

# REVISION OF *RHYSOTINA* (GASTROPODA: UROCYCLIDAE) LAND-SNAILS ENDEMIC TO THE WEST AFRICAN ISLAND OF SÃO TOMÉ

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*Abstract* *Rhysotina* (Urocyclidae) is a small genus endemic to the oceanic island of São Tomé in the Gulf of Guinea, off tropical west Africa. It is revised based on shell and spirit specimens collected by the authors in 2013. Two species have been recognised for many years, *R. hepatizon* (Gould 1845) and *R. welwitschi* (Morelet 1866). The second of these is shown to have been confused with a third species that is newly described here; they differ in several shell characters and their altitudinal ranges. The genital anatomy is redescribed and figured for all three species, which have similar genitalia despite their distinctive shells. The “unique character” of “a very peculiar structure” of the genital atrium that contributed to naming of the family Rhysotinidae Schileyko 2002 was most likely from a snail that was atypical or distorted in preservation. Nevertheless, because the genus has other peculiarities and the small amount of published molecular data suggest it forms a sister-group to other sampled Urocyclidae, it is tentatively separated from them here as the Subfamily Rhysotininae.

*Key words* *Rhysotina*, *Rhysotinidae*, *Urocyclidae*, São Tomé, oceanic island, endemics, new species, genital anatomy, shells

## INTRODUCTION

The two oceanic islands that form the small west African country of São Tomé and Príncipe are rich in endemic land snails. Gascoigne (1994a, 1994b) reported 39 species from São Tomé island alone, of which 25 were regarded as single-island endemics and 5 more as endemic to more than one of the Gulf of Guinea islands (76.9% endemics overall). Extensive exploration of the fauna and naming of the species was carried out mainly from 1853–1916 (see References), based mostly on shell specimens. Nevertheless, as in many tropical countries, detailed taxonomic re-evaluation of the fauna still needs to be carried out, based on anatomical, molecular and shell studies, as well as wider comparisons. However, the continuing poor knowledge of the land Mollusca of neighbouring African countries hinders this process.

*Rhysotina* Ancey 1887 (Urocyclidae) is a distinctive genus of medium-sized land snails with thick shells possessing apertural teeth. They are known only from São Tomé, where two species have been recognised for many years, *R. hepatizon* (Gould 1845) and *R. welwitschi* (Morelet 1866). Our material shows that the taxon treated as *R. welwitschi* by numerous authors consists of two superficially similar species, differing in several shell characters. Both *R. hepatizon* and *R. welwitschi* are redescribed and figured here and

the third species is named as *R. sublaevis* sp. nov. The literature is reviewed in an attempt to allocate older information to one or the other of these species.

Degner (1932) provided a detailed and careful account of the general morphology, genital anatomy and radula of *R. hepatizon* and *R. welwitschi sensu lato*. Very little has been published subsequently on the genus. Unfortunately, Schileyko (2002: 1233) overlooked Degner’s work and described the genital anatomy based on a single specimen that showed “a very peculiar structure” of the genital atrium, leading him to name the new family Rhysotinidae. The present paper redescribes, figures and to some extent reinterprets the genital anatomy for all three species, which differ very little from each other in anatomy.

## MATERIAL AND METHODS

Our specimens were collected on São Tomé island from 1<sup>st</sup> to 13<sup>th</sup> December 2013, by direct searching on and near the ground, mainly in wooded habitats, ranging from roadside banks, edges of cultivation and second-growth to well developed lowland and montane forests. Field sites were numbered ST1 to ST14. Coordinates and altitudes were measured using a hand-held GPS (“Garmin Etrex high sensitivity”) accurate to within <10m in open country. However, some

of our data are only approximate (prefaced by *ca*) because measurements were made from beneath a closed tree canopy inside forests. At each site, habitats were described and often photographed and collections of all Mollusca were made, preserved, and subsequently listed. Unless otherwise stated, all specimens are in the Collection of G.A. and D.T. Holyoak.

Adult shells of *Rhysotina* were separable from immatures by the strongly thickened peristome with a small tooth on the lower lip, most such specimens having mature genitalia. Shell measurements were made on adult shells with vernier callipers (accuracy  $\pm 0.05$ mm); the maximum breadth of the shell was easy to measure consistently; that of shell height is approximate because the maximum is offset laterally from the line downwards from the apex through the columellar axis. Shell whorls were counted using the method illustrated by Kerney & Cameron (1979: 13). Study of shells and dissections were made using Meiji RZ Series stereomicroscopes. The distal genitalia were removed from dissected bodies and drawn using a Meiji drawing tube. Coloration of the body was described from specimens that had been preserved in 70–80% alcohol for at least one year.

Abbreviations: **ad** adult; **alt.** altitude above sea-level; **B** shell breadth; **bod** bodies extracted from shells and preserved in alcohol; **Coll.** collected by; **DTH** D.T. Holyoak; **GAH** G.A. Holyoak; **H** shell height; **imm** immature; **Ma** millions of years before present; **n** number in sample; **NHMUK** The Natural History Museum, London, U.K.; **n.v.** original not verified; **s.d.** sample standard deviation; **sh** shells; **spm** specimens in alcohol (industrial methylated spirit); **syn.** synonym.

## RESULTS AND TAXONOMY

Family Urocyclidae Simroth 1889  
Subfamily Rhysotininae Schileyko 2002  
[as Family], p. 1233.

See Discussion below regarding treatment of Rhysotininae as a subfamily.

Genus *Rhysotina* Ancey 1887, p. 53

“Types” were listed as *Helix Welwitschi*, Mor, and *H. hepatizon*, Gould by Ancey *loc. cit.* *Helix welwitschi* Morelet 1866 was selected by subsequent

designation of Zilch (1959). The derivation of the name is uncertain but it appears to be a diminutive of *Rhysota* Martens 1860 (a synonym of *Ryssota* Albers 1850) which Ancey (*loc. cit.*) mentioned in the preceding paragraph. It is treated here as a feminine noun, like *Ryssota*.

*syn. Thomeonanina* Germain 1909, p. 99. Type species *Helix welwitschi* Morelet 1866, by subsequent designation of Schileyko (2002: 1233).

The genus possesses a unique combination of characters among Urocyclidae: the presence together of a thick, strongly sculptured shell, a muscular bursa copulatrix arising directly from the genital atrium with no intervening duct, along with absence of any atrial appendage or penial flagellum.

