

SYSTEMATICS, PHYLOGENY AND ZOOGEOGRAPHY OF BULIMULINAE (MOLLUSCA)

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With 182 text-figures, 5 tables and 3 plates

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ABSTRACT

In this publication a revision is given of the genera of the subfamily Bulimulinae (Gastropoda, Pulmonata, Bulimulidae).

The morphological variation of the shell, radula, pallial organs and genitalia is analyzed and 21 character transition series are recognized.

In the systematical part the following data are presented for each genus: description of shell and anatomy, distribution, ecology, bibliography and a list of taxa. The number of (sub)genera is reduced from 80 to 43 (+ two nomina inquirenda). A new synonymy is: *Paracochlea* Hylton Scott, 1967 = *Eudioptus* Albers, 1860. The following new species names are introduced: *Bostryx sophieae*, *Drymaeus (Drymaeus) marcapatensis*, *Drymaeus (Drymaeus) sophieae*, *Drymaeus (Mesembrinus) pseudobesus*. *Berendtia digueti* Mabilie is designated type species of *Teneritia* Mabilie; *Helix zoographica* d'Orbigny is designated type species of *Hamadryas* Albers.

Based on the transition series mentioned above, hypotheses of phylogenetic relationships are presented for the genus groups, using the methods of Hennig. The relationships between the five subfamilies of the Bulimulidae are also investigated but remain tentative.

In the zoogeographical section the various theories are reviewed and their relevance for the distribution of the Bulimulinae is treated, using the hypotheses of phylogenetic relationships and Croizat's vicariance theory.

I. INTRODUCTION

During a revision of some bulimulid genera from the West Indies (Breure, 1974a, 1975a), I became aware of the multiple taxonomic problems offered

by the mainland taxa. Especially the publications by Weyrauch (1956-1967) and Van Mol (1971) provoked my interest. Thanks to grants of the Foundation for the Advancement of Tropical Research (WOTRO) I could initiate a revision of the genera of Bulimulidae in 1975.

Because of the limited time available for this research, the present paper is entirely confined to the Bulimulinae. Data on the other subfamilies have partly been published (Breure, 1974c) or will be published in the near future (Breure & Schouten, in preparation).

In my view the anatomy yields indispensable information for a generic revision and, therefore, as very few preserved animals were available in collections, it was necessary to collect most material myself. This was made possible by grants of the Foundation for the Advancement of Tropical Research (WOTRO). The specimens which I collected during two field trips to South America were the basis for the results of my research.

Thanks to the monumental monograph of the Bulimulidae by Pilsbry (1895-1902), all descriptions previously published were readily available, which greatly facilitated the identification of the material. In Pilsbry's monograph the generic framework is based on one of the most important external morphological characters of the Bulimulidae, viz. the sculpture of the protoconch. Until now this character has retained its importance for identifications, but it proves to be of less value as indicator of phylogenetic relationships.

Thiele (1931) listed 11 genera and subgenera in the subfamily Bulimulinae (*Partula* and *Placostylus* now excluded). In Zilch's monograph on euthyneuran gastropods the number of (sub)generic taxa in the subfamily had grown to 80 (also induced by a changed concept of (sub)genera; *Diplomorpha*, *Placostylus* and *Aspastus* now excluded). With three genera classified sensu lato this number is now reduced to 43 (plus two nomina inquirenda). The various classifications are summarized in Table 1.

II. ECOLOGY

Field observations during January-June 1975 (see Breure, 1975b) and April-May 1976 indicate that bulimulid species frequent the following macrohabitats: (1) leaf litter layer; (2) herbaceous vegetation; (3) rock-faces; (4) trees.

The species of the leaf litter layer are characterized by their mostly uniform brownish colour, the unexpanded peristome and the straight rows of the radula. The species were collected by raking through leaves and debris on the ground.

Species that live in herbaceous vegetation may less frequently also be found in the leaf litter layer. They are characterized by their light (often whitish)

Pilsbry (1895-1902)*	Thiele (1931)*	Zilch (1960)*	Present classification *
<i>Neopetraeus</i>	<i>Bulimulus (Scansicochlea)</i> <i>Neopetraeus</i>	<i>Scansicochlea</i> <i>Neopetraeus</i>	[7] <i>Neopetraeus</i>
<i>Auris (Ostostomus)</i>	<i>Ostostomus</i>	? <i>Ostostomus</i>	<i>Laucaianus</i>
<i>Drymaeus (Zaplagius)</i>	<i>Zaplagius</i>	<i>Cochlorina</i>	<i>Ostostomus</i>
<i>Drymaeus (Drymaeus)</i>	<i>Drymaeus (Drymaeus)</i>	<i>Drymaeus (Drymaeus)</i>	<i>Cochlorina</i>
[<i>Stenostylus</i>]	[<i>Antidrymaeus</i>] [<i>Stenostylus</i>]	} } } <i>Drymaeus (Ornatimormus)</i> <i>Drymaeus (Metadrymaeus)</i> <i>Drymaeus (Orodrymaeus)</i> <i>Drymaeus (Leptomormus)</i> <i>Drymaeus (Leptodrymaeus)</i> <i>Drymaeus (Antidrymaeus)</i>	<i>Drymaeus (Drymaeus)</i>
<i>Drymaeus (Leiostracus)</i>	<i>Drymaeus (Leiostracus)</i>	<i>Stenostylus</i>	<i>Drymaeus (Mesembrinus)</i>
<i>Orychona</i>	<i>Orychona</i>	<i>Newboldius</i>	<i>Stenostylus</i>
<i>Bothriembryon</i>	<i>Bothriembryon</i>	<i>Newboldius</i>	<i>Newboldius</i>
<i>Simpulopsis (Simpulopsis)</i>	<i>Simpulopsis (Simpulopsis)</i>	<i>Lopesianus</i>	<i>Lopesianus</i> [3]
<i>Simpulopsis (Bulimulopsts)</i>	[<i>Eudiotypus</i>]	<i>Leiostracus (Leiostracus)</i>	<i>Leiostracus (Leiostracus)</i>
* (subgenera), [sections].	<i>Bothriembryon</i>	<i>Orychona</i>	[8]
Notes: [1] <i>Anitragus = Plekocheilus (Eudolichoitis)</i> .	<i>Simpulopsis (Simpulopsis)</i>	<i>Bothriembryon</i>	<i>Orychona</i>
[2] <i>Atahualpa = Thaumastus (Thaumastus)</i> .	[<i>Eudiotypus</i>]	<i>Simpulopsis (Simpulopsis)</i>	<i>Bothriembryon (Bothriembryon)</i>
[3] Nomen inquirendum.	<i>Bothriembryon</i>	<i>Simpulopsis (Eudiotypus)</i>	<i>Bothriembryon (Tasmanembryon)</i>
[4] <i>Xenothauma = Scutalus (Scutalus)</i> .	<i>Simpulopsis (Simpulopsis)</i>	<i>Simpulopsis (Eudiotypus)</i>	<i>Simpulopsis (Simpulopsis)</i> } [9]
[5] <i>Dentaris = Bostryx</i> sensu lato.	<i>Bothriembryon</i>	<i>Simpulopsis (Eudiotypus)</i>	<i>Simpulopsis (Eudiotypus)</i>
[6] <i>Protoglyptus = Naesiotus</i> sensu lato.	<i>Simpulopsis (Simpulopsis)</i>	<i>Simpulopsis (Eudiotypus)</i>	<i>Sphaeroconcha</i>
[7] <i>Scansicochlea = Bostryx</i> sensu lato.	<i>Bothriembryon</i>	<i>Simpulopsis (Eudiotypus)</i>	
[8] <i>Graptiostracus</i> is a non-bulimulid.	<i>Simpulopsis (Simpulopsis)</i>	<i>Simpulopsis (Eudiotypus)</i>	
[9] <i>Simpulopsis</i> was placed in the subfamily Amphibuliminae by Pilsbry, Thiele and Zilch.	<i>Simpulopsis (Simpulopsis)</i>	<i>Simpulopsis (Eudiotypus)</i>	

colour, the unexpanded peristome and the straight rows of the radula. When the specimens are aestivating they can easily be picked up from grasses and shrubs.

Only a limited number of species lives on rock-faces, where they probably feed on algae. The species are characterized by their elongate-globose shell shape, the light colour of their shell, the expanded peristome and the monocuspid teeth in the central part of the radula (see Breure & Gittenberger, in preparation).

Species that live on trees are usually well-hidden and then can only be collected alive during and shortly after heavy tropical showers. The species are mostly brightly coloured, have an expanded peristome and the transverse rows in the radula are more or less V-shaped.

Data on the seasonal distribution of the species are not available, but probably most species will have their highest activity during the rainy season. Altitudinal data were taken from collectors labels or gathered during my field work. Bulimulidae live from sea-level to near the snow-line at ca. 5200 m, most specimens being collected between 1000 and 3500 meters.

In this context attention may be drawn to the distribution of species living in arid valleys (most noticeably in Peru, both in valleys on the western escarpments of the Andes and in interandean valleys). Most of these species have a very limited distribution, both in area and in altitude, which is probably caused by their special dependence on the microclimate.

III. MATERIAL AND METHODS

The collections of bulimulids in the main European museums were studied to examine the variation in shell morphology and specimens of ca. 350 species were dissected to study the anatomical variation. The animals were fixed in neutral formalin (those collected by myself) or in alcohol 70% (presumably all those from museum collections). The greater part of the material studied anatomically is preserved in the Rijksmuseum van Natuurlijke Historie, Leiden.

From the animals studied the buccal mass, pallial organs and genitalia were dissected. The radula was studied following the procedure described by Ploeger & Breure (1977). The pallial organs and genitalia were drawn with a camera lucida attachment to a Wild M5 microscope. Part of the genitalia were studied histologically afterwards. They were embedded in paraffin, sectioned at 7 μ m and stained with 1% Alcian Blue after kalium permanganate oxidation, followed by staining with Haemalum and 0.8% Phloxine. Several sections were stained with Haemalum and Eosin-Erythrosin in ethanol 80%. The slides were mounted in malinol.

The following abbreviations are used to refer to the location of the specimens: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, Dept. of Geology, San Francisco; CM, Carnegie Museum, Pittsburgh; CMG, Museo Civico di Storia Naturale, Genua; DGM, Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro; DZSP, Departamento de Zoologia, Universidade de São Paulo, São Paulo; FMNH, Field Museum of Natural History, Chicago; IML, Instituto Miguel Lillo, Tucumán; IOC, Instituto Oswaldo Cruz, Rio de Janeiro; IRSN, Institut Royal des Sciences Naturelles, Brussels; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MCZ, Museum of Comparative Zoology, Cambridge (Mass.); MHNG, Musée d'Histoire Naturelle, Geneva; MIHS, private collection of Dr. M. I. Hylton Scott, La Plata; MLP, Museo La Plata, La Plata; MN, Museu Nacional, Rio de Janeiro; MNHN, Muséum National d'Histoire Naturelle, Paris; MRCN, Museu Rio-Grandense de Ciências Naturais, Porto Alegre; NMB, Naturhistorisches Museum, Basel; NMV, National Museum of Victoria, Melbourne; NRS, Naturhistoriska Riksmuseet, Stockholm; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SAM, South Australian Museum, Adelaide; SMF, Natur-Museum Senckenberg, Frankfurt am Main; UF, Florida State Museum, Gainesville; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor; USNM, National Museum of Natural History, Washington; WAM, Western Australian Museum, Perth; ZMA, Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam; ZMB, Zoologisches Museum der Humboldt-Universität, Berlin; ZMUZ, Zoologisches Museum, Universität Zürich, Zürich.

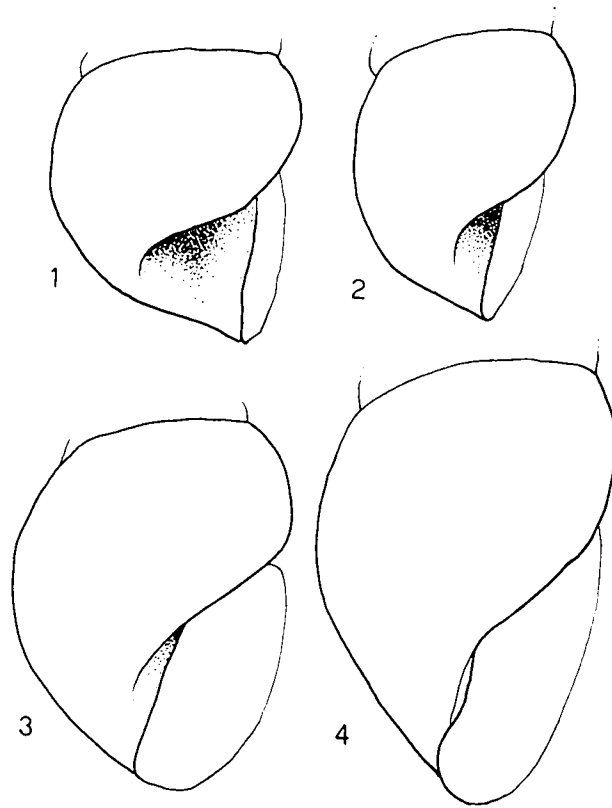
The status of the type species is abbreviated as follows: HT, holotype; LT, lectotype; NT, neotype; PT, paratype(s); ST, syntype(s).

The following abbreviations are used to refer to parts of the anatomy: EP, epiphallus; FL, flagellum; P, penis; PS, penis sheath.

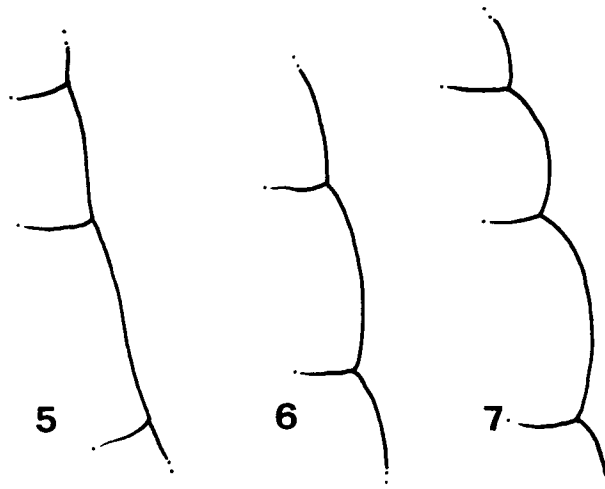
IV. TERMINOLOGY AND CHARACTER ANALYSIS

The terminology of the shell morphology is largely in accordance with that used by Pilsbry (1895-1902). Several morphological structures are nevertheless defined by figures, not only to facilitate the descriptions included in this paper, but also to provide a reference for future work.

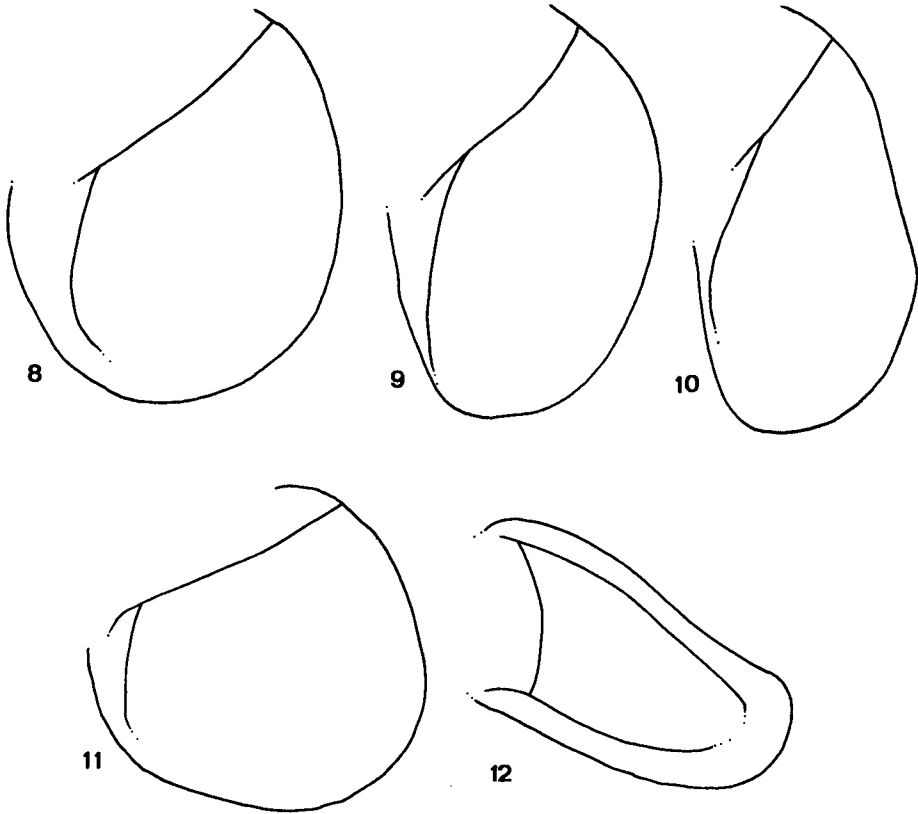
The shell shape may be ovate (fig. 71), elongate-ovate (fig. 111), ovate-conical (fig. 161), conical, globose (fig. 166), turrated (fig. 126), or fusiform (fig. 81). The umbilicus may be perforate, narrowly perforate, rimate or



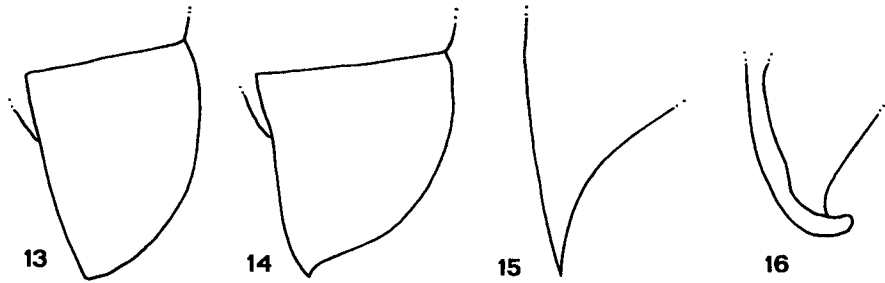
Figs. 1-4. The umbilicus is wide (1), narrow (2), rimate (3) or imperforate (4).



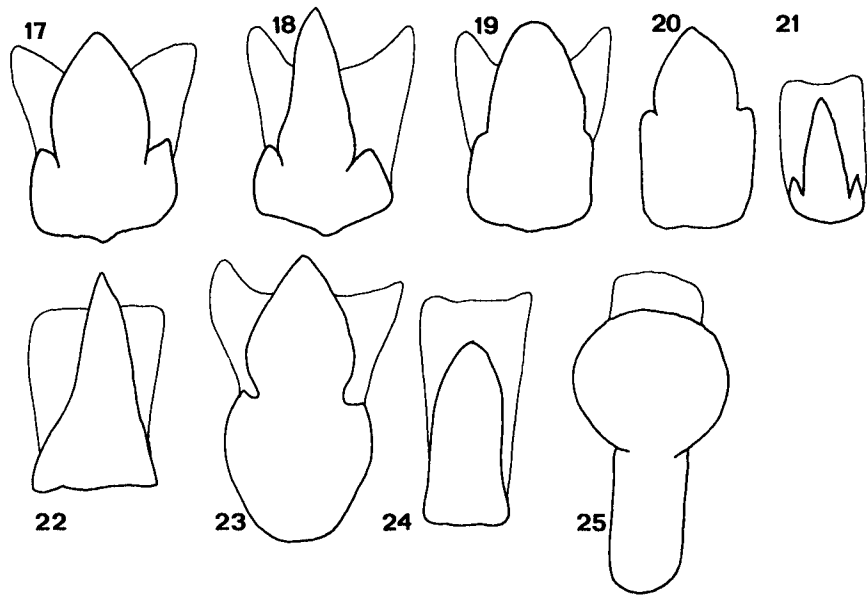
Figs. 5-7. The whorls are flat (5), slightly convex (6) or convex (7).



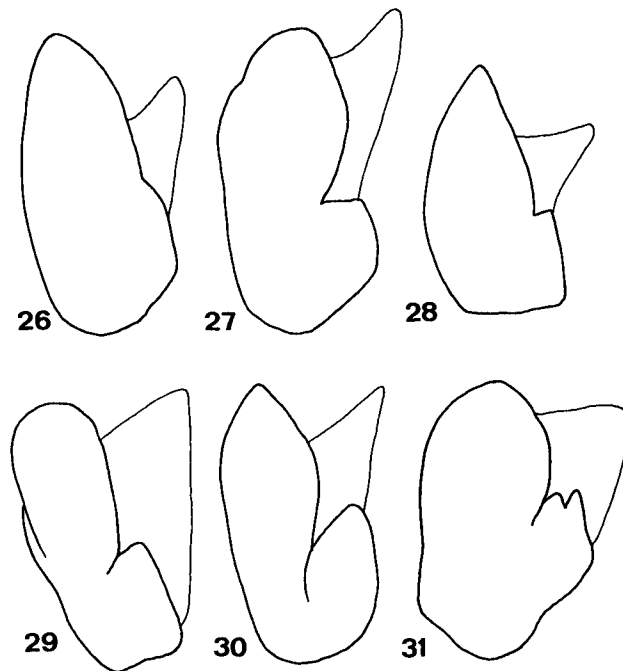
Figs. 8-12. The aperture is ovate (8), subovate (9), elongate-ovate (10), subcircular (11) or obliquely truncate-ovate (12).



Figs. 13-16. The peristome is simple (13), narrowly expanded (14), expanded (15) or reflexed (16).



Figs. 17-25. Different types of central radula teeth; respectively C-1, C-2, C-3, C-4, C-5, C-6, C-7, C-8 and C-9 (see Breure, 1978b, for descriptions).



Figs. 26-31. Different types of lateral radula teeth; respectively L-1, L-2, L-3, L-4, L-5 and L-6 (see Breure, 1978b, for descriptions).

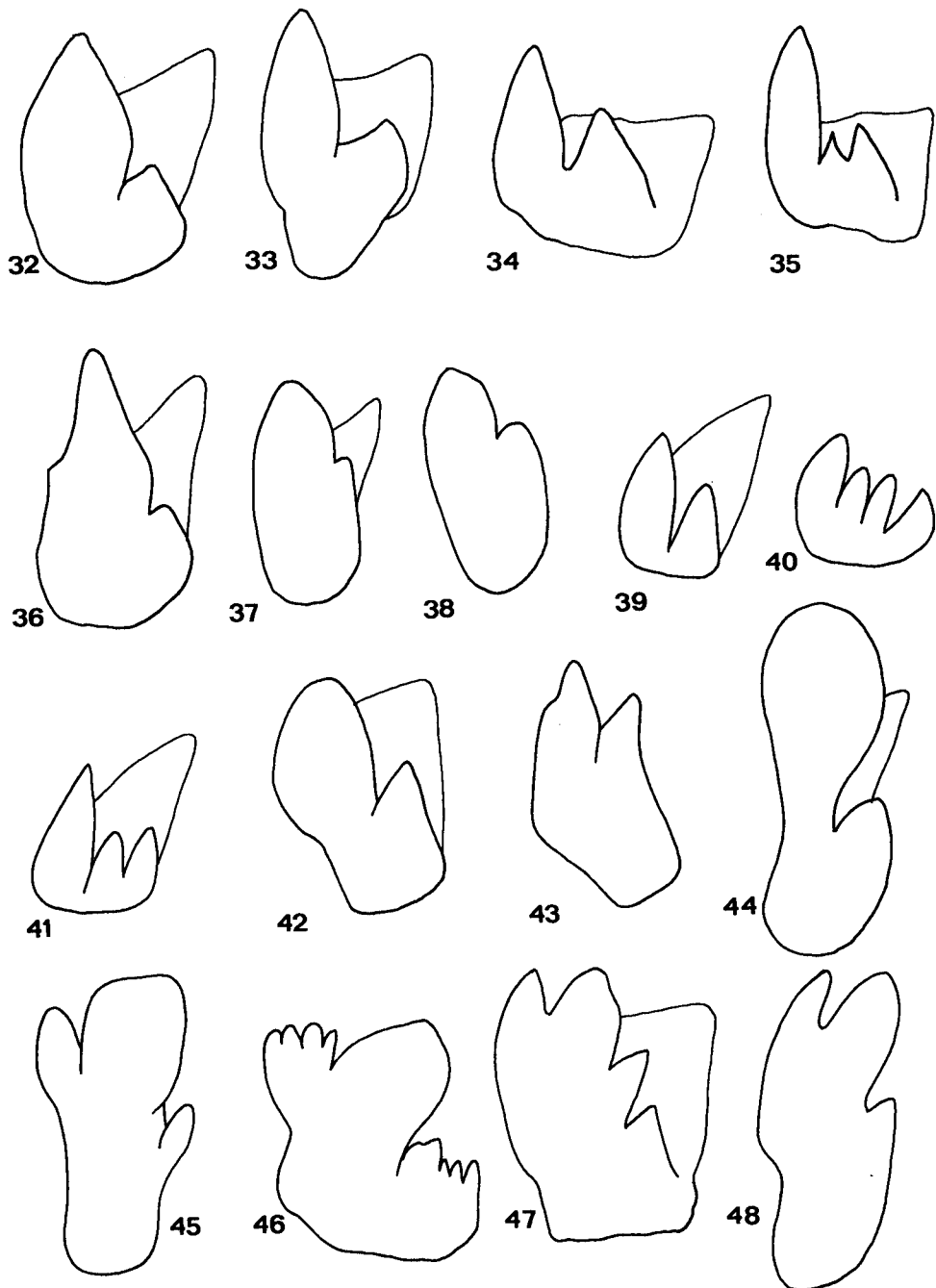
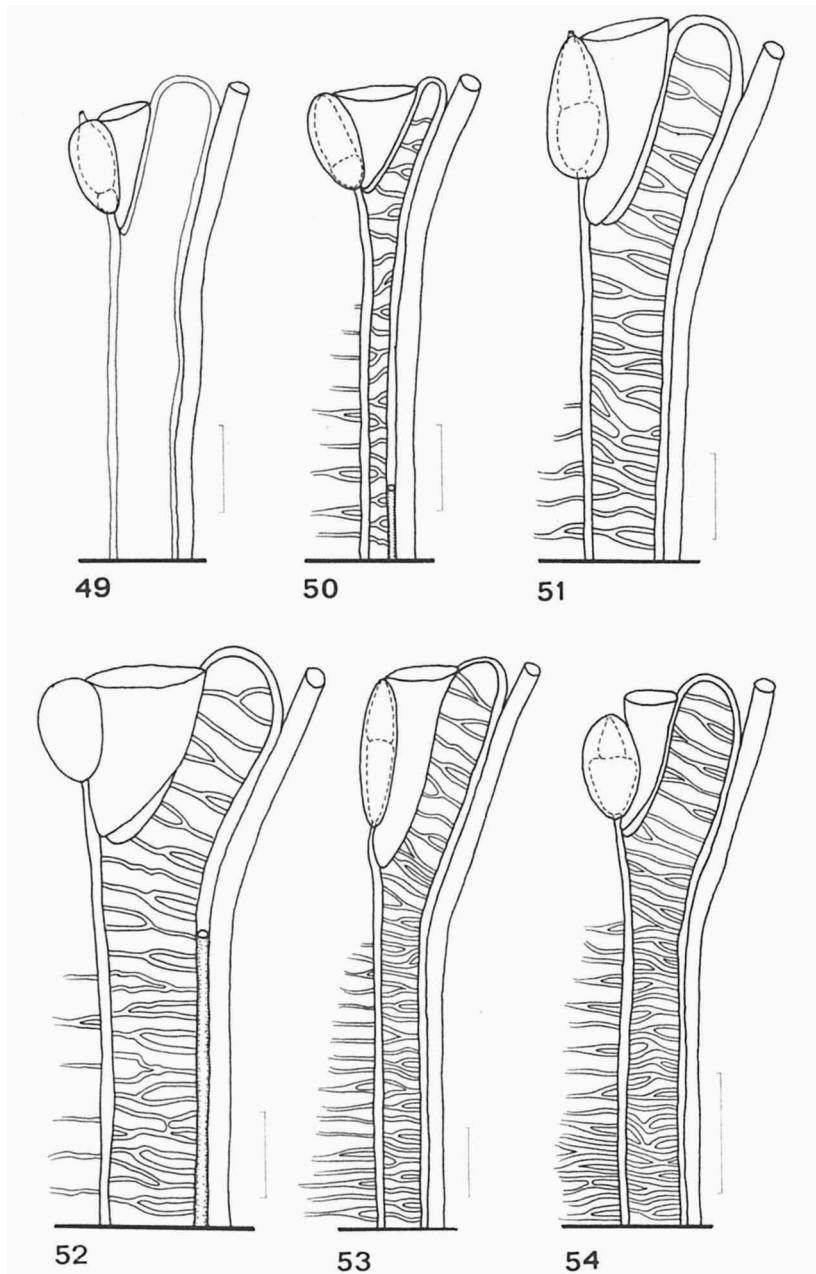
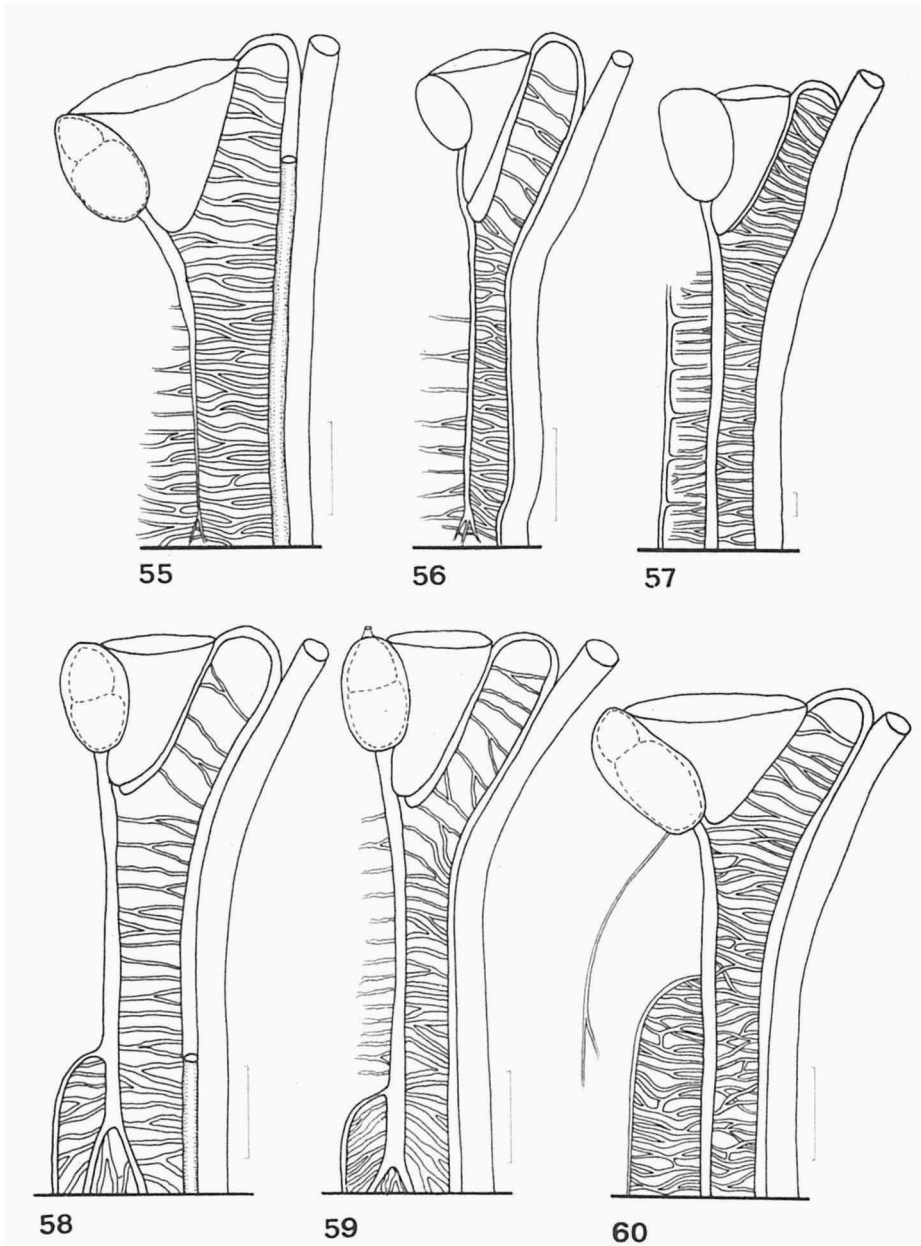


Fig. 32-48. Different types of lateromarginal radula teeth; respectively LM-1, LM-2, LM-3, LM-4, LM-5, LM-6, LM-7, LM-8, LM-9 (2x), LM-10, LM-11, LM-12, LM-13, LM-14, LM-15 and LM-16 (see Breure, 1978b, for descriptions).



Figs. 49-54. Pallial organs. Fig. 49. *Oxychona blanchetiana* (Moricand). Fig. 50. *Bostryx hamiltoni* (Reeve). Fig. 51. *Rhinus ciliatus* (Gould). Fig. 52. *Discoleus aguirrei* (Döring). Fig. 53. *Bulimulus jujuyensis* Holmberg. Fig. 54. *Leiostracus (Pseudoxychona) pileiformis* (Moricand). Scale = 5 mm.



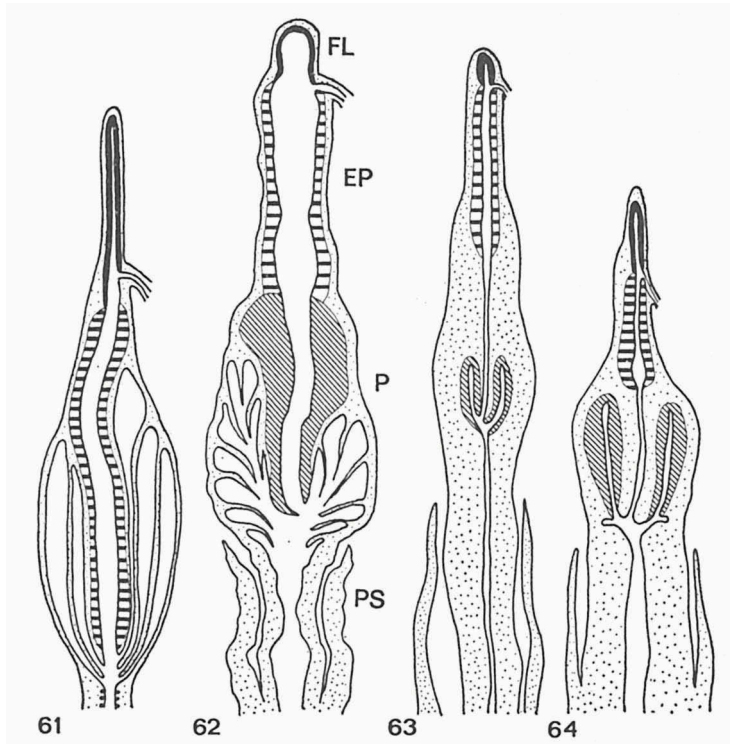
Figs. 55-60. Pallial organs. Fig. 55. *Plectostylus coquimbensis* (Broderip). Fig. 56. *Bostryx modestus* (Broderip). Fig. 57. *Stenostylus zilchi* Weyrauch. Fig. 58. *Scutalus (Kuschelenia) culmineus* (d'Orbigny). Fig. 59. *Bostryx virgultorum* (Morelet). Fig. 60. *Plekocheilus (Aeropictus) dissimulans* (Preston). Scale = 5 mm.

imperforate (figs. 1-4). The protoconch may be smooth, granulate, or sculptured with axial wrinkles, axial riblets, spiral lines, or is grated or pit-reticulate (pls. 1-3). The whorls are slightly convex, convex or flat (figs. 5-7). The aperture is, e.g., subovate, ovate, elongate-ovate, subcircular, truncate-ovate (figs. 8-12). The peristome is simple, narrowly expanded, expanded or reflexed (figs. 13-16). In side view the peristome may be parallel to the length axis of the shell or forming an angle ('skewed') of ca. 45 degrees at the utmost.

TABLE 2
Variation in pallial organs in Bulimulinae

	Adrectal ureter closed	Adrectal ureter partly open
Veins weakly to moderately developed	<i>Bostryx</i> , <i>Naesiotus</i> , <i>Scutalus</i> (<i>Suniellus</i>), <i>Neopetraeus</i> , <i>Oxychona</i> , <i>Leiostracus</i> , <i>Rhinus</i> , <i>Simpulopsis</i>	<i>Bostryx</i> , <i>Scutalus</i> (<i>Kuschelenia</i>), <i>Discoleus</i> , <i>Drymaeus</i> , <i>Neopetraeus</i>
Veins strongly developed	<i>Bostryx</i> , <i>Thaumastus</i> (<i>Thaumastiella</i>), <i>Bulimulus</i> , <i>Rabdatus</i> , <i>Scutalus</i> (<i>Scutalus</i>), <i>S.</i> (<i>Suniellus</i>), <i>Drymaeus</i> , <i>Newboldius</i> , <i>Leiostracus</i> (<i>Pseudoxychona</i>)	<i>Bostryx</i> , <i>Scutalus</i> (<i>Vermiculatus</i>), <i>Berendtia</i> , <i>Drymaeus</i> , <i>Plectostylus</i>
Veins strongly developed, anteriorly deltoid ramified + parallel veins	<i>Plekocheilus</i> , <i>Thaumastus</i> (<i>Thaumastus</i>), <i>T.</i> (<i>Paeniscutalus</i>), <i>T.</i> (<i>Scholvienea</i>), <i>Bostryx</i> , <i>Bulimulus</i> , <i>Scutalus</i> (<i>Scutalus</i>), <i>Bothriembryon</i> (<i>Bothriembryon</i>), <i>Otostomus</i> , <i>Stenostylus</i> , <i>Auris</i>	<i>Scutalus</i> (<i>Vermiculatus</i>), <i>S.</i> (<i>Kuschelenia</i>), <i>Discoleus</i>

The structure of the radula has been described by Breure (1978b) and Breure & Eskens (in preparation). See also figs. 17-48. Two, more or less independent, trends may be observed, viz. (1) the transverse rows vary from straight (in most species; RR 1) to V-shaped (in a limited number of species; RR 2) and (2) the (central) teeth are tricuspid (normally; RT 1) or moncuspid (in some groups; RT 2). Some authors, e.g. Solem (1974), have discussed the evolutionary trends in the structure of the radula and they agree that the occurrence of V-shaped transverse rows and moncuspid (central) teeth is rather exceptional (and may be regarded as apomorphic character states; see part VII). In most groups the teeth in the central part



Figs. 61-64. Schematic reconstruction of the penial complex. Fig. 61. *Bulimulus guadalupensis* (Bruguière). Fig. 62. *Rabdotus mooreanus* (Pfeiffer). Fig. 63. *Bostryx ignobilis* (Philippi). Fig. 64. *Bostryx tumidulus* (Pfeiffer).

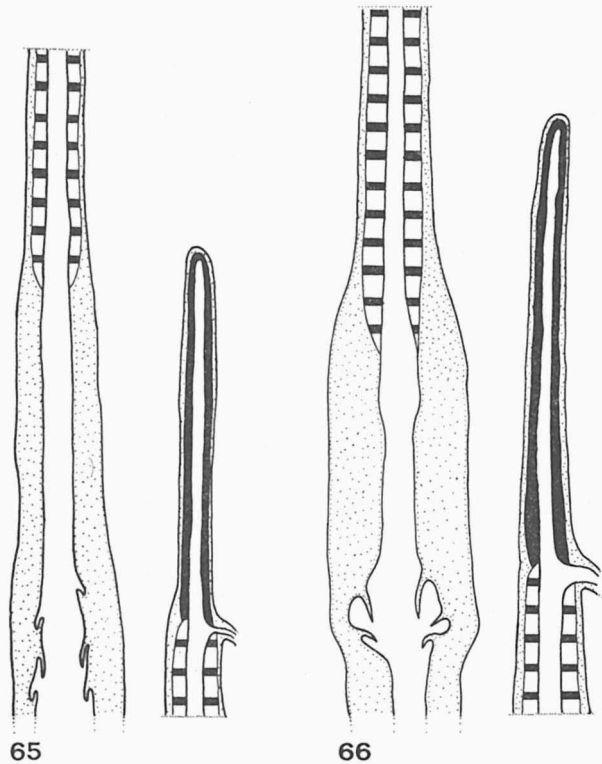
of the radula have 'supporting denticles' (RS 2; see Solem, 1972, for details on functioning). In some genera, however, this structure is absent (RS 1) [see pl. 3].

The variation in the pallial organs mainly concern the shape of the nephridium, the length of the pericard, the development of the veins and the structure of the adrectal ureter. The variation is shown in figs. 49-60 and summarized in table 2.

Compared with most other Stylommatophora the genitalia ¹⁾ of Bulimulidae are relatively simple. There are no appendages (at least not in the Bulimulinae) and the external morphological variation is limited to differences in relative length and thickness. The internal morphology and histology of the genitalia (especially the penis), however, offer a useful additional variation.

1) Terminology in accordance with Bayne (1973).

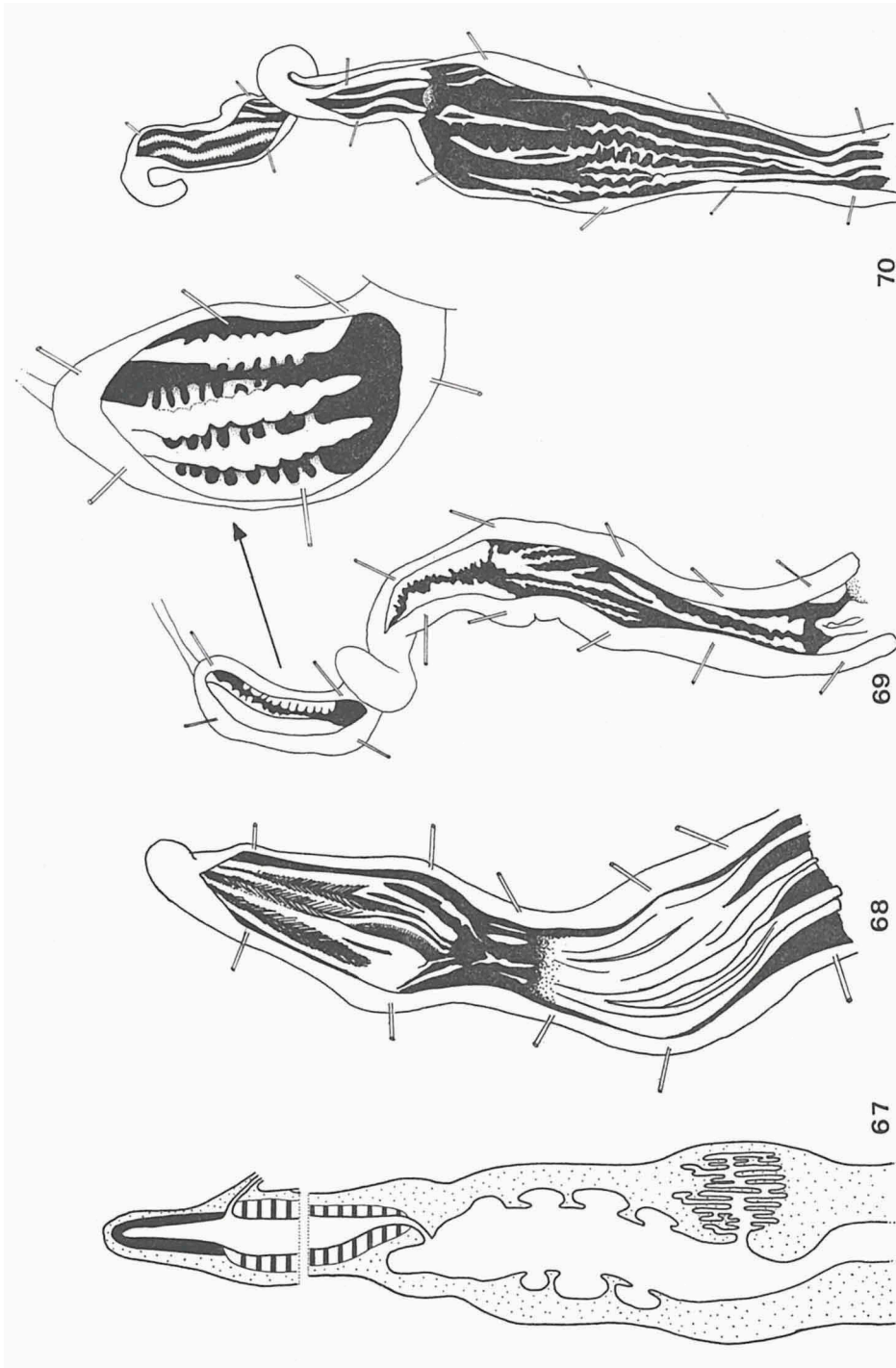
The penis may be with a proximal sheath (PS 1), of variable length, or without such a sheath (PS 2). The sheath may cover 1/3-1/15 of the length of the phallus (= penis + epiphallus + flagellum). In *Discoleus* the penis has a 'pseudo-sheath' over its entire length (PW 2). Internally the penis lumen may be simple (PL 1), constricted in its median part (PL 2) or with



Figs. 65-66. Schematic reconstruction of penial complex. Fig. 65. *Bothriembryon* (*Bothriembryon*) *indutus* (Menke). Fig. 66. *Plectostylus coquimbensis* (Broderip).

tubes parallel to the main lumen/pouches/parallel tubes /circular gland (PL 3; figs. 61-70). In several groups the subepithelial tissue in the distal part of the penis is made up of large, rounded (glandular) cells (PD 2). The epithelium in the penis is made up by one (P 1) or two different types of glandular cells (P 2). Details on these character states may be found in Breure (1978b).

The epiphallus and flagellum are rather constant in both external and internal morphology; in several groups the epiphallus intrudes the distal part of the penis (EP 2), while in some species the flagellum is embedded in



Figs. 67-70. Schematic reconstruction (67) and dissection of penial complex. Fig. 67. *Plekocheilus (Plekocheilus) blainvillaeus loveni* (Pfeiffer). Fig. 68. *Plekocheilus (Plekocheilus) elacodes* (Pfeiffer). Fig. 69. *Plekocheilus (Plekocheilus) delicatus* (Pilsbry). Fig. 70. *Plekocheilus (Plekocheilus) aurissilem* (Born).

muscular tissue (FL 2). Internally, the curved longitudinal fold in the flagellum is double-curved in some groups (CF 2). The retractor muscle is normally attached distally (RM 1), but in some groups subdistally or at the transition between flagellum and epiphallus (RM 2).

TABLE 3

Variation in character states in Bulimulinae (genera for which no anatomical data are available have been omitted). Abbreviations: P, penis epithelium; PL, penis lumen; RM, retractor muscle; PS, penis sheath; PD, distal part of penis; EP, transition epiphallus-penis; FL, flagellum; CF, curved fold in flagellum; SD, spermathecal duct; SA, spermathecal appendix; S, spermo-viduct; PW, penis wall; RR, radula rows; RT, radula teeth; RS, supporting denticles-system in radula. 1 = plesiomorphous; 2, 3 = apomorphous. See text and Table 4.

	P	PL	RM	PS	PD	EP	FL	CF	SD	SA	S	PW	RR	RT	RS
<i>P. (Plekocheilus)</i>	2	1/3	1	2	1	1	1	1	1	1	2	1	1	2	2
<i>P. (Eudolichotis)</i>	1	1	1	2	1	1	1	1	1	1	2	1	1	2	2
<i>P. (Eurytus)</i>	1	1	1	2	1	1	1	1	1	1	2	1	1	2	2
<i>P. (Aeropiectus)</i>	1	1	1	1	1	1	1	1	1	1	2	1	1	2	2
<i>Auris</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>T. (Thaumastus)</i>	2	3	1	1	1	2	1	1	1	1	2	1	1	1	2
<i>T. (Scholvienia)</i>	1	2	1	1	1	2	1	1	1	1	2	1	1	1	2
<i>T. (Quechua)</i>	2	3	1	2	1	2	1	1	1	1	2	1	1	2	2
<i>T. (Thaumastieilla)</i>	-	-	1	1	1	1	1	1	1	1	2	1	1	1	2
<i>T. (Paeniscutalus)</i>	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2
<i>Bostryx</i>	2	3	1	1	1	1	1	1	1	1	2	1	1	1/2	2
<i>Bulimulus</i>	2	3	1	1	1/2	2	1	1	1	1	2	1	1	1	2
<i>Naesiotos</i>	2	3	1	1	1	1/2	1	1	1	1	2	1	1	1	2
<i>Rabdotus</i>	2	3	1	1	1	1	1	1	1	1	2	1	1	1	2
<i>Berendtia</i>	-	-	1	1	1	-	1	1	1	1	2	1	1	1	2
<i>Spartocentrum</i>	-	-	1	1	1	-	1	1	1	1	2	1	1	1	2
<i>S. (Scutalus)</i>	2	2	1	1	1	1	1	1	1	1	2	1	1	2	2
<i>S. (Vermiculatus)</i>	2	2	1	1	2	1	1	1	1	1	2	1	1	1	2
<i>S. (Kuschelenia)</i>	2	2	1	1	2	2	1	2	1	2	1	1	1	1	2
<i>S. (Suriellus)</i>	1	1	1	2	2	2	1	1	1	1	2	1	1	1	2
<i>Plectostylus</i>	1	1	1	2	1	1	1	1	1	1	2	1	1	1	2
<i>Discoleus</i>	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2
<i>B. (Bothriembryon)</i>	1	1	1	2	1	1	1	1	1	1	2	1	1	1	2
<i>B. (Tasmanembryon)</i>	1	1	1	2	1	1	1	1	2	1	2	1	1	1	2
<i>Otostomus</i>	1	1	1	1	1	1	1	2	1	1	2	1	2	2	1
<i>Oxychona</i>	1	-	1	1	-	-	-	2	1	1	2	1	2	2	1
<i>Cochlorina</i>	-	-	1	1	1	1	1	2	1	1	2	1	2	2	1
<i>Newboldius</i>	1	1	1	1	-	1	1	2	1	1	2	1	-	2	1
<i>Neopetraeus</i>	1	1	1	1	1	1	1	2	1	1	2	1	1	2	1
<i>Stenostylus</i>	1	2	1	1	2	1	1	1	1	1	2	1	1	2	2
<i>D. (Drymaeus)</i>	1/2	2	1	1/2	2	1	1	1	1	1	2	1	1	1/2	1/2
<i>D. (Mesembrinus)</i>	1	2	1	1/2	2	1	1	1	2	1	2	1	2	2	1/2
<i>Sphaeroconcha</i>	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1
<i>Simpulopsis</i>	2	2	1/2	2	1	2	1	1	1	2	2	1	2	1/2	1/2
<i>L. (Leiostracus)</i>	1	1	2	2	1	2	1	1	1	2	2	1	1	2	2
<i>L. (Pseudoxychona)</i>	1	-	2	2	1	-	1	1	1	2	2	1	1	2	2
<i>Rhinus</i>	1	1	1	2	1	2	1	1	1	2	2	1	2	2	2

The spermathecal duct is usually more or less subcylindrical and as long as the spermoviduct (SD 1). In some groups this duct is reduced in length (SD 2). In other groups the proximal part of the duct is relatively stout, with a spermathecal appendix (SA 2) and a narrow distal part of the duct.

The vagina, oviduct and spermoviduct are all rather constant in both external and internal morphology. There is only one genus in which the glandular folds are arranged parallel to the length of the spermoviduct (S 1); in all other genera the glandular folds are perpendicular to the length axis (S 2). The differences that probably do exist in the internal morphology and histology of the spermoviduct can only be studied with specialized histochemical techniques, for which our material was not suitable.

This paper only presents figures of the genitalia of species of *Auris* and *Leiostracus* (*Pseudoxychona*), as these taxa were not treated in my previous papers. Details on the anatomy of species of other genera may be found in Breure (1975e, 1976d, 1977a, 1978b) and Breure & Coppo (1978).

The variation of the different character states is summarized in Table 3, as far as data are available.

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VI. SYSTEMATICS

In this part a systematic review is presented of the Bulimulinae. Each genus is briefly described and data are added on its synonymy, distribution and ecology. The main publications in which further data on the genus and its species may be found are also indicated. For each (sub)genus a list of the taxa belonging to that (sub)genus is given. In this list the type localities, as given in the original publication, are stated and data on type material are given, if available. Criteria to include taxa in these lists are: (a) type material seen; (b) (reputedly) correctly identified material seen; (c) on authority of another author; (d) on account of the original description; (e) on account of a redescription. At the end of this part a list of nomina inquirenda is given, as well as some data on fossil species and a list of taxa that are now excluded from the Bulimulinae.

Key to the genera of Bulimulinae

- | | |
|--|----------------------|
| 1a. Australian species | <i>Bothriembryon</i> |
| b. Neotropical species | 2 |
| 2a. Protoconch smooth | 3 |
| b. Protoconch sculptured | 5 |
| 3a. Shell small (height less than 40 mm) | <i>Bostryx</i> |
| b. Shell large (height more than 40 mm) | 4 |
| 4a. Shell surface granulate or malleate; aperture elongate-ovate — Colombia, Venezuela | <i>Dryptus</i> |
| b. Shell surface plicate, folded or granulate; aperture (broadly) ovate — Brazil | <i>Auris</i> |
| 5a. Protoconch granulate or pit-reticulate | 6 |
| b. Protoconch with axial and/or spiral components | 10 |
| 6a. Protoconch granulate | <i>Plekocheilus</i> |
| b. Protoconch pit-reticulate | 7 |
| 7a. Peristome simple | 8 |
| b. Peristome expanded | <i>Scutalus</i> |

- 8a. Shell elongate-ovate, relatively large *Thaumastus*
 b. Shell globose, relatively small *Sphaeroconcha*
- 9a. Axial and spiral components of protoconch sculpture equally strong 10
 b. Either axial or spiral components of protoconch sculpture dominating
 or present 16
- 10a. Axial components consisting of wrinkles *Simpulopsis*
 b. Axial components consisting of straight riblets 11
- 11a. Shell solid, large (ca. 70 mm high) *Newboldius*
 b. Shell (rather) thin, small (up to ca. 50 mm high) 12
- 12a. Shell (broadly) conical 13
 b. Shell more or less elongate-ovate 14
- 13a. Shell broadly conical, imperforate; aperture skewed,
 triangular *Oxychona*
 b. Shell conical, rimate; aperture elongate-ovate to triangular
 *Cochlorina*
- 14a. Aperture narrowed by a callous flange at the inner side of the
 peristome *Otostomus*
 b. Aperture not narrowed by a flange 15
- 15a. Inside of aperture with a pearly lustre; species living above
 3000 m *Stenostylus*
 b. Inside of aperture lustreless; species living below 3000 m . *Drymaeus*
- 16a. Both axial and spiral components in protoconch sculpture present
 and axial ones dominating 17
 b. Either axial or spiral components in protoconch sculpture present 22
- 17a. Axial components consisting of riblets 18
 b. Axial components consisting of wrinkles 20
- 18a. Protoconch more or less angled above; peristome broadly expanded
 *Neopetraeus*
 b. Protoconch regularly rounded; peristome not to weakly expanded 19
- 19a. Interstices on protoconch as broad as the riblets, spiral striae nearly
 as strong as axial riblets *Llaucanianus*
 b. Interstices on protoconch 1-5 times as broad as the riblets, spiral
 lines relatively weak *Naesiotus*
- 20a. Shell ovate-conical; last whorl more or less keeled . . . *Leiostracus*
 b. Shell elongate-ovate to globose; last whorl rounded 21
- 21a. Last whorl prominent; interstices on protoconch as broad as
 wrinkles *Simpulopsis*
 b. Last whorl not prominent; interstices on protoconch broader than
 the irregularly spaced wrinkles *Bostryx*
- 22a. Protoconch sculpture with only axial components 23

- b. Protoconch sculpture with only spiral components 30
- 23a. Axial components consisting of wrinkles 24
 - b. Axial components consisting of riblets *Rabdotus*
- 24a. Peristome broadly expanded and reflexed 25
 - b. Peristome simple or hardly expanded 26
- 25a. Axial wrinkles on protoconch undulating; last whorl prominent
. *Plekocheilus*
 - b. Axial wrinkles on protoconch zigzag; last whorl not prominent
. *Rhinus*
- 26a. Wrinkles on protoconch rather weakly developed, regular; shell rather
small (less than 50 mm) 27
 - b. Wrinkles rather strong, regular or broken into oblong, shorter wrinkles;
shell rather large (usually more than 50 mm) *Thaumastus*
- 27a. Shell uniformly coloured 28
 - b. Shell with axial streaks and/or spiral bands or variegated 29
- 28a. Shell unicoloured (whitish to brown); species living below 500 m,
mostly outside the Andes *Bulimulus*
 - b. Shell usually with a colour pattern of spots and/or spiral bands; species
living above 500 m in the Andes *Scutalus*
- 29a. Central teeth of radula monocuspid; species living below ca. 500 m in
North Chile *Plectostylus*
 - b. Central teeth of radula tricuspid; species living above 500 m in Andes
of Argentina, Bolivia, Peru and Ecuador *Scutalus*
- 30a. Protoconch with numerous spiral lines 31
 - b. Protoconch with few spiral lines *Lopesianus*
- 31a. Central teeth of radula tricuspid 32
 - b. Central teeth of radula monocuspid *Leiostracus*
- 32a. Penis with a sheath *Bostryx*
 - b. Penis without a sheath *Discoleus*

Plekocheilus Guilding, 1828

- Caprella* Guilding, 1824: 341. Type species by monotypy: *Caprella undulata* Guilding
[not *Caprella* Lamarck, 1801].
- Plekocheilus* Guilding, 1828a: 532. Type species by monotypy: *Caprella undulata* Guilding.
Plecocheilus Swainson, 1833: explanation pl. 103 [emendation].
- Pelekocheilus* Beck, 1837: 54. Type species by monotypy: *Voluta aurissileni* Born.
- Plecochilus* Agassiz, 1846: 297 [emendation].
- Pelecocheilus* Albers, 1850: 151 [emendation].
- Pelecychilus* Albers, 1860: 188. Type species by subsequent designation (Pilsbry, 1896):
Voluta aurissileni Born.
- Pleocheilus* M. E. Gray, 1874: pl. 74* fig. 1. Type species by monotypy: *Caprella*
undulata Guilding.

Plecocochilus Paetel, 1889: 207 [emendation].

Plechocheilus Leme, 1973: 307 [emendation].

Description. — Shell (elongate-)ovate; rimate to imperforate; thin to solid. Colour whitish to brownish, with axial zigzag streaks or oblique spiral series of spots. Surface smooth or malleate, in several species with cuticular cavities filled with air. Protoconch granulate or with axial wrinkles. Whorls slightly convex; suture hardly to well impressed, descending in front. Aperture sub- to elongate-ovate. Peristome thickened and more or less expanded and reflexed. Columella in several species with a fold.

The central teeth of the radula are monocuspid, with triangular to ovate mesocones and hardly developed ectocones. The lateromarginal teeth are (1) bicuspid with acute to truncate, spatulate mesocones and acute, ovate to deltoid ectocones; or (2) bicuspid, shifted, with rather blunt spatulate to elongate mesocones and acute, triangular to deltoid ectocones, which may be bifid in the outermost teeth; or (3) tricuspid, shifted, with rather blunt, ovate mesocones, acute elongate-ovate endocones and acute deltoid ectocones. Half-row formula: C/1 + L x/1 + M y/2 (x = 1-6, y = 38-106) or C/1 + LM x/2 (x = 50-59).

The pericard, which is strongly transversally disposed, is as long as the nephridium, which is broadly triangular. The main pulmonary vein is prominent, the side veins are strongly developed, especially at the anterior end where the veins are ramified and where one or two short veins are parallel to the main pulmonary vein. The adrectal ureter is closed.

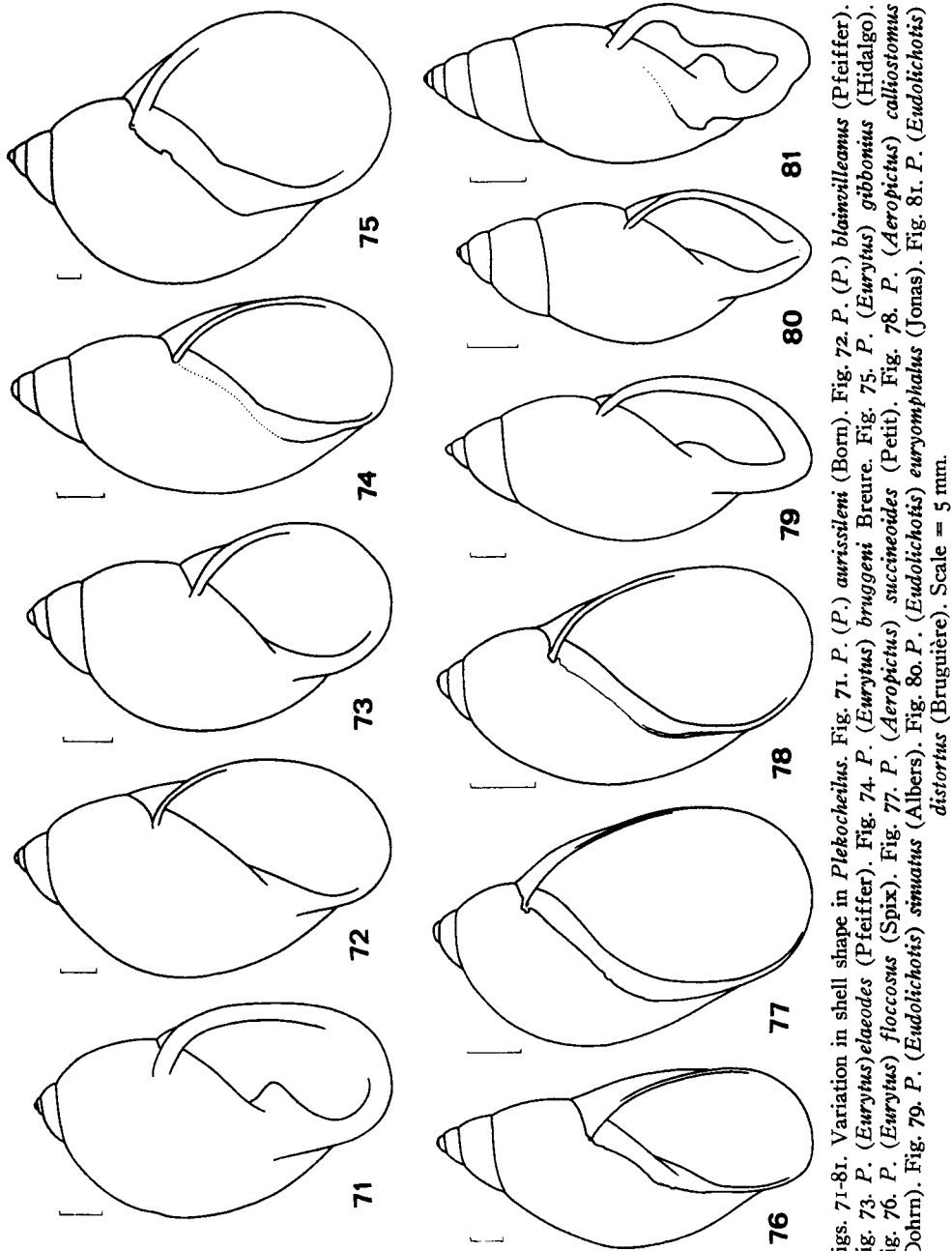
Penis with a proximal penis sheath (in *Eurytus* and *Aeropictus*) or without (in *Plekocheilus* s.str., *Eurytus* and *Eudolichotis*). The penis is more or less subcylindrical, in several species proximally swollen, and passing into the epiphallus without external differentiation. The flagellum is slender and rather long, but in some species it is short and stout (especially in *Aeropictus* and *Eudolichotis*). The vagina is relatively short. The spermathecal duct is more or less tapering, with an elongate-globose spermatheca at the distal end.

Distribution. — West Indies, Venezuela, Brazil, Bolivia, Peru, Ecuador, Colombia, Panama.

Relationships. — See page 147 for a discussion of the phylogenetic relationships of this genus.

Remarks. — The differences between the subgenera are but slight and the division of *Plekocheilus* into five subgenera is only tentative. Especially the status of *Sparnotion* Pilsbry, 1944, is uncertain.

Bibliography. — The main publications on this genus are: Breure, 1978b; Haas, 1955a; Oberwimmer, 1931; Pilsbry, 1895, 1939b; Solem, 1960; Weyrauch, 1967b.



Figs. 71-81. Variation in shell shape in *Plekocheilus*. Fig. 71. *P. (P.) aurissilemi* (Born). Fig. 72. *P. (P.) blasivillecomus* (Pfeiffer). Fig. 73. *P. (Eurytus) elaeodes* (Pfeiffer). Fig. 74. *P. (Eurytus) bruggeni* Breure. Fig. 75. *P. (Eurytus) gibbomus* (Hidalgo). Fig. 76. *P. (Eurytus) floccosus* (Spix). Fig. 77. *P. (Aeropictus) succineoides* (Petit). Fig. 78. *P. (Aeropictus) calliostomus* (Dohrn). Fig. 79. *P. (Eudolichotis) sinuatus* (Albers). Fig. 80. *P. (Eudolichotis) euryomphalus* (Jonas). Fig. 81. *P. (Eudolichotis) distortus* (Bruguère). Scale = 5 mm.

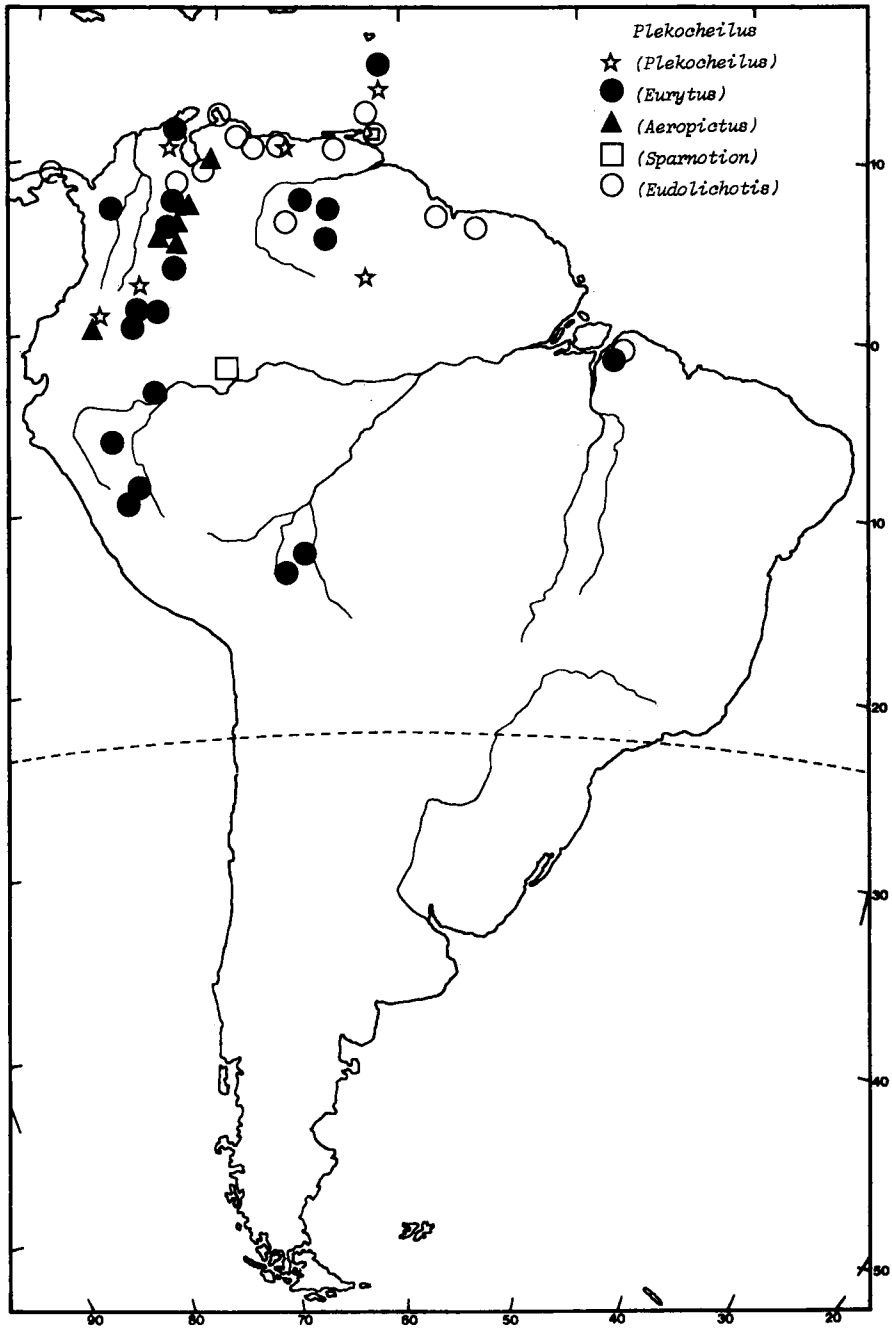


Fig. 82. Distribution of *Plekocheilus*.

Key to the subgenera of *Plekocheilus*

- 1a. Shell surface with cuticular cavities filled with air 2
 b. Shell surface without these cuticular cavities 3
 2a. Shell fusiform; aperture narrowly elongate-ovate, its basal margin produced *Plekocheilus (Sparnotion)*
 b. Shell elongate-ovate; aperture broadly elongate-ovate, its basal margin rounded *Plekocheilus (Aeropictus)*
 3a. Shell elongate-ovate to fusiform; surface smooth, granulate or with spiral series of puckered bands 4
 b. Shell (elongate-)globose; surface malleate
 *Plekocheilus (Plekocheilus)*
 4a. Aperture subovate, its basal margin rounded; columella simple or with a crescent-shaped channel *Plekocheilus (Eurytus)*
 b. Aperture narrowly elongate-ovate, its basal margin (rounded or) produced; columella with a fold at the basal-parietal margin
 *Plekocheilus (Eudolichotis)*

***Plekocheilus (Plekocheilus)* Guilding, 1828**

Description. — Shell (elongate-)globose; rimate; (rather) solid. Colour light (reddish-)brown (with greenish hues) and darker axial zigzag streaks. Surface with incrassate growth striae and malleation. Protoconch granulate. Whorls slightly convex; suture well impressed. Aperture subovate. Peristome expanded and reflexed. Columella with a fold at the parietal-basal margin.

Distribution. — West Indies (St. Vincent, Barbados), Venezuela, ?French Guyana, Ecuador, Colombia.

Ecology. — The species live in montane and cloud forest, presumably in leaf litter. The vertical distribution is ca. 900-2250 m.

Taxa. — The following taxa are placed in this subgenus:

alticola, *Plekocheilus (Plekocheilus) fulminans*, Haas, 1955a: 381, fig. 81 (Venezuela, [Estado Bolívar] Chimantá-massif, Torono-tepui, on the slopes bordering Caño Mojado, 2250 m) [HT FMNH 52442].

appuni, *Bulimus*, Dunker, 1875b: 220, pl. 6 figs. 1-2 ([Colombia] Sierra Nevada di Sta. Martha).

aurisilemi, *Voluta*, Born, 1780: 212, pl. 9 figs. 3-4 [no type locality given; HT NMW].

bellulus, *Bulimus*, Jonas, 1844: 36 (in vicinitate cavernae Guacharo, juxta vicum Caripe

Provinciae Cumana, Reipublicae Venezuela).

blainvilleanus, *Bulimus*, Pfeiffer, 1848a: 230 (Zaji, province of Merida, New Granada).

caprella, *Auricula*, Lamarck, 1822: 140 [indication; no type locality given].

cardinalis, *Bulimus*, Pfeiffer, 1853d: 316 ([Ecuador] Quito).

chrevotini, *Auricula*, Chenu, 1847: 163, fig. 531 [no type locality given].

fulminans, *Bulimus*, Nyst, 1843: 261, pl. 7 fig. 1 (la Colombie [sic, Venezuela], dans la

province de Cumana).

- linterae*, *Bulimus fulminans*, Sowerby, 1890: 582 (Br. Guyana, Mount Roraima) [LT BMNH 1889.4.25.1].
- loveni*, *Bulimus*, Pfeiffer, 1848a: 229 (New Granada, Colony of Tovar) (LT BMNH 1975285).
- lugubris*, *Bulimus*, Dunker, 1882: 378, pl. 11 figs. 1-2 (Pasto, Columbiae australis).
- plectostylus*, *Bulimus*, Pfeiffer, 1848a: 230 (New Granada, Prov. Merida, Chachopo) [LT BMNH 1975287].
- sileni*, *Plekocheilus*, Beck, 1837: 55 [emendation for *aurissileni* Born].
- speciosus*, *Bulimus*, Pfeiffer, 1855c: 290 ([Colombia] Sierra Nevada de S. Marta) [LT BMNH 1975300].
- undulatum*, *Carychium*, Leach, 1814: 84, pl. 37 [no type locality given].

Plekocheilus (Eurytus) Albers, 1850

Eurytus, Albers, 1850: 169. Type species by subsequent designation (Albers, 1860): *Helix pentadina* d'Orbigny.

Description. — Shell (elongate-)ovate; perforate to imperforate; thin to solid. Colour light to dark brown, uniformly coloured or with oblique spiral series of spots. Surface smooth, granulate or with spiral series of short lines and spirally arranged puckered bands. Protoconch granulate. Whorls slightly convex; suture well impressed. Aperture subovate (to elongate-ovate). Peristome slightly thickened and not to narrowly expanded. Columella simple or with a crescent-shaped channel.

Distribution. — West Indies (St. Lucia, St. Vincent), Venezuela, Brazil (Pará), Bolivia, Peru, Ecuador, Colombia.

Ecology. — Two species groups may be distinguished. The species of one group, including e.g. *Plekocheilus floccosus* (Spix), live mainly in rain forest at altitudes of up to ca. 1000 m, whereas species of the other group, including e.g. *Plekocheilus glandiformis* (Lea), live mainly in montane forest at ca. 1250-3500 m.

