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Article

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Five new *Napaeus* species (Gastropoda: Pulmonata: Enidae) from Gran Canaria and El Hierro (Canary Islands)

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Abstract

Five new species of *Napaeus* are described, four from Gran Canaria and one from El Hierro (Canary Islands): *Napaeus josei* **n. sp.**, *N. veneguerensis* **n. sp.**, *N. arinagaensis* **n. sp.**, *N. validoi* **n. sp.** and *N. grohi* **n. sp.** The main differences from the most similar species and data on distribution are presented. At least three of the new species disguise their shells with soil, presumably to avoid predation.

Key words: taxonomy, insular endemics, genital anatomy, shells, shell disguise

Introduction

The genus *Napaeus* has undergone a remarkable radiation in the Canary Islands (mid-Atlantic), with 65 living species (Yanes *et al*. 2009, 2011; Holyoak *et al*. in press; this paper) and two extinct species (Castillo *et al*. 2006; this paper) described, and we have collected specimens of some other as yet undescribed species.

The distribution of each species of *Napaeus* is typically restricted to a small area within a single island (i.e. they demonstrate "single island endemism"); some areas are well preserved but many other are not. The level of legal protection of species and their habitats is now lower than before, after a new Canarian law of 2010 abolished protection or reduced the level of protection of almost all the species included in the previous legislation.

The small island of La Gomera has the highest number (23) of living *Napaeus* species known for any single island whereas the two central islands, Tenerife and Gran Canaria, have only 16 and 13, respectively. The lowest numbers of living *Napaeus* species were described from El Hierro, the westernmost island, with 5 species (Grasset 1857; Mousson 1872; Wollaston 1878), La Palma, with 5 species (Shuttleworth 1852; Mousson 1872; Wollaston 1878; Henríquez *et al*. 1993a), and the two easternmost islands, Lanzarote, with 2 species (Wollaston 1878; Alonso *et al*. 1991) and Fuerteventura, with 1 species (Ibáñez *et al*. 2007). A complete list of the *Napaeus* species described to that date is found in Yanes *et al*. (2009); four additional species have been described by Yanes *et al*. (2011).

In the present study five new *Napaeus* species are described, four from Gran Canaria and one from El Hierro. They are not allocated to subgenera (*Napaeus* and *Napaeinus*) as described by Hesse (1933) because this has been shown to be problematical based on genital anatomy alone: anatomical study of six species revealed contradictions with Hesse's subgeneric descriptions (Alonso *et al*. 1995; Yanes *et al*. 2009). Different modes of classification (i.e. genital anatomy and molecular phylogeny) also yield different results (Alonso, Goodacre *et al*. 2006). Thus, the new species are not assigned to Hesse's subgenera until a phylogenetic analysis of the genus *Napaeus* is conducted.

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Methods

The snails were drowned in water and fixed in 80% ethanol. Maps of geographical distributions (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 analySIS® (Soft Imaging System GmbH). Abbreviations for shell characters and measurements are shown in Fig. 2. The angle at the upper peristome insertion between the columella and the upper palatal margin of the aperture has also been measured because a combination of this angle and the width of the peristome lip influences the shell breadth: if this angle is close to 90º, the aperture tends to be very prominent, but if it is close to 135º, the aperture tends not to be prominent. The lateral extension of the aperture beyond the penultimate whorl was measured in the corresponding photos and is expressed as a percentage obtained by using the formula: (U−T)×100/T, and also in millimetres (U−T) (Fig. 2). The number of shell whorls was counted using the methodology described by Kerney & Cameron (1979: 13). The terminology for the shape and proportions of shells is based on the biometric data provided in Table 1, following Henríquez *et al*. (1993b; 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 on the location of the insertion of the penial retractor muscle (as in Alonso & Ibáñez 2007).

Other 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
JSGC	J. Santana private collection, Las Palmas de Gran Canaria, Spain
MAGC	M. Artiles private collection, Arinaga, Gran Canaria, Spain
TFMC (MT)	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain
UTM	Universal Transverse Mercator cartographic projection system

TABLE 1. Data on the shell characters measured (in mm or mm^2). n, number of measured specimens; SD, standard deviation; Min., minimum; Max., maximum; other abbreviations as in Fig. 2.

Statistical parameter	Character / index	*N. josei*	*N. veneguerаensis*	*N. arinagaensis*	*N. validoi*	*N. grohi*	Character / index	*N. josei*	*N. veneguerаensis*	*N. arinagaensis*	*N. validoi*	*N. grohi*
Mean	SH	12,86	15,17	12,99	17,76	13,31	AP	17,63	16,74	11,83	17,83	16,72
SD		0,37	0,96	0,63	0,93	0,01		0,64	0,88	0,79	1,20	0,57
Min.		12,18	13,69	11,95	16,46	13,30		16,51	14,94	10,62	15,50	16,31
Max.		13,65	16,95	13,95	19,12	13,32		18,43	17,53	13	19,09	17,12
Mean	SB	8,05	7,14	4,99	7,43	7,42	FH	2,67	4,01	4,10	5,43	2,99
SD		0,25	0,29	0,31	0,39	0,23		0,23	0,41	0,23	0,42	0,37
Min.		7,77	6,75	4,43	6,59	7,25		2,31	3,43	3,7	4,78	2,72
Max.		8,54	7,46	5,41	7,83	7,58		3,14	4,75	4,5	6,17	3,25
Mean	SS	69,47	77,77	41,17	91,07	65,20	FB	4,32	5,23	2,91	5,36	4,00
SD		3,21	7,58	3,96	7,21	2,31		0,19	0,31	0,16	0,21	0,04
Min.		63,08	66,89	32,98	76,30	63,56		4,18	4,76	2,64	5,06	3,97
Max.		73,72	92,02	46,27	98,86	66,83		4,84	5,77	3,16	5,72	4,02

continued next page

TABLE 1. (continued)

Statistical parameter	Character / index	*N. josei*	*N. veneguerаensis*	*N. arinagaensis*	*N. validoi*	*N. grohi*	Character / index	*N. josei*	*N. veneguerаensis*	*N. arinagaensis*	*N. validoi*	*N. grohi*
Mean	SP	33,58	36,60	30,28	42,18	33,10	FS	7,48	14,00	8,02	20,43	7,32
SD		0,88	2,09	1,47	2,22	0,04		0,93	2,44	0,75	2,25	1,20
Min.		31,99	33,36	27,67	38,64	33,07		6,09	10,61	6,88	17,30	6,47
Max.		34,94	40,45	32,67	45,38	33,12		9,52	18,64	9,22	24,50	8,16
Mean	BH	7,96	8,47	6,74	9,17	8,32	FP	11,53	15,39	12,34	18,34	11,69
SD		0,22	0,54	0,37	0,47	0,32		0,65	1,07	0,62	1,02	0,81
Min.		7,62	7,54	5,99	8,20	8,09		10,86	13,82	11,43	16,84	11,11
Max.		8,40	9,13	7,22	9,72	8,54		13,25	17,28	13,5	19,90	12,26
Mean	BS	49,23	47,69	25,47	52,06	47,44	PH	2,15	2,70	2,18	3,15	2,02
SD		2,63	4,10	2,61	4,60	3,40		0,14	0,19	0,16	0,18	0,04
Min.		44,84	40,25	19,46	41,35	45,03		2,00	2,45	1,95	2,93	1,99
Max.		52,47	53,49	28,48	56,37	49,84		2,47	3,08	2,49	3,46	2,04
Mean	BP	28,00	27,48	20,14	28,96	26,78	PB	6,20	6,17	3,71	6,06	5,55
SD		0,68	1,26	1,03	1,40	0,81		0,20	0,19	0,20	0,23	0,08
Min.		26,43	25,31	17,95	25,81	26,20		5,78	5,95	3,25	5,58	5,49
Max.		28,50	29,49	21,55	30,61	27,35		6,34	6,55	3,91	6,30	5,60
Mean	AH	5,82	5,92	4,28	6,20	5,67	PS	12,27	16,07	7,68	18,58	10,45
SD		0,21	0,32	0,27	0,46	0,28		0,74	1,86	0,91	1,38	0,11
Min.		5,48	5,27	3,9	5,37	5,47		11,45	13,93	6,2	16,09	10,37
Max.		6,13	6,27	4,77	6,73	5,86		14,16	19,89	9,1	20,37	10,52
Mean	AB	5,35	4,92	3,36	5,30	5,12	PP	15,59	17,19	11,44	18,03	14,50
SD		0,18	0,27	0,26	0,32	0,13		0,43	0,90	0,69	0,65	0,13
Min.		5,18	4,42	2,97	4,66	5,02		14,94	16,23	10,14	16,80	14,40
Max.		5,68	5,26	3,7	5,67	5,21		16,38	19,01	12,41	18,86	14,59
Mean	AS	23,30	20,52	10,35	24,14	20,68	SB/SH	0,63	0,47	0,38	0,418	0,56
SD		1,45	2,08	1,46	3,22	1,26	BH/SH	0,62	0,56	0,52	0,52	0,63
Min.		20,35	16,42	8,15	18,10	19,79	AH/SH	0,45	0,39	0,33	0,35	0,43
Max.		24,67	22,79	12,34	27,75	21,57	AB/SB	0,67	0,69	0,67	0,71	0,69
n		10	7	13	9	2	BS/SS	0,71	0,61	0,62	0,57	0,73