Features of structure and anatomy that apply to all three species are described in the present section to avoid repetition. The shell is dextral, strong and lacks an umbilicus. Shells of the immature snails have a very sharp peripheral keel but the adults have the body-whorl rounded. Externally, the body has a pair of long ommatophores arising at the top of the front of the head, a much shorter second pair of tentacles beneath these. The mantle collar forms a wide flap extending around much of the circumference of the body. The external genital pore is often a conspicuously large opening, placed near the front of the right-hand side of the body; when the body is extended the location of the pore is behind the base of the right ommatophore, but much lower, not far above the foot-fringe at about the middle of the lower half of the flank. The tail is proportionately long with no ‘caudal horn’ but a prominent glandular pore on the dorsal surface just in front of the tip. Degner (1932: 226) also noted the absence of a caudal horn (noting: kein eigentliches, “Horn”) so it is unclear what Schileyko (2002: 1233) intended by commenting “caudal horn vestigial”. The sole of the foot is tripartite, with three zones of approximately similar width.

Degner (1932: 226) figured the radulae of *R. hepatizon* and *R. welwitschi* (*sensu lato*: see below) which seem to be typical for Urocyclidae with marginal teeth that are only weakly bicuspid. Schileyko (2002: 1233, fig. 1621D) figured the oxygnathous jaw of *R. welwitschi*.

In describing the genital anatomy below, proximal and distal refer to positions in relation to the

ovo-testis. Features of the genital anatomy similar in all three species include: right ommatophore retractor muscle passing through angle between penis and bursa-copulatrix; vagina absent because bursa copulatrix arises directly from genital atrium adjacent to distal end of free oviduct; limits of epiphallus and penis were judged by dissection as the distal part of the epiphallus is concealed within the penis sheath; interior of penis lacking any well-defined verge; penial retractor muscle arising from the distal end of the penis sheath at a sharp bend close to where the exposed part of the epiphallus leaves the sheath; this muscle is long and narrow, passing proximally alongside the spermoviduct to join the body wall. Spermatophores have not been described in the genus and none were found during the present study.

Our material appears to consist of three species, which can be separated on shell characters using the following key:

1. Greatest breadth of mature shells <25mm; upper spire with whorls flat to weakly convex so sutures almost indiscernible or very shallow; sculpture on upperside of shell nearly smooth to only moderately rough; adult shell with tooth on lower lip of aperture at middle or on outer half of length of lower lip 2.

Greatest breadth of mature shells >25mm; upper spire with whorls convex so suture shallow; sculpture on upperside of shell ~ rough; adult shell with tooth on lower lip of aperture on inner one-third of length of lower lip  
***R. hepatizon***

2. Greatest breadth of adult shell >18mm; whorls 1 and 2 of spire with regular radial ribs; whole upperside of shell with moderately rough sculpture; whorls 1–3 of spire nearly flat with suture very shallow or almost indiscernible; upper lip of adult shell aperture with prominent thickening that ends as low tooth directed outwards; at higher elevations (ca 610–1300m alt.)

***R. welwitschi* s. str.**

Greatest breadth of adult shell <18mm; whorls 1 and 2 of spire ~ smooth, or with few irregular growth lines; whole upperside of shell with weak sculpture; whorls 1–3 of spire slightly convex with evident suture; upper lip of adult shell aperture lacking any evident thickening that ends as tooth; at lower elevations (recorded at 68–236m alt.) ***R. sublaevis* sp. nov.**

### ***Rhysotina hepatizon* (Gould 1845)**

Figs 1A–C, 3A–D, 4C–D.

*Helix hepatizon* Gould 1845 (p. 38). Type locality: “near the mouth of the Gaboon river”, corrected to San-Thomé by Morelet (1868: 54) and Crosse (1868: 127).

*Helix hepatizon*– Pfeiffer (1853: 46, no. 122).

*Helix hepatizon*– Gould (1862: 197).

*Helix hepatizon* Gould, 1845– Morelet (1868: 54, pl. 2 fig. 7).

*Helix hepatizon* Gould, 1845– Crosse (1868: 126).

*Nanina hepatizon*– Fischer (1881: 226) n.v.

*Helix hepatizon* Gould– Greeff (1882: 521).

*Nanina hepatizon*, Gould– Nobre (1886: 214; p. 2 in offprint).

*Nanina hepatizon*– Tryon (1886: 34, pl. 9, fig. 34).

*Nanina hepatizon*, Gould– Crosse (1888: 15).

*Nanina hepatizon*, Gould– Nobre (1891: 932).

*Nanina hepatizon*, Gould– Girard (1893: 33).

*Nanina hepatizon* Gould– Germain (1908: 59).

*Thomeonanina hepatizon*– Germain (1909: 99).

*Nanina hepatizon*– Nobre (1909: 79).

*Thomeonanina hepatizon* Gould– Germain (1916: 156, 161, 167, 207).

*Rhysotina hepatizon* Gould– Degner (1932: 226; fig. 1, 228, fig. 3); specimens were in Hamburg Museum.