Taxa. — The following taxa are included in this subgenus:

- ameghinoi*, *Plekocheilus (Eurytus)*, Parodiz, 1962: 451 (New name for *Bulimus guildingi* Dohrn, 1875, not Pfeiffer, 1842).
- ampullaroides*, *Bulimus*, Mousson, 1873: 8 ([Colombia] Bogota) [LT ZMUZ].
- apolinari*, *Plectostylus*, Pilsbry, 1935: 83, pl. 6 figs. 1-2 (Colombia, region of Villa Vicencio) [HT ANSP 164566a].
- aristaceus*, *Bulimus*, Crosse, 1869a: 185 (Quito, reipublicae Aequatoris).
- aulacostylus*, *Bulimus*, Pfeiffer, 1853d: 316 ([West Indies] St. Lucia).
- aureonitens*, *Eurytus*, Miller, 1878: 181 ([Ecuador] Valli Pilatonensi, 1000 m).
- auriformis*, *Strophocheilus (Eurytus)*, Da Costa, 1904: 5, pl. 1 fig. 1 (Colombia, Bogotá) [HT BMNH 1907. 11.21.112].
- bruggeni*, *Plekocheilus (Eurytus)*, Breure, 1978b: 9, pl. 6 figs. 5-7 (Peru, Dept. Pasco, Huancabamba) [HT BMNH 1911.11.2.88].
- castaneus*, *Bulimus*, Pfeiffer, 1845a: 68 ([Colombia] Vegas of the River Quenden) [LT BMNH 1975279].
- coloratus*, *Bulimus*, Nyst, 1845a: 228, pl. fig. 2 (la province de Cumana, dans la Colombie [sic, Venezuela]).

- conspicuus*, *Plekocheilus*, Pilsbry, 1932: 390, pl. 27 figs. 4-5 (Peru, Dept. Tumbes, Bella Vista trail, Cascadero, near divide near Huasimal, 4000 ft.) [HT ANSP 141959].
- corticus*, *Bulimus* (*Eurytus*), Sowerby, 1895: 214, pl. 13 fig. 2 (Colombia, Bogota) [LT BMNH 1907.11.21.110].
- corydon*, *Bulimus*, Crosse, 1869a: 185 (Quito, reipublicae Aequatoris).
- couturesi*, *Eurytus*, Ancey, 1900: 42 (Bolivia).
- dalmasi*, *Plecochilus*, Dautzenberg, 1900: 151, pl. 9 fig. 1 [no type locality given].
- doliarius*, *Strophocheilus* (*Eurytus*), Da Costa, 1898: 84, fig. 1 (Ecuador, Paramba) [HT BMNH 1907.11.21.117].
- elaeodes*, *Bulimus*, Pfeiffer, 1853b: 256 (Andibus Novae Granada).
- episcopalis*, *Bulimus*, Pfeiffer, 1855h: 115 (Bogota, New Granada) [LT BMNH 1953.11.30.1].
- eros*, *Bulimus* (*Eurytus*), Angas, 1878: 312, pl. 18 figs. 6-7 (Ecuador) [HT BMNH 1879.1.21.2].
- floccosa*, *Achatina*, Spix, 1827: pl. 9 figs. 3-4 (sylvis Provinciarum septemtrionalium Brasiliae).
- fusitorsus*, *Eurytus*, Oberwimmer, 1931: 190, figs. 1, 4 (Venezuela, Territorium Amazonas, Río Padamo) [HT SMF 5142].
- gibbonius*, *Bulimus*, Lea, 1838: 85, pl. 23 fig. 99 (New Granada [Colombia, Dept. Huila], between La Plata and Tocaima).
- gibbonius*, *Bulimus*, Hidalgo, 1870: 54 (San José, Ecuador).
- glandiformis*, *Bulimus*, Lea, 1838: 83, pl. 23 fig. 92 (New Granada [Colombia, Dept. Huila], between La Plata and Tocaima) [HT USNM 105045].
- glandiformis*, *Bulimus*, Pfeiffer, 1848b: 49 (Nova Granada).
- guentheri*, *Bulimus*, Sowerby, 1892: 296, pl. 23 figs. 7-8 (U.S. of Colombia).
- guildingi*, *Bulimus* (*Plekocheilus*), Dohrn, 1875b: 306, pl. 10 figs. 5-6 (Neu Granada) [ST ZMB 101799].
- jacksoni*, *Plekocheilus*, Pilsbry, 1939: 1, fig. 2 (Ecuador, between Baeza and Archidona, Nachiyacu) [HT ANSP 170694].
- jimenezi*, *Bulimus*, Hidalgo, 1872: 93, pl. 5 figs. 2-3 [not seen].
- jucundus*, *Bulimus*, Pfeiffer, 1855c: 290 (Antioquia, Neu Granada).
- juliani*, *Plekocheilus* (*Eurytus*), Haas, 1955a: 375, fig. 78 (Venezuela, State of Bolívar, Chimantá-massif, summit of Apacará-tepui, 2100 m) [HT FMNH 49737].
- lacrimosus*, *Bulimus*, Heimbürg, 1884: 92 (bei Iquitos am oberen Amazonas in Peru).
- lamarckianus*, *Bulimus*, Pfeiffer, 1848a: 229 (Andes of New Granada, 8000 feet) [LT BMNH 1975295].
- lentiginosus*, *Bulimus*, Redfield, 1853: 14 (Trinidad, District San Fernando).
- lynciculus*, *Bulimus*, Deville & Hupé, 1850: 640, pl. 15 fig. 1 (Mission de Sarayacu, sur les bords de la rivière de l'Ucayali, Pérou).
- mabiliei*, *Bulimus*, Crosse, 1867: 197, pl. 6 fig. 4 (montibus Columbiae) [HT MNHN].
- mcgintyi*, *Plekocheilus*, Pilsbry, 1944a: pl. 9 fig. 6 [nomen nudum]; 'Pilsbry' H. B. Baker, 1963: 229 (Rio Napo, northeastern boundary of Ecuador) [HT ANSP 227455].
- mundiperditi*, *Plekocheilus* (*Eurytus*), Haas, 1955a: 378, fig. 80 (Venezuela, [State of Bolívar,] Chimantá-massif near Rio Tinca, 2100 m) [HT FMNH 52436].
- nachiyacu*, *Plekocheilus*, Pilsbry, 1939: 2, fig. 1 [Colombia (see Clench & Turner, 1962: 102); HT ANSP 170693a].
- nocturnus*, *Plekocheilus*, Pilsbry, 1939: 3, fig. 5 (Ecuador, Puyo) [HT ANSP 170695].
- oligostylus*, *Plekocheilus*, Pilsbry, 1939: 3, fig. 6 [Ecuador, Nachiyacu (see Clench & Turner, 1962: 109); HT ANSP 170696].
- onca*, *Helix*, d'Orbigny, 1835: 8 [no type locality given; in d'Orbigny, 1836 [1834-1847]: "... non loin ... de Tutulima" [Bolivia, NW Cochabamba].
- pentadina*, *Helix*, d'Orbigny, 1835: 8 (Yuracares, republica Boliviana) [HT MNHN].
- phoebus*, *Bulimus*, Pfeiffer, 1863a: 274 (Ecuador) [LT BMNH 1975143].

- piperatoides*, *Plekocheilus*, Pilsbry, 1901: 132, pl. 21 fig. 66 (Colombia) [HT ANSP 263536].
- piperitus*, *Bulimus*, Sowerby, 1833a: fig. 93 ([Peru] Huallaga).
- pirriensis*, *Plekocheilus*, Dall, 1912: 2, pl. 1 figs. 1-2 (Panama, Canal Zone, Pirri Range).
- prodeflexus*, *Plekocheilus superstriatus*, Pilsbry, 1895: 91, pl. 36 fig. 81 (Peru, valley of Marañon River, Balsas) [HT ANSP 66439].
- pseudopiperatus*, *Bulimus*, J. Moricand, 1858: 451, pl. 14 fig. 2 ([Peru] Moyobamba).
- pulicarius*, *Bulimus*, Reeve, 1848: pl. 42 fig. 267 (New Granada) [LT BMNH 1975281].
- roseolabrum*, *Bulimus*, E. A. Smith, 1877b: 362 (S. Ecuador, Malacatos) [LT BMNH 1975135].
- semipictus*, *Bulimus*, Hidalgo, 1869b: 188 (Baeza, reipublicae Aequatoris).
- semperi*, *Bulimus*, Dohrn, 1882: 103, pl. 3 figs. 3-5 (Sonson in provincia Antioquia Novae Granadae [Colombia]).
- subglandiformis*, *Bulimus*, Mousson, 1873: 6 [Colombia, Bogota; LT ZMUZ].
- subplicata*, *Bulimus coloratus*, Pfeiffer, ?1855 [1854-1860]: pl. 8 figs. 4-5 ([Colombia] Prov. Ocana).
- superstriatus*, *Bulimus*, Sowerby, 1890: 578, pl. 56 fig. 9 (Peru, YQUITOS) [LT BMNH 1889.11.19.1].
- taquinensis*, *Bulimus*, Pfeiffer, 1855c: 290 (Taquina, Sierra Nevada de Santa Martha, New Granada) [LT BMNH 1957.6.3.1].
- tatei*, *Plekocheilus (Eurytus)*, Haas, 1955a: 385, fig. 84 (Venezuela, Territory of the Amazon, Mount Duida, ledge 23B) [HT FMNH 73455].
- taylorianus*, *Bulimus*, Reeve, 1849: pl. 81 fig. 602 ([Ecuador] environs of Quito) [LT BMNH 1975142].
- taylorioides*, *Eurytus*, Miller, 1878: 180 ([Ecuador] circa Quito, Chimborazo).
- tetensii*, *Bulimus*, Dunker, 1875: 29 (Sierra Nevada di St. Martha [Colombia, Dept. Magdalena]).
- tricolor*, *Bulimus*, Pfeiffer, 1853d: 325 (Gualea, Neu Granada).
- virgatus*, *Plectostylus*, Pilsbry, 1935: 84, pl. 6 figs. 3-5 (Colombia, Valle de Tensa) [HT ANSP 164573a].

***Plekocheilus (Aeropictus)* Weyrauch, 1967**

- Aeropictus* Weyrauch, 1967b: 465. Type species by original designation: *Bulimus veranyi* Pfeiffer.
- Orcesiellus* Weyrauch, 1967b: 468. Type species by original designation: *Plekocheilus (Orcesiellus) tenuissimus* Weyrauch.

Description. — Shell elongate-ovate; rimate to imperforate; rather thin. Colour light brown, uniformly coloured or with axial or spiral series of spots of darker brown. Surface smooth or finely granulate, with cuticular cavities filled with air. Protoconch granulate or with axial wrinkles. Whorls slightly convex; suture well impressed. Aperture broadly elongate-ovate. Peristome slightly thickened, expanded. Columella simple.

Distribution. — Venezuela, Brazil, Ecuador, Colombia.

Ecology. — The species live in montane forest, cloud forest and páramo vegetation, in the leaf litter layer or on shrubs. One species lives under arid conditions and has been collected on *Opuntia* sp. The vertical distribution is 1000-4000 m, but the species are mainly found between 2500-3000 m altitude.

Remarks. — Justification of the synonymy may be found in Breure, 1977a.

Taxa. — The following taxa are included in this subgenus:

- argenteus*, *Euritus*, Jousseaume, 1900: 41, pl. 1 figs. 20-21 (Venezuela, Merida, 4000 m).
bulimoides, *Succinea*, Pfeiffer, 1842b: 131 [indication, refers to *Bulimus succinoides* [sic] Petit].
calliostoma, *Bulimus* (*Eurytus*), Dohrn, 1882: 103, pl. 3 figs. 1-2 (provincia Antioquia Novae Granadae).
cathartiae, *Bulimus*, Reeve, 1848: pl. 42 fig. 265 (New Granada, Prov. Merida) [LT BMNH 1975288].
cleeforum, *Plekocheilus* (*Aeropictus*) *succinoides* [sic], Breure, 1977a: 260, figs. 19-20 (Colombia, Dept. Cundinamarca, Páramo de Sumapaz, Cabeceras Río Bogotá, Alto de Torquita, ca. 3900 m) [HT ZMA].
delicatus, *Plectostylus*, Pilsbry, 1935: 84, pl. 6 figs. 6-8 (Colombia, Soacha near Bogota) [HT ANSP 164577a].
dissimulans, *Bulimus* (*Eurytus*), Preston, 1909: 509, pl. 10 fig. 5 (Venezuela, Merida) [LT BMNH 19144.3.37].
latilabris, *Bulimus*, Pfeiffer, 1855f: 7 (Santa Fé de Bogota [Colombia]) [LT BMNH 1975127].
manco, *Plekocheilus*, Pilsbry, 1930c: 356, pl. 31 fig. 4 (Peru) [HT ANSP 152287].
quadricolor, *Bulimus*, Pfeiffer, 1848a: 229 (New Granada, province of Merida, Chachopo) [LT BMNH 1975283].
rhodocheilus, *Bulimus*, Reeve, 1848: pl. 28 fig. 173 (Brazil) [LT BMNH 1975129].
scytodes, *Bulimus*, Pfeiffer, 1853b: 256 (Andes of Colombia).
succineoides, *Bulimus*, Petit, 1840: 75 ([Colombia] les environs de Bogota) [ST MNHN].
tenuissimus, *Plekocheilus* (*Orcesiellus*), Weyrauch, 1967b: 469, figs. 23, 50 (Ecuador, 20 km al oeste de Quito, Tandayapa, 2500 m) [HT IML 3364].
veranyi, *Bulimus*, Pfeiffer, 1848a: 230 (New Granada, province of Merida, Chachopo) [LT BMNH 1975297].
zilchi, *Plekocheilus* (*Aeropictus*), Breure, 1977a: 260, figs. 2, 21-22 (Colombia, Dept. Boyacá, SW Labranza Grande, Quebrada Comijoque) [HT SMF 245387].

***Plekocheilus* (*Sparnotion*) Pilsbry, 1944**

Sparnotion Pilsbry, 1944c: 30. Type species by monotypy: *Bulimus houxwelli* Crosse.

Description. — Shell fusiform; narrowly perforate; rather solid. Colour yellowish to light brown. Surface with some incrassate growth striae, irregularly spaced papillae and cuticular cavities filled with air. Protoconch ?granulate. Whorls slightly convex; suture well impressed. Aperture narrowly elongate-ovate, the basal margin produced. Peristome narrowly reflexed. The anatomy is unknown.

Distribution. — Peru (Dept. Loreto).

Ecology. — The species lives in tropical rain forest, probably in the leaf litter layer.

The only known taxon is:

- houxwelli*, *Bulimus*, Crosse, 1872: 211 (in vicinio fluminis Ambiyacu, ad locum Pebas, Peruviae) [HT MCZ].

Plekocheilus (Eudolichotis) Pilsbry, 1896

Eudolichotis Pilsbry, 1896b: 108. Type species by original designation: *Bulimus distortus* Bruguière.

Antitragus Oberwimmer, 1931: 194. Type species by monotypy: *Auris (Antitragus) gibber* Oberwimmer.

Eudolichotus Solem, 1960: 417 [emendation for *Eudolichotis*].

Description. — Shell elongate-ovate to fusiform; perforate; thin to solid. Colour whitish to yellowish with brown axial stripes and variegations. Surface smooth, with incassate growth striae or with diamond-shaped granules. Protoconch granulate. Whorls slightly convex; suture well impressed, crenulate. Aperture elongate-ovate, the basal and palatal margins rounded or more or less produced. Peristome thickened, expanded and narrowly reflexed. Columella with a (strong) fold at the basal-parietal margin.

Distribution. — West Indies (Grenada, Trinidad), Venezuela, Guyana, Surinam, French Guyana, Brazil (Pará), Colombia, Panama.

Ecology. — The species live mainly under arid conditions in the leaf litter layer of xerophytic shrub vegetation and in deciduous forests; also in gardens. Vertical distribution is 0-2000(-3000) m.

Remarks. — Justification of the synonymy of *Antitragus* may be found in Breure, 1978b.

Taxa. — The following taxa are placed in this subgenus:

aegotis, *Bulimus*, Menke, 1830: 26 [indication, refers to *Auricula silenii* Lamarck, 1822].
aegotis, *Bulimus*, Pfeiffer, 1855 in Küster & Pfeiffer, 1840-1865: 43, pl. 13 figs. 5-6 (Westindien).

auriscaprina, *Helix (Cochlogena)*, Férussac, 1821: 57 [indication].

aurissciuri, *Plekocheilus*, Guppy, 1866a: 51 (Trinidad) [ST BMNH 1975309].

bisuturalis, *Auris distorta*, Pilsbry, 1896b: 112, pl. 44 figs. 81-82 (Colombia, San José de Cúcuta) [LT ANSP 25421a].

caprinus, *Plekocheilus*, Beck, 1837: 55 [indication].

dillwynianus, *Bulimus*, Pfeiffer, 1853b: 258 (Andes of New Granada) [LT BMNH 1975144].

distortus, *Bulimus*, Bruguière, 1789: 344 (Indes orientales).

euryomphalus, *Bulimus*, Jonas, 1844: 36 (in vicinitate cavernae Guacharo, juxta vicum Caripe Provinciae Cumana Reipublicae Venezuela).

flammeum, *Ellobium*, Röding, 1798: 106 [indication].

gibber, *Auris (Antitragus)*, Oberwimmer, 1931: 192, figs. 2, 5 (Venezuela, Staat Orinoco, Sierra Maraguaca, 2170 m) [HT SMF 5143].

glabra, *Voluta*, Gmelin, 1791: 3436 [no type locality given].

gracilis, *Auris distorta*, Pilsbry, 1896b: 111, pl. 40 fig. 31 (Colombia, Cúcuta, Pamploma [sic]) [LT ANSP 25422].

grenadensis, *Plekocheilus glaber*, Guppy, 1868a: 436 ([West Indies] Island of Grenada).

guariensis, *Plecochilus*, Jousseaume, 1889: 244, pl. 9 fig. 11 ([Venezuela] La Guaira) [HT MNHN].

lacerta, *Bulimus*, Pfeiffer, 1855g: 94 (Brazil, Para) [LT BMNH 1975303].

midas, *Bulimus*, Albers, 1852: 32 (Venezuela) [ST ZMB 41456].

otostomus, *Bulimus*, Pfeiffer, 1855c: 291 (Venezuela) [LT BMNH 1975307].

panamensis, *Auris distorta*, Pilsbry, 1910: 507, pl. 37 figs. 8-9 (Panama, Canal Zone, between Tabernillo and San Pablo) [LT ANSP 101314].

- paraguanensis*, *Eudolichotus* [sic] *glabra*, Solem, 1960: 419, pl. 1 figs. 4-6 (Venezuela, Est. Falcon, Peninsula Paraguana, Pico Santa Ana, 550 m) [HT CMG CE37982].
- perdix*, *Bulimus*, Pfeiffer, 1848a: 230 (New Granada, Agua de Obispo) [LT BMNH 1975305].
- sileni*, *Auricula*, Lamarck, 1822: 138 (la Guyane et les Antilles).
- sinuatus*, *Bulimus*, Albers, 1854a: 32 (Venezuela) [HT ZMB 101794].
- spectrum*, *Bulimus*, Albers, 1854b: 219 (Neu Granada) [ST ZMB].
- sublaevis*, *Auris distorta*, Pilsbry, 1896b: 111, pl. 40 figs. 27-30 (Venezuela, La Guayra, Puerto Cabello, Arva) [HT ANSP 25414a].

Dryptus Albers, 1860

Dryptus Albers, 1860: 194. Type species by original designation: *Bulimus moritzianus* Pfeiffer.

Description. — Shell elongate-ovate; rimate to imperforate; solid and strong. Colour uniformly dark brown or yellow- to light brown with axial streaks of dark brown. Surface granulate to malleate (but comparatively smooth). Protoconch smooth. Whorls slightly convex; suture well impressed, crenulate. Aperture elongate-ovate. Peristome broadly expanded and reflexed. Columella with a strong fold. The anatomy is unknown.

Distribution. — Venezuela, ?Peru, Colombia.

Ecology. — The habitat of the species is unknown. The vertical distribution is ca. 500-2750 m.

Remarks. — Only a limited number of shells of this genus could be studied. The relationships to other genera remain therefore uncertain, although the shell morphology strongly suggests a relationship to *Plekocheilus*. I have treated *Dryptus* tentatively as a separate genus.

Taxa. — The following taxa are placed in this genus:

- adoptus*, *Bulimus*, Reeve, 1849: pl. 82 fig. 608 (Banks of the Orinoco).
- astrapoides*, *Bulimus*, Jonas, 1844: 35 (in vicinitate cavernae Guacharo, juxta vicum Caripe Provinciae Cumana, Reipublicae Venezuela).
- funckii*, *Bulimus*, Nyst, 1843: 262, pl. 7 fig. 2 (la Colombie [sic], dans la province de Cumana [Venezuela]).
- guerini*, *Bulimus*, Pfeiffer, 1846a: 40 (Neu Granada) [LT BMNH 1975272].
- jubeus*, *Strophocheilus* (*Dryptus*), Fulton, 1908: 86, fig. (Venezuela, Capas) [HT BMNH 1905.5.3.1].
- lasalleanus*, *Dryptus*, Haas, 1955a: 363, fig. 60 (Venezuela, Mérida, Mucurubá) [HT Mus. La Salle, Caracas].
- leptochilus*, *Bulimus*, Pfeiffer, 1848b: 534 (prope La Baja in prov. Pamplona, Novae Granadae [Colombia]).
- lindeni*, *Bulimus*, Reeve, 1848: pl. 31 fig. 189 (La Baja, Province of Pamplona, New Granada).
- marmoratus*, *Bulimus*, Dunker in Philippi, 1844: 157, pl. 2 figs. 1-2 (Venezuela) [LT BMNH 1975474].
- moritzianus*, *Bulimus*, Pfeiffer, 1847b: 66 (prope Caraccas [sic; Venezuela]).
- pardalis*, *Helix* (*Cochlostyla*), Férussac, 1821: 48 [no type locality given].
- pardalis*, *Bulimus*, Reeve, 1848: pl. 24 fig. 157 (Cumana, Venezuela; Varinas, Venezuela) [not *Helix pardalis* Férussac, 1821].

- stuebeli*, *Bulimus* (*Dryptus*), Martens, 1885: 172, pl. 32 figs. 6-8 (New Granada [Colombia], Fusagasugá, 1700 m).
superbus, *Bulimus*, Jonas, 1844: 35 (in vicinitate cavernae Guacharo, juxta vicum Caripe, Provinciae Cumana, Reipublicae Venezuela).
venetiolensis, *Bulimus*, Nyst, 1845a: pl. fig. 1 [emandation for *venezuelensis* Nyst].
venezuelensis, *Bulimus*, Nyst, 1845a: 227, (la province de Cumana, à la caverne de Guacharos [Venezuela]).
wilsoni, *Strophocheilus moritzianus*, Pilsbry, 1895: 39, pl. 21 fig. 48 [no type locality given; LT ANSP 7775].

Auris Spix, 1827

Auris Spix, 1827: 13. Type species by original designation: *Bulimus melastomus* Swainson.

Description. — Shell ovate; narrowly perforate to rimate; solid. Colour whitish, brownish or pink, with brown spots and/or axial streaks. Surface usually granulate, plicate or folded below the suture; last whorl in several species with oblique folds. Protoconch smooth. Whorls rather convex; suture hardly to well impressed. Aperture (broadly) ovate. Peristome thickened, expanded and reflexed, often bearing a callous flange. Columella receding, with a weak fold.

The central teeth of the radula are tricuspid, with rather acute, ovate mesocones and elongate-truncate ectocones. Lateromarginal teeth are bicuspid, with rather blunt to acute, elongate mesocones and elongate-truncate to ovate ectocones; without supporting denticles in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 30-32).

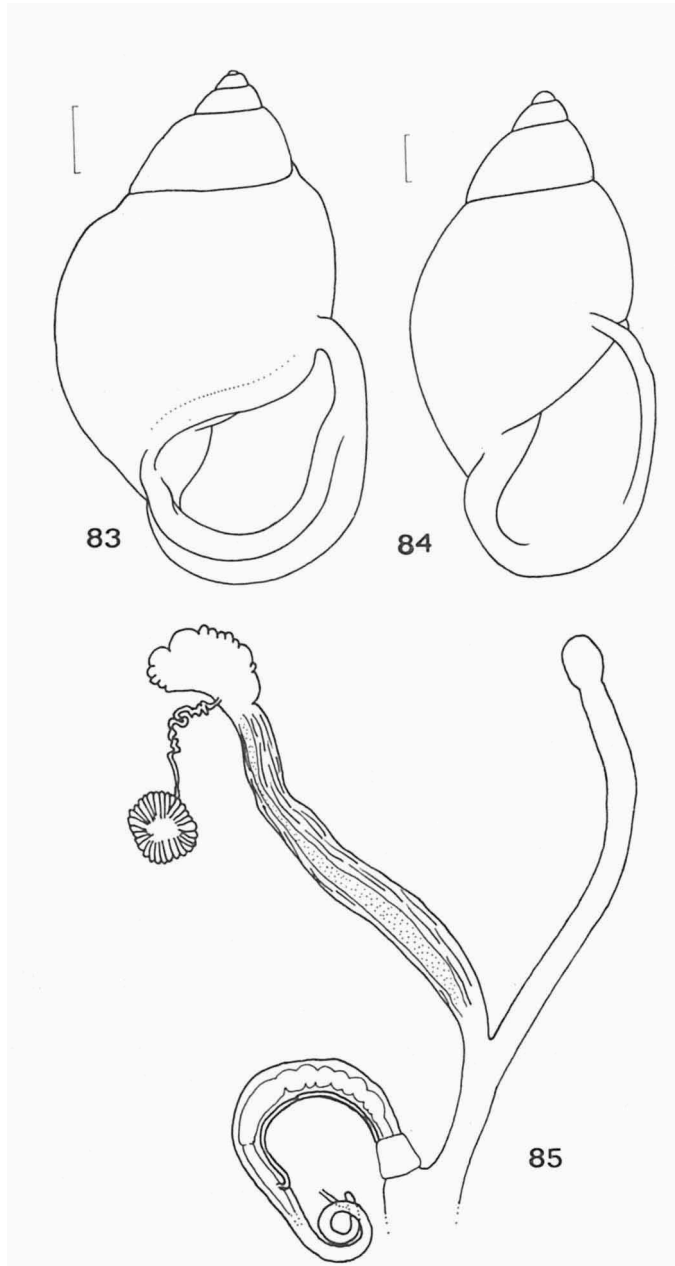
The pericard is transversally disposed and is as long as the nephridium, which is broadly triangular. The main pulmonary and side veins are well developed and prominently ramified at the anterior end, where two veins parallel to the main pulmonary vein are situated. The adrectal ureter is closed over its entire length.

Penis with a short proximal sheath, more or less subcylindrical and passing without external differentiation into the epiphallus. The flagellum is more or less tapering and is relatively long, as is the vagina. The spermathecal duct is subcylindrical, with a globose spermatheca at the distal end. The glandular folds of the spermoviduct are arranged parallel to the length axis of this duct.

Distribution. — Brazil.

Ecology. — Unknown.

Relationships. — The phylogenetic relationships of this genus are discussed on page 147. The genus is characterized by the shell shape, the sculpture of the surface and the smooth protoconch, the thickened peristome and the direction of the glandular folds of the spermoviduct.



Figs. 83-84. Variation in shell shape in *Auris*. Fig. 83. *A. bilabiata* (Broderip & Sowerby).

Fig. 84. *A. illheocola* (Moricand). Scale = 5 mm.

Fig. 85. Genitalia of *Auris bilabiata melanostoma* (Moricand); after Jurberg, 1964.

Bibliography. — The main publications on this genus are: Jurberg, 1964; Pilsbry, 1895.

- bernardii*, *Bulimus*, Pfeiffer, 1856b: 52 (Brasilia).
bilabiatus, *Bulimus*, Broderip & Sowerby, 1829: 49 (Brasilia).
brachyplax, *Auris melastoma*, Pilsbry, 1896b: 103, pl. 39 fig. 18 [no type locality given; HT ANSP 25394a].
chrysotoma, *Helix* (*Cochlogena*) *rhodospira*, S. Moricand, 1836: 428 ([Brazil] environs de Bahia).
egregia, *Pupa*, Jay, 1836: [81] pl. 1 fig. 4 [publication not seen].
illheocola, *Helix* (*Cochlogena*) *rhodospira*, S. Moricand, 1836: 428 ([Brazil, Bahia] Illheos).
listeri, *Bulimus*, Wood, 1828: pl. 7 fig. 23 [publication not seen].
maxiliana, *Helix*, 'Férussac' S. Moricand, 1836: 431 ([Brazil, Bahia] Illheos).
maxiliana, *Partula*, Potiez & Michaud, 1838: atlas p. 27, pl. 20 figs. 5-6 (le Brésil).
melanostomus, *Bulimus*, Deshayes, 1832 in Férussac & Deshayes, 1820-1851: pl. 155 figs. 4-5.
melanostoma, *Helix maximiliana*, S. Moricand, 1836: 431 ([Brazil, Bahia] Illheos).
melastomus, *Bulimus*, Swainson, 1820: pl. 4 (Brazil, province of Bahia).
minor, *Helix maximiliana*, S. Moricand, 1836: 431 ([Brazil, Bahia] Illheos).
nigrilabris, *Auris egregia*, Pilsbry, 1896b: 102, pl. 39 fig. 16 [no type locality given; HT ANSP 25390a].
rhodospirus, *Bulimus*, Potiez & Michaud, 1835: pl. 15 figs. 1-2 (Brésil).
scalaris, *Bulimus melanostomus*, Dohrn, 1883: pl. 11 fig. 4 ([Brazil, Bahia] Gebiete des Rio Francisco).
struthiolaris, *Bulimus*, Menke, 1830: 26 [indication].
swainsoni, *Bulimus*, Pfeiffer, 1845c: 156 (Brasilia).
vulgaris, *Helix rhodospira*, S. Moricand, 1836: 128, pl. 2 fig. 29 ([Brazil] environs de Bahia).

Thaumastus Albers, 1860

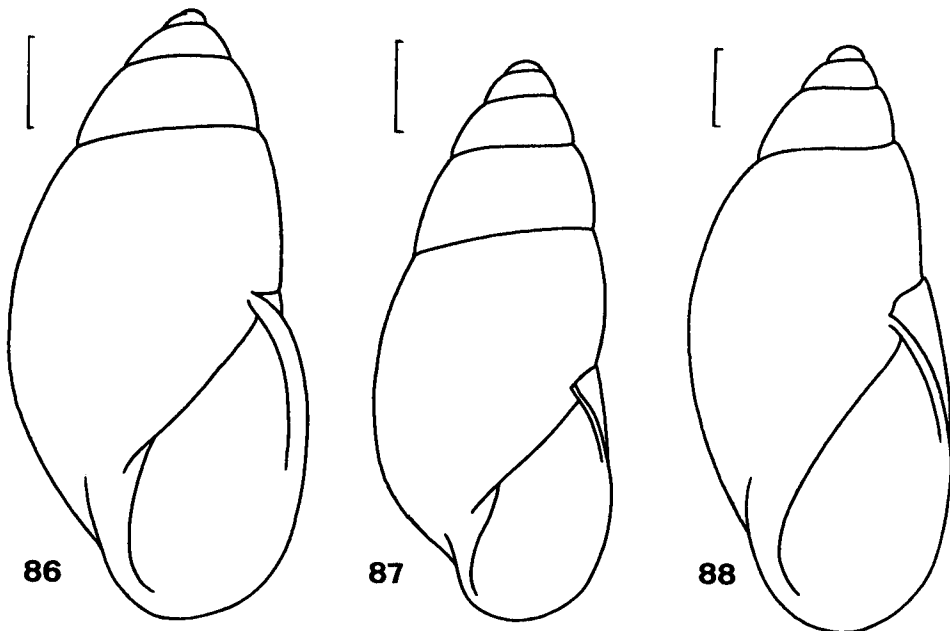
- Orphnus* Albers, 1850: 146. Type species by subsequent designation (Albers, 1860): *Helix taunaisii* Férussac [not *Orphnus* McLeay, 1819].
Thaumastus Albers, 1860: 215. Type species by original designation: *Bulimus hartwegi* Pfeiffer.
Orphaicus Schaufuss in Paetel & Schaufuss, 1869: 14. New name for *Orphnus* Albers, 1850 not McLeay, 1819.
Tatutor Jousseume, 1887b: 6. Type species by monotypy: *Tatutor tatutor* Jousseume.
Tholus Strebel, 1909: 137. Type species by monotypy: *Orthalicus* (*Porphyrobaphe*) *buckleyi* Higgins.
Pachytholus Strebel, 1909: 138. Type species by subsequent designation (Zilch, 1960): *Tholus* (*Pachytholus*) *pseudoiostomus* Strebel.
Atahualpa Strebel, 1910: 19. Type species by monotypy: *Atahualpa brunneus* Strebel.

Description. — Shell relatively large, elongate-ovate, with rather blunt apex; rimate to imperforate; (rather) solid. Colour brownish, mostly with axial streaks or spiral bands. Surface with incrassate growth striae or granulate. Protoconch pit-reticulate or with axial wrinkles. Whorls hardly to slightly convex; suture hardly to well impressed. Aperture subovate. Peristome thin to slightly thickened, not to hardly expanded.

Distribution. — Venezuela, Brazil, Bolivia, Peru, Ecuador.

Relationships. — The phylogenetic relationships of the subgenera are discussed on page 147.

Bibliography. — The main publications on this genus are: Breure, 1978b; Pilsbry, 1895, 1944b; Strebel, 1910; Weyrauch, 1956b, 1960a, 1967b; Zilch, 1953, 1954.



Figs. 86-88. Variation in shell shape in *Thaumastus*. Fig. 86. *T. (T.) sangoae* (Tschudi).
Fig. 87. *T. (T.) taunaisii achilles* (Pfeiffer). Fig. 88. *T. (T.) insolitus* (Preston).
Scale = 1 cm.

Thaumastus (Kara) Strebel, 1910

Kara Strebel, 1910: 16. Type species by original designation: *Bulimus thompsoni* Pfeiffer.

Description. — Shell elongate-ovate; imperforate; solid. Colour pale brown with darker axial streaks. Surface with some incrassate growth striae. Protoconch pit-reticulate. Whorls slightly convex; suture well impressed. Aperture subovate. Peristome thin and simple.

Distribution. — Peru, Ecuador.

Ecology. — Unknown.

Taxa. — The following taxa are included in this subgenus:

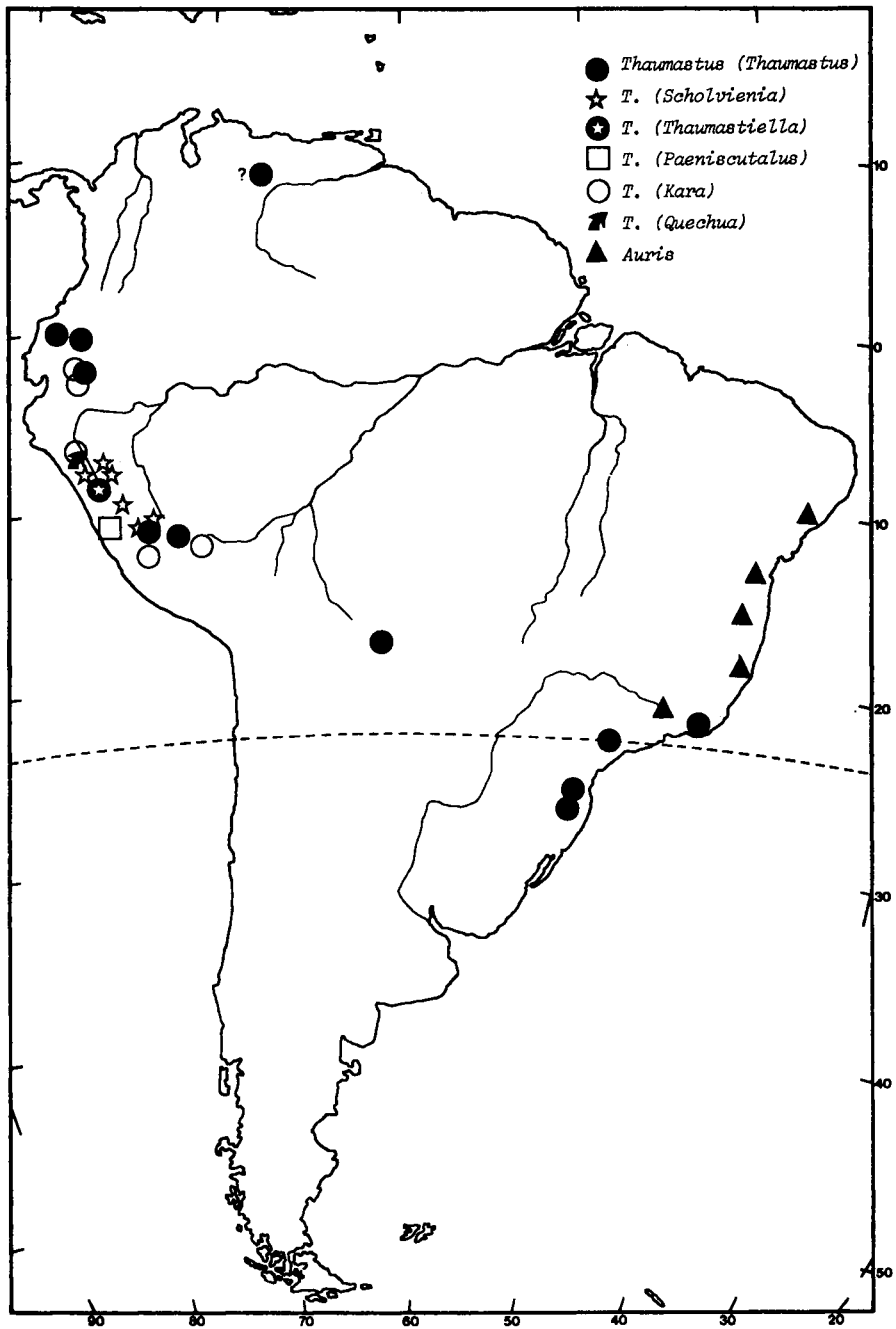


Fig. 89. Distribution of *Thaumastus* and *Auris*.

- lutea*, *Orphnus thompsoni*, Cousin, 1887 : 212 ([Ecuador] Cuença).
nigricans, *Orphnus thompsoni*, Cousin, 1887 : 212 ([Ecuador] Cuença).
olivacea, *Orphnus thompsoni*, Cousin, 1887 : 212 ([Ecuador] Cuença).
oriziamus, *Plecocheilus (Eurytus)*, Haas, 1955a : 366, fig. 73 (Peru, valley of Rio Chanay, between Chiclayo and Cutervo).
thompsonii *Bulimus*, Pfeiffer, 1845b : 74 ([Ecuador] Quito) [LT BMNH 1975464].
thompsonoides, *Thaumastus*, Oberwimmer, 1931 : 194, figs. 3, 6 (Ecuador, Loja) [HT SMF 5144].
viriatum, *Bulimus*, Morelet, 1863 : 170, pl. 7 fig. 4 ([Peru, Dept. Cuzco] vallée de Santa Anna, Niguapata).
yanamensis, *Bulimus*, Morelet, 1863 : 171, pl. 8 fig. 3 ([Peru] Yanama) [LT BMNH 1975127].
zebra, *Orphnus thompsoni*, Cousin, 1887 : 212 ([Ecuador] près Azagues).

Thaumastus (Scholvienia) Strebel, 1910

Scholvienia Strebel, 1910 : 20. Type species by subsequent designation (Pilsbry, 1932a) : *Bulimus bitaeniatum* Nyst.

Description. — Shell elongate-ovate; rimate; rather solid. Colour brown with yellowish spiral band(s). Surface with some incrassate growth striae. Protoconch (subexcavated) with strong axial wrinkles and short waved riblets. Whorls slightly convex; suture well impressed. Aperture subovate. Peristome thin and simple.

The central teeth of the radula are tricuspid, with acute, wedge-shaped mesocones and hardly developed ectocones. The lateromarginal teeth are bicuspid, with rather blunt to acute, elongate to wedge-shaped mesocones and acute, elongate to deltoid ectocones; without supporting denticles in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 31-38).

The pericard is transversally disposed and is as long as the nephridium, which is broadly triangular. The transition of the adrenal and adrectal ureters is relatively posteriorly situated. The main pulmonary vein is prominent, ramified at the anterior end, where a parallel vein is situated. The adrectal ureter is closed over its entire length.

The penis has a proximal sheath, is rather thick and subcylindrical and is passing without external differentiation into the epiphallus. The flagellum is tapering. The vagina is relatively short. The spermathecal duct is more or less subcylindrical, its distal part tapering towards the elongate-globose spermatheca.

Distribution. — Peru (Depts. Apurimac, Ayacucho, Junín, Pasco, Huánuco, Cajamarca and Amazonas).

Ecology. — The species live in open montane forest and steppe vegetations, in the leaf litter layer. The vertical distribution is (800-)1800-3500 m.

- alutaceus*, *Bulimus*, Reeve, 1850b : 99 (Peru, Cuzco) [LT BMNH 1975148].
argentinus, *Thaumastus (Scholvienia)*, Bequaert, 1949 : 114, pl. 7 fig. 6 (Argentina, Prov.

- Buenos Aires, Dept. Saavedra, 15 km N Pique, Hacienda Ducous [see remarks of Weyrauch, 1964: 50] [HT MCZ 132313].
- bambamarcaensis*, *Thaumastus* (*Scholvenia*), Breure, 1978b: 41, pl. 6 fig. 8 (Peru, Dept. Cajamarca, 7 km SW Bambamarca, 2920 m) [HT UF 22752].
- bifasciatus*, *Bulimus*, Philippi, 1845: 10, pl. 3 fig. 5 (sylvae peruanae).
- bitaeniatus*, *Bulimus*, Nyst, 1845b: 153 (New name for *Bulimus bivittatus* Philippi, not *Bulimus bivittatus* Sowerby).
- bivittatus*, *Bulimus*, Philippi, 1843: 62 (sylvae peruanae).
- brepheoides*, *Helix*, d'Orbigny, 1835: 17 (republica Peruviana).
- fusiformis*, *Bulimus*, Tschudi, 1852: 192 [nomen nudum].
- gittenbergerorum*, *Thaumastus* (*Scholvenia*), Breure, 1978b: 44, fig. 57, pl. 6 figs. 1-4 (Peru, Dept. Huánuco, 10.8 km W Huancapallac, 2950 m) [HT UF 22119].
- huancabambensis*, *Thaumastus* (*Scholvenia*), Strebel, 1910: 26, pl. 2 figs. 15, 19a (Peru, [Dept. Pasco] Huancabamba).
- iserni*, *Bulimus*, Philippi, 1867: 75 ([Peru, Dept. Junín] prope La Oroya).
- jaspideus*, *Bulimus*, Morelet, 1863: 180, pl. 7 fig. 7 ([Peru] vallée de Yucaï aux environs de Huancabelica).
- jelskii*, *Bulimus* (*Orphnus*), Lubomirski, 1880: 722, pl. 56 figs. 1-2 (Amable Maria, près de Tarma [Dept. Junín, Peru]).
- minor*, *Thaumastus* (*Scholvenia*) *jaspidea*, Strebel, 1910: 23, pl. 3 figs. 31-32, 36 (Peru, Quemia).
- pallida*, *Thaumastus* (*Scholvenia*) *bitaeniatus*, Strebel, 1910: 22, pl. 3 figs. 29-30 ([Peru, Dept. Junín] Chanchamayo, 1000 MeMter).
- porphyrius*, *Bulimus*, Pfeiffer, 1847a: 114 (Bolivia) [LT BMNH 1975277].
- taeniolus*, *Bulimus*, Nyst, 1845b: 151, pl. 2 fig. 4 (l'Amérique méridionale).
- tarmensis*, *Bulimus*, Philippi, 1867: 70 ([Peru, Dept. Junín] ad Oroya haud procul ab oppido Tarma).
- unicolor*, *Bulimus bifasciatus*, Philippi, 1869: 36 (Hacienda de Huaribamba, 14 leucas ad orientem oppidi Huancayo).
- weeksi*, *Bulimulus*, Pilsbry, 1930c: 357, pl. 31 fig. 9 (Peru, [La] Oroya, 12000 feet) [HT ANSP 140215a].
- weyrauch[i]*, *Thaumastus* (*Scholvenia*), Pilsbry, 1944b: 121, pl. 11 fig. 2 (Peru, Carpata on the Rio Tarma, 2300 m) [HT ANSP 179996a].

Thaumastus (Thaumastiella) Weyrauch, 1956

Thaumastiella Weyrauch, 1956b: 11. Type species by original designation: *Bulimulus sarcochrous* Pilsbry.

Description. — Shell ovate-conical; narrowly perforate; solid. Colour light brown, uniformly coloured or with a whitish band on the last whorl. Surface with incrassate growth striae. Protoconch with axial riblets, which become wavy, anastomosing and irregularly broken up into bead-like to oblong granules on the second whorl. Whorls slightly convex; suture crenulate, hardly to well impressed. Aperture (elongate-) ovate. Peristome thickened but unexpanded.

The central teeth of the radula are tricuspid, with acute, wedge-shaped mesocones and relatively small, triangular ectocones. Lateromarginal teeth are bicuspid, with elongate to deltoid ectocones; without supporting denticles in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 39).

The pericard is transversally disposed and is as long as the nephridium, which is broadly triangular. The main pulmonary vein and the side veins are moderately developed. The adrectal ureter is closed over its entire length.

Penis with a sheath (ca. 1/6 the length of the phallus), slightly swollen above the distal end of the sheath, but otherwise more or less subcylindrical and passing without external differentiation into the epiphallus. The flagellum is relatively short and tapering.

Distribution. — Peru (Depts. La Libertad, Cajamarca).

Ecology. — The species live in 'savannah forest', under stones. The vertical distribution is (1200-) 1600-2750 m.

Taxa. — The following taxa are placed in this subgenus:

debilisculptus, *Thaumastus* (*Thaumastiella*) *occidentalis*, Weyrauch, 1960a: 30, pl. 3 fig. 15 (N-Peru, bei Llama, an der Autostrasse von Chiclayo nach Cutervo, ca. 85 km nördlich Chiclayo, 2000-2250 m) [HT SMF 162029].

glyptocephalus, *Bulimulus*, Pilsbry, 1897d: 21 (Peru) [HT ANSP 25675].

koepckeii, *Thaumastus* (*Scholviencia*), Zilch, 1953: 53, figs. 7-9, pl. 14 fig. 3 (Peru, [Dept. Cajamarca] Hacienda Monteseo, ± 1200 m) [HT SMF 111487].

occidentalis, *Thaumastus* (*Thaumastiella*), Weyrauch, 1960a: 28, pl. 3 figs. 13-14 (N-Peru, Umgebung von Contumazá, 110 km nördlich Trujillo, 2750 m) [HT SMF 162026].

sarcochrous, *Bulimulus*, Pilsbry, 1897d: 21 (Peru) [HT ANSP 4705].

***Thaumastus* (*Paeniscutalus*) Wurtz, 1947**

Paeniscutalus Wurtz, 1947: 12. Type species by monotypy: *Megalobulimus* (*Microborus*) *incarum* Pilsbry.

Description. — Shell ovate; rimate; rather solid. Colour uniform whitish to light brown. Surface with more or less incrassate growth striae. Protoconch with indistinct axial wrinkles, which are partly broken into oblong granules. Whorls slightly convex; suture crenulate, hardly impressed. Aperture sub-ovate. Peristome slightly thickened and narrowly expanded.

The central teeth of the radula are tricuspid, with rather acute, ovate mesocones and elongate-truncate ectocones. Lateromarginal teeth are bicuspid, with rather blunt to acute, elongate mesocones and elongate-truncate to ovate ectocones; without supporting denticles in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 38).

The pericard is transversally disposed and is as long as the nephridium, which is broadly triangular. The main pulmonary vein and the side veins are prominent; the veins are ramified at the anterior end, where a vein parallel to the main pulmonary vein is situated. The adrectal ureter is closed over its entire length.

Penis with a sheath, more or less subcylindrical and passing without external differentiation into the epiphallus. The flagellum is rather short and

relatively thick. The spermathecal duct is thick and about half as long as the spermoviduct; the spermatheca is elongate-globose.

Distribution. — Peru (Depts. Ancash, La Libertad).

Ecology. — The species lives near cultivated grounds, under stones. The vertical distribution is 1850-3300 m.

Remarks. — This taxon was originally described as a subgenus of *Bulimulus* Leach, 1814. Zilch (1960) and Parodiz (1962) considered *Paeniscutalus* as a separate genus, but Weyrauch (in IML-collection) suggested its classification as a subgenus of *Thaumastus* Albers, 1860; I agree with this suggestion.

Taxa. — The following taxa are included in *Paeniscutalus*:

crenellus, *Bulimus*, Philippi, 1867: 67 (Peru [Dept. La Libertad, Distr. Santiago de Chuco] hacienda de Unigambal).

incarum, *Megalobulimus* (*Microborus*), Pilsbry, 1944c: 29, pl. 1 figs. 8-9 (Peru, [Dept. Ancash] Huaraz, 3000-3200 m) [HT ANSP 180677a].

Thaumastus (Thaumastus) Albers, 1860

Description. — Shell elongate-ovate; imperforate; solid. Colour light to dark brown, mostly with darker axial streaks or light spiral band(s). Surface with incrassate growth striae. Protoconch with fine, close axial wrinkles. Whorls hardly convex; suture well impressed, more or less crenulate. Aperture relatively small, subovate. Peristome slightly expanded.

The central teeth of the radula are tricuspid, with rather acute, ovate mesocones and elongate-truncate ectocones. The lateromarginal teeth are bicuspid, with rather blunt, elongate mesocones, rudimentary wing-like endocones and elongate-truncate ectocones or with acute, rather elongate meso- and ectocones; without supporting denticles in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 32-43).

The pericard is transversally disposed and is about as long as the nephridium, which is broadly triangular. The transition of adrenal and adrectal ureters is relatively posteriorly situated. The main pulmonary vein is prominent and ramified at the anterior end, where a parallel vein is situated. The adrectal ureter is closed over its entire length.

The penis has a proximal sheath and is rather thick and more or less subcylindrical; passing without external differentiation into the epiphallus. The flagellum is subcylindrical to tapering, up to half as long as the phallus length. The vagina is relatively short. The spermathecal duct is subcylindrical, with an elongate-truncate to globose spermatheca at the distal end.

Distribution. — Brazil, Bolivia, Peru, Ecuador.

Ecology. — In Peru the species live in cloud and montane forests, mainly

near rocky outcrop. The vertical distribution is 0-ca. 2300 m.

Taxa. — The following taxa are included in this subgenus:

- achilles*, *Bulimus*, Pfeiffer, 1853d: 378 (in ripis fluvii Amazonum) [LT BMNH 1975268].
- ascendens*, *Bulimus*, Pfeiffer, 1853d: 378 (Brasilia) [LT BMNH 1975274].
- ?*blanfordianus*, *Bulimulus*, Ancey, 1903: 90 (Bolivia, Iquico, 3500 m).
- brunneus*, *Thaumastus* (*Atahualpa*), Strebel, 1910: 19, pl. 2 fig. 25 (Ecuador).
- buckleyi*, *Orthalicus* (*Porphyrobaphe*), Higgins, 1872: 685, pl. 56 fig. 3 ([Ecuador] San Lucas) [ST BMNH].
- bulimea*, *Columna*, Spix, 1827: pl. 10 fig. 3 [no type locality given].
- cadwaladeri*, *Thaumastus*, Pilsbry, 1930c: 355, pl. 31 fig. 10 (Peru, Prov. Junin, Huacapistana, 6000-7000 feet) [HT ANSP 151812].
- consimilis*, *Bulimus*, Reeve, 1848: pl. 53 fig. 346 [no type locality given].
- contortuplicatus*, *Bulimus*, Reeve, 1850a: pl. 88 fig. 658 (Minas Geraes, Brazil).
- filocinctus*, *Bulimus* (*Dryptus*), Rolle, 1901: 93 (Peru, Chanchamayo).
- foveolatus*, *Bulimus*, Reeve, 1849: pl. 73 fig. 526 (Peru, Vitoe near Sarma [sic, Tarma]) [LT BMNH 1975275].
- fragilis*, *Bulimus*, Spix, 1827: pl. 6 fig. 3 [no type locality given].
- granocinctus*, *Strophocheilus* (*Thaumastus*), Pilsbry, 1901: 126 (New name for *Bulimus filocinctus* Rolle, 1901, not Reuss, 1861).
- hartwegi*, *Bulimus*, Pfeiffer in Philippi, 1846: 111, pl. 4 fig. 1 (respublica [sic] Aequatoris, ubi ad "El Catamaija" prope Loxa) [ST BMNH].
- hebes*, *Thaumastus*, Strebel, 1910: 9, pl. 2 fig. 22 ([Brazil] Sao Paulo; Sta. Catarina).
- hyalinus*, *Bulimus*, Wagner in Spix, 1827: 6 ([Brazil] sylvis Provinciae Minarum [Minas Gerais]).
- impressus*, *Bulimus*, Tschudi in Troschel, 1852: 188 (Urwälder Peru's).
- inca*, *Helix*, d'Orbigny, 1835: 16 (Tutulima, republica Boliviana) [ST MNHN].
- indentatus*, *Strophocheilus* (*Dryptus*), Da Costa, 1901: 239, pl. 24 fig. 8 (Ecuador) [HT BMNH 1907.11.21.115].
- insolitus*, *Bulimus* (*Thaumastus*), Preston, 1909: 509, pl. 10 fig. 9 (Peru, Chanchamayo) [HT BMNH 1947.3.11.1].
- integer*, *Bulimus*, Pfeiffer, 1855h: 114 (Quito, Ecuador) [LT BMNH 1975244].
- largillierti*, *Bulimus*, Philippi, 1845: 11, pl. 3 fig. 6 (Brasilien, Santa Catarina).
- loxostomus*, *Bulimus*, Pfeiffer, 1853d: 379 (Andibus Novae Granadae).
- magnificus*, *Bulimus*, Grateloup, 1839: 165, pl. 4 fig. 1 (Pérou) [LT BMNH 1907.11.21.24].
- mahogani*, *Bulimus*, Pfeiffer, 1842b: 42 (Chile).
- melanocheilus*, *Bulimus*, Nyst, 1845b: 149, pl. 2 fig. 3 (l'Amérique méridionale, au Pampas).
- monozonalis*, *Bulimus*, Deshayes, in Férussac & Deshayes, 1820-1851: pl. 144 figs. 2-3 [indication].
- nehringi*, *Bulimus achilles*, Martens, 1889: 12, pl. 40 figs. 9-10 ([Brazil] bei Piracicaba, Provinz S. Paulo) [HT ZMB 37675a].
- orcezi*, *Thaumastus* (*Thaumastus*), Weyrauch, 1967b: 473, fig. 2 (Ecuador, cuenca del río Esmeraldas, 35 km al noroeste de Quito, región de Nanegal, 1500 m) [HT IML 3165].
- plumbeus*, *Bulimus*, Pfeiffer, 1855h: 114 (Venezuela) [LT BMNH 1975130].
- pseudoiostomus*, *Tholus* (*Pachytholus*), Strobel, 1909: 139, pl. 21 fig. 338, pl. 26 figs. 397-398 (Chile).
- requieni*, *Bulimus*, Pfeiffer, 1853d: 389 (Brazil) [LT BMNH 1975301].
- sangoae*, *Bulimus*, Tschudi in Troschel, 1852: 189, pl. 6 fig. 1 (Urwäldern von Sangoa in Peru).

satipoensis, *Thaumastus robertsi*, Pilsbry, 1944b: 121, pl. 11 fig. 1 (Peru, near Huancayo, Satipo, 600 m) [HT ANSP 179990].

spixii, *Bulimus*, Wagner in Spix, 1827: 11 (Brasilia).

tatutor, *Tatutor*, Jousseau, 1887: 6, fig. 1 (Nouvelle Grenada) [HT MNHN].

taunaisii, *Helix* (*Cochlostyla*), Férussac, 1821: 48 (Brésil).

Thaumastus (Quechua) Strebel, 1910

Quechua Strebel, 1910: 17. Type species by original designation: *Bulimus salteri* Sowerby.

Description. — Shell elongate-ovate; rimate to imperforate; solid. Colour brownish, with light axial streaks and spots. Surface with incrassate growth striae and spiral lines. Protoconch with axial riblets and wrinkles, more or less anastomosing. Whorls slightly convex, the last whorl prominent; suture well impressed. Aperture elongate-ovate. Peristome unexpanded.

The central teeth of the radula are monocuspid, with triangular to ovate mesocones (some rudimentary ectocones may be observed). Lateral teeth monocuspid, with very acute, lanceolate mesocones. The marginal teeth are bicuspid, with blunt to acute mesocones, mostly rudimentary endocones and elongate(-truncate) ectocones. Half-row formula: C/1 + L x/1 + M y/2 (x = 2, y = 36-81).

The penis is broadly subcylindrical, without a proximal sheath; a weak constriction marks the transition to the epiphallus, which is subcylindrical. The flagellum is more or less tapering. The vagina is relatively long. The spermathecal duct is subcylindrical and rather short; the spermatheca is globose.

Distribution. — Peru (Depts. Junin, Cajamarca).

Ecology. — The species live in montane forest, in the leaf litter layer. The vertical distribution is 800-ca. 3000 m.

Taxa. — The following taxa are included in this subgenus:

maximus, *Thaumastus (Quechua) salteri*, Weyrauch, 1967a: 347, fig. 135 (Norte de Peru, 25 km NE Cutervo, camino de herradura de Súcota a San Andrés, Peña Blanca) [HT SMF 156381].

olmosensis, *Thaumastus (Quechua)*, Zilch, 1954: 76, 8, pl. 6 figs. 10-11 (Peru, am Weg von Olmos nach Jaén, 840 m) [HT SMF 123653].

salteri, *Bulimus*, Sowerby, 1890: 578, pl. 56 fig. 4 (Catamarca, Andes of Peru) [HT BMNH 1907.11.21.118].

taulisensis, *Thaumastus (Quechua)*, Zilch, 1953: 52, pl. 14 fig. 2 (Peru, [Dept. Cajamarca,] Hacienda Taulis, ± 1700 m) [HT SMF 111465].

tetricus, *Thaumastus (Quechua)*, Haas, 1951: 523, fig. 110 (Peru, Junín Prov., Río Tarma, Huacapistana) [HT FMNH 30920].

Nomen inquirendum

Thomsenia Strebel, 1910

Thomsenia Strebel, 1910: 26. Type species by monotypy: *Thomsenia claritae* Strebel.

Description. — Shell elongate-ovate; rimate; solid. Colour chestnutbrown,

the upper whorls paler. Surface with some incrassate growth striae. Protoconch with fine axial wrinkles and short waved riblets. Whorls slightly convex; suture well impressed. Aperture sub-ovate. Peristome thin and simple. [After Strebel].

Distribution. — Peru (Dept. Junín).

Ecology. — Unknown.

Remarks. — Only the type specimen was known and this is probably destroyed, together with most of Strebel's types, during the 1939-1945 war (Dance, 1966: 302). Judging from the description this taxon is most probably a synonym of *Scholviemia* Strebel, 1910 (page 40).

The sole taxon in this genus is:

claritae, Thomsenia, Strebel, 1910: 27, pl. 2 fig. 16 (Peru, Chanchamayo).

Nomen inquirendum

Lopesianus Weyrauch, 1958

Lopesianus Weyrauch, 1958: 120. Type species by monotypy: *Lopesianus crenulatus* Weyrauch.

Description. — Shell elongate-ovate; narrowly perforate; thin. Colour uniform brownish. Surface with slightly incrassate growth striae. Protoconch with relatively few, indistinct spiral lines. Whorls slightly convex; suture weakly crenulate, well impressed. Aperture elongate-ovate. Peristome thin and simple.

Distribution. — Brazil.

Ecology. — Unknown. The species lives at sea level.

Relationships. — The sculpture of the protoconch suggests a remote relationship with *Bostryx*, or possibly *Leiostracus*, but nothing can be said until the anatomy is known.

Remarks. — Only the type material of *Lopesianus crenulatus* Weyrauch is available and, despite all efforts, no further specimens have been found at the type locality (Rezende & Araujo, personal communication).

The sole taxon in this genus is:

crenulatus, *Lopesianus*, Weyrauch, 1958: 121, pl. 6 figs. 7-8 (Brasilien, Cabo Frio, Arrairal-Prainha, Estado do Rio) [HT SMF 156376].

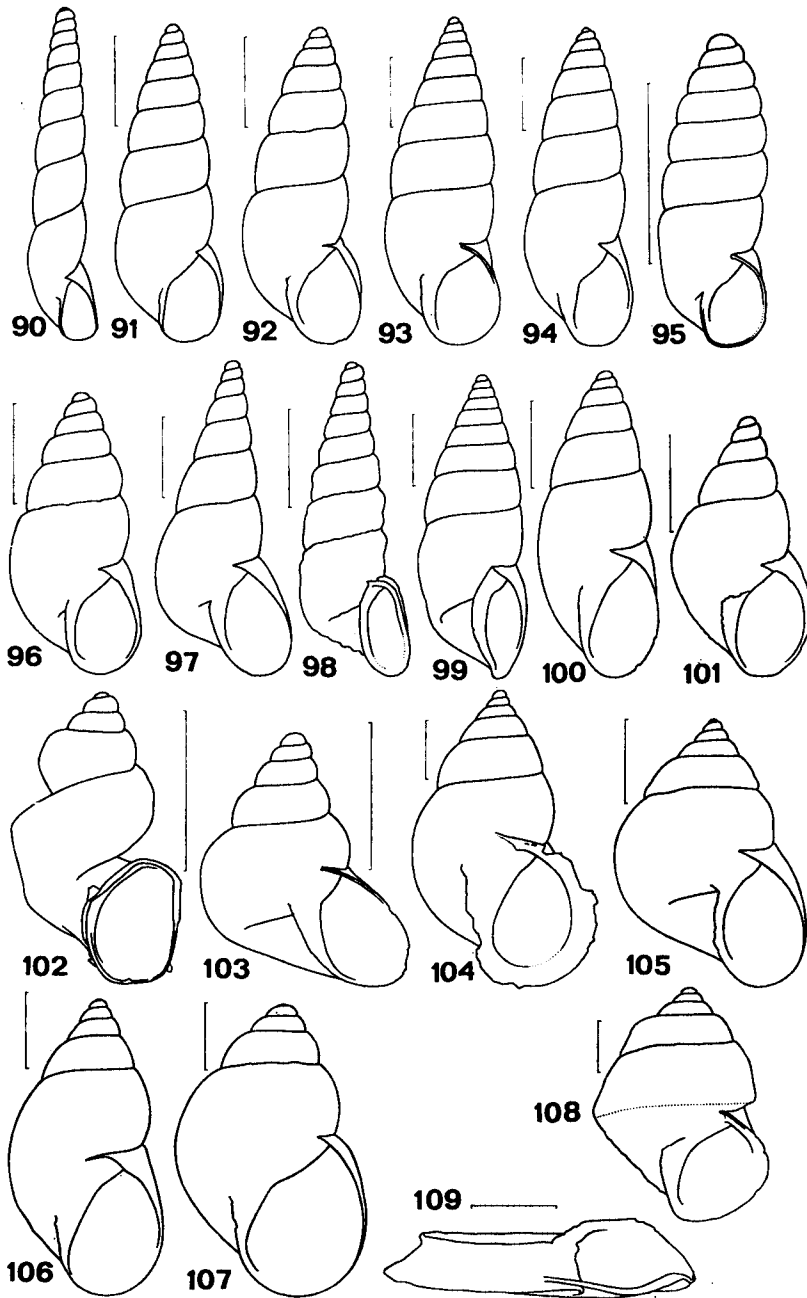
Bostryx Troschel, 1847

Bostryx Troschel, 1847: 49. Type species by monotypy: *Bulinus (Bostryx) solutus* Troschel.

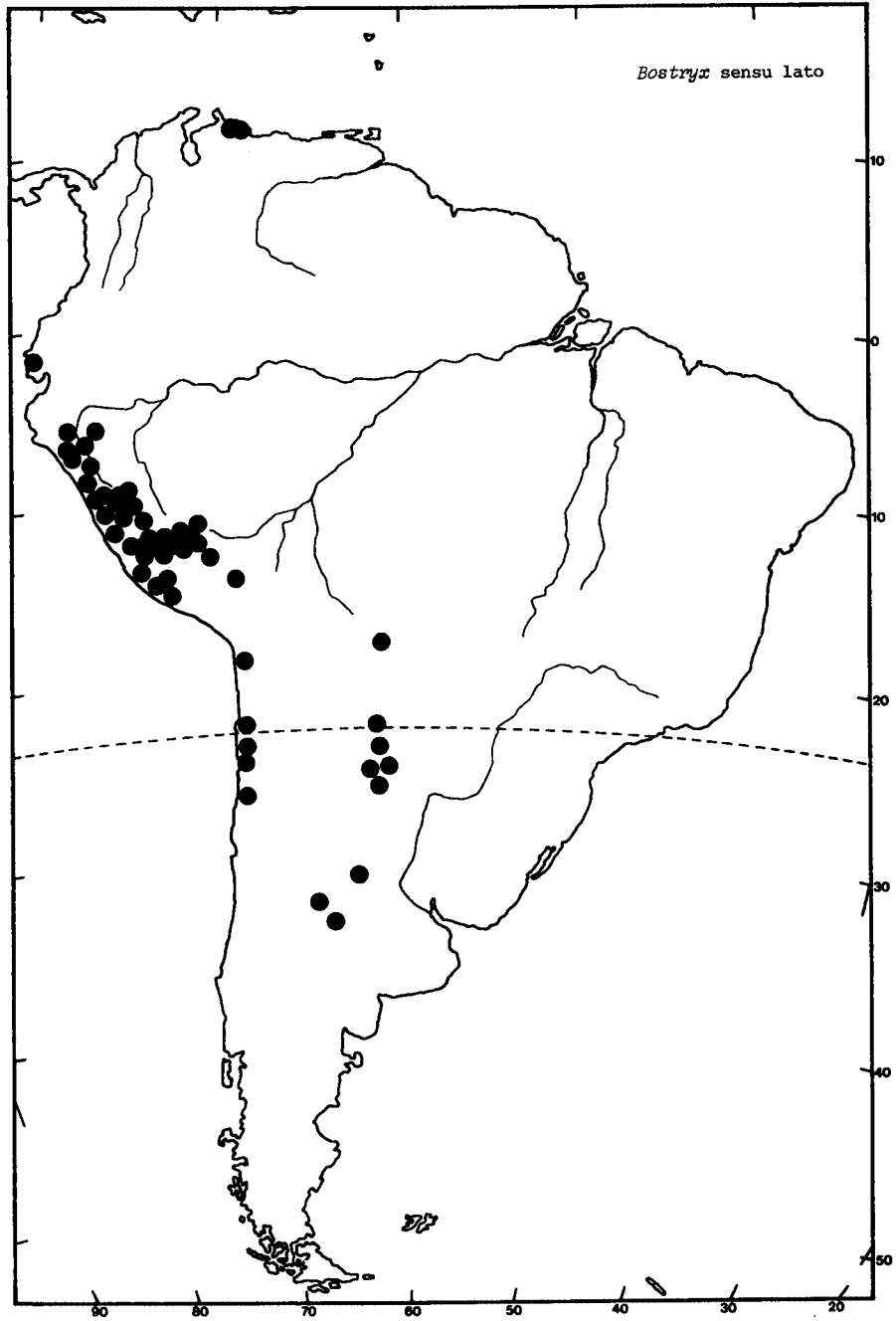
Peronaeus Albers, 1850: 163. Type species by subsequent designation (Albers, 1860): *Bulinus pupiformis* Broderip.

Ataxus Albers, 1850: 164. Type species by monotypy: *Bulinus umbilicaris* Souleyet.

Pyrgus Albers, 1850: 177. Type species by monotypy: *Bulinus turritus* Broderip.



Figs. 90-109. Variation in shell shape in *Bostryx*. Fig. 90. *B. bermudezae* Weyrauch. Fig. 91. *B. elatus* (Philippi). Fig. 92. *B. hamiltoni* (Reeve). Fig. 93. *B. obeliscus* Zilch. Fig. 94. *B. arcuatus* Breure. Fig. 95. *B. tschudii* (Troschel). Fig. 96. *B. pustulosus* (Broderip). Fig. 97. *B. obliquiportus* Weyrauch. Fig. 98. *B. tubulatus scalaricostus* (Morelet). Fig. 99. *B. infundibulum infundibulum* (Pfeiffer). Fig. 100. *B. chagualensis* Pilsbry. Fig. 101. *B. scalariformis* (Broderip). Fig. 102. *B. solutus* (Troschel). Fig. 103. *B. frederici* Breure. Fig. 104. *B. rhodolarynx apurimacensis* (Dall). Fig. 105. *B. megomphalus* Pilsbry. Fig. 106. *B. conspersus* (Sowerby). Fig. 107. *B. erythrostomus* (Sowerby). Fig. 108. *B. reentsi* (Philippi). Fig. 109. *B. planissimus* Pilsbry & Olsson. Scale = 5 mm.

Fig. 110. Distribution of *Bostryx sensu lato*.

- Geopyrgus* Pilsbry, 1896a: 114. New name for *Pyrgus* Albers, 1850 not Hübner, 1816.
- Lissoacme* Pilsbry, 1896a: 114. Type species by original designation: *Bulimus erythrostoma* Sowerby.
- Platybostryx* Pilsbry, 1896b: 129. Type species by monotypy: *Bulimulus eremothauma* Pilsbry.
- Geoceras* Pilsbry, 1896b: 136. Type species by original designation: *Bulimus columellaris* Reeve.
- Dentaxis* Pilsbry, 1902a: xxxi. Type species by monotypy: *Bulimulus dentaxis* Pilsbry.
- Phenacotaxus* Dall, 1912a: 7. Type species by original designation: *Bulimulus infundibulum umbilicatellus* Pilsbry.
- Ataxellus* Dall, 1912a: 7. Type species by original designation: *Phenacotaxus (Ataxellus) spiculatus pectinatus* Dall.
- Scansicohlea* Pilsbry, 1930c: 358. Type species by original designation: *Bulimulus (Scansicohlea) bromeliarum* Pilsbry.
- Scansicohlea* Thiele, 1931: 656. Type species by monotypy: *Bulimulus (Scansicohlea) bromeliarum* Pilsbry.
- Discobostryx* Pilsbry & Olsson, 1949: 11. Type species by monotypy: *Bostryx (Discobostryx) planissimus* Pilsbry & Olsson.
- Vermetellus* Haas, 1951: 520. Type species by monotypy: *Bostryx (Vermetellus) metagyra* Pilsbry & Olsson.
- Pseudoperonaeus* Weyrauch, 1958: 111. Type species by monotypy: *Bostryx (Pseudoperonaeus) bermudezae* Weyrauch.
- Elatibostryx* Weyrauch, 1958: 112. Type species by original designation: *Bostryx (Elatibostryx) imeldae* Weyrauch.
- Pampasimus* Weyrauch, 1958: 113. Type species by original designation: *Bostryx weyrauchi* Pilsbry.
- Multifasciatus* Weyrauch, 1958: 116. Type species by original designation: *Bulimus subroseus* Pfeiffer.
- Bilamelliferus* Weyrauch, 1958: 118. Type species by monotypy: *Bulimus tschudii* Troschel.
- Kionoptyx* Haas, 1966: 239. Type species by original designation: *Kionoptyx sagasteguii* Haas.
- Naesiotellus* Weyrauch, 1967a: 414. Type species by monotypy: *Naesiotus (Naesiotellus) latecolumellaris* Weyrauch.
- Floreziellus* Weyrauch, 1967b: 488. Type species by monotypy: *Floreziellus florezi* Weyrauch.

Description. — Shell (depressed-)conical to elongate-ovate, globose or discoid; (narrowly) perforate to rimate; rather thin. Colour whitish, brownish or bluish, uniform or with darker spiral lines and/or spots. Protoconch with numerous, fine spiral lines, sometimes smooth or with indistinct axial wrinkles or riblets (never as strong and regular as in *Naesiotus* species). Whorls slightly convex (in some species the last whorl is keeled); suture well impressed. Aperture (sub)ovate to triangular-ovate (in some species adnate). Peristome simple or slightly expanded, in some species continuous. Columella usually simple, sometimes with a lamella within the last whorls.

Central teeth of the radula are tricuspid (mesocones lanceolate and ectocones ovate to deltoid) or monocuspid (with blunt, deltoid cones). Latero-marginal teeth bicuspid (with elongate to lanceolate mesocones and ovate to

deltoid ectocones, which may be serrate in the outermost teeth) or monocuspid (with blunt, conical cones). Half-row formula: $C/3 + LM\ x/2$ ($x = 16-31$) or $C/1 + L\ x/1 + M\ y/2$ ($x = 6-19, y = 13-31$).

Pericard half as long as to as long as the nephridium, which is (narrowly) triangular. The main pulmonary vein is moderately to well developed, side veins are weakly to well developed. The adrectal ureter is closed or partially open ($1/10-1/3$ of its length).

Penis usually with a proximal sheath. The lumen of the penis is lined with two types of epithelium and is rather narrow, especially at the transition to the distal part of the penis. In the distal part a circular gland is present, which is externally visible as a swelling. The transition to the epiphallus, both internally and externally, is gradual. The flagellum is slender, with a distally attached retractor muscle. The spermathecal duct is more or less subcylindrical. The spermatheca is globose.

Distribution. — Venezuela (?), N-Argentina, Bolivia, Chile, Peru, Ecuador.

Ecology. — The species usually live on the ground in leaf litter or in shrubs, were they are generally found in dormancy. Some species live on rock-faces. The vertical distribution is 0-3600 m.

Relationships. — The phylogenetic relationships of this genus are discussed on page 151.

Remarks. — It has been mentioned before (Breure, 1978b) that a number of species groups may be recognized within *Bostryx* (sensu lato) that correspond more or less with some of the 'subgenera' listed in the above-mentioned synonymy. There are, however, a rather large number of taxa that can not be allocated to one of these species groups and it is preferred, therefore, to treat the genus here sensu lato.

Bibliography. — The main publications on this genus are: Breure, 1978b; Dall, 1912a; Haas, 1955b; Hylton Scott, 1967b; Parodiz, 1947; Pilsbry, 1896b, 1930c, 1932, 1944b; Rehder, 1945; Weyrauch, 1958, 1960a, 1960c, 1964, 1967a, 1967b.

Taxa. — The following taxa are placed in this genus:

abancayensis, *Bostryx*, Pilsbry, 1944b: 123, pl. 11 fig. 20 (Peru, Abancay, 2300 m) [HT ANSP 180001].

acalles, *Bulimus*, Pfeiffer, 1853b: 258 (Peruvian Andes).

acme, *Bulimulus* (*Peronaeus*), Haas, 1955b: 325, fig. 68 (Peru, Apurimac, Andahuaylas, Ongoy, altura de la Hacienda Mozobamba) [HT FMNH 51355].

acromelas, *Bulimus*, Morelet, 1863: 202, pl. 11 fig. 1. ([Peru] vallée d'Ayacucho et dans celle de l'Urubamba).

aequicostata, *Peronaeus*, Rehder, 1945: 5 (New name for *Bulimus scalarioides* Pfeiffer, 1867, not *Bulimus scalarioides* Reeve, 1849).

