A NEW SPECIES OF *VERMETUM* FROM GRAN CANARIA AND EVIDENCE THE GENUS SHOULD BE TRANSFERRED FROM PRISTILOMATIDAE TO GASTRODONTIDAE (GASTROPODA: PULMONATA)

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Abstract *An undescribed small land-snail discovered recently on Gran Canaria (Canary Islands) is named as* Vermetum tamadabaensis. *The generic placement is based on close similarity of its shells to those of* V. festinans, *which is known only by shells from La Palma in the same archipelago. The genital anatomy of* V. tamadabaensis *shows characters distinctive of Gastrodontidae rather than Pristilomatidae, including presence of a sarcobelum containing a dart and three "bridges", respectively joining the base of the penis to the free oviduct, the sarcobelum with duct of the bursa copulatrix, and the bursa duct to the epiphallus. Some of the anatomical features suggest affinity to* Zonitoides, *but others are peculiar.*

Key words *Canary Islands, land-snails, endemic, generic taxonomy, genital anatomy*

INTRODUCTION

During 2013 a hitherto unknown, small, discoid, tightly coiled land-snail was discovered by J. Santana and J. García in the hills of the north-west of the island of Gran Canaria, in the east-central part of the Canary Islands archipelago. Its shell characters showed obvious similiarities to those of *Vermetum festinans* (Shuttleworth 1852), a poorly known species described from shells from the hills of La Palma, one of the western islands of the Canary Islands archipelago. Live-collected material of the snail from Gran Canaria provided information on its genital anatomy. This showed characters of Gastrodontidae rather than the Pristilomatidae, the family which had been suggested for *V. festinans* (Bank, Groh & Ripken, 2002: 93, 111).

The Gastrodontidae is a family hitherto known in the Canary Islands only by the genus *Janulus* R.T. Lowe 1852 (currently endemic in Macaronesia: Bank *et al*., 2002: 111; Riedel, 1980; known as Tertiary fossil in Europe: Manganelli *et al*., 2011). Gastrodontidae genera known elsewhere in Macaronesia (Bank *et al*., 2002) are *Zonitoides* Lehmann 1862 known in Madeira and widespread also in Europe and over much of the Holarctic, the American *Striatura* Morse 1864 known only from the Azores where it is likely to be an introduction and *Atlantica* Ancey 1887 endemic on Madeira and the Desertas (Cameron *et al*., 2013). This paper describes and names the new species from Gran Canaria. Its taxonomic position is then assessed from characters of the distal genitalia and shells, leading to the tentative conclusion that *Vermetum* may be another endemic Macaronesian genus of Gastrodontidae, although the anatomy of its type species still needs to be confirmed.

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MATERIAL AND METHODS

Living specimens were drowned in water and preserved in 70% ethanol. Shell growth is indeterminate in these snails, so comparative measurements given are from a few of the largest shells available, mainly those where dissection revealed mature genitalia.

Methodology used in describing the specimens follows Kerney & Cameron (1979), Ibáñez *et al*. (2006) and Alonso *et al*. (2013). In descriptions of the genital system the terms "proximal" and "distal" refer to the position in relation to the ovotestis.

ABBREVIATIONS

AIT	Alonso and Ibáñez collection, Department of Animal Biology, University of La Laguna, Tenerife, Canary Islands, Spain.
CGAH	G.A. and D.T. Holyoak private collection, Cabeçudo, Portugal.
JGGC	J. García private collection, Las Palmas de Gran Canaria, Spain.
JMC	J.M. Castro private collection, Santa Cruz de La Palma, Spain.
JSGC	J. Santana private collection, Las Palmas de Gran Canaria, Spain.
MAGC	M. Artiles private collection, Arinaga, Gran Canaria, Spain.
NMBE	Naturhistorisches Museum, Bern, Switzerland.
sh	shell
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain.
UTM	Universal Transverse Mercator, cartographic projection system.

RESULTS AND SYSTEMATICS

Family Gastrodontidae Tryon 1866
Genus ***Vermetum*** Wollaston 1878

The generic name was introduced by Wollaston (1878: 323) as a new section of *Hyalina* Gray, apparently with the single species *Hyalina festinans* based on *Zonites festinans* Shuttleworth 1852. However, a list later in the same book (Wollaston, 1878: 569) added *Hyalina scintilla* Lowe to the section *Vermetum*, a species currently placed as *Lucilla scintilla* (R.T. Lowe 1852) in the Helicodiscidae (Bank, Groh & Ripken, 2002: 110; Seddon, 2008: 50). Thus, the type species of *Vermetum* was subsequently designated as *Zonites festinans* Shuttleworth 1852 by Bank *et al*. (2002: 142).

Several major reviews of zonitoid pulmonates (Pilsbry, 1946; Riedel, 1980, 1998; Schileyko, 2003) overlooked the generic name *Vermetum*. Bank *et al*. (2002: 111) included it in the Pristilomatidae, with the sole species *Vermetum festinans*, without any discussion of the reason for the family placement. The small, nearly discoid shell and narrow whorls are nevertheless suggestive of *Vitrea* of the Pristilomatidae, as noted by Wollaston (1878: 323) when he compared it to *Hyalina crystallina*. The large umbilicus and sculptured shell surface give an even greater similarity to *Hawaiia minuscula* (Binney 1841) of the Pristilomatidae, but the anatomy of *Vermetum festinans* has remained unknown so its allocation to any family has therefore been tentative at best.

