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Mysterious or confusing: enigmatic species in the Orthalicidae (Gastropoda, Pulmonata)

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Five enigmatic species that have remained unnoticed or proved confusing are treated: *Bostryx alausiensis* (Cousin), *Bulimulus gelidus* (Reeve), *Stenostylus colmeiroi* (Hidalgo), *Stenostylus nigrolimbatus* (Pfeiffer) and *Simpulopsis (S.) simula* (Morelet). *Drymaeus (D.) cleefi* Breure & Eskens is now synonymized with *Stenostylus nigrolimbatus* (Pfeiffer).

Key words: Gastropoda, Pulmonata, Orthalicidae, *Bostryx*, *Bulimulus*, *Stenostylus*, *Simpulopsis*, taxonomy, distribution, Colombia, Ecuador, Guatemala.

INTRODUCTION

Every family has its own 'ghost members', here considered enigmatic species as they often lead to misidentifications in collections or are taxonomically troublesome, e.g. because they are unrecognized after their original description, usually many decades ago.

This paper deals with several of these enigmatic species from the Neotropical land snail family Orthalicidae. The species in this paper occur in three countries of which the land snail fauna is hitherto relatively poorly known: Guatemala, Colombia and Ecuador.

Until the recapitulative work of Thompson (2008), the most recent comprehensive review of the land snail fauna of Guatemala is the work of Martens (1890-1901). He lists 33 taxa as belonging to the Orthalicidae from Guatemala. Goodrich & Van der Schalie (1937) dealt with the malacological results of the fourth Carnegie Institution-University of Michigan expedition in Petén and north Alta Vera Paz. They list 63 species in total, of which 4 belong to the Orthalicoidea. As the expedition visited Guatemala during the dry period, 15 species that were mentioned by Martens for this region were not collected, one of which is the enigmatic *Simpulopsis simula* (Morelet). Although this "hidden" species has been reported by Bequaert (1957) from Mexico, its ecology and distribution remained virtually unknown.

Colombian land snails are merely known from very scattered papers. No faunal overview has yet been published, although some papers are under way (Borrero, forthcoming; Borrero & Breure, in preparation). Vera-Ardila (2008) prepared a list of the genera occurring in Colombia, together with some biogeographical notes. Although much remains to be researched, it is clear that the complex oreography of the country is a factor in the relatively high endemism observed in several groups. Vascular plants, birds and amphibians are the best documented in this respect (Duellman, 1999; Gentry et al., 1995; Kattan & Franco, 2004; Kattan et al., 2004; Myers et al., 2000). Ongoing studies suggest that approximately 50% of the species in the Orthalicidae is endemic (Borrero & Breure, in preparation). One of these endemic species is the enigmatic *Stenostylus nigrolimbatus* (Pfeiffer).

Ecuador is a relatively small country that is known for its biodiversity (Myers et al., 2000; Brooks et al., 2006). Land snails from this country are not very well known; Cousin (1887) and Germain (1910) made the most comprehensive contributions so far. In their review of the Orthalicidae of Ecuador, Breure & Borrero (2008) list 168 taxa belonging to