- affinis*, *Bulinus*, Broderip in Broderip & Sowerby, 1832b: 106 (Peruviã, Mexillones, desert of Atacama).
- agueroi*, *Bostryx* (*Peronaeus*), Weyrauch, 1960c: 126, pl. 12 figs. 39-41 (M-Peru, Fundo Yacca, auf der rechten Seite des Río Canete, an der Autostrasse von Canete nach Yauyos, 2300 m) [HT SMF 162150].
- aguilari*, *Bostryx* (*Bostryx*), Weyrauch, 1967a: 349, figs. 2-6 (Peru, Lomas de Amancaes, 200-250 m) [HT SMF 162163].
- aileenae*, *Bostryx*, Breure, 1978b: 49, pl. 1 fig. 6 (Peru, Dept. Lima, Río Cañete valley, 1 km above Puente Auco, 2070 m) [HT RMNH 55158].
- albescens*, *Bulimulus* (*Bostryx*) *moniezi*, Dautzenberg, 1896: 225, pl. 7 figs. 4-5 (Haut-Pérou).
- albicolor*, *Bulinus*, Morelet, 1863: 199, pl. 11 fig. 9 ([Peru], Huanta et la vallée de l'Apurimac) [ST BMNH, MHNG].
- anachoreta*, *Bulinus*, Pfeiffer, 1856c: 208 (Paposo in deserto Atacamensi reipublicae Chilensis).
- andoicus*, *Bulinus*, Morelet, 1863: 198, pl. 11 fig. 13 ([Peru] vallée d'Ayacucho) [LT BMNH 1893.2.4.171].
- angelmaldonadoi*, *Bostryx* (*Bostryx*) *modestus*, Weyrauch, 1960a: 31, pl. 3 figs. 11-12 (M-Peru, Lomas ö. [E] Pachacamac, 450 m, auf der linken Seite des Río Lurin, 35 km sö [SE] Lima) [HT SMF 155595].
- angiportus*, *Bulimulus* (*Peronaeus*), Pilsbry, 1932: 393, pl. 28 figs. 11-13 (Peru, west side of the Marañon River, near Chagual, 4000-6000 ft.) [HT ANSP 159899a].
- angispira*, *Bostryx* (*Bostryx*) *obliquiportus*, Weyrauch, 1960c: 123, pl. 11 fig. 19 (M-Peru, Quichao, 5 km von Laraos, auf der linken Seite des Río Canete, 3450 m) [HT SMF 162183].
- angrandianus*, *Bulimulus*, Pilsbry, 1897a: 19 (New name for *Bulinus radiatus* Morelet, 1863, not Bruguière, 1789).
- anomphalus*, *Bostryx* (*Peronaeus*), Pilsbry, 1944b: 123, pl. 11 fig. 7 (Peru, Santa Eulalia valley, near Chosica) [HT ANSP 180002a].
- apertus*, *Neopetraeus stelzneri*, Hylton Scott, 1948a: 238, pl. 2 figs. 4-5 ([Argentina] Salta, Cerro Colorado) [HT MIHS].
- apurimacensis*, *Bulinus* (*Scutalus?*), Dall, 1917a: 10 (Peru, Apurimac valley, near Paseje) [HT USNM 251835].
- arcuatus*, *Bostryx*, Breure, 1978b: 52, pl. 7 figs. 6-7 (Peru, Dept. Cajamarca, Hacienda Montesecco (06°52' S 79°05' W)) [HT SMF 249625].
- ascendens*, *Bostryx derelictus*, Pilsbry, 1944b: 123, pl. 11 fig. 14 (Peru, Ninabamba near Ayacucho, 1900 m) [HT ANSP 180017].
- atacamensis*, *Bulinus*, Pfeiffer, 1856c: 207 (Paposo in deserto Atacamensi reipublicae Chilensis) [LT BMNH 1975312].
- avus*, *Peronaeus* (*Lissoacme*) *torallyi*, Parodiz, 1947: 20 ([Argentina] prov. Salta, Cachi) [HT MACN 3236].
- baeri*, *Peronaeus*, Dautzenberg, 1901a: 131 (Pérou, Iocos) [HT IRSN].
- balsanus*, *Bulinus*, Morelet, 1863: 192, pl. 9 fig. 8 ([Peru] Balsa de Cocharcas) [LT BMNH 1893.2.4.173].
- beltrani*, *Bostryx* (*Peronaeus*) *agueroi*, Weyrauch, 1964: 52, figs. 9-10 (Perú central, entre Laraos y Tintín, sobre la margen izquierda del río Canete, 3450 m) [HT SMF 162152].
- bermudezae*, *Bostryx* (*Pseudoperonaeus*), Weyrauch, 1958: 111, pl. 9 figs. 38-40 (M-Peru, Laraos, 3600 m, im Tale des Río Canete, 155 km ösö Lima [in Weyrauch, 1960c: 124 corrected to Quichao, 5 km from Laraos]) [HT SMF 156350].
- bicolor*, *Naesiotus* (*Naesiotus*), Weyrauch, 1967a: 408, fig. 83 (Sur de Perú, Sicuani, 3200 m) [HT IML (WW 3987)].
- bilineatus*, *Bulinus*, Sowerby, 1833b: 37 (Sanctam Elenam [Ecuador] et in Columbia Occidentali).

- binghami*, *Bulimulus* (*Lissoacme*), Dall, 1910: 180, fig. 2 (Peru, banks of the Rio Pampas) [HT USNM 209270].
- birabeni*, *Peronaeus* (*Lissoacme*), Hylton Scott, 1948b: 272, pl. 1 figs. 4-10 ([Argentina] Salta, Embarcación) [HT MIHS].
- bisculptus*, *Bulimus*, Pfeiffer, 1869: 89 (Huancayo Peruviae).
- bonneti*, *Bulimulus*, Ancey, 1902: 40, fig. 1 (Bolivie) [HT MNHN].
- bromeliarum*, *Bulimulus*, Pilsbry, 1930c: 358, fig. 1, pl. 31 figs. 11-12 (Peru, Dept. Lima, Rio Chillón, near Viscas, 2200-2300 m) [HT ANSP 142536].
- cactorum*, *Helix*, d'Orbigny, 1835: 10 (provincia Tacnacensi, rep. Peruviana).
- calchaquimus*, *Peronaeus*, Döring, 1879: 64 ([Argentina] Sierra de Belén (Catamarca)).
- carinatus*, *Bostryx*, Breure, 1978b: 54, pl. 10 figs. 3-5 (Peru, Dept. Ancash, 5 km SW Chavin de Huantar, 3300 m) [HT UF 22795].
- catamarcanus*, *Bulimulus* (*Scansicocchlea*), Parodiz, 1956: 77, fig. 6 ([Argentina] Concepción, provincia de Catamarca) [HT MACN].
- ceratacme*, *Bulimus*, Pfeiffer, 1855f: 8 (Peru?) [LT BMNH 1975347].
- cereicola*, *Bulimus*, Morelet, 1863: 192, pl. 9 fig. 7 ([Peru] vallées d'Abancay et d'Ayacucho, à l'ouest du Cuzco) [ST BMNH].
- ceroplasta*, *Bulimulus*, Pilsbry, 1896b: 159, pl. 50 figs. 38-39 (Peru, Marañon River, Balsas) [LT ANSP 25468].
- chacoensis*, *Bulimulus* (*Drymaeus*), Preston, 1907: 491, fig. 5 (Bolivia, Chaco, north of the Río Pilcomayo, 600 m).
- chagualensis*, *Bostryx* (*Peronaeus*), Pilsbry, 1932: 393, pl. 28 fig. 10 (Peru, west side of Marañon River, around Chagual, 4000-6000 ft.) [HT ANSP 159901a].
- chusgonensis*, *Bostryx* (*Bostryx*), Weyrauch, 1960a: 30, pl. 3 figs. 16-17 (N-Peru, Hacienda Santa Elena (1550 m), auf der rechten Seite des Río Chusgon, westlicher Zufluss des Marañon, 180 km nördlich Trujillo) [HT SMF 162013].
- cicheroi*, *Bulimulus* (*Scansicocchlea*), Hylton Scott, 1967b: 7, figs. 5-9 ([Argentina] San Luis, Quebrada de Cautana) [HT MIHS].
- circuliportus*, *Bostryx*, Breure, 1978b: 57, figs. 72-76, pl. 2 fig. 10 (Peru, Dept. Lima, Río Chillón, 11.5 km SW Canta, 2270 m) [HT RMNH 55169].
- claviformis*, *Bulimulus* (*Peronaeus*), Haas, 1951: 515, fig. 103 (Peru, Abancay) [HT FMNH 31212].
- climacographus*, *Bulimulus*, Holmberg, 1912b: 147, figs. 1-2 (Argentina, in Provincia Salta, prope marginem Río de las Piedras) [LT MACN 1349].
- coelhoi*, *Bostryx*, Breure, 1978b: 61, figs. 80-85 (Peru, Dept. Ancash, 7 km NE San Marcos, 2720 m) [HT UF 22799].
- coerulescens*, *Bulimus*, Pfeiffer, 1858: 257 (Peru, Andes of Prov. Patas).
- cokerianus*, *Bulimulus*, Dall, 1909: 164, pl. 23 fig. 3 ([Peru] peaks of Vieja Island, Independencia Bay, 1200 feet) [HT USNM 207700].
- columellaris*, *Bulimus*, Reeve, 1849: pl. 73 fig. 528 (Andes of Caxamarca, Peru, 12000 feet).
- columna*, *Neopetraeus coerulescens*, Pilsbry, 1898: 180, pl. 29 figs. 35-37 (Peru).
- compactus*, *Bostryx* (*Bostryx*) *zilchi*, Weyrauch, 1960c: 125, pl. 12 figs. 27-28 (M-Peru, am Fusspfad von Laraos nach Tintín, auf der linken Seite des Río Canete, 3450 m) [HT SMF 162156].
- compactus*, *Bulimulus*, Fulton, 1901: 69 (Bolivia, Chicani) [HT BMNH 1902.5.28.1].
- conospirus*, *Scutalus*, Döring, 1879: 67 ([Argentina] Sierra de Tucumán).
- conspersus*, *Bulimus*, Sowerby, 1833b: 73 ([Peru] collinis prope Lima).
- cordillerae*, *Bulimulus* (*Mesembrinus*), Strobel, 1874: 22, pl. 1 fig. 3 ([Argentina] Gola di Villa Vicencio e Casa de Piedra nella Preande Mendocine) [ST ZMB].
- corrugatus*, *Peronaeus* (*Lissoacme*) *torallyi*, Parodiz, 1947: 19, fig. 9 ([Argentina] prov. Tucumán, Villa Nougues) [HT MACN 25987].
- costatus*, *Bostryx* (*Bostryx*) *pygmaeus*, Weyrauch, 1960c: 122, pl. 11 figs. 12-16 ([Peru,

- Dept. Lima] Bei Alis, auf der rechten Seite des Río Alis, Zufluss des Río Canete, 3300 m) [HT SMF 162098].
- costellatus*, *Bulimulus* (*Scansicochlea*), Hylton Scott, 1971: 77, fig. 2c ([Argentina] Salta, Cerro de Cachi) [HT MACN 4221].
- costifer*, *Bostryx* (*Elatibostryx*) *imeldae*, Weyrauch, 1960c: 129, pl. 12 figs. 35-38 (M-Peru, Quichao, 5 km von Laraos, am Fusspfad nach Yauyos, im Tale des Río Canete, 3500 m) [HT SMF 162101].
- cracentis*, *Bostryx*, Breure, 1978b: 67, figs. 88-93 (Peru, Dept. Ancash, 5 km SW Chavin de Huantar, 3300 m) [HT UF 22816].
- crucilineatus*, *Bostryx* (*Peronaeus*), Weyrauch, 1967a: 361, fig. 14 (Peru central, 70 km al noroeste de Lima, valle del río Santa Eulalia, 2500 m) [HT IML 1241].
- cunyacensis*, *Bostryx*, Breure, 1978b: 68 (New name for *Floreziellus florezi* Weyrauch, 1967, not *Phenacotaxus* (*Ataxiellus*) *florezi* Weyrauch, 1967).
- curtus*, *Bulimus*, Koch in Philippi, 1844: 158, pl. 2 fig. 8 (Chili).
- cuspidatus*, *Bulimus*, Morelet, 1863: 210, pl. 11 fig. 7 ([Peru] à Cochabambilla sur les bords de l'Apurimac, et dans les gorges de Chachapoyas).
- cuyana*, *Helix*, Pfeiffer, 1867: 79 (in provincia Mendoza Peruviae [sic; Argentina]).
- cylindricus*, *Bostryx* (*Pseudoperonaeus*), Weyrauch, 1960c: 127, pl. 11 fig. 3 (M-Peru, 1 km von Laraos, auf der rechten Seite des Río Mayo, Zufluss des Río Canete, 3500 m) [HT SMF 162107].
- delicatulus*, *Bulimus*, Philippi, 1867: 73 ([Peru, Dept. La Libertad] hacienda de Ungambal).
- delumbis*, *Bulimus*, Reeve, 1849: pl. 76 fig. 555 [no type locality given; LT BMNH 1975558].
- dendritoides*, *Bulimus*, Pilsbry, 1896b: 186, pl. 50 figs. 60-61 (New name for *Bulimus monticola* Philippi, 1869, not Roth, 1856).
- denekei*, *Orthalicus* (*Rabdotus*), Adams & Adams, 1855: 158 [emendation for *denickei* Gray, 1852].
- denickei*, *Bulimus*, J. E. Gray, 1852: 92 ([Peru] Chala, near Callao) [ST BMNH].
- dentaxis*, *Bulimulus*, Pilsbry, 1901: 143, pl. 25 figs. 16-17 (Peru) [LT ANSP 25653a].
- depstus*, *Bulimus*, Reeve, 1849: pl. 73 fig. 525, text no. 524 (Chachapoyas, Peruvian plateau) [LT BMNH 1975318].
- derelictus*, *Bulimus*, Broderip, in Broderip & Sowerby, 1832b: 107 (Cobijam Bolivia [Chile, Cobija]).
- devians*, *Bulimus*, Dohrn, 1863: 155 [no type locality given].
- devillei*, *Bulimus*, Deville & Hupé, 1850: 641, pl. 15 fig. 3 (Pérou, mission de Sarayacu) [LT MNHN].
- doelloi*, *Bostryx* (*Platybostryx*), Hylton Scott, 1953: 412, figs. 1-4 (Argentina, Mendoza, Cerro Pelado) [HT MACN 9592].
- elatus*, *Bulimus*, Philippi, 1869: 33 (Peruvia, lectus est in Pampa inter Mayoc et Huanta . . . , et prope pontem Pichicna, 2 leucas ab Icucha, depti Huancavelica).
- emaciatius*, *Bulimus*, Morelet, 1863: 201, pl. 11 fig. 10 ([Peru] depuis Ayacucho jusqu'au Cuzco) [LT MHNG].
- endoplax*, *Bostryx* (*Phenacotaxus*), Pilsbry, 1944b: 124, pl. 11 fig. 9 (Peru, near Ayacucho, Ninabamba, 1900 m) [LT ANSP 180006a].
- endoptyx*, *Bulimulus* (*Phenacotaxus*), Pilsbry, 1940: 4, figs. 2b-d (Peru, Huánuco) [HT ANSP 175773].
- eremothauma*, *Bulimulus*, Pilsbry, 1896b: 129, pl. 44 figs. 83-86 (New name for *Helix reentsii* Philippi, 1855, not *Bulimus reentsii* Philippi, 1851).
- erythrostroma*, *Bulinus*, Sowerby, 1833b: 37 (Huasco, Chilae).
- extensus*, *Bulimulus* (*Peronaeus*), Haas, 1955b: 323, fig. 67 (Peru, Apurimac, Andahuaylas, Hacienda Palmira) [HT FMNH 51312].
- famatimus*, *Peronaeus*, Döring, 1879: 63 ([Argentina] Sierra de la Rioja, cuesta entre esta ciudad [La Rioja] y Chilecito, 2000 m) [ST MACN 3233].
- ferrugineus*, *Bulimus*, Reeve, 1849: pl. 62 fig. 424 (Peru) [LT BMNH 1975380].

- fisheri*, *Bostryx* (*Platybostryx*), Pilsbry, 1956: 92, pl. 5 figs. 4-5 (Peru, below Tarma, on the Tarma-Chanchamayo road) [HT ANSP 196550a].
- flagellatus*, *Bulimulus*, Pilsbry, 1896b: 166, pl. 50 figs. 44-45 (Peru, Marañon River, Balsas) [LT ANSP 25486a].
- florezi*, *Floreziellus*, Weyrauch, 1967b: 489, figs. 7-17 (Sureste de Peru, 60 km oeste de Cuzco, Puente Cunyac, 2100 m) [HT IML (WW) 101671a].
- florezi*, *Phenacotaxus* (*Ataxellus*), Weyrauch, 1967a: 369, figs. 49-50 (Peru, 25 km de Cuzco, Pisac, 3100 m) [HT IML 10522a].
- federici*, *Bostryx*, Breure, 1978b: 77, figs. 112-116, pl. 3 figs. 7-9 (Peru, Dept. Ancash, 5 km SW Chavin de Huantar, 3300 m) [HT UF 22801].
- fuliginus*, *Bostryx*, Breure, 1978b: 79, pl. 2 figs. 5-9 (Peru, Dept. Ancash, 6 km NE San Marcos, 2730 m) [HT UF 22788].
- gayi*, *Peronaeus*, Rehder, 1945: 4 ([Chile] Antofagasta) [HT USNM 537831].
- gladysae*, *Bulimulus* (*Scansicohlea*), Hylton Scott, 1967b: 8, figs. 1-3, 10 ([Argentina] Catamarca, Pie de la Cuesta de La Chilca) [HT MLP].
- globosus*, *Bostryx* (*Lissoacme*), Weyrauch, 1967a: 355, figs. 11-12 (Peru, paredones de Nazca) [HT IML (WW) 3972a].
- glomeratus*, *Bostryx* (*Bostryx*) *zilchi*, Weyrauch, 1960c: 124, pl. 12 figs. 29-34 (M-Peru, Quichao, 5 km von Laraos, am Fusspfad nach Yauyos, im Tale des Río Canete, 3500 m) [HT SMF 162104].
- gracilis*, *Bostryx* (*Scansicohlea*), Weyrauch, 1967a: 360, fig. 1 (Peru, río Rimac, cerca de Tambo Viso, 2750 m) [HT IML 1102].
- grandiportus*, *Bostryx* (*Bostryx*) *bromeliarum*, Weyrauch, 1958: 109, pl. 8 figs. 18-19 (M-Peru, auf der rechten Seite des Río Rimac bei Tambo Viso, 2700 m) [HT SMF 156367].
- haasi*, *Bostryx* (*Bostryx*), Weyrauch, 1960a: 33, pl. 5 fig. 35 ([Peru] Unterhalb Tambo Viso, Río Rimac, 2600 m) [HT SMF 156370].
- hamiltoni*, *Bulimus*, Reeve, 1849: pl. 83 fig. 610 (Bolivia, near the Lake of Titicaca) [LT BMNH 1975329].
- hector*, *Bulimulus*, Holmberg, 1909a: 11 ([Argentina] Jujuy, Tilcara, 2000 m).
- hennahi*, *Bulimus*, J. E. Gray, 1830: 5, pl. 5 fig. 5 (Peru, Arica [teste Pilsbry, 1896b: 156]).
- hirsutus*, *Bostryx*, Breure, 1978b: 82, figs. 125-127 (Peru, Dept. Cajamarca, Río Jequetepeque valley, near Chilate, Tambo Tingo, 1000 m) [HT IML].
- holostoma*, *Bulimus*, Pfeiffer, 1846a: 28 (Cobija, Bolivia [Chile]) [LT BMNH 1975345].
- huanucensis*, *Bostryx*, Breure, 1978b: 83, figs. 128-130, pl. 1 figs. 1-4 (Peru, Dept. Huánuco, 13.1 km N Huánuco, 2040 m) [HT UF 22757].
- huarazensis*, *Bostryx*, Pilsbry, 1944b: 121, pl. 11 fig. 17 (Peru, Santa valley, Huaraz, 3100 m) [HT ANSP 180000].
- huascensis*, *Bulimus*, Reeve, 1848: pl. 23 fig. 147 (Chili, Huasco) [LT BMNH 1975159].
- hybrida*, *Neopetraeus stelsneri*, Parodiz, 1948: 12 (Argentina, Cerro Velasco, Prov. La Rioja, 2700 m) [HT MACN 433].
- hyltonscottae*, *Bulimulus* (*Scansicohlea*), Parodiz, 1956: 59, figs. 1-4 ([Argentina] El Zapallar, Quines, Prov. San Luis) [HT MACN].
- ignobilis*, *Bulimus*, Philippi, 1867: 72 ([Peru, Dept. Junín] prope Chanchamayo).
- imeldae*, *Bostryx* (*Elatibostryx*), Weyrauch, 1958: 113, pl. 9 fig. 37 (M-Peru, Laraos, 3600 m, im Tale des Río Canete, 155 ösö Lima [corrected to Quichao, 5 km from Laraos (Weyrauch, 1960c: 124)]) [HT SMF 156347].
- inaquosum*, *Bostryx*, Breure, 1978b: 92 (New name for *Peronaeus philippii* Rehder, 1945, not *Bulimus philippii* Pfeiffer, 1842 [sec. homonymy]).
- inflatiportus*, *Bostryx* (*Bostryx*) *obliquiportus*, Weyrauch, 1960c: 123, pl. 12 figs. 22-26 (M-Peru, bei Alis, auf der rechten Seite des Río Alis, Zufluss des Río Canete, 3300 m) [HT SMF 162144].

- inflatus*, *Bulimus*, Broderip, 1836: 45 (Ambo, Peruviae).
- infundibuliformis*, *Bulimus*, Jay, 1848: 169, pl. 10 fig. 7 (interior of Bolivia).
- infundibulum*, *Bulimus*, Pfeiffer, 1853b: 255 (Andibus Peruvianis) [LT BMNH 1975163].
- iocosensis*, *Peronaeus*, Dautzenberg, 1901a: 131 (Pérou, Iocos) [ST IRSN].
- ischnus*, *Bulimulus*, Pilsbry, 1902a: lxxi (New name for *Bulimus terebralis* Pfeiffer, 1842, not Bruguière, 1789).
- izozoensis*, *Peronaeus*, Parodiz, 1947: 3, fig. 1 (Bolivia, Depto Santa Cruz de la Sierra, Llanos de Izozo, de Joseable a fortín El Puquio) [HT MACN 25953].
- juana*, *Thaumastus*, Cousin, 1887: 228, pl. 4 fig. 10 ([Ecuador] Gualacco, province de Cuenca) [LT MNHN].
- kathiae*, *Bostryx*, Breure, 1978b: 92, figs. 138-141 (Peru, Dept. Lima, Río Cañete valley, 1 km above Puente Auco, 2070 m) [HT RMNH 55175].
- kugleri*, *Leiostracus* (?), Forcart, 1954: 58, fig. 1 (Venezuela, Est. Falcón, Distr. Colina, Porta Juela near Cumarebo) [HT NMB 4950a].
- lactifluus*, *Bulimus*, Pfeiffer, 1857a: 330 (Chili).
- laraosensis*, *Bostryx* (*Bostryx*) *obliquiportus*, Weyrauch, 1960c: 124, pl. 11 figs. 20-21 (M-Peru, Quichao, 5 km von Laraos, am Fusspfad nach Yauyos, im Tale des Río Canete, 3500 m) [HT SMF 162187].
- latecolumellaris*, *Naesiotus* (*Naesiotellus*), Weyrauch, 1967a: 415, figs. 71-72 (Peru, 1 km más arriba del Puente El Auco, sobre la margen derecha del río Canete, 2100 m) [HT IML 1076].
- laurentii*, *Bulimus*, Sowerby, 1833b: 37 (Peruvia).
- lemniscatus*, *Bulimus*, Deshayes in Deshayes & Milne Edwards, 1838: 271 (Pérou).
- lentiformis*, *Bostryx*, Breure, 1978b: 96, fig. 143, pl. 10 figs. 8-10 (Argentina, Prov. San Juan, Sierra del Tontal, 3500 m) [HT MACN 12113a].
- lesueureanus*, *Bulimus*, Morelet, 1860: 374 [Peru, Pomacocha; ST BMNH].
- leucostictus*, *Bulimus*, Philippi, 1856: 53 (Paposo, reipublicae Chilensis).
- lichenorum*, *Bulimus*, Reeve, 1848: pl. 14 fig. 83 (Cobija; Chilon, Bolivia) [not *Helix lichenorum* d'Orbigny, 1835].
- lichenum*, *Cochlicella*, Beck, 1837: 63 [indication] (Bolivia).
- lichenorum*, *Helix*, d'Orbigny, 1835: 20 (Cobija, republica Boliviana [Chile]).
- limensis*, *Bulimus*, Reeve, 1849: pl. 77 fig. 563 (Lima and Quito, South America) [LT BMNH 1975326].
- limonoica*, *Helix*, d'Orbigny, 1835: 13 (provincia Chiquitensi, republica Boliviana) [LT MNHN].
- lizarasosae*, *Bostryx* (*Pseudoperonaeus*), Weyrauch, 1967a: 363, figs. 38-39 (Peru central, Cerro Arcupumco cerca de Ambo, valle del río Huallaga, 2200 m) [HT SMF 162009].
- lolae*, *Bulimulus* (*Scansicochlea*), Hylton Scott, 1967b: 11, figs. 4, 11 ([Argentina] Calamuchita, foot of Champaquí, borders of Río Reartes, 1500 m) [HT MACN].
- longinquus*, *Bulimus*, Morelet, 1863: 195, pl. 11 fig. 2 ([Peru] Limatambo, Ollantañambo, Yucay et Piré) [LT MHNG].
- longispira*, *Bostryx* (*Pseudoperonaeus*), Weyrauch, 1960c: 128, pl. 11 figs. 4-5 (M-Peru, an der Autostrasse von Magdalena nach Yauyos, auf der rechten Seite des Río Canete, 2600 m) [HT SMF 162112].
- lorenzii*, *Bulimus*, d'Orbigny, 1837: 281 [emendation for *laurentii* Sowerby].
- louisae*, *Bostryx*, Breure, 1978b: 100, figs. 146-147 (Peru, Dept. Apurímac, 19.5 km SW Abancay, 1960 m) [HT RMNH 55212].
- lychnorum*, *Bulimus*, Sowerby, 1838?: figs. 81-82 [no type locality given; not *Helix lichenorum* d'Orbigny, 1835].
- martinezi*, *Bulimulus* (*Scansicochlea*), Hylton Scott, 1965: 25, fig. ([Argentina] Chancani, Sierra de Pocho, Córdoba) [HT MIHS].
- megomphalus*, *Bostryx*, Pilsbry, 1944b: 122, pl. 11 figs. 15-16 (Peru, Acobamba near Tarma, 3200-3400 m) [HT ANSP 180036a].

- mejillonensis*, *Bulimus*, Pfeiffer, in Pfeiffer & Dunker, 1857: 230 (mejillones in deserto Atacamensi) [LT BMNH 1975322].
- metagyra*, *Bostryx*, Pilsbry & Olsson, 1949: 9, fig. 13 (Peru) [HT ANSP 184899].
- minor*, *Bostryx* (*Bostryx*) *haasi*, Weyrauch, 1960a: 35, pl. 5 fig. 34 (M-Peru, auf der rechten Seite des Río Rimac, gegenüber der Selterswasserquelle San Mateo (3300 m), 90 km nördlich Lima) [HT SMF 156371].
- minuta*, *Neopetraeus stelzneri conispirus*, Parodiz, 1948: 18 (Argentina, prov. Catamarca, Fiambalá) [HT MACN 6243].
- modestus*, *Bulimus*, Broderip, in Broderip & Sowerby, 1832b: 106 (Peruviae montibus, Huacho).
- moniezi*, *Bulimulus* (*Bostryx*), Dautzenberg, 1896: 224, pl. 7 fig. 3 (Haut Pérou) [ST BMNH].
- monticola*, *Bulimulus*, Döring, 1879: 69 ([Argentina] Sierra de los Granadillos (Catamarca) y en la cuesta de Tocina (Sierra de Famatina), 3300-4000 m).
- monticola*, *Bulimus*, Philippi, 1869: 33 (Peruviae, leucas ad orientem oppidi Huancayo, in regione "la Sierra").
- mordani*, *Bostryx*, Breure, 1978b: 103, pl. 3 fig. 3 (Peru, Dept. Lima, Río Santa Eulalia valley, 3 km above Autisha, 2500 m) [HT RMNH 55205].
- multilineatus*, *Bostryx*, Breure, 1978b: 103, pl. 7 figs. 11-13 (Peru, Dept. Ancash, below Colca, 2100 m) [HT IML 3080a].
- multivolvis*, *Bostryx* (*Geoceras*), Pilsbry, 1944b: 124, pl. 11 fig. 19 (Peru, near Ayacucho, Ninabamba, 2000 m) [HT ANSP 179994].
- nanus*, *Bulimus*, Reeve, 1849: pl. 79 fig. 585 (Chili) [ST BMNH].
- nigropileatus*, *Bulimus*, Reeve, 1849: pl. 73 fig. 524, text no. 525 (Chachapoyas Alto-Peru) [LT BMNH 1975335].
- nonogastanus*, *Neopetraeus stelzneri*, Parodiz, 1948: 13 (Argentina, prov. La Rioja, Nonogasta) [HT MACN 17591].
- obeliscus*, *Bostryx* (*Peronaeus*), Zilch, 1954: 78, pl. 6 figs. 12-16 (M-Peru, bei Autisha am Río Santa Eulalia, oberhalb Lima) [HT SMF 136762].
- obliquiportus*, *Bostryx* (*Bostryx*), Weyrauch, 1958: 110, pl. 9 figs. 35-36 (M-Peru, Laraos, 3600 m, im Tale des Río Canete, 155 km östlich [ESE] Lima) [HT SMF 156353].
- olmosensis*, *Bostryx*, Breure, 1978b: 106, pl. 7 figs. 8-9 (Peru, Dept. Lambayeque, road Olmos-Jaén (ca. 21 km ENE Olmos), 500-700 m) [HT SMF 249627].
- orophilus*, *Bulimus*, Morelet, 1863: 189, pl. 9 fig. 6 ([Peru] Talavera, Silque, Incahuasi et Mollepata) [LT BMNH 1893.2.4.188].
- ortizi*, *Bostryx* (*Bostryx*), Weyrauch, 1967a: 352, fig. 13 (Norte de Peru, Sotopampa, entre Huamboya y La Colmena, 1600 m) [HT IML 1126].
- papillatus*, *Bulimus*, Morelet, 1860: 372 (Pérou, Pucra) [ST BMNH].
- paposensis*, *Bulimus*, Pfeiffer, 1856c: 207 (Papos in deserto Atacamensi reipublicae Chilensis) [ST BMNH].
- paraconispirus*, *Neopetraeus stelzneri peristomatus*, Parodiz, 1948: 16 (Argentina, prov. San Luis, Sierra Gigante) [HT MACN 14086].
- paucicostatus*, *Bostryx spiculatus*, Breure, 1978b: 125, figs. 183-186 (Peru, Dept. Cuzco, Río Vilcanota valley, 2,8 km SE Pisac, 2980 m) [HT RMNH 55197].
- pauli*, *Bostryx*, Breure, 1978b: 107, fig. 151, pl. 3 figs. 4-6 (Peru, Dept. Ancash, 1 km N Recuay, 3410 m) [HT UF 22812].
- pectinatus*, *Phenacotaxus* (*Ataxellus*) *spiculatus*, Dall, 1912a: 10 (Peru, above Ollantaytambo) [HT USNM 250263].
- peliostrum*, *Bulimus*, Philippi, 1867: 77 ([Peru, Dept. Cajamarca] inter locum "Jocos" et fluvium Maranhon).
- perforatus*, *Bulimulus* (*Ataxus*), Haas, 1951: 518, fig. 106 (Peru, Río Pampas, Ninabamba, 2000 m) [HT FMNH 30906].

- pericanus*, *Orthalicus*, Adams & Adams, 1855: 159 [emendation for *piuranus* Albers, 1854].
- peristomatus*, *Scutalus*, Döring, 1879: 66 ([Argentina] Sierra de Pocho, Quebr. de Yatan, de Mermula, etc.).
- peruvianus*, *Drymaeus torallyi*, Pilsbry, 1944b: 126, pl. 11 fig. 13 (Peru, Santa valley, Huaraz, 3100 m) [HT ANSP 180008].
- philippi*, *Bulimus*, Pfeiffer, 1842b: 120 [indication].
- philippii*, *Peronaeus*, Rehder, 1945: 3 (Chile, near Copiapó) [HT USNM 537830].
- pictus*, *Bulimus*, Pfeiffer, 1855a: 58 (Peru) [LT BMNH 1975545].
- piuranus*, *Bulimus*, Albers, 1854a: 31 (Peruvia septentrionali, prope oppidum Piura) [ST ZMB 10289].
- placitus*, *Bostryx*, Breure, 1978b: 111, figs. 153-154 (Peru, Dept. Huánuco, 7.6 km S Ambo, 2360-2380 m) [HT RMNH 55207].
- planissimus*, *Bostryx (Discobostryx)*, Pilsbry & Olsson, 1949: 12, fig. 13 (Peru?) [HT ANSP 184269a].
- platycheilus*, *Neopetraeus*, Haas, 1955b: 311, figs. 60-61 (Peru, Apurimac Dept., Andahuaylas Prov., Hacienda Palmira) [HT FMNH 51315].
- ploegerorum*, *Bostryx*, Breure, 1978b: 115, figs. 163-166, pl. 2 fig. 4 (Peru, Dept. Ancash, 5 km SW Chavin de Huantar, 3300 m) [HT UF 22791].
- poveli*, *Bostryx huamucensis*, Breure, 1978b: 115, fig. 131, pl. 1 fig. 5 (Peru, Dept. Pasco, 42.5 km NNE Cerro de Pasco, 2800 m) [HT RMNH 55199].
- productus*, *Bulimus*, Philippi, 1867: 77 ([Peru] Sierra Cotahuasi).
- pruinosis*, *Bulimus*, Sowerby, 1833b: 36 ([Chile] Coquimbo) [ST BMNH].
- ptyalum*, *Bulimulus (Lissoacme)*, Dall, 1910: 181, fig. 3 (Peru, banks of the Río Pampas) [HT USNM 209271].
- pumilio*, *Peronaeus*, Rehder, 1945: 5 (New name for *Bulimus nanus* Reeve, 1848, not Lamarck, 1804).
- pumilus*, *Bostryx spiculatus*, Breure, 1978b: 126, figs. 187-190 (Peru, Dept. Cuzco, near Calca on the left side of the Río Vilcanota (ca. 2900 m)) [HT IML 1707a].
- punctilineatus*, *Bulimulus (Scutalus)*, Haas, 1951: 517, fig. 105 (Peru, Urubamba valley, Sahuayaco, 800 m) [HT FMNH 30914].
- puntanus*, *Peronaeus (Lissoacme)*, Parodiz, 1947: 13, fig. 8 (Argentina, prov. San Luis, Cerro de Morro) [HT MACN 9917].
- pupiformis*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 105 (Chili, Huasco).
- pustulosus*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 105 (Chili, Huasco).
- pygmaeus*, *Bostryx (Bostryx)*, Weyrauch, 1960c: 121, pl. 11 figs. 10-11 ([Peru, Dept. Lima] 1 km von Alis entfernt, an der Autostrasse nach Tintín, auf der rechten Seite des Río Alis, Zufluss des Canete, 3250 m) [HT SMF 162127].
- pyrgidium*, *Bulimulus (Peronaeus)*, Haas, 1955b: 321, fig. 66 (Peru, Apurimac Dept., Andahuaylas Prov., Ongoy Distr., Hacienda Mozobamba) [HT FMNH 51310].
- radiatus*, *Bulimus*, Morelet, 1863: 188, pl. 9 fig. 2 ([Peru] vallée de Jauja et des pentes du Cuzco) [LT BMNH 1893.2.4.198].
- raimondianus*, *Bulimulus*, Pilsbry, 1896b: 167, pl. 50 fig. 40 (New name for *Bulimus spretus* Philippi, 1869, not Reeve, 1850).
- reconditus*, *Bulimus*, Reeve, 1849: pl. 76 fig. 546 [no type locality given; LT BMNH 1975189 (labelled 'Peru')].
- reedii*, *Peronaeus (Lissoacme)*, Parodiz, 1947: 10, fig. 6 (Argentina, prov. Mendoza, La Cueva) [HT MACN 10001].
- reentsi*, *Bulimus*, Philippi, 1851: 30 (Peru, bei Chala).
- reentsi*, *Helix*, Philippi, 1855: 213 ([Chile] Cachinal de la Costa [teste Pilsbry, 1896b: 129]).
- rehderi*, *Bostryx (Elatibostryx)*, Weyrauch, 1960a: 35, pl. 3 figs. 4-5 (M-Peru, 2-3 km weit von Churin, an der Autostrasse nach Oyón, Río Huaura, 2400-2450 m, zwischen Huacho und Cerro de Pasco) [HT SMF 156386].

- rhodacme*, *Bulimus*, Pfeiffer, 1842b: 50 (Huasco, Chile: prope urbem Frierina).
- rhodolarynx*, *Bulimus*, Reeve, 1849: pl. 72 fig. 518 (Banks of the Apurimac, Alto-Peru) [LT BMNH 1975434].
- rimacensis*, *Bostryx circuliportus*, Breure, 1978b: 60, figs. 77-78 (Peru, Dept. Lima, Río Rimac valley, near Surco, ca. 75 km ENE Lima, 2100 m) [HT RMNH 55170].
- rodriguezae*, *Bostryx* (*Bostryx*), Weyrauch, 1967b: 475, figs. 33-48 (Peru central, 4 km de Laraos, en el camino de herradura a Quichao, sobre la margen izquierda del riachuelo Mayo, afluente del río Canete, 3500 m) [HT IML 1125a].
- ronaulti*, *Bulimus*, Hupé, 1854: 110, pl. 3 fig. 8 ([Chile] Copiapó) [LT MNHN].
- rubescens*, *Bulimus*, Reeve, 1848: pl. 23 fig. 148 (South America).
- rudisculptus*, *Bulimulus* (*Scansicochlea*), Parodiz, 1956: 78, fig. 7 ([Argentina] Baños de Villavil, provincia de Catamarca) [HT MACN].
- rudistriatus*, *Bulimulus* (*Lissoacme*), Haas, 1955b: 318, fig. 64 (Peru, Apurimac Dept., Andahuaylas Prov., Hacienda Palmira) [HT FMNH 51342].
- rusticellus*, *Bulimus*, Morelet, 1860: 373 ([no type locality given; Peru]).
- sagasteguii*, *Kionoptyx*, Haas, 1966: 239, fig. 57 (Peru, Dept. La Libertad, Prov. Huamachuco, Marcabal) [HT FMNH 131682].
- sandwicensis*, *Bulimus*, Pfeiffer, 1846a: 31 (Sandwich Islands).
- scaber*, *Neopetraeus stelzneri*, Parodiz, 1948: 14 (Argentina, prov. Salta, Cachi) [HT MACN 3217].
- scabiosus*, *Bulimus*, Sowerby, 1833b: 74 ([Chile] Cobijam).
- scalaricosta*, *Bulimus*, Morelet, 1860: 375 [no type locality given; Peru; LT BMNH 1893.2.4.1170].
- scalariformis*, *Bulimus*, Broderip in Broderip & Sowerby, 1832a: 31 (Peruvia, Ancon).
- scalarioides*, *Bulimus*, Philippi in Pfeiffer, 1867: 77 ([Peru] provincia Conchucos).
- scotophilus*, *Bostryx* (*Bostryx*), Weyrauch, 1967a: 353, fig. 10 (Peru central, puente El Diablo, río Chillón, 2300 m) [HT IML 1130].
- scutulatus*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 106 (Peru, [Dept. Arequipa] Islay).
- serotinus*, *Bulimus*, Morelet, 1860: 374 ([no type locality; Peru]) [LT BMNH 1893.2.4.204].
- simplex*, *Bulimus*, Hupé, 1857: 53, pl. 9 fig. 6 (Pérou) [LT MNHN].
- simpliculus*, *Bulimus*, Pfeiffer, 1855b: 124 [no type locality given; LT BMNH 1975340].
- smeurorum*, *Bulimulus*, Breure, 1974b: 15 (New name for *Bulimus simplex* Hupé, 1857, not Jonas, 1842, nor *Bulimulus simplex* Beck, 1837).
- solutus*, *Bulimus* (*Bostryx*), Troschel, 1847: 49 (Peru) [ST ZMB].
- sophieae**, **Bostryx**. New name for *Bulimulus monticola* Döring, 1879, not *Bulimus monticola* Philippi, 1869 [secondary homonymy].
- sordidus*, *Helix*, Lesson, 1826: pl. 13 fig. 3 (le mont San Christoval, à une lieu de Lima, au Pérou) [ST MNHN].
- spiculatus*, *Bulimus*, Morelet, 1860: 375 [no type locality given; Peru; LT BMNH 1893.2.4.1156].
- spretus*, *Bulimus*, Philippi, 1869: 34 (Peruvia, inter Mayoc et Huanta, nec non ad Huancayo).
- stelzneri*, *Bulimulus* (*Scutalus*), Dohrn, 1875: 202 (republica Argentina, Cerro de Chepe).
- stenacme*, *Bulimus*, Pfeiffer, 1857a: 333 (Bolivia) [LT BMNH 1975342].
- striatulus*, *Bulimus*, Sowerby, 1833b: 73 ([Peru] prope Lima).
- strobéli*, *Bulimulus* (*Scansicochlea*), Parodiz, 1956: 62, fig. 5 ([Argentina] Cerro del Morro, provincia de San Luis) [HT MACN].
- styliger*, *Bulimulus*, Beck, 1837: 70 [indication].
- subcactorum*, *Bulimulus*, Pilsbry, 1896b: 145, pl. 46 fig. 36 (New name for *Bulimus lichenorum* Reeve, 1848, not *Helix lichenorum* d'Orbigny, 1835).

- subelatus*, *Bulimulus* (*Peronaeus*), Haas, 1948: 189, fig. 38 (Peru, Dept. Huánuco, Ambo near Huánuco) [HT FMNH 29146].
- subroseus*, *Bulimus*, Philippi in Pfeiffer, 1869: 90 (inter S. Fernando et Patipampa Peruviae).
- superbus*, *Bostryx* (*Multifasciatus*), Weyrauch, 1967a: 365, figs. 15-19 (Peru central, a 4 km de Laraos en el camino de herradura a Quichao, sobre la margen izquierda del riachuelo Mayo, afluente del río Canete, 3500 m) [HT IML 1137a].
- tamboensis*, *Bostryx* (*Geopyrgus*) *turritus*, Zilch, 1953: 55, pl. 14 fig. 4 (Peru, bei El Tambo, Hacienda Casa Grande (ca. 07°40' S). Mittellauf des Río Chicama, ca. 1000 m) [HT SMF 105931].
- tarmensis*, *Naesiotus* (*Reclasta*), Weyrauch, 1967b: 479, figs. 51-52 (Peru central, en el valle del río Tarma, Cerro Huayuncayo cerca de La Florida, 3000-3100 m) [HT SMF 162017].
- terebralis*, *Bulimus*, Pfeiffer, 1842b: 51 (Coquimbo, Chile).
- tinogastanus*, *Neopetraeus stelzneri*, Parodiz, 1948: 13 (Argentina, prov. Catamarca, Tinogasta, La Coipita, 3440 m).
- torallyi*, *Helix*, d'Orbigny, 1835: 11 (provincia Valle-Grande, republica Boliviana) [LT MNHN].
- tortoranus*, *Bulimulus*, Döring, 1879: 71 ([Argentina] Sierra de Pocho).
- tricinctus*, *Bulimus*, Reeve, 1848: pl. 57 fig. 380 [no type locality; LT BMNH 1975182].
- trochiformis*, *Bostryx carinatus*, Breure, 1978b: 56, pl. 10 fig. 6 (Peru, Dept. Ancash, Río Pativilca, opposite Aquia (ca. 10° S 77°05' W), Racrachaca, 3600-3800 m) [HT SMF 162086].
- tschudii*, *Bulimus*, Troschel, 1852: 195, pl. 5 fig. 7 (Peru, Huaura und Huacho) [ST ZMB].
- tubulatus*, *Bulimus*, Morelet, 1860: 375 [no type locality given; Peru].
- tumidulus*, *Bulimus*, Pfeiffer, 1842b: 123 [indication].
- turritus*, *Bulinus*, Broderip in Broderip & Sowerby, 1832b: 106 (Peruviae montibus, Truxillo).
- tyleri*, *Bulimulus*, Dall, 1912a: 6 (New name for *Bulimus simplex* Hupé, 1857, not Jonas, 1842).
- umbilicaris*, *Bulimus*, Souleyet, 1842: 102 (Bolivie, environs de Cobija [Chile]) [LT MNHN].
- umbilicatellus*, *Bulimulus infundibulum*, Pilsbry, 1896b: 131, pl. 44 figs. 93-94 (Peru) [HT ANSP 62966].
- veruculum*, *Bulimus*, Morelet, 1860: 376 [no type locality given; Peru].
- viarins*, *Bulimulus* (*Lissoacme*), Pilsbry, 1932: 394, pl. 28 figs. 6-9 (Peru, San Marcos, 5 mi. S on trail to Cajabamba) [HT ANSP 159903a].
- vilchezi*, *Bostryx* (*Bostryx*), Weyrauch, 1960a: 32, pl. 3 figs. 8-10 (N-Peru, Sócota, 20 km nō Cutervo (1950 m), im Tale des Río Guineamaya, im Becken des Maranon) [HT SMF 155704].
- virginalis*, *Bulimus*, Morelet, 1860: 372 [no type locality given; Peru].
- virgula*, *Bulimulus* (*Peronaeus*), Haas, 1951: 514, fig. 102 (Peru, Río Pampas, Ninabamba, 2700 m) [HT FMNH 30917].
- virgultorum*, *Bulimus*, Morelet, 1863: 194, pl. 10 fig. 1 ([Peru] vallée de Santa Anna) [LT MHNG].
- vittatus*, *Bulinus*, Broderip in Broderip & Sowerby, 1832a: 31 (Peruviâ, Ilo).
- webbi*, *Bulimulus* (*Peronaeus*), Haas, 1951: 513, fig. 101 (Peru, [Dept. Huancavelica] Prov. Tayacaya, near Surcubamba) [HT FMNH 31335].
- weyrauchi*, *Bostryx*, Pilsbry, 1944a: 87, pl. 9 fig. 5 (Peru, near Ayacucho, Ninabamba, 2000 m) [HT ANSP 179979a].
- williamsi*, *Bulimus*, Pfeiffer, 1858: 257, pl. 42 fig. 1 (Province of Catamarca, Andes of Peru).

willinki, *Bostryx* (*Bostryx*), Weyrauch, 1964: 54, fig. 12 (Argentina, Prov. Catamarca, Quebrada de Tinogasta) [HT IML 121a].

zilchi, *Bostryx* (*Bostryx*), Weyrauch, 1958: 108, pl. 9 fig. 41-42 (M-Peru, Laraos, 3600 m, im Tale des Rio Cañete, 155 km ösö Lima [corrected to Quichao, 5 km von Laraos (Weyrauch, 1960c: 124)]) [HT SMF 156348].

Bulimulus Leach, 1814

Bulimulus Leach, 1814: 42. Type species by original designation: *Helix exilis* Gmelin. *Siphalomphix* Rafinesque, 1833: 165. Type species by monotypy: *Siphalomphix bonariensis* Rafinesque.

Loboa Ihering, 1917: 121. Type species by monotypy: *Loboa brunoii* Ihering.

Description. — Shell ovate to oblong; narrowly perforate to rimate. Colour uniformly brown to yellowish, sometimes with bands of darker (reddish-)brown. Surface with growth striae and often with fine spiral striae. Protoconch with axial wrinkles, sometimes with granulation or pit-reticulate on its lower part. Aperture (sub) ovate to squarish-ovate. Peristome simple, unexpanded or slightly expanded.

The central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. The central teeth are slightly smaller than the lateromarginal teeth, which are bicuspid with elongate to lanceolate mesocones and deltoid ectocones that may be serrate in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 20-31).

Pericard ca. 3/4 the length of the nephridium, which is (elongate) triangular. The main pulmonary vein is prominent and broad. Side veins are well developed, especially at the anterior end. The adrectal ureter is closed. The mantle collar is well developed.

Penis usually with a proximal sheath; the distal part of the penis is swollen; the lumen of the penis is divided into several parallel tubes. The epiphallus, which internally deeply penetrates into the penis, is slender and about two times as long as the penis. The flagellum is slender, with a distally attached retractor muscle. The vagina is relatively short. The median part of the spermathecal duct is widened; the duct tapers toward the distal end. The spermatheca is globose.

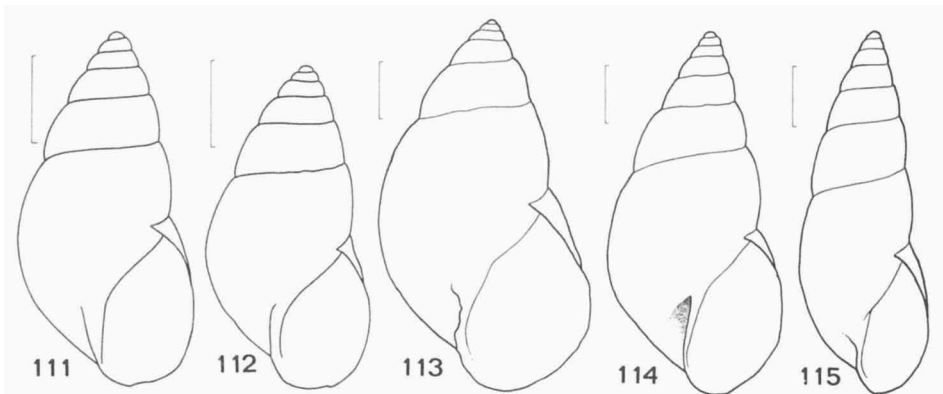
Distribution. — Antilles, Venezuela, Guyana, Surinam, French Guyana, Brazil, Paraguay, Uruguay, Argentina, Bolivia, Peru, Colombia, Central America, Mexico.

Ecology. — The species are usually ground-dwelling or live in shrubs, on stems and cacti. They are generally confined to secondary vegetation. The vertical distribution is 0-ca. 500(-ca. 800) m.

Remarks. — Zilch (1960) listed 25 subgenera under *Bulimulus*. Breure (1979) has shown that these taxa should either be given generic status or considered as synonyms. Two other taxa have been referred to *Bulimulus* as

subgenera viz. *Scansicohlea* Pilsbry, 1930 and *Paracochlea* Hylton Scott, 1967. In these taxa, however, the protoconch is sculptured with close spiral lines and only occasionally some wrinkles on the upper part of the protoconch have been observed. *Scansicohlea* Pilsbry, 1930 is considered a synonym of *Bostryx* Troschel, 1847 and *Paracochlea* Hylton Scott, 1967 is now referred to *Eudiotus* Albers, 1860; see p. 135 for a discussion.

Relationships. — Especially in the anatomy a remarkable resemblance with *Naesiotus* Albers, 1850 and *Rabdotus* Albers, 1850 is observed. Less clear is the resemblance with *Bostryx* Troschel, 1847. See p. 151 for a detailed discussion of the phylogenetic relationships between these genera.



Figs. 111-115. Variation in shell shape in *Bulimulus*. Fig. 111. *B. gittenbergeri* Breure. Fig. 112. *B. lehmanni* (Pfeiffer). Fig. 113. *B. apodemetes* (d'Orbigny). Fig. 114. *B. cacticolus* (Reeve). Fig. 115. *B. elatior* Hylton Scott. Scale = 5 mm.

The genus *Bulimulus* may be characterized by (1) the smooth surface of the shell; (2) the sculpture of the protoconch; (3) the structure of the radula: tricuspid central teeth and bicuspid lateromarginal teeth; (4) the presence of a proximal penis sheath; (5) the median widening of the spermathecal duct; (6) the internal structure of the penis: lumen divided into several parallel tubes; (7) the deep intrusion of the epiphallus into the penis.

Taxa. — The following taxa are placed in this genus:

[?] *acuta*, *Helix*, Chemnitz, 1786: 161, pl. 134 figs. 1224 1.2 [indication].

acutus, *Bulimulus*, Leach, 1814: 41, pl. 18 lower figs. [indication].

alba, *Bulini guadalupensis*, Sowerby in Sowerby & Gray, 1839: 144, pl. 38 fig. 13 (Brazil).

amoenus, *Bulimus*, Bonnet, 1864: 70 (Pérou) [not *Bulimus amoenus* Pfeiffer, 1847].

angustus, *Bulimulus* (*Bulimulus*) *vesicalis*, Weyrauch, 1966: 45, fig. 5 (Brasil, estado Rio Grande do Sul, São Leopoldo) [HT MRCN 1576a].

antiquensis, *Bulimulus*, Guilding in Swainson, 1840: 335 [nomen nudum].

antiquensis, *Bulimus*, Catlow & Reeve, 1845: 150 [indication; no type locality given].

apodemeta, *Helix*, d'Orbigny, 1835: 10 (republica Argentina; republica Boliviana) [ST MNHN].

- barbadensis*, *Bulimus*, Pfeiffer, 1853d: 435 ([West Indies] Barbados) [LT BMNH 197454].
- behrendti*, *Bulimus*, Pfeiffer, 1861b: 168, pl. 3 figs. 4-5 ([Mexico] Orizaba status Veracruz).
- bonariensis*, *Bulimulus* (*Thaumastus*) *sporadicus*, Strobel, 1874: 24 ([Argentina] Buenos Aires).
- bonariensis*, *Siphalomphix*, Rafinesque, 1833: 165 (Buenos Aires, South America [teste Parodiz, 1962: 432]).
- brunoi*, *Loboa*, Ihering, 1917: 121, pl. 4 fig. 7 (Brazil, Island of Trinity [Ilha da Trindade]) [HT MN].
- buenavistensis*, *Bulimulus*, Pilsbry, 1897d: 59, pl. 10 fig. 95 (New name for *Bulimus corneus* Lea, 1838, not Deshayes, 1836).
- cacticolus*, *Bulimus*, Reeve, 1849: pl. 58 fig. 393 (Venezuela, Curiana).
- castelmaui*, *Bulimus*, Pfeiffer, 1857a: 332 (Bolivia, Rio Pampas).
- concolor*, *Thaumastus exilis*, Piaget, 1914: 262 [no type locality given].
- corderoi*, *Bulimulus*, Parodiz, 1962: 430, pl. 2 fig. 15 (Uruguay, La Coronilla) [HT USNM 348777].
- coriaceus*, *Bulimus*, Pfeiffer, 1857a: 318 ([Mexico] Cordova).
- corneus*, *Bulimus*, Potiez & Michaud, 1835: pl. 14 figs. 11-12 ([Guyane française] Cayenne).
- corneus*, *Bulimus*, Lea, 1838: 66, pl. 23 fig. 111 (Buenavista, Colombia) [not *Bulimus corneus* Deshayes, 1836, nor Potiez & Michaud, 1835].
- corneus*, *Bulinus*, Sowerby, 1833b: 37 (America Centrali, Real Llejos).
- corumbaensis*, *Bulimulus*, Pilsbry, 1897a: 19 (New name for *Bulimus amoenus* Bonnet, 1864, not Pfeiffer, 1847).
- dendritis*, *Bulimus*, Morelet, 1863: 206, pl. 9 fig. 5 ([Peru] près de Huiro, vallée de Santa-Ana) [LT MHNG].
- dentrita*, *Helix*, Montagu, 1803: 384, pl. 11 fig. 1 [no type locality given].
- diaphanus*, *Bulimus*, Pfeiffer, 1855b: 125 ([West Indies] St. Thomas) [ST BMNH].
- dispar*, *Bulimulus apodemetes*, Hylton Scott, 1952: 23, pl. 1 fig. 5 ([Argentina] Salta, Pocitos) [HT MIHS].
- [?] *dukinfieldi*, *Bulimulus* (*Drymaeus*), Melvill, 1900: 116, fig. (Salto Grande do Rio dos Patos (upper waters of River Ivahy), Paraná, Brazil) [HT BMNH 1900.9.27.2].
- dysoni*, *Bulimus*, Pfeiffer, 1846c: 39 (Honduras) [ST BMNH 197453].
- effeminatus*, *Bulimus*, Reeve, 1848: pl. 51 fig. 338 [no type locality given; LT BMNH 1975508 (labelled 'valley of the Madeleine [= Río Magdalena, Colombia], N. Grenade')].
- eganus*, *Bulimus*, Pfeiffer, 1853b: 258 (Ega, Brasiliae).
- elatior*, *Bulimulus*, Hylton Scott, 1952: 21, pl. 2 fig. 4 ([Argentina] Formosa, Laguna Yema) [HT MIHS].
- ephippium*, *Bulimulus*, Ancey, 1904: 102 (Brazil, Bahia) [ST BMNH 1905.12.30.12].
- erectus*, *Bulimus*, Reeve, 1849: pl. 58 fig. 392 (Venezuela, Curiana).
- exilis*, *Helix*, Gmelin, 1791: 3668 [no type locality given; not *Helix exilis* Gmelin, 1791 (l.c.: 3616), nor Müller, 1774].
- eyriesii*, *Bulimus*, Drouët, 1859: 63, pl. 1 figs. 12-13 (Guyane française, Ilet-la-Mère).
- felipponei*, *Bulimulus* (*Bulimulus*), Marshall, 1930: 1, pl. 1 fig. 9 (Uruguay, Dept. Rio Negro, Fray Bentos) [HT USNM 380691] [not *Bulimulus felipponei* Ihering, 1928].
- fontainii*, *Bulimus*, d'Orbigny, 1837: 273 ([Ecuador] aux environs de Guayaquil).
- fraterculus*, *Bulimus*, Potiez & Michaud, 1835: pl. 13 figs. 7-8 ([West Indies] Guadeloupe) [LT MNHN].
- fraterculus*, *Helix* (*Cochlogena*), Férussac, 1821: 54 [nomen nudum].
- fuscus*, *Bulimulus*, Guilding, 1828b: 170 ([West Indies] insulae Barbadosensis).
- gelidus*, *Bulimus*, Reeve, 1849: pl. 76 fig. 553 (Central America?) [LT BMNH 1975402].

- gittenbergeri*, *Bulimulus* (*Bulimulus*), Breure, 1974a: 27, pl. 5 figs. 10-13, pl. 7 fig. 3 ([West Indies] St. Kitts, NW Brimstone Hill) [HT RMNH 54903].
- glandiniformis*, *Bulimulus*, Sowerby, 1892: 297, pl. 23 figs. 13-14 (U.S. of Colombia, Bogota).
- gorritiensis*, *Bulimulus*, Pilsbry in Pilsbry & Rush, 1896: 78 [nomen nudum]; Pilsbry, 1897a: 18 (Uruguay, Maldonado Bay, Gorriti Island).
- gracilis*, *Bulimulus sporadicus*, Hylton Scott, 1948a: 238, pl. 2 fig. 3 ([Argentina] Salta, Cerro Colorado) [HT MIHS].
- guadalupensis*, *Bulimus*, Bruguière, 1789: 313 ([West Indies] Guadeloupe).
- haplochrous*, *Bulimus*, Pfeiffer, 1855b: 125 [no type locality given; LT BMNH 1975405 (labelled 'New Granada')].
- houelmontensis*, *Bulimus*, [Crosse ms.] Mazé, 1883: 19, pl. 1 fig. 6 ([West Indies] Guadeloupe, Vieux-Fort, Houelmont, Monts Caraïbes, ca. 586 m) [HT MNHN].
- hummelincki*, *Bulimulus* (*Bulimulus*), Breure, 1974a: 28, figs. 61-71, pl. 3 figs. 1-5 ([West Indies] Barbuda, River Quarter W of Bull Hole) [HT RMNH 54905].
- ignavus*, *Bulimus*, Reeve, 1849: pl. 77 fig. 562 (Central America) [LT BMNH 1975411].
- inconspicuus*, *Bulimulus* (*Bulimulus*), Haas, 1949: 236, fig. 50a (Peru, Dept. Loreto, Río Ucayali, Contamana) [HT FMNH 30038].
- inermis*, *Bulimus*, Morelet, 1851: 10 ([Mexico] circa vicum Palizada provinciae Yucatanensis).
- inutilis*, *Bulimus*, Reeve, 1850a: pl. 86 fig. 639 [no type locality given; LT BMNH 1975162 (labelled '?Central America')].
- istapensis*, *Bulimulus*, Crosse & Fischer, 1873: 286 (Istapa, Guatemalae).
- jujuyensis*, *Bulimulus*, Holmberg, 1909a: 11 ([Argentina] Jujuy, Tilcara).
- juvenilis*, *Bulimus*, Pfeiffer, 1855g: 97 ([Colombia] Santa Fe de Bogota) [LT BMNH 1975161].
- krebsianus*, *Bulimulus*, Pilsbry, 1897d: 62, pl. 10 figs. 1-2 (Colombia, Cartagena).
- lehmanni*, *Bulimus*, Pfeiffer, 1865: 123 ([West Indies] Anguilla).
- lherminieri*, *Bulimus*, P. Fischer, 1857: 355, pl. 12 figs. 6-7 ([West Indies] Guadeloupe, montagnes de Petit-Bourg).
- limnaeoides*, *Bulimus* (*Leptomerus*), Albers, 1860: 222 [emendation for *limnoides* Férussac].
- limnoides*, *Helix*, Férussac, 1832 in Férussac & Deshayes, 1820-1851: pl. 142 figs. 9-10 ([West Indies] Guadeloupe) [LT MNHN].
- major*, *Bulimus inermis*, Martens, 1893: 250 (N. Guatemala, valley of the Rio Chisoy, Rancho Chisoy).
- marcidus*, *Bulimus*, Pfeiffer, 1853d: 435 (Brazil).
- marmatensis*, *Bulimus*, Pfeiffer, 1855b: 125 (U.S. of Colombia, Marmato).
- mendozianus*, *Bulimulus* (*Eudiotus*), Strobel, 1874: 23, pl. 1 fig. 4 ([Argentina] Gola di Villa Vicencio, Sierra de Mendoza).
- minor*, *Bulimulus corneus*, 'Martens' Pilsbry, 1897d: 56, pl. 10 figs. 71-72 (E. Mexico, near Vera Cruz, San Andres Tuxtla).
- moei*, *Bulimulus*, Parodiz, 1962: 431, pl. 2 fig. 13 (Argentina, northeastern part Prov. Salta) [HT USNM 349118].
- mollicellus*, *Bulimus*, Reeve, 1849: pl. 77 fig. 565 [no type locality given; LT BMNH 1975185].
- montevicensis*, *Bulimus*, Pfeiffer, 1846a: 33 (Montevideo, Buenos Ayres) [ST BMNH 1975401].
- nichollsi*, *Bulimus*, Brown, 1881: 57 [nomen nudum].
- nichollsi*, *Bulimus*, [Brown ms.] Angas, 1885: 596, figs. 2-3 ([West Indies] Dominica) [LT ANSP 9958].
- nuberculatus*, *Bulimus*, Pfeiffer, 1853b: 257 (America centrali) [LT BMNH 1975407].
- ochraspiris*, *Bulimulus*, Branson & McCoy, 1965b: 97 (Mexico, Campeche, 17.2 miles south of Champotón).

- orbignyi*, *Bulimus*, Pfeiffer, 1846a: 31 (Locality unknown) [LT BMNH 1975349].
 [?] *orthodoxus*, *Bulimus*, Drouët, 1859: 62, pl. 1 figs. 14-15 (Guyane française, Ilet-la-Mère).
- pervius*, *Bulimus*, Pfeiffer, 1853d: 651 [no type locality given; LT BMNH 1975165].
pessulatus, *Bulimus*, Reeve, 1848: pl. 23 fig. 153 (Bolivia, Santa Cruz de la Sierra) [LT BMNH 1975313].
petenensis, *Bulimus*, Morelet, 1851: 10 ([Guatemala] per campos Petenenses) [LT BMNH 1893.2.4.1176].
plicatulus, *Bulimus*, Pfeiffer, 1857c: 390 (Bolivia) [LT BMNH 1975390].
pliculatus, *Bulimus*, Pfeiffer & Clessin, 1881: 244 [emendation for *plicatulus* Pfeiffer].
pouyseguri, *Bulimulus*, Holmberg, 1912b: 150, figs. 5-6 (Argentina, Provincia Corrientes, insulam Curiyú in Laguna Yberá).
prosopidis, *Bulimulus*, Holmberg, 1912b: 150, figs. 3-4 ([Argentina] ad marginem dextrum fluminis Pilcomayo).
rüsei, *Bulimus*, Pfeiffer, 1855d: 103, pl. 4 figs. 7-8 ([West Indies] St. Croix, 'La Grange' prope Frederiksted).
rubrifasciatus, *Bulimus*, Reeve, 1848: pl. 44 fig. 227 [no type locality given; LT BMNH 1975393, shell height 23 mm, diameter 9.6 mm (figured specimen)].
rushii, *Bulimulus*, Pilsbry in Pilsbry & Rush, 1896: 78 [nomen nudum]; Pilsbry, 1897a: 18 (Uruguay, Maldonado).
sarcodes, *Bulimus*, Pfeiffer, 1846a: 30 (Honduras).
semicinctus, *Bulimulus*, Pilsbry, 1897d: 44, pl. 12 fig. 63 ([West Indies] Guadelupe [sic]) [LT ANSP 25602].
sepulcralis, *Bulimus*, Poey, 185?: 203, pl. 12 figs. 27-29 [Cuba, Havana and environs; teste Pilsbry, 1897d: 49].
simplex, *Bulimulus*, Beck, 1837: 66 (Antilles) [indication].
sporadica, *Helix*, d'Orbigny, 1835: 12 (provincia Corrientes, republica Argentina; provincia Chiquitensi, republica Boliviana).
subtropicalis, *Bulimulus sporadicus*, Döring, 1879: 74 ([Argentina] Rosario, Paraná).
tenuissima, *Helix*, Férussac, 1832 in Férussac & Deshayes, 1820-1851: pl. 142B fig. 8 [no type locality given; le Brésil et Cayenne (explanation of plate)].
tenuissimus, *Bulimulus*, Smith & Feilden, 1891: 252 [Barbados; not *Helix tenuissima* Férussac].
thoreyi, *Bulimulus*, Beck, 1837: 67 [indication] (Argentina, Bolivia).
transparentis, *Bulimus*, Reeve, 1849: pl. 77 fig. 556 [no type locality given; LT BMNH 1975397].
trifasciatus, *Bulimulus*, Leach, 1814: 42, pl. 18 upper figs. (West Indian).
trinidadensis, *Bulimulus*, Breure & Dos Santos Coelho, 1976: 3, figs. 1-4 (Brazil, Ilha da Trindade, Praia dos Cabritos) [HT MN 3711].
ucayalensis, *Bulimus*, Crosse, 1871a: 229 (ripas fluminis Ucayali dicti, Reipublicuae Aequatoris [sic, Peru]).
unicolor, *Bulimus*, Sowerby, 1833b: 73 (Insulam Perico in Sinu Panamensi).
uruguayanus, *Bulimulus vesicalis*, Pilsbry, 1897d: 69, pl. 12 figs. 38-39 (Uruguay, Montevideo).
vesicalis, *Bulimus*, Pfeiffer, 1853c: 58 (Brazil) [LT BMNH 1975395].
viatorum, *Bulimulus*, Holmberg, 1909b: 92 (Argentina, prope Boliviae limen via Yacuiva).
wiebesi, *Bulimulus*, Breure, 1978b: 149, figs. 239-245 (West Indies, Grenada, St. George Parish, 2.1 mi S St. George's) [HT UF 22764].

Naesiotus Albers, 1850

- Naesiotus* Albers, 1850: 162. Type species by subsequent designation (Dall, 1896b: 426):
Bulimus nux Broderip.
Omphalostyla sensu Adams & Adams (1855: 161) not Schlüter, 1838.

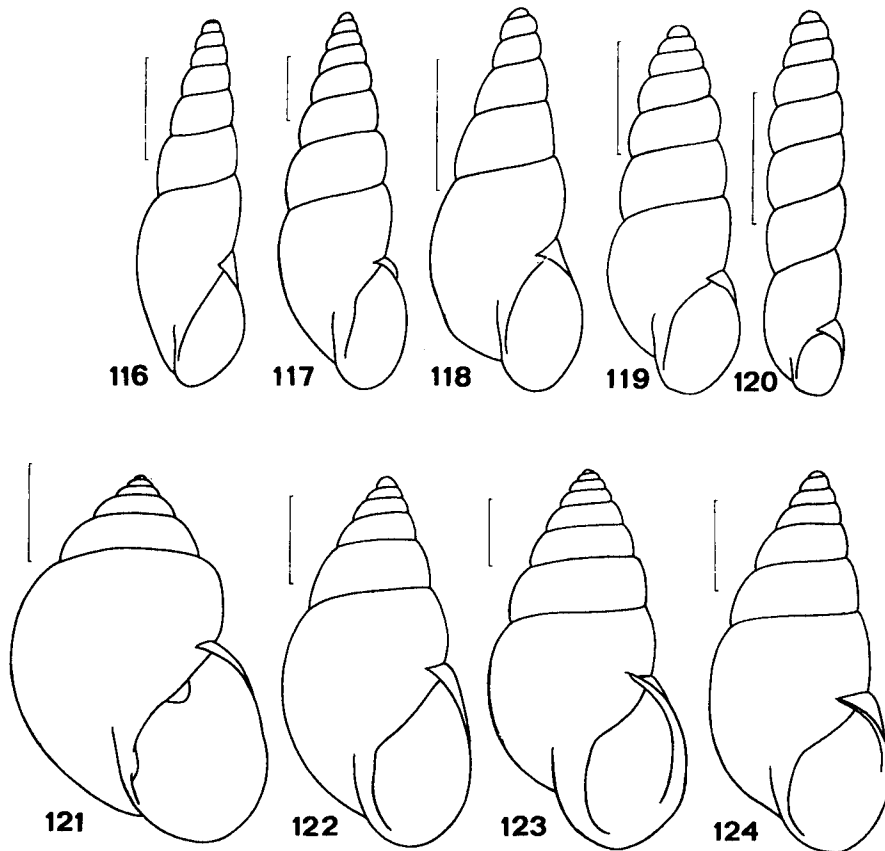
- Rhaphiellus* Pfeiffer, 1856a : 160. Type species by original designation : *Bulimus achatellinus* Forbes.
- Nesiotes* Albers, 1860 : 220. Type species by original designation : *Bulimus nux* Broderip.
- Pleuropyrgus* Albers, 1860 : 221. Type species by monotypy : *Bulimus chemnitzioides* Forbes.
- Nesiotes* Pfeiffer & Clessin, 1881 : 254 [error for *Nesiotes* Albers, 1860].
- Pelecostoma* Reibisch, 1892 : 25. Type species by original designation : *Bulimulus (Pelecostoma) canaliferus* Reibisch.
- Protoglyptus* Pilsbry, 1897d : 84. Type species by subsequent designation (Parodiz, 1946a : 312) : *Bulimulus pilosus* Guppy.
- Granucis* Dall, 1920 : 118. Type species by original designation : *Bulimulus rugulosus planospira* Ancey.
- Nuciscus* Dall, 1920 : 119. Type species by original designation : *Bulimus ustulatus* Sowerby.
- Reclasta* Dall, 1920 : 119. Type species by original designation : *Bulimus unifasciatus* Sowerby.
- Adenodia* Dall, 1920 : 119. Type species by original designation : *Bulimus eschariferus* Sowerby.
- Stemmodiscus* Dall, 1920 : 120. Type species by original designation : *Bulimulus snodgrassi* Dall.
- Olinodia* Dall, 1920 : 120. Type species by original designation : *Bulimulus (Naesiotus) amastroides* Ancey.
- Saeronia* Dall, 1920 : 120. Type species by original designation : *Bulimulus (Naesiotus) simrothi* Reibisch.
- Ochsneria* Dall, 1920 : 121. Type species by original designation : *Bulimulus (Naesiotus) wolfi* Reibisch.
- Granitza* Dall, 1920 : 121. Type species by original designation : *Bulimulus (Naesiotus) duncanus* Dall.
- Granella* Dall, 1920 : 121. Type species by original designation : *Bulimus sculpturatus* Pfeiffer.
- Rimatula* Parodiz, 1946a : 353. Type species by original designation : *Protoglyptus deletangi* Parodiz.
- Obstrusus* Parodiz, 1946a : 354. Type species by original designation : *Bulimus rocayanus* d'Orbigny.
- Maranhoniellus* Weyrauch, 1958 : 122. Type species by original designation : *Naesiotus (Maranhoniellus) pilsbryi* Weyrauch.

Description. — Shell turritid to elongate-ovate; with straight to slightly convex sides; (narrowly) perforate, rimate or imperforate. Colour whitish to brownish; uniformly coloured or with darker spiral bands, in some species with axial streaks. Surface smooth, with incrassate growth striae or rugose. Protoconch with (undulating) axial riblets and numerous fine spiral lines. Whorls nearly flat to slightly convex; suture hardly to well impressed. Aperture sub- to elongate-ovate, in some species with parietal dents. Peristome thin to rather thickened, simple to hardly expanded.

The central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. Lateromarginal teeth are bicuspid, with elongate to lanceolate mesocones and deltoid ectocones, which may be serrate in the outermost teeth. Half-row formula: C/3 + LM x/2 (x = 19-34).

Pericard nearly as long as the nephridium, which is (narrowly) triangular. Main pulmonary vein moderately developed, strongest at the anterior end; side veins weakly to moderately developed. The adrectal ureter is closed.

Penis with a proximal sheath. The lumen of the penis is divided into several parallel tubes or sac-like cavities and lined by two types of epithelium. The epiphallus is not to hardly intruding the penis. Externally the penis is more or less subcylindrical; a median ovoid swelling is present in several species. The flagellum is subcylindrical or divided into a stout and a slender part. The spermathecal duct is more or less subcylindrical, with a globose spermatheca at its distal end.



Figs. 116-124. Variation in shell shape in *Naesiotus*. Fig. 116. *N. rhabdotus* (Haas). Fig. 117. *N. cutisculptus* (Ancey). Fig. 118. *N. gracillimus* Weyrauch. Fig. 119. *N. deletangi* (Parodiz). Fig. 120. *N. fernandezae* Weyrauch. Fig. 121. *N. ochsneri* (Dall). Fig. 122. *N. quitensis* (Pfeiffer). Fig. 123. *N. carluccioi* (Rezende & Lanzieri). Fig. 124. *N. martinicensis* (Pfeiffer). Scale = 5 mm.

Distribution. — Lesser Antilles, Venezuela, Brazil, Paraguay, Uruguay, Argentina, Bolivia, Peru, Ecuador (including Galápagos), Colombia.

