

A REVIEW OF *RETINELLA* (*LYRODISCUS*): THE ENDEMIC ZONITIDAE OF THE CANARY ISLANDS

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Abstract The genital anatomy is described for all five island populations of *Retinella* (*Lyrodiscus*) endemic in the Canary Islands, revealing that it is mainly similar to that of the only species studied previously (*R. circumscissa*). Their shell characters, detailed distribution and habitat preferences are also described and reassessed. Five species are recognised. The population of El Hierro has hitherto been assigned to *R. lenis*, the species on La Palma, but it is named as a new species here. Descriptions of species from the south-west Alps by Giusti *et al.* (1986) revealed additional combinations of anatomical and shell characters that made it impossible to identify the limits of subgenera among the European *Retinella* species. *Lyrodiscus* was regarded by them as a possible exception to this because of its peculiar shell sculpture. Since our data show that the endemic Canary Islands species assigned to *Lyrodiscus* from conchological characters are also very similar to each other anatomically, it is useful to retain them together in the same subgeneric group until a phylogenetic study provides an adequate basis for a revised classification. Two additional *Lyrodiscus* species showing the characteristic shell sculpture are known from fossils in NW. Europe. Hence, it is argued that the species still living in the Canary Islands can most easily be regarded as relicts of a fauna that was widespread in NW. Europe in the Neogene and early Pleistocene. There, they apparently became extinct during the cold conditions of the Late Pleistocene glacial stages, whereas they survived in the milder climates within forest and scrub-covered habitats on the Canary Islands.

Key words Macaronesia, Canary Islands, *Retinella*, *Lyrodiscus*, subgenera, Zonitidae, genital anatomy, genital pore, shells, palaeobiogeography, island endemics, Tertiary relicts, Pleistocene fossils

INTRODUCTION

The archipelagos of the eastern Atlantic Ocean, known as the Macaronesian region, contain a richly diverse fauna of native land snails which has undergone extensive speciation. Nevertheless, many of these snail taxa remain poorly known. The subgenus *Retinella* (*Lyrodiscus*) of the Zonitidae, known living only in the Canary Islands, is among the poorly known groups. Although the subgenus occurs on five islands and has four species recognised in a recent checklist (Bank *et al.*, 2002: 113), a recent review of shell characters (Rousseau & Puisségur, 1990) covered only three of the species and accounts of the genital anatomy are available for only one species (*R. circumscissa*) and those are somewhat incomplete.

The description of *Retinella* (*Lyrodiscus*) *skertchlyi* Kerney (1976) from the Middle Pleistocene of southern England and attribution of *Helix jourdani* Michaud from the Lower Pliocene of France to the same subgenus by Rousseau & Puisségur (1990) has increased interest in the living relatives of *Lyrodiscus* and their palaeobiogeographical history.

Riedel (1977) subdivided *Retinella* into three subgenera (*Retinella* s. str., *Lyrodiscus* Pilsbry 1893 and *Retinelloides* Riedel 1977). This subdivision was questioned by Giusti *et al.* (1986), who regarded *Retinella* as “a very polymorphous taxon” and commented that it is impossible to identify the real limits of the subgenera “(perhaps with the exception of *Lyrodiscus*)”.

In the present study we describe and figure the genital anatomy of all five species of *Lyrodiscus*. Species differences in shell characters are also re-examined for all five island populations and their distribution and habitat preferences are described. The population of El Hierro has hitherto been assigned to *R. lenis* (Shuttleworth 1852), the same species as on La Palma: this is reassessed, leading to the conclusion that the population of El Hierro belongs to a new species that is named here. The relationships and subgeneric affinities of the species are then reviewed, with reference also to taxa known fossil in NW. Europe.

The palaeobiogeographic hypothesis is discussed that the *Retinella* (*Lyrodiscus*) living in the Canary Islands can most easily be regarded as relicts of a fauna that was widespread in NW. Europe in the Neogene and early Pleistocene. There, they apparently became extinct during

the cold conditions of the Late Pleistocene glacial stages, whereas they survived in the milder climates within forest and scrub-covered habitats on the Canary Islands.

METHODS

Snail specimens were drowned by immersion in water, then fixed in 70% industrial methyated

spirit or 80% ethanol. Maps of geographical distribution (Fig. 1) were produced using MapViewer software (Golden Software Inc.). The photographic methodology was described by Ibáñez *et al.* (2006). Shell growth is indeterminate in these Zonitidae, so comparative measurements given are from a few of the largest shells available, mainly those where dissection revealed mature genitalia. These standardised

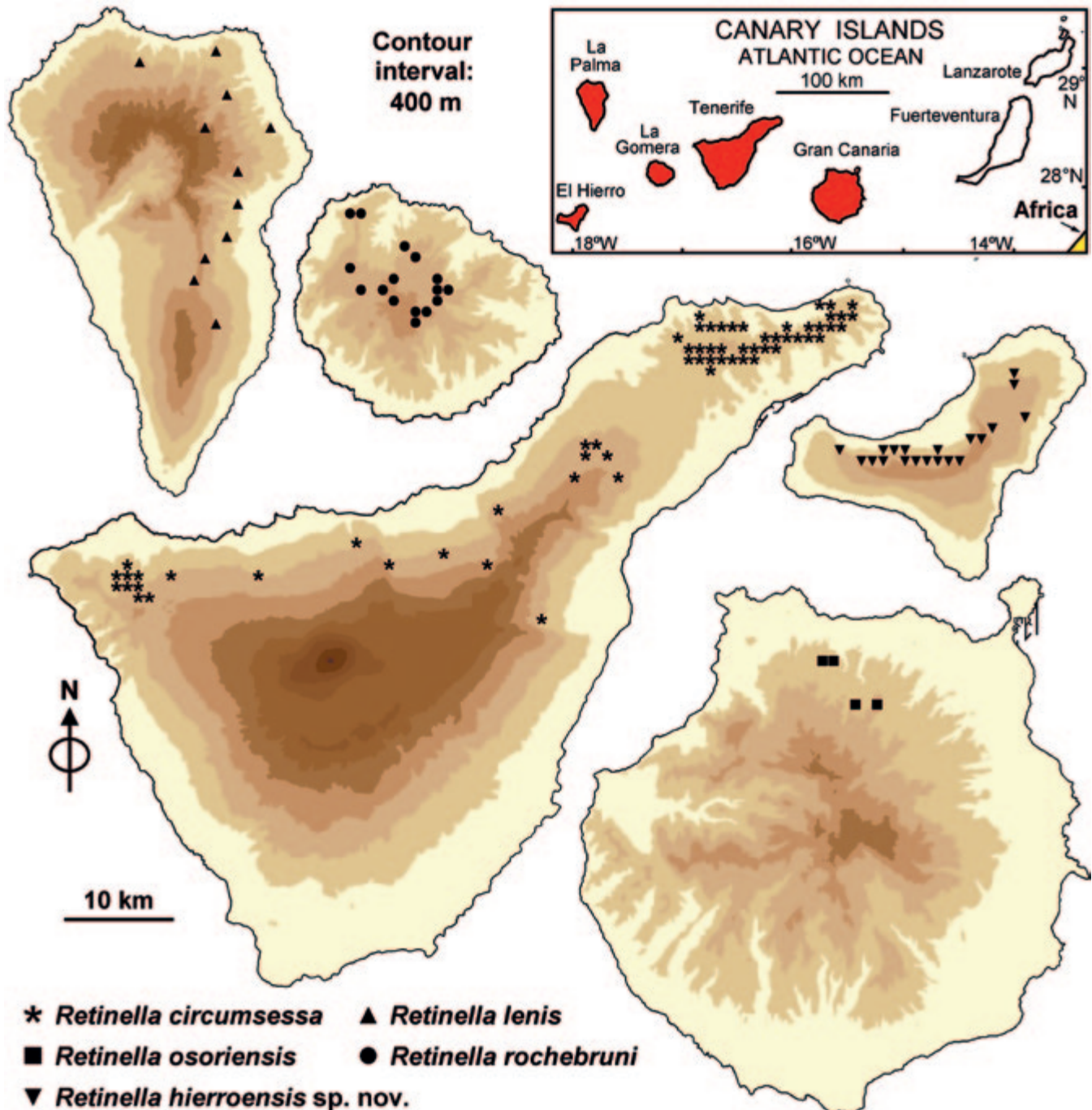


Figure 1 Geographical distribution of *Retinella* (*Lyrodiscus*) species in the Canary Islands, mapped by one-kilometre squares of the UTM grid.

measurements of the shells in the text and Table 1 were made either using an eyepiece graticule or the software analySIS® (Soft Imaging System GmbH) following Yanes *et al.* (2009). The number of shell whorls was counted using the methodology described by Kerney & Cameron (1979: 13).

