

FOUR NEW *NAPAEUS* SPECIES (GASTROPODA: PULMONATA: ENIDAE) FROM LA GOMERA (CANARY ISLANDS)

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Abstract Four new species of *Napaeus* are described from La Gomera (Canary Islands), which is one of the smaller islands of the archipelago but has the highest number of *Napaeus* species. The four new species can all disguise the shell with a cover of lichens, soil, or both, to reduce predation. When the covering is made of hygroscopic lichen, it might function as a water or humidity reservoir as well as for camouflage.

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

INTRODUCTION

The genus *Napaeus* has undergone a striking radiation in the Canary Islands (mid-Atlantic), with up to 55 living species (Yanes *et al.*, 2009) and one extinct species (Castillo *et al.*, 2006) described. Each species of *Napaeus* is typically restricted to a small area within a single island (i.e. they demonstrate “single island endemism”).

Within the Canary Islands, the richness of La Gomera (378 km², 1490 m altitude, 12 Myr old) is spectacular with 18 species, the largest number of living *Napaeus* species known for any single island, and includes both the biggest and the smallest species known in the genus (Mousson, 1872; Wollaston, 1878; Henríquez, Ibáñez *et al.*, 1993; Alonso *et al.*, 1995; Bank *et al.*, 2002; Yanes *et al.*, 2009). The neighbouring Tenerife, younger but the highest island and five times more extensive than La Gomera (2057 km², 7.5 Myr old, Mount Teide reaching 3718 m altitude), has 16 known living species, whereas Gran Canaria (1532 km², 1950 m altitude, 14.5 Myr old), the other central island of the Archipelago, has 10 species. The westernmost and youngest islands, La Palma (726 km², 2430 m altitude, 1.7 Myr old) and El Hierro (278 km², 1500 m altitude, 1.12 Myr old), with similar types of climate to the three islands mentioned above, have 4 species each. Finally the easternmost and

more arid islands, Lanzarote (15.5 Myr old), Fuerteventura (20.6 Myr old) and their islets (about 2600 km², 807 m altitude) as a whole (the oldest “Mahan island”, with an area of c. 5000 km² in the Last Glacial Maximum: García-Talavera, 1997) only have 3 species (Ibáñez *et al.*, 2007). The ages of the islands used here were derived from Carracedo *et al.* (2005).

In the present study four new *Napaeus* species are described from La Gomera. They are not allocated to the subgenera (*Napaeus* and *Napaeinus*) described by Hesse (1933) because these have 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 nominate subgenus *Napaeus* until a phylogenetic analysis of the genus is conducted.

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-

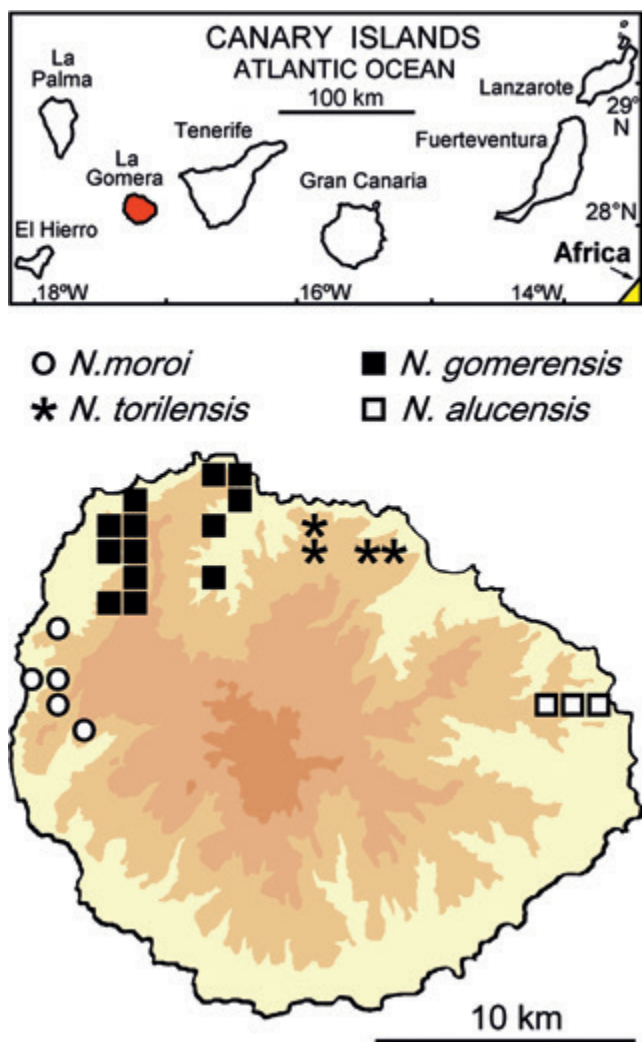


Figure 1 Geographic distribution of the four new species of *Napaesus*.

automatically, adopting the methods used by Yanes *et al.* (2009). Standardized 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 palatal corner between the columella and the upper palatal side of the aperture has also been measured because a combination of this angle and the width of the peristome lip influences shell breadth. 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

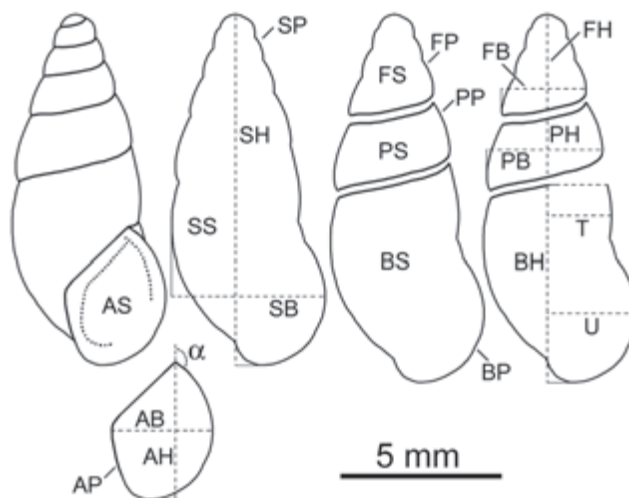


Figure 2 Drawings of the shell of the holotype of *Napaesus alucensis* sp. nov. showing the placement of the measurements obtained (in mm or mm²). AB, aperture breadth; AH, aperture height; AP, aperture perimeter; AS, aperture surface area (plane view); BH, body whorl height (at columella level); BP, 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.

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 (as in Alonso & Ibáñez, 2007), not the location of the insertion of the penial retractor muscle, as many early authors, such as Hesse (1918), and some recent researchers, have done.

