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Is being "blue" being different? The status of *Antidrymaeus* L. Germain, 1907 (Mollusca: Gastropoda: Bulimulidae), with notes on miscellaneous species of *Drymaeus* Albers, 1850 and *Mesembrinus* Albers, 1850

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Abstract. Phylogenetic analyses confirm the monophyly of a group of *Drymaeus* s.l. species that are characterised by tones of bluish or greenish colours of their bodies. This group is now considered as *Antidrymaeus* L. Germain, 1907, which was recently elevated from synonymy to generic status. Species of this group have been found from Florida to Brazil and Peru, but further fieldwork may show that more species belong to this genus than hitherto known. The following new taxa are described: *Antidrymaeus multifasciatus nevisensis* Robinson & Breure and *Antidrymaeus multifasciatus luciae* Robinson & Breure. The genus *Antidrymaeus* now includes *A. dormani* (W.G. Binney, 1857), *A. gereti* (C.M.F. Ancey, 1901), *A. immaculatus* (Reeve, 1850), *A. inusitatus* (Fulton, 1900), *A. multifasciatus christopheri* (Pilsbry, 1899), *A. multifasciatus laticinctus* (Guppy, 1868), *A. multifasciatus luciae* Robinson & Breure, 2024, *A. multifasciatus multifasciatus* (Lamarck, 1822), *A. multifasciatus nevisensis* Robinson & Breure, 2024, *A. pinchoti* (Pilsbry, 1930), *A. stramineus* (Guilding, 1824), and *A. sulphureus* (L. Pfeiffer, 1857). Additionally, several species of *Drymaeus* Albers, 1850 and *Mesembrinus* Albers, 1850 that also have bluish or greenish colours in their body are treated here. The hypothesis is posed that these also might be members of *Antidrymaeus*; however, this can only be corroborated through future phylogenetic studies.

Key words. Orthalicoidea, *Drymaeus* sensu lato, Central America, West Indies, South America, taxonomy, phylogeny, new taxa, body color

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Introduction

The genus *Drymaeus* Albers, 1850 is widely spread in the Neotropical region, from northern Argentina, Paraguay and Uruguay in the southern part of the region, to Mexico and Florida in the northern part. Currently there are approximately 600 nominal taxa classified at the species level within *Drymaeus*, and 14 taxa have been described at the subgeneric level. One of them is *Antidrymaeus* L. Germain, 1907, originally erected solely for a few sinistral species.

Breure (1979) critically revised the genus *Drymaeus* s.l. based on data later presented by Breure & Eskens (1981). Although anatomical data are known from a number of species, Breure (1979) only tentatively recognised 2 subgenera within *Drymaeus*, *Drymaeus* s.s. and *Mesembrinus* Albers, 1850. Later, Schileyko (1999) considered *Antidrymaeus* L. Germain, 1907 as a synonym

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of *D.* (*Mesembrinus*). Considering the large number of species in *Drymaeus* s.l., few molecular data have been generated.

While working on a paper on Dominica (Robinson et al. 2009), it became apparent to us that several *Drymaeus* species from the Neotropical region possess a peculiar body colour of various shades of blue, green, turquoise (green-blue), or even purple. We find that these colours can be present in the whole foot, head and tentacles included, or only in part of the body; and it may vary with a snail's age (Fig. 1; for a comparison of body colour with other *Drymaeus* and *Mesembrinus*, see fig. 1 at https://doi.org/10.6084/m9.figshare.26359921). The origin of the colour is not clear; however, small clusters of colour corpuscles can be seen in the skin (Fig. 1D–F). Colour may also vary in intensity between species and individuals and even between photographs of the same individual due to lighting and background of the photographs. Because the blue appearance of the body may depend on the available light, it may be necessary to view the animal from different angles.

Recently, material of several species has become available for further anatomical and molecular work that may augment our knowledge of this genus, which is not uncommon in the Neotropics (see also Breure & Romero 2012, Salvador et al. 2023). The aims of the present paper are to present the hypothesis that blue body colour is a synapomorphy of *Antidrymaeus*, to provide new data on a group of Central American and West Indian species and some miscellaneous notes on South American species, and to present a molecular framework for *Antidrymaeus*, which was recently elevated from synonymy to generic level (Salvador et al. 2023).

Material and Methods

Depositories of material

We used the following databases to check for occurrences: iNaturalist (https://inaturalist.org) and GBIF (https://GBIF.org; files of occurrences are indicated with their links in Table 1). Occurrences were downloaded from GBIF and include observations from iNaturalist.org, which were checked by the author team. Other identifications from GBIF could not be checked by us but are presented on maps if they lay within the known range of the species. Localities that were precise enough to be georeferenced with coordinates are included in the maps deposited at https://doi.org/10.6084/m9.figshare.26359921. QGIS v. 3.32 (QGIS.org 2023) was used to prepare the maps of relevant species using these coordinates. The position of these maps within the study area is given in Figure 2.

Besides the species' natural colour variation and that due to lighting, another issue with these snail photographs are the white shells, which cameras tend to overexpose, affecting also the overall colour balance. For this reason, we selected photographs that best reflected the colour perceived by the human eye according to our experience, and, whenever possible, photographs that included part of the environment (leaves, stones, logs, or even hands), to allow a better assessment of the true colouration.

The following abbreviations are used to refer to depositories of material: **ANSP** = Academy of Natural Sciences, Philadelphia, PA, USA; **CM** = Carnegie Museum, Pittsburgh, PA, USA; **CMRP** = Faculdade de Filosofia, Ciências e Lettras de Ribeirão Preto, Ribeirão Preto, Brazil; **FMNH** = Field Museum of Natural History, Chicago, IL, USA; **JG** = private collection of J. Grego, Banská Bystrica, Slovakia; **JHH** = private collection of J. Hortúa Herrera, Bogotá, Colombia; **MHNG** = Muséum d'histoire naturelle, Geneva, Switzerland; **MNCN** = Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN** = Muséum national d'Histoire naturelle, Paris, France; **MZSP** = Museu de Zoologia, São Paulo, Brazil; **MZUCR** = Museo de Zoología, Universidad de Costa Rica, Costa Rica; **MZUCRINB** = Museo de Zoología, Universidad de Costa Rica, Costa Rica, collected by Instituto Nacional de Biodiversidad, San Jose, Costa Rica; **NHMUK** = Natural History Museum, London, United Kingdom; **NMNZ** = Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; **NMW** = National Museum of Wales, Cardiff, United Kingdom; **RMNH**, Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands; **UF** = Florida Museum of Natural History, Gainesville, FL, USA; **USDA** = United States Department of Agriculture APHIS National Malacology Collection, Academy of Natural Sciences, Philadelphia, PA, USA; **VMA** = private collection, V. Mogollón, Lima, Peru; **ZMB** = Museum für Naturkunde, Berlin, Germany; **ZMUZ** = Zoologische Museum, Universität Zürich, Zurich, Switzerland.

Other abbreviations: **BC** = bursa copulatrix; **BCD** = bursa copulatrix duct; **bs** = bootstrap percentage; **EP** = epiphallus; **FL** = flagellum; **n.c.** = no code (vouchers not catalogued); **OD** = ovotestis duct; **P** = phallus; **PD** = distal part of phallus; **PP** = proximal part of phallus; **PS** = phallus sheath; **RM** = retractor muscle; **V** = vagina; **VD** = vas deferens. Proximal is used as closer to the genital pore, distal is further away.

Phylogenetic analysis

All sequences, and the methods used, were derived from those used by Breure et al. (2010), Breure & Romero (2012), and Salvador et al. (2023). See Table 2.

Sequences were aligned using the MUSCLE plugin (Edgar 2004) in Geneious Prime v. 2023.1 (Biomatters Ltd.) with default settings (i.e. optimised for accuracy). The resulting alignments were visually checked for inconsistencies. The ITS2+28S alignment was run through Gblocks (Talavera & Castresana 2007), with the least restrictive settings, to eliminate from the ITS2 portion poorly aligned or data-deficient positions that could introduce noise into the analysis. The alignments were then

Figure 1. Blue, green, and turquoise (green-blue) body colours in *Antidrymaeus* and related species. **A.** *Mesembrinus sallei* (Pilsbry, 1899), from Reserva Cientifica Ebano Verde, Dominican Republic (photograph: Francisco Paz, iNaturalist 117669022, CC by NC) with a medium-shade body colour. **B.** *Antidrymaeus multifasciatus laticinctus* (Guppy, 1868) Carnholm, Dominica, with a dark-shade body colour (photograph: D.G. Robinson). **C.** *Antidrymaeus sulphureus* (L. Pfeiffer, 1857) from La Selva, Sarapiquí, Costa Rica, with a light shade (photograph: Zaidett Barrientos). **D.** *Antidrymaeus sulphureus* from Ujarrás, Cartago, Costa Rica, with a very light shade (photograph: María de la Paz Angulo Irola). **E, F**. Same specimen as in Figure 1D with skin detail (photograph: María de la Paz Angulo Irola).

concatenated for the phylogenetic analysis. The molecular markers targeted for this study were the same as used by Breure & Romero (2012) and Salvador et al. (2023): (1) the barcoding fragment of the COI mitochondrial gene (c. 650 bp; primers LCO/HCO of Folmer et al. 1994); (2) a fragment of the nuclear histone 3 (H3) gene (c. 270 bp; primers H3pulF/H3pul3 of Uit de Weerd & Gittenberger 2013); (3) a continuous fragment of nuclear DNA including the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene (c. 1300 bp), amplified in 2 fragments (primers LSU-1/LSU-3 and LSU-2/LSU-5 of Wade & Mordan 2000, Wade et al. 2006). Further details regarding PCR settings and assembly can be found in the publications of Breure & Romero (2012) and Salvador et al. (2023).

The Bayesian analyses by Salvador et al. (2023) prompted additional analyses on a subset of sequences of *Drymaeus* and related genera. We executed a maximum-likelihood (ML) analysis in which we used the same concatenated sequences for Peltellinae as used by Salvador et al. (2023). The concatenated sequences (post trimming with Gblocks) consisted of 1988 bp (COI: 654 bp; H3: 267 bp; ITS2+28S: 1067 bp). As outgroup sequences, we used *Bulimulus guadalupensis* (Bruguière, 1798) and *Catracca uhlei* Simone, 2022. IQTree v. 1.6.12 was used for these analyses, with Modelfinder and ultrafast bootstrap (bs) options activated (Nguyen et al. 2015, Kalyaanamoorthy et al. 2017, Hoang et al. 2018). Evolutionary relationships of the COI sequences were further explored using SplitsTree4 v. 4.14.4 (Huson & Bryant 2006). Splitstree is an application for computing unrooted phylogenetic networks from molecular sequence data. Given an alignment of sequences, the program will compute a phylogenetic tree or network, in this case using

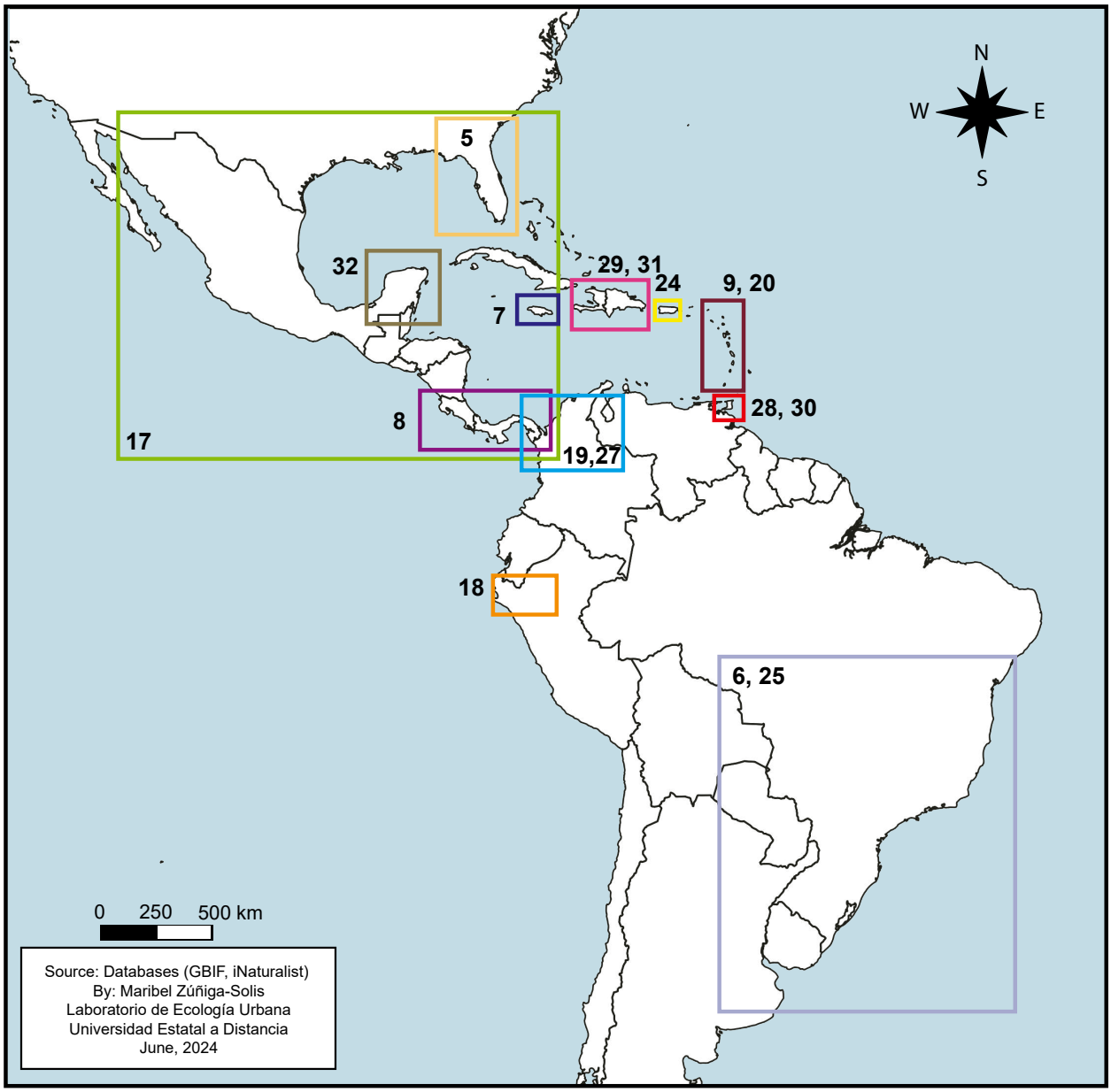

Figure 2. Study area. The position of distribution maps of several species is indicated. These can be found at https://doi.org/10.6084/m9.figshare.26359921. Numbers on this map refer to the figure numbers at that site, and the symbols on those maps match in colour the rectangles on this map.

the neighbour-net method. The network was constructed using K2P distances and EqualAngle settings.

Results

Phylogenetic analysis

The ML tree (Fig. 3) shows strong support (bs = 96) for the Peltellinae. The "basal" clade (bs = 96) has 3 species (*Scutalus chiletensis* Weyrauch, 1967, *Neopetraeus tessellatus* (Shuttleworth, 1852), and *Drymaeus vexillum* (W. Wood, 1828)); this contrasts with the topology of the Bayesian tree of Salvador et al. (2023: fig. 6), where *S. chiletensis* was sister to all other Peltellinae (although the sister-taxa relationship of the other 2 species (bs = 86) is the same). The second clade (bs = 97) consists of *Drymaeus dominicus* (Reeve, 1850) and *D.* cf. *schadei* Quintana & Magaldi, 1985, forming the sister clade to the remaining Peltellinae (Fig. 3); in Salvador et al. (2023), these 2 species were also sisters to one another, but contained within *Drymaeus* s. str.

The next clade (bs = 100) is the "blue *Drymaeus* group" of the same 9 species considered as monophyletic by Salvador et al. (2023: fig. 6), this time with nested subclades that are all reasonably to strongly supported. This clade represents *Antidrymaeus*. In the present tree (Fig. 3), *A. gereti* (Ancey, 1901) is the sister taxon to all other congeners, while in Salvador et al. (2023) it was sister to a clade formed by *A. dormani* (W.G. Binney, 1857) and *A. stramineus* (Guilding, 1824). Our tree

Table 1. Summary of species considered. Chirality: D = dextral; S = sinistral. Anatomy: available implies that information on at least part of the anatomy can be found. Georef. = link to excel sheets with GBIF data used for maps, coordinates were obtained from other sources in the internet, or coordinates are not available.

