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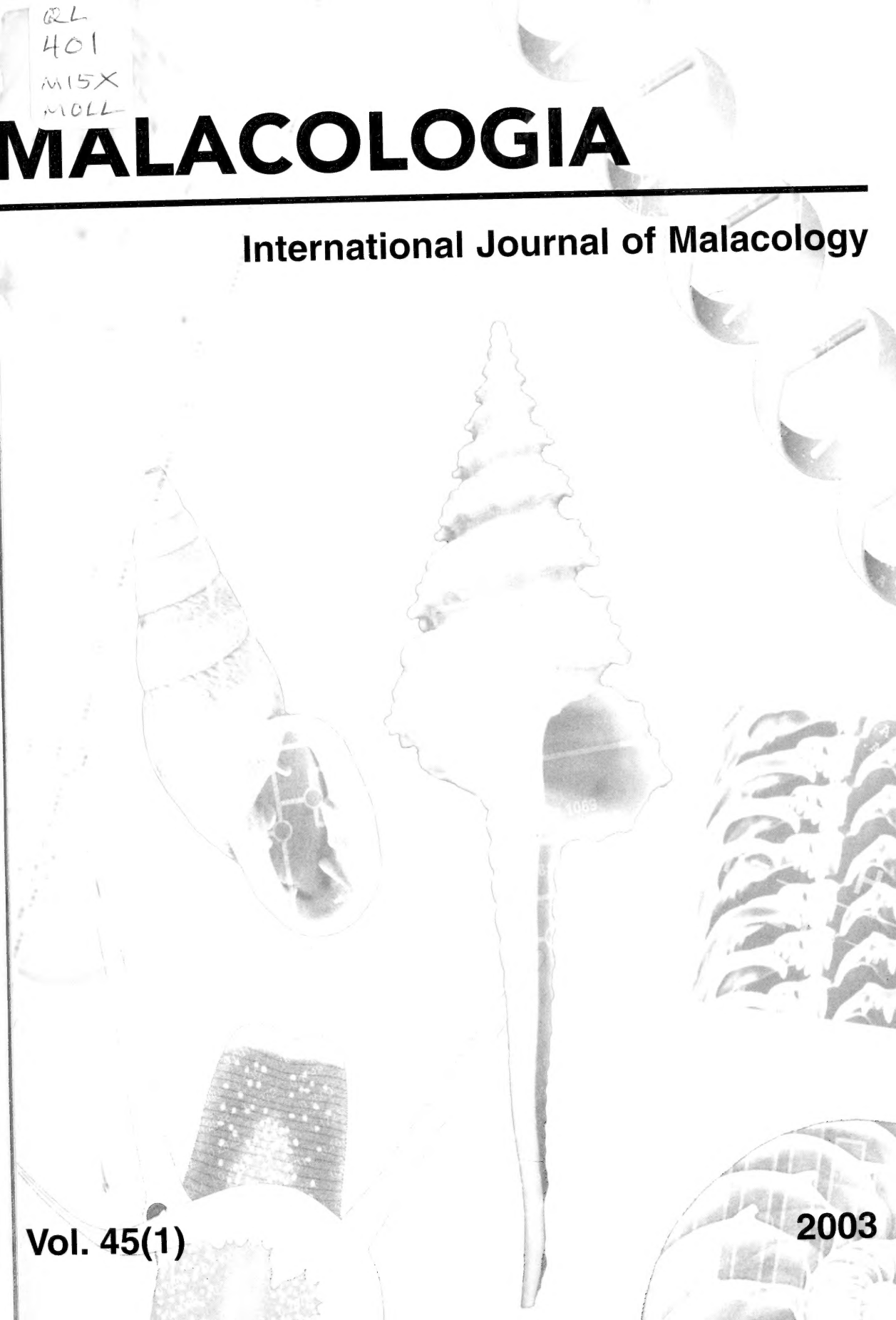

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TOWARD A SYSTEMATIC REVISION OF BROODING FRESHWATER CORBICULIDAE IN SOUTHEAST ASIA (BIVALVIA, VENEROIDA): ON SHELL MORPHOLOGY, ANATOMY AND MOLECULAR PHYLOGENETICS OF ENDEMIC TAXA FROM ISLANDS IN INDONESIA

Matthias Glaubrecht[1*], Thomas von Rintelen[1] & Alexei V. Korniushin[2]

ABSTRACT

The Indonesian island of Sulawesi, with its central zoogeographical position within the so-called "Wallacea", harbors a large number of endemic faunal elements, rendering this region a biodiversity hotspot. The present paper shows that this holds also true for limnic molluscs of the family Corbiculidae. Although less species-rich than previously assumed, we document here that the Indonesian corbiculids exhibit more anatomical and life-history variation than in the rest of their collective Old World distribution.

As a first step toward a comprehensive revision of the Southeast Asian corbiculids, morphological characters and molecular genetics are studied in the various taxa described from Sulawesi and Sumatra. Based on morphological studies of materials collected recently, especially in the central lakes on the island of Sulawesi and supplemented by historical museum collections, we conclude that *Corbicula* is represented on Sumatra by at least one and on Sulawesi by four endemic taxa. *Corbicula javanica* (Mousson, 1849), known from several islands of Indonesia, and *C. moltkiana* Prime, 1878, sampled in lakes Singkarak and Manindjau on Sumatra are similar in their anatomical characters and the mode of brooding to the widely distributed Asian *C. fluminea* (Müller, 1774), but differ from the latter in shell form and sculpture. The distinctness of *C. linduensis* Bollinger, 1914, restricted to the basin of the Palu River in North Sulawesi is confirmed in finding a peculiar mode of ovoviviparous reproduction, that is, incubation of embryos in the gills until juveniles are 1.3 mm long. *Corbicula matannensis* P. Sarasin & F. Sarasin, 1898, and *C. loehensis* Kruimel, 1913, both occurring within the Malili lake system on Sulawesi, as well as *C. possoensis* P. Sarasin & F. Sarasin, 1898, endemic to Lake Poso, all release small larvae, a reproductive mode similar to *C. fluminea*, but they differ from the latter in having broad siphons with slit-like apertures. *Corbicula loehensis* differs from *C. matannensis* in its very delicate sculpture and hinge, whereas *C. possoensis* is distinguished from other species in having big posterior adductors and especially broad inhalant siphon. In addition, only *C. possoensis* broods in both demibranchs, whereas all other known brooding corbiculids incubate in the inner demibranch only. Monoflagellate spermatozoa were observed in all studied Indonesian taxa except *C. javanica*, in which sperm structure remains unknown.

Phylogenetic analyses of COI sequences (MP and NJ) including now five Indonesian taxa studied herein show distinct clades occuring (i) on Sumatra, identified as *C. moltkiana*, and (ii) on Sulawesi with two seperate lineages of *C. possoensis* from Lake Poso being most distinct from *C. matannensis* and *C. loehensis* from the Malili lake system. The analyses also suggest a close relationship of *C. javanica* to the Korean *C. fluminea* within an Asian cluster, including also the Australian corbiculid. Systematic, biogeographical and evolutionary implications of these results are discussed.

Key words: freshwater Bivalvia, *Corbicula*, ovoviviparity, anatomy, systematics, biogeography, endemics, Sulawesi.

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INTRODUCTION

Limnic bivalves of the family Corbiculidae are widespread in tropical and subtropical regions of the Old and New worlds. The genus *Corbicula* is also widely distributed and abundant in fresh and brackish waters of Africa, the southern parts of Asia, extending from Turkey and Israel in the west to China, the Malayan Peninsula and the Sunda Archipelago, New Guinea and eastern Australia. Members of the genus were also introduced to both Americas and Western Europe (reviews: Morton, 1986; Araujo et al., 1993; Pfenninger et al., 2002).

Comprising brackish-water and freshwater species and, therefore, representing different stages of adaptation to freshwater environments, renders *Corbicula* an important model organism for evolutionary and ecological studies not only among molluscs. However, its taxonomy and systematics is far from being resolved and many aspects are still disputable. A great number of species were described, especially from Southeast Asia (e.g., Martens, 1897; P. Sarasin & F. Sarasin, 1898; Kruimel, 1913; reviews: Prashad, 1930; Morton, 1979), resulting in a plethora of named taxa. To date a comprehensive revision of these corbiculids is lacking.

While an earlier review (Prashad, 1930) dealt exclusively with conchological characters, recognizing many congeneric morphospecies, some later investigations focused on anatomy (Britton & Morton, 1979; Harada & Nishino, 1995) and particularly on reproductive biology (Morton, 1979, 1986), resulting in greatly reducing the number of species considered valid. For example, Morton (1986) recognized only two species, namely *C. fluminalis* Müller, 1774, and *C. fluminea* Müller, 1774. According to this author, *C. fluminalis* more frequently inhabits estuaries, tolerates higher salinity (thus, basically being a brackish-water representative) and releases free-swimming veliger larvae. In contrast, *C. fluminea* occurs in pure freshwater only and incubates embryos in the gills, which are not released before the foot of the juveniles is well developed. Summarizing the available biological data, Morton (1986) concluded that both *Corbicula* species are distributed throughout the range of the genus and include a great variety of conchological forms with overlapping characters.

A different taxonomic concept of *Corbicula* is accepted in Japan (Harada & Nishino, 1995). The estuarine, non-incubating species is referred to as *C. japonica* Prime, 1864, and the local freshwater incubating form as *C. leana* Prime, 1864, and *C. fluminea* is reported from several Japanese localities (Harada & Nishino, 1995; Komaru et al., 1998). Komaru et al. (1998) provided morphological characters to distinguish *C. leana* from *C. fluminea*. In addition, *C. sandai* Reinhardt, 1878, is recognized as an endemic species restricted to Lake Biwa in Japan.

To further complicate corbiculid systematics, new insights into the genetic structure of Asian *Corbicula* are salient to any taxonomic revision. As shown first by Okamoto & Arimoto (1986), Japanese taxa have different karyotypes, with *C. japonica* and *C. sandai* being diploid (with 2n = 38 and 36, respectively), whereas *C. leana* is triploid (3n = 54). Recently, polyploidy has also been discovered in several taxa from Korea (Park et al., 2000) and in two color forms of *C. fluminea* from China, Sechuan Province (Qiu et al., 2001). It has been repeatedly reported that polyploidy is associated with peculiar biflagellate spermatozoa and ameiotic reproduction, resulting in clonality (Komaru & Konishi, 1996, 1999; Komaru et al., 1997, 2000; Konishi et al., 1998; Siripattrawan et al., 2000; Qiu et al., 2001; Lee et al. 2002). For example, those investigations of the reproductive biology of *Corbicula* showed that biflagellate spermatozoa observed in *C. leana* from Japan and *C. fluminea* from China and Taiwan are non-reductional, and that these molluscs reproduce by means of androgenesis, that is, the elimination of the mother's genome from eggs and development of embryos from the genome of spermatozoon only. Similar biflagellate spermatozoa were reported for the *C. fluminea* samples from Thailand, Korea and the exotic forms introduced into the USA. Thus, apparently this taxon is a heterogeneous assemblage of variably polyploid and ameiotic clonal lineages (Siripattrawan et al., 2000). Spermatozoa of the Australian *C. australis* (Lamarck, 1818) are also biflagellate (Byrne et al., 2000), therefore indicating a clonal structure for this taxon as well (Siripattrawan et al., 2000).

All these clonal lineages, to our present knowledge, lack sexually reproducing parental taxa and, therefore, greatly complicate the meaningful application of specific names. Consequently, the name *C. fluminea* has been applied to multiple genetically distinct clonal lineages of unknown parentage in recent studies on European and introduced North American populations. In contrast, there is only one

documented sexual species of freshwater *Corbicula*, *C. sandai*, endemic to the "ancient" Lake Biwa (Hurukawa & Mitsumoto, 1953). Interestingly, at the same time only *C. sandai* has monoflagellate spermatozoa, thus allowing to correlate reproductive mode with sperm morphology (Konishi et al., 1998; Siripattrawan et al., 2000). In addition, *C. sandai* is also the only known gonochoric freshwater *Corbicula*, whereas all other taxa appear to be hermaphroditic (Komaru & Konishi, 1996; Byrne et al., 2000; Siripattrawan et al., 2000).

Surprisingly, only diploid karyotypes were reported for the two introduced European *Corbicula* morphotypes, traditionally identified as *C. fluminalis* and *C. fluminea* (Pfenninger et al., 2002). In the absence of direct evidence of clonality in these morphotypes, hybridization between those two morphotypes, which was discovered in this molecular study, might indicate sexual reproduction. Accordingly, clonality is widely distributed, especially among most Asian taxa, albeit not the universal feature among freshwater *Corbicula*. Therefore, the genetic structure of these limnic clams needs further investigation.

Furthermore, not only these new data on genetics, polyploidy and reproduction disagree with the two-species concept of Asian *Corbicula* as suggested by Morton (1979, 1986). Preliminary data from mitochondrial DNA sequences utilizing the COI gene (Siripattrawan et al., 2000; Lee et al., 2002) indicate that *C. leana*, *C. japonica* and *C. sandai* are distinct lineages alongside *C. fluminea*, whereas two North American morphotypes (forms A and B) might have different origin, with the first (form A) being closer related to Japanese *C. leana* and the second (form B) to *C. fluminea* from Korea. This analysis, as well as a later one that included samples from China, Israel and Europe (Pfenninger et al., 2002), demonstrated that all studied freshwater *Corbicula* form one single clade with poorly resolved relationships, though, with the exception of *C. madagascariensis* Smith, 1882, from Madagascar (erroneously referred to as *C. africana* from "Africa" in the latter paper as well as in GenBank). The modest levels of genetic divergence demonstrated for the freshwater lineages suggested evolutionary recent common origin (Siripattrawan et al., 2000; Pfenninger et al., 2002).

Despite these accounts, to date many regions remain poorly investigated with respect to *Corbicula* diversity and distribution, in particular islands of the Sunda Archipelago, such as the Indonesian islands of Sumatra and Sulawesi. This island chain is among the biologically most diverse regions in the world, representing one of the major hot spots of biodiversity, areas exceptionally rich in endemic species and harbouring rare and threatened species (Myers et al., 2000; Mittermeier et al., 2000; Reid, 1998). Due to its biogeographically central position within the so-called "Wallacea", in the heart of the complex crossroads of two continents Asia and Australia, Sulawesi not only harbours a number of unique and endemic faunal elements, but recently also figured prominently in palaeogeographical research providing new geological insights (Whitmore, 1981; Hall & Blundell, 1996; Metcalfe et al., 2001). Consequently, this region became a central focus of biogeographic interest again (Whitmore, 1987; Hall & Holloway, 1998; Metcalfe et al., 2001).

Although molluscs have unfortunately only rarely been considered in biogeographic research (Davis, 1982), especially limnic gastropods from the Sunda region were recently utilized as models in an approach to synthesize systematic and geological patterns (overview: Glaubrecht, 2000). For example, based on the known distributional pattern found in the constituent taxa for the mainly viviparous Pachychilidae which are widely distributed throughout the mainland of Southeast Asia and the Indo-Malayan Archipelago, reaching as far east as the Philippine Islands and Sulawesi, it has been hypothesized that the biogeography of these limnic snails (i) find their explanation in palaeogeographical events that go back to the Cretaceous and early Cenozoic instead of explaining the distribution as correlated to the forming of the so-called Sunda- and Sahulland, respectively, and (ii) that it implies vicariance over dispersal as causation (Glaubrecht, 2000; Köhler et al., 2000; Köhler & Glaubrecht, 2001, 2003; Glaubrecht & Rintelen, 2003).

In contrast, according to Siripattrawan et al. (2000) and Pfenninger et al. (2002), the known patterns of distribution and genetic divergence in *Corbicula*, based on data for continental Southeast Asia, Japan and Australia, suggest rather dispersal than vicariance scenario for these freshwater bivalves. Therefore, it is promising to test the mentioned scenario by extending the data set, and to compare the patterns of morphological and genetic divergence among Indonesian bivalves with that of the sympatric pachychilid snails. In this context,

the corbiculid bivalves provide a second model group that inhabits the same limnic environments in this crucial biogeographic region and, with them incubating eggs and embryos in their gills, also share a similar reproductive strategy with the ovoviviparous and viviparous pachychilid gastropods.

However, any zoogeographical evaluation has to be based on solid systematic knowledge. Unfortunately, any modern revision of the Corbiculidae is still lacking. For example, from Sulawesi a total of nine endemic corbiculid species have been described, especially from its ancient central lakes (Martens, 1897; P. Sarasin & F. Sarasin, 1898; Kruimel, 1913; Bollinger, 1914). In contrast, Prashad (1930) recognised only two endemic species on Sulawesi, assigning all lacustrine taxa to *C. subplanata* Martens, 1897. In his revision of the corbiculids from Sulawesi, Djajasasmita (1975, 1977) recognised four taxa – three endemic species living in lakes in addition to *C. subplanata* as the only riverine form. He also reported on one widely distributed Asian species, *C. javanica* (Mousson, 1849), as occurring on Sulawesi. From Sumatra, also a total of nine endemic species of *Corbicula* have been described (Prime, 1878; Clessin, 1887; Martens, 1897, 1900), of which Djajasasmita (1977) recognized four as valid – *C. moltkiana* Prime, 1878, *C. gustaviana* Martens, 1900, *C. sumatrana* Clessin, 1887, and *C. tobae* Martens, 1900, and, in addition, recorded four widely distributed Asian species on the island, viz. *C. javanica*, *C. pullata* Philippi, 1851, *C. rivalis* (Philippi, 1850), and *C. tumida* Deshayes, 1854.

However, none of these studies provided any sufficiently distinctive characters for the individual species. Although shell proportions, angle between lateral teeth, position of beaks, shell thickness and sculpture are usually used, the intraspecific variability of these characters remained largely unknown and, therefore, the taxonomic decisions appeared as being highly arbitrary. Consequently, Morton (1979, 1986) tentatively suggested conspecificy of the Indonesian species reviewed by Prashad (1930) and Djajasasmita (1975, 1977) with *C. fluminea*, synonymizing the species names listed above with the latter taxon. However, Morton did not discuss in detail the taxonomy, nor did he provide any new data on the morphology or biology of these Indonesian corbiculids. Thus, not only is the systematics and phylogenetic relationships of the presumably endemic insular Corbiculidae unknown, but the anatomy and reproductive biology of any of the disputable species from this region has remained undescribed.

The recent discovery of an endemic genus of Corbiculidae from Lake Poso with its unique cemented mode of life (Bogan & Bouchet, 1998) shows that the molluscan fauna at least of this lake on Sulawesi is much more specific than assumed earlier. This stimulated the present study of other Corbiculidae, namely species of the genus *Corbicula* inhabiting Poso and neighbouring lakes, as was suggested by Bogan & Bouchet (1998). Accordingly, we here integrate shell characters, new data on the anatomy, especially the reproductive biology, and molecular genetics (sequences of COI mitochondrial gene fragment) for six nominal taxa of *Corbicula* from Indonesia, namely *C. javanica*, *C. moltkiana*, *C. linduensis*, *C. matannensis*, *C. loehensis* and *C. possoensis*, based on recent sampling by the authors on Sumatra and Sulawesi, and we compare with historical material deposited in the museum collections. In addition, we report for the first time for any Indonesian *Corbicula* principal features of sperm morphology, as well as presence and localization of larvae in gills. We also provide a preliminary evaluation of the status and affinities of the studied taxa, but any final taxonomic decision is postponed until more molecular data on the diverse morphotypes from lacustrine and riverine habitats in the area are available. Some other taxa described by Martens (1897, 1900) from Sumatra and Sulawesi are also awaiting revision. However, because no fresh material on these taxa was available, these are beyond the scope of our current study. Nevertheless, we document here that the corbiculids endemic to the region (Fig. 1), although less species-rich than assumed before, exhibit more anatomical and life-history variation than in the rest of their collective Old World range.

MATERIALS AND METHODS

Material Studied

The material at hand (Fig. 1) was collected during two field trips to Sulawesi in August 1999 and March 2000 by M. G. and T. v. R., and on Sumatra in April 2000 by Frank Köhler and Sabine Schütt. It is housed in the Malacological collection of the ZMB, voucher material is also

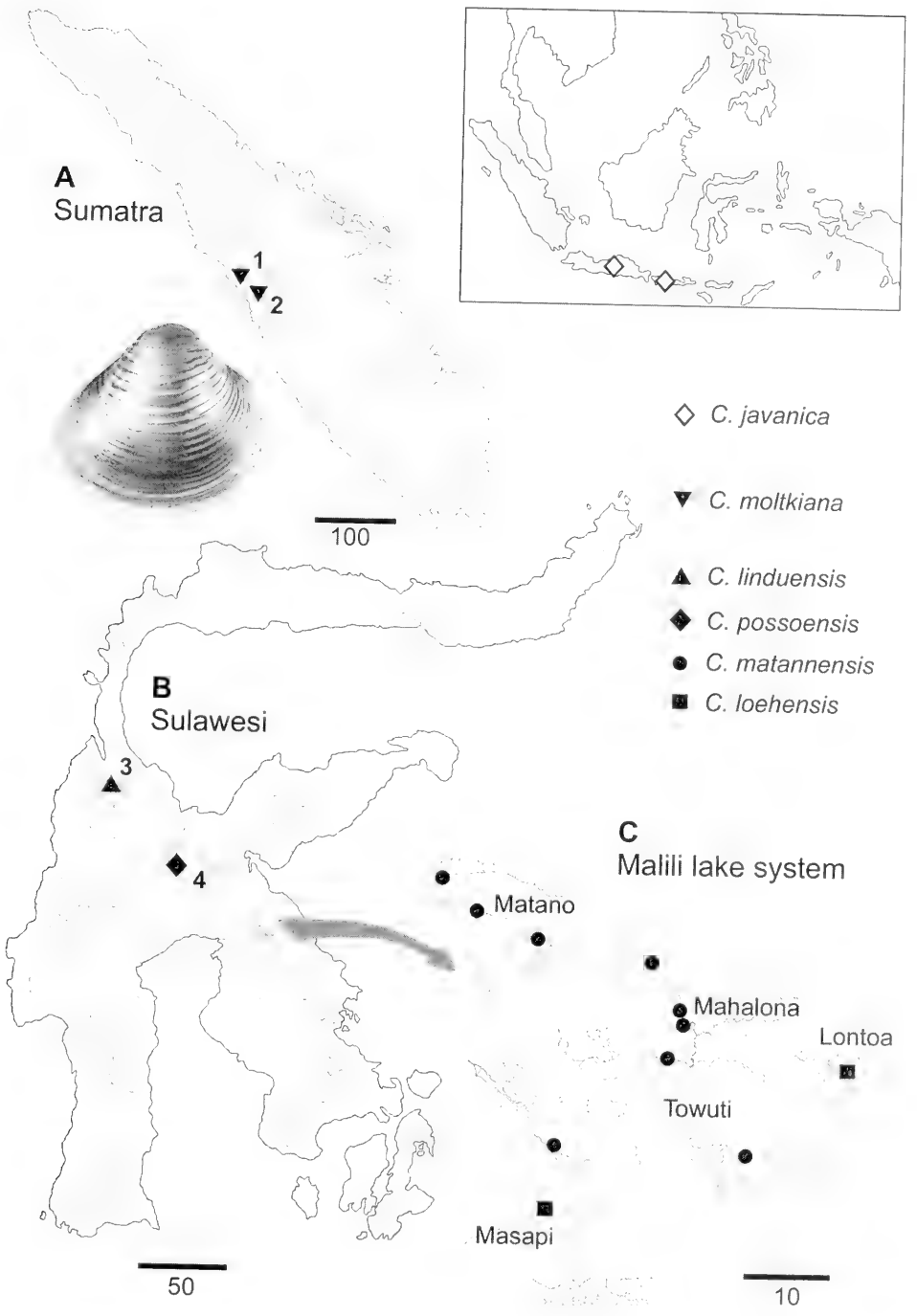

FIG. 1. The occurrence of freshwater bivalvia of the genus *Corbicula* on Indonesian islands based only on material examined in the present study; details are given for *C. moltkiana* on Sumatra (A) and four taxa on Sulawesi (B) and the Malili lake system (C), respectively. Numbers refer to the following locations: 1 - Lake Manindjau, 2 - Lake Singkarak, 3 - Palu River, 4 - Lake Poso. Scale bars given in km.

provided to the Zoological Museum in Bogor.

Type and other historical material representing *Corbicula* species from Sulawesi and Sumatra, including the type specimens of *C. subplanata* Martens, *C. celebensis* Martens, *C. lacustris* Martens, *C. possoensis* P. Sarasin & F. Sarasin, and *C. matannensis* P. Sarasin & F. Sarasin, also housed in the ZMB, were studied for comparison. This is supplemented by the relevant type materials recovered in other museums, including the lectotype of *C. fluminea* designated by Araujo et al. (1993), as well as type lots of *C. javanica* and *C. sumatrana*. Comparative alcohol material of *C. fluminea* was kindly provided by C. Ituarte (collected near Buenos Aires, Argentina).

Shell Morphology and Anatomy

All newly collected material was fixed in 70% ethanol after cracking the shells of some specimens per sample; this material is given as w = wet material in the Material sections below. Shell measurements were made with a caliper to a precision of 0.1 mm; size of adductor scar was measured as the distance between its uppermost point and junction with mantle line. Dissections were made under a Leica MZ 9.5 stereomicroscope, and anatomical structures illustrated using a camera lucida. Pieces of mantle for the study of musculature were stained by eosine (water solution) and mounted in Canada Balsam.

Sperm Morphology

Sperm was obtained from gonads of ethanol-fixed specimens. Its morphology was studied by means of interference contrast optics (DIC) and scanning electron microscopy (SEM), in the latter case applying hexamethyldisilazane (HMDS) following the procedure described by Nation (1983).

Molecular Genetics

DNA was purified from about 1–2 mm^3 of foot tissue by CTAB extraction (Winnepenninckx et al., 1993). Polymerase chain reaction (PCR) was used to amplify a region of ~710 bp at the 5'-end of the cytochrom oxidase subunit I gene (COI). PCR was performed in 25 µl volumes containing 1X Taq buffer, 1.5 mM MgCl2, 200 µM each dNTP, 1–2.5 U Taq polymerase, approximately 100 nM DNA and ddH_2O up to volume on a Perkin Elmer GeneAmp 9600 or 2400 thermocycler. After an initial denaturation step of 3 min at 94°C, cycling conditions were 35 cycles of 1 min each at 94°C, 45–53°C, and 72°C, with a final elongation step of 5 min.

Primers used were LCO 1490 [5' GCTCAA CAAATCATAAAGATATT 3'] and HCO2198 [5' TAAACTTCAGGGTGACCAAAAAATCA 3'] (Folmer et al., 1994). PCR products were purified with QiaQuick PCR purification kits (Qiagen) following the standard QiaQuick PCR purification protocol. Both strands were cycle sequenced with the original primers using ABI Prism BigDyeTM terminator chemistry and visualized on an ABI Prism 377 automated DNA sequencer. The resulting sequence electropherograms of both strands were corrected manually for misreads and merged into one sequence file using BioEdit Version 5.0.1 (Hall, 1999). Sequences were aligned manually and checked by translating the DNA sequences into amino acids in DAMBE 4.0.75 (Xia & Xie, 2001) using the genetic code for invertebrate mitochondrial DNA. The sequences obtained by this study were analyzed together with *Corbicula* sequences published by Siripattrawan et al. (2000) and Pfenninger et al. (2002); the latter included samples from Hong Kong, which is near to the type locality (Canton) of *C. fluminea*, and from Israel (presumably *C. fluminalis*).

Polymesoda caroliniana (Bosc, 1801) and *Neocorbicula limosa* (Maton, 1809) were used as outgroups. The latter taxon needs a nomenclatorial commentary. As pointed out by Parodiz (1996: 265), the generic name *Cyanocyclas* Blainville, 1818, is a senior subjective synonym of *Neocorbicula* Fisher, 1887, and, therefore, should have priority. Understanding that this taxon is in need of a taxonomic revision and possibly formal decision of the ICZN, we for the time being will use here the latter generic name, as done in recent molecular literature (e.g., Siripattrawan et al., 2000; Pfenninger et al., 2002). GenBank accession numbers of all sequences used and ZMB catalogue numbers for original material are provided in Table 1.

Aligned sequences were processed with PAUP* 4.0b10 (Swofford, 1998). Corrected sequence divergence levels were calculated by using a General Time Reversible model, to obtain the matrix comparable with that of Siripattrawan et al. (2000). Phylogenetic trees were reconstructed using neighbor joining (NJ, Saitou & Nei, 1987) and maximum parsimony (MP) methods as implemented in PAUP*. NJ

TABLE 1. Sources of the corbiculid material utilized in this study for COI sequence data analyses; numbers in brackets refer to analyses of sequence data as given in Table 4 and Figs. 18 and 19.

Taxon	Locality data	Museum catalog no.	GenBank accession no.	Reference
Corbicula javanica (Mousson, 1849)	Bogor, Java	ZMB 106449	AY275668	This study
C. moltkiana Prime, 1878 (1)	L. Singkarak, Sumatra	ZMB 103024	AY275660	This study
C. moltkiana (2)	L. Singkarak, Sumatra	ZMB 103034	AY275659	This study
C. moltkiana (3)	L. Manindjau, Sumatra	ZMB 103025	AY275657	This study
C. moltkiana (4)	L. Manindjau, Sumatra	ZMB 103032	AY275658	This study
C. matannensis Sarasin & Sarasin, 1898 (1)	L. Matano, Sulawesi	ZMB 103002	AY275663	This study
C. matannensis (2)	L. Matano, Sulawesi	ZMB 103003	AY275664	This study
C. matannensis (3)	L. Mahalona, Sulawesi	ZMB 103009	AY275665	This study
C. loehensis Kruimel, 1913 (1)	L. Lontoa, Sulawesi	ZMB 103033	AY275667	This study
C. loehensis (2)	L. Masapi, Sulawesi	ZMB 103011	AY275666	This study
C. possoensis Sarasin & Sarasin, 1898 (1)	L. Poso, Sulawesi	ZMB 190024	AY275661	This study
C. possoensis (2)	L. Poso, Sulawesi	ZMB 103028	AY275662	This study
C. fluminea (Müller, 1774)	Thailand	UMMZ 266691	AF196270	Siripattrawan et al., 2000
C. fluminea	Korea	UMMZ 266690	AF196269	Siripattrawan et al., 2000
C. fluminea	Hong Kong	-	AY097292	Pfenninger et al., 2002
C. leana Prime, 1864	Japan	UMMZ 266668	AF196268	Siripattrawan et al., 2000
C. sandai Reinhardt, 1878	L. Biwa, Japan	UMMZ 266689	AF196272	Siripattrawan et al., 2000
C. fluminalis?	Israel	-	AY097299	Pfenninger et al., 2002
C. australis (Lamarck, 1818)	NSW, Australia	UMMZ 266662	AF196274	Siripattrawan et al., 2000
Corbicula "form A"	Michigan, USA	UMMZ 266693	AF196280	Siripattrawan et al., 2000
Corbicula "form B"	Utah, USA	UMMZ 266695	AF196278	Siripattrawan et al., 2000
C. madagascariensis Smith, 1882	Madagascar	UMMZ 255293	AF196275	Siripattrawan et al., 2000
C. japonica Prime, 1864	Japan	UMMZ 266688	AF196271	Siripattrawan et al., 2000
Neocorbicula limosa (Maton, 1809)	Argentina	UMMZ 265500	AF196277	Siripattrawan et al., 2000
Polymesoda caroliniana (Bosc, 1801)	Florida, USA	UMMZ 265499	AF196276	Siripattrawan et al., 2000

analyses were conducted using the random initial seed option to break ties. The robustness of inferences was assessed through bootstrap resampling (1000 replicates) (Felsenstein, 1985). In the MP analyses, the heuristic search algorithm was employed with 10 random additions of taxa and tree bisection-reconstruction (TBR) branch swapping. All other settings were left at default values. Support for nodes was estimated by bootstrap resampling (500 replicates) with one random addition per replicate.

Abbreviations Used in Figures

aa – anterior adductor, es – exhalant siphon, is – inhalant siphon, mc – concentric mantle musculature, mp – papillae, mr – radial mantle musculature, p – papillae, pa – posterior adductor, pss – presiphonal suture, sr – siphonal retractor.

Museum Acronyms

MLP – Museo de La Plata, Buenos Aires, Argentina; MZB – Zoological Museum Bogor, Indonesia; SMF – Senckenbergsmuseum, Frankfurt/Main, Germany; UZMC – Universitetets Zoologisk Museum, Copenhagen, Denmark; ZMA – Zoological Museum Amsterdam, The Netherlands; ZMB – Museum für Naturkunde, Humboldt University, Berlin, Germany (formerly Zoological Museum Berlin); ZMZ – Zoologisches Museum, Universität Zürich, Switzerland.

SYSTEMATIC ACCOUNT

Species from the Sunda Islands

Corbicula javanica (Mousson, 1849)
Figs. 2A–C, 3D–F

Cyrena orientalis var. *javanica* Mousson, 1849: 86, pl. 15, fig. 2.

Corbicula ducalis Prime, 1862: 274; Martens, 1897: 114.

Corbicula javanica – Martens, 1897: 111; Prashad, 1930: 203, pl. 25, figs. 7–20; Djajasasmita, 1977: 6.

Type Locality: Tikojia (probably an error for Tjikoya), Java.

Type Material: Lectotype ZMZ 532199 (Fig. 2A) from Tijkoya, Java, leg. Zollinger, ex. coll. Mousson; corresponding to the specimen figured by Mousson (1849: pl. 15, fig. 2) with the following measurements: L = 39.5, H = 33.0, W/2 = 11.9 mm (present designation, to fix the status of this specimen as the sole name bearing type). Paralectotypes (2 specimens) from the same original lot, ZMZ 532199a. Paralectotypes ZMZ 532200 (2 specimens), the same locality and collector.

Other Material Examined: Java: Tjiponnas near Garut (ZMB Moll. 103054w; leg. M. Schmidt 1902); Bogor (ZMB Moll. 106459; leg. T. v. Rintelen, May 2002). Lombok: Narmada (ZMB Moll. 75535w; leg. Rensch, Sunda Expedition). Sulawesi: Lake Tempe (ZMB Moll. 103024; leg. Max Weber; originally identified as *Corbicula ducalis* Prime, 1862).

Taxonomic Remarks: In respect to the discrepancy of the spelling of the type locality for this taxon, we follow here Djajasasmita (1977), who interpreted it as Tjikoya. The latter author also synonymized *C. ducalis* Prime, 1862, which was reported earlier on as a valid species from several Indonesian islands (Martens, 1897; Prashad, 1930) with *C. javanica*. Our revision of specimens from Sulawesi originally identified by Martens as *C. ducalis* is consistent with this point of view, although some minor differences to the typical *C. javanica* are discernable. Specimens from Lombok included in this study (Fig. 2C) also correspond well to the published descriptions (Prashad, 1930) and revised type specimens of *C. javanica* (Fig. 2A, B).

Description

Shell: Oval or broad triangular, without angles, somewhat inequilateral, convex. Beaks broad, protruding, markedly shifted anteriorly. Periostracum yellow to brown, shiny. Internal coloration usually white or pale blue, with purple pattern at lateral teeth. Concentric sculpture coarse and widely spaced (8–11 ribs per 1 cm), ribs usually not sharp (wavelike). Hinge plate relatively narrow; cardinal teeth small; anterior lateral teeth long, arched. Specimens from Lombok and Sulawesi up to 20 mm long; Javanese specimens much larger, up to 50 mm long.

Anatomy: Adductors small, oval. Posterior adductor diameter about 0.13 length of shell (Table 2). Presiphonal suture not elongated, length equal to breadth of inhalant siphon. Siphons conical, with thick walls (when contracted) and circular or short oval apertures, both narrow; inhalant siphon with about 30

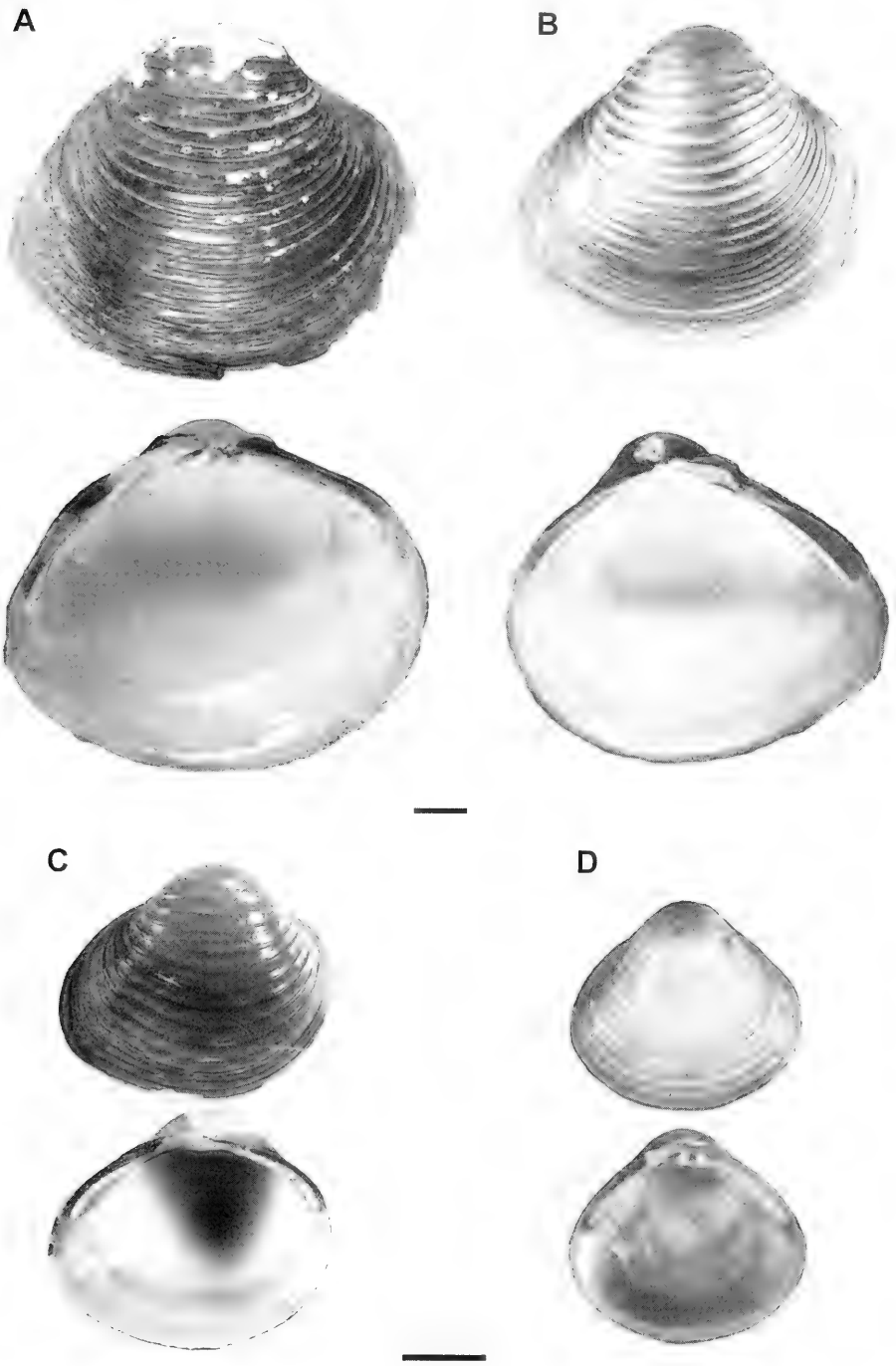

FIG. 2. Shells of *Corbicula javanica* in comparison with *C. fluminea*: A. *C. javanica*, Java, lectotype (ZMZ 532199); B. *C. javanica*, one of the paralectotypes (ZMZ 532200); C. *C. javanica*, Lombok (ZMB Moll.75535); D. *C. fluminea*, China, lectotype (UZMC). Scale bars = 5 mm.

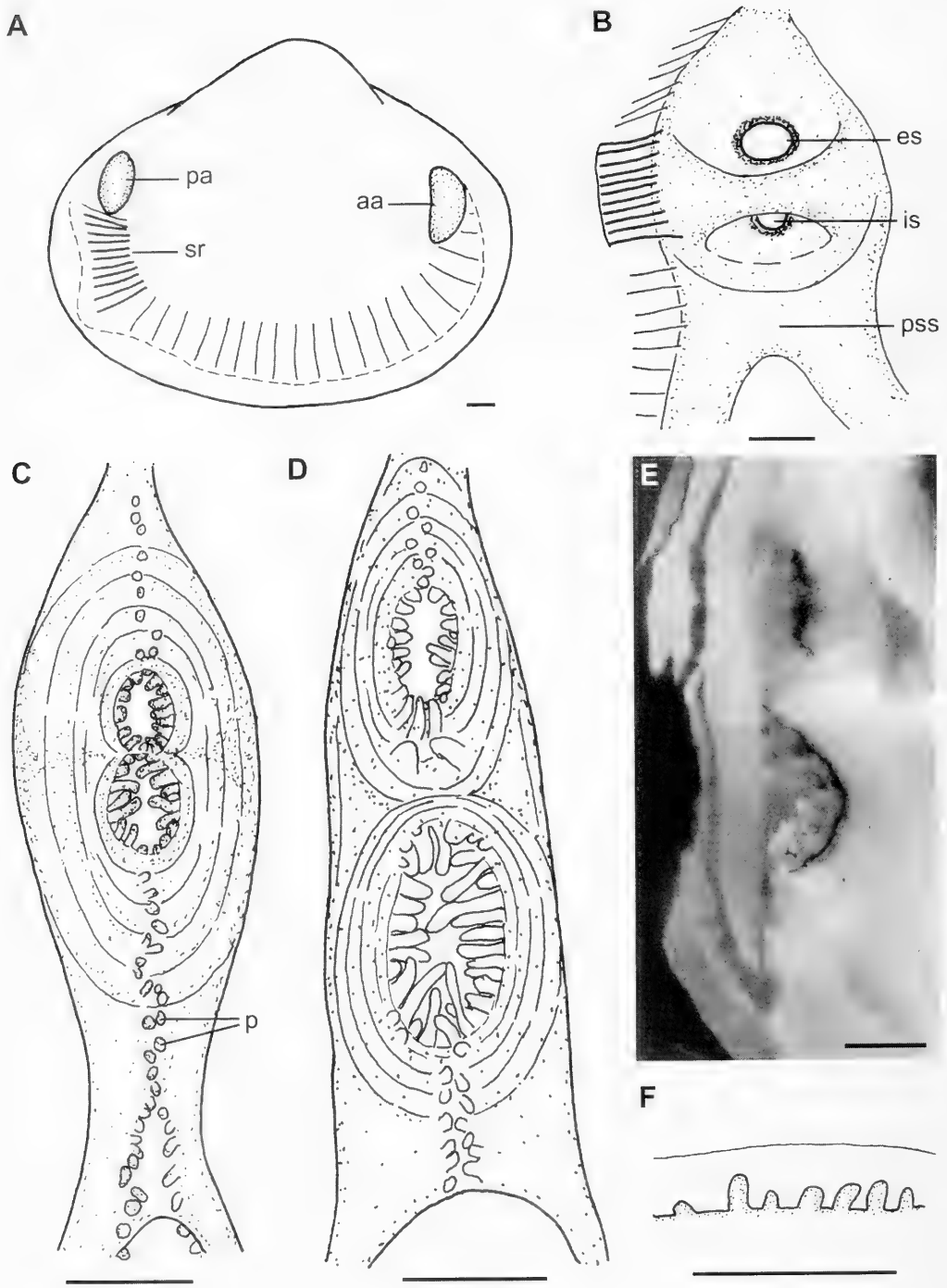

FIG. 3. Anatomy of *Corbicula fluminea*, Argentina (MLP 5329) (A–C) and *C. javanica*, Lombok (ZMB Moll. 75535) (D–F): A. Habitus of soft body; B. Siphons from inside; C, D. Siphons from outside; E. Section of siphons; F. Marginal mantle papillae. Scale bars = 1 mm.

TABLE 2. Morphometric indices (mean and standard deviation provided) calculated from measurements of shells and siphon structure of the *Corbicula* species studied: L - shell length; H - shell height; W - shell thickness (two valves); U - distance from beak to anterior end; HH - hinge plate length; A - diameter of the posterior adductor scar; S - breadth of siphons. Note that for the last two taxa only range is given for siphons.

Species	No. of measured specimens (dry/wet)	H/L	W/H	U/L	HH/H	A/L	S/L
C. fluminea (lectotype)	1	0.93	0.80	0.48	0.100	0.14	not measured
C. javanica ZMZ 532199, 532200 (type lot)	5/0	0.83 ±0.059	0.75 ±0.066	0.43 ±0.017	0.059 ±0.005	0.14 ±0.012	not measured
C. javanica ZMB 75535	3/0	0.82 ±0.035	0.81 ±0.022	0.39 ±0.021	0.057 ±0.006	0.13 ±0.009	not measured
C. javanica ZMB 106459	10/5	0.89 ±0.041	0.73 ±0.020	0.42 ±0.018	0.069 ±0.004	0.12 ±0.013	0.12 ±0.010
C. moltkiana ZMB 54370, 103058	10/2	0.78 ±0.056	0.68 ±0.020	0.47 ±0.022	0.080 ±0.016	0.14 ±0.007	0.24 ±0.05
C. moltkiana SMF 5994 (paratypes of *C. sumatrana*)	10/0	0.95 ±0.049	0.73 ±0.065	0.46 ±0.047	0.099 ±0.007	0.18 ±0.020	not measured
C. moltkiana ZMB 170000-01 (syntypes of *C. lacustris*)	6/0	0.94 ±0.126	0.80 ±0.033	0.44 ±0.069	0.111 ±0.016	0.18 ±0.043	not measured
C. moltkiana ZMB 103024	5/4	0.91 ±0.029	0.69 ±0.039	0.47 ±0.040	0.079 ±0.004	0.17 ±0.015	0.18 ±0.013
C. moltkiana ZMB 103032	7/4	0.84 ±0.049	0.69 ±0.039	0.50 ±0.032	0.073 ±0.008	not measured	0.19 ±0.030
C. linduensis ZMB 103016	10/4	0.77 ±0.022	0.63 ±0.039	0.49 ±0.029	0.081 ±0.007	0.14 ±0.015	0.18 ±0.033
C. matannensis ZMB 103002	10/6	0.84 ±0.043	0.64 ±0.035	0.42 ±0.022	0.098 ±0.005	0.15 ±0.010	0.24 ±0.015
C. matannensis ZMB 103009	9/7	0.83 ±0.045	0.59 ±0.041	0.39 ±0.031	0.96 ±0.013	0.13 ±0.017	0.26 ±0.034
C. matannensis ZMB 103006	4	0.96 ±0.050	0.70 ±0.090	0.42 ±0.052	0.111 ±0.016	0.15 ±0.016	not measured
C. loehensis ZMB 103010	5	0.88 ±0.028	0.68 ±0.034	0.44 ±0.011	0.078 ±0.015	0.14 ±0.023	not measured
C. loehensis ZMB 103011	8/3	0.88 ±0.040	0.68 ±0.026	0.47 ±0.046	0.075 ±0.011	0.12 ±0.010	0.32 ±0.032
C. loehensis ZMB 103033	3/2	0.87 ±0.047	0.60 ±0.040	0.44 ±0.026	0.070 ±0.014	0.12 ±0.004	0.27–0.33
C. possoensis ZMB 103028	10/7	0.93 ±0.028	0.65 ±0.033	0.41 ±0.033	0.115 ±0.007	0.23 ±0.019	0.32 ±0.022
C. possoensis ZMB190024	3/2	0.89 ±0.070	0.75 ±0.037	0.31 ±0.010	0.120 ±0.012	0.21 ±0.022	0.30–0.31

papillae usually arranged in one row (Fig. 3D), sometimes with additional row of short papillae. Black pigment concentrated in rings internally at base of both siphons (Fig. 3E); outer surface of siphons white or with pale brown pigment (in specimens from Lombok). Larger papillae of inhalant siphon with dark rings. Siphonal muscles strong, arranged in broad bands. Papillae on outer surface of presiphonal suture arranged in two rows (Fig.

TABLE 3. Comparative morphological characteristics of *Corbicula* taxa from Indonesia; ranges are given for indices in brackets (compare to Table 2).

Characters	*C. javanica*	*C. moltkiana*	*C. linduensis*	*C. matannensis*	*C. loehensis*	*C. possoensis*
Shell form	Oval or broad triangular, without angles	Triangular or tetragonal, with pronounced posteroventral angle	Oval, with rounded posteroventral angle	Tetragonal, with obtuse postero-ventral angle	Round, with obtuse posteroventral angle	Triangular or tetragonal, with posterior keel
Beaks	Broad, anterior	Narrow, central or subcentral	Narrow, central	Narrow, subcentral or anterior	Narrow, subcentral	Narrow, anterior
Sculpture	Wave-like ribs, 8–11 per 10 mm	Sharp ribs, 9–12 per 10 mm	Wave-like ribs, 10–12 per 10 mm	Sharp ribs, 15–20 per 10 mm	Delicate ribs, 30–40 per 10 mm	Delicate ribs, 25–30 per 10 mm
Hinge (HH/H index)	Narrow (0.05–0.07)	Moderately broad to broad (0.07–0.13)	Moderately broad (0.08–0.09)	Moderately broad to broad (0.07– 0.13)	Moderately broad (0.07–0.08)	Broad (0.09–0.13)
Adductor size (A/L index)	Small (0.10–0.14)	Small (0.13–0.21)	Small (0.12–0.17)	Small (0.11–0.18)	Small (0.10–0.15)	Large (0.20–0.27)
Siphons form (S/L index)	Conical, narrow (0.11–0.13)	Conical, somewhat broadened (0.15–0.25)	Conical, somewhat broadened (0.14–0.22)	Cylindrical, broad (0.22–0.32)	Cylindrical, broad (0.24–0.34)	Cylindrical, broad (0.29–0.35)
Inhalant siphon papillae	About 30, in one row	30-80, in two rows	About 50, in two rows	55–70, in two rows	About 50, in two rows	60–70, in two rows
Internal pigmentation of siphons	Dark rings	Dark rings and patches	Pale rings or absent	Entirely pigmented	Entirely pigmented	Entirely pigmented
Siphonal muscles	Strong, broad	Strong, broad	Strong, broad	Weak, narrow	Weak, narrow	Weak, narrow
Marginal mantle papillae	Numerous	Numerous	Numerous	Scarce	Scarce	Scarce
Radial mantle musculature	Strong, bundles not separated	Strong, bundles in large specimens separated	Strong, anterior bundles separated	Weak, bundles separated	Weak, bundles separated	Weak, bundles separated
Spermatozoa (type and head length)	Unknown	Monoflagellate, 11–12 μm	Monoflagellate, 8–9 μm	Monoflagellate, 11–12 μm	Monoflagellate, 9–10 μm	Monoflagellate, 10–11 μm
Location of brood	Inner demibranchs	Inner demibranchs	Inner demibranchs	Inner demibranchs	Inner demibranchs	Both demibranchs
Larval size	Small (final size unknown)	Small (0.25–0.35 mm)	Large (up to 1.5 mm)	Small (0.30–0.33 mm)	Small (about 0.25 mm)	Small (0.26–0.30 mm)

3D). Marginal mantle papillae well developed, densely arranged (Fig. 3F). Radial mantle muscles strong, arranged in band, individual bundles not separated.

Reproductive Biology: Only eggs were found in all dissected specimens, therefore sperm morphology remained unknown. One specimen from Java contained in its inner demibranchs several hundred small larvae (0.13–0.15 mm long) with uncalcified shells. Since these larvae were apparently not fully developed, the final size of released young remains unknown. Other studied specimens were not brooding.

Distribution and Ecology: According to Djajasasmita (1977), this taxon is widely distributed in Southeast Asia, from the Malay Peninsula to Timor and Aru Islands, as well as to the Philippines. It occurs in several different types of lentic and lotic habitats, that is, rivers, creeks and irrigation canals as well as lakes and ponds (Djajasasmita, 1977).

Remarks: This taxon is recognizable as a distinct morphotype, differing from the typical form of *C. fluminea* in its inequilateral shell, anterior shift of beaks, and relatively narrow hinge plate (Fig. 2, Table 3). Anatomical characters described here well agree with those reported for *C. fluminea* (Britton & Morton, 1979; Harada & Nishino, 1995) and observed in specimens of the latter species studied here for comparison (Fig. 3A–C), with the only difference of a darker pigmentation of the outer surface of siphons. In fact, we anticipate that *C. javanica* might probably just be a variety of *C. fluminea*. However, this supposition should be confirmed by investigating the reproductive biology and molecular genetics of the relevant forms in more detail.

Corbicula moltkiana Prime, 1878
Figs. 4–6, 7A, B, 8A, B

Corbicula moltkiana Prime, 1878: 43, pl. 2, fig. 2a, b, c; Prashad, 1930: 200, pl. 25, figs. 17–22; Djajasasmita, 1977: 4.

Corbicula sumatrana Clessin, 1887: 78, pl. 3, fig. 7; Prashad, 1930: 198, pl. 25, figs. 1–8; Djajasasmita, 1977: 7.

Corbicula verbecki Clessin, 1887: 79.

Corbicula moltkeana [sic] Prime – Martens, 1897: 111, pl. 7, figs. 1–6.

Corbicula lacustris Martens, 1897: 118, pl. 7, figs. 20–24.

Type Locality: "Sumatra", not exactly specified.

Type Material: Type specimens of *C. moltkiana* Prime located in UZMC are presumed to be lost (T. Schiotte, pers. comm.). Presumably syntypes (although catalogued as paratypes) of *C. sumatrana* Clessin, "Lake Singkarah" [sic!], leg. Verbeck 1880 (SMF 5994, 5995). Holotype of *C. verbecki*, Clessin, same locality data (SMF, not numbered). Syntypes of *C. lacustris* Martens, Lake Singkarah, leg. Weber (ZMB Moll. 170000, 170001, 170002).

Other Material Examined: Sumatra: Lake Manindjau (ZMB Moll. 54370w, 103058, 103059; leg. Max Weber; originally identified as *C. moltkiana* by E. v. Martens); Lake Manindjau, at shore near Manindjau (ZMB Moll. 103024, 103034; leg. Köhler & Schütt , April 2000); Lake Singkarak (0°32.89'S, 100°31.92'E) (ZMB Moll. 103025, 103032; leg. Köhler & Schütt, April 2000) (Fig. 1).

Taxonomic Remarks: We have at our disposal one alcohol lot and two dry lots coming from the collection of Eduard von Martens, bearing his identification. Obviously, the specimens are those cited in Martens' (1897) monograph as "*moltkeana*" (evidently a misspelling of Prime's original name). While characters of these specimens (Fig. 4E) well agree with the original description and figures of Prime (1878), we retain the original identificaton as *C. moltkiana*. Comparison of type specimens of the three taxa described from Lake Singkarak, namely *C. sumatrana* Clessin (Fig. 4B), *C. verbecki* Clessin, and *C. lacustre* Martens (Fig. 4C), as well as recent collections of *Corbicula* from this lake (Fig. 4D) with the available figures and material of *C. moltkiana* did not provide convincing distinctive characters and, thus, suggests that these taxa are conspecific.

Description

Shell: Variable in shape, but usually triangular or trapezoid, from high to markedly elongated, compressed. Posterior margin somewhat truncate, with characteristic posteroventral right or obtuse angle. Beaks narrow, central or somewhat shifted anteriorly, not protruding. Periostracum yellow, dark green or dark brown to black, shiny. Internal shell surface from white to dark purple. Concentric sculpture of variable spacing (9–12 ribs per 1 cm), ribs sharp. Hinge plate moderately broadened to broad (Table 2, 3). Cardinal teeth well developed; anterior lateral teeth thick, straight or slightly arched. Up to 30 mm long.

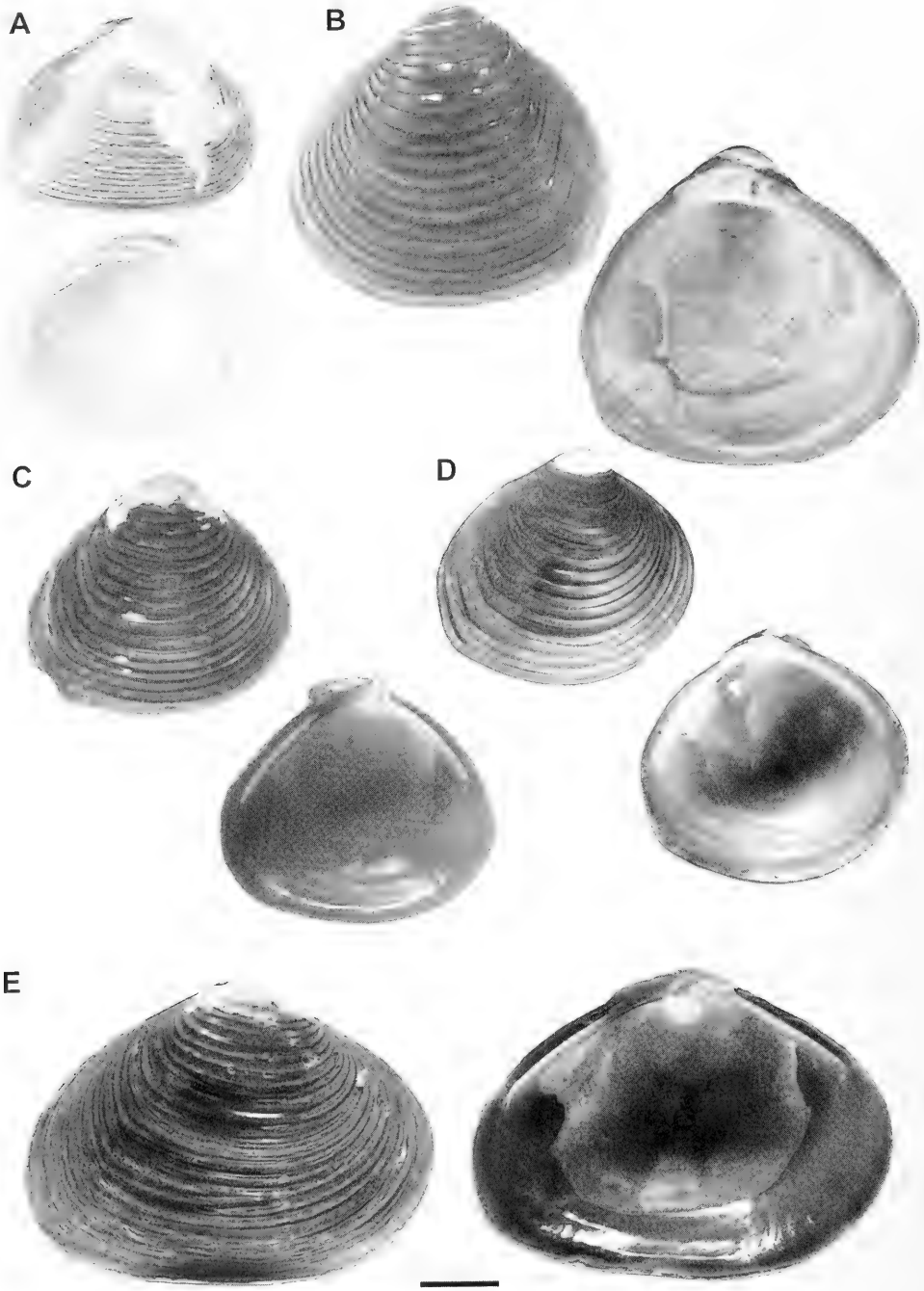

FIG. 4. Shells of *Corbicula moltkiana* from Sumatra with synonyms as suggested in the present paper: A. Original figure from Prime (1878), locality unknown (not to scale); B. One of the syntypes of *C. sumatrana*, Lake Singkarak (SMF 5995); C. One of the syntypes of *C. lacustre*, Lake Singkarak (ZMB Moll. 170000); D. *C. moltkiana*, Lake Singkarak (ZMB Moll. 103024); E. *C. moltkiana*, Lake Manindjau (ZMB Moll. 54370). Scale bar = 5 mm.

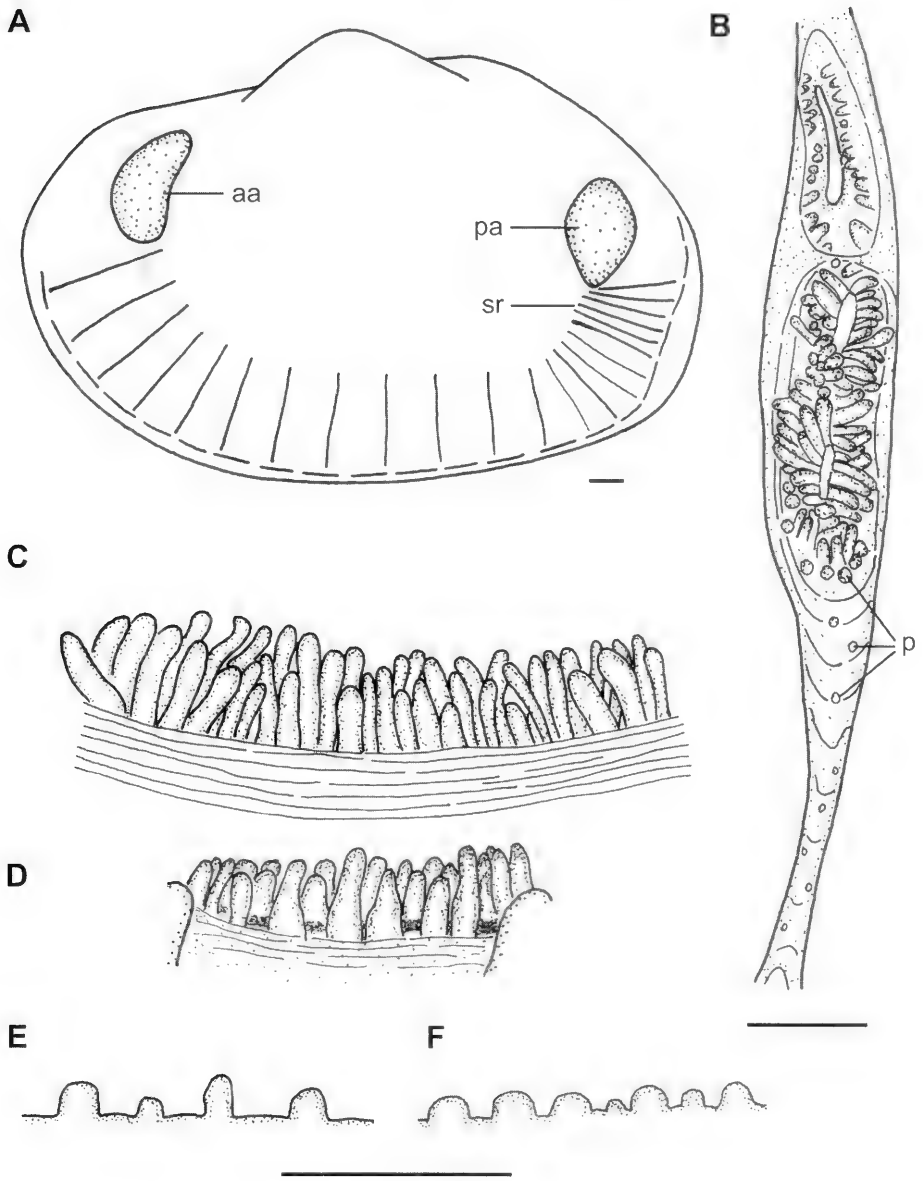

FIG. 5. Anatomy of *Corbicula moltkiana*, Sumatra, Lake Manindjau: A. Habitus of soft body; B. Siphons from outside; C–D. Papillae of inhalant siphon (C - ZMB Moll. 54370, D - ZMB Moll. 103034); E–F. Marginal mantle papillae (E - ZMB Moll. 54370, F - ZMB Moll. 103034). Scale bars = 1 mm.

Anatomy: Adductors small, oval (Fig. 5A, Table 2). Presiphonal suture longer than aperture of inhalant siphon. Siphons conical, narrow in small specimens and rather broad in full grown ones, with thick walls and circular or oval apertures; number of inhalant siphon papillae varies from 30 to about 80, arranged in one or two rows (Figs. 5B–D, 6B), in largest specimens additional row of small papillae may appear. Black pigment concentrated in rings at base of papillae in both siphons, but patches of pigment also seen around siphons

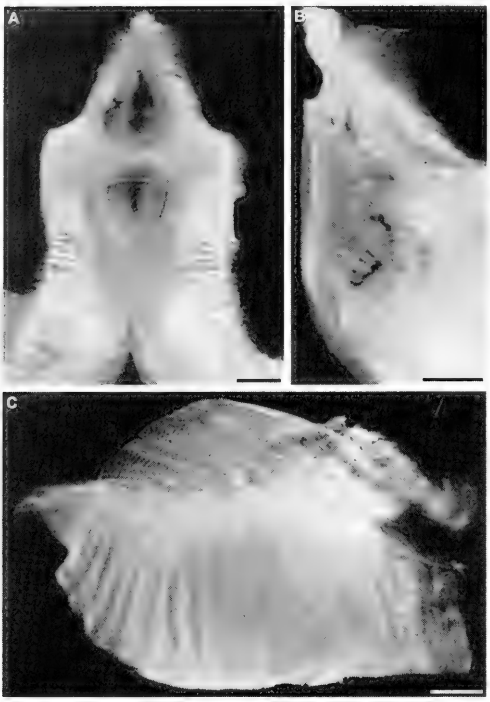

FIG. 6. *Corbicula moltkiana*, Sumatra, Lake Singkarak (ZMB Moll. 103025), view of mantle and gill: A. Siphons from inside, B. Section of siphons; C. Gill with incubated larvae, from inside. Scale bars = 1 mm.

(Fig. 6A, B), in some specimens internal surface of siphons almost entirely pigmented. Some papillae of inhalant siphon with dark rings. In specimens from Martens' collection pattern of pigmentation indistinguishable. Siphonal muscles strong, arranged in broad bands (Fig. 6A). Papillae on outer surface of presiphonal suture arranged in single row, sometimes in two rows. Marginal mantle papillae well developed, densely arranged. Radial mantle muscles strong, arranged in band, their bundles indistinguishable in smaller specimens but distinct in large animals (Fig. 7A, B).

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa (Fig. 8A–B) monoflagellate; head length 11.5 ± 0.58 μm (n = 7). Eight out of 15 specimens collected in Lake Singkarak (ZMB Moll. 103026) were brooding and their inner demibranchs contained several hundred larvae of approximately equal size (0.25–0.3 mm long). The only gravid specimen found in Lake Manindjau (ZMB Moll. 54370) contained larger larvae (about 0.35 mm long).

Distribution and ecology: To date known from several localities on Sumatra and the Malay Peninsula, according to Djajasasmita (1977). Material revised by this study was collected in lakes only (Fig. 1A), but the species was also recorded in rivers and ditches (Djajasasmita, 1977).

Remarks: This species is remarkably variable both in shell and anatomical characters. Specimens from Lake Manindjau differ from those collected in Lake Singkarak (type locality of *C. sumatrana* and *C. lacustris*) in their narrower hinge plate and densely arranged ribs. Moreover, the old lots from Lake Manindjau are distinguished from the new collections from the same lake by their elongated shells, broadened siphons, and weaker mantle muscles; anatomical differences might be associated with the larger size of animals collected by Weber, in comparison with those from our collections (26–28 and 15–18 mm, respectively). Furthermore, the purple form found in both sampled lakes (stored separately as ZMB Moll. 103032, 103034) alongside the yellow one (ZMB Moll. 103024, 103025) showed also somewhat more delicate ribs and darker internal pigmentation of siphons. The form described as *C. lacustre* is characterized by smaller size (up to 18 mm), high, thick-walled shell, and especially coarse sculpture; it is probably a deep water variety of the same species (Djajasasmita, 1977). While differences between the extreme forms from the localities discussed here are rather pronounced (Fig. 4), intermediate forms could be also found.

All forms assigned here to *C. moltkiana* can be recognized by their angulate compressed shell, narrow not protruding beak, relatively broad hinge plate and sharp ribs. These characters distinguish it from the widely distributed Southeast Asian taxon, *C. javanica* (Table 3), as well as from the typical form of *C. fluminea*. The differences from *C. javanica* in shell elongation and convexity, position of beaks, and relative breadth of hinge plate (Table 2) were significant at $p < 0.05$. Noteworthy, one specimen of *C. javanica* was found in Weber's lot from Lake Manindjau (ZMB Moll. 103.058), being well distinguishable from the sympatric *C. moltkiana* by its protruding beak, narrow hinge and widely spaced smoothened ribs.

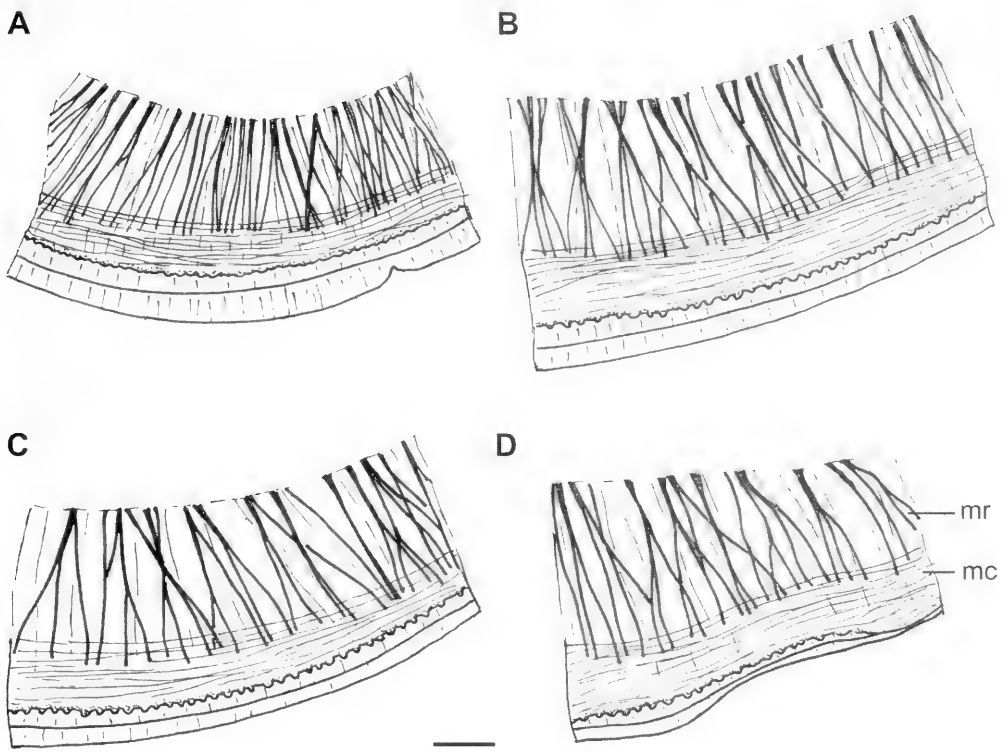

FIG. 7. Mantle musculature of Indonesian *Corbicula*: A. *C. moltkiana*, Sumatra, Lake Singkarak (ZMB Moll. 103024); B. *C. moltkiana*, Sumatra, Lake Manindjau (ZMB Moll. 54370); C. *C. matannensis*, Sulawesi, Lake Matano (ZMB Moll. 103002); D. *C. possoensis*, Sulawesi, Lake Poso (ZMB Moll. 103028). Scale bar = 1 mm. mc - concentric musculature, mr - radial musculature.

Large specimens of *C. moltkiana* are similar in some anatomical characters (form of siphons and patterns of mantle musculature) to the lacustrine taxa from Sulawesi (*C. matannensis* and *C. loehensis*). Dark rings of pigment seen at base of both siphons in *C. moltkiana* are similar to those of *C. fluminea* (Britton & Morton, 1979; Harada & Nishino, 1995), but the internal pigmentation of siphons in the former taxon is generally more intense than in the latter.

Sperm and eggs were not found in the same animal. We understand as functional males those animals producing sperm, while we did not find the relatively large eggs when inspecting the gonad. Although the exact expression of sexuality in this species remains to be verified by detailed seasonal observations and histological study of gonads, we anticipate that *C. moltkiana* is not a simultaneous hermaphrodite. In this aspect, it might be similar to *C. sandai* from Lake Biwa, but apparently differs from the other freshwater taxa studied so far (Konishi et al., 1998; Byrne et al., 2000; Qiu et al., 2001). It should be stressed again here, that our finding of monoflagellate sperm in this taxon provides an indication of meiosis and sexual reproduction (Siripattrawan et al., 2000).

Species from Sulawesi

Corbicula linduensis Bollinger, 1914
Figs. 8C, 9A, B, 10, 11

Corbicula moltkiana var. *linduensis* Bollinger, 1914: 575, pl. 18, fig. 12.
Corbicula linduensis Bollinger – Djajasasmita 1975: 84, fig. 1.
Corbicula lindoensis [sic!] Bollinger – Djajasasmita, 1977: 4.
Type Locality: Lake Lindu, Sulawesi.

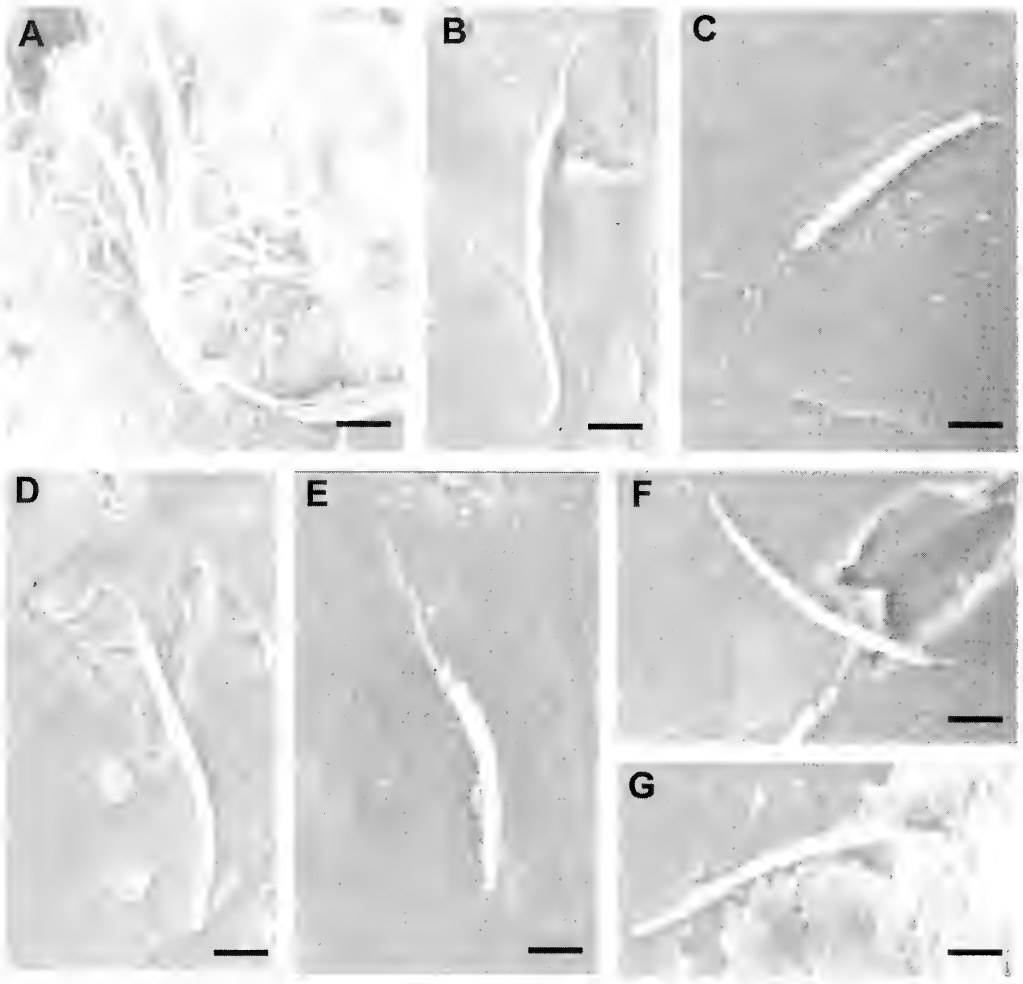

FIG. 8. Sperm morphology (SEM) of Indonesian *Corbicula* exhibiting monoflagellate spermatozoa: A, B. *C. moltkiana* (ZMB Moll. 103024); C. *C. linduensis* (ZMB Moll. 103016); D. *C. matannensis* (ZMB Moll. 103003); E. *C. loehensis* (ZMB Moll. 103010); F, G. *C. possoensis* (ZMB Moll. 103028). Scale bars = 2 μm.

Type Material: Syntypes deposited at the Natural History Museum Basel (Switzerland) are reported to be lost (U. Wüest, pers. comm.).

Material Examined: Sulawesi: river at the road from Palu to Gimpu, basin of the Palu River (01°13.75'S, 119°56.69'E) (ZMB Moll. 103016w; leg. Brinkmann & Rintelen, March 2000) (Fig. 1).

Description

Shell: Oval, usually markedly elongated, with rounded posteroventral angle (Fig. 9A, B). Periostracum yellow to brown. Internal coloration white or purple. Beaks central, narrow and not protruding. Surface sculpture with widely spaced, low ribs (n = 10–12 ribs per 1 cm); pronounced folds of periostracum noticeable between ribs. Hinge plate moderately broad. Cardinal teeth delicate; lateral teeth relatively short, straight. Largest specimen available for this study was 17 mm long. According to the literature, the specimens from Lake Lindu were on average 23 mm long.

Anatomy: Adductors small, round (Fig. 10A, Table 2). Presiphonal suture not elongated,

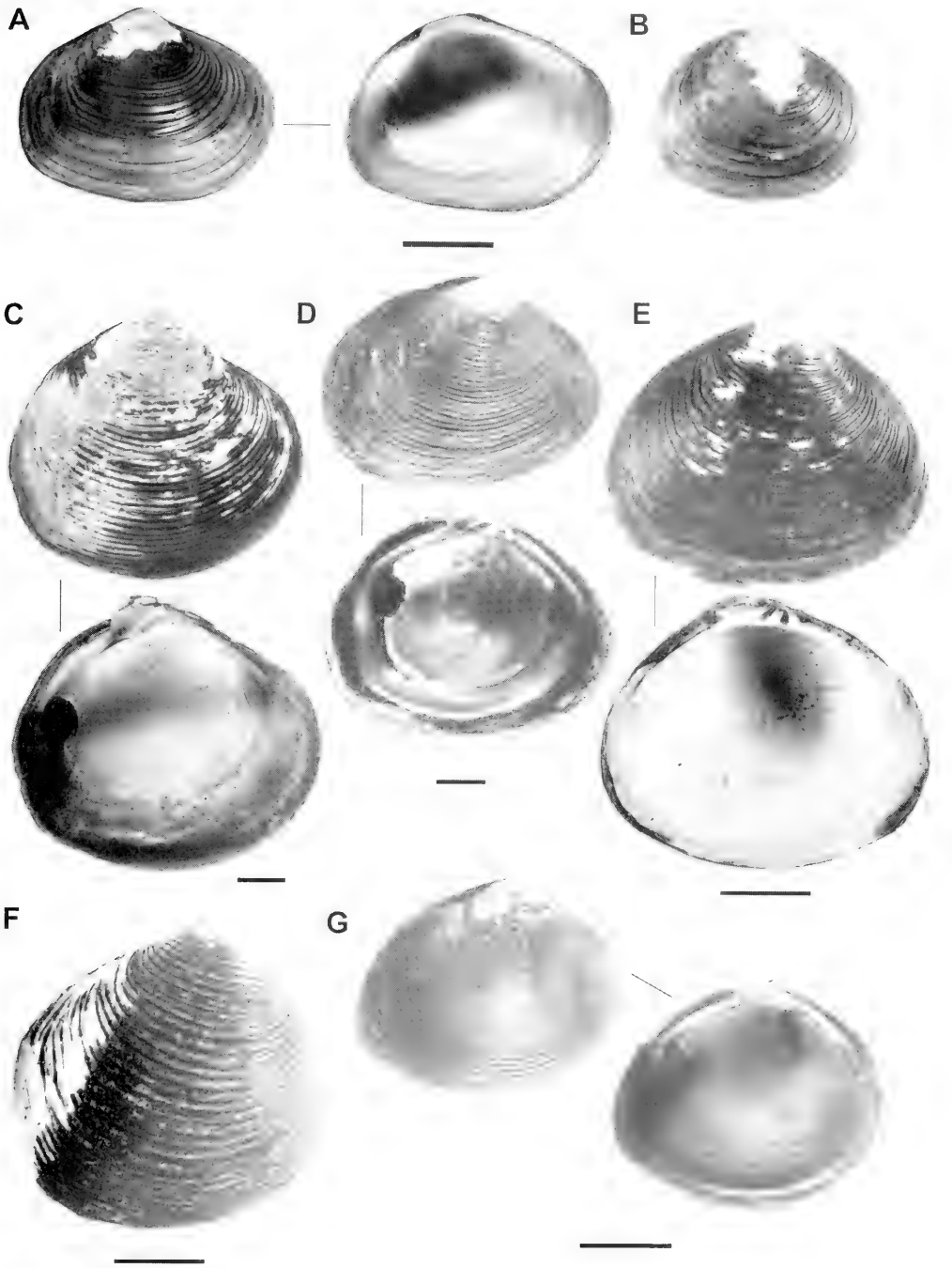

FIG. 9. Shells of *Corbicula* taxa from Sulawesi (right valve from outside, left valve from inside): A, B. *Corbicula linduensis*, Palu River system (ZMB Moll. 103016); C. Syntype of *C. matannensis*, Lake Matano (ZMB Moll. 50799); D. *C. matannensis*, Lake Matano (ZMB Moll. 103002); E. *C. matannensis*, Lake Mahalona (ZMB Moll. 103009); F. *C. matannensis*, Lake Towuti (ZMB Moll. 103006); G. Juvenile specimen of the same species from Lake Towuti (ZMB Moll. 103007). Scale bars = 5 mm.

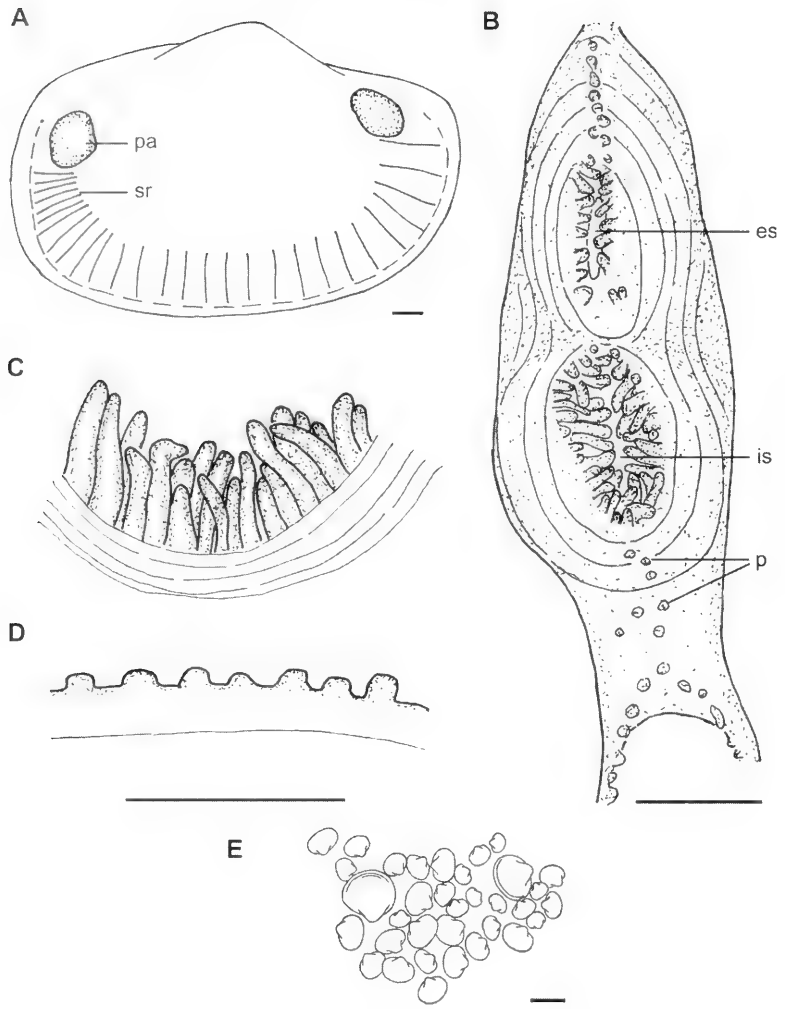

FIG. 10. Anatomy of *Corbicula linduensis*, Sulawesi (ZMB Moll. 103016): A. Habitus of soft body; B. Siphons from outside; C. Inhalant siphon papillae; D. Marginal mantle papillae; E. Clutch of juveniles from a gill. Scale bars = 1 mm (C and D to same scale).

length equal to diameter of inhalant siphon. Siphons conical, thin-walled, apertures circular or short oval, both somewhat broadened; inhalant siphon with about 50 papillae arranged in two rows (external row with shorter papillae) (Figs. 10B, C, 11A, B). Internal pigmentation of siphons weak, but pale internal ring sometimes noticeable around exhalant siphon. Papillae not pigmented. Siphonal muscles rather strong, arranged in broad bands. Papillae on outer surface of presiphonal suture arranged in two uneven rows (Fig. 10B). Marginal mantle papillae well developed, densely spaced (Fig. 10D). Radial mantle muscles strong, arranged in band, with only anterior bundles distinct, separated from each other.

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa (Fig. 8C) monoflagellate, relatively small (head length 8.8 $\pm$ 0.27 μm, n = 7). Eight of 12 studied specimens were brooding. Some of them contained several hundred larvae of usual size for *Corbicula*. However, most of the gravid animals carried in each inner demibranch 10 to 35 juveniles

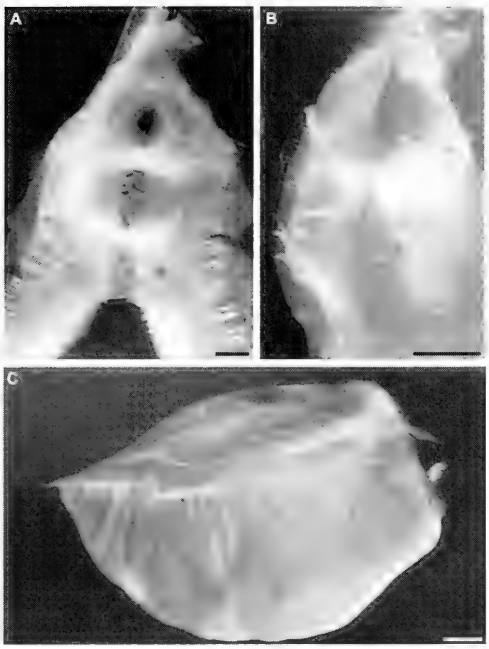

FIG. 11. View of mantle and gills of *Corbicula linduensis*, Sulawesi (ZMB Moll. 103016): A. Siphons from inside; B. Section of siphons; C. Gill with incubated larvae, from inside. Scale bars = 1 mm.

with up to 1.5 mm long shells (Fig. 10E, 11C).

Distribution and Ecology: Apparently restricted to the lake and river of the Palu basin. To date only known from lacustrine habitats (Djajasasmita, 1975, 1977). Our recent findings extend the known distribution from the lake proper to the Palu valley, though, since the specimens studied here were collected in a small river, on muddy bottom with vegetation.

Remarks: This species is similar in its elongated shell to some forms of *C. moltkiana*. However, the sculpture (smoothened ribs) and siphonal characters of *C. linduensis* are more similar to that in *C. fluminea* and *C. javanica* (Table 3). Sperm and eggs were not found in the same animal. Taking into account the monoflagellate type of sperm, we suggest that this species is meiotic, similarily to *C. moltkiana*. It is distinguished from the other taxa studied by the significantly smaller spermatozoa ($p < 0.01$, t-test). Characteristics of its brooding process, i.e. having the largest incubated juveniles known, are unique among *Corbicula* species. According to Djajasasmita (1975) the population from Lake Lindu has dramatically decreased since 1950, thus rendering conservation strategy for this unique bivalve an urgent task.

Corbicula matannensis P. Sarasin & F. Sarasin, 1898
Figs. 7C, 8D, 9C–G, 12, 13

Corbicula matannensis P. Sarasin & F. Sarasin, 1898: 92, pl. 11, figs. 158–160; Kruimel, 1913: 231; Djajasasmita, 1975: 84, fig. 3; Djajasasmita, 1977: 4.

Corbicula towutensis Kruimel, 1913: 231, pl. 4, fig. 3.

Corbicula mahalonensis Kruimel, 1913: 231, pl. 4, fig. 4.

Corbicula subplanata (partim) Martens – Prashad, 1930: 203, pl. 26, figs. 7–9, 13.

Type Locality: Lake Matano, Sulawesi.

Type Material: Syntype of *C. matannensis* P. Sarasin & F. Sarasin (ZMB 50799), from Lake Matano (Fig. 11A). Syntypes of *C. towutensis* Kruimel and *C. mahalonensis* Kruimel (ZMA) [vidi].

Other Material Examined: Sulawesi: Lake Matano: S shore, small bay (02°28.04'S, 121°14.04'E) (ZMB Moll. 103000w; leg. Glaubrecht & Rintelen, 15 August 1999); S shore (02°28.44'S, 121°15.78'E) (ZMB Moll. 103001w; leg. Glaubrecht & Rintelen, 15 August 1999); E bay, at outlet of Petea River (02°32.06'S, 121°28.50'E) (ZMB Moll. 103002w; leg. Glaubrecht & Rintelen, 16 August 1999); S shore, at Salonsa (02°30.49'S, 121°19.96'E) (ZMB Moll. 103003w; leg. Glaubrecht & Rintelen, August 1999); NW shore (2°26.01'S, 121°13.03'E) (ZMB Moll. 103004w; leg. Glaubrecht & Rintelen, 11–12 August 1999). Lake Towuti: W shore, bay at outlet of Larona River (02°46.09'S, 121°21.57'E) (ZMB Moll. 103006; leg. Glaubrecht & Rintelen, 18 August 1999); N shore, swamp W of Mahalona inlet, lake side of sand-bar (02°40'S, 121°31.8'E) (ZMB Moll. 103007w; leg. Bouchet, 1991). Lake Mahalona: at mouth of outlet (02°36.88'S, 121°30.98'E) (ZMB Moll. 103008; leg. Glaubrecht & Rintelen, 24 August 1999); E shore, cape (02°35.58'S, 121°30.68'E) (ZMB Moll. 103009w; leg. Glaubrecht & Rintelen, 24 August 1999) (Fig. 1).

Taxonomic Remarks: Comparison of the available material of *C. matannensis* to the

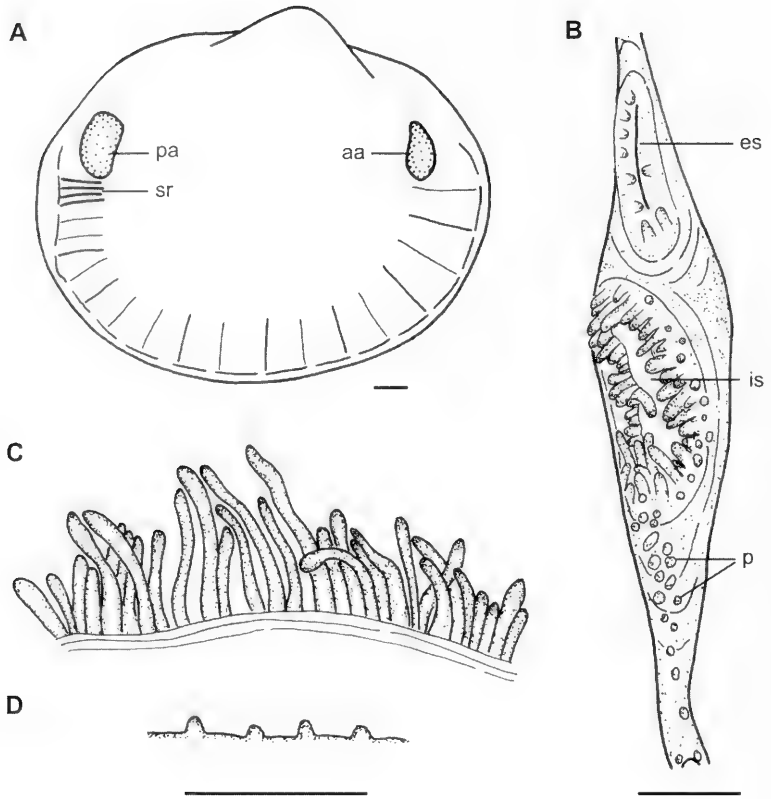

FIG. 12. Anatomy of *Corbicula matannensis* from Sulawesi, Lake Matano (ZMB Moll. 103002): A. Habitus of soft body; B. Siphons from outside; C. Papillae of inhalant siphon; D. Marginal mantle papillae. Scale bars = 1 mm (C and D to the same scale).

syntypes of *C. subplanata* Martens, 1897 (ZMB Moll. 103017, from Minralang River, near Tempe, Sulawesi), confirmed the differences in patterns of sculpture between these taxa mentioned by Djajasasmita (1975). However, the status of the latter taxon remains unclear, until its soft parts are available for anatomical and molecular study. Given that the differences between the respective taxa concern only shell proportions, which proved to be variable in *Corbicula* (Morton 1979, 1986; Harada & Nishino 1995), we accept here the synonymization of *C. mahalonensis* and *C. towutensis* under *C. matannensis* as suggested by Djajasasmita (1975).

Description

Shell: Circular in young specimens and tetragonal in fully grown ones, with obtuse posteroventral angle (Fig. 9C–G). Periostracum from pale yellow to dark violet in small shells and usually black in large ones, dull. Internal coloration from white to deep purple, usually darker on outer margin. Beaks central in young shells but markedly shifted forward in adults, narrow, not protruding. Concentric sculpture pronounced, densely spaced (15–20 ribs per 10 mm), ribs sharp. Hinge plate usually broad; cardinal teeth well developed; lateral teeth straight. Length up to 32.5 mm (syntype from Lake Matano).

Anatomy: Adductors small, oval (Fig. 12A, Table 2). Presiphonal suture relatively long. Siphons cylindrical, thin-walled, with broad slit-like apertures; inhalant siphon somewhat broader than exhalant, with 55 to 70 papillae arranged in two rows (internal row of long, external of short papillae) (Figs. 12B, C, 13A–C). Both inner and outer surface of siphons

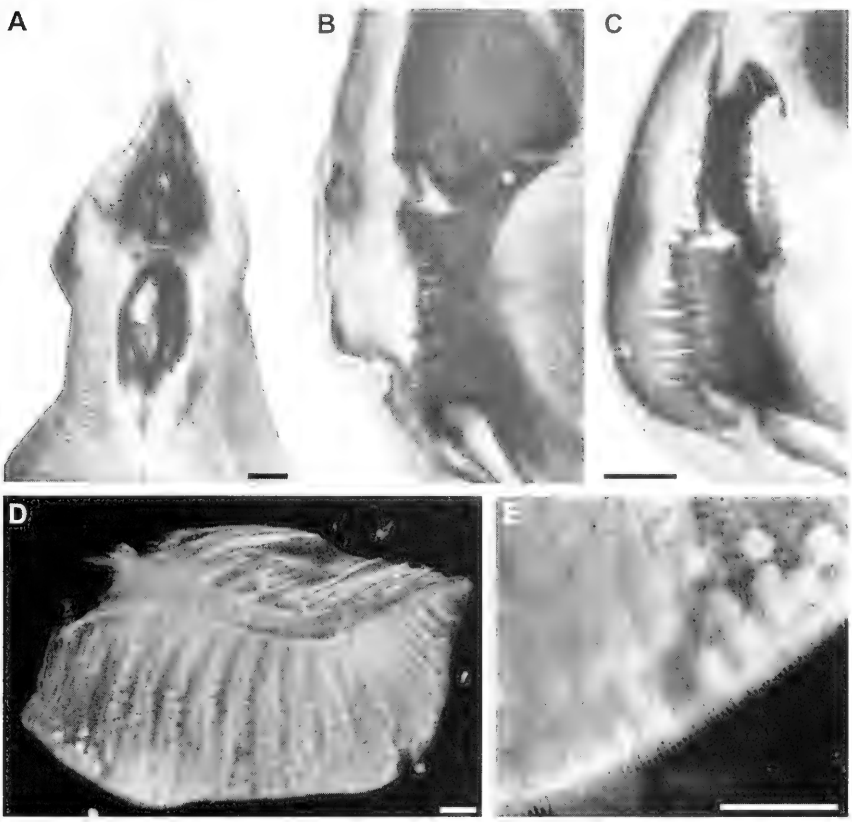

FIG. 13. *Corbicula matannensis* from Sulawesi, view of mantle and gill: A. Siphons from inside, Lake Matano (ZMB Moll. 103002); B. Section of siphons from specimen of the same locality; C. Section of siphons, Lake Towuti (ZMB Moll. 103006); D, E. Gill with incubated larvae, Lake Matano (ZMB Moll. 103002). Scale bars = 1 mm.

and papillae densely pigmented; with dark median internal stripe along presiphonal suture. Siphonal muscles weak, forming two narrow bands and dispersed fibers below and above these bands (Figs. 12A, 13A). Arrangement of papillae on outer surface of presiphonal suture variable: sometimes arranged in several rows, sometimes in single row or dispersed (Fig. 12B). Marginal mantle papillae small, widely spaced (Fig. 12D). Radial mantle muscles weak, forming separate bundles (Fig. 7C).

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa monoflagellate, head length 11.1 ± 0.30 μm (n = 7). Brooding specimens were found in three samples (two from Lake Matano and one from Lake Mahalona), representing a total of eight gravid specimens out of 30 specimens dissected. Numerous larvae (0.30–0.33 mm long) were located only in inner demibranchs (Fig. 13D, E).

Distribution and Ecology: Occurring in the larger lakes of the Malili system, that is, Lake Matano, Mahalona and Towuti. This species is known from lacustrine habitats only so far.

Remarks: This species is distinguished from *C. subplanata*, as described by Martens (1897), by its sculpture. *Corbicula matannensis* has much more densely placed ribs, and they are narrower and more sharp; because spacing between ribs in *Corbicula* increases with age, equally sized specimens should be compared. The latter taxon is also characterized by rather peculiar anatomical

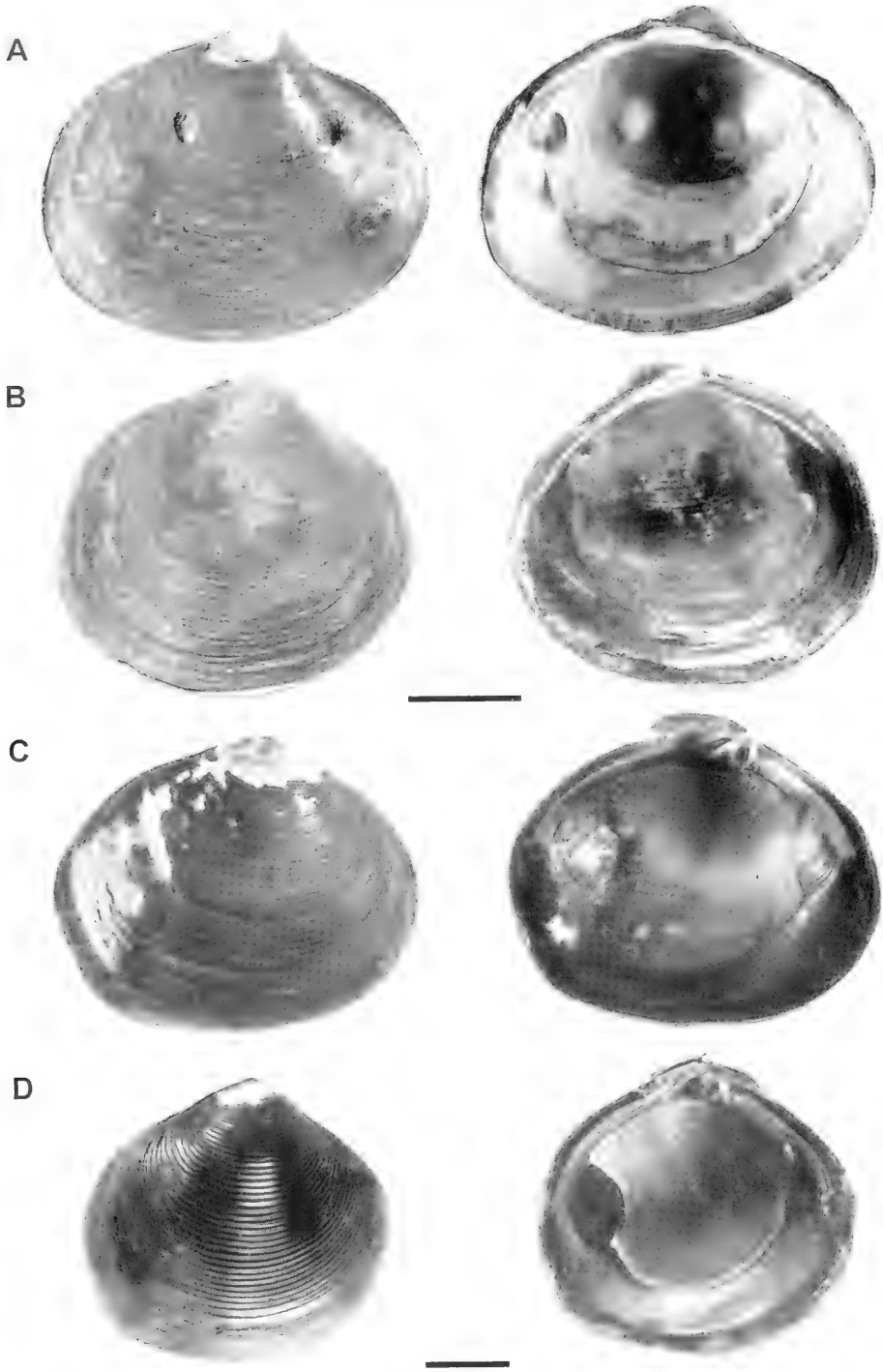

FIG. 14. Shells of *Corbicula* from Sulawesi: A. *C. loehensis*, Lake Masapi (ZMB Moll. 103010); B. *C. loehensis*, Lake Lontoa (ZMB Moll. 103005); C. Syntype of *Corbicula possoensis*, Lake Poso (ZMB Moll. 50798; D. *Corbicula possoensis*, Lake Poso (ZMB Moll. 190024). Scale bars = 5 mm.

