

# Folia conchyliologica

N° 52, décembre 2019



*Drymaeus (Mesembrinus) iris* (Piaget, 1914), Colombia, Calí. Photo G. Kattan.

## Sommaire

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**Abraham S.H. Breure & Francisco J. Borrero** - A review of *Stenostylus* Pilsbry, 1898 and *Drymaeus* Albers, 1850 (Mollusca: Gastropoda: Orthalicoidea: Bulimulidae) from Colombia, with description of new species.

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1-79

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La priorité est donnée aux articles traitant de malacologie continentale, autrement dit de la faune terrestre et dulcicole. Les articles traitant de la faune saumâtre ou marine sont acceptés afin de répondre à une demande croissante de lecteurs intéressés par l'ensemble de la malacologie.

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Il n'y a pas de recommandation particulière dans la rédaction des articles : nous nous chargeons de la mise en forme en accord avec vos souhaits. Dans la mesure du possible, inspirez vous de la mise en forme des numéros les plus récents.

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# A review of *Stenostylus* Pilsbry, 1898 and *Drymaeus* Albers, 1850 (Mollusca: Gastropoda: Orthalicoidea: Bulimulidae) from Colombia, with description of new species

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<http://zoobank.org/pub:4778E4BF-86D9-4956-B1D6-08CF32CCF6BA>

**Abstract** - The land snails of the genera *Drymaeus* Albers, 1850 and *Stenostylus* Pilsbry, 1898, both belonging to the family Bulimulidae, and occurring within northwestern South America are revised and notes on their distribution are given. 78 species of *Drymaeus* and two of *Stenostylus* are herein confirmed from Colombia, and are illustrated for comparison. Six new (sub)species are described: *Drymaeus (Drymaeus) denticulus*, *D. (D.) duplexannulus*, *D. (D.) felix restrepoensis*, *D. (D.) iniurius*, *D. (D.) intermissus*, *D. (D.) luciensis*.

*Drymaeus flexuosus* megas Pilsbry, 1944 is now upgraded to species level. A lectotype is designated for *Drymaeus roseatus montanus* Pilsbry, 1901.

The following nominal taxa are herein synonymised: *Bulimus antioquiensis* L. Pfeiffer, 1855 = *B. baranguillanus* L. Pfeiffer, 1853; *Bulimus hachensis* Reeve, 1850 = *B. virgo* Lea, 1838 = *B. columbianus* Lea, 1838; *Drymaeus eversus alata* Piaget, 1914 = *Drymaeus eversus subula* Piaget, 1914 = *Bulimus violaceus* Mousson, 1873 = *B. confluentis* L. Pfeiffer, 1855; *Drymaeus cantatus medianus* Pilsbry, 1935 = *D. tusagasuganus* Pilsbry, 1935 = *Bulimulus (Drymaeus) plicatoliratus* da Costa, 1898 = *Bulimus convexus* L. Pfeiffer, 1855; *Drymaeus fallax chicoensis* Breure, 1977 = *Bulimus fallax* L. Pfeiffer, 1853; *Bulimus trivittatus* Mousson, 1869 = *B. felix* L. Pfeiffer, 1862; *Bulimus andicola* L. Pfeiffer, 1847 = *B. multilineatus* Say, 1825; *Bulimulus (Drymaeus) comis* Preston, 1907 = *Bulimus pealianus* Lea, 1838; *Drymaeus incognita* da Costa, 1907 = *D. bellus* da Costa, 1906 = *D. blandi* Pilsbry, 1898 = *Bulimulus (Drymaeus) smithii* da Costa, 1898.

For the following species, precise localities are given for the first time: *Drymaeus (Drymaeus) angusta* da Costa, 1906, *D. (D.) auris* (L. Pfeiffer, 1866), *D. (D.) baranguillanus* (L. Pfeiffer 1853), *D. (D.) cognatus* Pilsbry, 1901, *D. (D.) geometricus* (L. Pfeiffer 1846), *D. (D.) inclinatus* (L. Pfeiffer 1862), *D. (D.) spadiceus* da Costa, 1906, *D. (Mesembrinus) koppelli* (G.B. Sowerby III, 1892), *D. (M.) muliebris* (Reeve 1849).

Newly recorded for the Colombian malacofauna are the following five taxa: *Drymaeus (Drymaeus) fordii* Pilsbry, 1898, *D. (D.) glaucostomus* (Albers, 1852), *D. (D.) volsus* Fulton, 1907, *D. (Mesembrinus) interruptus* (Preston, 1909).

The following 27 taxa are excluded from the Colombian fauna as we consider them based on erroneous or doubtful records: *Stenostylus meleagris* (L. Pfeiffer, 1853), *Drymaeus (Drymaeus) attenuatus* (L. Pfeiffer, 1853), *D. (D.) chimborasensis* (Reeve, 1848), *D. (D.) edmuelleri* (Albers, 1854), *D. (D.) linostoma* (d'Orbigny, 1835), *D. (D.) membielinus* (Crosse, 1867), *D. (D.) phryne* (L. Pfeiffer, 1863), *D. (D.) poecilus* (d'Orbigny, 1835), *D. (D.) protractus* (L. Pfeiffer, 1855), *D. (D.) rugistriatus* Haas, 1952, *D. (D.) strigatus* (Sowerby, 1833), *D. (D.) subinterruptus* (L. Pfeiffer, 1853), *D. (D.) trigonostomus* (Jonas, 1844), *D. (Mesembrinus) cactorivorus* (Broderip, 1832), *D. (M.) deshayesi* (L. Pfeiffer, 1845), *D. (M.) dubius* (L. Pfeiffer, 1853), *D. (M.) flavidus* (Menke, 1829), *D. (M.) granadensis* (L. Pfeiffer, 1848), *D. (M.) liliaceus* (Férussac, 1821), *D. (M.) loxanus* (Higgins, 1872), *D. (M.) manupictus* (Reeve, 1848), *D. (M.) multifasciatus* (Lamarck, 1822), *D. (M.) nitidus* (Broderip, 1832), *D. (M.) pertristis* Pilsbry, 1898, *D. (M.) pervariabilis* (L. Pfeiffer, 1853), *D. (M.) studeri* (L. Pfeiffer, 1847), *D. (M.) translucens* (Broderip, 1832).

**Key words** - Northwestern South America, Ecuador, Panama, Venezuela, Stylommatophora, taxonomy, distribution.

## Introduction

The land snail superfamily Orthalicoidea is a dominant element within the Neotropical malacofauna. Its taxonomy at the family level has seen several conflicting views, based on shell morphology and anatomy (Breure 1979, Schileyko 1999). Recently, Breure *et al.* (2010) and Breure & Romero (2012), presented phylogenetic studies covering representatives of the whole superfamily. Although some relationships need further study, the overall conclusion is that at present, seven families can be recognised within the Orthalicoidea. One of these families is the Bulimulidae, occurring in South and Central America, adjacent areas within the U.S.A., and the Caribbean. In this paper we deal with the genera *Stenostylus* Pilsbry, 1898, and *Drymaeus* Albers, 1850 of Colombia. While the former is a small genus with only a handful of species, the latter is one of the most species-rich genera of macro land snails in Colombia and also in the overall northern South American malacofauna. In the recent catalogue by Linares & Vera (2012) three *Stenostylus* respectively 99 *Drymaeus* species are listed; their list is, however, largely

based on literature and museum records from electronic databases, so the specimens were not critically examined and evaluated.

A few considerations motivated this study. First, many nominal taxa of *Drymaeus* have been described from the region, but most of these species are known only from the type material where the locality data is often very imprecise, such as a country, or often using places names now restricted to areas far from their namesakes, making it difficult to ascertain where these species actually lived or may live today. Furthermore, many species are known from few or single specimens so any intraspecific variability cannot be evaluated. A final motivation was that of producing a document that would allow a user to identify *Drymaeus* and *Stenostylus* snails from Colombia, by looking at (type) images provided for comparison, but also containing elements to understand the nomenclatural and taxonomical status of each taxon, including where relevant type and voucher material is housed.

The results of this study lead to a re-evaluation of the number of taxa recognised within this geographic region. The distinction between the two subgenera currently recognised (*Drymaeus* s.str. and *D. (Mesembrinus)* Albers, 1850) is followed in this paper, but it is understood that further molecular investigation is needed to ascertain its validity (Breure, unpublished data). For both genera, *Stenostylus* and *Drymaeus*, the overall aim of the present paper is to review the species known from Colombia and some species from adjacent areas as far as their understanding helps to decide on the systematics of species confirmed to have been collected within Colombia.

## Material and methods

This paper mainly relies on shell morphology since, with few exceptions, there is very little material suitable for anatomical studies of the taxa treated herein which has become available since Breure (1978) and Breure & Eskens (1981). Shells were studied from major museums in the USA and Europe, as well as from several institutions in Colombia, from additional private collections (P.C.s), and from recent field surveys. For a description of the study area and remarks on quality of the localities, see Borrero & Breure (2011: 3). Unless indicated as “[not seen]”, each vouchered specimen or images of the specimen were examined by us, and compared to photographs of other lots. For species described from Colombia the type material, where available, is illustrated with at least an apertural view; other views are presented only if not figured in recent publications. For several species listed herein no other photographs are available than those made by the second author during study visits; although these pictures are not always up to normal publication standards we have used them where necessary due to lack of alternatives. No data solely based on the museums’ databases (though these were consulted when applicable), or from data aggregators is listed.

The methodology follows that used by Breure & Borrero (2008) and Borrero & Breure (2011). Within each taxon, all voucher records are listed individually, with a collection acronym and record; records outside Colombia are also listed, but our searching for these in museum collections was not exhaustive, unless they were type material. Distributional data are given within the countries, arranged by the main political-administrative divisions indicated in bold type. Unless otherwise indicated; imprecise or untraceable locations are arranged under “?”. Distribution maps are provided for Colombian species for which precise localities are known and have been geo-referenced; only records from Colombia are shown in the maps. Records with vague localities (i.e., “Colombia”, or “Bogotá”) are excluded from this analysis unless there is certainty that the material came from such specific localities. In addition, only specimens examined directly by us were geo-referenced, and records based solely on published literature are not included in the maps, but are indicated in the text with a corresponding annotation. Altitudinal ranges are based on precise localities only; this may account for differences with those reported by Linares & Vera (2012), who used general type localities for their altitudinal ranges. When not stated in collection data, but enclosed in the text within square parenthesis, the values given correspond to our interpretation, based on such sources as local knowledge by colleagues in Colombia, as well as tools such as Google Earth.

Shell measurements are according to the method described by Breure (1974: figs 2–3). The following abbreviations are used to refer to shell dimensions (in mm, see also Breure 1974): D, diameter; H, shell height; HA, height of aperture; LW, height of last whorl; W, number of whorls; WA, width of aperture. Due to inaccessibility of some specimens measurements were taken from the photographs available. The following abbreviations were used in describing secondary administrative names of localities below the level of municipalities: Corr., Corregimiento, and Ver., Vereda.

Species are figured according to the following criteria: (i) Type material of all Colombian species if available; (ii) species that have not been properly illustrated before; (iii) species for which a synonymy is proposed, or an existing synonymy argued against; (iv) taxa that fall within closely related species complexes, or that are sufficiently similar to warrant photographic evidence as a tool for identification.

The following abbreviations are used to refer to depositories of material (PC indicates Private Collection): AI, PC Alan Pierre Infante, Bogotá, Colombia; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, USA; AQ, PC A. Quintero, Cali, Colombia; CC, PC C. Murcia, Cali, Colombia; CM, Carnegie Museum of Natural History,

Pittsburgh, USA; CMC, Cincinnati Museum Center, Cincinnati, USA; DMNH, Delaware Museum of Natural History, Wilmington, USA; FEM, Femorale (business collection), Sao Paulo, Brazil; FJ, Fundación Jocotoco, Quito, Ecuador; FMNH, Field Museum of Natural History, Chicago, USA; GK, PC Gustavo Kattan, Universidad Javeriana, Cali, Colombia; ICNB, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia; INHS, Illinois Natural History Survey, Urbana-Champaign, U.S.A.; IMCN, INCIVA-Museo Departamental de Ciencias Naturales, Cali, Colombia; JMR, Juan de Roux (business collection), Key Biscayne, FL, U.S.A.; JG, PC Jozef Grego, Banská Bystrica, Slovakia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MHNG, Muséum d'Histoire naturelle, Geneva, Switzerland; MLS-BOG, Museo La Salle de Ciencias Naturales, Universidad de La Salle, Bogotá, Colombia; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MUG, Museo de la Universidad de Guayaquil, Guayaquil, Ecuador; MHNN, Musée d'histoire naturelle, Neuchâtel, Switzerland; MNHN, Muséum national d'Histoire naturelle, Paris, France; NMW, National Museum of Wales, Cardiff, UK; NHMUK, Natural History Museum, London, UK; NMB, Naturhistorisches Museum Basel, Switzerland; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; RBINS, Royal Institute of Natural Sciences, Brussels, Belgium; RMNH, Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands; RZ, PC Raúl E.C. Zea, Caracas, Venezuela; SMF, Natur-Museum Senckenberg, Frankfurt am Main, Germany; UAM, Universidad de Antioquia, Medellín, Colombia; UMB, Universidad Militar Nueva Granada, Bogotá, Colombia; UF, Florida Museum of Natural History, Gainesville, USA; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; USDA, United States Department of Agriculture (ANSP), Philadelphia, USA; UVZ, Universidad del Valle, Departamento de Biología / Zoología, Cali, Colombia; ZMA, Naturalis Biodiversity Center (formerly Zoologisch Museum Amsterdam), Leiden, the Netherlands; ZMB, Zoologisches Museum der Humboldt-Universität, Berlin, Germany; ZMUZ, Zoologisches Museum, Universität Zürich, Zurich, Switzerland. The abbreviation n.c. (no code) is used for material without registration number in collections.

In some museums lots were found with several registration codes due to historic reasons. Although we have tried to be consistent in the choice of the most recent code, our efforts may not have been always successful. However, with the locality data supplied, and the accompanying photographs shown it should be possible to trace all samples we have studied.

## Systematics

### Superfamily Orthalicoidea Martens, 1860

#### Family Bulimulidae Tryon, 1867

**Remarks.** The classification of this family is based on data of Breure (1979), Breure *et al.* (2010) and Breure & Romero (2012). Nomenclature is in accordance with Bouchet *et al.* (2017). Taxa marked with double asterisks (\*\*) are new additions for Colombia. Species marked with an asterisk (\*) are species for which confirmation of presence in Colombia is still needed (this includes species with type locality 'Colombia' and 'New Granada', but not Bogota). Species for which we have no recent or precise records, but which have 'Bogota' and/or another seemingly precise location as type locality are not questioned as Colombian species, unless we have some strong reason to suspect their veracity (e.g., look suspiciously similar to a Peruvian taxon, etc.). Species that have been referred to being found in Colombia but are clearly errors, or are very unlikely to live in Colombia, are marked by a dagger (†). These are listed in a separate section with nominal taxa now excluded from the checklist of Colombian species for the two genera.

Full references for literature after 1995 are given for all species, in addition to those listed by Richardson (1995). Regarding the latter publication, i.e. a catalog of species of Bulimulidae, a general procedure is followed here when dealing with synonymies, as Richardson stated in his introduction: "Names that have been associated with a species (i.e., synonyms, varieties, subspecies, etc.) are listed with a "+" alphabetically under the species." We have interpreted his statement to mean that the grouping of taxa names under "+" by Richardson (1995) are not to be considered formal synonymisations, unless proposed elsewhere. It is possible that other workers have followed different interpretations.

## Genus *Stenostylus* Pilsbry, 1898

*Stenostylus* PILSBRY 1898 [1897–1898]: 184. Type species by original designation: *Bulimus nigrolimbatus* L. Pfeiffer, 1853.

**Distribution.** Peru, Ecuador, Colombia. Thus far all records are from relatively high elevations, i.e. more than 1500 m.

**Remarks.** The inclusion of Venezuela in the distribution list by BREURE (1979), was based on the reported, imprecise locality “Andes of New Grenada” for two species, viz. *S. meleagris* and *S. nigrolimbatus*. BREURE (2008) showed that the latter species occurs in the Cocuy area in Colombia, whereas no *Stenostylus* material is hitherto known from Venezuela. *S. meleagris* is a Peruvian species (BREURE 1978, 2011). *Bulimus goudoti* Petit de la Saussaye, 1843 is currently placed in *Suniellus* Breure, 1978 (Breure 2011); anatomical and molecular research is, however, still needed to confirm this classification.

### *Stenostylus colmeiroi* (Hidalgo, 1872)

Figs 2A–B, 3

*Bulimus colmeiroi* HIDALGO 1872: 122. Type locality: Ecuador, Baeza. Lectotype MNHN-IM-2000-20822 (BREURE 1975).

*Stenostylus colmeiroi* (Hidalgo); RICHARDSON 1995: 369 (references); BREURE 2008: 245, figs 9–10; BREURE & BORRERO 2008: 19; LINARES & VERA 2012: 207; BREURE & ARAUJO 2017: 86, fig. 32F.

**Material.** **Cauca**, Buenos Aires, Vereda El Silencio, Finca El Carmen [~1100–1300 m], R. Contreras, 17.x.1980 (UVZ 018 [partim]); **Cundinamarca**, Albán, Granjas Infantiles del Padre Luna, 2000 m, S. Obando leg., 27.x.2001 (ICNB n.c.); **Risaralda**, Santuario Flora y Fauna Otún-Quimbaya, P24–6, ~1,700 m, C. Murcia leg., x.2000 (CC); Ibidem, P3–6, ~1,700 m, vii.2000 (CC). **Ecuador**, Prov. Napo, Baeza, Martínez leg. (MNCN 15.05/3301, MNHN lectotype); Prov. Loja, San Francisco, near Malacatos [~1500–1700 m], A. Bianchi leg., 2013 (FEM 116345–116350).

**Altitudinal range.** All records are in the range 1500–2000 m.

**Ecology.** The Colombian records are all from Cauca Valley respectively Magdalena Valley montane forests ecoregions. The actual habitat is unknown.

**Remarks.** LINARES & VERA (2012: 207) listed this species from Valle del Cauca, Calima, 1600 m, on account of BREURE & ESKENS (1981: 55); the latter reference was re-interpreted by BREURE (2008: 246) as a misidentification of *Simpulopsis citrinovitrea* (Moricand, 1836). The record from Loja, Ecuador is the southernmost thus far known for this species.

### *Stenostylus nigrolimbatus* (L. Pfeiffer, 1853)

Figs 2C–D, 3

*Bulimus nigrolimbatus* L. PFEIFFER 1853b: 257. Type locality: “Andes of New Granada”. Lectotype NHMUK 1975549 (BREURE 1978).

*Stenostylus nigrolimbatus* (L. Pfeiffer); RICHARDSON 1995: 370; BREURE 2008: 247 (references, synonymy); BREURE & ABLETT 2014: 132, figs 75A–C, L40vii.

*Drymaeus (D.) cleefi* BREURE & ESKENS 1981: 14, figs 32–33, pl. 5 figs 7–8. Holotype RMNH 55375 (anatomy).

**Material.** **Santander**, Páramo de Almorzadero, Piedra de Molino, 4100–4350 m, A.M. Cleef leg. (RMNH 55375, 55376; ICNB n.c.); ?Colombia (NHMNH, lectotype of *B. nigrolimbatus*).

**Ecology.** This species is confined to the Northern Andean páramo ecoregion. The species was found on calcareous ridges (BREURE 2008: fig. 16).

**Remarks.** Placement of this species within *Stenostylus* rather than *Drymaeus*, was demonstrated by BREURE (2008).

### *Stenostylus* species 1

**Material.** **Valle del Cauca**, Páramo Pan de Azúcar, 3650 m, R. Contreras leg., 8.x.1983 (UVZ 83079).

**Ecology.** Found on Cyperaceae between paramo vegetation.

**Remarks.** The material of this and the following species is not sufficient to warrant definite identifications. The single specimen resembles most closely *S. nigrolimbatus* (L. Pfeiffer).

***Stenostylus* species 2**

**Material.** Antioquia, Municipio Caldas, Alto de San Miguel, Bosque #2, A. Sierra leg., 2045 m, 22.xi. 1996 (UAM n.c.). Caldas, Laguna Verde, between Laguna Santa Isabel and Paramo El Cisne, 4100 m, E. Peña leg., iii.1984 (UVZ 84049).

**Remarks.** The single specimen in each lot resembles most closely *S. nigrolimbatus* (L. Pfeiffer).

**Genus *Drymaeus* ALBERS 1850**

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

**Distribution.** Venezuela, Guyana, Suriname, French Guiana, Brazil, Uruguay, Paraguay, Argentina, Bolivia, Peru, Ecuador, Colombia, Panama, Costa Rica, Nicaragua, El Salvador, Honduras, Guatemala, Belize, Mexico, U.S.A., Caribbean (most islands).

**Key to the subgenera of *Drymaeus***

1 Peristome usually expanded, suture straight or ascending behind the peristome; mandibula with 13–18 plates, which are 4–5 times as long as wide; transverse row of radula straight, with relatively large, mono- to tricuspid central teeth and bi- to tricuspid lateromarginal teeth ... Subgenus *Drymaeus* s. str.

- Peristome usually simple, suture straight or descending in front; mandibula with more than 20 plates, which are ca. 8 times as long as wide; transverse rows of radula V- or W-shaped, with relatively small tri- to multicuspid central and lateromarginal teeth ... Subgenus *Drymaeus* (*Mesembrinus*)

**Remarks.** The shell morphological characters used in the key to subgenera provided above is based on the examination of a great number of taxa (several 100s); however, the radular morphology has been examined in only a much smaller subset of the known species. Therefore, while these distinctions are useful and reflect current knowledge, re-interpretation may be necessary as additional anatomical information becomes available.

**Subgenus *Drymaeus* s. str.**

**Distribution.** Venezuela, Guyana, Suriname, French Guiana, Brazil, Uruguay, Paraguay, Argentina, Bolivia, Peru, Ecuador, Colombia, Panama, Costa Rica, Guatemala, Belize, Mexico.

**Remarks.** The distribution in Central America is largely according to Thompson (2011) but also our own observations in museums and the field.

***Drymaeus* (*Drymaeus*) *aequatorianus* (E.A. Smith, 1877)\***

Fig. 14F

*Bulimulus* (*Drymaeus*) *aequatorianus* E.A. SMITH 1877: 363, pl. 39 fig. 7. Type locality: Ecuador. Lectotype NHMUK 1975137 (BREURE & ESKENS 1981).

*Drymaeus aequatorianus* (E.A. Smith); RICHARDSON 1995: 96 (references); BREURE & BORRERO 2008: 19; LINARES & VERA 2012: 180; BREURE & ABLETT 2014: 11, figs 28E–G, L2iii.

**Material.** Nariño, directly across river [río Caynacán] from Chical (Ecuador [Prov. Carchi]), 1220 m, Schupp leg., 1979 (UF 26613); Ecuador, Prov. Pichincha, 59 km W of Machachi, 1250 m, A.S.H. Breure leg., 13.iv.1975 (RMNH n.c.); Ibidem, Mindo, yellow house trails, 1200–1300 m, H. Mays & B. McKay leg. 24.iii.2008 (FJ 26); Ibidem, F.J. Borrero leg. 25.iii.2008 (FJ 34); Ibidem, San Nicolás [Cantón Mejía], A. Cousin leg., ex W.F. Webb (FMNH 31409); Canelos (DMNH 148431, ex Jackson).

**Remarks.** We found a number of lots corresponding to this taxon, all with “Ecuador” as the only locality data. We found one lot with a locality in Colombia (UF 26613), labeled as this species, and which we assign to *D. aequatorianus*, but it consists of a single shell, somewhat aberrant specimen (deformed). Its occurrence in Colombia remains to be confirmed. LINARES & VERA (2012) erroneously listed El Chical, Tangua as the collection

locality for lot UF 26613. A living animal and several shells were found in Mindo, Ecuador, in cloud forest. Body colouration off-white, with a light grey hue, and no other colour than the dark eye spots (F) 26).

***Drymaeus (Drymaeus) alabastrinus* da Costa, 1906**

Figs 14J, 21A

*Drymaeus alabastrinus* DA COSTA 1906b: 98, pl. 11 fig. 4. Type locality: Honda. Holotype NHMUK 1907.11.21.16.

*Drymaeus alabastrinus* da Costa; RICHARDSON 1995: 96 (references); LINARES & VERA 2012: 180; BREURE & ABLETT 2014: 14, figs 43J–L, L3iii.

**Material.** **Cordoba**, Upper Río Uré (FMNH 187572); **Santander**, [Cimitarra, circa 200 m] Puerto Olaya (MCZ 136485); Puerto Aquileo [circa 100 m] (ANSP 166118); “Magdalena River, SW Santander”, O.L. Haught leg. (USNM 472802); [Without specific locality], H. Palmer leg. (USNM 380791); **Tolima**, Honda (NHMUK, holotype).

**Ecology.** The records with precise data are located in Magdalena-Urabá moist forests, and Magdalena Valley dry forests ecoregions. The actual habitat is unknown.

**Remarks.** This species is characterised by the swollen last whorl, the ascending suture in front, and the very wide columellar plate. The records available are in the lower Magdalena river valley, at low elevations (200 m or less). The specimen from Upper Uré river is only tentatively referred to as this taxon, as it has a colour pattern of few, square brownish dots, arranged in bands. In addition its locality is isolated compared to the other known records.

***Drymaeus (Drymaeus) angustus* da Costa, 1906**

Figs 4A–D, 21A

*Drymaeus angustus* DA COSTA 1906a: 9, pl. 1 figs 7–8. Type locality: Bogotá. Holotype NHMUK 1907.11.21.14.

*Drymaeus angustus* da Costa; RICHARDSON 1995: 99 (references); LINARES & VERA 2012: 181 [*partim*]; BREURE & ABLETT 2014: 19, figs 37L–N, L4vi.

**Material.** **Antioquia**, Frontino, Corregimiento Nutibara, at a cave, 12.vii.1987 (ICNB n.c.); Yarumal, Ventanas, Nicéforo María leg., 1963 (MLS-BOG 21); Valdivia, 4500 ft. [~1370 m] on Cordillera Oriental, M.A. Carriker jr. leg., 1948 (USNM 590650). **Cundinamarca?**, Bogotá (NHMUK, holotype).

**Ecology.** Precise records for this species are located in Northwestern Andean and Cauca Valley montane forests ecoregions. The actual habitat is unknown.

**Remarks.** These are the first precise localities published for this species. It is unclear if the type locality may be trusted (see general remarks on quality of localities in BORRERO & BREURE 2011: 3). The record from “Piperál” (MCZ 136471) in LINARES & VERA (2012) has proven to be *Drymaeus* cf. *volsus* Fulton, 1907 (see below). There is some variability in this species as the specimens from Valdivia and Yarumal differ in having a broader and less elongated aperture, slightly more convex whorls and a slightly different colour pattern, consisting of broad, axial, reddish-brown stripes; on the body whorl these are present leaving a broad white band below the suture, and around the insertion of the columellar lip. The specimen from Frontino is very worn, and also has broad axial colour stripes. We refrain, however, from giving subspecific status to these specimens.

***Drymaeus (Drymaeus) auris* (L. Pfeiffer, 1866)**

Figs 11A, 21A

*Bulimus auris* L. PFEIFFER 1866: 831. Type locality: Venezuela. Lectotype NHMUK 1975499 (BREURE & ESKENS 1981).

*Drymaeus auris* (L. Pfeiffer); RICHARDSON 1995: 101 (references); BREURE & ABLETT 2014: 26, figs 37A–C, L7ii.

**Material.** **Boyacá**, Otanche, La Chuncala, Sitio La Grilla [1000–1200 m], E. Linares leg., 25.ix.1996 (ICNB 3377); **Cundinamarca**, Pasca, near Quebrada San Joaquin (RZ); **?Cundinamarca**, Bogotá (ANSP 107811), as *D. trigonostomus* (Jonas) ?, Colombia (NHMUK 1894.12.3.3); Venezuela (NHMUK, lectotype); **Norte de Santander**, [near Boyacá] (JMR).

**Ecology.** The species is known so far from the Magdalena Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** These are the first confirmed records with a precise locality for Colombia. The specimen from Pasca is only tentatively referred to as this species.



***Drymaeus (Drymaeus) baranguillanus* (L. Pfeiffer, 1853)**

Figs 5A–C, 22A

*Bulimus baranguillanus* L. PFEIFFER 1853a: 334. Type locality: “Baranguilla in Andibus Columbianus”. Lectotype NHMUK 1975452 (BREURE & ESKENS 1981).

*Drymaeus baranguillanus* (L. Pfeiffer); RICHARDSON 1995: 102 (references); LINARES & VERA 2012: 181; BREURE & ABLETT 2014: 27, figs 31A–C, L7v.

*Bulimus antioquiensis* L. PFEIFFER 1855b: 291. **Synon.n.** Type locality: “Prov. of Antioquia, New Grenada”. Lectotype NHMUK 1975450 (BREURE & ESKENS 1981).

*Drymaeus antioquiensis* (L. Pfeiffer); RICHARDSON 1995: 99 (references); LINARES & VERA 2012: 181; BREURE & ABLETT 2014: 20, figs 31D–F, L5iii.

**Material.** **Antioquia**, Frontino, 6000 ft. [~1800 m], G. Wallis leg., 1875 (ZMUZ 512115); “Prov. of Antioquia” (NHMUK, lectotype of *Bulimus antioquiensis*); **Atlántico**, Barranquilla (NHMUK, lectotype of *Bulimus baranguillanus*); **Bolívar**, Turquia, xi.2014 (FEM 155191); **Cundinamarca**, East of Bogotá, xii. 2014 (FEM 153598, 154858); Guatavita, xi.2014 (FEM 153560–153566, 153633–153635, 154767, 174101); road Topaipí–Yacopi, x.2014 (FEM 155192–155194); Alto de Tocotá, 1900 m, H. Pittier leg., xii.1905 (USNM 251160); mountains E of Bogotá, leg., 2006 (FEM 46936); Quebrada El Matadero, Gacheta, 1770 m (DRC 007); **Guajira**, Nat. Park Macuira, x.2014 (FEM 154800); **Magdalena**, Sierra de Santa Marta, xi.2014 (FEM 154776–154785); **Norte de Santander**, Ocaña, Wallis leg., 1875 (ZMUZ 512116).

**Altitudinal range.** Records with precise locations and altitudinal data are from 50–ca. 2700 m.

**Ecology.** The species is known so far from montane forests (Cordillera Oriental, and Magdalena Valley), and from Magdalena-Urabá moist forests ecoregions. The actual habitat is unknown.

**Remarks.** These are the first additional records for this species since its original description. See general remarks on Wallis’ localities in BORRERO & BREURE (2011: 3). This taxon exhibits many similarities with *D. (D.) confluens* (see below), and they may prove to be closely related or conspecific. However, specimens of the latter species tend to have a slightly more channeled base of the peristome, in some cases appearing ‘spouted’, although this character is not equally strong in all specimens. On the basis of this difference, and a seemingly restricted distribution of *D. baranguillanus* to northern Colombia, we have chosen to retain them as separate taxa. The altitudinal range given in LINARES & VERA (2012) for *D. baranguillanus* (“10 m”) is now shown to be questionable, as it is known from substantially higher elevations.

***Drymaeus (Drymaeus) bogotensis* (L. Pfeiffer, 1855)**

Fig. 5D

*Bulimus bogotensis* L. PFEIFFER 1855d: 93. Type locality: “Santa Fé de Bogotá”. Lectotype NHMUK 1975191 (BREURE & ESKENS 1981).

*Drymaeus bogotensis* (L. Pfeiffer); RICHARDSON 1995: 104 (references); LINARES & VERA 2012: 182 [*partim*]; BREURE & ABLETT 2014: 31, figs 42A–C, L9iii.

**Material.** **Cundinamarca**?, “Santa Fé de Bogota”, ex Cuming (NHMUK, lectotype).

**Remarks.** This species has been frequently misinterpreted in collections and is so far only known from the type material. The distribution records given by LINARES & VERA (2012: 182) do not belong to this species. *Drymaeus bogotensis* and *D. felix* are very similar and may prove to be a single taxon. We feel that the distinction between these taxa is somewhat arbitrary. For now, we have kept them separate, awaiting future studies that will hopefully resolve this issue of possible synonymy.

***Drymaeus (Drymaeus) caucaensis* (da Costa, 1898)**

Figs 10D, 22A

*Bulimulus (Drymaeus) caucaensis* DA COSTA 1898: 81, pl. 6 fig. 3. Type locality: “valley of the R. Cauca”. Lectotype NHMUK 1907.11.21.43 (BREURE 1979).

*Drymaeus caucaensis* da Costa; RICHARDSON 1995: 108 (references); LINARES & VERA 2012: 183; BREURE & ABLETT 2014: 40, figs 31G–I, L11vi.

**Material.** **Antioquia**, Jericó (UVZ 83021); **?Antioquia/?Caldas/?Cauca/?Risaralda/?Valle del Cauca**, Río Cauca valley (NHMUK, lectotype); **Caldas**, near Manizales, leg. xii.2015 (FEM 173093–173096, 173098, 194177); **?Cundinamarca**, Bogota, ex Brooklyn Museum (ANSP 268137).

**Ecology.** Records with precise locality are in Cauca Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** The records from Antioquia and Caldas are the first precise localities for this species, and are both within the eastern and western slopes of the two cordilleras that delimit the geographic valley of the Cauca River, at elevations in the 1800–2000 m range. Colour variation was observed among the few specimens examined; some specimens have a dark apex (first 2–3 whorls). In addition, the degree of connectedness of the three predominant concentric brown bands is variable, with some shells appearing nearly fully covered by the brown areas, while in others, more of the white background can be seen. PILSBRY (1898 [1897–1898]: 248) compared this species with *D. smithii* (da Costa, 1898) and *D. blandi* Pilsbry, 1898, and suggested that these taxa may be closely related. We concur with Pilsbry on the similarity with *D. blandi* (but see below under *D. smithii*); while the three species are similar in size and shape, *D. smithii*, known only from the type series, does not exhibit white dots within the dark stripes as in the other two taxa. Occurrence of this species near Bogotá remains to be confirmed, as Bogotá is across the Central Cordillera and the valley of the Magdalena River, relative to the other known localities.

***Drymaeus (Drymaeus) cognatus* Pilsbry, 1901**

Figs 8F–H, 24B

*Drymaeus cognatus* PILSBRY 1901 [1901–1902]: 155, pl. 23 figs 3–7. Type locality: Bogotá. Lectotype ANSP 78543 (H.B. BAKER 1963); LINARES & VERA 2012: 183 [*partim*].

**Material.** Boyacá, Region of Muzo [~800 m], P. Sanchez, 1935 (MCZ 136470); ?Cundinamarca, “Bogotá, Distrito Especial” (UF 161263 [not seen]); Sta. Fé de Bogotá, ex Sowerby & Fulton (MHNN 35.51); Bogotá (ANSP, lectotype of *Drymaeus cognatus*); Ibidem, ANSP 452359, three paralectotypes; Ibidem, FMNH 78764, paralectotype ex ANSP 78543; Ibidem, MCZ 64885, paralectotype ex ANSP 78543; Ibidem, ex Webb ex Sowerby and Fulton (FMNH 31408); Ibidem, ex Webb (FMNH 31476); Ibidem, ex Vassar (MCZ 156700); Ibidem (NHMUK n.c. [*partim*]); Ibidem, ex Sowerby (RMNH MOL.266131); Ibidem (UF 109117, 206150); Ibidem, ex Fulton (USNM 124981); Ibidem, ex Henderson (USNM 307610); Ibidem, ex Chamberlain ex Fulton (USNM 530530); Huila, Pital [~900 m], L.M. Murillo, 2.xi.1939 (MCZ 112467); San Agustín [~1700 m], leg., ix.2006 (FEM 44181); Ibidem, leg., i.2007 (FEM 46809); [without detailed locality] (JMR); Meta, 10 km NW of Villavicencio (towards Bogotá) [~1150 m], on vegetation on ground (JMR). Ecuador, “Ecuador” (ZMH 7269).

**Altitudinal range.** Based on the precise localities known, the range is ~800–~1700 m.

**Ecology.** The species is found in the Magdalena Valley and Cordillera Oriental montane forests ecoregions. Found alive on cocoa plants (MCZ 112467).

**Remarks.** The first precise localities cited are in the Departments of Meta, Boyacá and Huila. RICHARDSON (1995) grouped *D. cognatus* with *D. membielinus*. Judging from the description and comparing with the figure given by CROSSE (1868: pl. 1 fig. 2) and the syntypes, we disagree with his judgement. The type specimen of *D. membielinus* (BREURE & ARAUJO 2017: 77, figs 29G–J) lacks the strong columellar fold present in *D. cognatus*, and is also less elongate. It must be noted that the type localities of both *D. cognatus*, and *D. membielinus* are imprecise, and although *D. cognatus* may actually occur further south, we were unable to find specimens from further south than San Agustín, Colombia. Likewise, we have no records from Ecuador. The two species are undoubtedly closely related.

***Drymaeus (Drymaeus) confluens* (L. Pfeiffer, 1855)**

Figs 5E–K, 22B

*Bulimus confluens* L. PFEIFFER 1855e: 115. Type locality: “Marmato, New Grenada”. Lectotype NHMUK 1975196.

*Drymaeus confluens* (L. Pfeiffer); RICHARDSON 1995: 111 (references); LINARES & VERA 2012: 183; BREURE & ABLETT 2014: 48, figs 31J–L, L14i.

*Bulimus violaceus* MOUSSON 1873: 9. **Synon.n.** Type locality: “Nördlichem Süd-Amerika” [northern part of South America]. Lectotype ZMUZ 512087 (BREURE 1976).

*Drymaeus violaceus* (Mousson); RICHARDSON 1995: 195 (references); LINARES & VERA 2012: 192 [*partim*].

*Bulimus eversus* MOUSSON 1873: 10. **Synon.n.** Type locality: “Nördlichem Süd-Amerika”. The type of this taxon is considered lost (E. Neubert, pers. comm.).

*Drymaeus eversus* (Mousson); RICHARDSON 1995: 122 (references); LINARES & VERA 2012: 184.

*Drymaeus eversus alata* PIAGET 1914: 261, pl. 9 figs 3–4. **Synon.n.** Type locality: Antioquia, near Titiribi, Guaca, 1600 m. Syntypes MHNN 35.1650.

*Drymaeus eversus subula* PIAGET 1914: 261, pl. 9 figs 1–2. **Synon.n.** Type locality: Antioquia, near Titiribi, Guaca, 1600 m. Syntype MHNN 35.1651.

**Material.** **Antioquia**, near Titiribí, Guaca, 1600 m (Piaget 1914, Fuhrmann leg., MHNN, syntypes); Jericó, Hno. Daniel leg. (USNM 424479, 518428); near Medellín, El Picacho, Hno. Daniel leg. (USNM 518427); near Medellín, Prado, 24.iii.1970 (UVZ 83020); Frontino, G. Wallis leg., 1875 (ZMUZ 512086, ZMUZ 512088); **Boyacá**, Serranía de la Quinchas, xi.2014 (FEM 155184–155190); **Caldas**, Marmato, T. Bland leg., ex Swift (ANSP 25753–4); Manizales, xii.2015 (FEM 173422); Manizales, Los Yarumos, 2140 m, F.J. Borrero leg., 8.viii.2009 (USDA 144833); Marmato (NHMUK n.c.); **Cauca**, [Santander de] Quilichao (ex Preston; RMNH n.c.); slopes Nevada Huila, xi.2014 (FEM 155201); “Cauca” [no further locality], F. Bonis leg. (ANSP 91229, 91231, FMNH 78780); “Cauca” [without further specification] (ANSP 78546; FEM 173424, 174001–174002); **?Cundinamarca**, Bogota, Wallis leg., 1872 (ZMUZ, lectotype of *Bulimus violaceus*; 512085); **Quindío**, Ver. La Paloma, Corr. La Virginia, Calarcá, 1900 m, Borrero & T. Pearce leg., 29.vii.2012 (USDA 144868); Salento, vi.2014 (FEM 142780); Ibidem, v.2015 (FEM 163026, 193858); Ibidem, x.2016 (FEM 195858–195861); Valle del Cocora, x.2014 (FEM 155200); **Risaralda**, Pereira (RBINS 607767); near Marsella, Reserva Forestal Quebrada La Nona, 1600–2000 m, vi.2003 (GK); **Valle del Cauca**, North of El Aguila, between La Línea and El Granero, 1901 m, Borrero and Pearce leg., 20.vii.2010 (USDA 144831); El Aguila, 2100–2200 m, Borrero and Pearce leg., 8.vii.2011 (USDA 144832); Rio La Paila valley, 1300 m, H. Pottier leg. (USNM 251136a); Bugalagrande, Vereda La Morena, Galicia, Hacienda Chachafruto, 1800 m, V. Rochas leg., 23–28.ii.1999 (UVZ 99096); Palmira, vi.2014 (FEM 142749–142759); Ibidem, v.2015 (FEM 163027–163029, 165311, 174100). ?, New Granada (FMNH 77539); Ibidem, ex C.B. Adams (MCZ 154050), Ibidem, ex Dohrn (MCZ n.c.); U.S. of Colombia, Bland leg., ex Redfield ex Henderson (USNM 307622); Colombia (ANSP 362436, UF 206222, NHMUK 1907.8.29.10).