Taxon	Chirality	Sequences	Anatomy	Distribution	Georef.
Antidrymaeus dormani (W.G. Binney, 1857)	D	Available	Available	Florida	https://doi.org/10.6084/m9.figshare.24798945.v1
Antidrymaeus gereti (C.M.F. Ancey, 1901)	D	Available	Available	Brazil, Argentina	https://doi.org/10.6084/m9.figshare.24798945.v1
Antidrymaeus immaculatus (Reeve, 1850)	D	Available	Unknown	Jamaica	https://doi.org/10.6084/m9.figshare.24798945.v1
Antidrymaeus inusitatus (Fulton, 1900)	S	Available	Available	Costa Rica, Panama	https://doi.org/10.6084/m9.figshare.24798945.v1
Antidrymaeus multifasciatus christopheri (Pilsbry, 1899)	D	Unknown	Unknown	Saint Kitts	Other sources
Antidrymaeus multifasciatus laticinctus (Guppy, 1868)	D	Available	Unknown	Dominica	Other sources
Antidrymaeus. multifasciatus luciae Robinson & Breure ssp. nov.	D	Unknown	Unknown	Saint Lucia	Other sources
Antidrymaeus multifasciatus multifasciatus (Lamarck, 1822)	D	Available	Unknown	Martinique	Other sources
Antidrymaeus multifasciatus nevisensis Robinson & Breure ssp. nov.	D	Unknown	Unknown	Nevis	Other sources
Antidrymaeus pinchoti (Pilsbry, 1830)	D	Available	Available	Colombia	Not available
Antidrymaeus stramineus (Guilding, 1824)	D	Available	Available	Saint Vincent	Not available
Antidrymaeus sulphureus (L. Pfeiffer, 1857)	D	Available	Available	Mexico to Panama	https://doi.org/10.6084/m9.figshare.24798945.v1
Drymaeus ommatidia (Dorado & Roosen 2023)	D	Unknown	Unknown	Peru	Other sources
Drymaeus valentini (Breure & Vega-Luz, 2020)	D	Unknown	Unknown	Peru	Other sources
Mesembrinus alabastrinus (S.I. da Costa, 1906)	D	Unknown	Unknown	Colombia	Other sources.
Mesembrinus binominis (E.A. Smith, 1895)	D	Unknown	Unknown	Grenada, Grenadines	Other sources
Mesembrinus costaricensis (L. Pfeiffer, 1862)	D	Unknown	Unknown	Costa Rica, Nicaragua	Not available
Mesembrinus gabbi (Angas, 1879)	D	Unknown	Unknown	Costa Rica, Panama	Not available
Mesembrinus hjalmarsoni (L. Pfeiffer, 1856)	D	Unknown	Unknown	Puerto Rico	Other sources
Mesembrinus interpunctus (E. von Martens, 1886)	D	Unknown	Available	Brazil, Paraguay, Uruguay, Argentina	Other sources
Mesembrinus joubini L. Germain, 1907	S	Unknown	Unknown	Ecuador	Not available
Mesembrinus montanus (Pilsbry, 1901)	D	Unknown	Unknown	Colombia	Not available
Mesembrinus mossi (E.A. Smith, 1896)	D	Unknown	Unknown	Trinidad	https://doi.org/10.6084/m9.figshare.24798945.v1
Mesembrinus moussoni (L. Pfeiffer, 1853)	D	Unknown	Unknown	Hispaniola	https://doi.org/10.6084/m9.figshare.24798945.v1
Mesembrinus rawsoni (Guppy, 1871)	D	Unknown	Unknown	Tobago	https://doi.org/10.6084/m9.figshare.24798945.v1
Mesembrinus sallei (Pilsbry, 1899)	D	Unknown	Unknown	Hispaniola	https://doi.org/10.6084/m9.figshare.24798945.v1
Mesembrinus tropicalis (Morelet, 1849)	S	Unknown	Unknown	Mexico, Belize, Guatemala	https://doi.org/10.6084/m9.figshare.24798945.v1

Table 2. Species included in the phylogenetic analysis, with GenBank accession numbers for cytochrome oxidase (COI), histone 3 (H3), and internal transcribed spacer 2 plus 28S (ITS2+28S), museum vouchers, collection localities and references for earlier papers in which the references have been used. Note that SALVADOR et al. (2023) erroneously used *Drymaeus rufescens* (J.E. Gray, 1825) for *Antidrymaeus pinchoti* (Pilsbry, 1930). * = outgroup species.

Species	GenBank name	COI	H3	ITS2+28S	Voucher	Locality	Reference
Antidrymaeus dormani (W.G. Binney, 1857)	*Drymaeus dormani*	OP361019	OP381248	OP355608	UF 369107	USA, Florida, Gainesville	SALVADOR et al. 2023
Antidrymaeus gereti (Ancey, 1901)	*Drymaeus gereti*	OP361020	OP381249	OP355609	MZSP 137071	Brazil, Goiás, São Domingos, Angélica Cave	SALVADOR et al. 2023
Antidrymaeus gereti (Ancey, 1901)	*Drymaeus gereti*	OP361021	OP381250	OP355610	CMRP 877	Brazil, São Paulo, Jardinópolis, Rio Pardo	SALVADOR et al. 2023
Antidrymaeus immaculatus (Reeve, 1850)	*Drymaeus immaculatus*	OP361023	OP381252	OP355612	ANSP A23822	Jamaica, Saint Ann, Knutsford	SALVADOR et al. 2023
Antidrymaeus inusitatus (Fulton, 1900)	*Drymaeus inusitatus*	JF514648	—	HM027503	RMNH 114244	Costa Rica, Limón, south of Liverpool	BREURE et al. 2010, BREURE & ROMERO 2012
Antidrymaeus multifasciatus laticinctus (Guppy, 1868)	*Drymaeus lacinctus*	JF514646	JF514688	HM027492	RMNH 114177	Dominica, Saint Joseph, Carnholm	Breure et al. 2010, BREURE & ROMERO 2012
Antidrymaeus multifasciatus multifasciatus (Lamarck, 1822)	*Drymaeus multifasciatus*	JF514647	JF514689	JF514747	RMNH 114178	Saint Kitts, Christchurch	BREURE & ROMERO 2012
Antidrymaeus pinchoti (Pilsbry, 1930)	*Drymaeus rufescens*	OP361027	OP381256	OP355616	UF 271152	Colombia, Providencia Island	SALVADOR et al. 2023
Antidrymaeus stramineus (Guilding, 1824)	*Drymaeus stramineus*	—	JF514703	JF514759	RMNH 114179	Saint Vincent, Saint David, Trinity Falls trail	BREURE & ROMERO 2012
Antidrymaeus sulphureus (L. Pfeiffer, 1857)	*Drymaeus sulphureus*	OP361028	OP381257	OP355617	ANSP A18320	Costa Rica, Limon	SALVADOR et al. 2023
Drymaeus branneri F. Baker, 1914	*Drymaeus branneri*	—	JF514706	JF514762	RMNH 144422	Peru, Madre de Dios, Puerto Maldonado	BREURE & ROMERO 2012
Drymaeus dominicus (Reeve, 1850)	*Drymaeus dominicus*	OP361018	OP381246	OP355607	UF 449294	USA, Florida, Dade County	SALVADOR et al. 2023
Drymaeus expansus (L. Pfeiffer, 1848)	*Drymaeus expansus*	—	JF514704	JF514760	FIML BD521	Peru, Madre de Dios, Reserva Los Amigos	BREURE & ROMERO 2012
Drymaeus iheringi (Leme, 1968)	*Peltella iheringi*	OP361043	OP381279	OP355643	MZSP 139946	Brazil, São Paulo, Cunha	SALVADOR et al. 2023
Drymaeus palliolum (A. Férussac, 1821)	*Peltella palliolum*	—	JF514705	JF514761	MZSP 88759	Brazil, São Paulo, Santo André	BREURE & ROMERO 2012
Drymaeus pamplonensis Pilsbry, 1939	*Drymaeus pamplonensis*	—	JF514719	JF514768	UV 99061	Colombia, Cauca, Coconuco	BREURE & ROMERO 2012
Drymaeus papyraceus (Mawe, 1823)	*Drymaeus papyraceus*	OP361025	OP381254	OP355614	NMNZ M.328496	Brazil, Paraíba, Areia	SALVADOR et al. 2023
Drymaeus poecilus (d'Orbigny, 1835)	*Drymaeus poecilus*	OP361026	OP381255	OP355615	MZSP 108408	Brazil, Mato Grosso, Itiquira	SALVADOR et al. 2023
Drymaeus cf. *schadei* Quintana & Magaldi, 1985	*Drymaeus cf. schadei*	OP361022	OP381251	OP355611	NMNZ M.333508	Brazil, São Paulo, Jardinópolis, Rio Pardo	SALVADOR et al. 2023

Table 2. Continued.

Species	GenBank name	COI	H3	ITS2+28S	Voucher	Locality	Reference
Drymaeus serratus (L. Pfeiffer, 1855)	*Drymaeus serratus*	JF514649	JF514690	HM027499	RMNH 114194	Peru, Huánuco, Tingo Maria	BREURE et al. 2010, BREURE & ROMERO 2012
"*Drymaeus*" *vexillum* (Broderip, 1832)	*Drymaeus vexillum*	JF514625	JF514669	JF514733	RMNH 124038	Peru, Cajamarca, Puente Munuyac	BREURE & ROMERO 2012
Mesembrinus elongatus (Röding, 1789)	*Drymaeus elongatus*	—	OP381258	OP355618	ANSP A469939	Puerto Rico, Guánica, off Cueva Trail	SALVADOR et al. 2023
Mesembrinus elongatus (Röding, 1789)	*Drymaeus elongatus*	—	JF514710	JF514767	RMNH 127706	Bonaire, Goto Lake	BREURE & ROMERO 2012
Mesembrinus multilineatus (Say, 1825)	*Drymaeus multilineatus*	OP361024	OP381253	OP355613	FMNH 381507.1	USA, Florida, Florida City	SALVADOR et al. 2023
Neopetraeus tessellatus (Shuttleworth, 1854)	*Neopetraeus tessellatus*	JF514627	JF514671	JF514735	RMNH 124042	Peru, Ancash, Caño del Pato	BREURE & ROMERO 2012
Pseudoxychona dulcis (Ihering, 1912)	*Pseudoxychona dulcis*	—	OP381284	OP355648	MZSP 108880	Brazil, Espírito Santo, Sooretama	SALVADOR et al. 2023
Scutalus chiletensis Weyrauch, 1967	*Scutalus chiletensis*	JF514628	JF514672	JF514736	RMNH 124032	Peru, Cajamarca, Puente Munuyac	BREURE & ROMERO 2012
**Bulimulus guadalupensis* (Bruguière, 1789)	*Bulimulus guadalupensis*	JF514630	JF514674	JF514738	RMNH 106983	Dominican Republic, Santo Domingo	BREURE & ROMERO 2012
**Catracca uhlei* Simone, 2022	*Catracca uhlei*	OP361014	OP381236	OP355600	MZSP 151871	Brazil, Minas Gerais, Vargem Grande	SALVADOR et al. 2023

still has the latter 2 species as sister taxa (bs = 99). The arrangement of the rest of *Antidrymaeus* is exactly the same as in SALVADOR et al. (2023).

Finally, there are 2 unsupported clades containing some partially to strongly supported subclades: *Drymaeus papyraceus* (Mawe, 1823) + *D. branneri* F. Baker, 1914 (bs = 72), *Pseudoxychona dulcis* (Ihering, 1912) + *D. iheringi* (Leme, 1968) + *D. palliolum* (A. Férussac, 1821) (bs = 95), *Mesembrinus multilineatus* (Say, 1825) + *M. elongatus* (A. Férussac, 1821) (bs = 95). The species in the latter subclade were considered as *Mesembrinus* by SALVADOR et al. (2023) and were separate from *Drymaeus* s.s. in their tree. The other species are part of *Drymaeus* s.s. of SALVADOR et al. (2023), except for *P. dulcis*, which was outside *Drymaeus* s.l. In the present tree (Fig. 3), *D. iheringi* is sister to the slugs previously classified as *Peltella* J.E. Gray, 1855 (Fig. 3).

Drymaeus s.l. is in need of further studies, with an increased taxon sampling to resolve the classification of *Drymaeus* s.s. and the status of currently synonymized subgenera (e.g. *Leptodrymaeus* Pilsbry, 1946, *Mormus* E. von Martens, 1860, and *Peltella*).

The split network (Fig. 4) shows a clear separation between the 9 species of the "blue *Drymaeus* group" (i.e. *Antidrymaeus*) on one hand and the rest of the species on the other.

Systematics

Superfamily Orthalicoidea E. von Martens, 1860

Family Bulimulidae Tryon, 1867

The genus-level taxa

In this paper we treat the genera and species according to the results of SALVADOR et al. (2023); see also Table 1. Although we have some evidence that species treated in the current paper might all belong to *Antidrymaeus*, we keep them tentatively within their current classifications until further research provides more evidence. Species are allocated to *Mesembrinus* or *Drymaeus* following BREURE (1979), based on whether the peristome is expanded and on characters of the mandible and radula.

Genus *Antidrymaeus* L. Germain, 1907

Drymaeus (*Antidrymaeus*) GERMAIN 1907: 59. Type species by subsequent designation (PILSBRY 1926): *Bulimulus* (*Drymaeus*) *inusitatus* Fulton, 1900.

Species considered. *Antidrymaeus dormani* (W.G. Binney, 1857); *A. gereti* (C.M.F. Ancey, 1901); *A. immaculatus* (Reeve, 1850); *A. inusitatus* (Fulton, 1900); *A. multifasciatus* (Lamarck, 1822); *A. pinchoti* (Pilsbry, 1930); *A. stramineus* (Guilding, 1824); *A. sulphureus* (L. Pfeiffer, 1857).

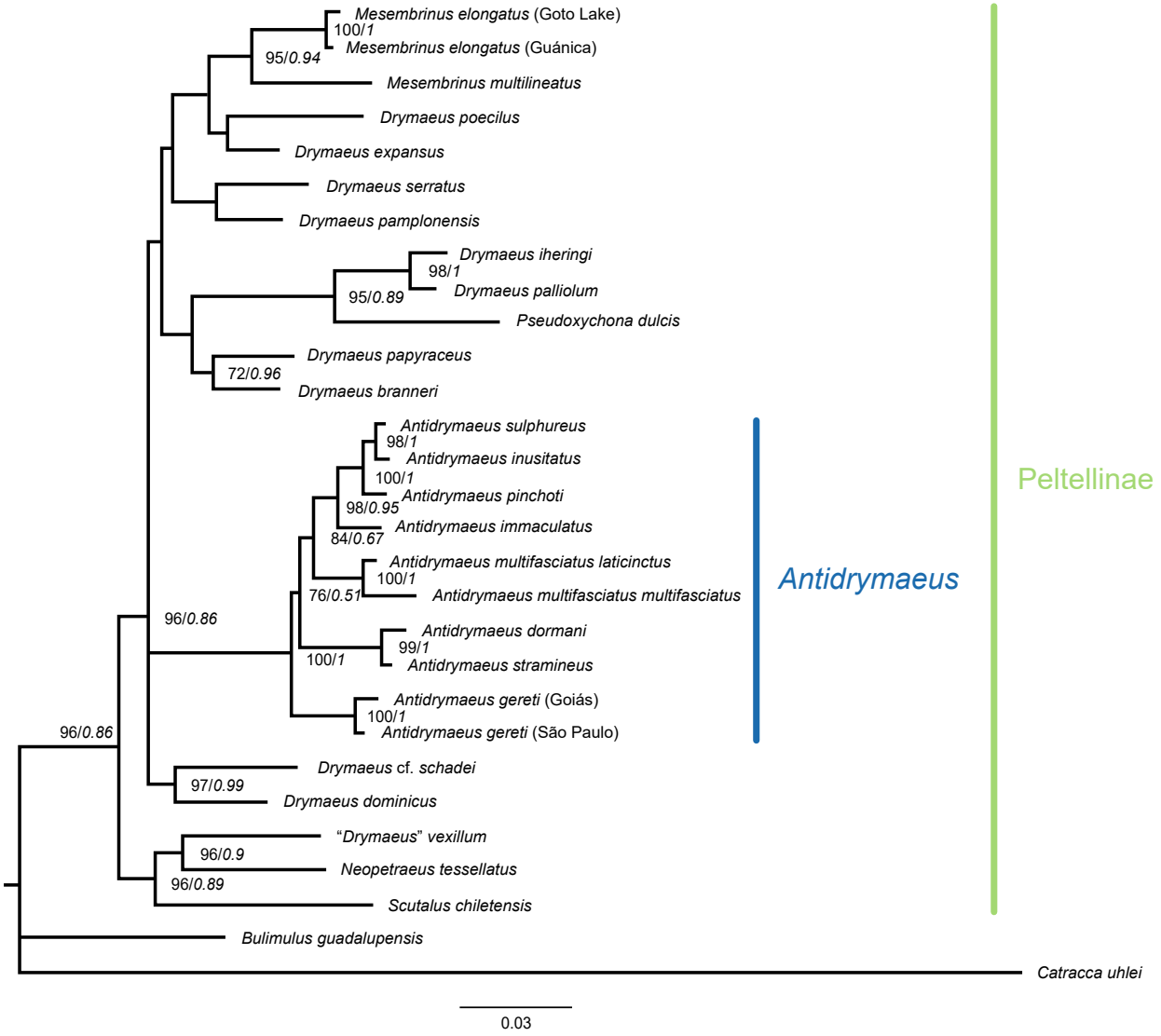

Figure 3. Maximum-likelihood tree of all concatenated sequences of Peltellinae, with bootstrap support percentages of 70 and higher. Support values from the Bayesian tree by SALVADOR et al. (2023: fig. 6) are added in italics. Sequences belonging to *Antidrymaeus* are indicated by the blue vertical bar.

