six species, but the largest aperture (as shown by all shell aperture parameters measured). It is the species with the widest shell for the genus, with shell breadth (SB) reaching a mean of 13 mm (Fig. 3C) and maximum of 14.09 mm in the specimens measured (Table 1).

The genital system is known only from another species of the *N. magnus* group, *N. bertheloti* (Fig. 9 D, E). Both genital systems have similar characters but differ in overall size (that of *N. magnus* being bigger than that of *N. bertheloti*), and also in the relative size of some parts as well as in the internal anatomy of the proximal part of the penis. Part A₁ of the penial appendix and the oviduct are shorter, and part A₄ and the bursa duct are longer in *N. magnus* (Fig. 9A) than in *N. bertheloti* (Fig. 9D). The length of the vagina is similar in these species. The main difference between them is in the pleated longitudinal folds inside the proximal part of the penis: they are much better developed and more voluminous in *N. bertheloti* (Fig. 9 E) than in *N. magnus* (Fig. 9C).

DISCUSSION

Many of the *Napaeus* species have small shells (Fig. 3). In the archipelago as a whole, 77% of the species have a mean shell height of less than half the shell height of the species with the tallest shell. This proportion is lower at 69% on La Gomera island, which not only has the species with the shortest shell for the genus (*N. minimus*), but also the one with the most slender shell (*N. beguirae* Henríquez 1995), the longest shell (*N. consecoanus*) and the widest shell (*N. magnus*).

The genital system of *Napaeus* species shows eight different patterns, named "A" to "H" (Table 3); pattern "H" (Fig. 10) was unknown until now and belongs to the species *Napaeus gruereanus* (Grasset 1857), from El Hierro island. The range of genital system variability is wider in the species of La Gomera island than in those of all of the rest of the archipelago. The genital anatomy has been described on 21 species from this island, with five different patterns present ("A" to "E": Table 3), in which the absence of both epiphallar caecum and bursa duct diverticulum are the only character-states common to all them.

In contrast to the situation on La Gomera Island, the number of different patterns of genital anatomy found so far in the *Napaeus* species from the other islands is thus lower: three are known on Tenerife, two on El Hierro, La Palma and Gran Canaria and one on Fuerteventura, Lanzarote and Alegranza islet.

The eight patterns found in the anatomy of the genital system of *Napaeus* are as follows:

(A) With two retractor muscles (penial and

Table 3 Distribution on the islands of the eight genital system patterns found in the genus *Napaeus*; the numbers correspond to the species equipped with each pattern.

PATTERN ISLAND/ ISLET	A	B	C	D	E	F	G	H
La Gomera	14	1	1	4	1			
Tenerife	3					5	6	
El Hierro	1							1
La Palma	1					1		
Gran Canaria	1						10	
Fuerteventura							1	
Lanzarote							1	
Alegranza							1	

appendicular); epiphallus without caecum; bursa copulatrix duct without diverticulum, lacking distal septum and distal chamber.

(B) With two retractor muscles; epiphallus without caecum; bursa copulatrix duct without diverticulum and with an inner, distal chamber. It is present in *N. alucensis* Santana & Yanes in Yanes *et al.* 2011.

(C) With two retractor muscles; epiphallus without caecum; bursa copulatrix duct without diverticulum and with a distal, incomplete septum; it is present in *N. avaloensis* Groh in Alonso *et al.* 2006.

(D) Without penial retractor muscle; epiphallus without caecum; bursa copulatrix duct without diverticulum and with an inner, distal chamber.

(E) Without penial retractor muscle; epiphallus without caecum; bursa copulatrix duct without diverticulum, lacking distal septum and distal chamber. It is present in *N. maculatus* Goodacre in Alonso *et al.* 2006.

(F) With two retractor muscles; epiphallus with a caecum; bursa copulatrix duct without diverticulum, lacking distal septum and distal chamber.

(G) With two retractor muscles; epiphallus with a caecum; bursa copulatrix duct with a diverticulum, lacking distal septum and distal chamber.