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; |
| GAH | Geraldine A. Holyoak private collection, Cabeçudo, Portugal; |

Table 1 Data for the shell characters measured (in mm or mm²) for *Napaeus* spp. sp1: *N. moroi*; sp2: *N. gomerensis*; sp3: *N. torilensis*; sp4: *N. alucensis*; 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	sp4	Character/index	sp1	sp2	sp3	sp4
Mean	SH	16.89	12.58	11.83	10.72	AP	20.29	15.54	10.51	11.46
SD		0.79	0.52	0.29	0.14		0.66	0.98	0.24	0.28
Min.		16.00	11.75	11.40	10.55		19.50	14.18	10.23	11.17
Max.		17.99	13.55	12.18	10.81		21.05	17.19	10.86	11.72
Mean	SB	8.40	6.42	4.29	4.79	FH	3.43	2.95	3.85	2.90
SD		0.15	0.35	0.12	0.08		0.34	0.18	0.37	0.16
Min.		8.16	6.10	4.19	4.72		2.97	2.71	3.55	2.72
Max.		8.55	7.09	4.47	4.88		3.91	3.37	4.47	3.02
Mean	SS	95.62	50.84	32.63	33.04	FB	5.09	3.25	2.53	2.58
SD		4.46	4.12	1.11	0.70		0.32	0.16	0.10	0.06
Min.		90.30	46.28	31.19	32.23		4.82	2.99	2.42	2.51
Max.		101.58	58.98	34.25	33.47		5.59	3.53	2.70	2.62
Mean	SP	41.32	30.89	27.25	25.47	FS	11.17	6.40	6.61	5.01
SD		1.41	1.34	0.63	0.38		1.67	0.64	0.90	0.38
Min.		39.43	29.13	26.52	25.04		9.71	5.31	5.82	4.58
Max.		43.21	33.36	28.23	25.69		13.86	7.66	8.11	5.29
Mean	BH	10.40	7.53	6.00	6.08	FP	14.08	10.49	11.22	9.37
SD		0.35	0.41	0.25	0.03		1.02	0.53	0.84	0.33
Min.		9.84	7.00	5.70	6.05		13.30	9.65	10.51	9.00
Max.		10.71	8.39	6.37	6.11		15.75	11.42	12.66	9.63
Mean	BS	65.53	35.65	19.91	22.28	FH	3.06	2.10	2.00	1.73
SD		1.92	3.17	0.60	0.36		0.21	0.11	0.05	0.06
Min.		62.53	32.37	19.47	22.05		2.85	1.96	1.93	1.68
Max.		67.83	42.46	20.93	22.69		3.36	2.3	2.07	1.80
Mean	BP	32.91	23.91	17.88	18.77	FB	6.50	4.42	3.23	3.55
SD		0.81	1.13	0.27	0.03		0.15	0.19	0.13	0.04
Min.		31.55	22.56	17.59	18.75		6.30	4.17	3.15	3.51
Max.		33.56	26.06	18.29	18.81		6.70	4.74	3.46	3.59
Mean	AH	7.14	5.39	3.88	4.16	FS	18.92	8.79	6.11	5.76
SD		0.29	0.36	0.12	0.15		1.79	0.77	0.39	0.29
Min.		6.90	4.91	3.79	3.99		17.58	7.63	5.70	5.58
Max.		7.58	6.01	4.10	4.27		21.91	10.23	6.66	6.10
Mean	AB	5.90	4.58	2.87	3.22	FP	18.45	12.43	10.17	10.21
SD		0.24	0.34	0.07	0.10		0.74	0.51	0.35	0.23
Min.		5.51	4.09	2.76	3.12		17.81	11.54	9.80	10.05
Max.		6.12	5.09	2.94	3.32		19.72	13.26	10.59	10.47
Mean	AS	31.06	18.35	8.11	9.38	SB/SH	0.49	0.51	0.36	0.45
SD		2.00	2.32	0.31	0.40	BH/SH	0.62	0.60	0.51	0.57
Min.		28.75	15.01	7.68	9.08	AH/SH	0.42	0.43	0.33	0.39
Max.		33.06	22.47	8.49	9.84	AB/SB	0.70	0.71	0.67	0.67
n		5	11	5	3	BS/SS	0.68	0.70	0.61	0.67

ICZN International Commission on Zoological Nomenclature;

JMTF J. Martín private collection, La Laguna, Tenerife, Spain;

JSGC J. Santana private collection, Las Palmas de Gran Canaria, Spain;

MAGC M. Artilles private collection, Arinaga, Gran Canaria, Spain;

NHM The Natural History Museum, London, U.K.;

TFMC Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain;

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		

UTM Universal Transverse Mercator, cartographic projection system;
sh shell;
sp specimens (in alcohol);
WRTG W. Rähle private collection, Tübingen, Germany.

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 moroi Martín, Alonso & Ibáñez sp. nov.

Holotype 1 sh, TFMC (MT 0420); leg. M. Ibáñez, 4 February 1994 (Fig. 3B).

Paratypes 1 sp, 1 sh (AIT), 4 sh (FDGC), 4 sp (GAH), 8 sh (JSGC), 3 sh (JMTF), 5 sh (MAGC), collected between July 1988 and December 2009 from the west of La Gomera.

Type locality Mountain Punta de Tejeleche (La Gomera; UTM: 28RBS 7116; 500 m altitude).

Diagnosis Shell nearly cylindrical, obese, pale brown coloured (greenish with living animal inside: Fig. 4A), with first whorls darker than rest. Penis without penial papilla, a sphincter between epiphallus and penis. Epiphallus without epiphallar caecum. Bursa copulatrix without a diverticulum.

Description Body pale greenish-brown (Fig. 4A). Shell (Fig. 3B) dextral, obese (SB/SH index),

nearly cylindrical because the last two whorls have similar breadth, with 5³/₄–6¹/₂ slightly convex whorls, marked suture. Body whorl large (BH/SH index), occupying slightly more than 2/3 of the shell surface area (BS/SS index). Protoconch smooth, shiny, with about 1¹/₂ whorls. Aperture long and wide (AH/SH and AB/SB indices), ovate-rounded, with elliptical section at palatal side, more curved at the union of the columellar and palatal edges. Angle of columella-upper palatal sides about 113°. Whitish discontinuous peristome expanded as wide lip, more developed on lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Older specimens with callosity between peristome edges and small nodule at union of parietal-palatal area. Edge of aperture projects about 40% (c. 1.5 mm) from start of body whorl (see Fig. 2, ratio T:U; due to combination of upper palatal angle and projection of peristomal lip). Shell colour pale brown (but greenish, because of transparency, with live animal inside), first whorls darker than rest. Ornamentation of first teleoconch whorl characterized by numerous, thin, radial oblique ribs. Ribs of second teleoconch whorl rather irregular with small protuberances which are more developed in penultimate whorl (Fig. 5A). Ornamentation of body whorl smoother and more regular, with radial rows provided with small granulations (Fig. 5B).

