

Struggling with shells: *Drymaeus* Albers, 1850 and *Mesembrinus* Albers, 1850 species (Mollusca, Gastropoda, Bulimulidae) from Peru—an illustrated checklist and descriptions of new species

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Abstract. We critically examine Peruvian taxa belonging to the genera *Drymaeus* Albers, 1850 and *Mesembrinus* Albers, 1850, verify their original reference, and figure type materials, if located in and available from museums. We include additional photographs of non-type material when they are deemed useful to show variation. Original figures from the literature are reproduced for some species where photographs of type material are unavailable. We list precise localities in Peru where each species has been collected and map each species. Where possible, the ecoregions in which each species occurs are indicated. A brief history of research on *Drymaeus* and *Mesembrinus* from Peru is included. We recognise 94 valid species of *Drymaeus* and *Mesembrinus*. Additionally, we list 10 taxa that have been erroneously or doubtfully reported from Peru, 10 that are *nomina inquirendi*, and four species that have been transferred to another genus. We believe that our checklist may serve as a baseline document for further research. It can be seen as an intermediate step in the revision of these genera, which will require additional anatomical or molecular study to achieve a stable classification.

The following new species are introduced: *Drymaeus araujoi* Vega-Luz, Breure & Mogollón; *Drymaeus nebulosum* Breure & Ablett; *Mesembrinus marmoratus* Breure, Mogollón & Vega-Luz; *Mesembrinus purpuralabrum* Breure, Mogollón & Vega-Luz.

Two species are reported from the Peruvian malacofauna for the first time: *Drymaeus fusoides* (d'Orbigny, 1835) and *Drymaeus tigrinus* (S.I. da Costa, 1898).

We propose the following new combinations: *Drymaeus combinai* (Weyrauch, 1958); *Mesembrinus acobambensis* (Weyrauch, 1967); *Mesembrinus anceps* (Albers, 1854); *Mesembrinus angulobasis* (Pilsbry, 1944); *Mesembrinus apicepunctata* (Preston, 1914); *Mesembrinus bequaerti* (Weyrauch, 1956); *Mesembrinus caktivorus* (Broderip, 1832); *Mesembrinus chrysomelas* (E. von Martens, 1867); *Mesembrinus clathratus* (L. Pfeiffer, 1858); *Mesembrinus coelestini* (F. Haas, 1952); *Mesembrinus cuzcoensis* (Reeve, 1849); *Mesembrinus cylindricus* (S.I. da Costa, 1901); *Mesembrinus eucosmetus* (F. Haas, 1955); *Mesembrinus farrisi* (L. Pfeiffer, 1858); *Mesembrinus inconspectus* (F. Haas, 1949); *Mesembrinus lamas* (Higgins, 1868); *Mesembrinus laxostylus* (Rolle, 1904); *Mesembrinus leucomelas* (Albers, 1854); *Mesembrinus libertadensis* (Pilsbry, 1898); *Mesembrinus mexicanus* (Lamarck, 1822); *Mesembrinus miltochrous* (Albers, 1854); *Mesembrinus nigroapicatus* (L. Pfeiffer, 1857); *Mesembrinus paeteli* (Albers, 1854); *Mesembrinus pergracilis* (Rolle, 1904); *Mesembrinus phryne* (L. Pfeiffer, 1863); *Mesembrinus praetextus* (Reeve, 1849); *Mesembrinus pseudobesus* (Breure, 1979); *Mesembrinus pulcherrimus* (H. Adams, 1867); *Mesembrinus rosalbus* (Pilsbry, 1932); *Mesembrinus sachsei* (Albers, 1854); *Mesembrinus scitulus* (Reeve, 1849); *Mesembrinus silvanus* (Zilch, 1953); *Mesembrinus succinea* (Pilsbry, 1901); *Mesembrinus trujillensis* (Philippi, 1867); *Mesembrinus vespertinus* (L. Pfeiffer, 1858); *Mesembrinus zilchi* (F. Haas, 1955); "*Mesembrinus*" *vexillum* (W. Wood Sr, 1828).

The following junior subjective synonyms are established: *Drymaeus aurantiostomus* Thompson & Deisler, 1982 = *Drymaeus branneri* F. Baker, 1914; *Drymaeus eusteirus* Pilsbry, 1944 = *Bulimus chanchamayensis* Hidalgo, 1870; *Drymaeus (Mormus) expansus* *flavilabrum* Weyrauch, 1967 = *Bulimus expansus* L. Pfeiffer, 1848; *Drymaeus (Orodrymaeus) farrisi* *quadritaeniatus* Weyrauch, 1956 = *Bulimus farrisi* Pfeiffer, 1858; *Drymaeus (Drymaeus) latitesta* F. Haas, 1952 = *Bulimus icterostomus* E. von Martens, 1901; *Drymaeus beyerleanus* mitchelli Dall 1912 = *Bulimus beyerleanus* Hupé 1857; *Bulimus (Liostracus) fuscobasis* E.A. Smith, 1877 = *Bulimus rectilinearis* L. Pfeiffer, 1855; *Bulimus recedens* L. Pfeiffer, 1864 = *Bulimus serratus* L. Pfeiffer, 1855; *Gonyostomus subhybridus* S.I. da Costa, 1906 = *Otostomus pulcherimus* H. Adams, 1867; *Mesembrinus (Ornatimormus) henrypilsbryi* *densestrigatus* Weyrauch, 1958 = *Mesembrinus (Ornatimormus) henrypilsbryi* *pichitacalugaënsis* Weyrauch 1958 = *Mesembrinus (Ornatimormus) henrypilsbryi* Weyrauch, 1958 = *Bulimulus pergracilis* Rolle, 1904; *Bulimus canarius* L. Pfeiffer, 1867 = *Bulimus trujillensis* Philippi, 1867; *Bulimus serenus* Philippi, 1867 = "Mesembrinus" *vexillum* (Wood, 1828).

The generic placements of "*Drymaeus*" *expansus* (L. Pfeiffer, 1848) and "Mesembrinus" *vexillum* (W. Wood Sr, 1828) are provisionally pending future molecular study.

The need for additional research is demonstrated by the fact that for 15 species only imprecise localities are known, while for 33 species no records are available within the last 50 years.

Key words. History of collecting, new combinations, new species, new synonyms, Orthalicoidea, Peltellinae

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CONTENTS

Introduction	295
Historical authors and collections of the Peruvian terrestrial malacofauna	297
Materials and Methods	299
Systematic Catalogue	300
Family Bulimulidae Tryon, 1867	300
Genus <i>Drymaeus</i> Albers, 1850	300
<i>D. abruptus</i> (Rolle, 1904)	300
<i>D. araujoi</i> Vega-Luz, Breure & Mogollón sp. nov.	300
<i>D. arcuatostriatus</i> (L. Pfeiffer, 1855)	301
<i>D. aurisratti</i> (Philippi, 1867)	302
<i>D. bartletti</i> (H. Adams, 1867)	303
<i>D. basitorus</i> F. Haas, 1951	303
<i>D. beyerleanus</i> (Hupé, 1857)	303
<i>D. branneri</i> F. Baker, 1914	304
<i>D. cantatus</i> (Reeve, 1848)	304
<i>D. castaneostrigatus</i> S.I. da Costa, 1906	305
<i>D. catenae</i> F. Haas, 1952	305
<i>D. chanchamayensis</i> (Hidalgo, 1870)	306
<i>D. combinai</i> (Weyrauch, 1958) comb. nov.	306
<i>D. costatus</i> Breure & Vega-Luz, 2021	307
<i>D. edmuelleri</i> (Albers, 1854)	307
<i>D. elsteri</i> S.I. da Costa, 1901	309
<i>D. eurystomus</i> (Philippi, 1867)	309
<i>D. expansus</i> (L. Pfeiffer, 1848)	309
<i>D. fordii</i> Pilsbry, 1898	312
<i>D. fusoides</i> (d'Orbigny, 1835)	312
<i>D. gibber</i> F. Haas, 1949	314
<i>D. gueinzii</i> (L. Pfeiffer, 1857)	314
<i>D. icterostomus</i> (E. von Martens, 1901)	314

<i>D. inaequalis</i> (L. Pfeiffer, 1857)	315
<i>D. inca</i> M. Smith, 1943	315
<i>D. interictus</i> (E. von Martens, 1867)	316
<i>D. jousseaumei</i> Dautzenberg, 1901	316
<i>D. lucculentus</i> Breure & Vega-Luz, 2021	317
<i>D. marcapatensis</i> Breure, 1979	317
<i>D. multiguttatus</i> Weyrauch, 1964	318
<i>D. nebulosum</i> Breure & Ablett sp. nov.	318
<i>D. ommatidia</i> Dorado & Roosen, 2023	319
<i>D. palassus</i> Breure & Eskens, 1981	320
<i>D. peelii</i> (Reeve, 1859)	320
<i>D. protractus</i> (L. Pfeiffer, 1855)	320
<i>D. punctatus</i> S.I. da Costa, 1907	321
<i>D. rectilinearis</i> (L. Pfeiffer, 1855)	322
<i>D. regularis</i> Fulton, 1905	322
<i>D. rosenbergi</i> S.I. da Costa, 1906	323
<i>D. rugistriatus</i> F. Haas, 1952	323
<i>D. schunkei</i> F. Haas, 1949	323
<i>D. scoliodes</i> Dautzenberg, 1901	324
<i>D. serratus</i> (L. Pfeiffer, 1855)	324
<i>D. similaris</i> (J. Moricand, 1856)	325
<i>D. sophiae</i> Breure, 1979	325
<i>D. strigatus</i> (G.B. Sowerby I, 1833)	326
<i>D. subeffusus</i> (Philippi, 1869)	327
<i>D. subsimilis</i> Pilsbry, 1898	327
<i>D. tigrinus</i> (S.I. da Costa, 1898)	328
<i>D. translucidus</i> Weyrauch, 1967	328
<i>D. valentini</i> (Breure & Vega-Luz, 2020)	328
<i>D. verecundus</i> Breure & Mogollón, 2019	329
<i>D. weeksi</i> Pilsbry, 1926	329
Genus <i>Mesembrinus</i> Albers, 1850	330
<i>M. acobambensis</i> (Weyrauch, 1967) comb. nov.	330
<i>M. aestivus</i> (L. Pfeiffer, 1857) comb. nov.	330

<i>M. alsophilus</i> (Philippi, 1867) comb. nov.	331
<i>M. anceps</i> (Albers, 1854) comb. nov.	331
<i>M. angulobasis</i> (Pilsbry, 1944) comb. nov.	331
<i>M. apicepunctata</i> (Preston, 1914) comb. nov.	332
<i>M. bequaerti</i> (Weyrauch, 1956) comb. nov.	333
<i>M. caktivorus</i> (Broderip, 1832) comb. nov.	333
<i>M. celendinensis</i> (Weyrauch, 1956)	334
<i>M. chrysomelas</i> (E. von Martens, 1867) comb. nov.	334
<i>M. clathratus</i> (L. Pfeiffer, 1858) comb. nov.	334
<i>M. coelestini</i> (F. Haas, 1952) comb. nov.	335
<i>M. cuzcoensis</i> (Reeve, 1849)	335
<i>M. cylindricus</i> (S.I. da Costa, 1901) comb. nov.	335
<i>M. eucosmetus</i> (F. Haas, 1955) comb. nov.	336
<i>M. farrisi</i> (L. Pfeiffer, 1858) comb. nov.	336
<i>M. inconspicuus</i> (F. Haas, 1949) comb. nov.	337
<i>M. lamas</i> (Higgins, 1868) comb. nov.	337
<i>M. laxostylus</i> (Rolle, 1904) comb. nov.	338
<i>M. leucomelas</i> (Albers, 1854) comb. nov.	338
<i>M. libertadensis</i> (Pilsbry, 1898) comb. nov.	338
<i>M. marmoratus</i> Breure, Mogollón & Vega-Luz sp. nov.	339
<i>M. mexicanus</i> (Lamarck, 1822) comb. nov.	340
<i>M. miltochrous</i> (Albers, 1854) comb. nov.	341
<i>M. nigroapicatus</i> (L. Pfeiffer, 1857) comb. nov.	341
<i>M. paeteli</i> (Albers, 1854) comb. nov.	342
<i>M. pergracilis</i> (Rolle, 1904) comb. nov.	342
<i>M. phryne</i> (L. Pfeiffer, 1863) comb. nov.	343
<i>M. ponsonbyi</i> (S.I. da Costa, 1907) comb. nov.	343
<i>M. praetextus</i> (Reeve, 1849) comb. nov.	344
<i>M. pseudobesus</i> (Breure, 1979) comb. nov.	344
<i>M. pulcherrimus</i> (H. Adams, 1867) comb. nov.	345
<i>M. purpuralabrum</i> Breure, Mogollón & Vega-Luz sp. nov.	345
<i>M. rosalbus</i> (Pilsbry, 1932) comb. nov.	346
<i>M. sachsei</i> (Albers, 1854) comb. nov.	347
<i>M. scitulus</i> (Reeve, 1849) comb. nov.	347
<i>M. silvanus</i> (Zilch, 1953) comb. nov.	348
<i>M. trujillensis</i> (Philippi, 1867) comb. nov.	348
<i>M. vespertinus</i> (L. Pfeiffer, 1858) comb. nov.	349
<i>M. zilchi</i> (F. Haas, 1955) comb. nov.	349
" <i>M.</i> " <i>vexillum</i> (W. Wood Sr, 1828) comb. nov.	350
Species erroneously or doubtfully reported from Peru	351
<i>Nomina inquirendi</i>	351
Species to be classified in other genera	352
Discussion	352
Acknowledgements	353
References	353
Appendix	357

INTRODUCTION

Drymaeus Albers, 1850 (*sensu lato*), recently the subject of molecular studies (Salvador et al. 2023), is a very species-rich group, occurring in South and Central America,

the Caribbean islands, and in the south of North America. *Drymaeus* species are usually variable, sometimes only in colour pattern, sometimes in their shape, and sometimes in both. This makes the classification of species from this genus often challenging and has led to a proliferation of available names, of which quite a substantial number have been put in the synonymy of earlier published species.

Drymaeus was first described by Albers (1850) who recognised two other taxa, *Mesembrinus* and *Hamadryyas*, of equal status. Martens (1860) placed the latter in synonymy with *Drymaeus* but kept *Mesembrinus* as a distinct group of species. Pilsbry (1897–1898: 192) wrote:

The passage of *Drymaeus* with expanded or reflexed peristome into *Mesembrinus* with its simple and acute [peristome], is a gradual one, and many species are arbitrarily assigned to one or the other section In some cases it is easy to see that species of both groups inhabiting one region are of common origin, and more nearly related to each other than to species of their respective sections in distinct locations.

Therefore, he adopted a geographic grouping of species into South American, Antillean and North American species. Subsequently, he described three new sections of *Drymaeus*: *Metadrymaeus*, *Orodrymaeus* (both Pilsbry 1926), and *Leptodrymaeus* (Pilsbry 1946). Further divisions were introduced by Germain (1907: *Antidrymaeus*) and Weyrauch (1958: *Ornatimormus*, *Leptomormus*; 1964: *Diaphanomormus*) (Table 1). The taxonomy of this group had been primarily based on external morphology, although Breure & Eskens (1981) studied both the external morphology and the anatomy and histology of several species. Other than *Drymaeus* and *Mesembrinus*, they failed to find clear distinctions among *Drymaeus* species. When molecular research became possible, the results for this genus (Breure & Romero 2012) were at first inconclusive due to the limited sampling of taxa. However, the phylogenetic analysis of Salvador et al. (2023), which included 21 species, suggested the division of *Drymaeus sensu lato* into *Drymaeus*, *Antidrymaeus*, and *Mesembrinus*. Breure et al. (2024) recently provided details on the monophyletic group of *Antidrymaeus* species and expected that additional research in the field might add to the number of species classified within this genus. Additional species available for DNA analysis is clearly needed and may result in more genus-level subdivisions.

We note that most *Drymaeus* taxa are challenging to identify on the basis of shells alone. Apart from some very recognisable taxa, many species are polymorphic in their colour pattern and some also show variation in their shell morphology, for example, in the shape of the aperture.

Table 1. Classification of *Drymaeus* and *Mesembrinus* through time. Implicit synonyms indicated by square brackets. Valid taxa in bold type. Blank cells indicate the need for DNA sequencing to ascertain the status of the taxon.

Taxon	Pilsbry 1897–1898, 1899	Weyrauch 1958	Zilch 1960	Breure 1960	Schileyko 1979	Schileyko 1999	Salvador et al. 2023	Type species
<i>Drymaeus</i> Albers, 1850	<i>Drymaeus</i> (<i>Drymaeus</i>) (1)	<i>Drymaeus</i>	<i>Drymaeus</i> (<i>Drymaeus</i>)	<i>Drymaeus</i> (<i>Drymaeus</i>)	<i>Drymaeus</i> (<i>Drymaeus</i>)	<i>Drymaeus</i> (<i>Drymaeus</i>)	<i>Drymaeus</i>	<i>hygrolyaeus</i>
<i>Bulimus</i> (<i>Goniognathmus</i>) P. Fischer & Crosse, 1875	[<i>Bulimus</i> (<i>Goniognathmus</i>)]		[<i>Goniognathmus</i>]	[<i>Goniognathmus</i>]	[<i>Goniognathmus</i>]	[<i>Goniognathmus</i>]		<i>lattrei</i>
<i>Bulimus</i> (<i>Semiclausaria</i>) L. Pfeiffer, 1856			[<i>Semiclausaria</i>]	[<i>Semiclausaria</i>]	[<i>Semiclausaria</i>]	[<i>Semiclausaria</i>]		<i>semiclausus</i>
<i>Bulimus</i> (<i>Mormus</i>) E. von Martens, 1860	[<i>Mesembrinus</i>]	<i>Mesembrinus</i> (<i>Mormus</i>)	[<i>Mormus</i>]	[<i>Mormus</i>]	[<i>Mormus</i>]	[<i>Mormus</i>]		<i>papyraceus</i>
<i>Drymaeus</i> (<i>Metadrymaeus</i>) Pilsbry, 1926				<i>Drymaeus</i> (<i>Metadrymaeus</i>)	[<i>Metadrymaeus</i>]	<i>Drymaeus</i> (<i>Metadrymaeus</i>)		<i>josephus</i>
<i>Drymaeus</i> (<i>Orodrymaeus</i>) Pilsbry, 1926				<i>Drymaeus</i> (<i>Orodrymaeus</i>)	[<i>Orodrymaeus</i>]			<i>farrisi</i>
<i>Mesembrinus</i> (<i>Ornatimormus</i>) Weyrauch, 1958				<i>Mesembrinus</i> (<i>Ornatimormus</i>)	[<i>Ornatimormus</i>]	<i>Drymaeus</i> (<i>Ornatimormus</i>)		<i>angulobasis</i>
<i>Mesembrinus</i> Albers, 1850				<i>Mesembrinus</i> (<i>Mesembrinus</i>)		<i>Drymaeus</i> (<i>Mesembrinus</i>)		<i>virginalis</i>
<i>Drymaeus</i> (<i>Leptodrymaeus</i>) Pilsbry, 1946				[<i>Leptodrymaeus</i>]	<i>Drymaeus</i> (<i>Leptodrymaeus</i>)	[<i>Leptodrymaeus</i>]	[<i>Leptodrymaeus</i>]	<i>dominicu</i> s
<i>Drymaeus</i> (<i>Antidrymaeus</i>) Germain, 1907				[<i>Antidrymaeus</i>]	<i>Drymaeus</i> (<i>Antidrymaeus</i>)	[<i>Antidrymaeus</i>]	[<i>Antidrymaeus</i>]	<i>inusitatus</i>
<i>Mesembrinus</i> (<i>Leptomormus</i>) Weyrauch, 1958				<i>Mesembrinus</i> (<i>Leptomormus</i>)	[<i>Leptomormus</i>]	[<i>Leptomormus</i>]	[<i>Leptomormus</i>]	<i>bequaerti</i>
<i>Drymaeus</i> (<i>Diaphanomormus</i>) Weyrauch, 1964					[<i>Diaphanomormus</i>]	[<i>Diaphanomormus</i>]	[<i>Diaphanomormus</i>]	<i>coelestini</i> <i>obesus</i>

Moreover, some authors in the past did not critically examine the protoconch sculpture, which is quite characteristic in *Drymaeus*, *Mesembrinus*, and *Antidrymaeus*, albeit also occurring in related genera such *Newboldius* Pilsbry, 1932 and *Stenostylus* Pilsbry, 1898. For these reasons, past authors may have named more species-level taxa than the number of valid species than we present in this paper.

In Ramírez *et al.*'s (2003) list of molluscs of Peru, 124 *Drymaeus* species were included, but without further data. More recently, additional species have been described and others have been placed in synonymy. We have tried to critically examine all taxa as part of our ongoing illustrated checklist of Peruvian land snails. This paper may serve as a baseline document for future research and as an intermediate step in a revision of the Peruvian species of *Drymaeus* and *Mesembrinus*.

Historical authors and collections of the Peruvian terrestrial malacofauna

One of the first dedicated shell collectors who visited the country (Fig. 1) was Hugh Cuming (1791–1865), who sailed along the west coast of South America during the years 1828–1830. Dance (1986: 113–115) wrote:

The details of this voyage are not available to us and it is necessary to delve into later zoological and botanical literature to ascertain something of its nature and extent ... Cuming's exact route is not known but it seems that he collected at frequent intervals along its entire coastline, often taking trips inland to collect non-marine shells and other animals and plants.

Cumingian localities are sometimes questioned on their veracity, and Dance (1986: 127–128) stated:

The confusion created by some of the Cumingian localities arise from their brevity, a common fault of locality information in nineteenth-century conchological literature, or from the failure to distinguish between localities sharing the same name but not the same geographical position. ... many other Cumingian localities have been shown to be completely erroneous, so many in fact that the accuracy of all Cuming's data is seriously impugned.

Dance continued with the story of Mrs Gray's mixing of locality labels and concluded, "I have no doubt the myth will prove to be virtually indestructible" (Dance 1986: 128–131). Cuming's collection is now in the Natural History Museum in London. Some of us, who have done considerable research on type material from the Cuming collection, feel that the conclusion of Dance is a bit of an overstatement

(at least for the genera treated in this paper), but we generally encourage a critical view of Cumingian localities based on their labels. Material from other collectors, who remain known solely by their surname, like Farris, Gueinzius, and Yates, to mention but a few, ended up in the Cuming collection. New species from that collection were described by several well-known malacologists such as William Broderip (1789–1859), Louis Pfeiffer (1805–1877), Lovell Reeve (1814–1865), and the Sowerby family.

Alcide d'Orbigny (1802–1857) visited Peru a few years after Cuming, in 1833, staying for only one week in Callao and Lima (Papavero 1971: 143). Shortly afterwards the expedition of HMS *Beagle* with Charles Darwin on board reached Callao in July 1835. Darwin found the country in a state of anarchy and only made brief excursions around Lima before the *Beagle* sailed further north to the Galápagos (Darwin 1845 [2021]: 626–631). In March 1839, Claude Gay (1800–1873) travelled to Peru and explored the regions of Tingo Maria, Cuzco, the Rio Urubamba, the valley of Santa Ana, Arequipa, and Lima (Papavero 1971: 149).

From 1843–1847 a French expedition led by François de Castelnau (1810–1880; but see Bajon 1995: 337) aimed to explore the Amazon and to find the watershed between the Amazon and the La Plata basins (Papavero 1971: 149–158, map 12; Bajon 1995: 340–343); they started in Rio de Janeiro and travelled through Brazil and Bolivia. In December 1845 they entered Peru along Titicaca Lake, went to Puno and then to Arequipa. From there they travelled in January 1846 along the coast to Lima. After a prolonged stay in that city they travelled to Cerro de Pasco, Junin, Huancavelica, Ayacucho, Abancay, Cuzco, and the Urubamba valley until they reached Sarayacu. From there they crossed the Andes via the Ucayali valley to the Marañón river, finally arriving at Pebas in December 1845. They went from there down the Amazon until they reached Belém. The malacological material collected was examined by Louis Hupé who published his results in 1857. Marius Porte (?–1866) travelled within Peru and supplied material to Jacques Moricand (1823–1877), who described new taxa in 1856 and 1858 (Breure & Tardy 2016). In the same period other individual collectors visited the country; among others we mention Józef Warszewicz (1812–1866), mostly known for his botanical work, whose shells were described by Johann Albers (1795–1857).

The Spanish Comisión Científica del Pacífico explored South America between 1862–1866 and visited Peru (Breure & Araujo 2017). The material was mainly described by Joaquín Hidalgo (1839–1923) and Hippolyte Crosse (1826–1898) and has been deposited in the Museo Nacio-



Figure 1. Physiography of Peru. Source: Perry-Castañeda Library Map Collection, University of Texas at Austin (modified; in public domain).

nal de Ciencias Naturales, Madrid and Muséum national d'Histoire Naturelle, Paris. Around the same time Arthur Morelet (1809–1892) published on Peruvian species from the collection of Léonce Angrand (1808–1886) in the Musée d'Histoire Naturelle, Geneva (Morelet 1863). Antonio Raimondi (1826–1890) emigrated to Peru in 1850 where he soon became professor of natural history. He made extensive journeys to all regions of the country and collected among other naturalia, shells that were described by Rudolph Philippi (1808–1904) and some by Louis Pfeiffer. In 1869 Konstanty Jelski (1837–1896) arrived in Peru where he conducted field work around Lima, and in Ayacucho, Junin and La Libertad departments. He was later seconded by Jan Sztolcman (1854–1928) who did further research along the Peruvian coast and in the Amazon basin after Jelski had returned to Europe in 1879 (Mierswa-Szymkowiak & Breure 2017). Their material was published by Władysław Lubomirski (1824–1882) in 1880.

Around the turn of the 20th century, we see contributions by Philippe Dautzenberg (1849–1935) based on a collection made by G.A. Baer. English authors also described several species, among them Solomon da Costa (1827–1907), Hugh Fulton (1861–1942), and Hugh Preston (1871–1945). In 1911, the Yale Peruvian Expedition searched for and re-found Machu Picchu, the last capital of the Inca. The shells collected during that expedition were studied by William Dall (1845–1927) and published in 1912. During this time, a Peruvian conchologist, José Bravo (1874–1927), was in contact with European and American colleagues, which facilitated the exchange of material; see Mogollón & Breure (2009) for his biography and details on his collection.

Henry Pilsbry (1862–1957), renowned for his *Manual of Conchology* which revised many groups of terrestrial snails, visited Peru in 1948. He wrote a series of papers on Peruvian species, some together with Axel Olsson (1889–1977), who was a geologist and invertebrate palaeontologist. A contemporary, Fritz Haas (1886–1969), also published in the late 1940s to mid-1950s a series of papers on Peruvian land snails; the material was collected by various persons, one of which was Wolfgang Weyrauch (1907–1970). This German biologist worked for many years in Peru and Argentina beginning in the 1940s until his death. He only collected at first and let others describe his material, but starting in the 1950s he initially collaborated with Adolf Zilch (1911–2006), then later published several large papers describing many new taxa as the sole author (Barbosa *et al.* 2008; Breure 2012). One of us (B. Breure) made extensive collecting trips in Peru during 1975–1976 (Breure 1975) and published regularly on the Peruvian malacofauna, with an interlude of some decades,

and with several papers together with Valentín Mogollón or Ricardo Vega. Rina Ramírez, who is currently the curator at the Museo Historia Natural in Lima, has contributed, with her students, several studies on land snails.

MATERIALS AND METHODS

This paper presents the published species-group and genus-group names found in literature, that have been applied to the molluscs of *Drymaeus* (*sensu lato*) of Peru, as well as unpublished records from museum collections and online databases that we were able to check. The main body of the text was finished in March 2024. The classification of *Drymaeus* (*sensu lato*) has changed over time and with different authors (Table 1).

In the checklist, names are alphabetically arranged by genus (and subgenus). Basionyms are included, but for chresonyms see Richardson (1995).

Where type materials have been located, we provide a figure. When types have not been found, or are lost, the original figures are reproduced.

The following abbreviations are used in the checklist to refer to public museum or private collections. For those collections preceded by an asterisk (*), their online databases were consulted.

AMNH, American Museum of Natural History, New York,
USA

ANSP*, Academy of Natural Sciences, Philadelphia, USA

CCD, Carlos Dorado (private collection)

CM, Carnegie Museum, Pittsburgh, USA

DMNH, Delaware Museum of Natural History, Wilmington,
USA

DMNS, Denver Museum of Nature and Science, Denver,
USA

FEM, Femorale (business collection)

FMNH, Field Museum of Natural History, Chicago, USA

FML / IFML-MOLL, Fundación Miguel Lillo, Tucumán,
Argentina

MCNB / MCNB-MZB, Museu de Ciències Naturals de Barcelona, Barcelona, Spain

MCZ*, Museum of Comparative Zoology, Cambridge, USA

MNCN, Museo Nacional de Ciencias Naturales, Madrid,
Spain

MHNG, Musée d'Histoire Naturelle, Geneva, Switzerland

MNHN*, Muséum national d'Histoire Naturelle, Paris, France

NHM / NHMUK*, Natural History Museum, London,
United Kingdom

RMNH / RMNH-MOL*, Naturalis Biodiversity Center
(formerly Rijksmuseum van Natuurlijke Historie), Leiden

den, the Netherlands
 RVL, Ricardo Vega-Luz (private collection)
 SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, USA
 SMF, Senckenberg Naturmuseum, Frankfurt am Main, Germany
 USNM*, National Museum of Natural History, Washington DC, USA
 VMA, Valentín Mogollón Ávila (private collection)
 ZMA / ZMA-MOLL*, Naturalis Biodiversity Center (formerly Zoologisch Museum Amsterdam), Leiden, the Netherlands
 ZSM, Zoologische Staatssammlung München, Germany
 Other online databases were searched for additional records:
 Invert-E-base (<http://www.invertebase.org>)
 GBIF (<https://doi.org/10.15468/>)
 iNaturalist (<https://www.inaturalist.org>)

As several species are prone to being misidentified, we accepted and included records in collection databases in the checklist if we could check the vouchers or if the localities were within the known range of the species. Observations from iNaturalist have only been included if they could be confirmed by one of us, and those that could not be confirmed have been omitted.

Localities are arranged according to department, the main administrative division of Peru. Except for type localities, records lacking precise locations have been disregarded, as a complete listing of all Peruvian records in museums is beyond the scope of this project.

Four gazetteers were used to find and georeference localities (see Appendix, Table A1):

Geonames (<http://www.geonames.org/>)
 Ornithological gazetteer of Peru (Stephens & Traylor 1983)

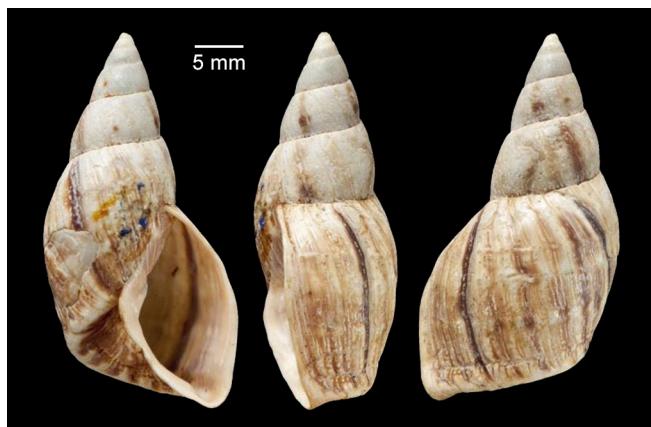


Figure 2. *Drymaeus abruptus* (Rolle, 1904). Syntype NHMUK 1904.1.12.1.

Toponimos quechua del Perú (Espinoza 1973)
 El Peru. Itinerarios de viajes (Raimondi 1879)

Distribution maps were made with SimpleMappr (Short-house 2010), with ecoregions shown in colour. A key to the ecoregions is provided in the Appendix, Table A2 and Figure A2. In Appendix Figure A1, all georeferenced records are plotted on ecoregion maps when precise localities are available that could be georeferenced.

Photographs of shells were taken with digital cameras by the staff at the respective institutions (see Acknowledgements).

SYSTEMATIC CATALOGUE

Family Bulimulidae Tryon, 1867

Genus *Drymaeus* Albers, 1850

Drymaeus Albers 1850: 155. Type species by subsequent designation (Pilsbry 1898 [1897–1898]: 182): *Helix hygrohylaeus* d'Orbigny, 1835.

Due to a lack of sufficient material for anatomical and phylogenetic study, several species are only tentatively placed in this genus and await future study that will allow for more definite classification.

Drymaeus abruptus (Rolle, 1904)

Figures 2, 6

Bulimus (*Drymaeus*) *abruptus* Rolle 1904: 35. “Huancabamba in Peru”. Syntypes NHMUK 1904.1.21.1 (1), 1947.2.10.1 (1), RBINS MT.2332 (1).

Diagnosis. Shell with straight sides; longitudinal axis of aperture skewed relative to shell axis; aperture contracted below, carinate at base.

Measurements. Shell height to 44 mm, diameter to 24 mm.

Occurrence records. JUNÍN, Maraynioc (MCZ 106782). PASCO, Huancabamba (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This species was not listed by Ramírez *et al.* (2003). The MCZ specimens were misidentified as *Drymaeus planibasis* Pilsbry, 1932, which is an Ecuadorian species (Breure *et al.* 2022: 164).

Drymaeus araujoi Vega-Luz, Breure & Mogollón sp. nov.

Figs 3, 6, Table 2

ZooBank identifier. urn:lsid:zoobank.org:act:AFDCB8F4-F4E5-4355-8344-0781A07B8037

Diagnosis. Shell to 54 mm high, with narrow axial bands,



Figure 3. *Drymaeus araujoi* Vega-Luz & Mogollón sp. nov. Holotype MNCN 15.05/200535.

crossed by two interrupted spiral bands on last whorl; lip whitish, inside of aperture with a purplish hue.

Description. Shell to 53.8 mm high, 2.47 times as long as wide, narrowly umbilicate, elongate, with almost straight sides, moderately solid. Colour whitish, with one spiral band of narrow, elongate dots just above periphery, and axial, partially undulating or zigzag bursts of dark brown; upper whorls with two broken spiral bands, with undulating axial streaks of brown, fading away above on spire. Surface slightly shiny, with prominent growth striae. Protoconch with reticulate sculpture of axial riblets and spiral striae, of equal strength. Whorls 7.7, hardly convex; suture impressed. Aperture subovate; basal margin relatively short; inside with purplish hue near peristome, otherwise whitish; 1.76 times as long as wide, 0.72 times total length. Peristome slightly expanded, whitish; outside with light beige band. Columellar margin expanded, receding above, triangularly broadened. Parietal region with thin, transparent callus.

Type locality. Peru, Amazonas Department, Limabamba District [ca -06.553, -077.576], 2000–2400 m alt.

Type material. Holotype MNCN 15.05/200535; paratype RVL (1), V. Castillo leg., October 2021.

Etymology. Named in memory of Rafael Araujo Armero (1960–2021), former curator of malacology at the MNCN, and who was a warm personality.

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This species resembles *Drymaeus jousseaumei* Dautzenberg, 1901, which has a slenderer and pointed shell, with the aperture 0.48–0.50 times the total length; the peristome is uniformly rounded and more extended than in *D. araujoi*, the side profile of the outer lip is curved and slightly sinuous at its base, the columellar margin curves inwards at the middle, and the axial striae are thicker and fewer than in *D. araujoi*.

Drymaeus arcuatostriatus (L. Pfeiffer, 1855)

Figures 4, 6

Bulimus arcuatostriatus Pfeiffer 1855: 95. “Peru”. Lectotype (Breure 1979: 106) NHMUK 1975455.

Table 2. Shell dimensions and number of whorls of type material of *Drymaeus araujoi* Vega-Luz, Breure & Mogollón sp. nov.

Specimen	Collection	Height (mm)	Diameter (mm)	Height of aperture (mm)	Width of aperture (mm)	Height of last whorl (mm)	No. of whorls
Holotype	MNCN	51.1	20.9	27.3	15.9	37.9	7.5
Paratype 1	RVL-DR11	53.8	21.5	28.8	15.9	38.1	8.0



Figure 4. *Drymaeus arcuatostriatus* (L. Pfeiffer, 1855). Lectotype NHMUK 1975455.

Bulimus strigatus Reeve 1848 [1848–1850]: pl. 44 fig. 280. Not *Bulinus strigatus* G.B. Sowerby I, 1833. Secondary homonymy.

Diagnosis. Shell closely arcuate-strigate, shiny, with wide, grey-brown, interrupted axial bands and angular streaks; suture somewhat ascending in front; aperture obliquely truncate-oval; peristome thin and expanded.

Measurement. Shell to 30.0 mm, diameter to 15.6 mm.

Occurrence record. HUÁNUCO, Tingo María, río Monson valley (FMNH 108289).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. This species may belong to the *D. expansus* group.

Drymaeus aurisratti (Philippi, 1867)

Figures 5, 6

Bulimus aurisratti Philippi 1867: 67. "Inter Lamas et Tarapoto repertus". Possible holotype SMF 156341 (Neubert & Janssen 2004: 200).

Diagnosis. Shell with conic spire; whorls hardly convex, with suture strongly ascending in front, rimate; sculptured with closely spaced axial lines; aperture oblique; lip expanded.

Measurements. Shell height 47.0 mm, diameter 26.9 mm.