(H) Without penial appendix retractor muscle; epiphallus without caecum; bursa copulatrix duct without diverticulum and with two parts of similar length to each other; proximal part tubular, with about 8 longitudinal folds inside and distal part very swollen, with 7–8 inner large, transverse septa; it is present in *N. gruereanus*.

Pattern "A" corresponds to the subgenus *Napaeus* (*Napaeus*) Hesse 1933; it is known from

20 species from La Gomera, Tenerife, El Hierro, La Palma and Gran Canaria. Pattern "G" corresponds to the subgenus *Napaeus* (*Napaeinus*) Hesse 1933; it is known from 19 species from Tenerife, Gran Canaria, Fuerteventura, Lanzarote and Alegranza.

ACKNOWLEDGEMENTS

Special thanks are due to Jonathan Ablett (NHMUK) for the photographic images of a syntype of *Bulimus savinosa*; to Harriet Wood (NMW) and James Turner, for those of the holotype of *Bulimus savinosa* var. *inflatuscula*; and to David T. Holyoak (Cabecudo, Portugal) for suggestions and comments that improved the manuscript. This study was partly supported by the project CGL2011-29898/BTE funded by the Spanish "Ministerio de Economía y Competitividad".

REFERENCES

- ALONSO MR, GOODACRE SL, EMERSON BC, IBÁÑEZ M, HUTTERER R & GROH K 2006 Canarian land snail diversity: conflict between anatomical and molecular data on the phylogenetic placement of five new species of *Napaeus* (Gastropoda, Pulmonata, Enidae). *Biological Journal of the Linnean Society* **89**: 169–187.
- ALONSO MR, HENRÍQUEZ F & IBÁÑEZ M 1995 Revision of the species group *Napaeus variatus* (Gastropoda, Pulmonata, Buliminidae) from the Canary Islands, with description of five new species. *Zoologica Scripta* **24**: 303–320.
- ALONSO MR, NOGALES M & IBÁÑEZ M 2006 The use of the computer-assisted measurements utility. *Journal of Conchology* **39**(1): 41–48.
- BANK RA, GROH K & RIPKEN TEJ 2002 Catalogue and bibliography of the non-marine Mollusca of Macaronesia. In Falkner M, Groh K & Speight MCD (eds) *Collectanea Malacologica. Festschrift für Gerhard Falkner*: 89–235, pl: 14–26. ConchBooks, Hackenheim.
- CAMERON RAD, TRIANTIS KA, PARENT CE, GUILHAUMON F, ALONSO MR, IBÁÑEZ M, MARTINS AM FRIAS, LADLE RJ & WHITTAKER RJ 2013 Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. *Journal of Biogeography* **40**(1): 117–130.
- CASTILLO C, YANES Y, ALONSO MR & IBÁÑEZ M 2006 *Napaeus lajaensis* sp. nov. (Gastropoda: Pulmonata: Enidae) from a Quaternary Aeolian Deposit of Northeast Tenerife, Canary Islands. *Zootaxa* **1307**: 41–54.
- GROH K, ALONSO MR, IBÁÑEZ M & HENRÍQUEZ FC 1992 Rediscovery of *Hemicycla saulcyi* (d'Orbigny, 1839), a revision of its fossil allies (Gastropoda: Helicidae), and a description of a new species of *Napaeus* (Enidae), both from La Isleta, Gran Canaria, Canary Islands. *Schriften zur Malakozoologie* **5**: 1–12, pl: 1–3.
- HENRÍQUEZ F, IBÁÑEZ M & ALONSO MR 1993 Revision of the genus *Napaeus* Albers, 1850 (Gastropoda Pulmonata: Enidae). I. The problem of *Napaeus* (*Napaeinus*) *nanodes* (Shuttleworth, 1852) and description of five new species from its conchological group. *Journal of Molluscan Studies* **59**: 147–163.
- HENRÍQUEZ F, ALONSO MR & IBÁÑEZ M 1993 Estudio de *Napaeus baeticatus* (Férussac) (Gastropoda Pulmonata: Enidae) y descripción de dos nuevas especies de su grupo conculológico. *Bulletin du Muséum national d'Histoire naturelle* (4) **15** A(1–4): 31–47.
- HESSE P 1933 Zur Anatomie und Systematik der Familie Enidae. *Archiv für Naturgeschichte, N. F.* **2**: 145–224.
- HOLYOAK GA, HOLYOAK DT, YANES Y, ALONSO MR & IBÁÑEZ M 2011 Two new *Napaeus* species from La Gomera and La Palma (Canary Islands) (Gastropoda: Pulmonata: Enidae). *Archiv für Molluskenkunde* **140**: 37–48.
- IBÁÑEZ M, ALONSO MR, YANES Y, CASTILLO C & GROH K 2007 Presence of the genus *Napaeus* (Gastropoda: Pulmonata: Enidae) living in all the islands of the Canarian archipelago: *Napaeus lichenicola* sp. nov. from Fuerteventura island. *Journal of Conchology* **39**(4): 381–389.
- IBÁÑEZ M, SIVERIO F, ALONSO MR & PONTE-LIRA CE 2006 Two *Canariella* species (Gastropoda: Helicoidea: Hygromiidae) endemic from the Northwest Tenerife (Canary Islands). *Zootaxa* **1258**: 33–45.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 2003 Opinion 2018 (Case 3192). Buliminidae Kobelt, 1880 (Mollusca, Gastropoda): spelling emended to Buliminidae, so removing the homonymy with Buliminidae Jones, 1875 (Rhizopoda, Foraminifera); and Enidae Woodward, 1903 (1880) (Gastropoda): given precedence over Buliminidae Kobelt, 1880. *Bulletin of Zoological Nomenclature* **60**: 63–65.
- KERNEY MP & CAMERON RAD 1979 *A field guide to the land snails of Britain and north-west Europe*. Collins, London. 288 pp.
- MOUSSON A 1872 Révision de la faune malacologique des Canaries. *Neue Denkschriften der allgemeinen schweizerischen Gesellschaft für die gesammten Naturwissenschaften* **25**: V+76 pp., 6 pls.
- SCHILEYKO AA 1984 Nazemnye molljuskij podotrjada Pupillina fauny SSSR (Gastropoda, Pulmonata, Geophila). *Fauna SSSR, Molljuskij* **3**(3): 1–399. Akademija Nauk, Leningrad.
- WEBB PB & BERTHELOT S 1833 Synopsis molluscorum terrestrium et fluviatiliium quas in itineribus per insulas Canarias, observarunt. *Annales des Sciences naturelles* **28**: 307–326.
- WOLLASTON TV 1878 *Testacea Atlantica or the land and freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes and Saint Helena*. L. Reeve, London. XI + 588 pp.