Vermetum festinans (Shuttleworth 1852)
Figs 1D, 2

Shuttleworth (1852: 138) named *Zonites festinans* on the basis of a single shell ("Diam. maj. 5, min. 4½, Alt. 2 mill.") from "Sub foliis emortuis, Palma". The holotype (and only original specimen: Bank *et al*., 2002: 163) is now housed at Natural History Museum, Bern (NMBE no. 18766) and is illustrated in our Fig 1D. The coloured illustrations which were intended to accompany Shuttleworth's description of this and other new species were not published until over a century later (Shuttleworth, 1975: pl. 1 fig. 4, in a volume edited by W. Backhuys; the original plates were made in 1853).

Wollaston (1878: 323) noted that "This little *Hyalina* appears to be peculiar (so far as at least has been observed hitherto) to the island of Palma, where it occurs in damp sylvan spots of intermediate and lofty altitudes. It was met with by Mr. Lowe and myself in the Barranco de Galga, and by the sides of the Vueltas (on the ascent to the Cumbre) above Buenavista; and Mr. Lowe obtained it (on May 26, 1858, in the wood of El Bucco, at El Monte, above Barlovento"). All these localities correspond approximately to the rectangular symbol in the north of La Palma island on our Fig. 2. In addition, we found a shell of this species (Fig. 1E) in the Barranco de La Traviesa, in the north of the island (UTM: 28RBS2090, at 800 m altitude) in "fayal-brezal" vegetation.

Tryon (1887: 160, pl. 51 figs 91, 92) described and illustrated the species as *Zonites festinans* in subgenus *Hyalinia*, section *Polita*.

Vermetum tamadabaensis sp. nov.
Figs 1A–C, 2–5

Holotype 1 sh, TFMC (MT 853); Leg. J. Santana, 29 December 2013 (Figs 1A, 3).

Paratypes 4 sh +bodies in spirit, and 9 specimens in spirit (CGAH), 14 sh +32 specimens (AIT), 60 sh (JSGC), 15 sh (JGGC), 3 sh (JMC) and 90 sh (MAGC); all collected between September 2009 and December 2013 from the type locality.