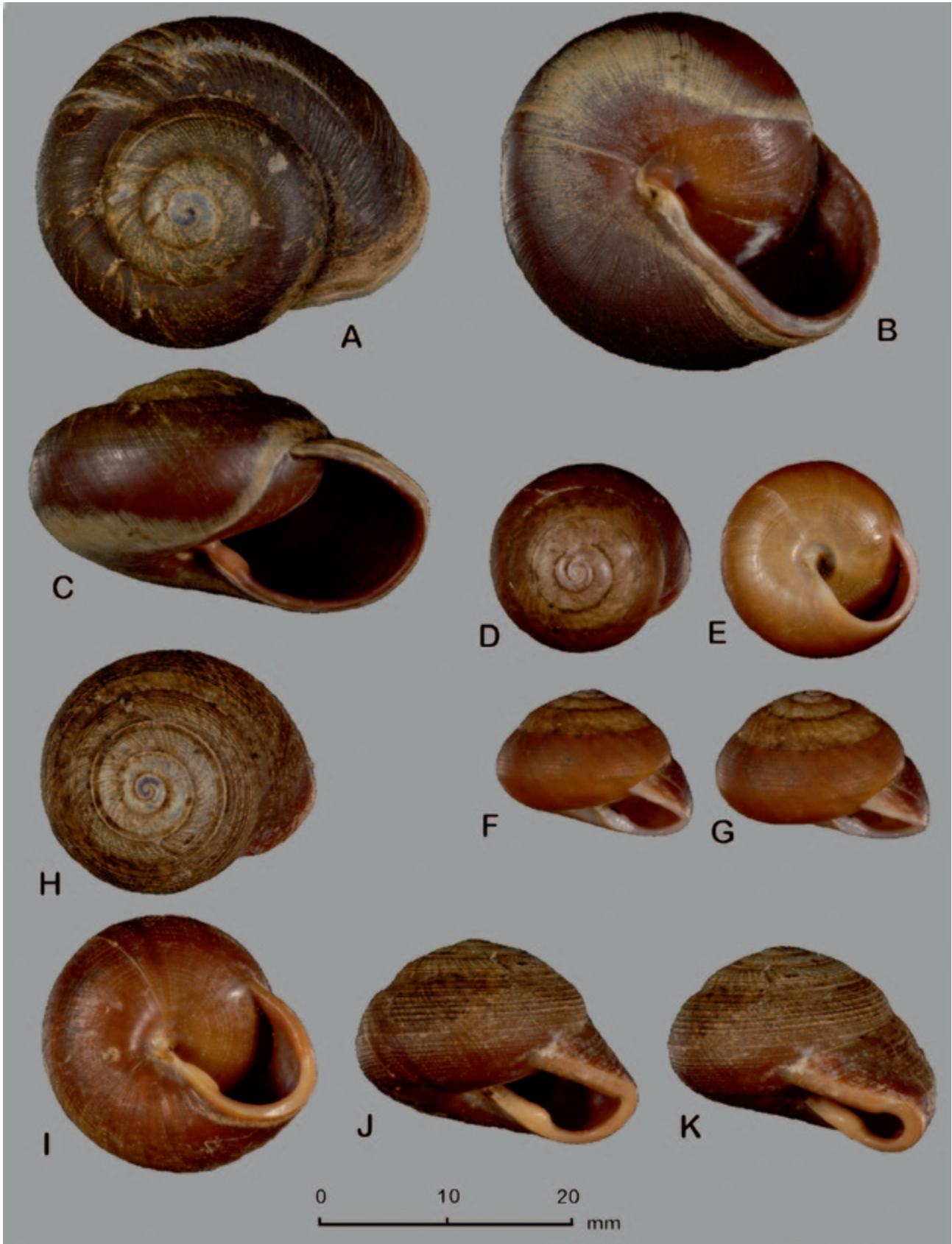
*Thomeonanina hepatizon* Gould, 1849– Cossignani (2014: 193); figs of three shells.

*Specimens examined* ST3, near Bom Successo Botanical Garden, 00°17'04.7"N., 006°36'35.2"E., trackside with scrub and grasses, cultivation edges and few small forest patches, 1149m alt., Coll. GAH, 2013.12.03, 14 sh (13 ad, 1 imm)+1 bod; ST4, path to Lagoa Amelia from Bom Successo Botanical Garden, ca 00°16'42.5"N., 006°36'00.2"E., montane forest on slope, with understory of saplings (collected from fallen branches and leaf-litter), ca 1300m, Coll. GAH, 2013.12.04, 2 sh +2 bod.

*Diagnosis* see key above.

*Description of shell* (n=12 measured) B 29.1–33.4mm, mean 31.45mm, s.d. 1.38mm; H 17.1–22.8mm, mean 20.49mm, s.d. 1.46mm; whorls 4.4–4.9, mean 4.62, s.d. 0.17. Depressed-conical, with whorls moderately swollen, separated by shallow sutures. Body whorl slightly expanded close to aperture. Aperture rather large, oval except where interrupted by penultimate whorl. Peristome mainly rather evenly thickened, but





**Figure 1** Shells of *Rhysotina* species from São Tomé: **A–C** *R. hepatizon*, Site ST4; **D–G** *R. sublaevis* sp. nov., Holotype, NHMUK 20150075, Site ST1; **H–K** *R. welwitschi* s. str., Site ST4; **G** and **K** are slightly oblique views to show shape of upper lip of peristome. See text for details of localities, etc.

scarcely reflected, twice as thick over *ca* 5mm near columellar margin with one short low tooth on inner third of lower lip (the tooth directed upwards into aperture where the peristome thickening ends). Shell thick, slightly translucent, glossy. Colour dark slightly reddish brown, interior of aperture dull brown, peristome paler brown to whitish on thickened area near columella; old shells become whitish where corroded or worn, especially on crests of periostracal ribs and papillae, at peristome edge and in grooves on body whorl near aperture. Protoconch smooth and glossy, with faint radial ribs from whorl 0.3 onwards. Teleoconch with sculpture of strong, somewhat irregular, closely spaced radial ribs intersected by weaker spiral grooves to give pattern of elongate papillae orientated obliquely along lines of growth; body whorl with roughest sculpture, especially towards aperture; sculpture on upper spire and underside of shell less rough.

Shell descriptions were also given by Morelet (1868: 54), Crosse (1868: 126) and Germain (1916: 207–208) and figures by Morelet (1868: pl. 2 fig. 7) and Cossignani (2014: 193, figs of three shells).

*External coloration of body* Head, ommatophores, top of forepart of body and top of forepart of flanks grey, shading downwards to whitish in middle of forepart of flanks; mantle-collar grey; rest of exposed body including foot, foot-fringe and tail whitish; exterior of mantle inside body-whorl with whitish ground-colour and bold blackish-streaks and blotches with a few smaller spots, the same coloration continuing on exterior of middle whorls of spire; uppermost whorls dull brown with fine whitish reticulation.

*Genital anatomy* Two dissected, from locality ST4. Vas deferens a thin tube, extending distally from position proximal to free oviduct to pass around distal part of bursa copulatrix, into angle between bursa and distal penis sheath (to which it is attached by thin connective tissue) then distally alongside penis sheath to join distal end of epiphallus. Epiphallus with exposed part about half the length of penis sheath, cylindrical, with two rounded projections respectively at and near proximal end that may be small caecae; concealed part of epiphallus inside proximal one-third of penis sheath, a tube enlarging distally to about half of diameter of distal end of penis (which

is abruptly larger), with two tight coils when *in situ*, so it fills proximal end of penis sheath. Penis sheath completely and rather tightly enveloping penis and concealed part of epiphallus, forming a cylindrical-clavate structure that is widest towards proximal end and narrowest at insertion onto genital atrium; wall of sheath opaque, whitish, mainly thin and flexible, but distal one-third with pronounced muscular thickening of wall, another much more restricted thickened area near proximal end. Penis sub-cylindrical, clavate, with thick muscular walls and rather narrow central canal; inner walls with numerous longitudinal ridges, each of which is the ~ sinuous crest (apparently glandular) of a tall longitudinal lamella. Genital atrium a very short wide cylinder with muscular walls, opening externally as a rather large genital pore and continuous proximally with the bursa copulatrix; inner wall with longitudinal ridges that also continue proximally into bursa; with opening from distal end of penis low down and that of free oviduct only slightly further proximally from genital pore. Bursa copulatrix large, ovoid, tapering abruptly at proximal end to a narrowly conical point which is attached to the lower part of the spermoviduct by a slender apical ligament and numerous strands of fine connective tissue; walls of bursa thick and muscular, internally with many longitudinal ridges, each the ~ sinuous crest (apparently glandular) of a thin lamella. Free oviduct rather short, somewhat narrowed at junction with genital atrium and more markedly towards spermoviduct.

