

# TAXONOMIC REVISION, HABITATS AND BIOGEOGRAPHY OF THE LAND SNAIL FAMILY DISCIDAE (GASTROPODA: PULMONATA) IN THE CANARY ISLANDS

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**Abstract** The endemic Macaronesian *Canaridiscus*, provisionally placed in the *Discidae* genus *Atlantica*, are closely linked to the peculiar laurel forest habitat of these islands. Knowledge of *Atlantica* (*Canaridiscus*) is increased here with the description, for the first time, of the genital system of three more of its species. The epiphallus is apparently lacking and the penis is much longer than that known from any of the *Discidae* of Europe and North America; generally it is too large to be more than partly accommodated in the distal female genital tract. *Keraea* has been regarded as an endemic Macaronesian genus of *Discidae* known only from a few shells, but its Madeiran species has been identified as a *Trochulus* (*Hygromiidae*) and its type species (from Tenerife) also matches *Hygromiidae*, not *Discidae*.

The origin and relationships of the Macaronesian *Discidae* are discussed. The simplest explanatory model is apparently that they represent the last living relicts of a more diverse fauna of *Discidae* that lived in Europe during the Tertiary; *Atlantica* (*Canaridiscus*) was probably isolated early on from the remaining *Discidae*. Recent literature reports multiple patterns of colonisation of Madeira and the Canaries that have varied between different groups of plants and animals. Hence, it is argued that it is unwarranted to expect to find only the single pattern of colonisation among the land snails of each of these archipelagos that was advocated by Waldén (1984).

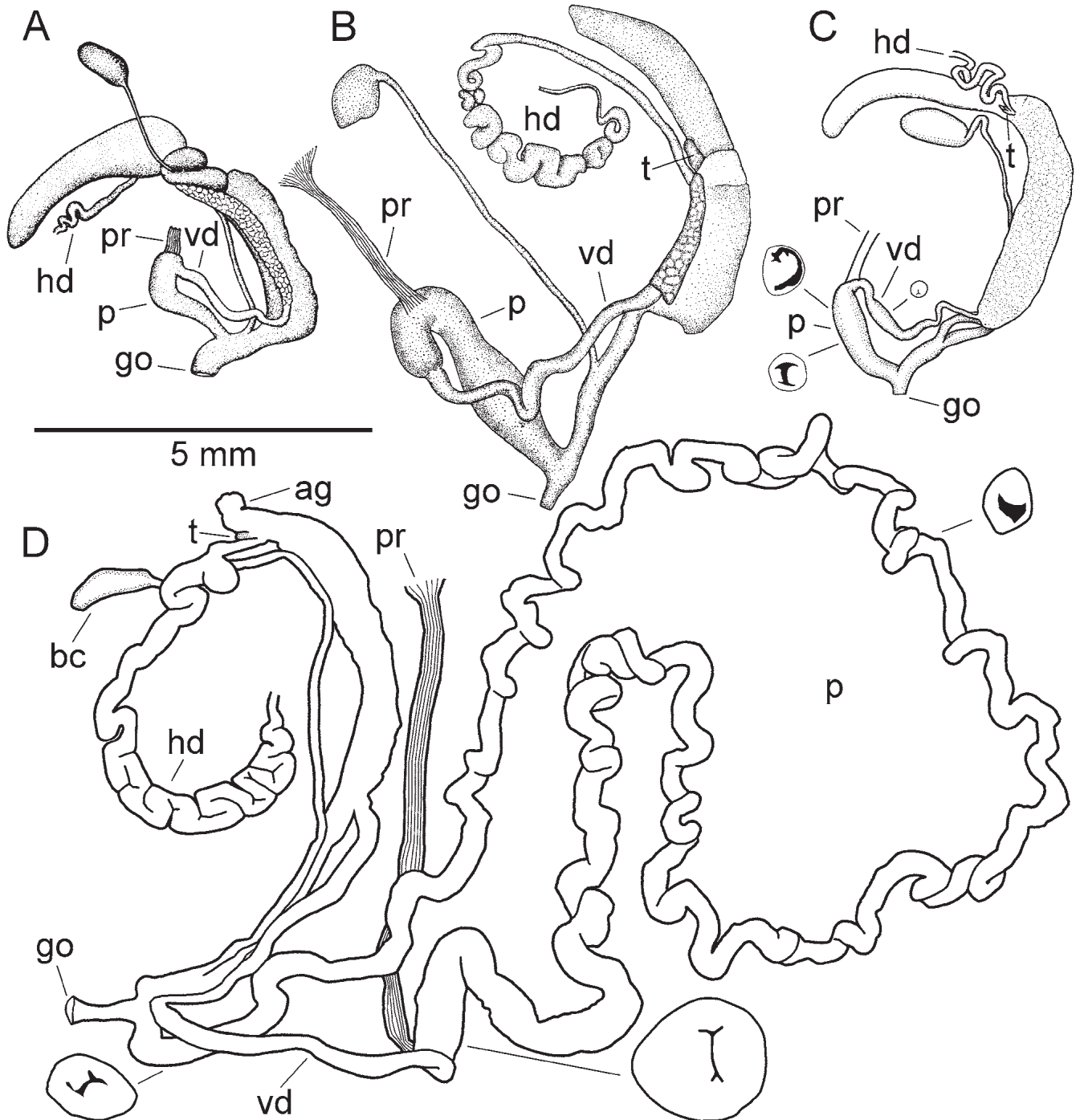
**Key words** Africa, *Atlantica*, *Canaridiscus*, genital anatomy, Laurasia, *laurisilva*, Macaronesia, Madeira, North America, paleobiogeography, penis length, Tertiary relict

## INTRODUCTION

The archipelagos located in the eastern Atlantic Ocean, known as the Macaronesian region, contain a rich and diverse native malacofauna that has undergone extensive speciation and adaptive radiation. However, many snail taxa are still poorly known, including the family *Discidae*. Recent checklists of the non-marine Mollusca of Macaronesia (Bank, Groh & Ripken, 2002; Seddon, 2008; Fauna Europaea database project, 2011), together with the data in Thiele (1931) recognise about 14 endemic species of *Discidae* from Macaronesia, which were grouped into the genera *Discus* Fitzinger 1833 and *Keraea* Gude 1911. Two species were cited for Madeira, nine in the Canary Islands and several in the Cape Verde Islands (Thiele, 1931), probably the three listed by Wollaston (1878) in *Patula* (*Iulus*). More recently, two new species from the Canary Islands grouped in the subgenus *Canaridiscus*, provisionally as *Atlantica* (*Canaridiscus*), were added to these checklists (Yanes *et al.*, 2011) as well as a

third species designated as *Discus* (*Canaridiscus*) by Rähle & Allgaier (2011).

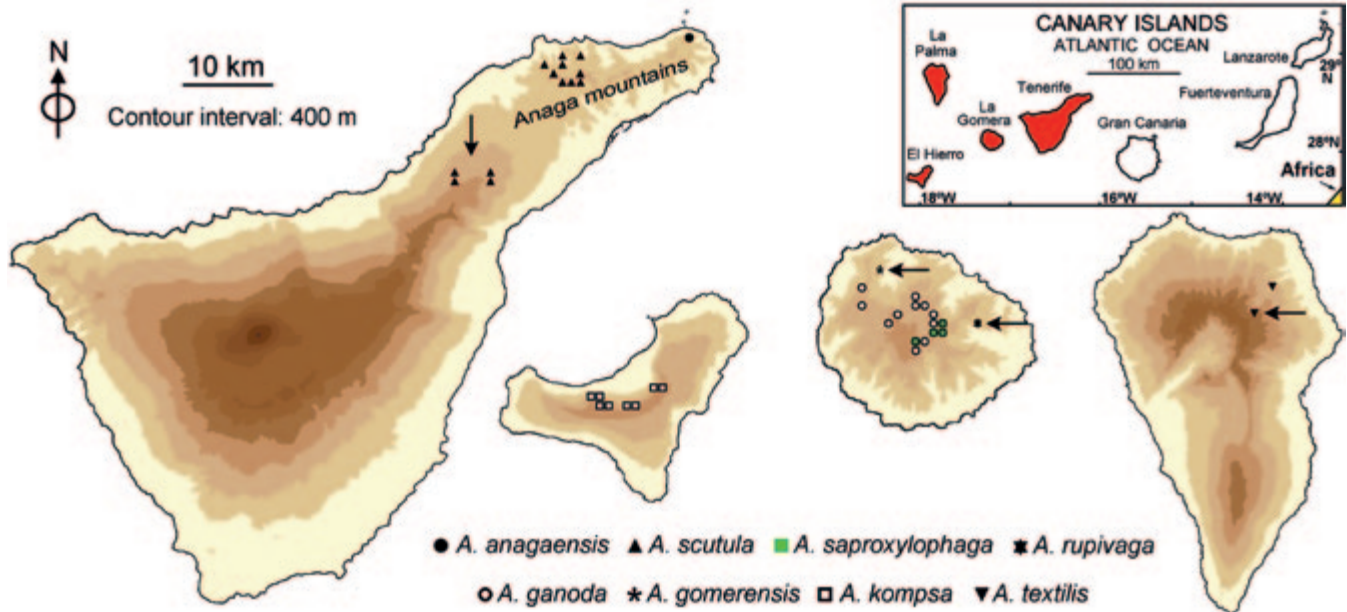
Despite the remarkable diversity of *Discidae* in these islands, representative specimens preserved and available in most collections of Mollusca are rather rare. Moreover, although intensive fieldwork has been performed in Madeira and the Canary Islands over the last few decades, *Discidae* taxa are infrequently encountered in field surveys. Indeed, four of the species were included in the list of European globally extinct taxa by Fontaine *et al.* (2007), namely *Discus engonatus* (Shuttleworth 1852), *D. retexus* (Shuttleworth 1852), *D. textilis* (Shuttleworth 1852) and *Keraea garachicoensis* (Wollaston 1878). In contrast with the anatomical data known for European and some North American *Discidae* (Fig. 1A–C), there has hitherto been no information published on the internal anatomy of the Canary Islands and Madeiran species (with the exception of the three species recently named by Yanes *et al.*, 2011 and Rähle & Allgaier, 2011), so they have been known only by their shell characters. Hence their affinities have remained mysterious.



