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Two new *Napaeus* species from La Gomera and La Palma (Canary Islands)

(Gastropoda: Pulmonata: Enidae)

Geraldine A. Holyoak, David T. Holyoak, Yurena Yanes, María R. Alonso & Miguel Ibáñez

Abstract

Two new species of *Napaeus* are described, from La Gomera and La Palma (Canary Islands). Both species are small, that from La Gomera being the smallest known *Napaeus*, its shell surface area (plane view) is more than ten times smaller than that of *N. bertheloti*. The two new species actively disguise their shells with lichens and soil, presumably to reduce predation.

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

Resumen

Se describen dos nuevas especies de *Napaeus*, de La Gomera y La Palma (Islas Canarias). Ambas son de pequeño tamaño, siendo la especie de La Gomera la más pequeña conocida del género, la superficie de su vista frontal es más de diez veces menor que la de *N. bertheloti*. Las dos nuevas especies disfrazan de forma activa sus conchas con líquenes y partículas pequeñas de tierra, probablemente como protección visual ante sus depredadores.

Palabras clave: Taxonomía, nuevos endemismos insulares, anatomía del reproductor, disfraz de la concha.

Introduction

The genus *Napaeus* has undergone a remarkable 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. 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"). La Gomera Island (378 km², 1490 m altitude, 12 my old) has the highest number (18) of living *Napaeus* species known for any single island (Mousson 1872, Wollaston 1878, Henríquez, Ibáñez et al. 1993, Alonso et al. 1995, Bank et al. 2002, Yanes et al. 2009):

N. avaloensis Groh 2006; *N. barquini* Alonso & Ibáñez 2006; *N. beguirae* Henríquez 1995; *N. bertheloti*

Authors' addresses:
Geraldine A. Holyoak, Dr. David T. Holyoak, Quinta da Cachopa, Barcoila, 6100-014, Cabeçudo, Portugal;
Dr. Yurena Yanes, Laboratorio de Biogeoquímica de Isótopos Estables, Estación Experimental del Zaidín (CSIC). Prof. Albareda 1, 18008 Granada, Spain.
Dr. Maria R. Alonso, Dr. Miguel Ibañez (Corresponding author, E-mail: mibanez@ull.es) Department of Animal Biology, La Laguna University, E-38206 La Laguna, Tenerife, Canary Islands, Spain.

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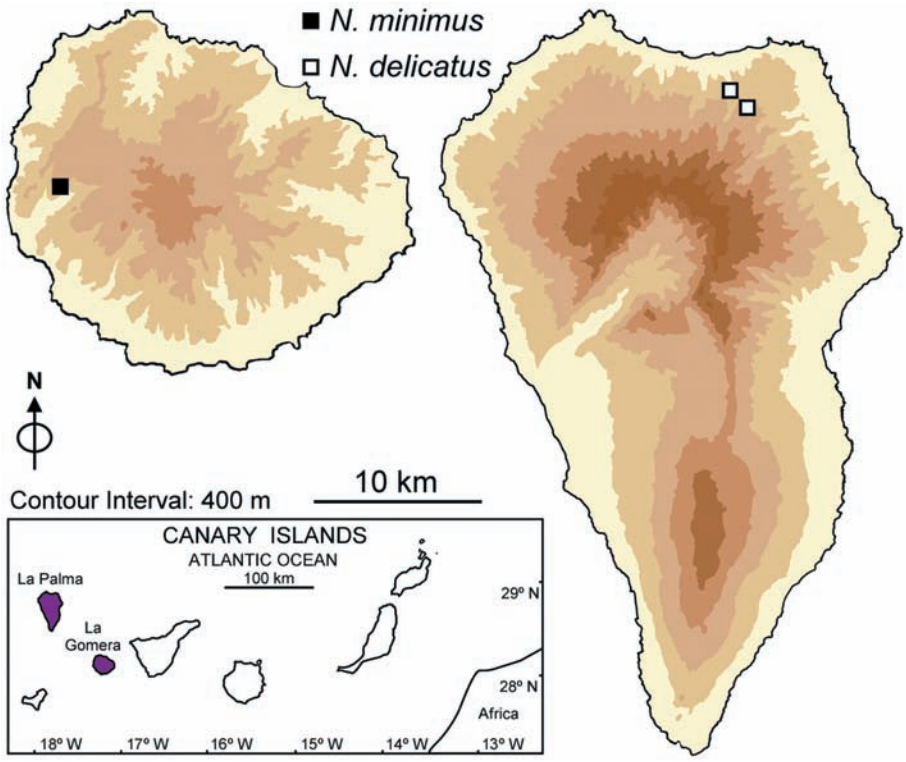
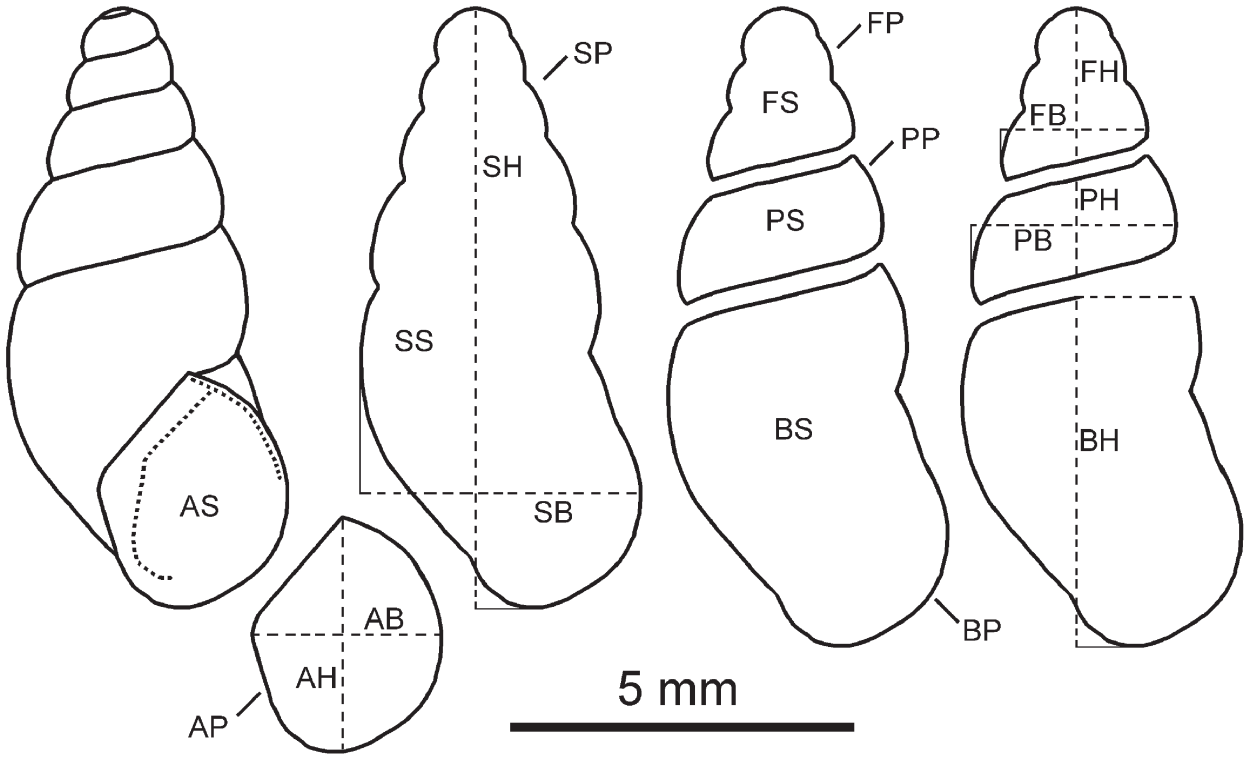