Ecology. — On the continent the species are usually ground-dwelling, whereas on the Galápagos Islands a strong radiation has taken place and the species live in shrubs, on stems, lava rocks, trees, etc. The vertical distribution is 0-1000(-2850) m.

Remarks. — The classification of *Naesiotus* has been very unstable through time; it has been regarded a subgenus or even a synonym of *Bulimulus*. Especially Dall (1920) has created many 'sections' in *Naesiotus*, but a preliminary revision (Breure & Coppo, 1978) has shown that it is not possible to divide *Naesiotus* unambiguously into subgenera. The genus is treated here, therefore, *sensu lato*.

Relationships. — The phylogenetic relationships are discussed on page 151. The genus is characterized by the protoconch sculpture: a regular pattern of axial riblets with fine, spiral lines.

Bibliography. — The main publications on this genus are: Breure, 1978b; Breure & Coppo, 1978; Dall, 1896b, 1900, 1917, 1920; Dall & Ochsner, 1928; Lanzieri & Rezende, 1971; Odhner, 1951; Parodiz, 1946a; Pilsbry, 1897d; Rehder, 1940; Rezende & Lanzieri, 1963; Rezende, Lanzieri & Inada, 1972; A. G. Smith, 1971, 1972; Vagvolgyi, 1977; Van Mol, 1972; Weyrauch, 1956a.

Taxa. — The following taxa are placed in this genus:

- achatellinus*, *Bulimus*, Forbes, 1850: 56, pl. 9 figs. 5a-b (Galapagos, Chatham Island).
achatinellinus, *Bulimus*, 'Forbes' Pfeiffer, 1853d: 429 [emendation].
achatinellus, *Bulimulus* (*Omphalostyla*), H. & A. Adams, 1855: 161 [emendation].
acutus, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 20, pl. 1 fig. 13 ([Galápagos] Chatham Island) [ST ZMB 47964].
adelphus, *Bulimulus* (*Naesiotus*), Dall, 1917b: 379 (Galapagos, Indefatigable Island) [HT CAS].
akamatus, *Bulimulus* (*Naesiotus*), Dall, 1917b: 378 (Galapagos, Indefatigable Island, 200-650 feet) [HT CAS].
albemarlensis, *Bulimulus* (*Naesiotus*), Dall, 1917b: 377 (Galapagos, [Isabela] near Villamil, 2300-3300 ft.) [HT CAS].
alethorhytidus, *Bulimulus* (*Naesiotus*), Dall, 1917b: 379 (Galapagos, Indefatigable Island, 350-400 feet) [HT CAS].
amastroides, *Bulimulus* (*Naesiotus*), Ancey, 1887: 293 (l'Archipel des Galapagos).
ambatensis, *Naesiotus quitensis*, Rehder, 1940: 117, pl. 13 figs. 12, 14 (Ecuador, Tunguragua, Ambato) [HT USNM 473973].
anceyi, *Bulimulus* (*Naesiotus*) *amastroides*, Dall, 1893b: 53 (Galapagos, Chatham Island, 1600 feet).
andivagus, *Naesiotus*, Weyrauch, 1956b: 5, pl. 1 fig. 2 (Central Peru, Río Huaura, near Churin, Cabracancha, 2200 m) [HT IML 1461].
antisana, *Naesiotus quitensis*, Rehder, 1942: 103 (Ecuador, Prov. Pichincha, slopes of Mt. Antisana) [HT USNM 516940].

- apertus*, *Bulimus*, Pfeiffer in Dunker et al., 1855: 107 [no type locality given; LT BMNH 1975317].
- approximatus*, *Bulimulus*, Dall, 1900: 90, pl. 8 fig. 4 (Galapagos, Hood Island).
- arnaldoi*, *Protoglyptus*, Lanzieri & Rezende, 1971: 255, figs. 1-4 ([Brazil] Ilha da Trindade, Pico do Desejado) [HT MN 3105].
- asperatus*, *Bulimus*, Albers, 1857: 98 (Insulis Gallopagos [sic]).
- avellana*, *Buliminus*, Beck, 1837: 70 [indication].
- bambamarcaensis*, *Naesiotus* (*Naesiotus*), Weyrauch, 1960a: 37, pl. 6 fig. 38 (Peru, Río Llaucan, Cerro Machaipungo, 4 km NW Bambamarca, 3000 m) [HT SMF 156220].
- bartolomensis*, *Naesiotus tanneri*, Vagvolgyi, 1977: 770, pl. 1 figs. 5a-b, pl. 2 fig. 3 (Ecuador, Archipiélago de Colón, off Santiago Island, Bartolomé Island, at western foot of main peak) [HT USNM 757717].
- basiplicatus*, *Bulimulus* (*Naesiotus*) *nux*, Dall & Ochsner, 1928: 157, pl. 9 figs. 9-10 Galapagos, Chatham Island, 1900-2500 ft.) [ST CAS].
- bauri*, *Bulimulus* (*Naesiotus*), Dall, 1893b: 54 (Galapagos, SW end Chatham Island).
- bizonalis*, *Bulimulus eschariferus*, Ancey, 1887: 295 [iles Galapagos].
- blombergi*, *Bulimulus*, Odhner, 1951: 255, figs. 1, 3-5, 8 (Galapagos, Santa Cruz Island, 200-300 m) [HT NRS].
- caliginosus*, *Bulimus*, Reeve, 1849: pl. 82 fig. 609 [no type locality given].
- calvus*, *Bulimus*, Sowerby, 1833b: 72 (Galapagos, James I.).
- canaliferus*, *Bulimulus* (*Pelecostoma*), Reibisch, 1892: 25, pl. 2 fig. 6 ([Galapagos] Chatham Island) [ST ZMB 47948].
- carluccioi*, *Protoglyptus*, Rezende & Lanzieri, 1963: 112, figs. 1-38 ([Brazil] Estado de Goiás, Planaltina Nova) [HT IOC 7780].
- caryonis*, *Bulimulus* (*Naesiotus*) *calvus*, Dall & Ochsner, 1928: 160, pl. 8 fig. 25 (Galapagos, Charles Island, 750 ft.) [HT CAS 1686].
- catlowiae*, *Bulimus*, Pfeiffer, 1853d: 427 ([Ecuador] Quito) [LT BMNH 1975414].
- cavagnaroi*, *Naesiotus*, A. G. Smith, 1972: 12, figs. 10-18 (Galapagos, Isla Santa Cruz, 7 km NE Santa Rosa) [HT CAS 13738].
- centralis*, *Bulimulus*, Döring, 1879: 69 ([Argentina] Sierra de Cordoba).
- cerrateae*, *Naesiotus* (*Raphiellus*), Weyrauch, 1967a: 410, fig. 77 (Peru central, río Pativilca, 10 km N Chiquián, Aquia, 3350 m) [HT SMF 162024].
- chacoensis*, *Bulimulus montivagus*, Ancey, 1897: 16 (Bolivie [sic], Gran Chaco, Caiza).
- chamayensis*, *Naesiotus* (*Naesiotus*) *subcostatus*, Weyrauch, 1967a: 409, figs. 97-99 (Norte de Peru, río Chamaya, cerca del pueblo Chamaya, 550-660 m) [HT SMF 162190].
- chemnitzoides*, *Bulimus*, Forbes, 1850: 55, pl. 9 figs. 6a-b (Galapagos, Chatham Island).
- chrysalis*, *Bulimus*, Pfeiffer, 1847b: 14 ([West Indies] Guadeloupe).
- chrysaloides*, *Bulimulus*, Pilsbry, 1897a: 20 ([West Indies] Martinique) [LT ANSP 3557].
- cinerarius*, *Bulimulus*, Dall, 1917a: 10 (New name for *Bulimulus cinereus* Reibisch, 1892, not *Bulimus cinereus* Reeve, 1848).
- cinereus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 19, pl. 1 fig. 10 ([Galapagos] James Island).
- cleeforum*, *Naesiotus*, Breure, 1978b: 160, pl. 2 fig. 1 (Colombia, Dept. Valle, 9 km N Dagua, Atunceto, 3500 ft.) [HT UF 22769].
- constrictus*, *Bulimus*, Reeve, 1848: pl. 47 fig. 307 ([Venezuela] Angostura).
- crepundia*, *Helix*, d'Orbigny, 1835: 14 (provincia Chiquitensi, republica Boliviana).
- crepundia*, *Bulimus*, Reeve, 1848: pl. 47 fig. 300 (Chiquitos, Bolivia).
- cucullinus*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 377 (Galapagos, Hood Island, 200-600 ft) [ST CAS].
- curtus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 21, pl. 1 fig. 14 ([Galapagos] Chatam [sic] Island) [ST BMNH 1894.6.8.8-9].
- cutisculptus*, *Bulimulus*, Ancey, 1901: 92 ([Brazil] Corumba, Matto-Grosso).

- cymatias*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 380 (Galapagos, Indefatigable Island, 400-650 ft.) [ST CAS].
- darwinii*, *Bulimus*, Pfeiffer, 1846a: 29 (Gallapagos [sic] Islands).
- deletangi*, *Protoglyptus*, Parodiz, 1946b: 3, fig. 1, pl. 1 fig. 4 (Argentina, Prov. Salta, Embarcación) [HT MACN 3131].
- deroyi*, *Naesiotus*, A. G. Smith, 1972: 9, figs. 2-9 (Galápagos, Isla Santa Cruz, on the NW side, 264 m) [HT CAS 13730].
- duncanus*, *Bulimulus* (*Naesiotus*), Dall, 1893b: 52 (Galapagos Islands, Duncan Island).
- durus*, *Bulimus*, Spix, 1827: pl. 6 fig. 2 (mediterraneis Provinciae Bahiensis [Brazil]).
- edenensis*, *Naesiotus tanneri*, Vagvolgyi, 1977: 769, pl. 1 fig. 3, pl. 2 fig. 4 (Ecuador, Archipiélago de Colón, off Santa Cruz Island, Eden Island, on southern slope, 100-150 feet) [HT USNM 757716].
- elaeodes*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 376 (Galapagos, Albemarle Island, near Banks Bay, 1500-2300 ft.) [ST CAS].
- elegantulus*, *Naesiotus*, Weyrauch, 1956b: 4, pl. 1 fig. 1 (Northern Peru, Mt. San Isidro W of Celendín, 2750-2800 m) [HT SMF 162023].
- eos*, *Bulimulus*, Odhner, 1951: 255, figs. 2, 9 (Galapagos, Santa Cruz Island) [HT NRS].
- eschariferus*, *Bulimus*, Sowerby, 1833a: fig. 85 (Galapagos) [ST BMNH 1975153].
- eudioptus*, *Bulimulus*, 'Thering' Pilsbry, 1897d: 89, pl. 14 figs. 16-17 (Brazil, Sao Paulo) [HT ANSP 71240a].
- exornatus*, *Bulimus*, Reeve, 1849: pl. 77 fig. 560 (Bolivia, Chilon) [LT BMNH 1975331].
- fernandezae*, *Naesiotus* (*Maranhoniellus*), Weyrauch, 1958: 122, pl. 9 figs. 45-46 (Peru, rechter Seite des Río Marañón, bei Balsas, 850 m) [HT SMF 157277].
- florschuetzi*, *Naesiotus*, Breure, 1978b: 160, pl. 2 fig. 2 (Ecuador, Prov. El Oro, 31 miles N Santa Rosa) [HT UF 22772].
- galapaganus*, *Bulimus*, Pfeiffer, 1855a: 58 (Galapagos Islands) [LT BMNH 1975146].
- geophilus*, *Naesiotus* (*Naesiotus*), Weyrauch, 1967b: 477, figs. 26-28 (Norte de Peru, valle del río Marañón, carretera de Chamaya a Bagua Grande y a Bagua Chica, Cruce Bagua Grande, 600 m) [HT IML 1074a].
- gerenorum*, *Naesiotus*, Breure, 1977a: 264, figs. 7-9, 13 (Colombia, Dept. Boyacá, Upper Río Chicamocha valley, few km S of Soatá, 2100 m) [HT RMNH 55115].
- gilderoyi*, *Bulimulus*, Van Mol, 1972: 2, fig. 1 (Galápagos, Santa Cruz, à proximité du Cerro Coralón) [HT IRSN].
- gracillimus*, *Naesiotus*, Weyrauch, 1956b: 6, pl. 1 fig. 3 (Central Peru, near Tingo Maria, Río Monzón near its confluence with Río Huallaga, 670 m) [HT SMF 155696].
- haasi*, *Naesiotus*, Weyrauch, 1956b: 7, pl. 1 fig. 5 (Northern Peru, Río Jequetepeque, mountain near Chilete, 850 m) [HT IML 2862].
- habeli*, *Bulimulus* (*Pleuropyrgus*), Dall, 1892: 98 (Galapagos).
- haematospira*, *Bulimulus*, Pilsbry, 1900a: 392 (locality unknown, probably Peru) [LT ANSP 78135a].
- hemaerodes*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 376 (Galapagos, Albemarle Island, Cowley Mountain, 2100-2300 ft.) [ST CAS].
- hirsutus*, *Naesiotus*, Vagvolgyi, 1977: 764, pl. 1 figs. 1a-b, pl. 2 figs. 1a-b (Ecuador, Archipiélago de Colón, Santa Cruz Island, southern slope, 2½ mi N of Puerto Ayora, 400-450 feet) [HT USNM 757715].
- hoodensis*, *Bulimulus*, Dall, 1900: 91, pl. 8 fig. 1 (Galapagos, Hood Island).
- incrassatus*, *Bulimus*, Pfeiffer, 1853d: 415 (insulis Gallapagos) [LT BMNH 1975157].
- indefatigabilis*, *Bulimulus* (*Naesiotus*), Dall, 1900: 92 (Galapagos, James and Indefatigable Islands).
- infuscata*, *Bulimulus* (*Naesiotus*) *rugulosus*, Ancey, 1887: 294 (îles Galapagos).
- invalidus*, *Bulimulus*, Reibisch, 1892: 17, pl. 1 fig. 6 ([Galapagos] Charles Island).
- irregularis*, *Bulimus*, Pfeiffer, 1848a: 231 (Quito, Ecuador).
- jacksoni*, *Naesiotus quitensis*, Rehder, 1940: 116, pl. 13 figs. 1, 5 (Ecuador, Pichincha, Guañillabamba) [HT USNM 473969].

- jacobi*, *Bulimus*, Reeve, 1848: pl. 21 fig. 135 (Jacob Island, Gallapagos).
- jacobi*, *Bulinus*, Sowerby, 1833b: 74 ([Galapagos] James Island).
- jacobinus*, *Bulimulus* (*Naesiotus*) *olla*, Dall & Ochsner, 1928: 163 [nomen nudum].
- jervisensis*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 381 (Galapagos, Jervis Island, 900-1000 ft.) [ST CAS].
- jullensorum*, *Naesiotus*, Breure, 1977a: 266, figs. 10-12, 14 (Colombia, Dept. Boyacá, Upper Rio Chicamocha valley, few km S Soatá, 2100 m) [HT RMNH 55113].
- lima*, *Bulimulus* (*Pleuropyrgus*), Reibisch, 1892: 25, pl. 2 fig. 5 ([Galapagos] Chatam [sic] Island).
- lopezi*, *Protoglyptus*, Rezende, Lanzieri & Inada, 1972: 374, figs. 1-3 ([Brazil] D[istrito] F[ederal], Brasília, Fercal) [HT MN 3555].
- luciae*, *Bulimulus sanctaeluciae*, Pilsbry, 1897d: 86, pl. 12 fig. 43 (British West Indies, St. Lucia) [HT ANSP 25667a].
- lycodus*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 379 (Galapagos, Indefatigable Island, 450-550 ft.) [ST CAS].
- lyelliae*, *Buliminus*, Beck, 1837: 70 [nomen nudum].
- manini*, *Bulimus*, 'Pfeiffer' Carpenter, 1857: 359 [emendation for *darwinii* Pfeiffer].
- maranonensis*, *Naesiotus subcostatus*, Breure, 1978b: 161, pl. 2 fig. 3 (Peru, Dept. Cajamarca, 25 km E Celendín, 2510 m) [HT UF 22774].
- martinicensis*, *Bulimus*, Pfeiffer, 1846d: 40 ([West Indies] Martinique) [LT BMNH].
- mazei*, *Bulimulus*, Crosse, 1874a: 118 ([West Indies] Martinique, Massif des Pitons, 730 m) [HT MNHN].
- minutissimus*, *Protoglyptus* (*Rimatula*), Parodiz, 1962: 445, pl. 1 fig. 6 (S. Bolivia, Choretirni [Choreti]) [HT USNM 361797].
- monotaenius*, *Bulimulus* (*Naesiotus*) *nux*, Dall & Ochsner, 1928: 157, pl. 9 figs. 3-8 (New name for *Bulimus unifasciatus* Reibisch, 1892, not *Bulinus unifasciatus* Sowerby, 1833).
- montivaga*, *Helix*, d'Orbigny, 1835: 14 (republica Boliviana, provincia Lagunensi; et republica Argentina, provincia Entre-Rios).
- naesioticus*, *Bulimulus* (*Naesiotus*), Dall, 1920: 121 [emendation for *nesioticus* Dall, 1896].
- nesioticus*, *Bulimulus* (*Naesiotus*), Dall, 1896: 443, pl. 16 fig. 1 ([Galapagos] James Island).
- nuciformis*, *Bulimus*, Petit, 1853b: 365, pl. 11 fig. 7 (îles Gallapagos) [HT MNHN].
- nucula*, *Bulimus*, Pfeiffer, 1854a: 60 (insulis Gallapagos) [LT BMNH 1975155].
- nudus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 21, pl. 1 fig. 15 ([Galapagos] Charles Island).
- nux*, *Bulinus*, Broderip, 1832: 125 (Galapagos, Charles Island) [LT BMNH 1975172].
- ochsneri*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 380 (Galapagos, Indefatigable Island, 200-650 ft.) [ST CAS].
- olla*, *Bulimulus* (*Naesiotus*), Dall, 1893b: 53 (New name for *Bulimus jacobii* Reeve, 1848, not *Bulinus jacobii* Sowerby, 1833).
- orinus*, *Naesiotus quitensis*, Rehder, 1940: 116, pl. 13 figs. 6, 10 (Ecuador, Chimborazo, near Riobamba, 12000 ft.) [HT USNM 473971].
- oxylabris*, *Scutalus*, Döring, 1879: 65 (la primera Sierra de Córdoba, La Calera, San Antonio, Maldonado, Alta Gracia [Argentina]).
- pachys*, *Bulimulus*, Pilsbry, 1897a: 20 (Brazil, Prov. of Bahia) [HT ANSP 25672].
- pallescens*, *Bulimulus* (*Naesiotus*) *ustulatus*, Dall & Ochsner, 1928: 160, pl. 9 figs. 13-14 (Galapagos, Charles Island, SW of Spring Mountain, 1650 ft.) [ST CAS].
- pallidus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 18, pl. 1 fig. 9 ([Galapagos] Albemarle Island).
- perchloris*, *Bulimulus* (*Naesiotus*) *nux*, Dall & Ochsner, 1928: 156, pl. 9 figs. 1-2 (Galapagos, Charles Island, 800-1000 ft.) [ST CAS].

- perrus*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 376 (Galapagos, Narborough Island, rim of the crater, 2000-4500 ft.) [ST CAS].
- perspectivus*, *Bulimus*, Pfeiffer, 1846a: 33 (Locality unknown) [LT BMNH 1975166].
- phlegonis*, *Bulimulus* (*Naesiotus*) *ustulatus*, Dall & Ochsner, 1928: 160, pl. 9 figs. 11-12, 15-17 (Galapagos, Charles Lsland, SW of Spring Mountain, 1650 ft.) [ST CAS].
- pileatus*, *Bulimulus* (*Naesiotus*) *eschariferus*, Dall, 1896: 434 ([Galapagos] Chatham Island).
- pilosus*, *Buliminus*, Guppy, 1871: 310, pl. 17 fig. 9 ([West Indies] Trinidad) [ST BMNH 1875.2.8.3].
- pilsbryi*, *Naesiotus*, Weyrauch, 1956b: 6, pl. 1 fig. 4 (Northern Peru, Río Marañon, near Chagual, Pampa Calquiche, 1200 m) [HT SMF 155698].
- pinzonensis*, *Naesiotus*, Vagvolgyi, 1977: 772, pl. 1 figs. 6a-b, pl. 2 fig. 2 (Ecuador, Archipiélago de Colón, Pinzón Island, northern and western cliffs of main peak, 1400-1500 ft.) [HT USNM 757718].
- pinzonopsis*, *Naesiotus*, Vagvolgyi, 1977: 774, pl. 1 figs. 7a-b (Ecuador, Archipiélago de Colón, Pinzón Island, northern and western cliffs of main peak, 1400-1500 ft.) [HT USNM 757719].
- planospira*, *Bulimulus* *rugulosus*, Ancey, 1887: 294 (Ile Chatham, archipel des Galapagos).
- pollonerae*, *Bulimulus*, Ancey, 1897: 17, fig. 10 (San Lorenzo, province de Jujuy, République Argentine).
- prepinguis*, *Naesiotus*, Vagvolgyi, 1977: 775, pl. 1 figs. 2a-b, pl. 2 fig. 5 (Ecuador, Archipiélago de Colón, Pinzón Island, secondary peak (864 ft.), north of the crater) [HT USNM 757720].
- punctistriatus*, *Protoglyptus*, Parodiz, 1946b: 5, fig. 2, pl. 1 figs. 5-6 (Argentina, Prov. Jujuy, Puesto Viejo) [HT MACN 991].
- quitensis*, *Bulimus*, Pfeiffer, 1848a: 230 (Quito) [LT BMNH 1975320].
- rabidensis*, *Bulimulus* (*Naesiotus*), Dall, 1917b: 381 (Galapagos, Jervis Island, 900-1000 ft.) [ST CAS].
- ramosae*, *Protoglyptus*, Hylton Scott, 1952: 23, pl. 1 fig. 6 ([Argentina] Prov. Salta, Pocitos) [HT MIHS].
- reibischii*, *Bulimulus* (*Naesiotus*), Dall, 1895: 126 (Galapagos, Indefatigable Island).
- rhabdotus*, *Bulimulus* (*Protoglyptus*), Haas, 1951: 512, fig. 100 (Peru, Ambo, near Huánuco, 2000 m) [HT FMNH 30915].
- rivasii*, *Bulimus*, d'Orbigny, 1836: 276, pl. 34 figs. 8-10 ([Bolivia] sur les coteaux des derniers contreforts des Andes boliviennes, avant de descendre dans les pleins de Santa Cruz de la Sierra, principalement à la Cuesta de Petaca).
- rocayana*, *Helix*, d'Orbigny, 1835: 13 (provincia Santa Cruz de la Sierra, republica Boliviana).
- rufescens*, *Bulimulus* (*Scutalus*) *quitensis*, Germain, 1910: C 35, pl. 4 figs. 1-2 ([Ecuador] Cujuja; valle de Tumbaco).
- rugatimus*, *Bulimulus* (*Naesiotus*), Dall, 1917a: 10 (New name for *Bulimulus acutus* Reibisch, 1892, not Leach, 1814).
- rugifer*, *Cochlicellus*, Beck, 1837: 63 [indication].
- rugiferus*, *Bulimus*, Sowerby, 1833b: 36 (Galapagos, James Island) [LT BMNH 1975178].
- rugulosus*, *Bulimus*, Sowerby, 1838? [1832-1841]: fig. 87 (Galapagos) [LT BMNH 1975176].
- saeronius*, *Bulimulus* (*Naesiotus*), Dall, 1917a: 9 (Galapagos, Indefatigable Island) [HT USNM 274097].
- sanctaeluciae*, *Bulimus* (*Leptomerus*), E. A. Smith, 1889: 403 ([West Indies] St. Lucia) [HT BMNH].
- scalesiana*, *Naesiotus*, A. G. Smith, 1972: 17, figs. 19-25 (Galápagos, Isla Santa Cruz, Horneman Farm area) [HT CAS 13745].
- sculpturatus*, *Bulimus*, Pfeiffer, 1846a: 29 (Galapagos Is.) [LT BMNH 1975174].

- silvaevagus*, *Naesiotus*, Weyrauch, 1960a: 36, pl. 4 fig. 20 (M-Peru, 2 km von Bergwerk Pichita Caluga (2200 m), im Chanchamayo-Becken [19.5 km WNW San Ramón]) [HT SMF 162001].
- simrothi*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 23, pl. 2 fig. 2 ([Galapagos] Albemarle Island).
- snodgrassi*, *Bulimulus*, Dall, 1900: 90, pl. 8 fig. 2 (Galapagos, Hood Island).
- subconoidalis*, *Bulimulus eschariferus*, Ancey, 1887: 295 (iles Galapagos).
- subcostatus*, *Bulimulus* (*Protoglyptus*), Haas, 1948: 190, fig. 39 (Peru, Dept. Cajamarca, Jaën, 1500-2100 feet) [HT FMNH 29148].
- sulcatus*, *Bulimulus* (*Naesiotus*) *incrassatus*, Reibisch, 1892: 16, pl. 1 figs. 4b-c ([Galapagos] Charles Island).
- tanneri*, *Bulimulus* (*Naesiotus*), Dall, 1895: 127 [as *fanneri*], iii (Galapagos, Indefatigable Island).
- terebra*, *Bulimulus* (*Pleuropyrgus*), Reibisch, 1892: 24, pl. 2 fig. 3 ([Galapagos] Chatam [sic] Island).
- tortuganus*, *Bulimulus* (*Naesiotus*), Dall, 1893b: 57 ([Galapagos] S Albemarle [Island], La Tortuga).
- trichodes*, *Helix*, d'Orbigny, 1835: 12 (Provincia Santa Cruz de la Sierra, republica Boliviana).
- trogonius*, *Bulimulus* (*Naesiotus*), Dall, 1917a: 10 (Galapagos, Albemarle Island, 1300 feet) [HT USNM 274096].
- tubularis*, *Bulimulus* (*Protoglyptus*), Pilsbry, 1930c: 357, pl. 31 figs. 5-8 (Bolivia, Dept. Santa Cruz, Prov. Cordillera, Questa del Limon) [HT ANSP 152288a].
- turritus*, *Naesiotus* (*Raphiellus*), Weyrauch, 1967a: 412, figs. 64-64a (Norte de Peru, valle del río Yanguate, 5 km NE Celendín, 2250 m) [HT IML 3976a].
- unifasciatus*, *Bulinus*, Sowerby, 1833b: 37 (Galapagos, Charles Id.) [LT BMNH 1975187].
- unifasciatus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 15, pl. 1 fig. 1 ([Galapagos] Charles Island) [not *unifasciatus* Sowerby].
- ustulatus*, *Bulinus*, Sowerby, 1833b: 72 ([Galapagos] Charles Id.).
- ventrosus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 19, pl. 1 figs. 12a-b ([Galapagos] Barrington Island) [ST ZMB 47949].
- venustus*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 17, pl. 1 fig. 7 ([Galapagos] Charles Island).
- vermiculatus*, *Bulimulus* (*Naesiotus*) *jacobi*, Dall, 1893b: 53 (Galapagos, James Island, James Bay).
- vermiculatus*, *Naesiotus quitensis*, Rehder, 1940: 117, pl. 13 figs. 17, 19 (Ecuador, Tunguragua, Agoyan near Baños) [HT MCZ 64957].
- verrucosus*, *Bulinus*, Pfeiffer, 1855h: 116 (Galapagos Island) [LT BMNH 1975168].
- vestalis*, *Bulinus*, Albers, 1854b: 218 (Columbia [sic, Peru] ad fluvium Maranhon).
- viridula*, *Bulimulus* (*Scutalus*) *subfasciatus*, Germain, 1910: C 29 ([Ecuador] Paramo de Pichincha).
- willinki*, *Naesiotus*, Breure, 1978b: 162, figs. 262-269, pl. 12 fig. 2 (Argentina, Prov. Salta, Estancia Lumbrera, 750 m) [HT IML 1263a].
- wolfi*, *Bulimulus* (*Naesiotus*), Reibisch, 1892: 22, pl. 2 figs. 1a-b ([Galapagos] Indefatigable Island) [ST BMNH 1894.6.8.7, ZMB 47950].
- zilchi*, *Naesiotus*, Weyrauch, 1956b: 9, pl. 1 fig. 6 (Northern Peru, Río Jequetepeque, Quinden, 600 m) [HT IML 1908].

Rabdotus Albers, 1850

- Rabdotus* Albers, 1850: 164. Type species by subsequent designation (Kobelt, 1880): *Helix dealbata* Say.
- Rhabdotus* Albers, 1860: 218 [emendation].

- Orthotomium* Crosse & Fischer, 1875 [1870-1894]: 473. Type species by original designation: *Bulimus sufflatus* Gould.
- Globulinus* Crosse & Fischer, 1875 [1870-1894]: 475. Type species by original designation: *Bulimus sufflatus* Gould.
- Leptobysrus* Crosse & Fischer, 1875 [1870-1894]: 475. Type species by original designation: *Bulimus spirifer* Gabb.
- Columna* Cooper, 1892a: 215. Type species by monotypy: *Rhodea californica ramentosa* Cooper [not *Columna* Perry, 1811].
- Plicolumna* Cooper, 1895: 164. New name for *Columna* Cooper, 1892, not Perry, 1811. (June).
- Pseudorhodea* Dall, 1895b: 51. Type species by original designation: *Rhodea californica ramentosa* Cooper. (September).
- Sonorina* Pilsbry, 1896a: 114. New name for *Leptobysrus* Crosse & Fischer, 1875, not *Leptobysrsa* Stål, 1873.
- Puritanina* Jacobson, 1958: 7. Type species by original designation: *Bulimulus (Scutalus) montezuma* Dall.
- Hannarabdotus* Emerson & Jacobson, 1964: 325. Type species by original designation: *Bulimulus slevini* Hanna.

Description. — Shell elongate-ovate to elongate-globose or turritid; perforate; thin to rather solid. Colour whitish to yellowish, uniformly coloured or with axial brown streaks. Surface smooth. Protoconch with straight axial riblets. Whorls slightly convex; suture well impressed. Aperture sub- to elongate-ovate. Peristome thin, simple to expanded and more or less reflexed. Columella with or without a fold.

Central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. Lateromarginal teeth are bicuspid, with elongate to lanceolate mesocones and ovate to deltoid ectocones. Half-row formula: $C/3 + LM \ x/2$ ($x = 28-36$).

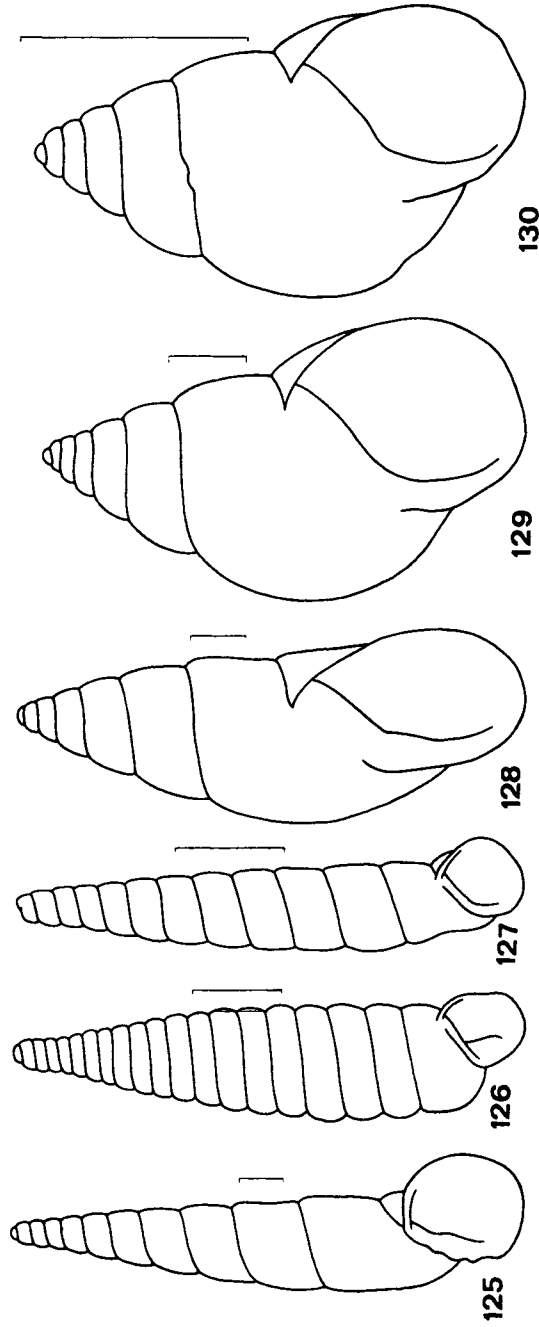
Pericard is ca. half as long as the nephridium, which is narrowly triangular. The main pulmonary vein is prominent and the side-veins are strongly developed, especially at the anterior end. The adrectal ureter is closed over its entire length.

Penis with a proximal sheath. The lumen of the penis is divided in a proximal part (broad, with pouches) and a distal part (narrow). The penis is swollen above the distal end of the sheath and the transition to the epiphallus is, both internally and externally, gradual. The epiphallus is relatively long. The flagellum is slender, with a distally attached retractor muscle. The spermathecal duct is subcylindrical, narrow, and with a globose spermatheca at the distal end.

Distribution. — Mexico, southern United States.

Ecology. — The species live on rocks or "upon bushes and other vegetation" (Pilsbry, 1946a: 6).

Relationships. — The phylogenetic relationships of this genus are discussed



Figs. 125-130. Variation in shell shape in *Berendtia*, *Spartocentrum* and *Rabdotus*. Fig. 125. *B. taylora* (Pfeiffer). Fig. 126. *S. vanduzeei* (Hanna). Fig. 127. *R. ramentosus* (Cooper). Fig. 128. *R. inscendens* (Binney). Fig. 129. *R. alternatus* (Say). Fig. 130. *R. dealbatus* (Say). Scale = 5 mm.

on page 151. The genus is characterized by the straight axial riblets on the protoconch.

Remarks. — A revision of *Rabdotus*, especially of the Baja California species, is forthcoming (Christensen, in press). This revision will present new data on the subgeneric division of *Rabdotus* and for this reason the genus is here treated sensu lato.

Bibliography. — The main publications on this genus are: Christensen & Miller, 1977; Cooper, 1891-1895; Dall, 1893c, 1897; Emerson & Jacobson, 1964; Hanna, 1923; Jacobson, 1958; Pilsbry, 1946a, 1953; Pilsbry & Ferriss, 1906, 1919, 1923; Pratt, 1969.

Taxa. — The following taxa are placed in this genus:

- abbreviata*, *Columna ramentosa*, Cooper, 1892a: 215 ([Mexico, Baja California] Sierra Laguna).
- acholus*, *Bulimulus (Scutalus)*, Mabile, 1895: 68 ([Mexico] montagnes de la Basse Californie) [LT MNHN].
- albidus*, *Bulimulus alternatus*, 'Taylor' Cockerell, 1891: 23 (Derby, Frio Co., Texas).
- alta*, *Bulimulus (Leptobyrus) inscendens*, Dall, 1893c: 643 [no type locality given].
- alternatus*, *Bulimus*, Say, 1830: 25 [publication not seen; type locality: Mexico, Monterrey (teste Pilsbry, 1946a)].
- artemisia*, *Bulimulus*, Binney, 1861: 331, fig. ([Mexico] peninsulae Californiae, San Lucas).
- baileyi*, *Bulimulus (Scutalus)*, Dall, 1893c: 640, pl. 71 fig. 1 (Mexico, Guaymas; Ortiz; Cape St. Lucas).
- bakeri*, *Bulimulus*, Hanna, 1923: 500, pl. 7 figs. 7-10 ([Mexico] Lower California, San Nicolas Bay, San Antonio Point) [HT CAS 1017].
- beldingi*, *Bulimulus inscendens*, Cooper, 1892a: 209 ([Mexico, Baja California] Punta Arena, near 25°30' [N], east coast).
- binneyanus*, *Bulimus*, 'Pfeiffer' Binney, 1859: 128 [Texas].
- bryanti*, *Bulimulus (Mesembrinus) inscendens*, Cooper, 1891: 101 ([Mexico, Baja California] on dry mountains 800 to 1000 ft high, between Cape St. Lucas and Margarita Bay; also for 350 miles farther north near San José del Cabo, twelve miles east of the Cape).
- cacoctycus*, *Bulimulus (Scutalus)*, Mabile, 1895: 69 ([Mexico, Baja California] Les Sierras du Sud de la presqu'île) [LT MNHN].
- carmen*, *Bulimulus*, Pilsbry & Lowe, 1932: 50 ([Mexico] Gulf of California, Salinas Bay, Carmen Island) [HT ANSP 158995a].
- ceralboensis*, *Bulimulus*, Hanna, 1923: 490, pl. 7 fig. 11, pl. 11 figs. 2, 4 ([Mexico] Gulf of California, Ceralbo Island, W of Ruffo's ranch house) [HT CAS 1021].
- chamberlini*, *Bulimulus*, Hanna, 1923: 494, pl. 8 fig. 21 ([Mexico] Gulf of California, San Diego Island) [HT CAS 1023].
- chinchensis*, *Bulimulus sufflatus*, Cooper, 1894: 140, pl. 5 fig. 10 ([Mexico, Baja California] El Chinche Mts., 2000 ft.).
- confinus*, *Bulimus*, Reeve, 1850a: pl. 86 fig. 643 (Texas, United States).
- cooperi*, *Bulimulus*, Dall, 1896a: 5 (New name for *Bulimulus pilula* Crosse & Fischer, not Binney).
- cosmicus*, *Bulimulus (Scutalus)*, Mabile, 1895: 68 ([Mexico, Baja California] Les Sierras du Sud de la presqu'île) [LT MHHN].

- dealbata*, *Helix*, Say, 1821: 159 [publication not seen; type locality: Missouri and Alabama, teste Pilsbry, 1946a].
- decipiens*, *Bulimulus*, Cooper, 1895: 164 ([Mexico, Baja California] San Lazaro Mt.).
- dentifer*, *Bulimulus* (*Leptobyrsus*), Mabille, 1895: 67 ([Mexico] Ile volcanique de la Tortuga, Basse Californie) [NT CAS 1048].
- digueti*, *Bulimulus* (*Thaumastus*), Mabille, 1895: 69 ([Mexico, Baja California] Sierra de la Victoria).
- dismenicus*, *Bulimulus* (*Leptobyrsus*), Mabille, 1895: 67 ([Mexico, Baja California] Sierra de la Puna, 1800 mètres) [LT MNHN].
- durangoanus*, *Bulimulus* (*Peronaeus*), Martens, 1893: 246, pl. 16 fig. 11 (N. Mexico, Villa Lerdo, State of Durango).
- elatus*, *Bulimus*, Gould, 1853: 408 [no type locality given].
- excelsus*, *Bulimus*, Gould 1853: 376, pl. 14 fig. 3 (California).
- gabbi*, *Bulimulus* (*Scutalus*), Crosse & Fischer, 1872: 223 (California Mexicana).
- gigantensis*, *Rabdotus*, Christensen & Miller, 1977: 131, figs. 1-3 (Baja California Sur, Mexico, at San Javier, 350-450 m) [HT CAS 57937].
- hannai*, *Bulimulus*, Pilsbry, 1927: 183, pl. 11 figs. 16-20, pl. 12 fig. 3 (Mexico, Lower California, Magdalena Bay, Margarita Island).
- harribaueri*, *Bulimulus* (*Puritanina*), Jacobson, 1958: 7, figs. 1-2 ([Mexico] Baja California, Fraile Bay) [HT AMNH 74003].
- hypodon*, *Bulimulus*, Pilsbry, 1897d: 102 ([Mexico] Lower California).
- inscendens*, *Bulimus*, Binney, 1861: 332, fig. ([Mexico] peninsulae Californiae inter Cape San Lucas et Margarita Bay).
- insularis*, *Bulimulus sufflatus*, Cooper, 1892a: 208, 212 ([Mexico, Baja California] Espiritu Santo Island).
- johnstoni*, *Bulimulus*, Hanna, 1923: 491, pl. 7 figs. 1-6, pl. 11 fig. 3 ([Mexico] Gulf of California, Santa Catalina Island) [HT CAS 1024].
- jonesi*, *Bulimulus dealbatus*, Clench, 1937: 18, pl. 3 fig. 4 (Alabama, Greene Co., 2 miles N of West Greene) [HT Univ. Alabama].
- juarezi*, *Bulimus*, Pfeiffer, 1866: 832 (provincia pacifica reipublicae Mexicanae) [ST BMNH].
- lactarius*, *Bulimus*, 'Menke' Pfeiffer, 1846c: 85 (Mexico).
- laevapex*, *Rabdotus*, Christensen & Miller, 1977: 132, figs. 4-7 (Baja California Sur, Mexico, on west side of Isla Cerralvo, approximately 0.5 km inland of the beach at El Limón anchorage, 50-100 m) [HT CAS 57942].
- lamellifer*, *Bulimulus*, Pilsbry, 1897d: 103 ([Mexico] Lower California) [HT ANSP 73646a].
- lapidivagus*, *Bulimulus* (*Leptobyrsus*), Mabille, 1895: 66 ([Mexico, Baja California] Sierra de Cacachila au sud de la Paz).
- levis*, *Bulimulus* (*Mesembrinus*) *xantusi*, Dall, 1893c: 642 [no type locality given].
- liquabilis*, *Bulimus*, Reeve, 1848: pl. 57 fig. 387 (Texas) [LT BMNH 1975422].
- mariae*, *Bulimus* (*Scutalus*), Albers, 1850: 160 [Texas, Brownsville; teste Pilsbry, 1946a].
- montezuma*, *Bulimulus* (*Scutalus*), Dall, 1893a: 26 (New name for *Bulimus proteus* Binney, 1869, not *Bulimus proteus* Broderip, 1832).
- monticola*, *Bulimulus* (*Leptobyrsus*) *inscendens*, Dall, 1893c: 643 [no type locality given].
- mooreanus*, *Bulimus*, 'W. G. Binney' Pfeiffer, 1868: 143 (Washington et De Witt Counties, Texas).
- neomexicanus*, *Bulimulus dealbatus*, Pilsbry, 1946a: 13, figs. 4e-f (New Mexico, western slope San Andreas Mts., Burkes Spring) [HT ANSP 175913].
- nigromontanus*, *Bulimulus alternatus*, Dall, 1897: 357 (Black Mountain, Sonora, Mexico) [HT USNM 129993].
- noctoleonis*, *Bulimulus* (*Rabdotus*), Pilsbry, 1953: 46, pl. 5 fig. 6 (Mexico, Nuevo Leon, near Galeana, Cerro Potosi) [HT ANSP 191020].

- orthelasmus*, *Bulimulus spirifer*, Pilsbry, 1898: 159 [Mexico, Baja California; teste Clench & Turner, 1962; HT ANSP 4270].
- ozarkensis*, *Bulimulus dealbatus*, Pilsbry & Ferriss, 1906: 136, pl. 6 figs. 14-15 (Missouri, Barry Co., Seligman) [LT ANSP 91358a].
- pallidior*, *Bulimus*, Sowerby, 1833b: 72 (South America).
- pasonis*, *Bulimulus dealbatus*, Pilsbry, 1902b: 32 (Texas, El Paso) [LT ANSP 83259a].
- patriarcha*, *Bulimus*, Binney, 1858: 116 (republica Mexicana).
- pecosensis*, *Bulimulus dealbatus*, Pilsbry & Ferris, 1906: 138, pl. 6 figs. 26-27 (Texas, Val Verde Co., 1½ mi SE High Bridge, So. Pacific R.R.) [LT ANSP 84618a].
- pilula*, *Bulimus*, Binney, 1861: 332, fig. ([Mexico] peninsulae Californiae, Todos Santos Mission et insula Marguerita) [HT USNM].
- pilula*, *Bulimulus*, Crosse & Fischer, 1875 [1870-1894]: 570, pl. 21 fig. 6 (Missione Todos Santos et in insula Margarita, Californiae Mexicanae).
- proteus*, *Bulimus*, Binney, 1861: 331 ([Mexico, Baja California] Cape San Lucas).
- ragsdalei*, *Bulimulus*, Pilsbry, 1890: 122 (Texas, St. Jo; Warren's Bend, 25 mi NW of Gainesville) [HT ANSP 58380a].
- ramentosa*, *Rhodea californica*, Cooper, 1891: 102 [no type locality given].
- recognitus*, *Bulimulus* (*Globulus*), Mabille, 1895: 69 ([Mexico] Basse Californie) [LT MNHN].
- rimatus*, *Bulimus*, Pfeiffer, 1847a: 112 (Locality unknown) [LT BMNH 1975418].
- sanmarcoensis*, *Bulimulus*, Pilsbry & Lowe, 1932: 49 ([Mexico] Gulf of California, San Marcos Island) [LT ANSP 158996a].
- santacruzensis*, *Bulimulus*, Hanna, 1923: 487, pl. 7 figs. 12-15 ([Mexico] Gulf of California, Santa Cruz Island) [HT CAS 1030].
- schiedeanus*, *Bulimus*, Pfeiffer, 1841: 43 (Mexico) [ST BMNH].
- sinaloae*, *Bulimulus excelsus*, Pilsbry, 1897d: 142, pl. 20 figs. 69-70 (Mexico, Sinaloa) [LT ANSP 25702a].
- slevini*, *Bulimulus*, Hanna, 1923: 488, pl. 7 figs. 16-19 ([Mexico] Gulf of California, Monserrate Island) [HT CAS 1034].
- sonorensis*, *Bulimulus*, Pilsbry, 1928: 115, fig. 1 (Mexico, Sonora, Carbo, Copete Mine) [HT ANSP 142647a].
- spirifer*, *Bulimus*, Gabb, 1868: 236 ([Mexico, Baja California] from San Antonio, below La Paz to near San Borja).
- striatulus*, *Bulimulus* (*Scutalus*) *pallidior*, Dall, 1893c: 640 ([Mexico, Baja California] Carmen and Margarita Islands).
- subspirifer*, *Bulimulus* (*Leptobyrsus*), Mabille, 1895: 67 ([Mexico] Basse Californie) [LT MNHN].
- sufflatus*, *Bulimus*, Gould in Binney, 1859: 25 (New name for *Bulimus vesicalis* Gould, 1853 (Oct.), not Pfeiffer, 1853 (March)).
- vegetus*, *Bulimus*, Gould, 1853: 375, pl. 14 fig. 2 ([Mexico] San Juan, Gulf of California).
- vegexpiza*, *Bulimulus vegetus*, Cooper, 1894: 134, pl. 5 fig. 1, pl. 6 fig. 27 ([Mexico, Baja California] Sierra El Taste (Meadow Mountains) in the central ridge north of Cape St. Lucas).
- veseyianus*, *Bulimulus* (*Leptobyrsus*), Dall, 1893c: 645, pl. 72 figs. 4-5 ([Mexico] Espiritu Santo Island, Gulf of California) [HT USNM 34122].
- vesicalis*, *Bulimus*, Gould, 1853: 375, pl. 14 fig. 1 ([Mexico] Lower California).
- xantusi*, *Bulimus*, Binney, 1861: 331, fig. ([Mexico] San Lucas, peninsulae Californiae).
- ximenez*, *Bulimulus*, Hanna, 1923: 497, pl. 8 figs. 4-9 ([Mexico] Gulf of California, Carmen Island, Marquer Bay) [HT CAS 1042].

Berendtia Crosse & Fischer, 1869

- Berendtia* Crosse & Fischer, 1869: 191. Type species by monotypy: *Clausilia*? (*Balea*?) *taylori* Pfeiffer.

Description. — “Shell rimate turrated, straightly tapering to an obtuse rounded apex which is retained in adult shells. Whorls about 11, the first 2 vertically costellate, the next having the riblets cut into spiral series of granules; last whorl becoming free in front, acutely keeled above. Aperture oblique, semicircular-ovate, the peristome broadly expanded and subreflexed. Internal axis imperforate, very slender and weakly sigmoid within each whorl” (Pilsbry, 1902c: 57).

Central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. Lateromarginal teeth are bicuspid, with elongate to lanceolate mesocones and ovate to deltoid ectocones. Half-row formula: $C/3 + LM\ x/2$ ($x = 30-34$).

Pericard nearly as long as the nephridium, which is triangular. The main pulmonary vein is prominent, especially at the anterior end, where the side veins are also strongly developed. The adrectal ureter is open at the anterior end over $1/5-1/6$ of its length.

The penis has a proximal sheath and is swollen above the distal end of the sheath. The epiphallus and especially the flagellum are relatively long. The spermathecal duct is narrow and subcylindrical, with a globose spermatheca at the distal end.

Distribution. — Mexico (Baja California).

Ecology. —The species aestivates sealed to rocks (Christensen, in litt.).

The only taxon included in this genus is:

taylori, *Clausilia?* (*Balea?*), Pfeiffer, 1861a: 27, pl. 2 fig. 7 (Localitas ignota).

Spartocentrum Dall, 1895

Spartocentrum Dall, 1895b: 51. Type species by original designation: *Cylindrella* (*Urocoptis*) *irregularis* Gabb.

Teneritia Mabille, 1897: 79. Type species by present designation: *Berendtia digueti* Mabille.

Description. — “Shell many-whorled, slender, cylindric below, tapering above, retaining the apex entire. Apex bulbous, the first $2\frac{1}{2}$ whorls vertically costellate, following 2 whorls decussated, granose, subsequent whorls ribbed, the last with no trace of a subperipheral cord, adnate or becoming free. Internal axis hollow, smooth, somewhat sinuous within each whorl, having a spiral swelling or convexity” (Pilsbry, 1902c: 51).

The central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. Lateromarginal teeth are bicuspid, with elongate to lanceolate mesocones and deltoid ectocones, which are serrate in the outermost teeth. Half-row formula: $C/3 + LM\ x/2$ ($x = 24$).

Penis with a proximal sheath, swollen above the distal end of the sheath. The vagina is short. The spermathecal duct is narrow, subcylindrical and with a globose spermatheca at the distal end.

Distribution. — Mexico (Baja California).

Ecology. — The species "aestivate free in the soil under rocks" (Christensen, in litt.).

Remarks. — The main differences between the species of *Spartocentrum* and *Berendtia* are: (1) the spiral swelling on the axis in *Spartocentrum*; (2) the different ecology [species of *Berendtia* and most *Rabdotus* aestivate sealed to the rocks (Christensen, in litt.)]. The shape of the shell, the sculpture of the protoconch and the anatomy, however, resemble each other strikingly and I expect that further research will show that these two genera are synonymous.

Taxa. — The following taxa are placed in *Spartocentrum*:

clavigeroi, *Coelocentrum*, Hanna, 1923: 512, pl. 9 figs. 29-30, pl. 11 fig. 6 ([Mexico] Lower California, Agua Verde Bay) [HT CAS 1082].

digueti, *Berendtia*, Mabille, 1895: 70 ([Mexico, Baja California] Plateau de San Xavier [sic, Javier]) [LT MNHN].

eiseni, *Coelocentrum*, Bartsch, 1907: 119 [emendation for *eisenianum* Pilsbry].

eisenianum, *Coelocentrum*, Pilsbry, 1900c: 553, fig. 2 ([Mexico] Lower California) [HT ANSP 77888].

gabbi, *Coelocentrum minorinum*, Pilsbry, 1900c: 551, fig. 1 ([Mexico] high table-land of the interior of Lower California, especially about Muleje) [HT ANSP 25077a].

insulare, *Coelocentrum*, Hanna, 1923: 509, pl. 9 figs. 9-28, pl. 11 fig. 5 ([Mexico] Gulf of California, Carmen Island, Puerto Bellandra) [HT CAS 1061].

irregularis, *Cylindrella (Urocoptis)*, Gabb, 1868: 238, pl. 16 fig. 4 [no type locality given].

minorina, *Berendtia*, Mabille, 1895: 70 ([Mexico, Baja California] plateaux situés su-dessus de l'Arroyo de la Purissima) [LT MNHN].

oweni, *Coelocentrum*, Hanna, 1923: 511, pl. 9 figs. 3-8, pl. 11 fig. 8 ([Mexico] Gulf of California, Carmen Island, Agua Grande) [HT CAS 1055].

vanduzeei, *Coelocentrum*, Hanna, 1923: 508, pl. 9 figs. 31-34, pl. 11 fig. 7 ([Mexico] Lower California, west side of Puerto Escondido) [HT CAS 1085].

Scutalus Albers, 1850

Scutalus Albers, 1850: 160. Type species by subsequent designation (Albers, 1860): *Bulinus proteus* Broderip.

Xenothauma Fulton, 1896: 102. Type species by monotypy: *Helix (Xenothauma) baroni* Fulton.

Spiroscutalus Pilsbry, 1932: 392. Type species by monotypy: *Bulimulus (Spiroscutalus) endospira* Pilsbry.

Description. — Shell elongate-ovate to globose, or depressed conical; broadly perforate to rimate; thin to solid. Colour yellowish, whitish or brownish, uniformly or with a colour pattern of darker spots or spiral bands. Surface with incrassate growth striae or granulation. Protoconch pit-reticulate or with anastomosing axial wrinkles. Whorls hardly to slightly convex; suture

well impressed. Aperture (sub)ovate. Peristome simple or expanded. Columella in some species with a fold.

Distribution. — N-Argentina, Bolivia, Peru, Ecuador.

Relationships. — The phylogenetic relationships of the subgenera are discussed on page 152ff.

Bibliography. — The main publications on this genus are: Breure, 1978b; Crawford, 1939; Haas, 1951, 1952, 1955a; Hylton Scott, 1951; Marshall, 1932; Pilsbry, 1897d, 1932; Pilsbry & Olsson, 1949; Weyrauch, 1960a, 1967a.

Key to the subgenera of *Scutalus*

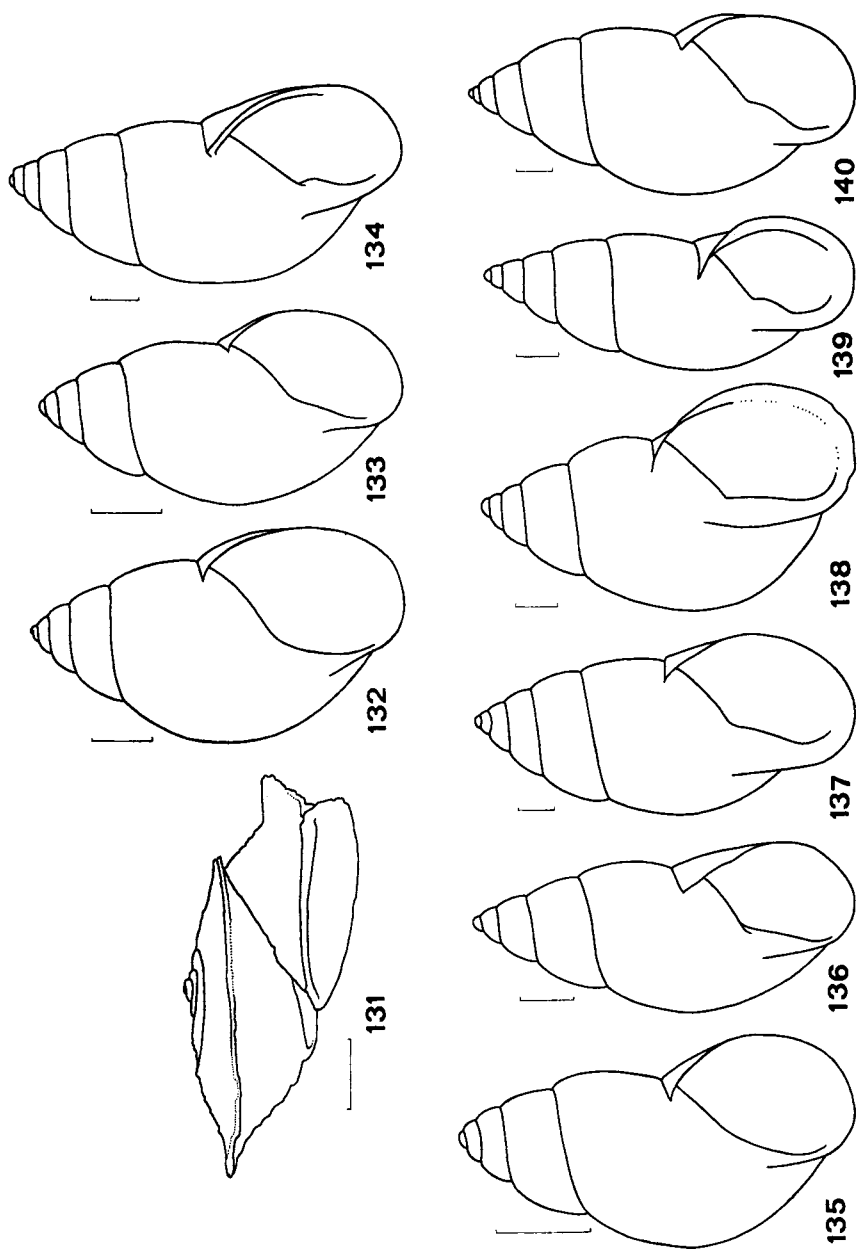
- 1a. Protoconch with axial wrinkles; peristome simple; central teeth of radula tricuspid 2
- b. Protoconch pit-reticulate; peristome more or less expanded; central teeth of radula monocuspid *Scutalus* (*Scutalus*)
- 2a. Shell thin; suture crenulate; penis with a single type of epithelium *Scutalus* (*Suniellus*)
- b. Shell (rather) solid; suture simple; penis with two types of epithelium 3
- 3a. Spermathecal duct $1/3-1/2$ the length of the spermooviduct; lateromarginal teeth with acute, elongate to deltoid mesocones and relatively small, deltoid ectocones *Scutalus* (*Kuschelenia*)
- b. Spermathecal duct as long as the spermooviduct; lateromarginal teeth with elongate to wedge-shaped mesocones and acute, ovate to deltoid ectocones *Scutalus* (*Vermiculatus*)

Scutalus (Scutalus) Albers, 1850

Description. — Shell elongate-ovate to rather globose or depressed conical; (broadly) perforate; solid. Colour whitish to brownish with darker spiral bands, in some species with axial streaks of coalescent spots. Surface granulate or with incrassate growth striae. Protoconch pit-reticulate. Whorls slightly convex. Aperture (sub)ovate. Peristome more or less expanded. Columella in some species with a fold within the last whorl.

The central and lateral teeth of the radula are monocuspid, with blunt conical to deltoid cones. The marginal teeth are bicuspid, with lanceolate mesocones and deltoid cones. Half-row formula: $C/I + L x/I + M y/2$ ($x = 10-16$, $y = 29-31$).

The pericard is about as long as the nephridium, which is narrowly triangular. The main pulmonary vein is moderately to well developed, the side veins are moderately developed. At the anterior end the veins are more



Figs. 131-140. Variation in shell shape in *Scutalus*. Fig. 131. S. (S.) *baroni* (Fulton). Fig. 132. S. (*Vermiculatus*) *angrandi* (Morelet). Fig. 133. S. (*Kuschelena*) *culmineus* (d'Orbigny). Fig. 134. S. (*Vermiculatus*) *omissus* Weyrauch. Fig. 135. S. (*Vermiculatus*) *macedoi* Weyrauch. Fig. 136. S. (*Vermiculatus*) *weddellii* (Hupé). Fig. 137. S. (S.) *grandiventris* Weyrauch. Fig. 138. S. (S.) *proteus* (Broderip). Fig. 139. S. (S.) *latecolumellaris* (Preston). Fig. 140. S. (*Kuschelena*) *tupacii* (d'Orbigny). Scale = 5 mm.

strongly developed and form a deltoid network. The adrectal ureter is closed.

The penis has a proximal sheath and is rather stout and more or less subcylindrical in form. The lumen of the penis is narrow; in the distal part of the penis, where a different type of epithelium is found, a short blind sac is present. The transition to the epiphallus, both internally and externally, is gradual. The flagellum is rather slender, with a distally attached retractor

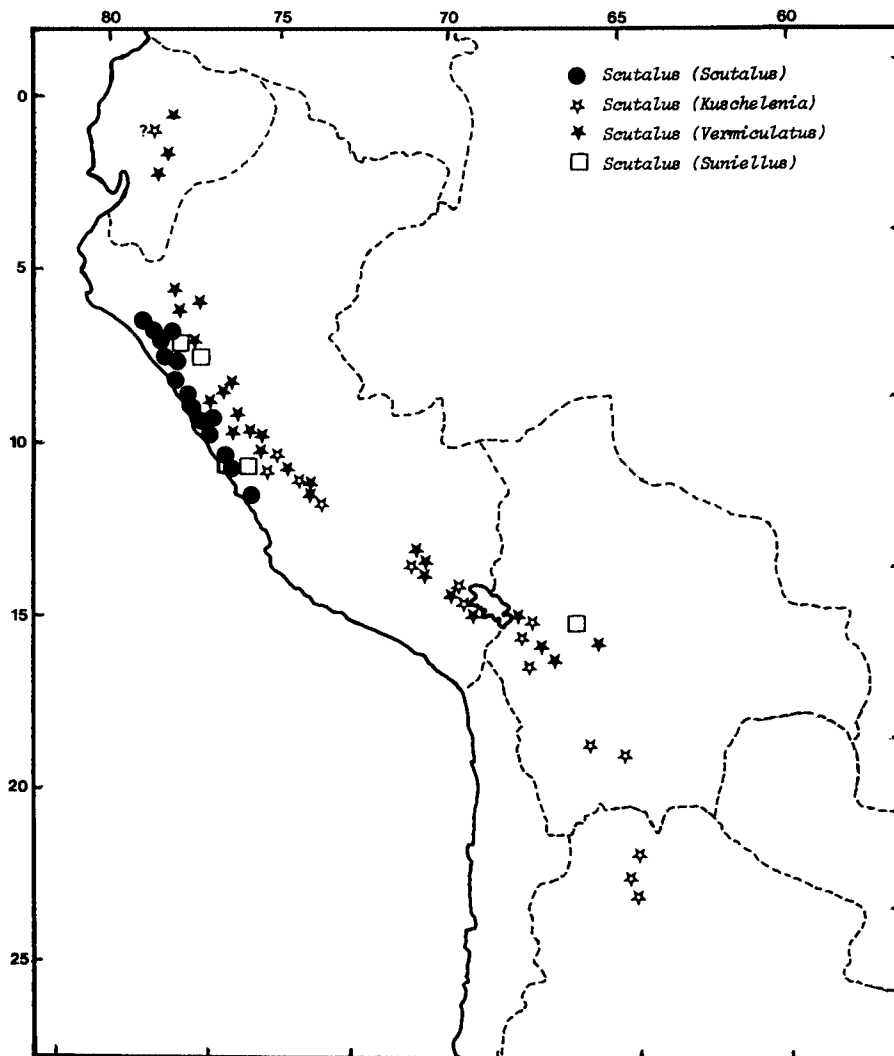


Fig. 141. Distribution of *Scutalus*.

muscle. The vagina is rather short. The spermathecal duct is more or less subcylindrical, with a globose spermatheca at its distal end.

Distribution. — Peru, coastal area (Dept. Lima, Ancash, La Libertad, Cajamarca).

Ecology. — The species are mainly living on rock-faces or on large stones in savannah habitat. The vertical distribution is 50-1850(-2700) m.

Taxa. — The following taxa are placed in this subgenus:

- baroni*, *Helix* (*Xenothauma*), Fulton, 1896: 101 (Rio Yonan, Peru, 4000 ft) [LT BMNH 1896.6.23.1].
- baroni*, *Bulimulus* (*Drymaeus*), Fulton, 1897: 213, pl. 6 fig. 8 (Peru, Rio Yonan) [LT BMNH 1897.8.3.177].
- broggii*, *Xenothauma*, Pilsbry & Olsson, 1949: 5, figs. 10-11 (Peru, Huacho, Cerro Colorado) [HT ANSP 184106].
- callaoensis*, *Bulimulus versicolor*, Pilsbry, 1897d: 16, pl. 1 fig. 15 (Peru, Callao) [LT ANSP 3464a].
- chiletensis*, *Scutalus* (*Scutalus*), Weyrauch, 1967a: 373, figs. 24-30 (Norte de Peru, río Jequetepeque, cerro encima del pueblo Chilete, 850-950 m) [HT IML 1354a].
- coraformis*, *Bulimulus*, Pilsbry, 1897d: 15, pl. 30 figs. 10-13 (Peru, Marañon River).
- cretaceus*, *Bulimus*, Pfeiffer, 1855b: 123 (Eastern Islands [sic, N-Peru]) [LT BMNH 1975388].
- debilisculptus*, *Scutalus* (*Scutalus*) *coraformis*, Weyrauch, 1967a: 376, figs. 20-23, 137-138 (Norte de Peru, río Jequetepeque, cerca de Quinden, 600-700 m) [HT IML 1964a].
- endospira*, *Bulimulus* (*Spiroscutalus*), Pilsbry, 1932: 392, pl. 28 figs. 14-16 (Peru, Dept. La Libertad, Samne, 6000 ft.) [HT ANSP 159904a].
- grandiventris*, *Scutalus*, Weyrauch, 1960a: 42, pl. 5 figs. 27-33 (N-Peru, oberhalb Cascas, ± 100 km nō. Trujillo, 1400 m) [HT SMF 155690].
- granulatus*, *Scutalus* (*Scutalus*) *chiletensis*, Weyrauch, 1967a: 375, figs. 31-32 (Norte de Peru, cerro situado en el valle de un río afluente de la margen derecha del río Jequetepeque, N de Chilete, 850 m) [HT IML 1362a].
- lachayensis*, *Scutalus* (*Scutalus*) *versicolor*, Weyrauch, 1967a: 383, figs. 109-115 (Peru central, lomas de Lachay cerca de Chancay, 90 km N de Lima, 300-350 m) [HT IML 147a].
- latecolumellaris*, *Bulimulus*, Preston, 1909: 510, pl. 10 fig. 11 (Peru) [HT BMNH 1922.2.4.39].
- mutabilis*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 108 (montibus Peruviae, Santos).
- mutabilis*, *Bulimus*, Sowerby, 1833a: fig. 15.
- nobilis*, *Xenothauma*, Pilsbry & Olsson, 1949: 7, fig. 9 (Peru, above Tembladera, Cerro de Sapo) [HT ANSP 183968].
- ortizpuenti*, *Scutalus* (*Scutalus*), Weyrauch, 1967a: 378, fig. 100 (Norte de Peru, valle del río Chancay, entre Chiclayo y Chota) [HT IML 10647].
- phaeocheilus*, *Bulimulus* (*Scutalus*), Haas, 1955b: 334, fig. 74 (Peru, Dept. Lambayeque, Chongoyape, 300 m) [HT FMNH 51918].
- proteiformis*, *Bulimus*, Dohrn, 1863: 154 [no type locality given].
- proteus*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 107 (Peruviae montibus, St. Jacinta, near Samanco).
- sordidus*, *Bulimus*, Deshayes in Deshayes & Milne Edwards, 1838: 267 (les montagnes du Pérou).
- steerei*, *Bulimulus*, Pilsbry, 1900a: 391 (Peru) [LT ANSP 78144a].

varians, *Bulimus*, 'Broderip' Küster, 1844 in Küster & Pfeiffer, 1840-1865: 41, pl. 13 figs. 3-4 [indication].

versicolor, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 108 (montibus Peruviae, Mongon near Casma).

Scutalus (Suniellus) Breure, 1978

Suniellus Breure, 1978b: 188. Type species by original designation: *Scutalus (Suniellus) chillu* Breure.

Description. — Shell ovate-conic to globose; rimate to imperforate; with slightly convex sides; thin. Colour yellowish to blackish-brown; uniformly coloured or, usually, with lighter axial streaks. Surface (slightly) shining, growth striae (partly) incrassate, often broken into oblong granules. Protoconch with axial wrinkles, sometimes more or less anastomosing. Whorls hardly convex; suture crenulate. Aperture subovate. Peristome thin and simple.

The central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. The lateromarginal teeth are bicuspid, with elongate to lanceolate mesocones and deltoid ectocones. Half-row formula: C/3 + LM x/2 (x = 34-43).

Pericard ca. $\frac{3}{4}$ the length of the nephridium, which is broadly triangular. The main pulmonary vein is well developed, the side veins are weakly to moderately developed.

The penis has a proximal sheath and is more or less subcylindrical in form. The lumen is lined by a single type of epithelium. The epiphallus intrudes the distal part of the penis. The external transition to the epiphallus is gradual. The flagellum is relatively short. The spermathecal duct is more or less tapering and has an elongate-globose spermatheca at its distal end.

Distribution. — Bolivia, Peru.

Ecology. — The habitat of the species is unknown. The vertical distribution is 2600-4100 m.

Taxa. — The following taxa are included in this subgenus:

chillu, *Scutalus (Suniellus)*, Breure, 1978b: 188, fig. 323, pl. 11 fig. 5 (Bolivia, Río Songo, Cuticucho, 3800-4100 m) [HT SMF 249640].

goudoti, *Bulimus*, Petit, 1843a: 239 (Nouvelle Grenade) [LT MNHN].

kochi, *Bulimus*, Pfeiffer, 1846b: 144 (republica chilensi?).

troscheli, *Bulimus*, Philippi, 1867: 71 (Peru, Hacienda de Unigambal [Dept. La Libertad, Distr. Santiago de Chuco]).

Scutalus (Vermiculatus) Breure, 1978

Vermiculatus Weyrauch, 1967a: 384 [nomen nudum]; Breure, 1978b: 166. Type species by original designation: *Bulimus bicolor* Sowerby.

Description. — Shell globose to elongate; with straight to slightly convex sides; rather thin to solid. Colour whitish to yellowish, uniformly coloured,

with spiral bands or a variegate pattern. Surface rather shining, growth striae incrassate or with axial riblets. Protoconch with axial wrinkles. Whorls rather flat, the last whorl more or less inflated. Aperture (sub)ovate. Peristome thin to slightly thickened, simple or hardly expanded.

The central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. The lateromarginal teeth are bicuspid, with elongate to lanceolate mesocones and deltoid ectocones, which are serrate in the outermost teeth. Half-row formula: $C/3 + LM \ x/2$ ($x = 26-33$).

The pericard is as long as the nephridium, which is (broadly) triangular. The main pulmonary vein is prominent and broad, the side veins are moderately to well developed, especially at the anterior end, where also a vein parallel to the main pulmonary vein may be found. The adrectal ureter is partially open ($1/10-1/2$ of its length).

The penis has a proximal sheath and is subcylindrical in form. The lumen of the proximal part is rather narrow by infoldings. More distally the lumen is wider, but narrow again at the transition to the distal part of the penis. The transition to the epiphallus, both internally and externally, is gradual. The flagellum is slender and rather long; the retractor muscle is distally attached. The spermathecal duct is more or less tapering, with a (elongate-) globose spermatheca at its distal end.

Distribution. — Bolivia, Peru, Ecuador.

Ecology. — The species live mainly on shrubs, mostly near rocky outcrops. The vertical distribution is 2600-5000 m.

Taxa. — The following taxa are included in this subgenus:

- achrous*, *Bulimulus* (*Scutalus*), Haas, 1952: 126, fig. 24 (Bolivia, Dept. Cochabamba, Tarata, 2800 m) [HT FMNH 39720].
- aequatorius*, *Bulimus*, Pfeiffer, 1853d: 420 (reipublicae Aequatoris, monte Schinchulagua) [LT BMNH 1975377].
- altorum*, *Bulimulus* (*Scutalus*) *revinctus*, Haas, 1951: 516, fig. 104 (Peru, puna between Andahuaylas and Abancay, 400 m) [HT FMNH 30912].
- angrandi*, *Bulimus*, Morelet, 1860: 372 (Pérou, Huancabelica).
- anthisanensis*, *Bulimus*, Pfeiffer, 1853d: 406 (reipublicae Aequatoris, monte Anthisana) [LT BMNH 1975372].
- aquilus*, *Bulimus*, Reeve, 1848: pl. 22 fig. 138 (Peru, Tacna) [LT BMNH 1975376].
- aureus*, *Scutalus* (*Vermiculatus*), Breure, 1978b: 170, pl. 10 fig. 12 (Peru, Dept. Cajamarca, 26 km NE Encañada, 3650 m) [HT UF 22754].
- badius*, *Bulimus*, Sowerby, 1835: 141 (provincia Peruviae Xagua).
- bicolor*, *Bulimus*, Sowerby, 1835: 141 (provincia Peruviae Xagua) [LT BMNH 1975151].
- bolivianus*, *Bulimulus* (*Scutalus*), Marshall, 1932: 2, pl. 1 figs. 3-4 (Bolivia, Ayapayo River, Tamañani, 85 miles NE Oruro) [HT USNM 382216].
- coagulatus*, *Bulimus*, Reeve, 1849: pl. 77 fig. 558 (Peru) [LT BMNH 1975351].
- confusus*, *Bulimus*, Reeve, 1848: pl. 48 fig. 316 [no type locality given; LT BMNH 1975194].