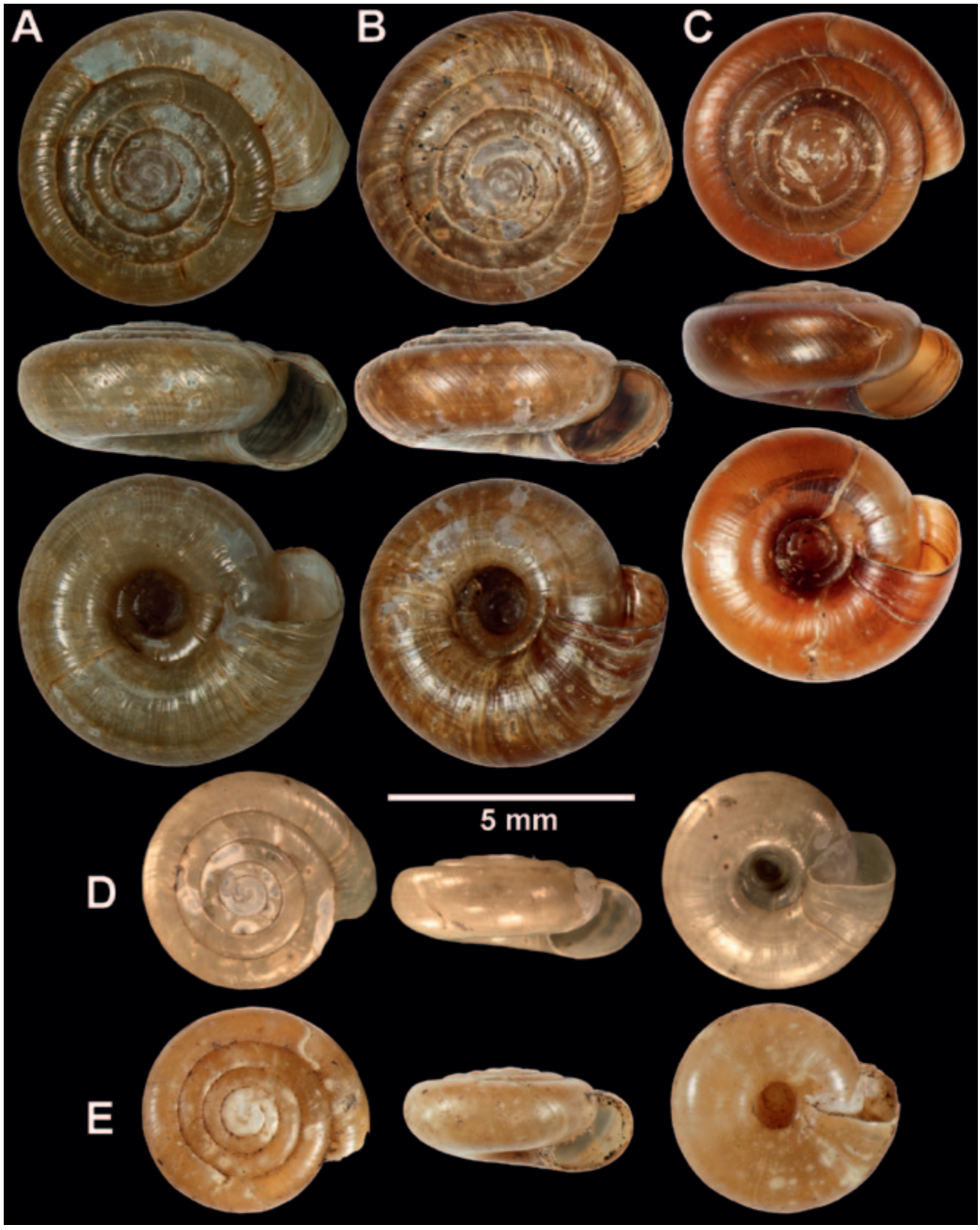

Figure 1 Shells of *Vermetum* species: **A–C** *V. tamadabaensis* sp. nov., **A** holotype, with whitish shell, **B** paratype, with pale brown shell, **C** paratype, with brown shell, all three from the type locality; **D, E** *V. festinans*, **D** holotype of *Zonites festinans* Shuttleworth 1852 (photo by Eike Neubert, © NMBE, zon0044, no. 18766, reproduced with permission), **E** from the Barranco de La Traviesa (La Palma).

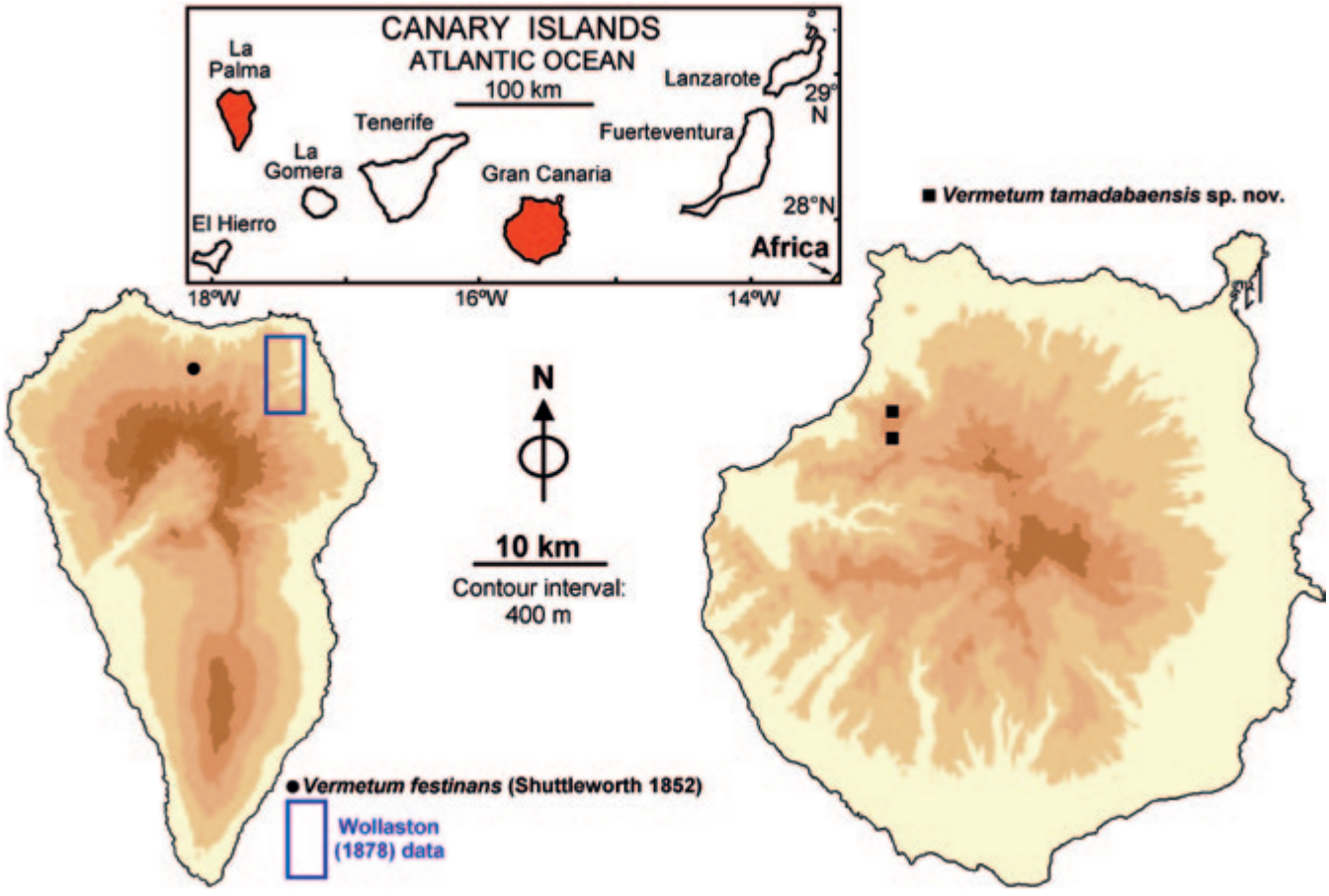

Figure 2 Map of distribution of *Vermetum* species in the Canary Islands. The approximate location of records of *V. festinans* from Wollaston (1878) is marked with a rectangle.

