Caracollina lenticula, *C. virilis* and *C. huloti* (Gastropoda: Trissexodontidae): the existence of three species of *Caracollina* H. Beck, 1837 on the Canary Islands

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Key words: *Caracollina*, Trissexodontidae, Macaronesia, Mediterranean area.

Because of the suspicion that *Caracollina lenticula* on the Canary Islands concerns more taxa, fossil and extant shells, as well as living specimens, were compared conchologically and anatomically. In addition to type material, specimens from the Canary Islands, Cape Verde Islands and Andalusia were included in the study. Three previously described species were identified: *Caracollina lenticula*, *C. virilis*, and *C. huloti*. These three species are being redescribed.

INTRODUCTION

In 1821, A. Férussac gave for the taxon *Helix* (*Helicigona*) *lenticula* only for the variant α the very limited description "striis valde notates" [= prominently striated] but no description for the nominate species at all. He cited specimens from Spain (Andalusia and Tenerife, Fig. 1a) and mentioned the variant from Egypt (Alexandria, Fig. 2) as well (Férussac, 1821: 37).

In a similar case with *Helix* (*Helicigona*) *barbata* Férussac, 1821, Kadolsky (1990: 101) commented on the current usage of the Greek lower-case letters for infra-specific categories, where in that case the species description was missing as well, and the name should therefore be invalid. The ICZN accepted this reasoning (Opinion 1690 from 1992), so it also applied to *Helix* (*Helicigona*) *lenticula*, which is 'described' on the same page. As no description was given for *H. lenticula*, and the variant was not named, the Férussac taxon is considered a nomen nudum (Opinion 1690 from 1992; Bank et al., 2002: 172; Bank, 2011: 20). The consistent application of the Code as stated by Kadolsky (1991: 244) therefore invalidates the later reasoning of Holyoak et al. (2019: 146-147) to consider Férussac 1821 as the author of *C. lenticula*.

Helicella ferruginea Risso, 1826 (Fig. 3), was wrongly considered a synonym of the invalid *Helix lenticula* A. Férussac by Caziot (1910: 122; 1919: 163). Even that *ferruginea* is the older name for what was later described by Michaud as *Helix lenticula*, regarding ICZN (1999) Article 23.9 (Reversal of precedence) the name should be supressed as a nomen oblitum as it never was used as a valid name for the species of Michaud and therefore will not become available. There are four syntypes present in MNHN; one of the syntypes is a *Trochulus* species. We have selected a lectotype from one of the remaining three syntypes.

Lowe (June 1831) provided a distinctive description of *Helix* (*Helicigona*) *subtilis* (Fig. 4), but Pfeiffer (1847: 212) and subsequent authors considered this name a synonym of *H. lenticula* A. Férussac, 1821. Although this name is older than the later accepted name *Helix lenticula* Michaud, 1831, *H. subtilis* has only been used as a synonym and has not been used as a valid name after 1860. As with *Helicella ferruginea*, Article 23.9 (Reversal of precedence) comes into place, making *H. subtilis* a nomen oblitum as well.

Michaud (December 1831: 43) was the next to provide a distinctive description for *Helix lenticula* (Figs 5-6). He mentions a few countries and Collioure (Pyrénées Orientales, France) as type locality. Next to the lectotype (Fig. 5) there are three paralectotypes, one with an unusually high teleoconch (Fig. 6). Prieto et al. (1993) noted that the 7 whorls in the description of Michaud must be a mis-

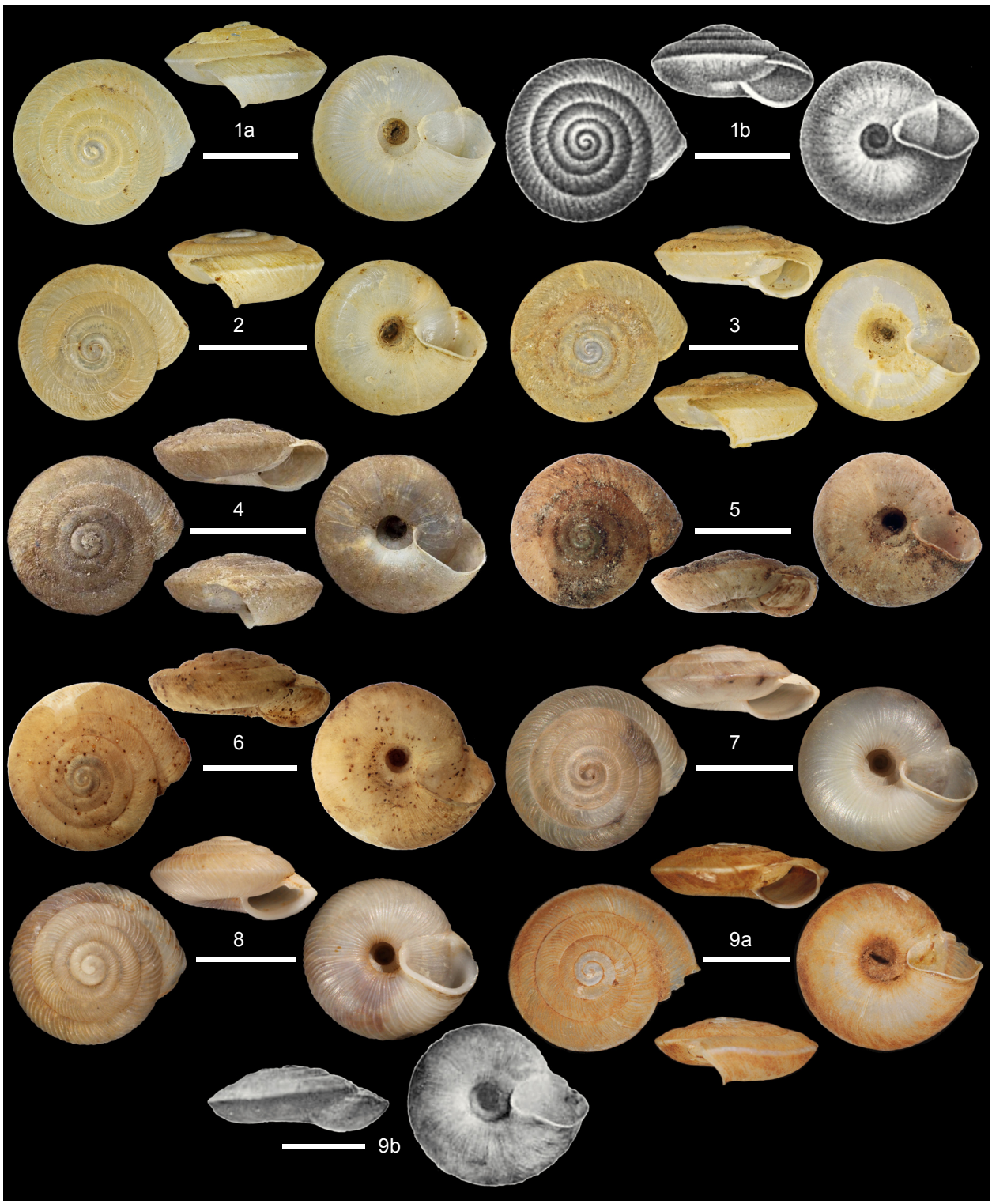


Fig. 1-14. *Caracollina* species. **1-9:** Type specimens; **10-14:** Extant and fossil specimens. **1a.** Lectotype of *Helix lenticula* A. Férussac, 1832, MNHN-IM-2000-28787, Andalusia – a representative of the large species. Photos PGB. **1b.** Original figure of *Helix lenticula* A. Férussac, 1832: pl. 66* fig. 1 (no locality mentioned in legend). **2.** "Type" of *Helix lenticula* var. α – A. Férussac, 1821, MNHN-IM-2000-28786, Alexandria (Egypt) – a representative of the small species. Photos PGB. **3.** Lectotype *Helicella ferruginea* Risso, 1826, MNHN-IM-2000-29117. Photos PGB. **4.** Syntype *Helix* (*Helicigona*) *subtilis* R. T. Lowe, 1831, NHMUK 1948.7.8.53, original from pl. V fig 13 in Lowe (1831) [= pl. 7 fig. 2 in Oliver et al., 2024]. **5.** Lectotype *Helix lenticula* Michaud, 1831, Collioure, MdCL 45002383 spmn 2. Photos CA. **6.** Paralectotype *Helix lenticula* Michaud, 1831, Collioure, MdCL 45002383 spmn 4. Photos CA. **7.** Syntype *Helix lenticula* var. *major* Mousson, 1872, TF, ZMZ 508700. Photos EN. **8.** Syntype *Helix lenticula* var. *virilis,* FV, ZMZ 508728. Photos EN. **9a.** Lectotype *Caracollina huloti* Pallary, 1913, ANSP 248297, Imi n' Takandout. **9b.** *Caracollina huloti* Pallary, 1913 figured in Pallary, 1922, pl. 5 figs 23-24 (from kaïd Embareck). Scale bars = 5 mm.

take because only 4.5 whorls are visible in the figure. Most authors quote Michaud as the author, but Férussac's authorship is also still used incorrectly. The species of Michaud is a relatively small species.

A year later, *Helix* (*Helicogena*) *lenticula* A. Férussac (thus not var. α!) was illustrated from three views by Férussac (1832: pl. 66* fig. 1; our Fig. 1b), and therefore Férussac nomenclaturally validated his species in 1832. This is a relatively large species, and much to our surprise, it turned out that it is different from *Helix lenticula* Michaud, 1831. So far, it was assumed that *Helix lenticula* Michaud, 1831 was the correct (i.e. older) name for *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832.

In the same decade, the species of Férussac is included in the genus *Caracollina* H. Beck, 1837. In a footnote, Ehrenberg (1831) already mentioned *Caracollina* as a name but did not provide a description and did not mention a species. It is a nomen nudum and therefore not available. Since *Caracollina* H. Beck, 1837 is not preoccupied by *Caracollina* Ehrenberg (1831), the substitution name *Caracollo* Strand, 1943 is not valid.

Beck (1837) mentions *Caracollina* as a subgenus in the tribe Helicida and the genus *Helix* Linnaeus, 1758, cites Férussac as the author of *Caracollina lenticula* and listed 11 taxa under the name *Caracollina*. The type species (*lenticula* A. Férussac) is selected by Herrmannsen (1846: 173).

Mousson (1872: 66-67) mentions two variations of *Helix lenticula* A. Férussac: var. *major* from Tenerife (Fig. 7) and var. *virilis* from Fuerteventura (Fig. 8). Although var. *major* has characteristics of the large specimens, the variant name '*major*' of Mousson, 1872 is not available, as the name *Helix major* is preoccupied already by a multitude of homonyms introduced between 1800 and 1870, in fact 26 times (see Sherborn 1928: 3831, Ruhoff 1980: 361).

Several new genera have been proposed: *Lenticulana* Fagot, 1890 (: 242), *Lensiana* Fagot, 1893 (: 176) (misspelled as *Lersiana* by Caziot (1912)), *Lenticulariana* Caziot, 1910 (: 122, 531), and *Caesarella* Pfeffer, 1930 (: 279-280). All these new names are considered junior synonyms because they are based on the monotypy of the same type species, *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832.