**Altitudinal range.** A range of 1300–2600 m can be ascertained from the few precise localities known.

**Ecology.** The species occurs in the Cauca Valley dry and montane forests ecoregion. The actual habitat is unknown.

**Remarks.** There are three places with the name “Marmato” in the Geonames gazetteer, in Antioquia, Caldas and Cauca. We follow the opinion of BREURE & ESKENS (1981) that this is Marmato in Department Caldas; it lies in the valley of the Cauca river. This is a variable species, both in shape, and in colouration. Differences in relative expansion of parts of the peristome result in some specimens appearing more laterally expanded, whereas some are more basally expanded. In addition, the intensity of purplish colouration inside the aperture, as well as the intensity of colour banding on the shell, varied widely among the material examined. We agree with PILSBRY (1898 [1897–1898]: 207) in grouping *Bulimus eversus* Mousson, 1873 with this species; we now consider *B. eversus* as a junior subjective synonym of *B. confluens*. Adult shells can vary substantially in size, as evidenced by a lot in MHNN (32.8–46.2 mm shell height). Piaget’s taxa, both described from the same locality Guaca, fall within the range of variation observed in this species and are now also considered junior subjective synonyms. Some specimens are only tentatively referred to as this species (ANSP 362436, USNM 518428, ZMUZ 512086).

### ***Drymaeus (Drymaeus) convexus* (L. Pfeiffer, 1855)**

Figs 13L–P, 21B

*Bulimus convexus* L. PFEIFFER 1855e: 115. Type locality: New Granada. Lectotype NHMUK 1975192 (BREURE 1979); LINARES & VERA 2012: 183.

*Drymaeus murrinus* (Reeve); RICHARDSON 1995: 156 [partim] (references); BREURE & ABLETT 2014: 50, figs 39A–C. L14iv.

*Bulimulus (Drymaeus) plicatoliratus* DA COSTA 1898: 80, pl. 6 fig. 1. **Synon.n.** Type locality: Bogotá. Holotype NHMUK 1907.11.21.120.

*Drymaeus plicatoliratus* (da Costa); RICHARDSON 1995: 162 (references); LINARES & VERA 2012: 189; BREURE & ABLETT 2014: 152, figs 57]–L, L46viii.

*Drymaeus fresnoensis* PILSBRY 1898 [1897–1898]: 304, pl. 40 fig. 18. **Synon.n.** Type locality: near Fresno. Holotype ANSP 25836; RICHARDSON 1995: 127 (references); LINARES & VERA 2012: 187.

*Drymaeus tusagasuganus* PILSBRY 1935: 85, pl. 6 fig. 14. **Synon.n.** Type locality: “Tusagasugá” [= Fusagasugá]. Holotype ANSP 164570; RICHARDSON 1995: 189 (references); LINARES & VERA 2012: 191.

*Drymaeus cantatus medianus* PILSBRY 1935: 85, pl. 6 fig. 13. **Synon.n.** Type locality: Region of Medina, E of Bogotá. Holotype ANSP 164572; RICHARDSON 1995: 108 (references); LINARES & VERA 2012: 182 [as *D. cantatus* (Reeve, 1848)].

**Material.** **Antioquia**, 16 km (linear distance) ENE Santa Rosa de Cabal, ca. 2500 m, in cloud forest, J. de Jager leg., 1988 (RMNH n.c.); **?Antioquia/Cundinamarca**, “Antiochia Bogota”, W. Reiss leg., 1879 (ZMUZ 512152); **Boyacá**, Iguaque Reserve (MEDINA & ARIAS 2007); Villa de Leiva: Cañón de Mamaramo near Carrizal, entrance to Santuario de Flora y Fauna Iguaque, Andean forest, 2920 m, B. Hausdorf leg., 2000 (ZMH 4224 [not seen]); Serranía de Las Quinchas, xi.2014 (FEM 155198); **Caldas**, near Manizales, xii.2015 (FEM 173444–173446); **Cauca**, Coconuco, 2000–2600 m, xii.2015 (FEM 173105–173106); Nevada del Huila, 2000–2400 m, xi.2014 (FEM 154768); Ibidem, xii.2015 (FEM 173399–173401); Sotara, Paispamba, 1700–2000 m, x.2014 (FEM 153541–153542, 153605);

**Cundinamarca**, La Calera, in primary forest, A. Infante leg. (AI, JG); Bojaca, Piedra del Indio, 2650 m, Infante leg. (AI); Guavio, Siberia, 2860 m, Infante leg. 17.ii.2003 (AI); Soacha, Infante leg. Xi.1994 (AI, JG); La Calera, circa 2700 m, found in the woods near Rio Teusacá, 11.xii.1955 (ANSP 323423); Region of Medina, M. González leg., 1930 (ANSP, holotype of *Drymaeus cantatus medinanus*); Medina, xii. 2015 (FEM 173143); Tusagasugá [= Fusagasugá], V. Guevara leg., pre-1935 (ANSP, holotype of *Drymaeus tusagasuganus*); Paramo de Cruz Verde, I. de Arévalo, 14.xii.1979 (ICNB 0917); near Gachetá, Infante leg. (JG; RMNH); N of Bogotá, i. 2013 (FEM 119497–119498); E of Bogotá, i.2011 (FEM 82986–82987); Páramo de Cruz Verde, near Bogotá, 3000 m, ex Bequaert (MCZ 179594); Páramo de Sumapaz, Chipaque, xii.2015 (FEM 173121–173130); Usaquén, E. Osorno leg., 15.vi.1931 (MCZ 145199); La Calera, Hno. Nicéforo María leg., xi.1958 (MLS-BOG n.c.); Ibidem, Aguas Claras, 13.ii.1973 (MLS-BOG 607); San José de Guausa, Chía, J. Espitia leg., 2003 (MLS-BOG n.c.); Nemocón, Vereda San Antonio, Aguas Claras, Finca Montecruz, P. Creutzberg leg., viii.2000 (RMNH n.c.); 6 km N Usaquén; valley E of Calle 82; 18 km N of Calle 79, H. Sturm leg. (SMF 245399–245404) (BREURE 1977); La Calera, just NE Bogota, O.L. Haight leg. (USNM 488856); Sitio Tequendama I, Municipio de Soacha (ZMA n.c.; CORREAL *et al.* 1977); La Calera 0.5 km towards Bogotá: farm La Cabrera, Vereda San Rafael, sandstones at forest margin, NW slope, 2820 m, B. Hausdorf leg., 2000 (ZMH 4016 [not seen]); Ibidem, Andean forest, NW slope, 2830 m (ZMH 4032 [not seen]); Ibidem, N slope, 2840m (ZMH 4064 [not seen]); La Calera: S of Entrada Fábrica de Cemento Samper, degraded Andean forest, NW slope, 2750 m, Hausdorf leg., 2000 (ZMH 4079 [not seen]); Bogotá: forest near brook above Escuela Militar de Caballería, 2750 m, Hausdorf leg., 2000 (ZMH 4320 [not seen]); Bosques de Torca: Andean forest, W slope, 2900 m, Hausdorf leg., 2000 (ZMH 4344 [not seen]); Silvania (Medina & Arias 2007); Tunquiza, xii.2015 (FEM 154766); Yacopi, x.2014 (FEM 155195–155197, 194189); Ibidem, xii.2015 (FEM 173144–173145); **?Cundinamarca**, Bogotá, Distrito Especial (UF 109324, 161268); Plateau de Bogota [= Sabana de Bogotá], 2600 m, ex Hemmen (ANSP 428818); Bogotá (ANSP 78544); Ibidem (DMNH 184294); Ibidem (FMNH 77538); Bogota, Chorro de Padilla, 2700 m, L.M. Murillo leg., 1938 (MCZ 145196); Ibidem (NHMUK, holotype of *Drymaeus plicatoliratus*); Ibidem, ex MacAndrew (NHMUK n.c.); Ibidem (RMNH n.c.); Ibidem, Petersen leg., 1878 (ZMUZ 512157); **Huila**, Parque Natural Cueva de los Guacharos, v.2015 (FEM 153551, 165304); **Nariño**, slopes Nevado del Ruiz, x.2014 (FEM 154760, 154762); Pasto, L. Taylor leg., 1879 (ZMUZ 512153); **Quindío**, near Calarca, xii.2015 (FEM 173452); **Tolima**, “Mountains towards Fresno”, ex Swift (ANSP, holotype of *Drymaeus fresnoensis*); Fresno, 1200–1600 m, x.2014 (FEM 153549–153550); Ibidem, v.2015 (FEM 165301); Rio Manso, 2800–3000 m, x.2015 (FEM 210513–210514); Ibidem, xii.2016 (FEM 193744, 194201); Yerbabuena, Páramo de Oasis (ICNB 10572); **Valle de Cauca**, near Palmira, xii.2016 (FEM 194429); near La Esmeralda, xii.2016 (FEM 193740); ?, Colombia, ex Cuming (NHMUK); Bogota (ANSP 78541). **?Ecuador**, “Ecuador (?)” (NHMUK, lectotype of *B. convexus*; two paralectotypes, NHMUK 1975193).

**Altitudinal range.** All precise localities known are in the range of 1200–3000 m.

**Ecology.** The species occurs in Cauca Valley, Magdalena Valley and Cordillera Oriental montane forests ecoregions. From specimens at Cundinamarca locations, the habitat is fragments of primarily secondary Andean forest, ranging from the humid Bogota plateau to dryer mountainous slopes.

**Remarks.** After careful comparison of the material of both *D. convexus* and *D. plicatoliratus*, we fail to see substantial differences, other than in the colour pattern. Therefore, we regard the latter taxon as a junior subjective synonym of *D. convexus*. Given the high variation within this species, both in colouration (including predominantly axially banded, spirally banded, and unbanded specimens, sometimes in the same lot), and in shell shape (specimens with varying flaring of the peristome at the base, including rather ‘spouted’ shells), we feel confident that *D. fresnoensis* (described from a single, subadult specimen), *D. tusagasuganus* and *D. cantatus medinanus* (both based on singletons) are also junior subjective synonyms of *D. convexus*. *D. cantatus medinanus* was regarded by Pilsbry to be “very similar to the figure of *D. cantatus* (Rve)”, probably a Peruvian species. Although the types of *D. cantatus* have not been found, we fail to see the similarity with Reeve’s figure; the Colombian specimen has a straighter aperture which is retracted at the narrow base. The material from Tolima, Yerbabuena is only tentatively placed here; it has a more spouted aperture and may be a teratological specimen, but it is too worn to make any definite conclusions. The record from Nariño, Pasto is doubtful, as the locality is far to the south from the majority of records for this species. From the Cundinamarca specimens (AI), the colouration of the live body is completely dark olive/brown, with clearly defined tubercles, and the eye stalks are the same colour even when fully extended; the end of the tail is white, from a swath of white pigmentation which starts on the sides of the end of the foot and becomes larger dorsally.

### ***Drymaeus (Drymaeus) dacostae* (G.B. Sowerby III, 1892)**

Figs 120–Q, 23A

*Bulimulus dacostae* G.B. SOWERBY III 1892: 297, pl. 23 figs 15–16. Type locality: “Bogota”. Holotype NHMUK 1907.11.21.51.

*Drymaeus dacostae* (Sowerby); RICHARDSON 1995: 113 (references); LINARES & VERA 2012: 184; BREURE & ABLETT 2014: 56, figs 33M–O, L16iv.

**Material.** Cundimarca, Suba, Hno. Nicéforo María leg., x.1959 (MLS-BOG 587); “Bogota” (NHMUK, holotype).

**Altitudinal range.** Around the locality above, altitudes range is 2550–2650 m.

**Ecology.** The species occurs in Magdalena Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** This is the first precise locality known for this species.

***Drymaeus (Drymaeus) decoratus (Lea, 1838)***

Figs 14A–C

*Bulimus decoratus* LEA 1838: 86, pl. 23 fig. 108. Type locality: “near Carthagena”. Syntypes USNM 105154.

*Drymaeus decoratus* (Lea); RICHARDSON 1995: 113 (references); LINARES & VERA 2012: 184.

*Drymaeus decoratus goniobasis* PILSBRY 1898 [1897–1898]: 262, pl. 40 fig. 4. Type locality: “Near Santa Ana”. Holotype ANSP 25803.

**Material.** Bolívar, near Cartagena, Gibbon leg. (USNM, syntypes of *Bulimus decoratus*), Caldas/Tolima, near Santa Ana (ANSP, holotype of *D. d. goniobasis*); Cundinamarca, Bogotá (ANSP 107812); Nariño, Rejoa, Buesaco (UVZ n.c.); Putumayo, Santa Lucia, Santiago, 2600 m, M.C. Cabrera leg., 25.i.2002 (UVZ n.c.).

**Remarks.** An older label accompanying the type lot of *Drymaeus decoratus goniobasis* reads: “... from mountains between[?] Salamina and S. Ana”. This leads us to assume that it refers to a place called Santa Ana 30 km (as the crow flies) WNW Manizales [05° 08' N 075° 47' W]; LINARES & VERA (2012) suggest this locality as NE Mariquita in Tolima. We tentatively refer the specimens from UVZ to this taxon; they differ somewhat in colour, but otherwise confirm to the description of *D. decoratus*. The type locality of this species may be misleading, as it is unknown to which areas Gibbon travelled. It is possible that the original type locality may not be as close to sea level, or as far north as may be inferred. Currently known with certainty from only four specimens, including the type material of both names. The record from Ecuador (BREURE & BORRERO 2008: 20) is in error.

***Drymaeus (Drymaeus) denticulus spec. n.***

Figs 11D–H <http://zoobank.org:act:107E4122-ADF6-47E9-835D-DBD80EE8071B>

**Diagnosis.** A relatively large species of *Drymaeus*, with a thin white line below the suture and a broad white band below the periphery; two interrupted spiral reddish-brown bands on the last whorl above the periphery, crossing weaker axial streaks of a less intense colour and forming V-like marks; one white spiral band at the periphery and one below starting at the insertion of the columellar margin. Aperture with a white, expanded lip and a curved columella, giving the appearance of a denticle.

**Description.** Shell up to 48.5 mm, 2.0 times longer than wide, narrowly rimate with rather flat sides, elongated, solid. Colour whitish-yellowish typically with two interrupted spiral colour bands on the last whorl above the periphery, crossing weaker axial streaks of a less intense colour and forming V-like marks; one spiral band at the periphery and one below starting at the insertion of the columellar margin; with a white line below the suture and below the periphery a broader white band with the axial streaks faintly continuing. Surface somewhat shining; the upper whorls smooth, on the remaining whorls the growth striae are slightly thickened. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 6.1, hardly convex; suture slightly impressed and bordered by a whitish to yellowish line below, ascending towards the aperture. Aperture elongate-ovate, 1.4 times longer than wide, 0.56 times the total length. Peristome thin, expanded throughout, whitish inside and outside. Columellar margin curved, reflexed, dilated above and receding. Parietal wall with a thin callus, transparent.

**Dimensions.** Holotype H 43.0 mm, D 22.9 mm, HA 24.0 mm, WA 17.0 mm, W 6.1; paratype H 48.5 mm, D 23.2 mm, HA 22.8 mm, WA 16.6 mm, W 6.5.

**Type material.** ?Antioquia/?Caldas/?Cauca/?Risaralda/?Valle del Cauca, “Cauca”, ex Preston (RBINS MT.2630, holotype; UMMZ 125081, one paratype).

**Remarks.** The paratype is somewhat larger, with a more obliquely protruding aperture. Although the locality data may refer to different Departments, we assume that the Department of Cauca is the most likely; the lack of a reference to the Río Cauca valley by Bryant Walker or Preston is supportive of this view. Despite the imprecise locality, we have decided to describe this new species as it is markedly different from any other that we have seen. This specimen resembles *Drymaeus (D.) flexuosus* (L. Pfeiffer, 1853) in its overall shape, but differs in having no white dots and no black patch behind the umbilicus. In apertural view it also resembles *D. (D.) spadiceus* da Costa, 1906, but differs from having no white dots. In addition the last whorl is inflated. The type specimens were found labeled as *Bulimulus mathildae*, an unpublished name by Preston.

**Etymology.** (*L.*) *denticulus* (denticle), referring to the curved columella, which appears as a denticle in the upper left corner of the aperture in apertural view. The epithet is used as a noun.

***Drymaeus (Drymaeus) duplexannulus spec. n.***Figs 9E–G, 23A <http://zoobank.org:act:0CC06643-39CC-4114-90D0-051352C33AF9>

**Diagnosis.** A medium-sized (~40 mm) species of *Drymaeus*, with a thin white line below the suture and dark- to reddish-brown and white-dotted zigzag colour bands on the last whorl. Aperture with a broadly expanded white lip, bordered dark-brown inside and partly on the peristome.

**Description.** Shell up to 40 mm, 2.2 times longer than wide, widely umbilicate with rather convex sides, rather elongated, solid. Colour whitish, with dark- to reddish-brown axial zigzag streaks, with unevenly spaced white dots; the white spaces in between 1–5 times as wide as the streaks. Upper whorls whitish, the colour pattern disappearing. Surface hardly shining, smooth. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 5.2, slightly convex; suture slightly impressed and bordered by a thin, whitish line below, ascending just before the aperture. Aperture elongate-ovate, 1.47 times longer than wide, 0.56 times the total length. Peristome thin, expanded throughout, white with a reddish- to dark brown border inside. Columellar margin curved, reflexed, dilated above and receding. Parietal wall with a thin, transparent callus, with a dark brown hue.

**Dimensions.** Holotype H 37.8 mm, D 17.8 mm, HA 21.4 mm, WA 14.9 mm, W 5.2; paratype H 40.0 mm, D 18.2 mm, HA 22.3 mm, WA 14.6 mm, W 5.4.

**Type material.** Norte de Santander, Santa Librada, Hno. Nicéforo María leg. (ANSP 170737, holotype); Pamplona, Hno. Nicéforo María (MLS-BOG 610 [*partim*], paratype).

**Ecology.** Localities where this species was found are in the Cordillera Oriental montane forests ecoregion. The actual habitat is unknown.

**Remarks.** In the paratype the whitish line below the suture is largely absent and the aperture is somewhat obliquely elongate-ovate. This taxon differs from *Drymaeus f. felix* (L. Pfeiffer, 1862) by (1) having a larger aperture, (2) being more slender, (3) having a narrower umbilicus, and (4) having an intense coloured band inside the aperture. This new species may also be compared to *D. felix restrepoensis* subspec. n., from which it differs in (1) being more slender, (2) having a darker colour band inside the aperture, and (3) the relative width of the white space between the zigzag bands. The new taxon shares similarities with *D. ziczac* (da Costa, 1898), from which it differs by (1) being more elongate, (2) having a more intense colour band inside the aperture, (3) having a more expanded lip. LINARES & VERA (2012: 186) located Santa Librada near Sarare, SE Toledo, at 750 m elevation.

**Etymology.** (L.) *duplex* (double), and *annulum* (ring); referring to the colouration of the aperture with a dark-brown band inside the white expanded lip, giving the impression of a double ring. The epithet is used as an adjective.

***Drymaeus (Drymaeus) exoticus da Costa, 1901***

Fig. 12K

*Drymaeus exoticus* DA COSTA 1901: 239, pl. 24 fig. 10. Type locality: “The hot country, Upper Magdalena River, Colombia”. Lectotype NHMUK 1907.11.21.38 (BREURE 1979); RICHARDSON 1995: 122 (references); LINARES & VERA 2012: 185; Breure & Ablett 2014: 70, figs 33D–F, L21v.

**Material.** ? “hot country, Upper Magdalena River, Colombia” (NHMUK, lectotype).

**Remarks.** The type locality is very general and several Departments could be involved; no material with a specific locality is known, and this species is known from just two shells.

***Drymaeus (Drymaeus) expansus* (L. Pfeiffer, 1848) species complex**

Figs 10E–K, 23A

*Bulimus expansus* L. PFEIFFER 1848b: 60. Type locality: Peru, Huallaga.

*Drymaeus expansus* (L. Pfeiffer); RICHARDSON 1995: 122 (references); LINARES & VERA 2012: 185; BREURE & ARAUJO 2017: 75, figs 30A–B.

*Drymaeus expansus vanattai* PILSBRY 1898 [1897–1898]: 223, pl. 34 fig. 6. Type locality: “Amazon River”. Lectotype ANSP 25762 (H.B. BAKER 1963).

*Drymaeus vanattai* Pilsbry; RICHARDSON 1995: 191 (references); SIMONE 2006: 145, fig. 484.

*Drymaeus expansus balboa* PILSBRY 1926: 82, pl. 10 figs 5–7. Type locality: Panama, Prov. Panama, Puerto Puerto. Holotype ANSP 140691; THOMPSON 2011: 108.

*Mesembrinus (Mormus) expansus orcesi* WEYRAUCH 1958: 130, pl. 7 fig. 15. Type locality: Ecuador, Montalvo, Rio Bobonaza, 314 m. Holotype SMF 156292; NEUBERT & JANSSEN 2004: 220, pl. 15 fig. 176; BREURE 2012: 10.

*Drymaeus rehderi* PARODIZ 1962: 435, pl. 1 figs 5, 8. Type locality: Antioquia, Valdivia. Holotype USNM 590653; RICHARDSON 1995: 171 (references); LINARES & VERA 2012: 190.

**Material.** **Antioquia**, Valdivia, 4500 ft. [~1370 m], M.A. Carriker leg., 1948 (USNM, holotype of *Drymaeus rehderi*). **?Cundinamarca**, Bogota? (CMC C13893); Santa Fé de Bogotá, ex Cuming (NHMUK n.c.); **Meta**, Serranía de la Macarena, Rio Duda, Centro de Investigaciones Primatólogicas La Macarena, Campamento Puerto Chamuza, Trail B1000, 350 m, E. Linares leg., x.1994 (ICNB 2841); **Nariño**, Santa Rosa de Sucumbios, Rio San Miguel, Intendencia Putumayo, B. Malkin and P. Burchard leg., 2–25.x.1970 (FMNH 187568); Between Alpichague and San Antonio, Santa Rosa de los Cofanes, below San Antonio del Guamués, H. LeNestour, ii.1965 (FMNH 187569); **Putumayo**, Puerto Asís, Upper Río Putumayo, F. Medem leg., 1958 (FMNH 114079). **?**, Amazon River (ANSP, lectotype of *D. e. vanattai*). New Grenada (Colombia), ex Cuming (NHMUK n.c.). **Ecuador**, Topo, ex Jackson (ANSP 306773, DMNH 142446); Rio Napo, ex Jackson (DMNH 147561); Santo Domingo de los Colourados, ex Jackson (DMNH 147570); Guarumos, ex Jackson (DMNH 150711); Nachiyacu, ex Jackson (DMNH 163667); Montalvo, Rio Bobonaza, 314 m, Ollala leg., (SMF, holotype of *D. e. orcesi*). **?**, Ecuador, ex Sowerby (ZMUZ 511962); Ibidem, ex B. Wright (MHNN 35.49). **Panama**, Right bank of Chagres river, junction with Rio Chico, J. Zetek leg., 1921 (ANSP 155413); Rio Puerco, A. Olsson leg. (ANSP 140691 & 451781, types of *D. e. balboa*); Rio Puerco, Darién, Olsson leg. (FMNH 117079). **Peru**, Tarapoto (UMMZ 4516); Valle de Chanchamayo, 1100 m, J. Schunke leg. (USNM 601807).

**Altitudinal range.** The few precise locations from which altitudinal data can be ascertained range 230–1370 m, suggesting that this taxon occurs at low to moderate elevations.

**Ecology.** The species is known from different montane forests ecoregions in Colombia. The actual habitat is unknown.

**Remarks.** With the (quite limited) material at hand, we conclude that *Drymaeus (D.) expansus* is a very variable species, with a seemingly huge distribution from central Panama to central Peru. Within its range, several varieties and subspecies have been recognised, which we are unable to evaluate fully with the scant material available. Therefore, we have grouped them together as without implying formal synonymisation. This species complex will benefit from anatomical and molecular studies based on material from throughout its distribution range. Also the relationship between *D. expansus* and *D. confluens*, suggested above, needs further study.

#### ***Drymaeus (Drymaeus) fabrefactus* (Reeve, 1848)**

Figs 13G–H

*Bulimus fabrefactus* REEVE 1848 [1848–1850]: pl. 49 fig. 319. Type locality: Venezuela, Estado Mérida. Lectotype NHMUK 1975531 (BREURE 1979).

*Drymaeus fabrefactus* (Reeve); RICHARDSON 1995: 123 (references); LINARES & VERA 2012: 185; BREURE & ABLETT 2014: 71, figs 38D–F, L22i.

**Material.** **Magdalena?** (“Unt Magdalena” [= lower Magdalena valley]), G. Wallis leg. (ZMUZ 512150); **Norte de Santander**, Ocaña, G. Wallis leg., 1875 (ZMUZ 512149 [*partim*]). **?**, Colombia, ex Calbert (USNM 515450). **Venezuela, ?**, “New Granada” (NHUK, lectotype).

**Remarks.** LINARES & VERA (2012) also have a record from Santander, Santa Bárbara (ICNB) for this species, but no specific voucher was given. No other precise localities are known.

#### ***Drymaeus (Drymaeus) fallax* (L. Pfeiffer, 1853)**

Figs 15A–C

*Bulimus fallax* L. PFEIFFER 1853a: 375. Type locality: Ecuador, Tungurahua. Syntype NHMUK 1969142.

*Drymaeus fallax* (L. Pfeiffer); RICHARDSON 1995: 124 (references, synonymy); LINARES & VERA 2012: 185; BREURE & ABLETT 2014: 72, figs 26D–F, L21vii; BREURE & ARAUJO 2017: 77, fig. 29K.

*Bulimus abscissus* L. PFEIFFER 1855e: 116. **Synon. nov.** Type locality: Ecuador, “Prov. of Quito”. Lectotype NHMUK 1975497 (BREURE 1979).

*Drymaeus abscissus* (L. Pfeiffer); RICHARDSON 1995: 95 (references); BREURE & ABLETT 2014: 8, figs 26A–C, L1ii.

*Drymaeus fallax chicoensis* BREURE 1977: 261, fig. 4. **Synon. nov.** Type locality: Cundinamarca, Bosque de Chicó. Holotype SMF 245405; RICHARDSON 1995: 124 (references); NEUBERT & JANSSEN 2004: 204, pl. 14 fig. 171; LINARES & VERA 2012: 185 [as *D. fallax*].

**Material.** **Cundinamarca**, Bosque de Chicó [NE of Bogotá], 2700–2800 m, H. Sturm leg. (SMF, holotype *chicoensis*); La Calera, 2820 m, E. Linares leg., iii.1978 (ICNB 674). **Ecuador**, Nono, R. Cousin leg., ex Clapp (CM 4 86212); Santo Domingo, ex Richardson (DMNH 76687); Canelos, ex Jackson (DMNH 135202, 147553); Mt. Chimborazo skirts, ex Jackson (DMNH 147555); Pichincha, ex Jackson (DMNH 147564); Mindo, close to the Rio Blanco, ex Jackson (DMNH 147567); Ibidem, Guarumos (DMNH 147563); Imbabura, A. González leg., vii.2011 (FEM 5023, 91168); Canelos (DMNH 135202, 135279); Puyo, ex Jackson (DMNH 147565); Topo, ex Jackson (DMNH 147571); Ibarra, ex Jackson (DMNH 150712); Santo Domingo de los Colourados (FMNH 85376); Ibidem, ex Jackson (MCZ 227645);

Ibidem, ex Jackson (DMNH 163666); Quito, Chiquilpe, ex Webb (FMNH 31299); Llou, A. Cousin leg., ex Webb ex Dautzenberg (FMNH 31350); Tumbaco, vi.2011 (FEM 91169 [subadult]); “Tunguragua” [sic, Tungurahua], ex Cuming (NHMUK, lectotype *fallax*); Naranjal, Quito road, above Yokuchaki, 2500 m, O.L. Haught leg. (USNM 534059). ?, Quito, ex E.R. Mayo (MCZ 88122), Ibidem, ex Evezard ex Henderson ex Cuming (USNM 316094); Ibidem, L. Taylor leg., 1879 (ZMUZ 512143); Ibidem, Vimont leg., 1882 (ZMUZ 512146); Ecuador, T. Prime leg., ex Clapp (CM 113637); Ibidem, ex Bequaert (MCZ n.c.); Ibidem, ex Sowerby (ZMUZ 512145); “Prov. of Quito” (NHMUK, lectotype of *abscissus*).

**Altitudinal range.** The few precise localities available range 1200–2500 m.

**Ecology.** The Colombian localities are situated within the Cordillera Oriental montane forests ecoregion. The actual habitat is unknown.

**Remarks.** Several specimens at DMNH were found under various MS-names by Jackson; with one exception, all fall within the morphological and colour variation of *Drymaeus fallax*. Specimens from some localities in Ecuador (DMNH 135197, 147556, 147569) seem to differ but we prefer herein to suggest further research before describing them formally as new taxon. The specimens from Colombia, previously distinguished as *D. fallax chicoensis*, are herein synonymised with the nominate taxon because the variation in shell shape observed seems to unite the two, despite there being no records from the intermediate region. This fact may need further study and consideration. Re-examination of the type material of *D. fallax fallax* and *D. abscissus*, as well as comparison with more recently collected material of *D. fallax*, makes evident that the ranges of shell shape, and of colouration variation of *D. fallax*, includes the morphology and colour of *D. abscissus*, making these taxa undistinguishable.

### ***Drymaeus (Drymaeus) felix felix* (L. Pfeiffer, 1862)**

Figs 6D–G, 23A

*Bulimus felix* L. PFEIFFER 1862: 387, pl. 37 fig. 2. Type locality: “New Grenada”. Lectotype NHMUK 1975206 (BREURE & ABLETT 2014).

*Drymaeus felix* (L. Pfeiffer); RICHARDSON 1995: 125 (references); LINARES & VERA 2012: 185 [partim]; BREURE & ABLETT 2014: 73, figs 45D–F, L22iii.

*Bulimus trivittatus* MOUSSON 1873: 11. **Synon.n.** Type locality: “Northlichen Süd-Amerika” [northern part of South America]. Possible syntype SMF 23456 (NEUBERT & JANSSEN 2004: 232, pl. 14 fig 166).

*Drymaeus trivittatus* (Mousson); RICHARDSON 1995: 189 (references); LINARES & VERA 2012: 191.

*Bulimus elegantissimus* MOUSSON 1873: 11. Type locality: “Nördlichem Süd-Amerika” [northern part of South America]. Possible syntypes ZMUZ 512110–512111.

*Drymaeus elegantissimus* (Mousson); RICHARDSON 1995: 120 (references); BREURE & BORRERO 2008: 20; LINARES & VERA 2012: 184 [partim].

**Material.** **Antioquia**, Frontino, G. Wallis, 1875 (ZMUZ 512109, 512111, possible syntype of *Bulimus elegantissimus*, 512136); Corregimiento San Antonio de Prado, Vereda Yurumalito (SW of Medellín), N. Uribe leg., 2008 (photographic voucher); **Cauca**, Buenos Aires, Vereda El Silencio, Finca El Carmen, 17.x.1980 (UVZ 018 [partim]); Ibidem, 8.x.1980 (UVZ n.c.); **Cundinamarca**, Fusagasugá, Vereda Bochica, above Chirimayó, 1800 m, H. García-Barriga leg., 1980 (ICNB 0094); San Antonio del Tequendama (JMR); Ibidem Vereda Chicaque, Parque Nacional Chicaque, Santuario de Flora y Fauna Montañas de Chicaque, 2400 m, E. Linares, 15.i.1991 (ICNB 2322–3); Bogotá (NHMUK 1894.2.28.9–22; Ibidem, ex Biggs (NHMUK n.c.); Guatavita, xi.2014 (FEM 153596); near Fusagasuga, 2000–2100 m (FEM 194408–194411); Tena, Laguna de Pedro Palo, oak forest, 2000 m, Linares, 14.vi.1998 (ICNB 3519 [partim]); Bogotá, Distrito Especial (UF 109230, 161241[both not seen]); near Zipaquirá, forest at 2000 m, leg. ix.2006 (FEM 44182); ibidem, leg. iv.2007 (FEM 48769); Norte de Santander, Ocaña, Wallis, 1875 (ZMUZ 512110, possible syntype of *B. elegantissimus*); **Risaralda**, La Cella, iii.2010 (FEM 79095). ?, Colombia (ANSP 362438, NHMUK 1907.8.29.13–17 [partim]); “New Grenada” (NHMUK, lectotype); U.S. of Colombia, ex Henderson ex Evezard (USNM 316129 [partim]). Boyacá, Caldas, near Neira, xii.2015 (FEM 173111–173115, 194067).

**Altitudinal range.** The few confirmed precise localities give an available range of 1800–2400 meters.

**Ecology.** Occurring in Cauca Valley and Magdalena Valley montane forests ecoregions. Collected in secondary rain forest, on moss-covered tree trunks (San Antonio de Prado, Antioquia).

**Remarks.** Mousson described *Bulimus trivittatus* without figuring it; L. PFEIFFER (1874 [1870–1876]: pl. 130 figs 3–4) figured it for the first time. The type material in Zürich is probably lost (E. Neubert, pers. comm.). This species was hitherto only known by the original description, until NEUBERT & JANSSEN (2004) located a possible syntype. The SMF specimen is not completely in agreement with L. Pfeiffer’s figure; the shells on which L. Pfeiffer based his figures are probably lost (DANCE 1966, but see RICHLING & GLAUBRECHT 2008). On the basis of L. Pfeiffer’s figures, we tentatively refer the material listed above in this taxon. Relatively constant in shape, specimens vary significantly in colouration, some specimens having a predominant pattern of dark concentric bands over a light background, whereas in other specimens the axial colour bands are more pronounced than the concentric pattern.



Body colouration olive green on the side of mantle and foot, increasingly darker dorsally; sole and eye-stalks lightly coloured (beige). The material from Cauca is tentatively assigned to this taxon, as this locality is substantially farther south than the rest of the available records, mainly in Central Colombia; however, we cannot observe any differences when comparing this material with the shells from Cundinamarca, and further collecting is needed to resolve this disjunct distribution. See also BORRERO & BREURE (2011: 3) for comments on Wallis' localities. The record by PILSBRY (1898 [1897–1898]: 246) for Bogotá was supposedly based on material from Wallis, but the latter author did not give Bogotá as a locality, and we have not been able to locate this material. The locality near Laguna de Pedro Palo (ICNB 3519) shows specimens that could be interpreted as intermediates between *Drymaeus (D.) smithii* and *D. (D.) felix*. A lot (DMNH 183910, six shells from “Bogotá”), labeled as *D. felix*, is not this species. Relying on museum databases, LINARES & VERA 2012: 186 listed additional lots from Bogotá, which belong to several other species; they also listed records from localities in Meta, near Villavicencio, that we consider different at the subspecific level (see below).

***Drymaeus (Drymaeus) felix restrepoensis* subspec. n.**

Figs 6H–I, 23A <http://zoobank.org:act:ADB17C3A-BD7D-484F-862B-F323865AD5C7>

**Diagnosis.** A medium-sized (29–38 mm shell height), umbilicated *Drymaeus* taxon characterised by the axial, white-dotted zigzag streaks, as wide as the intervals between them, and with V-shaped bulges on the left side. Aperture with a white, well expanded lip, bordered brownish to pinkish inside.

**Description.** Shell up to 38.5 mm, 1.9 times longer than wide, widely umbilicate with rather convex sides, rather elongated, solid. Colour whitish, with dark- to reddish-brown axial zigzag streaks, with unevenly spaced white dots; the white spaces in between 2–3 times as wide as the streaks. Upper whorls whitish, the colour pattern disappearing. Surface hardly shining, smooth. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 5.2, slightly convex; suture slightly impressed, ascending just before the aperture. Aperture elongate-ovate, 1.47 times longer than wide, 0.56 times the total length. Peristome thin, expanded throughout, white with a faint reddish- to dark brown border inside. Columellar margin curved, reflexed, dilated above and receding. Parietal wall with a thin, transparent callus, with a pinkish hue.

**Dimensions.** Holotype H 29.7 mm, D 15.6 mm, HA 17.3 mm, WA 13.1 mm, W 5.2; paratypes H 29.4 mm, D 14.9 mm, HA 15.4 mm, WA 10.8 mm, W 5.2; H 29.7 mm, D 13.8 mm, HA 15.4 mm, WA 10.5 mm, W 5.2 (both MCZ 370410); H 31.0 mm, D 14.3 mm, HA 16.7 mm, WA 11.0 mm, W 5.5 (MCZ 64780); H 38.5 mm, D 18.4 mm, HA 21.7 mm, WA 13.7 mm, W 6.0 (ANSP 164567); H 33.2 mm, D 16.1 mm, HA 18.6 mm, WA 12.2 mm, W 6.0 (FMNH 3377); H 37.2 mm, D 18.9 mm, HA 20.8 mm, WA 13.4 mm, W 6.1 (FMNH 78749).

**Type material.** Meta, Restrepo, [~500 m], Bequaert leg., 1936 (MCZ 64779, holotype; MCZ 370410, four paratypes, MCZ 64780, two paratypes); Villavicencio area, Hno. Apolinar María leg., 1933 (ANSP 164567, one paratype); Villavicencio, Dybas leg., 1938 (FMNH 3377, two paratypes); Villavicencio area, Hno. Guevara leg. (FMNH 78749, one paratype).

**Other material.** Acacías, Macizo de Sumapaz, San Cristóbal, Quebrada La Argentina, cerca campamento Las Blancas, 920 m, Th. van der Hammen & A.M. Cleef leg. (SUM 33), 1981 (RMNH n.c.).

**Ecology.** The type locality is in the Cordillera Oriental montane forests ecoregion. This taxon was found in Selva de *Brosnium* vegetation at station SUM 33 of the EcoAndes project (VAN DER HAMMEN 2008, RANGEL *et al.* 2008).

**Remarks.** This taxon may be distinguished from *Drymaeus f. felix* (L. Pfeiffer, 1862) by (1) the V-shaped bulges in the axial zigzag streaks, (2) the absence of prominent spiral bands in the colour pattern, and (3) the wider umbilicus, coloured dark (purple) inside. From *D. duplexannulus* spec. n., which occurs further north, it differs by (1) having a less prominent coloured border inside the aperture, (2) the whitish peristome throughout, (3) on average being smaller and somewhat less slender, (4) parietal callus with a pinkish hue. This subspecies only occurs on the eastern slopes of the Cordillera Oriental, at relatively lower elevations (circa 500–920 m), while the nominate form occurs at higher elevations (circa 1800–2400 m), westward of this region. The material at MCZ has been referred to as *Drymaeus violaceus restrepoensis* Bequaert and Clench, an unpublished name.

**Etymology.** The specific epithet refers to the type locality, Restrepo.

***Drymaeus (Drymaeus) flexuosus* (L. Pfeiffer, 1853)**

Figs 8A–E, 23B

*Bulimus flexuosus* L. PFEIFFER 1853a: 329. Type locality: “Marinata, Novae Grenadae” [corrected to Marmato in Pilsbry 1898]. Lectotype NHMUK 1975202 (BREURE & ESKENS 1981).

*Drymaeus flexuosus* (L. Pfeiffer); RICHARDSON 1995: 127 (references); LINARES & VERA 2012: 186 [*partim*]; BREURE & ABLETT 2014: 77, figs 34A–C, L23v.

