



## A checklist of the land Mollusca (Gastropoda) of the islands of São Tomé and Príncipe, with new records and descriptions of new taxa

### Listado de los moluscos terrestres (Gastropoda) de las islas de São Tomé y Príncipe, con nuevas citas y descripción de nuevos taxones

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Recibido el 8-XI-2019. Aceptado el 9-V-2020

#### ABSTRACT

The first comprehensive checklists since the works of Germain in 1916 are presented for the terrestrial Mollusca of São Tomé and Príncipe. The fauna currently known comprises 59 species for São Tomé, 45 for Príncipe, and a total of 86 species in the country as a whole. Seven species of terrestrial Gastropoda are newly described from the island of São Tomé and six more from the island of Príncipe. The genera involved are *Cyathopoma* (Cyclophoridae), *Maizania* and *Thomeomaizania* (Maizaniidae), *Pseudoveronicella* (Veronicellidae), *Nothapalus* (Achatinidae), *Gulella* and *Streptostele* (Streptaxidae), *Truncatellina* (Truncatellinidae), *Afroconulus* (Euconulidae), *Principicochlea* n. gen., *Principitrochoidea* n. gen., *Thomithapsia* n. gen. and *Thomitrochoidea* n. gen. (Urocyclidae). Most of these are from natural forest habitats and are likely to be single-island endemics. *Aporachis* n. gen. (Achatinidae s.l.) and *Apothapsia* n. gen. (Helicarionidae) are also described to accommodate previously known species. *Rachis burnayi* (Dohrn) and *R. eminula* (Morelet) are placed in the genus *Gittenouardia*. Additional new island records are of ten species on São Tomé, one on Príncipe and two more on both islands. These include six species of "microgastropods" with wider ranges in tropical Africa that are likely to be hitherto overlooked parts of the indigenous fauna and six anthropogenic introductions. *Pseudopeas crossei* previously known only from Príncipe and Bioko is newly recorded on São Tomé. More detailed taxonomic notes are provided on identification and delimitation of species and genera in Cyclophoridae/ Maizaniidae, Veronicellidae, Achatinidae, Cerastidae, Helicarionidae, and on the forgotten but apparently valid *Pseudoveronicella thomensis* (Veronicellidae).

#### RESUMO

São apresentadas as primeiras listas compreensivas dos moluscos terrestres de São Tomé e Príncipe desde os trabalhos de Germain em 1916. A fauna conhecida atualmente compreende 86 espécies, incluindo 59 em São Tomé e 45 no Príncipe. Sete novas espécies de gastrópodos terrestres são descritas da ilha de São Tomé e seis da ilha do Príncipe. Os géneros envolvidos

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são *Cyathopoma* (Cyclophoridae), *Maizania* e *Thomeomaizania* (Maizaniidae), *Pseudoveronicella* (Veronicellidae), *Nothapalus* (Achatinidae), *Gulella* e *Streptostele* (Streptaxidae), *Truncatellina* (Truncatellinidae), *Afroconulus* (Euconulidae), *Principicochlea* n. gen., *Principotrochoidea* n. gen., *Thomithapsia* n. gen. e *Thomitrochoidea* n. gen. (Urocyclidae). A maioria destes registos foram feitos em habitats de floresta natural e provavelmente são endémicos de uma única ilha. *Aporachis* n. gen. (Achatinidae s.l.) e *Apothapsia* n. gen. (Helicarionidae) também são descritos para acomodar duas espécies já conhecidas. *Rachis burnayi* (Dohrn) e *R. eminula* (Morelet) são realocados no género *Gittenedouardia*. Dez espécies adicionais são novos registos para São Tomé, uma para o Príncipe e duas para ambas as ilhas. Estes incluem seis espécies de “microgastrópodes” com ampla distribuição na África tropical, que provavelmente são parte da fauna indígena que tinha passado despercebida, e seis introduções antropogénicas. *Pseudopeas crossei* anteriormente conhecida apenas do Príncipe e Bioko é um novo registo para São Tomé. São fornecidas notas taxonómicas mais detalhadas sobre a identificação e delimitação de espécies e géneros de Cyclophoridae/ Maizaniidae, Veronicellidae, Achatinidae, Cerastidae, Helicarionidae e para a esquecida, mas aparentemente válida *Pseudoveronicella thomensis*.

## RESUMEN

Se presenta por primera vez desde los trabajos de Germain en 1916, un listado exhaustivo de los moluscos terrestre de São Tomé y Príncipe. La fauna actualmente conocida comprende 59 especies para São Tomé, 45 para Príncipe y un total de 86 especies para el país. Siete especies de gasterópodos terrestres se describen como nuevas en la isla de São Tomé y seis más en la isla de Príncipe. Los géneros abarcados son *Cyathopoma* (Cyclophoridae), *Maizania* y *Thomeomaizania* (Maizaniidae), *Pseudoveronicella* (Veronicellidae), *Nothapalus* (Achatinidae), *Gulella* y *Streptostele* (Streptaxidae), *Truncatellina* (Truncatellinidae), *Afroconulus* (Euconulidae), *Principicochlea* n. gen., *Principotrochoidea* n. gen., *Thomithapsia* n. gen. y *Thomitrochoidea* n. gen. (Urocyclidae). La mayoría de estos se encontraron en hábitats forestales naturales y es probable que sean endémicos de una sola isla. Se describen también *Aporachis* n. gen. (Achatinidae s.l.) y *Apothapsia* n. gen. (Helicarionidae) para acomodar especies previamente conocidas. *Rachis burnayi* (Dohrn) y *R. eminula* (Morelet) se reubican en el género *Gittenedouardia*. Además, se registran por primer vez diez especies en São Tomé, una en Príncipe y dos más en ambas islas. Estas incluyen seis especies de “microgastrópodos” con distribuciones más amplias en África tropical y que probablemente sean partes de la fauna indígena hasta ahora ignoradas, así como seis introducciones antropogénicas. *Pseudopeas crossei*, anteriormente conocido tan solo en Príncipe y Bioko, se registra ahora en São Tomé. Se proporcionan notas taxonómicas más detalladas sobre la identificación y delimitación de especies y géneros en Cyclophoridae / Maizaniidae, Veronicellidae, Achatinidae, Cerastidae, Helicarionidae y sobre *Pseudoveronicella thomensis* (Veronicellidae), un taxón olvidado pero aparentemente válido.

KEY WORDS: taxonomy, genital anatomy, endemic genera, endemic species, introduced species, land snails, slugs, microgastropods, Gulf of Guinea islands.

PALABRAS CLAVE: taxonomía, anatomía genital, géneros endémicos, especies endémicas, especies introducidas, caracoles terrestres, babosas, microgasterópodos, islas del Golfo de Guinea.

PALAVRAS-CHAVE: taxonomia, anatomia genital, géneros endémicos, espécies endémicas, espécies introduzidas, caracóis terrestres, lesmas, microgastrópodes, ilhas do Golfo da Guiné.

## INTRODUCTION

The Republic of São Tomé and Príncipe comprises two mountainous islands lying close to the Equator in the

Gulf of Guinea, off the west coast of central Africa. Both islands form part of the Cameroon Line of volcanos, and

both arose due to volcanic activity during the Tertiary. They rise from oceanic depths and have always been isolated from the nearest African coasts, which are no closer than 220 km and 255 km distant at the present day. Their natural vegetation was tropical rainforest, although cultivation has replaced most of this at lower altitude since human colonisation began in the fifteenth century. (JONES & TYE, 2006).

Both islands support rich land-snail faunas with a high proportion of endemic species. GASCOIGNE (1994a, 1994b) reported the faunas as comprising 39 species for São Tomé and 32 species for Príncipe, although he never published a full list for either island. Among these, he calculated for São Tomé that 25 species (64.1%) were single island endemics, with 19 (59.4%) for Príncipe; an additional 5 and 6 species respectively for each island were regarded as endemic to the Gulf of Guinea islands as a whole (i.e. present on more than one of the islands of São Tomé, Príncipe, Bioko or Annobón). GASCOIGNE (1993, 1996) also published useful bibliographies of the fauna of the islands.

Most of the land-snail species were discovered and named during the nineteenth century, in publications by RANG (1831), MORELET (1848, 1858, 1868), DOHRN (1866a, 1866b), GREEFF (1882), NOBRE (1886, 1891, 1894) and GIRARD (1893a, 1893b), with reviews by CROSSE (1868, 1888a, 1888b). In the early twentieth century, GERMAIN (1908, 1912a, 1912b, 1915, 1916) reported on additional large collections of specimens, but the proportion of new species he found was low, so one might gain the impression that faunal exploration had almost been completed. After this there was a long break in activity, until GASCOIGNE (1994a) became resident on São Tomé and reported new discoveries of a few species that had been introduced to the islands. The paper by GERMAIN (1916) was the last to give a comprehensive critical checklist of the land Mollusca of either of the islands. Hence there remains a need for a full checklist so we

give provisional full species lists for both islands in this paper, with a summary in Table I.

This paper describes the 13 new species discovered, along with other material representing new distributional records for either island. We found that very small snails (<3 mm) had often been overlooked by earlier workers, doubtless because they mainly occur at very low densities, sieving techniques were not used in the past, and the weak daylight reaching the ground inside the rainforests makes direct searching unproductive. However, some taxa with larger shells had also been overlooked, possibly because they resembled known species. More research is nevertheless needed in order to clarify and update the taxonomy of many of the endemic species, from molecular, anatomical and other characters, a process made more difficult by the poor level of taxonomic understanding of the faunas of neighbouring continental countries.

## MATERIAL AND METHODS

DTH and GAH visited both islands in December 2013 and made small collections of land Mollusca, and subsequently prepared a review of the endemic genus *Rhysotina* of São Tomé (HOLYOAK & HOLYOAK, 2016). RFL and MP made several longer visits to the islands over the next few years, partly to study *Archachatina*, during which small numbers of other molluscs were obtained. Unidentified taxa from the collections made in 2013 appeared to represent undescribed species, so DTH and GAH returned to both islands in November-December 2018 in order to collect more systematically. Their fieldwork on Príncipe was carried out with assistance from FS and his co-workers from the Fundação Príncipe who continued to collect molluscs in other areas during 2019. RFL and MP also continued to work on both islands in 2018 and 2019, resulting in more specimens found during studies focussed on *Archachatina*.

Table I. List to summarise systematic treatment, distribution and status of species of terrestrial Mollusca known from the islands of São Tomé and Príncipe. Key: X literature record confirmed herein, x literature record unconfirmed by present authors, \* newly recorded herein, ? occurrence doubtful, ! confirmed by present authors as still present from living or fresh material collected 2013-2019, <sup>a</sup> introduced, <sup>a2</sup> probably introduced, <sup>c</sup> probably single-island endemic, <sup>c2</sup> doubtful whether single island endemic, † endemic to São Tomé and Príncipe, <sup>m</sup> only on coastal beaches, SF Subfamily.

	São Tomé	Príncipe
CYCLOPHORIDAE J.E. Gray, 1847 or MAIZANIIDAE Tiecke, 1940		
<i>Afroditropis moller</i> (Nobre, 1886)	X <sup>e!</sup>	-
<i>Cyathopoma inexpectata</i> G. Holyoak & D. Holyoak n. sp.	-	X <sup>e!</sup> *
<i>Maizania furadana</i> G. Holyoak & D. Holyoak n. sp.	X <sup>e!</sup> *	-
<i>Thomeomaizania gascoignei</i> G. Holyoak & D. Holyoak n. sp.	X <sup>e!</sup> *	-
<i>Thomeomaizania vandellii</i> (Nobre, 1886)	X <sup>e!</sup>	-
TRUNCATELLIDAE J.E. Gray, 1840		
<i>Truncatella clathrus</i> R.T. Lowe, 1832	X <sup>m!</sup>	-
<i>Truncatella rostrata</i> Gould, 1847	-	X <sup>m</sup>
ASSIMINEIDAE H. Adams & A. Adams, 1856		
<i>Assiminea</i> sp.	X <sup>m</sup>	X <sup>m</sup>
ELLOBIIDAE L. Pfeiffer, 1854		
SF Melampodinae Stimpson, 1851 (1850)		
<i>Melampus flavus</i> (Gmelin, 1791)	X <sup>m</sup>	X <sup>m</sup>
<i>Melampus pusillus</i> (Gmelin, 1791)	X <sup>m</sup>	X <sup>m</sup>
<i>Melampus</i> sp.	X <sup>m!</sup> *	-
SF Pedipedinae P. Fischer & Crosse, 1880		
<i>Pedipes afer</i> (Gmelin, 1791)	X <sup>m</sup>	-
<i>Pedipes</i> sp.	-	X <sup>m</sup>
ONCHIDIIDAE Rafinesque, 1815		
<i>Onchidella</i> sp.	X <sup>m</sup>	-
VERONICELLIDAE J.E. Gray, 1840		
<i>Laevicaulis alte</i> (A. Férussac, 1822)	X <sup>a!</sup> *	X <sup>a!</sup> *
<i>Pseudoveronicella forcarti</i> D. Holyoak, G. Holyoak & F. Sinclair n. sp.	-	X <sup>e!</sup> *
<i>Pseudoveronicella liberiana</i> (Gould, 1850)	X!	X!
<i>Pseudoveronicella thomensis</i> (Girard, 1893)	X <sup>e!</sup>	-
ACHATINIDAE Swainson, 1840		
SF Achatininae		
<i>Archachatina bicarinata</i> (Bruguière, 1792)	X†!	X†!
<i>Archachatina marginata</i> (Swainson, 1821)	X <sup>a!</sup>	X <sup>a!</sup>
<i>Atopocochlis exaratus</i> (O.F. Müller, 1774)	X <sup>e!</sup>	-
<i>Columna columna</i> (O.F. Müller, 1774)	-	X <sup>e!</sup>
<i>Columna hainesi</i> L. Pfeiffer, 1856	-	X <sup>e</sup>
<i>Columna leai</i> Tryon, 1866	-	X <sup>e</sup>
<i>Lignus alabaster</i> (Rang, 1831)	-	X <sup>e!</sup>
<i>Limicolaria flammea</i> (O.F. Müller, 1774)	X <sup>a!</sup> *	-
SF Subulininae P. Fischer & Crosse, 1877		
<i>Ischnoglossula fuscicula</i> (Morelet, 1858)	x	x
<i>Striosubulina striatella</i> (Rang, 1831)	X!	X!

Tabla I. Lista para resumir el tratamiento sistemático, la distribución y el estado de las especies de moluscos terrestres conocidas de las islas de Santo Tomé y Príncipe. Clave: X registro bibliográfico confirmado en este trabajo, x registro bibliográfico no confirmado, \* registrado recientemente, ? presencia dudosa, ! confirmado como aún presente a partir de material vivo o fresco recolectado entre 2013 y 2019, <sup>a</sup> introducido, <sup>a2</sup> probablemente introducido, <sup>e</sup> probablemente endémica de una sola isla, <sup>e2</sup> dudoso si endémica de una sola isla, † endémica de Santo Tomé y Príncipe, <sup>m</sup> solo en playas costeras, SF subfamilia.

	São Tomé	Príncipe
<i>Subulina feai</i> Germain, 1912	-	X <sup>a</sup>
<i>Subulina moreleti</i> Girard, 1893	-	X <sup>e</sup> !
<i>Subulina newtoni</i> Girard, 1893	-	X <sup>e</sup> !
SF Cecilioidinae Mörch, 1864		
<i>Cecilioides</i> sp.	x?	-
SF Petriolinae Schileyko, 1999		
<i>Aporachis dohrni</i> (Greeff, 1882)	X <sup>e</sup> !	-
<i>Aporachis hispida</i> (Greeff, 1882)	X <sup>e</sup> !	-
<i>Bocageia lotophaga</i> (Morelet, 1848)	-	X <sup>a</sup>
<i>Nothapalus solitarius</i> G. Holyoak & D. Holyoak n. sp.	X <sup>e</sup> !*	-
<i>Petriola clavus</i> (L. Pfeiffer, 1864)	X <sup>e</sup> !	-
<i>Petriola marmorea</i> (Reeve, 1850)	X <sup>e</sup> !	-
<i>Petriola monticola</i> (Morelet, 1866)	X <sup>e</sup> !	-
SF Pyrginae Germain, 1916		
<i>Pyrgina umbilicata</i> Greeff, 1882	X <sup>e</sup> !	-
<i>Thomea newtoni</i> Girard, 1893	X <sup>e</sup> !	-
SF Opeatinae Thiele, 1931		
<i>Opeas dohrni</i> (Girard, 1893)	x	x
<i>Opeas greeffi</i> (Girard, 1893)	x	X!
<i>Opeas hannense</i> (Rang, 1831)	X!	-
<i>Opeas pauper</i> (Dohrn, 1866)	X!†	x†
<i>Opeas subpauper</i> Germain, 1912	-	X <sup>a</sup>
<i>Pseudopeas crosseii</i> (Girard, 1893)	X!*	X!
SF Thyrophorellinae Girard, 1895		
<i>Thyrophorella thomensis</i> Greeff, 1882	X <sup>e</sup> !	-
MICRACTAEONIDAE Schileyko, 1999		
<i>Micractaeon kaptawellensis</i> (Germain, 1934)	X!*	-
STREPTAXIDAE Gray, 1860		
SF Enneinae Bourguignat, 1883		
<i>Gulella azeitonae</i> D. Holyoak, G. Holyoak & F. Sinclair n. sp.	-	X <sup>e</sup> !*
<i>Gulella crystallum</i> (Morelet, 1848)	-	X <sup>e</sup> !
<i>Gulella joubini</i> (Germain, 1912)	-	X <sup>a</sup>
<i>Gulella sorghum</i> (Morelet, 1848)	-	X <sup>e</sup> !
<i>Streptostele abbreviata</i> D. Holyoak, G. Holyoak & F. Sinclair n. sp.	-	X <sup>e</sup> !*
<i>Streptostele fastigiata</i> (Morelet, 1848)	-	X <sup>e</sup> !
<i>Streptostele</i> (?) <i>feai</i> Germain, 1912	-	X <sup>a</sup>
<i>Streptostele folini</i> (Morelet, 1858)	-	X <sup>e</sup> !
<i>Streptostele</i> (?) <i>moreletiana</i> (Dohrn, 1866)	x†	x†
<i>Tomastele musaecola</i> (Morelet, 1860)	X <sup>a</sup> !*	-

Table I. Continuation.  
 Tabla I. Continuación.

	São Tomé	Príncipe
PUNCTIDAE Morse, 1864		
<i>Punctum camerunense</i> de Winter, 2017	X!*	-
CHAROPIDAE Hutton, 1884		
SF Charopinae		
<i>Trachycystis iredalei</i> Preston, 1912	X!*	-
SUCCINEIDAE Beck, 1837		
<i>Quickia concisa</i> (Morelet, 1848)	X!	X!
CERASTIDAE Wenz, 1923		
<i>Gittenedouardia burnayi</i> (Dohrn, 1866)	X!	X!
<i>Gittenedouardia eminula</i> (Morelet, 1848)	X!	X!
GASTROCOPTIDAE Pilsbry, 1918		
<i>Gastrocopta nobrei</i> (Girard, 1893)	X <sup>e</sup> !	-
TRUNCATELLINIDAE Steenberg, 1925		
<i>Truncatellina thomensis</i> D. Holyoak & G. Holyoak n. sp.	X <sup>e</sup> !*	-
VALLONIIDAE Morse, 1864 (15)		
<i>Pupisoma dioscoricola</i> (C.B. Adams, 1845)	X!*	-
<i>Pupisoma harpula</i> (Reinhardt, 1886)	X!*	-
AGRIOLIMACIDAE H.Wagner, 1935		
<i>Deroceras laeve</i> (O.F. Müller, 1774)	X <sup>a</sup> !*	-
EUCONULIDAE H.B. Baker, 1928		
<i>Afroconulus roseus</i> D. Holyoak & G. Holyoak n. sp.	X <sup>e</sup> !*	-
<i>Afropunctum seminium</i> (Morelet, 1873)	X!*	X!*
HELICARIONIDAE Bourguignat, 1877		
<i>Apothapsia moreleti</i> (Germain, 1915)	X <sup>e</sup> !	-
<i>Apothapsia thomensis</i> (Dohrn, 1866)	X <sup>e</sup> !	-
UROCYCLIDAE Simroth, 1889		
SF Urocyclinae		
<i>Dendrolimax greeffi</i> Simroth, 1889	X <sup>e</sup> !	-
<i>Dendrolimax heynemanni</i> Heynemann, 1868	-	X <sup>e</sup> !
SF Rhysotiniinae Schileyko, 2002		
<i>Rhysotina hepatizon</i> (Gould, 1845)	X <sup>e</sup> !	-
<i>Rhysotina sublaevis</i> G. Holyoak & D. Holyoak, 2016	X <sup>e</sup> !	-
<i>Rhysotina welwitschi</i> (Morelet, 1866)	X <sup>e</sup> !	-
SF Sheldoniinae Connolly, 1925		
<i>Africanar dumenticola</i> (Dohrn, 1866)	-	X <sup>e</sup> ?
<i>Principicochlea tenuitesta</i> D. Holyoak, G. Holyoak & F. Sinclair n. sp.	-	X <sup>e</sup> !*
<i>Principitrochoidea aglypta</i> (Dohrn, 1866)	-	X <sup>e</sup> !
<i>Principitrochoidea convexa</i> G. Holyoak, D. Holyoak & F. Sinclair n. sp.	-	X <sup>e</sup> !*
<i>Principitrochoidea folini</i> (Morelet, 1848)	-	X!
<i>Thomithapsia bomsuccisa</i> G. Holyoak & D. Holyoak n. sp.	X <sup>e</sup> !*	-
<i>Thomitrochoidea trindadensis</i> D. Holyoak & G. Holyoak n. sp.	X <sup>e</sup> !*	-
HELICIDAE Rafinesque, 1815		
SF Helicinae		
<i>Cornu aspersum</i> (O.F. Müller, 1774)	X <sup>a</sup> !*	-

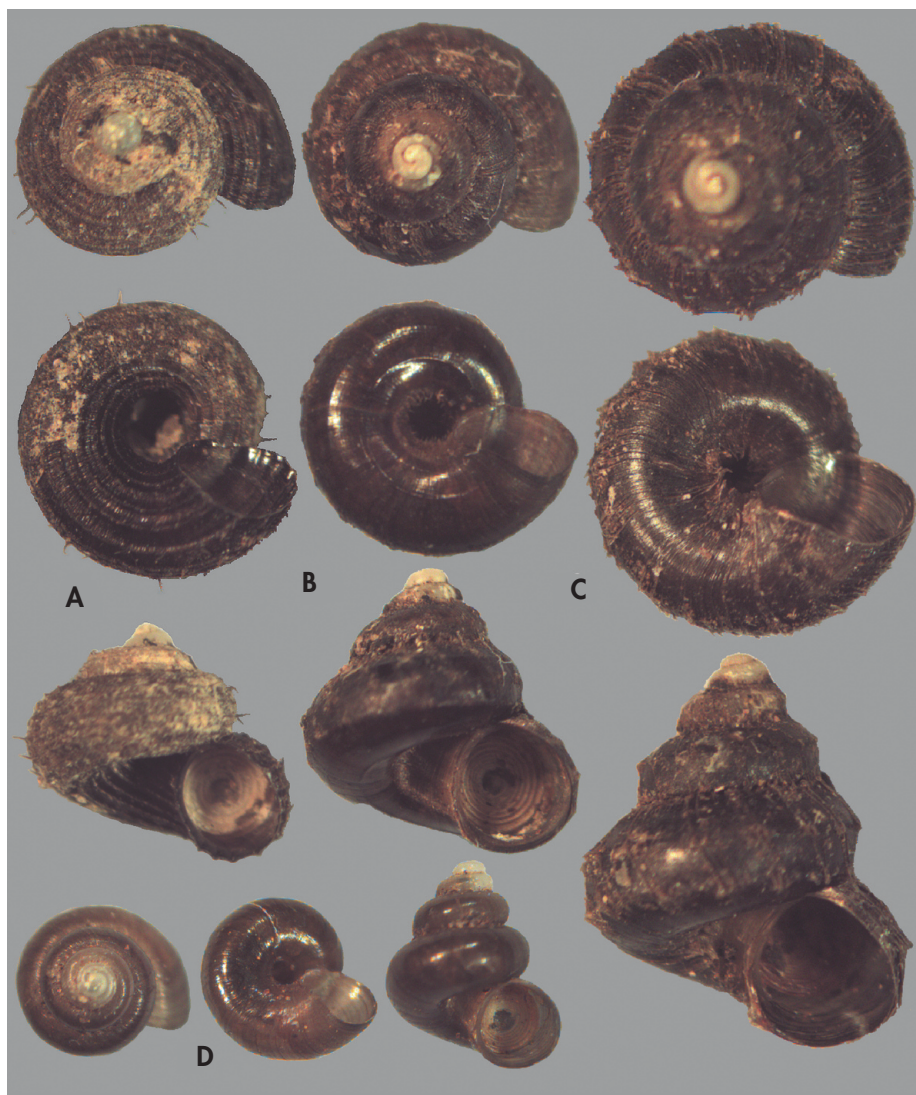


Figure 1. Shells of terrestrial Mollusca from São Tomé and Príncipe (1) Cyclophoridae and Maizaniidae. A: *Cyathopoma inexpectata* n. sp., holotype, Príncipe (B 2.82 mm); B: *Thomeomaizania gascoignei* n. sp., holotype, São Tomé (B 2.84 mm); C: *Thomeomaizania vandellii*, São Tomé, path from above Bom Sucesso Botanical Garden towards Lagoa Amélia, ca N0.2823° E6.5964°, montane forest, 1290-1415 m alt., 9 Dec. 2018, GAH & DTH 18-21, in CGAH (B 3.36 mm); D: *Maizania furadana* n. sp., holotype, São Tomé (B 1.77 mm). See text for details of other localities, etc.

Figura 1. Conchas de moluscos terrestres de Santo Tomé y Príncipe (1) Cyclophoridae y Maizaniidae. A: *Cyathopoma inexpectata* n. sp., holotipo, Príncipe (ancho 2,82 mm); B: *Thomeomaizania gascoignei* n. sp., holotipo, Santo Tomé (ancho 2,84 mm); C: *Thomeomaizania vandellii*, Santo Tomé, camino desde arriba del Jardín Botánico Bom Sucesso hacia Lagoa Amélia, aprox. N0,2823° E6,5964°, bosque montano, 1290-1415 m alt., 9 dic. 2018, GAH y DTH 18-21, en CGAH (ancho 3,36 mm); D: *Maizania furadana* n. sp., holotipo, Santo Tomé (ancho 1,77 mm). Véase el texto para detalles de otras localidades, etc.

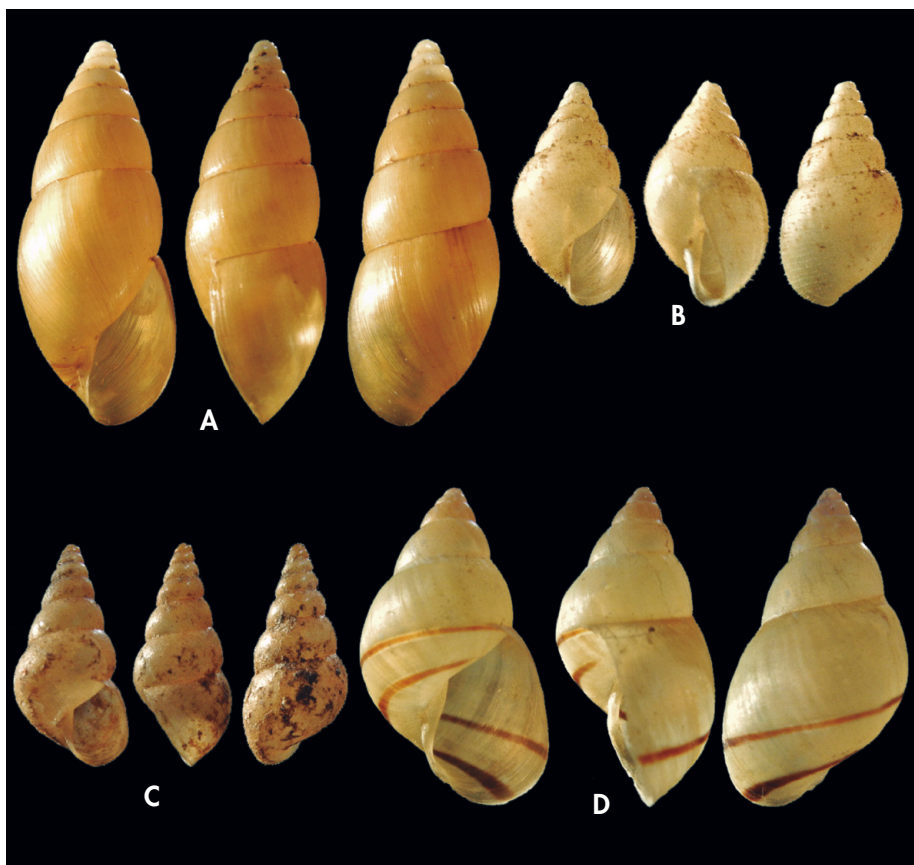


Figure 2. Shells of terrestrial Mollusca from São Tomé and Príncipe (2). A: *Aporachis dohrni*, São Tomé, near Lagoa Amélia, N0.2812° E6.5908°, low moist montane forest around infilled crater lake, 1416 m alt., 10 Dec. 2018, DTH, MP & FS 18-25 (H 20.42 mm); B: *Aporachis hispida*, São Tomé, Morro Claudina near Bom Sucesso, ca N 0.2912° E6.6057°, montane forest, ca 1289 m alt., 24 Nov. 2018, GAH, DTH, et al. 18-2 (H 12.03 mm, but part of first whorl missing); C: *Gittenedouardia eminula*, São Tomé, SW. of Trindade, N0.2766° E6.6598°, secondary-forest, abandoned cocoa plantations, etc., 398 m alt., 2 Dec. 2018, GAH & DTH 18-10 (H 11.70 mm); D: *Gittenedouardia burnayi*, Príncipe, just S. of Santo António on road to Bela Vista, N1.6307° E7.41790, edge of cultivation and secondary-forest, ca 24 m alt., 3 Dec. 2018, GAH, DTH & FS 18-11 (H 16.84 mm). All shells are in CGAH; all photos are from specimens dissected and drawn for Figure 6.

Figura 2. Conchas de moluscos terrestres de Santo Tomé y Príncipe (2). A: *Aporachis dohrni*, Santo Tomé, cerca de Lagoa Amélia, N0,2812° E6,5908°, bosque bajo húmedo montano alrededor del lago de cráter relleno, 1416 m alt., 10 dic. 2018, DTH, MP y FS 18-25 (H 20,42 mm); B: *Aporachis hispida*, Santo Tomé, Morro Claudina cerca de Bom Sucesso, aprox. N 0,2912° E6,6057°, bosque montano, aprox. 1289 m alt., 24 nov. 2018, GAH, DTH, et al. 18-2 (H 12,03 mm, pero falta parte de la primera vuelta); C: *Gittenedouardia eminula*, Santo Tomé, suroeste de Trindade, N0,2766° E6,6598°, bosque secundario, plantaciones de cacao abandonadas, etc., 398 m alt., 2 dic. 2018, GAH y DTH 18-10 (H 11,70 mm); D: *Gittenedouardia burnayi*, Príncipe, justo al S. de Santo António en el camino a Bela Vista, N1,6307° E7,41790, borde de cultivo y bosque secundario, aprox. 24 m alt., 3 dic. 2018, GAH, DTH y FS 18-11 (H 16,84 mm). Todos los ejemplares están en CGAH; todas las fotos son de especímenes diseccionados y dibujados para la figura 6.

Fieldwork sites were selected by DTH and GAH to represent a range of molluscan habitats, but with a preference for native forest in good condition. At each site we attempted to find and record a full list of all species of non-marine Mollusca present, including slugs, and to always collect samples of those that could not be reliably identified in the field. In wooded habitats the searching generally included foliage of herbs, ferns and saplings (extending up to five metres above the ground by bending thin saplings over), leaf-litter, trunks and exposed roots of trees, and beneath dead branches or any rocks lying on the ground. Locations were recorded with a hand-held GPS (Garmin eTrex high sensitivity) that was accurate to within 5 m horizontally and *ca* 10 m vertically on open ground. This GPS remained useable inside tall forest, but its accuracy was considerably reduced, especially in measuring altitude. Coordinates for localities have been converted to decimal degrees.

Paired sieves (meshes 2.0 and 0.5 mm) were regularly used in the field, although many of the sites sampled inside forests were so dark that the fine sieved fraction ("fines") was usually taken away in labelled plastic bags for drying and later searching. Very wet ground litter was also sometimes removed in bags for later drying and sieving. Since small snails were found to be generally scarce when present at all in the forest leaf-litter, sieving was soon focussed on the few places where accumulations of larger shells provided calcium and apparently increased the concentrations of small snails.

On São Tomé the anvil sites of the São Tomé Thrush *Turdus olivaceofuscus* provided these, where many tens of broken shells of *Rhysotina hepaticus* (Gould, 1845) were often accompanied by smaller numbers from *R. welwitschi* (Morelet, 1866), *Petriola* spp. and occasional immatures of *Archachatina bicarinata* (Bruguière, 1792). In forest on Príncipe, shells concentrated by Blue-breasted Kingfishers *Halcyon malimbica dryas* provided similar but less produc-

tive sieving opportunities, as did heaps of shells of *Archachatina marginata* collected for human food. The kingfisher "anvils" there included piles of old shells of *Columna columna* (O.F. Müller, 1774); "these are broken against rocks where hundreds of smashed shells may pile" (LEVENTIS & OLMOS, 2009: 86).

Living molluscs were drowned in water overnight then stored in industrial methylated spirit (IMS) or 80% ethanol, with bodies of the larger taxa being pulled wholly or partly from the shells. Most empty/dead shells collected into specimen tubes were also placed in IMS or 80% ethanol, then cleaned and dried later, although some of the largest were dried during the fieldwork. Samples of "fine fractions" dried during fieldwork were mostly searched later using a low-power stereomicroscope with large field of view and good lighting.

Descriptions of shells were made using Meiji RZ Series stereo-microscopes with fibre-optic light sources. Measurements were made with an eyepiece micrometer, drawings with assistance from a Meiji drawing tube, microphotography using Infinity (Lumenera Corporation) equipment. Shell whorls were counted following the method shown by KERNEY & CAMERON (1979: 13). Dissections were made under IMS using the same equipment, with genitalia drawn after they were removed from bodies. Proximal and distal refer to positions relative to the gonad.

### Abbreviations

alt.: altitude above sea level; AB: aperture breadth; AH: aperture height; B: shell breadth; bod: bodies in IMS; CGAH: Collection of G.A. and D.T. Holyoak; DTH: D.T. Holyoak; FS: F. Sinclair & co-workers from Fundação Príncipe; GAH: G.A. Holyoak; H: shell height; IMS: Industrial Methylated Spirit (80%); leg.: collected by; MNHNP Muséum National d'Histoire Naturelle, Paris; MP: M. Panisi; NHMUK: The Natural History Museum, London,

U.K.; n.v.: original not verified; RFL: R.F. de Lima; sh: shells; SMF: Senckenberg Museum, Frankfurt, Germany; spm: specimens in IMS; syn.: synonym; TL: type locality; UB: umbilicus breadth.

#### Additional abbreviations used for anatomy and external parts of body in the figures

aa: atrial appendage; ag: albumen gland; am: muscle attached to genital atrium; at: annular thickening on penis (in *Pseudoveronicella*); bc: bursa copulatrix; bcd: duct of bursa copulatrix; ch: caudal horn; chd: common hermaphrodite duct; cm: columellar muscle; cs: cylindrical sac (beside chd in *Streptostele*); dep: distal part of epiphallus; dg: digestive gland; em: embryo developing in oviduct; ep: epiphallus; epc: caecum on epiphallus; f: caudal fossa; fl: flagellum on penis; fo: free oviduct; ga: genital atrium; go: gonad; gp: external genital pore; gr: deep groove beneath head (*Helicarionoidea*); lc:

lateral caecum inside os; lt: lower tentacle; lu: lung; L1, L2, etc.: mantle laps (*Helicarionoidea*); m: mouth; ma: dorsal surface of mantle inside shell; ms: muscle attaching bc to pr; os: thin outer sheath of penis; osp: outer sheath of penis complex (in *Pseudoveronicella*); p: penis; pc: penial caecum; pcg: pericaudal groove; pep: proximal part of epiphallus; pi: pilaster; pg: penial gland; pr: prostatic part of sod; prm: penis retractor muscle; ps: penis sheath; rmaa: retractor muscle on atrial appendage; ro: right ommatophore; saa: thin sheath of atrial appendage; sod: spermoviduct; st: stimulator arising in atrial appendage; th: thickening on vas deferens; ut: upper tentacle; v: verge; va: vagina; vd: vas deferens; vi: villose organ, on sod.

All specimens collected by DTH and GAH in 2013 and 2018 except holotypes are currently in CGAH, as are all paratypes. Albeit not mandatory, ZooBank registrations were made for all the taxa described in this paper.

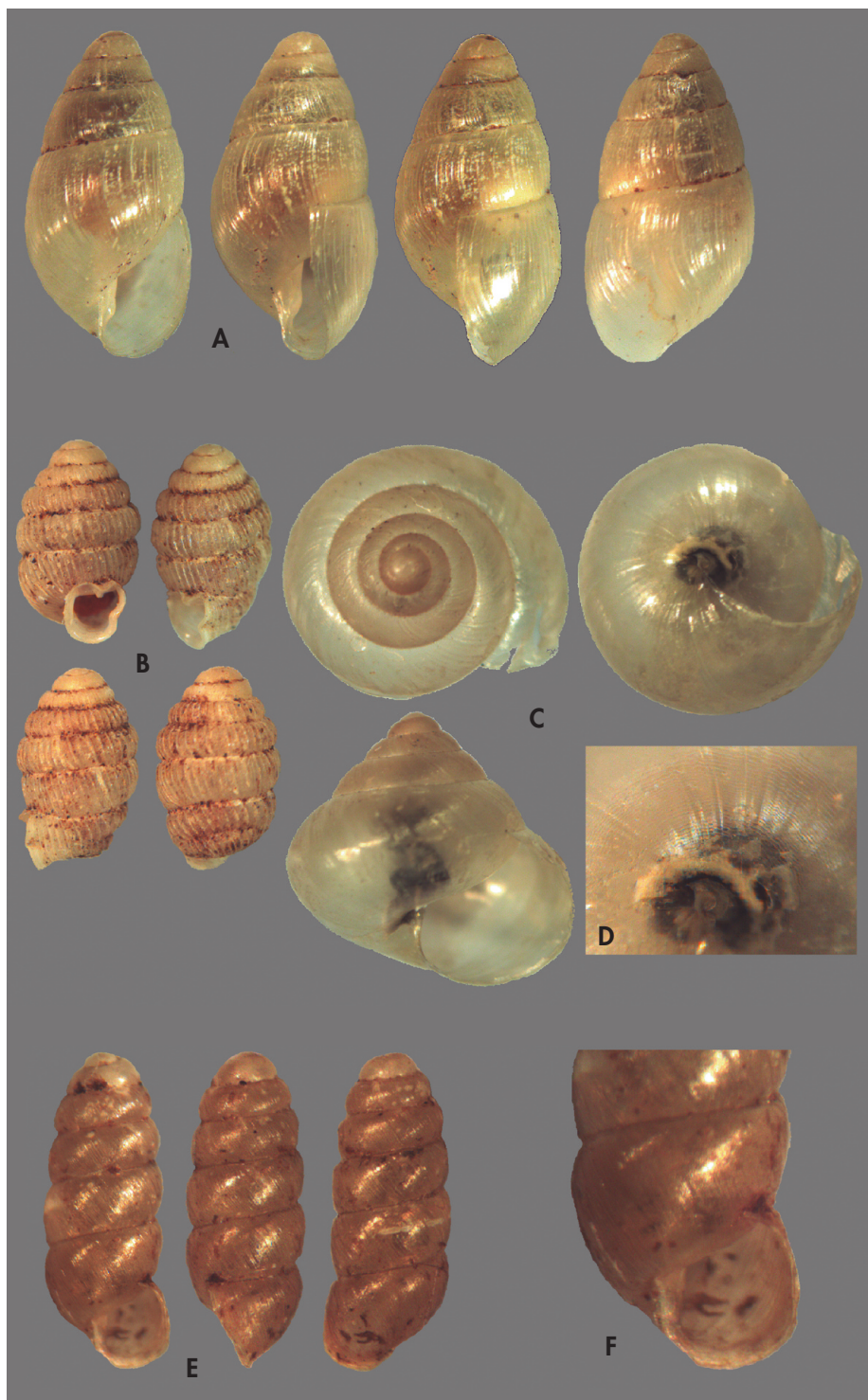
## TAXONOMIC PART & RESULTS

The supra-generic classification used here mainly follows BOUCHET *ET AL.* (2017). The text gives citations of original descriptions and detailed synonyms mainly for the endemic species and other names with their type locality on the islands. Other information provided is the first record for each island, reference to useful figures, and whether col-

lected by us 2013-2019 (species collected are marked ! if not otherwise evident). Additional information is sometimes noted for species rarely recorded. A brief note describes the global distribution of species that are not endemic. Nomenclatural details of genera are given mainly for those which are endemic.

(Right page) Figure 3. Shells of terrestrial Mollusca from São Tomé and Príncipe, (3). A: *Nothapalus solitarius* n. sp., holotype, São Tomé (H 4.69 mm); B: *Gulella azeitona* n. sp., holotype, Príncipe (H 2.90 mm); C: *Afroconulus roseus* n. sp., holotype, São Tomé (B 4.44 mm); D: ditto, showing umbilical area of base of shell at larger scale; E: *Truncatellina thomensis* n. sp., holotype, São Tomé (H 2.26 mm); F: ditto, showing shell aperture at large scale. See text for details of all localities, etc.

(Página derecha) Figura 3. Conchas de moluscos terrestres de Santo Tomé y Príncipe, (3). A: *Nothapalus solitarius* n. sp., holotipo, Santo Tomé (alto 4,69 mm); B: *Gulella azeitona* n. sp., holotipo, Príncipe (alto 2,90 mm); C: *Afroconulus roseus* n. sp., holotipo, Santo Tomé (ancho 4,44 mm); D: el mismo, mostrando el área umbilical de la base de la concha, ampliada; E: *Truncatellina thomensis* n. sp., holotipo, Santo Tomé (alto 2,26 mm); F: el mismo, mostrando la apertura de la concha ampliada. Véase el texto para detalles de otras localidades, etc.