Shell sculpture was studied using a Meiji RZ series stereo-microscope (at magnifications of up to $\times 56.25$) with a Schott KL1500 cold light source delivered through twin swan-neck fibre-optic cables that allowed high intensity illumination of shell surfaces from all angles. Measurements of microsculpture (reproducible to $\pm 2 \mu\text{m}$) were made using Infinity Analyze© software on images taken with an Infinity 1 camera on the same microscope. Three types of shell sculpture described in the species accounts are illustrated in Fig. 4 and named as follows: (a) very fine *incised spiral grooves*; (b) *raised spiral lines*, which are larger and more widely spaced, run parallel to each other and parallel to the incised grooves; sculpture of types (a) and (b) is superimposed on (c) *radial growth ribs*, \pm rounded in profile, variable in height and somewhat irregularly spaced. The spiral grooves and spiral lines are most strongly developed in *R. circumsessa* (Fig. 4A) allowing measurements of their spacing to be given below. In the other species (Figs 4B–E) these sculptural elements were similarly spaced but more weakly developed.

“Proximal” and “distal” refer to the position in relation to the ovotestis. The internal structure of the penis was investigated for those taxa where several mature specimens were available; that of the vagina only in *R. lenis*.

The sac forming an extension to the proximal end of the penis to which the penial retractor muscle is attached in *Retinella* was termed a flagellum by Forcart (1957: 114), Riedel (1980: 66, 68) and Giusti *et al.* (1986). However, the flagellum present for example in many Hygromiidae differs in arising from the epiphallus and in not being the point of attachment of their penial retractor muscle. Usage of the same term flagellum which is traditional in the anatomical literature of Zonitidae is therefore misleading. Presumably it was for this reason that Barker (1999: 109) referred to it as a “phallus flagellum” in *Oxychilus*; Frias Martins *et al.* (2013: 351, 353, 367) used the term “penial caecum” for it in *Oxychilus* (*Drouetia*). Schileyko (2003) described it both as a “flagellum” (p. 1412, in describing

subgenus *Lyrodiscus*) and as a “short caecum” (p. 1411, in describing genus *Retinella*). We follow Frias Martins *et al.* (2013) in using the term “penial caecum”.

Institutional and other abbreviations

AIT	Collection of M.R. Alonso & M. Ibáñez
CGAH	Collection of G.A. & D.T. Holyoak
ICZN	International Commission on Zoological Nomenclature
Ka	Thousands of years before present
Ma	Millions of years before present
NMBE	Naturhistorisches Museum, Bern, Switzerland
sh	shell(s)
sh+bod	shell(s) preserved dry with bodies preserved in spirit
spm	specimen(s) in alcohol
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain
UTM	Universal Transverse Mercator map projection system

SYSTEMATICS

Family Zonitidae Mörch 1864

Genus *Retinella* P. Fischer 1878 (in Shuttleworth, 1878 [“1877”]: 5, as subgenus of *Zonites*); the year of publication is given as 1877 in most of the literature, but Forcart (1967: 121) pointed out that it was 1878, as cited by Riedel (1980: 133, Footnote 1)

Type species: *Helix olivetorum* Gmelin 1791 (ICZN Opinion 335, 1955)

Subgenus *Lyrodiscus* Pilsbry 1893 (p. 48), as new name for *Lyra* Mousson 1872, non *Lyra* Cumberland 1816 (Brachiopoda)

syn. *Lyra* Mousson 1872 (p. 26) (as Sectio within *Patula*)

Type species: *Helix circumsessa* Shuttleworth 1852, by subsequent designation of Pilsbry (1893: 48) Rogers (1967: 15) introduced *Lyrodiscus* gen. nov. for species of fish parasites (Ancyrocephalinae, Trematoda: Monogenea). This name is an invalid junior homonym of *Lyrodiscus* Pilsbry 1893.

Retinella circumsessa (Shuttleworth 1852)

Figs 1, 2A, 4A, 5A, Table 1

Basionym *Helix circumsessa* Shuttleworth 1852 (p. 139).

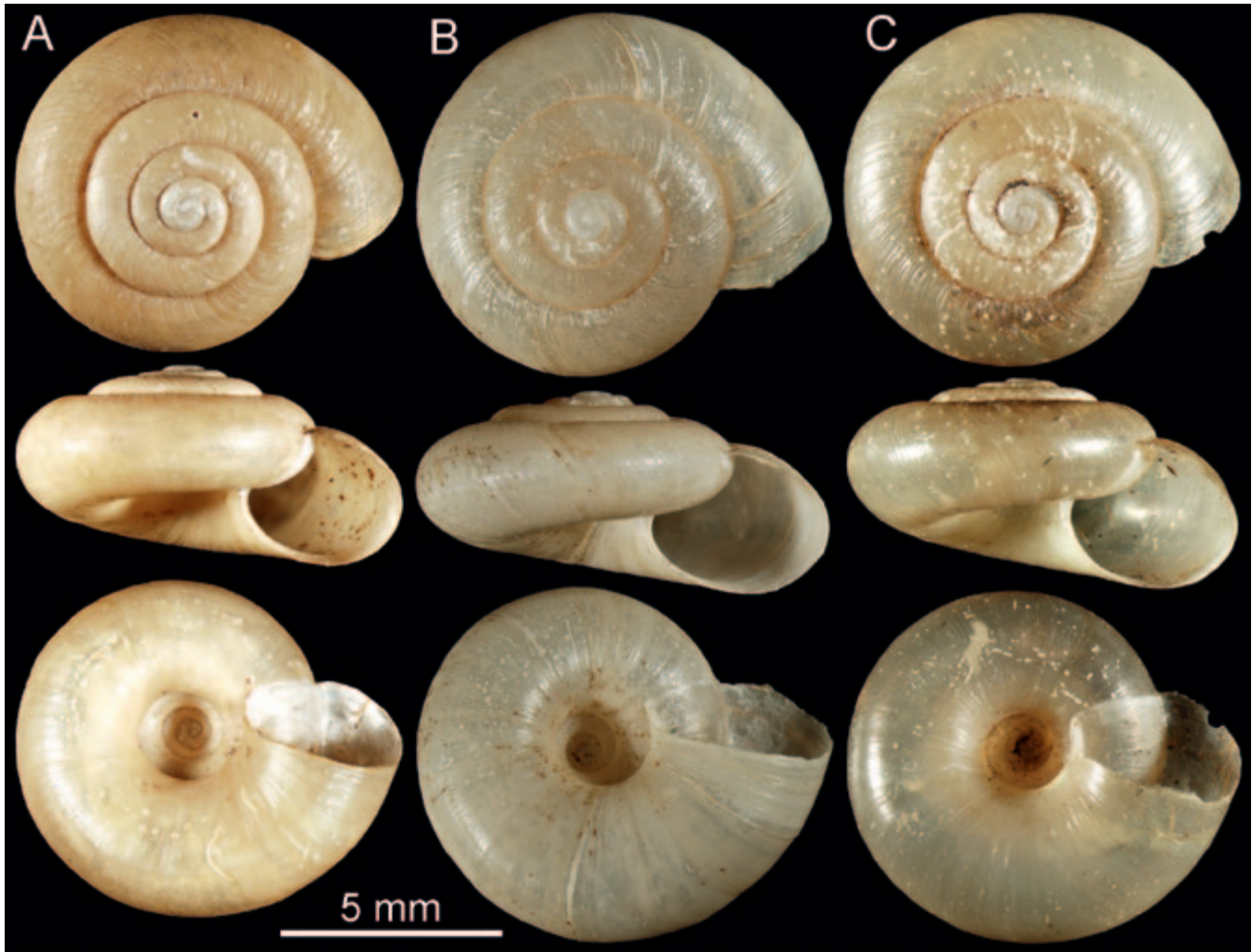


Figure 2 Shells of *Retinella* (*Lyrodiscus*) species: **A** *R. circumsessa* (Shuttleworth 1852), from Barranco del Agua, Anaga, Tenerife; **B** *R. osoriensis* (Wollaston 1878), from Brezal de Moya, Gran Canaria; **C** *R. lenis* (Shuttleworth 1852), from Roque Niquiomo, Mazo, La Palma.

Type locality “Hab. Sub saxis et foliis emortuis, Teneriffa”, restricted by Forcart (1960: 9, pl. 7a–d) through designation of lectotype NMBE 198791 (cf. Bank *et al.*, 2002: 154).

Material examined From Tenerife: 80 sh & 26 bod.

Shells Depressed-convex above, distinctly flattened below, height up to 4.55 mm, breadth up to 8.80 mm, with up to 4.3 whorls. Whorls strongly rounded (lacking peripheral keel even on immature shells), with deep sutures. Umbilicus very wide (up to 2.42 mm), representing 26.9–29.7% of shell breadth, symmetrical. Mouth rounded oval, except where interrupted by penultimate whorl, its maximum width up to 3.50 mm representing 38.5–40.3% of shell breadth; mouth edge thin, plane, slightly reflected only near umbilicus.

