

SHELL CHARACTERS AND GENITAL ANATOMY OF *ATLANTICA CALATHOIDES* AND TRANSFER OF THE GENUS *ATLANTICA* FROM DISCIDAE TO GASTRODONTIDAE (GASTROPODA: PULMONATA)

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Abstract The genus *Atlantica* from the Madeiran Islands contains two species, *A. gueriniana*, endemic on Madeira Island and *A. calathoides*, endemic to the Desertas. They have been regarded as members of the Discidae. The hitherto unknown genital anatomy of *A. calathoides* is described here from study of specimens collected on Deserta Grande. Comparisons with *Janulus bifrons* (Gastrodontidae) from the same island show that they have very similar genital systems, from which it is evident that both species belong to the Family Gastrodontidae. The Discidae of the Canary Islands have been placed provisionally in *Atlantica* subgenus *Canaridiscus*. Since the Madeiran *Atlantica* species are transferred to the Gastrodontidae, *Canaridiscus* is raised to generic rank in the Discidae. The “accessory duct” connecting penis and oviduct of *Janulus bifrons* and *Atlantica calathoides* (a structure regarded as a unique autapomorphy supporting the monophyly of the Gastrodontidae) is not a duct connection but a transverse bridge.

Key words Madeiran Islands, *Janulus bifrons*, *Atlantica*, Deserta Grande, Canary Islands, *Canaridiscus*.

INTRODUCTION

The Madeiran Islands have two endemic taxa grouped in the genus or subgenus *Atlantica* Ancey 1887. These were originally described by Lowe (1852, 1863) as *Helix gueriniana* R.T. Lowe 1852 from Madeira Island (the type species) and *Helix calathoides* R.T. Lowe 1863 (Fig. 1B) from Bugio and Deserta Grande islets (ca 22 km south-east of Madeira). Bank *et al.* (2002), Seddon (2008) and Bank (2009) treated the latter form as a subspecies, *Discus (Atlantica) guerinianus calathoides* and Abreu & Teixeira (2008) cited it as *Discus guerinianus calathoides*. Thiele (1931) placed *Atlantica* in the family Endodontidae, subfamily Discinae because the shell is similar to that of *Gonyodiscus* Fitzinger 1833 in being widely umbilicate with a low spire that is ribbed above and smooth below. Most recent studies (Bank *et al.*, 2002; Schileyko, 2002; Seddon, 2008; Bank, 2009; Holyoak *et al.*, 2011) have likewise placed them in the family Discidae (or its synonym the Patulidae). However, *Atlantica* differs from *Discus* and *Gonyodiscus* in the presence of raised lamellae forming a few paired radially elongate teeth on the inner palatal wall of the body whorl.

These teeth led Riedel (1998) to tentatively suggest that *A. calathoides* may be a species of *Janulus* R.T. Lowe 1852 since several species of that genus have similar shell teeth; Manganelli *et al.* (2011) also noted that its current allocation to *Discus* rather than *Janulus* (of the Gastrodontidae) is supported only by some shell characters.

The genus *Janulus* includes only three recent species, *J. bifrons* (R.T. Lowe 1831) (Fig. 1A) and *J. stephanophorus* (Deshayes 1850) from the Madeiran Islands and *J. pompylius* (Shuttleworth 1852) from La Palma in the Canary Islands. Several fossil species from continental Europe are also assigned to *Janulus*, with ages ranging from Oligocene to the end of the Pliocene (Manganelli *et al.*, 2011). Only one of the *Janulus* species is known anatomically, the Madeiran *J. bifrons*. It was placed in the Gastrodontoidea family Gastrodontidae because it has a penial dart-sac and a short duct from the oviduct connecting to the penis (Pilsbry, 1947). The Gastrodontoidea had its origins by the Eocene, in eastern Laurasia (Hausdorf, 2000: fig. 4), with different branches evolving in the western Palearctic and the eastern Palearctic/western Nearctic.