Type locality Tamadaba pine forest, in the north-western part of Gran Canaria Island, Canary Islands (UTM: 28R DS30) at 1195 to 1210 m altitude.

Description Exposed parts of body (Fig. 3) pale grey to light grey on head and dorsal surface of foreparts; eye-spots black, the blackish ommatophore retractor muscles visible by translucence; whitish to pale grey on upper flanks; tail, foot-fringe and sole of foot white; mantle-collar white; exterior of mantle white or pale grey; uppermost three whorls of spire light brown. Jaw minute, oxygnathous.

Shell almost discoid, with low rounded spire; breadth 5.4–6.7 mm, height 2.5–3.05 mm, breadth/height 2.0–2.3; of 4¾-5⅓ whorls that increase regularly in width. Whorls rounded overall, distinctly flattened above with sutures of moderate depth, somewhat less flattened below. Umbilicus broad, 1.5–1.8 mm (forming 28–30% of shell breadth), almost perfectly symmetrical, revealing interior of all whorls of spire. Mouth rounded overall, except where interrupted by penultimate whorl, but with flatter top and bottom of body whorl combined with steeply descending columellar margin giving a squared profile, maximum width 1.9–2.2 mm, maximum height 2.0–2.1 mm, width/height 0.97–1.05. Peristome simple, thin, extending further along body whorl on top of mouth than on bottom, often slightly reflected at umbilicus, not reflected upwards or outwards. Body whorl widens gradually and progressively to mouth, not descending near mouth. Interior of mouth and of body whorl lacking any internal teeth or ridges. Shell colour polymorphic (Figs 1A–C, 3), the dark shells bright medium-brown, the light shells whitish with a greenish tinge, a few intermediate shells light brown. Shell rather thin but strong, translucent, especially when brown pigment lacking. Surface somewhat glossy, especially below, on upperside the micro-sculpture tending to result in impression of a waxy lustre; upper whorls of spire often

Figure 3 Type locality of *Vermetum tamadabaensis* sp. nov. and live animals: the holotype with pale body coloration and the paratype (shell Fig. 1C) with darker body.

somewhat corroded on living adults, resulting in whitish spots and patches. Periostracum with moderately strong to rather weak transverse-oblique low ribs and growth lines that are somewhat irregular in height and spacing, generally weaker below, also rather weak above on some shells. A few stronger growth lines often present on later whorls, where emphasised by surface corrosion. Much finer microsculpture of even, closely spaced, spiral lines present on whole upperside of teleoconch where superimposed on the ribs to give a minutely decussate pattern; spiral sculpture much weaker and widely spaced or irregular beneath. Protoconch smooth; transverse ribs apparently begin at whorl 1.0, spiral microsculpture by whorl 1.2, but juvenile shells not studied and adult shells generally rather corroded apically.

Genital system (Figs 4, 5) Genital orifice a pore on right-hand side of body, behind base of right ommatophore, rather high on right flank about mid-way back to mantle-collar (location intermediate between that typical in Helicidae and the position further back that characterises *Retinella* (*Lyrodiscus*)), a C-shaped slit (opening forwards) bounded on a mature individual by inconspicuous low whitish lips. Atrium of short to medium length, widening proximally. The bursa duct, sarcobelum, penis and free oviduct all arise independently from the proximal end of the genital atrium, so there is no vagina. In a mature individual the penis formed a continuation of the proximal end of the atrium, with sarcobelum, bursa duct and free oviduct all arising on the same side, the bursa duct originating between the other two but much closer to base of free