Shell light brown. Periostracum with sculpture of *spiral grooves* (typically *ca* 10–18 μm apart), less prominent on underside of shell; *raised spiral lines* (*ca* 70–140 μm apart) which vary to scarcer, narrow, rather fragile, finely flexuose lamellae perpendicular to the shell surface and up to *ca* 105 μm high with a wavy crest (the raised spiral lines being weaker on underside of shell, where lamellae are lacking except towards the periphery of the whorl), and *radial growth ribs* that are rounded in profile, variable in height, somewhat irregularly spaced, typically 90–260 μm apart and weaker on the underside of the shell.

External features of body One preserved body and colour photos of one living snail examined. Head and top of foreparts of body dull grey, with ommatophores darker grey to blackish and darker lines of ommatophore retractor muscles



Figure 3 Shells of *Retinella* (*Lyrodiscus*) species: **A** *R. hierroensis* sp. nov., holotype, from Las Tabladas, El Golfo, El Hierro; **B** *R. rochebruni* (J. Mabilie 1882), from Montaña de La Caldera, Vallehermoso, La Gomera.

visible by translucence; lower foreparts of body, foot-fringe, tail and sole of foot whitish; mantle whitish with few small brown spots near anterior edge; upper whorls brown.

Genital anatomy Two dissected; the following notes are also based partly on Riedel (1980: 68, 172–173 fig. 166). Right ommatophore retractor muscle free of distal genitalia. Penial caecum short, elongate-ovoid, on proximal end of penis, with penis retractor muscle arising at its tip and terminating on diaphragm. Vas deferens a moderately slender tube, without internal papilla where it enters epiphallus. Epiphallus ending in oblique attachment directed proximally at proximal end of penis, noticeably wider than vas deferens and of similar length or slightly longer. Penis cylindrical, longer or much longer than the short vagina, but narrower. Interior of penis with low longitudinal ridges (“schmalen Längsfalten, ohne ‘Zotten’”), with radial folds (“Rundfalten”) near the epiphallus, exit of epiphallus lacks a papilla. Genital atrium a short or very short broad cylinder. Genital pore located posterior to middle of right flank of body. Vagina short to very short

(shorter than both penis and free oviduct). Free oviduct of similar length or shorter than penis, but wider, cylindrical. Bursa copulatrix duct narrow, cylindrical, *ca* 1.5 × length of penis, widening gradually into cylindrical or elliptical-clavate bursa copulatrix, somewhat thickened at distal end. The anatomy of this species was previously described by Hesse (1930: 142–144) and Riedel (1977: 506–508, 1980: 68, 172–173 fig. 166).

Geographical range and habitat Tenerife only (Fig. 1). Inclusion of La Palma by (Wollaston, 1878: 317–318) where “taken by both Blauner and Fritsch” was almost certainly an error. The authors’ records of living or fresh specimens were from 300–1150 m alt., within laurisilva (forest dominated by Lauraceae), scrub of *Erica arborea* L. (“Fayal-Brezal”), or in admixtures of these. It was also found at four localities in pine forest (*Pinus canariensis* Sweet ex Spreng.) and one (at 300 m alt.) in lowland vegetation (“piso basal”). They were collected from leaf-litter (including litter of *E. arborea* and *Hedera*), beneath dead branches lying on the ground, and creeping above ground on fern fronds (mainly of *Pteridium*

Table 1 Measurements of representative large individual shells of *Retinella* (*Lyrodiscus*) species. B = shell breadth (mm), H = shell height (mm), U = maximum width of umbilicus (mm), U% = 100U/B (as %), M = maximum width of aperture (mm), M% = 100M/B (as %), Sv = shell surface area in ventral view (mm²); Sf = shell surface area in frontal view (mm²); * = measurements made with eyepiece graticule; † = measurements made with analySIS® (Soft Imaging System GmbH) software.

Species	B	H	U	U%	M	M%	Sv	Sf	Sv/Sf	Sv/B
<i>R. circumsessa</i>	+8.80	4.55	2.37	26.9%	3.50	39.8%	48.97	28.03	1.75	5.56
	+8.44	4.55	2.31	27.4%	3.25	38.5%				
	*8.32	3.89	2.28	27.4%	3.36	40.3%				
	*8.32	3.62	2.42	29.0%	3.36	40.3%				
	*8.05	3.62	2.15	29.7%	3.22	40.0%				
<i>R. osoriensis</i>	†10.26	5.25	2.36	23%	4.50	43.9%				
	+9.43	4.60	2.13	22.6%	4.02	42.6%	54.49	29.77	1.83	5.78
<i>R. lenis</i>	*11.07	4.90	2.42	21.8%	4.97	44.8%				
	*10.67	4.90	2.42	22.6%	4.63	43.4%				
	+9.07	4.85	1.96	21.6%	3.82	42.1%				
	+8.97	4.78	1.92	21.4%	3.80	42.4%	52.71	29.66	1.78	5.88
<i>R. hierroensis</i> , holotype	+9.66	5.49	2.24	23.2%	4.02	41.6%	59.87	36.16	1.66	6.20
<i>R. hierroensis</i>	+8.71	5.05	2.04	23.4%	3.90	44.8%	51.37	28.10	1.83	5.90
<i>R. rochebruni</i>	*10.07	4.63	2.25	21.3%	4.50	44.7%				
	*9.66	4.30	2.08	21.5%	4.43	45.8%				
	+9.41	4.85	2.05	21.8%	3.97	42.2%				
	+9.22	4.82	2.08	22.6%	3.90	42.3%	55.23	30.36	1.82	5.99

aquilinum (L.) Kuhn). Two old shells were found at ca 517 m alt., amongst scree and in litter under low bushes at the base of a crag on a south-facing hillside with patchy *E. arborea*.

Remarks *R. circumsessa* stands somewhat apart from the other Canary Islands species of the subgenus in shell characters, mainly because of its rounder whorl profile giving very deep sutures, no trace of even a slight peripheral keel on juvenile shells and a relatively smaller, rounder aperture. The umbilicus is also relatively larger than in the other species ($U \times 100/B$ 27–30%, cf. 21–23%) and shell breadth at maturity is smaller. The spiral sculpture on the periostracum has raised lamellae up to >0.1 mm high (which easily wear away) among the lower raised lines; such lamellae are absent in most of the other species, but present on the upperside of immature shells of *R. osoriensis*. The mantle lacks blackish external pigmentation, as in *R. lenis* and *R. osoriensis*. Anatomically, it differs from *R. lenis* and *R. rochebruni* in the very short vagina.

***Retinella osoriensis* (Wollaston 1878)**

Figs 1, 2B, 4B, 5B, Table 1

Basionym *Hyalinia* [*Lyra*] *osoriensis* Wollaston 1878 (p. 319).

Type locality “in the woods on the Pico do Orsorio, in Grand Canary”.

Material examined From Gran Canaria: 4 sh + 5 bod + 2 spm.

Shells Depressed-convex above, distinctly flattened below, height up to 5.25 mm, breadth up to 10.67 mm, with up to 4.7 whorls. Whorls strongly rounded (lacking peripheral keel even on immature shells), with only moderately deep sutures. Umbilicus moderately wide (up to 2.36 mm), representing 15.7–23% of shell breadth, almost symmetrical. Mouth rounded oval, except where interrupted by penultimate whorl, its maximum width up to 4.50 mm representing 39.0–43.9% of shell breadth; mouth edge thin, plane, slightly reflected only near umbilicus. Shell light brown