TABLE 2. Terminology for shapes 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				

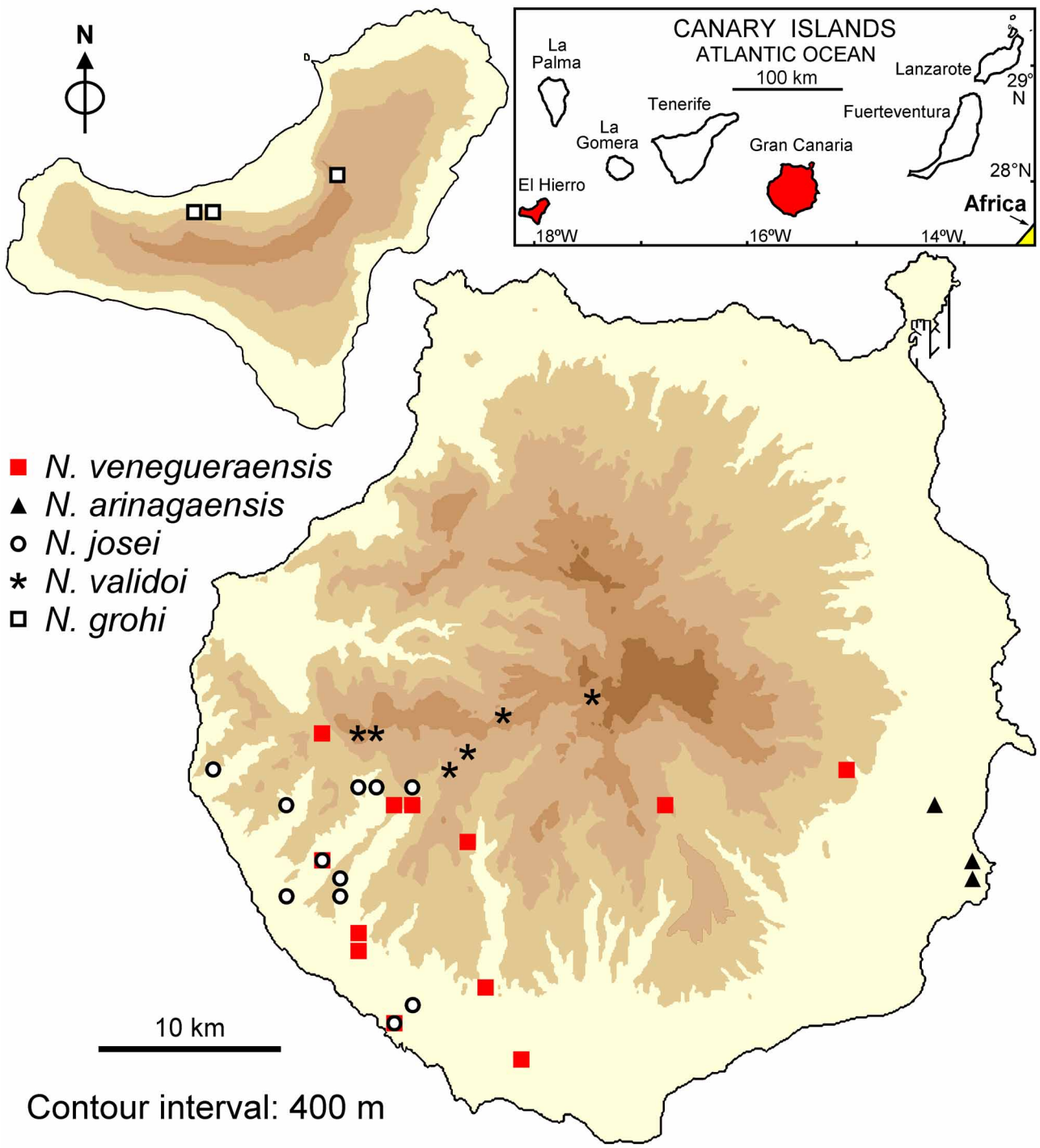

FIGURE 1. Geographical distribution of the new species.

Systematics

Family Enidae B. B. Woodward, 1903 (1880)

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

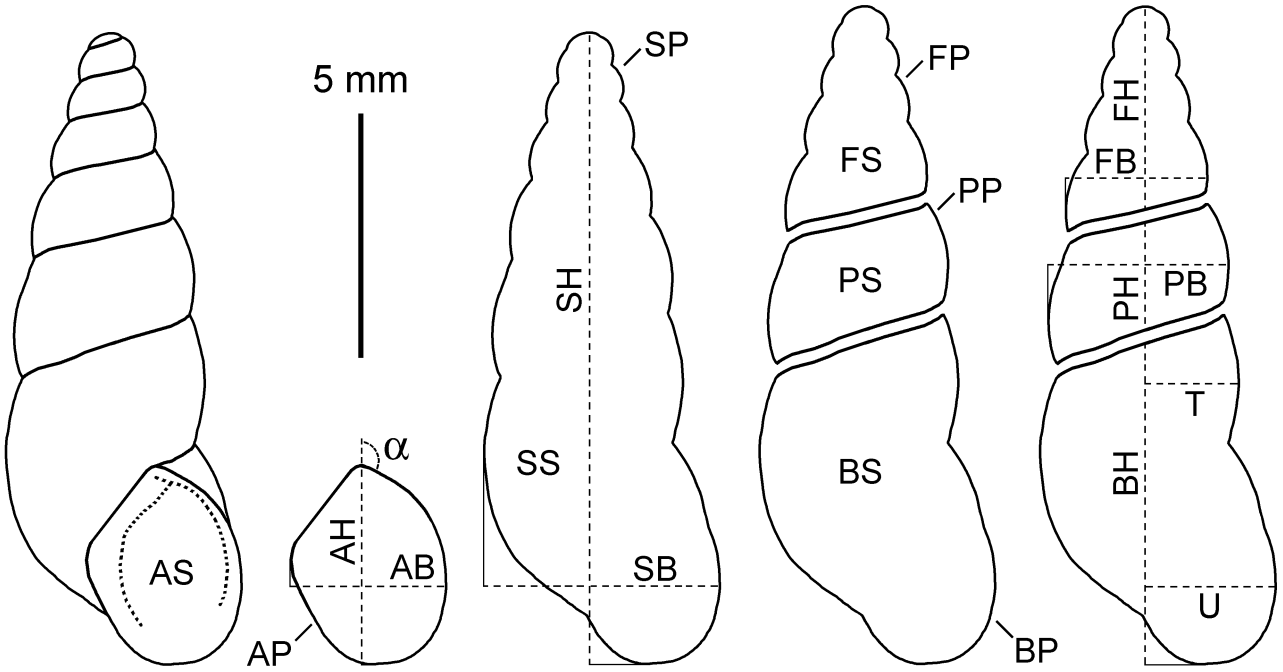

FIGURE 2. Drawings of the shell of the holotype of *Napaeus arinagaensis* **n. sp.**, showing the placement of the measurements obtained (in °, mm or mm^2). α, upper palatal angle (i.e. the angle between the columella and the upper palatal margin of the aperture); AB, aperture breadth; AH, aperture height; 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, distance between columella and periphery of penultimate whorl above aperture; U, highest distance between columella and palatal edge of aperture.

Genus *Napaeus* Albers, 1850

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

Napaeus josei Santana, Alonso & Ibáñez, n. sp.

Figs. 1, 3 A, 4 A–C, 5 A, B, 6 A, B, 7 A–C

Type locality. Barranco del Lechugal (Gran Canaria; UTM: 28RDR3075, 100 m altitude).

Holotype (Fig. 3 A; empty shell). TFMC (MT 0415). Leg. J. Santana, 26 January 2009.

Paratypes. 6 specimens and 102 shells, collected between 1998 and 2010 from the southwest of Gran Canaria, deposited in AIT (6 specimens, 5 shells) and the following collections: JSGC (68 shells); FDGC (9 shells); MAGC (20 shells).

Etymology. The specific name is dedicated to our late friend Jose María Hernández, marine malacologist from Gran Canaria.