Text Fig. 1. Geographic distribution of *Napaeus minimus* n. sp. and *N. delicatus* n. sp.



Text Fig 2. Drawings of the shell of the holotype of *Napaeus minimus* n. sp., showing the placement of the measurements obtained (in mm or mm^2). 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).

(L. PFEIFFER 1848); *N. consecoanus* (MOUSSON 1872); *N. inflatiusculus* (WOLLASTON 1878); *N. maculatus* GOODACRE 2006; *N. orientalis* HENRÍQUEZ 1995; *N. ornamentatus* MORO 2009; *N. procerus* EMERSON 2006; *N. pygmaeus* IBÁÑEZ & ALONSO 1993; *N. rupicola* (MOUSSON 1872); *N. servus* (MOUSSON 1872); *N. severus* (J. MABILLE 1898); *N. tagamichensis* HENRÍQUEZ 1993; *N. taguluchensis* HENRÍQUEZ 1993; *N. texturatus* (MOUSSON 1872); *N. voggenreiteri* HUTTERER 2006

It is noteworthy that the number of *Napaeus* species on La Gomera exceeds that of the neighbouring island of Tenerife, which only has 15 living species despite the latter island being higher (Mount Teide reaching 3718 m altitude) and five times more extensive. However, Tenerife is about 4.5 my younger than La Gomera (CARRACEDO et al. 2005) and its natural habitats have been much more degraded by human activity.

La Palma Island (726 km², 2430 m altitude, 1.7 my old) is located to the northwest of La Gomera and it only has four *Napaeus* species described to date (SHUTTLEWORTH 1852, MOUSSON 1872, WOLLASTON 1878, HENRÍQUEZ, ALONSO et al. 1993, BANK et al. 2002, YANES et al. 2009):

N. boucheti ALONSO & IBÁÑEZ 1993; *N. encaustus* (SHUTTLEWORTH 1852); *N. palmaensis* (MOUSSON 1872); *N. subgracilior* (WOLLASTON 1878)

In the present study two new *Napaeus* species are described, one from western La Gomera and the other from northern La Palma.

Methods

Maps of geographical distribution (Text Fig. 1) were produced using MapViewer software (Golden Software Inc.). The photographic methodology was described by IBÁÑEZ et al. (2006). Drawings of shell outlines (Text Fig. 2) were obtained semi-automatically, adopting the methods used by YANES et al. (2009). Standardized measurements of the shells (Table 1, Text Fig. 2) were made following ALONSO, NOGALES et al. (2006), using the software analySIS® (Soft Imaging System GmbH). Student's *t* tests was performed to compare the three main variables on shell height (SH), breadth (SB) and surface (SS) to contrast *N. minimus* and *N.barquini*; while ANOVA I tests were carried out for comparing *N. delicatus*, *N. roccellicola* and *N. rufobrunneus* (WOLLASTON 1878). All statistical analyses (Table 3) were carried out applying SPSS (v. 18.0).

Abbreviations for shell characters and measurements are shown in Text 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 on the location of the insertion of the penial retractor muscle (as in ALONSO & IBÁÑEZ 2007).

Other abbreviations:

AIT	ALONSO & IBÁÑEZ collection, Department of Animal Biology, University of La Laguna, Tenerife, Canary Islands, Spain;
GAH	GERALDINE A. HOLYOAK private collection, Cabeçudo, Portugal;
ICZN	International Commission on Zoological Nomenclature;
JSGC	J. Santana private collection, Las Palmas de Gran Canaria, Spain;
NHM	The Natural History Museum, London, U.K.;
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain;
SMF	Naturmuseum Senckenberg, Frankfurt, Germany
UTM	Universal Transverse Mercator, cartographic projection system.