**Figure 1** Genital anatomy of some European (A, B), North American (C) and Canarian (D) Discidae species: A *Discus (Discus) ruderatus* (Hartmann 1821) (from Riedel & Wiktor, 1974: fig. 117); B *D. (Gonyodiscus) rotundatus* (O.F. Müller 1774) (from Uminski, 1962: fig. 1); C *Anguispira kochi* (L. Pfeiffer 1845) (from Pilsbry, 1948: fig. 304); D *Atlantica (Canaridiscus) saproxylaphaga* Alonso, G. Holyoak & Yanes in Yanes *et al.* 2011 (drawn from Yanes *et al.*, 2011: fig. 3C). Parts: ag albumen gland; bc bursa copulatrix; go genital orifice; hd hermaphroditic duct; p penis; pr penis retractor; vd vas deferens. The scale bar corresponds only to A, B and D (C was drawn originally without a scale bar).

In this paper we revise the systematics of the Canary Islands species assigned to the Discidae. The genital system of three species is described

for the first time, confirming their allocation to the subgenus *Canaridiscus*. The relationships of the Macaronesian Discidae with those of Eurasia



**Figure 2** Geographical distribution of some *Atlantica* (*Canaridiscus*) species (only those species with precise recent data have been included). The arrows show the symbols of the only one-kilometre squares of the UTM grid with records located outside the laurel forest. Note: In the four one-kilometre UTM grid squares with *A. (C.) saproxylophaga* (on La Gomera Island), the species *A. (C.) ganoda* was also found.

and North America are discussed, leading to a consideration of their likely origins and history. Conservation status of the Macaronesian forms is also reassessed.

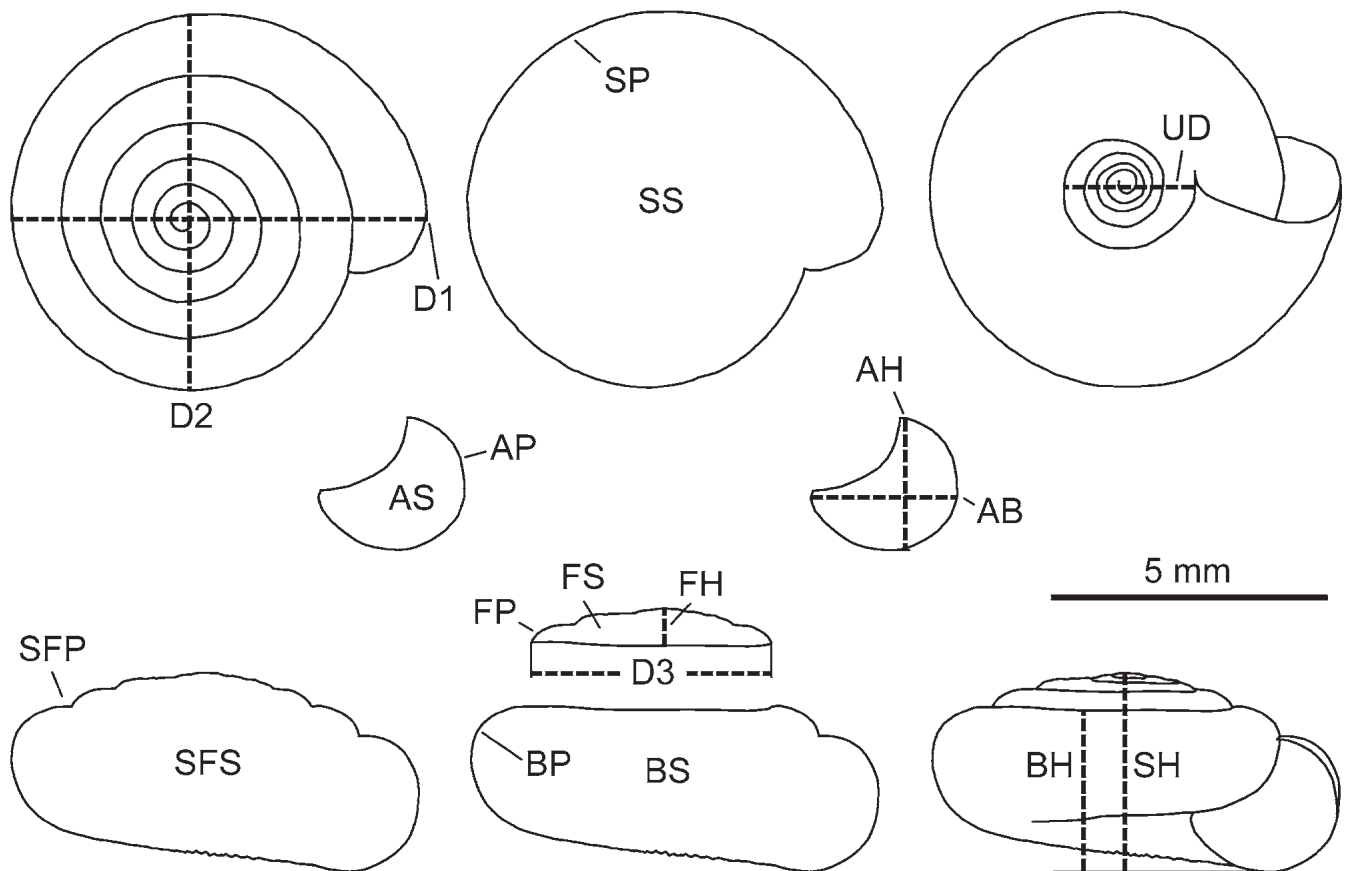
## METHODS

Snail specimens were drowned by immersion in water, then fixed in 80% ethanol. Maps of geographical distribution (Fig. 2) were produced using MapViewer software (Golden Software Inc.). The photographic methodology was described by Ibáñez *et al.* (2006). Drawings of shell outlines (Fig. 3) were obtained semi-automatically, adopting the methods used by Yanes *et al.* (2009b). Standardised measurements of the shells (Table 1, Fig. 3) were made following Yanes *et al.* (2009a), using the software analySIS® (Soft Imaging System GmbH). Abbreviations for shell characters and measurements are shown in Fig. 3. The number of shell whorls was counted using the methodology described by Kerney *et al.* (1979: 13). "Proximal" and "distal" refer to the position in relation to the ovotestis. Comparisons have been made with photographs of a syntype of *Patula (Iulus) garachicoensis* Wollaston 1878 (Fig. 4A), a possible syntype of *H. gueriniana* R.T. Lowe 1852 (Fig. 4B), a shell of *H. calathoides*

R.T. Lowe 1863 (Fig. 4C), a syntype of *H. retexta* Shuttleworth 1852 (Fig. 4D), a syntype of *H. engonata* Shuttleworth 1852 (Fig. 4E), a syntype of *H. putrescens* R.T. Lowe 1861 (Fig. 4F), a syntype of *H. scutula* Shuttleworth 1852 (Neubert & Gosteli, 2003: pl. 14, fig. 2), a syntype of *H. textilis* Shuttleworth 1852 (Neubert & Gosteli, 2003: pl. 14, fig. 3), the shell drawings of the holotype of *Discus gomerensis* Rähle 1994 (Rähle, 1994: figs 1–3), as well as a paratype of *Atlantica (Canaridiscus) saproxylophaga* Alonso, G. Holyoak & Yanes in Yanes *et al.* 2011 (Fig. 5A) and the holotypes of *A. (C.) anagaensis* Ibáñez & D. Holyoak in Yanes *et al.* 2011 (Fig. 5B) and *D. (C.) rupivagus* Rähle & Allgaier, 2011 (Fig. 4H).

## Institutional and other abbreviations

BDUNM	Biology Department, University of New Mexico, Albuquerque, U.S.A.
DBUA	Departamento de Biologia, Universidade dos Açores, Portugal
CMNH	Carnegie Museum of Natural History, Pittsburgh, U.S.A.
FMNH	Field Museum of Natural History, Chicago, U.S.A.
GBIF	Global Biodiversity Information Facility, Switzerland



**Figure 3** Drawings of the shell of *Atlantica (Canaridiscus) anagaensis* Ibáñez & D. Holyoak in Yanes *et al.* 2011, showing the placement of the measurements obtained (plane view, in mm or mm<sup>2</sup>). Measurements: AB aperture breadth; AH aperture height; AP aperture perimeter; AS aperture surface area; BH body whorl height; BP body whorl frontal perimeter; BS body whorl frontal surface area; D1 maximum shell diameter; D2 shell diameter perpendicular to D1; D3 maximum first whorls diameter; FH first whorls height; FP first whorls frontal perimeter; FS first whorls frontal surface area; SFP shell frontal perimeter; SFS shell frontal surface area; SH shell height; SP shell dorsal perimeter; SS shell dorsal surface area; UD umbilicus diameter.