Degner (1932: 228) described and figured generally similar genital anatomy, although with a proportionately narrower genital atrium and less coiling of the concealed part of epiphallus, differences which might have been due to a slightly less mature specimen.

*Distribution and ecology* Endemic at high elevations on São Tomé island, where found by us at 1149-*ca* 1300m alt. on and near ground in disturbed areas with plentiful vegetation bordering cultivation and in undisturbed montane forest with well developed understorey, coexisting with *R. welwitschi* s. str. Crosse (1888: 16) cited old records from Roça do Monte Café between 500–800m alt. and Roça Bom Sucesso at 1050m; the more general statement “et dans presque tout le reste de l’île, où l’espèce est commune (Moller)” may have been incorrect. According to



Exell (1944), the forests of São Tomé exist in three zones, a Lower Rainforest from sea-level to 800m, Montane Forest from 800–1400m and Mist-forest from 1400m to the top of the island at 2024m. On that basis, *R. hepatizon* may be known only from the Montane Forest zone, although it clearly does not require intact forest habitat.

*Etymology* Derivation of the name is not stated in the original description. However, *Hepatizon* was a highly valuable metal alloy in classical antiquity, thought to be an alloy of copper with the addition of a small proportion of gold and silver, mixed and treated to produce a material with a dark purplish patina, similar to the colour of liver (*Wikipedia*). This is exactly the colour of a fresh shell of the species. The species epithet is thus apparently a noun in apposition, so that it does not change to agree with the generic name.

***Rhysotina welwitschi* (Morelet 1866) s. str.**  
Figs 1H–K, 2, 3I–L, 4C–D.

*Helix welwitschi* Morelet 1866 (p. 153); type locality “*insula San-Thomé sinus Guineensis, ad 2,000 ped. altit. plagæ orientalis*”; the type shell was 21mm in major diameter, so apparently not referable to *R. sublaevis* sp. nov.

*Helix Welwitschii* [*sic*] Morelet, 1866– Morelet (1868: 55, pl. 2 fig. 4); with var. *magis globosa* ... named using a descriptive phrase; from “*dans les forêts élevées de San-Thomé*”.

*Helix Welwitschii* Morelet– Greeff (1882: 521); *pars*, material obtained with *H. hepatizon* “*in der Umgebung der Roça do Monte Cafe 500–800m über dem Meere*”.

*Nanina Welwitschi*, Morelet– Nobre (1886: 214, p. 2 in offprint); “*encontrados entre 600 e 1:300 metros de altitude*”.



**Figure 2** Upper whorls of spire of *Rhysotina* species from São Tomé: left, *R. sublaevis* sp. nov., immature shell from Site ST11; right *R. welwitschi* s. str., subadult shell from Site ST4.

*Nanina Welwitschi*, Morelet– Crosse (1888: 16), *pars*: from “zone élevée et zone moyenne de l’île, entre 600 et 1300 mètres d’altitude (Moller)”.

*Nanina Welwitschi* [sic], Morelet– Nobre (1891: 933), from “Roça Monte Cafe, de 700 a 1:500m. de altitude”.

*Rhysotina welwitschi* (Morelet, 1866) – Schileyko (2002: 1233, Fig. 1621); from Monte Café, 800–900m above sea level, São Thomé island, with figs of shell, jaw and genital anatomy.

*Rhysotina welwitschi* (Morelet, 1848 [sic]) – Cossignani (2014: 193), see below.

Additional or unverified citations referable to either *R. welwitschi* s. str. or *R. sublaevis* sp. nov.:

*Helix welwitschi* Morelet, 1866– Crosse (1868: 128, pl. 6 fig. 5).

*Nanina Welwitschi*– Fischer (1881: 226), n.v.

*Nanina Welwitschi*, Mrlt– Girard (1893: 31, 33).

*Thomeonanina Welwitschi*– Germain (1909: 99), n.v.

*Nanina Welwitschi*– Nobre (1909: 80), n.v.

*Rhysotina welwitschi* Morel. – Degner (1932: 226, figs. 1, 2). It is uncertain whether Degner (*op. cit.*: 227) described and figured the radula and anatomy of the montane species (*R. welwitschi* s. str.) or *R. sublaevis*, newly described below; his material was collected by Dr R. Greeff in 1879–80 who wrote that it was obtained from the lowlands up to 500–800m altitude (Greeff, 1882: 521); the specimens were in Hamburg Museum.

*Rhysotina welwitschi* (Morelet) – Gascoigne (1994b: 804).

*Specimens examined* ST3, near Bom Sucesso Botanical Garden, 00°17'04.7"N., 006°36'35.2"E., trackside with scrub and grasses, cultivation edges and few small forest patches, 1149m alt., Coll. GAH, 2013.12.03, 5 sh; ST4, path to Lagoa Amelia from Bom Sucesso Botanical Garden, ca 00°16'42.5"N., 006°36'00.2"E., montane forest on slope, with understorey of saplings (collected from fallen branches and leaf-litter), ca 1300m, Coll. GAH, 2013.12.04, 4 sh +4 bod.

*Diagnosis* see key above.