Genital system (Fig. 6A, B; one adult specimen dissected, the remaining 4 specimens were juveniles). Atrium very short. Penis with three parts, the middle one delimited by penial appendix connection and retractor muscle insertion; distal part (atrium–penial appendix connection) tubular, slender; middle part (penial appendix connection–retractor muscle insertion) wider and two times longer than distal part; proximal part (retractor muscle insertion–epiphallus) slightly swollen, with several small, longitudinal folds

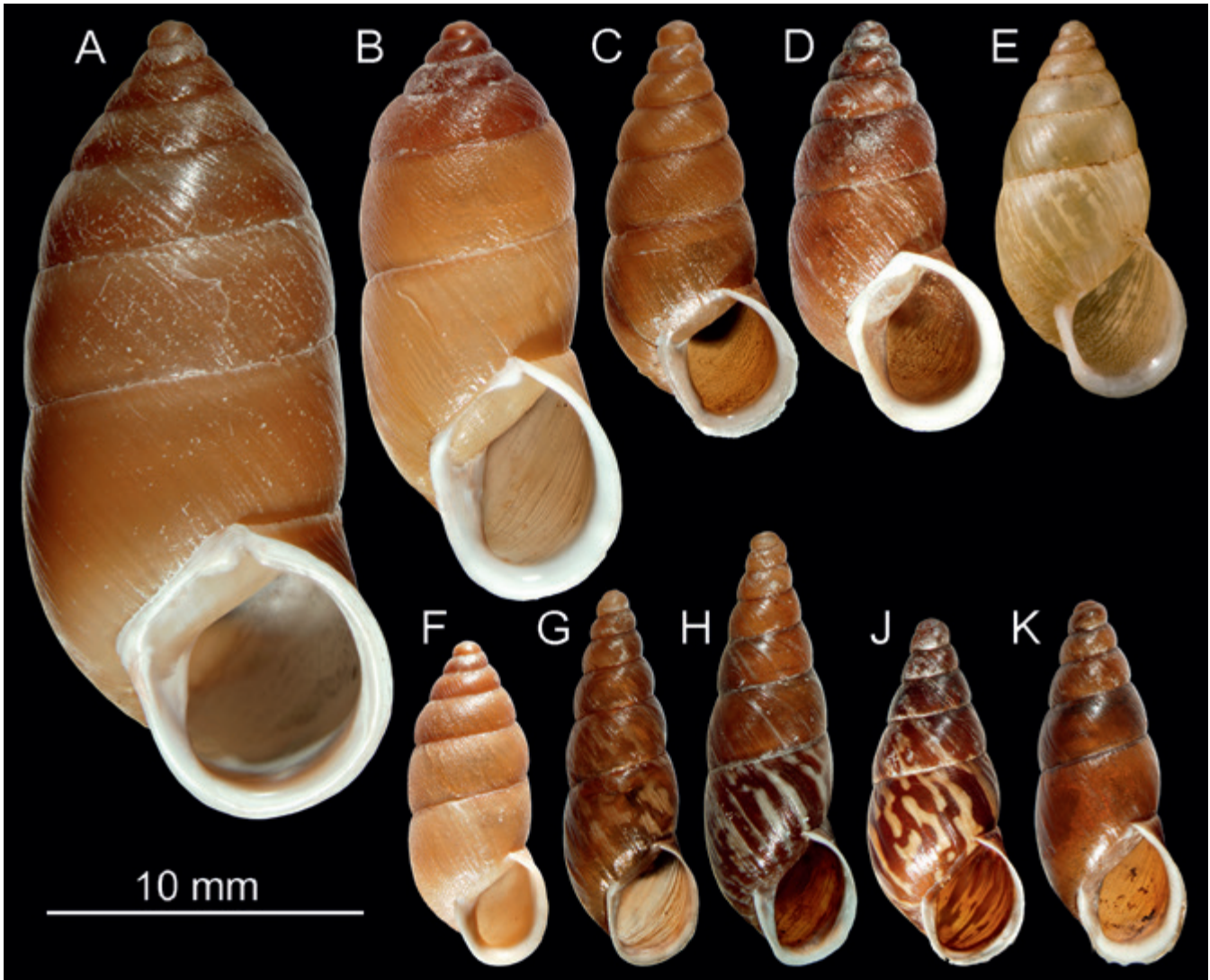


Figure 3 Shells of: A, *Napaeus bertheloti*, from Ismael Este Mountain, La Gomera; B, holotype of *N. moroi* sp. nov.; C, holotype of *N. teobaldoi* Martín 2009, from Tenerife (TFMC MT 0399) (from Yanes *et al.*, 2009); D, holotype of *N. gomerensis* sp. nov.; E, a syntype of *N. palmaensis* (NHM 1895.2.2.219; photo by J. Ablett), from La Palma; F, a paratype of *N. tagamichensis*, from Tagamiche, La Gomera; G, holotype of *N. torilensis* sp. nov.; H, *N. subgracilior*, from El Charco, Fuencaliente, La Palma; J, holotype of *N. alucensis* sp. nov.; K, holotype of *N. procerus*, from La Gomera (TFMC MT 0385).

inside. Penial papilla absent, but a small sphincter present between epiphallus and proximal penis portion. Epiphallus tubular, without caecum. Flagellum very short. Part A₁ of penial appendix similar in length to distal and middle penis portions together and with similar thickness to middle part of penis. Part A₂ small, globular. Part A₃ almost undifferentiated from part A₄. Parts A₃–A₅ as a whole, slightly longer than epiphallus. Appendicular retractor muscle inserts laterally near the proximal top of section A₁ and inserts on the lower lung wall fused with penis retractor. Free oviduct two times longer

than vagina. Bursa copulatrix duct short, without diverticulum.

Derivation of name The specific epithet *moroi* is dedicated to our friend Leopoldo Moro, a marine malacologist from Tenerife.

Distribution and habitat A species endemic to La Gomera, where it was collected under stones, in rock crevices and rocky slopes with sparse low vegetation and also pine forest, between 150 and 800 m altitude (Fig. 1). Some of the specimens collected had the shell slightly disguised with a



Figure 4 Undisguised (A, C, G, J) and disguised (B, D–F, H, K) shells of *Napaeus* spp. A, B, paratype of *N. moroi* sp. nov., from Arure; C–F, paratypes of *N. gomerensis* sp. nov., from several localities; C, D, adults; E, F, juveniles; G, H, paratypes of *N. torilensis* sp. nov., from Camino de Las Rosas and Altos del Toril, respectively; J, K, paratypes of *N. alucensis* sp. nov., from Ismael Este Mountain.

