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Napaeus lajaensis sp. nov. (Gastropoda: Pulmonata: Enidae) from a Quaternary Aeolian Deposit of Northeast Tenerife, Canary Islands

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Abstract

Napaeus lajaensis **sp. nov.** is the oldest *Napaeus* species found in the Canary Islands, with more than 130 ka. It is described from a Pleistocene aeolian deposit intercalated between two basaltic lava flows located at Mancha de La Laja (Tenerife Island). The new species is characterized mainly by the presence of two very prominent, spiral, semicylindrical ribs on the body whorl shell. The stratigraphic setting and taphonomic features of the land snail association to which *N. lajaensis* belongs, were also shown.

Key words: Gastropoda, *Napaeus*, taxonomy, Pleistocene, Canary Islands

Introduction

Island archipelagos continue to be a focal point for studies in evolutionary biology, with many research programs being directed towards understanding the origins of diversity (E merson 2002; Emerson & Kolm 2005). Island populations may diverge from their parental mainland populations to become endemic species. Therefore, land snails are one of the groups that often show high percentages of endemic forms. The Hawaiian Islands and the Galapagos Islands have both, for a long time, served as paradigmatic systems for conducting this type of research (Wagner & Funk 1995; Grant 1998), but recent years have seen an emerging interest in the Canary Islands as a further natural laboratory for the study of evolution owing to their discrete geographical nature and the diversity of species and habitats (Juan *et al*. 2000).

The Canary archipelago forms an island chain of seven main islands, approximately 500 km in length, in the Atlantic off the North West African coast at the western fringe of the Palaearctic, about 500 km north from the Tropic of Cancer, the easternmost island only 110 km from Morocco. The archipelago is clearly of volcanic origin, with geological

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support for a hotspot origin (Carracedo *et al*. 1998, 2005) or a hotspot, propagating fracture and uplifted block as unified explaining model (Anguita & Hernán 2000). The central and western islands, which are separated by deep water, have never been in contact with one another or the mainland. One of the central islands is Tenerife which has been dated between 11.9 and 8.9 million years old (Ma) (Guillou *et al*. 2004). In this geological context, the aeolian deposits constitute an important source of palaeontological information because of the good degree of preservation of both vertebrate and invertebrate Quaternary fossils (Michaux *et al*. 1991; De la Nuez *et al*. 1997; Castillo *et al*. 2003; Yanes *et al*. 2004). Sand dune invasions from the sea took place during arid periods, when sea level dropped and the wind mobilized the sands towards the island, palaeosols being intercalated between the dune deposits during more humid periods.

The alternation of aeolian deposits and palaeosols, which are related to abrupt transitions from arid to humid conditions (Meco *et al.* 1997; Damnati 1997; Castillo *et al*. 2002), are the reflection of globally induced changes in the palaeoenvironmental conditions of North Africa linked to the effect of African paleomonsoons in the trade winds and the Saharan Air Layer. These aeolian cycles, with a recurrence period of 5-7 ka, are probably the expression of multiples of the ~ 2,4 ka solar cycle (Ortiz *et al*. 2006).

Land snails are the main invertebrates of interest for palaeontological studies because of the excellent conservation of their shells. The majority of the Canarian land snail species (about 80%) are endemic to the archipelago (Ibáñez *et al*. 2001; Groh & García, 2004). Excluding human introductions, there are more than 40 genera naturally occurring on the archipelago, seven of which are endemic to the islands. Several endemic genera have experienced a remarkable radiation on the islands, *Napaeus* Albers, 1850 being the most species rich genus. *Napaeus* includes more than 60 nominal taxa of specific rank (which correspond to 50 species) described to date by several authors, 18 species being endemic to Tenerife. The main references of the *Napaeus* species are Webb & Berthelot (1833), Mousson (1872), Wollaston (1878), Krause (1895), Odhner (1931), Hesse (1933), Groh (1985), Alonso *et al*. (1991, 1995, 2006a), Groh *et al*. (1992), Henríquez *et al*. (1993 a,b) and Bank *et al*. (2002). Groh is the only author to show Quaternary localities of several *Napaeus* species, all of which also belong to the living malacofauna. Similarly to the majority of the endemic Canarian land snail species, the *Napaeus* species typically have a small distribution area, with each species normally restricted to a single area of one island.