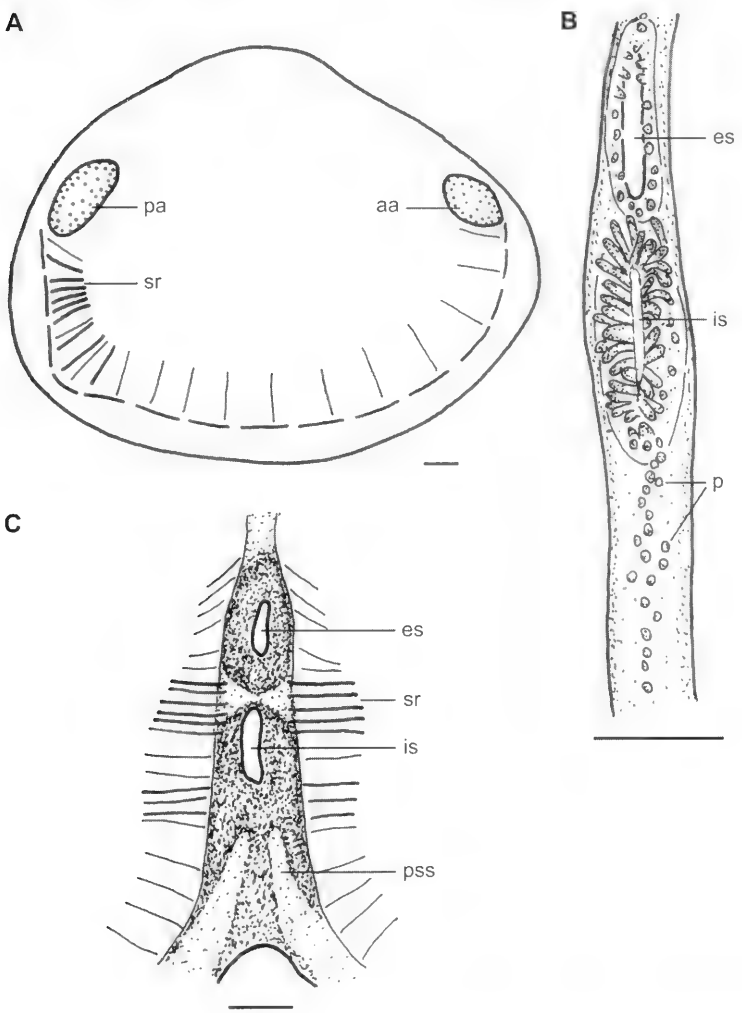

FIG. 15. Anatomy of *Corbicula loehensis*, Lake Masapi (ZMB Moll. 103010): A. Habitus of soft body; B. Siphons from outside; C. Siphons from inside. Scale bars = 1 mm.

characters (broad siphons with strong inside pigmentation, and widely spaced marginal papillae of mantle). One sample from Lake Towuti contained small shells (up to 16 mm long) with delicate sculpture (Fig. 9G) that show some similarity to *C. loehensis* (see below). However, none of these specimens were brooding, therefore, we conclude that all of them were young and could represent *C. matannensis*, in which juveniles have more delicate sculpture than adults. Noteworthy, the doubtful specimens from Towuti were similar to young *Corbicula* from Lake Matano and distinguished from *C. loehensis* of Lake Masapi and Lake Lontoa (older name: Wawontoa) by their broad hinge plate. The shells from Lake Matano are the largest (length up to 35 mm) characterised by well developed sculpture (n = 14–16 ribs per 10 mm in the middle and about 12 at the outer margin, near the beaks ribs are fine) and strong hinge. The specimens from Lake Towuti are very similar to that from Lake Matano, but they never reach such a large size (largest specimen found was 23 mm long) and are more round and convex (Fig. 11D, Table 2). This form is similar to

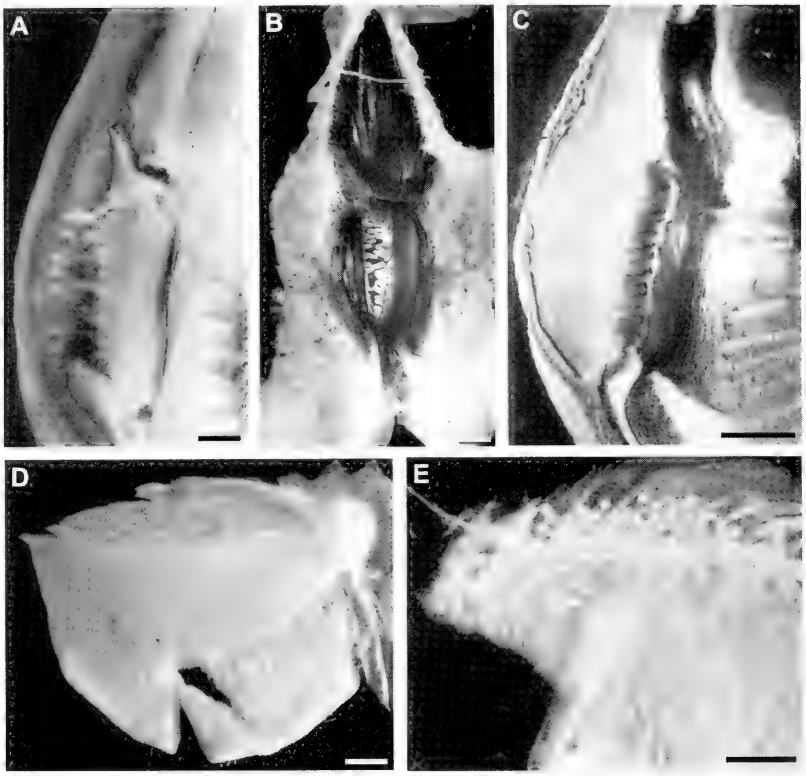

FIG. 16. *Corbicula loehensis* and *C. possoensis*, view of siphons and gills: A. *C. loehensis*, Lake Lontoa (ZMB Moll. 103005), section of siphons; B. *C. possoensis*, (ZMB Moll. 190024), siphons from inside; C. *C. possoensis* (ZMB Moll. 190024), section of siphons; D. *C. loehensis*, Lake Masapi (ZMB Moll. 103010), gill with incubated larvae from outside; E. *C. possoensis* (ZMB Moll. 190024), anterior portion of gill from inside (inner demibranch partly removed). Scale bars = 1mm.

small specimens of *C. possoensis*, but can be readily distinguished by the size of the adductors (see below). The corbiculids from Lake Mahalona are more elongated (especially posterior part) and flat (see Fig. 9E, Table 2). However, variation within one and the same lake (Matano) is also considerable (Fig. 11C, D, Table 2).

In features of reproductive biology (i.e., in presence of sperm and eggs in different animals, sperm morphology and mode of brooding) this species is similar to *C. moltkiana* from Sumatra.

Corbicula loehensis Kruimel, 1913
Figs. 8E, 14 A, B, 15, 16 A, D

Corbicula loehensis Kruimel, 1913: 232, pl. 4, figs. 2, 3; Djajasasmita, 1975: 84, fig. 3; Djajasasmita, 1977: 4.

Corbicula masapensis Kruimel, 1913: 232, pl. 4, fig. 1.

Corbicula subplanata Martens (part.) – Prashad, 1930: 203, pl. 26, figs. 11-12.

Type Locality: SE shore of Loeha Island, Lake Towuti.

Type Material: syntypes ZMA [vidi].

Other Material Examined: Sulawesi: Lake Masapi: S shore (02°50.84'S, 121°21.09'E) (ZMB Moll. 103011w; leg. Brinkmann & Rintelen, 30 March 2000); Lake Masapi, locality not specified (ZMB Moll. 103010w; leg. Bouchet, 1991). Lake Lontoa (= Wawontoa): SW shore (02°39.6'S, 121°44.8'E) (ZMB Moll. 103005w; leg. Bouchet, October 1991); W shore (02°39.90'S, 121°43.46'E) (ZMB Moll. 103033w; leg. Brinkmann & Rintelen, Mar 2000) (Fig. 1).

Taxonomic remarks: Djajasasmita (1975) synonymised *C. masapensis* with *C.*

loehensis. This point of view is tentatively accepted here, but we suggest to study Lake Towuti populations carefully before a final decision on the taxonomic status of the forms under consideration is possible. Identity of the form present in Lake Lontoa to *C. loehensis* was first shown by Djajasasmita (1975).

Description

Shell: Round to ovate, with somewhat obtuse posterior edge (Fig. 14A, B). Periostracum yellow in specimens from Lake Masapi and dark violet in those from Lake Lontoa, with silky glitter. Internal coloration white and purple, respectively. Beaks subcentral. Sculpture very fine, formed by delicate ribs (30–40 per 1 cm). Hinge plate moderately broad; cardinal teeth delicate; laterals relatively short, straight. The largest examined specimen was 18 mm long, but according to literature data the species may reach a length of 25 mm (Djajasasmita, 1975).

Anatomy: Adductors small, oval (Fig. 15A, Table 2). Siphons cylindrical, rather thin-walled, with broad oval apertures, inhalant siphon somewhat broader than exhalant, with about 50 papillae arranged in two rows. Internal surface of siphons, papillae and presiphonal suture usually strongly pigmented (Figs. 15B, C, 16A). Marginal mantle papillae small, widely spaced. Mantle musculature weak, muscle bundles well distinguishable and separated.

Reproductive biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa monoflagellate, head length 9.1 $\pm$ 0.21 μm (n = 7). The largest of the studied specimens was brooding. Larvae located in its inner demibranchs (Fig. 16D) were about 0.24 mm.

Distribution: Recorded ashore in Lake Towuti (Kruimel, 1913; Djajasasmita, 1975) and its satellite lakes Masapi and Lontoa.

Remarks: Anatomical characters of *C. loehensis* and *C. matannensis* are similar (Table 3), as well as are juvenile shells. However, the characters of juvenile shells in the former species (very fine sculpture and delicate hinge) are also retained in more advanced individuals of the latter species, which might indicate distinct developmental trends. Differences in coloration between the shells from Lakes Masapi and Lontoa are also noteworthy.

This species is similar in features of reproductive biology (structure of gonads, sperm type and mode of brooding) to *C. moltkiana* and *C. matannensis*, but differs in having significantly smaller spermatozoa ($p < 0.001$).

Corbicula possoensis P. Sarasin & F. Sarasin, 1898
Figs. 7D, 8F–G, 14C, D; 16B, C, E; 17

Corbicula possoensis P. Sarasin & F. Sarasin, 1898: 92, pl. 11, figs. 161–162; Kruimel, 1913: 231.

Corbicula subplanata Martens (part.) – Prashad, 1930: 203, pl. 26, figs. 10, 17–20.

Corbicula matannensis P. Sarasin & F. Sarasin (part.) – Djajasasmita, 1975: 84; Djajasasmita, 1977: 4.

Type Locality: Lake Poso, Sulawesi.

Type Material: syntype ZMB Moll. 50798 (Fig. 14C).

Other Material Examined: Lake Poso: S shore, Tentena, beach at Hotel "Pamona Indah" (01°45.92'S, 120°38.42'E) (ZMB Moll. 190024w; leg. Glaubrecht & Rintelen, September 1999); at Hotel "Mulia" (02°03.91'S, 120°41.50'E) (ZMB Moll. 103028w; leg. Brinkmann & Rintelen 23 September 2000); SW shore, Matawai (02°02.4'S, 120°38.1'E) (ZMB Moll. 103012w; leg. Bouchet, September 1991); E shore, Tolambo Bay (01°59.8'S, 120°42.1'E) (ZMB Moll. 103013w; leg. Bouchet, 1991); N shore, Saluopa (01°46.6'S, 120°32.9'E) (ZMB Moll. 103014w; leg. Bouchet, 1991) (Fig. 1).

Description

Shell: Triangular or short tetragonal, often with blunt keel at posterior end (Fig. 14C, D). Periostracum dark violet to black, sometimes yellowish in very young specimens, shiny. Internal coloration purple. Posterior margin truncate (diagnostic feature). Beaks markedly shifted forward, in small specimens relatively narrow while in large ones this can not be seen because shells are eroded. Hinge plate relatively broad, even in young specimens. Cardinal teeth well developed; lateral teeth somewhat shortened, straight. Sculpture: 25–30 delicate ribs per 1 cm.

Anatomy: Adductors large, posterior larger than anterior one (Figs. 14, 17A). Diameter of posterior adductor more that $^1/_5$ length of shell (Table 2). Presiphonal suture relatively short, not exceeding diameter of inhalant siphon.

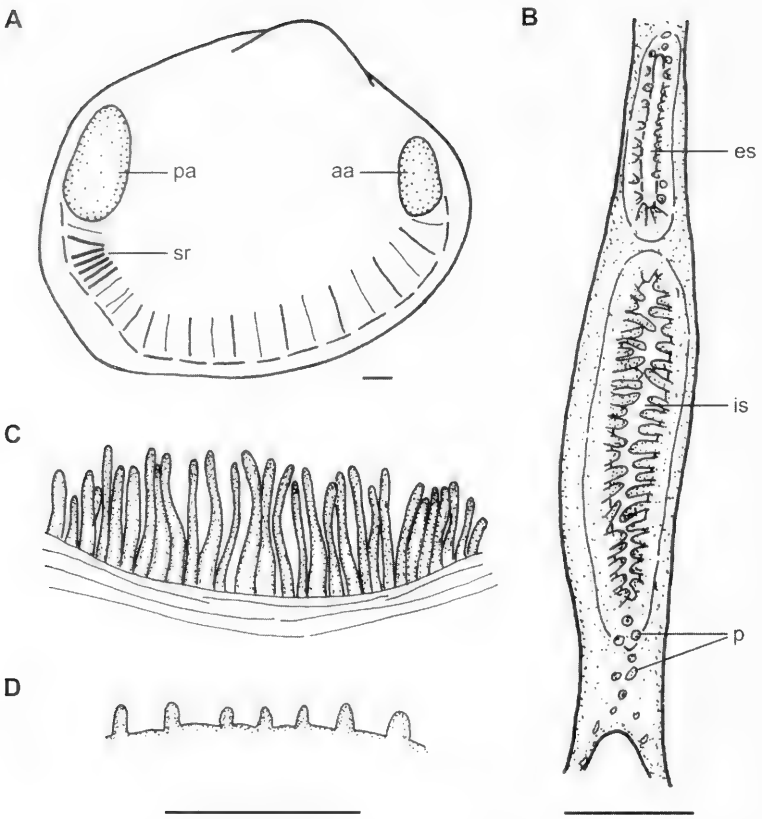

FIG. 17. Anatomy of *Corbicula possoensis*, Lake Poso: A. Habitus of soft body (ZMB Moll. 103014); B. Siphons from outside (ZMB Moll. 190024); C. Papillae of inhalant (ZMB Moll. 190024); D. Marginal mantle papillae (ZMB Moll. 190024). Scale bars = 1 mm (C and D to same scale).

Siphons broad, cylindrical, inhalant siphon markedly broader than exhalant, both with slit-like apertures; inhalant siphon with 60 to 70 papillae (depending on age), arranged in one or two rows (papillae of outer row always relatively smaller) (Figs. 16B, C, 17A, B). Both inner and outer surface of siphons and papillae densely pigmented, presiphonal suture also pigmented internally. Papillae on the outer surface of presiphonal suture scarce, unevenly arranged (Fig. 17B). Marginal mantle papillae small and widely spaced (Fig. 17D). Mantle musculature weak, muscle bundles separated, dispersed (Fig. 7D).

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa monoflagellate, head length 10.7 ± 0.37 μm (n = 6). Branchial incubation was observed in two samples containing larger specimens (exceeding 18 mm); 6 of 15 dissected specimens were brooding and contained larvae in both demibranchs of each gill (Figs. 16E), one gravid specimen had larvae in inner demibranch only, though. Larvae were 0.26–0.30 mm long.

Distribution: Restricted to Lake Poso in Central Sulawesi.

Remarks: Conchologically, this species is distinguished from *C. matannensis* by its truncate posterior edge, fine sculpture (more than 20 ribs per 10 mm) and larger posterior adductor scar (Table 3). Beaks in large shells are somewhat broader and placed more anteriorly than in all previous species; also the hinge plate is relatively higher. *Corbicula possoensis* differs from *C. matannensis* also in having broad siphons extending over about $^1/_3$ of the body length in the former and $^1/_4$ in the latter species. Differences in relative

height of hinge plate, adductor size, siphons breadth and number of ribs were confirmed by t-test ($p < 0.001$). These diagnostic characters were consistent among all examined specimens, which is, in concert with our molecular data, the argument against synonymization of *C. possoensis* with *C. matannensis* as was earlier on suggested by Djajasasmita (1975).

Corbicula possoensis differs from other studied congeners in characteristics of brooding, because it is the only *Corbicula* species known that incubates in both demibranchs, instead of only the inner demibranch. Slight but significant ($p < 0.05$) difference in sperm size between this taxon and *C. matannensis* is also noteworthy. Other reproductive features of *C. possoensis* are similar to those shown for the taxa from Sumatra and Sulawesi (Table 3).

MOLECULAR PHYLOGENETICS

Of a total of 614 base pairs included in the final alignment, 103 were parsimoniously informative. Heuristic search recovered 56 most parsimonious trees of 368 steps (CI = 0.742, RI = 0.685). The strict consensus tree (Fig. 18) shows that all newly sequenced taxa included in the present molecular study form a well supported monophyletic clade with those freshwater taxa of *Corbicula* studied earlier, with the exception of *C. madagascariensis*. Within this clade three distinct Indonesian taxa are supported in this study, occuring (i) on Sumatra, identified as *C. moltkiana*, and (ii) on Sulawesi with *C. matannensis* and *C. loehensis* from the Malili lake system. In addition, two different sequences with unresolved relationships were obtained from specimens identified morphologically as *C. possoensis* from Lake Poso. Furthermore, one other of the Indonesian taxa, *C. javanica*, is shown in the parsimony analysis as closely related to *C. fluminea* from Korea and the North American *Corbicula* "form B", a clade that is also well supported. The second sequence attributed to *C. fluminea*, originating from material from Thailand, a sequence of *C. australis* from Australian, and *C.* cf. *fluminalis* from Israel is also clustering with this clade; however, the bootstrap support for the joint group is weak.

The NJ tree (Fig. 19) is more resolved than the consensus tree recovered by the maximum parsimony analysis, but the clades supported by high bootstrap values are basically the same in both reconstructions. The two different morphotypes of *C. moltkiana* from Lake Manindjau cluster together, as well as the two different morphotypes from Lake Singkarak, irrespective of the morphological similarity between the corresponding morphotypes found in each of the two lakes; thus, the four samples from Sumatra cluster according to geography instead of morphology. The NJ analysis also indicates an outstanding position of *C. moltkiana* and a sister relationship between *C. loehensis* and *C. matannensis*, although the support of the relevant clades is below the 50% level. Heterogeneity of *C. possoensis* is found in this analysis as well.

Distance analyses show remarkable similarity in COI sequences (divergence levels not exceeding 1%) between the samples from the adjacent lakes Manindjau and Singkarak on Sumatra, as well Matano and Mahalona on Sulawesi (Table 4). The divergence between sequences obtained from different samples in Lake Matano was approximately of the same level as the difference between the samples from Matano and Mahalona. Only minor differences were recovered for *C. loehensis* from Masapi and Lontoa, while divergence level between this taxon and *C. matannensis* reaches 3.5%. The distance between two sequences of *C. possoensis* comprised 3.8%. Most of the pairwise sequence divergence levels calculated for the freshwater *Corbicula* taxa by this study did not exceed the level of 4.1% reported by Siripattrawan et al. (2000); only *C. moltkiana* showed greater distances, especially when compared with *C. possoensis* (up to 5.7%) and *C. australis* (up to 5.2%).

In conclusion, the molecular data agree with the morphological comparisons presented above in showing (i) distinctness of three lacustrine taxa from Sumatra (*C. moltkiana*) and Sulawesi (*C. matannensis* and *C. loehensis*), respectively, (ii) distinctness of these Indonesian taxa with respect to known continental Asian lineages, and (iii) the relationship of *C. javanica* and *C. fluminea*. However, the results concerning *C. possoensis* are equivocal, because no morphological characters correlated with the observed sequence differences were found. Plotting sperm morphology data on the trees based on COI sequence data suggests polyphyletic origin of the biflagellate condition, since no close relationship between the lineages sharing this state could be found.

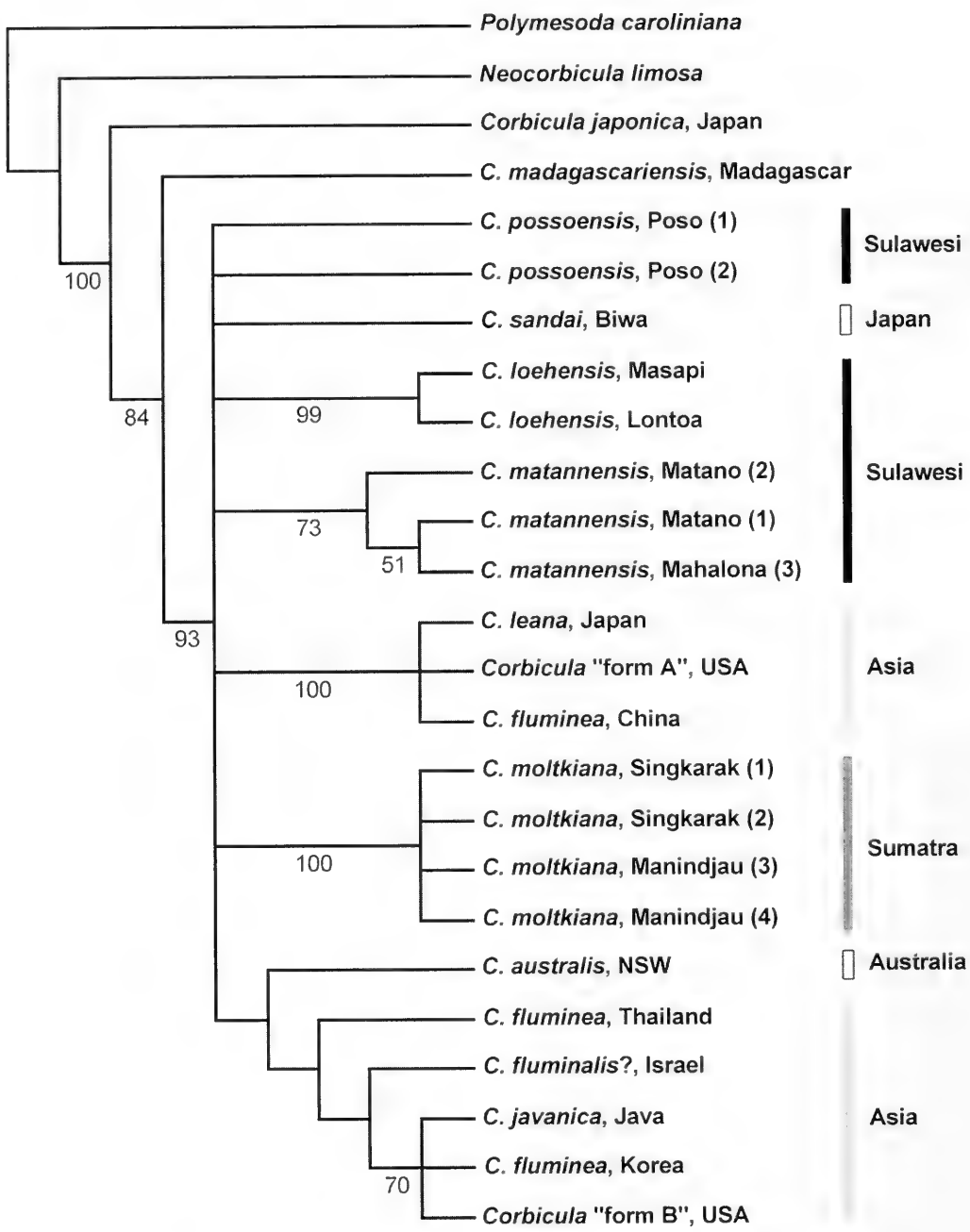

FIG. 18. Strict consensus of 56 maximum parsimony trees (368 steps, CI = 0.742, RI = 0.685) obtained for the corbiculid COI extended dataset. The numbers below branches show bootstrap support (if more than 50%).

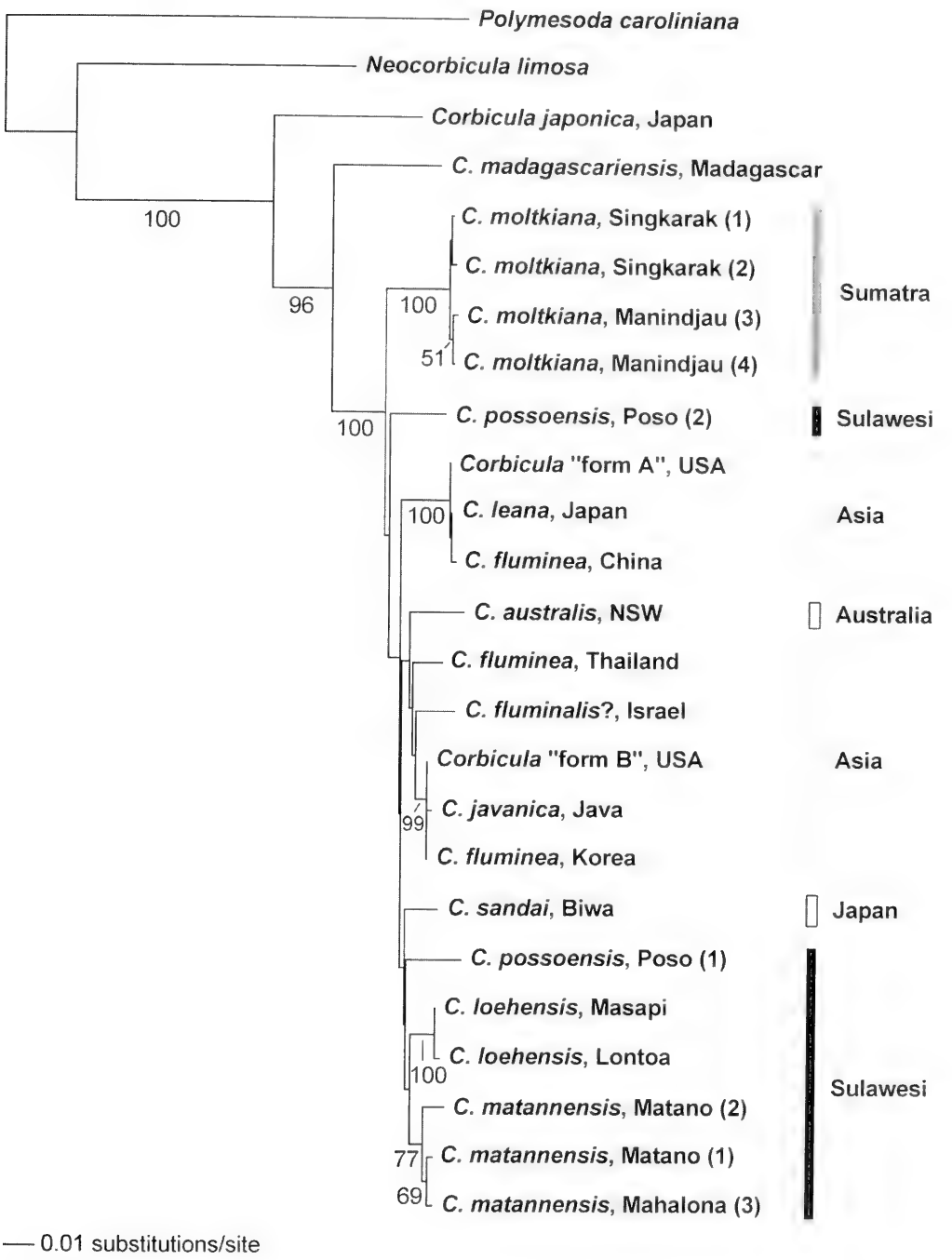

FIG. 19. A neighbor joining tree obtained for the corbiculid COI extended dataset. The numbers below branches show bootstrap support (if more than 50%).

TABLE 4. Corrected pairwise sequence divergences (General Time Reversible model utilized) among the COI haplotypes obtained for autochthonous freshwater *Corbicula* lineages (excluding those introduced to the Americas). Numbers in brackets refer to locality data given in Table 1.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. *C. moltkiana*, Singkarak (1)	-																			
2. *C. moltkiana*, Singkarak (2)	0.17	-																		
3. *C. moltkiana*, Manindjau (3)	0.16	0.34	-																	
4. *C. moltkiana*, Manindjau (4)	0.33	0.50	0.16	-																
5. *C. matannensis*, Matano (1)	4.29	4.40	4.48	4.29	-															
6. *C. matannensis*, Matano (2)	4.64	4.76	4.83	4.64	0.99	-														
7. *C. matannensis*, Mahalona (3)	4.29	4.40	4.48	4.29	0.33	0.99	-													
8. *C. loehensis*, Masapi (1)	3.60	3.69	3.78	3.96	1.34	2.02	1.34	-												
9. *C. loehensis*, Lontoa (2)	3.81	3,90	3.99	4.17	1.52	2.21	1.52	0.17	-											
10. *C. possoensis* (1)	5.55	5.69	5.74	5.55	2.17	2.86	2.88	2.88	3.08	-										
11. *C. possoensis* (2)	4.03	4.20	4.22	4.03	3.30	3.65	3.34	3.34	3.55	3.83	-									
12. *C. javanica*	3.42	3.52	3.60	3.42	2.17	2.52	2.17	2.19	2.38	3.05	3.47	-								
13. *C. fluminalis?* Israel	4.28	4.38	4.46	4.28	3.03	3.38	3.03	3.05	3.25	3.55	3.99	1.83	-							
14. *C. fluminea*, Hong Kong	4.23	4.46	4.43	4.23	2.91	3.27	2.91	2.54	2.72	3.83	4.27	3.09	3.45	-						
15. *C. fluminea*, Thailand	3.24	3.33	3.42	3.24	2.00	2.34	2.00	2.02	2.21	2.88	3.28	0.16	1.66	2.90	-					
16. *C. fluminea*, Korea	3.22	3.30	3.40	3.22	2.69	3.04	2.69	2.70	2.91	3.57	3.64	1.49	2.33	3.26	1.32	-				
17. *C. leana*	4.27	4.37	4.45	4.27	2.70	3.04	2.70	2.37	2.56	3.57	4.01	2.86	3.02	1.75	2.69	3.03	-			
18. *C. sandai*	3.75	3.85	3.93	3.75	2.00	2.34	2.00	2.01	2.20	2.85	3.27	1.82	3.37	3.45	1.66	2.33	3.37	-		
19. *C. australis*	5.03	5.16	5.22	5.03	3.38	3.03	3.38	4.41	3.62	3.91	4.37	2.86	3.38	4.05	2.69	2.68	3.75	3.02	-	
20. *C. madagascariensis*	7.77	7.99	7.98	7.77	7.11	7.47	6.71	6.57	6.80	8.40	7.76	3.36	7.04	6.72	6.16	6.91	6.84	7.30	8.48	-

DISCUSSION

Taxonomy and Systematics

Previous phylogenetic investigations suggested a common, monophyletic origin of all Old World freshwater *Corbicula*, with the estuarine *C. japonica* being the sister taxon (Siripattrawan et al., 2000; Pfenninger et al., 2002). This is confirmed in the present study by the inclusion of new sequence data from Indonesian taxa.

In an attempt to clarify the systematics of these Indonesian corbiculids, mainly of those species inhabiting Sumatra and Sulawesi, five taxa were found to possess specific distinctness and identity, based on shell morphology, anatomy and the features of reproductive biology (including brooding), as well as on molecular data. While the corbiculids studied from Sumatra are identified as *C. moltkiana*, four distinct taxa were identified on Sulawesi: *C. possoensis* (with two distinct lineages revealed in the NJ analysis) endemic to Lake Poso and *C. matannensis* plus *C. loehensis* occurring in the central Malili lake system. Suitable material of the fourth species, *C. linduensis* from the Lindu River, was not available for molecular investigation.

The species distinctness of *C. javanica* from the island of Java remains doubtful in the absence of data on sperm morphology and, thus, there is the possibility of clonality. Remarkable is its close affinity to Asian lineages of *C. fluminea* found in our study. However, the taxonomic status of the latter is also problematic, because it was shown to be an assemblage of several clonal lineages, probably of different origin, that also includes allochthonous populations introduced into North America and Europe (Siripattrawan et al., 2000; Pfenninger et al., 2002). Therefore, any synonymizations in this stage of investigation seem to be premature.

Corbicula taxonomy has historically been plagued by a plethora of nominal taxa described from numerous, at least partly ecophenotypic shell morphs. The occurrence of polyploidy, unisexual reproduction, hermaphroditism, and androgenesis recently reported for certain *Corbicula* populations (see Introduction) suggest that variation observed in these freshwater bivalvia could be the result of clonality and not necessarily imply species level differences, as discussed in Siripattrawan et al. (2000). Because polyploidy is prevalent in some freshwater molluscs, especially among bivalves, it is assumed to have played an important role in shaping their diversity and can pose significant challenges to reconstruct phylogenetic evolution also in Corbiculidae (Lee et al., 2002).

While the determination of presence or absence of meiosis is a rather laborious task applicable only in adequately fixed material, fortunately in *Corbicula* there is an exceptionally convenient morphological marker to help distinguish clonal forms, since, to the present knowledge, studied ameiotic lineages all have biflagellate spermatozoa (Komaru & Konishi, 1999; Siripattrawan et al., 2000; Qiu et al., 2001). Our preliminary observations suggest that Indonesian corbiculids reproduce sexually and have monoflagellate spermatozoa (with the exception of *C. javanica*, in which sperm structure remains unknown). In this respect, they appear to be similar to *C. sandai* from the "ancient" Lake Biwa in Japan, which is known to be diploid and reproduces sexually with monoflagellate sperm (Hurukawa & Mitsumoto, 1953; Okamoto & Arimoto, 1986). Interestingly, our NJ analysis revealed that *C. sandai* clusters together with the Sulawesi clade, whereas the topology of the MP tree is not resolved in this respect.

Given the notorious variability of morphological characters applied traditionally in *Corbicula* taxonomy, which is also shown in this study, and the incompleteness of data on reproductive biology as well as molecular genetics, any final decision about the systematics and taxonomic status of different forms (morphotypes) distributed across Australasia is still not possible. Uncertainties remain in particular for the Javanese form and the question concerning the existence, distribution and identity of *C. fluminea*. However, several of our systematic conclusions based on the new data on Indonesian taxa are in agreement with some of those already reached in previous revisions, mainly those by Djajasasmita (1975, 1977).

Implications from Morphology

Generally, confirming the presence of endemic taxa in several lacustrine habitats on Sumatra and Sulawesi, this study adds support to the recognition of the following taxa: *C. moltkiana*, *C. linduensis*, *C. possoensis*, *C. matannensis* and *C. loehensis*. The first of these taxa recorded in the lakes on Sumatra is similar to the widely distributed Asian *C.*

fluminea (Britton & Morton, 1979; Morton, 1986; Araujo et al., 1993; Chen et al., 1995; Harada & Nishino, 1995; Komaru et al., 1997, 2000), in anatomical characters and the features of brooding; however, its species status is supported by sperm morphology and COI sequence data.

Taxonomic distinctness of *Corbicula linduensis* from North Sulawesi, first suggested by Djajasasmita (1975), is supported here by characteristics of brooding (limited number of large juveniles incubated in gills) not known in any other *Corbicula*. However, in the absence of molecular data for this taxon, its relationships remain unknown. Noteworthy, brooding in *C. linduensis* seems to be somewhat similar to the South American *Neocorbicula limosa*, as described by Ituarte (1994). Since the latter represents an independent lineage within the family, judging from morphological study (Dreher Mansur & Meier-Brook, 2000) and molecular data (Siripattrawan et al., 2000; Figs. 18, 19), its mode of reproduction has apparently evolved independently.

The taxa inhabiting the Malili lake system on Sulawesi differ from their congeners not only in shell parameters, but also in anatomical characters, for example in the form and pigmentation of siphons. Although diagnostic applications of these characters in *Corbicula* is hindered by the considerable intraspecific variability (see, for example, the description of *C. moltkiana*), in this particular case anatomical differences are supported by molecular data. As shown in this study, the distinctness of *C. matannensis* occurring in Lake Matano and Lake Mahalona (connected through the Petea River; Fig. 1) from *C. loehensis* inhabiting the satellite lakes Masapi and Lontoa of Lake Towuti (but both connected via separate river systems) is in agreement with the taxonomy used by Djajasasmita (1975). Unfortunately, no molecular data are available to date for the latter species from Lake Towuti proper, where both taxa possibly live sympatrically according to Djajasasmita (1975).

The data on *C. possoensis* restricted to Lake Poso are controversial. While morphological observations show similarity of all available lots, molecular data suggest their heterogeneity. Although *Corbicula* from Lake Poso apparently needs further study, the outstanding position of *C. possoensis* in relation to corbiculids inhabiting the Malili lake system found in the present study is consistent with recent results on endemic pachychilid gastropods from Lake Poso, which exhibit a similar isolated position among the *Tylomelania* clade in morphological and molecular phylogenies (Rintelen & Glaubrecht, 1999, 2002; Rintelen et al., submitted).

Some anatomical characters, for example the broad cylindrical (fringe-like) form of siphons and the number and arrangement of the exhalant siphon papillae, which are common in *Corbicula* species inhabiting Lake Poso and the Malili Lakes on Sulawesi were also reported for the Japanese estuarine species *C. japonica* (Harada & Nishino, 1995). However, the internal coloration of siphons and papillae is remarkably similar in all Sulawesi taxa but differ from that of *C. japonica*, which is also very distinct karyologically (Okamoto & Arimoto, 1986), in its non-brooding reproduction (reviewed by Morton, 1986) and its molecular genetics (Siripattrawan et al., 2000). Therefore, any similarity in form of siphons between the freshwater corbiculids in question and their probable estuarine sister taxon are unlikely to be synapomorphic.

Spermatozoan Morphology

The new data on sperm morphology shown here for Indonesian taxa suggest that monoflagellate spermatozoa are more common among freshwater *Corbicula* than assumed in previous studies (Komaru & Konishi, 1996, 1999; Byrne et al., 2000; Siripattrawan et al., 2000). Interestingly, the monoflagellate type is known to occur in species inhabiting lacustrine habitats, such as, for example, Lake Biwa in Japan (*C. sandai*), lakes Singkarak and Manindjau on Sumatra (*C. moltkiana*), Lake Poso (*C. possoensis*) and the Malili lake system (*C. matannensis*, *C. loehensis*) on Sulawesi.

In addition, while all *Corbicula* with biflagellate spermatozoa are simultaneous hermaphrodites (Komaru & Konishi, 1996, 1999; Konishi et al., 1998; Byrne et al., 2000), the Indonesian corbiculids with monoflagellate sperm apparently have a different expression of sexuality. Since monoflagellate sperm is reported for the gonochoric *Corbicula sandai* (Siripattrawan et al., 2000, and literature cited therein), we hypothesize that the Indonesian taxa also have separate sexes.

However, sperm morphology of many riverine corbiculids, especially those occurring on other Sunda Islands, is still not studied; therefore, it is too early to judge on this habitat-sperm mor-

phology correlation. Our phylogenetic reconstruction does also not reveal a close relationship between lineages sharing the biflagellate type of sperm, because the latter occurs in clonal *Corbicula* within both Asian clades found in the analyses (Figs. 18, 19).

The diversity of head size in spermatozoa of *Corbicula* is remarkable, although no correlation between size and the monoflagellate/biflagellate type was found. The biflagellate spermatozoa of the Chinese *C. fluminea* and Japanese *C. leana* are distinguishable by their large size of 16–25 μm (Komaru & Konishi, 1996; Qiu et al., 2001), whereas biflagellate spermatozoa of *C. australis* are relatively small with 9.3 μm on average (Byrne et al., 2000). The latter are, thus, similar in size to the monoflagellate spermatozoa found here for *C. loehensis* (9.1 μm). Biflagellate spermatozoa of another Japanese form, *C.* aff. *fluminea*, are reported to be also relatively small compared with the sympatric *C. leana* (13.9 μm and 16.9 μm, respectively) (Konishi et al., 1998). Size difference in corbiculid sperm observed in taxa from China was found to be correlated with ploidy (Qiu et al., 2001) and in taxa from Japan with number of mitochondria (Konishi et al., 1998).

Brooding

Observations presented above on reproduction in Indonesian corbiculids agree with the literature data in showing prevalence of brooding among freshwater *Corbicula* (Morton, 1986; Byrne et al., 2000; Siripattrawan et al., 2000). To date, within the genus only the estuarine (i.e., brackish-water) sister taxon *C. japonica* is non-brooding and characterized by the development with free-swimming veligers (Byun & Chung, 2001). Among the freshwater corbiculids the endemic *C. sandai* from Lake Biwa with its benthic egg masses with direct developing young (Hurukawa & Mitsumoto, 1953) remains the only known exception of an ovoviviparous reproductive mode.

However, we here documented a greater diversity of brooding characteristics in taxa particularily from Sulawesi than was witnessed earlier for the rest of the collective Old World range of *Corbicula*. Remarkable is the presence of large juveniles being incubated in the gills of *C. linduensis* and the brooding utilizing both demibranchs in *C. possoensis*, which is both not known in any other congeners.

Historical Zoogeography

According to the phylogenetic systematics discussed above, two groups of taxa can be distinguished among Indonesian corbiculids. On one hand, there is at least one common widespread clade in Asia that includes populations identified as *C. fluminea* occuring in Korea and Thailand, as well as those populations from the Sunda Islands Java and Lombok assigned here tentatively to *C. javanica* and *C. australis* in Australia.

On the other hand, Sumatra and Sulawesi seem to harbour *Corbicula* species with fairly restricted occurrences that cluster according to their distribution not only on but within these islands. To the present knowledge, all lacustrine forms described herein are endemic to their respective lakes and lake systems with three separate regions to be distinguished (Fig. 1): (i) Northwest Sulawesi with the *graben* or basin of the Palu River and Lake Lindu where *C. linduensis* occurs, (ii) Lake Poso with the endemic *C. possoensis*, and (iii) the central lakes of the Malili system with *C. matannensis* (mainly in Lake Matano and Lake Mahalona) and *C. loehensis* (in the satellite lakes of and in Lake Towuti). Another species, *C. subplanata* was described based on shells only from a fourth region in southwest Sulawesi (area of Minralang), but its specific identity and status remains to be substantiated by anatomical and molecular data. In contrast, sampling on Sumatra is to date too scarce to allow for any solid judgement of an equally restricted occurrence of *C. moltkiana* in lakes Manindjau and Singkarak only. In addition, the specific identity and affinity of *C. tobae* endemic to Lake Toba in northern Sumatra remains unresolved.

The pattern of endemic occurrences of lacustrine corbiculids strongly correlates with the distribution recently studied in detail for pachychilid gastropods of the endemic *Tylomelania* clade on Sulawesi (Rintelen & Glaubrecht, 1999, 2002; Rintelen et al., submitted), as well as with the biogeography of Indonesian Ancylidae (Glaubrecht, unpub. data), and is, therefore, no artefact of insufficient data on the range of limnic molluscs in Southeast Asia. In case of the evolution of endemic corbiculid bivalves in separate areas within the geologically complex island of Sulawesi, it remains to be tested, based on further sampling and detailed molecular studies, whether this biogeographic pattern finds its historical expla-

nation in the spatial isolation over longer geological time in concert with the composite nature of this odd shaped island that formed by fusion of several microplates (terranes) in Late Miocene-Early Pliocene (palaeogeographical background: Whitmore, 1981; Hall & Bundell, 1996; Metclafe et al., 2001).

Using other limnic molluscs as models, it has recently been hypothesized that, for example, the phylogeny and biogeography of pachychilid gastropods of *Brotia, sensu lato*, in Southeast and Austral Asia reflect palaeogeographical events since the Cretaceous/Cenozoic rather than more recent geological history (Glaubrecht, 2000; Glaubrecht & Rintelen, 2003; Köhler et al., 2000; Köhler & Glaubrecht, 2001, 2003). The latter comprise, for example, those events related to the formation of Sundaland and its drowning during the Plio-Pleistocene. Accordingly, the distribution of taxa of the *Brotia, sensu lato,* complex might represent an ancient vicariance pattern caused by plate and terrane tectonics that has not been obscured subsequently, presumably due to comparatively restricted dispersal abilities of these viviparous snails in conjunction with ecological factors.

In contrast, the available evidence in case of the East Asian and Australian freshwater corbiculids was regarded incompatible with an ancient vicariance scenario. Above all, an assumed late Cenozoic origin of freshwater *Corbicula* restrict applicability of the studied group as indicator of a long and complex geological history and biogeography within the so-called "Wallacea" (as transitional zone between the Australian and Oriental region). Second, the mitochondrial COI sequences generated for those corbiculids collectively distributed from the Japanese Archipelago to Australia indicated a phylogenetically shallow polytomy, suggesting an evolutionary recent common origin to Siripattrawan et al. (2000) and Pfenninger et al. (2002). Showing rather low levels of genetic distances between different lineages of Asian freshwater *Corbicula*, our analyses including now the Indonesian taxa in general support this scenario of rather late divergence of freshwater lineages. Nevertheless, the higher sequence distances in particular shown by *C. moltkiana* on Sumatra may indicate that this divergence started earlier than Pleistocene age suggested by Pfenninger et al. (2002).

In summary, three statements of biogeographical importance are implied by the present study: (i) presence of distinct and, in relation to other Asian forms, old taxa on Sumatra and Sulawesi, (ii) a remarkable diversity of *Corbicula* on the island of Sulawesi with at least three distinct lineages and taxa, respectively, and (iii) presumably a relatively late colonization of the Sunda Islands Java and Lombok by *C. javanica* with its strong affinity to *C. fluminea*.

Evolutionary Ecology

The COI sequence data in conjunction with the new finding of exceptional life history and anatomical characteristics, including features of sperm morphology and incubation, presented herein for Indonesian *Corbicula* suggest an evolutionary ecology hypothesis on their origin (theoretical background, reviews: Glaubrecht, 1996; Streit et al., 1997). In particular, the diversity of *Corbicula* in the so-called "ancient" lakes on Sulawesi deserve such an explanation, while there is only one riverine corbiculid which has been collectively assigned to *C. subplanata* (see Introduction).

Accordingly, we anticipate colonization of Sumatra and Sulawesi by an early, sexual reproducing and incubating corbiculid ancestor with monoflagellate spermatozoa and subsequent radiation by speciation of individual corbiculids in situ particularly in Lake Poso and the Malili lake system, respectively, once these special habitats open up and provided new ecological opportunities. A time frame for this process can be given very tentatively only, with an estimated age of Lake Poso and the Malili lakes of about 1–2 myr (Rintelen et al., submitted).

Apparently, local ancient lakes with their temporally stable habitats facilitated an endemic radiation of specialized forms in case of *C. possoensis* in Lake Poso and *C. matannensis* and *C. loehensis* inhabiting the Malili lakes. The latter two lineages might originate from intralacustrine divergence within (at least temporarily) separated lakes and/or independent colonizations of the Malili system. In contrast, this specific intralacustrine speciation in an ancient lake setting is more unlikely in case of *C. linduensis* (for which riverine localities are also reported here for the first time), because Lindu is not known to fulfill the criteria of being an ancient lake. Nevertheless, the outstanding mode of brooding in *C. linduensis* may indicate rather long isolation.

Exceptional cases for lacustrine speciation and adaptive radiation on Sulawesi are pro-

vided by gastropods of known incidences in Pachychilidae (*Tylomelania*), Ancylidae (*Protancylus*) and Lymnaeidae (*Miratesta*)(P. Sarasin & F. Sarasin, 1898; Rintelen & Glaubrecht, 1999; Rintelen et al., submitted), and among bivalves also by the evolution of the endemic corbiculid genus *Possostrea* in Lake Poso (Bogan & Bouchet, 1998). On a more subdued scale, such a process that involves the evolution of several adaptations unknown for long in other freshwater congeners seems to have occurred only in *Corbicula sandai* of Lake Biwa. Although not brooding but laying benthic eggs masses with direct developing young, this endemic Japanese corbiculid share certain reproductive features (i.e., the monoflagellate sperm) with taxa endemic to Sulawesi, to which also its sequence data exhibit a certain affinity.

CONCLUSION

As shown in the present study, peculiarities of shell morphology, anatomy, sperm morphology and the brooding process, as well as available molecular data support the presence of several endemic *Corbicula* taxa on Sumatra (*C. moltkiana*) and particularly on Sulawesi (*C. linduensis*, *C. possoensis*, *C. matannensis* and *C. loehensis*). These taxa apparently represent relatively old and distinct genetic lineages which show no particularly close relationship to any previously studied *Corbicula* from the Japanese islands, Asian mainland or Australia. In contrast, *C. javanica* that is supposed to be widely distributed across the Sunda Archipelago, appears closely related to a Korean lineage identified as *C. fluminea* within an Asian cluster, and might be a later migrant in this region. Future additional morphological, biological and molecular investigations may provide more decisive information concerning the evolutionary pathways along which *Corbicula* species colonized freshwater habitats in Southeast and Austral-Asia.

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THE APPLE SNAILS OF THE AMERICAS (MOLLUSCA: GASTROPODA: AMPULLARIIDAE: *ASOLENE, FELIPPONEA, MARISA, POMACEA, POMELLA*): A NOMENCLATURAL AND TYPE CATALOG

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ABSTRACT

Ampullariidae are freshwater snails predominantly distributed in humid tropical and subtropical habitats in Africa, South and Central America and Asia. This catalog is concerned only with the American species, the majority of which are placed in the genus *Pomacea*. Species of *Pomacea* are found throughout most of South and Central America and the Caribbean, with a single species extending into southeastern USA. The other American genera are *Asolene*, *Felipponea*, *Pomella* and *Marisa*, all South American. The taxonomy of the group is heavily based on shell morphology but the true number of valid taxa remains unknown, pending revisionary work. This catalog provides the rigorous nomenclatural base for this future work by bringing together all the available and unavailable genus-group and species-group names that have been applied to American ampullariids, indicating their current nomenclatural status (species, subspecies, synonyms, etc.). The catalog lists 14 published genus-group and 307 published species-group names for American ampullariids. Of these, 7 genus-group (including 2 subgeneric) and 141 species-group (including 23 infraspecific) names are currently valid. There are 4 genus-group synonyms, 133 species-group synonyms, and 11 species-group homonyms. Also listed are 3 unavailable genus-group and 23 unavailable species-group names. The catalog provides bibliographic details for all names, details of type localities and locations of type material, and geographic distribution as far as can be ascertained given the confused state of the taxonomy. The catalog is a work of nomenclature; it is not a revisionary work of taxonomy.

Key words: Ampullariidae, freshwater snails, nomenclature, type material, North America, South America, Central America.

INTRODUCTION

Ampullariidae are freshwater snails predominantly distributed in humid tropical and subtropical habitats in Africa, South and Central America and Asia. They include the largest of all freshwater snails (*Pomacea urceus* can attain a shell height of 145 mm – Burky, 1974; *P. maculata* can exceed 155 mm – Pain, 1960) and frequently constitute a major portion of the native freshwater mollusk faunas of these regions. Among the seven to ten genera usually recognized, the two largest are *Pomacea*, perhaps with about 50 real species (but 117 nominally valid species recognized herein), and *Pila*, with about 30 (Berthold, 1991). Snails in these two genera particularly are frequently known as "apple snails" because many species bear large, round, often greenish shells. The term "apple-shell" was first used by Perry (1810c) in his introduction of the name *Pomacea*, for his new species *P. maculata*, because of "its general resemblance to … an apple" ("*Pomum*" in Latin), and not from the Greek *Πώμα*, which means an operculum.

Ampullariidae (junior synonym Pilidae; Cowie, 1997a; ICZN, 1999a) are operculate snails. They are most closely related to the Viviparidae, together with which they form the superfamily Ampullarioidea in the orders or superorders (depending on classification) Mesogastropoda of earlier authors and Caeno-

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gastropoda of more recent authors (Ponder & Warén, 1988; Berthold, 1989; Bieler, 1992; Ponder & Lindberg, 1997).

Traditional subdivision of the family, by various authors, has been into seven to ten genera, with the form of the siphon and the operculum considered diagnostically significant (e.g., Michelson, 1961). Pain (1972) briefly reviewed the history of taxonomic work on the family. More recently, Berthold (1991: 245–250) recognized ten genera (and three subgenera) with approximately 120 species. His detailed anatomical account treated representative species from each of these generic groupings. He divided the family into two subfamilies: the Afropominae (containing just a single Recent African species in the genus *Afropomus*); and the Ampullariinae, which he subdivided into the tribes Sauleini (one genus, *Saulea*, containing two African species, one Recent, one fossil) and Ampullariini (the remainder). He further subdivided the Ampullariini into the groups Heterostropha and Antlipneumata, but these divisions and names have been criticized by Bieler (1993), who reanalyzed Berthold's data using cladistic techniques. Bieler's reanalysis showed that the various groupings of genera remained more or less similar to those of Berthold, but the relationships among these groups were inconsistent. Given these inconsistencies, it seems unwise to force the various clades into a traditional hierarchy of family-group names. One of the ten genera recognized by Berthold (1991), *Pseudoceratodes* (African, fossil only), was included in the family only tentatively. Of the remaining nine genera, six contain fewer than six species each: *Afropomus* and *Saulea* are African; *Asolene*, *Felipponea*, *Pomella* and *Marisa* are South American. The three genera *Lanistes* Montfort, *Pila* (*Ampullaria* Lamarck and *Ampullarius* Montfort are junior synonyms; Cowie, 1997a; ICZN, 1999a) and *Pomacea*, containing 21, about 30, and about 50 species, respectively, comprise the great majority of species in the family. *Lanistes* (distinguished by its hyperstrophic and hence superficially sinistral shells) is African (including Madagascar). *Pila* is African and Asian. *Pomacea* is South and Central American.

This catalog is concerned only with the American species, the majority of which are placed in the genus *Pomacea*. Species of *Pomacea* are found throughout most of South and Central America and the Caribbean, with a single species, *Pomacea paludosa*, extending into the southeast USA. The genus is divided into two subgenera, *Pomacea sensu stricto* and *Pomacea* (*Effusa*). Berthold (1991) considered *Pomacea* to be monophyletic, with *Marisa* as its sister-group, and the similarities between *Marisa* and *Pomacea* subgenus *Effusa* to be convergent (see also Pilsbry, 1933: 72–73). However, the relationships among the two subgenera of *Pomacea* and the genus *Marisa* are not well resolved (Bieler, 1993) and, at least in terms of shell morphology, the three taxa intergrade. The distinctions among these and the other American genus-group taxa have been generally not well understood. This catalog follows Berthold (1991: 248–250) regarding validity and status of genus-group names, without necessarily implying support for his taxonomic views.

One or more species of *Pomacea*, introduced to Southeast Asia and islands of the Pacific, including the Hawaiian Islands, have become major agricultural pests, notably in rice and taro but also in other crops (Cowie, 2002). However, the true identity of the species involved is uncertain, having been treated variously as *Pomacea canaliculata* (Smith, 1992; Hendarsih et al., 1994), *P. lineata* (Cheng, 1989; Laup, 1991), *P. gigas* (see Guerrero, 1991), *P.* "*insularis*" (see Acosta & Pullin, 1991), *Pomacea* cf. *canaliculata* (Ng et al., 1993), simply *Pomacea* sp. (Acosta & Pullin, 1991), a "hybrid [of] *Ampullaria canaliculata* and *Ampullaria cuprina*" (Anderson, 1993), and even "*Ampularius* sp. a hybrid of undetermined origin" (Lacanilao, 1990). Keawjam & Upatham (1990) recognized three species of *Pomacea* introduced in Thailand: *P. canaliculata*, *P. insularum* and an unidentified species of *Pomacea*. Mochida (1991) indicated that as well as *P. canaliculata* (which he considered frequently to have been misidentified as *P. insularum*) two other species of *Pomacea* have also been introduced to the Philippines: *P. gigas* and *P. cuprina* (the latter possibly a misidentification of *P. bridgesii*, a species that has been carried all over the world by the domestic aquarium trade – Cowie, 1995). In Japan, three "strains of *Pomacea canaliculata*" have been identified, differing in shell colour and pattern, salinity tolerance, and in aspects of reproduction and growth (Brand et al., 1990; Fujio et al., 1991). In the Philippines, the snails have even been identified as species of *Pila* (see Guerrero, 1991). In Hawaii, where four ampullariid species are recorded (Cowie, 1995), snails in an aquaculture project have been reported as hybrids of *Pomacea canaliculata* and *P. paludosa* (Nishimura et al., in Tamaru, 1996).

Ampullariid species-level taxonomy has been heavily reliant on shell morphology, yet snail shells, and especially ampullariid shells, exhibit much intraspecific variation. The taxonomy and systematics of most species have not been adequately worked since their original descriptions. The pest species (even if it turns out to be more than one species) in Southeast Asia nevertheless appears to belong to a relatively well circumscribed group of more or less closely related species from South America. However, within this group, the species and their relationships are very poorly understood. The group comprises a large number of nominal species, including *P. canaliculata*. From time to time, some of the species within this "*canaliculata* group" have been formally synonymized, informally linked together, distinguished as separate species, and so on. This confusion was discussed but not resolved by Alderson (1925), the most recent author to revise *Pomacea* and *Pila* widely (referring to the two genera together as "*Ampullaria*"). He implicitly recognized most of the species in the "*canaliculata* group" as a more or less closely knit group. Within this group he further recognized a number of rather vaguely defined associations of species, for instance explicitly linking *Pomacea immersa*, *P. amazonica* and *P. haustrum*, although without formally synonymizing them; and informally referring to another subset of the group as "the *lineata* group". However, he did retain most species as valid. It is quite possible that, just as for the large number of Central American species synonymized under *Pomacea flagellata* by Pain (1964), many other "species" of Ampullariidae, including those in the "*canaliculata* group", do not deserve distinct specific status (Pain, 1960; Cazzaniga, 1987, 2002). A modern revision, involving not only conchology but also internal anatomy and molecular characters, might reduce the "*canaliculata* group" to as few as three species, possibly *P. canaliculata*, *P. lineata* and *P. gigas* (= *maculata* – see main catalog). Until such work is undertaken, however, the status of these various nominal species will remain obscure.

The purpose of this catalog, then, is to provide a rigorous base for this revisionary work by bringing together all the available and unavailable genus-group and species-group names in the large genus *Pomacea* and the other much smaller South American genera of Ampullariidae, indicating their current nomenclatural status (species, subspecies, synonyms, etc.) generally according to the most recent revisions; a total of 14 genus-group and 307 species-group names (Table 1). The catalog also provides bibliographic details for all names, details of type localities and locations of type material, if known, and geographic distribution as far as can be ascertained given the confused state of the taxonomy.

EXPLANATORY INFORMATION

Scope

This catalog lists all published genus-group and species-group names found in the literature, whether available or unavailable according to the *International Code of Zoological Nomenclature* (ICZN, 1999b), that have been applied to the Ampullariidae of North, Central, and South America, and the Caribbean region.

Arrangement and Treatment of Taxa

The sequence of genera is alphabetical. Subgenera appear in alphabetical order within genera. Genus-group synonyms are listed chronologically under the genus-group heading. All species-group names (valid and invalid, available and unavailable) are listed alphabetically within genera/subgenera. Incorrect spellings are listed only if confusion might be caused by their omission; they may also be mentioned in Remarks sections. Treatment of species-group names follows the major authoritative revisions, although few of these are recent. Names proposed as "forms", "va-

TABLE 1. Summary of the numbers of names of American ampullariid taxa (including names that are incerae sedis) treated in this catalog.

	Available		Unavailable
Genus-group names	Valid genus	5	
	Valid subgenus	2	3
	Synonym	4	
Species-group names	Valid species	117	
	Valid infra-specific	23	23
	Synonym	133	
	Homonym*	11	

*Includes homonyms considered to represent valid species (10) and valid infraspecific taxa (1).

rieties", etc., and neither already synonymized nor raised to subspecific status are simply treated, along with subspecies, as infraspecific. Treatment of genus-group names also follows the most recent authoritative revisions.

In some instances in which we treat a name as a junior synonym, one or more other names automatically become synonyms of the senior synonym because they had already been treated as synonyms of the junior synonym. In some cases this results in the introduction of a new synonymy, indicated in boldface by "**N. syn.**". However, no other revisionary work has been attempted and no new taxonomic decisions have been made.

Typographical Treatment of Names

Family and genus-group headings are centered in upper case type. Valid genus-group names are listed flush left in boldface upper case type. Valid, available species-group names are listed flush left in boldface, infraspecific names preceded by a "+". Synonyms are listed in italics flush left, upper case for family and genus-group names, lower case for species-group names. In the species-group, junior homonyms are also listed in italics flush left, or in boldface italics flush left if new or replacement names have not been provided. Nomenclaturally unavailable names are listed in plain type, flush left.

Taxonomic References

The citation for the original proposal of a genus-group name follows the name. The reference consists of author(s), date of publication and page number. For species-group names, on the line following the name and indented, the name is given in its original generic combination (including subgenus if in the original description, and using the original orthography, even if incorrect) and with its original status indicated (e.g., subspecies, "var.", as necessary). The name is followed by its author(s), date of publication, page number, and plate/figure number(s). When an author published the same name as new for the same taxon in more than one place, the later citation is given in square brackets following the first citation.

The author/date citation acts as a reference to the work as listed in the Literature Cited section. If an author published more than one work in the same year, a suffix (a, b, c, etc.), indicating chronological order of publication, is attached to the date in both the catalog text and the Literature Cited. Authors' names containing the terms "de", "d'", "von", if being of European continental origin, are cited and alphabetized in the Literature Cited by the main name, e.g., "*Ampullaria guadelupensis* Martens, 1857" in the main body of the catalog and "Martens, E. von. 1857" in the Literature Cited.

The page number cited is that on which the name first appeared. In some instances, the name first appeared on different pages, for instance in a list or key, with the actual description beginning on a subsequent page. In such cases, both page numbers are cited.

If the current status of a species-group name differs from that in the original description, this is indicated, with appropriate references, in a Remarks section below the standard entry for the species.

Type Species

For nomenclaturally available genus-group names, the type species and its method of fixation (following *Code* Arts. 66–70) are given following the literature citation.

Homonyms and Replacement Names

Homonymy of species-group names is indicated in the Remarks section under the name. In many cases, the junior homonym has already been synonymized with another earlier name, or a replacement name has already been provided. In cases in which a replacement name appears necessary, no replacement name is here provided, pending further research. We have not made an exhaustive search for possible senior homonyms.

Unavailable Names

Unavailable names are listed with full citation and a statement of why the name is unavailable, e.g., "*nom. nud.*", "first published as a junior synonym of ...", etc. No other information is provided except for explanatory details in the Remarks section, if necessary. Obviously incorrect spellings are not listed but may be mentioned in annotations.

Misidentifications

Misidentifications are not formally listed. No genus-group misidentifications are mentioned.

Species-group misidentifications are noted in square brackets or in Remarks sections, if necessary for clarity.

Miscellaneous Annotations

Under each genus-group heading, explanatory and other useful information is given immediately under the genus-group synonymy. Annotations other than those indicated in the above paragraphs are placed in square brackets immediately following the item to be clarified or, if the annotations are more extensive, placed in a Remarks section following the standard entry for the species.

Type Localities and Type Material

The type locality ("the geographical ... place of capture, collection or observation of the name-bearing type" [*Code* Art. 76]) is given for each available species-group name immediately following the author and citation. The location is given verbatim as published by the author, without translation. If no locality was given by the author, this is simply stated, in square brackets. Any additional intepretive or explanatory information regarding the type locality is placed in square brackets following the originally published locality, or, if extensive, in the Remarks section. However, an exhaustive attempt to determine the exact collection locality has not been made.

Location and catalog numbers of type material, if known, are given, following the type locality information. In many instances, the original descriptions did not designate a holotype or even identify a type series. Even though many of these descriptions were probably based on single specimens, it is rarely possible to determine this with certainty. Therefore, in most cases, the material known to have been used in describing a new species should be designated as a lectotype (or lectotype and paralectotype(s) if more than one specimen is present in the inferred type series) (*Code* Rec. 73F). Rather than designating lectotypes here, we consider such specimens to be syntypes, pending further study. The information provided is derived from the literature (citations given), and from enquiries made to numerous museums and our own study in various museums (see Acknowledgments); an exhaustive search for type material has not been made.

Distributions

The distribution (if known) of each species is given following the type locality and type material information. In most cases this information is not detailed, providing simply the country or region from which the species has been recorded in the literature. Citations for the sources of this information are provided, unless the only information available is the type locality, for which the reference has already been provided.

Museum Collection Acronyms and Type Material Holdings

The following acronyms are used for the various museum collections referred to in the catalog. The number of American taxa represented by type or possible type material in each collection, as known to us or referred to in the literature, is indicated in parentheses. Research will undoubtedly uncover additional type material in many of these collections.

AMNH	American Museum of Natural History, New York, U.S.A. (4)
ANSP	Academy of Natural Sciences, Philadelphia, U.S.A. (22)
BMNH	The Natural History Museum, London, U.K. (83)
CAS	California Academy of Sciences, San Francisco, U.S.A. (1)
CMNH	Carnegie Museum of Natural History, Pittsburgh, U.S.A. (1)
HUJ	Hebrew University of Jerusalem, Israel (5)
IMLA	Fundación e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina (1)
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (1)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. (29)
MCSN	Museo Civico di Storia Naturale, Milano, Italy (0)
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland (8)
MHNS	Museo de Historia Natural La Salle, Caracas, Venezuela (1)
MMUE	The Manchester Museum, University of Manchester, Manchester, U.K. (1)
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain (3)
MNHN	Muséum National d'Histoire Naturelle, Paris, France (30)
MNHNS	Museo Nacional de Historia Natural, Santiago, Chile (possibly 21)
MNRJ	Museu Nacional, Rio de Janeiro, Brasil (1)
MZUSP	Museu de Zoologia da Universidade de São Paulo, Brasil (0)

NMW	National Museum of Wales, Cardiff, U.K. (10)
NZSI	Zoological Survey of India, National Zoological Collection India, West Bengal, Calcutta, India (1)
RMNH	Nationaal Natuurhistorische Museum, Leiden, Netherlands (2)
SMFD	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany (possibly 2)
UF	Universisty of Florida, Florida Museum of Natural History, Gainesville, U.S.A. (1)
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor, U.S.A. (5)
USNM	National Museum of Natural History, Washington D.C., U.S.A. (11)
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (24)
ZMUH	Universität von Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg, Germany (0)
ZMZ	Zoologisches Museum der Universität, Zürich, Switzerland (1)
ZSM	Zoologische Staatssammlung München, Germany (14)

Abbreviations

The following abbreviations are used throughout the catalog.

Art(s).	Article(s) (of the *Code*)
Code	*International Code of Zoological Nomenclature* (ICZN, 1999b)
fig(s).	figure(s)
ICZN	International Commission on Zoological Nomenclature
nom. nud.	*nomen nudum*
N. syn.	New synonymy
pl(s).	plate(s)
p.	page
pers. comm.	personal communication
Rec.	Recommendation (of the *Code*)
s.l.	*sensu lato*
spm(s).	specimen(s)
s. str.	*sensu stricto*
subg.	subgenus

SYSTEMATIC CATALOG

Family AMPULLARIIDAE Gray, 1824

AMPULLARIIDAE Gray, 1824: 276. Type genus *Ampullaria* Lamarck, 1799 [= *Pila* Röding, 1798].

PILIDAE Preston, 1915: 96. Type genus *Pila* Röding, 1798.

ICZN (1999a), following Cowie (1997a: 83–88), confirmed the name Pilidae as a junior synonym of Ampullariidae and invalid.

Genus ASOLENE Orbigny, 1838

ASOLENE Orbigny, 1838d: 364. Type species: *Helix platae* Maton, 1811, by subsequent designation of Gray (1847: 148).

AMPULLOIDEA Orbigny, 1841e: 379. New name for *Asolene* Orbigny, 1838 (see Pilsbry, 1933: 74).

AMPULLOIDES Orbigny, 1842c: 1. Incorrect spelling of *Ampulloidea* Orbigny, 1841.

ASOLENA Herrmannsen, 1846a: 84. Incorrect spelling of *Asolene* Orbigny, 1838.

AMPULLAROIDES Gray, 1847: 148. Incorrect spelling of *Ampulloidea* Orbigny, 1841 (see Pilsbry, 1933: 74).

Treated as a full genus following Berthold (1991: 23). Orbigny (1841e: 379) replaced *Asolene* with *Ampulloidea*, treating only *platae* Maton, 1811, but without explicitly saying that this was the only species and hence not designating it as the type. Previously (Orbigny, 1838d: 364), he had included two species (*platae* Maton, 1811, and *celebensis* Quoy & Gaimard, 1834 [the latter is now placed in *Pila* Röding, 1798]).

brownii

Ampullaria Brownii Jay, 1839: 112, pl. 1, fig. 4. River Amazon [= Brasil]. Syntype: AMNH 56107 (Boyko & Cordeiro, 2001: 16) [labeled as "figd type" in Jay's handwriting (P. M. Mikkelsen, pers. comm. to RHC, 7 May 2002)]; possible additional syntype material: MCZ. Distribution: Brasil.

Remarks: Pain (1960: 430) stated that "[t]hrough the kindness of Dr. J. C. Bequaert and Dr. W. J. Clench [both of the MCZ], I have been able to examine the type". This is not considered an inadvertent lectotype designation because it is not specific as to the specimen examined (Boyko & Cordeiro, 2001: 16). Synonym of *crassa* Swainson, 1823, *teste* Philippi (1852a: 34), Paetel (1887: 477), Kobelt (1913f: 189) and Pain (1960: 429).

crassa

Ampullaria crassa Swainson, 1823a: pl. 136, upper and lower figs. [No locality given.] Syntypes ("the only specimen I have" and the specimen in "the figure of Martini" (Swainson, 1823a: pl. 136): possibly MMUE (Dean, 1936: 232; H. McGhie, pers. comm. to RHC, 28 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: Brasil, Bolivia, Peru, Equador, Colombia, Venezuela,

Guyana, Surinam, French Guiana (Baker, 1914: 661; Pain, 1960: 430; Geijskes & Pain, 1957: 45).

Remarks. Placed in *Limnopomus* Dall by Pain (1952: 31, 1960: 429) and Geijskes & Pain (1957: 45), but in *Asolene* Orbigny by Tillier (1980: 21), followed here.

crassa

Ampullaria crassa Orbigny, 1835a: 33. Rio Parana (republica Argentina). Syntypes: BMNH 1854.12.4.332 (13 spms.) [labeled "*roissyi*"].

Remarks. Junior primary homonym of *crassa* Swainson, 1823, and *crassa* Deshayes, 1830 [= *Melantho ponderosa* (Deshayes, 1825), *teste* Paetel (1887: 478); not Ampullariidae], replaced by *roissyi* Orbigny, 1841. Synonym of *pulchella* Anton, 1838, *teste* Gaudion (1879: 38), Ihering (1898: 50, 1919: 337) and Hylton Scott (1958: 310).

cyclostoma

Ampullaria cyclostoma Spix, in Wagner, 1827: 4, pl. 4, fig. 5. Brasilia. Syntype: ZSM 20012075 (E. Schwabe, pers. comm. to RHC, 28 July 2002; see also Fechter, 1983: 221). Distribution: Argentina, Paraguay, Uruguay, Bolivia, Brasil (Paraguay-Parana drainage) (Pain, 1960: 430).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.). Synonym of *platae* Maton, 1811, *teste* Hylton Scott (1958: 308) and S. C. Thiengo (unpublished), followed here, although contrary to Pain (1960: 430), who retained it as a valid species in *Limnopomus* Dall, 1904, which is here treated as a synonym of *Pomacea* Perry, 1810.

exumbilicata

Helicina exumbilicata Spix, in Wagner, 1827: 4, pl. 5, fig. 4. In aquis Provinciae Bahiensis. Type material: probably lost (S. C. Thiengo, unpublished).

Remarks: Authorship is given as "Spix, in Wagner", following Cowie et al. (in prep.), who also explain the publication history of this work. Spix illustrated *exumbilicata* as a valid species, but Wagner, in writing the description, treated it as a variety of *crassa* Swainson, 1823. Synonym of *crassa* Swainson, 1823, *teste* Philippi (1852a: 73) and Pain (1950b: 72), although the latter cited Spix's pl. 4, fig. 2.

fasciolata

Helix fasciolata Spix, in Wagner, 1827: 4, pl. 5, fig. 1. In aquis Provinciae Bahiensis. Type material: probably lost (S. C. Thiengo, unpublished).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.), who also explain the publication history of this work. Spix illustrated *fasciolata* as a valid species, but Wagner, in writing the descriptions, treated it as a variety of *crassa* Swainson, 1823. Synonym of *crassa* Swainson, 1823, *teste* Pain (1950b: 72), although he cited pl. 5, fig. 2.

+ **gallardoi**

Ampullaria pulchella Gallardoi Ihering, 1919: 337. curso inferior del río Paraná hasta Corrientes, del Chaco Argentina y del señor A. de W. Bertoni, de la Asunción. Type material: not found by us in MACN, not found by us in MZUSP (cf. Dance, 1986: 214). Distribution: Argentina, Bolivia (Hylton Scott, 1958: 311).

granulosa

Ampullaria granulosa Sowerby, 1894: 49, pl. 4, fig. 24. Cayenne. Lectotype (Pain, 1949b: pl. 2, figs. 5, 6; see also Tillier, 1980: 20): BMNH 1894.6.11.1. Distribution: Guyana, Surinam, French Guiana (Vernhout, 1914a: 43; Pain, 1952: 30; Geijskes & Pain, 1957: 46; Tillier, 1980: 20)

Remarks. Placed in *Limnopomus* Dall by Pain (1952: 31) and Geijskes & Pain (1957: 45). Placed here in *Asolene* following Tillier (1980: 17). The original description was not explicitly based on a single shell, so the specimen figured by Pain as the "type" must be considered a lectotype (*Code* Art. 74.6, Rec. 73F).

impervia

Ampullaria impervia Philippi, 1851: 17, pl. 4, fig. 7 [1852b: 21]. Brasilien. Syntype: ZSM 20012067 (E. Schwabe, pers. comm. to RHC, 28 July 2002). Distribution: "Brésil" (Gaudion, 1879: 31), "Bolivia, etc." (Sowerby, 1909a: 353).

Remarks. Synonym of *crassa* Swainson, 1823, *teste* Pain (1960: 429).

monticola

Ampullaria crassa var. *monticola* Vernhout, 1914b: 47, pl. 1 [not pl. 2, as indicated in the text], fig. 15a, b. Mount Cottica on the right bank of the Lawa ... altitude of 450 m ... French Guyana. Holotype: RMNH; paratype(s): RMNH. Distribution: French Guyana (Tillier, 1980: 21).

Remarks. Three specimens were mentioned in the text, but only two were figured. These were RMNH no. 132 (fig. 15a) and no.

131 (fig. 15b), but neither was specified as being the holotype. Synonym of *crassa* Swainson, 1823, *teste* Tillier (1980: 21).

naticoides

Ampullaria naticoides Orbigny, 1835a: 33. Unavailable name; first published as a junior synonym of *platae* [as "*Platea*"] Maton, 1811, not made available before 1961 (*Code*, Art. 11.6). Syntypes: BMNH 1854.12.4.337 (7 spms.).

Remarks. Locality given by Orbigny (1835a: 33) as "Rio de la Plata, provincia Buenos-Ayres (republica Argentina)". Treated as a synonym of *platae* Maton, 1811, by Orbigny (1841e: 379), Paetel (1887: 480), Sowerby (1909a: 356), Pilsbry (1933: 74) and Hylton Scott (1958: 308).

+ nubila

Ampullaria nubila Reeve, 1856c: pl. 14, fig. 65. River Salomoens. Syntypes: BMNH 20020672 (2 spms.). Distribution: Brasil, Bolivia, Peru (Pain, 1960: 430).

Remarks. Subspecies of *crassa* Swainson, 1823, *teste* Pain (1960: 430).

oblonga

Ampullaria (*Pomus*) *crassa* var. *oblonga* Nevill, 1884: 11. Brazil; Amazon Rv. Type material: possibly NZSI, not found by us in BMNH (cf. Dance, 1986: 220). Distribution: Brasil.

Remarks. Junior primary homonym of *oblonga* Swainson, 1823. Synonym of *crassa* Swainson, 1823, *teste* Paetel (1887: 480).

olivieri

Ampullaria Olivieri Deshayes, 1830a: 31. Cayenne. Type material: probably lost (Tillier, 1980: 16). Distribution: French Guiana.

Remarks. Synonym of *crassa* Swainson, 1823, *teste* Deshayes (1838: 548), Philippi (1852a: 34), Paetel (1887: 480) and Sowerby (1909a: 347).

ormophora

Ampullaria ormophora Morelet, 1857: 30. Novâ Caledoniâ [error]. Syntype: BMNH 1893.2.4.1805. Distribution: Brasil (from syntype label).

Remarks. No ampullariids are known from New Caledonia, which has therefore been considered in error (Crosse, 1871: 185). Tentatively place in *Asolene* Orbigny, based on the syntype label, on which is written "= *nubila* Reeve".

petiti

Ampullaria Petiti Crosse, 1891: 214, pl. 4, fig. 2. in flumine Amazonidum, Americæ meridionalis. Type material: MNHN (Sowerby, 1909b: 363) [not found by us]; topotype: MNHN ("coll. Jousseaume"; Tillier, 1980: 19).

Remarks. Sowerby (1909a: 356) thought it to be "perhaps a variety of *A. impervia*, Phil." but subsequently (Sowerby, 1909b: 363) considered the two taxa distinct. Synonym of *crassa* Swainson, 1823, *teste* Pain (1960: 429), but treated here as a valid species, following Berthold (1991: 250; see also Tillier, 1980: 21).

platae

Helix Platæ Maton, 1811: 331, pl. 24, figs. 16, 17. America australi ... Rio de la Plata. Type material: location not known to us. Distribution: Paraguay (Martens, 1857: 200; Paetel, 1873: 65, 1888: 481); Paraná (Pilsbry, 1933: 74); La Plata (Sowerby, 1909a: 356; Pilsbry, 1933: 74); La Plata and southern Brasil, "sistema del río Paraná" (Ihering, 1919: 333).

pulchella

Ampullaria pulchella Anton, 1838: 50. [No locality given]. Type material: location not known to us. Distribution: Rio Parana, La Plata, Bolivia (Sowerby, 1909a: 348).

Remarks. Synonym of *cyclostoma* Spix, in Wagner, 1827, *teste* Pain (1960: 430), but treated here as a valid species in *Asolene*, following Hylton Scott (1958: 310) and Berthold (1991: 250).

roissii

Ampullaria roissii Orbigny, 1838c, pl. 52, figs. 1–3. Unavailable name; incorrect original spelling of *roissyi* Orbigny, 1838.

roissyi

Ampullaria roissii Orbigny, 1838c, pl. 52, figs. 1–3 [given as "*Roissyi*" by Orbigny (1841e: 377)]. New name for *crassa* Orbigny, 1835, *non* Swainson, 1823, *non* Deshayes, 1830. Distribution: Rio Parana, Argentina (Orbigny, 1835a: 33).

Remarks. The name *roissyi*, as given by Orbigny (1841e: 377), was an incorrect subsequent spelling (*Code*, Art. 33.3); it was not an emendation, as it was not demonstrably intentional (*Code*, Art. 33.2). However, "*roissyi*" is in prevailing use, attributed to Orbigny, and is therefore deemed the correct original spelling (*Code*, Art. 33.3.1). Variety of *cyclostoma* Spix, 1827, *teste* Sowerby (1909a: 348). Synonym of *cyclostoma* Spix, 1827, *teste* Pain (1960: 430). Synonym of *pulchella* Anton, 1838, *teste* Philippi (1852a: 33), Ihering (1898: 50, 1919: 337) and Hylton Scott (1958: 310), followed here.

sloanii

Ampullaria Sloanii Férussac, 1827: 413. Unavailable name; *nom. nud.*

Remarks. Listed as from "Cayenne" by Férussac (1827: 413), Jay (1836: 47; 1839:

65; 1850: 283), Drouët (1859: 84), Gaudion (1879: 40) and Paetel (1888: 481). Listed as a synonym of *crassa* Swainson, 1823, by Tillier (1980: 21).

solida

Ampullaria solida Busch, 1859: 168. Ecuador. Syntypes: BMNH 20020683 (2 spms.). Distribution: Ecuador (Miller, 1879: 149).

Remarks. Synonym of *crassa* Swainson, 1823, *teste* Pain (1960: 429).

sowerbyi

Ampullaria sowerbyi Vernhout, 1914a: 29, pl. 1, fig. 13 [holotype]. Lawa. Holotype: RMNH. Distribution: Surinam.

Remarks. The description is explicitly based on only a single specimen. The "type" (i.e., the single specimen) is indicated as being in RMNH, and a specimen, which must be this single specimen, is figured. Synonym of *granulosa* Sowerby, 1894, *teste* Pain (1952: 30), Geijskes & Pain (1957: 45) and Tillier (1980: 20).

spixii

Ampullaria Spixii Orbigny, 1838d: 376, pl. 52, figs. 7, 8. New name for *zonata* Orbigny, 1835, *non* Spix, 1827. Distribution: "Sistema del Plata y del río Paraná ... Puerto Bertoni, Alto Paraná, en Río Grande do Sul ... y en el río Uruguay" (Ihering, 1919: 336).

Remarks. Synonym of *cyclostoma* Spix, 1827, *teste* Sowerby (1909a: 348), but treated here as a valid species, following Hylton Scott (1958: 312) and Berthold (1991: 250).

storeria

Ampullaria Storeria Jay, 1839: 112, pl. 1, fig. 5. River Amazon [= Brasil]. Probable syntype: AMNH 56107 (Boyko & Cordeiro, 2001: 16) [labeled as "figd type" in Jay's handwriting (P. M. Mikkelsen, pers. comm. to RHC, 7 May 2002)]. Distribution: Brasil.

Remarks. Considered a variety of *platae* Maton, 1811, by Jay (1850: 283). Philippi (1852a: 34, 63) could not decide its status as a real species or a synonym of *platae* Maton, 1811. Treated here as a synonym of *platae* Maton, 1811, following Martens (1857: 210) and Gaudion (1879: 37).

zonata

Ampullaria zonata Orbigny, 1835a: 32. Rio Parana (republica Argentina)...Lacubus provinciæ Corrientes (republica Argentina). Syntypes: BMNH 1854.12.4.327-329 (28 spms.) [labeled "*spixii*"], MNHN (2 lots, 8 spms.), MCZ (2 spms.) [labeled as paratypes].

Remarks. Junior primary homonym of *zonata* Spix, 1827; replaced by *spixii* Orbigny, 1838.

Genus FELIPPONEA Dall, 1919

FELIPPONEA Dall, 1919: 10. Type species: *Ampullaria* (*Felipponea*) *neritiniformis* Dall, 1919, by monotypy.

Considered a synonym of *Asolene* Orbigny, 1838, by Pilsbry (1933: 74), but treated here as a full genus with three included species, following Hylton Scott (1958: 317) and Berthold (1991: 23, 250).

elongata

Ampullaria (*Felipponea*) *elongata* Dall, 1921: 133. Uruguay River, Dept. of Paysandú. Holotype: USNM 333024. Distribution: Uruguay.

Remarks. Junior primary homonym of *elongata* Orbigny, 1842, which is here listed under *Pomacea* Perry, 1810.

iheringi

Asolene iheringi Pilsbry, 1933: 73, pl. 2, figs. 7 [paratype], 8 [paratype], 9 [holotype], 9a [holotype]. Rapids of Butni, Rio Uruguay, between San Borja and Uruguayana, Rio Grande do Sul, Brazil. Holotype [figured and distinguished by measurements given in the text]: ANSP 124615 ["124615a" (Baker, 1964: 168)]; paratypes: ANSP 365363 (3 spms.). Distribution: Southern Brasil.

neritiniformis

Ampullaria (*Felipponea*) *neritiniformis* Dall, 1919: 10. Rio Uruguay, Department of Paysandu. Holotype: USNM 332780; topotype: ANSP 141211 (Pilsbry, 1933: 76). Distribution: Uruguay River basin: Argentina, Brasil, Uruguay (Hylton Scott, 1958: 318; Faraco et al., 2002).

Genus MARISA Gray, 1824

MARISA Gray, 1824: 276. Type species: *Helix cornuarietis* Linnaeus, 1758, by subsequent designation of Gray (1847: 148).

CERATODES Guilding, 1828: 537, 540. Type species: *Helix cornuarietis* Linnaeus, 1758, by original designation.

Gray (1824: 276) established *Marisa* "for a genus of shells which has been confused with *Ampullaria*, but which differs from it in having a horny operculum and simple peristome". That is, he was establishing *Marisa* for American ampullariids, distinguishing them from Old World species with a calcified operculum, which are now placed in *Pila* Röding, 1798. [*Ampullaria* Lamarck, 1799, is a junior objective synonym of *Pila* Röding, 1798 (Cowie, 1997a;

ICZN, 1999a; and see below under *Pomacea* Perry, 1810)]. Martens (1899: 424) took Gray's *Marisa* to have been "intended for all American *Ampullariæ*", but incorrectly considered it junior to *Ceratodes* Guilding, 1828, because of the date of establishment of *cornuarietis* Linnaeus, 1758, as the type species. Dall (1904: 52) misinterpreted *Ampullaria* as referring to American species with a horny operculum, and *Marisa* to "cover *Ampullaria s.s.*" [what would now be called *Pomacea* Perry, 1810], and, incorrectly, to exclude *cornuarietis*, which he considered, again incorrectly, to have "so persistently and inaccurately been asserted to be the type of *Marisa*". Modern usage restricts *Marisa* Gray, 1824, to those species related to the type, *cornuarietis* Linnaeus, 1758, and places the majority of the remaining American species in *Pomacea* Perry, 1810 (with a small number in *Asolene* Orbigny, 1838, *Felipponea* Dall, 1919, and *Pomella* Gray, 1847).

The type species of *Marisa* Gray, 1824, has been considered as *Marisa intermedia* Gray, 1824, by monotypy (e.g., Pilsbry & Bequaert, 1927: 169; Baker, 1930: 11; Berthold, 1991: 249), whereas in fact *cornuarietis* Linnaeus, 1758, was also an originally included species, as Pilsbry (1933: 72) realized. Dall (1904: 52) misinterpreted *Marisa* Gray as not including *cornuarietis* Linnaeus, 1758. Gray (1847: 148) designated *cornuarietis* Linnaeus, 1758, as the type of *Marisa* Gray. *Ceratodes* Guilding, 1828, was established with two species included: *fasciatus* Guilding, 1828, and *cornuarietis* Linnaeus, 1758; the latter was explicitly designated as the type, contrary to the statement of Berthold (1991: 249) that the type was established by monotypy. Hence, *Ceratodes* Guilding, 1828, is a junior objective synonym of *Marisa* Gray, 1824.

Berthold (1991: 25, 159) included only two species (*cornuarietis* Linnaeus, 1758, and *planogyra* Pilsbry, 1933) in his summary of the genus, but although he illustrated (pp. 12–13) a third species, *chiquitensis* Orbigny, 1838, he apparently considered this (p. 249) to be part of the wide range of morphological variation in *cornuarietis* Linnaeus, 1758.

chiquitensis

Ampullaria Chiquitensis Orbigny, 1838d: 367, pl. 48, figs. 10, 11. sud-est de la province de Chiquitos (république de Bolivia) ... entre les Missions de San-Miguel e de San-José ... à peu près de la première Mission, dans le lac de los Migueleños, et dans les marais des environs. Syntypes: BMNH 1854.12.4.326 (9 spms.), MNHN (1 spm.). Distribution: Bolivia (Berthold, 1991: 13).

Remarks. Described in genus *Ampullaria*, subgenus *Ampullaria s. str.*, and within a section (*Ceratodes*) composed of "Espèces déprimées", but as the binomen "*Ceratodes Chiquitensis*". Thus, the original combination could be considered to be with either *Ampullaria* or *Ceratodes*. Since the species was explicitly described within the genus *Ampullaria*, we prefer *Ampullaria chiquitensis* as the original combination (cf. Petit & Harasewych, 1990: 69). Retained as a distinct species by Pilsbry (1933: 72) but here considered a synonym of *cornuarietis* Linnaeus, 1758, following Sowerby (1909a: 359) and Berthold (1991: 249).

contrarius

Planorbis contrarius Müller, 1774: 152. [No locality given]. Syntypes: the specimens figured by Seba, as cited by Müller; locations unknown, possibly Uppsala University (Dance, 1986: 225).

Remarks. Synonym of *cornuarietis* Linnaeus, 1758, *teste* Orbigny (1835a: 30), Anton (1838: 50) and Gaudion (1879: 27).

cornuarietis

Helix Cornu arietis Linnaeus, 1758: 771. O. Europæo [error; "probably Venezuela, but certainly somewhere between the Guianas and Colombia" (Pilsbry, 1933: 71)]. Type material: the specimen(s) figured by Lister, referred to by Linnaeus (1758: 771) (Pilsbry, 1933: 71); lost (Dance, 1967: 21). Distribution: northern South America, including Colombia, Venezuela, Guyana, Surinam [? error; Geijskes & Pain (1957: 47)], French Guiana, Bolivia, Brasil, Trinidad and Tobago (Pilsbry, 1933: 71–72).

Remarks. Ihering (1919: 333) appears to have incorrectly recorded this species south of the Amazon basin, from the Río Paraguay, Río de la Plata, and Río Grande do Sul.

fasciatus

Ceratodes fasciatus Guilding, 1828: 540, pl. supp. 28, figs. 4–7 in fluviis Americæ æquinoctialis. Type material: not found by us in BMNH (cf. Dean, 1936: 234; Dance, 1986: 213).

Remarks. Synonym of *cornuarietis* Linnaeus, 1758, *teste* Guppy (1866: 44), and here retained as such despite being considered a subspecies (as *knorrii* Philippi, 1852) of *cornuarietis* Linnaeus, 1758, by Baker (1930: 26). Junior secondary homonym of

fasciata Roissy, 1805, when both species are placed in *Pomacea* (e.g., Baker, 1930: 26).

intermedia

Marisa intermedia Gray, 1824: 276. Brazils. Syntype: BMNH 1895.11.6.1 [although Berthold (1991: 249) stated "Typus ... verschollen ist"].

Remarks. Pilsbry (1933: 72) considered *intermedia* Gray, 1824, to be "doubtless an *Effusa*, but ... unrecognizable specifically". Berthold (1991: 249) treated *intermedia* Gray, 1824 [*Marisa*] as different from *intermedia* Férussac [*Pomacea* subgenus *Effusa*], considering the former (incorrectly) as the type of the genus *Marisa* Gray. Either a junior synonym of *cornuarietis* Linnaeus, 1758, or a senior synonym of *planogyra* Pilsbry, 1933, *teste* Berthold (1991: 249).

knorrii

Ampullaria Knorrii Philippi, 1852a: 57, pl. 18, fig. 3 [1852b: 28]. die Insel Trinidad. Type material: probably MNHNS. Distribution: Venezuela, Guyana, Surinam, Trinidad, Colombia, Panama (Baker, 1930: 26).

Remarks. Synonym of *cornuarietis* Linnaeus, 1758, *teste* Guppy (1866: 44) and Sowerby (1909a: 359), or of *fasciatus* Guilding, 1828, *teste* Philippi (1852a: 57) and Baker (1930: 26).

planogyra

Marisa planogyra Pilsbry, 1933: 70, pl. 2, figs. 2–5a. Santa Rosa, in the Descalvados region of Matto Grosso. Holotype: ANSP 158776 [158776a (Baker, 1964: 168)]; paratypes: ANSP 158780 (16 spms.), 158787 (19 spms.), 365366 (3 spms., from holotype lot), MCZ (1 spm.). Distribution: Brasil.

rotula

Ampullaria rotula Mousson, 1869: 183. unteren Magdalenstrome [= Lower Magdalena river, Colombia]. Syntypes: ZMZ 525321 (3 spms.). Distribution: Panama, Costa Rica (Pilsbry, 1933: 71), Colombia (Martens, 1899: 425).

Remarks. Mousson (1873: 19) placed it in *Ceratodes* Guilding, 1828. Synonym of *cornuarietis* Linnaeus, 1758, *teste* Sowerby (1909a: 359), and retained here as such despite being considered a distinct, closely related species or subspecies of *cornuarietis* Linnaeus, 1758, by Pilsbry (1933: 71).

Genus POMACEA Perry, 1810

POMACEA Perry, 1810c: [unnumbered plate and text] [= pl. 12 (Mathews & Iredale, 1912: 11; Clench & Turner, 1956: 120; Geijskes & Pain, 1957: 42; R. E. Petit, pers. comm. to RHC, 16 October 2000); not pl. 11, as stated by Cowie (1997a: 84)]. Type species: *Pomacea maculata* Perry, 1810, by monotypy.

CONCHYLIUM Cuvier, 1816: 426. Type species *Nerita urceus* Müller, 1774, by subsequent designation of Pilsbry & Bequaert (1927: 170) [as *Bulimus urceus* Bruguière].

LIMNOPOMUS Dall, 1904: 52. Type species: *Ampullaria columellaris* Gould, 1848, by original designation.

The status of the genus-group names *Ampullaria* Lamarck, 1799, and *Ampullarius* Montfort, 1810, both frequently used incorrectly in combination with names of species of *Pomacea*, have been clarified by Cowie (1997a) and ICZN (1999a) as junior objective synonyms of *Pila* Röding, 1798 (see also Pain, 1956b: 79). *Pomus* "Humph." Gray, 1847, is also a junior objective synonym of *Pila* Röding, 1798. *Limnopomus* Dall, 1904, is here treated as a synonym of *Pomacea* Perry, 1810, following Berthold (1991).

The distinction between the two subgenera *Pomacea s. str.* and *Pomacea* (*Effusa*) is not clear. Only those species that have been explicitly placed in subgenus *Effusa* are listed under that heading. Others whose placement is uncertain are listed under *Pomacea s. str.*, pending further research. Many of the more obscure species-group names have never before been placed in combination with the genus-group name *Pomacea*, because of the traditional but incorrect use of the genus-group name *Ampullaria* for these American species (Cowie, 1997a; ICZN, 1999a). Hence many of the species listed here are probably new combinations with *Pomacea*.

Subgenus EFFUSA Jousseaume, 1889

EFFUSA Jousseaume, 1889: 255. Type species: *Helix glauca* Linnaeus, 1758, by subsequent designation of Baker (1930: 11).

Baker (1930: 20) considered *luteostoma* Swainson, 1823, to be distinct from *glauca* Linnaeus, 1758, but the *luteostoma* of most other authors, including Jousseaume (1889: 255), to be misidentifications of *glauca* Linnaeus, 1758. Subsequent authors have synonymized *luteostoma* Swainson, 1823, with *glauca* Linnaeus, 1758 (see below).

baeri

Ampullaria Baeri Dautzenberg, 1902: 312, pl. 9, figs. 12, 13. Rio Mixiollo [= Misciotto; Berthold, 1991: 13], province de Huallaga, Pérou. Lectotype (Fischer-Piette, 1950: 170): MNHN; paralectotypes: ANSP 99328 (1 spm.), MCZ (1 spm.), UMMZ 46767 [? error], ZMHB 59269 (1 spm.); possible paralectotypes: ZMHB 63631 (2 spms.), 109517 (1 spm.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: Peru (Berthold, 1991: 13).

Remarks. Probably synonymous with *glauca* Linnaeus, 1758, *teste* Boss & Parodiz (1977: 116), but not definitively synonymized.

balteata

Ampullaria balteata Philippi, 1851: 21, pl. 5, fig. 7 [1852b: 22]. [No locality given. Trinidad "chosen" by Baker (1930: 25).] Lectotype (Baker, 1930: 25): the specimen illustrated in "Philippi's first figure" [= pl. 5, fig. 7], probably MNHNS. Distribution: "Trinidad; also shells from Venezuela ..., Colombia ..., Tobago ..., and Martinique ... that are intermediate between this form and *neritina*" (Baker, 1930: 25); also "Venezuela - Guyane - Maroni - Orenoque" (Gaudion, 1879: 24).

Remarks. Baker (1930: 25) explicitly excluded the later figures of Philippi (1852a: 55, pl. 17, fig. 4). Although the precise origin of the designated lectotype is unknown, Baker's choice of Trinidad as the type locality follows *Code* Rec. 76A.1.4. Synonym of *luteostoma* Swainson, 1823 [= *glauca* Linnaeus, 1758], *teste* Paetel (1887: 477) and Alderson (1925: 6), but treated as a form of *glauca* Linnaeus, 1758, by Sowerby (1909a: 350) and Baker (1930: 25). Synonym of *glauca* Linnaeus, 1758. **N. syn.**

castanea

Ampullaria castanea Deshayes, 1830a: 31. [No locality given.] Syntype: MNHN. Distribution: "Orinocco" (Philippi, 1852a: 41); "La Guyane - Haut-Brésil = Haut-Amazone" (Gaudion, 1879: 26); "Guyana" (Paetel, 1873: 64, 1887: 477); "unknown" (Baker, 1930: 22).

Remarks. Synonym of *luteostoma* Swainson, 1823 [= *glauca* Linnaeus, 1758], *teste* Jay (1850: 36), or possibly of *neritina* Gmelin, 1791 [= *glauca* Linnaeus, 1758], *teste* Baker (1930: 22). Synonym of *glauca* Linnaeus, 1758. **N. syn.**

chlorostoma

Ampullaria chlorostoma Sowerby, 1825: 44. Unavailable name; first published as a junior synonym of *luteostoma* Swainson, 1823, not made available before 1961 (*Code* Art. 11.6).

cingulata

Ampullaria cingulata Philippi, 1851: 19, pl. 5, fig. 3 [1852b: 22]. [No locality given.] Syntype: ZMHB 1376 (1 spm.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: Venezuela (Martens, 1857: 203; 1873: 202).