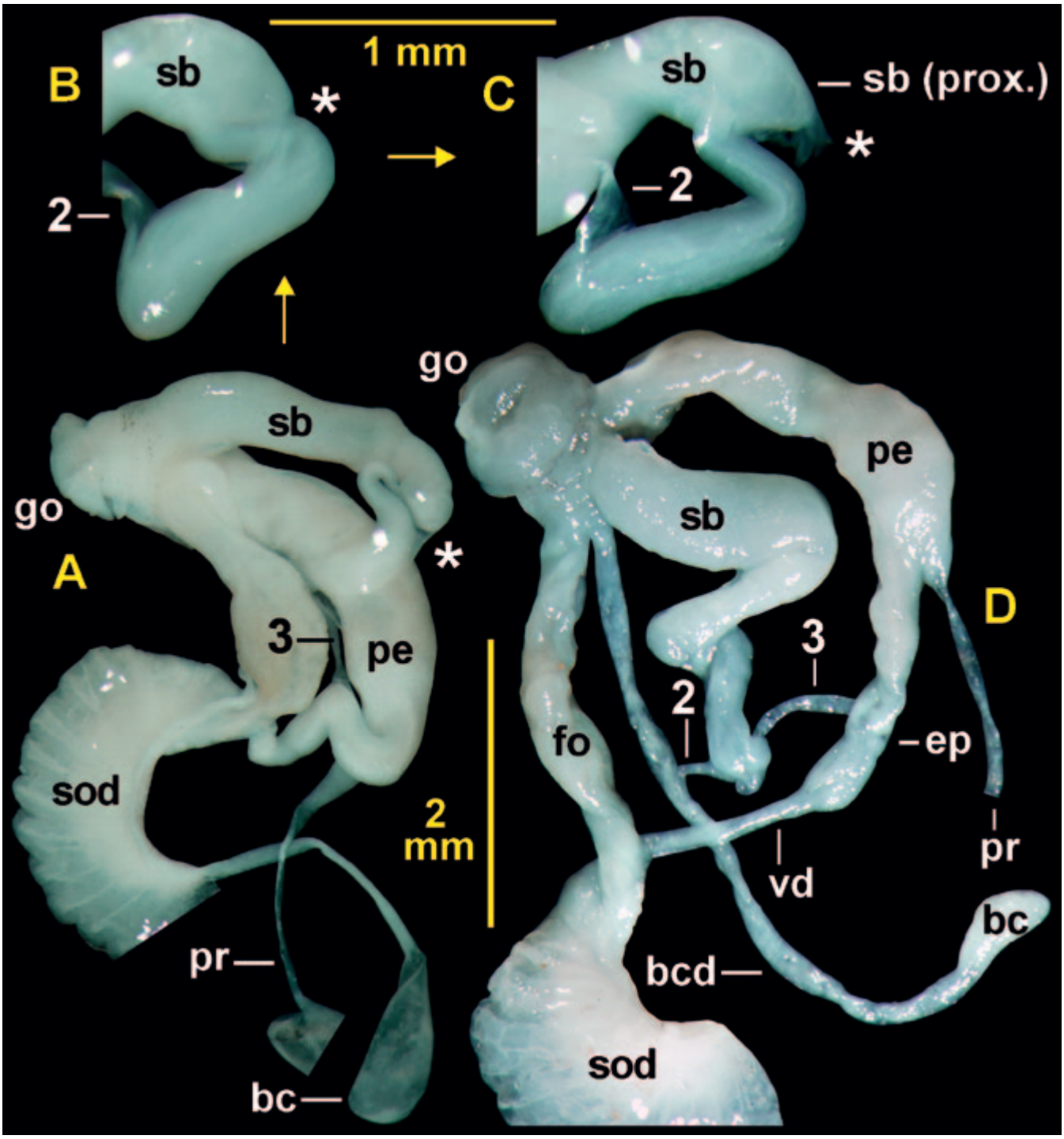

Figure 4 Photographs of distal genitalia of two paratypes (**A–C**, and **D**) of *Vermetum tamadabaensis* sp. nov.: **A** distal genitalia partly separated; **B**, **C** two views of sarcobelum; **D** distal genitalia of a different individual more widely separated. Abbreviations: bc bursa copulatrix; bcd duct of bursa copulatrix; ep epiphallus; fo free oviduct; go genital orifice; pe penis; pr penis retractor muscle; sb sarcobelum; sod spermoviduct; vd vas deferens; 2 "Bridge" 2; 3 "Bridge" 3; * distal end of sheath that covers proximal part of sarcobelum and continues as "Bridge" 2.

oviduct. Right ommatophore retractor muscle free from peni-oviducal angle.

Free oviduct moderately long, cylindrical. Bursa duct very long, the bursa copulatrix small, ovate, located close alongside proximal part of spermoviduct when *in situ*.

Sarcobelum large, nearly as long as penis overall, divided into three parts: distal part a wide

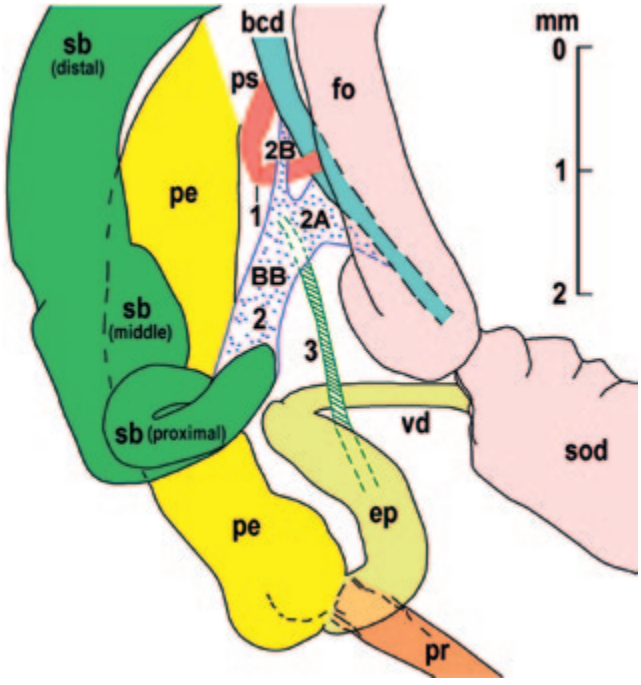

Figure 5 Semi-schematic drawing of part of distal genitalia of a paratype of *Vermetum tamadabaensis* sp. nov. to show details of "bridges", numbered 1, 2, 2A, 2B and 3. Abbreviations as in Fig. 4, plus: BB broad band (forming part of "Bridge" 2), ps penis sheath.