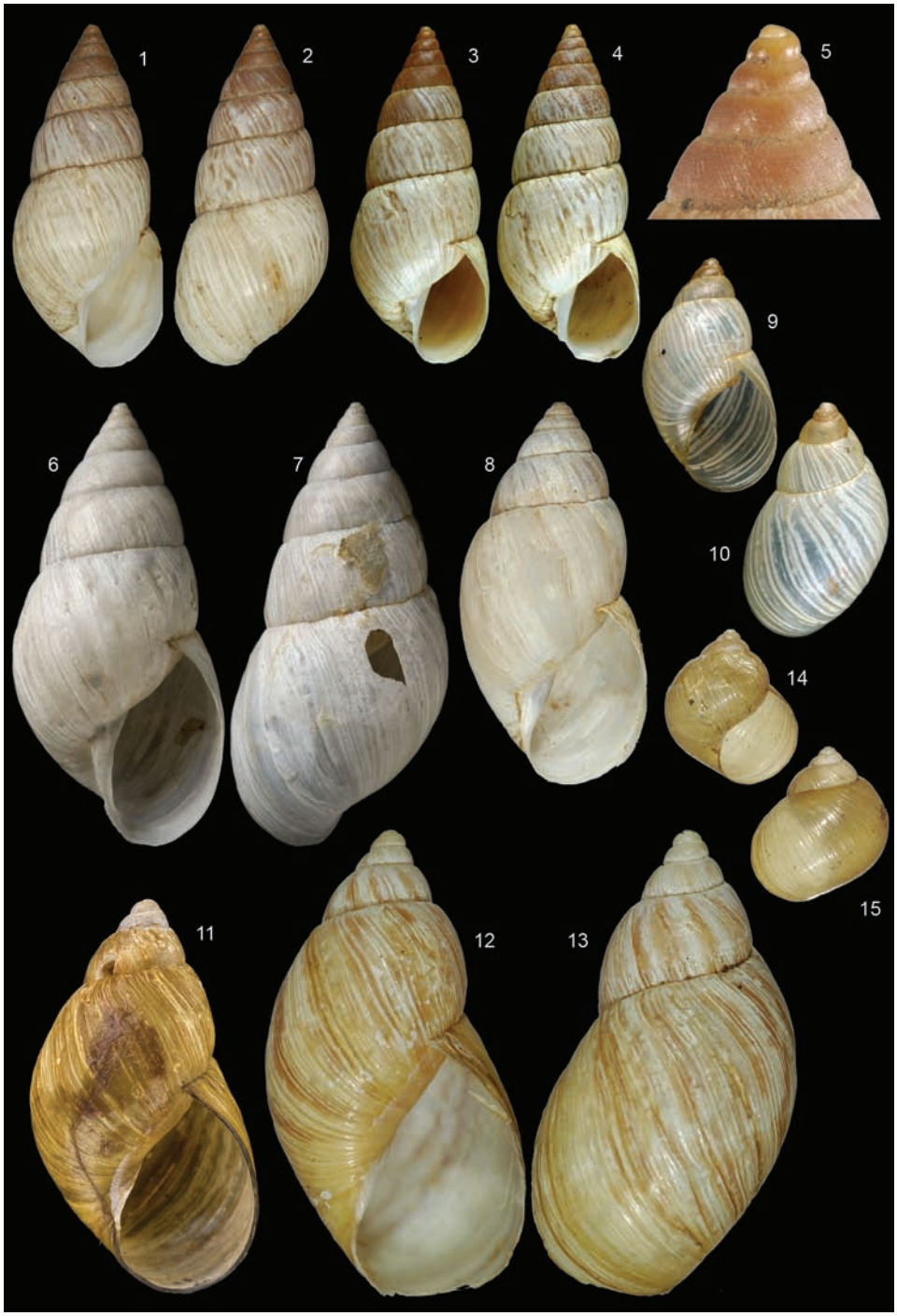
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Fig. **16**, *Stenotylus colmeiroi* on calcareous ridges with potteaceous mosses and *Andreaea rupestris* at c. 4300 m in humid lower superpáramo of Almorzadero (Dept. Santander). November 19, 1979. Leg. Antoine M. Cleef & Henry Hooghiemstra (Cleef diapos. 3985).

this family, of which 63 from the Galápagos; endemism is high: 79%. From the mainland species 30 are known from a single locality, and 11 of these species have not been recollected since their original description. Three species of this group are considered enigmatic, due to taxonomic indistinctness: *Bostryx alausiensis* (Cousin), *Bulimulus gelidus* (Reeve) and *Stenostylus colmeiroi* (Hidalgo).