Remarks. *Antidrymaeus* corresponds to the "blue *Drymaeus* group". All species in this clade are blue. Other *Drymaeus* that have been sequenced and whose colour is known are not blue. Part of *Antidrymaeus* was formerly considered as the *Drymaeus multifasciatus* species complex (ROBINSON et al. 2009). It cannot be excluded that other taxa of *Drymaeus* (s.l.) will appear to be part of *Antidrymaeus* once their body colour has been ascertained and more material suitable for molecular work becomes available. BREURE (1979) considered *Antidrymaeus* a synonym of *Drymaeus* (*Mesembrinus*). Based on the results of the phylogenetic analyses, SALVADOR et al. (2023) elevated the subgenus *Antidrymaeus* from a synonym of *Mesembrinus* to generic status. *Antidrymaeus* was originally described by GERMAIN (1907) as a subgenus of *Drymaeus*, defined by its members being sinistral. But eniantomorphy (shell morphs of a species differing in chirality) occurs in different Stylommatophoran groups, including the Orthalicoidea (GITTENBERGER et al. 2012, Breure unpubl. data). Within this superfamily this phenomenon may be found in different families, most notably in the Amphibulimidae (*Corona* and *Liguus*) and Bulimulidae (*Drymaeus*). Sinistrality alone is thus an insufficient basis for a subgeneric separation.

Genus *Drymaeus* Albers, 1850

Drymaeus ALBERS 1850: 155. Type species by subsequent designation (PILSBRY 1898 [1897–1898]): *Helix hygrohylea* d'Orbigny, 1835.

Species considered. *Drymaeus ommatidia* Dorado & Roosen, 2023; *D. valentini* Breure & Vega-Luz, 2020.

Genus *Mesembrinus* Albers, 1850

Mesembrinus Albers 1850: 157. Type species by subsequent designation (MARTENS 1860): *Helix virgulata* A. Férussac, 1821.

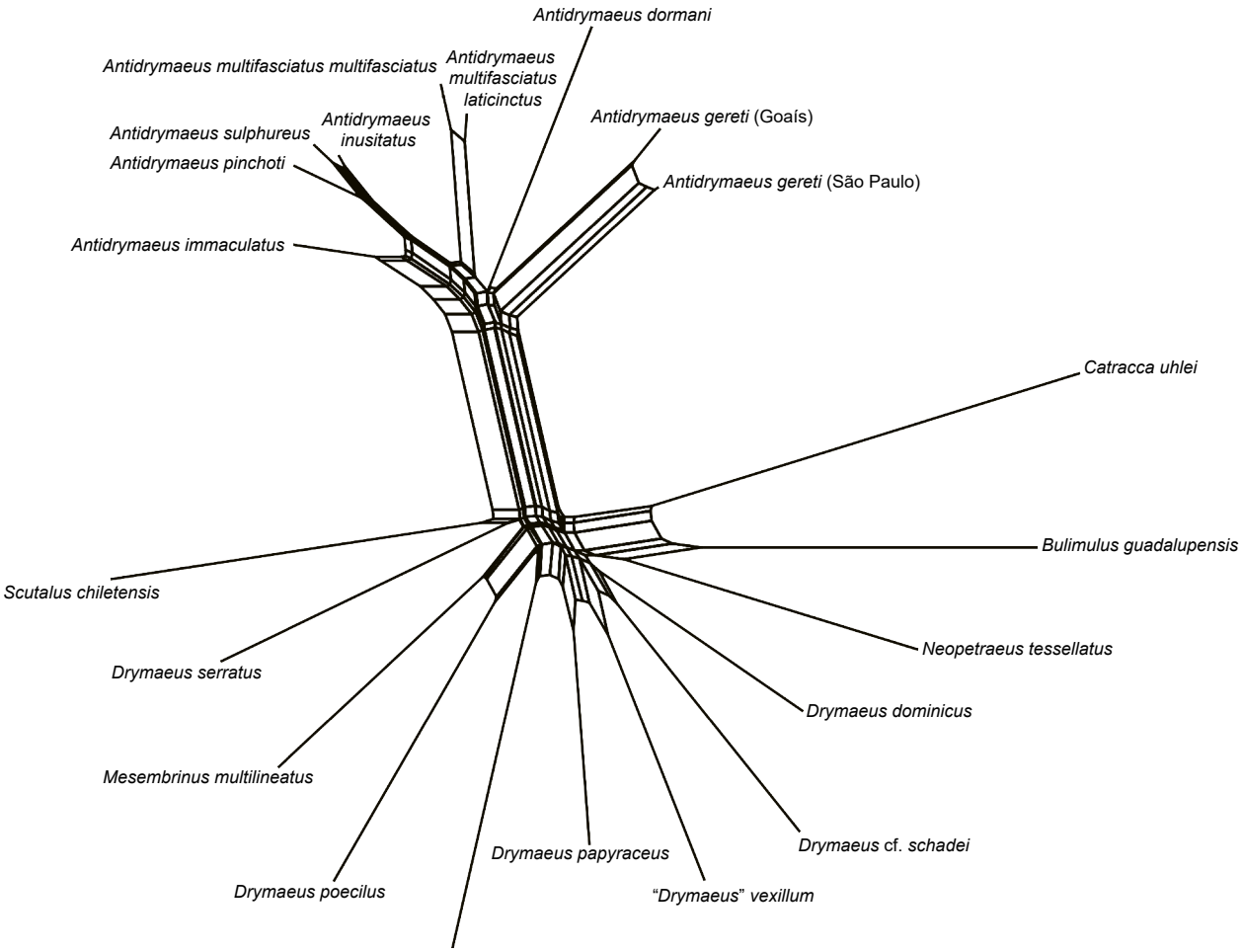

Figure 4. SplitsTree NeighborNet network of all COI sequences based on K2P distances and EqualAngle representation. For label information, see Table 2.

Species considered. *Mesembrinus alabastrinus* (S.I. da Costa, 1906); *M. binominis* (E.A. Smith, 1895); *M. costaricensis* (L. Pfeiffer, 1862); *M. gabbi* (Angas, 1879); *M. hjalmarsoni* (L. Pfeiffer, 1856); *M. interpunctus* (E. von Martens, 1886); *M. joubini* (L. Germain, 1907); *M. montanus* (Pilsbry, 1901); *M. mossi* (E.A. Smith, 1896); *M. moussoni* (L. Pfeiffer, 1853); *M. rawsoni* (Guppy, 1871); *M. sallei* (Pilsbry, 1899); *M. tropicalis* (Morelet, 1849). The section on *M. gabbi* considers also *M. tripictus* (Albers, 1857) and *M. irazuensis* (Angas, 1878).

Further notes on the genus *Antidrymaeus*

So far, the main evidence for a monophyletic clade of several blue-bodied species, including the type species for *Antidrymaeus*, has been the recent study by SALVADOR et al. (2023). Based on the available data on genitalia, on the histology of a few species, and on the radula structure (BREURE & ESKENS 1981), it must be concluded that it is difficult to define characteristics from these data that separate *Antidrymaeus* species from those classified in *Drymaeus* and *Mesembrinus.* The only morphological characteristic that we currently have is body colour, which seems a poor character to use at this level for classification. The only solution seems to be to wait for additional material that will allow molecular studies. Therefore, we can only include the already sequenced species as *Antidrymaeus* and formulate the hypothesis that other blue-bodied species will eventually prove to be *Antidrymaeus* once they are sequenced. We leave unsequenced species under their current classifications.

The species and subspecies

Species are arranged alphabetically under each genus name, following the sequence in Table 1.

Antidrymaeus dormani (W.G. Binney, 1857)

Figure 5, distribution map = "Fig5..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimus dormani BINNEY 1857: 188. "In peninsula Florida, prope St. Augustine". Type material not located.

Material. USA: Florida, Gainesville (UF 369107).

Distribution. USA: Florida.

Anatomy. Data on the genitalia (including their histology), radula, and mandibula were given by BREURE & ESKENS

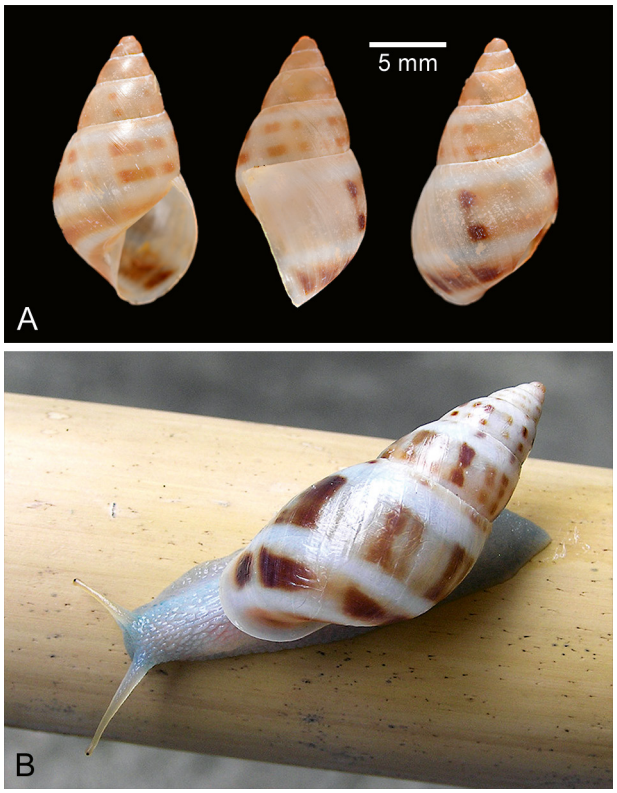

Figure 5. *Antidrymaeus dormani* (W.G. Binney, 1857). **A.** Shell of UF 369107 (photograph: John Slapcinsky). **B.** Living specimen from Twelve Mile Swamp, St. Johns County, Florida, USA (photograph: Bill Frank).

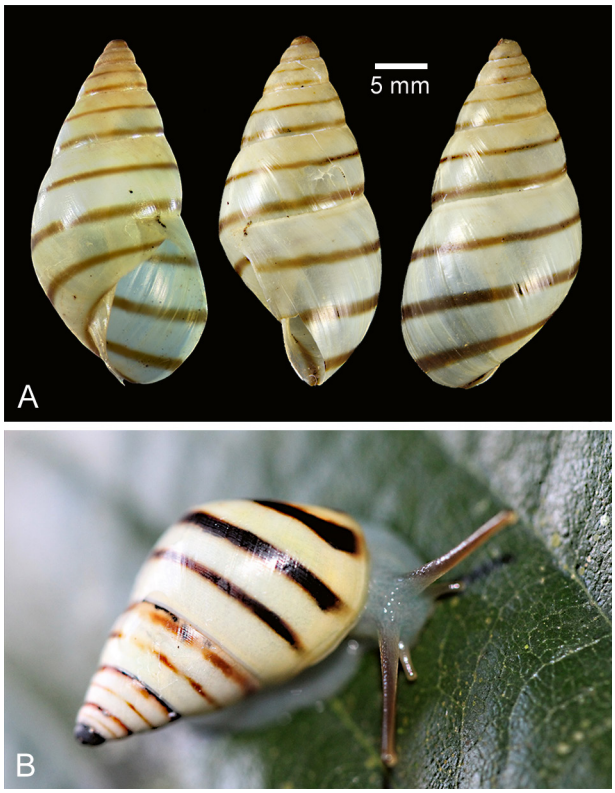

Figure 6. *Antidrymaeus gereti* (C.M.F. Ancey, 1901). **A.** Possible syntype, NMW 1955.158.12853. **B.** Living specimen from Guarani, Misiones, Argentina (photograph: R. Moyano).

(1981: 56–57, figs 190–199, 362, pl. 4 fig. 1, table 4).

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. A field photograph (Fig. 5B) shows the animal with bluish tints on the body and orange tints on the tentacles. This species is widespread within central peninsular Florida.

Antidrymaeus gereti (C.M.F. Ancey, 1901)

Figure 6, distribution map = "Fig6 and 25..." at https://doi.org/10.6084/m9.figshare.26359921

Drymaeus gereti Ancey 1901: 93. [Brazil] "Prov. de Goyaz". Possible syntype NMW.1955.158.12853 /1.

Material. Brazil: Goiás, São Domingos (13.39833° S, 046.31833° W) (MZSP 137071); São Paulo, Jardinópolis (21.0178° S, 047.7639° W), Rio Pardo (CMRP 877). **Argentina:** Missiones, Guarani, 27.20007° S 054.01703° W (iNaturalist 148479710).

Distribution. Brazil, Argentina.

Anatomy. Data on genitalia, radula, and mandibula were given by Breure & Eskens (1981: 71, figs 223–224, 366, table 4).

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. This species has a shell colour pattern that may be easily confused with some other species. Field photographs (e.g. iNaturalist 165659448) show that the blue body colour may not always be apparent in images.

Antidrymaeus immaculatus (Reeve, 1850)

Figure 7, distribution map = "Fig7..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimus immaculatus Reeve 1850 [1848–1850]: pl. 85 fig. 631. "Jamaica". Lectotype NHMUK 1975540.

Material. Jamaica: Saint Ann, Knutsford (ANSP A23 822).

Distribution. Jamaica.

Anatomy. Unknown.

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. This species has long been attributed to C.B. Adams, 1849 or to C.B. Adams in Reeve, 1850. Adams first published the name in a catalogue of Jamaican shells (Adams 1849b: 40) as a nomen nudum; it subsequently appeared with Adam's name as author in Reeve (1850 [1848–1850]) with the material mentioned as in "Amherst College". However, Adams (1852: 248) explicitly mentioned in the errata, "The description of *Bulimus immaculatus* was omitted from p. 29 [Adams 1849a]. The authorship of this name must therefore be ascribed to Mr. Reeve, who subsequently adopted it in the *Conchologica Iconica*". The status of the specimens in MCZ (lots

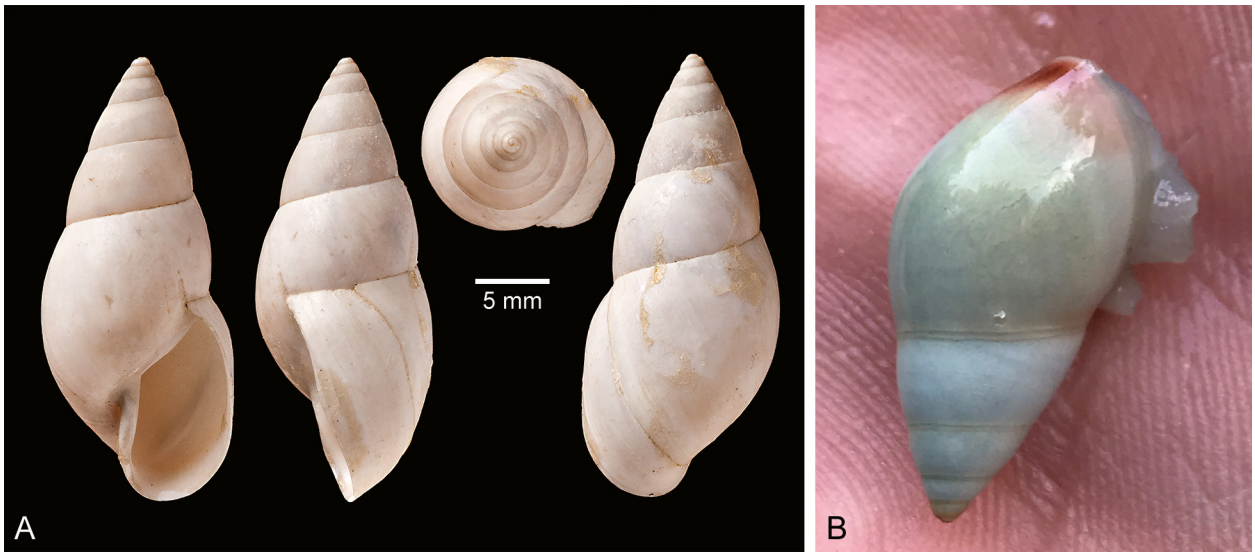

Figure 7. *Antidrymaeus immaculatus* (Reeve, 1850). **A.** Lectotype, NHMUK 1975540. **B.** Living specimen from Portland, Jamaica (iNaturalist 10302961, photograph: W. Fidler, CC by NC).