cylinder forming about half of total length; middle part a slightly wider cylinder forming about one-quarter of total length; proximal part much narrower (less than half width of distal part), cylindrical, white and firm, often curved *in situ*, enclosed by thin sheath (marked * in Fig. 4) that joins to middle part distally and continues proximally as "Bridge 2" (see below), at least sometimes separated from middle part internally by a short and much narrower neck. The sarcobelum lacks any laterally inserted coronal glands, but its narrow proximal part might have a similar function. The middle part of the sarcobelum contains a small dart (*ca* 0.47 mm long, slender, straight; one individual had point of dart projecting distally through external wall of its sarcobelum just distal to end of middle part).

The penis is long and cylindrical with a thin sheath, at least near the distal end. The penis is somewhat clavate proximally, one side of the terminal thickening giving rise to a retractor muscle (which is stout, long and continues proximally inside the body cavity to join the body wall). The other side of the proximal end of the penis gives rise to an epiphallus that is to some extent recurved laterally, about half the width of the penis and one-third to one-half of its length. The vas deferens continuing from the proximal end of the epiphallus is relatively short, about two-thirds length of epiphallus and less than half of its width, returning proximally to a position close to proximal end of free oviduct. There is no flagellum.

Three "bridges" of strong connective tissue (numbered 1 to 3 on Figs 4 and 5) link different organs of the distal genitalia. Bridge 1 joins distal end of penis to adjacent inner face of free oviduct (arising inside sheath at extreme base of penis where apparently cylindrical and forming a slender papilla or possibly a short duct; on leaving penis sheath it continues as thinner bridge of connective tissue). Bridge 2 arises at proximal end of proximal part of sarcobelum as a broad, flattened band (BB) of connective tissue, which passes distally and towards bursa duct (passing beneath free oviduct when *in situ*); the largest part of bridge (Bridge 2A) thins and widens to form an extensive attachment with bursa duct; a separate part of bridge branches off distally and continues as a narrower but thicker strap (Bridge 2B; crossing Bridge 1 without joining it) to form a narrow insertion more distally on bursa duct. Bridge 3 originates as part of the underside of Bridge 2 around the point where its narrow distal branch (2B) leaves; it continues as a narrow but clearly defined band to join the middle part of the epiphallus, crossing the vas deferens without joining it.

Three individuals with genitalia not fully mature had part BB of Bridge 2 shorter; the extensive sheet of tissue (Bridge 2A) thin and weakly developed so not forming an obvious bridge, whereas Bridge 2B was narrow and sharply defined. Bridge 1 was always present but in one individual it partly joined the nearest section of Bridge 2, in other two individuals it was free from Bridge 2, but looped around the narrow branch (2B) in one of these.

Comparisons The new species is very similar to *V. festinans* in shell characters, leaving little doubt that they are closely related. The only obvious differences are that *V. tamadabaensis* is larger and has an almost round rather than distinctly oval shell mouth (Figs 1A–C cf. D–E). Wollaston (1878: 323) mentioned that "*festinans* has somewhat the same whitish-green colour, or olivaceous-brown, as the *H. lenis*". This may imply that both

whitish and brown shell morphs exist in that species, as in *V. tamadabaensis*. The description of the holotype shell of *V. festinans* noted it as "lutescens" [yellowish] (Shuttleworth, 1852: 138) and the contemporary figures (Shuttleworth, 1975: pl. 1 figs 4) show it as whitish or very pale greenish-yellow.

Etymology The species epiphet *tamadabaensis* is an adjective derived from the name of the type locality.

Distribution and habitat The snails were collected at two adjacent localities at the "Pinar de Tamadaba", Artenara, in the north-western part of Gran Canaria, at 1195 m (28R DS3201) to 1210 m (28R DS3203) altitude. It is a wet area on rocky ground with pine forest (*Pinus canariensis* Sweet ex Spreng.) and sparse lower vegetation (*Cistus symphytifolius* Lam. var. *leucophyllus* (Spach) Dans., *Micromeria pineolens* Svent., *Erica arborea* L., *Allium subvillosum* Salzm. ex Schult. & Schult.f., etc.); some stone walls have a cover of lichens and fungi. The collection sites were covered with a thick layer of leaf-litter from the pine trees, which was wet because of rainfall brought by the northern trade winds in the winter. The snails were found deep among the layers of almost rotten leaf-litter, or during rain, climbing on and near rock faces and trunks of the pine trees (where whitish fungi were a possible food of the snails). Other landsnails found nearby included *Napaeus maffioteanus* (Mousson 1872), *Hemicycla* sp. (in rock crevices), *Monilearia* sp., *Gibbulinella dealbata* (Webb & Berthelot 1833) and *Testacella maugei* A.Férussac 1819.