Distribution and habitat (Fig. 1). Endemic to Gran Canaria, occupying an area of about 100 km^2 of the southwest of the island, with lowland vegetation, within an altitudinal range between 40 and 460 m. *Napaeus josei* (Fig. 4 A) is mainly a ground dweller, living associated with large *Euphorbia* species, sheltering during the day under stones or between *Euphorbia* roots. The majority of the specimens collected had the shell disguised by a covering of soil, which was sometimes very thick (Figs. 4 B, C), altering the appearance of the shell considerably as in other disguised *Napaeus* species (Yanes *et al*. 2010). This renders most living animals very inconspicuous in their normal resting places, presumably reducing the risk of visual detection by predators. The snails are part of the diet of the

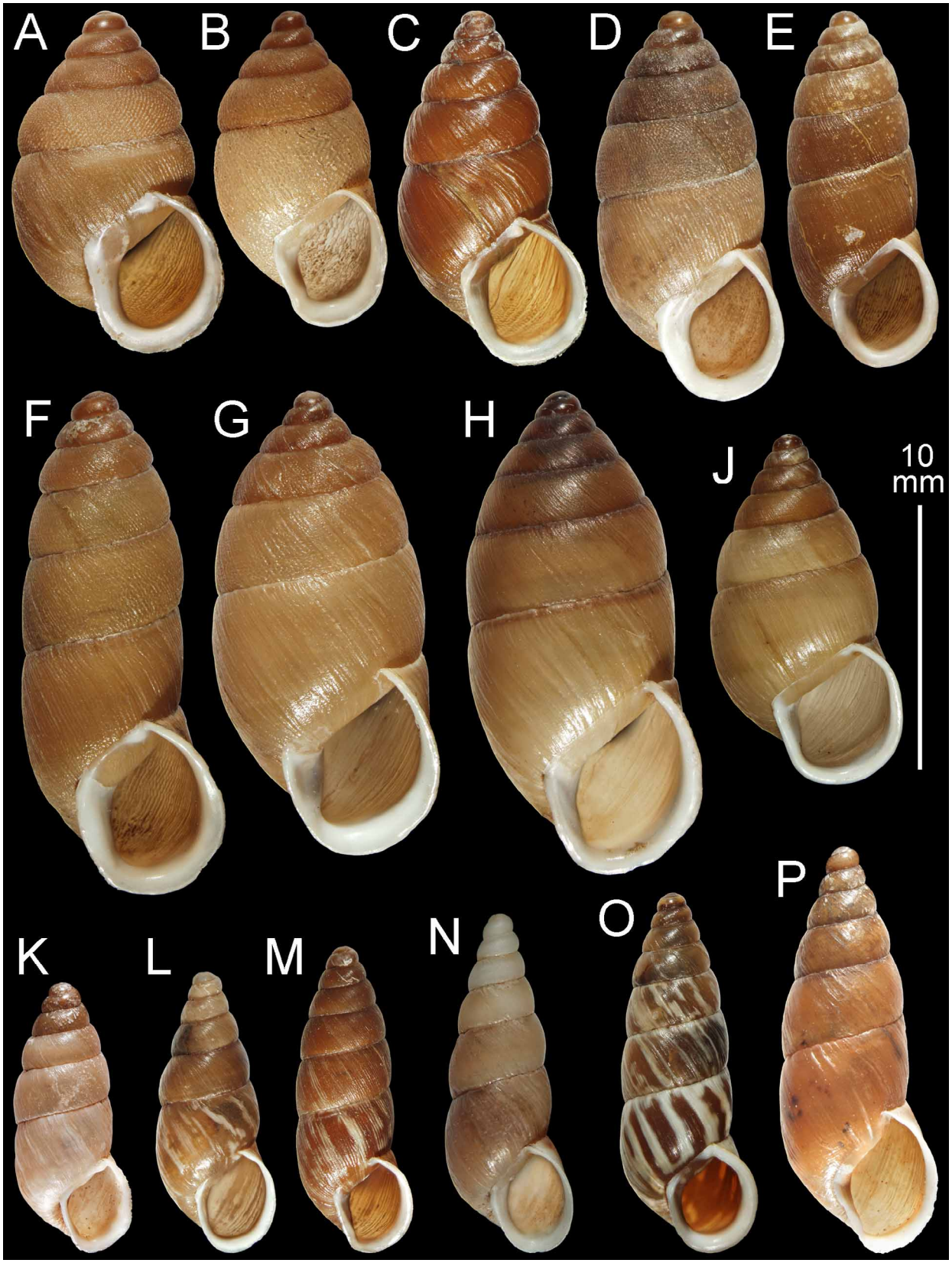

FIGURE 3. Shells of: A. *Napaeus josei* **n. sp.**, holotype. B. *N. nanodes*, from Barranco del Agua, Tenerife (AIT). C. *N. badiosus*, from Barranco de Valle Seco, Tenerife. D. *N. veneguerensis* **n. sp.**, holotype. E. *N. chrysaloides*, from Tamadaba, Gran Canaria (AIT). F. *N. validoi* **n. sp.**, holotype. G. *N. obesatus*, from Barranco del Pagador, Gran Canaria (AIT). H. *N. bajamarensis*, holotype (from Yanes *et al*. 2009). J. *N. grohi* **n. sp.**, holotype. K. *N. osoriensis*, from Osorio, Gran Canaria (AIT). L. *N. myosotis*, from Montaña de Guía, Gran Canaria (AIT). M. *N. exilis*, from Altos de Gáldar, Gran Canaria (AIT). N. *N. arinagaensis* **n. sp.**, holotype. O. *N. moquinianus*, from Brezal del Palmital, Gran Canaria (AIT). P. *N. isletae*, holotype.

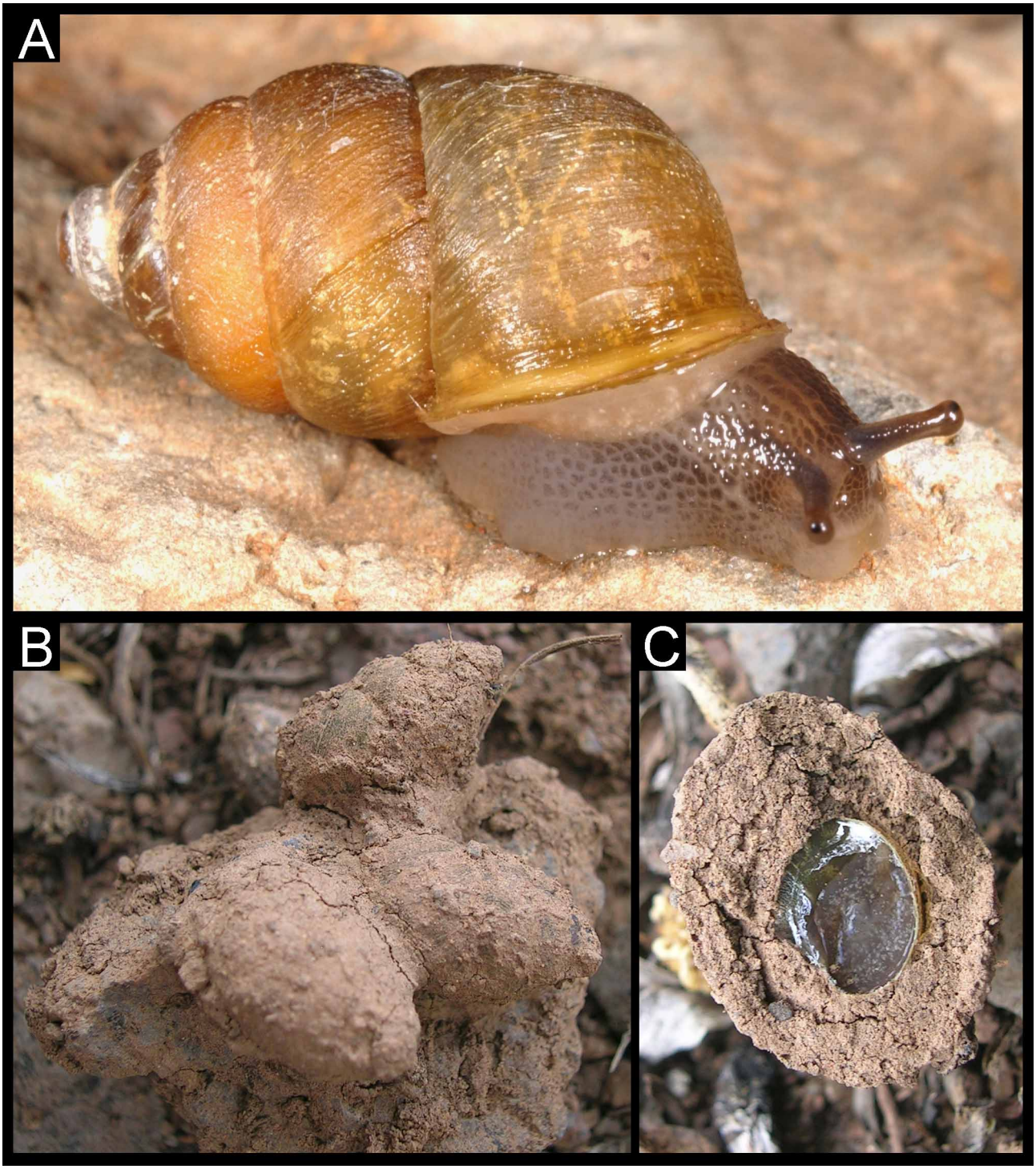

FIGURE 4. *Napaeus josei* **n. sp.** A. Paratype from the type locality (AIT). B. Three paratypes from the type locality, attached to a stone and disguised with a soil covering (JSGC). C. Disguised paratype with a very thick soil covering (JSGC).

Southern Grey Shrike, *Lanius meridionalis* Temminck (Aves, Passeriformes) (Padilla *et al.* 2009) and the omnivorous lizard, *Gallotia atlantica* (Peters & Doria), endemic to the eastern islands (Valido & Nogales 2003). Other species of *Gallotia*, which as a genus is present in all the islands of the Archipelago, probably also consume snails as part of their regular diet (Yanes *et al.* 2010).