Occurrence records. AMAZONAS, Rodriguez de Mendoza (FEM). SAN MARTÍN, between Lamas and Tarapoto (type locality; SMF 153338); Pardo Miguel (RVL).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. The specimen illustrated by Neubert & Janssen (2004: fig. 175) as *D. aurisratti* is larger than the measurements in the original description by Philippi. The figures given by Pfeiffer (1867 [1866–1869]: pl. 80 figs 10–11) dif-

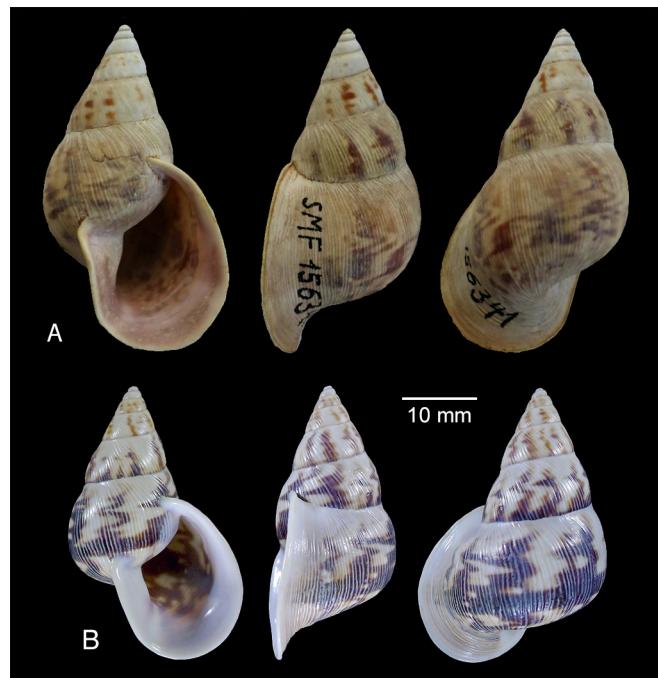


Figure 5. *Drymaeus aurisratti* (Philippi, 1867). **A**, possible syntype SMF 156341. **B**, Lamas–Tarapoto Road (VMA).

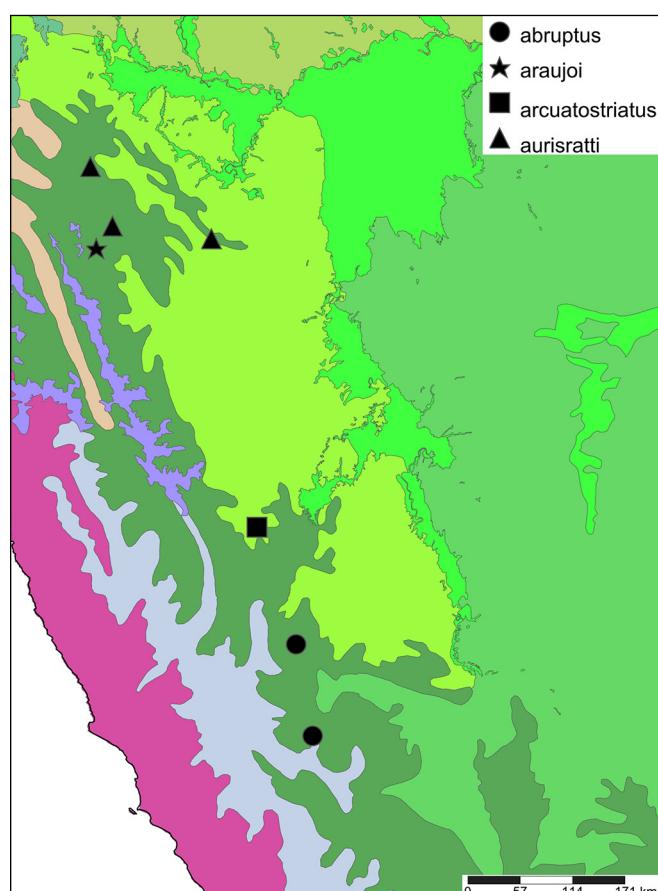


Figure 6. Distribution of *Drymaeus* species.

fer from the possible holotype specimen in SMF. *Drymaeus aurisratti* was placed in the synonymy of *D. expansus* by Pilsbry (1898 [1897–1898]: 223), but it was considered a valid species by Richardson (1995). It is part of the *D. expansus* species complex, which urgently needs molecular phylogenetic study to resolve this species complex.

***Drymaeus bartletti* (H. Adams, 1867)**

Figure 7

Otostomus bartletti Adams 1867: 442, pl. 38 fig. 4. “Upper Amazonas, and on the River Ucayali, Eastern Peru”. Lectotype NHMUK 1867.5.18.4 (Breure & Ablett 2014: 29).

Diagnosis. Shell with a relatively small, conic spire; whorls somewhat convex, sculptured with axial lines which are not continuous from suture to suture but partly broken into short elements; aperture oblique; lip broadly expanded; suture strongly ascending in front.

Measurements. Shell height 28.5 mm, diameter 26.7 mm.

Occurrence record. UCAYALI, along the Río Ucayali (type locality).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. We have not seen material other than the lectotype. The type locality is imprecise. This species is part of the *D. expansus* species complex, but it is decidedly smaller than the other species.

***Drymaeus basitorus* F. Haas, 1951**

Figures 8, 14

Drymaeus (Drymaeus) basitorus Haas 1951: 522, fig. 109A–C. “Peru, Chanchamayo, 1000 m”. Holotype FMNH 31354.

Diagnosis. Shell fragile, narrowly umbilicate; last whorl larger than spire; aperture elongate, pinched at base; suture slightly ascending in front.

Measurements. Shell height 30.2 mm, diameter 14.3 mm.

Occurrence records. JUNIN, Chanchamayo valley (type locality; MCZ 124833; 180461); Oreja de Capelo (IFML-MOLL 17083). PASCO, Oxapampa (IFML-MOLL 17084); Puente Paucartambo (RBINS no catalogue no.).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The relationship of *D. basitorus* with *D. pulcherimus* (H. Adams, 1867) may need additional anatomical or molecular phylogenetic study.

***Drymaeus beyerleanus* (Hupé, 1857)**

Figures 9, 14

Bulimus beyerleanus Hupé 1857: 50, pl. 6 fig. 6. “Pérou”. Lectotype (Breure 1976: 1149) MNHN-IM-2000-28009.



Figure 7. *Drymaeus bartletti* (H. Adams, 1867). Lectotype NHM UK 1867.5.18.4.



Figure 8. *Drymaeus basitorus* (F. Haas, 1951). Holotype FMNH 31354.

Drymaeus beyerleanus mitchelli Dall 1912: 6. “Lucma, 7000 ft., ... three leagues above Santa Ana, Eastern Peru”. Holotype USNM 250260. **New synonymy.**

Diagnosis. Shell subfusiform, rimate, smooth, glossy; last whorl with three spiral bands of sinuous brownish-black spots; aperture with a thin, expanded lip, especially basally.

Measurements. Shell height 42.5 mm, diameter 15 mm.

Occurrence records. CUZCO, La Convención (iNaturalist 102334701); Lares (IFML-MOLL 12097); Las Cruces (iNaturalist 67550445); Quillabamba (IFML-MOLL 10708, 12091, 17088; FMNH 30776; SMF 208325); Santa Ana (DMNH 147318).

Ecoregion. Peruvian Yungas [NT0153], Central Andean wet puna [NT1003].

Remarks. This species shows different colour patterns; shells have spiral bands of varying dominance, some have an axial pattern, or shells may be uniformly coloured. We consider *D. beyerleanus mitchelli* to be a colour morph and place it in the synonymy of *D. beyerleanus*.

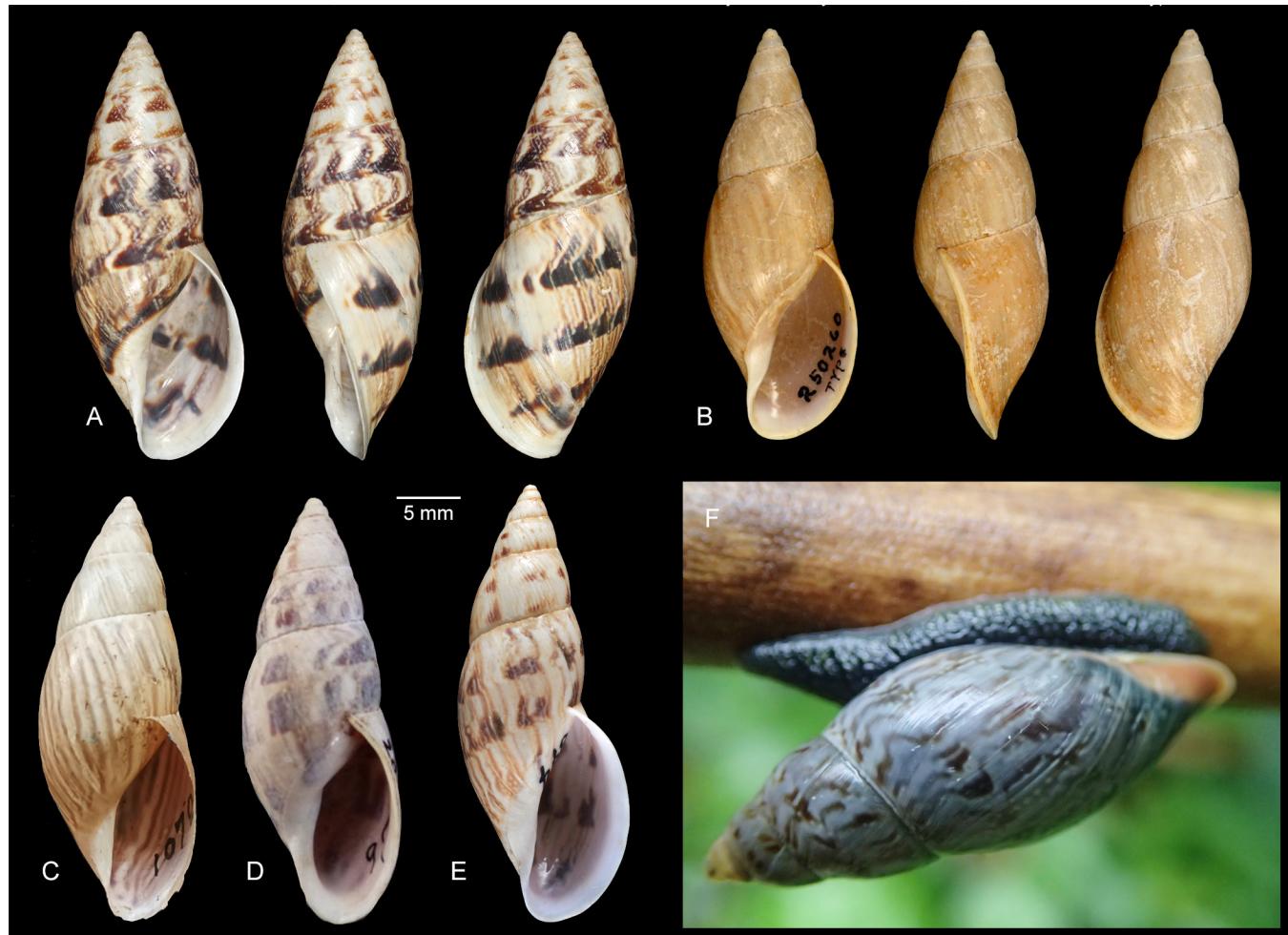


Figure 9. *Drymaeus beyerleanus* (Hupé, 1857). **A**, lectotype MNHN-IM-2000-28009. **B**, holotype of *Drymaeus beyerleanus mitchelli* Dall, 1912, USNM 250260. **C**, Quillabamba, Cuzco, IFML-MOLL 10708. **D**, *ibid.*, SMF 208325. **E**, Vilcanota, Cuzco, UF 161267. **F**, Paucartambo, Cuzco, (iNaturalist 67550445, © ingridcarmean CC-BY-MC 4.0).

Drymaeus branneri F. Baker, 1914

Figures 10, 14

Drymaeus branneri Baker 1914: 637, pl. 23 figs 1–4. “280 km above Porto Velho, Brazil”. Holotype ANSP 109308.

Drymaeus aurantiostomus Thompson & Deisler 1982: 265, fig. 1, 2, 5, 6. “Tambopata Reserve on Rio Tambopata at Rio La Torre, ca. 30 km SSW Puerto Maldonado”. Holotype UF 26605. **New synonymy.**

Diagnosis. Shell with prominent last whorl, openly rimate, glossy, with a brown spiral band below periphery of last whorl; sculptured with irregular, retractive costulae cut by close, finely incised, wavy lines; suture slightly ascending in front; peristome expanded, white, but edged with yellow.

Measurements. Shell height 25 mm, diameter 15 mm.

Occurrence records. BRAZIL (type locality). MADRE DE DIOS, 2 km S of Puerto Maldonado (iNaturalist 35528727);

30 km SSW of Puerto Maldonado (UF 26605, 41132, 41133); Quebrada Madama (VMA 0176); Tambopata (UF 26605; iNaturalist 41005237); S of Alegria (iNaturalist 189488973).

Ecoregion. Southwest Amazon moist forests [NT0166].

Remarks. This species was first mentioned from Peru by Breure & Mogollón (2010: 25). *Drymaeus aurantiostomus*, described by Thompson & Deisler (1982), is so similar that we place it in the synonymy of *D. branneri*.

Drymaeus cantatus (Reeve, 1848)

Figure 11

Bulimus cantatus Reeve 1848 [1848–1850]: pl. 56 fig. 375. “Habitat unknown”. Type material not located.

Remarks. This species has been mentioned from a precise locality only by Lubomirski (1880), based on material collected by Jelski at “Tarma” (presumably Santa Ana de la

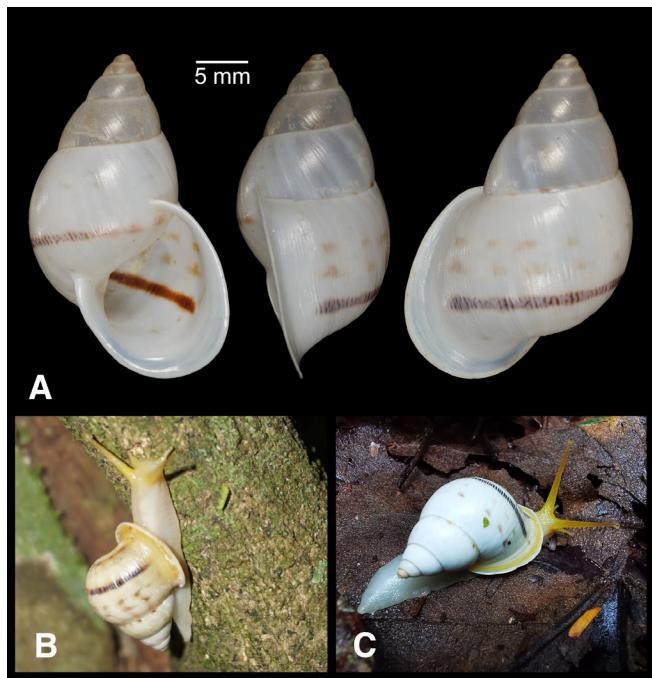


Figure 10. *Drymaeus branneri* F. Baker, 1914. A, holotype ANSP 109308. B, Tambopata, Madre de Dios (iNaturalist 192111759, © Alexander Sherer CC-BY-MC 4.0). C, 2 km S of Puerto Maldonado, Madre de Dios (iNaturalist 35528727, © Carlos G. Velazco-Macias CC-BY-MC 4.0).



Figure 12. *Drymaeus castaneostrigatus* S.I. da Costa, 1906. Holotype NHMUK 1907.11.21.19.

Drymaeus castaneostrigatus S.I. da Costa, 1906

Figures 12, 14

Drymaeus castaneostrigatus da Costa 1906: 98, pl. 11 fig. 5. "Pozuzo, Eastern Peru". Holotype NHMUK 1907.11.21.19.

Diagnosis. Shell slender, openly rimate; whorls hardly convex, smooth, with small axial, somewhat wavy brown bands; aperture relatively small, with a thin peristome, expanded especially at base; suture hardly ascending in front.

Measurements. Shell height 20.4 mm, diameter 8.6 mm.

Occurrence record. PASCO, Pozuzo (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Only known from the holotype. This species seems very closely related to *D. tigrinus* (S.I. da Costa, 1898).

Drymaeus catenae F. Haas, 1952

Figures 13, 14

Drymaeus (Drymaeus) catenae Haas 1952: 118, fig. 20. "Peru, Dept. Cuzco, Prov. Quispicanchi, Hacienda Cadena, 1000 m". Holotype FMNH 38121.

Diagnosis. Shell moderately solid, imperforate; colour pattern of wavy, zigzag, or bifid axial streaks on last two whorls; aperture higher than spire; peristome expanded; suture somewhat ascending in front.

Measurements. Shell height 30.0 mm, diameter 14.4 mm.

Occurrence records. CUZCO, Hacienda Cadena (type locality; ANSP 212214); Cosñipata (IFML-MOLL 17093).

Ecoregion. Peruvian Yungas [NT0153], Southwest Amazon moist forests [NT0166].

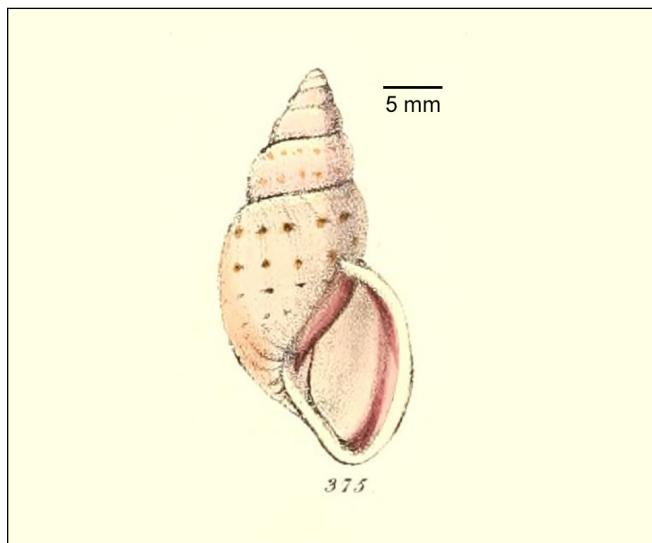


Figure 11. *Drymaeus cantatus* (Reeve, 1848). Figure reproduced from Reeve (1848 [1848–1850]: pl. 56 fig. 376).

Ribera de Tarma, Peru). We have been unable to locate the voucher material to check the identification, and the status of this species as a Peruvian one remains puzzling. See also Breure & Borrero (2019: 10) for why confusion exists with Colombian species.



Figure 13. *Drymaeus catenae* F. Haas, 1952. Holotype FMNH 38121.

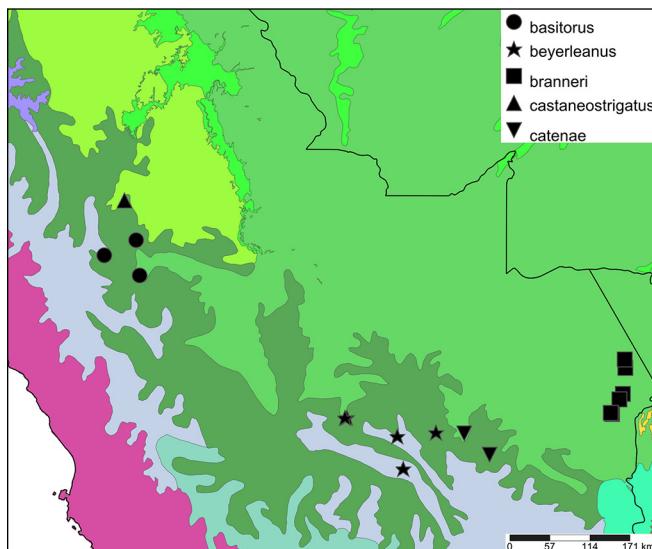


Figure 14. Distribution of *Drymaeus* species.

Remarks. Cosñipata is a new record for this species. It lies about 50 km north-west of the type locality.

Drymaeus chanchamayensis (Hidalgo, 1870)

Figures 15, 21

Bulimus chanchamayensis Hidalgo 1870: 40. "Chanchamayo, Pérou". Holotype MACN 15.05/3157.

Drymaeus eusteirus Pilsbry 1944: 29, pl. 1 fig. 7. "Oxapampa, Peru, at 1800 m". Lectotype ANSP 180674 (Baker 1963: 227). **New synonymy.**

Diagnosis. Shell solid, openly rimate, tawny-grey with two somewhat interrupted, brown-black bands, in some specimens spreading above; whorls roughly sculptured with axial

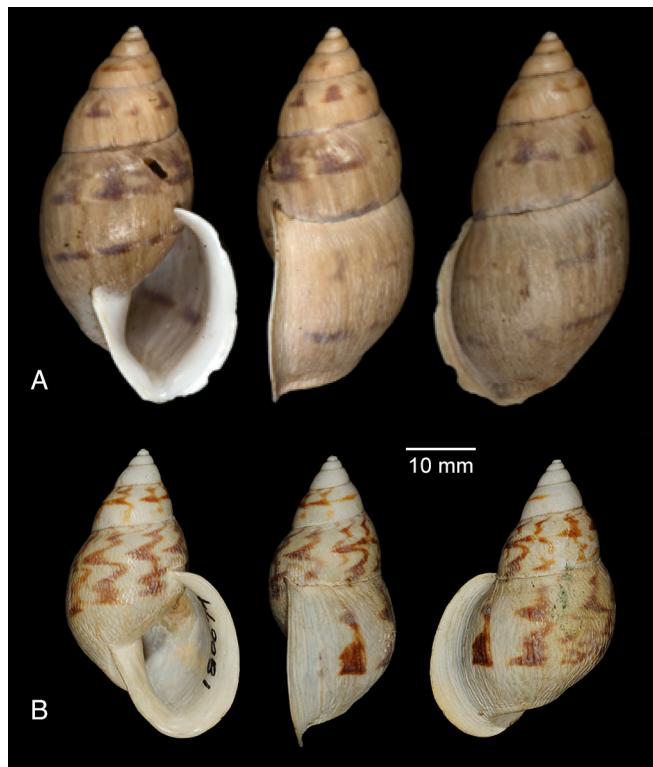


Figure 15. *Drymaeus chanchamayensis* (Hidalgo, 1870). A, Holotype MNCN 15.05/3157. B, Lectotype of *Drymaeus eusteirus* Pilsbry, 1944, ANSP 180674.

costulae; aperture ovate, narrowed at basal margin; peristome broadly expanded, white; suture strongly ascending in front.

Measurements. Shell height 50.5 mm, diameter 28.3 mm.

Occurrence records. JUNÍN, Chanchamayo valley (type locality; FMNH 78763; NHMUK 1904.1.30.27; SMF 24664; UF 109162); Pan de Azucar (SMF 156355). PASCO, Huanacabamba (ANSP 107813; FMNH 78774; RMNH. MOL.266018); Oxapampa (ANSP 180674).

Ecoregion. Peruvian Yungas [NT0153], Southwest Amazon moist forests [NT0166].

Remarks. Köhler (2007: 144) erroneously indicated that ZMB.MOLL 11833 was the holotype specimen of *D. chanchamayensis*. The holotype is, however, in the MACN collection and was collected by Isern (Breure & Araujo 2017: 73). This species is polymorphic with different colour patterns. *Drymaeus eusteirus* only differs from *D. chanchamayensis* in its colour pattern, and, therefore, we consider these taxa synonyms.

Drymaeus combinai (Weyrauch, 1958) comb. nov.

Figures 16, 87

Mesembrinus (Ornatimormus) combinai Weyrauch 1958: 135, pl. 8



Figure 16. *Drymaeus combinai* Weyrauch, 1958. Holotype SMF 156201.

fig. 16. "Mittel-Peru am Ostnag der östlichen Anden: Quimiri Sur (früher "Alto Quimiri" genannt), Valle de Chanchamayo, zwischen den Dörfern La Merced und San Ramón, 1300 m". Holotype SMF 156201.

Diagnosis. Shell thin, rimate, glossy; whorls somewhat convex, sculptured with growth striae and very fine spiral lines; colour whitish, with elongate brown dots at irregular intervals, three rows on last whorl; aperture ovate; peristome thin, slightly expanded at base; suture hardly ascending in front.

Measurements. Shell height 26.4 mm, diameter 12.5 mm.

Occurrence records. JUNÍN, Quimiri Sur (type locality). PASCO, Oxapampa (MCZ 133213).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This remarkable species has not been seen in more recent collections from the malacologically well-known Province of Chanchamayo. We place this species in *Drymaeus* on account of its expanded lip, but molecular analysis is needed to corroborate this systematic position.

***Drymaeus costatus* Breure & Vega-Luz, 2021**

Figures 17, 22

Drymaeus (*Drymaeus*) *costatus* Breure & Vega-Luz 2021: 19, figs 1–4. "Peru, Dept. Amazonas, Prov. Chachapoyas, District Omia, ca. 1800–1900 m". Holotype MNCN 15.05/200126; paratypes NHMUK 20210001 (1), RVL-DR2, VMA 1507.

Diagnosis. Shell rather thin, rimate; last whorl swollen, sculptured with shallow ribs; shell roseate to yellowish, with irregular, dark-reddish-brown blotches; aperture elongate-ovate; peristome expanded, reflected, white

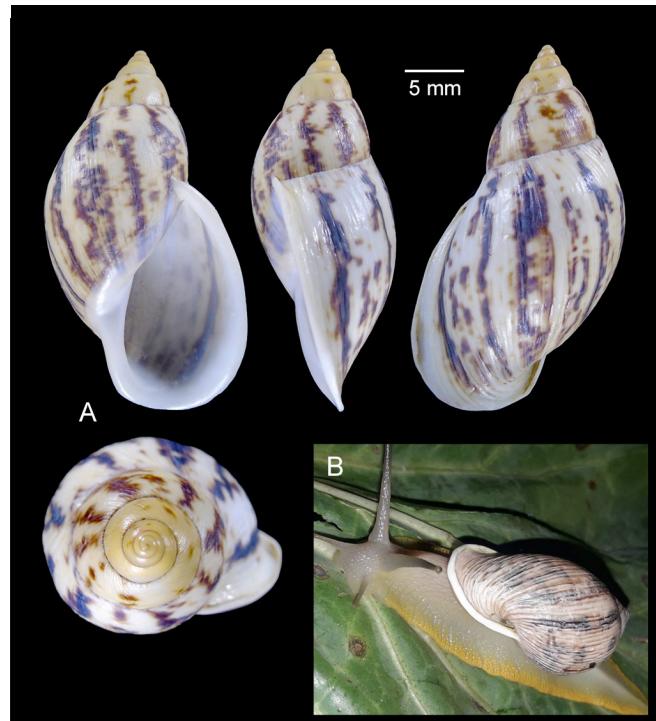


Figure 17. *Drymaeus costatus* Breure & Vega-Luz, 2020. **A**, Holotype MNCN 15.05/200126. **B**, Living specimen, topotype (VMA).

Measurements. Shell height 45.0 mm, diameter 25.8 mm.

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

Figures 18, 22

Bulimus edmüllerii Albers 1854: 218. "Columbia [sic], ad fluvium Maranhon". Lectotype ZMB.MOLL 111929a; paralectotypes ZMB.MOLL 111929b (3), 10340 (4) (Köhler 2007: 145).

Diagnosis. Shell rather thin, rimate; whorls hardly convex, whitish, with axial, wavy streaks crossed by a small and a broader spiral whitish band with dark dots; aperture oblong; peristome thin, slightly expanded below, whitish.

Measurements. Shell height 29.5 mm, diameter 10 mm.

Occurrence records. AMAZONAS, Yambrasbamba D istrict [ca -05.524, -077.860], ca. 1600 m alt. (RVL); N of Chachapoyas, near Cocachimba [-06.057, -077.895], 1790 m alt. (iNaturalist 45829598).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The original material was collected by Józef Warszewicz (1812–1866), one of the most prolific 19th-century plant collectors, who made an expedition through Panama, Colombia, Ecuador, Peru, Bolivia, and Brazil in 1851–1853, and who collected also zoological material (Nobis et al. 2022; Köhler 2014). Unfortunately, his itiner-



Figure 18. *Drymaeus edmuelleri* (Albers, 1854). A, Lectotype ZMB.MOLL 111929. B, Neugranada, ZMB.MOLL 22607.

ary was undocumented, and, therefore, we do not know the precise type locality of this species. The occurrence records above are the only precise localities known for this species.

Drymaeus edmuelleri is evidently related to *D. luculentus* Breure & Vega-Luz, 2021, as they occur in the same general area and have a similar general appearance. However, the aperture of *D. luculentus* is skewed (in some specimens protracted) and only purplish within, and outside behind the lip there is a narrow white band and a roseate zone.

Occurrence records. AMAZONAS, Cheto (NHMUK 202 10001); Omia District (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This is a polymorphic species, as shown in the original publication.



Figure 19. *Drymaeus elsteri* S.I. da Costa, 1901. Lectotype NHM UK 1907.11.21.34.

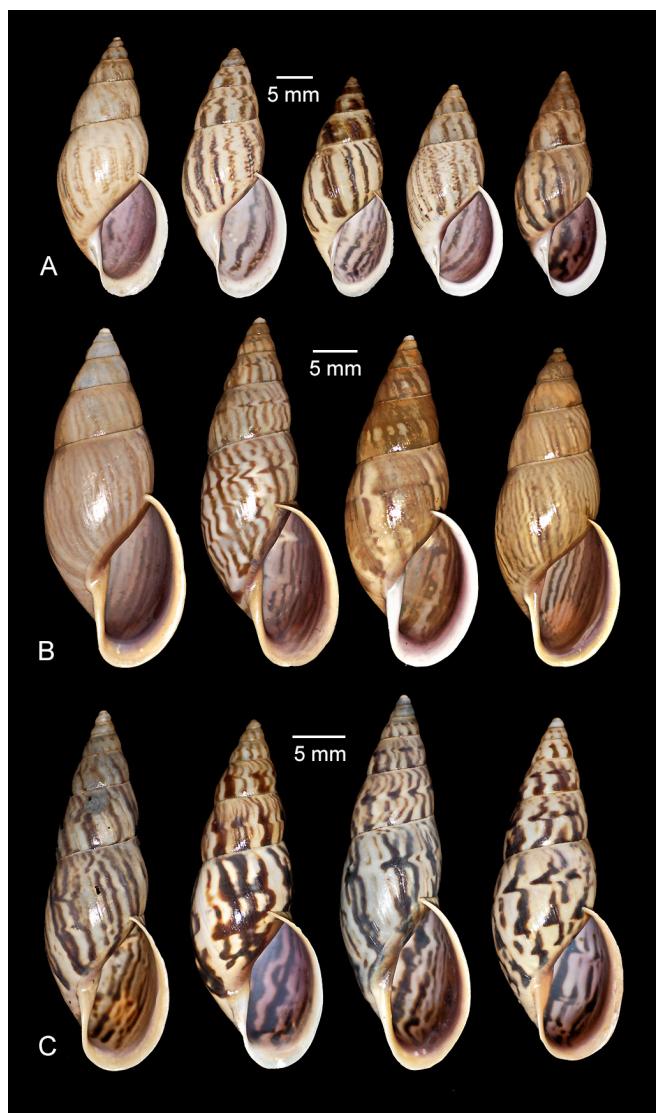


Figure 20. *Drymaeus* cf. *elsteri* S.I. da Costa, 1901. A, El Mirador, San Martín (RVL). B, Alto Mayo, San Martín (RVL). C, Villa Rica, Pasco (RVL).

***Drymaeus elsteri* S.I. da Costa, 1901**

Figures 19, 20, 22

Drymaeus elsteri da Costa 1901: 238, pl. 24 fig. 6. "Chachapoyas, prov. Amazonas, Peru". Lectotype (Breure 1979: 108) NHMUK 1907.11.21.34; paralectotypes NHMUK 1907.11.21.35–36 (2).

Diagnosis. Shell somewhat solid, imperforate; whorls hardly convex, whitish to brownish, with a variety of axial patterns (Fig. 20); aperture oblong-oval, purplish inside; peristome whitish, thin, somewhat expanded, especially basally.

Measurements. Shell height to 47.0 mm, diameter to 15.9 mm.

Occurrence records. AMAZONAS, Chachapoyas (type locality); Molinopampa (FEM 194396–194399, 197926); Asunción (RVL; VMA). SAN MARTÍN, Alto Mayo Protected Forest (RVL; VMA).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The type specimens are somewhat bleached by their long conservation, and for this reason, their original colour pattern cannot be seen. We tentatively consider the modern collected material (Fig. 20) as this species, which is characterised by a yellowish base colour that varies among specimens; axial lines vary in width and are light to dark brown. There is a light-coloured margin at the outside of the lip and a pink to purplish hue inside the aperture. There is also a great variation in size and height-width ratios. Further research is needed to determine the distribution of *D. elsteri* and if cryptic species are present.

***Drymaeus eurystomus* (Philippi, 1867)**

Figures 21, 22

Bulinus eurystomus Philippi 1867: 68. "Chanchamayo". Type material not located.

Bulinus hamadryas Philippi 1867: 68. "Chanchamayo". Type material not located.

Diagnosis. Shell narrowly perforate, with growth striae crossed by very fine transverse lines; whorls hardly convex, uniformly whitish or whitish with varying patterns of brownish spots; aperture ovate, compressed below and subangular basally; peristome thin, somewhat expanded below; suture slightly ascending in front.

Measurements. Shell height 31.5 mm, diameter 15 mm.

Occurrence records. JUNÍN, Chanchamayo valley (type locality; FMNH 78756; NHMUK 1904.1.30.20–27; RMNH.MOL 114070, 265682; SMF 25846; ZMB.MOLL no catalogue no.). PASCO, Huancabamba (FMNH 78774); Paucartambo (FEM).

Ecoregion. Peruvian Yungas [NT0153], Southwest Amazon moist forests [NT0166].

Remarks. *Drymaeus eurystomus* has varied colour forms, and *Bulinus hamadryas* was synonymised by Richardson (1995: 121). We republished the original figures (Pfeiffer 1867 [1866–1869]: pl. 81 figs 1, 2, 7, 8) of these taxa, due to lack of type material available.

Living specimens show a brown body edged near the foot by an orange band, orange tentacles, and an orange area on the head between the tentacles (Fig. 23E).

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

Figures 23, 24, 28

Bulinus pulchellus Sowerby I 1838: fig. 91. "Huallaga". Not *Bulinus pulchellus* Broderip in Broderip & G.B. Sowerby I, 1832.

Bulinus expansus Pfeiffer 1848: 60. "Huallaga". Type material not located.

Bulinus iodostomus Deville & Hupé 1850: 641, pl. 15 fig. 2. "au village de Pebas, sur la rivière des Amazones". Syntype MNHN-IM-2000-28069 (1).

Drymaeus expansus perenensis da Costa 1901: 239, pl. 24 fig. 5. "Perene, Peru". Lectotype (Breure 1979: 112) NHMUK 1907.11.21.39.

Drymaeus expansus (var.) *subprotractus* Pilsbry 1901 [1901–1902]: 155, pl. 25 figs 27–29. "Peru". Lectotype ANSP 78127 (Baker 1963: 231).

Mesembrinus (Mormus) expansus altorum Weyrauch 1958: 129, pl. 7 figs 12, 13. "Mittel-Peru, am Osthang der östlichen Anden: Quimiri Sur, Valle de Chanchamayo ... oberhalb Puente Herrería, zwischen den Dörfern La Merced und San Ramón, 1100–1300 m". Holotype SMF 156295; paratypes SMF 156294 (1), IFML-MOLL 1333 (5).

Drymaeus (Mormus) expansus flavilabrum Weyrauch 1967: 484, fig. 29. "Peru central, río Aguaytía, en la carretera de Tingo María a Pucallpa, 300 m". Holotype IFML-MOLL 1197.

Diagnosis. Shell umbilicate; spire conic; last whorl swollen; surface with raised, thread-like costulae; colour whitish, variously streaked or maculate with brownish; aperture broadly ovate, purplish inside; peristome broadly expanded throughout; columella strongly twisted; suture well ascending in front.

Measurements. Shell height 44 mm, diameter 22 mm.