Within the Helicoidea Rafinesque, 1815, there was long uncertainty about the systematic position of the genus *Caracollina* in ranking. The genus has been placed in the Helicidae Rafinesque, 1815 – Helicodontinae Kobelt, 1904 (in Backhuys, 1975 and Kerney et al., 1983), Hygromiidae Tryon, 1866 – Ciliellinae Schileyko, 1970 (e.g. in Fechter & Falkner, 1990; Nordsieck, 1993), Helicodontidae Kobelt, 1904 (e.g. in Heller, 1993), Helicodontidae Kobelt, 1904 – Caracollininae H. Nordsieck, 1987 (e.g. in Schileyko, 2005), the Hygromiidae (e.g. in Yanes et al., 2005; Audibert & Bertrand, 2015) and the Trissexodontidae H. Nordsieck, 1987 (e.g. in Bank et al., 2001; Heller, 2009). Nowadays and in most of the references, the Trissexodontidae is considered the family of the genus (MolluscaBase).

Caracollina lenticula (Michaud, 1831) is known as a species of dry rocky habitat with a wide distribution around the Mediterranean and the Macaronesian archipelagoes (Azores, Madeira and the Canary Islands) and the Cape Verde Islands (e.g. Backhuys, 1975: 40, 223, 263; Kerney et al., 1983: 304; Fechter & Falkner, 1990: 218, 219-fig 3; Prieto et al., 1993; Heller, 1993: 324; Falkner, Ripken & Falkner, 2002: 48; Bank et al., 2002: 117, pl 20 - figs 1-2, 172; Yanes et al., 2005: 133*; Talaván Serna & Talaván Gómez, 2008: 214*; Talaván Serna & Talaván Gómez, 2010: 133; Gargominy & Ripken, 2011: 84; Groh, 2012: 50; Welter-Schultes, 2012: 484; Audibert & Bertrand, 2015: 166; Cadevall & Orozco, 2016: 529; Bank et al., 2025; MolluscaBase; Malacowiki). In references with an asterisk, photos and measurements seem to confirm that also large specimens from > 9 mm are found on the Canary Islands. In recent literature is assumed that there is only one species of *Caracollina* in Europe including Macaronesia. Prieto et al. (1993) provide information of *C. lenticula* on the microsculpture and variation in the genitals from different areas in Spain. The only other accepted *Caracollina* is *C. huloti* Pallary, 1913 (Figs 9a-b), described from Morocco. Ortiz de Zárate Rocandio & Ortiz de Zárate López (1961) placed *huloti* in *Oestophora* Hesse, 1907. Based on anatomical differences in the genitalia, Nordsieck (1993) placed *huloti* back in *Caracollina* and created the subgenus *Paroestophora* for this species and included *Helix tarnieri* Morelet, 1854 as well. Puente (1996) and Ruiz et al. (2008) confirm that *huloti* belongs to *Caracollina* (*Paroestophora*). Anyhow, *Oestophora* is now considered as the genus for *O. tarnieri* (Cadevall & Orozco, 2016; Holyoak et al., 2021). Razkin et al. (2015) demonstrate with molecular research that *Oestophora* should even be considered a different tribe than Caracollinini and thus confirm that *O. tanieri* is not a *Caracollina* (*Paroestophora*). Bank et al. (2025: 452) state that the subgeneric separation between *C. lenticula* and *C. huloti* is based on anatomical criteria, as the shell is hardly different.

The recognition of two clearly different forms on the Canary Islands led to the suspicion that there are two extant species within the genus *Caracollina*. To substantiate this suspicion, syntypes and shells from various collections were examined.

METHODS

The following abbreviations for collections or persons are used: ANSP = The Academy of Natural Sciences Philadelphia, USA, AR = Anette Rosenbauer, CA = Cédric Audibert, CGD = collection Klaus Groh, Bad Dürkheim, Germany, CMB = collection Kees Margry, Boxtel, The

Netherlands, EN = Eike Neubert, IK = Ingo Kurtz, IMM = Ingrid Margry-Moonen, KG = Klaus Groh, KK = Klaus Kittel, KM = Kees Margry, MdCL = Muséum des Confluences Lyon, France, MI = Miguel Ibáñez, MNHN = Muséum national d'Histoire naturelle, Paris, France, NHMUK = The Natural History Museum, London, United Kingdom, NMBE = Naturhistorisches Museum der Burgergemeinde Bern, Switzerland, PGB = Priscilla Gaël Bourguignon, RMNH = Rijksmuseum van Natuurlijke Historie (Naturalis Biodiversity Center), Leiden, The Netherlands, TdW = Ton de Winter, ZMZ = Zoological Museum Zürich, Switzerland.

For islands, the following abbreviations are used: GR = La Graciosa, FV = Fuerteventura, GC = Gran Canaria, TE = Tenerife, LG = La Gomera, CV = Cape Verde Islands.

Abbreviations in the figures of genitalia: ab = albumen gland, as = accessory sac, at = atrium, bc = bursa copulatrix, bd = bursa copulatrix duct, bw = body wall, d = dart, ds = dart sac, e = epiphallus, hd = hermaphrodite duct, hg = hermaphrodite gland, hp = hepatopancreas, mg = mucous gland, pd = part of the diaphragm, pe = penis, pp = protruding part of the genitals, pr = penial retractor muscle, so = spermoviduct, ta = talon, va = vagina, vd = vas deferens.

The research is concentrated on shells of *Caracollina* from the Macaronesian islands, supplemented with specimens from the Cape Verde Islands, Spain and France.

For a comparison of shells, the following characteristics were investigated: The size of the protoconch in relation to the first whorl, the height of the dorsal side of the teleoconch above the keel, the convexity of the whorls, the depth of the suture, the sharpness of the keel on the body whorl, the shape of the aperture, and the shape of the umbilicus. The form of the shell is as defined by Herbert & Kilburn (2004: 67).

Using photos from the dorsal, frontal, and ventral side of 34 specimens (CMB) from LG (n = 28) and Andalusia (n = 6), measurements were taken in Adobe Photoshop. The measurements are shown in Fig. 15. Only specimens that could be unambiguously assigned to different taxa based on shell characteristics were selected; additionally, only complete specimens with a fully developed peristome were used. In addition, the same measurements were taken from photos of type specimens from Risso (1826, MNHN), Lowe (1831, NHMUK from Oliver, Groh & Audibert, 2024), Michaud (1831, MdCL), Mousson (1872, ZMZ) and Pallary (1913, ANSP from internet) (Table 1). For photos where a scale

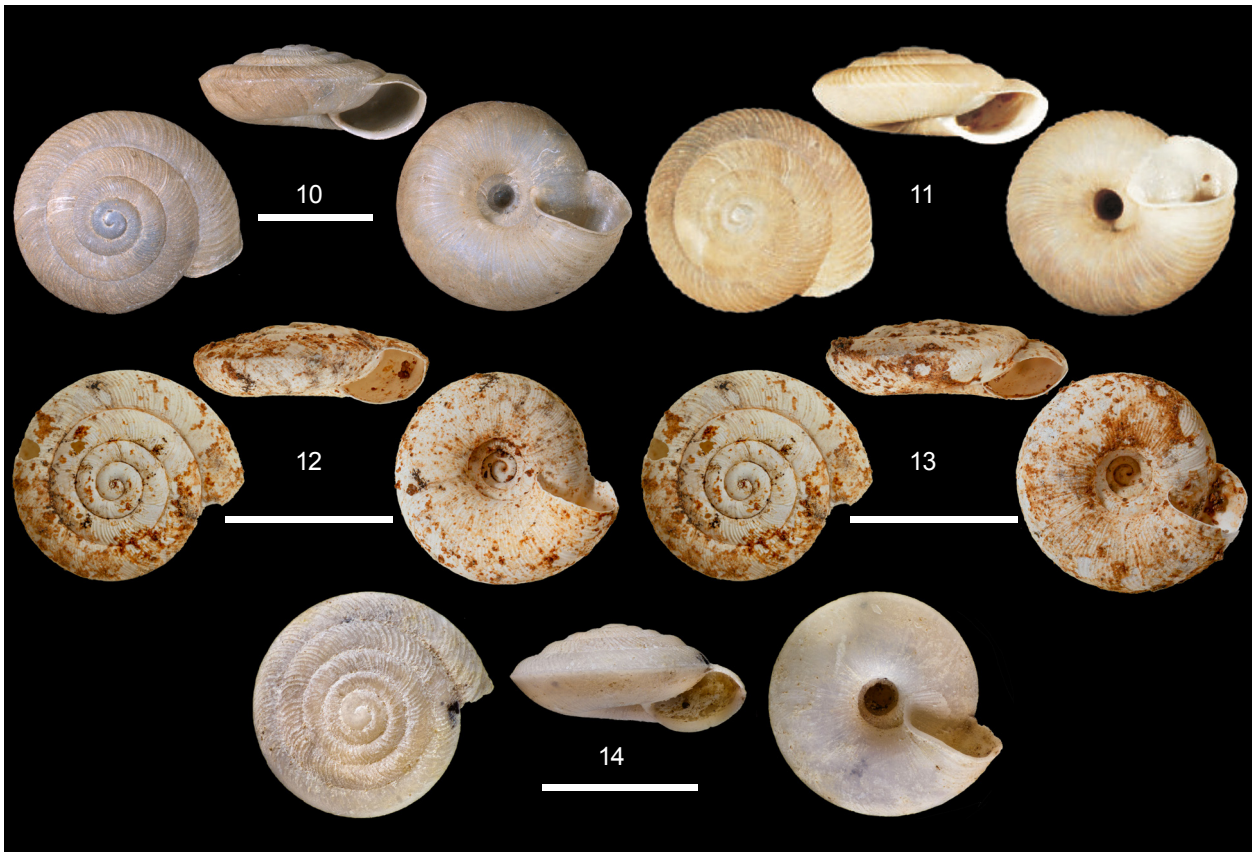


Fig. 10. *Caracollina lenticula*, topotype Collioure, RMNH.MOL.289507, photos TdW. **Fig. 11.** *Caracollina virilis?* from Yanes et al., 2005: fig 11; 2011: fig. 3J (as *lenticula*). Photo MI. **Fig. 12-13.** Two fossil specimens of *Caracollina lenticula* from Chinguarime, LG, 14.iii.2025, legit KM & IMM. Photos IMM. **14.** Fossil specimen of *Caracollina huloti* from Caleta de Milan, TF, legit KG, CGD 03530. Photos IK.