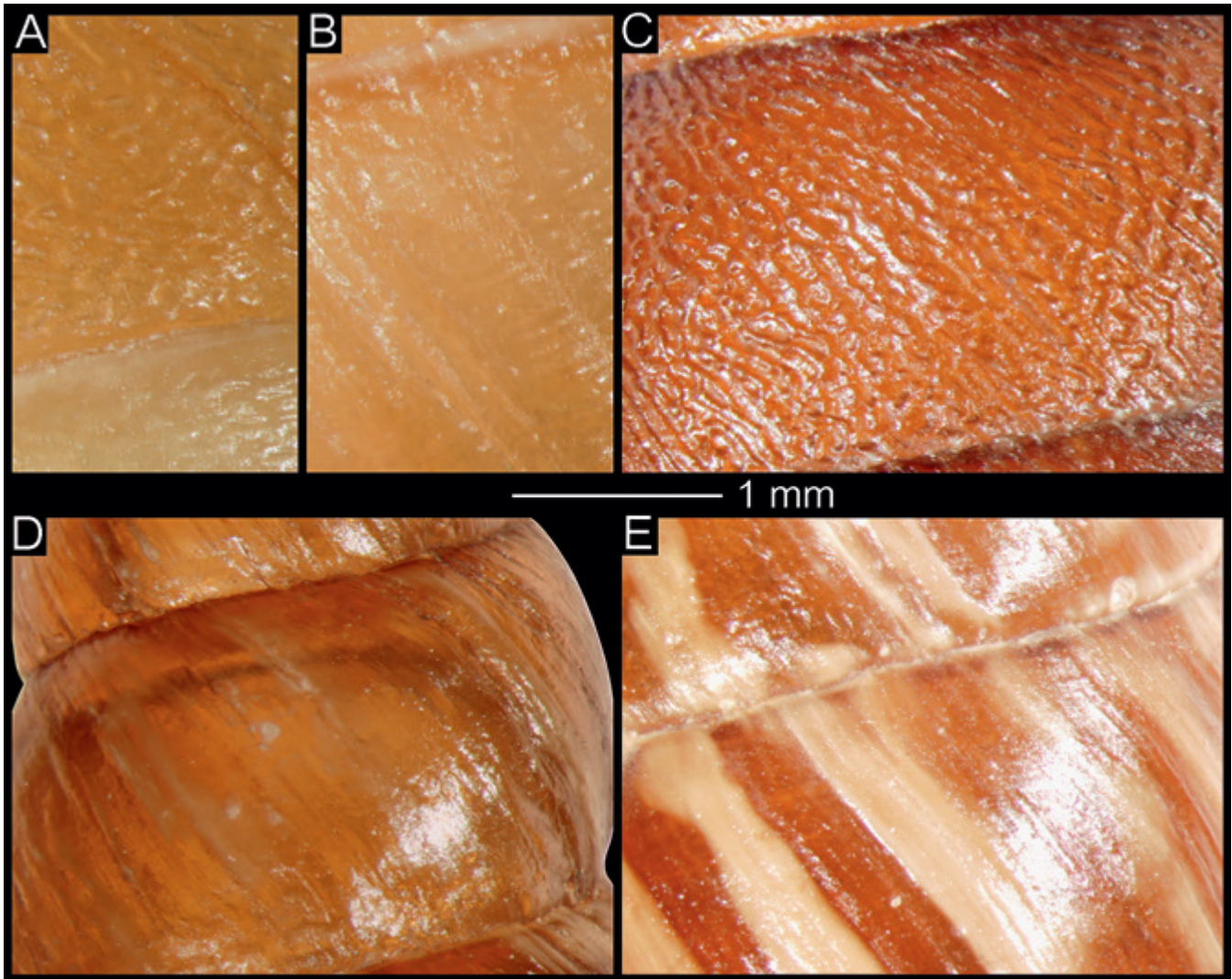


Figure 5 Details of shell ornamentation of holotypes. A, C–E, penultimate whorl; B, body whorl; A, B, *Napaeus moroi* sp. nov.; C, *N. gomerensis* sp. nov.; D, *N. torilensis* sp. nov.; E, *N. alucensis* sp. nov.

fine soil cover (Fig. 4B), more complete in juveniles. Other specimens appeared undisguised.

Comparisons *Napaeus moroi* sp. nov. is comparable only with *N. bertheloti* (L. Pfeiffer 1848) in both shell form and genital system, but *N. moroi* is unambiguously smaller in all the parameters studied (Figs 3A, B; 6A, C). These species differ also in shell colour and ornamentation, *N. bertheloti* having the shell uniformly coloured and almost smooth, without protuberances (Fig. 3A).

***Napaeus gomerensis* G. A. Holyoak & D. T. Holyoak sp. nov.**

Holotype 1 sh, TFMC (MT 0421); Leg. G. A. Holyoak & D. T. Holyoak, 12 February 2006 (Fig. 3D).

Paratypes 2 sp, 15 sh (AIT), 13 sp (+ many juveniles), 30 sh (GAH), 5 sh (FDGC), 6 sp, 49 sh (JSGC), 6 sh (MAGC) collected between December 1978 and April 2010 from the north of La Gomera.

Type locality W. of Montaña Blanca (La Gomera; UTM: 28RBS 7418; 785 m altitude).

Diagnosis Shell dextral, very obese, conic-ovate, with very wide, prominent aperture and small protuberances in penultimate whorl. Epiphallus without epiphallar caecum. Bursa copulatrix without a diverticulum.

Description Body grey to dark grey, even blackish (Fig. 4C). Shell (Fig. 3D) dextral, very obese (SB/SH index), conic-ovate, with 6–6¾ convex