IZUC	Institute for Zoology, University of Cologne, Germany
ICZN	International Commission on Zoological Nomenclature
JSGC	J. Santana private collection, Las Palmas de Gran Canaria, Spain
Kya	thousands of years ago
Mya	millions of years ago
NHMK	The Natural History Museum, London, U.K.
NHNV	Natural History Museum Vienna, Austria
NMBE	Naturhistorisches Museum, Bern, Switzerland
PAS	Polish Academy of Sciences, Poland
UMA	Universidade da Madeira, Funchal, Madeira, Portugal
UTM	Universal Transverse Mercator cartographic projection system

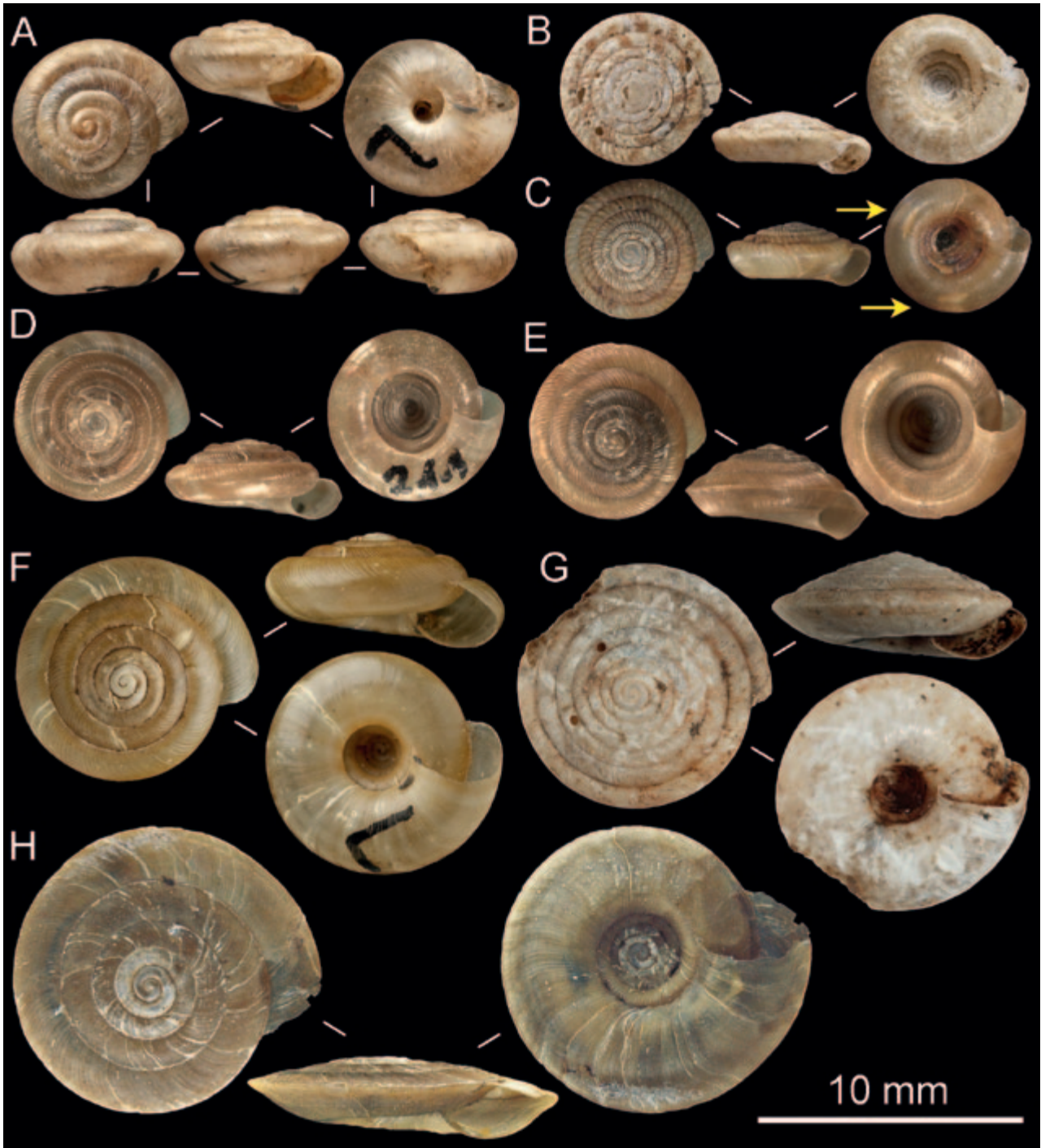
#### REVIEW OF SYSTEMATICS OF DISCIDAE

The generic names *Discus* and *Gonyodiscus* were introduced by Fitzinger (1833) for European Discidae. The widespread (apparently) Holarctic species *Helix rudrata* Hartmann 1821 became the type species of *Discus* by subsequent designation of Gray (1847), and the central and southeastern European *Helix perspectiva* Megerle von Mühlfeld 1816 the type species of *Gonyodiscus* by monotypy. Adams & Adams (1858) united these genera into *Discus*.

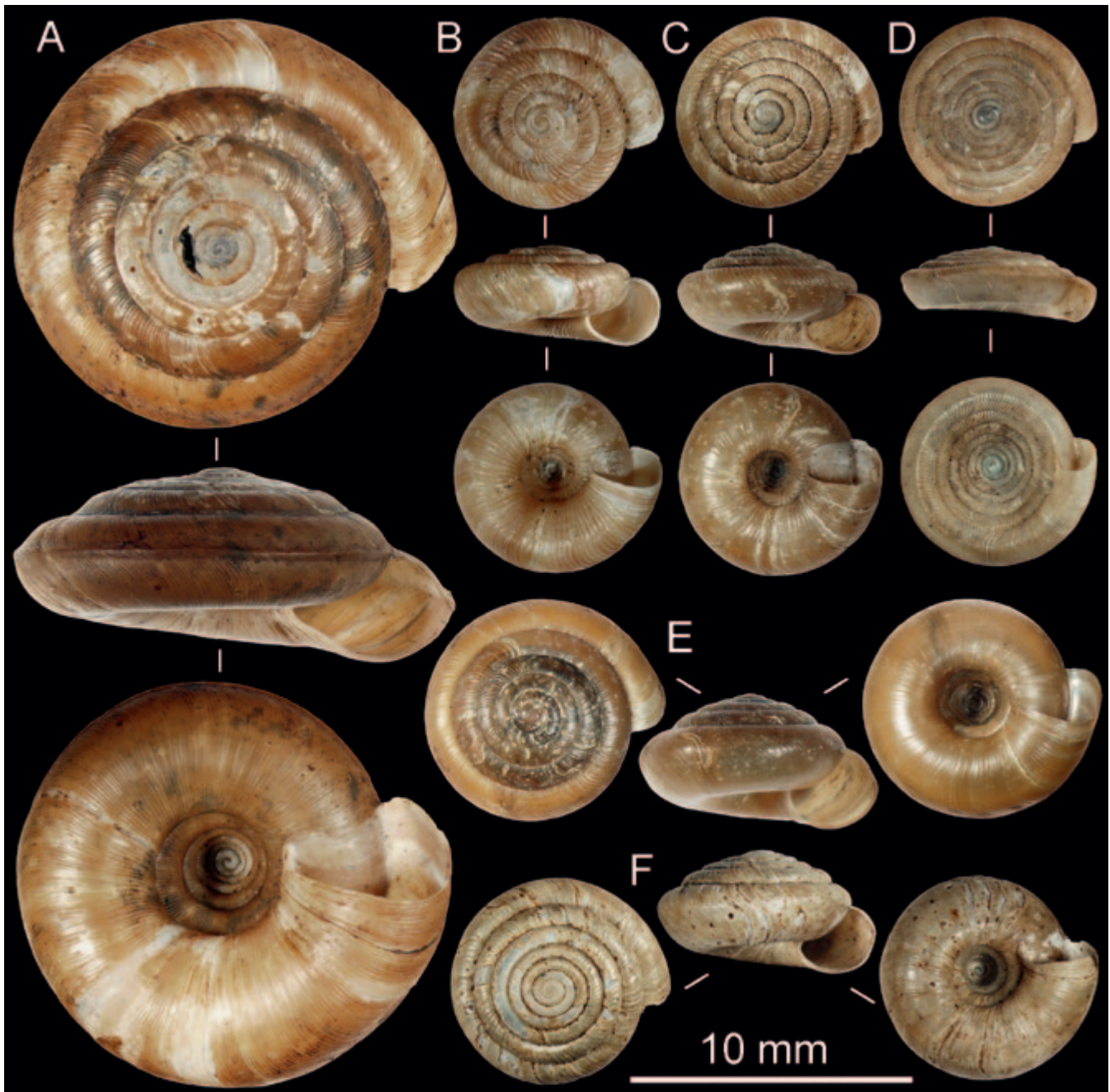
The family Discidae Thiele 1931 of current lists comprises species from various parts of the Holarctic that were all placed by Thiele (1931) in the family Endodontidae, subfamily Discinae, genus *Discus*. Adoption of the name Discidae in preference to Patulidae (based on Patulinae Tryon 1866) follows Bouchet & Rocroi (2005). Thiele grouped the Discinae species in several

**Table 1** Data on the shell characters measured (minimum – maximum, in mm or mm<sup>2</sup>): AB aperture breadth; AH aperture height; AP aperture perimeter; AS aperture surface area; BH body whorl height; BP body whorl frontal perimeter; BS body whorl frontal surface area; D1 maximum shell diameter; D2 shell diameter perpendicular to D1; D3 maximum first whorls diameter; FH first whorls height; FP first whorls frontal perimeter; FS first whorls frontal surface area; SFP shell frontal surface area; SFS shell frontal surface area; SH shell height; SP shell dorsal perimeter; SS shell dorsal surface area; UD umbilicus diameter; n number of specimens measured.