***Caracollina* species original name, author and year**	**(type) locality**	**"types" in**	**remarks**	**taxon**
Helix (*Helicigona*) *lenticula* A. Férussac, 1821	Andalusia and Tenerife	MNHN	nomen nudum	large
Helix (*Helicigona*) *lenticula* var. α — A. Férussac, 1821	Alexandria	MNHN		small
Helicella ferruginea Risso, 1826	Nice	MNHN	nomen oblitum	small
Helix subtilis R. T. Lowe, 1831	Madeira	NHMUK	nomen oblitum	small
Helix lenticula Michaud, 1831	Collioure	MDCL	nomen protectum	small
Helix lenticula A. Férussac, 1832	Andalusia	MNHN	homonymy	large
Helix lenticula var. *major* Mousson, 1872	Tenerife	NMB	homonymy	large
Helix lenticula var. *virilis* Mousson, 1872	Fuerteventura	NMB	valid name	large
Caracollina huloti Pallary, 1913	Imi n' Takandout	ANSP	valid name	large

Table 1. Type specimens of *Caracollina*.

characteristic	**"small" *Caracollina***	**"large" *Caracollina***
The size of the protoconch in relation to to the first whorl	wide	narrow
The height of the dorsal side of the teleoconch	more flattened	more elevated
The convexity of the whorls	more convex	less convex
The depth of the suture	Prominent and deep	Prominent but more superficial
The sharpness of the keel on the bodywhorl	less sharp	more sharp
The shape of the umbilicus	all whorls become progressively wider and the last whorl is more elongated	first whorls slowly increase in width, only last whorl more elongated

Table 2. Characteristics of the two taxa of *Caracollina*.

species	**width**	**height**	**whorls**
Caracollina lenticula	5.8 - 8.8 (spmn 4 = 9.7)	2.2 - 4.2 (spmn 4 = 4.2)	3.7 - 4.95 (spmn 4 = 5.20)
Caracollina huloti	7.0 - 11.2	2.2 - 5.2	4.8 - 5.8
Caracollina virilis	8.5	3.5 - 4.2	4.90 - 5.05

Table 3. Measurements of the three species of *Caracollina*.

bar was missing, the width of the shell was given on request and used as a basis for other measurements. In some cases, the angle of the shell on the photo was different and distorted, so the exact measurement had to be taken approximately. Additional photos were used from one topotype of *C. lenticula* (Fig. 10, RMNH.MOL.289507, 3.ix.1980, legit. TdW), two fossil shells from Lanzarote (CGD, Bateria, 27.iii.1997, Figs 29-30) and a specimen (Fig. 11) from archipiélago Chinijo (Yanes et al., 2005: fig. 11; 2011: fig 3J).

The diameter (D) and the height (H) of other shells (n = 248, CGD and CMB) from Andalusia (n = 6), the Canary Islands (FV (n = 46), GC (n = 11), TF (n = 57), LG (n = 110)), and Cape Verde Islands (n = 18) were taken with a caliper to the nearest 0.1 mm as explained in Fig. 15.

The counting of whorls follows Kerney et al. (1983: 21) but is not counted in quarters of a turn but in decimals by using a transparent with 20 parts in a circle.

For the radula, the jaw, and anatomical study of the genitals, five specimens (2 of the small form, 3 of the large form) from La Gomera were used (CMB). The nomenclature of the genital morphology is according to Prieto et al. (1993). The two stylophores as named by Schileyko (1991: 225; 2005: 1914-1915) refer to the mucous gland and the accessory sac. The proximal parts of the genitals are being located closer to the hermaphroditic gland and the distal parts are located closer to the genital orifice.

The living specimens, the shells, and the dissected material were photographed with a Canon EOS 7D camera with an EF 100 mm lens. Stacked images were obtained using Adobe Photoshop. To photograph the love dart, the jaw, and the radula, SEM images of the radula were made with a Jeol jsm-it510 after coating with Palladium and Platin.

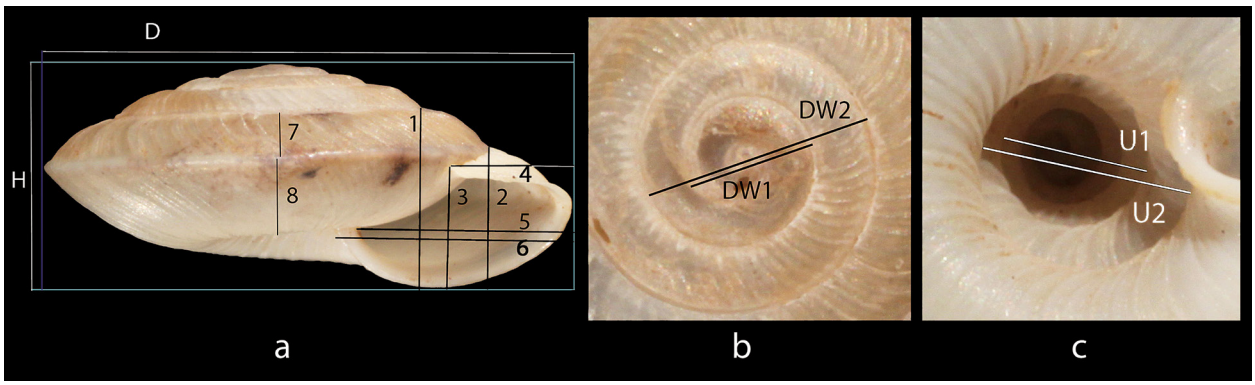


Fig. 15. Shell measurements. In Adobe Photoshop: **a:** frontal measured; **b:** dorsal measured; **c:** ventral measured. With a calliper: H and D in Fig. 15a.

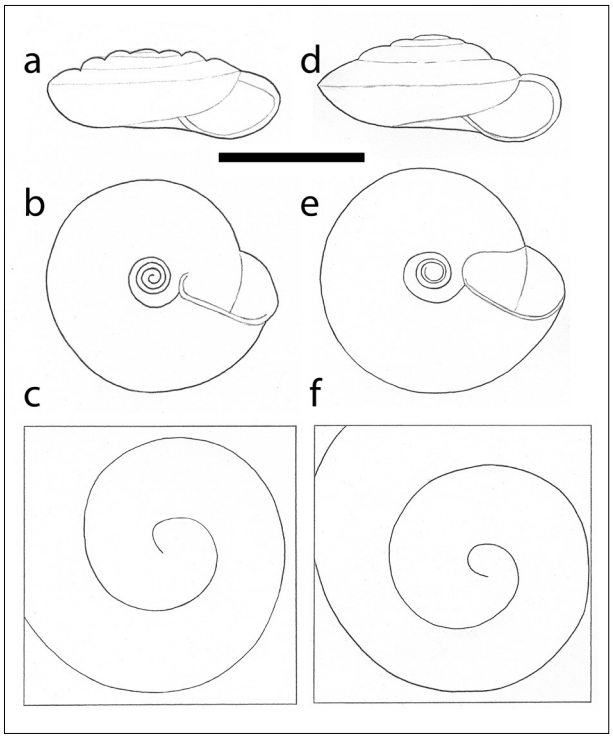


Fig. 16. Drawing of the schematic characteristics of *Caracollina*. **a-c:** *C. lenticula*; **d-f:** *C. huloti*; **a-d:** height of the apex and depth of the suture; **b-e:** whorls in the umbilicus. Scale bar a,b,d,e is 5 mm, c-f: the protoconch in a square of 2 × 2 mm. Drawing KM.

RESULTS

When comparing the shape of the shells, six characteristics can be seen as discriminating in these two groups (Fig. 16, Table 2).

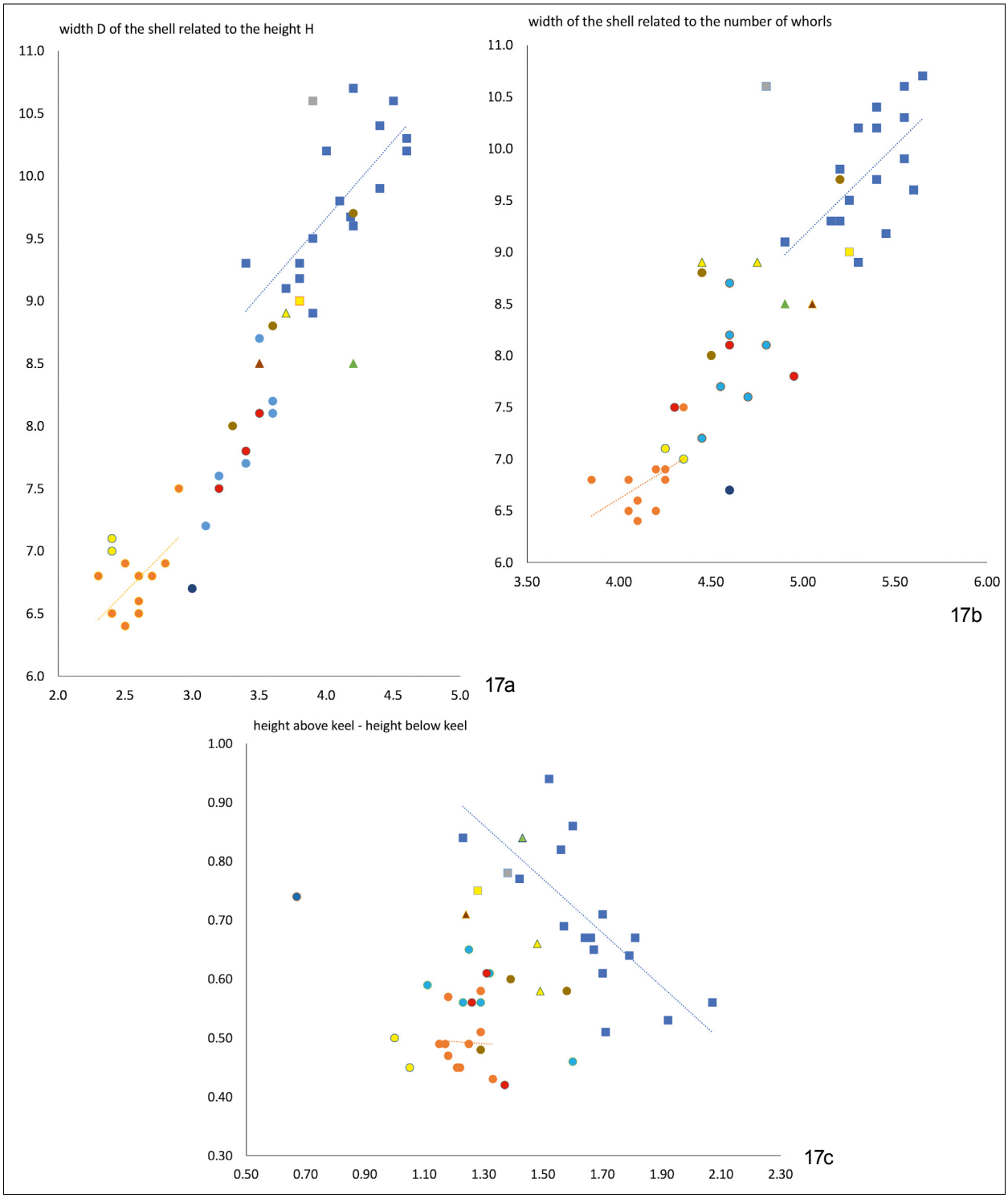
Based on the measurements of photos of 28 shells from La Gomera, two groups can be distinguished; small: specimens with less than 4.4 whorls and less than 7.6 mm wide; large: specimens with almost always more than 4.9 whorls and more than 9.1 mm wide (Figs 17a-c). Two fossil specimens from Chinguarime fit in the group of the small specimens but have an umbilicus with more evenly increasing whorls (Figs 12-13). Specimens from Andalusia have intermediate sizes but less than 5 whorls (Figs 17a-c) and correspond in characteristics to the small specimens. For the mainland, even the 'small' shells can be relatively large.