**Material.** **Antioquia**, Tamésis, Hno. D. González leg. (MLS-BOG 609 [*partim*]); Ibidem, ex Colegio de San José (RMNH n.c.); Puerto Nare, 300 m, L. Richter leg. (MCZ 146360); Sonsón, Hno. Daniel (USNM 517846); Jericó, 15.iii.1980 (UVZ 8161); **Caldas**, Marmato, T. Bland leg., ex Swift (ANSP 25755; DMNH 25595); Ibidem, Bland leg., ex Amherst College (MCZ 146106); Ibidem, ex Richardson (DMNH 67690); Valley of Magdalena river, 1200 m, Richter leg. (MCZ 145208); Ibidem, UF 109239 [not seen]; Chinchiná, Vereda La Esmeralda, Embalse San Francisco, Bosque La Esmeralda, 1023 m, J. Martínez leg. (UVZ n.c.); **Cauca**, Coconuco, xii.2015 (FEM 173423); near Santander de Quilichao, piedmont of Cerro La Chapa, 1700 m, F.J. Borrero leg., 1.viii.2009 (USDA 144837–144838); “Quilichao”, ex McAndrew (NHMUK n.c.); Ibidem (UF 109238, 161244); Puerto Tejada (UVZ 81239 [not seen]) (Restrepo *et al.* 1983, as *D. rugistriatus* Haas); “Cauca”, F. Bonis leg. (ANSP 91230); **Quindío**, Salento, vi.2014 (FEM 153595, 154855, 154857); **Risaralda**, Santuario, in coffee plantation, 1300–1400 m, J. Pineda leg., iv.2007 (GK); Santa Rosa de Cabal, Parque Los Nevados, Finca La Miranda, O. Rangel leg., 20.vi.1980 (ICNB 0109); Pereira, ex Bequaert (MCZ 113837); Ibidem (RBINS 613297); **Tolima** San Juan de las Herosas, xi.2014 (FEM 153554); La Tigrera, Valle (JMR); **Valle del Cauca**, La Cumbre, Finca La Esmeralda, on live fence, 1591 m, Borrero leg., 12.viii.2007 (USDA 144830); Ver. El Topacio, Pance, 1700 m, F. Montoya leg., 2008 (USDA 144834); Ibidem, Montoya leg., 15.i.2007 (USDA 144835); Ibidem, Montoya leg. iii.2007 (USDA 144836); Pance, 1676 m, H. Montoya leg., 3.ii.2011 (UVZ n.c.); Ver. El Topacio, Pance, Borrero leg. 18.vii.2005, 1550 m (USDA 144839); SW of El Aguila, between La Línea and El Granero, 1901 m, Borrero and T. Pearce leg., 20.vii.2010 (USDA 144840); 1.4 km NW Lago Calima, 1458 m, viii.2011 (USDA 144841); Jamundí, Hacienda “El Castillo”, 1000 m, Borrero leg., 8.x.1979 (RMNH n.c., UVZ 82054); Ibidem, xii.1979 (UVZ 8164) (last two localities: Restrepo *et al.* 1983, misidentified as *D. rugistriatus* Haas); 3 km W Atuncela, 4500 ft. [~1370 m], F.G. Thompson leg., 1969 (UF 176885 [not seen]); Rio La Paila valley, 1300 m, H. Pittier leg., i.1906 (USNM 251163); 20 kms above Trujillo, Vereda La Débora, 4.8 kms above Venecia, 2050 m, P. Silverston leg., 6.iii.1981 (UVZ 82047); Paso de la Bolsa, Rio Cauca margin, 1000 m, R. Neira leg., 28.v.1982 (UVZ 82152); Calima-Darién, Finca Las Carmelitas, 1 km from Lago Calima, trail to Campo Alegre, 1600 m, E. Velasco leg., 20.xi.1982 (UVZ 82271); Sevilla, road Barragán–Sevilla, Hacienda Cristales, 2100 m, V. Rojas leg., 13–20.i.1999 (UVZ 99106); ; near Zarzal, Hacienda El Medio, 950 m, 21.iii.2005 (UVZ n.c.). ?, New Granada, ex Dohrn (MCZ n.c.); Colombia (NHMUK 1895.6.29.2–3, 1907.8.29.13–17 [*partim*]); Ibidem, ex Webb (FMNH 31482); U.S. Colombia, ex Evezard ex Henderson (USNM 316129 [*partim*]); Bogota, ex Biggs (NHMUK n.c.); Ibidem, ex Chamberlain ex Fulton (USNM 530510).

**Altitudinal range.** From the data above, the range is 300–1900 m; most records are from 1000 m and above. LINARES & VERA (2012) gave a range to 2600 m, based partly on misidentified material.

**Ecology.** The localities where this species is recorded are predominantly in the dry and moist forests ecoregions of Cauca and Magdalena Valley. Found alive on tree trunks (UVZ 8161), and in a seasonally flooded, mixed hardwood/bamboo forest, on *Ficus* trees, between 1–5 m from the ground (UVZ 82054); see also OREJUELA 1979.

**Remarks.** Another species which shows substantial variation in colour, specifically the extend of lateral extensions of axial dark stripes (i.e., zigzag pattern), which give the appearance of interrupted concentric bands; most specimens have a noticeable dark colour band just behind the umbilicus, although this feature is also present in other taxa. Body colouration beige, slightly lighter from the fringe of the foot, towards the sole; last third of eyestalks slightly darker, with a brownish hue. There appear to be a number of populations in the southern part of Valle del Cauca (i.e., Pance, Jamundí) and parts of Cauca (i.e., near Santander de Quilichao) with shorter spired specimens, which we tentatively refer to as this species. Material from Coconuco is without white dots but also tentatively identified as this species. Finally, the specimens from the MacAndrew collection in NHMUK and lot USNM 517846 are tentatively referred to as this species, given their difference in overall shape (lower height/diameter ratio). A lot from Cúcuta (FEM 46920) is not included as it needs further corroboration.

### ***Drymaeus (Drymaeus) fordii* Pilsbry, 1898\*\***

Figs 12L–N, 24A

*Drymaeus fordii* PILSBRY 1898 [1897–1898]: 205, pl. 38 figs 1–3. No type locality. Lectotype ANSP 72368.

**Material.** **Putumayo**, Colón, El Salado, M.C. Barrera leg., i.2002 (UVZ n.c.). ?, [No locality data], J. Ford leg., 1894 (lectotype ANSP, and paralectotype, ANSP 451941).

**Ecology.** The species occurs in the Eastern Cordillera real montane forests ecoregion.

**Remarks.** The UVZ material is subadult and has a colour pattern of axial streaks, but the shell shape agrees well with the lectotype. The Putumayo record is the first precise locality for this taxon, which is now known from just three specimens.

***Drymaeus (Drymaeus) fucatus* (Reeve, 1849)\***

Fig. 13E

*Bulimus fucatus* REEVE 1849 [1848–1850]: pl. 83 fig. 615. Type locality: “New Granada, Sebundoi”. Lectotype NHMUK 1874.12.11.224 (BREURE 1979).

*Drymaeus fucatus* (Reeve); RICHARDSON 1995: 128 (references); BREURE & BORRERO 2008: 21; LINARES & VERA 2012: 187; BREURE & ABLETT 2014: 79, figs 45G–I, L24v.

**Material.** Putumayo, Sibundoy (NHMUK, lectotype). Ecuador, “Ecuador”, Sowerby leg. (ZMZ 512130–31).

**Remarks.** LINARES & VERA (2012) list this species from Dept. Nariño, Tumaco without reference to a voucher. This species has been recorded from Ecuador (BREURE & BORRERO 2008); its presence in Colombia needs confirmation.

***Drymaeus (Drymaeus) geometricus* (L. Pfeiffer, 1846)**

Figs 11B, 24A

*Bulimus geometricus* L. PFEIFFER 1846: 84. Type locality: “Novae Granadae, vallis Magdalenae”. Lectotype NHMUK 1975564 (BREURE 1979).

*Drymaeus geometricus* (L. Pfeiffer); RICHARDSON 1995: 129 (references); LINARES & VERA 2012: 187; BREURE & ABLETT 2014: 83, figs 46J–L, L25iv.

**Material.** Antioquia, San Luis, around Rio Claro cement plant, 300 m, E. Linares leg., 10.x.1987 (ICNB 685); Frontino, G. Wallis leg., 1875 (ZMUZ 511969); ?Antioquia, “Antiochia Bolivia”, W. Reiss leg., 1877 (ZMUZ 512092); Caldas, Marmato, T. Bland leg., ex C.B. Adams (MCZ 155819); ?Cundinamarca, Bogota (FMNH 77575); Norte de Santander, Ocaña, Wallis leg., 1876 (ZMUZ 511968); Tolima, Herveo [“Forests in the mountains below Ervé, on the road to Santa Ana (Bland)” (Pilsbry 1898 [1897–1898]: 235)]; “between Páramo of Herve and Fresno”, Bland leg., ex Swift (ANSP 25770); Ibagué (ICNB 0030). ?, “Valley of the Madeleine” (NHMUK, lectotype); New Granada, Bland leg. (ANSP 25772; FMNH 78750); New Granada, ex Sowerby (ZMUZ 512091); Colombia, ex S. Putzeys (MCZ 75346); Ibidem (UF 206172 [not seen]); U.S. Colombia, Bland leg., ex Henderson ex Redfield (USNM 307546); [without locality], ex Swift (ANSP 25771). Venezuela. ?, [without specific locality], ex Petit (ZMUZ 512090).

**Altitudinal range.** The precise localities where this species has been found are 300–~2300 m.

**Ecology.** Localities for this species are in the montane forests ecoregions of the Cauca and Magdalena Valley. The actual habitat is unknown.

**Remarks.** Combining the note by PILSBRY (1898 [1897–1898]) with the text of the label from Bland, it becomes clear that this species has been collected just north of Herveo, in the border region with Caldas. This locality and Ibagué (both in Tolima), and San Luis (Antioquia) are the only specific localities known for this species. See also remarks on Santa Ana under *Drymaeus decoratus goniobasis*. Colour variation was observed among the samples examined, consisting in the relative intensity and width of colour bands, and of the axial zigzagging elements that connect them. Some specimens are devoid of either type of bands.

***Drymaeus (Drymaeus) glaucostomus* (Albers, 1852)\*\***

Figs 6A–C

*Bulimus glaucostomus* ALBERS 1852: 32. Type locality: “in montibus Venezuela”. Lectotype ZMB 101784 (KÖHLER 2007); KÖHLER 2007: 145, fig. 91.

**Material.** Norte de Santander, Ocaña, G. Wallis leg., 1876 (ZMUZ 511967).

**Remarks.** The ZMUZ material can be assigned to this well-known Venezuelan species. This is the first Colombian record, but with an imprecise Wallis locality, which needs further confirmation.

***Drymaeus (Drymaeus) inaequalis* (L. Pfeiffer, 1857)**

Figs 14G–H, 24A

*Bulimus inaequalis* L. PFEIFFER 1857: 330. Type locality: Banks of the Maranhon.

*Drymaeus inaequalis* (L. Pfeiffer); RICHARDSON 1995: 138 (references); BREURE & BORRERO 2008: 21; BREURE & ARAUJO 2017: 77, fig. 30E.

**Material.** Huila, San Agustín, leg. 1977 (UVZ 8157); **Meta**, region of Villavicencio, V. Guevara, leg. (ANSP 164568). ?, “Maranhon”, M.J. Landauer, 1868 (ZMUZ 512099). **Ecuador**, Antisana, ex Jackson (DMNH 148428); Canelos, ex Jackson (DMNH 148430); Chimborazo, 7 miles below Huigra, S.N. Rhoads leg., 1911 (ANSP 14873); Nachiyacu, Napo region, ex Jackson (ANSP 170711); Pachijal, Rhoads leg., 1911 (ANSP 148442); Pomasqui, ex Jackson (DMNH 164083); Napo, Oriente, ex Jackson (DMNH 164084); Guarumos, ex Jackson (DMNH 164085).

**Ecology.** The species occurs in the Magdalena Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** The Huila record is the first precise Colombian locality for this taxon. The ZMUZ material is accompanied by a second label “Kolumbien” [Colombia]. The ANSP 164568 material is only tentatively referred to as this species.

### ***Drymaeus (Drymaeus) inclinatus* (L. Pfeiffer, 1862)**

Figs 14I, 24A

*Bulimus inclinatus* L. PFEIFFER 1862: 387. Type locality: “New Granada”. Lectotype NHMUK 1975532 (BREURE 1979).

*Drymaeus inclinatus* (L. Pfeiffer); RICHARDSON 1995: 138 (references); LINARES & VERA 2012: 187; BREURE & ABLETT 2014: 94, figs 47A–C, L28iv.

**Material.** Valle del Cauca, El Cairo, Serranía de Los Paraguas, Corregimiento El Boquerón, 7400–8200 ft. [~2255–2500 m], M.S. Alberico and J.M. Restrepo leg., 26.ii.1987 (UVZ 97042); Ibidem, Vereda Las Amarillas, ca. 20 km NW El Cairo, Cerro El Inglés, M.S. Alberico et al. leg., 26.ii.1987 (UVZ 97040); Ibidem, Alto de Galápagos, 2300 m, V. Rojas leg., 27.iv.1994 (UVZ 97039); Vereda Las Amarillas, border El Cairo and El Boquerón, W. Bolívar, 21.ix.1996 (UVZ 97027); El Aguila, Paso de Galápagos, ~1900 m (UVZ n.c.).?, New Grenada (NHMUK, lectotype; two paralectotypes, NHMUK 1975533).

**Altitudinal range.** The records suggest a range ~1900–2500 m.

**Ecology.** The species is recorded from the Northwestern Andean montane forests ecoregion. Found 1.50 m above ground on vegetation (UVZ 97027).

**Remarks.** This species may be compared with *D. angustus* with which it shares the elongated shell, but differs from this species in the less open umbilicus, and less expanded peristome. The material was partly found stored in ethanol; due to a prolonged stay in ethanol, the surface of the shells generally has become dull. The exact locality of the two shells from Paso de Galápagos (UVZ n.c.) is unknown as this pass extends between the Departments of Valle del Cauca and Chocó; it is part of Serranía de Los Paraguas. The precise localities mentioned above are the first ones for this species.

### ***Drymaeus (Drymaeus) intermissus* spec. n.**

Figs 11I–K, 24A <http://zoobank.org:act:56EC77D1-F45C-412E-9507-8273B6D6820E>

**Diagnosis.** A relatively small *Drymaeus* species characterised by the large umbilicus, the flared lip, the spire longer than the aperture and the reddish-black-tipped apex.

**Description.** Shell 27.1 mm, 2.2 times longer than wide, umbilicate with slightly convex sides, rather elongated, solid. Colour whitish-yellowish with waving and partly interrupted, axial chestnut-brown streaks; upper whorls in the same ground colour as the rest of the shell. Surface somewhat shining, smooth, the growth striae visible as subcontinuous whitish lines over the axial streaks. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 5.9, hardly convex, last whorl 0.7 total height; suture slightly impressed. Aperture ovate, 1.9 times longer than wide, 0.63 times the total length. Peristome thin, expanded, especially below, rounded at the base, whitish with a pink border inside. Columellar margin curved, reflexed, dilated above and receding. Parietal wall with a thin callus, with a pink hue, continuous with the columella and the interior edge of the aperture.

**Dimensions.** Holotype H 27.1 mm, D 12.2 mm, HA 17.1 mm, WA 8.8 mm, W 5.9.

**Type material.** **Meta**, Serranía de la Macarena, Rio Duda, Centro de Investigaciones Primatólogicas La Macarena, Campamento Puerto Chamuza, Trail B1000, 350 m, E. Linares leg., x.1994 (ICNB 2840, holotype).

**Ecology.** The type locality is in the Cordillera Oriental montane forests ecoregion. The actual habitat is unknown.

**Remarks.** This species is seemingly related to *Drymaeus (D.) yapacanensis* Breure & Eskens, 1981 from Venezuelan Guayana, but differs by (1) being smaller (27.1 vs. 31.2 mm), (2) having a larger umbilicus, (3) having the aperture relatively smaller and more ovate. Known thus far from a single, dead-collected, but relatively fresh shell, which appears to be a fully developed adult. The Serranía de la Macarena is part of the Colombian Guayana Shield area (ARMENTERAS *et al.* 2009).

**Etymology.** (L.) *intermissus* (isolated), referring to the isolated Serranía de la Macarena, from which hitherto very few malacological collections are known. The epithet is used as an adjective.

***Drymaeus (Drymaeus) iniurius spec. n.***

Figs 15J–L, 24B <http://zoobank.org:act:97CB6DFD-E9E7-4B66-B9B3-114B86BED41C>

**Diagnosis.** A medium-sized species of *Drymaeus*, with one white spiral band below the suture and a broader one below the periphery on the last whorl, bordered by a smaller brownish spiral band above; lower part of last whorl dark chestnut-brown, the upper part of this whorl yellowish-white to marron-brown interspersed with lighter, axial patches of yellowish. Aperture more or less protruded basally, with a white, slightly expanded lip at the basal margin.

**Description.** Shell up to 31.9 mm, 2.2 times longer than wide, imperforate to narrowly rimate, with hardly convex sides, rather elongated, solid. Colour pattern with one light coloured spiral band below the suture and a broader one below the periphery on the ultimate whorl, bordered by a smaller brownish spiral band above; lower part of last whorl dark chestnut-brown, the upper part of this whorl yellowish-white to marron-brown interspersed with lighter, axial patches of yellowish. Upper whorls in the same ground colour as the upper part of the last whorl, becoming somewhat lighter towards the apex. Surface rather shiny, the growth striae slightly thickened. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 6.0, rather flat; suture slightly impressed and bordered by a whitish band below. Aperture elongate-ovate, more or less protruded basally, 1.5 times longer than wide, 0.47 times the total length. Peristome thin, slightly expanded at the basal margin, the lip whitish or pink. Columellar margin straight, hardly reflexed, dilated above and receding. Parietal wall with a thin, transparent callus.

**Dimensions.** Holotype H 29.8 mm, D 13.5 mm, HA 14.7 mm, WA 8.9 mm, W 6.0; paratypes H 29.8 mm, D –, HA 13.5 mm, WA 8.7 mm, W 5.9 (UVZ 84036); H 31.9 mm, D 12.7 mm, HA 14.8 mm, WA 9.7 mm, W 5.8 (UVZ n.c.).

**Type material.** **Valle del Cauca**, Palmira, La Sirena, western slope of Central Cordillera, 2700 m, T. Grant leg., 15.v.1997 (UVZ 97026, holotype, previously alcohol preserved); Ibidem, watershed of Rio Nima, 2800 m, G. Corredor et al., 31.vii.1999 (UVZ n.c., two paratypes); Northeast of Tenerife, road to television antenna, 3000 m, C. Restrepo leg., 6.iv.1984 (UVZ 84036, one paratype); Ibidem, 8.vii.1984 (UVZ 84073, two paratypes).

**Other material.** **Tolima**, Parque Nacional Nevado del Huila, 1200–1600 m, leg. x.2014 (FEM 1535;24–153531, 173428); Ibidem leg. xii.2016 (FEM 194178).

**Altitudinal range.** Records indicate a range 1200–3000 m.

**Ecology.** The species occurs in the Cauca Valley montane forests ecoregion. Found alive on understory vegetation in secondary forest (UVZ 97026, UVZ n.c.). The lots found northeast of Tenerife were collected in cloud forest on a carpet of moss.

**Remarks.** The shell figured by REEVE 1848 [1848–1850]: pl. 44 fig. 275 and copied by PILSBRY 1898 [1897–1898]: pl. 40 fig. 1 as *Drymaeus chimborasensis* does not correspond to the type material labelled as such (BREURE & ABLETT 2014: 43). Reeve's figure matches, however, the material listed above very well, except for having a pink lip. This is a very characteristic species, which may be compared with *Drymaeus murrinus* (Reeve, 1848); it differs from that taxon by (1) having the columellar margin receding, (2) the absence of a (pink) colour band behind the lip inside the aperture, and (3) being more rimate to imperforate. This novelty bears also some resemblance to forms of *D. convexus* (L. Pfeiffer, 1855), from which it differs in (1) having the whorls less convex, (2) the relatively larger aperture, and (3) the absence of axial elements in the colour pattern. The subperipheral concentric band is yellow in the material from Tolima, whereas this band is white in the material from Valle del Cauca, but the thinner subsutural bands are white in all specimens examined; it is possible that this may be related with freshness of the material. The body of the holotype specimen (collected alive) is dried inside the shell. Lots UVZ 84036 and 84073 are fragments; the shells have probably been preyed upon by a bird.

**Etymology.** (L.) *iniuria* (wrong one); referring to the error made by Reeve and copied in subsequent literature. The epithet is used as an adjective.

***Drymaeus (Drymaeus) leai* Pilsbry, 1898**

Figs 12A–C

*Bulimus gracilis* LEA 1838: 85, pl. 23 fig. 102. Type locality: “near Carthagera”. Syntype USNM 105143; LINARES & VERA 2012: 187. Not *Bulimus gracilis* Hutton, 1834.

*Drymaeus leai* PILSBRY 1898 [1897–1898]: 213, pl. 40 figs 15–17; RICHARDSON 1995: 142 (references).

**Material.** Bolívar, “6 miles from Cartagena”, Gibbon leg., ex Lea (USNM, syntype).

**Remarks.** LINARES & VERA (2012) incorrectly considered *Drymaeus leai* Pilsbry, 1898 a junior synonym of *D. gracilis* (Lea, 1838), apparently overlooking the homonymy with Hutton's taxon. The locality of the species remains questionable as Gibbon's itinerary is unknown. The species remains only known from the type specimen.

***Drymaeus (Drymaeus) luciensis spec. n.***

Figs 14M–O, 24B <http://zoobank.org:act:E9426E34-6E01-4C45-A4D8-16B73BFF91F8>

**Diagnosis.** A relatively medium-sized species of *Drymaeus*, with rather swollen and saccate last whorl and a closed umbilicus. Aperture with a white, slightly expanded and broad lip, rimmed inside.

**Description.** Shell up to 30.1 mm, 1.76 times longer than wide, imperforate with rather convex sides, rather elongated, solid. Colour whitish-greyish, (the colours in the type material have been faded away, but there is a pattern of widely separated axial brown bands (possibly up to ten in the body whorl). Upper whorls in the same ground colour as the rest of the shell. Surface dull; the upper whorls smooth; from the third whorl onwards, sculpture consists of fine concentric incised lines which are crossed by growth striae which are slightly thickened in parts, giving the appearance of slight bumps, most noticeable on the last whorl. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 5.5, slightly convex, except the last one, which is swollen and saccate below; suture slightly impressed and bordered by a lighter line below. Aperture ovate, 1.5 times longer than wide, 0.49 times the total length. Peristome slightly thickened, expanded, especially below, with a low ridge inside the aperture that transforms into the columella. Columellar margin curved, reflexed, receding. Parietal wall with a thin callus, with a brownish colouration, not extending into the peristome.

**Dimensions.** Holotype H 30.1 mm, D 17.2 mm, HA 14.8 mm, WA 9.6, W 5.5; paratype H 29.2 mm, D 16.0 mm, HA 15.6 mm, WA 8.5 mm, W 5.4.

**Type material.** Valle del Cauca, Tuluá, Santa Lucía, Hacienda Las Vegas, 3000 m, E. Velasco leg., 21.ii.1984 (UVZ 84019, holotype and one paratype).

**Other material.** Caldas, near Neira, 1800–2000 m, leg., xii.2016 (FEM 194082–194088, 194482, 194484).

**Altitudinal range.** The two localities are on the western slopes of the Central Cordillera, and range 1800–3000 m.

**Ecology.** The species occurs in the Cauca Valley montane forests ecoregion. Collected among leaf litter, in rain forest (FEM).

**Remarks.** Although the type material of this species consists of two not fresh, discoloured specimens, we believed it was different from all other species examined, when we first saw the material in 2008. Since then, we have become aware of six fresh specimens which were available for sale in the shell trade, and their photographs attest to the colouration and sculpture, and variation among individuals, not evident in the type material. Sculpture consists of rather coarse growth lines, crossing over incised spiral lines. All specimens have axial, broad brownish, subvertical stripes, which are variable in number and in intensity and width of individual bands. The bands stop short of reaching the lower parietal area and the expanded peristome, such that the whitish background shell colour is unbanded in the lower part of the body whorl; this can not be observed in the type material. These Caldas specimens are smaller (H ~22 mm) than those from the type locality. This new taxon resembles *Drymaeus (D.) subsemiclausus* in the overall shape and saccate body whorl below but differs in (1) being larger; (2) having a more acute spire; (3) having the last whorl more regularly rounded (especially as seen in dorsal view); (4) having the peristome more sinuous in side view. As with the latter species, the precise localities known are at relatively high elevations.

**Etymology.** The specific epithet refers to the type locality, Santa Lucía.

***Drymaeus (Drymaeus) megas* Pilsbry, 1944**

Figs 9A–C, 24B

*Drymaeus flexuosus megas* PILSBRY 1944: 127, pl. 11 fig. 3. Type locality: Dept. Huila, Upper Magdalena Valley, Suesa. Holotype ANSP 179981.

*Drymaeus flexuosus* Pilsbry; RICHARDSON 1995: 127 (references); LINARES & VERA 2012: 186.

**Material.** Huila, Upper Magdalena Valley, near Suesa [03°15'N 075°15'W, ~ 400 m], A.A. Olsson leg., 1943 (ANSP, holotype).

**Ecology.** The species is known from the Magdalena valley dry forests ecoregion.

**Remarks.** We observe the lack of the characteristic black band behind the umbilicus, distinctive of *Drymaeus flexuosus*. Moreover, the overall shape is different from that species, the shell is considerably larger, and the single locality in the low valley (Suesa is at 380 m), east of the Central Cordillera, is outside the range of *D. flexuosus*, which is distributed on the Western Cordillera and the valley between these two mountain chains.

Contrary to Pilsbry we regard this as a distinct species (**status n.**), but note that it has not been re-collected in this comparatively well-known area during the past ca. 70 years.

***Drymaeus (Drymaeus) murrinus* (Reeve, 1848)**

Figs 14D, 24B

*Bulimus murrinus* REEVE 1848 [1848–1850]: pl. 43 figs 273b. Type locality: “Santa Fé de Bogotá”. Lectotype NHMUK 1975213 (BREURE 1979).

*Drymaeus murrinus* (Reeve); RICHARDSON 1995: 156 [*partim*] (references); LINARES & VERA 2012: 188 [*partim*]; BREURE & ABLETT 2014: 129, figs 38J–L, L40i.

**Material.** Caldas, “Marinata” [Marmato] (NHMUK, lectotype).

**Ecology.** The species is known from the Cauca Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** Reeve published two different species under this name. The type specimen found in the NHMUK collection corresponds to REEVE 1848 [1848–1850]: pl. 43 fig. 273b (contrary to figure 273a as mentioned by RICHARDSON 1995). The type locality of this species was published as “Santa Fé de Bogota”; however, the original label states “Marinata / New Granada”, which most likely refers to Marmato [~ 1300 m] in the Department of Caldas (see BREURE & ESKENS 1981: 26). In the material studied we have seen many specimens mislabeled as *Drymaeus murrinus*; after comparing them to the type we conclude that none corresponds to this taxon, which is thus known only from the type material.

***Drymaeus (Drymaeus) narcissus* (Albers, 1854)**

Figs 14K–L, 25A

*Bulimus narcissus* ALBERS 1854: 217. Type locality: “Nova Grenada”. Lectotype ZMB 114315 (KÖHLER 2007).

*Drymaeus narcissus* (Albers); RICHARDSON 1995: 156 (references); KÖHLER 2007: 147, fig. 102; LINARES & VERA 2012: 188.

**Material.** Antioquia, Municipio Caldas, Alto de San Miguel, A. Sierra leg., 2045 m, 22.xi. 1996 (UAM n.c.); Medellín, Vereda Santa Elena, Piedras Blancas, 2200 m, in oak forest, Parra and Posada leg., 10.xi.2003 (UAM n.c.); [without specific locality] (UAM n.c.). ?, “Nova Granada” (ZMB, lectotype); U.S. of Colombia, ex Nelson (FMNH 94876).

**Altitudinal range.** The records known indicate a range ~2000–2200 m.

**Ecology.** All records are situated in the Magdalena Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** Köhler observed contradictions between the original label of Albers (“*Bul. narcissus* Alb. Columbia ad fluv. Maranhon”), the label given in the Pätel collection (“Nova Granada”, corresponding to the type locality published by Albers), and information in the literature (“U.S. of Colombia”, PILSBRY 1898 [1897–1898]: 227). He concludes that the original locality data must be erroneous, which is not necessarily correct, since in the early 19th century New Granada extended to the borders of Río Marañon, now in Peru (BREURE 2019). KÖHLER (2007) considers New Granada as the type locality and interprets this as Venezuela. With the data at hand it is, however, impossible to assess whether this is a correct interpretation. The localities in the Municipalities of Caldas and Medellín are the first precise localities known for this species, and provide confirmation of its occurrence in Colombia.

***Drymaeus (Drymaeus) notabilis* da Costa, 1906**

Fig. 7G

*Drymaeus notabilis* DA COSTA 1906a: 7, pl. 1 fig. 2. Type locality: Antioquia. Lectotype NHMUK 1907.11.21.5 (BREURE 1979); RICHARDSON 1995: 157 (references); LINARES & VERA 2012: 188; BREURE & ABLETT 2014: 134, figs 32J–L, L41v.

**Material.** Antioquia, [no precise locality known] (NHMUK, lectotype).

**Remarks.** This species is only known from the type material.

***Drymaeus (Drymaeus) notatus* da Costa, 1906**

Figs 11C, 25A

*Drymaeus notatus* DA COSTA 1906a: 7, pl. 1 fig. 3. Type locality: Antioquia. Holotype NHMUK 1907.11.21.6; RICHARDSON 1995: 157 (references); LINARES & VERA 2012: 189; BREURE & ABLETT 2014: 134, figs 32G–I, L41vi.

**Material.** **Antioquia**, [no precise locality known] (NHMUK, holotype); **Quindío**, Filandia, A. Quintero leg. (AQ); **Valle del Cauca**, Jamundí, Villa Colombia, Rio Claro, Quebrada Las Pilas, 1700 m, xi.1989 (UVZ n.c.); Rio Velez, 16.v.1989 (UVZ n.c.).

**Altitudinal range.** Localities where this species occurs range from ~1000–1800 m.

**Ecology.** The species is found in Cauca Valley dry and montane forests ecoregions. The actual habitat is unknown.

**Remarks.** These are the first precise localities for this species. Only five specimens found, all adults. The holotype (NHMUK 1907.11.21.6) has a considerably more expanded and reflected basal portion of the peristome than the other four shells. Colouration fairly constant, with two concentric brown bands on the body whorl, and finer axial patterns.

***Drymaeus (Drymaeus) pamplonensis* Pilsbry, 1939**

Figs 13I–K, 25A

*Drymaeus pamplonensis* PILSBRY 1939: 4, fig. 10. Type locality: Pamplona. Holotype ANSP 170699; RICHARDSON 1995: 159 (references); LINARES & VERA 2012: 189.

**Material.** **Norte de Santander**, Pamplona, Hno. Nicéforo María leg. (ANSP, holotype).

**Altitudinal range.** Around Pamplona altitudes range from ~2000–2800 m.

**Ecology.** The type locality is in the Cordillera Oriental montane forests ecoregion. The actual habitat is unknown.

**Remarks.** Known from the type specimen only. There is little probability of confusion with other Colombian *Drymaeus* species, since this taxon seems so distinctive.

***Drymaeus (Drymaeus) pealianus* (Lea, 1838)**

Figs 4E–H, 25A

*Bulimus pealianus* LEA 1838: 65, pl. 33 fig. 105. Type locality: Colombia, near the rapids of Angostura. Holotype ANSP 192929.

*Drymaeus pealianus* (Lea); RICHARDSON 1995: 161 (references); LINARES & VERA 2012: 189.

*Bulimulus (Drymaeus) comis* PRESTON 1907: 494, fig. 8. **Synon.n.** Type locality: “Bogota”. Holotype USNM 202514. *Drymaeus comis* (Preston); RICHARDSON 1995: 111 (references); LINARES & VERA 2012: 183.

**Material.** **Antioquia**, San Roque, San José del Nus, Quebrada Guaico, ~1475 m (UAM n.c.); **Boyacá/Antioquia**, “near the rapids of Angostura, Colombia”, T.R. Peale leg. (ANSP, holotype of *pealianus*). **?Cundinamarca**, Bogota, ex Preston (USNM, holotype of *comis* [as *conus* (*sic*)]); **Santander**, Between Carare and [Rio] Magdalena, near Puerto Aquileo, A.A. Olsson leg., v.1935 (ANSP 166117).

**Altitudinal range.** Precise records suggest a range of ~100–1500 m.

**Ecology.** The species is known from the Magdalena Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** The type locality of *Bulimus pealianus* may be located along the Río Magdalena, which was the route that Peale followed on his collecting trip (ABBOTT 1955). There is an Isla de Angostura near Puerto Boyacá (= Puerto Serviez), which might be the general area to which Lea referred. LEA (1838) wrote “[d]uring Mr. Peale’s travels in Colombia he found a single specimen”. PILSBRY (1898 [1897–1898]: 217) stating that “[t]he type of this species was placed by Peale in his Philadelphia Museum. It was lost either in the fire which destroyed a large portion of that collection, or at the final disposal of the remainder”. The specimen in the ANSP collection was donated with a remainder of the Peale collection, and is considered the holotype (ABBOTT 1955). The specimen of *Bulimulus (Drymaeus) comis* Preston in the USNM collection is not accompanied by an original label in Preston’s hand, but it corresponds to his figure 8 and is considered the holotype.

The localities from the ANSP and UAM material are the first modern, precise localities for this species based on verified material. LINARES & VERA (2012) record this species from Puerto Nare, Antioquia, and from Salto del Tequendama, near Bogotá, without mentioning voucher depositories.



***Drymaeus (Drymaeus) pseudofusoides* da Costa, 1906**

Figs 13F, 25A

*Drymaeus pseudofusoides* DA COSTA 1906a: 8, pl. 1 fig. 6. Type locality: Bogotá. Holotype NHMUK 1907.11.21.11; RICHARDSON 1995: 165 (references); LINARES & VERA 2012: 189; BREURE & ABLETT 2014: 158, figs 44J–L, L49ii.

**Material.** ?Cundinamarca, Bogota (NHMUK, holotype); Cauca, Valle Tigre, 2000–2400 m, v.2015 (FEM 161442–161450); Valle del Cauca, Parque Nacional Farallones de Cali, Campamento Corea, 2500 m, C. Restrepo and A. Gonzalez leg., 27.xi.1982 (UVZ 82282, 82277); Ibidem, A. Palacios leg., 27.xi.1982 (UVZ 8294); Ibidem, 2300 m, A. Burbano leg., x.1981 (UVZ 82006); Ibidem, 2300 m, A. Gonzalez, 22.i.1982 (UVZ 82007); Ibidem, 2500 m, C. Restrepo leg., xi.1982 (UVZ 82288); Ibidem, G. Cantillo leg., xi.1982 (UVZ 82291); Ibidem, ca. 2700 m, 19.iv.1981 (UVZ 81132); Ibidem, G. Bolívar leg., 20.vii.1981 (UVZ 81240); Ibidem, 2300 m, O. Ceballos, 21.i.1982 (UVZ 82010); Ibidem, 2600 m, O. Ceballos leg., 21.i.1982 (UVZ 82011); Ibidem, 2700 m, 7.xii.1980 (UVZ 8102); Ibidem, La Cuchilla, 3000 m, 17.viii.1980 (UVZ 8173); near Palmira, xii.2016 (FEM 194187–194188); between Dagua and El Queremal, Hacienda San Pedro, ca. 2100 m, L.A. Neira (UVZ 99003).

**Altitudinal range.** The material listed above suggests a range from 2300–3000 m.

**Ecology.** The species occurs in the Cauca Valley montane forests ecoregion. Collected live in montane cloud forest, at 1.20–1.70 m above the ground on leaves and trunks, and on leaf litter at ground level.

**Remarks.** This species was hitherto only known from the type material. With very little doubt we refer the material mentioned above to this species, based on the following shared characteristics: a) general shape; b) size (shell height *D. pseudofusoides* type material ~ 36 mm); c) surface very smooth. All of the new, precise localities are within a relatively small area in Valle del Cauca, on the eastern side of the Cordillera Occidental; it is still to be confirmed if this species is also found in the vicinity of Bogotá. Overall shape somewhat variable; some shells appear proportionally taller because of varying lateral reflection of the peristome among adult shells, mainly in the palatal area; in addition, some specimens exhibit a somewhat broadly ‘spouted’ base, whereas in others the base is more rounded. Shell colouration highly variable, but with a constant, white polished background, superimposed with light brown patterns of broad concentric bands, and finer axial elements, but including specimens with no colour bands. Live body colouration dark, grey-brown, slightly lighter dorsally and on the eyestalks; light colouration on the foot sole, edge of foot sole (visible from side), and tail end.

***Drymaeus (Drymaeus) sanctaemarthae* Pilsbry, 1901**

Figs 12 G–J

*Drymaeus sanctaemarthae* PILSBRY 1901 [1901–1902]: 161, pl. 48 figs 49–50. Type locality: Jiracasaca, NW slope of Santa Marta Mountains. Holotype CM 46613; RICHARDSON 1995: 173 (references); LINARES & VERA 2012: 190.

**Material.** Magdalena, Jiracasaca, south of Santa Marta, 2500 ft. [~750 m], H.H. Smith leg., 1900 (CM, holotype); Finca Don Amo [E of Santa Marta], mountain forest, 3500 ft. [~1067 m], Smith leg. (ANSP 47610); mountains near Santa Marta (UF 109285).

**Altitudinal range.** The localities above suggest a range ~750–1100 m. The seemingly precise localities, however, could not be found in gazetteers and have not been geo-referenced.

**Ecology.** Presumably occurring in the Santa Marta montane forests ecoregion. The actual habitat is unknown.

**Remarks.** The ANSP and UF specimens are the first records collected after the description of this species, from the same area of the Sierra Nevada de Santa Marta. LINARES & VERA (2012) reported an incorrect depository for the type material.

***Drymaeus (Drymaeus) signifer* (L. Pfeiffer, 1855)\***

Figs 15H–I, 27B

*Bulimus signifer* L. PFEIFFER 1855c: 8. Type locality: Venezuela? Lectotype NHMUK 1975216 (BREURE 1979).

*Drymaeus (Mesembrinus) signifer* (L. Pfeiffer); BREURE & ESKENS 1981: 88; RICHARDSON 1995: 178; LINARES & VERA 2012: 200 [partim]; BREURE & ABLETT 2014: 179, figs. 25I–K, L55i.

**Material.** Boyacá, Muzo, ex Melvill-Tomlin (NMW 1955.158.25126).

**Ecology.** This locality is within the Magdalena Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** This taxon is now transferred to the nominate subgenus on the basis of the expanded peristome and the ascending suture in front. The specimen mentioned above may indeed correspond to this taxon, and it

would be the first Colombian record, and the first with a precise locality for this taxon. However, because of lack of additional material that would allow to ascertain variation in this species, this identification needs further corroboration. Linares & Vera (2012) cited this lot, without seeing it, and also cited another lot (FMNH 3378, from Meta, Villavicencio) as corresponding to this species; upon examination, the three specimens included in FMNH 3378 are juvenile, and are not assignable to a particularly species; they certainly are not *D. signifer*. The presence of this species in Colombia remains to be confirmed.

***Drymaeus (Drymaeus) smithii* (da Costa, 1898)**

Figs 12D–F, 25B

*Bulimulus (Drymaeus) smithii* DA COSTA 1898: 81, pl. 6 fig. 8 [July 1898]. Type locality: Bogotá. Lectotype NHMUK 1907.11.21.52 (BREURE 1979).

*Drymaeus smithii* (da Costa); RICHARDSON 1995: 178 (references); LINARES & VERA 2012: 190; BREURE & ABLETT 2014: 180, figs 30G–I, L55iv.

*Drymaeus blandi* PILSBRY 1898 [1897–1898]: 248, pl. 43 figs 73–76, 79–80 [7 Dec. 1898]. **Synon.n.** Type locality: near Fresno. Lectotype ANSP 25780 (H.B. BAKER 1963); RICHARDSON 1995: 104 (references); LINARES & VERA 2012: 182 [partim].

*Drymaeus bellus* DA COSTA 1906a: 8, pl. 1 fig. 5. **Synon.n.** Type locality: San Martín. Holotype NHMUK 1907.11.21.8; RICHARDSON 1995: 103 (references); LINARES & VERA 2012: 181; BREURE & ABLETT 2014: 30, figs 28H–J, L8v.