The anatomy of the genital system of *J. bifrons* was described by Pilsbry (1947) as follows: “The

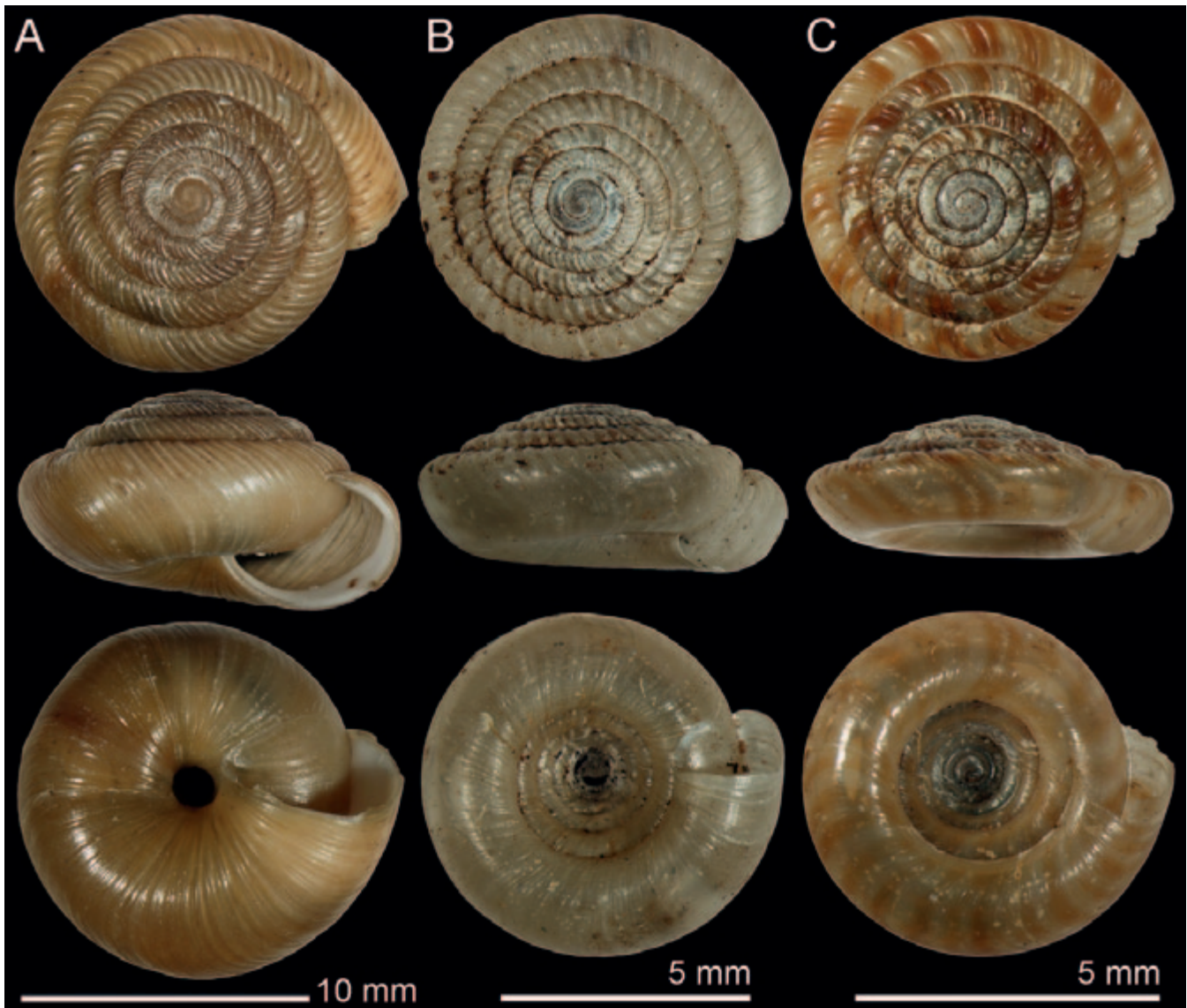


Figure 1 Shells of: A *Janulus bifrons* (R.T. Lowe 1831); B *Atlantica calathoides* (R.T. Lowe 1863); C *Atlantica guerini-ana* (R.T. Lowe 1852) [C from Melvill-Tomlin Collection, NMW.Z 1955.158.25072].

genitalia (figs. 1, 2) show a long atrium from which the oviduct, spermathecal duct, penis and dart-sac branch at about the same level, no vagina being developed. The long, rather thick penis terminates in a short stout epiphallus leading to a short vas deferens. The penial retractor is terminal on the penis. The dart-sac seated on the base of the penis, is arcuate, a very short connective from its summit to the spermathecal duct. No dart present (probably dissolved by the preservative). There are no coronal glands. A short duct (d) from the oviduct enters a sheath which envelops the lower part of the penis (stippled in figure 1). It has no connection with the spermathecal duct. The free oviduct is long. The spermatheca is ovate, on a rather long duct."