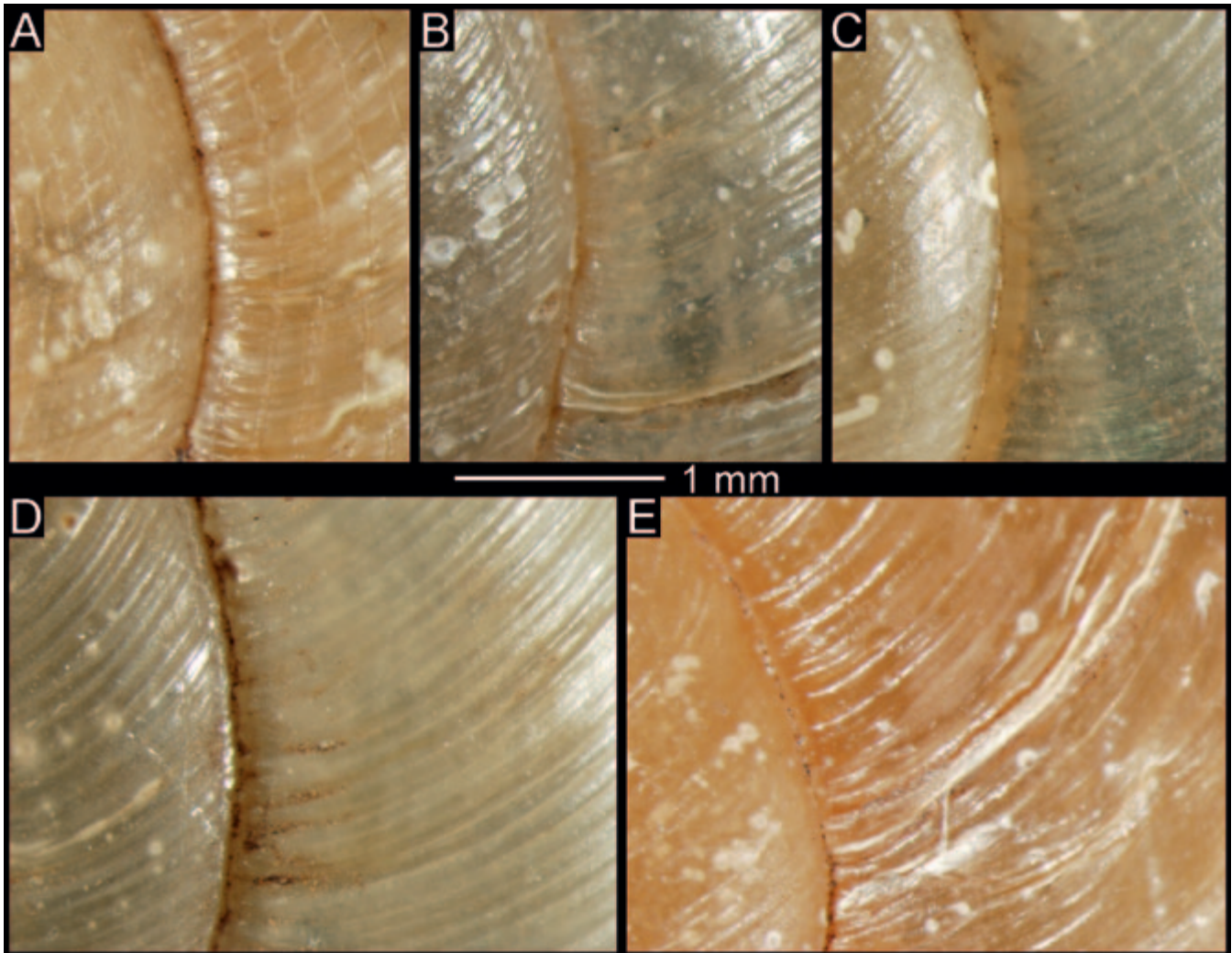


Figure 4 Details of the surface ornamentation of shells of *Retinella* (*Lyrodiscus*) species: **A** *R. circumsessa* (Shuttleworth 1852); **B** *R. osoriensis* (Wollaston 1878); **C** *R. lenis* (Shuttleworth 1852); **D** *R. hierroensis* sp. nov.; **E** *R. rochebruni* (J. Mabile 1882); the specimens are the same as those listed in Figs 2 and 3, respectively.

above, pale brown to almost whitish beneath. Periostracum glossy, with sculpture of *spiral grooves*, present both on upperside and underside of shell; *raised spiral lines* that are low and often rather inconspicuous on body whorl of adult shell, or more obvious as two to five lines well spaced around periphery of body whorl (immature shell has raised lines forming low irregular lamellae on upperside, especially towards periphery of whorls, from whorls 1.0–3.5); *radial growth ribs* moderately developed but rather irregular on upperside, especially on body whorl, weaker on underside.

External features of body One preserved body and two preserved specimens examined. Top of head, dorsal surface of forepart of body and top of tail whitish or pale grey shading to

whitish below; sides or body, foot-fringe, tail and sole of foot whitish; mantle whitish to pale grey without dark pigmentation; upper whorls pale.

Genital anatomy Two dissected. Right ommatophore retractor muscle free of distal genitalia. Penial caecum on proximal end of penis, its distal part cylindrical and of similar width to penis, becoming somewhat conical as it tapers towards proximal end. Penis retractor muscle attached to proximal end of caecum and terminating on diaphragm, apparently rather short and slender. Vas deferens a thin tube, somewhat convoluted *in situ*. Epiphallus ending in oblique attachment directed proximally near proximal end of penis, much wider than vas deferens but much narrower than penis, mainly cylindrical but

becoming narrower towards the junction with proximal end of penis. Penis of medium length or rather long (two-thirds to slightly longer than vagina plus free oviduct). Interior of penis not studied. Genital atrium very short, broadly cylindrical. Genital pore located posterior to middle of right flank of body. Vagina long, wider and much longer than free oviduct, cylindrical but apparently wider proximally or at both proximal and distal ends compared to middle. Free oviduct cylindrical, narrow, short (one-half to one-third length of vagina). Bursa copulatrix duct cylindrical, markedly thicker at distal end, length varying from similar to that of penis to twice as long. Bursa copulatrix ovoid (and thin walled) to irregularly cylindrical.

Geographical range and habitat Gran Canaria (Fig. 1). The authors' records were from 495–700 m alt., in laurisilva and *Erica arborea* scrub ("Fayal-Brezal").

Remarks *Retinella osoriensis* resembles *R. lenis* and *R. rochebruni* (and differs from *R. circumscissa*) in the shallow sutures, widely oval aperture and relatively narrow umbilicus. It differs from them in the slightly flatter shell and absence or weak development of a peripheral keel. The weak spiral lines usually present on the body whorl of adult shells are similar to those in *R. lenis*, whereas the lamellae on immature shells resemble those in *R. circumscissa*. The external colouration of the body is paler in *R. osoriensis* than usual in the other four species (approached on the foreparts of the body only by the palest individuals of *R. rochebruni*); it resembles *R. circumscissa* and *R. lenis* in lacking the dark pigment markings on the mantle that are present in *R. hierroensis* and *R. rochebruni*. The genital anatomy of *R. osoriensis* shows apparently distinctive features compared to other members of the subgenus: cylindrical-conical rather than ovate shape of the penial caecum, the vagina much longer and markedly wider than free oviduct, and marked thickening at the distal end of the bursa copulatrix duct (similar thickening present but less developed in *R. circumscissa*).

Retinella lenis (Shuttleworth 1852)
Figs 1, 2C, 4C, 5C, 8, Table 1

Basionym *Zonites lenis* Shuttleworth 1852 (p. 138).

Type locality "Hab. Palma, sub foliis emortuis". Syntypes NMBE 18767/1 + 18768/10 + 18769/1 + 18770/8 (Bank *et al.*, 2002: 172).

Material examined From La Palma: 36 sh + 14 bod.

Shells Depressed-convex above, distinctly flattened below, height up to 4.90 mm, breadth up to 11.07 mm, with up to 4.6 whorls. Whorls rounded (but with periphery weakly keeled above middle on immature shells), with sutures of moderate depth. Umbilicus wide (up to 2.42 mm), representing 21.8–22.6% of shell breadth, nearly symmetrical. Mouth rounded-oval, except where interrupted by penultimate whorl, its maximum width up to 4.97 mm representing 42.1–44.8% of shell breadth; mouth edge thin, plane, slightly reflected only near umbilicus. Shell light brown. Periostracum glossy, with sculpture of *spiral grooves*, prominent both on upperside and underside of shell; *raised spiral lines*, obvious on upperside of shell but occurring there only as lines (lamellae lacking), absent or weakly developed on underside of shell, present but weak on body whorl of mature shells, and *radial growth ribs*, obvious on upperside of shell, often weakly developed on underside.

External features of body Nine preserved bodies and colour photos of one living snail examined. Head and top of forepart of body grey, with ommatophores (and their retractor muscles visible by translucence) dark grey; sides of forepart of body and tail light grey; broad foot-fringe and sole of foot whitish; mantle whitish to cream, sometimes with light brown anterior edge; upper whorls brown or grey and brown.