Remarks. Sowerby (1909a: 347) considered it a "doubtful species which may possibly be young of *A. gigas*", but it was considered a valid species and placed in subgenus *Effusa* by Baker (1930: 10). Baker (1930: 10) considered "Lago de Valencia, Ven. [= Venezuela]" as the type locality. This was probably correct because Philippi (1851: 19) described the species from material in the Berlin Museum, and Martens (1873: 202) gave this as the only known locality for material in the Berlin Museum. However, Martens (1873: 202) also indicated that some of the material was without locality data. Strictly then, the type locality probably includes the above location but may not be restricted to it.

conica

Ampullaria effusa variety *conica* Guppy, 1866: 44 [by bibliographic reference to Guppy, 1864: 244]. Trinidad. Type material: probably Victoria Inst., Trinidad [destroyed], not found by us in BMNH (cf. Dance, 1986: 213). Distribution: Trinidad.

Remarks. Junior primary homonym of *conica* Lamarck, 1804 [also 1822] (now placed in family Naticidae), *conica* Swainson, 1823 [= *virens* Lamarck, 1822 (Philippi (1852a: 73)] (now placed in *Pila* Röding, 1798), and *conica* Wood, 1828 [*Ampullaria conica* selected as the correct original combination by Cowie (1997b: 4)] (now placed in *Pila* Röding, 1798). Synonym of *neritina* Gmelin, 1791 [= *glauca* Linnaeus, 1758], *teste* Baker (1930:22). Synonym of *glauca* Linnaeus, 1758. **N. syn.**

crocostoma

Ampullaria crocostoma Philippi, 1852a: 42, pl. 12, fig. 3 [1852b: 26]. Caraccas. Possible syntypes: ZMHB 109501 (3 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003) [the largest shell is very similar to the original figure (F. Köhler, pers. comm. to RHC, 6 March 2003)]; possibly also MNHNS. Distribution: Venezuela, Guyana (Pain 1950b: 71).

Remarks. Synonym of *glauca* Linnaeus, 1758, *teste* Baker (1930: 18) and Starmühlner (1988: 253), followed here, although treated as a variety of that species by

Pain (1950b: 69). See also Boss & Parodiz (1977: 116).

cuprina

Ampullaria cuprina Reeve, 1856e: pl. 1, fig. 1. [No locality given.] Syntypes: BMNH 20020652 (2 spms.). Distribution: unknown.

Remarks. Synonym of *glauca* Linnaeus, 1758, *teste* Starmühlner (1988: 253), followed here, although considered a variety of that species by Sowerby (1909a: 351).

dubia

Ampullaria dubia Guilding, 1828: 539, pl. supp. 27, figs. 7, 8. in fluviis Americæ æquinoctialis ... small river in the Gulph of Paria ... canals of Demerara [Baker (1930: 15–16), in designating the lectotype, restricted the type locality to the "Gulf of Paria, probably one of distributaries of Rio Orinoco"]. Lectotype (Baker, 1930: 15): the specimen in Guilding's fig. 7, not found by us in BMNH (cf. Dean, 1936: 234; Dance, 1986: 213). Distribution: Guyana, Surinam, Rio Orinoco, St. Lucia (Lesser Antilles), Guadeloupe (Baker, 1930: 16).

Remarks. Synonym of *luteostoma* Swainson, 1823 [= *glauca* Linnaeus, 1758], *teste* Sowerby (1909a: 350). Synonym of *glauca* Linnaeus, 1758, *teste* Starmühlner (1988: 254), followed here (see also Baker, 1930: 12, 15), despite Alderson (1925: 3) and Pain (1950b: 70) considering it unidentifiable.

effusa

Nerita effusa Müller, 1774: 175. [No locality given. Rio Yaracuy, Ven. [= Venezuela] chosen by Baker (1930: 17).] Syntypes: the specimens figured by Seba and Geve, as cited by Müller, and the specimens "In Museo Moltkiano" (Müller, 1774: 176; see also Baker, 1930: 17) [not in the Copenhagen Museum (O. S. Tendahl, pers. comm. to RHC, 18 April 2002)]; not the specimen illustrated by Lister, as cited by Müller, nor ANSP 50596 (Baker, 1930: 17). Distribution: French Guiana [? error], Surinam [? error] (Drouët, 1859:79), Martinique (Saulcy, 1854: 141; Paetel, 1887: 478), Venezuela (Baker, 1930: 17), Guyana (Pain, 1950b: 65).

Remarks. Baker (1930: 17) considered the locality of ANSP 50596 as the type locality, but although this action was not a valid neotype designation (*Code* Art. 75) and the origin of the true type material is unknown, his choice of the type locality appears to follow *Code*, Rec. 76A.1.4. Synonym of *glauca* Linnaeus, 1758, *teste* Swainson (1823a: pl. 157), Philippi (1852a: 43) and Starmühlner (1988: 253), followed here (see also Baker, 1930: 12, 17), contrary to Sowerby (1909a: 350) who treated it as a variety of that species. Gmelin (1791: 3626) listed *effusa* Müller, 1774, as variety "γ" of *ampullacea* Linnaeus, 1758, which is now placed in *Pila* Röding, 1798. However, Philippi (1852a: 43) and Starmühlner (1988: 253), in listing Gmelin's variety as a synonym of *glauca* Linnaeus, 1758, gave it as "*ampullaria* var. γ. Gm" and "*Helix ampullaria* var. j", respectively; and Gaudion (1879: 29), in listing it as a synonym of *effusa* Müller, 1774, gave it as "*Helix ampullaria* var Gmel". These usages of "*ampullaria*" are misspellings of "*ampullacea*".

expansa

Ampullaria expansa Miller, 1879: 152, pl. 15, fig. 6. Rio Santiago prope Playa de oro, in provincia Esmeraldas. Type material: location not known to us. Distribution: Ecuador (Miller, 1879: 152; Sowerby, 1909a: 349).

Remarks. Placed in subgenus *Effusa* following Kobelt (1913a: 147), who placed it in his "Formenkreis der *Ampullaria glauca* L. (Effusae Martens)". Junior primary homonym of *expansa* Nevill, 1877, which is now placed in *Pila* Röding, 1798.

geveana

Ampullaria Geveana Philippi, 1852a: 26. Unjustified emendation of *gevesensis* Deshayes, 1838.

Remarks. Philippi (1852a: 26) explicitly made the emendation. However, the original name is here considered a result of incorrect latinization, which is not treated as an inadvertent error and therefore not a justification for emendation (*Code* Art. 32.5.1). As an emendation, *geveana* Philippi, 1852, is available and a junior objective synonym of *gevesensis* Deshayes, 1838 (*Code* Art. 33.2.3.), and hence a synonym of *glauca* Linnaeus, 1758, as indicated by Starmühlner (1988: 253).

gevesensis

Ampullaria Gevesensis Deshayes, 1838: 541. [No locality given.] Syntype: MNHN. Distribution: French Guiana (Sowerby 1909a: 350), Guyana, Venezuela "in all probablility ... from Venezuela in the north, southwards to the Amazon Valley" (Pain, 1950b: 71), Surinam (Pain, 1952; 31; Geijskes & Pain, 1957: 44).

Remarks. Variety of *glauca* Linnaeus, 1758, *teste* Sowerby (1909a: 350 [as "*Geveanensis*"]), Pain (1950b: 69) and

Geijskes & Pain (1957: 44). Synonym of *effusa* Müller, 1774 [= *glauca* Linnaeus, 1758], *teste* Baker (1930: 17). Synonym of *glauca* Linnaeus, 1758. **N. syn.**

glauca

Helix glauca Linnaeus, 1758: 771. [No locality given. Rio Tuca, near Tucacas, Venezuela "chosen" by Baker (1930: 12, 18).] Type material: lost (Dance, 1967: 21). Distribution (*glauca* Linnaeus, 1758, and its varieties): Brasil, Bolivia, Colombia, Venezuela, Guyana, Surinam, French Guiana, Trinidad, Grenada, Barbados, Guadeloupe, Dominica, Martinique, St. Lucia (Vernhout, 1914a: 43; Pain, 1950b: 69; Geijskes & Pain, 1957: 44; McKillop & Harrison, 1980: 271; Tillier, 1980: 24; Starmühlner, 1984: 89–91, 1988: 254).

Remarks. The designation by Baker (1930: 19) of Knorr's figure as a neotype ["type"] was invalid (*Code* Art. 75). However, although the origin of the type material is unknown, Baker's choice of the type locality appears to follow *Code*, Rec. 76A.1.4. Baker (1930: 12–13) recognized nine "forms" of *glauca* Linnaeus, 1758, considering that "at least the first six of these are not geographic subspecies". Some of these "forms" are here treated as synonyms, others as undetermined infraspecific taxa. Because *glauca* Linnaeus, 1758, is highly variable (e.g., Arias, 1952: 64) revisionary study would probably synonymize all nine "forms".

guadelupensis

Ampullaria guadelupensis Martens, 1857: 199. Caripe auf Guadeloupe. Syntypes: ZMHB 1385 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); no type material found by us in BMNH or MCZ (cf. Dance, 1986: 218). Distribution: Guadeloupe.

Remarks. Synonym of *glauca* Linnaeus, 1758, *teste* Baker (1930: 18) and Starmühlner (1988: 253).

intermedia

Ampullaria intermedia Férussac, in Quoy & Gaimard, 1825d: 489, pl. 68, figs. 1–3. Brésil. Syntypes: MNHN (2 spms.). Distribution: Brasil (Berthold, 1991: 12).

Remarks. Synonym of *sordida* Swainson, 1823, *teste* Orbigny (1835a: 31), Philippi, (1852a: 38), Sowerby (1909a: 357) and Thiengo (1989: 351), followed here, although contrary to Berthold (1991: 23), who treated it as a valid species in subgenus *Effusa*.

luteostoma

Ampullaria luteostoma Swainson, 1823a: pl. 157, top and bottom figs. [No locality given.] Type material: possibly MMUE (Dean, 1936: 232; H. McGhie, pers. comm. to RHC, 29 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: Venezuela, Guyana, French Guiana, Martinique, Guadeloupe (Pain, 1950b: 71).

Remarks. Variety of *glauca* Linnaeus, 1758, *teste* Pain (1950b: 69, 71). Synonym of *glauca* Linnaeus, 1758, *teste* Boss & Parodiz (1977: 116), followed here.

+ **minuscula**

Pomacea (*Effusa*) *glauca* form *minuscula* Baker, 1930: 24, pl. 30, fig. 8. Quebrada Sucremo, a small, swampy brook in heavy forest near Boquerón, Venezuela (station number "H, VIII, b, 29"). Holotype: UMMZ 92069; paratypes: ANSP 147706 (2 spms.), MCZ (1 lot, 3 spms.). Distribution: Venezuela.

Remarks. Retained as a distinct infraspecific taxon, following Baker (1930: 12, 24) and pending further research.

neritina

Helix neritina Gmelin, 1791: 3638. [No locality given. Belmont, near Port of Spain, Trinidad "chosen" by Baker (1930: 22).] Holotype: the specimen illustrated in "Kaemerer Conch. Rudolst. p. 185. n. 2. t. 11. f. 7." (cited by Gmelin), location not known to us. Distribution: ? Colombia, Venezuela, Trinidad, Tobago, St. Lucia, Martinique, Guadeloupe (Baker, 1930: 22).

Remarks. Synonym of *glauca* Linnaeus, 1758, *teste* Philippi (1852a: 43), Paetel (1887: 480) and Starmühlner (1988: 253) (see also Baker, 1930: 12, 22). Although the locality of the holotype is unknown, Baker's choice of the type locality appears to follow *Code*, Rec. 76A.1.4.

oculuscommunis

Helix oculus communis Gmelin, 1791: 3621. [No locality given. Rio Yaracuy, Venezuela, "chosen" by Baker (1930: 14).] Lectotype (Baker 1930:14): the specimen illustrated by "Seba (Thes., pl. 40, figs. 3–5)"; paralectotypes: the specimens illustrated in the other figures cited by Gmelin (1791: 3621). Distribution: Venezuela, Guyana, French Guiana (Baker, 1930: 14).

Remarks. Baker (1930: 14) designated the lectotype; and, although the locality of this specimen is unknown, his choice of a type locality appears to follow *Code* Rec. 76A.1.4. Synonym of *glauca* Linnaeus, 1758, *teste* Philippi (1852a: 43), Sowerby (1909a: 350) and Starmühlner (1988: 253) (see also Baker, 1930: 12, 14). Synonym of *gevesensis*

Deshayes, 1838 [= *glauca* Linnaeus, 1758], *teste* Pain (1950b: 69).

oligista

Pomacea (*Effusa*) *oligista* Pilsbry & Olsson, 1953: 98, pl. 6, fig. 6. on the road ... from Cartagena to Barranquilla ... a freshwater lake known as the Cienaga de Luruaco. Holotype: ANSP 189546 ["189546a" (Baker, 1964: 168)]; paratypes: ANSP 189547 (10 spms.), 365367 (3 spms., figured). Distribution: Colombia.

Remarks. Pilsbry & Olsson (1953: 98) gave measurements of the "type" and the largest "paratype" but gave no catalog numbers. Synonym of *planorbula* Philippi, 1852, *teste* Pain (1956a: 76–77).

orinoccensis

Ampullaria orinoccensis Troschel, 1848: 548. am obern Pomeroon. Syntypes: ZMHB 1384a (1 spm.), 1384b (3 spms.), 1384c (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); possible syntypes: MCZ [labeled as paratypes, but as "*oronocoensis* Reeve"]; type material possibly also in the Dohrn collection, Stettin Museum [destroyed; Dance, 1986: 210: 229]; no type material found by us in BMNH (cf. Dance, 1986: 210). Distribution: Guyana, Surinam, Venezuela (Vernhout, 1914a: 43; Pain, 1952: 30–31; Geijskes & Pain, 1957: 45), French Guiana (Tillier, 1980: 27).

Remarks. Name attributed to Ziegler by Troschel (1848: 548). Variously misspelled, e.g., as "*Oronocensis*" by Reeve (1856b: pl. 10, fig. 45) and "*Orinocensis*" by Martens (1873: 204). Synonym of *dubia* Guilding, 1828 [= *glauca* Linnaeus, 1758], *teste* Baker (1930: 15). Variety or subspecies of *glauca* Linnaeus, 1758, *teste* Pain (1950b: 70; 1952: 31), Geijskes & Pain (1957: 44) and Tillier (1980: 26). Synonym of *glauca* Linnaeus, 1758, *teste* Starmühlner (1988: 253 [as "*oronocensis* Reeve"]), followed here.

pachystoma

Ampullaria pachystoma Philippi, 1849: 17. Brasilia [? error]. Type material: probably MNHNS. Distribution: Brasil [? error].

Remarks. Synonym of *luteostoma* Swainson, 1823 [= *glauca* Linnaeus, 1758], *teste* Paetel (1887: 480) and Alderson (1925: 6). Variety of *glauca* Linnaeus, 1758, *teste* Sowerby (1909a: 350). Retained as a distinct species by Baker (1930: 16–17). Synonym of *glauca* Linnaeus, 1758, *teste* Starmühlner (1988: 253), followed here.

pattersoni

Pomacea (*Effusa*) *pattersoni* Boss & Parodiz, 1977: 112, figs. 7–9. Vicinity of Yarina (6°172' S; 75°172' W), upstream from Isla Navarro, close to Río Huallaga, Department of San Martín, Peru. Holotype: MCZ 272900; paratype: MCZ 272918. Distribution: Peru.

philippiana

Pomacea (*Effusa*) *glauca* form *philippiana* Baker, 1930: 14. canal near Georgetown, British Guiana. Holotype ANSP 70016 ["170016a" (Baker, 1964: 168)]; paratypes: ANSP 365368 (14 spms.). Distribution: Surinam to Orinoco and Guadeloupe (Baker, 1930: 14).

Remarks. Synonym of *glauca* Linnaeus, 1758 (see Baker, 1930: 12, 14). **N. syn.**

+ planorbula

Ampullaria planorbula Philippi, 1852a: 26, pl. 7, fig. 3 [1852b: 23]. [No locality given.] Syntype: ZMHB 2131 (M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: "Payta" (Paetel, 1888: 481), "Para." (Sowerby, 1909a: 359).

Remarks. Retained as a distinct infraspecific taxon, following Baker (1930: 12, 24) and pending further research. Pilsbry (1933: 72) considered it "to be the young stage of some variety of *P.* (*Effusa*) *glauca* (L.)".

prunulum

Ampullaria prunulum Reeve, 1856c: pl. 18, fig. 82. New Granada [in 1856 = present-day Colombia and Panama]. Syntypes: BMNH 20020679 (3 spms.). Distribution: Colombia and/or Panama.

Remarks. Synonym of *glauca* Linnaeus, 1758, *teste* Starmühlner (1988: 253), followed here, although considered a variety of that species by Pain (1950b: 69).

quinindensis

Ampullaria quinindensis Miller, 1879: 151, pl. 15, fig. 5. Rio Quinindé qui influit in fluminem Esmeraldas. Type material: location not known to us. Distribution: Ecuador (Miller, 1879: 152; Sowerby, 1909a: 357 [as "*quinquidensis*"]).

rhodostoma

Ampullaria rhodostoma Appun, 1871: 141, 548. Unavailable name; *nom. nud.*

Remarks. Treated as a synonym of *luteostoma* Swainson, 1823, by Alderson (1925: 6).

suprafasciata

Ampullaria geveana var. *suprafasciata* Kobelt, 1913b: 157, pl. 57, figs. 7, 8. [No locality given.] Type material: possibly SMFD, ZMHB (Dance, 1986: 215), but not found in ZMHB (M. Glaubrecht, pers. comm. to RHC, 1 March 2003).

Remarks. Synonym of *glauca* Linnaeus, 1758, *teste* Baker (1930: 18).

tamsiana

Ampullaria Tamsiana Philippi, 1852a: 51, pl. 16, figs. 1, 2 [1852b: 27]. Puerto Cabello. Syntype: ZMHB 109502 (1 spm.) [= pl. 16, fig. 2], 109503 (2 spms.); possible syntypes 109503 (2 spms.) [one of these ? = pl. 16, fig. 1] (M. Glaubrecht, pers. comm. to RHC, 1 March 2003; F. Köhler, pers. comm. to RHC, 6 March 2003), possibly also MNHNS. Distribution: Venezuela (Berthold, 1991).

Remarks. Name attributed to Dunker by Philippi (1852a: 51; 1852b: 27). Synonym of *glauca* Linnaeus, 1758, *teste* Baker (1930: 18, 20).

teres

Ampullaria teres Philippi, 1849: 19. [No locality given.] Syntype: ZMHB 109504 (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); type material possibly also in MNHNS. Distribution: Cuba [? error] (Gaudion, 1879: 40; Paetel, 1888: 482), "La Plat." [? error] (Paetel, 1873: 65).

Remarks. "Form" of *glauca* Linnaeus, 1758, *teste* Pilsbry (1927a: 251). Synonym of *neritina* Gmelin, 1791 [= *glauca* Linnaeus, 1758], *teste* Baker (1930: 22) (see also Baker, 1930: 12). Synonym of *glauca* Linnaeus, 1758. **N. syn.**

tristis

Ampullaria effusa variety *tristis* Guppy, 1866: 44. Trinidad [in title of publication]. Type material: probably Victoria Inst., Trinidad [destroyed], not found by us in BMNH (cf. Dance, 1986: 213). Distribution: Trinidad.

Remarks. Synonym of *neritina* Gmelin, 1791 [= *glauca* Linnaeus, 1758], *teste* Baker (1930: 22) (see also Baker, 1930: 12). Synonym of *glauca* Linnaeus **N. syn.**

villata

A. villata Sowerby, 1909a: 350. Unavailable name; first published as a junior synonym of *gevesensis* Deshayes, 1838 [as "*geveanensis*"], not made available before 1961 (*Code* Art. 11.6).

Remarks. Name attributed to Martens by Sowerby (1909a: 350) and listed as a synonym of *gevesensis* Deshayes, 1838 [= *glauca* Linnaeus, 1758]. Not listed under Martens' authorship by Ruhoff (1980: 564), the *Zoological Record* or Kabat & Boss (1997: 365).

Subgenus POMACEA Perry, 1810

Details as for genus *Pomacea* Perry, 1810.

acuta

Ampullaria acuta Paetel, 1873: 64 [1887: 476]. Unavailable name; *nom. nud.*

Remarks. Name attributed to Menke by Paetel (1873: 64, 1887: 476), and by Gaudion (1879: 23), with locality "Vera Cruz". Not listed by Sowerby (1916: 70), Sherborn (1922–1933) or Ruhoff (1980: 123).

aldersoni

Pila (*Pomacea*) *aldersoni* Pain, 1946a: 180; pl. 6, figs. 1, 2. Ecuador, in a marsh near Santa Barbara, about 170 miles S.E. of Quito. Holotype and paratype (distinguished as such in the text and the only two specimens on which the description was based): BMNH 1946.6.24.25 (1 spm.), possibly NMW.Z.1981.118.00091 (1 spm.) or NMW.1955.158.02411 (Melvill-Tomlin collection, 1 spm.). Distribution: Ecuador.

Remarks. The original label of NMW. 1955.158.02411 states that it was collected in November 1939, whereas the type series was collected in January 1939; however, it does say "co-type". NMW.Z.1981.118.00091 is small compared to the type dimensions and is not the specimen figured (H. Wood, pers. comm. to RHC, 30 October 2001).

amazonica

Ampullaria Amazonica Reeve, 1856b: pl. 12, fig. 55. River Amazon. Syntype: BMNH 20020645. Distribution: Amazon (Sowerby, 1909a: 346).

angulata

Ampullaria angulata Jay, 1836: [85 (explanation of pl. 3)], pl. 3, fig. 7. Mexico [error]. Syntype: AMNH 56108 (Boyko & Cordeiro, 2001: 16) [labeled as "figd pl. 3, fig. 7" in Jay's handwriting (P. M. Mikkelsen, pers. comm. to RHC, 7 May 2002)].

Remarks. Synonym of *scalaris* Orbigny, 1835, *teste* Jay (1839: [116]), Martens (1857: 202), Gaudion (1879: 23) and Ihering (1898: 48), which has never been found as far north as Mexico. We therefore consider Jay's locality to be incorrect.

angulata

Ampullaria angulata Dunker, 1845: 188. reipublicae Argentinae. Type material: not in ZMHB (F. Köhler, pers. comm. to RHC, 6 March 2003), not found by us in BMNH (cf. Dance, 1986: 210).

Remarks. Junior primary homonym of *angulata* Jay, 1836.

angulata

Ampullaria angulata Deshayes, 1850: 45, pl. 72, fig. 23. [No locality given.] Type material: possibly École des Mines, not found by us in

BMNH or MNHN (cf. Dance, 1986: 210). Distribution: unknown.

Remarks. Junior primary homonym of *angulata* Jay, 1836, and *angulata* Dunker, 1845. Probably a synonym of *scalaris* Orbigny, 1835, and hence retained here as a South American species.

angulata

Pomus angulata H. Adams & A. Adams, 1854c: 347. Unavailable name; *nom. nud.*

Remarks. Name attributed to Jonas by H. Adams & A. Adams (1854c: 347). Not listed by Sowerby (1916: 70), Sherborn (1922–1933) or Trew (1992: 16). Perhaps the attribution to Jonas was in error, or Jonas' concept of the species was a misidentification of one of the three taxa listed above.

arata

Ampullaria malleata var. *Arata* Fischer & Crosse, 1890: 235 [1888: pl. 44, fig. 6d, 6e; plate published without name]. in Laguna de los Cocos, provinciæ Vera Cruz ..., in paludibus prope Palizada et San Geromino, provinciæ Yucatan ..., in paludibus fluminis Usumasinta, prope Balancan, provinciæ Tabasco. Type material: Sallé collection, not found by us in BMNH, MNHN, etc. (cf. Dance, 1986: 209, 225). Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Baker (1922: 37) and Pain (1964: 227).

+ archimedes

Ampullaria Archimedes Spix, in Wagner, 1827: 1, pl. 2, fig. 2. [No locality given.] Type material: probably lost (Philippi, 1851: 10; Fechter, 1983: 221; S. C. Thiengo, unpublished). Distribution: unknown.

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.), who also explain the publication history of this work. Spix illustrated *archimedes* as a full species, but Wagner, in writing the descriptions, treated *archimedes* "Spix" as a variety of *zonata* "Wagner". We retain it as an infraspecific taxon of *zonata* Spix, 1827, following Philippi (1851: 10) and Sowerby (1909a: 359), though they were synonymized by Martens (1857: 202).

armeniacum

Ampullaria armeniacum Hupé, 1857: 69, pl. 13, fig. 5. le fleuve des Amazones. Distribution: "Haut-Amazone" (Gaudion, 1879: 24). Type material: not found by us in MNHN (cf. Dance, 1986: 214).

aulanieri

Ampullaria Aulanieri Deville & Huppé, 1850: 642, pl. 15, fig. 4. lac de Cruz Playa, sur la rivière de l'Ucayali (Pérou). Syntypes: MNHN (3 lots, 15 spms.). Distribution: Peru (Pain, 1960: 424).

auriformis

Ampullaria auriformis Reeve, 1856e: pl. 28, fig. 133a, b. Honduras. Syntype: BMNH 20020646. Distribution: Honduras.

Remarks. May be a variety of *hopetonensis* Lea, 1834, *teste* Sowerby (1909a: 346), but note the skepticism of Pain (1964: 225) regarding this.

aurostoma

Ampullaria aurostoma Lea, 1856: 110. Carthagena. Syntypes: USNM 106299 [figured by Lea (1866, pl. 22, fig. 4), labeled in the USNM as the holotype], USNM 106273 (11 spms.) [labeled as paratypes], MCZ (1 lot) [labeled as paratypes]. Distribution: Mexico [? error] (Paetel, 1887: 477), Colombia, Venezuela (Baker, 1930: 9; Pain, 1956a: 78).

Remarks. Also published by Reeve (1856e: pl. 28, fig. 131a, b), who said "Lea MS". Retained as a distinct species following Baker (1930: 8) and Pain (1956a: 78), contrary to Sowerby (1909a: 347) and Kobelt (1913a: 145) who synonymized it with *cerasum* Hanley, 1854. Placed in subgenus *Limnopomus* Dall by Baker (1930: 8).

australis

Ampullaria australis Orbigny, 1835a: 32. lacubus Pampas meridionalibus Buenos-Ayres (republica Argentina). Syntype: BMNH 1854.12.4.335. Distribution: Argentina.

Remarks. Synonym of *insularum* Orbigny, 1835, *teste* Sowerby (1909a: 353), or a variety of *hopetonensis* Lea, 1834 [= *paludosa* Say, 1829], *teste* Sowerby (1909a: 352; but see Pain, 1964: 225). Synonym of *canaliculata* Lamarck, 1822, *teste* Hylton Scott (1958: 299) and Cazzaniga (2002: 73).

autumnalis

Ampullaria autumnalis Reeve, 1856a: pl. 4, fig. 16. [No locality given.] Syntype: BMNH 20020647. Distribution: unknown.

Remarks. Synonym of *sordida* Swainson, 1823, *teste* Sowerby (1909a: 357) and Kobelt (1913h: 206).

avellana

Ampullaria avellana Sowerby, 1909a: 346 [name], 360 [description], text fig. Lagunella, Venezuela. Syntypes: BMNH 1909.10.19.34 (1 spm.) (see also Sowerby, 1909a: 359), HUJ 21519 (1 spm.) (H. Mienis, pers. comm. to RHC, 4 August 2002), MHNG 1093/99 (2 spms.) (Y. Finet, pers. comm. to RHC, 22 August 2002). Distribution: Venezuela.

Remarks. Junior primary homonym of *avellana* Lamarck, 1822 [not Ampullariidae (Sowerby, 1825: 44; Jay, 1850: 294)].

batabana

Ampullaria batabana Paetel, 1887: 477. Unavailable name; *nom. nud.*

Remarks. Listed as from Cuba by Paetel (1887: 477).

belizensis

Ampullaria Belizensis Crosse & Fischer, in Fischer & Crosse, 1888: [explanation of] pl. 45, fig. 2, 2a–c [Crosse & Fischer, 1890: 110; see also Fischer & Crosse (1890: 231, pl. 48, fig. 9, 9a)]. [No locality given. in coloniâ anglicâ Belize (Crosse & Fischer (1890: 110).] Syntypes: MNHN (5 lots, 36 spms.) (see also Sowerby, 1909b: 363). Distribution: Belize.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

brasiliensis

Ampullaria Brasiliensis Paetel, 1887: 477. Unavailable name; *nom. nud.*

bridgesii

Ampullaria Bridgesii Reeve, 1856b: pl. 11, figs. 50, 51. Rio Grande, Bolivia. Lectotype (Pain, 1960: 425): BMNH 20010487 (shell figured as no. 50 by Reeve); paralectotype: BMNH 20010488. Distribution: Brasil (Baker, 1914: 660), Bolivia.

Remarks. Pain (1960: 425) considered the nominotypical subspecies of *bridgesii* Reeve, 1856, to be a rare and local form, with the subspecies *diffusa* Blume, 1957, being much more widespread. Sometimes synonymized with *scalaris* Orbigny, 1835 (e.g., Ihering, 1898: 48), but almost certainly incorrectly.

bulla

Ampullaria bulla Reeve, 1856d: pl. 22, fig. 104a, b. [No locality given but type material labeled as from Mexico.] Syntypes: BMNH 20020648 (2 spms.). Distribution: Ecuador [? error] (Paetel, 1887: 477), Mexico (Sowerby, 1909a: 346).

buxea

Ampullaria buxea Reeve, 1856e: pl. 23, fig. 112. [No locality given.] Syntype: BMNH 1907.10.28.210. Distribution: Colombia (Paetel, 1887: 477), Jamaica (Sowerby, 1909a: 346).

Remarks. Synonym of *fasciata* Roissy, 1805, *teste* Pilsbry (1927a: 247), although considered a possible synonym of *hopetonensis* Lea, 1834, by Martens (1857: 203).

caliginosa

Ampullaria caliginosa Reeve, 1856e: pl. 25, fig. 118. [No locality given.] Type material: not found by us in BMNH. Distribution: Florida (Walker, 1918: 124).

Remarks. Synonym of *paludosa* Say, 1829, *teste* Sowerby (1916: 70), followed here, though Pilsbry (1927a: 250) was not certain of this synonymy.

camena

Pomacea camena Pain, 1949a: 258; pl. 13, figs. 5, 6. shallow stream near Lagunella, Venezuela, at 800 metres. Holotype: BMNH 1946.10.2.4 (Pain, 1949a: 258; incorrectly citing BMNH 1946.10.2.3, which is the number of the holotype of *vickeryi* Pain, 1949, in both his paper and the BMNH register); paratypes (1 only mentioned by Pain (1949a: 258)): HUJ 21516 (1 spm.) (H. Mienis, pers. comm. to RHC, 4 August 2002), NMW.Z.1981.118.00108 (Pain collection, 2 spms.), NMW.1955.158.02412 (Melvill-Tomlin collection, 1 spm.), MCZ. Distribution: Venezuela.

Remarks. The holotype in the BMNH is not a close match to the specimen illustrated by Pain (1949a: figs. 5, 6), although the other two holotypes illustrated in Pain's paper are of the BMNH specimens (P. B. Mordan, pers. comm. to RHC, 2 November 2001, 7 February 2003).

canaliculata

Ampullaria canaliculata Lamarck, 1822a: 178. les rivières de la Guadeloupe [? error; perhaps Lago Guadeloupe, Argentina, not the Caribbean island of Guadeloupe (Pain, 1946b: 58; Hylton Scott, 1958: 300; Thiengo et al., 1993: 68; Cazzaniga, 2002: 74)]. Possible holotype: MHNG 1093/91 (Sowerby, 1909b: 363; Mermod, 1952: 88; Y. Finet, pers. comm. to RHC, 24 October 1994, 22 August 2002). Distribution: Argentina, Bolivia, Brazil, Paraguay, Uruguay (Hylton Scott, 1958: 301–303) [but ascertaining the true distribution of this variable species depends on detailed taxonomic study; e.g., Cazzaniga (1987)].

Remarks. Lamarck (1804: 32) also described a marine fossil from the Eocene of France as *Ampullaria canaliculata*, this species being the type species of *Amauropsina* Chelot, 1885, which is either in the Naticidae (Kabat, 1991: 426) or Ampullospiridae (Tracey et al., 1996: 116). An application (Cowie et al., 2001) was submitted to the ICZN to retain both names as valid (*Code* Art.

23.9.5), and this was so ruled by the ICZN (2002: 137).

cassidiformis

Ampullaria Cassidiformi Reeve, 1856b: pl. 12, fig. 56. Lake of Maracaibo, Venezuela. Syntype: BMNH 20020649. Distribution: Venezuela.

Remarks. The original spelling, as given above, is considered incorrect, as it was clearly an inadvertent error [*Code* Art. 32.5.1] inasmuch as other species published by Reeve at the same time with similarly formed names did not lack the "s". The index to Reeve's work has "*cassidiformis*", but this was published later and therefore is to be considered as evidence external to the original publication. Synonym of *eximia* Dunker, 1853, *teste* Baker (1930: 6).

castelloi

Ampullaria Castelloi Sowerby, 1894: 48, pl. 4, fig. 22. River Meta, S.E. of Bogota. Lectotype (Pain, 1949b: pl. 1, figs. 1, 2): BMNH 1893.5.29.3 [possibly part of the type series but not the specimen originally figured by Sowerby; P. B. Mordan, pers. comm. to RHC, 7 February 2003]; possible paralectotypes: MCZ (1 lot) [labeled "? paratypes"]. Distribution: Colombia, Surinam (Vernhout, 1914a: 29, 41, 43) [? error; Geijskes & Pain, 1957: 45).

Remarks. Placed in *Limnopomus* Dall by Pain (1949b: 39). Sowerby (1894: 48) based his description on more than one shell ("... in some specimens [the umbilicus is] completely closed"). Therefore, the specimen figured by Pain (1949b: pl. 1, figs. 1, 2) as the "type" must be considered a lectotype (*Code* Art. 74.5, Rec. 73F).

castelnaudii

Ampullaria castelnaudii Hupé, 1857: 65, pl. 11, fig. 1. le fleuve des Amazones. Syntypes: MNHN (4 lots, 7 spms.). Distribution: "Haut-Amazone" (Gaudion, 1879: 26).

catamarcensis

Ampullaria catamarcensis Sowerby, 1875: 600, pl. 72, fig. 4. Catamarca (on the Andes of Peru) [? = Cajamarca (Peru); Cazzaniga (1987: 59–61)]. Syntypes: BMNH 1875.4.19.2 (2 spms.). Distribution: Peru.

Remarks. Placed in subgenus *Limnopomus* Dall by Cazzaniga (1987: 59–61).

+ **catemacensis**

Ampullaria patula catemacensis Baker, 1922: 39, pl. 14, figs. 2–4, pl. 15. fig. 7. Lake Catemaco. Holotype (Baker, 1922: pl. 14, fig. 2): UMMZ 31850; paratypes: UMMZ 31850 (5 spms., not separated from the holotype), ANSP 133680 (4 spms.); topotypes: MCZ. Distribution: Lake Catemaco, Mexico (Naranjo-García & García-Cubas, 1986: 603).

cerasum

Ampullaria cerasum Hanley, 1854: [unnumbered page], *Ampullaria* pl. 2, fig. 7. [No locality given.] Syntype: BMNH 1907.11.21.83. Distribution: Mexico (Martens, 1899: 421; Sowerby, 1909a: 347).

Remarks. Not listed among Hanley's taxa by Norris & Dance (2002: 370).

+ **chamana**

Ampullaria lattrei chamana Hinkley, 1920: 53 [1921: pl. 4, fig. 5]. Guatemala [in publication title]. Lectotype (Baker, 1964: 168): ANSP "46231" [error; correctly 46321] ; paralectotypes: Bryant Walker collection, Museum of the Illinois University, Hinkley collection (Hinkley, 1920: 54), ANSP 76238 (2 spms.; originally 3 spms. in this lot), MCZ. Distribution: Guatemala.

chaquensis

Pomacea canaliculata chaquensis Hylton Scott, 1948: 242. Madrejón de Ingeniero Juárez, Chaco salteño. Formosa. Syntypes ["Cotipos"]: IMLA. Distribution: Argentina, Bolivia (Hylton Scott, 1958: 304).

Remarks. Synonym of *canaliculata* Lamarck, 1822, *teste* Cazzaniga (1987: 56).

chemnitzii

Ampullaria Chemnitzii Philippi, 1852a: 39, pl. 10, fig. 5 [1852b: 25]. [No locality given. 4.5 kilometers south ... from Tucacas "chosen" by Baker (1930: 5)] Lectotype: the specimen illustrated in "Philippi's figure" (Baker, 1930: 5) Type material: probably MNHNS. Distribution: Ecuador, Colombia, Venezuela (Pain, 1956a: 75).

Remarks. Although the origin of the designated lectotype is unknown, Baker's (1930: 5) type locality choice (the locality being that of his own material) appears to follow *Code* Rec. 76A.1.4. Synonym of *lineata* Spix, 1827, *teste* Sowerby (1909a: 354) and Vernhout (1914a: 27), but retained here as a distinct species, following Baker (1930: 5).

chiapasensis

Ampullaria malleata var. *Chiapasensis* Fischer & Crosse, 1890: 235, pl. 48, fig. 5. in paludibus prope Las Playas, in provincia Chiapas. Type material: Morelet collection, not found by us in BMNH or MNHN, not found in MHNG by Y. Finet (pers. comm. to RHC, 5

August 2002) (cf. Dance, 1986: 219). Distribution: Mexico.

Remarks. Synonym of *livescens* Reeve, 1856, *teste* Pain (1964: 228).

cincta

Ampullaria cincta Cristofori & Jan, 1832: [Section IIa, Pars Ia] 7, [Mantissa] 3. Jamaica. Type material: formerly MCSN [destroyed; A. Garassino, pers. comm. to RHC, 5 September 2002]. Distribution: Jamaica.

Remarks. Synonym of *fasciata* Roissy, 1805, *teste* Pilsbry (1927a: 247).

citreum

Ampullaria citreum Reeve, 1856e: pl. 24, fig. 116a, b. [No locality given.] Syntype: BMNH 1907.11.21.83. Distribution: "Western Hemisphere" (Sowerby, 1909a: 347).

columbensis

Ampullaria Columbensis Jay, 1836: 47 [1839: 65; 1850: 282]. Unavailable name; *nom. nud.*

Remarks. South America given as locality by Jay (1836: 47).

columbiensis

Ampullaria columbiensis Philippi, 1851: 20, pl. 5, fig. 5. [No locality given; "Westkolumbien" on label in ZMHB] Syntypes: ZMHB 1343 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003), possibly also MNHNS. Distribution: possibly "Rio Pastása in Andibus orientalibus" (Miller, 1879: 150), Colombia.

Remarks. Name attributed to Sowerby by Philippi (1851: 20). Miller (1879: 150) discussed his material under "*Ampullaria* aff. *Columbiensis* Phil.". Alderson (1925: 53) considered it "unrecognized" but discussed it under *interrupta* Sowerby, 1909, which was placed in *Limnopomus* Dall, 1904, by Sowerby (1909a: 361). We therefore include it tentatively in *Pomacea* Perry, 1810.

columbiensis

Ampullaria columbiensis Reeve, 1856b: pl. 5, fig. 25. Chiriqui, Veragua [Colombia]. Syntypes: BMNH 20020650 (2 spms.), MNHN (3 spms.).

Remarks. Name attributed to Sowerby, MS. Junior primary homonym of *columbiensis* Philippi, 1851; replaced by *martensiana* Nevill, 1884. Also replaced by *tristrami* Fischer & Crosse, 1890, Fischer & Crosse (1890: 245) apparently being unaware of Nevill, 1884. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

columellaris

Ampullaria columellaris Gould, 1848: 74. Province of Maynas, Peru. Lectotype (Johnson, 1964: 57): USNM 5547. Distribution: Peru, Bolivia, ? Ecuador (Pain, 1960: 429).

Remarks. Unless it can be determined that Gould based his description on only a single specimen, Johnson's (1964: 57) listing of the "holotype" in fact designated a lectotype (*Code* Art. 74.6, Rec. 73F). The type species of *Limnopomus* Dall, 1904, which is here considered a synonym of *Pomacea* Perry, 1810.

commissionis

Amp. decussata var. *commissionis* Ihering, 1898: 51. Iguape. Syntypes: ZMHB 109513 (1 spm.), 109514 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); no type material in MZUSP (cf. Dance, 1986: 214). Distribution: Brasil (Pilsbry, 1933: 74).

Remarks. Raised to full species level and placed in *Asolene* Orbigny, 1838, by Kobelt (1913h: 202), but removed from *Asolene* Orbigny, 1838, by Ihering (1919: 341).

conoidea

Ampullaria conoidea Martens, 1899: 423, pl. 24, figs. 10, 11. Costa Rica. Possible syntypes (description based explicitly on 2 spms. only): ZMHB 21857 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 4 May 2002, 1 March 2003). Distribution: Costa Rica.

consolatrix

Ampullaria consolatrix Ihering, 1919: 338. Fl. Uruguay, prope Itaquy, Río Grande do Sul. Type material: not found by us in MZUSP (cf. Dance, 1986: 214). Distribution: Brasil.

contamanoensis

Ampullaria contamanoënsis Preston, 1914: 527. Contamano, Rio Ucayali, Eastern Peru. Syntypes: BMNH 1915.1.6.84, NMW.Z.1981.118.00096 (Pain collection, 1 spm.), not in HUJ, not found by us in UMMZ (cf. Dance, 1986: 206, 222). Distribution: Peru.

Remarks. Synonym of *aulanieri* Deville & Huppé, 1850, *teste* Pain (1960: 424).

cornucopia

Ampullaria cornucopia Reeve, 1856e: pl. 1, fig. 4. Columbia [= Colombia]. Syntype: BMNH 20020651. Distribution: Colombia (Sowerby, 1909a: 347).

costaricana

Ampullaria costaricana Martens, 1899: 418, pl. 24, figs. 14–17. Nicaragua: Lake of Nicaragua ... N.W. Costa Rica: Rio Saveyre, at Boca Culebra ... S.W. Costa Rica: Palmar, south of the Rio Grande de Terraba ... N.

Panama: Chiriqui. Syntypes: ZMHB 109507 (1 spm.) [= fig. 16], 109508 (1 spm.) [= fig. 15], 109509 (1 spm.) [= fig. 17], 109510 (1 spm.) [= fig. 14], 109511 (7 spms.), 109512 (1 spm.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003; F. Köhler, pers. comm. to RHC, 6 March 2003); no type material found by us in BMNH or MCZ (cf. Dance, 1986: 218). Distribution: Nicaragua, Costa Rica, Panama.

Remarks. Additional localities in Costa Rica given by Martens (1901: 644).

cousini

Ampullaria Cousini Jousseaume, 1877: 185, pl. 3, fig. 3. la République de l'Équateur. Syntypes: MNHN (2 lots, 3 spms.). Distribution: Ecuador (Sowerby, 1909a: 347).

crosseana

Ampullaria Crosseana Hidalgo, 1871: 206 [1872: 142, pl. 7, fig. 1]. in fluvio Amazonum dicto, Americæ meridionalis. Syntypes: MNCN 15.05/11485 (1 spm., figured), 15.05/1047 (1 spm.) (Villena et al., 1997: 75). Distribution: River Amazon (Sowerby, 1909a: 348).

Remarks. Synonym of *maculata* Perry, 1810, *teste* Pain (1960: 423).

cubensis

Ampullaria cubensis Morelet, 1849: 24. prov. borealis insulæ Cuba. Syntypes: BMNH 1893.2.4.1675-6 (2 spms.). Distribution: Cuba [? error; Pilsbry, 1927a: 252].

Remarks. Synonym of *teres* Philippi, 1849, *teste* Paetel (1887: 478), and according to the syntype labels. However, Pilsbry (1927a: 252) conclusively demonstrated that it is not *teres* Philippi, 1849 (nor *cubensis* Reeve, 1856), but he was unable to locate the type material (see also *cubensis* Reeve, 1856) and hence considered the species too poorly known to place it in the synonymy of any known species.

cubensis

Ampullaria Cubensis Reeve, 1856c: pl. 18, fig. 83a, b. Cuba. Type material: not found by us in BMNH. Distribution: Cuba.

Remarks. Junior primary homonym of *cubensis* Morelet, 1849, replaced by *poeyana* Pilsbry, 1927. Treated as a variety of *glauca* Linnaeus, 1758, by Sowerby (1909a: 350) and placed in the "Formenkreis" of *glauca* Linnaeus, 1758, by Kobelt (1913a: 150). Synonym of *glauca* Linnaeus, 1758, *teste* Starmühlner (1988: 253 [as "*culemsis*"]). Pilsbry (1927a: 251–252), followed here, retained *poeyana* Pilsbry, 1927, as a distinct species not in the "same section of the genus [as *glauca* Linnaeus, 1758]" (i.e., subg. *Effusa*). It is possible that the syntypes listed under *cubensis* Morelet, 1849, although labeled "Morelet", are syntypes of *cubensis* Reeve, as we found no type material labeled "*cubensis* Reeve" in the BMNH. If Pilsbry had thought this to be the case, it would explain his inability to find Morelet's material. However, neither specimen matches Reeve's figures.

cumingii

Ampullaria Cumingii King & Broderip, 1831: 344. in Sinu Panamæ, (Island of Saboga, in a small hill-stream). Type material: not found by us in BMNH (cf. Dance, 1986: 215); topotype: USNM 4673 (Morrison, 1946: 6). Distribution: Mexico [? error], Panama, Ecuador [? error] (Sowerby, 1909a: 348).

Remarks. Confusion over the type locality was clarified by Morrison (1952: 105–106), who considered the locality as originally published ("Saboga") to be correct.

dacostae

Ampullaria Da Costæ Sowerby, 1909a: 348 [name], 359 [description], text fig. Costa Rica. Syntype: BMNH 1909.10.19.35 (see also Sowerby, 1909a: 359). Distribution: Costa Rica.

decussata

Ampullaria decussata Moricand, 1836: 445, pl. 2, figs. 26, 27. Bahia [in publication title; Lake Baril, Brasil, according to the label associated with the MHNG syntypes]. Syntypes: HUJ 21518 (2 spms.) (H. Mienis, pers. comm. to RHC, 4 August 2002), MCZ (2 lots; one of them is 141866), MHNG 33484 (9 spms.) (Y. Finet, pers. comm. to RHC, 26 August 2002), MNHN (2 lots, 13 spms.), ZMHB 109516 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: Brasil (Sowerby, 1909a: 348).

delattrei

Ampullaria Delattrei Fischer & Crosse, 1890: 246, pl. 48, fig. 7, 7a [1888: pl. 45, fig. 4, 4a]. Unjustified emendation of *lattrei* Reeve, 1856.

Remarks. Although the name was given as "*Delattrei*" by Fischer & Crosse (1888: [explanation of] pl. 45, fig. 4), this was not explicitly an emendation. The emendation was explicit in Fischer & Crosse (1890: 246), and therefore dates from 1890. Reeve (1856b: pl. 5, fig. 22) gave the collector's name incorrectly as "Lattre" and spelled the species name as "*Lattrei*". However, there is no evidence in the original publication of an inadvertent error

(*Code* Art. 32.5.1) that would justify the emendation. Although accepted by some (e.g., Martens, 1899: 419; Alderson, 1925: 31), the emendation has not been accepted by others (e.g., Hinkley, 1920: 53; Pain, 1964: 229) and so cannot be considered to be in prevailing use; it is therefore an unjustified emendation (*Code* Art. 33.2.3.1) and a junior objective synonym of *lattrei* Reeve, 1856.

depressa

Ampullaria depressa Say, 1824: 264, pl. 14, fig. 2. East Florida ... tributary to St. John's river, and on the plantation of Mr. Fatio ... Lake George. Lectotype (Clench & Turner, 1956: 121; see also Baker, 1964: 168): ANSP 50580; paralectotype: ANSP 365373.

Remarks. Junior primary homonym of *depressa* Lamarck, 1804 [not Ampullariidae]. Replaced by *paludosa* Say, 1829.

+ **diffusa**

Pomacea bridgesi diffusa Blume, 1957: 1, [unnumbered text figs.; holotype]. Lagune mitten in der Stadt St. Cruz, Bolivia. Holotype: ZSM 20011991; paratypes: ZSM 20011990 (4 spms.) [? ex coll. Blume]; possible paratypes: ZSM 20011989 (c. 110 spms.) [? the "alle anderen Paratypoide" (Blume, 1957: 2)]; Pain collection (1 spm.) (Blume, 1957: 2; E. Schwabe, pers. comm. to RHC, 28 July 2002). Distribution: Brasil, Peru, Bolivia (Pain, 1960: 425).

Remarks. Possibly a valid species (F. Naggs, pers. comm. to RHC, 9 July 2002). The true identity and origin of the snails currently referred to widely as *bridgesii* Reeve, 1856, in the domestic aquarium trade (Perera & Walls, 1996) is not known; they may be more correctly referred to *diffusa* Blume, 1957.

dilatata

Ampullaria fasciata variété *dilatata* Orbigny, 1842c: 4. Cuba [in publication title]. Type material: not found by us in BMNH (nor listed by Gray, 1855: 27–29) or MNHN; not in MHNG (Y. Finet, pers. comm. to RHC, 20 August 2002) (cf. Dance, 1986: 219, 220). Distribution: Cuba.

Remarks. Synonym of *paludosa* Say, 1829, *teste* Pilsbry (1927a: 250).

disseminata

Ampullaria disseminata De Kay, 1843: 124. Unavailable name; first published as a junior synonym of *paludosa* Say, 1829, not made available before 1961 (*Code* Art. 11.6).

Remarks. DeKay (1843: 124) attributed the name to Say as a manuscript name, but the name does not occur in Say's published writings (Binney, 1858: [237], 1865: 5).

dolioides

Ampullaria Dolioides Reeve, 1856c: pl. 16, fig. 75a, b. Bombay [error]. Syntypes: BMNH 20020653 (2 spms.). Distribution: Guyana, Surinam, French Guiana, Venezuela (Pain, 1950b: 65; Geijskes & Pain, 1957: 43; Tillier, 1980: 29).

Remarks. For a history of the interpretation of this species see Prashad (1925: 83; 1931: 167). Considered a synonym of *lineata* Spix, 1827, by Pain (1952: 31) but in error according to Geijskes & Pain (1957: 43), followed here, who treated it as a valid species, as did Tillier (1980: 29).

dolium

Ampullaria dolium Philippi, 1852a: 40, pl. 11, fig. 1 [1852b: 25]. Guyana, namentlich der Orinoco. Type material: probably MNHNS. Distribution: Guyana.

Remarks. Synonym of *urceus* Müller, 1774, *teste* Gaudion (1879: 41), Sowerby (1909a: 358), Alderson (1925: 10) and Baker (1930: 2).

dorbignyana

Ampullaria Dorbignyana Philippi, 1852a: 65, pl. 21, fig. 4. [The locality of Orbigny's specimen; "die La Plata Staaten" (Philippi, 1852a: 66)]. Holotype: the specimen illustrated in Orbigny's (1835a) figure (pl. 4, fig. 4), location not known to us. Distribution: "Brésil – Parana – Plata" (Gaudion, 1879: 35).

Remarks. Philippi (1852a: 65) explicitly described this species on the basis of Orbigny's (1835a) figure. Philippi (1852a: 49) also named it "*d'Orbignyi*" [= *dorbignyi*]. We select *dorbignyana*, the heading of Philippi's description and the more widely used alternative (e.g., Alderson, 1925: 21), as the correct original spelling. Synonym of *canaliculata* Lamarck, 1822, *teste* Ihering (1898: 49) and Sowerby (1909a: 348; 1909b: 363).

dorbignyi

Ampullaria d'Orbignyi Philippi, 1852a: 49. Incorrect original spelling of *dorbignyana* Philippi, 1852.

+ **dysoni**

Ampullaria Dysoni Hanley, 1854: [unnumbered page], *Ampullaria* pl. 2, fig. 5. Honduras. Syntype: BMNH 1907.11.21.65. Distribution: Honduras (Martens, 1899: 417; Pain, 1964: 230).

Remarks. Subspecies of *flagellata* Say, 1829, *teste* Pain (1964: 230). Not listed among Hanley's taxa by Norris & Dance (2002: 371).

electrina

Ampullaria electrina Reeve, 1856c: pl. 20, fig. 95a, b. [No locality given.] Syntypes: BMNH 20020654 (3 spms.). Distribution: unknown.

Remarks. Sowerby (1909a: 349) placed it in *Pomacea* [as *Ampullaria*].

elegans

Ampullaria elegans Orbigny, 1835a: 33. Rio Piray, provincia Santa Cruz de la Sierra (republica Boliviana). Syntypes: BMNH 1854.12.4.330 (3 spms.), MNHN (4 lots, 14 spms.). Distribution: Bolivia.

Remarks. Synonym of *cyclostoma* Spix, 1827, *teste* Pain (1960: 430).

elongata

Ampullaria fasciata variété *elongata* Orbigny, 1842c: 4. Cuba [in publication title]. Type material: not found by us in BMNH (nor listed by Gray, 1854: 17) or MNHN, not in MHNG (Y. Finet, pers. comm. to RHC, 20 August 2002) (cf. Dance, 1986: 220). Distribution: Cuba.

Remarks. Synonym of *paludosa* Say, 1829, *teste* Pilsbry (1927a: 250).

+ erogata

Ampullaria erogata Crosse & Fischer, in Fischer & Crosse, 1888: [explanation of] pl. 46, figs. 6, 6a, 7 [Crosse & Fischer, 1890: 113; see also Fischer & Crosse (1890: 251)]. [No locality given. Peten, Guatemalae ... Cacoprieto, in isthmo de Tehuantepecensi, reipublicae Mexicanae (Crosse & Fischer, 1890: 113)]. Holotype: the specimen illustrated by Crosse & Fischer, in Fischer & Crosse (1888, fig. 6, 6a), not found by us in MNHN. Distribution: as for *flagellata* Say, 1829 (Pain, 1964: 230).

Remarks. Treated by Pain (1964: 229) as an "ecological race" of *flagellata* Say, 1829, occupying the same geographic range. Determining its true taxonomic status requires further study.

erronea

Ampullaria erronea Nevill, 1877: 17. S. America. Holotype: NZSI. Distribution: South America.

erythrostoma

Ampullaria erythrostoma Reeve, 1856c: pl. 13, fig. 59. Zanzibar [error (Sowerby, 1909a: 349; Pain, 1950b: 68)]. Type material: not found by us in BMNH. Distribution: Peru (Sowerby, 1909a: 349).

Remarks. Synonym of *guyanensis* Lamarck, 1822, *teste* Sowerby (1909a: 349), Kobelt (1913f: 186) and Pain (1960: 427), and hence of *urceus* Müller, 1774 (see Tillier, 1980: 27). **N. syn.**

eumicra

Ampullaria eumicra Crosse & Fischer, 1890: 113 [see also Fischer & Crosse (1890: 243, pl. 48, fig. 10, 10a)]. provinciâ Oajaca dictâ, reipublicae Mexicanae. Syntypes: MNHN (4 spms.). Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

exculpta

Ampullaria malleata var. *Exculpta* Fischer & Crosse, 1890: 235 [1888: pl. 44, fig. 6, 6a–c; plate published without name]. in Laguna de los Cocos, provinciæ Vera Cruz ..., in paludibus prope Palizada et San Geromino, provinciæ Yucatan ..., in paludibus fluminis Usumasinta, prope Balancan, provinciæ Tabasco. Type material: Sallé collection, not found by us in BMNH, MNHN, etc. (cf. Dance, 1986: 209, 225). Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Baker (1922: 37) and Pain (1964: 227).

eximia

Ampullaria eximia Dunker, 1853: 93. die Provinz Coro am See von Maracaybo, Republik Venezuela. Syntypes: MCZ 125225, ZMHB 4039 (3 spms.) (M. Glaubrecht, pers. comm. to RHC, 4 May 2002, 1 March 2003). Distribution: Venezuela (Baker, 1930: 6).

falconensis

Pomacea falconensis Pain & Arias, 1958: 6, pl. 1, figs. 1–4, pl. 2, figs. 1–7. 5 km. SW de Chichiriviche, Estado Falcón, Venezuela (68°152' W; 10° 502' N). Holotype: MHNS 4000 (female); paratypes: MHNS 3499 (7 spms.), NMW.Z.1981.118.00116 (Pain collection, 4 spms.), MCZ 224267 (2 spms.); ZSM 20012070 (1 spm.) (E. Schwabe, pers. comm. to RHC, 28 July 2002). Distribution: Venezuela.

fasciata

Ampullaria fasciata Roissy, 1805: 374. les rivières de la Jamaïque, de la Guadeloupe et de Saint-Domingue [Haiti]. Type material: location not known to us. Distribution: Jamaica only, Guadaloupe and Haiti being incorrect (Pilsbry, 1927a: 248).

Remarks. Pilsbry (1927a: 247) clarified the status of this species as being from Jamaica, as Roissy had stated, and that it is not an Asian species in the synonymy of *ampullacea* Linnaeus, 1758 (which is now placed in *Pila*) as Sowerby (1909a: 354) had considered; that is, Roissy (1805: 374; see also Schumacher, 1817: 200) mistakenly included *ampullacea* Linnaeus, 1758, in his synonymy.

fasciata

Ampullaria fasciata Reeve, 1856b: pl. 9, fig. 41. [No locality given.] Lectotype (Kobelt, 1914b: 220): BMNH 20020655.

Remarks. Junior primary homonym of *fasciata* Roissy, 1805, and *fasciata* Lamarck, 1816 [*incertae sedis* in family Ampullariidae]. Synonym of *insularum* Orbigny, 1835, *teste* Sowerby (1909a: 353). Kobelt (1914b: 220) designated the specimen in Reeve's pl. 9, fig. 41 as a lectotype, copying the figure as his own pl. 77, fig. 1.

ferruginea

Ampullaria ferruginea Martens, 1857: 205. Unavailable name; *nom. nud.*

Remarks. Attributed to "R. pl. 14" [= Reeve, 1856b, pl. 14] with locality "Laplata". However, the name "*ferruginea*" does not appear in Reeve's work. Gaudion (1879: 29) also listed the name and said "Reev [*sic*] Hab: La Plata" but with no other information. Not listed by Sowerby (1916: 71), Ruhoff (1980: 271) or Kabat & Boss (1997: 208).

figulina

Ampullaria figulina Spix, in Wagner 1827: 3, pl. 4, fig. 4. [Type locality as for *lineata* Spix, 1827]. Syntypes: ZSM 20012063-5 (3 lots, 4 spms.) (E. Schwabe, pers. comm. to RHC, 28 July 2002; cf. Fechter, 1983: 221). Distribution: Brasil (Baker, 1914: 659).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.), who also explain the publication history of this work. Spix illustrated *figulina* as a full species, but Wagner, in writing the description, treated *figulina* "Spix" as a variety of *lineata* "Wagner". Wagner at first sight appears to have also treated it as a synonym of his own new species-group name "minor". Cowie et al. (in prep.) discuss why this is not the case and why "minor" is not an available name. Alderson (1925: 29) considered *figulina* Spix, 1827, impossible to identify with certainty. Synonym of *lineata* Spix, 1827, *teste* Pain (1960: 422), followed here, although he cited pl. 6, fig. 4.

flagellata

Ampullaria flagellata Say, 1829c: 260. Mexico ... a short distance below Vera Cruz. Lectotype (Pilsbry, 1891a: 325–326): ANSP 50645 ["50645a" (Baker, 1964: 168)]; paralectotype: ANSP 50645; topotypes: MCZ 139677. Distribution: Central America, from central Mexico to Panama, extending into northern Colombia (Magdelana drainage area) (Pain, 1964: 228; Naranjo-García & García-Cubas, 1986: 603).

Remarks. Although Baker (1964: 168) considered the type as fixed by monotypy ["TOM" (Baker, 1964: 149)], he also noted that this specimen was the "smaller and fresher of type lot", implying that there were additional specimens. Thus, Pilsbry (1891a: 325–326) in referring to a single specimen as "Say's type", and providing dimensions for it, designated a lectotype (*Code* Art. 74.6), for which Baker (1964: 168) gave the catalog number.

flatilis

Ampullaria flatilis Reeve, 1856b: pl. 7, fig. 31. Tabasco, Mexico. Syntype: BMNH 20020656. Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

flava

Pomacea paludosa flava Smith, 1937: 147. canals near Pinecrest on the Tamiamai Trail. Central Everglades and near Miami, Florida. Lectotype (Baker, 1964: 168): ANSP 188992 [as "188992a"]; paralectotype: ANSP 365372 (2 spms.). Distribution: Florida.

Remarks. Synonym of *paludosa* Say, 1829, *teste* Clench & Turner (1956: 120).

fumata

Ampullaria fumata Reeve, 1856e: pl. 26, fig. 124a, b. Province of Chiapes [= Chiapas], Mexico. Type material: not found by us in BMNH. Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227). Discussed briefly by Strebel (1873: 32).

+ **garciae**

Pomacea paludosa garciae Richards, 1933: 169, fig. 21. swamp near the town of Mendoza (or Paso Real) about five kilometers from the terminus of the Ferro-Cariles Unidos de la Habana at Guane, Pinar del Rio, Cuba. Holotype: ANSP 160873 ["160873a" (Baker, 1964: 168)]; paratypes: ANSP 365371 (2 spms.); topotype: MCZ. Distribution: Cuba.

georgii

Ampullaria Georgii Williams, 1889: 47. marshes near the La Plata, at Buenos Ayres, in the Argentine Republic. Type material: location not known to us. Distribution: Argentina.

Remarks. Synonym of *insularum* Orbigny, 1835, *teste* Sowerby (1909a: 353).

ghiesbreghti

Ampullaria Ghiesbrechtii Reeve, 1856e: pl. 26, fig. 123. Province of Chiapes [= Chiapas], Mexico. Syntype: BMNH 20020657. Distribution: Mexico, Guatemala (Pain, 1953: 222).

Remarks. Originally spelled "*Ghiesbrechtii*" but explicitly emended to "*Ghiesbreghti*" by Fischer & Crosse (1890: 233). Although there is no evidence in the original publication of an inadvertent error (*Code* Art. 32.5.1) that would justify the emendation, the emendation is in prevailing use attributed to Reeve (e.g., Pilsbry, 1893: 338; Alderson, 1925: 44; Pain, 1953: 222, 1964: 228) and is therefore deemed to be a justified emendation (*Code* Art. 33.2.3.1). Synonym of *livescens* Reeve, 1856, *teste* Pain (1964: 228).

gigantea

Ampullaria ? *gigantea* Barbosa Rodrigues, 1892: 52. avec l'*Emys macrococcygeana* ... à la même époque geologique ... ; dans les ravins des environs du Río Nanay; Loreto-Yacu, dans l'étage tertiaire [probably near Loreto on the upper Amazon in Peru, above the junction with the Río Javari (Boss & Parodoz, 1977: 111)]. Type material: may have been lost (Patterson, 1936: 50; Boss & Parodiz, 1977: 111). Distribution: Peru.

Remarks. Fossil, probably Pliocene (Boss & Parodiz, 1977: 111). Junior secondary homonym of *giganteus* Tristram, 1864.

giganteus

Pomus giganteus Tristram, 1864: 414. Lake Peten, Vera Paz [Guatemala]. Type material: not found by us in BMNH (cf. Dance, 1986: 229). "Paratype" (Pain, 1953: 222) [? = syntype]: NMW.Z.1981.118.00125 (Pain collection, 1 spm.). Distribution: Guatemala.

Remarks. Synonym of *livescens* Reeve, 1856, *teste* Pain (1964: 228).

gigas

Ampullaria gigas Spix, in Wagner, 1827: 1, pl. 1, figs. 1, 2. In flumine Amazonum. Type material: formerly in ZSM but probably lost (Alderson, 1925: 16; Fechter, 1983: 221; S. C. Thiengo, unpublished); possible syntype: MHNG 33489 (1 spm.) (Y. Finet, pers. comm. to RHC, 26 August 2002). Distribution: Brasil (Sowerby, 1909a: 350; Baker, 1914: 659).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.). Synonym of *maculata* Perry, 1810, *teste* Pilsbry (1927b: 63), Pain (1956a: 79, 1960: 423), Geijskes & Pain (1957: 42) and Boss & Parodiz (1977: 112), *contra* Ihering (1919: 334), who synonymized it with *insularum* Orbigny, 1835.

gossei

Ampullaria Gossei Reeve, 1856c: pl. 20, fig. 93a, b. Jamaica. Syntypes: BMNH 20020658 (3 spms.). Distribution: Jamaica (Sowerby, 1909a: 351; Pilsbry, 1927a: 249).

guaduasensis

Ampullaria guaduasensis Anderson, 1928: 23, pl. 1, figs. 19, 20. near San Juan de Rio Seco, on the east border of the upper valley of the Magdalena River, Colombia. Holotype: CAS 2721. Distribution: Colombia.

Remarks. Pleistocene fossil (Boss & Parodiz, 1977: 118).

gualtieri

Amp. Gualtieri Orbigny, 1835a: 32. Unavailable name; first published as a junior synonym of *canaliculata* Lamarck, 1822, not made available before 1961 (*Code*, Art. 11.6).

Remarks. Name attributed to Sowerby by Orbigny (1835a: 32) but we have been unable to find it in any Sowerby work.

guatemalensis

Ampullaria flagellata var. *guatemalensis* Martens, 1899: 413, pl. 22, fig. 11, 11a. N. Guatemala: Panzos ... Cahabon ... W. Guatemala: Paso Antonio, in the lower part of the Rio Michatoya, near the Pacific coast ... Cerro Zunil. Syntypes: MCZ [labeled as paratypes], ZMHB 109505 (4 spms.), 109506a (8 spms.), 109506b (1 spm.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003; F. Köhler, pers. comm. to RHC, 6 March 2003); no type material found by us in BMNH (cf. Dance, 1986: 218). Distribution: Guatemala.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Sowerby (1909a: 352 [as "Morelet ?"]).

guyanensis

Ampullaria Guyanensis Lamarck, 1822a: 176. les rivières de la Guyane. Lectotype (Tillier, 1980: 27): MHNG 1093/90 (Y. Finet, pers. comm. to RHC, 27 August 2002) (see also Sowerby, 1909a: 349; Mermod, 1952: 84; Pain, 1960: 427); probable paralectotypes: MNHN (2 spms., "coll. Lamarck"; 1 spm., "coll. Buffon"; see also Tillier, 1980: 27). Distribution: Brasil, Peru, Colombia, Venezuela, Guyana, French Guiana (Pain, 1960: 427).

Remarks. Subspecies of *urceus* Müller, 1774, *teste* Pain (1960: 426) and Geijskes & Pain (1957: 47). Synonym of *urceus* Müller, 1774, *teste* Tillier (1980: 27), followed here.

haemastoma

Ampullaria hæmastoma Reeve, 1856b: pl. 7, fig. 34. Peru. Syntype: BMNH 20020659. Distribution: Peru.

Remarks. Synonym of *guyanensis* Lamarck, 1822, *teste* Sowerby (1909a: 351; 1909b: 363) and Alderson (1925: 12), and

hence of *urceus* Müller, 1774 (see Tillier, 1980: 27). **N. syn.**

hanleyana

Ampullaria hanleyana Alderson, 1926: 42. Type material: lost ["Hanley's type" is lost (Pain 1951: 146)]. Distribution: Brasil (Pain, 1960: 424).

Remarks. Introduced as a new name for *swainsoni* Hanley, 1854. However, Hanley (1854: [unnumbered page], *Ampullaria* pl. 1, fig. 1) clearly indicated that he thought he was illustrating *swainsoni* Philippi, 1852, not a new species. Thus, *swainsoni* Hanley, 1854, is not a homonym of *swainsoni* Philippi, 1852, as Alderson (1926: 42) thought, but a misidentification. Alderson's (1926: 42) new name and citing of Hanley's figure therefore constitutes the original description of this species. Not listed by Norris & Dance (2002: 377).

hanleyi

Ampullaria Hanleyi Reeve, 1856e: pl. 23, fig. 113. [No locality given.] Type material: not found by us in BMNH. Distribution: Río Paraná (Ihering, 1919: 336).

Remarks. Synonym of *pulchra* Griffith & Pidgeon [as "Gray"], 1834, *teste* Alderson (1925: 33, 1926: 42).

haustrum

Ampullaria haustrum Reeve, 1856b: pl. 5, fig. 23. River Marañon. Possible syntype: BMNH 20020660. Distribution: Brasil, Bolivia, Peru (Pain, 1960: 422–423).

Remarks. Synonym of *canaliculata* Lamarck, 1822, *teste* Ihering (1898: 49) and Thompson (1997: 91), but here retained as a distinct species because of its reported production of green eggs, in contrast to the pink eggs of *canaliculata* Lamarck, 1822 (Cowie, 2002).

hollingsworthi

Pila (*Pomacea*) *hollingsworthi* Pain, 1946a: 180; pl. 6, figs. 3–5. Colombia, in a swiftly flowing stream with a rocky bed near Bogota. Holotype: BMNH 1946.6.24.24; paratype: NMW.Z.1981.118.00198 (H. Wood, pers. comm. to RHC, 30 October 2001). Distribution: Colombia.

Remarks. Belongs in *Limnopomus* Dall, 1904, *teste* Pain (1946a: 181), although Pain agreed with Alderson (1925: 1) that *Limnopomus* Dall, 1904, is not a distinguishable taxon.

hondurasensis

Ampullaria Hondurasensis Reeve, 1856a: pl. 3, fig. 15. Honduras. Syntypes: BMNH 20020662 (2 spms.). Distribution: Honduras, Guatemala (Nevill, 1884: 9), Nicaragua (Martens, 1899: 420).

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

hopetonensis

Ampullaria Hopetonensis Lea, 1834: 115, pl. 19, fig. 84. Hopeton, near Darien, Georgia. "Paratypes": MCZ 151580 (Clench & Turner, 1956: 121). Distribution: USA (Georgia).

Remarks. Synonym of *paludosa* Say, 1829, *teste* Alderson (1925: 29), Pilsbry (1927a: 249) and Clench & Turner (1956: 120).

immersa

Ampullaria immersa Reeve, 1856b: pl. 11, fig. 52. Rio Grande, Bolivia. Syntypes: BMNH 20020663 (1 spm.), MCZ [labeled as "cotypes"]; topotypes: MCZ. Distribution: Bolivia (Sowerby, 1909a: 351).

Remarks. Synonym of *canaliculata* Lamarck, 1822, *teste* Ihering (1898: 49). Synonym of *haustrum* Reeve, 1856, *teste* Pain (1960: 422).

innexa

Ampullaria innexa Crosse & Fischer, in Fischer & Crosse, 1888: [explanation of] pl. 44, fig. 7, 7a–c [Crosse & Fischer, 1890: 111; see also Fischer & Crosse (1890: 242)]. [No locality given. Monte de Mistan, propè Coapan, in provinciâ Oajaca, reipublicæ Mexicanæ (Crosse & Fischer (1890: 111).] Type material: not found by us in MNHN. Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

insularum

Ampullaria insularum Orbigny, 1835a: 32. Rio Parana (republica Argentina). Syntypes: BMNH 1854.12.4.309-313 (7 spms.), MNHN (3 lots, 5 spms.), MHNG 33487 (2 spms.) (Y. Finet, pers. comm. to RHC, 26 August 2002). Distribution: Argentina, Brasil (Baker, 1914: 659).

Remarks. Synonym of *gigas* Spix, 1827, *teste* Ihering (1898: 49) and S. C. Thiengo (unpublished), followed here, although contrary to various authors (e.g., Baker, 1914: 659), who treated it as a valid species.

interrupta

Ampullaria interrupta Sowerby, 1909a: 353 [name], 361 [description], text fig. Laguna Urao, Venezuela. Syntype: BMNH 1909.10.19.33 (see also Alderson, 1925: 52; Pain, 1950a: 110). Distribution: Venezuela.

Remarks. Placed in *Limnopomus* Dall, 1904, by Sowerby (1909a: 361) and discussed as such by Pilsbry (1933: 75).

intropicta

Ampullaria intropicta Reeve, 1856d: pl. 21, fig. 101a, b. [No locality given.] Syntypes: BMNH 20020664 (3 spms.). Distribution: Brasil (syntype label).

Remarks. Synonym of *decussata* Moricand, 1836, *teste* Sowerby (1909a: 348).

labiosa

Ampullaria labiosa Philippi, 1852a: 58, pl. 18, fig. 5 [1852b: 28]. [No locality given.] Holotype ["das einzige Exemplar" (Philippi, 1852a: 58)]: Koch collection, location not known to us. Distribution: unknown.

Remarks. Philippi (1852a: 58) attributed the name to Koch. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227), though listed as from India by Paetel (1887: 479) and "Indes orientales" by Gaudion (1879: 32).

lamarckii

Ampullaria Lamarckii Philippi, 1852a: 67, pl. 21, fig. 5. [No locality given.] Type material: probably MNHNS. Distribution: unknown.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

lattrei

Ampullaria Lattrei Reeve, 1856b: pl. 5, fig. 22. Coban, Guatemala. Syntypes: BMNH 20020665 (2 spms.). Distribution: Guatemala (Martens, 1899: 419; Sowerby, 1909a: 354; Pain, 1964: 229).

Remarks. See *delattrei* Fischer & Crosse, 1890.

lemniscata

Ampullaria lemniscata Crosse & Fischer, in Fischer & Crosse, 1888: [explanation of] pl. 44, fig. 5, 5a–c [Crosse & Fischer, 1890: 112; see also Fischer & Crosse (1890: 248)]. [No locality given. coloniâ anglicâ Belize (Crosse & Fischer (1890: 112).] Syntypes: MNHN (4 spms.) (see also Sowerby, 1909b: 363). Distribution: Belize, Mexico (Sowerby, 1909a: 352).

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

leucostoma

Ampullaria leucostoma Swainson, 1823a: pl. 175. [No locality given.] Type material: possibly MMUE (Dean, 1936: 232; H. McGhie, pers. comm. to RHC, 29 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: Venezuela (Paetel, 1887: 479).

Remarks. Synonym of *urceus* Müller, 1774, *teste* Philippi (1852a: 54), Gaudion (1879: 41), Sowerby (1909a: 358) and Alderson (1925: 10).

levior

Ampullaria levior Sowerby, 1909a: 354 [name], 361 [description], text fig. Amazon River. Syntype: BMNH 1909.10.19.36. Distribution: Amazon River; Surinam, Brasil (Vernhout, 1914a: 28, 43).

Remarks. Synonym of *lineata* Spix, 1827, *teste* Pain (1960: 422).

lineata

Helix lineata Spix, in Wagner, 1827: 3, pl. 5, fig. 2. in aquis Provinciae Bahiensis, e.g. in fluvio Itahype [see also Thiengo (1987: 563)]. Syntypes: ZSM 20012054 (1 spm.), 20012066 (1 spm.), 20012074 (1 spm.) (E. Schwabe, pers. comm. to RHC, 28 July 2002; cf. Fechter, 1983: 221), MNHN (2 spms.). Distribution: Brasil, Guyana, French Guyana, Surinam (Sowerby, 1909a: 354; Baker, 1914: 660; Vernhout, 1914a: 43) [Brasil only, *teste* Pain (1960: 422)].

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.), who also explain the publication history of this work. Pain (1950b: 72) listed "*Helix liniata* Spix" in the synonymy of *crassa* Swainson, 1823 (although he cited Spix's pl. 5, fig. 1), but subsequently (Pain, 1960: 422), followed here, treated *lineata* Spix, 1827, as a valid species. Misspelled "*lineolata*" by Deshayes (1850: 44).

linnaei

Ampullaria Linnaei Philippi, 1852a: 62, pl. 20, fig. 6 [1852b: 29]. [No locality given.] Holotype ["eines … Exemplares" (Philippi, 1852a: 62)]: probably MNHNS. Distribution: unknown.

Remarks. Synonym of *lineata* Spix, 1827, *teste* Sowerby (1909a: 354).

+ **livescens**

Ampullaria livescens Reeve, 1856b: pl. 5, fig. 21. [No locality given.] Syntype: BMNH 1986214. Distribution: Tabasco and Chiapas, Mexico; Lake Petén, northern Guatemala (Pain, 1964: 228).

Remarks. Subspecies of *flagellata* Say, 1829, *teste* Pain (1964: 228).

lutea

Poomacea [*sic*] *paludosa* Say var. *lutea* Farfante, 1942: 51. Unavailable name; *nom. nud.*

Remarks. Listed as a synonym of *paludosa* Say, 1829, by Clench & Turner (1956: 120).

lymnaeaeformis

Ampullaria lymnææformis Reeve, 1856b: pl. 8, fig. 39. River Marañon. Syntypes: BMNH 20020666 (2 spms.). Distribution: Peru.

Remarks. Synonym of *aulanieri* Deville & Huppé, 1850, *teste* Pain (1960: 424). Frequently spelled "*lymnaeformis*".

maculata

Pomacea maculata Perry, 1810c: [unnumbered plate and text] [= pl. 12 (Mathews & Iredale, 1912: 11; Geijskes & Pain, 1957: 42; R. E. Petit, pers. comm. to RHC, 16 October 2000)]. the South Sea [error; Mathews & Iredale, 1912: 11]. Type material: not found by us in BMNH (cf. Dance, 1986: 221). Distribution: Brasil, Peru (Pain, 1960: 423).

Remarks. Possibly a synonym of *urceus* Müller, 1774, *teste* Berthold (1991: 248).

malleata

Ampullaria malleata Jonas, 1844: 35 [1846: 122, pl. 10, fig. 11, 11a, 11b]. Juxta Tabasco, urbem Mexicanum. Lectotype ["le type de Jonas" (Fischer & Crosse, 1890: 237)]: probably ZMHB 109515 (M. Glaubrecht, pers. comm. to RHC, 1 March 2003; F. Köhler, pers. comm. to RHC, 6 March 2003, 20 March 2003); possible paralectotypes [labeled paratypes]: MCZ. Distribution: Mexico.

Remarks. Fischer & Crosse (1890: 237) stated that the "type" of Jonas was collected in Tabasco by Fokkes. Martens (1899: 412) mentioned two specimens, one collected from Tabasco by Fokkes and given by Jonas to Dunker, and another, from the Dunker collection, illustrated by Martens (1899: pl. 22, fig. 10) but with no mention of its collector or whether it had ever been in Jonas' possession. Although Martens (1899: 412) suggested that the latter specimen might be Jonas' "type", it seems more likely that the former is the "type" and that it is the specimen indicated as such by Fischer & Crosse (1890: 237). Martens' figure and that of Jonas (1846: fig. 11) are almost identical. Jonas gave his collection to ZMUH, which would explain the statement of Fischer & Crosse (1890: 237) that Jonas' "type" was there. Martens, however, stated that both his specimens were from the Dunker collection, in ZMHB, and the specimen ZMHB 109515 almost perfectly matches Jonas' figure, even to the small depression in the lower rim of the aperture (F. Köhler, pers. comm. to RHC, 20 March 2003). This probably came about through donation or exchange, as Dunker certainly exchanged material with collectors in Hamburg, because there is material of other taxa from him that ZMUH obtained from the Altonaer Museum (another museum in Hamburg) after the ZMUH collections were destroyed in the Second World War (B. Hausdorf, pers. comm. to RHC, 10 March 2003). However, it yet could be that Fischer & Crosse (1890: 237) and Martens (1899: 412), although both referred to the "type", were actually referring to different shells. Synonym of *flagellata* Say, 1829, *teste* Baker (1922: 37) and Pain (1964: 226).

manco

Pomacea manco Pilsbry, 1944: 145, pl. 11, figs. 31, 32. collecting station 161, on the Pachitea River, about one mile upstream from Quebrada Sungarillo. Holotype: ANSP Invertebrate Paleontology 4596 ["4596a" (Baker, 1964: 168)]; paratypes: ANSP Invertebrate Paleontology 78898 (2 spms.). Distribution: Peru (Boss & Parodiz, 1977: 110).

Remarks. Fossil. Placed in *Limnopomus* Dall, 1904, by Parodiz (1969: 110).

manetou

Pila Manetou Röding, 1798: 145. [No locality given.] Type material: possibly Art and Natural History Museum, Gotha (Stewart, 1930: 35; Dance, 1986: 206). Distribution: unknown.

Remarks. Synonym of *urceus* Müller, 1774, *teste* Baker (1930: 2).

+ **marginatra**

Ampullaria marginatra Jonas, 1845: 169. [No locality given.] Type material: "in Museo hon. Gruner" (Jonas, 1845: 169), ZMHB 29964 (lost; M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: unknown.

Remarks. Variety of *zonata* Spix, 1827, *teste* Philippi (1851: 10; 1852a: 63, 74) and Sowerby (1909a: 359).

martensiana

Ampullaria (*Pomus*) *martensiana* Nevill, 1884: 10. New name for *columbiensis* Reeve, 1856; *non* Philippi, 1851. Distribution: Colombia.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

martinezi

Ampullaria Martinezi Hidalgo, 1866: 345, pl. 14, fig. 5. Santa-Rosa, Reipublicæ Æquatoris [Ecuador]. Lectotype: MNHN (Fischer-Piette, 1950: 68); paralectotypes: MNHN (1 spm) (Fischer-Piette, 1950: 68), MNCN 15.05/7524 (1 spm.), 15.05/12306 (7 spms.) (Villena et al., 1997: 75). Distribution: Ecuador (Miller, 1879: 151; Sowerby, 1909a: 354).

melanocheila

Ampullaria melanocheila Reeve, 1856b: pl. 5, fig. 24. [No locality given.] Syntype: BMNH

20020667. Distribution: Brasil (Paetel, 1887: 480).

Remarks. Synonym of *sordida* Swainson, 1823, *teste* Sowerby (1909a: 357).

melanostoma

Ampullaria reflexa Var. melanostoma Philippi, 1852a: 35, 58, pl. 18, fig. 4. [No locality given.] Syntype: ZMHB 109500 (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); type material possibly also in MNHNS. Distribution: unknown.

Remarks. Philippi (1852a: 35) attributed the name to "Parr. in litt." Synonym of *malleata* Jonas, 1844, *teste* Martens (1857: 189, 207), but a variety of *flagellata* Say, 1829, *teste* Martens (1899: 411). Treated here as a synonym of *flagellata* Say, 1829. **N. Syn.**

meridaensis

Pomacea (*Limnopomus*) *meridaensis* Pain, 1950a: 109. Merida, Venezuela. Holotype (Pain, 1950a: 110): the specimen figured by Alderson (1925: pl. 11, fig. 7); paratypes: Alderson collection (Pain, 1950a: 110), HUJ 21517 (1 spm.) (H. Mienis, pers. comm. to RHC, 4 August 2002), MCZ 171558 (2 spms.), FMNH (1 spm.), ZSM 20012068 (1 spm.; ex Alderson collection) (E. Schwabe, pers. comm. to RHC, 29 July 2002). Distribution: Venezuela.

Remarks. Synonym of *camena* Pain, 1949, *teste* Pain (1957: 175).

mermodi

Ampullaria mermodi Sowerby, 1919: 152, [unnumbered text figure]. Central America. Syntypes: MHNG 33490 (3 spms.) (Y. Finet, pers. comm. to RHC, 26 August 2002; see also Tillier, 1980: 19 [as "Sowerby, 1905"]). Distribution: ? Guyana, ? Central America (Pain, 1950b: 72).

Remarks. Pain (1950b: 72) stated that this species was founded on a single specimen. However, this was not made explicit by Sowerby (1919: 152–153), who described it from "photographs" sent to him by Mermod. Tillier (1980: 19) indicated that Sowerby's (1919: 152) figure illustrated the largest of three syntypes.

meta

Ampullaria meta Ihering, 1915: 12, pl. [3], figs. 6, 7. Cidade da Barra, Rio S. Francisco River, Bahia. Holotype: MNRJ. Distribution: Brasil.

+ metcalfei

Ampullaria Metcalfei Reeve, 1856e: pl. 25, fig. 119a, b. [No locality given.] Type material: not found by us in BMNH. Distribution: Venezuela (Baker, 1930: 4).

Remarks. Possibly a synonym of *vexillum* Reeve, 1856, *teste* Alderson (1925: 14). Subspecies of *swainsoni* Philippi, 1852, *teste* Baker (1930: 4), although he noted collections containing both forms and a "good series of intermediates".

mexicana

Ampullaria Mexicana Martens, 1857: 207. Unavailable name; *nom. nud.*

Remarks. Listed by Martens (1857: 207) as a manuscript name of Philippi; also listed by Gaudion (1879: 33). Treated as a synonym of *malleata* Jonas, 1844, by both these authors. Also listed by Paetel (1873: 65, 1887: 480).

+ miamiensis

Ampullaria miamiensis Pilsbry, 1899: 365 [1927a: 252, pl. 22, figs. 5 (lectotype), 6, 7]. creek flowing from the Everglades near Miami, Dade County, in southeastern Florida. Lectotype (Pilsbry, 1927a: 253; see also Baker, 1964: 168): ANSP 77369; paralectotypes: ANSP 361441 (59 spms., uncounted juveniles), CMNH 62.19966 (1 spm.), 62.33743 (1 spm.) (Parodiz & Tripp, 1988: 141), USNM (1 spm.) [labeled as "cotype"], MCZ ("paratypes"; Clench & Turner, 1956: 122). Distribution: Florida.

Remarks. Treated by Clench & Turner (1956: 122) as a "race" or "local population" of *paludosa* Say, 1829, but not formally synonymized.

miltocheilus

Ampullaria miltocheilus Reeve, 1856e: pl. 25, fig. 120a, b. Province of Chiapes [= Chiapas], Mexico. Lectotype ["Le type"; Fischer & Crosse (1890: 248)]: BMNH 20020668/1; paralectotypes: 20020668/2-5 (5 spms.); based on our study of the BMNH material. Distribution: Mexico.

Remarks. Variety of *ghiesbreghti* Reeve, 1856, *teste* Martens (1899: 418). Synonym of *cumingii* King & Broderip, 1831, *teste* Sowerby (1909a: 348). Probably a synonym of *quitensis* Busch, 1859, *teste* Alderson (1925: 44). Not a synonym of *ghiesbreghti* Reeve, 1856, *teste* Pain (1953: 223), who also remarked on its shell "resembling species of *Limnopomus*".

miltochilus

Ampullaria miltochilus Fischer & Crosse, 1890: 247. Unjustified emendation of *miltocheilus* Reeve, 1856.

+ *minor*

Ampullaria (*Pomus*) *gigas* var. *minor* Nevill, 1884: 9. les environs de Corrientes, et sur les

rivages de la Plata, près de Buenos-Ayres [locality given by Orbigny (1838d: 372) for the variety illustrated in his pl. 50, fig. 5]. Holotype/syntypes: the specimen(s) illustrated by Orbigny (1838e: pl. 50, figs. 5, 6) [the two figures probably illustrate a single (live) specimen but this is not certain], location not known to us. Distribution: La Plata (Orbigny, 1838d: 372), Rio Parana (Nevill, 1884: 9).

Remarks. Name proposed by bibliographic reference to Orbigny (1838e: pl. 50, figs. 5, 6). Junior primary homonym of *minor* Nevill, 1877, which is now placed in *Pila* Röding, 1798.

modesta

Ampullaria modesta Busch, 1859: 168. Ecuador. Type material: location not known to us. Distribution: Ecuador (Miller, 1879: 150).

monachus

Ampullaria monachus Crosse & Fischer, in Fischer & Crosse, 1888: [explanation of] pl. 46, fig. 5, 5a [Crosse & Fischer, 1890: 112 [as "*monacha*"]; see also Fischer & Crosse (1890: 250)]. [No locality given. Santa Efigenia, in Isthmo Tehuantepecensi, reipublicae Mexicanae (Crosse & Fischer (1890: 113)]. Holotype: the specimen illustrated by Crosse & Fischer, in Fischer & Crosse (1888, fig. 5, 5a), not found by us in MNHN. Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

monstrosa

Ampullaria fasciata var. *monstrosa* Sowerby, 1825: 44. Unavailable name; *nom. nud.*

Remarks. Not listed by Sherborn (1922–1933).

nais

Pomacea nais Pain, 1949a: 257; pl. 13, figs. 3, 4. small stream on the south bank of the Amazon near Obidos, Brasil. Holotype: BMNH 1947.2.3.1 [not 1946.2.3.1, as stated by Pain (1949a: 257)]; paratype: NMW.Z.1981.118.00093 (Pain collection, 1 spm.). Distribution: Brasil (Pain, 1960: 424).

Remarks. May be a "local race" of *lineata* Spix, 1827, *teste* Pain (1960: 424).

nigrilabris

Ampullaria nigrilabris Philippi, 1852a: 65, pl. 21, fig. 2 [1852b: 29]. [No locality given.] Type material: probably MNHNS. Distribution: "Rio Janeiro" (Gaudion, 1879: 34; Sowerby, 1909a: 355; see also Paetel, 1873: 65, 1887: 480).

nobilis

Ampullaria nobilis Reeve, 1856a: pl. 2, fig. 8. River Marañon. Possible syntype: BMNH 20020669; topotypes: ANSP 120276 (Baker, 1930:3). Distribution: Venezuela (Baker, 1930: 3), East Peru (Sowerby, 1909a: 354), Brasil (Baker, 1914: 660).

Remarks. Synonym of *guyanensis* Lamarck, 1822, *teste* Pain (1960: 427), and hence of *urceus* Müller, 1774 (see Tillier, 1980: 27). **N. Syn.**

notabilis

Ampullaria notabilis Reeve, 1856c: pl. 14, fig. 63. [No locality given.] Syntype: BMNH 20020670. Distribution: Peru (Sowerby, 1909a: 355) [? error; Alderson, 1925: 45; Pilsbry, 1927a: 250].

Remarks. Synonym of *nubila* Reeve, 1856, *teste* Paetel (1887: 480). Possibly a synonym of *paludosa* Say, 1829, *teste* Alderson (1925: 45) and Pilsbry (1927a: 250). Retained here as a distinct species, pending further study.

novaegranadae

Ampullaria novæ-granadæ Busch, 1859: 169. New Granada [in 1859 = present-day Colombia and Panama]. Syntypes: BMNH 20020671 (2 spms.). Distribution: Colombia and/or Panama.

oajacensis

Ampullaria malleata var. *Oajacensis* Fischer & Crosse, 1890: 235 [1888: pl. 46, fig. 3, 3a, 3b; plate published without name]. Monte de Mistam, prope Coapam, provinciæ Oajaca. Type material: Sallé collection, not found by us in BMNH, MNHN, etc. (cf. Dance, 1986: 209, 225). Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

oblonga

Ampullaria oblonga Swainson, 1823a: pl. 136, middle figs. [No locality given.] Syntypes: "in the late Mrs. Bligh's collection" (Swainson, 1823a: pl. 136), location not known to us. Distribution: Venezuela (Philippi, 1851: 21; Sowerby, 1909a: 355), Guadeloupe (Gaudion, 1879: 35).

Remarks. Synonym of *urceus* Müller, 1774, *teste* Pain (1960: 426), but retained here as a valid species based on our own observations (S. C. Thiengo, unpublished).

ocanensis

Ampullaria (aurisformis var. ?) *ocanensis* Kobelt, 1914b: 222, pl. 77, figs. 4, 5 [1914e: 177]. Ocaña in Neu-Granada [= Colombia]. Figured specimen (Kobelt, 1914b: figs. 4, 5): ZMUH [destroyed; B. Hausdorf, pers. comm. to RHC, 3 May 2002]. Distribution: Colombia.

occlusa

Ampullaria occlusa Crosse & Fischer, in Fischer & Crosse, 1888: [explanation of] pl. 45, fig. 3, 3a–c [Crosse & Fischer, 1890: 111; see also Fischer & Crosse (1890: 244)]. [No locality given. Tanesco, Guatemalæ (Crosse & Fischer (1890: 112).] Syntypes: MNHN (2 lots, 11 spms.) (see also Sowerby, 1909b: 363). Distribution: Guatemala.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

ochracea

Ampullaria ochracea Jay, 1836: [85 (explanation of pl. 3)], pl. 3, fig. 8 [1839: [explanation of pl. 3, fig. 8]. Spanish Maine [= isthmus of Panama to mouth of Orinoco River]. Syntypes: AMNH 56106 (1 spm.) [labeled as "figd type" in Jay's handwriting (P. M. Mikkelsen, pers. comm. to RHC, 7 May 2002)], 56106A (1 spm.); additional 6 syntypes [Jay (1839: 116) mentioned 8 spms. in total]: location not known (Boyko & Cordeiro, 2001: 16).

Remarks. Synonym of *flagellata* Say, 1829, *teste* Martens (1899: 405) and Pain (1964: 226).

+ *olivacea*

Ampullaria olivacea Spix, in Wagner, 1827: 2, pl. 3, fig. 1. in fluminibus Amazonum, Solimoès, Japurá alliisque in interiore continente Brasiliae aequatorialis. Type material: probably lost (Fechter, 1983: 221; S. C. Thiengo, unpublished). Distribution: Brasilian Amazon (Pain, 1960: 428).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.). Junior primary homonym of *Ampullaria olivacea* Lamarck, 1816. However, Lamarck (1822a: 178), followed by Philippi (1852a: 28), placed *olivacea* Lamarck, 1816, in the synonymy of *Ampullaria guinaica* Lamarck, 1822, which has long been placed in the African genus *Lanistes* (e.g., Nevill, 1884: 14). Thus, because *olivacea* Spix, 1827, and *olivacea* Lamarck, 1816, have not been considered congeneric after 1899, no replacement name is provided and the case must be referred to the ICZN for a ruling (*Code*, Art. 23.9.5). Wagner (1827: 2) listed the older name *guyanensis* Lamarck, 1822, in synonymy. However, Pain (1960: 427), followed here, treated *olivacea* Spix, 1827, as a subspecies of *urceus* Müller, 1774, and distinct from *guyanensis* Lamarck, 1822.

oviformis

Ampullaria oviformis Deshayes, 1830a: 34. Cayenne. Syntypes: MNHN (2 lots, 2 spms.). Distribution: French Guiana (Sowerby, 1909a: 355) [? error; Tillier, 1980: 16].

Remarks. The two syntypes are clearly two different species, indicating the need for further study to clarify this species' true identity (see also Tillier, 1980: 16).

palmeri

Ampullaria palmeri Marshall, 1930: 4, pl. 1, figs. 5, 8. small stream in dense jungle, 13 kilometers south of Puerto Santos, Province of Santander del Norte, Republic of Colombia. Holotype: USNM 380696; paratypes: USNM 380697. Distribution: Colombia.

paludosa

Ampullaria paludosa Say, 1829c: 260. New name for *depressa* Say, 1824, *non* Lamarck, 1804. Distribution: USA (Alabama, Georgia, Florida), Cuba (Clench & Turner, 1956: 122; Cowie, 1997b: 5).

papyracea

Ampullaria papyracea Spix, in Wagner, 1827: 3, pl. 4, figs. 1, 2. in fluviis et stagnis Provinciarum Bahiensis, Pernambucanae et Piauhiensis. Syntypes: ZSM 20012059 (2 spms.) (E. Schwabe, pers. comm. to RHC, 28 July 2002; see also Fechter, 1983: 221). Distribution: Brasil, Peru, Venezuela, Guyana, Surinam, French Guiana (Pain, 1950b: 66, 1960: 429).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.).

patula

Ampullaria patula Reeve, 1856d: pl. 21, fig. 100a, b. [No locality given.] Syntypes: BMNH 20020673 (3 spms.). Distribution: Amazon, Brasil, New Granada [= Colombia and Panama] (Walker, in Baker, 1922: 39).

Remarks. Junior primary homonym of *patula* Lamarck, 1804, which is now placed in the family Naticidae (see also Lamarck, 1822b: 549). Not listed by Sowerby (1912: 72).

pealiana

Ampullaria pealiana Lea, 1838: 16, pl. 23, fig. 77. Turbaco, Colombia, South America. Lectotype [as "Figured holotype"] (Abbott, 1955: 126, pl. 4, fig. 2): ANSP 192933; paralectotypes: MCZ 161600. Distribution: Ecuador, Colombia (Pain, 1956a: 78), Venezuela (Paetel, 1887: 480), Panama (Martens, 1899: 423).

Remarks. We treat "*pealeana*" Philippi, 1852 (1852a: 62) as an incorrect subsequent spelling.

penesma

Ampullaria penesma DeKay, 1843: 124. Unavailable name; first published as a junior synonym of *paludosa* Say, 1829, not made available before 1961 (*Code* Art. 11.6).

Remarks. DeKay (1843: 124) attributed the name to Say as a manuscript name, but the name does not occur in Say's published writings (Binney, 1858: [237], 1865: 5).

periscelis

Pila periscelis Röding, 1798: 146. [No locality given.] Type material: possibly Art and Natural History Museum, Gotha (Stewart, 1930: 35; Dance, 1986: 206).

Remarks. Possibly a synonym of *chemnitzii* Philippi, 1852, *teste* Baker (1930: 5).

peristomata

Ampullaria peristomata Orbigny, 1835a: 33. Guarayos (republica Boliviana). Syntypes: BMNH 1854.12.4.331 (10 spms.), MNHN (2 lots, 6 spms.). Distribution: Brasil (Baker, 1914: 660), Peru (Paetel, 1888: 481), Bolivia.

Remarks. Synonym of *cumingii* King & Broderip, 1831, *teste* Sowerby (1909a: 348) and Kobelt (1912h: 141), and of *elegans* Orbigny, 1835, *teste* Gray (1855: 29), but treated as a valid species by Baker (1914: 660), followed here. The BMNH and MNHN syntype lots are clearly two different species, indicating the need for further study to clarify this species' true identity.

pernambucensis

Ampullaria Pernambucensis Reeve, 1856d: pl. 22, fig. 103. Pernambuco. Syntypes: BMNH 20020674 (3 spms.). Distribution: Brasil.

+ **pertusa**

Ampullaria pertusa Sowerby, 1894: 48, pl. 4, fig. 22. [No locality given.] Holotype (the single specimen on which the description was explicitly based): BMNH 20020675 (figured also by Pain, 1949b: pl. 1, figs. 3, 4). Distribution: Venezuela (Sowerby, 1909a: 355, Pain, 1949b: 39).

Remarks. Variety of *castelloi* Sowerby, 1894, *teste* Pain (1949b: 39).

phaeostoma

Ampullaria phaeostoma Philippi, 1852a: 45, pl. 13, fig. 3 [1852b: 26]. [No locality given.] Type material: probably MNHNS. Distribution: "Haut-Amazone" (Gaudion, 1879: 37) [? error].

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

physis

Ampullaria physis Hupé, 1857: 67, pl. 12, fig. 2 [two figs.]. le fleuve des Amazones. Syntypes: MNHN (2 lots, 4 spms.). Distribution: Amazon River (Sowerby, 1909a: 356).

Remarks. Synonym of *lineata* Spix, 1827, *teste* Pain (1960: 422).

physoides

Ampullaria Physoides Reeve, 1856d: pl. 22, fig. 107a, b. Pernambuco. Syntypes: BMNH 20020676 (4 spms.). Distribution: Brasil, India [error; one of the BMNH syntypes has a horny operculum, indicating its New World origin] (Paetel, 1888: 481).

picta

Ampullaria picta Reeve, 1856e: pl. 24, fig. 117a, b. [No locality given.] Syntypes: BMNH 1907.11.21.91-92 (2 spms.). Distribution: Mexico (Mazatlan) (Sowerby, 1909a: 356).

pinei

Ampullaria Pinei Dall, 1898: 75. Homosassa River, Florida. Possible syntype: USNM 152699 [labeled as the figured "type", although Dall (1898: 75–76) did not designate or figure a type]. Distribution: USA.

Remarks. Synonym of *paludosa* Say, 1829, *teste* Clench & Turner (1956: 120).

poeyana

Ampullaria poeyana Pilsbry, 1927a: 251, pl. 21, figs. 7, 8 ["Type"], 9. New name for *cubensis* Reeve, 1856, *non* Morelet, 1849. Distribution: Cuba.