Systematic section

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

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

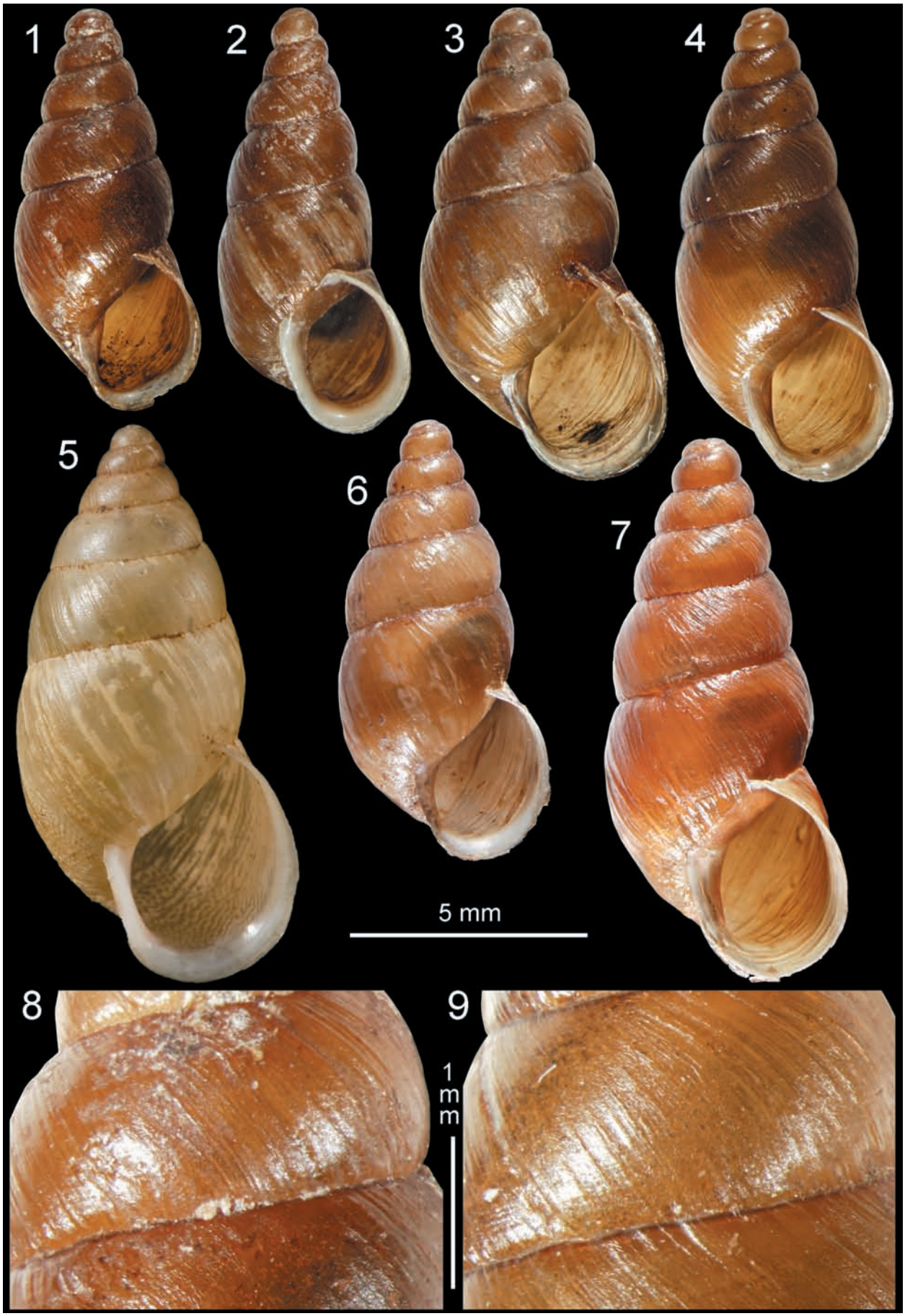
Genus ***Napaeus*** ALBERS, 1850

Type species by subsequent designation of HERMANNSEN (1852): *Bulimus baeticatus* WEBB & BERTHELOT 1833.

Napaeus minimus D. HOLYOAK & G. HOLYOAK n. sp.

Text Figs 3A, 4, 5A, B, Plate 1, Figs 1, 8, Plate 2, Figs 1–7

Holotype (Plate 1, Fig. 1): TFMC (MT 0413); Leg. G. HOLYOAK and D. HOLYOAK, 13 February 2006; type locality (Text Fig. 3A): Mirador CÉSAR MANRIQUE (La Gomera; UTM: 28RBS7212; 720 m altitude). — paratypes: 30 specimens + 25 shells collected between February 2006 and June, 2010 from the western part of La Gomera; deposited in GAH (21 speci-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Text Fig. 3. Type localities of A: *Napaeus minimus* n. sp. B: *N. delicatus* n. sp.

mens + 12 shells), JSGC (2 specimens + 9 shells), and AIT (7 specimens + 2 shells and SMF (2 shells).