*Description of shell* (n=7 measured) B 18.6–21.9mm, mean 19.60mm, s.d. 1.19mm; H 11.8–13.4, mean 12.46mm, s.d. 0.54mm; mean H/mean B 0.64; whorls 4.7–5.2, mean 4.91, s.d. 0.16. Subglobose-conical with rounded spire. Whorls 1–3 of spire nearly flat with suture very shallow to almost indiscernible; body whorl somewhat

flattened above and at periphery, separated from penultimate whorl by moderately deep suture. Aperture ovate-rectangular except where interrupted by penultimate whorl, with strongly curved outer margin, less curved upper and lower margins. Peristome rather evenly thickened throughout but not reflected; on upper-side of aperture thickest at 7–8mm from parietal margin with long low tooth directed outwards over shell aperture; on lower side of aperture peristome thickest at 6–7mm from columellar margin where there is a higher rounded tooth directed upwards into shell aperture. Shell thick and strong, slightly translucent, glossy when fresh. Colour deep reddish-brown, slightly lighter toned beneath and lighter inside aperture; peristome pale brown, or whitish near columellar margin; old shells become whitish due to corrosion or wear, especially on apex, peristome and spiral cords of spire. Protoconch glossy with close regular radial ribs developed from ~ whorl 0.4 onwards, which also form the dominant sculpture on whorls 1–2. Rest of teleoconch with strong spiral ridges, several of which form slightly raised cords; this spiral sculpture intersects closely set lower radial ribs, to give pattern of mainly short oblique riblets (locally also of varied small papillae). Underside with sculpture much less prominent, but including strong spiral microsculpture close to aperture.

The shell of *R. welwitschi* s. str. was also described and figured by Morelet (1868: 55, pl. 2 fig. 4) and Cossignani (2014: 193; figs of first and third shell given as 23mm so surely *R. welwitschi* s. str., the second shell given as 19mm so probably also this species). Either *R. welwitschi* s. str. or *R. sublaevis* sp. nov. was described and figured by Crosse (1868: 128, pl. 6 fig. 5).

*External coloration of body* Head, top of forepart of body, top of forepart of flanks and base of ommatophores grey, shading downwards to whitish in middle of forepart of flanks; foot and foot-fringe pale brown to pale greyish or nearly whitish; mantle-collar grey-brown to dull grey with pale outer edge; one of four bodies with tail lightly marked with grey dorsally near tip; rest of exposed body, lower tentacles and tips of ommatophores whitish; exterior of mantle inside body-whorl with whitish ground-colour nearly obscured by blackish-grey spots, blotches and short streaks.

*Genital anatomy* Three dissected, from locality ST4. Vas deferens a thin tube, originating just proximal to the free oviduct, continuing distally, passing around bursa copulatrix to near base of penis sheath to which it is loosely attached by connective tissue then returning proximally to join proximal end of epiphallus. Epiphallus with exposed part consisting of tube about one-third length of penis sheath, having two rounded lateral projections respectively at and near the proximal end that may represent small caecae; concealed part within proximal end of penis sheath, straight, similar in width to exposed part or slightly wider (approximately half diameter of proximal end of penis), with length varying in different individuals from two to six times the width. Penis sheath completely and tightly enveloping all of penis and concealed part of epiphallus, a whitish, curved cylindrical structure that is somewhat clavate, being widest in proximal half; walls of sheath opaque, thin and flexible over most of sheath, but much thicker and muscular in distal third and also somewhat thicker over small area at proximal end. Penis cylindrical-clavate, with thick muscular walls and relatively narrow central lumen; interior of penis with many longitudinal ridges formed by crests of ~ sinuous (apparently glandular) thin lamellae, some of which extend full length of penis (many surface cells of lamellae loose, friable, possibly not well preserved). Genital atrium a short wide cylinder with muscular walls, opening in external genital pore that is rather large to medium-sized in different individuals, the exit from distal penis quite close to pore, that from free oviduct somewhat further from it (more proximal); outline of atrium continuous with that of bursa in one individual, narrower in another. Bursa copulatrix ovoid, with thick muscular walls, giving rise apically (proximally) to a short to rather long, narrow, conical to subcylindrical point from which a thin strand of ligament and various fine connective tissues extend to the spermoviduct. Free oviduct rather short, narrowed at junction with atrium and at proximal end.

It is uncertain whether Degner (1932: 227) described and figured the genital anatomy of *R. welwitschi* (*s. str.*: the montane species) or *R. sublaevis* (the lowland species) newly described below. His material was collected by Dr R. Greeff in 1879–80 who wrote that it was obtained from the lowlands up to 500–800m altitude (Greeff,

1882: 521). Degner's account is of genitalia very similar to those that we found in both of these species.

Schileyko (2002: 1233) apparently overlooked Degner's publication. He described and figured the distal genitalia of a single specimen (Moscow Lc-19629, ex Leiden) that was collected at 800–900m alt. and had the strong spiral cords on the shell characteristic of *R. welwitschi s. str.* This specimen had "a very peculiar structure of atrium", which was "enormously swollen, sac-like". This differs markedly from the atrium structure described by Degner (*loc. cit.*) and from our material. Since a total of 14 adult individuals of *Rhysotina* representing three species have now been found to lack the "enormously swollen, sac-like" atrium found by Schileyko it seems unlikely that it is normal in the genus at any stage of development. Therefore, it appears to represent either an abnormal individual or possibly distortion during preservation. Schileyko also appears to have overlooked the concealed portion of the distal epiphallus inside the penis sheath. He described the penis as thin-walled (perhaps as a slip for the penis sheath, since he figures thick penis walls) and "with a strong axial pilaster" internally; the latter seems less conspicuous in our material.

*Distribution and ecology* Endemic on São Tomé island, where found by us only at 1149–ca 1300m alt., on and near the ground in disturbed areas with plentiful vegetation bordering cultivation and in undisturbed montane forest with well developed understorey, coexisting with *R. hepatizon* in both habitats. Morelet's (1866: 154) type was from "2,000 *ped. altit. plagæ orientalis*", i.e. ca 610m alt. above the eastern coast. The species thus appears to be characteristic of the Montane Forest zone of Exell (1944) from 800–1400m, perhaps also occurring somewhat lower into the upper part of the Lower Rainforest zone, but it is clearly not restricted to forest habitats.

*Etymology* The epithet honours the collector Dr Friederich Welwitsch.

***Rhysotina sublaevis* sp. nov. G.A. Holyoak & D.T. Holyoak**

Figs 1D–G, 2, 3E–H, 4A–B.

*Holotype* NHMUK 20150075 (shell, B 16.1mm, H 10.6mm), collected by G.A. Holyoak on 2013.12.01 at site ST1.



*Type locality* São Tomé island, by NW. coastal road (EN1) well S. of Santa Catarina and inland of coast, 00°14'25.7"N., 006°28'20.0"E., on slopes at edge of tall open secondary forest, 68m alt.

*Paratypes* 80 sh +13 bod in CGAH from localities ST1, ST2, ST7, ST10, ST11 and ST13 listed below.

*Previous citations*

*Helix Welwitschii* Morelet– Greeff (1882: 521); *pars*, material from “ca 300m über dem Meere auf Roça Boa Entrada, Rio do Ouro”.