	<i>A. (A.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>	<i>A. (C.)</i>
	<i>gueriniana</i>	<i>saprophylophaga</i>	<i>anagaensis</i>	<i>textilis</i>	<i>ganoda</i>	<i>kompsa</i>	<i>scutula</i>	<i>putrescens</i>	<i>gomerensis</i>	<i>retexta</i>	<i>engonata</i>	<i>rupivaga</i>	
D1	5.5–6.1	12.1–15.8	7.1–7.5	7.1–8.0	8.4–8.8	7.8–7.9	7.1–8.0	8.9–9.5	7.8	6.7	6.7	11.8	
D2	5.2–5.8	10.9–14.5	6.6–6.8	6.5–7.7	7.9–8.3	7.3–7.4	6.7–7.6	8.2–8.7	7.6	6.5	6.7	10.8	
SS	21.3–26.8	96.3–169.0	34.7–37.4	34.5–44.9	49.5–54.7	42.5–43.9	35.8–45.3	54.0–61.2	45.5	32.5	34.1	94.1	
SP	16.9–18.9	35.8–49.5	21.6–22.7	21.3–24.9	25.6–27.2	23.7–24.2	21.8–25.6	27.3–29.8	25.4	21.5	22.1	35.5	
SH	2.4	5.4–6.9	3.3–3.6	3.6–4.5	4.4–5.6	4.3–4.6	2.7–3.0	4.2–4.5	3.5	3.1	3.7	3.1	
SFS	8.9–9.5	43.1–72.2	17.9–19.4	17.7–23.8	26.5–33.2	24.2–25.6	13.0–16.1	24.2–27.3	18.2	13.7	15.2	24.6	
SFP	12.8–14.0	27.4–36.7	17.4–18.4	17.4–20.1	20.7–22.7	19.6–20.0	16.3–19.0	20.9–22.6	18.7	16.6	17.3	25.2	
FH	0.7–0.8	1.2–1.7	0.5–0.7	0.8–1.1	0.7–1.1	0.9–1.0	0.6–0.8	0.9	1.2	0.9	1.1	0.5	
D3	3.6–4.0	7.2–9.9	4.2–4.3	4.6–5.4	5.1–5.7	5.2–5.3	5.0–5.6	4.9–5.1	5.7	4.4	4.6	6.4	
FS	1.8–2.0	5.3–11.0	1.5–2.0	2.5–3.9	2.4–4.1	2.9–3.6	2.2–3.0	2.7–3.0	4.0	2.9	3.1	2.3	
FP	7.6–8.4	15.1–20.7	8.8–9.1	10.0–11.6	10.6–12.5	11.1–11.5	10.5–11.9	10.3–10.8	12.2	9.7	10.1	12.8	
BH	1.5–1.7	4.2–5.3	2.7–2.9	2.6–3.4	3.7–4.4	3.3–3.7	2.0–2.2	3.3–3.6	2.4	2.1	2.6	2.6	
BS	6.9–7.6	37.8–61.3	16.3–17.4	14.5–19.9	24.0–29.1	20.6–22.7	10.8–13.2	21.3–24.6	14.2	10.8	12.1	22.3	
BP	12.5–13.8	26.8–35.8	17.2–18.0	16.7–19.2	20.2–21.8	18.7–19.5	15.9–18.4	20.9–22.3	18.0	15.7	16.4	25.1	
UD	2.4–2.9	3.4–4.5	2.1–2.4	1.9–2.5	2.4–2.6	2.1–2.5	4.3–5.0	2.5–2.8	2.1	3.1	3.3	3.8	
AH	1.4	3.2–4.0	2.2–2.4	1.9–2.4	2.6–2.9	2.4–2.5	1.5–1.9	2.2–2.4	1.7	1.5	1.9	2.1	
AB	1.6–2.0	4.7–6.0	2.6–2.8	2.6–3.0	3.1–3.4	2.9–3.2	1.3–1.8	3.2–3.3	2.8	2.0	1.9	4.5	
AS	1.2–1.4	9.0–13.0	3.5–3.7	3.2–4.6	4.9–6.1	3.9–4.6	1.2–2.0	4.5–5.1	3.1	2.1	2.2	5.7	
AP	4.8–5.3	12.8–15.6	7.9–8.0	7.3–8.8	9.1–10.1	8.3–8.9	4.3–5.5	8.5–9.0	7.1	5.6	5.7	10.4	
n	2	4	3	4	4	2	4	3	1	1	1	1	1



**Figure 4** Shells of: A *Keraea garachicoensis*, a syntype of *Patula (Iulus) garachicoensis* Wollaston 1878 (NHMUK 1985.2.2 73–75; photo by J. Ablett) from Tenerife; B possible syntype of *Helix gueriniana* R.T. Lowe 1852 (NHMUK 1875.12.31.219; photo by J. Ablett) from Madeira; C specimen of *Helix calathoides* R.T. Lowe 1863 (photo by Dinarte Teixeira, UMA), from Deserta Grande Islet, Madeiran Archipelago, currently considered as a subspecies of *A. gueriniana* (Bank *et al.*, 2002) – the arrows mark the location of two pairs of palatal tooth-shaped lamellae, visible by transparency on the outer wall of the body whorl; D syntype of *Helix retexta* Shuttleworth 1852 (NMBE 18783; © 2006 GBIF Switzerland/Eike Neubert), from La Palma (firstly published by Neubert & Gosteli, 2003: pl. 14 fig. 4); E syntype of *Helix engonata* Shuttleworth 1852 (NMBE 18790; © 2006 GBIF Switzerland/Eike Neubert), from Tenerife (firstly published by Neubert & Gosteli, 2003: pl. 14, fig. 1); F syntype of *Helix putrescens* (NHMUK 1875–12–31–299; photo by J. Ablett), from La Palma; G specimen of *Discus gomerensis* Rähle 1994, from drift debris of a stream in Las Rosas ravine, La Gomera; H holotype of *Discus (Canaridiscus) rupivagus* Rähle & Allgaier 2011 (from Rähle & Allgaier, 2011: fig. 1A).



**Figure 5** Shells of *Atlantica* (*Canaridiscus*) species: A paratype of *A. (C.) saproxylophaga* Alonso, G. Holyoak & Yanes in Yanes *et al.* 2011 (JSGC), from La Gomera (first published by Yanes *et al.*, 2011: fig. 2A); B holotype of *A. (C.) anagaensis* Ibáñez & D. Holyoak in Yanes *et al.* 2011, from Tenerife (first published by Yanes *et al.*, 2011: fig. 2B); C specimen of *A. (C.) textilis*, from La Palma (first published by Yanes *et al.*, 2011: fig. 2C); D specimen of *A. (C.) scutula*, from Montaña Grande, Tenerife; E specimen of *A. (C.) ganoda*, from Mériga, La Gomera; F specimen of *A. (C.) kompsa*, from Los Corchos, El Hierro.

sections mainly on the basis of shell characters. His Nearctic sections comprise *Anguispira* Morse 1864, *Mexicodiscus* Pilsbry 1926 and *Planogyra* Morse 1864. The Palearctic sections were *Discus* s. str., *Gonyodiscus*, *Atlantica* Ancey 1887 and *Keraea*. Section *Atlantica* of Thiele included only

the Madeiran species *Helix gueriniana* R.T. Lowe 1852, as *D. (A.) semiplicatus* (L. Pfeiffer 1852), which has 2–3 pairs of tooth-shaped lamellae on the interior of the outer wall of the shell body-whorl (see Fig. 4C). Section *Keraea* of Thiele included *Patula* (*Iulus*) *garachicoensis* Wollaston

1878 from Tenerife and some species from the Cape Verde Islands, without providing their names.

Pilsbry (1948) raised *Anguispira* to the rank of genus in the Discidae, added a new Nearctic subgenus *Discus* (*Nematodiscus*) based on shell characters and described the pallial complex in *Anguispira* and *Discus*, which have the lung long and narrow without large or noticeable branches on the pulmonary vein, kidney triangular, a little longer than the pericardium and the secondary ureter closed. Pilsbry also presented drawings of the jaw and radula of *Discus patulus* (Deshayes 1830) as well as those of the genital system and some details of *Anguispira alternata* (Say 1816) and *A. kochi* (Fig. 1C). Uminski (1963) reported on the taxonomy of *D. marmorensis* H.B. Baker 1932, and Solem (1976) made a detailed anatomical study of the distal genitalia and radula of three *Anguispira* species, *A. alternata*, *A. cumberlandiana cumberlandiana* (I. Lea 1840) and *A. picta* (G.H. Clapp 1920). Contrary to earlier literature, Solem found that the vas deferens enters the penis directly through a simple pore (without an epiphallus) and the penial retractor muscle arises from the diaphragm, not the columellar muscle. He also noted that the marginal radular teeth of *Anguispira* are not multicuspid, maintaining a basically bicuspid condition, the outermost marginals showing splitting of side cusps. On some individual outer marginal teeth there is a weak endocone. Schileyko (2002) raised *Discus* (*Gonyodiscus*) section *Antediscus* Baker in Pilsbry 1948 to the rank of a subgenus of *Discus* and gave detailed drawings of the genital systems of *Anguispira alternata*, *A. (Zonodiscus) kochi* and *Discus (Discus) ruderatus*.

Bank *et al.* (2002) grouped eight Canary Islands species in "*Discus (Gonyodiscus?)*" and included *Patula garachicoensis* in *Keraea*. Their allocation to *Discus (Gonyodiscus)* and *Keraea* has since been adopted by the Fauna Europaea database project (2011), which also included *Helix deflorata* R.T. Lowe 1854 from Madeira in *Keraea*, a species previously classified in *Iulus* by Wollaston (1878). Yanes *et al.* (2011) raised *Atlantica* to the rank of a genus of Discidae and described a new subgenus, *Canaridiscus*, provisionally allocated as *Atlantica (Canaridiscus)*, and two new species from the Canarian Islands. Rähle & Allgaier (2011) described a new *Canaridiscus* species, retaining the genus *Discus* with subgenera *Atlantica* and

*Canaridiscus*. Hence, current understanding of the Discidae species from the Canary Islands can be summarised in Table 2, which also presents data on distribution for each island and refers to the figures of their shells in this paper.