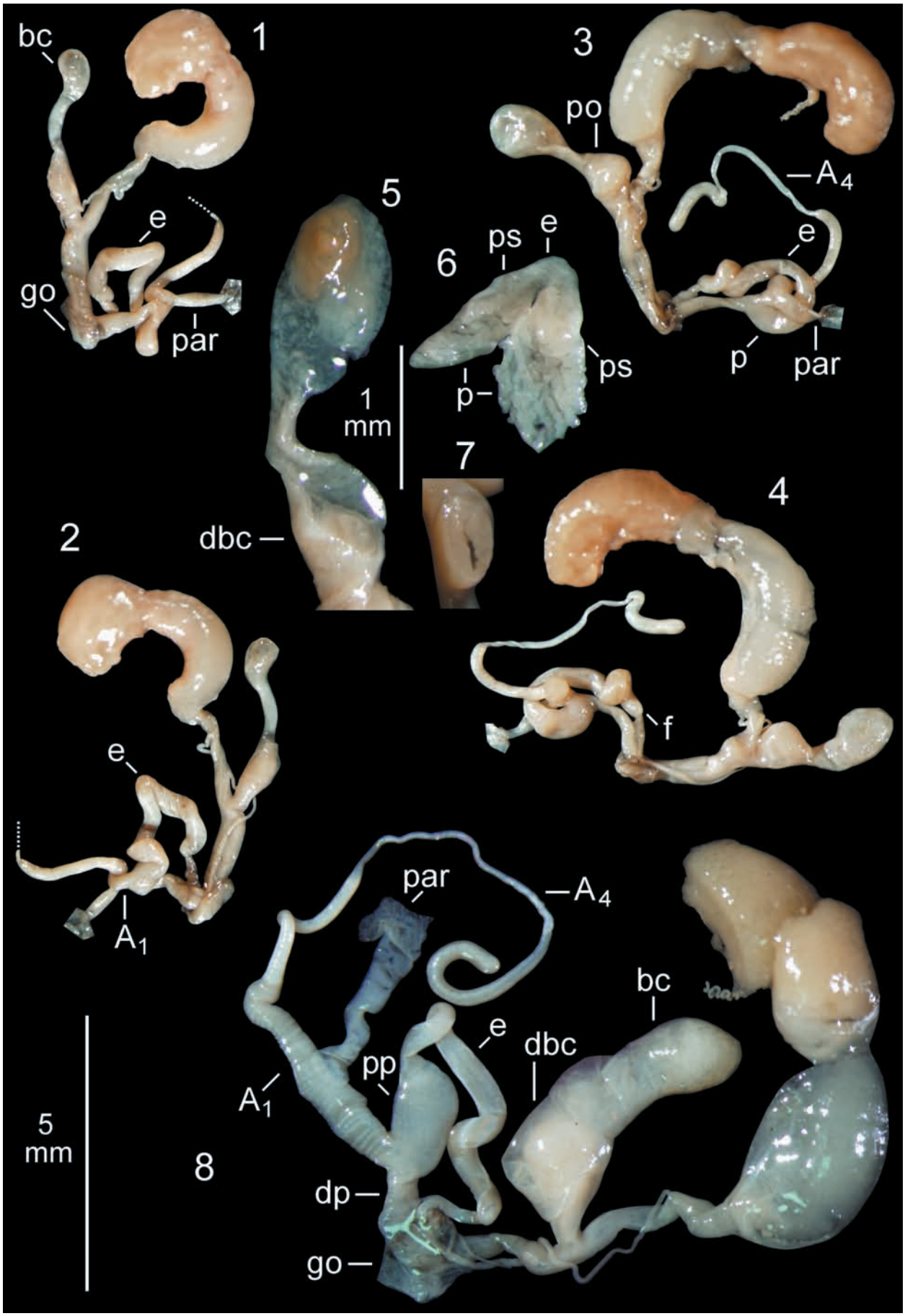
Diagnosis: Shell very small, slightly elongated, obese, uniform corneous-brown in colour. Penis without penial retractor muscle. Part A_1 of the penial appendix extremely short. Epiphallus without epiphallar caecum. Bursa copulatrix without a diverticulum, with three parts, distal part with an inner chamber.

Description: The species has the smallest shell known in *Napaeus*. The animal has a dark grey body. The shell (Plate 1, Fig. 1) is very small, slightly elongated, uniform corneous-brown in colour, obese (SB/SH index: Table 2), with 6–6½ convex whorls and a deeply marked suture. The body whorl is intermediate (BH/SH index: Table 2), occupying about ⅔ of the shell surface (BS/SS index: Table 1). The protoconch is smooth, with 1¾ whorls. The aperture is short and wide (AH/SH and AB/SB indices, respectively: Table 2), elliptical in section at the palatal side and slightly angular at union of columellar and palatal edges. The upper palatal side forms an angle of about 105º with the parietal side but at once arches; because of this, the aperture juts out only slightly from the start of the body whorl, producing an ovate appearance. The peristome has an incipient lip more developed in lower part of palatal edge, where it partially covers the umbilical slit. The shell surface is shiny with a weak obliquely radial striation (Plate 1, Fig. 8).

The genital system is shown in Plate 2, Figs 1–7 (two adult specimens dissected). The atrium is very short and the penis, which has no penial retractor muscle, is clearly shorter than the epiphallus and longer than the A_1 part of the penial appendix. The penis has two portions, a distal tubular region and a swollen, proximal region, which has several inner folds and an incipient, proximal penial papilla shown as a small sphincter between the epiphallus and penis. The epiphallus is tubular, without a caecum or distinguishable regions. The flagellum is very short and globular, as a small protuberance subterminal in the conexion with the vas deferens. The penial appendix opens laterally on the penis. Part A_1 is extremely short, tubular. Part A_2 is small, muscular, globular. The appendicular retractor muscle inserts in the middle zone of A_1.

The vagina and free tubular oviduct are similar in length and also similar in length to the penis. The vagina is fixed to the body tegument by short vaginal connective fibres. The bursa copulatrix duct is very short and lacks a diverticulum. The bursa copulatrix is large, with three