72315 and 156071) needs further study as there is doubt if they were part of the material seen by Reeve. Field photographs show bluish tints when the animal is nearly retracted (Fig. 7B).

Antidrymaeus inusitatus (Fulton, 1900)

Figure 8, distribution map = "Fig8..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimulus (*Drymaeus*) *inusitatus* FULTON 1900: 87. "Costa Rica". Lectotype NHMUK 1901.4.25.28.

Material. Costa Rica: Limón, Pococi (iNaturalist 198 342179).

Distribution. Panama, Costa Rica.

Anatomy. Data on genitalia were given by BREURE & ESKENS (1981: 75–76, figs 245–246).

Sequences. See Table 2 (COI, ITS2+28S).

Remarks. This is the type species of *Antidrymaeus*. Images of the blue-bodied animals have not been published before, but Figure 8B shows an animal photographed in the field. The relationship of this species with *M. tropicalis* needs special attention. Both taxa are about the same size and have similar shapes. They may prove to be synonyms, in which case the name *M. tropicalis* has priority.

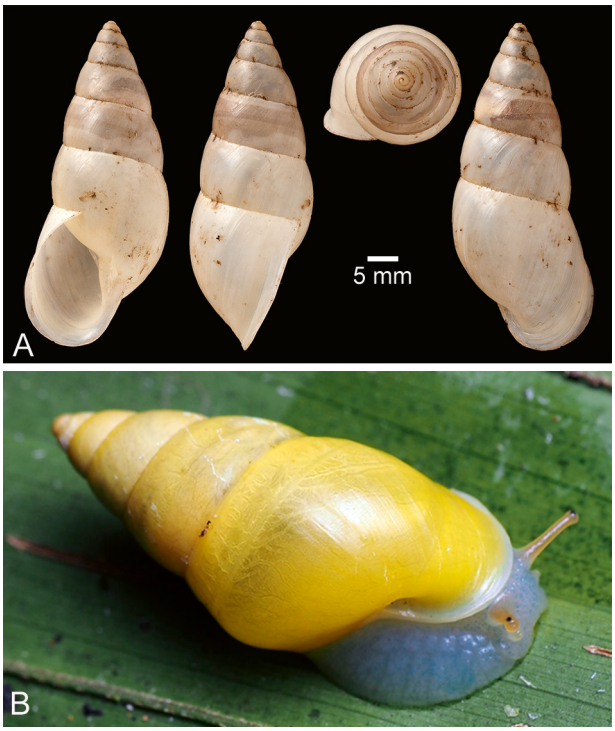

Figure 8. *Antidrymaeus inusitatus* (Fulton, 1900). **A.** Lectotype, NHMUK 1901.4.25.28. **B.** Living specimen from Pococí, Limón, Costa Rica (iNaturalist 198342179, photograph: thirty_legs, CC by NC).

Antidrymaeus multifasciatus christopheri (Pilsbry, 1899) comb. nov.

Figures 9, 10

Drymaeus multifasciatus christopheri PILSBRY 1899: 16, pl. 13 figs 98–99. [Saint Kitts] "St. Christopher". Lectotype ANSP 25857.

Material. Saint Kitts: Saint Paul Capisterre, crater trail up Mount Liamuiga, 17°22′57.7″N 062°49′36.5″W, D.G. Robinsonleg.,8.iii.2004(USDA100629/7);approximately same locality, D.G. Robinson leg., 8.iii.2004 (USDA 100775/2); Christchurch Nichola Town, trail to Phillips Level, on *Heliconia* leaves and other vegetation, 17°21′10.6″N 062°46′26.8″W, D.G. Robinson leg., 9.iii.2004 and 15.iii.2004 (USDA 100685/8); Trinity Pametto Point, on top of Ottley's level, 17°18′38.2″N 062°46′06.8″W, D.G. Robinson leg., 13.iii.2004 (USDA 100628/1).

Distribution. Saint Kitts.

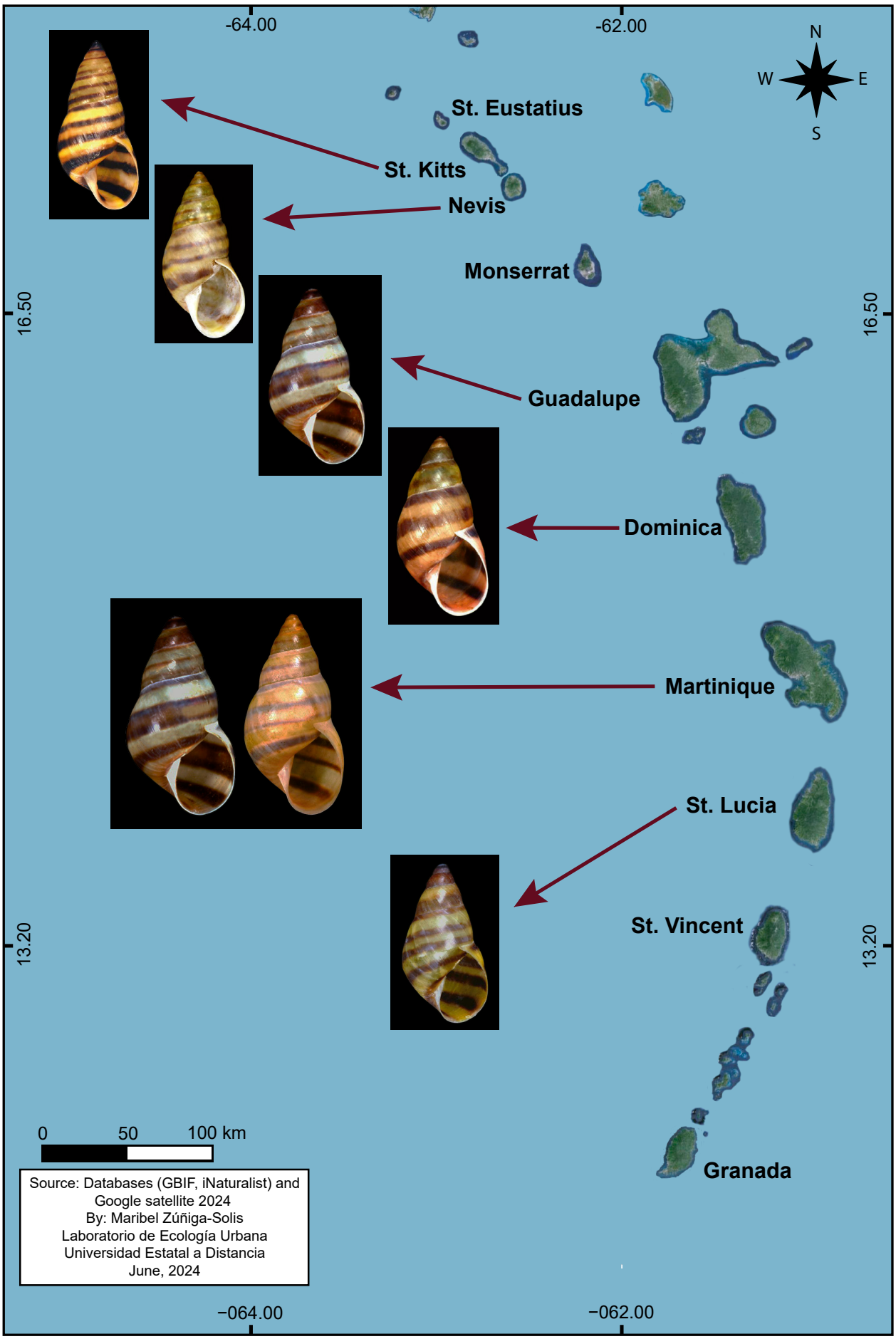

Figure 9. Overview of the *Antidrymaeus multifasciatus* species complex (striped forms).

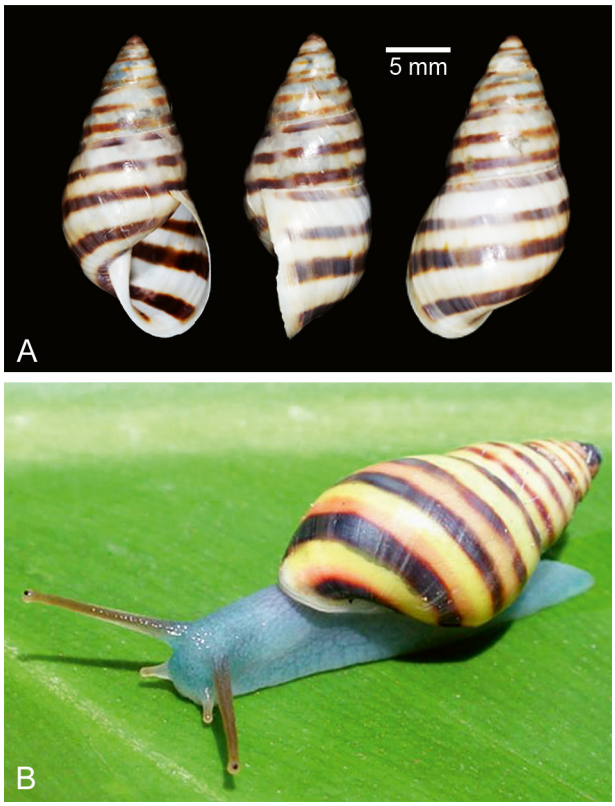

Figure 10. *Antidrymaeus multifasciatus christophori* (Pilsbry, 1899). **A.** Holotype, ANSP 25857. **B.** Living specimen from Saint Kitts (photograph: D.G. Robinson).

Anatomy. Unknown.

Sequences. Unknown.

Remarks. The shell of this subspecies may be pure white, pale yellow, or yellow to orange-rose and can have 5 brown stripes. Immatures of all shell morphs have the blue body colouration characteristic of the genus. In museum specimens the colour of the shell fades to white or pale yellow. For distribution details see Breure et al. (2016: fig. 54).

Antidrymaeus multifasciatus laticinctus (Guppy, 1868) comb. nov.

Figures 1B, 11

Bulimus laticinctus Guppy 1868: 431. “Dominica”. Type material not located.

Material. Dominica: Saint George, Bellevue Chopin (USDA n.c.); Saint Joseph, Carnholm (USDA n.c.).

Distribution. Dominica.

Anatomy. Unknown.

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. To bring the systematic position in line with the closely morphologically related taxa from neighbouring islands, Guppy’s species is now treated as a subspecies. The distribution on Dominica has been reported by Robinson et al. (2009).

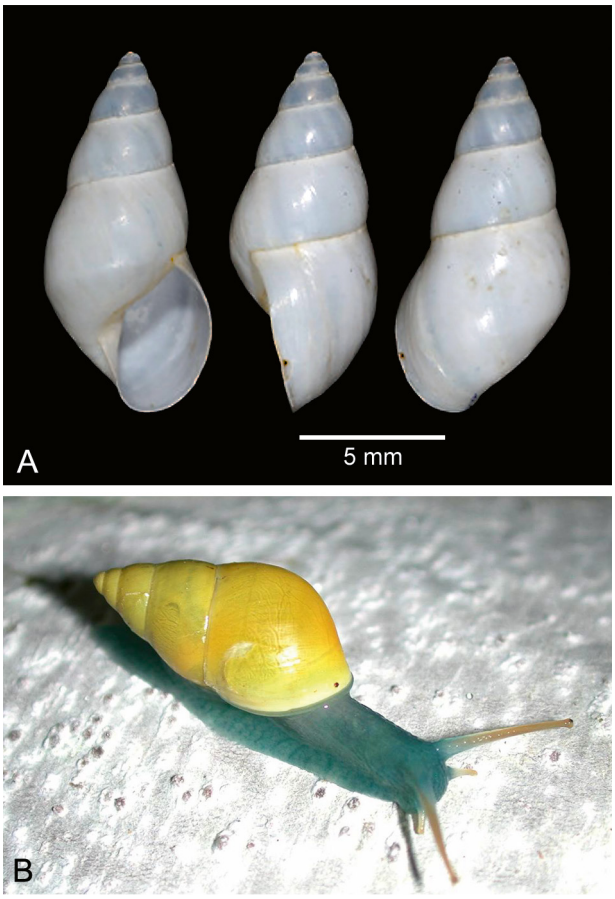

Figure 11. *Antidrymaeus multifasciatus laticinctus* (Guppy, 1868). **A.** Holotype of *Drymaeus virginalis dominicanus* Pilsbry, 1899, ANSP 25853. **B.** Living specimen from Bellevue Chopin, Dominica (photograph: D.G. Robinson).

Antidrymaeus multifasciatus luciae Robinson & Breure ssp. nov.

Figures 9, 12

Zoobank registration. urn:lsid:zoobank.org:act:88783EB8-1EDC-4142-9344-B69033585E5B

Type material. Saint Lucia, Soufrière Quarter, summit of Gros Piton, 13.8033° N 061.0669° W, 169 m, N. Ramnath leg., 2001 (holotype ANSP 494853; Fig. 12A); same locality, D.G. Robinson leg., 3.xii.2002 (paratype ANSP 494854 /1).

Diagnosis. Up to 17.5 mm in height, and 9.0 mm in maximum diameter.

This is the smallest of the *A. multifasciatus* subspecies. It has the typical *Drymaeus*-like crowded, spiral incised lines, although the shell is not as elongate as other subspecies of *A. multifasciatus* and has an overall squatter outline. It also differs from the nominate subspecies by the thinner and more delicate shell, the golden yellow colour pattern, and the lack of pink banding. On the last whorl there are 5 reddish-brown spiral bands, one at the suture and the fifth outlining the columella; the ones on the lower part of the body whorl are somewhat broader. Early whorls are entirely blackish purple. Figure 12B shows a form with a pure white shell lacking any visible

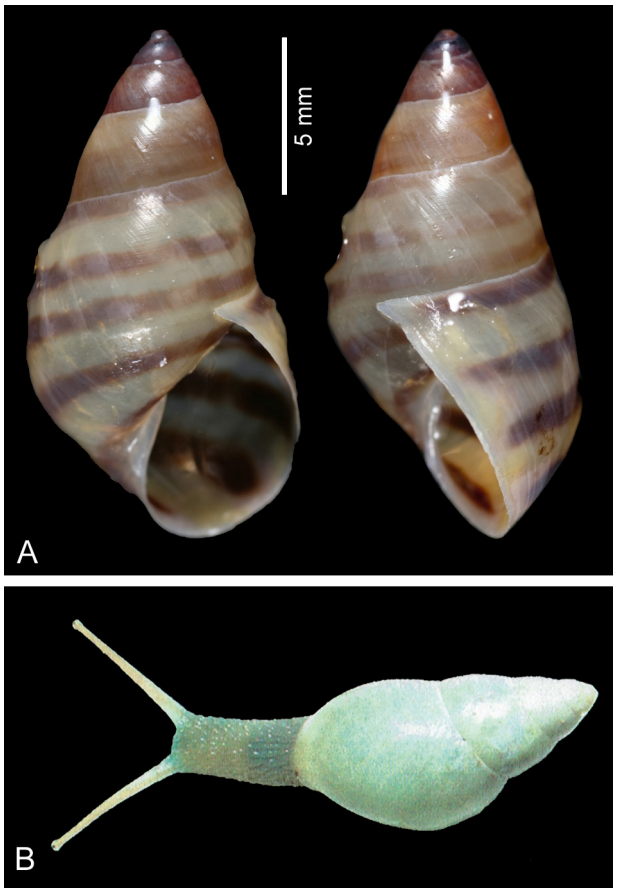

Figure 12. *Antidrymaeus multifasciatus luciae* Robinson & Breure ssp. nov. **A.** Holotype, ANSP 494853 (photograph: K. Seizova). **B.** Living specimen from Gros Piton, Saint Lucia (photograph: D.G. Robinson).