Remarks. Pilsbry (1927a: 251, 253) provided this name as a "n. sp." and designated a "holotype" (ANSP 50618) ["50618a" (Baker, 1964: 168)]. Two specimens from the same lot are now ANSP 365370. However, Pilsbry was simply providing a replacement name for *cubensis* Reeve, 1856, so the type material of this species is Reeve's and Pilsbry's designation of a holotype is invalid. Although *cubensis* Reeve, 1856, has been considered a variety or synonym of *glauca* Linnaeus, 1758 (which is listed here under *Pomacea* subg. *Effusa* Jousseaume, 1889), we follow Pilsbry (1927a: 251–252) in retaining *poeyana* Pilsbry, 1927, as a valid species in *Pomacea s. str.*

pomatia

Ampullaria pomatia Martens, 1857: 194. Brasilien. Syntypes: ZMHB 1366a (3 spms.), 1366b (3 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: Brasil.

pomum

Ampullaria pomum Philippi, 1851: 13, pl. 3, figs. 3, 4 [1852b: 20]. [No locality given.] Type

material: probably MNHNS. Distribution: unknown.

porphyrostoma

Ampullaria porphyrostoma Reeve, 1856b: pl. 6, fig. 30. [No locality given.] Syntypes: BMNH 20020677 (3 spms.). Distribution: Venezuela (Baker, 1930: 5), New Granada [= present-day Colombia and Panama from 1830 to 1903 and Colombia only from 1903 on] (Sowerby, 1909a: 353).

Remarks. Synonym of *chemnitzii* Philippi, 1852, *teste* Baker (1930: 5) and Pain (1956a: 74).

prasina

Ampullaria malleata var. *Prasina* Fischer & Crosse, 1890: 235, pl. 48, fig. 4, 4a. Misantla, provinciæ Vera Cruz. Type material: not found by us in MNHN. Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

producta

Ampullaria producta Reeve, 1856c: pl. 15, fig. 68a, b. [No locality given.] Syntypes: BMNH 20020678 (3 spms.). Distribution: "F. Magdalen" [= Colombia] (Paetel, 1888: 481), Amazon River (Sowerby, 1909a: 356), Neu-Granada [= Colombia and/or Panama] (Kobelt, 1913h: 205).

prourceus

Pomacea (*Pomacea*) *prourceus* Boss & Parodiz, 1977: 110, figs. 1–4. Chicocoa (a single farmhouse on the east bank of the Río Huallaga ...), east of Chasuta [Chazuta] (6° 352' S; 76° 112' W), the Río Huallaga, Department of San Martín, Peru. Holotype: MCZ 272899. Distribution: Peru.

Remarks. Tertiary fossil, possibly middle or late Eocene (Boss & Parodiz, 1977: 110).

pulchra

Paludina pulchra Griffith & Pidgeon, 1834b: 599, pl. 1, fig. 6 [pl. 1 predated p. 599 and was possibly published in 1833 (Cowan, 1969: 139)]. [No locality given.] Syntype: BMNH 20020680. Distribution: South America (Sowerby, 1909a: 356).

Remarks. Name attributed to Gray by Griffith & Pidgeon (1834b: 599). Placed in *Pomacea* [as *Ampullaria*] by Sowerby (1909a: 356).

puncticulata

Ampullaria puncticulata Swainson, 1823a: pl. 143, figs. 3, 4 [middle figs.]. [No locality given.] Type material: possibly MMUE (Dean, 1936: 232; H. McGhie, pers. comm. to RHC, 28 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: Brasil [error] (Drouët, 1859: 81), Colombia, Guyana, French Guiana (Pain, 1950b: 72); also Venezuela (Gaudion, 1879: 38). Spelled as "*punctulata*" by Mousson (1873: 18), Paetel (1888: 481) and Ihering (1919: 332).

Remarks. Synonym of *guyanensis* Lamarck, 1822, *teste* Pain (1960: 426), and hence of *urceus* Müller, 1774 (see Tillier, 1980: 27). **N. Syn.**

puntaplaya

Ampullaria puntaplaya Cousin, 1887: 278, pl. 4, fig. 2. Punta-Playa. Syntypes: MNHN (2 lots, 4 spms.). Distribution: Ecuador (Sowerby, 1909a: 356).

+ purpurascens

Ampullaria purpurascens Guppy, 1864: 243. Trinidad [in publication title]. Syntypes (Guppy, 1864: 248): BMNH, not found by us. Distribution: Trinidad (Sowerby, 1909a: 356).

Remarks. Treated as a variety of *urceus* Müller, 1774, by Guppy (1866: 44).

+ pyrum

Ampullaria pyrum Philippi, 1851: 18, pl. 5, fig. 2 [1852b: 21]. Brasilien. Syntype: ZSM 20012060 (E. Schwabe, pers. comm. to RHC, 28 July 2002). Distribution: Brasil (Gaudion, 1879: 38).

Remarks. Variety of *hopetonensis* Lea, 1834 (= *paludosa* Say, 1829), *teste* Sowerby (1909a: 353), but note the skepticism of Pain (1964: 225) regarding this. Either it is not a variety (or synonym) of *paludosa* Say, 1829, or the locality (Brasil) is incorrect.

quercina

Ampullaria quercina Spix, in Wagner, 1827: 2, pl. 3, fig. 2. in fluminibus Amazonum, Solimoès, Japurá alliisque in interiore continente Brasiliae aequatorialis [as for *olivacea* Spix, 1827]. Syntype: ZSM 20012061 (E. Schwabe, pers. comm. to RHC, 28 July 2002; cf. Fechter, 1983: 221). Distribution: Amazon drainage (Pain, 1960: 428).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.), who also explain the publication history of this work. Spix illustrated *quercina* as a full species, but Wagner, in writing the description, treated *quercina* "Spix" as a variety of *olivacea* Spix, 1827. Retained as a variety by Sowerby (1909a: 355), but treated here as a distinct species, following Pain (1960: 428). Berthold (1991: 23) placed *quercina* "Wagner non Spix" in *Pomacea* subg. *Effusa* Jousseaume, 1889.

quitensis

Ampullaria quitensis Busch, 1859: 168. Ecuador. Type material: location not known to us. Distribution: Ecuador (Miller, 1879: 149).

Remarks. Synonym of *cumingii* King & Broderip, 1831, *teste* Sowerby (1909a: 348).

reflexa

Ampullaria reflexa Swainson, 1823b: 377 [1823a: pl. 172]. [No locality given.] Type material: possibly MMUE (Dean, 1936: 232; H. McGhie, pers. comm. to RHC, 28 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: Cuba (Paetel, 1873: 65, 1888: 481; Sowerby, 1909a: 353; Henderson, 1916: 322) [error; Alderson, 1925: 34]; Colombia (Alderson, 1925: 34; Pain, 1964: 224).

Remarks. Alderson (1925: 31, 34) discussed the confused history of misidentification of *reflexa* Swainson, 1823, confusion that apparently continues, as it was considered a synonym of *paludosa* Say, 1829, by Yong & Perera (1984: 121). Considered either a variety of *flagellata* Say, 1829, or a distinct species by Alderson (1925: 34). Retained here as a distinct species, following Pain (1964: 224).

retusa

Ampullaria retusa Philippi, 1851: 18, pl. 5, fig. 1 [1852b: 21]. Guyana, namentlich der Rio Rupunin, und Brasilien [? error]. Syntype: ZMHB 1339 (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); type material possibly also in MNHNS. Distribution: Brasil, Guyana (Martens, 1857: 188, 1899: 424; Gaudion, 1879: 39) [? error].

Remarks. Name attributed to Olfers by Philippi (1851: 18; 1852b: 21). Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227). However, *flagellata* Say, 1829, is a Central American species, extending southwards only into northern Colombia (Pain, 1964: 228), suggesting either that the localities given for *retusa* Philippi, 1851, are incorrect or that Pain was incorrect in synonymizing the two species.

reyrei

Ampullaria Reyrei Cousin, 1887: 279, pl. 4, fig. 7. Napo. Probable syntype: MNHN; topotype: MCZ 92312. Distribution: Ecuador (Sowerby, 1909a: 357).

robusta

Ampullaria robusta Philippi, 1852a: 50, pl. 15, figs. 4, 5 [1852b: 27]. [No locality given.] Type material: probably MNHNS. Distribution: unknown.

Remarks. Synonym of *columellaris* Gould, 1848, *teste* Alderson (1925: 54).

rugosa

Ampullaria rugosa Lamarck, 1801: 93. [No locality given; "Mississipi" [? error] (Lamarck, 1822a: 177)]. Syntypes: the specimens illustrated in the works cited by Lamarck (1801: 93); possible syntype: MHNG 1093/93 (Y. Finet, pers. comm. to RHC, 22 August 2002; see also Mermod, 1952: 85). Distribution: unknown.

Remarks. Synonym of *urceus* Müller, 1774, *teste* Valenciennes (1833: 258), Gaudion (1879: 41), Paetel (1888: 481), Sowerby (1909a: 358), Alderson (1925: 10), Prashad (1925: 72) and Mermod (1952: 86).

+ **sanjosensis**

Pomacea cumingii sanjosensis Morrison, 1946: 6, pl. 1, fig. 1. three small streams (not of contiguous drainage) on the west side of San José Island. Holotype: USNM 542136; paratypes: ANSP 190947 (5 spms.), 215480 (3 spms.), 386773 (4 spms.), BMNH 1951.11.1.6-9 (4 spms.), MNCN 15.05/23733 (2 spms.) (Villena et al., 1997: 76), UF (1 lot, 3 spms.), USNM 598924, ZSM 20012076 (3 spms.) (E. Schwabe, pers. comm. to RHC, 28 July 2002), MCZ, UMMZ. Distribution: Panama.

scalaris

Ampullaria scalaris Orbigny, 1835a: 31. Rio Parana (republica Argentina) ... Guarayos (republica Boliviana) ... provincia Santa-Cruz de la Sierra (republica Boliviana). Syntypes: BMNH 1854.12.4.333-4 (9 spms.), MNHN (4 lots, 10 spms.), MHNG 33488 (1 spm.) (Y. Finet, pers. comm. to RHC, 26 August 2002). Distribution: Bolivia, Paraguay, Argentina, Brasil, Uruguay (Paraguay-Parana drainage) (Pain, 1960: 425).

scholvieni

Ampullaria scholvieni Kobelt, 1914b: 223, pl. 77, figs. 6, 7 [1914e: 178]. Puerto Cabello. Holotype: ZMUH 15880 [destroyed; B. Hausdorf, pers. comm. to RHC, 3 May 2002]. Distribution: Venezuela (Baker, 1930: 5).

Remarks. Synonym of *chemnitzii* Philippi, 1852, *teste* Baker (1930: 5) and Pain (1956a: 74).

semitecta

Ampullaria semitecta Mousson, 1873: 18. nördlichen Süd-Amerika [in publication title]. Type material: location not known to us, not in ZMZ (T. Meier, pers. comm. to RHC, 15 August 2002), not found by us in MNHN (cf.

Dance, 1986: 220). Distribution: Colombia, Venezuela (Pain, 1956a: 75).

semperi

Ampullaria (? *figulina* var.) *semperi* Kobelt, 1914b: 221, pl. 77, figs. 2, 3 [1914e: 176]. [No locality given. "Fundort nicht genau bekannt, doch sicher in Brasilien" (Kobelt, 1914e: 176)]. Type material: possibly SMFD, ZMHB (Dance, 1986: 215), but not found in ZMHB (M. Glaubrecht, pers. comm. to RHC, 1 March 2003); possible syntype(s): ZMUH [all ZMUH dry material destroyed in the second world war; B. Hausdorf, pers. comm. to RHC, 3 May 2002]. Distribution: ? Brasil.

Remarks. In the group of *lineata* Spix, 1827, *teste* Kobelt (1914b: 221).

simplex

Ampullaria simplex Reeve, 1856d: pl. 21, fig. 98a, b. [No locality given.] Syntype: BMNH 20020682. Distribution: unknown.

Remarks. Synonym of *lineata* Spix, 1827, *teste* Pain (1960: 422).

sordida

Ampullaria sordida Swainson, 1823a: pl. 143, figs. 1, 2 [top and bottom figs.]. [No locality given.] Type material: possibly MMUE EM265907 (1 spm.) (H. McGhie, pers. comm. to RHC, 29 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: "Brésil - Rio-Janeiro - Plata" (Gaudion, 1879: 40), French Guiana (possibly introduced; Tillier, 1980: 24).

spirata

Ampultaria [*sic*] *spirata* Deville & Huppé, 1850: 643. [No locality given.] Type material: location not known to us. Distribution: unknown.

Remarks. Name attributed to Orbigny. By comparing it with *Ampullaria aulanieri* Deville & Huppé, 1850, sufficient description was provided to make the name available. Junior primary homonym of *Ampullaria spirata* Lamarck, 1804, which is now placed in family Naticidae (see also Lamarck, 1822b: 549). Not listed by Sherborn (1922–1933) or Ruhoff (1980: 504).

sprucei

Ampullaria Sprucei Reeve, 1856e: pl. 28, figs. 134a, b. Tarapoto, east side of the Andes. Syntypes: BMNH 20020684 (2 spms.); topotype: ANSP. Distribution: Peru (Paetel, 1888: 481).

Remarks. Synonym of *columellaris* Gould, 1848, *teste* Alderson (1925: 54).

strebeli

Ampullaria malleata var. *Strebeli* Fischer & Crosse, 1890: 235. Misantla, provinciæ Vera Cruz. Syntypes: ZMHB 23203 (1 spm.; ? = Strebel, 1873, pl. 3a, fig. 13a) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003; F. Köhler, pers. comm. to RHC, 6 March 2003), location of the 5 other spms. listed by Strebel (1873: 26) not known to us. Distribution: East Mexico (Martens 1899: 415).

Remarks. Described by bibliographic reference to Strebel (1873: 25, pl. 3, fig. 13, pl. 3a, fig. 13a, b). Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227). Martens (1899: 415) considered it a full species and gave more detailed locality information.

superba

Ampullaria superba Marshall, 1926: 3, pl. 1, fig. 9 [holotype]. Cienaga Totuma, Department of Atlantico, United States of Columbia [= Colombia]. Holotype: USNM 362863. Distribution: Colombia (Pain, 1956a: 77).

swainsoni

Ampullaria Swainsoni Philippi, 1852a: 53, pl. 16, fig. 5. [No locality given; Brasil given by Swainson (1831–1832, pl. 64)]. Holotype: MMUE (Swainson, 1831–1832: pl. 64). Distribution: Brasil, Guyana [error] (Baker, 1930: 3).

Remarks. Philippi (1852a: 53) explicitly based his description on Swainson's (1831–1832) figure of "*Ampullaria fasciata* var." [not *fasciata* Swainson, 1822; see *swainsonii* Hupé, 1857], which he copied, and although Swainson had given the locality as Brasil, Philippi stated that the locality was unknown. Baker (1930: 3) mistakenly gave the locality as Demerara [Guyana], which Swainson (1831–1832: pl. 64) had mentioned but in reference to other specimens. See also Swainson (1822c: 12 [Appendix]). Synonym of *lineata* Spix, 1827, *teste* Sowerby (1909a: 354), but treated here as a distinct species, following Baker (1930: 3). See also *hanleyana* Alderson, 1926.

swainsonii

Ampullaria swainsonii Hupé, 1857: 66. Brasil. Holotype: the shell illustrated by Swainson (1821–1822a: pl. 103, fig. 2), possibly MMUE (H. McGhie, pers. comm. to RHC, 28 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: Brasil.

Remarks. Introduced as a new name for *fasciata* Swainson, 1822, which Hupé considered preoccupied by Lamarck, 1816 [also Roissy, 1805]. However, *fasciata* Swainson,

1822 (see Swainson, 1821–1822a: pl. 103) is a misidentification of *fasciata* Roissy, 1805, so Hupé's citation of Swainson's figure constitutes the original description of this species. Junior primary homonym of *swainsoni* Philippi, 1852.

tenuissima

Ampullaria tenuissima Jousseaume, 1894: 120, text fig. La Coca, province d'Orient (Équateur) [Ecuador]. Type material: not found by us in MNHN (cf. Dance, 1986: 215). Distribution: Ecuador (Sowerby, 1909a: 358).

testudinea

Ampullaria testudinea Reeve, 1856e: pl. 24, fig. 114. [No locality given.] Syntype: BMNH 1900.2.13.20. Distribution: "Amazons" (Sowerby, 1909a: 358); Brasil (Baker, 1914: 660).

Remarks. Synonym of *lineata* Spix, 1827, *teste* Pain (1960: 422).

tristrami

Ampullaria tristrami Crosse & Fischer, in Fischer & Crosse, 1890: 245. New name for *columbiensis* Reeve, 1856, *non* Philippi, 1851. Distribution: Columbia; also "Pérou [error] - Guatemala" (Gaudion, 1879: 26); also ? Panama.

Remarks. Martens (1899: 413) considered that *tristrami* Crosse & Fischer, 1890, referred to the shell given to Tristram by Salvin, which Tristram (1864: 414) had misidentified as *columbiensis* Reeve, 1856. Martens argued, therefore, that *tristrami* Crosse & Fischer, 1890, should not be accepted as a replacement name for *columbiensis* Reeve, 1856, but should stand as a valid name for Tristram's shell. However, the misidentification notwithstanding, the nomenclatural act of Crosse & Fischer was valid, even despite there already being a new name for *columbiensis* Reeve, 1856 (i.e., *martensiana* Nevill, 1884). Pain (1964: 228), placed Tristram's "*columbiensis*" in the synonymy of *livescens* Reeve, 1856. Because *columbiensis* Reeve, 1856, is treated here as a synonym of *flagellata* Say, 1829, *tristrami* Crosse & Fischer, 1890, is also a synonym of *flagellata* Say, 1829. **N. syn.**

+ **unicolor**

Ampullaria gigas Var. *unicolor* Philippi, 1852a: 47, pl. 10, fig. 2. [No locality given.] Type material: probably MNHNS. Distribution: unknown.

+ **urabaensis**

Pomacea cumingi urabaensis Pain, 1956a: 75, text fig. (holotype). Golfo de Uraba, northern Antioquia, Colombia. Holotype and three paratypes (listed with dimensions by Pain (1956a: 75) but without giving their location): NMW.Z.1981.118.00114 (Pain collection, 3 spms. only); additional paratypes: MCZ (1 lot, 2 spms.). Distribution: Colombia.

Remarks. None of the NMW specimens is large enough to be the holotype (H. Wood, pers. comm. to RHC, 30 October 2001), the location of which is therefore unknown.

urceus

Nerita urceus Müller, 1774: 174. in insulis Indiae. Syntypes: the specimen figured by Lister, as cited by Müller, and the specimen(s) "In Museo Moltkiano" (Müller, 1774: 175), location not known to us, not in the Copenhagen Museum (O. S. Tendahl, pers. comm. to RHC, 18 April 2002). Distribution: Brasil, Peru, Ecuador, Colombia, Venezuela, Guyana, French Guiana, Trinidad (Pain, 1960: 426), ? Surinam (Vernhout, 1914: 30) [? error; Geijskes & Pain, 1957: 46, Tillier, 1980: 29], Mexico [error] (Paetel, 1873: 65).

venetus

Ampullaria venetus Reeve, 1856b: pl. 4, fig. 17. [No locality given.] Syntypes: BMNH 20020686 (2 spms.). Distribution: Guatemala (Paetel, 1888: 482).

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

vermiformis

Ampullaria vermiformis Reeve, 1856b: pl. 12, fig. 54. Paraguay. Syntype: BMNH 20020687. Distribution: Paraguay.

Remarks. Synonym of *canaliculata* Lamarck, 1822, *teste* Martens (1857: 210). Synonym of *gigas* Spix, 1827, *teste* Ihering (1898: 49). Synonym of *insularum* Orbigny, 1935, *teste* Sowerby (1909a: 353; 1909b: 363).

vexillum

Ampullaria vexillum Reeve, 1856a: pl. 4, fig. 20. [No locality given; locality unknown (Baker, 1930: 7; Pain, 1950b: 72).] Syntypes: BMNH 20020688 (2 spms.). Distribution: Venezuela (Baker, 1930: 7).

Remarks. Synonym of *puncticulata* Swainson, 1823, *teste* Sowerby (1909a: 356) and Kobelt (1913e: 180), but retained here as a valid species, following Pain (1950b: 72).

vickeryi

Pomacea vickeryi Pain, 1949a: 257; pl. 13, figs. 1, 2. marsh near Buenos Aires, La Plata. Holotype: BMNH 1946.10.2.3; paratypes:

NMW.Z.1981.118.00107 (Pain collection, 2 spms.). Distribution: Argentina.

Remarks. Synonym of *insularum* Orbigny, 1935, *teste* Scott (1958: 295). Neither of the two NMW specimens is large enough to be the paratype for which Pain (1949a: 257) gave measurements; presumably they are two others of the total of 10 that were collected (H. Wood, pers. comm. to RHC, 30 October 2001).

violacea

Ampullaria violacea Valenciennes, 1833: 260. in sylvis Americæ. (Nova Hispania.). Lectotype (Fischer & Crosse, 1888: [explanation of] pl. 46, fig. 4, 4a): MNHN. Distribution: Mexico (Martens, 1899: 415; Sowerby, 1909a: 358).

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 226).

welwitschiana

Ampullaria Welwitschiana Drouët, 1859: 82, pl. 3, figs. 33, 34. la rivière du Diamant, les environs de Cayenne. Type material: not found by us in MNHN, not mentioned by Tillier (1980: 27–29). Distribution: French Guiana.

Remarks. Synonym of *urceus* Müller, 1774, *teste* Tillier (1980: 27).

woodwardi

Ampullaria Woodwardi Dohrn, 1858: 134. Ceylon [in publication title; error]. Lectotype (Prashad, 1931: 168): BMNH 20020689. Distribution: South America (Prashad, 1931: 168).

Remarks. "Probably an abnormal and somewhat eroded shell of *Pomacea* (*Marisa*) *cyclostoma*" (Prashad, 1931: 168). This statement does not definitively synonymize *woodwardi* Dohrn, 1858, so it is retained here as a valid species pending further research. Prashad (1925: 85) could only find one shell in the BMNH (as could we) and (Prashad, 1931: 168) mentioned "the unique type", hence designating that specimen the lectotype.

+ **yatesii**

Ampullaria Yatesii Reeve, 1856b: pl. 6, fig. 28. River Marañon. Type material: not found by us in BMNH. Distribution: Peru (Pain, 1960: 427).

Remarks. Subspecies of *urceus* Müller, 1774, *teste* Pain (1960: 427). Boss & Parodiz (1977: 111) implied that they are synonyms, without formally synonymizing them. The single specimen labeled as *yatesii* Reeve, 1856, in the BMNH type collection does not fit the hardened glue on the board in its box, nor does it look like *urceus* Müller, 1774, nor does it match Reeve's figure. This specimen is therefore not *yatesii* Reeve, 1856, the type material of which must be considered lost.

yucatanensis

Ampullaria yucatanensis Crosse & Fischer, 1890: 110 [see also Fischer & Crosse (1890: 240, pl. 48, fig. 3, 3a)]. San Geronimo, provinciae Yucatan dictae, reipublicae Mexicanae. Type material: not found by us in MNHN. Distribution: Mexico.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

yzabalensis

Ampullaria yucatanensis var. *yzabalensis* Martens, 1899: 420, pl. 24, fig. 9. E. Guatemala: Lake of Yzabal. Syntypes: ZMHB 47109 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 3 March 2002); type material not found by us in BMNH or MCZ (cf. Dance, 1986: 218). Distribution: Guatemala.

Remarks. Synonym of *flagellata* Say, 1829, *teste* Pain (1964: 227).

zeteki

Pomacea zeteki Morrison, 1946: 8, pl. 1, fig. 3. Chagres River near Gatuncilla, Republic of Panamá. Holotype: USNM 542137; paratypes: ANSP 190941 (5 spms.), BMNH 1951.11.1.10-15 (6 spms.), HUJ 21515 (1 spm.) (H. Mienis, pers. comm. to RHC, 4 August 2002), USNM 542138, ZSM 20012055 (4 spms.) (E. Schwabe, pers. comm. to RHC, 28 July 2002). Distribution: Panama (Pain, 1956a: 76).

zischkai

Pomacea zischkai Blume & Pain, 1952: 267, pl. 7. Chapara Region, at 400 m. Bolivia tropica. Holotype: ZSM 20012062 (E. Schwabe, pers. comm. to RHC, 28 July 2002); paratypes: ANSP 212117 (2 spms.), FMNH 35467 (1 spm.), 38001 (3 spms.), MHNG 33486 (1 spm.) (Y. Finet, pers. comm. to RHC, 26 August 2002), NMW.Z.1981.118.00117 (Pain collection, 2 spms.) (H. Wood, pers. comm. to RHC, 30 October 2001), ZMHB 98762 (2 spms.) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003), ZSM 20012050 (24 spms.) 20012051 (2 spms.), 20012052 (101 spms.), 20012053 (155 spms.), 20012057 (9 spms), 20012058 (2 spms.) (E. Schwabe, pers. comm. to RHC, 28 July 2002). Distribution: Bolivia (Pain, 1960: 428).

zonata

Ampullaria zonata Spix, in Wagner, 1827: 1, pl. 2, fig. 1. in rivulis ... Provinciae Bahiensis. Syntype: ZSM 20012056 (E. Schwabe, pers. comm. to RHC, 28 July 2002; see also Fechter, 1983: 221). Distribution: Columbia, Brasil (Gaudion, 1879: 43; Sowerby, 1909a: 359).

Remarks. Authorship is given here as "Spix, in Wagner", following Cowie et al. (in prep.).

Genus POMELLA Gray, 1847

POMELLA Gray, 1847: 148. Type species: *Ampullaria neritoides* Orbigny, 1835 [= *megastoma* Sowerby, 1825], by original designation.

Treated as a full genus, with two subgenera (*Pomella s. str.*, *Surinamia*) following Berthold (1991: 24, 250).

Subgenus POMELLA Gray, 1847

Details as for genus *Pomella* Gray, 1847.

americanista

Ampullaria americanista Ihering, 1919: 330, [unnumbered text figure ("Cotipo")]. Río Paraná (Encarnación e Iguazú). Syntype: MACN 8776a (Ihering, 1919: 331). Distribution: Argentina, Brasil, Paraguay (Ihering, 1919: 335; Hylton Scott, 1958: 316).

Remarks. Placed in *Pomella* following Hylton Scott (1958: 316) and S. C. Thiengo (unpublished).

megastoma

Ampullaria megastoma Sowerby, 1825: 44 [name], x [description]. [No locality given.] Holotype ("The only specimen ... that we have seen"): not found by us in BMNH. Distribution: Uruguay (Sowerby, 1909a: 359), Argentina (Ihering, 1919: 333).

neritoides

Ampullaria neritoides Orbigny, 1835a: 31. Rio Uruguay (republica Uruguayensi orientali). Syntypes: BMNH 1854.12.4.306-7 (4 spms.), MNHN (2 lots, 3 spms.). Distribution: Uruguay.

Remarks. Synonym of *megastoma* Sowerby, 1825, *teste* Pilsbry (1933: 74) and Hylton Scott (1958: 314).

Subgenus SURINAMIA Clench, 1933

SURINAMIA Clench, 1933: 71. Type species: *Asolene* (*Surinamia*) *fairchildi* Clench, 1933 [= *sinamarina* Bruguière, 1792], by original designation.

fairchildi

Asolene (*Surinamia*) *fairchildi* Clench, 1933: 71, pl. 7, figs. 1, 2. in the cataract of the Surinam River below Kedjo, Dutch Guiana (100 miles up river from Paramaribo). Holotype: MCZ 80515; paratypes: MCZ 80516, ANSP 161782 (1 spm.), UMMZ (Clench, 1933: 72) [not found by us]. Distribution: Surinam.

Remarks. Synonym of *sinamarina* Bruguière, 1792, *teste* Geijskes & Pain (1957: 46) and Tillier (1980: 17).

schrammi

Ampullaria Schrammi Crosse, 1876: 102. in flumine Oyapock, Guyanae Gallicae. Lectotype (Fischer-Piette, 1850: 150, pl. 5, fig. 81): MNHN. Distribution: French Guiana.

Remarks. Synonym of *sinamarina* Bruguière, 1792, *teste* Tillier (1980: 17).

sinamarina

Bulimus Sinamarinus Bruguière, 1792: 342, pl. 18, figs. 2, 3. la rivière de Sinamari dans la Guyane française. Type material: not found by us, nor by Tillier (1980: 17), in MNHN. Distribution: Guyana, Surinam, French Guiana (Vernhout, 1914: 43; Pain, 1950b: 73, 1952: 31; Geijskes & Pain, 1957: 46).

Remarks. Placed in *Surinamia* Clench, 1933, by Pain (1952: 31) and Tillier (1980: 17).

Incertae sedis in family AMPULLARIIDAE Gray, 1824

The following species are not well enough known to place them in a particular genus or in some cases to definitively include or exclude them as South American.

bilineata

Ampullaria bilineata Reeve, 1856e: pl. 23, fig. 110a, b. [No locality given.] Type material: not found by us in BMNH. Distribution: unknown.

Remarks. Gaudion (1879: 24) gave "Manille" [= Manila, Philippines] as the locality. Placed in *Pila* Röding, 1798, by Sowerby (1910: 56–57) and, confusingly, considered to be "based on young shells" of *globosa* Swainson (which is now placed in *Pila* Röding, 1798) by Prashad (1925: 72; see also Nevill, 1877: 2) but "certainly the same" as *gracilis* Lea (also now placed in *Pila* Röding, 1798) by Prashad (1925: 81). However, Alderson (1925: 30) treated it as a synonym of *buxea* Reeve, 1856, considering it

"nothing more than a stunted specimen of this variety [*buxea*]". Pilsbry (1927a: 247) treated *buxea* Reeve, 1856, as a synonym of *fasciata* Roissy, 1805 [*Pomacea*] and considered *bilineata* Reeve 1856, as a possible synonym of *fasciata* Roissy, 1805.

equestris

Pila equestris Röding, 1798: 145. [No locality given.] Type material: possibly Art and Natural History Museum, Gotha (Stewart, 1930: 35; Dance, 1986: 206). Distribution: unknown.

Remarks. Not listed by Gaudion (1879) or Sowerby (1916: 71).

fasciata

Ampullaria fasciata Lamarck, 1816: 12 [liste], pl. 457, fig. 3a, b [1822a: 177]. [No locality given. "les rivières de l'Inde, des Moluques et des Antilles" (Lamarck, 1822a: 177)]. Lectotype ["die von Lamarck citirte Figur der Encyclopädie" (Philippi, 1852a: 53)]: MHNG (Mermod, 1952: 88) [not MHNG 1093/92, *teste* Y. Finet (pers. comm. to RHC, 22 August 2002)].

Remarks. Junior primary homonym of *fasciata* Roissy, 1805. Its correct placement is unclear (e.g., Alderson, 1925: viii, 60) and depends on further study. Mermod (1952: 87) considered it probably a synonym of *ampullacea* Linnaeus, 1758, which is now placed in *Pila* Röding, 1798. Misidentified by Swainson (1821–1822a: pl. 103); see *swainsonii* Hupé, 1857.

gibbosa

Ampullaria gibbosa Paetel, 1887: 478. Unavailable name; *nom. nud.*

Remarks. Attributed to "Sw." [= Swainson], with reference to "Ad. Gen." [= H. Adams & A. Adams, 1853–1854], by Paetel (1887: 478). However, it is not listed by H. Adams & A. Adams (1853–1854), Sowerby (1916: 71), Sherborn (1922–1933) or Ruhoff (1980: 288) and appears never to have been made available. Paetel (1887: 480) listed "*pachystoma* Benson" as a synonym, suggesting that the species is Asian, since Benson worked in India (Naggs, 1997).

hepataria

Ampullaria hepataria Reeve, 1856c: pl. 17, fig. 77. [No locality given.] Syntype: BMNH 20020661. Distribution: unknown.

Remarks. Synonym of *corrugata* Swainson (which is now placed in *Pila* Röding, 1798), *teste* Nevill (1884: 2). Listed as a "Western Hemisphere" species and possibly a form of *hopetonensis* Lea, 1834, by Sowerby (1909a: 351). However, Alderson (1925: 46) excluded it from the synonymy of *hopetonensis* Lea, 1834 [= *paludosa* Say, 1829]. Also note the skepticism of Pain (1964: 225) regarding Sowerby's synonymies.

ignota

Pila ignota Röding, 1798: 146. [No locality given.] Type material: possibly Art and Natural History Museum, Gotha (Stewart, 1930: 35; Dance, 1986: 206). Distribution: unknown.

Remarks. Not listed by Gaudion (1879) or Sowerby (1916: 71).

imperforata

Ampullaria imperforata Swainson, 1823b: 377. [No locality given.] Type material: possibly MMUE (Dean, 1936: 232; H. McGhie, pers. comm. to RHC, 28 July 2002), not found by us in BMNH (cf. Dance, 1986: 227). Distribution: unknown.

Remarks. Sowerby (1916: 70) was unable to identify this species. Swainson (1823b: 377) said "operculum horny ?", which would suggest a New World species.

nucleus

Ampullaria nucleus Philippi, 1852a: 25, pl. 7, fig. 1 [1852b: 23]. [No locality given.] Syntypes: ZMHB 1374 (2 spms.; larger spm. = original illustration) (M. Glaubrecht, pers. comm. to RHC, 1 March 2003). Distribution: unknown.

Remarks. Considered close to *crasssa* Swainson, 1823, and with a horny operculum (Philippi, 1852a: 25), so included here as a New World species.

obtusa

Ampullaria obtusa Deshayes, 1850: 45, pl. 72, fig. 24. [No locality given.] Type material: not found by us in MNHN or BMNH (cf. Dance, 1986: 210). Distribution: unknown.

pachystoma

Ampullaria pachystoma Paetel, 1887: 480. Unavailable name; *nom. nud.*

Remarks. Attributed to Benson, but not listed by Sowerby (1916: 72), Sherborn (1922–1933) or Ruhoff (1980: 415) and appears never to have been made available. Material not in Cambridge (R. C. Preece, pers. comm. to RHC, 27 August 2002), not found by us in BMNH. May be *pachystoma* Philippi [*Pomacea*] or possibly an Asian species (see *gibbosa* Paetel, 1887).

planorboides

Ampullaria planorboides Cristofori & Jan, 1832: [Section IIa, Pars Ia] 7. Unavailable name; *nom. nud.*

Remarks. Name attributed to Ziegler by Cristofori & Jan (1832: 7), who gave "Austr. N. Holl." as the locality. Martens (1857: 208)

was unsure of the locality, saying "Botanybay (?) Quid [= where]?". Gaudion (1879: 37) gave the locality as "Nouv. Hollande". Not listed by Sowerby (1916: 72). Material formerly in MCSN [destroyed; A. Garassino, pers. comm. to RHC, 5 September 2002]. May not be an ampullariid.

rufilineata

Ampullaria rufilineata Reeve, 1856a: pl. 2, fig. 7. [No locality given.] Syntypes: BMNH 20020681 (3 spms.). Distribution: uncertain.

Remarks. Sowerby (1916: 69) placed this species in *Pila*, giving "Pegu" as the locality (the locality on the BMNH label). Martens (1857: 209) and Gaudion (1879: 39), however, gave Venezuela as the locality. Blume & Pain (1952: 267) considered the location and generic placement uncertain.

sepulta

Pila sepulta Röding, 1798: 146. [No locality given.] Type material: possibly Art and Natural History Museum, Gotha (Stewart, 1930: 35; Dance, 1986: 206). Distribution: unknown.

Remarks. Not listed by Gaudion (1879) or Sowerby (1916: 72).

tristis

Ampullaria tristis Gaudion, 1879: 41. Unavailable name; *nom. nud.*

Remarks. Name attributed to Say, although Say appears never to have published it (Binney, 1858: [237]). "Amérique Septentrionale" given as locality. Possibly *Bulimus tristis* Jay, 1839 [now placed in the genus *Lanistes* Montford, 1810, which is African].

trochulus

Ampullaria trochulus Reeve, 1856c: pl. 14, fig. 66. [No locality given.] Syntype: BMNH 20020685. Distribution: unknown.

Remarks. Listed as a New World species by Sowerby (1909a: 358).

Non-American species in family AMPULLARIIDAE Gray, 1824

To prevent confusion, we list those non-American ampullariids that have at some time been considered as American or possibly American. The list may not be comprehensive.

adusta

Ampullaria adusta Reeve, 1856a: pl. 3, fig. 11. [No locality given.] Type material: BMNH 20020690 [labeled "Zanzibar"].

Remarks. Nevill (1884: 10) gave the locality as "South America". Confirmed as African (and hence to be placed in *Pila* Röding, 1798) by Alderson (1925: 86).

aperta

Ampullaria aperta Philippi, 1849: 18. [No locality given.] Type material: probably MNHNS.

Remarks. Gaudion (1879: 24) and Paetel (1873: 64, 1887: 476) gave the locality as Venezuela. Considered Indian and placed in *Turbinicola* Annandale & Prashad, 1921 [= *Pila*, *teste* Berthold, 1991: 247], by Prashad (1925: 88).

bruguieri

Ampullaria Bruguieri Deshayes, 1830a: 32. Cayenne [?]. Syntypes: MNHN (3 spms.).

Remarks. One of the syntypes has a calcified operculum and the label says "= *A. kordofana* Parreyss" suggesting that it is a species of *Pila* from Africa (see also Tillier, 1980: 16).

exigua

Ampullaria exigua Philippi, 1852a: 46, pl. 13, fig. 4 [1852b: 26]. [No locality given.] Type material: probably MNHNS.

Remarks. Sowerby (1909a: 349), following Philippi (1852b: 27), first considered that it "may be a variety of *A. crassa*, Swainson" but subsequently (Sowerby, 1910: 58) treated it as a species of *Pila* from Egypt. Listed from Egypt by Paetel (1887: 478).

+ pallens

Ampullaria pallens Philippi, 1849: 17. Indiae orientalis. Type material: probably MNHNS.

Remarks. Gaudion (1879: 36) gave Mexico as the locality. Philippi (1852a: 32) had previously said "wahrscheinlich Ostindien" and Martens (1901: 644) stated that it was from the Philippines. Variety of *virens* Lamarck, 1822 (which is now placed in *Pila* Röding, 1798), *teste* Sowerby (1910: 62).

paludinoides

Ampullaria paludinoides Cristofori & Jan, 1832: [Section IIa, Pars Ia] 7, [Mantissa] 3. Am. mer. Type material: formerly MCSN [destroyed; A. Garassino, pers. comm. to RHC, 5 September 2002].

Remarks. The locality was reiterated as "America meridionalis" by Philippi (1852b: 24) and "Amer. m." by Paetel (1873: 65). Martens (1857: 213) considered it African. Paetel (1887: 480) listed it from "Moulmein" and it was considered Indian by Nevill (1877: 7–9), though perhaps based on misidentifications by the previous authors he cited. Placed in

Pila Röding, 1798, by Sowerby (1910: 57, 62).

prunella

Ampullaria prunella Hupé, 1857: 67, pl. 12. fig. 4, 4a. les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para [in publication title]. Syntypes: MNHN (7 spms.; see also Tillier, 1980: 16); possible syntype: MNHN (1 spm.).

Remarks. The syntypes are labeled as from "Cayenne" but have calcified opercula, indicating that this is not an American species (Tillier, 1980: 16).

rotundata

Ampullaria rotundata Say, 1829b: 245. St. John's River in Florida. Type material: "not found" (Baker, 1964: 168).

Remarks. Sowerby (1909a: 357) considered it "most likely a form of *Hopetonensis*" [= *paludosa* Say, 1829], but it was subsequently synonymized with *globosa* Swainson (which is now placed in *Pila* Röding, 1798) by Pilsbry (1953: 60; see also Walker, 1918: 124; Clench, 1955: 107; Clench & Turner, 1956: 120). Spelled by Binney (1858: 147) as "*Ampluria rotundata*".

Unpublished names in family AMPULLARIIDAE Gray, 1824

The following names of ampullariids, some of them perhaps referring to American species, have been found by us on museum collection labels. They appear never to have been published and are not nomenclaturally available.

"adjusta". No author. Treated as a synonym of *sordida* Swainson, 1823 in ANSP.
"burmeisteri". Attributed to Ihering. ZMHB 109518 (M. Glaubrecht, pers. comm. to RHC, 1 March 2003).
"gualteriana". No author. "nov. Pernambuco *A. fasciata* Sw. var.?" on label in MNHN.
"miquitensis". Attributed to Spix in UMMZ.
"palmieri". Attributed to Preston in UMMZ.
"tacarigua". Attributed to Pilsbry. ANSP 161137, labeled "Holotype".
"undata". No author. USNM.
"unicolor". Attributed to Martens in UMMZ.
"venezullum". No author. UMMZ.

Non-ampullariids described originally in family AMPULLARIIDAE Gray, 1824

The following taxa were described originally in *Ampullaria* or *Pomacea* but are not now considered to belong to the Ampullariidae. Some may be nomenclaturally unavailable. The list is not comprehensive.

Ampullaria acuminata Lamarck, 1804
Ampullaria acuta Lamarck, 1804
Pomacea annularis Perry, 1811
Ampullaria avellana Lamarck, 1822
Ampullaria buccinoidea Young & Bird, 1828
Ampullaria bulimoides Deshayes, 1842
Ampullaria canaliculata Lamarck, 1804
Ampullaria canalifera Lamarck, 1822
Pomacea bibliana Marshall & Bowles, 1932
Ampullaria borealis Valenciennes, 1833
Ampullaria conica Lamarck, 1804
Ampullaria crassa Deshayes, 1830
Ampullaria crassatina Lamarck, 1804
Ampullaria depressa Lamarck, 1804
Ampullaria elongata Bennett, 1831
Ampullaria excavata Lamarck, 1804
Ampularia faujasii Serres, 1829
Ampullaria fragilis Lamarck, 1822
Ampullaria galloprovincialis Matheson, 1843
Ampullaria hybrida Lamarck, 1804
Ampullaria laevigata Deshayes, 1842
Pomacea linearis Perry, 1811
Ampullaria media Bennett, 1831
Ampullaria patula Lamarck, 1804
Ampullaria perovata Conrad, 1846
Ampullaria ponderosa Deshayes, 1825
Ampullaria proboscidea Matheson, 1843
Ampullaria pygmaea Lamarck, 1804
Ampullaria rosea Spix, 1827
Ampullaria scalariformis Deshayes, 1825
Ampullaria sigaretina Lamarck, 1804
Ampullaria spirata Lamarck, 1804
Ampullaria tasmaniae Guillou, 1842
Pomacea variegata Perry, 1811

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We have seen all the references listed, thereby ensuring accuracy of citation. Dates of publication in some cases have been taken from Evenhuis & Cowie (1995) and Cowie (1998); other dates derive from subsequent research. Citation is given verbatim, unless a publication represents a presentation made at a meeting, in which case it cannot be cited verbatim and a paraphrased title is provided and placed in square brackets. The date of publication, as accurately as could be ascertained from the publication itself and from outside sources, is placed in square brackets at the end of the citation. The dates recorded here are the earliest found for each citation. If the year of publication was different from that printed in the publication itself, the actual year of publication is placed in square brackets. In many instances of works published in parts (Lieferungen, livraisons, etc.), the original wrappers have not been seen, only the complete bound work. Dating has then been obtained from other, secondary sources. The dates that were printed on the original wrappers have therefore not always been verified. The year(s) of publication of the entire work, if different from that which actually appeared in the work (usually on the frontispiece) are therefore not placed in square brackets, pending further research on the original wrappers. If no date other than year could be found, the publication date must be treated as 31 December until such time as evidence of earlier publication is discovered. Sources for dates listed here are held by the first author. When an author published more than one paper in a year, the papers are listed chronologically and the year given a letter suffix corresponding to the citation in the catalog. Where tabular collation is given for publications issued in parts, the date letter for each part is given in the "Date of publication" column. An author's initials are placed in square brackets if not given in the publication. Publications of the International Commission on Zoological Nomenclature are cited with authorship as "ICZN" in the catalog but spelled out in this bibliography.

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3	9–12	65–96	June 1853c
4	13–16	97–128	August 1853d
5	17–20	129–160	September 1853e
6	21–24	161–192	October 1853f
7	25–28	193–224	November 1853g
8	29–32	225–256	December 1853h
9	33–36	257–288	January 1854a
10	37–40	289–320	February 1854b
11	41–44	321–352	March 1854c
12	45–48	353–384	April 1854d
13	49–52	385–416	May 1854e
14	54–56	417–448	June 1854f
15	57–60	449–484	July 1854g

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1	101	i–vii, 1–256	1 February 1830a
2	101	1–144	1 February 1830b
2	102 [part]	145–594	29 September 1832

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1	1	1–19	1–152	1–6	1870
	2	20–38	153–304	7–12	1872
	3	39–48	305–384	13–16	1873a
	4	49–58	385–464	17–20	1873b
	5	59–68	465–546	21–24	1875
	6	69–78	457–624	25–28	1877
	7	79–88	625–702	29–31	1878
2	8	1–10	1–80	32–36	1880
	9	11–16	81–128	37–42	1886
	10	17–22	129–176	43–46	1888
	11	23–32	177–256	47–48	1890
	12	33–39	257–312	49–52	1891
	13	40–49	313–392	53–54	1892
	14	50–61	393–488	55–58	1893
	15	62–72	489–576	59–62	1894a
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38	December 1833
39	March 1834a
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1	i–xxvii, 1–104	1 September 1846a
2	105–232	1 December 1846b
3	233–360	1 March 1847a
4	261–488	18 April 1847b
5	489–616	25 May 1847c
6 (part)	617–637	17 July 1847d

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Section	Pages	Part	Printed date	Date in other lists
1	1–8	550	13 March 1911a	1911
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4	25–32	556	24 May 1911d	1912
5	33–40	556	15 October 1911e	1912
6	41–48	556	2 November 1911f	1912
7	49–56	557	4 November 1911g	1912
8	57–64	557	25 November 1911h	1912
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10	73–80	560	2 December 1911j	1912
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12	89–96	560	12 January 1912b	1912
13	97–104	560	10 January 1912c	1912
14	105–112	563	30 June 1912d	1913
15	113–120	563	12 September 1912e	1913
16	121–128	563	12 September 1912f	1913
17	129–136	563	1 November 1912g	1913
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19	145–152	565	4 March 1913a	October 1913
20	153–160	567	8 July 1913b	November 1913
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22	169–176	567	14 July 1913d	November 1913

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Section	Pages	Part	Printed date	Date in other lists
23	177–184	570	4 August 1913e	1913
24	185–192	570	21 December 1913f	1913
25	193–200	570	23 December 1913g	1913
26	201–208	574	29 December 1913h	1914
27	209–216	574	12 January 1914a	1914
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Pages	Plates	Date of publication
1–40	1	1890
41–96	2–5	1891
97–176	6–9	1892
177–248	10–12	1893
-	13–15	1894
249–288	16	1897
289–368	17–20	1898
369–472	21–28	1899
473–608	29–41	1900
609–706, i–xxviii	42–44	1901

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Pages	Date of publication
1–228	8 March 1810
229–414 (with index and title page)	7 September 1811

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Published in livraisons as follows:

Livraison	Pages	Plates	Wrapper date	Date of publication (Evenhuis & Cowie, 1995)
1	-	1, 2	1834	15 May 1835b
3	-	4	1835	15 May 1835c
4	-	3	1835	Before 31 August 1835d
5	-	5, 6, 7	1835	31 August 1835e
6	1–48	10, 12	1834	14 September 1835f
7	49–72	-	1835	23 November 1835g
8	73–104	-	1834	7 December 1835h
9	105–128	9, 11, 13	1834	4 January 1836a
11	129–152	17, 21	1835	18 April 1836b
12	153–176	8	1835	30 May 1836c
13	-	18, 19, 22	1835	-
14	-	20, 25	1835	11 July 1836e
15	-	23	1835	1 August 1836f
16	-	15, 16	1834	26 September 1836g
17	177–184	27, 28	1836	3 October 1836h
18	-	14, 26	1836	7 November 1836i
21	-	31	1836	-
22	-	24, 35	1836	27 February 1837a
23	-	30, 32, 34	1836	3 April 1837b
24	-	35, 37	1836	5 June 1837c
25	-	38, 41	1837	19 June 1837d
26	-	38, 39	1837	7 August 1837e
27	-	40, 45	1837	18 September 1837f
28	-	29, 46	1837	-
29	-	40, 42, 43	1837	6 November 1837h
31	185–232	44	1837	5 March 1838a
32	233–280	47	1837	23 April 1838b
33	281–328	48, 52	1837	6 May 1838c
34	329–376	-	1837	11 June 1838d
35	-	49, 50, 51	1837	15 October 1838e
36	-	55	1835	12 November 1838f
37	-	56	1834	8 April 1839a
38	-	57	1837	29 April 1839b
39	-	58	1836	24 June 1839c
42	-	59	1839	11 November 1839d
43	-	64, 65	1939	21 November 1839e
44	-	54, 60–63	1839	6 September 1841a
46	-	66	1839	8 November 1841b
47	-	68, 69	1839	8 November 1841c
48	-	70	1940	8 November 1841d
49	377–408	-	1840	15 November 1841e
50	-	53, 67, 71	1840	15 November 1841f
51	409–424	72	1841	15 November 1841g
52	425–472	73, 74, 79	1841	15 November 1841h
53	473–488	75, 76, 80	1841	14 February 1842a
82	489–528	-	1846	-
83	529–600	-	1845	-
84	601–656	-	1846	-
85	657–704	-	1846	-
86	705–728	-	1846	-
-	729–758	-	-	-
88	-	83, 85	1842	-
89	-	78, 81	1847	-
90	-	79, 82	1847	-

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Published in livraisons. Few details are available; the following are from G. Rosenberg (pers. comm. to RHC, October 2001):

Pages	Date of publication
1–112	1842c
113–128	8 November 1844
129–208	16 February 1848
209–380	1853

PAETEL, F., 1873, *Catalog der Conchylien-Sammlung von Fr. Paetel. Nebst Uebersicht des angewandten Systems*. Gebrüder Paetel, Berlin. [iv] + 172 pp. [after April]

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Lieferung	Pages	Date of publication
1–6	1–480	after June 1887
7, 8	481–639	before 22 October 1888

PAIN, T., [1946]a, Two new species of *Pila* (= *Ampullaria*) from South America. *Proceedings of the Malacological Society of London*, 26: 180–181, pl. 6. [31 January]

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PAIN, T., 1949a, Three new species of *Pomacea* from South America. *Proceedings of the Malacological Society of London*, 27(6): 257–258, pl. 13. [14 January]

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Issued in monthly parts of unnumbered plates and associated text. The plates were numbered by Mathews & Iredale (1912) and monthly dates are here given following those authors. *Pomacea maculata* appears on pl. 12.

However, Cowie (1997a: 84) indicated that *P. maculata* appeared on pl. 11, based on pencilled numbers in the BMNH copy. Neave (1940: 866) indicated that it appeared in signature G5. A full collation is in preparation and confirms that *P. maculata* appeared on pl. 12 in signature G5 (R. E. Petit, pers. comm. to RHC, 16 October 2000).

Plates	Date of publication
[1–4]	1 January 1810a
[5–8]	February 1810b
[9–12]	1 March 1810c
[13–16]	April 1810d
[17–20]	May 1810e
[21–24]	June 1810f
[25–28]	July 1810g
[29–32]	August 1810h
[33–36]	September 1810i
[37–40]	October 1810j
[41–44]	November 1810k
[45–48]	December 1810l
[49–52]	January 1811a
[53–56]	February 1811b
[57–60]	March 1811c
[61–64]	April 1811d
[65–68]	May 1811e
[69–72]	June 1811f
[73–76]	July 1811g
[77–80]	August 1811h
[81–84]	September 1811i

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Published in parts as follows:

Part	Pages	Plates	Date of publication
104	1–24	A, 1–5	1851
107	25–48	6–11	1852a
110	49–74	12–17	1852a
113		18–21	1852a

PHILIPPI, R. A., 1852b, Centuria quinta testaceorum novorum. (Contin.) *Zeitschrift für Malakozoologie*, 9(2): 20–29. [25 March]

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Published in two parts as follows:

Pages	Date of publication
310–328	25 August 1891a
329–334	22 September 1891b

PILSBRY, H. A., 1893, Notes on a collection of shells from the state of Tabasco, Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 44[1892]: 338–341, pl. 14. [24 January]

PILSBRY, H. A., 1899, A new *Ampullaria*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 51: 365. [8 September]

PILSBRY, H. A., 1927a, Revision of the Ampullariidae of Jamaica and Cuba. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 79: 247–253, pls. 21–22. [10 September]

PILSBRY, H. A., 1927b, On *Pomacea* Perry (Ampullariidae). *The Nautilus*, 41(2): 63–64. [27 October]

PILSBRY, H. A., 1933, Zoological results of the Matto Grosso expedition to Brazil in 1931, – II. Mollusca. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 85: 67–76, pl. 2. [17 July]

PILSBRY, H. A., 1944, Molluscan fossils from the Rio Pachitea and vicinity in eastern Peru. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 96: 137–153, pls. 9–11. [11 August]

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QUOY, J. R. C. & L. P. GAIMARD, 1824–[1826], Zoologie. Pp. i–vii, 1–712, 96 pls., in: L. C. D. DE FREYCINET, *Voyage autour du monde, entrepris par ordre du Roi sous le ministère et conformément aux instructions de S. Exc. M. le Vicomte du Bouchage, Secrétaire d' État au Département de la Marine, exécuté sur les corvettes de S. M.* l'Uranie *et* la Physicienne*, pendant les années 1817, 1818, 1819 et 1820; publié sous les auspices de S. E. M. le Comte Corbière, Secrétaire d'État de l'Intérieur, pouv la partie historique et les sciences naturelles, et de S. E. M. le Marquis de Clermont-Tonnerre, Secrétaire d'État de la Marine et des Colonies, pouv la partie nautique*. Pillet Aîné, Paris.

Published in livraisons as follows:

Livraison	Pages	Date of publication
1	1–40	26 June 1824a
2	41–88	31 July 1824b
3	89–128	28 August 1824c
4	129–184	18 September 1824d
5	185–232	9 October 1824e
6	233–280	20 November 1824f
7	281–328	18 December 1824g
8	329–376	29 January 1825a
9	377–424	26 March 1825b
10	425–464	7 May 1825c
11	465–496	18 June 1825d
12	497–536	6 August 1825e
13	537–576	1 October 1825f
14	577–616	17 December 1825g
15	617–664	26 April 1826a
16	665–712	14 June 1826b

In the "Préface" to this work (unnumbered page 3), Quoy & Gaimard thank Férussac for the nomenclature of the terrestrial mollusks. In the introduction to the terrestrial and freshwater mollusks, Quoy & Gaimard state (pp. 463–464) that "Nous devons à M. de Férussac la description des espèces que nous avons rapportées, dont il a fait figurer plusiers dans son magnifique ouvrage sur les mollusques terrestres et fluviatiles." Thus, authorship of the descriptions of the terrestrial and freshwater mollusks (pp. 465–496, including *Ampullaria*) is Férussac, in Quoy & Gaimard, though Quoy & Gaimard are the authors of the introductory text to that chapter (pp. 462–464).

REEVE, L. [A.], 1856, Monograph of the genus *Ampullaria*. Pls. 1–28, in: L. [A.] REEVE, *Conchologia Iconica: or, illustrations of the shells of molluscous animals. Vol. X.* Lovell Reeve, London.

This is a lambda book (a book in which plates were published separately, along with unnumbered pages of explanatory text, as the plates were ready). After all plates were completed, they were bound into volumes. Dates of publication as given on the bottom of the explanatory text for each plate are as follows for *Ampullaria*.

Plates	Date of publication
2–4	June 1856a
5–12	August 1856b
13–20	October 1856c
21, 22	November 1856d
1, 23–28	December 1856e

RICHARDS, H. G., 1933, A conchological expedition to Cuba. *Proceedings of the Pennsylvania Academy of Science*, 7: 167–172. [4 December]
RÖDING, P. F., 1798, *Museum Boltenianum*. Pars Secunda. J. C. Trapp, Hamburg. viii + 199 pp. [September]

Authorship of this work determined by ICZN Direction 48.

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SAULCY, E. de, 1854, Note sur l'ampullaire œil d'Ammon, *Ampullaria effusa* (Lamarck). *Bulletin de la Société d'Histoire Naturelle du Département de la Moselle*, 6: 139–147, 1 pl.
SAY, T., 1824, Appendix. Part I. – Natural History. 1. Zoology. Pp. 253–378, pls. 14–15, in: W. H. KEATING, ed., *Narrative of an expedition to the source of St. Peter's River, Lake Winnepeek, Lake of the Woods, &c. &c. Performed in the year 1823, by order of the Hon. J. C. Calhoun, Secretary of war, under the command of Stephen H. Long, Major U.S.T.E.* Vol. II. H.C. Carey & I. Lea, Philadelphia.
SAY, T., 1829, Descriptions of some new terrestrial and fluviatile shells of North America. *The Disseminator of Useful Knowledge* [New Harmony], 2.

Published in parts, as follows:

Pages	Date of publication
229–230	29 July 1829a
244–246	12 August 1829b
259–261	26 August 1829c
275–277	9 September 1829d
291–293	23 September 1829e
308–310	7 October 1829f
323–325	21 October 1829g
339–341	4 November 1829h
355–356	18 November 1829i

SCHUMACHER, C. F., 1817, *Essai d'un nouveau système des habitations des vers testacés avec XXII planches*. Schultz, Copenhague. [ii] + 287 pp., 22 pls.
SHERBORN, C. D., 1922–1933, *Index animalium sive index nominum quae ab A.D. MDCCLVIII generibus et speciebus animalium imposita sunt. Sectio secunda a kalendis ianuariis, MDCCI usque ad finem decembris, MDCCCL*. British Museum, London. cxlvii + vii + [i] +7056 + 1098 pp.
SMITH, B. D., 1992, Introduction and dispersal of apple snails (Ampullariidae) on Guam. *Pacific Science Association Information Bulletin*, 44: 12–14.
SMITH, M., 1937, *East coast marine shells. Descriptions of shore mollusks together with many living below tide mark, from Maine to Texas inclusive, especially Florida.* Edwards Brothers, Inc., Ann Arbor. vii + 308 pp. [before 12 June]
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This index includes all ampullariid names listed in the main body of the catalog. Family-group names are in **BOLDFACE** capitalized letters. Genus-group names are in all CAPITALIZED letters. Unavailable names are in *italics*. Unpublished names are listed in quotes in plain type.

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ASSESSMENT OF GENETIC HETEROGENEITY WITHIN LABORATORY-MAINTAINED *SCHISTOSOMA MANSONI*-RESISTANT STOCKS OF *BIOMPHALARIA GLABRATA* SNAILS BY RAPD-PCR

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ABSTRACT

Random amplified polymorphic DNA (RAPD)-PCR analysis was used to assess the extent of genetic diversity within two laboratory-maintained *Schistosoma mansoni*-resistant stocks of *Biomphalaria glabrata* (10-R2 and BS-90). Both stocks routinely serve as parents in crosses with susceptible snails for studying the genetics of parasite resistance in the snail host. Genomic DNA was isolated from individual adult 10-R2 and BS-90 snails. From RAPD-PCR conducted with 16 anonymous primers, no polymorphisms were detected within the BS-90 stock, whereas 13 primers revealed considerable intrastrain variations showing different sized bands among the 10-R2 snails. The polymorphisms in the 10-R2 stock allowed us to identify three distinct groups (Types 1, 2 and 3) within these snails. Random screening of individual 10-R2 snails revealed that, of the three distinct types, Types 1 and 2 snails were found at similar frequencies (approximately 45%), whereas 10% fell into the third group (Type 3). The identification of genetic variants within the 10-R2 stock demonstrates the need for careful assessment of the existence of diverse forms in this stock prior to conducting genetic crosses with these snails.

Key words: genetic heterogeneity, *Biomphalaria glabrata*, *Schistosoma mansoni*, intermediate snail host, intrastrain variation, resistance, DNA polymorphisms, RAPD-PCR.

INTRODUCTION

Much of the research on the genetics of the interrelationship between the parasitic helminth *Schistosoma mansoni* and the snail host *Biomphalaria glabrata* has been made possible because of the availability of several genetically defined *B. glabrata* stocks that breed true for a variety of traits (Richards, 1970). From crosses conducted between many different snail stocks, these have been grouped into four categories (Types I–IV) based on susceptibility to *S. mansoni* (Richards & Shade, 1987, review). Snails in the Type I category are resistant to parasite infection at any age. Type II snails are susceptible as juveniles, but adult resistant. Type III snails are susceptible at any age, whereas Type IV snails are juvenile susceptible and adult variable. Of all these categories, snails from categories Types I and III have received the most attention by investigators studying the molecular basis of resistance and susceptibility to infection. Accordingly, many of these studies have been done using either the prototype Type I resistant stocks 10-R2, 13-16-R1 or the "Salvador" strain (also referred to as BS-90), or the susceptible Type III M-line and NMRI snail stocks.

It is known that genes of both the snail and parasite affect the outcome of this host/parasite relationship. Based on this, it was suggested as early as the late 50s (Hubendick, 1958) that one method for reducing transmission may involve the use of parasite resistant snails to replace susceptible ones in an endemic area. Whether or not this form of control will become reality, studying the molecular biology of the snail and parasite has become the focus of considerable research in recent years. For the emerging field of molecular malacology, the existence of genetically defined *B. glabrata* snail stocks has therefore been invaluable.

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Although recent success has been achieved in defining molecular markers for resistance in *B. glabrata* (Knight et al., 1999), there is evidence that molecular heterogeneity may exist between individual snails within either resistant or susceptible laboratory-maintained stocks, potentially complicating interpretation of experimental results. In earlier studies, while searching for RFLPs in the small ribosomal gene, we reported on a smaller scale the genetic diversity within both resistant (10-R2) and susceptible (M-line) snail stocks (Knight et al., 1991). Later, Mulvey & Bandoni (1994) reported differences in allozyme frequencies among nine enzymes from M-line snails obtained from several different laboratories.

For this study, we were interested in further documenting the genetic variability among our resistant snail stocks. Our goal was to assess the extent of genetic diversity in the present laboratory-maintained resistant stocks by means other than RFLP analysis before using them to conduct crosses with the susceptible M-line snails. Although the original 10-R2 stock was maintained in the laboratory for many generations without loss or reduction of the refractory trait (Richards, personal communication), some stocks in other laboratories occasionally show partial susceptibility, especially when they are exposed as juveniles.

The RAPD-PCR method only detects dominant alleles and has the potential to show inconsistencies in results if assays have not been optimized (Williams et al., 1990; Welsh & McClelland, 1990). On the other hand, the method has been used effectively in assessing genetic diversity in both laboratory maintained and field populations of *B. glabrata* (Larson et al., 1996; Vidigal et al., 1994). Moreover, in comparison to other DNA genotyping tools available, for example RFLP analysis and examination of polymorphic microsatellite (simple sequence repeats) loci, RAPD-PCR requires no prior sequencing or cloning steps, uses negligible amounts of DNA, and requires no radioactive isotopes in the assay.

Here, we compare the genotypes of individual schistosome-resistant BS-90 and 10-R2 snails using RAPD-PCR analysis. Of the two stocks, no genetic diversity was found between snails of the BS-90 stock by this analysis. Genetic heterogeneity however was found in the 10-R2 stock, allowing us to identify three distinct substocks (herein after referred to as Types 1–3).

MATERIALS AND METHODS

Snails

The two different *S. mansoni*-resistant stocks of *B. glabrata* used in this study were the 10-R2 (Richards, 1975) and BS-90 (Paraense & Correa, 1963) snails. Adult snails (10–14 mm in diameter) were reared as individuals in self-fertilizing lineages in beakers (400 ml) with petri dish covers in aerated tap water, and fed romaine lettuce. Cohorts of the snails used in this study, after exposure to *S. mansoni* miracidia, have always displayed the resistance phenotype.

Genomic DNA Extraction

Genomic DNA was prepared from the whole body of individual snails (Knight et al., 1998). Snails were cleaned with a Q-tip and maintained overnight in sterile deionized water (DW) containing 100 μg/ml of ampicillin at room temperature. In some cases, DNA was isolated from snail tentacles. For this, tentacles were snipped off live snails with a pair of fine tipped forceps under a dissecting microscope, placed in siliconized tubes and kept frozen at –70°C until required. The frozen tentacles were thawed into 200μl CTAB buffer (2% w/v of cetyltrimethylammonium bromide, 1.4 M NaCl, 20 mM EDTA, 0.2% v/v of β-mercaptoethanol, 100 mM Tris-HCl, pH8.0) containing proteinase K (0.1mg/ml), homogenized with a motorized pestle (Kimble, Illinois), and incubated at 55°C for 1 h and processed further as described previously (Knight et al., 1998).

DNA was recovered by centrifugation and washed in cold 70% ethanol, air dried and resuspended in an appropriate volume of sterile distilled water. The quality of DNA was determined by horizontal flat-bed gel electrophoresis (0.8% agarose) resolved in TBE buffer (89 mM Tris-base, 89 mM Boric acid and 2 mM EDTA, pH 8.0). DNA concentration was measured under UV illumination (Eagle Eye, Stratagene, California) from the intensities of ethidium bromide staining of the extracted DNA samples compared to that of known amounts of standard DNA spotted (1.0 μl) onto agarose plates incorporated with ethidium bromide.

Random Amplified Polymorphic DNA (RAPD)-PCR

Genetic diversity between individual resistant snails was analyzed by RAPD-PCR as described previously (Larson et al., 1996). The genotypes

TABLE 1. The frequency of detecting variant forms (%) of 10-R2 snails based on genotypying DNA from individual snails assayed by RAPD-PCR with random oligonucleotide decamer primers. Some primers produced no product (N/P) and others detected no genetic diversity within the snails (indicated by 0).

Primer	Sequence 5'→3'	Variants (%)		
		Type 1	Type 2	Type 3
OPM-05	GGGAACGTGT	45	45	10
OPM-07	CCGTGACTCA	45	45	10
OPZ-05	TCCCATGCTG	45	45	10
OPM-01	GTTGTTGGCT	45	45	N/P
OPM-04	GGCGGTTGTC	45	45	N/P
OPM-08	TCTGTTCCCC	45	45	N/P
OPM-09	GTCTTGCGGA	45	45	N/P
OPM-10	TCTGGCGCAC	45	45	N/P
OPZ-01	TCTGTGCCAC	45	45	N/P
OPZ-03	CAGCACCGCA	45	45	N/P
OPZ-06	GTGCCGTTCA	45	45	N/P
OPZ-07	CCAGGAGGAC	45	45	N/P
OPZ-10	CCGACAAACC	45	45	N/P
OPM-06	CTGGGCAACT	0	0	0
OPM-11	GTCCACTCTC	0	0	0
OPZ-11	GTCCACTGTG	0	0	0

of individual 10-R2 and BS-90 snails were determined by anonymous 10-mer oligonucleotide primers (listed in Table 1) obtained from Operon Technologies (Alameda, California). The control (no template DNA) was sterile distilled water. After amplification, the reaction was mixed with 5 µl of loading buffer (40% sucrose, 0.25% bromophenol blue and 0.25% xylene cyanol) and run on a 1.2% agarose gel containing 0.5 µg/ml of ethidium bromide in TBE buffer (voltage at 100V). The amplified bands were visualized by UV illumination and sizes estimated based on the migration of a 100-base pair (bp) ladder (Gibco BRL, Gaithersburg, Maryland).

RESULTS AND DISCUSSION

RAPD analysis was performed using DNA extracted from two different stocks of *B. glabrata*. DNA samples from 24 individuals of the 10-R2 stock and 20 individual BS-90 snails were compared using 16 random primers. The results revealed that with all of the random primers tested, no polymorphisms were found between individual BS-90 snails, whereas 13 of 16 primers revealed variations (different sized bands) between the 10-R2 snails analyzed (Table 1). Thirteen of the primers revealed that approximately 45% of the individuals analyzed could be grouped into one of two genotypes (Types 1 or 2). Three primers (OPM-05, OPM-07, OPZ-05) revealed a third type (Type 3) but at a lower frequency (10%). Only three primers (OPM-06, OPM-11 and OPZ-11) showed no polymorphisms between all individual 10-R2 snails tested.

Results of specific bands obtained for the three 10-R2 types, using the 13 primers that produced amplified products, are summarized in Table 2. Seven primers (OPM-04, OPM-05, OPM-07, OPM-08, OPM-10, OPZ-03 and OPZ-10) amplified different sized products for Type 1 snails, but not for Type 2, thus allowing differentiation between the two types. Six primers produced bands specific for Type 2 snails and three primers amplified specific products for Type 3 snails.

Representative examples of the polymorphisms that enabled us to segregate the 10-R2 snails into three distinct groups using three different primers OPM-05, OPM-07 and OPZ-05, can be seen in Figures 1A–C, respectively. Primer OPM-05 (Fig. 1A), revealed the presence of high molecular weight bands (shown by the arrows) in Type 1 (approximately, 1600bp), and Type 3 (1550bp) snails that were absent in Type 2 snails. Amplification using primer OPM-07 (Fig. 1B) showed (indicated by arrows) two specific bands (1500bp and 700bp) in Type 1 snails that were absent in Types 2 and 3 snails and the presence of Type 3 specific bands (1600bp, 1500bp, 900bp and 750bp). DNA from the 3 types amplified using primer OPZ-05 (Fig. 1C) produced specific markers for each (a band of 550bp for Type 1, 650bp and 800bp for Type 2,and a 1600bp fragment and a doublet at approximately 1500bp/1550bp for Type 3). Amplification with the same three primers (OPM-05, OPM-07 and OPZ-05) using DNA from individual BS-90 snails (Figs. 2A–C, respectively) showed that unlike the 10-R2 snails, intrastrain variation was not detected within this stock. In some cases, results showed differences in the intensities of bands but because the same size bands were amplified from all individual BS-90 snails, these differences in band intensities may be due to minor inconsistencies in the amount of template DNA utilized rather than inherent genetic differences in this stock.

Using RAPD-PCR, we thus revealed considerable molecular diversity between individual

TABLE 2. The detection of Type-specific bands by RAPD-PCR analysis of individual 10-R2 snails. The sizes of the various substock specific bands were determined by agarose gel electrophoresis as described in Materials and Methods. No amplified products (N/P) were produced by ten of the primers.

	Specific bands (bp)		
Primer	Type 1	Type 2	Type 3
OPM-05	1,550		1,500
OPM-07	1,400, 650		800
OPZ-05	550	650, 800	1,600, 1500 (db)
OPM-01	750, 400	500	N/P
OPM-09	1,400	700, 550, 500	N/P
OPZ-07	1,550, 400	350	N/P
OPM-04	1,550, 1,500		N/P
OPM-08	1,550, 700		N/P
OPM-10	1,550		N/P
OPZ-03	650		N/P
OPZ-10	1,550, 550, 500, 400		N/P
OPZ-01		900 (db), 1,100	N/P
OPZ-06		600 (db)	N/P
OPM-06 OPM-11 OPZ-11	no polymorphisms detected		

10-R2 snails, one of the most commonly used resistant stocks in investigations of the molecular basis of the *B. glabrata/S. mansoni* relationship. Similar genetic heterogeneity was not detected between snails of another commonly used resistant stock (BS-90). Because of current research interest in these snails in the search for genes that define the resistance phenotype, we felt that a thorough background of their genetic diversity/stability was warranted in order to avoid misscoring of genotypes in future molecular genetic studies. Although our focus is not population genetics, we also point to findings that may be pertinent for furthering our understanding of the population biology of these organisms.

From our earlier crosses between the resistant (BS-90) snails and the susceptible (M-line) snails we were able to demonstrate that RAPD-markers segregated with the adult resistant phenotype (Knight et al., 1999). We hoped that crosses generated with other resistant snail stocks (e.g., 10-R2) would enable us to not only confirm our earlier results but help identify other DNA markers that may be associated with the refractory phenotype.

The level of variability observed in the 10-R2 snails was higher than expected, given that these snails were laboratory selected and maintained for many years by selfing. However, Mulvey & Vrijenhoek (1981) previously reported polymorphisms for four of 16 allozyme loci studied in this stock. In addition, the 10-R2 snails are derived in part from the M-line stock developed by Newton (1955) (Richards, 1973). M-line snails have been shown, by allozyme analysis, to display a high degree of genetic heterogeneity (Mulvey & Vrijenhoek, 1981; Mulvey & Bandoni, 1994). Earlier molecular studies in our laboratory using the 10-R2 snails, based on RFLP analysis of ribosomal RNA genes, had also revealed a certain degree of genetic heterogeneity within this stock (Knight et al., 1991). Our earlier study was limited in scope, however, and the fact that we can distinguish three distinct subgroups within the stock with only a small subset of primers by RAPD-PCR was unexpected.

Contamination might explain the variability observed in the 10-R2 stock, and has previously been reported in the M-line stock of *Biomphalaria glabrata* (Mulvey & Bandoni,

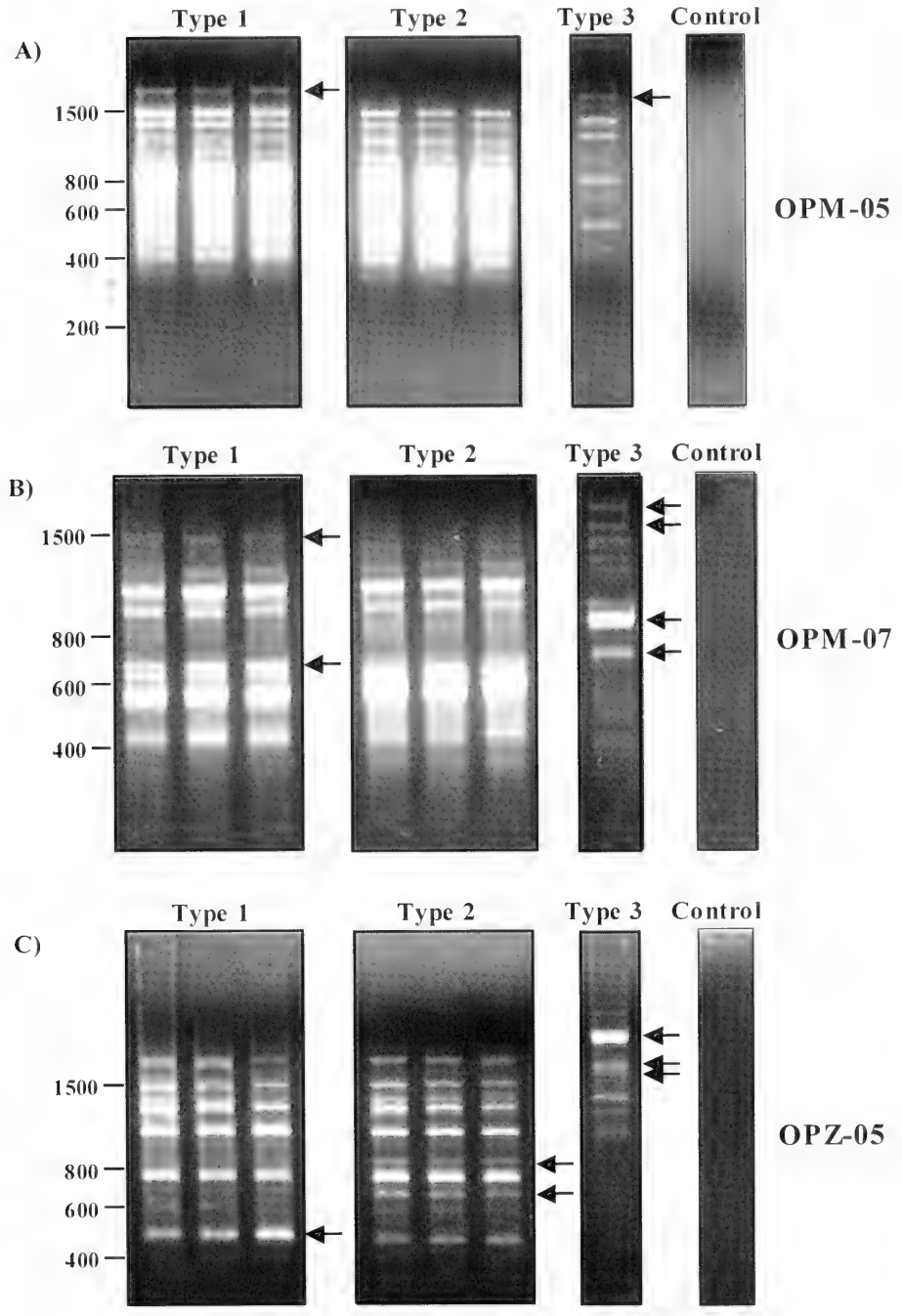

FIG. 1. Ethidium bromide stained agarose gels showing RAPD-PCR products amplified by anonymous primers (A) OPM-05, (B) OPM-07, and (C) OPZ-05 using DNA from individual 10-R2 snails that segregated into three different substocks (Types 1–3). The different Type-specific bands identified with these primers are indicated by the arrows. Control lanes represent amplifications done in the absence of template DNA.

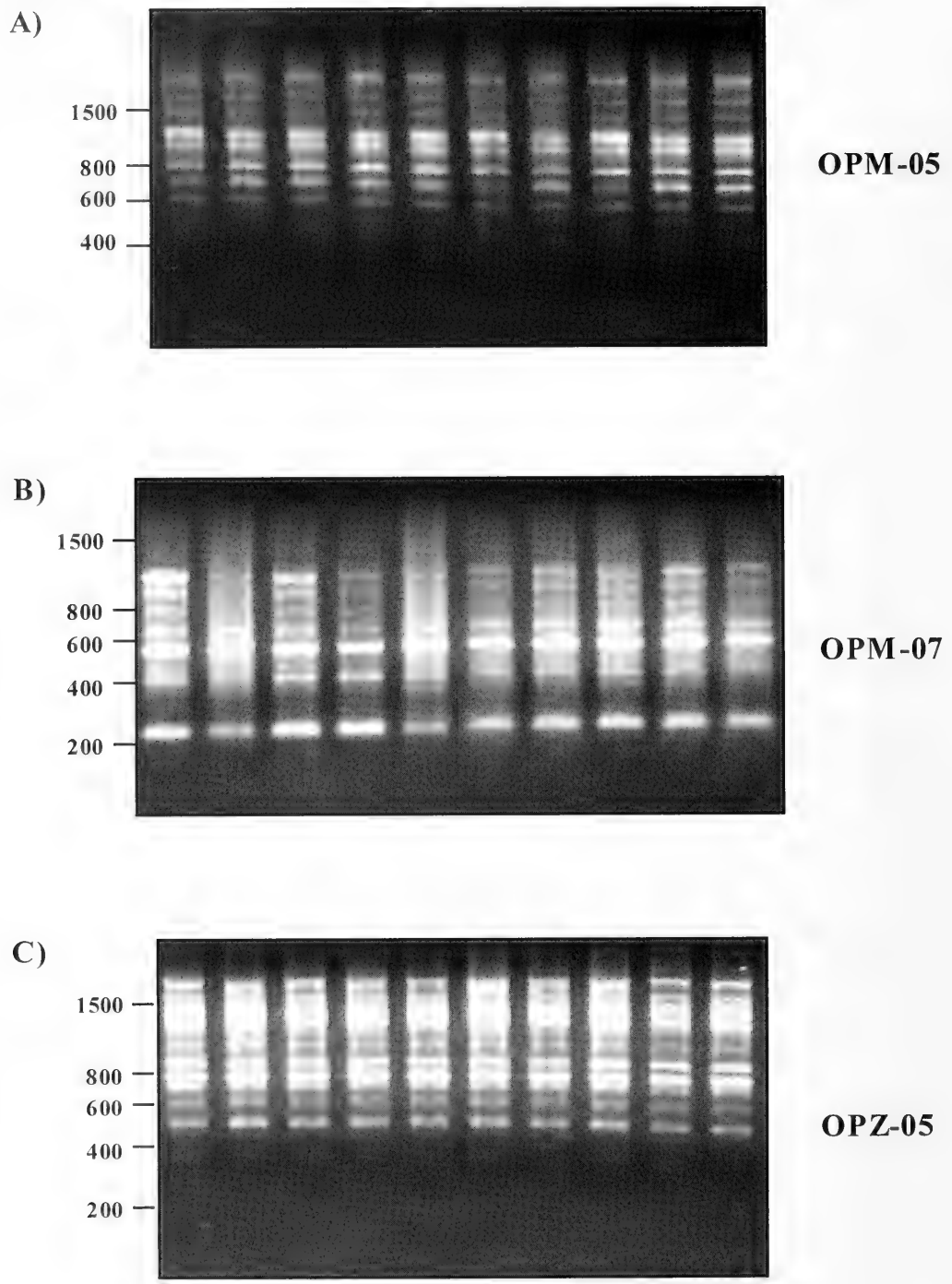

FIG. 2. Ethidium bromide stained agarose gels showing RAPD-PCR products using primers (A) OPM-05, (B) OPM-07 and (C) OPZ-05 and DNA from individual BS-90 snails. Control lanes represent amplifications done with the same primers without DNA template as control.

1994). However, because the 10-R2 snails were reared as individual selfing lineages, it is very unlikely that the within-population variation seen in this stock is due to contamination. The black-eye pigmentation of these snails makes them readily distinguishable from albino stocks maintained in the laboratory.

Several genetic mechanisms might explain the presence of the three multilocus genotypes observed. The occurrence of only three multiple locus genotypes would be consistent with the history of selfing in the snails that we studied. It is possible that the three genotypes found within these snails may reflect derivation from separate self-fertilizing lineages. Further study of these markers using progeny from selfing and outcrossing individuals would be needed to establish this. It is also possible that inbreeding has produced distinctive combinations of alleles at multiple loci that work best in concert, without disruption. Again, further research is needed in order to investigate this possibility. Finally, spontaneous genetic mutations within other susceptible stocks have also been reported. For example, selection of mutants from the NMRI stock gave rise to the LAC-line snails, which display the non-susceptible phenotype, in addition to other abnormalities (Cooper et al., 1994; Cousin et al., 1995).

In contrast to our observations for the BS-90 snails, the laboratory-derived resistant 10-R2 stock, on which considerable research has been reported, has proven to be morphologically more variable (Richards, personal communication). This stock was selected for juvenile resistance and maintained in self-fertilizing lineages. Frequent exposure of snails from our 10-R2 stock, either as adults or juveniles, has revealed no susceptibility to the parasite, and snails from the three types reported here do not have obvious phenotypic differences. Several morphologic differences have, however, been detected in this stock over the years. These include deformed, everted mouthparts, abnormal intestine, variations in egg clutch size, abnormal position of the aorta, unusual shell development, and abnormal tentacles (Patterson & Richards, unpublished). It is also not clear if any of these morphological abnormalities may be related to inbreeding depression in this stock, and warrants further investigation.

The mechanism(s) by which genome plasticity occurs in 10-R2 snails remains unknown. In unrelated, ongoing studies in our laboratory, however, we have identified several expressed sequence tags (ESTs) showing a high degree of sequence identity to genes normally associated with transposable elements, such as transposase and reverse transcriptase (Miller et al., 2001; Raghavan, in preparation). Future studies will compare the frequency (copy-number) and gene activity of some of these retrotransposon-like sequences between 10-R2 and BS-90 snails.

The BS-90 snail stock, which has been used for most of the resistance-related genetics conducted in our laboratory, was derived from snails that were isolated by Paraense & Correa (1963) in the field (Salvador, Brazil). Since its arrival in our laboratory 12 years ago, this stock has remained robust and stable, with no detectable changes either in morphology or fecundity, regardless of whether they are kept as pedigree selfing snails or in a group.

The inability to detect polymorphisms within the BS-90 stock was surprising, as allozyme polymorphisms were detected in a previous study (Bandoni et al., 1995). It is possible that additional variation at the level of the DNA may be revealed using a more sensitive tool, such as the examination of polymorphic microsatellite loci. The analysis of variations within microsatellite loci of *B. glabrata* as a means of assessing diversity among snails is steadily gaining significance (Jones et al., 1999; Malvares et al., 2000). In recent years, genome sequencing projects for several organisms have been initiated. It is hoped that, as is being done for the mosquito vectors of malaria, a genome project may be forthcoming for *B. glabrata*. In view of the present study, we hope that the inherent intra-strain diversity that exists within these snails will be taken into consideration before a particular snail stock is chosen as representative of this organism.

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DEPTH EFFECTS ON ZEBRA MUSSEL REPRODUCTION

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ABSTRACT

Male and female *Dreissena polymorpha* from 2 m depth in Lake Iseo, northern Italy, spawned synchronously, and their gametogenic cycle followed the annual pattern previously observed in other Italian and European populations. Water temperature of 12°C and phytoplankton blooms triggered spawning, and seasonal variation in gametogenesis was related to photoperiod. Some mussels at 25 m depth always had active gonads, and reproduction continued all year, with no seasonal gametogenic phases. Hypolimnetic environmental conditions, such as slight variation in water temperature, darkness and low food availability, may cause this reproductive strategy. No evidence of hermaphroditism or modified sex ratios were noted at either depth. Gametogenesis and spawning ability of zebra mussels in the hypolimnion must be reconsidered.

Key words: *Dreissena polymorpha*, reproduction, depth, gametogenesis, histology.

INTRODUCTION

For the last two centuries, the zebra mussel, *Dreissena polymorpha*, has been steadily spreading over Europe (Stanczykowska, 1977). In Italy, *D. polymorpha* was first detected at the end of the 1960s in Lake Garda (Giusti & Oppi, 1972), and from then on, it reached all the great subalpine lakes, the major northern rivers, and, recently, Lake Trasimeno in central Italy. By the 1980s, it had also invaded the major river systems and numerous inland lakes throughout the northeastern USA (Ram & McMahon, 1996).

Among the factors that favor such a wide geographic distribution, high fecundity is one of the most important (Sprung, 1989). But the mechanisms that regulate zebra mussel reproductive behavior are not well understood. Many authors have investigated its reproduction, both in Europe (Tourari et al., 1988; Borcherding, 1991; Neumann et al., 1993; Bacchetta et al., 2001) and North America (Haag & Garton, 1992; Gist et al., 1997), and all have found an annual cycle involving a gamete development phase in winter and early spring, spawning events in late spring and summer, followed by a gonad resting stage.

Temperature is considered the main environmental factor that regulates both gametogenesis and the start of spawning in *D. polymorpha* (Borcherding, 1991; Bacchetta et al., 2001), whereas such other factors as food availability and phytoplankton bloom are involved in regulating the number of reproductive events (Gist et al., 1997) and the onset of spawning (Ram & Nichols, 1993). In laboratory experiments, the gonadal cycle is not closely associated with photoperiod variation (Borcherding, 1995).

In lakes, *D. polymorpha* forms a characteristic belt around the shores, usually covering the littoral and upper sublittoral zones. The area occupied by this species varies greatly, depending on the littoral zone width and slope. In shallow lakes, it can occupy both inshore areas and mid-lake zones, whereas in deep lakes it has been found to 30 m (Lake Geneva) and 55 m (Lake Constance) (Stanczykowska, 1977). Although zebra mussels are most common between 2 and 8 m, they have been reported from the wave zone to 110 m (Claxton & Mackie, 1998).

In Lake Iseo, also known as Sebino (45°39–49'N, 2°21–30'W), *D. polymorpha* forms dense populations along the wave zones and occurs to at least 50 m, although density progressively decreases from 5 m and is very low at 30–40 m. Lake Iseo lies in the foothills of the Alps and reaches a maximum depth of 251 m. Limno-

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logically, Lake Iseo is classified as warm monomictic, and like other deep lakes, it is distinctively holo-oligomictic. Because of its geographic location in the temperate belt and its morphology, complete overturn is uncommon, only occurring in particularly cold, windy winters (Ambrosetti et al., 1992). The lake is stratified for a long period during summer-autumn and is eutrophic (Garibaldi et al., 1997). These attributes, and observations that depth may control bivalve reproductive cycles (Mackie, 1984), led us to investigate possible differences in reproductive behavior between shallow and deep water mussels. To this end, and because only one work (Claxton & Mackie, 1998) has considered depth variation in gametogenesis and spawning, we used qualitative histological methods to follow the *D. polymorpha* reproductive cycle from two depths and over two spawning seasons in a Lake Iseo population.

MATERIALS AND METHODS

Sampling

To investigate the timing of gonadal development, 20 samples of mussels were collected from a densely settled site in Lake Iseo, near the town of Tavernola Bergamasca, from March 1999 to September 2000. Scuba divers brought up rocks covered with *D. polymorpha* from about 2 and 25 m depths, above and below the summer thermocline. On each sampling occasion, about 60 specimens of *D. polymorpha* > 18 mm in length were detached from the rocks and fixed in aqueous Bouin's for histological analysis.

Histological Methods

After nearly one week in Bouin's fluid, about 30 mussels were randomly selected to determine gonadal condition. Specimens were washed overnight in running tap water, and then their visceral sacs were separated from the remaining tissues, dehydrated in an ascending alcohol series, and embedded in Bio-Plast tissue embedding medium (melting point 57°C). Using a rotary microtome, samples were cut in 7 µm transverse sections at the proximal, central and distal levels of the gonad in order to detect any heterogeneous development within the ovaries. About ten serial sections from each portion were placed on microscope slides and dried overnight at 37°C. The slides were then stained with Mayer's Haemalaun (Merck), counterstained with alcoholic Eosin (Merck), mounted in Eukitt (Kindler GmbH, Freiburg), and observed using a light microscope with calibrated eyepiece. A total of 1,163 mussels were histologically examined.

Maturity Index and Sex Ratio

The stage of gametogenic development for both males and females was described using a four-step qualitative evaluation, as given by Gist et al. (1997): stage 0 = gonad inactive, stage 1 = developing, stage 2 = prespawn, stage 3 = postspawn. The Maturity Index (MI) was calculated for both sexes as the mean gonadal stage for all the specimens examined on each sampling occasion.

Mussels were sexed by microscopic examination of the histological slides and sex ratios were estimated for all the samples.

Environmental Parameters

From February 1999 to September 2000, we recorded water temperature, food availability, photoperiod, and water transparency. Water temperature was measured at 1, 10, 20 and 30 m. To evaluate food availability, chlorophyll-*a* (Chl-*a*) concentration was determined in integrated samples from six depths from 0 to 20 m collected in a Van Dorn sampling bottle. After collection, the samples were placed in polyethylene bottles, put in thermic bags in the dark, and transported to the laboratory. Once in the laboratory, each sample was filtered through a GF/F glass microfibre filter (WHATMAN, pore size 0.45 µm) and then stored at –4°C until processing. Chl-*a* concentrations were measured with a standard spectrophotometric method (Lorenzen, 1967) after 24 h extraction with 90% acetone. Daylength on each sampling occasion was calculated from sunrise and sunset times published by the Italian Airforce Weather Bureau and reported as light-minutes per day. A Secchi disk was used to estimate water transparency. The epilimnion of Lake Iseo was taken to be the upper 15 m, representing 10% of the lake's volume; the hypolimnion was the water mass below 15 m (Garibaldi et al., 1997).

Statistical Analysis

Ninety-five percent confidence intervals were calculated for the MI at each date and depth. Thus, when the confidence intervals of two MIs

TABLE 1. Number of adult mussels histologically examined and variations in sex ratios 2 and 25 m deep. Stage 0, 1, 2, 3 = Gonadal developmental stages according to Gist et al., 1997. M = Mixed stage. DO = Mussels with degenerating oocytes. Sex R = Sex ratios (Females / (Females + Males)). The critical value for χ^2 goodness of the test of equal numbers of females and males, (1 d.f.) at 95% significance is 3.84. * = $p < 0.05$.

	♀♀	Stage						♂♂	Stage					Sex R	X^2	♀♀	Stage						♂♂	Stage					Sex R	X^2
	-2m	0	1	2	3	M	DO	-2m	0	1	2	3	M	-2m	-2m	-25m	0	1	2	3	M	DO	-25m	0	1	2	3	M	-25m	-25m
28/03/99	15	0	15	0	0	0	0	15	0	15	0	0	0	0.50	0	15	0	3	3	9	0	0	15	1	14	0	0	0	0.50	0
08/05/99	14	0	5	6	3	0	2	15	0	1	10	4	0	0.48	0.03	18	0	2	8	8	0	1	11	1	3	4	0	3	0.62	1.69
29/05/99	19	0	1	7	11	0	1	11	0	0	10	1	0	0.63	2.13	13	0	2	3	8	0	0	15	1	6	2	2	4	0.46	0.14
20/06/99	11	0	0	2	9	0	1	19	0	0	6	13	0	0.37	2.13	16	0	2	0	14	0	3	14	1	0	0	10	3	0.53	0.13
10/07/99	15	0	0	4	11	0	0	15	1	0	2	12	0	0.50	0	15	0	1	7	7	0	1	14	2	2	5	5	0	0.52	0.03
25/07/99	18	3	3	1	11	0	0	12	3	0	2	7	0	0.60	1.2	20	0	0	10	10	0	5	10	0	0	8	2	0	0.67	3.33
19/08/99	17	8	9	0	0	0	0	12	12	0	0	0	0	0.59	0.86	15	0	0	8	7	0	6	14	2	0	6	6	0	0.52	0.03
06/09/99	15	6	9	0	0	0	0	21	21	0	0	0	0	0.42	1	23	0	0	8	15	0	6	14	2	0	6	6	0	0.62	2.19
25/09/99	17	0	17	0	0	0	0	11	11	0	0	0	0	0.61	1.29	18	0	1	9	8	0	5	13	5	0	3	5	0	0.58	0.81
16/10/99	14	0	14	0	0	0	0	15	14	1	0	0	0	0.48	0.03	13	0	0	4	9	0	1	17	4	1	7	5	0	0.43	0.53
14/11/99	10	0	10	0	0	0	0	18	15	3	0	0	0	0.36	2.29	16	0	3	0	13	0	2	14	8	0	1	5	0	0.53	0.13
09/01/00	13	0	13	0	0	0	0	14	1	13	0	0	0	0.48	0.07	14	0	11	1	2	0	0	16	8	8	0	0	0	0.47	0.13
20/02/00	14	0	14	0	0	0	0	15	0	15	0	0	0	0.48	0.03	13	0	11	0	2	0	0	17	6	9	1	0	1	0.43	0.53
25/03/00	10	0	6	4	0	0	0	11	0	11	0	0	0	0.48	0.05	21	0	6	0	3	12	3	10	3	6	1	0	0	0.68	3.9*
07/05/00	15	0	1	0	14	0	0	11	0	0	4	7	0	0.58	0.62	10	0	2	0	8	0	0	20	1	9	1	9	0	0.33	3.33
04/06/00	19	0	0	0	19	0	0	10	0	0	8	2	0	0.66	2.79	16	0	2	0	14	0	0	14	0	4	4	6	0	0.53	0.13
01/07/00	12	0	0	1	11	0	0	10	1	0	2	7	0	0.55	0.18	18	0	2	0	16	0	1	12	2	2	5	3	0	0.60	1.2
29/07/00	14	0	0	5	9	0	0	10	2	0	6	2	0	0.58	0.67	16	0	3	0	13	0	2	13	1	0	1	11	0	0.55	0.31
19/08/00	16	1	14	0	1	0	0	10	9	0	0	1	0	0.62	1.38	12	0	1	0	11	0	0	16	0	0	10	6	0	0.43	0.57
23/09/00	16	4	12	0	0	0	0	13	13	0	0	0	0	0.55	0.31	20	0	6	0	14	0	3	10	5	0	4	1	0	0.67	3.33
Total	294						4	268						0.52	1.20	322						39	279						0.54	3.07

overlapped, we considered there to be no significant difference between them. The relationship between the MIs of the two depths was tested using Spearman's Rank correlation analysis (Snedecor & Cochran, 1980), and a pairwise Pearson correlation matrix (Sokal & Rohlf, 1981) was used to determine the correlation between the environmental parameters and the gonadal cycle. A Chi square goodness-of-fit test (Snedecor & Cochran, 1980) was used to test the hypothesis of a 1:1 sex ratio and to determine the relationships between the presence of oocyte degeneration in females from the two depths. Differences were considered significant at the 5% level ($p \leq 0.05$).

RESULTS

The number of specimens at each gonadal stage and the sex ratio on each sampling occasion and at each depth are given in Table 1. The histological appearance of the ovary and testis at different maturity stages is illustrated in Figures 1 and 2.

Reproductive Behavior at 2 m

The gonadal phases of development, maturation, spawning, and inactivity were temporally well defined (Fig. 3). Spawning events occurred in spring/summer starting in May, when the first postspawned specimens were seen, and ending in July (1999) or August (2000). During these periods, samples in pre- and postspawned stages were observed and showed a continuous process of maturation and gamete release. The onset of spawning was always preceded by a period with gonads in the developing stage, followed by a quick gamete maturation phase, highly synchronized among individuals. At the end of the spawning season, testes of all males became inactive until the end of September; October signaled the restart of gametogenesis (Fig. 3). The resting stage of ovaries is shorter than that of testes and involved only a few mussels. At the time of the last spawning, some females were already developing gonads, and by late September all were (Fig. 3). The MI trend confirmed these observations. During the reproductive season,

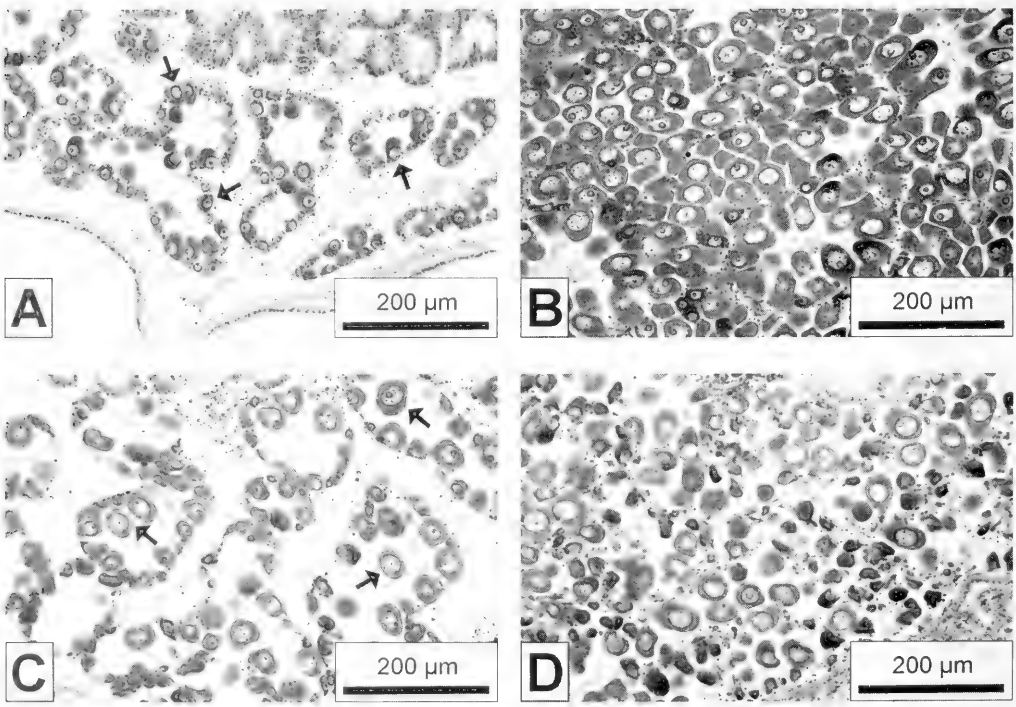

FIG. 1. Histology of the *Dreissena polymorpha* ovary. A. Developing stage: developing oocytes (➡) attached to wall of acini; B. Prespawn stage: acini filled with mature oocytes; C. Postspawned stage: enlarged acini contain only few large oocytes in lumen (➡); D. Mixed stage: acini filled with oocytes at different maturity levels.