Diagnosis. Shell very obese, conic-ovate, brown-coloured, with first whorls slightly darker than rest. Teleoconch granulated. Penis short and thick, with large penial papilla. System of penial appendix parts A_1–A_3 very short. Appendicular retractor muscle inserts laterally in proximal tip of part A_3. Epiphallus with epiphallic caecum. Bursa copulatrix duct inflated, with long diverticulum.

Description. Body pale brown-greyish, covered with brown spots, denser in cephalic area (Fig. 4 A). Shell (Fig. 3 A) dextral, robust, very obese (SB/SH index), conic-ovate, with sharp apex, irregularly increasing whorls (penultimate whorl and body whorl giving oval appearance), 5¾–6 convex whorls and deeply marked suture. Body whorl large (SB/SH index) occupying more than ⅔ of shell surface area (BS/SS index). Protoconch smooth, with 1¾–2 whorls. Aperture long, very wide (AH/SH and AB/SB indices), rounded at palatal side, more curved at junction of columellar and palatal edges. Angle (Fig. 2) between columella and upper palatal margin about 122º. Peristome discontinuous, expanded as a wide, whitish lip, more developed in lower part of the palatal and columellar edges, reflected on columellar edge, where it partly covers umbilical slit. Older specimens with a callosity between peristome edges and a nodule at junction of parietal and palatal margins. Aperture extending laterally beyond penultimate whorl by about 32% (*ca*. 1 mm). Colour brown, with first whorls slightly darker than rest.

Ornamentation of first teleoconch whorl characterised by numerous, thin, radial, oblique ribs with small, irregular protuberances. Protuberances from second teleoconch whorl to body whorl more developed, and those of penultimate whorl (Fig. 5 A) broader and usually equidistantly placed, giving appearance of granular rows perpendicular to radial shell ribs. Body whorl mainly with radial ribs provided with irregular granulation on the upper side (Fig. 5 B).

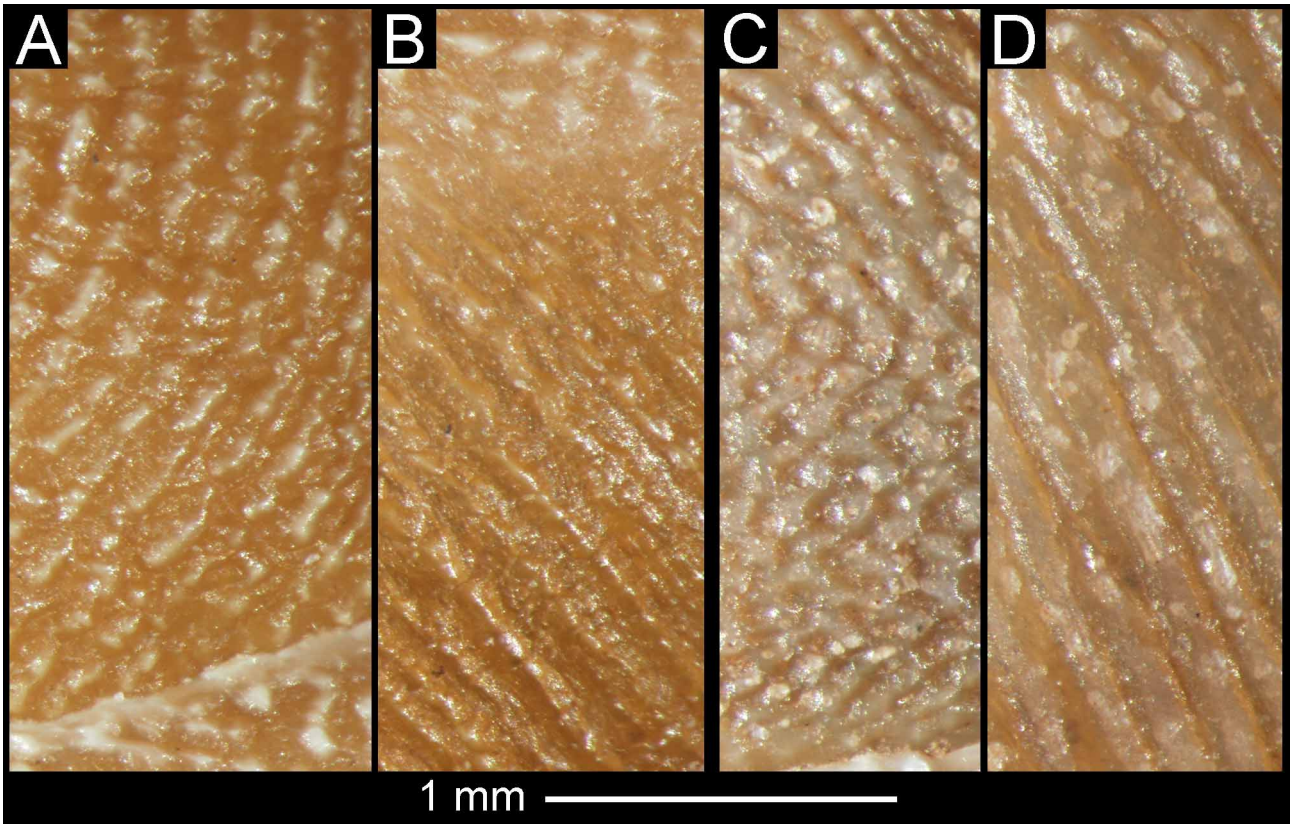

FIGURE 5. Details of shell ornamentation of holotypes (A, C: penultimate whorl; B, D: body whorl). A–B. *Napaeus josei* **n. sp.** C–D. *N. veneguerensis* **n. sp.**

Genital system (Figs. 6 A, B; two specimens dissected). Atrium very short. Penis short and thick, without evident division into separate portions and about a third of the length of the epiphallus. Penial papilla large, well-developed, occupying almost all of penial cavity. Penial retractor muscle inserts apically into proximal penis tip, next to epiphallus-penis connection. Epiphallus opening distally into penis, tubular, slender, with epiphallic caecum inserting in its proximal third. Flagellum very short, globular. Vas deferens opens sub-terminally on proximal end of epiphallus. Penial appendix long, arising obliquely in distal portion of penis near atrium, longer than penis and epiphallus together. System of penial appendix parts A_1–A_3 very short, boundary between them scarcely visible. Parts A_3 and A_4 clearly separated from each other, A_4 long and thin, passing gradually into expanded A_5. Appendicular retractor muscle inserts laterally in proximal tip of short part A_3, joined to penial retractor just before insertion on lower lung wall.

Vagina tubiform, similar in length to free oviduct and proximal third of epiphallus, respectively. Bursa copulatrix duct inflated, with diverticulum longer than duct and branching off in proximal quarter of duct, surmounting the vesicle of the bursa copulatrix.