Occurrence records. AMAZONAS, Puerto Galilea (UF 28031, 28032, 28034, 28035, 28037, 29454); Rio Cenepa (UF 24939). HUANCABELICA, Huancavelica (ANSP 25758). HUÁNUCO, Pachitea Province (RVL); Panao Province (RVL); Tingo Maria (FMNH 106306); 14.9 km NE of Tingo Maria (UF 176883). JUNÍN, Chanchamayo (ANSP 78151, 204473; DMNH 58080, 135196; FMNH 72604; MCZ 139834; SMF 208332, 284348; UF 109223; USNM

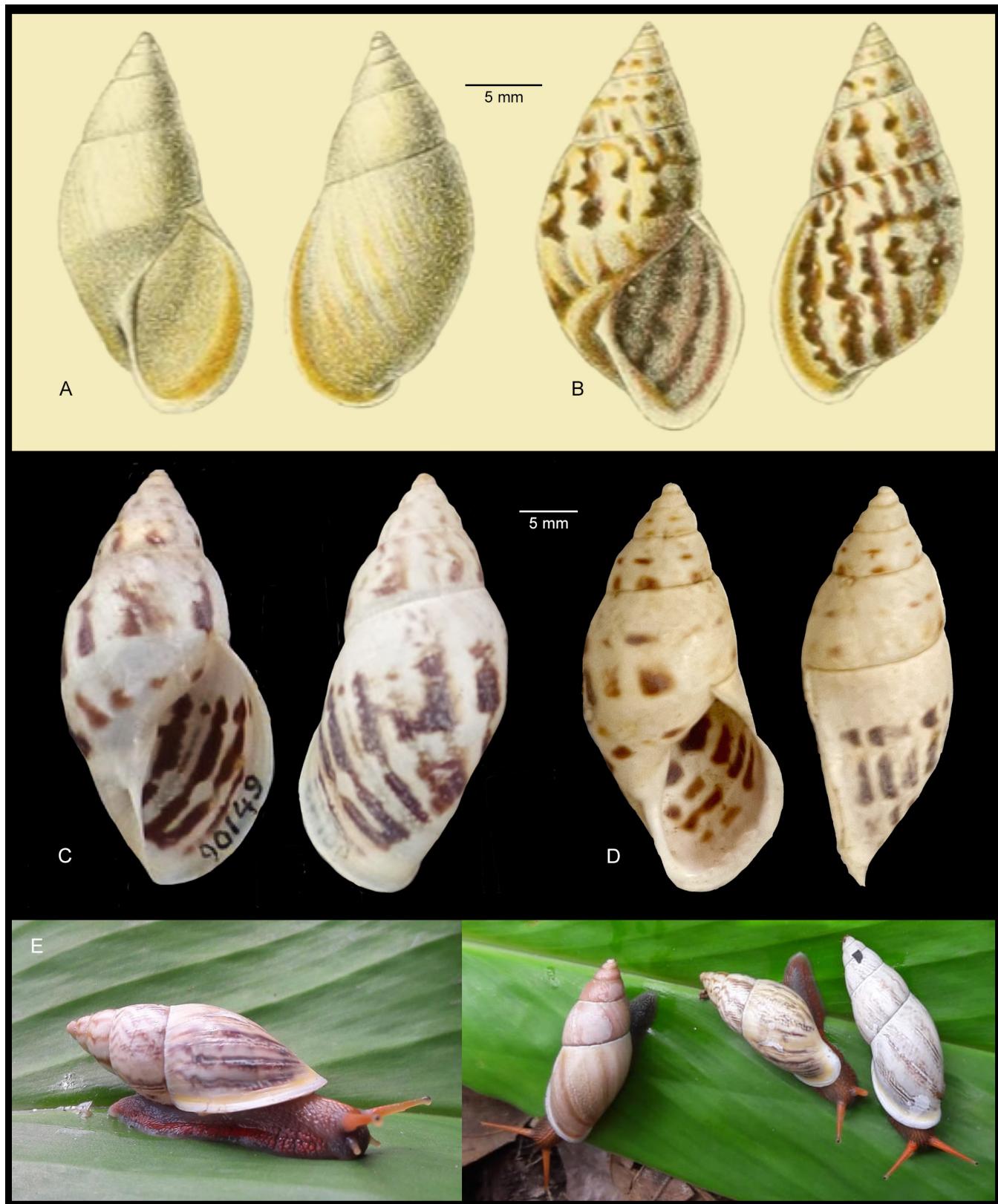


Figure 21. *Drymaeus eurystomus* (Philippi, 1867). **A**, Figures of *Bulimus eurystomus* reproduced from Pfeiffer (1867: pl. 81 figs 7, 8). **B**, Figures of *Bulimus hamadryas* Philippi, 1867 reproduced from Pfeiffer (1867: pl. 81 figs 1, 2). **C**, Chanchamayo, Junin, SMF 90149. **D**, Same locality as C, RMNH.MOL 114070. **E**, Living snails. Oxapampa, Pasco (RVL).

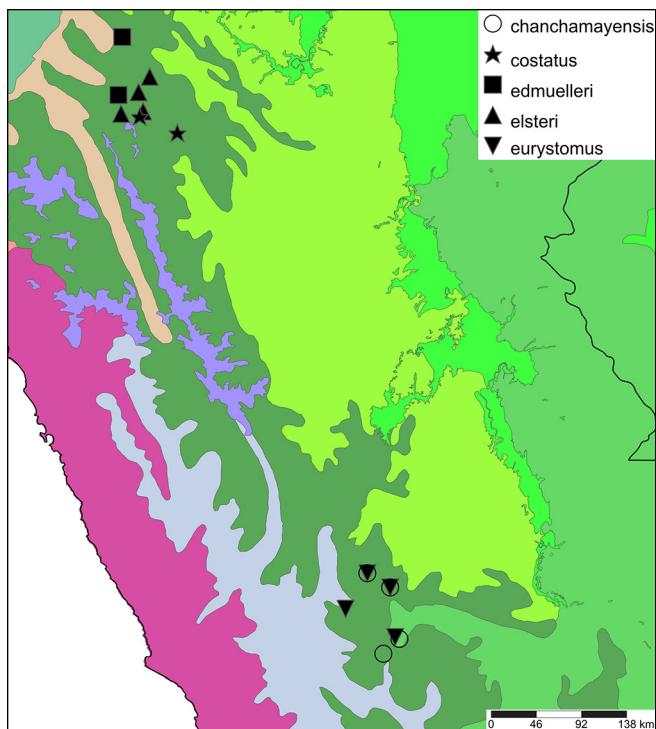


Figure 22. Distribution of *Drymaeus* species.

601807); Perené (NHMUK 1907.11.21.39); Quimiri Sur (SMF 156294, 156295); Satipo (FEM). LORETO, Alto Javari (FMNH 67896); Mariscal Ramón Castilla (iNaturalist 19505481); Pebas (MNHN-IM-2000-28069). MADRE DE DIOS, Reserva Los Amigos (IFML-MOLL 14941). PASCO, Oxapampa (RVL); Pozuzo (UMMZ 124358). SAN MARTÍN, Moyobamba (UMMZ 124355); Huallaga Province (type locality); Río Mishollo (RBINS); Rioja (FEM); Tarapoto (DMNH 163637; FMNH 72603, 94880; UMMZ 4514, 124357); Tarapoto to Lamas (RBINS no catalogue no.; UMMZ 124356). UCAYALI, Tingo María–Pucallpa road, Río Aguaytia (IFML-MOLL 1197).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174], Napo moist forests [Napo moist forests [NT0142], Iquitos várzea [NT0128], Southwest Amazon moist forests [NT0166].

Remarks. In the Bayesian-inference tree by Salvador *et al.* (2023: fig. 6), this species is part of a multifurcation with *Drymaeus*, *Antidrymaeus*, and *Mesembrinus* as subtrees. As only a further DNA study with increased taxon sampling can solve the position of this and related species, we retain it in *Drymaeus*, but its genus-level classification may change with new phylogenetic results.

Pfeiffer introduced the name *expansus* in 1848 while he thought Sowerby's name was preoccupied by "*B. expansus*

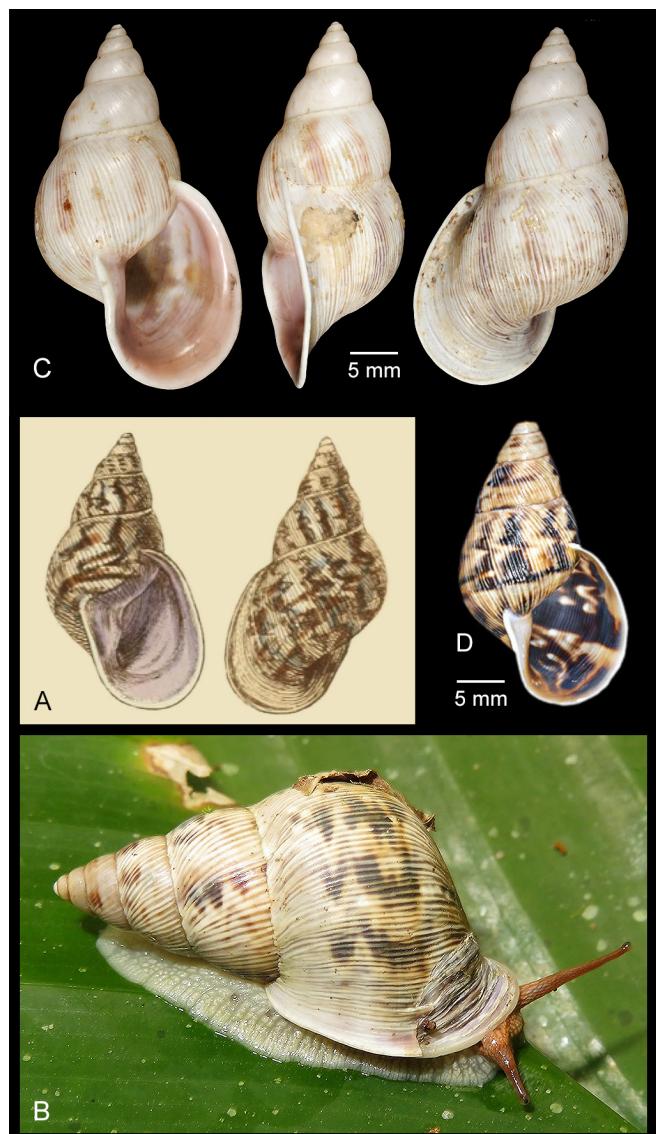


Figure 23. *Drymaeus expansus* (L. Pfeiffer, 1848) species complex. **A**, figures of *Bulinus pulchellus* G.B. Sowerby I, 1838 reproduced from Sowerby (1838: pl. 143 fig. 91). **B**, living specimen, Rioja Province, San Martín (iNaturalist 38292095, © Rob Westerduijn). **C**, *Bulinus iodostylus* Deville & Hupé, 1850. Syntype MNHN-IM-2000-28069. **D**, Satipo, Junín. FEM.

Spix" (in Spix & Wagner 1827). However, this is erroneous, as there was no such name in Spix and Wagner's publication. Instead, a new name was needed to solve a junior homonymy with *Bulinus pulchellus* Broderip in Broderip & Sowerby I, 1832. In the NHM a lot is present from the Cuming collection where both the names *pulchellus* Sowerby and *expansus* Pfeiffer have been written in Pfeiffer's handwriting. However, the locality (in another handwriting) is "Santa Fé da Bogotá" and not Huallaga. While the locality might be in (Cumingian) error, this lot is evidently very similar in

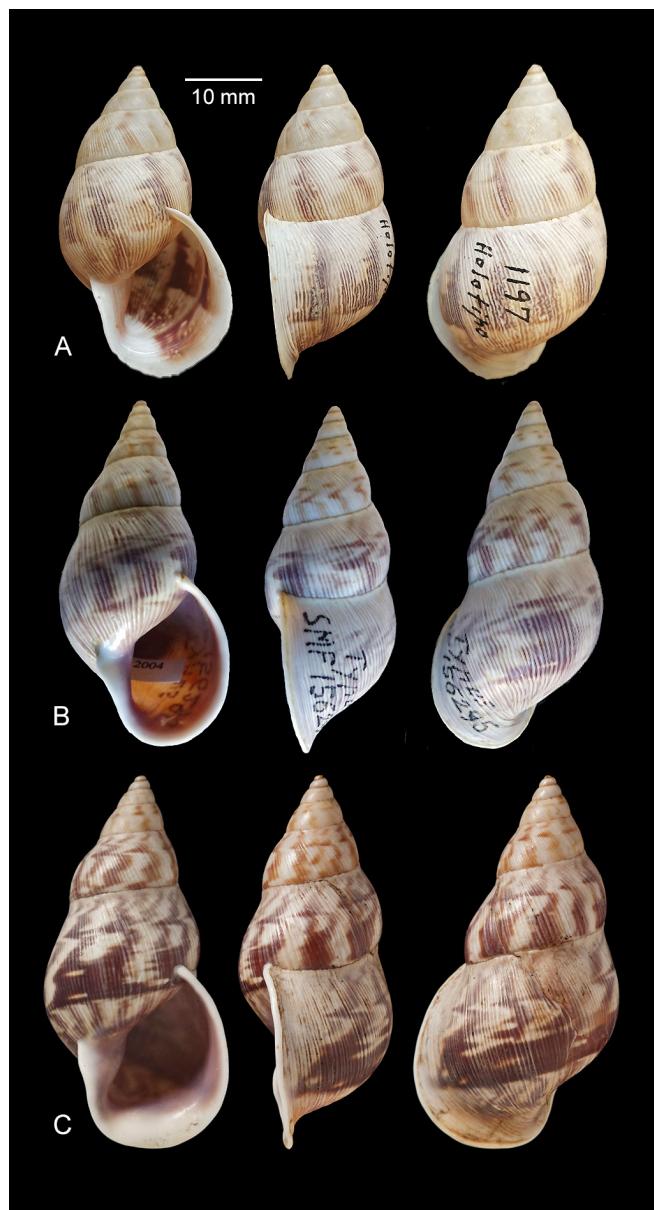


Figure 24. *Drymaeus expansus* (L. Pfeiffer, 1848) (species complex). **A**, *Drymaeus (Mormus) expansus flavilabrum* Weyrauch, 1967. Holotype IFML 1197. **B**, *Mesembrinus (Mormus) expansus altorum* Weyrauch, 1958. Holotype SMF 156295. **C**, *Drymaeus expansus perenensis* S.I. da Costa, 1901. Lectotype NHMUK 1907.11.21.39.

appearance to the original description.

The specimen illustrated by Neubert & Janssen (2004: fig. 175) as *D. aurisratti* is larger than the measurements given by Philippi in his description of *D. aurisratti*. The figures given by Pfeiffer (1867 [1866–1869]: pl. 80 figs 10, 11) are different than this specimen in SMF. *Drymaeus aurisratti* was placed in the synonymy of *D. expansus* by Pilsbry (1898 [1897–1898]: 223), but it was later considered a valid spe-

cies by Richardson (1995). Weyrauch (1967: 485) also considered *D. protractus* as a separate species.

As treated here, *D. expansus* is a species complex, and we provisionally list all taxa of this complex under the heading of *D. expansus*. However, multiple distinct species are possible, but anatomical or molecular studies are needed to resolve the taxonomic relationships of the nominate taxa included in the complex. If *D. expansus* is found to contain more than one species, this may explain why this complex occurs in different ecoregions. This species complex occurs also in Brazil, Ecuador, Colombia, and Panama (Simone 2006; Linares & Vera 2012; Breure et al. 2022).

Drymaeus fordii Pilsbry, 1898

Figures 25, 28

Drymaeus fordii Pilsbry 1898 [1897–1898]: 205, pl. 38 figs 1–3. “Habitat unknown”. Lectotype ANSP 72368 (Baker 1963: 227).

Diagnosis. Shell moderately solid, rimate, whitish, with varying black-brown patterns (Fig. 25B); aperture roughly ear-shaped; peristome somewhat expanded throughout; suture ascending in front.

Measurements. Shell height 57.1 mm, diameter 24.4 mm.

Occurrence record. AMAZONAS, Yambrasbamba (VMA; RVL).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Richardson (1995: 162) placed this species in the synonymy of *D. peeli* (Reeve, 1859), which was followed by Breure et al. (2022: 161). Based now on Peruvian materials, we consider *D. fordii* as a valid species; however, as Reeve did not publish a figure of his material, nor have we located the material on which he based his species, doubt remains about its status. Pilsbry’s *D. fordii* differs mainly from *D. peeli* in having no spiral elements in the colour pattern and a pink-purplish peristome, which is also less expanded than in *D. peeli*. It cannot be excluded that the lectotype specimen is an aberrant *D. peeli*. The lectotype seems partly bleached, which is why it does not fully conform to the original description. The shape of the aperture is especially variable in this species.

Drymaeus fusoides (d’Orbigny, 1835)

Figures 26, 28

Helix fusoides d’Orbigny 1835: 19. “provincia Yungacensi, república Boliviana”. Lectotype MNHN-IM-2000-28047; paralectotype NHMUK 1854.12.4.133 (Breure 1976: 1151).

Diagnosis. Shell elongate, thin, rimate; whorls somewhat convex, whitish, with a few small, slender, brown axial

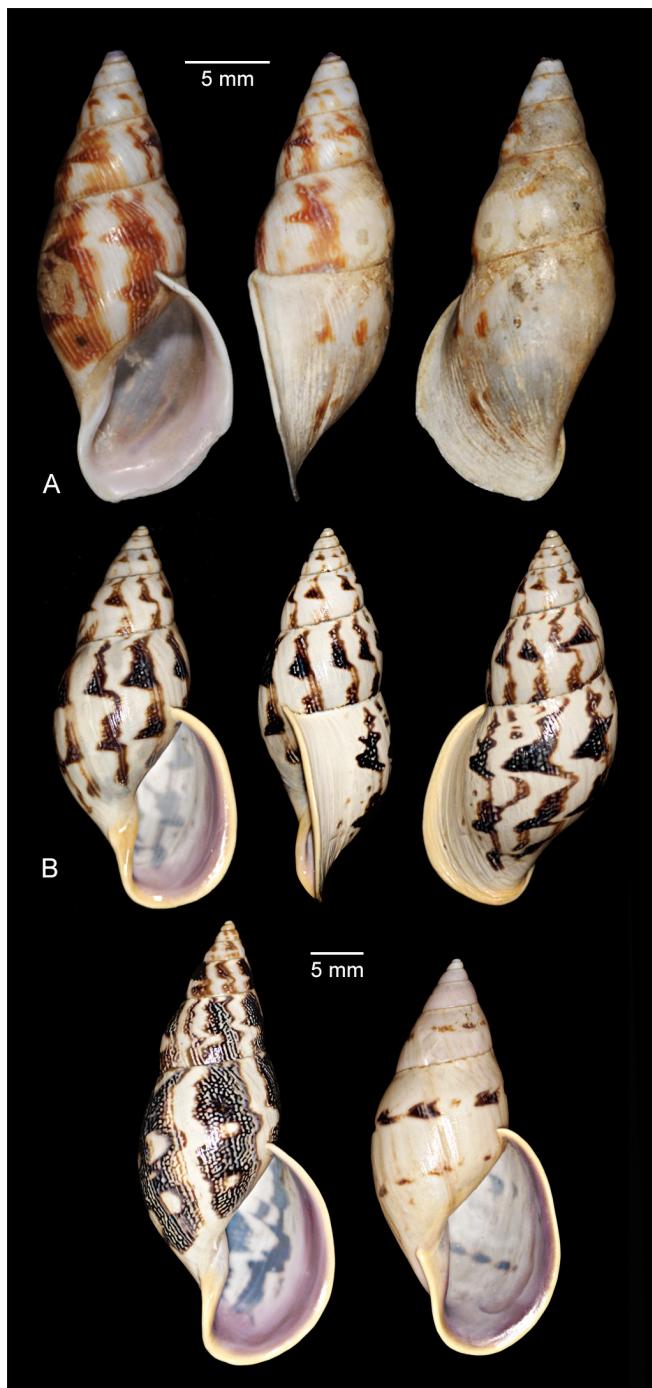


Figure 25. *Drymaeus fordii* Pilsbry, 1898. **A.** lectotype ANSP 72368. **B.** Yambrasbamba, Amazonas (RVL).

streaks; aperture oblong, oblique, bordered with purplish inside; peristome expanded; suture hardly ascending in front.

Measurements. Shell height 42.0 mm, diameter 14.6 mm.

Occurrence records. BOLIVIA, Yungas del Palmar (type locality; IFML-MOLL 12002). PUNO, San Juan del Oro (FEM).

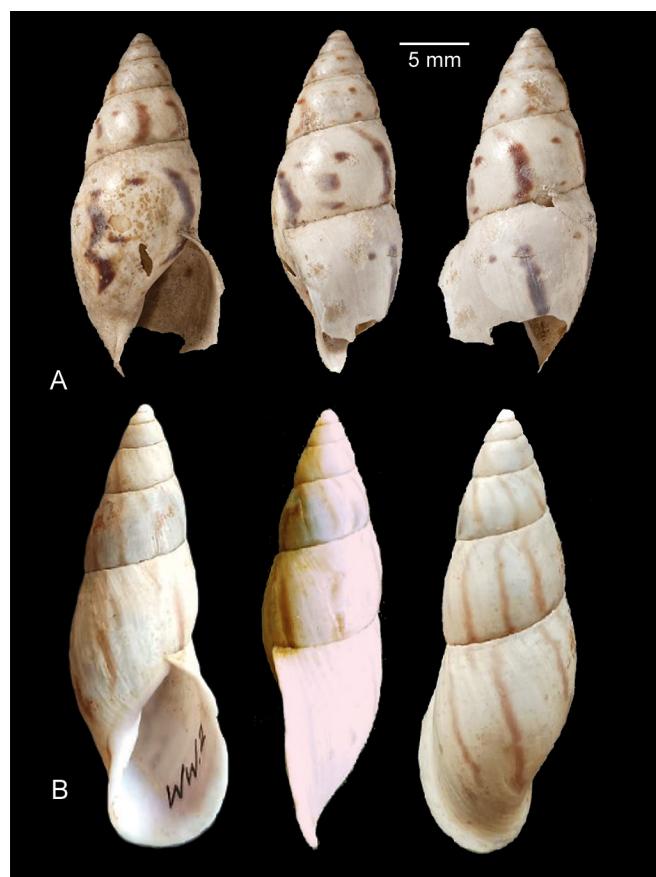


Figure 26. *Drymaeus fusoides* (d'Orbigny, 1835). **A.** paralectotype NHMUK 1854.12.4.133. **B.** topotype IFML-MOLL 12002.

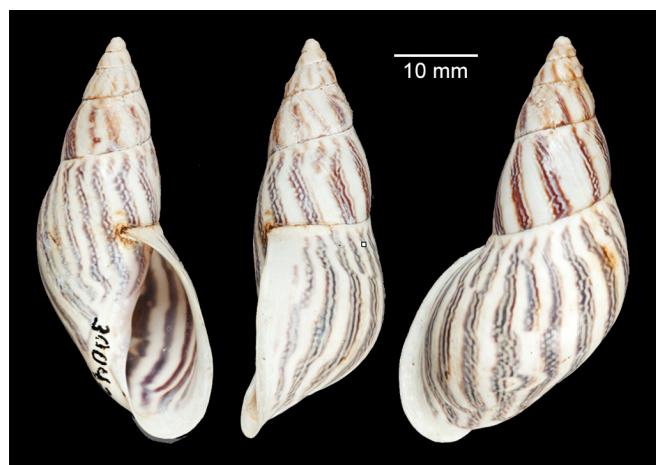


Figure 27. *Drymaeus gibber* F. Haas, 1949. Holotype FMNH 30042.

Ecoregion. Bolivian Yungas [NT0105].

Remarks. This species is reported here for the first time from Peru. Other records in collections, from GBIF, proved to be misidentifications.

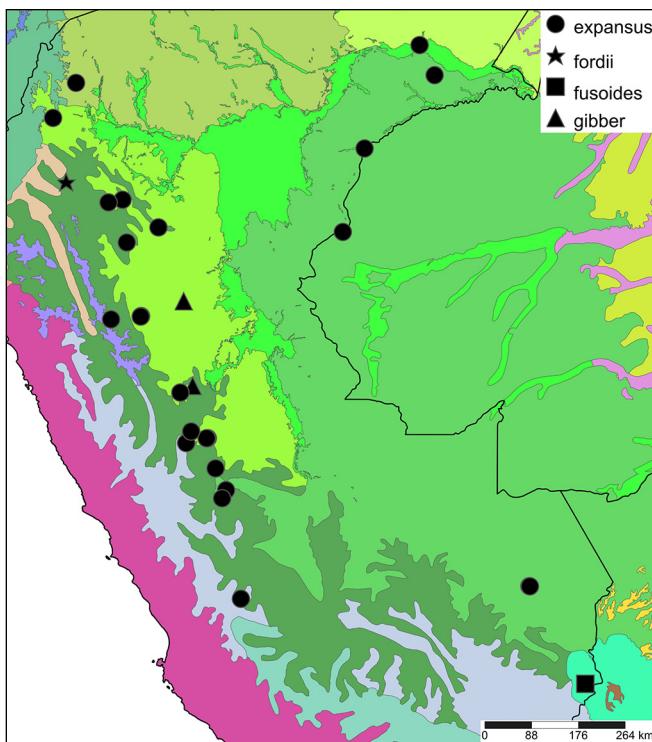


Figure 28. Distribution of *Drymaeus* species.

Drymaeus gibber F. Haas, 1949

Figures 27, 28

Drymaeus (*Drymaeus*) *gibber* Haas 1949: 238, figs 50c, 51a–d.
“Divisória, Dept. Huanuco, Peru, at 5,000 ft elevation”. Holotype FMNH 30042; paratypes FMNH 30043, 30044.

Diagnosis. Shell imperforate, thin, with rather flat whorls; last whorl with a gibbosity that irregularly inflates its last part and deviates last whorl from the shell axis; aperture slanting forward, ovate-oblong; peristome expanded below.

Measurements. Shell height 38.1 mm, diameter 19.4 mm.

Occurrence records. HUÁNUCO, Cordillera Azul (ANSP 204467); Divisoria (type locality; ANSP 212211; CM 43258; DMNH 58090, 148417; IFML 12813; MCZ 202186; SBMNH 141117; UF 109247); road from Tingo Maria to Pucallpa (UF 486914).

Additional material. Without locality (ZSM 110618).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. In the original paper, Haas (1949) showed that this species is polymorphic species in the shape of the shell and aperture. MCZ 202186 is marked as “paratype”; lot ZSM 110618 is labelled without locality but is considered to be a “syntype”. This lot was not mentioned as a paratype in Haas’ (1949) original publication.



Figure 29. *Drymaeus gueinzii* (L. Pfeiffer, 1857). Lectotype NHMUK 1975539.

Drymaeus gueinzii (L. Pfeiffer, 1857)

Figures 29, 35

Bulimus gueinzii Pfeiffer 1857: 330. “Meobamba, Peru”. Lectotype NHMUK 1975539 (Breure 1979: 109).

Diagnosis. Shell thin, shiny, rimate; whorls rather convex, yellowish, with narrow brown axial streaks, some bifid or undulating; aperture ovate, lilac inside; peristome expanded; suture hardly ascending in front.

Measurements. Shell height 23.2 mm, diameter 10.9 mm.

Occurrence records. SAN MARTÍN, Bellavista (RBINS no catalogue no.); Moyobamba (type locality); Sauce District (RBINS no catalogue no.).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. This species is characterised by its upright subovate aperture; expanded, white lip; broad, white margin on the outside of the lip; axial colour pattern; skewed aperture in lateral view; and relatively small size.

Drymaeus icterostomus (E. von Martens, 1901)

Figures 30, 35

Bulimus icterostomus Martens 1901: 149. “Gebiet des Urubamba, eines der oberen Zuflüsse des Amazonasstroms im östlichen Peru”. Lectotype ZMB.MOLL 52736 (Köhler 2007: 146).

Drymaeus (*Drymaeus*) *latitestata* Haas 1952: 117, fig. 19. “Hacienda Cadena, Distr. Marcapata, Prov. Quispicanchi, Dept. Cuzco, Peru in Rio Marcapata valley at 1,000 meters elevation”. Holotype FMNH 38120. **New synonymy.**

Diagnosis. Shell rather solid, perforate; whorls rather convex, with last one swollen; colour white-yellowish, with three narrow, brown spiral bands and some axial elements; aperture ear-shaped; peristome broadly expanded; suture ascending in front.

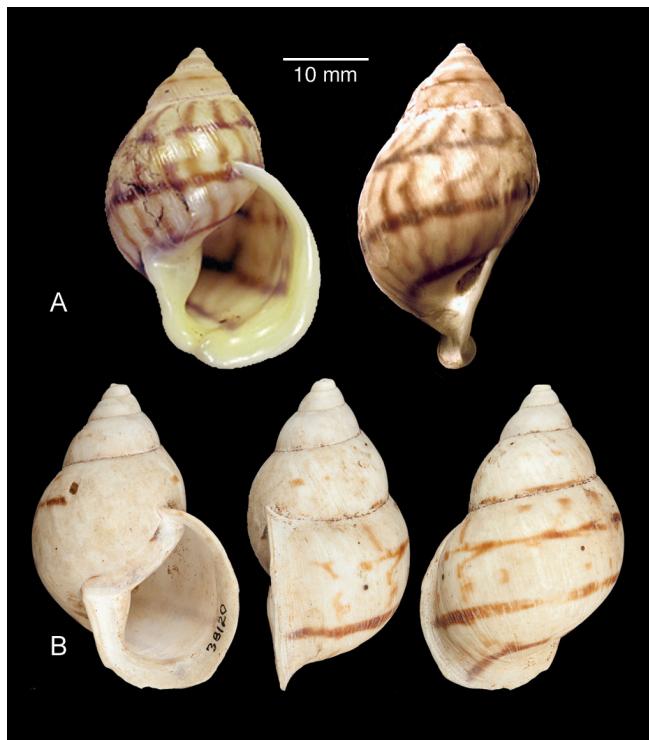


Figure 30. *Drymaeus icterostomus* (E. von Martens, 1901). **A**, lectotype ZMB.MOLL 52736. **B**, holotype FMNH 38120 of *Drymaeus (Drymaeus) latitesta* F. Haas, 1952.

Measurements. Shell height 37 mm, diameter 24 mm.

Occurrence record. Cuzco, Marcapata, Hacienda Cadena (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. *D. latitesta* is evidently the same species as *Drymaeus icterostomus*. Both taxa are known only from one specimen each.

Drymaeus inaequalis (L. Pfeiffer, 1857)

Figure 31

Bulimus inaequalis Pfeiffer 1857: 330. "Banks of the Maranon". Syntypes AMNH 41212 (3).

Diagnosis. Shell rather thin, rimate; whorls somewhat convex, whitish, with wide, branching purplish-brown axial streaks; aperture elongately ear-shaped, bordered with purple inside; peristome broadly expanded throughout; suture slightly ascending in front.

Measurements. Shell height 43 mm, diameter 13 mm.

Occurrence records. Unknown.

Ecoregion. Several ecoregions, but mainly Peruvian Yungas [NT0153].

Remarks. The Marañon River runs for more than 1400 km



Figure 31. *Drymaeus inaequalis* (L. Pfeiffer, 1857). Syntype AMNH 41212.

through several departments. This species was described from the H. Cuming collection without further data. When Pfeiffer illustrated the species in his second volume of the *Novitates Conchologicae* (Pfeiffer 1860 [1860–1866]: 158, pl. 42 figs 3–5), he mentioned "Aus der Sammlung des Hrn. Haines in Newyork" [from the collection of Mr Haines in New York]. This material, which are syntypes, has been located in the AMNH collection. The type locality is imprecise; see the section on historical authors and collections above for data on the collector, Józef Warszewicz.

Drymaeus inca M. Smith, 1943

Figures 32, 35, 51

Drymaeus inca Smith 1943: 61, pl. 7 fig. 10. "Collected at an elevation of 1100 meters in the Department of Junin, Province of Jaugo [sic, Jauja], Peru". Holotype UF 174303; paratypes UF 137954 (2).

Diagnosis. Shell rather thin, perforate-rimate; whorls hardly convex, with last one prominent, subcarinate at a flattened base; colour yellowish-white, with undulating reddish-brown axial streaks overlaid with interrupted, narrow, white axial lines; aperture ovate, oblique; peristome expanded throughout; suture hardly ascending in front.

Measurements. Shell height 30 mm, diameter 18 mm.

Occurrence records. JUNÍN, no specific locality (ANSP 180233); Chanchamayo valley (ZMB.MOLL 59661); Prov. Jauja (type locality); Satipo (IFML-MOLL 17090; FMNH 30778; VMA).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The size and colour pattern are characteristic for

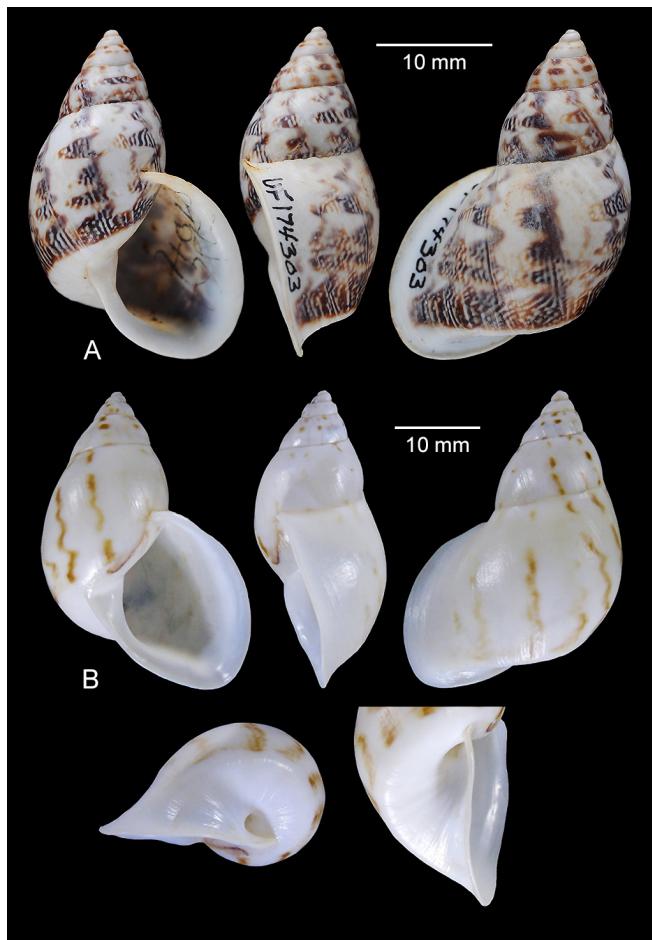


Figure 32. *Drymaeus inca* M. Smith, 1943. A, holotype UF 174303. B, Satipo, Junín (VMA); black arrows point to disappearing lines. See also Figure 53.

this species. The white lines or spots in the dark-coloured parts of the colour pattern are present in the type material and some other specimens, but these white lines are missing in some populations, and different colour patterns do occur (see Fig. 51B, which is tentatively identified as this species; see also *D. schunkei*.

Drymaeus interictus (E. von Martens, 1867)

Figures 33, 35

Bulimulus (Drymaeus) interictus Martens 1867: 144. "oberen Amazonenstromgebiet" [from title of paper]. Lectotype ZMB.MOLL 11834a; paralectotypes ZMB.MOLL 11834b (3) (Köhler 2007: 146).

Drymaeus interictus form *diversipictus* Pilsbry 1944: 125, pl. 11 fig. 11. "Orejo de Capelo, Peru, 1600 meters elevation". Holotype ANSP 180021.

Diagnosis. Shell elongate, thin, shiny, imperforate; whorls rather convex, yellowish, with axial streaks speckled with



Figure 33. *Drymaeus interictus* (E. von Martens, 1867). Lectotype ZMB.MOLL 11834a.

yellowish dots; aperture elongate-ovate, purplish inside; peristome white, expanded throughout; suture hardly ascending in front.

Measurements. Shell height 40 mm, diameter 15 mm.

Occurrence records. JUNÍN, Chanchamayo Valley (MCZ 139836); Orejo de Capelo (ANSP 180021, MCZ 125551).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This is a polymorphic species with different colour patterns, all with axial elements. Pilsbry's *diversipictus* is clearly a colour form and was placed by Richardson (1995: 139) in the synonymy of *Drymaeus interictus*.

Drymaeus jousseae Dautzenberg, 1901

Figures 34, 35

Drymaeus jousseae Dautzenberg 1901: 308, pl. 9 figs 4–5. "Rio Mixollo, Province Huallaga, Pérou". Lectotype MNHN-IM-2000-28065; paralectotype RBINS MT.2356 (Fischer-Piette 1950: 170).

Diagnosis. Shell solid, rimate, sculptured with low costulae; whorls rather convex, whitish, with wavy, brown axial streaks; aperture ear-shaped, purplish inside; peristome expanded throughout; suture ascending in front.

Measurement. Shell height 49 mm, diameter 22 mm.

Occurrence record. SAN MARTÍN, Rio Mishollo (type locality).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. The type material is the only specimens known.



Figure 34. *Drymaeus jousseaumei* Dautzenberg, 1901. Lectotype MNHN-IM-2000-28065.

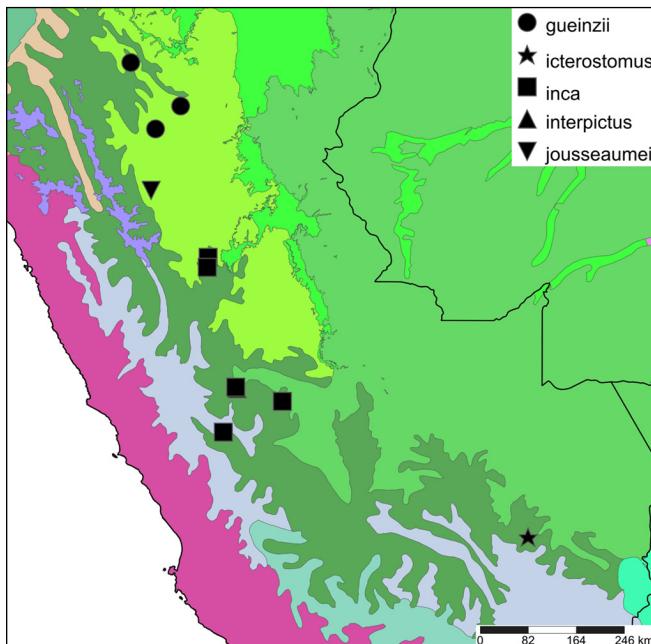


Figure 35. Distribution of *Drymaeus* species.

Drymaeus luculentus Breure & Vega-Luz, 2021

Figures 36, 41

Drymaeus (Drymaeus) luculentus Breure & Vega-Luz 2021: 21, figs 5–8. “Peru, Dept. Amazonas, Prov. Chachapoyas, District Molinopampa, ca. 2600 m”. Holotype NHMUK 20210002; paratypes MNCN 15.05/200127 (1), RVL-DR3 (1).