The accessory duct connecting penis and oviduct has been regarded as the unique autapomorphy supporting the monophyly of the gastrodontids (Hausdorf, 1998) but a robust phylogeny of these land snails is still lacking (Manganelli *et al.*, 2011). This duct may not be homologous in all Gastrodontidae, since it is absent in *Pilsbryna* H.B. Baker 1929, and connects the penial dart-sac and spermathecal duct in *Gastrodonta* Albers 1850, the penis and free oviduct in *Janulus*, and the penis and spermathecal duct in other genera. In *Zonitoides* Lehmann 1862 a second accessory duct joins the spermathecal duct and free oviduct according to Baker (in Pilsbry, 1946), Riedel, (1980) and Gittenberger *et al.* (1984). Yakovlev (2005) made a histological

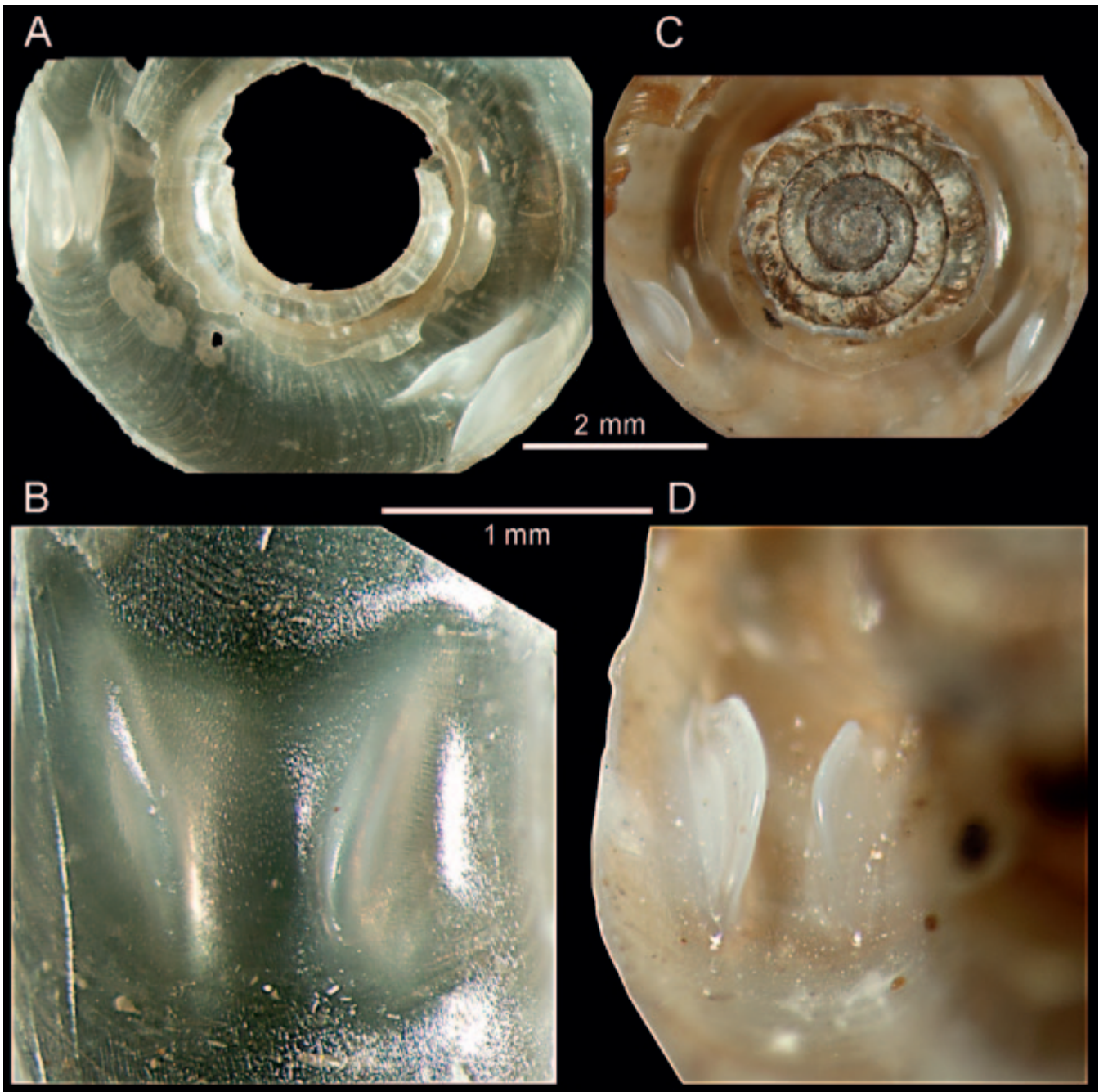


Figure 2 Shell details: A, B *Atlantica calathoides* (R.T. Lowe 1863), C, D *Atlantica gueriniana* (R.T. Lowe 1852) [C, D specimen from Melvill-Tomlin Collection, NMW.Z 1955.158.25072]; A, C inside of palatal part of body whorl, showing the two pairs of palatal lamellae; B, D detail of the outermost pair of palatal lamellae.

study of the connections of the spermathecal duct in two morphs of *Zonitoides nitidus* (O.F. Müller 1774), respectively with two and three stalks of the spermathecal duct, showing that only one of them is a genuine spermathecal duct, the other stalks being merely strands of connective tissue.

Yanes *et al.* (2011) and Holyoak *et al.* (2011) have recently transferred all the endemic Discidae of the Canary Islands to the taxon

Canaridiscus Alonso & Ibáñez 2011 and provisionally classified *Canaridiscus* as a subgenus of *Atlantica*. Nevertheless, the absence of information on the anatomy of the genital system of the Madeiran species of *Atlantica* led to continuing uncertainty about the correct systematic position of *Canaridiscus*. In this paper we describe and compare the anatomy of the genital systems of *Janulus bifrons* and *Atlantica calathoides* in order