- WOODWARD BB 1903 List of British non-marine Mollusca. *Journal of Conchology* **10**(12): 352–367.
- YANES Y, MARTÍN J, MORO L, ALONSO MR & IBÁÑEZ M 2009 On the relationships of the genus *Napaeus* (Gastropoda: Pulmonata: Enidae), with the description of four new species from the Canary Islands. *Journal of Natural History* **43**: 2179–2207.
- YANES Y, MARTÍN J, DELGADO JD, ALONSO MR & IBÁÑEZ M 2010 Active disguise in land snails: *Napaeus badiusus* (Gastropoda, Pulmonata, Enidae) from the Canary Islands. *Journal of Conchology* **40**(2): 143–148.
- YANES Y, MARTÍN J, SANTANA J, HOLYOAK GA, HOLYOAK DT, ARTILES M, DENIZ F, ALONSO MR & IBÁÑEZ M 2011 Four new *Napaeus* species (Gastropoda: Pulmonata: Enidae) from La Gomera (Canary Islands). *Journal of Conchology* **40**(4): 393–407.
- YANES Y, SANTANA J, ARTILES M, DENIZ F, MARTÍN, J, ALONSO MR & IBÁÑEZ M 2011 Five new *Napaeus* species (Gastropoda: Pulmonata: Enidae) from Gran Canaria and El Hierro (Canary Islands). *Zootaxa* **2901**: 35–51.