Diagnosis. Shell rather thin, rimate, slender; colour ranging from yellowish at top to multicolour on base and crossed on last whorl by spiral bands of arrow-like brown and whitish parts; aperture elongate-ovate, compressed below; peristome

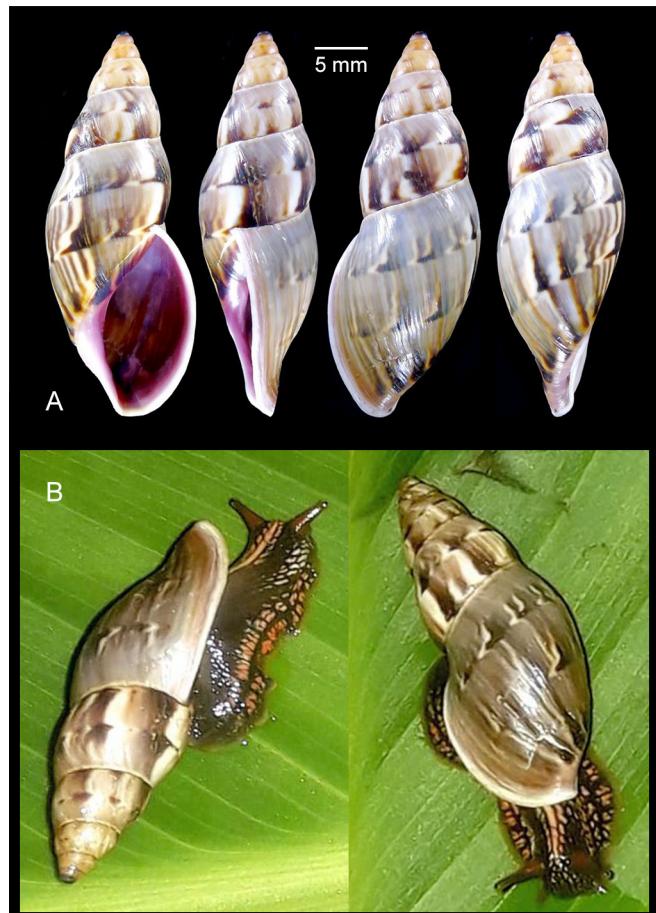


Figure 36. *Drymaeus luculentus* Breure & Vega-Luz, 2021. A, holotype NHMUK 20210002. B, living specimen, Cocachimba, Amazonas (iNaturalist 45829598).

white, slightly expanded; suture hardly ascending in front.

Measurements. Shell height 35 mm, diameter 15 mm.

Occurrence records. AMAZONAS, Molinopampa District (type locality); Omia District (MNCN 15.05/200127; RVL); Bongará Province, Cocachimba (iNaturalist 45829598).

Ecoregion. Peruvian Yungas [NT0153].

Animal. The body of the animal is greenish beige, with latticed areas of beige “dots” and beige tentacles, which are darker at the tips.

Remarks. This is a polymorphic species, as shown in the original publication.

Drymaeus marcapatensis Breure, 1979

Figures 37, 41

Drymaeus (Drymaeus) schmidti Haas 1955: 314, fig. 62. “Ccachabamba, Marcapata, Cuzco, Peru”. Holotype FMNH 51323.



Figure 37. *Drymaeus marcapatensis* Breure, 1979. Holotype FM NH 51323.

Not *Bulimus schmidti* L. Pfeiffer, 1854.
Drymaeus (Drymaeus) marcapatensis Breure 1979: 111. Nom. nov.
 for *Drymaeus (Drymaeus) schmidti* Haas 1955.

Diagnosis. Shell thin, rimate, with a rounded, pinched-up keel around umbilical chink; colour creamy white; aperture oval, pointed at both ends, channelled at base; peristome slightly expanded; suture hardly ascending in front.

Measurements. Shell height 28 mm, diameter 12 mm.

Occurrence record. CUZCO, Marcapata District, Ccachubamba (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The holotype is the only specimen known.

Drymaeus multiguttatus Weyrauch, 1964

Figures 38, 41

Drymaeus (Ornatimormus) multiguttatus Weyrauch 1964: 55, fig. 8. "Perú central, Boquerón de Abad, en la carretera entre Tingo María y Pucallpa, 550 m". Holotype IFML-MOLL 1200.

Diagnosis. Shell thin, rimate; whorls rather convex, whitish, with spiral rows of rectangular, light-brown spots; aperture oval; peristome slightly expanded at base; suture hardly ascending in front.

Measurements. Shell height 19.8, diameter 11 mm.

Occurrence record. HUÁNUCO, Boquerón de Abad (type locality).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. The holotype is the only specimen known.



Figure 38. *Drymaeus multiguttatus* Weyrauch, 1964. Holotype IFML-MOLL 1200.



Figure 39. *Drymaeus nebulosum* Breure & Ablett sp. nov. Holotype NHMUK 1928.12.6.97.

Drymaeus nebulosum Breure & Ablett sp. nov.

Figures 39, Table 3

ZooBank identifier. urn:lsid:zoobank.org:act:8945D4BF-B009-480A-93CF-68759D558529

Diagnosis. A *Drymaeus* species up to 35.7 mm, characterised by its colour pattern of spiral colour bands and bursts of dark purplish brown with whitish spots, whitish lip, and aperture with a purplish hue.

Description. Shell up to 35.7 mm, 1.95 times as long as wide, narrowly umbilicate, with almost straight sides; elongate, moderately solid. Colour whitish, patterned with spiral bands and bursts of dark purplish brown with whitish spots;

Table 3. Shell dimensions and number of whorls of type material of *Drymaeus nebulosum* Breure & Ablett sp. nov.

Specimen	Collection	Height (mm)	Diameter (mm)	Height of aperture (mm)	Width of aperture (mm)	Last whorl height (mm)	No. of whorls
Holotype	NHMUK	35.0	19.6	17.4	14.3	23.9	7.3
Paratype 1	RVL-DR8	31.3	14.7	16.8	9.8	23.1	6.25
Paratype 2	RVL-DR9	35.7	18.3	17.6	10.6	24.8	6.75

in some specimens one or more bands may be broader and besides the whitish spots there is a network of straight or undulating lines of differing length. Surface rather shiny, with growth striae somewhat incrassate. Protoconch with a reticulate sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 6.4, hardly convex; suture impressed and ascending in front. Aperture subovate, inside with a purplish hue, showing the dark bands (but without whitish spots); 1.55 times as long as wide, 0.51 times total shell length. Peristome broadly expanded, whitish; with a light band on its outside. Columellar broadly expanded, receding above, triangularly broadened. Parietal region with thin, transparent callus.

Type locality. Peru, Amazonas Department, Rodriguez de Mendoza Province, Vista Alegra, Puca Tambo [ca -06.16, -077.26], 1555 m a.s.l.

Additional locality. Peru, Amazonas Department, Bongará Province, Yambrasbamba [ca -05.73, -077.92], ca 1850 m a.s.l. (RVL, paratypes).

Ecoregion. Peruvian Yungas [NT0153].

Type material. Holotype NHMUK 1928.12.6.97, Godman–Thomas Expedition leg., 1926. Paratypes RVL (2), V. Castillo leg., July 2020.

Remarks. This novel species is only known from the type locality and the additional locality where the paratypes were found. We have seen images of shells sold by Femorale, a shell-dealership (<http://www.femorale.com>, pers. comm.), that are also likely this species. These specimens come from the area around Chachapoyas. The new species resembles *D. arcuatostriatus* (L. Pfeiffer, 1855) in shell shape, however, that species is smaller and has more prominent whitish axial lines on the darker parts of the irregular colour pattern (Breure & Ablett 2014: fig. 41A–C). Mogollón & Breure (2019: 15) discussed material that was collected at San Martín Department, Cueva Pequeña and misidentified by Guevara (2008: figs 2.64–2.67) as *D. glaucostomus* (Albers, 1852), which is a Venezuelan species. Her shell looks like our new species, except that the dark-brown spiral bands are without white dots or lines and are crossed by dark-brown axial streaks.

Etymology. Latin: *nebulosum*, cloudburst. The colour pattern gives the impression of spiral cloud bands.

Drymaeus ommatidia Dorado & Roosen, 2023

Figures 40, 63

Drymaeus ommatidia Dorado & Roosen 2023: 114, figs 1, 2D.

“Peru, departamento de Amazonas, provincia de Bagua, nordeste de Bagua, entre 1,600–2,200 m s.n.m.” Holotype MCNB-MZB 2023-0666; paratypes MCNB-MZB 2023-0667 (1), RBINS MT.4006 (1), CCD (1).

Diagnosis. Shell thin, imperforate, whitish-yellow, translucent; aperture oval; peristome thin, slightly expanded basally; suture hardly ascending in front.

Measurements. Shell height 23 mm, diameter 12.2 mm.

Occurrence record. AMAZONAS, near Bagua (type locality).

Ecoregion. Marañon dry forests [NT0223].

Remarks. The body is green in living specimens. This species, together with *D. valentini* Breure & Vega-Luz, 2020, are closely related and seem characterised by the green animal. This warrants further molecular and anatomical research better to understand the relationship with other *Drymaeus* species.

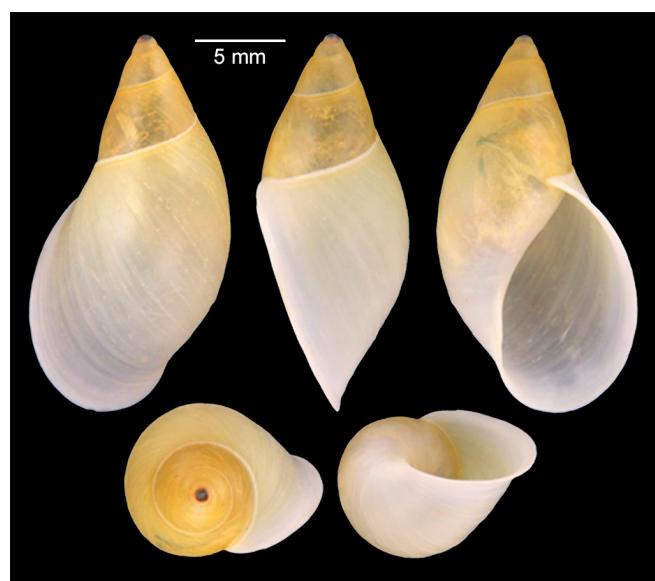


Figure 40. *Antidrymaeus ommatidia* (Dorado & Roosen, 2023). Holotype MCNB/MZB 2023-0666.

***Drymaeus palassus* Breure & Eskens, 1981**

Figures 41, 42

Drymaeus (Drymaeus) palassus Breure & Eskens 1981: 32. "Peru, Dept. Cajamarca, 30 km NE Cutervo, 2650 m". Holotype SMF 156377a; paratypes IFML-MOLL 3198 (4), SMF 156377b (1).

Diagnosis. Shell rather thin, shiny; whorls slightly convex, last whorl prominent; colour beige to brownish, with lighter, irregularly spaced dots and spots; aperture ear-shaped; peristome white, expanded, reflected; columellar margin with fold.

Measurements. Shell height 38.7 mm, diameter 17.4 mm.

Occurrence record. CAJAMARCA, Cutervo (type locality; RVL).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Different colour forms exist of this species, ranging from uniform to a pattern of dark axial bands with irregular lighter spots.

***Drymaeus peelii* (Reeve, 1859)**

Figures 43, 48

Bulimus peelii Reeve 1859: 123. "Peruvian side of Amazonas". Type material not located.

Diagnosis. Shell rather solid, shiny, rimate, whitish, with wavy, light-brown axial streaks, on last whorls crossed by two interrupted, dark-brown-black spiral bands overlayed by narrow, interrupted whitish lines; aperture ear-shaped; peristome orange-yellow, expanded; suture hardly ascending in front.

Measurements. Shell height 58.5 mm, diameter 23.4 mm.

Occurrence records. AMAZONAS, Abra Patricia (RVL). SAN MARTÍN, Oriente Nuevo (ZMH 10284).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. This is a large species (54–58.5 mm high), which may have a disjunct distribution in Peru and Ecuador (Breure et al. 2022: 161, 163). See also *D. fordii* Pilsbry, 1898, which is now considered as a separate species.

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

Figures 44, 48

Bulimus protractus Pfeiffer 1855: 94, pl. 34 fig. 1. "Meobamba, Eastern Peru". Lectotype NHMUK 1975494 (Breure 1979: 113).

Diagnosis. Shell rather thin, perforate, uniform buff or with narrow, light-brown axial streaks; aperture ovate, purplish-bordered inside; peristome buff, expanded throughout; suture slightly ascending in front.

Measurements. Shell height 26.0 mm, diameter 12.5 mm.

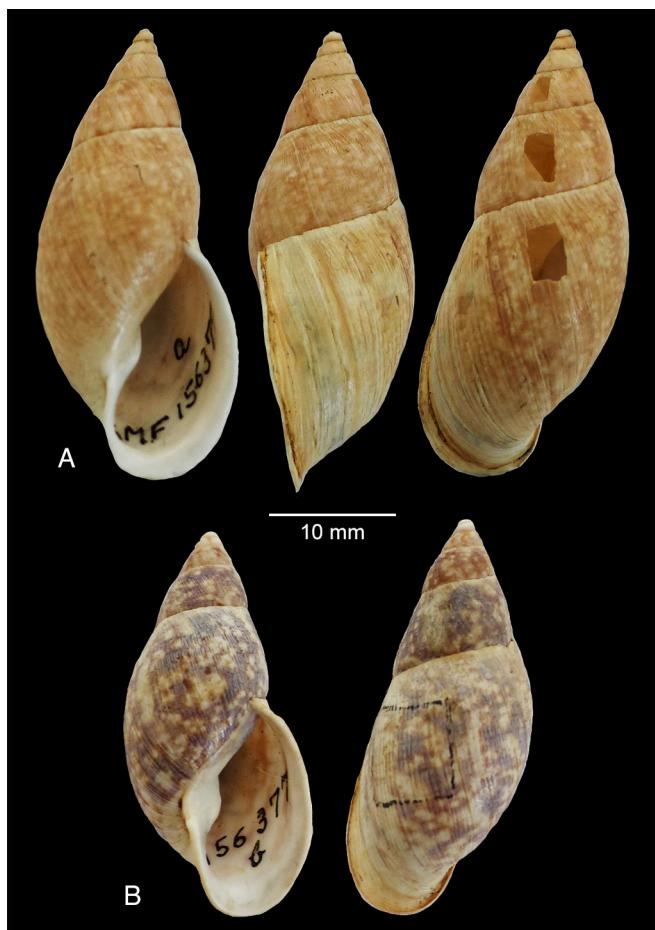


Figure 41. *Drymaeus palassus* Breure & Eskens, 1981. A, holotype SMF 156377. B, paratype 156377b.

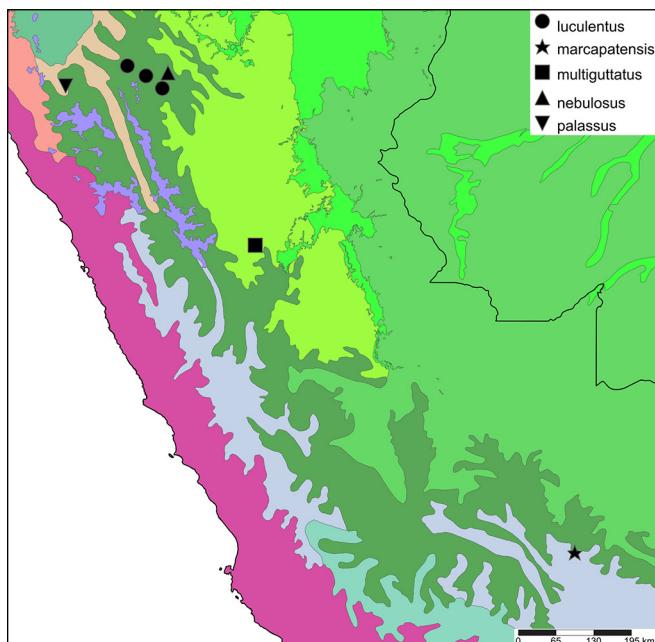


Figure 42. Distribution of *Drymaeus* species.



Figure 43. *Drymaeus peelii* (Reeve, 1859). Abra Patricia, Amazonas (RVL).

Occurrence records. SAN MARTÍN, Moyobamba (type locality); Tarapoto to Bellavista (FEM); Tarapoto to Sauce.

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Tentatively we follow Weyrauch (1967: 485) to consider this taxon as a valid species, but it is closely related to the *Drymaeus expansus* species complex.



Figure 44. *Drymaeus protractus* (L. Pfeiffer, 1855). Lectotype NHMUK 1975494.



Figure 45. *Drymaeus punctatus* S.I. da Costa, 1907. Lectotype NHMUK 1907.11.21.20.

***Drymaeus punctatus* S.I. da Costa, 1907**

Figures 45, 48

Drymaeus punctatus da Costa 1907: 304, pl. 26 figs 1–1a. “Chanchamayo, Peru”. Lectotype (Breure 1979: 113) NHMUK 1907.11.21.20; paralectotypes NHMUK 1907.11.21.21 (1), ZMB.MOLL S9262 (1).

Drymaeus punctatus (var.) *albida* da Costa 1907: 304, pl. 26 figs 2–2a. “Chanchamayo, Peru”. Syntype ZMB.MOLL 59263 (1).
Drymaeus punctatus (var.) *ventricosa* da Costa 1907: 304, pl. 26 figs 3–3a. “Chanchamayo, Peru”.

Diagnosis. Shell fusiform, imperforate, yellowish white, with wavy axial streaks and yellowish-white dots; aperture ovate, purplish-bordered inside; peristome white, expanded throughout; suture hardly ascending in front.

Measurements. Shell height 34 mm, diameter 11 mm.

Occurrence records. JUNÍN, Chanchamayo valley (type locality; ANSP 98109; RMNH.MOL 266088; UMMZ 125087). PASCO, Huancabamba (ANSP 107814; MCZ 64888; UF 161288; UMMZ 125090; USNM 530534); Pozuzo (RMNH.MOL 114280).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The two varieties are regarded as colour forms; they were already listed under the nominal form by Richardson (1995: 165).

Drymaeus rectilinearis (L. Pfeiffer, 1855)

Figures 46, 48

Bulimus rectilinearis Pfeiffer 1855: 96, pl. 31 fig. 7. “Meobamba, Eastern Peru”. Type material: see Breure & Ablett (2014: 166).

Bulimus (Liostracus) fuscobasis Smith 1877: 365, pl. 39 fig. 6. “Tarapoto, Andes of Peru”. Lectotype (Breure 1979: 119) NHMUK 1975139; paralectotype NHMUK 1975140 (1).

New synonymy.

Diagnosis. Shell thin, perforate, whitish, with a small spiral band at periphery and two broader bands below; aperture oval-elliptical; peristome thin, outer and basal margins narrowly expanded; suture slightly ascending in front.

Measurements. Shell height 24.0 mm, diameter 11.5 mm.

Occurrence records. AMAZONAS, Bagua (VMA). SAN MARTÍN, Moyobamba (type locality); Tarapoto (ANSP 78155; DMNH 164074, 176840; FMNH 72598, 78773, 94765, 95371; MCZ 9220; NHMUK 1975139–140); Rio Mayo, Leinas [sic, Lamas] (ZMB.MOLL 25577).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. Records in GBIF from other countries are mis-identifications. Given the shell shape and the colouration, we regard *B. fuscobasis* as a junior subjective synonym of *D. rectilinearis*.

Drymaeus regularis Fulton, 1905

Figures 47, 48

Drymaeus regularis Fulton 1905: 25, pl. 6 fig. 6. “Chanchamayo, Peru”. Lectotype (Breure 1979: 113) NHMUK 1905.11.17.2; paralectotype ZMB.MOLL 55982 (1).



Figure 46. *Drymaeus rectilinearis* (L. Pfeiffer, 1855). Lectotype of *Bulimus (Liostracus) fuscobasis* E.A. Smith, 1877, NHMUK 1975139.



Figure 47. *Drymaeus regularis* Fulton, 1905. A–D, lectotype NHM UK 1905.11.17.2.

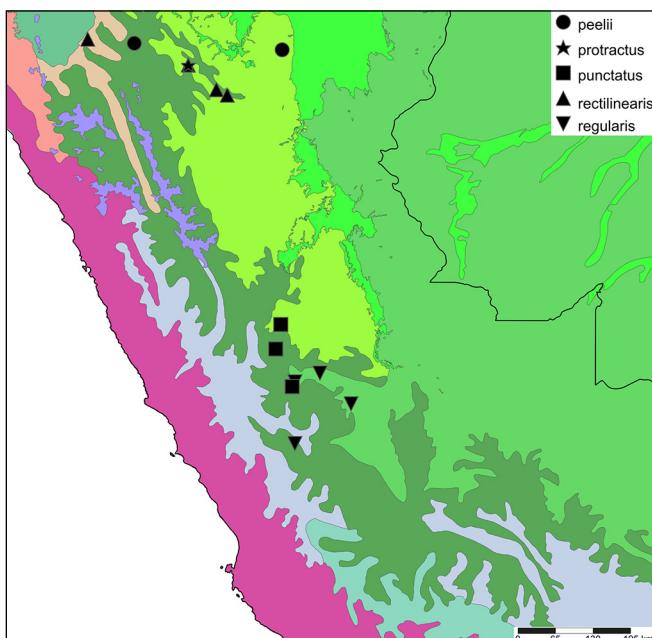


Figure 48. Distribution of *Drymaeus* species.

Diagnosis. Shell rather solid, rimate, with rather convex whorls, the last one swollen; colour whitish, with spiral series of small, dark-brown spots just above periphery and zigzag stripes below; aperture oval, violet within; peristome thin, broadly expanded throughout; suture ascending in front.

Measurements. Shell height 31 mm, diameter 16 mm.

Occurrence records. JUNÍN, Chanchamayo Valley (type locality; FMNH 31413, 31481; MCZ 145188; NHMUK 1904.1.30.33–34; UF 109132, 161291; USNM 530513; ZMB.MOLL no catalogue no.); Quimiri Sur (IFML-MOLL 17090); Alto Guacamayo (ZMA.MOLL 77900); Alto Zotani (FEM); Concepcion (FEM); Rio Colorado (IFML-MOLL 17132); between Satipo and Puerto Ocopa (MCZ 105970).

Ecoregion. Southwest Amazon moist forests [NT0166].

Remarks. This is a polymorphic species. Most colour patterns have axial elements, but in some populations, only spiral elements are present. This species closely resembles *D. schunkei* Haas, 1949, which has a more swollen last whorl and occurs further north.

Drymaeus rosenbergi S.I. da Costa, 1906

Figures 49, 55

Drymaeus rosenbergi da Costa 1906: 98, pl. 11 fig. 6. “Pozuzo, Eastern Peru”. Lectotype (Breure 1979: 113) NHMUK 1907.11.21.17.

Diagnosis. Shell thin, rimate, whitish, with narrow, undulating axial streaks; aperture oval-elliptical; peristome thin, with outer and basal margins narrowly expanded; suture slightly ascending in front.

Measurements. Shell height 19 mm, diameter 9 mm.

Occurrence records. JUNÍN, San Ramón, Guacamayo (ZMA.MOLL 77897). PASCO, Pozuzo (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This seems to be a rare species in the well-collected Chanchamayo area.

Drymaeus rugistriatus F. Haas, 1952

Figures 50, 55

Drymaeus (Drymaeus) rugistriatus Haas 1952: 120, fig. 21. “Hacienda Cadena, Valley Rio Marcapata, Dist. of Marcapata, Prov. Quispicanchi, Dept. Cuzco, Peru, at 1,000 meters elevation”. Holotype FMNH 38123.

Diagnosis. Shell rather solid, perforate, sculptured with low, interrupted costulae, whitish with a coarse pattern of brown axial streaks, festooned at periphery; aperture ear-shaped; peristome expanded throughout; suture ascending in front.

Measurements. Shell height 32.5 mm, diameter 15 mm.



Figure 49. *Drymaeus rosenbergi* S.I. da Costa, 1906. Lectotype NHMUK 1907.11.21.17.



Figure 50. *Drymaeus rugistriatus* F. Haas, 1952. Holotype FMNH 38123.

Occurrence records. CUZCO, río Marcapata Valley, Hacienda Cadena (type locality). MADRE DE DIOS, Puerto Maldonado, Quebrada La Cachuela, 175 m (VMA).

Ecoregion. Peruvian Yungas [NT0153].

Drymaeus schunkei F. Haas, 1949

Figures 51, 55

Drymaeus (Drymaeus) schunkei Haas 1949: 237, fig. 50b. “Cerro Azul, on Rio Ucayali, Dept. Loreto, Peru”. Holotype FMNH 30040.

Diagnosis. Shell thin, perforate, whitish, with dark-brown, undulating axial streaks; whorls slightly convex, the last prominent; aperture oval, oblique; peristome broadly expanded throughout; suture ascending in front.

Measurements. Shell height 28 mm, diameter 14 mm.

Occurrence records. HUÁNUCO, 27.4 km SSE of Aucayacu (UF 176993); Cerro Azul (type locality of *schunkei*; IFML-

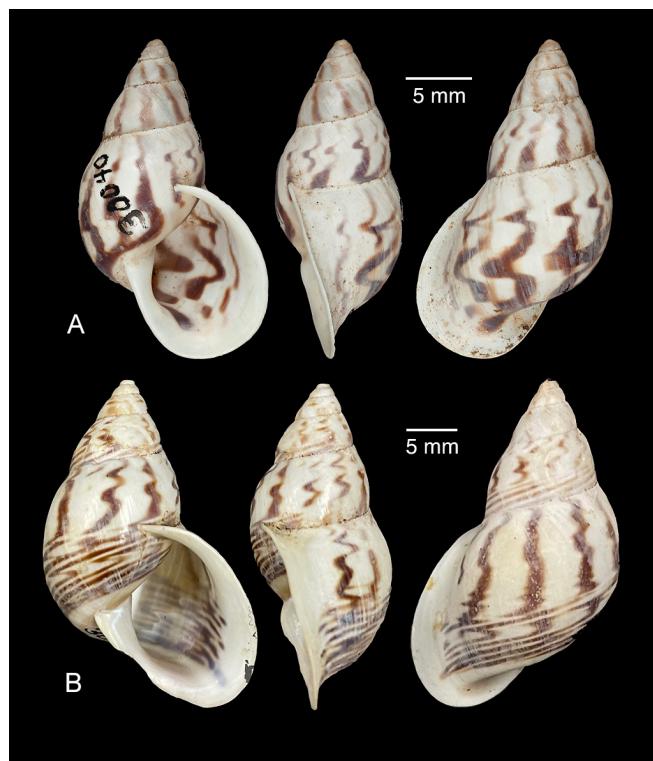


Figure 51. *Drymaeus schunkei* F. Haas, 1949. A, holotype FMNH 30040. B, *Drymaeus* cf. *inca* M. Smith, 1943. Divisoria, Huánuco (FMNH 30051).

MOLL 17086); 70–80 km NE of Tingo María (RMNH. MOL.266091). UCAYALI, Pucallpa (RMNH.MOL.266090; SMF 164017).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. There is some variation in colour pattern, the pointedness of the aperture, and the angle of the aperture to the axis of the columella. Specimens from Divisoria (FMNH 30051) are tentatively identified as *D. schunkei* (Fig. 51B). The relationship between this species and related ones, like *D. inca* M. Smith, 1943 and *D. regularis* Fulton, 1905, needs further research.

Drymaeus scoliodes Dautzenberg, 1901

Figures 52, 55

Drymaeus scoliodes Dautzenberg 1901: 309. “Rio Mixiollo, Province de Huallaga, Pérou”. Lectotype (Fischer-Piette 1950: 170) MNHN-IM-2000-28114; paralectotype RBINS/MT 2377 (1).

Diagnosis. Shell rather solid, umbilicate, whitish, with relatively few dark-brown axial streaks; last whorl carinate at base; aperture ovate, oblique to shell axis; peristome expanded; suture ascending in front.

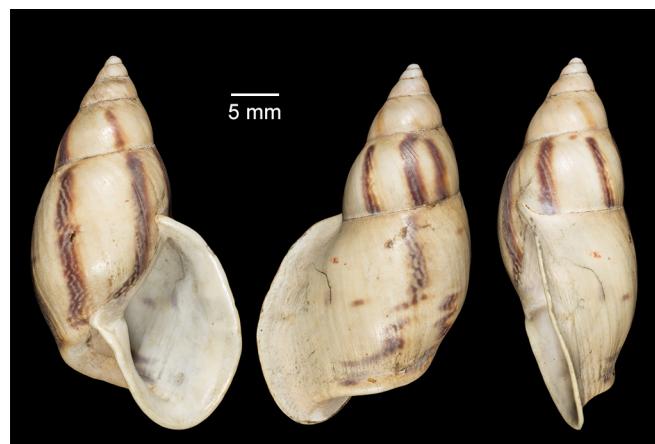


Figure 52. *Drymaeus scoliodes* Dautzenberg, 1901. Lectotype MNHN-IM-2000-28114.

Measurements. Shell height 42.5 mm, diameter 22.5 mm.

Occurrence records. SAN MARTÍN, prov. Huallaga, rio Mishollo (type locality).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. Known only from the type specimens. Dautzenberg (1901: 309) gave as measurements of “Long. 63, diam. maj. 22 millim.”; we suppose the shell height is in error, as Breure (1976: 1149) gave the shell height as 42.5 mm and diameter as 22.5 mm, the latter in accordance with Dautzenberg’s measurements.

Drymaeus serratus (L. Pfeiffer, 1855)

Figures 53, 55

Bulimus serratus Pfeiffer 1855, Proc. zool. Soc. London 23: 94, pl. 31 fig. 6. “Meobamba, Eastern Peru”. Lectotype (Breure 1979: 114) NHMUK 1975475; paralectotypes NHMUK 1975476 (2).

Bulimus recedens Pfeiffer 1864: 525. “Meobamba”. Lectotype (Breure 1979: 113) NHMUK 1975477. **New synonymy.**

Diagnosis. Shell rather thin, rimate, whitish, with narrow axial stripes ending at periphery and interrupted in two places by sharp, arrow-shaped zigzags; aperture oval, pale roseate-purplish inside; peristome somewhat expanded, especially at basal margin; suture slightly ascending in front.

Measurements. Shell height 27.3 mm, diameter 13.3 mm.

Occurrence records. HUÁNUCO, Tingo María (DMNH 164 073; UF 176999, 486916); near Tingo María, road to airport (RMNH.MOL 264815); *ibid.*, Cueva de las Pavas (RMNH.MOL 114914); 4.6 km N of Tingo María (UF 177 000); 4 km NE of Tingo María (UF 177001); 9.2 km S of Tingo María (UF 176998). SAN MARTÍN, Moyobamba (type locality; FMNH 31357; MCZ 142938; NHMUK 1975477).



Figure 53. *Drymaeus serratus* (L. Pfeiffer, 1855). Lectotype NHMUK 1975475.



Figure 54. *Drymaeus similaris* (J. Moricand, 1856). A, syntype MHNG-MOLL 63531. B, Rioja, San Martín (RVL).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. The type material of *B. recedens* is similar in shape, size, and colour pattern, and from the same type locality as *Drymaeus serratus*; we consider these taxa to be synonyms.

Drymaeus similaris (J. Moricand, 1856)

Figures 54, 55

Bulimus similaris Moricand 1856: 177, pl. 6 fig. 8. "Moyobamba".
Syntypes MHNG-MOLL-63531 (7).

Redescription. Shell up to 26 mm, 2.0 times as long as wide, narrowly umbilicate, with almost straight sides; elongate, moderately solid. Colour whitish, its colour pattern with one spiral colour band, broken into narrow elongate dots, just above the periphery, and axial, partial undulating or zig-zag, bursts of dark brown; on the upper whorls there are two broken spiral bands, with axial undulating streaks of brown, fading away above. Surface slightly shiny, with hardly visible growth striae. Protoconch with a grating sculpture of axial

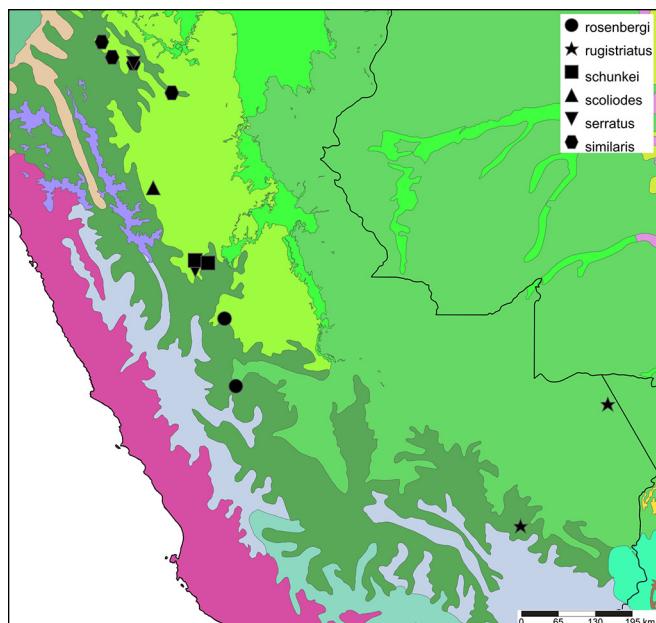


Figure 55. Distribution of *Drymaeus* species.

riblets and spiral striae, which are of equal strength. Whorls 5.7, hardly convex; suture impressed. Aperture subovate, inside showing dark bands through shell wall; 1.6 times as long as wide, 0.52 times shell length. Peristome expanded, yellowish; on outside with a light-yellow band. Columellar margin expanded, receding above and triangularly broadened. Parietal region with a thin, somewhat yellowish callus.

Occurrence records. SAN MARTÍN, Mirador, Alto Mayo (RVL; VMA 1569); Moyobamba (type locality); Nueva Cajamarca (FEM); Tarapoto (ZMB.MOLL without catalogue no.).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The relationship of this taxon with *D. strigatus* (G.B. Sowerby I, 1833), occurring in the same general area, needs further study. This species resembles *D. nebulosum* Breure & Ablett sp. nov., but it differs in being smaller, lacking white dots or lines in the dark brown colour pattern, having a purple hue inside of the aperture, and above all, having a yellow peristome.

Drymaeus sophiaeae Breure, 1979

Figures 56, 65

Drymaeus (Drymaeus) pergracilis Haas 1952: 122, fig. 23. "Hacienda Cadena, Dist. Marcapata, Prov. Quispicanchi, Dept. Cuzco, Peru, at 1,000 meters elevation in the valley of Rio Marcapata". Holotype FMNH 38128, paratypes 38128a-k/11. Not *Bulimus pergracilis* Rolle, 1904.

Drymaeus (Drymaeus) sophiaeae Breure 1979: 114. Nom. nov. for



Figure 56. *Drymaeus sophiaeae* Breure, 1979. Holotype of *Drymaeus* (*Drymaeus*) *pergracilis* F. Haas, 1952, FMNH 38128.

Drymaeus (*Drymaeus*) *pergracilis* Haas 1952.

Diagnosis. Shell elongate, thin, rimate, whitish, with a few small, slender, brown axial streaks; whorls somewhat convex; aperture oblong, oblique, bordered with purplish inside; peristome expanded; suture hardly ascending in front.

Measurements. Shell height 46 mm, diameter 14 mm.

Occurrence records. CUZCO, Prov. Marcapata, Hacienda Cadena (type locality); Santa Ana (MCZ 133209).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. An unconfirmed identification, possibly this species, near Aguas Calientes (iNaturalist 37821804) makes us suspect that this species can also show a colour pattern of a few spiral bands.

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

Figures 57, 65

Bulinus strigatus Sowerby I 1833 [Sowerby I & II 1832–1841]: figs 95–96. “Huallaga”. Possible syntypes NHMUK 20090168 (3).

Bulinus saccatus Pfeiffer 1955: 94, pl. 31 fig. 2. “Meobamba, Eastern Peru”. Lectotype (Breure 1979: 114) NHMUK 1975207; paralectotypes NHMUK 1975218 (2).

Bulinus musivus Pfeiffer 1855: 95, pl. 31 fig. 3. “Meobamba, Eastern Peru”. Lectotype (Breure 1979: 111) NHMUK 1975292.

Bulinus ceciliae Moricand 1858: 452, pl. 14 fig. 4. “Tarapoto”. Syntypes MHNG-MOLL-63436 (9).

Bulinus delphinae Moricand 1858: 452, pl. 14 fig. 3. “Tarapoto”.

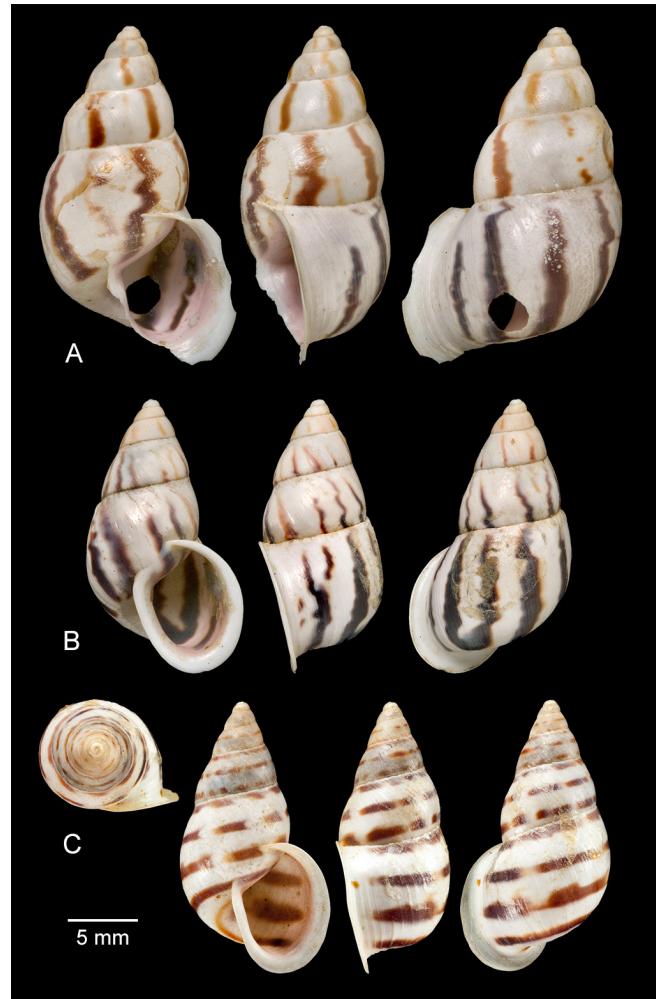


Figure 57. *Drymaeus strigatus* (G.B. Sowerby I, 1833). A, possible syntype NHMUK 20090168. B, lectotype of *Bulinus musivus* L. Pfeiffer, 1855, NHMUK 1975292. C, lectotype of *Bulinus saccatus* L. Pfeiffer, 1855, NHMUK 1975207.

Syntypes MHNG-MOLL-63443 (3).