to establish the family allocation of *Atlantica* and, in turn, decide the correct systematic position for *Canaridiscus*.

MATERIAL AND METHODS

Living specimens of *Janulus bifrons* and *Atlantica calathoides* were collected from two separate locations on Deserta Grande in April 2012. The first species (Fig. 1A) was collected live by RADC from a population nearer the centre of the island, on a gentle rocky slope with grasses and bracken *Pteridium aquilinum* (L.) Kuhn. *A. calathoides* (Fig. 1B) was rediscovered alive and also collected on this occasion by Mr Isamberto Silva. It occurred on a very steep boulder slope with very sparse vegetation at the south end of the island.

Of the six living *A. calathoides* obtained, only two appeared to approach adult size. These were drowned in water and preserved in 70% ethanol. Two surviving juveniles are currently being maintained alive at the Agricultural University of Wrocław. Specimens of *Janulus bifrons* were killed immediately in the field by immersion in 70% ethanol, as anatomical studies were not anticipated.

To allow taxonomic comparisons, we also studied 56 shells of *Atlantica gueriniana* (Fig. 1C), from Madeira Island, belonging to the Melvill-Tomlin Collection (NMW.Z 1955.158.25072). One specimen was broken to examine the structure of the internal palatal lamellae.

Methodology used in describing the specimens follows Kerney & Cameron (1979), Ibáñez *et al.* (2006) and Yanes *et al.* (2009). In descriptions of the genital system the terms “proximal” and “distal” refer to the position in relation to the ovotestis.

RESULTS

Taxonomy of *Atlantica*

Shells of *A. calathoides* (Fig. 1B) and *A. gueriniana* (Fig. 1C) have similar form (small, depressed and widely umbilicate) and similar ornamentation (spire strongly ribbed above and almost smooth below) to that of the Gastrodontidae *Janulus stephanophorus* (Deshayes 1850), from Madeira (see Manganelli *et al.*, 2011, fig. 9).