- costifer*, *Bulimulus* (*Scutalus*), Pilsbry, 1932: 392, pl. 28 figs. 2-3 (Peru, south of Oroya, near Llocllapampa, 13000 ft.) [HT ANSP 147390a].
- costulatus*, *Scutalus* (*Vermiculatus*), Weyrauch, 1967a: 395, fig. 45 (Peru central, Huarmipiquio cerca de Junín, 4200 m) [HT SMF 162068].
- cotopaxiensis*, *Bulimus*, Pfeiffer, 1853d: 419 (reipublicae Aequatoris, montem Cotopaxi) [LT BMNH 1975370].
- cousini*, *Rhabdotus*, Jousseau, 1887: 167, pl. 3 fig. 18 (Equateur, Concha) [HT MNHN].
- cuzcoensis*, *Scutalus* (*Vermiculatus*), Weyrauch, 1967a: 396, figs. 47-48 (Sur de Peru, 7 km S de Cuzco, Huancaro, Kachuna, 3500 m) [HT IML 10522a].
- feisthameli*, *Bulimus*, Hupé, 1854: 114, pl. 3 fig. 7 (Chile).
- filaris*, *Bulimus*, Pfeiffer, 1853d: 653 [no type locality given; ST BMNH].
- haenkei*, *Bulimulus* (*Scutalus*), Haas, 1955a: 372, fig. 76 (Bolivia, Alto Plano, 3800 m) [HT FMNH 50732].
- hendeensis*, *Bulimulus* (*Scutalus*), Pilsbry, 1926a: 7, pl. 2 fig. 8 (Peru, Dept. Junín, [La] Oroya, 12000 ft.) [HT ANSP 140101].
- hessi*, *Bulimulus* (*Scutalus*), Marshall, 1932: 1, pl. 1 figs. 1-2, 5-6 (Bolivia, Ayapayo River, Tamañani, 85 miles NE Oruro) [HT USNM 382217].
- longitudinalis*, *Bulimulus* (*Scutalus*), Haas, 1955b: 316, fig. 63 (Peru, Ayacucho, San Miguel, Tambo, Polanco) [HT FMNH 51328].
- macedoi*, *Scutalus* (*Vermiculatus*), Weyrauch, 1967a: 398, figs. 42-44 (Peru central, Lago Junín, Capillacocho, 4150 m) [HT SMF 162070].
- marasensis*, *Scutalus* (*Vermiculatus*) *cuzcoensis*, Weyrauch, 1967a: 398, fig. 33 (Sur de Peru, Dept. Cuzco, Maras, 3000 m) [HT IML 10641a].
- meridionalis*, *Bulimus*, Reeve, 1848: pl. 21 fig. 131 (Chili).
- minutus*, *Scutalus* (*Vermiculatus*), Breure, 1978b: 179, figs. 305-307 (Peru, Dept. Amazonas, 11 km SSW Leimebamba, 2180 m) [HT UF 22805].
- naggsi*, *Scutalus* (*Vermiculatus*) *costifer*, Breure, 1978b: 173, pl. 11 fig. 15 (Peru, Dept. Pasco, 1 km NE Cerro de Pasco, 4100 m) [HT UF 22803].
- nucinus*, *Bulimus*, Reeve, 1850a: pl. 85 fig. 629 [no type locality given; LT BMNH 1975379].
- ochraceus*, *Bulimus*, Morelet, 1863: 176, pl. 7 fig. 6 ([Peru] Sorai et Salcantai) [LT BMNH 1893.2.4.164].
- omissus*, *Scutalus* (*Vermiculatus*), Weyrauch, 1967a: 400, figs. 116-120 (Peru central, algunos km SE Huarás, Shaurama, 3200-3300 m) [HT SMF 155586].
- peakei*, *Scutalus* (*Vermiculatus*), Breure, 1978b: 180, figs. 308-313 (Peru, Dept. Ancash, 20 km W Huaráz, 3750 m) [HT UF 22807].
- pentlandi*, *Bulimus*, Reeve, 1849: pl. 83 fig. 614 (Near the Lake of Titicaca, Bolivia).
- petiti*, *Bulimus*, Pfeiffer, 1846a: 31 (Peru) [LT BMNH 1975374].
- pilosus*, *Scutalus* (*Vermiculatus*), Weyrauch, 1967a: 403, figs. 40-41 (Peru central, Inca Pirca, 43 km OE [W] Junín, 4200 m) [HT SMF 162065].
- polymorpha*, *Helix*, d'Orbigny, 1835: 20 (republica Peruviana).
- promethus*, *Bulimus*, Crosse, 1860b: 423 (Pérou) [HT MNHN].
- purpuratus*, *Bulimus*, Reeve, 1849: pl. 71 fig. 517 (Andes of Caxamarca [sic], Peru) [LT BMNH 1975364].
- pyramidalis*, *Scutalus* (*Vermiculatus*), Breure, 1978b: 184, pl. 10 figs. 16-19 (Peru, Dept. Pasco, 4.7 km S Huariaca, 3000 m) [HT UF 22117].
- quechuarum*, *Bulimulus* (*Scutalus*), Crawford, 1939: 330, pl. 19 figs. 11-12 ([Peru, Dept. Puno] Capachica) [HT BMNH 1939.4.17.226].
- sanborni*, *Bulimulus* (*Scutalus*), Haas, 1947: 176, fig. 33 (Peru, Dept. Loreto [sic, Junín], basin of Lake Junín, Carhuamayta, 15000-18000 feet) [HT FMNH 25880].
- schmidti*, *Thaumastus* (*Scholviencia*), Haas, 1955b: 309, fig. 59 (Peru, Hacienda Piso, Lacroja, Huancavelica) [HT FMNH 51305].

thamnoica, *Helix*, d'Orbigny, 1835: 16 (Cavari, republica Boliviana; provincia Chuquisacasensi, republica Boliviana).

voithianus, *Bulimus*, Pfeiffer, 1847a: 114 (Chile).

weddellii, *Bulimus*, Hupé, 1857: 45, pl. 7 fig. 5 (Pérou, environs de Lag. Titicaca) [LT MNHN].

Scutalus (Kuschelenia) Hylton Scott, 1951

Kuschelenia Hylton Scott, 1951: 539. Type species by monotypy: *Kuschelenia simulans* Hylton Scott.

Description. — Shell elongate-ovate; narrowly perforate; (rather) solid. Colour yellowish to light brown; uniformly coloured or, usually, with darker spiral bands. Surface shining, with incrassate growth striae. Protoconch with (anastomosing) axial wrinkles. Whorls rather flat; suture well impressed. Aperture (sub)ovate. Peristome thin to slightly thickened, simple or hardly expanded.

The central teeth of the radula are tricuspid, with lanceolate to wedge-shaped mesocones and ovate to deltoid ectocones. The lateromarginal teeth are bicuspid, with elongate to deltoid and lanceolate mesocones and deltoid ectocones. Half-row formula: C/3 + LM $x/2$ ($x = 35-54$).

The pericard is as long as the nephridium, which is (broadly) triangular. The main pulmonary vein is prominent and broad, the side veins are moderately to well developed, especially at the anterior end, where also a vein parallel to the main pulmonary vein may be observed. The adrectal ureter is partially open ($1/10-1/2$ of its length).

The penis has a proximal sheath and is subcylindrical. The lumen of the proximal part of the penis is narrow; more distally the lumen is wider, but it is narrow again at the transition to the distal part of the penis, where large, rounded cells have been observed in the subepithelial tissue. The transition to the epiphallus, both internally and externally, is gradual. In most species the lumen of the distal part of the epiphallus and of the flagellum are surrounded by muscle fibres, which is externally visible as a swollen structure. The flagellum is relatively short. The length of the vas deferens is in most species shorter than the length of the penis and epiphallus, which are thus contorted. The spermathecal duct is $1/3-1/2$ the length of the spermoviduct. The spermatheca is ovoid.

Distribution. — N-Argentina, Bolivia, S- and C-Peru, ?Ecuador.

Ecology. — The species live mainly on shrubs, mostly near rocky outcrops. The vertical distribution is (600-) 3100-5000 m.

Remarks. — The classification and relationships of *Kuschelenia* have been puzzling. It was described as a genus and said to be characterized by a smooth protoconch. A study of the single type specimen in the collection of

Dr. Hylton Scott showed, however, that the protoconch is sculptured with fine, undulating, oblique wrinkles. Moreover, in both the description and the figure of the genitalia it was suggested that a flagellum be absent. The figure, however, clearly shows that the distal part of the phallus is swollen and this suggests that the flagellum is embedded in muscular fibres (cf. Breure, 1978b: figs. 291-292, 300). These observations, the presence of a short spermathecal duct and the structure of the radula all suggest that *Kuschelenia* is a subgenus of *Scutalus* (see Breure, o.c., for additional anatomical data).

Taxa. — The following taxa are placed in this subgenus:

- alauda*, *Bulimus*, Hupé, 1857: 39, pl. 7 fig. 3 [indication].
culminans, *Bulimus*, Reeve, 1848: pl. 17 fig. 98 [emendation for *culmineus* d'Orbigny].
culminea, *Helix*, d'Orbigny, 1835: 13 (republica Boliviana) [LT MNHN].
edwardsi, *Bulimus*, Morelet, 1863: 182, pl. 9 fig. 1 ([Peru] Huancabelica, Huanta) [ST BMNH].
gayi, *Bulimus*, Pfeiffer, 1857c: 389 (Bolivia) [LT BMNH 1975382].
jussieui, *Bulimus*, Pfeiffer, 1846a: 33 (Cusco [Peru]) [ST BMNH].
jussieui, *Bulimus*, 'Valenciennes' Hupé, 1857: 48, pl. 7 fig. 4 (la province de Cuzco, Pérou) [LT MNHN].
lithoica, *Helix*, d'Orbigny, 1835: 13 (provincia Pazensi, republica Boliviana) [LT MNHN].
major, *Orphnus tupacii*, Döring, 1876: 338 ([Argentina] Sierra de Tucuman y ... de Salta).
minor, *Orphnus tupacii*, Döring, 1876: 339 ([Argentina] Sierra de Tucuman y ... de Salta).
nemorensis, *Bulimus*, Philippi, 1867: 78 ([Peru] Punas, inter Ayapata et Ollachea).
pluto, *Bulimus*, Crosse, 1869b: 422 (Pérou) [HT MNHN].
revinctus, *Bulimus*, Hupé, 1857: 39, pl. 7 fig. 2 [indication].
simulans, *Kuschelenia*, Hylton Scott, 1951: 540, fig. 1-4 (Bolivia, Potosí, 3400 m) [HT MIHS].
subfasciatus, *Bulimus*, Pfeiffer, 1853d: 408 (republicae Aequatoris, monte Anthisana) [LT BMNH 1975368].
subjussieui, *Bulimulus culmineus*, Pilsbry, 1897d: 26, pl. 5 figs. 59-60 (New name for *Bulimus jussieui* 'Valenciennes' Hupé, 1857, not Pfeiffer, 1846).
tupacii, *Helix*, d'Orbigny, 1835: 16 (republica Boliviana, provincia Yungaseni).
zilchi, *Scutalus (Vermiculatus) culmineus*, Weyrauch, 1967a: 393, figs. 139-140 (Perú central, cerca de Alis, sobre la margen derecha del río Alis, afluente del río Cañete) [HT IML 3328a].

Plectostylus Beck, 1837

- Plectostylus* Beck, 1837: 58. Type species by subsequent designation (Gray, 1847): *Bulimus peruvianus* Bruguière.
Plectostylus Wurtz, 1947: 12 [error for *Plectostylus*].

Description. — Shell elongate-globose; imperforate; rather solid. Colour whitish to yellowish with a pattern of axial and spiral streaks/spots in (dark) brown. Surface finely granulate, with incrassate growth striae. Protoconch with hardly undulating axial wrinkles. Whorls slightly convex; suture hardly

impressed, usually descending in front. Aperture subovate. Peristome thin and simple.

The central teeth of the radula are monocuspid, with blunt, conical to deltoid mesocones. The lateromarginal teeth are (1) tricuspid, shifted, with blunt elongate mesocones, slightly curved endocones and triangular ectocones; or (2) bicuspid, with blunt to acute, elongate to lanceolate mesocones and slightly acute deltoid ectocones; or (3) monocuspid, shifted, with elongate mesocones. Half-row formula: $C/1 + L \ x/1-2 + M \ y/3$ ($x = 6-16$, $y = 55-56$).

The pericard is transversally disposed and about $4/5$ the length of the nephridium, which is broadly triangular. The pulmonary vein is prominent, the side veins are, especially at the anterior end, well developed. The adrectal ureter is an open gutter over the greater (ca. $3/4$) part of its length.

Penis without a sheath, rather swollen, tapering towards the epiphallus and passing into this structure without external differentiation. The flagellum is more or less subcylindrical. The vagina is relatively short. The spermathecal duct is more or less subcylindrical, its distal part narrow; the spermatheca is globose.

Distribution. — Chile.

Ecology. — Unknown. The vertical distribution is probably 0-ca. 500 m.

Relationships. — The phylogenetic relations of this genus are discussed on page 154ff. The genus is characterized by the imperforate shell, the colour pattern, the sculpture of the protoconch, the monocuspid central teeth of the radula and the absence of a penis sheath.

Bibliography. — The main publications are: Breure, 1978b; Pilsbry, 1897d.

Taxa. — The following taxa are included in this genus:

- alduneata*, *Helix* (*Bulimus*) *chilensis*, Hupé, 1854: 100, pl. 1 fig. 6 (Chile, Concepcion).
broderipii, *Bulinus*, Sowerby in Broderip & Sowerby, 1832a: 30 (fissuris rupium prope Copiapu Chilensium).
buschii, *Succinea*, Pfeiffer, 1842b: 56 [no type locality given].
chilensis, *Bulimus*, Lesson, 1826: pl. 7 fig. 3 (l'ancienne ville de Penco, dans la province de la Concepcion, au Chili).
coquimbensis, *Bulinus*, Broderip in Broderip & Sowerby, 1832a: 30 (Chili, Coquimbo).
corrugatus, *Bulinus*, King in King & Broderip, 1831: 341 ([Chile] Concepcion).
coturnix, *Bulinus*, Sowerby in Broderip & Sowerby, 1832a: 30 (Chili, Huasco).
elegans, *Succinea*, Pfeiffer, 1842b: 56 (Huasco, Chili) [LT BMNH 1975360].
elongata, *Bulimus broderipi*, d'Orbigny, 1837: 266 (Bolivia [Chile], Cobija).
flavescens, *Partula*, King in King & Broderip, 1831: 342 (oras Americae meridionalis, Valparaiso).
graniger, *Bulimulus*, Beck, 1837: 67 [indication] (Chili).
granulosus, *Bulimus*, Potiez & Michaud, 1835: pl. 13 figs. 9-10 (Ilo, république Peruvienne).
granulosus, *Bulinus*, Broderip in Broderip & Sowerby, 1832a: 31 ([Chile] ad Valparaiso et in montibus Conceptionis).

- gravesii*, *Bulinus*, King in King & Broderip, 1831: 340 ([Chile] Valparaiso).
mariae, *Plectostylus*, Brooks, 1936: 124, fig. (Chile, San Esteban) [HT CM 6228184].
moestai, *Bulinus*, Dunker, 1864: 156 (Cerro bravo vallis Copiapo in deserta Atacama provincia Chilensi) [ST ZMB 101810].
ochsenii, *Bulinus*, Dunker in Dunker et al., 1855: 107 (in provincia Valdivia Chilensi) [ST ZMB].
perelegans, *Plectostylus coquimbensis*, Pilsbry, 1897d: 11, pl. 8 figs. 18-22 (New name for *Succinea elegans* Pfeiffer, 1842, not Risso, 1826).
peruvianus, *Bulinus*, Bruguière, 1789: 320 (Pérou) [LT MNHN].
prolatus, *Bulinus*, Gould, 1846b: 191 (Chili, Santiago).
pulicarius, *Plectostylus*, Beck, 1837: 58 [indication].
punctulifer, *Bulinus*, Sowerby, 1833b: 36 (Chili) [ST BMNH].
reflexa, *Succinea*, Pfeiffer, 1842b: 30 ([Chile] Pichidanque near Coquimbo).
rupicolus, *Bulinus*, Reeve, 1848: pl. 16 fig. 93 (Valleys in the north of Coquimbo).
vagabondiae, *Plectostylus*, Brooks, 1936: 125, fig. (Chile, San Esteban) [HT CM 6228185].
variegata, *Succinea*, Pfeiffer, 1842b: 56 (Chile, prov. septentr.) [LT BMNH 1975362].

Discoleus Breure, 1978

Discoleus Breure, 1978b: 195. Type species by original designation: *Eudioptus aguirrei* Döring.

Description. — Shell ovate-conical; rimate; (rather) thin. Colour yellowish, uniformly coloured or, usually, with brownish axial streaks at irregular intervals. Surface with more or less incrassate growth striae (partly broken into oblong granules). Protoconch with fine spiral lines. Whorls hardly convex, the last whorl inflated; suture well impressed. Aperture subovate. Peristome thin and simple.

The central teeth of the radula are tricuspid, with acute, ovate mesocones and hardly differentiated, more or less triangular ectocones. The lateral teeth are bicuspid, with elongate to wedge-shaped mesocones and acute, ovate to deltoid ectocones. The marginal teeth are tricuspid, shifted, with elongate mesocones, slightly curved endocones and triangular ectocones. Half-row formula: $C/3 + Lx/2 + My/3$ ($x = 9, y = 28-29$).

The pericard is $1/2-4/5$ times the length of the nephridium, which is broadly triangular. The main pulmonary vein is well developed, but the side veins are weakly developed. The anterior half of the adrectal ureter is open.

Penis without a sheath, subcylindrical and passing without external differentiation into the epiphallus, which is more or less tapering. The flagellum is relatively short. The spermathecal duct is more or less subcylindrical, with a globose to truncate-globose spermatheca at the distal end.

Distribution. — Argentina.

Ecology. — The ecology is unknown. The vertical distribution is 0-ca. 1250 m.

Relationships. — The relationships of this genus with *Plectostylus* and

Bothriembryon are discussed on page 154ff. The genus is characterized by the conical shell shape, the inflated last whorl, the absence of a penis sheath, the presence of a 'pseudo-sheath' and the shape of the marginal teeth of the radula.

Remarks. — According to Parodiz (1944c: 1) the most southern locality for a bulimulid species is the record of *Discoleus ameghinoi* (Ihering) from Bahía Sanguineto, Golfo de San Jorge (47°05' S 66°30' W) in the province of Santa Cruz, Argentina.

Taxa. — The following taxa are placed in this genus:

- aguirrei*, *Eudioptus*, Döring, 1884: 112, pl. 2 fig. 2 ([Argentina] Sierra de La Tinta).
ameghinoi, *Bulimulus*, Ihering, 1908: 430, fig. 1 ([Argentina, Buenos Aires] étage bonaëreen du ruisseau Chapalmalal).
azulensis, *Eudioptus mendozanus*, Döring, 1884: 111 ([Argentina] Sierra Baya).
bonaerensis, *Bulimulus*?, Holmberg, 1909a: 10 ([Argentina] Prov. Buenos Ayres, in montibus australibus, Sierra de Curá-malal).
bonaerensis, *Eudioptus mendozanus*, Döring, 1884: 111, pl. 2 fig. 1 ([Argentina] Sierra del Tandil, Escalones de las Aguilas).
curamalalensis, *Peronaeus (Lissoacme)*, Parodiz, 1957: 23 (New name for *Bulimulus bonaerensis* Holmberg, 1909, not *Eudioptus mendozanus bonaerensis* Döring, 1884).
fayssianus, *Bulimus*, Petit, 1853a: 250, pl. 8 fig. 7 (république Argentine?) [LT MNHN].
madrynnensis, *Bulimulus (Lissoacme) ameghinoi*, Parodiz, 1944c: 3, figs. 8-9 ([Argentina, Chubut] El Doradillo, 100 m, frente a punta Dorada, 9 kms a norte de puerto Madryn) [HT MACN 25878].
pampa, *Bulimulus sporadicus*, Ihering, 1914: 70 ([Argentina] Buenos Aires).
ventanensis, *Bulimulus*, Pilsbry, 1896b: 189, pl. 1 fig. 8 (Argentina, Buenos Ayres, Sierra de la Ventana) [LT ANSP 60842a].

Bothriembryon Pilsbry, 1894

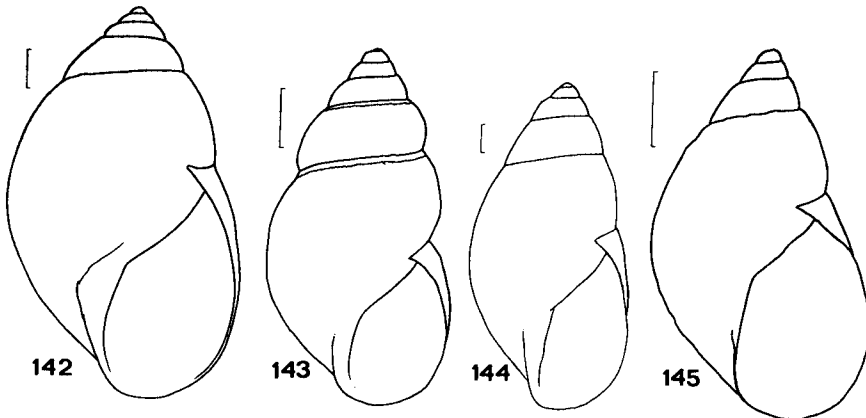
- Liparus* Albers, 1860: 229. Type species by original designation: *Bulimus inflatus* Lamarck.
Bothriembryon Pilsbry, 1894: 36. New name for *Liparus* Albers, 1860, not Olivier, 1807, nor Albers, 1850.
Hartogembryon Iredale, 1933: 41. Type species by original designation: *Bulimus onslowi* Cox.
Larapintembryon Iredale, 1933: 41. Type species by original designation: *Liparus spenceri* Tate.
Satagembryon Iredale, 1933: 41. Type species by original designation: *Buliminus (Liparus) gratwicki* Cox.
Dialembryon Iredale, 1939: 16. Type species by original designation: *Bulimus indutus* Menke.
Ponembryon Iredale, 1939: 16. Type species by original designation: *Bulimus dux* Pfeiffer.
Telebryon Iredale, 1939: 16. Type species by original designation: *Bulimus kingii* Gray.
Celatembryon Iredale, 1939: 36. Type species by original designation: *Bothriembryon distinctus* Iredale.

Description. — Shell ovate to oblong-conical; rimate to imperforate; rather solid to thin. Colour whitish to brownish, usually with axial streaks of darker

colours, sometimes with spiral bands. Surface with uneven, wrinkled growth striae, usually stronger below the suture, often crossed by spiral lines of variable strength. Protoconch with axial wrinkles or reticulate. Aperture ovate. Peristome thin and simple.

Distribution. — Australia: Northern Territory, Palm Valley near Hermannsburg (fossil record, see McMichael, 1968); Tasmania; South Australia, Kangaroo Island, Eyre Peninsula and westward; Western Australia, entire southern coast, northward to the Hamersley Range.

Remarks. — Zilch (1960) only listed the taxa described by Iredale and did not place them in his system. Burch (1976) considered Iredale's subgenera of *Bothriembryon* as usable, but study of the shell morphology and of the anatomy (see Breure, 1978b) has convinced me that the taxa are synonymous with *Bothriembryon* s.str., except *Tasmanembryon*.



Figs. 142-145. Variation in shell shape in *Bothriembryon*. Fig. 142. *B. (B.) dux* (Pfeiffer). Fig. 143. *B. (B.) inflatus* (Lamarck). Fig. 144. *B. (B.) indutus* (Menke). Fig. 145. *B. (Tasmanembryon) gunnii* (Sowerby). Scale = 5 mm.

Key to the subgenera of *Bothriembryon*

- a. Protoconch pit-reticulate or with anastomosing wrinkles. Spermatheca more or less globose *Bothriembryon (Bothriembryon)*
- b. Protoconch with oblique axial wrinkles, the intervals about as broad as the wrinkles, crossed by weaker spiral lines. Spermatheca broadly elongate-ovate. Spermathecal duct relatively short
 *Bothriembryon (Tasmanembryon)*

***Bothriembryon (Bothriembryon)* Pilsbry, 1894**

Description. — Shell elongate-ovate to oblong-conical; rather solid. Colour variable, with shades of yellow, brown, red, lillac and white, often in patterns

of irregular axial streaks and, less frequently, spiral bands. Protoconch pit-reticulate or with anastomosing wrinkles. Whorls rather convex; suture well to rather deeply impressed. Aperture subovate. (Modified after Kendrick & Wilson, 1975).

The central teeth of the radula are tricuspid, with acute, ovate mesocones and hardly differentiated, more or less triangular ectocones. Lateromarginal teeth bicuspid (with blunt to acute, elongate to lanceolate mesocones and slightly acute, deltoid ectocones) to tricuspid (shifted, with elongate mesocones, slightly curved endocones and triangular ectocones). Half-row formula: $C/3 + Lx/2 + My/3$ ($x = 8-13$, $y = 21-36$).

The pericard is as long as the nephridium, which is narrowly triangular and curved. The main pulmonary vein is prominent, with strong side veins. Two veins run parallel to the main pulmonary vein, one of them being connected with the side veins. The adrectal ureter is closed.

The penis is without a sheath, sometimes swollen at the proximal end, but always long and slender throughout; passing without external differentiation into the epiphallus. The flagellum, which is about half as long as penis and epiphallus together, is slender and with a distally inserted retractor muscle. The spermathecal duct is as long as the spermoviduct, slender and with a more or less globose spermatheca at its distal end.

Distribution. — Australian mainland, see page 92.

Ecology. — The species live mainly in heath and *Acacia* vegetation (Kendrick & Wilson, 1975).

Taxa. — The following taxa are included in this subgenus:

- angasianus*, *Bulimus*, Pfeiffer, 1864: 528 (Port Lincoln, South Australia) [ST BMNH].
baconi, *Bulimus*, Benson, 1854: 99 (Australia occidentali).
balteolus, *Bothriembryon*, Iredale, 1939: 21, pl. 2 fig. 9 (W. Australia, Esperance Mallu Belt district, 50 mi S of Norseman, Madura, Salmon Gums) [LT WAM 9876].
barretti, *Bothriembryon*, Iredale, 1930: 119, fig. 1 (Australia, Nullabor Plain).
bradshawi, *Bothriembryon*, Iredale, 1939: 24, pl. 2 fig. 14 (W. Australia, Tambellup, N of Stirling Range).
brazieri, *Bulimus*, Angas, 1871: 19, pl. 1 fig. 28 ([Australia] Sinclair's Range, King George's Sound) [ST BMNH].
bullia, *Bulimus*, Menke, 1843: 7 [W. Australia, summit of Darling Range; teste Pilsbry, 1900b: 15].
castanea, *Bulimus melo*, Deshayes in Deshayes & Milne Edwards, 1838: 245 (Nouvelle Hollande).
conispira, *Bothriembryon inflatus*, Pilsbry, 1900b: 6, pl. 1 figs. 15-17 ([W. Australia] King George Sound) [LT ANSP 8453a].
costulata, *Helix (Cochlogena)*, Férussac, 1821: 58 [nomen nudum].
costulata, *Helix*, Lamarck, 1822: 122 [indication; LT MHNG].
decesensis, *Bothriembryon*, Cotton, 1940: 42, fig. ([S. Australia] Kangaroo Island, Cape Cassini) [HT SAM D-13773].
distinctus, *Bothriembryon*, Iredale, 1939: 36, pl. 2 fig. 43 (W. Australia, Cardanumbi, W of Eyre).

- dux*, *Bulimus*, Pfeiffer, 1861a : 24 (King George's Sound, Australia) [LT BMNH 19598].
- esperantia*, *Bothriembryon*, Iredale, 1939 : 21, pl. 2 fig. 8 (W. Australia, Esperance).
- eventus*, *Bothriembryon leeuwinensis*, Iredale, 1939 : 25, pl. 2 fig. 18 (W. Australia, Margaret River).
- fuscus*, *Bothriembryon*, Thiele, 1930 : 588, pl. 4 fig. 68 (SW Australia, Torbay).
- glauerti*, *Bothriembryon*, Iredale, 1939 : 29, pl. 2 fig. 24 (W. Australia, Stirling Ranges) [HT WAM 10127].
- grantianus*, *Bothriembryon rhodostomus*, Iredale, 1939 : 21, pl. 2 fig. 5 (W. Australia, Recherche Group, Charley Island).
- gratwicki*, *Bulimus* (*Liparus*), Cox, 1899 : 435, figs. 1-3 (Western Australia, about 50 miles east of Israelite Bay).
- hartogensis*, *Bothriembryon onslowi*, Kobelt, 1901 : 770 (West Australien, Dirk Hartogs Island).
- hullianus*, *Bothriembryon rhodostomus*, Iredale, 1939 : 20, pl. 2 fig. 4 (W. Australia, Recherche Group, Gunton Island).
- humilis*, *Bothriembryon physoides*, Pilsbry, 1900b : 10, pl. 2 figs. 33-34 (Western Australia, Kings George Sound) [LT ANSP 65568a].
- indictus*, *Bothriembryon barretti*, Iredale, 1939 : 36 (W. Australia, Eucla).
- indutus*, *Bulimus*, Menke, 1843 : 6 [publication not seen].
- inflatus*, *Bulimus*, Lamarck, 1822 : 122 [indication] (Nouvelle Hollande) [LT MHNG].
- irvineanus*, *Bothriembryon*, Iredale, 1939 : 24, pl. 2 fig. 16 (W. Australia, Cape Riche).
- jacksoni*, *Bothriembryon*, Iredale, 1939 : 31, pl. 2 fig. 30 (W. Australia, Nornalup, Deep River).
- kingii*, *Bulimus*, J. E. Gray, 1825 : 414 (New Holland) [LT BMNH 195910].
- leeuwinensis*, *Bulimus*, E. A. Smith, 1894 : 94, pl. 7 fig. 27 (Cape Leeuwin, S.W. Australia) [LT BMNH 1891.11.21.128].
- maculiferus*, *Bothriembryon inflatus*, Pilsbry, 1900b : 5, pl. 1 figs. 12-14 (Australia, King George Sound) [LT ANSP 8450a].
- martensi*, *Bothriembryon*, Kobelt, 1901 : 764, pl. 112 figs. 3-4 (Neu Holland) [HT ZMB 101818].
- mastersi*, *Bulimus*, Cox, 1867 : 39 (Port Lincoln, South Australia).
- maxwelli*, *Bothriembryon*, Kobelt, 1901 : 781, pl. 112 figs. 4-5, 17 (West Australien, King George Sound, Doubtful Island).
- melo*, *Helix*, Quoy & Gaimard, 1832 : 109, pl. 9 figs. 4-5 ([W. Australia] au port du Roi Georges, principalement sur le sommet de Bald Head) [LT MNHN].
- melones*, *Helix* (*Cochlogena*), Férussac, 1821 : 58 [nomen nudum].
- minor*, *Bothriembryon onslowi*, Pilsbry, 1900b : 12, pl. 3 figs. 45-46 (Western Australia).
- multispirus*, *Bothriembryon*, Macpherson, 1951 : 30, fig. (W. Australia, 20 miles west of Cocklebidy Waterhole) [HT NMV F-5716].
- naturalistarum*, *Bothriembryon kingii*, Kobelt, 1901 : 781, pl. 113 figs. 22-23 (West Australien, Cape Naturaliste).
- notatus*, *Bothriembryon*, Iredale, 1939 : 31, pl. 2 fig. 29 (W. Australia, Pallinup River).
- onslowi*, *Bulimus*, Cox, 1864 : 185 (Dirk Hartog's Island, Shark Bay, Western Australia) [HT AM].
- ovum*, *Bulimus*, Deshayes, (1836-1849) : pl. 23 fig. 1 [no type locality given].
- pallidus*, *Bulimus indutus*, Tate, 1879 : 135 [South Australia, Bunda plateau; teste Pilsbry, 1900b : 15].
- perditus*, *Bothriembryon*, Iredale, 1939 : 32 (W. Australia, 70 miles E of Israelite Bay).
- perobesus*, *Bothriembryon*, Iredale, 1939 : 28, pl. 2 fig. 22 (W. Australia, mouth of Moore River) [HT WAM 10217].
- perspectus*, *Bothriembryon rhodostomus*, Iredale, 1939 : 21, pl. 2 fig. 7 (W. Australia, Recherche Group, Woody Isle).
- physoides*, *Bulimus*, Reeve, 1849 : pl. 70 fig. 507 [no type locality given; ST BMNH].

- praeceus*, *Bothriembryon*, Iredale, 1939: 22, pl. 2 fig. 11 (W. Australia, Kellerberrin) [HT WAM 9321].
- quoyi*, *Bulimus*, Cox, 1864: 23 [indication; teste Pilsbry, 1900b: 8].
- revecus*, *Bothriembryon*, Iredale, 1939: 33, pl. 2 fig. 37 (W. Australia, Bow River).
- rhodostomus*, *Bulimus*, J. E. Gray, 1834: 65 (Nova Hollandia?) [LT BMNH 1874.10.28.1].
- sayi*, *Bulimus*, Pfeiffer, 1847a: 114 (locality unknown).
- sedgwicki*, *Bothriembryon*, Iredale, 1939: 22, pl. 2 fig. 12 (W. Australia, Nangeenan via Merredin).
- serpentinus*, *Bothriembryon*, Iredale, 1939: 22, pl. 2 fig. 10 (W. Australia, Darling Range, Serpentine Falls).
- solidus*, *Bothriembryon kingii*, Pilsbry, 1900b: 9, pl. 2 fig. 28 (Western Australia).
- spenceri*, *Liparus*, Tate, 1894: 192 [no type locality given; Central Australia].
- trilineata*, *Helix*, Quoy & Gaimard, 1832: 107, pl. 9 figs. 1-3 (le port du Roi Georges, Nouvelle Hollande) [LT MNHN].
- whitleyi*, *Bothriembryon*, Iredale, 1939: 27, pl. 2 fig. 21 (W. Australia, Geraldton).
- wrightianus*, *Bothriembryon rhodostomus*, Iredale, 1939: 21, pl. 2 fig. 6 (W. Australia, Recherche Group, Rabbit Island).

Bothriembryon (Tasmanembryon) Iredale, 1933

Tasmanembryon Iredale, 1933: 41. Type species by original designation: *Bulimus tasmanicus* Pfeiffer.

Description. — Shell elongate-ovate; imperforate; thin. Colour whitish with yellowish to brownish axial streaks, the upper whorls pink-brown. Protoconch with oblique wrinkles, more or less anastomosing and crossed by weaker spiral lines. Whorls rather convex; suture well impressed. Aperture broadly ovate.

The radula is as in the nominal subgenus, but in the half-row formula is $x = 5$ and $y = 60$. The genitalia are as in *Bothriembryon* s.str., except that the spermathecal duct is short and relatively less slender and that the spermatheca is broadly elongate-ovate.

Distribution. — Reported as a fossil of probably Pliocene age from the Yellow Limestone near Hobart, Tasmania and from the Kent's Group in Bass Strait. Recent from the east coast of Tasmania and from Maria Island.

Ecology. — According to Pilsbry (1900b: 18) the species have arboreal habits.

Relationships. — Differs from *Bothriembryon* (*Bothriembryon*) in (1) the structure of the protoconch; (2) the greater number of teeth in the radula; (3) the short and less slender spermathecal duct and the stout spermatheca.

Remarks. — Burch (1976: 132) listed *Tasmanembryon* as a separate genus. In my opinion the above-mentioned differences with *Bothriembryon* (*Bothriembryon*) justify only a subgeneric division.

Taxa. — The following taxa are placed in this subgenus:

- brachysoma*, *Bothriembryon gunni*, Pilsbry, 1900b: 19, pl. 3 fig. 53 (East coast of Tasmania) [HT ANSP 8461].
gunnii, *Bulinus*, Sowerby, 1845: 298, pl. 19 fig. 5 [Tasmania, near Hobart; Pliocene; teste Pilsbry, 1900b: 18].
tasmanicus, *Bulinus*, Pfeiffer, 1853b: 260 (Van Diemen's Land).

Oxychona Mörch, 1852

Oxychona Mörch, 1852: 14. Type species by monotypy: *Trochus bifasciatus* Burrow.

Description. — Shell conical; imperforate; (rather) thin. Colour uniformly whitish or with purplish-brown spiral bands. Surface (malleate,) with spiral lines. Protoconch with a grating sculpture of axial riblets and spiral striae that are of equal strength. Whorls (nearly) flat, the last whorl sharply keeled and with a flat to concave base; suture hardly impressed. Aperture very oblique and skewed, triangular. Peristome partly expanded and reflexed.

Central teeth of the radula monocuspid, with rather blunt, spatula-shaped mesocones. The lateral teeth are bicuspid, with blunt spatula-shaped mesocones and small, acute, ovate to triangular ectocones that are posteriorly situated at the basal plate. Half-row formula: C/1 + LM x/2 (x = 37).

Penis with a proximal sheath, more or less subcylindrical and passing without external differentiation into the epiphallus. The flagellum is subcylindrical and relatively long, internally with a double-curved longitudinal fold.

Distribution. — Brazil.

Ecology. — The species live on trees.

Taxa. — The following taxa are included in this genus:

- bifasciatus*, *Trochus*, Burrow, 1815: 188, pl. 27 fig. 2 [publication not seen].
blanchetiana, *Helix*, Moricand, 1833: 539, pl. 1 fig. 3 (Brésil, aux environs de Bahia) [ST ZMB].
bosciana, *Helix*, Férussac, 1821: 37 [nomen nudum].
currani, *Oxychona pyramidella*, Bartsch, 1916: 53 (Brazil, Bahia, Rio Grungogy [Grungogy]) [HT USNM 322281].
gyrina, *Helix*, 'Valenciennes' Deshayes, in Férussac & Deshayes, 1820-1851: pl. 63B fig. 4 (Brésil).
lonchostoma, *Caracolla*, Menke, 1828: 76 (intes[sic] Rio et Campo, Brasilia).
minarum, *Drymaeus* (*Oxychona*) *bifasciatus*, Ancey, 1901a: 93 ([Brazil] Minas Geraes).
pyramidella, *Helix*, Wagner in Spix, 1827: 22 (sylvis mediterraneis inter montem sanctum et flumen S. Francisci, in Provincia Bahiensi).

Otostomus Beck, 1837

Otostomus Beck, 1837: 55. Type species by subsequent designation (Gray, 1847): *Auris signata* Spix.

Description. — Shell obliquely elongate-ovate; perforate; solid. Colour whitish, with broad brown spiral bands on the last whorl. Surface with granules and incrassate growth striae. Protoconch with a grating sculpture

of axial riblets and spiral striae, that are of equal strength. Whorls slightly convex; suture well impressed, ascending in front. Aperture ear-shaped, skewed. Peristome expanded and reflexed, with a callous flange on the inner side of palatal and basal margin. Columella with a lamellar fold.

Central teeth of the radula are monocuspid, with rather blunt, spatula-shaped mesocones. The lateral teeth are tricuspid, with blunt, spatula-shaped mesocones, acute, curved, elongate endocones and acute, ovate to triangular ectocones that are posteriorly situated on the basal plate. Half-row formula: $C/1 + LM x/3$ ($x = 42$).

The penis has a short, proximal sheath; the penis is swollen above the distal end of the sheath and the transition to the subcylindrical epiphallus is gradual. The flagellum is more or less tapering and relatively long, internally with a double-curved longitudinal fold.

Distribution. — Brazil.

Ecology. — Unknown, but probably arboreal.

The only known taxon is:

signata, *Auris*, Spix, 1827: 17, pl. 12 fig. 3 ([Brazil] sylvis Provinviae Bahiensis).

Cochlorina Jan, 1830

Navicula Spix, 1827: 22. Type species by monotypy: *Navicula fasciata* Spix = *Helix navicula* Wagner [not *Navicula* De Blainville, 1825].

Cochlorina Jan, 1830: 5. Type species by subsequent designation (Bequaert, 1948): *Bulimus aurisleporis* Bruguière.

Zaplagius Pilsbry, 1896a: 115. Type species by original designation: *Helix navicula* Wagner.

Description. — Shell (ovate-)conical; rimate; thin to solid. Colour whitish to reddish-brown, uniformly coloured or banded, streaked or maculated with (black-)brown. Surface with slightly incrassate growth striae, malleate to granulate and/or with spiral lines. Protoconch with a grating sculpture of axial riblets and spiral striae that are of equal strength. Whorls hardly convex, the last whorl rounded or keeled and with a flat to concave base; suture weakly impressed, ascending in front. Aperture ear-shaped or (obliquely) triangular. Peristome expanded (and reflexed).

Central teeth of the radula are monocuspid, with rather blunt, spatula-shaped mesocones. The lateral teeth are bi- to tricuspid, with blunt, spatula-shaped mesocones, acute, curved, elongate endocones (and acute, ovate to triangular ectocones that are posteriorly situated on the basal plate). Half-row formula: $C/1 + LM x/2-3$ ($x = 33$).

The penis has a short proximal sheath, is more or less subcylindrical and passing without external differentiation into the epiphallus. The lumen of the penis is not constricted in its median part. The flagellum is more or less

tapering and relatively long, internally with a double-curved longitudinal fold.

Distribution. — Brazil.

Ecology. — The species live on trees. The vertical distribution is 0-ca. 500 m.

Relationships. — This genus was classified as a subgenus of *Drymaeus* by Pilsbry (1898) or considered closely related to *Drymaeus* (Weyrauch, 1960a) [Weyrauch (1958) erroneously synonymized *Drymaeus* with *Cochlorina*]. Anatomical research shows that *Cochlorina* closely resembles *Oxychona* and *Otostomus* (Breure & Eskens, in preparation). See page 158 for a discussion of the phylogenetic relationships.

Taxa. — The following taxa are placed in this genus:

- aurisleporis*, *Bulimus*, Bruguière, 1792: 346 (l'île de Madagascar [sic]).
aurismuris, *Helix*, S. Moricand, 1839: 140, pl. 3 figs. 1-3 ([Brazil] province de Bahia, à la fazenda de Palmeirinha, entre Caxoeira et Jacobina).
auritum, *Stenostoma*, Spix, 1827: 18, pl. 13 figs. 1-2 ([Brazil] Provincia Sebastianopolitana).
fasciata, *Navicula*, Spix, 1827: pl. 15 figs. 2-3 ([Brazil] sylvis aboriginibus Provinciae Bahiensis).
intensor, *Drymaeus* (*Zaplagius*) *aurisleporis*, Pilsbry, 1898: 190, pl. 28 fig. 4 [no type locality given].
involutus, *Bulimulus*, Martens, 1867a: 63 (Brasilien).
lagotis, *Bulimus*, Menke, 1828: 15 [indication].
lateralis, *Bulimus*, Menke, 1828: 76 (Brasilia).
lateritius, *Drymaeus* (*Zaplagius*), Pilsbry, 1898: 320 (Brazil, Prov. of Bahia) [HT ANSP 73553].
leporis, *Auricula*, Lamarck, 1822: 138 (Madagascar [sic]).
lyonnetianus, *Bulimus*, Küster in Küster et al., 1840-1865: 23, pl. 5 figs. 5-7 (Insel Frankreich [?]).
myotis, *Otostomus*, Beck, 1837: 55 [indication].
navicula, *Helix*, Wagner in Spix, 1827: 22 ([Brazil] sylvis aboriginibus Provinciae Bahiensis).
uranops, *Drymaeus* (*Zaplagius*), Pilsbry, 1898: 188, pl. 27 figs. 24-27 (Brazil).

Newboldius Pilsbry, 1932

Newboldius Pilsbry, 1932: 398. Type species by original designation: *Newboldius inca* Pilsbry.

Description. — Shell elongate-ovate; imperforate; thick and solid. Colour whitish to lightbrown, the last whorl with 3-4 brownish spiral bands. Surface with more or less incrassate growth striae; sometimes with spiral lines and/or malleation. Protoconch [with a grating sculpture of axial riblets and spiral striae, which are of equal strength]. Whorls hardly convex; suture weakly impressed. Aperture elongate-ovate, slightly oblique, a sulcus at the basal-columellar margin. Peristome broadly expanded and reflexed, thick; brownish to pink coloured. A callus at the parietal region.

The central teeth of the radula are monocuspid, relatively small with blunt elongate to triangular mesocones. Lateromarginal teeth bi- to tricuspid, (slightly) shifted, with (rather) blunt elongate to lanceolate or ovate mesocones, acute elongate-ovate endocones and deltoid ectocones. Half-row formula: $C/1 + L \ x/2 + y/3$ ($x = 1, y = 54$).

The pericard is about half as long as the nephridium, which is triangular and curved. The main pulmonary vein is rather prominent and ramified at its anterior end. The rectum is very broad, largely covering the adrectal ureter, which is closed over its entire length.

Penis with a sheath (ca. 1/7 the length of the phallus), subcylindrical and passing without external differentiation into the epiphallus. The flagellum is slightly tapering, about as long as the penis sheath. The vagina is relatively long and the spermathecal duct is subcylindrical.

Distribution. — Peru (Dept. Cuzco, Junín, Pasco, Puno).

Ecology. — The species live mainly in cloud forest, at altitudes of 1700-2200 m.

Relationships. — The relationships of this genus are dealt with on page 158ff. The genus is characterized by the thick and solid shell, the colour-pattern, the shape of the aperture and the thick peristome.

Taxa. — The following taxa are included in this genus:

angiportus, *Newboldius*, Weyrauch, 1960b: 53, pl. 8 figs. 5-6 (M-Peru, 2 km von Bergwerk Pichita Caluga, 2200 m [19.5 km WNW San Ramón]) [HT SMF 162045].
crichtoni, *Bulinus*, Broderip, 1836: 44 (Ambo, Peruviae) [LT BMNH 1958.9.3.4].
illustris, *Bulinus* (?), Rolle, 1905: 36 (Peru, Huancabamba) [HT BMNH 1922.2.24.40].
inca, *Newboldius*, Pilsbry, 1932: 398, pl. 27 fig. 2 (Peru, Dept. Puno, Rio Quitun (a branch of the Rio Inambari), Oconeque) [HT ANSP 156230].

Neopetraeus Martens, 1885

Neopetraeus Martens, 1885c: 194. Type species by subsequent designation (Pilsbry, 1898): *Otostomus millegranus* Martens.

Description. — Shell ovate(-conical); (broadly) perforate; rather solid. Colour whitish to pink with brown spots and streaks in various patterns. Surface slightly malleate, plicate or with spiral series of granules; with spiral series of lines. Protoconch more or less angled above, with axial riblets, predominating over the closer set, fine spiral striae of the interstices. The upper whorls are keeled below, the last whorl is large and more or less inflated. Aperture (rounded-)ovate. Peristome (broadly) expanded (and reflexed). Columella more or less strongly folded. At the parietal region a thin callus may be observed.

The central teeth of the radula are monocuspid, relatively small, with blunt elongate to triangular mesocones. Lateral teeth are bicuspid, slightly shifted,

with rather blunt, elongate to lanceolate mesocones and triangular to deltoid ectocones. The marginal teeth are tricuspid, shifted, with rather blunt, ovate mesocones, acute elongate-ovate endocones and acute, deltoid ectocones, which may be bifid in the outermost teeth. Half-row formula: $C/1 + L x/2 + M y/3$ ($x = 2-6$, $y = 76-84$).

The nephridium is broadly triangular, its pericardial side strongly curved. The main pulmonary vein is prominent, ramified at its anterior end. The adrectal ureter is closed except for a short distance near the urinary opening.

Penis with a very short sheath, more or less subcylindrical and passing without external differentiation into the epiphallus, which is slightly tapering. The flagellum is (rather) slender. The spermathecal duct is subcylindrical, with a globose spermatheca at the distal end.

Distribution. — Peru (Dept. Ancash, La Libertad, Cajamarca, Amazonas).

Ecology. — The ecology of only one species is known, which lives on trees and shrubs in xerophytic savannah vegetation. The vertical distribution is 800-1900(-3200) m.

Relationships. — The phylogenetic relationships of this genus are discussed on page 158ff. The genus is characterized by the shell shape, the protoconch sculpture and the expanded peristome.

Taxa. — The following taxa are included in *Neopetraeus*:

- altoperuvianus*, *Bulimus*, Reeve, 1849: pl. 72 fig. 521 (Chachapoyas, Alto-Peru) [LT BMNH 1975437].
- arboriferus*, *Neopetraeus*, Pilsbry, 1898: 175, pl. 32 figs. 32-33 (Andes of Peru) [LT ANSP 4684a].
- atahualpa*, *Bulimulus*, Dohrn, 1863: 153 [no type locality given; ST BMNH].
- binneyanus*, *Bulimus*, Pfeiffer, 1857d: 229 (Andibus prov. Patas, Peru) [LT BMNH 1975426].
- brownii*, *Neopetraeus decussatus*, Pilsbry, 1898: 179, pl. 32 figs. 40-41, pl. 33 fig. 39 (Peru) [LT ANSP 4692a].
- camachoi*, *Neopetraeus*, Weyrauch, 1967a: 418, figs. 68-70 (Norte de Peru, río Chotano, Cuesta de Chuguid, 1500 m) [HT IML 1541a].
- catamarcanus*, *Bulimus*, Pfeiffer, 1858: 256, pl. 42 fig. 5 (Peru, Andes of the province Caxamarca [sic]).
- cora*, *Helix*, d'Orbigny, 1835: 15 (republica Peruviana).
- cremnobates*, *Neopetraeus*, Pilsbry, 1949: pl. 3 fig. 9 [nomen nudum]; 'Pilsbry' H. B. Baker, 1963: 227 (hydroelectric plant on Rio Santa, near southern edge of Dept. de Libertad, Peru) [HT ANSP 185841a].
- decussatus*, *Bulimus*, Reeve, 1849: pl. 72 fig. 519 (Andes of Caxamarca [sic] Peru) [LT BMNH 1975180].
- excoriatus*, *Bulimus*, Pfeiffer, 1855b: 123 (Andes of Peru) [LT BMNH 1975500].
- filiola*, *Drymaeus (Neopetraeus)*, Pilsbry, 1897a: 22 (Peru) [HT ANSP 25724].
- gracilior*, *Neopetraeus altoperuvianus*, 'Pfeiffer' Pilsbry, 1898: 173, pl. 33 figs. 37-38 [no type locality; HT ANSP 63081].
- heterogyrus*, *Bulimus*, Philippi, 1869: 42 ([Peru] inter Sartimbamba et Chusgon in departamento de la Libertad).
- latistrigatus*, *Neopetraeus arboriferus*, Pilsbry, 1898: 176, pl. 32 figs. 34-35 (Andes of Peru) [LT ANSP 4685a].

- lobbii*, *Bulimus*, Reeve, 1849: pl. 72 fig. 516 (Banks of the Marañon near Balsas, Peru) [LT BMNH 1975431].
- millegranus*, *Otostomus*, Martens, 1883: 177, pl. 32 figs. 1-4 (Balzas, Peruviae orientalis, 963 meter) [HT ZMB 36493].
- myristicus*, *Bulimus*, Reeve, 1849: pl. 72 fig. 520 (Andes of Caxamarca, Peru) [LT BMNH 1975433].
- obesus*, *Neopetraeus arboriferus*, Weyrauch, 1967a: 416, figs. 62-63 (Peru) [HT IML 1244a].
- orientalis*, *Neopetraeus catamarcanus*, Breure, 1978b: 212, fig. 364, pl. 4 figs. 3-4, pl. 5 (Peru, Dept. Amazonas, 18 km ENE Balsas, 1880 m) [HT UF 22779].
- patasensis*, *Bulimus*, Pfeiffer, 1858: 257, pl. 42 fig. 6 (Province of Patas, Andes of Peru) [LT BMNH 1975439].
- paucistrigatus*, *Neopetraeus arboriferus*, Weyrauch, 1967a: 417, figs. 65-67 (Norte de Peru, valle del río Marañon, ruta de Huamachuco a Pataz, Chagual, 1300 m) [HT IML 1239a].
- perincrassatus*, *Neopetraeus tessellatus*, Pilsbry, 1898: 169, pl. 31 figs. 18-19, pl. 33 fig. 48 (Peru) [HT ANSP 72113].
- platystomus*, *Bulimus*, Pfeiffer, 1858: 256, pl. 42 fig. 2 (Province of Patas, Andes of Peru) [LT BMNH 1975428].
- ptychostylus*, *Bulimus*, Pfeiffer, 1858: 256, pl. 42 fig. 7 (Province of Patas, Andes of Peru) [LT BMNH 1975430].
- rectistrigatus*, *Neopetraeus arboriferus*, Pilsbry, 1898: 176, pl. 32 figs. 36-37 (Andes of Peru) [LT ANSP 4683a].
- tessellatus*, *Bulimus*, Shuttleworth, 1852: 200 [no type locality given].
- unicolor*, *Bulimus cora*, Pfeiffer in Pfeiffer & Clessin, 1881: 245 [indication].
- vadum*, *Neopetraeus*, Pilsbry, 1898: 165, pl. 29 figs. 32-34 (Peru) [LT ANSP 5260a].
- weyrauchi*, *Neopetraeus*, Pilsbry, 1944a: 88, pl. 9 fig. 4 (Peru, Santa valley, Huaraz, 3200 m) [HT ANSP 179980].

Llaucanianus Weyrauch, 1967

Llaucanianus Weyrauch, 1967a: 420. Type species by monotypy: *Llaucanianus haasi* Weyrauch.

Description. — Shell ovate-conical; narrowly perforate; solid. Colour pink, uniformly coloured or with oblique brown streaks on the upper whorls. Surface with very fine spiral lines. Protoconch with axial riblets and less prominent spiral striae. Last whorl relatively large and slightly inflated. Aperture elongate-ovate, skewed, orange coloured inside. Peristome expanded, white. The anatomy is unknown.

Distribution. — Peru (Dept. Cajamarca).

Ecology. — The species lives in rock-chasms at 2700 m altitude.

Remarks. — This genus, which is more or less intermediate between *Neopetraeus* and *Drymaeus*, may prove to be better classified as a subgenus of *Neopetraeus* once the anatomy has been studied.

Taxa. — The only taxon is:

haasi, *Llaucanianus*, Weyrauch, 1967a: 421, figs. 34-36 (Peru, [Dept. Cajamarca] Peña Rota, margen izquierda del río Llaucan, 8 km NE Bambamarca, 2700 m) [HT SMF 162046].

Stenostylus Pilsbry, 1898

Stenostylus Pilsbry, 1898: 184. Type species by subsequent designation (Pilsbry, 1898):
Bulimus nigrolimbatus Pfeiffer.

Description. — Shell ovate; imperforate; (rather) thin. Colour yellowish to light brown, with axial streaks of (darker) brown. Surface with incrassate growth striae and/or spiral lines. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls slightly convex; suture slightly crenulate, well impressed. Aperture (elongate-)ovate, with a pearly layer inside. Peristome thin and simple.

The central teeth of the radula are monocuspid, relatively small, with blunt, elongate to triangular mesocones. Lateral teeth are bicuspid, slightly shifted, with (rather) blunt, elongate to lanceolate mesocones and small, triangular to deltoid ectocones. The marginal teeth are tricuspid, shifted, with rather blunt, ovate mesocones, acute elongate-ovate endocones and acute deltoid ectocones. Half-row formula: $C/1 + L \ x/2 + M \ y/3$ ($x = 7-8$, $y = 64$).

Penis with a short sheath ($1/5-1/11$ the length of the phallus), more or less subcylindrical and passing without external differentiation into the epiphallus. The flagellum is (rather) short, subcylindrical. The spermathecal duct is more or less subcylindrical, with an elongate-globose spermatheca at the distal end.

Distribution. — ?Venezuela, Peru, ?Ecuador, ?Colombia.

Ecology. — The species live under stones and in rock-chasms. The vertical distribution is 3000-ca. 4000 m.

Remarks. — *Stenostylus* was described as a section of *Drymaeus*, but Weyrauch (1956a) has convincingly shown that it is justified to regard this taxon as a separate genus. Some of the species included by Pilsbry (1898) in *Stenostylus* proved to belong to *Scutalus* (*Sumiellus*) Breure, 1978. This latter taxon closely resembles *Stenostylus* in the shell morphology, but may be readily distinguished by the sculpture of the protoconch, and the structure of the radula.

Relationships. — The phylogenetic relationships are discussed on page 158ff. The genus is characterized by the shell shape, the colour and the sculpture of the protoconch.

Bibliography. — The main publications are: Breure, 1978b; Pilsbry, 1898; Weyrauch, 1956a.

Taxa. — The following taxa are included in *Stenostylus*:

- colmeiroi*, *Bulimus*, Hidalgo, 1872: 122 (Baeza, República del Ecuador).
[?] *guttula*, *Bulimus*, Pfeiffer, 1854b: 154 (Gualea, reipublicae Aequatoris) [this taxon may prove to belong to *Simpulopsis* (*Eudiptus*)].
meleagris, *Bulimus*, Pfeiffer, 1854b: 157 (Andes of New Granada).

- nigrolimbatus*, *Bulimus*, Pfeiffer, 1854b: 157 (Andes of New Granada) [LT BMNH 1975549].
tapadoides, *Bulimus*, Philippi, 1867: 71 ([Peru, Dept. Junín] prope Tarma).
zilchi, *Stenostylus*, Weyrauch, 1956a: 156, pl. 11 fig. 18 (Peru, Tapacocha, 3250 m, 280 km n. Lima, an der Autostraße von Barranca nach Huaraz) [HT SMF 155314].

Drymaeus Albers, 1850

- Drymaeus* Albers, 1850: 155. Type species by subsequent designation (Pilsbry, 1898): *Helix hygrophylaea* d'Orbigny.
Hamadryas Albers, 1850: 155. Type species by present designation: *Helix zoographica* d'Orbigny [not *Hamadryas* Hübner, 1806].
Semiclausaria Pfeiffer, 1856a: 162. Type species by monotypy: *Bulimus semiclausus* Petit.
Mormus Albers, 1860: 216. Type species by original designation: *Helix papyracea* Mawe.
Otostomus sensu Martens (1873: 23), not Beck, 1837.
Goniognathmus Fischer & Crosse in Crosse & Fischer, 1875 [1870-1894]: 473. Type species by original designation: *Bulimus lattarei* Pfeiffer.
Metadrymaeus Pilsbry, 1926b: 87. Type species by original designation: *Bulimus josephus* Angas.
Orodrymaeus Pilsbry, 1926b: 87. Type species by original designation: *Bulimus farrisi* Pfeiffer.
Ornatimormus Weyrauch, 1958: 131. Type species by original designation: *Drymaeus angulobasis* Pilsbry.

Description. — Shell (elongate-)ovate; perforate to rimate; thin to solid. Colour whitish, yellowish or pink usually with a colour pattern of streaks, spiral bands or spots. Surface smooth or with incrassate growth striae. Protoconch with a grating sculpture of axial riblets and spiral striae, which are of equal strength. Whorls slightly convex; suture well impressed. Aperture sub- to (elongate-)ovate. Peristome simple to broadly expanded.

Distribution. — Venezuela, Guiana, Surinam, French Guyana, Brazil, Paraguay, Argentina, Bolivia, Peru, Ecuador, Colombia, Panama, Costa Rica, Nicaragua, El Salvador, Honduras, Guatemala, Belize, Mexico, USA, West Indies.

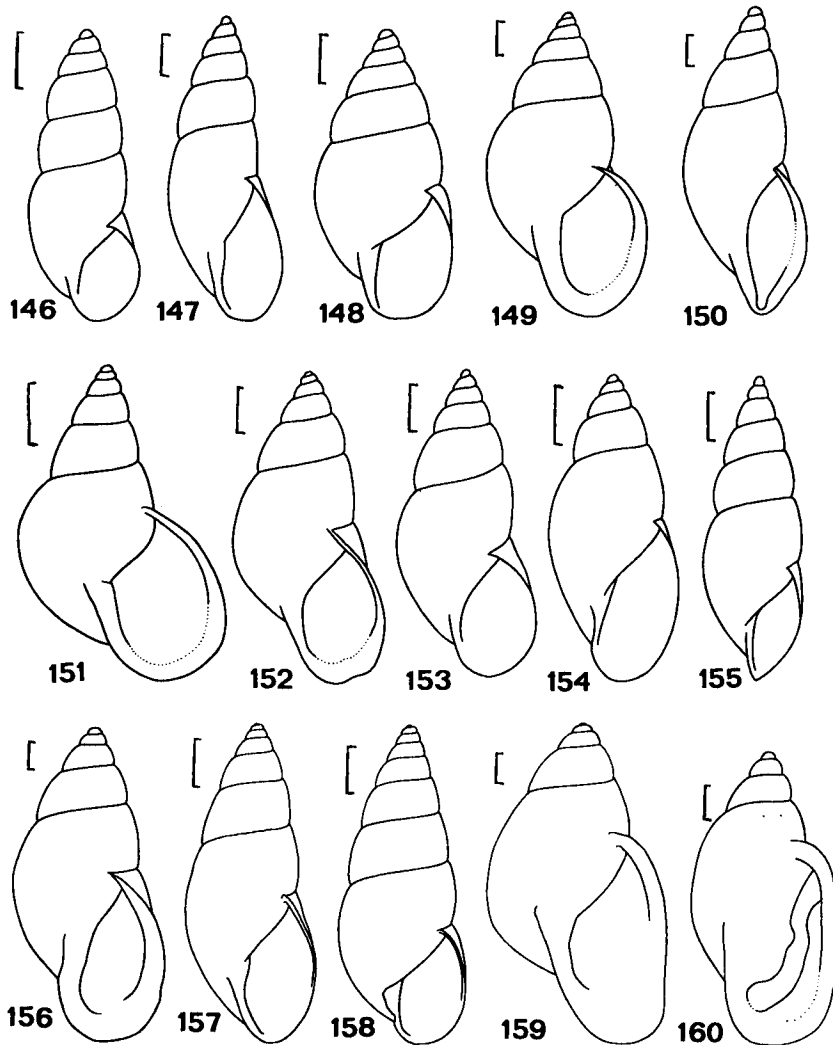
Remarks. — Details on the anatomy may be found in Breure & Eskens (in preparation).

Relationships. — The phylogenetic relationships of the genus are discussed on page 158ff.

Bibliography. — The main publications on this genus are: Da Costa, 1906a, 1906b, 1907; Haas, 1951, 1952, 1955a, 1955b; Pilsbry, 1930a, 1939, 1946a; Preston, 1907, 1909; Weyrauch, 1956a, 1958, 1964, 1967a.

Key to the subgenera of *Drymaeus*

- a. Peristome usually expanded; mandibula with 13-18 plates, which are 4-5 times as long as wide; transverse rows of radula straight, with relatively large, mono- to tricuspid central teeth and bi- to tricuspid lateromarginal



Figs. 146-160. Variation in shell shape in *Drymaeus*, *Cochlorina* and *Otostomus*. Fig. 146. *D. (Mesembrinus) virgo* (Lea). Fig. 147. *D. (D.) trujillensis* (Philippi). Fig. 148. *D. (D.) mexicanus* (Lamarck). Fig. 149. *D. (D.) fenestratus* (Pfeiffer). Fig. 150. *D. (D.) pulcherrimus* (H. Adams). Fig. 151. *D. (D.) expansus* (Pfeiffer). Fig. 152. *D. (D.) confluens* (Pfeiffer). Fig. 153. *D. (D.) ghiesbreghti* (Pfeiffer). Fig. 154. *D. (D.) attenuatus* (Pfeiffer). Fig. 155. *D. (D.) henrypilsbryi* (Weyrauch). Fig. 156. *D. (D.) colimensis* (Rolle). Fig. 157. *D. (D.) angulobasis* Pilsbry. Fig. 158. *D. (D.) celendinensis* Weyrauch. Fig. 159. *C. aurisleporis* (Bruguère). Fig. 160. *O. signatus* (Spix).
Scale = 5 mm.

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

Drymaeus (Drymaeus) Albers, 1850

Description. — Shell elongate-ovate; (narrowly) perforate; thin to solid. Colour whitish, yellowish or pink, with axial streaks, spiral bands and/or spots of brown, red, black or yellow. Surface with incrassate growth striae. Aperture elongate- to obliquely ovate, inversed ear-shaped or triangular. Peristome (simple to) broadly expanded.

Mandibula with 13-18 plates, which are 4-5 times as long as wide. Transverse rows of radula usually straight, in some species slightly V-shaped. Central teeth are (1) tricuspid, with elongate-ovate to lanceolate mesocones and rather blunt, triangular ectocones; or (2) monocuspid, with triangular to deltoid mesocones. Lateral teeth are bi- to tricuspid, slightly shifted, with (rather) blunt elongate-ovate mesocones, (curved, acute, lanceolate endocones) and triangular to deltoid ectocones that are posteriorly situated on the basal plate. Marginal teeth tricuspid, shifted, with lanceolate to elongate-ovate mesocones, curved lanceolate endocones and relatively small deltoid ectocones that may be bifid. Half-row formula: $C/1 + L x/2 + M y/3$ ($x = 1-4$, $y = 40-67$) or $C/3 + LM x/3$ ($x = 52-87$).

Penis with a (relatively) short sheath, which is absent in a few species; subcylindrical and passing without external differentiation into the epiphallus. Flagellum, subcylindrical, relatively short; the retractor muscle is distally inserted. Vagina relatively long. Spermathecal duct subcylindrical or tapering, usually as long as spermoviduct, but in some species reduced in length. The spermatheca is more or less globose, but normally not differentiated in species with a reduced spermathecal duct.

Distribution. — Venezuela, Brazil, Uruguay, Argentina, Bolivia, Peru, Ecuador, Colombia, Panama, Costa Rica, Nicaragua, Honduras, Guatemala, Mexico.

Ecology. — The species live on shrubs (and trees?). The vertical distribution is up to 2900 m.

Taxa. — The following taxa are placed in this subgenus (taxa tentatively referred to this subgenus are marked by an asterisk):

- **abruptus*, *Bulimulus* (*Drymaeus*), Rolle, 1905: 35 (Peru, Huancabamba) [HT 1947.2.10.1].
- abscissus*, *Bulimulus*, Pfeiffer, 1855h: 116 (Prov. of Quito, Ecuador) [LT BMNH 1975497].

- abyssorum*, *Helix*, d'Orbigny, 1835: 17 (provincia Lagunacensi, republica Boliviana).
- acervatus*, *Bulimus*, Pfeiffer, 1857b: 157 (Brasilien).
- acobambensis*, *Drymaeus*, Weyrauch, 1967b: 482, figs. 24-25 (Peru central, río Tarma, entre Tarma y Acobamba, Huailahuichán, 2900 m) [HT SMF 155694].
- **acuminatus*, *Drymaeus*, Da Costa, 1906a: 8, pl. 1 fig. 4 (Brazil, Matto Grosso) [HT BMNH 1907.11.21.10].
- aequatorianus*, *Bulimus* (*Drymaeus*), E. A. Smith, 1877b: 363, pl. 39 fig. 7 (Ecuador) [LT BMNH 1975137].
- aestivus*, *Bulimus*, Pfeiffer, 1857a: 331 (Meobamba, Peru) [ST BMNH].
- alabastrinus*, *Drymaeus*, Da Costa, 1906b: 98, pl. 11 fig. 4 (Colombia, Honda) [HT BMNH 1907.11.21.16].
- alabastrinus*, *Drymaeus*, Hylton Scott, 1952: 25 ([Argentina] Salta, Tartagal) [HT MIHS].
- albida*, *Drymaeus punctatus*, Da Costa, 1907: 304, pl. 26 figs. 2-2a (Peru, Chanchamayo).
- albiaricosus*, *Otostomus* (*Drymaeus*) *palpaloensis*, Martens, 1885c: 190 (E. Mexico, Playa Vincente).
- albolabiatus*, *Bulimus* (*Drymaeus*), E. A. Smith, 1877b: 363, pl. 39 fig. 4 (South Ecuador, Malacatos) [HT BMNH 1877.3.28.3].
- alcantarae*, *Bulimus*, Bernardi, 1853: 35, pl. 3 fig. 1 (Salomon Islands [sic]).
- alsophilus*, *Bulimus*, Philippi, 1867: 69 ([Peru] inter Lomas et Tarapoto).
- altorum*, *Mesembrinus* (*Mormus*) *expansus*, Weyrauch, 1958: 129, pl. 7 figs. 12-13 (Peru, Quimiri Sur, Valle de Chanchamayo, oberhalb Puente Herrería, zwischen ... La Merced und San Ramón, 1100-1300 m) [HT SMF 156295].
- ambustus*, *Bulimus*, Reeve, 1849: pl. 74 fig. 535 [no type locality given].
- andai*, *Drymaeus*, Jousseau, 1898: 14 (Tena, Équateur).
- angulobasis*, *Drymaeus*, Pilsbry, 1944b: 125, pl. 11 fig. 10 (Peru, [Dept. Junín, near San Ramón] Oreja de Capelo, 1600 m) [HT ANSP 180022].
- angusta*, *Drymaeus*, Da Costa, 1906a: 9, pl. 1 figs. 7-8 ([Colombia] Bogotá) [HT BMNH 1907. 11. 21.14].
- antioquiensis*, *Bulimus*, Pfeiffer, 1855c: 291 (Prov. of Antioquia, New Granada) [LT BMNH 1975450].
- arcuatostratus*, *Bulimus*, Pfeiffer, 1855g: 95 (Peru) [LT BMNH 1975455].
- attenuatus*, *Bulimus*, Pfeiffer, 1853a: 256 ([Mexico] Veracruz) [LT BMNH 1975458].
- auris*, *Bulimus*, Pfeiffer, 1866: 831 (Venezuela) [LT BMNH 1975499].
- aurisratti*, *Bulimus*, Philippi, 1867: 69 ([Peru] inter Lomas et Tarapoto).
- baeensis*, *Bulimus*, Hidalgo, 1869b: 189 (Baeza, reipublicae Aequatorius).
- balboa*, *Drymaeus expansus*, Pilsbry, 1926b: 82, pl. 10 figs. 5-7 (Panama, Prov. Panama, Río Puerco) [HT ANSP 140691].
- balteatus*, *Drymaeus acervatus*, Pilsbry, 1898: 255, pl. 51 fig. 13 (Brazil) [HT ANSP 72645].
- baranguillanus*, *Bulimus*, Pfeiffer, 1853d: 334 (Baranguilla in Andibus Columbianus) [LT BMNH 1975452].
- bariletti*, *Otostomus*, H. Adams, 1867: 442, pl. 38 fig. 4 (E. Peru).
- basitorus*, *Drymaeus* (*Drymaeus*), Haas, 1951: 522, fig. 109 (Peru, Chanchamayo, 1000 m) [HT FMNH 31354].
- bellus*, *Drymaeus*, Da Costa, 1906a: 8, pl. 1 fig. 5 (Colombia, San Martín) [HT BMNH 1907.11.21.32].
- beyerleanus*, *Bulimus*, Hupé, 1857: 50, pl. 6 fig. 6 (Pérou).
- bivittatus*, *Bulimus*, Sowerby, 1833a: fig. 46 (Brazil).
- blandi*, *Drymaeus*, Pilsbry, 1898: 248, pl. 43 figs. 73-76, 79-80 (Colombia, near Fresno) [LT ANSP 25780a].
- bogotensis*, *Bulimus*, Pfeiffer, 1855g: 93 (Santa Fé de Bogotá) [LT BMNH 1975191].
- bolivariü*, *Helix*, d'Orbigny, 1835: 17 (provincia Cochabambacensi, republica Boliviana).

- bolivianus*, *Bulimus*, Pfeiffer, 1846a: 34 (Merida, Andes of Bolivia [sic]) [LT BMNH 1975444].
- botterii*, *Bulimulus* (*Drymaeus*), Crosse & Fischer, 1875: 52 (in vicinio civitatis Orizaba, reipublicae Mexicanae).
- boucardi*, *Drymaeus*, Da Costa, 1907: 305, pl. 26 figs. 5-5a ([Panama] Chiriqui) [HT BMNH 1907.11.21.26].
- bourcierii*, *Bulimus*, Pfeiffer, 1853d: 314 (Pichincha, reipublicae Aequatorius) [LT BMNH 1975446].
- brachystoma*, *Helix*, d'Orbigny, 1835: 18 (provincia Santa Cruz de la Sierra, republica Boliviana).
- branneri*, *Drymaeus*, F. Baker, 1914: 637, pl. 23 figs. 1-4 (280 km above Porto Velho, Brazil) [HT ANSP 109308].
- bucia*, *Bulimus*, Pfeiffer, 1859: 39 (Brasilia).
- buckleyi*, *Bulimus* (*Drymaeus*), Sowerby, 1895: 214, pl. 13 figs. 3-4 (Ecuador) [LT BMNH 1907.11.21.48].
- canaliculatus*, *Bulimus*, Pfeiffer, 1845a: 68 (Bolivia) [LT BMNH 1975514].
- canarius*, *Bulimus*, Pfeiffer, 1867: 76 ([Peru] Trujillo).
- cantatus*, *Bulimus*, Reeve, 1848: pl. 56 fig. 375 [no type locality given].
- carandaitiensis*, *Bulimulus* (*Drymaeus*), Preston, 1907: 491, fig. 4 (Carandaiti, province of Cordillera, Bolivia, 1000 m).
- castaneostriatus*, *Drymaeus*, Da Costa, 1906b: 98, pl. 11 fig. 5 (Eastern Peru, Pozuzo) [HT BMNH 1907.11.21.19].
- catamayensis*, *Mormus*, Miller, 1879: 120, pl. 12 fig. 4 (Catamayo (prov. Loja) [Ecuador]).
- catenae*, *Drymaeus* (*Drymaeus*), Haas, 1952: 118, fig. 20 (Peru, Dept. Cuzco, Prov. Quispicanchi, Hacienda Cadena, 1000 m) [HT FMNH 38121].
- caucaensis*, *Bulimulus* (*Drymaeus*), Da Costa, 1898: 81, pl. 6 fig. 3 (Colombia, valley of the R. Cauca) [HT BMNH 1907.11.21.43].
- cecileae*, *Bulimus*, J. Moricand, 1858: 452, pl. 14 fig. 4 ([Peru] Tarapoto).
- celendinensis*, *Drymaeus*, Weyrauch, 1956a: 151, pl. 11 figs. 10-11 (N-Peru, Hgel 2 km w. Celendin, 2700 m) [HT SMF 155307].
- chamaeleon*, *Bulimus*, Pfeiffer, 1855h: 116 (Quito [Ecuador]) [ST BMNH].
- championi*, *Otostomus*, Martens, 1893: 222, pl. 14 fig. 5 (Guatemala, Hacienda de las Nubes, Cerro Zunil) [LT BMNH 1901.6.22.451].
- chanchamayensis*, *Bulimus*, Hidalgo, 1870: 49 (Chanchamayo, Prou) [ST ZMB].
- chaperi*, *Bulimulus*, Crosse & Fischer, 1893: 31, pl. 1 figs. 1-2 (Mexique, ile de Mescala, sur le lac Chapala dans l'Etat de Jalisco).
- chenui*, *Bulimus*, Philippi, 1867: 72 ([Peru] Pachicamac prope Lima).
- chiapasensis*, *Bulimus*, Pfeiffer, 1866: 81 (Chiapas, republica Mexicanae).
- chiapensis*, *Otostomus*, Martens, 1893: 205, pl. 15 fig. 12 (E. Mexico, Cordova).
- chicoensis*, *Drymaeus fallax*, Breure, 1977a: 261, fig. 4 (Colombia, Cundinamarca, Bosque de Chic, 2700-2800 m) [HT SMF 245405].
- chimborasensis*, *Bulimus*, Reeve, 1848: pl. 44 fig. 275 (Chimborazo, Columbia [sic], Ecuador), New Granada) [ST BMNH].
- chiriquiensis*, *Drymaeus*, Da Costa, 1901: 238, pl. 24 fig. 1 (Panama, Chiriqui, Boqueti) [HT BMNH 1907.11.21.119].
- chrysomelas*, *Bulimulus* (*Thaumastus*), Martens, 1867b: 145 [oberen Amazonenstromgebieten; ST ZMB].
- citrinellus*, *Bulimus scitulus*, 'Philippi' Pfeiffer, 1853d: 411 (inter Macanya et fluvium Maranon).
- clarus*, *Bulimus*, Pfeiffer, 1857a: 330 (Meobamba, Peru).
- clathratus*, *Bulimus*, Pfeiffer, 1858: 258 (Prov. of Patas, Andes of Peru) [LT BMNH 1975449].