Bulinus mariae Moricand 1858: 453, pl. 14 fig. 5. “Tarapoto”. Syntypes MHNG-MOLL-64389 (7). Not *Bulinus mariae* Albers, 1850.

Drymaeus strigatus (var.) *purus* Pilsbry 1898 [1897–1898]: 229, pl. 42 fig. 41. “Peru”. Lectotype (Baker 1963: 230) ANSP 264300.

Drymaeus marieanus Pilsbry 1898 [1897–1898]: 230, pl. 42 fig. 51. Nom. nov. for *Bulinus mariae* J. Moricand, 1858.

Diagnosis. Shell rather thin, perforate, whitish, with either narrow, brown axial or spiral bands, or brownish, with a white spiral band just below periphery, aperture ovate, somewhat compressed at base; peristome white, expanded; suture ascending in front.

Measurements. Shell height 19–24 mm, diameter 9–12 mm.

Occurrence records. SAN MARTÍN, Moyobamba (NHM UK 1975207, 1975218, 1975292; ZMB.MOLL no catalogue no.); Prov. Huallaga (type locality); Rumizapa near Tarapoto (RBINS no catalogue no.); Tarapoto (ANSP 24300, 78152; DMNH 164062, 176841, 183908; FMNH 30859, 94814, 94862, 94875, 95321, 95319, 95322, 95326, 95375, 95379, 95391, 95392, 95393; MCZ 9221, 140270, 160226; MHNG-MOLL-63436, 64343, 64389; SMF 90194; SMF 90195; UF 487287); Traquillo (RBINS no catalogue no.). UCAYALI, Prov. Ucayali (ZMB.MOLL 37647).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174], Iquitos várzea [NT0128].

Remarks. This is a polymorphic species with much variation in the colour pattern among populations. See also Breure (2016) and Breure & Ablett (2016).

Drymaeus subeffusus (Philippi, 1869)

Figures 58, 65

Bulimus subeffusus Philippi 1869: 36. “in nemoribus Peruviae de Huancayo dictis, loco Coyllorbamba”. Type material not located.

Diagnosis. Shell rather thin, rimate, whitish, with brown axial stripes; aperture ovate-oblong; peristome thin, right and basal margins narrowly expanded.

Measurements. Shell height 40.5 mm, diameter 17.5 mm.

Occurrence record. JUNÍN, Coyllorbamba (type locality).

Ecoregion. Central Andean wet puna [NT1003].

Remarks. We could not find “Coyllorbamba” in gazetteers available to us, but we did find a lake named “Coyllorcocha” southwest of Huancayo, the well-known city in the Department of Junin (Espinoza 1973). We also found the name of a farm, “Coyllorbamba”, where Raimondi (1879: 349) collected; likely, this is near Lake Coyllorcocha; this area is at an altitude of 4500–4600 m a.s.l.

The spire shape and the colour pattern resembles some species of *Bostryx* Troschel, 1847. Locating the type locality and collecting fresh topotypic material is needed.

Drymaeus subsimilis Pilsbry, 1898

Figures 59, 65

Drymaeus subsimilis Pilsbry 1898 [1897–1898]: 22, pl. 44 figs 15–16. “probably western Brazil or eastern Peru”. Holotype ANSP 25751.

Diagnosis. Shell moderately solid, imperforate, whitish, with two spiral series of small brown spots and darker axial stripes connecting the two spiral series on last whorl; aperture long-ovate, lilac-purple on near lip; peristome expanded, especially basally; suture slightly ascending in front.

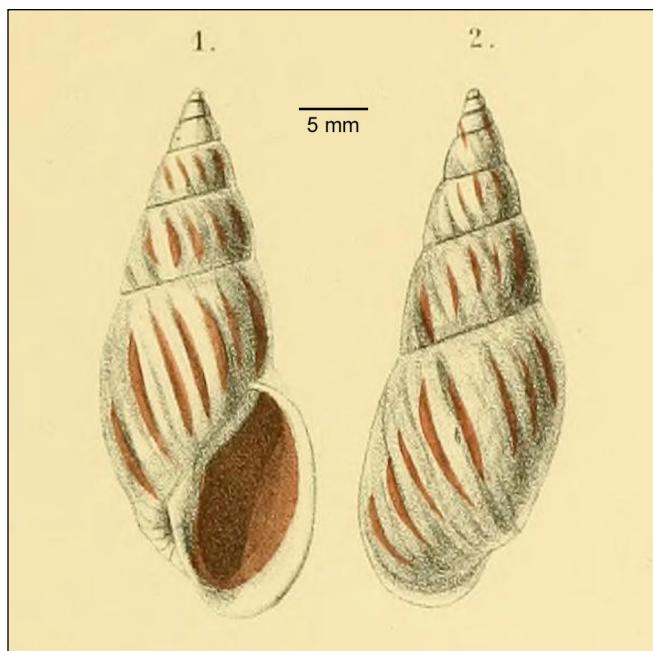


Figure 58. *Drymaeus subeffusus* (Philippi, 1869). Original figures reproduced from Pfeiffer (1869 [1866–1869]: pl. 102 figs 1, 2).



Figure 59. *Drymaeus subsimilis* Pilsbry, 1898. Holotype ANSP 25751.

Measurements. Shell height 23.0 mm, diameter 9.5 mm.

Occurrence record. AMAZONAS, Aramango (IFML-MO LL 17100).

Ecoregion. Marañon dry forests [NT0223].

Remarks. The type locality is imprecise, but the IFML material, which was collected by Weyrauch, reveals the area where this species occurs. We have not seen this species in other collections.

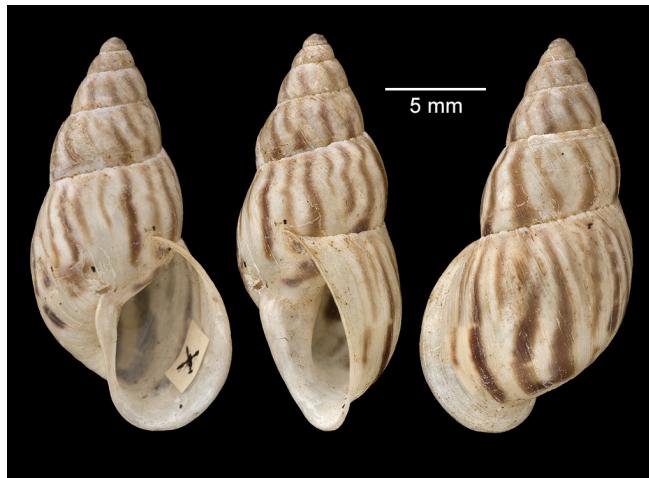


Figure 60. *Drymaeus tigrinus* (S.I. da Costa, 1898). Lectotype NHMUK 1907.11.21.55.

Drymaeus tigrinus (S.I. da Costa, 1898)

Figures 60, 65

Bulimulus (*Drymaeus*) *tigrinus* da Costa 1898: 82, pl. 6 fig. 6. “Ecuador”. Lectotype (Breure 1979: 115) NHMUK 1907.11.21.55, parlectotype NHMUK 1907.11.21.56 (1).

Diagnosis. Shell thin, perforate, whitish, with narrow, wavy axial stripes; aperture ovate; peristome thin, narrowly expanded at outer and basal margins; suture ascending in front.

Measurements. Shell height 21 mm, diameter 10 mm.

Occurrence records. AMAZONAS, near Galilea on Rio Santiago (UF 28028, 28029), Poza on Rio Santiago (UF 29457), Rio Yutupis, Shiringa (UF 29462). LORETO, Rio Curaray (RMNH.MOL 114184).

Ecoregion. Napo moist forests [NT0142].

Remarks. This species was previously only known from an unspecified locality in Ecuador (Breure *et al.* 2022: 168), and we report it from the Peruvian malacofauna for the first time. The specimens from northern Peru are somewhat variable in their colour pattern, but otherwise they show the same characteristics as the type material.

Drymaeus translucidus Weyrauch, 1967

Figures 61, 65

Drymaeus (*Drymaeus*) *translucidus* Weyrauch 1967: 422, figs 78, 79. “Peru central, Boquerón de Abad en la carretera entre Tingo María y Pucallpa, 500 m”. Holotype IFML-MOLL 1202a; paratypes IFML-MOLL 1202b (1), SMF 162158 (1).

Diagnosis. Shell thin, imperforate, semi-translucent, colour whitish, either uniform or with broad brownish axial streaks, on the last whorl leaving the shell whitish below the

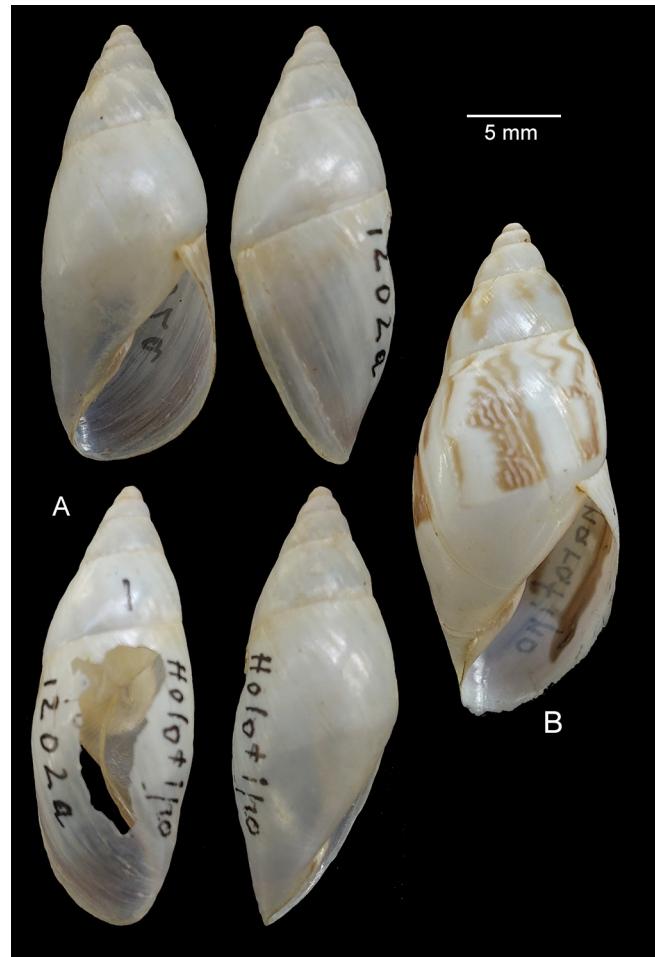


Figure 61. *Drymaeus translucidus* Weyrauch, 1967. A, holotype IFML-MOLL 1202a. B, paratype IFML-MOLL 1202b.

periphery, aperture long-ovate, oblique to the left related to the shell axis, peristome hardly expanded.

Measurements. Shell height 27.8 mm, diameter 11.1 mm.

Occurrence records. HUÁNUCO, Boquerón de Abad (type locality; RMNH.MOL 266086).

Ecoregion. Ucayalí moist forests [NT0174].

Remarks. The type material shows a bend at the periphery and the aperture is oblique to the left, which are characters that suggest subadult specimens. However, topotypic specimens (RMNH.MOL 266086) also have these characters.

Drymaeus valentini (Breure & Vega-Luz, 2020)

Figures 62, 63

Drymaeus (*Drymaeus*) *valentini* Breure & Vega-Luz 2020: 2, figs 2–4. “Peru, Dept. Amazonas, near Molinopampa, -06.208 S, -077.667 W, ca. 2600 m”. Holotype MNCN 15.05/200118H.

Diagnosis. Shell rather thin, imperforate, yellowish with irregularly spaced whitish lines of variable width; last whorl very swollen; aperture round-ovate; peristome whitish, expanded, and reflected throughout; suture slightly ascending in front.

Measurements. Shell height 27.0 mm, diameter 20.5 mm.

Occurrence records. AMAZONAS, near Molinopampa (type locality); Alto Mayo reserve (CCD); S of Chachapoyas (CCD); Jazan, Kingoyacu (J. Richards observation).

Ecoregion. Peruvian Yungas [NT0153].



Figure 62. *Antidrymaeus valentini* (Breure & Vega-Luz, 2020). Holotype MACN 15.05/200118H.

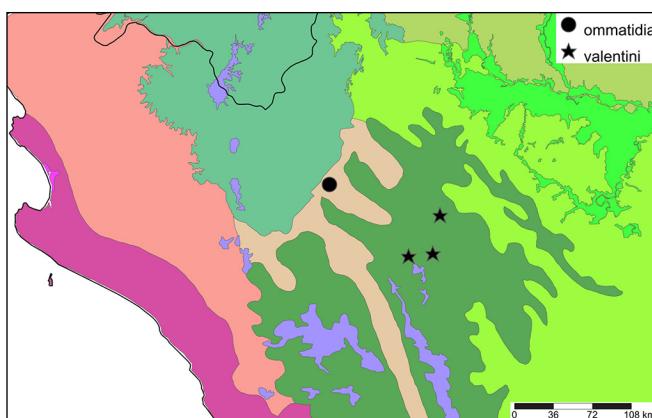


Figure 63. Distribution of *Drymaeus* species.

Remarks. The animal of this species is green when alive. It was known only from the type locality, but has since been collected at other localities in the same region.

Drymaeus verecundus Breure & Mogollón, 2019

Figures 64, 65

Drymaeus (Drymaeus) verecundus Breure & Mogollón in Mogollón & Breure 2019: 16, figs 12–15. “Peru, Dept. Loreto, Iquitos, Quistococha, 104 m, -73.322086 W, -3.826123 S”. Holotype RBINS MT.3654; paratypes RBINS MT.3655 (3), 3656 (1), RMNH.MOL 282881 (2), VMA 1148 (4).

Diagnosis. Shell thin, fragile, imperforate, whitish, with three narrow, brown spiral bands (band at periphery most prominent); aperture ovate; peristome expanded at base; suture slightly ascending in front.

Measurements. Shell height 18.7 mm, diameter 9.7 mm.

Occurrence record. LORETO, Quistococha (type locality).

Ecoregion. Iquitos várzea [NT0128].

Remarks. There is one iNaturalist observation (74684935) near Maynas in the same department as the type locality. However, as the shell is only shown in dorsal view, the identification cannot be confirmed. Its colour pattern is slightly different, with all three spiral bands of equal width.

Drymaeus weeksi Pilsbry, 1926

Figure 66

Drymaeus weeksi Pilsbry 1926: 8, pl. 2 fig. 4. “Peru”. Holotype ANSP 140302.

Diagnosis. Shell rather thin, umbilicate, whitish, with faint, pinkish-buff axial streaks; aperture round-ovate; peristome broadly expanded throughout; suture ascending in front.



Figure 64. *Drymaeus verecundus* Breure & Mogollón, 2019. Holotype RBINS MT.3654.

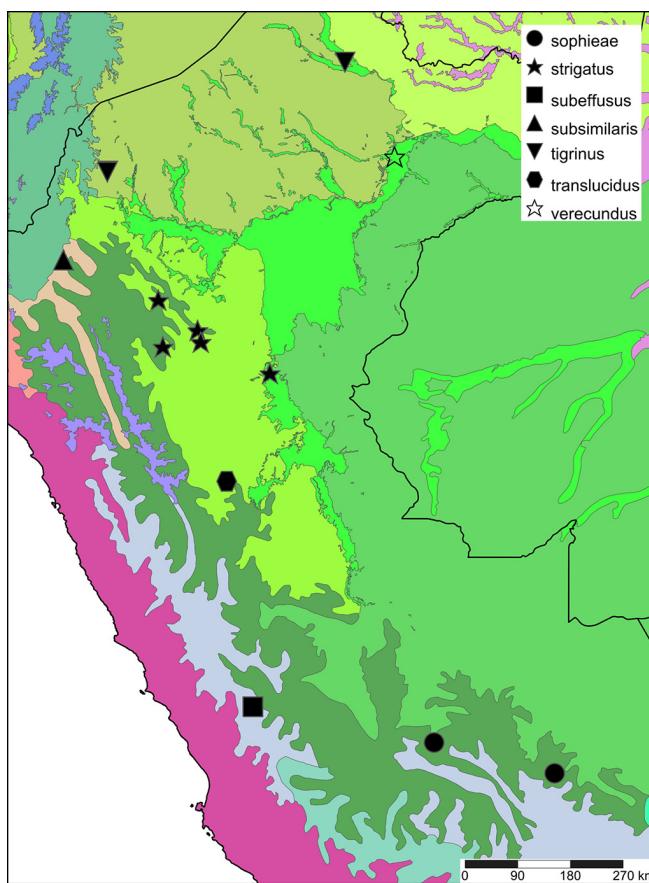


Figure 65. Distribution of *Drymaeus* species.

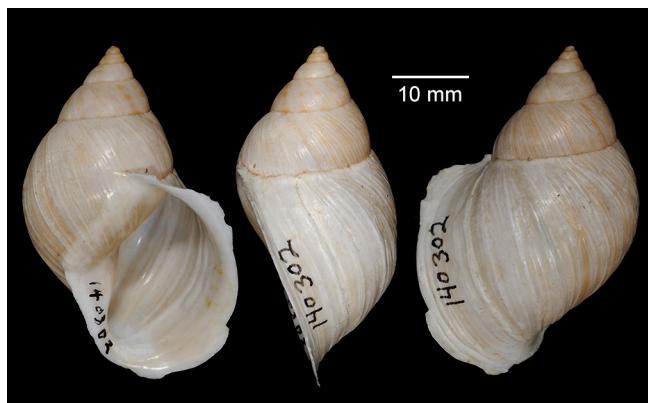


Figure 66. *Drymaeus weeksi* Pilsbry, 1926. Holotype ANSP 140302.

Measurements. Shell height 45.5 mm, diameter 31 mm.

Occurrence records. Unknown.

Ecoregion. Unknown.

Remarks. This species is known only from the type material and, since its description, has not been seen among other material from Peru.

Genus *Mesembrinus* Albers, 1850

Mesembrinus Albers 1850: 157. Type species by subsequent designation (Martens 1860: 214): *Helix virgulata* A. Féruccac, 1821.

In their molecular phylogenetic analysis, Salvador *et al.* (2023) found this group to be monophyletic and elevated the rank of *Mesembrinus* to a genus. Due to insufficient anatomical and molecular data, the allocation of other taxa to *Mesembrinus* remains tentative. We provisionally place species with a simple peristome in this genus.

Mesembrinus acobambensis (Weyrauch, 1967) comb. nov.

Figures 67, 74

Drymaeus acobambensis Weyrauch 1967: 482, figs 24–25. “Peru central, río Tarma, entre Tarma y Acobamba, Huailahuichán, 2900 m”. Holotype SMF 155604.

Diagnosis. Shell rather solid, rimate, whitish, with irregular pattern of partly fused or zigzag axial streaks; aperture ovate; peristome simple.

Measurements. Shell height 29.0–35.5 mm, diameter 15.5–17.5 mm.

Occurrence records. JUNÍN, between Tarma and Acobamba (type locality); mountain above Tarmatambo (DMNS 37620).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This species is tentatively placed now in the genus *Mesembrinus* on account of the relatively simple peristome. Anatomical or molecular data are needed to confirm this generic placement.

Mesembrinus aestivus (L. Pfeiffer, 1857) comb. nov.

Figures 68, 74

Bulimus aestivus Pfeiffer 1857: 331. “Meobamba, Peru”. Syntype NHMUK 1975462.

Diagnosis. Shell thin, perforate, colour whitish uniformly, whorls moderately convex, aperture ovate, peristome simple.

Measurements. Shell height 17, diameter 8 mm.

Occurrence record. SAN MARTÍN, Moyobamba (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Breure & Ablett (2014) have shown that “Ecuador”, the label locality on the type specimen, is likely erroneous. The specimen is uniformly whitish, but we do not know if other colour patterns occur in this species. No other specimens, other than the syntype, are known.



Figure 67. *Mesembrinus acobambensis* (Weyrauch, 1967). Holotype SMF 155604.

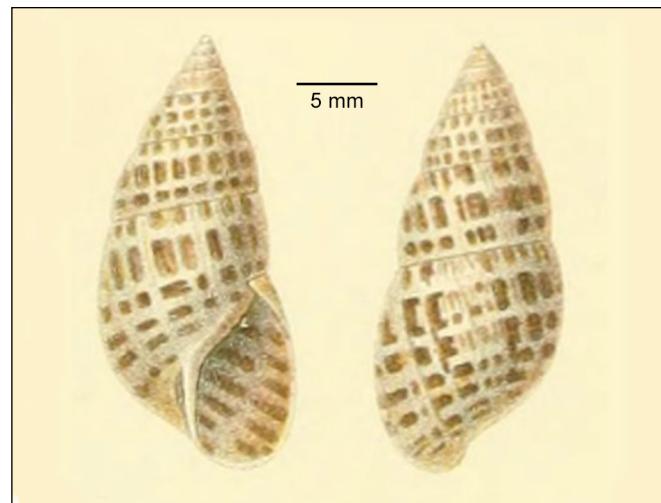


Figure 69. *Mesembrinus alsophilus* (Philippi, 1867). Figures reproduced from Pfeiffer (1867 [1866–1869]: pl. 80 figs 3, 4).



Figure 68. *Mesembrinus aestivus* (L. Pfeiffer, 1857). Syntype NHMUK 1975462.

Mesembrinus alsophilus (Philippi, 1867) comb. nov.

Figures 69, 74

Bulimus alsophilus Philippi 1867: 67. “Inter Lamas et Tarapoto”.
Type material not located.

Diagnosis. Shell thin, rimate, whitish, with spiral rows of elongate, reddish-brown spots; whorls rather flat; aperture ovate; peristome simple.

Measurements. Shell height 30.5 mm, diameter 14.0 mm.

Occurrence records. SAN MARTÍN, between Lamas and Tarapoto (type locality); without locality (UF 176769).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. We know of only the records given here, although the region where this species occurs is well collected.

Mesembrinus anceps (Albers, 1854) comb. nov.

Figure 70

Bulimus anceps Albers 1854: 217. “Columbia [sic] ad fluvium Maranon”. Syntypes ZMB.MOLL 101788 (2), 101789 (1).

Diagnosis. Shell rather solid, rimate, pale buff, with brown spots arranged in spiral bands and axial streaks, obsolete on lower half of last whorl; aperture ovate-elliptical; peristome thin, simple.

Measurements. Shell height 26.0–28.5 mm, diameter 10.0 mm.

Occurrence records. Unknown.

Ecoregion. Unknown, but likely Peruvian Yungas [NT0153].

Remarks. The Marañón River runs for 1400 km through several departments of Peru. The material was collected by Warszewicz, but we do not know his itinerary. This species has not been recently collected. Martens (1860: 213) corrected the type locality by stating “am ob.[eren] Maranon” [on the upper Marañón].

Mesembrinus angulobasis (Pilsbry, 1944) comb. nov.

Figures 71, 74

Drymaeus angulobasis Pilsbry 1944: 125, pl. 11 fig. 10. “Peru, Oreja de Capelo, 1600 m”. Holotype ANSP 180022.

Diagnosis. Shell rather strong, perforate, whitish, festooned with dark-purple axial stripes speckled with white and crossed by three narrow, interrupted, purple spiral bands; aperture oval, angular at both ends, spout-like at base; peristome white, slightly expanded at base, suture hardly ascending in front.



Figure 70. *Mesembrinus anceps* (Albers, 1854). Syntype ZMB. MOLL 101788.

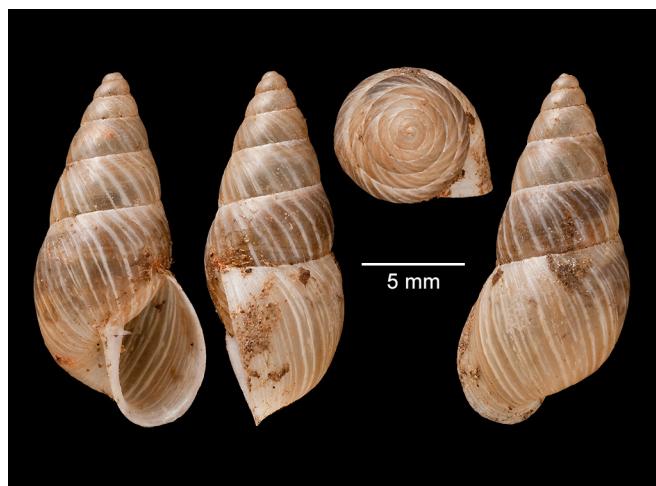


Figure 72. *Mesembrinus apicepunctata* (Preston, 1914). Holotype NHMUK 1915.1.6.23.



Figure 71. *Mesembrinus angulobasis* Pilsbry, 1944. Holotype ANSP 180022.

Measurements. Shell height 37.0 mm, diameter 13.5 mm.

Occurrence records. JUNÍN, near San Ramón, Oreja de Capelo (type locality). PASCO, Pozuzo (DMNH 58083, 177746; FMNH 193441, 216835; MCZ 221149; UF 109138, 485742; USNM 601800, 653344; ZMA. MOLL.214394, 385761).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. *Mesembrinus angulobasis* is the type species of Weyrauch's (1958) subgenus *Ornatimormus*, which is said to have "embryonic and postembryonic whorls without regular sculpture" (Schileyko (1999: 318-319). We refrain



Figure 73. *Mesembrinus bequaerti* (Weyrauch, 1956). A–C, holotype SMF 155309.

from making a conclusion on the systematic position of this subgenus until anatomical and molecular data are available. The relationship of *M. angulobasis* with *M. pulcherrimus* and *D. basitorus* may need resolution. *Mesembrinus phryne* and several species in Colombia, Ecuador and Bolivia have a similar external morphology and may be closely related ; this should be corroborated by future research. The shape of the aperture varies with the amount of protraction of the basal margin, which may cause confusion in identifying these species.

***Mesembrinus apicepunctata* (Preston, 1914) comb. nov.**
Figures 72, 74

Bulimulus apicepunctata Preston 1914: 523. "Santa Rita, E. Peru".

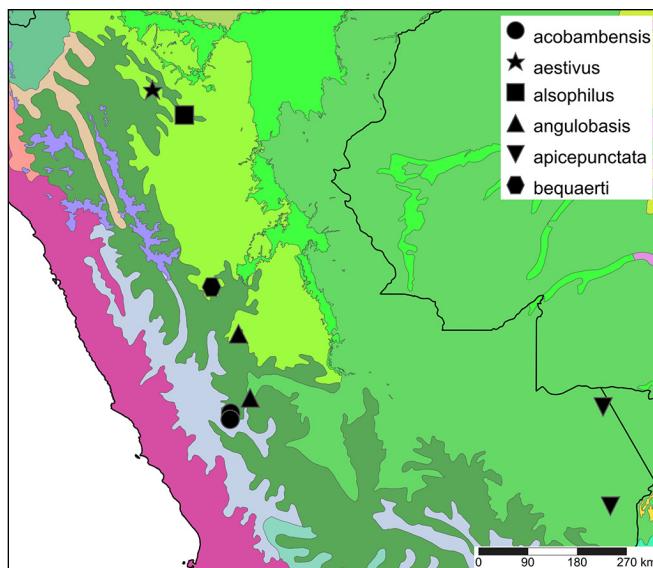


Figure 74. Distribution of *Mesembrinus* species.

Holotype NHMUK 1915.1.6.23.

Diagnosis. Shell rather thin, perforate, reddish-brown, with oblique, transverse cream-coloured bands; aperture elongate-ovate; peristome thin, hardly expanded at base; suture slightly ascending in front.

Measurements. Shell height 17.5, diameter 9 mm.

Occurrence record. See Remarks.

Ecoregion. Unknown.

Remarks. There are several localities in Peru at the eastern side of the Andes that are named “Santa Rita”, and the type locality cannot be known with certainty.

Mesembrinus bequaerti (Weyrauch, 1956) comb. nov.

Figures 73, 74

Drymaeus bequaerti Weyrauch 1956: 154, pl. 11 figs 12–14. “Mittel-Peru, rechten Seite des Rio Monzon, 670 m, nahe seinem Zusammenfluss mit dem Rio Huallaga, unweit von Tingo Maria”. Holotype SMF 155309; paratypes SMF 155305 (1), 155310 (2), IFML-MOLL 511 (1).

Diagnosis. Shell rather thin, rimate, dark brown, with narrow, a reddish-brown spiral band at periphery; aperture elongate-oval; peristome thin and simple.

Measurements. Shell height 19.1 mm, diameter 7.1 mm.

Occurrence records. HUÁNUCO, Rio Monzon near Tingo Maria (type locality); 4.0 km NE of Tingo Maria (UF 176785); 9 km S of Tingo Maria, Cueva de las Pavas (RMNH.MOL. 255900).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. In the SMF type material, the colour is faded.

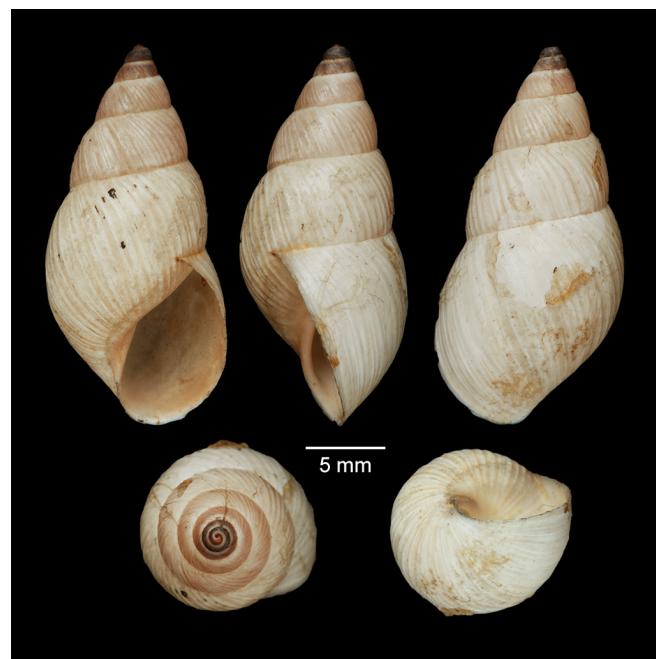


Figure 75. *Mesembrinus caktivorus* (Broderip, 1832). Possible syntype of *Bulinus nitidus* Broderip, 1832 NHMUK 1975551.

Mesembrinus caktivorus (Broderip, 1832) comb. nov.

Figures 75, 80

Bulinus caktivorus Broderip in Broderip & Sowerby I 1832: 32. “ad montem Chris”. Type material not located.

Bulinus nitidus Broderip in Broderip & Sowerby I 1832: 31. “Peruvia”. Possible syntypes NHMUK 1975551 (5), 1842.5.10.135–138 (4+2).

Diagnosis. Shell rimate, whitish, with or without numerous oblique, axial, black-brown or reddish-brown streaks; surface coarsely, irregularly costulate-striate; aperture ovate; peristome thin and simple.

Measurements. Shell height 23 mm, diameter 11 mm.

Occurrence records. PIURA, 45 km W of Ayabaca, Río Quiros (MCZ 125502); 25 km NE of Negritos (MCZ 89078). TUMBEZ, no specific locality (SMF 10059; USNM 104861).

Ecoregion. Tumbes-Piura dry forests [NT0232].

Remarks. The type locality of Broderip’s taxon is in Ecuador, Montecristi ($-01.045, -080.658$) in Manabí Province (Breure et al. 2022: 170). The occurrence records listed above are only tentatively identified as this species. An additional lot was found in the NHM collection, acquired from Cuming and with locality “Peru” (NHMUK 20230893). This species may be expected at more localities in the northern coastal departments of the country, notably Piura and Tumbes.

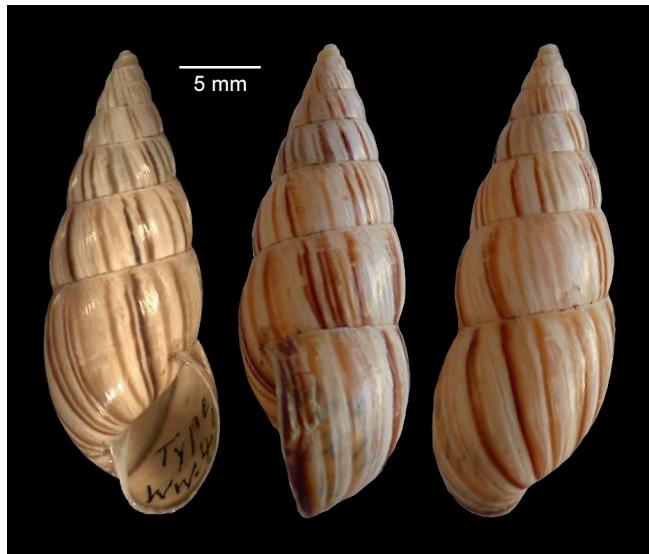


Figure 76. *Mesembrinus celendinensis* (Weyrauch, 1956). Holotype SMF 155307.

Mesembrinus celendinensis (Weyrauch, 1956)

Figures 76, 80

Mesembrinus celendinensis Weyrauch 1956: 151, pl. 11 figs 10–11.
“N-Peru, Hügel 2 km w. Celendin, 2700 m, ö. Cordillera Cumulca, der östlichen Andenkette, welche die Tiefebene um Cajamarca und Celendin voneinander trennt”. Holotype SMF 155307; paratypes SMF 155308 (1), 69498 (4), ANSP (5), CM (17), MCZ (5), IFML-MOLL (12).

Diagnosis. Shell rimate, thin, cream-coloured, with narrow, light- or dark-brown axial stripes, or creamy, with interrupted, dark-brown spiral bands (two very narrow and two broader on last whorl); aperture subvertical, ovate; peristome thin and simple.

Measurements. Shell height 30.7 mm, diameter 12 mm.

Occurrence records. CAJAMARCA, 2 km W of Celedin (type locality; ANSP 355514, 204500; CM 43260; DMNH 58098; IFML-MOLL 12492; MCZ 211950; SMF 69498, 155307, 155308; 3 km E of Celendin (UF 176789); around Celendin (UF 109742).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This species resembles *M. scitulus* and *M. trujillensis*, but it differs in having more convex whorls and a more rounded aperture.

Mesembrinus chrysomelas (E. von Martens, 1867) comb. nov.

Figures 77, 80

Bulimus (Thaumastus) chrysomelas Martens 1867: 145. “Chanchamayo”. Lectotype (Köhler 2007: 144) ZMB.MOLL 11



Figure 77. *Mesembrinus chrysomelas* (E. von Martens, 1867). Lectotype ZMB.MOLL 11835a.

835a; paralectotypes SMF 90121 (1), ZMB 11835 (3).

Diagnosis. Shell perforate, glossy, dark brown, with irregular, yellow axial streaks; aperture subvertical, ovate-elliptical; peristome thin and hardly expanded at base.

Measurements. Shell height 47.5 mm, diameter 18.0 mm.

Occurrence records. JUNÍN, Chanchamayo valley (type locality; SMF 90121; ZMB 11835); Huancapistana (IFML-MOLL 1255, 17089); Pichita Caluga (IFML-MOLL 17094).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This is a distinctive species, which has some variation in colour pattern. The population at Huancapistana has lighter-coloured shells.

Mesembrinus clathratus (L. Pfeiffer, 1858) comb. nov.

Figures 78, 80

Bulimus clathratus PFEIFFER 1858, Proc. zool. Soc. London 26: 258. “Province of Pataz, Andes of Peru”. Lectotype (BREURE 1979: 107) NHMUK 1975449.

Diagnosis. Shell umbilicate, whitish, somewhat latticed with light-brown axial streaks and narrow spiral bands; aperture subrhombic-oval; peristome thin and simple.

Measurements. Shell height 30.0 mm, diameter 12.2 mm.

Occurrence records. CAJAMARCA, Cajabamba (UMMZ 45843, not seen). LA LIBERTAD, Prov. Pataz (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This species resembles *M. laxostylus* in shell shape but smaller. It also resembles *M. praetextus*, but *M. clathratus*



Figure 78. *Mesembrinus clathratus* (L. Pfeiffer, 1858). Lectotype NHMUK 1975449.



Figure 79. *Mesembrinus coelestini* (F. Haas, 1952). Holotype FMNH 38125.

differs in being smaller and having the suture slightly more impressed, especially at the last whorl.

Mesembrinus coelestini (F. Haas, 1952) comb. nov.

Figures 79, 80

Drymaeus (Drymaeus) coelestini Haas 1952: 121, fig. 22. "Huayumbe, Dist. Marcapata, Prov. Quispicanchi, Dept. Cuzco, Peru, at 630 meters elevation in Valley Rio Marcapata". Holotype FMNH 38125; paratypes FMNH 38126/2.

Diagnosis. Shell rimate, thin, uniformly greyish-brown; aperture round-ovate; peristome simple, hardly expanded at base.

Measurements. Shell height 12.9 mm, diameter 6.1 mm.

Occurrence record. CUZCO, Marcapata dist., Huayumbe (type locality).

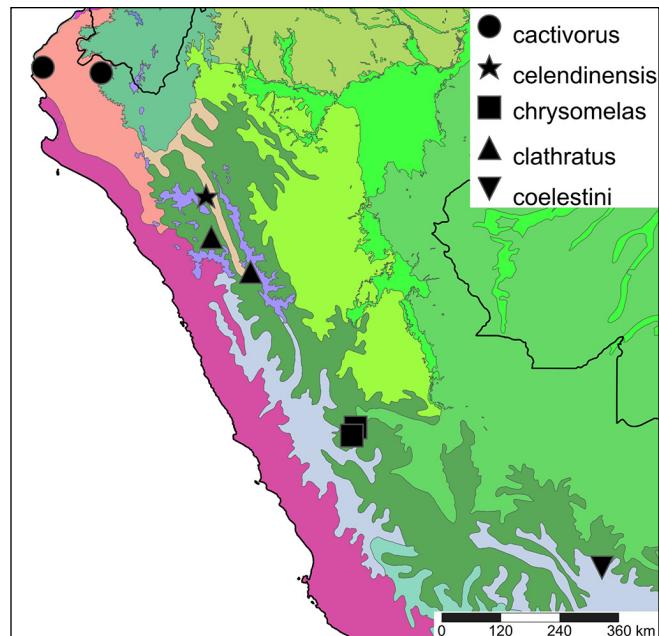


Figure 80. Distribution of *Mesembrinus* species.