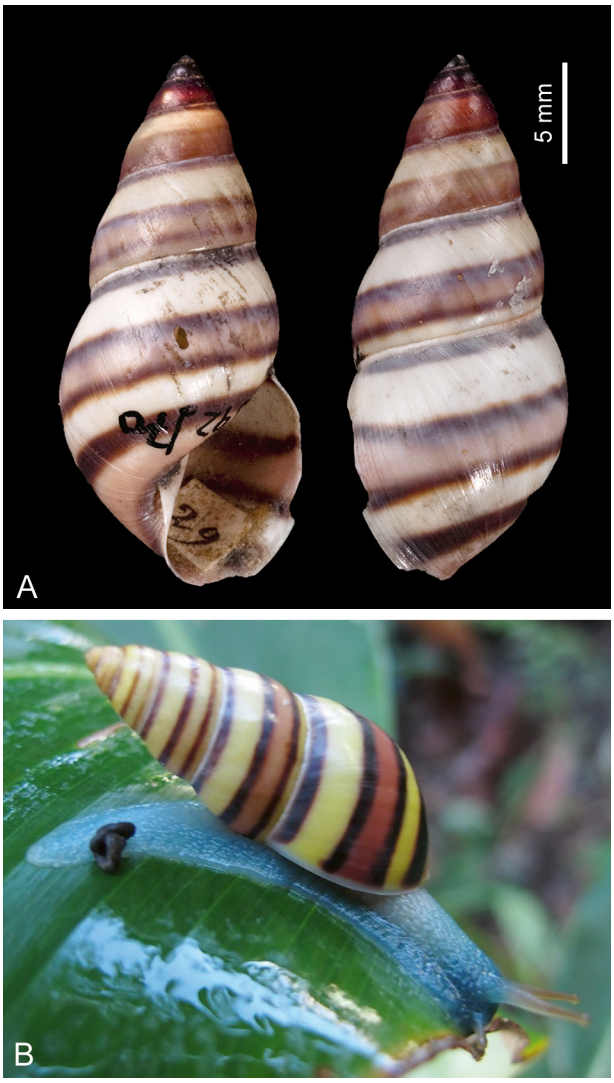

Figure 13. *Antidrymaeus multifasciatus multifasciatus* (Lamarck, 1822). **A.** Syntype, MHNG-MOLL- 51167. **B.** Living specimen from Circuit d'Absalon, Fort de France, Martinique (photograph: B. Duprée).

banding. The periostome is thin and somewhat expanded. The body colour is sky blue.

Anatomy. Unknown.

Sequences. Unknown.

Etymology. Named after Saint Lucia, the island where this endemic taxon was found. The epithet is a noun in the genitive.

Antidrymaeus multifasciatus multifasciatus (Lamarck, 1822)

Figures 9, 13

Bulimus multifasciatus Lamarck 1822: 123. "Les Antilles". Syntype MHNG-MOLL-51167.

Bulimulus multifasciatus albicans Mazé 1874: 163. [Martinique] "Saint Pierre, hauteurs du Parnasse, 200 mètres environs". Type material not located.

Material. Martinique: Anse Couleuvre, 150–250 m, A. & S. Tillier leg., 9.iv.1984 (MNHN n.c. /22); Anse Couleuvre, 320 m, A. & S. Tillier leg., 9.iv.1984 (MNHN n.c. /6); Morne Gardier, 350 m, L. Morice leg., 15.ix.1984 (MNHN n.c. /2); Morne Rose, Grand Fond, 600 m, L. Morice leg., iv–v.1984 (MNHN n.c. /2). Martinique, without specific locality (MHNG-MOLL 51167, lectotype).

Distribution. Martinique.

Anatomy. Unknown.

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. Pilsbry (1899: 15) remarked that "Larmarck's types probably come from Martinique, as they agree perfectly with specimens from that island". Mazé (1874: 163) reported a white-shelled variety (var. *albicans*) from an elevation of 200 m at Saint Pierre as "rare". However, from the material listed above, only the specimens from Morne Gardier are coloured like the type material; all other material is (nearly) pure white, sometimes with faint (pinkish) traces of parts of the spiral bands, usually 3. Additional images with living snails from this island were published by Delannoye et al. (2015: pl. 42).

Antidrymaeus multifasciatus nevisensis Robinson & Breure ssp. nov.

Figures 9, 14

Drymaeus (*Antidrymaeus*) *multifasciatus* subspecies—Breure et al. 2016: fig. 46.

ZooBank registration. urn:lsid:zoobank.org:act:6EBBF000-DFB8-4442-BF98-8FC96B94CDE3

Type material examined. Nevis: Saint James Windward, cloud forest above Prison Farm, 17.1656° N 062.51° W, 270 m, D.G. Robinson leg., 12.iii.2004 (holotype ANSP 494849, Fig. 14A [body only, shell lost after photographing]; paratype ANSP 494851 /1 [body only]).

Diagnosis. Up to 25.4 mm in height, and 12.6 mm in maximum diameter.

Similar to *A. multifasciatus* from Martinique in shape and with the typical *Drymaeus*-like crowded, spiral incised lines, the *nevisensis* subspecies is duller in colouration as an adult, with an overall pale-yellow to pinkish shell with 5 brown bands, which are somewhat poorly defined and, in some specimens broken up into square, brown spots. Small immature specimens are brighter in colour, approaching the colouration of the nominate *A. multifaciatus*. The periostome is thin and somewhat expanded.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. Although Saint Kitts and Nevis are separated by a channel little more than a few kilometres wide, the subspecies from each island are recognisably distinct. Shells from Nevis are not as brightly coloured, with the various bands less well defined. A whitish form exists and appears to be characterised by transparent bands. In juvenile specimens, the body colour is sky blue, while in adults the body loses its blue colouration. The Nevisian form seems closest to the form from Guadeloupe. For distribution details see BREURE et al. (2016: fig. 54).

Etymology. The subspecific epithet refers to the island Nevis, the locality of this endemic taxon. The name is used as an adjective.

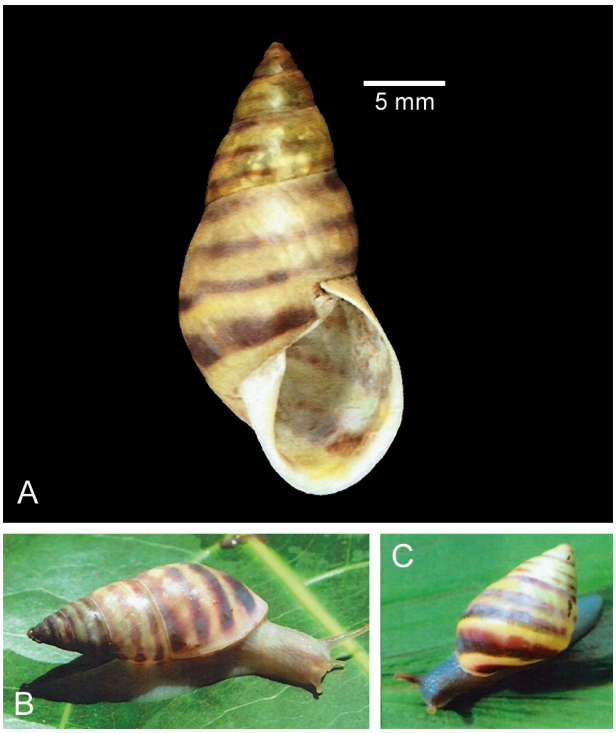

Figure 14. *Antidrymaeus multifasciatus nevisensis* Robinson & Breure ssp. nov. **A.** Holotype, ANSP 494849. **B, C.** Living specimens (adult and juvenile) from Nevis (photographs: D.G. Robinson).

Antidrymaeus multifasciatus subspecies?

Figure 9

Bulimulus multifasciatus (Lamarck) var.—MAZÉ 1883: 16.
Drymaeus cf. *multifasciatus*—TILLIER & TILLIER 1985: 65.

Material. Guadeloupe: Basse Terre (vouchers lost; see remarks).

Distribution. Guadeloupe.

Ecology. TILLIER & TILLIER (1985) reported this taxon from "fôret hygrophyle inférieure" (fig. 26), also termed "peuplement mésophyle" (p. 78); the annual rainfall was given as 3000 mm/year.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. MAZÉ (1883) noted that the specimens from Guadeloupe differed from those of Martinique and reported the blue body colour without further conclusions. His specimens originated from 375–610 m on the western side of Basse-Terre; the taxon was reported as rather rare. TILLIER & TILLIER (1985) were able to find this species only at 1 place at a slightly higher elevation, despite intensive sampling in the forests of Basse-Terre. However, the altitude reported by them may be erroneous, as Google Earth gives an elevation that is considerably lower and fits within the range reported by MAZÉ (1883). Despite considerable efforts, neither Mazé's nor the Tilliers' material was located in the MNHN collection (V. Héros pers. comm.).

Antidrymaeus pinchoti (Pilsbry, 1930) comb. nov.

Figure 15

Drymaeus rufescens pinchoti PILSBRY 1930: 252, pl. 18 figs 13–24. "Old Providence: about half a mile inland from Southwest Bay". Holotype ANSP 150852.

Material. Colombia: Providencia Island (UF 271152).

Distribution. Providencia Island, Colombia.

Anatomy. Data on genitalia and histology, radula, and mandibula are given (as *Drymaeus* (*Mesembrinus*) *rufescens pinchoti*) by BREURE & ESKENS (1981: 83–84, figs 269–277, 374, pl. 1 fig. 2, table 4).

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. When PILSBRY (1930) introduced *pinchoti* he considered it as a subspecies of *Drymaeus rufescens* (J.E. Gray, 1825). The latter was originally described as *Bulimus rufescens* from Jamaica (GRAY 1825: 414), and it may be noted that PILSBRY (1899: 9) earlier considered Gray's taxon "insufficiently diagnostic" and

Figure 15. *Antidrymaeus pinchoti* (Pilsbry, 1930). Holotype, ANSP 150852.

treated it as a nomen nudum; in 1899 he had used the name *Drymaeus erubescens* (L. Pfeiffer, 1847) instead, but in 1930 he treated that as a junior synonym of *D. rufescens*. *Drymaeus erubescens* was described from a "locality unknown", but Adams (1849b) associated its illustration with a Jamaican species; in 1930 Pilsbry also referred this species to Jamaica, and subsequently Breure & Ablett (2014: 69, fig. 25D) found the type specimen labelled "Jamaica" in a later handwriting. Rosenberg & Muratov (2006: 128) excluded *Drymaeus rufescens* (and *D. erubescens*) from the Jamaican fauna and stated that "the only authentic locality for the species is Old Providence Island (Isla de Providencia, Colombia)". When we compare the holotype of Pilsbry's taxon with the lectotype of Pfeiffer's *D. erubescens*, it is clear they are different species. We consider Gray's taxon as a nomen inquirendum. Therefore, we have raised Pilsbry's taxon to species status. This species has been sequenced and falls within the *Antidrymaeus* clade, but we have not yet seen convincing field photographs showing a blue-bodied snail.

Antidrymaeus stramineus (Guilding, 1824) comb. nov.

Figure 16

Bulimulus stramineus Guilding 1824: 340. "St. Vincent". Type material not located.

Material. Saint Vincent: Saint David Parish, along Trinity Falls trail, D.G. Robinson leg., 31.vii.2003 (RMNH 114179 /2). Vermont Nature Trail, 27.v.2022 (iNaturalist 204927819).

Distribution. Saint Vincent.

Anatomy (Fig. 16D, E). Phallus relatively long, with an indistinct, short sheath, its proximal part somewhat swollen and light brown under outer layer; distal part subcylindrical, whitish, with longitudinal folds. Transition to epiphallus externally indiscernible. Flagellum relatively long, tapering only at distal end, with an extremely short retractor muscle attached. Vagina relatively long. Bursa copulatrix duct rather narrow, short (½ length of spermoviduct), terminating in a knob-like reservoir.

Sequences. See Table 2 (H3, ITS2+28S).

Antidrymaeus sulphureus (L. Pfeiffer, 1857)

Figures 1C–E, 17, distribution map = "Fig17..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimus sulphureus Pfeiffer 1857: 318, pl. 35 fig. 11. [Mexico] "Cordova". Lectotype NHMUK 20100585.

Bulimus citronellus Angas 1879: 479, pl. 40 fig. 5. "Uren to Lipurio, Costa Rica". Lectotype NHMUK 1879.7.21.19.

Material. Costa Rica: Prov. Heredia, Puerto Viejo de Sarapiquí, 50 m, J. Slapcinsky leg., (UF 310110, 310112); Prov. Limón, S of Liverpool, 190 m, I. Richling leg., 13.iii.1997 (MZUCRINB n.c., RMNH 144244 /1); between Bibri and Uatsi, 90 m, I. Richling leg., 15.ix.1999 (MZUCRINB n.c.); Guayacán, 700 m, I. Richling leg., 12.ix.1999 (MZUCRINB n.c.). **Honduras:** Depto. Copán, Munic. Santa Rosa de Copán, Mayan ruins of Copán, 14° 50′21.5″ N 089° 08′45.3″W, D.G. Robinson leg., 29.vi.2010 (USDA 110232 /1); Depto. Santa Bárbara, along Honduras highway P20, between El Mogote and Pito Solo, 14° 47′34.1″ N 088° 10′45.5″W, D.G. Robinson leg. (USDA n.c.).

Distribution. Mexico, Belize, Guatemala, Honduras, Costa Rica, Panama.

Anatomy. Data on the radula structure were given by Breure & Eskens (1981: table 4).

Sequences. See Table 2 (COI, H3, ITS2+28S).

Remarks. Two coloured shell morphs are known, a white and a yellow one. Figure 19C shows a living specimen of the yellow shell morph. Photographs of living snails from Belize predated by snail-eating snakes were published by Dourson et al. (2018: 115–117).

Drymaeus ommatidia (Dorado & Roosen, 2023)

Figure 18A, B, distribution map = "Fig18..." at https://doi.org/10.6084/m9.figshare.26359921

Drymaeus ommatidia Dorado & Roosen 2023: 114, figs 1, 2D. "Perú, departamento de Amazonas, provincia de Bagua, noreste de Bagua, entre 1.600–2.200 m s.n.m. Cerca del límite con el departamento de Cajamarca (−5.634 S, −78.530 O)". Holotype MCNB (MZB 2023-0666).

Material. Peru: Amazonas, Bagua (Dorado & Roosen 2023).

Distribution. Peru.

Anatomy. Unknown.

Sequences. Unknown.

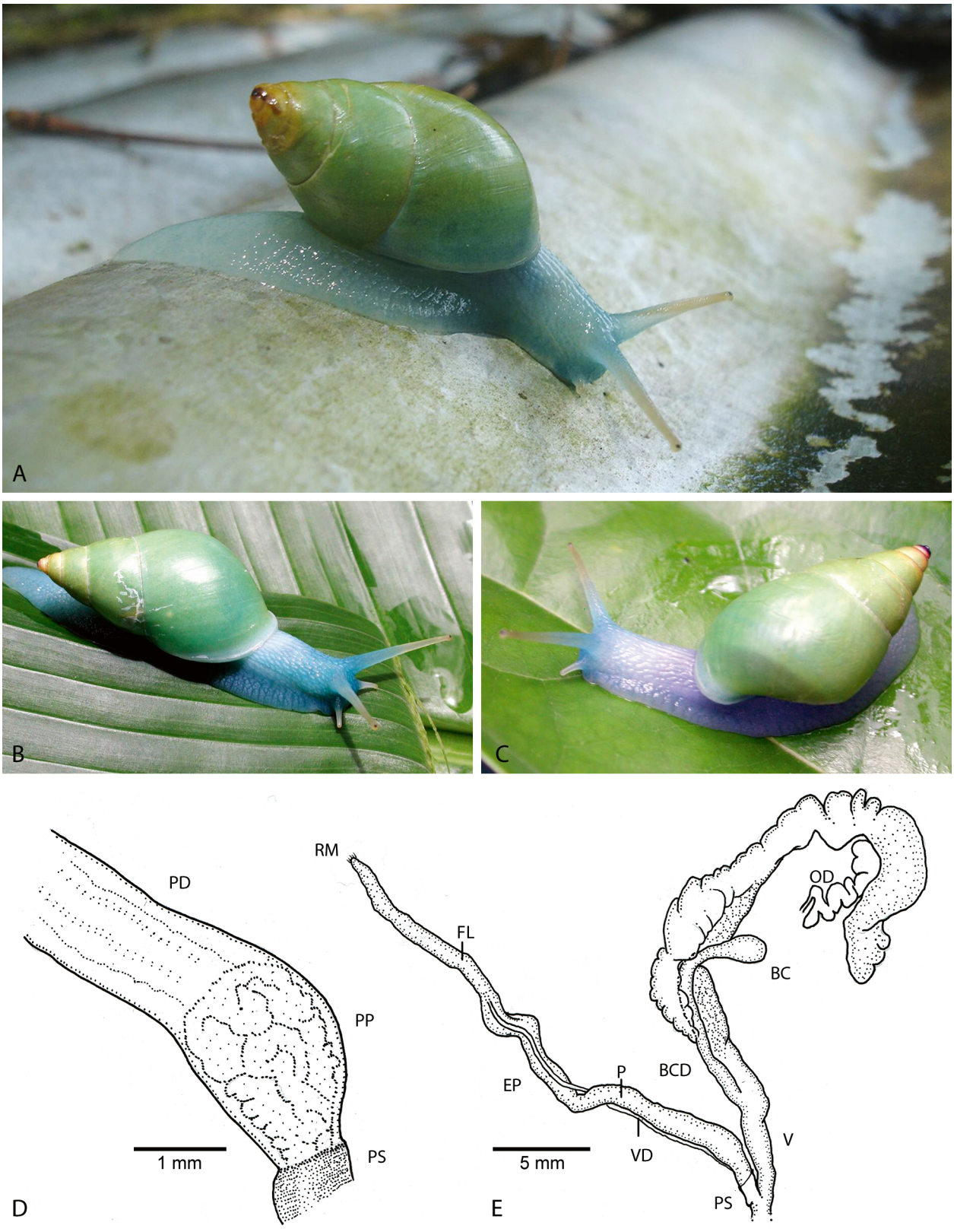

Figure 16. *Antidrymaeus stramineus* (Guilding, 1824). **A.** From Saint Vincent, Charlotte (iNaturalist 171056696, photograph: Islander784, CC by NC). **B, C.** From Trinity Falls trail (photographs: D.G. Robinson). **D, E.** Genitalia (RMNH.MOL 114176): (**D**) detail of phallus; (**E**) overview.