- coarctatus*, *Bulimus*, Pfeiffer, 1845b: 73 (Locality unknown) [LT BMNH 1975560].
- coarctatus*, *Bulimus*, Reeve, 1848: pl. 41 fig. 260 [no type locality given].
- cognatus*, *Drymaeus*, Pilsbry, 1901: 155, pl. 23 figs. 3-7 (Colombia, Bogota) [LT ANSP 78543a].
- colimensis*, *Otostomus*, Rolle, 1895: 130 (Mexiko) [ST ZMB].
- comis*, *Bulimulus* (*Drymaeus*), Preston, 1907: 494, fig. 8 (Colombia, Bogota).
- concolor*, *Otostomus attenuatus*, Martens, 1893: 215 (E. Mexico).
- concolor*, *Otostomus josephus*, Martens, 1893: 202, pl. 12 figs. 8-10 (SW Costa Rica, banks of Rio Pacuare del Sur, about 500 m).
- confluens*, *Bulimus*, Pfeiffer, 1855h: 115 (Marmato, New Granada) [LT BMNH 1975196].
- conicus*, *Drymaeus*, Da Costa, 1907: 305, pl. 26 figs. 7-7a (Mexico, Oaxarca [sic]) [LT BMNH 1907.11.21.32].
- convexus*, *Bulimus*, Pfeiffer, 1855h: 116 (New Grenada) [LT BMNH 1975192].
- correctus*, *Bulimus*, Pfeiffer, 1852b: 93 (Venezuela).
- costaricensis*, *Bulimus*, Pfeiffer, 1862b: 153 (Costa Rica).
- crebristriga*, *Bulimulus* (*Thaumastus*) *chrysomelas*, Martens, 1867b: 145 [oberen Amazonenstromgebieten].
- crosei*, *Otostomus* (*Drymaeus*) *lilacinus*, Martens, 1885c: 191 (Alta Vera Paz, N Guatemala).
- cuticula*, *Bulimus*, Pfeiffer, 1855g: 95 (Brazil, Rio [de Janeiro]) [LT BMNH 1975451].
- cuzcoensis*, *Bulimus*, Reeve, 1849: pl. 71 fig. 514 (Cuzco, Bolivia [sic]) [LT BMNH 1975453].
- **cygneus*, *Bulimus*, Philippi, 1867: 68 (Lomas de Supe, Peru).
- **cylindricus*, *Drymaeus*, Da Costa, 1901: 238, pl. 24 fig. 3 (Peru, San Pablo) [HT BMNH 1907.11.21.42].
- dacostae*, *Bulimulus*, Sowerby, 1892: 297, pl. 23 figs. 15-16 (Bogota [Colombia]) [HT BMNH 1907.11.21.51].
- dacostianus*, *Drymaeus*, Pilsbry, 1898: 219, pl. 50 fig. 87 (New name for *Bulimulus lucidus* Da Costa, not *Bulimus lucidus* Reeve).
- decoratus*, *Bulimus*, Lea, 1838: 86, pl. 23 fig. 108 (near Carthagen, S.A.).
- delattreii*, *Bulimulus* (*Drymaeus*), Fischer & Crosse in Crosse & Fischer, 1875 [1870-1894]: 481, pl. 20 figs. 3-4, pl. 22 figs. 1-14 [emendation for *lattrei* Pfeiffer].
- delphinae*, *Bulimus*, J. Moricand, 1858: 452, pl. 14 fig. 3 ([Peru] Tarapoto).
- densestrigatus*, *Mesembrinus* (*Ornatimormus*) *henrypilsbryi*, Weyrauch, 1958: 134, pl. 8 fig. 20 (M-Peru, Quimiri Sur, Valle de Chanchamayo, oberhalb Puente Herreria, zwischen ... La Merced und San Ram6n, 1300-1400 m) [HT SMF 156293].
- diversipictus*, *Drymaeus interpictus*, Pilsbry, 1944b: 125, pl. 11 fig. 11 (Peru, [Dept. Jun6n, near San Ram6n] Orejo de Capelo, 1600 m) [HT ANSP 180021].
- dombeyana*, *Helix*, 'F6russac' Pfeiffer, 1842: 76 (Peru).
- draparnaudi*, *Bulimus*, Pfeiffer, 1847a: 113 (Chilon, Bolivia).
- dunkeri*, *Bulimus*, Pfeiffer in Philippi, 1846: 112, pl. 4 fig. 10 (respublica [sic] Mexicana, Michoacan) [LT BMNH 1975512].
- edmuelleri*, *Bulimus*, Albers, 1854b: 218 (Columbia [sic, Peru], ad fluvium Maranhon).
- elegantissimus*, *Bulimus*, Mousson, 1873: 11 (N6rdlichem S6d-Amerika).
- elsteri*, *Drymaeus*, Da Costa, 1901: 238, pl. 24 fig. 6 (Peru, Chachapoyas (prov. Amazonas)) [LT BMNH 1907.11.21.34].
- errans*, *Drymaeus josephus*, Pilsbry, 1926b: 84, fig. 15a (Panama, Prov. Boca del Toro, Mono Creek) [HT ANSP 140832].
- eucosmetus*, *Drymaeus* (*Drymaeus*), Haas, 1955b: 331, figs. 71-72 (Peru, Lambayeque, Cambache near Chongoyape, 460 m) [HT FMNH 51920].
- eusteuris*, *Drymaeus*, Pilsbry, 1944c: 29, pl. 1 fig. 7 (Peru, Oxapampa, 1800 m) [HT ANSP 180674].

- eversus*, *Bulimus*, Mousson, 1873: 10 (Nördlichem Süd-Amerika).
- exoticus*, *Drymaeus*, Da Costa, 1901: 239, pl. 24 fig. 10 (Upper Magdalena River, Colombia) [HT BMNH 1907.11.21.38].
- expansus*, *Bulimus*, Pfeiffer, 1848b: 60 ([Peru] Huallaga).
- expatriatus*, *Bulimulus* (*Drymaeus*), Preston, 1909: 510, pl. 10 fig. 4 (E. Bolivia) [LT BMNH 1975201].
- fabrefactus*, *Bulimus*, Reeve, 1848: pl. 49 fig. 319 (New Granada, Province of Merida) [LT BMNH 1975531].
- fairchildi*, *Drymaeus* (*Drymaeus*), Bequaert, 1949: 114, pl. 7 fig. 7 (Panama, Coclé Prov., El Valle) [HT MCZ 175763].
- fallax*, *Bulimus*, Pfeiffer, 1853d: 375 (Tunguragua reipublicae Aequatoris).
- farrisi*, *Bulimus*, Pfeiffer, 1858: 258, pl. 42 fig. 8 (Province of Patas, Andes of Peru) [LT BMNH 1975506].
- felix*, *Bulimus*, Pfeiffer, 1862a: 387, pl. 37 fig. 2 (New Granada).
- fenestralis*, *Bulimus* (*Mesembrinus*), Albers, 1850: 157 [emendation for *fenestratus* Pfeiffer].
- fenestratus*, *Bulimus*, Pfeiffer, 1846a: 29 (Mexico) [LT BMNH 1975525].
- fenestrellus*, *Bulimulus* (*Scutalus*), Martens, 1864: 541 (Hochebene von Mexico) [ST ZMB].
- feriatus*, *Bulimus*, Reeve, 1848: pl. 48 fig. 314 [no type locality given; LT BMNH 1975204].
- flavilabrum*, *Drymaeus* (*Mormus*) *expansus*, Weyrauch, 1967b: 484, fig. 29 (Peru central, carretera de Tingo Maria a Pucallpa, Río Aguaytía, 300 m) [HT IML 1197].
- flexilabris*, *Bulimus*, Pfeiffer, 1853d: 652 (Brasilia) [LT BMNH 1975559].
- flexuosus*, *Bulimus*, Pfeiffer, 1853d: 329 (Marinato, Novae Granadae, in valle Pomasqui) [LT BMNH 1975202].
- focillatus*, *Bulimus*, Reeve, 1848: pl. 36 fig. 211 ([Mexico] Vera Cruz).
- fordii*, *Drymaeus*, Pilsbry, 1898: 205, pl. 38 figs. 1-3 [no type locality given; LT ANSP 72368a].
- forreri*, *Bulimulus*, Mousson, 1883: 217, pl. 9 fig. 2 ([Mexico] Ventanas, Durango).
- fresnoensis*, *Drymaeus*, Pilsbry, 1898: 304, pl. 40 fig. 18 (Colombia, near Fresno) [HT ANSP 25836].
- fucatus*, *Bulimus*, Reeve, 1849: pl. 83 fig. 615 (New Granada, Sebundoi) [LT BMNH 1874.12.11.224].
- fusoides*, *Helix*, d'Orbigny, 1835: 19 (provincia Yungacensi, republica Boliviana).
- gealei*, *Bulimus*, H. Adams, 1867: 309, pl. 19 fig. 21 (Mexico).
- geometricus*, *Bulimus*, Pfeiffer, 1846c: 84 (Novae Granadae, vallis Magdalenae) [LT BMNH 1975564].
- germaini*, *Bulimulus*, Ancey, 1892: 91 (Matto Grosso, Brazil).
- ghiesbreghti*, *Bulimus*, Pfeiffer, 1866b: 82 (Chiapas, reipublicae Mexicanae).
- gibber*, *Drymaeus* (*Drymaeus*), Haas, 1949: 238, fig. 50c (Peru, Dept. Huánuco, Divisoria, 5000 feet [NE Tingo Maria]) [HT FMNH 30042].
- glaucostomus*, *Bulimus*, Albers, 1852: 32 (in montibus Venezuela) [ST ZMB].
- goniobasis*, *Drymaeus decoratus*, Pilsbry, 1898: 262, pl. 40 fig. 4 (Colombia, near Santa Ana) [HT ANSP 25803].
- gracilior*, *Bulimus mexicanus*, Pfeiffer, 1848b: 102 (prov. Tabasco, Mexicana).
- gracilis*, *Bulimus*, Lea, 1838: 85, pl. 23 fig. 102 ([Colombia] near Carthagen).
- gueinzii*, *Bulimus*, Pfeiffer, 1857a: 330 (Meobamba, Peru) [LT BMNH 1975539].
- hamadryas*, *Bulimus*, Philippi, 1867: 68 ([Peru] Chanchamayo).
- harringtoni*, *Drymaeus*, Marshall, 1930: 2, pl. 1 fig. 7 (Argentina, Prov. Salta, General Ballivian) [HT USNM 380701].
- henrypilsbryi*, *Mesembrinus* (*Ornatimormus*), Weyrauch, 1958: 134, pl. 8 fig. 20 (New name for *Drymaeus pilsbryi* Weyrauch, 1956, not Zetek, 1934) [and type locality corrected to "Pan de Azucar" (near San Ramón)].

- henselii*, *Bulimulus*, Martens, 1868: 180 ([Brazil] Costa da Serra) [HT ZMB 13702].
- hepaticus*, *Bulimus*, Albers, 1854b: 218 (Columbia [sic, Peru], ad fluvium Maranhon) [ST ZMB].
- **hepatostomus*, *Bulimus*, Pfeiffer, 1861a: 23, pl. 3 fig. 4 (Mexico) [LT BMNH 1975571].
- hiabundus*, *Otostomus* (*Drymaeus*) *delattrei*, Martens, 1893: 204, pl. 12 figs. 11-14 (W. Guatemala, Cerro Zunil) [ST ZMB].
- hidalgoi*, *Bulimulus* (*Drymaeus*), Da Costa, 1898: 81, pl. 6 fig. 2 (Ecuador) [HT BMNH 1907.11.21.28].
- humboldtii*, *Bulimus*, Reeve, 1849: pl. 58 fig. 391 (Mexico) [ST BMNH].
- hyematus*, *Bulimus*, Reeve, 1848: pl. 49 fig. 324 [no type locality given].
- hygrohyla*, *Helix*, d'Orbigny, 1835: 18 (provincia Chiquitensi, republica Boliviana).
- hygrophilaeus*, *Bulimus*, Hupé, 1857: 50 [emendation for *hygrohyla* d'Orbigny].
- hyltoni*, *Drymaeus*, Parodiz, 1957: 25 (New name for *Drymaeus alabastrinus* Hylton Scott, 1952, not Da Costa, 1907).
- icterica*, *Bulimulus poecilus*, Ancey, 1892: 92 (Brazil, Matto-Grosso).
- ictericus*, *Otostomus* (*Drymaeus*) *lilacinus*, Martens, 1893: 202 (W. Guatemala, Cerro Zunil).
- icterostomus*, *Bulimus*, Martens, 1901: 149 (Urubamba, im östlichen Peru) [HT ZMB 52736].
- inaequalis*, *Bulimus*, Pfeiffer, 1857a: 330 ([Peru] Banks of the Maranhon).
- inca*, *Drymaeus* (*Drymaeus*), M. Smith, 1943: 61, pl. 7 fig. 10 (Junín, prov. Jauja, Peru, 1100 m).
- inclinatus*, *Bulimus*, Pfeiffer, 1862a: 387, pl. 37 fig. 3 (New Granada) [LT BMNH 1975532].
- incognita*, *Drymaeus*, Da Costa, 1907: 304, pl. 26 figs. 4-4a ([Colombia] Bogota) [HT BMNH 1907.11.21.24].
- interpticus*, *Bulimulus* (*Drymaeus*), Martens, 1867: 144 ([Bolivia] Yungasensis) [HT ZMB 11834].
- iodostomus*, *Bulimus*, Deville & Hupé, 1850: 641, pl. 15 fig. 2 [Peru, Dept. Amazonas, Pebas; ST MNHN].
- iodostylus*, *Bulimus*, Pfeiffer, 1861a: 23 (Mexico) [ST BMNH].
- jansoni*, *Otostomus* (*Drymaeus*) *lilacinus*, Martens, 1893: 201, pl. 12 fig. 3 (Nicaragua) [LT BMNH 1901.6.22.951].
- josephus*, *Bulimus*, Angas, 1878a: 73, pl. 5 figs. 13-14 (San José, Costa Rica) [ST BMNH].
- jousseaumei*, *Drymaeus*, Dautzenberg, 1901c: 308 (Rio Mixiollo, Province Huallaga, Pérou).
- kefersteini*, *Bulimus*, Pfeiffer, 1866b: 82 (Mexiko).
- lamas*, *Bulimus* (*Otostomus*), Higgins, 1868: 179, pl. 14 figs. 3-3a (Jouctabamba, Peru) [ST BMNH].
- laticus*, *Bulimulus papyraceus*, 'Martens' Strebel in Strebel & Pfeiffer, 1882: 81 [no type locality given].
- latitesta*, *Drymaeus* (*Drymaeus*), Haas, 1952: 117, fig. 19 (Peru, Dept. Cuzco, Prov. Quispicanchi, Hacienda Cadena, 1000 m) [HT FMNH 38120].
- lattrei*, *Bulimus*, Pfeiffer in Philippi, 1847: 112, pl. 4 fig. 11 (America centralis, prope Veracruz) [LT BMNH 1975555].
- **lautus*, *Bulimus*, Gould, 1856: 12 (From the mountains of Equador, near Quito).
- laxostylus*, *Bulimulus*, Rolle, 1905: 37 (Peru, Huancabamba) [HT BMNH 1922.2.24.32].
- leai*, *Drymaeus*, Pilsbry, 1898: 213, pl. 40 figs. 15-17 (New name for *Bulimus gracilis* Lea, 1838, not Hutton, 1834).
- libertadensis*, *Drymaeus hepaticus*, Pilsbry, 1898: 291, pl. 51 figs. 16-17 (New name for *Bulimus taenitus* Philippi, 1869, not Mörch, 1850).

- liebmanni*, *Bulimus*, Pfeiffer, 1846a: 158 (Mexiko).
- lilacinus*, *Bulimus*, Reeve, 1849: pl. 74 fig. 532 [no type locality given].
- limicolarioides*, *Drymaeus* (*Drymaeus*), Haas, 1936: 150, figs. 12-13 (Staat São Paulo, Brasilien) [HT SMF 10077].
- linostoma*, *Bulimus*, Bland, 1852: 230 [not seen].
- linostoma*, *Helix*, d'Orbigny, 1835: 19 (provincia Chiquitensi, republica Boliviana).
- lita*, *Helix*, Férussac, 1821: 54 (les îles Sandwich [sic]).
- literatus*, *Bulimus*, Spix, 1827: 7, pl. 7 fig. 3 (Provincia septentrionalibus Brasiliae).
- lophoica*, *Helix*, d'Orbigny, 1835: 19 (provincia Yungacensi, republica Boliviana).
- lucidus*, *Bulimulus* (*Drymaeus*), Da Costa, 1898: 82, pl. 6 fig. 4 (Ecuador) [HT BMNH 1907.11.21.44].
- maculosus*, *Otostomus josephus*, Martens, 1893: 292, pl. 12 fig. 7 (SW Costa Rica, banks of Rio Pacuare del Sur, about 500 m).
- magus*, *Bulimus*, Wagner in Spix, 1827: 6, pl. 7 fig. 1 (Provinciarum Riauiensis et Maraquariensis [Brazil]).
- major*, *Bulimus poecilus*, d'Orbigny, 1836: 268, pl. 31 figs. 7-8 ([Bolivia] à la porte de Tasajos et du bourg de Pampa grande).
- malleatus*, *Bulimulus* (*Drymaeus*), Da Costa, 1898: 82, pl. 6 fig. 7 (Bolivia, La Paz) [HT BMNH 1907.11.21.130].
- marcapatensis**, ***Drymaeus* (*Drymaeus*)**. New name for *Drymaeus* (*Drymaeus*) *schmidti* Haas, 1955, not *Bulimus schmidti* Pfeiffer, 1854.
- mariae*, *Bulimus*, J. Moricand, 1858: 453, pl. 14 fig. 5 ([Peru] Tarapoto).
- mariaenus*, *Drymaeus strigatus*, Pilsbry, 1898: 230, pl. 42 fig. 51 (New name for *Bulimus mariae* J. Moricand, 1858, not Albers, 1850).
- marmarina*, *Helix*, d'Orbigny, 1835: 18 (provincia Yungacensi, republica Boliviana).
- medinanus*, *Drymaeus cantatus*, Pilsbry, 1935: 85, pl. 6 fig. 13 (Region of Medina, E of Bogota, Columbia) [HT ANSP 164752].
- meesi*, *Drymaeus glaucostomus*, Breure, 1976d: 113, pl. 1 (Surinam, Nassau Mountains, ca. 530 m) [HT RMNH 55077].
- megas*, *Drymaeus flexuosus*, Pilsbry, 1944b: 127, pl. 11 fig. 3 (Colombia, Dept. Huila, Suesa) [HT ANSP 179981].
- megastomus*, *Drymaeus*, Parodiz, 1962: 435, pl. 1 fig. 7 (Costa Rica) [HT USNM 98230].
- melanoscolops*, *Otostomus*, Dohrn, 1882: 108, pl. 3 figs. 6-8 ([Brazil] in provincia Pará ad fluvium Tapajos) [ST ZMB].
- membielinus*, *Bulimus*, Crosse, 1867b: 445 (Republica Aequatoris).
- mexicanus*, *Bulimus*, Lamarck, 1822: 123 (Mexique).
- minor*, *Bulimus poecilus*, d'Orbigny, 1836: 268, pl. 31 figs. 9-10 ([Bolivia] ... entre Santa Cruz de la Sierra et Chiquitos).
- mittelli*, *Drymaeus beyerleanus*, Dall, 1912a: 6 (Lucma, 7000 ft., ... three leagues above Santa Ana, Eastern Peru) [HT USNM 250260].
- morbidus*, *Bulimus*, Philippi, 1867: 70 (hacienda de Sunchobamba prope Cajamarca [Peru]).
- muelleggeri*, *Drymaeus*, Jaeckel, 1927: 136, fig. 2 ([Brazil] Wälder zwischen den Flüssen Rio Santa Rosa und Rio Santo Christo, bei Santa Rosa im Staate Rio Grande do Sul) [HT ZMB 64916].
- multiguttatus*, *Drymaeus* (*Ornatimormus*), Weyrauch, 1964: 55, fig. 8 (Perú central, Boquerón de Abad, entre Tingo Maria y Pucallpa, 550 m) [HT IML 1200].
- murrinus*, *Bulimus*, Reeve, 1848: pl. 43 figs. 273a-b (Santa Fé di Bogota) [LT BMNH 1975213].
- musivus*, *Bulimus*, Pfeiffer, 1855g: 95, pl. 31 fig. 3 (Meobamba, E Peru) [LT BMNH 1975292].
- napo*, *Bulimus* (*Otostomus*), Angas, 1878b: 312, pl. 18 figs. 4-5 (Ecuador) [HT BMNH 1879.1.21.4].

- narcissus*, *Bulimus*, Albers, 1854b: 217 (Nova Granada).
- navarrensis*, *Bulimus*, Angas, 1878a: 73, pl. 5 figs. 15-16 (Navarro, Costa Rica).
- **nebulosus*, *Otostomus chiapensis*, Martens, 1893: 205, pl. 12 fig. 15 (Central Mexico, Cuantitlan).
- nigricans*, *Thaumastus nystianus*, Cousin, 1887: 220 (entre Pomasqui et Chilquiltina, canton de Quito, Rep. l'Equateur).
- nigrogularis*, *Otostomus*, Dohrn, 1882: 107, pl. 3 figs. 10-13 (Juraty provinciae Pará prope ad ripam dextram fluvii Amazonas [Brazil]) [ST ZMB].
- nigroumbilicatus*, *Bulimulus (Drymaeus)*, Preston, 1907: 491, fig. 6 (Bolivia, Chaco, north of Rio Pilcomayo, 600 m).
- nigroumbilicatus*, *Peronaeus (Lissoacme) torallyi*, Parodiz, 1947: 20, fig. 10 ([Argentina] prov. Salta, Embarcación) [HT MACN 8848].
- notabilis*, *Drymaeus*, Da Costa, 1906a: 7, pl. 1 fig. 2 (Colombia, Antioquia) [HT BMNH 1907.11.21.5].
- notatus*, *Drymaeus*, Da Costa, 1906a: 7, pl. 1 fig. 3 (Colombia, Antioquia) [HT BMNH 1907.11.21.6].
- nubilus*, *Bulimulus (Drymaeus)*, Preston, 1903: 4, fig. (Costa Rica) [HT BMNH 1903.5.4.1].
- nystianus*, *Bulimus*, Pfeiffer, 1853d: 374 (Reipublicae Aequatoris) [LT BMNH 1975573].
- ochrocheilus*, *Bulimus (Drymaeus)*, E. A. Smith, 1877b: 362, pl. 39 fig. 1 (South Ecuador, Malacatos) [HT BMNH 1877.3.28.4].
- orcei*, *Mesembrinus (Mormus) expansus*, Weyrauch, 1958: 130, pl. 7 fig. 15 (Ecuador, Montalvo, Río Bobonaza, Zufluß des Río Pastaza, 314 m, 270 km sw Quito) [HT SMF 156292].
- **orobaena*, *Helix*, d'Orbigny, 1835: 17 (provincia Yungacensi, republica Boliviana).
- orthostoma*, *Bulimus (Drymaeus)*, E. A. Smith, 1877b: 364, pl. 39 fig. 5 (Ecuador?) [HT BMNH 1975132].
- pallidior*, *Bulimulus (Scutalus)*, Dall, 1893c: 640 (Zeledon, Costa Rica).
- pamplonensis*, *Drymaeus*, Pilsbry, 1939: 4, fig. 10 (Colombia, Pamplona) [HT ANSP 170699].
- papyracea*, *Helix*, Mawe, 1823: 168, fig. 7 (Bahia, Brazil).
- papyrifactus*, *Drymaeus papyraceus*, Pilsbry, 1898: 252, pl. 51 fig. 4-5 (Brazil, Paraná, Curitiba) [HT ANSP 72656a].
- patricius*, *Bulimus*, Reeve, 1849: pl. 81 fig. 600 [no type locality given; LT BMNH 1874.12.11.220].
- peakamus*, *Bulimus*, Lea, 1838: 65, pl. 33 fig. 105 (near the rapids of Angostura, Colombia).
- peeli*, *Bulimus*, Reeve, 1859: 123 (Peruvian side of Amazonas).
- percandidus*, *Drymaeus poecilus*, Dall, 1912a: 4 (Santa Ana, Peru) [HT USNM 250245].
- perenensis*, *Drymaeus expansus*, Da Costa, 1901: 239, pl. 24 fig. 5 (Peru, Peréné) [HT BMNH 1907.11.21.39].
- pergracilis*, *Bulimulus*, Rolle, 1905: 37 (Peru, Huancabamba) [HT BMNH 1922.2.4.33].
- pergracilis*, *Drymaeus (Drymaeus)*, Haas, 1952: 122, fig. 23 (Peru, Dept. Cuzco, Prov. Quispicanchi, Hacienda Cadena, 1000 m) [HT FMNH 38127].
- petasites*, *Drymaeus*, Miller, 1878: 189 (Nanegal, Sebondoï, in valli Pilatonensi [Ecuador]).
- phryne*, *Bulimus*, Pfeiffer, 1863: 274 (Andes of Peru) [LT BMNH 1975214].
- pichitacalugaensis*, *Mesembrinus (Ornatimormus) henrypilsbryi*, Weyrauch, 1958: 135, pl. 8 fig. 17 (M-Peru, 2 km vom Bergwerk Pichita Caluga, 2200 m [19.5 km WNW San Ramón], im Chanchamayo-Becken) [HT SMF 156388].
- pictus*, *Bulimus*, Bonnet, 1864: 69, pl. 5 figs. 4-6, pl. 6 fig. 1 (Pérou).
- piescheli*, *Bulimulus (Otostomus)*, Martens, 1864: 541 ([Mexico] an der Westküste bei Manzanillo).

- pilsbryi*, *Drymaeus*, Weyrauch, 1956a: 153, pl. 11 fig. 7 (Peru, Pan de Azucar, 1350 m, Río Tarma, Oberlauf des Río Chanchamayo) [HT SMF 155303].
- pittieri*, *Otostomus attenuatus*, Martens, 1893: 216, pl. 16 fig. 1 (SW Costa Rica, Alto de Mango Tigre, near Terraba, 690 m).
- planibasis*, *Drymaeus*, Pilsbry, 1932: 395, pl. 28 fig. 18 (Ecuador, above Chunchi, Pagma Forest) [HT ANSP 148436a].
- plicatoliratus*, *Bulimulus* (*Drymaeus*), Da Costa, 1898: 80, pl. 6 fig. 1 (Colombia, Bogota) [HT BMNH 1907.11.21.120].
- poecila*, *Helix*, d'Orbigny, 1835: 11 (provincia Chiquitensi, republica Boliviana).
- ponsonbyi*, *Drymaeus*, Da Costa, 1907: 305, pl. 26 figs. 6-6a (Peru, Sarco) [HT BMNH 1907.11.21.27].
- praecilius*, *Bulimus*, Anton, 1839: 41 [emendation for *poecilus* d'Orbigny].
- praetextus*, *Bulimus*, Reeve, 1850: 98 (Andes of Caxamarca, Peru).
- primularis*, *Bulimus*, Reeve, 1849: pl. 73 fig. 527 (Chachapoyas, Alto Peru).
- prostratus*, *Bulimulus*, Paetel & Schaufuss, 1869: 81 [emendation for *protractus* Pfeiffer].
- protractus*, *Bulimus*, Pfeiffer, 1855g: 94, pl. 34 fig. 1 (Meobamba, Eastern Peru) [LT BMNH 1975494].
- pseudelatus*, *Drymaeus* (*Drymaeus*), Haas, 1951: 520, fig. 108 (Peru, Mantaro River, Anco, 2500 m) [HT FMNH 30908].
- pseudofusoides*, *Drymaeus*, Da Costa, 1906a: 8, pl. 1 fig. 6 (Colombia, Bogota) [HT BMNH 1907.11.21.11].
- pulchellus*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 106 (in Peruviae montibus, Truxillo).
- pulchellus*, *Bulinus*, Sowerby, 1833a: fig. 91 ([Peru] Huallaga).
- pulcherrimus*, *Otostomus*, H. Adams, 1867: 442, pl. 38 fig. 3 (Eastern Peru) [HT BMNH 1867.5.18.3].
- punctatus*, *Drymaeus*, Da Costa, 1907: 304, pl. 26 figs. 1-1a (Peru, Chanchamayo) [HT BMNH 1907.11.21.20].
- purus*, *Drymaeus strigatus*, Pilsbry, 1898: 229, pl. 42 fig. 41 (Peru) [LT ANSP 264300a].
- **quadrifasciatus*, *Bulimus* (*Otostomus*), Angas, 1878b: 312, pl. 18 figs. 2-3 (Ecuador) [LT BMNH 1879.1.21.3].
- quadrifasciatus*, *Otostomus chiapensis*, Martens, 1893: 205 (E. Mexico, Matlaquihahuitl, in the State of Vera Cruz; Cerro de Plumas near Cordova).
- quadritaeniatus*, *Drymaeus* (*Orodrymaeus*) *farrisi*, Weyrauch, 1956a: 150, pl. 11 fig. 9 (N-Peru, Hacienda Santa Elena, 1550 m, auf der rechten Seite des Río Chusgon, westlicher Zufluß des Río Marañon) [HT SMF 155306].
- rabuti*, *Hamadryas*, Jousseume, 1898: 14 (Tena, Équateur).
- raristriga*, *Bulimulus* (*Thaumastus*) *chrysomelas*, Martens, 1867: 145 [oberen Amazonenstromgebiets].
- recedens*, *Bulimus*, Pfeiffer, 1864: 525 (Peru, Moyobamba) [LT BMNH 1975477].
- regularis*, *Drymaeus*, Fulton, 1905b: 25, pl. 6 fig. 6 (Peru, Chanchamayo) [LT BMNH 1905.11.17.2].
- rehderi*, *Drymaeus*, Parodiz, 1962: 435, pl. 1 figs. 5, 8 (Colombia, Antioquia, Valdivia) [HT USNM 590653].
- rhoodsi*, *Drymaeus*, Pilsbry, 1932: 394, pl. 28 fig. 5 (Ecuador, Pachijal) [HT ANSP 148440].
- ribeiroi*, *Drymaeus nigrogularis*, Ihering, 1915: 6 ([Brazil] Estado do Pará, Juruty).
- rosenbergi*, *Drymaeus*, Da Costa, 1906b: 98, pl. 11 fig. 6 (Eastern Peru, Pozuzo) [LT BMNH 1907.11.21.17].
- rubellus*, *Bulinus*, Broderip, 1832: 124 (in Peruviae montibus, Truxillo).
- rubrovariegatus*, *Bulimus*, Higgins, 1868: 178, pl. 14 figs. 2-2a (Peru, Huamachuco) [ST BMNH].
- rudis*, *Bulimus*, Anton, 1839: 43 [no type locality given].

- rugistriatus*, *Drymaeus* (*Drymaeus*), Haas, 1952: 120, fig. 21 (Peru, Dept. Cuzco, Prov. Quispicanchi, Hacienda Cadena, 1000 m) [HT FMNH 38123].
- rugosa*, *Lymnaea*, Valenciennes, 1827: 250, pl. 56 fig. 5 [no type locality given].
- saccatus*, *Bulimus*, Pfeiffer, 1855g: 94, pl. 31 fig. 2 (Meobamba, E. Peru) [LT BMNH 1975127].
- sachsei*, *Bulimus*, Albers, 1854a: 30 (Columbia australi [sic, Peru] ad fluvium Maranhon) [ST ZMB].
- **sanctaemarthae*, *Drymaeus*, Pilsbry, 1901: 161, pl. 48 figs. 49-50 (Colombia, NW slope of Santa Marta Mts., Jiracasaca).
- santanensis*, *Drymaeus poecilus*, Dall, 1912a: 4 (Peru, Santa Ana).
- **schmidti*, *Bulimus*, Pfeiffer, 1854a: 65 [no type locality given].
- schmidti*, *Drymaeus* (*Drymaeus*), Haas, 1955b: 314, fig. 62 (Peru, Dept. Cuzco, Marcapata, Ccachabamba) [HT FMNH 51323].
- schunkei*, *Drymaeus* (*Drymaeus*), Haas, 1949: 237, fig. 50b (Peru, Dept. Loreto, Río Ucayali, Cerro Azul) [HT FMNH 30040].
- scitulus*, *Bulimus*, Reeve, 1849: pl. 71 fig. 513 (Peru, Chachapoyas).
- scitus*, *Otostomus*, H. Adams, 1867: 442, pl. 38 fig. 5 (E. Peru).
- scoliodes*, *Drymaeus*, Dautzenberg, 1901c: 309 (Río Mixiollo, province Huallaga, Pérou).
- selli*, *Bulimulus* (*Drymaeus*), Preston, 1909: 511, pl. 10 fig. 3 (British Guiana) [HT BMNH 1915.1.6.36].
- semistriatus*, *Drymaeus* (*Drymaeus*), Haas, 1955a: 374, fig. 77 (Brazil, São Paulo, Varnhagen Distr., Fazenda Ipanema) [HT FMNH 49784].
- serratus*, *Bulimus*, Pfeiffer, 1855g: 94, pl. 31 fig. 6 (Peru, Moyobamba) [LT BMNH 1975475].
- silvanus*, *Drymaeus* (*Orodrymaeus*), Zilch, 1953: 56, pl. 14 fig. 5 (Peru, [Dept. Cajamarca] Bergurwald der Hacienda Taulis, 1700 m) [HT SMF 108567].
- similaris*, *Bulimus*, J. Moricand, 1856: 177, pl. 6 fig. 8 ([Peru] Moyobamba).
- solii*, *Drymaeus* (*Drymaeus*), Haas, 1952: 108, fig. 14 (Brazil, Pará, Cacaual Grande, Furo Piapó) [HT FMNH 38170].
- smithii*, *Bulimulus* (*Drymaeus*), Da Costa, 1898: 81, pl. 6 fig. 8 ([Colombia] Bogota) [LT BMNH 1907.11.21.52].
- solidus*, *Bulimulus* (*Drymaeus*), Preston, 1907: 494, fig. 9 (Colombia, Bogota) [ST BMNH].
- sophieae**, *Drymaeus* (***Drymaeus***). New name for *Drymaeus* (*Drymaeus*) *pergracilis* Haas, 1952, not *Bulimulus pergracilis* Rolle, 1905 [secondary homonymy].
- souzalopesi*, *Drymaeus* (*Drymaeus*), Weyrauch, 1965: 74, figs. 4-5 (Brasil, Estado de Goyaz, Planaltina Nova) [HT IML 10622a].
- spadiceus*, *Drymaeus*, Da Costa, 1906b: 97, pl. 11 figs. 2-3 ([Colombia] Bogota) [HT BMNH 1907.11.21.15].
- spectatus*, *Bulimus*, Reeve, 1849: pl. 81 fig. 601a (New Granada) [LT BMNH 1874.12.11.226].
- sporadicus*, *Bulimus*, Reeve, 1848: pl. 49 fig. 325 (Bolivia, [Argentina] Patagonia [sic]).
- steyermarki*, *Plecocheilus* (*Eurytus*), Haas, 1955a: 377, fig. 79 (Venezuela, State of Bolívar, northwest part of Chimantá-massif, plateau below Apacará-tepui, 1800 m) [FMNH 49735].
- stolli*, *Otostomus ghiesbreghtii*, Martens, 1893: 209, pl. 13 figs. 5-10 (Central Guatemala, Llano of Quezaltenango, 6000 to 9000 feet).
- strigatus*, *Bulimus*, Reeve, 1848: pl. 44 fig. 280 ([Peru] Huallaga).
- strigatus*, *Bulimus*, Sowerby, 1833a: figs. 95-96 (Peru, Huallaga).
- subeffusus*, *Bulimus*, Philippi, 1869: 36 (in nemoribus Peruviae de Huancayo dictis, loco Coyllorbamba).
- subhybridus*, *Gonyostomus*, Da Costa, 1906b: 97, pl. 9 fig. 1 (Eastern Peru, Pozuzo) [HT BMNH 1907.11.21.127].

- **subinterruptus*, *Bulimus*, Pfeiffer, 1853b: 256 (Bolivian Andes) [LT BMNH 1975470].
subprotractus, *Drymaeus expansus*, Pilsbry, 1901: 155, pl. 25 figs. 27-29 [Peru; teste
 Clench & Turner, 1962; LT ANSP 78127a].
- **subsemiclausus*, *Bulimus*, Petit, 1843a: 239 (Nouvelle Grenade) [ST MNHN].
subsularis, *Drymaeus*, Pilsbry, 1898: 222, pl. 44 figs. 15-16 (probably western Brazil or
 eastern Peru) [HT ANSP 25751].
subventricosus, *Drymaeus*, Da Costa, 1901: 239, pl. 24 fig. 4 ([Colombia] Bogota) [HT
 BMNH 1907.11.21.37].
succinea, *Drymaeus*, Pilsbry, 1901: 160, pl. 26 fig. 38 (Amazon River) [HT ANSP
 78180a].
sulcosus, *Bulimus*, Pfeiffer, 1841: 43 (Tacubaya, Mexico).
suprapunctatus, *Drymaeus limostoma*, F. Baker, 1914: 637, pl. 23 figs. 5-8 (280 km above
 Porto Velho, Brazil) [HT ANSP 109307a].
taeniatus, *Bulimus*, Philippi, 1869: 35 ([Peru, Dept. La Libertad] hacienda de Mariebal).
tigrinus, *Drymaeus*, Da Costa, 1898: 82, pl. 6 fig. 6 (Ecuador) [HT BMNH 1907.11.21.55].
tigris, *Bulinus*, Broderip in Broderip & Sowerby, 1832b: 107 (in Peruviae montibus,
 Truxillo).
translucidus, *Drymaeus (Drymaeus)*, Weyrauch, 1967a: 422, figs. 78-79 (Peru central,
 entre Tingo Maria y Pucallpa, Boquerón de Abad, 500 m) [HT IML 1202a].
tricinctus, *Drymaeus poecilus*, Parodiz, 1962: 442, pl. 2 fig. 11 (Bolivia) [HT USNM
 307436].
trivittatus, *Bulimus*, Mousson, 1873: 11 (Nördlichen Süd-Amerika).
trujillensis, *Bulimus*, Philippi, 1867: 73 ([Peru] prope Trujillo).
tusagasuganus, *Drymaeus*, Pilsbry, 1935: 85, pl. 6 fig. 14 (Colombia, Tusagasugá) [HT
 ANSP 164570].
undulosus, *Otostomus (Drymaeus) lilacinus*, Martens, 1893: 201 (W. Guatemala, Ha-
 cienda de las Nubes, Cerro Zunil).
vanattai, *Drymaeus expansus*, Pilsbry, 1898: 223, pl. 34 fig. 6 [no type locality given;
 HT ANSP 25762].
varians, *Bulinus*, Broderip in Broderip & Sowerby, 1832b: 107 (Americâ meridionali,
 Kings and Sabogo Islands, Bay of Panama).
varicosus, *Bulimus*, Pfeiffer, 1853b: 256 (Mexico) [LT BMNH 1975466].
ventricosa, *Drymaeus punctatus*, Da Costa, 1907: 304, pl. 26 figs. 3-3a (Peru, Chancha-
 mayo).
ventricosus, *Bulimulus (Drymaeus)*, Preston, 1907: 495, fig. 10 (Colombia, Bogota).
vespertinus, *Bulimus*, Pfeiffer, 1858: 257, pl. 42 fig. 3 (Peru, Province of Patas) [LT
 BMNH 1975471].
vexillum, *Helix*, Wood, 1828: pl. 8 fig. 78a [not seen].
**vicinus*, *Bulimulus (Drymaeus)*, Preston, 1907: 495, fig. 11 (Colombia, Bogota).
villavicencioensis, *Drymaeus*, Breure, 1977a: 269, figs. 23-24 (Colombia, Dept. Meta,
 Villavicencio) [HT SMF 245417].
violaceus, *Bulimus*, Mousson, 1873: 9 (Nördlichen Süd-Amerika).
vittata, *Helix (Cochlogena)*, 'Humboldt' Férussac, 1821: 54 [nomen nudum].
volsus, *Drymaeus*, Fulton, 1907: 153, pl. 10 fig. 2 (Ecuador) [HT BMNH 1907.5.3.162].
weeksi, *Drymaeus*, Pilsbry, 1926a: 8, pl. 2 fig. 4 (Peru) [HT ANSP 140302].
xanthostoma, *Helix*, d'Orbigny, 1835: 18 (provincia Yungacensi, republica Boliviana).
yungasensis, *Bulimus*, d'Orbigny, 1837: 316, pl. 40 fig. 8 ([Bolivia] dans les bois qui
 bordent le Rio de Meguilla, près de son confluent avec le Rio de la Paz).
zeledoni, *Bulimulus (Leptobyrsus)*, Dall, 1893c: 644, pl. 71 fig. 2 (Costa Rica, Zeledon)
 [HT USNM 98231].
zhorquinensis, *Bulimus*, Angas, 1879: 478, pl. 40 fig. 4 ([Costa Rica] Middle Zhorquin
 to Cuabre) [HT BMNH 1879.7.22.15].
ziczac, *Bulimulus (Drymaeus)*, Da Costa, 1898: 81, pl. 6 fig. 5 (Colombia, valley of the
 R. Cauca) [HT BMNH 1907.11.21.46].

zilchi, *Drymaeus* (*Drymaeus*), Haas, 1955b: 333, fig. 73 (Peru, Dept. Tumbes, Huasimo, 220 m) [HT FMNH 51927].
zoogeographicus, *Drymaeus*, Zischka, 1953: 82 [emendation for *zoographica* d'Orbigny].
zoographica, *Helix*, d'Orbigny, 1835: 19 (provincia Yungacensi, republica Boliviana).

Drymaeus (Mesembrinus) Albers, 1850

Mesembrinus Albers, 1850: 157. Type species by subsequent designation (Albers, 1860): *Helix virgulata* Férussac.
Antidrymaeus Germain, 1907: 59. Type species by subsequent designation (Pilsbry, 1926b): *Bulimulus* (*Drymaeus*) *inusitatus* Fulton.
Leptodrymaeus Pilsbry, 1946a: 23. Type species by original designation: *Bulimus dominicus* Reeve.
Leptomormus Weyrauch, 1958: 136. Type species by original designation: *Drymaeus bequaerti* Weyrauch.
Diaphanomormus Weyrauch, 1964: 57. Type species by original designation: *Drymaeus* (*Diaphanomormus*) *coelestini obesus* Weyrauch.

Description. — Shell elongate-ovate to ovate; narrowly perforate to rimate; thin to rather solid. Colour whitish to yellowish, uniformly coloured or with brownish spiral bands or brownish axial streaks (that may be divided into series of spots). Surface smooth or with incassate growth striae and/or fine spiral lines. Aperture elongate- to subovate. Peristome thin and simple (to expanded).

Mandibula with more than 20 plates, which are ca. 8 times as long as wide. Transverse rows of the radula are V- to W-shaped. Central teeth tricuspid, with lanceolate mesocones and but slightly smaller triangular to lanceolate ectocones. Lateromarginal teeth tricuspid, shifted, with elongate-ovate to lanceolate mesocones, curved lanceolate endocones and triangular to deltoid ectocones that may be bifid or serrate. Half-row formula: C/3 + LM x/3 (x = 56-146).

Penis with or without a proximal sheath, subcylindrical and passing without external differentiation into the epiphallus. The flagellum is subcylindrical and (usually) relatively short. Vagina relatively long. Spermathecal duct tapering, with a more or less globose spermatheca or reduced in length, in which case the spermatheca may be undifferentiated.

Distribution. — Venezuela, Guiana, Surinam, French Guyana, Brazil, Peru, Colombia, Panama, Costa Rica, Nicaragua, El Salvador, Honduras, Guatemala, Belize, Mexico, USA, West Indies.

Ecology. — The species live on trees and shrubs. The vertical distribution is 0-ca. 1000 m.

Taxa. — The following taxa are placed in this subgenus (taxa tentatively referred to this subgenus are marked by an asterisk):

albescens, *Bulimulus aureolus*, Guppy, 1871: 308 [no type locality given; Trinidad].
albicans, *Bulimulus multifasciatus*, Mazé 1874: 163 ([West Indies, Martinique] Saint Pierre, hauteurs du Parnasse, 200 mètres environs).

- albida*, *Bulimulus dormani*, Wright, 1890: 61 (Florida).
- albostrigatus*, *Bulimulus*, Strebel in Strebel & Pfeiffer, 1882: 94, pl. 6 fig. 3 ([Mexico] Tehuantepec).
- altenai*, *Drymaeus*, Breure, 1976d: 112 (Surinam, near Lucie River) [HT ZMA].
- alternans*, *Bulimus* (*Bulimulus*), Beck, 1837: 65 (I. Saboga ad Panamam).
- alternatus*, *Bulimus*, Forbes, 1850: 54 [nomen nudum].
- amandus*, *Bulimus*, Pfeiffer, 1855g: 96, pl. 31 fig. 4 (Venezuela) [LT BMNH 1975457].
- amoenus*, *Bulimus*, Pfeiffer, 1847d: 82 [no type locality given].
- *anceps*, *Bulimus*, Albers, 1854b: 217 (Columbia [sic, Peru] ad fluvium Maranhon) [ST ZMB].
- andicola*, *Bulimus*, Pfeiffer, 1847a: 115 (Andes of Bolivia) [LT BMNH 1975315].
- angasi*, *Otostomus*, Martens, 1893: 207 (NE Costa Rica, La Paz on the road to the Río Sarapiquí).
- anguillensis*, *Bulimus*, Pfeiffer, 1865: 123 ([West Indies] insula Anguilla).
- annulatus*, *Bulimus*, Reeve, 1849: pl. 81 fig. 599 (Andes of Bolivia).
- apicepunctata*, *Bulimulus*, Preston, 1914: 523 (E. Peru, Santa Rita) [HT BMNH 1915.1.6.23].
- apiculatus*, *Bulimus*, J. E. Gray, 1834: 66 [no type locality given].
- aureolus*, *Bulimus*, Guppy, 1866a: 49 (Trinidad, Savana Grande) [ST BMNH].
- aurifluus*, *Bulimus*, Pfeiffer, 1857a: 319, pl. 35 fig. 10 (Cordova, Veracruz, Mexico).
- bahamensis*, *Bulimus*, Pfeiffer, 1862b: 204 (New Providence, insularum Bahamensium).
- bahamensis*, *Bulimulus*, Bland, 1875b: 199 ([Hispaniola] Port au Prince, Fort Jaques).
- beattyi*, *Drymaeus elongatus*, Clench, 1951a: 273, figs. 4-6 (Mona Island, Puerto Rico, West Indies) [HT MCZ 171032].
- bequaerti*, *Drymaeus*, Weyrauch, 1956a: 154, pl. 11 figs. 12-14 (M-Peru, rechten Seite des Río Monzon, 670 m, nahe seinem Zusammenfluß mit dem Río Huallaga, unweit ... Tingo Maria) [HT SMF 155309].
- binominis*, *Bulimulus*, Guppy, 1868a: 436 ([West Indies] Grenada).
- bolivianus*, *Bulimus*, Reeve, 1848: pl. 44 fig. 281 (Andes of Bolivia).
- borealis*, *Otostomus uhdeanus*, Martens, 1893: 233, pl. 15 figs. 1-6 (NW Mexico, Ventanas, State of Durango, 2000 feet) [ST ZMB].
- *borellii*, *Bulimulus*, Ancey, 1897: 13, figs. 8-9 (Bolivia, haut-Pilcomayo).
- bourgeoisae*, *Drymaeus*, Rehder, 1943: 28, pl. 6 fig. 10 (Mexico, Vera Cruz, near Cordoba, Paraje Nuevo) [HT USNM 517550].
- broadwayi*, *Bulimulus* (*Drymaeus*), E. A. Smith, 1896: 243, pl. 8 fig. 9 ([West Indies] Trinidad) [HT BMNH 1895.11.28.10].
- bugabensis*, *Otostomus*, Martens, 1893: 218, pl. 13 figs. 21-21a (Panama, Depto. Chiriqui, Bugaba) [LT BMNH 1901.6.22.958].
- cactivorius*, *Bulinus*, Broderip in Broderip & Sowerby, 1832a: 31 (ad montem Chris in Columbia).
- californicus*, *Bulimus*, Reeve, 1848: pl. 56 fig. 378 (California).
- cancellata*, *Drymaeus prestoni*, Da Costa, 1906a: 9, pl. 1 fig. 10 (Panama, Chiriqui) [HT BMNH 1907.11.21.13].
- carabaeorum*, *Bulimus*, Lamarck, 1822: 124 (les Antilles).
- carnea*, *Bulimulus virgulatus*, Mörch, 1852: 23 [nomen nudum].
- castrensis*, *Bulimus*, Pfeiffer, 1847a: 115 [no type locality given].
- castus*, *Bulimus*, Pfeiffer, 1847a: 112 (Central America?) [LT BMNH 1975197].
- cerussatus*, *Bulimus*, Reeve, 1849: pl. 74 fig. 536, text fig. 537 [no type locality given].
- chevallieri*, *Drymaeus*, Breure, 1976d: 113, figs. 5-9 (French Guyana, Saint Hermine, Maroni) [HT MNHN].
- christopheri*, *Drymaeus multifasciatus*, Pilsbry, 1899: 16, pl. 13 figs. 98-99 ([West Indies] St. Christopher [St. Kitts]) [HT ANSP 25857a].
- citronellus*, *Bulimus*, Angas, 1879: 479, pl. 40 fig. 5 (Uren to Lipurio, Costa Rica) [LT BMNH 1879.7.22.19].

- clarissimus*, *Drymaeus dominicus*, Pilsbry, 1946a: 25, fig. 14f (Florida, [Everglades Nat. Park] Royal Palm Park) [LT ANSP 166283a].
- coelestini*, *Drymaeus (Drymaeus)*, Haas, 1952: 121, fig. 22 (Peru, Dept. Cuzco, Prov. Quispicanchi, Huayumbe, 630 m) [HT FMNH 38125].
- columbianus*, *Bulimus*, Lea, 1838: 66, pl. 23 fig. 110 (about one hundred miles up the Magdalena River, Colombia) [LT ANSP 192932].
- columbiensis*, *Bulimus*, Pfeiffer, 1855b: 124 (Columbia) [LT BMNH 1975521].
- combinai*, *Mesembrinus (Ornatimormus)*, Weyrauch, 1958: 135, pl. 8 fig. 16 (M-Peru, Quimiri Sur, Valle de Chanchamayo, zwischen . . . La Merced und San Ramón, 1300 m) [HT SMF 156201].
- coniformus*, *Bulimus*, Pfeiffer, 1847a: 114 (Merida, Andes of Bolivia [sic, Venezuela]).
- conus*, *Drymaeus*, Pilsbry, 1902a: lxxi (New name for *Bulimus coniformis* Pfeiffer, 1847, not Bruguière, 1789).
- cozumelensis*, *Drymaeus shattucki*, Richards, 1936: 253, pl. 4 fig. 4 ([Mexico] Cozumel, San Miguel to Santa Rita) [HT ANSP 167744].
- cuernavacensis*, *Bulimulus (Scutalus)*, Fischer & Crosse, 1874: 283, pl. 23 fig. 11 (Cuernavaca, Mexique).
- curianianus*, *Bulimus*, Reeve, 1849: pl. 58 fig. 390 (Curiana, Venezuela).
- debilis*, *Bulimulus*, Beck, 1837: 65 [indication].
- decoloratus*, *Bulimus*, Sowerby, 1833b: 73 (prope Lima, Peruviae).
- deletus*, *Drymaeus droueti*, Solem, 1955: 13, pl. 1 fig. 12 (Mexico, Sumidero) [HT UMMZ 181389].
- demotus*, *Bulimus*, Reeve, 1850a: xi [New name for *Bulimus feriatus* Reeve, 1848 (Nov.), not Reeve, 1848 (Dec.)].
- depictus*, *Bulimus*, Reeve, 1849: pl. 74 fig. 529 (New Granada) [LT BMNH 1975529].
- deshayesi*, *Bulimus*, Pfeiffer, 1845b: 73 [no type locality given; LT BMNH 1975526].
- discrepans*, *Bulimus*, Sowerby, 1833b: 72 (America Centrali).
- dominicanus*, *Drymaeus virginalis*, Pilsbry, 1899: 12, pl. 12 fig. 24 ([West Indies] Dominica) [LT ANSP 25853a].
- dominicus*, *Bulimus*, Reeve, 1850: pl. 88 fig. 659 (St. Domingo [West Indies]).
- dormani*, *Bulimus*, Binney, 1857: 188 (in peninsula Florida, prope St. Augustine).
- droueti*, *Bulimus*, Pfeiffer, 1857a: 319, pl. 35 fig. 12 (Cordova, Veracruz, Mexico).
- dubius*, *Bulimus*, Pfeiffer, 1853b: 257 (Andes of New Granada) [LT BMNH 1975519].
- dutaillyi*, *Bulimus*, Pfeiffer, 1857c: 390 (Brazil) [LT BMNH 1975516].
- eboreus*, *Drymaeus multilineatus*, Grimshawe, 1951: 34, pl. 2 fig. 6 (NE end of Little Pine Key, Monroe County, Florida).
- **electrum*, *Bulimus*, Reeve, 1848: pl. 56 fig. 373 (Venezuela) [LT BMNH 1975510].
- elongata*, *Helix*, Röding, 1798: 107 [indication].
- elongatulus*, *Drymaeus nigrofasciatus*, Pilsbry, 1898: 307, pl. 50 fig. 100 [no type locality given; HT ANSP 4346a].
- emeus*, *Bulimus*, Say, 1829: 26 [Road from Veracruz to Mexico City; teste Solem, 1955].
- erubescens*, *Bulimus*, Pfeiffer, 1847a: 112 (Jamaica) [LT BMNH 1975562].
- eurystomus*, *Bulimus*, Philippi, 1867: 68 ([Peru] Chanchamayo).
- exalbidus*, *Bulimulus fluctuatus*, Beck, 1837: 66 [nomen nudum].
- extinctus*, *Bulimus*, Pfeiffer, 1855d: 103, pl. 4 figs. 9-10 ([West Indies] insulae St. Croix).
- extraneus*, *Bulimulus (Lissoacme)*, Haas, 1955a: 382, fig. 82 (Venezuela, summit of Apacará-tepui, NW part of Chimantá-massif, State of Bolívar, 2100 m) [HT FMNH 49736].
- fasciarum*, *Drymaeus*, Pilsbry, 1939: 5, fig. 9 (Colombia, Cúcuta) [HT ANSP 168429a].
- fasciata*, *Bulimulus stramineus*, E. A. Smith, 1895: 305, pl. 21 fig. 9 ([West Indies] St. Vincent Island).
- fasciatus*, *Bulimulus aureolus*, Guppy, 1871: 308 [no type locality given; Trinidad].
- feriatus*, *Bulimus*, Reeve, 1848: pl. 54 fig. 354 (Venezuela) [LT BMNH 1975504].

- fidustus*, *Bulimus*, Reeve, 1849: pl. 76 fig. 557 (New Granada, Sebundoi) [LT BMNH 1975517].
- flavescens*, *Helix liliacea*, Férussac, 1821: 54 (les Antilles, Porto Rico).
- flavidulus*, *Bulimus (Liostracus)*, E. A. Smith, 1877b: 364, pl. 39 fig. 3 (South Ecuador, Zarama) [LT BMNH 1975134].
- flavidus*, *Bulimus*, Menke, 1829: 6 [not seen].
- flavotinctus*, *Drymaeus vincentinus*, Pilsbry, 1899: 18, pl. 12 fig. 11 ([West Indies] Trinidad) [HT ANSP 25859].
- floridanus*, *Bulimus*, Pfeiffer, 1857a: 330 (Florida) [LT BMNH 1975199].
- floridianus*, *Bulimus*, Binney, 1859: 134 (Florida).
- fluctuatus*, *Bulimulus*, Beck, 1837: 66 [indication].
- **funeralis*, *Bulimus*, Bruguère, 1789: 321 (l'intérieur de l'Amérique méridionale).
- fuscobasis*, *Bulimus (Liostracus)*, E. A. Smith, 1877b: 365, pl. 39 fig. 6 (Andes of Peru, Tarapoto) [LT BMNH 1975139].
- gabbi*, *Bulimus*, Angas, 1879: 477, pl. 40 fig. 3 ([Costa Rica] Pico Blanco, 3000-6000 ft) [LT BMNH 1879.7.22.23].
- gabbianus*, *Bulimulus*, Binney, 1884: 124, pl. 12 fig. F (Costa Rica).
- gereti*, *Drymaeus*, Ancey, 1901a: 93 ([Brazil] Prov. de Goyaz).
- gorgonensis*, *Drymaeus*, Haas, 1966: 233, fig. 49 (Colombia, Cauca, Island of Gorgona) [HT FMNH 114164].
- gracilior*, *Otostomus (Drymaeus) sulfureus*, Martens, 1893: 225 (Guatemala, Nicaragua).
- gratus*, *Bulimus (Mesembrinus)*, Pfeiffer, 1856a: 159 [New name for *Bulimus columbiensis* Pfeiffer, 1855, not Lea, 1838].
- grenadensis*, *Bulimus*, Pfeiffer, 1848a: 231 [no type locality given].
- griffini*, *Drymaeus (Drymaeus)*, Haas, 1955a: 383, fig. 83 (Venezuela, western side of Abacapa-tepui, Chimantá-massif, State of Bolívar, 1300 m) [HT FMNH 49734].
- gruneri*, *Bulimus*, Pfeiffer, 1846a: 30 (Mexico).
- guttulatus*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- hachensis*, *Bulimus*, Reeve, 1850a: pl. 85 fig. 627 (Guatemala, banks of the Rio Hacha) [LT BMNH 1975392].
- haitensis*, *Drymaeus sallei*, Pilsbry, 1899: 12, pl. 39 fig. 4 (Haiti, Port-au-Prince, Fort Jacques) [LT ANSP 3552].
- havanensis*, *Drymaeus multilineatus*, Jaume & Borro, 1941: 404 (Cuba, provincia de la Habana, cerca de San Francisco de Paula, Reparto "Diezmero").
- hegewischi*, *Bulimus*, Pfeiffer, 1842: 46 (Mexico, Michoacan, Parquaro).
- hemphilli*, *Bulimulus*, Wright, 1889: 8 [indication].
- herrerae*, *Drymaeus*, Bartsch, 1907: 119 (Bonanza Zimapan, Hidalgo, Mexico) [HT USNM 192992].
- heterogeneous*, *Bulimus*, Pfeiffer, 1866b: 83 ([Mexico] in regione "savannarum" prope Veracruz).
- heyнемanni*, *Bulimus*, Pfeiffer, 1866b: 83 (Mexico, Orizaba).
- hjalmarsoni*, *Bulimus*, Pfeiffer, 1856b: 51 (in insula Portorico, plantatione "Pajas" prope Manati).
- hoffmanni*, *Otostomus tripictus*, Martens, 1893: 225, pl. 14 figs. 11-11a (Central Costa Rica, woods of San Lorenzo de Bota, 1300 m).
- honduranus*, *Otostomus*, Martens, 1893: 232 (Honduras).
- hondurasanus*, *Bulimus*, Pfeiffer, 1846a: 29 (Honduras) [LT BMNH 1975265].
- honduratanus*, *Bulimus*, Tristram, 1861: 230 (Guatemala).
- hyalinoalbida*, *Bulimulus (Drymaeus) moricandi*, Crosse & Fischer, 1875 [1870-1894]: 497, pl. 24 figs. 9-9a (in provincia Chiapas, reipublicae Mexicanae).
- hypozonus*, *Otostomus (Drymaeus) palpaloensis*, Martens, 1893: 223 (East Mexico [several localities mentioned]).
- ictericus*, *Otostomus depictus*, Martens, 1873: 183, pl. 1 figs. 16-17 ([Venezuela] Caracas).

- immaculatus*, *Bulimus*, C. B. Adams in Reeve, 1850: pl. 85 fig. 631 (Jamaica) [LT BMNH 1975540].
- imperfectus*, *Bulimus multifasciatus*, Guppy, 1866a: 49 (southern parts of the island of Trinidad).
- incarnatus*, *Bulimus*, Pfeiffer, 1855g: 95 (Venezuela) [LT BMNH 1975566].
- indistinctus*, *Bulimulus*, Guppy, 1868a: 436 [West Indies, Grenada].
- indistinctus*, *Bulimus*, Pfeiffer, 1852a: 63 [New name for *Bulimus monilifer* Reeve, 1848, not *Bulimus moniliferus* Gould, 1846].
- inglorius*, *Bulimus*, Reeve, 1848: pl. 55 fig. 368 [no type locality given; LT BMNH 1975536].
- insulaecygni*, *Drymaeus*, Clapp, 1914: 98, pl. 6 fig. 5 ([West Indies] Swan Island) [HT MCZ 22877].
- interpunctus*, *Bulimulus*, Martens, 1887: 161 (Piracicaba, São Paulo, Brasilien) [HT ZMB 38952].
- interruptofasciatus*, *Drymaeus*, Vernhout, 1914a: 11, pl. 1 figs. 5-6 (Surinam, environs of Paramaribo) [HT RMNH].
- interruptus*, *Bulimulus* (*Drymaeus*), Preston, 1909: 511, pl. 10 fig. 1 (Venezuela, Merida) [HT BMNH 1914.4.3.38].
- interstitialis*, *Otostomus ghiesbreghti*, Martens, 1893: 209, pl. 13 figs. 5-10 (C. Guatemala, Cumbre de San Martin, on the SW slope of the Cordillera, 6000 feet).
- intrapictus*, *Drymaeus*, Pilsbry, 1930b: 341, pl. 30 fig. 8 (Panama, Los Santos Prov., Tonosi) [HT ANSP 140834].
- inuitatus*, *Bulimulus* (*Drymaeus*), Fulton, 1900: 87 (Costa Rica) [HT BMNH 1901.4.25.28].
- irazuensis*, *Bulimus*, Angas, 1878a: 73, pl. 5 figs. 17-20 (volcano of Irazu, Costa Rica; Mexico).
- jonasi*, *Bulimus*, Pfeiffer in Philippi, 1847: 125, pl. 5 fig. 4 (Americae centralis, Vera Cruz) [ST BMNH].
- juquilensis*, *Drymaeus alternans*, 'Martens' Pilsbry, 1899: 88, pl. 15 fig. 40 (S. Mexico, State of Oaxaca, Juquila).
- kaemmereri*, *Bulimus*, Mörch, 1852: 23 [nomen nudum].
- keppelli*, *Bulimus*, Pfeiffer, 1853d: 654 (in *Andibus Peruvianus*).
- knorri*, *Bulimus*, Pfeiffer in Philippi, 1846: 115, pl. 4 fig. 3 (La Guyana).
- koppeli*, *Bulimus*, Sowerby, 1892: 297, pl. 23 figs. 9-12 ([Colombia] Bogota) [LT BMNH 1907.11.21.133].
- lacteus*, *Bulimus*, Lea, 1838: 65, pl. 23 fig. 100 (about one hundred miles up the Magdalena River, Colombia) [LT ANSP 192930].
- laetus*, *Bulimus*, Reeve, 1849: pl. 83 fig. 616 (New Granada, Sebundoi) [LT BMNH 1975534].
- lascellesiana*, *Bulimulus* (*Drymaeus*) *binominis*, E. A. Smith, 1895: 316, pl. 21 fig. 14 ([West Indies] Grenada, 1000-2000 feet).
- laticinctus*, *Bulimulus*, Guppy, 1868a: 431 ([West Indies] Dominica).
- latizonatus*, *Drymaeus multilineatus*, Pilsbry, 1936: 69 (Florida, Lower Matecumbe Key) [LT ANSP 160880a].
- lentiginosus*, *Bulimus*, Philippi, 1869: 32 ([Peru] inter Cajamarca et Contumaza).
- leucomelas*, *Bulimus*, Albers, 1854b: 219 (Columbia [sic, Peru] ad fluvium Maranhon) [HT ZMB 101785].
- liliacea*, *Helix*, Férussac, 1821: 54 (les Antilles, Porto Rico).
- limpidus*, *Bulimus*, Drouët, 1859: 64, pl. 2 figs. 23-24 (Guyane française, Ilet-la-Mère).
- lineolatus*, *Bulimus*, Conrad, 1856: 32 (volcano of Cartago, Costa Rica).
- lineolatus*, *Otostomus reclusianus*, Martens, 1893: 213 (Central Costa Rica, San José).
- lirinus*, *Bulimus*, Morelet, 1851: 11 ([Guatemala] Petenensium San Luis) [ST BMNH].
- lituratus*, *Bulimulus fluctuatus*, Beck, 1837: 66 [indication].

- livescens*, *Bulimus*, Pfeiffer, 1842: 175 (Mexico).
- lividus*, *Bulimus*, Reeve, 1850: pl. 85 fig. 626 (Venezuela) [LT BMNH 1975208].
- loxanus*, *Otostomus*, Higgins, 1872: 685, pl. 56 figs. 2-2a ([Ecuador] Loxa) [LT BMNH 1975552].
- loxensis*, *Bulimus*, Pfeiffer, 1846c: 85 (El Catamajja prope Loxa reipublicae Aequatorius) [LT BMNH 1975553].
- lucidus*, *Bulimus*, Reeve, 1848: pl. 40 fig. 245 ([West Indies] St. Vincents) [ST BMNH].
- lusorius*, *Bulimus*, Pfeiffer, 1855c: 291 (Banks of Amazon, Brazils) [LT BMNH 1975543].
- lynchi*, *Drymaeus*, Parodiz, 1946b: 1, pl. 1 figs. 1-3 (Bolivia, Pozo de Vargas) [HT MACN 1344].
- maculatus*, *Bulimus*, Lea, 1838: 86, pl. 23 fig. 112 (near Carthagena [Colombia]).
- manupictus*, *Bulimus*, Reeve, 1848: pl. 55 fig. 369 (Andes of Columbia) [LT BMNH 1975522].
- marielinus*, *Bulimus*, Poey, 1851: 204 [Cuba, teste Pilsbry, 1899].
- martensianus*, *Drymaeus recluzianus*, Pilsbry, 1899: 56 (New name for *Otostomus recluzianus lineolatus* Martens, 1893, not *Bulimus lineolatus* Conrad, 1856).
- mayaorum*, *Drymaeus*, Rehder, 1966: 287, figs. 3-4 (Isla Mujeres, Quintana Roo, Mexico) [HT USNM 251656].
- membranaceus*, *Bulimus*, Philippi, 1846: 126, pl. 5 fig. 2 [no type locality given].
- membranaceus*, *Bulimus*, Reeve, 1849: pl. 75 fig. 544.
- membranaceus*, *Otostomus (Mormus)*, Martens, 1873: 186 (Venezuela, Caracas).
- menkei*, *Bulimus*, Gruner, 1841: 277, pl. 11 fig. 2 (Reipublicae Venezuela, prov. Orinoco).
- meridanus*, *Bulimus*, Pfeiffer, 1846a: 33 (Merida, Bolivian Andes [sic]) [ST BMNH].
- mexicanus*, *Bulimus*, Reeve, 1848: pl. 40 fig. 244 (Mexico).
- miliaris*, *Bulimus*, Philippi, 1867: 74 ([Peru, Dept. La Libertad] hacienda de Unigambal).
- mitochrous*, *Bulimus*, Albers, 1854b: 217 (Columbia [sic, Peru] ad fluvium Maranhon) [HT ZMB 101791].
- misellus*, *Drymaeus translucens*, Pilsbry, 1926b: 83, fig. 14b (Panama, Prov. Los Santos, Tonosi) [HT ANSP 140281a].
- modesta*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- monachus*, *Bulimus*, Pfeiffer, 1857a: 333 (Meobamba, Peru).
- monilifer*, *Bulimus*, Reeve, 1848: pl. 48 fig. 318 [no type locality given; LT BMNH 1975403].
- montagnei*, *Bulimus*, d'Orbigny, 1836: 286, pl. 32 figs. 5-7 ([Bolivia] principalmente à la côte de Petaca [= Dept. Santa Cruz, Prov. Florida, Cuevas Petacas, ca. 23 km E Samaipata]).
- montagnei*, *Bulimus*, Reeve, 1848: pl. 23 fig. 146 (Bolivia, Chilon) [not *montagnei* d'Orbigny].
- montaguae*, *Otostomus sargi*, Martens, 1893: 218 (C. Guatemala, valley of the Rio Montagua).
- montanus*, *Drymaeus roseatus*, Pilsbry, 1901: 161, pl. 48 fig. 51 (Colombia, western part of Santa Marta Mts., Las Pantidas).
- **morenoi*, *Bulimulus (Drymaeus)*, Preston, 1907: 494, fig. 7 (Argentina).
- moricandi*, *Bulimus*, Pfeiffer, 1847a: 113 (Mount Coban, C-America) [LT BMNH 1975212].
- moritinctus*, *Otostomus*, Martens, 1893: 228, pl. 14 figs. 9-10 (Mexico, State of Guerrero, Chilpancingo) [LT BMNH 1901.6.22.841].
- mossi*, *Bulimulus (Drymaeus)*, E. A. Smith, 1896: 243, pl. 8 fig. 8 ([West Indies] Trinidad).
- moussoni*, *Bulimus*, Pfeiffer, 1853a: 147 ([West Indies] St. Domingo) [LT BMNH 1975210].
- **muliebris*, *Bulimus*, Reeve, 1849: pl. 81 fig. 598 (New Granada).

- multifasciatus*, *Bulimus*, Lamarck, 1822: 123 (les Antilles).
- multilineatus*, *Bulimus*, Say, 1825: 120 [not seen].
- multispira*, *Drymaeus*, Da Costa, 1904: 1, pl. 1 fig. 4 (Bolivia, Chuco Chaca) [HT BMNH 1907.11.21.31].
- necaxanus*, *Drymaeus*, Solem, 1955: 14, pl. 1 fig. 9 (near Salto Grande, Necaxa, Puebla, Mexico) [HT UMMZ 181377].
- **niceforonis*, *Drymaeus*, Pilsbry, 1939: 4, figs. 3-4 (Colombia, Santa Librada) [LT ANSP 170697a].
- nigroapicatus*, *Bulimus*, Pfeiffer, 1857a: 333 (Bolivia, Rio Pampas).
- nigrofasciatus*, *Bulimus*, Pfeiffer in Philippi, 1846: 125, pl. 5 fig. 7 (Novae Granadae, vallis Magdalena) [ST BMNH].
- nitelinus*, *Bulimus*, Reeve, 1849: pl. 59 fig. 398 (Mexico).
- nitidulus*, *Bulimulus*, Beck, 1837: 67 [indication].
- nitidus*, *Bulinus*, Broderip in Broderip & Sowerby, 1832a: 31 (Peruvia) [ST BMNH].
- obesus*, *Drymaeus* (*Diaphanomormus*) *coelestini*, Weyrauch, 1964: 58, fig. 11 (Perú central, Boquerón de Abad, 550 m, vertiente oriental de la Cordillera Azul, en la carretera entre Tingo María y Pucallpa) [HT IML 1196a].
- obesus*, *Otostomus* (*Drymaeus*) *sulfureus*, Martens, 1893: 225, pl. 14 figs. 14-18 (E Mexico, Huatusco, in the State of Vera Cruz).
- occidentalis*, *Mormus*, Miller, 1879: 121, pl. 13 fig. 2 ([Ecuador] Guayaquil).
- oreades*, *Helix*, d'Orbigny, 1835: 11 (provincia Corrientes, republica Argentina).
- pachecensis*, *Drymaeus translucens*, Pilsbry, 1930b: 340, pl. 30 fig. 11 (Panama, Pearl Islands, Pacheca Island) [HT ANSP 151302].
- paeteli*, *Bulimus*, Albers, 1854a: 31 (insula Lobosad oram Peruviae septentrionalis) [HT ZMB 101792].
- paivanus*, *Bulimus*, Pfeiffer, 1866b: 81 (Vera Cruz, reipublicae Mexicanae).
- palpaloensis*, *Bulimulus*, Strebel in Strebel & Pfeiffer, 1882: 85, pl. 5 figs. 12a-c ([Mexico] Arroyo del Obispo, Rancho de Querrero).
- panamensis*, *Bulinus*, Broderip in Broderip & Sowerby, 1832b: 105 (Panamae).
- parvicignyi*, *Drymaeus*, Pilsbry, 1930a: 245, pl. 18 figs. 10-11 ([West Indies] Little Swan Island) [HT ANSP 150859a].
- parvus*, *Bulimus*, Lea, 1838: 84, pl. 23 fig. 96 (near Carthagenae [Colombia]).
- paucipunctus*, *Drymaeus acervatus*, Pilsbry, 1898: 255, pl. 51 fig. 14 (Brazil, ? Sao Paulo) [HT ANSP 71235].
- paziana*, *Helix*, d'Orbigny, 1835: 12 (provincia Sicasica, republica Boliviana).
- percomis*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- perductorum*, *Drymaeus*, Rehder, 1943: 29, pl. 6 figs. 6-9 (Las Grutas de Cacahuamilpa, Guerrero [Mexico]) [HT USNM 517552].
- pereirai*, *Drymaeus*, Parodiz, 1958: 1 (El Carmen, between Palmito and Santa Ana, on the railroad Corumbá-Santa Cruz, Prov. Chiquitos, Depto Santa Cruz, southeastern Bolivia) [HT MCZ 168843].
- pertristis*, *Drymaeus*, Pilsbry, 1898: 301 (New name for *Bulimus tristis* Pfeiffer, 1854, not Jay, 1839).
- pervariabilis*, *Bulimus*, Pfeiffer, 1853d: 337 (Novae Granadae) [LT BMNH 1975547].
- perversus*, *Drymaeus semimaculatus*, Pilsbry, 1926b: 84, fig. 15c (Panama, Prov. Panama, Garachino) [HT ANSP 140833].
- picturata*, *Helix*, Férussac, 1821: 54 [indication].
- **pilsbryi*, *Drymaeus*, Zetek, 1934: 93, pl. 13 fig. 1 (Panama Canal Zone, Gutun Lake, Barro Colorado Island).
- pinchoti*, *Drymaeus rufescens*, Pilsbry, 1930a: 252, pl. 18 figs. 13-24 ([West Indies] Old Providence Island, ½ mi inland from Southwest Bay) [HT ANSP 150852].
- pluviatilis*, *Bulimus*, Pfeiffer, 1862b: 153 (Costa Rica).
- pochutlensis*, *Bulimulus* (*Thaumastus*) *tryoni*, Fischer & Crosse in Crosse & Fischer, 1875 [1870-1894]: 565, pl. 24 figs. 3-3a (Pochutla, reipublicae Mexicanae).