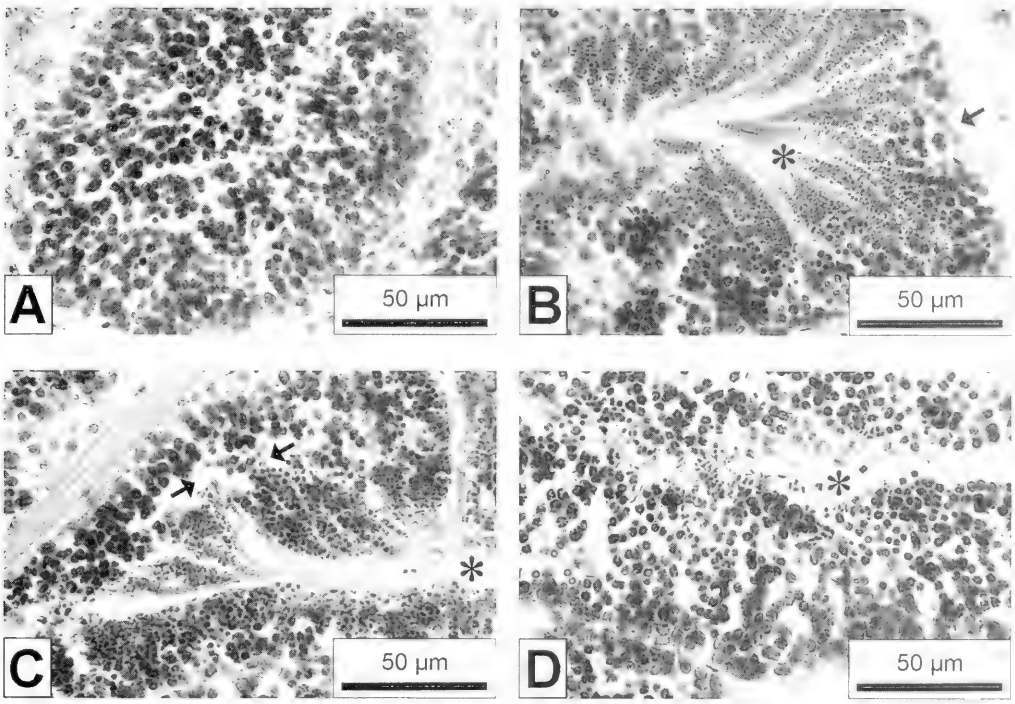

FIG. 2. Histology of the *Dreissena polymorpha* testis. A. Developing stage: detail of an acinus filled with undifferentiated cells, arranged radially; B. Prespawn stage: villi-like processes with spermatozoa (*), spermatocytes on periphery (➡); C. Postspawned stage: villi detached from underlying generative layers (➡), spermatozoa free in lumen (*); D. Mixed stage: detail of an acinus with radially arranged cells, together with mature spermatozoa (*).

both males and females showed values around 2 or greater, but in the other months the MIs were around 1, with lower values for males. Only just before the spawning period were the male and female MIs similar (Fig. 4). The Spearman's Rank correlation analysis showed highly significant synchrony between the MI trends of the two sexes ($r = 0.91$; $p < 0.01$).

Reproductive Behavior at 25 m

Postspawned females were present in all samples, and none with inactive ovaries was ever observed (Fig. 3). The frequency of the postspawn stage was always high, except in winter when the developing stage was dominant. Prespawned ovaries were recorded throughout 1999, whereas except for one specimen in January they were not observed in 2000. This indicates that during 1999, female mussels had spawned successfully following massive oocyte maturation. This did not happen in 2000, suggesting a slackening in reproduction. In March 2000, a new gametogenic stage was observed in which the ovary condition could not be assigned to any of the four stages. We call these morphologies "mixed stages", because the ovary acini were filled with oocytes at different maturity levels. Even though no maturity stage predominated, we underline the spawning activity initiated by 12 mussels, by classifying them as postspawned (Fig. 3, Table 1).

Prespawned, postspawned, and inactive male mussels were almost always present. Synchrony among individuals was low. All four stages of testis maturity occurred contemporaneously at seven different times (Fig. 3). Thus, we hypothesize a tendency towards continuous male gamete production and release even if, contrary to the females, individual mussels often underwent a brief inactive period. The frequency of inactive males increased in the fall and was maximal in November 1999. By winter

and until March, reproductive activity was reduced, with most males in an inactive or developing stage.

The tendency towards continuous reproduction was confirmed by the presence of "mixed stages" in males in May and June 1999, and in February 2000. Their testes had acini with radially arranged cells, typical of the developing stage, together with mature sperm, typical of the postspawned stage, but without the usual detachment between generative layers (Fig. 2). These, too, were classified as postspawned.

In both sexes, MI values were almost always high, particularly in females, for which they exceeded 2 except in January and February 2000 (Fig. 4). The MI trends of the two sexes were synchronous (Spearman $r = 0.62$; $p < 0.01$).

Significantly, more mussels from 25 m depth showed oocyte degeneration than those from 2 m ($\chi^2 = 25.73$, $p < 0.01$). Specimens with this histopathological condition were frequently observed in the 25 m mussels, while it was detected only in May and June 1999 in the 2 m mussels (Table 1). Degenerating oocytes presented a vacuolated apical portion that detached from the lower cytoplasm and accumulated in the lumen of the acini. At times, the oocytes were completely disgregated.

Sex Ratio

Of the 562 mussels from the 2 m depth, 294 were females and 268 males, whereas of 601 mussels from 25 m, 322 were females and

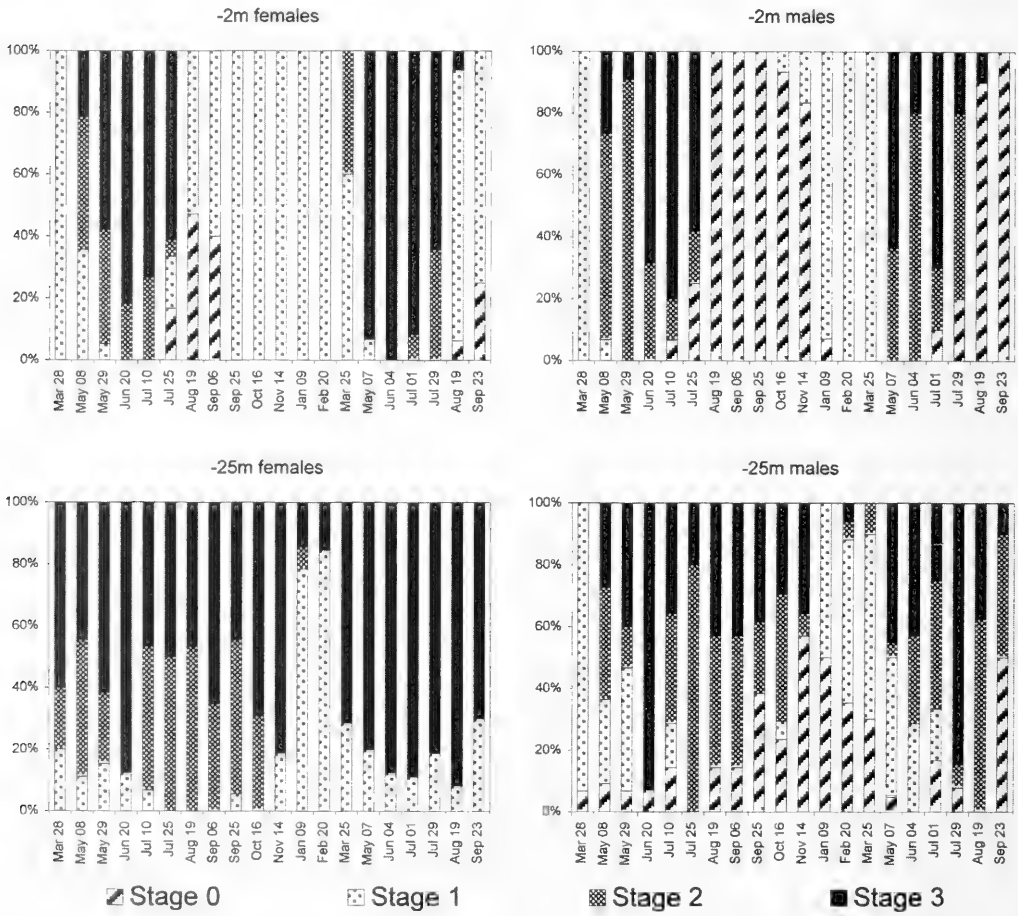

FIG. 3. Gametogenic cycles of adult mussels from 2 (upper panels) and 25 m in depth (lower panels). Histograms show relative frequency of the four gonadal stages for each sampling. Stage 0 = gonad inactive; stage 1 = developing; stage 2 = prespawn; stage 3 = postspawn.

279 males (Table 1). At both depths, there was no significant difference in the total number of males and females (χ^2 = 1.20, p > 0.05 for mussels from 2 m; χ^2 = 3.07, p > 0.05 for mussels from 25 m). The monthly comparisons showed no statistical difference in male and female numbers, except in March 2000 for the 25 m deep mussels (χ^2 = 3.90, p < 0.05). No evidence of hermaphroditism was found.

Environmental Parameters

At 2 m, water temperature showed the same trend in both years, with a rapid increase in spring-summer, reaching the highest values in August 1999 (22.6°C) and July 2000 (23.0°C), with a clear decrease in autumn to a minimum of 6.3°C in winter (Fig. 5). At the beginning of May in both years, temperature rose above

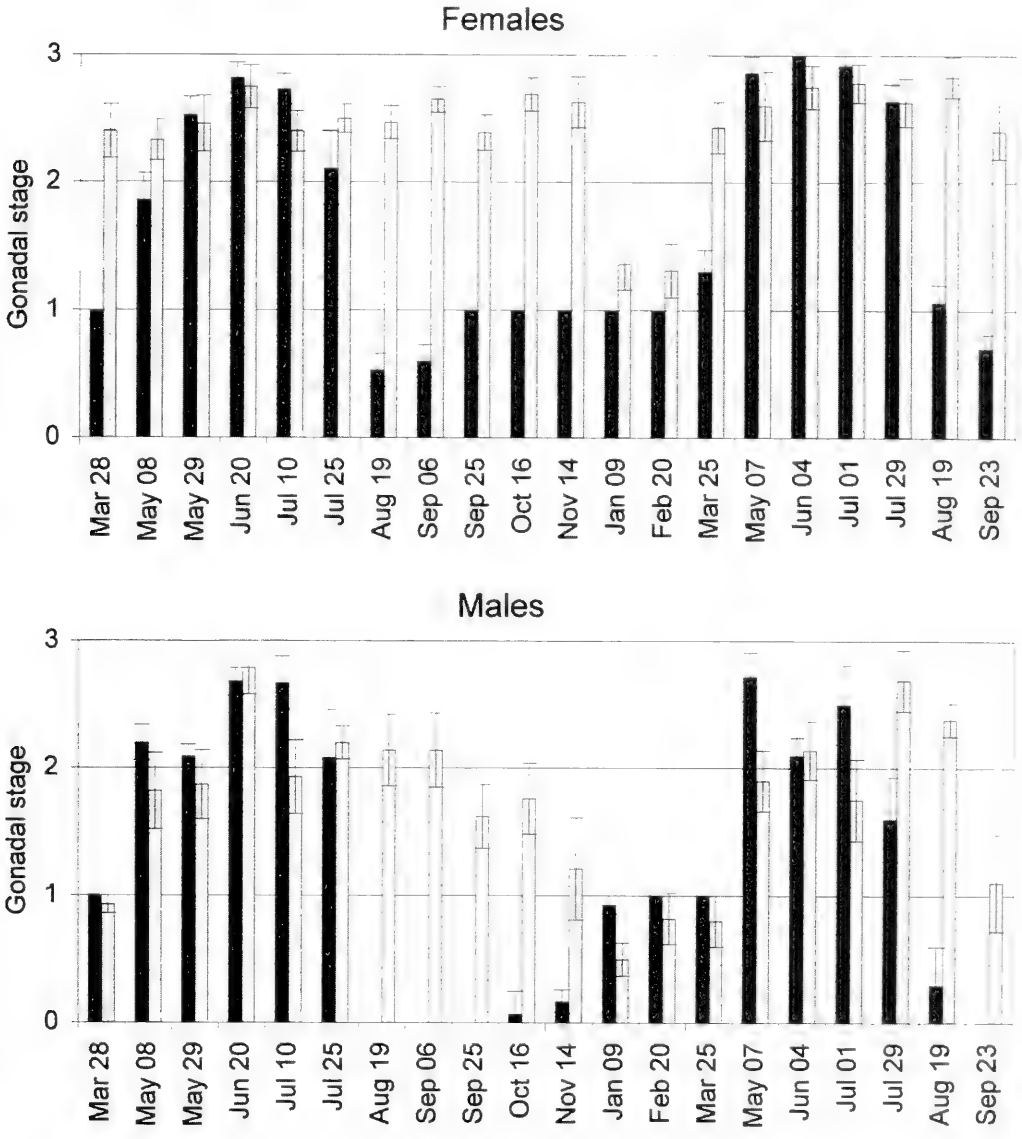

FIG. 4. Maturity Index values from the two depths. Data are presented as the mean gonadal stage ± 95% c.i. Black bars = mussels from 2 m depth. Shaded bars = mussels from 25 m depth.

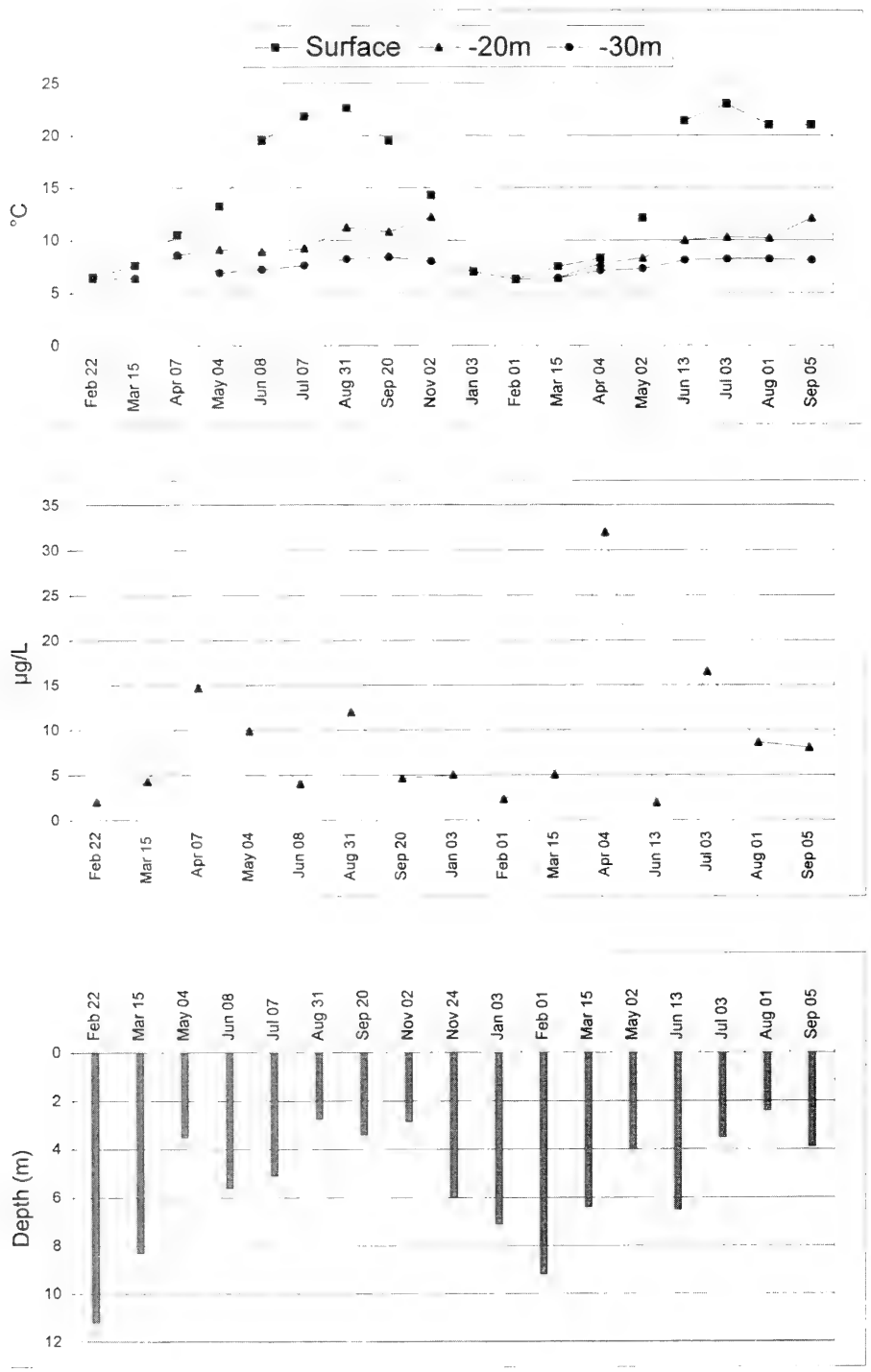

FIG. 5. Environmental parameters. Water temperature (upper panel), chlorophyll-*a* concentration (mid panel), transparency (lower panel).

12.0°C, which has been considered the temperature that triggers spawning (Borcherding, 1991). At 20 m, the temperature stayed below 10.0°C for most of the year and varied minimally, reaching 12.0°C only in November 1999 and September 2000. At 30 m, the temperature curve flattened even more and ranged only between 6.4°C and 8.4°C.

Chl-*a* concentrations showed two peaks per year, one in April before the onset of spawning (especially high in 2000), and one in summer. During the 2000 spring bloom, the highest Chl-*a* concentration value recorded was 32 µg/L. Minimum values occurred in winter, except for the June 2000 sample, when the Chl-*a* was 2 µg/L (Fig. 5).

Transparency showed an opposite trend from Chl-*a*, indicating that algae were the main component of suspended matter. Minimum values were observed in August, concurrent with the summer algal bloom, whereas the highest values were in February. However, transparency never exceeded 11.2 m, indicating that 25 m mussels were always in the dark.

DISCUSSION

The reproductive cycle of zebra mussels in northern Italian waters is annual, as in the rest of Europe (Bacchetta et al., 2001). This was confirmed for the 2 m mussels from Lake Iseo, where the spawning period started in May and ended in July, in both 1999 and 2000. This period followed well-synchronized phases of gamete development and maturation. Oogenesis restarted soon after the end of the last spawning, while spermatogenesis began later. In general, males and females showed similar reproductive patterns, culminating in synchronous spawning, except for the longer resting gonad period in males than in females. In fact, females had empty gonads only in a few cases, indicating that they began gamete production for the next season just before the end of the late spawning events.

These results corroborate those from other Italian water bodies (Bacchetta et al., 2001), suggesting that in shallow waters a similar course of reproductive events may be generalized for all subalpine populations of *D. polymorpha*.

Reproductive behavior at 25 m differed greatly from that at 2 m. Intense spawning activity occurred throughout the study period, except during winter months, when reproduction slackened. The constant presence of spawning mussels indicates a much reduced annual reproductive pattern for *D. polymorpha* at this depth. The female MI trend confirmed this (Fig. 4), and MI values always exceeded 2, except in January and February 2000. In these two months, the MI was still over 1, which agreed with the reduction in spawning activity, in contrast to clear reproductive inactivity.

The lack of prespawn females at 25 m in 2000 may indicate different reproductive behavior in the two years. By March 2000 females may be unable to mature large numbers of oocytes simultaneously, modifying the reproductive event from an "explosive" phenomenon to a slow and continuous release of gametes. But why such behavior? At 25 m, environmental conditions may prevent a regular annual course of gamete maturation and spawning. Thus, reproductive events may only happen once in two or more years. The high frequency of mussels with developing ovaries in January and February 2000, not followed by prespawn specimens, support this assertion. Moreover, the "mixed stages" observed in females after these months strengthen this hypothesis.

Regarding males, their reproductive pattern was similar in the two years and, as in the females, differed from that of those living near the surface (Fig. 3). The presence of all four stages of testis maturity in many samples indicated a very low level of synchronization, but suggests a tendency towards continuous reproduction. Nevertheless, the course of the male gonadal cycle at 25 m also differed from that of the females, mainly in the percentage of inactive gonads observed in males all year round. The difference between sexes may be a result of the major energy demand to mature oocytes, which at 25 m, could be a limiting factor.

The loss of seasonality in deep water may result from the environmental conditions in the hypolimnion, including small variation in water temperature, darkness, and low food availability (perhaps because of the stable deep water environment, contrasting with the shallow water wave movement). In the epilimnion, many environmental factors contribute to regulate gametogenesis and spawning in bivalves. The most important are usually considered to be water temperature, food availability, photoperiod, and depth (Giese & Pearse, 1979; Mackie, 1984). It is commonly held that for *D. polymorpha* water temperature is the main factor involved in triggering spawning, whereas food availability plays a role in determining the num-

ber and intensity of reproductive events (Borcherding, 1991; Ram et al., 1996). Although photoperiod does not affect gametogenesis in laboratory experiments (Borcherding, 1995), it has well-recognized regulatory properties in many other invertebrate species (Bohlken & Joosse, 1982; Olive & Pillai, 1983; Foster & Hodgson, 1995), including bivalves (Giese, 1959). With regard to depth, the temporal aspects of breeding strategy vary with depth, although it is often difficult to separate the effect of temperature and depth (Mackie, 1984; Claxton & Mackie, 1998).

In many European, Russian, and American populations, breeding starts when water temperature exceeds 12°C, even if other environmental conditions differ markedly according to the populations examined. Stanczykowska (1977) indicated 15°C as the temperature when spawning starts, whereas Sprung (1987) stated that a range of 12–14°C is suitable for spawning, with an optimum around 18°C. Tourari et al. (1988) observed that gamete spawning occurs when temperature reaches 16–17°C, whereas Borcherding (1991) and Neumann et al. (1993) reported the onset when water temperature exceeds 12°C. In North America, Haag & Garton (1992) found that spawning started between 22°C and 23°C, even if in the same waterbody, Lake Erie, disjunct populations start spawning at different temperatures (Nichols, 1996). McMahon (1996) indicated that spawning can begin at 12°C, but is maximized around 17–18°C, whereas Gist et al. (1997) reported the onset of the breeding season when water temperature is above 20°C.

Our results indicate that 2 m deep mussels started spawning in May when water temperature reached 13.2°C (1999) and 12.1°C (2000), thus triggering the event, confirming the observations of Borcherding (1991) and Neumann et al. (1993) in central Europe, and of Bacchetta et al. (2001) in other north Italian water bodies.

The lack of data about the relationship between photoperiod and the *D. polymorpha* reproductive cycle does not permit speculation about the role of this factor on the onset of gamete deposition. However, previous data by Bacchetta et al. (2001) show delayed spawnings in a river population compared to a lacustrine population, despite the same light conditions. In fact, while in Lake Como gamete release started at the beginning of May, when water temperature reached 13°C, in the Adda River this threshold was reached only two weeks later.

Photoperiod played a major role in regulating gametogenic phases, because in 2 m deep mussels, this factor was correlated with MIs trend ($r = 0.75$; $p < 0.001$ for females, $r = 0.69$; $p < 0.01$ for males).

Even if Chl-*a* concentration was not significantly related to the reproductive cycle, we suggest that the two Chl-*a* peaks preceding the spawning season may be involved in spawning induction by signaling the trophically advantageous conditions for success of the subsequent larval developmental period. In *D. polymorpha*, phytoplankton blooms, with their associated chemicals, may be the first inducer of gamete release, followed by further chemical stimulus associated with gametes that induces spawning in the opposite sex (Ram & Nichols, 1993). In conclusion, the *D. polymorpha* gametogenic events strictly followed the seasonal variations of photoperiod, while spawning events were mainly regulated by food availability and water temperature.

At 25 m depth, below the thermocline, this reproductive pattern vanished. Water temperature never exceeded the threshold of 12–13°C for the onset of spawning, but stayed for most of the year below 10°C, the value that has been considered the minimum spawning and fertilization temperature for *D. polymorpha* (Sprung, 1987). We can say nothing about fertilization and larval developmental success at this depth, but both males and females matured and released their gametes, as evidenced by the presence of spawning specimens, even when temperature was 6–7°C. *Dreissena polymorpha* also reproduces at low temperatures in other regions: in Lake Constance, at 4.5–5.5°C, and in Lake Grosser Plöner at 2.5°C (Walz, 1978). Nichols (1996) reported that zebra mussel larvae were collected at temperatures below 5°C, and that *D. polymorpha* is theoretically able to produce larvae at temperatures below 10°C.

Another dreissenid, the quagga mussel, *Dreissena bugensis*, has been reported to spawn at low temperatures in deep waters (Roe & MacIsaac, 1997). These authors observed gonadal development and spawning at 4.8°C in Lake Erie, and Claxton & Mackie (1998) found that *D. bugensis* and *D. bugensis* "*profunda*" spawned in the same lake at 9–10°C.

While it has now been shown that *D. bugensis* spawns in the hypolimnion at tem-

peratures below the minimum dreissenid spawning and fertilization temperature (Claxton & Mackie, 1998), our findings suggest that this minimum must also be reconsidered for *D. polymorpha*, and that the zebra mussel is able to reproduce in a hypolimnion environment. This contrasts with the findings of Claxton & Mackie (1998), who found no gametogenic development or spawning in hypolimnetic Lake Erie zebra mussels.

In our study, significantly more females with degenerating oocytes were observed at 25 m than at 2 m ($\chi^2 = 25.73$, $p < 0.01$). Oocyte degeneration in *D. polymorpha* is triggered by several cues, among them, low temperature and low food availability (Borcherding, 1995). The presence of degenerating oocytes in the ovaries, together with detritus clearly visible in the lumen of the acini, indicates intense recycling activity by the gonad in disadvantageous environmental conditions. This has been previously observed in *D. polymorpha* (Bielefeld, 1991), as well as in other mollusks, for example, *Mytilus edulis* (Pipe, 1987) and *Mactra veneriformis* (Chung & Ryou, 2000). The hermaphroditic state in gonochoristic bivalves is also determined by environmental factors (Mackie, 1984), but even if the particular hypolimnetic conditions in Lake Iseo caused oocyte degeneration and altered spawning activity, they did not seem to influence sex determination. In fact, the sex ratio, even in deep waters, was not significantly different from 1:1, and no hermaphrodites were seen, contrary to Antheunisse (1963), who found 4% hermaphroditic mussels in the Amstel River.

In conclusion, the reproductive behavior of 25 m deep mussels differed significantly from that of those in shallow water, where an annual pattern was confirmed. In deep water, at the low limit of the thermal discontinuity, reproduction continued all year, without seasonal changes of gametogenic phases. Elsewhere, reproduction can continue throughout the year, depending mainly on the geographic locality of a given water body and its thermal condition, as in warmer reservoirs, where the reproductive period is longer (Stanczykowska, 1977). Even in the hypolimnetic waters of Lake Iseo, where temperatures were always low, zebra mussels were observed to spawn continuously, suggesting that variations in water temperature are more important in regulating the timing of reproduction than absolute temperature.

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THE EGG OF *OXYCHILUS* (*DROUETIA*) *ATLANTICUS* (PULMONATA: ZONITIDAE): SURFACE STRUCTURE AND CARBOHYDRATE COMPOSITION

Armindo S. Rodrigues[1*], Regina T. Cunha[1] & Benjamin J. Gómez[2]

ABSTRACT

Oxychilus atlanticus is an oviparous species with eggs of the heavily calcified type. The eggshell is formed of calcite crystals and is endowed with large amounts of neutral polysaccharides, galactogen and glycogen, providing nutritive reserves for embryo development. The egg is surrounded by mucopolysaccharides as it passes along the spermoviduct. This component probably acts as a mechanical support element, as well as a chelation promoter of calcium ions during eggshell construction.

Key words: oviparous snail; calcite crystals; galactogen; glycogen; mucopolysaccharides.

INTRODUCTION

Apart from the works of Bayne (1966, 1968), Tompa (1974, 1976, 1979), Baur (1994), Baur & Baur (1998), and Heller (2001), little is known about the structure and composition of pulmonate eggs, and no information exists about egg formation inside the spermoviduct of oviparous species. This could be due to the fact that, in oviparous species, such as the stylommatophoran land snails and slugs, the eggs are laid as they are made inside the spermoviduct and distal female genital ducts (Tompa, 1979).

The surface structure, composition and function of molluscan eggs have received little attention. In general, the egg is known to protect the embryo against adverse environmental effects, but it is also considered to act as a calcium reserve for itself and the newly hatched juvenile (Fournié & Chétail, 1982a). Baur & Baur (1998) consider that eggs are decisive for the survival of the offspring in invertebrates, especially when the species do not have post-laying egg care.

After studying a great number of eggs from different gastropods, Hall & Taylor (1971) concluded that the eggshell is generally made by calcite or aragonite crystals, although they refer to a new form of calcium carbonate crystals, vaterite, in the eggshell of four species of *Ampullaria* Lamarck, 1799, for the first time. According to Tompa (1976), 36 of 65 stylommatophoran families have eggshells made of calcium carbonate, that is, in calcareous eggs, commonly in the form of calcite. Tompa (1974) suggests that the reason for the common presence of aragonite in the body shell is due to its higher resistance to the abrasion by soil particles, whereas calcite, frequently found in the eggshell, involves less investment because it occupies more space per mole of $CaCO_3$ secreted.

Tompa (1976) classified the eggs of the Stylommatophora into three types – heavily calcified (*Cepaea nemoralis* Linnaeus 1758), partly calcified, and uncalcified (Limacidae), according to the degree of calcification. In the same work, the size of the egg and its surface ultrastructure were considered to be of taxonomic value, even between closely related species.

Concerning the resources of the eggs, Heller (2001) considers that they are rich in energy and nutrients, including proteins, mucopolysaccharides and calcium.

This study describes the carbohydrate composition of the egg of *Oxychilus (Drouetia) atlanticus* (Morelet & Drouët 1857) (Pulmonata Zonitidae) during its formation inside the spermoviduct, as well as the structure and composition of its surface after being laid.

The aim of this work is to contribute to the knowledge of the reproductive biology of an endemic species from São Miguel Island, Açores.

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MATERIALS AND METHODS

Specimens of *O. atlanticus* were collected at Abelheira, 3 km north of Ponta Delgada, between June and September. The species reaches maturity between June and November, with a shell diameter of 7 mm (Rodrigues et al., 1998). From over 200 specimens analysed, only two adults had eggs inside the spermoviduct, observable through the translucent shell. Therefore, only these two specimens were used for histochemical tests.

Genitalia with eggs were dissected and fixed in Baker's formol (Culling, 1974), embedded in paraffin, and sectioned at 7 μm thickness. Sections were routinely processed for light microscopy and stained using various histological and histochemical methods.

The following histochemical methods were carried out: The Periodic acid-Schiff (P.A.S.) technique was used as a general method for identifying neutral carbohydrates (Culling, 1974). Acetylation, followed by saponification and diastase treatment, were used as controls (Martoja & Martoja-Pierson, 1970). Alcian blue staining was used at pH = 0.5 to stain strongly sulphated mucosubstances and at pH = 2.5 for carboxylated and weakly sulphated mucosubstances (Martoja & Martoja-Pierson, 1970). Best's carmine was used to identify glycogen deposits, with previous digestion with diastase as a control. Best's carmine was also used to detect the presence of galactogen, according to Grainger & Shillitoe (1952).

In order to study the eggshell structure, individuals of *O. atlanticus* were collected from the field and laid eggs under laboratory conditions from November 1997 to January 1998. The diameter of 40 eggs was measured under a stereomicroscope with the aid of a camera lucida. To perform scanning electron microscope (SEM) observations, the shells of ten eggs were broken and their fragments placed in a chamber with silica gel for two days of dehydration. The material was then mounted on specimen-stubs, coated with carbon and gold-palladium (60–40%) in a vacuum evaporator (JEE 400) for observation with a JEOL SEM (JSM 5410) at 15 kV or 25 kV.

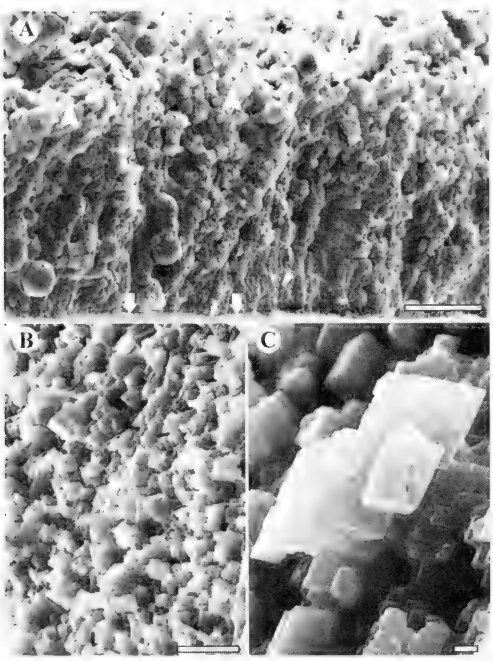

FIG. 1. A. Cross section of a fractured egg of *Oxychilus (Drouetia) atlanticus*. Arrowheads indicate the outer surface; arrows show the inner border (scale bar = 10 μm). B. Surface view of the egg showing the large calcite crystals (scale bar = 10 μm). C. Surface view of the egg showing individual calcite crystals (scale bar = 1 μm).

RESULTS

The eggs of *O. atlanticus* are 1.5 ± 0.05 mm in diameter, with a hard and brittle surface, and a thickness of 34.1 ± 1.9 μm (Fig. 1A). The egg surface consists of a continuous layer of calcium carbonate, which reacts with hydrochloric acid. The calcium carbonate develops as geometric forms (Fig. 1B, C), with a symmetry that fits into a hexagonal system, typical of calcite (Almeida, personal communication). Solids of calcite show a perfect cleavage in three directions that may originate rhombohedral habits (Dana, 1969), as shown in Figure 1B and C.

The histochemical tests reveal the presence of an organic layer, 5 μm in thickness, over the calcified shell, mainly composed of acid mucopolysaccharides and some neutral polysaccharides, which react strongly with alcian blue solution (pH 2.5) and Best's carmine, respectively. The inner shell membranes between the calcified shell and the perivitelline fluid show a high positivity for P.A.S. and a moderate positivity for Best's carmine, revealing the presence of neutral carbohydrates. The histochemical composition of this layer is very similar to that of the perivitelline fluid, the most important feature of which is a complete maintenance of the

TABLE 1. Staining reactions of *O. atlanticus* eggs pulled from the spermoviduct. P.A.S. = Periodic acid-Schiff; Acetyl./P.A.S. = control Acetylation/P.A.S.; Acetyl./S/P.A.S. = control Acetylation/saponification/P.A.S.; gr. = granules; - = no reaction; ± = weak positivity; + = moderate positivity; ++ = high positivity ; +++ = very intense positivity.

Stain	Carbohydrates detected	Outer shell layer	Calcified shell	Inner shell membranes	Perivitelline fluid	Vitellus
Alcian blue pH 0.5	Strongly sulphated mucosubstances	+	-	- gr. ±	-	-
Alcian blue pH 2.5	Carboxylated and weakly sulphated mucosubstances	++	-	±	-	-
Best's carmine	Glycogen and galactogen	++	-	+	+	+
Control		+	-	±	+	-
P.A.S.	Neutral carbohydrates	±	-	++	gr. ++	gr. ++
Acetyl./P.A.S.		-	-	-	-	-
Acetyl./S/P.A.S.		+	-	+	gr. ++	gr. ++
P.A.S.-without oxidation		-	-	-	-	-

reaction intensity with Best's carmine test and control, indicating the presence of galactogen. In the vitellus, the observed polysaccharide is glycogen because it shows a high positivity for Schiff's reagent and Best's carmine, but it is digested by diastase (Table 1).

DISCUSSION

Oxychilus atlanticus is an oviparous species in which a sequential synthesis and release of each egg occurs, with a clutch consisting of 5–6 eggs (Rodrigues & Cunha, unpubl. data). The difficulty in finding gravid individuals in *O. atlanticus* may be related to its oviparity, as stated by Tompa (1979) for other oviparous species. He reports that, in thousands of specimens analysed, not a single individual from the oviparous species was found to be gravid, in contrast with the ovoviviparous and viviparous species.

The eggshells of *O. atlanticus* bear a compact and brittle construction of calcite crystals, which we classify as of the heavily calcified type (Tompa, 1976; 1984). This strong structure may function as a protection against predators and desiccation, in addition to its role in the support of the internal components (Bayne, 1966). Furthermore, the eggshell may also function as a calcium reserve to supply the developing embryo with enough calcium to form its embryonic shell (Heller, 2001).

In the egg of *O. atlanticus,* mucopolysaccharides prevail in the vicinity of the shell, whereas neutral polysaccharides are the main elements internally.

According to Grainger & Shillitoe (1952), diastase digests the polysaccharide glycogen, but it is unable to digest galactogen. Thus, this methodology is suitable for detecting the presence of galactogen, indicating that the perivitelline fluid and vitellus mainly contain galactogen and glycogen, respectively. Wijsman & Wijck-Batenburg (1987) mentioned that galactogen and proteins are the major components of the egg of *Lymnaea stagnalis* Linnaeus, 1758. According to Bayne (1968), neutral polysaccharides, as well as proteins, are abundant in the perivitelline fluid, whereas mucopolysaccharides occur in the external layers of the egg; the neutral polysaccharides and proteins are mainly involved with the nutrition of the embryo, and the mucopolysaccharides are more involved in mechanical support. We suggest that the mucopolysaccharides found between the eggshell and the spermoviduct epithelium may also act in the chelation of the

calcium ions (Chétail et al., 1982; Fournié & Chétail, 1982b), promoting eggshell mineralization.

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INFLUENCE OF INORGANIC COMPOUNDS ON FOOD SELECTION BY THE BROWN GARDEN SNAIL *CORNU ASPERSUM* (MÜLLER) (GASTROPODA: PULMONATA)

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ABSTRACT

Cornu aspersum's (synonym: *Helix aspersa*) ingestion rates were determined for 19 wild plant species and revealed strong feeding preferences. The plant species were classified according to their palatability. The inorganic contents of 3 appetent and 3 inappetent plants, analysed by ICP-MS, revealed significant differences, the appetent species being poorer in zinc and richer in calcium than inappetent ones.

Trials facing isolated snails with a test solution against distilled water as control were performed. Farm snails previously fed with a calcium-rich food did not react differently towards two solutions of different calcium carbonate concentrations, whereas wild snails fed with a calcium-lacking food significantly preferred a 1 mg x ml^{-1} calcium carbonate solution. Farm snails were significantly repelled by a 13 mg x ml^{-1} zinc sulphate solution.

The detection of inorganic compounds by snails and its possible influence on feeding regulation is discussed.

Key words: *Cornu aspersum*, *Helix aspersa*, food selection, inorganic compounds, calcium, zinc

INTRODUCTION

Chemoreception via the tentacles, lips and foot (Croll, 1983; Kohn, 1983; Chase, 2002) enables a snail to direct itself towards the food source (olfaction), to analyse it by touch and taste, and to determine whether it is a suitable food or not. This analysis requires the intervention of a specialized olfactory neuronal system (Chase, 2002) and learning capacities linked with previous feeding history (Balaban, 1993; Desbuquois & Daguzan, 1995; Ungless, 1998). Associative learning and post-ingestive effects may also modify future food selection (Gelperin, 1975; Chevalier et al., 2000).

Several factors may influence the feeding choices of terrestrial molluscs. Secondary metabolites produced by plants, such as terpenoids (Gouyon et al., 1983; Linhart & Thompson, 1995), glucosinolates (Glen et al., 1990) or alkaloids (Speiser et al., 1992; Chevalier et al., 2000), were recognized as deterrent for slugs and snails, and physical features of plants such as height (Rathcke, 1985) or texture (Wadham & Wynn Parry, 1981) may also constitute a barrier against feeding activity. Some inorganic compounds, such as copper, calcium and trace metals, are necessary nutrients for molluscs (Johannsen & Solhøy, 2001), whereas chrome, nickel or selenium are not essential (Simkiss & Mason, 1983). Because of seasonal needs for calcium, snails store this mineral mainly as calcium carbonate and possess high reallocation capacities (Tompa & Wilbur, 1977; Fournié & Chétail, 1984). As calcium phosphate, it constitutes the mineral rings of the spherites located in the calcium (crypt) cells of the digestive gland (Almendros & Porcel, 1992) that have a heavy metal detoxifying function (Beeby & Richmond, 1988).

Few studies have dealt with the role that inorganic compounds might play in snail nutrition. Williamson & Cameron (1976) and Wadham & Wynn Parry (1981) hypothesized that the silica content of grasses may be responsible for their rejection by the snail *Cepaea nemoralis* and the slug *Deroceras reticulatum*, respectively. High levels of cadmium, copper and zinc

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were found to reduce the food intake of snails and be toxic (Laskowski & Hopkin, 1996; Gomot-de Vaufleury, 2000). Iglesias & Castillejo (1999) have suggested that the appetence of *Urtica dioica* for *Cornu aspersum* was linked with its richness in calcium.

The aims of this study were to investigate the plant preferences of *C. aspersum* and relate these preferences to the mineral composition of six selected food plants. Trials were then performed to observe the snail's gustatory sensitivity when faced with the most important minerals revealed by the analysis.

MATERIALS AND METHODS

Consumption of Plants

Samples of 19 plant species were collected in two coastal sites where populations of *C. aspersum* were well established. Three plant species were common to the two sites. Those sites were in the salt-pans of Guérande, France, and in the polders of the Mont-Saint-Michel bay, where we determined previously the diet of *C. aspersum* (Chevalier et al., 2001). Twenty-two groups of farmed snails, each of 15 snails of equivalent sizes (32.4 ± 1.0 mm) and weight (11.0 ± 1 g) were used (ANOVA on sizes: df = 21, F = 0.218, p = 0.99). These snails were considered as naive as they originated from a snail farm, had always been fed with a cereal-based flour and had never experienced any fresh plant material. They were starved two days before the experiment.

Snails were kept individually in plastic boxes and received a fresh sample of one plant species weighing around 2 g. The relationships between fresh and dry plant weights were established with plant samples oven-dried to constant mass. After 48 h, plant remains were weighed, dried and the dry weight of plant ingested calculated. It was then divided by the fresh weight of the snail to obtain ingestion rates. Each snail was used once and each plant was tested against 15 snails.

ICP-MS Analysis

Six of the 19 plant species studied were chosen according to their strong appetence or inappetence: three from Guérande: *Picris echioides* and *Carduus tenuifloris* (Asteraceae) and *Beta maritima* (Salsolaceae), and three from the Mont Saint-Michel polders: *Urtica dioica* (Urticaceae), *Brachythecium rutabulum* (Bryophyta Brachytheciaceae), and *Elytrigia repens* (Poaceae).

Leaf samples of those six plants were collected in the field, rapidly frozen in liquid nitrogen, and dried by lyophilisation. Each powdered sample (nominally 100 mg) was digested in a screw-top Teflon® bomb (Savillex®, USA) on a hot-plate by three treatments using: (1) nitric acid (HNO_3 14N sub-boiling grade); (2) hydrogen peroxide (Analytical reagent 30%); (3) nitric acid together with hydroxyfluoric acid (HF 29N sub-boiling grade). The sample was dissolved in HNO_3 and evaporated to dryness. The completely mineralised samples were dissolved in 100ml of HNO_3 0.37N (HNO_3 14N diluted with ultrapure deionized water Milli-Q® system).

Samples spiked with 100 ppb of indium (Internal standard), were analyzed with an Inductively Coupled Plasma Mass Spectrometer (ICP-MS Agilent-Technologie® model HP4500) (Table 1). Calibrations were determined using synthetic multi-element solutions. To quantify the accuracy of our ICP-MS analyses, we used the NIST standard SRM 1573a (Standard Reference Material of Tomato leaves – National Institute of Standards and Technology, USA), and a reagent blank.

Calcium Carbonate and Zinc Sulphate Experiments

Six batches of 35 to 50 adult snails of equivalent sizes (30.6 ± 1.0 mm) and weights

TABLE 1: ICP-MS operating conditions

Instrument parameters:	
Plasma gas	15L/min
Auxiliary gas	1.0L/min
Carrier gas	1.13L/min
Nebulizer	Cross flow
Spray chamber	Scott
T° spray chamber	2°C
CeO^+/Ce^+	0.6%
Ce^{++}/Ce^+	1%
Data acquisition parameters:	
Quantitative analysis	3s/mass
Repetition	2

(8.9 ± 1.0 g) (ANOVA, df = 59, F = 0.01, p = 0.991) were used. These snails, originating from different clutches were maintained at 20°C, 80% relative humidity under a 12 h light-12 h dark period. Two days before the experiment, they were starved in order to enhance their feeding motivation. 30 min before the test, their locomotion was stimulated by a gentle spray of tepid distilled water. At the beginning of the experiment, carried out during the scotophase, they were individually placed at the bottom of a plastic box (11.5 x 8.5 x 4.5 cm) between two nylon gauzes of 24 cm^2 each. One gauze was impregnated with 2 ml of distilled water, the other with 2 ml of the test solution. Boxes were covered with a transparent glass sheet. They were observed in dim-light for 30 min and the time spent on the gauzes was checked. Time was recorded when snails remained active, not retracted into their shells, head and lips in contact with the gauze.

Among the six batches, two comprised naïve snails reared with a specific meal rich in calcium carbonate (20% $CaCO_3$) ("farm snails"). Two other batches comprised wild snails from Rennes, France, fed with lettuce for two months before the experiment ("wild snails"). Lettuce is well known as attractive to snails and also poor in calcium, between 300 and 500 mg x kg^{-1} (Feinberg et al., 1991; Couplan, 1998). A batch of farm snails and a batch of wild snails were tested with a 0.1 mg x ml^{-1} $CaCO_3$ solution, while the two others were tested with a 1 mg x ml^{-1} $CaCO_3$ solution.

One of the two remaining batches of farm snails was tested with a 1 mg x ml^{-1} $ZnSO_4$ solution, that roughly corresponds to the zinc concentration of lettuce (Dallinger & Wieser, 1984) and the second with a 13 mg x ml^{-1} $ZnSO_4$ solution, a value higher than the toxic threshold of zinc determined by Gomot-de Vaufleury (2000) in the food of *C. aspersum*. This high value compensated for the short time of exposure (30 min), the objective being to demonstrate the perception of this metal by the snail.

Statistical Analysis

Differences in ingestion rates among plant species were evaluated using ANOVA followed by a Fisher's PLSD test when a significant difference was detected. The normality of the data was checked by the Wilk-Shapiro method.

ICP-MS data from Guérande and Mont-Saint-Michel, and data from preferred and rejected plants, were compared by a Student t-test.

The trials data were analyzed using a Wilcoxon, Mann & Whitney test for paired samples. The total activities of the snails – time spent on the test gauze + time spent on the control – were compared between different concentrations by a Student t-test.

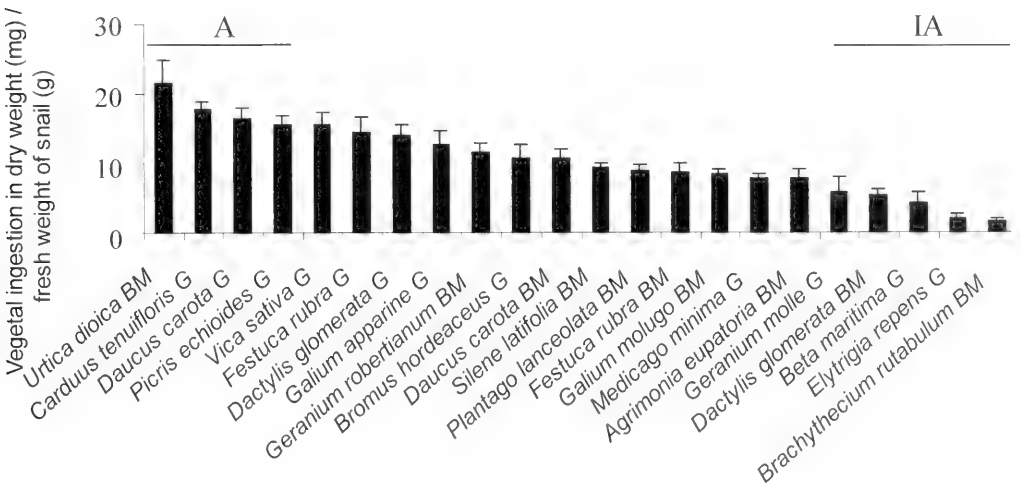

FIG. 1. Laboratory feeding trials showing the ingestion of 19 plant species by 15 adult *Cornu aspersum*. Values are means ± S.E. G = saltpans of Guérande, BM = polders of the Mont-Saint-Michel bay. A group = appetent plants; IA group = inappetent plants; ANOVA, $p < 0.05$.

RESULTS

Consumption of Plants

The results, figured according to decreasing ingestion rates were recorded for 19 species: 14 dicotyledonous, four monocotyledons (Poaceae), and one Bryophyta (Fig. 1). Significant differences between ingestion rates were highlighted by ANOVA ($df = 21$, $F = 12.205$, $p < 0.0001$) but data were continuous so that we could not separate all the plants species into different groups according to their appetence. From the ingestion rates, we could only consider two groups: the A group of four appetent plants that were significantly more ingested than the IA group of 5 inappetent plants (Fig. 1). Then, the ICP-MS analysis was performed on three plants belonging to the A group (*Urtica* sp., *Carduus* sp., *Picris* sp.) and the three others belonging to the IA group (*Beta* sp., *Elytrigia* sp., *Brachythecium* sp.).

Among the 11 most ingested plants, Poaceae were represented by *Festuca rubra, Dactylis glomerata* and *Bromus hordeaceus*, whereas the tough *Elytrigia repens* figured among the less eaten species. *Festuca rubra* and *Dactylis glomerata* seemed to be less palatable for *C. aspersum* when they came from the Mont-Saint-Michel than from Guérande.

Inorganic Compounds

Forty-two elements were quantified in the plant samples, but we show only the 12 elements having biological interest, that is, Na, Mg, K, Ca, Mn, Ni, Cu, Zn, As, Sr, Cd, Pb (Table 2).

With 52 and 21 g x kg^{-1} respectively, *B. maritima* and *P. echioides* from Guérande showed high sodium contents compared to the other species (Table 2). The lead content of the moss *B. rutabulum* reached ten times the level found in *E. repens* or *U. dioica*; *B. maritima* was about eight times richer in cadmium than *E. repens* or *B. rutabulum*.

Plants from Guérande were significantly richer in sodium than Mont-Saint-Michel plants (t-test, $p = 0.049$). No other significant difference, for any compound, was observed between the plants from the two sites (t-test, $n = 6$, $p > 0.05$). IA plants showed significantly lower concentrations of calcium and strontium than the A ones. A plants were roughly ten times richer as the IA plants. On the other hand, IA plants had a high zinc concentration (t-test, $n = 6$, $p = 0.049$).

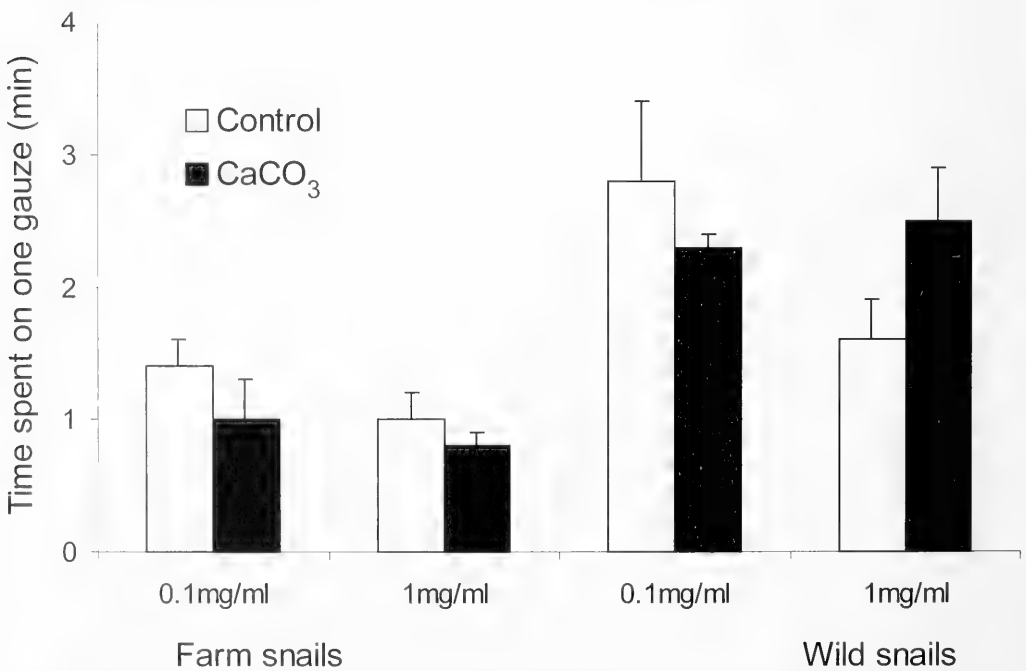

FIG. 2. Time spent by adult snails on a gauze impregnated with $CaCO_3$ solutions compared to a control gauze saturated with distilled water. Values are means ± S.E.

TABLE 2: Quantitative results obtained by ICP-MS analysis. The concentrations (mg x kg ^{1} dry sample) were corrected by a dilution factor. DL (detection limits) were calculated from three times the standard deviation of the blank water signal counts, divided by the sensibility factor based on analysis of 10 ppb standard. *indicates a significant difference between appetent and inappetent plants for the related compound.

Isotope			Na 23	Mg 25	K 39	Ca 43*	Mn 55	Ni 60
Standard	SRM 1573a tomato leaves	Average n = 4	138	11,635	26,590	50,688	254	1.57
		SD	2	220.7	416	253	4	0.02
		RSD%	2	2	2	0	1	2
Standard	SRM 1573a tomato leaves	Certified values	136	12,000	27,000	50,500	246	1.59
		Uncertainties	4	proposed value	500	900	8	0.07
Blank	Blank reagent		0.01056	450 x 10^{-6}	8,900 x 10^{-6}	< DL	20 x 10^{-6}	40 x 10^{-6}
DL	Detection limits		191 x 10^{-6}	5 x 10^{-6}	400 x 10^{-6}	230 x 10^{-6}	2.5 x 10^{-6}	5 x 10^{-6}
Inappetent	*Elytrigia repens* BM		3,248	1,373	23,880	2,769	24	0.47
	Brachythecium rutabulum BM		597	1,576	5,535	8,256	21	3.42
	Beta maritima G		52,130	9,944	23,270	6,633	342	0.84
Appetent	*Urtica dioica* BM		1,299	3,657	21,380	31,210	26	0.52
	Picris echioides G		20,840	2,814	22,400	14,670	32	1.16
	Carduus tenuifloris G		7,345	3,306	48,470	13,030	26	1.01
Isotope			Cu 63	Zn 66*	As 75	Sr 88*	Cd 111	Pb 208
Standard	SRM 1573a tomato leaves	Average n = 4	4.80	30.4	0.127	85.5	1.42	0.573
		SD	0.06	0.4	0.003	0.3	0.00	0.05
		RSD%	1	1	3	0	0	1
Standard	SRM 1573a tomato leaves	Certified values	4.70	30.9	0.112	85	1.52	-
		Uncertainties	0.14	0.7	0.004	proposed value	0.04	-
Blank	Blank reagent		50 x 10^{-6}	320 x 10^{6}	16 x 10^{-6}	40 x 10^{-6}	1 x 10^{-6}	42 x 10^{-6}
DL	Detection limits		5 x 10^{-6}	6 x 10^{-6}	10 x 10^{-6}	1 x 10^{-6}	2.5 x 10^{6}	1 x 10^{-6}
Inappetent	*Elytrigia repens* BM		6.82	30.0	0.027	21.9	0.03	0.28
	Brachythecium rutabulum BM		4.80	40.2	0.453	63.6	0.06	2.81
	Beta maritima G		6.73	49.8	0.058	19.4	0.56	0.27
Appetent	*Urtica dioica* BM		4.41	28.6	0.022	230.3	0.02	0.25
	Picris echioides G		9.30	25.8	0.312	271.1	0.13	0.72
	Carduus tenuifloris G		8.87	25.6	0.761	220.4	0.15	1.81

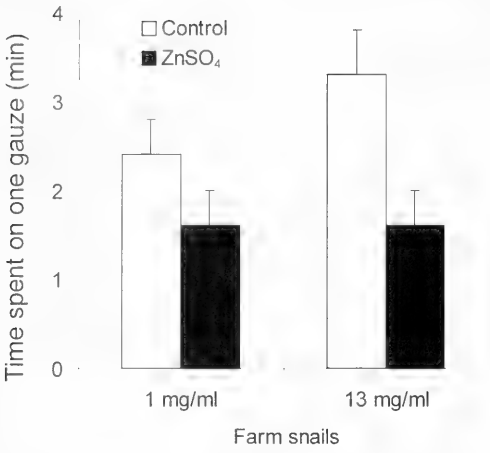

FIG. 3. Time spent by adult farm snails on a gauze impregnated with $ZnSO_4$ solutions compared to a control gauze saturated with distilled water. Values are means ± S.E.

Calcium Carbonate and Zinc Sulphate Experiments

The total activities – that is, time spent on both gauzes – of the wild and the farm snails for the four $CaCO_3$ trials were similar (t-test, n = 140, p = 0.32). Wild snails significantly preferred the gauze impregnated with the 1mg x ml^{-1} calcium carbonate concentration (Wilcoxon, Mann & Whitney test, n = 35, p = 0.036). Wild snails subjected to 0.1 mg x ml^{-1} $CaCO_3$ and farm snails for both concentrations did not behave differently towards the two gauzes (Fig. 2).

The total activities of the two batches of farm snails exposed to two different concentrations of zinc sulphate were not significantly different (t-test, n = 100, p = 0.44). During the 1 mg x ml^{-1} $ZnSO_4$ trials, snails showed a non-significant tendency to avoid the zinc sulphate solution (Wilcoxon Mann & Whitney, n = 50, p = 0.16) (Fig. 3). This reaction became significant with the 13 mg x ml^{-1} $ZnSO_4$ concentration which was tasted half as often as the control (Wilcoxon Mann & Whitney, n = 50, p = 0.04).

DISCUSSION

Amongst the plant species eaten by snails, grasses were represented by *Festuca rubra* and *Dactylis glomerata,* whereas the tough grass *Elytrigia repens* was less appreciated. This result is consistent with our previous data (Chevalier et al., 2001). Williamson & Cameron (1976) and Waddham & Wynn-Parry (1981) hypothesized that the tough texture of some grasses may be responsible for their deterrence towards slugs and snails. Differences in the ingestion rates of the same grass species from the two different locations may be due to the fact that grass species often present subspecies (Metcalfe, 1960). The soil and climate differences between the two sites could also induce phenological and/or toughness differences.

The rejection of the bryophyte *Brachythecium rutabulum* and the sea beet *Beta maritima* could be linked to their richness in lead and cadmium respectively. Bryophyta are known to accumulate heavy metals but the much higher concentrations known to be toxic to *C. aspersum* – 146 mg x kg^{-1} for cadmium (Russell et al., 1981), 12700 mg x kg^{-1} for lead (Laskowski & Hopkin, 1996) – cannot support this hypothesis.

The sodium content of *B. maritima* and *P. echioides*, representing nearly 50% and 30% respectively of the total amount of inorganic compounds recorded may be related to the proximity of the saltpans. Some halophytes were also met near our studied area: *Suaeda* sp., *Obione* sp. or *Salicornia* sp. Considering that free salt (NaCl) is often used as a barrier for molluscs, we may hypothesize that a deterrence threshold for sodium could take place for concentrations around 50 g x kg^{-1} found in *Beta maritima*.

Although other chemical (secondary metabolites) and physical (height, hairiness) characteristics might account for differences in consumption, it seems that inorganic compounds and especially calcium, strontium and zinc could play a role in *C. aspersum*'s feeding choices. Calcium and strontium values are often expressed as Sr/Ca ratios in the literature, as they show similar variations (Klein et al., 1996). In this study, "farm snails" were reared with a flour supplemented with calcium carbonate. Since snails have strong calcium storage and reallocation capacities, especially from their shells (Fournié & Chétail, 1984), it is difficult to assess precisely whether a snail lacks calcium. This becomes possible with wild snails fed with lettuce, 10-fold poorer in calcium compared to industrial snail food. The positive reaction towards calcium carbonate shown by wild snails can therefore be related to this lack. Snails may thus be able to detect the $CaCO_3$ available in the soil or in the plants and

to balance their diet in order to optimize their calcium intake. In term of optimal foraging, nutrients constraints sometimes drive feeding decision (Boyer, 1997). Such an active balance was observed in slugs towards amino-acids (Cook et al., 2000) and was suggested in snails for calcium by Iglesias & Castillejo (1999). Recently, damages made by *C. aspersum* have been observed on house paints in different regions of Brittany. The work carried out with 16 water-based house paints proved that the more calcium they contained, the more snails ingested them (Chevalier & Charrier, 1999; Charrier, in Chesnais, 1999). A comparison between two groups of snails living in Brittany, one group originating from a narrow band of soil rich in calcium and the other from a chalky poor soil, supported the hypothesis that snails lacking this mineral ate more calcium-rich paints. Many works and the present study allow us to state that calcium is one of the major mineral elements governing the feeding strategy of *C. aspersum*, regardless of which factors are controlling its cellular incorporation.

Like copper, zinc is an essential nutrient for snails but over a certain threshold it has inhibitory effects on the growth, development and fitness of snails (Laskowski & Hopkin, 1996; Gomot-de Vaufleury, 2000). Those effects are often accompanied by a decrease in food ingestion (Russell et al., 1981; Simkiss & Watkins, 1991; Laskowski & Hopkin, 1996). The 13 mg x ml^{-1} zinc concentration that deterred snails during our no-choice trials is higher than those found in the three deterrent plant species, but within 30 minutes, the duration of the trial, the response was a fast rejection after contact chemoreception. In contrast, in nature, the snails are regularly exposed to the metals in plants and soil. Therefore, post-ingestive effects may occur after several days, the compounds being stored and becoming toxic by a cumulative pattern.

Our experiment accounts for oral chemoreception, but uptake of calcium (Fournié & Chétail, 1984) and water (Prior et al., 1989) can also be integumental, suggesting the presence of Ca^{2+} channels and aquaporines in the snail integument.

This study has shown that gastropods can use inorganic compounds as clues for deciding whether or not to feed. Nutritional quality of the plants may influence the distribution of the snails in their environment. Snails' pressure on their food plants may in turn influence the balance of competition between plants, resulting in modifications of their distribution. Such studies might contribute to the knowledge of ecological niche occupancy in relation to food resources.

Further investigations on inorganic compounds are needed by using complete artificial diets with different ratios in elements (Ca, Na, Zn) concentrations and by testing these diets on snails deprived specifically of such elements. This could help us to assess whether snails have the capacity to respond to the inorganic compounds contents of plants and to regulate their intake.

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SHELL-BAND COLOR POLYMORPHISM IN *CEPAEA VINDOBONENSIS* AT THE NORTHERN LIMIT OF ITS RANGE

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ABSTRACT

The distribution of black-, brown- and faint-banded morphs in populations of *Cepaea vindobonensis* (Férussac) was established at the northwestern edge of the species' distribution. In the Czech Republic, the species was sampled at 132 localities in the Morava and Elbe river basins, between 48°45' and 50°15'N. Even in this narrow zone, there was a significant trend for increasing frequency of the black-banded morph with increasing geographic latitude and altitude. The variation paralleled the decreasing length of sunshine (April–August), which is > 10% shorter at the northern than at the southern localities. The habitats occupied by northern populations (grassy steppe-like stands) differed from those preferred by southern populations (synanthropic weed stands, mostly stinging nettle). Geographic trends and habitat differences in morph frequencies may be affected by climatic selection. Other possible causes of variation are discussed, comparisons are made with other species, and gaps in evidence are identified.

Key words: *Cepaea*, Helicidae, shell-band color, polymorphism, geographic distribution. climatic selection, microclimate, vegetation.

INTRODUCTION

Cepaea vindobonensis (Férussac) is a medium-sized helicid snail (shell diameter 20–25 mm) living in steppe or ruderal localities of southeast Europe. In the northwest, its distribution extends to north Carpathian, Sudete and east Alp mountains, and only a few populations pass this limit along the Danube and Elbe rivers (Schilder & Schilder, 1953; Lozek, 1956; Kerney & Cameron, 1999). *Cepaea vindobonensis* has been studied less than its close relatives, *C. nemoralis* (L.) and *C. hortensis* (Müller), although this species is common in the area of its distribution. Consequently, geographic variation and ecological significance of shell banding and color polymorphisms are less understood. Variation of these characters is, however, simpler and less marked than in the two congeners, which should make interpretation easier.

The shell of *C. vindobonensis* is whitish with five dark bands. Two or more bands may fuse together, but individuals with confluent bands are rare. The polymorphism consists usually in differences of band color, which varies between black and pale yellow. As the band color becomes paler, the sharpness of band margins decreases so that finally the color of the shell becomes uniformly yellowish. The decolorized "faint-banded" individuals dominate some populations of the Balkan Peninsula and southern central Europe (Zimmermann, 1919; Lozek, 1956; Schilder & Schilder, 1957), whereas northern populations consist of dark-banded individuals. Detailed studies of morph distribution in the northern Balkan Peninsula (Jones, 1973, 1974; Jones et al., 1977) revealed that proportion of morphs in local populations depends on microclimate.

Cepaea vindobonensis is abundant in lowland areas of the basin of the Morava River (Lisicky, 1991). This eastern part of the Czech Republic (Moravia, approx. east of 16°E) is essentially a valley opening to the south. In the western part of the Czech Republic (Bohemia), *C. vindobonensis* lives in north-central lowland parts, mainly along the Elbe River. Earlier investigation (Zimmermann, 1919; Lozek, 1956) showed that Moravian and Bohemian populations differ in the proportion of faint-banded individuals. However, the precise distribution of forms and its environmental correlates were not known. Assuming the effect of climatic selection, I ex-

pected a north-south cline of increasing proportion of faint-banded morph in local populations. The existence of this variation was studied in 106 Moravian and 26 Bohemian populations of *C. vindobonensis* that were sampled and for which geographic and climatic conditions were established.

MATERIALS AND METHODS

Color Morphs

Shell pattern and coloration of *C. vindobonensis* has been illustrated (Jones, 1973; Kerney & Cameron, 1999) and described (Jones, 1973, 1975; Cook, 1998; Staikou, 1998, 1999; Kerney & Cameron, 1999) several times. The descriptions require some precision with respect to variation encountered in populations of the Czech Republic. The shell has five bands conventionally indicated band 1 (dorsal) to 5 (ventral). In populations of the Czech Republic, the occurrence of shells with absent or confluent bands was very rare. Considering this variation was therefore immaterial for quantitative description of the composition of populations, and only differences in band and shell ground color were important. The categories used here are based on bands 3–5 because bands 1 and 2 are narrow and often paler. I distinguish three morphs with respect to color of bands 3–5: (i) black-banded morph with black or dark-violet-black bands (violet coloration often appears in worn living and dead weathered shells), (ii) brown-banded morph, and (iii) faint-banded morph with yellow bands. The ground coloration in black-banded individuals is always white. In band morphs (ii) and (iii) the band margins may be blunted. Brown or yellow color then becomes "diffuse" and "spreads" into areas of white coloration between bands so that final shell coloration may become uniformly pale brown or yellow.

Sampling and Habitat Description

The snails were sampled in 1990–2001 at localities (Appendix) of southern and central Moravia and central Bohemia (Fig. 1). Search for localities started in areas where species occurrence was already established (Lozek, 1956; Lisicky, 1991) and progressed to neighboring territories up to the edge of the species distribution. The sampling was made in April–June when snails are most active. At each locality, living animals and well-preserved dead shells were collected at a plot of usually

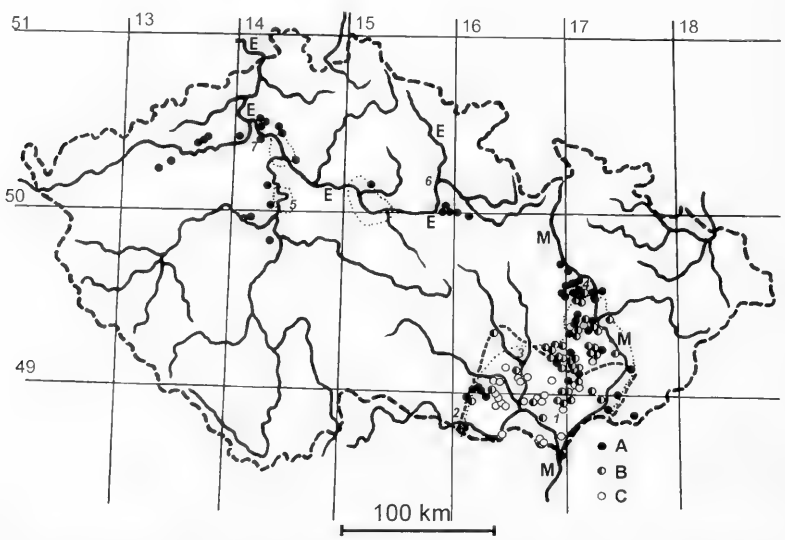

FIG. 1. The presence of shell-band color morphs at local *C. vindobonensis* populations (Appendix). A. Black-banded individuals only. B. Brown-banded individuals present. C. Faint-banded (and brown-banded) individuals present. Dashed line: isotherm of 17°C mean June temperature. Dotted line: isotherm of 15°C mean April–September temperature. Numbers 1–7 indicate the position of meteorology stations (Table 2). The reaches of Elbe (E) and Morava (M) rivers are indicated.

< 1000 m^2 size. The number of animals of each morph was recorded together with geographic coordinates, altitude (established by Global Position System or read from 1:50,000 maps) and vegetation of the locality. Vegetation stands were divided into four categories: grassy closed (grass sward with no or few small spots of bare ground), grassy open (sparse grassy vegetation with large parts of bare ground), forb closed (dense forb stands with no bare ground between the plants) and forb open (forb stands not closed, with large spots of bare ground). Climatic data were taken from published sources. *The Atlas of the Climate of Czechoslovakia* (Anonymous, 1958) indicates the isotherms of mean monthly temperatures or mean temperatures accumulated over selected longer periods, calculated from data of 1901–1950. *The Statistical Yearbook of the Czech Republic 2001* (Anonymous, 2001) indicates average monthly temperatures and sunshine hours for selected meteorology stations, calculated from data of 1961–1990.

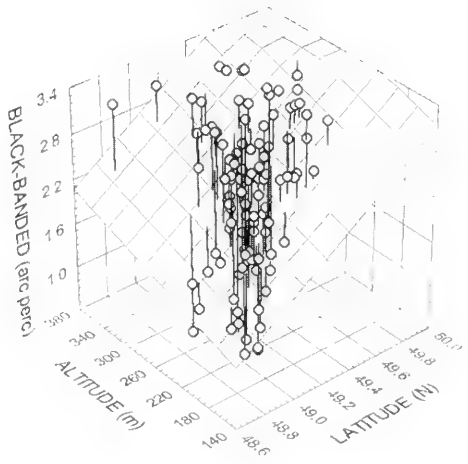

FIG. 2. The regression of the proportion of black-banded individuals (arcsin transformation) on the geographic latitude and altitude of the locality of collection. Data for populations of Moravia.

Data Processing

The multiple linear regression of proportion of the black-banded morph in local populations (arcsin transformed) on geographic latitude and altitude of the locality and the second order regression ($P = b_0+b_1S+b_2S^2$, where P is arcsin transformed proportion of black-banded morph and S is sunshine hours) of this characteristic on sunshine hours recorded at the nearest meteorology station were calculated. The differences in morph frequency on localities with different types of plant cover were tested by G-test and Fisher exact test. All calculations were made using Statistica for Windows (StatSoft, 1994).

RESULTS

Geographic Distribution of Shell-Band Color Forms

The distribution of populations containing faint-banded and brown-banded morphs (Fig. 1) was limited to south Moravia. The faint-banded animals were found at 26 localities situated below 49°20'N and 320 m altitude (average altitude 217 m a.s.l.). The brown-banded morph was found at all these and further 44 localities, that is, at a total of 70 localities situated below 49°30'N and 340 m (average altitude 230 m a.s.l.). The populations consisting only of black-banded morph were found at 36 localities between 48°48'N and 49°46'N and 180 to 360 m (average altitude 260 m a.s.l.). The occurrence of morphs was thus not geographically separated. Nevertheless, within Moravia, the proportion of the black-banded morph in *C. vindobonensis* local populations (Fig. 2) significantly increased ($R^2 = 0.3166$, $F_{(2,102)} = 23.628$, $p < 0.001$) with geographic latitude ($t_{102} = 4.67$, $p < 0.001$) and altitude ($t_{102} = 2.31$, $p < 0.05$) of the locality. In Bohemia only populations consisting of black-banded individuals were found (Fig. 1).

Habitats

The vegetation cover of localities occupied by *C. vindobonensis* populations changes with latitude. In south Moravia (< 49°10'N), half of the populations lived in open or closed forb stands (Fig. 3). The latter were in most cases the patches of stinging nettles (*Urtica dioica* L.) growing on eutrophic soils surrounding human settlements. As a consequence, the occurrence of *C. vindobonensis* was largely synanthropic. By contrast, in the north Moravia and Bohemia about 80% of populations occupied closed or open grassy stands. Thus, the preferred sites changed from ruderal to steppe localities.

The relationship between plant cover and frequency of shell color morphs was investigated for 59 localities of south Moravia. The populations with faint-banded and brown-banded

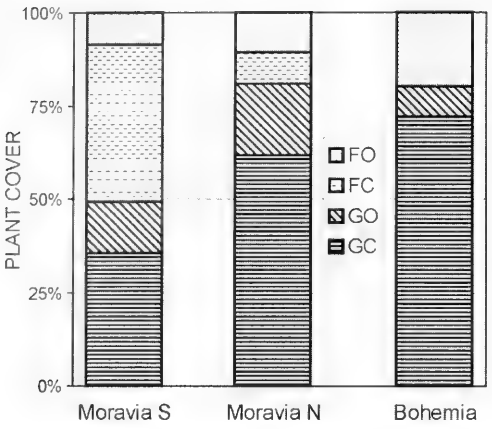

FIG. 3. The proportion of *C. vindobonensis* localities covered by different types of vegetation in the southern Moravia (left), northern Moravia (middle), and Bohemia (right). The localities of Moravia were partitioned into south and north by 49°0'N parallel (northern edge of a common occurrence of the faint-banded morph). The patterns filling the columns represent types of vegetation cover: FO: forb open, FC: forb closed, GO: grassy open, GC: grassy closed.

morphs were significantly more represented at localities with grassy stands than in forb stands (Table 1). By contrast, populations consisting only of black-banded morphs were frequently found at localities grown with forb stands.

Climatic Correlates of Morph Distribution

In Moravia, the geographic distribution of shell- band color morphs was correlated with climatic characteristics of the localities. The faint-banded morph was present (with few exceptions) at localities situated south of the 17°C isotherm of mean June temperature (Fig. 1). The northern limit of the area where populations of brown-banded morph were found was approximately the 15°C isotherm of mean April–September temperature (Fig. 1). In Bohemia there exist small areas where mean April–September temperatures also exceed 15°C (Fig. 1). However, the brown-banded shells were not found at the Bohemian localities.

The increase of the frequency of black-banded morph was parallel to the geographic trend in the change of climate (Table 2). As one moves from south to north average April–August temperature decreased only slightly by about 1°C. A consistent trend was found in the decrease of sunshine hours with a total of

TABLE 1. The frequency of south Moravia (below 49°10'N) populations containing particular shell-band color morphs in relation to plant cover at the locality. Above: populations where faint-banded morph was present vs. populations where only brown and/or black-banded (not faint-banded) morphs were present. Below: populations where only black-banded morph was present vs. populations where faint- and/or brown-banded morphs were present. Expected frequencies for each category are in brackets.

	Plant cover			
	Forb	Grass	Total	P
Not faint-banded	22 (17.7)	14 (18.3)	36	
Faint-banded	7 (11.3)	16 (11.7)	23	
Total	29	30	59	< 0.05a
Black-banded	11 (6.4)	2 (6.6)	13	
Brown- or faint-banded	18 (22.6)	28 (23.4)	46	
Total	29	30	59	< 0.01b

a: G-test on 2x2 contingency table
b: Fisher exact test

TABLE 2. Mean temperature and mean monthly sunshine duration in April–August at seven meteorology stations situated inside the area of *C. vindobonensis* distribution (Fig. 1), Velké Pavlovice (48°50'N; 180 m a.s.l.), Kucharovice (48°50'N; 300), Brno (49°10'N; 230), Olomouc (49°40'N; 220), Praha (50°00'N; 260), Hradec Králové (50°10'N; 240), Doksany (50°20'N; 160). Both climatic characteristics were calculated as means of 1961–1990 data.

	Temperature (°C)	Sunshine duration (h)
1 Velké Pavlovice	16.1	223
2 Kucharovice	15.1	219
3 Brno	15.3	212
4 Olomouc	15.4	208
5 Praha	15.7	202
6 Hradec Králové	14.9	203
7 Doksany	14.8	190

> 10% smaller in northern than southern areas. There was a highly significant regression of arcsin transformed percentage of black-banded morph on average sunshine hours of the nearest meteorology station ($b_0 = 53.89$, $b_1 = 0.5959$, $b_2 = 0.00155$, $R^2 = 0.3817$, $p < 0.001$).

DISCUSSION

This study demonstrates a latitudinal trend in the frequency distribution of shell banding morphs of *C. vindobonensis* near the edge of its range. It confirms, in more detail, the earlier finding that shells are all dark-banded at the northwestern extreme of distribution (Schilder & Schilder, 1957; Honek, 1995b), whereas more southerly populations contain proportions of brown or pale-banded individuals. Where polymorphism is usual (Moravia, south of 49°10'N), populations living in open, grassy habitats are more likely to include pale morphs, and to hold them at higher frequencies, than those in dense stands of forbs. The frequency of black-banded forms also increases with altitude, although this is a much smaller trend, and the range of altitude slight.

These trends all suggest the operation of climatic selection in response to both macro- and microclimatic differences. However, some problems should be discussed before such a conclusion is accepted. Over the whole range of the species, the effects of local microclimatic differences seem to be more consistent than any response to regional macroclimates. Thus, pale morphs are rare in northern Italy (Sacchi, 1984), but abundant in some populations of the Balkan Peninsula. In Croatia, populations in valley bottoms subject to temperature inversions are black-banded, whereas those on insolated slopes nearby have up to 50% of pale-banded shells (Jones, 1973, 1974). A similar association, reinforced by altitude, was found in northern Greece (Staikou, 1999). Only in one study in Romania was no association found (Jones, 1975).

In the closely related *C. nemoralis* and *C. hortensis*, there is also evidence for climatic selection (Jones, 1973; Vicario et al., 1988; Stine, 1989). In these species, however, systematic differences between regions of contrasting climate are clearer than associations with local microclimates (Cook, 1998). There exist large-scale geographic trends between shell color (Jones, 1973; Jones et al., 1977) or body color (Cowie & Jones, 1985) and local climate. Studies of shell color (e.g., Falniowski et al., 1993; Gardner et al., 1995) or body color (Cowie, 1990) of other species also demonstrated association between climate and snail color.

Local differences in morph frequencies associated with habitats are more usually accounted for as a product of visual selection for crypsis by predators (Cain & Sheppard, 1954; Cook, 1998). In this context, there is, as yet, no direct evidence on the selectiveness of predation on *C. vindobonensis*. It is worth noting, however, that at the northwestern extremity of its range, black-banded shells dominate in populations confined to open grassy habitats, whereas further south, they are most frequent in shadier places, and decline in the open habitats. This is not consistent with strong selection for crypsis, but it is with climatic selection.

Genetic drift and the history of colonization may also be significant, especially in small isolated or marginal populations (Honek, 1995a; Cameron et al., 1998). Monomorphy of marginal populations (e.g., in Bohemia) could derive from small founding populations.

Studies on the possible mechanisms of climatic selection, however, strengthen the case for its operation in this case. In other species, variation in thermal equilibria and/or rate of heating in sunshine is related to the degree of melanism in the shell (Etter, 1988; Honek, 1993), and such morphs may also differ in resistance to desiccation (Arad et al., 1993a, b). There is evidence that this applies to *C. vindobonensis*. The thermal equilibrium of the black-banded morph under sunshine has twice been shown to be about 1°C higher than that of paler morphs (Jones, 1973; Staikou, 1999), and in the latter case, the rate of desiccation in the black-banded morph was also higher. In Staikou's study, however, differences between populations were greater than differences between morphs. Other factors clearly affect the balance, and help to explain why local differences in the proportion of morphs are more consistent than regional ones.

The consequences of these differences need further study. Snails are generally nocturnal (Bailey, 1981; Blanc et al., 1989; Lorvelec et al., 1991), as is *C. vindobonensis*, with activity usually ceasing in the morning, later in pale-banded individuals than in those with dark bands (Staikou, 1999). We have no evidence to distinguish between selection due to increased activity of dark forms under cool conditions and that due to superior survival of pale forms under insolation (Jones, 1974). Resting snails are sometimes exposed to direct sun when resting on plants, rocks or walls. Despite these gaps in our knowledge, the evidence overall indicates that climate has a strong influence on visible variation in this snail.

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APPENDIX

Proportion of shell-band color morphs at local *C. vindobonensis* populations considered in this study. For each locality the information is provided as:
Nearest village (geographic latitude of the collection site [degrees and minutes N], geographic longitude [degrees and minutes E], altitude [m above sea level], black-banded [no. individuals]-brown-banded [no. individuals]-faint-banded [no. individuals])

Localities in Moravia

Lanžhot (4843, 1658, 160, 4-3-1); Úvaly (4844, 1642, 230, 6-10-12); Úvaly (4844, 1642, 220, 21-21-12); Hevlín (4846, 1626, 180, 7-10-2); Načeratice (4848, 1606, 230, 5-0-0); Suchovské Mlýny (4848, 1735, 360, 7-0-0); Zaječí (4853, 1647, 220, 5-3-0); Strážnice (4853, 1723, 180, 14-0-0); Čejkovice (4855, 1655, 270, 4-3-6); Troskotovice (4855, 1625, 190, 5-8-11); Hustopeče (4855, 1644, 200, 9-6-0); Kurdějov (4856, 1646, 250, 8-7-3); Horní Bojanovice (4857, 1647, 200, 1-8-1); Vlasatice (4857, 1628, 180, 10-10-36); Vlasatice (4857, 1628, 180, 20-41-55); Hovorany (4857, 1700, 220, 15-1-0); Hostěradice (4857, 1615, 220, 20-5-0); Pouzdřany (4858, 1638, 180, 7-7-10); Mistřín (4858, 1705, 200, 14-1-0); Bzenec (4858, 1717, 190, 8-1-0); Brumovice (4858, 1654, 200, 62-7-0); Morašice (4858, 1613, 270, 26-0-0); Diváky (4900, 1649, 220, 10-23-7); Cvrčovice (4900, 1632, 180, 47-37-8); Žeravice (4900, 1715, 230, 25-4-0); Olbramovice (4900, 1623, 220, 13-0-0); Hluk (4900, 1731, 240, 7-0-0); Židlochovice (4902, 1636, 180, 28-13-3); Jezeřany (4902, 1626, 220, 6-2-0); Loděnice (4902, 1628, 200, 4-3-0); Želetice (4902, 1700, 190, 48-5-0); Archlebov (4903, 1703, 200, 14-7-1); Trboušany (4903, 1627, 210, 18-11-1); Blučina (4903, 1640, 200, 6-12-2); Hrušovany u Brna (4903, 1635, 220, 28-13-3); Němčičky (4903, 1630, 190, 81-13-5); Násedlovice (4903, 1658, 190, 25-2-0); Moravský Krumlov (4903, 1620, 260, 23-0-0); Lovčice (4904, 1703, 240, 5-14-2); Bohuslavice (4904, 1708, 210, 55-6-4); Bohuslavice (4904, 1708, 210, 30-9-0); Rokytná (4904, 1620, 270, 40-0-0); Otnice (4905, 1650, 230, 15-14-3); Ždánice (4905, 1702, 230, 18-0-0); Mohelno (4906, 1611, 360, 14-0-0); Rašovice (4907, 1653, 240, 64-5-0); Silůvky (4908, 1628, 280, 32-42-9); Nesovice (4908, 1705, 240, 61-3-0); Brankovice (4908, 1708, 260, 26-8-0); Vícemilice (4908, 1702, 230, 31-25-0); Křižanovice (4909, 1656, 230, 40-2-0); Slavkov (4909, 1653, 220, 80-4-0); Hajany (4909, 1634, 260, 11-6-0); Nesovice (4909, 1703, 260, 69-9-0); Bučovice (4909, 1659, 220, 126-15-0); Slavkov (4909, 1652, 220, 10-0-0); Milonice (4910, 1705, 260, 38-2-0); Lísky (4910, 1714, 320, 63-0-0); Napajedla (4910, 1731, 210, 18-0-0); Rosťoutky (4911, 1703, 290, 51-1-0); Kozlany (4911, 1702, 310, 24-0-0); Strabenice (4912, 1714, 320, 42-8-3); Rosťoutky (4912, 1703, 270, 19-3-0); Holubice (4912, 1650, 280, 19-4-0); Rousínov (4912, 1653, 250, 26-8-0); Rousínov (4913, 1653, 270, 24-2-0); Zdounky (4914, 1717, 230, 22-2-0); Morkovice (4914, 1714, 280, 19-2-0); Kvasice (4914, 1730, 200, 8-4-0); Skržice (4915, 1720, 210, 16-1-0); Netčice (4915, 1717, 240, 61-4-0); Rostěnice (4915, 1658, 260, 5-8-0); Zborovice (4915, 1716, 260, 30-0-0); Vyškov (4917, 1701, 240, 49-0-0); Heroltice (4918, 1704, 240, 18-2-0); Těšice (4918, 1710, 210, 60-0-0); Pustiměř (4919, 1702, 290, 44-7-1); Křenovice (4919, 1715, 200, 48-2-0); Dřevnovice (4920, 1709, 240, 27-36-2); Nezamyslice (4920, 1800, 250, 64-4-0); Želeč (4921, 1704, 340, 121-15-0); Tišnov (4922, 1623, 290, 44-22-0); Brodek u Prostějova (4921, 1705, 290, 64-0-0); Brodek u Prostějova (4922, 1705, 280, 22-0-0); Pivín (4923, 1710, 280, 20-2-0); Polkovice (4923, 1719, 200, 74-0-0);

Vranovice (4924, 1706, 250, 11-0-0); Henčlov (4926, 1723, 200, 17-1-0); Prostějov (4930, 1705, 240, 24-5-0); Kostelec na Hané (4930, 1704, 250, 30-7-0); Zdětín (4930, 1659, 350, 13-0-0); Ptení (4930, 1658, 340, 14-0-0); Čelechovice (4931, 1706, 280, 11-15-0); Čelechovice (4931, 1704, 280, 14-0-0); Smržice (4931, 1709, 250, 45-0-0); Blatec (4932, 1715, 230, 57-0-0); Blatec (4932, 1715, 230, 51-0-0); Slatinice (4933, 1706, 250, 28-0-0); Čechy pod Kosířem (4933, 1701, 290, 18-0-0); Pěnčín (4934, 1701, 330, 11-0-0); Olomouc (4935, 1717, 210, 17-0-0); Drahanovice (4935, 1705, 250, 53-0-0); Ludéřov (4935, 1703, 280, 25-0-0); Ludéřov (4935, 1703, 330, 25-0-0); Cholina (4940, 1702, 270, 26-0-0); Bílá Lhota (4946, 1658, 290, 16-0-0)

Localities in Bohemia

Malá Lečice (4950, 1422, 280, 10-0-0); Srbsko (4957, 1408, 260, 39-0-0); Karlštejn (4957, 1410, 260, 17-0-0); Vysoké Mýto (4957, 1610, 270, 20-0-0); Kostěnice (5000, 1554, 240, 20-0-0); Uhersko (5000, 1602, 240, 20-0-0); Platenice (5001, 1557, 240, 20-0-0); Praha (5002, 1420, 300, 40-0-0); Dašice (5002, 1556, 230, 20-0-0); Hradčany (5009, 1517, 250, 20-0-0); Podmoráň (5010, 1420, 290, 24-0-0); Blšany (5014, 1327, 280, 15-0-0); Měcholupy (5016, 1333, 290, 15-0-0); Veltrusy (5016, 1420, 180, 20-0-0); Kly (5018, 1433, 220, 60-0-0); Nová Ves (5020, 1418, 200, 20-0-0); Roudnice (5025, 1417, 210, 9-0-0); Raná (5025, 1347, 380, 40-0-0); Libochovice (5026, 1403, 170, 11-0-0); Charvatce (5026, 1348, 350, 25-0-0); Charvatce (5026, 1349, 330, 25-0-0); Štětí (5027, 1423, 170, 20-0-0); Vrbice (5028, 1417, 160, 36-0-0); Chcebuz (5029, 1423, 230, 72-0-0); Vrutice (5030, 1417, 160, 20-0-0); Polepy (5031, 1419, 160, 20-0-0)

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KARYOTYPES OF EUROPEAN SPECIES OF *RADIX* (GASTROPODA: PULMONATA: LYMNAEIDAE) AND THEIR RELEVANCE TO SPECIES DISTINCTION IN THE GENUS

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ABSTRACT

Karyotypes of *Radix auricularia* (Linnaeus, 1758) and three disputable taxa considered by different authors as distinct species or assigned as forms of *Radix peregra* (Müller, 1774), *sensu lato* – *R. labiata* (Rossmässler, 1835), *R. balthica* (Linnaeus, 1758), and *R. ampla* (Hartmann, 1821) – were studied with preparations obtained from gonad tissues by the air-drying method. The studied taxa have the same diploid number (2n = 34), but are characterized by different morphology of some chromosome pairs. In particular, *R. labiata* (traditionally identified as *R. peregra, s. s.*) and *R. balthica* (= *R. ovata* in traditional understanding) differ in the number of subtelocentric chromosomes (1 and 5, respectively), species status of these taxa being also supported by pronounced differences in centomeric indexes of chromosome pairs 4 and 16. Species distinctness of *R. ampla* is supported by differences in three chromosome pairs, and karyological similarity between this taxon and *R. balthica* is also noted. FN values varied among the studied taxa from 56 in *R. ampla* to 66 in *R. labiata*. The known karyological characters are traced on phylogenetic trees suggested by recent molecular reconstructions. This study demonstrates that karyology can be an effective tool for aiding taxonomic distinctions of historically problematic groups of molluscs.

Key words: *Radix*, karyotypes, taxonomy, species distinctions.

INTRODUCTION

The group of lymnaeid species bearing the name *Radix* Montfort, 1810, is defined mainly by its thin-walled fragile shell with a relatively large aperture (Falkner, 1990; Glöer & Meier-Brook, 1998; Jackiewicz, 1998; Glöer, 2002). The distinctive karyological character of *Radix*, namely its chromosome number (n = 17) deviating from the other members of the family (typically n = 18, or in some taxa n = 16 or 19), has also been known for a long time (Inaba, 1969; Choudhary et al., 1992).

Despite intensive research by different methods (Hubendick, 1951; Inaba, 1969; Patterson & Burch, 1978; Kruglov & Starobogatov, 1983, 1993; Remigio & Blair, 1997; Jackiewicz, 1998; Bargues et al., 2001), many taxonomic problems of *Radix* remain unresolved. In particular, the rank of the group is alternatively defined as subgeneric within *Lymnaea* (Hubendick, 1951; Kruglov & Starobogatov, 1983, 1993; Jackiewicz, 1998; Kerney, 1999) or generic (Patterson & Burch, 1978; Falkner, 1990; Glöer & Meier-Brook, 1998; Bargues et al., 2001; Falkner et al., 2002). A distinct subgenus *Peregriana* was recognized in *Lymnaea* alongside *Radix* by Kruglov & Starobogatov (1983). Still uncertain also is the number of species within this group. Stressing the lack of distinctive anatomical characters and existence of intermediate shell morphotypes, British (Kerney, 1999) and Polish (Jackiewicz, 1998) authors recognized only two European species, namely *Lymnaea (Radix) auricularia* (Linnaeus, 1758) and *L. (R.) peregra* (Müller, 1774), distinguishing in the latter up to four ecological forms: *L. peregra s. s.* (= f. *typica, sensu* Jackiewiecz, 1998), f. *ovata* (Draparnaud, 1805), f. *lagotis* (Schrank, 1803), and f. *ampla* (Hartmann, 1821). Evidence for species distinctness of *Radix ovata* was provided by Glöer & Meier-Brook (1998), whereas Falkner (1990) also recognized *R. ampla* as a full species. Five European taxa are supported by recent molecular studies (Bargues et al., 2001) and have been

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TABLE 1. Material for karyological investigation.

Taxon	Synonymy	Locality	No. of specimens studied	No. of metaphases studied*	Remarks
Radix auricularia (Linnaeus, 1758)	*Lymnaea auricularia*	Zhitomyr, River Teterev	50	16	first studied by Garbar (1998)
		Vinnitsa Region, Shyroka Greblya, River Yuzhny Bug (South Bug)	14	9	
R. labiata (Rossmässler, 1835)	*R. peregra, auctt.* *L. peregra, auctt.* *L. peregra* f. *typica*, *sensu* Jackiewicz, 1998	Zhitomyr, small pond	45	29	first studied by Garbar (2000)
		Vorokhta, Ivano-Frankivsk Region, small pond	20	11	
R. balthica (Linnaeus, 1758)	*R. ovata* (Draparnaud, 1805) *L. ovata* *L. peregra* f. *ovata*, *sensu* Jackiewicz, 1998	Olevsk, Zhitomyr Region, River Ubort	30	15	first studied by Garbar (2000)
		Kiev, River Dnieper	9	6	
R. ampla (Hartmann, 1821)	*L. peregra* f. *ampla*, *sensu* Jackiewicz, 1998	Zhitomyr, River Teterev	65	17	
		Kharkiv, River Udy	5	9	

* In some specimens no metaphases could be observed.

included as species in the latest European checklists (Falkner et al., 2002; Glöer, 2002) with the following names: *Radix auricularia, R. labiata* (Rossmässler, 1835) (substituting *R. peregra, s. s.* of previous authors), *R. balthica* (Linnaeus, 1758) (= *R. peregra* of Müller, = *R. ovata, auctt.*), *R. ampla,* and *R. lagotis.* An even more profound subdivision was suggested by Kruglov & Starobogatov (1983, 1993) but not supported by any of the later studies.

Until now, chromosome numbers were mainly involved in discussions about taxonomy and relationships among freshwater gastropods. However, interspecific differences in chromosome morphology were recently found in *Viviparus* (Baršiene et al., 2000). Furthermore, preliminary investigations of Garbar (1998, 2000) on *Radix* and on *Stagnicola* (Garbar & Korniushin, 2002) have shown that morphological characters of chromosomes may be also helpful by species distinction in lymnaeids. This paper summarizes results of karyological investigation in four European taxa of *Radix*, designated in modern reviews as *R. auricularia, R. labiata, R. balthica* and *R. ampla*.

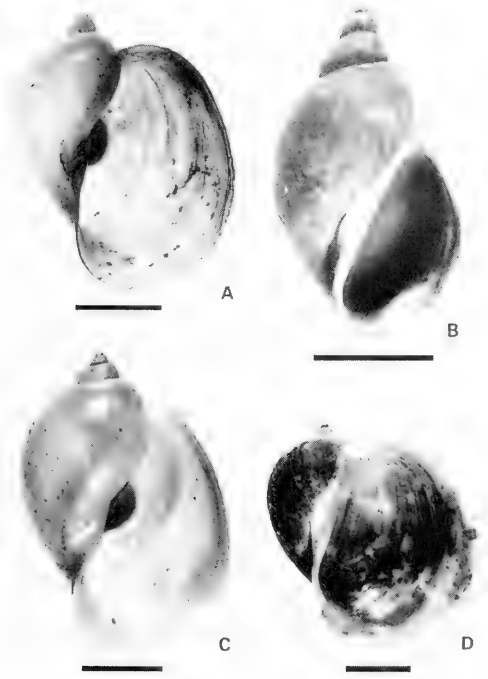

FIG. 1. Shells of the studied species: A. *Radix auricularia* (Linnaeus, 1758); B. *R. labiata* (Rossmässler, 1835); C. *R. balthica* (Linnaeus, 1758); D. *R. ampla* (Hartmann, 1821). Scale bar, 5 mm.

MATERIAL AND METHODS

Material was collected by the first author in 1997–2000 in western and central Ukraine (Table 1). In order to minimize the influence of local factors, each species was sampled in two remote (at a distance of at least 150 km) localities; the sampled populations inhabit different river systems (of the Danube, Yuzhny Bug, and Dnieper drainages) and live under somewhat different climatic conditions. Some populations included in the earlier karyological studies (Garbar, 1998, 2000) were re-sampled. Species identification was based on traditional conchological and anatomical characters (Glöer & Meier-Brook, 1998; Jackiewicz, 1998). The studied group is treated in our work as a genus and the studied forms as species, following the latest systematic and phylogenetic works (Remigio & Blair, 1997; Bargues et al., 2001; Falkner et al., 2002). Nomenclature of the latest European monographic review (Glöer, 2002) is used herein; in order to avoid misunderstanding, we provide the list of the studied taxa with synonyms used in the cited publications (Table 1).

Pictures of shells are provided in Figure 1. Voucher specimens have been deposited in the mollusc collection of the Museum für Naturkunde, Humboldt Universität zu Berlin, Germany.

Chromosome preparations were obtained from the gonad tissue according to the recommendations of Baršiene et al. (1996) and Garbar (1998). Molluscs were placed for 17 h in a 0.002% solution of colchicine. Pieces of gonad were fixed in a mixture of ethanol and acetic acid (3:1). The cell suspension was prepared by maceration in a mixture of concentrated acetic and 60% lactic acids (30:1) and dispersed with a capillar pipette on microscopic slides heated at 50°C. Dried preparations were stained 10–15 min in 10% solution of azur-eosine after Romanovski, prepared on 0.01M phosphate buffer. Stained preparations were placed for short time in xylol and embedded in Canada Balsam. These preparations were studied under a Biolam-L-212 microscope with magnification 10 x 90. The plates with a good dispersion of chromosomes and moderate degree of spiralization were selected for photographing and measuring. The relative length and centromeric index were then calculated for each chromosome. Chromosomes were classified according to Levan et al. (1964). The Fundamental Number (FN) was calculated as the number of autosome arms in haploid complement, with a value of 4 given to metacentric and

submetacentric chromosomes, and a value of 2 to subtelocentric chromosomes (no telocentric chromosomes were found in the studied taxa). Quantitative data from the most numerous samples were processed statistically using standard methods.

RESULTS

Descriptions of Karyotypes

Radix auricularia. 2n = 34. Chromosomes of adjacent pairs similar in size, their relative length varies between 9.21% and 4.15% (Table 2). Karyotype includes 11 pairs of metacentric, four pairs of submetacentric, and two pairs of subtelocentric chromosomes (Fig. 2, Table 2). FN = 64.

Radix labiata. 2n = 34. Chromosomes of adjacent pairs similar in size, with relative length between 9.69% and 3.74% (Table 2). Karyotype includes 12 pairs of metacentric, four pairs of submetacentric, and one pair of subtelocentric chromosomes (Fig. 3, Table 2). FN = 66.

Radix balthica. 2n = 34. Chromosomes of adjacent pairs similar in size, with relative length between 9.29% and 3.95% (Table 2). Karyotype includes eight pairs of metacentric, four pairs of submetacentric, and five pairs of subtelocentric chromosomes (Fig. 4, Table 2). FN = 58.

Radix ampla. 2n = 34. Chromosomes of adjacent pairs similar in size, with relative length of chromosomes between 9.32% and 4.05% (Table 2). Karyotype includes eight pairs of metacentric, three pairs of submetacentric, and six pairs of subtelocentric chromosomes (Fig. 5, Table 2). FN = 56.

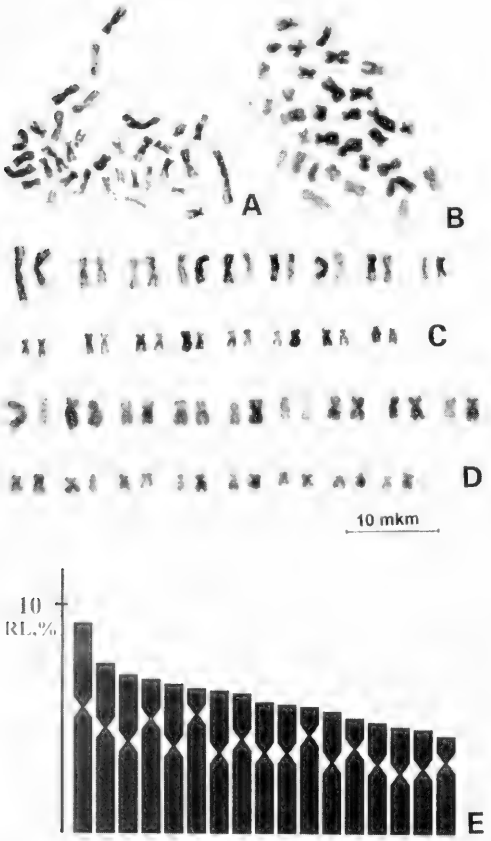

FIG. 2. Chromosomes of *Radix auricularia*: A. Mitotic metaphase of a specimen from Zhitomyr; B. The same of a specimen from Vinnitsa; C, D. Karyotypes of specimens from Zhitomyr and Vinnitsa region, respectively; E. Ideogram (based on data from Table 2). Scale bar, 10 μm.