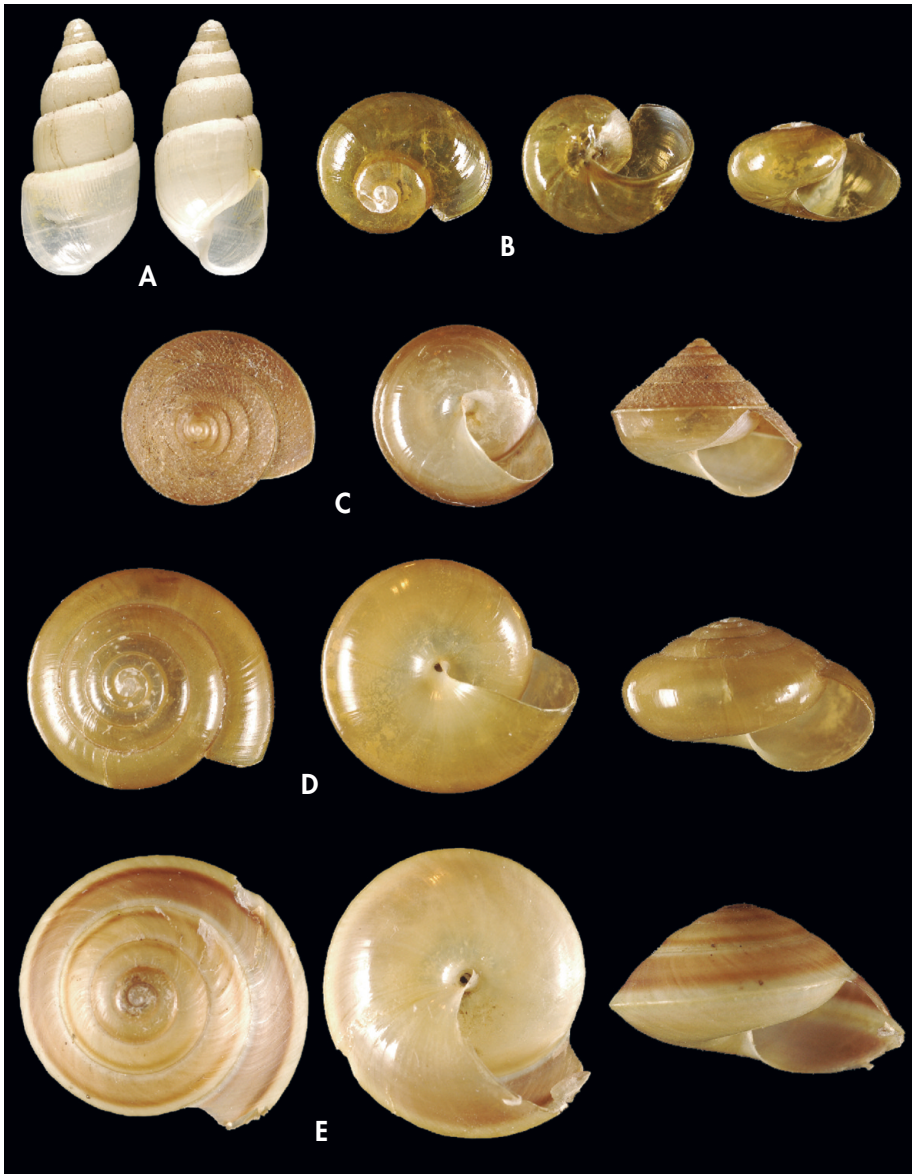


Figure 4. Shells of terrestrial Mollusca from São Tomé and Príncipe (4). A: *Streptostele abbreviata* n. sp., holotype, Príncipe (H 12.29 mm); B: *Principicochlea tenuitesta* n. sp., holotype, Príncipe (B 8.38 mm); C: *Principitrochoidea convexa* n. sp., holotype, Príncipe (B 9.51 mm); D: *Thomithapsia bomsucessica* n. sp., holotype, São Tomé (B 12.33 mm); E: *Thomitrochoidea trinidadensis* n. sp., holotype, São Tomé (B 14.4 mm). See text for details of all localities, etc.

Figura 4. Conchas de moluscos terrestres de Santo Tomé y Príncipe (4). A: *Streptostele abbreviata* n. sp., holotipo, Príncipe (alto 12,29 mm); B: *Principicochlea tenuitesta* n. sp., holotipo, Príncipe (ancho 8,38 mm); C: *Principitrochoidea convexa* n. sp., holotipo, Príncipe (ancho 9,51 mm); D: *Thomithapsia bomsucessica* n. sp., holotipo, Santo Tomé (ancho 12,33 mm); E: *Thomitrochoidea trinidadensis* n. sp., holotipo, Santo Tomé (ancho 14,4 mm). Véase el texto para detalles de otras localidades, etc.

CYCLOPHORIDAE J.E. Gray, 1847 or MAIZANIIDAE Tielecke, 1940

Two endemic species from São Tomé named and described in *Cyclophorus* by NOBRE (1866) were placed in separate genera as *Afroditropis mollerii* and *Maizania* (*Thomeomaizania*) *vandellii* by BEQUAERT & CLENCH (1936). TIELECKE (1940) used anatomical characters of other species to recognise two separate families, the Cyclophoridae and Maizaniidae. VAN BRUGGEN (1986) followed Tielecke's recognition of two families and treated *Thomeomaizania* as a full genus within the Maizaniidae, despite the absence of anatomical information for either of the two species hitherto reported from São Tomé. He also provided detailed new descriptions and figures of both species which were known from São Tomé.

VAN BRUGGEN (1986: 359) attempted to define characters of the shell and operculum to discriminate Maizaniidae from Cyclophoridae at family level, but it appears that he was only partly successful in doing so. He noted (following BOSS, 1982: 979) "that the operculum of the Maizaniidae is always thin, corneous and simple", while that of Cyclophoridae is "corneous or calcareous, generally multispiral, and occasionally with external processes". However, the two species already known from São Tomé and two new species named below all have a similar operculum: it is concave externally, with a small smooth central circle (nucleus) surrounded by a lamellar ridge which spirals tightly for up to 11 full turns. The edge of the operculum has a rounded concave groove in its outer half, a flat edge on its inner part. The whole structure usually appears corneous and typically whitish or buff or pale brown in colour; in *Thomeomaizania vandellii* it is whitish externally in some populations but

brown in other samples of the same species, possibly reflecting varying extents of calcification. Thus it matches the Cyclophoridae type rather than the Maizaniidae type, despite VAN BRUGGEN (1986: 359-363) having placed this genus in Maizaniidae. However, the genus *Thomeomaizania* Bequaert & Clench, 1936 appears to have been defined by VAN BRUGGEN (1986: 364) on the basis of a single shell that has lost most of its periostracal sculpture (see below), so its affinities are likely to have been misinterpreted. Shell characters of the four species now known from São Tomé seem to span much of the diversity known hitherto in both families, with respectively, predominantly spiral sculpture of three strong ridges, predominantly axial sculpture plus either two strong or at least five weak spiral keels, or a smooth surface without obvious spiral or axial structures.

As a provisional arrangement in the absence of both molecular and anatomical data, we therefore name the two new species from São Tomé and a third from Príncipe in the existing genera to which their shells show the strongest resemblance. The similarity in the opercula may imply that at least the four species from São Tomé represent a single endemic radiation of forms; if so, they should probably all be placed in *Thomeomaizania*. Nevertheless, we avoid changing their nomenclature here because a reliable classification into families and genera cannot be provided. It may be possible in future from molecular and anatomical studies that should include comparisons with taxa from the African mainland. A key to identify shells of the five species now known from the islands is presented at the end of this section.

*Afroditropis* Bequaert & Clench, 1936

*Afroditropis mollerii* (Nobre, 1886)

*Cyclophorus mollerii* Nobre, 1886, Bol. Soc. Geographia Lisboa, (6) 4, p. 15; TL ilha de S. Thomé.

Shell figures in NOBRE (1894: pl. 5 “fig. 6”; the figures are useless because too small; the text gives fig. 6 for both

this species and *C. Vandellii*). Shell redescribed by VAN BRUGGEN (1986). Endemic on São Tomé!

*Cyathopoma* W. & H. Blanford, 1861

*Cyathopoma inexpectata* n. sp. G. Holyoak & D. Holyoak (Fig. 1A)

**Type material:** Named and described only from the unique holotype shell, NHMUK 20200230, collected 4 Dec. 2018 by GAH at site 18-12.

**Type locality:** Príncipe Island, path to Santa Joaquina, N1.6157° E7.3976°, 216 m alt., tall native forest with understorey of saplings, found on leaf-litter at base of steep flushed bank.

**Etiymology:** The species epithet *inexpectata* (Latin, meaning unexpected) refers to our surprise at finding a distinct undescribed cyclophorid at an easily accessible locality on an island where land snails were well studied historically, and further surprise on later realising that it may represent a different genus to the Cyclophoridae known from São Tomé.

**Description:** Based on holotype shell which is apparently mature and in fresh condition: H 2.57 mm, B 2.82 mm, H/B 0.91; AH 1.25 mm, AB 1.09 mm, AH/AB 1.14; UB 0.72 mm (UB/B 25.5%); whorls 3.6. Shell depressed-conical, with rapidly expanding whorls descending regularly. Whorl profile rounded, with deep suture. Aperture nearly round (slightly higher than broad). Peristome thin, not reflected, curving smoothly in ventral view; continuous where it meets penultimate whorl and narrowly fused with latter externally; in oblique view, a shallow recess apparent around umbilicus. Umbilicus comparatively large and open, symmetrical, exposing interior of whorls of spire. Protoconch raised, of *ca* 1.5 whorls, with microsculpture of minute low rounded papillae. Teleoconch of much of upper part of spire partly concealed (encrusted), but with six spiral cords projecting, the three cords on outer part of penultimate whorl bearing well-spaced perpendicular hairs resembling those on body-whorl. Upper and outer surfaces of body-whorl with *ca* nine spiral cords,  $\pm$  evenly spaced, with raised crests, reaching peristome edge, the four outermost bearing rather evenly-spaced but sparse hairs (hairs 0.11–0.18 mm long, brownish, mainly straight, very narrowly conical and tapering to tip, mostly perpendicular to shell surface, but those near shell aperture recurved from base);

finer axial sculpture of closely-spaced riblets is continuous across the cords and the wider spaces between them, these riblets having much weaker spiral lines just visible at  $\times 56$  magnification. Underside of body-whorl with five spiral cords, plus four more in umbilicus, all  $\pm$  evenly spaced, extending outwards to edge of peristome, the external cords with lamella-like crests and the two outermost with a few hairs as on upper part of body-whorl; whole basal surface also with finer axial sculpture, resembling that on adapical surface of whorl. Protoconch whitish; teleoconch blackish-brown, glossy; interior of aperture dark brown with external cords showing as pale lines, the thin shell slightly translucent. Operculum closing interior of body-whorl 0.2 whorl back from aperture (perhaps attached to dried body internally), with two-layered structure similar to that noted in family account above revealed by damage along one edge; externally whitish, concave, darker smooth central ‘nucleus’ forming  $\frac{1}{3}$  of diameter; raised lamella spiralling outwards from nucleus with six closely appressed near-circular coils visible, but true number probably greater because surface apparently damaged or eroded.

The exterior of the body, genital anatomy, radula, etc., remain unknown.

**Discussion:** The identity of this single small caenogastropod specimen as a dis-

tinctive taxon new for Príncipe was apparent in the field. However, close searching around the immediate area where it was found failed to reveal any more individuals and two large bags of leaf-litter taken away, dried and then sieved were also unproductive.

VAN BRUGGEN (1986: 360, 374-377) regarded presence on the body-whorl of strong spiral keels, reticulate sculpture and a hirsute periostracum as characters of the genus *Chondrocyclus*, but recent research implies that genus is restricted to South Africa (COLE, RAHEEM & VILLET, 2018; COLE, 2019). The recent work also confirms that the operculum

of the South African species is a “spirally coiled fringe of strong, flattened, usually fused bristles; bristles project around the edge, forming a tight seal ...” (HERBERT & KILBURN, 2004: 90), different to that described above from the Príncipe specimen. A species from Cameroon with strong spiral keels on the body whorl and a raised spiral lamella on the exterior of the operculum was placed in *Cyathopoma* by DE WINTER (2002), along with several other species from tropical Africa. Until molecular or anatomical comparisons are available, it therefore seems best to also place the Príncipe species in *Cyathopoma*.

### *Maizania* Bourguignat, 1889

#### *Maizania furadana* n. sp. G. Holyoak & D. Holyoak (Fig. 1D)

**Type material:** Holotype, shell (H 2.59, B 1.77 mm) in NHMUK 20200231, collected 26 Nov. 2018 by GAH & DTH at site 18-5.

**Type locality:** São Tomé Island, near Ponta Furada, N0.23665° E6.46775°, 240 m alt., on flushed, steep rock of trackside cutting, part-shaded by secondary forest.

**Paratypes:** 30 shells from the type locality, mainly with opercula, mostly found alive, with *Thomeomaizania vandellii* (Nobre, 1886).

**Etymology:** The species epithet *furadana* is an adjective constructed from the name of Ponta Furada, a coastal headland near the type-locality.

**Description:** Apparently mature shells: H 1.83-2.59 mm, B 1.44-1.95 mm, H/B 1.15-1.46; AH 0.72-1.01 mm, AB 0.72-0.99 mm, AH/AB 0.96-1.02; UB 0.23-0.51 mm (UB/B 15.7-26.2%); whorls 3.5-4.3. Shell conical with whorls rapidly expanding and descending; whorls evenly rounded in profile, separated by very deep suture; body-whorl descending gradually to aperture. Umbilicus narrow, interior of top of spire just visible, in largest shells becoming eccentric at body whorl. Umbilicus with 0-3 distinct low narrow ridges formed of periostracum, with rough tops, well-separated from each other, all emerging to almost reach the outer edge of the peristome. Aperture almost circular (varying from slightly higher than wide to slightly wider than high, sometimes a slight blunt point at top, near where exterior touches penultimate whorl; peristome thin, not reflected, in oblique basal

view with shallow recess adjacent to umbilicus. Protoconch minutely rough with low rounded papillae; teleoconch appearing almost smooth at low magnification but with weak, close, rather irregular axial growth lines; at high magnification ( $\times 56$ ) faint close spiral lines are just visible. Protoconch of 1.3-1.5 whorls whitish, teleoconch externally  $\pm$  dark brown, sometimes nearly blackish, glossy; interior of aperture on mature shells whitish and almost opaque, although shell rather thin. Operculum closing interior of body-whorl *ca* 0.1-0.3 of whorl back from aperture, attached internally to dried body; general structure as described above under family heading; concave externally, whitish to light yellow-brown; smooth ‘nucleus’ forming central  $\frac{1}{4}$ - $\frac{1}{3}$  of width, remainder with narrow raised lamella or ridge spiralling outwards in *ca* 11 tightly appressed near-circular coils.

External coloration of the body of living animals was mainly pale grey. Their tentacles were long, slender and blackish, remaining visible through the translucent shell. Eye spot at base of and external to each tentacle was black. The operculum carried on top of the tail appeared whitish. Moist shells containing bodies of the living snails appeared dark olive-brown to blackish. Characters of the genital anatomy remain undescribed. Dried bodies are present in numerous paratype shells, so study of the radula should be possible in future.

**Discussion:** The new species is known only from its type-locality. The living snails were resting or moving on moist dead leaves and stems in places with dripping water on the volcanic rock of the old cutting.

This species is provisionally placed in the genus *Maizania* on the basis of

the shell lacking distinct sculpture. Following VAN BRUGGEN (1986: 360-362), its small size (<4 mm) would also imply it belongs in subgenus *Micromaizania* Verdcourt, 1964. Again, following VAN BRUGGEN (1986: 359), the present species would be assigned to Maizaniidae rather than Cyclophoridae on the basis of the absence of “major spiral sculpture in the form of keels, ridges or cords”. Nevertheless, the operculum is not thin, corneous and simple which he regarded as characteristic for that family. Evidence from elsewhere also shows that lack of spiral shell sculpture is not always a reliable character pointing to Maizaniidae, since HERBERT & KILBURN (2004: 92) characterised *Chondrocyclus exsertus* (Melvill & Ponsonby, 1903) of the Cyclophoridae from KwaZulu-Natal as having a smooth shell but a duplex operculum.

### *Thomeomaizania* Bequaert & Clench, 1936

#### *Thomeomaizania gascoignei* n. sp. G. Holyoak & D. Holyoak (Fig. 1B)

**Type material:** Holotype, shell (H 3.25, B 2.84 mm) in NHMUK 20200232, collected 4 Dec. 2013 by GAH & DTH at site ST4.

**Type locality:** São Tomé Island, path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2786° E6.6000°, ca 1300 m alt., in montane forest on slope with understorey of saplings, 23 sh (mainly live-collected, along with 36 sh of *T. vandellii*).

**Paratypes:** 22 sh from type-locality collected with holotype on 4 Dec. 2013, GAH & DTH at site ST4. Also: 7 Dec. 2013, path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2825° E6.5969°, ca 1400 m alt., montane forest on ridge, with closed canopy & understorey of saplings, GAH & DTH ST8, 1 sh (live-collected, along with 11 sh of *T. vandellii*); 9 Dec. 2018, ditto, ca N0.2823° E6.5964°, 1290-1415 m alt., montane forest, GAH & DTH 18-21, 19 sh (live-collected, along with 55 sh of *T. vandellii*); 10 Dec. 2018, near Lagoa Amélia, N0.2812° E6.5908°, 1416 m alt., low moist montane forest around infilled crater-lake, DTH, MP & FS 18-25, 3 sh (live-collected, along with 4 sh of *T. vandellii*).

**Etymology:** The species epithet honours the late Angus Gascoigne, a former resident on São Tomé whose publications helped to revive interest in the land Mollusca of the islands after the decades of inactivity throughout the mid-twentieth century.

**Description:** Apparently mature shells: H 2.65-3.31 mm, B 2.18-2.84 mm, H/B 1.14-1.34; AH 1.05-1.32 mm, AB 1.09-1.32, AH/AB 0.96-1.00; UB 0.43-0.62 mm (UB/B 19.2-23.0%); whorls 3.5-4.6. Shell conical, whorls increasing and descending rapidly, sutures deep. Whorl profile externally with several weak spiral keels: three at and above

periphery of body-whorl, two more beneath periphery, all separated by flatter bands of shell and ending just before the peristome edge. Aperture almost round, with peristome thin to very thin, plane, not reflected, sometimes (in subadults?) interrupted at point of contact with penultimate whorl, in oblique view from below

showing shallow recess adjoining umbilicus. Umbilicus narrow, internally just exposing whorls of spire, becoming somewhat eccentric at body-whorl in larger shells. Exterior of lowest part of body-whorl in umbilicus with up to five more weak spiral keels, each forming a thin ridge of periostracum extending outwards to end close to edge of peristome lip, the crest of each ridge with tiny elongate pointed scale (up to 0.07 mm long) arising where ridge meets axial sculpture. Protoconch (up to whorl 1.5) with closely spaced low weak axial ridges and minute low rounded papillae. Teleoconch whorls 2-3 with  $\pm$  regular fine axial ribs; an immature shell has minute (0.06 mm) hair-like projections on the periostracum in a row where the ribs approach the suture. Lower whorls of spire and body-whorl with microsculpture of minute closely spaced axial riblets crossed by closely-spaced minute ( $\times 56$ ) spiral lines; this sculpture interrupted at intervals by prominent axial bands formed of 3-5 much stronger axial ribs grouped together, each of them bearing erect scales where it intersects a spiral keel (although scales fragile and soon lost). Basal surface of body-whorl lacking strong axial ribs, but with closely spaced pattern of minute axial riblets and even finer spiral lines (just visible at  $\times 56$ ). Protoconch white, teleoconch brown to blackish-brown, glossy on areas of adapical surface lacking strong ribs and on most of basal surface. Interior of aperture brown, the shell rather thin and somewhat translucent. Operculum inside aperture 0.2-0.3 whorl in from peristome, attached internally to tail of dead body. See family heading for general characters of opercula, which externally whitish to yellow-brown, concave, with flat central 'nucleus' forming less than  $\frac{1}{4}$  of total diameter, surrounded by a sharp lamella spiralling outwards in 10-11 closely appressed near-circular coils.

No information was recorded on characters of the exterior of the body

or on genital anatomy because the specimens were intermixed with those of *T. vandellii* and not recognised as distinct until after fieldwork was completed.

*Discussion:* Our shell samples clearly demonstrate that two superficially similar species occur together in montane forest on São Tomé which both resemble *Thomeomaizania vandellii*. Differences in the whorl profile and sculpture on the upper surface of the shells (see Key below) allow immature individuals to be assigned to separate species, so it is apparent that they do not represent different stages of maturity of a single species. The possibility of the difference between them being due to sexual dimorphism of shells can also be discounted since *T. gascoignei* appears to be restricted to montane forest where it lives intermixed with *T. vandellii*, while large samples of shells demonstrate that only the latter species occurs in the lowlands (see below). However, we found initially that there was scope for serious doubts about which of the two species should now be identified as *T. vandellii*, but believe these have subsequently been resolved as discussed below. Hence, the second species is named here as *Thomeomaizania gascoignei* n. sp. and the Key below sets out the characters used to separate it from *T. vandellii*.

VAN BRUGGEN (1986: 364-366, figs. 4-6) selected a lectotype for *Cyclophorus vandellii* Nobre, 1886 as BM [now NHMUK] 98.1.22.11, "Presd. by Mr. Aug. Nobre", and redescribed and figured this specimen. CROSSE (1888a: 27-28, pl. 1 figs. 2, 2a) also described and figured "*Cyclophorus Vandellii*, Nobre" independently of the original valid description by NOBRE (1886: 14-15). Besides the specimen sent to the BM and another to Crosse, Nobre is likely to have retained others in Portugal, but his collection went to the Lisbon Museum (DANCE, 1986: 220) where it was apparently lost in the fire which destroyed the Zoology Collection in March 1978.

Comparison of van Bruggen's detailed re-description and good figures of the lectotype with the descriptions by Nobre and Crosse (and the good figures in CROSSE, 1888a) suggested at first sight that the lectotype might represent a different species: it has much weaker vertical ribbing, less prominent spiral keels, and no sign of projections ("tubercles") arising from the spiral keels (the last difference being noted by VAN BRUGGEN (1986: 366) himself), and these features appear more similar to the characters of *T. gascoignei*. The description by Nobre suggested more prominent ribs and keels than did van Bruggen's new description ("coberta de uma epiderma lamelosa e sobreposta em camadas espaçadas verticais; and [for body whorl profile] "ultima fortemente subquadrangular"); Crosse's description likewise emphasised strong keels and prominent sculpture ("dernier tour muni de 3 rangées de tubercules sailants, dont la plus rapprochée de la base est la plus faible, et qui le font paraître comme bicaréné") and his figures showed these characters well (cf. our Fig. 1B and C).

Nonetheless, VAN BRUGGEN (1986) referred to periostracum wrinkles ... "being crowded and forming a fringe around the umbilicus" (p. 365, repeated on p. 366) and these appear to be indicated in his figs. 4 and 6. This "fringe" is a decisive character, formed of a comb-like or lamella-like band curving around the edge of the widest part of the umbilicus on the underside of the body whorl, formed of elongate closely spaced periostracal projections (see our Fig. 1C, middle photo). *T. gascoignei* lacks this, having instead two to five

much lower spiral ridges deeper within the umbilicus (Fig. 1B middle and lower photos). Hence it appears that the lectotype does indeed represent *C. vandellii*, but with a specimen having most of the periostracal sculpture worn, corroded or rubbed off the body whorl and spire. We can match this shell with a proportion of our recently collected specimens.

As noted above, *T. vandellii* was found living with *T. gascoignei* at all four sites where the latter was recorded, at 1300-1416 m altitude in montane forest. However, *T. vandellii* has a much wider range on São Tomé, extending from 1416 m alt. beside Lagoa Amélia to the southern end of the island at low altitudes (e.g. 11 Dec. 2013, by EN2 ca 2 km S. of Monte Mário "praia", N0.0694° E6.5522, ca 101 m alt., roadside bank at foot of slope with secondary forest, GAH & DTH ST11, 15 sh).

*Maizania* (*Thomeomaizania*) was named by Bequaert & Clench, 1936, Rev. Zool. Bot. Afr., 29, p. 99, with type species by original designation and monotypy *Cyclophorus vandellii* Nobre, 1866. VAN BRUGGEN (1986: 364) treated *Thomeomaizania* as a full genus within the Maizaniidae, which he evidently characterised on the basis of the worn lectotype shell discussed above, showing: "small size and turbate shape (l/d about 1.00), the presence of weak costulae and an intensely wrinkled, deciduous periostracum, which shows two faint keels." This seriously misrepresented the strong ribbing and two prominent spiral keels of an unworn shell of the type species, which, following the discussion and key by VAN BRUGGEN (1986: 359-360), would instead lead to its identification as a genus in the Cyclophoridae.

### *Thomeomaizania vandellii* (Nobre, 1886) (Fig. 1C)

*Cyclophorus Vandellii* Nobre, 1886, Bol. Soc. Geographia Lisboa, (6) 4, p. 14; TL ilha de S. Thomé.

Other shell figures: CROSSE (1888: pl. 1 figs. 2, 2a), NOBRE (1894: pl. 5 "fig. 6"; the figures useless because too small and the text gives fig. 6 for both this

species and *C. Molleri*), VAN BRUGGEN (1986: 364-366, figs. 4-6 of lectotype, but a worn shell as discussed above). Endemic on São Tomé!

# Key to species of Cyclophoridae and Maizaniidae of São Tomé and Príncipe

The following key to Cyclophoridae and Maizaniidae is to be used with unworn adult shells, if necessary after carefully cleaning away adhering soil.

1. - Shell wider than high (Fig. 1A); umbilicus *ca* 25% of shell breadth; periostracum with longer hair-like projections (>0.1 mm long); Príncipe Island only . . . . . *Cyathopoma inexpectata* n. sp.  
 - Shell usually higher than wide; umbilicus <25% of shell breadth; periostracum lacking hair-like projections, or with these restricted to minute hairs (<0.1 mm long) on immature shells; São Tomé Island only . . . . . 2
2. - Upper surface of shell with sharp axial ribs bearing scales (that may form rough papillae at crests of the spiral keels) (Fig. 1 B, C) . . . . . 3  
 - Upper surface of shell without sharp axial ribs bearing scales,  $\pm$  smooth (Fig. 1D) . . 4
3. - Body-whorl rounded with 5 weak spiral ridges (3 at and above periphery, 2 below it) (Fig. 1B); 2-5 ridges prominent within umbilicus (behind columellar side of aperture); comb-like lamella lacking from entrance to umbilicus; most shells not heavily encrusted with soil . . . . . *Thomeomaizania gascoignei* n. sp.  
 - Body-whorl sub-quadrangular (with 2 strong spiral keels above periphery); underside of shell and interior of umbilicus lacking spiral ridges (Fig. 1C); ridges lacking within umbilicus but entrance to umbilicus fringed externally by curved comb-like lamella formed of narrow scales; shells often encrusted with soil . . . . . *Thomeomaizania vandellii*
4. - Shell with three spiral cords on upper surface . . . . . *Afroditropis molleri*  
 - Shell lacking spiral cords on upper surface (Fig. 1D) . . . *Maizania furadana* n. sp.

## TRUNCATELLIDAE J.E. Gray, 1840

### *Truncatella* Risso, 1826

#### *Truncatella clathrus* R.T. Lowe, 1832

São Tomé, on seashores (TOMLIN & SHACKLEFORD, 1914: 253; FERNANDES & ROLÁN, 1993: 34; CGAH). Species also reported e.g. from south-eastern U.S.A.

#### *Truncatella rostrata* Gould, 1847

A species from Atlantic coasts of Africa, with original description by Gould giving Rio de Janeiro erroneously as type locality (CLENCH & TURNER, 1948). On seashore of Príncipe: syn. *Truncatella princeps* Dohrn, 1866, TL Prinzenseln (DOHRN, 1866b: 134); GERMAIN (1912b: 394, with shell description, from Bahia do Este); FERNANDES & ROLÁN (1993: 34).

## ASSIMINEIDAE H. Adams & A. Adams, 1856

### *Assiminea* J. Fleming, 1828

#### *Assiminea* sp.

Seashores; species listed as a new record from both São Tomé and Príncipe by FERNANDES & ROLÁN (1993: 34).

ELLOBIIDAE L. Pfeiffer, 1854

Subfamily MELAMPODINAE Stimson, 1851 (1850)

*Melampus* Montfort, 1810

Taxonomic revision of specimens is desirable to clarify species limits in taxa of this genus from the Atlantic coast of Africa

and which names should be applied. Reports from São Tomé and Príncipe have been made under the following names.

*Melampus flavus* (Gmelin, 1791)

Seashores: reported from São Tomé (TOMLIN & SHACKLEFORD, 1914: 240, common; FERNANDES & ROLÁN, 1993: 41) and

Príncipe (DOHRN, 1866b: 133; GERMAIN, 1912b: 387; TOMLIN & SHACKLEFORD, 1914: 240; FERNANDES & ROLÁN, 1993: 41).

*Melampus pusillus* (Gmelin, 1791)

Seashores: reported from São Tomé (TOMLIN & SHACKLEFORD, 1914: 240, fairly common; FERNANDES & ROLÁN,

1993: 41) and Príncipe (DOHRN, 1866b: 133; NOBRE, 1894: 92; GERMAIN, 1912b: 388; FERNANDES & ROLÁN, 1993: 41).

*Melampus* sp.

NOBRE (1894: 92) reported *Melampus liberianus* H. Adams & A. Adams, 1854 from São Tomé with doubt. Specimens collected in 2018 from São Tomé were also identified as *M. liberianus* (CGAH);

other specimens coexisting with them collected at same locality in 2018 on São Tomé (CGAH) have been identified tentatively as *Melampus* cf. *lividus* (Deshayes, 1830) (CGAH).

Subfamily PEDIPEDINAE P. Fischer & Crosse, 1880

*Pedipes* A. Férussac, 1821

*Pedipes afer* (Gmelin, 1791)

São Tomé, on seashore (TOMLIN & SHACKLEFORD, 1914: 240, fairly common;

FERNANDES & ROLÁN, 1993: 41, including new record or records).

*Pedipes* sp.

Specimens collected in 2018 from the seashore on São Tomé have been tentatively identified as *P. dohrnii*

D'Ailly, 1896 (CGAH). *Pedipes* sp. was reported from Príncipe by DOHRN (1866b: 133).

ONCHIDIIDAE Rafinesque, 1815

*Onchidella* J.E. Gray, 1850

*Onchidella* sp.

Reported from seashore of São Tomé

by FERNANDES & ROLÁN (1993: 41).

## VERONICELLIDAE J.E. Gray, 1840

The review of African Veronicellidae by FORCART (1953) recorded only *Pseudoveronicella liberiana* (Gould, 1850) for São Tomé and Príncipe. Our study recognises four species of the family from the islands, adding a species which is newly described here, a poorly-known taxon rescued from synonymy and an alien that may be a relatively recent arrival. A key to identify these is given below. We mainly follow the terminology of FORCART (1953: 16-18) for the external morphology and the genital organs of this family (with upper side of body termed notum, underside comprising sole of the foot with hyponotum forming band on each side of it, separated from foot by a pedal groove). The methodology he suggested (p. 19) for dissection was also adopted, consisting of opening the skin by cutting along the left-hand pedal groove, before turning

back the skin over the full length of the body. The distal male genitalia were located along the right-hand side of the buccal mass and just proximal to it, with the oesophagus often passing through the digitiform branches of the penial gland. The distal male genitalia were removed for study, the penial sheath then being opened longitudinally from the base upwards to expose the verge. Additional anatomical terminology translated from GOMES (2007: 4) is adopted for the parts of the vas deferens: anterior vas deferens (“ducto deferente anterior”) being the section extending from near the external male genital pore to the proximal end of the penis, middle vas deferens (“deferente medio”) the part passing concealed within the body wall from near the external male pore proximally to near the posterior end of the body.

*Laevicaulis* Simroth, 1919

*Laevicaulis alte* (A. Férussac, 1822)

*Vaginulus alte* A. Férussac, 1822, Tableaux systématiques des animaux mollusques ..., part 2, section 1 [Limaces], livraison 16, p. 14. TL “environs de Pondichéry” [= Puducherry, India].

New to Príncipe: 3 Dec. 2018, just S. of Santo António on road to Bela Vista, N1.6307° E7.4179°, ca 24 m alt., edges of secondary forest, trackside banks, cultivation, GAH, DTH & FS 18-11, 1 spm.

New to São Tomé: 28 Apr. 2008, Chácara, city of São Tomé, photo by RFL, 1, not kept; 27 Aug. 2016, Monte Café, photo by RFL, 1, not kept; 24 Nov. 2018, by Bom Sucesso Botanical Garden, N0.28829° E6.61193°, 1159 m alt., trackside with herbs near hedges, scrub, wall & cultivation, GAH & DTH *et al.* 18-1, 1 spm; 27 Nov. 2018, on path above Bom Sucesso Botanical Garden, N0.28° E6.61°, 1159 m alt., on muddy path through herbs and scrub near cultivation, GAH & DTH 18-6F, 1 spm; 10 Dec. 2018, in Bom Sucesso Botanic Garden, N0.2886° E6.6121°, 1156 m alt., botanical garden with groves of trees, lawns & cultivated patches, GAH & DTH 18-22, 1 spm.

Identification of the four specimens was confirmed by dissection with all of them having mature male genitalia, despite large differences in body size (length of notum in preserved material 37.5-73 mm). They all showed the very long penial verge tapering to an almost terete point figured by FORCART (1953: pl. 4 fig. 7a) and GOMES (2007: 89 fig. 14), along with other characters set out in the key below. Our material differs from many illustrations of *L. alte* in having the pale (buff) mid-dorsal line on the notum less conspicuous, but close examination reveals that a narrow and sometimes discontinuous line can be seen along at least part of the posterior half of all four specimens.

The species may be a recent arrival on São Tomé and possibly also on Príncipe, the first evidence of its presence being from a photo taken in 2008. Although the

type of the species was from India, FORCART (1953: 68) noted that the main development of the genus *Laevicaulis* is in eastern and central Africa, so he concluded that *L. alte* was primarily an African species and that its wider distribution (Madagascar, Mascarene Is., India, Sri Lanka, China, Taiwan, Indonesia, New Caledonia, Loyalty Is., Australia)

may have been caused by spread with cultivated plants. Since the 1950s it has been recorded in many other parts of the tropics and subtropics, including Malaysia, Philippines, New Guinea, Fiji, Vanuatu, W. Samoa, Hawaii and Bermuda, being regarded as a pest of cultivated plants in some countries (GOMES & THOMÉ, 2004; COWIE ET AL., 2009).

### *Pseudoveronicella* Germain, 1908

*Pseudoveronicella* Germain, 1908, Bull. Mus. Nat. Hist. Nat., Paris, 14, p. 59; type species *Veronicella Gravieri* Germain, 1908 (= *V. thomensis* Girard, 1893, see below), by monotypy.

### *Pseudoveronicella forcarti* n. sp. D. Holyoak, G. Holyoak & F. Sinclair (Figs. 5C, D, 12D)

**Type material:** Holotype, NHMUK 20200233, spm in IMS (notum length 34 mm) with male genitalia separated, collected 3 July 2019, by FS, A. Pedronho & A. Andrade at type locality (site 2019-07-03-01).

**Paratypes:** Two spm in IMS collected with the holotype at the type-locality.

**Type locality:** Príncipe Island, saddle beneath Pico Mesa, N1.58151° E7.35421°, 414 m alt., mid-elevation native forest on exposed ridge.

**Etymology:** The species epithet honours Lothar H. E. W. Forcart (1902-1990), a zoologist and malacologist from Switzerland, who provided a detailed illustrated monograph of African Veronicellidae (FORCART, 1953) that was fundamental to our work on the family.

**Description:** Slugs lacking a shell; specimens preserved in IMS with notum 30.5-34 mm long, maximum width 10.5-11 mm; body strongly dorso-ventrally flattened throughout, tapering to narrow translucent lateral margins; outline elliptical/narrowly oval, with notum rounded at anterior and posterior ends; upper tentacles projecting a few millimetres beyond anterior end of notum. Preserved specimens have notum light grey, with scattered small and rather indistinct darker spots, the holotype alone having more obvious irregular whitish blotches along midline in posterior one-third of body; surface of notum with even pattern of low rounded tubercles visible at low magnification ( $\times 7$ ). Hyponotum pale grey without markings; sole of foot whitish; head pale grey dorsally, whitish at front; upper tentacles grey or grey with white tips and a small black eye-spot centrally near tip. Anus a rather large crescentic opening close to posterior end of right hyponotum, not or slightly concealed beneath end of foot. Female pore in lower

half of right hyponotum, slightly anterior of middle of (preserved) body length (at 16.5 mm from front of 34 mm holotype, 14 mm from front of 30.5 mm paratype), inconspicuous, or with distinct whiter rim.

Several additional living slugs collected in Nov. 2019 near the type-locality and photographed soon afterwards (e.g. Fig. 12D) confirm that the body is flattened dorso-ventrally, relatively wide and tapering to thin lateral margins. It is conspicuously translucent with dark gut contents along interior of mid-line of body easily visible from above or below. Dorsally the notum was dull pale to light greenish-yellow in colour, marked with pale cream blotches concentrated around the dorsal mid-line and more extensive tiny pale spots on the tip of each low rounded tubercle; tentacles grey, with eye-spot black; sole of foot and hyponotum whitish. The greenish-yellow dorsal coloration is evidently lost following preservation in IMS.

External pore of male genitalia below and to right of right upper tentacle. Geni-

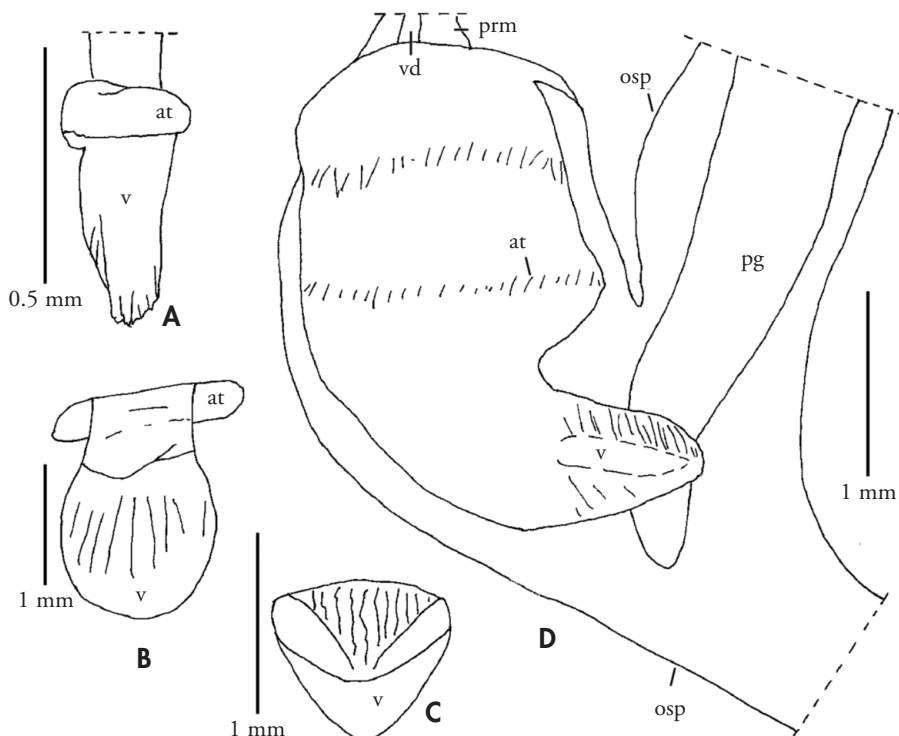


Figure 5. Penial anatomy of *Pseudoveronicella*. A: *P. liberiana* (São Tomé, by EN2 just NE of Monte Mário “roça”, N0.0606° E6.5561°, ca 236 m alt., forest on slopes by road, 13 Dec. 2013, GAH & DTH ST13); B: *P. thomensis* (São Tomé, path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2786° E6.6000°, ca 1300 m alt., in montane forest, 4 Dec. 2013, GAH & DTH ST4); C, D: *P. forcarti* n. sp. (Príncipe, holotype). A and B show convex dorsal surface of verge; C shows apex of verge viewed from beyond its tip, dorsal surface uppermost; D shows view from side, dorsal surface uppermost.

Figura 5. Anatomía penial de *Pseudoveronicella*. A: *P. liberiana* (Santo Tomé, por EN2 justo al NE de la “roça” Monte Mário, N0.0606° E6.5561°, aprox. 236 m alt., bosque en laderas junto a carretera, 13 dic. 2013, GAH y DTH ST13); B: *P. thomensis* (Santo Tomé, camino a Lagoa Amélia desde el Jardín Botánico Bom Sucesso, N0.2786° E6.6000°, aprox. 1300 m alt., en bosque montano, 4 dic. 2013, GAH & DTH ST4); C-D: *P. forcarti* n. sp. (Príncipe, holotipo). A y B muestran la superficie dorsal convexa de la verga; C muestra la punta de la verga vista desde más allá de su punta, la superficie dorsal arriba; D muestra una vista lateral, la superficie dorsal arriba.

talia studied in holotype (Fig. 5C, D) and larger of the two paratypes. Thin-walled penial outer sheath encloses most of penis and distal part of the large penial gland, dividing proximally into separate sheaths enveloping each of these organs, the part covering penial-gland becoming a thick muscular wall proximally. Penis (inside sheath) a short muscular cylinder

(less than twice as long as wide), with distinct single annular thickening towards distal end, before narrowing into short, blunt, curved verge almost as long as wider part of penis. Apical portion of verge with two broad blunt apical wings converging towards tip, enclosing a shallow central depression with longitudinal ridges, the opposite side deeply

convex. Proximal end of penis with strong retractor muscle attached to outside of penial sheath and passing proximally along body. Distal part of penial gland a long-conical papilla (pointed and probably perforated “stimulator”, longer and narrower than verge); middle part longer, muscular, expanding proximally to give clavate structure; large proximal part attached by narrow neck, comprised of group of *ca* 16 tubular glands, when *in situ*, running  $\pm$  parallel to each other, loosely conjoined laterally and somewhat convoluted or curved. Retractor muscle of penial gland arising on proximal end of external sheath of its clavate structure, running proximally to join (larger) penial retractor muscle. Anterior vas deferens starting concealed in body wall close to genital pore, initially thin, then widening to a narrow, long tube, convoluted *in situ*, passing proximally alongside exterior of penis sheath, ending in centre of proximal end of penis adjacent to attachment of retractor muscle [middle vas deferens not seen; it can be assumed to pass proximally to posterior end of body concealed within the body wall as in other Veronicellidae: GOMES, 2007: 4].

*Comments:* *P. forcarti* resembles *P. thomensis* externally in its size and greenish notum, but differs from it markedly in structure of the penial verge (see couplet 3 of Key below; Fig. 5). FORCART (1953: 54-55, pl. 4 fig. 2) recorded that *P. (Congoveronicella) schoutedeni* Forcart, 1953 has the notum light greenish with indistinct spots, but the verge of that

species is peculiar with a wide “spatha” near its tip. All other congeners from the African mainland also differ from *P. forcarti* in penis structure.

The review by FORCART (1953) recognised four subgenera within *Pseudoveronicella*, the name of one (*Hoffmannia* Forcart, 1953 non *Hoffmannia* Heinemann & Wocke, 1877, Lepidoptera) later being replaced by *Afroveronicella* (FORCART, 1954). Differentiation of those subgenera was based mainly on the form of the penial verge: *Vaginina* Simroth, 1897 having a fine elongated distal part, the monotypic *Congoveronicella* Forcart, 1953 having a wide distal spathe, *Afroveronicella* Forcart, 1954 having the verge “glandiform” (enlarged relative to base of penis), whereas *Pseudoveronicella sensu stricto* has it “utricular” (narrow relative to base, with *P. liberiana* (Gould, 1850) placed here). On such criteria, all three species known from São Tomé and Príncipe would be placed in *Pseudoveronicella sensu stricto*, although both “green” taxa approach subgenus *Afroveronicella* in having wider verges than *P. liberiana*.