*Drymaeus incognita* DA COSTA 1907: 304, pl. 26 figs 4–4a. **Synon.n.** Type locality: “Bogotá”. Holotype NHMUK 1907.11.21.24; LINARES & VERA 2012: 188.

*Drymaeus incognitus* (da Costa); RICHARDSON 1995 (references); BREURE & ABLETT 2014: 94, figs 33A–C, L28v.

**Material.** **Antioquia**, Frontino (ANSP 362098 [partim]); Támesis, Hno. D. González leg. (MLS-BOG 609 [partim]); Municipio Caldas, Alto de San Miguel, A. Sierra leg., 2045 m, 22.xi.1996 (UAM n.c.); Medellín, Vereda Santa Elena, Piedras Blancas, 2200 m, in oak forest, Parra and Posada leg., 10.xi.2003 (UAM n.c.); Sonsón, Cerro Las Palomas (UAM n.c.); Támesis, 1964 (UVZ 83016); Frontino, G. Wallis leg., 1875 (ZMUZ 512114); “Antioquia”, T. Bland leg., 1870 (ANSP 25776); **Boyacá**, Muzo (UF 161214 [not seen]); Iguaque, 3100 m, E. Constantino leg., 12.ii.1985 (UVZ 97044); Iguaque, x.2014 (FEM 154764–154765, 194425); **Cundinamarca**, Tequendama near Bogotá, Bland leg. (ANSP 25777; PILSBRY 1898 [1897–1898]: pl. 43 fig. 80); San Antonio del Tequendama (JMR); Páramo de Usaquén, Cordillera Oriental, N of Bogotá, 3000 m, Idrobo leg., 1961 (FMNH 114078); Bojacá, Las Mercedes, road to Fute, 2600–2700 m, Camacho leg., 13.xii.1962 [partim] (FMNH 187571); Tena, Laguna de Pedro Palo, oak forest, 2100 m, E. Linares leg., 30.x.1995 (ICNB 954); Ibidem, 2000 m, Linares leg., 14.vi.1998 (ICNB 3519 [partim]–3543); San Francisco, Vereda Sabaneta, 2550 m, Linares leg., 12.vi.1990 (ICNB 2090); San Antonio del Tequendama, Vereda Chicaque, Mountains of Chicaque, 2400 m, Linares leg., 15.i.1991 (ICNB 2324, 2336, 2339); San Antonio del Tena, P. [Parque] Chicaque, 2350 m, Linares leg., 27.v.1991 (ICNB 2596); Ibidem, 2600 m, Linares leg., 27.i.1997 (ICNB 3404); Mesitas del Colegio [~ 950 m], Soler de Neira leg. (RMNH MOL.266016); Cerro de Manjui, near Facatativá [2700–3000 m], Petersen leg., 1878 (ZMUZ 512017); **Huila**, near Garyzon [= Garzón], Upper Magdalena valley, A.A. Olsson leg., 1945 (ANSP 331965); **Tolima**, Mountains W Fresno, ex Swift (ANSP 25780, lectotype of *Drymaeus blandi*); Ibidem (ANSP 451944, paralectotype); Ibidem (FMNH 78761, paralectotype ex ANSP 25780); **Tolima/Caldas**, “mountains near [sic?, West] Fresno” and “between Salamina and Cabuyal”, Bland leg. (ANSP 25779 [see Remarks]). ?, Bogotá (NHMUK, holotype of *D. incognita*, 1 paratype, NHMUK 1907.11.21.25); Bogotá (NHMUK, holotype of *D. smithii*); Yericó” [Jericó?], ex Jackson (DMNH 164056); Bogotá (ANSP 78542); Ibidem, Bland leg., ex Swift (ANSP 25778); Bogotá, ex Swift (ANSP 25756); Ibidem (ANSP 78542); Bogotá (CMC C13890); Ibidem (DMNH 194935); Ibidem (FMNH 31419); Ibidem, ex C.B. Adams (MCZ 47); Ibidem, ex Preston (UMMZ 124261); San Martín (NHMUK, holotype of *Drymaeus bellus*; NHMUK 1907.11.21.9, paratype); Santa Fé de Bogotá (ZMA n.c.); Colombia (MCZ n.c.); [Label states Bogotá] (USNM 530538a, ex Fulton).

**Altitudinal range.** Among the precise localities cited, the known range is broad, 950–3100m.

**Ecology.** The species was predominantly found in the Cauca Valley and Magdalena Valley montane forests ecoregions. The actual habitat is unknown.

**Remarks.** Of the four taxa listed under this species, *Drymaeus smithii* has priority. This species does not have the little white lines (three specimens in the type series); variation in colour among the three type specimens includes expression of concentric versus axial colour bands, with one paralectotype exhibiting virtually no colour bands. *D. smithii* looks smoother, but has very much the same shape as *D. blandi* and *D. bellus*. The shape of *D. incognita* is also the same; colouration falls in range of variation, salmon hue inside, and a white somewhat expanded peristome. The holotype has little white lines, similar to *D. bellus* (not present in the types of *D. blandi*). The published type locality of *Drymaeus blandi* “near Fresno” appears to be west of that place, according to the original label. Lot ANSP 25779 has two labels. Cabuyal is a vereda [in general, not referring to a specific vereda] within the Municipio Salamina; Fresno is in Tolima, Salamina is in Caldas, and they are about 57 km apart (linear distance). Thus, the location may be in the mountainous area between the Departments of Tolima and Caldas, or one of the two labels does not belong with this lot. However, both places are in the same general area. Studying the variation in the material available, we feel confident in regarding *Drymaeus bellus* as a junior subjective

synonym of *D. smithii*. The variation is mainly in colouration, in the differing strength of axial and concentric colour stripes, including specimens that have elements of both, but also which are devoid of one or the other, or both. The light-coloured and expanded peristome, most often with reddish brown inside, as well as in the parietal area, are present in most specimens. We have been unable to pinpoint with certainty the type locality of *Drymaeus bellus* ("San Martín"), as there are too many places with that name within the range of *D. blandi*. Possibly due to being the better known of such places, LINARES & VERA (2012: 181) suggested that this locality may be in Meta, where there is a municipality with that name and the region is known as Los Llanos de San Martín. However, this seems far outside the range of the known localities. This species resembles *Drymaeus (D.) felix*, and the locality near Laguna de Pedro Palo (ICNB 3519) shows specimens that could be interpreted as intermediate between these two taxa. The lot from "Yerico" (DMNH 164056) is probably from Jericó, but it is impossible to tell which of the many places of that name is meant.

***Drymaeus (Drymaeus) solidus* (Preston, 1907)**

Figs 7A–D

*Bulimulus (Drymaeus) solidus* PRESTON 1907: 494, fig. 9. Type locality: Bogotá. Syntypes NHMUK 1908.7.2.72–73; RBINS MT.2259 (BREURE 2011: 40, fig. 13C, 13iii); USNM 202511; ZMB 59599 (KÖHLER 2007: 148, fig. 109).

*Drymaeus solidus* (Preston); RICHARDSON 1995: 178 (references); LINARES & VERA 2012: 190; BREURE & ABLETT 2014: 181, figs 32D–F, L55v.

*Bulimulus (Drymaeus) ventricosus* PRESTON 1907 [Dec.]: 495, fig. 10. **Synon.n.** Type locality: Bogotá. Holotype USNM 202513.

*Drymaeus ventricosus* (Preston); RICHARDSON 1995: 192 (references); LINARES & VERA 2012: 191. Not *Mesembrinus ventricosus* Paravicini, 1894 nor *Drymaeus punctatus* var. *ventricosa* da Costa, 1907 [June].

**Material.** ?Cundinamarca, Bogotá, ex Preston (NHMUK, RBINS, USNM, ZMB, syntypes of *Drymaeus solidus*); Ibidem, ex Bryant Walker ex Preston (UMMZ 124260); Bogota, U.S. of Colombia, ex Preston (USNM, holotype of *D. ventricosus*); Bogota (FMNH 77577 [partim], 146882).

**Remarks.** This is yet another species of which only material with vague, or uncertain localities is known. Whether *Mesembrinus ventricosus* Paravicini, 1894 is actually a homonym of Preston's name remains somewhat doubtful. Paravicini's species was regarded by PILSBRY (1898 [1897–1898]: 279) as a synonym of *Helix torallyi* d'Orbigny, 1835; it may prove to belong either to *Drymaeus* or *Bostryx*, but the whereabouts of Paravicini's type material is unknown to us. *Drymaeus punctatus* var. *ventricosa* da Costa, 1907 [p. 304: June] was published a few months before Preston's paper [Dec. 1907]. The FMNH lots are only tentatively referred to as this species. Typos in LINARES & VERA (2012: 190), make their text appear as if stating a different type locality for this taxon.

***Drymaeus (Drymaeus) spadiceus* da Costa, 1906**

Figs 7E–F, 25B

*Drymaeus spadiceus* DA COSTA 1906b: 97, pl. 11 figs 2–3. Type locality: Bogotá. Holotype NHMUK 1907.11.21.15; RICHARDSON 1995: 178 (references); LINARES & VERA 2012: 190; BREURE & ABLETT 2014: 182, figs 34D–F, L56i.

**Material.** Boyacá, Muzo, P. Sanchez leg., 1925 (DMNH 164093); Cundinamarca, Yacopí, Vereda La Oscula, Quebrada Chipola, E. Linares, 11.iii.2000 (ICNB n.c.); ?Cundimarca, Bogota (NHMUK, holotype); Santander, near Boyacá (JMR).

**Ecology.** The species is found in the Magdalena Valley montane forests ecoregion.

**Remarks.** The record from Cundinamarca (~ 1300 m in elevation) and the record from Boyacá (~ 700–900 m), both new precise localities for this species, are considerably lower in elevation than what could be expected on the sole basis of the type locality (~ 2600 m).

***Drymaeus (Drymaeus) spectatus* (Reeve, 1849)**

Figs 14E, 25B

*Bulimus spectatus* REEVE 1849 [1848–1850]: pl. 81 fig. 601a. Type locality: "New Granada". Lectotype NHMUK 1874.12.21.226 (BREURE 1979).

*Drymaeus spectatus* (Reeve); RICHARDSON 1995: 178 (references); LINARES & VERA 2012: 191; BREURE & ABLETT 2014: 182, figs 48G–I, L56ii.

**Material.** **Cauca**, “road between Popayan to the Hacienda Sotara [= Paispamba, 02° 15' 24" N 076° 37' 07" W] at about 2400 m (Stübel)” (PILSBRY 1898 [1897–1898]: 213); Popayan, xii.2015 (FEM 173116, 173427); slopes Volcán Purace near Coconuco, v.2015 (FEM 165306–165310); Popayan, v.2015 (FEM 162969–162971); Nevada de Huila, 2000–2400 m, xi.2014 (FEM 154768); Sotara, Paispamba, 1700–2000 m, v.2015 (FEM 165323); Purace, Termales de San Juan, Visitors Center, 3200 m, M. Giraldo leg., 16.xii.1988 (UVZ 99061); Ibidem, A.A. Vasquez leg., 11.vii.2008 (UVZ n.c.); **Nariño**, Galeras near San Juan de Pasto, 1700–2000 m, x.2014 (FEM 153599–153603, 154859); slopes Nevado del Ruiz, x.2014 (FEM 154718, 155218); **Quindío**, Alto de La Linea, v.2015 (FEM 163372–163373); near Calarca, vi. 2014 (FEM 14308–143112); Ibidem, x.2014 (FEM 153567–153571, 173429–173430); **Risaralda**, Between Ucumarí and La Pastora, Santuario de Flora y Fauna Otún-Quimbaya, 2400–2600 m, 1995–1996 (UVZ n.c.); Ibidem, 2400 m, G. Kattan leg. (GK); La Pastora, 2600 m, Kattan leg. (GK, UVZ n.c.); **Valle de Cauca**, Páramo Las Hermosas, 2000 m, x.2014 (FEM 153503, 153505, 156111, 156113–156114, 210516–210517); Ibidem, v.2015 (FEM 163374); ?, “New Granada” (NHMUK, lectotype).

**Altitudinal range.** The localities above suggest a range from 1700–2600 m.

**Ecology.** Records for this species are situated in the Northwestern Andean and Cauca Valley montane forests ecoregions. The actual habitat is unknown.

**Remarks.** Including the lectotype, we found only a few specimens in public collections. LINARES & VERA (2012) also record this species from Dept. Tolima, Mariquita (‘Forest in the mountains below Ervé, on road to Santa Ana’), which suggests material collected by Bland; however, this cannot be evaluated as no voucher information is given. Two lots referred to this taxon were found at ZMUZ (512109, 512114) both from “Frontina”, ex Wallis; we have interpreted this material as belonging to *Drymaeus felix* and *D. smithii* respectively. PILSBRY (1898 [1897–1898]) mentioned the Cauca locality based only on Martens’ text. Overall shell shape and sculpture is relatively constant among adult shells. On the contrary, the pattern of colouration in this species is variable, including variable-width dark axial bands over a beige background. In some specimens, the axial pattern is accompanied by concentric swats devoid of colouration, giving an overall effect of having mainly a concentric pattern of clear colouration. Constant features are the subsutural light concentric bands, as well as a light coloured area around the umbilicus. Predominantly spirally, and or axially coloured individuals coexisted in some samples from the Santuario de Flora y Fauna Otún-Quimbaya. We found one lot with uniformly reddish-brown shells and a whitish subsutural line

### ***Drymaeus (Drymaeus) subsemiclausus* (Petit de la Saussaye, 1843)**

Figs 15E–G, 26A

*Bulimus subsemiclausus* PETIT DE LA SAUSSAYE 1843: 239. Type locality: “montagne de Kindiou, province de Bogota”. Syntype MNHN-IM-2000-21316 (BREURE & ESKENS 1981); syntype NMB 8170a.

*Drymaeus subsemiclausus* (Petit de la Saussaye); RICHARDSON 1995: 181 (references); LINARES & VERA 2012: 191.

**Material.** **Antioquia**, Santa Rosa de Cabal, ca. 16 km ENE linear distance, ~3000 m, in cloud forest, J. de Jager, 1988 (RMNH n.c.); **?Cundinamarca**, Bogotá, G. Wallis leg., 1872 (ZMUZ 512142); Province of Bogota (PILSBRY 1898 [1897–1898]: 239); **Nariño**, Volcan Galeras near Pasto, 1700–2000 m, x.2014 (FEM 153496); Ibidem, v.2015 (FEM 153498, 153499, 168251–168255); **Quindío**, Between Salento and La Cocora, 6 kms N end of road, Hacienda Alaska, Finca Rincón Santo, 2750 m, C. Restrepo leg., 29.ix.1982 (UVZ 82248); “Montagne de Kindiou” [= Nevado de Quindío], ex Goudot (syntype MNHN), Bogota, ex Boissier ex P. Bohny, ex Petit de la Saussaye (syntype NMB); **Valle del Cauca**, NE of Tenerife, 3000 m, Restrepo and C. Murcia leg., 6.iv.1984 (UVZ 84034–5); Ibidem, Restrepo, 8.vii.1984 (UVZ 84074); Páramo Pan de Azúcar, 3500 m, dwarf forest, transition to tall grass, V. Rojas leg., 30.i.1998 (UVZ 99086). ?, Colombia, ex Chamberlain ex Calbert (USNM 515451).

**Altitudinal range.** Precise and confirmed records range 2750–3500 m. It is unknown whether this species may be found at lower elevations.

**Ecology.** The species occurs in the Cauca Valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** It is unknown upon how many specimens Petit de la Saussaye described this taxon. BREURE & ESKENS (1981) reported on finding a syntype in Paris. An additional specimen, housed at NMB [not seen], is regarded as part of the type series. There is variation in colour among the 19 specimens we examined. The majority, including the syntypes, and the specimen figured in Guerin’s *Magazin de Zoologie* (pl. 66) are nearly pure white, with colouration limited to the inner edge of the peristome, and to the columellar/parietal zones. In contrast, the specimen illustrated by REEVE (1848 [1848–1850]: species 254, later reproduced by PILSBRY 1898 [1897–1898]) exhibits multiple, well separated, dark(er), concentric colour bands over a white background. The two patterns of colouration may be seen in specimens collected from the same locality and collection event (UVZ 84034–84035).

***Drymaeus (Drymaeus) subventricosus* da Costa, 1901**

Fig. 13A

*Drymaeus subventricosus* DA COSTA 1901: 239, pl. 24 fig. 4. Type locality: Bogotá. Lectotype NHMUK 1907.11.21.37 (BREURE 1979); RICHARDSON 1995: 182 (references); LINARES & VERA 2012: 191; BREURE & ABLETT 2014: 188, figs 33J–L, L57vii.

**Material.** ?Cundinamarca, Bogotá (NHMUK, lectotype).

**Remarks.** Another species of which only the type specimen and no precise locality is known. The elevation data given by LINARES & VERA (2012) assumes that Bogotá was the actual collection locality, which is not at all certain.

***Drymaeus (Drymaeus) sykesi* da Costa, 1906**

Fig. 9H

*Drymaeus sykesi* DA COSTA 1906a: 7, pl. 1 fig. 1. Type locality: Bogotá. Holotype NHMUK 1907.11.21.4; RICHARDSON 1995: 183 (references); LINARES & VERA 2012: 200; BREURE & ABLETT 2014: 190, figs 35J–L, L58iii.

**Material.** ?Cundinamarca, Bogotá (NHMUK, holotype); Bogota (USNM 307633).

**Remarks.** We have found no additional material other than the type specimen and the single specimen in the USNM lot. When giving an altitudinal range, LINARES & VERA (2012) assumed that the type locality is correct, which is unlikely.

***Drymaeus (Drymaeus) vicinus* (Preston, 1907)**

Figs 13B–D

*Bulimulus (Drymaeus) vicinus* PRESTON 1907: 495, fig. 11. Type locality: Bogotá. Syntypes USNM 202512, ZMB 59603 (KÖHLER 2007).

*Drymaeus vicinus* (Preston); RICHARDSON 1995: 194 (references); KÖHLER 2007: 148, fig. 111; LINARES & VERA 2012: 192.

**Material.** ?Cundinamarca, “Bogota, Colombia”, ex Preston (USNM, ZMB, syntypes).

**Remarks.** Another species of which only the type material and no precise locality is known. The elevation data given by LINARES & VERA (2012) assumes that Bogotá was the actual collection locality, which we doubt. Variation in colour pattern is seen among the two syntype specimens examined, i.e., mainly one single colour, unbanded (USNM 202512), and banded, with both concentric and axial colour elements (ZMB 59603). This species seems closely related to *Drymaeus (D.) fabrefactus* (Reeve, 1848), and their relationship needs further study.

***Drymaeus (Drymaeus) villavicencioensis* Breure, 1977**

Figs 11M, 26A

*Drymaeus villavicencioensis* BREURE 1977: 269, figs 23–24. Type locality: Dept. Meta, Villavicencio. Holotype SMF 245417; RICHARDSON 1995: 194 (references); NEUBERT & JANSSEN 2004: 234, pl. 14 fig. 167; LINARES & VERA 2012: 192.

**Material.** Meta, Villavicencio, Schremmer leg., 1970 (SMF, holotype).

**Altitudinal range.** Villavicencio is at ~400 m altitude; however, the precise locality is unknown and to the west of the city, substantially higher elevations occur.

**Ecology.** Unknown as the precise collecting locality was not specified.

**Remarks.** No additional material is known. This species has a very distinct shape and colouration, unlikely to be confused with other known species of *Drymaeus* from Colombia.

***Drymaeus (Drymaeus) volsus* Fulton, 1907\*\***

Figs 9D, 26A

*Drymaeus volsus* FULTON 1907: 153, pl. 10 fig. 2. Type locality: Ecuador. Lectotype (BREURE 1979) NHMUK 1907.5.3.162; RICHARDSON 1995: 196 (references); BREURE & BORRERO 2008: 23; BREURE & ABLETT 2014: 208, figs 35A–C, L64vii.

**Material.** Meta, Pipiral (MCZ 136471). Ecuador, “Ecuador” (NHMUK, lectotype).

**Altitudinal range.** Pipiral is at ~900 m elevation.

**Ecology.** The locality lies in the Cordillera Oriental montane forests ecoregion. The actual habitat is unknown.

**Remarks.** This single specimen, listed in MCZ's database, and cited by LINARES & VERA (2012) as *Drymaeus angustus*, is in fact the first confirmed precise locality of *D. volsus* in Colombia.

***Drymaeus (Drymaeus) ziczac* (da Costa, 1898)**

Fig. 6J

*Bulimulus (Drymaeus) ziczac* DA COSTA 1898: 81, pl. 6 fig. 5. Type locality: "valley of the R. Cauca". Lectotype NHMUK 1907.11.21.46 (BREURE 1979).

*Drymaeus ziczac* (da Costa); RICHARDSON 1995: 197 (references); LINARES & VERA 2012: 192; BREURE & ABLETT 2014: 212, figs 30J–L, L66v.

**Material.** ?Antioquia/?Caldas/?Cauca/?Risaralda/?Valle del Cauca, "valley of the R. Cauca" [no specific locality known] (NHMUK, holotype, and 1907.11.21.46, paralectotype).

**Remarks.** Given that the Río Cauca runs through different Departments, the locality remains very imprecise without further material. The label accompanying the type material states "Llanos de Cavariari" (BREURE & ABLETT 2014: 212, fig L66v); we have been unable to find such a locality in Colombia, even accepting localities with somewhat similar spellings. The Department of Guaviare, Colombia is one such locality, and includes areas considered as "Llanos" (i.e, extensive, relatively flat areas), but the Río Cauca is far to the west of this region. We found no additional material of this taxon.

***Drymaeus (Drymaeus) zingarensis* Restrepo & Breure, 1987**

Figs 10A–C, 26A

*Drymaeus zingarensis* RESTREPO & BREURE 1987: 141, figs 1–2. Type locality: Valle del Cauca, Finca Zíngara (3°31'N 76°36'W), 2000m. Holotype UVZ 83010, paratypes see below; LINARES & VERA 2012: 192.

**Material.** Valle del Cauca, Finca Zíngara, km 6 on the trail km19 road Cali–Buenaventura–La Paz, 2000 m, M. Giraldo leg. (UVZ 81252, 82032, 82194, 83007; all paratypes); Locations on road Cali–Buenaventura: km 14, Bosque de San Antonio, W of Cerro de la Horqueta, 2100 m (UVZ 82131, 82133, 82164, 83036, 83115; RMNH 55838; all paratypes); km 16, Bosque de San Pablo, 1900 m (UVZ 8160, 82210; RMNH 55839; all paratypes); km 23, Reserva El Refugio, Dagua, 1945 m, F.J. Borrero & T. Pearce leg., 4.vii.2013 (USDA 144885); La Cumbre, Chicoral, Dapa, J.M. Riascos leg., 18.xi.1994 (IMCN 0013); Cerro El Inglés, El Cairo, on rocks under vegetation, leg. iii.2010 (FEM 709061, 79062, 79075).

**Altitudinal range.** 1900–2100 m, according to the material studied.

**Ecology.** The species is known from localities in the Northwestern Andean montane forests ecoregion. The actual habitat is unknown.

**Remarks.** During a visit to the UVZ collection, the holotype appeared to be broken into pieces.

**Morphospecies**

**Remarks.** The following morphospecies are not described; see the remarks under each for more details.

***Drymaeus (Drymaeus) species 1***

Fig. 16A

**Material.** Valle del Cauca, Palmira, road from Tenerife to Paramo Pan de Azucar, 3500 m, R. Contreras leg., 8.x.1983 (UVZ 83078); Ibidem, north-east of Tenerife, 3000 m, C. Restrepo leg., 8.vii.1984 (UVZ 84076); Buga, Vereda Janeiro, La Magdalena, Hacienda Santelina, V. Rojas, 28.ii–6.iii.1999 (UVZ 99102); Parque Nacional Farallones, Corea, 2500 m, C. Restrepo and A. Gonzalez, 27.xi.1982 (UVZ 82282); Florida, Hacienda Los Alpes, 2450 m, Y. Solarte and A. Gonzalez leg., 15.v.1983 (UVZ 83058).

**Ecology.** Found live in bromeliad species (UVZ 83078).

**Remarks.** This morphospecies may actually belong to *Stenostylus*, but the only shell that seems full-grown is broken and a final evaluation has to be postponed until additional material becomes available.

***Drymaeus (Drymaeus) species 2***

Figs 16B–D

**Material.** Nariño, Ricaurte, Parque Nacional Natural La Planada, G. Cantillo leg., ix.1987 (UVZ 97035).

**Remarks.** The single specimen is an old, worn shell. We have not been able to match it to other taxa known from Colombia or Ecuador, but no further action is warranted until additional material becomes available.

***Drymaeus (Drymaeus) species 3***

Fig. 16E

**Material.** Huila, Finca Meremberg, 2200 m, viii.1979 (UVZ 8153); Ibidem, Borrero leg., xii.1979 (UVZ 8154–5, 8257); Ibidem, 2300 m, (UVZ 8156); Ibidem, M. Giraldo, 7–8.iv.1982 (UVZ 82098–100); Ibidem, G. Kattan leg., 10.x.1981 (UVZ 82069); Ibidem, Kattan leg., xi.1982 (UVZ 82295–6); Ibidem, Kattan leg., iv.1983 (UVZ 83051–2); Reserva de Fauna and Flora Meremberg, km 100 road Popayán–La Plata, Kattan leg., iv.1982 (UVZ 84001); Ibidem, C. Restrepo, ix.1984 (UVZ 84091); San Agustín, leg., i.2007 (FEM 46809). ?, “Marmoto”, ex Hinckley (INHS Z25724).

**Ecology.** Found alive on a tree at 0.60 m (UVZ 82100), on *Cecropia* tree at 10 m (UVZ 8154), and on ‘platanillo’ leaf (UVZ 82098).

**Remarks.** These specimens resemble the lectotype of *D. (D.) fordii* (Pilsbry 1898) (ANSP 72368). However, we refrain from using this name for the material above, due to a lack of locality data for *D. fordii*, as well as of additional specimens, which would allow us to assess morphological variability within this species. The specimens from INHS resemble this morphospecies; however, with the imprecise locality “Marmoto” [probably Marmato, which in this case could be either in Caldas or Cauca] it is difficult to ascertain their affinities.

***Drymaeus (Drymaeus) species 4***

Fig. 16J

**Material.** Cundinamarca, La Calera, towards the mine, R. Jaramillo, iv.1980 (ICNB 0004); San Miguel, 2900 m, L. Richter leg. (MCZ 145207); Guadalupe, 2650 m, E. Osorno leg., 10.vii.1944 (MCZ 147223); Aguadita, Hno. Apolinar María leg. (MCZ 178142). ?, Colombia (MCZ n.c.).

**Ecology.** Found alive on *Senecio* sp. tree (ICNB 0004), and on a bromeliad (MCZ 147223).

**Remarks.** These specimens resemble *Drymaeus (D.) convexus* (L. Pfeiffer, 1855), but are not typical of the morphological variation observed in that species. Given the fact that the localities are within the distributional range of this known to be variable species, we list them here as a morphospecies. Among the five lots there are two colour patterns discernible, namely axial, and concentric colour bands, which may be connected.

***Drymaeus (Drymaeus) species 5***

Fig. 16F

**Material.** Cauca, Belalcazar, Termal Inderena, 2800 m, I. de Arebalo leg., 29.x.1980 (ICNB 0164); Ibidem, 3000 m, 28–29.x.1980 (ICNB 0182, 0185); Coconuco, Parque Nacional Natural Munchique, 3050 m, M. Losano leg., 2.viii.1980 (ICNB 0187); Headwaters of Rio Palo, Central Cordillera, 3200 m, H. Pittier leg., i.1906 (USNM 251161); **Huila**, Moscopán, Hacienda El Chuscal, 2300 m, C. Roman, 1.x.1984 (ICNB 0382); **Valle del Cauca**, Pance, Campamento Corea, 2900 m, iii.2007 (USDA n.c.); Pance, trail to Corea, 2500 m (USDA n.c.).

**Remarks.** These specimens also resemble *D. (D.) convexus* in the large, elongated, shells, rimate umbilicus and similar heights of the aperture and the spire. The colouration is variable among the specimens observed, and falls within the variation observed in *D. convexus*. We refrain to include them in the later species, due to their more southerly distribution, relative to the majority of the available records of *D. convexus*.

***Drymaeus (Drymaeus) species 6***

Fig. 16G

**Material.** Antioquia, Frontino, Wallis leg. 1875 (ZMUZ 512118); ?, New Granada, G. Wallis leg. 1875 (ZMUZ 512117).

**Remarks.** These lots somewhat resemble *Drymaeus (D.) confluens* (L. Pfeiffer, 1855), but the basal part of the expanded peristome is rounded, not slightly spouted. Because of this difference and the imprecise localities of the only two lots found, we prefer not to list them under *D. confluens*. These lots also bear resemblance to *D. geometricus* (L. Pfeiffer, 1846), differing mainly by being less elongate.

***Drymaeus (Drymaeus) species 7***

Fig. 16H

**Material.** Cundinamarca, San Miguel [Fusagasugá], L. Richter leg., 1943, 1000–1200 m [*sic*, ca. 2800 m] (FMNH 114105); Santa Fé de Bogotá, ex Fulton (MHNN 35.50).

**Remarks.** The San Miguel sample is comprised of only two shells, one of which is a subadult. These two lots may correspond to a distinct, unrecognised species of *Drymaeus* (s.s.), but the material available is insufficient for further assessment.

***Drymaeus (Drymaeus) species 8***

Fig. 16I

**Material.** Nariño, 5 mi E of Santiago, Ross and Schlinger leg., 3.iii.1955 (FMNH 106317).

**Remarks.** This single specimen, has the unusual feature not seen in any other specimens examined, that the main colour pattern consisting of interrupted concentric bands, continues onto the parietal callus, which also exhibits a pink hue.

**Subgenus *Drymaeus (Mesembrinus) Albers, 1850***

*Mesembrinus* ALBERS 1850: 157. Type species by subsequent designation (ALBERS & MARTENS 1860): *Helix virgulata* Férussac, 1821 = *Helix elongatus* Röding, 1789.

**Distribution.** Venezuela, Guyana, Suriname, French Guiana, Brazil, Peru, Ecuador, Colombia, Panama, Costa Rica, Nicaragua, El Salvador, Honduras, Guatemala, Belize, Mexico, U.S.A., Caribbean (most islands).

***Drymaeus (Mesembrinus) cf. amandus (L. Pfeiffer, 1855)\****

Figs 17A–B, 26B

*Bulimus amandus* L. PFEIFFER 1855d: 96, pl. 31 fig. 4. Type locality: Venezuela. Lectotype NHMUK 1975457 (BREURE 1979).

*Drymaeus amandus* (L. Pfeiffer); RICHARDSON 1995: 97 (references); BREURE & ABLETT 2014: 17, figs 19C, L4ii.

**Material.** Magdalena, Sierra Nevada de Santa Marta, Onaca Estate, 2500 ft. [~760 m], H.H. Smith leg. (ANSP 47608); Ibidem, 3500 ft [~1065 m] (ANSP 47609); Ibidem, trail to Buritaca 201, 1000 m, 1981 (UVZ 81222).

**Venezuela,** Santo Domingo, 3000 m, Gabaldón leg. (USNM 109522a, h). ?, [no specific locality], ex Cuming (NHMUK, lectotype).

**Remarks.** The specimens from ANSP and UVZ are only tentatively referred to as this species. These Colombian records thus need further confirmation. They differ by the more expanded and slightly reflexed peristome, the slightly larger last whorl, and the lack of the pink colour described in L. Pfeiffer's specimen. The USNM lots are also tentatively placed here; the shells are stouter than the lectotype.

***Drymaeus (Mesembrinus) columbianus (Lea, 1838)***

Figs 18A–F, 26B

*Bulimus columbianus* LEA 1838: 66, pl. 23 fig. 110. Type locality: "about 100 miles up the Magdalena River, Colombia". Lectotype ANSP 192932 (H.B. BAKER 1963).

*Drymaeus columbianus* (Lea); RICHARDSON 1995: 111 (references); LINARES & VERA 2012: 193 [as *D. columbianus* (Lea 1839), *sic*].

*Bulimus virgo* LEA 1838: 84, pl. 23 fig. 97. **Synon.n.** Type locality: near Carthagen. Syntype USNM 105076.

*Drymaeus virgo* (Lea); RICHARDSON 1995: 196 (references); LINARES & VERA 2012: 201.

*Bulimus gruneri* L. PFEIFFER 1846: 30. Type locality: Mexico; Richardson 1995: 196. Lectotype NHMUK 20100563/1 (BREURE & ABLETT 2014).

*Drymaeus gruneri* (L. Pfeiffer); BREURE & ABLETT 2014: 84, figs 24E, L25vii.

*Bulimus hachensis* REEVE 1850 [1848–1850]: pl. 85, fig. 627. Type locality: Guatemala, Rio Hacha. Lectotype NHMUK 1975392 (BREURE 1979).

*Bulimulus hachensis* (Reeve); RICHARDSON 1995: 75; LINARES & VERA 2012: 195; BREURE & ABLETT 2014: 86, figs 19K–L, L26ii.



**Material.** **Bolívar**, near Cartagena (USNM, syntype of *Bulimus virgo* Lea); Rioviejo [= Rio Viejo], F. Medem leg., 13.vi.1956 (FMNH 115803); **Cesar**, near [Agustín] Codazzi, 100–300 m, O.L. Haught leg., x.1943 (FMNH 117070); Western side of Sierra Perijá, 200–500 m, Haught leg. (USNM 473938); **Cundinamarca**, Apulo, A.A. Olsson leg., v.1935 (ANSP 166142); Jerusalem–Tocaima, Olsson, 1935 (ANSP 166146); **Magdalena**, S of Fundación, A.G. Ruthven leg., 11.viii.1913 (ANSP 333208); Rio Cesar valley, Haught leg. (USNM 534072); **?Magdalena/Bolívar**, “100 miles up the Magdalena R.” [25–75 m], T.R. Peale leg. (ANSP, lectotype of *B. columbianus* Lea); **Tolima**, [Guayabal,] Méndez, T. Bland leg., ex Swift (ANSP 25837; FMNH 78783); *Ibidem*, ex C.B. Adams (MCZ 155820); Alvarado, 310 m, O. Rangel leg., vi.1980 (ICNB 093, 0112); *Ibidem*, vi.1981 (ICNB 0104). **Panama**, Arraiján, Rio Caseres, Finca Bergerón, E.S. Bergerón leg., 10.x.1961 (FMNH 117201); *Ibidem* (FMNH 117542); Alhajueta, H. Pittier leg., v.1911 (USNM 515852). *?*, Colombia, ex Cuming (NHMUK n.c.); “Rio Hacha Guatemala” (NHMUK, lectotype of *B. hachensis*) [see Remarks].

**Altitudinal range.** The precise localities indicate a range up to ~300 m.

**Ecology.** Recorded from different ecoregions. Predominantly from Guajira-Barranquilla xeric scrub, and from Sinú Valley and Magdalena valley dry forests ecoregions. The actual habitat is unknown.

**Remarks.** ABBOTT (1955) reported on the type specimen of *Bulimus columbianus* Lea, which was previously thought to be lost. It appears that a wealthy donor purchased the leftovers of Peale’s collection for the Academy when it went up for sale during Abbott’s tenure (see also under *lacteus* below). The locality “Rio Hacha Guatemala” is problematic, as no related names could be found in gazetteers; there are, however, places of that name—or “Riohacha” or “Hacha”—e.g. in Panama and in Colombia (Dept. La Guajira). PILSBRY (1898 [1897–1898]: pl. 45 fig. 40) had a picture drawn from a specimen with a darker band around the umbilicus which is also visible inside the aperture, which he regarded as *D. virgo*. We found one lot (ANSP 333208) which he regarded as *D. virgo*; the type of *D. columbianus* does not have this characteristic. We found several lots (e.g., FMNH 78783, 115803) within which some specimens show the same colouration. According to LINARES & VERA (2012) the type locality of *D. columbianus* might be located between Córdoba / Magangué (Dept. Bolívar) and Plato / Santa Bárbara de Pinto (Dept. Magdalena). In BREURE & ABLETT’s (2014) assessment of the type material of *D. gruneri*, they questioned the veracity of its type locality (“Mexico”), which was handwritten on the original label at a later date. For a discussion on the relation of *D. columbianus* and *D. lacteus* see the Remarks under the latter.

### ***Drymaeus (Mesembrinus) columbiensis* (L. Pfeiffer, 1855)**

Fig. 17C

*Bulimus columbiensis* L. PFEIFFER 1855a: 124. Type locality: “Columbia”. Lectotype NHMUK 1975521 (BREURE 1979).

*Drymaeus columbiensis* (L. Pfeiffer); LINARES & VERA 2012: 193; BREURE & ABLETT 2014: 47, figs 19I–J, L25v.

*Bulimus gratus* L. PFEIFFER 1856a: 159. New name for *Bulimus columbiensis* L. Pfeiffer, 1855, not *Bulimus columbianus* Lea 1838 [See remarks].

*Drymaeus gratus* (L. Pfeiffer); RICHARDSON 1995: 134 (references).

**Material.** *?*, Colombia (NHMUK, lectotype).

**Remarks.** The new name introduced by L. PFEIFFER (1856a) to replace his *Bulimus columbiensis* not *B. columbianus* Lea, 1838, was unnecessary as his spelling is sufficiently different. Therefore, we regard *Bulimus gratus* as a junior subjective synonym (**Synon.n.**) of *B. columbiensis*. The specimens reported by CORREAL *et al.* (1977) from Soacha, Sitio Tequendama I (Cundinamarca), and referred to by LINARES & VERA (2012) are not *D. gratus*. We have not seen any other material apart than the type lot that can be assigned with certainty to this species.

### ***Drymaeus (Mesembrinus) depictus* (Reeve, 1849)**

Figs 19A–B, 26B

*Bulimus depictus* REEVE 1849 [1848–1850]: pl. 74 fig. 529. Type locality: “New Granada”. Lectotype NHMUK 1975529 (BREURE 1979).

*Drymaeus depictus* (Reeve); RICHARDSON 1995: 131 (references; as *D. granadensis* (L. Pfeiffer, 1848), see remarks); LINARES & VERA 2012: 193 [*partim*]; BREURE & ABLETT 2014: 59, figs 22C, L17v.

*Otostomus depictus ictericus* MARTENS 1873: 183, pl. 1 figs 16–17. Type locality: [Venezuela] Caracas.

**Material.** **Norte de Santander**, Guamalitos, 1500–2000 ft. [~470–610 m], M.A. Carriker leg. (USNM 517806); **Sucre**, Puerta de Hierro, Rose leg., 6.ix.1959 (FMNH 115839); *?*, New Granada, ex A.D. Brown (ANSP 5240); *Ibidem*, ex Swift (ANSP 25831–2); *Ibidem* (NHMUK, lectotype). **Venezuela, Mérida**, Quebrada de Jají, 1800 m, O. Ravello leg., iii.2015 (FEM 198491–198493); El Marcho, 2200 m, Ravello leg., iii.2015 (FEM 198669); [without further

locality], ex Webb, ex Sowerby and Fulton (FMNH 31362); Ibidem, ex Chamberlain ex Fulton (USNM 530520); Ibidem (USNM 530580); Sierra Nevada Mountains, 8400 ft [~2560 m], Gabaldón and Sons leg., (USNM 206489 [partim]); ?, Caracas, F. Cocking leg., ex Swift (ANSP 25833).

**Altitudinal range.** The Colombian locality at low elevations contrast with the records from Venezuela (1800–~2600 m).

**Ecology.** The Colombian record is located in the Catatumbo moist forests ecoregion.

**Remarks.** This species has been grouped together with *Bulimus granadensis* L. Pfeiffer, 1848 by RICHARDSON (1995). However, since no type of that species seems to exist, and no material has been examined that fits the description, we treat *B. depictus* as a valid species. See also *Drymaeus (Mesembrinus) granadensis* (q.v.) *Otostomus depictus ictericus* has been recognized as a variety by von Martens and Pilsbry; however, with the material at hand it is impossible to evaluate its subspecific status. *D. (M.) depictus* is clearly a variable species in colouration; both banded and uniformly whitish specimens occur. The lots FMNH 31362, and FMNH 115839 are tentatively referred to this species. At this time, the only precise Colombian locality for this species is in Norte de Santander.