*Nanina Welwitschi*, Morelet– Crosse (1888: 16), *pars*: record from “Roça Boa Entrada, à 300 mètres d’altitude, Rio do Ouro”.

*Helix Welwitschi* Morelet– Germain (1908: 59), from “Bords du Rio de Ouro” [presumably a lowland locality].

*Thomeonanina Welwitschi* Morelet– Germain (1916: 156, 161, 167, 208), with (p. 209) *depressa*, *alta* described as both “mutations” and “formes”; *pars*?: on p. 209 the species is described as “assez polymorphe”; specimens from Ribeira Palma collected by L. Fea from 0–300m alt. and 400–700m alt. were studied, at least those from low altitudes and with shell diameters <19mm were presumably the present species.

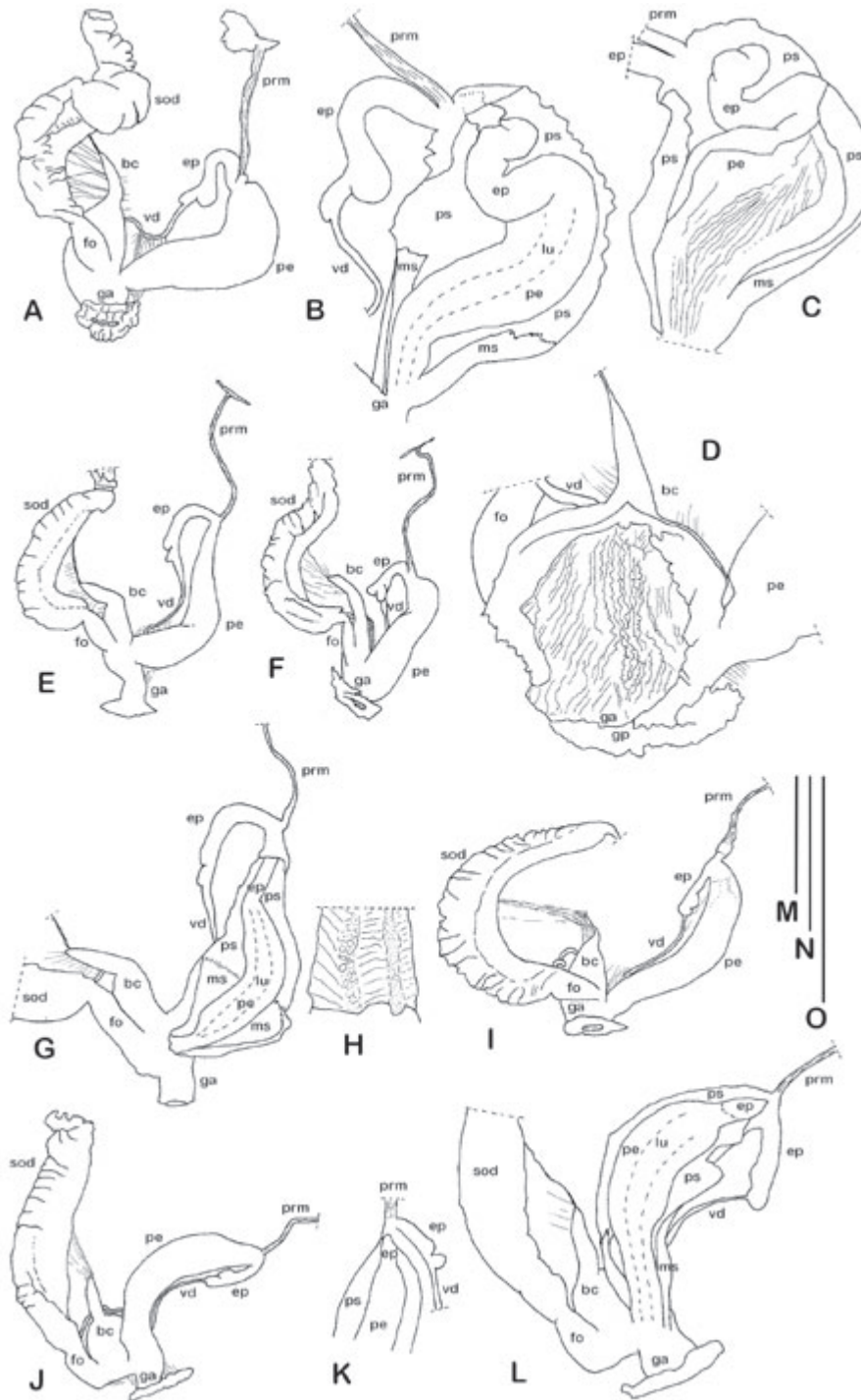
*Specimens examined* ST1, by NW. coastal road (EN1) well S. of Santa Catarina and inland of coast, 00°14'25.7"N., 006°28'20.0"E., tall open secondary forest on slopes (collecting from roadside banks, etc.), 68m alt., Coll. GAH, 2013.12.01, 10 sh (4 ad, 6 imm)+3 bod; ST2, S. of EN2 and NW. of Ribeira Peixe, 00°05'35.3"N., 006°35'20.2"E., edge of tall primary forest on hill above young oil palms (from backs of fallen leaves and fallen stems), 126m alt., Coll. GAH, 2013.12.02, 2 sh +2 bod (imm); ST7, S. of EN2 and NW. of Ribeira Peixe, 00°05'23.3"N., 006°35'25.2"E., tall primary forest on ridge and slopes, understorey of saplings, rocky banks, ca 181m alt., Coll. GAH, 2013.12.06, 4 sh +2 bod (imm); ST10, by EN2 ca 0.5km NE. of Montemario, 00°04'30.9"N., 006°33'52.1"E., second-growth woodland and oil-palm plantation on rocky slope, with ferns in ground-layer, 56m alt., Coll. GAH & DTH, 2013.12.11, 6 sh; ST11, by EN2 ca 2km S. of Montemario, 00°04'09.8"N., 006°33'08.1"E., roadside bank with ferns and herbs at foot of slope with secondary forest above, ca 101m alt., Coll.

GAH (mainly) & DTH, 2013.12.11, 37 sh (6 ad, 31 imm)+8 bod; ST12, by EN1 ca 0.5km SW. of Lagoa Azul, 00°24'02.2"N., 006°36'26.6"E., dead and perhaps drifted shells from soil surface and debris by small dried stream course above shore in lower edge of valley with cover of dry woodland, ca 5m alt., Coll. GAH & DTH, 2013.12.12, 3 old sh; ST13, by EN2 ca 2km N. of Ponta Baleia, 00°03'37.6"N., 006°33'21.8"E., forest on slopes by road, with understorey of saplings and ground-layer of ferns, 236m alt., GAH & DTH, 2013.12.13, 22 sh (9 ad, 13 imm)+3 bod.