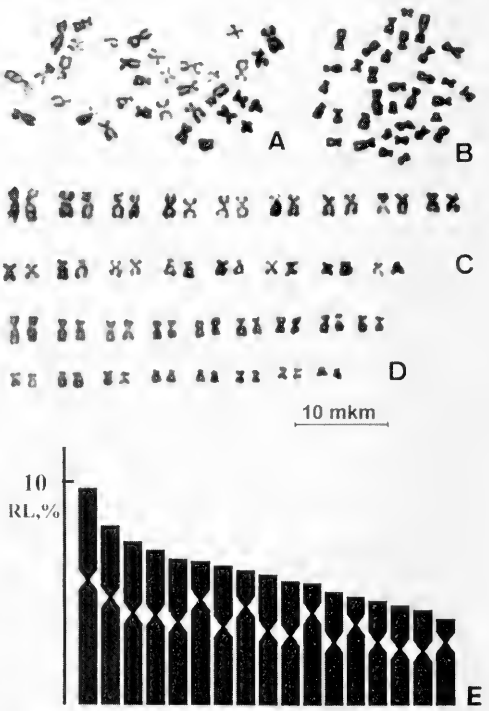

FIG. 3. Chromosomes of *Radix labiata*: A, B. Mitotic metaphases of specimens from Zhiomyr and Vorokhta, respectively; C, D. Karyotypes of specimens from Zhitomyr and Vorokhta, respectively; E. Ideogram (based on data from Table 2). Scale bar, 10 μm.

Comparisons

All studied taxa are characterized by the same chromosome number (2n = 34). Morphological similarity is demonstrative also in some individual chromosome pairs, that is, pairs 1, 3, 5, 7, 9, 11, 12 and 15, belonging to one and the same type in all these taxa. On the other hand, distinctive features of chromosome morphology were noted not only for the doubtless species *Radix auricularia*, but also for three taxa of disputable status – *R. labiata, R. balthica,* and *R. ampla*. The karyotype of *R. labiata* (= *R. peregra, auctt.*) differs from that of *R. balthica,* and *R. ampla* in morphological type in seven to nine pairs. The higher rate of subtelocentric chromosomes in two latter species (five to six out of 17 pairs) is also reflected in the lower values of FN (58 and 56, respectively), compared to FN of *R. labiata* (66). In some cases, such as in the pairs 2, 6, and 13, mean values of centromeric indexes in the compared species were close (Table 2), and assignment of chromosomes to different types might be influenced by individual variation. However, that was not the case in chromosome pairs 4 and 16, for which interspecific differences were the most pronounced. Taking into account that chromosomes adjacent to the mentioned pairs in the ideograms (Figs. 2–5) were morphologically similar among the studied taxa, we conclude that observed differences could not be caused by errors in identification of individual chromosomes. Therefore, they are further referred to as taxonomic characters.

Similarity in chromosome morphology between *R. labiata* and *R. auricularia* is noteworthy: only two pairs (4 and 6) were assigned to

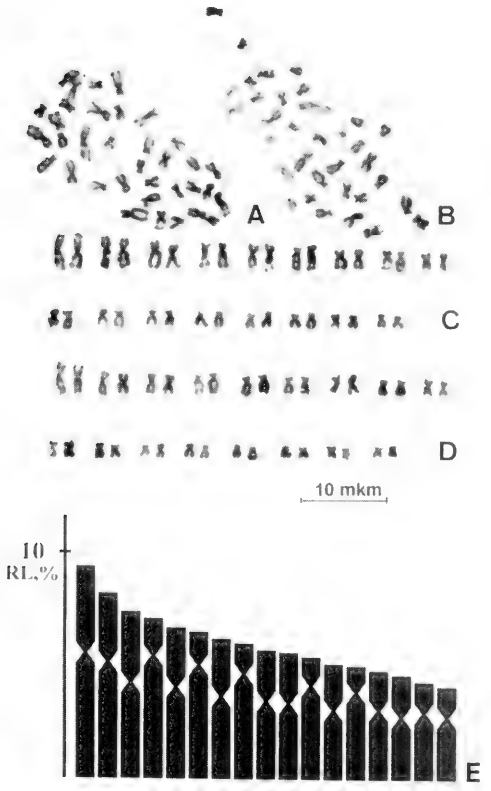

FIG. 4. Chromosomes of *Radix balthica*: A, B. Mitotic metaphases of specimens from Olevsk and Kiev, respectively; C, D. Karyotypes of specimens from Olevsk and Kiev, respectively; E. Ideogram (based on data from Table 2). Scale bar, 10 μm.

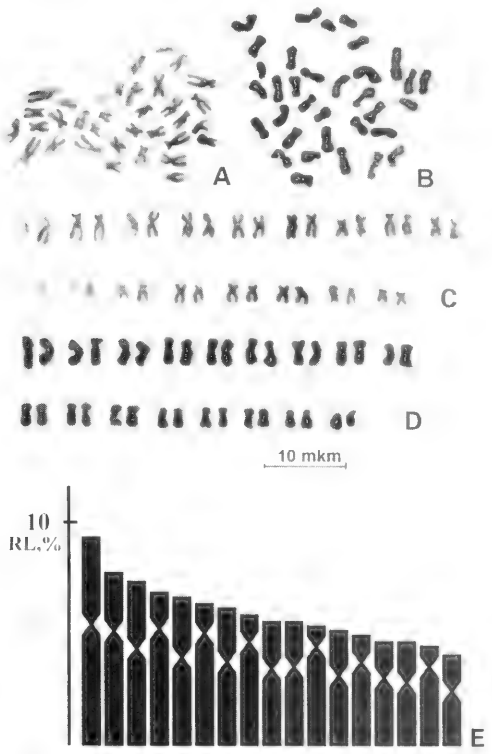

FIG. 5. Chromosomes of *Radix ampla*: A, B. Mitotic metaphases of specimens from Zhitomyr and Kharkiv, respectively; C, D. Karyotypes of specimens from Zhytomyr and Kharkiv, respectively; E. Ideogram (based on data from Table 2). Scale bar, 10 μm.

TABLE 2. Measurements (RL - relative length, Ci - centromeric index, SD - Standard Deviation) and classification of chromosomes (m - metacentric, sm - submetacentric, st - subtelocentric chromosome) of *Radix auricularia* from Zhitomyr, River Teterev, *R. labiata* from Zhitomyr, and *R. balthica* from Zhitomyr Region, Olevsk, and *R. ampla* from Zhitomyr, River Teterev.

	R. auricularia			*R. labiata*			*R. balthica*			*R. ampla*		
Pair no.	RL % (± SD)	Ci % (± SD)	Type	RL % (± SD)	Ci % (± SD)	Type	RL % (± SD)	Ci % (± SD)	Type	RL % (± SD)	Ci % (± SD)	Type
1	9.21 ± 0.27	40.23 ± 1.11	m	9.69 ± 0.08	41.81 ± 0.69	m	9.29 ± 0.11	41.23 ± 0.73	m	9.32 ± 0.19	41.60 ± 1.21	m
2	7.38 ± 0.11	38.07 ± 1.50	m	8.00 ± 0.09	39.59 ± 0.96	m	8.07 ± 0.08	37.38 ± 1.38	sm	7.71 ± 0.09	34.27 ± 1.50	sm
3	6.88 ± 0.08	42.73 ± 1.49	m	7.33 ± 0.07	43.30 ± 0.80	m	7.34 ± 0.06	42.45 ± 0.74	m	7.28 ± 0.06	41.57 ± 1.19	m
4	6.65 ± 0.08	25.43 ± 1.10	sm	6.89 ± 0.06	42.71 ± 0.69	m	7.01 ± 0.07	22.22 ± 1.16	st	6.82 ± 0.11	23.03 ± 1.55	st
5	6.45 ± 0.05	42.47 ± 1.41	m	6.54 ± 0.04	43.35 ± 0.69	m	6.59 ± 0.05	39.07 ± 0.82	m	6.57 ± 0.05	41.07 ± 1.55	m
6	6.30 ± 0.03	16.61 ± 1.43	st	6.42 ± 0.05	25.88 ± 1.07	sm	6.43 ± 0.05	21.35 ± 1.12	st	6.32 ± 0.08	20.56 ± 1.75	st
7	6.15 ± 0.05	43.90 ± 0.89	m	6.20 ± 0.04	43.86 ± 0.74	m	6.13 ± 0.05	40.97 ± 0.86	m	6.05 ± 0.06	39.80 ± 1.16	m
8	5.07 ± 0.04	33.6 ± 1.05	sm	6.02 ± 0.05	26.28 ± 0.84	sm	5.87 ± 0.04	22.65 ± 1.07	st	5.81 ± 0.04	20.54 ± 1.60	st
9	5.72 ± 0.06	37.52 ± 1.46	m	5.75 ± 0.04	42.94 ± 0.67	m	5.61 ± 0.04	40.01 ± 0.78	m	5.52 ± 0.04	38.23 ± 1.81	m
10	5.55 ± 0.05	38.13 ± 1.49	m	5.52 ± 0.04	43.06 ± 0.68	m	5.49 ± 0.03	40.09 ± 1.01	m	5.50 ± 0.04	35.72 ± 1.56	sm
11	5.45 ± 0.06	22.55 ± 1.63	st	5.35 ± 0.05	23.52 ± 1.02	st	5.27 ± 0.04	22.66 ± 1.09	st	5.35 ± 0.05	19.33 ± 0.89	st
12	5.25 ± 0.07	41.24 ± 1.40	m	5.01 ± 0.05	43.67 ± 0.67	m	5.00 ± 0.05	40.57 ± 0.98	m	5.12 ± 0.06	38.60 ± 0.94	m
13	5.00 ± 0.08	26.21 ± 1.40	sm	4.78 ± 0.05	25.27 ± 1.07	sm	4.85 ± 0.05	23.09 ± 1.12	st	4.90 ± 0.04	24.81 ± 0.92	st
14	4.79 ± 0.06	38.10 ± 1.44	m	4.59 ± 0.06	39.50 ± 1.22	m	4.67 ± 0.05	35.75 ± 1.31	sm	4.63 ± 0.06	34.53 ± 0.97	sm
15	4.58 ± 0.05	42.56 ± 1.38	m	4.36 ± 0.06	42.55 ± 0.78	m	4.46 ± 0.04	41.11 ± 0.74	m	4.56 ± 0.06	38.31 ± 1.50	m
16	4.46 ± 0.09	37.75 ± 1.28	m	4.16 ± 0.05	43.40 ± 0.83	m	4.24 ± 0.04	31.04 ± 1.32	sm	4.37 ± 0.08	20.74 ± 0.83	st
17	4.15 ± 0.09	25.63 ± 1.44	sm	3.74 ± 0.04	26.99 ± 1.21	sm	3.95 ± 0.05	33.98 ± 1.11	sm	4.05 ± 0.07	38.38 ± 1.07	m

different types in these two taxa, and values of FN were also close. The karyotype of *R. ampla* is close to that of *R. balthica*, differing in morphological type of three chromosome pairs; presence of one more subtelocentric pair (16) is the most characteristic feature of the former taxon.

DISCUSSION

Diploid numbers of all studied species (2n = 34) agree well with the published literature on the genus *Radix* (Inaba, 1969; Patterson & Burch, 1978; Coudhary et al., 1992; Baršiene et al., 1996; Garbar, 1998, 2000). No cases of hypodiploidy or polyploidy were observed by our study, this result being in contrast with data on Spanish populations identified as *R. peregra* (Baršiene et al., 1996). The presence of telocentric (t) chromosomes in the karyotype of *R. auricularia* from the Zhitomyr population reported by Garbar (1998) was also not confirmed by this study. In all probability, this work dealt with an artifact caused by very profound spiralization of chromosomes. At the same time, our present observations on *R. labiata* and *R. balthica* agree with the data of Garbar (2000) on these species (for correspondence of nomenclature: Table 1). The karyotype of *R. ampla* has been studied here for the first time.

Differences in the chromosome morphology (most pronounced in the pairs 4 and 16) support species status of *R. balthica* (= *R. ovata*) and *R. labiata* (traditionally referred to as *R. peregra*) – two taxa considered conspecific by many taxonomists dealing with shell and anatomical characters (Hubendick, 1951; Jackiewicz, 1998; Kerney, 1999). However, karyological distinction between *R. labiata* and *R. balthica* shown by this study should be checked on the representative material taken throughout their distributions. Noteworthy, chromosome pair 4 is apparently of the same type in the karyotype of Spanish *R. peregra* shown by Baršiene et al. (1996) and Ukrainian specimens of *R. labiata* included in this study, but similarities/differences in other chromosome pairs cannot be evaluated, because centromeric indexes for the Spanish specimens were not provided.

Species status of *R. ampla* is also supported by this study, but the karyological differences between this taxon and *R. balthica* were apparently less pronounced than those reported for *R. balthica* and *R. labiata*. Furthermore, the karyotype of *L. (Peregriana) fontinalis* (Studer, 1820), as described by Garbar (2000), is similar to that of *R. ampla* (especially in having subtelocentric chromosome pair 16), with moderate (about 6%) difference in mean values of centromeric indexes of chromosome pair 2. This result is surprising, because *L. fontinalis* (in the understanding of Russian authors) corresponds in its conchological and anatomical characters (Kruglov & Starobogatov, 1983: fig. 2, 3; Garbar, 2000: fig. 1) to *R. balthica* of modern western European reviewers (Glöer, 2002) and is apparently different from *R. ampla*. Thus, correlation between chromosome morphology and the other characters in the *R. balthica*/*R. ampla* complex should be checked by further studies.

The observed pattern of karyological differences in *Radix* is consistent with the phylogenetic trees based on ITS-2 sequences (Bargues et al., 2001), supporting the following topology in the clade of European *Radix* species (nomenclature as used here): (*R. labiata*, (*R. auricularia*, (*R. lagotis, R. ampla, R. balthica*))). In particular, the peculiar karyotype of *R. labiata* and the karyological similarity between *R. ampla* and *R. balthica* corroborate this phylogenetic hypothesis. In particular, the overwhelming prevalence of meta- and submetacentric chromosomes characterizes the basal taxa *R. labiata* and *R. auricularia*, whereas the high number of subtelocentric chromosomes is a common feature of *R. balthica* and *R. ampla*, which belong to the terminal clade. Thus, the state of the karyotype of the former may be interpreted as plesiomorphic, and the latter as apomorphic within the analysed group. The results of our investigation are also consistent with the molecular analysis (Bargues et al., 2001) in suggesting, that *R. ampla* is a valid species alongside *R. balthica*. Neither karyological nor molecular characters support the subgenus *Peregriana* of Kruglov & Starobogatov (1983, 1993) as including, among other species, *R. labiata*, *R. balthica*, *R. lagotis* and *R. ampla*, but not *R. auricularia*. Broad understanding of *Lymnaea peregra* (Jackiewicz, 1998) also contradicts both data sets.

The results of this work, as well as earlier observations on other freshwater gastropods (Baršiene et al., 2000; Garbar & Korniushin, 2002), show that the study of chromosome morphology may provide additional characters for species diagnosis and phylogenetic analysis. Karyological study of Lymnaeidae should be continued, given the parasitological importance of this group and remaining uncertainty about its species-level taxonomy.

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USE OF MICROSATELLITE VARIATION AND RAPD-PCR TO ASSESS GENETIC POLYMORPHISM IN *BIOMPHALARIA GLABRATA* SNAILS FROM A SINGLE LOCALE IN A SCHISTOSOMIASIS ENDEMIC AREA

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ABSTRACT

Genetic variation was assessed in *Biomphalaria glabrata* snails using variations in microsatellite loci and by RAPD-PCR analysis. Populations of snails examined were field-collected isolates from a small pond in a schistosomiasis endemic region in Brazil, after standard conditions were developed for analyzing snails from two laboratory-maintained stocks. The analyses were performed using a total of 60 microsatellite primer sets and, for RAPD-PCR, a total of 19 random primers. We show that genetic diversity can readily be detected by both molecular methods among the field-collected snails from this small site. In addition, RAPD-PCR bands that were found in another study to segregate with parasite resistance were not detected in any of the field-collected snails analyzed.

Keywords: *Biomphalaria glabrata*, RAPD-PCR, microsatellites, genetic diversity, AMOVA, schistosomiasis.

INTRODUCTION

Schistosomiasis is a parasitic disease of global significance. Nearly every stage of the schistosome's life cycle, which alternately involves mammalian and snail hosts, has been the target for intervention, but often these control efforts result in short-term success. Although combined efforts to reduce transmission, for example by molluscicide and mass chemotherapy, are initially effective, rapid recolonization by the snails and reinfection in the human population make long-term control difficult to achieve. Developing an effective vaccine against schistosomes is a challenging task (Bergquist, 1998), making it even more important to explore other control measures. The strategy of replacing susceptible snails in schistosomiasis-endemic areas with parasite-resistant snails is a suggested form of biological control (Hubendick, 1958). Implementation of these control methods and the need to better understand the epidemiology of schistosomiasis has stimulated interest in better characterizing the population genetic structures of both the snail hosts and parasites (Bandoni et al., 1990; Johnston et al., 1993; Hoffman et al., 1998; Langand et al., 1999; Curtis & Minchella, 2000; Sire et al., 2001).

Some degree of genetic diversity in snail field populations has been noted using a variety of methods, including allozyme analysis, RAPD-PCR, and variations in microsatellite loci (Bandoni et al., 1990; Vidigal et al., 1994; Jones et al., 1999; Bandoni et al., 2000; Mavares et al., 2000; Charbonnel et al., 2000). Applying RAPD-PCR and microsatellite analysis to study snail population structure is relatively new, but both methods have found wide use for examining the frequency of genotypes in relation to disease, genetics and ecology in numerous species of medical and agricultural importance. Over the last several years, however, less frequent use has been made of multi-locus molecular markers, such as RFLPs and RAPDs, than of microsatellites for population genetic studies (review: Jarne & Theron, 2001). This has occurred even though

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RAPD-PCR has some obvious advantages, notably the ability to identify genetic loci (scored as the presence or absence of bands) without prior cloning or sequencing steps (Williams et al., 1993). Detecting microsatellite loci, on the other hand, depends on initial time-consuming cloning and sequencing steps to identify the simple sequence repeats (SSR, or microsatellite loci), and the design of primers flanking SSRs for amplification and detection of polymorphic loci (Jarne & Lagoda, 1996).

Most of the studies on snail hosts have analyzed the genetic structure of *Biomphalaria glabrata* populations, the major intermediate host for *Schistosoma mansoni* in South America and several Caribbean islands. Recently, this species was also found in Egypt, where it could complicate the extensive control efforts that have been in place there for the last several years (Yousif et al., 1996). Vidigal et al. (1994) showed that snails in a population in one geographic region were more homogeneous (based on RAPD-PCR analysis) than snails from different geographic regions. However, for the African species *B. pfeifferi*, Hoffman et al. (1998) found considerable heterogeneity in populations even within a few hundred meters along a river system. Assessing genetic diversity in *B. glabrata* by targeting polymorphic SSRs in the genome is less established (Jones et al., 1999; Mavares et al., 2000), but has been shown to be a powerful tool for linkage analysis for certain traits in other species. The purpose of this study was to use RAPD-PCR and microsatellite variation in assessing the genetic diversity among *B. glabrata* snails collected in a single, small field site. Our goal was to determine the sensitivity of each method to detect genetic diversity in a single population. We have begun by examining genomic polymorphisms on a small scale in order to better understand patterns of variation where geographic distance is not a complicating factor. By beginning on a small scale before applying these methods to analyze snails from a broad geographic region, we will be better able to choose markers and sampling protocols for larger-scale analyses. Furthermore, the occurrence of previously identified RAPD markers that segregate with resistance to *S. mansoni* infection in laboratory maintained snails (Knight et al., 1999) was assessed in field collected snails for the first time in this study.

MATERIALS AND METHODS

Snails

Initial standardization of techniques was performed on laboratory-maintained *B. glabrata* snails from two well-established stocks: (1) the BS-90 snails, a pigmented, parasite-resistant stock that was isolated from Salvador, Brazil (Paraense & Correa, 1963), and (2) the M-line snails, an albino stock highly susceptible to *S. mansoni* infection (Newton, 1953).

Field-collected *B. glabrata* snails were obtained from a schistosomiasis endemic area in Corrego de Melquiades, Governador Valadares municipality, Minas Gerais, Brazil. The epidemiology of schistosomiasis in this area has been documented by others (Kloos et al., 2001; Bethony et al., 2001). Snails (> 5 mm shell dia.) were collected from a single fishpond (approx. 40 m^2 surface area) fed by a single small stream. Before being transferred to the laboratory, the snails were maintained in plastic jars containing water collected from their respective sites and fed lettuce or decaying aquatic vegetation. To detect trematode infection in field-collected snails, the snails were placed individually in water in 24-well plates and exposed to incandescent light for 1–2 hr at room temperature. The water was then examined under a dissecting microscope for the presence of cercariae. Snails exhibiting signs of trematode infection were excluded from the DNA analysis.

DNA Isolation

Snails were placed overnight in water containing 0.1 mg/ml of ampicillin for preparation for DNA extraction. The shells were removed after gently crushing the snails between two glass slides and, in the case of field-collected snails, the tissues further examined microscopically for evidence of trematode infections. The headfoot of individual snails was severed from the posterior region of the body with a sharp scalpel blade, then the headfoot either used immediately for DNA extraction, or frozen in liquid nitrogen and stored at –70°C until required. DNA was extracted as described previously (Knight et al., 1998). Genotypes of individual laboratory and field-collected snails were initially established by RAPD-PCR using the 10-mer primers OPM-04 and OPZ-11, as described by Knight et al. (1999).

Construction of Small Insert Genomic Library

Small insert genomic DNA libraries were constructed either by using restriction enzyme *Sau* 3AI to generate small fragments (0.5–2.0 kb), or by multiple enzyme digestions, as described by Ostrander et al. (1992). Restriction enzyme digestions were performed using 10 μg genomic DNA from an individual BS-90 snail according to manufacturer's instructions (Life Technologies). DNA concentration was determined by spotting samples (1 μl) on agarose plates impregnated with ethidium bromide (0.2 μg/ml) and compared with DNA samples of known concentration under UV light. The DNA fragments generated by *Sau* 3AI digestion were ligated into *Bam* HI linearized pUC-18 vector (Amersham Pharmacia Biotech) under standard conditions. In the case of DNA fragments generated by multiple enzyme digestions, blunt-ended fragments, filled in by a standard method using the Klenow fragment of DNA polymerase, were ligated into the *Sma* I site of pUC-18.

Transformation of heat-inactivated ligation reactions into *E. coli* strain DH5α was performed according to manufacturer's instructions (Life Technologies). Libraries were plated on LB agar (Invitrogen) containing ampicillin, X-gal, and IPTG and stored with 15% glycerol at –70°C until required. For screening, libraries were thawed, diluted and plated at a density of 2,000 colonies/plate (180 mm dia.) onto LB agar containing ampicillin, and colonies screened by lifting onto nitrocellulose filters according to manufacturer's instructions (Schleicher & Schull).

Baked filters were hybridized under moderate to low stringency conditions (Benton & Davis, 1977) using $\gamma[^{32}P]$ labeled oligonucleotides containing -$[AT]_{10}$, -$[GT]_{10}$, and -$[AAT]_7$ repeats (Pharmacia). Positive colonies were detected by autoradiography on Kodax X-Omat film at –70°C for 2 days using intensifying screens. Plasmid DNA was isolated from positive clones using the Wizard plasmid DNA kit (Promega) from overnight cultures grown in LB medium containing 0.1mg/ml amplicillin. Nucleotide sequences of recombinant plasmids were determined using M13 primers (forward and reverse) by the dideoxy-chain termination Sequenase Kit (Amersham). From this information, primers flanking potential microsatellite sites were designed and obtained commercially (Genosys). University of Wisconsin Genetics Computer Group (UWGCG) software (Deveraux et al., 1987) was used to mine existing sequences of potential *B. glabrata* microsatellite loci from EST sequences in GenBank (dbEST).

Detection of Microsatellite Variation and RAPD-PCR Analysis

Genetic diversity between snails was assessed by RAPD-PCR analysis, using 19 arbitrary primers, and by variations in microsatellite loci. Variations in microsatellite loci were evaluated by PCR using primer sets flanking either 15 previously described loci (Jones et al., 1999; Mavares et al., 2000) or 45 new loci identified for this study. Genomic DNA was amplified using 'touchdown' PCR (Don et al., 1991) with oligonucletide primer pairs (17–19 mers) obtained from Sigma-Genosys Ltd. The negative control was sterile distilled water. PCR was performed in a total volume of 5.0 μl containing 5 ng of DNA template, 0.5 μl of 10X PCR buffer (same as in 10X RAPD buffer), 1.0 μl of 1mM dNTPs, 0.25 μl α-^{35}S dATP (Specific Activity, 1000Ci/μmol Amersham Pharmacia Biotech, U.K.) and 0.002 units of Taq DNA polymerase (Promega, Wisconsin). "Touchdown" PCR was performed as follows: denaturation, 30 sec at 95°C; annealing, 30 sec (temperature was decreased by 1°C every two cycles from an initial temperature of 10°C above optimal Ta as determined from the manufacturers for the new 45 primer pairs or as previously published by Jones et al. (1999) and Mavares et al. (2000), then held at optimal annealing temperature for 20 cycles; extensions were at 72°C for 30 sec. Stop buffer (1.0 μl, 0.1% xylene cyanol 0.1% bromophenol blue, 10mM EDTA in 95% deionized formaldehyde) was then added to each reaction. Amplified alleles were separated by electrophoresis on 6% urea/polyacrylamide sequencing gels in conjunction with known standards: (1) a 25 bp DNA ladder (Invitrogen) end-labelled with γ-^{32}P; and (2) a sequencing ladder of pUC-19 generated using the universal M13 (reverse) primer. Gels were fixed in 10% (v/v) acetic acid and 10% (v/v) methanol for 15 minutes at room temperature prior to drying at 80°C. Dried gels were set up for autoradiography on X-ray film (X-OMAT, Kodak) overnight at room temperature without intensifying screens. RAPD-PCR using 25 ng of genomic DNA was performed as previously described (Larson et al., 1996). The control was distilled water, and amplified samples were resolved by gel electrophoresis on agarose gels (1.2% w/v). The bands were stained by ethidium bromide and visualized by UV transillumination.

AMOVA Analysis

Phenotypic variation of RAPD products (primers OPX-6, OPM-19, OPAW-07) was investigated by analyses of molecular variance (AMOVA; Excoffier et al., 1992) implemented in the computer package ARLEQUIN Ver. 2.001 (Schneider et al., 2000). Only those bands that could be unequivocally scored across all samples were included in the analysis. Subsequent AMOVA analysis proceeded with 13 markers for three BS-90 snails, three M-line snails and 36 field-collected snails. A matrix of Euclidian square distances was computed using the pairwise difference method. This matrix was used for the analysis of genetic structure including partitioning of variation (A) within the three populations, (B) among the three populations, and (C) among groups of populations (i.e., lab strains versus field strain). Statistical significance of variance components was assessed with 10,000 random permutations.

RESULTS

Assessing Genetic Differences Between Laboratory Snails from Two Different Stocks

Before embarking on the analysis of field population snails, we tested our ability to detect genetic differences, by variations in microsatellite loci and RAPD-PCR analysis, between laboratory-maintained snails. DNA profiles of two well-established laboratory stocks of *B. glabrata* were used as reference samples to test all RAPD-PCR primers and microsatellite primer sets for consistency in amplification. These snails, from stocks BS-90 and M-line, are fully resistant or susceptible, respectively, to the NMRI strain of *S. mansoni* used in our laboratory. Previously, we have shown considerable genetic homogeneity between individuals within each stock by RAPD-PCR with numerous primers (Knight et al., 1999; Ittiprasert et al., 2003). Here we determined the occurrence of polymorphisms between them by examining variations at 60 microsatellite loci and by RAPD-PCR using 19 random primers. The new loci were identified either by screening a small insert library, or *in silico* by mining for simple sequence repeats (SSR) from *B. glabrata* sequences deposited in GenBank.

Primer sets and annealing temperatures (Ta) used for the present study for all 60 microsatellite loci are given in Table 1. Variations in the microsatellite loci examined between the two laboratory maintained snails, listing the number of alleles and their observed sizes, are shown in Table 2. Of the six loci previously described by Jones et al. (1999), null alleles (N/A) were observed for three of these (μBg1, Bgμ10 and Bgμ16) in both snails, and unscorable multiple products (MP) were detected in both stocks with primer sets flanking locus Bgμ8. For the two other loci (μBg2 and Bgμ15) single alleles that were polymorphic between the two laboratory snails were identified. Allelic size ranges observed were more consistent with the size seen in the BS-90 stock compared to M-line stock. For locus Bgμ15, the single allelic band of 178 bp (previously reported) appeared as two bands (176 bp and 178 bp) in the BS-90 snail, and a single band of 161 bp in the M-line snail.

For the nine microsatellite loci reported previously by Mavares et al. (2000), two (BgE2, BgE3) were undetected (null alleles), and primer sets corresponding to locus BgC8 produced multiple products in both snail stocks. Of the remaining six loci, all except one (locus BgE5) were detected in both stocks. The primer set corresponding to the BgE5 locus produced no detectable band in the M-line snail, but produced two allelic bands of 204 bp and 234 bp in the BS-90 snail, thus demonstrating polymorphism in this locus between the two laboratory strains. Similarly, genetic differences between the two stocks were detected with the primer sets corresponding to loci BgC7, BgE1, BgE4 and BgE6. For these sites, the allelic size range detected fell within the expected size range as previously described (Mavares et al., 2000), with the BS-90 snail showing better correspondence in size expected than the M-line stock.

Data in Table 2 describe the presence of the 45 previously unreported, potential microsatellite loci (BGMSCA series, BGMSAT series, and BGMSGATA series). Included are the number of alleles and observed sizes amplified from the two laboratory stocks using primers flanking these loci. Of these, variations were detected in 20 of the sites between the two laboratory snails. Null alleles were observed with 14 primer sets (combined data from BS-90 and M-line snails), and multiple products were detected with primer sets corresponding to four sites.

The results of the RAPD-PCR comparison, using 19 random primers, are summarized in

TABLE 1. Summary of microsatellite loci for the present study.

Locus	Repeat	Flanking Primers (5'–3')	Ta (°C)	Expected Size (bp)	Source	GenBank Accession Number
*m*Bg1	$(TC)_{20}$	F:TTAATTCTACTGGACTCACATGG R:CTGCCAATGTTTACATGCTG	57	186	Jones et al., 1999	AF157698
*m*Bg2	$(GT)_{20}$	F:AGTCTGCTCCAGATTCATTACG R:GCTTATTTTCACCTCTGAATGC	58	254	"	AF157699
Bg*m*8	$(TG)_7TT(TG)_{10}$	F:GCACGAATGTTTGTTGAC R:CCTATTGATTGAAGTGTTTCC	53	131	"	AF157700
Bg*m*10	$(CA)_{11}$	F:AAACACCCACTCACTCTCC R:GTTCAATAAGGTCAGGCAAG	55	95	"	AF157701
Bg*m*15	$(GA)_{14}(G)_{11}$	F:AGGTTTGTATGTCTTGCTG R:GGTTCACTCAGATACATCC	50	178	"	AF157703
Bg*m*16	$(TC)_{24}(TATC)_6$	F:CTGTTATTCATTATTTCATAGAGC R:GGGGATCTAACACATCAG	52	138	"	AF157704
BgC6	$(CA)_4TT(CA)_2CT(CA)_5(TACA)_2$	F:GAGTCTGCGTTTAGCGTACAG R:TGCAGTGATTTGTTCCGTTC	58	302–304	Marvares et al., 2000	AF216279
BgC7	$(AG)_3G(GA)_8GGGAGG(GA)_5$	F:AAACGGGATTGTGTGAATGG R:GCCCAGCAGCAGAGATTG	54	317–321	"	AF216280
BgC8	$(AG)_4N_{23}(AG)_8G(GA)_3N_{13}(AG)_5$	F:AGCCAGCACACCATGTTAGG R:GAAGCGAGCGTTTTGTTTTG	54	269–271	"	AF216274
BgE1	$(GT)_5(GA)_{15}(GACA)_6$	F:GATTGTAAGCTCAGGTGAATAGAAG R:ACACTCGAAAAACACACGAAC	54	133–148	"	AF216275
BgE2	$(GATA)_{18}TGGA(GATA)_9$ TAG$(GATA)_5$	F:TTCCATATTCACGAACCAAC R:GGAACTTTGTGGAGACTGC	54	310–398	"	AF216270
BgE3	$(GATA)_{25}$	F:GGCACCTTTTTCAATGTGG R:TTAGGGTTATTGTCTGTGAGGTTAG	60	221–253	"	AF216269
BgE4	$(GATA)_{13}$	F:GTCAGGACTGTGTGTAAAAGGAAG R:AGAGGGCAGATGATGCAAAG	60	185–246	"	AF216272
BgE5	$(GATA)_{34}$	F:CAGCCTTAGCACCTCTAGTCG R:TCTCATGGAAGTGAAGCTGTG	60	273–345	"	AF216271
BgE6	$(GATA)_{39}N_3(GATA)_{22}$	F:CAGCATTTACCACGAAGAGC R:CACCGCGCCTCTCTACTAC	54	328–526	"	AF216273

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Locus	Repeat	Flanking Primers (5'–3')	Ta (°C)	Expected Size (bp)	Source	GenBank Accession Number
BGMSCA01	$(CA)_7$	F:CTCTCTCCCATAATCCC R:GAATCTGAAATATTTTTA	48	116	BRI	RBGIA11TF
BGMSCA02	$(CA)_8$	F:CAAAATGGTATTTTAAAC R:GTTAGCGATCGGCTGGTG	50	191	"	RBGIA55TR
BGMSCA03	$(CA)_7$	F:CTATGTTTCAGATTTAT R:CAAATGGACAATCTCACG	50	158	"	RBGIA61TF
BGMSCA04	$(CA)_9AA(CA)_2$	F:CCCCATGCCTCTTTCAC R:GCTATGCCCGAAAACGG	50	166	"	RBGIB18TR
BGMSCA05	$(AC)_7$	F:CGAGCGAAGGAACCCGGTC R:GGGTCCCCTTCCCCCTG	48	161	"	RBGIB42TF
BGMSCA06	$(CA)_5$	F:CATTGATATAACACAGA R:GCAGAAAGTAGAACTCTG	50	149	"	RBGIB78TF
BGMSCA07	$(AC)_9$	F:CATATCTTGCATCATTC R:GCGCACTTGGCCTCTCG	55	149	"	RBGIC42TR
BGMSCA08	$(CA)_6GACAAA(CA)_5CT(CA)_2$ CTCA	F:CAATAGCCGGTCGGGTC R:GCACGAGGTCACGTGAT	50	168	"	RBGIC68TF
BGMSCA09	$(CA)_8$	F:CTCTCTTTTTAGTTAGC R:GTTTATTTGTCTTGCGG	55	155	"	RBGID54TF
BGSMCA10	$(CA)_7$	F:CAAAACCAGCTACCCAGC R:CTTTGCATTTAATATTG	48	155	"	RBGIF86TR
BSMGCA11	$(CA)_6$	F:CTATTCTTTTTAAAAGAAC R:CTGTCTCCATAACATCA	50	140	"	RBGIFH81TR
BGMSCA12	$(TA)_3(TG)_{12}GA(CT)_3(GTAT)_2$ TTCAT$(CT)_2(GTAT)_2$TTCA	F:CTGGATGGATCCAGACC R:CTCACAAGTCCACTTAGAA	48	204	"	N/A
BGMSCA13	$(GT)_6$	F:GCGAAAGAAATTGAAGGG R:GTGTACGCTCATAGTAGC	48	393	"	AW739582
BGMSCA14	$(TG)_{12}$	F:CAAGCTACCCTCAAAAAG R:CTCTGTTGTTATCAGCGTG	53	197	"	AW739856
BGMSCA15	$(CA)_6$	F:GTAGACATGAGAAACGTGCC R:GCAAAGACCAGCGAAAAAC	57	222	"	AW739948

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Locus	Repeat	Flanking Primers (5'–3')	Ta (°C)	Expected Size (bp)	Source	GenBank Accession Number
BGMSCA16	$(CA)_7$	F:GCTCTGGTTTCAACACACTCTGC R:GGCAACCCATTCCATTCTCC	63	338	"	AW739597
BGMSCA17	$(TG)_6$	F:GGTCGATTGACGATTTGCCAG R:CGGTTCTTAACCTTTTATGCTCGG	65	158	"	AW739693
BGMSCA18	$(GT)_6$	F:CGATGTAATCGTCTGAATGGGC R:CATGGTAGAGTGACCTCACCTGTG	63	162	"	AW739886
BGMSCA19	$(GT)_7$	F:CGAATTGAACCGCTGTCCAG R:GGTCACCATGACTTAACCCAGTTC	63	151	"	AW740047
BGMSCA20	$(GT)_6GC(GT)_2$	F:ACGTGTGCGTGTTTGGATGG R:TGTAGGAGTGGAACGTCAGCAATC	65	157	"	AW740050
BGMSCA21	$(CA)_8$	F:GCACGAGAAAGAAACAAATCTTGTG R:CGTTGTGTGAATGATGCAATATGAG	61	203	"	AW740079
BGMSCA22	$(CA)_9$	F:TCACTTAGATCGACGCCGTAGG R:GGAAGCTATGCCCGAAAACG	64	154	"	AW740121
BGMSCA23	$(GT)_7$	F:CCCCACCAAAACGTCACAACTC R:CCAGTATATCCACTGCCCAGGTATG	65	112	"	AW740152
BGMSCA24	$(AC)_9$	F:TCCACATATCTTGCATCATTCCC R:TCTAGGTAGCCAAGCCAAGCC	62	182	"	AW740220
BGMSCA25	$(TG)_6$	F:TGGCGATTGTCATTTTTCAACC R:GTCGGGTCATTTGGATACATGC	64	134	"	AW740245
BGMSCA26	$(CA)_6$	F:TCCACGTCGTACTACTCTCCATTTC R:GATCTGCCTTTGGGTCAATCAG	61	151	"	AW740423
BGMSCA27	$(CA)_7$	F:CGAGAACAAAACCAGCTACCCAG R:TGTGCTATTGAGGAGTGTCGTGC	54	196	"	AW740496
BGMSAT01	$(TA)_6$	F:CATATTTATTTATTGAT R:GTTTGTAATCTTAATAT	48	188	"	RBGIA41TF
BGMSAT02	$(AT)_{10}$	F:CTTCTAGGTAGCCAAGA R:GTATTGGTTAGGTAAGA	48	130	"	RBGIA62TF
BGMSAT03	$(TA)_9$	F:CGACGGTATCGATAAGC R:CAGATTAGTTAGAAAAT	48	150	"	RBGIC90TF

(*Continues*)

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Locus	Repeat	Flanking Primers (5'–3')	Ta (°C)	Expected Size (bp)	Source	GenBank Accession Number
BGMSAT04	$(TA)_6$	F:CTGGGGCTGCGCAGCCA R:GTATAGTTATATATTGT	48	149	"	RBGID73TF
BGMSAT05	$(TA)_6$	F:CAGTGGGGATAAAGAAT R:GTGTTAGGAAAATATGA	48	146	"	RBGIF69TF
BGMSAT06	$(AT)_{10}N_{23}(CT)_7$	F:CGGTTTGTTTTATTAGAC R:CAAGACTGGGAAGTGGG	55	199	"	RBGIG94TR
BGMSAT07	$(TA)_{31}$	F:CAGGAAGGATTACAAGAC R:CGTCTCTCAAGACATAAAG	48	214	"	AW739491
BGMSAT08	$(AT)_7$	F:GGGCGACTCGATATAAG R:ACGAATTGTGGCAAAGTC	53	230	"	AW740012
BGMSAT09	$(AT)_{10}N_{23}(CT)_7$	F:ATATCGGGGAGGCATTGC R:GTGCAAATTTTAAACTGGC	54	299	"	AW740375
BGMSAT10	$(AT)_7$	F:CGATGATGACTATTGCTAAAGGG R:TCAAAAAGAAAACGAACGCC	61	136	"	AW739712
BGMSAT11	$(AT)_6$	F:CGACAAATCTTGCCTGGTGC R:TCGAGTCATAGGTAGTCAAGCCAAG	65	163	"	AW739850
BGMSAT12	$(AT)_{10}$	F:CGAGATCTTATTCTGAGAG R:GTGCAAATTTTAAACTGGCTCC	48	368	"	RBGIG94TR
BGMSAT13	$(TA)_6$	F:CAAAAGAAAATCCGCTGCC R:TGTGAGCTAAAGCCCTCTCC	48	322	"	RBGID73TF
BGMSAT14	$(TA)_9$	F:TCGACGGTATCGATAAGCTTG R:ATGTGTGCCAGAAAGCGGAG	48	439	"	RBGIC90TF
BGMSAT15	$(AT)_5$	F:GAGTTGTAGGCCTACACAATG R:AGGTCTGTCGCCAGTAATTATC	52	431	"	RBGIC86TF
BGMSAT16	$(TA)_5$	F:TTGATCTGAGATTGGGCAATG R:GGAATTCGGCACGAGGTTG	49	449	"	RBGIB13TF
BGMSGATA01	$(TATC)_7$	F:AGGAATTCGGCACGAGTC R:CTCAGTGGCTAATGCGTC	57	291	"	AW739497
BGMSGATA02	$(AACC)_6AA(TCTA)_{18}(TCTG)_7$ $TT(TGTC)_2$	F:GAGTAGACATGGACAACAC R:GGCCAAGGAATGTCTAATGG	49	239	"	AW740338

Table 3 (column 3). All but one primer (OPV-20) revealed polymorphisms between strains. In all cases, the polymorphisms detected were major and readily observed by ethidium bromide staining of agarose gels. Representative examples of the DNA profiles from RAPD-PCR using two random primers are shown in Figure 1A and B. Major differences could be detected with both primers in the RAPD profiles of both the BS-90 and M-line snails. For example, primer OPAW-07 reveals a major band of 700 bp that is absent from the M-line snail. Using primer OPZ-05 a band of 1.0 kb was detected only in the M-line snail.

In summary, it was clear that both microsatellite variation and RAPD-PCR analysis were adequate in assessing polymorphisms between snails from the two laboratory stocks. Of the microsatellite sites analyzed, 26 loci were found to be polymorphic, while 8 sites were monomorphic between the two stocks. With RAPD-PCR, all but one primer revealed polymorphisms between the two lab stocks.

Assessing Genetic Diversity in Field-Collected Snails from a Single Locality

After conditions were optimized, DNA polymorphisms were evaluated following the established procedure among field isolates of *B. glabrata*. Results in Table 4 describe microsatellite variations (observed allelic sizes and number of alleles) between 20 different individual field collected snails for 26 primer sets. The primer pairs used for field evaluation were those that gave consistent results either when amplifications were performed at different times or by different investigators on the same field-collected snail DNA template. Primer sets that failed to show amplified products (null alleles) when laboratory snail stock DNA was used as template were omitted from the field study. In addition, 24 primer sets that produced multiple products when field collected samples were analyzed have not been included in Table 4. In comparison to the laboratory snails, field-collected snails showed significant variations for several of the loci examined. For example, for two loci previously identified by Mavares et al. (2000) (BgE1 and BgE5), we detected more intrastrain variation at these loci compared to the laboratory stocks, where only one allele was detected. Correspondence in the observed size range to the expected size was consistent between laboratory-maintained and field-collected samples, although the number of alleles varied between them for the majority of loci analyzed. Invariant alleles (in size and number) between the laboratory snails and field isolates were found with only two loci (BGMSCA05 and

TABLE 2. Observed allelic sizes and number of alleles for 60 microsatellite loci in resistant (BS-90) and susceptible (M-line) laboratory-maintained snails.

	BS-90 (R)		M-line (S)	
Locus	Observed Sizes (bp)	Number of Alleles	Observed Sizes (bp)	Number of Alleles
mBg1	N/A	N/A	N/A	N/A
mBg2	249	1	259	1
Bgm8	MP	MP	MP	MP
Bgm10	N/A	N/A	N/A	N/A
Bgm15	176, 178	2	161	1
Bgm16	N/A	N/A	N/A	N/A
BgC6	N/A	N/A	N/A	N/A
BgC7	321	1	325	1
BgC8	MP	MP	MP	MP
BgE1	131, 137	2	103, 135	2
BgE2	N/A	N/A	N/A	N/A
BgE3	N/A	N/A	N/A	N/A
BgE4	205	1	177	1
BgE5	204, 234	2	N/A	N/A
BgE6	539	1	289	1

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Locus	BS-90 (R)		M-line (S)	
	Observed Sizes (bp)	Number of Alleles	Observed Sizes (bp)	Number of Alleles
BGMSCA01	126, 128	2	MP	MP
BGMSCA02	N/A	N/A	N/A	N/A
BGMSCA03	158, 160	2	166, 168	2
BGMSCA04	135, 164	2	164	1
BGMSCA05	152	1	152	1
BGMSCA06	152,154	2	152,154	2
BGMSCA07	149	1	153	1
BGMSCA08	N/A	N/A	N/A	N/A
BGMSCA09	155	1	171	1
BGSMCA10	N/A	N/A	N/A	N/A
BSMGCA11	MP	MP	MP	MP
BGMSCA12	N/A	N/A	N/A	N/A
BGMSCA13	N/A	N/A	N/A	N/A
BGMSCA14	199	1	193, 195	2
BGMSCA15	224	1	190	1
BGMSCA16	334	1	334	1
BGMSCA17	N/A	N/A	N/A	N/A
BGMSCA18	162	1	162	1
BGMSCA19	151	1	151	1
BGMSCA20	162	1	164	1
BGMSCA21	203	1	N/A	N/A
BGMSCA22	154	1	154	1
BGMSCA23	112	1	112	1
BGMSCA24	180, 182	2	185, 187	2
BGMSCA25	134	1	138	1
BGMSCA26	151	1	153	1
BGMSCA27	196	1	204, 212	2
BGMSAT01	N/A	N/A	N/A	N/A
BGMSAT02	130	1	N/A	N/A
BGMSAT03	N/A	N/A	N/A	N/A
BGMSAT04	N/A	N/A	N/A	N/A
BGMSAT05	140, 146	2	140, 146	2
BGMSAT06	MP	MP	MP	MP
BGMSAT07	MP	MP	MP	MP
BGMSAT08	220, 230	2	224, 234	2
BGMSAT09	307	1	332	1
BGMSAT10	136	1	136	1
BGMSAT11	MP	MP	MP	MP
BGMSAT12	335	1	N/A	N/A
BGMSAT13	319, 333	2	333	1
BGMSAT14	N/A	N/A	N/A	N/A
BGMSAT15	431	1	431	1
BGMSAT16	232	1	185, 233	2
BGMSGATA01	MP	MP	MP	MP
BGMSGATA02	372	1	374	1

TABLE 3. Detection of polymorphisms (+/-) by RAPD-PCR analysis among laboratory stocks and among field-collected snails.

RAPD Primers	Sequence 5' to 3'	Lab Interstrain Variation (+/-)	Field Intrastrain Variation (+/-)
OPAL-10	AAGGCCCCTG	+	-
OPAJ-17	ACCCCCTATG	+	-
OPAV-11	GACCCCGACA	+	-
OPT-11	TTCCCCGCGA	+	-
OPS-04	CACCCCCTTG	+	+
OPV-12	ACCCCCCACT	+	+
OPAQ-09	AGTCCCCCTC	+	+
OPX-04	CCGCTACCGA	+	+
OPM-18	CACCATCCGT	+	-
OPAJ-08	GTGCTCCCTC	+	-
OPAP-08	ACCCCCACAC	+	-
OPAW-07	AGCCCCCAAG	+	+
OPV-20	CAGCATGGTC	-	-
OPM-19	CCTTCAGGCA	+	+
OPX-06	ACGCCAGAGG	+	+
OPV-15	CAGTGCCGGT	+	+
OPZ-20	ACTTTGGCGG	+	-
OPZ-05	TCCCATGCTG	+	+
OPAH-04	CTCCCAGAC	+	-

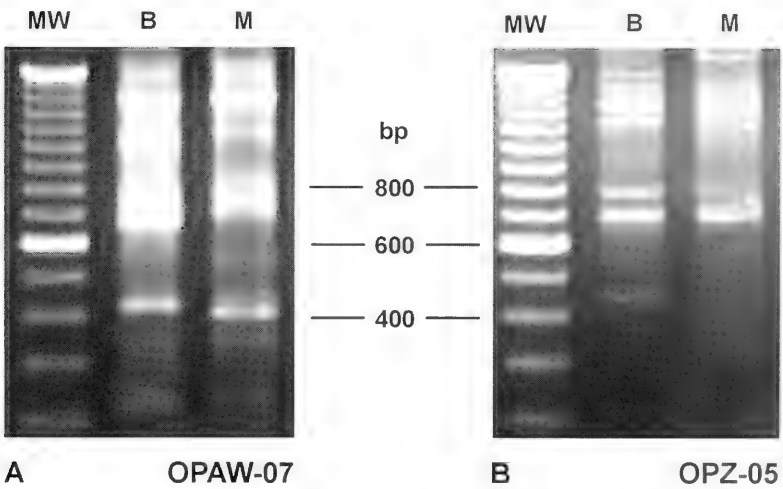

FIGURE 1. RAPD-PCR amplification of BS-90 (B) and M-line (M) snail DNA with random primers (A) OPAW-07 and (B) OPZ-05. For molecular weight markers (MW), a 100 bp ladder was used.

TABLE 4. Observed allelic sizes and number of alleles for 44 microsatellite loci of field-collected *B. glabrata* snails.

Locus	Number of Snails	Observed Allelic Sizes (bp)	Number of Alleles
mBg2	19	275	1
	1	259, 275	2
Bgm15	13	175	1
	5	175, 176	2
	1	176	1
	1	N/A	
BgC7	4	326, 327	2
	15	327	1
	1	N/A	
BgE1	2	99, 103	2
	3	99, 107	2
	1	99	1
	7	103	1
	7	N/A	
BgE4	14	181	1
	6	181, 209	2
BgE5	4	230	1
	1	230, 234	2
	1	230, 242	2
	4	234	1
	4	234, 242	2
	6	N/A	
BGMSCA01	20	126, 128	2
BGMSCA03	19	166, 168	2
	1	N/A	
BGMSCA05	20	152	1
BGMSCA14	18	197	1
	2	197, 198	2
BGMSCA18	20	162	1
BGMSCA19	19	160	1
	1	N/A	
BGMSCA20	20	N/A	
BGMSCA22	20	152	1
BGMSCA23	20	N/A	
BGMSCA25	20	144	1
BGMSCA26	20	N/A	
BGMSCA27	17	200	1
	3	N/A	
BGMSAT05	14	130, 136	2
	6	N/A	
BGMSAT08	10	230	1
	5	230, 231	2
	3	231	1
	2	N/A	
BGMSAT10	20	154	1
BGMSAT12	12	335	1
	8	N/A	
BGMSAT15	4	429	1
	1	429, 437	2
	2	437	1
	13	N/A	
BGMSAT16	11	184	1
	6	184, 211	2
	3	N/A	
BGMSGATA02	19	520, 521	2
	1	N/A	

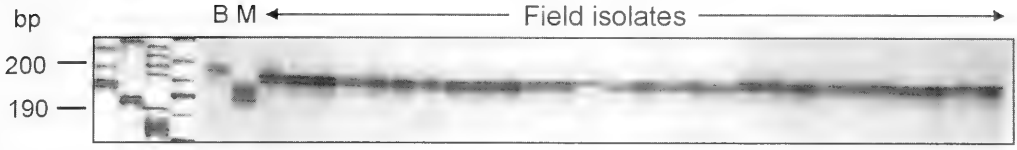

FIGURE 2. Microsatellite variation of locus BGMSCA14. Sequencing ladder of pUC-19 was used as standard. B and M represent lanes showing allelic bands amplified at this locus for the BS-90 and M-line laboratory stocks, respectively. Amplification at the same locus for DNA from 29 field-isolated snails, isolated from a single site, is shown. Note the difference in number and size of alleles between the lab stocks and among the field-collected samples.

BGMSCA18), where single allelic size bands of 152 bp and 162 bp, respectively, were detected with all DNA samples analyzed.

In several cases, multiple products were obtained for the same loci in snails from both laboratory and field, that is, Bgμ8 and BgC8. Although null alleles were infrequent for the majority of loci, these were associated more with the M-line snail than with either the BS-90 or field-collected snails. A representative example of microsatellite variation in the locus BGMSCA14 is shown in Figure 2. As can be seen, polymorphisms in this locus were detected between the laboratory-maintained snails, manifested by differences in sizes of allelic bands in the BS-90 (199 bp) compared to the M-line snail (193 bp and 195 bp). Diversity within this locus for field-collected snails was also clearly visible. In this case, most samples examined from this population (29 snails) either displayed allelic size bands of 197 bp and 198 bp or, as seen in one snail from this population, a single allelic band of 198 bp was detected.

A summary of the results obtained using RAPD-PCR to assess genetic diversity among the field-collected snails is shown in Table 3 (column 4). Of the 19 random primers utilized, we observed intra-strain variation with nine of them. Figure 3 shows a representative ex-

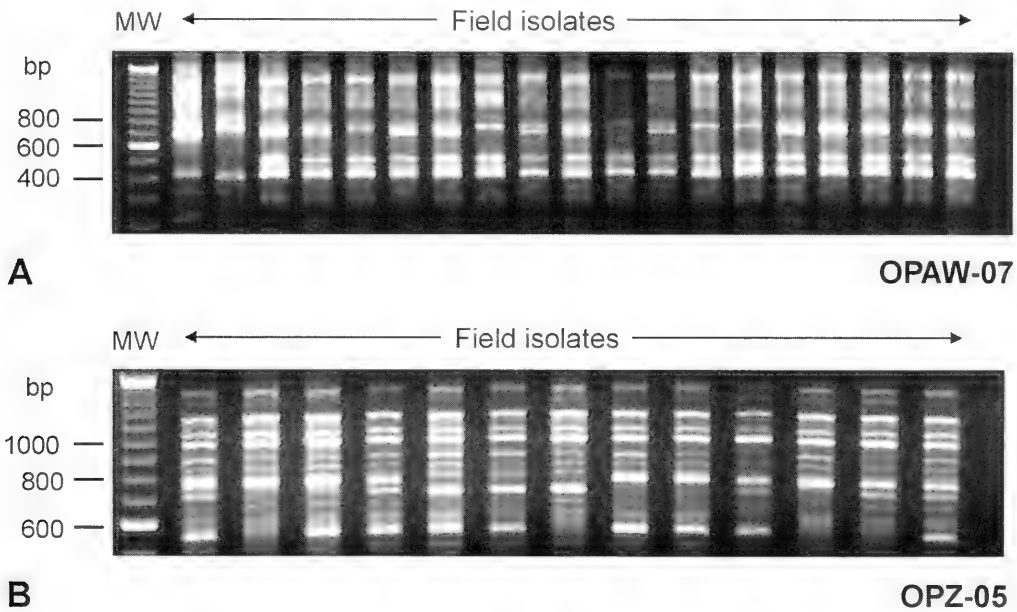

FIGURE 3. RAPD-PCR amplification of DNA from individual field isolates of *B. glabrata* snails, using random primers (A) OPAW-07 and (B) OPZ-05. For molecular weight markers (MW), a 100 bp ladder was used.

ample of RAPD-PCR analysis of field-collected snails, using random primers OPAW-07 and OPZ-05. Of the 19 DNA samples analyzed, both primers revealed major intrastrain variation among them. For primer OPAW-07, two bands (doublet) of 700 bp and 750 bp were present in most snails analyzed, but a single 750 bp band was seen in five snails examined. Also, with this primer, a major 500 bp band seen in most snails was absent in two analyzed (lanes 1 and 2). Variations with primer OPZ-05 were clearly visible in several bands. For example, polymorphisms were detected in bands at 550 bp and 750 bp in these field-collected snails.

Assessing Population Structure Based on RAPD Data

The analysis of molecular variance (AMOVA) showed that most of the variation resides within populations (68%) and the permutation tests indicated that the within-population differences are highly significant ($P < 0.00001$). The variation among populations accounts for 54% of the total variation ($P = 0.0283$). However, the difference between the two lab-strain populations and the field-strain population (–22% of the total variation) is not significant (Table 5). A pairwise AMOVA differentiation test between populations showed that all three comparisons were significant (BS-90 snails vs. M-line snails 0.02712; BS-90 snails vs. field-collected snails 0.00157, and M-line snails vs. field-collected snails 0.00161).

DISCUSSION

The genetics of both the snail host and the parasite determine the outcome of the molluscan stage of parasite development. For this reason, more is being done to understand how the genetic structures of the parasite and snail host populations affect transmission and epidemiology of this complex disease. In this study, we have compared the relative sensitivities of two DNA fingerprinting methods to assess genetic heterogeneity among snails from a single, restricted field site in a schistosomiasis-endemic area. This analysis was done following establishment of the profiles of representative snails from two well-established laboratory stocks that are either resistant or susceptible to parasite infection, and on which considerable molecular profile data already exist (Knight et al., 1999; Ittiprasert et al., 2003). The genome wide scanning tools we used in this study (microsatellite variation and RAPD-PCR) are particularly useful for studying organisms in which only limited molecular information is available. From our results it was clear that both methods showed significant polymorphisms between snails in this restricted field site.

In previous work, we showed by RAPD-PCR the segregation of two markers (1.2 kb and 1.0 kb) with the inheritance of adult resistance (Knight et al., 1999), a known Mendelian single gene trait in *B. glabrata* (Richards, 1984). Included in our study here was the first analysis to assess the potential frequency of these markers in field-collected snails from a known endemic area for schistosomiasis. We had hoped that by extending these studies to the field, the presence, if any, of resistant snails and their role in the dynamics of transmission can start to be evaluated. However, neither marker was detected in any of the field-isolated snails we analyzed. Whether these markers universally segregate with resistance in all *B. glabrata* populations, or whether resistant snails were absent from the present population studied is not known.

TABLE 5. Summary of AMOVA analysis. Statistics include: degrees of freedom (*df*), sum of squares (SSD), variance-component estimates (CV), and percentages of the total variance (% Total) contributed by each component.

Source of Variation	*df*	SSD	CV	% Total
within populations	37	14.500	0.39189	68.15
among populations	1	1.625	0.30828	53.61
among groups	1	1.750	–0.12511	–21.76*

*not significant after 100172 permutations; the negative value reflects that this statistic is actually a covariance where negative values can occur when the actual values are close to zero (Excoffier et al., 1992).

Several explanations may account for the absence of the 1.2 kb and 1.0 kb markers in our field population. One possible explanation is that the markers do not universally segregate with resistance in all *B. glabrata* populations. Differences between the M-line, BS-90 and the field population may also reflect intraspecific diversity in *B. glabrata* as a whole. Previously, Paraense (1959) found reduced infertility among some populations of *B. glabrata*, suggesting there may be considerable genetic heterogeneity in this species. A second explanation that might account for the absence of the 1.2 and 1.0 kb markers in the field population would be evolution in the laboratory stocks. It is possible that when these stocks were founded that alleles that were rare in natural populations became more common, either by chance or because of the removal of selection against them. Laboratory stocks can be extremely useful for working out patterns that are difficult to see in natural populations because there may be more pronounced and less variable responses, that is, a more favorable ratio of signal to noise. However, a potential pitfall of using laboratory stocks is that they may not be reflective of what actually happens in nature. Our findings therefore point to a critical need for further comparisons of laboratory and field populations of *B. glabrata*. Our results also show that not all microsatellite primer sets that were developed using laboratory stock DNA were useful when field collected snails were analyzed, thus indicating that more work needs to be done on field collected snails in developing more representative markers.

Finally, it is possible that the markers of resistance were simply absent from the sample we examined. Experimental studies suggest that resistance may be costly to snails (Minchella & LoVerde, 1983). Mulvey & Vrijenhoek (1984) have also proposed that genetic drift in populations of *B. glabrata* might produce patchy susceptibility and resistance over time and space.

For population genetic analysis of schistosome snail hosts by RAPD-PCR, evidence for the existence of both inter- and intrapopulation diversity has been reported. Vidigal et al. (1994), using four primers, showed that diversity between snail populations can readily be assessed by this method, but it was not as revealing among snails from the same geographic region. With another *Biomphalaria* species, however, Hoffman et al. (1998) reported that this method could reveal a high frequency of genetic diversity in *B. pfeifferi* populations that resided only a short distance apart in the same river. Likewise, studies examining *Bulinus* snails involved in transmission of *S. haematobium* have shown similar intrapopulation genetic diversity by RAPD-PCR (Davies et al., 1999). Our study clearly shows that RAPD-PCR analysis can be a legitimate tool to reveal polymorphisms between snails collected from a single site, in which mating would presumably be restricted, and to study population structure of groups of populations.

As stated earlier, limitations to the RAPD-PCR method for population studies exists, especially because it allows for the detection of only dominant alleles. In earlier studies on laboratory snail stocks, we detected reproducible polymorphisms between schistosome-resistant and -susceptible snails with 90% of the primers utilized in the RAPD-assay. In the present study, we found that by using RAPD-PCR a somewhat higher frequency of diversity is seen between our laboratory stocks, compared to variation observed in the field isolated snails – a not altogether unexpected finding. This may reflect the fact that, compared to the field snails, the two laboratory snails used here originated from very different geographic lineages; the albino M-line was derived by a cross between Puerto Rican and Brazilian isolates (Newton, 1953), whereas the wildtype BS-90 snails are descendents of an original field collection from Brazil (Paraense & Correa, 1963).

In addition to the *B. glabrata* microsatellite loci previously described by others (Jones et al., 1999; Mavares et al., 2000), we now show results of genetic variation in 45 new microsatellite loci. Population genetic studies with microsatellites for other schistosome transmitting species have been carried out, especially for *Bulinus* sp., measuring parameters such as mating systems and geneflow (Viard et al., 1996; Stothard et al., 2001). Invariant loci detected were further evaluated by SSCP to determine the unequivocal evidence of homoplasy (Angers et al., 2000). Our study shows that two loci (BGMSCA05 and BGMSCA18) appear to be fixed between both laboratory stocks and in field snails. Whether the same size bands are identical by descent remains to be seen, but nucleotide sequence analysis of the same sized bands should reveal their relationship.

The value of data mining for SSRs in expressed sequence tags (ESTs) is evident from the results of our study, allowing us to generate

44 microsatellite primer sets. This data mining strategy for SSRs has also been used with success in plant molecular biology for identification of potential microsatellite loci in barley, maize, rice, sorghum and wheat (Kantety et al., 2002). With current interest in a genome project for *B. glabrata*, it is anticipated that the availability of more sequence information from this snail will increase the output of microsatellite markers, thus benefiting high density mapping efforts. It is envisaged that high throughput analysis of *B. glabrata* DNA will facilitate the development of other modern genome analysis tools, such as single nucleotide polymorphisms (SNPs), another useful tool for studying the diversity of complex genomes (Wang et al., 1998).

It is not known what role SSRs play in mRNA transcripts, because one would expect the gene coding region of the transcript to remain neutral. Polymorphisms, manifested by the expansion of tri-nucleotide repeats in the coding region of mRNA, have been shown, however, to play a role in certain human genetic disorders, such as Huntington's disease and muscular dystrophy (Maat-Kievit et al., 2001; Margolis et al., 2001). In humans, the most abundant di-nucleotide repeat motif found is the CA/GT repeat (Weber, 1990). In the new sites described in this study, 15 repeat motifs were CA/GT, but most were AT/TA rich. Compound and interrupted repeats were also detected.

We found that null alleles were infrequent for most microsatellite loci examined. In the case of the loci described by Jones et al. (1999), amplification of our laboratory snails showed no product for three out of the six loci reported by these investigators. We likewise observed null alleles with several of the loci described by Mavares et al. (2000) in BS-90 and M-line snails. With the newly described loci we obtained *in silico*, we were surprised to observe null alleles for some of them, since these sequences reside in functional transcripts of the snail. One explanation for this could be that these sequences may not be readily detected using the amplification conditions employed in this analysis.

We found that several loci were non-scorable, and amplification of these showed multiple bands with sizes that deviated significantly from the size expected. Because microsatellites have been defined as highly polymorphic single locus regions in the genome, we omitted primers that produced these multiple products from our study. It is likely, however, that these may constitute hypervariable sites in the *B. glabrata* genome. Nucleotide sequence analysis should help to clarify the nature of these repetitive bands.

In summary, we found that RAPD-PCR is a practical method for assessing population structure of lab- and field-collected strains of *Biomphalaria glabrata*. In addition, variations in previously described and newly identified microsatellite loci are useful for assessing genetic differences between two laboratory maintained snails, and among snails collected from a single field site. With the substantial variation shown by microsatellite analysis in the field-collected snails, however, it will be important to select only those primer sets that do not display hypervariability for detailed population studies. Before settling on primer sets to use for studying snail population structure in other geographic regions, it may be important to prescreen representative snails from that region. The extensive variation in snails we showed through microsatellite analysis may be magnified by geographic distance, revealing even more profound differences than what we demonstrated even in this very restricted field collection site.

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RESEARCH NOTES

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A NEW PANAMIC SPECIES OF THE BIVALVE GENUS *SEMELINA* (SEMELIDAE)

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ABSTRACT

A new species of *Semelina*, *S. campbellorum*, is described from the Panamic province, differing from *S. subquadrata* (Carpenter, 1857) in having a longer, more tapered posterior end, orthogyrate rather than opisthogyrate beaks, more lamellar commarginal ribs with fine commarginal threads between the larger lamellae, and a longer, more confluent pallial sinus that reaches the anterior adductor muscle scar. *Semelina subquadrata* is very similar to the western Atlantic *S. nuculoides* (Conrad, 1841). An internal ligament has probably evolved more than once within the Tellinoidea, and the Semelidae is probably polyphyletic. The genus *Semelina* is one of several genera that are of somewhat uncertain position.

Key words: *Semelina*, Semelidae, Panamic province.

INTRODUCTION

In identifying material in connection with preparation of a manual on the Panamic Bivalvia, it was realized that there are two tropical eastern Pacific species of the genus *Semelina*. Study of Carpenter's type material of "?*Montacuta*" *subquadrata* was necessary to be certain which of the two species he described.

As first suggested by Maxwell (1991) in a talk and accompanying abstract, the Semelidae as presently constituted is probably polyphyletic. He cited several pairs of genera with similar external shell morphology, differing chiefly in the presence of only an external ligament (Tellinidae) or also having an internal resilifer (Semelidae). Whereas some examples that he cited may actually represent convergence in general shell morphology, it is likely that an internal ligament has evolved more than once among taxa now allocated to the Semelidae. Indeed, Kamenev & Nadtochy (1999) demonstrated that juvenile *Macoma* have a small internal ligament and are not very different from species allocated to *Abrina* in the Semelidae. Gustav Paulay (personal communication, 19 December 2002) has pointed out that some IndoPacific species, mostly as yet undescribed, now allocated to the tellinid genera *Exotica* and *Semelangulus* actually have both an external and an internal ligament, and some of these are similar to the New World genus *Semelina*, although only the three taxa discussed in this paper have been allocated to *Semelina* in the literature. Additional studies are clearly much needed to sort out the clades within the Tellinoidea.

The following institutional abbreviations are used here: BMNH, British Museum of Natural History collection, The Natural History Museum, London, England; CAS, California Academy of Sciences, San Francisco, California, U.S.A.; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; USNM, United States National Museum collection, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

SYSTEMATIC TREATMENT

Semelina Dall, 1900: 986, 994

Type species (original designation): *Amphidesma nuculoides* Conrad, in Hodge, 1841: 347; Conrad, 1845: 73, pl. 41, fig. 7. Natural Well, Duplin County, North Carolina; Duplin Formation (*sensu stricto*), 3.2 Ma, late Pliocene. Synonyms: *Semele nuculoidea, auctt., nom. null.*; "*Semele*?" *virginiana*

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Meyer, 1888: 143; *S. nuculoidea lirulata* Dall, 1900: 994; *S. sirulata* Dall, *auctt., nom. null.*

Diagnosis

Small, longer anteriorly; internal ligament in a short to elongate resilifer, not produced ventrally beyond the hinge plate; external ligament in a narrow groove; right valve with elongate anterior and posterior lateral teeth, the left valve fitting into the grooves between them and the dorsal margin; lunule and escutcheon present; right valve with a narrow, inconspicuous anterior cardinal and a large posterior cardinal; left valve with a large anterior cardinal and a narrow posterior cardinal that defines the posterior edge of the resilifer; pallial sinus large, deep. Sculpture of fine, dense commarginal ribs.

This genus first appears in the early Miocene Chipola Formation of Calhoun County, Florida, with *Semelina cythereoidea* Dall, 1900 (p. 994, pl. 44, fig. 5). The eastern U.S./western Atlantic *Semelina nuculoides* is treated by Campbell (1993: 42, pl. 17, fig. 156), Díaz M. & Puyana H. (1994: 97, pl. 28, fig. 268), Gardner (1944: 102–103, pl. 17, figs. 18–21), Lamy (1915), Redfern (2001: 231–232, pl. 99, fig. 948), and Rios (1994: 275, pl. 94, fig. 1352). It now occurs from North Carolina to the West Indies and Brazil, and is recorded as early as the early Pliocene (3.8 Ma) in the southeastern U.S.A.

Semelina subquadrata (Carpenter, 1857)
Figures 1–4

"?*Montacuta*" *subquadrata* Carpenter, 1857a: 248, *nom. nud.*; Carpenter, 1857b: 113; Brann, 1966: 35, pl. 10, fig. 162

"?*Mysella*" *subquadrata* (Carpenter) – Dall, 1899: 881

Rochefortia subquadrata (Carpenter) – Hertlein & Strong, 1947: 135 [in part; their specimen from Bahía Santa Inez, Baja California Sur, is a *Mysella* – CAS 162714; Loc. 17746]

Semelina nuculoides Conrad, *non* Conrad, in Hodge, 1841 – Hoffstetter, 1952: 41

Mysella subquadrata (Carpenter) – Keen, 1958: 107

Semelina subquadrata (Carpenter) – Olsson, 1961: 375, pl. 66, fig. 11; Keen, 1968: 395, fig. 11, 400; Keen, 1971: 259, 260, fig. 661

Description

Ovate-elongate, evenly inflated; beaks almost at posterior end, opisthogyrous; posterior end subtruncate; surface with fine, even, rounded commarginal ribs, some of which become lamellar on posterior slope, while others die out before reaching the posterior slope; pallial sinus ending well short of anterior adductor muscle scar and confluent with the pallial line for only about a third of its length; shell white, sometimes with a pinkish flush. Length to 6.6 mm.

Type Material & Locality

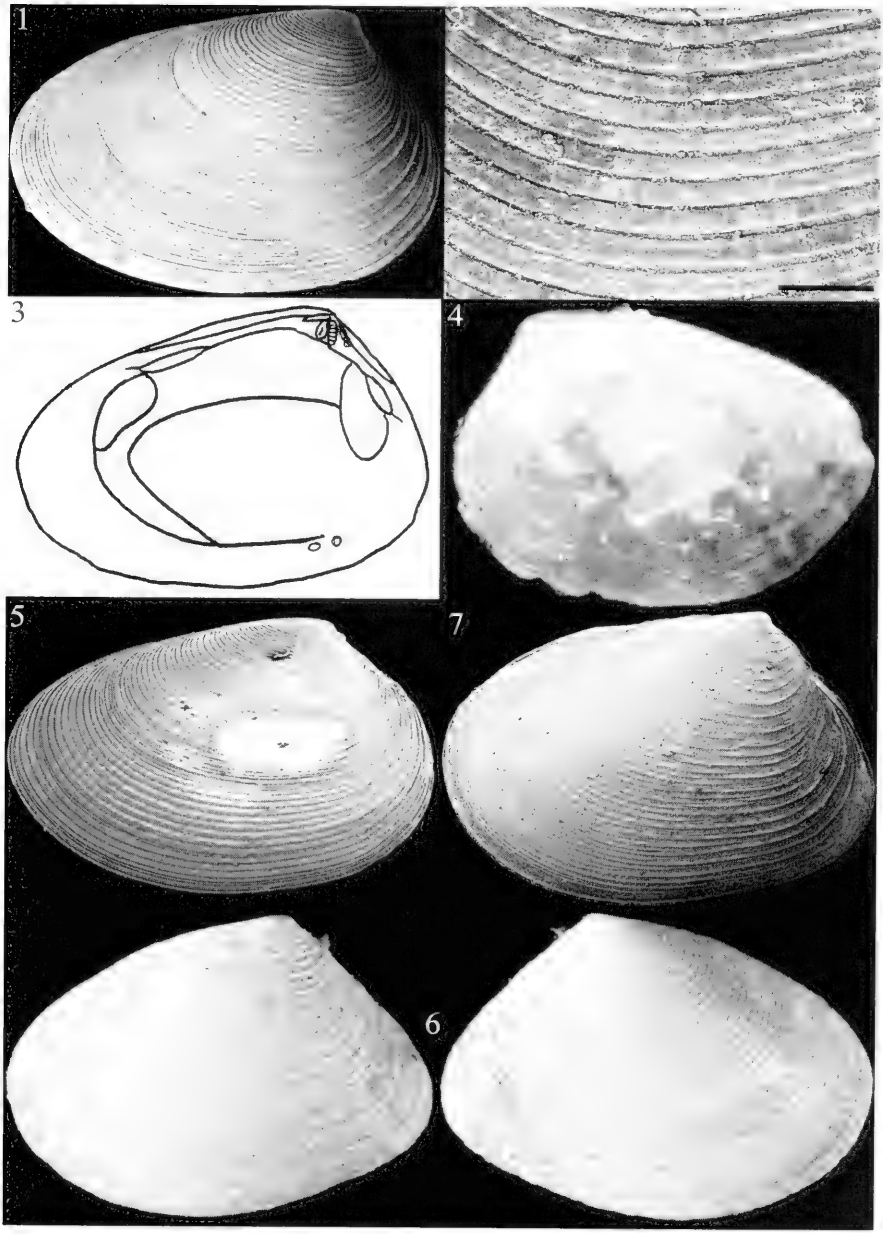
BMNH 1857.6.4.503/1, **lectotype herein**, the larger specimen, a right valve, length = approximately 3.2 mm (Fig. 4); BMNH 1857.6.4.503/2, paralectotype, a smaller left valve measuring approximately 1.2 mm. Both specimens remain glued to Carpenter's original glass slide. Mazatlán, Sinaloa, México (32.2°N); Frederick Reigen. A lectotype is designated because the small glue-covered left valve is too small to be reliable identified.

Distribution

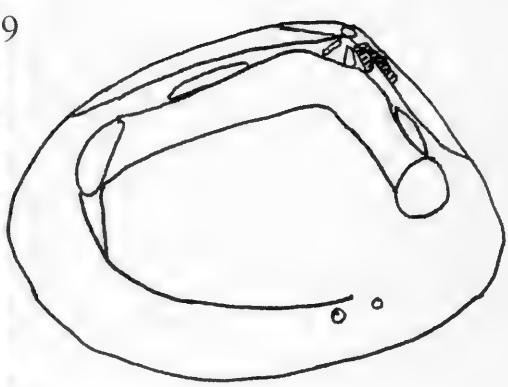
Bahía Magdalena, Pacific coast of Baja California Sur (24.5°N) [LACM 49-234.1], into the Golfo de California as far north as Isla Danzante, Baja California Sur (25.8°N) (Skoglund Collection), and Estero Soldado, Sonora (27.9°N) [LACM 73-5.45], México, to Manglaralto, Guayas, Ecuador (1.9°S) [CAS 162257]; probably as far south as Punta Santa Elena, Guayas, Ecuador (2.2°S), where it has been recorded as a subfossil (Hoffstetter, 1952: 41); Isla Marchena, Islas Galápagos, Ecuador (0.3°N) [LACM 34-285.5]; from the intertidal zone to 220 m (mean = 43.1 m; n = 17); no bottom types noted on labels. I have seen 20 lots; Carol Skoglund provided data for 4 additional lots.

Referred Material

Stations in México: LACM 49-234.1 – Bahía Magdalena, Baja California Sur – 33 m; Skoglund Collection – Isla Danzante, Baja California Sur – 30–45 m; Skoglund Collection – Los Frailes, Baja California Sur – 50–66 m; LACM 73-5.45 – Estero Soldado, Sonora – intertidal zone; Skoglund Collection – Bahía San Carlos, Sonora – 15–30 m; BMNH 1857.6.4.503 – Mazatlán, Jalisco – type lot; CAS 161375 – Mazatlán, Jalisco – "dredged"; Skoglund Collection – Cuastecomate, Jalisco – 12–30 m; LACM 38-263.1, CAS 164336 – Black Rocks,



FIGS. 1–4. *Semelina subquadrata*. FIG. 1. External view of left valve; length, 4.6 mm. SBMNH 348120; Balboa, Panamá; commercial dredgings; *ex* Skoglund Collection. FIG. 2. Same specimen; close-up of sculpture on border between central and posterior slopes; width of ribs approximately 60 µm. FIG. 3. Sketch showing hinge, adductor muscle scars, pallial sinus, pallial line, and cruciform muscle scars of right valve; CAS 161375; Mazatlán, Sinaloa, México; length, 5.1 mm. FIG. 4. Lectotype of "?*Montacuta*" *subquadrata* Carpenter; BMNH 1857.6.4.503/1, right valve approximately 3.2 mm long. FIG. 5. *Semelina nuculoides*. External view of left valve; length, 4.5 mm. SBMNH 348121; 40 miles SE of Charleston, South Carolina; 60 m; *ex* Campbell Collection.
FIGS. 6–7. *Semelina campbellorum*. FIG. 6. Holotype; external views of left and right valves; SBMNH 348119; Bahía de Santiago, Colima, México; length, 4.4 mm. FIG. 7. Paratype; SBMNH 348119; external view of left valve; same station; length, 3.7 mm.



FIGS. 8, 9. *Semelina campbellorum*. FIG. 8. Same specimen as Fig. 7; close-up of sculpture on border between central and posterior slopes; distance between higher ribs approximately 100 µm. FIG. 9. Sketch showing hinge, adductor muscle scars, pallial sinus, pallial line, and cruciform muscle scars of right valve; LACM 37-218.2; Bahía San Ignacio, Sinaloa, México; length, 5.0 mm.

Jalisco – 37 m; LACM 65-16.18 – Bahía Banderas, Jalisco; LACM 33-136.1 – Petatlán, Guerrero – 11 m; LACM 34-241.1 – Petatlán, Guerrero – 183–256 m; LACM 38.9.12 – Bahía Guatulco, Oaxaxa – 73–128 m

Stations in Nicaragua: CAS 164337 – Corinto, Chinandega – no depth recorded; CAS 164338 – Corinto, Chinandega – no depth recorded

Stations in Costa Rica: LACM 72-19.39 – Bahía de Salinas, Guanacaste – 1.5–11 m; LACM 80-60.17 – Cabo Santa Elena, Guanacaste – intertidal zone; LACM 86-26.33 – Playa Nancite, Guanacaste – beach drift; Skoglund Collection – Playa Tamarindo, Guanacaste – 6–15 m; LACM 84-152.5 – Bahía Ballena, Puntarenas – 15–21 m.

Stations in Panamá: LACM 39-259.2 – Isla Ladrones, Chiriquí – 99 m, Skoglund Collection – Balboa, Panamá

Stations in Ecuador: CAS 162257 – Manglaralto, Guayas – no depth recorded; LACM 34-285.5 – Isla Marchena, Islas Galápagos – 37 m

Discussion

As pointed out by Olsson (1961: 375), this species is very similar to the western Atlantic *Semelina nuculoides* (Conrad, in Hodge, 1841), and the two may be indistinguishable. Resolution of this question would require more abundant material of *Semelina nuculoides* from its type locality in the Pliocene of North Carolina than was at my disposal. (Conrad's type material was not located in the Academy of Natural Sciences of Philadelphia by Moore, 1962: 80.) Eastern Pacific material of *S. subquadrata* differs from Recent specimens from North Carolina identified as *S. nuculoides* (Fig. 5) in having higher, more pointed, more posteriorly placed beaks.

Semelina campbellorum Coan, 2002, new species
Figures 6–9

Description

Subtrigonal; anterior end more inflated; beaks about two-thirds of way to posterior end, orthogyrous; posterior end tapered, slightly sinuous, subtruncate ventrally; surface with lamellar commarginal ribs, becoming broader ventrally, and with fine commarginal threads between them; major lamellar ribs more higher near and on posterior slope, whereas some of them become thread-like and end anterior to posterior slope; pallial sinus just touching anterior adductor muscle scar, and confluent with the pallial line for most of its length; internal ligament in a short to elongate resilifer, not produced ventrally beyond the hinge plate; external ligament in a narrow groove; right valve with elongate anterior and posterior lateral teeth, the left valve fitting into the grooves between them and the dorsal margin; lunule and escutcheon present; right valve with a narrow, inconspicuous anterior cardinal and a large posterior cardinal; left valve with a large anterior cardinal and a narrow posterior cardinal that defines the posterior edge of the resilifer. Length to 7.0 mm.

Type Material & Locality

SBMNH 348118, holotype; length, 4.4 mm; height, 3.3 mm; width, 2.0 mm (Fig. 6); SBMNH 348119, paratypes, 7 pairs, including the two figured herein (Figs. 7, 8); USNM 1008293; paratype, 1 pair. Skoglund Coll., paratypes, 5 pairs. Off Punta de Juluapan, Bahía de Santiago, Colima, México (19°5'N, 104°23'W); 30–60 m; Paul & Carol Skoglund; December 1975 and later.

Distribution

In the Golfo de California as far north as Bahía de los Angeles, Baja California (29.1°N) [LACM 86-195.5], and Bahía San Ignacio, Sinaloa (25.4°N) [LACM 37-218.2], México, to Islas Lobos de Afuera, Lambayeque, Perú (6.9°S) [LACM 35-161.1]; Isla Socorro, Islas Revillagigedos, México [LACM 34-246.3, 34-247.5]; Isla Marchena, Islas Galápagos, Ecuador (0.3°N) [LACM 34-285.6]; 5–100 m (mean = 44 m; n = 29). The only bottom type noted on labels is sand. I have seen 28 lots, and Carol Skoglund provided data for an additional lot.

Referred Material

Stations in México: LACM 86-195.5 – Bahía de Los Angeles, Baja California – 5 m; Skoglund Collection – Bahía Concepción, Baja California Sur – 8–15 m; LACM 39-99.10 – Bahía Coyote, Baja California Sur – 4–5 m; LACM 37-185.5 – Isla Ildefonso, Baja California Sur – 91 m; LACM 49-238.1 – Bahía San Francisco, Baja California – 46 m; LACM 78-120.20 – Isla Danzante, Baja California – 43–55 m; LACM 36-144.3 – Isla San Francisco, Baja California – 42 m; LACM 49-237.1 – Bahía Frailes, Baja California Sur – 91 m; LACM 34-247.5 – Isla Socorro, Islas Revillagigedos – 7–18 m; LACM 34-246.3 – Isla Socorro, Islas Revillagigedos – 37 m; LACM 37-218.2 – Isla San Ignacio, Sinaloa – 42 m; SBMNH 348118, 348119, USNM 1008293, Skoglund Collection – Punta de Juluapan, Bahía de Santiago, Colima – 30–60 m – Type lot; LACM 38-265.4 – Bahía Chacahua, Oaxaca – 75 m

Stations in Costa Rica: LACM 72-13.30 – Bahía Juanilla, Guanacaste – 37 m; LACM 72-7.31 – Bahía Santa Elena, Guanacaste – 1.2–11 m; LACM 72-30.26 – Punta Santa Elena, Guanacaste – 12–15 m; LACM 72-57.37 – Punta Quepos, Puntarenas – 21 m; LACM 72-66.38 – Isla del Caño, Puntarenas – 56 m.

Stations in Panamá: LACM 39-259.1 – Isla Ladrones, Chiriquí – 99 m; LACM 38-184.2 – Islas Secas, Chiriquí – 22 m; LACM 34-251.5 – Islas Secas, Chiriquí – 34–146 m; LACM 34-252,9 – Bahía Honda, Veraguas – 55–64 m; LACM 34-114.17 – Isla Jicarita, Veraguas – 44 m

Stations in Colombia: LACM 35-179.5 – Bahía Octavia, Choco – 82 m; LACM 38-224.2 – Isla Gorgona, Nariño – 18–37 m

Stations in Ecuador: LACM 33-180.1 – Bahía Santa Elena, Guayas – 46 m; LACM 34-307.4 – Isla Santa Clara, Guayas – 64 m; LACM 34-285.6 – Isla Marchena, Islas Galápagos – 37 m

Station in Perú: LACM 35-161.1 – Bahía Norte, Islas Lobos de Afuera, Lambayque – 22 m

Discussion

This species differs from *S. subquadrata* (Carpenter, 1857) in having a longer, more tapered posterior end, orthogyrate rather than opisthogyrate beaks, more lamellar commarginal ribs with fine commarginal threads between the larger ribs, and a more elongate pallial sinus. It differs from small specimens of *Semele*, such as *S. jamesi* Coan, 1988 (pp. 33–35, figs. 62, 63), which never attains a large size, in having more prominent lateral teeth, especially the anterior lateral, in the right valve and in having a less conspicuous posterior cardinal in the left valve.

Etymology

This species is named for the Campbell clade of Spartanburg, South Carolina, U.S.A., all of whom have studied and published on the Mollusca – Lyle D. Campbell, Sarah C. Campbell, David C. Campbell, Matthew R. Campbell, and Andrew C. Campbell.

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Lyle D. Campbell kindly provided Pliocene and Recent specimens of *Semelina nuculoides* for examination. Kathie Way of The Natural History Museum, London, loaned Carpenter's type material of *Semelina subquadrata*; Lindsey Groves of the Natural History Museum of Los Angeles County, California, and Elizabeth Kools of the California Academy of Sciences, San Francisco, California, loaned material from those collections. Carol Skoglund made material and data from her collection available to me, including the specimens that became the type lot of *S. campbellorum*. Gustav Paulay provided information about systematic relations in the Tellinoidea. Yolanda Camacho took the SEM photographs, and Daniel L. Geiger prepared the plates.

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A FIELD STUDY OF THE LIFE HISTORY OF AN ENDEMIC HAWAIIAN SUCCINEID LAND SNAIL

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The Hawaiian land snail fauna is noted for its diversity and high level of endemism (Cowie, 1995). Almost nothing, however, is known of the ecology of any of the species, with the exception of the life histories of a few achatinelline tree snail species (Hadfield et al., 1993). The Hawaiian Succineidae comprise about 42 species found in diverse habitats from arid coastal dune-land to rainforest (Cowie et al., 1995), but the only published work on their ecology is a laboratory study of growth and reproduction in *Succinea thaanumi* Ancey, 1899, and *Catinella rotundata* (Gould, 1846) (Rundell & Cowie, in press).

Here, we report a field study of the life history of *S. thaanumi*. Unlike many Hawaiian land snail species, *S. thaanumi* remains relatively common. It occurs on the eastern side of the island of Hawaii, the largest in the Hawaiian chain. The study was conducted in the Pu'u Maka'ala Natural Area Reserve in two areas (10 m^2 and 2 m^2 about 12 m apart) at an elevation of 1,067 m. The under-story consisted of native plants of the following genera: *Cyanea*, *Broussaisia*, *Pipturus*, *Straussia*, *Freycinetia*, and *Cibotium*. The over-story consisted primarily of the Hawaiian endemic tree *Metrosideros polymorpha*. Snails and their egg clutches were found on all plants but mostly on *Broussaisia*, one of the most common under-story plants in the study site. Data were collected, usually twice weekly, from 22 February 2000 to 4 June 2001, a total of 104 occasions. In addition, rainfall was recorded on 88 occasions with a rain gauge placed in a clearing on the perimeter of the study site, temperature on 68 occasions, and humidity on 37 occasions.

Each plant in the study site was examined for the presence of snails and egg clutches. Egg clutches consisted of transparent, viscous material containing developing embryos and were laid primarily attached to leaf tips but also occasionally on the stems and other parts of the plants. This contrasts with other land snails, which lay their eggs primarily in moist soil (Tompa, 1984), and with *Succinea putris* Linnaeus, 1758, which lays its eggs among the roots of rushes (Rigby, 1965). Maximum shell length of each snail was measured with calipers, with a minimum amount of contact and without moving the snail. The number of embryos in each clutch was recorded. In addition, the location of the snail on a plant (e.g., on the top, bottom, or petiole of a leaf, or on the stem) and whether the snail's body was retracted into the shell or not were recorded.

Average snail size ($F_{(11,92)} = 19.6$; $p < 0.0001$) and the number of new egg clutches ($F_{(11,44)} = 2.8$; $p < 0.008$) varied through the year. In February and March of 2000 and 2001, the size-frequency distribution was unimodal, with the highest numbers in the 5–6 mm range (Fig. 1). Few egg clutches were observed in February, but by March, the number of clutches had increased (Fig. 2). By April of both years, mean snail size had increased but the size-frequency distribution remained unimodal. In May, however, the distribution became bimodal, with the appearance of large numbers of very small (1 mm) snails, which we interpret as the offspring of the snails in the larger size-class (Fig. 1). Numbers of egg clutches also increased in April (Fig. 2). The distributions remained bimodal through August, but by this time fewer large snails were observed, presumably because they were dying off. The numbers of egg clutches increased from April to August (Fig. 2). From September through November, the size distribution became skewed by the increased numbers of newly emerged snails. These snails appeared to be growing about 1 mm per month because the modal size of this size-class increased from 1 mm in September to 3 mm in November. Growth continued through December and January (Fig. 1). Numbers of egg clutches decreased from September through January (Fig. 2). The number of embryos found in a clutch ranged from 1 to over 16. In most months, the average was 6–8, except for February and March when it averaged 1–2. This difference is significant ($F_{(11,33)} = 6.3$; $p < 0.001$).

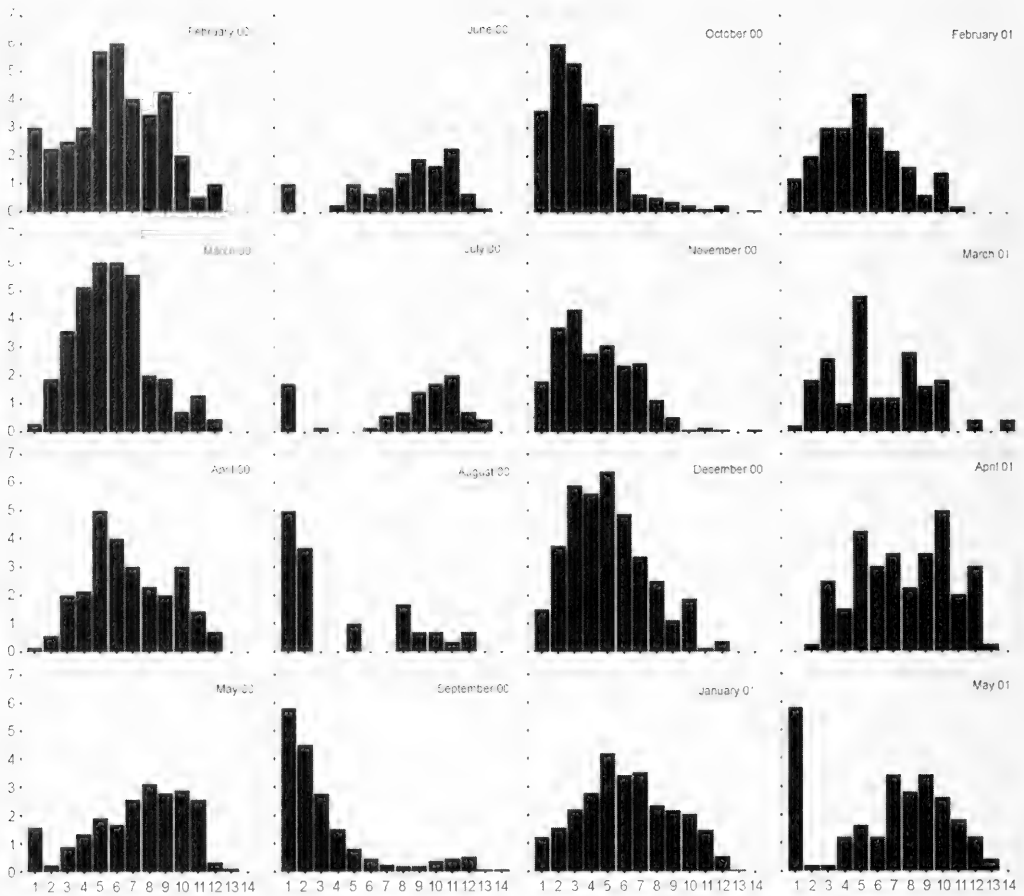

FIG. 1. Monthly size-frequency distributions of snail size. The Y-axis is the number of snails of a particular size, averaged over data collecting occasions. The X-axis is snail size.

In 2000, copulations were first observed on 13 June and in 2001 on 30 May. Most copulations were between pairs of snails (succineids are hermaphrodites) with the top snail acting as the male, mating by "shell mounting" (Asami et al., 1998). In one case, we observed three snails with the middle one acting as both a male and a female. We observed one snail laying an egg clutch. The viscous material containing the eggs was exuded from the snail's genital pore. The completed clutch was about three times larger than the snail, which may be explained if the viscous material absorbed moisture from the air, as reported for *Ovachlamys fulgens* (Gude, 1900) (Barrientos, 1998). We interpret these patterns as representing an annual, semelparous life-cycle, which agrees well with the results of the laboratory study of *S. thaanumi* of Rundell & Cowie (in press). Reproduction is primarily in the May–November period, but snails of all sizes and some egg clutches were observed throughout the year. Therefore, at least some snails were growing and reproducing out of synchrony with the overall population.

Snail behavior was related to the microclimate of the study area. Numbers of snails recorded were negatively related to temperature ($r = -0.44$; $F_{(1,65)} = 15.8$; $p < 0.0001$), suggesting that the snails moved into a different part of the habitat as the temperature increased. However, temperature did not vary significantly through the year ($F_{(11,55)} = 0.86$; $p = 0.59$), possibly because the study site was in the interior of an upland rainforest. The number of new clutches dropped to essentially zero when the humidity was below 80% (Fig. 3). Regression analyses

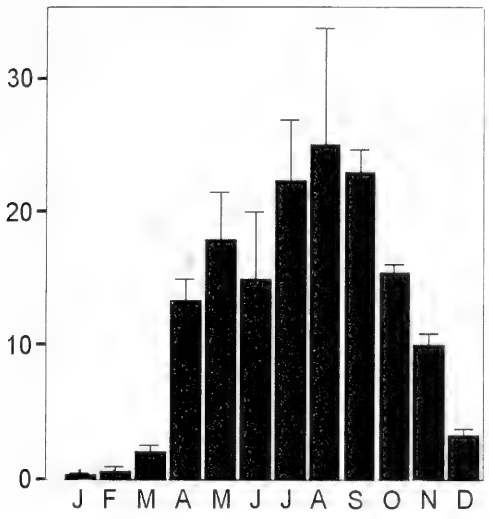

FIG. 2. Frequency distribution of the number of egg clutches observed during a month, averaged over the two years of the study. The letters on the X-axis are the first letters of the month. Bars are standard errors of the means.

showed that the percent of snails observed on the tops of leaves ($F_{(3,30)} = 9.4$; $p < 0.0001$) and the bottoms of leaves ($F_{(3,30)} = 33.6$; $p < 0.0001$), and the percent of snails observed with their bodies extended out of their shells ($F_{(3,30)} = 32.5$; $p < 0.0001$) were significantly related to temperature and humidity. In low humidity, the snails tended to be on the bottoms of leaves; as humidity increased, especially if it was raining, they tended to be on the tops. When humidity reached 80%, nearly all of the snails' bodies were extended out of their shells. Snails on the bottoms of leaves were usually retracted into their shells, whereas snails on the tops of leaves were usually extended. Presumably this behavior is related to one of the major problems faced by terrestrial snails, desiccation (Riddle, 1983).

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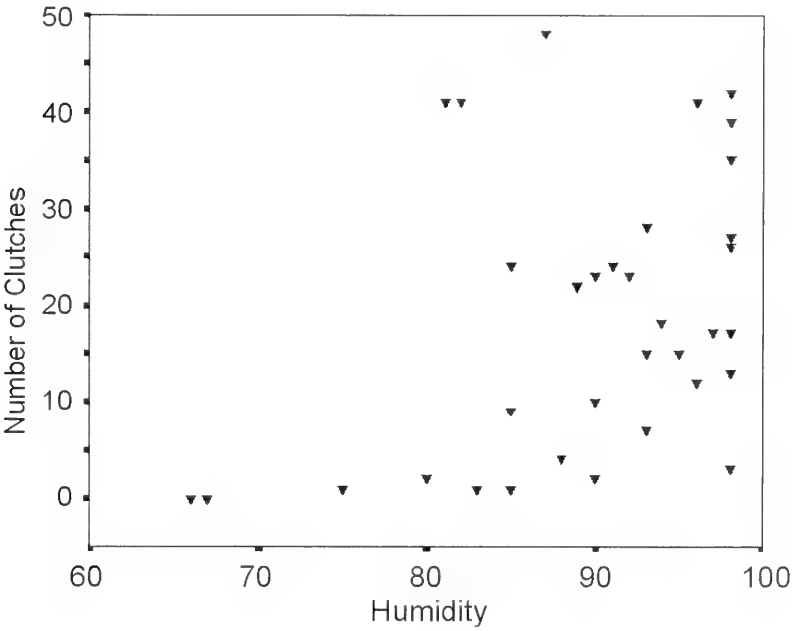

FIG. 3. Scatterplot of the relationship between number of new clutches recorded on an observation occasion and humidity.

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DRY SEASON SURVIVAL IN A FLORIDA APPLE SNAIL (*POMACEA PALUDOSA* SAY) POPULATION

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ABSTRACT

Previous reports concluded that Florida apple snails (*Pomacea paludosa* Say) have little tolerance to dry conditions, which stands in contrast to other Ampullariidae studied to date. Given that inconsistency, and the fact that we do find snails in wetlands that periodically dry down, we were interested in elucidating dry season survival patterns in this species. We conducted a field study in 1995 in which snails with miniature radio transmitters were monitored weekly in flooded and dry marsh. Snails from this same wetland were collected during the 1996 dry season and monitored during a laboratory study designed to simulate a marsh in dry down conditions. We found that apple snails die at a rate of approximately 10–15% per week in May and June regardless of water levels. Dry conditions exacerbated snail mortality in the laboratory study (χ^2 = 6.53, df = 1, P = 0.011), but not in the field (χ^2 = 0.48, df = 1, P = 0.49). The mean size of snails still alive at the end of the laboratory study were significantly smaller than those that had died during the study (T = 2.25, 9 df, P = 0.025), indicating they were young of the year. Our data support previously unsubstantiated reports that *Pomacea paludosa* is essentially an annual species that experiences a post-reproductive die-off near the end of the dry season. It appears previously reported apple snail deaths attributed to dry conditions were confounded by an annual post reproductive die-off. Florida apple snails may be well equipped to survive in these fluctuating wetland environments, but how drying events affect their population demography remains largely unanswered.

Key words: *Pomacea paludosa*, apple snail, survival, water level, wetland, Florida.

INTRODUCTION

Estimates of survival are critical to understanding population dynamics and the relationship between population density, environmental gradients, and the impacts of environmental fluctuations. Freshwater snails of the genera *Pila* and *Pomacea* (Caenogastropoda: Ampullariidae) commonly referred to as apple snails, inhabit tropical and subtropical wetlands, some of which are subject to periodic drying events (i.e., the water table falls below ground level). *Pila* and *Pomacea* species studied to date can survive dry conditions for 3 to 25 months (Cowie, 2002), although direct comparisons of survival under wet versus dry conditions have not been made for any apple snail species. Apple snails have drawn attention because of their critical role as prey items for wetland vertebrate fauna (e.g., Snyder & Snyder, 1969; Donnay & Beisinger, 1993) and because they are considered pests in rice and taro agriculture (Cowie, 2002). Information linking survival with hydrology is fundamental to understanding apple snail autecology and the potential impacts of water management practices on snail populations.