Genital anatomy Three dissected. Right ommatophore retractor muscle free of distal genitalia. Penial caecum elongate-ovoid, on proximal end of penis, with penis retractor muscle arising at its tip and terminating on diaphragm. Vas deferens a slender tube, twisted *in situ*. Epiphallus ending in oblique attachment directed proximally at proximal end of penis, noticeably wider than vas deferens and longer. Penis cylindrical, appreciably longer than vagina but narrower. Interior of penis (one examined) with three paired low longitudinal ridges that widen at proximal end and continue into atrium at distal end; other low ridges radiate from exit of epiphallus, which lacks

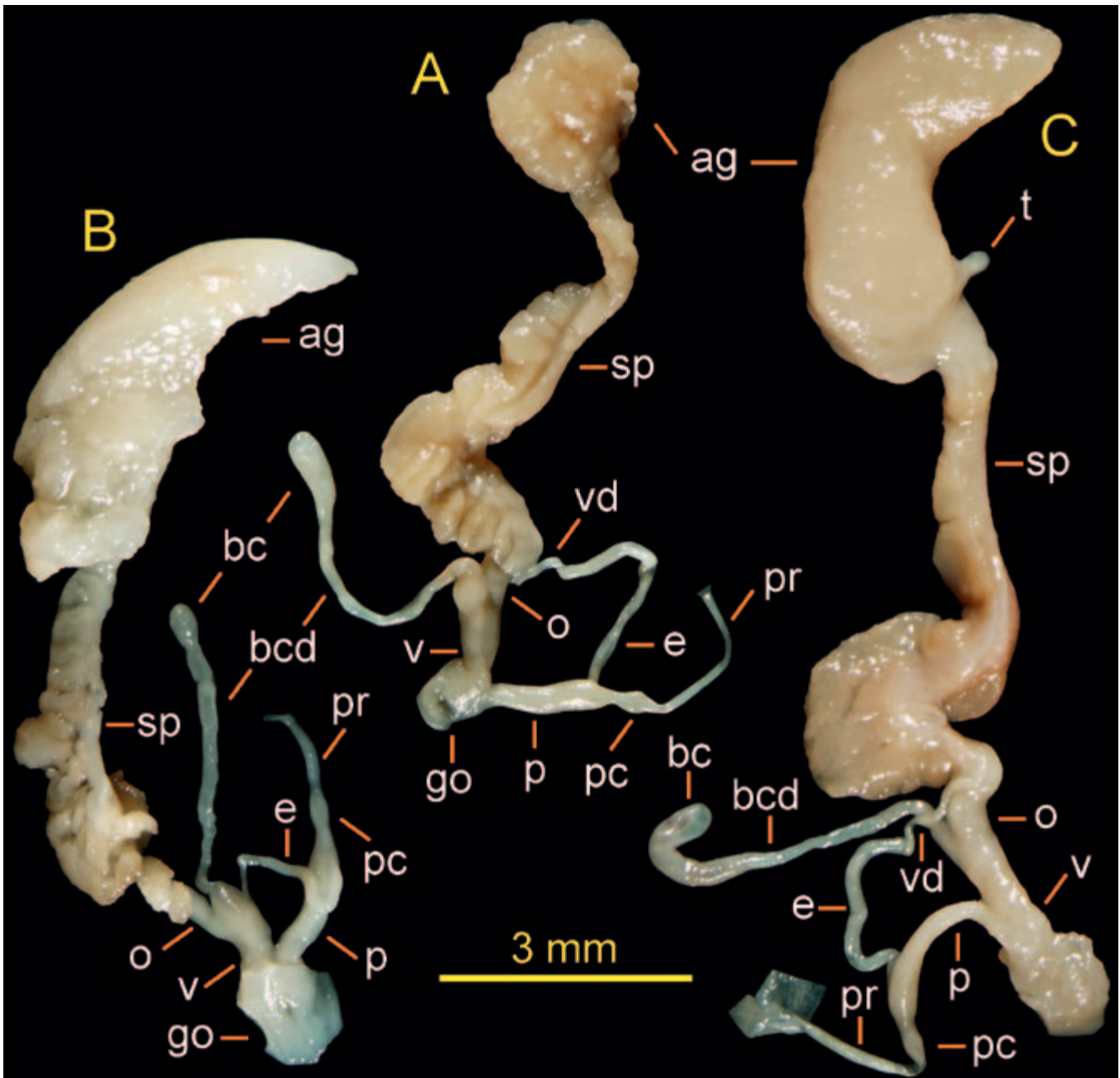


Figure 5 Genital anatomy of *Retinella (Lyrodiscus)* species: **A** *R. circumsesta* (Shuttleworth 1852), from El Pijaral, Anaga, Tenerife; **B** *R. osoriensis* (Wollaston 1878), from Brezal de Moya, Gran Canaria; **C** *R. lenis* (Shuttleworth 1852) from Roque Niquiomo, Mazo, La Palma; ag albumen gland; bc bursa copulatrix; bcd bursa copulatrix duct; e epiphallus; go genital orifice; o oviduct; p penis; pc penial caecum; pr penis retractor; sp spermoviduct; t talon; v vagina; vd vas deferens.

a papilla. Genital atrium a short broad cylinder, ending in slit-like genital pore located near the middle of the right flank of the extended body of the snail. Vagina rather short (shorter than penis, longer than free oviduct), approximately cylindrical, internally (one examined) with five or six low rather irregular ridges that grade into papillae distally and are replaced by papillae in the atrium. Free oviduct short. Bursa copulatrix duct

narrow, cylindrical, 1.0–1.5 × length of penis, widening gradually into broadly cylindrical to somewhat clavate bursa copulatrix, with both bursa copulatrix and much of duct lying closely appressed to spermoviduct.

Geographical range and habitat La Palma (Fig. 1). The authors' records were from ca 300–1500 m in laurisilva (with some *Pinus canariensis* at highest

elevation), *Erica arborea* scrub ("Fayal-Brezal"; including low scrubby evergreen woodland of *Erica arborea*, *Myrica*, etc. at ca 1280 m below scattered *Pinus* trees) and in pine forest.

Remarks The shell characters of *R. lenis* are close to those of *R. rochebruni*, since both share (when compared to *R. circumscissa*) shallower sutures, slightly keeled periphery to juvenile shells, a proportionately smaller umbilicus, a proportionately wider, more oval aperture and absence of tall spiral lamellae. They differ from each other mainly in sculpture, the raised spiral lines being better developed in *R. lenis* where they are present but inconspicuous on much of the body whorl of fully mature shells, whereas they are absent from the body whorl of mature *R. rochebruni* although present on the periphery of its juvenile shells. *R. osoriensis* differs more in sculpture, with much stronger spiral ribs on the upperside of the shell than in either of those species, its ribs forming irregular lamellae in juveniles. The mantle lacks blackish external pigmentation, as in *R. circumscissa* and *R. osoriensis*. The main anatomical difference from *R. circumscissa* is the longer vagina, which is appreciably longer than the free oviduct in this species.

Retinella hierroensis Alonso and Ibáñez, sp.
nov.

Figs 1, 3A, 4D, 6A–C, 7A, Table 1

Holotype Sh , TFMC (MT 0848); Leg. M. R. Alonso and M. Ibáñez, 11 February 1993.

Type locality Las Tabladas, El Golfo, El Hierro, Canary Islands, Spain, (UTM: 28RAR9671; 900 m altitude; vegetation of laurisilva (laurel forest).

Synonym *Hyalina lenis*: Wollaston (1878: 320), *pars*, non Shuttleworth 1852.

Material examined From El Hierro: 60 paratypes (sh+bod) and 28 paratypes (sh), and the holotype (sh).

Shells Depressed-convex above, distinctly flattened below. Holotype dimensions (mm): breadth 9.66, height 5.49, umbilicus 2.24, representing 23.2% of total shell breadth, maximum width of mouth 4.02. Two paratypes: heights 4.56, 5.05 mm, breadths 8.71, 8.86 mm, with 4.4 whorls. Whorls rounded, with weak peripheral keel even on immature shells but keel slight

or lacking on body whorl of adult, with deep sutures. Umbilicus wide (up to 1.88–2.24 mm), representing 21.2–23.4% of shell breadth, symmetrical. Mouth rounded oval, except where interrupted by penultimate whorl, its maximum width up to 4.02–4.03 mm representing 41.6–45.5% of shell breadth; mouth edge thin, plane, slightly reflected only near umbilicus. Shell light brown. Periostracum with waxy lustre, with sculpture of *spiral grooves* above and below; *raised spiral lines* few, with two or three evident around periphery of body whorl and one visible above periphery on earlier whorls of spire; *radial growth ribs* conspicuous on upper side of shell where closely spaced but rather irregular, less conspicuous beneath.

External features of body Two preserved bodies, two preserved specimens and colour photographs of one living snail examined. Top of head, dorsal surface of forepart of body and top of tail dull grey to light grey, shading to whitish near foot-fringe on darker individuals but shading to whitish higher on flanks of paler individuals; foot-fringe and sole of foot whitish; mantle whitish with few irregular but moderately bold lines of blackish pigmentation; upper whorls brown with large areas of blackish pigmentation.