From measurements on photos of the type material it can be concluded that the type specimens of Risso (1826) (Fig. 3), Lowe (1831) (Fig. 4), and Michaud (1831) (Figs 5-6) correspond to the small taxon. The sizes of the syntypes originating from France are, like some specimens from Andalusia, sometimes relatively large (Fig. 17). One specimen of Michaud (spmn 4, Fig. 17b) even falls within the group of large specimens but still has the characteristics for the small taxon. A topotype (RMNH.MOL.289507, Fig. 10) represents the small taxon. *Helix lenticula* var. *major* (Fig. 7), *H. lenticula* var. *virilis* (Fig. 8), *Caracollina huloti* (Figs 9a-b), and the figured specimen in Yanes et al. (2005, 2011) (Fig. 11) have the sizes and characteristics of the large taxon.

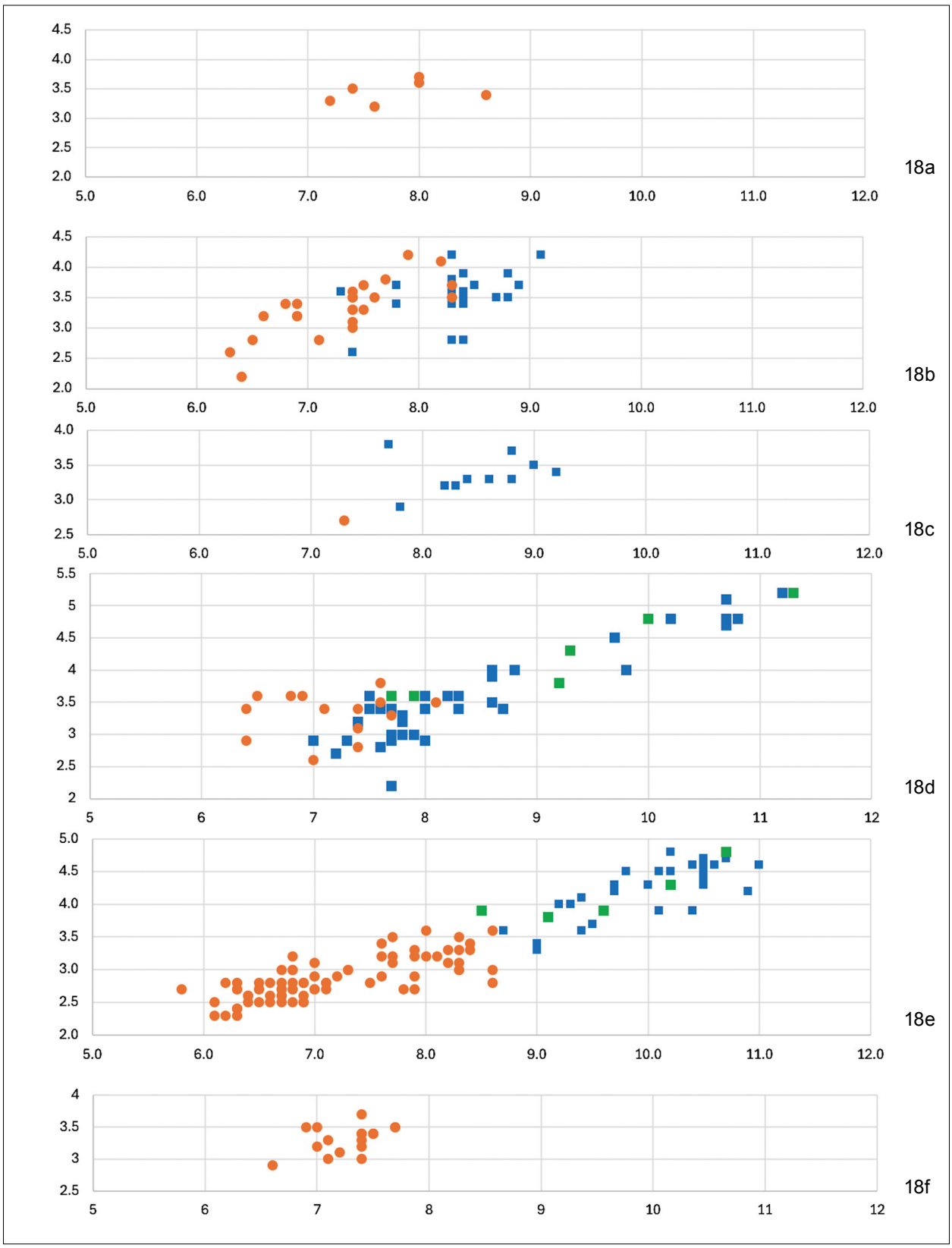
The ratio between width and number of whorls gives the best distinction. The height in relation to the width usually also gives a good distinction. With the measurements of the height of the last whorl above and below the keel, the large spmn 4 of Michaud (1831) corresponds even clearer to the small species (Fig. 17c). But, this characteristic is very dependent on the position of the shell when photographing and is therefore not a good characteristic to use.

The genitals of the small specimens (Fig 19) show similarity to images of *Caracollina lenticula* in Schileyko (2005: 1914-1915, fig. 2434) and the most common form in Prieto et al (1993: fig. 3).

The genitals of the large specimens (Fig. 20) show strong similarity to the images of *Caracollina huloti* in Hesse (1931: pl. 8, figs 64a-b). In addition to the strongly thickened dart sac, it is striking that the accessory sac is much thicker than either of the two branches of the mucous gland.



Figs 17a-c. Graphs with measurements and number of whorls of shells from the Canary Islands, Madeira, Andalusia, France and Morocco. **a:** width (D) of the shell related to the height (H); **b:** width (D) of the shell related to the number of whorls; **c:** height of body whorl above keel related to the height of the body whorl below keel.
Squares: the large *Caracollina* = *C. huloti*; gray: lectotype *C. huloti* Pallary (1913), Morocco; blue: *C. huloti* La Gomera; yellow: type specimen *H.* var. *major* Mousson (1872), Tenerife.
Triangles: the large *Caracollina* = *C. virilis*; green: *H.* var. *virilis* (Mousson, 1872), Fuerteventura; yellow: *C. virilis*, Lanzarote, CGD redbrown: '*C. lenticula*' = cf. *C. virilis* from Yanes et al. (2005; 2011), Chinijo archipelago.
Circles: the small *Caracollina* = *C. lenticula*; brown: 4 syntypes *C. lenticula* Michaud (1831) and topotype RMNH, Collioure, France; orange: *C. lenticula* from La Gomera; yellow: *C. lenticula* fossil from La Gomera; blue: *C. lenticula* from Andalusia; dark blue: syntype *H. subtilis* Lowe (1831), Madeira; red: lectotype and 2 paratypes *H. ferruginea* Risso (1826), Nice, France.



Figs 18a-f. Measurements with caliper of the height (H) related to the width (D) of *Caracollina* shells from Andalusia (AN), the Canary Islands (FV, GC, TF, LG) and Cape Verde (CV). **a:** Andalusia; **b:** Fuerteventura; **c:** Gran Canaria; **d:** Tenerife; **e:** La Gomera; **f:** Cape Verde. Square: the large *Caracollina* = *C. huloti*, ■ blue = extant, ■ green = fossil; circle: the small *Caracollina* = *C. lenticula*, ● orange = extant.

The conclusion is that the syntypes of Michaud (1831) belongs to the small species and therefore retains the name *Caracollina lenticula*. For the large taxon, only *Helix lenticula* var. *virilis* and *Caracollina huloti* Pallary, 1913 remain. *Helix lenticula* var. *virilis* however has noticeably coarser ribs and is known as a fossil from Fuerteventura. All other large specimens resemble *Caracollina huloti*. The variation in measurements of the three species is shown in Table 3.

SYSTEMATIC PART

Superfamily Helicoidea Rafinesque, 1815
Family Trissexodontidae H. Nordsieck, 1987
Subfamily Trissexodontinae H. Nordsieck, 1987

Genus *Caracollina* H. Beck, 1837

Caracollina H. Beck, 1837: 28. Type species (selected by Herrmannsen, 1846: 173): *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832. Remark: *Caracollina* Ehrenberg, 1831 is a nomen nudum; therefore, the name of Beck is not a junior homonym.

Lenticulana Fagot, 1890: 242, Type species (by monotypy – Article 68.3): *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832. Remark: Fagot (1893: 176) later erected *Lensiana* for *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832.

Lensiana Fagot, 1893: 176. Type species (by monotypy): *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832. Remark: misspelled as *Lersiana* by Caziot (1912: 151).

Lenticulariana Caziot, 1910: 122, 531. Type species (by monotypy): *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832.

Caesarella Pfeffer, 1930: 279-280. Type species (by monotypy): *Helix* (*Helicogena*) *lenticula* A. Férussac, 1832.

Caracollo Strand, 1943: 95. Unnecessary new name (nomen novum) for *Caracollina* H. Beck, 1837.

Paroestophora H. Nordsieck, 1993: 9. Type species (by original designation): *Caracollina huloti* Pallary, 1913: 361 (monotypic).

Remarks. — Nordsieck did not realize that the type species of *Caracollina* H. Beck, 1837, is not *Helix lenticula* Michaud, 1831, but *Helix* (*Helicigona*) *lenticula* A. Férussac, 1832. The latter is a preoccupied name, and is a synonym of *Caracollina huloti* Pallary, 1913. If one wants to place the two extant *Caracollina* species into two subgenera, a new name must be created for the species of Michaud. Since the two subgenera are based on differences in the genital system only, and given the variability of the genital system of *Caracollina lenticula* (Michaud) as illustrated by Prieto et al. (1993), and given that the variability of the genital system of *Caracollina huloti* is currently unknown, we refrain from introducing a new name, until more data are available.

***Caracollina lenticula* (Michaud, 1831)**
(Figs 2-6, 10, 12-13, 19, 21c-d, 22b, 23, 25, 27)

Helix (*Helicigona*) *lenticula* var. α — Férussac, 1821: 37 (Quarto edition) [Folio edition: 41]. Locality: "Alexandrie en Égypte". Two shells (coll. Férussac) in MNHN-IM-2000-28786 (Fig. 2); two shells (coll. Olivier) in MNHN-IM-2000-29038.

Helicella ferruginea Risso, 1826: 72. Type locality: "Nos environs" [= Nice]. Lectotype (out of 4 syntypes; here selected): MNHN-IM-2000-29117 (Fig. 3).

Helix [*Helicigona*] *subtilis* R. T. Lowe, 1831 [June]: 45, pl. 5 fig. 13 (shell). Type locality: "Hab. in Maderae maritimis". Syntype NHMUK 1948.7.8.53, original from pl. V fig 13 in Lowe (1831) [= pl. 7 fig. 2 in Oliver et al., 2024] (Fig. 4).

Helix lenticula Michaud, 1831 [December]: 43-44, pl. 15 figs 15-17. Type locality (here restricted because of lectotype selection): "Collioure (Pyrénées Orientales)". Lectotype (here selected): MdCL 45002383 spmn 2 (Fig. 5).