On the northeast coast of Tenerife (Fig. 1), a Quaternary aeolian deposit intercalated between two basaltic lava flows constitutes a small yet interesting fossil site named Mancha de La Laja. This paper includes a preliminary presentation of the stratigraphic and taphonomic features of that site, allowing the historic reconstruction of its palaeoclimatic habitat; the taxonomic composition of its land snails is also shown and a new fossil *Napaeus* species is described.

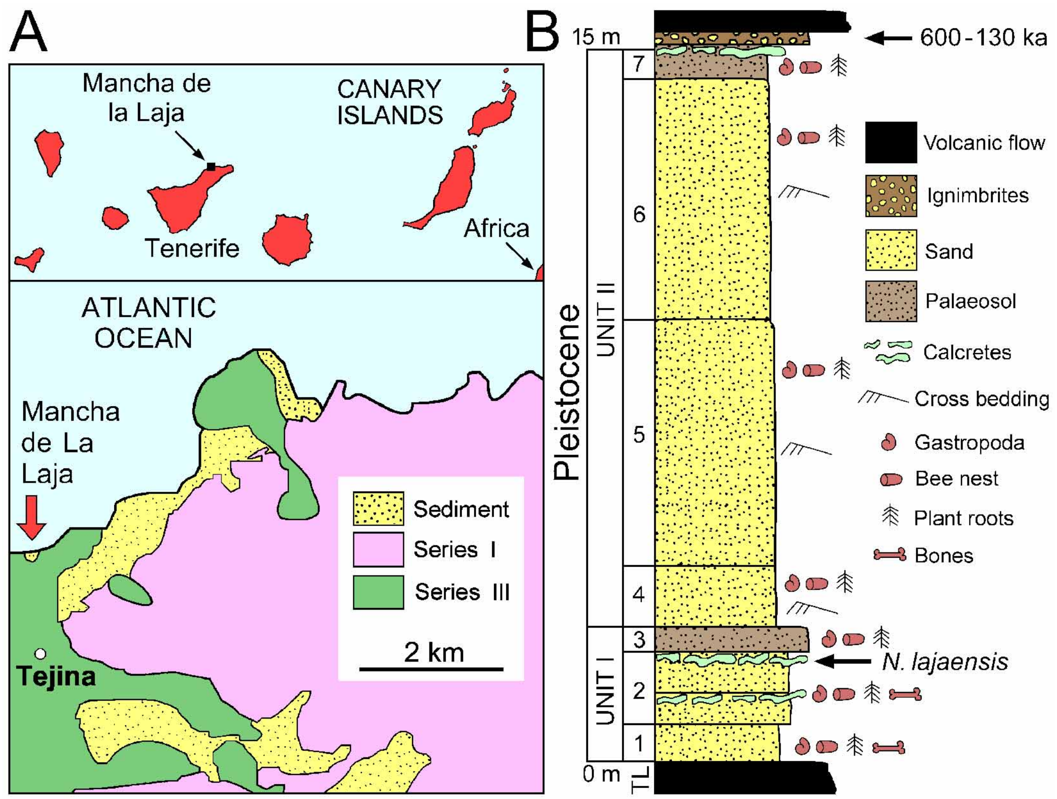

FIGURE 1. A: Geographical and geological setting of the Mancha de La Laja fossil site. B: Stratigraphic column of the *Napaeus lajaensis* type locality.