METHODS

The following abbreviations are used to refer to museum collections: BMNH — Natural History Museum, London, UK; FLMNH — Florida Museum of Natural History, Gainesville, USA; MACN — Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN — Muséum National d'Histoire Naturelle, Paris, France; RMNH — National Museum of Natural History/Naturalis, Leiden, The Netherlands; UVZ — Universidad del Valle, Zoología, Cali, Colombia.

Other abbreviations are referring to the dimensions of the shells, measured with a digital sliding gauge and following the methods as described by Breure (1974: figs 2-3): D, diameter of the shell; H, height of the shell; HA: height of aperture; LW, height of last

◀ Figs **1-5**. *Bostryx alausiensis* (Cousin). **1-2**, lectotype (MNHN 20820, shell height 24.3 mm), **3-4**, paralectotypes (MNHN 20821, shell height 23.9 mm; photo: Virginie Héros), **5**, structure on upper whorls showing spiral lines of oblong granules. **6-8**. *Bulimulus gelidus* (Reeve). **6-7**, lectotype (BMNH 1975402, shell height 31.4 mm; photos: NHM), **8**, Ecuador, Alausí (RMNH, shell height 27.0 mm). **9-14**. *Stenostylus* spec. **9-10**, *Stenotylus colmeiroi* (Hidalgo), syntype (MNHN 20822, shell height 16.7 mm; photos: MNHN, Virginie Héros); **11**, *Stenostylus nigrolimbatus* (Pfeiffer), lectotype (BMNH 1975549, shell height 28.0 mm; photo: NHM); **12-13**, do., Colombia, Páramo de Almorzadero (RMNH 55375, shell height 33.0 mm). **14-15**. *Simpulopsis (S.) simula* (Morelet), Guatemala, 11 km W Lanquín (FLMNH 190137, shell height 11.0 mm).

whorl; W, number of whorls; WA, width of aperture. All measurements are in mm.

Geo-referenced locality data (following National Geospatial-Intelligence Agency, 2008) were used as input in Maxent 3.2.1 (Phillips et al., 2004, 2006; Phillips & Dudik, 2008; see also http://www.cs.princeton.edu/~schapire/maxent), together with environmental data layers. As default settings the following variables were used: annual diurnal temperature range; annual frost frequency; January, April, July, October, and annual precipitation; minimum, maximum and mean annual temperature; annual vapor pressure; elevation and ecoregions (all based on data as resampled by Phillips et al., 2006, who also discusses the use of environmental variables). Models were generated using the following settings: random test percentage 25, regularization multiplier 1, maximum iterations 500 and convergence treshold 0.00001 (see also Phillips et al., 2006). The resulting distribution was a grid file with logistic values, used as input for DIVA-GIS 5.4 (Hijmans et al., 2007). Within DIVA-GIS a multi-layered data analysis was performed combining the grid file output from Maxent as basis, plus shape files of Central and South America, combined with the relevant localities of species. The result was viewed using the Design tab of DIVA-GIS and saved as a tiff-file for further processing. For further discussion of methodology see Breure & Borrero (2008).

SYSTEMATICS

Family Orthalicidae Albers, 1860

Bostryx alausiensis (Cousin, 1887) (figs 1-5)

Thaumastus alausiensis Cousin, 1887: 228, pl. 4 fig. 13 (MNHN 20820/lectotype and 20821/17 paralectotypes).

Bulimulus (Bostryx) alausienis Cousin; Pilsbry, 1896: 180, pl. 50 fig. 59.

Peronaeus (Lissoacme) alausiensis (Cousin); Breure, 1976: 1141, pl. 6 fig. 4 (designation and figure of lectotype).

Thaumastus alausiensis Cousin; Breure, 1979: 135 (as *nomen inquirendum*).

Thaumastus alausiensis Cousin; Breure & Borrero, 2008: 29 (under *incertae sedis*).

Material studied. — "Équateur", A. Cousin leg., ex Jousseaume Colln (MNHN).