From the shell characters, we consider these to represent two different species of the genus *Atlantica*. In comparison to *A. gueriniana*, *A. calathoides* has the shell higher and the body

whorl more rounded in cross-section, as well as a smaller umbilicus. They also differ in shell colouration, since the dorsal surface of the shell of *A. gueriniana* has darker red-brown flammulations (Fig. 1C; Seddon, 2008: 113, pl. 12D) like those of typical *Discus rotundatus* (O.F. Müller 1774) or the American *Anguispira* Morse 1864, whereas *Atlantica calathoides* has an unmarked cream shell (Fig. 1B), so separation of the two at species rank appears to be appropriate.

Moreover, the interior of the outer (palatal) wall of the body whorl of the *A. calathoides* shell has two paired, radial-oblique lamellae at 130 degrees to each other (one specimen measured; Fig. 2A). Each pair consists of two tooth-like lamellae diverging from each other towards the shell mouth (by about 25 degrees in the outermost pair of the specimen photographed: Fig. 2B). In *A. gueriniana*, the paired lamellae (Fig. 2C) are located at 100 and 122 degrees to each other in the two specimens measured. Each pair consists of two small tooth-like lamellae diverging from each other towards the shell mouth (by about 14 degrees in the outermost pair of the specimen photographed: Fig. 2D).

Both *Atlantica* species were placed in *Discus* Fitzinger 1833 subgenus *Atlantica* by Thiele (1931), Bank *et al.* (2002), Seddon (2008) and Bank (2009), whereas Yanes *et al.* (2011) and Holyoak *et al.* (2011) raised *Atlantica* to generic rank. From their shell characters and the anatomy of the genital system of *A. calathoides* (described below), we consider that *Atlantica* belongs in the Family Gastrodontidae not the Discidae.

Janulus bifrons genital system

Pilsbry (1947) described a [distal] “short duct (d) from the oviduct [that] enters a sheath which envelopes the lower part of the penis”. However, this connection is not a duct, but a transverse bridge (Fig. 3B, C: br1). The same interpretation was suggested by Schileyko (2003) in his description of *Janulus*, and demonstrated by Yakovlev (2005) in his histological study of *Zonitoides nitidus*. The arrow of Fig. 3C shows the penial insertion of this transverse distal bridge of *J. bifrons*. There is also a second (proximal) bridge similar to the distal one (Fig. 3A: br2), between the epiphallus and the dart sac. The distal part of the spermathecal duct is located parallel and very near to the oviduct and the distal bridge (Fig. 3A, C), while its proximal part is very near to the