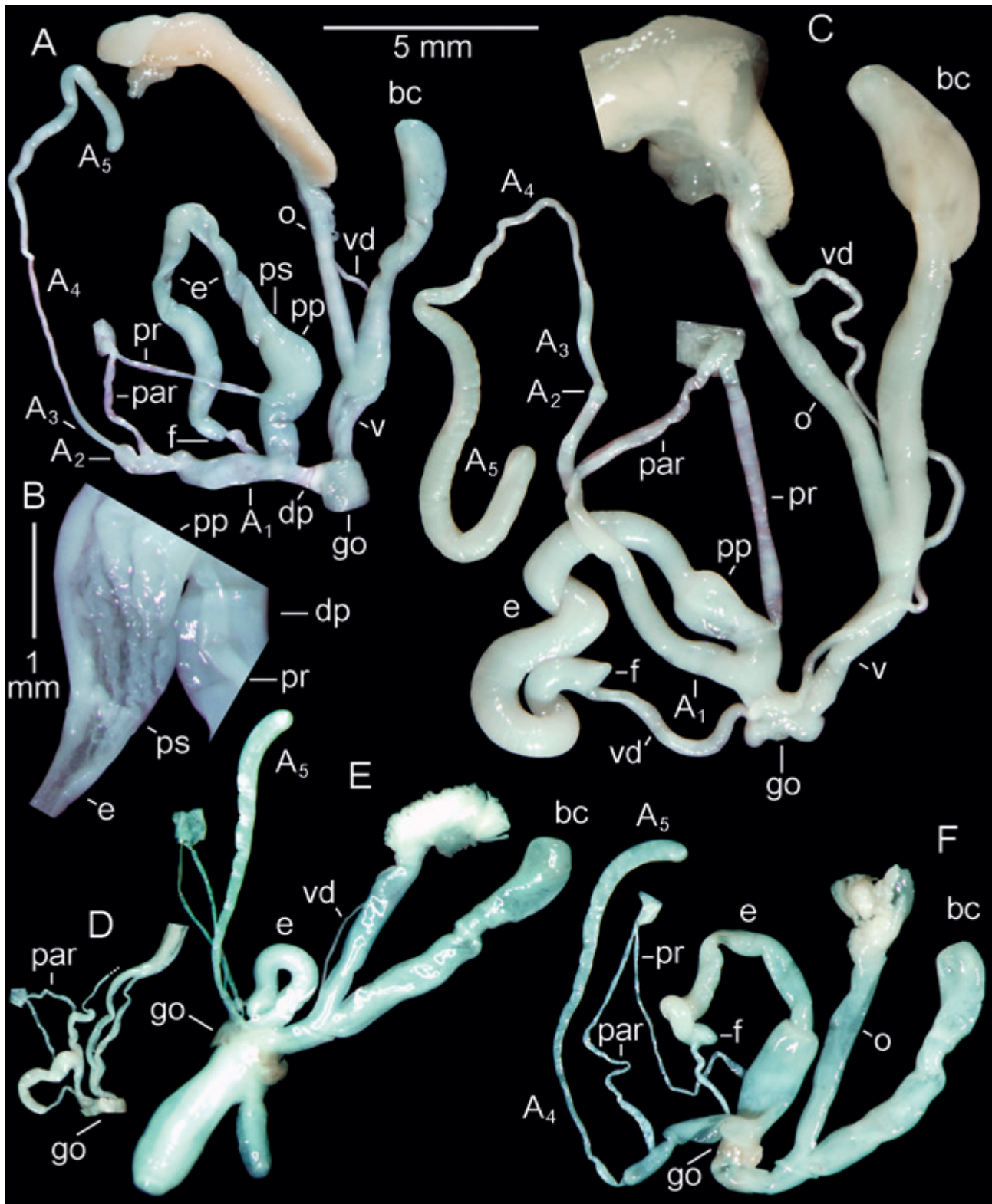


Figure 6 Genital systems of: A, *Napaeus moroi* sp. nov., from Mirador de Taguluche; B, Detail of distal penis, dissected and pleated over proximal penis, showing a sphincter in the epiphallus–penis connexion; C, *N. bertheloti*, from Ismael Este Mountain; D–F, *N. gomerensis* sp. nov., from Beguira Mountain; D, immature; E, mature specimen with male genital system partially evaginated through the genital orifice; F, the same mature specimen, after desinvagination in laboratory. 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.

whorls and deeply marked suture. Body whorl large (BH/SH index), occupying about 70% of the shell surface area (BS/SS index). Protoconch smooth, shiny, with about 1½–1¾ whorls. Aperture long and very wide (AH/SH and AB/SB indices), prominent, ovate-rounded, with elliptical section at palatal side, more curved at the union of the columellar and palatal edges. Angle of columella-upper palatal side about 110°. Whitish discontinuous peristome expanded as a wide lip, more developed on lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Older specimens with callosity between peristome edges and small nodule at union of parietal-palatal area. Edge of aperture projects about 70% (1.7 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 uniform dark reddish brown with the animal inside (Fig. 4C) but reddish brown in the empty shell (Fig. 3D). Ornamentation of first two teleoconch whorls weak, with numerous, thin, radial oblique ribs and shiny surface. Penultimate whorl with ribs more developed, sinuous, irregularly interrupted, forming small protuberances (Fig. 5C). Protuberances smaller on body whorl, disappearing in some specimens, ribs being more regular except surrounding the umbilical slit, the last with ornamentation similar to that of the penultimate whorl (Figs 3D, 4C).

Genital system (Fig. 6D–F; two specimens dissected). Unfortunately, the only mature specimen obtained had the male genitalia partly evaginated through the genital orifice (penis and penial appendix evaginated, Fig. 6E), but after dissection this was laid out in its natural position (Fig. 6F). The second specimen was apparently adult although the shell was immature, being usable only as a general reference (Fig. 6D). Atrium very short. Penis with three parts, middle part delimited by penial appendix connection and retractor muscle insertion; they are visible in the immature specimen but not in the evaginated specimen, probably because of dilation of tissue during the evagination process. Epiphallus tubular, without caecum. Flagellum very short. Part A₁ of penial appendix also dilated by the evagination process. Part A₂ undifferentiated, probably for the same reason. Part A₃ almost undifferentiated from part A₄. Parts A₃–A₅ as a whole 1.5 times longer than epiphallus. Appendicular retractor muscle inserts laterally near the proximal top of the part

A₁ and inserts on the lower lung wall fused with penis retractor. Free oviduct three times longer than vagina. Bursa copulatrix duct short, without diverticulum.

Derivation of name *gomerensis* is derived from La Gomera island.

Distribution and habitat A species endemic to La Gomera, where it was collected under stones, in rock crevices or on open, lichen-covered rock faces exposed to the humid trade winds, with vegetation varying from sparse low growths to laurel forest and pine forest, between 300 and 785 m altitude (Fig. 1). Some immature specimens carried very large loads of lichen on their shells, as in other actively disguised *Napaeus* species (Yanes *et al.*, 2010) such that they were virtually invisible until the head or body emerged from the shell mouth (Fig. 4E, F). Their covering of hygroscopic lichen might function as a water or humidity reservoir as well as for camouflage. The adults carried much less lichen cover (Fig. 4D) and some specimens none at all.