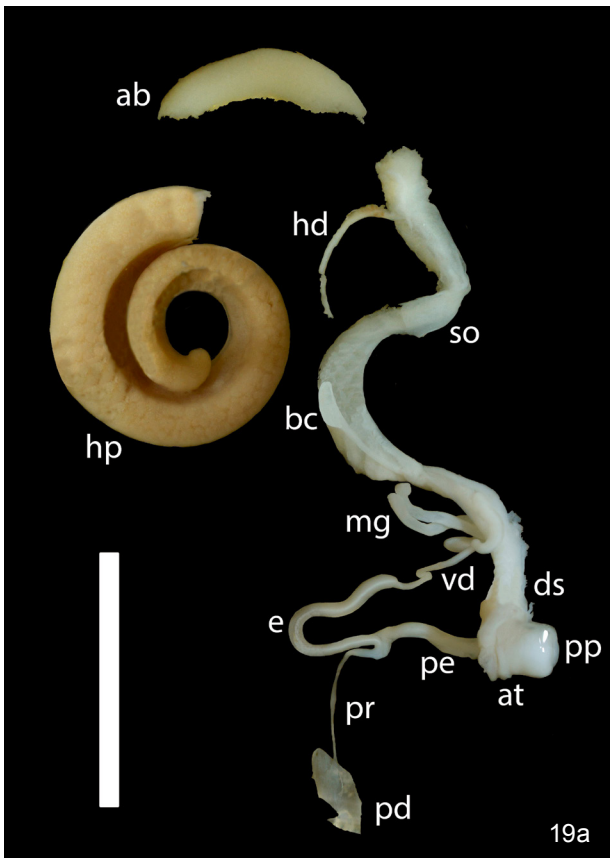
Diagnosis. — Shell with fewer than 5 whorls and usually less than 8.5 mm wide. Shell with flattened teleoconch and convex whorls with a deep suture. The mucous gland is branched into two equal parts, each almost as thick as the accessory sac. The penis retractor muscle is long. Extant and fossil.

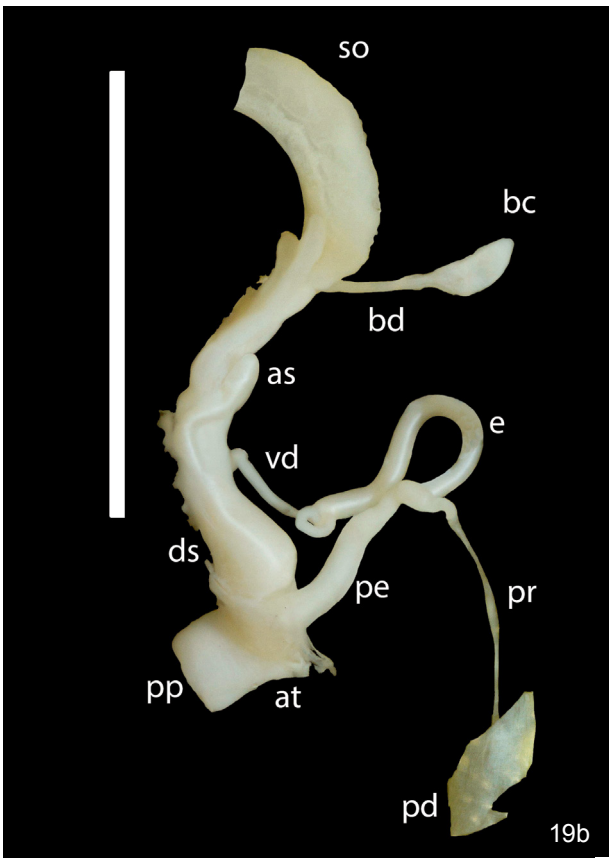
Animal (Fig. 25, 27.iii.2025, Tazo, LG, legit KM & IMM). — The animal is beige from the lower side to dark brown on the top and the head. The sole is grey brown.

Shell (Fig. 27, 20.v.2018, Tazo, legit KM & IMM. D = 6.9 mm, H = 2.5 mm, whorls 4.25). — The shell is discoidal and slightly flattened on the upper side. The shells usually have less than 5 whorls. The whorls are clearly convex and have a deep suture. The last whorl is keeled. The shells are usually less than 8.5 mm wide. In the umbilicus the gradual regular rotation of the whorls is visible. all whorls become progressively wider and the last whorl is more elongated. The start of the protoconch is usually wide compared to the first whorl. The aperture has a slightly reflected lip. The protoconch has small, interrupted, spiral crests. The teleoconch has regularly spaced radial ribs with a superposed reticulated microsculpture. The shell is light horn coloured.

Anatomy (Fig. 19, 27.iii.2025, Tazo, LG, legit KM & IMM) (see also Odhner, 1931: 85, fig 36; Giusti, 1970: 103, fig 20). — The hermaphrodite duct is highly convoluted, the talon is elongated. The bursa copulatrix is elongated oval with a long narrow duct. The vas deference becomes increasingly smaller from the spermoviduct and opens into the more than twice thicker epiphallus. At the transition to the penis there is a long retractor muscle connected to the diaphragm. The penis is thicker and hardly shorter than the epiphallus. The thickened dart sac contains one dart.

Both the mucous gland and the accessory sac open into





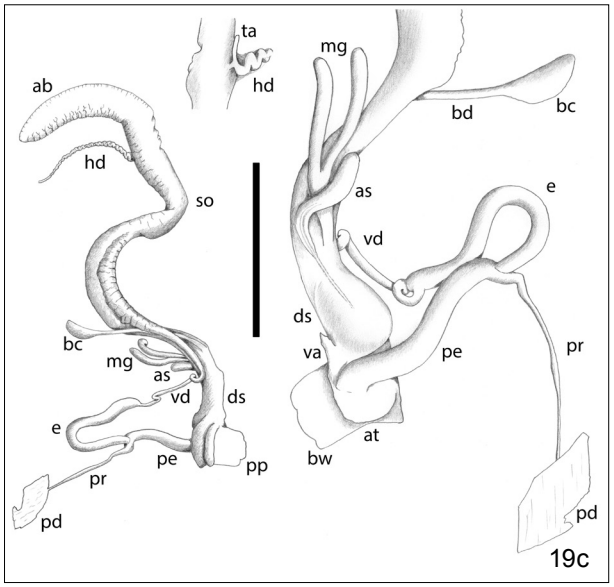


Fig. 19. *Caracollina lenticula*. Tazo, LG, 27.iii.2025. **a-c.:** genitals. Scale bar is 5 mm. See Methods section for abbreviations. Photos: a, b: IMM, drawing c: KM.

the dart sac. The duct of the accessory sac is about as wide as either of the two branches of the mucous gland. The terminal part of the accessory sac is thicker. The common part of the mucous gland is shorter than the accessory sac.

Love dart (Figs 21c-d, 5.x.2022, Antoncojo, LG, legit KM & IMM) (see also Odhner, 1931: 85, fig 36). — The love dart of an adult specimen (shell width 8.5 mm) is 0.66 mm long, curved and thickened from the base to the middle part, and tapers to a point. A foramen at the dorsal side gives access through a cavity to an opening at the top. The base is attached to tissue connected to the accessory sac.

Jaw (Fig. 22b, 5.x.2022, Antoncojo, LG, legit KM & IMM) (see also Pilsbry, 1894: pl 36 fig. 6). — The odontognathous jaw of an adult specimen (shell width 8.5 mm) is 0.43 mm wide and has about nine ribs that are irregular in thickness. A micro sculpture of coarse lines runs across the ribs, often with thicker elevations at the intersections. It has a red-brown colour.

Radula (Fig. 23a-c, shell width is 6.3 mm, 5.x.2022, Antoncojo, LG, legit KM & IMM) (see also Pilsbry, 1894: pl 36 fig. 5; Giusti, 1970: 103-104, pl 14, figs 1-3). — The central tooth has a large mesocone and two small ectocones. The approximately ten laterals are slightly larger than the central tooth and have a large mesocone and a small, wide ectocone that gradually lengthens towards the margins. The outer laterals have the beginning of a long, narrow endocone. There are approximately eight marginals in which the mesocone is barely larger than the ectocone and the long narrow endocone. Sometimes the apex of a marginal cone splits into two points.

Localities (studied material only). — Cape Verde Islands, extant: **Brava**: Mte. Fontainha. **São Vicente**: Mte. Verde. **São Nicolau**: Ribeira Brava; Mte. Gordo.

Canary Islands, fossil: **Fuerteventura**: sandpit Las Costillas E Cotillo; Bco. de los Molinos. **La Gomera**: Bco. Chinguarime E Playa Santiago; Bco. de los Zarzales, Pie de la Cuesta, Agulo.

Canary Islands, extant: **El Hierro**: 2 km W Valverde. **La Palma**: Bco. Salto de las Pinas; Mte. Tinuine; Laderos de Doña Maria; Mte. Feran do Porto; Mte. Aparicio N Los Sauces and N El Castillo S Pto. Naos; N Fuencaliente; Bco. de la Transa E Tijarafe; Pta. de los Roques below Cumbrecita; Mte. Todoque N Los Barriales. **La Gomera**: Mtña. de la Zarza 6 km SW Vallehermoso; El Faro 1.5 km NE San Sebastian; Playa de la Caleta; Playa de Hermigua; Bco. Revolcadero E San Sebastian; El Guro close to Valle Gran Rey; Arure viewpoint; Mtña Beguira; Bco. Biquillo; Lomo de Majona; between Cuevas Blancas and Riscos de Cuevas Blancas; Bco. del Rincon; Tamolde NW San Sebastian; Mtña Tesselinde; Bco. de los Zarzales; Punta de Sepultura; E and NE Tazo; Antoncojo; Playa de Arguamul; Bco. de Higuera S of Arguamul; El Molinito; Cañada de Tehetas; Taguluche; Agulo; between Jerdune and Seima; Lomo del Higueral SW San Sebastian; Bco. de Avalo; Las Casitas N of tunnel Agulo; Garimen N Epina; La Manteca N Arguayoda; Bco. de Almagrero; Pie de la Cuesta, La Mérica; Las Rosas; Exit K6 GM2; N La Dama, N of airport; Las Nuevitas E Hermigua; La Cabezada NW San Sebastian; Bco. de la Era Nueva W Vallehermoso; Roque Placeres W San Sebastian; Epina; GM3 at Hernia; Tagamiche; between Ayamosna and Roque Magro; San Pedro N Vallehermoso; Tamargada; Quise – Piedras Salen; Tejiade. **Tenerife**: Bco. del Rio; 1.5 km NW Buenavista; Los Silos; Ladera de Guïmar; Bajamar; 3 km N Los Valles, 200 m above Masca; Parque San Antonio; Taganana; San Andres. **Gran Canaria**: between Maspalomas and Artenara. **Fuerteventura**: Cortijo de Tetui; Mte. Manza W La Mantilla; Bco. de Juanicó; Playa de Inses; Isthmus de la Pared; Bco. de la Salina; 4 km W Corralejo, Mte. Caracol. **Lanzarote**: Hacha Grande; N of Bateria; Caminho Guatifay; Mtña. Blanca; Urbanicacion Famara; Bco. la Porcela/El Corillejo; El Jable 500 m N Caleta; Bco. de la Horca; El Golfo; Bco. de Fuente; Caldera Traesera; Mtña. de Guanapay above Teguise; Embalse W Mala; Las Breñas. **La Graciosa**: Agujas Grande [KK].

Spain, extant: **Andalusia**: Bco. de la Coladilla Nerja; Rio Chillar Nerja.

Caracollina huloti Pallary, 1913

(Figs 1, 7, 9, 14, 20, 21a-b, 22a, 23-24, 26, 28)

Helix (*Helicigona*) *lenticula* A. Férussac, 1821: 37 (Quarto edition) [Folio edition: 41] (without var. α). Localities: "L'Andalousie" and "Ténériffe". Nomen nudum.