Methods

The stratigraphy of the fossil site distinguishes seven stratigraphic beds, from TL-1 (the oldest) to TL-7 (the most recent) belonging to two main sedimentary episodes (Fig. 1B). Subsequently, a semiquantitative analysis of taphonomic features of land snails assemblages has been achieved based on the methodology of Kidwell *et al*. (1986) and Brett & Baird (1986). The taphonomic data were obtained from ten 30 cm by 30 cm plots. Four taphonomic indexes on the land snail assemblages: breakage, coating, colour conservation and rounding were studied. Also, we checked the mineralogical shell composition by X-Ray diffraction. The sampling has been made from the beds TL-1 and TL-2 of unit I (Fig. 2). The sediment samples were sieved in dry conditions through a 1 mm mesh size and then examined with a stereomicroscope.

The photographic methodology is the same as that of Ibáñez *et al*. (2006). For the shell measurements of the new species (Table 1), shells were oriented with the shell axis (columella) to the Y axis of coordinates and the maximum shell breadth represented accurately in plane view. The shell measurements were obtained with the program analySIS® (Soft Imaging System GmbH 2002). The image preparation and placement of measurements are shown in Figure 3, the straight linear shell measurements being obtained by the analySIS® program as the projections on the X and Y axes of the respective structures. Some computer-assisted measurements of plane views of shells, such as those related to surface and perimeter, were added to the common straight linear measures because these provide more reliable and less variable data than traditional ones (Alonso *et al*. 2006b). Shell whorls numbers were calculated following Kerney & Cameron (1979: 13). The conchological terminology, based on the biometric data shown in Table 1, is the same as that of Henríquez *et al*. (1993b; see Table 2).

Abbreviations

AB	aperture breadth (mm)
AH	aperture height (mm)
AIT	Alonso & Ibáñez collection, Department of Animal Biology, University of La Laguna, Tenerife, Canary Islands, Spain
AP	aperture perimeter (mm)
AS	aperture surface (plane view; mm^2)
a.s.l.	above sea level
BH	body whorl height (at columella level; mm)
BP	body whorl perimeter (mm)
BS	body whorl surface (plane view; mm^2)
I.C.Z.N.	International Commission on Zoological Nomenclature
ICZN	International Code of Zoological Nomenclature
ka	kilo years ago
Ma	million years ago
n	number of measured specimens
SB	shell breadth (mm)
SH	shell height (mm)
SP	shell perimeter (mm)
SS	shell surface (plane view; mm^2)
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain
TL 1-7	stratigraphical beds (fossiliferous levels)
unit I-II	dune-formation episodes

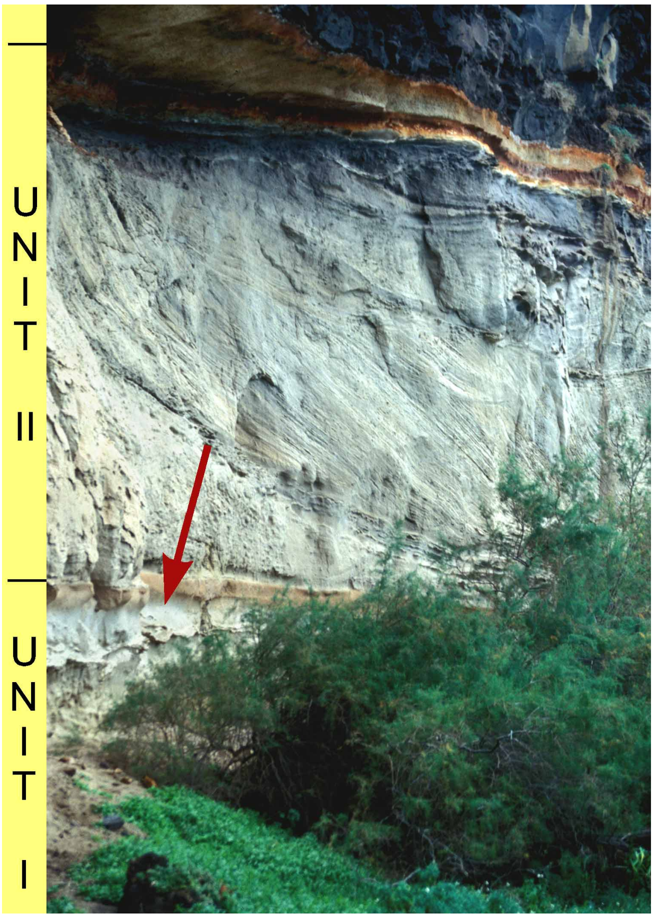

FIGURE 2. General picture of the Mancha de La Laja aeolian deposit, showing the Units I and II. The arrow indicates the location of *Napaeus lajaensis* **sp. nov.**