Comparisons The shell form of *Napaeus gomerensis* sp. nov. is different from that of all congeners on La Gomera. It is comparable only with those of *N. teobaldoi* Martín 2009 from Tenerife (Fig. 3C) and *N. palmaensis* (Mousson 1872) from La Palma (Fig. 3E), appearing intermediate between them, but having a larger surface area in both shell and aperture (Fig. 7A, B, D), whereas the body whorl is broader and has a greater surface area than those of both other species (Fig. 7C). *N. teobaldoi* and *N. gomerensis* have similar ornamentation, *N. palmaensis* is almost smooth. *N. teobaldoi* has a cone-shaped shell, showing very regular growth and is uniform brown in colour, without the dark-reddish tone of the *N. gomerensis* shell. The genital system of *N. gomerensis* is of the same type as that of *N. bertheloti* and *N. moroi*, whereas that of *N. teobaldoi* has an epiphallar caecum (Yanes *et al.*, 2009: fig. 11C); the genital system of *N. palmaensis* is not yet described; in *N. gomerensis* the epiphallus is shorter than that of *N. bertheloti* and *N. moroi*.

Napaeus torilensis Artiles & Deniz sp. nov.

Holotype 1 sh, TFMC (MT 0422); Leg. J. Santana, 27 December 2009 (Fig. 3G).

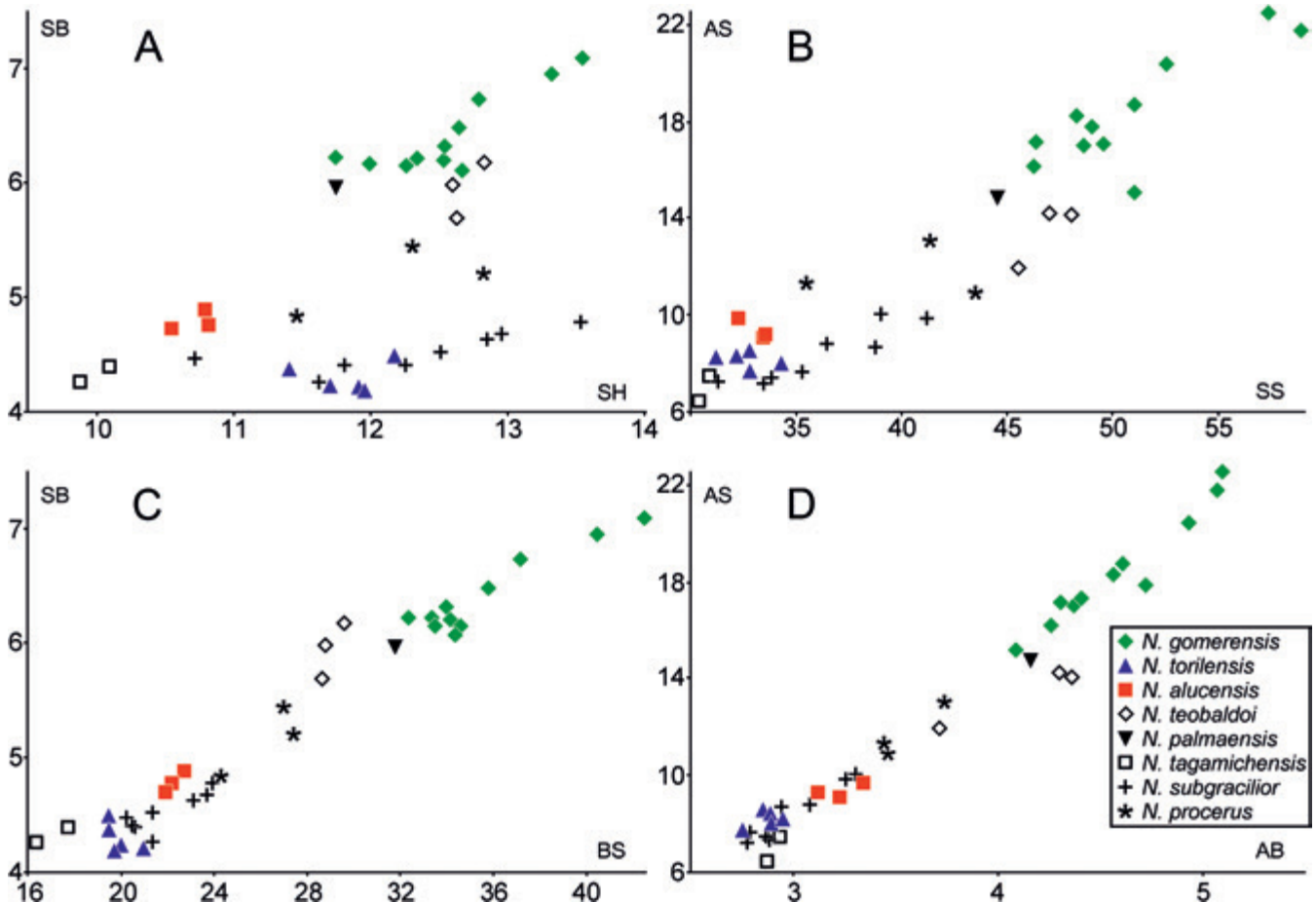


Figure 7 Scatter plots of some shell measurements for the new species of *Napaeus* and similar species. AB, aperture breadth; AS, aperture surface area (plane view); BS, body whorl surface area (plane view); SB, shell breadth; SH, shell height; SS, shell surface area (plane view). Data on measurements of *N. bertheloti* and *N. moroi* sp. nov. are not included in the plots because their dimensions are very different to those of the other species studied here.

Paratypes 2 sp, 5 sh (AIT), 49 sh (FDGC), 23 sh (JSGC), 16 sh (MAGC), 1 sh (WRTG), collected between March 2005 and April 2010 from the north of La Gomera.

Type locality Altos del Toril (La Gomera; UTM: 28RBS 8119; 662 m altitude).

Diagnosis Shell slender, shiny, with weak radial oblique striation, regular growth mode and convex whorls, colour brown, sometimes with small yellowish patches. Penis and epiphallus extremely short. Epiphallus without epiphallar caecum. Flagellum very small. Bursa copulatrix small, without diverticulum.