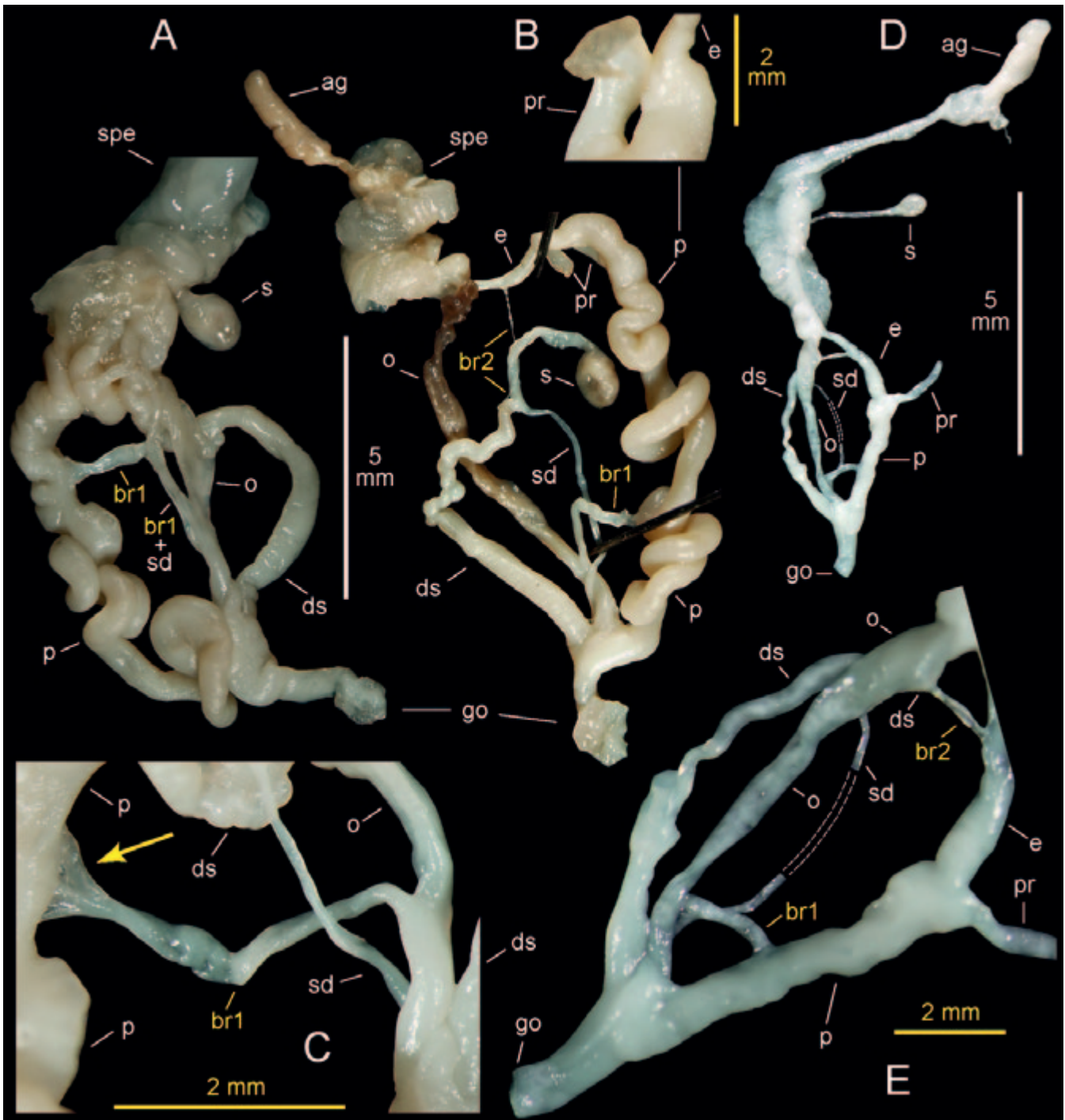


Figure 3 Anatomy of genital system. A–C *Janulus bifrons* (R.T. Lowe 1831), A genitalia of two specimens, viewed from opposite sides, B detail of the penis retractor muscle and epiphallus, C detail of the distal genitalia, showing the distal transverse bridge between penis and oviduct (arrow shows the bridge insertion on to wall of penis), D–E *Atlantica calathoides* (R.T. Lowe 1863), D genital system perhaps not fully developed, E detail of distal part of genitalia. Distal genitalia: a atrium; ag albumen gland; br1 distal transverse bridge between oviduct and penis; br2 proximal transverse bridge between epiphallus and dart sac; ds dart sac; e epiphallus; go genital orifice; o oviduct; p penis; pr penis retractor muscle; s spermatheca; sd spermathecal duct; spe spermoviduct.

proximal bridge. As described by Pilsbry (1947), it is fixed to the end of the dart sac through a very short connective. The penial retractor is not

terminal on the penis, but subterminal (Fig. 3B). As quoted above, Pilsbry (1947) also noted the absence of a vagina.

Genital system of *Atlantica calathoides*

The genitalia (Fig. 3D, E) of the two specimens dissected appears not to be fully developed, but the main features are apparent. It has a similar anatomy to that of *J. bifrons*. The atrium is conspicuous. From its proximal end, the oviduct, spermathecal duct, penis and dart-sac all branch off at about the same level. As in *Janulus bifrons*, there is no vagina, because the bursa copulatrix inserts at the atrium. The penis is tubular, without folds (in contrast to the long, much folded penis of *J. bifrons*), with a well developed penial retractor muscle inserted on its proximal end, at the junction with the epiphallus. There is no external differentiation between the epiphallus and vas deferens. The dart-sac is slightly arcuate, with a very short connective from its proximal end to the spermathecal duct. There are two transverse bridges similar to the bridges of *J. bifrons*, one distal between the penis and the oviduct (Fig. 3E: br1), the other proximal between the epiphallus and the dart sac (Fig. 3C, E: br2).

REMARKS

The genital system of *Atlantica gueriniana calathoides* has a similar pattern to that of *Janulus bifrons*, with the oviduct, spermathecal duct, penis and dart-sac all branching off from the distal end of the atrium at about the same level. Both species also possess two transverse bridges as described above. Hence they undoubtedly belong to the same family, the Gastrodontiidae. Although the genitalia of the *Atlantica* specimens shown in Fig. 3D–E were apparently somewhat immature, it is likely their shorter penis than in *Janulus bifrons* lacking the complex folding of that species' penis (Fig. 3A, B), will prove to be characters that are also present in mature individuals.