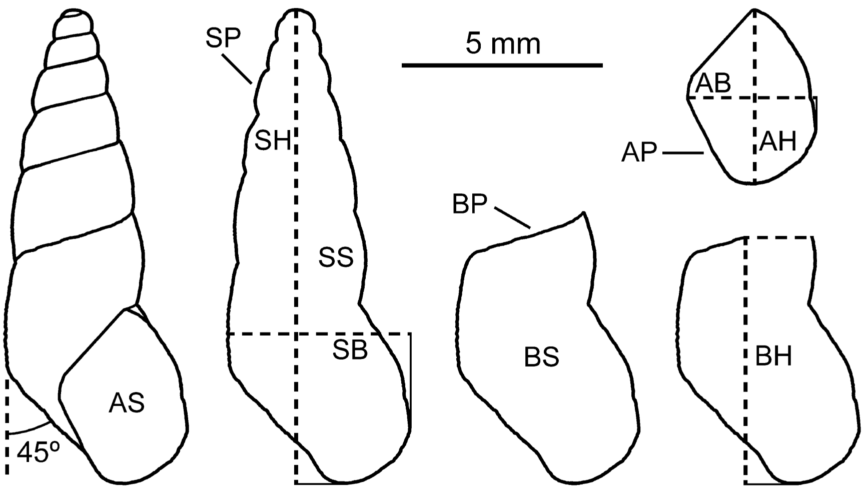

FIGURE 3. Drawings of the *Napaeus lajaensis* holotype shell, showing the placement of the measurements obtained.

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TABLE 1. Biometric data of the adult *Napaeus lajaensis* **sp. nov.** shell (n = 9)

Character or index	Statistical parameter	Population measured	Holotype
SH	Mean	11,08	11,87
	SD	0,49	
	Min.	10,37	
	Max.	11,87	
SB	Mean	4,47	4,62
	SD	0,22	
	Min.	4,14	
	Max.	4,85	
SS	Mean	30,50	32,96
	SD	1,61	
	Min.	27,95	
	Max.	32,96	
SP	Mean	26,25	28,01
	SD	1,09	
	Min.	24,72	
	Max.	28,01	
BH	Mean	5,85	6,19
	SD	0,21	
	Min.	5,45	
	Max.	6,19	
BS	Mean	19,42	20,66
	SD	1,13	
	Min.	17,72	
	Max.	21,24	
BP	Mean	17,85	18,67
	SD	0,56	
	Min.	16,89	
	Max.	18,67	
AH	Mean	4,03	4,39
	SD	0,24	
	Min.	3,66	
	Max.	4,39	
AB	Mean	3,04	3,30
	SD	0,19	

to be continued.

TABLE 1 (continued).

Character or index	Statistical parameter	Population measured	Holotype
	Min.	2,74	
	Max.	3,30	
AS	Mean	8,42	9,79
	SD	0,9	
	Min.	6,89	
	Max.	9,79	
AP	Mean	10,96	11,82
	SD	0,58	
	Min.	9,93	
	Max.	11,82	
SB/SH	Mean	0.36	0.39
BH/SH	Mean	0,53	0,52
AH/SH	Mean	0,36	0,37
AB/SB	Mean	0,68	0,71

TABLE 2. Conchological terminology, based on the indexes of Table 1.