- porrectus*, *Otostomus castus*, Martens, 1893: 206, pl. 12 figs. 16-21 [no type locality given].
- prestoni*, *Drymaeus*, Da Costa, 1906a: 9, pl. 1 fig. 9 (Panama, Chiriqui) [HT BMNH 1907.11.21.12].
- primula*, *Bulimus*, Reeve, 1848: pl. 57 fig. 385 (Merida, New Granada) [LT BMNH 1975478].
- proteus*, *Bulimus*, Guilding in Swainson, 1840: 335 [no type locality given].
- pseudobesus**, **Drymaeus (Mesembrinus)**. New name for *Drymaeus (Diaphanomormus) coelestini obesus* Weyrauch, 1964, not *Otostomus (Drymaeus) sulfureus obesus* Martens, 1893.
- pseudonyma*, *Drymaeus pazianus*, Pilsbry, 1898: 278, pl. 44 fig. 96 (New name for *Bulimus montagnei* Reeve, 1848, not d'Orbigny, 1836).
- puellaris*, *Bulimus*, Reeve, 1850: pl. 86 fig. 637 (Brazil) [LT BMNH 1975400].
- puncticulatus*, *Bulimus*, Pfeiffer, 1857c: 390 (Bolivia).
- purissimus*, *Drymaeus vincentinus*, Pilsbry, 1899: 18 ([West Indies] Trinidad) [LT ANSP 25861a].
- quadrifasciatus*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- quadrifasciatus*, *Drymaeus*, Vernhout, 1914a: 12, pl. 1 fig. 4 (Surinam, Jan Basi Gado) [HT RMNH].
- quincefasciatus*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- rawsoni*, *Bulimulus aureolus*, Guppy, 1871: 308, pl. 17 fig. 6 ([West Indies] Island of Tobago) [LT BMNH 1878.1.28.209].
- recluzianus*, *Bulimus*, Pfeiffer, 1847d: 82 [no type locality given].
- rectilinearis*, *Bulimus*, Pfeiffer, 1855g: 96, pl. 31 fig. 7 (Meobamba, Eastern Peru) [ST BMNH].
- rhodotrema*, *Bulimulus*, Martens, 1868: 463, pl. 101 figs. 10-11 (Costa Rica) [HT ZMB 14410].
- rosalbus*, *Drymaeus*, Pilsbry, 1932: 395, pl. 28 fig. 4 (Peru, Dept. San Martin, Rio Jelashte, E of Leymebamba, 4500 ft.) [HT ANSP 159897a].
- roseatus*, *Bulimus*, Reeve, 1848: pl. 54 fig. 353 (Venezuela) [LT BMNH 1975309].
- rubicunda*, *Bulimulus (Mesembrinus) virgulatus*, Albers, 1860: 214 [nomen nudum].
- rubra*, *Bulimus elongata*, Pfeiffer, 1859: 482 (Porto Rico, St. Thomas).
- rufescens*, *Bulimus*, J. E. Gray, 1825: 414 (Jamaica).
- rufolineatus*, *Bulimus*, Drouët, 1859: 61, pl. 1 figs. 10-11 (Guyane française, Ilet-la-Mère).
- sallei*, *Drymaeus*, Pilsbry, 1899: 11, pl. 12 fig. 15 ([West Indies] Santo Domingo [city] and Rancho Arriba [cf. Clench & Turner, 1962]) [HT ANSP 57002a].
- sargi*, *Bulimulus*, Crosse & Fischer, 1875: 52 (Guatemala, Tamaju).
- semifasciatus*, *Bulimus*, Mousson, 1869: 175 [no type locality given].
- semimaculatus*, *Drymaeus*, Pilsbry, 1898: 297 (New name for *Bulimus maculatus* Lea, 1838, not Bruguière, 1789).
- semipellucidus*, *Bulimus*, Tristram, 1861: 230, pl. 26 fig. 8 (Guatemala).
- serenus*, *Bulimus*, Philippi, 1867: 72 ([Peru, Dept. La Libertad] hacienda de Sunchabamba).
- serperastrus*, *Bulimus*, Say, 1829: 25 [between Veracruz and Mexico City; teste Solem, 1955].
- sexfasciatus*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- shattucki*, *Drymaeus*, Bequaert & Clench, 1931: 424 (Chichen Itzá, Yucatan [Mexico]) [HT MCZ 79396].
- signifer*, *Bulimus*, Pfeiffer, 1855f: 8 (Venezuela?) [LT BMNH 1975216].
- sisalensis*, *Bulimus*, Morelet, 1849: 9 (circa Sisalensem pagum Yucutaneorum [Mexico]) [LT BMNH 1893.2.4.1655].
- sororcula*, *Drymaeus translucens*, Pilsbry, 1926b: 83, fig. 14c (Panama, Taboga Island) [HT ANSP 45238a].

- sporlederi*, *Bulimus*, Pfeiffer, 1866: 83 ([Mexico] Mirador prope Veracruz).
- stigmaticus*, *Bulimus*, Philippi, 1867: 74 ([Peru, Dept. La Libertad] hacienda de Unigambal).
- stramineus*, *Bulimulus*, Guilding, 1824: 340 ([West Indies] Sti Vincentii).
- studerii*, *Bulimus*, Pfeiffer, 1847a: 112 (Venezuela, Merida) [LT BMNH 1975480].
- subfasciatus*, *Bulimulus dormani*, Cockerell, 1891: 18 [no type locality given].
- subfasciatus*, *Bulimulus fluctuatus*, Beck, 1837: 66 [nomen nudum].
- subfloccosus*, *Drymaeus translucens*, Pilsbry, 1899: 90, pl. 24 figs. 26-27 (Nicaragua and Honduras) [LT ANSP 25949a].
- subpellucidus*, *Bulimus (Liostracus)*, E. A. Smith, 1877b: 364, pl. 39 fig. 2 (Ecuador).
- subunicolor*, *Otostomus fenestrellus*, Martens, 1893: 215 [no type locality given].
- sulphureus*, *Bulimus*, Pfeiffer, 1857a: 318, pl. 35 fig. 11 ([Mexico] Cordova).
- surinamensis*, *Drymaeus*, Vernhout, 1914a: 13, pl. 1 fig. 3 (Surinam, Post Groningen) [HT RMNH].
- sykesi*, *Drymaeus*, Da Costa, 1906a: 7, pl. 1 fig. 1 ([Colombia] Bogota) [HT BMNH 1907.11.21.4].
- tenuilabris*, *Bulimus*, Pfeiffer, 1866a: 831 (Venezuela) [LT BMNH 1975338].
- tepecensis*, *Otostomus uhdeanus*, Martens, 1893: 233, pl. 15 figs. 1-6 (West Mexico, Tepic, State of Jalisco).
- tonosiensis*, *Drymaeus translucens*, Pilsbry, 1930b: 340 (Panama, Los Santos Prov., Tonosi) [HT ANSP 151288].
- tortugensis*, *Drymaeus bahamensis*, Pilsbry & Vanatta, 1928: 477, pl. 27 figs. 11-13 ([West Indies] Haiti, Tortuga Island) [HT ANSP 146700a].
- totonacus*, *Bulimulus*, Strebel in Strebel & Pfeiffer, 1882: 84, pl. 5 figs. 13-13a ([Mexico] Rancho de Quilate und Aguacaliente, Umgegend Misantla).
- translucens*, *Bulimus*, Broderip in Broderip & Sowerby, 1832a: 31 (in America meridionali, Kings and Saboga Islands, Bay of Panama).
- **tribalteatus*, *Bulimus*, Reeve, 1848: pl. 43 fig. 269 (Santa Fé di Bogota).
- tricingulatus*, *Bulimus*, Anton, 1839: 43 (Saboja Islands).
- tricolor*, *Bulimus knorri*, Schaufuss, 1881: 178 (Venezuela).
- trigonostomus*, *Bulimus*, Jonas, 1844: 36 (Provinciae Cumana, Reipublicae Venezuela).
- trimarianus*, *Otostomus*, Martens, 1893: 216, pl. 13 fig. 17 (Mexico, Tres Marias Islas) [LT BMNH 1901.6.22.950].
- trinitarius*, *Bulimulus (Drymaeus)*, E. A. Smith, 1896: 242, pl. 8 fig. 7 ([West Indies] Trinidad).
- tripictus*, *Bulimus*, Albers, 1857: 97 (Costa Rica).
- tristis*, *Bulimus*, Pfeiffer, 1855b: 124 (New Granada) [ST BMNH].
- tropicalis*, *Bulimus*, Morelet, 1849: 9 ([Mexico] ad plagam civitatis Campêche) [LT BMNH 1893.2.4.210].
- tryoni*, *Bulimulus (Thaumastus)*, Crosse & Fischer, 1875 [1870-1894]: 565 ([Mexico] provincia Tabasco; Papanla; Misantla; Oajaca; Cinaloa).
- uhdeanus*, *Bulimulus (Mesembrinus)*, Martens, 1864: 541 [no type locality given; ST ZMB].
- umbraticus*, *Bulimus*, Reeve, 1849: pl. 77 fig. 559 (Central America) [LT BMNH 1975184].
- undulatus*, *Bulimulus*, Guilding, 1828b: 169 ([West Indies] Sti Vincentii, radices montis "Bon Homme").
- unicolor*, *Otostomus lilacinus*, Martens, 1893: 192 (W. Guatemala).
- vencuelensis*, *Otostomus*, Martens, 1893: 224 (Mirador, Mexico).
- venosus*, *Bulimus*, Reeve, 1848: pl. 45 fig. 285 (Angostura, Banks of the Orinoco).
- veracruzensis*, *Drymaeus herrerae*, Bartsch, 1907: 119 (Cordova, Vera Cruz, Mexico) [HT USNM 192993].
- vernhouti*, *Drymaeus*, Breure, 1976d: 111, fig. 4 (New name for *Drymaeus quadrifasciatus* Vernhout, 1914, not *Bulimus quadrifasciatus* Angas, 1878).

- vexillum*, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 105 (Sinu Panamae, Kings and Saboga Id).
- vincentinus*, *Bulimus*, Pfeiffer, 1846a: 30 ([West Indies] St. Vincent) [LT BMNH 1975219].
- virginalis*, *Bulimus*, Pfeiffer, 1856b: 46 ([Venezuela] Caracas).
- virgo*, *Bulimus*, Lea, 1838: 84, pl. 23 fig. 97 (near Carthagena [Colombia]).
- virgulata*, *Helix*, Férussac, 1821: 54 [indication].
- waldoschmitti*, *Drymaeus*, Parodiz, 1962: 436, pl. 2 fig. 16 (Peru) [HT USNM 609317].
- wintlei*, *Drymaeus*, Finch, 1929: 275, figs. (Ecuador) [HT BMNH 1929.6.11.1].
- xantholeucus*, *Otostomus castus*, Martens, 1893: 206, pl. 12 figs. 16-21 (N. Guatemala, Saboma, valley of the river Polochic, 3800 feet).
- zieglerei*, *Bulimus*, Pfeiffer, 1847a: 113 [no type locality given].
- zieglerei*, *Bulimus*, Reeve, 1849: pl. 58 fig. 389 (Central America).

Sphaeroconcha Breure, 1978

Sphaeroconcha Breure, 1978b: 153. Type species by monotypy: *Bulimulus* (*Bulimulus*) *araozi* Weyrauch.

Description. — Shell globose; rimate; thin. Colour uniform brown. Surface with epidermal spiral striae. Protoconch pit-reticulate. Whorls rather convex; suture well impressed. Aperture subcircular, relatively large. Peristome slightly thickened, simple.

The central teeth of the radula are tricuspid, with very acute, conical to lanceolate mesocones and relatively small, acute, triangular ectocones. The lateromarginal teeth are bi- to multicuspid, with acute, elongate to lanceolate mesocones and 1-5 acute, triangular to deltoid ectocones. Half-row formula: $C/3 + LM \ x/2-6$ ($x = 53$).

Penis without a sheath, more or less subcylindrical.

Distribution. — Peru (Dept. Huánuco).

Ecology. — The species lives in tropical rain forest, possibly on leaves, at 500-700 m.

Relationships. — This genus is not closely related to any of the other bulimulid genera. It is characterized by the globose shell shape, the sculpture of the protoconch, the subcircular shape of the aperture, the absence of a penis sheath, the absence of parallel tubes in the penis and the structure of the radula.

The only known taxon is:

araozi, *Bulimulus* (*Bulimulus*), Weyrauch, 1956a: 149, pl. 11 fig. 8 (M-Peru, Tingo Maria, 670 m, auf der linken Seite des Río Huallaga) [HT SMF 155304].

Leiostracus Albers, 1850

Leiostracus Albers, 1850: 156. Type species by subsequent designation (Albers, 1860): *Bulimus vittatus* Spix.

Liostracus Mörch, 1852: 26 [emendation for *Leiostracus* Albers].

Description. — Shell ovate-conical; with straight sides; (narrowly) perforate; (rather) thin. Surface smooth or with epidermal spiral striae. Protoconch with axial wrinkles and/or fine spiral lines. Whorls nearly flat to slightly convex, last whorl more or less keeled; suture hardly impressed. Aperture oblique, sub- to elongate-ovate. Peristome narrowly expanded.

Distribution. — Guyana, Surinam, Brazil.

Key to the subgenera of *Leiostracus*

- a. Shell surface smooth; protoconch with fine spiral lines and occasionally some low axial wrinkles on upper part of whorl; lateral teeth of the radula bicuspid *Leiostracus (Leiostracus)*
- b. Shell surface mostly with epidermal spiral striae; protoconch with axial wrinkles and fine spiral lines; lateral teeth of the radula monocuspid *Leiostracus (Pseudoxychona)*

***Leiostracus (Leiostracus)* Albers, 1850**

Description. — Shell perforate; rather thin. Colour whitish to yellowish, uniformly coloured or with axial and/or spiral brownish bands. Surface smooth. Protoconch with fine spiral lines and occasionally some low axial wrinkles on the upper part of whorl. Aperture elongate-ovate. Peristome narrowly expanded.

The central teeth of the radula are monocuspid, relatively small, with blunt, elongate to triangular mesocones. Lateral teeth are bicuspid, with spatula-shaped to truncate mesocones and triangular to deltoid ectocones. The marginal teeth are tricuspid, shifted, with elongate mesocones, curved, elongate endocones and triangular ectocones. Half-row formula: $C/1 + L \ x/2 + M \ y/3$ ($x = 8, y = 17-29$).

The pericard is ca. $\frac{3}{4}$ the length of the nephridium, which is narrowly triangular. The main pulmonary vein is well developed, but not prominent, while the side veins are weakly developed. The adrectal ureter is closed over its entire length.

The penis is without a sheath, more or less subcylindrical and passing without external differentiation into the epiphallus. The flagellum is relatively short. The proximal part of the spermathecal duct is thick, with a spermathecal appendix; the distal part of the spermathecal duct is long and narrow. The spermatheca is (elongate-)globose.

Distribution. — Guyana, Surinam, Brazil (Bahia, Espírito Santo).

Ecology. — The species live on trees. The vertical distribution is 0-ca. 500 m.

Remarks. — Pilsbry (1899) was the first to restrict the name *Leiostracus*

to the Brazilian species. The anatomy shows, however, that Pilsbry's classification of *Leiostracus* as a subgenus of *Drymaeus* was incorrect.

Graptostracus Pilsbry, 1939, described as a subgenus of *Leiostracus*, is a non-bulimulid.

Relationships. — The phylogeny of *Leiostracus* is discussed on page 161ff. The nominate subgenus is characterized by the sculpture of the protoconch, the smooth surface and the structure of the radula.

Bibliography. — The main publications are: H. B. Baker, 1926; Breure, 1978b; Pilsbry, 1899.

Taxa. — The following taxa are included in this subgenus:

- angulosa*, *Helix* (*Cochlogena*), Férussac, 1821: 58 [nomen nudum].
candidus, *Bulimus*, M. E. Gray, 1874: 27, pl. 302 fig. 4 [nomen nudum].
caxoeirana, *Helix* (*Cochlogena*), S. Moricand, 1841: 59 ([Brazil] Caxoeira, dans la province de Bahia, et dans les bois de S. Gonzales).
cinnamomeolineata, *Helix* (*Cochlogena*), S. Moricand, 1841: 60, pl. 4 figs. 6-7 ([Brazil] province de Bahia).
clouei, *Bulimus*, Pfeiffer, 1857c: 390 (Brazil) [LT BMNH 1975491].
coxeirana, *Helix* (*Cochlogena*), S. Moricand, 1836: 433, pl. 2 figs. 7-11 ([Brazil] Caxoeira, dans la province de Bahia).
coxiramus, *Bulimus*, Potiez & Michaud, 1835: pl. 13 figs. 1-2 (le Brésil).
demerarensis, *Bulimus*, Pfeiffer, 1861a: 24 ([Guyana] Demerara) [LT BMNH 1975501].
dizona, *Helix* (*Cochlogena*) *coxeirana*, S. Moricand, 1836: 433 ([Brazil] Caxoeira, province de Bahia et dans les bois de S. Gonzales).
goniotropis, *Bulimulus*, Ancey, 1904a: 102 (Brazil, Espirito Santo) [ST IRSN].
jeffreysi, *Bulimus*, Pfeiffer, 1852b: 93 (Brasilia).
lineatus, *Bulimus*, Spix, 1827: pl. 7 fig. 6 ([Brazil] Bahiensis et Pernambucanae).
manoeli, *Helix* (*Cochlogena*), S. Moricand, 1841: pl. 4 figs. 4-5 ([Brazil] Bahia).
monozona, *Drymaeus obliquus*, Ancey, 1901a: 93 ([Brazil] Bahia).
nigrescens, *Helix* (*Cochlogena*) *coxeirana*, S. Moricand, 1836: 433 ([Brazil] Caxoeira, province de Bahia et dans les bois de S. Gonzales).
obliquus, *Bulimus*, Reeve, 1849: pl. 76 fig. 551 (Brazil) [LT BMNH 1975493].
omphalodes, *Bulimus*, Menke in Pfeiffer & Menke, 1846: 144 [no type locality given].
onager, *Bulimulus*, Beck, 1837: 64 [indication].
opalinus, *Bulinus*, Sowerby, 1833a: fig. 47.
perlucidus, *Bulimus*, Spix, 1827: pl. 7 fig. 2 (Brasilia).
poecilogramma, *Drymaeus obliquus*, Ancey, 1901a: 93 ([Brazil] Minas Geraes).
polygramma, *Helix* (*Cochlogena*), S. Moricand, 1836: 436, pl. 2 figs. 12-14 ([Brazil, Bahia] Caxoeira).
purpurascens, *Helix* (*Cochlogena*) *coxeirana*, S. Moricand, 1836: 433 ([Brazil] Caxoeira, province de Bahia et dans les bois de S. Gonzales).
ruthveni, *Drymaeus* (*Leiostracus*), H. B. Baker, 1926: 48 (British Guiana, near Dunoon).
sarcochilus, *Bulimus*, Pfeiffer, 1857b: 157 (Brasilia septentrionali) [LT BMNH 1975398].
subtuszonata, *Drymaeus onager*, Pilsbry, 1899: 95, pl. 14 fig. 17 (Brazil, Prov. Bahia).
trizona, *Helix* (*Cochlogena*) *coxeirana*, S. Moricand, 1836: 433 ([Brazil] Caxoeira, province de Bahia et dans les bois de S. Gonzales).
unicolor, *Helix* (*Cochlogena*) *coxeirana*, S. Moricand, 1836: 434 ([Brazil] province de Bahia, Caxoeira et les bois de S. Gonzales).

- unicolor*, *Helix* (*Cochlogena*) *vittata*, S. Moricand, 1836: 433 ([Brazil, Bahia] les forêts de Ilheos).
- viminea*, *Helix* (*Cochlogena*), S. Moricand, 1833: 540, pl. 1 fig. 5 (Brésil, province de Bahia) [ST ZMB].
- vitreus*, *Bulimus*, Spix, 1827: pl. 8 fig. 2 (Brasília).
- vittatozonata*, *Helix* (*Cochlogena*) *coxeirana*, S. Moricand, 1836: 433 ([Brazil, Bahia] les forêts de Ilheos).
- vittatozonata*, *Helix* (*Cochlogena*) *vittata*, S. Moricand, 1836: 432 ([Brazil, Bahia] les forêts de Ilheos).
- vittatus*, *Bulimus*, Spix, 1827: 7, pl. 7 fig. 4 ([Brazil] sylvis... Provinciarum Bahiensis et Pernambucanae).
- zebra*, *Bulimus*, Spix, 1827: pl. 7 fig. 5 ([Brazil] sylvis mediterraneis Provinciae Bahiensis).

Leiostracus (Pseudoxychona) Pilsbry, 1930

Pseudoxychona Pilsbry, 1930c: 356. Type species by original designation: *Oxychona spiritualis* Ihering.

Description. — Shell ovate-conical; with straight sides; narrowly perforate to rimate; rather thin. Colour yellowish to brownish, uniformly coloured or with darker spiral band(s). Surface with epidermal spiral striae. Protoconch with spiral lines and axial riblets, which are ca. three times as strong as the lines. Whorls hardly to slightly convex, the last whorl keeled; suture hardly impressed. Aperture oblique, truncate-ovate. Peristome hardly to narrowly expanded.

The central teeth of the radula are monocuspid, with deltoid to triangular mesocones of which the apex is acute and pointed. The lateral teeth are monocuspid, with acute and pointed, triangular mesocones. Marginal teeth tricuspid, shifted, with elongate mesocones, slightly curved endocones and triangular ectocones. Half-row formula: C/1 + L x/1 + M y/3 (x = 8, y = 16-18).

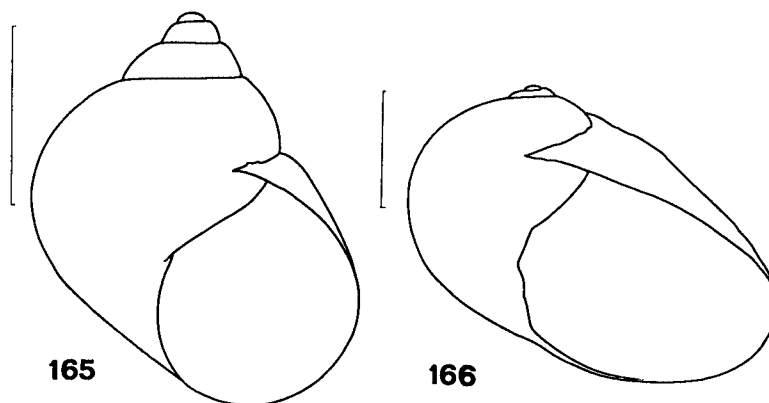
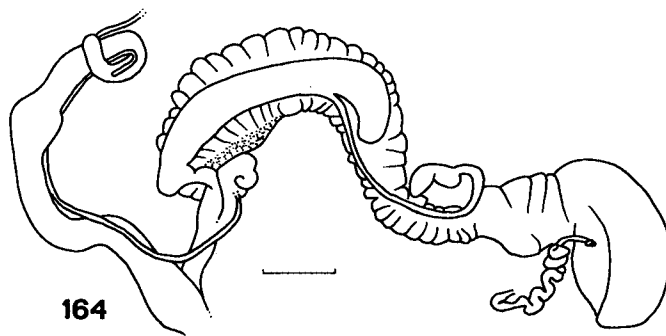
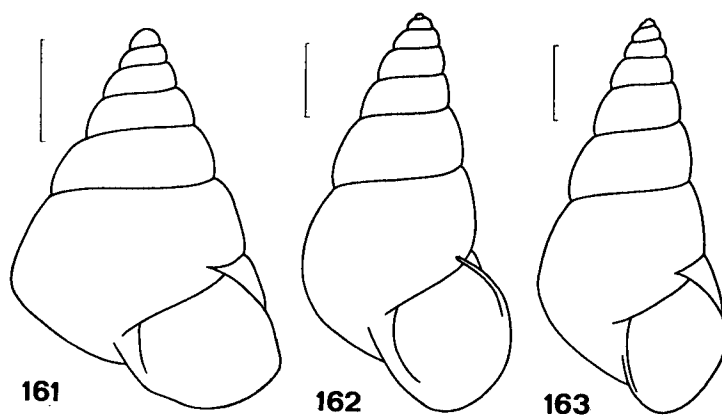
The pericardium is 1/2-4/5 the length of the nephridium, which is narrowly triangular. The main pulmonary vein is moderately, the side veins are weakly to moderately developed. The adrectal ureter is closed over its entire length.

Penis without a sheath, subcylindrical and slightly swollen at the transition to the epiphallus, which is ca. half as long as the penis. The flagellum is relatively very short. The vagina is rather long. The proximal part of the spermathecal duct is subcylindrical and rather thick, with an elongate spermathecal appendix; the distal part of the duct is narrow. The spermatheca is elongate-ovate.

Distribution. — Brazil (Bahia, Espírito Santo).

Ecology. — Unknown.

Remarks. — Zilch (1960) considered this taxon a subgenus of *Bulimulus*. The anatomy, however, demonstrates that this classification is incorrect and



Figs. 161-163. Variation in shell shape in *Leiostracus*. Fig. 161. *L. (Pseudoxychona)* spec. Fig. 162. *L. (L.) perlucidus* (Spix). Fig. 163. *L. (L.) onager* (Beck). Scale = 5 mm. Fig. 164. Genitalia of *Leiostracus (Pseudoxychona) spiritualis* (Ihering). After a drawing by courtesy of Dr. H. E. B. Rezende. Scale = 2 mm. Figs. 165-166. Variation in shell shape in *Simpulopsis*. Fig. 165. *S. (S.) decussata* Pfeiffer. Fig. 166. *S. (S.) atrovirens* (Moricand).

that *Pseudoxychona* is more properly placed with *Leiostracus*, *Rhinus* and *Simpulopsis*.

Relationships. — See page 161ff for a discussion of the phylogenetic relationships. The subgenus is characterized by the sculpture of the protoconch, the shape of the aperture and the structure of the radula.

Bibliography. — The main publications are: Ihering, 1912; Pilsbry, 1930c.

Taxa. — The following taxa are included in this subgenus:

dulcis, *Oxychona pileiformis*, Ihering, 1912: 485, pl. 42 fig. 14 [Brazil, Espirito Santo; teste Morretes, 1949].

pileiformis, *Helix*, S. Moricand, 1836: 420, pl. 2 fig. 2 ([Brazil, Bahia] Ilheos) [ST MHNG].

polytricha, *Oxychona*, Ihering, 1912: 486, pl. 42 figs. 16-18 ([Brazil] Espirito Santo, Cachoeira am Rio Doce) [HT DZSP].

spiritualis, *Oxychona*, Ihering, 1912: 485, fig. 1, pl. 41 figs. 10-13, pl. 42 fig. 15 ([Brazil] Espirito Santo, Cachoeira am Rio Doce) [HT DZSP].

Rhinus Albers, 1860

Rhinus Albers, 1860: 223. Type species by original designation: *Bulimus heterotrichus* Moricand.

Description. — Shell (elongate-)ovate to globose; perforate to rimate; rather thin to solid. Colour brownish to yellowish. Surface with slightly incrassate growth striae and spiral series of hairs. Protoconch with axial waved or zigzag wrinkles. Aperture (rounded) ovate. Peristome expanded and usually narrowly reflexed.

The central teeth of the radula are monocuspid, relatively small, with blunt elongate to triangular mesocones. Lateromarginal teeth are bi- to tricuspid, with blunt spatula-shaped mesocones, acute, curved elongate endocones and (rather) acute, ovate to triangular ectocones, which are posteriorly situated on the basal plate. Half-row formula: C/1 + LM x/2-3 (x = 32).

The pericard is slightly shorter than the nephridium, which is triangular and slightly curved. The pulmonary vein is rather prominent, but the side veins are weakly developed. The adrectal ureter is closed over its entire length.

The penis is without a sheath and club-shaped. The epiphallus is as long as and half as broad as the distal part of the penis, subcylindrical and slightly swollen towards the transition to the flagellum. The flagellum is short (ca. 1/3 the length of the epiphallus) and tapering towards the distal end. The vagina is very short. The proximal part of the spermathecal duct is half as broad as the median part, which has a spermathecal appendix. The distal part of the duct, which bears the ovoid spermatheca, is relatively narrow.

Distribution. — Venezuela, Brazil, ?Argentina.

Ecology. — Unknown.

Relationships. — The phylogenetic relationships of this genus are discussed on page 161ff. The genus is characterized by the shell shape, the spiral series

of hairs, the sculpture of the protoconch, the expanded peristome, the structure of the radula and the presence of a spermathecal appendix.

Bibliography. — The main publications on this genus are: Breure, 1978b; Pilsbry, 1897d.

Taxa. — The following taxa are included in this genus:

- angosturensis*, *Bulimus*, Gruner, 1841: 278, pl. 11 fig. 3 (republicae Venezuela, provincia Orinoco).
- argentinus*, *Bulimulus* (*Rhinus*), Ancey, 1901: 92 ([Argentina] province d'Entrerios, Gualaguaychu) [ST IRSN].
- ciliatus*, *Bulimus*, Gould, 1846b: 191 (Brazil, Organ Mountains).
- constrictus*, *Bulimus*, Pfeiffer, 1841: 43 (Angostura [Venezuela, Ciudad Bolívar]).
- heterogramma*, *Helix* (*Cochlogena*), S. Moricand, 1836: 437, pl. 2 figs. 15-17 ([Brazil, Bahia] Caxoeira).
- heterotricha*, *Helix* (*Cochlogena*), S. Moricand, 1836: 430, pl. 2 figs. 5-6 [no type locality given].
- hirtus*, *Bulimus*, Beck, 1837: 51 [indication].
- hyaloideus*, *Bulimus*, Pfeiffer, 1855c: 292 (Mendez, Andes of New Granada) [LT BMNH 1975412].
- koseritzi*, *Bulimus* (*Rhinus*), Clessin, 1888: 168 (Brasilien).
- longiseta*, *Helix* (*Bulimus*), S. Moricand, 1846: 156, pl. 5 figs. 18-20 ([Brazil] la province de Bahia).
- obeliscus*, *Bulimulus* (*Rhinus*), Haas, 1836: 150, figs. 15-16 (Brasilien, Staat Sta. Catharina) [HT SMF 10078].
- ovulum*, *Bulimus*, Reeve, 1849: pl. 46 fig. 556 (Philippine Islands [sic]) [LT BMNH 1975416].
- pubescens*, *Helix* (*Bulimus*), S. Moricand, 1846: 157, pl. 5 figs. 21-23 ([Brazil] les environs de Bahia).
- rochai*, *Bulimulus* (*Rhinus*), F. Baker, 1914: 636, pl. 23 figs. 19-20 ([Brazil] Jacoco, 7 km from Ceará-Mirim) [HT ANSP 109058].
- scobinata*, *Helix*, Wood, 1828: pl. 8 fig. 77 [publication not seen].
- subtenuis*, *Bulimulus heterotrichus*, Pilsbry, 1897d: 76, pl. 13 figs. 2, 25, pl. 15 fig. 19 [Brazil, teste Clench & Turner, 1962; LT ANSP 25658a].
- suturalis*, *Bulimulus* (*Rhinus*) *rochai*, F. Baker, 1914: 637, pl. 23 figs. 13-14 ([Brazil] Mongúba, Ceará & Baturité R.R., about 27 km from Ceará) [HT ANSP 109322a].
- taipuensis*, *Bulimulus* (*Rhinus*) *rochai*, F. Baker, 1914: 636, pl. 23 fig. 17 ([Brazil] fossil beds on the Central R.R., 46 km from Natal) [HT ANSP 109321].
- tateanus*, *Bulimus constrictus*, Guppy, 1875b: 322 (Venezuelan Guiana).
- thomei*, *Bulimulus* (*Rhinus*), Weyrauch, 1967b: 481, figs. 3-5 (Sureste de Brasil, estado Rio Grande do Sul, Livramento) [HT MRCN 1021a].
- velutinohispida*, *Helix* (*Cochlogena*), S. Moricand, 1836: 429, pl. 2 fig. 6 [no type locality given; ST MNHN].

Simpulopsis Beck, 1837

- Simpulopsis* Beck, 1837: 100. Type species by subsequent designation (Albers, 1860): *Helix sulculosa* Férussac.
- Simulopsis* Gray, 1847: 171 [emendation for *Simpulopsis* Beck].

Description. — Shell elongate-ovate to globose; narrowly perforate to imperforate; thin. Surface smooth or corrugate. Protoconch with fine spiral lines that more or less cut the low, oblique riblets or wrinkles into granules. Whorls slightly to moderately convex, the last whorl prominent; suture well

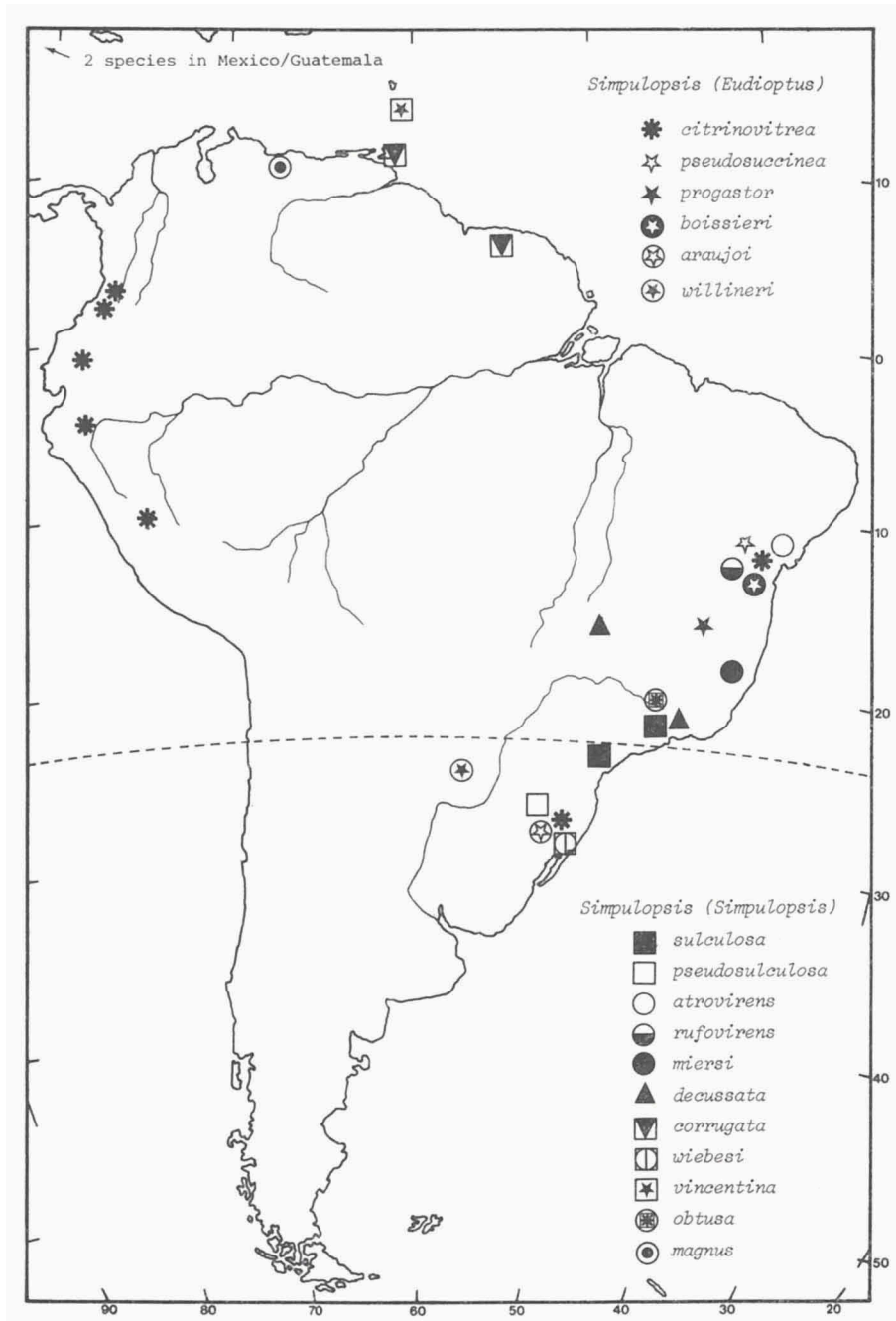


Fig. 167. Distribution of *Simpulopsis*.

impressed. Aperture (oblique) (elongate-)ovate. Peristome thin and simple.

The central teeth of the radula are (1) monocuspid, with blunt, elongate to triangular mesocones; (2) monocuspid, with rather blunt, spatula-shaped mesocones; or (3) tricuspid, with elongate to lanceolate mesocones and triangular ectocones. Lateral teeth are (1) tricuspid, with acute, spatula- to wedge-shaped mesocones, small triangular endocones and triangular to deltoid ectocones; or (2) bi- to tricuspid, with acute lanceolate mesocones, (small triangular endocones) and triangular to deltoid ectocones. Marginal (and lateromarginal) teeth are (1) tricuspid, with blunt, spatula-shaped mesocones, acute, curved elongate endocones and acute, ovate to triangular ectocones, which may be serrate in the outermost teeth; (2) tricuspid, shifted, with elongate mesocones, curved elongate endocones and triangular ectocones; or (3) bicuspid, with elongate mesocones and triangular, bifid ectocones. Half-row formulas: $C/1 + LM \ x/3$ ($x = 35-48$), $C/1 + L \ x/2-3 + M \ y/3$ ($x = 7-10$, $y = 24-31$), $C/3 + L \ x/3 + M \ y/3$ ($x = 10$, $y = ca. 20-28$) or $C/3 + LM \ x/2$ ($x = 24$).

The pericard is $1/2-4/5$ the length of the nephridium, which is broadly triangular to deltoid. The main pulmonary vein and the side veins are moderately to weakly developed. The adrectal ureter is closed over its entire length.

Penis without a sheath (in some species with a tunica), more or less swollen. The epiphallus is slender and subcylindrical, the flagellum is tapering or subcylindrical. The proximal part of the spermathecal duct is more or less subcylindrical and relatively thick, with a spermathecal appendix; the distal part of the duct is narrow; the spermatheca is (elongate-)globose.

Distribution. — Mexico, Guatemala, West Indies, Venezuela, Surinam, French Guyana, Brazil, Paraguay, Argentina, Peru, Ecuador, Colombia.

Remarks. — The division in subgenera is mainly based on the shell morphology; the structure of the radula and the morphology of the genitalia are remarkably variable and do not parallel the subgeneric division.

Relationships. — The phylogenetic relationships are discussed on page 161ff. The genus is characterized by the thin shell, the sculpture of the protoconch, the presence of a spermathecal appendix and the structure of the radula.

Bibliography. — The main publications on the genus are: Araujo, 1971, 1975; Araujo & Breure, 1977; Breure, 1975e, 1978b; Breure & Ploeger, 1977; Hylton Scott, 1967; Pilsbry, 1899; Van Mol, 1971.

Key to the subgenera of *Simpulopsis*

- a. Shell globose; surface more or less corrugate *Simpulopsis* (*Simpulopsis*)
- b. Shell elongate-ovate; surface smooth . . . *Simpulopsis* (*Eudioptus*)

Simpulopsis (Simpulopsis) Beck, 1837

Description. — Shell globose; rimate to imperforate; thin to fragile. Colour yellowish-green to olive-brown. Surface more or less corrugate, in some species with 'numerous revolving dull and lustreless bands about as broad as the glossy intervals'. Protoconch with closely set, oblique wrinkles crossed by spiral lines of about equal strength. Whorls slightly convex, the last whorl inflated. Aperture oblique, ovate to rounded.

Distribution. — Mexico, Guatemala, West Indies (St. Vincent, Trinidad), Venezuela, Surinam, French Guyana, Brazil.

Ecology. — The ecology of the species is not known, but presumably most species are living on trees. The vertical distribution is 0-ca. 1100 m.

Taxa. — The following taxa are included in this subgenus:

- aenea*, *Simpulopsis*, Pfeiffer, 1861a: 27 (Mexico, [Estado Oaxaca] La Parada) [ST BMNH].
- atrovirens*, *Helix* (*Cochlohydra*), S. Moricand, 1836: 416, pl. 2 fig. 1 ([Brazil] Portao).
- brasiliensis*, *Helix*, S. Moricand, 1836: 416 [nomen nudum].
- brasiliensis*, *Succinea*, S. Moricand, 1846: 160, pl. 5 fig. 5 ([Brazil] S. Gonzalves).
- corrugatus*, *Simpulopsis*, Guppy, 1866a: 53 ([West Indies] Trinidad) [ST BMNH].
- cumingi*, *Simpulopsis*, Pfeiffer, 1861a: 27, pl. 3 fig. 2 (Mexico) [ST BMNH].
- decussata*, *Simpulopsis*, Pfeiffer, 1856d: 260 ([Brazil] Petropolis prope Rio de Janeiro) [LT BMNH 1975488].
- magnus*, *Simpulopsis*, Thompson, 1957: 4, pl. 1 (Venezuela, Estado Aragua, Rancho Grande) [HT UMMZ 191736].
- membranacea*, *Succinea*, 'Michaud' Villa & Villa, 1841: 9 ([Brazil] Bahia).
- miersi*, *Simpulopsis*, Pfeiffer, 1856d: 260 ([Brazil] Esperito Santo) [LT BMNH 1975489].
- obtusa*, *Succinea*, Sowerby, 1821/1822 [1821-1834]: pl. *Succinea* fig. 2 [= *ovata*].
- ovata*, *Succinea*, Sowerby, 1821/1822 [1821-1834]: 2 (Brazil).
- pseudosulculosa*, *Simpulopsis* (*Simpulopsis*), Breure, 1975e: 101, figs. 2-3, 12 (Brazil, Santa Catarina, Nova Teutonia) [HT NRS 2503].
- rufescens*, *Simpulopsis*, 'Moricand' Adams & Adams, 1855: 128 [emendation for *rufovirens* Moricand].
- rufovirens*, *Helix* (*Succinea*), S. Moricand, 1846: 147, pl. 5 fig. 4 (Brésil, dans la province de Bahia) [PT MHNG].
- salomonina*, *Vitrina*, Pfeiffer, 1853c: 51 (insulis Salomonis) [LT BMNH 1975485].
- simulus*, *Bulimus*, Morelet, 1851: 11 (sylvis Petenensis [Guatemala, Dept. Petén]) [ST BMNH].
- sulculosa*, *Helix* (*Cochlohydra*), Férussac, 1821: 27 (Brésil) [ST MNHN].
- tryoni*, *Simpulopsis*, Pilsbry, 1899: 218, pl. 64 fig. 92 (Brazil) [HT ANSP 26033].
- vincentina*, *Simpulopsis*, E. A. Smith, 1895: 305, pl. 21 figs. 4-5 ([West Indies] St. Vincent, Upper Richmond Valley, 2000 feet) [HT BMNH 1895.6.17.458].
- wiebesi*, *Simpulopsis* (*Simpulopsis*), Breure, 1975e: 101, figs. 4-5, 10-11 (Brazil, Santa Catarina, Nova Teutonia) [HT NRS 2505].

Simpulopsis (Eudiptus) Albers, 1860

Eudiptus Albers, 1860: 223. Type species by original designation: *Helix pseudosuccinea* Moricand.

Bulimulopsis Pilsbry, 1899: 220. New name for *Eudioptus* Albers, 1860, not *Eudioptis* Hübner, 1816.

Bulimolopsis Parodiz, 1944c: 6 [error for *Bulimulopsis* Pilsbry].

Pseudoglandina Weyrauch, 1967b: 485. Type species by monotypy: *Pseudoglandina agitata* Weyrauch.

Paracochlea Hylton Scott, 1967a: 89. Type species by monotypy: *Bulimulus* (*Paracochlea*) *willineri* Hylton Scott. **New synonymy.**

Description. — Shell elongate-ovate; perforate to rimate; thin. Colour uniform yellowish to brownish. Surface smooth or with delicate spiral striae. Protoconch with spiral lines and (rather indistinct) axial wrinkles. Aperture sub- to elongate-ovate.

Distribution. — Brazil, Paraguay, Argentina (Prov. Jujuy), Peru, Ecuador, Colombia.

Ecology. — The species live in rain and cloud forests, on leaves. The vertical distribution is up to 1500 meters.

Remarks. — *Paracochlea* Hylton Scott is now considered a junior subjective synonym of *Eudioptus* Albers, on account of the shell shape and the structure of the radula.

Taxa. — The following taxa are included in this subgenus:

agitata, *Pseudoglandina*, Weyrauch, 1967b: 486, fig. 53 (Peru central, valle de Chanchamayo entre La Merced y San Ramón, 1100 m) [HT IML 1066].

araujoii, *Simpulopsis* (*Eudioptus*), Breure, 1975e: 108, figs. 8-9, 13-14 (Brazil, Santa Catarina, Nova Teutonia) [HT NRS 2371].

boissieri, *Helix* (*Bulimus*), S. Moricand, 1846: 156, pl. 5 figs. 24-25 ([Brazil] Bahia) [PT MHNG].

citrinovitrea, *Helix* (*Cochlogena*), S. Moricand, 1836: 436, pl. 2 fig. 19 ([Brazil] aux environs de Bahia [= Salvador]) [ST MNHN].

luteolus, *Bulimulus*, Ancey, 1901a: 82 ([Brazil] Goyaz) [ST IRSN].

moricandi, *Succinea*, Pfeiffer, 1842b: 131 [indication].

prokastor, *Helix*, d'Orbigny, 1835: 2 (Brasilianis oris [= Brazil, coastal area]).

pseudosuccinea, *Helix* (*Cochlogena*), S. Moricand, 1836: 435, pl. 2 fig. 18 ([Brazil] aux environs de Bahia [= Salvador]) [HT MHNG].

vitrinoides, *Bulimus*, Reeve, 1848: pl. 46 fig. 290 [no type locality given; ST BMNH].

willineri, *Bulimulus* (*Paracochlea*), Hylton Scott, 1967a: 90 (Paraguay, San Estanislao) [HT MIHS] [also mentioned as *Scansicochlea willineri*].

Nomina inquirenda

The following taxa could not unambiguously be assigned to one of the genera. As far as the available data permit I have indicated to which genus they possibly belong.

alausiensis, *Thaumastus*, Cousin, 1887: 228, pl. 4 fig. 13 ([Ecuador] le versant du mont Hacu, entre Achapallas et la rivière Sula, Alausi, province de Chimborazo) [LT MNHN] [?*Scutalus*?/??*Naesiotus*].

albicans, *Bulimus*, Broderip in Broderip & Sowerby, 1832b: 105 (Copiapo, Chili) [?*Bostryx*].

albus, *Bulimus*, Sowerby, 1833b: 73 (arenosis prope Copiapo) [?*Bostryx*].

arrosus, *Bulimus*, Sowerby, 1833a: fig. 34 [error for *erosus* Broderip?].

biformis, *Bulimus*, Pfeiffer, 1854e: 223 (Peru?).

- callosus*, *Bulimus*, Pfeiffer, 1846: 128 [locality unknown].
- cinereus*, *Bulimus*, Reeve, 1848: pl. 56 fig. 372 (Bolivia).
- erosus*, *Bulinus*, Broderip in Broderip & Sowerby, 1832b: 106 (Peruviã, Huantajaya near Iquiqui) [?Bostryx].
- fasciata*, *Scutalus conospirus*, Döring, 1879: 67 ([Argentina] Sierra de Tucuman) [?Bostryx stelzneri].
- felipponei*, *Bulimulus* (*Scutalus*), Ihering, 1928: 95 (Republic of Uruguay, Canelones) [?Naesiotus].
- flossdorfi*, *Bulimulus*, Holmberg, 1909a: 11 ([Argentina] Chaco, Territorio de Formosa, prope Nueva Pompeya) [?Bostryx].
- fonsecanus*, *Bulimulus* (*Rhabdotus*), Haas, 1961: 20, figs. 11a-b (San Salvador or Nicaragua, Gulf of Fonseca) [HT FMNH 106702].
- fourmiersi*, *Bulimus*, d'Orbigny, 1836: 273, pl. 30 figs. 12-14 ([Argentina] la province de Corrientes, non loin du Rio de Santa Lucia, au lieu nommé Pasto reito) [?Naesiotus].
- fusca*, *Bulimulus heloicus*, Ancey, 1901a: 82 (aux environs de Gualaguaychu, province Entrerios, République Argentine).
- guttatus*, *Bulinus*, Broderip in Broderip & Sowerby, 1832a: 31 (Peruviã, Cobija or Puerto de la Mar) [?Bostryx].
- heloica*, *Helix*, d'Orbigny, 1835: 11 (provincia Chiquitensi, republica Boliviana).
- joergenseni*, *Bulimulus*, Holmberg, 1912b: 150, figs. 7-8 (Argentina, Misiones, Colonia Bonpland).
- metamorphus*, *Bulimulus*, Pilsbry, 1896b: 157, pl. 1 figs. 6-7 (Chili) [LT ANSP 69455a] [?Bostryx].
- munsterii*, *Bulimus*, d'Orbigny, 1836: 278, pl. 34 figs. 4-7 ([Bolivia] côte de Petaca).
- nivalis*, *Helix*, d'Orbigny, 1835: 12 [no type locality given; Potosí, Bolivia (cf. d'Orbigny, 1836: 260)] [?Scutalus].
- obliquistriatus*, *Drymaeus*, Da Costa, 1901: 238, pl. 24 fig. 2 (Peru, San Pablo) [HT BMNH 1907.11.21.41] [?Bostryx].
- olorinus*, *Bulimus*, Duclos, 1833: pl. 24 [= *albus* Sowerby].
- pliculosa*, *Bulimulus turritella*, Ancey, 1901a: 92 ([Brazil] Matto-Grosso).
- robertsi*, *Thaumastus*, Pilsbry, 1932: 390, pl. 27 figs. 3, 6 (Peru, Dept. San Martin, Rio Jelashte, 4500 ft.) [HT ANSP 159920a].
- saltensis*, *Bulimulus*, Holmberg, 1909b: 91 ([Argentina] Salta, ad ripam Rio de los Horcones et Rio de las Piedras).
- sowerbyi*, *Bulimus*, Pfeiffer, 1847a: 114 (Andes of Colombia).
- spixii*, *Bulimus*, Potiez & Michaud, 1835: pl. 15 figs. 13-14 (république Argentine et Bolivienne) [?Bostryx].
- stenogyroides*, *Bulimulus*, Guppy, 1868: 431 (Dominica).
- stilbe*, *Bulimulus*, Pilsbry, 1901: 145, pl. 25 fig. 18 (Brazil, State of Sao Paulo) [HT ANSP 73434].
- striatellus*, *Buliminus*, Beck, 1837: 70 [indication].
- striatus*, *Bulinus*, King in Sowerby, 1833a: fig. 56 (Santos, Peru) [?Bostryx].
- tenebrosa*, *Thaumastus onca*, Pilsbry, 1926a: 7, pl. 2 figs. 9-10 (Bolivia, Dept. Cochabamba) [HT ANSP 138107] [?Plekocheilus].
- turritella*, *Helix*, d'Orbigny, 1835: 13 (provincia Chiquitensi, republica Boliviana).
- turritellatus*, *Bulimulus*, Beck, 1837: 67 (New name for *Helix turritella* d'Orbigny, 1835, not Férussac, 1821).
- ulloae*, *Bulimus*, Philippi, 1869: 34 (Peruvia in pampa inter Mayoc et Huanta).
- umbilicatus*, *Thaumastus*, Miller, 1879: 122, pl. 12 fig. 5, pl. 13 fig. 1 ([Ecuador] Prov. Loja, Rio Catamayo, 2000-3000 ft.) [?Scutalus].
- ventricosus*, *Mesembrinus*, Paravicini, 1894: 6 ([Argentina] provincia di Salta, S. Rosa) [?Drymaeus/?Bostryx].
- woodwardi*, *Bulimus*, Pfeiffer, 1857b: 332 (Andes of Peru) [LT BMNH 1975334] [?Bostryx].

The following taxa are excluded from the Bulimulidae:

- cucullus*, *Bulimus*, Morelet, 1849. Testacea novissima, 1: 9.
gracilior, *Bulimulus (Scutalus) cucullus*, Fischer & Crosse, 1875. Mission scientifique au Mexique, Mollusques, 1: 519, pl. 20 fig. 12.
Graptostracus Pilsbry, 1939. Nautilus, 53: 29.
hector, *Bulimus*, Pfeiffer, 1857. Malakozoologische Blätter, 4: 157.
visendus, *Bulimus*, Hidalgo, 1869. Journal de Conchyliologie, Paris, 17: 50, pl. 5 fig. 8.
webberi, *Leiostracus*, Pilsbry, 1939. Nautilus, 53: 28, pl. 7 fig. 3.

FOSSIL SPECIES

The fossil record of the Bulimulidae is rather scarce and mainly concerns Odontostominae. The fossils referable to the Bulimulinae are listed below.

Data on fossil Bulimulinae may be found in Breure (1978b), Brito (1967), Camancho (1967), Ferreira & Coelho (1971), Herm (1970), Ihering (1904, 1908, 1914), Magalhães & Mezzalira (1953), Maury (1935), Muniz & Ramirez (1971), Palma & Brito (1974), Parodiz (1946c, 1949, 1969), Trindade (1956).

List of fossil taxa:

- carvalhoi*, *Bulimulus*, Brito, 1967: 18, pl. 2 figs. 4-6 (Brasil, Edo. Rio de Janeiro, São José de Itaboraí) [HT DGM 4995].
coelhoi, *Bulimulus*, Palma & Brito, 1974: 396, pl. 2 figs. 2, 4 (Brasil, Edo. Rio de Janeiro, São José de Itaboraí) [HT DGM 5410].
eocenicus, *Paleobulimulus*, Parodiz, 1949: 177, figs. 1-2 (Argentina, Chubut, region de Mallin Blanco) [HT MACN].
fazendicus, *Bulimulus*, Maury, 1935: 7, figs. 10-11 (Brazil, State of Rio de Janeiro, Municipality of Itaborahy, Fazenda Sao José) [HT AMNH 24243].
ferreirai, *Bulimulus*, Palma & Brito, 1974: 393, pl. 2 figs. 1, 6 (Brasil, Edo. Rio de Janeiro, São José de Itaboraí) [HT DGM 5409].
Itaborahia Maury, 1935: 9. Type species by monotypy: *Itaborahia lamegoi* Maury.
lamegoi, *Itaborahia*, Maury, 1935: 10, figs. 6-7 (Brazil, State of Rio de Janeiro, Municipality of Itaborahy, Fazenda Sao José) [HT AMNH 24240].
othoni, *Thaumastus magnificus*, Maury, 1935: 15, figs. 14-15 (Brazil, State of Sao Paulo, vicinity of Ribeira do Iguape, near Iporanga) [HT AMNH 24245].
Paleobulimulus Parodiz, 1949: 177. Type species by monotypy: *Paleobulimulus eocenicus* Parodiz.
patagonicus, *Thaumastus*, Parodiz, 1946c: 307, pl. 1 figs. 1-4 (Argentina, Chubut, Cañodón Hondo del Rio Chico) [HT MACN 4521].
sommeri, *Bulimulus*, Palma & Brito, 1974: 396, pl. 2 figs. 3, 5 (Brasil, Edo. Rio de Janeiro, São José de Itaboraí) [HT DGM 5411].
trindadeae, *Bulimulus*, Ferreira & Coelho, 1971: 470, fig. 7 (Brasil, Edo. Rio de Janeiro, São José de Itaboraí) [HT MN-Geol. 5022-1].
variabilis, *Bostryx (Bostryx)*, Herm, 1970: 194, pl. 4 figs. 1-3 (Nordchile, N Antofagasta, Halbinsel Mejillones, 2400 m SE Cuesta del Burro, 250 m) [HT Bayerische Staatssammlung für Paläontologie und historische Geologie, München].

Some recent species are also known as fossils, e.g.: *Bulimulus gorritiensis* Pilsbry, *B. sporadicus* (d'Orbigny) and *Discoleus ameghinoi* (Ihering) [see Camancho, 1967].

Thaumnastus limneiformis tenuis Warren (1926: 7) and *T. l. procerior* Russell (1926: 220) are only mentioned here. It is not clear whether they are correctly referred to the Bulimulidae.

VII. PHYLOGENY AND ZOOGEOGRAPHY

"Ideas deserving to be called 'original' in the strictest sense probably do not exist"

Ghiselin, 1974: 9.

PHYLOGENY

In this section the methods outlined by Hennig (1966) are used. Comments on these methods may be found in Ashlock (1971, 1973, 1974), Colless (1967, 1969a, 1969b, 1970), Cracraft (1974), Darlington (1970), Engelmann & Wiley (1977), Farris et al. (1970), Farris (1976), Hennig (1971, 1974, 1975), Mayr (1974), Nelson (1971a, 1971b, 1972a, 1972b, 1973b, 1974), Peters (1970, 1972), Peters & Gutmann (1971, 1973), Platnick (1976a, 1977), Remane (1971), Rosen (1974b), Schlee (1969, 1971), Sokal (1975), Van der Steen & Boontje (1973).

This is the first time that Hennigian principles are applied to Bulimulidae. I have tried to justify the transition series (key-notions of these principles), which I recognize, as well as possible. In most instances I have been forced to make decisions on account of the frequency of the various character states in the Bulimulinae. In some other cases, e.g. the presence or absence of a penis sheath, I had to take an arbitrary decision. I hope that further research will improve my transition series and their argumentation.

The following character transition series have been recognized (summarized in Table 4):

Radula. — (1) The central teeth of the radula are normally tricuspid, not only in Bulimulidae but in many other pulmonate families as well (cf. Solem, 1974: 170). The presence of monocuspid central teeth is generally hypothesized to be an apomorphic character, which presence in different genera is best understood as the result of convergent evolution (Breure & Gittenberger, in preparation); (2) the same applies to monocuspid lateral teeth. (3) The length axis of the mesocones of (lateral and) marginal teeth is normally parallel to the length axis of the basal plate. In some groups, however, the length axis of the mesocone (and normally also of the endo- and ectocones) is shifted, i.e., turned ca. 20-30 degrees with respect to the length axis of the basal plate. This character state, which I consider apomorphic, is not correlated to the ecology of the species (it occurs both in ground dwelling and in arboreal species. Its presence in different genus groups is most probably the result of convergent evolution. (4) The transverse

TABLE 4
Summary of character transition series in Bulimulinae

Character	Plesiomorphous (1)	(2)	Apomorphous (3)
RADULA			
1. Central teeth	tricuspid	monocuspid	
2. Lateral teeth	bi/tricuspid	monocuspid	
3. (Lateral) marginal teeth	length axis parallel	length axis 'shifted'	
4. Transverse rows	straight	V- or W-shaped	
5. Supporting denticles	present	absent	
PALLIAL ORGANS			
6. Pulmonary veins	weakly to moderately developed	strongly developed, anteriorly ramified	pericard transversally disposed
GENITALIA			
7. Penis sheath	absent	present	
8. "pseudo-sheath"	absent	present	
9. Glandular cell types in penis epithelium	one	two or more	
10/11. Penis lumen	undivided	'simply' constricted in median part	'complex' constricted in median part
12/13. Penis lumen	'divided', with pouches	parallel tubes	circular gland
14. Subepithelial tissue in distal penis	muscular fibers	glandular cells	
15/16. Epiphallus-penis	gradual change	intrudes in distal penis	do., in distal + proximal penis
17. Curved fold in flagellum	single	double	
18. Retractor muscle	distally inserted	subdistally inserted	
19. Spermathecal duct	as long as spermoviduct	reduced in length	
20. Spermathecal appendix	absent	present	
21. Glandular folds of sperm-oviduct	parallel to length axis of spermoviduct	perpendicular to length axis of spermoviduct	
SHELL			
22. Protoconch	sculptured	smooth	

rows of the radula are usually straight or slightly bent in the outermost teeth. In some genera the transverse rows are V- or W-shaped and this is hypothesized to be an apomorphous character. (5) In most genera the central part of the radula is provided with an interrow interlocking system by the presence of 'supporting denticles'. The absence of this system is hypothesized to be apomorphous.

Pallial organs. — (6) The main pulmonary veins and side veins are normally weakly to moderately well developed; veins parallel to the main pulmonary vein are absent. In some genera, however, the veins are strongly developed and ramified at the anterior end, where one or two veins parallel to the main pulmonary vein may be present (in part of the genera, moreover, the pericard is transversally disposed); this situation is considered apomorphous.

Genitalia. — (7) The function of the proximal penis sheath, which is present in most genera, is not clear. It is not possible to decide *a priori* between the two possibilities: either the presence or the absence of a sheath is an apomorphous character state. I have chosen for the presence of the sheath to be apomorphous. [It may be noted that, if the absence of the sheath is hypothesized to be apomorphous, the resulting cladograms do not alter substantially]. (8) In transverse sections of the penis the outer layer is made up by muscular fibres. Normally this layer is united, but in one genus it is divided into an inner and outer layer, which are unconnected over the greater length of the penis. The outer layer is here named 'pseudo-sheath' and its presence is considered apomorphous. (9) The epithelium bordering the penis lumen has a glandular function. Usually the epithelium is made up by one cell type and the presence of two or more glandular cell types is hypothesized to be apomorphous. (10) The shape of the penis lumen in longitudinal section leads to two transition series that, in my opinion, are independent. In the first series the presence of a 'simple', undivided lumen that is more or less cylindrical qua width is considered primitive. When the lumen is 'constricted' in its median part, which is hypothesized to be apomorphous, this may be either 'simple' (10) or 'complex' (11). (12) In the second series the lumen is 'divided' either into a broad and narrow part or into a 'central' lumen and 'side lumina'. The presence of pouches is then hypothesized to be plesiomorphous and parallel tubes are apomorphous; (13) a specialized form of these parallel tubes is the presence of a circular gland, where the tubes are reduced in length and (nearly totally) united. (14) The subepithelial tissue in the distal part of the penis may be made up of muscular fibers, which is considered the plesiomorphous situation, or by large, rounded cells that probably have a glandular function; the presence of these (glandular) cells is hypothesized to be apomorphous. (15) The distal part of the penis gradually

changes into the epiphallus or, hypothesized to be apomorphic, the epiphallus intrudes the distal part of the penis; (16) when the epiphallus not only intrudes into the distal part but also into the proximal part of the penis this is hypothesized to be relatively apomorphic. (17) The flagellum has internally a curved, longitudinal fold that has a function in the formation of the spermatophore (Breure & Eskens, 1978). In some genera this fold is double-curved and this situation is hypothesized to be apomorphic. (18) The penis retractor muscle is normally attached to the distal end of the flagellum. In some groups, however, the muscle is subdistally inserted at the flagellum or at the transition between epiphallus and flagellum; this is considered an apomorphic character state. (19) The spermathecal duct is usually about as long as the spermoviduct. The reduction in length of this duct is hypothesized to be apomorphic and the presence of this character state in different genus groups may be the result of convergent evolution. (20) The spermathecal duct is normally subcylindrical or tapering. In some genera, however, the proximal part of the duct is relatively thick and has an appendix; the distal part of the duct is narrow and originates below the distal end of the proximal part. The presence of a spermathecal appendix is hypothesized to be apomorphic. (21) The glandular folds of the spermoviduct are normally perpendicular to the length axis of the duct. For reasons of parsimony (Peters & Gutmann, 1971) this is considered an apomorphic character state. When the glandular folds are arranged parallel to the length axis of the spermoviduct this is considered plesiomorphous. (22) The presence of protoconch sculpture is hypothesized to be plesiomorphous; a smooth protoconch is considered an apomorphic character state.

The cladograms presented below are based on the above-mentioned transition series. As these series only concern anatomical characters the genera for which no anatomical data are available are left out of these cladograms.

The cladograms represent the least rejected hypotheses of phylogenetic relationships among the (sub)genera of each group. With the present data at hand it was impossible to fit the cladograms of the different genus groups into one cladogram for the whole subfamily. There are, moreover, some groups of which the monophyly is not corroborated by synapomorphic characters; these groups are treated as such on account of other characters, e.g. the sculpture of the protoconch (a transition series of the different sculptures is too hypothetical), or out of tradition.

ZOOGEOGRAPHY

The available zoogeographical (or, more correctly perhaps: biogeographical) theories have recently been reviewed by Cracraft (1975b; see also Ball, 1976). These theories may be summarized as follows:

A. Theories involving the center of origin concept.

1. Evolutionary biogeography. This theory, applied by Darlington (1957, 1959, 1965), Matthew (1915), Mayr (1952), Simpson (1940) and others, has not been explicitly formulated. Cracraft (1975b: 229) lists the following principles: a) the center of origin of a taxon is that area showing the greatest specific and generic diversity; b) the degree of differentiation of a group is roughly proportional to the length of time that group has occupied the area in question; c) the area occupied by a group is more or less proportional to the age of the group; d) distributions of peripheral groups that are more nearly continuous with the distribution of the "central" populations are probably younger than those peripheral populations with widely separated (relict) distributions; e) related, competing or "associated" taxa tend to arise in the same areas as the taxon under consideration; f) the distribution of primitive groups are not trustworthy for recognizing centers of origin; g) fossils provide the best clues for biogeography if the record is "adequate". The hypotheses forwarded by evolutionary biogeographers are usually weakly formulated in that they do not have predictive value nor aim at finding any regularity in distributions. These hypotheses may be called "narrative" (sensu Ball, 1976).

2. Phylogenetic biogeography. The distribution of the species in question and their hypothetical phylogenetic relationships given, one can hypothesize the center of origin and the direction of dispersal which are most probable for the given phylogenetic hypothesis. To explain disjunct distributions Hennig (1960) proposed three "rules": a) the progression rule; b) the phylogenetic intermediate rule and c) the multiple sister-group rule (see Ashlock, 1974, for comments). See also Brundin (1972). One of the main differences between these two theories is that most evolutionary biogeographers suppose stationary continental outlines, whereas the phylogenetic biogeographers accept continental drift. It may be mentioned that, in the end, acceptance of the theory of continental drift (= plate tectonics) is only partially relevant; what really matters in this context is a cautious use of this theory to explain certain types of distribution.

B. Theories involving vicariance.

3. Ecological biogeography. With this name I designate the theory of dispersal centers advocated by De Lattin (1957, 1967) and applied by Müller (1973a, 1973b, 1974) to the Neotropics. The theory, not mentioned by Cracraft (1975b) and only implicitly formulated by De Lattin and Müller, may be summarized as follows. Species are confined to a certain biome ["Großlebens-

räume" of De Lattin; Müller (1974: fig. 49) lists for the Neotropics the Hylaea (rain forest), savannah, steppe, desert and orcal biomes]; the areas of these biomes are influenced by climate-oscillations and vegetations-fluctuations and so are the areas of the species which form part of these biomes. Under unfavourable environmental conditions (e.g., an arid period for rain-forest species) species may survive in a restricted area (= dispersal centre¹); in these areas speciation²) may have taken place so that, e.g., populations of the same species which survived in different areas prove to differ at the subspecies level when they make contact under more favourable conditions afterwards.

4. Historical biogeography, with which I designate the theory of Croizat (1958, 1964, 1976; also Croizat, Nelson & Rosen, 1974; cf. Nelson, 1973a). The main principles of this theory are (see Croizat et al., 1974): a) the distribution of a group can be represented by one or more tracks connecting the ranges of all members of that group; b) many overlapping individual tracks form a generalized track which estimates an ancestral biota that, because of changing geography, has become subdivided into descendant biotas; c) overlap (sympatry) of generalized tracks, or any of the components of different generalized tracks, reflects geographical overlap of different biotas due to dispersal.

The three last mentioned theories may be called analytical (sensu Ball). A descriptive biogeographical publication on the Neotropics is Cabrera & Willink (1973).

The evolutionary biogeographical theory is here repudiated because of its non-analytical nature.

The phylogenetic biogeographical theory has its merits because of the prior phylogenetic analysis carried out of the group in question. As Brundin (1966) says, knowledge of phylogenetic relationships is a prerequisite for the discussion on distribution patterns, as the value of biogeographical conclusions depends on the value of phylogenetic arguments. Howden (1972: 130) has pointed out that "Hennig's methodology merely shows relationships, it does not explain the dispersal mechanisms". There are two other points to comment on. The theory involves the concept of centre of origin in the form of the

1) Müller (1973b: 3) states: "I do not assume at the outset that dispersal centres represent centres where faunas and flora were preserved during regressive phases", while the same author (1974: 157) defines: "Dispersal centres are areas in which animals and plants survived unfavourable environmental conditions". The latter statement was expressed in his earlier papers as well and is used, therefore, to summarize the theory.

2) According to Müller (1973a: 232) there are two types of differentiation (speciation): a) allopatric differentiation within a continuous distribution area on account of different selection forces; b) differentiation by geographical isolation.

'progression rule': ancestral forms remain at, or near, the point of origin and the derived forms migrate. A contrariwise opinion has been expressed, e.g., by Darlington (1963) and Ball (1976: 420) correctly remarked that "it is difficult to decide a priori between these two possibilities". Secondly, reticulate evolution (although possibly more common in plants than in animals) may cause some problems, as Sneath (1975) has shown, which cannot be solved with the present phylogenetic theory.

The two theories that involve the concept of vicariance have been compared so far only by Croizat (1976: 519 ff.). It cannot be denied that Müller, although his theory is 'analytical' (sensu Ball), often allows himself 'narrative' explanations (several examples in Croizat, o.c.). Yet, the differences between the two theories are perhaps less than Croizat supposes. Both accept vicariance as a principal factor underlying distribution patterns (Müller only implicitly, Croizat explicitly). Furthermore, as the dispersal centres of Müller are a priori correlated to certain vegetational formations these centres represent in some way the biotas of Croizat³). A point also to be taken into account is the comment by Müller (1974: 6) that "ecological and historical zoogeography are nevertheless not opposed to each other. Any argument about which of the two is more important is, as de Lattin (1967) said, quite beside the point". The main differences between the two theories are that Müller assigns relative importance to ecological factors which occurred in the Plio-Pleistocene⁴), whereas Croizat maintains that geological events which occurred as early as the Tertiary are responsible for "differential form making"⁵). It is not possible to decide a priori which of these viewpoints is correct and it is likely that both are correct (e.g., ecological factors of the Pleistocene to explain the distribution of certain subspecies and geological events of the Tertiary explaining the distribution pattern shown by a certain genus). There are, however, some severe drawbacks to Müller's theory, which make it difficult to accept it as a general theory, viz. (1) the theory only explains intracontinental distribution; (2) the theory heavily depends [in my opinion to a far greater extent than does the theory of Croizat] on the taxonomic quality of the group in question, i.e., the availability of a stable taxonomy at the species level; for this reason Müller was only able to analyse the distribution of vertebrate (sub)species; (3) the "relationships" between the different centres depend on polytypic and polycentric species which are "correlated with the particular vegetational formations or climatic

3) Croizat (1958, I: 461) also speaks of "center of dispersal"; these centres are not correlated to vegetational formations but (more or less vaguely) to geological history.

4) Müller seems well aware of the importance of geological factors (1972: 106; 1973b: 153), but hardly mentions any.

5) According to Croizat a succession of comparatively rapid climatic cycles may cause immediate extinction, but does not affect form making (e.g., Croizat 1958, I: 29).

types to which the elements are adapted" (Müller, 1973b: 166). This means that the distribution of taxa that cannot be correlated to a certain vegetational formation or of which the ecology is unknown, cannot be explained. It also means that this theory is a self-fulfilling prophecy: if species are correlated with certain ecological factors then the centres in which these species occur will be related according to the same ecological factors (e.g., arboreal, oréal and non-forest centres; Müller, 1973b: 173, figs. 93-95). Furthermore, (a) the correlation that Müller lies between distribution and phylogenetic relationships (o.c.: fig. 86) is incorrect, as his "phylogenetic relationships" are not based on an analysis using the methods of Hennig, but probably only indicate morphological resemblance; (b) Müller's theory is merely zoogeographical (also "zoogeographical" sensu Croizat), rather than biogeographical, in that it does not explain plant distributions; (c) to say that "the degree of relationships between centres does not only depend on the ecological distinctiveness of a group. It equally depends on the vagility, the course of evolution and the geographical isolation of the faunal elements", rational as it may seem, it is as 'narrative' as the land-bridges of most evolutionary biogeographers.

From the above discussion it may be concluded that I accept the vicariance theory advocated by Croizat. This does not mean that I entirely repudiate all other theories as such. They probably each contain several elements that are acceptable and applicable in certain cases. Nevertheless some additional remarks need to be made.

As Ball (1976: 421) has pointed out, Croizat did not regard the phylogenetic relationships of the taxa; of course he could hardly do so because he compiled his data from the works of evolutionary biologists. Once phylogenetic principles are applied "we find that the method [of Croizat] is little different from the multiple sister-group rule of Hennig" (Ball, l.c.). Phylogenetic principles have been applied to the vicariance theory by Rosen (1974a, 1976), convincingly showing the strength of the method. Croizat, however, still rejects the phylogenetic principles and writes (1976: 815): "los caracteres "diagnósticos" de un taxon siempre figuran una combinación; razón por la cual no hay "especie madre" que se parta en dos "especies-hijas" necesariamente "monofiléticas"; sino, al contrario, los *caracteres* de las "especies" que forman parte del grupo se combinan en sus descendientes en medidas que escapan a toda definición previa" 6) (*italics of Croizat*).

Finally, Ball (o.c.) has given an adequate discussion of the inductive versus deductive approach to biogeographical hypotheses.

6) "The "diagnostic" characters of a taxon always form a combination; and this is why there is not a "mother species" splitting into two "daughter species" in a monophyletic way; but, on the contrary, the characters of the "species" forming part of the group, combine in the descendants in a way that cannot be defined a priori".

BULIMULINAE

The phylogeny and zoogeography of the Bulimulinae will now be discussed, especially of the genus groups.

Three main distribution patterns may be distinguished: (a) an austral pattern (*Plectostylus*-group); (b) a strictly South American pattern that is principally Andean (*Auris*- and *Scutalus*-groups); (c) a Neotropical/Nearctic pattern (*Simpulopsis*-, *Bulimulus*- and *Cochlorina*-groups).

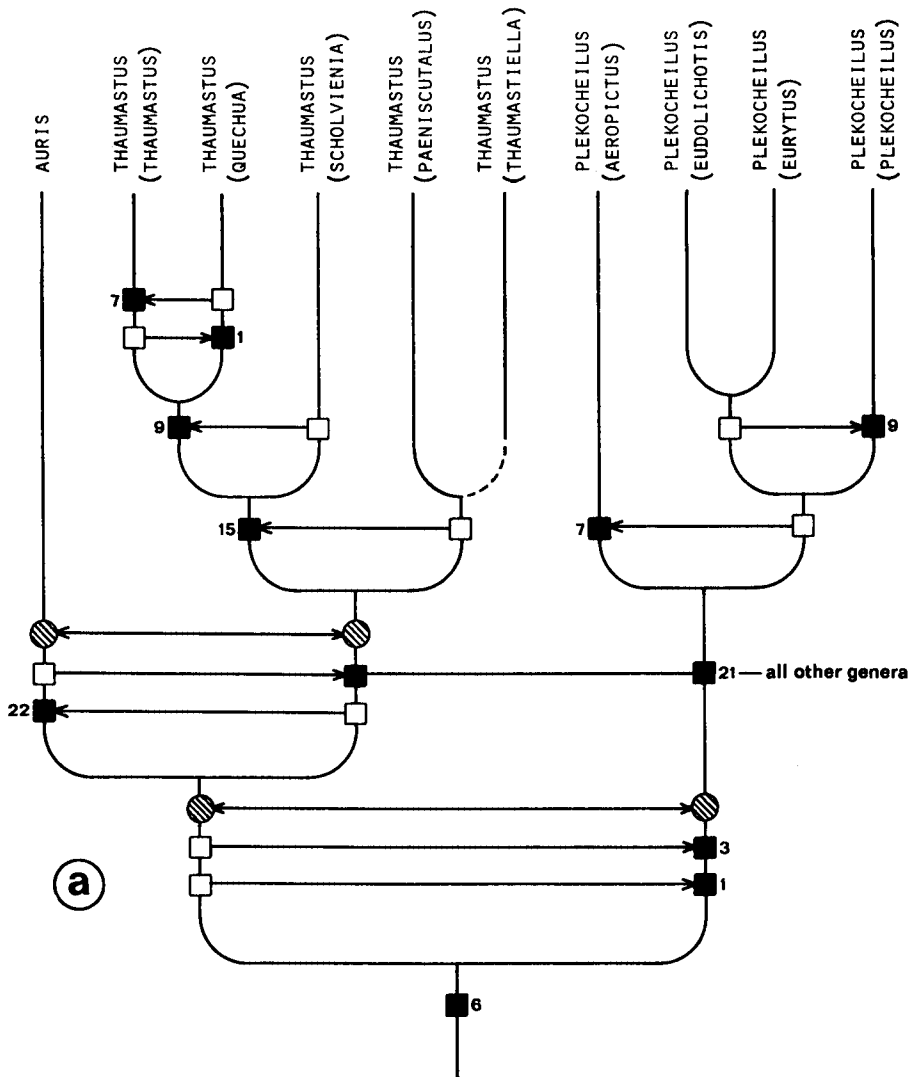


Fig. 168a. Hypothesis of phylogenetic relationship in the *Auris*-group. Vicariant distribution indicated by hatched circles.