The three specimens of *P. forcarti* from July 2019 were collected from “tops of saplings (probably all of the same species), at about shoulder height” in native forest on an exposed ridge. Although more observations are needed, the greenish-yellow coloration of the living slugs and their presence above ground on foliage may imply a partly arboreal micro-habitat, as also tentatively suggested below for *P. thomensis*.

### *Pseudoveronicella liberiana* (Gould, 1850) (Figs. 5A, 12C)

*Vaginulus liberianus* Gould, 1850, Proc. Boston Soc. Nat. Hist., 3, p. 193, TL Liberia.  
Syn. *Veronicella myrmecophila* Heynemann (HEYNEMANN, 1868: 37, pl. 1 fig. 2), TL Príncipe.

Other figures of whole animal: HEYNEMANN (1868: pl. 1 fig. 2), FORCART (1953: pl. 1 figs. 1a-d), other figures of genital anatomy: FORCART (1953: pl. 3 figs. 2a-f, description p. 28).

First record on Príncipe by HEYNEMANN (1868, see above), still present in 2018 (CGAH!); first record on São Tomé

much later, in GASCOIGNE (1994a: 2), also recorded e.g. 2013 and 2018 (CGAH), as discussed further below in account of *P. thomensis*. Range elsewhere: Bioko (GASCOIGNE, 1994a: 2); W. and C. Africa from Liberia to Uganda and southwards to N. Angola (FORCART, 1953: 34 Map 1 and pp. 34-36).

*Pseudoveronicella thomensis* (Girard, 1893) (Figs. 5B, 12A, B)

*Veronicella thomensis* Girard, 1893, *Jornal Sci. Math., Phys. Nat.*, (2) 3 (10), p. 113; TL Binda, St. Thomé [= Bindá, São Tomé].

Syn. *Veronicella Gravieri* Germain, 1908, *Bull. Mus. Nat. Hist. Nat.*, Paris, 14, p. 55; TL São Thomé Island, San Nicolas [probably = São Nicolau].

GIRARD (1893b: 113) gave a short description of a single veronicellid slug specimen from São Tomé that was in poor condition and not dissected, but he noted the coloration as “uniforme jaune verdâtre” (uniformly greenish-yellow), which in combination with the locality suffices to distinguish it from *Pseudoveronicella liberiana* and other congeners and validates the name *Veronicella thomensis*. GERMAIN (1908: 55) named the same species as *V. gravieri* and gave a very detailed account of the single specimen available to him which was collected by Ch. Gravier in 1906. Germain described (p. 55) the coloration of this taxon as “d’un vert pomme clair” (i.e. light apple-green; italicised by Germain), apparently based on a much older account by BRANDT (which could not be traced). The monograph by FORCART (1953: 26-36, pl. 3) discounted the name *V. thomensis* Girard, “1895” (*sic*) as “so insufficient that the species can not be surely recognised” and treated *V. gravieri* as one of the numerous synonyms of *P. liberiana*, which was mapped by him as having a wide range in tropical Africa extending from [the former French] Guinea and Liberia eastwards to Uganda and southwards to N. Angola.

Dissection of our only fully adult *P. thomensis* revealed that the apical part of its penial verge was bluntly spatulate (Fig. 5B), whereas several immature and near-adult *P. liberiana* from São Tomé had a narrower, bluntly pointed end to the verge (Fig. 5A). There are several other reasons for regarding *P. thomensis* as a distinct species from *P. liberiana*, in addition to the former being distinctive in its light green coloration dorsally (Fig. 12A, B), whereas the island populations of the latter are light or dull brown dorsally, commonly with dark grey or

black blotches and fine dots of blackish-grey (Fig. 12C). The first record on São Tomé for *P. liberiana* was not until the report by GASCOIGNE (1994a: 2), despite it being known on Príncipe since HEYNEMANN (1868: 37, pl. 1 fig. 2) named it from that island as *Veronicella myrmecophila*. This late date perhaps indicates that *P. liberiana* is a recent anthropogenic introduction to São Tomé.

Records during 2013-2018 show that *P. liberiana* is now widespread on São Tomé and that it apparently has a different altitudinal range to that of *P. thomensis* and they possibly also differ in habitat preferences. Our finds of *P. liberiana* extend from lowlands near the southern end of the island (68 m alt.) to those of the north-western coastal regions (just S. of Santo António, at ca 24 m, sample 18-14), and upwards to near Monte Café (24 Nov. 2018, near Quinta da Graça, N0.29921° E6.64174°, 678 m alt., scrub, cultivated gardens, roadside banks, few trees, GAH & DTH 18-3, 3 spm). It has been found in secondary forest, but not inside closed forest or in montane forest.

In contrast, *P. thomensis* has been recorded from ca 500 m up to 1380 m. The lowest records were of slugs photographed by RFL in June 2019 (ca 500 m alt.: near stream in secondary forest, above Mirante, São João, Santa Catarina [Lembá district], N0.24364° E6.50242°; ca 530 m alt.: in shade of cocoa plantation, between Java and Abade [Mé Zóchi district], N0.25820° E6.65029°). Otherwise it was recorded only from higher ground, with four records at 700-1093 m alt. in secondary forest and numerous finds at up to 1380 m alt. inside montane forest. Its few records from more open habitats were from inside Bom Sucesso Botanic Garden (at 1156 m) and on a shaded trackside nearby.

Whereas *P. liberiana* was commonly but not exclusively found on the ground, most of the numerous records of *P. thomensis* were of immature slugs up to 2 m above the ground on leaves of saplings or shrubs, although our only fully adult specimen was from the ground inside

montane forest and the slug photographed at ca 530 m was on a dead log. The taxa thus appear to differ in altitudinal ranges (with some overlap between 500 and 678 m alt.), in the habitats occupied, and possibly also in the extent to which they climb up onto vegetation.

### Key to species of Veronicellidae of São Tomé and Príncipe

Within the islands, identification of species from coloration and locality (island) appears to be reliable, but

anatomical characters useful to confirm determinations are also given here.

1. - Notum almost uniformly dull grey to blackish-grey, lacking conspicuously darker blotches or fine spots, with narrow and sometimes indistinct buff line along mid-line of posterior half; anus close to mid-line of underside of body, generally concealed by back of foot, rounded with marginal flaps; female opening behind centre of right hyponotum; verge long (> half of penis length), tapering to almost terete point . . . . . *Laevicaulis alte*  
 - Notum (a) yellowish or green (bright, light, or dull) or (b) light to deep brown with darker blotches and small blackish spots; anus offset from mid-line of underside of body in right hyponotum, more posterior, so not concealed by back of foot, widely lunate; female opening in front of centre of right hyponotum; verge shorter (> half of penis length), towards the point flattened, spatulate or angled, but not terete . . . . . 2 (*Pseudoveronicella* spp.)
2. - Notum light to deep brown with darker blotches, and evenly dotted with small blackish spots which may form papillae; body rather opaque (Fig. 12C); verge short, with narrow canaliculate point (Fig. 5A) . . . . . *P. liberiana*  
 - Notum green or greenish-yellow, lacking conspicuous dark markings, sometimes with small whitish spots or cream blotches; margins of body translucent; verge flattened and spatulate or short, thick and angular . . . . . 3
3. - Verge longer; tip of verge wide, spatulate (Fig. 5B); known only on São Tomé . . . . .  
 . . . . . *P. thomensis*  
 - Verge shorter; tip of verge thick and blunt, with two broad blunt angular wings on either side of central depression (Fig. 5C, D); known only from Príncipe . . . . .  
 . . . . . *P. forcarti* n. sp.

### ACHATINIDAE Swainson, 1840

#### Subfamily Achatininae

#### *Archachatina* Albers, 1850

#### *Archachatina bicarinata* (Bruguière, 1792)

*Bulinus bicarinatus* Bruguière, 1792, Enycl. méth., hist. nat. vers, (1789-1792), 1, p. 359, no. 102.

Older but unavailable names exist from Lister (Conch., pl. 37, fig. 36), Tournefort (Voy., vol. II, p. 446; from "Le Levant", error) and as *Bulla Achatina sinistrorsa maxima* Chemnitz, 1786 (9 (1), p. 28, pl. 103, figs. 875, 876, work not binominal).

Syn. *Achatina sinistrorsa* L. Pfeiffer (1848, Mon. helic. viv., 2, p. 239 no. 2, 248 no. 13), was derived from Chemnitz.

RANG (1831, Ann. Sc. Nat., 24, pp. 23-27) reported it from his own observations on Príncipe as *H[elix] bicarinata*: “l’île du Prince ... commune sur les montagnes” and also commented “On m’a assuré qu’elle vit à la côte correspondante du continent d’Afrique, dans le voisinage du Gabon, ce qui me semble de toute probabilité.” MORELET (1858: 20) noted that on Príncipe: “n’est point rare à l’île du Prince; toutefois, on ne la rencontre guère que dans le voisinage du piton granitique qui domine la baie de Santo-Antonio”. Several early authors subsequently recorded it also from São Tomé and the neighbouring Ilha de Rolas. Good figures of shells were given e.g. by PILSBRY (1904: 107-109, pl. 19, fig. 27; 1905: pl. 46, fig. 4) and GERMAIN (1916: pl. 7 figs. 10-11, pl. 9 fig. 13). SCHILEYKO (1999: 483 fig. 619) figured the genital anatomy based on an illustration by Deshayes (in A. Férussac, 1819, Hist. nat. gen. part. moll. terr. & fluv., vol. 2, pp. 1-96); we have confirmed the general accuracy of this from a modern specimen (CGAH).

MORELET (1858: 20) long ago commented that it is very unusual to find

such a large snail as a supposed native on an oceanic island, and this remains true today. Since RANG (1831) rather tentatively accepted reports of it from the African mainland (see above) there might be some doubt about its native status on both islands, although there are no subsequent confirmed records from the “mainland”. GASCOIGNE (1994a: 5, 1994b: 798) suggested that the presence of this species on both São Tomé and Príncipe is likely to have resulted from anthropogenic introduction to one island or the other, resulting from its importance as a food source. DALLIMER & MELO (2010: fig. 2), recorded it on Príncipe only in primary forest in southern part of island and provided evidence that it was declining. Intensive surveys by FUNDAÇÃO PRÍNCIPE (2019: 15-17) have documented further decline there and investigated its causes, among which collection of the snails for human food is probably important. PANISI (2017 and in preparation) has made a detailed study of its distribution and status on São Tomé, likewise documenting a large decline. Thus its threat status globally should be increased at least to Endangered.

### *Archachatina marginata* (Swainson, 1821)

*Achatina marginata* vary Swainson, 1821, Exotic conchology ..., 1 (1,2), plate with no number; TL stated as “coast of Guinea” by Swainson.

New to Príncipe: 9 Dec. 2013, just NW. of Cidade de Santo António, N1.6444° E7.4203°, 42 m alt., from base of bank above road, with secondary-forest and cultivation, GAH & DTH ST9, 2 sh (from *ca* 15 seen).

The species is native in continental West Africa where it is widespread (e.g. PILSBRY, 1904: 109, 1905: pl. 24 figs. 22, 23, pl. 25 fig. 26; SCHILEYKO, 1999: 484; COSSIGNANI, 2014: 156-158). It was not found on São Tomé or Príncipe by collectors in the nineteenth- or early twentieth-centuries. GASCOIGNE (1994a: 3-4) cited anecdotal evidence that it had been introduced to São Tomé within the preceding 30-40 years and gave a map

of its range, which was then restricted to the lower elevations in the north and centre of that island. In 2013 we also found it in the extreme south of the island. A detailed study of its colonisation has been carried out since then by PANISI (2017).

Our record from Príncipe in 2013 confirmed that it had also been introduced and become established there. In 2018 it was clearly widespread on the island and well known to local people. Accumulations of scores of shells of snails collected for food by local people were seen by us in native forest (e.g. 4 Dec. 2018, along path to Santa Joaquina, N1.61313° E7.39683°, at 240 m alt.).

*Atopocochlis* Crosse & Fischer, 1888

*Atopocochlis exaratus* (O.F. Müller, 1774)

*Buccinum exaratum* O.F. Müller, 1774, Verm. terr. et fluv., 2, p. 148, no. 337; TL not stated.  
Syn. *Bulimus crystallinus* Greeff (1882: 520), based on immature shells of this species according to GIRARD (1893a: 38); *Pseudachatina vitrea* Greeff, 1884, Sitz. d. Ges. Naturw. zu Marburg, p. 51, nota (see GIRARD 1893a: 38-39 for identification).

Endemic on São Tomé! The origin of old specimens was uncertain until it was confirmed by MORELET (1868: 59).

Shell figures: CROSSE (1868: pl. 6 fig. 2), PILSBRY (1904: pl. 9 figs. 1, 2), PARKINSON *et al.* (1987: pl. 21 fig. 11), SCHILEYKO (1999: 491); figures of genital anatomy:

SCHILEYKO (1999: 491). COSSIGNANI (2014: 194-195) figured shells as *Atopocochlis* [*sic*] *lexarata* variously as “São Tomé, Guinée Equatoriale” and “São Tomé e Príncipe”, both of which apparently involve errors in the localities.

*Columna* Perry, 1811

Conchology, pl. 51. Type species *Buccinum columna* O.F. Müller, 1774 by absolute tautonymy according to SCHILEYKO (1999: 475); PETIT (2003: 20-21) designated *Columna marmorea* Perry, 1811, considering this name to be a junior synonym of *Buccinum columna* O.F. Müller, 1774.

*Columna columna* (O.F. Müller, 1774)

*Buccinum columna* O.F. Müller, 1774, Verm. terr. fluv., 2, p. 151, no. 341; TL not given, based on Lister (Conch., pl. 38, fig. 37 & pl. 39, fig. 37b).

Syn. *Limax flammeus* Martyn, 1789, Universal conchologist, 3, p. 122, pl. 41, fig. 1, n.v. (Reprinted in Ed. Chenu, Bibl. Conch., 2, p. 28; publication details are confirmed in DALL, 1906: 421; adopted as a valid name by DOHRN, 1866b: 124, apparently in preference to *B. columna* Müller, of which it is a junior subjective synonym); *Helix pyrum* Gmelin, 1790, Syst. Nat., ed. 13, p. 3665, no. 204; *Helix Listeri* Bolten, 1798, Museum Boltenianum, p. 108, no. 1393; *Columna grisea* Perry, 1811, Conchology, pl. 51, fig. 6, *Columna* no. 1 on plate explanation (PETIT, 2003: 38 noted that this = *Columna columna* (Müller, 1774) *fide* DESHAYES, 1838: 305, as *Achatina columellaris* Lamarck, the figure probably being copied from CHEMNITZ, 1786, pl. 112, fig. 955); *Columna marmorea* Perry, 1811, Conchology, pl. 51, fig. 7, *Columna* no. 2 on plate explanation (PETIT, 2003: 40 noted that this = *Columna columna* (Müller, 1774) *fide* DESHAYES, 1838: 305, as *Achatina columellaris* Lamarck, the figure probably being copied from CHEMNITZ, 1786, pl. 112, fig. 955); *Columna flammea* Schumacher, 1817, Essai nouv. système vers testacés, p. 188; *Lymnea columnaris* Lamarck, 1822, Hist. nat. anim. s. vert., 6, part 2, p. 159, no. 1, pl. 6, 2nd p., no. 1; *Achatina columellaris* Lamarck: Deshayes (1838: 305), apparently a spelling error; *A.[gathina] columnaris*: Morelet (1858: 10), spelling error.

Endemic on Príncipe!: Through his personal observations of it on Príncipe, RANG (1831: 37) established that previous reports from the West Indies (“Antilles”), Brazil and coasts of W. Africa (“Guinée”) were erroneous. RANG (1831: 36-38) also provided notes on its body coloration, biology and habitats: in woods, reaching middle levels of the mountains, but not their summits. MORELET (1858: 25) described it as “Très-commune à l’île du

Prince” and DOHRN (1866b: 124, no. 6) reported “Ile du Prince (Dr J. Wilson); sous les feuilles mortes, dans les bois (de Folin).” GERMAIN (1912b: 340, 361-363) recorded it from Roça Infante D. Henrique, 100-300 m alt. and Bahia do Oeste, 100-200 m alt. In 2018 we found accumulations of old shells at kingfisher “anvils” locally in native forest (see above under Material and Methods heading; CGAH), but living individuals were seen at only a

single remote locality during extensive fieldwork by FUNDAÇÃO PRÍNCIPE (2019) researchers.

Shell figures: PILSBRY (1905: pl. 46, figs. 5-9), SCHILEYKO (1999: 476, fig. 610). COSSIGNANI (2014: 196) published good

photographs of shells of all three species of *Columna* from “Isola Príncipe, Guinea Equatoriale”, thus giving the correct island, but the wrong country. Genital anatomy: undescribed; a description of the CGAH specimen is in preparation

### *Columna hainesi* L. Pfeiffer, 1856

*Columna Hainesi* L. Pfeiffer, 1856, Malak. Blätt., 3, p. 256; TL “Cape Palmas” (southern part of Liberia, W. Africa).

TRYON (1866: 278) reported that he saw several specimens, belonging to Mr. Lea’s cabinet, collected by Dr J. Wilson at Prince’s Isle; Pfeiffer’s locality of “Cape Palmas” must therefore have been erroneous, or based on a drifted shell; *Columna Hainesii* [sic], Pfeiffer: Girard (1894: 201), spelling error.

Endemic on Príncipe. Apparently a rare species in collections for which there are no recent records; none of the few old reports gave any details of localities or habitats on Príncipe. Shell figures: TRYON (1866: pl. 20, fig. 1), PILSBRY (1905: pl. 46, figs. 10, 11), COSSIGNANI (2014: 196). Genital anatomy: undescribed.

E. von Martens (1866, Zool. Record, Moll., p. 198) questioned the recognition of more than one species in this genus, since the hundreds of shells collected by earlier authors did not lead to recognition of additional spp. CROSSE (1888b: 301) expressed similar doubts: “*Obs.* Les trois espèces de *Columna*, qui vivent dans l’île du Prince, sont toutes à peu près semblables, sous le rapport du système de coloration, qui se compose de bandes brunes, disposées longitudi-

nalement en zigzags plus ou moins obliques, sur un fond jaune. Le *C. flammea* présente une surface granuleuse, par suite de l’entrecroisement de ses stries. Le *C. Leai*, à peu près de même taille que le précédent, est entièrement lisse. Ses flammules longitudinales sont aussi un peu plus larges, proportionnellement. Le *C. Hainesi* est plus petit et, en même temps, plus large à la base, et plus turbiné que les deux autres formes. Ses flammules sont plus grandes et son dernier tour de spire subanguleux. Peut-être découvrira-t-on ultérieurement des individus intermédiaires entre ces trois formes, ce qui permettra de n’en faire qu’une seule espèce?”. However, GIRARD (1893b: 110) examined two shells of *C. hainesi* and was convinced that it is really distinct. Two old shells of *C. leai* found in 2018 (see below) also show distinct characters matching the figures and descriptions of old specimens. The possibility of intermediate shells suggested by Crosse has never been confirmed and they are unlikely to be found now that living snails of the genus have become very rare.

### *Columna leai* Tryon, 1866

*Columna leai* Tryon, 1866, American J. Conch., 2, pp. 297-298, pl. 20, fig. 1; TL Prince’s Isle, W. Coast of Africa.

A rare species in collections, endemic on Príncipe, but see notes under preceding species regarding its potentially uncertain taxonomic validity. The few old reports did not give any details of its local-

ities or habitats on the island. A single recent find was of two old shells lacking periostracum: 5 Dec. 2018, by road N. from Santo António, N1.64506° E7.41998°, on ground by plantation of bananas, etc., 58

m alt. (site 18-17). This was remarkable in differing from all of the recent finds of *C. columna* shells, which were from native forest in the southern part of the island. This implies that *C. leai* may have had a

different range and habitat to those of *C. columna*. Shell figures: TRYON (1866: pl. 20, fig. 1), PILSBRY (1905: pl. 46, figs. 12, 13), COSSIGNANI (2014: 196). Genital anatomy: undescribed.

### *Lignus* J.E. Gray, 1834

*Lignus* J.E. Gray, 1834, Proc. Zool. Soc. Lond., 2, p. 66; type species *Lignus tenuis* J.E. Gray, 1834, by monotypy.

### *Lignus alabaster* (Rang, 1831)

*H.[elix] alabaster* Rang, 1831, Ann. Sci. Nat., 24, pp. 20-23, no. 9, pl. 1 figs. 2, 2a; TL: l'île du Prince, très -commune ... dans les bois, à la partie moyenne et à celle inférieure des montagnes. Syn. *Lignus tenuis* J.E. Gray, 1834, Proc. Zool. Soc., London, 2, p. 66; TL "in Africâ ?".

Endemic on Principe! CROSSE (1888b: 301, no. 16) reported it: "Dans toute la partie septentrionale de l'île, sur les feuilles des arbres et des buissons, entre 15 et 20 pieds de hauteur (H. Dohrn)." GERMAIN (1912b: 340. 359-361) recorded it from Roça Infante D. Henrique, 100-300 m alt. and Bahia do Oeste, 100-200 m alt. We found it living on undersides of leaves high up on banana plants in gardens on low ground at the edge of Santo António in 2018 (CGAH).

Shell figures: RANG (1831, pl. 1 figs. 2, 2a), PILSBRY (1904: 221, no. 1, pl. 16, figs. 70, 71, 73, 74), SCHILEYKO (1999: 488-489, fig. 627 A); figures of genital anatomy: SEMPER (1870: 1, p. 145, pl. 12, fig. 3, incorrectly indicated as fig. 1 in text, pl. 16, fig. 15, radula, "2 exemplare von der Prinzeninsel"), SCHILEYKO (1899: 488-489, fig. 627B) based on SEMPER (1870).

COSSIGNANI (2014: 194) figured a shell labelled as "São Tomé e Príncipe", but there is no record from São Tomé.

### *Limicolaria* Schumacher, 1817

### *Limicolaria flammea* (O.F. Müller, 1774)

*Helix flammea* O.F. Müller, 1774, Verm. terr. fluv., 2, p. 87; TL "Senegal" (*fide* Adanson) & "In Guinea ad arcem Christiansburgensem" [a fortress near Accra, Ghana].

New to São Tomé: Nov. 2018, around Mesquita, Água Grande District, plentiful in gardens, leg. MP, 2 sh (in plantations and found to be present in gardens all along the main street that goes from Mesquita up to the border of Mé-Zochi District); 9 Nov. 2018, garden outside the National Herbarium, Boa Nova, Alto Potó [Mé Zóchi district], N0.33678° E6.65057°, ca 500 m alt., RFL; 28 Nov. 2018, Mesquita, N0.34299° E6.70533°, 69 m alt., waste-ground around industrial building, among low weedy herbs, with bananas planted along edge, DTH, GAH, RFL & MP 18-8, 3 sh & bod, 7

spm; 2 Oct. 2019, Água Crioula, Mé-Zochi District, in shade plantation, RFL.

Native of continental Africa, known from Sierra Leone, Guinea, Nigeria, Cameroon and Zaïre (CROWLEY & PAIN, 1970; SCHILEYKO, 1999: 474; COSSIGNANI, 2014: 165-166). Broader shells figured by COSSIGNANI (2014: 166) from Tanzania are only tentatively placed as this species. *L. flammea* has been known as an introduction in Singapore since 2006 (TAN & CLEMENTS, 2011; TAN & LOW, 2011), where it is potentially damaging to the valuable horticultural industry.

Local people in São Tomé date its introduction in Água Grande District to around three to five years ago. They complain that it causes damage to cultivated plants and in 2019 some were using baits of jackfruits (*Artocarpus heterophyllus*) combined with pesticides to

remove the species. However, others are deliberately spreading *L. flammea* in the mistaken belief that they are juveniles of the edible *Archachatina marginata*. On 28 Nov. 2018 (see above) we found *L. flammea* living at high density accompanied by smaller numbers of *A. marginata*.

#### Subfamily SUBULININAE P. Fischer & Crosse, 1877

*Ischnoglessula* Pilsbry, 1919 (as subgenus of *Pseudoglessula* O. Boettger, 1892)

#### *Ischnoglessula fuscidula* (Morelet, 1858)

*Achatina fuscidula* Morelet, 1858, Séries conchyliologiques, 1, p. 26, no. 25, pl. 1 fig. 9; TL “la côte du Gabon”.

Syn. *Pseudoglessula fuscidula* Morelet var. *thomensis* Germain, 1916 (GERMAIN, 1916: 156, 163, 280, pl. 7 fig. 3 *bis*, pl. 11 fig. 1; TL: Ilha San-Thomé: Ribeira Palma, entre 400 et 700 mètres d’altitude, leg. L. Fea, un exemplaire).

Reported in literature from both Príncipe (GERMAIN, 1912b: 338, 340, 381-383, at Roça Infante D. Henrique, at 100-300 m alt., leg. L. Fea, trois individus) and São Tomé (GERMAIN, 1916, see above). Range elsewhere includes

Gabon, Cameroon and Liberia (D’AILLY, 1896: 106; PILSBRY, 1904: 160; GERMAIN, 1912b: 382-383). Shell figures: PILSBRY (1904: pl. 61 fig. 98), GERMAIN (1912b: pl. 4, figs. 9, 10; 1916: pl. 7 fig. 3 *bis*, pl. 11 fig. 1), BREURE *ET AL.* (2018: 291 fig. 431).

#### *Striosubulina* Thiele, 1933

Type species *Helix striatella* Rang, by monotypy. Originally introduced as sect. *Striosubulina* Thiele, 1933 of genus *Homorus*, subgenus *Neoglessula*.

#### *Striosubulina striatella* (Rang, 1831)

*Helix striatella* Rang, 1831, Ann. Sci. Nat., 24, pp. 38-39, no. 15, pl. 3, fig. 7; TL ile du Prince (= Príncipe), “très commune” ... “au pied des montagnes, proche le bord de la mer”.

Syn. *Stenogyra* (*Subulina*) *angustior* Dohrn, 1866(b), Malak. Blätt., 13, pp. 127-128; TL “am Baumwurzeln, am Fusse von Mauern etc.”, doubtless on Príncipe judging from the title of the paper, but this is not explicitly stated.

Common on São Tomé! (also recorded historically from Ilhéu de Rolas) and Príncipe! Known elsewhere as apparently native from Annobón, Bioko and tropical W. Africa (Sierra Leone to Angola) (e.g. D’AILLY, 1896: 141; PILSBRY 1906: 78; GERMAIN, 1916: 163, 290; GASCOIGNE, 1994a: 2); as introduction in Mascarene Islands (GRIFFITHS & FLORENS, 2006) and Pemba Island (ROWSON, WARREN & NGEREZA, 2010), and in greenhouses elsewhere (England, France). Shell figures: RANG (1831: pl. 3,

fig. 7), PILSBRY (1906: pl. 11 figs. 89-92, 96, 98-101), GERMAIN (1912b: pl. 4 figs. 1, 2), KERNEY & CAMERON (1979: 207), SCHILEYKO (1999: 519). Fig. of genital anatomy: SCHILEYKO (1999: 519).

SCHILEYKO (1999: 519) described and figured the genital anatomy of this species and promoted *Striosubulina* to the status of a full genus. F. Naggs (in ANDERSON, 2005: 633) commented that Schileyko based his study on introduced material from Kew Gardens (England) which has a pale yellow

body, whereas the original description was accompanied by a coloured figure showing a dark animal (RANG, 1831: pl. 3 fig. 7). However, he appears to have overlooked Rang's accompanying text (p. 38) which stated "Corpore albosordido" and then "L'animal est d'un blanc sale qui tient un peu de la teinte générale de la coquille", establishing that the dark body shown in the figure was likely to be an error made by the artist. Topotypical specimens in CGAH from several localities on Príncipe are indeed like those from São Tomé in having exposed parts of the body pale (whitish in spirit). Furthermore, SCHILEYKO (1999: 519 fig. 676) figured only a shell from Kew, with his drawing of genital anatomy clearly described as

based on a specimen from Sri Lanka. Thus it was unwarranted for NAGGS ET AL. (2014) to give the name of the introduced British snail as *Subulina striatella* because "*Striosubulina* has been shown to be conspecific [meaning congeneric?] with *Subulina*".

GIRARD (1893b: 103, no. 2) suggested *Stenogyra* (*Subulina*) *angustior* Dohrn, 1866 from Príncipe may not be worthy of taxonomic recognition ("je crois qui c'est une simple variation mais comme M. Newton ne l'a pas recueille je l'admets sur l'autorité de MM. Dohrn et Pfeiffer"). We also regard it as a synonym of *S. striatella* because shape and size of shells intergrade in some samples collected in 2018 (CGAH).

### *Subulina* Beck, 1837

#### *Subulina feai* Germain, 1912

*Subulina feai* Germain, 1912(a), Bull. Mus. Hist. nat., Paris, 18 (5), pp. 320-321; TL Île du Prince; Roça Infante D. Henrique, entre 100 et 300 mètres d'altitude (leg. L. Fea, quelques exemplaires).

Endemic on Príncipe. The shell has apparently never been figured but is described well by GERMAIN (1912a: 320-321; 1912b: 372-373). Genital anatomy: undescribed. GERMAIN (1916: 156, 163)

listed "*Pseudopeas Feai* Germain" in the table on his p. 163, apparently in error; *Subulina Feai* Germain was listed on the same page and there is no separate taxon named *Feai* in *Opeas* or *Pseudopeas*.

#### *Subulina moreleti* Girard, 1893

*Subulina Moreleti* Girard, 1893(b), J. Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 104, pl. 1 fig. 12; TL "Île du Prince. Un individu recueilli à Quilala-Faluiha à 500 m d'alt. (F. Newton)."

Endemic on Príncipe! Shell figures: GIRARD (1893b: pl. 1 fig. 12), PILSBRY

(1906: 74-75, pl. 11, fig. 86). Genital anatomy: undescribed.

#### *Subulina newtoni* Girard, 1893

*Subulina Newtoni* Girard, 1893(b), J. Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 104, pl. 1 fig. 11; TL "Île du Prince, à Ferreiro Velho (100 m d'alt.); Ó que S. João (200 m alt.); Quilala Faluiha à 500 m d'alt. (F. Newton)".

Endemic on Príncipe! Also recorded there by GERMAIN (1912b: 340, 373-374), at Roça Infante D. Henrique, 100-300 m

alt. (leg. L. Fea). Shell figures: GIRARD (1893b: pl. 1 fig. 11), PILSBRY (1906: 75, pl. 11, fig. 87). Genital anatomy: undescribed.

Subfamily CECILIOIDINAE Mörch, 1864

*Cecilioides* A. Férussac, 1814

*Cecilioides* sp.

GASCOIGNE (1994b: 798) noted that it was “recently recorded on São Tomé for the first time”; we have not found it.

Subfamily PETRIOLINAE Schileyko, 1999

*Aporachis* n. gen. D. Holyoak

Type species: *Bulimus* (*Leptomerus*) *Dohrni* Greeff, 1882.

**Etymology:** Based on the comment by MARTENS (1860: 231, “Rhachis - Rückgrat, Spindel - Albers erste Ausg. S. 182”) it was made clear that the genus name *Rachis* Albers, 1850 (ALBERS, 1850: 182; Cerastidae) was based on the Greek *Rachis* (or *Rhachis*) meaning backbone (spine) or spindle. The new genus name *Aporachis* is thus based on the genus name *Rachis* Albers, 1850 in combination with the Greek *Apo-* (meaning apart, or separate from) and, like *Rachis*, it is a feminine noun.

**Description:** Shells ovoid-conical to broadly cylindro-conical; shell growth apparently indeterminate, but with mature genitalia at shell H 12-21 mm, B 7-8 mm, and 6-7 whorls. Shell rather thin,  $\pm$  translucent, brown to pale brown. Whorls of upper spire increasing rather gradually in size (giving almost flat to moderately convex profile to spire), but body-whorl disproportionately large; sutures moderately deep. Aperture rather narrowly oval in outline, but broadly interrupted by penultimate whorl; peristome thin and mainly simple, narrowly reflected over upper part of columellar axis; umbilicus nil or a narrow chink. Columella smoothly curved basally, not truncated; apertural teeth lacking. Protoconch and second whorl with sculpture of spiral grooves; teleoconch sculpture variable: with only weak axial growth lines, with low axial ribs, or with spiral rows of short hairs.

Foot and lower exposed part of body white; exposed dorsum of body grey or spotted with grey. Mantle with white margin, the remainder with light grey to blackish blotches that often fuse upwards into broad dark axial bands; body inside spire externally pale pinkish or brown, sometimes with bold blotches of blackish-brown.

Genital pore about mid-height on front right-hand side of body, just posterior to lower tentacle. Genital atrium very short. Penis long, cylindrical,  $\pm$  tapering proximally, rather tightly enclosed inside thin membranous sheath, lacking epiphallus or flagellum; penial retractor muscle stout, flattened, strap-like, arising from proximal end of penis, passing proximally and downwards to join columellar musculature. Vas deferens ending close to proximal end of penis; its distal portion a very narrow tube, passing distally alongside penis enclosed within penial sheath, exiting at penial/vaginal angle where vas deferens widens slightly; widening further as it passes alongside vagina and free oviduct, then narrowing proximally before widening again near to where it leaves distal part of spermooviduct. Vagina cylindrical distally with conspicuous thickened muscular annulus; above annulus vagina widening markedly and asymmetrically; free oviduct rather wide, very short in *A. hispidus*, longer in *A. dohrni*. Reservoir of bursa copulatrix a thin-walled ovoid to somewhat D-shaped sac appressed to side of distal end of spermooviduct (or free oviduct in one of two *A. dohrni* dissected, which had duct of bursa passing back distally); duct of bursa copulatrix a

narrow tube about as long as the reservoir. Spermoviduct large, much of its length enclosed along one side in “villose organ” formed of thickened whitish carpet of densely packed, variably curved villi (one *A. dohrni* had oviducal part of spermoviduct containing ten large white spherical eggs each ca 1.9 mm in diameter, arranged as five pairs regularly and rather closely spaced along length of oviduct; the carpet of villi covered the exterior wall of the egg-filled oviduct). Common hermaphrodite duct arising from gonad inside digestive gland, passing distally to near proximal extremity of spermoviduct; the proximal portion a very thin tube; the distal portion (near albumen gland) much thicker, convoluted in tight coils. Albumen gland rather small. Right ommatophore retractor passing through angle between distal end of penis and distal vagina.

The two species placed in this genus were both originally described in *Bulimus* (*Leptomerus*) by GREEFF (1882). GERMAIN (1916) transferred both of them to *Rachis* Albers, 1850; the latter genus being placed in the Cerastinae Wenz, 1923 in the review by MORDAN (1992). However, features of the genital anatomy (Fig. 6A-D) show *Aporachis* n. gen. differs markedly from Cerastidae and is better placed in the broadly defined Achatinaceae adopted by BOUCHET ET AL. (2017: 361). In particular,

*Aporachis* has a simple penis lacking epiphallus or flagellum, the vas deferens running alongside the penis in the penial sheath; stout penial retractor muscle attached proximally to the columellar musculature; vagina with annular thickening distally; bursa copulatrix with short duct. In contrast, Cerastidae have a complex penis with appendages commonly including epiphallus, flagellum and caecum; a long, slender penial retractor muscle attached to the inner wall of the lung, and vagina lacking a distal annular thickening but possessing a characteristic dark-pigmented spongy and fibrous tissue covering most of the vagina and the collateral part of the atrium (Fig. 6E, F).

The new genus is only provisionally assigned to Subfamily Petriolinae, which is the closest subfamily in shell characters as well as having all three species of its type genus similar in being endemic on São Tomé island. The closest match in shell characters is actually with *Bocageia* from Príncipe, for which the genital anatomy remains unknown. DNA sequence data reported for *Bocageia* in FONTANILLA ET AL. (2017: fig. 1) almost undoubtedly came from *Petriola* sp. (see below under that genus). *Nothapalus* (see below) from the Congo basin is likewise unknown from genital anatomy and molecular data. So far as is known the “villose organ” is peculiar to *Aporachis* n. gen.

### *Aporachis dohrni* (Greeff, 1882) n. comb. (Figs. 2A, 6A, B)

*Bulimus* (*Leptomerus*) *Dohrni* Greeff, 1882, Zool. Anzeiger, 5, p. 520; TL S. Thomé auf Roça do Monte Café und Santa Luzia.

Syn. *Buliminus* (*Rachis*) *Castroi* Nobre, 1891, O Instituto, Coimbra, 2nd ser., 38, p. 933 (p. 25 in off-print); TL “Pico de S. Thomé a 2:100 m. de altitude” (São Tomé).

Endemic on São Tomé! A poorly known species that has apparently never been figured before in the literature. Shell Fig. 2A; genital anatomy Fig. 6A, B. CROSSE (1888a: 17-18) commented on the poor original description and difficulty in placing it taxonomically. GERMAIN (1916: 162, 168) merely listed

it. Our records were from forests at 1022-1490 m elevation, with a single old shell tentatively identified from 959 m. At the upper levels it was found in montane forest, sometimes where it was low and mossy as near Lagoa Amélia; at the lower levels it occurred in secondary forest.

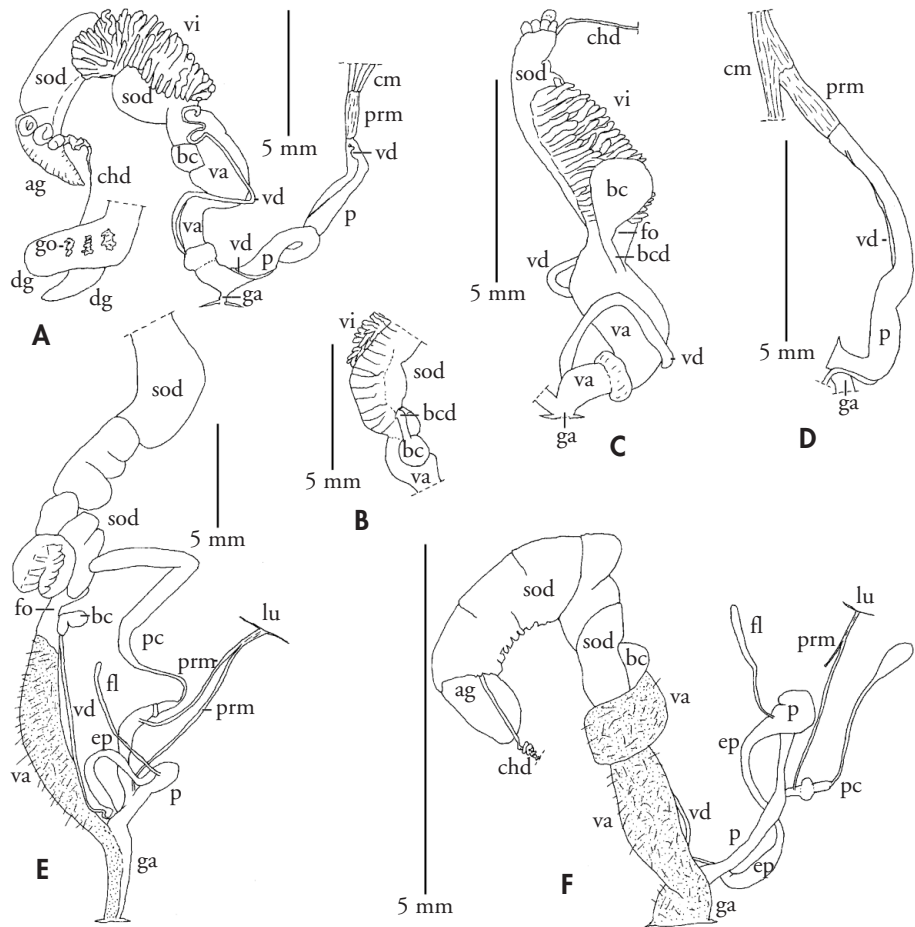


Figure 6. Genital anatomy of *Aporachis* (Achatinidae: Petriolinae) and *Gittenedouardia* (Cerastidae). A, B: *A. dohrni* (São Tomé, near Lagoa Amélia, N0.2812° E6.5908°, 1416 m alt., low moist montane-forest around infilled crater lake, 10 Dec. 2018, DTH, MP & FS 18-25 (B: shows opposite side of proximal part of vagina and distal part of spermooviduct of same specimen as in A); C, D: *A. hispida* (São Tomé, Morro Claudina, N0.2912° E6.6057°, ca 1289 m, lower montane forest on ridges & slopes, 24 Nov. 2018, GAH, DTH, et al. 18-2 (C: shows hermaphrodite and female tracts; D: shows male tract of same specimen); E: *G. burnayi* (Príncipe, just S. of Santo António on road to Bela Vista, N1.63075° E7.41794°, 24 m alt., edges of secondary-forest and cultivation, 2 Dec. 2018, GAH & DTH 18-11); F: *G. eminula* (São Tomé, SW of Trindade, N0.27667° E6.65986°, 398 m alt., secondary forest on slopes & old plantations, 3 Dec. 2018, GAH & DTH 18-10).

*Figura 6. Anatomía genital de Aporachis (Achatinidae: Petriolinae) y Gittenedouardia (Cerastidae). A, B: A. dohrni (Santo Tomé, cerca de Lagoa Amélia, N0,2812° E6,5908°, 1416 m alt., bosque bajo húmedo montano alrededor del lago de cráter relleno, 10 dic. 2018, DTH, MP y FS 18-25 (B: muestra el lado contrario de la parte proximal de la vagina y de la parte distal del espermooviducto, mismo ejemplar que en A); C, D: A. hispida (Santo Tomé, Morro Claudina, N0,2912° E6,6057°, aprox. 1289 m, bosque montano inferior en crestas y laderas, 24 nov. 2018, GAH, DTH, et al. 18-2 (C: muestra tractos hermafrodita y femenino; D: muestra tracto masculino del mismo ejemplar); E: G. burnayi (Príncipe, justo S. de Santo António en el camino a Bela Vista, N1,63075° E7,41794°, 24 m alt., bordes de bosque secundario y cultivo, 2 dic. 2018, GAH y DTH 18-11); F: G. eminula (Santo Tomé, SO de Trindade, N0,27667° E6,65986°, 398 m alt., bosque secundario en laderas y plantaciones antiguas, 3 dic. 2018, GAH y DTH 18-10).*

*Aporachis hispida* (Greeff, 1882) n. comb. (Figs. 2B, 6C, D)

*Bulimus* (*Leptomerus*) *hispidus* Greeff, 1882, Zool. Anzeiger, 5, p. 521; TL S. Thomé, Roça do Monte Café.

Endemic on São Tomé! A poorly known species that has apparently never been figured before in the literature. Shell Fig. 2B; genital anatomy Fig. 6C, D. CROSSE (1888: 18) commented on the poor original description and difficulty in placing it taxonomically; GIRARD (1893a: 33) and GERMAIN (1916: 162, 168) merely listed it.

Our records were mainly from montane forest at 1289-1416 m elevation, including occurrence in low mossy forest near Lagoa Amélia where it coexisted with *A. dohrni*. It was also found once lower down at 885 m near Cascata de São Nicolau, in secondary forest on steep rocky slopes receiving spray from a large waterfall.

**Key to shells of species from São Tomé and Príncipe formerly placed in genus *Rachis***

These comprise the two species of *Aporachis* n. gen. (Achatinidae) discussed above which are endemic on São Tomé and two species of *Gittenedouardia* (Cerastidae) discussed below which both occur on São Tomé, Príncipe, and

the mainland of central Africa. Fig. 2 illustrates shells of all four species; Fig. 6 shows conspicuous differences between the genera in genital anatomy, but little or no difference among the congeneric species.