Description Body dark brown to blackish (Fig. 4G). Shell (Fig. 3G) dextral, small, slender (SB/SH index), with regular growth mode, 6–7¼

convex whorls and marked suture. Body whorl intermediate (BH/SH index), occupying about 61% of the shell surface area (BS/SS index). Protoconch smooth, shiny, with about 1½–1¾ whorls. Aperture short and wide (AH/SH and AB/SB indices), ovate, with elliptical section at palatal side, more curved at the union of the columellar and palatal edges. Angle of columella-upper palatal sides about 116°. Whitish discontinuous peristome expanded as a small lip, more developed on lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Older specimens with callosity between peristome edges and small nodule at union of parietal-palatal area. Edge of aperture projects about 36% (0.7 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 generally uniform brown

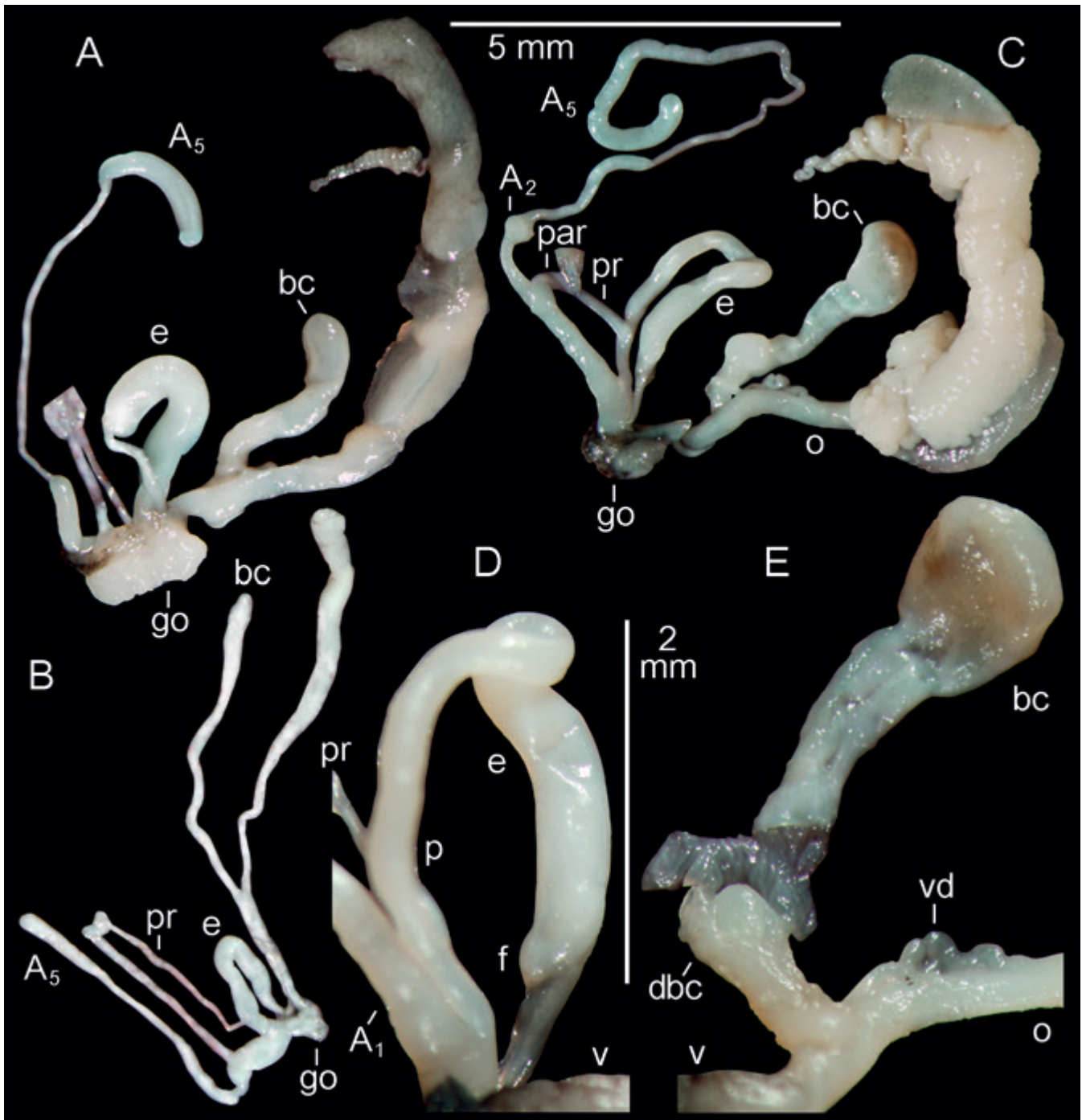


Figure 8 Genital systems of: A–B, *N. torilensis* sp. nov., from Altos del Toril; C–E, *N. alucensis* sp. nov., from Ismael Este Mountain; B, immature specimen; D, detail of penis–epiphallus–flagellum; E, detail of bursa copulatrix complex, showing the inner distal chamber; A₂, A₅, parts of the penial appendix; bc, bursa copulatrix; dbc, distal bursa copulatrix chamber; e, epiphallus; f, flagellum; go, genital orifice; p, penis; par, penial appendix retractor; pr, penial retractor; o, free oviduct; v, vagina; vd, vas deferens.

in first whorls, the remainder can show small, irregular, yellowish patches, more developed in body whorl; some specimens have all the shell uniform brown. The shell surface is shiny with a weak radial oblique striation (Fig. 5D).

Genital system (Fig. 8A, B; two specimens dissected). One specimen immature and the other well developed but showing the beginning of an evagination process. Atrium very short. Penis externally undifferentiated from epiphallus.

Penis and epiphallus together extremely short in relation to penial appendix length. Epiphallus without epiphallar caecum. Flagellum very small, vas deferens opens subapically on proximal end of epiphallus. Penial appendix arising from distal part of penis, near the atrium. Parts A_1 and A_2 and penial appendix not visible because they are partially evaginated. Part A_3 similar to A_5 in length and thickness. Free oviduct longer than vagina. Bursa copulatrix small, without diverticulum.

Derivation of name Derived from the name of the type locality of this species, Altos del Toril.

Distribution and habitat A species endemic to La Gomera, where it was collected on north-facing open, lichen-covered rocks exposed to the moist trade winds coming from the north-east, of an area with laurel forest and pine wood, between 510 and 665 m altitude (Fig. 1). Some specimens had covered their shells with a thin layer of soil, others with lichens (Fig. 4H), altering the appearance of the shell considerably as in other disguised *Napaeus* species (Yanes *et al.*, 2010). In some specimens the shell was not covered.

Comparisons The shell of *N. torilensis* sp. nov. is similar only to that of *N. subgracilior* (Wollaston 1878) from La Palma (Fig. 3H), but smaller and more slender (Fig. 7A, C) and the yellowish patches of the body whorl are less clear. The genital system of *N. subgracilior* is of the same type as that of *N. bertheloti*, *N. moroi* and *N. gomezensis*, whereas that of *N. torilensis* is very similar only to that of *N. tagamichensis* Henríquez 1993 (Henríquez *et al.*, 1993: fig. 7B). Genital systems of the latter two species stand out because the penis and epiphallus together are extremely short in relation to the penial appendix length. However, the shells of these two species have few similarities (Fig. 3F, G).

***Napaeus alucensis* Santana & Yanes sp. nov.**

Holotype 1 sh, TFMC (MT 0423); Leg. J. Santana, 15 November 2008 (Fig. 3J).