The entire genital systems of some of the European *Discus* species were figured by Uminski (1962) and Riedel & Wiktor (1974) (Fig. 1A, B), these being similar to those of the North American *Discus* and the *Anguispira* species figured by Pilsbry (1948) (Fig. 1C). Uminski (1962) showed differences in the structure of the genital organs of *Discus ruderatus*, *D. perspectivus* and *D. rotundatus*, justifying their taxonomic arrangement in the subgenera *Discus* s. str. (the first-named species) and *Gonyodiscus* (the other two species). The penis of *D. (Discus)* (Fig. 1A) is an elongated cone with the narrow distal end communicating with the genital atrium and the penial retractor inserted on the wider proximal end of the penis and arising from the diaphragm. The vas deferens joins the penis laterally, at one side of the wide proximal end and the prostate is distinctly elongated. In *D. (Gonyodiscus)* (Fig. 1B) the penis is cylindrical and elongated, the penial retractor is attached to the penis laterally and the vas deferens connects with the penis terminally. The prostate is triangular or semicircular in shape. Schileyko (2002) described some additional characters of the *Discus* genital system, mainly related to the internal anatomy of the penis (without penial papilla) and free oviduct (with several pilasters, folds and plicae). He also showed (Schileyko, 2002: fig. 1384B) the presence of a markedly swollen distal zone of the bursa duct and a small stimulator in the proximal end of the penis in *Anguispira (Zonodiscus) kochi*. Finally, the two *Atlantica (Canaridiscus)* species as well as the new species recently described by Rähle & Allgaier (2011) differ from the other Discidae mainly by their remarkably long penis, ca. eight times the maximum shell diameter in *A. (C.) saproxylophaga* (Fig. 1D). It is much longer than that known from any of the Discidae of Europe and North America and too large to be more than partly accommodated in the distal female genital tract.

The absence of the epiphallus was noted by Uminski (1962) in the subgenera *Discus (Discus)* and *D. (Gonyodiscus)* and by Solem (1976) in *Anguispira*. The connection between the vas deferens and the penis in *A. (C.) saproxylophaga* (Yanes



Table 2 Current understanding of the Discidae species from the Canary Islands.

Original name	Usual name (bibliography)	Current name (this paper)	Island	Figure (this paper)
<i>Patula (Iulus) garachicoensis</i> Wollaston 1878	<i>Keraea garachicoensis</i>	<i>Microxeromagna?</i> <i>Xerotricha?</i> <i>garachicoensis</i>	Tenerife	4A
<i>Helix retexta</i> Shuttleworth 1852	<i>Discus (Gonyodiscus) retextus</i>	<i>Atlantica (Canaridiscus) retexta</i>	La Palma	4D
<i>Helix engonata</i> Shuttleworth 1852	<i>D. (G.) engonatus</i>	<i>A. (C.) engonata</i>	Tenerife	4E
<i>Helix (Lucilla) putrescens</i> R.T. Lowe 1861	<i>D. (G.) putrescens</i>	<i>A. (C.) putrescens</i>	La Palma	4F
<i>Discus gomerensis</i> Rähle 1994	<i>D. (G.) gomerensis</i>	<i>A. (C.) gomerensis</i>	La Gomera	4G
<i>Discus (Canaridiscus) rupivagus</i> Rähle & Allgaier 2011	<i>D. (C.) rupivagus</i>	<i>A. (C.) rupivaga</i>	La Gomera	4H
<i>Atlantica (C.) saproxylophaga</i> Alonso, G. Holyoak & Yanes in Yanes <i>et al.</i> 2011	<i>A. (C.) saproxylophaga</i>	<i>A. (C.) saproxylophaga</i>	La Gomera	5A
<i>Atlantica (C.) anagaensis</i> Ibáñez & D. Holyoak in Yanes <i>et al.</i> 2011	<i>A. (C.) anagaensis</i>	<i>A. (C.) anagaensis</i>	Tenerife	5B
<i>Helix textilis</i> Shuttleworth 1852	<i>D. (G.) textilis</i>	<i>A. (C.) textilis</i>	La Palma	5C
<i>Helix scutula</i> Shuttleworth 1852	<i>D. (G.) scutulus</i>	<i>A. (C.) scutula</i>	Tenerife	5D
<i>Helix ganoda</i> J. Mabilie 1882	<i>D. (G.) ganodus</i>	<i>A. (C.) ganoda</i>	La Gomera	5E
<i>Helix kompsa</i> J. Mabilie 1883	<i>D. (G.) kompsus</i>	<i>A. (C.) kompsa</i>	El Hierro	5F

*et al.*, 2011: fig. 3F) is similar to that described by Solem (1976) in *Anguispira*, so an epiphallus is apparently also absent in the subgenus *Canaridiscus*.

#### OBSERVATIONS

##### Family Hygromiidae Tryon 1866

Genus *Keraea* Gude 1911

Type species by original designation: *Patula (Iulus) garachicoensis* Wollaston 1878 (Gude, 1911: 271). [syn: *Iulus* Wollaston 1878, non Linnaeus 1758].

We studied photographs of a syntype of *Patula garachicoensis* (Fig. 4A), which apparently belongs to a species of the Hygromiidae, not to the Discidae. The shell is somewhat immature, with nearly 4½ whorls and maximum diameter of 6.7 mm. It shows irregular ribs above, apparently with some hair-pits and perhaps faint hints of a blotched colour pattern, and looks like an old shell of a hygromiid of the genera *Microxeromagna* Ortiz de Zárate López 1950 or *Xerotricha* Monterosato 1892.

*Patula garachicoensis* and *Helix deflorata* share similar shell characters, differing in dimensions. Wollaston (1878) indicated that the shell diameter of the only specimen of *H. deflorata* (a single adult shell with a large umbilicus and the basal whorl conspicuously – though not very greatly – deflexed at the aperture) is about “5½ lines” (11.6 mm) and that of *P. garachicoensis*, with 5–5½ whorls, is “3½ lines” (7.4 mm). Seddon (1996a) considered *H. deflorata* to be a junior synonym of the European species now known as *Trochulus striolatus* (C. Pfeiffer 1828) following comments from the late H. W. Waldén, who had seen the specimen and commented that it is a shell of that species (*in lit.* to Wells & Chatfield, 1992). Whereas Bank *et al.* (2002) listed *H. deflorata* as a valid taxon, Bank (2009) does not include *H. deflorata* or *Trochulus striolatus* in a list of recent terrestrial gastropods of the Madeiran archipelago.

Besides *P. garachicoensis* and *H. deflorata*, three species from the Cape Verde Islands were grouped by Wollaston (1878) in *Patula (Iulus)*: *Helix gorgonarum* Dohrn 1869; *H. bertholdiana* (M. Pfeiffer 1852); and *H. bouvieri* (A. Morelet 1873). These are also likely to be species of Hygromiidae rather than of Discidae.

##### Family Discidae Thiele 1931 (1866)

[syn: Patulidae, see Bouchet & Rocroi, 2005: 11, 268; ICZN, 1999: Art. 40.2].

Type genus: *Discus* Fitzinger 1833.

Genus *Atlantica* Ancey 1887

Type species by monotypy: *Helix gueriniana* R.T. Lowe 1852, from Madeira Island.

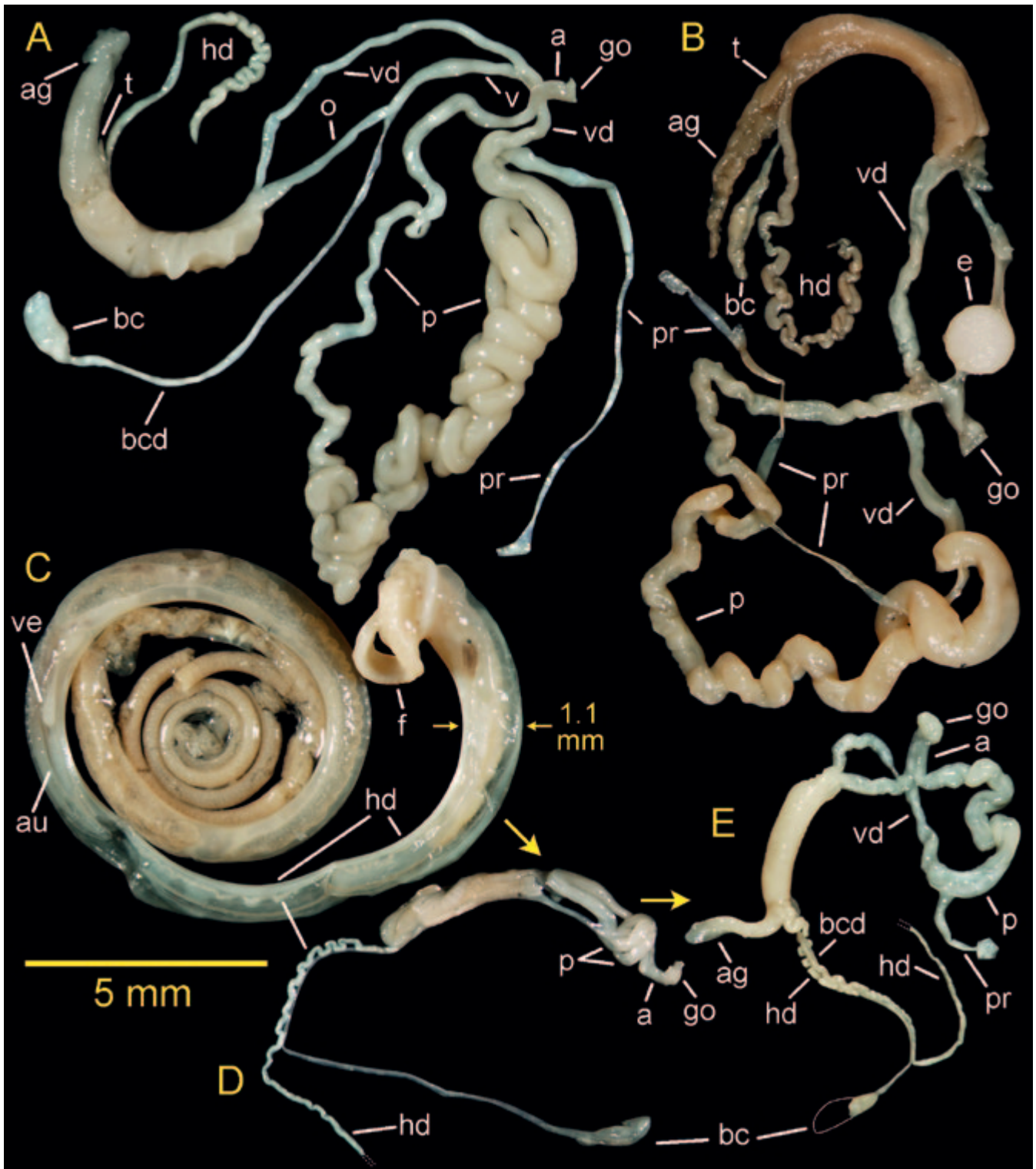
Subgenus *Atlantica* (*Canaridiscus*) Alonso & Ibáñez in Yanes *et al.* 2011

Type species by original designation: *Atlantica (Canaridiscus) saproxylaphaga* Alonso, G. Holyoak & Yanes in Yanes *et al.* 2011, from La Gomera Island.