Discussion. — This species was described by Cousin, who lived for many years in Ecuador, on the basis of material collected by him in Prov. Chimborazo, between Achapallas [Achupallas, 02° 17′ 05″ S 078° 45′ 25″ W, 3550 m] and Río Sula, near Alausí [02° 12′ 40″ S 078° 50′ 36″ W, 2550 m], under stones and at the base of cacti at 2800m. Since the type material was described, no additional specimens are known to have been collected and the status of this taxon remained somewhat problematic. Recently a specimen was found in the RMNH-collection, collected near Alausí, that at first sight was considered to belong to this taxon. After comparison with the type material it is clear that this specimen belongs to another enigmatic species.

Bostryx alausiensis is characterized by (1) being slender, (2) having a relatively small aperture, (3) having the growth striae strong and irregular, giving a marbled appearance, (4) the upper whorls reddish to grey-brown coloured, exceptionally corneous, and (5) the growth-striae on these whorls crossed by spiral bands of oblong granulae. These granules could be an indication that as a juvenile the shell is hairy.

The lectotype is here refigured according to present-day standards.

Dimensions: see table 1.

	H	D	HA	WA	LW	W	H/D	HA/WA	HA/H	LW/H
M	22,8	10	8,5	5,2	13,1	7,7	2,28	1,64	0,37	0,58
s	1,41	0,50	0,73	0,41	0,80	0,38	0,09	0,10	0,03	0,02
max	25,6	11	10,4	5,8	15,4	8,2	2,44	1,82	0,41	0,61
min	20,5	9,3	7,5	4,5	12,1	6,7	2,15	1,45	0,33	0,53

Table **1**. Dimensions of *Bostryx alausiensis* (Cousin). Type material, MNHN (N = 17).

Bulimulus gelidus (Reeve, 1849) (figs 6-8)

Bulimus gelidus Reeve, 1849: pl. 76 fig. 553 (BMNH 1975402/lectotype).
Bulimulus sporadicus montevidensis (Pfeiffer); Pilsbry, 1898: 320.
Bulimulus gelidus (Reeve); Breure, 1979: 62 (designation of lectotype).

Material studied. — Ecuador, Prov. Chimborazo, Alausí, Luis E. Peña leg., 13.xii.1971 (RMNH/1); "Chimborazzo", Hoffmann leg., 1852 ex Mousson Colln (ZMZ 512237/2); "Central America", ex Cuming Colln (BMNH 1975402).

Discussion. — This taxon, described from "Central America?" by Reeve, remained unnoticed until Pilsbry placed it in the synonymy of *Bulimulus sporadicus montevidensis* (Pfeiffer, 1846). He notes "Mr. E.A. Smith, from an examination of the type, considers it probably identical with the Montevideo variety" (Pilsbry, 1898: 320). Recently three specimens turned up that have been compared to the lectotype in the BMNH. They all originate from Ecuador, one revealing the area where this species really occurs: Prov. Chimborazo, near Alausí. This is a new record for the Ecuadorian malacofauna and an addition to Breure & Borrero (2008).

Dimensions: see Table 2.

Collection	H	D	HA	WA	LW	W
BMNH	31,4	15	14	8,9	20,7	7,7
RMNH	27	13,2	12,2	8,8	19,7	6
ZMZ	27,5	13,4	12,2	7,6	18,5	6,1
ZMZ	26,1	12,4	11,5	7,3	18	5,4

Table **2**. Dimensions of *Bulimulus gelidus* (Reeve).

Stenostylus colmeiroi (Hidalgo, 1872) (figs 9-10)

Bulimus colmeiroi Hidalgoi, 1872: 122 (MNHN 20822/lectotype; MACN 15.05/3301/1 paralectotype).
Drymaeus colmeiroi (Hidalgo); Pilsbry, 1898: 316, pl. 46 fig. 54-55.
Stenostylus colmeiroi (Hidalgo); Breure, 1976: 1153, pl. 10 fig. 6 (designation and figure of lectotype).
Stenostylus colmeiroi (Hidalgo); Breure, 1979: 102.
Drymaeus (Mesembrinus) colmeiroi (Hidalgo); Breure & Schouten, 1981: 55.
Bulimus colmeiroi Hildalgo; Templado et al., 1993: 214.
Stenostylus colmeiroi Hidalgo; Richardson, 1995: 369.