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Known only from the type material.

Mesembrinus cuzcoensis (Reeve, 1849)

Figure 81

Bulimus cuzcoensis Reeve 1849 [1848–1850]: pl. 71 fig. 514. "Cuzco, Bolivia [sic]". Lectotype (Breure 1979: 108) NHMUK 1975453; paralectotypes NHMUK 1975454 (2).

Diagnosis. Shell rather thin, rimate, tawny-reddish; aperture oval; peristome thin, with basal margin hardly expanded.

Measurements. Shell height 36.6 mm, diameter 115.7 mm.

Occurrence record. CUZCO, no specific locality known.

Ecoregion. Unknown.

Remarks. This species has not been collected in Peru since its original description.

Mesembrinus cylindricus (S.I. da Costa, 1901)

comb. nov.

Figure 82

Drymaeus cylindricus da Costa 1901: 238, pl. 24 fig. 3. "San Pablo, Peru". Holotype NHMUK 1907.11.21.42.

Diagnosis. Shell rather solid, rimate, dull rosy-corneous; growth striae irregularly thickened; aperture oblique, subvertical, narrowly ovate; peristome thin and simple.

Measurements. Shell height 30 mm, diameter 11 mm.

Occurrence records. There are several places called "San



Figure 81. *Mesembrinus cuzcoensis* (Reeve, 1849). Lectotype NHMUK 1976453.



Figure 83. *Mesembrinus eucosmetus* (F. Haas, 1955). Holotype FMNH 51920.



Figure 82. *Mesembrinus cylindricus* (S.I. da Costa, 1901). Holotype NHMUK 1907.11.21.42.

Pablo” in Peru; unfortunately, there are no data available to pinpoint the type locality of this species.

Ecoregion. Unknown.

Remarks. Only the holotype is known.

Mesembrinus eucosmetus (F. Haas, 1955) comb. nov.

Figures 83, 87

Drymaeus (*Drymaeus*) *eucosmetus* Haas 1955: 331, figs 71, 72. “Cambache near Chongoyape, Lambayeque, Peru”. Holotype FMNH 51920.

Diagnosis. Shell rather solid, perforate, polymorphic, with yellow-whitish background ornamented with four chestnut

spiral bands, or with irregular axial streaks, or yellowish pink, with cloud-like axial streaks; aperture narrowly ovate; peristome thin and simple.

Measurements. Shell height 25.4 mm, diameter 11.6 mm.

Occurrence records. LAMBAYEQUE, Chongoyape (type locality); “Cambache” (ANSP 212212); PIURA, Olmos-Chamaya road (RBINS no catalogue no.).

Ecoregion. Tumbes-Piura dry forests [NT0232].

Remarks. We could not find “Cambache” in the gazetteers available to us. *Mesembrinus eucosmetus* resembles very much *M. paeteli*, known from the upper Marañón valley, and further studies may be needed to determine if they are both valid species.

Mesembrinus farrisi (L. Pfeiffer, 1858) comb. nov.

Figures 84, 87

Bulimus farrisi Pfeiffer 1858: 258. “Province of Pataz, Andes of Peru”. Lectotype (Breure 1979: 109) NHMUK 1975506; paralectotype NHMUK 1975507 (1).

Drymaeus (*Orodrymaeus*) *farrisi quadritraeniatus* Weyrauch 1956: 150, pl. 11 fig. 9. “N-Peru, Hacienda Santa Elena, 1550 m, auf der rechten Seite des Río Chusgon, westlicher Zufluss des Río Marañón”. Holotype SMF 155306. **New synonymy**.

Diagnosis. Shell rather solid, rimate, roseate-whitish, densely speckled and streaked with pink, sculptured with rather coarse wrinkles; last whorl prominent; aperture oblique, bright orange to brown inside; peristome thin and simple.

Measurements. Shell height 47.0 mm, diameter 18.4 mm.

Occurrence records. ANCASH, Pomabamba (DMNH 142453); 2 km S of Puente Chagual (FMNH 78744, 143961). LA LIBERTAD, Province of Pataz (type locality); Río Chusgon (DMNH 76688, 164071, 164371; UF 167371; ZMA.

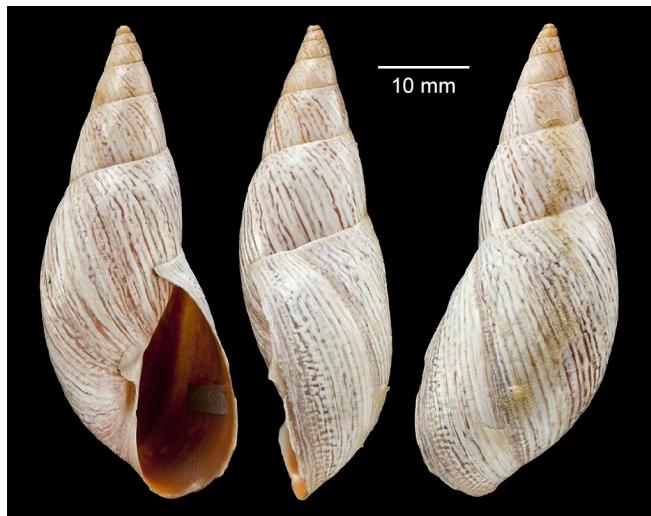


Figure 84. *Mesembrinus farrisi* (L. Pfeiffer, 1858). Lectotype NHMUK 1975506.

MOL 214373); near Chagual (ANSP 159916; FMNH 78744, 143961; MCZ 95703; SBMNH 141113; ZMA. MOL 55562); Hacienda Elena (SMF 155306); Hacienda Marcabal (DMNH 147976; UF 109229; USNM 601803); Hacienda Santa Rosa (ANSP 204493, 232510; CM 20621; DMNH 7313, 58069; FMNH 193635, 216833; MACN 28097; MCZ 202202); Huamachuco (FMNH 53999, 216827); Patipampa (IFML-MOLL 17087, FMNH 216834).

Ecoregion. Peruvian Yungas [NT0153], Maranon dry forests [NT0223].

Remarks. The shape of the shell is very characteristic of this species. We consider the subspecies *quadritaeniatus* a synonym of *M. farrisi*. Weyrauch (1956: 151) wrote:

Obwohl ich nach dem Funde des ersten Stückes von *quadritaeniatus* eine Stunde lang in einem grossen Raume in ihrem Biotope nach ihr suchte, konnte ich nur ein zweites Stück finden" [Although I searched for it for an hour in a large area of its biotope after finding the first piece of *quadritaeniatus*, I could only find a second specimen].

Although the holotype of *quadritaeniatus* is not quite typical in shell shape, this is a rare colour form of *M. farrisi*, exemplified by the lot IFML-MOLL 17087. Material labelled by Weyrauch with the manuscript name *aureolabris* is also considered to be *M. farrisi*.

This species is the type species of *Orodrymaeus* Pilsbry, 1926, but molecular data are needed to confirm this taxon as a valid group in a modern phylogeny. We include *M. farrisi* in *Mesembrinus* for now, owing to its simple peristome.

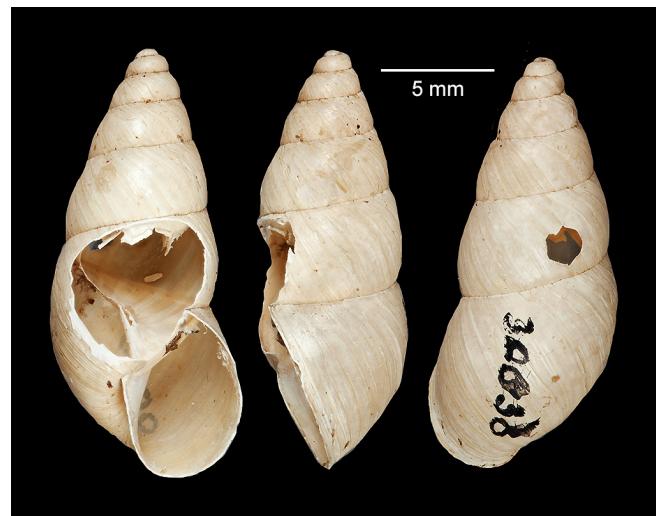


Figure 85. *Mesembrinus inconspicuus* (F. Haas, 1949). Holotype FMNH 30038.

***Mesembrinus inconspicuus* (F. Haas, 1949) comb. nov.**

Figures 85, 87

Bulimulus (Bulimulus) inconspicuus Haas 1949: 236, fig. 50a. "Contamana on Ucayali River, Dept. Loreto, Peru". Holotype FMNH 30038.

Diagnosis. Shell thin, rimate, dull-corneous; aperture oval; peristome thin and simple.

Measurements. Shell height 17.0 mm, diameter 7.5 mm.

Occurrence records. LORETO, Contamana (type locality); Quistococha (VMA 0186).

Ecoregion. Iquitos várzea [NT0128].

Remarks. This species was first recognised as belonging to *Mesembrinus* by Mogollón & Breure (2019).

***Mesembrinus lamas* (Higgins, 1868) comb. nov.**

Figures 86, 87

Bulimus (Otostomus) lamas Higgins 1868: 179, pl. 14 fig. 3–3a. "Juctabamba, Peru". Possible syntypes NHMUK 1868.4.3.3 (3).

Diagnosis. Shell rather thin, rimate, whitish, with chestnut axial streaks; aperture narrowly oval; peristome thin and simple.

Measurements. Shell height 33 mm, diameter 10 mm.

Occurrence records. LA LIBERTAD, "Jauctabamba" [=? Jucusbamba] (type locality); Huayllillas (FMNH 131675); 4 mi W of Otuzco (FMNH 106268).

Ecoregion. Central Andean wet puna [NT1003].

Remarks. We have not found "Jauctabamba" in the gazetteers available to us. This locality might be a misspelling for Jucusbamba, which is in Pataz Province.



Figure 86. *Mesembrinus lamas* (Higgins, 1868). Possible syntype NHMUK 1868.4.3.3.



Figure 88. *Mesembrinus laxostylus* (Rolle, 1904). Lectotype NHMUK 1922.2.24.32.

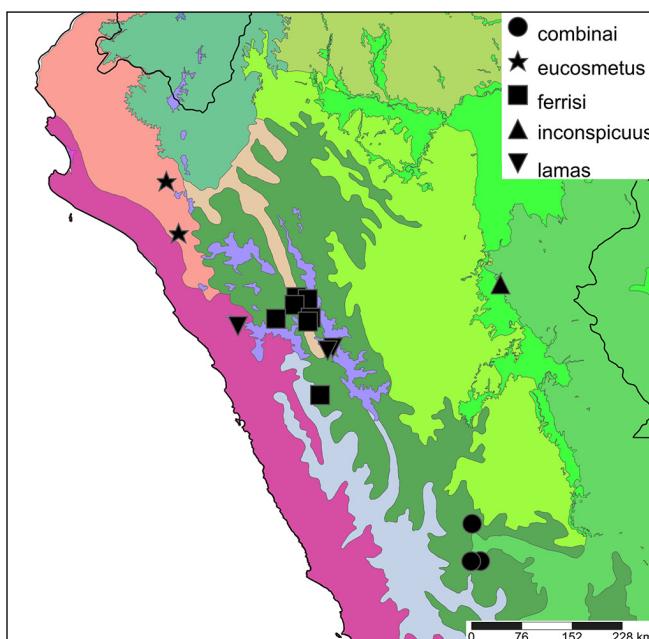


Figure 87. Distribution of *Drymaeus combinai* and *Mesembrinus* species.

Mesembrinus laxostylus (Rolle, 1904) comb. nov.

Figures 88, 98

Bulimus laxostylus Rolle 1904: 37. "Huancabamba in Peru". Lectotype (Breure 1979: 110) NHMUK 1922.2.24.32.

Diagnosis. Shell rather thin, glossy, rimate, chestnut-brown, with small, irregular yellowish spots and narrow axial lines plus some broader yellowish streaks; aperture oval; peristome white, thin, and simple.

Measurements. Shell height 40.0 mm, diameter 16.5 mm.

Occurrence records. PASCO, Huancabamba (type locality). HUÁNUCO, Tingo María (FEM). JUNÍN, Huacapistana (MCZ 136250).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. Until now, this species was only known from the type locality. These two additional localities extend the distribution by about 140 km to the north and about 90 km to the south of the type locality.

Mesembrinus leucomelas (Albers, 1854) comb. nov.

Figure 89

Bulimus leucomelas Albers 1854: 219. "Columbia [sic, Peru] ad flumen Maranhon". Holotype ZMB.MOLL 101785.

Diagnosis. Shell rather thin, perforate, whitish to pale buff, with dark-brown axial streaks and some white spots; aperture narrowly oval; peristome thin and simple.

Measurements. Shell height 29 mm, diameter 10 mm.

Occurrence records. See Remarks.

Ecoregion. Unknown.

Remarks. The Marañón River runs for 1400 km through various departments of Peru. The material was collected by Warszewicz, but we do not know his itinerary, and the collection locality is not precisely known. This species has not been recognised in more recent collections. Martens (1860: 213) corrected the type locality by stating "am ob.[eren] Maranhon" [on the upper Marañón].

Mesembrinus libertadensis (Pilsbry, 1898) comb. nov.

Figure 90

Bulimus taeniatus Philippi 1869: 35. "In departamento peruviano



Figure 89. *Mesembrinus leucomelas* (Albers, 1854). Holotype ZMB.MOLL 101785.

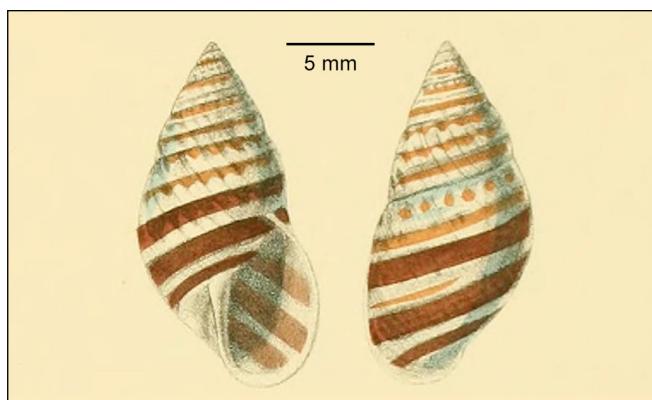


Figure 90. *Mesembrinus libertadensis* (Pilsbry, 1898). Original figures of *Bulimus taeniatus* Philippi, 1869 reproduced from Pfeiffer (1869 [1866–1869]: pl. 102 figs 3, 4).

Libertad in hacienda de Mariabal lectus (Sierra)". Type material not located. Not *Bulimus taeniatus* Mörch, 1850.

Drymaeus libertadensis Pilsbry 1898 [1897–1898]: 291, pl. 51 figs 16, 17. New name for *Bulimus taeniatus* Philippi, 1869 non Mörch, 1850.

Diagnosis. Shell rather thin, perforate, whitish, with five or six reddish-chestnut spiral bands (upper ones ragged); aperture oval; peristome thin and simple.

Measurements. Shell height 25.0 mm, diameter 10.5 mm.

Occurrence record. LA LIBERTAD, Marcabal (type locality; see remarks).

Ecoregion. Marañon dry forests [NT0223].

Remarks. The original spelling "Mariabal", which was emended by Pilsbry (1898) to "Mariebal", could not be found in the gazetteers, and the only name in the Department of Libertad that we found which is similar is "Marcabal". There are two places named Marcabal; one, at -07.61, -077.81, is a populated place and the other, at -07.70, -078.03, is the seat of a third-order administrative division. Both are at elevations of 2800–3000 m a.s.l. Philippi (1869) described the shell as having a simplex peristome, which gives us reason to include the species in *Mesembrinus*.

***Mesembrinus marmoratus* Breure, Mogollón & Vega-Luz sp. nov.**

Figures 91, 92, 98, Table 4

ZooBank identifier. urn:lsid:zoobank.org:act:83A4CECF-101C-47AD-9FDB-D04D990C7AB6

Diagnosis. A *Mesembrinus* species up to 45.0 mm, characterised by its marbled, yellowish- to dark-brown colour pattern and a lip with a light-coloured outer margin and a pink inner margin.

Table 4. Shell dimensions and number of whorls of type material of *Mesembrinus marmoratus* Breure, Mogollón & Vega-Luz sp. nov.

Specimen	Collection	Height (mm)	Diameter (mm)	Height of aperture (mm)	Width of aperture (mm)	Height of last whorl (mm)	No. of whorls
Holotype	NHMUK	38.3	18.3	18.7	11.8	27.6	7.5
Paratype 1	MNCN	37.4	16.6	19.2	11.8	28.2	6.5
Paratype 2	MNCN	31.9	14.4	15.6	9.9	22.9	6.5
Paratype 3	RBINS	37.8	16.1	17.4	10.6	26.7	7.5
Paratype 4	RVL-DR4	39.3	16.7	19.5	11.2	29.1	7.5
Paratype 5	RVL-DR5	32.6	14.8	16.1	10.1	24.4	6.8
Paratype 6	RVL-DR6	36.9	16.1	17.8	10.4	26.9	7.0
Paratype 7	RVL-DR7	36.5	15.9	17.9	10.9	26.5	7.0
Paratype 8	VMA 1703	40.3	20.2	19.2	12.1	30.1	7.1
Paratype 9	VMA 1704	43.4	19.6	20.6	12.2	32.3	7.6

Description. Shell up to 45.0 mm, 2.2 times as long as wide, imperforate, with almost straight sides; elongate, moderately solid. Colour yellowish to dark brown, in some

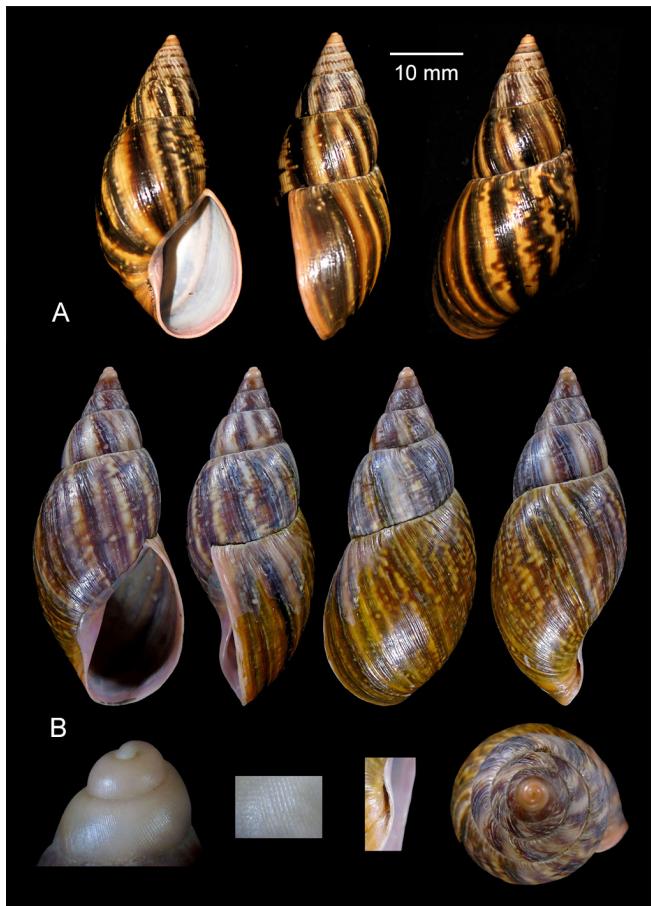


Figure 91. *Mesembrinus marmoratus* Breure, Mogollón & Vega-Luz sp. nov. **A**, holotype NHMUK 20240087. **B**, paratype (VMA).

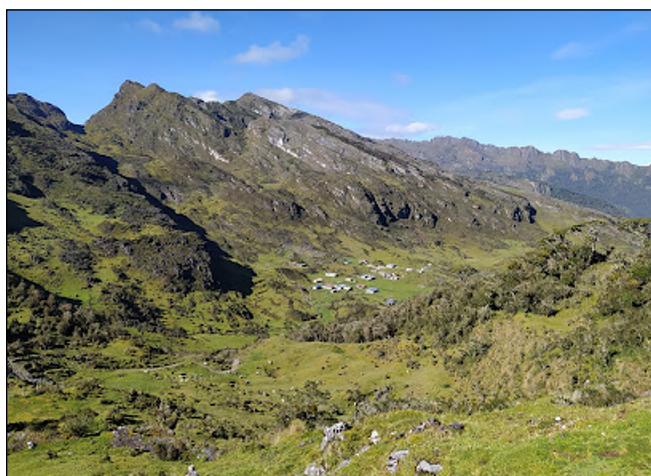


Figure 92. *Mesembrinus marmoratus* Breure, Mogollón & Vega-Luz sp. nov. Type locality.

specimens with hues of pink, the pattern giving a marbled impression by dispersed yellowish dots, with predominantly darker axial streaks which are straight, undulating or merging with each other. Surface rather shiny, with growth striae somewhat incrassate, in some specimens giving a puckered impression. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls 7.0, hardly convex; suture impressed. Aperture subovate, skewed; 1.64 times as long as wide, 0.49 times the total length. Peristome thin and simple; on the outside with a light band, on the inside with a pinkish zone. Columellar margin thin, receding. Parietal region with a thin, transparent callus.

Type locality. Peru, Huánuco Department, Pachitea Province, Tambo de Vaca [ca -09.87, -075.75], 3300–3500 m elev.

Type material. Holotype NHMUK 20240087. Paratypes MNCN 15.05/200536–37 (2), RBINS MT.4057 (1), RVL (4), VMA (2). All material V. Castillo leg., March 2021.

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This novelty is hitherto only known from the type locality. It resembles *M. acobambensis* but is more elongate and has a pink zone behind the lip. *Mesembrinus laxostylus* but *M. marmoratus* is somewhat larger, with a more prominent last whorl, and with the pinkish zone inside the peristome.

Etymology. Latin, *marmoratus*, marbled, referring to the colour pattern.

Mesembrinus mexicanus (Lamarck, 1822) comb. nov.

Figures 93, 98

Bulimus mexicanus Lamarck 1822: 123. “Mexique” [sic]. Syntypes MHNG-MOLL-51166 (2).



Figure 93. *Mesembrinus mexicanus* (Lamarck, 1822). Syntype MHNG-MOLL-51166.

Bulimus humboldtii Reeve 1849 [1848–1850]: pl. 58 fig. 391. “Mexico” [sic]. Lectotype (Breure & Ablett 2014: 90) NHMUK 1975528; paralectotype NHMUK 1975528 (1).
Bulimus primularis Reeve 1849 [1848–1850]: pl. 73 fig. 527. “Chachapoyas, Alto Peru”. Type material not located.

Diagnosis. Shell rather thin, narrowly perforate, whitish or yellowish to light orange, with 2–5 chestnut-brown spiral bands, white or yellowish crossed by white lines; aperture oval; peristome thin and simple.

Measurements. Shell height 31 mm, diameter 15 mm.

Occurrence records. AMAZONAS, 7 km below Caclic (FMNH 148807); 34 km on road Chachapoyes–Pedro Ruiz (FEM); Chirimoto (FEM); Luya (iNaturalist 25896598); Pongo de Rentema (RBINS no catalogue no.); Roca San Lorenzo (FMNH 136521); 7 km NNW of Tingo Nuevo (UF 177230); Utcubamba Province (UF 161264; USNM 110065). CAJAMARCA, Bellavista (FMNH 113316; MCZ 64724); Jaén (ANSP 322770; DMNH 58088; FMNH 29134; MCZ 211039; UF 109295); Pucará (FMNH 113315, 148810); Rio Chamaya (ANSP 322792; FMNH 148364); Rio Chinchipe (USNM 601804); Socota (RVL).

Ecoregion. Peruvian Yungas [NT0153], Napo moist forests [NT0142], Marañon dry forests [NT0223].

Remarks. This is a polymorphic species, which is restricted to northern Peru.

Mesembrinus miltochrous (Albers, 1854) comb. nov.

Figure 94

Bulimus miltochrous Albers 1854: 217. “Columbia [sic] ad fluvium Maranhon”. Lectotype (KÖHLER 2007: 152) ZMB.MOLL 101791a; paralectotype ZMB.MOLL 101791b (1).

Diagnosis. Shell rather thin, rimate, brownish, with two blackish spiral bands, crossed by white lines; one spiral band at suture, another at base, and a narrow white band at periphery; aperture oval; peristome thin and simple.

Measurements. Shell height 31 mm, diameter 13 mm.

Occurrence records. Unknown.

Ecoregion. Unknown, but likely Peruvian Yungas [NT0153].

Remarks. The Marañón River runs through 1400 km several departments of Peru. The material was collected by Warszewicz, but we do not know his itinerary. Martens (1860: 213) corrected the type locality by stating “am ob.[eren] Maranhon” [on the upper Marañón], and Pilsbry (1898 [1897–1898]: 290) modified the type locality by adding “or Ecuador”, but both emendations were made without any supporting evidence. This species has not been recently collected.

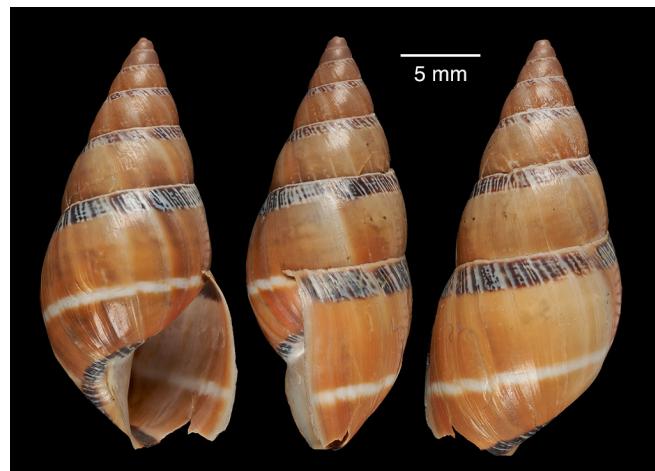


Figure 94. *Mesembrinus miltochrous* (Albers, 1854). Lectotype ZMB.MOLL 101791.



Figure 95. *Mesembrinus nigroapicatus* (L. Pfeiffer, 1857). Syntype NHMUK 20230556.

Mesembrinus nigroapicatus (L. Pfeiffer, 1857) comb. nov.

Figure 95

Bulimus nigroapicatus Pfeiffer 1857: 333. “Rio Pampas, Bolivia”. Syntypes NHMUK 20230556 (2).

Diagnosis. Shell rather thin, rimate, whitish, with 5–7 interrupted light- to dark-brown spiral bands and with areas between bands partly coloured with yellowish; aperture subvertical, elliptical-oval; peristome thin and simple.

Measurements. Shell height 22.0 mm, diameter 11.5 mm.

Occurrence records. See Remarks.

Ecoregion. Unknown.

Remarks. This previously unfigured species was described

from the Cuming collection but was collected during the expedition of Castelnau (Ablett & Breure 2024). Although Pfeiffer located the rio Pampas in Bolivia, Pilsbry (1898 [1897–1898]: 284) placed the type locality in Peru. After studying the itinerary of Castelnau (Papavero 1971: 149–159), we consider it more plausible that this species was collected in Peru. The rio Pampas is a tributary of the rio Apurímac and runs north–south for 424 km. Its source is the Choclococha Lagoon in the Department of Huancavelica; it crosses the Department of Ayacucho, Peru, through the Provinces of Víctor Fajardo, Cangallo, and Vilcashuamán, and finally joins with the Apurímac River. As Castelnau travelled through both departments, it is impossible to say where he may have collected the syntypes of this species. We consider *M. nigroapicatus* a valid species for now, but as the syntypes are not mature, fully developed, mature material is needed to confirm the validity of this taxon.

Mesembrinus paeteli (Albers, 1854) comb. nov.

Figure 96

Bulimus paeteli Albers 1854: 31. “insula Lobos oram Peruviae septentrionalis” (see Remarks). Lectotype (Köhler 2007: 152) ZMB.MOLL 101792; paralectotypes ZMB.MOLL 101793 (2).

Diagnosis. Shell thin, perforate, yellowish-white, with four purple-brown bands; aperture oblong-oval; peristome thin, hardly expanded at base.

Measurements. Shell height 25.0 mm, diameter 10.5 mm.

Occurrence records. “Ob. Maranhon” (ZMB.MOLL 10336).

Ecoregion. Unknown.

Remarks. Lobos Island, off the coast of the Department of Lambayeque, was said to be the type locality, but no *Drymaeus* or *Mesembrinus* species are known to occur there. Martens (1860: 212) corrected the locality and gave it as “Am ob.[eren] Maranhon” [on the upper Marañón River].

Mesembrinus pergracilis (Rolle, 1904) comb. nov.

Figures 97, 98

Bulimulus pergracilis Rolle 1904: 37. “Huancabamba in Peru”. Lectotype (BREURE 1979: 112) NHMUK 1922.2.24.33.

Drymaeus pilsbryi Weyrauch 1956: 153, pl. 11 fig. 7. “Peru, Pan de Azucar, 1350 m, Rio Tarma, Oberlauf des Río Chanchamayo”.

Holotype SMF 155303. Not *Drymaeus pilsbryi* Zetek, 1934.

New synonymy.

Mesembrinus (Ornatimormus) henrypilsbryi Weyrauch 1958: 134. Nom. nov. for *Drymaeus pilsbryi* Weyrauch 1956. **New synonymy.**

Mesembrinus (Ornatimormus) henrypilsbryi densestrigatus Wey-



Figure 96. *Mesembrinus paeteli* (Albers, 1854). Lectotype ZMB. MOLL 101792.



Figure 97. *Mesembrinus pergracilis* (Rolle, 1904). A, lectotype NHMUK 1922.2.24.33. B, *Mesembrinus (Ornatimormus) henrypilsbryi* Weyrauch, 1958. Holotype SMF 155303. C, *Mesembrinus (Ornatimormus) henrypilsbryi pichitacalugaensis* Weyrauch, 1958. Holotype SMF 156388. D, *Mesembrinus (Ornatimormus) henrypilsbryi densestrigatus* Weyrauch, 1958. Holotype SMF 156293.

rauch 1958: 134, pl. 8 fig. 20. "Mittel-Peru am Osthang des östlichen Anden: Quimiri Sur, Valle de Chanchamayo, auf der rechten Seite des Río Chanchamayo, oberhalb Puente Herrería". Holotype SMF 156293. **New synonymy.**

Mesembrinus (Ornatimormus) henrypilsbryi pichitacalugaënsis Weyrauch 1958: 135, pl. 8 fig. 17. "Mittel-Peru am Osthang des östlichen Anden: 2 km vom Bergwerk Pichita Caluga entfernt, 2200 m, im Chanchamayo-Becken". Holotype SMF 156388; paratype IFML-MOLL 3110 (2). **New synonymy.**

Diagnosis. Shell thin, rimate, yellowish white, with brown axial streaks at intervals 2–3 times as broad; aperture oval; peristome thin and simple.

Measurements. Shell height 36.7, diameter 11.5 mm.

Occurrence records. PASCO, Huancabamba (type locality); Oxapampa (MCZ 211374); 17 km from Oxapampa to Huancabamba (RBINS no catalogue no.). JUNÍN, Chanchamayo valley, Orejo de Capelo (MCZ 211371); Pan de Azucar (SMF 155303); Quimiri Sur (SMF 156293); near Pichita Caluga (SMF 156388, IFML-MOLL 3110).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. *Mesembrinus henrypilsbryi* is a polymorphic species, which also presents unicoloured or nearly unicoloured shells, but as this species has a similar size and shape as *M. pergracilis*, we consider these taxa synonyms. They occur in the same general area.

Mesembrinus phryne (L. Pfeiffer, 1863) comb. nov.

Figures 99, 104

Bulimus phryne Pfeiffer 1863: 274. "Andes of Peru". Lectotype (BREURE 1979: 112) NHMUK 1975214; paratypes NHMUK 1975215 (2).

Diagnosis. Shell rather thin, perforate, yellowish white, with reddish-brown axial streaks, some of which are bifid, interrupted, or fused; aperture subrhombic, rose-coloured; peristome thin and simple.

Measurements. Shell height 15 mm, diameter 7 mm.

Occurrence records. JUNÍN, Chanchamayo valley (MCZ 124833, not seen). PASCO, Huancabamba (ANSP 107815, not seen; FMNH 78711; MCZ 180461); Oxapampa (FMNH 72589, not seen)

Ecoregion. Peruvian Yungas [NT0153].

Remarks. The material listed above was found identified as *D. canaliculatus* (L. Pfeiffer, 1845), which, however, occurs in Bolivia. *Mesembrinus phryne* is most similar to *D. abruptus* (Rolle, 1904), *D. basitorus*, and *D. chanchamayensis*, which occur in the same region. Anatomical study or molecular genetics are needed to clarify the systematic position of these taxa.

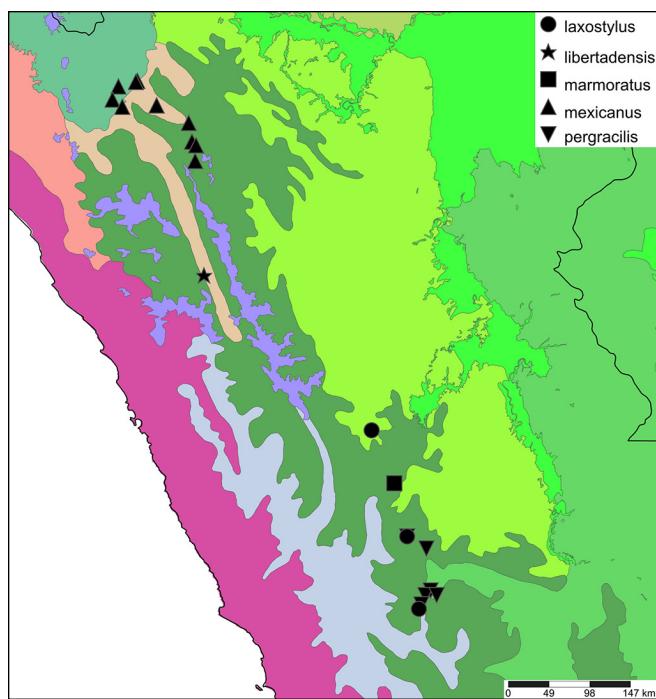


Figure 98. Distribution of *Mesembrinus* species.



Figure 99. *Mesembrinus phryne* (L. Pfeiffer, 1863). Lectotype NHMUK 1975214.

Mesembrinus ponsonbyi (S.I. da Costa, 1907) comb. nov.

Figures 100, 104

Drymaeus ponsonbyi da Costa 1907: 305, pl. 26 figs 6–6a. "Peru, Sarco". Holotype NHMUK 1907.11.21.27.

Diagnosis. Shell rather thin, glossy, narrowly perforate, buff, with a faint, narrow, whitish spiral band above periphery; ornamented with irregular thickened growth striae giving shell a malleated appearance; aperture elliptical-ovate; peristome thin and simple.

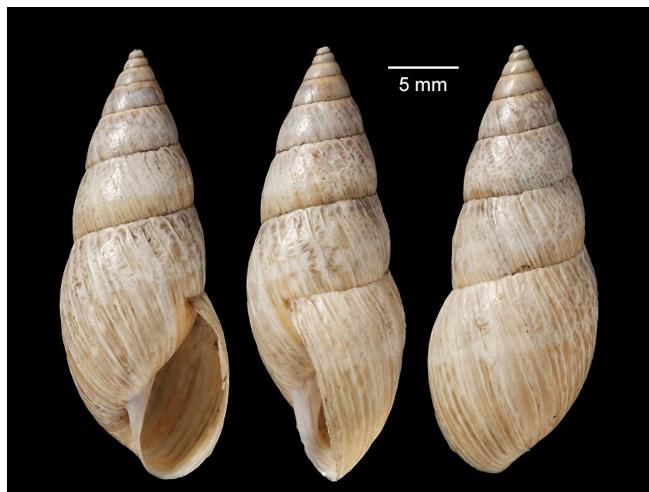


Figure 100. *Mesembrinus ponsonbyi* (S.I. da Costa, 1907). Holotype NHMUK 1907.11.21.27.

Measurements. Shell height 33 mm, diameter 12 mm.

Occurrence record. LIMA, Surco (type locality).

Ecoregion. Sechura desert [NT1315].

Remarks. Breure & Ablett (2014: 155) were uncertain about the locality. However, Surco is the name of a third-order administrative District in the valley of the rio Rimac. Da Costa (1907) gave the altitude of the type locality as 2050 m, which is plausible for this high valley. Surco is also the name of a locality in Arequipa, but it lies at an elevation of about 950 m a.s.l. Thus, this species likely originates from the valley of the rio Rimac, which is well-travelled. However, it is somewhat puzzling that *M. ponsonbyi* is only known from the type material.

Mesembrinus praetextus (Reeve, 1849) comb. nov.

Figures 101, 104

Bulimus praetextus Reeve 1849 [1848–1850]: pl. 71 fig. 515. “Andes of Caxamarca Peru”. Lectotype (Breure & Ablett 2014: 155) NHMUK 198340.

Diagnosis. Shell rather solid, perforate, whitish, marbled with violaceous-brown axial streaks and some dispersed whitish spots; aperture oblong; peristome narrowly expanded at outer lip and base.

Measurements. Shell height 39 mm, diameter 14 mm.

Occurrence record. CAJAMARCA, Rio Yonan (FMNH 31465).

Ecoregion. Tumbes-Piura dry forests [NT0232].

Remarks. The locality included above is the first precise locality for this species. However, *M. praetextus* may only be a colour form of “*M.* vexillum” (W. Wood Sr, 1828). Both taxa occur at the same locality.



Figure 101. *Mesembrinus praetextus* (Reeve, 1849). Lectotype NHMUK 198340.

Mesembrinus pseudobesus (Breure, 1979) comb. nov.