Genital anatomy Two dissected. Right ommatophore retractor muscle free of distal genitalia. Penial caecum on proximal end of penis, ovoid-cylindrical, somewhat narrower than penis, with penis retractor muscle arising at its tip and terminating on diaphragm. Vas deferens slender. Epiphallus ending in oblique attachment directed proximally near proximal end of penis, cylindrical, narrower than penis, wider and slightly longer than vas deferens. Penis cylindrical, of similar length to that of vagina plus free oviduct. Interior of penis with three raised longitudinal ridges that extend full length of penis and three more that apparently extend only along its proximal half. Genital atrium a very short wide cylinder. Genital pore located behind the middle of the right flank of the forepart of the body. Vagina cylindrical, wider than penis, less than one-half length of free oviduct and one-third length of penis. Free oviduct cylindrical, wider than penis. Bursa copulatrix duct a slender cylindrical tube, length less than twice or somewhat more than twice that of penis, widening near proximal end. Bursa copulatrix cylindrical, about three times as long as wide.

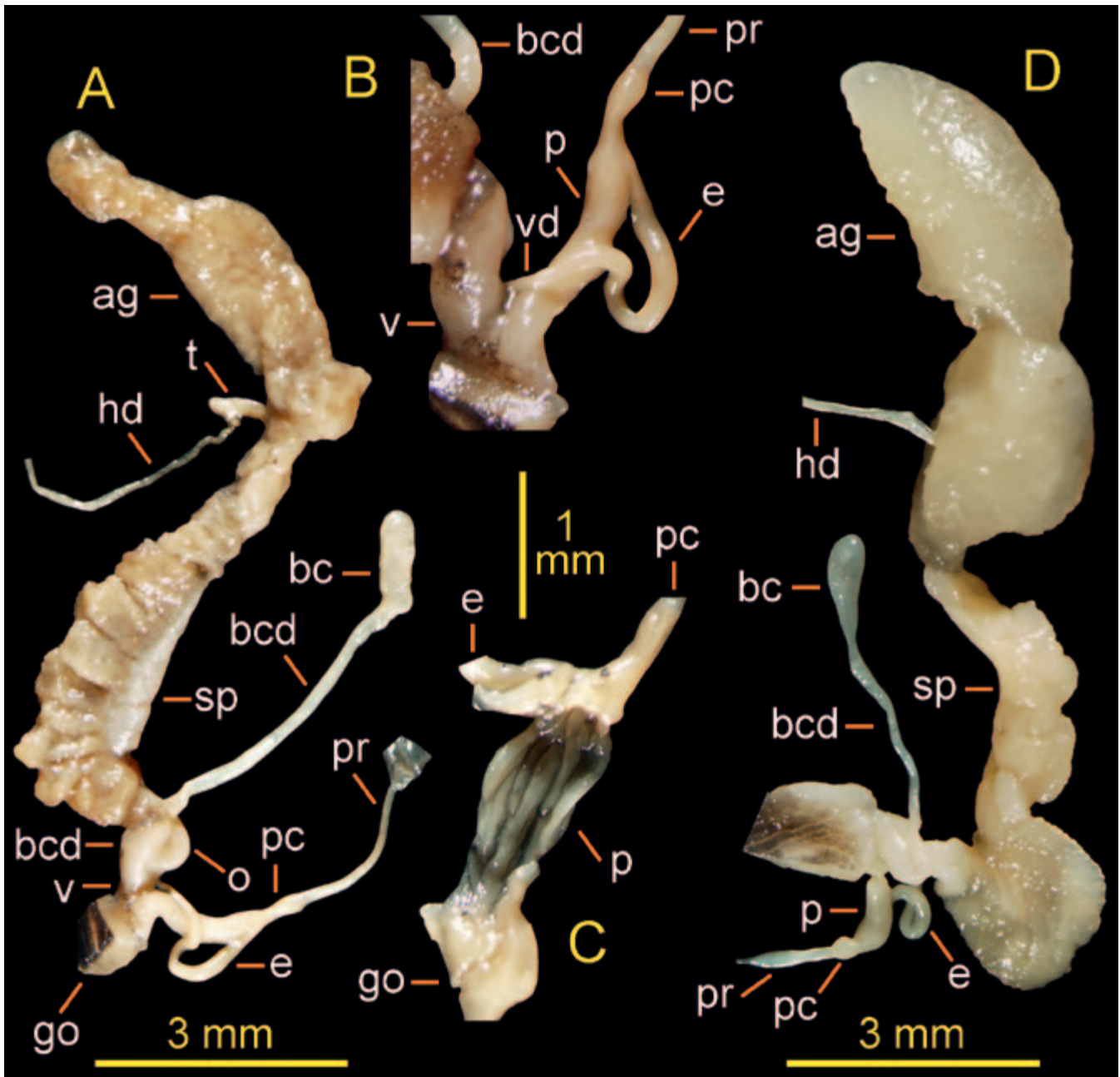


Figure 6 Genital anatomy of *Retinella (Lyrodiscus)* species: **A–C** *R. hierroensis* sp. nov., from Bajada de Jinama, El Golfo, El Hierro; **B** distal genitalia; **C** dissection of penis showing the internal longitudinal folds; **D** *R. rochebruni* (J. Mabille 1882), from Montaña de La Caldera, Vallehermoso, La Gomera; hd hermaphroditic duct; the other abbreviations for anatomical structures as in Fig. 5.

Geographical range and habitat El Hierro (Fig. 1). The authors' records were from 600–1250 m alt., in laurisilva and *Erica arborea* scrub ("Fayal-Brezal").

Remarks The *Retinella (Lyrodiscus)* of El Hierro have hitherto been regarded as conspecific with *R. lenis* from La Palma (e.g. Bank *et al.*, 2002). *Retinella hierroensis* is indeed close in shell

characters to *R. lenis* (see above), but it is less glossy and with spiral lines better developed on the periphery of the body whorl in mature shells; it may also mature at a smaller size. *R. hierroensis* may also tend to have a larger shell surface area (in ventral view) than in the other species, including *R. lenis*, although sample sizes were very small (Table 1). The generally rather dark external body colouration of *R. hierroensis*

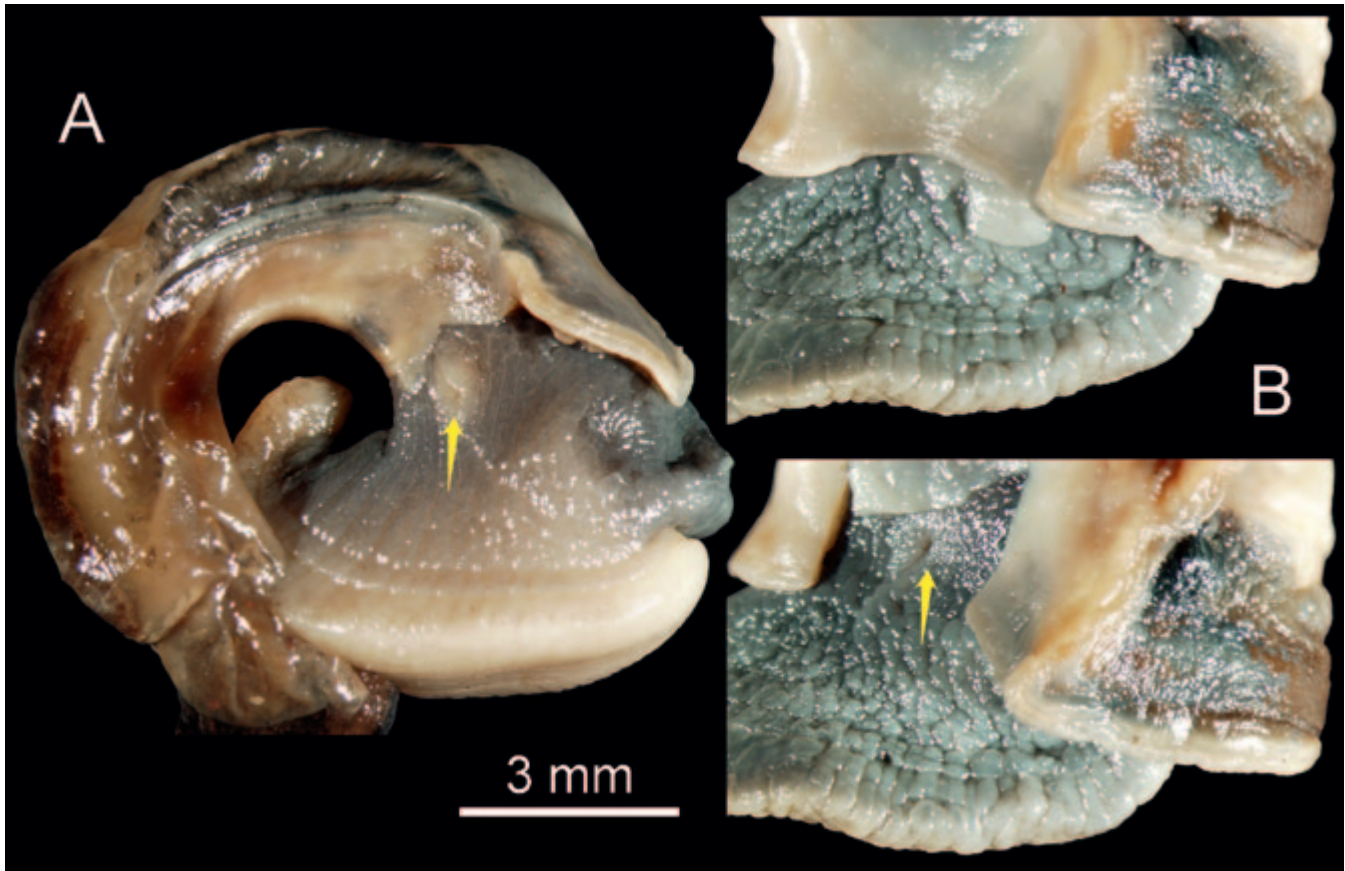


Figure 7 Location of the genital pore (yellow arrow) in *Retinella* species: **A** *Retinella (Lyrodiscus) hierroensis* sp. nov., from Bajada de Jinama, El Golfo, El Hierro; **B** specimen of *R. incerta* (Draparnaud 1805) from Dept. Pyrénées-Atlantiques, France.