Material studied. — [Ecuador, Prov. Napo, Baeza], ex Journal de Conchyliologie Colln (MNHN 20822).

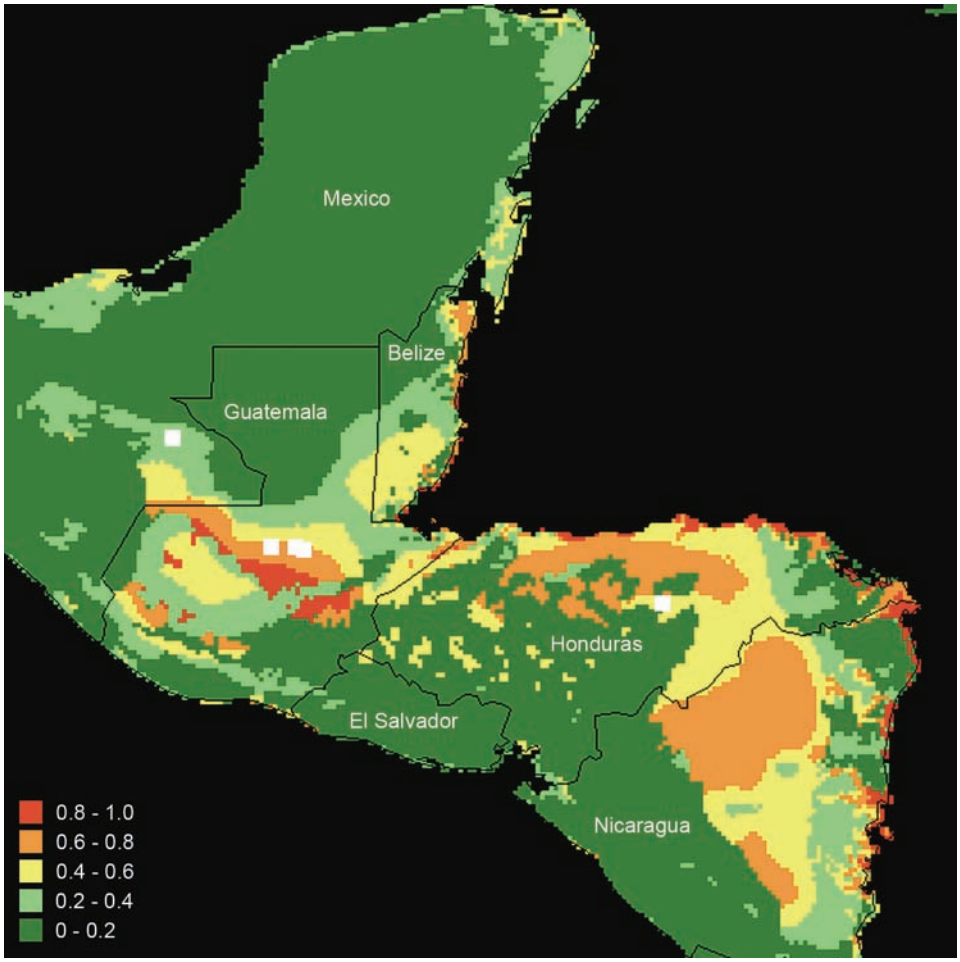

Fig. **17**. Potential distribution range of *Simpulopsis* in Mexico, Guatemala and Honduras, using Maxent modelling; squares are localities where specimens of *Simpulopsis simula* (Morelet) have been found.

Discussion. — The publication date of this species has been a first source of confusion. Richardson (1995) lists 1869 as the year of publication, apparently overlooking that the 'Moluscos del viaje al Pacífico' contained three parts of which the number did not correspond to the sequence of publication. Part one by Hildalgo on the terrestrial molluscs, was published in 1872; part two by F.P. Martínez y Sáez on marine bivalves was published earlier, in 1869, and part three, again by Hidalgo, on marine gastropods was published in 1879 (López-Ocón & Badía, 2003).