In addition to *A. (C.) saproxylaphaga*, *A. (C.) anagaensis* and *A. (C.) rupivaga*, we were able to study the genital systems of three other Discidae species from the Canary Islands: *A. (C.) ganoda* (Fig. 6A) from La Gomera, *A. (C.) kompsa* (Fig. 6B) from El Hierro and *A. (C.) scutula* (Fig. 6D, E) from Tenerife. These last three species have the basic structure and arrangement of the genitalia similar to those of the three former species, although there are differences mainly in the penis length. Hence they can be shown to belong in the subgenus *Canaridiscus*. The remaining Discidae species from the Canary Islands for which the genital anatomy remains unknown are also likely, therefore, to be species of this subgenus.

The longest penis is that of *A. (C.) saproxylaphaga*, followed in turn by *A. (C.) ganoda*, *A. (C.) rupivaga*, *A. (C.) anagaensis*, *A. (C.) kompsa* and *A. (C.) scutula*. The shortness of the penis of *A. (C.) scutula* is perhaps related to the thinness of the soft part body (Fig. 6C, its maximum diameter being 1.1–1.2 mm), but it is proportionally longer than those of the genera *Discus* and *Anguispira*. The “ampulla” of the hermaphroditic duct has been found only in *Atlantica saproxylaphaga* and *A. (C.) ganoda*. The talons of *A. (C.) saproxylaphaga*, *A. (C.) anagaensis*, *A. (C.) ganoda* and *A. (C.) kompsa* are similar to, but seemingly less developed, than those of *Anguispira alternata* and *A. kochi* drawn by Pilsbry (1948: figs 304D, E), as well as that of *A. cumberlandiana cumberlandiana* drawn by Solem (1976).

*Affinities of the Discidae genera:* *Discus*, *Anguispira* and *Atlantica (Canaridiscus)* share many shell



**Figure 6** A, B, D, E, genital systems; C, body of the animal extracted from the shell. A *Atlantica* (*Canaridiscus*) *ganoda*; B *A. (C.) kompsa*; C–E *A. (C.) scutula*. Parts: a atrium; ag albumen gland; au auricle; bc bursa copulatrix; bcd bursa copulatrix duct; e egg; f foot; go genital orifice; hd hermaphroditic duct; o oviduct; p penis; pr penis retractor; t talon; v vagina; vd vas deferens; ve ventricle.

and anatomical character-states, as follows: a shell moderately to strongly depressed, radially ribbed, with the base having a widely open

umbilicus that reveals all the whorls including the nucleus; lung long and narrow, without large or noticeable branches on the pulmonary vein;

kidney triangular, a little longer than the pericardium; secondary ureter closed; male genital system lacking flagellum and epiphallus; penis without penial papilla; bursa copulatrix small; bursa duct long and very thin, without diverticulum.

The genera *Discus* and *Anguispira* share similar characters of the genital system, notably a short penis (Fig. 1A–C), whereas *Atlantica* (*Canaridiscus*) clearly differs from both of them because it has a much longer penis (Fig. 1D). Therefore the relationship of *Atlantica* (*Canaridiscus*) with *Discus* and *Anguispira* is apparently more distant than that between the last two genera.

### GENERIC CLASSIFICATION

Due to the unknown anatomical and genetic characteristics of *Atlantica gueriniana* from Madeira (the type-species of the genus *Atlantica*), the existence of close relationships between the Madeiran and Canary Islands Discidae can only be surmised. Nevertheless, they have generally similar shell characters as described above and both are related to the peculiar laurel forest vegetation type (*laurisilva*) of these archipelagos in northern Macaronesia (Wollaston, 1878), although the Madeiran species was recently found outside the *laurisilva*, in drier but well vegetated regions (Cameron & Cook, 1999) and *A. gueriniana calathoides* occurs in dry habitats of the Desertas (which have their maximum altitude at 442 m). Thus, we provisionally group *Canaridiscus* in *Atlantica*, raising the latter to generic rank in the Discidae, because *Canaridiscus* is not closely related to the genera *Discus* and *Anguispira*. Future study of the genital system of the Discidae species from Madeira is needed to either confirm the position of *Canaridiscus* as a subgenus of *Atlantica* or raise it to generic rank. However, future studies of the Discidae combining anatomical and molecular techniques may modify our understanding of the systematics of the whole family.

### HABITATS

The Canarian Discidae species have a narrow range of habitats. The Canary Islands species mostly live in the *laurisilva*, a forest found in

subtropical or warm-temperate areas with high humidity and relatively stable temperatures. The older literature indicates that they were generally found on the ground beneath the trunks of decaying trees, pieces of rotten wood, dead leaves, or sometimes beneath stones (Mousson, 1872; Wollaston, 1878). Recent finds were mostly in undisturbed, humid laurel forest, closely associated with rotting wood. The two recently described species, *A. (C.) saproxylophaga* and *A. (C.) anagaensis*, were found inside the humid trunks of decaying trees, beneath them, or in both types of site.

Exceptional finds in other habitats include the holotype of *A. (C.) gomerensis* (an empty white shell) and the species *A. (C.) rupivaga*. *A. (C.) gomerensis* was found in a ravine outside the *laurisilva*, near the Macizo de Teselinde (La Gomera Island), but about 2 km to the north-east of the Epina mountain, which has laurel forest (Fig. 2, the arrow on La Gomera map). Some specimens of this species were also collected by J. Santana (JSGC; Fig. 4G) in Las Rosas ravine (UTM: 28RBS8420, 250 m altitude), about 8 km east of the type locality; the latter locality is not included on the map because the shells were from stream deposits. *A. (C.) rupivaga* was found hidden in narrow crevices of shattered, northeast-exposed volcanic rocks, as well as between stones at the base of these rocks, at an altitude of 600 m; it is the only *A. (Canaridiscus)* species known to live in narrow rock crevices.

The main vegetation type at the *A. (C.) rupivaga* locality nowadays is pine forest (Rähle & Allgaier, 2011: fig. 1C) but this forest results from re-forestation begun between 1960 and 1970 (Del Arco *et al.*, 1990, 2006) on an area where the ancient vegetation was mainly *laurisilva*. Although the species has evidently survived this change from *laurisilva* to pine forest, its survival was probably due to the adaptation to living in rock crevices.

In addition, some specimens of *A. (C.) scutula* from Tenerife (localities outside the Anaga mountains, between 1000 and 1250 m altitude) and *A. (C.) textilis* from La Palma (to 1500 m altitude), were found outside the *laurisilva*, in pine forest (Fig. 2, see arrows on Tenerife and La Palma maps). In the case of *A. (C.) scutula*, it is possible that these few occurrences are from areas where laurel forest occurred formerly but regressed mainly as a consequence of human impacts much as in the *A. (C.) rupivaga* locality;

there is abundant evidence of historic reduction in extent of the laurel forests (Parsons, 1981; de Nascimento *et al.*, 2009; Fernández-Palacios *et al.*, 2011). In the case of *A. (C.) textilis*, it is more likely that a natural regression of the higher-altitude laurel forests has occurred due to changes in the moist trade winds, which are essential for the presence and development of the *laurisilva*, since there is currently no *laurisilva* in the Canary Islands above 1200 m altitude (Yanes *et al.*, 2009c: Fig. 2). Survival of *A. (C.) scutula* and *A. (C.) textilis* could perhaps be related to the presence of trunks of decaying trees and pieces of rotten wood in the pine forest that has replaced *laurisilva*.

## DISCUSSION

*Evolution and biogeographical history of Discidae*  
The occurrence of endemic Discidae in the Canary Islands, which differ widely in anatomy from the living European and North American species, is described above. All of the Canary Islands they inhabit have ages of less than 12 Mya, so we are confronted with a problem in explaining the occurrence there of taxa more distinctive than any of those on the geologically much older European and North American continents. This is addressed in the following sections of the Discussion, through consideration of: time-scales for evolution of Stylommatophora and of Discidae in particular, based on fossil records and “molecular-clock” studies; timing of separation of the European and American continents and the European-African connection, as deduced from geochronological, geomagnetic and other geological data; evidence of the volcanic origins and ages of the Canary and Madeiran archipelagos; origins of the land snails and other biota of Madeira and the Canaries, including evidence that Canaries Discidae were mainly restricted to relict laurel forests; the history of *laurisilva* in the western Palearctic; and the most parsimonious model to explain distributional history of Discidae in the Canaries and other regions. Terminology for divisions of the geological record and the ages assigned to them here follow Gradstein *et al.* (2005) and Ogg *et al.* (2008).