Plate 1. Figs 1–7: Shells of: 1: holotype of *Napaeus minimus* n. sp., 2: holotype of *N. beguirae*, 3: *N. barquini*, from Acantilado La Gerode (La Gomera), 4: holotype of *N. delicatus* n. sp., 5: syntype of *N. palmaensis* (NHM 1895.2.2.219; photo by J. Ablett), 6: *N. roccellicola*, from Tamargo (Teno, Tenerife), 7: *N. rufobrunneus*, from El Castillejo (Lanzarote). Figs 8–9: Details of the ornamentation of the penultimate whorl of the shells of holotypes of 8: *Napaeus minimus* n. sp., 9: *N. delicatus* n. sp. Figs 6 and 7, from Ibáñez et al. (2007).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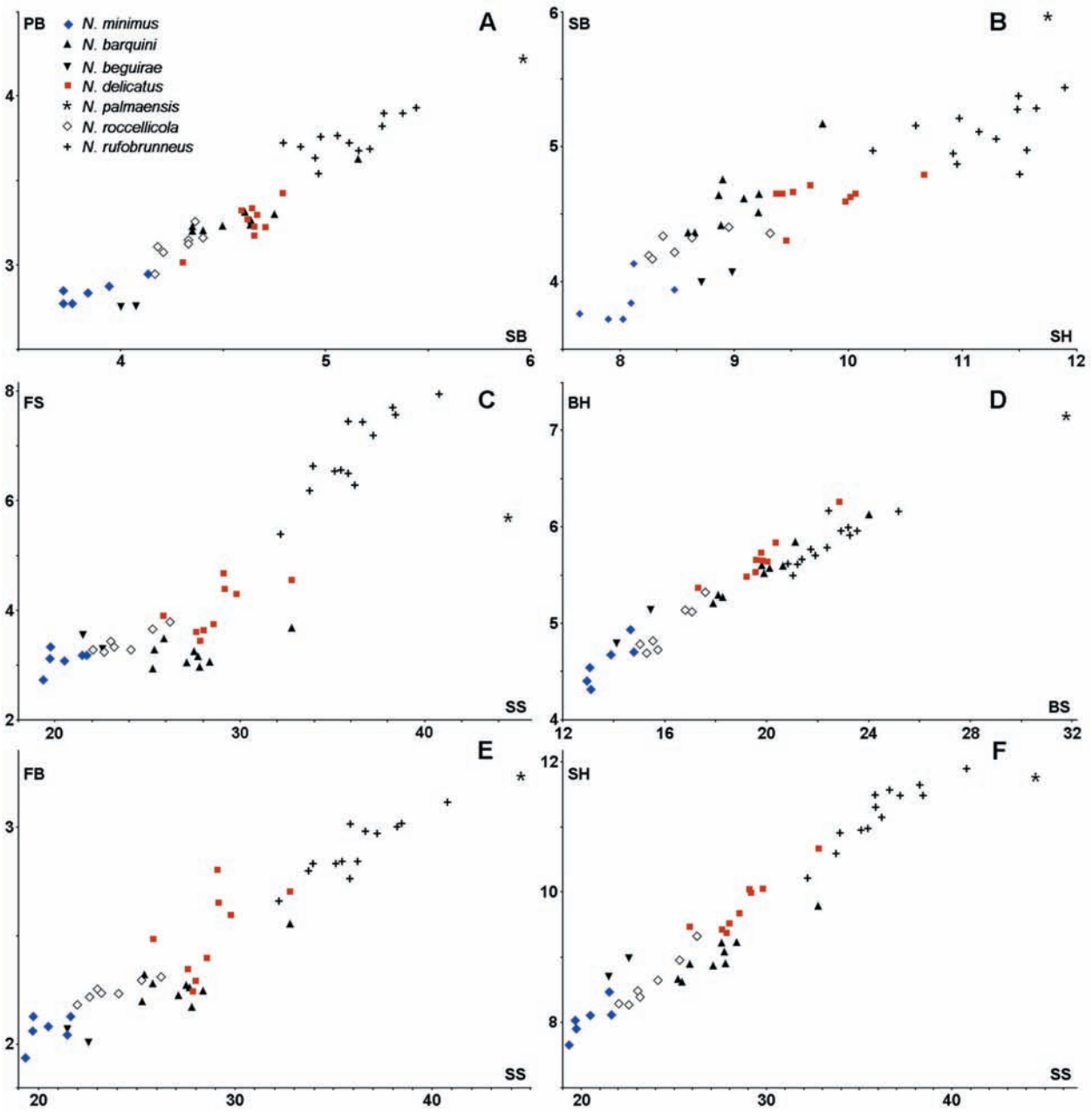


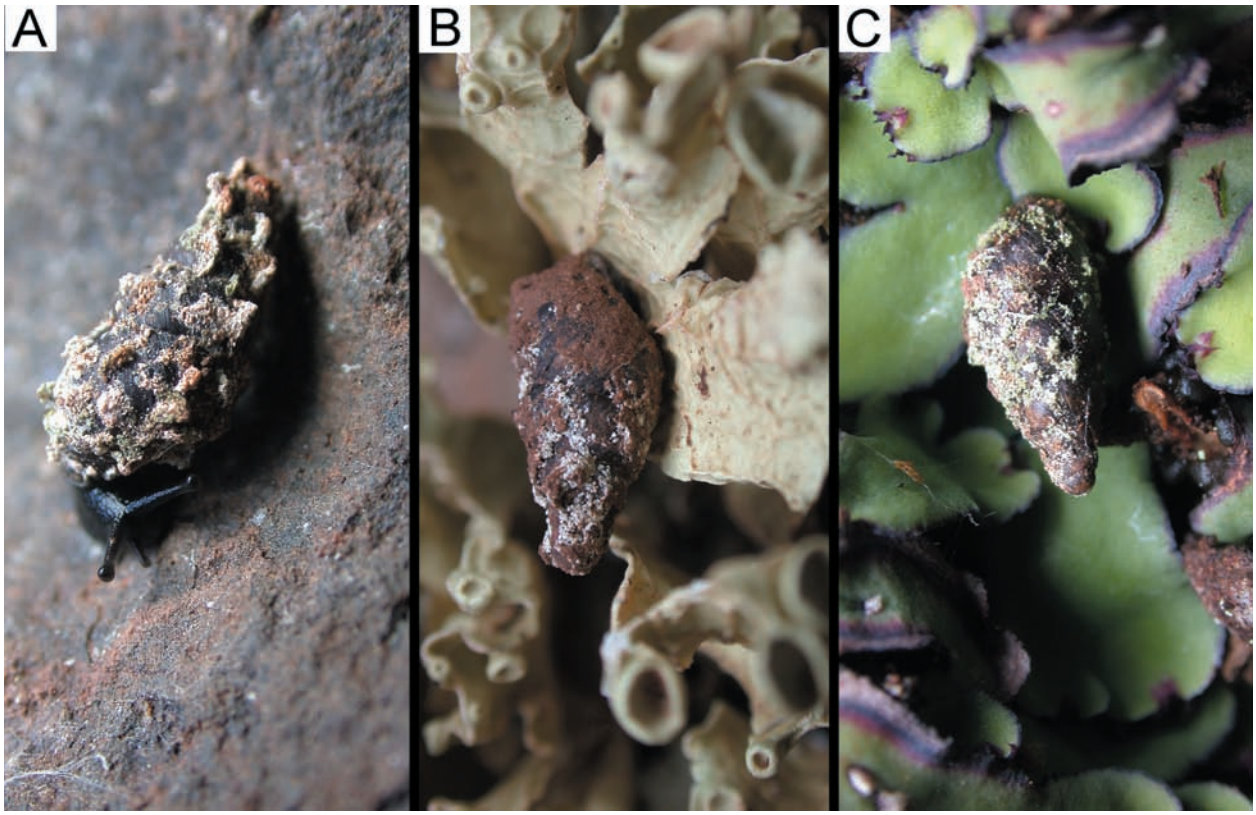
Text Fig. 4. Scatter plots of some shell measurements for the new species of *Napaeus* and similar species. BH, body whorl height (at columella level); BS, body whorl surface area (plane view); FB, first whorls breadth; FS, first whorls surface area (plane view); PB, penultimate whorl breadth; SB, shell breadth; SH, shell height; SS, shell surface area (plane view).