A second source of confusion has been the generic placement of this taxon. Breure & Eskens (1981) transferred this species to *Drymaeus (Mesembrinus)* on account of material from Colombia, Valle del Cauca, Lago Calima, road to Campo Alegre (UVZ). This appears to be a misidentification for *Simpulopsis (Eudioptus) citrinovitrea* (Moricand, 1836), an error also observed in museum collections (Breure & Borrero, 2008). After restudy of the type

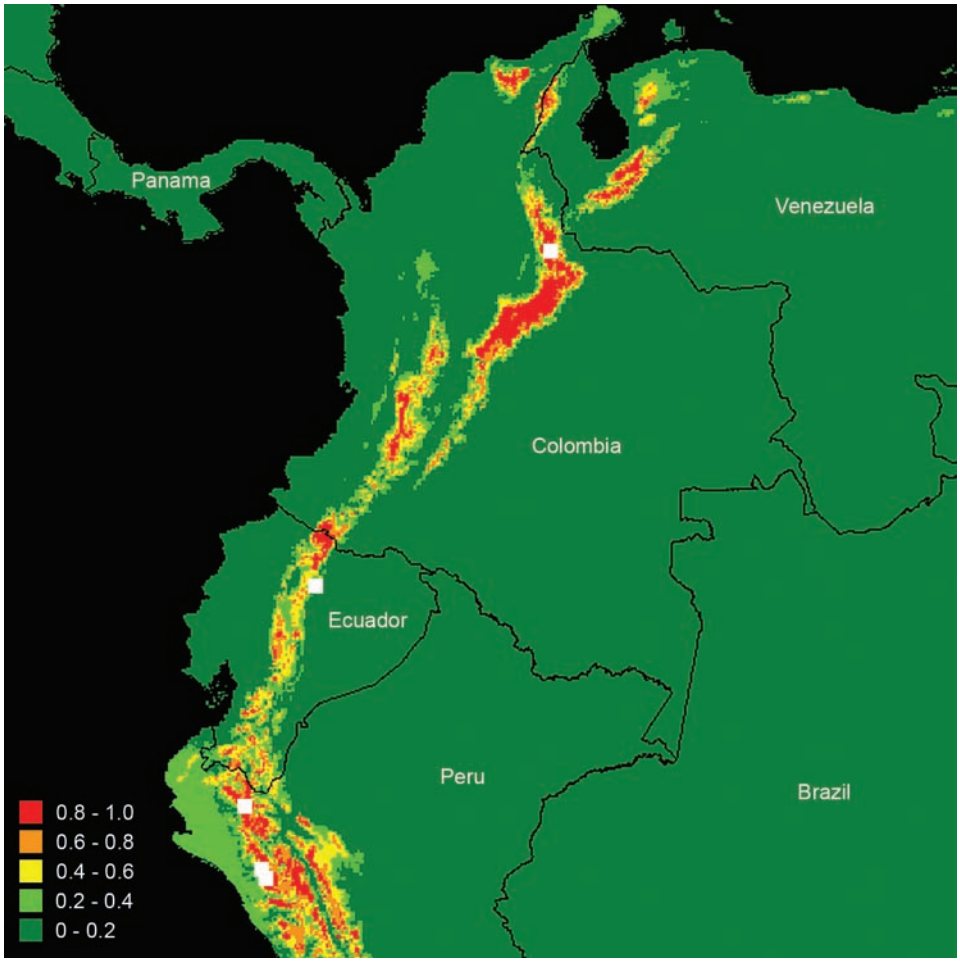

Fig. **18**. Potential distribution range of *Stenostylus* in northwestern South America, using Maxent modelling; squares are localities where species of this genus have been recorded.

material in the MNHN-collection, this error is here corrected and the species is placed in *Stenostylus* again.