*Time-scales for evolution of Stylommatophora and of Discidae* Records of fossil terrestrial pulmo-

nates from the Carboniferous coal forests (*ca* 300 Mya) were regarded as representing the earliest Stylommatophora by Solem & Yochelson (1979), but some of these have been reidentified as non-stylommatophoran eupulmonates by Bandel (1991, 1997) and attribution of Carboniferous fossils to several Recent stylommatophoran families is now regarded as highly controversial (Mordan & Wade, 2008). The suggestion has been made that no land snails survived the mass extinction event at the end of the Permian (250 Mya) with a loss of up to 95% of all species (Wade *et al.*, 2006). However, not all animal taxa were equally affected by this event and terrestrial invertebrates appear to have survived the crisis better than marine animals or terrestrial tetrapods (Stworzewicz *et al.*, 2009); for example, only eight of the 27 orders of Paleozoic insects became extinct, and nearly half of the remaining ones survived to the present day (Labandeira & Sepkoski, 1993).

Solem & Yochelson (1979), in their detailed study of North American Upper Paleozoic land-snail fossils, placed *Protodiscus priscus* (Carpenter 1867) within the Discidae based on its shell sculpture. Subsequent workers have regarded it as belonging to an uncertain family but possible the Pleurodiscidae (Nordsieck, 1986), or perhaps the Valloniidae (Stworzewicz *et al.*, 2009). This species has also been found in Early Permian (250–260 Mya) sediments of the Upper Silesian-Cracow Upland (Karniowice, S. Poland), indicating it occurred not only in proto-N. America, but also in the European part of the Pangea supercontinent (Stworzewicz *et al.*, 2009). There are additional records of fossil pulmonates from the Middle Jurassic (Planorbidae representing the *Hygrophila* from the Doggerian Epoch, 188–163 Mya) and Late Jurassic (Ellobiidae and Siphonariidae from the Malm Epoch, 163–144 Mya), but no undisputed fossil Stylommatophora from before the Cretaceous (130 Mya: Bandel, 1991, 1997; Zilch, 1959). Fossils of species assigned to the Discidae have been recognised from the Upper Cretaceous (65–100 Mya), Eocene, Oligocene and Miocene in America (Henderson, 1935; Pilsbry, 1948; Pierce & Constenius, 2001), and there were many Tertiary species reported from Europe (Wenz, 1923; Zilch, 1959; Harzhauser & Binder, 2004; Harzhauser *et al.*, 2008).

On the basis of a “molecular-clock” approach, Tillier *et al.* (1996) suggested that divergence and

rapid early diversification of the Stylommatophora occurred around 90–60 Mya (Late Cretaceous to Paleocene), which is at least roughly congruent with the 130 Mya demonstrated by fossils. Wade *et al.* (2001) and Wade *et al.* (2006) presented the fullest molecular studies currently available of the Pulmonata. They revealed an early separation into an “achatinoid clade” and a “non-achatinoid” lineage, both of which contain families originating in the Mesozoic southern supercontinent of Gondwanaland. Some of these had a wide distribution in Gondwanaland before its fragmentation in the Late Jurassic (around 150 Mya), from which it is reasonably assumed that the initial diversification of Stylommatophora took place even earlier. Wade *et al.* (2001) showed that the Discidae are not closely related to Punctidae, Charopidae or Otoconchidae as suggested by previous studies. Instead, the Discidae appears as an early offshoot of a very large clade that later gave rise successively to Cerionidae, Haplotrematidae, Spiraxidae and eventually to all Helicoidea. In addition, it is clear that the Discidae are not only known exclusively from the Holarctic (living or as fossils), but that they show no close affinity with any group originating in Gondwanaland, strengthening the likelihood that they originated in the northern supercontinent Laurasia.

*Timing of separation of the European and American continents and the European-African connection*  
Prior to the separation of Gondwanaland and Laurasia (Triassic, 248–213 Mya) the single large land mass (Pangea II) comprised Laurasia in the north (with proto-North America as its southern part, proto-Europe as its northern part) and Gondwanaland in the south (with its northern part comprised of proto-South America in the west, proto-Africa in the east) (Scotese, 2001). During the Jurassic, Gondwanaland and Laurasia separated and the developing Atlantic Ocean separated Laurasia into proto-North America and proto-Europe. By the Late Jurassic (152 Mya) the Atlantic Ocean was still much narrower than at the present day and seas of approximately similar width separated North America from South America and Europe from Africa (Smith *et al.*, 1973). Geological and paleobiogeographical data show that Africa was isolated from the Mid-Cretaceous to Early Miocene, i.e. for ca. 75 Mya, but also that this isolation was broken intermit-

tently by discontinuous filter routes that linked it mainly to Laurasia until the Early Miocene (ca. 23 Mya), when a definitive connection with Eurasia was established (Gheerbrant & Rage, 2006). This connection was interrupted on its western side at the start of the Pliocene (ca. 5 Mya), when the Straits of Gibraltar were formed.

*Volcanic origins and ages of the Canaries and Madeira*  
The Canarian and Madeiran archipelagos are comprised exclusively of volcanic islands that rose above sea-level in the Tertiary, after the Atlantic had almost reached its present-day width. The oldest dated rocks known to still exist on land that is subaerially exposed are in the eastern Canaries (15.5–20.6 Mya), but these islands lack laurel forests and also Discidae. This is no doubt because the moist trade winds ascend to altitudes higher than those of both islands (with the exception of a small peak on each of them). Although Fuerteventura now has a maximum altitude of 806 m (La Zarza Peak), it is estimated to have reached about 3000 m high in the Miocene (Stillman, 1999). The western Canaries range from 1.1 Mya (El Hierro) and 1.7 Mya (La Palma) to 7.5 Mya (Tenerife) and 12 Mya (La Gomera) (Carracedo *et al.*, 2005). The small island of Porto Santo is the oldest of the Madeiran islands (10 Mya) and it lacks Discidae; the larger Madeira island is up to 5 Mya but has suffered renewed vulcanism as recently as 2.5 Mya. However, Fernández-Palacios *et al.* (2011) have recently argued from geological evidence that large and high islands may have been continuously available in northern Macaronesia for very much longer than is indicated by the surface of the oldest current island of the region, possibly for as long as 60 Mya.

*Origins of the land snails and other biota of Madeira and the Canaries*  
Currently, because of the unknown anatomical and genetic characteristics of *Atlantica gueriniana* from Madeira, the existence of close relationships between the Madeiran and Canarian Discidae can only be surmised. Nevertheless, as discussed above, we provisionally group all of these taxa in *Atlantica* based on the similarities in shell shape and main habitats.

Waldén (1984) indicated that “the most conspicuous difference between the land-mollusc faunas of Madeira and the Canary Islands is the

complete absence of taxa with north-west African affinities on Madeira, despite the fact that they hold a similar position relative to the African continent". Indeed, Porto Santo, the oldest island of the Madeiran archipelago, was susceptible to colonisation for over 10 Mya without major volcanic activity and colonists are thought to have arrived by island-hopping from Europe (i.e. the south-west Iberian Peninsula) through a former island chain now remaining as seamounts (Cook, 2008). It has been suggested that the Canary Islands were colonised by land-snails from neighbouring north-west Africa, possibly on floating vegetation rafts (Alonso *et al.*, 2000; Arnedo *et al.*, 2001; Yanes *et al.*, 2009b). An Afrotropical origin seems likely for the endemic Canary Islands genus *Gibbulinella* (Rowson *et al.*, 2011). However, the Canarian Discidae have close ecological ties to the laurel forest, as do several other genera of land snails present in both the Canaries and Madeira (*Craspedopoma* L. Pfeiffer 1847, *Lauria* J.E. Gray 1840, *Leiostyla* R.T. Lowe 1852, *Columella* Westerlund 1878). Hence greater similarity of the land-snail faunas of these archipelagos is evident than was implied by Waldén's (1984) analysis.

Different groups of plants show differing patterns of phytogeographical affinity between the archipelagos in northern Macaronesia. There are relatively few endemic genera of angiosperms compared to older island archipelagos or continental fragments: ca 15 of them being found only in the Canaries, 4 only in the Madeiran archipelago (*Chamaemeles*, *Monizia*, *Musschia*, *Parafestuca*), none only in the Azores, three in both the Canaries and Madeira, one in the Canaries and the Azores (*Lytanthus*), one in Madeira and the Azores (*Melanoselinum*) and one in all three archipelagos (*Aichryson*) (Good, 1964; Press & Short, 1994). Analyses of floristic data sets for liverworts (Hepaticophyta) and Pteridophyta support (or cannot reject) existence of an Azorean-Madeiran-Canarian clade, whereas a similar analysis of the mosses (Bryophyta) resolves the Canary Islands as sister to North Africa (Vanderpoorten *et al.*, 2007). Even within the liverworts, *Plagiochila stricta* (Dickson) Dumortier from the Canaries has been demonstrated to have close Neotropical affinities and origin by a wealth of molecular, phytochemical and morphological data (Rycroft *et al.*, 2002); its microscopic spores might of course have been wind-blown across the Atlantic. In con-

trast, the liverwort *Radula lindenbergiana* Gottsche ex C. Hartmann may have had a refugium in the Macaronesian archipelagos during Quaternary glaciations, from which it subsequently recolonised the European continent (Laenen *et al.*, 2011). Among angiosperms, the four genera of Lauraceae that characterise the Macaronesian *laurisilva* all occur in both the Canaries and Madeira, with *Apollonia* and *Ocotonia* absent from both the Azores and neighbouring continental regions, whilst *Persea* and *Laurus* also occur in the Azores and the latter is present additionally in southern Europe and north-west Africa (Hohenester & Weiss, 1993; Fernández-Palacios *et al.*, 2011). All of these trees have large fleshy fruits that are likely to be dispersed primarily by frugivorous birds, principally pigeons, so it is surely no coincidence that endemic frugivorous pigeons occur in the *laurisilva* of Madeira (*Columba trocaz* Heineken 1829) and the Canaries (*C. bollii* Godman 1872, *C. junoniae* Hartert 1916). All three of these birds specialise in Lauraceae fruits and all are thought to have derived from the European and North African continental species *C. palumbus* Linnaeus 1758 (Goodwin, 1977; Cramp *et al.*, 1985; Emmerson, 1985; Oliveira *et al.*, 2002; Marrero *et al.*, 2004).