*Diagnosis* see key above.

*Description of shell* (n=29 measured) B 15.7–17.8mm, mean 16.77mm, s.d. 0.61mm; H 10.5–13.4mm, mean 12.20mm, s.d. 0.83mm; mean H/mean B 0.73; whorls 4.8–5.3, mean 4.98, s.d. 0.14. Depressed globose with rounded spire; whorls 1–3 of spire slightly convex with evident suture; body whorl rounded, separated from penultimate whorl by shallow suture. Aperture rounded to broadly oval except where interrupted by penultimate whorl, the lower margin less curved than upper. Peristome rather evenly thickened throughout, not reflected, upper edge without any obvious tooth or additional thickening, lower edge thicker at 5–6mm from the columellar margin where there is an obvious low tooth directed upwards into shell aperture. Shell thick and strong, slightly translucent, lustrous rather than glossy when fresh because of close microsculpture, except for glossy apex (whorls 0–2) and interior of aperture. Colour brown to dull brown, lighter inside aperture, with peristome pale brown to whitish (old shells often become extensively whitish on spire due to corrosion or wear). Protoconch smooth, lacking any sculpture; whorl 1 similar but with faint growth ridges. Teleoconch generally weakly sculptured, with continuous low spiral ribs intersecting weaker and rather irregular radial riblets. Underside with sculpture less prominent, mainly of very low and rather even spiral ribs, the spaces between these with microsculpture of elongate (straight or curved) papillae. Shell descriptions by Germain (1916: 209–210) presumably included the present species in his account of *R. welwitschi* (see above).

*External coloration of body* Head, top of forepart of body, top of forepart of flanks and base of ommatophores light grey; foot and foot-fringe



**Figure 3** Drawings of distal genitalia of *Rhysotina* species from São Tomé: **A–D** *R. hepatizon*, Site ST4 (A distal genitalia; B penis and epiphallus with penis sheath opened; C penis and part of epiphallus, with penis opened to show internal structures; D bursa copulatrix and genital atrium opened to show internal structures); **E–H** *R. sublaevis* sp. nov., paratypes from Site ST1 (E, F distal genitalia of two individuals; G same snail as E with penis sheath opened; H as G, with penis opened to show structures on inner wall, somewhat schematically); **I–L** *R. welwitschi* s. str., Site ST4 (I, J distal genitalia of two individuals; K epiphallus and proximal part of penis of a third individual, with penis sheath opened; L same snail as J, with penis sheath opened); **M–O** are scale bars representing 10mm (M for Fig. 3A; N for figs 3E, F, I and J; O for figs 3B, C, D, G, H, K and L). Abbreviations: **bc** bursa copulatrix, **ep** epiphallus, **fo** free oviduct, **ga** genital atrium, **gp** genital pore, **lu** lumen of penis, **ms** thick (muscular) part of penis sheath, **pe** penis, **prm** penis retractor muscle, **ps** thin penis sheath, **sod** spermoviduct, **vd** vas deferens. See text for details of localities, etc.

pale brown; mantle-collar brown-grey with pale outer edge; rest of exposed body whitish; exterior of mantle inside body-whorl whitish with blackish-grey spots and small blotches or streaks ~ throughout (the dark markings covering less than half of the total area); middle whorls of spire similar to body-whorl; uppermost whorls dull light brown with fine whitish reticulation. Generally, the body coloration of this species is lighter in tone with somewhat smaller dark markings than in *R. hepatizon* or *R. welwitschi* s. str.

*Genital anatomy* Seven mature individuals dissected, from localities ST1, ST11, ST13. Vas deferens a thin tube, somewhat wider near distal end where joined to proximal end of epiphallus, originating above proximal end of free oviduct, continuing distally to pass around bursa copulatrix to distal end of penis sheath (to which it is joined by thin connective tissue), then returning proximally to join epiphallus. Epiphallus with exposed part cylindrical, curved, overall about one-third length of penis sheath, having two rounded lateral projections (probably small caecae) respectively at and near proximal end; concealed part inside proximal one-third to one-quarter of length of penis sheath, about half diameter of proximal end of penis (from which it is sharply demarcated) and similar in overall length to exposed part, in one individual straight, in second individual tightly coiled through one complete turn so that proximal end of penis sheath filled. Penis sheath cylindrical in one individual, tapering proximally in another; a whitish, opaque structure; the wall thin, flexible for distal two-thirds of length, abruptly and markedly thicker and more muscular in distal one-third of length; more narrowly thickened also near proximal end. Penis cylindrical, tapering somewhat at proximal and distal ends, with thick muscular walls and relatively narrow central lumen; interior walls of penis with many longitudinal and transverse ridges, forming tops (apparently glandular) of lamellae; a central elongated band of lamellae forming an internal ridge (perhaps a weakly developed pilaster); an impression of transverse ridges (Fig. 3H) may be have resulted from contraction during preservation. Genital atrium a short to very short cylinder, opening outwards in a rather large genital pore; the exit from distal end of penis very close

to pore in one individual, further proximal in another, the exit from free oviduct somewhat higher (more proximal) in both of them. Bursa copulatrix apparently a continuation proximally of the genital atrium, forming a rather small narrowly-ovoid structure with thick walls, terminating proximally in a cylindrical-conical point from which a long thin strand of ligament passes proximally to join spermoviduct and numerous slender threads of connective tissue form similar but shorter links. Free oviduct rather short, sub-cylindrical, narrowed at both ends.

*Distribution and ecology* Endemic on São Tomé island, where our records (listed above) are only from the lowlands, at 68–236m alt., from edges of primary forest, secondary forest, and its edges including roadside banks bordering forest. The species is therefore known only from the Lower Rainforest zone which Exell (1944) defined as from sea-level to 800m, whereas *R. welwitschi* (q.v.) is characteristic of the Montane Forest above 800m (with a possible old record at 610m), although neither species now requires intact forest habitat. It will be interesting in future to ascertain whether the altitudinal ranges of the two species meet or overlap.

*Etymology* The epithet *sublaevis* refers to the almost smooth shell, based on *laevis* (adj. B); a distinction from the other two species of the genus that have rougher shell sculpture.