### ***Drymaeus (Mesembrinus) fasciarum* Pilsbry, 1939**

Figs 19F–H

*Drymaeus fasciarum* PILSBRY 1939: 5, fig. 9. Type locality: Cúcuta. Lectotype ANSP 168429 (H.B. BAKER 1963); RICHARDSON 1995: 125 (references); LINARES & VERA 2012: 194.

**Material.** Norte de Santander, Cúcuta, Hno. Nicéforo María leg., 1936 (ANSP, lectotype, two paralectotypes ANSP 466281); Santander, Piedecuesta, Inspección de Policía Pescadero, 3 km on trail Cespitá, border of Rio Chicamocha, 500 m, E. Linares leg., 2.xii.1997 (ICNB 3433–3435); Cañón de Chicamocha, near Pescadero, Linares leg. 4.v.1998 (ICNB 714); Ibidem, 600–700 m, S. Obando leg., xi.2001 (ICNB n.c.); Pamplona, Hno. Nicéforo María leg. (MLS-BOG 610 [partim]); approx. 15 km S of Málaga, Río Servitá valley, ca.1800 m [*sic*, 1150 m], A.S.H. Breure leg., 1975 (RMNH n.c.). ?, Bogotá (DMNH 183909).

**Altitudinal range.** Precise localities are in the range 350–1150 m.

**Ecology.** Recorded from Magdalena Valley and Cordillera Oriental montane forests ecoregions. The species occurs in arid habitats among species of *Lippia* (Verbenaceae), *Stenocereus* (Cactaceae) and *Prosopis* (Fabaceae).

**Remarks.** The colouration and shape of this species is somewhat variable. Within a single population, specimens may show interruptions in the colour bands to different degrees; within the same region specimens may also vary in shell elongation. In contrast, the sculpture of (slightly) oblique axial elements appears to be constant within the material studied.

### ***Drymaeus (Mesembrinus) fidustus* (Reeve, 1849)**

Figs 19E, 27A

*Bulimus fidustus* REEVE 1849 [1848–1850]: pl. 76 fig. 557. Type locality: “New Granada, Sebundoi”. Lectotype NHMUK 1975517 (BREURE 1979).

*Drymaeus fidustus* (Reeve); RICHARDSON 1995: 126 (references); LINARES & VERA 2012: 194; BREURE & ABLETT 2014: 75, figs 23G–H, L23i.

**Material.** Putumayo, Sibundoy (NHMUK, lectotype; one paralectotype, NHMUK 1975518).

**Remarks.** Although the type locality is sufficiently precise to suggest a southern Colombian-Ecuadorian distribution, no additional material is available for corroboration.

### ***Drymaeus (Mesembrinus) gorgonensis* Haas, 1966**

Figs 17K–M, 27A

*Drymaeus gorgonensis* HAAS 1966: 233, fig. 49. Type locality: Dept. Cauca, Island of Gorgona. Holotype FMNH 114164; RICHARDSON 1995: 130 (references); LINARES & VERA 2012: 195.

**Material.** Cauca, Island of Gorgona, “northern part of the island, near camp” [03°N 78°11’W], F. Medem leg., 1961 (FMNH, holotype).

**Remarks.** Known only from the type material. The maximum elevation in Gorgona Island in ~330 m; the northern part is lower; most of the island is covered in native, rain forest. No species similar to *D. gorgonensis* have been found in the mainland of Colombia.

***Drymaeus (Mesembrinus) interruptus (Preston, 1909)\*\****

Figs 19C–D, 26B

*Bulimulus (Drymaeus) interruptus* PRESTON 1909: 511, pl. 10 fig. 1. Type locality: Merida, Venezuela. Lectotype NHMUK 1914.4.3.38 (BREURE 1979).

*Drymaeus interruptus*; RICHARDSON 1955: 132 (references); BREURE & ABLETT 2014: 96, figs 18A–B, L29iii.

*Bulimulus (Drymaeus) interruptus pallidus* PRESTON 1909: 511, pl. 10 fig. 2. Type locality: Merida, Venezuela. Lectotype NHMUK 1914.4.3.41 (BREURE & ABLETT 2015: 62).

**Material.** Cesar, Pueblo Bello, San Sebastian de Rabago, 1950 m, F.J. Borrero et al. leg. 13.vii.2010 (USDA 144876, 144880); Ibidem, 1925 m (USDA 144881); Ibidem, 1943–1993 m (CMC C14236). **Venezuela**, Merida (NHMUK, lectotype of *D. interruptus*; ANSP 98092, paralectotype); Ibidem (NHMUK, lectotype of *D.i. pallidus*; ANSP 98100, paralectotype); Ibidem, ex Fulton (USNM 530523); Ibidem, road Quebrada La Sucia to Jají, 1700 m, O.Ravello leg., iii.2015 (FEM 181794–181795, 198495, 198497).

**Altitudinal range.** The Colombian localities are in the range 1925–~2000 m.

**Ecology.** In Colombia this species occurs in the Santa Marta montane forests ecoregion. Observed live on fique plants (*Furcraea* sp., Asparagaceae), and on fences along an unpaved road, up to 3 m from ground.

**Remarks.** This is the first record of this species from Colombia. Two of the colour morphs distinguished by Preston were found sympatrically. This species is similar to, and shares part of the range of *Drymaeus (Mesembrinus) fasciarum*. *D. interruptus* can sometimes be distinguished by the presence of a reddish-brown band around the umbilicus, present in the two colour forms observed in the Cesar samples. However, the lectotype of *D. interruptus pallidus* (Preston) does not have this reddish band; further, a sample from near Jají (five specimens) included two light-coloured shells without the basal colour band, but with very faint concentric squared markings of similar disposition as in other specimens of the nominal form. *D. interruptus* is also very similar to *D. depictus* (Reeve), with which it shares part of its known distribution between Venezuela and Colombia. Additional material of these, and of seemingly related taxa from the region (i.e. *D. depictus*, *D. fasciarum*, *D. granadensis*, and *D. interruptus*), suitable for anatomy and molecular analysis, would be necessary to further ascertain their relations.

***Drymaeus (Mesembrinus) iris (Piaget, 1914)***

Figs 19L–M, 27A

*Leiostracus studeri iris* PIAGET 1914: 261, pl. 9 fig. 6. Type locality: Antioquia, El Cairo near [Río] Cauca, 892 m. Holotype MHNN 35.1645.

**Material.** **Antioquia**, Palermo, Hno. L.E. Ordóñez, vii.1977 (MLS-BOG 22.); Medellín, Girardota, Autopista Norte, M.I. Gomez, iv.1997 (UAM n.c.); near Medellín, Hno. Daniel leg. (USNM 424795); El Cairo (MHNN, holotype); **Caldas**, Marmato, T. Bland leg., ex C.B. Adams (MCZ 154055); **Cauca**, Timba, R. Contreras, i.1979 (UVZ 8175); Santander de Quilichao, A.E. Baca, 15.v.1987 (UVZ 97038); “Cauca, Colombia” (NHMUK 1909.4.26.12); **Risaralda**, Puerto Caldas, Parque de los Nevados, 1000 m, O. Rángel, 1981 (ICNB 0099); **Valle del Cauca**, along via Cali-La Buitrera, Corr. La Buitrera, 1258 m, F.J. Borrero & T. Pearce leg., 6.vii.2013 (USDA 144893); Vereda El Vergel, along road Ansermanuevo-El Aguila, 1012 m, Borrero and Pearce leg., 20.vii.2010 (USDA 144842); Club de Golf Los Andes, km 35 road Cali–Popayán, Borrero leg., 2008 (USDA 144843); Cali, Menga, 950 m, Juan de Roux leg., v.2017 (JMR); Cali, Barrio Santa Teresita, Carrera 2A Oeste #12–111, 1064 m, G. Kattan leg., 2.viii.2008 (USDA 144844); Ibidem, xii.2006 (GK); Ibidem, 2009 (USDA 144866); Jamundí, 1050 m, A. Salazar leg., vi.1968 (MLS-BOG n.c.); Cali, Vivero Meléndez, i.1979 (UVZ 8181); Ibidem, along Avenida Guadalupe, 1000 m, Borrero leg. 4.vi.1982 (UVZ 82162); Ibidem, C. Restrepo, 3.i.1984 (UVZ 84004); Palmira, Potrerillo, i.1979 (UVZ 8178); near Palmira, vi.2014 (FEM 143128–143131); near Felidia, A. Velasco leg., viii.1982 (UVZ 82204); Timba, Hacienda La Arabia, R. Contreras leg., 1980 (UVZ 8179); La Paila, ca. 1000 m, 29.xi.1979 (UVZ 8174, 8180); Yotoco, Reserva Forestal de Yotoco, 1400–1600 m, i.1977 (UVZ 8177); between Cartago and Ansermanuevo, Hacienda Formosa, ca. 1300 m, C. Restrepo and M. Giraldo leg., iii.1982 (UVZ 82041); Ibidem, xi.1981 (UVZ 81273); Ansermanuevo, Rio Catarina, 1000–1200 m, W. Bolívar leg., 13–16.iii.2005 (UVZ n.c.).

**Altitudinal range.** All records range 1000–1300 m.

**Ecology.** All localities lies in the Cauca Valley dry or montane forests ecoregions. Found alive in an urban bamboo patch (GK), on moss-covered trunks (UVZ 8175), and on sugar-cane and -stems (UVZ 8174).

**Remarks.** This taxon has long remained unrecognised. LINARES & VERA (2012), who followed grouping with Venezuelan *Drymaeus (Mesembrinus) studeri* (L. Pfeiffer, 1847) by RICHARDSON (1995: 207), as an informal synonymisation, state that El Cairo is a location SW of Santa Bárbara. There are six places of this name and two 'El Cairo' listed within Dept. Antioquia in the Geonames gazetteer, but this is likely El Cairo situated at 05° 49' N 075° 36' W. PIAGET (1914) stated he had a single specimen, and compared this taxon with *D. (M.) studeri* from which he said it could be differentiated by the slightly greater size (shell height 26 vs. 25 mm for L. Pfeiffer's type). In our opinion the main differences with L. Pfeiffer's species are the less impressed suture and the last whorl being less convex. He also compared his taxon with *Bulimus primula* Reeve, 1848, stating that it differs by the bands being darker and more numerous, and by the yellow base colour. The lectotype of *D. (M.) primula* (NHMUK 1975478) proves to have more convex whorls; however, it resembles the holotype of *D. (M.) iris* in having a reddish-brown apex. This species is similar in appearance to *Drymaeus rufolineatus* Drouët 1859, from the Guyana Plateau, as per a possible syntype (MNHN), and specimens from Cayenne, Guyana (SIMONE 2006: 142, fig. 472; MASSEMIN *et al.* 2009: pl.6, figs. C–D), in its overall shape, and light colour background with five brown spiral bands. It differs slightly from the latter species in being light yellow in background colour (instead of white or near transparent), and being smaller. A more in-depth study of these three taxa, inclusive of anatomical and molecular research, would be needed to reach a substantiated conclusion about their relationship and systematic position.

***Drymaeus (Mesembrinus) koppeli* (G.B. Sowerby III, 1892)**

Figs 170–S

*Bulimus koppeli* G.B. SOWERBY III 1892: 297, pl. 23 figs 9–12. Type locality: Bogotá. Lectotype NHMUK 1907.11.21.133.

*Drymaeus koppeli* (Sowerby); RICHARDSON 1995: 141 (references); LINARES & VERA 2012: 195; BREURE & ABLETT 2014: 103, figs 24H, L32iv.

**Material.** Cundinamarca, Soacha, El Soche, 2920 m, E. Linares leg., 15.x.2004 (ICNB 10556); ?Cundinamarca, Bogota, ex Sowerby and Fulton (ANSP 78540); Ibidem, ex Clapp ex da Costa (CM 90283); Ibidem, ex Webb (FMNH 31393); Ibidem, ex P.E. Humbert ex Preston (MHNN 35.53); Ibidem, ex Sowerby (NHMUK, lectotype and one paralectotype, 1907.11.21.134); Ibidem, RMNH n.c.); Ibidem (UF 109131); Bogotá, Distrito Especial (UF 109279, 109280 [both not seen]). ?, "Cauca", ex Bryant Walker ex Preston (UMMZ 125084).

**Ecology.** The only locality suitable for georeferencing is located in the Magdalena valley montane forests ecoregion. The actual habitat is unknown.

**Remarks.** Soacha is the first precise locality for this species. The locality "Cauca" of the UMMZ specimen is not assignable to a specific Department, but may be anywhere in the Cauca river valley, including localities not too far from Cundinamarca; this specimen was found labeled as as type of *Bulimulus osculans* Preston, an unpublished name. Some morphological variability was observed, with most specimens having the last whorl slightly saccate below, whereas in other shells, the columella is straighter, so the shell appears more elongated below. Colour variability included presence, and/or absence of axial brown bands, and of brown colour dots at various locations on the shell.

***Drymaeus (Mesembrinus) lacteus* (Lea, 1838)**

Figs 18M, 27A

*Bulimus lacteus* LEA 1838: 65, pl. 23 fig. 109. Type locality: "about 100 miles up the Magdalena River". Lectotype? ANSP 192930 (see Remarks).

*Drymaeus lacteus*; RICHARDSON 1995: 141 (references); LINARES & VERA 2012: 195 [*partim*].

**Material.** Bolívar, tree close to bridge over Río Pechilín, road from Tolviejo to Sincelejo, F. Medem and Velásquez leg., 1964 (FMNH 187575); ?Bolívar/Magdalena, "100 miles up the Magdalena R." [25–75 m elevation], T.R. Peale leg. (ANSP, lectotype?); ?Norte de Santander, Ocaña, M.J. Landauer leg., 1875 (ZMUZ 512283).

**Altitudinal range.** Available information suggests this species occurs at very low altitudes below ~100 m.

**Ecology.** The single precise locality is located in the Guajira-Barranquilla xeric scrub ecoregion. The actual habitat is unknown.

**Remarks.** PILSBRY (1898 [1897–1898]: 303) wrote about *Bulimus lacteus*: "Lea's type was immature", and "The type of *B. lacteus* has been lost from the Lea Collection." Since Lea specifically referred to several specimens, Pilsbry's action constitutes a lectotype selection. However, since Lea gave a single set of measurements, and a figure that is unsuitable to recognise an individual shell, it is unclear which shell is Pilsbry's lectotype. ABBOTT (1955: 125, pl. 4 fig. 1) reported on a specimen (ANSP 192930), considered to be part of the original series, as part

of the purchase of portions of the Titian Peale Collection for the Academy of Natural Sciences, in 1944. This collection contains the types of several Colombian taxa by Lea, including two other species of *Drymaeus*, namely *D. (D.) columbianus* and *D. (M.) pealianus*. The specimen is considered the possible lectotype, but it could be a paralectotype. This remains an enigmatic species, despite the rather precise locality, which is the same as the type locality of *D. columbianus*. The figures of PILSBRY (1898 [1897–1898]: pl. 45 figs 38–39) correspond to two specimens from lot ANSP 25830 (“Venezuela”, ex Swift); they are larger, and one of the figures shows traces of axial streaks, clearly seen in various degrees in all the shells in this lot. The lectotype? (ANSP 192930) does not have the axial colour streaks; this specimen has a broad red-brown colouration at the base of the aperture, also seen in all specimens in lot ANSP 25830. The lectotype? indeed appears to be immature. LINARES & VERA (2012) attributed lot FMNH 117070 to this species; upon verification this proved to be *Drymaeus columbianus* (Lea, 1838). This latter species may be closely related to *D. lacteus* or part of a continuum, but both are known from few specimens at present. Hence additional sampling is needed to come to any further conclusions. The material from FMNH and ZMUZ is tentatively referred to as this species; if conspecific, FMNH 187575 would be the first modern precise locality for this species after the type collection. “Ocaña” (ZMUZ 512283) was used as a vague locality by various authors (*cf.* BORRERO & BREURE 2011: 3) and may not correspond to the actual collection locality.

***Drymaeus (Mesembrinus) laetus* Reeve, 1849**

Fig. 19N

*Bulimus laetus* REEVE 1849 [1848–1850]: pl. 83 fig. 616. Type locality: “New Granada, Sebundoí”. Lectotype NHMUK 1975534 (BREURE 1979).

*Drymaeus laetus* (Reeve); RICHARDSON 1995: 141 (references); LINARES & VERA 2012: 195; BREURE & ABLETT 2014: 104, figs 18E, L32v.

**Material.** Cundinamarca, Soacha, Sitio Tequendama I (CORREAL *et al.* 1977) [see Remarks]; Nariño, Pasto (PILSBRY 1898 [1897–1898]: 245); Putumayo, Sibundoy (NHMUK, lectotype, two paralectotypes NHMUK 1975535); *Ibidem*, L. Taylor leg., 1879 (ZMUZ 512223).

**Ecology.** The type locality lies in the Eastern Cordillera real montane forests ecoregion. The actual habitat is unknown.

**Remarks.** Specimens from aboriginal middens excavated near Bogotá were identified by CORREAL *et al.* (1977) as this taxon; the specimens (ZMA n.c.) are very worn and are partially broken shells, and may or may not be *D. laetus*. However, considering the archaeological context of this material, the actual occurrence of the snails is not certain as they may have been collected elsewhere. PILSBRY (1898 [1897–1898]) gave Pasto as a locality, on the authority of Lehmann, but we have not found any vouchered material. Thus far, the only confirmed locality we have found for this species is the type locality in southern Colombia (Sibundoy), at an elevation of possibly ~ 2000 m. As pointed out by BREURE & ABLETT (2014), the original label with the lectotype has an additional locality, interpreted by these authors as “in Abejónal”. We have re-interpreted this to read “in Abejorral”, but this issue remains unresolved since the only locality we can find with that name is in Antioquia (not southern Colombia), and we did not find any such name in Ecuador. Colour variation was observed within the four known specimens, specifically differences in the width of the white spiral and brown bands, and one of the white bands is obsolete in a paralectotype.

***Drymaeus (Mesembrinus) cf. lividus* (Reeve, 1850)\***

Figs 19O–P

*Bulimus lividus* REEVE 1850 [1848–1850]: pl. 83 fig. 616. Type locality: “Venezuela”. Lectotype NHMUK 1975208 (BREURE 1979).

*Drymaeus lividus* (Reeve); RICHARDSON 1995: 132 (references); BREURE & ABLETT 2014: 112, figs 18C–D, L34ix.

**Material.** Norte de Santander, Ocaña, Landolt leg., 1875 (ZMUZ 512285). Venezuela, [no further locality] (NHMUK, lectotype, two paralectotypes, NHMUK 1975209).

**Remarks.** The ZMUZ specimen is subadult and only tentatively referred to as this species. Whether this species occurs in Colombia remains to be confirmed.

***Drymaeus (Mesembrinus) membranaceus* (Philippi, 1846)**

Figs 17Z–AA

*Bulimus membranaceus* PHILIPPI 1846 [1845–1847]: 126, pl. 5 fig. 2. No type locality given.

*Otostomus venezuelensis* MARTENS 1893 [1890–1901]: 224. Type locality: Mexico, Mirador.

**Material.** **Antioquia**, Frontino, G. Wallis leg., 1875 (ZMUZ 512248); **Bolívar?/Magdalena?**, “Unt. Magdalena” [lower valley of River Magdalena], Wallis leg. (ZMUZ 512247). **Norte de Santander**, Ocaña, Wallis leg., 1875 (ZMUZ 512277), ?, New Granada (ZMUZ 512281).

**Remarks.** This species has been synonymised with *Drymaeus venezuelensis* by PILSBRY (1898 [1897–1898]); the name of this taxon is confusing, as the type was described from Mexico; the location of the type material is unknown. Although several lots were examined, these do not allow us to resolve this issue as no type material of either taxa is known to exist and no additional material resembling this species is available. The precise occurrence in Colombia remains uncertain due to the vague localities given by Wallis (see BORRERO & BREURE (2011: 3) for remarks).

***Drymaeus (Mesembrinus) muliebris* (Reeve, 1849)**

Figs 17H–J, 27B

*Bulimus muliebris* REEVE 1849 [1848–1850]: pl. 81 fig. 598. Type locality: “New Grenada”. Lectotype NHMUK 1879.2.26.251 (BREURE & ABLETT 2014).

*Drymaeus muliebris* (Reeve); RICHARDSON 1995: 152 (references); LINARES & VERA 2012: 197; BREURE & ABLETT 2014: 127, figs 18K–L, L39iii.

**Material.** **Santander**, Los Santos, El Barbosa, J.L. Fernández, 22.ix.2004 (ICNB n.c.); Cañón de Chicamocha, near Pescadero, E. Linares leg., 4.v.1998 (ICNB 715); ?, Andes of Colombia (PILSBRY 1898 [1897–1898]); Colombia, ex Cuming (NHMUK n.c.); New Granada, E.J. Penny leg., 1862 (ANSP 25757); Ibidem (lectotype NHMUK).

**Remarks.** These are the first precise records for this species from Colombia. The specimen ICNB 715 is tentatively referred to as this species.

***Drymaeus (Mesembrinus) multilineatus* (Say, 1825)**

Figs 17T–W

*Bulimus multilineatus* SAY 1825: 120. Type locality: [U.S.A.] southern part of East Florida.

*Drymaeus multilineatus* (Say); RICHARDSON 1995: 154 (references, synonymy); PÉREZ & LÓPEZ 2003: 413; LINARES & VERA 2012: 197.

*Bulimus parvus* LEA 1838: 84, pl. 23 fig. 96. Type locality: near Carthagen. Holotype USNM 105077.

*Drymaeus parvus* (Lea); LINARES & VERA 2012: 198.

*Bulimus menkei* GRÜNER 1841: 277, pl. 11 fig. 2. Type locality: Venezuela, Orinoco. Probable syntype ZMB 10285 (KÖHLER 2007: 151, fig. 124).

*Bulimus andicola* L. PFEIFFER 1847: 115. Type locality: Andes of Colombia. Lectotype NHMUK 1975315 (BREURE 1979). **Synon.n.**

*Drymaeus andicola* (L. Pfeiffer); RICHARDSON 1995: 98 (references); LINARES & VERA 2012: 193; BREURE & ABLETT 2014: 18, figs 23A, L4iv.

*Bulimus sisalensis* MORELET 1849: 9. Type locality: Mexico, Yucatan, Sisal. Lectotype MNHN-IM-2000-28111 (BREURE 1975); BREURE & ABLETT 2014: 180, figs 24G, L55iii; BREURE *et al.* 2018: 432, fig. 1054.

**Material.** **Atlántico**, Barranquilla, T. Bland leg., 1857 (ANSP 25901); Savanilla [= Sabanilla] (PILSBRY 1899: 27); **Bolívar**, Cartagena, Gibbon leg., ex Lea (USNM, holotype of *Bulimus parvus*); Ibidem, San Juan, on secondary forest, leg. iv.2006 (FEM 44187, 72044); **Cesar**, near Valledupar, Barker leg. (FMNH 109677); Rio Cesar valley, O.L. Haught leg. (USNM 538061); 5 km N Becerril, along Quebrada Boquete, Haught leg. (USNM 599484); near Codazzi, 100–300 m, Haught, x.1943 leg. (USNM 599508); **La Guajira**, Rancheria, NE Magdalena, A.A. Olsson leg. (ANSP 184063); Uribia, H.B. Baker leg. (ANSP 342342); 2 km S Rio Hacha, Baker, i.1937 (ANSP 342345); near Carraipía, Haught leg. (USNM 543486); **Magdalena**, Bonda, 150 ft., H.H. Smith leg., 1900 (ANSP 79793); Bonda, 150 ft. [~45 m], dry forests, on trees, Smith leg., 1899 (CM 90281); Bonda, 150 ft., 8 miles SE Station Santa Marta, Smith leg., viii.1908 (CM 90282); Ibidem, ex Clapp ex Henderson (USNM 307434); Santa Marta, Las Tinajas area, Finca Kalashe, 139 m, F.J. Borrero and T. Pearce leg., 10.vii.2010 (USDA 144848); Bahía Concha, hills with cacti and thorny bushes, Borrero leg., vii.2008 (USDA 144849); Santa Marta, Vereda Mosquito, Reverva La Iguana Verde, 110 m, Borrero *et al.* leg., 11.vii.2010 (USDA 144850); Ibidem, above La Iguana Verde, 270 m, Borrero *et al.* leg., 30.vi.2013 (USDA 144883); Tayrona, near Santa Marta, leg. vii.2014 (FEM 143143); Santa Marta, Vereda El Campano, Minca, Hacienda La Victoria, V. Perez leg. 18.x.2007 (ICNB n.c.); near Santa Marta, Smith leg. (UF 109323); Bahía de Neguange, K.-J. Götting leg., 1976–1978 (GÖTTING 1978); between Santa Marta and El Rodadero (SMF 245414); between Santa Marta and Ciénaga (SMF 245415) (both BREURE 1977); Riofrio, H. Pittier leg., 1906 (USNM 192905). **Venezuela**, Puerto Cabello, ex Parreys (ZMUZ 512407). ?, San Juan, M. Smith leg. (ANSP 323495);

Colombia, C.M. Yoden leg., 1976 (CM 73989); “Andes of Columbia”, ex Cuming (NHMUK, lectotype of *Bulimus andicola*); Colombia, ex Cuming (NHMUK n.c.); Bogota (NHMUK n.c.); Ibidem, L. Taylor leg., 1879 (ZMUZ 512297); Bolivia, ex Bryant Walker ex Geret (UMMZ 123300); Angostura (ZMB, probable syntype of *Bulimus menkei*).

**Altitudinal range.** Recorded from localities up to ~ 300 m.

**Ecology.** The Colombian localities are situated in the Guajira-Barranquilla xeric scrub and Sinú Valley dry forests ecoregions. The species has been found on trees and in secondary forests.

**Remarks.** This taxon has one of the widest geographical distributions among species of the genus *Drymaeus*, extending from the USA (Florida), to northern South America (Colombia and Venezuela) and several Caribbean islands. Say's original material of *Bulimus multilineatus* has not been located; PILSBRY (1946: 27) designated a specimen at ANSP as a neotype, however it does not satisfying the current requirements of the ICZN, 4th edition (1999). This species exhibits substantial colour variation, particularly in the presence and strength of black and reddish-brown bands and stripes, and the colour band around the umbilical area; a few specimens are nearly white, and some very dark.

### *Drymaeus (Mesembrinus) niceforonis* Pilsbry, 1939

Figs 18J–L

*Drymaeus niceforonis* PILSBRY 1939: 4, figs 3–4. Type locality: Santa Librada. Holotype ANSP 170697; RICHARDSON 1995: 156 (references); LINARES & VERA 2012: 197.

**Material. Norte de Santander,** Santa Librada, Hno. Nicéforo María leg., 1938 (ANSP, holotype; ANSP 462280, paralectotype).

**Remarks.** LINARES & VERA (2012: 186, 197) argued that Santa Librada may correspond to a location in the region of Sarare, Norte de Santander, at an elevation of ~ 750 m, with which we concur. No additional material has been located since the type collection. The unique morphology and colouration of this species separates it readily from all other Colombian *Drymaeus*.

### *Drymaeus (Mesembrinus) nigrofasciatus* (L. Pfeiffer, 1846)

Figs 19Q–S, 27B

*Bulimus nigrofasciatus* L. Pfeiffer in PHILIPPI 1846 [1845–1847]: 125, pl. 5 fig. 7. Type locality: “Novae Granadae, vallis Magdalenae”. Lectotype, “largest specimen in lot NHMUK 1975542” (BREURE & ABLETT 2014).

*Drymaeus nigrofasciatus* (L. Pfeiffer); RICHARDSON 1995: 157 (references); LINARES & VERA 2012: 198 [partim]; BREURE & ABLETT 2014: 131, figs 21]. L40v–vi.

*Drymaeus nigrofasciatus elongatulus* PILSBRY 1898 [1897–1898]: 307, pl. 50 fig. 100. No type locality given. Lectotype ANSP 4346 (H.B. BAKER 1963).

**Material. Boyacá,** Alto de Vereá–Suscón, about 7 km NW Sogamoso, 2850 m, A.A. Olsson leg., 1935 (FMNH 166114); [without further locality data], Hno. Roque Caselles leg., xii.1965 (MLS-BOG 591, 593); **Cundinamarca,** Gachetá, A. Infante leg. (AI, JG); Guavio, La Calera, La Siberia, 2780 m, Infante leg. 5.xii.2002 (AI); La Calera, just NE of Bogotá, O.L. Haught leg. (FMNH 72764); Laguna de Hernández, Sabana de Bogotá, F. Medem leg., 1958 (FMNH 114080); Ubaté, Carvajal leg., 1958 (FMNH 115897); Suba (FMNH 187577); Mosquera, La Herrera, 2580 m, M.L. Vera leg., 1.ii.2003 (ICNB 1144); Ibidem, Laguna de La Herrera, M. Bueno leg., 24.vii.1981 (ICNB 0107); Ibidem, Jaramillo leg., 18.ix.1979 (ICNB 0118); Suba, La Conejera, C. and G. Diaz, 14.i.1981 (ICNB 0120); Suesca, Vereda Susatá, Hacienda Susatá, 2700 m, vii.2000 (ICNB n.c.); Nemocón, Rio Chucua, 2700 m, Linares leg., 12.vi.1998 (ICNB 3494); Fúquene, Capellanía (JMR); Ibidem, G. Losano leg., 1.i.2001 (ICNB n.c.); Bogotá, Yomasa, Hno. Apolinar María leg. (MCZ 192450); Soacha, km 1, variante Soacha (MLS-BOG n.c.); Suba (MLS 585 [partim]); Gachetá (RMNH n.c.); Chingaza (UMB n.c.); La Calera, NE Bogotá, Haught leg. (USNM 488853); Mosquera: arid SW slope with sandstone rocks and *Opuntia* at the shore of Laguna de La Herrera SW of near quarry, 2610 m, B. Hausdorf leg., 2000 (ZMH 4002 [not seen]); Soacha, Hacienda Tequendama, T. van der Hammen and G. Correal leg. (ZMA n.c.; CORREAL *et al.* 1977); Facativá, Petersen leg. 1878 (ZMUZ 512304, 512367); ?**Cundinamarca,** Bogotá, Distrito Especial (UF 109325, 109326, 161271); Bogotá, ex MacAndrew (NHMUK 1891.10.6.1–5); Ibidem (CM 42.422; FMNH 77560, 102483; RBINS n.c.; RMNH n.c.; USNM 713046; ZMH 7320); **Santander,** Capitanejo, 1300 m, Acosta leg., 1960 (FMNH 114081). ?, New Grenada [locality data degraded], Seymour leg. (ANSP, lectotype of *D. n. elongatulus*, two paralectotypes ANSP 451947; New Granada (ANSP 25834); Ibidem, ex Morelet (MCZ n.c.); Colombia, V. Sterki leg. (CM 62.28101); Columbia (ANSP 217109); Colombia, ex Hinkley (INHS Z21027); Ibidem, Hno. Apolinar María leg. (MCZ n.c.). **Ecuador,** W. Reiss leg., 1877 (ZMUZ 512303); **Venezuela,** ex Cuming (ZMUZ 512302).

**Altitudinal range.** Records are in the range of ~ 2500–2850 m.

**Ecology.** Precise localities are in the Magdalena Valley and Cordillera Oriental montane forests ecoregions. Found dead among *Verbena* sp. (Verbenaceae) in subxerofytic, rocky habitats (ICNB 1144); found live on bushes (ICNB 1020); found among a Rhamnaceae species (ICNB 3494).

**Remarks.** This species has been misinterpreted to some extent, mainly by the inclusion of specimens of other, as yet unrecognised, taxa. Comparison with the type material leads us to believe that only material from Boyacá, Cundinamarca and Santander (as listed above) agree well with the type specimens examined in the NHM collection. Although substantial variation in colour can be observed among *D. nigrofasciatus*, including few specimens with mostly white shells and little to no dark bands, as well as the typical darkly banded shells, there may also be other morphologically similar species involved. For instance, specimens from southwestern Colombia have colour bands that are less wide, are generally lighter in colouration, and exhibit a different sculpture (see *Drymaeus (Mesembrinus)* species 6, *q.v.*). Also in northern Colombia (Cesar, see *Drymaeus (Mesembrinus)* species 5, *q.v.*) specimens are also lighter in colouration, and have a different shape; we do not consider these conspecific with *D. nigrofasciatus*. The record from Chocó (ICNB 1784) has to be regarded with suspicion, as it is well outside the range of the species. *Drymaeus nigrofasciatus elongatulus* falls within the variation shown by this species. The form was reported from “Tequendano, Ecuador” on the authority of Strebel by PILSBRY (1898 [1897–1898]: 308). This is apparently an error for Tequendama in Cundinamarca. It is possible that this report was based on one lot (ZMUZ 512303, ex Mousson), collected by Reiss in 1877, which is labelled “Ecuador”. We consider this as probably mislabelled, since Ecuador is well outside the range of the species. Similarly, we consider the locality of lot FMNH 114083 (“Venezuela”), and ZMUZ 512302 (“Venezuela”, ex Cuming 1855) as incorrect.

### ***Drymaeus (Mesembrinus) roseatus montanus* Pilsbry, 1901**

Figs 17D–G

*Drymaeus roseatus montanus* PILSBRY 1901 [1901–1902]: 161, pl. 48 fig. 51. Type locality: Colombia, western part of Santa Marta Mountains, Las Pantidas, about 4000 ft. Elevation. Lectotype CM 46614 (**design.n.**); RICHARDSON 1995: 133 (references); LINARES & VERA 2012: 199 (as *Drymaeus roseatus* (Reeve, 1848)).

**Material. Magdalena,** Las Pantidas [sic, Partidas], western part of Sierra Nevada de Santa Marta, ~ 4,000 feet [1,200 meters], H.H. Smith leg., 1900 (CM 46614, lectotype).

**Remarks.** The type locality of the nominate subspecies, *Drymaeus (M.) roseatus roseatus* (Reeve, 1848) is Venezuela, but it is also known from Brazil (SIMONE 2006). There is a lot under this name from “Andes of New Granada” in the Cuming collection (NHM), which we consider misidentified. Due to lack of sufficient material, it remains unclear whether the two forms are indeed conspecific, although we are inclined to consider Pilsbry’s taxon as a separate species. PILSBRY (1901 [1901–1902]) did not select a type specimen, nor did he indicated the number of specimens he used in his description; although it is likely that the only specimen available to him was the single specimen now at the Carnegie Museum, this is not clear from his writing. CM 46614 matches well the figured specimen, but only imperfectly the measurements given by Pilsbry (height to within 0.2, diameter to within 2.4 mm). To stabilise this ill-understood taxon we now designate this specimen as the lectotype.

### ***Drymaeus (Mesembrinus) rufescens pinchoti* Pilsbry, 1930**

Figs 18G–I

*Drymaeus rufescens pinchoti* PILSBRY 1930: 252 pl. 18 figs 13–24. Type locality: Isla de Providencia, 800 m inland from Bahía Suroeste. Holotype ANSP 150852; RICHARDSON 1995: 172 (as *Drymaeus rufescens* (Gray, 1825)); KÖHLER 2007: 152, fig. 130; LINARES & VERA 2012: 199 (as *Drymaeus rufescens* (Gray, 1825)).

**Material. San Andrés y Providencia,** Providence Isld., ½ mi. inland from Southwest Bay, H.A. Pilsbry leg., 1929 (ANSP, holotype); Providencia Isld. (13°30N 081°30W), Emberton leg., 1987 (ANSP A121261); Providencia, Southwest Harbor (DMNH 164079); Saddle between Split Hill [Alto Peña Rajada] and next peak, Pilsbry leg., iv.1929 (DMNH 007344, 026872, 030138, 135067); Ibidem, Barbour *et al.* leg., 1931 (DMNH 164080); Providencia Isld., mount back of [Santa] Isabel, Pilsbry leg., 1929 (FMNH 78770); Saddle near Split Hill (FMNH 146662); Hills near center of island, Gilbert *et al.* leg., 1971 (UF 176978); Manchioneel Hill, Geister leg., 1970 (UF 176977); Providencia Isld., Ebel leg., 1998 (UF 271152, 271153); Providence Island, Pilsbry leg., 1929 (ZMB 79213, paratypes).

**Altitudinal range.** The maximum elevation on Providencia Island is ~360 m.

**Ecology.** Found on trunks of smooth-barked, greenwood trees, primarily Cockspur (UF 176977); on ‘Cockspur’ (*Acacia*), one [specimen] on bromeliad (ANSP A121261).

**Remarks.** The nominate species occurs on Jamaica and the relationship with the Providence Island taxon may need further study.



***Drymaeus (Mesembrinus) semifasciatus (Mousson, 1869)***

Figs 19T–V, 27A

*Bulimus semifasciatus* MOUSSON 1869: 175. No type locality given. Lectotype ZMUZ 512301 (BREURE 1976).  
*Drymaeus semifasciatus* (Mousson); RICHARDSON 1995: 175 (references); LINARES & VERA 2012: 199 [partim].

**Material.** Putumayo, Puerto Asis, 2200 m [sic, 220 m?], leg., 2007 (FEM 46810). ?, “Kolumbia”, G. Wallis leg., 1869 (ZMUZ, lectotype); Maranhon, Müller leg., 1869 (ZMUZ 512298).

**Remarks.** Although the specimen that was listed on the Femorale website could only be judged by its photograph, its locality (M. Coltro, pers. commun.) leaves no doubt about the region where this species occurs. It is the first precise record for Colombia but the altitude given is wrong as Puerto Asis is at ~250 m elevation. Lot FMNH 3378, attributed by Linares & Vera (2012: 199) to this species [and also to *D. (M.) signifer* on p. 200], is considered unassignable (see below), but it certainly is not *D. semifasciatus*.

***Drymaeus (Mesembrinus) semimaculatus Pilsbry, 1898***

Figs 17AB–AC, 27B

*Drymaeus semimaculatus* PILSBRY 1898 [1897–1898]: 297. New name for *Bulimus maculatus* Lea 1838 not Bruguière, 1789. Type locality: near Carthagen. Syntypes USNM 105153; RICHARDSON 1995: 175 (references, synonymy); LINARES & VERA 2012: 196 (as *Drymaeus maculatus* (Lea, 1839 [sic]) [partim]).

**Material.** Bolívar, near Cartagena (USNM, syntypes); Ibidem, ex Anthony (MCZ 64731); Casanare, Caño Garzón, S. Renjifo leg., iv.1946 (MCZ 177963); Cundinamarca, Tocaima, Jaramillo leg. (MCZ 177982); La Guajira, 18 km SW Carraipía, Quebrada Paradero, 100–200 m, O.L. Haught leg., 1943 (USNM 599644); Sierra Perijá, above Airoca [?], 6000 ft. [~1830 m], M.A. Carriker jr. leg. (USNM 488790); near Becerril, Quebrada Boquete (USNM 599489); Tolima, Alvarado, 310 m, O. Rangel leg., vi.1980 (ICNB 0122). Panama, Canal Zone, Barro Colourado Island, J. Zetek leg., 20.ii.1942 (DMNH 164045); Ibidem, ex Jackson (FMNH 63681); Ibidem, G.B. Fairchild leg., 9.ii.1939 (MCZ 100645); Prov. Panama, Arraiján, Rio Caseres, Finca Bergerón, E.S. Bergerón leg., 10.x.1961 (FMNH 126949). ? Colombia, ex Cuming (NHMUK n.c.).

**Ecology.** The records for this species are situated in Guajira-Barranquilla xeric scrub, Sinú Valley dry forests, and Llanos ecoregions. The actual habitat is unknown.

**Remarks.** This species appears to be limited in distribution within Colombia to generally low elevations, with two exceptions (FMNH 187576, and USNM 488790). It has been reported from Guatemala, Nicaragua, Costa Rica and Panama (Thompson 2011); we have evaluated some lots from the latter country, but its occurrence in the other countries remain to be confirmed with the type material. The lot from Tocaima (MCZ 177982) is identified as this species but we doubt if its collecting locality is correct as the altitude is far outside the known range (therefore not included in the distribution map). Lots ICNB 0122, and FMNH 126949 are tentatively placed here; the latter is a juvenile. LINARES & VERA (2012) overlooked the new name introduced by PILSBRY 1898 [1897–1898] to solve the homonymy of *Bulimus maculatus* Lea, 1838.