1. - Shell whitish, marked near base (except in small immatures) with conspicuous spiral brown band; commonly also with brown blotches or spots dorsally; shape broadly conical with rapidly enlarging whorls, so last whorl forms >60% of shell height . . . . . *G. burnayi*  
 - Shell brown or brownish, lacking darker markings; shape more narrowly conical with whorls enlarging more gradually, so last whorl <60% of shell height . . . . . 2
2. - Shell narrower, B <6 mm in largest shells; mature shells with >6 whorls; body-whorl forming <50% of height of mature shells; apical whorls almost smooth; mantle not boldly marked with black blotches . . . . . *G. eminula*  
 - Shell broader, B >6 mm at maturity; mature shells with 6 or fewer whorls; body-whorl forming >50% of shell height of mature shells; apical whorls with spiral sculpture (often lost as shells age); mantle often boldly marked with black blotches (sometimes lacking) . . . . . 3
3. - Shell with short hairs in regular spiral rows (hairs soon lost, but traces of spiral lines more persistent); axial ribs weak; whorls 1-2 of apex with <8 low narrow spiral ridges that are widely separated . . . . . *A. hispida*  
 - Shell lacking hairs; spiral sculpture absent from body-whorl; axial ribs weak to moderately strong; whorls 1-2 of apex with >11 stronger spiral ridges that are closely spaced . . . . . *A. dohrni*.

*Bocageia* Girard, 1893

Jornal Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 100; type species *Bulimus lotophagus* Morelet by original designation.

*Bocageia* is currently a junior objective synonym of *Streptostele* Dohrn, 1866, as discussed below under the latter genus heading. We maintain exist-

ing usage of both generic names here because the ICZN will be requested to set aside older but overlooked designations of the type species of *Streptostele*.

*Bocageia lotophaga* (Morelet, 1848)

*Bulimus lotophagus* Morelet, 1848, Rev. Zool., 11, p. 352; TL insulam Principis in sinu Guineensi; 3 syntypes in NHMUK (BREURE *ET AL.*, 2018: 330, fig. 605).

Endemic on Príncipe. Recorded by GIRARD (1893b: 100-102) "Ó que S. João à 200 m d'altitude (F. Newton) ... pas adultes", by GERMAIN (1912b: 338, 340, 368-370) from "Roça Infante D. Henrique, 100-300 m (leg. L. Fea)". Shell figures:

MORELET (1858: pl. 1, fig. 7), PILSBRY (1905: pl. 56, figs. 18-20), GERMAIN (1912b: pl. 4 figs. 5, 6), BREURE *ET AL.* (2018: 330 fig. 605). Genital anatomy: undescribed. GIRARD (1893b: 100-102, no. 1, pl. 1, fig. 10) figured the radula.

*Nothapalus* von Martens, 1897

*Nothapalus solitarius* n. sp. G. Holyoak & D. Holyoak (Fig. 3A)

**Type material:** Named and described only from the unique holotype shell: NHMUK 20200234, collected 4 Dec. 2013, GAH ST4.

**Type locality:** São Tomé Island, path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2786° E6.6000°, ca 1300 m alt., montane forest on slope with understorey of saplings.

**Etymology:** The species epithet uses the Latin *solitarius* (meaning alone, or by itself) referring to the single shell specimen found despite repeated visits, and its distinctness from other species.

**Description:** Shell dextral, H 4.69 mm, B 2.40 mm, H/B 1.96; body-whorl height 3.29 mm (70.1% of H); AH 2.06 mm (43.9% of H), AB 1.03 mm, AH/AB 2.00; whorls 3.9. Shell shape rather narrowly conical, with rounded base. Whorls of spire slightly rounded, with definite shoulder close below suture; suture somewhat oblique, impressed but shallow, appearing as narrow double line. Body-whorl large, approximately oval. Aperture ear-shaped with rounded lower palatal margin, gently curved outer palatal margin, curved parietal margin; columellar margin almost straight in upper half sharply truncate just below middle, the lower half with strongly curved shallow recess. Peristome (apparently not fully mature) thin, plane, with membranous fringe except on columellar margin, which widely reflected in upper half, overlapping but not closing umbilicus. Umbilicus a narrow deep chink, the interior visible only in ventral view. Protoconch small, slightly domed, with faint granular microsculpture. Teleoconch with low, rather irregular axial ribs that are slightly curved on upper whorls and more strongly curved on

body-whorl; spiral microsculpture (of thin grooves) crossing the low ribs, rather indistinct on body-whorl, more conspicuous on whorls 2 and 3. Shell thin, translucent, whitish with weak yellow tinge, moderately glossy.

Body (dried inside shell) and anatomy unknown.

**Comments:** The single shell does not appear to be fully mature but it cannot be matched by immatures of *Petriola* or other "subulinids" from São Tomé. Because the anatomy is unknown, allocation to a genus or subfamily is tentative. It appears to be a species of one of the groups formerly treated as Subulinidae (now placed within Achatinidae) from the thin, elongate, whitish shell, axial ribbing and lack of apertural barriers, and this family also seems likely in view of its wide radiation and prolific speciation on São Tomé and Príncipe. The provisional assignment to *Nothapalus*, represented by several species in the Congo basin, is based on the narrowly conical/ovoid shell outline, few whorls, flattened whorl profiles and especially, the markedly truncate columella (cf. PILSBRY, 1919: 129-134, pl. 19 figs. 1-6). Nevertheless, *Nothapalus* differs in its larger

shells (H 13-22.3 mm), closed umbilicus and lack of spiral shell sculpture. Some species of the genus *Curvella* Chaper, 1885 are similar in having few whorls, axial ribbing, whitish shells and also rather small size (H 6 mm in some South African species: HERBERT & KILBURN, 2004: 136), but none of them have the columella truncated. *Neoglessula* Pilsbry, 1909 has several species known in west Africa, but none of them matches the shell from São Tomé.

Outside the Achatinidae (which now includes the former Subulinidae), *Micractaeon* shows a conspicuous similarity in shell form (VAN BRUGGEN & DE

WINTER, 1995), but it differs in having a relatively tiny shell (H up to 2.1 mm), brown shell coloration and spiral sculpture on the shell consisting of distinctive lines of rounded pits (clearly visible at  $\times 56$  with strong oblique illumination using our microscopes, whereas *Nothapalus solitarius* shows faint spiral grooves and continuous lines not rows of pits). Some genera of the family Ferussaciidae also have shells of similar general form, but the family is not known in tropical west Africa. Thus, more material is needed to use anatomical or molecular characters to establish the affinities of this species.

### *Petriola* Dall, 1905

*Nautilus*, 18 (12), p. 143, type species *Achatina marmorea* Reeve, 1850, by typification of replaced name. Syn. *Trichodina* Ancy in VIGNON (1888: 71), preoccupied, non Ehrenberg (Ciliophora).

DALL (1905: 143) introduced the generic name *Petriola* as a replacement name for *Trichodina* Ancy, 1888 which is preoccupied by *Trichodina* Ehrenberg, 1831 (Ciliophora). PILSBRY (1905) and GERMAIN (1916) treated these large subulinids which are endemic on São Tomé as forming the subgenus *Petriola* within *Bocageia* Girard, 1893. However, this seems to be unwarranted since the type of *Bocageia* is *Bulimus lotophagus* Morelet, 1848 an endemic of Príncipe, having a shell with fewer whorls than the São Tomé species and a very shallow suture (BREURE ET AL., 2018: 330 fig. 605); its genital anatomy is unknown. The São Tomé species had also been placed in *Homorus* Albers, 1850 (by CROSSE, 1888a; NOBRE, 1891; GIRARD, 1893a, 1893b), but that genus has narrowly-conical rather than subcylindrical shells, with a proportionately longer mouth which is pointed rather than rounded below. Also, the scanty information on its genital anatomy (PILSBRY, 1919: 114; SCHILEYKO, 1999: 522-523, fig. 681) shows it differs in having the free oviduct a little longer than the vagina, whereas the free oviduct is "very short" in *Petriola clavus* (SCHILEYKO, 1999: 521-522, fig. 679) or absent (our Fig. 7D and I of *P. marmorea* and 7H of *P. monticola*). Other anatomical

features of *Petriola* as a whole are the penis which can be extruded from genital pore, containing a short distal verge (at least in *P. clavus* and *P. marmorea*); well-defined epiphallus; penial retractor muscle attached to epiphallus / vas deferens junction [*contra* SCHILEYKO, 1999: 522-523, fig. 681], the muscle rather short and descending to join columellar muscles; short genital atrium; rather long vagina; small bursa copulatrix on very short duct, the reservoir lying alongside distal end of spermoviduct; spermoviduct large and long; some mature individuals with 1-5 embryos developing shells inside oviducal part of spermoviduct; common hermaphrodite duct long, narrow, convoluted in distal portion, almost straight in proximal portion. Hence, we retain the São Tomé species in the endemic genus *Petriola* for now, although more extensive research on genital anatomy and molecular-sequence data for *Bocageia lotophaga* and the numerous poorly known nominal taxa from the African mainland may lead to changes in the future.

SCHILEYKO (1999: 520) named the subfamily Petriolinae within the Subulinidae mainly on the basis of the structure of the penis, since "no one other subfamily has such conspicuous organization of copula-

tory apparatus", presumably referring to possession of a distinct epiphallus and a verge inside the distal penis. Molecular-phylogenetic data presented by FONTANILLA ET AL. (2017: fig. 1) for "*Bocageia* sp." gave additional justification for recognition of Subulinidae (Petriolinae) as a subfamily, which became Achatinidae subfamily Petriolinae in BOUCHET ET AL. (2017), but the "*Bocageia* sp." which provided the only sequence data involved was a specimen from São Tomé that doubtless represented a *Petriola* sp. SCHILEYKO (1999: 521-522, fig. 679) published the only detailed account of the genital anatomy of any of the *Petriola*

species, based on *P. clavus*. Besides revising that description (using 11 specimens from 4 populations), we have obtained the first data on the genital anatomy (Fig. 7) of other congeneric species from São Tomé recognised by PILSBRY (1905) and on *Achatina* (*Subulina*) *costulata* Greeff, 1882 (GREEFF, 1882: 519). These fall into three natural groups according to length of the penis and epiphallus, but they all show a general similarity, so we retain them in the same genus. Along with study of numerous shell samples (see below), this leads us to recognise three species in *Petriola* which may be distinguished as follows:

1. - Periostracum dark brown to blackish, in fresh shells with narrow axial riblets and higher lamellae bearing spines, intersecting spiral riblets to give decussate pattern; shell broad (B >11.0 mm in mature snails; breadth 5 mm below apex >4.4 mm); penis shorter than vagina (Fig. 7D-F, I); small section of vas deferens passing inside outer sheath of penis (Fig. 7I) . . . . . *P. marmorea*  
- Periostracum brown to whitish, smooth or bearing regular or irregular axial riblets or ribs, but without spines or decussate pattern; shell narrower (B <11.5 mm in mature snails; breadth 5 mm below apex <5.5 mm); penis shorter or longer than vagina; all of vas deferens passing outside outer sheath of penis . . . . . 2
2. - Shell wider (B >7.7 mm in mature snails; breadth 5 mm below apex 3.9-5.4 mm); body-whorl almost smooth or with wavy axial lines; periostracum of fresh shells brown, glossy; proximal part of distal portion of epiphallus not slender, not markedly convoluted *in situ* (Fig. 7A) . . . . . *P. clavus*  
- Shell narrower (B <7.0 mm in mature snails; breadth 5 mm below apex <3.9 mm); body-whorl smooth, with axial riblets or ± strong axial ribs; periostracum of fresh shells whitish to pale brown; proximal part of distal portion of epiphallus slender, convoluted *in situ* (Fig. 7H) . . . . . *P. monticola*

### *Petriola clavus* (L. Pfeiffer, 1846) (Fig. 7A-C)

*Achatina clavus* L. Pfeiffer, 1846, Symbolae ad Historiam Heliceorum, 3, p. 90 no. 398; TL unknown. *Petriola clava* is an incorrect subsequent spelling in GERMAIN (1908, Bull. Mus. Natn. Hist. Nat., 14, p. 61); *clavus* is a classical noun (masculine, meaning a nail) used in apposition to the genus name.

Endemic on São Tomé! Shell figures: 195, figures of two shells). Figures of PILSBRY (1905: pl. 56 figs. 9-11), SCHILEYKO (1999: 521), COSSIGNANI (2014: genital anatomy: SCHILEYKO (1999: 521), Fig. 7A-C, see comments above.

### *Petriola marmorea* (Reeve, 1850) (Fig. 7D-F, I)

*Achatina marmorea* Reeve, 1850, Conch. icon., 5, pl. 23 fig. 125; TL unknown (MORELET, 1868: 756-76 considered Reeves' type of *marmorea* to be a worn specimen of his own *A. barbigera*, a conclusion accepted by PILSBRY, 1905: 182-183 and GERMAIN, 1916: 262).

Syn. *Achatina barbigera* Morelet, 1866, J. Conchyl., (3rd ser.) 6, p. 160; TL "In dumetis silvestribus San-Thomé, ad 2,500 ped. altitudinis"; 2 syntypes in MNHN & 2 syntypes in NHMUK (BREURE ET AL., 2018: 214, fig. 103); *Homorus Massonianus* Crosse, 1888, J. Conchyl., 36, p. 22, pl. 1, fig. 3; TL San-Thomé (GERMAIN, 1916: 264 suggested this may be a variety of *P. marmorea* with less developed shell sculpture); *Bocageia (Petriola) Massoni* is an incorrect subsequent spelling in GERMAIN (1916: 163, 168, 264).

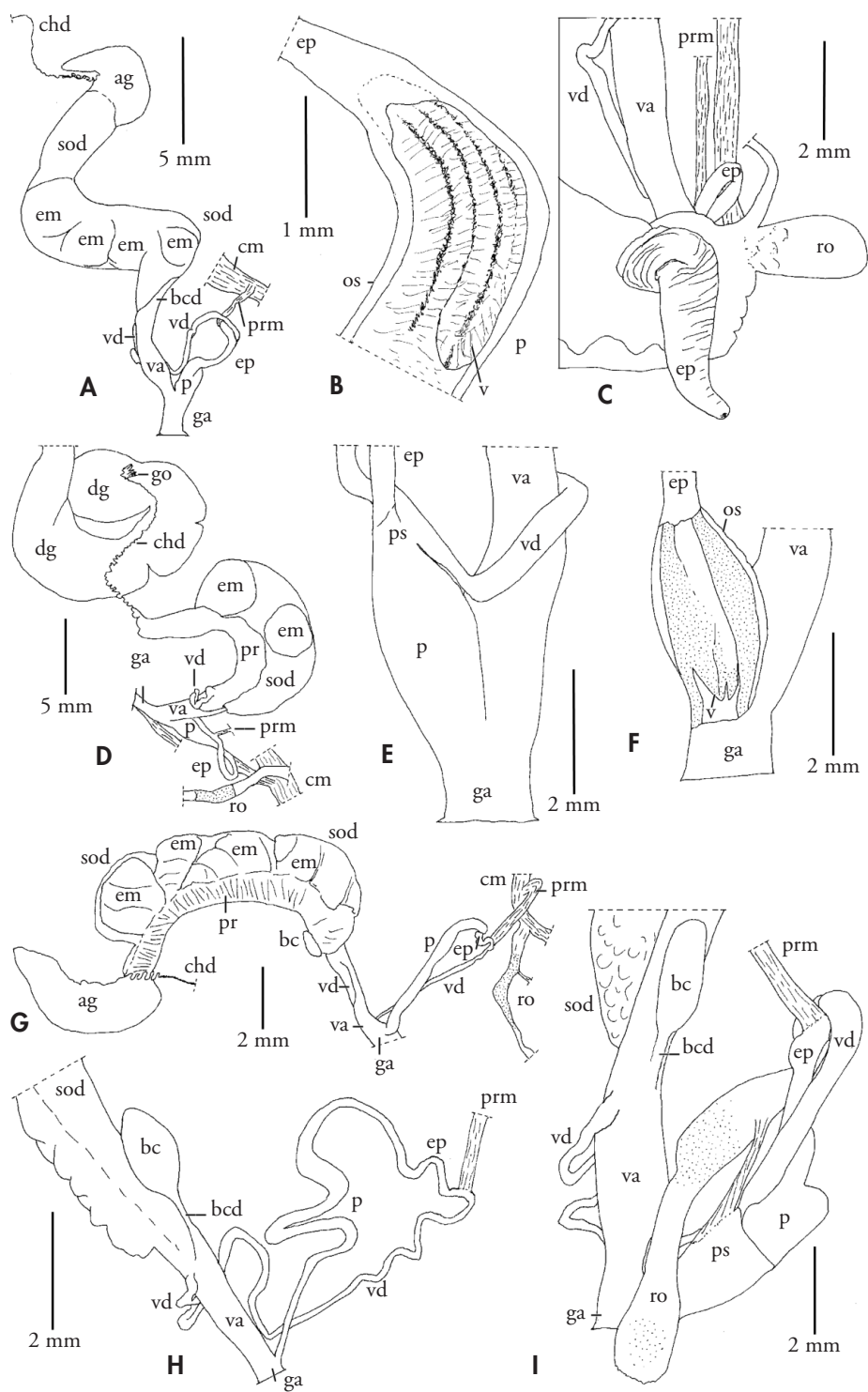
Endemic on São Tomé! Shell figures: MORELET (1868: pl. 9 fig. 5), CROSSE (1888: pl. 1 figs. 3, 3a), PILSBRY (1905: pl. 55 figs. 94-96, pl. 56 figs. 13-15), BREURE ET AL. (2018: 214, fig. 103), COSSIGNANI (2014: 195, figures of two shells as *massoni*). Figures of genital anatomy: Fig. 7D-F, I.

PILSBRY (1905: 184, pl. 56 figs. 13-15) treated *Homorus massonianus* Crosse, 1888 (CROSSE, 1888a: 22, pl. 1 fig. 3) as a valid species, but GERMAIN (1916: 264) was probably correct in suggesting it

may be a variety of *P. marmorea* with less developed shell sculpture, since Crosse gave the maximum diameter of the shell as 13 mm. GERMAIN (1916: 163, 168, 264) also emended the species epithet to *Bocageia (Petriola) massoni* Crosse, but the change was unnecessary. COSSIGNANI (2014: 195) figured two shells as *Bocageia massoni* (Crosse, 1868 [sic]), but they are clearly *P. marmorea* because they show coarsely decussate periostracal sculpture with some small spines visible.

(Right page) Figure 7. Genital anatomy of *Petriola* from São Tomé. A-C: *P. clavus*; A: distal genitalia (just S of Milagrosa, on road between Trindade and Bombaim, N0.27667° E6.65986°, 398 m alt., tall secondary forest & abandoned cocoa plantations, 2 Dec. 2018, GAH & DTH 18-10); B: longitudinal section of penis to show wall of lumen (path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2825° E6.5969°, ca 1400 m alt., montane forest, 7 Dec. 2013, GAH & DTH ST8); C: partial dissection of foreparts of snail with epiphallus extended out of genital pore (path between Bom Sucesso and Macambrará, near Rio Manuel Jorge, N0.2847° E6.6097°, ca 1149 m alt., cultivation edges & small forest patches, 3 Dec. 2013, GAH & DTH ST3). D-F, I: *P. marmorea*; D: genitalia with attached right ommatophore and associated muscles (Morro Claudina, N0.2912° E6.6057°, 1289 m, montane forest, 24 Nov. 2018, DTH & GAH 18-2); E: detail of penis, vagina and vas deferens (18-2); I: details of distal genitalia and muscle attaching it to right ommatophore (ST8). G,H: *P. monticola*; G: distal genitalia with attached right ommatophore and associated muscles (Morro Claudina, N0.2918° E6.6059°, 1254-1292 m, montane forest, 27 Nov. 2018, DTH & GAH 18-6); H: details of distal genitalia (by EN2 just NE of Monte Mário "roça", N0.0606° E6.5561°, ca 236 m alt., forest on slopes by road, 13 Dec. 2013, GAH & DTH ST13).

(Página derecha) Figura 7. Anatomía genital de *Petriola* de Santo Tomé. A-C: *P. clavus*; A: genitalia distal (justo al S de Milagrosa, en la carretera entre Trindade y Bombaim, N0,27667° E6,65986°, 398 m alt., bosque secundario alto y plantaciones de cacao abandonadas, 2 dic. 2018, GAH y DTH 18-10); B: sección longitudinal del pene para mostrar la pared del lumen (camino a Lagoa Amélia desde el Jardín Botánico Bom Sucesso, N0,2825° E6,5969°, aprox. 1400 m alt., Bosque montano, 7 dic. 2013, GAH & DTH ST8); C: disección parcial de las partes delanteras del caracol con epífalo extendido fuera del poro genital (camino entre Bom Sucesso y Macambrará, cerca de Río Manuel Jorge, N0,2847° E6,6097°, aprox. 1149 m alt., bordes de cultivo y pequeños parches de bosque, 3 dic. 2013, GAH y DTH ST3). D-F, I: *P. marmorea*; D: genitalia unida al ommatóforo derecho y músculos asociados (Morro Claudina, N0,2912° E6,6057°, 1289 m, bosque montano, 24 nov. 2018, DTH y GAH 18-2); E: detalle del pene, la vagina y el conducto deferente (18-2); I: detalle de la genitalia distal y músculos que la unen al ommatóforo derecho (ST8). G,H: *P. monticola*; G: D: genitalia distal unida al ommatóforo derecho y músculos asociados (Morro Claudina, N0,2918° E6,6059°, 1254-1292 m, bosque montano, 27 nov. 2018, DTH y GAH 18-6); H: detalles de la genitalia distal (por EN2, justo al NE del Monte Mário "roça", N0,0606° E6,5561°, aprox. 236 m alt., bosque en laderas por carretera, 13 dic. 2013, GAH y DTH ST13).



*Petriola monticola* (Morelet, 1866) (Fig. 7G, H)

*Achatina monticola* Morelet, 1866, J. Conchyl., (3rd ser.) 6, p. 160; TL insulae San Thomé, ad 2,500 ped. altitudinis; 2 syntypes at NHMUK (BREURE ET AL., 2018: 358, fig. 719).  
 Syn. *Achatina* (*Subulina*) *costulata* Greeff (1882, p. 519); *Achatina* (*Subulina*) *subcrenata* Greeff (1882, p. 519) (PILSBRY, 1905: 187 and GERMAIN, 1908: 62 listed this as a syn. of *P. monticola*); *Stenogyra subcrenulata* [sic] Greeff: CROSSE (1888: 25), spelling error; *Bocageia* (*Petriola*) *monticola* Morelet et vars. *sculptisuturata* Germain, *costulata* Greeff [sic] et *maxima* Germain (1916, pp. 156, 163, 168); *Bocageia* (*Petriola*) *monticola* Morelet mutation *marginata* Germain (1916, p. 268, 322, pl. 11 fig. 11; p. 119, pl. 6 fig. 11 in reprint), a name not based on an obviously teratological specimen (so not needing to be excluded under ICZN Art. 1.3.2, indeed Germain apparently intended merely a variant form (since, e.g., under var. *costulata* on p. 270, he commented "Cette variété est également polymorphe et il est facile de séparer des mutations *elata* ou *ventricosa*": both of the latter being nomina nuda); TL Is. San-Thomé: Vista Alegre, entre 200 et 300 mètres d'altitude, found with type and var. *sculptisuturata* Germain; *Bocageia* (*Petriola*) *monticola* Morelet var. *sculptisuturata* Germain (1916, p. 269); TL: Is. San-Thomé: Ribeira Palma, entre 400 et 700 mètres d'altitude; Ribeira Palma, dans la forêt, entre 500 et 600 mètres d'altitude; Vista Alegre, entre 200 et 300 mètres d'altitude [with type at first and last of these localities]; *Bocageia* (*Petriola*) *monticola* Morelet var. *maxima* Germain, 1916 (p. 270, pl. 10 figs. 10, 13); TL: Is. San-Thomé: Ribeira Palma, entre 0 et 300 mètres d'altitude, with type and var. *costulata* Greeff.

Endemic on São Tomé! Shell figures: MORELET (1868: pl. 5 fig. 7), GIRARD (1893b: pl. 1 figs. 5-8), PILSBRY (1905: pl. 56 figs. 4-8), GERMAIN (1916: pl. 8 fig. 15, pl. 11 figs. 6, 10, 11, 13), COSSIGNANI (2014: 195), BREURE ET AL. (2018: 358, fig. 719). Figures of genital anatomy: Fig. 7G, H.

A syntype of *Achatina monticola* Morelet, 1867 is figured by BREURE ET AL. (2018: 358 fig. 719). Although immature, this shell clearly shows axial ribs well developed beneath the suture on the spire but weak or absent in the middle of each whorl. GREEFF (1882: 519) named a strongly ribbed form as *Achatina* (*Subulina*) *costulata* and another with weaker ribs as *Achatina* (*Subulina*) *subcrenata*, the latter being treated as a synonym of *P. monticola* by PILSBRY (1905: 187) and GERMAIN (1908: 62). *Stenogyra costulata* Greeff was retained as a species by CROSSE (1888: 25) and GIRARD (1893a: 33), but it was reduced to *Homorus monticola* var. *costulata* Greeff by GIRARD (1893b: 96) and also treated at varietal rank by PILSBRY (1905: 187) and GERMAIN (1916: 156). GERMAIN (1916: 269-271) named an additional variety as *Bocageia* (*Petriola*) *monticola* Morelet var. *sculptisuturata*, with specimens from "Ribeira Palma, entre 400 et 700 mètres d'altitude, Ribeira Palma,

dans la forêt, entre 500 et 600 mètres d'altitude and Vista Alegre, entre 200 et 300 mètres d'altitude". However, his new variety occurred with typical shells at the first and last of those localities and its characters seem to be similar to those of the syntype we mention above.

Although the type locality of *P. monticola* was in the hills ("ad 2,500 ped. altitudinis" = 762 m: MORELET, 1866: 161) and we have collected it up to 1416 m alt. in low montane forest near Lagoa Amélia (our sample 18-10), we can also confirm reports that it occurs down to near sea-level (0-300 m: GERMAIN, 1916: 270), so the species epithet is not always appropriate. Our own material includes a majority of samples with smooth shells lacking ribs or with them only slightly developed, two samples with strong axial ribs continuous across the whorls, along with others having weak ribs or ribbing only just below the suture. Shells from a wet basalt cliff at ca 6 m alt. near the shore N. of Santa Catarina (sample ST6) have striking strong almost regular axial ribs. The only shells we have found with equally strong (but less regular) ribbing are from the upper altitudinal extreme in sample 18-10 from near Lagoa Amélia and the latter locality, also produced nearly smooth shells from close by along with a few interme-

diates. Dissection of a strongly ribbed adult individual from 18-10 did not disclose any differences in genital anatomy from smooth-shelled individuals from lower altitudes in montane forest. The

lack of any anatomical difference and the occurrence of populations at other localities with ribbing developed to intermediate extents leads us to regard all these forms as conspecific.

### Subfamily PYRGININAE Germain, 1916

#### *Pyrgina* Greeff, 1882 (p. 518)

Type species *Pyrgina umbilicata* Greeff, 1882 by monotypy.

#### *Pyrgina umbilicata* Greeff, 1882

*Pyrgina umbilicata* Greeff, 1882, Zool. Anzeiger, 5, p. 518; TL S. Thomé.

Endemic on São Tomé! Shell figures: (1907: pl. 49 figs. 15, 16), SCHILEYKO (1999: GIRARD (1893b: pl. 1 figs. 19, 20), PILSBRY 503). Genital anatomy: undescribed.

#### *Thomea* Girard, 1893 (1893b: 106)

Type species *Thomea Newtoni* Girard, by monotypy.

#### *Thomea newtoni* Girard, 1893

*Thomea Newtoni* Girard, 1893(b), Jornal Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 107, pl. 1 figs. 16-18; TL "Ile St. Thomé à Bindá, Morro do Gentio, Gumbella (250m alt.), Rio Quija (530m), (F. Newton)."

Endemic on São Tomé! Shell figures: GIRARD (1893b: pl. 1 figs. 16-18), PILSBRY (1907: pl. 49 figs. 17, 18), GERMAIN (1916: pl. 11 figs. 4, 5, 7, 8, 14, 15), SCHILEYKO (1999: 503). Genital anatomy: undescribed.

PILSBRY (1907: 333) and GERMAIN (1916: 302) commented that it might

more justly be ranked as a subgenus of *Pyrgina*, from which it differs only in the narrower axial perforation (umbilicus). ZILCH (1959-1960) followed by GASCOIGNE (1994b: 797) treated *Thomea* as a subgenus of *Pyr-gina*.

### Subfamily OPEATINAE Thiele, 1931

#### *Opeas* Albers, 1850

Die Heliceen, p. 175, type species *Helix goodalli* Miller, 1822 (non A. Férussac, 1821) = *Bulimus pumilus* L. Pfeiffer, 1840, by SD of Martens in Albers (1860, Die Heliceen, ed. 2, p. 265).

#### *Opeas dohrni* (Girard, 1893)

*Opeas Dohrni* Girard, 1893(b), Jornal Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), pp. 105-106, no. 3, pl. 1, fig. 14; TL "Ile du Prince à Ó que S. João a 200 m d'altitude (F. Newton). Ile St. Thomé sur les collines du littoral du Nord-ouest, St. Miguel, Cachoeira (F. Newton)."

Syn. *Opeas Dohrni* Girard var. *conoidea* Germain (1912b: 376); TL Príncipe, “Roça Infante D. Henrique, 100-300 m (leg. L. Fea)”, found along with typical form.

Reported in literature from São Tomé (sur les collines du littoral du Nord-ouest, St. Miguel, Cachoeira: GIRARD, 1893b: 106) and Príncipe (see above). Known else-

where from Annobón (GERMAIN, 1916: 164, 296). Shell figures: GIRARD (1893b: pl. 1 fig. 14), PILSBRY (1906: pl. 15 fig. 63). Genital anatomy: undescribed.

### *Opeas greeffi* (Girard, 1893)

*Opeas Greeffi* Girard, 1893(b), Jornal Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 106, no. 4, pl. 1 fig. 15; TL “Ile du Prince à Ó que S. João a 200 m d’altitude (F. Newton). Ile St. Thomé: Cafini (F. Newton).” *Allopeas greeffi* [sic] is a spelling error in GASCOIGNE (1994a: 2).

Reported in literature from São Tomé (Cafini; Vista Alegre) and Príncipe (see above); we have found it only on Príncipe. Known elsewhere from

Annobón (GERMAIN, 1916: 164, 294). Shell figures: GIRARD (1893b: pl. 1 fig. 15), PILSBRY (1906: pl. 15 figs. 64, 65). Genital anatomy: undescribed.

### *Opeas pauper* (Dohrn, 1866)

*Stenogyra* (*Opeas*) *pauper* Dohrn, 1866(b), Malak. Blätt., 13, p. 126, no. 9, pl. 5 figs. 14-16; TL “Habitat cum praecedente”, i.e., *Buliminus eminulus*, which was “in einem bewaldeten Schlucht” (doubtless on Príncipe judging from the title of the paper but this is not explicitly stated).

Endemic, reported in literature from Príncipe (TL, see above; also by GIRARD, 1893b: 105, no. 2, from “Ô que S. João á 200 m d’alt., F. Newton”; by GERMAIN, 1912b: 340, 376-377, at Roça Infante D. Henrique, 100-300 m alt., leg. L. Fea) and São Tomé (GERMAIN, 1916: 156,

163), where there is one recent record (N0.39561° E6.56686°, in non-forested habitat, 74 m alt., leg. Leonor Tavares, 24 Oct. 2019), 3 sh, CGAH. Shell figures: DOHRN (1866b: pl. 5 figs. 14-16), PILSBRY (1906: pl. 15 fig. 62). Genital anatomy: undescribed.

### *Opeas hannense* (Rang, 1831)

*Helix* (*Cochlicella*) *hannensis* Rang, 1831, Annales Sci. Nat., 24 (93), p. 41, pl. 3, fig. 8; TL “au village de Hann sur la presqu’île du Cap-Verd ...”.

Syn. *Helix goodalli* J.S. Miller, 1822 (non A. Férussac, 1821); *Bulimus clavulus* Turton, 1831; *Bulimus pumilus* L. Pfeiffer, 1840; *Opeas pumilum* (L. Pfeiffer): GASCOIGNE (1994a: 2, 3; 1994b: 798).

WOLLASTON (1878: 510) commented: “After a very careful comparison of the minute *Stenogyra* of the Cape-Verde archipelago, which has been identified by Morelet with the *Helix hannensis*, of Rang, from Cape Verde on the opposite coast of Africa, I have come to the conclusion that it is absolutely identical with the *S. Goodallii*, Mill., - a species

which has been naturalized in various widely-separated countries, probably through the transmission of plants, ... I have several of Mr. Miller’s original types in my possession, ... and which so completely resemble those from the Cape Verdes that I do not think it would be possible (if intermingled) to re-adjust the two sets.” RANG (1831: 41-42) col-

lected his living specimens from a habitat (on C. Vert peninsula, now in Senegal) that was evidently disturbed by man: “au village de Hann ... voisinage des eaux douces, particulièrement de celles que l’on y recueille dans des barriques enfoncées dans la terre”. There is nothing in the original description or figure that does not match *O. goodalli* and Rang himself (p. 42) commented that: “*hannensis* paraît très voisine de l’*H. clavulus* qui est de l’Île-de-France, cependant elle s’en distingue par des caractères suffisants”. Although PILSBRY (1906: 141-142) thought Wollaston’s proposed synonymisation “a question which must remain unsettled until specimens from Rang’s original locality

can be compared”, it has been accepted by VON PROSCHWITZ (1983, 1994) and GROH (2012: 50).

São Tomé! (first recorded from collections by GASCOIGNE, 1994a: 3 from two locations in São Tomé city, det. F. Naggs). Elsewhere, native in tropical C. and S. America, but now widely dispersed by man, e.g. to Cape Verde Is., St. Helena, Rodrigues, Hawaiian Is. (PILSBRY, 1906: 200-201); also reported e.g. from Egypt, Galapagos Is., Samoa; in greenhouses in Europe and U.S.A. Shell figures: PILSBRY (1906: pl. 28 figs. 72-74, as *O. goodalli*), KERNEY & CAMERON (1979: 207, as *O. pumilum*), SCHILEYKO (1999: 493, fig. 631A, as *O. pumilum*). Genital anatomy: undescribed.

### *Opeas subpauper* Germain, 1912

*Opeas subpauper* Germain, 1912(a), Bull. Mus. Hist. nat., Paris, 18 (5), pp. 321-322; TL Île du Prince: Bahia do Oeste, entre 100 et 200 mètres d’altitude (leg. L. Fea).

Endemic on Príncipe, where known only from original material comprising two specimens, one adult and one young (GERMAIN, 1912a;

1912b: 340, 377-379, text figs. 1, 2). Shell figures: GERMAIN (1912b: 378, text figs. 1, 2). Genital anatomy: undescribed.

### *Pseudopeas* S. Putzeys, 1899

#### *Pseudopeas crossei* (Girard, 1893)

*Opeas Crossei* Girard, 1893(b), Jornal Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 105, pl. 1, fig. 13; TL Príncipe “Ô que S. João à une altitude de 200 m.”

New to São Tomé: 10 Dec. 2018, on path between Bom Sucesso and Macambrará, near Rio Manuel Jorge, N0.28571° E6.60912°, 1114 m alt., horticulture areas with bananas, groves of scrub & trees alongside track, GAH 18-23, 1 sh (live-collected), resembling our material from Príncipe comprised of six

shells from two localities in native forest. A species previously known from Príncipe (GIRARD, 1893b: 105, pl. 1, fig. 13; 1894: 201; PILSBRY, 1906: 115, pl. 15, figs. 60, 61; GERMAIN, 1912b: 340; 1916: 167) and also reported from Bioko (GASCOIGNE, 1994a: 2, 5; WRONSKI *ET AL.*, 2014: 164, Table 1).

### Subfamily THYROPHORELLINAE Girard, 1895

#### *Thyrophorella* Greeff, 1882 (p. 517)

Type species *T. thomensis* Greeff, 1882 by monotypy.

*Thyrophorella thomensis* Greeff, 1882 (Fig. 12E)

*Thyrophorella thomensis* Greeff, 1882, Zool. Anzeiger, 5, p. 517; TL S. Thomé auf der Roça do Monte Café 800-900 m über dem Meere, am rande eines hier sich erhebenden und in das höhere Gebirge übergehenden Urwaldes.

Endemic on São Tomé! Shell figures: GIRARD (1895: pl. figs. 2-5), SCHILEYKO (2001: 928 fig. 1215), COSSIGNANI (2014: 194, figures of three shells). Fig. of genital anatomy: GIRARD (1895: pl. fig. 8).

*Thyrophorella* was until recently treated in the monotypic family Thyrophorellidae, endemic on São Tomé. It attracted special interest from the time of its discovery because of the presence in a land-snail of an unusual discoid-planorboid shell shape reminiscent in outline of that of the aquatic *Segmentina nitida* (O.F. Müller, 1774) (Planorbidae), but sinistral and composed of fewer whorls, in combination with a unique stiff flap of periostracum hinged to the dorsal half of the peristome (Fig. 12E) that functions to close the shell aperture when the body is withdrawn in the same manner as the operculum of a caenogastropod. CROSSE (1888: 29) expressed grave doubts about the position of this taxon, even questioning its placement as a mollusc. However, GIRARD (1895) confirmed its position as a pulmonate mollusc with descriptions of the radula and genital anatomy, the latter apparently being generally similar to Helicarionoidea. Subsequently, FONTANILLA *et al.* (2017) have confirmed an earlier molecular study showing the closest affinity of *Thyrophorella* is with *Pyrgina umbilicata*, also endemic on São Tomé, thus establishing the position of both within the Achatinidae *sensu lato*. It is nonetheless radically different in shell shape from *Pyrgina*, which has a turricu-

late shell of about 13 very narrow whorls, conical towards the apex, the remaining part cylindrical.

Other than the original reports by Dohrn indicating occurrence in montane rainforest, the literature has hitherto given no indication of the micro-habitat of *Thyrophorella*, so it has been unclear exactly where and how to look for it. MP found one live subadult individual on her clothing on 16 Jan. 2017 while working inside montane rainforest at Morro Claudina above Bom Sucesso. The first time we saw it *in situ* was again at Morro Claudina, on 27 Nov. 2018, inside closed montane rainforest at ca 1267 m alt. (N0.29048° E6.60530°). Individual snails were found there by GAH at 50 cm above the ground on leaves of a fern and 80 cm up on those of a large herb, in rather heavy shade in a humid hollow, where large leaves of understory plants supported plenty of tiny epiphyllous liverworts (two samples of these were identified later as *Cololejeunea cuneifolia* Steph.). Several more of the snails were found in the same area on leaves of other plants in the forest understory. The *Thyrophorella* held their shells against the leaf surfaces with the flattened basal part of the shell against the underside of a leaf, sometimes in a thin meniscus of water. During fieldwork in 2019 Leonor Tavares and RFL also found it near Ribeira Peixe in the south of the island at much lower elevations, both in the forest (Monte Carmo), and in the oil palm monoculture (EMOLVE).

MICRACTAEONIDAE Schileyko, 1999

*Micractaeon* Verdcourt, 1993

*Micractaeon koptawelilensis* (Germain, 1934)

*Pseudopeas koptawelilensis* Germain, 1934, Bull. Mus. Natn. Hist. Nat., Paris, (2) 6, p. 380; TL Kenya, "Mount Elgon, vallée de la Koptawelil, à 2.300 mètres d'altitude, au nord de la rivière Koitoboss". VAN BRUGGEN & DE WINTER (1995: 80) pointed out that the correct orthography of the name would be *Pseudopeas koptawelilense*.

New to São Tomé: 24 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.2900° E6.6055°, 1257 m alt., montane rainforest (sieving from shelly debris at thrush anvil), GAH, DTH *et al.* 18-2C, 5 sh; 27 Nov. 2018, Morro Claudina, N0.28909° E6.60442°, ca 1290 m alt., montane forest with understorey (sieving from shelly debris at thrush anvil), GAH & DTH 18-6A, 5 sh; ditto, N0.29181° E6.60592°, 1288 m alt., floor of montane forest near tiny clearing (sieved from shelly debris at thrush anvil among buttress roots of tree), sample 18-6C, 3 sh; ditto, N0.29036° E6.60537°, 1254 m alt., floor of rather open montane forest with some alien trees (sieving from shelly debris at thrush anvil), sample 18-6D, 2 sh; ditto, N0.29011° E6.60537°, 1255 m alt., floor of

montane forest with some alien trees, near edge of recent clearing (sieved from shelly debris at thrush anvil), sample 18-6E, 2 sh; 28 Nov. 2018, Cascata de São Nicolau, N0.2857° E6.6257°, 885 m alt., around waterfall on steep rocky slopes with secondary forest, GAH, DTH *et al.* 18-7, 1 sh.

VAN BRUGGEN & DE WINTER (1995) provided good illustrations and revised the nomenclature, taxonomy and distributional data on this species, showing that it has a wide range in tropical Africa from Ghana and Cameroon south-eastwards to western Kenya, south-eastern Zaïre and Malawi. Although recorded from Bioko (WRONSKI *ET AL.*, 2014: 164, Table 1) there were no records hitherto from oceanic islands offshore of Africa.

#### STREPTAXIDAE J.E. Gray, 1860

##### Subfamily ENNEINAE Bourguignat, 1883

##### *Gulella* L. Pfeiffer, 1856

##### *Gulella azeitonae* n. sp. D. Holyoak, G. Holyoak & F. Sinclair (Fig. 3B)

**Type material:** Described only from the unique holotype, NHMUK 20200235, sh & (incomplete) bod, collected 3 May 2019, by A. Pedronho & R. Fernandes, 2019-05-03-02.

**Type locality:** Príncipe Island, Floresta de Azeitona, N1.64968° E7.39879°, 194 m alt., tall secondary forest.

**Etymology:** The species epithet *azeitonae* is based on the type-locality in the Floresta de Azeitona.

**Description:** Shell dextral, H 2.90 mm, B 1.74 mm, H/B 1.66; AH 0.73 mm, AB 0.67 mm, AH/AB 1.09; whorls 6.9. Other measurements (from the same positions as those used by DE WINTER & VASTENHOUT, 2013: 608 fig. 1): body-whorl height 1.46 mm, peristome height 0.93 mm, peristome width 0.91 mm, width across five successive rib-intervals and six ribs (RD) in middle of penultimate-whorl 1.46 mm). Shell shape biconical, with apex somewhat rounded and base of shell broadly rounded. Whorls increasing gradually in width and descending gradually up to start of body-whorl; most of body-whorl narrower than penultimate-whorl and not descending. Whorls of spire rounded in profile; suture moderately deep. Body-whorl somewhat constricted

behind aperture. Middle of exterior of last half of body-whorl with prominent external groove just below mid-height that disappears towards aperture. Aperture asymmetrically heart-shaped, with broadly rounded base, rounded sinus around parietal-upper palatal junction and somewhat straighter columellar and parietal margins. Peristome continuous, reflected on palatal and columellar sides of aperture, not reflected on parietal side; section above parietal lamella with flap raised away from aperture beyond line of rest of peristome. Two apertural barriers clearly visible: a long low parietal lamella with serrated crest running into aperture from line of peristome, and a rounded mid-palatal projection inwards of the unthickened peristome corresponding to external hollow. Exter-

nal groove on body-whorl apparently corresponding to deep-set mid-palatal lamella (dry body prevents clear view from aperture). Protoconch and start of teleoconch (up to whorl 2.5) almost smooth, with granular or somewhat decussate microsculpture (lacking clear spiral elements). Rest of teleoconch with strong sculpture of rather evenly spaced axial ribs (*ca* 30 counted around underside of body-whorl), the ribs nearly straight to slightly curved, mainly with slight transverse orientation. Interstices between ribs smooth (no trace of spiral microsculpture). Protoconch, early whorls of teleoconch, peristome and interior of aperture whitish; rest of teleoconch pale brownish. Shell not thick, slightly translucent; somewhat glossy, especially on crests of axial ribs.