Slenderness index (SB/SH)		Body whorl height index (BH/SH)		Aperture height index (AH/SH)		Aperture breadth index (AB/SB)	
very slender	< 0.350	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	0.426–0.500	large	0.61–0.66	long	> 0.38	very wide	> 0.70
very obese	> 0.50	very large	> 0.66				

Results

Geological and paleontological setting

1. Sedimentary and stratigraphic descriptions

The Mancha de La Laja section (Fig. 1) is located on the northwest coast of Tenerife (Canary Islands; 1 km^2 UTM coordinates: 28RCS6758), at 20 m a.s.l., intercalated between two basaltic Pleistocene lava flows (Araña *et al*, 1978). The top of the aeolian deposit studied is overlain by a layer of ignimbrites belonging to the Cañadas Edifice (Ancochea *et al*. 1990, 2000), which last volcanic activity (C-III phase) was dated by K/Ar and Ar/Ar between 600-130 ka (Cantagrel *et al*. 1999). Thus, the fossil site studied is older than 130 ka.

This section shows two alternation cycles of aeolian sands and reddish clayey palaeosols, the last developed when the sands were stabilizing. These cycles can be related to the paleoclimatic records of the area.

The Quaternary dune deposit studied has a total outcrop length of ca. 100 m and a maximum thickness of 15 m. Two dune-formation episodes (units I and II) were identified (Fig. 1B). Unit I (first dune-formation episode) is ca. 3 m thick, with 3 fossiliferous levels, defined and numbered TL-1 to TL-3 from bottom to top. The oldest level (TL-1) consists of well-cemented cross-bedded grayish sands. TL-2 is a deposit of massive yellowish sands (Fig. 2) and is subdivided into several beds by the presence of a discontinuous calcareous crust. These aeolian deposits contain land snail shells, ichnofossils (fossil bee brood cells) and some remains of reptiles (a giant *Gallotia*) and birds (García Talavera *et al.* 1989; Castillo *et al.* 2000). The upper limit of this unit is a palaeosol (TL-3) which belongs to a humid episode.

The second dune-formation episode (Unit II) consists in ca. 12 m of main cross-bedded organic sands. Two beds of greyish sands (TL-4 and TL-6) separated by a vast deposit of yellowish sands (TL-5) can been differentiated. The upper limit of this unit (TL-7) is a palaeosol with fewer land snail shells than the other beds.

The presence of an alternating fossiliferous aeolian deposit and palaeosols in this locality suggests that two dry-wet climate cycles occurred. Nevertheless, the presence of several calcareous crusts in TL-2 indicates short warm periods intercalated in the oldest dry cycle, with rainfall and hot temperatures. These climatic conditions advanced the first wet period represented by the first palaeosol.

2. Paleontological setting

A preliminary sampling was carried out in TL-1 and TL-2 beds. The fossil shell remains of Mancha de La Laja are scattered in the sand matrix (< 0.1 bioclasts/cm^2 in TL-1 and <0.03 in TL-2). The percentage of fragmented shells in TL-1 is greater than that of TL-2 (breakage: 42.5% and 31%, respectively). The majority of land snail shells are complete at the top of TL-2 and the low part of the palaeosol (ca. 80%), and the fragments have practically no edge rounding. Furthermore, several shells have good color preservation and shell composition is aragonitic in all cases. Therefore, they did not undergo fossil diagenetic processes, except carbonate precipitation crusting during the arid seasons. X-ray diffraction analysis confirming that shell composition is aragonite in all the cases, analogous to that of current individuals.

On the basis of taphonomic properties, two types of concentrations of land snails could be identified: A) the highest percentage of shell fragmentation in the massive sands of TL-1 indicates a sedimentological concentration (Kidwell *et al.* 1986) where the wind transport is the main agent responsible for accumulation. B) the preservation of the colour pattern and original shell mineralogy indicates a rapid burial and a biological concentration of land snails in TL-2 (Castillo *et al.* 2003). These results allow us to deduce that the land snail assemblages were concentrated by the influence of high aeolic energy, underwent quick burial and were scarcely displaced from their original habitat, being Parauthocthonous-authocthonous fossil assemblages, according to Kidwell *et al.* (1986) classification.

Systematics

Enidae B. B. Woodward, 1903

Woodward (1903): 354, 358; I.C.Z.N. (2003), Opinion 2018.