***Drymaeus (Mesembrinus) tenuilabris (L. Pfeiffer, 1866)***

Figs 17X–Y, 27B

*Bulimus tenuilabris* L. PFEIFFER 1866: 831. Type locality: Venezuela. Lectotype NHMUK 197538 (BREURE 1979).  
*Drymaeus tenuilabris* (L. Pfeiffer); RICHARDSON 1995: 183 (references); LINARES & VERA 2012: 200; BREURE & ABLETT 2014: 190, figs 21F, L59ii.

**Material.** Antioquia, Sonsón, G. Wallis leg., 1875 (ZMUZ 512267); Cesar, Pueblo Bello, next to Rio Ariguani, 1125 m, F.J. Borrero and T. Pearce leg., 14.vii.2010 (USDA 144851); El Roncón, 10–12 km E Becerril, foothills of Sierra de Perijá, 200–300 m, B. Malkin leg., 15–22.ix.1969 (FMNH 173009); Cundinamarca, Rd. Girardot to Bogotá, A.A. Olsson leg. 1935 (ANSP 166140 partim); Chinauta (JMR); Norte de Santander, Ocaña, Wessel leg., ex Webb ex ZMB (FMNH 31388); Ibidem, Wallis leg., 1875 (ZMUZ 512263); Ibidem, Landolt leg., 1875 (ZMUZ 512264–512265); Ibidem, Wallis leg., 1875 (ZMUZ 512266).

**Remarks.** PILSBRY (1898 [1897–1898]: 310) based his work on MOUSSON (1869) for the Colombian record from “Lower Magdalena”. All lots mentioned here are tentatively referred to as this species. Remarkably constant in shape, size, and shine among adult shells; a varied range of colourations was observed, including spiral bands of variable width, axial streaks, and absence of banding on variable colour background.

***Drymaeus (Mesembrinus) tribalteatus* (Reeve, 1848)**

Figs 19I–K

*Bulimus tribalteatus* REEVE 1848 [1848–1850]: pl. 43 fig. 269. Type locality: “Santa Fé de Bogotá”.*Drymaeus tribalteatus* (Reeve); RICHARDSON 1995: 186 (references); LINARES & VERA 2012: 201.**Material.** ?, New Granada, Colombia, L. Taylor leg., 1879 (ZMUZ 512289).**Remarks.** The ZMUZ material is the only lot that we, tentatively, can refer to this species. LINARES & VERA (2012) give the locality Dept. Putumayo, Santiago, without voucher information; this location seems to be based on PILSBRY (1898 [1897–1898]: 246), who quoted it on the authority of Dunker. The precise occurrence of this species in Colombia still has to be confirmed. An additional subadult specimen was collected from Nariño (Piedrancha Chucunés, La Planada, 1800 m, Linares leg., 26.iii.1995 (ICNB 2850, see *D. (M.)* species 3 below), if correctly identified by us, it would lend support to the notion that this taxon occurs in southern Colombia.**Morphospecies****Remarks.** The following morphospecies are not described; see the remarks for each for more details.***Drymaeus (Mesembrinus) species 1***

Figs 20A–B

**Material.** Magdalena, between Ciénaga and Aracataca, 281 m, F.J. Borrero leg., 30.vii.2008 (USDA 144852–3).**Remarks.** This species could not be matched to any of the above species, but further material is needed to reach a final conclusion.***Drymaeus (Mesembrinus) species 2***

Figs 20C–D

**Material.** Santander, Suaita, Inspección San José de Suaita, Sector Flandes, Finca Marbella, ca. 2000 m, S. Albesiano leg., 21.iii.2004 (ICNB n.c.).**Remarks.** The single 40hell found resembles very much the previous morphospecies.***Drymaeus (Mesembrinus) species 3***

Figs 20E–F

**Material.** Nariño, Piedrancha Chucunés, La Planada, 1800 m, E. Linares leg., 26.iii.1995 (ICNB 2850).**Remarks.** This specimen resembles *D. (M.) tribalteatus* Reeve, 1848. However, we refrain from assigning it to that species, on account of being a single subadult, somewhat broken shell.***Drymaeus (Mesembrinus) species 4***

Figs 20G–H

**Material.** Antioquia, Frontino, G. Wallis leg., 1869 (ZMUZ 512274); Cesar, Socorpa Mission area, Sierra de Perijá, 1300 m, B. Malkin leg., 22.vii.1968 (FMNH 187585); Ibidem, Finca San José, 1500–1600 m, Malkin leg., 15–17.viii.1968 (FMNH 187597); Rio Cesar valley, low altitudes, viii.1938, O.L. Haught leg. (USNM 534074); ?Magdalena, “Unit Magdalena” [= Lower Magdalena valley], Wallis leg., 1869 (ZMUZ 512273); Norte de Santander, Ocaña, La Pradera, M. Calle leg., vii.1971 (ICNB 0195); Guamalitos, 1500–2000 ft. [~470–610 m], M.A. Carriker leg. (USNM 517809); Ocaña, Wallis leg., 1875 (ZMUZ 512269 [*partim*]).**Remarks.** This morphospecies resembles the Venezuelan *Drymaeus (Mesembrinus) studeri* (L. Pfeiffer, 1847), of which we have examined the type material in NHMUK (BREURE & ABLETT 2014: 185, figs 180–P). The material listed above is relatively constant in shell shape and colour pattern; it differs from the type by having smaller spiral bands, the suture more impressed and having the columellar margin less dilated than most material listed above. These differences, however, are only small in comparison with the infraspecific variation known to exist in some *Drymaeus* species, and it cannot be excluded that at least part of the material listed from Colombia may prove to fall within the range of variation once more material of *D. studeri* from western Venezuela becomes known.

***Drymaeus (Mesembrinus) species 5***

Fig. 20I

**Material.** Valle del Cauca, Serranía de Paraguas, El Cairo, Vereda Las Amarillas, W. Bolivar, 2220–2460 m, 20–21.ix.1996 (UVZ n.c.).

**Remarks.** Only a single shell has been found, which is broken at the basal part of the last whorl. However, it differs from anything else we have seen. It appears to have a thin white line lining the suture.

***Drymaeus (Mesembrinus) species 6***

Figs 20J–K

**Material.** Valle del Cauca, Cali, Parcelación Miravalle, ca. 1087 m, F.J. Borrero leg., 11.viii.2009 (USDA 144845); Calima-Darién, near Lago Calima, trail to Campo Alegre, Zona Las Campanas, 1300 m, Borrero leg., 6.ix.1979 (UVZ 82068); La Paila, ca. 1000 m, 26.xi.1979 (UVZ 8107). ?, [no locality data] G. Kattan leg. (GK).

**Remarks.** Besides the figured light yellow morph we have seen material that is darker yellowish in colour. Although this material is unlike any other *Drymaeus* species we have seen from Colombia, we refrain from describing it at present.

**Unassignable lots with useful data**

**Remarks.** The following lots are currently unassignable to any specific *Drymaeus* species. These lots, however, have accurate locality data that may be useful for an analysis of where collecting in Colombia has been done for this genus (see Fig. 1E).

**Cesar**, Pueblo Bello, next to Rio Ariguani, 1125 m, F.J. Borrero and T. Pearce leg., 14.vii.2010 (USDA 144855); Sierra de Perijá, trail El Roncón, Finca San José, 10–25 km E Becerril, B. Malkin leg., 1969 (FMNH 163702, 173004, 173005, 173007–173011, 173857–173860); 15 km S of Becerril, La Jagua (FMNH 187593, 187600); Socorpa Mission area, Sierra de Perijá [Becerril], Malkin leg., 1968 (FMNH 157906, 187555, 187581, 187602–187604); Ibidem, 1300–1400m, (FMNH 187596).; Valledupar, Malkin leg., 1968 (FMNH 187601); Sierra Nevada de Santa Marta, San Sebastián de Rábago [=Nabusimake], Malkin leg., 1968 (FMNH 157540, 161099); El Pueblito, Parque Nacional Tairona, Malkin and Burchard leg., 1970 (FMNH 187599); La Calera del Cerro Chimichagua, 8.i.2007 (ICNB n.c.); **Chocó**, Acandí, Keep leg. (UF 109122); Riosucio, La Balsa, E. Linares leg., 1.vi.1988 (ICNB 1784); **Córdoba**, Upper Río Uré, tributary of Río San Jorge, Cepeda leg., 1963 (FMNH 187572); **Cundinamarca**, Guavito, Gachetá, Resguardo II, Finca Sastre, 2780 m, A. Infante leg. (AI); region of Medina (ANSP 164571); Las Mercedes, road to Fute, SW slope of Tena, Municipality Bojacá, Camacho leg., 1962 (FMNH 187571); Las Mercedes, road to Fute, S. of Laguna de Herrera at limit of Sabana de Bogotá, 2600–2700m, J. Hernández leg., 1962 (FMNH 187576); Suba, Sabana de Bogotá, Mejía leg., 1962 (FMNH 187577); Vereda Santa Lucia (ICNB 1809); Quebrada Vieja, near Bogota (RZ); Macizo de Sumapaz, 1120 m, T. van der Hammen and A.M. Cleef leg. (SUM 29), 1981 (RMNH n.c.); **Guainía**, Caranocoa, P. Galvez leg. (ICNB n.c.); **Huila**, Altamira, 500 m, xii.1979 (UVZ 8158); **Magdalena**, Mountains near Santa Marta, 3600 ft. [~1100 m], H.H. Smith leg. (UF 109285); road Santa Marta-Riohacha, Vereda Cacaguelito, Borrero and Pearce leg., 2010 (USDA 144856); **La Guajira**, 5–6 km above Manaure, western side of Perijá Range, A.A. Olsson leg., 1943 (ANSP 217537); La Cueva, on old trail from Fonseca to Riohacha, 4000 ft. [~1220 m; erroneous], Carriker jr. leg. (USNM 488801); Serranía Macuira, 1984 (UVZ 84102); **Meta**, Upper Rio Guëjar, Medem leg. (ANSP 196266); Villavicencio, Dybas leg., 23.v.1938 (FMNH 3378); near Villavicencio, Renjifo leg., 18.iii.1946 (MCZ 177967); **Nariño**, Sandoná, Uribe leg. (MCZ 157441); Cúcuta, leg. 2007 (FEM 46920); **Putumayo**, Santa Rosa de Sucumbios, Río San Miguel, Malkin and Burchard leg., 1970 (FMNH 187568); between Alpichaque and San Antonio, Santa Rosa de los Cofanes, below San Antonio del Guamués, trib. of Upper Río Putumayo, LeNestour leg., 1965 (FMNH 187569); **Tolima**, Santa Isabel, Vereda La Pava, Finca La Pavita (ICNB 0102); **Valle del Cauca**, Atuncelo, 9 km N Dagua, 2800 ft. [~850 m], F.G. Thompson leg., 1969 (UF 24412); 3 km W Cisneros, 1500 ft. [~455 m], Thompson leg., 1969 (UF 176762); [El] Carmelo, 1000 ft. [sic, 1000 m], F.G. Thompson leg., 1969 (UF 176964); Venticas del Dagua, Dagua valley, 1000 m, H. Pittier leg., ii.1906 (USNM 251159); Rio Bravo, tributary of Rio Calima, 1150 m, P.A. Silverston leg., i.1982 (UVZ 82031); Estación Agroforestal Bajo Calima, live on Musaceae ('platanillo'), A. Rios, 10.x.1981 (UVZ 81275).

**Unassignable lots, attributed to Colombian species in error.**

**Remarks.** The following lots have been attributed to either Colombian species or species that are listed below as doubtfully or in error for Colombia. We have been unable to identify them to any species known to us.

Bogota (FMNH 77538); Colombia (FMNH 77559); New Granada / Colombia, ex Dorhn (MCZ 57054); Ocaña (ZMUZ 512135); New Granada (ZMUZ 512286)

**Species doubtfully or erroneously recorded from Colombia**

**Remarks.** The following species are listed here as probably erroneous for Colombia or with doubtful localities; they are marked with a dagger (†).

***Stenostylus meleagris* (L. Pfeiffer, 1853)†**

*Bulimus meleagris* L. PFEIFFER 1853b: 157. Type locality: "Andes of Colombia".

*Stenostylus meleagris* (L. Pfeiffer); RICHARDSON 1995: 370 (references); LINARES & VERA 2012: 207.

**Remarks.** This species is only known with precise localities from Peru (BREURE 1978, 2011). As it has not been recorded from Ecuador, the occurrence in Colombia remains doubtful.

***Drymaeus (Drymaeus) attenuatus* (L. Pfeiffer, 1853)†**

*Bulimus attenuatus* L. PFEIFFER 1853b: 256. Type locality: Mexico, Veracruz. Lectotype NHMUK 1975458 (BREURE & ESKENS 1981).

*Drymaeus attenuatus* (L. Pfeiffer); RICHARDSON 1995: 99 (references); LINARES & VERA 2012: 181; BREURE & ABLETT 2014: 24, figs 17F–H, L6vi.

**Material.** Arauca/?Meta, "Villavicencia", M. Medem-Cortez leg., 1975 (USNM 853418) [not seen].

**Remarks.** It is unlikely that this species occurs in Colombia, so it is most likely a misidentification.

***Drymaeus (Drymaeus) chimborasensis* (Reeve, 1848)†**

*Bulimus chimborasensis* REEVE 1848 [1848–1850]: pl. 44 fig. 275. Type locality: Ecuador, Chimborazo. Syntypes NHMUK 1975460.

*Drymaeus chimborasensis* (Reeve); RICHARDSON 1995: 109 (references); LINARES & VERA 2012: 183; BREURE & ABLETT 2014: 43, figs 38A–C, L12v.

**Material.** Ecuador, Chimborazo (NHMUK, syntypes).

**Remarks.** The figure given by Pilsbry (1898 [1897–1898]: pl. 40 fig. 1) is taken from REEVE (1848 [1848–1850]). However, this figure does not match the type material (BREURE & ABLETT 2014). The shells figured from Sitio Tequendama I, Soacha (ZMA; CORREAL *et al.* 1977) and said to be *D. chimborasensis* were misidentified; they are *Drymaeus (D.) convexus* (L. Pfeiffer, 1855). We have seen no other material originating from Colombia that can be referred to *D. chimborasensis*.

***Drymaeus (Drymaeus) edmuelleri* (Albers, 1854)†**

*Bulimus edmuelleri* ALBERS 1854: 218. Type locality: "in Columbia ad fluvium Maranhon". Lectotype ZMB 111929a (KÖHLER 2007).

*Drymaeus edmuelleri* (Albers); SIMONE 2006: 136, fig. 447; KÖHLER 2007: 144, fig. 89.

**Material.** Ecuador, Rio Napo region (MCZ 92321); ?, "Colombia, valley of the Upper Maranhon", ex Pätel ex ZMB (FMNH 31417).

**Remarks.** The Marañon valley is entirely in Peru; however, the downstream part running along southeastern Colombia has erroneously been called "Maranhon" in the past, and this may have added to the confusion of the type locality. The presence of this species in Colombia still needs to be ascertained.

***Drymaeus (Drymaeus) linostoma* (d'Orbigny, 1835)†**

*Helix linostoma* D'ORBIGNY 1835: 19. Type locality: provincia Chiquitensi, republica Boliviana.

**Remarks.** This species has been erroneously listed from Colombia, Marmato by BLAND (1852: 230) on the basis of specimens collected by him. PILSBRY (1898 [1897–1898]: 218) already stated “*D. linostoma* is not known to occur in that country”. Two lots examined by us ZMUZ 512136 (Ocaña, G. Wallis leg., 1875), and ZMUZ 512136 (Frontina, Wallis leg., 1875) are listed as *D. linostoma*, but neither corresponds to this taxon. We consider ZMUZ 512136 as *D. (D.) felix felix* (see above).

***Drymaeus (Drymaeus) membielinus* (Crosse, 1867)†**

*Bulimus membielinus* CROSSE 1867: 445. Type locality: “In Republica Aequatoris”. “Ecuador”, MNCN 15.05/7355, syntype; “Napo” MNCN 15.05/20344, syntype.

*Drymaeus membielinus*; RICHARDSON 1995: 149 (references); LINARES & VERA 2012: 188 [*partim*]; BREURE & ARAUJO 2017: 77, figs 29G–J.

**Remarks.** See also the remarks under *Drymaeus (D.) cognatus* Pilsbry, 1901. The reference to a type at ZMH by LINARES & VERA (2012) is erroneous.

***Drymaeus (Drymaeus) phryne* (L. Pfeiffer, 1863)†**

*Bulimus phryne* L. PFEIFFER 1863: 274. Type locality: Andes of Peru. Lectotype NHMUK 1975214 (BREURE 1979).

*Drymaeus phryne* (L. Pfeiffer); BREURE & ABLETT 2014: 151, figs 39G–I, L46v.

**Remarks.** This species was regarded as a variety of *Drymaeus murrinus* (Reeve, 1848) by PILSBRY (1898 [1897–1898]: 215), while he noted “Mr. DaCosta states that this is not separable from *B. murrinus* Reeve”. Studying both type specimens in the NHMUK, we disagree and consider this a distinct (Peruvian) species, which may bear more external similarity with *Drymaeus convexus* L. Pfeiffer 1855, than with *D. murrinus*.

***Drymaeus (Drymaeus) poecilus* (d'Orbigny, 1835)†**

*Helix poecila* D'ORBIGNY 1835: 11. Type locality: Bolivia, Dept. Santa Cruz, around Pampa Grande (BREURE 1973). Syntypes MNHN-IM-2000-24675–24679.

*Drymaeus poecilus* (d'Orbigny); RICHARDSON 1995: 163 (references); LINARES & VERA 2012: 189; BREURE & ABLETT 2014: 153, figs 45M–N, L47iii.

**Material.** ?, “Columbia [locality data degraded]”, ex J. Jeanes (ANSP 25824).

**Remarks.** This is an easily recognisable species, ranging from southern Brazil through Paraguay and Bolivia into northern Argentina (SIMONE 2006: 141). It is highly unlikely that it occurs in Colombia so the locality with the ANSP specimen must be in error.

***Drymaeus (Drymaeus) protractus* (L. Pfeiffer, 1855)†**

*Bulimus protractus* L. PFEIFFER 1855d: 94, pl. 34 fig. 1. Type locality: Peru, Meobamba. Lectotype NHMUK 1975494.

*Drymaeus protractus* (L. Pfeiffer); BREURE & ABLETT 2014: 157, figs 49G–I, L48vii.

**Remarks.** We have found one lot labelled New Granada, Colombia, ex Sowerby (ZMUZ 512125) as *D. protractus*, and consider the locality erroneous. This Peruvian species most likely does not occur in Colombia.

***Drymaeus (Drymaeus) rugistriatus* Haas, 1952†**

*Drymaeus (Drymaeus) rugistriatus* HAAS 1952: 120, fig. 21. Type locality: Peru, Cuzco, Hacienda Cadena. Holotype FMNH 38123; LINARES & VERA 2012: 190.

**Remarks.** This Peruvian species is recorded from southern Colombia by LINARES & VERA (2012) without further voucher information, on account of RESTREPO *et al.* (1983). It is simply a misidentification by the latter authors (see *D. (D.) flexuosus*).

***Drymaeus (Drymaeus) strigatus* (G.B. Sowerby I, 1833)†**

*Bulinus strigatus* G.B. SOWERBY I 1833 [1832–1841]: figs. 95–96. Type locality: Peru, Huallaga.

*Bulimus musivus* L. PFEIFFER 1855d: 95, pl. 31 fig. 3. Type locality: Meobamba, E. Peru. Lectotype NHMUK 1975292.

*Drymaeus musivus* (L. Pfeiffer); BREURE & ABLETT 2014: 129, figs 29J–L, L39vi.

**Material.** ?, New Granada, ex Henderson (USNM 307563).

**Remarks.** The USNM material was found under the name *Drymaeus musivus*, and clearly belongs to this Peruvian species, but its locality data must be in error.

***Drymaeus (Drymaeus) subinterruptus* (L. Pfeiffer, 1853)†**

*Bulimus subinterruptus* L. PFEIFFER 1853b: 256. Type locality: Bolivian Andes. Lectotype NHMUK 1975470.

*Drymaeus subinterruptus* (L. Pfeiffer); RICHARDSON 1995: 181 (references); BREURE & ABLETT 2014: 187, figs 490, L57v.

**Remarks.** This presumably Bolivian species has been associated with Colombian material, but this seems to be erroneous.

***Drymaeus (Drymaeus) trigonostomus* (Jonas, 1844)†**

*Bulimus trigonostomus* JONAS 1844: 36. Type locality: Curiana, Venezuela (BREURE 1979).

*Drymaeus trigonostomus* (Jonas); RICHARDSON 1995: 187 (references).

*Bulimus knorri* L. Pfeiffer in PHILIPPI 1846 [1845–1847]: 115, pl. 4 fig. 3. Type locality: La Guayra. Possible syntypes, NHMUK 20100654; BREURE & ABLETT 2014: 103, figs 51D–F, L32iii (as *Drymaeus trigonostomus* (Jonas)).

**Material.** ?, Bogota, Colombia (CMC C13891); Colombia, Müller leg. (ZMUZ 512159).

**Remarks.** This is a Venezuelan species that has been erroneously referred to as being collected from Colombia in some collections. The CMC material is labelled as *Drymaeus knorri*. The material from Zürich is labeled as *Drymaeus curianianus* (a synonym of *D. trigonostomus*), and with locality “Colombia”. We have not found other Colombian material and consider the presence of this species in Colombia uncertain.

***Drymaeus (Mesembrinus) cattivorus* (Broderip, 1832)†**

*Bulimus cattivorus* Broderip in BRODERIP & G.B. SOWERBY I 1832: 31. Type locality: “ad Montem Chris in Columbia”.

*Drymaeus cattivorus* (Broderip); RICHARDSON 1995: 106 (references); BREURE & BORRERO 2008: 23; LINARES & VERA 2012: 193.

**Remarks.** This species occurs in western Ecuador in lowland areas under dry conditions (BREURE & BORRERO 2008). The type locality thus could therefore refer to Montecristi in Ecuador [01° 03' 00" S 080° 40' 00" W], not Colombia, although there are 11 places in this country called “Montecristo” and one place “Monte Cristo” with “Cristo” as variant in the Geonames gazetteer. We have not found other Colombian material and feel that the presence of this species in Colombia needs to be confirmed.

***Drymaeus (Mesembrinus) deshayesi* (L. Pfeiffer, 1845)†**

*Bulimus deshayesi* L. PFEIFFER 1845: 73. Type locality: Locality unknown. Lectotype NHMUK 1975526 (BREURE 1979).

*Drymaeus deshayesi* (Pfeiffer); RICHARDSON 1995: 131; BREURE & ABLETT 2014: 61, figs 24D, L18i (label info ‘New Granada’).

*Drymaeus deshayesii* [sic]; LINARES & VERA 2012: 194.

**Material.** Venezuela, [without specific locality], ex Henderson ex Evezard (USNM 316266). ?, “New Granada” (NHMUK, lectotype).

**Remarks.** RICHARDSON (1995) grouped this species with *Bulimus depictus* Reeve, 1849 and *B. granadensis* L. Pfeiffer, 1848. Comparing the two lectotypes in NHMUK we fail to see any reason for this. Its presence in Colombia remains uncertain.

***Drymaeus (Mesembrinus) dubius* (L. Pfeiffer, 1853)†**

*Bulimus dubius* L. PFEIFFER 1853b: 257. Type locality: Andes of New Granada. Lectotype NHMUK 1975519 (BREURE 1979).

*Drymaeus dubius* (L. Pfeiffer); RICHARDSON 1995: 118 (references); LINARES & VERA 2012: 194; BREURE & ABLETT 2014: 62, figs 25C, L18iv.

**Material.** ?, New Granada, ex Luders (ANSP 5259); Ibidem (NHMUK, lectotype).

**Remarks.** We tentatively refer the ANSP specimen to this species. Another shell from “Colombia” (ZMUZ 512366, see below) may belong to this species but cannot be fully assessed. Without additional material and precise localities, the presence of this species in Colombia remains uncertain.

***Drymaeus (Mesembrinus) flavidus* (Menke, 1829)†**

*Bulimus flavidus* MENKE 1829: 6. Type locality: “?”.

*Drymaeus flavidus* (Menke); RICHARDSON 1995: 127 (references).

**Remarks.** HAAS (1966: 233) writes “from Venezuela to Panamá”, which would imply that this taxon might occur in northern Colombia. However, as no material with specific Colombian localities is known to us, the presence of this species in Colombia remains uncertain. Material from near Bogotá resembles this species, but is a new taxon waiting to be described.

***Drymaeus (Mesembrinus) granadensis* (L. Pfeiffer, 1848)†**

*Bulimus granadensis* L. PFEIFFER 1848a: 231. Type locality: “Merida, New Granada”.

*Drymaeus granadensis* (L. Pfeiffer); RICHARDSON 1995: 130 (references, synonymy).

**Material.** La Guajira, La Cueva, on old trail from Fonseca to Riohacha, 4000 ft. [~1220 m ], M.A. Carriker jr. leg. (USNM 488801); ?, New Granada, Coulon leg., 1849 (ZMUZ 512287).

**Remarks.** The USNM is an old subadult shell, and does not appear to belong to this taxon; we consider it “unassignable”. The ZMUZ material is tentatively referred to as this species. Richardson (1995) followed the suggestion of von Martens and Pilsbry (see PILSBRY 1898 [1897–1898]: 300) and grouped *Bulimus depictus* with *B. granadensis* L. Pfeiffer, 1848; we consider *B. depictus* to be a distinct species (*q.v.*). *Drymaeus granadensis* has been reported from La Fría in Venezuela (ANSP 140956), and the present-day occurrence of this species in Colombia is somewhat doubtful. BREURE (1979: 119) listed this species as *D. (M.) grenadensis* [*sic*].

***Drymaeus (Mesembrinus) liliaceus* (Férussac, 1821)†**

*Helix lilacea* FÉRUSSAC 1821: 54. Type locality: Les Antilles, Puerto Rico.

*Drymaeus liliaceus* (Férussac); RICHARDSON 1995: 144 (references, synonymy); LINARES & VERA 2012: 196.

**Material.** Cesar, “Socorpa Mission, Sierra de Perijá, Magdalena” [Becerril], 1300–1400m, B. Malkin leg., 22.viii.1968 (FMNH 187596).

**Remarks.** This species has hitherto been reported with certainty from the West Indies only. Listing this species as from Colombia appears to be based on misidentifications. The single specimen from Cesar (labeled as “*D. sp aff. liliaceus*”) belongs to a different taxon, and is a subadult shell; at this time we consider it unassignable. A specimen in NHMUK (n.c.) from “Colombia”, ex Cuming, is a rather bleached juvenile and could be referred to a number of species.

***Drymaeus (Mesembrinus) loxanus (Higgins, 1872)***†

*Otostomus loxanus* HIGGINS 1872: 685, pl. 56 figs 2–2a. Type locality: Ecuador, Loja. Lectotype NHMUK 1975552 (BREURE 1979).

*Drymaeus loxanus* (Higgins); RICHARDSON 1995: 147 (references); LINARES & VERA 2012: 196; BREURE & ABLETT 2014: 113.

**Material.** Cauca, between Popayán and Hacienda Sotará, at about 2400m (Pilsbry, 1898 [1897–1898]: 270). Ecuador, Loja (NHMUK 1975552).

**Remarks.** Pilsbry quoted the locality from MARTENS (1885: 160); we have not been able to verify the actual specimens, and so this remains a doubtful Colombian record. No material we have examined resembles this very distinctive species from southern Ecuador.

***Drymaeus (Mesembrinus) manupictus (Reeve, 1848)***†

*Bulimus manupictus* REEVE 1848 [1848–1850]: pl. 55 fig. 369. Type locality: “Andes of Columbia”. Lectotype NHMUK 1975522 (BREURE 1979).

*Drymaeus manupictus* (Reeve); RICHARDSON 1995: 148 (references); LINARES & VERA 2012: 196; BREURE & ABLETT 2014: 117, figs 21E, L36iv.

**Material.** ? Venezuela, “Merida, Columb.” [see Remarks] (NHMUK, lectotype).

**Remarks.** BREURE & ESKENS (1981) have shown that the type material is labelled “Venezuela” and “Merida, Columbia” [*sic*, Venezuela]. The locality “Andes of Colombia (Cuming coll.)” mentioned by PILSBRY (1898 [1897–1898]: 304) on the authority of Reeve, is possibly based on the erroneous assignment of Mérida to Colombia due to political-administrative changes in the mid-19th century. The same locality of material at NMW, referred to by LINARES & VERA (2012), may be similarly explained. It is possible however, that this species may be found in the large area bordering the two countries.

***Drymaeus (Mesembrinus) multifasciatus (Lamarck, 1822)***†

*Bulimus multifasciatus* LAMARCK 1822: 123. Type locality: Antilles. Syntype MHNG-MOL-51167. *Drymaeus (Mesembrinus) multifasciatus*; BREURE 2016: 75, figs 66–67.

**Remarks.** One lot labelled “Cauca, Colombia” (NHMUK 1909.4.26.12) has been misidentified as this species, which is only known from the Lesser Antilles.

***Drymaeus (Mesembrinus) nitidus (Broderip, 1832)***†

*Bulimus nitidus* Broderip in BRODERIP & G.B. SOWERBY I 1832: 31. Type locality: Peru. Syntype NHMUK 1975551; RICHARDSON 1995: 107 (as *Drymaeus cactoris* (Broderip, 1832)).

*Drymaeus nitidus* (Broderip); LINARES & VERA 2012: 198; BREURE & ABLETT 2014: 133, figs 23M, L41iii.

**Material.** ?, Colombia, ex Sowerby (ZMUZ 512366).

**Remarks.** The material listed (a single bleached, broken shell) has been misidentified as this Peruvian species, which does not occur in Colombia.

***Drymaeus (Mesembrinus) pertristis Pilsbry, 1898***†

*Drymaeus pertristis* PILSBRY 1898 [1897–1897]: 301. New name for *Bulimus tristis* L. Pfeiffer, 1855 not Jay, 1839, Type locality: “New Granada”. Syntypes NHMUK 1975299; RICHARDSON 1995: 162 (references); LINARES & VERA 2012: 201 (as *Drymaeus tristis*) [*partim*]; BREURE & ABLETT 2014: 197, figs. 22B, L62i.

**Remarks.** We have not found material that can be assigned to this species. The Colombian references in collections cannot be fully evaluated at this time. Lot FMNH 31388 (Ocaña, labeled as *D. pertristis*), listed uncritically as this species by LINARES & VERA (2012), is *Drymaeus (M.) tenuilabris* (L. Pfeiffer, 1866). Lot ZMUZ 512281 (“New Granada”, ex Sowerby, 1878) resembles *D. (M.) membranaceus*. Although the type material is possibly from Colombia, we currently consider the occurrence of this taxon in Colombia as unconfirmed.



***Drymaeus (Mesembrinus) pervariabilis* (L. Pfeiffer, 1853)†**

*Bulimus pervariabilis* L. PFEIFFER 1853a: 337. Type locality: “Novae Granadae”. Lectotype NHMUK 1975547 (BREURE 1979).

*Drymaeus pervariabilis* (L. Pfeiffer); RICHARDSON 1995: 133 (references); LINARES & VERA 2012: 199 [partim]; BREURE & ABLETT 2014: 147, figs 21I, L45iv.

**Material.** ?, New Granada (NHMUK, lectotype).

**Remarks.** Pilsbry treated this taxon as a variety of *Drymaeus (M.) depictus* (Reeve), while RICHARDSON (1995) grouped *D. pervariabilis* with *D. granadensis*. BREURE & ESKENS (1981: 81, pl. 6 fig. 3)—after having compared the type material of both—argued why it should be considered a valid species. The shell shape and the (slightly) expanded lip resembles some *Drymaeus (D.)* species. We have not seen material from Colombia that can be assigned to this species with any certainty. LINARES & VERA (2012) listed lot ANSP 5240 as this species; examination of the material leads us to attribute it to *Drymaeus (M.) depictus* (Reeve, 1849).

***Drymaeus (Mesembrinus) studeri* (L. Pfeiffer, 1847)†**

*Bulimus studeri* L. PFEIFFER 1847: 112. Type locality: Venezuela, Merida. Lectotype NHMUK 1975480 (BREURE & ESKENS 1981).

*Leiostracus studeri* (L. Pfeiffer); RICHARDSON 1995: 207 (references).

*Drymaeus studeri* (L. Pfeiffer); LINARES & VERA 2012: 200 [partim]; BREURE & ABLETT 2014: 185, figs 18o–P, L57ii.

*Bulimus primula* REEVE 1848 [1848–1850]: pl. 57 fig. 385. Type locality: Venezuela. Lectotype NHMUK 1975478 (BREURE & ESKENS 1981).

*Leiostracus primulus* (Reeve); RICHARDSON 1995: 207 (references).

*Drymaeus (Mesembrinus) studeri* (L. Pfeiffer); BREURE & ABLETT 2014: 156, figs 18H–I, L48v.

**Remarks.** We have not found material from Colombia that can be assigned to this *Drymaeus (Mesembrinus)* species. By uncritical use of museum databases, LINARES & VERA (2012) attributed the following lots to *D. (M.) studeri*, none of which closely resemble this species: FMNH 115803 (see *D. (M.) columbianus*), MCZ 154055 (*D. (M.) iris*), ANSP 217537 (unassignable lot). After examining the type series, we suggest that *Bulimus primula* Reeve, 1848 might indeed be considered a junior synonym of this species.

***Drymaeus (Mesembrinus) translucens* (Broderip, 1832)†**

*Bulinus translucens* Broderip in BRODERIP & G.B. SOWERBY I 1832: 31. Type locality: Panama, “King and Saboga Islands” [Archipelago de las Perlas]. Lectotype NHMUK 20100634 (BREURE & ABLETT 2014).

*Drymaeus (Mesembrinus) translucens translucens* (Broderip); THOMPSON 2011: 122 (references); LINARES & VERA 2012: 200; BREURE & ABLETT 2014: 194, figs 18R, L61i.

**Remarks.** This species was described from Panama and is known to occur in the north to Oaxaca, Mexico (THOMPSON 2011); its occurrence in Colombia is dubious. A specimen labeled as this taxon (FMNH 140279), from near Popayán, southern Colombia, appears to belong to a different species.

**Discussion**

When looking at all localities where material of the material mentioned in this study was found (Fig. 1E), it is clear that most have been collected in areas that are relatively accessible. Nonetheless, at 74% of the 183 localities only one *Drymaeus* species was recorded, two co-occurring species respectively were found at 20% of the localities, three species at 6%, and only two localities are known where four or five species respectively were found. Although the data are limited, 95 localities could be ascertained where collecting was recently (*i.e.* post-1950) done (Fig. 28A).

Of the 78 *Drymaeus* species now recorded from Colombia, 15 are known only from their type material which was collected during the 19th century, while of 15 additional species the records are at least 100 years old. This raises the question whether these species are extremely short-range endemics or whether their habitat has been destroyed, and therefore it remains questionable if these taxa will ever be re-collected. Although for most species of this genus the exact habitat is still unknown, it is obvious from the known precise localities that most of the *Drymaeus* species do occur in (montane) forests ecoregions (Fig. 28B). From the literature regarding land cover change and deforestation in Colombia, we know that the regions where most species in this study have been

recorded have (substantially) changed over the past century, and several areas are still under threat of continued deforestation (e.g., VIÑA *et al.* 2004; ETTER *et al.* 2006, 2008; ARMENTERAS *et al.* 2011; SÁNCHEZ-CUERVO *et al.* 2012; RODRÍGUEZ *et al.* 2013). It cannot be excluded that the habitat of species, which have not recently been re-collected or are only known from 19th century records, has drastically changed; they may now be extinct but the current data does not allow a full evaluation.

Although the data for these two genera in Colombia is now fairly substantial, it is clear that many taxa are still poorly known, and their anatomical and molecular data unknown in most cases. We hope that this review will act as a stimulus for (local) malacologists to further research.

## Acknowledgements

We thankfully acknowledge the input of Jenny de Jager (Nieuwegein), Andrés Quintero (Cali), M.M. Ruíz and R. Rios (Cali), Marcus and José Coltro (Brazil) with specimens or data on localities. Museum curators and collection managers at each of the institutions listed (you know who you are) are gratefully acknowledged for allowing visiting and using the collections under their charge, and for answering questions and providing photographs or additional information as needed. Photo credits are due, other than those of the second author, to Yves Barette, Celia Bueno, Eike Neubert, and John Taylor, and to the ANSP, MNHN, and NMW. This research received support, with a grant to ASHB to visit the London museum in 2010, from the SYNTHESYS Project (<http://www.synthesys.info>) which is financed by European Community Research Infrastructure Action under the FP7 Integrating Activities Programme. The first author is grateful to Jan van Tol (Naturalis Biodiversity Center, Leiden) for partly financing a visit to Cincinnati in 2011, which led to a first draft of this manuscript. FJB thanks Glenn Storrs and Jane MacKnight (CMC Cincinnati) for providing logistic support and facilitating loans of specimens during the early part of this project, Gary Rosenberg (ANSP) for discussion about records at the Academy, and Timothy A. Pearce, Luz Adriana Velasco and Lyda Castro (Univ. Magdalena, Santa Marta) and Ines Borrero for assistance in the field.

The preparation of this manuscript took many years due to unforeseen circumstances, which have partly prevented to make this text as extensive as we originally had envisaged. The comments of Jonathan Ablett and reviewers has led to further improvements and is thankfully acknowledged.