Figures 102, 104

Drymaeus (*Diaphanomorphus*) *coelestini obesus* Weyrauch 1964: 58, fig. 11. “Perú central, Boquerón de Abad, 550 m”. Holotype IFML-MOLL 1196a; paratypes IFML-MOLL 1196b (2), SMF 162119 (1). Not *Otostomus* (*Drymaeus*) *sulfureus obesus* E. von Martens, 1893.

Drymaeus (*Mesembrinus*) *pseudobesus* Breure 1979: 123. Nom. nov. for *D. coelestini obesus* Weyrauch 1964.

Diagnosis. Shell perforate, glossy, thin, uniformly pale-yellowish; aperture round-ovate; peristome simple, hardly expanded at base.

Measurements. Shell height 11.3 mm, diameter 7.4 mm.

Occurrence records. HUÁNUCO, Boquerón de Abad (type locality). UCAYALI, Colonia Calleria (FMNH 121891).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. We could not find “Colonia Calleria” in gazetteers, but the District of Calleria lies east of the Ucayali River opposite Pucallpa.

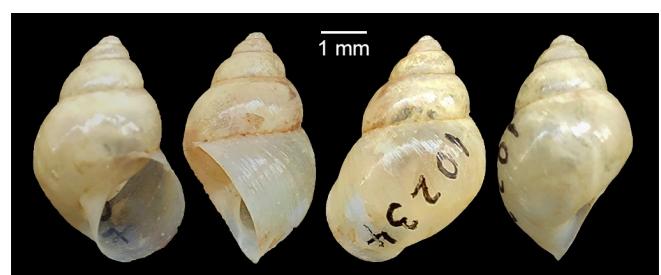


Figure 102. *Mesembrinus pseudobesus* (Breure, 1979). Holotype of *Drymaeus* (*Diaphanomorphus*) *coelestini obesus* Weyrauch, 1964 IFML-MOLL 1196a.

***Mesembrinus pulcherrimus* (H. Adams, 1867) comb. nov.**

Figures 103, 104

Otostomus pulcherrimus Adams 1867: 442, pl. 38 fig. 3. "Eastern Peru". Holotype NHMUK 1867.5.18.3.

Gonyostomus subhybridus da Costa 1906: 97, pl. 9 fig. 1. "Pozuzo, Eastern Peru, 800 meters". Holotype NHMUK 1907.11.21.127.

New synonymy.

Diagnosis. Shell rather thin, rimate, whitish, with white-dotted, dark-chestnut axial streaks, which are sinuate above and broken into two series of spots below; aperture rhombic-oval; peristome simple.

Measurements. Shell height 50 mm, diameter 19 mm.

Occurrence records. PASCO, Huancabamba (RMNH.MOL 266085; UF 109156, 109157; 161216); Pozuzo (IFML-MOLL 12660; NHMUK 1907.11.21.127; RMNH.MOL 266009–266010; SMF 69496, 181801). JUNÍN, Chanchamayo (RBINS no catalogue no.; ZMB/Mol no catalogue no., 11833); Chanchamayo valley, Rio Torro (MCZ 133210).

Ecoregion. Peruvian Yungas [NT0153], Ucayalí moist forests [NT0174].

Remarks. The specimen which Adams used for his description of *M. pulcherrimus* has since been broken, and only the lower part of the specimen exists today. The holotype of *G. subhybridus* is similar in shape and height, which is similar to the measurements of Adams' shell prior to being broken. We place *G. subhybridus* in the synonymy of *M. pulcherrimus*. The relationship of *M.* with *D. angulobasis* and *D. basitorus* to *M. pulcherrimus* may need more study, and if these taxa, prove to belong to a monophyletic group, that group might be called *Ornatimormus* Weyrauch, 1958.

***Mesembrinus purpuralabrum* Breure, Mogollón & Vega-Luz sp. nov.**

Figures 105, 110, Table 5

ZooBank identifier. urn:lsid:zoobank.org:act:63019F4A-5CAD-4CC1-A865-B5D0FBD9BE93

Diagnosis. A *Mesembrinus* species up to 30 mm, characterised by its polymorphic colour pattern of yellowish to dark brown, with a light-coloured margin on the outside of the lip and a pinkish or purple zone around the peristome.

Description. Shell up to 30.1 mm, 2.4 times as long as wide, imperforate, elongate, with almost straight sides, moderately solid. Colour whitish, with well-marked greyish to intensely dark-brown axial streaks and, in most specimens, with traces of small, interrupted spiral bands (two on the last whorl, one on spire whorls); axial streaks greyish to intense dark brown in colour. Surface rather shiny. Protoconch with equally strong

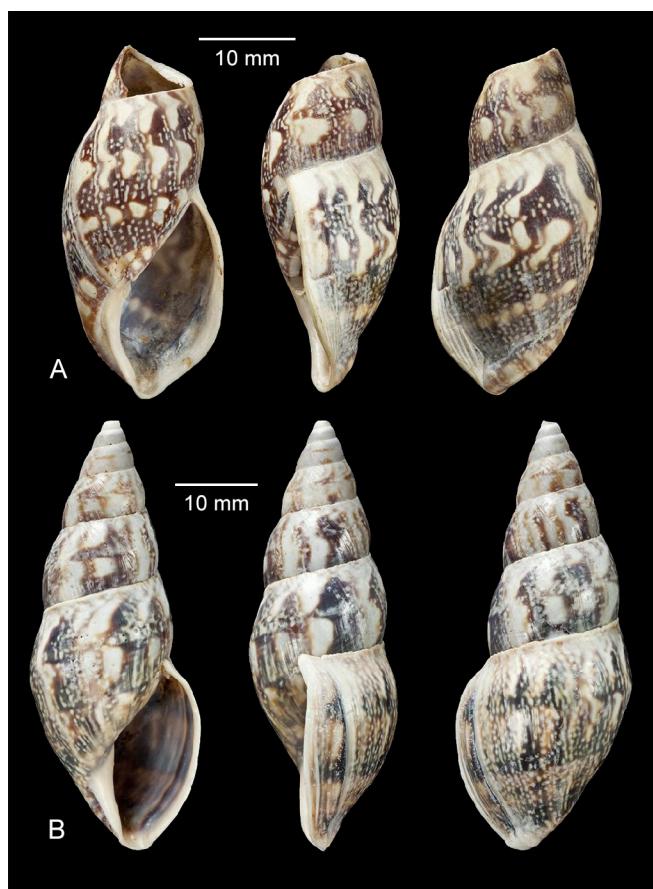


Figure 103. *Mesembrinus pulcherrimus* (H. Adams, 1867). **A**, holotype NHMUK 1867.5.18.3. **B**, holotype of *Gonyostomus subhybridus* S.I. da Costa, 1906.

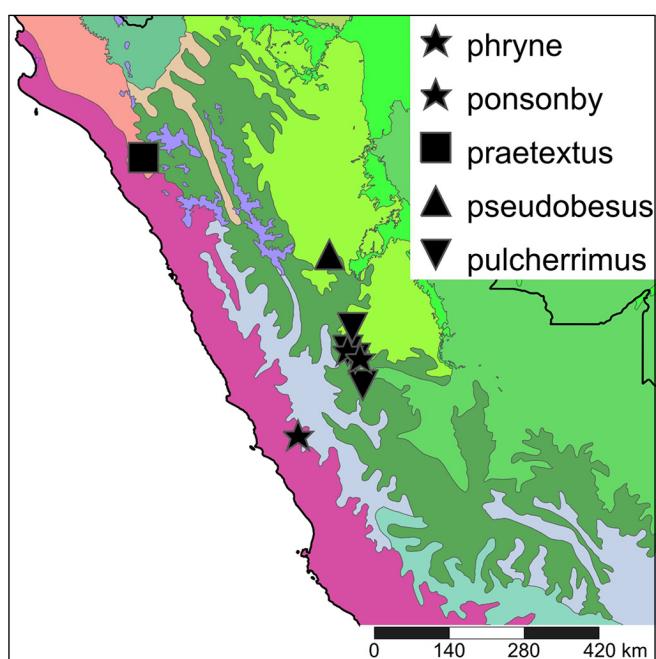


Figure 104. Distribution of *Mesembrinus* species.

Table 5. Shell dimensions and number of whorls of type material of *Mesembrinus purpuralabrum* Breure, Mogollón & Vega-Luz sp. nov.

Specimen	Collection	Shell height (mm)	Diameter (mm)	Height of aperture (mm)	Width of aperture (mm)	Height of last whorl (mm)	No. of whorls
Holotype	NHMUK	26.3	11.2	10.9	6.4	16.3	7.0
Paratype 1	NHMUK	29.1	11.8	11.6	7.5	17.4	7.5
Paratype 2	MNCN	26.5	10.6	10.5	6.7	16.2	7.0
Paratype 3	RBINS	26.9	11.4	10.6	6.8	15.9	7.25
Paratype 4	RVL-DR12	30.1	11.9	11.5	7.2	17.2	7.75
Paratype 5	RVL-DR13	26.7	11.4	11.4	7.2	17.2	7.0
Paratype 6	VMA 1705	28.2	10.9	11.9	7.3	18.1	6.75

axial riblets and spiral striae forming a reticulate sculpture. Whorls 7.2, hardly convex; suture impressed. Aperture subovate, 1.6 times as long as wide, 0.4 times shell length. Peristome thin and simple, with pinkish or purple zone around inside the aperture; outer side of lip with a light-purple band. Columellar margin thin, receding. Parietal region with a thin, transparent callus.

Type locality. Peru, Amazonas Department, Bongará Province, Yambrasbamba area [ca -05.7358, -077.9248], 1800–2000 m alt.

Ecoregion. Peruvian Yungas [NT0153].



Figure 105. *Mesembrinus purpuralabrum* Breure, Mogollón & Vega-Luz sp. nov. **A**, holotype NHMUK 20240088. **B**, topotypes (RVL).

Type material. Holotype NHMUK 20240088. Paratypes NHMUK 20240089 (1), MNCN 15.05/200538 (1), RBINS MT.4054 (1), RVL (2), VMA (1). All material V. Castillo leg., July 2020.

Remarks. The pinkish or purple zone, especially on the outside of the lip tend to fade over time. This species resembles *M. leucomelas*, from which it differs in having more prominently impressed sutures. From *M. scitulus*, it differs in the more rounded aperture.

Etymology. Latin *purpura*, purple, and *labrum*, lip; referring to the purple zone around the inside of the peristome.

Mesembrinus rosalus (Pilsbry, 1932) comb. nov.

Figure 106

Drymaeus rosalus Pilsbry 1932: 395, pl. 28 fig. 4. “Rio Jelashte, E of Leymebamba, Dept. of San Marten, Peru, at 4,500 ft.” Holotype ANSP 159897.

Diagnosis. Shell thin, umbilicate, uniformly buff on spire to whitish on lower whorls; aperture ovate; peristome thin and simple.



Figure 106. *Mesembrinus rosalus* (Pilsbry, 1932). Holotype ANSP 159897.

Measurements. Shell height 16.3 mm, diameter 7.8 mm.

Occurrence record. SAN MARTÍN, Rio Jelashte (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. We have not found in gazeteers a river by the name of "Jelashte" (Pilsbry 1932). However, we assume that the type locality is in the northern part of San Martín, east of Leymebamba and the Cordillera Yasgolga, which forms the border of the departments of Amazonas and San Martín. The species has not been re-collected since its description.

Mesembrinus sachsei (Albers, 1854) comb. nov.

Figures 107, 110

Bulimus sachsei Albers 1854: 30. "Columbia australis [sic], ad flumen Maranhon". Lectotype ZMB.MOLL 10290a; paratypes MHNG-MOLL-63524 (1), ZMB.MOLL 10290b (13) (Köhler 2007: 148).

Diagnosis. Shell rather thin, perforate, whitish, with dark-chestnut streaks, dotted with white; aperture oval-oblong, with a dull, purplish band inside the aperture; peristome simple.

Measurements. Shell height 27.5 mm, diameter 12.5 mm.

Occurrence records. Upper Marañon valley (type locality; SMF 90180; ZMB.MOLL 111920, 114317). AMAZONAS, Bagua Province, La Peca (RVL; VMA); Tingo Nuevo (UF 177229).

Ecoregion. Peruvian Yungas [NT0153], Marañon dry forests [NT0223].

Remarks. The simple peristome and the shell shape has led us to classify this species as belonging to *Mesembrinus*. The type locality is imprecise, and there is no data about it in the itinerary of the collector, Warszewicz. Breure *et al.* (2022: 168, fig. 224) mentioned this species from Chimborazo and Loja Provinces in Ecuador. However, we have no records for this species from southernmost Ecuador, nor from northernmost Peru. Given this apparent distribution gap, we cannot exclude the possibility that the Ecuadorian records are a local look-alike, in which case they might be a new species.

Mesembrinus scitulus (Reeve, 1849) comb. nov.

Figures 108, 110

Bulimus scitulus Reeve 1849 [1848–1850]: pl. 71 fig. 513. "Chachapoyas, Alto-Peru". Lectotype NHMUK 1975217, paratypes NHMUK 1975217 (2) (Breure & Eskens 1981: 39).

Bulimus citrinellus Pfeiffer 1868: 114 (ex Philippi). "inter Macanya et fluvium Maranon". Type material not located.



Figure 107. *Mesembrinus sachsei* (Albers, 1854). Lectotype ZMB. MOLL 10290.

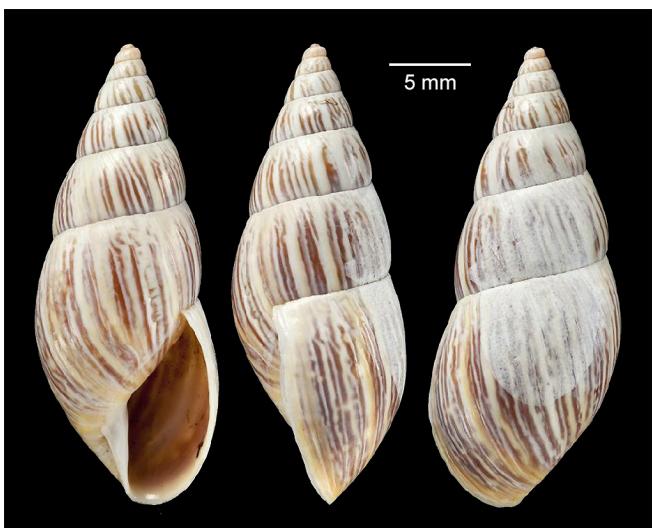


Figure 108. *Mesembrinus scitulus* (Reeve, 1849). Lectotype NHMUK 1975217.

Bulimus (Otostomus) rubrovariegatus Higgins 1868: 178, pl. 12 figs 2–2a. "Huamachuco, Peru". Possible syntypes NHMUK 1868.4.3.1 (3). **New synonymy.**

Diagnosis. Shell rather thin, glossy, rimate, whitish, with numerous axial, arcuate, narrow purple-brown stripes, leaving a white band below suture; aperture subvertical, narrowly ovate, somewhat truncate below; peristome thin, simple.

Measurements. Shell height 28 mm, diameter 10.5 mm.

Occurrence records. AMAZONAS, Chachapoyas (type locality; IFML-MOLL 1253), Utcubamba (SMF 23359). CAJAMARCA, Bambamarca (RBINS.INV 32219), Cajabamba (ZMB.MOLL 47399, 47400, 55976), Cajamarca

(ZMB.MOLL 55981), near Celendin (MCZ 202220), Choropampa (SMF 90192, 90193), Cochambul (ANSP 204495, 355511; DMNH 1122, 7343, 58079, 58087, 148419, 148420, 164069; FMNH 30777, 72605, 125148, 126922, 147302, 150826, 193598; MACN 28098; MCZ 167371, 222190; SMF 69495, 208361, 277340; UF 109350, 184712, 501068; USNM 601801, 601802). LA LIBERTAD, Huamachuco (NHMUK 1868.4.3.1), Huayllillas (SMF 164320, 164321), Las Gramas (Hacienda) (ANSP 204484, 355510; DMNH 58099; MCZ 202189, 222192); Patipampa (ANSP 204492, 232512; CMN 020622; DMNH 7312, 58077, 76699, 135199; SMF 156382, 156383, 162015, 208360, 277339).

Ecoregion. Peruvian Yungas [NT0153], Cordillera Central páramo [NT1004].

Remarks. This species is a highly variable in its colour patterns and the shape of the aperture. Quebrada Macanya, the locality where Raimondi collected is in La Libertad, which is near where the material originated on which Pfeiffer based his *citrinellus*. “Huamachuco” occurs in other departments of Peru, but we assume that Higgins’ material originated also from La Libertad. As the type specimens of *B. rubrovariegatus* fall within the variation of *M. scitulus*, we synonymise these taxa.

Mesembrinus silvanus (Zilch, 1953) comb. nov.

Figures 109, 110

Drymaeus (Orodrymaeus) silvanus Zilch 1953: 56, pl. 14 fig. 5. “Peru, Bergurwald der Hacienda Taulis, 1700 m”. Holotype SMF 108567.

Diagnosis. Shell rather thin, rimate, yellowish white, with dark-brown axial streaks of varying width, crossed by three spiral bands and a white band below suture; aperture ovate; peristome thin, simple.

Measurements. Shell height 36.0 mm, diameter 13.7 mm.

Occurrence record. CAJAMARCA, Hacienda Taulis (type locality).

Ecoregion. Peruvian Yungas [NT0153].

Remarks. This species may be allied to *M. farrisi* (L. Pfeiffer, 1858), but it has a distinctive colour pattern and incrassate growth lines.

Mesembrinus trujillensis (Philippi, 1867) comb. nov.

Figures 111, 115

Bulimus trujillensis Philippi 1867: 73. “Propa [sic] Trujillo”. Type material not located.

Bulimus canarius Pfeiffer 1867: 76 (ex Philippi). “Trujillo”. Type material not located. **New synonymy.**



Figure 109. *Mesembrinus silvanus* (Zilch, 1953). Holotype SMF 108567.

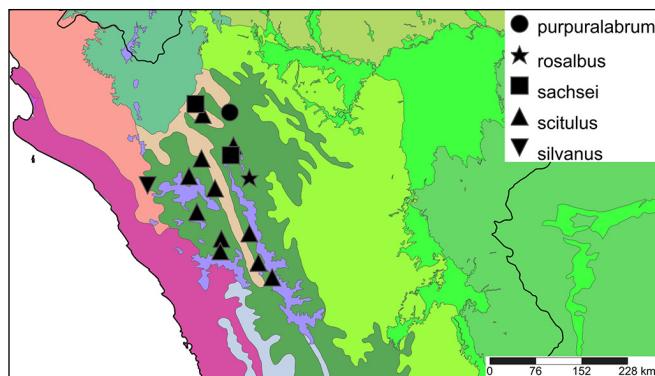


Figure 110. Distribution of *Mesembrinus* species.

Diagnosis. Shell thin, shiny, perforate, whitish, with close-set, light-reddish to dark-brown axial stripes or with three spiral bands of dark brown; aperture oblong; peristome thin, simple.

Measurements. Shell height 37 mm, diameter 12 mm.

Occurrence records. LA LIBERTAD, Cerro Campana (FM NH 30774; SMF 153385, 164347); Cerro La Cumbre (MCZ 177506; UF 109447); Trujillo (type locality; DMNH 164075; USNM 591535). LAMBAYEQUE, 10 km E of Olmos (FMNH 106155).

Ecoregion. Tumbes-Piura dry forests [NT0232].

Remarks. *Bulimus canarius* was published by Pfeiffer (1867) on the same date in a “Nachschrift” (a postscript) to Philippi’s paper. The two nominate species are similar in shape and have the same type locality, and *B. canarius* is now consid-

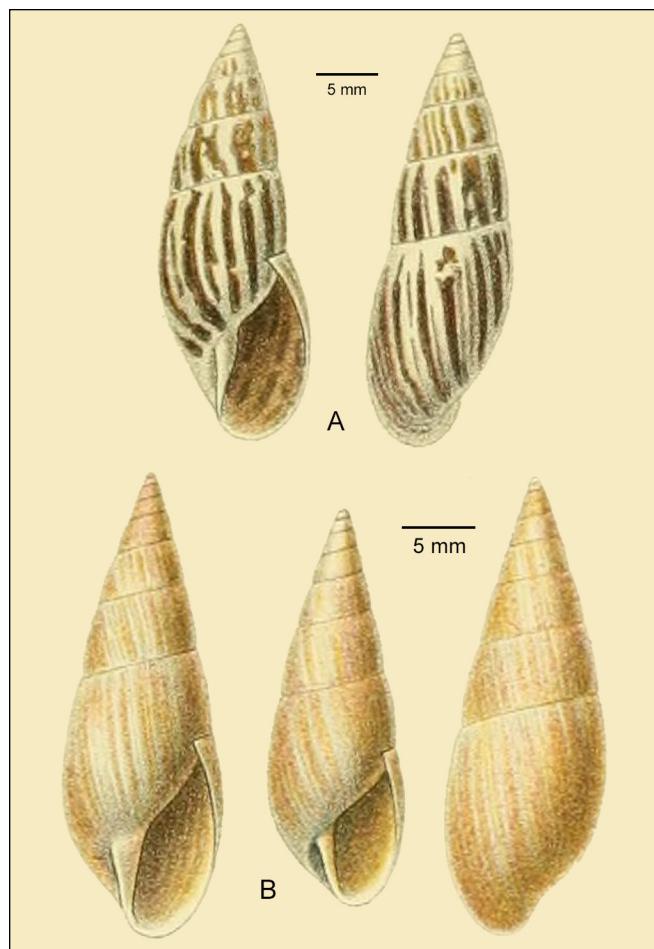


Figure 111. *Mesembrinus trujillensis* (Philippi, 1867). **A**, original figures reproduced from Pfeiffer (1867 [1866–1869]: pl. 80 figs 1, 2). **B**, original figures of *Bulimus canarius* L. Pfeiffer, 1867 reproduced from Pfeiffer (1867 [1866–1869]: pl. 80 figs 5–7).



Figure 112. *Mesembrinus vespertinus* (L. Pfeiffer, 1858). Lectotype NHMUK 1975471.

ered as a junior subjective synonym of *B. trujillensis*. *Mesembrinus trujillensis* is believed to be restricted to low altitudes along the coast. The relationship with *M. lamas* and “*M.*” *vexillum* (Broderip, 1832) needs further study.

***Mesembrinus vespertinus* (L. Pfeiffer, 1858) comb. nov.**

Figures 112, 115

Bulimus vespertinus Pfeiffer 1858: 257, pl. 42 fig. 3. “Province of Patas, Andes of Peru”. Lectotype NHMUK 1975171, paratypes NHMUK 1975472 (2) (Breure 1979: 115).

Diagnosis. Shell thin, rimate, creamy-white, with axial, dark-reddish streaks profusely dotted with white; aperture subvertical, narrowly ovate; peristome thin, simple.

Measurements. Shell height 35 mm, diameter 15 mm.

Occurrence records. ANCASH, Pomabamba (DMNH 58095; SMF 149095). LA LIBERTAD, Jocos (MCZ 102260), Pataz Province (type locality; ANSP 25818; FMNH 78776, ZMB/Mol no catalogue no.).

Ecoregion. Peruvian Yungas [NT0153], Marañon dry forests [NT0223].

Remarks. This species resembles some morphs of “*M.*” *vexillum*, and their relationship needs further study.

***Mesembrinus zilchi* (F. Haas, 1955) comb. nov.**

Figures 113, 115

Drymaeus (Drymaeus) zilchi Haas 1955: 333, fig. 73. “Huasimo, Tumbes, Peru, at 220 meters elevation”. Holotype FMNH 5197.

Diagnosis. Shell rather thin, rimate, yellowish white, with four chestnut spiral bands broken into rectangular dots; aperture ovate; peristome thin, simple.



Figure 113. *Mesembrinus zilchi* (F. Haas, 1955). Holotype FMNH 51927.

Measurements. Shell height 24.1 mm, diameter 10.4 mm.

Occurrence record. TUMBES, Huasimo (type locality).

Ecoregion. Tumbes-Piura dry forests [NT0232].

Remarks. This species is only known from the type locality.

"Mesembrinus" vexillum (W. Wood Sr, 1828) comb. nov.

Figures 114, 115

Bulimus vexillum Wood 1828: 32, pl 8 fig. 78a. No type locality given. Type material not located. Not *Bulinus vexillum* Broderip, 1832.

Bulinus pulchellus Broderip in Broderip & Sowerby I 1832: 106. "in Peruviae montibus (Truxillo)". Type material not located.

Bulinus varians Broderip in Broderip & Sowerby I 1832: 107. "in Peruviae montibus (Truxillo)". Type material not located.

Bulinus tigris Broderip in Broderip & Sowerby I 1832: 107. "in Peruviae montibus (Truxillo)". Type material not located.

Bulinus rubellus Broderip in Broderip & Sowerby I 1832: 124. "in Peruviae montibus (Truxillo)". Type material not located.

Bulimus keppelii Pfeiffer 1853: 653. "in Andibus Peruanis". Lectotype NHMUK 1975538 (Breure & Eskens 1981: 76).

Bulimus serenus Philippi 1867: 72. "In praedio 'hacienda de San-chobamba' lectus". Type material not located. **New synonymy.**

Diagnosis. Shell thin, perforate, variable in colour, creamy-white, yellowish, or light reddish, with or without axial or spiral bands; aperture subvertical, narrowly oblong-ovate.

Measurements. Shell height 37 mm, diameter 13 mm.

Occurrence records. CAJAMARCA, 15 mi. W of Cajamarca (NHMUK 1929.4.9.5–10, 1929.4.9.12–13, 1929.4.9.48–67); 5 km W of Chilote (UF 177223, UF 177231); near Chilote (ZMA.MOLL 214392); 10 km E of Chilote (UF 177225, 177228); 16 km E of Chilote (UF 177224, 177227, 177232); Choropampa (SMF 208350; ZMA.MOLL 77893); Contumazá (UF 482783, 482946, 482971); Currunday near Samne (SMF 156374); Hacienda Monteseco (ZMB/Mol 100914); 2 km E of Magdalena (UF 177233); rio Yonan (ANSP 78529, 78531; FMNH 31373–4, 31412, 77566, 78752; MCZ 64890; NHMUK 20230937; RBINS no catalogue no.; UF 109442, 161311, 161312, 161313, 161314, 161316; ZMB/Mol 48623); 20 km ESE of Magdalena (UF 177226, 177234, 177235); San Bernardino to San Pablo (FMNH 148808; ZMA.MOLL 77145, 77890, 77898). LA LIBERTAD, Trujillo (DMNH 150753, 164065, 164066; SMF 10065; UF 109455; USNM 104823, 104850, 104865, 105103, 591532, 591533, 591534); Hacienda Santo Domingo (DMNH 135203, 153677; FMNH 84723, 216836; MACN 28088; MCZ 233531; SMF 156384); Mt Cumbre near Trujillo (ANSP 182104; MCZ 109643, 177505, 177507; UF 109452, 109453, 203090); Mt Campana near Trujillo (MCZ 105969, 109641, 177504); Samne

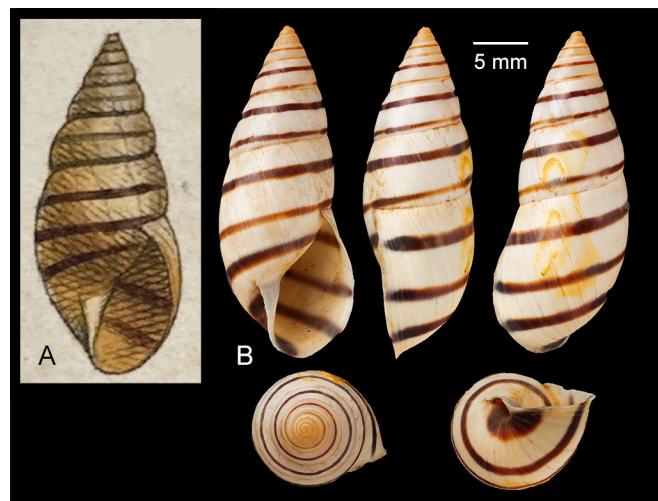


Figure 114. '*Mesembrinus*' *vexillum* (W. Wood Sr, 1828). **A**, copy of the original figure. **B**, various views of NHMUK 20230937 from Rio Yonan, Cajamarca (ex MacAndrew).

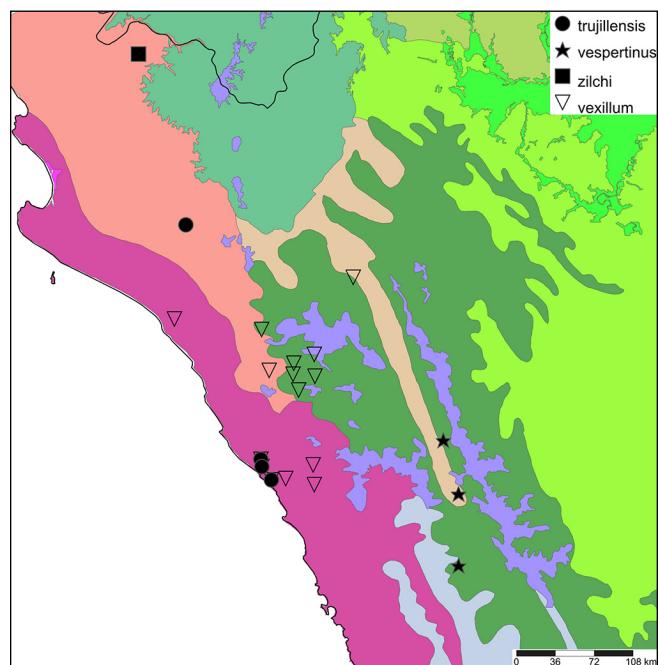


Figure 115. Distribution of *Mesembrinus* species.

near Trujillo (ANSP 159911, 159912, 159913; DMNH 58096, 135204; FMNH 29135, 78759; MCZ 95704, 177501; UF 167377; USNM 601802A). LAMBAYEQUE, near Chiclayo (ZMA.MOLL 214378).

Ecoregion. Cordillera Central páramo [NT1004], Peruvian Yungas [NT0153], Marañón dry forests [NT0223], Tumbes-Piura dry forests [NT0232], Sechura desert [NT1315].

Remarks. Wood (1828) described *Bulimus vexillum* using

material from the collections of “British Museum” (now NHM), Mrs Mawe, and J.E. Gray, as well as some figures from literature. He did not indicate in his publication on what specimens and collection each of his figures were based. Earlier, we did not locate the type of Wood’s *Bulimus vexillum* in the NHM (Breure & Ablett 2014), and we reproduced the original figure from Wood. In the NHM collection, we found one lot (ex MacAndrew) from “Rio Yonan”, of which we have illustrated a specimen (Fig. 114B) that resembles Wood’s figure.

This species shows varied colour patterns; the several taxa that have been tentatively placed in the synonymy of this species need additional study. Philippi based his description of *B. serenus* on a single specimen; the figure given by Pfeiffer (1867 [1866–1869]: pl. 80 figs 19, 20) shows a subadult specimen.

In the phylogeny presented by Salvador *et al.* (2023: fig. 6), this species is outside the three clades corresponding to *Drymaeus*, *Antidrymaeus*, and *Mesembrinus* and sister to *Neopetraeus tessellatus* (Shuttleworth, 1852), which points to a placement in another genus. There are several subgeneric names potentially available, which need to be evaluated before one can be elevated to the level of genus to contain “*M.*” *vexillum*. We indicate this species’ uncertain generic position by the use of “*Mesembrinus*” in quotation marks; however, a molecular study sampling additional taxa is needed to solve the generic position of this and related species.

Species erroneously or doubtfully reported from Peru

All species listed in this section were reported from Peru by Ramírez *et al.* (2003: 279–280) but are misidentifications or otherwise included in the malacofauna of Peru without evidence. They are all indicated as *Drymaeus* (*sensu lato*) until their proper systematic position is re-evaluated.

***Drymaeus canaliculatus* (L. Pfeiffer, 1845).** This species was described from Bolivia, and we have not seen any material from Peru that could be identified as this species.

***Drymaeus dombeyanus* (L. Pfeiffer, 1846).** This species is generally considered as belonging to the Mexican malacofauna; see Breure & Ablett (2014: 62).

***Drymaeus fallax* (L. Pfeiffer, 1853).** This species belongs to the malacofauna of Ecuador. See Breure *et al.* (2022: 158).

***Drymaeus granadensis* (L. Pfeiffer, 1848).** The record for this species, erroneously listed as “*grenadensis*” by Ramírez *et al.* (2003), is based on a misidentification. *Drymaeus granadensis* belongs to the fauna of Venezuela and Colombia. See Breure & Borrero (2019: 47).

***Drymaeus maculatus* (I. Lea, 1838).** This taxon is a

junior homonym of *Bulimus maculatus* Bruguière, 1792 and has been replaced by *Drymaeus semimaculatus* Pilsbry, 1898, which occurs in Colombia and Panama; see Breure & Borrero (2019: 41).

***Drymaeus montagnei* (d’Orbigny, 1835).** This taxon was described from Bolivia and appears to belong to *Bostryx* (Breure & Ablett 2014: 123–124). Records from Peru are considered to be misidentifications.

***Drymaeus murrinus* (Reeve, 1848).** This often-misinterpreted species is known from Colombia. See Breure & Borrero (2019: 9, 21).

***Drymaeus orthostoma* (E.A. Smith, 1877).** This is a species which belongs to the malacofauna of Ecuador. See Breure *et al.* (2022: 160).

***Drymaeus subinterruptus* (L. Pfeiffer, 1853).** The type locality of this species is “Andes of Bolivia”. The colour pattern of four spiral bands makes it very similar to some other species in northern Peru.

***Drymaeus succinea* (Pilsbry, 1901).** The type locality (“Amazon River”) is very imprecise and Pilsbry (1901 [1901–1902]: 160, pl. 26 fig. 38) did not mention Peru at all; he compared it with the French Guinean *Drymaeus limpidus* Drouët, 1859. Ramirez *et al.* (2003) listed it for the Peruvian malacofauna without further evidence. It is likely that this species is restricted to eastern Brazil.

***Drymaeus vexillum* (Broderip, 1832).** This junior homonym of *Bulimus vexillum* (now “*Mesembrinus*” *vexillum* (W. Wood Sr, 1828)) is a Panamanian species and was placed in the synonymy of *Drymaeus translucens* (Broderip, 1832) by Richardson (1995: 186).

***Drymaeus ziegleri* (L. Pfeiffer, 1847).** This taxon belongs to the Mexican fauna. See Breure & Ablett (2014: 212–213).

***Drymaeus zoographicus* (d’Orbigny, 1835).** This Bolivian species has been misidentified in a number of cases found in museum collections. For the original type material, see Breure (1976: 1153, pl. 1 fig. 6) and Breure & Ablett (2014: 213, fig. 28D).

Nomina inquirendi

Several species are difficult to interpret due to lack of original or type material. We have chosen to consider them *nomina inquirendi* until authentic or topotypic material allows to determine their status.

***Bulimus clarus* Pfeiffer, 1857:** 330. “Meobamba, Peru”. Possible syntype NHMUK 1975487 (1). The lot in NHM consisted of two specimens, one of which belonged to the genus *Naesiota* (s.l.); the *Drymaeus* specimen proved to be subadult. Also the label did not mention the type locality (“Meobamba,

Peru") given by Pfeiffer in his original description.

***Bulinus decoloratus* Sowerby I, 1833:** 73. "prope Lima, Peruviae". Possible syntypes SMF 9989 (2). The shell figured by Neubert & Janssen (2004: pl. 16 fig. 201; SMF 9989) does not look like the figure given by Reeve (1848 [1848–1850]: pl. 21 fig. 128), which was based on material in the Cuming collection from where Sowerby described *B. decoloratus*. The specimen in SMF is more likely a juvenile *Bostryx* species, and therefore we disagree with the type status of SMF 9989.

***Bulimus lentiginosus* Philippi, 1869:** 32. "inter Cajamarca et Contumaza". Type material not located. This taxon has not been figured. Pilsbry (1901: 159) wrote "Described from a single imperfect species The embryonic whorls are smooth and corneous". It may belong to *Bostryx*, but data are insufficient to make determine the systematic position.

***Bulimus miliaris* Philippi, 1867:** 74. "hacienda de Unigambal". Type material not located. Shell shape and colour pattern is more indicative of a *Bostryx* species.

***Bulimus morbidus* Philippi, 1867:** 70. "Hacienda de Sunchobamba". Type material not located.

There is much doubt about this species given the remarks and figures presented by Pilsbry (1898 [1897–1898]: 283); it may either be an unicoloured form of "*Mesembrinus*" *vexillum* (W. Wood Sr, 1828) or is possibly not a *Drymaeus*. The protoconch of topotypic material, when this becomes available, may help to judge on the systematic position.

***Bulimus pictus* Bonnet, 1864:** 69, pl. 5 figs 4–6, pl. 6 fig. 1. "Peru". Type material not located. Not *Bulimus pictus* L. Pfeiffer, 1855. Shell shape and colour pattern is also indicative of a *Bostryx* species.

***Bulimus stigmaticus* Philippi, 1867:** 74. "hacienda de Unigambal". Type material not located. Shell shape and colour pattern is more likely indicative of a *Bostryx* species.

***Drymaeus waldoschmidti* Parodiz, 1962:** 436, pl. 2 fig. 16. "Peru". Holotype USNM 609317. This taxon was described based on one specimen found among a lot of "*Drymaeus poecilus* d'Orbigny". Parodiz stated that "The specimen is a perfect, well-developed adult, not a young of *poecilus*, as one might think from its carination". The contextual data are too imprecise to consider this a well-defined taxon, which is why we consider it to be a *nomen inquirendum*.

Species to be classified in other genera

The following species do not belong to *Drymaeus*. They are now assigned to other genera.

"*Drymaeus*" *hepaticus* (Albers, 1854) (Ramírez *et al.* 2003: 279). On examination of the type material of *Bulimus*

hepaticus (ZMB.MOLL 101790), the protoconch appears to be smooth. This taxon is now placed in *Bostryx* Troschel, 1847.