parts; proximal part glandular, the gametolytic gland and distal part with an inner chamber similar to that of *N. barquini* and intermediate part tubular, connecting the proximal and distal parts.

Etymology: The specific name is derived from the shell dimensions, this being the smallest species known in the genus, its shell surface area (plane view: SS parameter) is more than ten times smaller than that of *N. bertheloti* (20/213 mm^2).

Geographic range and habitat: Endemic to La Gomera, where it was collected in two nearby localities, on north-facing open, lichen-covered rocky

Plate 2. Genital systems of *Napaeus minimus* n. sp. (Figs 1–7) and *N. barquini*, paratype (Fig. 8) from Benchijigua (La Gomera), ventral view (from ALONSO, GOODACRE et al. 2006). 1–4: two specimens (1–2 and 3–4), each of them shown in dorsal (1, 3) and ventral (2, 4) views; 5: longitudinal section of the bursa copulatrix; 6: longitudinal section of the proximal penis; 7: cross section of the proximal penis. A1, A4, 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; ps: penial sphincter.



Text Fig. 5. A: specimen of *Napaeus minimus*, with incomplete cover mainly of lichens adherent to the shell and forming protuberances; B: another specimen of *N. minimus*, resting on the lichen *Ramalina bourgaeana*, with lichens and soil adherent to the shell; C: Specimen of *N. delicatus* partly disguised with lichens, resting on the liverwort *Mannia androgyna*.

slopes exposed to the humid trade winds, with succulent vegetation, between 720 and 780 m altitude (Text Fig. 3A).

Relationships. *Napaeus minimus* n. sp. shares with the species *N. voggenreiteri*, *N. barquini* and *N. procerus* the character states "male genital system with only one retractor muscle, the appendicular retractor muscle", "bursa copulatrix with three parts, the proximal part being glandular, the gametolytic gland" and "distal part of bursa copulatrix with an inner chamber which opens proximally in the cavity of the medium bursa part". Compared to those species, the shell of *N. minimus* is similar in form and size only to that of *N. barquini* (Plate 1, Fig. 3), but it is more slender and almost all its parameters measured are smaller than those of *N. barquini* (Text Fig. 4, Table 2). The genital system of *N. minimus* is also of the same type as that of *N. barquini* (Plate 2, Fig. 8) but smaller, the main difference being with the part A_1 of the penial appendix, which in *N. barquini* is well developed, wide, and longer than the penis, whereas that of *N. minimus* is extremely short.

The shell size of *N. minimus* is also comparable to that of *N. beguirae* (Plate 1, Fig. 2) which is also from La Gomera, but the latter species has a conical shell, the whorls flatter and the penultimate whorl narrower (Text Fig. 4B). Moreover the genital system of *N. beguirae* has two retractor muscles (penial and appendicular) and its bursa copulatrix lacks the parts present in *N. minimus* and *N. barquini.*

N. minimus is mainly a rock-dwelling species, living on lichen-covered rock surfaces and in rock crevices. The majority of the specimens collected had the shell disguised by a covering made from the surrounding crustose lichens, forming protuberances (Text Fig. 5A) and altering the appearance of the shell considerably as in other disguised *Napaeus* species (YANES et al. 2010). This renders most of the living animals very inconspicuous in the normal resting places on rock surfaces and presumably serves to avoid predation. Two atypical specimens had the shell covered predominantly with fine powdery soil. A third specimen had a cover of both lichen and soil and was photographed resting in an atypical place, on the lichen *Ramalina bourgaeana* MONTAGNE EX NYLANDER, where its camouflage did not work (Text Fig. 5B).

Napaeus delicatus ALONSO, YANES & IBÁÑEZ n. sp.