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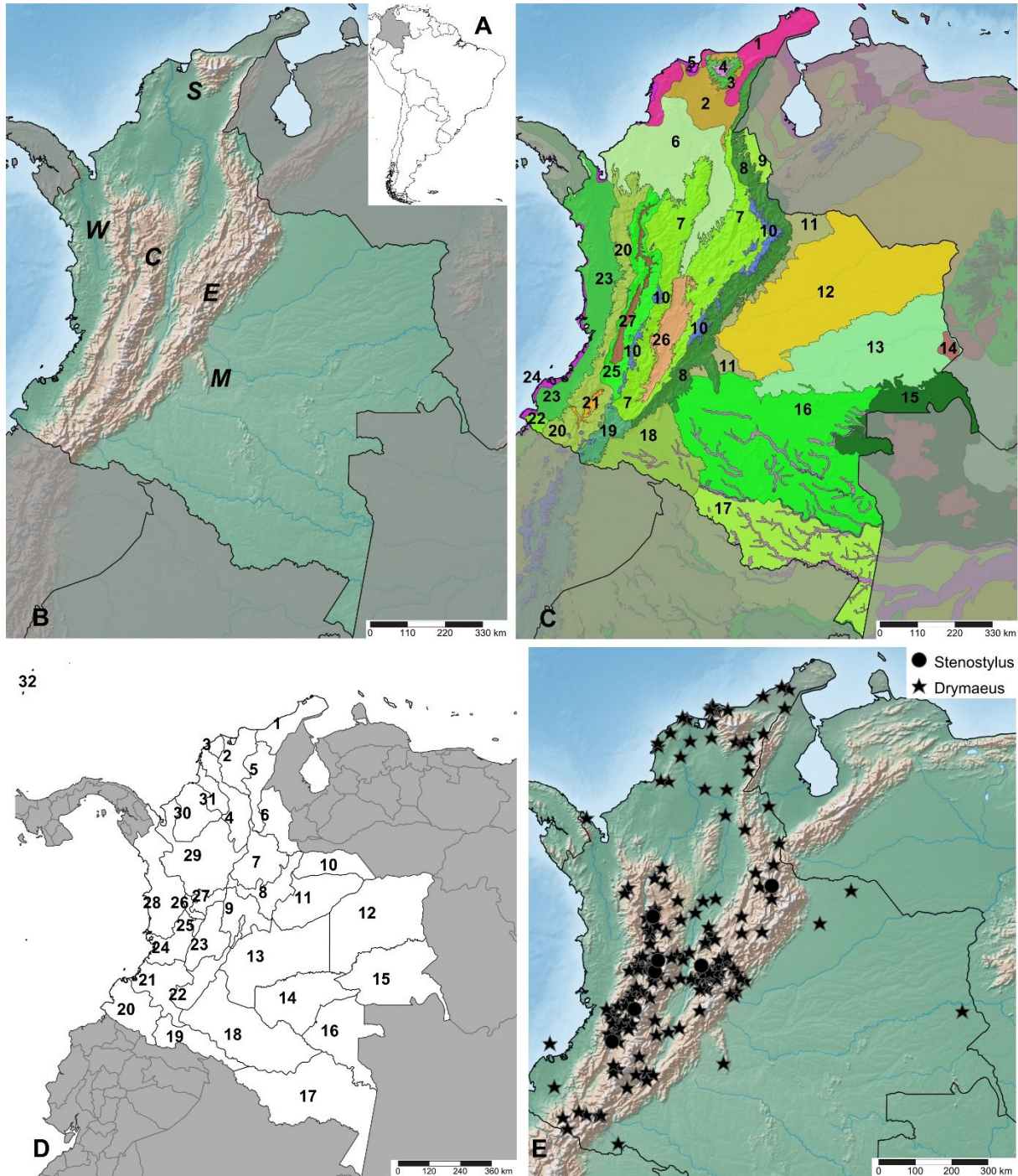
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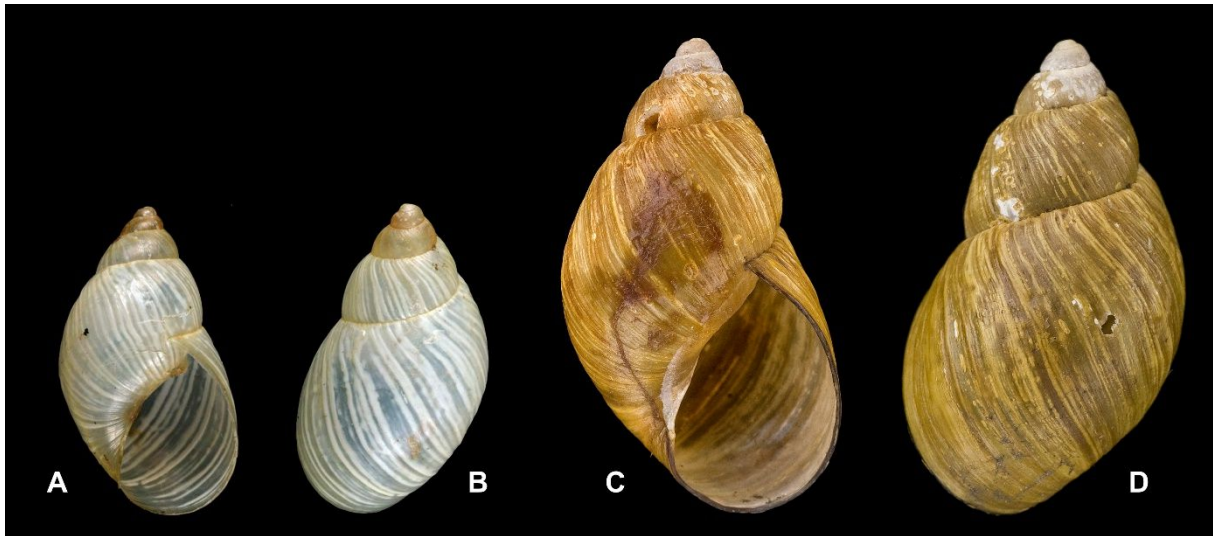
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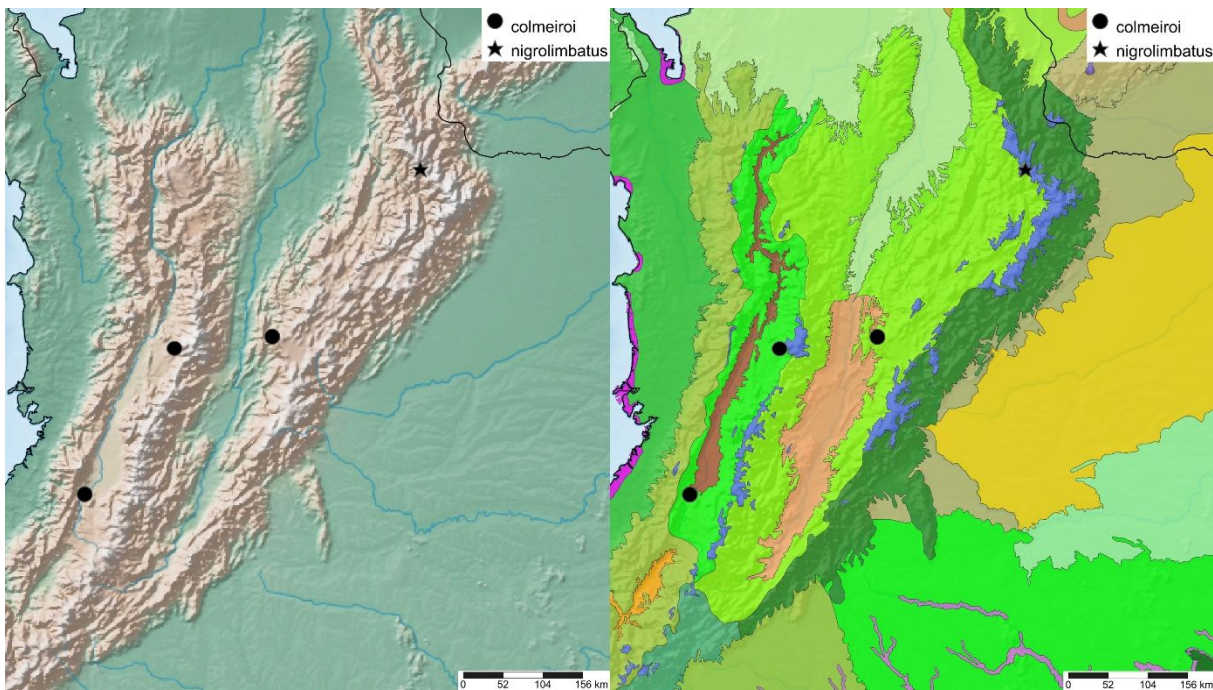


**FIGURE 1.** Colombia. **A.** Situation within South America. **B.** Main topographic features: C, Central Cordillera; E, Eastern Cordillera; M, Serranía de la Macarena; S, Sierra Nevada de Santa Marta; W, Western Cordillera. **C.** Main ecoregions: 1, Guajira-Barranquilla xeric scrub; 2, Sinú valley dry forests; 3, Santa Marta montane forests; 4, Santa Marta páramo; 5, Central American dry forests; 6, Magdalena-Urabá moist forests; 7, Magdalena Valley montane forests; 8, Cordillera Oriental montane forests; 9, Catatumbo moist forests; 10, Northern Andean páramo; 11, Apure-Villavicencio dry forests; 12, Llanos; 13, Negro-Branco moist forests; 14, Rio Negro campinarana; 15, Japurá-Solimões-Negro moist forests; 16, Caqueta moist forests; 17, Japurá-Solimões moist forests; 18, Napo moist forests; 19, Eastern Cordillera real montane forests; 20, Northwestern Andean montane forests; 21, Patía Valley dry forests; 22, Western Ecuador moist forests; 23, Chocó-Darién moist forests; 24, South American Pacific mangroves; 25, Cauca Valley montane forests; 26, Magdalena Valley dry forests; 27, Cauca Valley dry forests. For more information see WWF (2015). **D.** Political-administrative division: 1, La Guajira; 2, Magdalena; 3, Atlántico; 4, Bolívar; 5, Cesar; 6, Norte de Santander; 7, Santander; 8, Boyacá; 9, Cundinamarca; 10, Arauca; 11, Casanare; 12, Vichada; 13, Meta; 14, Guaviare; 15, Guainia; 16, Vaupés; 17, Amazonas; 18, Caquetá; 19, Putumayo; 20, Nariño; 21, Cauca; 22, Huila; 23, Tolima; 24, Valle del Cauca; 25, Quindio; 26, Risaralda; 27, Caldas; 28, Chocó; 29, Antioquia; 30, Córdoba; 31, Sucre; 32, San Andrés y Providencia. **E.** All localities which were precise enough to be geo-referenced (n = 247).





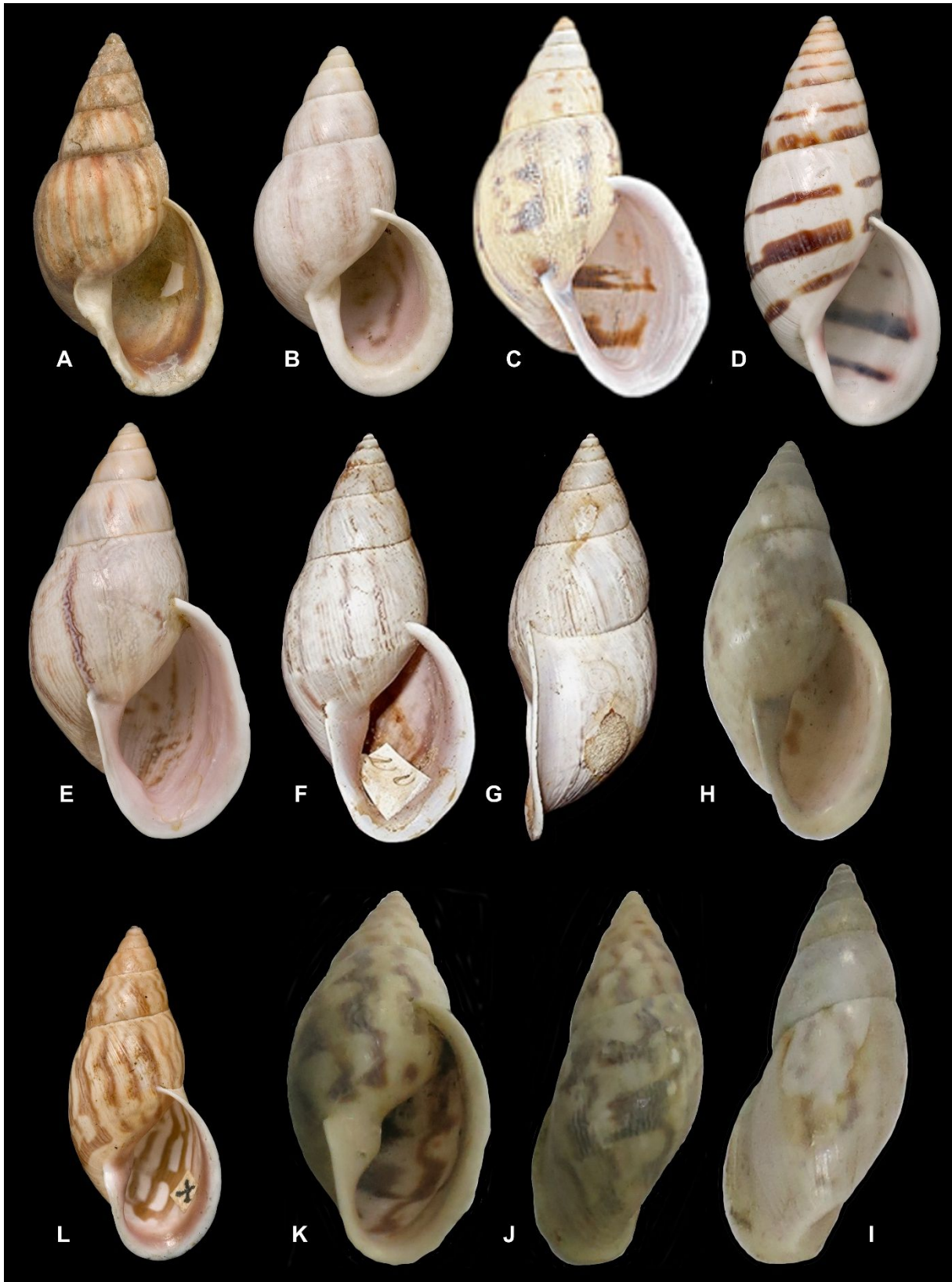
**FIGURE 2.** *Stenostylus* species. **A–B.** *S. colmeiroi* (Hidalgo, 1872), MNHN-IM-2000-2 (H = 16.7 mm). **C–D.** *S. nigrolimbatus* (L. Pfeiffer, 1853), NHMUK 1975549, lectotype (H = 28.0 mm).



**FIGURE 3.** Distribution of *Stenostylus* species, respectively in topographic and ecoregions view.



**FIGURE 4.** *Drymaeus (Drymaeus)* species. **A–D.** *D. (D.) angustus* da Costa, 1906. **A.** NHMUK 1907.11.21.14, holotype (H = 31.5 mm). **B–D.** MLS-BOG 21 (H = 28.7). **E–H.** *D. (D.) pealianus* (Lea, 1838). **E–G.** ANSP 192929, holotype (H = 29.1 mm). **H.** USNM 202514, holotype of *Bulimulus (Drymaeus) comis* Preston, 1907 (H = 29.4 mm).



**FIGURE 5.** *Drymaeus (Drymaeus)* species. **A–C.** *D. (D.) baranguillanus* (L. Pfeiffer, 1853). **A.** NHMUK 1975452, lectotype (H = 31.5 mm). **B.** NHMUK 1975450, lectotype of *Bulimus antioquiensis* L. Pfeiffer, 1855 (H = 29.6 mm). **C.** FEM 154777 (H = 35.4 mm). **D.** *D. (D.) bogotensis* (L. Pfeiffer, 1853), NHMUK 1975191, lectotype (H = 37.4 mm). **E–K.** *D. (D.) confluens* (L. Pfeiffer, 1855). **E.** NHMUK 1975196, lectotype (H = 39.5 mm). **F–G.** ZMUZ 512087, lectotype of *Bulimus violaceus* Mousson, 1873 (H = 36.0 mm). **H–I.** MHNN 35.1650, syntype of *Drymaeus eversus alata* Piaget 1914 (H = 35.6 mm). **J–K.** MHNN 35.1651, syntype of *Drymaeus eversus subula* Piaget 1914 (H = 32.1 mm) [Note the abnormal view in K.]. **L.** *D. (D.) incognitus* da Costa, 1907, NHMUK 1907.11.21.24, holotype (H = 29.8 mm).



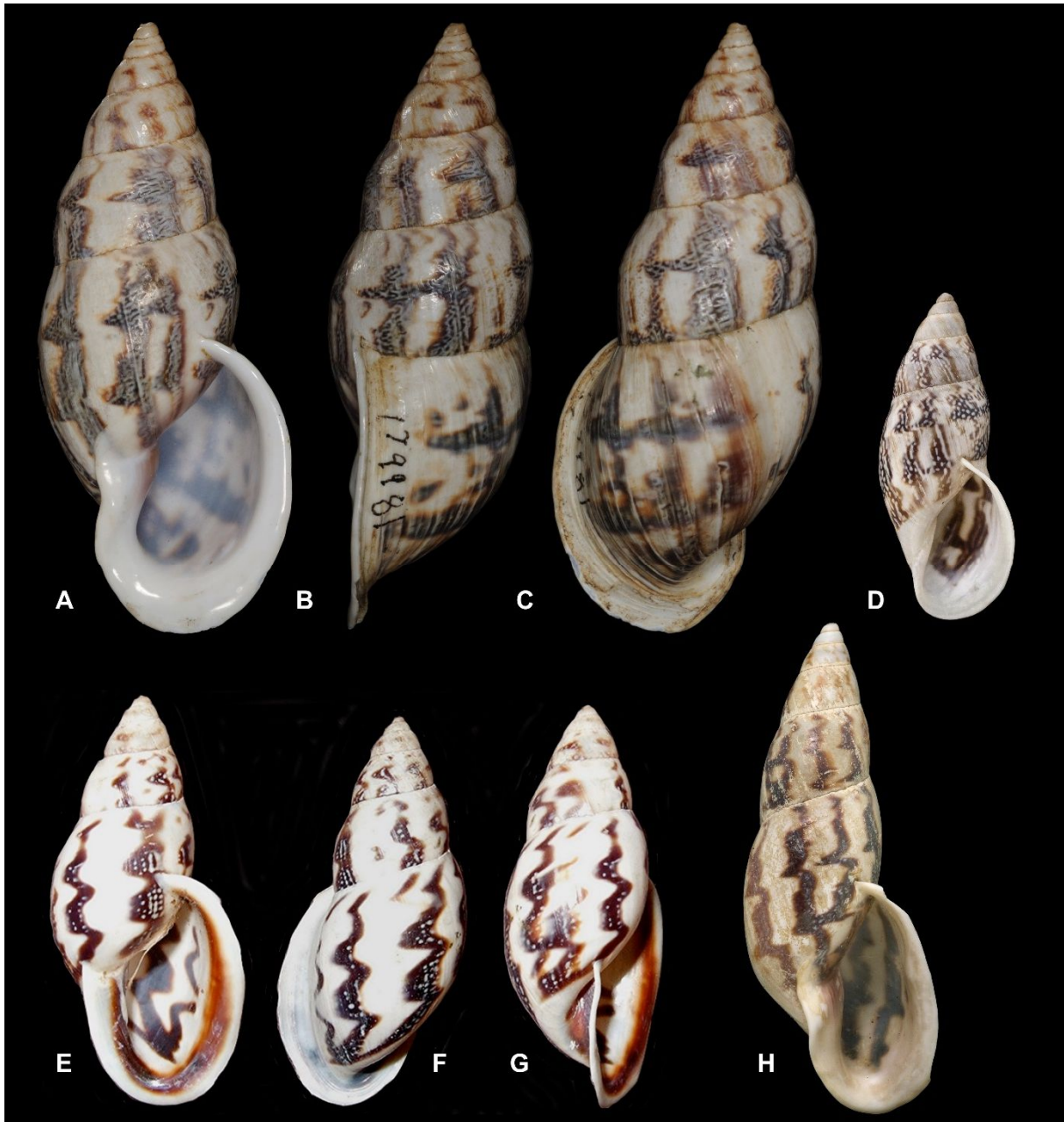
**FIGURE 6.** *Drymaeus* (*Drymaeus*) species. **A-C.** *D. (D.) glaucostomus* (Albers, 1852), ZMUZ 511967 (H = 36.7 mm). **D-G.** *D. (D.) felix felix* (L. Pfeiffer, 1862). **D-F.** ICNB 0094 (H = 34.6 mm). **G.** NHMUK 1975206, lectotype of *Bulimus felix* L. Pfeiffer, 1862 (H = 34.0 mm). **H-I.** *D. (D.) felix restrepoensis* subsp.n., MCZ 64779, holotype (H = 31.5 mm). **J.** *D. (D.) ziczac* (da Costa, 1898), NHMUK 1907.11.21.46, lectotype (H = 26.5 mm).



**FIGURE 7.** *Drymaeus (Drymaeus)* species. **A–D.** *D. (D.) solidus* (Preston, 1907). **A.** NHMUK 1908.7.2.72, lectotype (H= 32.8 mm). **B–D.** USNM 202513, holotype of *Bulimulus (Drymaeus) ventricosus* Preston 1907 (H = 30.7 mm). **E–F.** *D. (D.) spadiceus* da Costa, 1906. **E.** NHMUK 1907.11.21.15, holotype (H = 37.3 mm). **F.** ICNB n.c. (H = 39.5 mm). **G.** *D. (D.) notabilis* da Costa, 1906, NHMUK 1907.11.21.5, lectotype (H = 32.8 mm).



**FIGURE 8.** *Drymaeus (Drymaeus)* species. **A-E.** *D. (D.) flexuosus* (L. Pfeiffer, 1853). **A.** NHMUK 1975202, lectotype (H = 43.0 mm). **B-C.** DMNH 76690 (H = 47.0 mm). **D-E.** MCZ 113837 (H = 31.5 mm). **F-H.** *D. (D.) cognatus* Pilsbry, 1901, ANSP 78543, lectotype (H = 36.0 mm).



**FIGURE 9.** *Drymaeus (Drymaeus)* species. **A-C.** *D. (D.) megas* Pilsbry, 1944, ANSP 179981, holotype (H = 58.0 mm). **D.** *D. (D.) volsus* Fulton, 1907, NHMUK 1907.5.3.162, lectotype (H = 30.3 mm). **E-G.** *D. (D.) duplexannulus* spec.n., ANSP 170737, holotype (H = 37.8 mm). **H.** *D. (D.) sykesi* da Costa, 1906, NHMUK 1907.11.21.4, holotype (H = 51.7 mm).

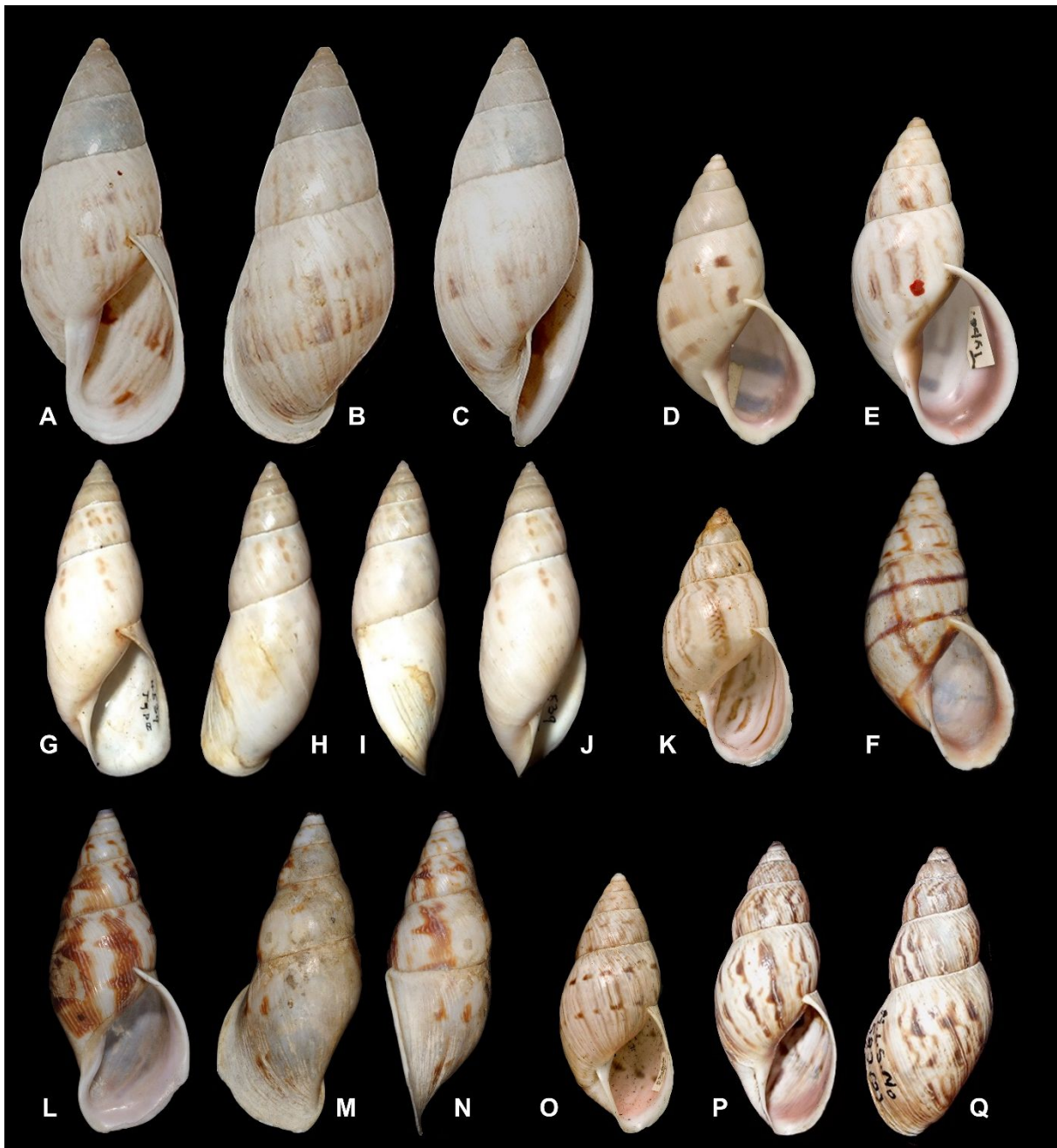


**FIGURE 10.** *Drymaeus (Drymaeus)* species. A–C. *D. (D.) zingarensis* Restrepo and Breure, 1987, IMCN 0013 (H = 25.7 mm). D. *D. (D.) caucaensis* (da Costa, 1898), NHMUK 1907.11.21.43, lectotype (H = 34.8 mm). E–K. *D. (D.) expansus* (L. Pfeiffer, 1853). E–F. FMNH 187569 (H = 40.8 mm). G–H. ICNB 2841 (H = 37.0). I–K. USNM 590653, holotype of *Drymaeus rehderi* Parodiz, 1962 (H = 37.0 mm).





**FIGURE 11.** *Drymaeus* (*Drymaeus*) species. **A.** *D. (D.) auris* (L. Pfeiffer, 1866), NHMUK 1975499, lectotype (H = 38.8 mm). **B.** *D. (D.) geometricus* (L. Pfeiffer, 1846), NHMUK 1975564, lectotype (H = 34.6 mm). **C.** *D. (D.) notatus* da Costa, 1906, NHMUK 1907.11.21.6, holotype (H = 34.5 mm). **D–H.** *D. (D.) denticulus* spec.n. **D.** UMMZ 125081, paratype (H = 48.0 mm). **E–H.** RBINS MT.2630, holotype (H = 43.0 mm). **I–K.** *D. (D.) intermissus* spec.n., ICNB 2840, holotype (H = 27.1). **L.** *D. (D.) incognitus* da Costa, 1907, NHMUK 1907.11.21.24, holotype (H = 29.8 mm). **M.** *D. (D.) villavicencioensis* Breure, 1977, SMF 245417, holotype (H = 29.0 mm).



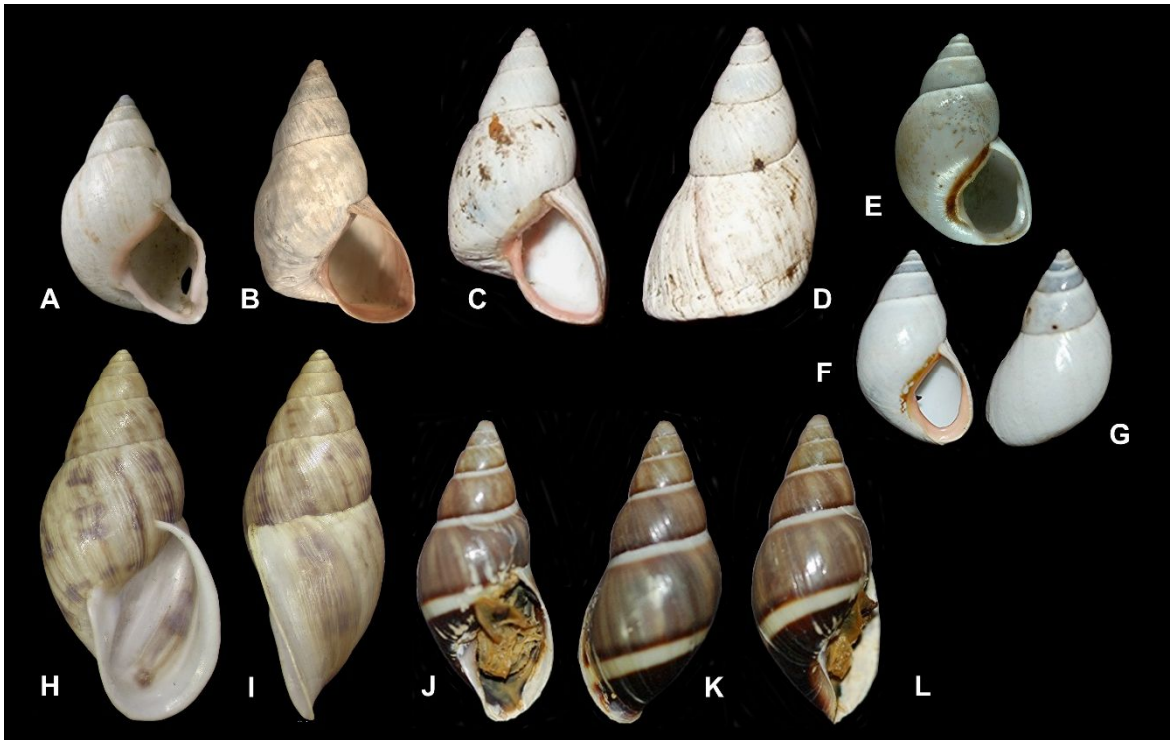
**FIGURE 12.** *Drymaeus* (*Drymaeus*) species. **A–C.** *D. (D.) leai* Pilsbry, 1901, USNM 105143, syntype (H = 41.6 mm). **D–F.** *D. (D.) smithii* (da Costa, 1898). **D.** NHMUK 1907.11.21.52, holotype (H = 29.5 mm). **E.** NHMUK 1907.11.21.8, holotype of *Drymaeus bellus* da Costa, 1906 (H = 33.2 mm). **F.** ANSP 25780, lectotype of *Drymaeus blandi* Pilsbry, 1898 (H = 30.0 mm). **G–J.** *D. (D.) sanctaemartae* Pilsbry, 01, CM 46613, holotype (H = 33.9 mm). **K.** *D. (D.) exoticus* da Costa, 1901, NHMUK 1907.11.21.38, lectotype (H = 24.8 mm). **L–N.** *D. (D.) fordii* Pilsbry, 1898, ANSP 72368, lectotype (H = 34.0 mm). **O–Q.** *D. (D.) dacostae* (G.B. Sowerby III, 1892). **O.** NHMUK 1907.11.21.51, holotype (H = 26.3 mm). **P–Q.** MLS-BOG 587 (H = 31.7).



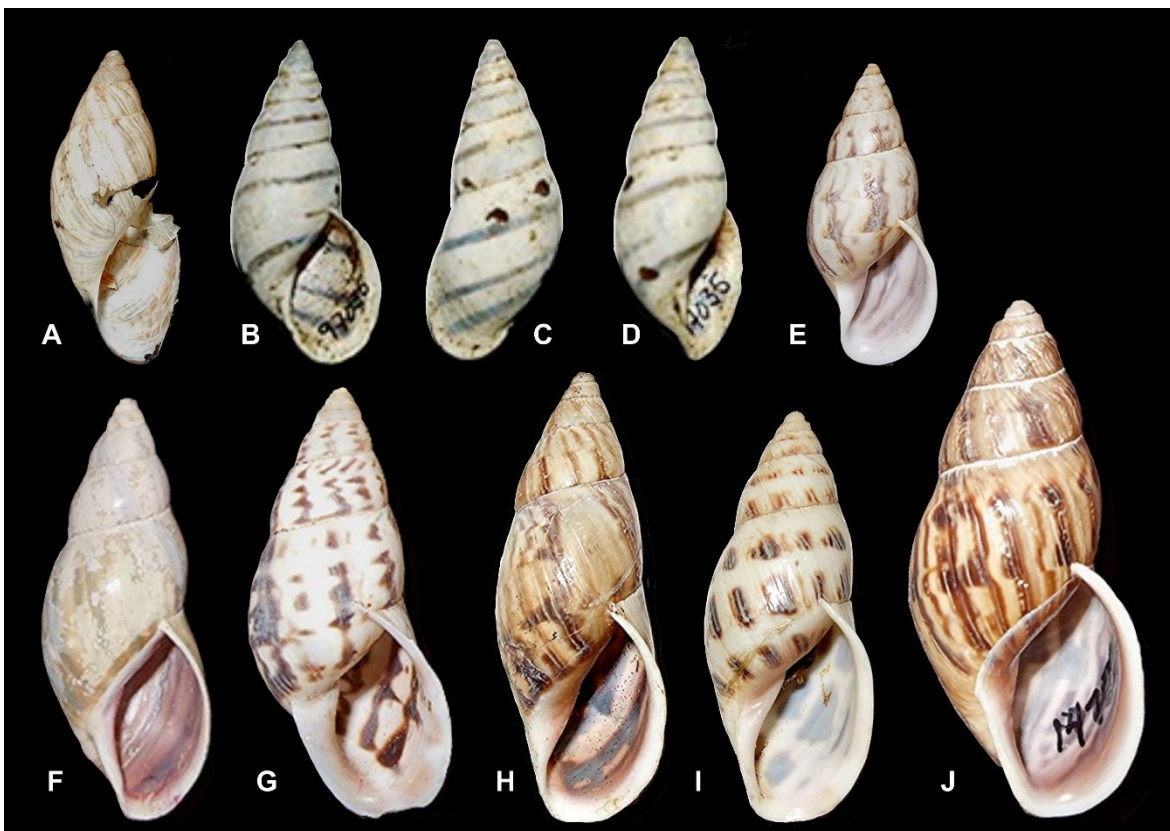
**FIGURE 13.** *Drymaeus* (*Drymaeus*) species. **A.** *D. (D.) subventricosus* da Costa, 1901, NHMUK 1907.11.21.37, lectotype (H = 30.1 mm). **B–D.** *D. (D.) vicinus* (Preston, 1907), USNM 202512, syntype (H = 35.8 mm). **E.** *D. (D.) fucatus* (Reeve, 1849), NHMUK 1874.12.11.224 (H = 23.5 mm). **F.** *D. (D.) pseudofusoides* da Costa, 1906, NHMUK 1907.11.21.11, holotype (H = 33.6 mm). **G–H.** *D. (D.) fabrefactus* (Reeve, 1848), ZMUZ 512150 (H = 39.3 mm). **I–K.** *D. (D.) pamplonensis* Pilsbry, 1939, ANSP 170699, holotype (H = 38.6 mm). **L–P.** *D. (D.) convexus* (L. Pfeiffer, 1855). **L.** NHMUK 1975192, lectotype (H = 38.4 mm). **M.** NHMUK 1907.11.21.120, holotype of *Bulimulus (Drymaeus) plicatoliratus* da Costa, 1898 (H = 36.6 mm). **N.** ANSP 25836, holotype of *Drymaeus fresnoensis* Pilsbry, 1898 (H = 27.7 mm). **O.** ANSP 164572, holotype of *Drymaeus cantatus medinanus* Pilsbry, 1935 (H = 35.0 mm). **P.** ANSP 164570, holotype of *Drymaeus tusagasuganus* Pilsbry 1935 (H = 29.8 mm).



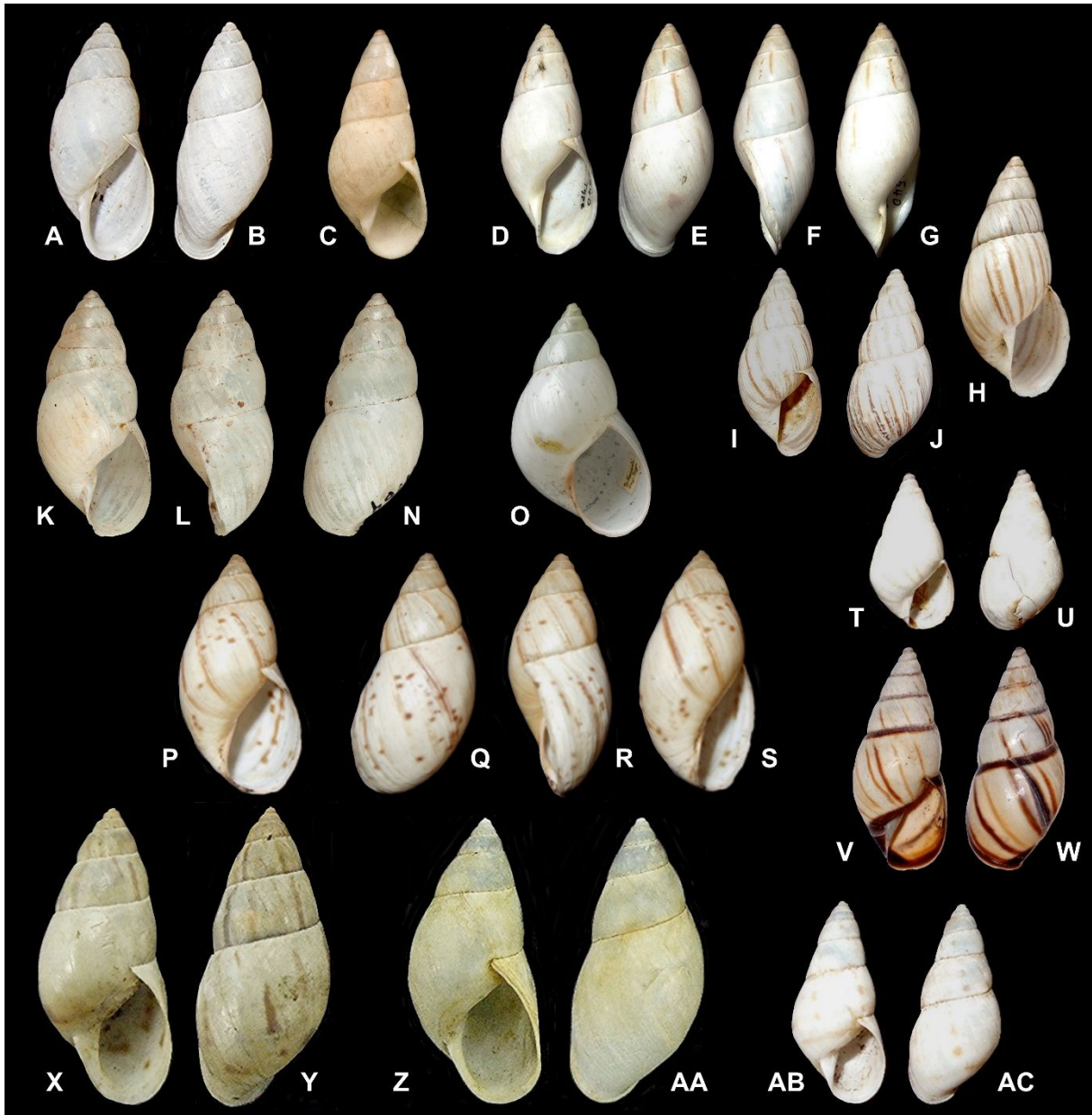
**FIGURE 14.** *Drymaeus* (*Drymaeus*) species. **A-C.** *D. (D.) decoratus* (Lea, 1838), USNM 105154, syntype (H = 28.3 mm). **D.** *D. (D.) murrinus* (Reeve, 1848), NHMUK 1975213, lectotype (H = 37.1 mm). **E.** *D. (D.) spectatus* (Reeve, 1849), NHMUK 1874.12.11.226, lectotype (H = 39.2 mm). **F.** *D. (D.) aequatorianus* (E.A. Smith, 1877), NHMUK 1975137, lectotype (H = 26.6 mm). **G-H.** *D. (D.) inaequalis* (L. Pfeiffer, 1857), UVZ 8157 (H = 52.5). **I.** *D. (D.) inclinatus* (L. Pfeiffer, 1862), NHMUK 1975532, lectotype (H = 33.1). **J.** *D. (D.) alabastrinus* da Costa, 1906, NHMUK 1907.11.21.16, holotype (H = 33.0 mm). **K-L.** *D. (D.) narcissus* (Albers, 1854), UAM n.c. (H = 32.2 mm). **M-O.** *D. (D.) luciensis* spec.n. **M-N.** UVZ 84019, holotype (H = 30.1 mm). **O.** FEM 194084 (H = 23.0 mm).