Exterior of body (described from visible parts pulled from specimen that had been drowned in water then kept in 80% ethanol for four months): sole of foot white; exterior of body orange; eyespot in upper tentacle black; dorsum of mantle from inside shell orange. Genital anatomy unknown; preserved foreparts of body may contain the radula but they are too incomplete for study of the genitalia.

*Discussion:* The new species differs strikingly from the three species of *Gulella* hitherto known from Príncipe (*G. crystallum* Morelet, 1848, see BREURE *ET AL.*, 2018: 262 fig. 305 for syntype; *G. sorghum* Morelet, 1848, see BREURE *ET AL.*, 2018: 435 fig. 1064 for syntype; *G. joubini* (Germain, 1912), see SCHILEYKO, 2000: 812 fig. 1062 for shell figure) in possessing strong axial ribs on the shell and in the number or position of its apertural barriers.

Unlike the three *Gulella* species already known from Príncipe, *G. azeitonae* n. sp. somewhat resembles the

segregate genera *Avakubia* Pilsbry, 1919 and *Pseudavakubia* de Winter & Vastenhout, 2013, in its combination of small shell size, biconical shell profile, strong axial ribs, few apertural barriers, as well as having a range in west or tropical Africa. However, comparisons of the unique holotype with the detailed monograph of those genera by DE WINTER & VASTENHOUT (2013) reveal numerous differences: it lacks spiral sculpture on the protoconch and in the interstices between ribs on the teleoconch; the body-whorl narrows towards the aperture; the back of the body-whorl has an external groove; the visible part of the parietal lamella has a serrated rather than smooth edge; the peristome has a prominent flap projecting outwards over the aperture; the umbilicus is closed (as in *Pseudavakubia*, but unlike *Avakubia*; but differing from *Pseudavakubia* and resembling *Avakubia* more in the regular increase of early whorls of the spire). Because of these differences, we prefer to place the new species in *Gulella*, since this remains a “catch-all” genus containing disparate elements. Much more study of this largest of African land-snail genera is needed to resolve its internal relationships and to place the four apparently endemic Príncipe species in a wider context, although ROWSON & HERBERT (2016) have made a valuable start.

The shell of *G. azeitonae* also resembles some species of *Ptychotrema* L. Pfeiffer, 1853 in overall shape and the form of the parietal tooth and its affinities might be with that genus rather than *Gulella*. SCHILEYKO (2000: 823-826) recognised six subgenera within *Ptychotrema*, five of which are represented in west or central Africa with three of them on Bioko; its numerous nominal species are in need of a modern revision.

### *Gulella crystallum* (Morelet, 1848)

*Pupa crystallum* Morelet, 1848, Rev. Zool., 11, p. 354; TL in insula Principis sinus Guineensis; 8 syntypes at NHMUK & 4 syntypes at MNHN (BREURE *ET AL.*, 2018: 261-262, fig. 305).  
Syn. *Pupa hyalina* L. Pfeiffer, 1849, Zeitschr. Malak., 1849, p. 52.

Endemic to Príncipe! Shell figures: MORELET (1858: pl. 3, fig. 3), TRYON (1885: pl. 18 fig. 50), GERMAIN (1912b: pl. 4 figs. 7, 8), BREURE *ET AL.* (2018: 261-262, fig. 305). Genital anatomy: undescribed.

COSSIGNANI (2014: 194) figured three similar shells as “*Ennea joubini*

(Germain, 1923), São Tomé, 7 mm”. These appear to be of misidentified *G. crystallum*, otherwise known only as an endemic on Príncipe, so an error of both identification and locality was likely to have been involved.

### *Gulella joubini* (Germain, 1912)

*Ennea (Sphinctostrema) Joubini* Germain, 1912(a), Bull. Mus. Hist. Nat., Paris, 18 (5), pp. 318-319; TL Île du Prince; Roça Infante D. Henrique, entre 100 et 300 mètres d’altitude (leg. L. Fea, based on single shell).

Reliably reported only as endemic to Príncipe and apparently known only from the holotype. See note under preceding species regarding shells figured by COSSIGNANI (2014: 194-195) as *Ennea joubini* supposedly from São Tomé. Shell

figures: GERMAIN (1912b: pl. 4 figs. 13-15), SCHILEYKO (2000: 812, fig. 1062). Genital anatomy: undescribed.

Listing of *Ennea Bocagei* by GERMAIN (1916: 161) in a table was apparently an error for *E. Joubini*.

### *Gulella sorghum* (Morelet, 1848)

*Pupa sorghum* Morelet, 1848, Rev. Zool., 11, p. 354; TL in insulam Principis. One syntype at NHMUK (BREURE *ET AL.*, 2018: 434-435, fig. 1064).

Endemic to Príncipe! Shell figures: MORELET (1858: pl. 3, fig. 10); BREURE *ET*

*AL.* (2018: 435, fig. 1064). Genital anatomy: undescribed.

### *Streptostele* Dohrn, 1866(b)

Malak. Blätt., 13, pp. 128-129.

DOHRN (1866b: 128-133) treated three species that had formerly been placed in the genus *Bulimus* in his new genus *Streptostele*, successively as *S. lotophaga*, *S. fastigiata* and *S. folini*, but did not designate a type species. He stated that he had not seen *Bulimus lotophagus*, which he did not describe, whereas he gave detailed descriptions of the other two species and his description of the new genus *Streptostele* was clearly based on those and not on *B. lotophagus*. In a publication that has been widely overlooked, NEVILL (1878: 8) stated “Genus *Streptostele*, Dohrn (type *S. lotophaga*)”, so the genus was unambiguously typified by subsequent designation, albeit with the species corresponding least

well to the protologue. GIRARD (1893b: 102) was evidently unaware of Nevill’s publication when he cited several authors who had pointed out that *B. lotophagus* was only distantly related to *S. fastigiata* and *S. folini*, leading to his comment: “le *Bulimus lotophagus* ne peut être considéré comme le type du genre *Streptostele*.” Hence, GIRARD (1893b: 100) introduced the new genus *Bocageia* with *B. lotophaga* as its type (by monotypy), but he did not fix the type of *Streptostele*. As a result of Nevill’s earlier publication, *Bocageia* would become a junior objective synonym of *Streptostele*. Subsequently, C.F. ANCEY (in VIGNON, 1888: 68 footnote) again designated *Bulimus lotophagus* Morelet, 1848 as type species

of *Streptostele*, without any explanation, apparently unaware of the previously published works by both Nevill and Girard. PILSBRY (1919: 181 footnote) also wrote in apparent ignorance of both those works when he stated: "I am not accepting Ancey's name-juggling because it appears to me that he erred in selecting as type of Dohrn's group a species which that author expressly states that he had not seen, and which disagrees in conspicuous and essential characters with Dohrn's diagnosis. PILSBRY (1919) thereby established what has become contemporary usage (e.g. SCHILEYKO, 2000: 802-806) in regarding the first valid fixation of the type species of *Streptostele* as being that by E.A. SMITH (1890: 96) who selected *Bulimus fastigia-*

*tus* Morelet, 1848, but he clearly overlooked the earlier valid designation by NEVILL (1878: 8).

Since the genus *Streptostele* is well known and in current use for numerous species it would be confusing to restrict its use to *Bulimus lotophagus*, an endemic on Príncipe, currently placed in a different family (Achatinidae). Hence, the ICZN should be asked to set aside the earlier typifications of *Streptostele* by NEVILL (1878: 8) and C.F. ANCEY (in VIGNON, 1888: 68 footnote) in favour of the later but widely adopted designation by E.A. SMITH (1890: 96) of *Bulimus fastigiatus* Morelet, 1848. We therefore maintain currently accepted usage of the genera *Streptostele* and *Bocageia* here, pending a decision by the ICZN.

*Streptostele abbreviata* n. sp. D. Holyoak, G. Holyoak & F. Sinclair (Figs. 4A, 8A-C)

**Type material:** Described only from the unique holotype, NHMUK 20200236, sh & bod, collected 3 July 2019, by FS, A. Pedronho & A. Andrade, site 2019-07-03-01.

**Type locality:** Príncipe Island, saddle beneath Pico Mesa, N1.58151° E7.35421°, 414 m alt., mid-elevation native forest on exposed ridge.

**Etymology:** The generic name *Streptostele* has been treated as a feminine noun. The species epithet is from *abbreviatus* (Latin, meaning shortened), because its shell shape is much shorter than in the allied *S. fastigiata* (Morelet, 1848).

**Description:** Shell H 12.29 mm, B 5.89 mm, H/B 0.46; AH 4.87 mm, AB 2.84 mm, AH/AB 1.71; maximum height of body-whorl (in apertural view) 7.7 mm (60.2% of H). Shell dextral, with 5.7 whorls; outline narrowly-ovate with conical spire. Upper whorls rounded, body whorl with flatter outline; suture moderately deep. Aperture with rounded base, columellar and palatal margins almost parallel and both approximately straight, long almost straight parietal margin and rounded sinus near junction of palatal and parietal regions. Peristome slightly thickened, reflected on lower-palatal and columellar margins; a thin callus extending from reflected columellar lip across parietal area. Umbilicus lacking. Protoconch small and rounded with spiral microsculpture that continues onto third whorl (teleoconch) where longitudinal riblets begin. Rest of teleoconch with strong low longitudinal

ribs; also faint traces of spiral microsculpture on parts of body-whorl. Shell thin, somewhat translucent, moderately glossy; pale cream, shading to whitish on peristome and base of body-whorl.

Body (and anatomy) were described from specimen drowned in water then preserved in 80% ethanol before being pulled from shell about three weeks later. This body was partly contracted, with head withdrawn under mantle-collar. During dissection coloration was noted: skin on external foreparts and front of flanks white, tail-tip white and back of sole of foot white. The mantle-collar and surface of mantle inside shell were also mainly white, but a wide band across front half of dorsum of mantle was bright yellow. Two other small areas on dorsum of mantle (corresponding to position of retracted upper tentacles inside the body-wall) each formed a yellow streak con-

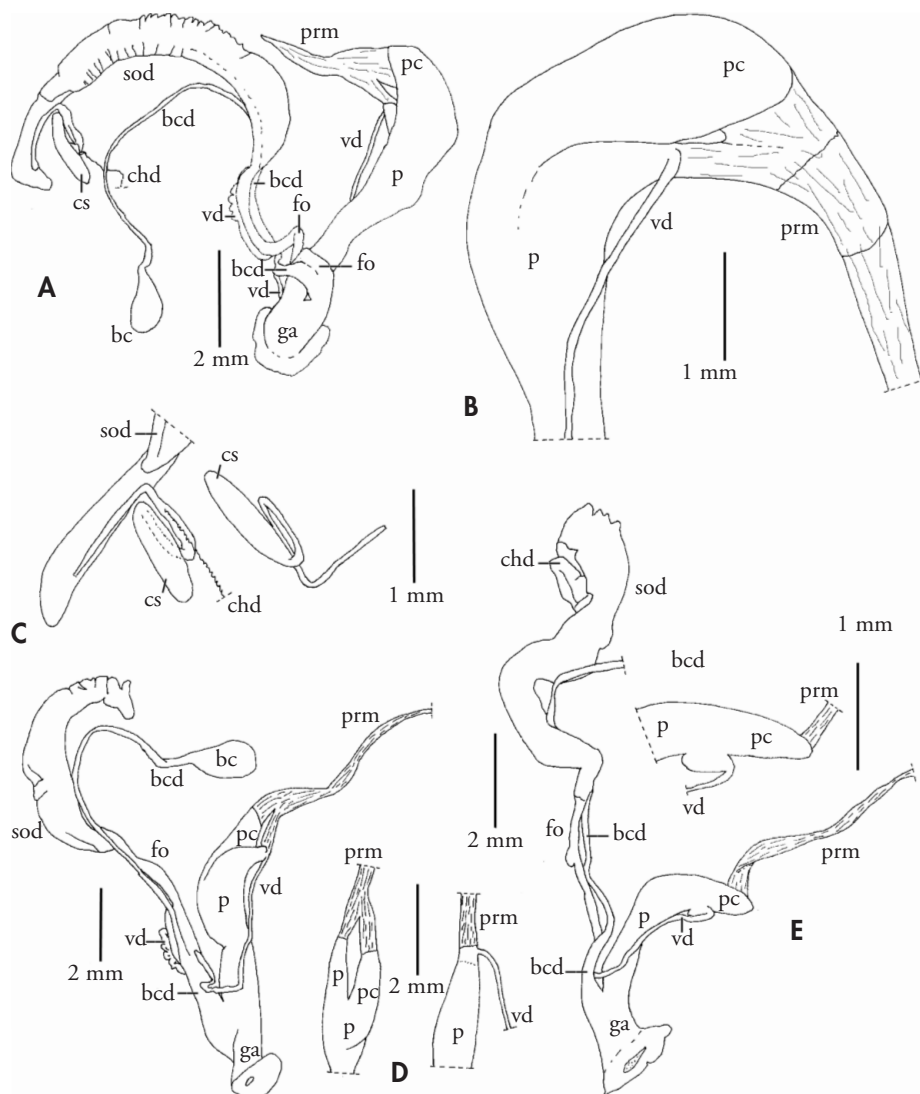


Figure 8. Genital anatomy of *Streptostele* from Príncipe. A-C: *S. abbreviata* n. sp. (holotype); A: distal genitalia; B: different view of penis; C: details of “cylindrical sac” and associated structures; D: *S. fastigiata* (path to Santa Joaquina, N1.6157° E7.3976°, 216 m alt., tall native forest, 4 Dec. 2018, GAH, DTH & FS 18-12), distal genitalia and two different views of penis of same snail, rotated; E: *S. folini* (just S of Santo Antonio on road to Bela Vista, N1.6300° E7.4177°, ca 24 m alt., cultivation & edges of secondary forest, 4 Dec. 2018, GAH 18-14), distal genitalia and different view of proximal end of penis of same snail.

Figura 8. Anatomía genital de *Streptostele* de Príncipe. A-C: *S. abbreviata* n. sp. (holotipo); A: genitalia distal; B: vista diferente del pene; C: detalles del “saco cilíndrico” y de las estructuras asociadas; D: *S. fastigiata* (camino a Santa Joaquina, N1,6157° E7,3976°, 216 m alt., bosque nativo alto, 4 dic. 2018, GAH, DTH y FS 18-12), genitalia distal y dos vistas diferentes del pene del mismo caracol, girado; E: *S. folini* (justo al S de Santo Antonio en el camino a Bela Vista, N1,6300° E7,4177°, aprox. 24 m alt., cultivo y bordes de bosque secundario, 4 dic. 2018, GAH 18-14), genitalia distal y otra vista del extremo proximal del pene del mismo caracol.

taining a small black eye-spot. Upper three whorls of spire containing digestive gland, pale brown with weak network pattern of thin darker lines (in intricate pattern suggestive of alveoli of mammalian lungs).

As in dissections of the congeners *S. fastigiata* and *S. folini* (Morelet, 1848), the interior of the front of the body was dominated by a very large muscular buccal mass continuing proximally as a large and muscular-walled oesophagus. The distal genitalia were small compared to the digestive organs, with the female tract conspicuously more slender than the male tract.

Genital pore on right flank of forepart of body. Genital atrium a short and rather wide cylinder, dividing proximally into distal penis and distal vagina. Penis a large, long organ, muscular inside a firm sheath, widening proximally to give clavate, curved outline. Proximal part of penis forked (Fig. 8A, B), to give larger penial caecum and smaller, shorter proximal penis, each with a separate retractor muscle arising apically before the muscles fuse into a flat fan of muscle which becomes narrower as it continues proximally as the combined penial retractor muscle to join other muscles along columellar axis of the body in mid-spire. Epiphallus and flagellum lacking. Vas deferens a thin tube, starting near distal end of spermoviduct, passing distally alongside free oviduct into the angle formed with distal part of penis, then passing proximally alongside penis, without entering penis sheath until it does so almost at tip of proximal penis (adjacent to insertion of its retractor muscle). Vagina very short, its precise point of separation from distal end of duct of bursa copulatrix unclear since both organs thin-walled, flattened *in situ*, bound side by side with connective tissue and too delicate to separate. Distal part of free oviduct narrow, convoluted into several folds, a thin-walled (translucent), flattened tube about half as long as penis overall. Duct of bursa copulatrix rather wide but thin-walled and flattened in distal part alongside free oviduct; its proximal part a very thin long tube, when *in situ* following course proximally along distal half of spermoviduct,

then diverging widely to cross externally over the oesophagus, returning back over it further proximally, with bursa reservoir lying partly on spermoviduct. Reservoir oval, tapering into duct, thin-walled. Spermoviduct long, flattened tapering at proximal end without passing into a clearly defined albumen gland. Peculiar cylindrical sac *ca* 1.5 mm long (Fig. 8A, C) resting against proximal end of spermoviduct is whitish, opaque and firm-walled, connected by folded duct that becomes thin as far as it could be traced proximally; the duct with a distinct thin strand passing proximally that may represent retractor muscle. Function and hence terminology of the sac unclear: possibly a very long talon, possibly a seminal vesicle.

*Comments:* The two large endemic species of *Streptostele* hitherto known from Príncipe both have elongate, very narrowly conical shells, *S. fastigiata* being conspicuously larger (H 14-29, mostly 18-19 mm, B 6-7 mm: MORELET, 1848: 352-353, 1858), *S. folini* usually smaller and always narrower (H 17 mm, B 5 mm: MORELET, 1858: 16-17; H 16 mm, B 4.5 mm: DOHRN, 1866b: 131). BREURE *ET AL.* (2018: 284 fig. 399, 287 fig. 415) provided good illustrations of Morelet's syntypes of both species. In our experience, the narrower apical whorls of *S. folini* allow immature as well as adult individuals to be separated easily by direct comparisons. *S. abbreviata* n. sp. differs from both in having a much shorter shell when adult (holotype H 12.29 mm, B 5.89 mm) with a narrowly-ovate rather than very narrowly conical outline; the mature holotype has 5.7 whorls compared to 8-10 whorls in mature individuals of the other species; its body whorl forms 60% of shell height, compared to much less than 50% in the other species. Indeed, it differs from them so conspicuously in shape that our first impressions suggested it might be a white-shelled specimen of Cerastidae.

Our field collections show that both *S. fastigiata* (11 sites) and *S. folini* (7 sites) are widespread in wooded habitats on the island, with both recorded from

plantations, secondary-forest and native forests, often living together in ground-litter. Whereas *S. fastigiata* had a wide altitudinal range recorded (24-860 m) including low mossy forest in the mountains, *S. folini* was found only at 24-194 m. The only record for *S. abbreviata* was from 414 m alt., in mid-elevation native forest on an exposed ridge. Body coloration in living individuals of *S. fastigiata* and *S. folini* is conspicuously pink to almost orange, as in the other common streptaxid, *Gulella crystallum* (Morelet, 1848), which commonly coexists with both of these *Streptostele* species. The body colour of living *S. abbreviata* remains to be confirmed, since pink and orange colours of the other streptaxids disappear quickly after preservation in alcohol.

Dissections of specimens of *Streptostele fastigiata* from Príncipe (two snails from different populations), *S. folini* (one) and *S. abbreviata* n. sp. (holotype) showed they have generally similar genital anatomy (Fig. 8), so they may represent an endemic radiation on Príncipe island. Taking account of different degrees of maturity among the

specimens dissected, the main anatomical difference among these species is that *S. folini* has the penial retractor muscle undivided at its distal end and attached only to the proximal end of its penial caecum (Fig. 8E), whereas *S. fastigiata* (Fig. 8D) and *S. abbreviata* (Fig. 8A, B) have a divided distal end to the penial retractor consisting of a larger portion attached to the penial caecum and a smaller portion attached to the apex of the penis itself (close to the insertion of the vas deferens). The difference in the retractor muscle is rather clearly associated with the smaller size of the free part of the proximal penis in *S. folini* than in the other two species. If in future separate generic (or sub-generic) rank is thought useful for *S. folini*, it is the type species by monotypy of *Campylaxis* Ancey in Vignon, 1888 (March), Bull. Soc. Malac. France, 5, p. 68 footnote. ANCEY (IN VIGNON, 1888: 68) wrote "Ancey 1885" for his new name, but apparently in error since although ANCEY, 1885: 143-144 discussed *Streptostele*, including *folini*, and named the new genus *Tomostele*, he did not use the name *Campylaxis*.

### *Streptostele fastigiata* (Morelet, 1848) (Fig. 8D)

*Bulimus fastigiatus* Morelet, 1848, Rev. Zool., 11, pp. 352-353; TL insulam Principis; 3 syntypes at NHMUK (BREURE *ET AL.*, 2018: 284, fig. 399).

Endemic on Príncipe! Shell figures: MORELET (1858: pl. 1, fig. 8), PFEIFFER (1867-1869: Bd 3, pl. 76, figs. 6, 7), TRYON (1885: pl. 20, fig. 74), SCHILEYKO (2000: 805, fig. 1050A), BREURE *ET AL.* (2018: 284, fig. 399). Fig. of genital anatomy: Fig. 8D (see account of *S. abbreviata* above for comments on genital anatomy of *S. fastigiata*). HEYNE-MANN (1869, Nachr. d. Malak.

Ges., p. 178, taf. I, fig. 5) figured radula.

COSSIGNANI (2014: 195) figured a shell as *Streptostele fastigiata* with locality as São Tomé, but apparently as an error of locality. GERMAIN (1916: 161) listed *Streptostele Buchholzi* Martens, 1876 for Cameroun, Fernando Poo [Bioko] and Príncipe in a table, the last apparently in error since it is not mentioned elsewhere.

### *Streptostele* (?) *feai* Germain, 1912

*Streptostele Feai* Germain, 1912(a), Bull. Mus. Hist. nat. Paris, 18 (5), pp. 319-320, fig. 60; TL Ilha do Príncipe; Roça Infante D. Henrique, entre 100 et 300 mètres d'altitude (leg. L. Fea, quelques exemplaires). GERMAIN (1912b: 350-351) repeated the description, adding a comparison with "S. Moreleti Dohrn."

Endemic on Príncipe and apparently known only from the original specimens. Shell figures: GERMAIN (1912a: 320 fig. 60; 1912b: pl. 4 figs. 11, 12).

Genital anatomy: undescribed. This is a distinctive species with a small shell (H 6½, B 1¾ mm) that may not belong in the genus *Streptostele* s.s.

### *Streptostele folini* (Morelet, 1858) (Fig. 8E)

*Bulimus folini* Morelet, 1858, *Séries Conchyliologiques*, livr. 1, pp. 16-17, no. 14, pl. 1, fig. 5; TL l'île du Prince; 2 syntypes at NHMUK (BREURE ET AL., 2018: 287, fig. 416).

Syn. ? *Bulimus fastigiatus* Pfr. var. *minor*: Dohrn (1866b: 131); *Streptostele Folinii* [sic], Morelet: GIRARD (1893a: 33), orthographic error.

Príncipe! where apparently endemic. Although *S. folini* was listed by GERMAIN (1916: 161) for São Tomé in a table, it was perhaps in error for *S. Moreleti* [sic] which was listed on the following line. Shell figures: MORELET (1858: pl. 1, fig.

5), PFEIFFER (1867-1869: Bd. 3, pl. 76, figs. 8, 9), TRYON (1885: pl. 20, figs. 72, 73), BREURE ET AL. (2018: 287, fig. 416). Fig. of genital anatomy: Fig. 8E (see account of *S. abbreviata* above for comments on genital anatomy of *S. folini*).

### *Streptostele* (?) *moreletiana* (Dohrn, 1866)

*Streptostele moreletiana* Dohrn, 1866(b), *Malak. Blätt.*, 13, p. 132, pl. 5, figs. 17-19; TL stated only as "mit der vorigen Art zusammen" (i.e. with *Streptostele folini*, p. 131, which was "auf der Pflanzung Azeitona", i.e. Azeitona Plantation, on Príncipe). *Streptostele Moreleti* [sic] Dohrn: GERMAIN (1912b: 339, 340) is an incorrect subsequent spelling.

Endemic species, reported in literature from both São Tomé (GIRARD, 1893b: 99, who commented "Les recherches de M. Newton me permettent d'inscrire ce genre intéressant dans la faune de St. Thomé. Les individus de cette île ne diffèrent en rien de ceux du Prince"; GASCOIGNE, 1994a: 2, 1994b: 796) and Príncipe (TL, see above; GIRARD, 1893b: 99; also reported "Ó que

S. João à 200m d'alt., F. Newton"). Shell figures: DOHRN (1866b: pl. 5, figs. 17-19). Genital anatomy: undescribed. GIRARD (1893b: pl. 1 fig 9) figured the radula.

SCHILEYKO (2000: 802-806) recognised six subgenera in *Streptostele*, but the allocation of the present species is uncertain. Like *S. feai*, it has a small shell (H 6½, B 1¾ mm) and it may not belong in the genus *Streptostele* s.s.

### *Tomostele* Ancey, 1885

*Tomostele* Ancey (ANCEY, 1885: 143) has *Achatina musaecola* Morelet, 1860 as type by original designation (albeit misspelled as *Achatina muscola* [sic] as it was by PFEIFFER, 1868, *Mon. Helic. viv.*, 6: 239). We treat *Tomostele* at generic rank rather than as a subgenus of *Streptostele* because it is a much smaller shell, differing from the Príncipe taxa also in having the base of the columella markedly truncate; its genital anatomy has apparently not

been described. We adopt the generic name *Tomostele* here for *T. musaecola*, but leave it to others to seek appropriate generic placements for numerous other species from the African mainland and Malagasy region currently lumped together in *Streptostele*. This task is perhaps best left until anatomical or molecular data is obtained for them, since placements based on shell characters alone seem unlikely to be reliable.

*Tomostele musaecola* (Morelet, 1860)

*Achatina musaecola* Morelet, 1860, J. Conchyl., 8, p. 190; TL “Guineam”. BREURE, AUDIBERT & ABLETT (2018: 361) figured one of three syntypes in NHMUK and its label in Morelet’s handwriting giving the locality as “Gabon”, so we herewith restrict the type-locality to Gabon.

New to São Tomé: 6 Dec. 2013, S. of EN2 and ca 0.4 km W. of Vila Aida, N0.0897° E6.5903°, ca 181 m alt., tall forest on ridge & slopes with understorey of saplings, GAH ST7, 1 sh (live-collected); 11 Dec. 2013, by EN2 ca 1.2 km N. of Monte Mário “roça”, N0.0694° E6.5522°, ca 101 m alt., roadside bank with ferns & herbs at foot of slope with secondary forest, GAH & DTH ST11, 1 sh (live-collected).

HAUSDORF & BERMÚDEZ (2003) found that *Luntia insignis* E.A. Smith, 1898 from the Caribbean island of Trinidad was a synonym of *Streptostele* (*Tomostele*) *musaecola* (Morelet, 1860). It

had been widely reported under the name *L. insignis* as an introduction in tropical and subtropical America (Bermuda, Nicaragua to Colombia, Lesser Antilles, Guyana, Surinam). GERBER & CLARK (2015) reported the first record of *S. musaecola* becoming established in the continental U.S.A. (from Florida) and also cited published reports of it from Melanesia (Vanuatu, Fijian Is., American Samoa) and Polynesia (Cook Is., Society Is.). COWIE (1998) cited an unpublished report by Miller that this carnivorous alien species might have been implicated in the extinction of a native species in American Samoa.

PUNCTIDAE Morse, 1864

*Punctum* Morse, 1864

*Punctum camerunense* de Winter, 2017

*Punctum camerunense* de Winter, 2017, Arch. Molluskenk., 146, pp. 204-206, fig. 1A-I, table 1; TL Cameroon, South West Region, ca 7 km SW. of Buea; undisturbed cloud forest; 04°08'N., 009°11'E; 1300-1400 m a.s.l.

New to São Tomé: 27 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.28909° E6.60442°, ca 1290 m alt., floor of montane forest with understorey (sieved from shelly debris at thrush anvil), GAH & DTH 18-6A, 5 sh; ditto, N0.2890° E6.6044°, sieved from ground-litter on floor of montane forest, sample 18-6B, 2 sh; ditto, N0.29181° E6.60592°, 1288 m alt., floor of montane forest near tiny clearing (sieved from shelly debris at thrush anvil among buttress roots of tree), sample 18-6C, 1 sh; ditto, N0.29011° E6.60537°, 1255 m alt., floor of montane forest with some alien trees,

near edge of recent clearing (sieved from shelly debris at thrush anvil), sample 18-6E, 1 sh; 9 Dec. 2018, path from above Bom Sucesso Botanical Garden towards Lagoa Amélia, ca N0.2823° E6.5964°, 1290-1415 m alt., montane forest (sieved), GAH & DTH 18-21, 2 sh.

DE WINTER (2017) described this species from four shells found at two adjacent localities in the Mount Cameroon complex (South West Region, Cameroon), in forest at 1300-1400 m alt. and it has not hitherto been reported elsewhere.

CHAROPIDAE Hutton, 1884

Subfamily CHAROPINAE

*Trachycystis* Pilsbry, 1893

*Trachycystis iredalei* Preston, 1912

*Trachycystis iredalei* Preston, 1912, Proc. Zool. Soc. London, 1912, pp. 187-188, pl. 32 fig. 8; TL Between the Igembi Hills and Nyeri, British East Africa.

New to São Tomé: 24 Nov. 2018, São Tomé Island, Morro Claudina (near Bom Sucesso), N0.2900° E6.6055°, 1257 m alt., on ground in montane rainforest (sieved from shelly debris of thrush anvil), DTH, GAH, *et al.* 18-2C, 1 sh; 27 Nov. 2018, Morro Claudina, N0.29181° E6.60592°, 1288 m alt., on ground among buttress-roots of tree near tiny clearing in montane rainforest (sieved from shelly debris of thrush anvil), GAH & DTH 18-6C, 1 sh.

*Description:* Site 18-2C, shell: H 0.78 mm, B 1.77 mm, H/B 0.44; AH >0.56 mm, AB >0.64 mm; UB 0.66 mm, UB/B 37.4%, 3.1 whorls. Site 18-6C, shell: H 0.74 mm, B 1.60 mm, H/B 0.46; AH 0.56 mm, AB 0.54 mm, AH/AB 1.04; UB 0.53 mm, UB/B 32.9%, 2.9 whorls. Although the 18-6C shell is smaller than the one from 18-2C, it has a fully formed peristome and may represent an adult; it is a fresh shell with intact peristome. The 18-2C shell has much of the periostracum missing from the dorsal surface and most of the aperture broken away.

Shell discoid, with protoconch and spire scarcely raised above the top edge of the body-whorl. Whorls expanding slowly at first, with body whorl increasing more rapidly; suture deep. Body-whorl with distinct shoulder above the suture but otherwise with evenly rounded periphery. Umbilicus wide, open, almost symmetrical, internally exposing much of underside of protoconch and some of inner part of all whorls. Aperture broadly oval except where interrupted by penultimate whorl. Peristome thin, mainly plane but slightly reflected over extreme edge of umbilicus, its upper edge arching forwards beyond the outer and lower edges,

its ventral end extending further around whorl than the distal end. Protoconch of 1.3-1.5 whorls minutely granular or pitted or appearing smooth; teleoconch from about whorl 1.6 onwards with strong rather regular axial ribs (body whorl having *ca* 64 ribs on smaller shell, *ca* 57 on larger shell); each rib raised as a cord of even width that arcs backwards towards shell periphery, with its height greatest on periphery; periostracum between ribs nearly smooth but with fine grid-like pattern of 4-6 neat axial lines between each pair of ribs and running parallel to them, the axial lines being intersected by spiral lines. Sculpture on basal surface of teleoconch generally as on adapical surface, but axial lines between ribs tend to be stronger near aperture; similar sculpture also visible inside umbilicus on inside of whorls of spire. Protoconch translucent, becoming whitish on older shell, teleoconch light brown, slightly glossy; inside of aperture brown, translucent because shell thin. Known only from shells, so features of the exterior of the body, genital anatomy, etc., remain unknown.

*Trachycystis iredalei* was described from Kenya (PRESTON, 1912); VERDCOURT (1991: 373 figs. 12a-c) figured a lectotype. VAN BRUGGEN & VAN GOETHEM (2001: 161 figs. 19-21) reported its range as D.R. Congo, Kenya and perhaps Cameroon (the last based on two shells tentatively reported by DE WINTER & GITTENBERGER, 1998) and WRONSKI *ET AL.* (2014: 163, 165: table 1) reported it from Bioko. Our specimens from São Tomé thus represent the first confirmed records from oceanic islands off western Central Africa.

SUCCINEIDAE Beck, 1837

*Quickia* Odhner, 1950

Proc. Malac. Soc., London, 28 (4-5), p. 206; type species *Succinea concisa* Morelet, 1848 by original designation.

*Quickia concisa* (Morelet, 1848)

*Succinea concisa* Morelet, 1848, Rev. Zool., 11, p. 351; TL ad ripas fluvii Gabon prope lineam aequinoxialem in sinu Guineensi emergentis; 3 syntypes at NHMUK (BREURE *ET AL.*, 2018: 249, fig. 252).

Syn. *Succinea spurca* Gould, 1850, Proc. Boston Soc., 3, p. 193.

Present on São Tomé! and Príncipe! (CGAH), and either native there or long established since DOHRN (1866b: 133, no. 18) reported it from both islands. Also known from Annobón, Guinea Bissau [“Bissau (Guinée portugaise)”], Cameroon, Gabon, and Congo (GIRARD 1893a: 33, 1894: 208, GERMAIN 1912b: 385–386, 1916: 303, GASCOIGNE 1994a: 2, SCHILEYKO 2007: 2078). PATTERSON (1975: 184) gave a map of its distribution showing occurrence in W. Africa from Sierra Leone to Angola and in W. Indian Ocean from Zanzibar and Seychelles to Mauritius, La Réunion and Rodrigues. BROOK (2010: 207) also reported it as a recent introduction (first recorded 1992–94) in Polynesia from Samoa to the Marquesas Is., where its identity was confirmed by molecular data in addition to anatomical study.

Shell figures: SCHILEYKO (2007: 2078 fig. 2616A), BREURE *ET AL.* (2018: 249, fig. 252). Figures of genital anatomy: QUICK (1936), SCHILEYKO (2007: 2078: fig. 2616 B–D). PATTERSON (1975: 183) provided a key to *Quickia* species and stated that *Q. concisa* has a white shell, whereas it is variably white to somewhat translucent and pale yellowish or brownish in our live-collected material from São Tomé and Príncipe. BREURE *ET AL.* (2018: 249, fig. 252) do indeed illustrate white shells for syntypes of the species from Gabon, but these may simply have been empty shells that had become bleached through prolonged exposure to sunlight, as is normal in old shells of *Quickella arenaria* (Bouchard-Chantereaux) (Succineidae) collected in Europe.

CERASTIDAE Wenz, 1923

syn. Pachnodidae Steenberg, 1925; Cerastuidae Wenz, 1930

SCHILEYKO (1998: 166, 174, 176) regarded the name Cerastinae Wenz, 1923 as invalid because he regarded the type genus *Cerastus* E. von Martens, 1860 (in ALBERS, 1860: 232) as a junior homonym of *Cerastus* Dejean, 1821 (Curculionidae, Coleoptera). Hence he adopted the family name Pachnodidae Steenberg, 1925 (STEENBERG, 1925: 202). This appears to follow logically from the older literature: STRAND (1928: 67) provided *Cerastua* as a replacement name for *Cerastus* E. von Martens in Albers, 1860; WENZ (1930: 3034) provided Cerastuidae as a replacement family-group name for his Cerastinae (WENZ, 1923: 1072), but Pachnodidae would have had priority. Nevertheless, *Cerastus* Dejean, 1821 is now regarded as a *nomen nudum* (<http://taxonomicon.taxonomy.nl/TaxonTree.aspx?id=990683>, accessed

18 Apr. 2020) so that *Cerastus* E. von Martens, 1860 is after all an available name and hence Cerastidae Wenz, 1923 has priority since it complies with ICZN Art. 11 and 39. MORDAN (1992), BOUCHET *ET AL.* (2017: 363) and MOLLUSCABASE (<http://www.marinespecies.org/aphia.php?p=taxdetails&id=1057476>, accessed 17 Apr. 2020) gave Cerastidae precedence over Pachnodidae without any explanation, but their treatment is correct.

Seven nominal species resembling cerastids have been reported from São Tomé, Príncipe, or both islands. These appear to represent four different species actually occurring there and are distinguishable on shell characters which are described in the Key above (under *Aporachis* n. gen. in Achatinidae). GERMAIN (1916) placed them in the

genus *Rachis*. The review of Cerastinae by MORDAN (1992) did not consider any of the species from São Tomé or Príncipe and the genital anatomy of all of them has remained undescribed in the literature until now. Our studies show that the genitalia of two of these species resembles that of Achatinidae *s.l.* instead, and these are discussed above under *Aporachis* n. gen. The other two species have genital anatomy closely resembling that of "*Edouardia*" *meridionalis* (L. Pfeiffer, 1847) described and

figured by SCHILEYKO (1998: 172-173, fig. 210C) and also resembling figures for "*E.*" *tumida* Taylor and "*E.*" *natalensis* (L. Pfeiffer) given by MORDAN (1992: 9), differing from *Rachis* and all other cerastid genera covered in those publications. We therefore transfer them to *Gittenedouardia* for reasons explained below.

*Rhachistia neurica* (Reeve) was listed by GASCOIGNE (1994a: 2) for Príncipe, São Tomé and Bioko, but the basis for this appears to be unclear.

### *Gittenedouardia* Bank & Menkhurst, 2008

Basteria, 72 (4-6), p. 101; type species *Bulimus spadiceus* L. Pfeiffer, 1846, by original designation.

MORDAN (1992) and SCHILEYKO (1998: 172) used the generic name *Edouardia* Gude, 1914, but BANK & MENKHORST (2008: 101) found that name to be unsuitable for the species involved. This is because GUDE (1914: 280) published *Edouardia* as a supposed nom. nov. for *Conulinus* E. von Martens, 1895, for which the type species (by subsequent designation of Woodward, 1896, Zool. Record 1895, Mollusca, p. 59) is *Buliminus ugandae* E. von Martens, 1895. Instead, however, GUDE (1914: 280) designated the type species of *Edouardia* as *Bulimus conulus* Reeve, 1849, a species which was not originally included by VON MARTENS (1895: 180) when he named *Conulinus*. ICZN Art. 67.8 states that when a *nomen novum* is declared for a genus name, that name inherits the type of the replaced name. Consequently, Gude's type designation is invalid because there is an earlier one and *Edouardia* is an objective synonym of *Conulinus*.

There was actually no need for a new name to be introduced by Gude since *Conulinus* E. von Martens, 1895 is not a homonym of *Conulina* Bronn, 1835. Hence, BANK & MENKHORST (2008: 101) were able to retain the genus *Conulinus* for eight east African taxa, which differ from *Gittenedouardia* in shell characters they describe and anatomical characters tabulated by MORDAN (1994: 4, table 3). BANK & MENKHORST (2008: 101) described the distribution of the genus *Gittenedouardia* as "restricted to Madagascar (*rufoniger*, *vesconis*), Seychelles (*tumida*), India (*orbis*) and the southeastern part of Africa (*tumida* and remaining taxa)". On the basis of characters of the genital anatomy noted under the family heading above, *Rachis burnayi* (Dohrn) and *R. eminula* (Morelet) are treated here as new combinations in the genus *Gittenedouardia*. Hence the present study extends the range of that genus to include São Tomé, Príncipe, and western central Africa from Bioko and Cameroon to Angola and the (former) Congo.

### *Gittenedouardia burnayi* (Dohrn, 1866) n. comb. (Figs. 2D, 6E)

*Buliminus* (*Rhachis*) *Burnayi* Dohrn, 1866(b), Malak. Blätt., 13, pp. 124-126, no. 7, pl. 5, figs. 11-13; TL "in vallibus et collibus usque ad 800 pedum altitudinem" (i.e. Ilha do Príncipe). *Rachis Burnayi* Dohrn with Mutation *zebra* and Mutation *fasciata* named and described: GERMAIN (1916: 156, 162, 233-235); his account makes it clear that the "Mutation" are groups of the common phenotypes differing in the pattern of dark bands on their shells, so they are infraspecific forms rather than teratological specimens.

Recorded on both São Tomé! and Príncipe! Range elsewhere includes Bioko, Cameroon and (former) Congo (D'Ailly, 1896: 58; Germain, 1916: 156, 162, 168, 233-235). Shell figures: DOHRN (1866b: pl. 5, figs. 11-13), Fig. 2D. For genital anatomy see Fig. 6E.

Our records from Príncipe were at 5-240 m elevation on edges of secondary forest adjoining cultivation and inside

native forest with understorey of saplings. On São Tomé we found it at three sites, from 22-398 m elevation, twice in old cocoa plantations with some tall trees, once in secondary forest with some planted trees and palms intermixed (NE. of Ponta Baleia). The live snails were collected above the ground on leaves, often high up on saplings.

*Gittenouardia eminula* (Morelet, 1848) n. comb. (Fig. 2C, 6F)

*Bulimus eminulus* Morelet, 1848, Rev. Zool., 11, p. 353; TL "littus Guineense ad ostia fluminis Gabon"; 3 syntypes at NHMUK (Breure *et al.*, 2018: 278).

Syn. *Buliminus (Rachis) Crossei* Nobre, 1891, O Instituto, Coimbra, 2nd ser., 38, p. 934; TL "Região media da ilha de S. Thomé".

Recorded on both São Tomé! and Príncipe! Range elsewhere Gabon, Angola, Cameroon (D'Ailly, 1896: 59; Germain, 1912b: 357), possibly Ethiopia (Jickeli, 1874: 103). Shell figures: MORELET (1858: pl. 1, fig. 6), BREURE *ET AL.* (2018: 278, fig. 377), Fig. 2C. For genital anatomy see Fig. 6F.

On Príncipe we found it in two localities, at 24 m elevation in secondary forest adjoining edges of cultivation and

at 185 m inside secondary forest. Numerous finds of it on São Tomé ranged from 96-1477 m elevation. At the highest elevations it lived inside montane forest, at lower elevations it was found in secondary forest, at forest edges, and in a plantation with shade trees. Spires of the shells of the live snails were commonly covered with fine dark detritus which tended to camouflage them when they were climbing on trunks and branches.

GASTROCOPTIDAE Pilsbry, 1918

*Gastrocopta* Wollaston, 1878

*Gastrocopta nobrei* (Girard, 1893)

*Pupa Nobrei* Girard, 1893b, Jornal Sci. Math., Phys. Nat., Lisboa, (2) 3 (10), p. 111, pl. 1 fig. 21; TL "Ile St. Thomé à Bindá sous l'écorce des arbres (F. Newton)".