Genus *Napaeus* Albers, 1850

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

Napaeus lajaensis sp. nov.

Type material: Holotype (Fig. 4): TFMC (MT 0381). Leg. C. Castillo and Y. Yanes (27-01-2004). Paratypes: 8 shells and several fragments collected between 2001 and 2004 (AIT).

Type locality: Mancha de La Laja, Bajamar (Tenerife, Canary Islands; UTM coordinates: 28RCS6758 [28º 54 16N, 16º 35 94W]; 10-15 m altitude).

Stratigraphy: The new species has been found at the bed top of TL-2 (unit I), belonging to the Pleistocene.

Etymology: This species is named after its type locality.

Diagnosis: Small, slender *Napaeus* with body whorl shell laterally 45°- 52° tilted, angle vertex located on left side of very prominent spiral, semicylindrical rib (*torus*). Body whorl basis with one second spiral *torus*, surrounding partially umbilicus. Aperture laterally protruding because of body whorl inclination.

Description (Figs. 4 A, B; Table 1): Shell small, dextral, slender (SB/SH index), conical, with 6½-7 slightly convex whorls (almost flat), slightly marked suture. Body whorl intermediate (BH/SH index) and protoconch smooth, with 1½ whorls.

A very prominent spiral, semicylindrical rib (*torus*) begins over aperture parietal side running over near entire body whorl, ending dorsally just before aperture palatal lip. Body whorl laterally tilted, forming 45°-52° angle with columellar axis, angle vertex located on left side of spiral *torus* (Fig. 3). Second spiral *torus* appearing on basis of body whorl, surrounding partially umbilicus; shorter, wider than first one.

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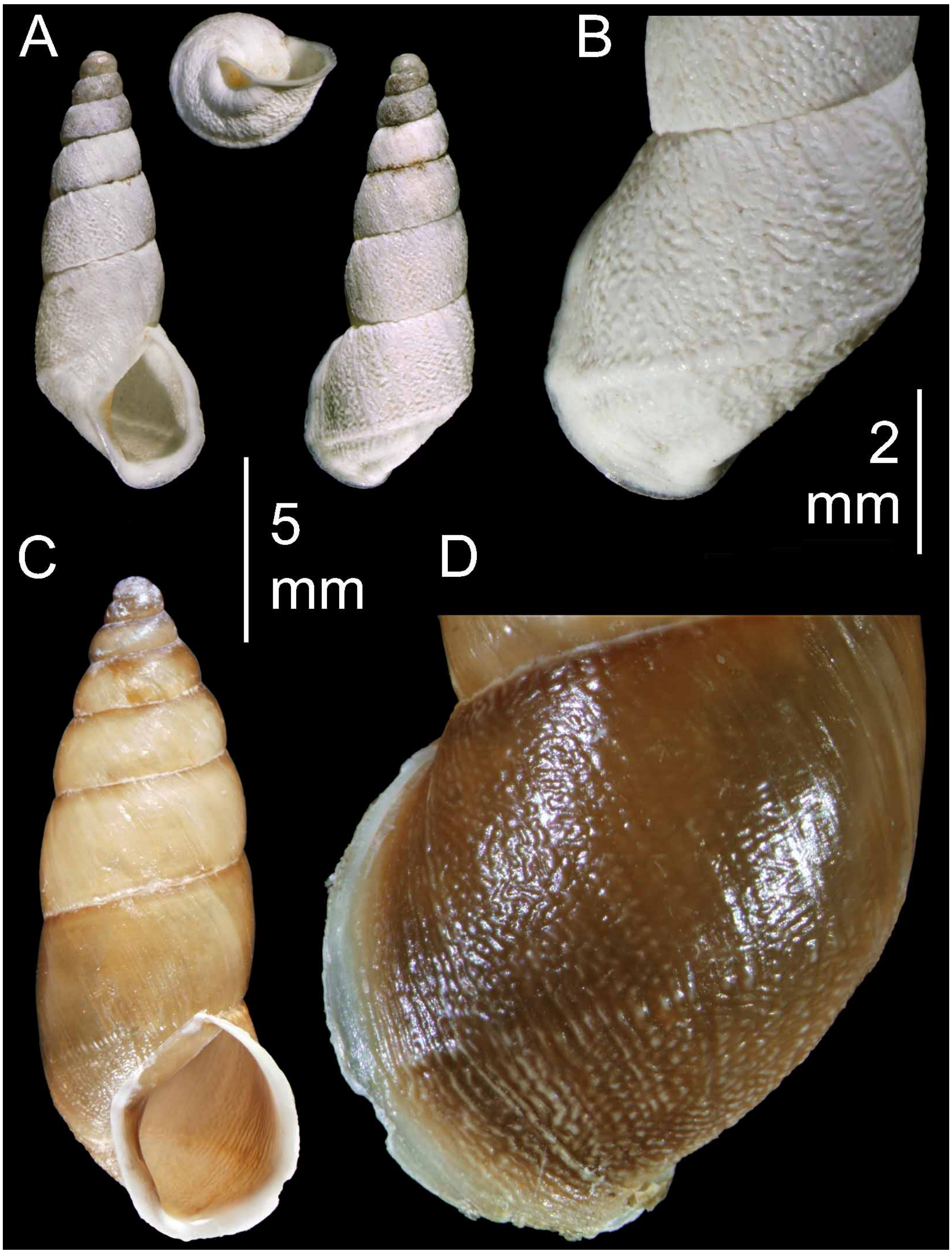