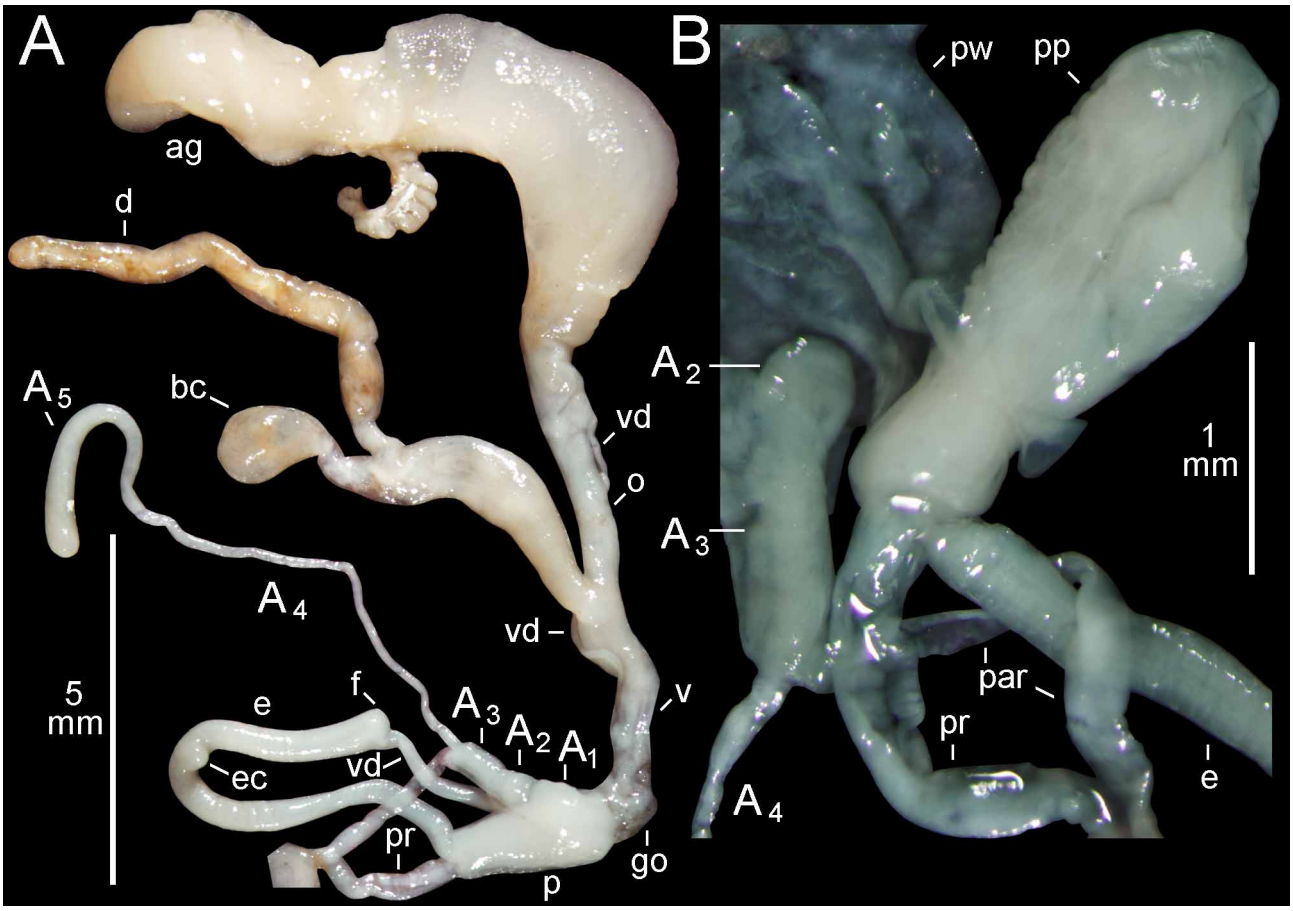

FIGURE 6. *Napaeus josei* **n. sp.**, paratype from Barranco del Lechugal, Gran Canaria (AIT). A. Genital system. B. internal anatomy of penis, showing the penial papilla; A_1–A_5, parts of the penial appendix; ag, albumen gland; bc, bursa copulatrix; d, diverticulum; e, epiphallus; ec, epiphallic caecum; f, flagellum; go, genital orifice; o, free oviduct; par, penial appendix retractor; p, penis; pp, penial papilla; pr, penis retractor; pw, penis wall; v, vagina; vd, vas deferens.

Comparison with other taxa. Shell morphology: The shell of *N. josei* **n. sp.** (Fig. 3 A) is comparable in shape and size mainly to that of *N. nanodes* (Shuttleworth, 1852) (Fig. 3 B) and *N. badiosus* (Webb & Berthelot, 1833) (Fig. 3 C), both from Tenerife. The shell of *N. josei* is clearly more obese than that of both species (Figs. 3 A–C, 7 A). The shell aperture of *N. josei* is similar to that of *N. badiosus* and bigger than that of *N. nanodes* (Figs. 3 A, B, 7 C). The shell ornamentation is clearly different in the three species, the granulation of *N. josei* (Figs. 3 A, 5 A, B) contrasting with the sinuous, undulating ribs surrounding large depressions in *N. nanodes* (Fig. 3 B) and the more or less uniformly ribbed, not granulated shell of *N. badiosus* (Fig. 3 C).

Genital anatomy: *N. josei* has an enormous penial papilla (Fig. 6 B), the largest known in the genus, occupying almost the entire penial cavity.

***Napaeus veneguerensis* Artiles, Santana & Deniz, n. sp.**
Figs. 1, 3 D, G, 5 C, D, 7 A–C, 8 A

Type locality. Barranco de Veneguera (Gran Canaria; UTM: 28RDR2583, 100 m altitude).

Holotype (Fig. 3 D; empty shell): TFMC (MT 0416). Leg. M. Valido and M. Ibáñez, 29 December 1988.

Paratypes. 3 specimens and 107 shells, collected between 1988 and 2010 from the south of Gran Canaria; deposited in AIT and the following collections: FDGC (7 shells); JSGC (67 shells); MAGC (20 shells).

Etymology. The specific name is derived from its type locality, Veneguera.

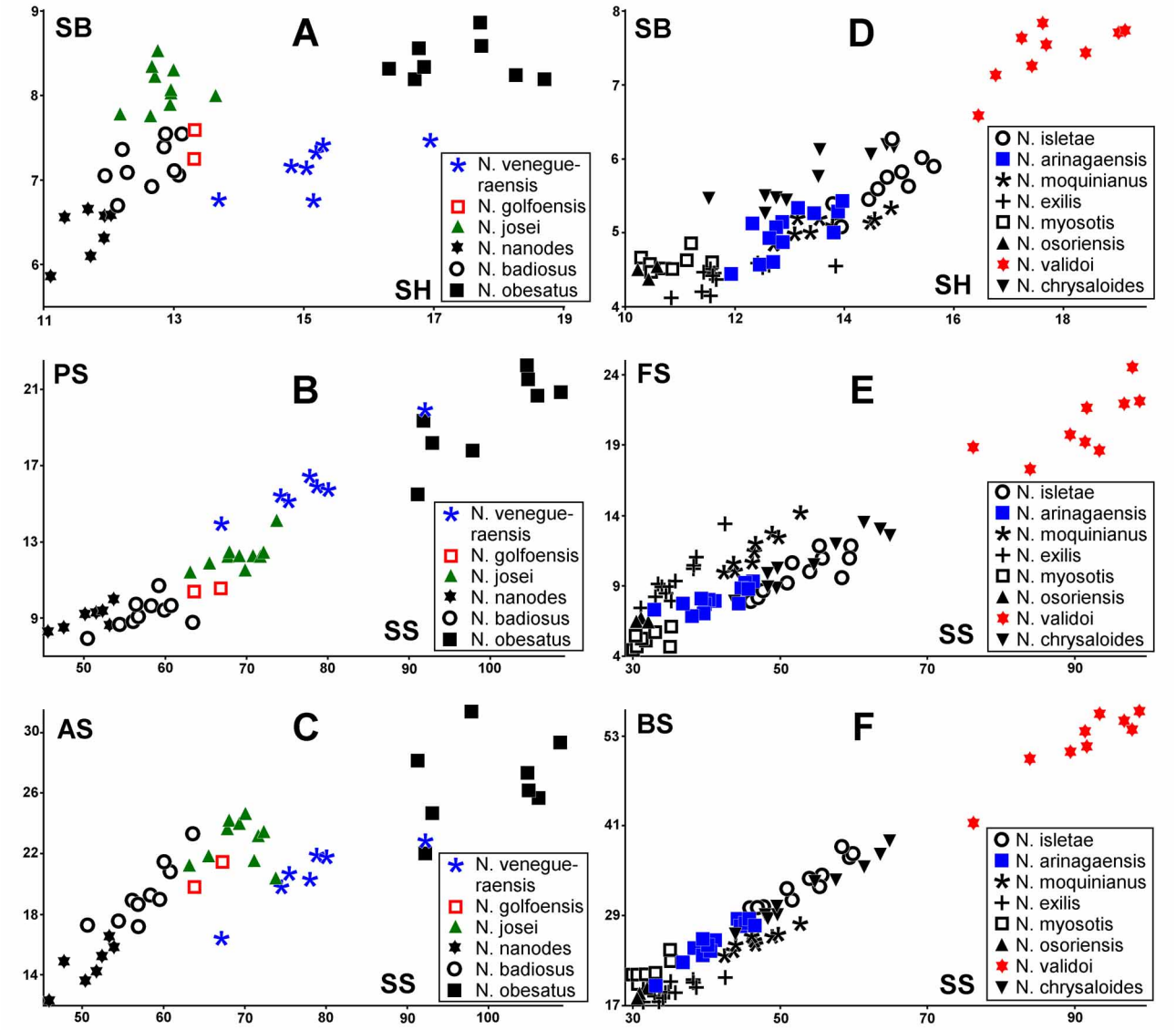

FIGURE 7. Scatter plots of some shell measurements for the new species and the most similar species. AS, aperture surface area (plane view); BS, body whorl surface area (plane view); FS, first whorls surface area (plane view); PS, penultimate whorl surface area (plane view); SB, shell breadth; SH, shell height; SS, shell surface area (plane view). The dimensions are in mm (lengths) or mm^2 (surface areas).

Distribution and habitat (Fig. 1). Endemic to Gran Canaria, occupying an area of about 200 km^2 of the south of the island, associated mainly with lowland vegetation and also pine forest, within an altitudinal range between 80 and 715 m. *Napaeus veneguerae*nsis is mainly a ground dweller, living in pine forest and "cardonal" (*Euphorbia canariensis* L.), sheltering during the day under stones or between *Euphorbia* roots. Some specimens collected together with *N. josei* in the Barranco del Lechugal had the shell disguised by a thick soil covering, but *N. veneguer-aensis* has usually been found undisguised.

Diagnosis. Shell ovate, with whorls increasing regularly in size. Teleoconch ribbed with protuberances irregularly distributed on first whorls and regularly placed on the body whorl. Epiphallus with epiphallic caecum. Penial appendix slightly shorter than penis and epiphallus together. Bursa copulatrix duct similar in length to or slightly shorter than diverticulum.