Endemic on São Tomé! No other finds of *G. nobrei* have been reported since its original description and the types may have been lost. The original specimens came from beneath the bark of trees (see above), but GAH found it at two localities amongst plant litter on or near the ground, at low altitudes on almost opposite ends of the island: 2 Dec. 2013, site ST2, S. of EN2 and NW. of Ribeira Peixe (N0.9314° E6.5889°), edge of tall forest on hill above young oil palms, ca 126 m alt., 15 sh; 5 Dec. 2013, site ST6, by EN1 road in NW. of

island a few km N. of Santa Catarina (N0.2716° E6.4789°), base of wet basalt cliff above shore & road, saplings on ledges, planted bananas locally, ca 6 m alt., 2 sh. The 17 shells collected in 2013 are a good match for the original description and figure.

Shell fig.: GIRARD (1893b: pl. 1 fig. 21). Genital anatomy: undescribed. The systematic position of *G. nobrei* requires further study as part of a wide-ranging revision: Pilsbry (in PILSBRY & COOKE 1918-1920: 368, pl. 34 fig. 10) placed it as one of five species in genus *Costigo* O. Boettger,

1891, the other four species being from the Philippines, Moluccas and Mascarene Islands, with a comment (p. 366) that *Costigo* "is probably not a natural group in its present limits - merely a conve-

nience". The generally similar *G. annobonensis* (GIRARD, 1894) of Annobón differs in having three or four palatal teeth (cf. GIRARD 1894: 207, PILSBRY 1916-1918: 124), compared to two in *G. nobrei*.

# TRUNCATELLINIDAE Steenberg, 1925

## *Truncatellina* R.T. Lowe, 1852

### *Truncatellina thomensis* n. sp. D. Holyoak & G. Holyoak (Fig. 3E, F)

**Type material:** Holotype NHMUK 20200237, shell (H 2.26 mm, B 0.88 mm), 24 Nov. 2018, GAH, DTH, *et. al.*, site 18-2C.

**Type locality:** São Tomé Island, Morro Claudina (near Bom Sucesso), N0.2900° E6.6055°, 1257 m alt., on ground in montane rainforest (sieved from shelly debris at thrush anvil).

**Paratypes:** From type-locality, collected with holotype, site 18-2C, 7 sh + 2 fragments; 27 Nov. 2018, Morro Claudina, N0.28909° E6.60442°, ca 1290 m alt., floor of montane forest with understorey (sieved from shelly debris at thrush anvil), GAH & DTH 18-6A, 3 sh; ditto, N0.29036° E6.60537°, 1254 m alt., floor of rather open montane forest with some alien trees (sieved from shelly debris at thrush anvil), GAH & DTH 18-6D, 9 sh.

**Etymology:** The species epithet *thomensis* is an adjective derived from the type-locality on São Tomé.

**Description:** H 1.71-2.26 mm, B 0.82-0.93 mm, H/B 2.04-2.58; body-whorl height 0.82-1.05 mm (44.0-55.1% of H); AH 0.47-0.56 mm, AB 0.39-0.54 mm, AH/AB 1.0-1.27; whorls 5.7-6.1. Shell dextral, sub-cylindrical with sub-conical upper-spire (body-whorl and penultimate-whorl similar in width but peristome extends slightly further; whorl 4 slightly narrower; whorls 0-3 sub-conical with bluntly rounded apex); whorl height increasing  $\pm$  gradually. Whorls somewhat rounded, but with weak shoulder below suture. Umbilicus a shallow chink (slit) under columellar side of peristome; back of body-whorl mainly rounded, but with short keel above umbilicus. Aperture broadly ovate to ovate-oblong except where interrupted by penultimate-whorl, the columellar border, palatal border, or both, often straighter than basal margin. Peristome thin to slightly thickened throughout, gently reflected on palatal margin, more strongly reflected on columellar margin, but sharply turned inwards to meet penultimate-whorl at top of palatal margin; outer palatal edge convex and rounded. In side view the peristome usually arched upwards along middle part of palatal margin.

Aperture without any trace of teeth or denticles, even when viewed obliquely and none visible by translucence on concealed parts of body-whorl. Protoconch (whorl 1) smooth; teleoconch with numerous closely-spaced fine riblets or striae, which somewhat irregular, nearly straight, passing somewhat obliquely downwards to right (with shell viewed with spire pointed upwards and aperture on top). Protoconch whitish; teleoconch light-brown, glossy; interior of aperture of freshest shells light brown with the thin shell translucent, although columellar edge whitish; on older shells interior of aperture more extensively whitish, less translucent.

Features of the exterior of the body, genital anatomy, etc., remain unknown.

**Discussion:** The only previous reports of *Truncatellina* from islands in the Gulf of Guinea were by VAN BRUGGEN (1994: 23-24, figs. 24, 25, 29, see pp. 377-378 for corrected version of figs) for *T. adami* van Bruggen, 1994 from Fernando Poo (now Bioko), but that species has a wider shell (B 1.0-1.1 mm) which is almost smooth on later whorls ("no sculpture beyond some very faint growth lines"). In West Africa,

the genus was reported only by DE WINTER (1990: 306-307), who named *T. silvicola* as a new species, apparently still known only from its holotype, from 600 m altitude in forest of the western Ivory Coast. Compared to *T. thomensis* n. sp., that species is smaller (H 1.64 mm), has the whorls more swollen, and ribs more widely spaced on the teleoconch.

All other *Truncatellina* described from tropical Africa are known only from localities that are much more distant geographically from São Tomé: *T. pygmaeorum* (Pilsbry & Cockerell, 1933) from central Kenya through east and south-east Zaïre to south-west Angola and north-eastern South Africa has a sinistral shell (e.g. VAN BRUGGEN, 1994; HERBERT & KILBURN, 2004: 113) whereas *T. thomensis* n. sp. has a dextral shell. *T. naivashaensis* (Preston, 1911) from Kenya has a fold on the columella visible when the shell aperture is viewed obliquely (ADAM, 1954; VAN BRUGGEN, 1994); *T. ruwenzoriensis* Adam, 1957 has strong axial sculpture on the upper part of the spire and weak irregu-

lar sculpture on the body-whorl (ADAM, 1957: 6, fig. 5; VAN BRUGGEN, 1994); *T. ninagongonis* (Pilsbry, 1935) from Zaïre (L. Kivu in former Belgian Congo) and Malawi has fine striae on the shell that are stronger behind the peristome (ADAM, 1957: 3-4, 6 fig. 4; VAN BRUGGEN, 1994). *T. upembae* Adam, 1954 was figured and described by VAN BRUGGEN (1994: 19, figs. 9-12, 22-23, 29, see pp. 377-378 for corrected version of figs) and reported to be widely distributed in Central Africa (NE. Angola, S., E. and NE. Zaïre) in that paper and by VAN BRUGGEN & VAN GOETHEM (2001: 154). Although different populations of *T. upembae* are rather variable in shell characters, and the overall shell measurements for that species broadly overlap those of *T. thomensis*, comparisons with the published figures shows that *T. thomensis* differs in having much closer and finer axial ribbing on the later whorls, the outer palatal edge of the peristome convex and rounded rather than slightly concave or straight, and usually a shallower suture.

## VALLONIIDAE Morse, 1864

Syn. Pupisomatidae Iredale, 1940

### *Pupisoma* Stoliczka, 1873

A single tiny shell apex from Príncipe collected in 2018 (CGAH) apparently

represents a *Pupisoma* sp., a genus otherwise unrecorded on the island.

### *Pupisoma dioscoricola* (C.B. Adams, 1845)

*Helix dioscoricola* C.B. Adams, 1845, Proc. Boston Soc. Nat. Hist., 2, p. 16; TL Jamaica.  
Syn. *Helix orcula* Benson, 1850, Ann. Mag. Nat. Hist., (2) 6, p. 251; TL India.

New to São Tomé: 26 Nov. 2018, near Ponta Furada, N0.23665° E6.46775°, 240 m alt., flushed steep rock of trackside cutting, part-shaded by secondary forest, GAH & DTH 18-5, 1 sh; 27 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.28909° E6.60442°, ca 1290 m alt., floor of montane forest with understorey (sieved from shelly debris

at thrush anvil), GAH & DTH 18-6A, 1 sh; 28 Nov. 2018, Cascata de São Nicolau, N0.2857° E6.6257°, 885 m alt., around waterfall on steep rocky slopes with secondary forest, GAH, DTH *et al.* 18-7, 1 sh.

*Helix orcula* is treated as a synonym of *H. dioscoricola* here following [www.molluscabase.org](http://www.molluscabase.org) (accessed 7 July

2019). HERBERT & KILBURN (2004: 114-115) gave the range of *Pupisoma orcula* as extending widely over eastern South Africa, northwards to Zimbabwe, Mozambique and central Africa, and occurring elsewhere in Asia, Hawaii and Australia. VERMEULEN & WHITTEN (1998: 83) placed it in the genus *Parazoo-genetes* Habe, 1956 (an arrangement not accepted on MolluscaBase in 2019) and described the species as “common and widespread in Africa, Asia, Australia,

Pacific”. It was tentatively reported from West Africa by DE WINTER (1990: 307-308), who figured *Pupisoma* cf. *orcule* from the western Ivory Coast, based on a single shell from undisturbed forest habitat at 600 m alt. HAUSDORF (2007) revised New World *Pupisoma*, giving the range there of *P. dioscoricola* as extending from southern U.S.A. through the Caribbean and Central America to the Galapagos Is., S. Brazil and N. Argentina.

### *Pupisoma harpula* (Reinhardt, 1886)

*Helix* (*Acanthinula*) *harpula* Reinhardt, 1886, Sitzungsab. Ges. Naturf. Fr. Berlin, p. 115; TL Tokio, Kanda [Japan]; PILSBRY (1926, Man. Conch., 2 (27) p. 198) recombined it as *Zoögenetes* (?) *harpula* (Reinh.) but this was corrected by HAAS (1937: 10-11, pl. 3 figs. 25-27) who figured “Typus SMF 3443”.

Syn. *Pupisoma japonicum* Pilsbry, 1902, Nautilus, 16, p. 21; TL Hirado, Hizen [Japan].

New to São Tomé: 24 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.2900° E6.6055°, 1257 m alt., montane rainforest (sieved from shelly debris at thrush anvil), GAH, DTH *et al.* 18-2C, 5 sh; 27 Nov. 2018, Morro Claudina, N0.28909° E6.60442°, ca 1290 m alt., montane forest with understorey (sieved from shelly debris at thrush anvil), GAH & DTH 18-6A, 1 sh; ditto, N0.2890° E6.6044°, sieved from ground-litter on floor of montane forest, sample 18-6B, 1 sh; ditto, N0.29036° E6.60537°, 1254 m alt., floor of rather open montane forest with some alien trees (sieved from shelly debris at thrush anvil), sample 18-6D, 1 sh; 28 Nov. 2018, Cascata de São Nicolau, N0.2857° E6.6257°, 885 m alt., around waterfall on steep rocky slopes with secondary forest, GAH, DTH *et al.* 18-7, 3 sh; 9 Dec. 2018, path from above Bom Sucesso Botanical Garden towards Lagoa Amélia, ca N0.2823° E6.5964°, 1290-1415 m alt., montane forest (sieved), GAH & DTH 18-21, 1 sh.

PILSBRY (1920: 25-26, pl. 2, figs. 11, 12) again treated this species as *P. japonicum*, separating it from *P. orcula* by the wider umbilicus (one-seventh of shell diameter) and giving its range as Japan and South Africa. HERBERT & KILBURN (2004: 114-115) described and figured both *P. harpula* and *P. orcula* (regarding *P. japonicum* as a synonym of *P. harpula*). They noted that they are very similar, but that *P. harpula* differs in being smaller than *P. orcula* (up to 1.65 mm, cf. 2.0, rarely 2.2 mm), with shell more elevated, having a wider umbilicus and lacking spiral sculpture. They gave the range of *P. harpula* as extending from Japan to central and southern Africa, reaching the southern Cape, occurring in similar habitats in S. Africa to *P. orcula* and sometimes living with it on the same tree. VERDCOURT (2006) listed *P. harpula* for East Africa. This species has also been reported as *P. japonicum* from Central Africa (e.g. ADAM, 1954: 806), E. Madagascar (EMBERTON *ET AL.*, 2010) and the Mascarene Is. (GRIFFITHS & FLORENS, 2006: 86).

AGRIOLIMACIDAE H.Wagner, 1935

*Deroceras* Rafinesque, 1820

*Deroceras laeve* (O.F. Müller, 1774)

*Limax laevis* O.F. Müller, 1774, Verm. terr. fluv., 2, p. 1; TL restricted by WIKTOR (2001: 107) to Frideriksdal near Copenhagen (Denmark).

New to São Tomé: 3 Dec. 2013, on path between Bom Sucesso and Macambrará, near Rio Manuel Jorge, N0.2847° E6.6097°, ca 1149 m alt., trackside, cultivation edges, scrub & small forest patches, GAH & DTH ST3, 6 spm (2 dissected were both aphyallid, but with spermoduct well developed); Mar. 2017, surroundings of Jardim Botânico at Bom Sucesso, non-forested, with bananas & fields of vegetables, leg. Martina Panisi #1, 5 spm; ditto, #2, 6 spm; 24 Nov. 2018, near Quinta da Graça, N0.29921° E6.64174°, 678 m alt., scrub, cultivated gardens, roadside banks, few trees, GAH & DTH 18-3, 1 examined alive (not kept); 2 Dec. 2018, just S. of Milagrosa, on the road between Trindade and Bombaim, N0.27667° E6.65986°, 398 m alt., tall secondary forest on slopes, track edges with flushed rocky cuttings & abandoned cocoa plantations, GAH & DTH 18-10, examined alive (not kept); 10 Dec. 2018, in Bom Sucesso Botanic

Garden, N0.2886° E6.6121°, 1156 m alt., botanic garden with groves of trees, lawns & cultivated patches, GAH & DTH 18-22, examined alive (not kept); 10 Dec. 2018, on path between Bom Sucesso and Macambrará, near Rio Manuel Jorge, N0.28571° E6.60912°, 1114 m alt., horticulture areas with bananas, groves of scrub & trees alongside track, GAH 18-23, examined alive (not kept).

WIKTOR (1999: 463) noted that “the original distribution range of *D. laevis* seems to be the Palearctic, which is practically wholly inhabited by the species, from the subpolar zone up to its southern fringes, including China. Owing to its short life cycle and high ecological tolerance, the slug is extraordinarily susceptible to introduction. It can be encountered on all continents, except for Antarctic. It occurs quite locally but all over the globe, even on tropical islands such as New Guinea or others in the Pacific”.

#### EUCONULIDAE H.B. Baker, 1928

##### *Afroconulus* Van Mol & van Bruggen, 1971

##### *Afroconulus roseus* n. sp. D. Holyoak & G. Holyoak (Figs. 3C-D, 9A-D)

**Type material:** Known only from the unique holotype, NHMUK 20200238, dry sh + bod in IMS, collected 10 Dec. 2018, by DTH (with FS & MP), site 18-24.

**Type locality:** São Tomé Island, path from above Bom Sucesso Botanical Garden to Lagoa Amélia, N0.2835° E6.5981°, ca 1353 m alt., found alive ca 1.5 m above ground on large glossy green leaf of herb in understory of montane rainforest.

**Etymology:** The genus *Afroconulus* has been treated as a masculine noun. The epithet *roseus* is from the Latin (meaning pink), alluding to pink dorsal coloration of the body of the living snail.

**Description:** Shell B 4.44 mm, H 4.06 mm, H/B 0.91; AB 2.35 mm, AH 2.18 mm, AH/AB 0.93; whorls 5.0. Dextral, conical, convex below; protoconch small, whorls increasing regularly; suture moderately deep. Body-whorl rounded, with definite angle just above periphery that becomes less obvious near aperture. Aperture broadly oval, except where interrupted by penultimate whorl. Peristome thin, plane except short columellar part which is reflected to conceal the tiny

umbilicus. Protoconch with microsculpture of fine close axial riblets intersected by spiral ridges. Teleoconch above and below periphery with fine closely-spaced spiral ridges, intersecting coarser, less regular, ill-defined, low riblets and lines. Shell very thin, fragile, translucent; pale brown; spire appearing to have waxy lustre that becomes glossy on body whorl, especially the underside.

Exterior of body described from living animal as having striking pattern

produced by blackish ommatophores and their retractor muscles, blackish spot dorsally at tail tip and bright pink dorsal surface of other exposed parts of body, shading to lighter pinkish on face and whitish on flanks, foot-fringe and sole of foot. The mantle visible through the translucent shell was mainly whitish but marked with a strong blackish line along the mantle-collar.

Body of holotype drowned and preserved in IMS (partly contracted) was 7.1 mm long, of which tail formed 3.7 mm. All trace of pink coloration has vanished. Sole of foot narrow, tripartite, white; front of foot separated from base of head by deep transverse groove (as in other *Helicarionoidea* studied). Thin groove bordering upper edge of foot-fringe continuous along sides of body and around tail. Tail appears long, rather narrow (higher than wide), white with light grey dorsal area around tip; no distinct caudal horn, only a slight subapical protuberance; caudal fossa visible only as very small pore high on steep end of tail. Front of head with two pairs of tentacles, the lower pair short. Mantle-collar raised around front edge and on sides of body as thin continuous flap, narrowing posteriorly on both sides and absent above base of tail; lacking separate mantle-laps; white, except for blackish line along the front right-hand half. Mantle inside shell white with two black blotches towards rear of dorsum (Fig. 9D).

Genital pore tiny, on front right-hand flank of body at one-third height, a short distance behind base of upper tentacle. Genital atrium a short but rather wide tube, dividing proximally into distal end of penis and distal end of vagina. Penis a short tube only twice as long as wide, with opaque wall. Distal epiphallus an opaque narrow white tube enclosed in a translucent thin muscular cylindrical sheath almost twice as wide that appears well defined at both proximal and distal ends. Proximal part of epiphallus tightly convoluted *in situ*, with strands of connective tissue joining its folds; comprised of three short wide portions separated by two

narrower necks; penial retractor muscle widely attached near proximal end of epiphallus, extending onto inside of mantle wall; proximal end of epiphallus narrows into vas deferens; flagellum lacking. Vas deferens starts near distal end of spermoviduct, passes distally alongside free oviduct and then returns proximally to reach only the proximal part of epiphallus (not passing into vaginal-penial angle). Vagina just over twice as long as wide, somewhat swollen, with distal end narrower; free oviduct at least three times length of vagina, stout, the distal two-thirds thicker-walled because encased in an opaque cylindrical gland. Duct of bursa copulatrix a tube somewhat narrower than free oviduct or epiphallus-sheath, lying alongside free oviduct; reservoir of bursa not distinct from the duct, its proximal apex reaching distal end of spermoviduct, with a thread-like strand extending proximally from tip of reservoir to inner edge of mid-part of spermoviduct. The spermoviduct large and stout with distinct folds, attaching proximally to large curved albumen-gland that tapers to bluntly pointed apex. Part of broken-off common hermaphrodite duct remains on inner surface of albumen gland towards its inner, distal end. Right ommatophore retractor muscle passing through distal genitalia between epiphallus-sheath and duct of bursa copulatrix.

*Comments:* The genus *Afroconulus* was named by VAN MOL & VAN BRUGGEN (1971: 286) with *Sitala diaphana* Connolly, 1922 as type species by original designation. DE WINTER & VAN BRUGGEN (1992) recognised three genera of Euconulidae in Africa (*Afropunctum* F. Haas, 1934, *Afroguppya* de Winter & van Bruggen, 1992 and *Afroconulus*). Among these genera, *Afroconulus* is distinctive anatomically in possessing a well-developed vagina; in having most of the free-oviduct surrounded by a perivaginal gland; in having most of the length of the penial epiphallus enclosed in a long cylindrical muscular sheath, and in lacking a penial flagellum (VAN MOL & VAN BRUGGEN, 1971; DE WINTER & VAN

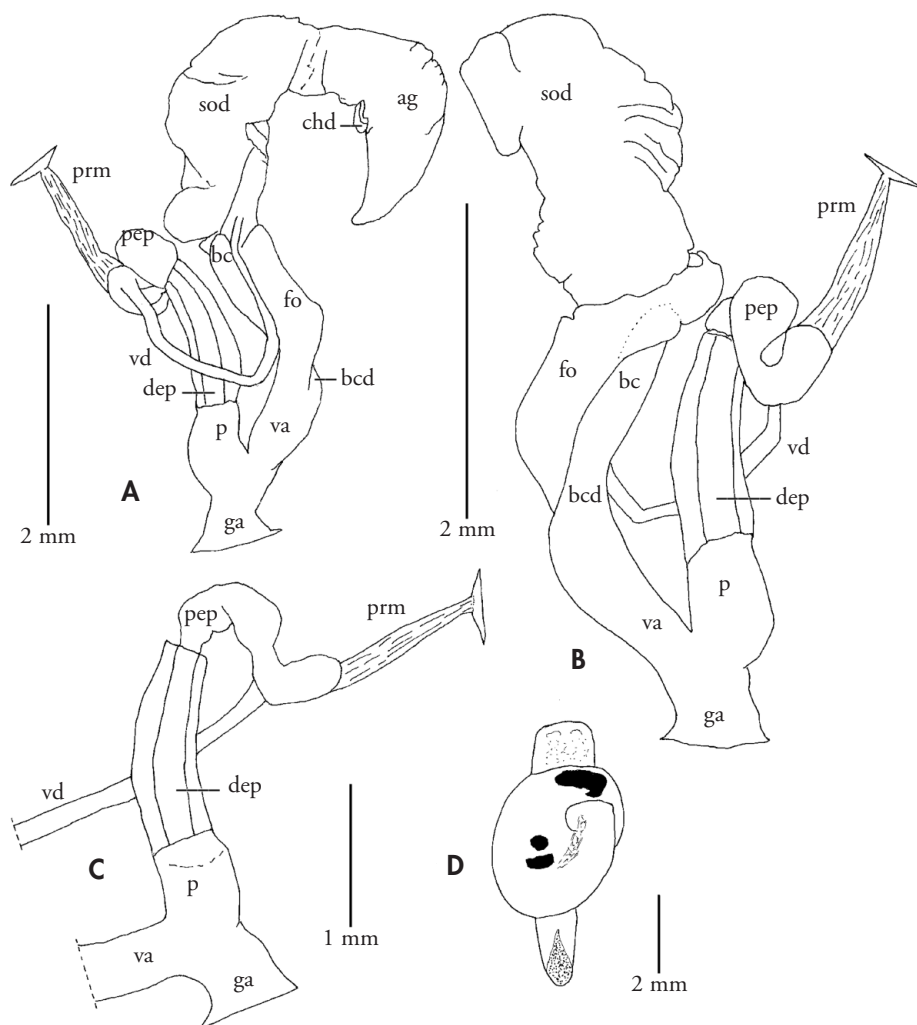


Figure 9. Genital anatomy and pattern of body coloration of *Afroconulus roseus* n. sp. from São Tomé (all based on holotype). A, B: distal genitalia, viewed from opposite sides; C: detail of penis and epiphallus with epiphallus extended; D: dorsal coloration of body preserved in IMS and removed from shell (stipple represents grey coloration; black areas shown as black).

*Figura 9. Anatomía genital y patrón de coloración corporal de Afroconulus roseus* n. sp. de Santo Tomé (todo basado en el holotipo). A, B: genitalia distal, vista desde lados opuestos; C: detalle del pene y epífalo, con el epífalo extendido; D: coloración dorsal del cuerpo preservado en alcohol industrial metilado y retirado de la concha (el punteado representa coloración gris; las áreas negras se muestran en negro).

BRUGGEN, 1992; SCHILEYKO, 2002a: 1135-1136). Whereas both *Afropunctum* and *Afroguppya* are known to bear live young because shelled embryos are found in the free oviduct (DE WINTER & VAN BRUGGEN, 1992), *Afroconulus* may differ

in laying eggs, since HERBERT & KILBURN (2004: 255) refer to "tiny, round, white eggs" as "retained within the parent for some time" in *A. diaphanus*; although the distal female tracts of the mature holotype of *A. roseus* were not opened they

certainly lacked shelled embryos. *Helix jenynsi* L. Pfeiffer, 1846 has also been placed in *Afroconulus*, but it is now regarded as *Sitala jenynsi* (L. Pfeiffer, 1846) and placed in the Helicarionidae on MolluscaBase (<http://www.marine-species.org/aphia.php?p=taxdetails&id=1262369>, accessed 13 Aug. 2019).

The shell characters and distal genital anatomy of *A. roseus* n. sp. generally match those of *Afroconulus diaphanus* (Connolly, 1922) (VAN MOL & VAN BRUGGEN, 1971; SCHILEYKO, 2002a: 1135-1136; HERBERT & KILBURN, 2004: 255). However, it is treated as a distinct species here because *A. roseus* has the shell lower than wide (H/B 0.91 in holotype), whereas figures of *A. diaphanus* show its shell is higher than wide (H/B 1.05). Also, comparison with the figure by SCHILEYKO (2002a: 1136 fig. 1494B) shows that the proximal part of the

epiphallus (part outside the sheath) of *A. roseus* is much longer compared to the sheath length than in *A. diaphanus* ( $>0.5\times$  sheath, cf.  $<0.3\times$ ); its proximal epiphallus has three wide portions separated by two narrow “necks” (Fig. 9B, C) and is tightly convoluted *in situ*, not a single wide portion which is C-shaped; also, the reservoir of the bursa copulatrix is not swollen so as to be distinct from adjoining parts of the bursa duct. All these characters of course need to be compared from more specimens than the unique holotype of *A. roseus*, but the large gap in geographical distribution between its type locality in montane rainforest on São Tomé and the range of *A. diaphanus* (montane forests from Kenya to Transkei: HERBERT & KILBURN, 2004: 255) also encourages us to regard it at least provisionally as a distinct species.

#### *Afropunctum* F. Haas, 1934

##### *Afropunctum seminium* (Morelet, 1873)

*Helix seminium* Morelet, 1873, J. Conchyl., 21 (4), p. 329; TL “prov. Gabon”. BREURE ET AL. (2018: 424, fig. 1015) figured a syntype from NHMUK.

New to São Tomé: 7 Dec. 2013, path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2825° E6.5969°, ca 1400 m alt., montane forest on ridge, with closed canopy & understorey of saplings, GAH & DTH ST8, 2 sh; 13 Dec. 2013, by EN2 just NE of Monte Mário “roça”, N0.0606° E6.5561°, ca 236 m alt., forest on slopes by road with understorey of saplings & ferns beneath, GAH & DTH ST13, 1 sh; 27 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.28909° E6.60442°, ca 1290 m alt., floor of montane forest with understorey (sieved from shelly debris at thrush anvil), GAH & DTH 18-6A, 3 sh; ditto, N0.29181° E6.60592°, 1288 m alt., floor of montane forest near tiny clearing (sieved from shelly debris at thrush anvil among buttress roots of tree), sample 18-6C, 3 sh; ditto, N0.29036° E6.60537°, 1254 m alt., floor of rather open montane forest with some alien trees (sieved from shelly debris at thrush anvil), sample 18-

6D, 1 sh; 28 Nov. 2018, Cascata de São Nicolau, N0.2857° E6.6257°, 885 m alt., around waterfall on steep rocky slopes with secondary forest, GAH, DTH et al. 18-7, 6 sh & 1 spm; 1 Dec. 2018, just before the Cascata de Bombaim (Rio Abade), on the road between Trindade and Bombaim, N0.2534° E6.6318°, 485 m alt., flushed rock of low trackside cutting, part-shaded by bamboo & secondary forest, GAH, DTH & RFL 18-9, 1 spm; 2 Dec. 2018, just S of Milagrosa, on the road between Trindade and Bombaim, N0.2766° E6.6598°, 398 m alt., secondary forest on slopes, abandoned cocoa plantations, trackside rock cuttings, GAH & DTH 18-10, 44 sh & 7 spm; 9 Dec. 2018, path from above Bom Sucesso Botanical Garden towards Lagoa Amélia, ca N0.2823° E6.5964°, 1290-1415 m alt., montane forest, GAH & DTH 18-21, 4 sh.

New to Príncipe: 5 Dec. 2018, 1.5 km SW of Terreiro Velho, close to Oquê Pipi,

N1.59965° E7.41082°, 308 m, tall native forest, GAH 18-16A, 1 sh.

The identification characters, systematic position and geographical range of this species were reviewed by DE WINTER & VAN BRUGGEN (1992), who also provided good illustrations of its

shells, genital anatomy and radula. Their study revealed that the species has an extensive range in tropical Africa, with west African records from countries including Ghana, Nigeria and Gabon, but no reports hitherto from offshore islands.

## HELICARIONIDAE Bourguignat, 1877

The supra-generic classification by BOUCHET *ET AL.* (2017) recognised three families within the Helicarionoidea Bourguignat, 1877 as Helicarionidae, Ariophantidae Godwin-Austen, 1888 and Urocyclidae Simroth, 1889. Although the slug genus *Dendrolimax* Heynemann, 1868 clearly belongs in Urocyclidae subfamily Urocyclinae and the large thick-shelled snails of the genus *Rhysotina* endemic on São Tomé form the subfamily Rhysotininae Schileyko, 2002 of the Urocyclidae, allocation of the remaining mainly endemic snails and semi-slugs from São Tomé and Príncipe to families is less clear.

This is partly because the genital anatomy of the four hitherto known species has remained undescribed except for a single small drawing for *Nanina thomensis* Dohrn in a largely overlooked paper (GIRARD, 1895: 32-33) otherwise devoted to *Thyrophorella thomensis* Greeff, 1882. The present study therefore describes the genital anatomy of three of the four known species along with that of four new species. This reveals that they form five undescribed and presumably mainly

endemic genera each with distinctive genital anatomy. It is difficult to place some of them within the recent classifications by VAN MOL (1970), VAN GOETHEM (1977), SCHILEYKO (2002b) and DE WINTER (2008). The present arrangement is therefore provisional and based on overall resemblance of characters of the distal genitalia, since it is clear that the helicarionoid group is in need of a phylogenetic analysis using both morphological and molecular data (DE WINTER, 2008: 474).

For Helicarionoidea, terminology of the mantle lobes and other external soft parts used here follows SOLEM (1966) and DE WINTER (2008). In all taxa described below the tail was longer than the forepart of the body; the foot sole was tripartite with a narrow central zone; the front edge of the sole separated from base of head by deep transverse groove. All these taxa also had two long upper tentacles with a small black eyespot near the tip when tentacle is expanded and two short hemispherical to very shortly cylindrical lower tentacles. Head warts or other protuberances on the front of the head were not seen.

## *Apothapsia* n. gen. D. Holyoak & G. Holyoak

**Type species:** *Nanina thomensis* Dohrn, 1866 (see below).

**Material examined:** >100 specimens of *A. thomensis*, from 16 localities on São Tomé, all in CGAH.

**Etymology:** Based on snail genus *Thapsia* Albers, 1860 of Helicarionidae, originally published as a subgenus of *Nanina* Gray, 1834 non Risso, 1826. Albers (in MARTENS, 1866: 56) did not state the derivation of the word *Thapsia*, but it appears to be Greek in origin. The new generic name therefore combines the Greek *Apo-* (meaning apart, or separate from) with *Thapsia*. Hence, like *Thapsia*, it is a feminine noun.

**Diagnosis:** Shell dextral, depressed-conical to nearly conical; breadth 9.3-13.0 mm at maturity; umbilicus deep, very

narrow to narrow; peristome simple; shell thin, somewhat translucent; periostracum whitish to brown, glossy, with weak and

inconspicuous sculpture. Body elongate, possessing tail horn; mantle-collar wide; left and right shell laps on mantle edges large, together covering most of exterior of shell when body fully extended. Distal

genitalia with long penis convoluted *in situ*, long epiphallus much convoluted *in situ*, lacking flagellum or caecum; vagina and free oviduct both moderately long; duct of bursa copulatrix short.

*Apothapsia thomensis* (Dohrn, 1866) n. comb. (Figs. 11A-C 12H-J)

*Nanina thomensis* Dohrn, 1866(a), Malak. Blätt., 13, p. 114-115, pl. 5 figs. 8-10; TL insula St. Thomé ad radices arborum.

Syn. *Helix chrysosticta* Morelet 1868, Voy. Fr. Welwitsch, Mollusques, p. 56, pl. 1 fig. 5; TL: "île San-Thomé avec la précédente" [i.e. with *H. welwitschii*, "dans les forêts élevées de San-Thomé"]; 5 syntypes in NHMUK (BREURE, ET AL., 2018: 240, fig. 208); *Nanina Molleri* Nobre, 1894 (p. 93, pl. 5 figs. 4); TL: Ile de S. Thomé; *Thapsia thomensis* var. *carinata* Germain, 1908 (p. 60); TL Bords du Rio Ouro (Ile de San-Thomé), described as a var. nov. on the basis of a single specimen; *Thapsia thomensis* Dohrn Var. *subthomensis* Germain, 1915 (p. 286); TL Agua Izè, entre 400 et 700 mètres d'altitude (Ile de San-Thomé); *Thapsia germaini* Connolly, 1925, Ann. Mag. nat. Hist., (9) 15 (88), p. 457, pl. 28 fig. 2; TL San Thomé (CONNOLLY 1925); holotype in MNHNP. *Nanina thomensis* Dohrn was treated as *Thapsia thomensis* (Dohrn) in later literature (e.g. GERMAIN, 1908: 60; 1916: 216-218, pl. 10 figs. 5-7).

Endemic on São Tomé! Shell figures: DOHRN (1866a: pl. 5 figs. 8-10), MORELET (1868: pl. 1 fig. 5), NOBRE (1894: pl. 5 figs. 4, as *N. Molleri*), GERMAIN (1916: pl. 10 figs. 5-7), BREURE ET AL. (2018: 240, fig. 208). Figures of genital anatomy: GIRARD (1895: pl. fig. 9), Fig. 11A-C.

MORELET (1868) described *Helix chrysosticta* without any reference to the description of *Nanina thomensis* by DOHRN (1866a). CROSSE (1868: 130) did not see specimens of either taxon, but after careful comparison of the original descriptions and figures noted that they "semble excessivement voisine". Subsequent authors have nevertheless recognised both species on the basis of small differences in the shells.

Although GERMAIN (1916: 313-314) recognised three species, it is clear from his comments that he regarded *Nanina Molleri* Nobre, 1894 as the end-point of a series of shell types with progressively higher spires, passing from *Thapsia chrysosticta* ("forma subdepressa"), through *T. thomensis* ("forma normalis") and *T. thomensis* var. *subthomensis* ("forma elata") to *T. Molleri* ("forma perelata"). CGAH material shows no differences in genital anatomy or body coloration between high-shelled and low-shelled animals. The shell shapes also intergrade completely in our material.

*Description:* Shell dextral, depressed-conical to nearly conical, with rounded spire and flatter base. At maturity, H 7.5-11.0 mm, B 10.4-13.0 mm, with 4.2-4.8 whorls. Protoconch small; whorls of spire rounded with shallow suture (which forms conspicuous narrow band or double line), increasing gradually, but with relatively larger body whorl that is evenly rounded in profile or with slight but definite angle forming upper edge of its periphery. Aperture rounded-oval except where interrupted by penultimate whorl; peristome thin, plane except for narrow reflected area around about half of umbilicus. Umbilicus very narrow (< 1 mm) but deep and usually exposing interior of spire. Shell thin, rather fragile, translucent when fresh but becoming opaque and whitish when old. Fresh shells pale brown to yellow-brown above, paler to whitish beneath, very glossy throughout. Protoconch smooth; teleoconch with inconspicuous sculpture comprised of faint irregular axial lines (mainly close below suture) and very faint irregular spiral microsculpture.

Body relatively long and slender, long tail ending dorsally in short-conical caudal horn (ca 1.5 mm long, raised, or near-horizontal and directed backwards in live snails), with large fossa in rear

end beneath. Mantle-collar wide, with left shell-lap and right shell-lap both large, thin, together covering much of exterior of shell of undisturbed live snails including top of spire, hence leaving minority of shell surface visible as broad arc (Fig. 12H); these shell-laps are withdrawn inside shell when snails are approached closely or touched (Fig. 12I, J). Snails preserved in IMS have exposed parts of body mainly whitish to pale pink, top of head and upper foreparts pale grey in some individuals; shell-laps dull pale pinkish to pale pinkish-grey; mantle-collar and mantle surface inside body-whorl and penultimate whorl marked with fine speckling and lines giving grey ground-colour (blackish-grey in darkest individuals), with large spots or conspicuous blotches of white. When living snails are disturbed the body flushes with orange-pink (Fig. 12J); when they are handled copious orange body-slime is produced that briefly stains human hands and the water in which specimens are drowned.

Distal genitalia were studied in six individuals, all from different localities. Genital pore on right-hand side of forepart of body, behind lower tentacle, directly beneath base of upper tentacle. Genital atrium short, dividing proximally on one side into distal end of penis, on opposite side into distal end of vagina, with narrow but well-defined short band of muscle attached to its outer proximal wall between those organs. Penis large, appearing broadly cylindrical in outline within a thin flexible outer sheath covering all but most distal part; coiled inner contents clearly visible through central portion of sheath. In two fully mature snails the distal penis and penis sheath were opened longitudinally, both specimens revealing (Fig. 11A-C): a short wide penis in distal part with thick muscular walls; this passing into central portion with narrower epiphallus coiled *in situ*; this in turn continuing into more slender epiphallus in proximal one-third of penis complex, where its tight and rather irregularly intertwined coils were firmly bound together with threads, bands and small sheets of strong connective tissue

suggestive of spider's web; at proximal end a small epiphallic caecum with penis retractor muscle attached terminally (muscle broken off in one snail; long, slender and passing proximally to columellar musculature in the other). Flagellum lacking. Vas deferens a slender tube throughout, passing from near distal end of spermoviduct distally alongside free oviduct then through vaginal-penial angle, returning proximally alongside exterior of penis sheath to pass through it close before proximal end of penis outer sheath, and so continue into proximal end of epiphallus. Vagina cylindrical, about two-thirds length of free oviduct, somewhat convoluted, with strong muscular wall; free oviduct of similar thickness to vagina, with thick muscular wall. Duct of bursa copulatrix short, less than half length of vagina and thinner than vagina; reservoir of bursa shortly ovoid, positioned alongside free oviduct, with thin strand of muscle arising at its proximal tip and passing proximally to join central part of prostate which is adherent to columellar side of spermoviduct. Right ommatophore retractor muscle passes through angle between distal penis and distal vagina.

*Comments:* The study by DE WINTER (2008) began the process of revising the large and heterogeneous assemblage of species that have been placed in *Thapsia* Albers, 1860 mainly on the basis of genital anatomy and to a lesser extent on shell characters. He did not discuss *A. thomensis*; although the figure of its genital anatomy by GIRARD (1895: 32-33) was accurate, it did not portray any features inside the penis sheath. Comparison of our observations with those of DE WINTER (2008) shows that *A. thomensis* resembles *Thapsia* s.s., *Saphtia* de Winter, 2008 and *Pseudosaphtia* de Winter, 2008 in having a distinct vagina and long penial epiphallus, with penial retractor muscle arising from end of a short epiphallic caecum. However, *A. thomensis* differs from all taxa placed in those genera in having a much smaller bursa copulatrix on a much shorter duct (so the reservoir lies alongside free oviduct not central part of spermoviduct), not having a

penial flagellum, and especially in having the very long proximal part of the epiphallus tightly bound into an ovoid mass inside the penis sheath, rather than free or much more loosely convolute *in situ*. Despite having a very similar shell, *Vanmolina* de Winter, 2008 differs markedly from all of these genera in lacking a vagina (so duct of bursa copulatrix and free oviduct both arise from genital atrium), penis with a large verge internally and a shorter epiphallus, characters perhaps suggestive of Urocyclidae rather than Helicarionidae.

In *A. thomensis* the total length of penis + epiphallus *in situ* before dissection was *ca* 12 mm, but after complete dissection of the very long epiphallus of the figured individual it was *ca* 37 mm ( $>3 \times$  shell diameter;  $ca\ 2 \times$  total length of extended body). However, only the distal part of the penis is likely to be everted during mating, so that the length of the intromittent organ will be

5-6 mm, approximately corresponding to the length of the vagina. The very short duct of the bursa copulatrix might imply that the (unknown) spermatophore is equally short, but this needs further study since a long epiphallus would normally imply that the spermatophore is equally long.

The following species is unknown anatomically and only tentatively referred to *Apothapsia*. Hence, only the type species *Apothapsia thomensis*, is securely referred to this genus. It is endemic to São Tomé, where it is probably the most common land snail in wooded habitats on the island, occurring in montane primary-forest, lowland secondary-forest and plantations, from near sea-level to at least 1400 m alt. Living snails are faster-moving than most land snails and climb freely on foliage of herbs, ferns, saplings, or banana plants, and on dead wood and tree trunks. They also rest under dead wood lying on the ground.

### *Apothapsia moreleti* (Germain, 1915) n. comb.

*Trochonanina* (*Trochozonites*) *Moreleti* Germain, 1915, Bull. Mus. d'Hist. Nat., 21 (7), p. 287; TL Vista Alegre, entre 200 et 300 mètres d'altitude; Água Izè, entre 400 et 700 mètres d'altitude (Ile de San-Thomé); GERMAIN (1916: 221-223, pl. 9 figs. 6-8, 12).

Syn. *Trochonanina* (*Trochozonites*) *Moreleti* Germain var. *fasciata* Germain, 1915 (p. 287); TL apparently as for the typical variety, but "beaucoup plus rare"; GERMAIN (1916: 222).

**Material examined:** All from São Tomé Island: 12 Dec. 2013, by EN1 between Lagoa Azul [Morro Carregado is the name on the military maps] and Praia Mutamba, N0.4006° E6.6075°, *ca* 5 m alt., dead/drifted shells from soil surface & debris by small dry stream-course above shore in lower edge of valley with cover of dry woodland, GAH & DTH ST12, 1 sh & 1 sh fragment; 24 Nov. 2018, near Quinta da Graça, N0.29928° 6.64174°, 678 m alt., scrub, gardens, roadside banks, with few trees, GAH & DTH 18-3, 1 sh; 2 Dec. 2018, São Tomé Island, just S of Milagrosa on the road between Trindade and Bombaim, N0.2766° E6.6598°, 398 m alt., secondary forest on slopes, abandoned cocoa plantations, trackside rock cuttings. GAH & DTH site 18-10, 1 sh; 11 Dec. 2018, by S. side of EN2 between the "roças" Fraternidade and Soledade (*ca* 1.6 km due S. of São João dos Angolares, centre), N0.1262° 6.6371°, 22 m alt., old cocoa plantations & bananas, under tall trees & palms, near stream (Água São Pedro), GAH & DTH 18-26, 1 sh.