Remarks. This species seems to be morphologically similar to the next species, *D. valentini*, also from northern Peru. DORADO & ROOSEN (2023) did not provide an image of a crawling snail, but the similarity is so evident (greenish shell when fresh, yellowish when older) that we have no doubt to consider this taxon as a close relative.

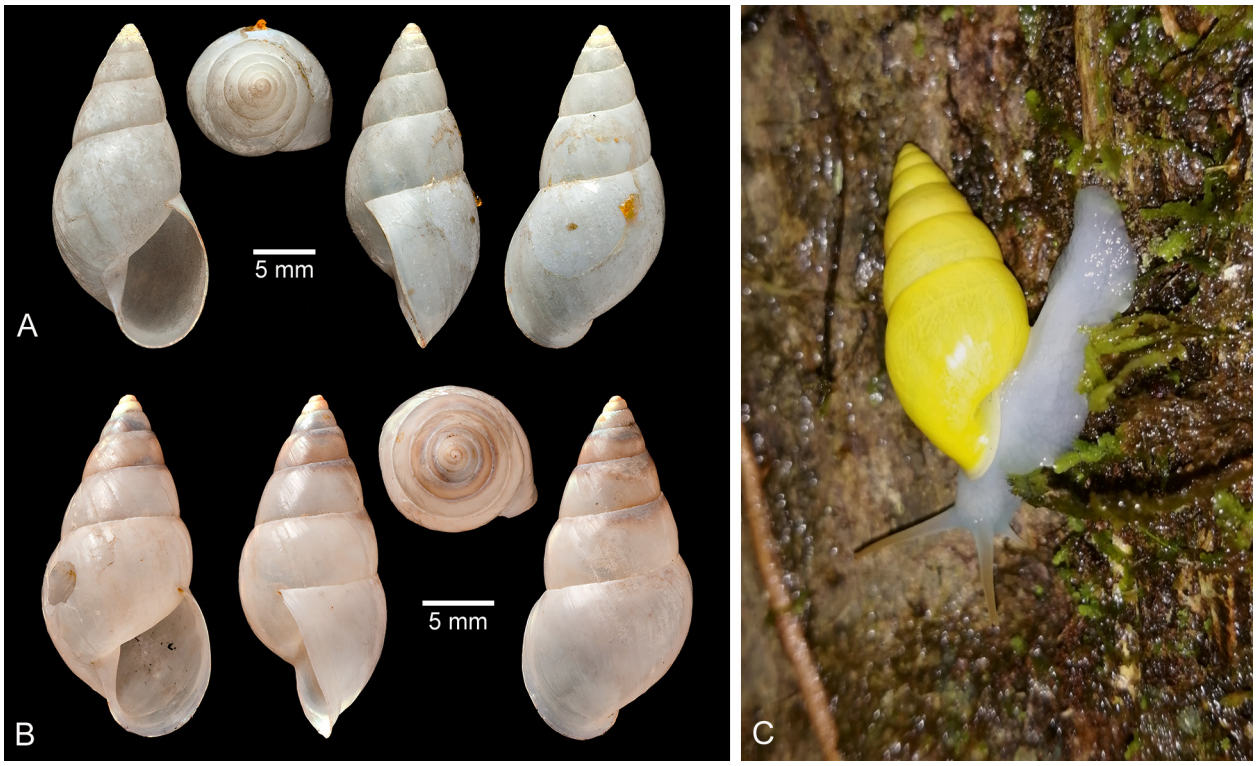

Figure 17. *Antidrymaeus sulphureus* (L. Pfeiffer, 1857). **A.** Lectotype, NHMUK 20100585. **B.** Lectotype of *Bulimus citronellus* Angas, 1879, NHMUK 1879.7.22.19. **C.** Living specimen, from Altos de Rasgos, Costa Rica (iNaturalist 146543863, photograph: Sergio Villegas, CC by NC).

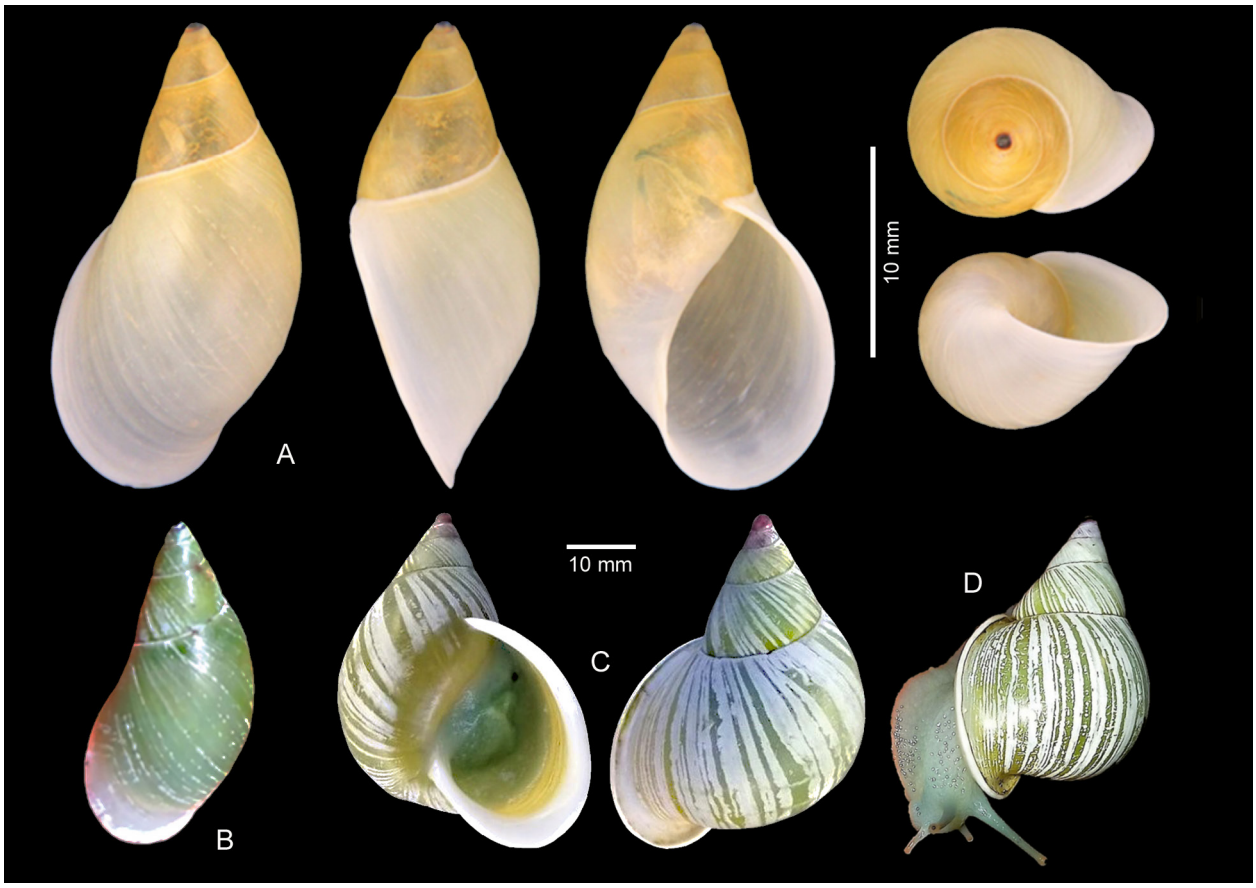

Figure 18. A, B. *Drymaeus ommatidia* (Dorado & Roosen, 2023): (**A**) holotype, MCNB MZB 2023-0666; (**B**) living specimen showing body colour through shell (A, B modified from Dorado & Roosen 2023: fig. 1). **C, D.** *Drymaeus valentini* (Breure & Vega-Luz, 2020): (**C**) apertural and dorsal views of holotype, MNCN 15.05/200118H; (**D**) live specimen from Molinopampa, Peru (photograph: V. Castillo).

Drymaeus valentini (Breure & Vega-Luz, 2020)

Figure 18C, D, distribution map = "Fig18..." at https://doi.org/10.6084/m9.figshare.26359921

Drymaeus (*Drymaeus*) *valentini* Breure & Vega-Luz 2020: 2, figs 2–4. "Peru, Dept. Amazonas, near Molinopampa, −6.208 S, −77.667 W, ca. 2600 m". Holotype MNCN 15.05/200118H.

Material. Peru, Amazonas, Molinopampa (VMA).

Distribution. Peru.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. This species has a very restricted range and is known only from a few localities. Figure 18C and D show the species when fresh; for photographs of non-fresh specimens, with yellowish shells, see Breure & Vega-Luz (2020).

Mesembrinus alabastrinus (S.I. da Costa, 1906)

Figure 19, video taken in the field at https://doi.org/10.6084/m9.figshare.21995660.v1, distribution map = "Fig19 and 27..." at https://doi.org/10.6084/m9.figshare.26359921

Drymaeus alabastrinus da Costa 1906: 98, pl. 11 fig. 4. "Honda, Colombia". Holotype NHMUK 1907.11.21.16.

Material. Colombia: Ibagué (iNaturalist 186988359).

Distribution. Colombia.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. Until now this species was known from shells only, which are whitish when found empty. Field images on iNaturalist (observation 186988359) show a greenish shell when alive, while the body of the snail extending from it has blueish tints (Fig. 19B; see also the video listed above). This observation falls within the known distribution of this species.

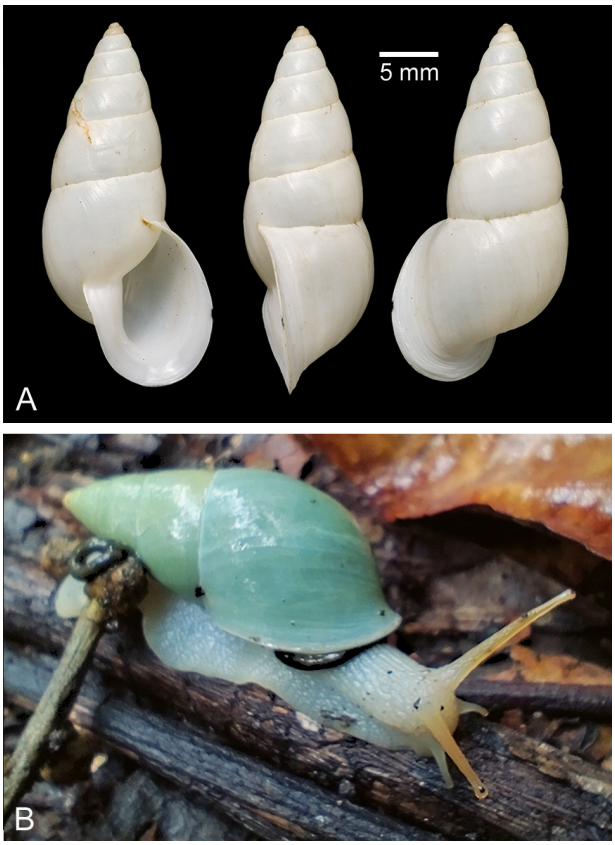

Figure 19. *Mesembrinus alabastrinus* (S.I. da Costa, 1906). **A.** Holotype, NHMUK 1907.11.21.16. **B.** Living specimen from near Ibagué, Colombia (photograph: N. Sanabria).

Mesembrinus binominis (E.A. Smith, 1895)

Figure 20, distribution map = "Fig20..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimulus indistinctus Guppy 1868: 436, not *Bulimus indistinctus* L. Pfeiffer, 1852. "Grenada". Type material not located.

Bulimulus (Drymaeus) binominis Smith 1895: 316, pl. 21 fig. 13. New name for *Bulimulus indistinctus* Guppy, 1868 non L. Pfeiffer, 1852.

Bulimulus (*Drymaeus*) *binominis lascellesiana* Smith 1895: 316, pl. 21 fig. 14. [Grenada] "Annandale estate". Lectotype NHMUK 1895.9.10.1.

Material. Bequia: Spring Estate, 13.0235° N 061.2261° W, D.G. Robinson leg., 4.viii.2003 (USDA 110224 /1). **Mustique.** A. Fields leg., 25.xi.2003 (USDA 100687 /3). **Canouan.** A. Fields leg., 28.xi.2003 (USDA 100670 /3). **Grenada:** Saint David Parish, Saint David's Harbour, D.G. Robinson leg., 2.vii.2003 (USDA 100829 /2, RMNH 114176 /1); Saint David Parish, scrub forest opposite Saint David's Harbour, D.G. Robinson leg., 1.xii.2003 (USDA 100690 /2); Saint George Parish, Annandale Estate, D.G. Robinson leg., 30.vi.2003 (USDA 100 669 /2).

Distribution. Grenada, Saint Vincent and the Grenadines.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. New records from the Grenadines (Bequia, Union Island, Mustique, and Canouan) show that this species is more common than hitherto assumed. Part of the collected material has been accidentally lost at the Holetown campus of the University of West Indies and is, therefore, not included in the material listed above. Field photographs, however, show that shells have 2 colour morphs, yellow and white. The specimens are faintly blue in the head and tail, but the mantle inside the shell is clearly blue, affecting the overall appearance of the shell. On Union Island the shell is much thicker, which makes the blue less visible.

Mesembrinus costaricensis (L. Pfeiffer, 1862)

Figure 21

Bulimus costaricensis Pfeiffer 1862: 153; Pfeiffer 1868 [1866–1869]: 419, pl. 95 figs 11–12. "Costa Rica". Type material not located.

Figure 20. *Mesembrinus binominis* (E.A. Smith, 1896). **A.** Shell from Grenada. **B–D.** Living animals from Grenada, Bequia, and Union Island respectively (photographs: D.G. Robinson).

Material. Costa Rica: unknown locality (voucher not collected).

Distribution. Costa Rica, Nicaragua (Thompson 2011).

Anatomy. Unknown.

Sequences. Unknown.

Remarks. In the field photographs, the blue tints are visible on the head, but other images showing the body are not available to us.

Mesembrinus gabbi (Angas, 1879)

Figure 22

Bulimus gabbi Angas 1879: 477, pl. 40 fig. 3. Flanks of Pico Blanco [Costa Rica], at an altitude from 3000 to 6000 feet [910–1830 m]. Lectotype NHMUK 1879.7.22.23.

Material. Costa Rica: San José, Pérez Zeledón, Rivas, trail to Parque Nacional Chirripó, 1740 m, M. Zuñiga, Z. Barrientos leg., 21.x.2021 (MZUCR). Photograph of specimen from Cerro Kámuk, Limón, Costa Rica, Parque Internacional La Amistad, subpáramo, R. González photographer, 24.xi.2022 (Fig. 22C).

Distribution. Panama, Costa Rica.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. Angas (1879: 477) described *Bulimus gabbi* based on material collected by W.M. Gabb. This material is present in the NHMUK (Fig. 22A). Angas (1879) wrote: "Animal varies with the colour of the shell from white to ash-colour, greenish white, or light brown". Recent observations of living specimens show 2 unicoloured shell morphs, a whitish and a green one (Fig. 22B, C). Both shell morphs, but especially the white morph, have bodies that show a very light, bluish colour on the dorso-caudal area of the foot (Fig. 22B, C).