Text Figs 3B, 4, 5C; Plate 1, Figs 4, 9

Holotype (Plate 1, Fig. 4): TFMC (MT 0414); Leg. G. HOLYOAK and D. HOLYOAK, 22 February 2006; type locality (Text Fig. 3B): A north-facing slope near the Gallegos ravine, in the

Table 1. Data for the shell characters measured (in mm or mm^2). sp1: *N. barquini*; sp2: *N. minimus*; sp3: *N. delicatus*; sp4: *N. palmaensis* (NHM 95.2.2.219-21 syntype). sp5: *N. roccellicola*; sp6: *N. rufobrunneus*; n, number of measured specimens; SD, standard deviation; Min., minimum; Max., maximum; 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); StP, Statistical parameter; C/P, Character/Index

StP	C/P	sp1	sp2	sp3	sp4	sp5	sp6	C/P	sp1	sp2	sp3	sp4	sp5	sp6
Mean	SH	9.03	8.05	9.80	11.75	8.62	11.21	AP	10.17	8.41	10.45	14.22	9.28	10.87
SD		0.36	0.27	0.42		0.39	0.47		0.50	0.54	0.46		0.39	0.52
Min.		8.62	7.65	9.37		8.26	10.22		9.29	7.78	9.52		8.62	9.97
Max.		9.78	8.48	10.67		9.32	11.9		10.71	9.27	11.25		9.70	11.76
Mean	SB	4.60	3.85	4.62	5.97	4.28	5.12	FH	2.04	2.11	2.50	2.83	2.27	3.44
SD		0.25	0.16	0.13		0.09	0.20		0.09	0.08	0.20		0.10	0.24
Min.		4.35	3.72	4.30		4.17	4.8		1.94	1.97	2.24		2.16	2.95
Max.		5.16	4.14	4.79		4.40	5.44		2.19	2.18	2.80		2.42	3.72
Mean	SS	27.56	20.43	28.78	44.54	23.82	36.14	FB	2.28	2.07	2.35	3.23	2.25	2.90
SD		2.26	0.97	1.90		1.52	2.25		0.11	0.07	0.09		0.05	0.13
Min.		25.31	19.38	25.88		22.07	32.21		2.17	1.94	2.23		2.18	2.66
Max.		32.80	21.67	32.82		26.28	40.8		2.55	2.13	2.46		2.31	3.12
Mean	SP	22.06	19.55	23.67	28.59	21.07	27.39	FS	3.19	3.10	4.02	5.68	3.42	6.88
SD		0.99	0.69	0.96		0.88	1.18		0.25	0.20	0.46		0.22	0.74
Min.		21.01	18.74	22.69		20.23	25.21		2.93	2.74	3.44		3.23	5.39
Max.		24.29	20.63	25.69		22.60	29.38		3.67	3.33	4.67		3.79	7.96
Mean	BH	5.55	4.60	5.68	7.15	4.94	5.83	FP	7.45	7.17	8.47	10.08	7.67	11.05
SD		0.29	0.22	0.26		0.25	0.21		0.34	0.31	0.50		0.23	0.69
Min.		5.21	4.32	5.36		4.69	5.5		7.06	6.59	7.79		7.44	9.8
Max.		6.12	4.94	6.26		5.32	6.17		8.20	7.46	9.30		8.02	11.98
Mean	BS	20.02	13.76	19.87	31.80	16.18	22.41	PH	1.45	1.35	1.61	1.77	1.46	1.91
SD		1.89	0.83	1.42		0.99	1.23		0.07	0.02	0.07		0.09	0.10
Min.		17.95	12.96	17.35		15.04	20.85		1.35	1.32	1.49		1.37	1.74
Max.		24.04	14.81	22.88		17.60	25.19		1.55	1.37	1.73		1.63	2.09
Mean	BP	17.21	14.51	17.51	22.56	15.80	18.92	PB	3.28	2.84	3.25	4.22	3.11	3.75
SD		0.87	0.53	0.72		0.60	0.57		0.13	0.06	0.12		0.09	0.11
Min.		16.16	13.83	16.28		15.15	17.81		3.19	2.77	3.01		2.94	3.54
Max.		18.83	15.16	19.03		16.82	20		3.62	2.94	3.43		3.25	3.93
Mean	AH	3.71	3.00	3.69	5.11	3.27	3.75	PS	4.40	3.58	4.88	7.06	4.22	6.80
SD		0.18	0.21	0.16		0.16	0.21		0.34	0.09	0.35		0.38	0.51
Min.		3.45	2.69	3.47		3.10	3.32		4.04	3.48	4.39		3.76	5.73
Max.		3.91	3.33	3.98		3.46	4.09		5.16	3.69	5.39		4.90	7.6
Mean	AB	2.94	2.46	3.11	4.14	2.77	3.23	PP	9.05	7.92	9.30	11.53	8.69	10.88
SD		0.15	0.18	0.17		0.12	0.17		0.43	0.17	0.35		0.38	0.48
Min.		2.65	2.27	2.74		2.51	2.94		8.79	7.68	8.83		8.17	9.84
Max.		3.16	2.72	3.36		2.89	3.51		10.15	8.15	9.83		9.32	11.65
Mean	AS	7.15	5.18	8.14	14.88	6.27	8.73	SB/SH	0.51	0.48	0.47	0.51	0.50	0.46
SD		0.72	0.72	0.70		0.55	0.79	BH/SH	0.61	0.57	0.58	0.61	0.57	0.52
Min.		5.85	4.39	6.67		5.28	7.5	AH/SH	0.41	0.37	0.38	0.43	0.38	0.33
Max.		8.01	6.29	9.29		6.96	9.85	AB/SB	0.64	0.64	0.67	0.69	0.65	0.63
n		9	6	9	1	7	13	BS/SS	0.73	0.67	0.69	0.71	0.68	0.62

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				

northern part of the island (La Palma; UTM: 28RBS2390, 500 m altitude). — paratypes: 9 specimens and 43 shells, collected 22 February 2006 from northern La Palma; deposited in GAH (41 shells), AIT (9 specimens) and SMF (2 shells).

Diagnosis: Shell small, delicate, elongated, obese, uniform corneous-brown in colour; body whorl occupies rather more than ⅔ of the shell surface; aperture rounded.