#### AFFINITIES, EVOLUTION AND CONSERVATION OF *RHYSOTINA*

*Rhysotina* appears to be a taxonomically rather isolated genus, with no close relatives evident in the land-snail faunas of the other Gulf of Guinea islands or indeed on the adjacent parts of the African continent. Nevertheless, the arguments for recognition of the monogeneric family Rhysotinidae (Schileyko, 2002: 1233) appear to be based partly on the genital anatomy of an atypical individual, as discussed above. A resemblance of *Rhysotina* to the genus *Plegma* Gude 1911 from the Mascarene islands has been noted (Degner, 1932; F. Naggs in Gascoigne, 1994b: 797), and this was supported by the first molecular phylogenetic data to include these genera, which placed both of them in the Helicarionidae (Wade, Mordan & Clarke, 2001: 416; Wade, Mordan & Naggs, 2006). However, a





**Figure 4** Habitats of *Rhysotina* on São Tomé island, December 2013; **A, B** in Lower Rainforest zone, **C** in Montane Forest zone, **D** at transition from Montane Forest zone to Mist-forest zone. **A** (site ST1) by NW. coastal road (EN1) well S. of Santa Catarina and inland of coast, 00°14'25.7"N., 006°28'20.0"E., tall open secondary forest on slopes, 68m alt., *R. sublaevis* collected here at type-locality from roadside banks, etc.; **B** (ST2) S. of EN2 and NW. of Ribeira Peixe, 00°05'35.3"N., 006°35'20.2"E, inside edge of tall primary forest on hill, 126m alt., *R. sublaevis* collected from backs of fallen leaves and fallen stems; **C** (ST3) near Bom Successo Botanical Garden, 00°17'04.7"N., 006°36'35.2"E., trackside with scrub and grasses, cultivation edges and few small forest patches, 1149m alt., *R. hepatizon* and *R. wewitschi* s. str. collected here, at base of low vegetation; **D** primary forest bordering Lagoa Amelia, above Bom Successo Botanical Garden, ca 1430m, above site ST4 where *R. hepatizon* and *R. wewitschi* s. str. collected from fallen branches and leaf-litter in montane forest on slope, with understory of saplings at ca 1300m, ca 00°16'42.5"N., 006°36'00.2"E.

subsequent molecular study including more taxa places *Rhysotina* in a clade with the African genera *Elisolimax* Cockerell 1893, *Gymnarion* Pilsbry 1919 and *Sheldonia* Ancey 1887 which are together labelled as Urocyclidae (Herbert & Mitchell, 2009: 213). Although that study (*loc. cit.*, fig. 9) brackets *Rhysotina* with the Helicarionidae the branching pattern shown would render this family paraphyletic since the genus is shown as the sister group of the Urocyclidae, whereas placement of *Rhysotina* within the Urocyclidae results

in the latter family being enlarged but remaining monophyletic. It is therefore unsurprising that *Rhysotina* was assigned to the Urocyclidae (Subfamily Sheldoniinae) by Bouchet & Rocroi (2005: 269).

As discussed above, the “unique character” of “a very peculiar structure” of the genital atrium that was emphasised for naming of the family Rhysotinidae Schileyko 2002 was most likely from a snail that was atypical or distorted in preservation. Nevertheless, among those few

genera of Urocyliidae that are known anatomically (cf. Schileyko, 2002), the combination of shell and genital characters of *Rhysotina* appear distinctive, as described above under the genus heading. Because of these peculiarities and the small amount of published molecular data suggesting it forms a sister-group to other sampled Urocyliidae (Herbert & Mitchell, 2009: 213), it is tentatively maintained here as a separate Subfamily Rhysotininae, rather than as a distinct family.

Restriction of the taxonomically isolated genus *Rhysotina* to a single oceanic island that arose from the deep ocean floor as a result of volcanic activity during the Tertiary (Fitton & Dunlop, 1985) is remarkable. The most likely explanation may be that it has survived as a relict there following colonisation by a taxon formerly occurring on the African continent where it has become extinct (or not yet been discovered). The flowering plants of São Tomé include afro-montane elements showing striking range disjunctions with close relatives on mountains in eastern Africa as well as presence of palaeoendemic taxa (Figueiredo *et al.*, 2011: 41–42).

Development of three species of *Rhysotina* on a single rather small island (857 km<sup>2</sup>) may also need an explanation. Repeated geographical speciation by isolation of populations within São Tomé seems surprising because the island has a rather simple topography with central mountains surrounded by a continuous band of lowland. However, there is evidence of repeated volcanic activity there since the Tertiary, from rocks dated to 15.7 Ma, 13.0 Ma and between 7.6 and 0.1 Ma (Fitton & Dunlop, 1985), so that lava flows or other areas with no vegetation might have formed barriers to dispersal of snails across the island at various times in the past, providing opportunities for geographical speciation. Alternatively, there is evidence that the neighbouring island of Príncipe (111 km distant, area 139 km<sup>2</sup>) was much larger at times of lower ocean levels during the Pleistocene (Jones & Tye, 2006: 1, 7), so that former occurrence of the genus there is possible. This might have allowed repeated invasions of São Tomé from Príncipe, followed by extinction on the latter island, giving another possible scenario for producing several species.

The presence of a very strong shell in all three *Rhysotina* species is at first sight puzzling, since they are all endemic on an island with no native

mammals other than bats and no other likely predators with strong jaws. Nevertheless, the endemic thrush (*Turdus olivaceofuscus olivaceofuscus*) is known to eat land snails (Jones & Tye, 2006: 102) and to smash them on rocks (Atkinson *et al.*, 1994; Leventis & Olmos, 2009: 90); land-crabs also occur widely on the island and they are likely to be snail predators.

When the island was discovered in 1470 it was said to be uninhabited and Exell (1944) thought that rainforest would have uniformly covered almost all of the island, although much of the lowland area is now deforested (Jones & Tye, 2006: 12–13). Our observations show that although *Rhysotina* still occur in pristine primary forest (e.g. Figs 4B, 4D) they have also occupied secondary habitats extensively, including edges of plantations (e.g. Fig. 4C), so they are unlikely to be seriously threatened by habitat loss at present. Unlike many snails of oceanic islands, they presumably now coexist successfully with introduced mammals (monkeys *Cercopithecus mona*, feral cats, African Civet *Civettictis civetta*, weasels *Mustela nivalis numidica*, feral pigs, *Rattus rattus*, *Rattus norvegicus* and *Mus musculus* are all recorded on the island: Frade, 1958; Jones & Tye, 2006: 15), against which the thick shell might have been a fortuitous and useful pre-adaptation.

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