Description. Body pale brown, covered with brown spots, denser in cephalic area. Shell (Fig. 3 D) dextral, robust, obese (SB/SH index), ovate, cone-shaped above, with whorls increasing regularly in size, 6½–7 weakly convex whorls separated by shallow sutures. Body whorl intermediate (BH/SH index), occupying less than ⅔ of the shell surface area (BS/SS index). Protoconch smooth, shiny, with 1½–1¾ whorls. Aperture long, wide (AH/SH and AB/SB

indices, respectively), with elliptical section at palatal side, more curved at junction of columellar and palatal edges. Angle (Fig. 2) between columella and upper palatal margin about 135º. Peristome discontinuous, moderately expanded as whitish lip, more developed in lower part of palatal edge, reflected on columellar edge, partly covering umbilical slit. Older specimens with a callosity between peristome edges and a nodule at junction of parietal and palatal margins. Aperture extending laterally beyond penultimate whorl by about 22% (*ca* 0.74 mm).

Shell colour pale brown. Ornamentation characterised by numerous oblique, sinuous radial ribs, interrupted on the first teleoconch whorls forming irregularly distributed protuberances, whereas they are regularly placed on the body whorl (Figs. 5 C, D).

Genital system (Fig. 8 A; three specimens dissected). Atrium very short. Penis about a quarter of the length of the epiphallus, with two portions. Distal portion tubular, located between atrium and insertion of penial retractor muscle. Proximal portion swollen. Epiphallus tubular, opening distally into penis, two regions of similar length defined by presence of epiphallic caecum. Flagellum very short. Vas deferens thicker in its distal portion. Penial appendix arising in distal portion of penis near genital orifice, slightly shorter than penis and epiphallus together. Part A_1 of penial appendix clearly differentiated from globular part A_2, similar in length to penis. Appendicular retractor muscle inserting laterally in middle zone of part A_1, joined to penial retractor on diaphragm walls. 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, distally very thin, passing gradually into expanded A_5.

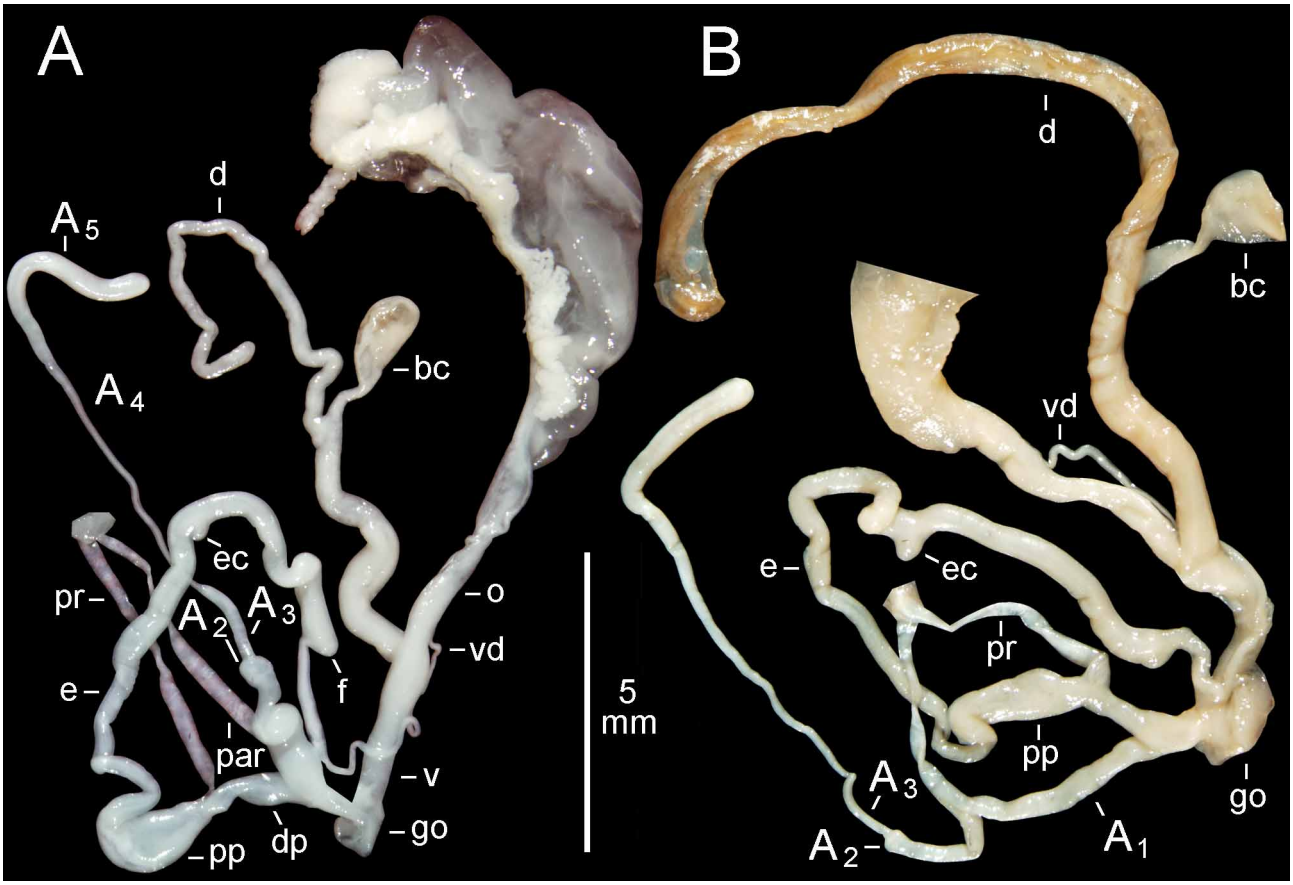

FIGURE 8. Genital systems of: A. *N. veneguerensis* **n. sp.**, paratype from Barranco de Taurito, Gran Canaria (AIT). B. *N. validoi* **n. sp.**, paratype from Monte de Inagua, Gran Canaria (AIT). A_1–A_5, parts of the penial appendix; bc, bursa copulatrix; d, diverticulum; dp, distal penis; e, epiphallus; ec, epiphallic caecum; f, flagellum; go, genital orifice; o, free oviduct; par, penial appendix retractor; pp, proximal penis; pr, penis retractor; v, vagina; vd, vas deferens.

Free oviduct shorter than vagina. Vagina firmly fixed to body tegument by short connective fibres. Bursa copulatrix complex with well-developed diverticulum, branching off near proximal end of bursa duct, more slender and similar in length to or slightly longer than bursa duct.

Comparison with other taxa. Shell morphology: The shell shape of *N. veneguerensis* **n. sp.** (Fig. 3 D) is comparable mainly to that of *N. obesatus* (Webb & Berthelot, 1833), from Gran Canaria (Fig. 3 G), and *N. bajama-*

rensis Ibáñez & Alonso, 2009, from Tenerife (Fig. 3 H). The last two species are similar to each other in dimensions and clearly bigger than *N. veneguerensis* (Figs. 3 G, H, 7 A). The three species differ also in shell ornamentation, *N. veneguerensis* being rough, without gloss, with the radial ribs irregularly distributed on the first teleoconch whorls (Figs. 5 C, D); *N. obesatus* has the ribs more widely spaced and regularly disposed (Fig. 3G), and *N. bajamarensis* has the teleoconch almost smooth (Fig. 3 H).

Genital anatomy: *N. veneguerensis* is similar to *N. bajamarensis* (Yanes *et al*., 2009, fig. 9), but the latter species has an exceptionally long bursa copulatrix duct, several times longer than the diverticulum. In contrast, the bursa duct of *N. veneguerensis* is similar in length to or slightly longer than the diverticulum. The proximal penis portion of *N. veneguerensis* is more swollen than that of *N. bajamarensis.*

Napaeus arinagaensis Artiles, Deniz & Martín, n. sp.

Figs. 1, 2, 3 N, 7 D–F, 9 A

Type locality. North slope of Arinaga Mountain (Gran Canaria; UTM: 28RDR6182, 180 m altitude).

Holotype (Figs. 2, 3 N; empty shell): TFMC (MT 0417). Leg. M. Valido and M. Ibáñez, 9 July 1989.

Paratypes. 36 shells collected between 1989 and 2010 from Arinaga Mountain (east of Gran Canaria); deposited in AIT and the following collections: JSGC (12 shells); MAGC (10 shells).

Etymology. The specific name derives from its type locality, Arinaga Mountain.

Distribution and habitat (Fig. 1). Endemic to Gran Canaria, occupying an area of about 6 km^2 of the Arinaga mountain and its surroundings (southeast of the island), associated with lowland vegetation, within an altitudinal range between 30 and 180 m. We only found empty shells of this species, which is possibly extinct as living specimens were not recorded during the fieldwork since 1989, despite intensive searching.

Diagnosis. Shell slender, conic, almost smooth, shiny, with whorls increasing regularly in size. Aperture ovate, rounded at junction of columellar and palatal edges.