Description: Unfortunately, all the specimens collected were juvenile or sub-adult but immature; thus, only a conchological description is made. The shell (Plate 1, Fig. 4) is small, delicate, elongated, obese (SB/SH index: Table 2), with 6½–7¼ convex whorls, a marked suture and uniform corneous-brown in colour. The body whorl is intermediate (BH/SH index: Table 2), occupying something more than ⅔ of the shell surface (BS/SS index: Table 1). The protoconch is smooth, with 1½ whorls. The aperture is short and wide (AH/SH and AB/SB indices, respectively: Table 2), rounded at the palatal side and slightly angular at union of columellar and palatal edges. The upper palatal side forms an angle of about 110º with the parietal side and the aperture projects clearly from the start of the body whorl, giving a nearly circular appearance. The peristome is expanded as a small lip, more developed in the lower part of the palatal edge and reflected on the columellar edge, where it partially covers the umbilical slit. The shell surface is shiny with a weak radial oblique striation (Plate 1, Fig. 9).

Etymology: The specific name derives from the delicate appearance of the shell.

Geographic range and habitat: A species endemic to La Palma, where it was collected in two nearby localities, on steep north-facing crags beside road, on slopes with *Erica arborea* L. and other scrub (Text Fig. 3B).

Relationships: Among *Napaeus* occurring on La Palma island, the form of the *N. delicatus* shell is comparable only with that of *N. palmaensis* (Plate 1, Fig. 5, Text Fig. 4, Table 2), but it is clearly smaller; e.g., the aperture of the *N. palmaensis* shell is almost twice as large as that of *N. delicatus*. The *N. delicatus* shell is also comparable with that of *N. roccellicola* (WEBB & BERTHELOT 1833) (Plate 1, Fig. 6), from Tenerife, and *N. rufobrunneus* (Plate 1, Fig. 7), from Lanzarote. In *N. roccellicola* the whorls are more convex and the suture is deeper than in *N. delicatus*. Similarly, *N. rufobrunneus* has both of the same characters more pronounced than in *N. delicatus*. Also, the aperture of *N. delicatus* is rounded whereas the other two species have it ovate; the new species also occupies a position intermediate between the other two species in respect of the parameters SH, SS and FB (Text Figs 4B, C, E, F).

Lichen covered juveniles of *N. delicatus* were mostly found on the rock of crags, some in the open on vertical surfaces, others partly or well hidden in crevices. A few were also found behind *Aeonium* rosettes and three were on thalli of the liverwort *Plagiochasma rupestre* (J. R. FORSTER & J. G. A. FORSTER) STEPHANI (Text Fig. 5C). Five subadults (i.e., differing from the adults only in the develop of the genital system, but the shell is already fully grown) had the shell disguised with soil particles, with bits of crustose lichen also present on two of the shells (Text Fig. 5C). However, *N. delicatus* appeared to carry much less camouflaging material on the shell than did most of the *N. minimus* (this paper) or *N. barquini* specimens (ALLGAIER 2007, for *N. barquini*).

Taxonomic complexity of *Napaeus*

Allocation of *Napaeus* species into the two subgenera of HESSE (1993) (*Napaeus* and *Napaeinus*) has been shown to be problematical because different modes of classification (i.e. genital anatomy and molecular phylogeny) yield different results (ALONSO et al. 2006). Their subgeneric allocation has also been problematical based on genital anatomy alone because anatomical study of six species revealed contradictions with HESSE's subgeneric descriptions (HENRÍQUEZ, ALONSO et al. 1993, HENRÍQUEZ, IBÁÑEZ et al. 1993, YANES et al. 2009).

The genital systems of the species *N. voggenreiteri*, *N. barquini*, *N. procerus* and *N. maculatus*, listed above from La Gomera share the character states "male genital system with only one retractor muscle, the appendicu-

Table 3. Statistical results obtained for the comparisons of the *Napaeus* species studied.

Species	Statistical (Student's *t* tests)			p-level		
	SS	SH	SB	SS	SH	SB
sp1 vs. sp2	- 7.22	- 5.66	- 6.37	< 0.001	< 0.001	< 0.001
	Statistical (ANOVA I)			p-level		
	SS	SH	SB	SS	SH	SB
sp3 vs. sp5 vs. sp6	94.18	83.86	66.64	< 0.001	< 0.001	< 0.001

lar retractor muscle" and "bursa copulatrix with three parts, the proximal part being glandular, the gametolytic gland". The first three species of that list also share the character state "distal part of bursa copulatrix with an inner chamber which opens proximally in the cavity of the middle bursa part". A new supraspecific taxon grouping these species seems to be justified from the anatomical point of view. However, when considering anatomical data in conjunction with molecular phylogenetic data, disparities are apparent in that neither of the subgenera *Napaeinus* or *Napaeus*, or the possible new supraspecific taxon, are monophyletic within the molecular phylogeny, despite being distinguishable from each other by a suite of morphological characters (ALONSO et al. 2006). Thus, the new species are not assigned to HESSE's subgenera or the possible new supraspecific taxon mentioned above until a phylogenetic analysis of the genus is conducted.

Statistical analyses

The results obtained indicate that there are clear differences among the species when the variables shell height (SH), shell breadth (SB) and shell surface (SS), are analysed (see Tables 1 and 3). *Napaeus minimus* is shorter in size than *N. barquini*. In the case of the other group, *N. rufobrunneus* is larger than *N. delicatus* and *N. rufobrunneus*; and *N. delicatus* is larger than *N. rocellicola*. The differences in shell proportions shown in the plots of Fig. 4 are clear.

The Student's *t* and ANOVA I tests performed show that the shell characters of each *Napaeus* species are very constant. The shell differences compared to the most similar species on the same island (*N. palmaensis*) are clearly big. The other two species, *N. rufobrunneus* and *N. roccellicola*, inhabit different islands (so far as is known, each *Napaeus* species only lives in a small part of one island), and in their respective islands these species have not developed ecological variants/morphotypes.

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