"*Drymaeus*" *monachus* (L. Pfeiffer, 1857) (Ramírez *et al.* 2003: 280). This taxon appears to be a *Bulimulus* species; see Breure & Ablett (2014: 122).

"*Drymaeus*" *poecilus percandidus* Dall, 1912 (Ramírez *et al.* 2003: 279). The protoconch of the type material appears to be smooth and the species is a *Bostryx*. This name is a junior synonym of *Bostryx virgultorum* (Morelet, 1863).

"*Drymaeus*" *poecilus santanensis* Dall, 1912 (Ramírez *et al.* 2003: 279). Dall studied material collected by the Yale expedition to southern Peru and newly described this taxon without selecting a holotype. He listed a number of "mutations", which all appear to misidentified *Bostryx virgultorum*.

"*Drymaeus*" *pseudelatus* F. Haas, 1951 (Haas 1951: 520, fig. 108). The shape of the shell, the presence of axial riblets, and the colouration are all uncommon for *Drymaeus*. This taxon likely belongs to either *Naesiota* Albers, 1850 or *Bostryx*.

DISCUSSION

Our project to prepare an illustrated checklist for the terrestrial mollusc species of Peru, similar to the one we published for Ecuador (Breure *et al.* 2022), was initiated several years ago (Breure & Mogollón 2016). This project was hindered by the large number of species known from the country, which forced us to split the work across separate publications, the inability to collect new materials in Peru for anatomical and molecular research, and the restrictions to visit several relevant museum collections during the COVID-19 pandemic. This second contribution treats 94 species (Appendix, Table A4), of which 87 (92%) are endemic to Peru. Of the total number of species, 33 (35%) were not represented by modern (i.e. <50-year-old) records in literature or collections; the majority of these (27 species) have not been found since their description (often during the 19th century). Although increased collecting efforts could once again bring to light some of these species, it cannot be excluded that some small-range endemics have become extinct due to habitat destruction.

Drymaeus and *Mesembrinus* tree snails may act as a proxy for the conservation of Andean forest landscapes in Peru. We have made a preliminary overlay of the localities used in the present study with the map of national-level protected areas (SERNANP 2024). It shows that only a few of the records of the species in this study overlap with protected areas (Appendix, Figs A4, A5). For a fuller understanding of this apparent lack of protection to the land-snail fauna

of Peru, it will be necessary first to produce the checklists of other genera in our project. According to Fajardo *et al.* (2014), the National System of State Protected Areas provides protection to 15.2% of the Peruvian territory, with a bias towards Amazonian ecosystems and humid forests. Their study was based on data for amphibians, birds, butterflies, mammals, and plants and resulted in the proposition of many new conservation areas and a priority system for their selection. High-priority areas in their study are concentrated on the Coast and in the Andes regions, and these are the regions where most of the land snails have been described. However, a recent study by Golden Kroner *et al.* (2019) showed that within protected areas in Peru, there have been 64 events of downgrading, downsizing, loss of legal protection between 1900 and 2017. Such actions can accelerate habitat loss and fragmentation. Moreover, there are indications that regionally protected areas extensively overlap with concessions of extractive mining (Bax *et al.* 2019). On the long-term prospect for the Amazon biome, which extends into eastern Peru, Flores *et al.* (2024) concluded that the Amazon forest system could possibly reach a tipping point, including a large-scale ecological collapse, within the next few decades. This is worrying, as a collapse of the Amazonian ecosystem would have devastating effects on biodiversity, including the malacofauna. Currently, no endemic species of land snails from Peru are included in the IUCN Red List of Threatened Species.

Finally, Peruvian malacologists with access to facilities for DNA research are strongly encouraged to obtain data from Peruvian species not yet sequenced and to preserve specimens for anatomical research. These actions will allow for further insights into the relationships among species and improve their classification. A taxonomy firmly based on an integrative approach to classification will help to promote conservation actions and effective legislative mechanisms (Thomson *et al.* 2018). The poorly protected malacofauna of Peru could only benefit from such research activities.

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APPENDIX

I. Localities

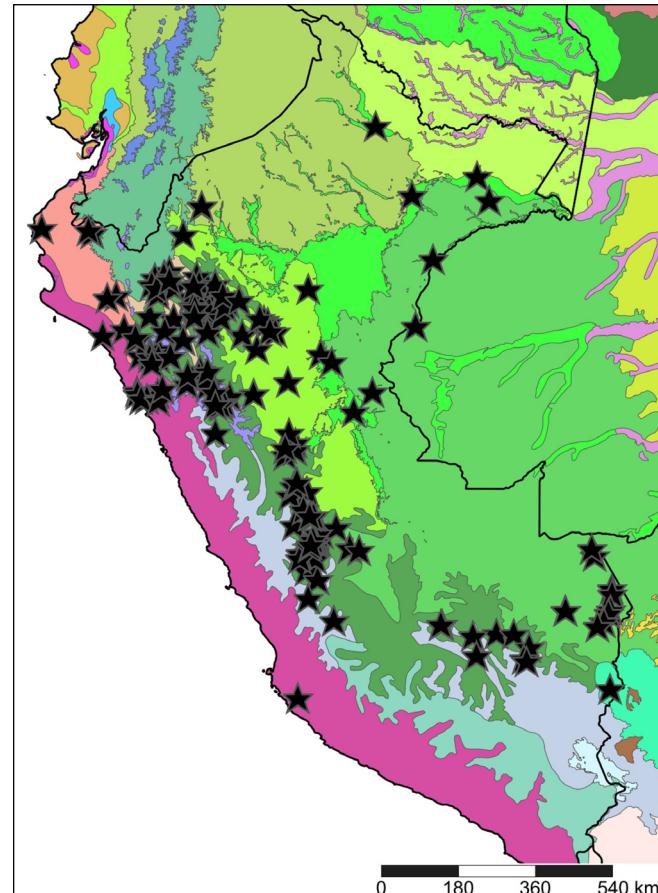
Table A1. Localities mentioned in the text that can be georeferenced. Geographic coordinates, and altitude in metres above sea level have been found using the Geonames gazetteer (<http://www.geonames.org/>). See also Figure A1.

Locality	Latitude	Longitude	Alt. (m)	Locality	Latitude	Longitude	Alt. (m)
"Rio Jelashte"	-06.71	-077.63	2350	Coyllorbamba	-12.31	-075.51	4580
10 km E of Olmos	-05.98	-079.74	320	Curunday	-08.15	-078.67	2500
15 mi. W of Cajamarca	-07.07	-078.67	3520	Cutervo	-06.37	-078.85	2880
2 km S of Puerto Maldonado	-12.63	-069.19	190	Cuzco	-013.52	-071.97	3360
4 mi W of Otuzco	-07.90	-078.58	3000	Divisoria	-09.18	-075.79	1400
Abra Patricia	-05.69	-077.81	2300	Finca Las Piedras	-012.22	-069.11	260
Alegría	-12.11	-069.12	250	Huacapistana	-011.23	-075.48	2500
Alto Javari	-05.17	-072.88	110	Huallaga Province	-06.756	-076.90	1280
Alto Mayo	-05.89	-077.61	880	Huamachuco	-07.8	-078.07	3340
Alto Zotani	-10.82	-074.92	1080	Huancabamba	-010.44	-075.61	1890
Aramango	-05.42	-078.43	530	Huancavelica	-012.78	-074.97	3700
Asunción	-06.03	-077.71	2800	Huasimo	-04.56	-080.14	390
Aucayacu, 27.4 km SSE of	-09.15	-075.99	670	Huayllillas	-08.19	-077.29	2360
Ayabaca, 45 km W of	-04.62	-080.06	420	Jaén	-05.71	-078.81	730
Bagua	-05.63	-078.53	430	Jauja Province	-011.72	-075.55	3470
Bambamarca	-06.68	-078.53	2740	Jocos	-08.23	-077.47	2290
Bellavista	-07.06	-076.59	310	Jucusbamba	-08.23	-077.36	3030
Bellavista District	-05.56	-078.74	850	La Cachuela	-011.41	-069.48	260
Bongará Province	-06.04	-077.89	2070	La Peca	-05.61	-078.43	890
Boquerón de Abad	-08.83	-075.91	1700	La Poza	-05.91	-078.68	600
Caclic	-06.20	-077.90	1690	Lamas	-06.42	-076.53	810
Cadena	-13.34	-070.86	890	Lamas-Tarapoto	-06.46	-076.44	300
Cajabamba	-07.61	-078.05	2630	Lares	-013.10	-072.04	3660
Celendín	-06.86	-078.14	2630	Las Cruces	-013.05	-071.55	1480
Cerro Campana	-07.94	-079.12	300	Limabamba	-06.55	-077.58	2000–2400
Cerro La Cumbre	-08.01	-079.11	290	Los Amigos	-012.57	-070.10	270
Chachapoyas	-06.23	-077.87	2360	Luya	-06.16	-077.94	2310
Chagual	-07.84	-077.63	1250	Macanya	-07.97	-077.50	2330
Chanchamayo valley	-11.03	-075.36	870	Madama	-012.56	-069.14	210
Cheto	-06.25	-077.70	2130	Magdalena	-07.25	-078.67	1240
Chiclayo	-06.77	-079.84	30	Maraynioc	-011.35	-075.45	3520
Chilete	-07.23	-078.85	1130	Marcabal	-07.61	-077.81	3080
Chongoyape	-06.64	-079.39	210	Marcapata	-013.59	-070.97	3380
Chontabamba	-10.58	-075.48	2350	Marcapata District	-013.64	-070.91	3300
Choropampa	-06.42	-078.35	2140	Mariscal Ramón Castilla	-03.93	-071.70	110
Cocachimba	-06.06	-077.89	1790	Molinopampa	-06.21	-077.67	2400
Cochanbul	-07.22	-078.41	2570	Molinopampa District	-06.21	-077.61	2460
Colonia Calleria	-07.96	-074.16	200	Monteseco (Hacienda)	-06.86	-079.11	1190
Concepcion	-11.92	-075.31	3280	Moyobamba	-06.03	-076.97	870
Contamana	-07.33	-075.02	140	Negritos, 25 km NE of	-04.52	-081.12	70
Contumazá	-07.36	-078.80	2700	Nueva Cajamarca	-05.94	-077.31	1480
Cordillera Azul N.P.	-07.75	-075.94	680	Olmos–Chamaya road	-05.93	-079.55	820
Cosñipata	-013.07	-071.18	930	Omia District	-06.40	-077.35	1900
				Oreja de Capelo	-011.03	-075.36	1540

Table A1. Continued.

Locality	Latitude	Longitude	Alt. (m)
Oriente Nuevo	-05.79	-075.51	1180
Oxapampa	-010.58	-075.40	1810
Pachitea Province	-09.95	-075.81	2630
Pan de Azucar	-011.18	-075.46	1630
Panao Province	-010.15	-075.90	3720
Pardo Miguel Province	-05.75	-077.63	1820
Pataz Province	-07.78	-077.59	2640
Patipampa	-07.53	-077.63	2280
Paucartambo	-010.77	-075.81	3050
Pebas	-03.42	-071.95	70
Pedro Ruiz	-05.96	-077.98	1360
Perené	-010.94	-075.22	610
Pichita Caluga	-011.08	-075.41	2020
Pomabamba	-08.83	-077.47	3380
Pongo de Rentema	-05.50	-078.54	820
Pozuzo	-010.07	-075.53	1130
Puca Tambo	-06.17	-077.27	1550
Pucallpa	-08.38	-074.55	150
Puerto Galilea	-04.06	-077.76	190
Quillabamba	-012.86	-072.69	1050
Quimiri Sur	-011.08	-075.29	1200
Quistacocha	-03.82	-073.33	100
Rio Cenepa	-04.65	-078.15	220
Rio Chamaya	-05.78	-078.70	410
Rio Chinchipe	-05.51	-078.55	350
Rio Colorado	-010.96	-075.31	820
Rio Curaray	-02.36	-074.09	120
Rio Mishollo	-08.00	-076.66	450
Rio Yonan	-07.20	-079.05	590
Rio Yutopiza, Shiringa	-04.04	-077.75	170
Rioja	-08.06	-077.16	830
Rodriguez de Mendoza Prov.	-06.33	-077.42	2580
Samne	-07.99	-078.68	1490
San Bernardino-San Pablo	-07.14	-078.84	1950
San Juan del Oro	-014.22	-069.15	1330
San Ramon	-011.13	-075.35	830
Santa Ana	-012.87	-072.72	1650
Santa Elena	-07.51	-077.79	1530
Santa Rita	-011.27	-069.54	300
Santo Domingo (Hacienda)	-08.10	-078.91	130
Satipo	-011.25	-074.64	630
Satipo-Puerto Ocopa	-011.30	-074.44	520
Sauce District	-06.70	-076.20	600
Sinchoco	-09.03	-075.78	1500
Surco	-011.88	-076.44	2580
Tambillo	-011.48	-075.36	3960

Locality	Latitude	Longitude	Alt. (m)
Tambo de Vaca	-09.87	-075.75	3300–3500
Tambopata	-012.91	-069.42	210
Tambopata Reserve	-012.80	-069.30	220
Tarapoto	-06.50	-076.36	270
Tarma-Acobamba	-011.37	-075.68	3070
Tarmatambo	-011.48	-075.69	3460
Taulis	-06.82	-079.15	1710
Tingo Maria	-09.29	-075.99	650
Tingo Nuevo	-06.37	-077.91	1970
Traquillo	-06.68	-076.32	270
Trujillo	-08.11	-079.03	30
Ucayali Province	-07.17	-075.25	140
Utcubamba Province	-05.77	-078.33	560
Yambrasbamba	-05.73	-077.92	1870
Yambrasbamba District	-05.52	-077.86	1600

**Figure A1.** Georeferenced localities mentioned in the main text; see also Table A1.

II. Terrestrial ecoregions

Ecoregions (Table A2, Fig. A2), as defined by the World Wildlife Fund, have been indicated wherever possible for the distribution records in the text. However, the following caveats apply (Olson et al. 2001). Firstly, no single biogeographic framework is optimal for all taxa. Ecoregions reflect the best compromise for as many taxa as possible. Secondly, in nature, the boundaries of ecoregions rarely form abrupt

edges, but rather, ecotones and mosaic habitats form at the edges of ecoregions. Thirdly, most ecoregions contain habitats that differ from their assigned biome (e.g., for example, rainforest ecoregions in Amazonia often contain small edaphic savannas). With these caveats in mind, ecoregions can form useful units for biological analysis and for conservation planning and action.

Table A2. The numbers used in Figure A2 are given between brackets; between square brackets the corresponding WWF codes are given (see WWF 2015).

Ecoregion	Number in Fig. A2	Ecoregion code	Ecoregion	Number in Fig. A2	Ecoregion code	
TROPICAL AND SUBTROPICAL MOIST BROADLEAF FORESTS						
Bolivian Yungas	(15)	[NT0105]	Marañon dry forests	(9)	[NT0223]	
Eastern Cordillera real montane forests	(3)	[NT0121]	Tumbes-Piura dry forests	(1)	[NT0232]	
Iquitos várzea	(7)	[NT0128]	MONTANE GRASSLAND AND SHRUBLANDS			
Napo moist forests	(4)	[NT0142]	Central Andean puna	(14)	[NT1002]	
Peruvian Yungas	(10)	[NT0153]	Central Andean wet puna	(12)	[NT1003]	
Purus várzea	(5)	[NT0156]	Cordillera Central páramo	(11)	[NT1004]	
Solimões-Japurá moist forests	(6)	[NT0163]	DESERTS AND XERIC SHRUBLANDS			
Southwest Amazon moist forests	(13)	[NT0166]	Sechura desert (Peru)	(2)	[NT1315]	
Ucayalí moist forests	(8)	[NT0174]				

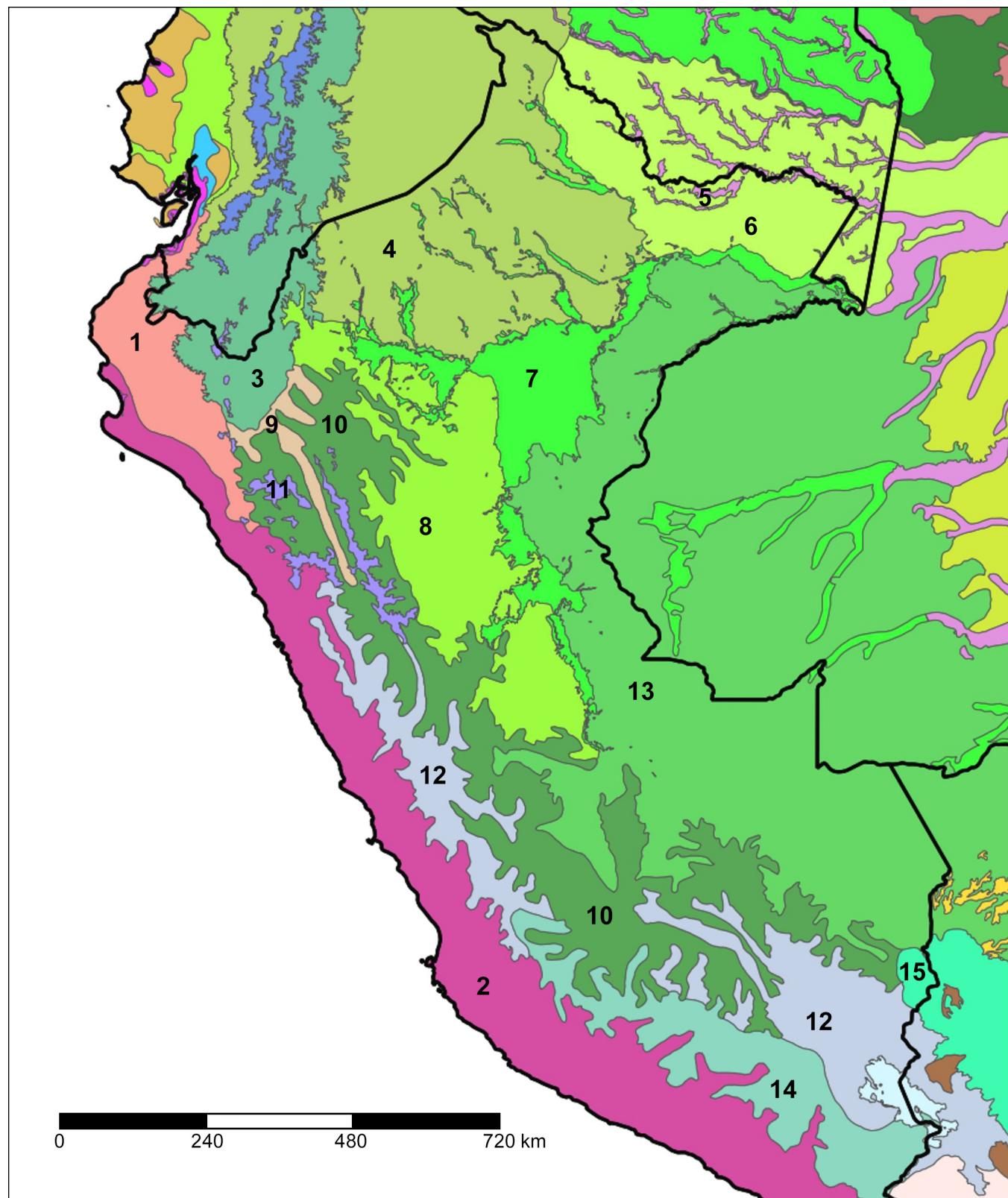


Figure A2. Ecoregions of Peru, numbered 1–15; see Table A2. 1 = Tumbes-Piura dry forests, 2 = Sechura desert, 3 = Eastern Cordillera real montane forests, 4 = Napo moist forests, 5 = Purus várzea, 6 = Solimões-Japurá moist forests, 7 = Iquitos várzea, 8 = Ucayalí moist forests, 9 = Marañon dry forests, 10 = Peruvian Yungas, 11 = Cordillera Central páramo, 12 = Central Andean wet puna, 13 = Southwest Amazon moist forests, 14 = Central Andean puna, 15 = Bolivian Yungas,

Table A3. *Drymaeus* and *Mesembrinus* species occurrences by ecoregion (see Table A2, Fig. A2). These data may allow for studies on ecological communities or biogeography, but see Munguía-Ortega *et al.* (2021).

Table A3. Continued.

Species	Moist forests							Dry forests		Grasslands		Desert			
	NT0105	NT0121	NT0128	NT0142	NT0153	NT0156	NT0163	NT0166	NT0174	NT0223	NT0232	NT1002	NT1003	NT1004	NT1315
<i>D. sophiaeae</i>					x										
<i>D. strigatus</i>		x			x				x						
<i>D. subeffusus</i>												x			
<i>D. subsimilaris</i>											x				
<i>D. tigrinus</i>				x							x				
<i>D. translucidus</i>									x						
<i>D. valentini</i>					x										
<i>D. verecundus</i>		x													
<i>D. weeksi</i>															
<i>M. acobambensis</i>					x										
<i>M. aestivus</i>					x										
<i>M. alsophilus</i>					x										
<i>M. anceps</i>															
<i>M. angulobasis</i>					x										
<i>M. apicepunctata</i>															
<i>M. bequaerti</i>					x										
<i>M. caktivorus</i>										x					
<i>M. celendinensis</i>					x										
<i>M. chrysomelas</i>					x										
<i>M. clathratus</i>					x										
<i>M. coelestini</i>					x										
<i>M. cuzcoensis</i>											x				
<i>M. cylindricus</i>															
<i>M. eucosmetus</i>											x				
<i>M. farrisi</i>			x							x					
<i>M. inconspicuus</i>	x												x		
<i>M. lamas</i>													x		
<i>M. laxostylus</i>					x										
<i>M. leucomelas</i>															
<i>M. libertadensis</i>										x					
<i>M. marmoratus</i>				x		x									
<i>M. mexicanus</i>	x			x						x					
<i>M. miltochrous</i>															
<i>M. nigroapicatus</i>															
<i>M. paeteli</i>													x		
<i>M. pergracilis</i>					x										
<i>M. phryne</i>					x										
<i>M. ponsonbyi</i>						x									x
<i>M. praetextus</i>										x					
<i>M. pseudobesus</i>					x										
<i>M. pulcherrimus</i>					x				x						
<i>M. purpurealabrum</i>					x										
<i>M. rosalbus</i>					x										
<i>M. sachsei</i>					x				x						

Table A3. Continued.

Species	Moist forests							Dry forests		Grasslands		Desert			
	NT0105	NT0121	NT0128	NT0142	NT0153	NT0156	NT0163	NT0166	NT0174	NT0223	NT0232	NT1002	NT1003	NT1004	NT1315
<i>M. scitulus</i>					x									x	
<i>M. silvanus</i>					x										
<i>M. trujillensis</i>											x				
<i>M. vespertinus</i>					x					x					
<i>M. zilchi</i>											x				
" <i>M.</i> " <i>vexillum</i>					x					x	x		x	x	

III. Protected areas in Peru

According to SERNANP (2024), the following areas are protected in Peru (Fig. A4):

- National parks: areas that constitute representative samples of the country's natural diversity. They provide intangible protection for one or more ecosystems, associations of wild flora and fauna, as well as other associated landscape and cultural features. They are protected natural areas of indirect use in which scientific research and tourism are allowed in appropriately designated areas.
- National sanctuaries: areas where the habitat of a species or a community of flora and fauna, as well as natural forma-

tions of scientific and landscape interest, are protected on an intangible basis. These are protected natural areas of indirect use in which scientific research and tourism are allowed in appropriately designated areas.

- National reserves: areas destined for the conservation of biodiversity and the sustainable use of wild flora and fauna resources. These are natural protected areas of direct use in which, through management plans, the traditional use and sustainable exploitation of natural resources by local populations is permitted.

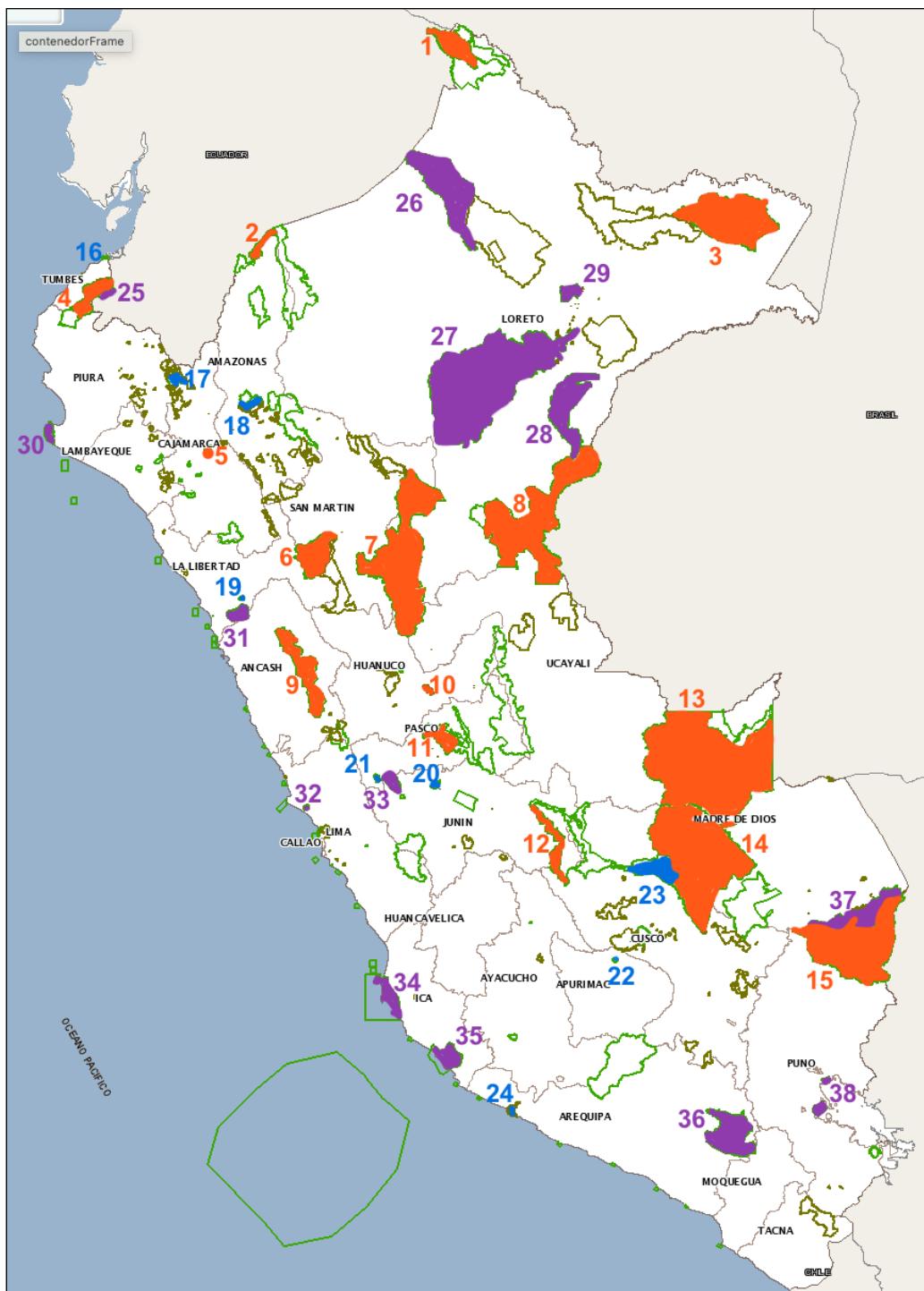


Figure A4. Protected natural areas in Peru. National Parks (P.N.) are numbered in red: 1 = P.N. Gueppí-Sekime, 2 = P.N. Ichikat Muja-Cordillera del Condor, 3 = P.N. Yaguas, 4 = P.N. Cerros de Amotape. 5 = P.N. Cutervo, 6 = Rio Abiseo, 7 = P.N. Cordillera Azul, 8 = P.N. Sierra del Divisor, 9 = P.N. Huascarán, 10 = P.N. Tingo Maria, 11 = P.N. Yanachaga Chemillén, 12 = P.N. Otishi, 13 = P.N. Alto Purús, 14 = P.N. del Manu, 15 = P.N. Bahuja Sonene. National sanctuaries (S.N.) are numbered in blue: 16 = S.N. Los Manglares de Tumbes, 17 = S.N. Tabaconas Namballe, 18 = S.N. Cordillera de Colán, 19 = S.N. de Calipuy, 20 = S.N. de Huayllay, 21 = S.N. Pampa Hermosa, 22 = S.N. de Ampay, 23 = S.N. Megantoni, 24 = S.N. Lagunas de Mejia. National reserves (R.N.) are numbered in purple: 25 = R.N. de Tumbes, 26 = R.N. Pucacuro, 27 = R.N. Pacaya Samiria, 28 = R.N. Matsés, 29 = R.N. Allpahuayo Mishana, 30 = R.N. Illescas, 31 = R.N. de Calipuy, 32 = R.N. de Lachay, 33 = R.N. de Junin, 34 = R.N. Paracas 35 = R.N. San Fernando, 36 = R.N. Pampa Galeras Barbara D'Achille, 37 = R.N. Tambopata, 38 = R.N. del Titicaca.

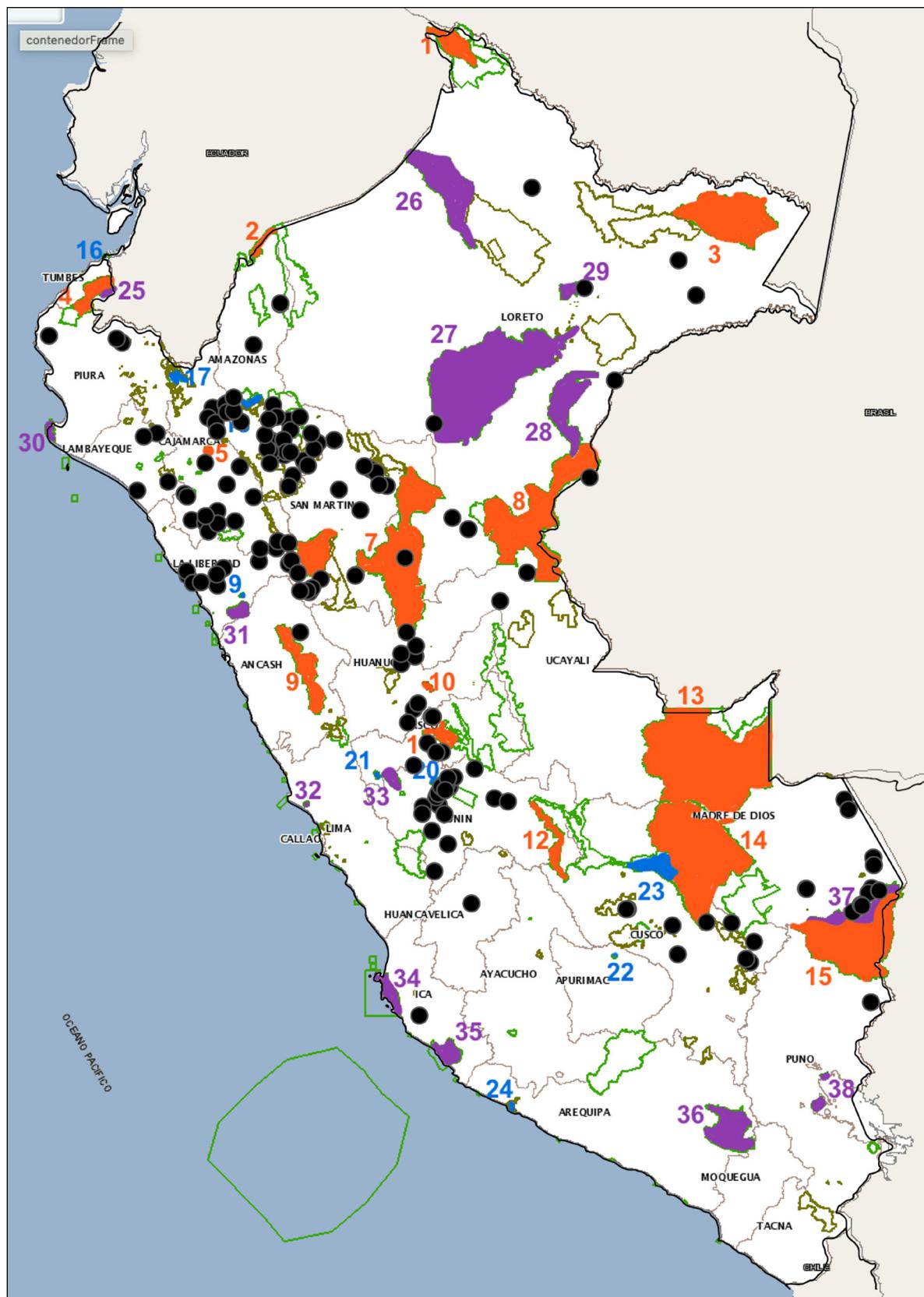


Figure A5. Peruvian protected areas overlayed by the localities of *Drymaeus* and *Mesembrinus* species in the main text. Most of localities where materials have been collected are from unprotected areas.

IV. Status of *Drymaeus* and *Mesembrinus* species of Peru

Here we list the status of the species treated (Table A4). While the majority are endemic, several have not been re-collected within the last 50 years, which may either be due to insufficient collecting, insufficient reporting, a combination of these two factors, or a decline in occurrences due to, for instance, alterations in habitat. For some species collect-

ing may be hampered by the lack of knowledge about where they occur. This is especially true for species described in the 19th century when less attention was given to the value of precise localities. Additionally, for some species the type material has not been found in museum collections or the material is presumed lost.

Table A4. Status of *Drymaeus* and *Mesembrinus* species of Peru.

Species	Endemic	No records <50 years old	Imprecise locality	New record
<i>D. abruptus</i>	x	x		
<i>D. araujoi</i>	x			
<i>D. arcuatostriatus</i>	x			
<i>D. aurisratti</i>	x			
<i>D. bartletti</i>	x	x	x	
<i>D. basitorus</i>	x			
<i>D. beyreleanus</i>	x			
<i>D. branneri</i>				
<i>D. cantatus</i>	?	x	x	
<i>D. castaneostrigatus</i>	x	x		
<i>D. catenae</i>	x			
<i>D. chanchamayensis</i>	x			
<i>D. combinai</i>	x	x		
<i>D. costatus</i>	x			
<i>D. edmuelleri</i>	x			
<i>D. elsteri</i>	x			
<i>D. eurystomus</i>	x			
<i>D. expansus</i>	x			
<i>D. fordii</i>				x
<i>D. fusoides</i>			x	
<i>D. gibber</i>	x			
<i>D. gueinzii</i>	x			
<i>D. icterostomus</i>	x	x		
<i>D. inaequalis</i>	x	x	x	
<i>D. inca</i>	x			
<i>D. interictus</i>	x			
<i>D. jousseaumei</i>	x	x	x	
<i>D. luculentus</i>	x			
<i>D. marcapatensis</i>	x	x		
<i>D. multiguttatus</i>	x	x		
<i>D. nebulosum</i>	x			
<i>D. ommatidia</i>	x			
<i>D. palassus</i>	x			
<i>D. peelii</i>				
<i>D. protractus</i>	x			

Species	Endemic	No records <50 years old	Imprecise locality	New record
<i>D. punctatus</i>	x			
<i>D. rectilinearis</i>	x			
<i>D. regularis</i>	x			
<i>D. rosenbergi</i>	x		x	
<i>D. rugistratus</i>	x			
<i>D. schunkei</i>	x			
<i>D. scolioides</i>	x		x	x
<i>D. serratus</i>	x			
<i>D. similaris</i>	x			
<i>D. sophiaeae</i>	x			
<i>D. strigatus</i>	x			
<i>D. subeffusus</i>	x		x	
<i>D. subsimilaris</i>	x		x	
<i>D. tigrinus</i>				x
<i>D. translucidus</i>	x		x	
<i>D. valentini</i>	x			
<i>D. verecundus</i>	x			
<i>D. weeksi</i>	x		x	x
<i>M. acobambensis</i>	x			
<i>M. aestivus</i>	x		x	
<i>M. alsophilus</i>	x		x?	
<i>M. anceps</i>	x		x	x
<i>M. angulobasis</i>	x			
<i>M. apicepunctata</i>	x			
<i>M. bequaerti</i>	x			
<i>M. cactivorus</i>				x
<i>M. celendinensis</i>	x			
<i>M. chrysomelas</i>	x			
<i>M. clathratus</i>	x		x	
<i>M. coelestini</i>	x		x	
<i>M. cuzcoensis</i>	x		x	x
<i>M. cylindricus</i>	x		x	x
<i>M. eucosmetus</i>	x			
<i>M. farrisi</i>	x			
<i>M. inconspicuus</i>	x			

Table A4. Continued.

Species	Endemic	No records <50 years old	Imprecise locality	New record	Species	Endemic	No records <50 years old	Imprecise locality	New record
<i>M. lamas</i>	x				<i>M. praetextus</i>	x	x		
<i>M. laxostylus</i>	x				<i>M. pseudobesus</i>	x			
<i>M. leucomelas</i>	x	x	x		<i>M. pulcherrimus</i>	x			
<i>M. libertadensis</i>	x	x	x		<i>M. purpuralabrum</i>	x			
<i>M. marmoratus</i>	x				<i>M. rosalbus</i>	x	x	x	
<i>M. mexicanus</i>	x				<i>M. sachsei</i>	x			
<i>M. miltochrous</i>	x	x	x		<i>M. scitulus</i>	x			
<i>M. nigroapicatus</i>	x	x	x		<i>M. silvanus</i>	x	x		
<i>M. paeteli</i>	x	x	x		<i>M. trujillensis</i>	x			
<i>M. pergracilis</i>	x				<i>M. vespertinus</i>	x			
<i>M. phryne</i>	x				<i>M. zilchi</i>	x	x		
<i>M. ponsonbyi</i>	x				“ <i>M.</i> ” <i>vexillum</i>	x			