In contrast to the vast Tertiary colonisation of northern Macaronesian islands deduced for many of the plants discussed above, a molecular study of *Erica arborea* Linnaeus (Ericaceae) demonstrates colonisation of both Madeira and the Canaries during the Pleistocene *via* the Mediterranean basin, from refugia in East Africa (Désamoré *et al.*, 2011). *Erica arborea* has very small dry seeds and it may be surmised that these are readily dispersed over long distances. Overall, it is probably unsurprising to find multiple patterns of colonisation of Madeira and the Canaries that have varied between different groups of organisms, partly no doubt due to their differing propagules and dispersal agents, partly due to differing climatic or ecological tolerances, but perhaps also sometimes due only to chance. Consequently, it is unwarranted to expect to find only a single pattern of colonisation among the land snails of each of these archipelagos.

*History of laurisilva in the western Palearctic* In the western Palearctic the laurel forest vegetation type is now restricted to middle levels (600–1200 m a.s.l.) in the mountains of the

Azores, Madeira and the western Canary Islands. A varied evergreen forest vegetation of similar subtropical affinities, but richer in plant genera, was widespread in Europe (northwards to the London basin: Reid & Chandler, 1933) during the Early and Middle Tertiary, 65–24.6 Mya. Thereafter, the forest became progressively less diverse and apparently retreated southwards by the Miocene (24.6–5.1 Mya) and especially the Pliocene (5.1–2.0 Mya) (e.g. Krutzsch, 1967; West, 1968; Flenley, 1979; Nilsson, 1983; Fernández-Palacios *et al.*, 2011).

By the Early Pleistocene, the subtropical evergreen forest had disappeared from the mainland of Europe and north-west Africa. However, some of its characteristic plants persisted as relicts characterising the *laurisilva* on the Azores, Madeira and Canaries (Fernández-Palacios *et al.*, 2011). Four Late Pleistocene marine pollen records from offshore of Portugal and Morocco representing the period 250–5 Kya demonstrate that in the presumed mild (interglacial) stages (respectively 240–190, 125–70, 10–5 Kya) a Mediterranean oak forest was widespread in the continental areas to the east, whereas during colder (glacial) stages a steppe-like vegetation (*Artemisia* rich, partly wooded with *Pinus*) formed a transition zone between the Sahara to the south and the tree-less tundras of western Europe (Hooghiemstra *et al.*, 1992). Roucoux *et al.* (2001) have subsequently demonstrated that the changes in the marine pollen record offshore of continental Portugal from 65–9 Kya closely tracked temperature changes deduced from marine oxygen-isotope data, with Mediterranean oak forest occurring only during the warm stages. Neither study showed palynological evidence for anything resembling *laurisilva* on the European and north-west African mainland during the past 240 Kya and it seems highly unlikely that most of its characteristic plants could have survived there during the cold stages (a few exceptions probably included *Laurus nobilis* Linnaeus and *Prunus lusitanica* Linnaeus, both of which still grow in the Iberian Peninsula).

Iberia and the Maghreb are of course rich in endemic biota and the region has repeatedly been demonstrated as a likely “Atlantic-Mediterranean refugial area” allowing survival of species through the Late Pleistocene cold stages (e.g. Schmitt, 2007), but these are animals and plants of varied open or aquatic habitats or

deciduous woodlands, not stenophiles requiring floristically-rich, broadleaved, evergreen forests. Colonisation of the Canaries by Discidae was apparently restricted to *laurisilva* habitats so that it almost certainly followed the arrival of this vegetation type, while persistence of their Discidae to the present day was doubtless related to continuing presence of the *laurisilva* throughout the Late Tertiary and Pleistocene.

*A model of distributional history of the Discidae*  
Much of the information that would allow a detailed understanding of the evolution and biogeographical history of Discidae is lacking. The fossil record of the family is probably very incomplete, the known fossils (shells) cannot provide the data on genital anatomy that would allow better assessment of their generic affinities, and there has been no molecular study of the phylogeny of the extant taxa. Attempts at reconstructing the history of the family must therefore be generalised and somewhat speculative, accompanied by recognition that the simplest explanation may not be the correct one.

The earliest radiation of taxa in the Discidae was probably no older than Upper Cretaceous (ca. 100–65 Mya), as established by fossils from America (Henderson, 1935; Pilsbry, 1948; Pierce & Constenius, 2001), but it could be much older than this. Numerous fossil taxa (Wenz, 1923) also confirm that the range extended to Europe through much of the Tertiary (65–5 Mya). By the Late Cretaceous the widening north Atlantic Ocean was still much narrower than at the present day, with relatively narrow sea gaps separating the British Isles from Newfoundland, Labrador and southern Greenland (e.g. Smith *et al.*, 1973). By the Eocene (54.9–38 Mya) the sea gaps involved were wider, but considerably narrower than they are today. Throughout the Late Cretaceous and Early Tertiary the vegetation at the palaeo-latitude of 30°–40° N was essentially subtropical broad-leaved forest. The Eocene flora of the London Clay (Reid & Chandler, 1933) gives detailed evidence of this, and Pearson (1964) provided data suggesting this flora had clear tropical affinities. However, Steenis (1962) has argued that much of this flora may consist of material drifted across the Tethys; Muller (1970) found that European Eocene pollen and spore micro-floras are very different to the few known Indo-Malayan ones; likewise, Krutzsch



(1967) found that there is evidence of only a few Indo-Malayan taxa penetrating Europe in warm phases. Thus, Daley (1972) was led to suggest that the London Clay climate of the Eocene was seasonal but frostless, with higher rainfall than today (for the palaeo-latitude that was then 40° N.), warmer than now, but not as warm as in tropical rainforest regions. Occurrence of Eocene coral reefs in the London basin nevertheless strengthens the evidence for at least a moderately warm climate. The early Discidae could therefore have had ample opportunity to cross the narrow north Atlantic Ocean of the Late Cretaceous and Early Tertiary and find suitable habitats on both sides. The much later overseas colonisation of the Canaries and Madeira demonstrates that representatives of the family have the ability to cross substantial sea gaps.

It might seem simpler to imagine early Discidae occurring in the Triassic (248–213 Mya) or Early Jurassic, when proto-Europe and proto-North America were a single land mass. However, this is much earlier than any fossils assignable to Discidae. An additional objection to the hypothesis of such ancient existence and spread of Discidae is that their broad-leaved forest habitat did not exist until much later, when a diverse flora of angiosperms evolved during the Cretaceous and gradually replaced vegetation dominated by cycads, conifers and ferns (e.g. Axelrod, 1959, 1963; Muller, 1970; Wolfe *et al.*, 1975; Hughes, 1976).

The following hypothetical outline of biogeographical history of Discidae in Europe and northern Macaronesia since the Early Tertiary can therefore be suggested as the simplest scenario accounting for the evidence available. (1) The numerous species of the family present in the Tertiary of Europe (Wenz, 1923; Zilch, 1959), included lineages allied to those still extant in North America. (2) The emergent Madeiran islands and Canaries were colonised in the Tertiary from Europe, North Africa, or both, by Discidae of a lineage no longer present in these continental areas. (3) On the European continent Discidae were reduced to three surviving species (one of them also in NW. Africa) by the Late Pleistocene (250–0 Kya), none of which is closely related to the relict taxa present in the Canaries and, probably, also in Madeira. These extinctions resulted from climatic and vegetational changes (cf. discussion above). (4) Subsequent evolution

probably accounts for some of the characters of each of the Madeiran and Canaries species, all of which are distinctive single-island endemics.

*Conservation of Macaronesian Discidae* The morphological and taxonomic uniqueness of the Discidae of the Canary Islands, their relict nature and restriction predominantly to the *laurisilva* habitats, emphasise the importance of their conservation.

Fontaine *et al.* (2007) showed that most of the recent extinctions in Europe have affected taxa with small geographical ranges, along with others having strict ecological requirements. Similarly, most European species listed as threatened in the IUCN Red List have small ranges. Most Canarian Discidae have small ranges and *D. engonatus*, *D. retextus*, *D. textilis* and *Keraea garachicoensis* were included in the list of European globally extinct taxa by Fontaine *et al.* (2007), as was *Janulus pompylius* (Shuttleworth 1852) of the Gastrodontidae, but without details being given of the reasons for them being regarded as extinct.

Fortunately, among the Discidae species listed by Fontaine *et al.* (2007) as globally extinct, at least *Atlantica (Canaridiscus) textilis* is known to still survive since we collected several fresh shells at two localities on La Palma Island (e.g. Fig. 5C). Similarly, the Madeiran *A. gueriniana* was originally listed as possibly extinct (Wells & Chatfield, 1992; Groombridge, 1994; Seddon, 1996b), then reassessed as extinct (E) in the 1996 *Red List* (Baillie & Groombridge, 1996) because it had not been recorded since the 1860s despite intensive searching since 1983. However, Cameron & Cook (1999) rediscovered it at the western end of Madeira island at two close, but separate locations. It was found there outside the *laurisilva*, in drier but well vegetated regions, on highly disturbed precipitous hillsides facing the ocean, differing from the habitats described in Wollaston (1878). Apparently only shells have been recorded recently, but these are sufficiently fresh to assume the species is living at these sites (Seddon, 2000). *A. gueriniana calathoides* might possibly also survive in the Desertas and it remains possible that several of the other species currently listed as extinct will be refound living because all of them were from locations which have remained undisturbed, or relatively undisturbed.

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