Helix (*Helicogena*) *lenticula* A. Férussac, 1832: ii, pl. 66* fig. 1. Type locality (here restricted because of lectotype selection): "Andalousie". Lectotype (out of four syntypes; here selected) MNHN-IM-2000-28787 (Fig. 1a). Remark: name unavailable (junior homonym); preoccupied by *Helix lenticula* Michaud, 1831.

Helix [*Gonostoma*] *lenticula* var. *major* Mousson, 1872: 67. Type locality: "observe dans Ténérife". Syntypes ZMZ 508700/4 (labelled Sta-Cruz) (Neubert, Gosteli & Bank, 2023: 95-96, pl. 35 fig. 7) (Fig. 7). Remark: name unavailable because of multiple primary homonymy.

Caracollina huloti Pallary, 1913: 361. Type locality (restricted because of lectotype selection): Morocco, "Imi n' Takandout". Lectotype (selected by Baker, 1963: 255): ANSP 248279a (Fig. 9a).

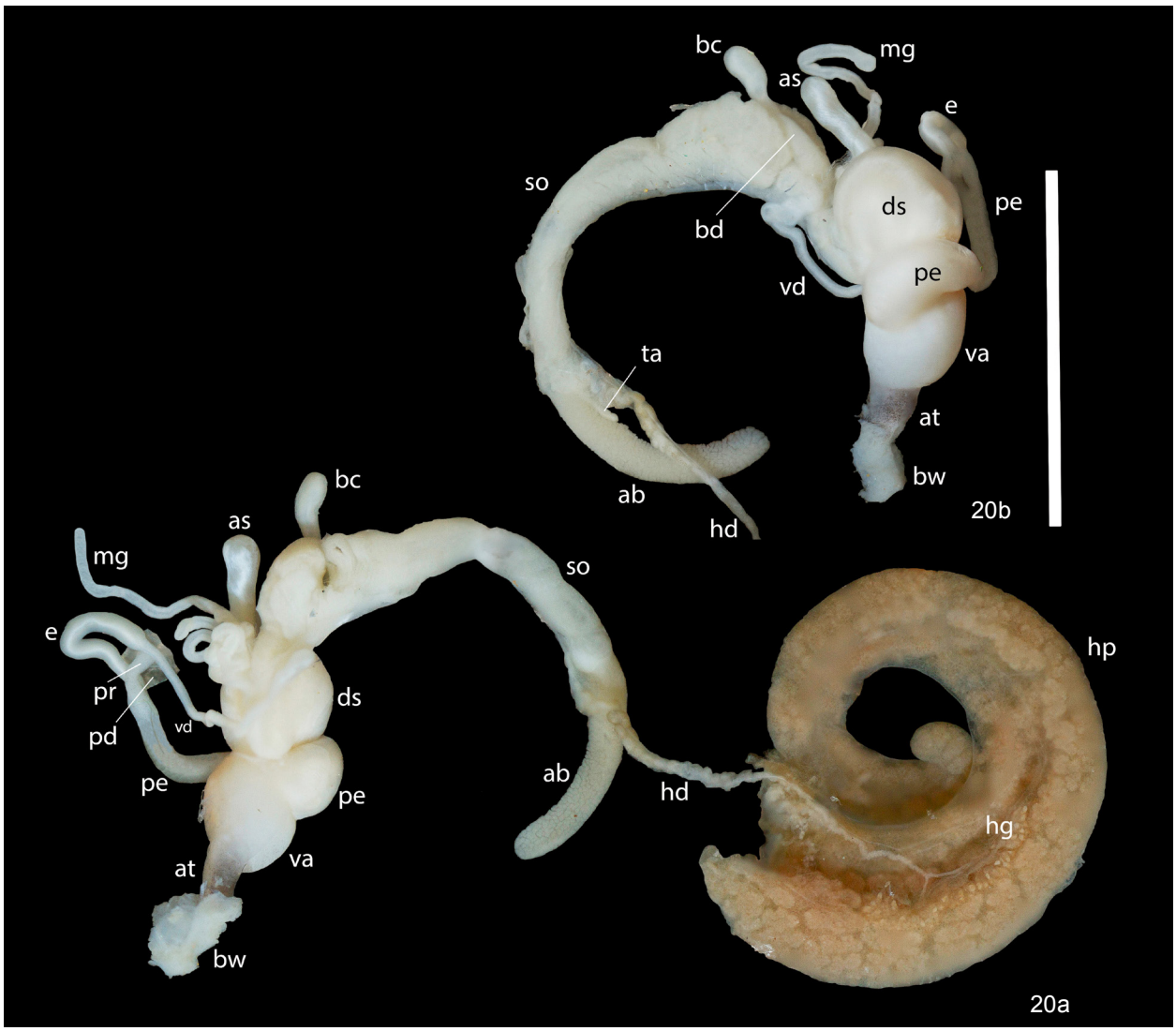
Caracollina huloti — Pallary, 1922: 105, pI. 5 figs 23-24.

Diagnosis. — A *Caracollina* species with at least 4.5 whorls. Shell usually more than 8 mm wide. The shell has slightly convex whorls and the suture is not very deep. The mucous gland is branched into two equal parts, each much thinner and longer than the accessory sac. The retractor penis muscle is stout and short. Extant and fossil.

Animal (Fig. 26, 5.iii.2025 #2, Tamargada, LG, legit KM & IMM). — The animal is beige from the lower side to dark brown on the top and the head. The sole is grey brown.

Shell (Fig. 28, 23.vi.2028, Montaña Tesselinde, LG, legit KM & IMM. D = 9.2 mm, H = 3.8 mm, whorls 5.45). — The shell is lenticular and has usually at least 4.5 whorls. The whorls are weakly concave and have no deep suture. The last whorl is keeled. The shells are usually more than 8.0 mm wide. In the umbilicus, the first whorls slowly increase in width, only the last whorl is more elongated. The aperture has a slightly reflected lip. The protoconch has small, interrupted, spiral crests. The teleoconch has regularly spaced radial ribs with a superposed reticulated microsculpture. The shell is light horn coloured.

Genitals (Figs 20a-d, shell width is 9.1 mm, 5.iii.2025 #3, Tamargada, LG, legit KM & IMM) (see also Hesse, 1931: 53, pl 8, figs 64a-b). — The hermaphrodite duct is strongly convoluted. The talon is elongated. The broad attachment to the vagina of the relatively short bursa copulatrix duct narrows towards the middle and widens terminally to the elongated oval bursa copulatrix. The long vas deference becomes increasingly thinner from the spermoviduct and opens into the more than twice as thick epiphallus. At the transition to the penis there is a very short retractor muscle that is broadly anchored to the diaphragm. The penis is thicker and longer than the epiphallus. The strongly thickened dart sac contains one dart. Both the mucous gland and the accessory sac open into this dart sac. The duct of the accessory sac is approximately as wide as either of the two branches



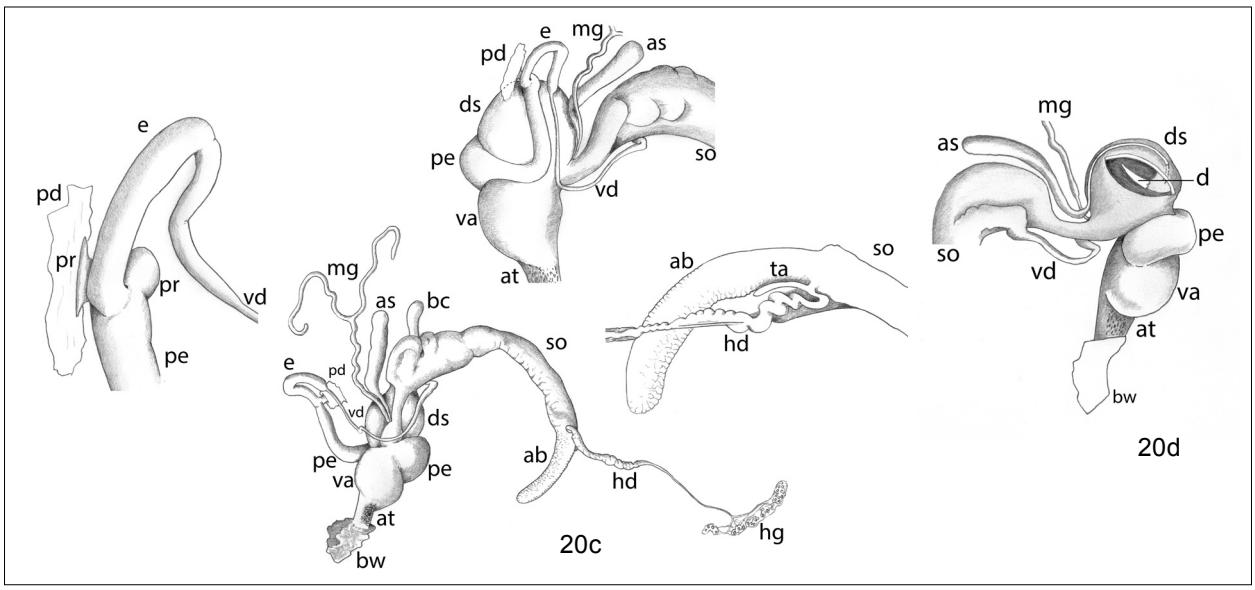


Fig. 20. *Caracollina huloti*. Tamargada, 5.iii.2025. **a-d:** genitals. Scale bar a, b = 5 mm. See Methods section for abbreviations. Photos a, b: IMM, drawings c, d: KM.

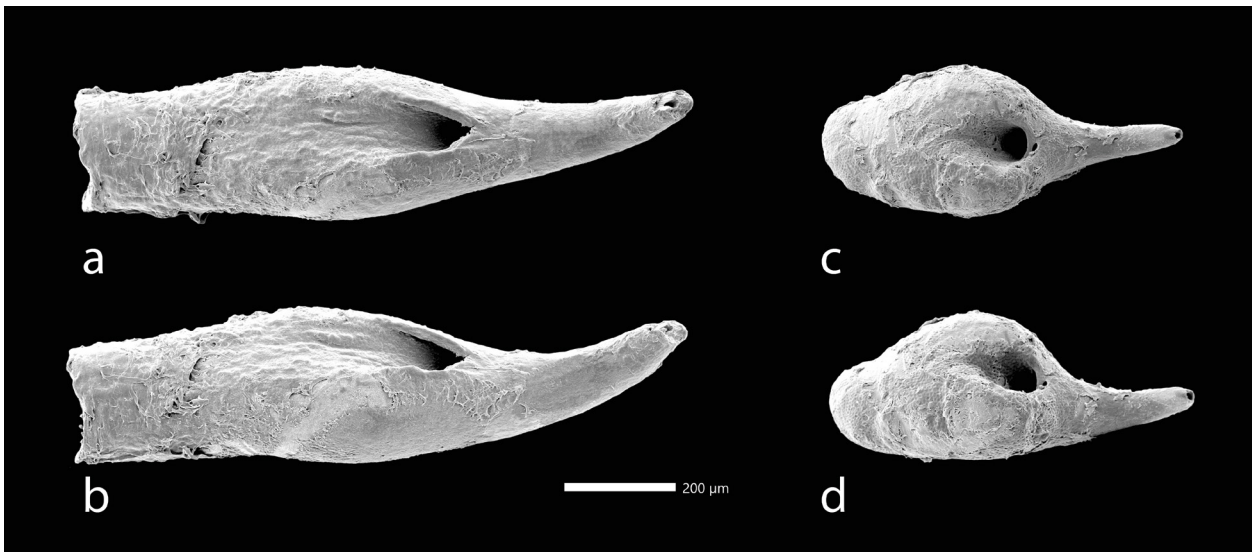


Fig. 21. Love darts of *Caracollina*. **a-b:** *C. huloti*; **c, d:** *C. lenticula*. Scale bar 200 µm.