**Description:** Based on four shells (+ one fragment) from four localities. H 4.02-4.42 mm, B 9.31-10.32 mm, H/B 0.42-0.45; AH 3.28-3.75 mm, AB 4.49-5.09 mm, AH/AB 0.73-0.76; UB 0.40-0.47 mm (UB/B 4.3-5.0%); whorls 4.2-4.6. Shell dextral, very depressed-conical with flatter base and rounded spire. Proto-

conch small, whorls of spire increasing regularly in size, slightly rounded above; suture shallow and appearing to form distinct narrow band or double line. Body-whorl not much wider than last part of penultimate whorl, with prominent angle at upper edge of periphery forming distinct keel; top

edge of keel concave, defining a rather indistinct narrow peripheral cord. Aperture oval in outline, with angle formed at periphery by keel and parietal area widely interrupted by penultimate whorl. Peristome thin, plane throughout except for narrow reflection of columellar margin near umbilicus. Umbilicus narrow, deep, exposing interior of spire, symmetrical, slightly overhung by edge of peristome. Protoconch somewhat corroded but remaining periostracum smooth; teleoconch with inconspicuous sculpture of fine irregular axial lines and very fine irregular microsculpture of spiral lines; periostracum of body-whorl also with minute closely-spaced granular or decussate pattern just visible at  $\times 56$  under intense light from low angles. Shell thin, apparently fragile, translucent when fresh. Protoconch whitish, teleoconch light brown and glossy throughout.

Because only empty shells have been found, features of the exterior of the body, genitalia, etc. remain unknown.

*Discussion:* The taxonomic position of this species in *Apothapsia* is provisional, awaiting revision when the genital anatomy can be described, since distinct genera that appear to be allied to *Thapsia* show few differences in shell characters (DE WINTER, 2008). Shells of *A. moreleti* differ from those of *A. thomensis* in having an obvious peripheral keel, whereas the keel in the latter species is commonly absent or at most very weak. The other consistent difference from *A. thomensis* is the darker brown shell coloration, while the flatter shells with lower spire, less swollen whorls of the spire and smaller adult shell size are almost consistent. All four of our localities for *A. moreleti* are in lowland habitats (5-678 m alt.), with altered vegetation, with no records from

intact native forests, whereas *A. thomensis* occurs up to at least 1400 m and it is plentiful in montane primary-forest as well as in lowland plantations. *A. moreleti* also appears to be much scarcer than *A. thomensis*, with single shells from three localities and two shells from the fourth. *A. thomensis* was present alongside *Thomitrochoidea trinidadensis* n. sp. at three of the four localities for the latter species (but unrecorded at 18-10, the type-locality). The disturbed habitats of *A. moreleti* probably increase the possibility that this taxon is an introduction to São Tomé from elsewhere in tropical Africa, but no obvious match for it has been found, its few sites were geographically well separated on the island and native endemic species were present at the same localities.

The two papers by GERMAIN (1915: 287; 1916: 223) gave partly conflicting localities on São Tomé for his new species, although all were in lowlands (700 m alt. at most). He also noted (GERMAIN, 1916: 223) that the species had probably been described but not named by MORELET (1868: 57). Var. *fasciata* Germain, 1915 was described as having “agrémentés, au dernier tour, d’une étroite fascie brune rigoureusement appliquée sur la carène et visible, par transparence, à l’intérieur de l’ouverture” and also noted as “beaucoup plus rare que le type”. None of our specimens has a brown shell band, which would be unusual in any genus allied to *Thapsia*. There is a possibility therefore that he had based var. *fasciata* on misidentified immature shells of the taxon we describe below as *Thomitrochoidea trinidadensis*, which are keeled and often possess a brown band such as he described, but we think this unlikely because that taxon differs in shell size, shape and sculpture.

UROCYCLIDAE Simroth, 1889  
Subfamily UROCYCLINAE Simroth, 1889  
*Dendrolimax* Heynemann, 1868 (p. 32)

Type species *Dendrolimax Heynemanni* Heynemann, 1868, by monotypy.

### *Dendrolimax greeffi* Simroth, 1889

*Dendrolimax Greeffi* Simroth, 1889, Nova Acta Acad. Leopoldino-Carolinae Germanicae Naturae Curiosorum, 54, p. 60, pl. 4 figs. 1, 2; TL: S. Thomé (based on a specimen collected by Greeff, so perhaps from Roça Santa Luzia [cf. GREEFF, 1882: 521, below], which VAN GOETHEM 1977: 106 accepted as TL). The following publications all listed *Dendrolimax Heynemanni* for São Tomé in the apparently erroneous belief that it was the same species as on Príncipe: GREEFF (1882: 521), CROSSE (1888a: 15), GIRARD (1893a: 33; 1893b: 111-112), GERMAIN (1916: 161).

Endemic on São Tomé! (VAN GOETHEM, 1977: 106, map 8, excluded specimens described from Rhodesia as *greeffi* by FORCART, 1967). Field observations and photographs of >20 slugs on São Tomé show this species is medium-sized and predominantly light brown, with irregular large whitish surficial patches: Specimens preserved in IMS (in CGAH) retain the light brown coloration. In contrast, the Príncipe species (*D. heynemanni*, see below) is all-white dorsally, sometimes larger, and it remains whitish when preserved in IMS. Figures of whole slug and of genital anatomy: SIMROTH (1889: pl. 4 figs. 1, 2).

SIMROTH (1889: 60) named the taxon from São Tomé as *D. greeffi* and pointed out differences from the taxon from Príncipe. The review by VAN GOETHEM (1977: 106) treated *D. greeffi* as a separate species but noted that the mainly anatomical differences described by Simroth may be at least partly due to the action of the liquid preservative or the degree of development of the animals examined. In conclusion, VAN GOETHEM (1977: 107) noted that “Quant au problème de savoir si *D.*

*greeffi* et *D. heynemanni* sont ou ne sont pas des espèces différentes, nous ne prenons pas encore de décision. Nous préférons d’abord examiner du matériel topotypique”. Thus, both species were listed by him despite the validity of *D. greeffi* being unconfirmed.

A mature specimen in CGAH dissected in 2014 (collected 3 Dec. 2013, on path towards Macambará, near Rio Manuel Jorge, N0.2847° E6.6097°, ca 1149 m alt., trackside, cultivation edges, scrub & small forest patches, GAH & DTH ST3) has genitalia much like those shown by VAN GOETHEM (1977: fig. 132) from Príncipe material, but the latter specimen is clearly immature whereas the ST3 specimen is mature. The only differences from the ST3 specimen appear to be (1) vagina and free oviduct appear longer; (2) flagellum appears shorter relative to caecum; (3) epiphallus 2 appears longer relative to epiphallus 1. These differences in proportions are likely to result from differing degrees of development, the somewhat stylised drawing by Van Goethem, or a combination of these.

### *Dendrolimax heynemanni* Heynemann, 1868

*Dendrolimax Heynemanni* “Dohrn” Heynemann, 1868, Malak. Blätt., 15, p. 35; TL Prinzeninsel [= Príncipe].

Endemic on Príncipe (see under previous species for erroneous reports from São Tomé). CROSSE (1888b: 299), noted it as “très abondante sur quelques points isolés de l’île du Prince. On la trouve sous et sur les feuilles des arbres et des buissons, à une hauteur qui varie entre 1 et 7 mètres. Elle rampe avec vivacité (H. Dohrn).”

Fig. of genital anatomy: SEMPER (1870: pl. 4, fig. 12); figures of genital

anatomy and shell: VAN GOETHEM (1977: figs. 131, 132).

VAN GOETHEM (1977: 102) gave the authorship as “Dohrn in Heynemann, 1868”. However, HEYNEMANN (1868: 35) stated: “Die einzige von Dohrn beobachtete Art saudte er mir, als *Dendrolimax Heynemanni* Dohrn.” Since there is no evidence that Dohrn supplied the description of the new species

(rather than just the name and specimens) for the paper in which Heyne-mann was sole author, it is appropriate to regard the latter as the author of the name.

Observations and photos of a living *Dendrolimax* found on Príncipe in 2018 showed it is sometimes larger than the São Tomé species and all-white externally, remaining whitish after preservation in IMS (CGAH). The coloration was confirmed by four specimens collected subsequently by FS and co-workers from Fundação Príncipe (now in CGAH), although one of them has the lateral fields of the sole of the foot dark grey.

This coloration matches the “schneewiss, selten citrongelb” described by HEYNE-MANN (1868). The persistent difference in dorsal coloration implies that the Príncipe and São Tomé populations should not be regarded as conspecific.

The genital anatomy of *Dendrolimax newtoni* Ortiz de Zárate & Alvarez, 1960 from Annobón was figured by VAN GOETHEM (1977: fig. 137). Although based on immature material, this taxon appears to differ from the endemic São Tomé and Príncipe taxa in possessing a distinct genital atrium rather than having it extremely short to absent as in *D. greeffi* and *D. heyne-manni*.

### Subfamily RHYSOTININAE Schileyko, 2002

#### *Rhysotina* Ancey, 1887 (p. 53)

“Types” listed as *Helix Welwitschi*, Mor[e]let, and *H. hepatizon*, Gould by ANCEY (1887: 53); *Helix welwitschi* Morelet, 1866 was selected by subsequent designation of ZILCH (1959). Syn. *Thomeonanina* Germain, 1909, p. 99; type species *Helix welwitschi* Morelet, 1866, by subsequent designation of SCHILEYKO (2002b: 1233).

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

*Helix hepatizon* Gould 1845, Proc. Boston Soc. Nat. Hist., 2, p. 38; TL “near the mouth of the Gaboon river”, corrected to San-Thomé by MORELET (1868: 54) and CROSSE (1868: 127).

Endemic on São Tomé! See HOLYOAK & HOLYOAK (2016) for synonymy, figures of shells and of distal genitalia.

#### *Rhysotina sublaevis* G. Holyoak & D. Holyoak, 2016

*Rhysotina sublaevis* G. Holyoak & D. Holyoak, 2016, J. Conch., 42 (3), p. 66, figs. 1D-G, 2, 3E-H; TL 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.

Endemic on São Tomé! See HOLYOAK & HOLYOAK (2016) for synonymy, figures of shells and of distal genitalia.

#### *Rhysotina welwitschi* (Morelet, 1866)

*Helix welwitschi* Morelet, 1866, J. Conchyl., (3rd ser.) 6, p. 153; TL “insula San-Thomé sinus Guineensis, ad 2,000 ped. altit. plagæ orientalis”; 5 syntypes at MNHN, 3 at NHMUK (figured), BREURE *ET AL.* (2018: 482).

Endemic on São Tomé! See HOLYOAK & HOLYOAK (2016) for synonymy, figures of shells and of distal genitalia.

Subfamily SHELDONIINAE Connolly, 1925

*Africarion* Godwin-Austen, 1883

*Africarion dumeticola* (Dohrn, 1866)

*Vitrina dumeticola* Dohrn, 1866, Malak. Blätt., 13, p. 119, pl. 5, figs. 1-4; TL "im Norden der Insel [Príncipe] auf der Pflanzung Azeitona".

Endemic on Príncipe. CROSSE (1888b: 299-300), based on translation of part of Dohrn's account, noted for *V. dumeticola*: "Hab. Azeitona, plantation située au Nord de l'île du Prince (H. Dohrn). Obs. Cette espèce vit sur les feuilles d'arbres, à une hauteur de 4 à 10 pieds. L'animal est jaune avec des tâches blanchâtres: il rampe avec vivacité H. Dohrn)." GERMAIN (1916: 161)

treated it as *Helicarion* (*Africarion*) *dumeticola* Dohrn, doubtless based on the reasonable assumption that the shells represent a vitriniform semi-slug from the Helicarionoidea rather than a member of the Vitrinidae. Nevertheless, the taxon is known only from shells, so its position in *Helicarion* (*Africarion*) should be regarded as provisional.

*Principicochlea* n. gen. D. Holyoak & G. Holyoak

**Type species:** *Principicochlea tenuitesta* n. sp.

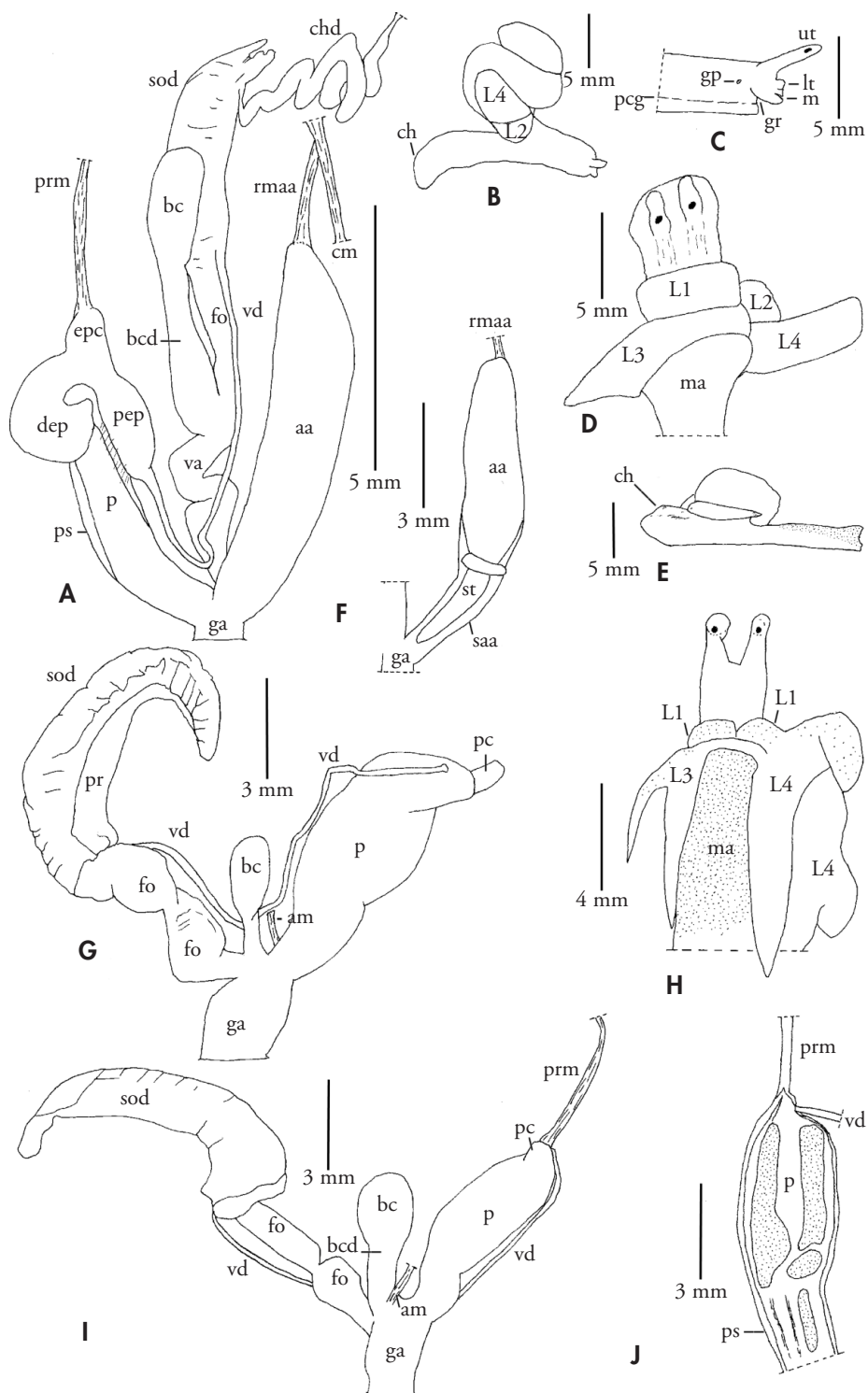
**Etymology:** *Principi-* is derived from the name of the island of Príncipe; combined with *cochlea* (snail shell, Latin, feminine). Like *cochlea*, the new name is thus a feminine noun.

**Diagnosis:** Shell dextral, subglobular with low spire, oval in outline, of up to 3.1 rapidly expanding whorls, maxi-

mum breadth up to 8.4 mm; umbilicus absent; aperture large with thin peristome. Shell very thin, transparent, un-

(Right page) Figure 10. Genital anatomy and external structures of bodies of *Principicochlea tenuitesta* n. sp. from Príncipe and *Tomithapsia bomsucessica* n. sp. from São Tomé. A-F: *P. tenuitesta* (holotype, except E); A: anatomy of distal genitalia; B: right-hand side of preserved specimen (shell removed) to show form of body and mantle laps; C: detail of forepart of right-hand side of body; D: dorsal view of forepart of body of preserved specimen with shell removed and mantle laps extended; E: right-hand side of specimen (paratype) preserved in IMS with shell present, the mantle laps retracted into shell; F: partly diagrammatic longitudinal section of atrial appendage. G-J: *T. bomsucessica*, paratypes; G, H: (site ST4); I, J: (site 18-6); G, I: distal genitalia (the penis retractor muscle broken off in G); H: dorsal view of forepart of body of preserved specimen with shell removed and mantle laps extended (grey pigmentation shown by stippling); J: partly diagrammatic longitudinal section of penis to show pilasters (stippled).

(Página derecha) Figura 10. Anatomía genital y estructuras corporales externas de *Principicochlea tenuitesta* n. sp. de Príncipe y *Tomithapsia bomsucessica* n. sp. de Santo Tomé. A-F: *P. tenuitesta* (holotipo, excepto E); A: anatomía de la genitalia distal; B: lado derecho del ejemplar preservado (sin concha) para mostrar la forma del cuerpo y los lóbulos del manto; C: detalle de la parte delantera derecha del cuerpo; D: vista dorsal de la parte delantera del cuerpo del ejemplar preservado con la concha retirada y los lóbulos del manto extendidos; E: lado derecho del ejemplar (paratipo) preservado en alcohol industrial metilado, con la concha presente, los lóbulos del manto retraídos en la concha; F: sección longitudinal parcialmente esquemática del apéndice atrial. G-J: *T. bomsucessica*, paratipos; G, H: (sitio ST4); I, J: (sitio 18-6); G, I: genitalia distal (el músculo retractor del pene roto en G); H: vista dorsal de la parte delantera del cuerpo del ejemplar preservado con la concha retirada y los lóbulos del manto extendidos (pigmentación gris mostrada por punteado); J: sección longitudinal parcialmente esquemática del pene para mostrar pilastras (punteadas).



calcified; periostracum dull yellow with weak sculpture. Body long; caudal horn a low blunt papilla; mantle lobes cover part of front and right-hand side of shell when snails active. Distal genitalia with short genital atrium dividing proximally into three: (1) a large atrial appendage (containing conical stimulator) terminating in a retractor muscle; (2) a moderately long vagina, and (3) a moderately long penis. Proximal end of penis with short caecum giving rise apically to penial retractor muscle and short epiphallus; flagellum lacking. Free oviduct and duct of bursa copulatrix both moderately long.

*Principicochlea tenuitesta* is placed in a new genus here because it shows a distinctive combination of characters of the genital anatomy different to those among the numerous other helicarioid semislugs known from tropical Africa (cf. VAN MOL, 1970; SCHILEYKO,

2002b). Thus, no other African genus combines: penis with well-developed epiphallus and retractor muscle arising from epiphallic caecum; lack of penial flagellum; vagina longer than free oviduct; presence of large atrial appendage with extrudable conical-cylindrical stimulator. The closest match appears to be with *Ratnadvipia* Godwin-Austen, 1899, a Sri Lankan endemic genus placed in Ariophantidae by SCHILEYKO (2002b: 1287), with a second species described by RAHEEM & NAGGS (2006). This would be a zoogeographically improbable ally, especially since both *Ratnadvipia* species have a much larger shell (B >18 mm), the bursa copulatrix lacking a separate duct, a much longer sarcobelum [atrial appendage] and apparently different penis structure, so they seem more likely to show convergent affinities rather than be closely related to *Principicochlea*.

***Principicochlea tenuitesta* n. sp.** D. Holyoak, G. Holyoak & F. Sinclair (Figs. 4B, 10A-F, 12F, G)

**Type material:** Holotype NHMUK 20200239, shell (B 8.38 mm) + bod, collected 19 Apr. 2019 by FS, A. Pedronho and A. Andrade.

**Type locality:** Príncipe Island, high on Pico Príncipe, N1.58202° E7.38262°, 860 m alt., in low mossy forest.

**Paratypes:** 1 sh (damaged) + bod, 6 spm in IMS and 1 spm in 96% ethanol, all collected with the holotype on same day at type locality.

**Etymology:** The species epithet derives from *tenui-* (meaning thin, Latin adjective) and *testa* (shell, Latin, feminine). The new species epithet *tenuitesta* thus agrees with the feminine generic name with its ending unchanged.

**Description:** Shell of holotype: H 4.29 mm, B (max.) 8.38 mm, B (min.) 6.97 mm, H/B 0.51, AH 4.22 mm, AB 4.96 mm, AH/AB 0.85, with 3.1 whorls; damaged shell of a paratype: B (max.) 7.91 mm, B (min.) 6.37 mm, with 3.0 whorls. Shell dextral, subglobular, with low rounded spire and flatter base, oval in outline. Protoconch small, whorls increasing rapidly and regularly, so body-whorl forms most of shell; whorls rounded at periphery; suture shallow, appearing as narrow band or double line. Aperture rounded-oval except where interrupted by penultimate whorl, in ventral view aperture not

extending beyond columellar axis, so interior of spire not visible in ventral view. Periostracum thin, plane except for minute reflected band close to columellar axis, the outer and lower palatal margins with narrow membranous fringe that shrinks when shell dries. Umbilicus absent. Sculpture low and weak on whole shell. Strong oblique lighting reveals protoconch with low closely-spaced axial riblets; teleoconch also with low irregular axial riblets and lines, with weak and very irregular spiral lines in few places (mainly near suture, visible at ×56). Protoconch whitish, teleoconch dull yellow, glossy

throughout. Shell very thin, transparent, uncalcified, flexible when moist, fragile and somewhat deformed when dry.

Body long relative to that of small shell, which is carried on body with the spire on right-hand side. Body of relaxed snails preserved in alcohol 18.5–20.0 mm long, of which tail forms up to 11 mm and slightly contracted forepart forms up to *ca* 9 mm. Tail somewhat higher than wide, rounded dorsally, tapering towards tip, the end of its dorsum with caudal horn forming low blunt papilla (Figs. 10E, 12G), beyond which extreme tip of tail appears rounded in dorsal view. Mantle lobes extend to cover a small part of exterior of right-hand side and front of shell when living snails are active and disturbed (Fig. 12F, G) and also in some specimens preserved in alcohol (Fig. 10B, E), but it is unclear whether they cover more of shell when the snails are undisturbed. Drowned and relaxed specimens in alcohol have four lobes that can be pulled outwards from the mantle edge (Fig. 10D), (1) a thick low frontal shell-lap, (2) low thick crescentic lobe 2.0 mm long on front right-hand side of body below #1, (3) a left shell-lap extending above #1 around front of body and continuing for *ca* 5 mm to end in point directed outwards and posteriorly on left-hand side of body, (4) a large thin oblong right shell-lap 5.5 mm long, above and mainly posterior to #2 on right-hand side of body. Sole of foot white. Exterior of body whitish, but light grey-brown dorsally on upper one-third to one-half of tail (the dark colouring widest posteriorly), top of foreparts and front of head pale brown, the ommatophore retractor muscles giving darker grey-brown streaks visible through translucent skin. Mantle surface inside shell dull yellow on outer part of body-whorl with few irregular blackish streaks, on inner part of body-whorl dark olive-brown with bold irregular bands of light yellow forming variable network of coarse markings. Digestive gland inside whorls 0–1.5 pale brown; a band of light yellow extending alongside inner suture to protoconch.

Genital anatomy (Fig. 10A–F) studied in holotype and a paratype. Genital pore located near mid-height on right-hand side of fore-part of body close behind base of upper tentacle. Genital atrium very short, dividing proximally into a long atrial appendage on one side, the distal penis on the other side, with distal vagina inserting between these organs. Atrial appendage very large (*ca* 8.5 mm long; longer than penis + epiphallus, equalling vagina + free oviduct, wider than both distal male and distal female tracts), thick-walled, with slender retractor muscle attached to proximal end; one specimen with thickened collar evident near distal end of appendage, from which a cylindrical stimulator with bluntly conical tip was extruded. Penis a long stout tube with muscular wall inside a thin outer sheath; epiphallus rather thin-walled throughout, curved, distal portion wider than penis, proximal portion thinner and separated by constriction (with outer wall of proximal portion attached by connective tissue to outer wall along proximal end of penis); epiphallic caecum near middle of curved epiphallus with retractor muscle attached to end of it which extends to insert on inside wall of diaphragm. Flagellum lacking. Vas deferens a thin tube, starting near distal end of spermoviduct, passing distally alongside free oviduct and vagina to near distal end of penis, returning proximally alongside penis to enter end of epiphallus. Vagina moderately long (somewhat longer than penis), with two bends when *in situ*, longer and stouter than free oviduct. Spermoviduct rather short (about equal to penis length); albumen gland not seen. Gonad inside digestive gland close to apex of spire, linked by convoluted tube of common hermaphrodite duct to near proximal end of spermoviduct. Duct of bursa copulatrix a stout cylinder just proximally to where it arises from junction of vagina with free oviduct, becoming thinner proximally. Bursa copulatrix shortly cylindrical, distinctly wider than adjacent portion of its duct, the reservoir

appressed to side of distal half of spermoviduct. Right ommatophore retractor passes between distal penis and vagina.

**Comments:** *Principicochlea tenuitesta* n. sp. is clearly different to Dohrn's *Vitrina dumeticola*, which has apparently not been refound. DOHRN (1866b: 119, pl. 5, fig. 1) figured a shell of that taxon with the aperture in ventral view extending beyond the columellar axis as a large rounded sinus, exposing the inside of the penultimate whorl of the spire, a feature lacking in *P. tenuitesta*. Furthermore, his text confirmed this in detail as he noted "columellaris recedens, valde arcuatus; margo anfractuum internus conspicuus" and "Unter den mir bekannten Arten steht ihr *V. nitida* Gould ziemlich nahe, auch unsere *V. diaphana* Drap. ähnelt ihr in der form", i.e. with receding columellar margin

resembling that in *Madeirovitrina nitida* (Gould, 1847) and *Eucobresia diaphana* (Draparnaud, 1805) as shown in his pl. 5 fig. 1.

Only the type species *Principicochlea tenuitesta* from Príncipe is referred to this genus, since *Vitrina dumeticola* Dohrn is clearly different, as discussed above. The type material and only specimens known of *P. tenuitesta* were collected from leaves in foliage above the ground in low mossy forest at 860 m alt. high on Pico Príncipe, which at 947 m forms the highest point of the island. Further research is needed to establish the extent of its range on the mountains of the island. Attempts to refind *Vitrina dumeticola* in the lowland Azeitona of north Príncipe are also needed in order to collect anatomical specimens to establish its taxonomic position.

### *Principitrochoidea* n. gen. D. Holyoak & G. Holyoak

**Type species:** *Helix folini* Morelet, 1848 (MORELET, 1848: 352).

**Etymology:** *Principi-* is derived from the name of the island of Príncipe; *Trochoidea* Brown, 1827 is the name of a genus of land snails (Geomitridae) that are similar in having the shell shaped like a spinning top toy. Like *Trochoidea*, the new generic name is a feminine noun.

**Diagnosis:** Shell dextral, conical to depressed conical with pointed apex, of small to medium size. Body elongate with long tail possessing a caudal-horn; rear end of body with deep caudal fossa. Mantle with well-developed collar, right mantle-lap and left mantle-lap. Distal genitalia having short genital atrium with penis, free oviduct and duct of bursa copulatrix all arising directly from its proximal end (vagina lacking). Large penis tapering proximally to long slender terminal caecum that ends in slender retractor muscle attaching to proximal end of spermoviduct nearby. Epiphallus and flagellum lacking. Free oviduct a rather thin tube shorter than penis. Duct of bursa copulatrix nearly as long as penis. Reservoir of bursa copulatrix wider than adjacent part of duct.

The new genus contains three species, *P. aglypta*, *P. folini* and *P. convexa* n. sp. All three occur on the island of Príncipe, reports from elsewhere being

only of *P. folini* from Angola, Gabon and Cameroon (GERMAIN, 1912b: 353-354) and Bioko (ORTIZ DE ZARATE, 1951; GASCOIGNE, 1994a: 2; DE ANDRÉS COBETA, 2001: 136-137; WRONSKI ET AL., 2014: 165, table 1). Separation of *Principitrochoidea* from other genera of Helicarionoidea is based mainly on characters of the distal genital anatomy, which has not been described previously. The literature is also unclear regarding the shell characters useful for identifying the species. We therefore give separate accounts of the bodies and genital anatomy of each species here, ending with a key for species identification based mainly on shells. The reasons why neither *Trochonanina* Mousson, 1869 or *Trochozonites* Pfeffer, 1883 are regarded here as earlier names for *Principitrochoidea* n. gen. are explained in the *Comments* under *P. folini*, since details of the genital anatomy and synonymy of that species are required for discussion.

*Principitrochoidea convexa* n. sp. G. Holyoak, D. Holyoak & F. Sinclair  
(Figs. 4C, 11D-G)

**Type material:** Holotype, NHMUK 20200240, shell (H 6.83, B 9.51 mm) + bod, collected 3 Dec. 2018, DTH, GAH & FS, at site 18-11.

**Type locality:** Príncipe Island, just S. of Santo António on road to Bela Vista, N1.6307° E7.4179°, ca 24 m alt., edges of secondary forest, trackside banks & cultivation.

**Paratypes:** All from Príncipe Island: from type locality (site 18-11) 3 sh; 4 Dec. 2018, path to Santa Joaquina, N1.6157° E7.3976°, 216 m alt., tall native forest with understorey of saplings, found on leaf-litter at base of steep flushed bank, GAH, DTH & FS 18-12, 12 sh (including 3 imm.) + 4 spm; 4 Dec. 2018, just S. of Santo António on road to Bela Vista, N1.6300° E7.4177°, ca 24 m alt., banana cultivation, edges of secondary forest by track, GAH 18-14, 9 sh (including 2 old & 1 imm.), 1 spm; 5 Dec. 2018, 1.5 km SW of Terreiro Velho, close to Oquê Pipi, N1.59965° E7.41082°, 308 m alt., tall native forest, GAH 18-16A, 6 sh (including 2 imm.) 1 sh + bod; 3 May 2019, Floresta de Ponto do Sol, N1.65121° E7.39728°, 198 m alt., tall secondary forest, leg. A. Pedronho & R. Fernandes 2019-05-03-1, 1 sh; 15 May 2019, Morro de Leste trail 2, N1.59631° E7.41166°, 375 m alt., tall disturbed native forest, leg. A. Pedronho, A. Andrade & R. Fernandes 2019-05-15-2, 3 sh.

**Other material examined:** From Príncipe Island, 4 Dec. 2018, path to Santa Joaquina, N1.6131° E7.3968°, 240 m alt., tall native forest with understorey of saplings (sampled by sieving), GAH, DTH & FS 18-13B, 3 sh (imm.).

**Etymology:** The epithet *convexa* is based on *convexus* (Latin, meaning convex or curved outwards), referring to the shell being more convex beneath than in the two congeneric species.

**Description:** Based on holotype and paratypes (with measurements only from mature shells), H 6.63-7.44 mm, B 9.11-9.92 mm, H/B 0.72-0.75; AH 4.49-5.09 mm, AB 4.76-5.03 mm, AH/AB 0.94-1.03; UB 0-0.34 mm (UB/B 0-3.5%); whorls 5.4-6.2. Shell dextral, above slightly depressed conical with pointed spire, below convex. Protoconch small; whorls increasing gradually at first, more rapidly in penultimate-whorl and body-whorl; whorls slightly rounded above; suture of moderate depth, appearing as narrow band or double line. Body-whorl slightly convex above periphery, deeply convex below it, with prominent peripheral keel above middle of whorl height; top edge of keel bordered with narrow concavity or flat area, resulting in low peripheral cord around outermost edge. Aperture almost round except where intersected by penultimate-whorl and at just above mid-height of palatal margin where keel forms angle of ca 120° with small internal sinus. Peristome thin, mainly plane, but end of columellar margin widely reflected at umbilicus. Umbilicus narrow and deep, most often fully overlapped by reflected peristome in mature shells, although usually visible in

oblique view. Protoconch smooth or sometimes with faint spiral microsculpture. Teleoconch often with low, rather widely and evenly spaced, axial-tangential ribs which are almost straight; rib-crests in some shells with small curved hairs up to 0.3 mm high; in other populations ribs weak or almost lacking. Shell surface between ribs with minutely decussate sculpture just visible at ×56 using strong oblique illumination. Underside of shell smooth except for very low irregular axial riblets. Shell thin, rather fragile, translucent; colour light brown to brown; waxy lustre above, glossy below.

Body elongate with long tail; caudal-horn long (2.5 mm), tapering apically to slender point that extends backwards beyond end of body; end of body with deep caudal fossa with large diamond-shaped external opening. Mantle-collar a broad flap extending around most of periphery of body, widest anteriorly. At front edge its lower part is thicker and muscular, upper part thinner, the latter ending at each side in mantle-laps directed backwards. The right mantle-lap starts in a more posterior position than the left mantle-lap, but they are variable between individual snails in length (2-3

mm) and either right-lap or left-lap may be widest. Exterior of body mainly whitish, but pale brown on dorsum of front end and caudal-horn light grey. Mantle-laps whitish; mantle inside shell very pale brown with scatter of large white spots on right-hand half; body inside middle of spire blackish-brown; digestive-gland in upper spire light brown.

Genital pore located just below mid-height towards front of right flank of body, slightly in front of base of upper tentacle; its external lips slightly swollen around the concealed pore. Genital atrium a short tube, dividing proximally on one side into distal penis, on opposite side into distal end of free oviduct, with exit from large duct of bursa copulatrix in between these organs. Penis large, its distal portion tubular, widening at distal end of longer proximal portion, which then tapers proximally to long slender terminal caecum that ends in slender retractor muscle attaching to proximal end of spermoviduct nearby. Epiphallus and flagellum lacking. Longitudinal section of penis (Fig. 11G) reveals distal portion with single muscular wall, longer proximal portion with double muscular wall (inner wall joined to outer wall by many strands of connective tissue); interior surface of (inner) wall of most of penis with longitudinal muscular pilaster, largest in distal portion where semi-circular in cross-section, becoming lower and narrower proximally as it extends along most of length of lumen of proximal penis. Vas deferens starts near distal end of spermoviduct, passing distally alongside free oviduct to distal end of duct of bursa copulatrix and near distal end of distal penis, returning proximally alongside penis and entering tip of penis at base of its terminal caecum. Vas deferens a  $\pm$  narrow tube throughout almost all of its length, but at level of distal penis a prominent bulge somewhat longer than wide begins and ends rather abruptly, its thickness about double that on each side. The bulge present in both specimens studied; the most mature specimen also had vas deferens thickened and convoluted alongside proximal penis, with conspicuous white contents.

Vagina lacking. Free oviduct a rather thin tube only about half length of penis, its distal section slightly wider with a thin translucent external wall, its proximal section thinner but with a thicker wall. Duct of bursa copulatrix wide and thick-walled, tapering proximally, nearly as long as penis; reservoir of bursa copulatrix wider than adjacent part of duct, in one specimen joined apically to proximal end of prostatic part of spermoviduct by thin strands of tissue; in other specimen not obviously joined and reservoir swollen (with remains of spermatophore?). Spermoviduct rather short (wide part only two-thirds length of penis, but with shorter and more slender proximal section); albumen-gland short, arcuate; common hermaphrodite duct a narrow tube (broken-off proximally). Right ommatophore retractor passes between distal penis and duct of bursa copulatrix.

*Comments:* The terminology of organs of the penis complex in this genus is problematical, partly because their functions are uncertain. The proximal continuation of the penis is described as a "terminal caecum" here because it appears to arise directly from the penis and a small muscle attached to its most proximal part is likely to function as a penial retractor. The alternative of terming it an epiphallus is avoided because the vas deferens inserts at or just beyond its distal end. Nevertheless, it is possible that the tail of the spermatophore forms within this "terminal caecum" and if so the term "flagellum" might be more appropriate, although a retractor muscle arising apically would not be expected when that term is used.

*P. convexa* shares the distinctive characters of *P. folini* which support separation of *Principitrochoidea* from *Trochonanina*. However, the two species differ considerably in the internal structure of the penis, with a distal verge and small lateral caecum present in *P. folini*, whereas *P. convexa* n. sp. lacks both but has a muscular longitudinal pilaster on the inner wall of the penis lumen.

Our records of *P. convexa* were from a wide variety of habitats at 24-375 m

alt., including gardens with banana plants and bushes, secondary forest and its edges and (repeatedly) in tall native forest. At least some of the living individuals were collected from foliage above the ground. At site 18-12 it was living in forest with both *P. aglypta* and *P. folini*.

The Key below differentiates *P. convexa* from congeners. Since this

species was not reported by collectors active on Príncipe during the nineteenth century, it is unclear whether it was overlooked by them or it has arrived on the island since then as an introduction. Its occurrence at several sites in native forest far from human habitation may imply that it was previously overlooked, or if it is not native, that it has spread widely.

### *Principitrochoidea folini* (Morelet, 1848) (Fig. 11H, I)

*Helix Folini* Morelet, 1848, Rev. Zool., 11, p. 352; TL insulam Principis sinus Guineensis. Syntypes were formerly in NHMUK, but they were not re-located by BREURE *ET AL.* (2018: 287).

*Trochonanina* (*Trochozonites*) *Folini* Morelet: GERMAIN (1912b: 353-354), giving records from Príncipe from Roça Infante D. Henrique, 100-300 m alt.; Bahia do Oeste, 100-200 m alt.; in footnote 2, he treated *Trochonanina percarinata* of MARTENS (1876, Monatsb. Königl. Akad. Wiss. Berlin, p. 256, pl. 1, figs. 16-18) as *Trochonanina* (*Trochozonites*) *Folini* var. *percarinata* Martens but this appears to be incorrect (see *Comments* below).

*Trochonanina aglypta* (Dohrn, 1866) *sensu* COSSIGNANI (2014: 194), non Morelet, 1848 (error of identification; the locality "São Tomé" given by Cossignani is presumably also erroneous).

*Trochozonites folini* (Morelet, 1848): BREURE *ET AL.* (2018: 287, fig. 417).

**Material examined:** All from Príncipe Island, 3 Dec. 2018, just S. of Santo António on road to Bela Vista, N1.6307° E7.4179°, ca 24 m alt., edges of secondary forest, trackside banks, cultivation, GAH, DTH & FS 18-11, 1 sh + bod; 4 Dec. 2018, path to Santa Joaquina, N1.6157° E7.3976°, 216 m alt., tall native forest with understorey of saplings, found on leaf-litter at base of steep flushed bank, GAH, DTH & FS 18-12, 6 sh (including 2 old & 3 imm.); 4 Dec. 2018, just S. of Santo António on road to Bela Vista, N1.6300° E7.4177°, ca 24 m alt., banana cultivation, edges of secondary forest by track, ca 24 m alt., GAH 18-14, 9 sh (including 2 old & 1 imm.), 1 sh + bod, 1 spm; 5 Dec. 2018, by road N. from Santo António, N1.64506° E7.41998°, 58 m alt., by plantation of bananas, etc., GAH 18-17, 2 sh (old).

**Description:** Compared to the somewhat larger *P. convexa* n. sp. described in more detail above, the caudal-horn of *P. folini* is longer (3.5 mm). The arrangement of its mantle-collar and laps is similar, although the mantle-collar is less wide and the mantle-laps are shorter (right-lap 1.7 mm, left-lap 1.3 mm). Its body coloration is darker, with exterior of body light grey, shading to pale grey on foot fringe and dorsum of rear part of body beneath shell; tail horn is grey. Mantle-collar grey; mantle surface inside shell (sample 18-14) pale grey-brown with only small and faint dark markings or (sample 18-11) grey with minute blackish speckling.

Genital anatomy (Fig. 11H, I) has similar general structure to that of *P. convexa* described in more detail above.

Its penial terminal caecum is even longer in proportion to penis length, when *in situ* resting against spermiduct; proximal tip of terminal caecum missing in one specimen and likely to be incomplete in other, so no muscular attachment seen. Terminal caecum thinner-walled than penis. Penis large with narrower distal portion forming only one-fifth of total penis length; proximal portion mainly cylindrical, but tapering proximally into terminal caecum. Longitudinal section of penis studied in one specimen (Fig. 11I) reveals thin muscular outer sheath along full length of proximal penis, continuing as thinner membranous sheath over distal penis. Inside sheath, central axis formed by thick muscular-walled tube running almost full length of penis,

with small rounded lateral caecum directed backwards just distal of the middle. Middle part of the tube free of penis sheath, but proximal one-third of it and the distal end firmly attached to inside of sheath by connective tissues; tube widening at its distal extremity, apparently forming a verge. Thus penis probably partly eversible with verge forming intromittent organ. Vas deferens stout and convoluted in section adjacent to proximal penis; with white "globular process" on section near distal penis. Bursa copulatrix larger, ovate, when *in situ* appressed to prostatic side of sperмовидuct.

*Comments:* *Trochonanina percarinata* Martens, 1876 was described from Bonjongo ["im Camerun-Gebirge"]. GERMAIN (1912b: 353-354, footnote 2) treated this taxon as *Trochonanina* (*Trochozonites*) *Folini* var. *percarinata* Martens. The original description of the genus *Trochozonites* Pfeffer, 1883 (p. 23) included only two species, both from Bonjongo, *T. percarinatus* and *T. ibuensis* L. Pfeiffer, without designating a type species; CONNOLLY (1912) subsequently designated *T. percarinata* Martens, 1876 as the type species. In view of this history, it is unsurprising that VERDCOURT (1982) placed *P. folini* in the genus *Trochozonites* Pfeffer, 1883.

In the protologue, PFEFFER (1883: 23) referred to "Genitalen s. Archiv. l. c. p. 421" but the citation followed his reference to *Archiv für Naturgeschichte* given erroneously as 1877 instead of 1878. This may explain why details of the genitalia presented by PFEFFER (1878: 421-422, pl. 13 fig. 5) have been overlooked, e.g. by SCHILEYKO (2002: 1245). From the clear description and figure of genitalia provided for *T. percarinata* by Pfeffer it is evidently not conspecific with *P. folini*, and indeed too widely different to be regarded as congeneric with it. Pfeffer figured genitalia with a long bursa copulatrix duct arising proximally to a definite vagina (not from the genital atrium as in *P. folini*); he figured and described a penis sheath enclosing a highly convoluted inner penis (not the simpler and nearly straight inner penis of *P. folini*);

he figured and described a penial flagellum originating at the proximal end of the penis opposite the junction with the vas deferens (whereas a flagellum is lacking in *P. folini*); and the penis was not continued proximally into a very long caecum as it is in *P. folini*. It remains possible that either Pfeffer or Germain had misidentified material of *percarinata* in front of them, although PFEFFER (1883: 23) gave only the locality "Bonjongo, Buchholz" for *percarinatus*, which is likely to imply he studied the original material of the species, or at least topotypes. Thus Germain was apparently incorrect in regarding *T. percarinata* as a variety of *folini*, which might have resulted from *T. percarinata* having a rather featureless thin corneous shell with almost flat whorls that have only weak sculpture.

VERDCOURT (1984) and SCHILEYKO (2002b: 1245, fig. 1637) described and figured the anatomy of *Trochozonites medjensis* (Pilsbry, 1919), which differs markedly from *P. folini* in the structure of its penis, with a well-developed epiphallus bearing a short caecum, a long flagellum, and penial retractor muscle that arises directly from the epiphallus near the base of the caecum. *Principitrochoidea folini* also shows several clear differences in its distal genital anatomy from *Trochonanina mozambicensis* (L. Pfeiffer, 1855), the type-species of *Trochonanina* Mousson, 1869 described and figured by SCHILEYKO (2002b: 1278-1279, fig. 1682). Thus, *T. mozambicensis* has a moderately long vagina, a distinct epiphallus, a short free flagellum and a large penial gland, all lacking in *P. folini*. Nevertheless, they share the peculiar swelling in the middle part of the vas deferens (termed "globular process on middle portion" by Schileyko), lacking so far as known in other helicarionoids. Along with the shared trochoid shell shape, this character is likely to suggest affinity of these genera. However, it seems best to introduce a new genus for the three species occurring on Príncipe which all have rather similar genital anatomy and shells.