DISCUSSION

Comparisons of the distal genitalia of *Vermetum tamadabaensis* with those of Pristolomatidae (described and figured in Riedel, 1980; Schileyko, 2003) reveal obvious differences, since that family always lacks a sarcobelum, dart and "bridges" joining different parts of the distal genitalia, whereas the presence of these characterises several genera of Gastrodontidae.

Riedel (1980: 13–26, 153–157) and Schileyko (2003: 1366–1378) provided descriptions and illustrations of shells and genital anatomy of most of the genera of Gastrodontidae that allow the likely affinities of *V. tamadabaensis* to be assessed. Further comparative information was provided by Cameron *et al*. (2013) on the characters of *Atlantica* and of a second species of *Janulus*.

Two American genera, *Pseudohyalina* Morse 1864 and *Striaturops* Baker 1928, differ conspicuously from *V. tamadabaensis* in lacking a sarcobelum, both being small snails that may have secondarily reduced genitalia; the American *Striatura* has the sarcobelum inserted high on the penis; *Nastia* Riedel 1989 from NE. Turkey has the sarcobelum arising from near the middle of the penis and several other obvious differences (right ommatophore retractor passing through peni-oviducal angle, vagina present, no "bridges" in distal genitalia).

Thus, five genera of Gastrodontidae remain that resemble *V. tamadabaensis* in possessing a sarcobelum arising directly from the genital atrium, three of them occurring in the Palearctic (*Atlantica*, *Janulus*, some *Zonitoides*) and two that are essentially American (*Poecilozonites* O. Boettger 1884 comprising only Bermudan endemics; *Gastrodonta* Albers 1850 known only from eastern N. America). Neither of these American genera appears to have much in common with *V. tamadabaensis*, since both have a small or very small umbilicus; *Gastrodonta* has a strongly ribbed shell with apertural teeth, an apical caecum on the penis, two coronal glands on the sarcobelum and only one "bridge"; *Poecilozonites* has a very short penis with long twisted epiphallus and only one "bridge"; some of its species have apertural teeth, a keeled shell, or a narrow umbilicus. The Macaronesian *Janulus* differs in having shell teeth, a strongly ribbed shell, a small umbilicus, a longer penis and one or two "bridges" in the distal genitalia, albeit in similar positions to two of the bridges in *V. tamadabaensis* (cf. Cameron *et al*., 2013: figs 3A–C). The Madeiran genus *Atlantica* is much like *Janulus* in most of those characters, but with a shorter penis and much larger umbilicus.

Only *Zonitoides* remains as a genus sharing a large proportion of its characters with *V. tamadabaensis*, although comparisons are complicated because five subgenera are currently recognised, some of them so different from each other anatomically that further study may reveal that more genera are justified (as e.g. in Pilsbry, 1946). Four of these subgenera have exclusively North American ranges: *Zonitoides* (*Ventridens* Binney & Bland 1869) mostly comprises species not known anatomically, but immature shells of many of them have apertural teeth, unknown elsewhere

in the genus, and a large majority of species have a small or very small umbilicus; in *Z.* (*V.*) *acera* (Lewis 1875) the sarcobelum arises low on the penis (not on the atrium) and has one or two laterally inserted coronal glands; "bridges" join the sarcobelum to the bursa duct and the same point on the bursa duct to the sheath on the lower part of the penis (Pilsbry, 1946: 434–471); *Z.* (*Elliottius* Pilsbry 1946) has a single species *Z. elliotti* (Redfield 1856) with an elongate coronal gland on the sarcobelum, a peculiar swollen annulus in the distal half of the sarcobelum, a "bridge" connecting the proximal end of the sarcobelum to the bursa duct and another bridge (or duct) connecting the same point on the bursa duct to the base of the free oviduct; *Z.* (*Ventricallus* Pilsbry 1946) has a pair of well separated coronal glands on the sarcobelum, a long vagina, a long atrium and the lower part of bursa duct with two "bridge" connections, respectively to lower part of vagina and to penis sheath; *Z.* (*Pseudohyalus* Baker 1929) has a large penial caecum, sarcobelum with a small bifurcate coronal gland and a very long dart, and one "bridge" extending from bursa duct to near the middle of the penis. Overall therefore, none of the four American subgenera of *Zonitoides* gives evidence of close similarity to *V. tamadabaensis*.

The Holarctic *Zonitoides* (*Zonitoides*) would appear to be the most likely of the subgenera to include close relatives of *V. tamadabaensis*, because of its much less distant geographical range, with *Z. nitidus* (O.F. Müller 1774) reaching SW. Europe and NW. Africa as a native species. However, there are several clear-cut differences: all of its species lack pronounced spiral microsculpture on the shell, the penis retractor muscle is not attached terminally on the penis, the sarcobelum has a small coronal gland inserting laterally and it lacks a discrete narrower proximal part. The arrangement of the two "bridges" in the distal *Zonitoides* (*Zonitoides*) genitalia is similar in that one "bridge" joins the bursa duct to proximal end of sarcobelum, but quite different in that a second "bridge" passes from the bursa duct to the sheath of the distal part of the penis, both these "bridges" sometimes forming ducts (Schileyko, 2003: 1374, Yakovlev, 2005, Shikov, 2013), but apparently often not fully connecting the organs involved (e.g. Pilsbry, 1946: 474, footnote). However, *Zonitoides* (*Zonitoides*) lacks "bridges" corresponding to "Bridge 1" in *V. tamadabaensis* (between base of penis and free oviduct) and its "Bridge 3" (between bursa duct or at least part of "Bridge 2" and epiphallus).