Pilsbry (1899) grouped *M. gabbi* with *M. tripictus* and *M. irazuensis*. These taxa, native to Costa Rica, dwell above 1500 m and are similar in shape and size. They have a rose or reddish band around the lip and columella, and polymorphic shell colouration. *Mesembrinus tripictus* was described by Albers (1857: 97) as *Bulimus tripictus* (syntype ZMUZ 512562 /1) (Fig. 23A). Subsequently, Martens (1893 [1891–1901]: 225) wrote: "Some years ago [referring to his 1868 paper] I was led into an error concerning this species, owing to the original label "*tripictus"* being attached to a very different species, *O. meridanus,* Pfr., from Colombia, in the collection left by Albers …; therefore I described "*rhodotrema"* as new. But afterwards I satisfied myself that Albers's original description could not be applied at all to the shells in his collection, but very well to the specimens of *rhodotrema*". The type of this latter species was located in ZMB by Köhler (2007) (holotype ZMB 14410; Fig. 23B). Martens (1893 [1891–1901]: 225, pl. 14 figs 11,

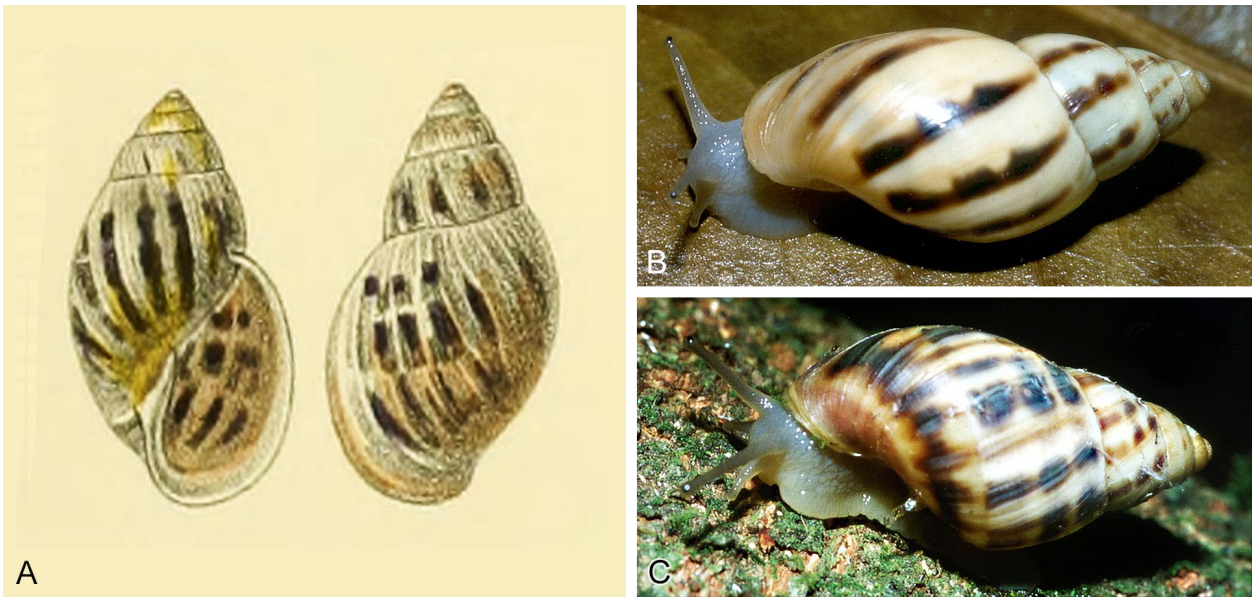

Figure 21. *Mesembrinus costaricensis* (L. Pfeiffer, 1862). **A.** Original figures (Pfeiffer 1868 [1866–1869]: pl. 95 figs 11, 12. **B, C.** Living specimens from Costa Rica (photographs: I. Richling).

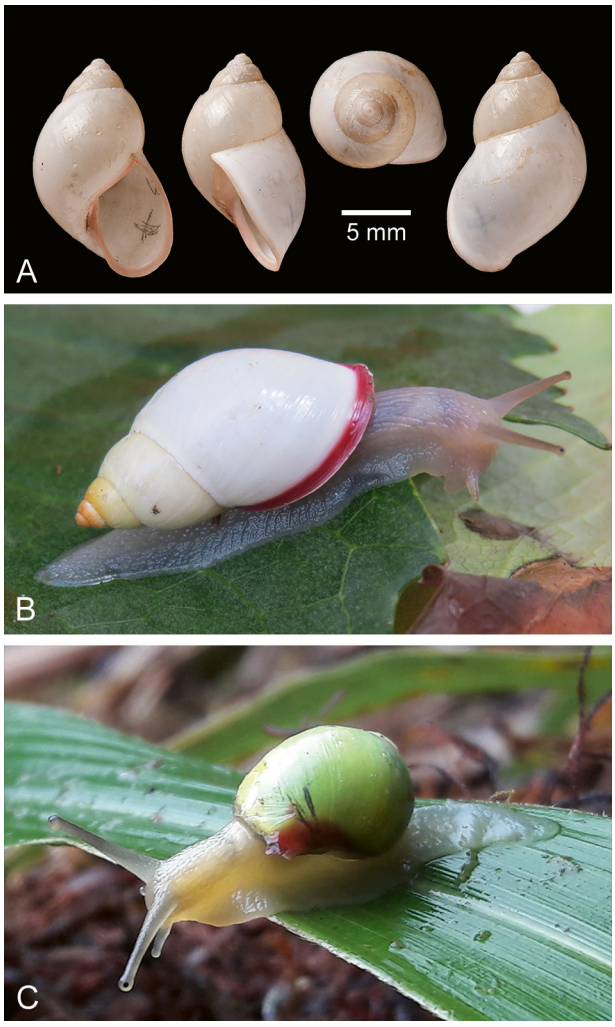

Figure 22. *Mesembrinus gabbi* (Angas, 1879). **A.** Lectotype of *Bulimus gabbi* Angas, 1879, NHMUK 1879.7.22.23. **B.** From Chirripó National Park, Costa Rica (photograph: Z. Barrientos). **C.** From Cerro Kámuk, La Amistad International Park, Costa Rica; this specimen's lip is partially broken (photograph: R. González).

11a) described *Otostomus tripictus* var. *hoffmanni*, which he placed in the synonymy of Albers' taxon but which RICHARDSON (1995: 136) considered as a valid species. However, Martens' material has not been located. Since we have been unable to check this material, we refrain from conclusions on the systematic position of this taxon. Details on the ecology, mating behaviour, and reproductive anatomy of *M. tripictus* were published by BARRIENTOS (2016). The body of this species is mainly beige or greyish, with no traces of blue (Fig. 23C).

Mesembrinus irazuensis (Angas, 1878) was described from the "volcano of Irazu" (ANGAS 1878: 73, pl. 5 figs 17–20). We have thoroughly checked it in the field, and it has a beige body near the head and a greyish colour on the dorso-caudal area of the foot, without traces of blue (Fig. 23E). Neither *M. tripictus* nor *M. irazuensis* have been sequenced.

Mesembrinus hjalmarsoni (L. Pfeiffer, 1856)

Figure 24, distribution map = "Fig24..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimus hjalmarsoni PFEIFFER 1856: 51. "In insula Portorico, plantatione 'Pajas' prope Manati". Type material not located.

Material. Puerto Rico: Municipio Utuado, Barrio Ángeles, along road between Utuado and Camuy, 18° 19′ 23.7″ N 066° 49′ 32.3″ W, 320 m, D.G. Robinson leg. (USDA n.c. /8); Municipio Arecibo, Bosque Estatal de Río Abajo, along road PR-10, steep forested slope adjacent to lay-by at km 72.6, 18° 21′ 29.9″ N 066° 41′ 23.2″ W, 220 m, R. Torres & D.G. Robinson leg., 17.i.2008 (USDA n.c. /5).

Distribution. Puerto Rico.

Anatomy. Unknown.

Sequences. Unknown.

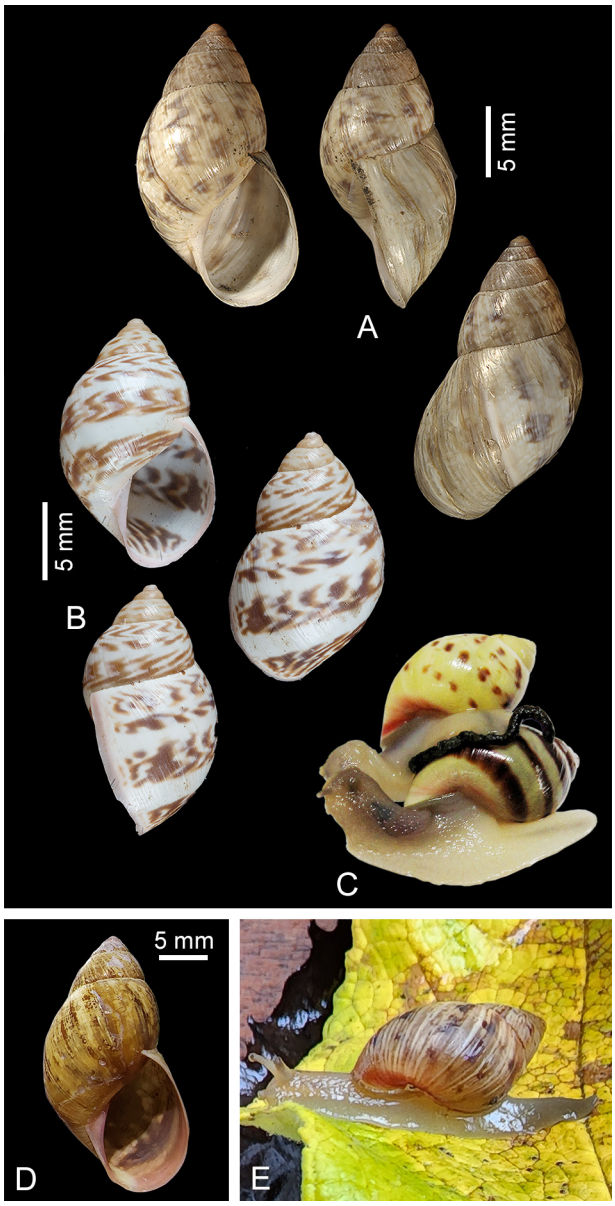

Figure 23. A. *Mesembrinus tripictus* (Albers, 1857), syntype of *Bulimus tripictus* Albers, 1857, ZMUZ 512562. **B.** *Bulimus rhodotrema* E. von Martens, 1868, holotype, ZMB 14410. **C.** Mating of 2 shell-colour morphs of *M. tripictus* from Reserva Forestal Río Macho, Cartago, Costa Rica (photograph: Z. Barrientos). **D.** Apertural view of *Mesembrinus irazuensis* (Angas, 1878) from Cerro Buena Vista, Cartago, Costa Rica (photograph: Z. Barrientos). **E.** Living specimen of *M. irazuensis* (Angas, 1878) from Cascajal de Vásquez de Coronado, San José, Costa Rica (photograph: Z. Barrientos).

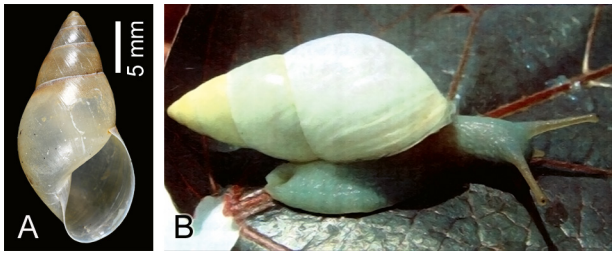

Figure 24. *Mesembrinus hjalmarsoni* (L. Pfeiffer, 1856). **A.** From Bosque Estatal de Rio Abajo (USDA n.c.). **B.** Living specimen from Ceiba, Puerto Rico (photograph: D.G. Robinson).

Figure 25. *Mesembrinus interpunctus* (E. von Martens, 1886). **A.** Lectotype, ZMB 38952. **B.** From Florianopolis, Brazil (iNaturalist 187907036, photograph: Kaurenju, CC by NC).

Remarks. The type locality is near Manatí (18.4275° N 066.4779° W), at a sugar-cane plantation that no longer exists. Some, perhaps all, type specimens were present in Pfeiffer's collection but destroyed during World War II. The new records are from an area approximately 26 km west-south-west of the type locality, and these are the first precise localities of this species since its original description. It may be easily confused with uniformly whitish forms of *Mesembrinus elongatus* (Röding, 1798) but differs in having a thinner shell, and a rounder and somewhat more flared aperture.

Mesembrinus interpunctus (E. von Martens, 1886)

Figure 25, distribution map = "Fig6 and 25..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimulus interpunctus Martens 1886: 161. "Piracicaba, Prov. S. Paulo, Brasilien". Lectotype ZMB 38952.

Material. Brazil: Paraná, Capanema, Cristo Rei (iNaturalist 190109881); Santa Catarina, Florianópolis (iNaturalist 187907036).

Distribution. Brazil, Paraguay, Uruguay, Argentina.

Anatomy. Data on genitalia and histology, radula and mandibula are given in Breure & Eskens (1981: 74–75, 235–244, 368, pl. 4 fig. 4, table 4).

Sequences. Unknown.

Remarks. Macedo et al. (2023: fig. 3) presented a de-

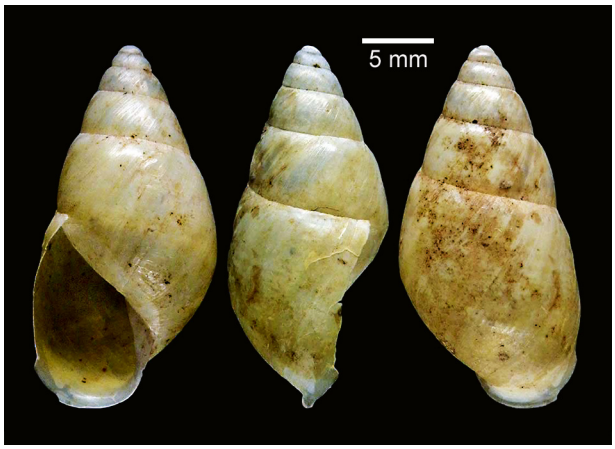

Figure 26. *Mesembrinus joubini* (L. Germain, 1907), holotype, MNHN 23014.

tailed report on the distribution in Brazil. They also published new anatomical data. Field photographs (Fig. 25B, iNaturalist 190109881) show that this species has some bluish tints on the body, as well as orange-tinted tentacles (particularly near the tips), which are also observed in some *Antidrymaeus* species. Due to the lack of sequences, we tentatively keep this species in *Mesembrinus.*

Mesembrinus joubini L. Germain, 1907

Figure 26

Drymaeus (*Antidrymaeus*) *joubini* Germain 1907: 59, fig. 2. [Ecuador] “République de l’Équateur”. Holotype MNHN-IM-2000-23014.

Material. Ecuador: “Équateur” (MNHN n.c.).

Distribution. Ecuador.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. This enigmatic species is known only from the type material, which is here refigured. It may prove to be a sinistral form of one of the Ecuadorian *Drymaeus* species. However, Germain had only imprecise locality data, so it is uncertain whether further sinistral specimens can be collected in Ecuador.

Mesembrinus montanus (Pilsbry, 1901)

Figure 27, distribution map = “Fig19 and 27...” at https://doi.org/10.6084/m9.figshare.26359921

Drymaeus roseatus montanus Pilsbry 1901 [1901–1902]: 161, pl. 48 fig. 51. “Colombia, western part of Santa Marta mountains, Las Pantidas [sic, Las Pavitas], about 4000 ft. elevation”. Lectotype CM 46614.

Material. Colombia: Santander, Florián (JHH).

Distribution. Colombia.

Anatomy. Unknown.

Sequences. Unknown.

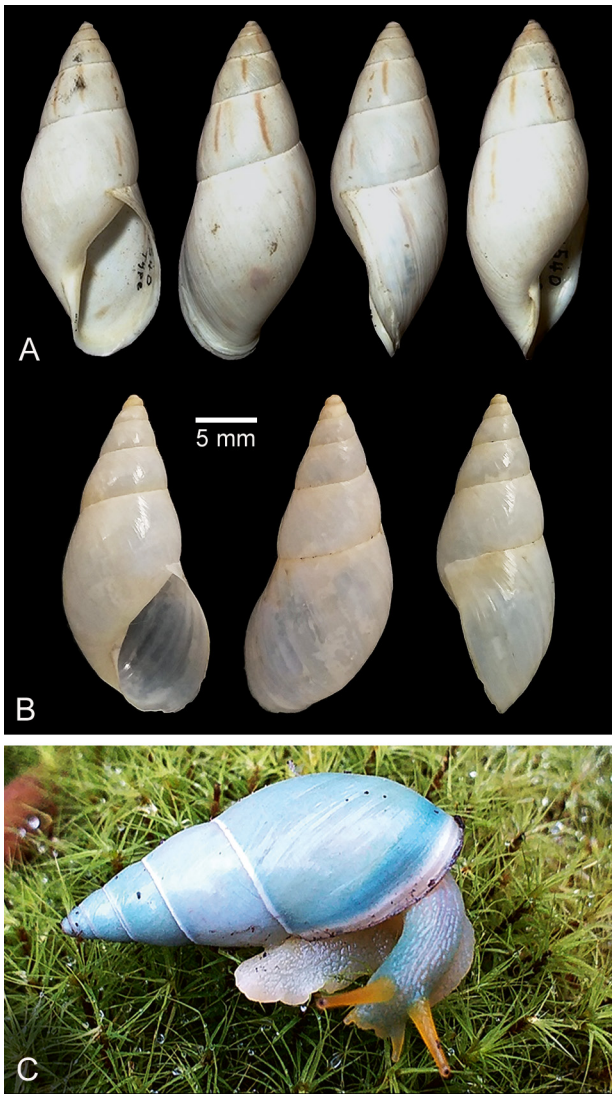

Figure 27. *Mesembrinus montanus* (Pilsbry, 1901). **A.** Lectotype, CM 46614. **B.** From Florián, Colombia (photographs: J. Hortua). **C.** Living specimen from Florián, Colombia; be aware light may affect colours in photographs especially when shells are white (photograph: J. Hortua).