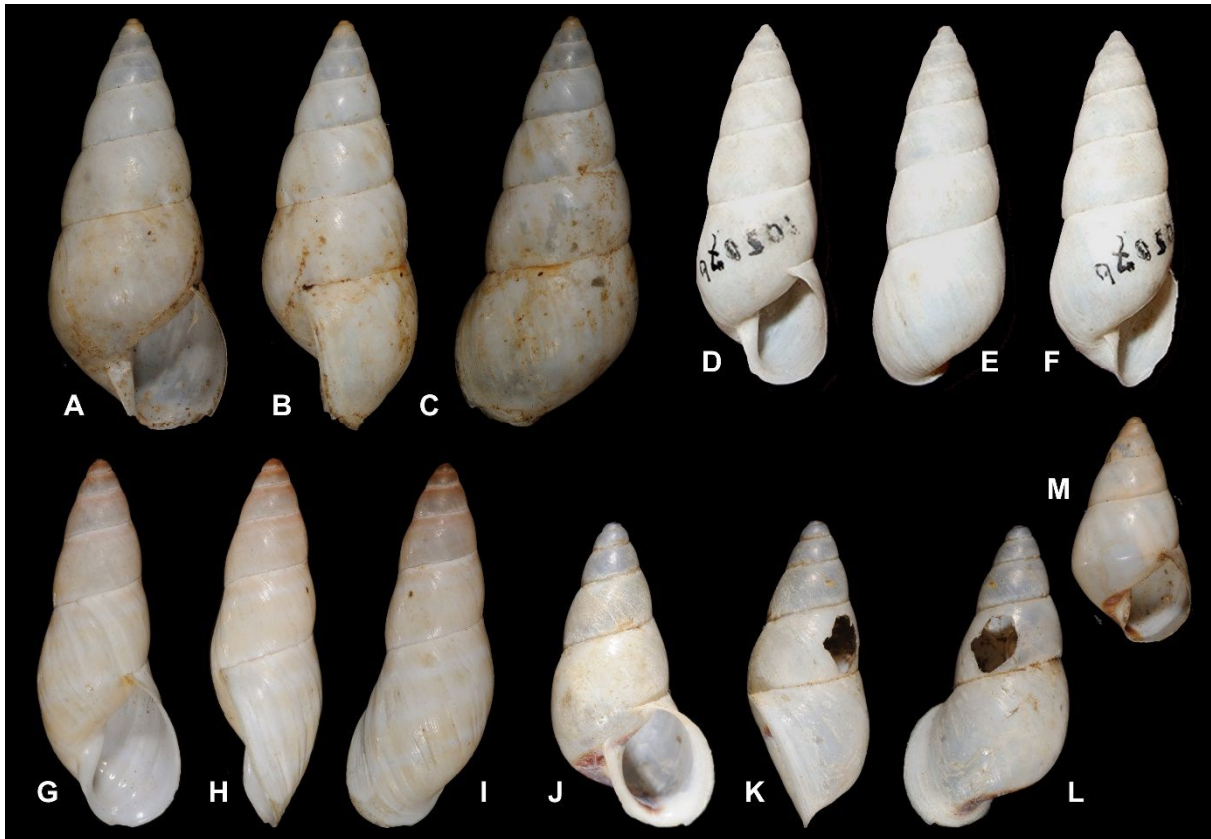
**FIGURE 15.** *Drymaeus (Drymaeus)* species. **A-C.** *D. (D.) fallax* (L. Pfeiffer, 1853). **A.** NHMUK 1969142, lectotype (H = 22.4 mm). **B.** SMF 245405 holotype of *Drymaeus fallax chicoensis* Breure, 1977 (H = 23.5 mm). **C-D.** ICNB 674 (H = 27.1 mm). **E-G.** *D. (D.) subsemiclausus* (Petit de la Saussaye, 1843). **E.** MNHN-IM-2000-21613, syntype (H = 22.4 mm). **F-G.** UVZ 84035 (H = 20.2 mm). **H-I.** *D. (D.) signifer* (L. Pfeiffer, 1855), NMW 1958.158.25126 (H = 32.7 mm). **J-L.** *D. (D.) iniurius* spec.n., UVZ 97026, holotype (H = 27.6 mm).



**FIGURE 16.** *Drymaeus (Drymaeus)* morphospecies. **A.** *D. (D.)* species 1, UVZ 83078 (H = 28.0). **B-D.** *D. (D.)* species 2, UVZ 97035 (H = 28.0 mm). **E.** *D. (D.)* species 3, UVZ 82098 (H = 26.0 mm). **F.** *D. (D.)* species 5, ICNB 0185 (H = 37.2 mm). **G.** *D. (D.)* species 6, ZMUZ 512117 (H = 34.0 mm). **H.** *D. (D.)* species 7, FMNH 114105 (H = 38.2 mm). **I.** *D. (D.)* species 8, FMNH 106317 (H = 35.9 mm). **J.** *D. (D.)* species 4, MCZ 147223 (H = 37.0 mm).



**FIGURE 17.** *Drymaeus* (*Mesembrinus*) species. **A-B.** *D. (M.)* cf. *amandus* (L. Pfeiffer, 1855), ANSP 47608 (H = 29.2 mm). **C.** *D. (M.) columbiensis* (L. Pfeiffer, 1855), NHMUK 1975221, lectotype (H = 28.0 mm). **D-G.** *D. (M.) roseatus montanus* Pilsbry, 1901, CM 46614, lectotype (H = 28.7 mm). **H-J.** *D. (M.) muliebris* (Reeve, 1849). **H.** NHMUK 1879.2.26.251, lectotype (H = 29.9 mm). **I-J.** ICNB n.c. (H = 22.6 mm). **K-M.** *D. (M.) gorgonensis* Haas, 1966, FMNH 114164, holotype (H = 25.6 mm). **O-S.** *D. (M.) koppeli* (G.B. Sowerby III, 1892). **O.** NHMUK 1907.11.21.133, lectotype (H = 25.5 mm). **P-S.** UMMZ 125084 (H = 25.8 mm). **T-U.** *D. (M.) multilineatus* (Say, 1825). **T-U.** USNM 105077, holotype of *Bulimus parvus* Lea, 1838 (H = 14.6 mm). **V-W.** CM 90282 (H = 23.5 mm). **X-Y.** *D. (M.) tenuilabris* (L. Pfeiffer, 1866), ZMUZ 512266 (H = 35.8 mm). **Z-AA.** *D. (M.) membranaceus* (Philippi, 1846), ZMUZ 512277 (H = 33.0 mm). **AB-AC.** *D. (M.) semimaculatus* Pilsbry, 1898, USNM 105153, syntype (H = 22.2 mm).



**FIGURE 18.** *Drymaeus* (*Mesembrinus*) species. **A-F.** *D. (M.) columbianus* (Lea, 1838). **A-C.** ANSP 192932, lectotype (H = 31.7 mm). **D-F.** USNM 105076, holotype of *Bulimus virgo* Lea, 1838 (H = 25.7 mm). **G-I.** *D. (M.) rufescens pinchoti* Pilsbry, 1930, ANSP 150852, holotype (H = 24.6 mm). **J-L.** *D. (M.) niceforonis* Pilsbry, 1939, ANSP 170697, holotype (H = 20.6 mm). **M.** *D. (M.) lacteus* (Lea, 1838), ANSP 192930, ?lectotype (H = 16.6 mm).

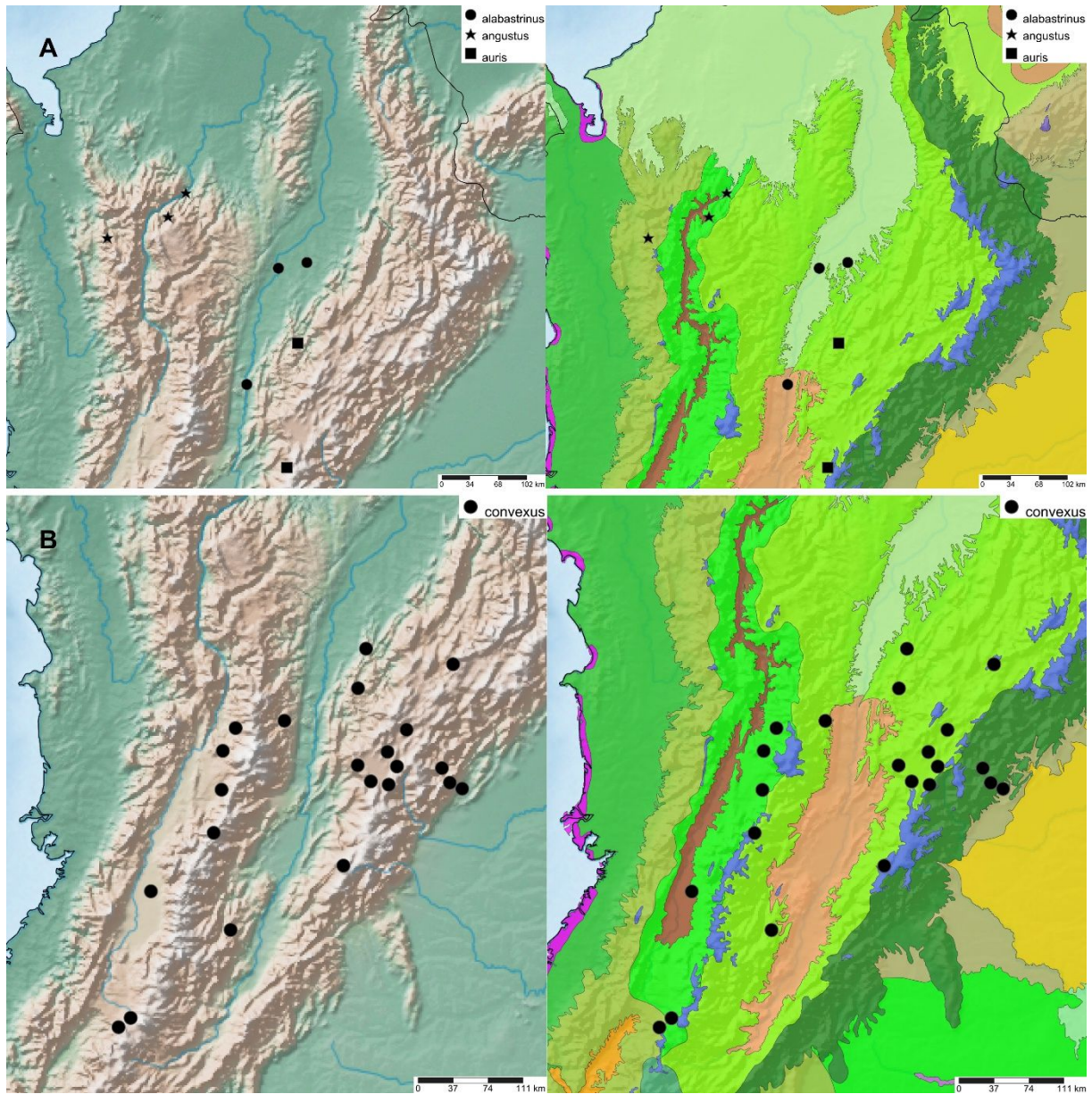


**FIGURE 19.** *Drymaeus* (*Mesembrinus*) species. **A–B.** *D. (M.) depictus* (Reeve, 1849). **A.** NHMUK 1975529, lectotype (H = 27.9 mm). **B.** ANSP 25831 (H = 33.7 mm). **C–D.** *D. (M.) interruptus* (Preston, 1909), USDA 144876 (H = 30.4 mm). **E.** *D. (M.) fidustus* (Reeve, 1849), NHMUK 1975517, lectotype (H = 22.5 mm). **F–H.** *D. (M.) fasciarum* Pilsbry, 1939, ANSP 168429, lectotype (H = 22.0 mm). **I–K.** *D. (M.) tribalteatus* (Reeve, 1848), ZMUZ 512289 (H = 25.3). **L–M.** *D. (M.) iris* (Piaget, 1914), MHNN 35.1645, syntype (H = 26.2 mm). **N.** *D. (M.) laetus* (Reeve, 1849), NHMUK 1975534 (H = 26.6 mm). **O–P.** *D. (M.) cf. lividus* (Reeve, 1850), ZMUZ 512285 (H = 22.5 mm). **Q–S.** *D. (M.) nigrofasciatus* (L. Pfeiffer, 1846). **Q.** NHMUK 1975542, lectotype (H = 23.5 mm). **R–S.** FMNH 114081 (H = 20.0 mm). **T–V.** *D. (M.) semifasciatus* (Mousson, 1869), ZMUZ 512301 (H = 27.9 mm).

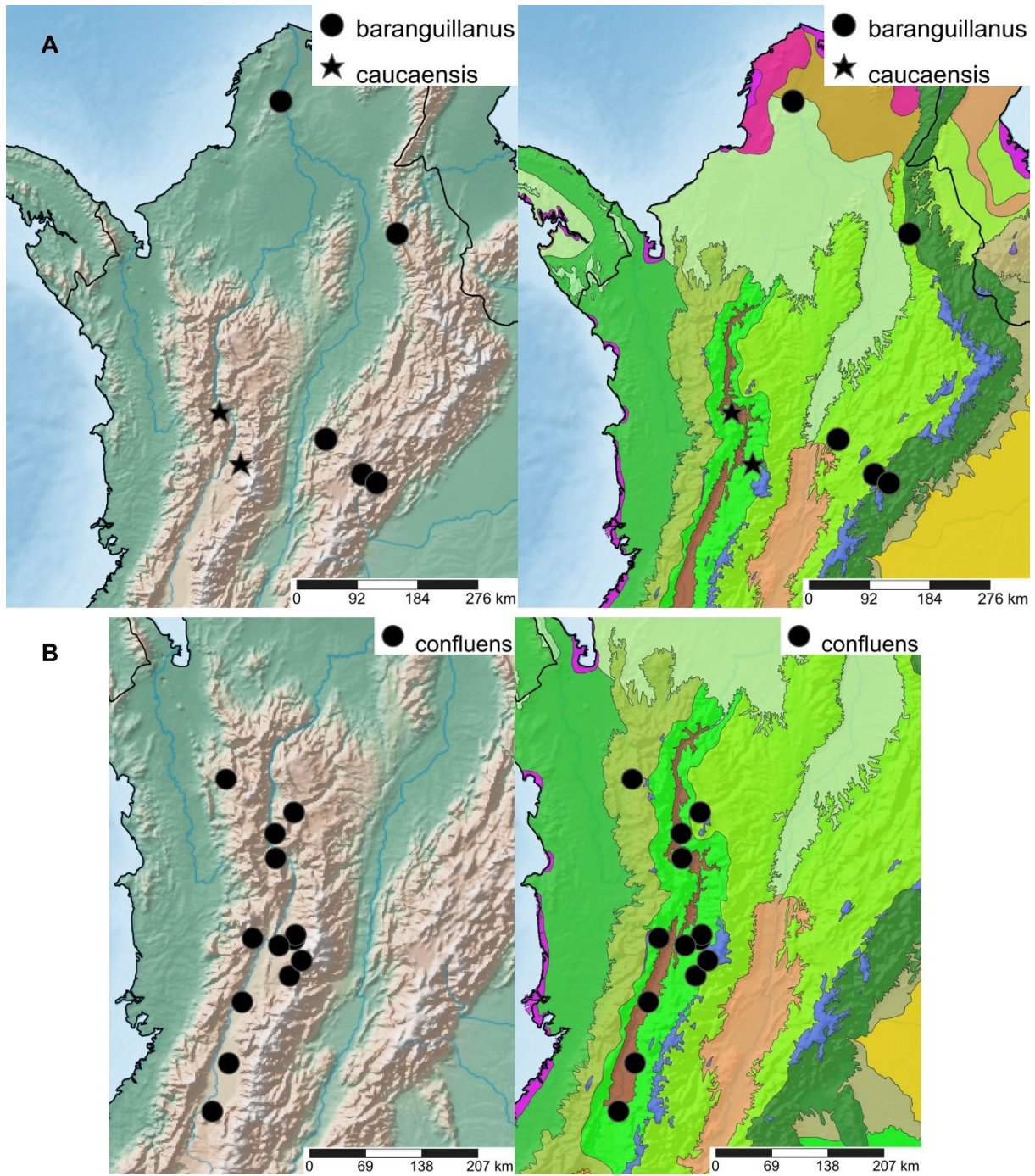




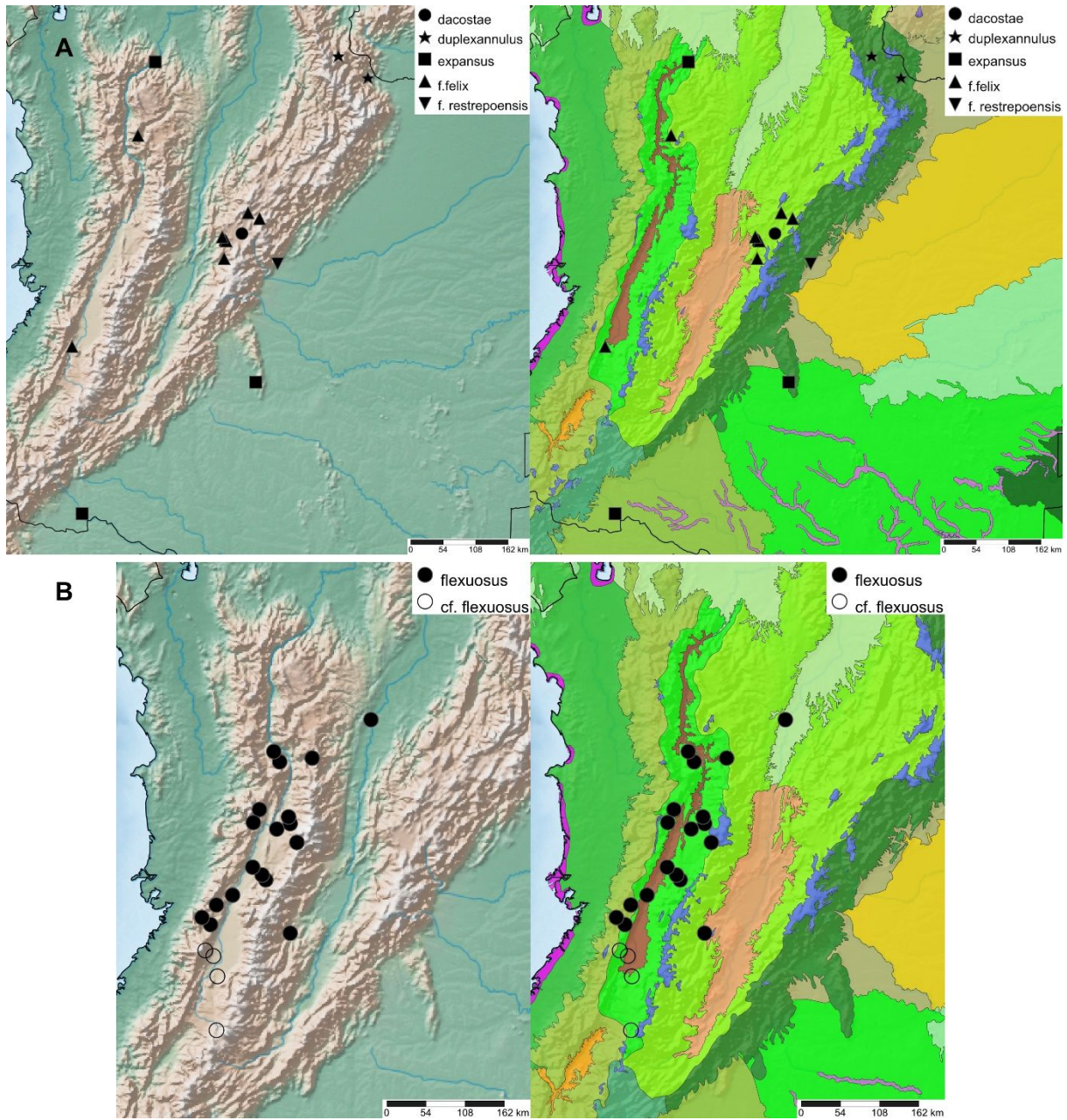
**FIGURE 20.** *Drymaeus (Mesembrinus)* species. **A-B.** *D. (M.)* species 1, USDA 144852 (H = 28.6 mm). **C-D.** *D. (M.)* species 2, ICNB n.c. (H = 23.8 mm). **E-F.** *D. (M.)* species 3, ICNB 2850 (H = 19.8 mm). **G-H.** *D. (M.)* species 4, FMNH 187585 (H = 36.8 mm). **I.** *D. (M.)* species 5, UVZ n.c. (H = ~ 24 mm). **J-K.** *D. (M.)* species 6, GK n.c. (H = 19.0 mm).



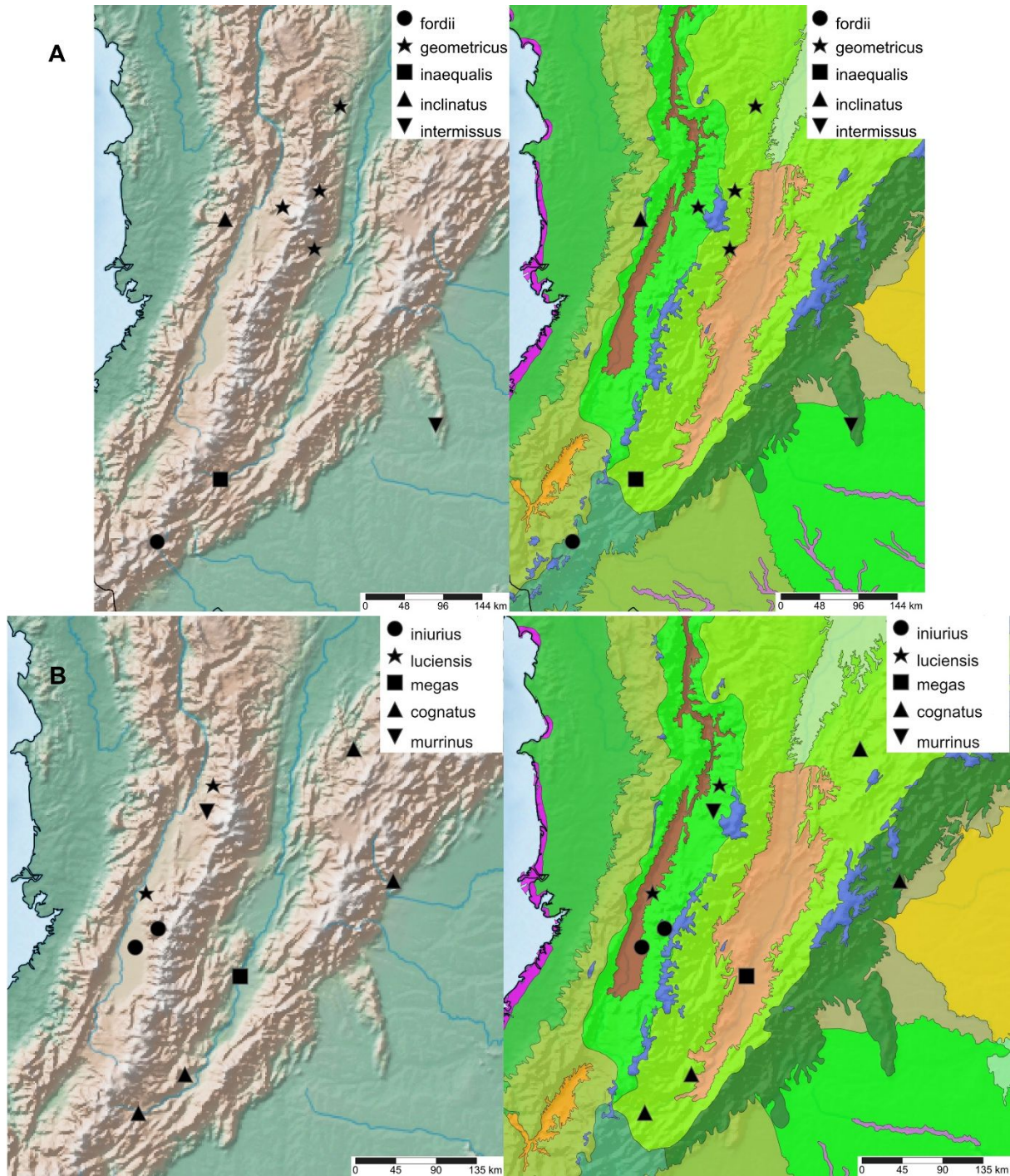
**FIGURE 21.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (D.) alabastrinus* da Costa, 1906, *D. (D.) angustus* da Costa, 1906, and *D. (D.) auris* (L. Pfeiffer, 1866). **B.** *D. (D.) convexus* (L. Pfeiffer, 1855).



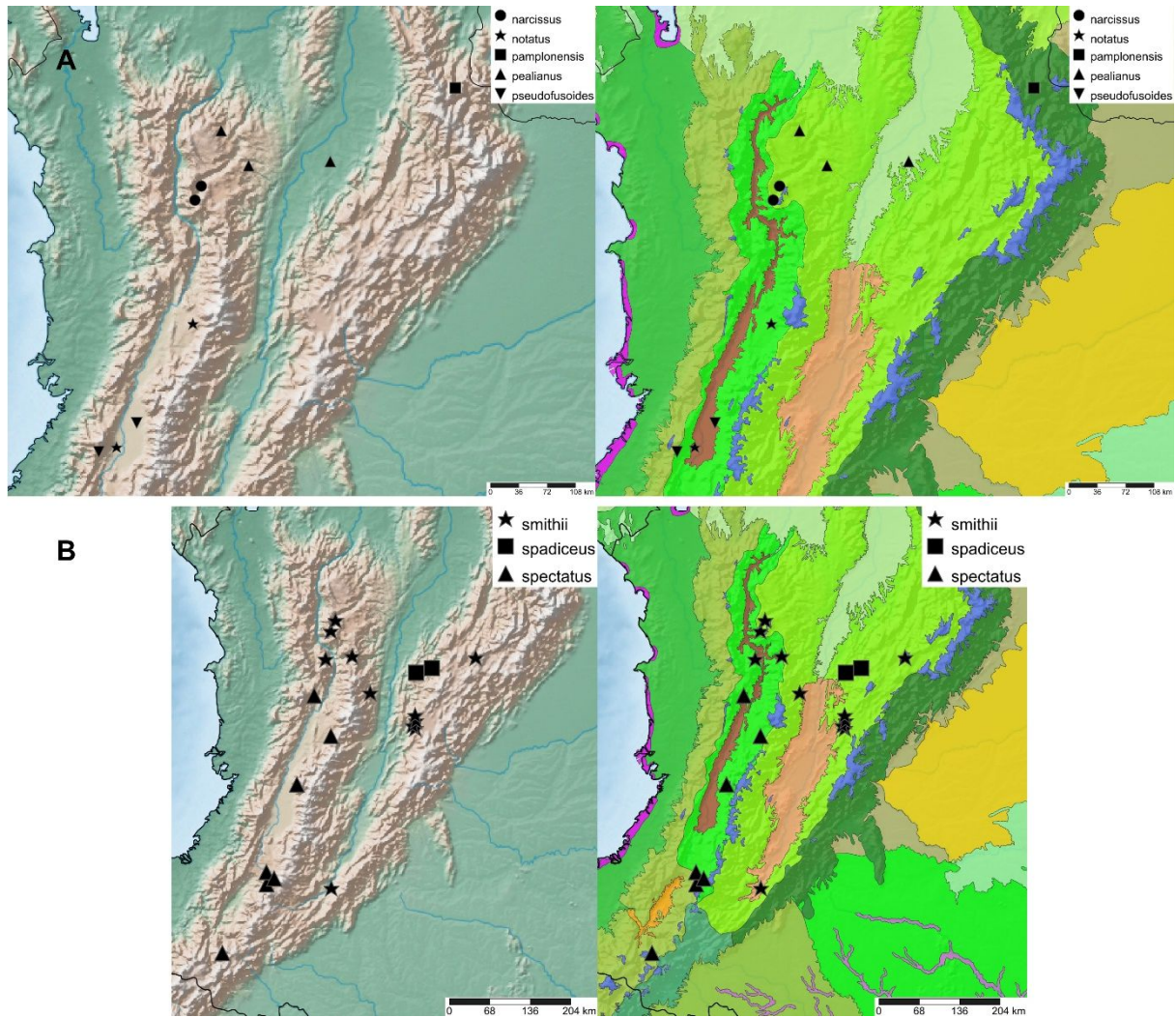
**FIGURE 22.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (D.) baranguillanus* (L. Pfeiffer, 1853), and *D. (D.) caucaensis* (da Costa, 1898). **B.** *D. (D.) confluens* (L. Pfeiffer, 1855).



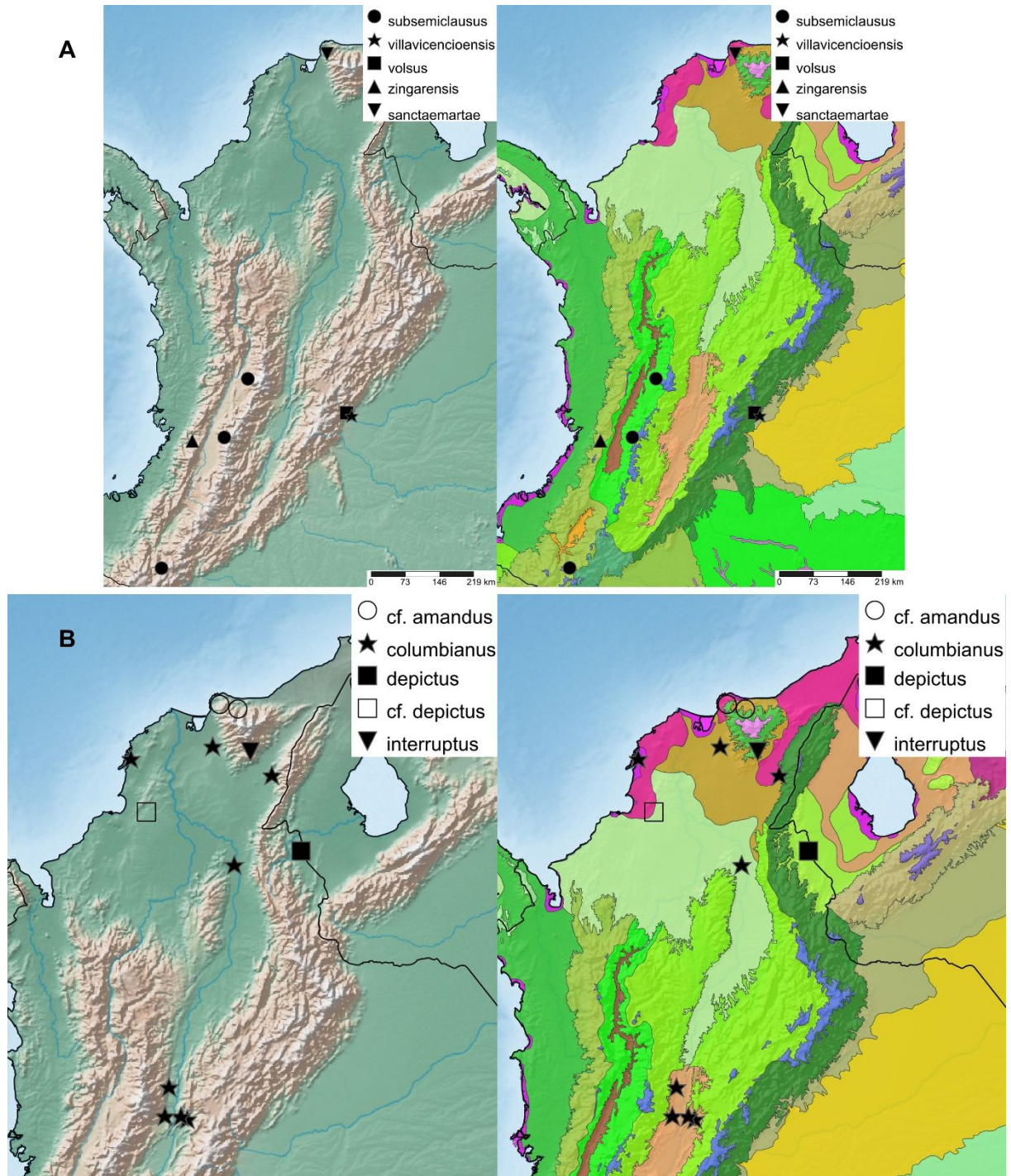
**FIGURE 23.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (D.) dacostae* (G.B. Sowerby III, 1892), *D. (D.) duplexannulus* spec.n., *D. (D.) expansus* (L. Pfeiffer, 1853), *D. (D.) felix felix* (L. Pfeiffer, 1862), and *D. (D.) felix restrepoensis* subsp.n. **B.** *D. (D.) flexuosus* (L. Pfeiffer, 1853).



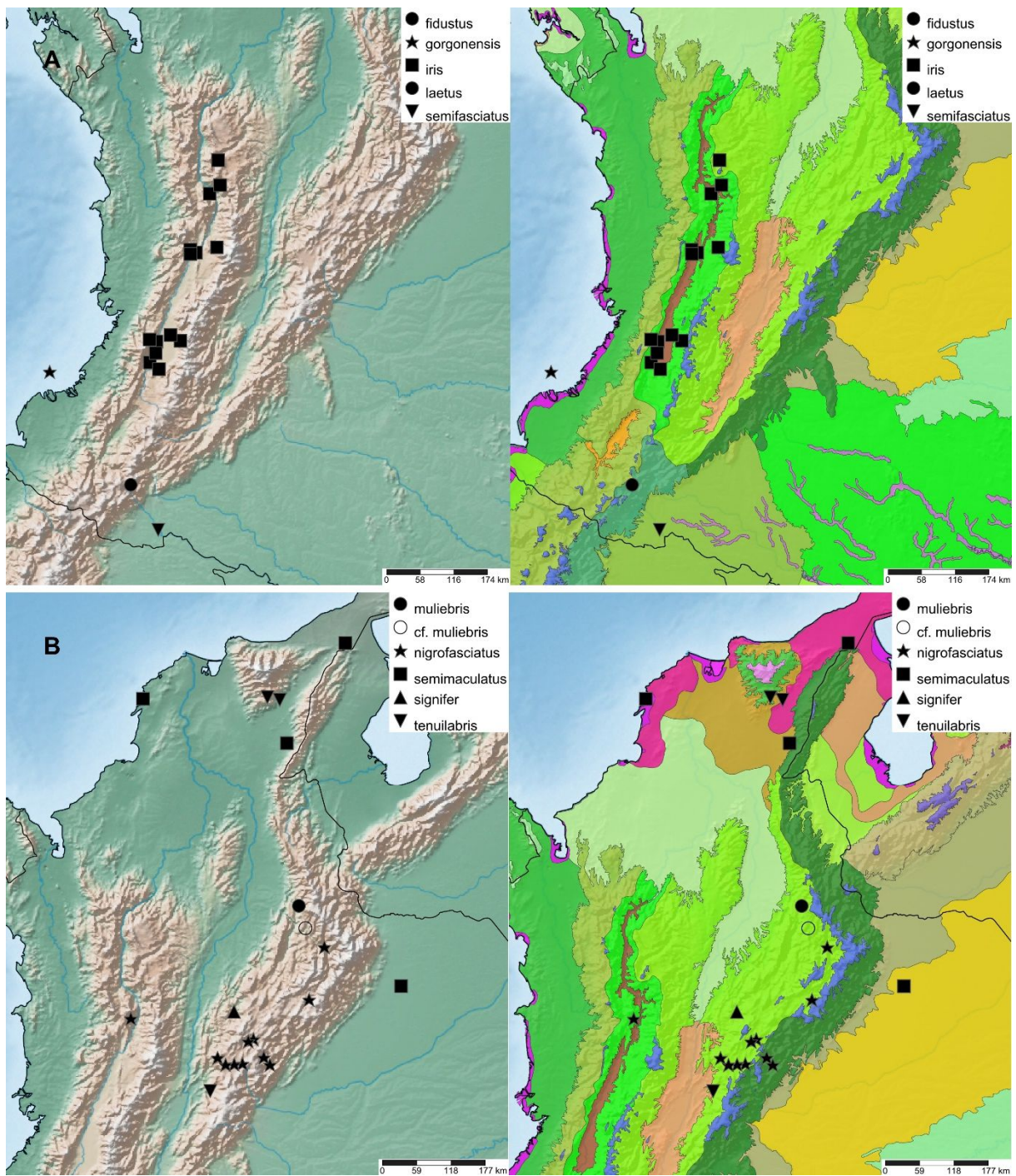
**FIGURE 24.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (D.) fordii* Pilsbry, 1898, *D. (D.) geometricus* (L. Pfeiffer, 1846), *D. (D.) inaequalis* (L. Pfeiffer, 1857), *D. (D.) inclinatus* (L. Pfeiffer, 1862), *D. (D.) intermissus* spec.n. **B.** *D. (D.) iniurius* spec.n., *D. (D.) luciensis* spec.n., *D. (D.) megas* Pilsbry, 1944, *D. (D.) cognatus* Pilsbry, 1901, and *D. (D.) murrinus* (Reeve, 1848).



**FIGURE 25.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (D.) narcissus* (Albers, 1854), *D. (D.) notatus* da Costa, 1906, *D. (D.) pamplonensis* Pilsbry, 1939, *D. (D.) pealianus* (Lea, 1838), and *D. (D.) pseudofusoides* da Costa, 1906. **B.** *D. (D.) smithii* (da Costa, 1898), *D. (D.) spadiceus* da Costa, 1906, and *D. (D.) spectatus* (Reeve, 1849).

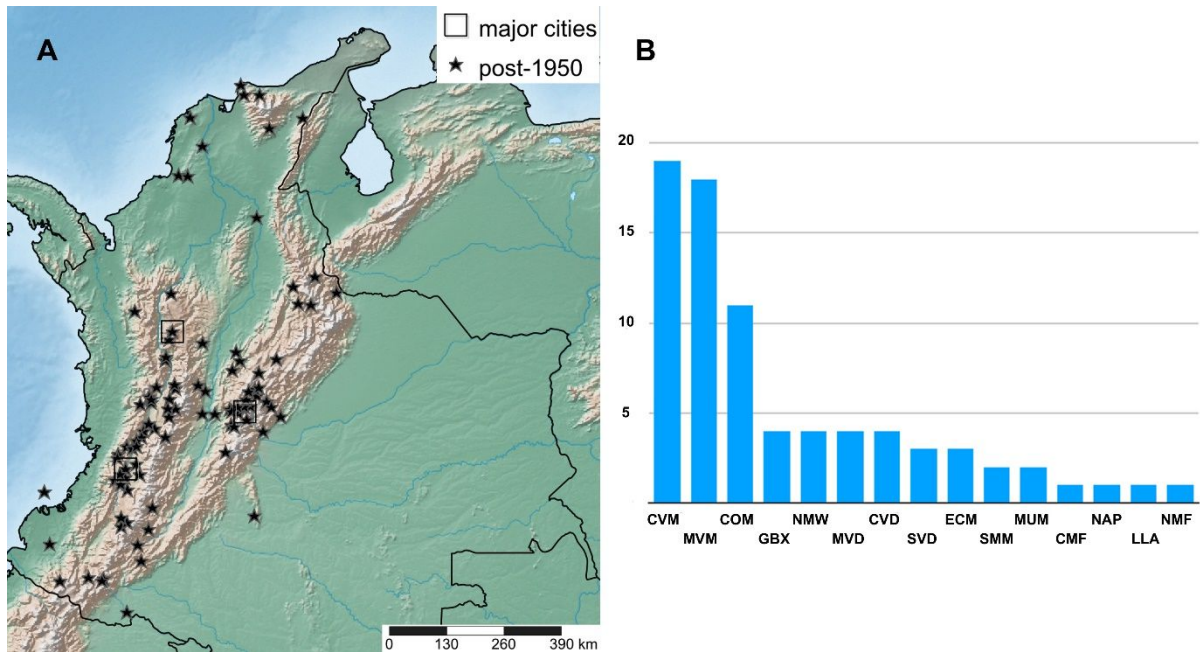


**FIGURE 26.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (D.) subsemiclausus* (Petit de la Saussaye, 1843), *D. (D.) villavicencioensis* Breure, 1977, *D. (D.) volsus* Fulton, 1907, *D. (D.) zingarensis* Restrepo and Breure, 1987, and *D. (D.) sanctaemartae* Pilsbry, 1901. **B.** *D. (M.) cf. amandus* (L. Pfeiffer, 1855), *D. (M.) columbianus* (Lea, 1838), *D. (M.) depictus* (Reeve, 1849), and *D. (M.) interruptus* (Preston, 1909).



**FIGURE 27.** Distribution of *Drymaeus* species in Colombia, respectively in topographic and ecoregions view. **A.** *D. (Mesembrinus) fidustus* (Reeve, 1849), *D. (M.) gorgonensis* Haas, 1966, *D. (M.) iris* (Piaget, 1914), *D. (M.) laetus* (Reeve, 1849), and *D. (M.) semifasciatus* (Mousson, 1869). **B.** *D. (M.) muliebris* (Reeve, 1849), *D. (M.) nigrofasciatus* (L. Pfeiffer, 1846), *D. (M.) semimaculatus* Pilsbry, 1898, *D. (M.) signifer* (L. Pfeiffer, 1855), and *D. (M.) tenuilabris* (L. Pfeiffer, 1866).





**FIGURE 28. A.** Localities where material from this study has been collected in 1950 or later ( $n = 183$ ; only georeferenced localities used). Major cities shown are Bogotá, Cali and Medellín. **B.** Number of species for recorded ecoregions per species ( $n = 51$ ). CMF, Catatumbo moist forests; COM, Cordillera Oriental montane forests; CVD, Cauca Valley dry forests; CVM, Cauca Valley montane forests; ECM, Eastern Cordillera real montane forests; GBX, Guajira-Barranquilla xeric scrub; LLA, Llanos; MUM, Magdalena-Urabá moist forests; MVD, Magdalena Valley dry forests; MVM, Magdalena Valley montane forests; NAP, Northern Andean páramo; NMF, Napo moist forests; NMW, Northwestern Andean montane forests; SMM, Santa Marta montane forests; SVD, Sinú valley dry forests.



*Xerosecta cespitum*, avril 2005, Leucate, Aude © Alain Bertrand

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