resembles that of *R. rochebruni* and differs from the other three species (including *R. lenis*) in having blackish markings on the mantle and upper whorls. It differs anatomically from *R. lenis* in having a proportionately shorter vagina, which is less than one-half length of free oviduct and one-third length of penis in *R. hierroensis*, longer than free oviduct and about one-half length of penis in *R. lenis*.

Etymology The species epithet is based on the island of El Hierro.

Retinella rochebruni (J. Mabille 1882)
Figs 1, 3B, 4E, 6D, Table 1

Basionym *Hyalina rochebruni* J. Mabille 1882 (p. 132).

Type locality «l'Ile de Gomera l'une des Canaries».

Material examined From La Gomera: 24 sh + 13 bod.

Shells Depressed-convex above, distinctly flattened below, height up to 4.85 mm, breadth up to 10.07 mm, with up to 4.5 whorls. Whorls rounded (but with periphery weakly keeled above middle on immature shells), with sutures of moderate depth. Umbilicus wide (up to 2.08 mm), representing 21.3–22.6% of shell breadth, nearly symmetrical. Mouth rounded oval, except where interrupted by penultimate whorl, its maximum width up to 4.50 mm representing 42.2–45.8% of shell breadth; mouth edge thin, plane, slightly reflected only near umbilicus. Shell light brown. Periostracum with sculpture of *spiral grooves*, present both on upperside and underside of shell; *raised spiral lines*, that are always low (lamellae lacking), obvious on protoconch, well developed around periphery of whorls on young shells, elsewhere often few and weakly developed, usually absent on undersurface of shell and absent from body whorl of mature shells, and *radial growth ribs*, obvious on upperside of shell, often weaker on underside.



Figure 8 Living individual of *Retinella (Lyrodiscus) lenis* (Shuttleworth 1852), from Roque Niquiomo, Mazo, La Palma.

External features of body Nine preserved bodies studied. Head and top of forepart of body deep grey; sides of forepart of body dark grey, grey or light grey in different individuals; broad foot-fringe and sole of foot whitish; mantle whitish with light brown anterior edge; in different individuals, dorsally more or less heavily pigmented grey to blackish; upper whorls dark brown, in different individuals more or less heavily marked with blackish dorsally.

Genital anatomy Three dissected, but one of them immature. Right ommatophore retractor muscle free of distal genitalia. Penial caecum elongate-ovoid, on proximal end of penis, with penis retractor muscle arising at its tip and terminating on diaphragm. Vas deferens a slender tube, twisted *in situ*. Epiphallus ending in oblique attachment directed proximally at proximal end of penis, about twice width of vas deferens and longer. Penis cylindrical, at least $1.5 \times$ length of vagina but narrower. Interior of penis (one examined was poorly fixed and broken) with low longitudinal ridges; exit of epiphallus lacks

a papilla. Genital atrium a short broad cylinder, ending in slit-like genital pore located near the middle of the right flank of the extended body of the snail. Vagina short (shorter than penis and shorter than free oviduct), approximately cylindrical, internally (one examined) with low, sinuous, somewhat irregular longitudinal ridges. Free oviduct of medium length (nearly as long as penis or slightly longer). Bursa copulatrix duct narrow, cylindrical, at least $2.0 \times$ length of penis, widening gradually into broader cylindrical to rather irregular or somewhat clavate bursa copulatrix, with both bursa copulatrix and much of duct lying closely appressed to spermoviduct.

Geographical range and habitat La Gomera (Fig. 1). The authors' records were from 500–1365 m alt., mainly in laurisilva (sometimes under tall old trees) and *Erica arborea* scrub ("Fayal-Brezal"), but once at 500 m alt. under chestnuts (*Castanea sativa* Mill.). The snails were collected from beneath stones and amongst leaf-litter.

Remarks As noted above, the shell characters of *R. rochebruni* are close to those of *R. lenis*, since both share (when compared to *R. circumscissa*) shallower sutures, slightly keeled periphery to juvenile shells, a proportionately smaller umbilicus, a relatively wider, more oval aperture and absence of tall spiral lamellae. They differ from each other mainly in sculpture, the raised spiral lines being better developed in *R. lenis* where they are present but inconspicuous on much of the body whorl of fully mature shells, whereas they are absent from the body whorl of mature *R. rochebruni* although present on the periphery of its juvenile shells. *R. osoriensis* differs more in sculpture, with much stronger spiral ribs on the upperside of the shell than in either of those species (forming irregular lamellae on juvenile shells). The external colouration of the body differs from that of *R. circumscissa*, *R. lenis* and *R. osoriensis*, but resembles *R. hierroensis* in having individually variable grey to blackish pigmentation on the mantle and upper whorls. Anatomically, *R. rochebruni* differs from *R. circumscissa* in having a longer vagina, more like that of *R. lenis* although somewhat shorter than in the latter species. Since the free oviduct is longer in *R. rochebruni* than in *R. lenis*, the free oviduct of *R. rochebruni* is a little longer than its vagina (much longer in *R. circumscissa*, slightly shorter in *R. lenis*).

SPECIES DIFFERENCES, SUBGENERIC
CLASSIFICATION AND HISTORICAL BIOGEOGRAPHY
OF (*RETINELLA*) *LYRODISCUS*

Comparative data on the genital anatomy of the Canary Islands taxa of *Retinella* (*Lyrodiscus*) can now be added to a reappraisal of shell characters to review species limits. It is demonstrated that four species (*R. circumsesta*, *R. hierroensis*, *R. lenis*, *R. rochebruni*) apparently show small differences from each other in relative lengths of the vagina and free oviduct, even though statistical treatment of measurements from larger samples might in future show there is some overlap. *R. osoriensis* differs more from those species, in having the penial caecum cylindrical-conical rather than ovate, its vagina much longer and markedly wider than the free oviduct, and marked thickening at the distal end of the bursa copulatrix duct (also present but less developed in *R. circumsesta*). It is also shown that mantle colouration of *R. rochebruni* and *R. hierroensis* is different to that of the other three species listed in having markings formed by blackish pigmentation. The detailed analysis of shell characters by Rousseau & Puisségur (1990) failed to include *R. rochebruni* or specimens from El Hierro, but showed that *R. circumsesta*, *R. lenis* and *R. osoriensis* all differ from each other in features of periostracal sculpture. Our examination of *R. rochebruni* has established that it also shows some peculiarities, differing from the rather similar *R. lenis* in lacking raised spiral lines on the body whorl of mature shells. *R. hierroensis* also shows small differences from *R. lenis* in shell characters, to add to the differences in external body colouration and anatomy of their distal genital.

To summarise, the Canary Islands species can be distinguished using the characters set out in the following key:

1. Umbilicus wide (>25% of breadth of mature shell); aperture relative small (maximum width of aperture <41% of breadth of mature shell); periostracum on body whorl of mature shell with (fragile) raised spiral lamellae among raised lines
R. circumsesta (Tenerife)
- Umbilicus narrower (<25% of breadth of mature shell); aperture relative large (maximum width of aperture >41% of breadth of mature shell); periostracum on body whorl of mature shell with or without raised lines but always lacking raised spiral lamellae 2

2. Juvenile shell with rounded whorl profile (peripheral keel absent); immature shells with (fragile) raised spiral lamellae; dorsal surface of forepart of body whitish or pale grey; penial caecum cylindrical-conical; distal end of bursa copulatrix duct markedly thickened

R. osoriensis (Gran Canaria)

- Juvenile shell with peripheral keel; immature shells with raised spiral lines but lacking raised spiral lamellae; dorsal surface of forepart of body pale grey to dark grey; penial caecum ovate; distal end of bursa copulatrix duct not markedly thickened 3

3. Raised spiral lines absent from body whorl of fully mature shells, although present on periphery of juvenile shells; exterior of mantle with variable grey to blackish markings; vagina somewhat shorter than free oviduct

R. rochebruni (La Gomera)

- Raised spiral lines present but inconspicuous on body whorl of fully mature shells; exterior of mantle unmarked or with variable blackish markings; vagina longer than free oviduct or less than half of its length 4

4. Shell less glossy; raised spiral lines better developed (on mature shells, 2 or 3 evident around periphery of body whorl, 1 visible above periphery on earlier whorls of spire); blackish markings present on surface of mantle and upper body whorls; vagina less than one-half length of free oviduct and one-third of length of penis

R. hierroensis (El Hierro)

- Shell more glossy; raised spiral lines obvious but weaker (on mature shells, present around periphery); surface of mantle and upper body whorls lacking blackish markings; vagina longer than free oviduct and about one-half length of penis
R. lenis (La Palma)

Recognition of five species thus appears justified from the morphological data. This therefore suggests that the familiar pattern of predominantly single-island endemism found in other Canary Islands land snails (Enidae, Discidae, Vitrinidae, Hygromiidae, Helicidae) is likely to be true also of the endemic taxa of Zonitidae.