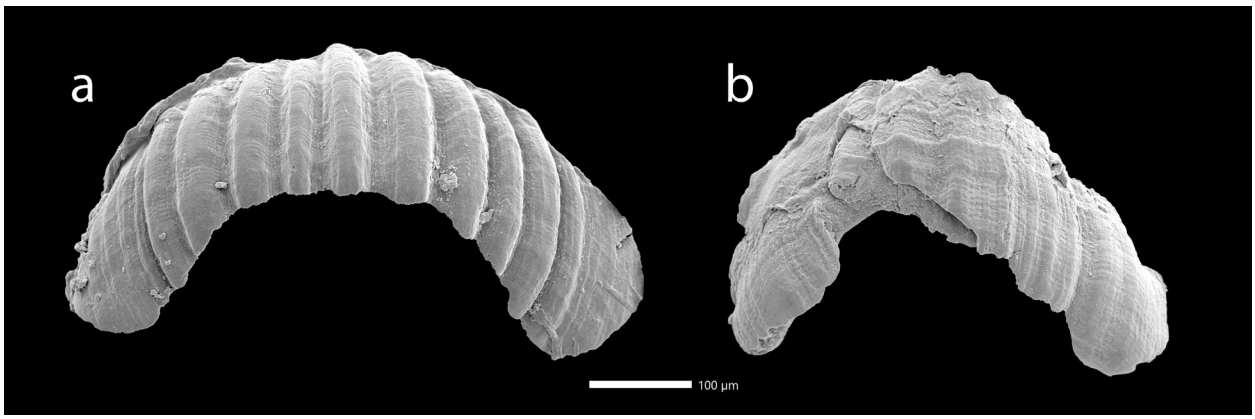


Fig. 22. Jaws of *Caracollina*. **a:** *C. huloti*; **b:** *C. lenticula*. Scale bar 100 µm.

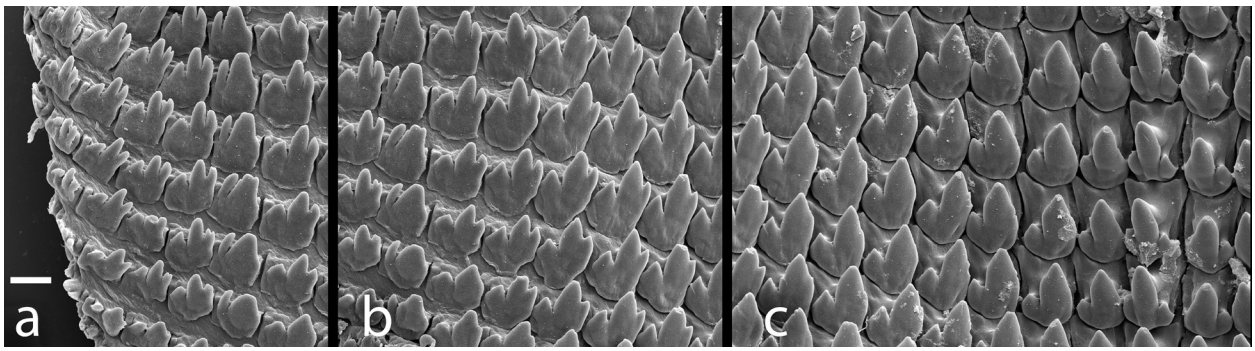


Fig. 23. Radula of *Caracollina lenticula*. **a:** marginals; **b:** transition from laterals to marginals; **c:** central tooth with laterals. Scale bar 10 µm.

of the mucous gland. The terminal part of the accessory sac is considerably thicker than the parts of the mucous gland. The common convoluted portion of the mucous gland is thin and of equal length to the accessory sac, and the two branches are each equally thin, long, and convoluted.

Love dart (Fig. 21a, b, 5.iii.2025 #3, Tamargada, LG, legit KM & IMM). — The love dart of an adult specimen (shell width 9.1 mm) is 1.14 mm long and elongated. It is somewhat thickened at the middle part, and tapers to a curved point. A foramen at the dorsal side gives access through a

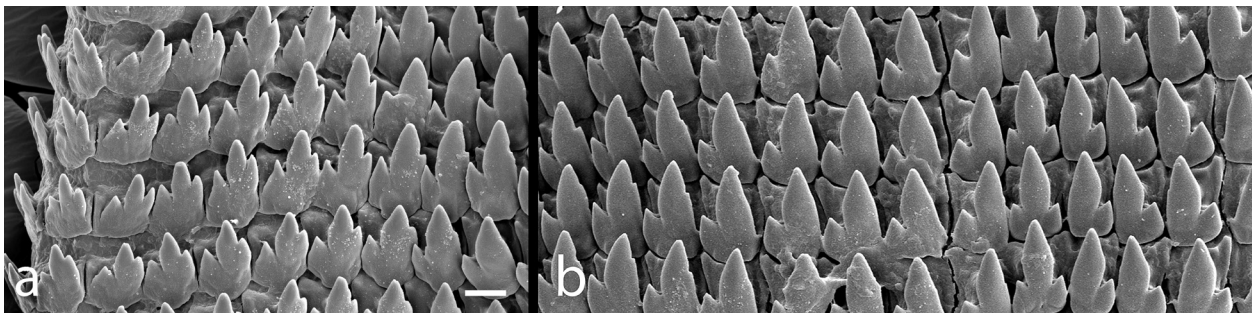


Fig. 24. Radula of *Caracollina huloti*. **a:** marginals and transition to laterals; **b:** central tooth with laterals. Scale bar 10 µm.

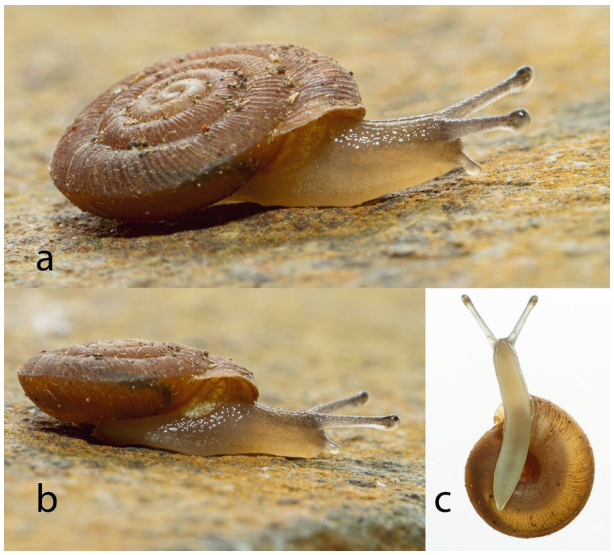


Fig. 25. *Caracollina lenticula*. Tazo, LG, 27.iii.2025. **a, b:** side view; **c:** sole of the foot. Photos: IMM.

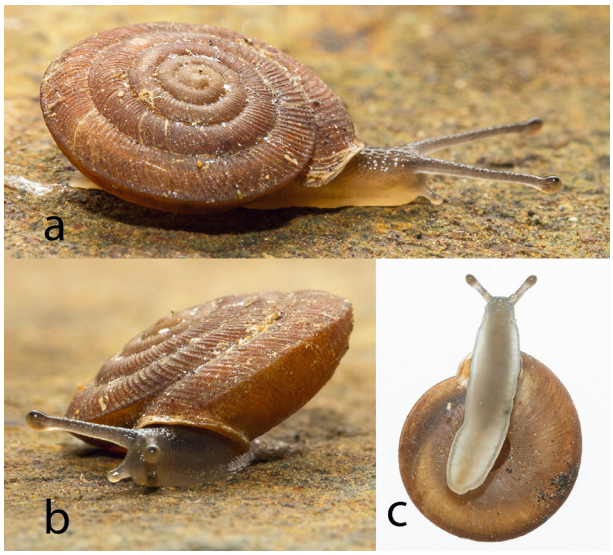


Fig. 26. *Caracollina huloti*. Tamargada, LG, 5.iii.2025. **a, b:** side view; **c:** sole of the foot. Photos: IMM

cavity to an opening at the top. The base is connected to tissue attached to the accessory sac.

Jaw (Fig. 22a, 5.iii.2025 #3, Tamargada, LG, legit KM & IMM) (see also Hesse, 1931: 53, pl 8, fig. 64c). — The odontognatous jaw of an adult specimen (shell width 8.9 mm) is 0.56 mm wide, half-moon-shaped, light horn yellow, and transparent. It has 9 larger ribs and a few lower ribs at the edge of both sides. On each rib is a fine micro sculpture of crossing lines.

Radula (Fig. 24, shell width 8.9 mm, 5.iii.2025 #4, Tamargada, LG, legit KM & IMM) (see also Hesse, 1931: 53). — The central tooth has a large mesocone and two small ectocones. The approximately 10 laterals are slightly larger than the central tooth and have a large mesocone and a wide but lower ectocone. From about the 6th lateral, the beginning of an endocone is visible. From the 9th or 10th lateral, a long, narrow endocone with a clear cusp is present. From about the 10th lateral, the mesocone becomes smaller and there is a transition to the approximately 7 marginals, where the meso-, endo-, and ectocone reach approximately the same height. Towards the verge of the radula, the margins become increasingly smaller and more irregular.

Localities (studied material only). — Canary Islands, fossil: **Tenerife**: fossil dune Bajamar; fossil dune Tejina. **La Gomera**: Las Casitas N of tunnel Agulo; Bco. de la Era Nueva W Vallehermoso.