FIGURE 4. Shells. A, B: *Napaeus lajaensis*, holotype. C, D: *N. helvolus*, a specimen from Bajamar (Tenerife).

Aperture edentate, short, very wide (AH/SH and AB/SB indices, respectively), laterally protruding because of body whorl inclination. Aperture curved, slightly angular at union of columellar, palatal edges. Columellar side of aperture forming 17°-28° angle with columellar axis. Discontinuous peristome expanded as lip, better developed, reflected in

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lower portion of palatal edge, columellar lip not covering the umbilicus. Small callosity appearing at union of parietal-palatal area.

Ornamentation characterized by radial oblique striation, with varying regularity in early whorls. Starting from third whorl, shell with some ribs regularly disposed but majority of ribs sinuous, irregularly undulating, frequently broken, also connected with adjacent ribs, producing reticulation surrounding small, irregular depressions. This ornamentation decreasing or even disappearing at top of spiral ribs on body whorl.

Remarks: *Napaeus lajaensis* is the oldest *Napaeus* species found in the Canary Islands. It differs from each other *Napaeus* species in the following shell character states: A) body whorl laterally tilted, B) presence on the body whorl of a very prominent spiral, semicylindrical rib (*torus*) beginning over the parietal side of the aperture and ending dorsally just before the palatal lip, and C) presence of a second spiral *torus* on the body whorl basis, surrounding partially the umbilicus. Of the remaining *Napaeus* species, only *N. helvolus* (Webb & Berthelot, 1833) (Figs. 4 C, D), a species living on the same area, has a shell with a single spiral riblet on the body whorl located similarly to the main *N. lajaensis* spiral *torus*, but scarcely differentiated.

The fossil assemblages of terrestrial gastropods from Mancha de La Laja are composed of eight species of which *N. lajaensis* and *Hemicycla collarifera* Boettger, 1908, are currently extinct while the others also have living specimens: *Plutonia lamarckii* (A. Férussac, 1821), *Canariella hispidula* (Lamarck, 1822), *Xerotricha* sp., *Pomatias laevigatus* (Webb & Berthelot, 1833), *Hemicycla consobrina* (A. Férussac, 1821) and *Canariella planaria* (Lamarck, 1822). The last three species are the only living today on the area whereas the first two species are restricted to a higher altitude and a more humid climate. This different faunistic composition suggests that a drier, semiarid microclimate is present today, with scarce precipitation, high temperatures (less than 300 mm and 20ºC, respectively) and slight herbaceous vegetation-spread, near the sea coast.

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