The research described here was prompted by several reports about the inability of Florida apple snails, *Pomacea paludosa* Say, to tolerate drying events, in contrast to other *Pila* and *Pomacea* species. Florida wetlands experience a dry season that generally extends from November through May or June (Chen & Gerber, 1990), and in some years culminates in a dry down (Kushlan, 1990; Duever et al., 1994). Despite the persistence of snail populations in these wetlands, one field study (Kushlan, 1975) and two lab studies (Little, 1968; Turner, 1994) concluded that Florida

apple snails were intolerant to dry downs, even those less than one month in duration. However, there is also indirect evidence (accumulations of empty shells in the field) of an annual spring adult die-off that would typically coincide with the May–June drying events (Hanning, 1979). If Florida apple snails were an annual species, previous reports of dry down intolerance may have been confounded by a coincidental adult die-off. The objective of this study was to compare survival of *P. paludosa* in wet versus dry marsh in order to address the contradictory available information on dry down tolerance in this species.

METHODS

Field Study

We conducted a field study in 1995 in the easternmost portion of the Blue Cypress Water Management Area (BCWMA), a wetland unit that is part of the Upper St. Johns River Basin, Indian River County, Florida. Darby et al. (2002) described the study site, which had the highest ground elevation of the basin wetlands and was therefore most likely to dry out. Areas that eventually went dry were adjacent to areas that remained inundated (Darby et al., 2002).

We studied the same snails from BCWMA for which movements were monitored (Darby et al., 2002). Snails were located weekly via miniature radio transmitters affixed to their shells. Maximum transmitter battery life was 60 d. We documented weekly survival for four months by releasing transmitters in a staggered fashion (six in March, four in April, 26 in May, nine in June). We skewed transmitter release in May to maximize the probability of the snails encountering a dry down. We also monitored six snails that were initially found in May via hand searches in dry marsh (the 45 snails described above were found in flooded marsh). Snails in dry marsh do not move (Darby et al., 2002), so we could monitor them without transmitters by flagging their location. Snail survival was assessed first by tapping the shell to look for the behavioral response of retracting the operculum and, if there was no response, gently prying one corner of the operculum away from the aperture to inspect the soft body tissue. If an empty shell was found, evidence of predation was noted as described by Snyder & Snyder (1969). We measured water depth and temperature throughout the study, as described by Darby et al. (2002).

Laboratory Study

In 1996, we assessed survival for stranded snails in tanks designed to simulate a dry down. A laboratory setting permitted control over moisture conditions and eliminated factors (e.g., precipitation, predation) that confounded interpretation of field data.

Snails were collected from eastern BCWMA via wire traps (Darby et al. 2001) from 29 April through 10 May 1996 (n =232). Snail shell widths were 22–42 mm (mean ± SD = 34.1 ± 3.2 mm). Based on size/maturation relationships reported by Hanning (1979) and our own observations of snails mating and laying eggs, snails > 30 mm were considered adults. Approximately 10% of our lab study population were juveniles.

On 12 May, a total of 18–24 snails were placed in each of twelve 120 cm L x 61 cm W x 46 cm H polyethylene tanks. All tanks started with 15 cm (above the substratum) of filtered, aerated well water. The substratum consisted of a 5 cm layer of stone in a size gradation (diameter) from 1.9 cm to 0.6 cm (upper layer) and topped by a 13 cm layer of either sand (n = 6 tanks) or unprocessed commercial peat (n = 6). Two substrata were included in order to see if peat, with its greater moisture holding capacity, would enhance survival for stranded snails relative to sand. Tank locations were randomized for substratum type and water regime.

Water was replaced every 3 to 7 days during the experiment. Snails were fed *Utricularia* sp. in excess of demand. Uneaten food and waste were removed every 3 days. The tanks were outdoors and therefore subject to ambient temperatures, but covered to prevent rain from entering. Well water was allowed to reach ambient temperature prior to tank distribution.

For each substratum (peat and sand), we had three control tanks with continuous 15 cm water depths and three dry down tanks wherein water was dropped from 15 cm to 0 cm over 28 days. The water withdrawal rate approximated the 28 d period prior to dry down conditions in BCWMA in 1995. Water depths reached 0 cm on 10 June. On 11 June all the water was drained and the substratum began drying.

We measured water and substratum temperatures three times weekly. Substratum moisture levels were measured three times weekly in three locations per tank as percent saturation using a moisture meter (Lincoln Industries, NE) inserted 5 cm below the surface. Snail survival was checked weekly as de-

scribed for the telemetry study. All tanks containing water were inspected daily to remove dead snails.

Statistical Analyses

Cumulative survival for the laboratory snails was estimated at weekly intervals using the Kaplan & Meier procedure (1958). A variation of this procedure to accommodate staggered transmitter release and failed transmitters was used to estimate survival in the telemetry study (Pollock et al. 1989). We used the approach described by Bennetts et al. (1999) to accommodate situations in which animals previously found in one condition (e.g., flooded marsh) were subsequently found in another (e.g., dry marsh). The hypothesis that survival for snails in dry down conditions (19 May–7 July) was lower than in flooded conditions over the same period was tested using a log-rank test (Pollock et al., 1989). We tested for sex differences and tank effects using the same approach. In all cases we report the most conservative χ^2 values of the three log-rank tests described in Pollock et al. (1989), but for all tests the conclusions were the same regardless of how χ^2 was calculated.

RESULTS

Snail survival in both the field and the laboratory studies declined to less than 10% (Fig. 1), regardless of water levels. Survival in the field study remained at 100% for the initial six-week period through mid-April before declining at an average rate of 14% per week through June. Water levels declined steadily (Darby et al. 2002) and water temperatures rose from 23°C in March to a peak of 38°C (afternoon measurements) in late May. Nine of these snails were eaten by predators (snail kites and limpkins). [There may have been more preyed upon, but for several dead snails the evidence for predation was not clear]. Survival for males (n = 24) did not differ from females (n = 27) (χ^2 = 0.048, df = 1, P = 0.83). Survival of the twelve snails stranded in dry down was not different from snails remaining in flooded marsh over the same period (χ^2 = 0.48, df = 1, P = 0.49). The mean survival time in dry down conditions was 3.9 ± 2.2 weeks.

Substratum type had no effect on survival (χ^2 = 0.121, df = 1, P = 0.73 and χ^2 = 0.08, df = 1, P = 0.78, for controls and dry down tanks, respectively), despite the fact that moisture levels in the peat substratum remained 3–5 times higher than the sand substratum (data not shown). The peat and sand tank survival data were therefore pooled to examine the overall effects of drying. Survival for all laboratory snails declined approximately 10–15% per week by late May, prior to the 11 June dry down. The simulated dry down did, however, appear to exacerbate death rates (χ^2 = 6.53, df = 1, P = 0.011). Tank water temperatures ranged from 23°C to 30°C over the study period.

At the end of the lab study, it appeared that surviving snails were smaller than those that had died. We used a T-test for groups with unequal variance (F-test: F = 0.27, P = 0.0002) to test for size differences between surviving and dead snails. The mean (± SD) size of the ten snails living at the end of the lab study was significantly smaller (30.1 ± 3.1 mm) than that of those that had died (34.3 ± 5.9 mm) (T = 2.25, df = 9, P = 0.025). Sizes were similar for the 47 dead (35.9 ± 2.4 mm) and four living snails (34.9 ± 2.5 mm) at the end of the field study (T = 0.70, df = 3, P = 0.27). At the end of both studies, aestivating snails were removed from their dry conditions and placed in water. They became active within 2 to 24 h.

DISCUSSION

Florida apple snails, regardless of hydrologic conditions, exhibit a steady decline in survival late in the dry season (May–June). Dry down conditions exacerbated mortality in these snails, but dry down intolerance clearly was not the primary cause of mortality for snails observed in the lab or the field. Our data from both the field and lab studies support previously unsubstantiated estimates of a 1–1.5 year life span for *P. paludosa* (Hanning, 1979; Ferrer et al., 1990). It appears that the life cycle of apple snails terminates in a post-reproductive die-off. Egg cluster surveys by Hanning (1979), Odum (1957) and Darby et al. (1999) consistently show an April–May peak in egg production. In our study, steepest declines in survival occurred in May and June. The telemetry study was initiated early in the breeding season, so this would explain the six-week period of high survival prior to the May–June die-off. Snails alive at the end of the lab study were likely young of the year that had reached sufficient size to be captured in the wire traps.

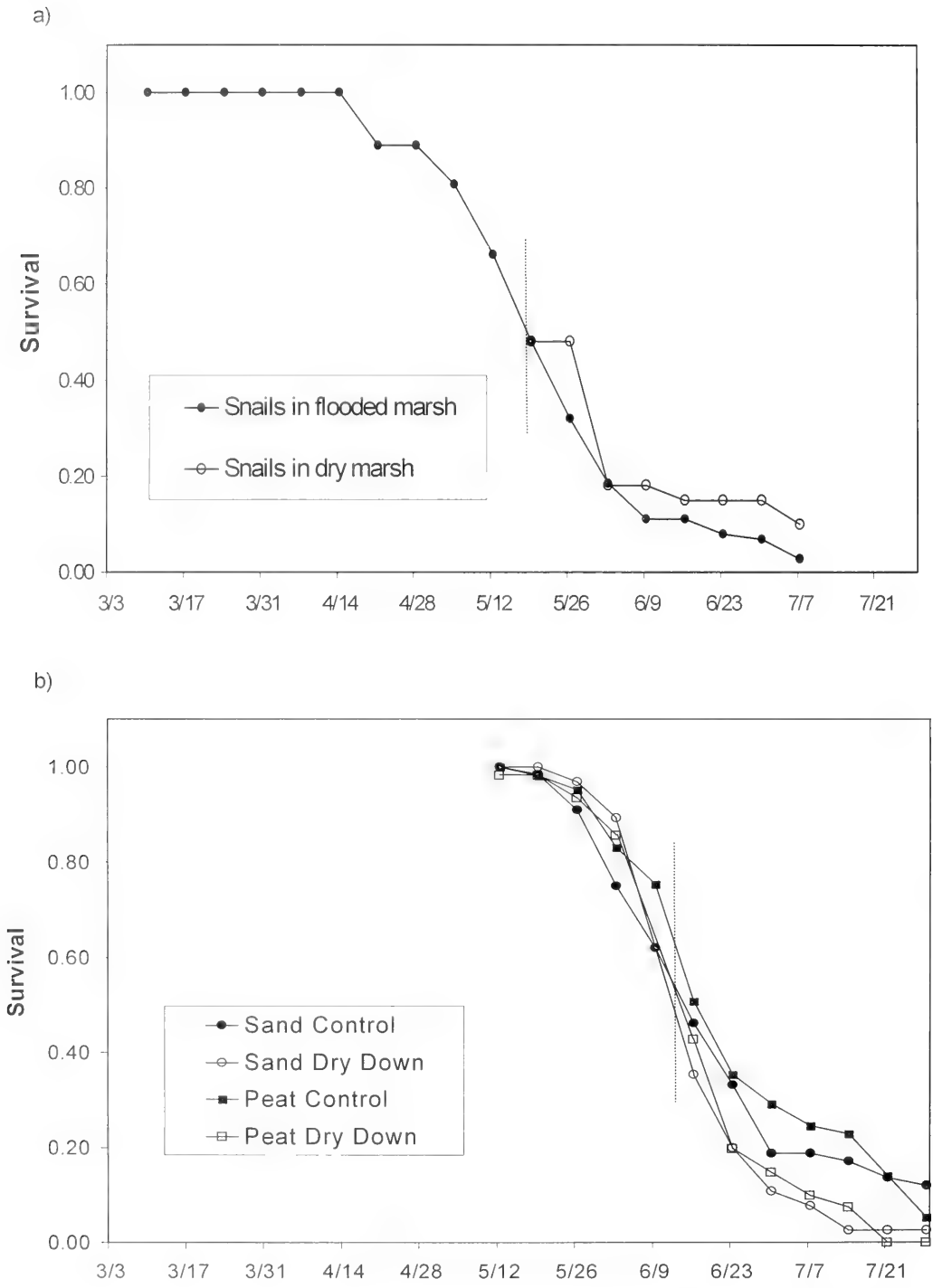

FIG. 1. Cumulative survival for apple snails monitored in wet and dry conditions in a) the 1995 field study and b) the 1996 laboratory study. Dashed vertical lines indicate the date on which snails first became stranded in dry conditions.

Bearing transmitters could influence survival. However, the staggered entry design meant that snails in any given week had carried transmitters for a range of different times. For example, in the first week of June, eight snails that died had worn transmitters from 1 to 8 weeks and 11 snails still alive had worn transmitters 1 to 9 weeks. Four of the snails were initially found via hand searches in dry marsh, demonstrating that snails do get stranded without bearing transmitters.

We also considered that high water temperatures (33–38°C) we measured in the field in May 1995 might have contributed to the steep decline in survival. In the lab study, however, we found that a similar survival pattern emerged even when water temperatures stayed < 30°C. Lethal temperatures of 35°C to 45°C have been reported for other apple snail species (Cowie, 2002).

It appears previously reported apple snail deaths attributed to dry conditions (Little, 1968; Turner, 1994) were confounded by an annual post reproductive die-off. Apple snails may be well equipped to survive in these fluctuating wetland environments, but how drying events affect Florida apple snail population demography remains largely unanswered.

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LUNTIA INSIGNIS SMITH, 1898, IS A SYNONYM OF *STREPTOSTELE* (*TOMOSTELE*) *MUSAECOLA* (MORELET, 1860) (GASTROPODA: STREPTAXIDAE) - AN AFRICAN TRAMP AND ITS DISTRIBUTION IN AMERICA

Bernhard Hausdorf[1] & Clara Inés Medina Bermúdez[2]

Smith (1898) described *Luntia insignis* as a new genus and new species of the family Stenogyridae (= Subulinidae) from Trinidad. This species has been recorded as probably introduced in Aruba (Hummelink, 1940a, b), Guyana (Morrison, 1943), Suriname (van Regteren Altena, 1960, 1964, 1975), Nicaragua (López & Pérez, 1996), and in a greenhouse in the Netherlands (Meeuse & Hubert, 1949, as *Varicella clappi* [*non* Pilsbry, 1907]; see van Regteren Altena, 1964). It has also been recorded from Saba (Haas, 1962) and Barbados (Chase & Robinson, 2001).

Thiele (1931) included *Luntia* Smith, 1898, as a subgenus in *Leptinaria* Beck, 1837 (Subulinidae), whereas Baker (in van Regteren Altena, 1975), who examined the radula of the species, transferred it to *Varicella* L. Pfeiffer, 1856 (Oleacinidae).

Pilsbry (1930) was the first to record the African *Streptostele* (*Tomostele*) *musaecola* (Morelet, 1860) (Streptaxidae) as an introduced species in Panama. The native range of *Streptostele musaecola* extends in western Africa from Guinea to the Congo (Pilsbry, 1919). Pilsbry (1930) recognized that this might be a "tramp" species carried around on bananas, on which it was originally discovered (Morelet, 1860). Later, *Streptostele musaecola* has been recorded as introduced in Bermuda (Bieler & Slapcinsky, 2000), Vanuatu (= New Hebrides) (Solem, 1989), American Samoa (Solem, 1989; Cowie, 1998, Cowie & Rundell, 2002; Cowie et al., 2003), and the Society Islands (Solem, 1989).

We have examined the holotype of *Luntia insignis* Smith (The Natural History Museum, London, NHM 1898.12.5.18; Fig. 1) and three specimens labelled as syntypes of *Achatina musaecola* Morelet in The Natural History Museum (NHM 1893.2.4.276-8; Fig. 2). As locality of the putative syntypes of *A. musaecola*, "Gabon" is given in Morelet´s handwriting, whereas Morelet (1860: 190) gives Guinea as type locality. However, Ancey (1885) also said that *A. musaecola* is from Gabon. It is unclear whether this was an error or whether Ancey knew that the type locality actually was Gabon and not Guinea.

A comparison of these type specimens, new material from Colombia (Zoologisches Museum der Universität Hamburg, ZMH 2918; Fig. 3), and figures of shells identified as *Luntia insignis* (Meeuse & Hubert, 1949; Haas, 1962) and *Streptostele musaecola* (Pilsbry, 1919, 1930; Solem, 1989; Bieler & Slapcinsky, 2000),

FIGS. 1–3. *Streptostele* (*Tomostele*) *musaecola* (Morelet). FIG. 1. Trinidad: Port of Spain (holotype of *Luntia insignis* Smith, NHM 1898.12.5.18). FIG. 2. Gabon (syntype? of *Achatina musaecola* Morelet, NHM 1893.2.4.276-8). FIG. 3. Colombia: Finca Torreblanca near Silvania (ZMH 2918). Scale bar = 1 mm.

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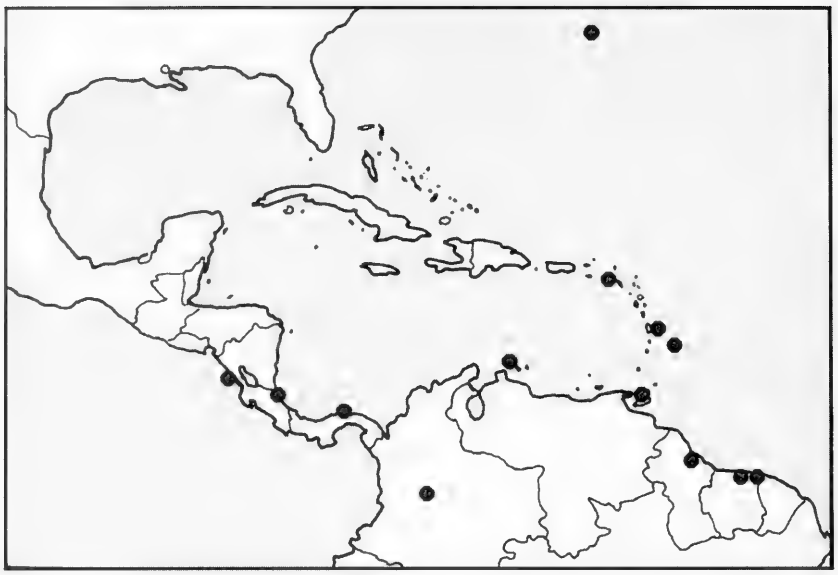

FIG. 4. Distribution of *Streptostele* (*Tomostele*) *musaecola* (Morelet) in America (1°-grid).

show that *Luntia insignis* Smith, 1898 is a synonym of *Streptostele* (*Tomostele*) *musaecola* (Morelet, 1860). Consequently, *Luntia* Smith, 1898, is a synonym of *Tomostele* Ancey, 1885, of which *Achatina musaecola* Morelet, 1860, is the type species.

Streptostele musaecola is known from the following American localities (Fig. 4): Bermuda: Hamilton, 32°18'N, 64°47'W (Bieler & Slapcinsky, 2000). Nicaragua: Masatepe, El Arenal, El Pochote, 455 m altitude, 11°55'N, 86°08'46"W (López & Pérez, 1996); Masatepe, El Arenal, El Mango, 455 m altitude, 11°55'N, 86°08'46"W (López & Pérez, 1996). Costa Rica: La Lola, 28.3 miles W of Puerto Limón, 10°N, 83°W (Florida Museum of Natural History FLMNH 211842). Panama: Mount Hope, 9°20'N, 79°54'W (Pilsbry, 1930); Colon, 9°22'N, 79°54'W (FLMNH 211843). Colombia, Departamento Cundinamarca: Finca Torreblanca near Silvania, 1560 m altitude, forest, 4°24'14"N, 74°23'12"W (ZMH 2918). Aruba: Fontein, 12°30'N, 69°54'W (Hummelink, 1940a). Saba: Road to Bottom, 17°38'N, 63°15'W (Haas, 1962). Saint Lucia: Grande Anse, 14°00'N, 60°54'W (FLMNH 281110). Barbados: Holetown, Porter´s House, 2–4 m altitude, 13°11'44"N, 59°38'18"W (Chase & Robinson, 2001); Holetown, hill NE of Royal Westmoreland Landscape Garden Centre, 10 m altitude, 13°12'01"N, 59°38'04"W (Chase & Robinson, 2001); Bathsheba, Andromeda Botanic Gardens, 60–90 m altitude, 13°12'25"N, 59°31'04"W (Chase & Robinson, 2001); 200 m S of Harrison Point Lighthouse, 30 m altitude, 13°18'23"N, 59°38'58"W (Chase & Robinson, 2001). Trinidad: Port of Spain, 10°39'N, 61°31'W (holotype of *Luntia insignis* Smith, NHM 1898.12.5.18). Guyana: Kyk over Al Island, 6°23'N, 58°41'W (Morrison, 1943). Suriname: Jodensavanne, 5°25'N, 54°59'W (van Regteren Altena, 1964, 1975); Albina, 5°30'N, 54°03'W (van Regteren Altena, 1975); Paramaribo, 5°50'N, 55°10'W (van Regteren Altena, 1964, 1975); Tambaredjo, 5°50'N, 55°33'W (van Regteren Altena, 1960).

The newly discovered occurrence near Silvania in Colombia represents probably the highest locality from which *Streptostele musaecola* has been recorded. However, we do not know whether a stable population has been established there or whether there was only an unsuccessful introduction.

Streptostele musaecola is widespread throughout tropical America. Its impact on the native fauna should be monitored, especially because it is a carnivorous species. Actually, it might have been implicated in the extinction of a native species in American Samoa (Miller, unpublished report, quoted in Cowie, 1998).

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CLASSIFICATION OF THE HELICINIDAE: REVIEW OF MORPHOLOGICAL CHARACTERISTICS BASED ON A REVISION OF THE COSTA RICAN SPECIES AND APPLICATION TO THE ARRANGEMENT OF THE CENTRAL AMERICAN MAINLAND TAXA (MOLLUSCA: GASTROPODA: NERITOPSINA)

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ABSTRACT

The present study combines a taxonomical revision of the poorly known Costa Rican Helicinidae, with a detailed investigation of certain morphological structures with respect to their relevance for systematics, culminating in a discussion of the arrangement of the Central American mainland species.

The revision of the Costa Rican species is based on the examination of nearly all type material, coupled with extensive field work and investigations of the collections of the Instituto Nacional de Biodiversidad de Costa Rica and the Florida Museum of Natural History, Gainesville, along with perusal of additional historical material. With minor exceptions, all these species were investigated with respect to the features of shell, operculum, surface sculpture of embryonic shell and teleoconch, internal shell structures, radula, and female reproductive system. In addition, analyses of morphometry and sexual dimorphism were carried out. Faced with a limited amount of material, it became necessary to develop a new preparation method to separate the soft body from the shell without damaging either.

For the higher classification and comparative analysis of the different morphological characteristics, similar examinations emphasizing formerly poorly studied or neglected characteristics, such as embryonic shell and female reproductive system, were carried out for 17 additional species representing the most important related Central American supraspecific taxa using their type species when available. For taxa with inaccessible material, data from the available literature were critically incorporated.

For Costa Rica, 15 species were recognized, among them seven new species, partially published in Richling (2001) – *Helicina echandiensis*, *H. talamancensis*, *H. monteverdensis*, *H. chiquitica*, *H. escondida*, *Alcadia* (*Microalcadia*) *hojarasca*, and *A.* (*M.*) *boeckeleri* – and two new subspecies – *H. punctisulcata cuericiensis*, and *H. beatrix riopejensis*. Other previously subspecifically separated taxa (*H. funcki costaricensis* Wagner, 1905; *H. tenuis pittieri* Wagner, 1910) were shown to fall within the range of intraspecific variability. Records of the Guatemalan and Mexican species *Helicina oweniana* L. Pfeiffer, 1849, and subspecies, *H. amoena* L. Pfeiffer, 1849, as well as those of *H. fragilis* Morelet, 1851, were proven to be based on faulty identifications and were therefore excluded from the Costa Rican fauna. This fact, together with the recognition of the several new species, shows that the faunal composition of Costa Rica is much more distinct from that of the northern areas than previously assumed. The transitional zone of Nicaragua, however, still remains widely uninvestigated. Only *Helicina tenuis* L. Pfeiffer, 1849, being ecologically very tolerant, *Lucidella lirata* (L. Pfeiffer, 1847), and *Pyrgodomus microdinus* (Morelet, 1851) are widespread, extending from Mexico to Costa Rica, perhaps even farther south. The distribution of the typical Costa Rican species follows the topographical subdivision created by the Central Cordilleras, along with its corresponding effects on the climate.

Contrary to former assumptions, certain features of the female reproductive system proved very useful for the classification of the Helicinidae. For the first time, monaulic conditions have been recognized for *Helicina* and *Eutrochatella*, necessitating the correction of previous descriptions in this respect. Furthermore, the monaulic or diaulic state is characteristic of the genera and is paralleled by consistent changes in the embryonic shell struc-

ture. Because primitive members of the Helicinidae possess a diaulic system, the monaulic condition is regarded as the derived state. The Central American genera *Helicina*, *Alcadia*, *Eutrochatella*, *Lucidella* and *Schasicheila* were properly distinguished and described by this, as well as by other differences in the female reproductive system. The anatomies of the type species of *Helicina* and *Alcadia* were examined for the first time, and earlier descriptions of *Eutrochatella* and *Lucidella* were corrected in major points. On the basis of this new evidence, the assignment of traditional subgeneric units of *Helicina* and *Alcadia*, previously based mainly on vague radula and shell characteristics, was especially reassessed. The subgenera *Sericea* and *Analcadia* were transferred to *Helicina*, as well as the mainland land species summarized under the preoccupied taxon "*Gemma*". *Tristramia*, *Oxyrhombus*, *Pseudoligyra*, *Oligyra*, *Succincta*, "*Cinctella*" [also preoccupied] and *Punctisulcata* were confirmed in their association with *Helicina*. Due to its monaulic condition, the former genus *Ceochasma* is reduced to a subgenus of *Helicina*. In addition, exemplary non-type Antillean species were studied, including *Helicina jamaicensis* Sowerby, 1841, which had to be shifted to *Alcadia s.l.*, and *Alcadia* (*Analcadia*) *platychila* (von Mühlfeldt, 1816), which is now assigned to *Helicina s.s.* On one hand, the new arrangement excludes *Alcadia* as previously known from the Central American mainland, but, on the other hand, examination of the newly discovered Costa Rican species *Helicina hojarasca* and *H. boeckeleri* required the establishment of a new subgenus of *Alcadia*, *Microalcadia* n. subgen. on the mainland, based mainly on the features of the female reproductive system and embryonic shell structure. The occurrence of *Alcadia* with only a few diminutive species on the mainland of Central America corresponds to the distribution of the genera *Eutrochatella/Pyrgodomus* and *Lucidella*.

The Central American mainland species of *Helicina* seem to show a closer relationship among each other than to the northern South American subgenera *Analcadia* and *Sericea*. The Brazilian taxon *Angulata*, previously a subgroup of *Helicina*, deviates remarkably in embryonic shell structure and shows differences in anatomy that still require final confirmation, and it thus deserves recognition as a separate genus.

Contrary to the well-supported differentiation at the generic level, the attempt to characterize subgroups of the Central American mainland species of *Helicina* has been only partially successful. Certain similarities in teleoconch surface structure, relative development of the accessory structures of the female reproductive system, and the degree of sexual dimorphism become obvious and are discussed to some extent, but intermediate characteristics complicate a satisfactory solution. Besides *Ceochasma*, three Central American mainland subgenera are recognized: *Oligyra*, *Tristramia* most closely resembling *Helicina s.s.*, and "*Gemma*". The latter preoccupied name is tentatively retained, because the proposal of a new name seems inappropriate at this stage.

Investigation of the morphological features other than the embryonic shell sculpture and the female reproductive system revealed the following additional results, mainly based on the Costa Rican species of *Helicina*:

Characteristics of teleoconch, operculum, and radula, previously regarded as substantial for classification, were repeatedly demonstrated to be subject to convergent development, thus limiting their value for systematics. Different examples are given, such as the T-shaped lateral of the radula or periostracal hairs, and further evidence is provided by the necessary re-arrangements outlined above. Nevertheless, these features play a supplementary or supporting role.

The mantle pigmentation of arboreal Helicinidae is closely related to the transparency of the shell and functionally replaces shell color in thin shells. The physiological possibility of an obviously adaptable mantle pigmentation could provide the opportunity for survival with thin, transparent shells as adaptation to the limited availability of calcium carbonate. Whereas varying and patterned mantle color are characteristic for arboreal thin-shelled species, the color of the head and foot is seldom species specific.

Size differences of the embryonic shell have not previously been studied for Helicinidae. Embryonic shell size is shown to increase with the shell size within a group of related species and also altitude within different populations of a species. Furthermore, it may show

a certain species specificity. Preliminary data on *Lucidella* and *Eutrochatella/Pyrgodomus* suggest a consistently smaller embryonic shell size than in *Helicina* or *Alcadia*.

Internal shell structures – axial cleft and muscle attachments – seem characteristic for certain systematic units, for example, *Lucidella* and *Schasicheila*. The length of the axial cleft is confirmed to be constant within a species, but, contrary to former assumption, it is not related to the whorl count.

The data on sexual dimorphism given in this study represent the most comprehensive approach to date to analyze this phenomenon for Helicinidae. The sexual dimorphism may manifest itself in differences in volume, a male's size being only about 62–70% of that of the female's, but formerly assumed deviations in shape could not be proved to be of significance for species of *Helicina*. A certain value for the degree of differences in uncovering systematic affinities is indicated.

Keywords: Helicinidae, Costa Rica, Central America, classification, reproductive system, radula, embryonic shell, new species.

RESUMEN

El presente estudio combina una revisión de los poco conocídos helicínidos de Costa Rica con un análisis detallado de varias estructuras morfológicas y su utilización para resolver preguntas sistemáticas. Con base en esto se discute a profundidad la clasificación de las especies continentales de Centroamérica.

La revisión de las especies costarricenses se basa en un exhaustivo trabajo de campo, en el análisis de casi todo el material tipo, de las colecciones del Instituto Nacional de Biodiversidad de Costa Rica y del Museo de Historia Natural de Gainesville, asi como de material histórico. Con pocas excepciones se estudiaron para todas las espécies los carácteres de la concha, del opérculo, de la estructura superficiál de la concha embriónica, asi como de la teleoconcha, estructuras internas de la concha, la rádula, y el tracto reproductor femenino. También se efecturon estudios sobre morfometría y dimorfismo sexúal. Considerando la escacéz de material, para efectuar un estudio a gran envergadura, fue necesario desarollar una metodología de disección para separar el cuerpo blando de la concha sin ningún detrimento.

Para efectuar una clasificación más amplia y una comparación de las diferentes estructuras morfológicas se tomaron los mismos datos de otras 17 especies, que representan los taxa supraespecíficos emparentados más importantes de Centroamérica.

Énfasis se puso en las estructuras poco estudiadas hasta ahora como la concha embriónica y el tracto reproductor femenino. Hasta donde se pudo se trabajo con material de especies que corresponden a los tipo. En donde no se pudo obtener material anatómico para estudiar se interpretaron cuidadosamente los datos de la literatura.

Para Costa Rica se determinaron 15 especies, entre las cuales siete son nuevas, y en parte publicadas en Richling (2001) – *Helicina echandiensis*, *H. talamancensis*, *H. monteverdensis*, *H. chiquitica*, *H. escondida*, *Alcadia* (*Microalcadia*) *hojarasca* y *A.* (*M.*) *boeckeleri*, además dos nuevas subespécies *H. punctisulcata cuericiensis* y *H. beatrix riopejensis*. Los taxa subespecíficos, hasta ahora separados, *H. funcki costaricensis* Wagner, 1905, y *H. tenuis pittieri* Wagner, 1910, caen dentro de la variación intraespecífica. La presencia de las especies mejicanas y guatemaltécas *Helicina oweniana* L. Pfeiffer, 1849 con sus subespécies, *H. amoena* L. Pfeiffer, 1849 y *H. fragilis* Morelet, 1851 no fue confirmada ya que el material estaba mal identificado y por esto se las elimina del listado faunístico de Costa Rica. Debido a este hecho y al descubrimiento de algunas nuevas espécies se puede distinguir la fauna de Costa Rica más claramente de otras regiones más al norte de lo que se suponia hasta ahora. Nicaragua que es el territorio de transición está casi inexplorado. Solamente las espécies *Helicina tenuis* L. Pfeiffer, 1849, que presenta una gran tolerancia ecológica, asi como *Lucidella lirata* (L. Pfeiffer, 1847) y *Prygodomus microdinus* (Morelet, 1851) se distribuyen desde México hasta Costa Rica y también más hacia el sur. La distribución de las espécies típicas costarricenses sigue la subdivisión topográfica de las cordilleras centrales y sus efectos correspondientes al clima.

Contrario a supociciones anteriores, se pudo demostrar que los carácteres del tracto reproductor femenino son muy útiles en la clasificación de los helicínidos. Por primera vez se pudieron reconocer condiciones monáulicas en *Helicina* y *Eutrochatella* por lo que descripciones previas se deben corregir a este respecto. Además la condición monáulica o diáulica son característicos para cada género y paralelamente hay cambios consistentes el la estructura de la concha embriónica. Ya que los miembros primitivos de los helicínidos poseen un sistema diáulico, la condición monáulica es considerada como derivada. Los géneros centroamericanos *Helicina*, *Alcadia*, *Eutrochatella*, *Lucidella* y *Schasicheila* se distinguen claramente y son descritos por estos y otros carácteres de la genitalia femenina. La anatomía de las espécies tipo de *Helicina* y *Alcadia* se estudiaron por primera vez y las descripciones anteriores de *Eutrochatella* y *Lucidella* se debieron corregir en varios puntos importantes. Sobre esta nueva base, especialmente la asignación de las tradicionales unidades subgenéricas de *Helicina* y *Alcadia*, que estaban previamente basadas en carácteres vagos de la rádula y la concha, fueron reordenaron. Los subgéneros *Sericea* y *Analcadia* se transfirieron a *Helicina* asi como las especies continentales comprendidas bajo el taxón preocupado "*Gemma*". La pertenencia a *Helicina* de *Tristamia*, *Oxyrhombus*, *Pseudoligyra*, *Oligyra*, *Succincta*, "*Cinctella*" (también preocupada) y *Punctisulcata* se confirma. Debido al tracto genital monáulico, el género *Ceochasma* se ordena como subgénero de *Helicina*. Espécies de la Antillas solo se estudiaron ejemplarmente, *Helicina jamaicensis* Sowerby, 1841, se incluyó dentro de *Alcadia s.l.* y *Alcadia* (*Analcadia*) *platychila* (von Mühlfeldt, 1816) se le asigna a *Helicina s.s.* Por una parte estos datos excluyen al género *Alcadia* del continente centroaméricano, por otra parte el análisis de las nuevas espécies costarricenses encontradas de *Helicina hojarasca* y *H. boeckeleri* requirieron la instauración del subgénero *Alcadia*, *Microalcadia* n. subgen., para el continente basandose mayormente en los carácteres del tracto reproductor femenino y de la concha embriónica. La presencia de *Alcadia* con solo unas cuantas pequeñas especies en el continente corresponde a la distribución de *Eutrochatella/ Pyrgodomus* y *Lucidella*.

Las espécies continentales centroaméricanas de *Helicina* parecen estar más emparentadas entre si, qué con los subgéneros *Analcadia* y *Sericea* del norte de Suramérica. El taxón brasilero *Angulata*, subordinado a *Helicina*, posee una estructura de la concha embriónica claramente distinta y diferencias anatómicas todavia por corroborar, por esto se le considera como un género aparte.

Contraria a la clara diferenciación a nivel genérico, el intento de agrupar las espécies continentales de *Helicina* ha sido solo en parte exitoso. Algunas similitúdes en la estructura superficial de la teleoconcha, el desarróllo relativo de las estructuras accesórias del aparato reproductor femenino,y el grado de dimorfismo sexúal son obios y se discuten en parte, pero estadios intermedios complican la solución satisfactoria de este problema. Además de *Ceochasma*, se reconocen tres subgéneros centroaméricanos continentales: *Oligyra*, *Tristramia* muy parecido a *Helicina s.s.* y "*Gemma*". Este último está preocupado pero se le retiene tentatívamente, ya que proponer un núevo nombre a este nivel no se considera apropiado.

El estudio de otros carácteres morfológicos diferentes a la estructura de la concha embriónica y del aparato reproductivo femenino revelan los siguientes resultados adicionales, basados especialmente en las espécies costarricenses de *Helicina*:

Se demostró repetidamente que las características de la teleoconcha, opérculo y rádula, previamente considerados fundamentales para la clasificación, son objeto de desarrollos convergentes, limitando asi su valor sistemático. Diferentes ejemplos son dados como el diente lateral en forma T de la rádula o los filamentos del perióstraco. Evidencia adicional es dada en la reorganización requerida mencionada anteriormente. Sin embargo estos carácteres juegan un papel suplementario o de soporte.

La pigmentación del manto de los helicínidos arbóreos está fuertemente relacionada con la transparencia de la concha y reemplaza funcionalmente la coloración de la concha en conchas delgadas. La posibilidad fisiológica de la pigmantación del manto se considera como una adaptación obia que permite la supervivencia con conchas delgadas, en ambientes con poco calcio. Mientras que los patrónes de coloración del manto son

característicos para las espécies arbóreas con conchas delgadas, la coloración de la cabeza y el pié son raramente característicos a nivel de espécie.

Las diferencias del tamaño de la protococnha no se habian estudiado previamente en los helicínidos. Se demuestra que el tamaño de la concha embriónica aumenta con el tamaño de la concha en un grupo de espécies relacionadas y con la altitúd de la localidad de differentes poblaciones de una espécie. En algunos casos el tamaño de la concha embriónica puede ser característico para una espécie. Primeros datos de *Lucidella* y *Eutrochatella*/*Pyrgodomus* muestran constantemente una concha embriónica más pequeña que en *Helicina* o *Alcadia*.

Las estructuras internas de la concha – apertura axíal e inserción de los músculos – parecen ser característicos para algunas unidades sistemáticas, e. j. *Lucidella* y *Schasicheila*. La longitud de la apertura axíal es constante dentro de las espécies, pero, contrariamente a lo que se suponia, no está relacionada con el número de vueltas.

Los datos sobre dimorfismo sexúal dados en este trabajo representa la aproximación más amplia hasta la fecha para analizar este fenómeno en los helicínidos. Este estudio muestra diferencias significativas en el volúmen, en donde los machos en casos extremos solamente alcanzan aproximadamente entre el 62 y el 70% del tamaño de las hembras. Contrariamente a las suposiciónes anteriores no se pudieron comprobar diferentes formas en el género *Helicina*. El grado de dimorfismo sexúal parece tener también valor al determinar las relaciones de parentesco.

INTRODUCTION

The Helicinidae and a few related families belonging to the Neritopsina represent the earliest branch of gastropods evolved to terrestrial existence from as-yet unknown diotocardian marine ancestors. Their recent distribution encompasses two main regions – the subtropical and tropical zones of North and South America and the Indopacific and Pacific islands and small areas of the Asian and Australian continents. A particular high diversity has developed on the Caribbean Islands and on the Philippines. The family is comprised of approximately 550 species, of which a little more than half occur in the New World. Most species are small, with only the largest representatives reaching nearly 3 cm.

Early classifications of the Helicinidae were based on shell characters only (e.g., L. Pfeiffer, 1850–1853). Later, Wagner (1907–1911) provided the still most extensive, but much criticized (e.g., Fulton, 1915; Solem, 1959: 166–167) monograph on the family worldwide, incorporating features of the operculum for his systematic arrangement. At about the same time, a very detailed, comprehensive anatomical investigation of several New and Old World species of different genera, including histology, was published by Bourne (1911). His study demonstrated a considerable uniformity of the morphological structures within the Helicinidae, indicating their very limited value for revealing systematic affinities, especially with respect to the reproductive system. In conclusion, Bourne (1911) favored radular characteristics as the safest feature for a classification. Baker (1922a, 1923) followed this concept to clarify the relationships of the American mainland taxa (United States to northern South America) and nomenclaturally corrected, modified and consolidated the system of Wagner (1907–1911) through radula characteristics that were believed to provide systematically relevant information. Subsequent anatomical studies on the same group of species with emphasis on the reproductive system (Baker, 1926, 1928) did not allow similar conclusions to be drawn due to the uniformity of the structures and the limited material. Later authors interpreted the results in the sense of Bourne (1911) and stated that the "... general uniformity of the genitalia of the Helicinidae makes them useless for diagnostic purposes" (Boss & Jacobson, 1974: 6). The radula characteristics were partly accepted, but other authors questioned their value for certain taxonomical units (Rehder, 1966; Boss & Jacobson, 1973). The most recent contribution to systematic issues of Helicinidae by Thompson (1982) highlights the conservative character of embryonic shell sculptures as a criterion for determining relationships, but its further application was beyond the scope of his study on a species-group from the West Indies. The few publications dealing with the classification of the Australasian and Pacific

species are based on shell structures or vague differences in the radula, respectively. In conclusion, it can be stated that the systematics within the Helicinidae still remain controversial, and due to the fact that the studies of the different structures were mostly based on different taxa, they are not comparable and any interpretation is, at the very least, partially questionable.

Faced with the absence of a detailed investigation of the applicability of different features to reveal affinities within the Helicinidae and a comparison of all these characteristics for one and the same group of species, this study tries to bridge this gap. Furthermore, preliminary studies on the female reproductive system of a Costa Rican species showed deviations from the previous results, rendering these organs more informative than described above. Therefore, the present study intends to investigate several morphological characters for their value in determining relationships on the species level (rather highly adaptable) and in higher systematics (rather conservative). The chosen characteristics will encompass widely applied aspects, such as shell in general, operculum and radula, but will also focus on less investigated or neglected structures, such as teleoconch surface structure, embryonic shell, internal shell structures, female reproductive system, and the phenomenon of sexual dimorphism.

Because single structures can only partially be assessed in their possible adaptability by their complexity and functionality alone, they also have to be discussed within the context of the best possible, well-founded synthesis of all possible characteristics, that is, the proposed classification. Therefore, the analysis of structures is based on revision of one group of closely related species (species level) and study of other related supraspecific taxa (higher systematics, e.g., type species of respective genera and subgenera). This will result in a new proposal for the classification of the taxa studied, which is compared with possibly deviating previous concepts.

This study will be based on the Costa Rican representatives of Helicinidae, which encompass a reasonable number of species for detailed analysis. According to Wagner (1907–1911) and Baker (1922a, 1926), most of the species belong to one or two genera, *Helicina* or *Helicina* and *Alcadia*. Single species of *Lucidella* and *Pyrgodomus* represent relatives of genera with otherwise Antillean distributions. Two newly discovered species (Richling, 2001) still await proper classification. Thus, a fairly wide scope of systematic units is included and, with respect to the Costa Rican species, part of the Central American mainland fauna has been chosen for which the most data for comparison, mainly from the works of Baker, are available.

The focus on the Costa Rican species provided the opportunity to carry out a revision of the Helicinidae of a poorly investigated area as well. Because von Martens (1901: xii) still has characterized the molluscan fauna as "one of the best known within Central America", a few scattered publications in the 1930s (e.g., Pilsbry) remained in complete neglect until recently, when the growing interest in tropical biodiversity, spearheaded by the foundation and work of the Instituto Nacional de Biodiversidad de Costa Rica (INBio), resulted in a new approach. The cooperation with the Zaidett Barrientos of the Malacology Section of INBio in providing access to the comprehensive collection of national molluscs greatly ameliorated the disadvantage of the unfavorable geological conditions of Costa Rica for collecting terrestrial snails which result in extremely low abundances and therefore present practical difficulties for obtaining sufficiently large numbers of specimens for certain aspects of the study.

MATERIALS AND METHODS

Area of Investigation

Costa Rica is situated in southern Central America adjacent to Nicaragua to the north and Panama to the south (about 8° to 11°15'N). Located between the Pacific Ocean and the Caribbean Sea, small area of just 51,100 square kilometers rises up to 3,820 m above sea level. The central mountain chain, northwest to southeast in orientation, separates a larger Caribbean from a hilly Pacific plain. The mountains are subdivided into the northern Cordillera de Guanacaste, the Cordillera de Tilarán, and the Cordillera Central, a chain of volcanoes, some of them still active, and the southern Cordillera de Talamanca which has been uplifted as a result of the subduction of the Cocos Ridge (Fig. 1).

The climate is characterized by a dry and a rainy season, with the dry season lasting from about December to May. Whereas the northwestern and central parts of the country really experience a dry period, the southern Pacific

side as well as the Caribbean side always have humid conditions. This is reflected in the variation of the vegetation, the tropical dry forest only being found in the northwestern area in the transition to the Península de Nicoya. The vegetation of the remaining part of the country is classified as moist, wet or rain forest (Tosi, 1969), with the humidity mainly increasing with the altitude (Fig. 2). The distribution of the annual precipitation is given in Fig. 3.

Materials

Fieldwork:

Costa Rica. The field work was carried out on five visits of about 4 to 9 weeks each to Costa Rica between 1998 and 2001. With one exception during the rainy season of July to September, the field trips were carried out during the dry season in February and March. Several localities scattered around the country were investigated for distributional data. Selected areas were visited several times in order to gather sufficient material of certain populations for comparative studies, because their abundance in the tropical rain forests is very low. Due to the arboreal life-style of most of the Costa Rican species, manual searches had to be conducted. The detailed material and localities are listed under each species. Main collecting sites are shown on the general map (Fig. 1).

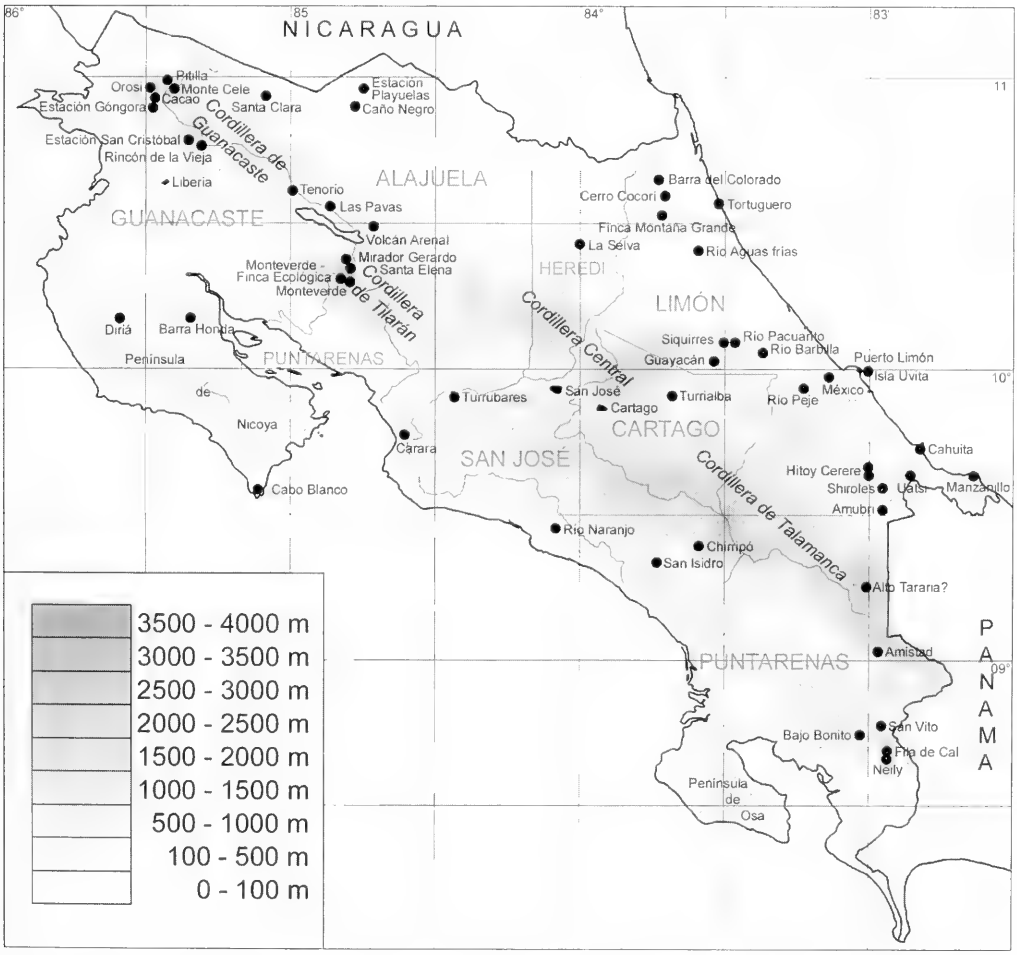


FIG. 1. Map of Costa Rica, including the most important collecting sites, the central mountain chains, and the provinces.

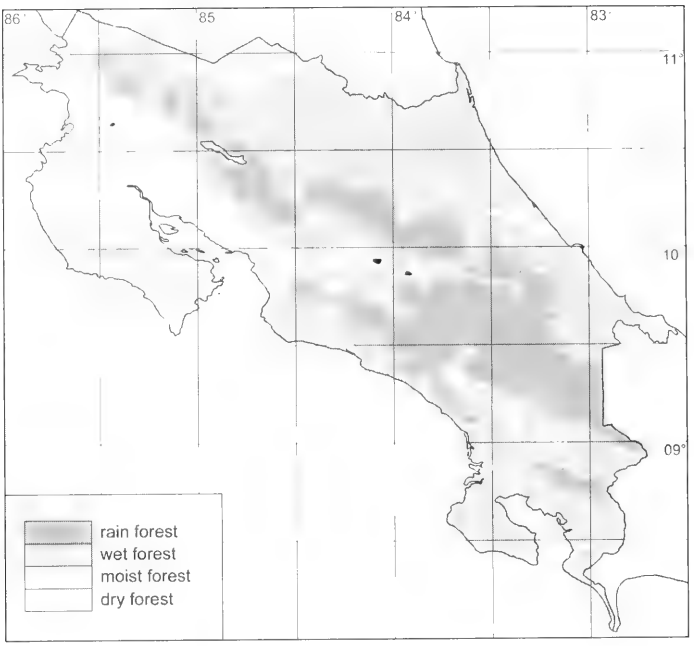


FIG. 2. Vegetation zones of Costa Rica (based on Tosi, 1969).

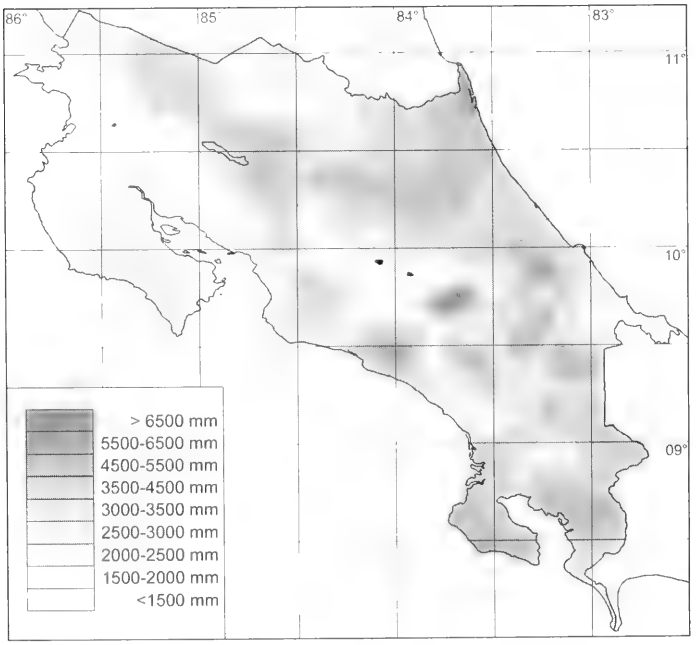


FIG. 3. Annual precipitation in Costa Rica [mm/year] (based on Ministerio de Agricultura y Ganaderia & Instituto Meteorologico Nacional, 1985).

JAMAICA/UNITED STATES. Because the type species of the most important Central American genera (*Helicina*, *Alcadia*, *Lucidella*, *Eutrochatella*) occur in Jamaica, and preserved material was not available in collections, supplementary research was carried out during two weeks in May/June 2001. Specimens of *Helicina orbiculata* (Say, 1818) were collected in Gainesville, Florida, in May 2001.

Museum Collections: Material of the following institutions has been studied, subsequently only the abbreviations will be used:

ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, USA (Dr. Gary Rosenberg, Dr. Igor Muratov)
APHIS-PPQ USDA	Malacological Collection of United States Department of Agriculture, Philadelphia, USA (Dr. David G. Robinson)
BMNH	The Natural History Museum, London (formerly British Museum, Natural History), Great Britain (Dr. Fred Naggs, Richard Williams)
HNC	Haus der Natur Cismar, Germany (Dr. Vollrath Wiese)
INBio	Instituto Nacional de Biodiversidad de Costa Rica, Santo Domingo, Costa Rica (Dr. Zaidett Barrientos)
IR	Material collected by Ira Richling, partially deposited as vouchers at INBio, otherwise accessible through the collection of the HNC; a few of the numbers refer to field observations only
MHNN	Musée d'Histoire Naturelle, Neuchâtel, Switzerland (Dr. Jean-Paul Haenni)
MIZ	Museum and Institute of Zoology of the Polish Academy of Sciences in Warszawa, Poland (Prof. Dr. Adolf Riedel)
NMBE	Naturhistorisches Museum Bern, Bern, Swiss (Dr. Margret Gosteli)
RMNH	Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Natuurlijke Historie), The Netherlands (Wim Maassen)
SMF	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt a.M., Germany (Dr. Ronald Janssen)
UF	Florida Museum of Natural History, Gainesville, USA (Dr. Fred G. Thompson, John Slapcinsky)
USNM	United States National Museum, Washington, D.C., USA (Dr. Robert Hershler)
ZMB	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (formerly Zoological Museum Berlin) (Dr. Matthias Glaubrecht)
ZMH	Zoologisches Museum, Universität Hamburg, Hamburg, Germany (Dr. Bernhard Hausdorf)

INBio: Within a context of considerable recent efforts towards an inventory of the biodiversity of Costa Rica, the institute houses a very extensive collection of molluscs. All available specimens of Helicinidae from this material were studied, partially during personal visits in Costa Rica, partially by loans to Germany.

UF: This institution houses probably one of the most comprehensive collections of Central American terrestrial molluscs. During a two-week visit, about 1,100 lots of Helicinidae were studied with the emphasis on the mainland species yielding considerable distributional data.

ZMB/MHNN: The only important historical collections in Costa Rica were made by the Swiss naturalists Biolley and Pittier at the end of 19th century. Their material ended up in different collections, parts of it in the ZMB and MHNN respectively, other parts remained in the Museo Nacional in San José, Costa Rica (see under *Helicina pitalensis*). The ZMB collection was visited personally, whereas material in the MHNN was searched for by J.-P. Haenni, Neuchâtel, and kindly loaned to the author. According to J.-P. Haenni, an up-to-date catalogue of the mollusc collection does not exist and the materials of Pittier and Biolley are scattered throughout the collection, which has never actually been catalogued and which was moved in the past, and it is possible that some of the material has not yet been found. A detailed list of material studied is given under each species.

Locations/Maps: During the field work, coordinates of the localities were registered using the Global Positioning System (Magellan GPS 3000) whenever possible, otherwise

they were taken from maps in 1:50,000 scale produced by the Instituto Geografico Nacional, San José, Costa Rica, in different editions, but all based on data from between 1961 and 1966. The staff of INBio uses the same maps. All Costa Rican records from literature or other sources without exact data were localized as accurately as possible and coordinates were estimated based on the map: Los Parques Nacionales y otras areas protegidas de Costa Rica. – Fundación Neotrópica, San José, 1993, I Reimpressión 1995. Information on some historical collecting sites was provided by Zaidett Barrientos and Maribel Zuñiga, INBio. All further explanations that were subsequently added are given in brackets.

The map of Costa Rica used throughout this study is based on: Costa Rica. Mapa fisicopolitico 1:500.000 – Instituto Geográfico Nacional, San José, edition 1987.

Methods

Measurements: The following linear measurements (Fig. 4) were used, when measurements of single species given, the following sequence is given, separated by "/" (unless otherwise stated):

height
major diameter
greatest diameter
minor diameter
expansion of outer lip
height of last whorl
height of columellar axis

Because some helicinid species display variation in the development of the outer lip which mainly influences the measure of the greater diameter, measurement of "major diameter" has been introduced. This measurement was taken just behind the reflection of the outer lip (Fig. 4). For the height, this modification was not applied, because it is not affected as much and is furthermore not uniformly practicable.

The greatest diameter is usually included only in measurements given for single specimens to comply with traditional measurements.

Measurements were taken with a micrometer gauged on 0.01 mm scale. In view of the deviation shown below that were minimized by personal experience, values given to characterize single specimens were rounded to a 0.1 mm scale. Deviations are mainly due to effects of an imperfect perpendicular orientation of the shell with respect to the measuring axis, a problem that can be minimized with experience if the same person carries out the measurements. However, errors probably cannot be excluded in globular shells, but their range is tolerable. To check the average deviations, three shells of different shapes were measured the different times and the mean value, the standard deviation and absolute deviations were analyzed (Table 1).

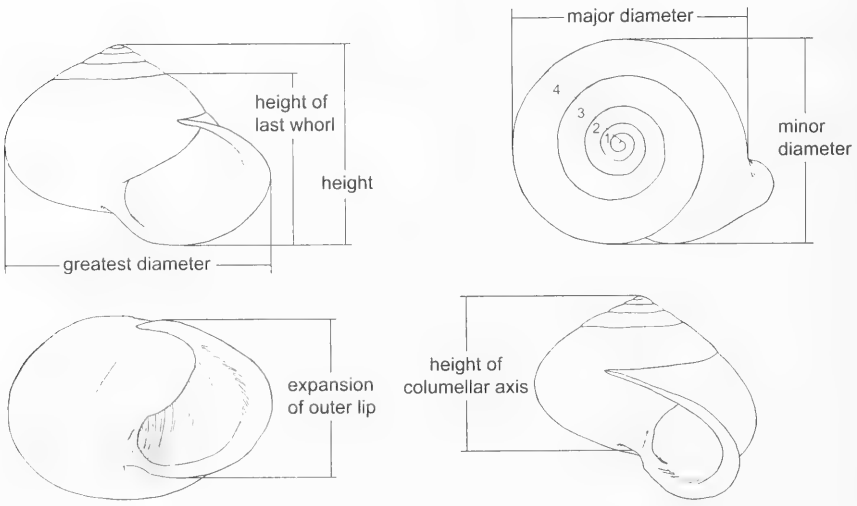


FIG. 4. Measurements and counting of postembryonic whorls.

TABLE 1. Analysis of deviations in measuring procedure of Helicinidae for three individuals of different species, all measurements in mm, maj./min. diam. = major/minor diameter, col. axis = columellar axis.

	Helicina beatrix confusa lot IR 1113					*Helicina funcki* lot IR 1555					*Helicina gemma* lot IR 1460				
	Mean value	Standard deviation	Min	Max	Number	Mean value	Standard deviation	Min	Max	Number	Mean value	Standard deviation	Min	Max	Number
Height	8.30	0.02	8.27	8.33	10	10.78	0.04	10.72	10.85	10	6.61	0.03	6.57	6.66	10
Maj. diam.	7.38	0.03	7.34	7.43	10	12.33	0.09	12.18	12.53	10	6.13	0.01	6.12	6.15	10
Greatest diameter	7.75	0.03	7.70	7.81	10	13.49	0.03	13.44	13.56	10	6.47	0.01	6.43	6.49	10
Min. diam.	7.05	0.02	7.02	7.08	10	11.06	0.02	11.03	11.10	10	5.69	0.01	5.67	5.71	10
Outer lip	4.80	0.03	4.74	4.85	10	7.81	0.02	7.78	7.84	10	3.86	0.02	3.82	3.90	10
Last whorl	6.14	0.03	6.10	6.18	10	8.87	0.04	8.78	8.94	10	4.91	0.05	4.83	4.98	10
Col. axis	6.53	0.03	6.46	6.60	10	8.17	0.05	8.09	8.36	10	5.13	0.03	5.08	5.22	10

In addition to the linear measurements, the weight and volume of empty shells were analyzed. Sartorius scales (scale 0.001 g) were used. The volume was measured as the difference of weight of the shell filled with distilled water and the weight of the empty shell. To obtain comparable data, shells were always filled until the water showed a plain surface in the aperture. In the weight measurements, the hole caused by the preparation procedure did not influence the results, because the wall at the beginning of the last whorl is thin and the amount of material removed was below the scale of resolution.

Except for the specimens studied with the SEM, the diameter of the embryonic shell was measured under a stereomicroscope (scale 20 µm). Otherwise, measurements were taken from photographs, which are much more exact. Whorls were counted according to Fig. 4.

Fixation: The preservation of the live collected material was carried out in two ways:

(1) Collections until 1999: Specimens were relaxed in water for several hours and subsequently transferred to isopropanol (about 80%).

This method has disadvantages: It is difficult to find the right time to stop the relaxation process, because it depends on so many factors, such as specimen size, water volume and temperature. Under the conditions of field work and travel by bus, it is difficult to carry out lengthy procedures. Furthermore, the shocks received during transport also influence timing. As a result, the specimens may be badly preserved or contracted. In case they close their opercula again, there remains the risk that the alcohol will not penetrate into the shell.

Beginning in 2000, I developed the new method to remove the body from its shell described below, which allowed another preservation method mitigating these disadvantages.

(2) Collections after 1999: Specimens were removed from the shell alive and immediately dropped in isopropanol.

It has the advantage that specimens can be preserved immediately and with a constant result. The problem of the closure of the operculum becomes irrelevant. If a relaxation is required for subsequent investigations, the body can still be dropped in water or other solutions and will be anaesthetized much faster due to the greater unprotected surface for medium exchange. For the present study and due to the need of a fast working method, a relaxation process has usually not been applied, because retractions are limited to the foot and the two portions of the retractor muscle and do not greatly affect other organs.

Preparation and Storage of Material: Against the background of the low abundance of Helicinidae in Costa Rica and the various aims of the study (e.g., aspects of anatomy, sexual dimorphism), two requirements had to be met at the same time: the shell and the animal had to be separated and they had to be kept as intact as possible.

When normally pulling a more or less relaxed animal out of its shell, in most cases the head-foot and the anterior pallial portion will be released, but the remaining part will be torn off within the shell. This is due to the fact that in the Helicinidae, contrary to most other gastropods, by the dissolution of the inner whorls of the shell, the visceral mass forms one large complex, which has a greater diameter than the remaining part of the last whorl or aperture respectively, through which it has to pass. Furthermore, air cannot penetrate to allow the body to be released. Besides the obvious disadvantages, the resulting rupture of the body directly divides the pallial gonoduct at an important section and often makes its study impossible.

In a newly developed method, a small hole is made on the periphery within about the second quarter of the last whorl (Fig. 5, arrow) with a nail file or insect needle of different size, depending on the shell thickness. This can be performed without injury to the animal when applying the method to live individuals. Subsequently, a needle, curved if necessary, is carefully inserted between shell wall and body and the two retractor muscles are detached. Afterwards, the ani-

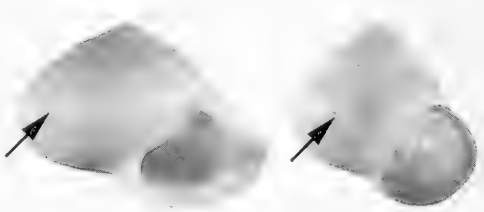


FIG. 5. Hole for removal of the body.

mal can easily be removed by pulling the operculum (live animals) or by a needle inserted in the foot (preserved animals). One must be careful to allow air to enter the hole. Live animals can then be fixed. In preserved specimens, it is usually more complicated during the final removal to avoid the damage described above, because the visceral mass is no longer very flexible or may suffer from poor preservation. By the aid of the needle (through the hole), the visceral mass then has to be squeezed through the remaining part of the last whorl. The success in preserved specimens greatly depends on the shell shape (relation of shape and volume of visceral mass to the diameter of the aperture) and the prior fixation. During the present study, the method seldom failed.
In my own material, shells were separated from the bodies in all adult and live collected specimens. They were individually stored, enumerated and labeled.

Sex Determination: The determination of the sex was done by external inspection of the soft body. According to Baker (1926) and personal experience, in most cases and many species a dissection is not necessary. Females are recognized by the comparatively small lobes of the ovary, widely spaced, regular constrictions of the pallial gonoduct (not in all species), and the dark color of a distinct portion of the distal pallial gonoduct. Males are characterized by the comparable larger lobes of the testis, the absence of the distinct dark color, a very densely lobed apical, and smooth distal part of the pallial gonoduct. In some cases, the shiny white vas deferens may shimmer through the visceral mass. Normally not all these features are visible in one and the same specimen, but each one may be unequivocal. It mainly depends on the body pigmentation, the species and the individual development. In ambiguous cases, the specimen was dissected.

Reproductive System: Dissections were made in 70% isopropanol or ethanol. For the investigation of the reproductive system, the mantle cavity was opened along the left side of the intestine, with the latter remaining along the pallial gonoduct. A second cut was made between the pallial gonoduct and the right retractor muscle, along or through the hypobranchial gland up to the apical part of the pallial portion of the reproductive system (Fig. 6).

Histology: The separated female reproductive system was dehydrated through a series of ethanol, transferred to paraffin via acetone (100%) and embedded in paraffin. Serial sectioning was done at 5–7 µm with a sliding microtome. The tissue was subsequently stained with a sequence of paraldehyde fuchsin solution, nuclear fast red and orange G/ light-green.

Preparation of Shells for SEM: In order to reduce lasting effects to the shell by gold coating, the specimens were usually mounted on aluminum specimen stubs using adhesive conductive tape. Subsequently, they were tightly covered with laboratory film (Parafilm "M"®), which adhered to the remaining surface of the adhesive conductive tape. Finally, the embryonic shell or other areas of interest were uncovered and coated. After the SEM investigation the laboratory film can easily be removed and the shell extracted.

Preparation of the Radula: The radula was removed from the buccal mass. It was cleaned

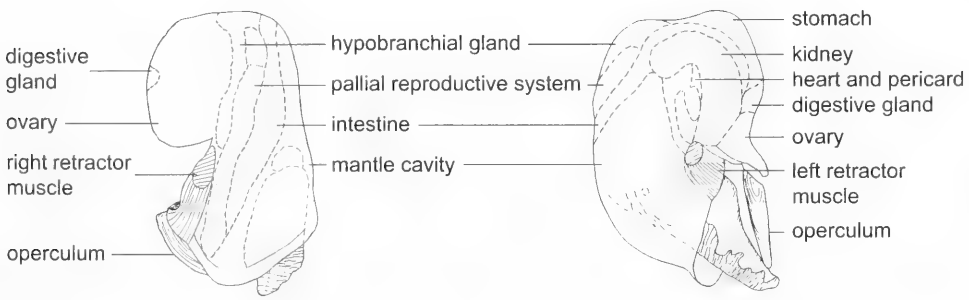


FIG. 6. General anatomy of the Helicinidae.

from remaining tissue in NaOH-solution (1 N) for about 24 h at 50°C. Subsequently the radula ribbon was washed in distilled water several times and dehydrated through a series of ethanol (70%, 80%, 96%, 100%). After the pure alcohol, it was dried and arranged to the final mounting position with the marginal teeth turned up by using preparation needles. Finally, the radula was mounted with conductive carbon cement on the aluminum specimen stubs for SEM examination. Only a few radulae were studied with the light microscope. For light microscopy, the radulae were transferred to the slides directly after removal.

SEM Investigation of Shells and Radulae: Samples were sputtered with gold for 140 sec by using a BALTEC SCD 050 Sputter Coater. Investigations were carried out with a LEO 420 scanning electron microscope (LEO V 02.04). Radulae had to be studied under low voltage conditions (about 2.5 kV), because the structure of the rhipidogloss radula causes extremely high charge distributions, rendering adequate studies and exposures under high voltage conditions impossible.

Figures: Unless otherwise stated, all drawings, maps and photographs in the study were made by the author. Drawings were made at a LEICA MZ 8 stereomicroscope by the aid of a camera lucida. Except for Figures 140, 228, 249, 257, and all live animals photographed with a 35 mm SLR camera, all shells were digitized with a Sony Digital Still Camera DSC-F505V.

Addditional Abbreviations:
ad./ads. – adult/s
coll. – collection
juv./juvs. – juvenile/s
SEM – scanning electron microscope

RESULTS

The results are presented into two parts: (1) Revision of all Costa Rican species of Helicinidae including the investigation of the shell – general aspects, internal structure, surface structure, embryonic shell, morphometry and sexual dimorphism – the radula, the soft body color, the female reproductive system, and data on the habitat and distribution. (2) The morphological characters of the supraspecific taxa relevant for the classification of the Central American mainland Helicinidae.

GENERAL ASPECTS

The discussion under each species will focus on the species-relevant data. Aspects of the morphological characteristics will be discussed in context with the classification subsequent to the Results, as will some general results for the Costa Rican fauna and the classification of the Helicinidae. The account for each species has the following outline, in which I have here included an overview of the morphological characters.

Literature Records (without heading): All literature records of the respective species are listed. In some cases of questionable determinations, attempts to re-examine the original material were made. Some citations nevertheless remained uncertain, those are marked by a "?".

Synonymy: For clarity, the synonyms are reitterated from the Literature Records. This includes only synonyms that were proved and accepted during this study.

Original Description: Complete citation of the original description.

Type Material: This exclusively includes the type material of the respective species.

Type Locality: Only the type locality of the respective species is given under this heading.

Type Material of Synonymous Taxa or Similar Species: If necessary for comparison, information on the type material of synonymous taxa or similar species is also provided, because for many Central American taxa adequate figures cannot be found in the literature. For those species, the type locality is given here.

Examined Material: For a better finding of the data of the lots, the material is arranged according to the collections (leg. I. Richling, collection INBio, other sources) and, only secondarily, according to localities (Costa Rica: different provinces; other countries).

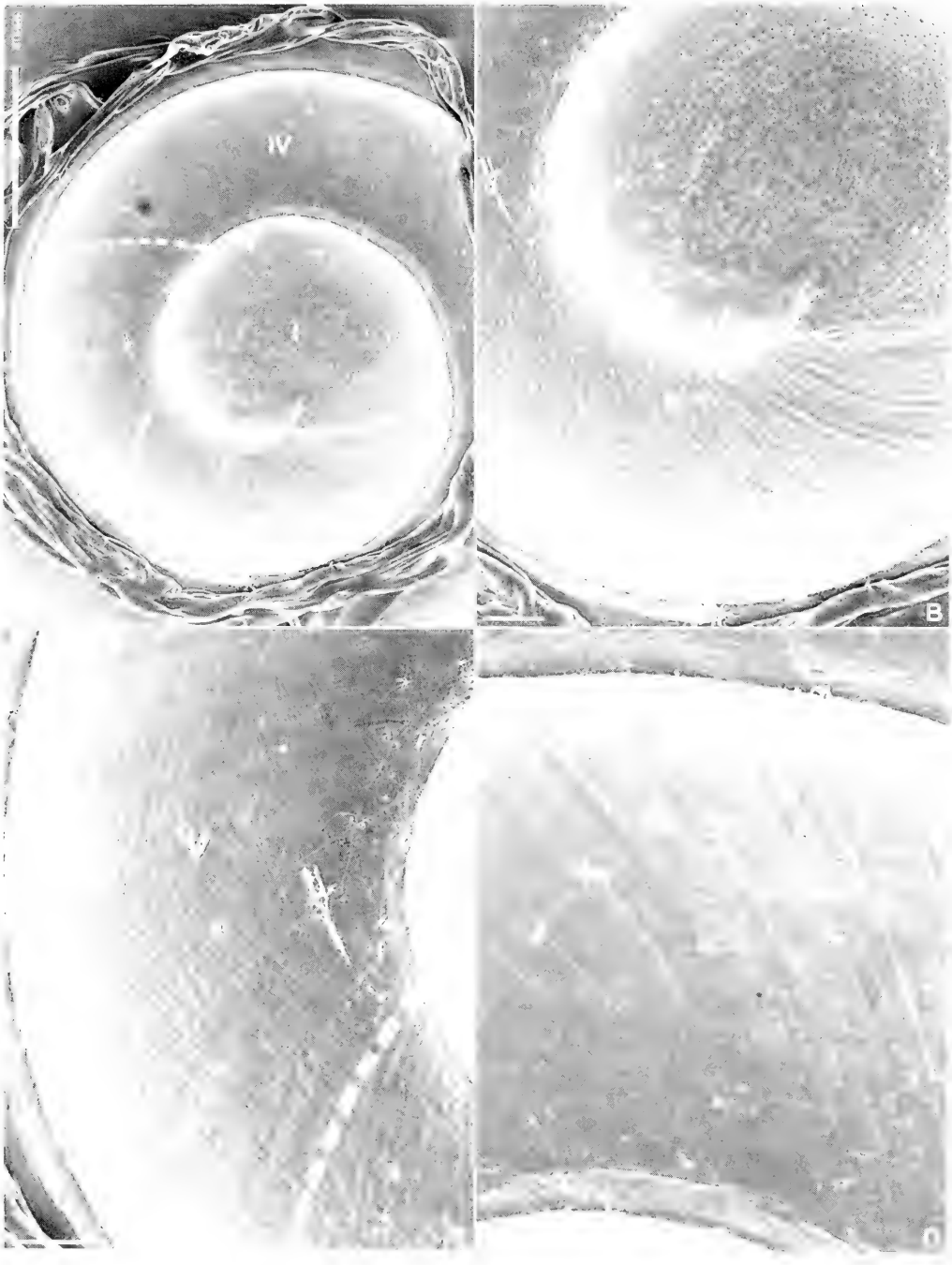


FIG. 7. Changes in shell surface structure exemplary shown for *Helicina gemma*. A. I: Embryonic shell; II: Transitional structure; III: Oblique diverging grooves; IV: Smooth surface with fine growth lines. B. Enlarged view of the transitional structure (section II). C. Pattern of oblique diverging grooves with transformation of section II. D. Enlarged view of the smooth surface with fine growth lines (section IV); scale bars 500 µm (A); 100 µm (B–D).

To shorten the descriptions of the localities and to facilitate the search for the complete locality data mentioned in the text, the following typological convention is used for the Richling and INBio material. In the case of a single locality for lot(s), only a shortened name of the locality is set in italics. In the case of several lots from sublocalities, the entire general description is in italics, followed by a colon; the colon is then followed by further specifications in italics applying to the lots following the second colon. In some cases, there is a further subdivision, such as altitude, given in the same format. Locality data in roman type refer only to the subsequent lot.

Description:

Shell: General description of the species.

Internal Shell Structures: Contrary to most other gastropods, Helicinidae dissolve the inner parts of their shells so completely that only a septum of a certain length subdivides the shell internally. This septum extends from the remains of the columella to the suture of the last whorl. The length of the septum or, referring to the soft body, of the axial cleft is figured here. Additionally, the positions of the attachments of the retractor muscles are shown. In Helicinidae, the columellar muscle in separated in two portions, one attaching somewhere in the umbilical area, the other in the upper part of the shell, often close to the beginning of the axial cleft.

Teleoconch Surface Structure: During growth, the Helicinidae produce different shell surface structures. A possible sequence of different patterns is shown for *Helicina gemma* (Fig. 7) covering the variations among in Costa Rican helicinids.

The embryonic shell (Fig. 7A: I) is sharply distinguished from the teleoconch by a distinct pattern and a more or less clear growth mark. The subsequent part exhibits an irregular, coarse and wrinkled surface ("transitional structure") (Figs. 7A: II, B). It changes continuously with pits elongating to grooves to a pattern consisting of groups of parallel grooves that diverge acutely with other obliquely orientated groups of grooves (Figs. 7A: III, C). The grooves follow two main orientations (this structure will subsequently be referred to as "pattern of oblique diverging grooves"). Finally, this pattern is predominated by fine growth lines forming an otherwise smooth, shiny surface (Figs. 7A: IV, D). Only a vestige of the oblique grooves may still be visible. This surface structure is maintained to the aperture.

This general scheme is not completely realized in all Costa Rican Helicinidae, certain sections may be absent, for example, the pattern of oblique diverging grooves continues for the rest of the postembryonic shell and the smooth surface is absent. Apart from differences in detail, the pattern of the major part of the postembryonic shell does not change again and starts at the latest at the beginning of the second whorl (Fig. 7A, III–IV). Therefore, a section of this whorl is preferably described for species comparisons.

Embryonic Shell: If available, at least three specimens of each species or subspecies respectively were investigated for embryonic shell structures. Individuals were chosen randomly and depending on the preservation. Especially in cloud forest areas, the embryonic shell seems to erode very quickly.

Unless otherwise stated, relative descriptions refer to the structures of *Helicina funcki*.

Operculum: The operculum of most species of the Helicinidae is concentric and consists of two plates, an inner horny plate (attached to the foot) and an outer calcareous plate. The horny plate projects beyond the margins of the calcareous plate. In all Costa Rican species except for *Pyrgodomus*, the calcareous plate is thin and becomes thickened only towards the columellar edge, determining the shape of this margin, whereas the palatal margin is shaped by the further extending horny layer; the calcareous layer becomes indistinguishable and normally does not reach this margin.

Animal: Expecting species-specific differences in the mantle color of certain species, as many specimens as possible were documented as to their color, but due to considerable variation, especially among different populations, the comparison did not reveal many species-specific differences. A generalized description will be given for each species.

Radula: The helicinid radula consists of three groups of teeth: the centrals, the laterals and the marginals (Fig. 8). The central field is composed of an unpaired central or rhachidian tooth (R), which is flanked by three paired teeth, called A-, B-, and C-cen-

FIG. 8. Part of radula ribbon (shown in *Helicina funcki*); "A"–"C": respective central teeth, ap: accessory plate, cl: comb-lateral, R: rhachidian tooth; scale bar 100 µm.

tral with the A-central aside to the rhachidian tooth (some authors such as Keen, 1960; Thompson, 1980, but not 1982; Stanisic, 1997, include the three paired teeth into the laterals). The laterals, also called the capituliform complex, are formed by two partially fused teeth, the inner comb-lateral (cl) and the accessory plate (ap). Within the Helicinidae, the comb-lateral is developed in two main types: (1) the true "comb"-lateral: a broad tooth with numerous cusps at the cutting edge (Fig. 8) or (2) a very strong tooth T- or mushroom shaped (also called T-lateral) without cusps (Fig. 246B). The marginals encompass numerous long, slender teeth in oblique rows that bear a varying number of accuminate cusps. The terminology follows Baker (1922a).

The radulae of the Costa Rican species of *Helicina* do not show many differences among the individual species, but within populations of the species themselves, there is some variation, especially regarding the number of cusps on the central teeth. A certain number of cusps is usually not exceeded, but the cusps are often vestigial or absent, forming a crenulate margin at the cutting edge. Throughout each radula, the different teeth are very uniformly developed with a very constant numbers of cusps.

The rhachidian tooth is triangular to trapezoid shaped and lacks cusps. The A- and B-centrals project laterally, with broad faces forming an oblique cutting edge. The C-central narrows towards its face and represents the outer tip of the central cutting edge.

The two teeth of the capituliform complex were always observed to be fused, and, under the conditions and the magnifications studied with the SEM, the demarcation line between the teeth was not visible. The cusps on the comb-lateral only show intraspecific fluctuations of one or two, but aberrant developments do occasionally occur (e.g., many more cusps or lacking any at all). The relative size of the cusps appears to be constant. In most species, the cusps slightly decrease in length towards both ends of the edge, with the inner a little longer. The accessory plate is usually slightly smaller than the comb-lateral and projects laterally.

With the occasional exception of the innermost tooth, the marginals increase in number of cusps outwards starting with 2–3 to more than 10. Two tendencies were recognized: (1) slowly and (2) rapidly increasing number of cusps; in the first, there are remarkably more teeth with 2, 3 and 4 cusps, that is, also more teeth with pronounced terminal cusps, whereas in teeth with more cusps the latter tend to arrange themselves laterally along the tip which is therefore turned sidewards to bring the cutting edge into action.

In the account on the radula for the species, only the distinguishing features are outlined in addition to the figures.

Unless otherwise stated, the radulae of at least three specimens of each species and in some cases also of different populations were investigated. For *Helicina funcki* and *H. beatrix riopejensis* n. subsp. eight specimens were studied to check for intraspecific variability.

Female Reproductive System: Parts of the reproductive system of the Helicinidae show several peculiarities for which authors have introduced special terminology (Bourne, 1911; Baker, 1925 & 1926). Because terms were exchanged and confused, a summary is given, and the present use is indicated (Table 2, Fig. 9). The terminology implies certain functional aspects, but the function has been controversially discussed for different taxa (e.g., Bourne, 1911) and still remains partially doubtful, especially with respect to the structures for sperm storage. The terms used in this study follow the traditional usage and strike a balance between possible confusions, but will not be modified for functional correctness to avoid any fur-

TABLE 2. Terminology of the female reproductive system in Helicinidae.

Anatomical position	BOURNE (1911)	BAKER (1925)	BAKER (1926)	THOMPSON (1980)	Present study
	Parts of oviduct				
Direct continuation of slender primary oviduct	descending limb	first limb	right limb	ascending limb	ascending limb
Limb of V-organ leading into pedicel	ascending limb	-	left limb	pedicel**	descending limb
Basal portion of V-organ from invaginated constriction up to reception chamber	-	-	pedicel	pedicel**	pedicel
Portion of oviduct receiving several accessory organs	-	fertilization chamber	reception chamber	seminal receptacle***	reception chamber
Distal part of oviduct, parallel to rectum	ootype	secondary gonoduct or uterus	uterus	pallial oviduct	pallial oviduct
	Accessory structures				
On top of V-organ	-	accessory sperm sac	-	accessory sperm sac	accessory sperm sac
On descending limb just above pedicel	receptaculum seminis	-	accessory sperm sac	accessory sperm sac	receptaculum seminis
Sac entering directly into reception chamber	-	-	secondary accessory sperm sac (for *Schasicheila*)	-	no specific term
Ventral, associated with reception chamber	caecum of ootype*	spermatheca or bursa copulatrix	ventral bursa	bursa copulatrix/ copulatory bursa	bursa copulatrix
Dorsal, associated with reception chamber or provaginal duct	provaginal sac*	provaginal sac	provaginal sac	provaginal sac	provaginal sac

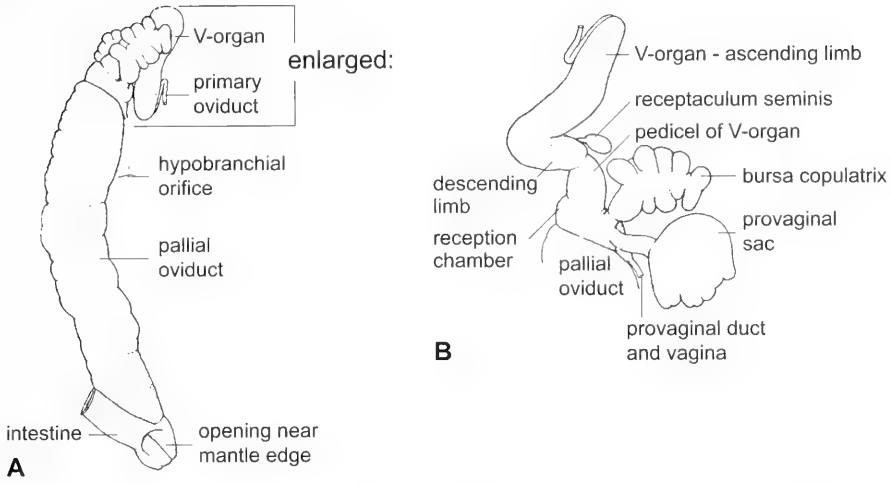


FIG. 9. Female reproductive system in Helicinidae (*Helicina orbiculata*), ovary to slender portion of the oviduct omitted, ventral view. A. Organs in natural position. B. Apical complex enlarged and artificially arranged to show the different organs and their connections (modified after Baker, 1926).

ther confusion until these aspects have been finally clarified. Furthermore, the term "pallial" only refers to the topographical position and not to ontogenetic origin.

The reproductive system of female Helicinidae consists of a folliculous ovary that discharges into a thin-walled spherical structure, which continues as the slender primary oviduct. This oviduct is curved anteriad before it enters the V-organ. The V-organ is subdivided in an ascending limb, a descending limb, and a pedicel and leads into the reception chamber. The oviduct continues as an elongated pallial part parallel to the intestine and opens near the mantle edge. The descending limb of the V-organ may receive the duct of a receptaculum seminis, or is associated with sac-like structures (accessory sperm sac) at its very beginning (e.g., *Lucidella*). Besides the oviduct (pedicel), the reception chamber is connected with a ventral bursa, a dorsal provaginal sac, and a provaginal duct that opens into the mantle cavity. Because of the two openings, the female system is called diaulic.

Because the general structure is similar in Costa Rican *Helicina*, it is described as follows, and only specific deviations are added under each species.

The ascending limb of the V-organ is straight and a little longer than descending limb and

(*Continued from opposite page*)

* The caecum of the ootype and the provaginal sac *sensu* Bourne (1911) were differently interpreted by Baker. In 1925, he assigned the organs correctly as given in my Table, whereas in 1926, he exchanged this assignment of the terms, regarding his former interpretation as wrong. He pointed out that in Bourne's figure (1911: pl. XXXV, fig. 25) the caecum would clearly be located dorsally (as only is the provaginal sac) with respect to the oviduct. Actually, he disregarded the accurate description of the position of the organs. He was probably misled by the fact that in *Alcadia palliata* (C. B. Adams, 1849) the general appearance of this apical complex with both ventral bursa and provaginal sac elongated and without lobes differs somewhat from the mainland species that he had dissected.

** Thompson misinterpreted the pedicel (term introduced by Baker, 1926) as the whole descending limb of the V-organ. In Helicinidae, it is demarcated by an invaginated constriction and subsequent distal swelling before entering into the reception chamber, also histologically differentiated. In the Ceresidae and Proserpinidae, which Thompson studied, the descending limb and a pedicel are not externally demarcated, but since histological data are lacking, the identification of the "descending" limb with the pedicel only (and absence of the "non-pedicel" part) is not verified for the two families.

*** Thompson intended to comply with other prosobranch terminology, but because both Latin and English terms were used (e.g., bursa copulatrix and copulatory bursa) for the same organ, "seminal receptacle" would be synonymous with "receptaculum seminis", a term being already in use for an accessory structure. Furthermore, as far as it is known just the reception chamber is not a place for sperm storage, i.e. a receptaculum seminis.

pedicel together, and in natural position it approximately reaches the transition of the reception chamber to the pallial oviduct. Situated between the limbs of the V-organ, a comparatively small, always simple sac-shaped receptaculum seminis enters the descending limb with a slender duct. The ventral bursa copulatrix is always lobed, but to a different extent. The provaginal sac is well developed, but rather simple shaped, and possesses a fairly long stalk as connection to the reception chamber. Contrary to the general scheme given above and the descriptions of other Central American species of *Helicina* by Baker (1926), the provaginal duct or vagina does not exist and the system is monaulic. The thick walls of the pallial oviduct are always variously folded, which is reflected in surface constrictions. A short, distinct portion just before the distal opening is dark brownish, whereas the remaining part of the reproductive system is whitish-opaque if not otherwise stated.

If material was sufficient the reproductive system of at least three females of each species or population were dissected. In addition, serial sections were studied for *Helicina funcki*, *H. tenuis*, *H. beatrix confusa*, *H. beatrix riopejensis* n. subsp., *H. gemma*, *Alcadia hojarasca*, and *Lucidella lirata* to confirm the results of the dissections.

In the drawings, the reproductive system is normally shown from the ventral side and the accessory organs of the apical part were artificially separated to allow an adequate presentation of this complex structure (Fig. 9B). If not otherwise stated, relative descriptions refer to the structures of *Helicina funcki*.

Morphometry and Sexual Dimorphism: Due to the paucity of material, the number of specimens of each population/species studied could not be standardized, but, as far as possible, maximized; the number of specimens is indicated in each case. The following measurements were analyzed: height, minor diameter, height of last whorl and columellar axis, extension of outer lip, volume and weight, if available. The major diameter is given only for comparison, but it is not included in diagrams, because the shells increase regularly in size, and it is therefore correlated with the minor diameter, which can be measured more exactly.

For the comparison with populations of unknown sex (e.g., INBio material, type material) the sex-independent mean value is always indicated in the diagrams by shading, it is given as the average of the mean values of both sexes. In this way, it more closely approaches the theoretical 1:1 distribution of females and males than the mean value of the total population.

When relations of the shell size of the different populations of one species to other parameters will be analyzed, the minor diameter is preferred over the shell height, because it is better correlated to the volume (shown for *Helicina funcki*, Fig. 30). The latter would display the size best, but the volume is normally not available for all populations.

Habitat: The description of the habitat is nearly exclusively based on the author's own field observations.

Distribution: In addition to the description, for the distribution within Costa Rica a detailed map is provided based on all records critically revised and the material studied. The sources of the localities will be indicated divided into recent collections (IR, INBio), and literature records and the other material examined.

Discussion: Here, mainly the taxonomical problems of each species will be discussed. For broader aspects, see the general Discussion.

REVISION OF THE COSTA RICAN HELICINIDAE

The following species are recognized for Costa Rica:

Helicina (*Tristramia*) *funcki* L. Pfeiffer, 1849
Helicina (*Tristramia*) *pitalensis* Wagner, 1910
Helicina (*Tristramia*) *tenuis* L. Pfeiffer, 1849
***Helicina* (*Tristramia*) *echandiensis* n. sp.**
***Helicina* (*Tristramia*) *punctisulcata cuericiensis* n. subsp.**
Helicina (*"Gemma"*) *beatrix beatrix* Angas, 1879
Helicina (*"Gemma"*) *beatrix confusa* (Wagner, 1908)
***Helicina* (*"Gemma"*) *beatrix riopejensis* n. subsp.**

Helicina (*"Gemma"*) *talamancensis* (Richling, 2001)
Helicina (*"Gemma"*) *gemma* Preston, 1903
***Helicina* (*"Gemma"*) *monteverdensis* n. sp.**
***Helicina* (*"Gemma"*) *escondida* n. sp.**
Helicina (*"Gemma"*) *chiquitica* (Richling, 2001)
Pyrgodomus microdinus (Morelet, 1851)
Alcadia (*Microalcadia*) *hojarasca* (Richling, 2001)
Alcadia (*Microalcadia*) *boeckeleri* (Richling, 2001)
Lucidella (*Perenna*) *lirata* (L. Pfeiffer, 1847)
Questionable:
Helicina (*Oligyra*) *flavida* Menke, 1828

Helicina (*Tristramia*) *funcki*
L. Pfeiffer, 1849

Helicina funcki L. Pfeiffer, 1849: 121 (not figured)
Helicina funcki – L. Pfeiffer, 1850: 33, pl. 9, figs. 1, 2
Helicina funcki – L. Pfeiffer, 1852a: 361
Helicina tuncki [sic] – L. Pfeiffer, 1852b: 261–262
Helicina funckii [sic] – Sowerby, 1866: 288, pl. 273, fig. 271
Helicina funcki – Bland, 1866: 9
Helicina funcki – Reeve, 1874: pl. 17, fig. 152
Helicina funki [sic] – Angas, 1879: 484, pl. XL, fig. 7 (living animal): Costa Rica: Talamanca, all the coast region, and to the lower hills (Gabb)
Helicina funcki – von Martens, 1890: 33: Costa Rica: Talamanca, all the coast region, and to the lower hills (Gabb); Cache [Cachí? 09°50'N, 83°48'W, Cartago Province] (Rogers)
Helicina funcki var. a, b – Biolley, 1897: 4–5: Costa Rica: San Miguel, Sarapiqui, 200 m [about 10°19'N, 84°11'30"W, Alajuela Province], Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province]
Helicina funcki var. c, d – Biolley, 1897: 4–5: Costa Rica: Azahar de Cartago, 1,500 m, Tarbaca, 1,600 m [09°49'25"N, 84°06'39"W, San José Province]
Helicina funcki – Ancey, 1897: 87: E-Nicaragua: Greytown, N-Panama: Monkey Hill, near Colon (leg. Aillaud)
Helicina funcki – von Martens, 1900: 603-604: E-Nicaragua: Greytown; NE-Costa Rica: San Miguel, valley of the Sarapiqui, 200 m [about 10°19'N, 84°11'30"W, Alajuela Province]; Puerto Viejo [about 10°28'N, 84°00'30"W, Heredia Province] (Biolley), on the borders of the Río San Juan [along borderline to Nicaragua in Alajuela, Heredia, Limón provinces, cannot be specified] (Pittier), E-Costa Rica: Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] (Biolley, Pittier); Turrialba, 750 m [about 09°54'30"N, 83°41'W, Cartago Province] (Biolley), central Costa Rica: Azahar de Cartago [not clear, if referring to the town Cartago, ?about 09°52'N, 83°55'W, Cartago Province] and Tarbaca, 1,500-1,600 m [09°49'25"N, 84°06'39"W, San José Province], only the smaller varieties (Biolley); N-Panama: Monkey Hill, near Colon [in part]
Helicina (*Retorquata*) *funcki* – Wagner, 1905: 232-233
Helicina (*Retorquata*) *funcki costaricensis* Wagner, 1905: 233, pl. XIII, fig. 12 a–c: Costa Rica ("von San José [14 km NW of Upala, about 10°58'N, 85°08'W, Alajuela Province] in Costarica besitze ich Exemplare dieser Form, welche größer und einfarbig weiß sind, ferner ¼ bis ½ Umgang mehr aufweisen")
Helicina fucki [sic] – Wagner, 1910a: 306307, pl. 61, figs. 11–15: Neu Granada (obviously only in part of Panama), Costa Rica: Azachar Centajo, Tarbaca
Helicina funcki costaricensis – Wagner, 1910a: 307, pl. 61, fig. 16: Costa Rica: St. José [see above] and Sta. Clara [7.5 km NW of Upala, about 10°56'N, 85°05'W, Alajuela Province]; "eine ähnliche Form, jedoch mit deutlicher Kante am letzten Umgang und höherem Gewinde liegt in meiner Sammlung mit der Fundartsangabe Ylalag in Mexico"
Helicina funcki – Pilsbry, 1910: 503: Panama: Canal Zone: Tabernillo (Brown)
Helicina funcki – Pilsbry, 1920a: 3: Costa Rica: Guapiles, 980 ft. [about 10°14'N, 83°47'W, Limón Province] (Calvert)
Helicina deppeana parvidens Pilsbry, 1920a: 3 (not figured): Costa Rica: Juan Viñas, farther waterfall, 3300 ft., also on the road to Río Reventazon, 3000 ft. [about 09°54'N, 83°44'30"W, Cartago Province] (Calvert)
Helicina (*Tristramia*) *funcki funcki* – Baker, 1922a: 51
Helicina (*Tristramia*) *funcki parvidens* – Baker, 1922a: 51
Helicina (*Tristramia*) *funcki costaricensis* – Baker, 1922a: 51
Helicina funcki – Pilsbry, 1926a: 59, 69, 71, fig. 3C: Panama: Escobal on Gatun Lake (Chapin), Bocas del Toro Province: Mono Creek (Olsson), Gatun (Harrower), Canal

Zone: Barro Colorado Island and near Darien (Zetek)

Helicina funcki – Pilsbry, 1926b: 127: Costa Rica: Talamanca Valley, < 100 ft. [approximately 09°34'N, 83°W, not specified, Limón Province] (Olsson)

Helicina (*Tristramia*) *funcki* – Baker, 1926: 42: Panama: Gatun, Canal Zone (Harrower), pl. V fig. 8, pl. VI, fig. 9 (female and male reproductive system)

Helicina funcki – Pérez, 1994: 746: Costa Rica: La Selva [about 10°26'N, 84°W, Heredia Province]

Helicina funki [sic] – Monge-Nájera, 1997: 113: Costa Rica

Helicina funcki – Robinson, 1999: 434: USA: sometimes mistakenly imported

Synonymy

Helicina funcki costaricensis Wagner, 1905
Helicina deppeana parvidens Pilsbry, 1920

Original Description

"Hel. testa conico-subglobosa, tenuiuscula, sub lente tenuissime oblique striatula, vix nitidula, flavida, roseo-nebulosa; spira conoidea, obtusiuscula; anfractibus 5,5 planiusculis, ultimo utrinque convexiore, obsolete angulato; apertura obliqua, semiovali; columella subarcuata, linea impressa verticali notata, basi subnodosa, in callum sensim tenuiorem retrorsum abiente; peristomate late expanso, margine supero subrepando.
Diam. 13,5, altit. 9 mill.
From San Yago, New Granada (Funck)."

Type Material

BMNH 20010497.1–4: Santiago, New Granada, Funk, H. Cuming collection

The type lot contains four similar specimens. The shell that is slightly larger than the other three is **herein selected as lectotype** of *Helicina funcki* (Fig. 10). It shows the traces of some lead pencil painting which could have been applied to the specimen as a drawing aid, probably reflected in the dark shading visible in the figure in L. Pfeiffer (1850: pl. 9, figs. 1, 2). Furthermore, it is the only specimen that attains 13.5 mm in its greatest extension (not perpendicular to the shell axis). The height given in the original description cannot be attributed to a conventional adjustment of the shell. The specimen is yellowish, and the reddish tinge is barely visible, whereas it is well developed in the three paralectotypes in the second half of the body whorl between suture and the periphery.
Dimensions:
Lectotype BMNH 20010497.1:
10.6/11.9/13.2/10.7/7.9/8.8/8.2 mm
Paralectotypes BMNH 20010497.2–4:
10.1/11.5/12.6/10.2/7.3/8.3/7.7 mm
10.0/11.0/12.4/10.0/7.1/8.2/7.6 mm
10.0/11.1/12.4/10.1/7.4/8.2/7.9 mm

Type Locality

"San Yago, New Granada", this most probably refers to Santiago, which today belongs to Panama, Veraguas Province.

Type Material of Synonymous Taxa or Similar Species

Helicina funcki costaricensis Wagner, 1905

Type Material: MIZ 8989: Costa Rica, Sta. Clara, 250 m alt., Biolley legit
In the original description Wagner gives Costa Rica as the origin of the new subspecies and mentions additional specimens from San

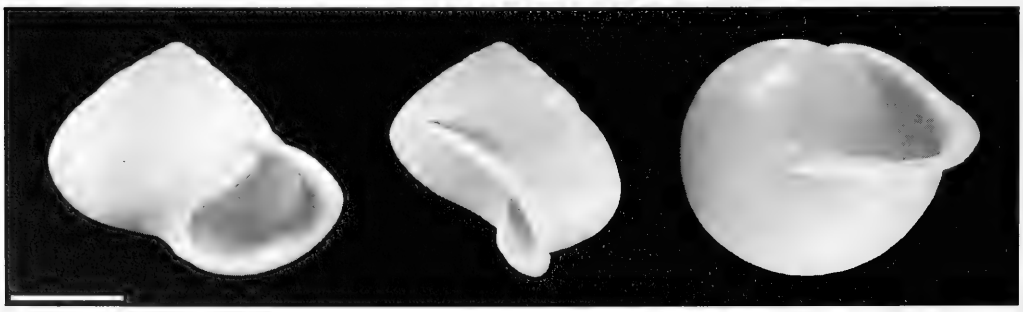


FIG. 10. *Helicina funcki*, lectotype, BMNH 20010497.1, height 10.6 mm; scale bar 5 mm.

José, which are said to be of greater size and of uniformly white color, the description being obviously based on further unspecified material. In his collection stored in the MIZ, there are two lots: the typical one with the locality mentioned later (Wagner, 1910a), as given above and the one from San José. The syntypes MIZ 8989 consist of two specimens, a yellowish-greenish one and a reddish tinged one. In comparing the figures in Wagner (1905, 1910a), it is obvious that different specimens were illustrated: the later figure shows a yellowish-greenish specimen somewhat more elevated and with a more strongly developed denticle at the transition of the outer lip into the columella. Thus, the reddish specimen was first to be depicted and has therefore been **selected here as lectotype** (Fig. 11). It displays a slight crack in the last whorl which, however, did not result in any deformation or damage in the shell. The specimen was dead collected, whereas the paralectotype was collected alive, complete with its operculum.
Dimensions:
Lectotype MIZ 8989a:
12.0/13.2/14.6/11.8/8.7/9.7/9.3 mm
Paralectotype MIZ 8989b:
12.3/13.1/14.6/11.9/8.9/10.1/9.5 mm

Type Locality: "Costa Rica"; restricted by type selection to Sta. Clara, 250 m a.s.l. [7.5 km NW of Upala, about 10°56'N, 85°05'W, Alajuela Province]
"Santa Clara" is a name used for various localities in Costa Rica. Biolley mentions it several times as a collecting site, also "Delicias near Santa Clara" and a "San José" (see "Discussion" for *Helicina funcki costaricensis*) that is definitively not the capital. This combination suggests the identification with the village of Santa Clara near Upala, because Las Delicias and San José are nearby. The exact altitude of Santa Clara is 40 m, but it is known that in former times (personal communication with Zaidett Barrientos) the whole region was called "Llanuras de Santa Clara" [plains of ...]. Therefore, in case it was not just an inaccurate measurement of the altitude, it is likely that the specimens were collected a little to the southeast of the village approaching the Cordillera de Guanacaste.