Hence, *Vermetum tamadabaensis* shows several distinctive features which may justify maintaining it in a separate genus of Gastrodontidae, resulting in the Macaronesian fauna possessing a third endemic genus of the family. Further studies are nevertheless needed to assess the phylogenetic relationships of the genera of Gastrodontidae and better judge the significance of the differing arrangements of "bridges" and other characters of their distal genital anatomy. A study combining morphological and molecular analyses would therefore be especially valuable. It also remains highly desirable to investigate the genital anatomy of *Vermetum festinans*, the type species of *Vermetum*, to confirm that its conchological similarity to *V. tamadabaensis* reflects real affinity.

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References

Alonso MR, Holyoak DT, Holyoak GA, Yanes Y & Ibáñez M 2013 A review of *Retinella* (*Lyrodiscus*): the endemic Zonitidae of the Canary Islands. *Journal of Conchology* **41** (4): 493–509.

Bank RA, Groh K & Ripken TEJ 2002 Catalogue and bibliography of the non-marine Mollusca of Macaronesia. *In*: Falkner M, Groh K & Speight MCD *Collectanea Malacologica. Festschrift für Gerhard Falkner*. ConchBooks: Hackenheim. pp. 89–235.

Cameron RAD, Holyoak GA, Holyoak DT, Yanes, Y, Alonso MR & Ibáñez M 2013 Shell characters and genital anatomy of *Atlantica calathoides* and transfer of the genus *Atlantica* from Discidae to Gastrodontidae (Gastropoda: Pulmonata). *Journal of Conchology* **41** (3): 287–294.

Ibañez M, Siverio F, Alonso MR & Ponte-Lira CE 2006 Two *Canariella* species (Gastropoda: Helicoidea: Hygromiidae) endemic to the Northwest Tenerife (Canary Islands). *Zootaxa* **1258**: 33–45.

Kerney MP & Cameron RAD 1979 *Land snails of Britain and north-west Europe*. Collins (Collins Field Guide): London. 288 pp., 24 pls. (reprinted 1987, 1994, by HarperCollins).

Manganelli G, Martini I & Benocci A 2011 A new *Janulus* species (Gastropoda, Pulmonata, Gastrodontidae) from the Zanclean (early Pliocene)

of Tuscany (central Italy). *Bollettino della Società Paleontologica Italiana* **50** (3): 165–173.

PILSBRY HA 1946 *Land Mollusca of North America (north of Mexico)*. Academy of Natural Sciences of Philadelphia, Monographs No. **3**: Philadelphia. **2** (1). vi +520 pp.

RIEDEL A 1980 *Genera Zonitidarum. Diagnosen supraspezifischer Taxa der Familie Zonitidae (Gastropoda, Stylommatophora).* Dr W. Backhuys: Rotterdam. 197 pp., 2 pls.

RIEDEL A 1998 *Genera Zonitidarum – Addenda et corrigenda (Gastropoda, Stylommatophora).* Muzeum i Instytut Zoologii PAN: Warszawa. 91 pp.

SCHILEYKO AA 2003 Treatise on recent terrestrial pulmonate molluscs. Part 10. Ariophantidae, Ostracolethidae, Ryssotidae, Milacidae, Dyakiidae, Staffordiidae, Gastrodontidae, Zonitidae, Daudebardiidae, Parmacellidae. *Ruthenica*, Suppl. **2**: 1308–1466.

SEDDON MB 2008 The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago. *Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales*, *Biotir Reports* **2**: 1–204.

SHIKOV EV 2013 The penial stalk of the *Zonitoides nitidus* (O. F. Müller, 1774) (Gastropoda: Pulmonata: Gastrodontidae) spermathecal duct as an allosperm container. *Folia Malacologica* **21** (3): 121–125.

SHUTTLEWORTH RJ 1852 Diagnosen neuer Mollusken. *Mittheilungen der naturforschenden Gesellschaft in Bern* **260 & 261**: 289–304. [Reprinted in Shuttleworth, 1975: 19–23].

SHUTTLEWORTH RJ 1975 *Tabulae ineditae Molluscorum Insularum Canariensium*. Edited by W. Backhuys. Goecke & Evers: Krefeld. 43 pp., 8 pls.

TRYON GW, JR 1887 *Manual of Conchology, structural and systematic, with illustrations of the species. Second series: Pulmonata.* vol. 3. Helicidæ:– vol.I. published by the author: Philadelphia.

WOLLASTON TV 1878. *Testacea Atlantica, or the land and freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena*. L. Reeve & Co.: London. xi +588 pp.

YAKOVLEV AA 2005 [Organization of spermathecal duct in *Zonitoides nitidus* (Müller, 1774) (Gastropoda, Pulmonata, Gastrodontidae)]. *Ruthenica* **15** (1): 61–64. [in Russian].