The shells of *Janulus* (Fig. 1A) and *Atlantica* (Fig. 1B, C) share the same type of dorsal sculpture and a peristome that is simple and not reflexed (although internally thickened in *J. bifrons*). Very similar, radial, paired, tooth-shaped palatal lamellae are present in *Atlantica calathoides* and in *A. gueriniana* (Fig. 2; also illustrated for the latter by Seddon, 2008: 113, pl. 12 D). Palatal lamellae are lacking in *J. bifrons*, but they are present in several other *Janulus* species (*J. stephanophorus*, *J. spadinii* Manganelli, Martini & Benocci 2011, *J. schottleri* Wenz 1922), although these have three

or four teeth in each group rather than a pair (Manganelli *et al.*, 2011).

The most conspicuous conchological difference between *Janulus* and *Atlantica* is in the size of the umbilicus. *Janulus* has a small umbilicus, quite different to the very wide umbilicus of *Atlantica*. This may be an important character for retaining *Atlantica* as a separate genus from *Janulus* within the Madeiran Gastrodontiidae, since it is related to the much smaller body mass in *Atlantica* compared to that of *Janulus*.

Yanes *et al.* (2011) and Holyoak *et al.* (2011) showed that the *Canaridiscus* endemic in the Canary Islands are characterised by a much longer penis than other Discidae. None of its species show lamelliform teeth inside the palatal part of the body whorl and none of them show the characters of the distal genitalia set out above that are shown by *Atlantica* and *Janulus* and point to affinity of the two latter genera being with Gastrodontiidae. Until now *Canaridiscus* was provisionally located as a subgenus of *Atlantica*, but as a consequence of *Atlantica* being transferred to the Gastrodontiidae, *Canaridiscus* should be raised to generic rank in the family Discidae.

A relation could be suggested between *Canaridiscus* and the Tertiary genus *Calogoniodiscus* Pfeffer 1929, as the keeled shell form of the *Calogoniodiscus* type species, *C. perelegans* (Deshayes) (figures in Pfeffer, 1929 and Zilch, 1959) is comparable with those of some *Canaridiscus* species, as *C. engonatus* (Shuttleworth 1852) and *C. rupivagus* (Rähle & Allgaier 2011). Such keeled forms, however, can be found in many genera, such as *Canariella*, *Candidula*, *Eremina* and *Oestophora*, and seem to represent repeated adaptations to life in rock fissures. Other members of these genera lack the keeled form, as do other species of *Canaridiscus*. Relationships to Tertiary species remain indeterminate.

Atlantica must be treated as a feminine noun. Therefore when *Helix guerinianus* and *Helix calathoides* are transferred to this genus the correct forms become *Atlantica gueriniana* and *A. calathoides* (the latter epithet has the same form for all genders in the singular). The Latin word *Discus* is a masculine noun and the same applies to the generic name *Canaridiscus* derived from it, for Discidae of the Canary Islands. When transferred to the genus *Canaridiscus*, *Atlantica* (*Canaridiscus*) *saproxylophaga* thus becomes *C.*

saproxyllophagus whereas *Atlantica* (*Canaridiscus*) *anagaensis* retains the ending to its epithet unchanged as *C. anagaensis*.

ACKNOWLEDGEMENTS

Special thanks are due to the National Museum of Wales, Cardiff, (UK NMW.Z), for the loan of 56 shells of *A. gueriniana* from the Melvill-Tomlin Collection, and for permission to break one shell to examine the internal lamellae. This study was partly supported by the project CGL2011–29898/BTE funded by the Spanish “Ministerio de Economía y Competitividad”. We are grateful to Isamberto Silva for the discovery and collection of *A. calathoides*, to the Parque Natural da Madeira for permissions and assistance on Deserta Grande, and to Dinarte Teixeira and Regina Tristão da Cunha with whom RADC worked on Deserta Grande. Thanks are also due to Tom Blockeel for advice on nomenclature, and to Ruud Bank and two anonymous referees for pertinent comments.

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