Remarks. This species was hitherto known only from the type locality in Department of Cesar, near Las Pavitas (Pilsbry erred in the spelling of the locality). Breure & Borrero (2019), who designated a lectotype to stabilise the name, were inclined to consider Pilsbry’s taxon as a separate species from the Venezuelan *Drymaeus roseatus* (Reeve, 1848). We follow their judgement due to the lack of additional data for *D. roseatus*. A new locality, c. 500 km to the south, is Florián in the Department of Santander, where a living example was observed with blue tones in the body (Fig. 27C).

Mesembrinus mossi (E.A. Smith, 1896)

Figure 28, distribution map = “Fig28 and 30...” at https://doi.org/10.6084/m9.figshare.26359921

Bulimulus (*Drymaeus*) *mossi* Smith 1896: 243, pl. 8 fig. 8. “Trinidad”. Holotype NHMUK 1912.5.11.1.

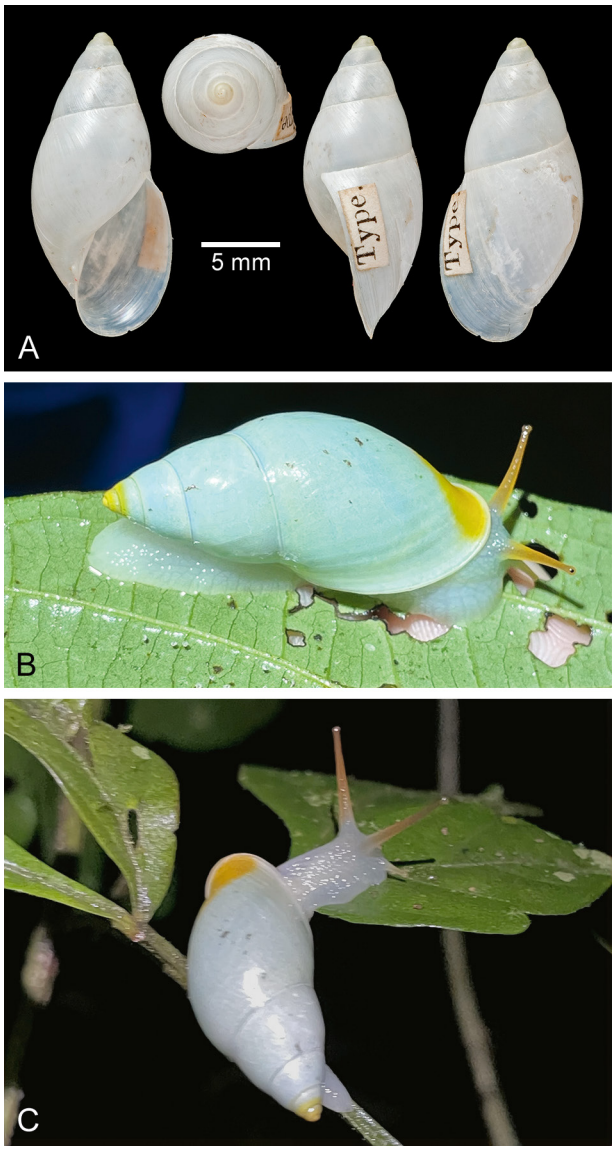

Figure 28. *Mesembrinus mossi* (E.A. Smith, 1896). **A.** Holotype, NHMUK 1912.5.11.1. **B, C.** From Tunapuna, Trinidad; both images are of the same animal, showing that light and a camera's automatic colour balance may affect colours (photographs: S. Tran).

Material. Trinidad: Tunapuna (iNaturalist 131683522).

Distribution. Trinidad.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. The observer of the living animal photographed it from different angles, which resulted in pictures where the animal appeared pale and another where the typical blue in the body was visible (Fig. 28B, C). We suppose that the pale colour is due to colour adjustment of the photograph. The species identity is based on the orange-yellow apex and the spot of the same colour at the outside of the lip around the umbilicus.

Mesembrinus moussoni (L. Pfeiffer, 1853)

Figure 29, distribution map = "Fig29 and 31..." at https://

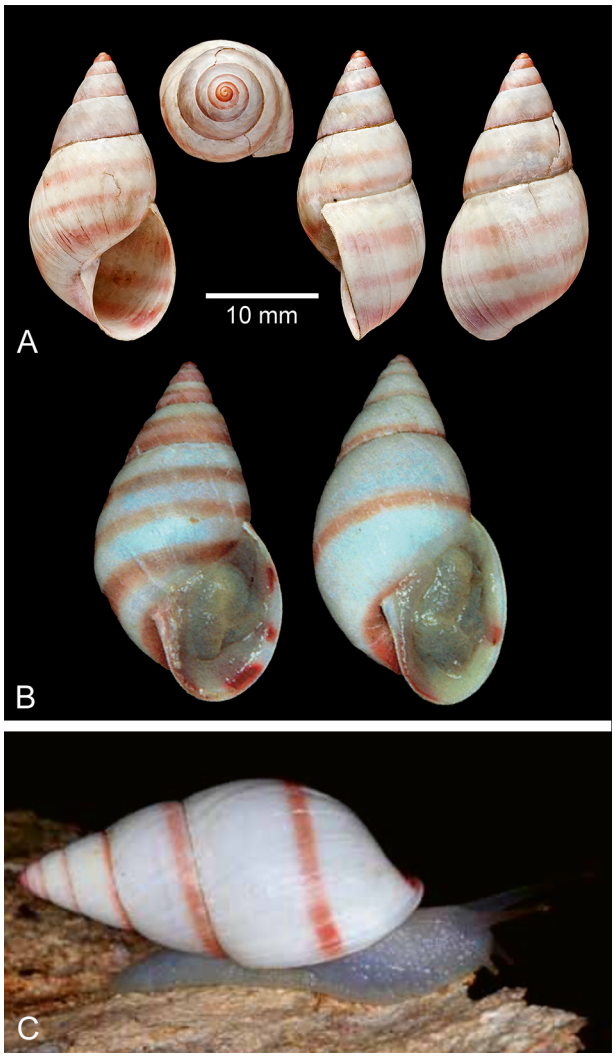

Figure 29. *Mesembrinus moussoni* (L. Pfeiffer, 1853). **A.** Lectotype, NHMUK 1975210. **B.** Two shell-colour morphs from Dominican Republic (USDA biotic survey). **C.** Living specimen from Bánica, Dominican Republic (source: Espinosa 2012: fig. 1A, CC by NC).

doi.org/10.6084/m9.figshare.26359921

Bulimus moussoni Pfeiffer 1853: 147. "St. Domingo". Lectotype NHMUK 1975210.

Material. Dominican Republic: "Las Yareyes, 2.3 km de la entrada de Bánica" (Espinosa 2012). **Haiti:** 1 km NE of Dufailly (UF 32894); 9 km NE of Dufailly (UF 32872); near Gonaives (UF 176955); 2 km SE of Las Cahobas (UF 32617).

Distribution. Hispaniola.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. Crosse (1891: 129) reported this species from "Yaquesi (A. Sallé)", Nord-Est Province, Haiti [Yaquezy, or in the current spelling: Jacquezy]. Pilsbry & Vanatta (1928: 478) mentioned they had seen a specimen from Bertrand Plantation, near Pont Sondé, [Artibonite Province], Haiti (ANSP 44519, 44520; this material was collected in 1917). Suitable habitat for this species may have

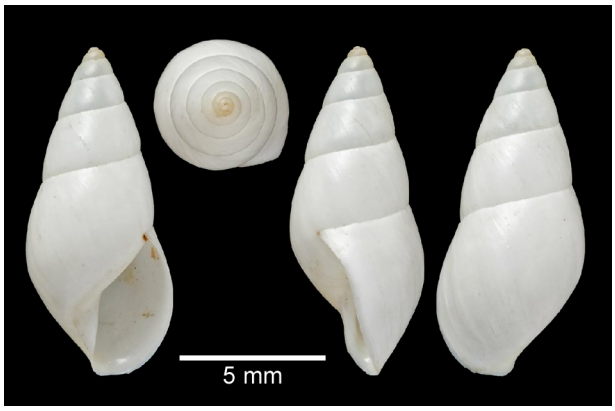

Figure 30. *Mesembrinus rawsoni* (Guppy, 1868). Lectotype, NHMUK 1878.1.28.209.

disappeared at both localities. There is a third Haitian locality known, from mountains near Marché Canard, Centre Province, at c. 180 m (ANSP 251105; collected in 1960).

Mesembrinus rawsoni (Guppy, 1871)

Figure 30, distribution map = "Fig28 and 30..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimulus aureolus var. *rawsoni* Guppy 1871: 308, pl. 17 fig. 6. "Tobago". Type material not located.

Bulimulus aureolus rawsoni H. Adams 1873: 208, pl. 13 fig. 12. "Tobago". Syntypes NHMUK 1866.1.3.8 /2.

Material. Tobago: Delaford (USDA n.c.).

Distribution. Tobago, Little Tobago.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. Both Guppy and H. Adams obtained their material from the same source, Sir Rawson William Rawson, who was Governor of Barbados and the Windward Islands from 1869 to 1875. This species is morphologically related to *Mesembrinus mossi* but differs in being smaller and having a slightly less flared apertural lip.

Mesembrinus sallei (Pilsbry, 1899)

Figures 1A, 31, distribution map = "Fig31..." at https://doi.org/10.6084/m9.figshare.26359921

Drymaeus sallei Pilsbry 1899: 11, pl. 12 fig. 15. [Hispaniola] "Santo Domingo [city] and Rancho Arriba" [Santo Domingo, according to Clench & Turner 1962: 132]. Holotype ANSP 57002.

Drymaeus sallei haitensis Pilsbry 1899: 12, pl. 39 fig. 4. [Hispaniola] "Haiti, Port-au-Prince, Fort Jacques". Lectotype ANSP 3552.

Material. Haiti: Province Sud, 3 km W of Formond, Morne Cavelier, 1100 m, J. Grego & J. Šteffek leg., 5.ii. 2006 (JG, RMNH 106894 /1).

Distribution. Hispaniola.

Anatomy. Unknown.

Sequences. Unknown.

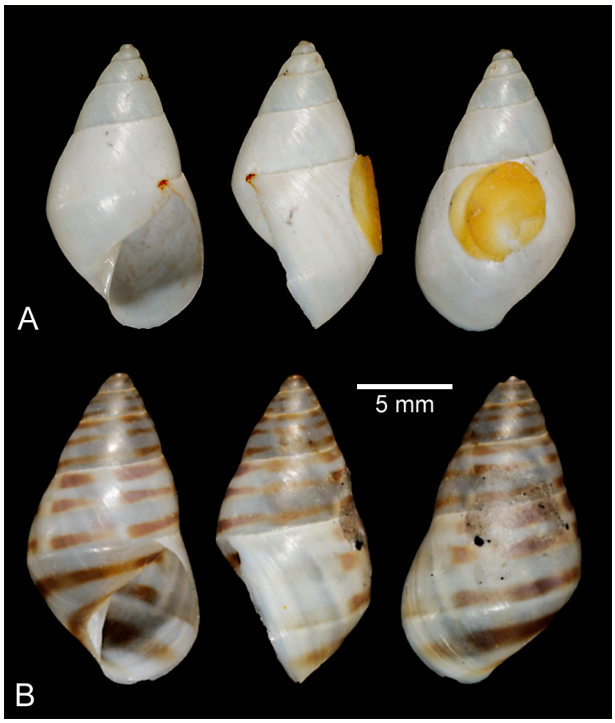

Figure 31. *Mesembrinus sallei* (Pilsbry, 1899). **A.** Lectotype of *Drymaeus sallei* Pilsbry, 1899 (ANSP 57002); **B.** Lectotype of *D. sallei haitensis* Pilsbry, 1899 (ANSP 3552).

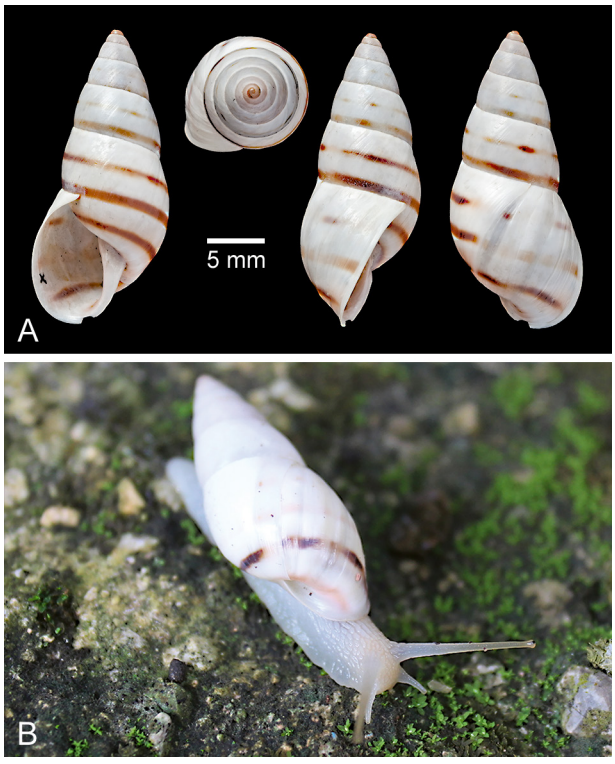

Figure 32. *Mesembrinus tropicalis* (Morelet, 1849). **A.** Lectotype, NHMUK 1893.2.4.210. **B.** Living specimen from Flores, Guatemala (photograph: R. Busquets Reverte).

Remarks. Pilsbry (1899: 11) wrote about his variety *haitensis*, "The exact position and status of this form are not easily decided". We tentatively regard this as the

banded form of *Drymaeus sallei*; it was recorded from Fort Jacques, Province Ouest at 1300 m. It is not known if the locality has been deforested since Pilsbry's material was collected.

Mesembrinus tropicalis (Morelet, 1849) comb. nov.

Figure 32, distribution map = "Fig32..." at https://doi.org/10.6084/m9.figshare.26359921

Bulimus tropicalis Morelet 1849: 9. [Mexico] "adpagam civitatis Campeche". Lectotype NHMUK 1892.2.4.210.

Otostomus tropicalis (Morelet)—Martens 1893 [1891–1901]: 233.

Drymaeus tropicalis (Morelet)—Pilsbry 1899: 85–86; pl. 6 figs 21–23.

Material. Guatemala: Petén, Flores (iNaturalist 95266 963).

Distribution. Mexico, Belize, Guatemala.

Anatomy. Unknown.

Sequences. Unknown.

Remarks. The only available images of a living animal show hints of blue in the body (Fig. 32B); the photographs were taken near Flores in Guatemala. We await further DNA research to ascertain the systematic position of this taxon and its relationship with *A. inusitatus*.

Discussion

Mazé's (1883) observation of a blue-bodied snail has long (140 years!) been ignored in the literature. Is blue colouration something substantially different that has taxonomic value? This has been met with much scepticism. For example, local malacologists in Costa Rica consider that there are 3 similar species, *Mesembrinus tripictus*, *M. gabbi* and *M. irazuensis*. *Mesembrinus gabbi* has a blue colouration, but *M. tripictus* and *M. irazuensis* do not. Non-experts of the fauna doubt whether the blue coloration is significant biologically and taxonomically. Since we could not examine the body colour of live specimens in more detail, this remains an open question for the moment. However, the availability of material suitable for sequencing from several other blue-bodied species has finally allowed us to conclude that these form a monophyletic group and to draw the consequence of this observation in their classification: that is to group them together in the genus *Antidrymaeus* (Salvador et al. 2023).

While the distribution of *Antidrymaeus* shows a marked focus in Central America and the Caribbean, with only a few scattered species on the mainland of South America, we suspect that additional field observations could increase the species list, especially from the latter area. We envisage that future sequencing will lead to the discovery that more species belong to this clade. Interestingly this group is now composed of morphologically different species, which were hitherto placed in either *Drymaeus* s.s. or *Mesembrinus*; the latter was until very recently classified as a subgenus of *Drymaeus* s.l., but then raised to the genus level (Salvador et al. 2023). Therefore, we strongly suggest that increased taxon sampling and sequencing is needed in this species-rich *Drymaeus* genus to improve its classification.

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