Description. Shell (Figs. 2, 3 N) dextral, slender (SB/SH index), conic, with whorls increasing regularly in size; 6¾–7¼ convex whorls, deeply marked suture. Body whorl intermediate (BH/SH index), occupying less than ⅔ of the shell surface area (BS/SS index). Protoconch smooth, shiny, with about 1½ whorls. Aperture short and wide (AH/SH and AB/SB indices), ovate, rounded at junction of columellar and palatal edges. Angle (Fig. 2) between columella and upper palatal margin about 117º. Peristome discontinuous, expanded as narrow whitish lip, more developed in lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Older specimens with a callosity between peristome edges and a small nodule at junction of parietal and palatal margins. Aperture extending laterally beyond penultimate whorl by about 42% (*ca* 0.8 mm).

The majority of the shells collected were bleached and whitish, but some of them, including the holotype, retain a part of the original coloration, being uniformly pale brown, without blotches. Shell ornamentation almost smooth (Fig. 9 A), characterised by numerous weak, radial oblique ribs, only a few stronger on the body whorl. The shell has some gloss despite ribs.

Comparison with other taxa. The *N. arinagaensis* shell (Fig. 3 N) is comparable in form and size to five species from Gran Canaria. It is clearly smaller than *N. isletae* Groh & Ibáñez, 1992 (Fig. 3 P) and larger than *N. exilis* Henríquez, 1995 (Fig. 3 M), *N. myosotis* (Webb & Berthelot, 1833) (Fig. 3 L) and *N. osoriensis* (Wollaston, 1878) (Fig. 3 K). *Napaeus arinagaensis* is similar in shell size to *N. moquinianus* (Webb & Berthelot, 1833) (Fig. 3 O), however, the latter has irregular whitish blotches on its shell and the surface areas of the first whorls and the entire shell of *N. arinagaensis* are smaller than those of *N. moquinianus*. *Napaeus arinagaensis* (Fig. 3 N) and *N. myosotis* (Fig. 3 L) are similar in the degree of convexity of their whorls whereas the other four species have flatter whorls.

Napaeus validoi Ibáñez, Alonso & Martín, n. sp.

Figs. 1, 3 F, 7 D–F, 8 B, 9 B

Type locality. Ñameritas (Gran Canaria; UTM: 28RDR3389, 1000 m altitude).

Holotype (Fig. 3 F; empty shell): TFMC (MT 0418). Leg. M. Nogales, 10 November 1984.

Paratypes. 14 specimens and 11 shells, collected between 1984 and 2010 from the central-western part of Gran Canaria; deposited in AIT and the JSGC collection (1 shell).

Etymology. The specific name is dedicated to our friend Manuel Valido, malacologist from Gran Canaria.

Distribution and habitat (Fig. 1). Endemic to Gran Canaria, occupying an area of about 25 km^2 of the Reserva Natural Integral de Inagua, the Monumento Natural del Roque Nublo and their surroundings, associated mainly with pine forest, within an altitudinal range between 950 and 1450 m. *Napaeus validoi* is a ground dweller; the specimens collected had the shell disguised by a covering of vertic soil (a type of clayey soil), altering its appearance considerably as in other disguised *Napaeus* species.

Diagnosis. Shell slender, nearly cylindrical, with prominent aperture and wide lip. Epiphallus with epiphallic caecum. Penial appendix shorter than penis and epiphallus combined. Bursa copulatrix duct shorter than diverticulum.

Description. Shell (Fig. 3 F) dextral, slender (SB/SH index), nearly cylindrical, with 7–7½ slightly convex whorls. Body whorl intermediate in size (BH/SH index), occupying about 4/7 of the shell surface area (BS/SS index). Protoconch smooth, shiny, with about 1½ whorls. Aperture short and very wide (AH/SH and AB/SB indices), rounded, with elliptical section at palatal side, more curved at the junction of the columellar and palatal margins. Angle (Fig. 2) between columella and upper palatal margin about 114º. Peristome discontinuous, expanded as wide, whitish lip, more developed in lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Older specimens with a callosity between peristome edges and a small nodule at the junction of parietal and palatal margins. Aperture extending laterally beyond penultimate whorl by 50% (*ca* 1.6 mm).

Shell colour brown. Ornamentation characterised by numerous oblique radial ribs, regularly placed on body whorl and sinuous, sometimes interrupted in remainder of teleoconch whorls, forming small protuberances that are irregularly distributed (Fig. 9 B).

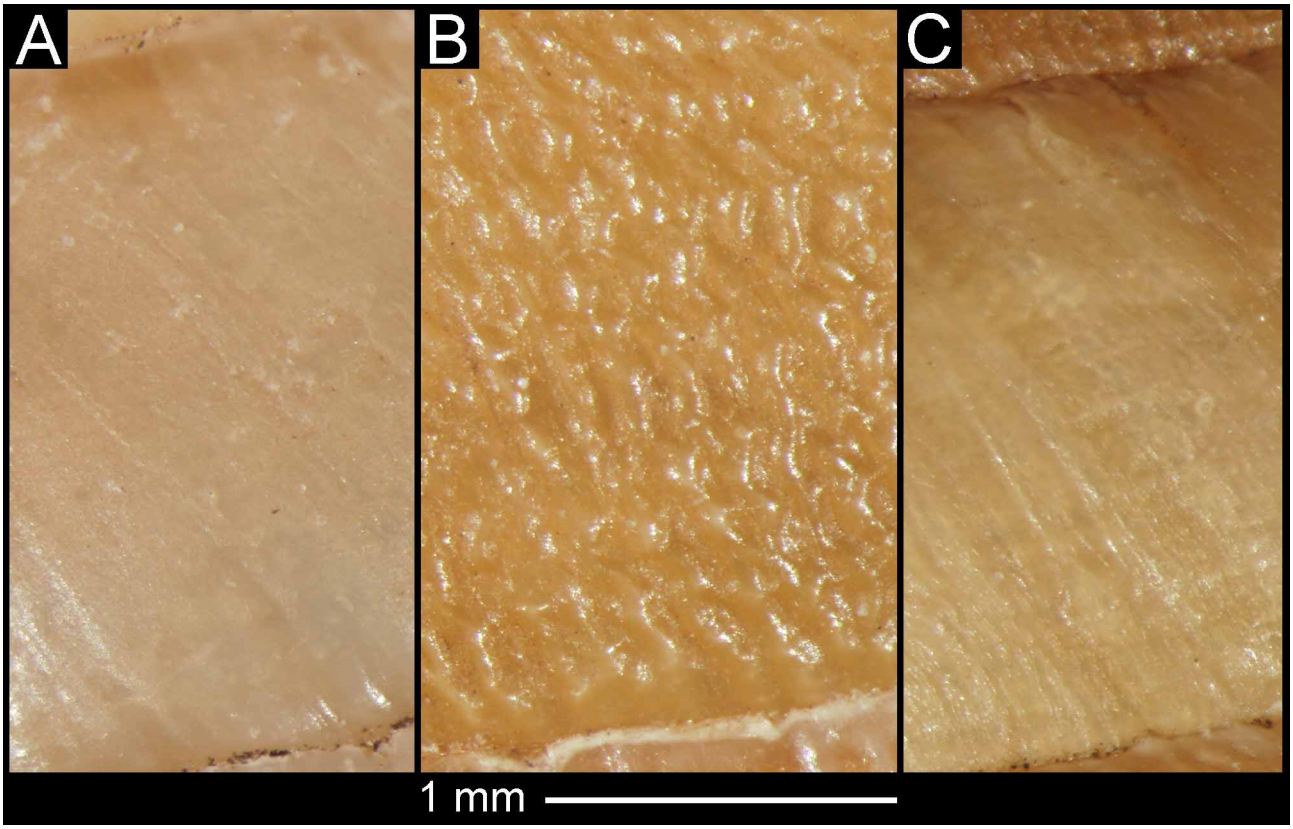

FIGURE 9. Details of shell ornamentation of holotypes (penultimate whorl). A. *Napaeus arinagaensis* **n. sp.** B. *N. validoi* **n. sp.** C. *N. grohi* **n. sp.**

Genital system (Fig. 8 B; two specimens dissected). Atrium very short. Penis about one quarter of length of epiphallus, with two portions. Distal portion tubular, located between atrium and insertion of penial retractor muscle. Proximal portion slightly swollen. Epiphallus tubular, opening distally into penis, two regions defined by presence of epiphallic caecum, distal region slightly longer and more slender than proximal region. Flagellum very short. Penial appendix arising from distal penis portion near genital orifice, shorter than penis and epiphallus com-

bined. Part A_1 of penial appendix not much differentiated from small, globular part A_2, slightly longer than penis. Appendicular retractor muscle inserting laterally in the proximal zone of part A_1, joining penial retractor on diaphragm walls.

Free oviduct longer than vagina. Bursa copulatrix complex with well-developed diverticulum, branching off near proximal end of bursa duct, longer than bursa duct and similarly inflated when accommodating partner's spermatophore.