Fig. 168 is a summary of alternate hypotheses of phylogenetic relationships in the *Auris*-group. The monophyly of the group is corroborated by one character (6), but there are no synapomorphies to corroborate the monophyly of *Thaumastus* as a genus. *Thaumastus* (*Scholvienia*), *T.* (*Paeniscutalus*) and *T.* (*Thaumastiella*) are separated on account of the shell morphology; the same applies to *Plekocheilus* (*Eurytus*) and *P.* (*Eudolichotis*). The hypothesis shown in fig. 168b is rejected because of character (21); more-

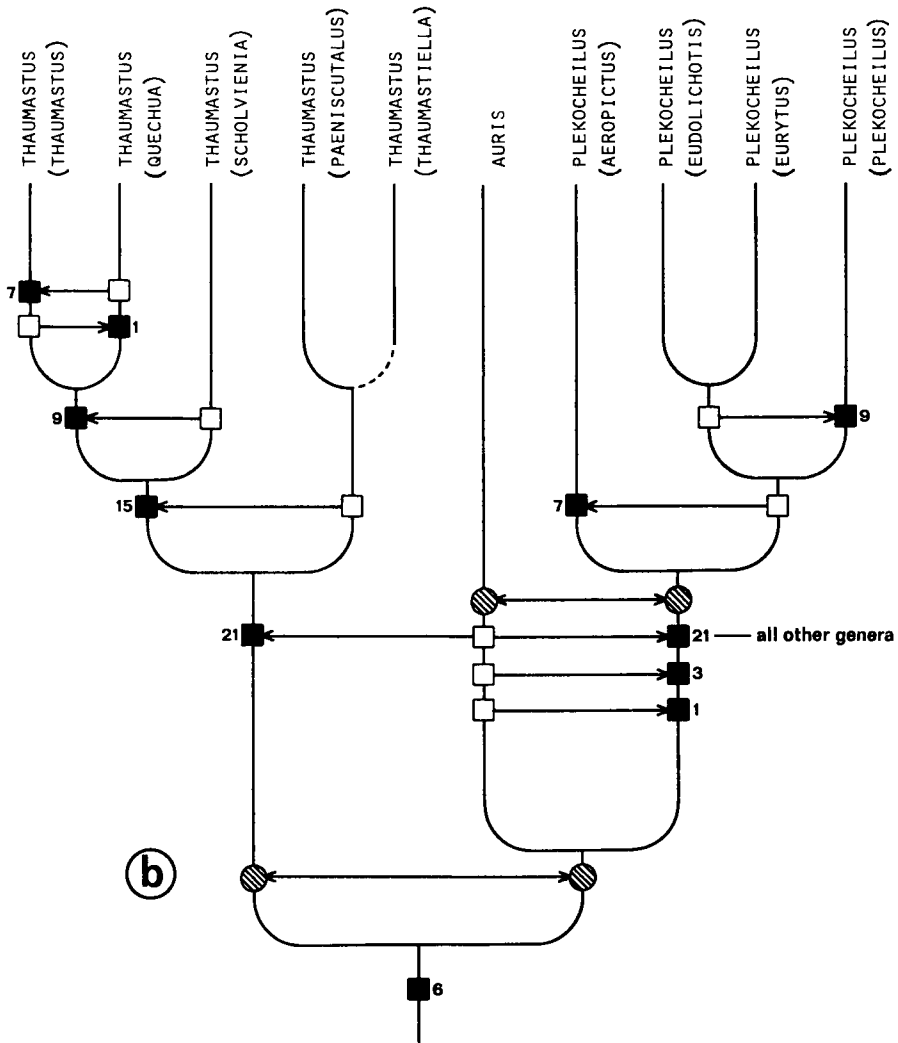


Fig. 168b. Hypothesis of phylogenetic relationship in the *Auris*-group.

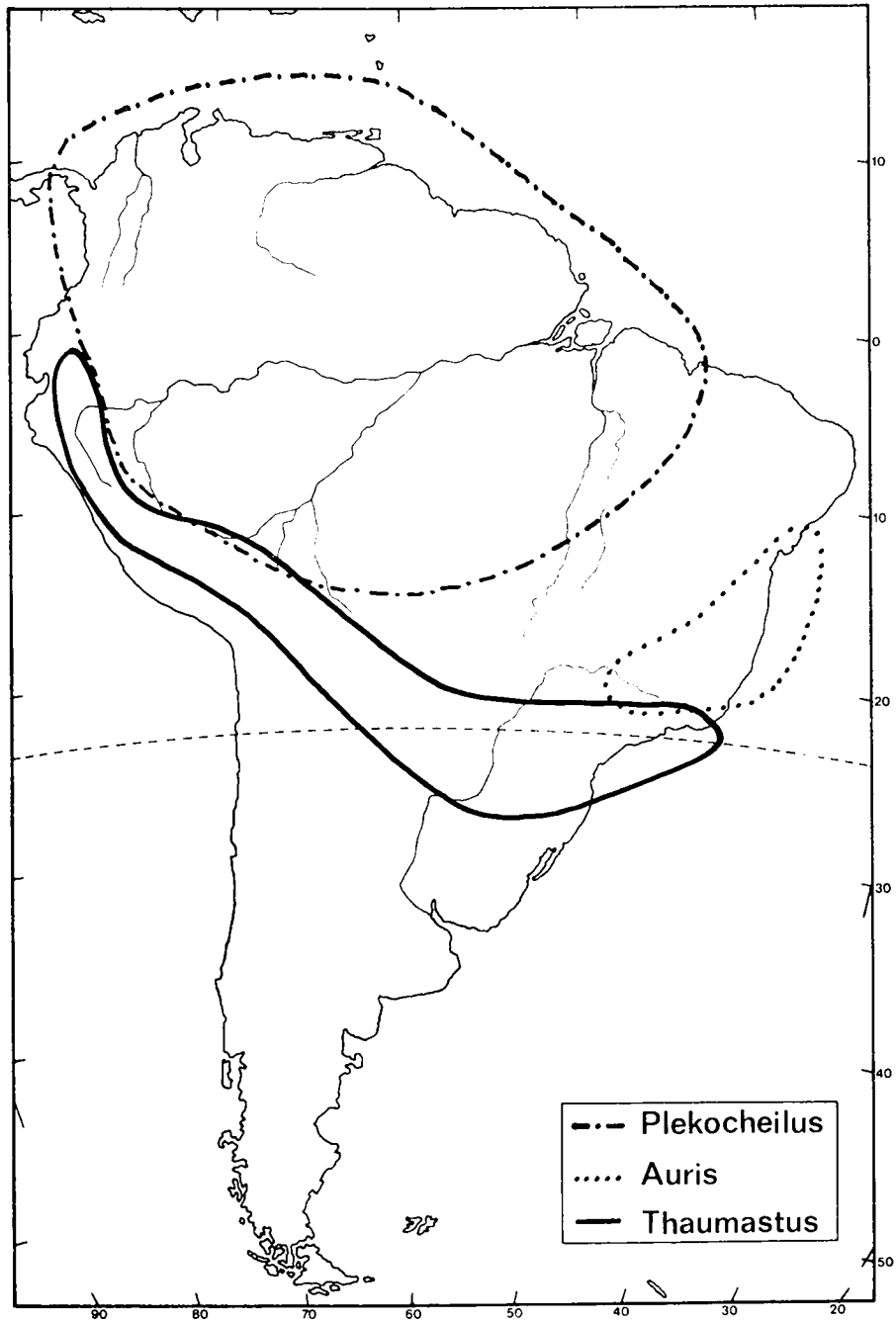


Fig. 169. Distribution of the *Auris*-group.

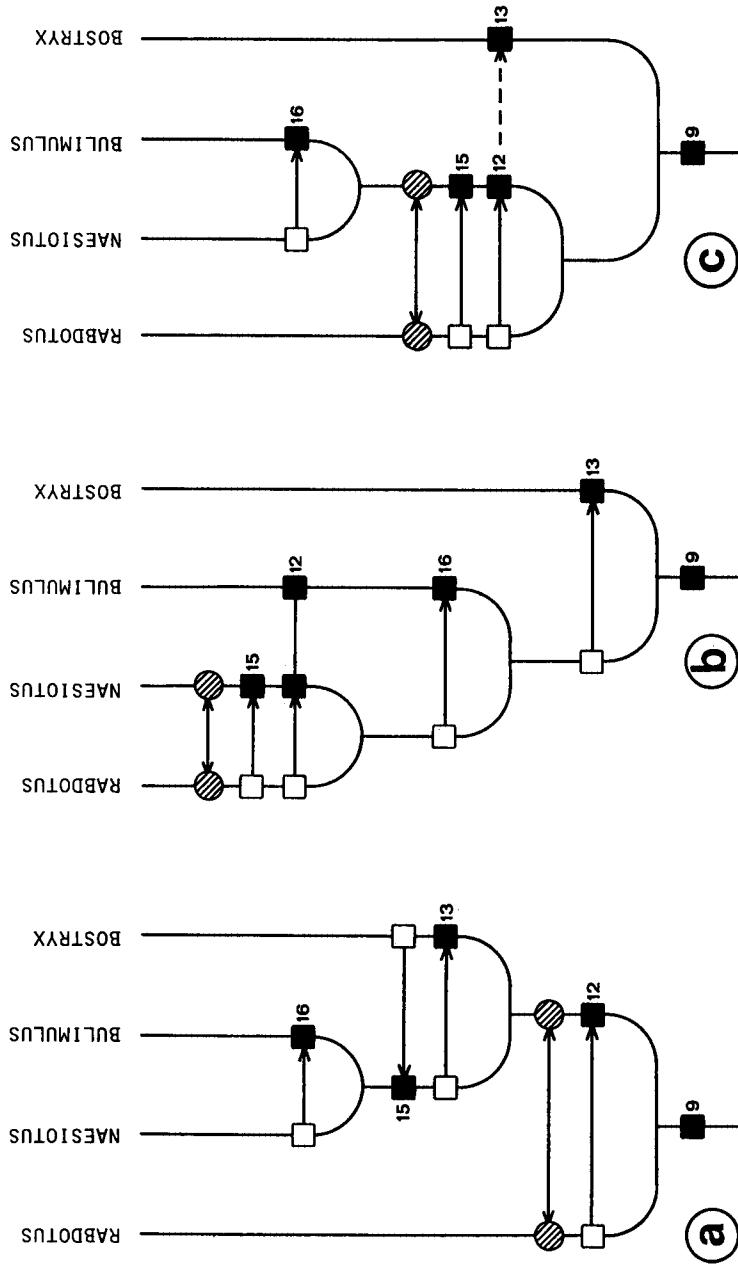


Fig. 170. Hypotheses of phylogenetic relationships in the *Bulimulus*-group.

over, the radula structure is the same in *Auris* and *Thaumastus*, differing from that in *Plekocheilus* (Breure, 1978b). The vicariant distribution of the three genera (fig. 169) is not in contradiction with the hypothesis of fig. 168b, nor with that of fig. 168a. *Auris*, which is probably the relatively oldest



Fig. 171. Distribution of the *Bulimulus*-group.

group, is restricted to the Coastal Brazilian Shield [see Harrington (1962) for palaeogeographical data]. *Thaumastus* s.str. ranges from the Coastal Brazilian Shield into the Andes; the other subgenera of *Thaumastus* are restricted to parts of the Andes and their existence is probably correlated with Andean orogenesis. *Plekocheilus* s.str. and *P. (Aeropictus)*, which are relatively apomorphous, are restricted to the Andes; *P. (Eurytus)* and *P. (Eudolichotis)* are mainly found on the Guiana Shield [*P. (Eurytus)* seems to be intermediate: one species group in the Amazon basin and on the eastern escarpments of the Andes, another species group at higher altitudes in the Andes]. This possibly indicates that the direction of dispersal (sensu Platnick, 1976b) is from the Guiana Shield to the Andes. The occurrence of subspecies of *Plekocheilus (P.) fulminans* (Nyst) on the Roraima-massif is not in contradiction to this hypothesis. [Cf. Croizat, 1958, I: 298; Croizat, 1976].

Fig. 170 summarizes the alternative hypotheses of phylogenetic relationship in the *Bulimulus*-group. The monophyly of the group is corroborated by one character (9). Fig. 170b shows a hypothesis that is rejected because of parallelism in *Naesiotus* and *Bulimulus* (character 12 and characters 15/16 partly) and *Bostryx* (partly: characters 12/13). The hypothesis shown in fig. 170c is also rejected because of partial convergence. The least rejected hypothesis is shown in fig. 170a. The monophyly of *Rabdotus* and *Naesiotus* could not be corroborated with the data at hand. It is now hypothesized that both *Bulimulus* and *Naesiotus* are of pre-Andean origin. If one prefers an indication of the geological period ⁷⁾, the Lower Tertiary could be suggested. For *Naesiotus* this is corroborated by its distribution on the Coastal Brazilian Shield (see fig. 171); the Andean distribution of the genus seems to be in contradiction to such a hypothesis, but may be the result of the ecological requirements of the species: all live in the lowest part of (interandean) valleys and are correlated to arid vegetational formations. The disjunct distribution of *Bulimulus* may be the result of the upheaval of the Andes and the ecological requirements of the species (viz. relatively high temperature conditions). *Bostryx*, too, is possibly of pre-Andean origin (it is represented by some species groups in the coastal areas of Peru and Chile [unless this is explained as secondary dispersal]), but evolved more in accordance with the orogenesis of the Andes than *Bulimulus* and *Naesiotus*. Finally, the distribution of *Rabdotus* is not easily explained. The vicariant distribution with the other genera corroborates the phylogeny shown in fig. 170a, but I do not

7) Geological periods and times are only mentioned here to give an approximate idea on the absolute age of a genus or a subfamily. My data are based on Harrington (1962) and Cracraft (1975a); further research will undoubtedly alter these data to a certain degree.

know of a geophysical event that may account for this distribution pattern, nor for the disjunct distribution of the genus itself.⁸⁾ Croizat (1976: 541) has suggested that a vicariance between Baja California and South America (i.e. Peru) may be explained by "horstian distribution" (see also Croizat, 1958, I: 762-763, 797, and Rosen, 1976: figs. 18-19).

Fig. 172 is a summary of alternate hypotheses of phylogenetic relationships in the *Scutalus*-group. If relative importance is assigned to character (9) the hypothesis as shown in fig. 172b emerges. In this hypothesis character (14) may only be explained by convergent evolution between *Scutalus* (*Suniellus*), *S.* (*Vermiculatus*) and *S.* (*Kuscheleonia*). The least rejected hypothesis is

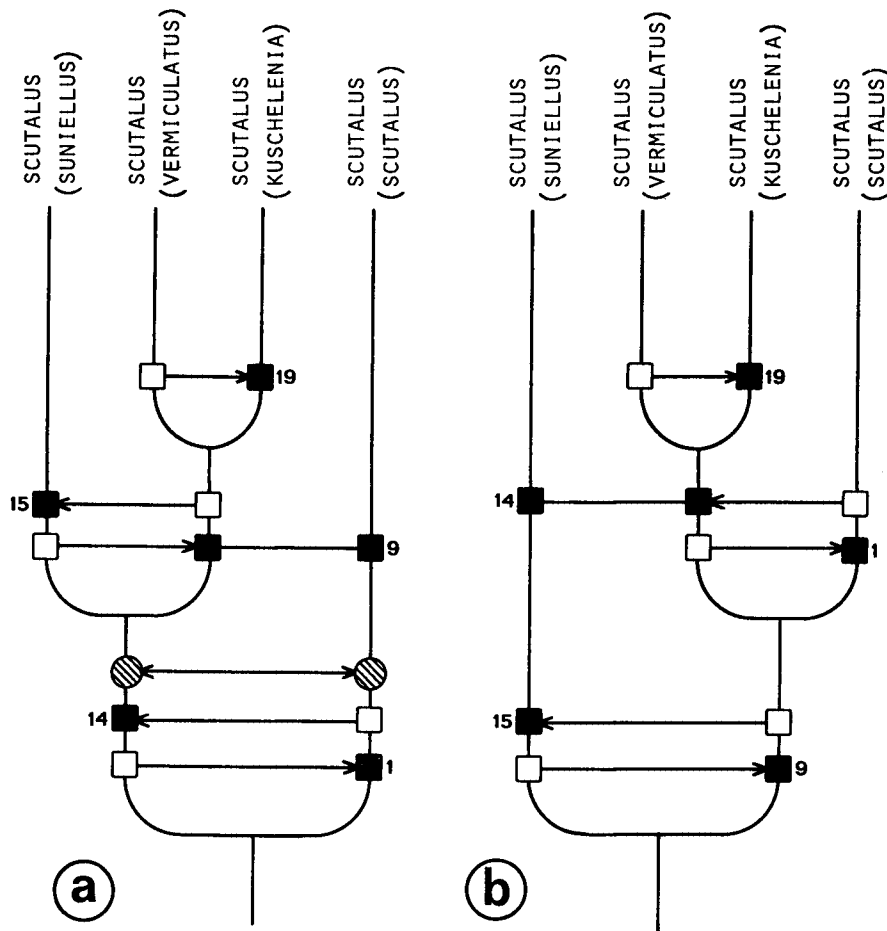


Fig. 172. Hypotheses of phylogenetic relationship in *Scutalus*.

8) The relationships of *Berendtia* and *Spartocentrum* with *Rabdatus* have not been considered, awaiting the revision of Christensen (in press).

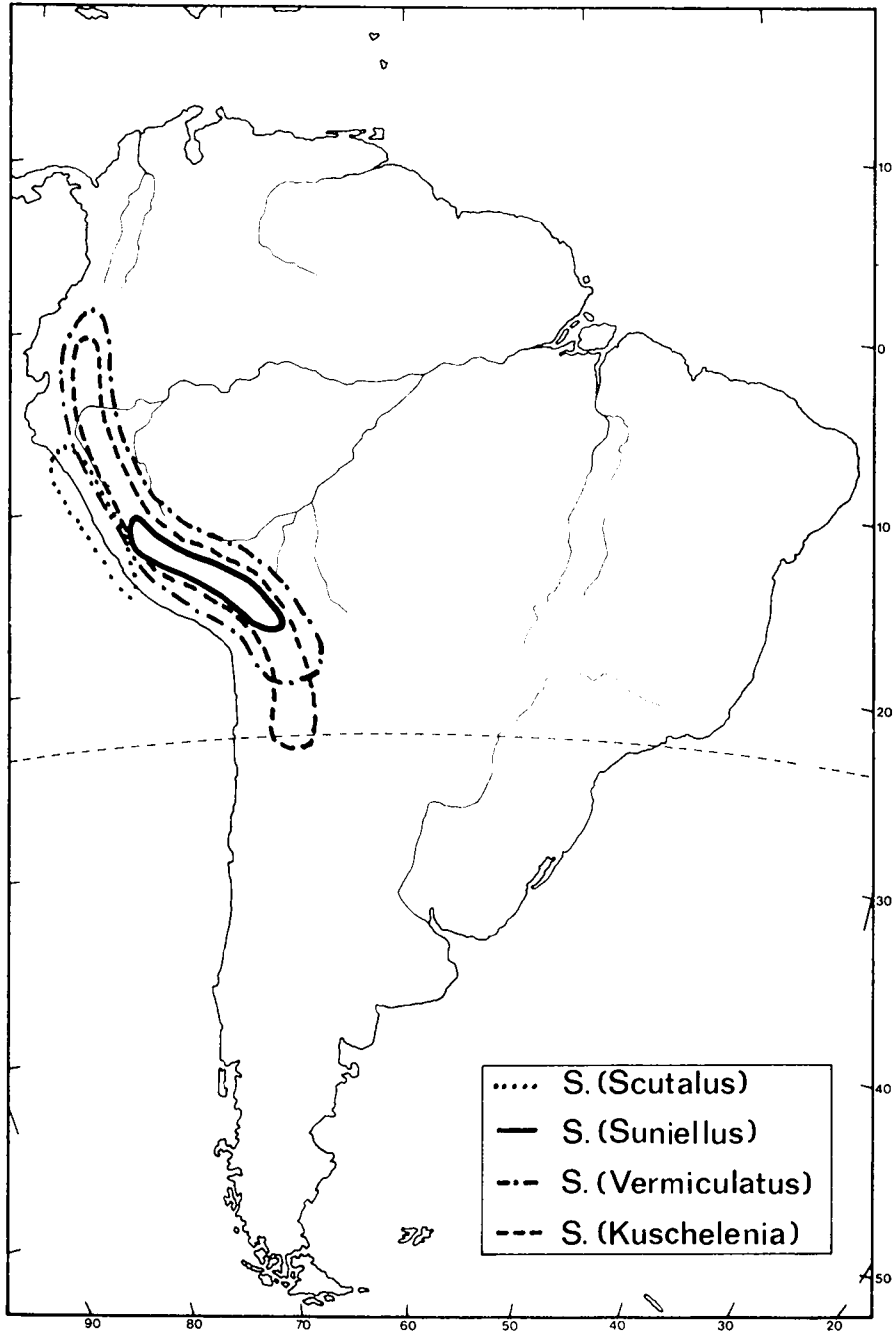


Fig. 173. Distribution of *Scutalus*.

presented in fig. 172a. It implies that character (14) is relatively important and that the occurrence of character (9) is a case of convergent evolution. This hypothesis, however, neatly shows the vicariance between *Scutalus* s.str. and the other subgenera (see fig. 173). It is not possible to decide *a priori* between the two possibilities that (1) *Scutalus* s.str. is the oldest group, which also lived in pre-Andean biota and that the three other subgenera arose with the upheaval of the Andes; or (2) the group has an Andean origin and *Scutalus* s.str. arose secondary in the coastal region of Peru. The occurrence of two apomorphic character states in *Scutalus* s.str., viz. the presence of two glandular cell types in the penis epithelium and the monocuspid teeth in the central part of the radula [correlated to the ecology: species living on rock-faces], suggests that the second possibility is more plausible.

In fig. 174 the alternative hypotheses of phylogenetic relationships in the *Plectostylus*-group are summarized. The monophyly of the group is corro-

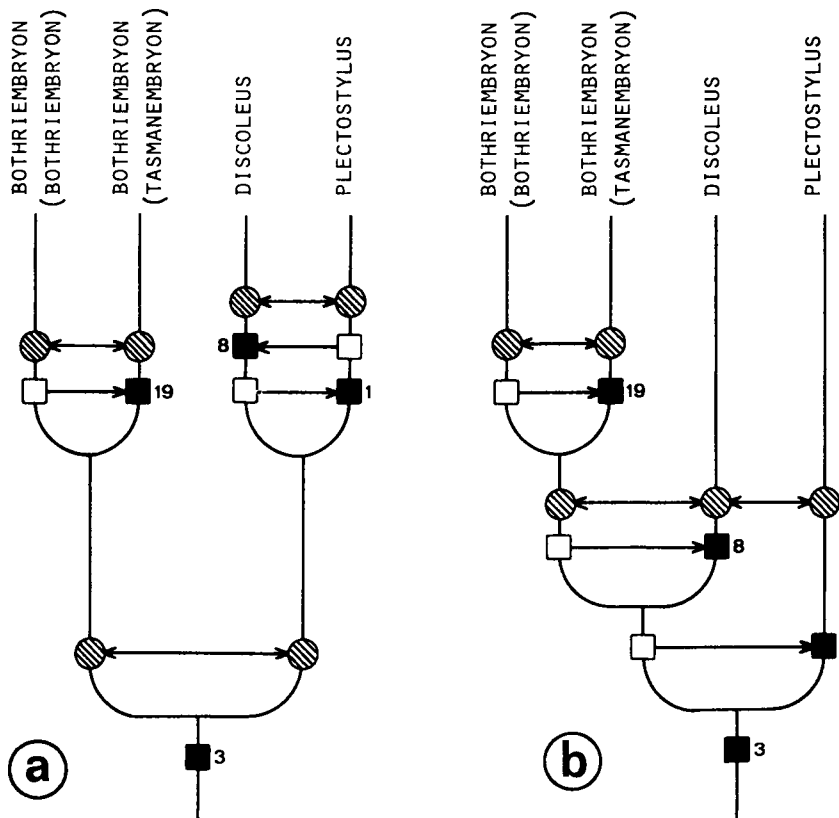


Fig. 174. Hypotheses of phylogenetic relationships in the *Plectostylus*-group.

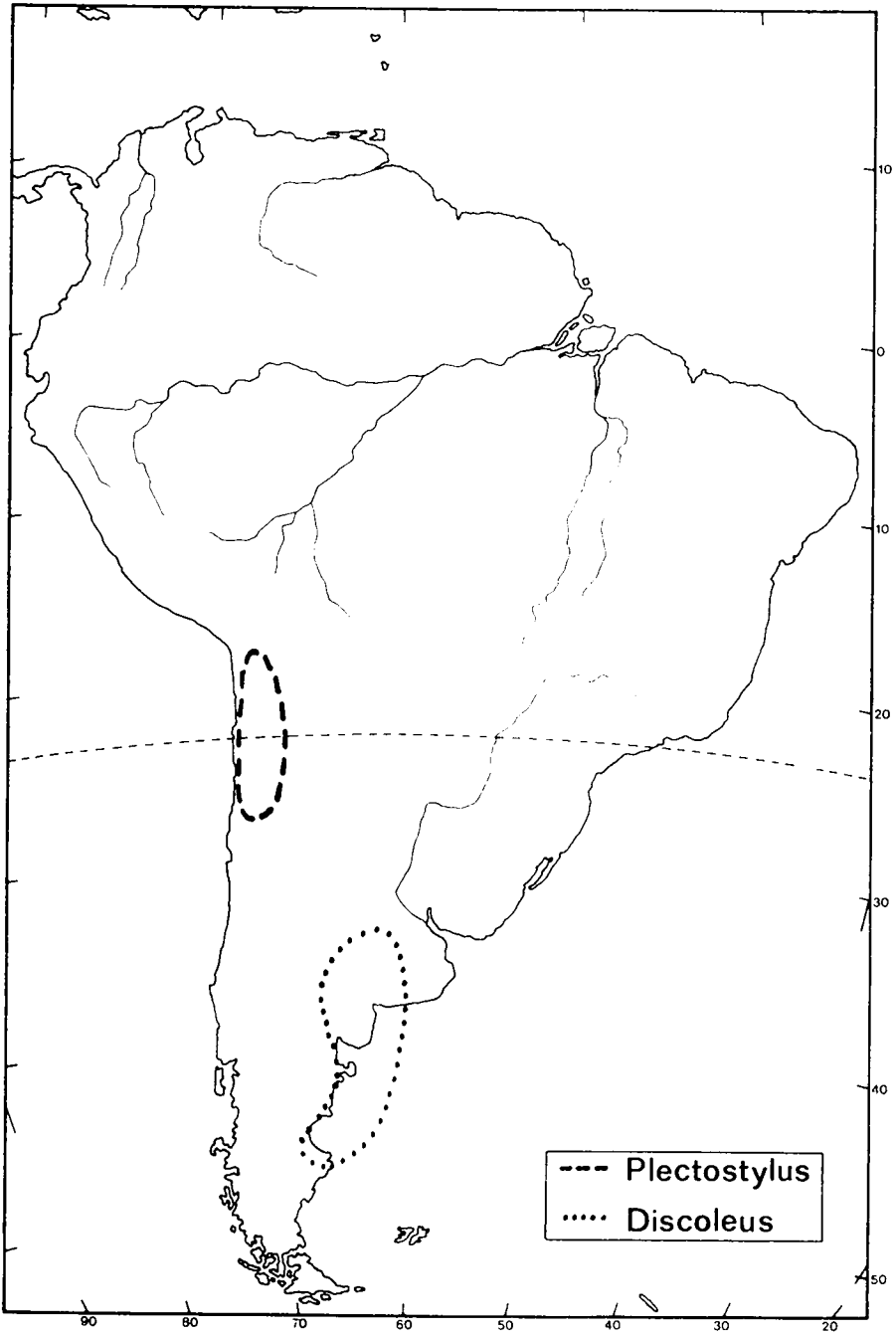


Fig. 175. Distribution of *Plectostylus* and *Discoleus*.

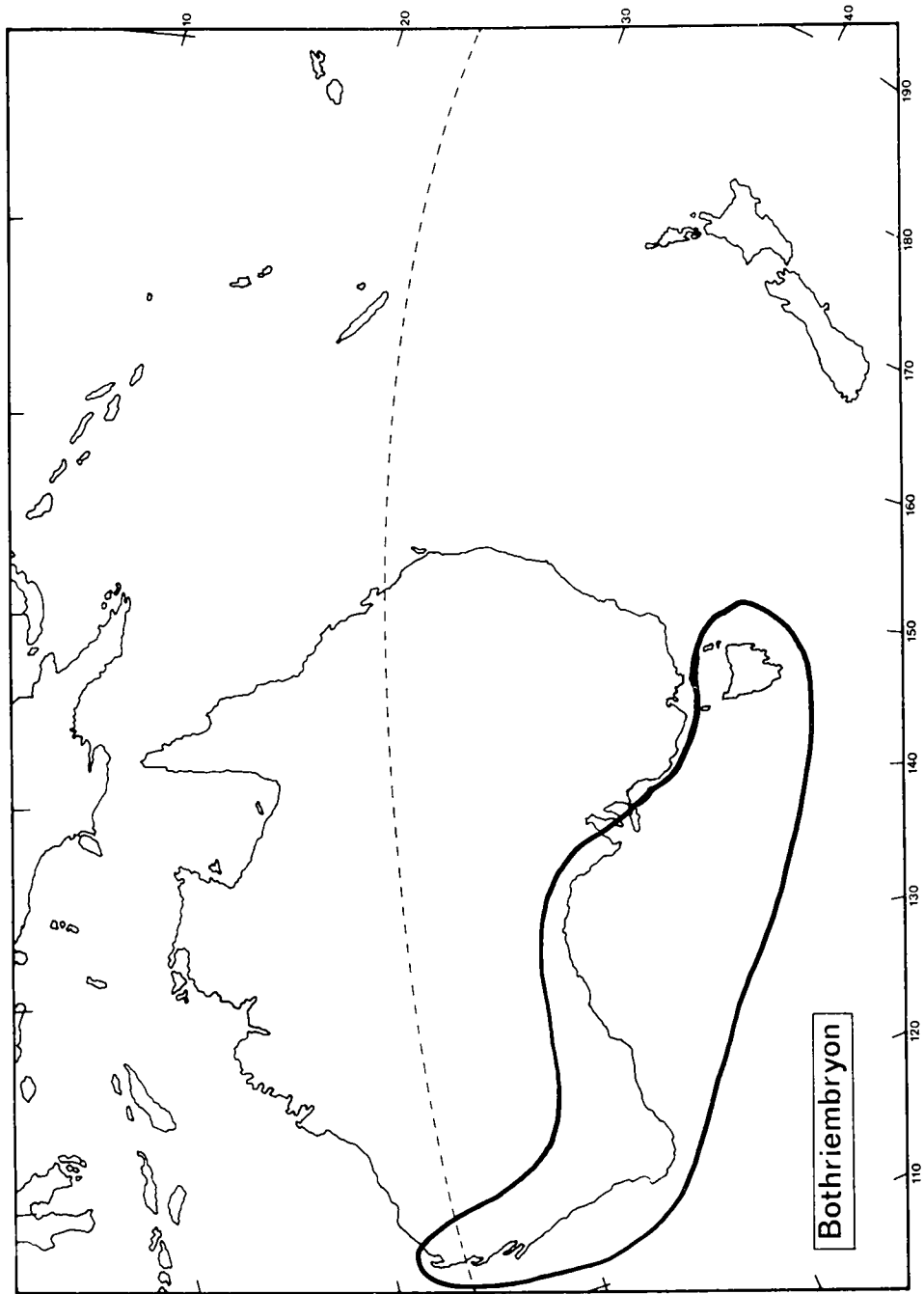


Fig. 176. Distribution of *Bothriembryon*.

borated by one character (3), but the present data do not corroborate the monophyly of *Bothriembryon* s.str. The hypothesis shown in fig. 174a is preferable, in my opinion, because it expresses the vicariant distribution of *Bothriembryon* (Australian Region) versus *Discoleus* + *Plectostylus* (Neotropical Region) more adequately. The austral distribution pattern shown by this group (figs. 175 and 176) is found in other animal groups as well (see Keast, 1973) and may be the result of continental drift. According to Cracraft

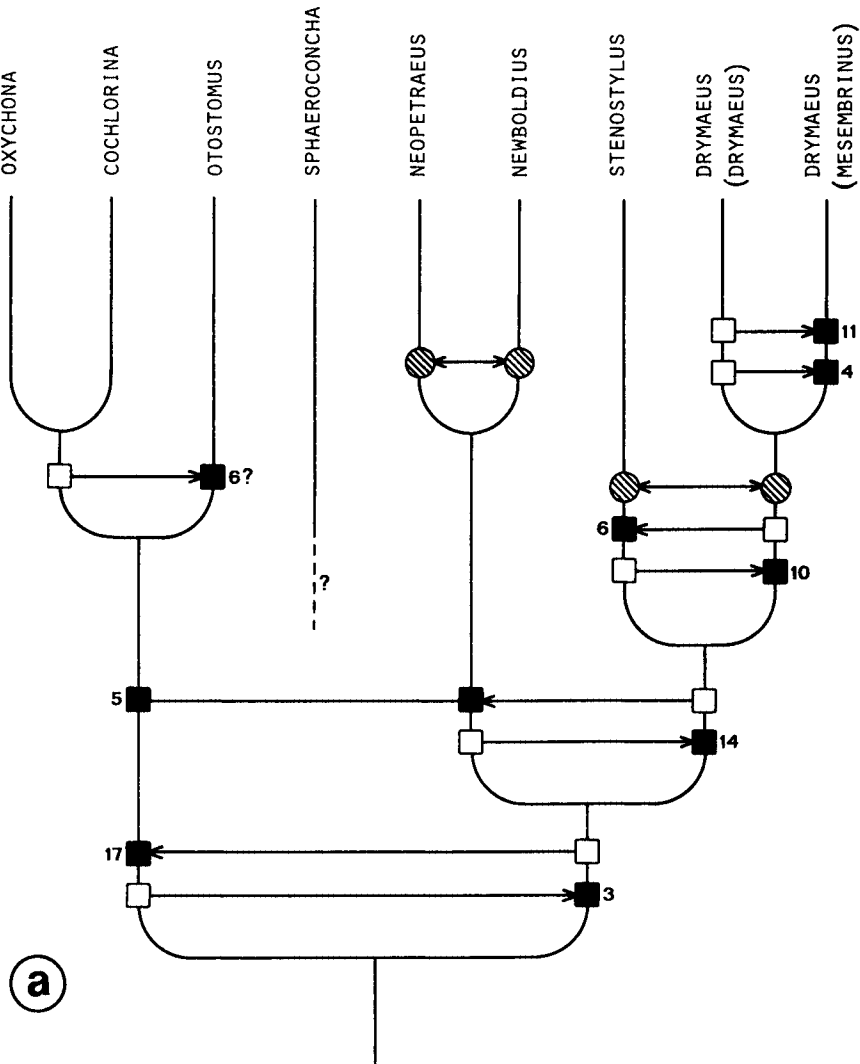


Fig. 177a. Hypothesis of phylogenetic relationships in the *Cochlorina*-group.

(1975a) the separation between Antarctica and Australia (i.e., between the *Bothriembryon*-stock and other Bulimulinae) took place ca. 55 m.y. ago.

Fig. 177 summarizes alternate hypotheses of phylogenetic relationships in the *Cochlorina*-group. In fig. 177b relative importance is assigned to character (5), in fig. 177a to character (3). The occurrence of these characters in different groups in the respective hypotheses may be the result of convergent evolution. The monophyly of *Newboldius* and *Neopetraeus* is not corro-

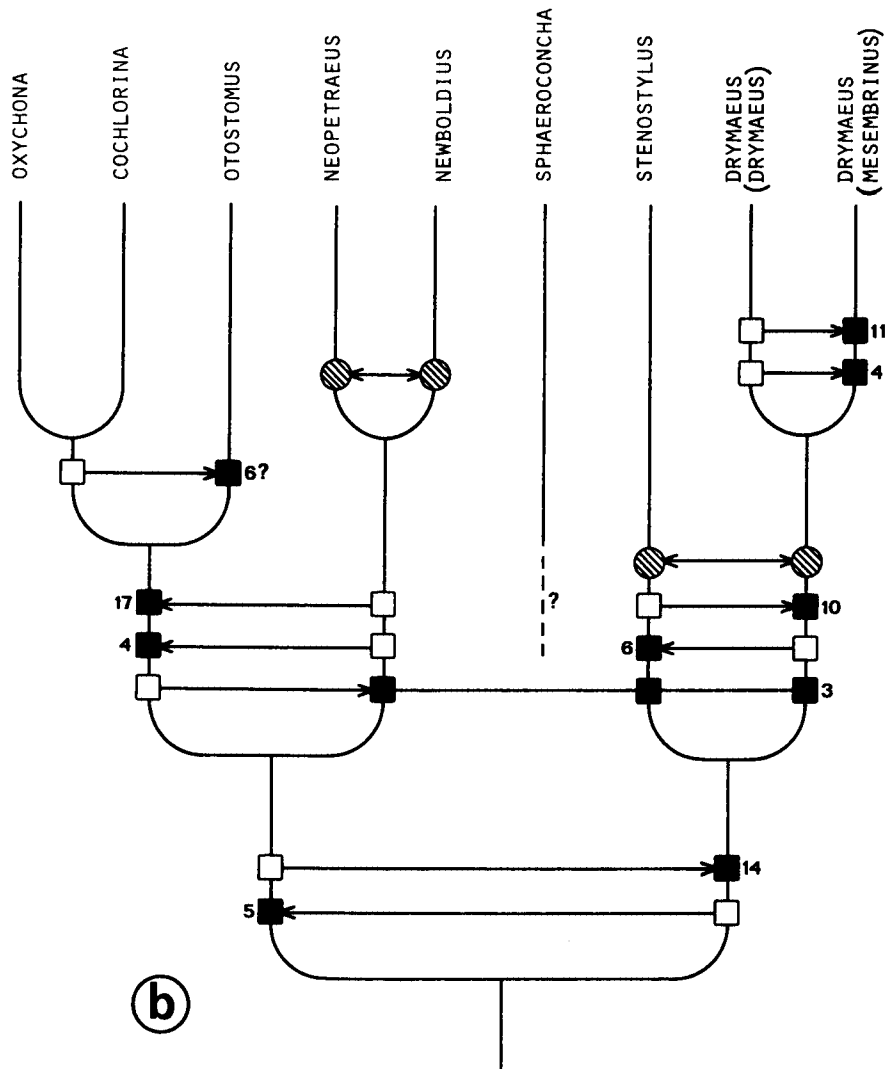


Fig. 177b. Hypothesis of phylogenetic relationships in the *Cochlorina*-group.

borated; they are separated on account of the shell morphology. The same applies to *Oxychona*, *Otostomus* and *Cochlorina*. The relationships of *Sphaeroconcha* are not clear and the genus is only tentatively incorporated in this genus group. The genera *Otostomus*, *Oxychona* and *Cochlorina* are



Fig. 178. Distribution of the *Cochlorina*-group.

restricted to eastern Brazil (Coastal Brazilian Shield). *Neopetraeus* and *Newboldius* are restricted to small areas in the Andes, while the distribution of *Stenostylus* is rather disjunct but also limited to the same mountain range. *Drymaeus* connects these two distribution areas, ranging from eastern Brazil via the Andes into Central America, the West Indies and Florida (fig. 178). This genus is divided into two subgenera: (a) *Drymaeus* s.str., which is found mainly in South America and extending its range into Central America as north as Central Mexico, and (b) *Drymaeus* (*Mesembrinus*), of which most species live in Central America, Florida and the West Indies, with some species scattered in South America. The relative abundance of apomorphic

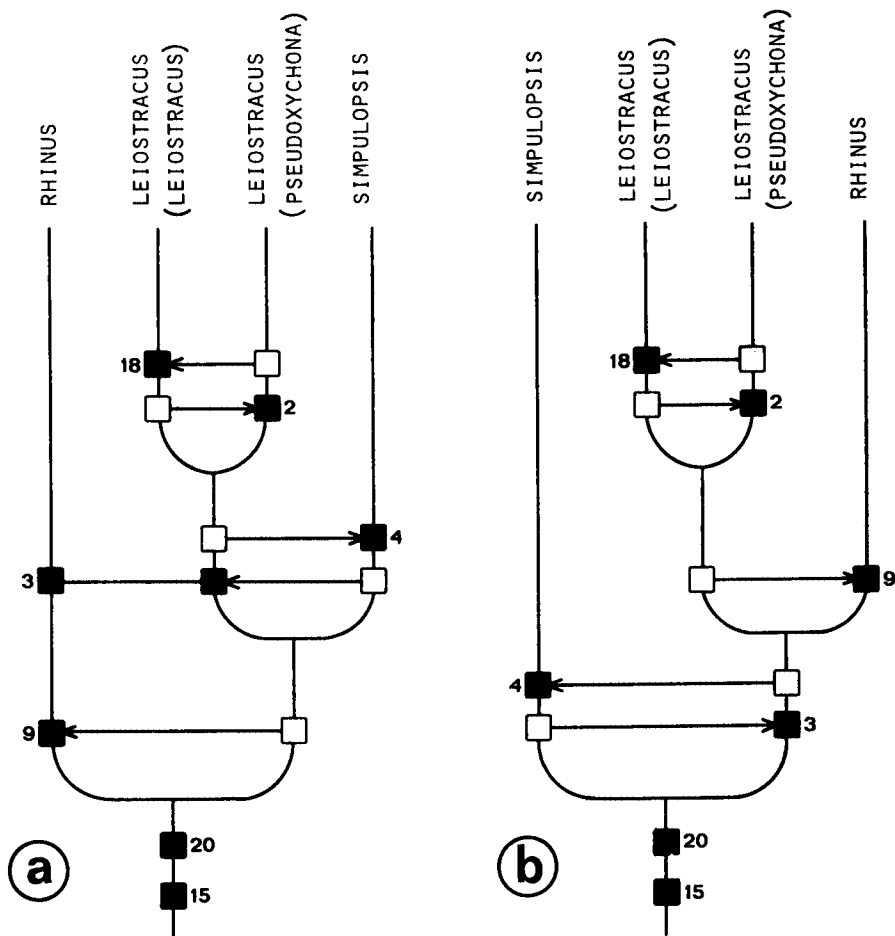


Fig. 179. Hypotheses of phylogenetic relationships in the *Simpulopsis*-group.

character states in *Drymaeus* (*Mesembrinus*) suggests that dispersal was primarily directed from South America to Central America.

Fig. 179 summarizes alternate hypotheses of phylogenetic relationships in the *Simpulopsis*-group. The monophyly of the group is corroborated by two

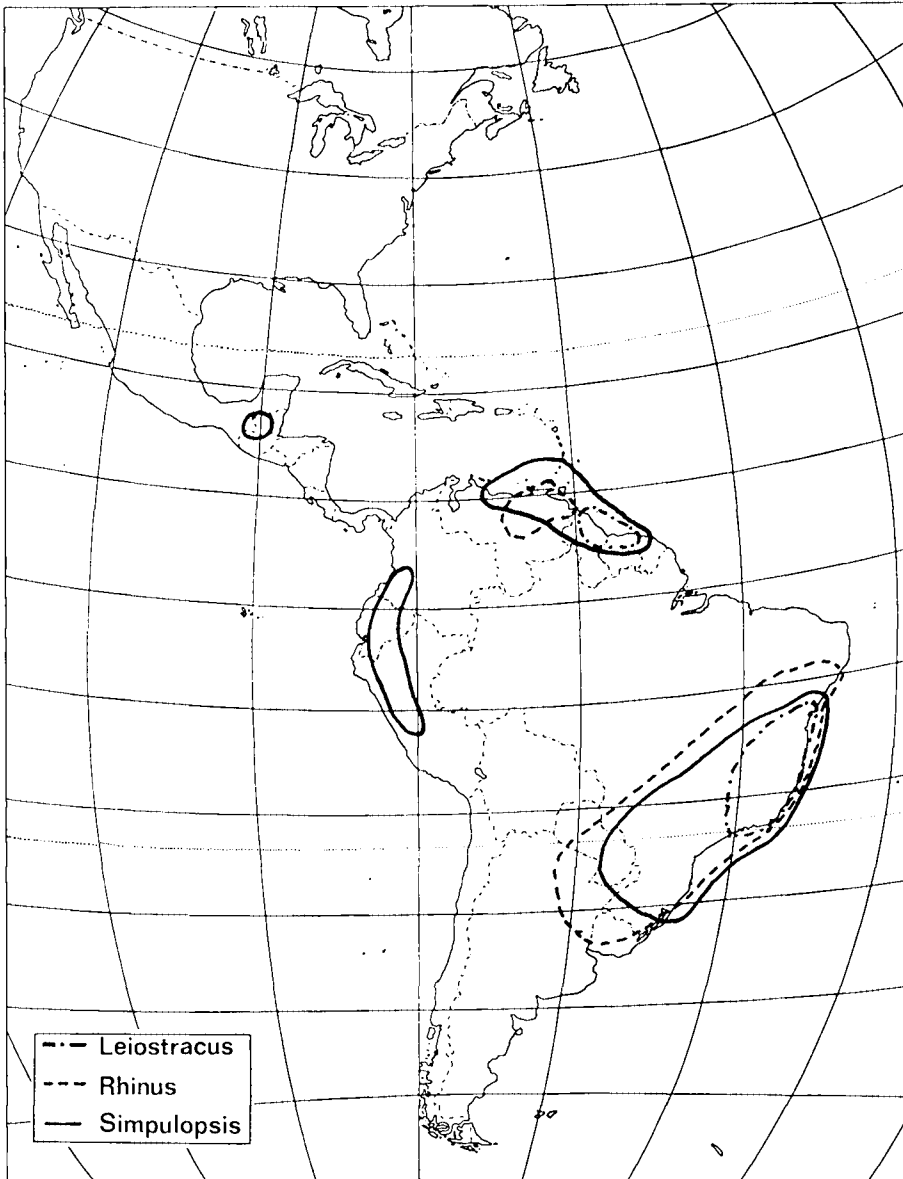


Fig. 180. Distribution of the *Simpulopsis*-group.

characters (15, 20). In fig. 179a relative importance is assigned to character (9) and the occurrence of character (3) may be the result of convergent evolution. If relative importance is assigned to character (3) the result as shown in fig. 179b emerges. The genus *Simpulopsis* shows a disjunct distribution (fig. 180): Mexico/Guatemala (Nuclear Central America), northern Andes, coastal part of the Guiana Shield, eastern Brazil (Coastal and Central Brazilian Shield). This possibly indicates that *Simpulopsis* is an old group (see, e.g., Croizat, 1976: figs. 57, 70, 77, etc. for similar distribution patterns). *Leiostracus* is found in Guiana/Surinam (Guiana Shield) and eastern Brazil (Coastal Brazilian Shield); *Rhinus* is found in the latter region and in Venezuela (Llanos Plain + Margarita Island). These distribution patterns are not in contradiction to the hypothesis shown in fig. 179a, but are more in accordance, in my opinion, with the hypothesis of fig. 179b.

VIII. INTRAFAMILIAR RELATIONSHIPS

In the present study the family Bulimulidae is considered *sensu lato*, viz. comprising five subfamilies: Bulimulinae, Placostylinae, Odontostominae, Orthalicinae and Amphibuliminae. Previous authors, e.g. Zilch (1960), have given part of these subfamilies familiar rank (all except Placostylinae that were integrated with Bulimulidae). Iredale (1937) has erected a family (Bothriembryontidae) for the Australian members of the Bulimulinae; anatomical research (Pilsbry, 1946b; Breure, 1978b) has shown that this classification is incorrect.

The relationships of the five subfamilies are now investigated, using own observations (Breure & Schouten, in preparation) and data from literature (Bulimulinae: see references. Placostylinae: Clapp, 1923; Climo, 1973; Kondo, 1948; Rensch & Rensch, 1935; Solem, 1959a; Starmühlner, 1970; Turner & Clench, 1972. Odontostominae: Araujo, 1963, 1973, 1975b; Heath, 1914; Hylton Scott, 1951, 1952, 1966, 1967c. Orthalicinae: Van Mol, 1971. Amphibuliminae: Breure, 1974c; Ihering, 1886; Leme, 1968; Van Mol, 1971).

With the data at hand the relationships of the subfamilies can only tentatively be indicated and further research is required.

The character transition series that have been recognized are summarized in Table 5 and concern the mandibula, radula, genitalia and protoconch [characters that involve convergence (e.g., radula structure, penis sheath, spermathecal duct) are left out of the transition series]: (1) the number of plates of the mandibula is usually relatively large (20 or more). A reduction in the number of plates is hypothesized to be apomorphic. (2) The surface of the mandibula may be smooth or granulate. The latter character state is

TABLE 5
Summary of character transition series in Bulimulidae

Character	Bulimulinae	Placostylinae	Odontostominae	Orthalicinae	Amphibuliminae
MANDIBULA					
1. Number of plates	large	large	small	large	large
2. Surface	smooth	granulate	smooth	smooth	smooth
3. Internal structure	amorphous	amorphous	amorphous	columnar	amorphous
RADULA					
Central teeth	mono/tricuspid	tricuspid	tricuspid	monocuspid	mono/tricuspid
Transverse rows	straight/V-shaped	straight	straight	V-shaped	straight/V-shaped
GENITALIA					
4. Genital atrium	absent	absent	absent	present	absent
5. Penis shape	cylindrical	club-shaped	cylindrical	conical	cylindrical
6. Penis appendix	absent	absent	absent	present	absent
Prox. penis sheath	present/absent	absent	present	absent	absent
7. Flagellum	present	reduced/absent	present	present	present
8. Retractor muscle	slender, thin	broad, thick	slender, thin	slender, thin	slender, thin
9. Torsion spermoviduct	absent	present	absent	intermediate	absent
Length spermathecal duct	normal ¹⁾ /reduced	normal/reduced	normal	normal	normal/reduced
Ovotestis size	intermediate	intermediate	small	large	intermediate
PALLIAL ORGANS					
10. Disposition ureters	sigmurethrous	sigmurethrous	sigmurethrous ²⁾	sigmurethrous	heterurethrous
11. Pulmonary veins	weak to strong	strong	weak	very strong	very strong
Adrectal ureter	open/closed	closed	open/closed	closed	closed
MUSCLE SYSTEM					
12. Columellar muscle	present	present	present	present	absent
SHELL					
13. Protoconch	sculptured	sculptured	sculptured	smooth	smooth
14. Dents/lamellae aperture	absent	absent	present	absent	absent

1) Normal is: as long as spermoviduct.

2) Some species show a mesurathrous disposition.

considered apomorphous. (3) The internal structure of the mandibula is normally more or less amorphous. In one subfamily the internal structure is columnar (Breure & Schouten, in preparation) and this is hypothesized to be apomorphous. (4) The presence of a relatively large genital atrium (in some species with the ♂- and ♀-openings separated) is hypothesized to be apomorphous. (5) The penis shape is cylindrical or conical; a club-shaped penis is considered apomorphous. (6) Usually the penis is without an appendix; the presence of such a structure is considered apomorphous. (7) The reduction or absence of the flagellum is hypothesized to be apomorphous. (8) The penis retractor muscle is normally slender and rather thin. A broad and relatively thick retractor muscle is considered an apomorphous character state. (9) The spermoviduct is usually hardly contorted. A strong torsion of this duct is hypothesized to be apomorphous. (10) The organisation of the adrenal and adrectal ureters is sigmurethrous [some species in the Odontostominae show a mesurethrous pattern; cf. Leme, 1973: fig. 13], except in the Amphibuliminae where their disposition is called heterurethrous by Van Mol (1971: 194); this disposition, caused by a process of limacisation, is hypothesized to be apomorphous. (11) The development of the pulmonary veins varies from weak (plesiomorphous) to very strong (Van Mol, o.c.: figs. 4-5), which is hypothesized to be apomorphous. (12) In the free muscular system the right and left eye retractor muscles and the pharyngeal retractor muscle are usually united into the columellar muscle. In the Amphibuliminae the muscles remain separated (Van Mol, o.c.: figs. 6B-E) and this is considered apomorphous. (13) The protoconch may be sculptured (plesiomorphous) or not (apomorphous). (14) The presence of dents and/or lamellae that narrow the aperture is considered an apomorphous character state.

The least rejected hypothesis of phylogenetic relationships between the five subfamilies is summarized in fig. 182. The family is hypothesized to be monophyletical.

The monophyly of the Placostylinae is corroborated by five characters (2, 5, 7, 8, 9), the monophyly of the Odontostominae by two (1, 14), the monophyly of the Orthalicinae + Amphibuliminae by two (11, 13), the monophyly of the Orthalicinae by three (3, 4, 6), the monophyly of the Amphibuliminae by two (10, 12). Nor the monophyly of the Odontostominae + Bulimulinae nor the monophyly of the Bulimulinae is corroborated by apomorphous character states, with the data at hand.

Solem (1959b: 305, 327) suggested a relationship between the southwestern Australian *Bothriembryon* and New Hebridian *Diplomorpha* and *Placostylus*, basing himself on anatomical data. The present data, however,

do not justify such a relationship. Solem (o.c.: 318, 327) also suggested that *Placostylus* has a northern origin. New data on continental drift and plate tectonics make a northern origin for this group unlikely (cf. Cracraft, 1975a). Instead, my suggestion is, (although hypothetical too) that the Placostylinae reached their present distribution area via West Antarctica and New Zealand and that *Bothriembryon* reached Australia via East Antarctica. This hypothesis makes the distribution of "primitive" and "advanced" *Placostylus* (Solem, o.c.: fig. 20) more plausible and, moreover, makes clear that *Bothriembryon* and *Placostylus* cannot be closely related.

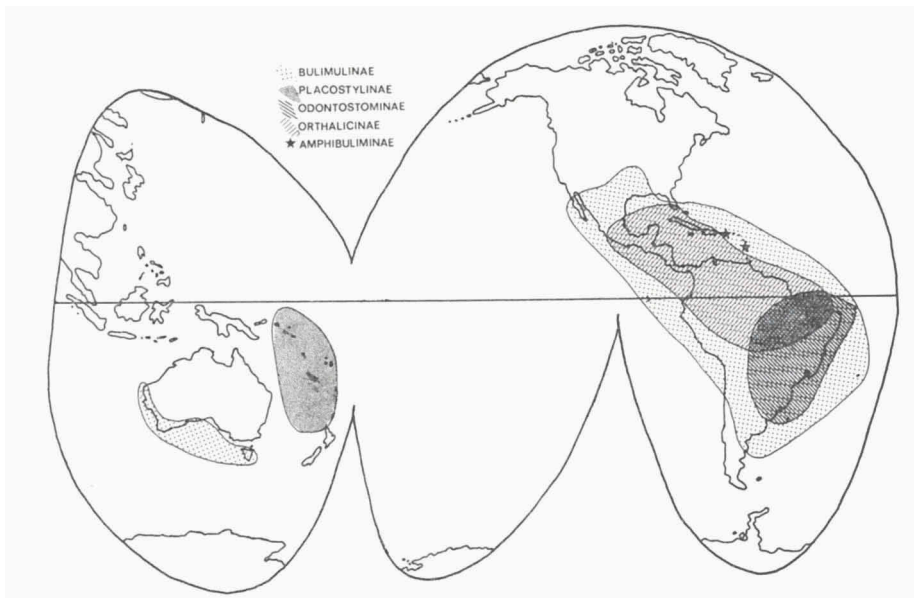


Fig. 181. Distribution of Bulimulidae.

An interesting question that remains is: how old are the subfamilies? The answer is only partially possible and is rather speculative, but Cracraft (1975a: fig. 4 and addendum) gives some useful data. Basing myself on his data, the origin of the family lies between 80-95 m.y. ago (as no bulimulids are present in Africa), i.e., in the Cretaceous. The Placostylinae are ca. 80 m.y. old, as New Zealand separated about that time from Antarctica. Lack of geophysical data, however, prevents speculation as regards the time of origin of the other subfamilies.

IX. SUMMARY

The relatively large family Bulimulidae is mainly distributed in the Neotropics. The family may be divided into five subfamilies: Bulimulinae (South

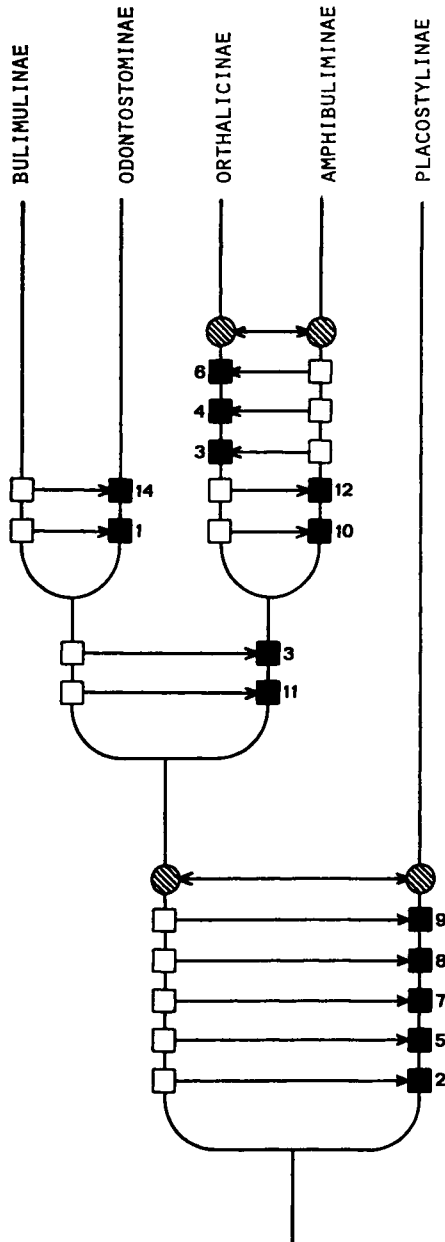


Fig. 182. Hypothesis of phylogenetic relationships of the subfamilies of Bulimulidae.

and Central America, southern United States, Australia; 43 (sub)genera), Odontostominae (eastern South America; 18 (sub)genera; Zilch, 1960), Orthalicinae (northern South America, Central America; 15 (sub)genera; Zilch, o.c.), Amphibuliminae (eastern South America, West Indies; 4 genera; Breure, 1974c) and Placostylinae (New Zealand, Melanesia; 15 (sub)genera; Zilch, o.c.).

So far the classification of the genera was mainly based on the sculpture of the protoconch (Pilsbry, 1896a). This character is still useful for identification, but it cannot be used for a phylogenetic analysis, nor can any other morphological character of the shell. On the contrary, the radula shows a variation that phylogenetically may be analyzed. The variation mainly concerns the shape of the teeth, the number of cusps, the presence or absence of supporting denticles and the shape of the transverse rows.

The pallial organs show variation in the prominence of the veins, the position of the pericard and the structure of the adrectal ureter (open or closed).

Further variation in the anatomy is found in the genitalia, viz. the spermiduct (position of glandular folds), spermathecal duct (relative length; presence or absence of an appendix), penis (presence or absence of a proximal sheath; shape of penis lumen; number of glandular celltypes), epiphallus (in some groups intruding the penis) and flagellum (place of insertion of the retractor muscle).

In the systematical part a synonymy, description, the distribution and a list of taxa are presented for each (sub)genus of the Bulimulinae. The number of (sub)generic taxa used so far (80) is now reduced to 43.

Accepting the methods of Hennig the genera can be divided into six groups. The present data do not allow these groups to be fitted into one phylogenetic scheme for the whole subfamily. The relationships between the five subfamilies also remain tentative.

The conclusion of an analysis of the existing biogeographical theories is that, after prior phylogenetic analysis, the vicariance theory of Croizat may be adopted. The distribution of the Bulimulinae is explained, using this theory, in the light of the geological history of the southern continents.

RESUMEN

La familia Bulimulidae, que es relativamente grande, se halla principalmente en la región neotropical. Se puede dividir la familia en cinco subfamilias: Bulimulinae (América del Sur y Central, la parte sur de los Estados Unidos, Australia; 43 (sub)géneros), Odontostominae (la parte este de América del Sur; 18 (sub)géneros), Orthalicinae (la parte norte de América

del Sur, América Central; 15 (sub)géneros), Amphibuliminae (la parte este de América del Sur, las Indias occidentales; 4 géneros) y Placostylinae (Nueva Zelandia, Melanesia; 15 (sub)géneros).

Hasta ahora la clasificación de los géneros estaba fundada sobre la escultura de la protoconcha. Se puede todavía usar esta característica para la identificación, pero no para el análisis filogenético ni otras características morfológicas de la concha. Al contrario, la rádula muestra una variación que se puede analizar filogenéticamente. Esta variación concierne la forma de los dientes, el número de cúspides, la presencia o la ausencia de "supporting denticles" y la forma de las hileras transversales.

Los órganos paleales muestran variación en la red circulatoria del pulmón y en la estructura de la uretra secundaria (abierta o cerrada).

Otra variación se muestra en los órganos genitales: el espermo-oviducto (posición de los pliegues glandulares), el pedúnculo (largura relativa; presencia u ausencia de un apéndice), penis (presencia u ausencia de una vaina muscular; forma del lumen; número de tipos de células glandulares), epiphallus (penetrando el penis en algunos grupos) y flagello (posición del fásículo muscular).

En la parte sistemática se presenta la sinonimia, una descripción, la distribución y una lista de taxa de cada (sub)género de la Bulimulinae. El número de los (sub)géneros era 80 y es reducido hasta 43.

Aceptando los métodos de Hennig se pueden dividir los géneros en seis grupos. Los datos actuales no se permiten reunir estos grupos en un esquema filogenético de toda la subfamilia. Asimismo las relaciones entre las cinco subfamilias quedan provisionarias.

La conclusión del análisis de las teorías biogeográficas existentes es que, después de un análisis filogenético precedente, se puede aceptar la teoría de vicariancia de Croizat. Usando esta teoría la distribución de las Bulimulinae es aclarada, a la luz de la historia geológica de los continentes australes.

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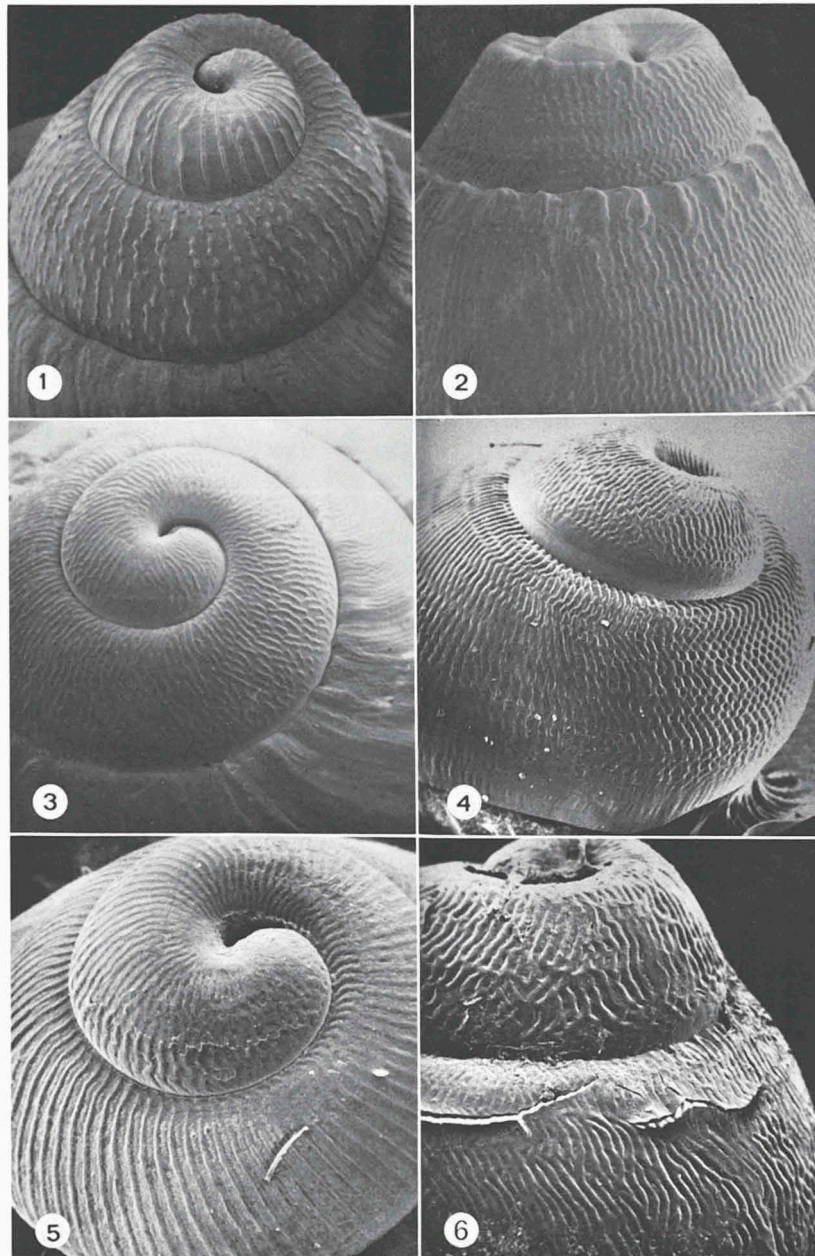


Fig. 1. *Thaumastus (Thaumastiella) occidentalis* Weyrauch, protoconch, $\times 26$. Fig. 2. *Thaumastus (Quechua) taulisensis* Zilch, protoconch, $\times 23$. Fig. 3. *Thaumastus (Paeniscutalus) crenellus* (Philippi), protoconch, $\times 24$. Fig. 4. *Bulimulus guadalupensis* (Bruguière), protoconch, $\times 58$. Fig. 5. *Rabdotus* spec., protoconch, $\times 57$. Fig. 6. *Scutalus (Suniellus) troscheli* (Philippi), protoconch, $\times 61$.

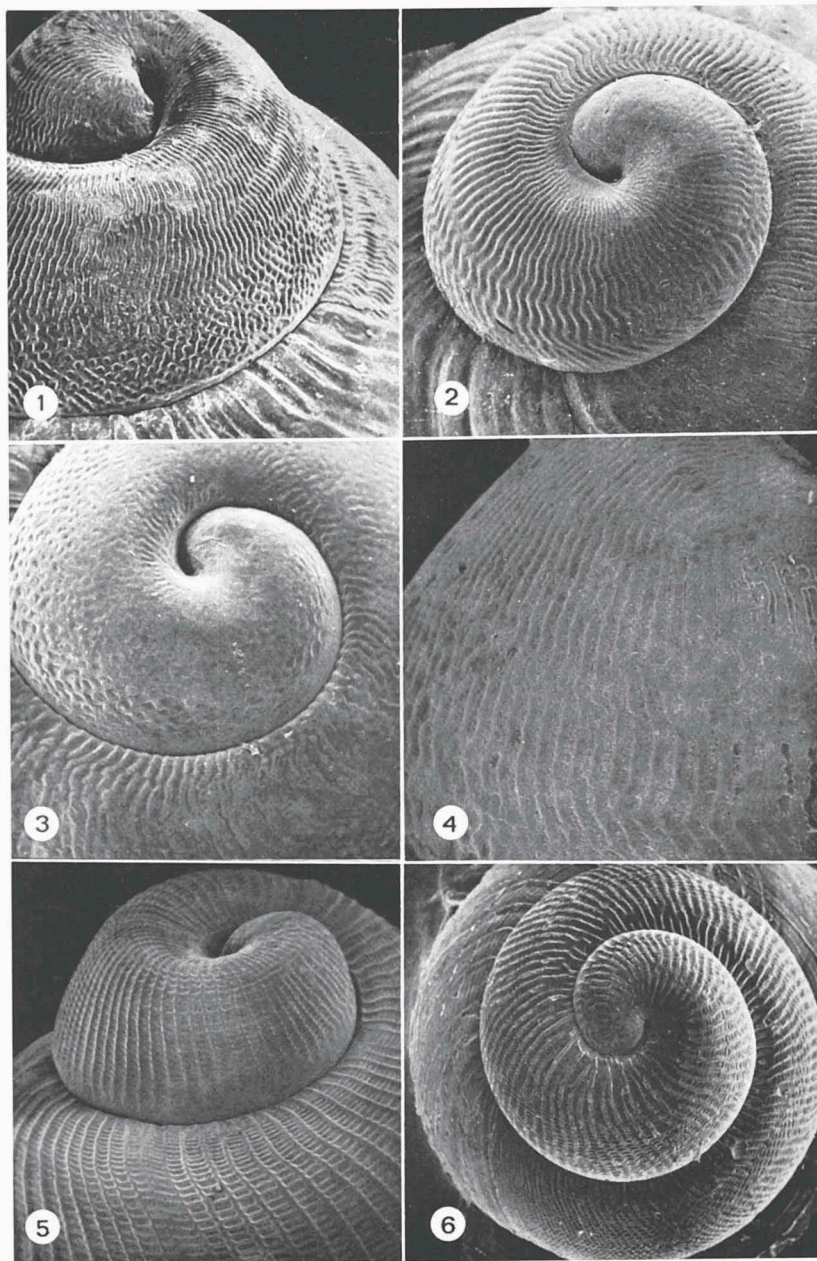


Fig. 1. *Scutalus (Vermiculatus) zeddellii* (Hupé), protoconch, $\times 63$. Fig. 2. *Plectostylus variegatus* (Pfeiffer), protoconch, $\times 71$. Fig. 3. *Bothriembryon (Bothriembryon) onslowi* (Cox), protoconch, $\times 100$. Fig. 4. *Bothriembryon (Tasmanembryon) gunnii* (Sowerby), protoconch, $\times 125$. Fig. 5. *Neopetraeus tessellatus* (Shuttleworth), protoconch, $\times 65$. Fig. 6. *Leiostracus (Pseudoxychona) spec.*, protoconch, $\times 53$.

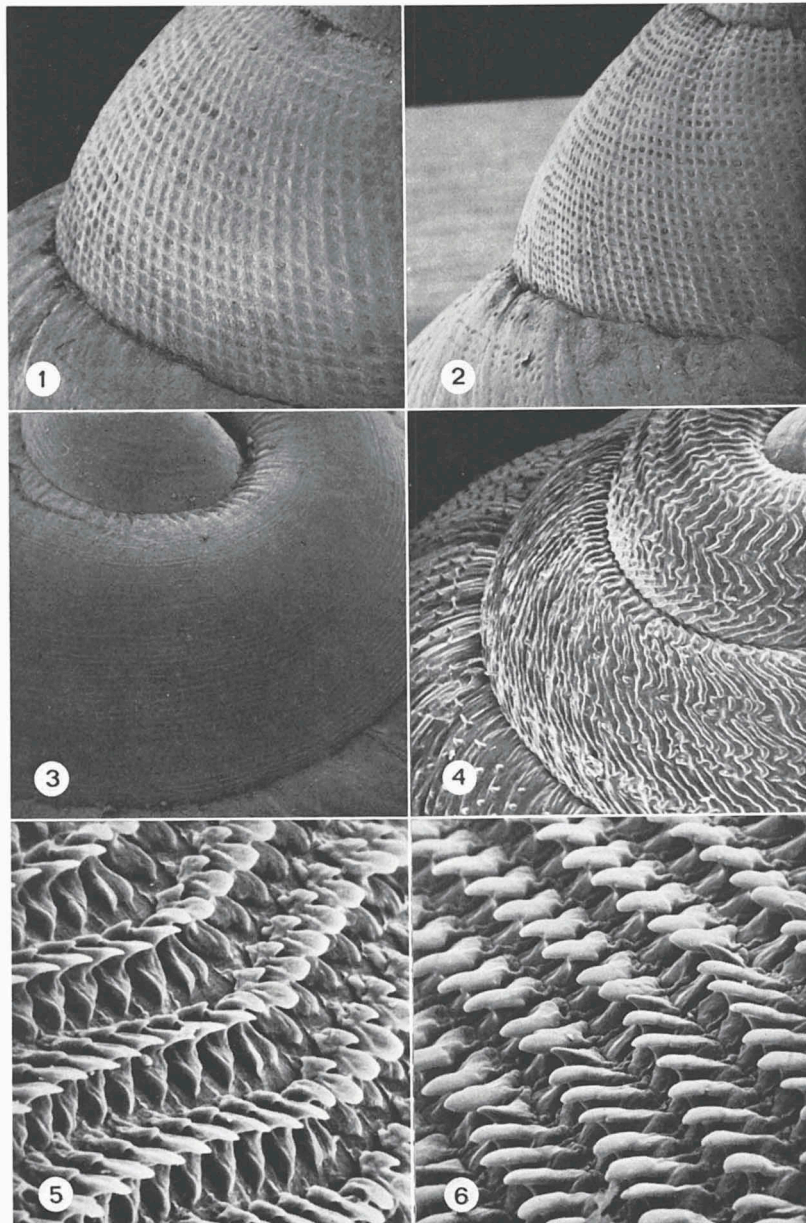


Fig. 1. *Drymaeus (Drymaeus) poecilus* (d'Orbigny), protoconch, $\times 56$. Fig. 2. *Drymaeus (Mesembrinus) emeus* (Say), protoconch, $\times 58$. Fig. 3. *Simpulopsis (Simpulopsis) decussata* Pfeiffer, protoconch, $\times 115$. Fig. 4. *Rhinus constrictus* (Reeve), protoconch, $\times 58$. Fig. 5. *Stenostylus meleagris* (Pfeiffer), central part of radula, $\times 580$. Fig. 6. *Neopetraeus camachoi* Weyrauch, central part of radula, $\times 530$.