*P. folini* was recorded by us from 24–216 m alt., mainly in disturbed habitats and cultivated areas, but also in numbers at a site in tall native forest with understorey of saplings, away from human habitation. At the latter locality, it was living near both *P. aglypta* and *P. convexa*. Since the species is well known on Bioko and in neighbouring countries of the African mainland (see

above under genus heading), it might have originally been introduced to Príncipe, despite its first discovery on the island being in 1848 or earlier.

COSSIGNANI (2014: 194) figured a shell as “*Trochonanina aglypta*” with locality given as São Tomé that clearly represents a misidentified *P. folini*, but this species has never been reported otherwise from São Tomé

### *Principitrochoidea aglypta* (Dohrn, 1866)

*Nanina aglypta* Dohrn, 1866, Malak. Blätt., 13, pp. 119–120, pl. 5, figs. 5–7; TL Ilha do Principe in “silvis montosis ad Lappa d’Oeste”. Treated as *Trochonanina aglypta* Dohrn by Germain (1912b: 340) and *Trochonanina* (*Trochozonites*) *aglypta* Dohrn by Germain (1916: 162).

**Material examined:** All from Príncipe Island, 4 Dec. 2018, path to Santa Joaquina, N1.6157° E7.3976°, 216 m alt., tall native forest with understorey of saplings, found on leaf-litter at base of steep flushed bank, GAH, DTH & FS 18–12, 3 sh + 1 bod; 15 Apr. 2019, Pico Príncipe campsite, N1.59665° E7.37301°, 265 m alt., tall native forest, leg. Y. dos Santos 2019-04-19-2, 2 spm; 3 May 2019, Floresta de Ponta do Sol, N1.65121° E7.39728°, 198 m alt., tall secondary forest, leg. A. Pedronho & R. Fernandes 2019-05-03-2, 1 sh; 15 May 2019, Morro de Leste trail 2, N1.59967° E7.41085°, 344 m alt., tall disturbed native forest, leg. A. Pedronho, A. Andrade & R. Fernandes 2019-05-15-3, 1 spm.

**Description:** Largest specimen drowned and preserved in alcohol has partly hunched body 9.5 mm long; another smaller but less hunched specimen preserved in the same way has body 12.5 mm long. Caudal-horn is proportionately very long (3.3 mm on largest body, 4.2 on smaller body), conical basally with filiform tip 1.4 mm long, erect, arched forwards, but it would project considerably beyond tail tip if lowered. Beneath the caudal-horn the caudal fossa is evident as a round hole on the end of the tail. Mantle-laps proportionately long, very elongate triangular tapering to sharp point, in largest specimen right-lap 2.4 mm, left-lap 3.5 mm with separate 2.0 mm process conjoined to outer edge. External parts of body mainly light grey, shading to pale grey on foot-fringe; caudal horn grey; dorsum whitish beneath shell on base of tail and on sole of foot; dorsum of front of body blackish, with blackish ommatophore retractor muscles showing through translucent skin. Mantle-collar and flaps light grey with whitish middle band. Mantle

surface inside shell pale but with blackish closely spaced minute spiral lines giving greyish effect overall. External body-wall of whorls inside spire with blackish spiral lines.

An apparently immature specimen has genital pore on right-hand side of body, one-third up from base of foot below base of upper tentacle. Genital anatomy studied in single specimen which nearly mature but with damage around head and genital atrium. Penis large and long, with structure ± as in *P. folini*; membranous sheath lost from distal end where verge with slit-like end pore remains intact; terminal caecum nearly as long as penis, curved, cylindrical, thin, when *in situ* attached to prostatic side of spermiduct, with fine retractor muscle arising at its proximal tip and passing distally to join underside of proximal part of spermiduct. Vas deferens passes distally as thin tube alongside free oviduct, with white “globular process” level with distal penis, becoming thick and convoluted where passing alongside inner edge of penis, inserting at tip of penis. Vagina

nil or almost nil, with free oviduct arising as thin tube alongside thicker tube of bursa copulatrix duct from (remains of) genital atrium beside distal end of penis. Bursa copulatrix large and ovoid with thin wall.

*Comments:* DOHRN (1866b: 119-120, pl. 5, figs. 5-7) described this species on the basis of a single shell containing a dried body found by a local helper. There have been no subsequent reports of it being collected. Our discovery of a third species of the genus on Príncipe necessitates critical reassessment of the identity of Dohrn's material. This is made more difficult because his main collection was formerly housed in the Museum at Stettin (now Szczecin, Poland) and destroyed in the 1939-45 war (DANCE, 1986: 210), although some Dohrn material is still in the Museum and Institute of Zoology of the Polish Academy of Sciences in Warsaw (HERBERT & MOUSSALLI, 2010: 114). Fortunately, however, Dohrn made it clear that his shell was as high as wide with aperture wider than high ("Diam. maj. 10, min. 9, alt. 10, apert. lat. 5, alt. 4 mill.") and his figures confirm these pro-

portions. He also described the sculpture as "radiato-striatulus" and followed the account of *N. aglypta* with comments on newly collected *Nanina Folini*, pointing out that the latter had the suture "vielmehr canalförmig" with a weak spiral rib beneath, and thus making it clear that the two species were different.

The dissection of our single damaged subadult specimen of *P. aglypta* shows enough of its genital anatomy closely resembles that of *P. folini* to confirm the place of this species in genus *Principitrochoidea*. Furthermore, it resembles *P. folini* rather than *P. convexa* n. sp. in having a well-developed distal verge in the penis.

Unlike the other two species we place in this genus, *P. aglypta* is known only from forest habitats, at 198-344 m alt. All of our four records were from tall forest, three of them noted as native forest (disturbed forest at one locality) the fourth as secondary forest. At site 18-12 it occurred with both *P. folini* and *P. convexa* n. sp. The only previous record was of the type specimen, recorded as from "silvis montosis" (mountain forest).

#### Key to species of *Principitrochoidea* based mainly on shell characters

1. - Upper edge of body-whorl just below suture with concave channel bordered below by spiral rib; periostracum of body-whorl with coarse sculpture of axial ribs bearing stiff erect hairs, the longest of them >0.5 mm long . . . . . *P. folini*  
 - Upper edge of body-whorl just below suture often with narrow flatter strip but lacking concave channel bordered by spiral rib; periostracum of body whorl smooth or with sculpture of axial ribs; if erect hairs present these <0.5 mm long . . . . . 2
2. - Shell wider than high (H/B 0.7-0.8); base of shell usually more convex (so keel in apertural view normally on upper half of peristome); body-whorl smooth above or with  $\pm$  strong axial ribs; penis lacking distal verge (Fig. 11G) . . . . . *P. convexa* n. sp.  
 - Shell about as wide as high (H/B 0.8-1.1); base of shell less convex (so keel in apertural view usually around middle of peristome or on its lower half); body-whorl with sculpture of fine axial riblets; penis with distal verge . . . . . *P. aglypta*

#### *Thomithapsia* n. gen. D. Holyoak & G. Holyoak

Type species: *Thomithapsia bomsucessica* n. sp.

**Etymology:** Based on *Thomi-* from an old name (île de Saint Thomas) for São Tomé island and snail genus *Thapsia* Albers, 1860 of Helicarionidae (see comments above under *Apothapsia* regarding apparent Greek origin of *Thapsia*). Like *Thapsia*, it is a feminine noun.

**Diagnosis:** Shell dextral, depressed-conical with rounded spire, breadth up to 13.3 mm; umbilicus narrow but deep. Up to 5.7 whorls that increase gradually in width; upper edge of periphery weakly keeled in immature shells, almost rounded in adults; suture moderately deep. Aperture rather large; peristome thin, plane except close to umbilicus. Shell thin, slightly translucent, glossy, with weak sculpture. Body with caudal horn up to 2 mm long; mantle-collar wide with two lobes projecting

forwards; each side of body with a separate free shell-lap. Distal genitalia with well-developed genital atrium dividing into three at proximal end: (1) penis, rather long and bulky, with short caecum at proximal end giving rise to penial retractor muscle; epiphallus and flagellum lacking; (2) bursa copulatrix with ovate reservoir, on duct slightly longer than the reservoir; (3) moderately long free oviduct, its distal portion distinctly thicker-walled than proximal portion.

***Thomithapsia bomsucessica* n. sp.** G. Holyoak & D. Holyoak (Fig. 4D, 10G-J)

**Type material:** Holotype NHMUK 20200241, shell (H 6.97, B 12.33 mm) & bod, collected 4 Dec. 2013, by GAH & DTH at site ST4.

**Type locality:** São Tomé Island, path to Lagoa Amélia from Bom Sucesso Botanical Garden, N0.2786° E6.6000°, ca 1300 m alt., montane forest on slope with understorey of saplings.

**Paratypes:** All from São Tomé Island: 1 sh (dead when found) from type-locality; 3 Dec. 2013, on path towards Macambará, near Rio Manuel Jorge, N0.2847° E6.6097°, ca 1149 m alt., trackside, cultivation edges, scrub & small forest patches, GAH & DTH ST3, 1 sh; 24 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.2912° E6.6057°, ca 1289 m alt., montane rainforest on ridges & slopes, GAH, DTH, *et al.*, 18-2, 3 spm; 24 Nov. 2018, near Quinta da Graça, N0.29928° E6.64174°, 678 m alt., scrub, gardens, roadside banks, with few trees, GAH & DTH 18-3, 1 sh; 27 Nov. 2018, Morro Claudina (near Bom Sucesso), N0.2918° E6.6059°, 1254-1292 m alt., montane rainforest, GAH & DTH 18-6, 1 sh & bod; 9 Dec. 2018, path to Lagoa Amélia from above Bom Sucesso Botanical Garden, N0.2823° E6.5964°, 1290-1415 m alt, montane forest, GAH & DTH 18-21, 2 sh & 2 spm.

**Etymology:** The epithet *bomsucessica* is an adjective based on the name of Bom Sucesso (in distrito de Mé-Zóchi), on São Tomé island, the location of the famous Botanical Garden and close to the collection localities of most specimens of the new species.

**Description:** Based on holotype and paratypes (with measurements only from mature shells), H 6.97-8.31 mm, B 12.33-13.33 mm, H/B 0.57-0.64; AH 5.03-5.90 mm, AB 5.90-6.70 mm, AH/AB 0.85-0.91; UB 0.27-0.47 mm (UB/B 2.2-3.5%); whorls 5.2-5.7. Shell dextral, depressed-conical with rounded spire and flatter base. Protoconch small; whorls increasing gradually, with body-whorl expanding more rapidly to rather wide aperture; suture moderately deep, appearing as narrow band or double line. Body-whorl rounded at periphery, with slight hint of weak keel on upper edge of periphery that is much more obvious in immature shells. Aperture broadly oval except where interrupted by penultimate whorl. Peristome thin and plane, narrowly reflected close to adjacent half of umbilicus; lower palatal

margin with convex edge in ventral view. Umbilicus funnel-shaped above the narrow interior (where UB measured), deep, exposing spire internally, almost symmetrical, slightly overlapped by reflected peristome. Shell sculpture weak throughout; protoconch mainly smooth, with weak spiral microsculpture in places; adapical and basal surface of teleoconch with low irregular axial riblets and closely-spaced fine spiral grooves. Shell thin, rather fragile, slightly translucent. Protoconch and inside of umbilicus whitish, otherwise shell colour a rather bright light brown; periostracum glossy on upper whorls, with less gloss or waxy lustre on body-whorl.

Body relatively long and slender; long tail ending dorsally in caudal horn (moderately tall, nearly erect, 2.0 mm

high at front edge), with large caudal fossa in rear end beneath. Mantle-collar wide, with two small rounded lobes projecting forwards over fore-part of body (L1) and large projecting shell-laps on both sides of body (Fig. 10H). The left shell-lap (L3) ca 4 mm wide, with long loose flap having pointed tip directed posteriorly; the right shell-lap (L4) ca 5 mm wide, with long loose flap directed posteriorly having pointed tip and another round-tipped free flap extending outwards from anterior edge. The shell-laps are withdrawn inside shell when snails are approached closely or touched.

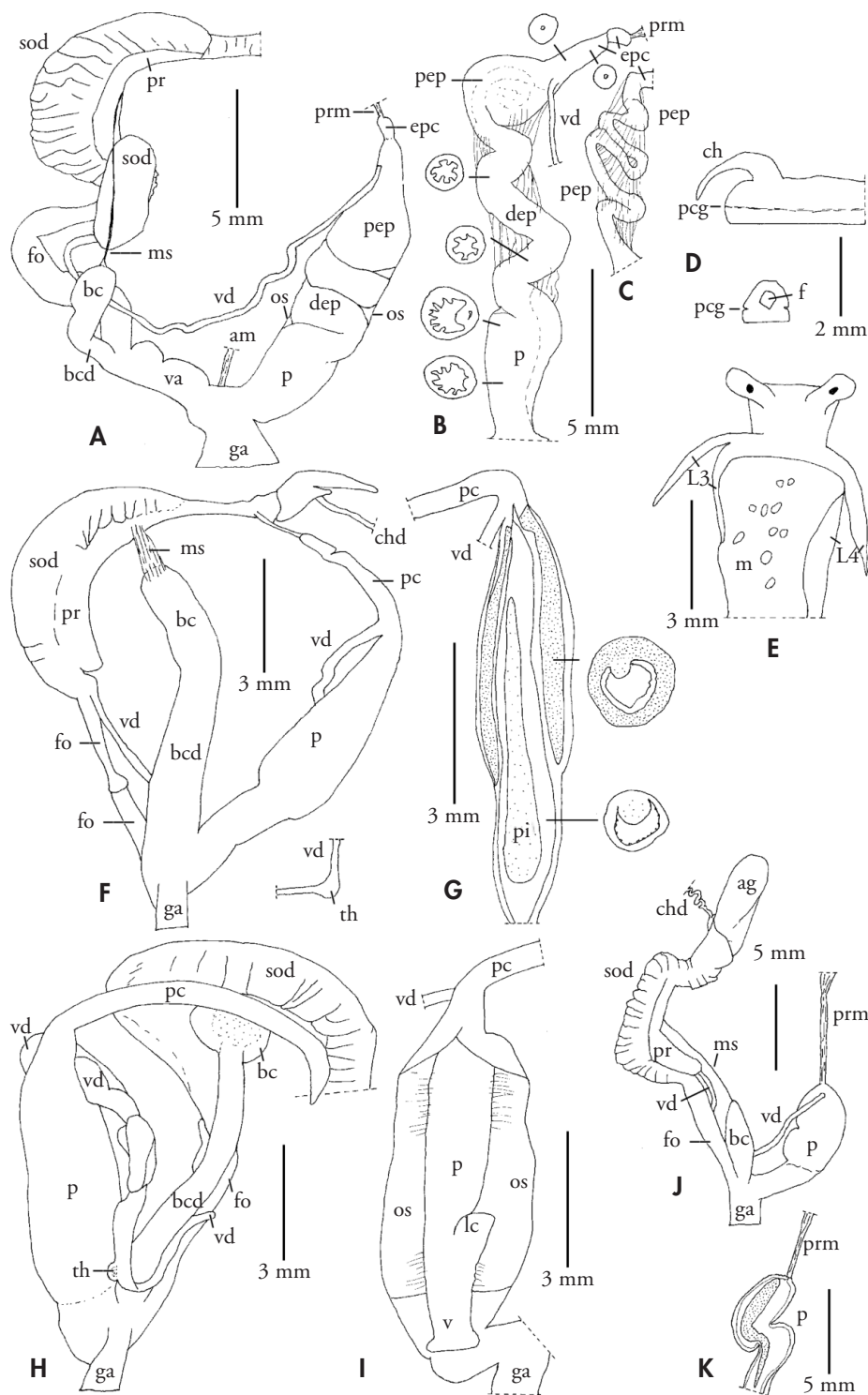
Bodies of darker specimens preserved in IMS have exposed parts of body pale grey above, whitish on foot-fringe and sole of foot, mantle-laps pale to light grey dorsally, dorsal surface of mantle inside shell dark grey to nearly

blackish with pale lower fringe. Bodies of lighter specimens are mainly whitish externally, shading to very pale brown high on flanks and on mantle-laps, to light brown on dorsum of fore-part and front of face; the ommatophore retractor muscles showing as dark grey through translucent skin. These have mantle inside shell dorsally blackish-grey, its left-hand edge whitish; digestive gland inside spire dark brown.

Genital anatomy studied in two mature individuals (sites ST4, ST18-6). Genital pore on right flank of forepart of body below base of right ommatophore at about one-third height, with surrounding tubercles whitish. Genital atrium a cylinder of medium length, its proximal end dividing into distal end of penis and distal end of vagina, with duct of bursa copulatrix inserting between these. A short but definite

(Right page) Figure 11. Genital anatomy and external features of body of Helicarionoidea. A-C: *Apothapsia thomensis* (São Tomé, by EN1 well S. of Santa Catarina & inland of NW. coast, N0.2405° E6.4722°, ca 68 m alt., secondary-forest, 1 Dec. 2013, GAH site ST1), all based on same snail; A: distal genitalia; B: detail of penis with coils of epiphallus partly separated and with diagrammatic transverse sections; C: detail of proximal epiphallus only, with coils separated further. D-G: *Principitrochoidea convexa* n. sp. (Príncipe, site 18-16A, paratypes); D: lateral view of tail to show caudal horn and diagram of caudal fossa viewed from rear; E: dorsal view of foreparts of preserved body with shell removed and mantle laps spread (also showing white spots on mantle); F: distal genitalia with detail of thickened part of vas deferens; G: partly diagrammatic longitudinal section of penis (showing pilaster on inner wall of lumen with light stipple, muscular thickening of wall of penis with heavier stipple) and two transverse sections. H, I: *Principitrochoidea folini* (Príncipe, site 18-14, see text); H: distal genitalia; I: detail of penis with outer sheath opened. J, K: *Thomitrochoidea trindadensis* n. sp. (holotype, São Tomé, site 18-10); J: distal genitalia; K: diagrammatic longitudinal section of penis to show pilaster (stippled) on inner wall of lumen.

(Página derecha) Figura 11. Anatomía genital y características externas del cuerpo de Helicarionoidea. A-C: *Apothapsia thomensis* (Santo Tomé, por EN1 pozo S. de Santa Catarina y tierra adentro de la costa noroeste, N0,2405° E6,4722°, aprox. 68 m alt., bosque secundario, 1 dic. 2013, sitio ST1 de GAH), todo basado en el mismo caracol; A: genitalia distal; B: detalle del pene con vueltas de epifalo parcialmente separadas y con secciones transversales esquemáticas; C: detalle del epifalo proximal solamente, con vueltas aun más separadas. D-G: *Principitrochoidea convexa* n. sp. (Príncipe, sitio 18-16A, paratipos); D: vista lateral de la cola para mostrar el asta caudal y un diagrama de la fosa caudal vista desde atrás; E: vista dorsal de las partes delanteras del cuerpo preservado con la concha retirada y los lóbulos del manto extendidos (también mostrando manchas blancas en el manto); F: genitalia distal con detalle de la parte engrosada del conducto deferente; G: sección longitudinal parcialmente esquemática del pene (que muestra la pilastra en la pared interna de la luz con punteado ligero, el engrosamiento muscular de la pared del pene con punteado más denso) y dos secciones transversales. H, I: *Principitrochoidea folini* (Príncipe, sitio 18-14, véase texto); H: genitalia distal; I: detalle del pene con vaina exterior abierta. J, K: *Thomitrochoidea trindadensis* n. sp. (holotipo, Santo Tomé, sitio 18-10); J: genitalia distal; K: sección longitudinal esquemática del pene para mostrar la pilastra (punteada) en la pared interna de la luz.



muscle also attached to exterior of wall of proximal end of atrium adjacent to base of bursa duct or base of distal end of penis. Penis moderately large and bulky, with shorter and narrower distal portion (one-third of penis length) extending proximally into longer and wider proximal portion (two-thirds of penis length), giving clavate outline. Short thinner penial caecum on proximal extremity of penis with penial retractor muscle arising from its end as long slender muscle that passes proximally through body cavity alongside other genitalia. Longitudinal section of penis (Fig. 10J) reveals rather thin muscular outer wall, the interior of which has two longitudinal muscular pilasters attached to it throughout most of length of proximal penis; another small rounded pilaster lies close to junction of proximal with distal penis; inner wall of distal penis has a fourth pilaster forming longitudinal ridge, larger than several other lamellae running parallel to it. Thus there is no distinct epiphallus, no penial flagellum and no verge inside penis. Vas deferens a slender tube throughout its length, begins near distal end of spermooviduct, passes distally alongside free oviduct into angle near bursa copulatrix duct and distal part of penis, before returning proximally alongside penis and entering wall of proximal penis close to its end. Vagina absent. Free oviduct slightly longer than penis but more slender, divided into thicker-walled distal part and thin-walled (translucent) proximal part, with constriction in between. Duct of bursa copulatrix short and narrow or somewhat wider, a tube, passing into small ovoid or long-ovoid bursa reservoir which is of approximately the same length. Spermooviduct as long as penis

or somewhat longer; albumen gland not studied. Right ommatophore retractor muscle passes proximally between base of distal part of penis and base of duct of bursa copulatrix.

*Comments:* The genus *Thomithapsia* recalls *Vanmolina sjoestedti* (D'Ailly, 1896) from Cameroon in having a shell with raised spire, tiny umbilicus and spiral periostracal sculpture combined with distal genitalia lacking a vagina and possessing a large clavate penis (DE WINTER (2008: 468-475). However, *Thomithapsia* differs: (a) in lacking a short penial epiphallus (its vas deferens enters the proximal penis wall directly), (b) in lacking a verge inside the proximal penis, and (c) having a smaller duct of the bursa copulatrix lacking the peculiar thickened walls of its counterpart in *Vanmolina*. Since the combination of its shell and anatomical characters appear to be unique (cf. SCHILEYKO, 2002b), we treat *Thomithapsia* as an independent monotypic genus, which is so far as known endemic to São Tomé.

*T. bomsucessica* is distinct conchologically from the other species of Helicarioidea known from São Tomé in having adults that show a combination of a thin rather glossy shell, light brown rather than pale brown shell coloration, more than 5 shell whorls, and absence of an obvious peripheral keel (although immatures have keeled shells). It has been found in rather small numbers at sites from ca 678 m up to at least 1300 m alt., inside montane forest and in disturbed places at lower altitudes without woodland cover. The living specimens were obtained from beneath fallen wood and amongst leaf-litter and other debris on the ground. Unlike the much more common *Apothapsia thomensis*, none were found on vegetation above ground.

### *Thomitrochoidea* n. gen. D. Holyoak & G. Holyoak

Type species: *Thomitrochoidea trinidadensis* n. sp. D. Holyoak & G. Holyoak, see below.

**Etymology:** *Thomi-* is derived from an old name (île de Saint Thomas) for the island of São Tomé; *Trochoidea* Brown, 1827 is the name of a genus of land snails (Geomitridae) that are similar in having a shell shaped like a spinning top toy. Like *Trochoidea*, the new generic name is a feminine noun.

*Diagnosis:* Shell dextral, depressed-conical to very depressed-conical; breadth when mature up to 16.4 mm; umbilicus very narrow; whorls up to 4.9, increasing regularly in width, with keeled periphery, and shallow suture. Peristome thin, plane except on columellar margin. Shells rather thin, variable in coloration, cream, sometimes with dark spiral band, or predominantly red-brown; teleoconch mainly with weak

sculpture. Body with short caudal horn; mantle-collar forming large free flap around front and sides of body. Distal genitalia with short genital atrium dividing proximally into three: (1) penis of medium-length, lacking epiphallus, flagellum or caecum, with retractor muscle attached to its proximal end; (2) bursa copulatrix that is narrowly ovoid and lacks any distinct duct; (3) free oviduct that is cylindrical and rather long.

***Thomitrochoidea trinidadensis* n. sp.** D. Holyoak & G. Holyoak (Figs. 4E, 11J, K)

*Trochonanina moreleti* Germain, 1921 [sic] *sensu* COSSIGNANI (2014: 193), photographs of two shells from São Tomé, a 13 mm, b 14 mm, is a misidentification, non *T. moreleti* Germain, 1915.

**Type material:** Holotype NHMUK 20200242, shell (H 8.6, B 14.4 mm) + bod, collected 2 Dec. 2018, by GAH & DTH at site 18-10.

**Type locality:** São Tomé Island, just S. of Milagrosa, on the road between Trindade and Bombaim, N0.27667° E6.65986°, 398 m alt., tall secondary forest on slopes, track edges with flushed rocky cuttings & abandoned cocoa plantations.

**Paratypes:** All from São Tomé Island: 2 Dec. 2018, from type-locality at site 18-10, 2 spm, 42 sh found dead; 1 Dec. 2013, by EN1 well S. of Santa Catarina & inland of NW. coast, N0.2405° E6.4722°, ca 68 m alt., roadside banks, etc., in tall open secondary-forest on slope, GAH ST1, 1 sh + bod; 2 Dec. 2013, S. of EN2 and NW. of Ribeira Peixe, N0.9314° E6.5889°, ca 126 m alt., edge of tall secondary forest on hill above young oil palm plantation, GAH ST2, 1 sh + bod; 6 Dec. 2013, S. of EN2 and ca 0.4 km W. of Vila Aida, N0.0897° E6.5903°, ca 181 m alt., tall forest on ridge & slopes with understorey of saplings, GAH ST7, 2 sh (imm); 13 Dec. 2013, by EN2 just NE of Monte Mário “roça”, N0.0606° E6.5561°, ca 236 m alt., forest on slopes by road with understorey of saplings & ferns beneath, GAH & DTH ST13, 3 sh + 2 bod; 11 Dec. 2018, by S. side of EN2 between the “roças” Fraternidade and Soledade (ca 1.6 km due S. of São João dos Angolares, centre), N0.1262° 6.6371°, 22 m alt., old cocoa plantations & bananas, under tall trees & palms, near stream (Água São Pedro), GAH & DTH 18-26, 1 sh + bod.

**Other material examined:** 11 Dec. 2013, by EN2 ca 2 km S. of Monte Mário “praia”, N0.0694° E6.5522°, ca 101 m alt., roadside bank at foot of slope with secondary forest, GAH & DTH ST11, 1 sh (old); 12 Dec. 2013, by EN1 between Lagoa Azul [Morro Carregado is the name on the military maps] and Praia Mutamba, N0.4006° E6.6075°, ca 5 m alt., dead/drifted shells from soil surface & debris by small dry stream-course above shore in lower edge of valley with cover of dry woodland, GAH & DTH ST12, 2 sh; 1 June 2019, Cão Pequeno, Caué, N0.0996° E6.5306°, 200 m, native forest, RFL, 1 sh (adult, broken).

**Etymology:** The epithet *trinidadensis* is adjectival, based on the name of the town of Trindade (Portuguese for the Trinity), which is near to the type-locality and the administrative centre of Mé-Zóchi District.

*Description:* Shell dextral, depressed-conical to very depressed-conical with apex to spire rounded and underside moderately convex. When mature H 8.6-9.6 mm, B 14.4-16.4 mm, with 4.3-4.9 whorls. Protoconch small, whorls increasing gradually and regularly in width, except that body-whorl expands disproportionately towards aperture.

Whorl-profile only slightly convex above, with shallow suture forming a narrow band or double line. All whorls keeled at periphery and body-whorl sharply angled with blunt-edged keel in middle of periphery; a slight concavity above the keel and an almost plane area just below it, but outer edge of keel not ending in a distinct cord. Aperture elong-

gate-oval except where widely interrupted by penultimate whorl, and externally with sharp angle of *ca* 70° inside the peripheral keel; peristome thin, plane except for reflection of columellar margin around the adjacent half of the umbilicus, the reflection extending slightly onto palatal margin of aperture. Umbilicus very narrow (*ca* 1 mm), deep, exposing spire internally, partly overlapped by peristome edge. Protoconch nearly smooth, teleoconch with weak sculpture of axial-oblique lines, low irregular riblets, or both; faint irregular spiral microsculpture just visible at high magnification ( $\times$  42) on parts of some shells, apparently absent on others. Shell rather thin, translucent when immature, less so when adult. Proto-

conch whitish to pale brown; teleoconch variable in colour between different localities: all shells in large sample from TL dull cream with single (mainly narrow, broader on few sh) spiral band of red-brown just above keel; second sample with single shell (ST1) was similar but without the dark band; four other small samples were of much darker shells (ST2, ST7, ST13, 18-26) with early whorls and first part of penultimate whorl dull cream, remainder including all of body-whorl chestnut or dull chestnut with irregular axial-oblique lines (between riblets) of cream, and cream outer edge to peripheral keel; underside of shell bright chestnut without markings, except white interior of umbilicus. Fresh shells are glossy

(Right page) Figure 12. Living terrestrial Mollusca photographed on São Tomé and Príncipe. A,B: *Pseudoveronicella thomensis*, São Tomé; A: immature, *ca* 30 mm, 27 Nov. 2018, Morro Claudina, site 18-6; B: smaller immature, *ca* 25 mm, 9 Dec. 2018, by path from Bom Sucesso to Lagoa Amélia (photos © DTH). C: *Pseudoveronicella liberiana*, *ca* 25 mm, São Tomé; 26 Nov. 2018, along track near Ponta Furada, N0.23665° E6.46775° (photo © DTH). D: *Pseudoveronicella forcarti* n. sp., *ca* 25 mm, Príncipe, close to type-locality at saddle beneath Pico Mesa, Nov. 2019 (photo © FS & Fundação Príncipe). E: *Thyrophorella thomensis*, shell breadth *ca* 9 mm, São Tomé, 27 Nov. 2018, Morro Claudina, site 18-6 (creeping on underside of leaf, with hinged periostracum flap attached to dorsum of aperture pushed upwards by extruded forepart of body) (photo © DTH). F, G: *Principicochlea tenuitesta* n. gen. et n. sp., shell breadth *ca* 6-8 mm, Príncipe, holotype and paratypes (photos © FS). H-J: *Apothapsia thomensis*, São Tomé; H: undisturbed snail with mantle laps covering most of shell, I: disturbed subadult snail fleeing, with mantle laps mainly withdrawn into shell; J: threatened snail, body partly withdrawn into shell and flushed with orange-pink colour; shell breadth of H, J *ca* 11 mm, of I *ca* 9 mm (photos © RFL). The photographs were taken during fieldwork so that only rough approximations can be provided of the size.

Figura 12. Moluscos terrestres vivos fotografiados en Santo Tomé y Príncipe. A,B: *Pseudoveronicella thomensis*, Santo Tomé; A: inmaduro, aprox. 30 mm, 27 nov. 2018, Morro Claudina, sitio 18-6; B: inmaduro más pequeño, aprox. 25 mm, 9 dic. 2018, al borde de camino desde Bom Sucesso a Lagoa Amélia (fotos © DTH). C: *Pseudoveronicella liberiana*, aprox. 25 mm, Santo Tomé, 26 de noviembre de 2018, en un sendero cerca de Ponta Furada, N0.23665 ° E6.46775 ° (foto © DTH). D: *Pseudoveronicella forcarti* n. sp., aprox. 25 mm, Príncipe, cerca de la localidad tipo en la vaguada debajo de Pico Mesa, nov. 2019 (foto © FS y Fundação Príncipe). E: *Thyrophorella thomensis*, concha aprox. 9 mm ancho, Santo Tomé, 27 nov. 2018, Morro Claudina, sitio 18-6 (repta en la parte inferior de la hoja, con una solapa abisagrada de periostraco unida al dorso de la abertura, empujada hacia arriba por la parte delantera del cuerpo extendido) (foto © DTH). F, G: *Principicochlea tenuitesta* n. gen. y n. sp., concha aprox. 6-8 mm ancho, Príncipe, holotipo y paratipos (fotos © FS). H-J: *Apothapsia thomensis*, Santo Tomé; H: caracol sin molestar, con los lóbulos de manto que cubren la mayor parte de la concha; I: caracol subadulto perturbado, huyendo con la mayor parte de los lóbulos del manto retirados en la concha; J: caracol asustado, cuerpo parcialmente retirado dentro de la concha y enrojecido con un color naranja-rosado; conchas en H, J aprox. 11 mm ancho, en I aprox. 9 mm (fotos © RFL). Las fotografías se tomaron durante el trabajo de campo por lo que solo se pueden proporcionar valores aproximados del tamaño.



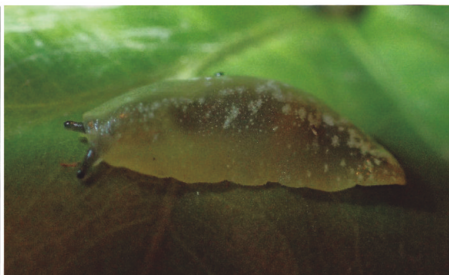
A



C



B



D



E



F



G



H



I



J

beneath but they lack gloss above, except on and near protoconch.

Body elongate with relatively long tail ending in short caudal horn that forms rounded tubercle on dorsal surface of tip, beneath which caudal fossa has large opening (triangular, with point on lower edge). Mantle-collar forms large flap continuous all around front and sides of body, except where deeply incised by slit at front of right-hand edge. In pale-bodied specimens from type locality, sole of foot, foot-fringe and most of exposed part of body whitish, at front pale brown dorsally and on upper flanks, the ommatophore retractor muscles showing as dull dark grey-brown areas through the translucent skin. Exposed mantle-collar whitish; mantle inside body-whorl very pale brown with scattered small grey-brown spots and short longitudinal streaks, with a continuous dark line along the columellar edge. In darker-bodied specimens (site 18-26), exposed foreparts of body pale grey dorsally, mantle-collar pale grey, mantle surface inside body-whorl whitish to pale grey with small spots and irregular small longitudinal streaks of dull grey concentrated along columellar edge.

Genitalia studied in single specimens from type-locality (Fig. 11J, K) and site ST2, another from site 18-26 had immature genitalia. External genital pore at mid-height on right-hand side of forepart of body, below back edge of base of right upper tentacle. Genital atrium a short cylinder, dividing proximally into distal penis on one side and distal end of free oviduct on opposite side, with bursa copulatrix inserting between them. Penis clavate proximally, with two distinct portions: the distal penis a short tube, the proximal penis nearly twice as wide and twice as long and sharply bent just above its junction with distal penis. Penial retractor muscle inserted on proximal end of outer wall of penis, extending proximally alongside spermoviduct to deep within body cavity, apparently ending amongst columellar musculature. Penis opened longitudinally in one mature specimen (Fig.

11K), revealing a moderately thick muscular outer wall throughout; almost the full length of the inner wall of proximal penis with two high curved raised longitudinal lamellae (pilasters), both extending into distal penis and becoming lower there before ending in its distal half; within proximal penis the crests of the lamellae extend across more than half of the width of the lumen. Penial caecum, epiphallus and flagellum all absent; no trace of external glandular tissue around penis. Vas deferens a thin tube beginning near distal end of spermoviduct, passing distally alongside free oviduct, then in turn passing close to bursa copulatrix and into angle near base of distal penis, returning proximally alongside penis, finally entering proximal wall of penis just distal to insertion of its retractor muscle. Vagina lacking; free oviduct a tube about as long as the penis. Bursa copulatrix narrowly ovoid, rather small (only about half length of penis and much narrower than proximal penis), narrowed towards insertion onto genital atrium but lacking a distinct duct, the outer wall of the proximal end giving rise to a long slender thread of strong tissue that passes proximally to join onto surface of proximal half of prostatic part of spermoviduct. Spermoviduct large, curved *in situ*; albumen gland moderately long, approximately ellipsoidal; common hermaphrodite duct a thin convoluted tube arising near distal end of albumen gland. Right ommatophore retractor passing proximally between distal part of penis and bursa copulatrix. No anatomical differences were detected between single mature specimens from populations consisting entirely of pale shells with a brown band (TL) and a population with dark shell coloration (site 18-26).

*Comments:* *Thomitrochoidea* is described as a new genus here because we cannot match its characters with those of any other genus of *Helicarioidea*. Although its shell characters recall those of *Principitrochoidea* n. gen. from Príncipe described and discussed above, they do not match it closely and their distal genitalia show important dif-

ferences. The type species of *Trochonanina* Mousson, 1869, *T. mozambicensis* (L. Pfeiffer, 1855), shows some similarity in shell characters, but differs markedly in having a distinct vagina and penis with a caecum, epiphallus, flagellum and large penial gland (SCHILEYKO, 2002b: 1278-1279), all lacking in *Thomitrochoidea*. PILSBRY (1919: 245) had presented similar anatomical data to those for *T. mozambicensis* for two other species from the Congo, placing them in the genus *Ledoulxia* Bourguignat, 1885 which is a synonym of *Trochonanina*. *Plicatonanina* Verdcourt, 1961 has a very short vagina, but its penial caecum, epiphallus and duct of the bursa copulatrix are all well-developed (VERDCOURT, 1961). Other African helicarionoid genera with trochoid shells (*Trochozonites* L. Pfeiffer, 1883; *Sjostedtina* Verdcourt, 1961; *Carinazingis* van Bruggen & de Winter, 1990; *Tropidocochlion* Verdcourt, 1998) likewise differ in having an epiphallus and flagellum, among various other distinctive characters (SCHILEYKO, 2002b).

Based on recent records from ten localities on São Tomé at 22-900 m alt., *T. trinidadensis* n. sp. appears to be restricted to the lowlands and middle elevations at sites with woody vegetation, including secondary-forest and its edges and old cocoa plantations. Except at the type locality, only a few specimens were found at each site and the living ones were mainly picked off vegetation

above the ground. The type-locality is in an old cocoa plantation with tall *Artocarpus* trees where we initially collected 42 mainly fresh shells found scattered on the ground. Sustained searching did not reveal any living on or near the ground, so we examined saplings by bending them over to check their upper leaves and branches and this technique yielded three live specimens from 2.3 m above ground which were resting together inside an empty, decaying cocoa *Theobroma cacao* "pod" (fruit). Hence, it seems that the species might previously have been overlooked on the island because of its arboreal habitat. However, since it has moderately large shells that were perhaps unlikely to have been overlooked by the nineteenth-century collectors, there is also a strong possibility that the species is a recent introduction to São Tomé from elsewhere in tropical Africa, where there are numerous poorly known nominal species of Helicarionoidea with trochoid shells. Nevertheless, the wide scatter of our localities from the northern to the southern end of the island would imply it may not have arrived recently. Also, there has been one find of it in a remnant of native forest at low elevation (1 June 2019, Cão Pequeno, N0.0996° E6.5306°, in native forest at 200 m alt., a fresh broken shell, leg. RFL) and another at ca 900 m alt. (Oct. 2019, Chamiço, in north of island, photographed by RFL).

## HELICIDAE Rafinesque, 1815

### Subfamily HELICINAE

#### Tribe OTALINI Pfeffer, 1830

##### *Cornu* Born, 1778

##### *Cornu aspersum* (O.F. Müller, 1774)

*Helix aspersa* O.F. Müller, 1774, Verm. terr. fluv., p. 59; TL Italy.

New to São Tomé: 3 Dec. 2013, ca 1.5 km E. of Botanic Gardens at Bom Sucesso, ca 1100 m alt., among grass & weeds by track, GAH & DTH [E. of ST3], 1 typical living individual ca two-thirds adult size recorded but not

collected; 24 Nov. 2018, by Bom Sucesso Botanical Garden, N0.28829° E6.61193°, 1159 m alt., trackside with herbs near hedges, scrub, wall & cultivation, GAH & DTH *et al.* 18-1, 2 sh & 1 bod.

The species is now widespread in S. and W. Europe, where it has been regarded as native. Nevertheless, MADEC, BELLIDO & GUILLER (2003: 225) and GUILLER & MADEC (2010) concluded from evidence of loss of genetic variation and lack of convincing fossil evidence from Europe that the European popula-

tions result from historical introduction from NW. Africa by man. Elsewhere, it occurs eastwards to Turkey and the Middle East and is established as an introduction in S. Africa (widespread) and locally also in N. America, Mexico, Haiti, Argentina, Chile, Australia, New Zealand, Macaronesia and on St. Helena.

## DISCUSSION

The accounts above and Table I present the first comprehensive checklists since the work of GERMAIN (1916) for the terrestrial Mollusca of both islands, comprising 86 species in total, with 59 known for São Tomé and 45 for Príncipe. Many of these are endemic, including several endemic genera, but an accurate assessment of the percentages of endemics will need more research on the other islands of the Gulf of Guinea as well as neighbouring countries of the mainland of Central Africa.

Furthermore, the faunas of both São Tomé and Príncipe are certainly not fully known yet. Our sieved material from forests on Príncipe includes two tiny land-shell apices that definitely do not represent species known on the island, one probably of Cerastidae, the other possibly Charopidae, but the material available is so poor that it would be unhelpful to future researchers to give names to such fragments. Among the species receiving new names here, five are as yet known only from the unique type specimens, two from montane forest on São Tomé and three from Príncipe. Furthermore, our existing knowledge for São Tomé relies on intensive study at very few sites which happen to combine species-rich habitats and relatively easy access, notably the Bom Sucesso to Lagoa Amélia path and neighbouring Morro Claudina forest. Wider searching on both islands will doubtless reveal more undescribed species.

The recent declines of some large endemic snails, including *Archachatina bicarinata* (DALLIMER & MELO, 2010) and *Columna columna* (pers. obs.) emphasise

that the native faunas of these islands are not safe and static, while deleterious habitat changes and more introductions of alien species are occurring. As elsewhere on oceanic islands (CHIBA & COWIE, 2016; YEUNG & HAYES, 2018), it is urgent to find out more before the opportunity to do so is lost forever as endemic species become extinct. More taxonomic knowledge is still needed to inform effective conservation.

## ACKNOWLEDGEMENTS

We are grateful for energetic practical assistance from the Fundação Príncipe, especially colleagues of FS in the fieldwork team (Aramis Andrade, Ayres Pedronho, Davide Dias, Yodiney dos Santos), whose work was supported by a grant from the French Facility for Global Environment (FFEM). The fieldwork by RFL in São Tomé had the support of BirdLife International, through the ECOFAC6 and Rainforest Trust (4875) projects. RFL and MP were also supported by the Portuguese Government through the “Fundação para a Ciência e a Tecnologia” (FCT/MCTES – SFRH/BPD/91494/2012 & PD/BD/140814/2018, respectively), which funded this work within the framework of the project UID/BIA/00329/2019. MP also received support from the Critical Ecosystem Partnership Fund (109607), the Mohamed bin Zayed Species Conservation Fund (190521916), Alisei NGO, and assistance from Gabriel Oquiongo, and Vasco Pissarra. Permits to collect and export specimens were provided by Eng. Arlindo de Carvalho,

Diretor Geral of Ministério das Infraestructuras Recursos Naturais e Ambiente, Direção Geral do Ambiente of the Republic of São Tomé and Príncipe. Leonor Tavares allowed study of specimens she collected in São Tomé in 2019. Rui Mendes assisted in obtain-

ing literature. Tom Blockeel kindly advised us on formation and orthography of the new scientific names. Thanks are also due to Dr David Herbert, another reviewer, and Prof. Serge Gofas for detailed comments on an earlier draft.

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