Paratypes 2 sp, 2 sh (AIT), 2 sp, 12 sh (JSGC), 1 sh (WRTG), collected between March 2005 and April 2010 from the east of La Gomera.

Type locality Ismael Este Mountain, near Casas de Aluce (La Gomera; UTM: 28RBS 9113; 325 m altitude).

Diagnosis Shell dextral, small, obese, shiny, with a weak radial oblique striation, regular growth mode and slightly convex whorls; colour brown with irregular, oblique elongated yellowish patches. Epiphallus tubular, without caecum. Combines characters of "male genital system with two retractor muscles" and "distal part of the bursa copulatrix with an inner chamber".

Description Body dark greyish-brown (Fig. 4J), even blackish. Shell (Fig. 3J) dextral, obese (SB/SH index), with regular growth mode, 6–6½ slightly convex whorls and marked suture. Body whorl intermediate (BH/SH index), occupying about ⅓ of the shell surface area (BS/SS index). Protoconch smooth, shiny, with 1¼–1½ whorls. Aperture long and wide (AH/SH and AB/SB indices), ovate, with elliptical section at palatal side, more curved at the union of the columellar and palatal edges. Angle between columellar and upper palatal sides about 130°. Whitish discontinuous peristome expanded as lip, more developed on lower part of palatal edge and reflected on columellar edge, partly covering umbilical slit. Older specimens with callosity between peristome edges and small nodule at union of parietal-palatal areas. Edge of aperture projects about 35% (0.7 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 uniform brown in first whorls; penultimate whorl and body whorl with irregular, oblique elongated yellowish patches, more developed on body whorl. The shell surface is shiny with a weak radial oblique striation and, occasionally, some small granulation (Fig. 5E).

Genital system (Fig. 8C–E; two specimens dissected). Atrium very short. Distal penis (atrium–penial appendix connection), short and broad; proximal penis tubular, slender, externally undifferentiated from epiphallus. Epiphallus tubular, without caecum. Flagellum very short. Part A_1 of penial appendix as broad as distal penis. Part A_2 clearly swollen. Part A_3 long, slightly shorter than part A_4 . Parts A_4 – A_5 as a whole, similar in length to epiphallus. Appendicular retractor muscle inserts laterally near the proximal top of the part A_1 and inserts on the lower lung wall

fused with penis retractor. Free oviduct similar in length to vagina, or slightly longer. Bursa copulatrix duct very short, without diverticulum. Distal part of bursa copulatrix with an inner chamber having several small folds inside.

Derivation of name Derives from Casas de Aluce, the name of the human settlement nearest to the type locality.

Distribution and habitat A species endemic to La Gomera, where it was collected on a north-facing slope on rocks of an area with sparse low vegetation, between 325 and 340 m altitude (Fig. 1). The specimens disguised their shells actively, with lichens and soil (Fig. 4K).

Comparisons The shell of *N. alucensis* sp. nov. is comparable in form and dimensions only with that of *N. procerus* Emerson 2006, from La Gomera (Fig. 3K), but that species is more slender (Fig. 7A), with a less regular growth mode, a larger aperture (Fig. 7D) and uniform chestnut-brown colour. The genital system of *N. alucensis* shares with those of *N. procerus*, as well as *N. voggenreiteri* Hutterer 2006 and *N. barquini* Alonso & Ibáñez 2006 the presence of an inner chamber in the distal part of the bursa copulatrix (Fig. 8E; Alonso, Goodacre *et al.*, 2006). However, *N. alucensis* differs from all them because it has two retractor muscles, penial and appendicular – as in the majority of the *Napaeus* species – whereas the other three species only have one, the appendicular retractor muscle.

DISCUSSION

The high number (22) of living *Napaeus* species now known from the small island of La Gomera (with a surface area of only 378 km²) might at first sight appear “too good to be true”, so it demands evolutionary and ecological explanations.

Part of the evolutionary explanation relies on geographical comparisons with neighbouring islands of the archipelago, since a number of topographical and geological features of La Gomera as well as its location appear to be especially favourable for promoting and maintaining a diversity of *Napaeus*. Thus, La Gomera is a sufficiently old island (12 Myr) for the development of the evolutionary process, yet it has suffered

less from Quaternary volcanic activity than the neighbouring islands of La Palma, El Hierro or Tenerife (with no vulcanism in past 1 Myr on La Gomera, whereas all three other islands have records of eruptions in past 500 yr: Mangas, 2007). Nevertheless, like those islands it is mountainous and high enough to intercept the humid trade winds coming from the north east, resulting in a considerable range of habitats from the arid subtropical conditions of some areas in the south of the island to temperate and humid conditions in the evergreen laurel forest that is well preserved in Garajonay National Park. Another significant factor allowing repeated speciation of *Napaeus* on La Gomera may have included particularly good opportunities for isolation of local populations, due both to its radial pattern of valleys separated by ridges or high ground with laurel forest, and the high potential for isolation of rupestral species on separate large rocky crags. Furthermore, unlike all other islands of the archipelago, La Gomera is relatively close to three other islands (Tenerife to the east; La Palma to the north-west; El Hierro to the south-west), offering opportunities for past colonisation from three separate sources.

Kokshoorn & Gittenberger (2010) have recently re-emphasised the proverbial inertness of many land snails, implying lack of active dispersal and resulting in a relatively high degree of local endemism and thus species diversity. There is no doubt that local endemism is more pronounced in the genus *Napaeus* than the other Canarian land snails. As discussed above, the explanation for this richness lies partly in the opportunities for geographical isolation, promoting geographical speciation, and also millennia of stable environmental history allowing the new species to survive. However, ecological factors allowing adaptive radiation and coexistence of species are also likely to have contributed to the persistence of so many species, as in other island archipelagos (e.g. Cameron *et al.*, 1996; Goodacre & Wade, 2001; Richards & Davison, 2010). The richer habitats on La Gomera often have four *Napaeus* species living close together: comprising a small and a large rupestral species occupying microhabitats like those respectively of a *Chondrina* and an *Albinaria* (Clausiliidae), accompanied by small and large ground-living species occupying niches variously like those of *Cochlicopa*, *Ena* or *Rumina*. The absence of numerous

continental land-snail families from the native fauna of the western Canary Islands (e.g. Azecidae, Chondrinidae, Clausiliidae, Cochlicopidae, Ferussaciidae, Orculidae, Stenogyridae) appears to have left unfilled niches, allowing this wide adaptive radiation of ecological types in *Napaeus*, which has evolved approximate ecological counterparts for several of the missing snail families.

Finally, recent observations have shown that shell disguise is widespread among species of the genus *Napaeus* in the Canary Islands and this has doubtless been an important contributory factor to the evolutionary success of the genus.

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