Lyra Mousson and the replacement name *Lyrodiscus* Pilsbry were originally distinguished from otherwise rather similar Zonitidae by the presence of pronounced spiral ribs on the external

surface of the shell whorls. Wollaston (1878: 318) referred to [*H.*] *circumsessa*, *osoriensis*, and *lenis* as “intimately bound together by the very peculiar and significant character” of these “spiral lines”. Subsequent anatomical studies of *R. circumsessa* revealed distal genitalia generally resembling those of *Retinella* s. str., with the penial retractor muscle arising apically from a well defined caecum and no papilla where the epiphallus enters the side of the proximal part of the penis. Hence, following the early reassessment by Hesse (1930: 142–144), *Lyrodiscus* has consistently been treated as a subgenus of *Retinella* by subsequent authors (Forcart, 1957: 117–188, 1960: 9–10; Zilch, 1959: 251; Kerney, 1976: 49; Riedel, 1977: 506–508, 1980: 68, 172–173, 1998: 10; Rousseau & Puisségur, 1990; Bank *et al.*, 2002: 113; Schileyko, 2003: 1412).

The review by Riedel (1980) recognised three subgenera within *Retinella*, comprising *Lyrodiscus*, *Retinella* s. str. (with three species, occurring in S. Switzerland, Italy, Sicily and N. Morocco) and *Retinelloides* Riedel 1977 (monotypic, with *R. incerta* (Draparnaud 1805) restricted to the Pyrenees and N. Spain: Altonaga, 1989). At that time, these groups appeared to be distinct and clearly defined from characters of the shells and genital anatomy. However, the description by Giusti *et al.* (1986) of *R. pseudoaegopinella* Giusti, Boato & Bodon 1986 as a new species of *Retinella* and reassignment of *R. stabilei* (Pollonera 1886) to this genus, both from the SW. Alps, revealed additional combinations of anatomical and shell characters. These authors concluded (*op. cit.*: 178) that “In such a situation it is impossible not only to identify the real limits of the subgenera (perhaps with the exception of *Lyrodiscus*) but also to identify a boundary line between *Retinella* and other taxa such as the N.-American genus *Glyphyalinia*.” They therefore “prefer to abstain from using a subgenerical subdivision and simply to regard *Retinella* as a very polymorphous taxon”. It would appear that a modern phylogenetic study using a combination of molecular and morphological characters is needed to improve understanding of relationships among these and other Zonitidae.

Our data show that the endemic Canary Islands species assigned to *Lyrodiscus* from conchological characters are also very similar to each other anatomically. Although their genital anatomy mainly appears similar to that e.g. in *Retinella pseudoaegopinella* from Italy, the narrow glandular

covering of the genital atrium of that species was not seen in *Lyrodiscus*. Hence, it is useful to retain the Canary Islands species together in the same subgeneric group until a phylogenetic study provides an adequate basis for a revised classification of the allied genera.

The genital pore was found to be located further back on the forepart of the right hand side of the body in *Retinella hierroensis* (well behind the middle of the right flank: Fig. 7A) than usual in other Zonitidae such as *Aegopinella nitidula* (Draparnaud 1805) and *Oxychilus draparnaudi* (H. Beck 1837). A posterior location of the pore was found to be present in preserved specimens of all the Canary Islands *Retinella* (*Lyrodiscus*). Study of five preserved individuals of *Retinella incerta* (Draparnaud 1805) from three localities also showed its genital pore was located well behind the middle of the right flank on the retracted bodies (e.g. Fig. 7B), an unusual location not mentioned in the account by Altonaga (1989). It is difficult to assess the taxonomic significance of this feature in the absence of comparative data on position of the pore in other European or Moroccan *Retinella* and a general lack of information on its location in other genera of Zonitidae. The functional significance of the pore being located further back from the front of the animal is also uncertain, since it might be expected to hinder reciprocal mating in the usual position with snails facing each other head to head.

Retinella (*Lyrodiscus*) *skertchlyi* Kerney 1976 (p. 49) was named from fossils from a Pleistocene interglacial tufa at Icklingham in Suffolk, England that show strong spiral ribs similar to those of *R. circumsessa*. Holyoak *et al.* (1983) summarised additional evidence that this tufa and two other English deposits from which *R. skertchlyi* was subsequently recorded are of Middle Pleistocene age (perhaps Hoxnian). Later, Kerney (1980) suggested that *R. skertchlyi* may be a synonym of *R. jourdani* (Michaud 1882) from the Lower Pliocene of Hauterives (France). However, detailed studies by Rousseau & Puisségur (1990) established that *R. skertchlyi* and *R. jourdani* are clearly distinct. They confirmed that *R. skertchlyi* shows the strong conchological similarities to the endemic Canary Islands *Retinella* (*Lyrodiscus*) reported by Kerney (1976) and therefore retain them together in the same subgenus, in which they also included *R. (L.) jourdani* (Michaud 1882) (*op. cit.*: 62). Rousseau & Puisségur (1990) showed that fossil

R. skertchlyi occurred over a geographical range extending from S. England to C. France and SW. Germany, in deposits dated from 2.3 Ma (Upper Pliocene at Cessey-sur-Tille, Côte d'Or, France) to ca 400 Ka (the Hoxnian/ Holsteinian/ marine isotope stage 11, of the Middle Pleistocene).

As stressed by Rousseau & Puisségur (*op. cit.*), it is noteworthy that all of the European fossil occurrences are associated with species-rich fossil land-snail faunal assemblages characteristic of temperate forest habitats. Thus, Truc (1972) demonstrated this for Cessy-sur-Tille and the assemblages associated with the Middle Pleistocene occurrences were described e.g. by Kerney (1959, at Hitchin, with *R. skertchlyi* subsequently recorded by Holyoak & Preece, 1986), Kerney (1976) and Rousseau (1987). Furthermore, most records are from tufas deposited from shallow freshwater, a type of sedimentation that has occurred in NW. Europe only when the climate was warm.

The fossil specimens from Cessey-sur-Tille had been determined as *R. jourdani* by Schlickum (1975) but were reidentified as *R. skertchlyi* by Rousseau & Puisségur (1990: 61–62). Since these specimens were those used by Schlickum & Strauch (1975: 39–40, pl. 3 figs 1–2) as the basis for introducing *Retinella* (*Riedeliella*) as a new monotypic subgenus with *R. jourdani* named as its supposed type, it is clear that subgenus *Riedeliella* is a junior synonym of *Lyrodiscus*.

The close conchological resemblance between the *Retinella* (*Lyrodiscus*) that are known living only as endemics in the Canary Islands and the Pliocene to Middle Pleistocene fossil taxa from north-western Europe gives valuable evidence of the likely origins of the living forms. These can most easily be regarded as geographically marginal relicts of a fauna that was widespread in NW. Europe in the late Tertiary and early Pleistocene. *Retinella* (*Lyrodiscus*) apparently became extinct in continental Europe during the cold conditions of the Late Pleistocene glacial stages, when temperate forest habitats were drastically reduced in extent, whereas on the Canary Islands they survived as forests persisted under milder climates. As pointed out by Rousseau & Puisségur (1990: 67–68), *Janulus* [Gastrodontidae] provides a comparable example of post-Pleistocene survival only in Macaronesia of a European land-snail genus that was widespread in the Tertiary. Holyoak *et al.* (2011: 595–599) discussed the

likelihood of a similar history for the Discidae endemic in the Canary Islands. Those Discidae, occur on the islands mainly as stenophiles of the humid laurel-forest habitats that are peculiar to the higher islands of northern Macaronesia, whereas *Retinella* (*Lyrodiscus*) are commonest in the same habitat but also occur more widely in the woodland and scrub habitats at middle elevations on the larger Canary Islands.

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