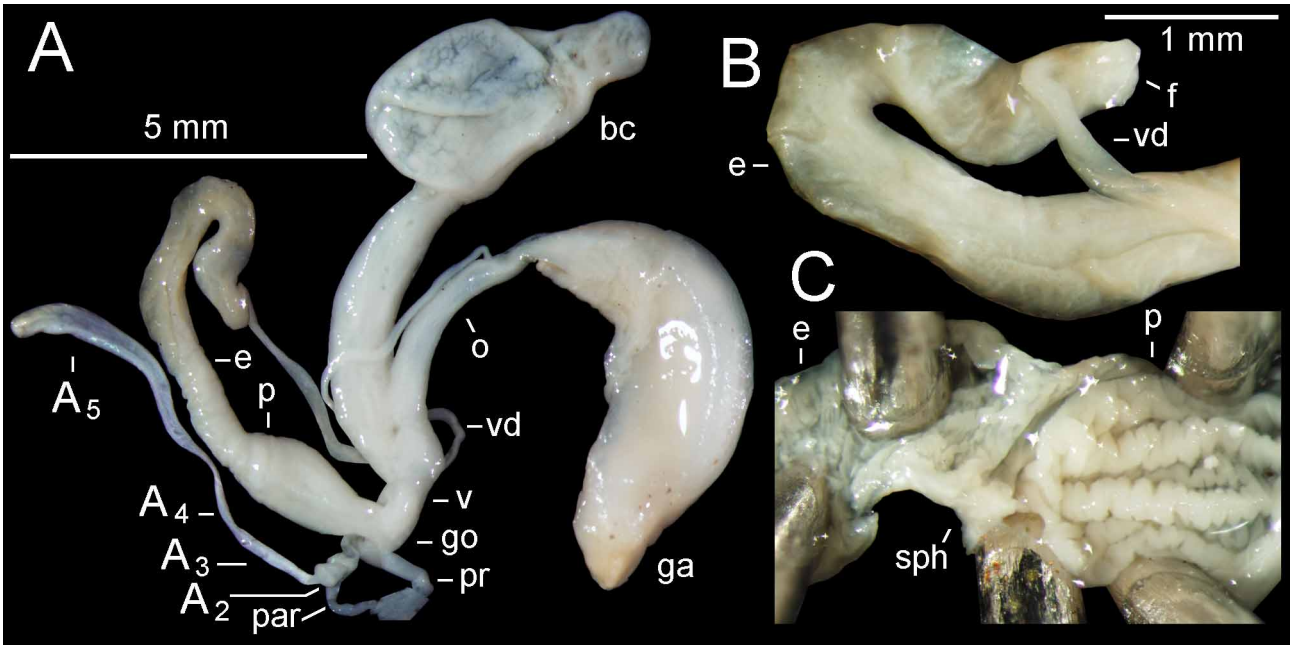

FIGURE 10. *Napaeus grohi* **n. sp.**, holotype. A. Genital system. B. Detail of the flagellum. C. Internal anatomy of penis. A_4–A_5, parts of the penial appendix; ag, albumen gland; bc, bursa copulatrix (although this appears be bent it is in fact only wrinkled); e, epiphallus; f, flagellum; go, genital orifice; o, free oviduct; par, penial appendix retractor; p, penis; pr, penis retractor; sph, sphincter between epiphallus and penis; v, vagina; vd, vas deferens.

Comparison with other taxa. Shell morphology: *Napaeus validoi* (max. SH = 19.1 mm) has almost the same height but is more slender (SB/SH index = 0.42) than *N. interpunctatus* (Wollaston, 1878) (max. SH = 20.0 mm; SB/SH index = 0.46), which is the biggest *Napeus* species from Gran Canaria. The *N. validoi* shell (Fig. 3 F) has a form similar to that of *N. chrysaloides* (Wollaston, 1878) (Fig. 3 E), but is clearly higher, has a stronger ornamentation, and its rounded aperture is nearly twice as large as that of *N. chrysaloides*.

Genital anatomy: *N. validoi* is similar to *N. veneguerensis* and *N. chrysaloides*, without important differences between them. The apparently greater length of the diverticulum of the bursa copulatrix in *N. validoi* (Fig. 8) can be attributed to the remains of a spermatophore inside the dissected specimens.

Napaeus grohi Alonso, Ibáñez & Santana, n. sp.

Figs. 1, 3 J, 7 A–C, 9 C, 10

Type locality. Pista del Derrabado (El Hierro; UTM: 28RDR6182, 850 m altitude).

Holotype. (Fig. 3 J; ethanol-preserved specimen): TFMC (MT 0419, shell and dissected soft body). Leg. M. Ibáñez, 5 January 1993. **Paratypes**. 2 shells (JSGC) collected in 2006 from the Ermita de La Caridad and Lomo Blanco (northwest of the island); deposited in the JSGC collection.

Etymology. The specific name is dedicated to our friend Klaus Groh, who has spent several decades working in malacology.

Distribution and habitat (Fig. 1). Endemic to El Hierro, occupying an area of about 10 km^2 of the humid laurel forest on the El Golfo northern slopes, within an altitudinal range between 850 and 1200 m. This species is a ground-dweller, associated with the humid laurel forest.

Diagnosis. Shell obese, conic-ovate, with weakly convex whorls increasing regularly in size and shallow but distinct suture. Body whorl large. Aperture with five-sided appearance. Penis globose, without penial papilla but with sphincter between epiphallus and penis. Penial cavity with eight longitudinal, wrinkled folds, four of these thickened and alternating with the other four. Penial retractor muscle inserting on distal end of penis. Bursa copulatrix very large, pear shaped, without diverticulum.

Description. Body brown, covered with blackish-brown spots, denser in cephalic area. Shell (Fig. 3 J) dextral, obese (SB/SH index), conic-ovate, with whorls increasing regularly in size, 6½–7 weakly convex whorls. Body whorl large (BH/SH index), comprising almost ¾ of shell surface area (BS/SS index). Protoconch smooth, shiny, with 1½ whorls. Aperture long and wide (AH/SH and AB/SB indices). Angle (Fig. 2) between columella and start of upper palatal margin about 120º; upper palatal margin transitioning into central part of palatal margin with a rounded, blunt angle (ca. 50º), so that the central part is almost parallel with the columella; (angle between them *ca.* 170º); junction of palatal and columellar edges also slightly angular, resulting in a five-sided appearance of the aperture. Peristome discontinuous, expanded as moderate whitish lip, more developed in lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Holotype with callosity between peristome edges and small nodule at junction of parietal and palatal margins. Aperture extending laterally beyond penultimate whorl by about 28% (*ca* 0.95 mm).

Shell colour pale-brown, with first whorls darker than rest. Shell ornamentation almost smooth, characterised by numerous weak, radial oblique ribs (Fig. 9 C). Shell with gloss despite ribs.

Genital system (Fig. 10; only one specimen dissected, the holotype). Atrium very short. Penis globose, without sections, about one-third the length of epiphallus, without penial papilla but with sphincter between epiphallus and penis. Penial cavity with eight longitudinal, wrinkled folds, four of them thickened and alternating with the other four which are narrower. Penial retractor muscle inserting on distal end of penis. Epiphallus tubular, not subdivided into portions, opening distally into penis. Flagellum short. Vas deferens opens laterally into proximal end of epiphallus. Penial appendix arising from distal portion of penis near atrium, slightly shorter than penis and epiphallus combined. Part A_1 of penial appendix short, tubular, clearly differentiated from globular part A_2. Short appendicular retractor muscle inserting laterally in middle zone of part A_1, joined to short penial retractor on diaphragm walls. Part A_3 slender, shorter than penis. Part A_4 shorter and more slender than A_3, passing gradually into expanded and longer A_5. Free oviduct three to four times longer than vagina. Vagina firmly attached to body tegument by short connective fibres. Bursa copulatrix complex without diverticulum, vesicle pear shaped, very large, ca. twice as long as wide; bursa duct tubular and very thick.

Comparison with other taxa. Shell morphology: *Napaeus grohi* (Fig. 3 J) is comparable in form and size with *N. josei* (Fig. 3 A) and *N. badiosus* (Fig. 3 C), its whorls being flatter and the ornamentation weaker than in both of those species. In *N. josei* the shell is broader and in *N. badiosus* it is more slender (excluding the aperture) than in *N. grohi*.

Genital anatomy: *N. grohi* differs from all species of the genus for which the anatomy is known by the insertion of the penial retractor muscle on the distal end of the penis, near the genital orifice and by the very large, pear shaped vesicle of the bursa copulatrix complex.

Final remarks

The evolutionary capacity of *Napaeus* has been assisted by a number of topographical and geological features of the Canarian Archipelago, resulting in a considerable range of habitats which contribute to the rich diversity of *Napaeus* species. The Archipelago comprises seven main islands and some islets. The islands show great differences in age (from 1 to 20 My), surface area (from 278 to 2057 km^2), altitude (from 670 to 3.718 m), volcanic activity (from several years since the last eruption to 1 My without volcanic activity) and climate (from hot and arid to subalpine conditions).

The two eastern islands are considered to be the western outpost of the Saharan Zone (Ortiz *et al*. 2006). They are the oldest islands and have an area of about 2600 km^2 (slightly more than 1/3 of the total area of the Archipelago), but only support three *Napaeus* species whereas the other five islands receive the moist trade winds coming from the north-east and they support at least 62 living species. These data emphasise that the evolutionary capacity of *Napaeus* is clearly favoured by the humidity supplied by the trade winds.

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