Breure (1976) considered the type specimen in the MNHN as holotype, but as Hidalgo did not mention on how many specimens the original description was based, it should be considered a lectotype according to ICZN-rules. Templado et al. (1993) have indeed mentioned another specimen from the Hidalgo collection, present in the MACN-collection.

Stenostylus nigrolimbatus (Pfeiffer, 1853) (figs 11-13, 16)

Bulimus nigrolimbatus Pfeiffer, 1853: 257 (BMNH 1975549/lectotype, BMNH 1975550/paralectotype).
Bulimus nigrolimbatus Pfeiffer; Pfeiffer [1853] in Küster & Pfeiffer, 1845-1855: 81, pl. 21 figs 26-30.

Drymaeus nigrolimbatus (Pfeiffer); Pilsbry, 1898: 315, pl. 46 fig. 47-48, 50-51, 56.
Stenostylus nigrolimbatus (Pfeiffer); Breure, 1978: 219 (designation of lectotype).
Stenostylus nigrolimbatus (Pfeiffer); Breure, 1979: 103.
Drymaeus (Drymaeus) cleefi Breure & Eskens, 1981: 14, figs 32-33, pl. 5 figs 7-8 (description, reproductive anatomy, ecology). New synynomy.

Material studied. — Colombia, Dept. Santander, Páramo de Almorzadero, Piedra de Molina, 4225 m, A.M. Cleef, J. Aguirre C. & H. Hooghiemstra leg., 17.xi.1978 (RMNH 55375/1, 55376/8 subadults). "Andes of New Granada" (BMNH 1975549/lectotype).

Discussion. — Pfeiffer's description was originally read for the Zoological Society of London in 1851 but published in December 1853 (Duncan, 1937). Later he figured the original series in the Conchylien-Cabinet, describing two colour forms. The material originates from "Andes of New Granada" without further specification, thus leaving doubt on where it might actually occur. The description — translated by Pilsbry, who copied the figures from the Conchylien-Cabinet – suggested it to be based on adult specimens. When I found part of the type series in the BMNH collection, I had no reason to question this. However, in hindsight the types are subadults that do not show the full coloration that belongs to this taxon and which may be observed when the shells are collected fresh. According to Weyrauch (1956), *Stenostylus* is characterized by having (1) a thin cuticula that peels off the shell, (2) the surface of the postembryonic whorls with incrassate growth striae, (3) a pearly luster on the inside of the aperture. In the shells that Cleef et al. collected at one of the highest parts of the Cordillera Oriental in Colombia, the first characteristic is not very noticeable, while the inside of the aperture is whitish. This may have confused Breure & Eskens (1981), who described this material as *Drymaeus (Drymaeus) cleefi*. This taxon appears to be the adult form of *nigrolimbatus*, thus we may now conclude the enigma of *Bulimus nigrolimbatus* to be resolved.

Simpulopsis (Simpulopsis) simula (Morelet, 1851) (figs 14-15)

Bulimus simulus Morelet, 1851: 11 (BMNH 1893.2.4.1128-1129/2 syntypes).
Simpulopsis simula (Morelet); Pilsbry, 1899: 219, pl. 63 fig. 56-57.
Simpulopsis simula (Morelet); Goodrich & Van der Schalie, 1937: 21 (expected but not found in region of type locality).
Simpulopsis simula (Morelet); Bequaert, 1957: 221 (new locality record).
Simpulopsis simula (Morelet); Breure, 1979: 134.

Material studied. — Guatemala, Dept. Alta Verapaz, 15 km N Cobán [15° 37′ 14″ N 090° 19′ 10″ W], F.G. Thompson leg., 18.ii.1991 (FLMNH/189910/1 juv.); 3 km W Pajál [15° 35′ 11″ N 090° 04′ 16″ W], F.G. Thompson & S.P. Christman leg., 20.ii.1991 (FLMNH 190028/1); 11 km W Lanquín [15° 33′ 29″ N 090° 04′ 02″ W], F.G. Thompson & S.P. Christman leg., 22.ii.1991 (FLMNH 190137/2). Honduras, Dept. Olancho, vicinity of Magua Cave [14° 56′ 50″ N 086° 07′ 50″ W], circa 15 km SSW Gualaco, F.G. Thompson & H.G. Lee leg., 11.iii.1993 (FLMNH 194333/1).