Canary Islands, extant: **La Palma**: above Sta. Cruz; Bco. de la Transa E Tijarafe; Mte. Tinuine; Mte. Aparicio N El Castillo S Pto. Naos; Mte. Todoque N Los Barriales; Bco. Salto de las Pinas. **La Gomera**: S Lepe [AR]; Roque Bianco N Vallehermoso [AR]; Hermigua below Roque Pedro [AR]; Mtña. de la Zarza 6 km W Vallehermoso; El Faro NE San Sebastian; Playa de la Caleta; Playa de Hermigua; Bco. Revolcadero E San Sebastian; Ibo Alfaro, Hurona; Embalse de Hermigua; 1 km below Vallehermoso; 1 km above San Sebastian; near km 17 of road from San Sebastian to Hermigua; 800 m below Vallehermoso in direction Playa; Roque Cano near Vallehermoso; E Tazo, S Arguamul; between Ermita St. Clara and Epina; Bco. de los Zarzales; Bco. de la Era Nueva; Las Casitas N of tunnel

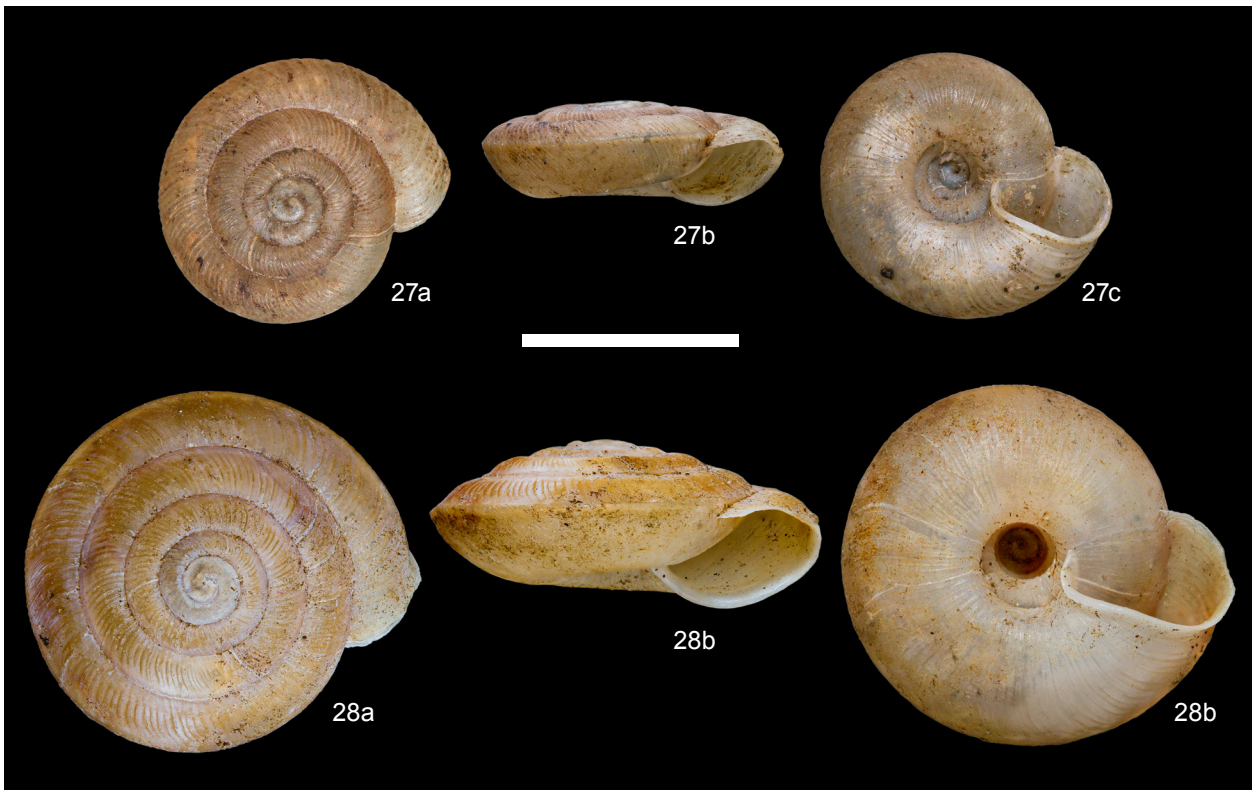


Fig. 27. Shell of *Caracollina lenticula*. Tazo, LG, alt. 250 m a.s.l., 20.v.2018, legit IMM & KM. **a:** dorsal view, **b:** frontal view; **c:** ventral view. CMB20180520.A. **Fig. 28.** Shell of *Caracollina huloti*. Montaña de la Caldera, LG, alt. 544 m a.s.l., 23.vi.2018, legit IMM & KM. **a:** dorsal view, **b:** frontal view; **c:** ventral view. CMB20180623.c. Scale bar is 5 mm. Photos: IMM.

Agulo; Mtña. Tesselinde; Alto de Toril Las Rosas; N Erm. St. Clara; Cumbre de Chijere; La Quilla N Vallehermoso; Nat. Parc El Cano; between El Cano and El Tion; between Hermigua and El Cedro; path to Pie de la Cuesta E Vallehermoso; Mtña. Alcala; Ruta 38 between Las Rosas and Agulo; Bco. de Monteforte; Pescante Agulo; Las Rosas; Montaña de la Caldera; Pie de la Cuesta; Tamargada; Bco. del Clavo; between Hermigua and viewpoint Carbonera; N of Mtña. Montañeta; Bco. del Rincon; Playa de Vallehermoso. **Tenerife**: Bco. del Rio; Ladera de Guïmar; 1.5 NW Buenavista; Mtña. Guasa; 1 Semaforo; 1, 3 and 6 km above San Andres; Bco. de las Monjas E Grenadilla; Bco. del Infierno; Mtña. Taco between Los Silos and Buenavista. **Gran Canaria**: Valle de Mogan; Bco. de Tocodonán; Palmiras Parque W Bco. de la Gato. **Fuerteventura**: Ladera N Mte. Tegú'; Huertas de las Palmas; Ladera N Pico Fortaleza; Pico de la Palma; Betancuria; Bco. del Ciervo; Bco. de Los Molinos. **Lanzarote**: Hacha Grande; N of Bateria; Caminho Guatifay; Mirador Guinate; Mtña. Blanca; doline Los Molinos; Haria; Orzola; El Golfo; Atalaya de Femes; 1 km N Ye; Eremita de las Nieves; Mirador del Rio; Mtña. de Chimia.

***Caracollina virilis* (Mousson, 1872)**

(Figs 8, 11?, 29-30)

Helix [*Gonostoma*] *lenticula* var. *virilis* Mousson, 1872: 67, 153, 162. Type locality: "Fuerteventura". Syntypes ZMZ 508727/1? + ZMZ 508728/1 (Neubert, Gosteli & Bank, 2023: 151, pl. 35 fig. 6) (Fig. 8).

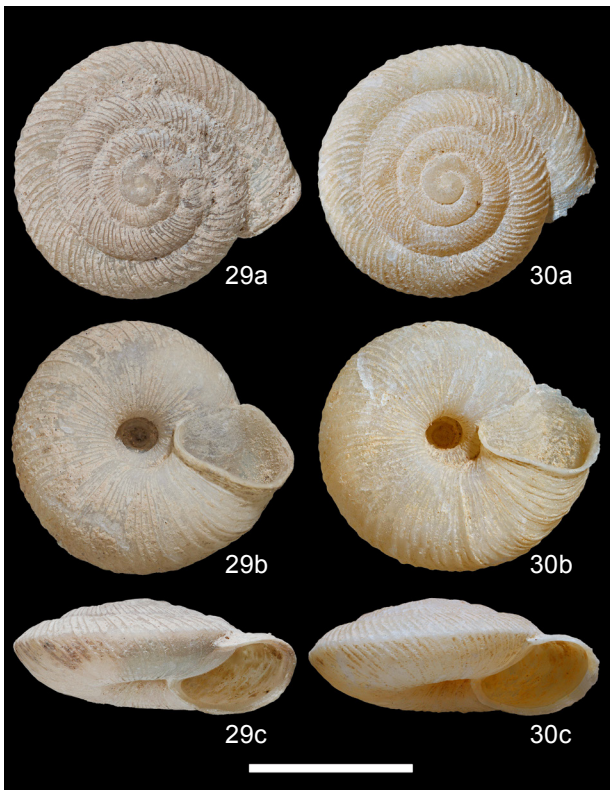
Helix lenticula var. *virilis* — Wollaston, 1878: 149, 395.

Caracollina lenticula — Yanes et al., 2005: fig. 11; 2011: fig. 3J ? (Chinijo archipelago) (Fig. 11).

Helix [*Gonostoma*] *lenticula* var. *virilis* — Neubert et al., 2023: 151, pl. 35 fig. 6 (in error mentioned "fig. 7").

Diagnosis. — A solid *Caracollina* shell with remarkably strong ribs. Fossil.

Shell. — The figured syntype shell (ZMZ 508728/a) is lenticular and has about 4.7 whorls, which are weakly concave and have no deep suture. The last whorl is strongly angled. This solid shell is 8.4 mm wide. In the umbilicus, the first whorls slowly increase in width, only the last whorl is more elongated. The aperture has a reflected lip and shows a tubercle in the palatal corner of the aperture. The teleoconch has remarkable strong ribs on the dorsal and ventral side. These are at the base more numerous than in strongly



Figs 29-30. Shells of *Caracollina virilis*. Fossil dune W Bateria, LZ, 27.iii.1997 legit KG, CGD 04044. **a:** dorsal view; **b:** ventral view; **c:** frontal view. Scale bar is 5 mm. Photos: IMM.

ribbed specimens e.g. from LG or of var. *major* from TF (56 vs. 45 at the base. This fossil shell is light horn coloured.

Localities (studied material only). — Canary Islands, fossil: **Lanzarote**: sandpit S Tinajo; fossil dune W Bateria + **La Graciosa**: NW La Sociedad.

Remarks. — According to Neubert et al. (2023: 151), one shell collected by Wollaston (ZMZ 508727) might be a syntype as well. However, Wollaston (1878: 395) only cited the collector Fritsch and the description of Mousson and did not mention his finding of a solid form like *Caracollina virilis* in his book. The specimen depicted in Yanes et al. (2005: fig. 11; 2011: fig 3J) (Fig. 11), is considered to be *C. virilis*. The solid shell has the characteristic strong ribs. This find also fits with the type locality, which means that the distribution area now runs from Fuerteventura to the Chinijo archipelago.

FINAL REMARKS

The following can be concluded from the measurements with the caliper (Fig. 18): For all Canarian Islands, all shells with the characteristics for *Caracollina lenticula* are less than 8.8 mm wide, and shells with the characteristics for *C. huloti* are more than 7.0 mm wide. There is an overlap between 7.0 and 8.8 mm. The overlap is the largest in the east (FV) and the smallest in the west (LG). With their sizes, fossil specimens fall within the extant specimens. Towards the West, *C. huloti* seems to become larger (Fig. 18). The shells from Cape Verde Islands all have the flattened shape and belong to *C. lenticula*.

The fossil *Caracollina virilis* is tentatively accepted as a valid species. It might also be only a chrono-subspecies of the large species named *C. huloti*, but in that case the latter has to become a subspecies of *C. virilis* as it is the younger name.

On La Gomera, both extant and fossil specimens of *C. lenticula* and *C. huloti* have been found. From Tenerife, *C. huloti* is known from Pleistocene deposits (in CGD 03530, Fig. 14) of 600 Ka (Miller et al., 2022), which makes it unlikely that this species is introduced by humans.

In Iberian specimens of *Caracollina*, a large variation in genital morphology has been established (Prieto et al., 1993). Based on the figures used, it can be determined that they have examined *C. lenticula*. The extent to which the described variation in the mucous gland, the appendix and the dart sac also occurs in specimens in other parts of the distribution area and *C. huloti* in particular, is the subject of further research.

No spermatophore was found in any of the examined bursa copulatrix.

Hardly any differences were found in the radula and jaw between both species. The difference lies mainly in the size of the radula and the number of laterals.

Due to the distinction between both species, it is now possible to investigate their distribution and it will especially have to become clear to what extent *Caracollina huloti* also occurs outside Morocco, the Canary Islands and Andalusia. The depicted shell of *C. lenticula* in Bank et al. (2025: 754, pl. 90 fig. 1) from Palamut, Antalya, southwest Türkiye (NMBE 23916, D = 7.8 with 4.7 whorls), e.g., has the most features of *C. huloti*.

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