Discussion. — This species was for many years only known from the type material, until Bequaert reported it from Mexico, Chiapas, Laguna Ocotal [16° 49′ 00″ N 091° 27′ 00″ W] to El Censo, 700-1000 m; it was collected on leaves of epiphytic plants (*Philodendron* sp.). The collection of the Florida museum proved to house specimens that were found by Thompson during several collecting trips. Described from the "forests of Petén" by Morelet, the first precise localities in Guatemala are: (1) Dept. Alta Verapaz, 15 km by road

north of Cobán, 1050 m, in leaf-litter on a very steep north-facing limestone slope with a cut-over rainforest thicket; (2) do., 3 km W of Pajál, 1130 m, in leaf-litter in a deep limestone ravine with large trees and open understory; (3) do., 11 km W of Lanquín, 1000 m, collected at the base of a slope covered with tropical broad-leaf forest with little understory in a zone with numerous sink-holes and caves. Whereas the species was hitherto only known from southeastern Mexico and northern Guatemala, a new record is: (4) Honduras, Dept. Olancho, vicinity of Magua Cave, 940 m, in mesic forest near the cave amoung limestone boulders and ledges.

All material was collected as empty shells. It may be noted that species of this genus are usually hard to find, especially alive. According to Morelet this species lives on the leaves of trees, suggesting an arboreal habitat preference. The record of Bequeart (1957) corroborates this preference.

DISTRIBUTIONAL OBSERVATIONS

The additonal distribution data that became available during this study, make predictions possible about potential distribution ranges using Maxent for ecological niche modelling. Given the low number of occurrences, the analyses have been made at the generic level. The results are expressed as logistic values, represented on the maps (figs 17-18) in five classes, ranging from very unlikely (0-0.2, dark green) to very likely (0.8-1.0, red).

Simpulopsis Beck, 1837

Until now the records for this genus from Central America (two other species are known from Mexico) were unconfirmed. Adding the precise localities to those of other *Simpulopsis* species and modelling its total range in Central and South America, also helps to better predict the potential distribution of *S. simula* (fig. 17). Environmental variables that have a comparatively high influence on the distribution model are maximum annual temperature and ecoregions. When we analyse the range using the distribution of ecoregions (National Geographic Society, 2008), it becomes clear that this genus seems to be confined to montane forests. This concurs with the known ecology of South American species (Gomes et al., 2004). *Simpulopsis cumingi* Pfeiffer, 1861, which could either be synonymous or a sister species of *S. simula*, might prove to occur in Mexico, Chiapas, close to the border of Guatemala. The taxonomic status of the third taxon, *Simpulopsis aenea* Pfeiffer, 1861, reported from Mexico, Oaxaca, needs further clarification.

Stenostylus Pilsbry, 1898

Locality records were taken from literature and analyzed. As the number of precise localities is rather low, the available data of the following species have been used: *colmeiroi, nigrolimbatus* (this publication); *meleagris* Pfeiffer, 1854 (Breure, 1978); *tapadoides* Philippi, 1867, *zilchi* Weyrauch, 1956 (both type localities as given by Breure, 1979). The resulting model is presented in fig. 18, showing that *Stenostylus* is potentially widely distributed in the Andes but restricted to the higher parts (usually above 3000 m). The lowest occurence regards *S. colmeiroi* from Baeza, which lies on 2000 m; it may hypothesized that its actual occurrence is at higher altitudes west of this locality.

The environmental variable that predominantly influences the distribution model is the altitude, with January percipitation as a minor factor.

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