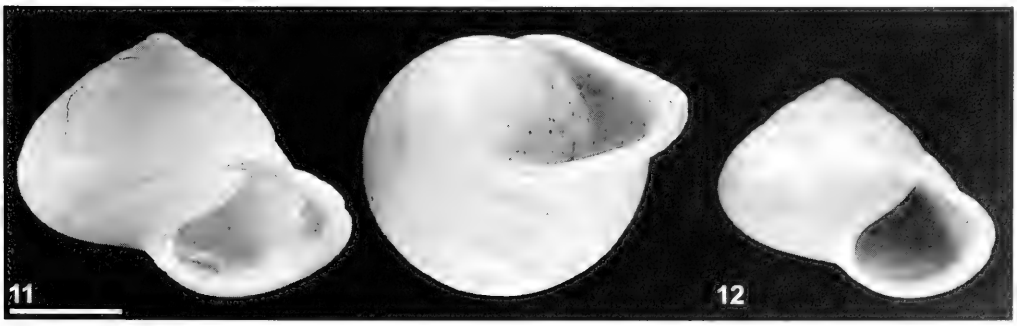
Helicina deppeana parvidens Pilsbry, 1920

Type Material: Holotype ANSP 105286 (Fig. 12), Paratype ANSP 105252 (original designation)

Type Locality: Costa Rica: "Juan Viñas, farther waterfall, 3300 ft." [about 09°54'N, 83°44'30"W, Cartago Province]

Examined Material

Leg. I. Richling
Guanacaste: *N Santa Elena*: *Reserva Sta. Elena, Sendero Río Negro, about 10°20'31"N, 84°47'53"W, 1,550 m a.s.l.*: 14.08.1999: (IR 924); *Sendero at Mirador Gerardo, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l.*: 14.08.1999: (IR 928); 19.02.2000: (IR 1230)
N of Nuevo Arenal: *area of primary rain forest, 10°33'32"N, 84°51'40"W, 800 m a.s.l.*: 05.03.1999: (IR 737); *"Las Pavas" (private reserve in preparation), secondary rain for-*



FIGS. 11–12. *Helicina* spp. FIG. 11. *Helicina funcki costaricensis*, lectotype, MIZ 8989a, height 12.0 mm; scale bar 5 mm. FIG. 12. *Helicina deppeana parvidens*, holotype, ANSP 105286, height 10.0 mm; scale bar 5 mm (photograph: D. Robinson).

est, about 10°33'30"N, 84°51'53"W, 800 m a.s.l., to 10°33'26"N, 84°51'57"W, 760 m a.s.l.: 05.03.1999: (IR 742); 17.08.1999: (IR 952): 24.02.2000: (IR 1273); (IR 1331); 03.2001: (IR 1637)

NW Nuevo Arenal, "Eco Lodge", Sendero Cabana, about 10°34'37"N, 84°55'35"W, 750 m a.s.l., 18.08.1999: (IR 955)

Parque Nacional Rincón de Vieja: *trail from Aquas calientes to Las Pailas, about 10°46'00"N, 85°19'13"W, 800 m a.s.l.*: 20.08.1999: (IR 972); *E Casona Sta. Maria, trail to Canal, 10°45'57"N, 85°17'06"W, 750 m a.s.l.*: 21.08.1999: (IR 979)

Alajuela: *Near Volcán Arenal*, trail along volcano in rainforest, about 10°29'07"N, 84°42'55"W, 720 m a.s.l.: 24.02.1998: (IR 390); 01.08.1999: (IR 884); on Heliconiaceae, 25.02.2000: (IR 1286)

Heredia: *S Puerto Viejo de Sarapiqui*, Zona Protectora La Selva, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1061); 06.09.1999: (IR 1062); 13.02.2000: (IR 1182); (IR 1184)

Limón: *Parque Nacional Cahuita, trail from Cahuita to Puerto Vargas, coastal forest with coco palms and swampy areas*: *09°44'01"N, 82°49'48"W, 1–5 m a.s.l.*: 11.03.1997: (IR 107); (IR 106); (IR 108); *about 09°43'27"N, 82°50'28"W, 4 m a.s.l.*: 10.03.1999: (IR 757); 07.08.1999: (IR 897); 08.08.1999: (IR 898); 04.03.2000: (IR 1312); 14.03.2001: (IR 1555), (IR 1630), (IR 1639); 15.03.2001: (IR 1557), (IR 1648); *09°43'13"N, 82°50'39"W, 4 m a.s.l.*: 13.09.1999: (IR 1095); *near Puerto Vargas, 09°42'49"N, 82°49'20"W, 1 m a.s.l.*: 08.08.1999: (IR 907)

Refugio Nacional de Fauna Silvestre Gandoca-Manzanillo, *S Manzanillo*, trail along coast line to S, coastal forest, about 09°38'06"N, 82°38'26"W, 50 m a.s.l., 14.9.1999: (IR 1096); 5.3.2000: (IR 1320); (IR 1322); (IR 1642)

Near Cruce Penshurt, mouth delta of Río Estrella, Aviarios del Caribe, about 09°48'30"N, 82°54'W, 20 m a.s.l., 09.08.1999: (IR 912)

About 9 km W of Matina, road Limón to Siquirres, a little stream up *Río Barbilla*, small banana plantation, about 10°03'29"N, 83°22'24"W, 70 m a.s.l., 12.03.2001: (IR 1545)

S Siquirres, road Limón to Siquirres, along footpath stream up *Río Pacuarito*, 10°05'38"N, 83°28'11"W, 110 m a.s.l., 18.03.2001: (IR 1612); (IR 1613)

Siquirres, along footpath stream up *Río Siquirres* and along a southern tributary, 10°05'37"N, 83°30'32"W, 100 m a.s.l., 11.03.2001: (IR 1623); 19.03.2001: (IR 1617)

W Guayacán, abandoned banana plantation, 10°01'53"N, 83°32'14"W, 520 m a.s.l., 03.09.1999: (IR 1079); (IR 1080); 12.09.1999: (IR 1090): 17.03.2001: (IR 1608)

W Liverpool, Mexico: *near Río Blanco, 09°56'37"N, 83°09'41"W, 35 m a.s.l.*: 13.03.1997: (IR 150); *near Río Blanco, abandoned area with bananas and some old trees, 09°58'32"N, 83°08'32"W, 35 m a.s.l.*: 14.02.1998: (IR 274): 21.02.1999: (IR 627); *footpath along small creek and through bush, 09°59'04"N, 83°08'04"W, 40 m a.s.l.*: 16.02.2000: (IR 1191); 22.02.2001: (IR 1406); (IR 1408)

S Liverpool: *near Río René, swampy area and forest, 09°57'33"N, 83°08'15"W, 20 m a.s.l.*: 13.03.1997: (IR 148); (IR 140); *along Río Victoria, 09°56'01"N, 83°10'24"W, 80 m a.s.l.*: 05.03.1998: (IR 465)

SW Liverpool: *Río Quito, at bridge, 09°57'11"N, 83°10'37"W, 40 m a.s.l.*: 04.03.1998: (IR 448); *E of Río Peje, forest on little hill, 09°57'46"N, 83°13'26"W, 270 m a.s.l.*: 12.03.1997: (IR 131); *Río Peje and small tributary, 09°56'35"N, 83°14'01"W, 110 m a.s.l.*: 12.03.1997: (IR 126); (IR 127); *Río Peje, bordering forest, 09°56'23"N, 83°14'06"W, 160 m a.s.l.*: 09.03.1999: (IR 753); *along Río Peje, bordering forest with palms, 09°55'46"N,83°13'15"W, 135 m a.s.l.*: 04.03.1998: (IR 441); 09.03.1999: (IR 751); 03.03.2000: (IR 1300); (IR 1302); 13.03.2001: (IR 1552)

N Shiroles: *along Quebrada Kirio, 09°35'38"N, 82°57'20"W, 100 m a.s.l.*: 12.03.1999: (IR 763); 09.08.1999: (IR 911); 16.03.2001: (IR 1596); (IR 1644); *Cerro Mirador, along trail, 09°36'37"N, 82°57'43"W, 430 m a.s.l.*: 16.03.2001: (IR 1599)

W Bribri, road to Uatsi, about 09°38'11"N, 82°51'48"W, 30 m a.s.l.: *abandoned field with Heliconiaceae and Eucalyptus*: 12.03.1999: (IR 766); 15.09.1999: (IR 1114); *wooded valley within banana plantation, 50 m a.s.l.*: 15.3.2001: (IR 1572); *at crossing with Río Carbón, 30 m a.s.l.*: 17.3.1997: (IR 183);

W Uatsi, along Río Uatsi, 09°37'30"N, 82°53'30"W, 60 m a.s.l., 15.03.2001: (IR 1632)

Zona Protectora Tortuguero, near Tortuguero, about 10°34'N, 83°31'W, 10 m a.s.l.: *Sendero Ranita*: 10.3.2000: (IR 1348); *N of village*: 16.03.2001: (IR 1620); 21.03.2001: (IR 1653)

Cartago: W Turrialba, *near Catie*, forest along road Turrialba to Siquirres, 09°53'01"N, 83°39'17"W, 610 m a.s.l., 15.03.2000: (IR 1350)

Puntarenas: *Near Monteverde, about 10°17'24"N, 84°48'04"W: small piece of forest along road to reserve, 1,330 m a.s.l.*: 27.02.1997: (IR 22); *1 km before entrance on road to reserve, 1,500 m a.s.l.*: 26.07.1999: (IR 826); 1999: (IR 1391); 13.8.1999: (IR 927); *Bosque de los Niños, 10°17'59"N, 84°48'44"W, 1,380 m a.s.l.*: 29.07.1999: (IR 860)

Zona Protectora Arenal-Monteverde: *Reserva Biológica Bosque Nuboso Monteverde (about 10°18'08"N, 84°47'41"W, 1,500–1,650 m a.s.l.)*: 27.07.1999: (IR 843); 18.02.2000: (IR 1194); (IR 1199); (IR 1627): *Sendero Bosque Nuboso*: 25.02.1997: (IR 14); 24.02.1999: (IR 628); *Sendero Roble*: 18.02.1998: (IR 301); *Sendero Chomogo*: 25.02.2001: (IR 1435)

Monteverde, Cerro Plano, *Finca Ecologica*, Sendero Mirador, 10°18'47"N, 84°49'30"W, 1,330 m a.s.l., 25.02.1999: (IR 651); 28.07.1999: (IR 859); 15.08.1999: (IR 946); 20.02.2000: (IR 1246)

About 4 km N Santa Elena, Skywalk, 10°18'33"N, 84°49'42"W, 1,330 m a.s.l., 20.02.1998: (IR 332)

INBio Collection

Guanacaste: Zona Protectora Arenal-Monteverde: *Santa Elena*, sendero Encantado, 10°21'57"N, 84°47'27"W, 1,200 m a.s.l., leg. Kattia Martinez, 21.06.1996: 8 ads. (INBio 1498638)

Zona Protectora Tenorio: Río San Lorenzo, Tierras Morenas, 10°36'38"N, 84°59'42"W, 1,050 m a.s.l., leg. Gladys Rodriguez, 28.10.1995: 1 ad. (INBio 1485411); Tenorio, Alrededores de la estación, 10°36'51"N, 85°00'07"W, 900 m a.s.l., leg. Gladys Rodriguez, 18.09.1996: 1 ad. (INBio 1498593)

Parque Nacional Rincón de la Vieja: *Sector Las Pailas*: 4.5 km SW del Volcán Rincón de la Vieja, 10°46'36"N, 85°21'07"W, 800 m a.s.l., leg. malacological staff of INBio, 09.12.1992: 1 ad. (INBio 1466644); sendero Pailas, 10°46'36"N, 85°21'07"W, 800 m a.s.l., leg. Karla Taylor, 23.08.1995: 3 ads., 1 s.ad. (INBio 1498739); *Sector Santa María*: 10°45'58"N, 85°18'19"W, 800 m a.s.l., leg. Dunia Garcia, 14.10.1995: 1 ad. (INBio 1487945); sendero Bosque Encantado, 10°46'36"N, 85°21'07"W, 800 m a.s.l., leg. Karla Taylor, 23.08.1995: 1 ad. (INBio 1498744)

Parque Nacional Guanacaste: *Estación Góngora, 10°53'22"N, 85°28'33"W, 580 m a.s.l.*: leg. Zaidett Barrientos, 11.02.1994: 2 ads. (INBio 1480300); leg. Dunia Garcia, 20.10.1994: 1 juv. (INBio 1478682); 2 juvs. (INBio 1478739); 2 ads. (INBio 1483409); leg. Dunia Garcia, 28.10.1994: 1 ad. (INBio 1480475); leg. Dunia Garcia, 08.03.1995: 1 ad. (INBio 1488083); leg. Dunia Garcia, 28.06.1995: 1 ad., 3 juvs. (INBio 1484993); *Sector Góngora [río Góngora], 10°53'22"N, 85°28'33"W, 580 m a.s.l.*: leg. Kattia Martinez, 26.05.1995: 1 juv. (INBio 1498514)

Parque Nacional Guanacaste: Sector Orosi (antes: Maritza), sendero Casa Fram, 10°57'40"N, 85°29'45"W, 600 m a.s.l., leg. Zaidett Barrientos, 15.07.1996: 3 ads. (INBio 1494681); Río Tempisquito, 10°57'45"N, 85°29'05"W, 600 m a.s.l., leg. Dunia Garcia, 08.03.1996: 1 juv. (INBio 1488078)

Parque Nacional Guanacaste: *La Cruz, 9 km S de Santa Cecilia, Estación Pitilla*: *10°59'25"N, 85°25'38"W, 700 m a.s.l.*: leg. Petrona Rios, 09.12.1994: 1 ad. (INBio 1480289); Lado S del Río Orosí, leg. Calixto Moraga, 16.08.1994: 3 ads. (INBio 1480319); leg. Calixto Moraga, 23.08.1994: 1 ad. (INBio 1480318); *10°59'33"N, 85°25'46"W, 700 m a.s.l.*: leg. malacological staff of INBio, 08.01.1993: 1 ad. (INBio 1463787); leg. Calixto Moraga, 10.07.1993: 1 juv. (INBio 1467560); *Sendero Nacho, 10°59'33"N, 85°25'46"W, 700 m a.s.l.*: leg. malacological staff of INBio, 13.10.1993: 1 ad. (INBio 1463946); *Sendero Mena, 400 m W de la Estación Pitilla, 10°59'25"N, 85°25'51"W, 700 m a.s.l.*: leg. Calixto Moraga, 09.01.1994: 1 ad. (INBio 1480043); *Fila Orosilito, 10°59'02"N, 85°26'01"W, 900 m a.s.l.*: leg. Calixto Moraga, 20.04.1994: 1 ad. (INBio 1480329); *Finca del Estado*: *Casa de Roberto, 11°00'09"N, 85°25'33"W, 600 m a.s.l.*: leg. Calixto Moraga, 22.08.1994: 1 s.ad. (INBio 1480342)

La Esperanza, 6 km E de Santa Cecilia de la Cruz, 11°00'42"N, 85°22'45"W, 400 m a.s.l., leg. Calixto Moraga, 09.01.1994: 1 ad. (INBio 1480050)

Alajuela: *Reserva Biológica Los Angeles*, 7 km NE de los Angeles Norte de San Ramón, 10°12'12"N, 84°29'10"W, 1,100 m a.s.l., leg. Zaidett Barrientos, 06.11.1995: 1 ad., 2 s.ads. (INBio 1482570)

Reserva Biológica San Ramón, 10°13'30"N, 84°35'17"W, 800 m a.s.l.: leg. malacological

staff of INBio, 15.02.1994: 1 ad. (INBio 1477816); leg. Gerardo Carballo, 10.07.1994: 1 ad. (INBio 1476150); Sendero Liz, leg. Gerardo Carballo, 08.08.1994: 1 ad. (INBio 1476214)

Sector Colonia Palmareña, 10°14'09"N, 84°33'15"W, 700 m a.s.l., leg. Eida Fletes, 13.04.1995: 1 ad. (INBio 1485385)

Zona Protectora Arenal-Monteverde: *Sector Alemán, Finca dos Ases, 10°17'56"N, 84°46'08"W, 1,140 m a.s.l.*: leg. Zaidett Barrientos, 13.10.1994: 1 ad. (INBio 1468276); leg. Kattia Martinez, 04.12.1995: 2 ads. (INBio 1485227); *Sendero Alemán, 10°17'59"N, 84°45'38"W, 1,080 m a.s.l.*: leg. Kattia Martinez, 18.08.1994: 1 ad. (INBio 1480101); 19.08.1994: 1 ad. (INBio 1478523); *Sector Peñas Blancas, Estación Alemán, 10°18'09"N, 84°44'52"W, 900 m a.s.l.*: leg. Kattia Martinez, 11.10.1994: 2 ads. (INBio 1498802); 11.12.1994: 1 ad. (INBio 1480605)

Parque Nacional Guanacaste-Rincón de la Vieja, *Estación San Cristóbal*, 10°52'55"N, 85°23'26"W, 600 m a.s.l.: leg. Dunia Garcia, 08.01.1995: 5 ads., 2 s.ads. (INBio 1488065); leg. malacological staff of INBio, 18.08.1995: 8 ads., 5 s.ads. (INBio 1498494)

Sector las Cubas, Bosque Urbina, 10°53'41"N, 84°47'20"W, 40 m a.s.l., leg. Kattia Martinez, 25.04.1994: 1 ad. (INBio 1466940)

Caño Negro: *Veracruz, 10°50'22"N, 84°52'52"W, 35 m a.s.l.*: leg. Kattia Flores, 14.02.1997: 1 juv. (INBio 1487125); *Finca Delicias, 10°54'01"N, 84°47'20"W, 35 m a.s.l.*: leg. Kattia Flores, 14.12.1996: 1 ad. (INBio 1487043); 01.11.1997: 1 ad. (INBio 1487611); *en el Pueblo, 10°53'38"N, 84°47'20"W, 35 m a.s.l.*: leg. Kattia Flores, 09.10.1994: 1 ad. (INBio 1480029); 07.04.1995: 5 ads. (INBio 1501040)

Refugio Nacional de Vida Silvestre Caño Negro: Caño Negro, San Antonio, Finca Juan Cubano 2, 10°54'50"N, 84°45'12"W, 35 m a.s.l., leg. Kattia Flores, 16.11.1996: 1 ad. (INBio 1487878)

Monte Cele, sendero La Tepezcuintle, 10°57'27"N, 85°24'20"W, 700 m a.s.l., leg. Dunia Garcia, 09.09.1995: 4 ads. (INBio 1488042)

Estación Playuelas, 50 m del Río Frío, 10°57'29"N, 84°44'55"W, 40 m a.s.l., leg. Kattia Martinez, 08.01.1994: 4 ads. (INBio 1479506)

Sector Playuelas, 10°57'29"N, 84°45'15"W, 35 m a.s.l.: leg. Kattia Martinez, 21.08.1996: 2 ads. (INBio 1498571); leg. Kattia Flores, 08.11.1996: 1 ad. (INBio 1487809)

Heredia: *Frente al bosque de la hoja*, 10°04'13"N, 84°05'40"W, 1,800 m a.s.l., leg. Zaidett Barrientos, 14.05.2000: 1 ad. (INBio 3562231)

Limón: *Reserva Indígena Talamanca*: *Sector Amubri, 09°30'53"N, 82°57'19"W, 70 m a.s.l.*: 14.06.1994: 1 ad. (INBio 1477585); 15.06.1994: 1 ad. (INBio 1477569); 26.09.1994: 1 ad. (INBio 1483302); 4 s.ads. (INBio 1483303); 1 juv. (INBio 1483376); 1 ad. (INBio 1483382); 1 s.ad. (INBio 1483388); 2 ads. (INBio 1483392); 1 ad. (INBio 1483407); 2 s.ads. (INBio 1483408); 27.09.1994: 1 ad. (INBio 1483381); 1 ad. (INBio 1483389); 2 s.ads. (INBio 1483402); 29.09.1994: 2 s.ads. (INBio 1483403); 1 ad. (INBio 1483394): 30.09.1994: 2 s.ads. (INBio 1483395); 2 s.ads. (INBio 1483401); 18.10.1994: 1 ad. (INBio 1483390); 1 ad. (INBio 1483386); 19.10.1994: 1 s.ad. (INBio 1483383); 1 ad. (INBio 1483387); 1 s.ad. (INBio 1483396); 27.11.1994: 1 ad. (INBio 1483398); 28.11.1994: 1 s.ad. (INBio 1483378); 1 s.ad. (INBio 1483385); 29.11.1994: 1 s.ad. (INBio 1483397); 30.11.1994: 1 ad. (INBio 1483400) (all leg. Gerardina Gallardo); *Amubri, Sendero Soki, 09°30'53"N, 82°57'19"W, 70 m a.s.l.*: leg. Angela Mora Maroto, 17.04.1995: 1 ad. (INBio 1484735); leg. Gerardina Gallardo, 17.05.1994: 4 ads. (INBio 1467294); 4 ads. (INBio 3395382); leg. Angela Mora Maroto, 22.04.1995: 3 ads. (INBio 1485382); leg. Angela Mora Maroto, 04.08.1995: 1 ad. (INBio 1485365); leg. Gerardina Gallardo, 27.11.1996: 3 ads., 1 s.ad. (INBio 1493444)

Reserva Indígena Talamanca: *Cerca Río Lari, 09°32'57"N, 82°58'25"W, 80 m a.s.l.*: leg. Gerardo Carballo, 17.06.1994: 1 ad. (INBio 1476073); *Suirí, orillas del Rio Telire, 09°33'56"N, 82°55'50"W, 30 m a.s.l.*: leg. Gerardina Gallardo, 25.11.1996: 1 ad., 2 s.ads. (INBio 1487336)

Reserva Biológica Hitoy Cerere: *Sector Miramar*: *09°38'03"N, 83°00'45"W, 300 m a.s.l.*: leg. Zaidett Barrientos, 08.10.1994: 1 ad. (INBio 1475720); 1 ad. (INBio 1475725); *Senderos a Río Moín, 09°37'44"N, 83°00'32"W, 150 m a.s.l.*: leg. Zaidett Barrientos, 08.11.1994: 2 juvs. (INBio 1475228); 1 ad. (INBio 1475234); *Hitoy Cerere, 09°37'50"N, 83°00'52"W, 300 m a.s.l.*: leg. Gerardo Carballo, 12.05.1994: 3 ads., 1 s.ad. (INBio 1476376); leg. Gerardo Carballo, 13.06.1994: 4 ads. (INBio

1476490); leg. Gerardo Carballo, 04.07.1994: 2 ads. (INBio 1475694); leg. Marianella Segura, 07.12.1994: 1 ad. (INBio 1480272); *Sendero Moín, 09°37'50"N, 83°00'52"W, 300 m a.s.l.*: 14.01.1994: 3 ads. (INBio 1475930); 27.02.1994: 1 ad. (INBio 1476687); 1 ad. (INBio 1476688) (all leg. Gerardo Carballo)

Reserva Biológica Hitoy Cerere: *Cruce entre Sendero Revienta Pechos y Sendero Espavel, 09°39'12"N, 83°00'58"W, 600 m a.s.l.*: leg. Alexander Alvarado Mendez, 24.04.1999: 1 ad. (INBio 1497851); *Sector Hitoy Cerere, Sendero Catarata, 09°40'18"N, 83°01'45"W, 100 m a.s.l.*: leg. Gerardo Carballo, 22.02.1994: 1 ad. (INBio 1476262); *Sendero Tepezcuintle, 09°40'22"N, 83°01'40"W, 140 m a.s.l.*: 25.04.1999: 2 ads. (INBio 1497862); 2 ads. (INBio 3090624); 05.07.1999: 1 ad. (all leg. Alexander Alvarado Mendez) (INBio 1497905); *Sendero Bobócara, 09°40'31"N, 83°00'31"W, 200 m a.s.l.*: leg. malacological staff of INBio, 10.01.1993: 1 ad. (INBio 1466444); *Sendero Toma de Agua, 09°40'31"N, 83°01'36"W, 100 m a.s.l.*: 20.04.1994, leg. Zaidett Barrientos: 2 ads. (INBio 1473832); leg. Gerardo Carballo: 1 ad. (INBio 1476246); leg. Zaidett Barrientos, 08.09.1994: 1 ad. (INBio 1475438); *Estación Hitoy Cerere, 09°40'35"N, 83°01'36"W, 100 m a.s.l.*: leg. malacological staff of INBio, 15.11.1993: 3 ads. (INBio 1463392); *400 m NE de la Estación de Hitoy Cerere, Sendero la "Finca", 09°40'35"N, 83°01'26"W, 110 m a.s.l.*: 03.06.2000: 1 ad. (INBio 3098418); 20.07.1999: 1 s.ad. (INBio 1497844); 27.09.2000: 2 ads. (INBio 3091789) (all leg. Alexander Alvarado Mendez); *Sendero Chato*: 09°40'41"N, 83°01'26"W, 100 m a.s.l., leg. Marianella Segura, 14.07.1994: 1 s.ad. (INBio 1478197)

Refugio Nacional de Vida Silvestre Gandoca-Manzanillo: *Sector Gandoca, Camino a Gandoca, 09°38'04"N, 82°38'37"W, 10 m a.s.l.*: 28.04.1999: 5 juvs. (INBio 3097941); *Sector Manzanillo*: 1 km S de la escuela, 09°37'31"N, 82°39'36"W, 4 m a.s.l., 02.02.2000: 2 ads. (INBio 3097906); Camino a Gandoca, 09°38'13"N, 82°38'40"W, 100 m a.s.l., 28.01.2000: 2 ads. (INBio 3097895); Sendero a Gandoca, 09°38'04"N, 82°38'43"W, 8 m a.s.l., 04.02.2000: 2 s.ads. (INBio 3097899) (all leg. Alexander Alvarado Mendez)

1 km S de Punta Cocles, 09°38'17"N, 82°43'25"W, 40 m a.s.l., leg. Zaidett Barrientos, 20.08.1996: 1 ad., 1 juv. (INBio 1487850)

Parque Nacional Cahuita: *Sector Cahuita*: 800 m E de la Casetilla, 09°44'00"N, 82°49'57"W, 10 m a.s.l., 05.11.1999: 1 s.ad., 1 juv. (INBio 3096430); *Sector Puerto Vargas*: Sendero a Cahuita, 09°43'43"N, 82°49'11"W, 0 m a.s.l., 01.09.1999: 3 ads. (INBio 3095846); 600 m E de la Casetilla, 09°42'54"N, 82°48'58"W, 8 m a.s.l., 27.09.2000: 1 juv. (INBio 3091796) (all leg. Alexander Alvarado Mendez)

Isla Uvita, frente al muelle de Limón, 09°59'45"N, 83°00'50"W, 5 m a.s.l., leg. Alexander Alvarado Mendez, 11.10.2000: 2 ads., 1 juv. (INBio 3315386)

Zona Protectora Río Pacuare: 1.3 km NW de la Estación Barbilla, 09°59'25"N, 83°28'04"W, 500 m a.s.l., leg. Alexander Alvarado Mendez, 02.11.2000: 1 ad. (INBio 3315302)

Reserva Indígena Barbilla-Dantas: Sector Colonia Puriscaleña, 10°00'17"N, 83°23'02"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 03.03.2000: 2 juvs. (INBio 3098016)

Sector Guápiles: 10°11'51"N, 83°51'22"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 08.03.2000: 2 ads., 1 s.ad. (INBio 3097950)

Orillas del río Aguas Frías, 10°24'05"N, 83°35'60"W, 10 m a.s.l.: leg. Elias Rojas, 29.11.1996: 3 ads. (INBio 1487980)

Finca Montaña Grande, 10°31'39"N, 83°43'33"W, 10 m a.s.l.: *400 m N de la estación, a orillas de la quebrada*: 13.09.1993: 3 ads. (INBio 1498610); *300 m N de la estación*: 21.09.1996: 1 ad. (INBio 1501097); *600 m N de la estación Cedrales*: 13.11.1996: 2 juvs. (INBio 1501055); 14.12.1996: 1 juv. (INBio 1498623) (all leg. Elias Rojas)

Finca Toty Castro, 1.7 km S de la estación Cedrales, 10°31'39"N, 83°43'33"W, 10 m a.s.l., leg. Elias Rojas, 16.10.1996: 1 ad. (INBio 1501098)

Refugio Nacional de Vida Silvestre Barra del Colorado: Pococí, Colorado, Sector *Cerro Cocorí*, 30 km N de Cariari, 10°35'39"N, 83°42'59"W, 160 m a.s.l.: leg. malacological staff of INBio, 10.12.1993: 6 ads. (INBio 1465446); leg. malacological staff of INBio, 04.10.1994: 3 ads. (INBio 1478061); leg. Elias Rojas, 10.05.1994: 5 ads. (INBio 1483360); leg. Elias Rojas, 24.08.1994: 1 ad., 1 s.ad. (INBio 1480255); leg. Elias Rojas, 10.09.1994: 1 ad. (INBio 1483208); 1

juv. (INBio 1483209); leg. Elias Rojas, 13.09.1994: 2 ads. (INBio 1480261); 1 juv. (INBio 1480281); leg. Elias Rojas, 10.10.1994: 1 ad. (INBio 1483017); leg. Elias Rojas, 05.12.1994: 1 ad. (INBio 1467174)
Refugio Nacional de Vida Silvestre Barra del Colorado: *Barra del Colorado, Estación Sardinas*: *10°38'52"N, 83°43'52"W, 50 m a.s.l.*: 05.01.1994: 1 ad. (INBio 1478283); 10.02.1994: 4 ads. (INBio 1484010); 12.05.1994: 1 ad., 1 s.ad. (INBio 1484585); 5 ads., 1 s.ads. (INBio 1484587); 6 ads. (INBio 1484589); 24.05.1994: 1 s.ad. (INBio 1478305); 11.07.1994: 4 s.ads., 2 juv. (INBio 1484432); 25.07.1994: 1 ad. (INBio 1478294); 28.08.1994: 1 ad. (INBio 1480051); 12.10.1994: 3 juv. (INBio 1484372); 3 ads., 1 s.ad., 2 juv. (INBio 1484372); 12.10.1994: 3 ads., 1 s.ad., 2 juv. (INBio 1484374); 16.10.1994: 3 ads. (INBio 1484013); 22.10.1994: 2 ads. (INBio 1484991); 7 ads., 1 s.ad. (INBio 1485284); 5 ads., 1 s.ad., 2 juvs. (INBio 1485285); 7 ads., 1 s.ad., 2 juvs. (INBio 1485289); 2 juvs. (INBio 1485290); 09.11.1994: 2 s.ads. (INBio 1480044); 09.12.1994: 1 ad. (INBio 1480041); 01.02.1995: 1 ad., 1 s.ad. (INBio 1485145); 02.06.1995: 1 ad. (INBio 1484748); 4 ads. (INBio 1484749) (all leg. Flor Araya); *10°39'11"N, 83°44'21"W, 15 m a.s.l.*: leg. malacological staff of INBio: 13.01.1994: 1 ad. (INBio 1478017); 16.04.1994: 1 ad. (INBio 1477915); *800 m N de la Estación Sardinas, Sendero Tono, 10°39'05"N, 83°44'31"W, 50 m a.s.l.*: leg. malacological staff of INBio, 21.11.1993: 1 juv. (INBio 1465699); 1 ad. (INBio 1465700)

Cartago: *Parque Nacional Tapantí-Macizo de La Muerte*: *Sendero Oropéndola, 09°45'09"N, 83°47'08"W, 1,260 m a.s.l.*: leg. Rosa Guzman, 03.10.1997: 1 ad. (INBio 1488194); *Estación Quebrada Segundo, 09°45'45"N, 83°47'18"W, 1,360 m a.s.l.*: leg. Roberto Delgado, 18.10.1994: 1 ad. (INBio 1479646); leg. Roberto Delgado, 03.07.1995: 1 ad. (INBio 1487842)
Monumento Nacional Guayabo: Turrialba, Santa Teresita, 09°58'26"N, 83°41'42"W, 1,000 m a.s.l., leg. Zaidett Barrientos, 16.12.1994: 1 ad. (INBio 1476052)

Puntarenas: *Quebrada Chanchera*, 800 m W de la Playa, 08°37'26"N, 83°26'39"W, 1 m a.s.l., leg. Socorro Avila, 08.12.1996: 1 ad. (INBio 1486976)
San Luis, Finca Buen Amigo, 10°16'36"N, 84°47'48"W, 1,100 m a.s.l., leg. Zobeida Fuentes, 26.06.1995: 1 ad. (INBio 1484382)
Zona Protectora Arenal-Monteverde: *Reserva Biológica Bosque Nuboso Monteverde*: *Sendero Brillante, 10°17'59"N, 84°47'10"W, 1,520 m a.s.l.*: leg. Kattia Martinez, 17.06.1994: 2 ads. (INBio 1466835); *Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,600 m a.s.l.*: 24.05.1994: 5 ads. (INBio 1466884); 3 ads. (INBio 1466954); 2 ads. (INBio 1467003); 25.05.1994: 1 ad. (INBio 1466842); 1 ad. (INBio 1466870); 2 ads. (INBio 1466891); 1 ad. (INBio 1466905); 1 ad. (INBio 1467024); 14.06.1994: 3 ads., 2 sads. (INBio 1467031); 15.07.1994: 2 ads. (INBio 1479528); 16.07.1994: 2 ads. (INBio 1479539); 25.09.1995: 1 ad. (INBio 1498806); 28.10.1995: 1 ad. (INBio 1498590); 20.10.1996: 4 ads. (INBio 1498828) (all leg. Kattia Martinez); *Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,520 m a.s.l.*: leg. Zaidett Barrientos, 14.10.1994: 1 s.ad., 1 juv. (INBio 1468141); 1 ad. (INBio 1468211); 1 ad. (INBio 1468212); *Sendero el Camino, 10°18'03"N, 84°47'15"W, 1,560 m a.s.l.*: 23.05.1994: 5 ads., 1 s.ad. (INBio 1466912); 1 s.ad. (INBio 1466947); 23.05.1994: 1 s.ad. (INBio 1466996); 2 ads. (INBio 1467010); 25.05.1994: 1 ad. (INBio 1466863); 1 s.ad. (INBio 1466968); 10.06.1994: 7 ads. (INBio 1480426); 14.07.1994: 2 ads., 1 s.ad. (INBio 1480126); 2 ads. (INBio 1480128); 5 ads. (INBio 1480129); 1 ad. (INBio 1480149); 08.08.1994: 3 ads. (INBio 1479517); 2 ads. (INBio 1479550); 1 juv. (INBio 1479838); 16.09.1994: 1 ad. (INBio 1480098); 10.10.1994: 1 ad. (INBio 1485422); 26.09.1995: 1 ad. (INBio 1498807) (all leg. Kattia Martinez); *Sendero el Roble, 10°18'16"N, 84°47'27"W, 1,600 m a.s.l.*: leg. Kattia Martinez, 08.11.1994: 1 ad. (INBio 1480132); *Sendero Chomogo, 10°18'22"N, 84°47'23"W, 1,640 m a.s.l.*: 13.08.1994: 1 ad. (INBio 1480152); 10.10.1994: 1 ad. (INBio 1485426); 08.12.1994: 1 ad. (INBio 1477521); 15.12.1994: 1 ad. (INBio 1484687); 06.03.1995: 1 ad. (INBio 1485441) (all leg. Kattia Martinez); *Sendero Bosque Eterno, 10°18'22"N, 84°47'40"W, 1,600 m a.s.l.*: 09.06.1994: 1 ad. (INBio 1480119); 06.08.1994: 1 s.ad. (INBio 1466793); 28.10.1995: 1 ad. (INBio 1498581) (all leg. Kattia Martinez); *Sendero el Río, 10°18'29"N, 84°47'37"W, 1,600 m a.s.l.*: 15.07.1994: 1 juv. (INBio 1479353); 08.12.1994: 3 ads. (INBio 1480127); 1 ad. (INBio 1480130); 1 ad. (INBio 1480131);

04.07.1995: 1 s.ad. (INBio 1485234); 1 ad. (INBio 1485235) (all leg. Kattia Martinez); *Estación la Casona, 10°18'11"N, 84°47'50"W, 1,520 m a.s.l.*: 08.09.1994: 1 ad. (INBio 1479451); 22.09.1995: 3 ads. (INBio 1498804); 28.10.1998: 3 ads. (INBio 1498632) (all leg. Kattia Martinez); 10°18'15"N, 84°47'46"W, 1,520 m a.s.l., leg. malacological staff of INBio, 28.07.1994: 5 ads. (INBio 1477749)

Finca tomas, por Casa Boby, 10°18'12"N, 84°48'22"W, 1,520 m a.s.l., leg. Kattia Martinez, 24.10.1995: 1 s.ad. (INBio 1498808)

Cerro Plano, 10°18'58"N, 84°49'09"W, 1,300 m a.s.l., leg. Kattia Martinez, 02.09.1996: 1 ad. (INBio 1498652)

Other Sources

COSTA RICA

Guanacaste: Tilaran [about 10°28'30"N, 84°58'30"W], leg. Univ. Alabama, M. Smith coll.: 6 ads. (UF 95283)

1.7 mi S Tilaran on road to Quebrado Grande [about 10°27'N, 84°58'W], leg. R.W. McDiarmid, 28.08.1971: 2 ads., 1 s.ad. (UF 214166)

10 mi W Tilaran [about 10°26'N, 85°06'W], leg. Ronald Heyer, 06.08.1964: 1 ad. (UF 214163)

Monte Verde [about 10°18'N, 84°47'W], leg. Savage & Scott, 13–16.05.1964: 6 ads., 3 s.ads. (UF 214170)

Alajuela: San Carlos [about 10°20'N, 84°26'W], leg. McGinty coll., *ex* Preston & Tomlin: 3 ads. (UF 160150)

Cariblanca [about 10°17'N, 84°12'W], Sarapiqui, 600 m a.s.l., P. Biolley (#267): 5 ads. (MHNN)

Chemin de Sarapiqui, S. Miguel [about 10°19'N, 84°11'30"W], leg. P. Biolley: 11 ads. (MHNN)

Tesalia [Tetsalia?, about 10°21'N, 84°24'W], leg. R. W. McDiarmid, 18–20.07.1971: 1 ad. (UF 214164)

Heredia: Puerto Viejo [de Sarapiqui, about 10°28'N, 84°00'30"W], leg. P. Biolley: 2 ads. (ZMB 103242)

Río Frio, Standard Fruit Co., 10°20'N, 83°53'W, 300 ft., leg. Michael J. Corn, 21.11.1969: 1 ad. (UF 214160); 22.11.1969: 2 s.ads. (UF 214172)

[not: "Alajuela"], Río Frio [about 10°20'N, 83°53'W], leg. Michael J. Corn, 05.05.1970: 1 ad. (UF 214161); 15.05.1970: 1 ad. (UF 214171)

Limón: Los Diamantas Farm, 11.08.1971: 1 ad. (UF 69846); Los Diamantes Farm, 12 mi SE Guapiles [about 10°11'N, 83°37'W], leg. R.W. McDiarmid, 13.08.1971: 1 ad. (UF 214167)

Moin, hill #1 [about 10°N, 83°04'W], leg. C. Little, 29.09.1967: 1 ad. (UF 214158)

Cueva Castil, near Limon [about 10°N, 83°02'W], leg. Colin Little, 30.08.1967: 5 ads. (UF 214165)

Puerto Limon, football field adjacent to Standard Fruit Box Factory [about 10°N, 83°02'W], leg D.G. Robinson (TU-954), 19.05.1984: 1 ad. (UF 155820)

Along road cut, along south side of Río Banano, opposite La Bomba, 09°54'49.7"N, 83°03'56.4"W, leg. D.G. Robinson & J.M. Montoya, 21.09.1998 (APHIS PPQ USDA)

Pandora [about 09°43'N, 82°58'W], leg. Jay Savage, 01.05.1964: 1 ad. (UF 214156); leg. F. G. Thompson (FGT-100), 05.08.1964: 3 ads. (UF 214157)

3.2 km N Pandora [about 09°45'N, 82°58'W], leg. F.G. Thompson (FGT-98), 04.08.1964: 8 ads, 1 s.ad. (UF 214155)

1 km NW of Cahuita, 09°44.5'N, 82°50.9'W", leg. F.G. Thompson (FGT-5616), 25.02.1996: 1ad. (UF 258427)

Trib[utary] to Río Moin [Valle de Talamanca!], 572 500 E, 397 600 S, 430 m a.s.l. [09°37'45"N, 83°00'18"W], leg. E.L. Raiser (ELR-082), 10.08.1994: 1 ad. and in alcohol (UF 41438) (UF 41437); leg. F. Alvando (ELR-087), 11.08.1994: 2 ads. (UF 41442)

Amubre [about 09°32'N, 82°57'30"W], leg. Norman Scott, 16.03.1964: 1 ad. (UF 214168)

San José: Tarbaca [about 09°49'25"N, 84°06'39"W], leg. P. Biolley: 2 ads. (ZMB 103246)

2 lots mixed: Cartago: 1. Azahar de Cartago [not clear, if referring to the town Cartago, ?about 09°52'N, 83°55'W], San José: 2. Tarbaca [about 09°49'25"N, 84°06'39"W], leg. P. Biolley: 10 ads. (MHNN)

Cartago: 2 lots mixed: Cartago: 1. Azahar de Cartago [not clear, if referring to the town Cartago, ?about 09°52'N, 83°55'W], San José: 2. Tarbaca [about 09°49'25"N, 84°06'39"W], leg. P. Biolley: 10 ads. (MHNN)

Tapanti, 4300 ft. [about 09°47'N, 83°48'W], leg. F. G. Thompson (FGT-23), 26.06.1963: 1 ad. (UF 214169)

Turrialba [about 09°54'30"N, 83°41'W], *ex* coll. S.G.A. Jaeckel: 2 ads. (HNC 39842);

coll. Bosch, *ex* Rolle, *ex* Wagner: 6 ads. (SMF 180790/6); Turrialba, versant de l'Atlantique, 750 m [about 09°54'30"N, 83°41'W], leg. P. Biolley (#146), 07.1893: 4 ads. (MHNN)
Valleé de Tuis [about 09°51'N, 83°35'W], H. Pittier, 9.1893 *ex* coll. Wiegmann: 1 ad. (ZMB 70633)
Cartago?: Cache [Cachí?, about 09°50'N, 83°48'W], leg. Roger, *ex* Godwin & Salvin: 1 ad. (ZMB 40836)
Puntarenas: 1.5 mi NE Monte Verde [about 10°19'N, 84°47'W], leg. R.W. McDiarmid (RWM-11), 17.02.1966: 6 ads. (UF 214162)
Costa Rica, without locality further specified: leg. Beal-Maltbie coll., *ex* W. F. Webb coll.: 4 spec. (UF 237539); leg. H. G. Lee, *ex* G.D. Robinson, W.F. Webb: 1 ad. (UF 166943); leg. Univ. Alabama, T.H. Aldrich coll. (THA-8213), *ex* Webb: 1 ad. (UF 95254); 1 ad. (UF 214110); leg. P. Biolley: 4 ads. (MHNN); leg. Carmiol: 2 ads. (ZMB 103244); *ex* Fulton: 3 ads. (ZMB 64488); 1 ad. (ZMB 103245)

NICARAGUA
Not further specified: Sumichrast: 2 ads. (UF 214108)

PANAMA
Bocas Del Toro: Colon Island, leg. McGinty coll.: 2 ads. (UF 185608); Isla Colon, ca. 12 km NNW of Bocas del Toro, 09°25'00"N, 82°16'23"W, leg. F.G. Thompson (FGT-4726), 19.09.1990: 1 ad. (UF 167537); Isla Colon, limestone knoll along E coast, 5 km NNE of Bocas del Toro, 09°23'05"N, 82°14'09"W, leg. F.G. Thompson (FGT-4727), 20.09.1990: 1 ad. (UF 167538)
N end of Isla San Cristobal, 09°17'28"N, 82°15'51"W, leg. F.G. Thompson (FGT-4730), 21.09.1990: 1 ad. (UF 167541)
Isla Bastimentos, 0.5 km NE of Bastimentos Town on trail to Wizard Beach, 09°20'59"N, 82°12'15"W, 60 m a.s.l., leg. F.G. Thompson (FGT-4731), 22.09.1990: 1 ad. (UF 167544)
Ojo de Agua, Filo Almirante, 09°17'32"N, 82°27'43"W, 300 m a.s.l., leg. F.G. Thompson (FGT-4733), 24.09.1990: 6 ads. (UF 167551)
Colón, Canal Zone: 0.5 mi SE Achiote, S. R. Telford, 12.1969, 1 ad. (UF 214173); 4.8 km SE Achiote, leg. F.G. Thompson (FGT-1130), 27.04.1969: 20 ads. (UF 214154)
0.8 km SW Madden Dam, leg. F.G. Thompson (FGT-1131), 02.05.1969: 1 ad. (UF 214159)
N bank Chagres River, 6 km NNE Gamboa, leg. S.R. Telford, 22.04.1969: 1 ad. (UF 214174)
Canal Zone, not further specified: leg. Univ. Alabama, M. Smith coll., *ex* Clark 5 ads., 1 s.ad. (UF 95284); leg. Univ. Alabama, M. Smith coll.: 11 ads. (UF 95285)
Panama, without locality further specified: leg. Beal-Maltbie coll., *ex* W. Webb coll. (UF 237401)

Description

Shell (Fig. 335A–C): Conical-subglobose, solid, relatively large sized and dull to slightly shiny. Color: basic color yellowish to whitish-opaque, towards apex and on upper half of whorls often a more or less intensive tinge ranging from reddish-brown to flesh colored, in some specimens involving the whole shell with exception of outer lip. The color is slightly overlapped with fine light to transparent patches and lines giving the shell a special ornamentation. Surface textured with fine growth lines and oblique grooves of different individual orientations but of same general direction (Fig. 14), causing the dull appearance. Embryonic shell of about 1 whorl; 4–4$^{5}/_{8}$ (lectotype: 4½) subsequent whorls nearly straight and only very slightly convex; last whorl with a touch of angulation on the periphery; whorls equally extending in size, forming a very regular, blunt spire. Suture very slightly impressed. Aperture oblique and nearly straight, last whorl only very slightly descending, inserting exactly at periphery or just below it. Outer lip independent of color of whorls, always yellowish-whitish, remarkably thickened and broadly expanded, upper palatal region slightly sinuate. Reflection nearly rectangular to the whorl; transition to columella with a more or less pronounced denticle. Columella slightly curved, its tran-

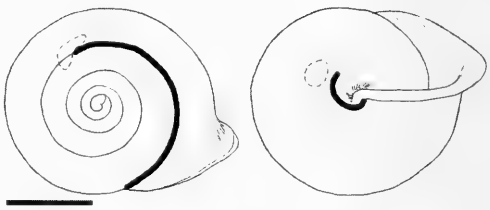


FIG. 13. Axial cleft and muscle attachments of *Helicina funcki*, IR 757; scale bar 5 mm.

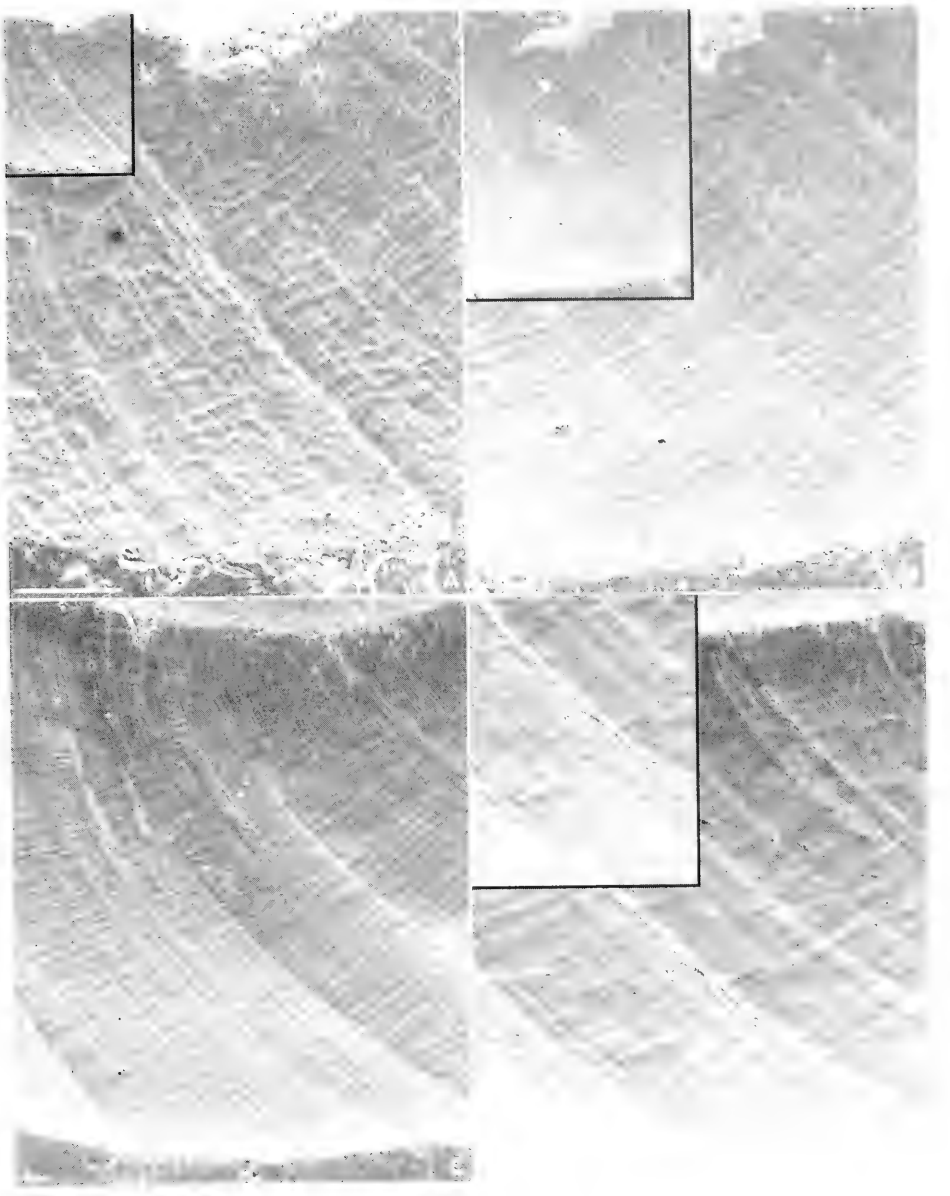


FIG. 14. Teleoconch surface structure of *Helicina funcki*. A. On 1st whorl. B. On 2nd whorl. C. On 3rd whorl. D. On 4th whorl (inset same magnification as in C); scale bar 100 µm.

sition to body whorl marked with a perpendicularly impressed line or even a groove. Basal callus weakly developed and nearly completely smooth or very slightly granulated.

Juvenile specimens exhibit a roundly carinated periphery sometimes bearing periostracal spiral lines.

Internal Shell Structures: (Fig. 13)

Teleoconch Surface Structure: In *Helicina funcki*, the transitional structure is followed by a pattern of oblique diverging grooves, which is maintained in all whorls (Fig. 14B–D). The grooves only increase in length and become more widely spaced.

Embryonic Shell: The surface is structured with pits arranged in concentric lines (Fig. 15A). The diameter of these pits is approximately equal to the interspacial distance between the pits in a line as well as between the lines of pits themselves, although the arrangement is somewhat irregular. This is the typical structure for *Helicina funcki*, but deviations also occur (Fig. 15B). The "compressed" pattern obviously results from irregularities experienced during growth (in the present case, during the younger part) which caused a different form of the embryonic shell and more closely spaced growth lines resulting in a reduction of the diameter (Fig. 15A: 1040 µm, Fig. 15B: 930 µm).

Concerning the size of the embryonic shell, the type material falls within the range of Costa Rican lowland populations (e.g., Cahuita), whereas specimens from higher altitudes of Monteverde consistently develop a much larger embryonic shell.

Diameter: 954 µm (± 41) (870–1,040) (n = 16) (IR 1630, IR 1639, IR 1642, IR 1648, Cahuita); 1,160 µm (± 43) (1,060–1,240) (n = 20) (IR 843, Monteverde); 980 µm (± 40) (940–1,040) (n = 4) (BMNH 20010497.1–4, type lot, lectotype: 1,000 µm); 970 µm (± 50) (9201,020) (n = 2) (MIZ 8989, type lot of *Helicina funcki costaricensis*, lectotype: 1020 µm).

Operculum (Fig. 16): Only slightly calcified, calcareous plate not fully extended over horny plate, leaving a free margin, thickened towards columellar side. Color dark reddish-brown to nearly black, only the margin transparent. Columellar side slightly S-shaped, upper end acute and pointed or nearly rectangular, lower end rounded, but slightly truncated towards the columella.

Animal (Fig. 337A, B): The color of the animal does not show any great variation, either at different sites or within the populations. Sole

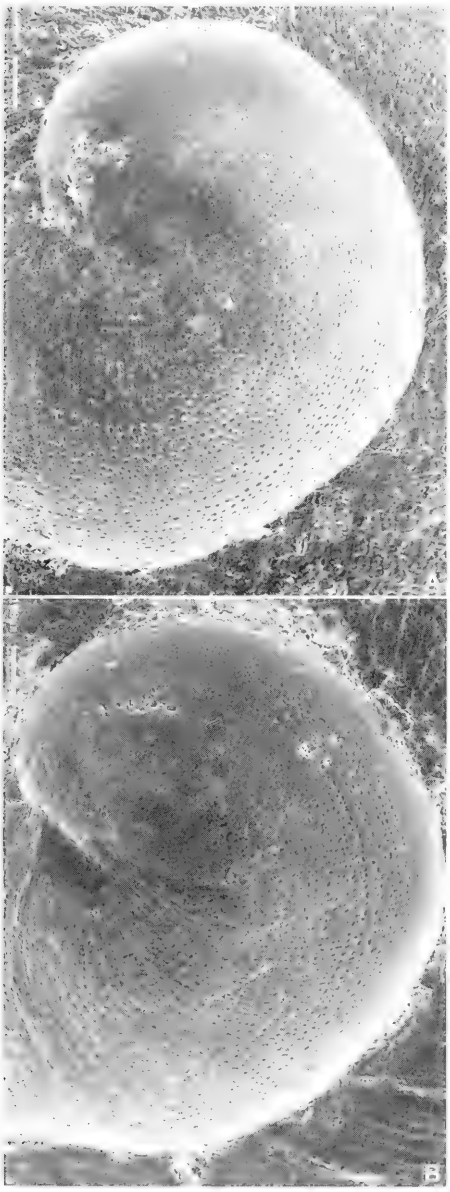


FIG. 15. Embryonic shell of *Helicina funcki*, A. Typical. B. Irregularities during growth; scale bar 100 µm.

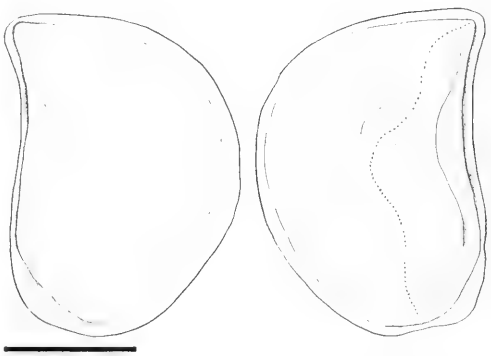


FIG. 16. Operculum of *Helicina funcki*, IR 757; scale bar 2.5 mm.

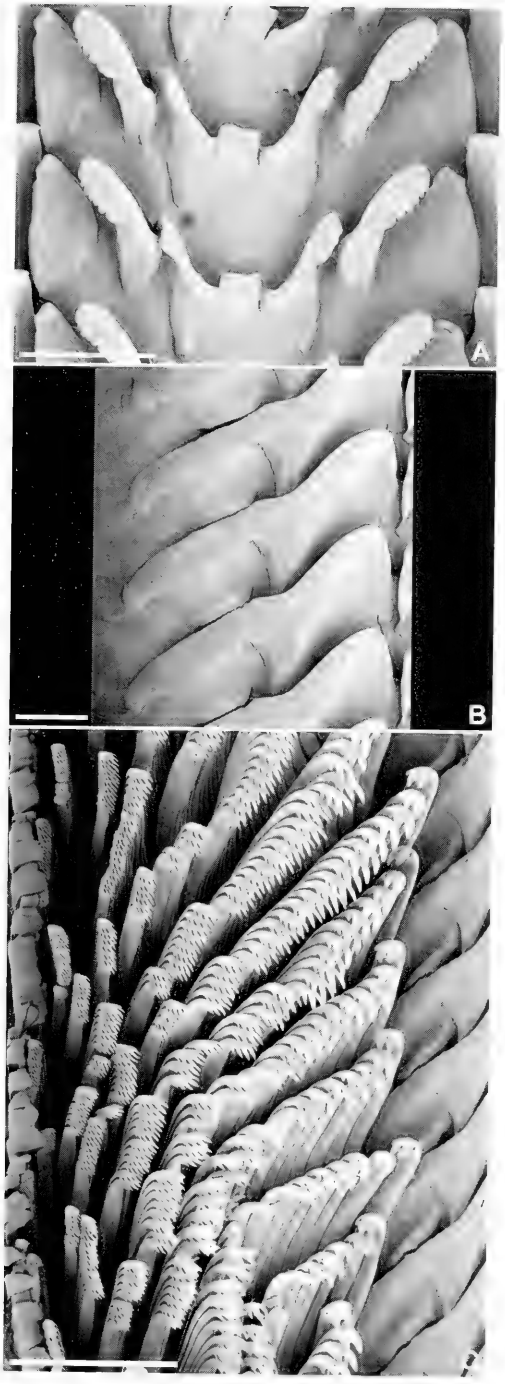


FIG. 17. Radula of *Helicina funcki*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm (A, B), 100 µm (C).

and sides of the foot are whitish-yellowish changing gradually to dark brown-greyish towards the upper side and head. The tentacles are also dark brown-greyish with a light tip. The mantle has a whitish-greenish pigmentation shining through the shell, thus providing the live specimens with a somewhat greenish appearance. The mantle only bears a dark color in juvenile specimens (Fig. 337B), being sometimes spotted with yellow, thus causing those juvenile individuals to appear darker.

Radula (Fig. 17): The cusps on the A- and C-central are vestigial, only the B-central with 4–5 more or less-well developed cusps. Comb-lateral with 7–9 cusps, cusps on marginals slowly increasing in number. Radula with about 70–105 rows of teeth.

Female Reproductive System (Figs. 18, 19): The receptaculum seminis enters at the middle of the inner side of the descending limb of the V-organ. It is a cylindrical, slender

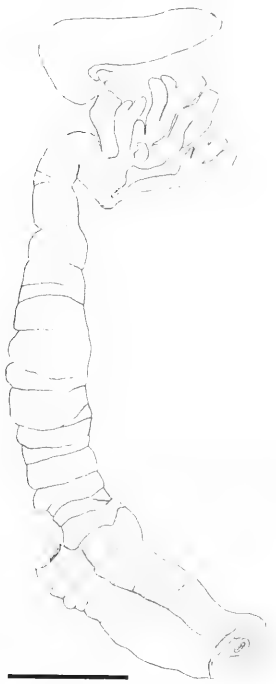


FIG. 18. Female reproductive system of *Helicina funcki*, IR 1312; scale bar 2 mm.

FIG. 19. Variability of the female reproductive system of *Helicina funcki*, IR 1312; scale bar 2.5 mm.

sac. The bursa copulatrix consists of numerous remarkably elongated lobes, some of which are always further subdivided. The provaginal sac is irregularly shaped, dorsoventrally flattened and bears lobe-structures at its distal side. The stalk is comparatively long and deeply curved anteriorly, as is the adjacent part of the reception chamber. The pallial oviduct is relatively long and shows mainly transversal constrictions. In Figure 19, the right drawing shows the genital for a slightly immature specimen. The main difference consists in the much less thickened pallial oviduct, in which, except for a slight enlargement, the final shape of the accessory structure is already developed.

Morphometry and Sexual Dimorphism (Tables 3–4, Figs. 21–28)

From my own material, all adult specimens of known sex and populations with at least a few specimens of each sex were compared. A few populations with scanty material were included because of their otherwise undocumented origin.

The measurement of the weight is especially difficult in *Helicina funcki*, because a considerable part of the weight results from the strongly developed, broadly expanded outer lip. In Fig. 20, the increase of weight during growth is illustrated for the population from Cahuita (juveniles were studied from lot IR 1312). An additional non-mature shell from Río Peje is included as an example for heavy-shelled specimens to demonstrate that the increase of weight during juvenile growth period continues at about the same rate. Shells

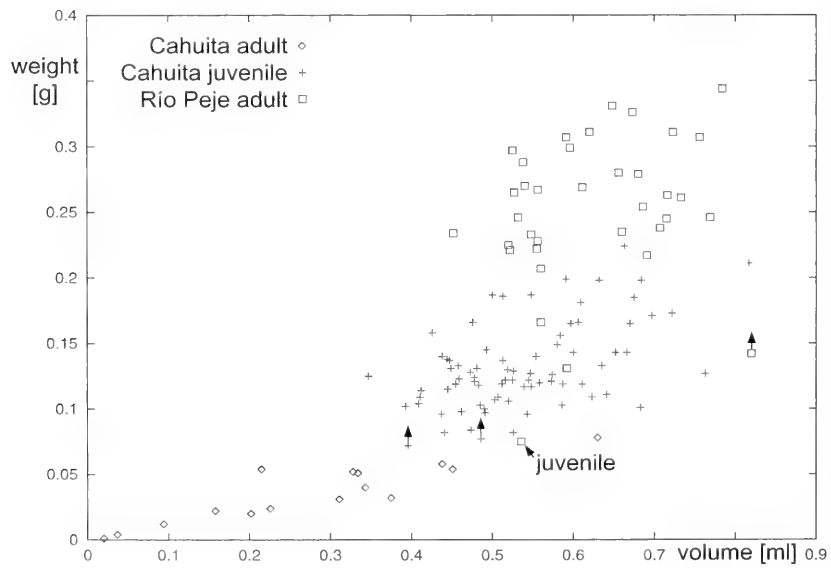


FIG. 20. Increase of weight during growth of *Helicina funcki* from Cahuita (juveniles IR 1312), compared also with adults from Río Peje (one juvenile included); arrows indicate "thin-lipped" adults; juvenile = shells without expanded lip.

TABLE 3. Measurements of different populations of *Helicina funcki* from material collected by the author, given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		"Rincón de la Vieja" (altitude 800 m) lots IR 972, IR 979					"Mirador Gerardo" (altitude 1450 m) lots IR 924, IR 928, IR 1230				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	11.14	0.33	10.80	11.52	4	11.05	0.48	10.55	11.74	4
Height	m	10.60	0.32	10.22	11.04	4	10.17	0.11	10.04	10.34	4
Maj. diam.	f	12.02	0.31	11.57	12.63	4	12.42	0.36	11.96	12.96	4
Maj. diam.	m	11.56	0.69	10.66	12.36	4	11.90	0.12	11.67	12.07	4
Min. diam.	f	10.84	0.23	10.53	11.22	4	11.19	0.31	10.78	11.67	4
Min. diam.	m	10.39	0.56	9.58	11.05	4	10.48	0.08	10.36	10.65	4
Outer lip	f	7.95	0.20	7.56	8.11	4	8.17	0.14	7.92	8.36	4
Outer lip	m	7.83	0.52	7.13	8.76	4	7.83	0.26	7.49	8.25	4
Last whorl	f	9.08	0.17	8.78	9.30	4	9.15	0.27	8.82	9.48	4
Last whorl	m	8.86	0.27	8.43	9.30	4	8.61	0.06	8.49	8.68	4
Col. axis	f	8.73	0.17	8.50	8.97	4	8.62	0.32	8.08	9.10	4
Col. axis	m	8.14	0.13	7.96	8.29	4	7.89	0.11	7.67	8.09	4
Weight	f	0.078	0.008	0.066	0.094	4	0.137	0.025	0.117	0.187	4
Weight	m	0.093	0.032	0.032	0.132	4	0.142	0.015	0.125	0.162	4
Volume	f	0.471	0.031	0.435	0.515	4	0.491	0.031	0.452	0.553	4
Volume	m	0.409	0.053	0.342	0.471	4	0.400	0.005	0.390	0.408	4

		"Monteverde - Finca Ecológica" (altitude 1330 m) lots IR 859, IR 946, IR 1246					"Monteverde" (altitude 1500 m) lots IR 843, IR 927, IR 1194, IR 1435, IR 1627				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	10.96	0.22	10.65	11.31	4	11.31	0.33	10.24	12.17	18
Height	m	10.03	0.22	9.70	10.32	3	10.29	0.38	9.71	11.55	15
Maj. diam.	f	11.91	0.43	11.33	12.54	4	12.73	0.36	11.70	13.38	18
Maj. diam.	m	11.09	0.44	10.43	11.70	3	12.10	0.34	11.54	12.98	15
Min. diam.	f	11.16	0.36	10.45	11.72	4	11.45	0.34	10.25	12.35	18
Min. diam.	m	9.94	0.33	9.45	10.34	3	10.77	0.37	10.19	11.55	15
Outer lip	f	8.04	0.21	7.75	8.30	4	8.16	0.20	7.40	8.65	18
Outer lip	m	7.65	0.30	7.34	8.09	3	7.85	0.23	7.15	8.54	15
Last whorl	f	9.02	0.25	8.56	9.30	4	9.39	0.25	8.57	10.09	18
Last whorl	m	8.32	0.30	7.88	8.55	3	8.71	0.32	8.26	9.74	15
Col. axis	f	8.55	0.19	8.16	8.86	4	8.82	0.27	8.14	9.45	18
Col. axis	m	7.88	0.27	7.58	8.28	3	7.98	0.26	7.62	8.81	15
Weight	f	0.156	0.037	0.105	0.198	4	0.174	0.018	0.137	0.235	18
Weight	m	0.126	0.046	0.057	0.177	3	0.132	0.024	0.075	0.188	15
Volume	f	0.444	0.028	0.407	0.490	4	0.521	0.039	0.385	0.653	18
Volume	m	0.345	0.020	0.315	0.365	3	0.420	0.035	0.368	0.518	15

(*Continues*)

(*Continues*)

		"Las Pavas" (altitude 800 m) lots IR 952, IR 955, IR 1273, IR 1637					"Tortuguero" (altitude 0–10 m) lots IR 1348, IR 1620, IR 1653				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.12	0.22	11.81	12.75	7	12.22	1.13	11.09	13.34	2
Height	m	11.11	0.48	10.15	12.08	5	11.73	0.21	11.52	11.94	2
Maj. diam.	f	13.38	0.32	12.93	14.08	7	14.08	0.78	13.31	15.25	3
Maj. diam.	m	12.30	0.35	11.85	13.00	5	13.27	0.09	13.17	13.36	2
Min. diam.	f	12.11	0.18	11.61	12.44	7	12.66	0.77	11.84	13.82	3
Min. diam.	m	11.03	0.34	10.60	11.60	5	11.78	0.16	11.62	11.93	2
Outer lip	f	8.74	0.23	8.32	9.23	7	9.40	0.85	8.55	10.25	2
Outer lip	m	8.40	0.28	7.99	8.75	5	8.81	0.01	8.80	8.82	2
Last whorl	f	10.14	0.10	10.00	10.40	7	10.36	0.86	9.50	11.22	2
Last whorl	m	9.31	0.32	8.76	9.96	5	9.69	0.03	9.66	9.72	2
Col. axis	f	9.33	0.13	9.17	9.75	7	9.24	0.48	8.52	9.81	3
Col. axis	m	8.49	0.40	7.51	9.23	5	8.72	0.08	8.64	8.80	2
Weight	f	0.152	0.035	0.103	0.233	7	0.147	0.081	0.061	0.268	3
Weight	m	0.151	0.020	0.128	0.197	5	0.177	0.062	0.115	0.239	2
Volume	f	0.636	0.035	0.593	0.703	7	0.731	0.089	0.602	0.865	3
Volume	m	0.473	0.042	0.404	0.549	5	0.568	0.003	0.565	0.570	2

		"La Selva" (altitude 60 m) lots IR 1061, IR 1062, IR 1182					"Guayacán" (altitude 520 m) lots IR 1079, IR 1090, IR 1608				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.65	0.29	12.16	13.06	9	12.14	0.34	11.47	12.55	5
Height	m	11.62	0.36	10.92	12.26	9	11.50	0.31	11.19	11.80	2
Maj. diam.	f	14.06	0.21	13.56	14.37	9	13.18	0.36	12.69	13.62	5
Maj. diam.	m	13.37	0.23	12.78	13.82	9	12.70	0.17	12.45	12.89	3
Min. diam.	f	12.88	0.14	12.51	13.09	9	11.97	0.27	11.65	12.42	5
Min. diam.	m	12.00	0.18	11.51	12.32	9	11.41	0.10	11.27	11.56	3
Outer lip	f	9.56	0.24	9.03	10.18	9	8.73	0.11	8.48	8.88	5
Outer lip	m	9.08	0.29	8.30	9.47	9	8.52	0.04	8.48	8.55	2
Last whorl	f	10.58	0.19	10.21	10.95	9	10.14	0.29	9.66	10.43	5
Last whorl	m	9.86	0.27	8.98	10.22	9	9.61	0.07	9.54	9.68	2
Col. axis	f	9.77	0.17	9.38	10.00	9	9.34	0.24	8.88	9.56	5
Col. axis	m	8.93	0.21	8.37	9.35	9	8.76	0.11	8.63	8.92	3
Weight	f	0.236	0.036	0.134	0.277	9	0.191	0.032	0.138	0.233	5
Weight	m	0.219	0.044	0.141	0.278	9	0.175	0.004	0.171	0.179	2
Volume	f	0.729	0.037	0.652	0.783	9	0.615	0.040	0.533	0.669	5
Volume	m	0.580	0.041	0.505	0.638	9	0.534	0.001	0.533	0.534	2

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		"México" (altitude 40 m) lots IR 274, IR1191, IR 1406					"Río Peje" (altitude 160 m) lots IR 751, IR 1300, IR 1552				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	11.22	0.23	10.92	11.68	4	12.54	0.33	11.56	13.64	17
Height	m	10.40	0.16	10.15	10.62	6	11.68	0.40	10.88	12.55	20
Maj. diam.	f	13.21	0.30	12.82	13.64	4	13.91	0.32	13.17	14.65	17
Maj. diam.	m	12.11	0.37	11.32	12.55	6	13.13	0.31	12.61	13.97	20
Min. diam.	f	11.98	0.29	11.59	12.40	4	12.74	0.29	11.93	13.27	17
Min. diam.	m	10.90	0.28	10.36	11.29	6	11.80	0.24	11.34	12.44	20
Outer lip	f	8.68	0.15	8.49	8.98	4	9.45	0.28	8.75	9.98	17
Outer lip	m	8.01	0.26	7.41	8.41	6	8.98	0.28	8.42	9.87	20
Last whorl	f	9.70	0.24	9.43	10.08	4	10.61	0.28	9.84	11.47	17
Last whorl	m	8.90	0.13	8.65	9.09	6	9.97	0.25	9.54	10.66	20
Col. axis	f	8.67	0.16	8.49	8.99	4	9.59	0.32	8.86	10.66	17
Col. axis	m	8.05	0.09	7.93	8.17	6	8.95	0.29	8.13	9.78	20
Weight	f	0.200	0.030	0.175	0.260	4	0.259	0.036	0.142	0.344	17
Weight	m	0.200	0.034	0.130	0.238	6	0.249	0.040	0.131	0.331	20
Volume	f	0.574	0.030	0.542	0.624	4	0.703	0.050	0.548	0.820	16
Volume	m	0.432	0.036	0.371	0.494	6	0.562	0.038	0.452	0.686	19

		"Río Barbilla" (altitude 70 m) lot IR 1545					"Uatsi" (altitude 30 m) lots IR 766, IR 1114, IR 1632				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.22	0.00	12.21	12.22	2	12.61	0.18	12.28	12.79	6
Height	m	11.32	0.50	10.75	12.12	5	11.94	0.18	11.59	12.15	5
Maj. diam.	f	13.93	0.00	13.93	13.93	2	14.04	0.15	13.78	14.33	6
Maj. diam.	m	12.73	0.47	11.97	13.61	5	13.36	0.60	12.64	14.35	5
Min. diam.	f	12.60	0.02	12.58	12.62	2	12.68	0.19	12.45	12.97	6
Min. diam.	m	11.37	0.43	10.73	12.09	5	12.05	0.44	11.52	12.98	5
Outer lip	f	9.29	0.02	9.27	9.30	2	9.50	0.19	9.16	9.95	6
Outer lip	m	8.57	0.29	8.04	8.95	5	9.19	0.35	8.32	9.68	5
Last whorl	f	10.31	0.10	10.21	10.41	2	10.51	0.20	10.04	10.81	6
Last whorl	m	9.60	0.45	8.78	10.30	5	9.98	0.30	9.56	10.57	5
Col. axis	f	9.41	0.25	9.16	9.66	2	9.53	0.12	9.36	9.81	6
Col. axis	m	8.62	0.35	8.11	9.32	5	8.89	0.16	8.71	9.11	5
Weight	f	0.240	0.012	0.228	0.251	2	0.263	0.036	0.219	0.335	6
Weight	m	0.157	0.041	0.089	0.219	5	0.148	0.049	0.087	0.226	5
Volume	f	0.688	0.019	0.669	0.707	2	0.708	0.021	0.681	0.744	6
Volume	m	0.547	0.073	0.442	0.695	5	0.631	0.074	0.546	0.764	5

(*Continues*)

(*Continues*)

	"Shiroles" (altitude 100 m) lots IR 911, IR 1596, IR 1599, IR 1644						"Cahuita" (altitude 0–10 m) lots IR 107, IR 757, IR 897, IR 898, IR 907, IR 1095, IR 1312, IR 1555, IR 1557, IR 1630, IR 1639, IR 1648				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.54	0.57	11.97	13.10	2	11.31	0.53	10.21	12.73	63
Height	m	12.04	0.30	11.67	12.50	4	10.66	0.54	9.20	12.08	51
Maj. diam.	f	14.16	0.63	13.53	14.79	2	12.76	0.52	11.59	14.55	63
Maj. diam.	m	13.49	0.25	13.14	13.82	4	12.26	0.53	10.85	14.43	51
Min. diam.	f	12.81	0.29	12.52	13.10	2	11.67	0.46	10.62	13.26	63
Min. diam.	m	12.21	0.19	11.82	12.41	4	11.04	0.45	9.88	12.67	51
Outer lip	f	9.24	0.06	9.18	9.30	2	8.63	0.41	7.76	9.89	63
Outer lip	m	9.16	0.21	8.76	9.48	4	8.37	0.41	7.39	9.73	51
Last whorl	f	10.63	0.40	10.22	11.03	2	9.56	0.47	8.44	10.71	63
Last whorl	m	10.27	0.13	10.10	10.45	4	9.05	0.44	8.17	10.19	51
Col. axis	f	9.53	0.30	9.23	9.82	2	8.68	0.43	7.93	9.91	63
Col. axis	m	9.24	0.15	9.07	9.49	4	8.12	0.41	7.11	9.18	51
Weight	f	0.298	0.030	0.268	0.328	2	0.134	0.026	0.077	0.224	63
Weight	m	0.292	0.014	0.274	0.306	4	0.141	0.039	0.057	0.282	51
Volume	f	0.718	0.060	0.658	0.777	2	0.564	0.070	0.437	0.817	60
Volume	m	0.622	0.025	0.572	0.656	4	0.471	0.058	0.329	0.662	51

	"Manzanillo" (altitude 0–10 m) lots IR 1096, IR 1320, IR 1642					
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	11.81	0.43	10.43	12.45	10
Height	m	11.17	0.34	10.44	12.45	19
Maj. diam.	f	13.43	0.43	12.39	14.43	10
Maj. diam.	m	12.79	0.45	12.01	13.70	19
Min. diam.	f	12.11	0.40	11.25	12.96	10
Min. diam.	m	11.48	0.33	10.99	12.25	19
Outer lip	f	9.11	0.47	7.97	9.76	10
Outer lip	m	8.66	0.28	8.03	9.23	19
Last whorl	f	9.97	0.33	9.28	10.55	10
Last whorl	m	9.31	0.24	8.79	10.03	19
Col. axis	f	8.93	0.34	7.91	9.57	10
Col. axis	m	8.56	0.27	7.96	9.29	19
Weight	f	0.180	0.018	0.132	0.217	10
Weight	m	0.168	0.031	0.128	0.257	19
Volume	f	0.615	0.053	0.486	0.719	10
Volume	m	0.522	0.043	0.452	0.630	19

still lacking their thickened outer lip but otherwise being fully grown weigh from approx. 50 to 100 mg depending on the size, with adults ranging up to 344 mg. Thus, the weight is mainly influenced by the thickness of the outer lip, which not only depends on the age of the individual but also on size. A recently developed outer lip is probably thinner than the one of a truly fully grown individual, a factor that cannot be differentiated in field collections, although the attempt was made to at least exclude non fully grown adult shells in populations with sufficient material. The arrows in the figure exemplary indicate such

"thin-lipped" adults. In fact, this may have resulted in too low measurements, thereby reducing the mean value.

In the diagrams, the populations are roughly grouped according to their locations: Rincón de la Vieja to Monteverde (NW-Costa Rica: mountain chains of Guanacaste and Tilarán), Las Pavas to La Selva (western and northern Caribbean plain), Guayacán to Barbilla (middle Caribbean plain), and Uatsi to Manzanillo (southern Caribbean plain).

Because the sex of the additional populations from the INBio material could not be determined, they have to be compared to the average value of both sexes.

Morphometry: The comparison of the populations showed that they differ in all characteristics. Except for weight, these differences between the populations exhibit a similar pattern in each characteristic (Figs. 21–28); that is, "Monteverde – Finca Ecológica" always has the smallest dimensions, suggesting that relations between the measurements at each locality are constant. In fact, several relations were tested and, except for the size, no significant differences were found at the different locations. The individual data can diverge remarkably from the mean value and as may be expected, due to the fact that as more specimens are

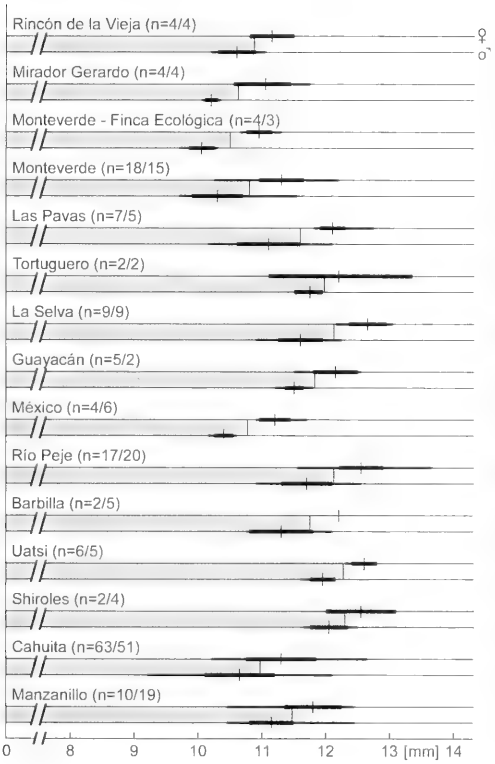


FIG. 21. Shell height of different populations of *Helicina funcki* in Costa Rica according to Table 3; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex.

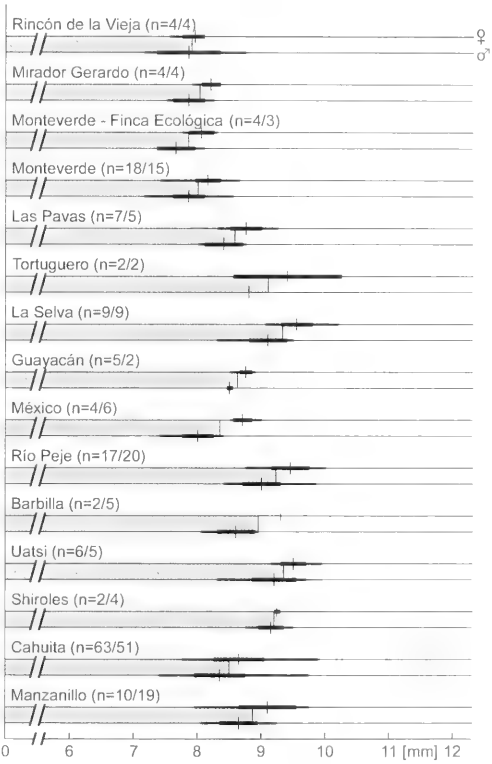


FIG. 22. Expansion of outer lip of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

included in the investigation, the wider the range of the data can become.

Regarding these size differences, the volume appears to illustrate them best, especially because it is the only measurement directly reflecting the actual living conditions of the animal. The extrema: the biggest individual from Tortuguero (0.865 ml) had a shell with 2.75 times the volume of the smallest from Monteverde – Finca Ecológica (0.315 ml); the mean value of the population of Shiroles is 1.7 times higher than that of Monteverde – Finca Ecológica. At the upper four locations in Fig. 27 (mountain chains of Guanacaste and Tilarán), representing the highest altitudes, consistently smaller-shelled populations are found, as well as at two far distant localities in the Caribbean plain (México and Cahuita). Shells from Las Pavas, Guayacán and Manzanillo are of intermediate size (Fig. 29).

Additional populations from the collection of INBio were subsequently compared only in the minor diameter, because the volume could not be measured and – as previously demonstrated – other characteristics varied in the same way. The minor diameter was chosen instead of the height, because it can be measured more exactly and it is better correlated with the volume (Fig. 30, Cahuita population). The populations show similar differences in size at different sites (Figs. 24, 29). The two individuals of Isla Uvita represent the smallest *Helicina funcki* measured in this study. The few corresponding localities (Monteverde, Manzanillo, Rincón de la Vieja, Mirador Gerardo – Santa Elena, Shiroles close to Hitoy Cerere) agree sur-

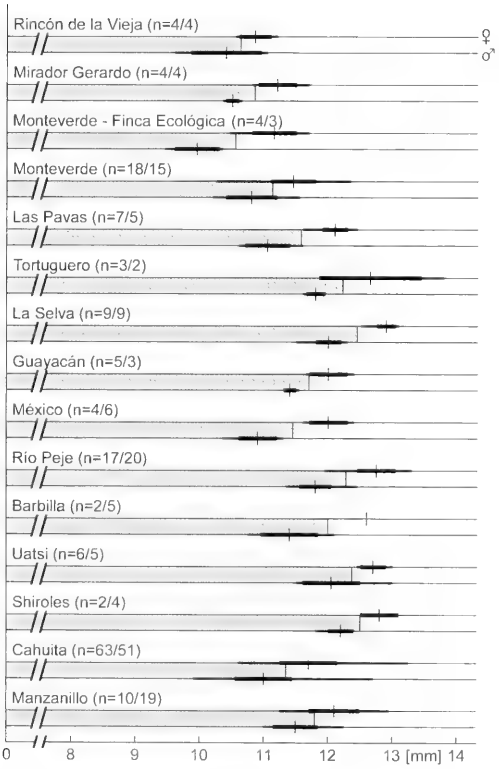


FIG. 23. Minor diameter of shell of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

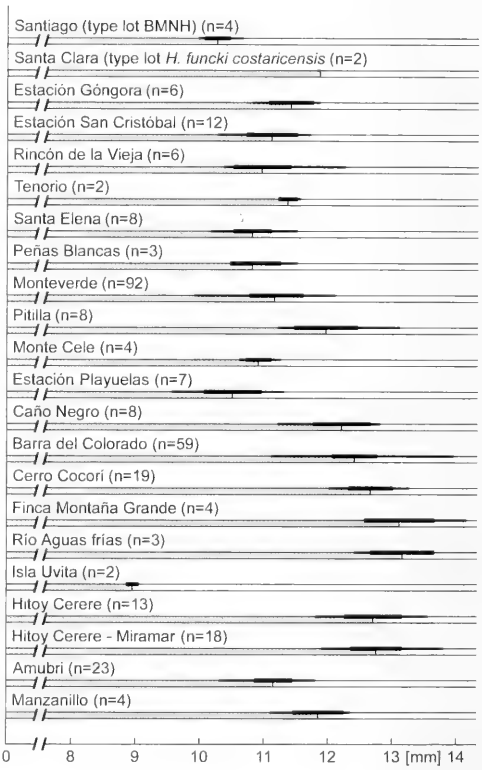


FIG. 24. Minor diameter of shell of different populations of *Helicina funcki* in Costa Rica, INBio collection, according to Table 4, and type material of *Helicina funcki* and *Helicina funcki costaricensis*; for explanations see Fig. 21.

prisingly well in their mean values, although this is often not supported by very extensive data in my own material or INBio's, respectively. This even agrees with the results of the analysis of "non-statistical" numbers of specimens.

Following up the fact that the highest localities always had the small-shelled populations, the average minor diameter of the 34 populations (Isla Uvita excluded) was plotted against the elevation (Fig. 31). A constant decline of the maximum values with increasing elevation is clearly visible, suggesting an influence by elevation. Furthermore, all the data scattered below this decline in maximum size indicate that altitude is not the only important parameter. The range of possible influences is too wide, and *Helicina funcki*, although widely distributed, occurs at very scattered locations so that very detailed and local studies of environmental conditions would be required to trace any further correlation.

Sexual Dimorphism: Besides weight, females in all measurements and in all populations are clearly bigger than males, although the range of measurements overlaps widely, as exemplified for Cahuita by the minor diameter-height-relation (Fig. 32). Even with a small sample size of sometimes as few as two individuals, this result is always confirmed. Furthermore, the range of the differences is often about the same as in the more extensively supported data of the populations from Cahuita, Río Peje and Monteverde. The males have a volume of about 81% of females.

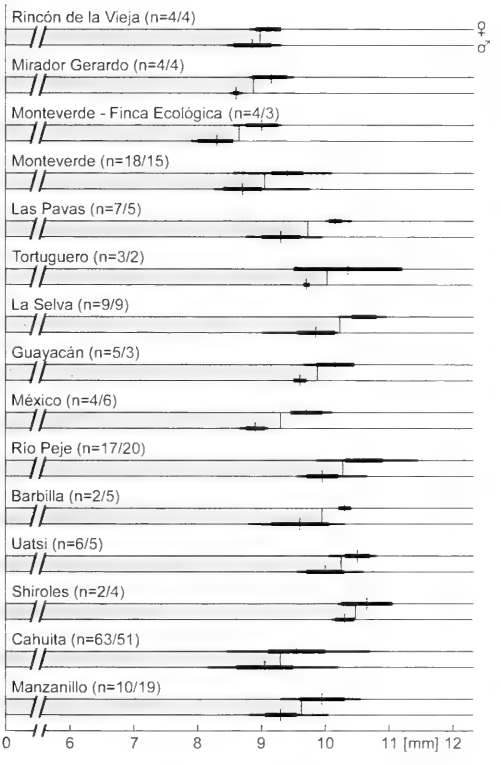


FIG. 25. Height of last whorl of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

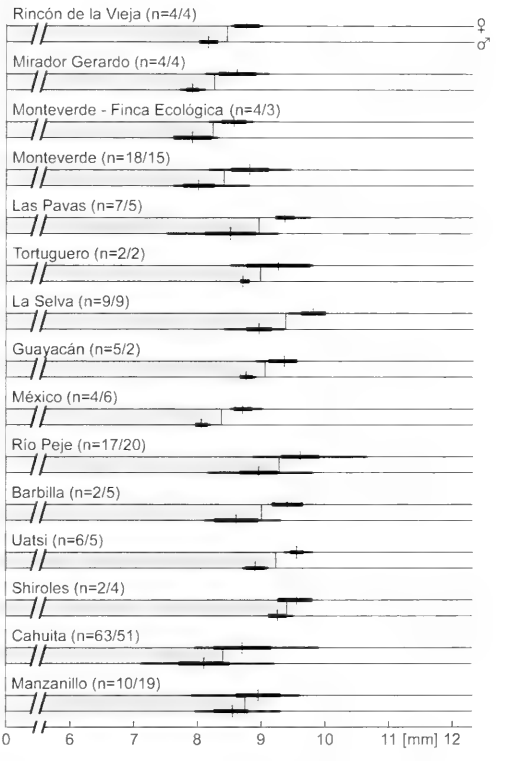


FIG. 26. Height of columellar axis of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

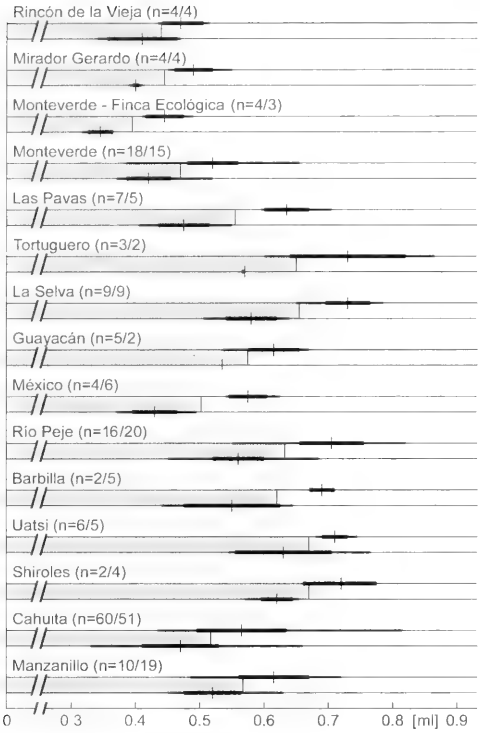


FIG. 27. Shell volume of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

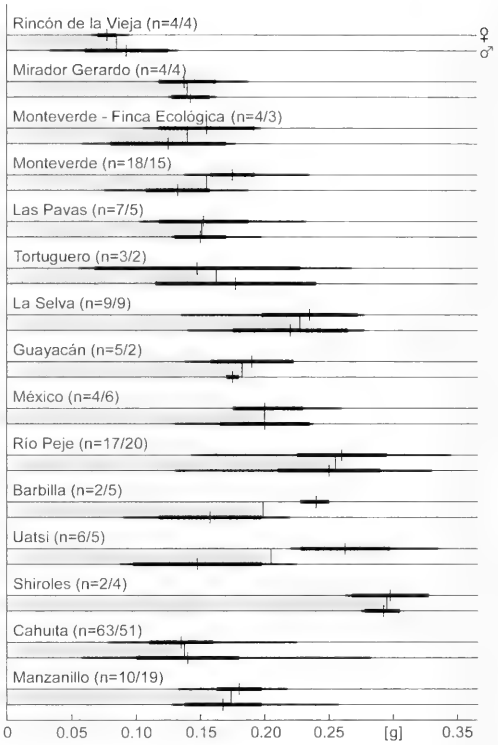


FIG. 28. Shell weight of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

TABLE 4. Minor diameter measurements [mm] of different populations of *Helicina funcki* from the INBio collection and type material, given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens.

Locality	Mean value	Deviation	Min	Max	Number	Lots
Santiago (type lot BMNH)	10.24	0.22	9.95	10.67	4	BMNH 20010497.1-4
Santa Clara (type lot *H. funcki costaricensis*)	11.84	0.02	11.82	11.86	2	MIZ 8989
Estación Góngora	11.42	0.34	10.80	11.85	6	INBio 1480300, 1480475, 1483409, 1484993, 1488083
Estación San Cristóbal	11.09	0.38	10.26	11.68	12	INBio 1488065, 1498494
Rincón de la Vieja	10.95	0.47	10.34	12.27	6	INBio 1466644, 1487945, 1498739, 1498744
Tenorio	11.37	0.17	11.20	11.54	2	INBio 1485411, 1498593
Santa Elena	10.81	0.30	10.13	11.48	8	INBio 1498638

(*Continues*)

(*Continued*)

Locality	Mean value	Deviation	Min	Max	Number	Lots
Peñas Blancas	10.82	0.44	10.45	11.48	3	INBio 1480605, 1498802
Monteverde	11.13	0.45	9.89	12.08	92	INBio 1466835, 1466842, 1466863, 1466870, 1466884, 1466891, 1466905, 1466912, 1466954, 1467003, 1467010, 1467031, 1468211, 1477521, 1477749, 1479517, 1479528, 1479539, 1479550, 1480098, 1480119, 1480126, 1480127, 1480128, 1480129, 1480130, 1480131, 1480132, 1480149, 1480152, 1480426, 1484687, 1485422, 1485426, 1485441, 1498581, 1498590, 1498632, 1498804, 1498806, 1498807, 1498828
Pitilla	11.94	0.49	11.22	13.08	8	INBio 1463787, 1463946, 1480043, 1480289, 1480318, 1480319
Monte Cele	10.91	0.22	10.58	11.26	4	INBio 1488042
Estación Playuelas	10.49	0.44	9.53	11.32	7	INBio 1479506, 1487809, 1498571
Caño Negro	12.20	0.47	11.18	12.78	8	INBio 1466940, 1480029, 1487043, 1487611, 1487878, 1501040
Barra del Colorado	12.39	0.35	11.09	13.97	59	INBio 1465700, 1477915, 1478017, 1478283, 1478294, 1480041, 1480051, 1484010, 1484013, 1484372, 1484374, 1484585, 1484587, 1484589, 1484748, 1484749, 1484991, 1485145, 1485284, 1485285, 1485289
Cerro Cocorí	12.67	0.34	11.98	13.25	19	INBio 1465446, 1467174, 1478061, 1480255, 1480261, 1483017, 1483208, 1483360
Finca Montaña Grande	13.08	0.53	12.53	14.15	4	INBio 1498610, 1501098
Río Aguas frías	13.16	0.50	12.41	13.66	3	INBio 1487980
Isla Uvita	8.95	0.09	8.86	9.03	2	INBio 3315386
Hitoy Cerere	12.72	0.44	11.82	13.55	13	INBio 1463392, 1466444, 1473832, 1475438, 1476246, 1476262, 1497862, 1497905, 3091789
Hitoy Cerere - Miramar	12.73	0.39	11.91	13.81	17	INBio 1475234, 1475694, 1475720, 1475725, 1475930, 1476376, 1476490, 1476687, 1476688, 1480272
Amubri	11.13	0.28	10.32	11.81	24	INBio 1467294, 1477569, 1477585, 1483302, 1483381, 1483382, 1483386, 1483387, 1483389, 1483390, 1483392, 1483394, 1483398, 1483400, 1483407, 1485365, 1485382, 1493444
Manzanillo	11.86	0.39	11.08	12.33	4	INBio 3097895, 3097906

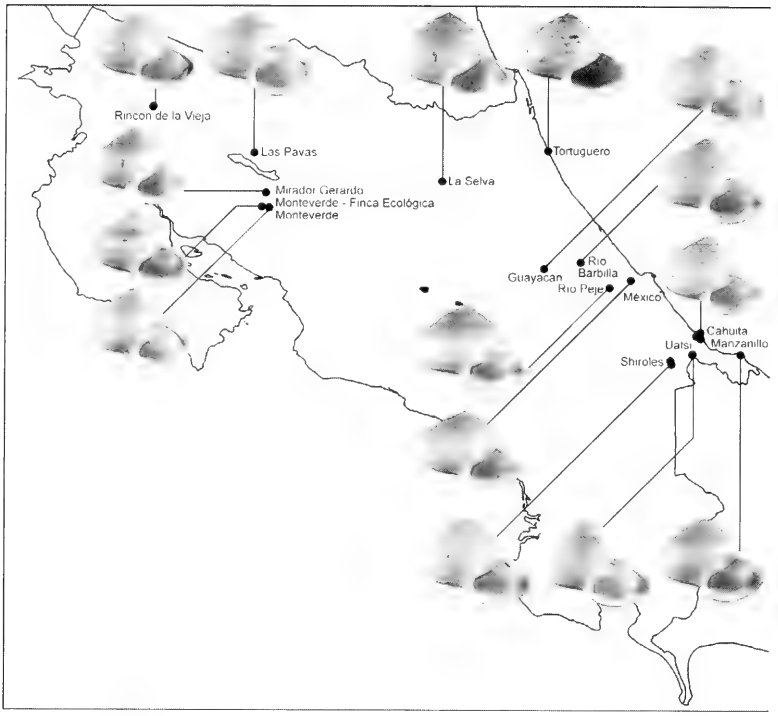


FIG. 29. Size variations in Costa Rican populations of *Helicina funcki*: shell height in figures reflects the mean value of the respective females; each shell originates from the respective locality and is randomly chosen according to the approximation of the mean value.

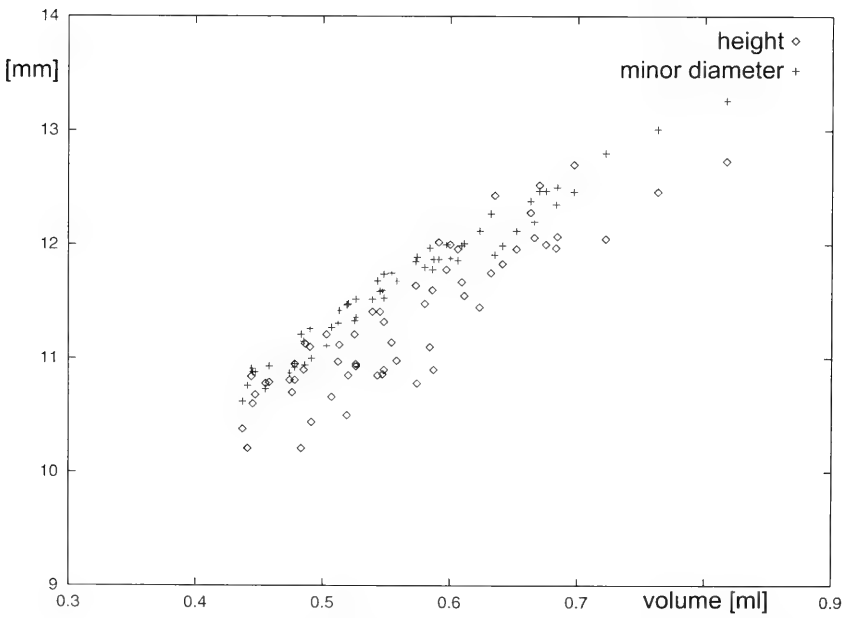


FIG. 30. Relation of shell height and minor diamater respectively to the volume in *Helicina funcki* exemplary for the females of the population from Cahuita.

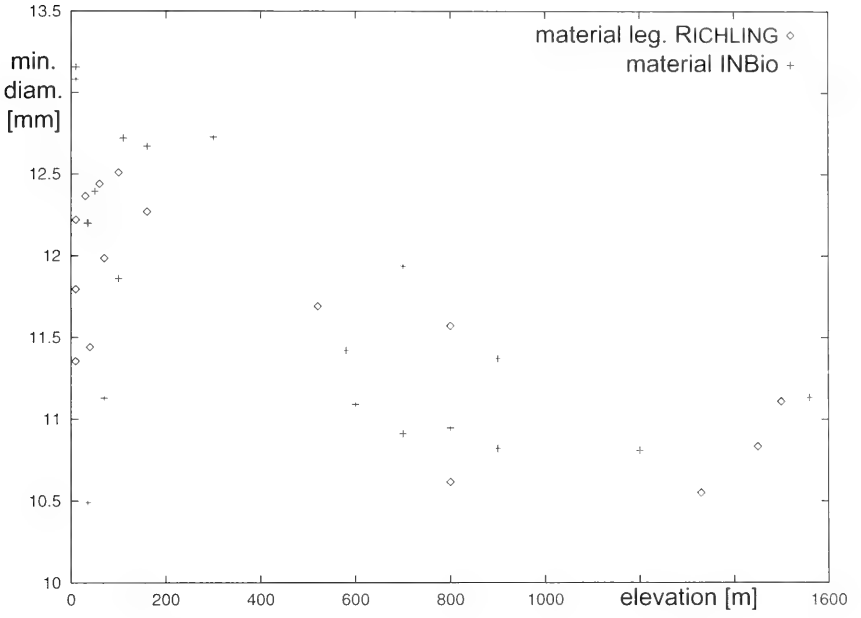


FIG. 31. Relation of minor diameter of shell to elevation of locality of different populations of *Helicina funcki* in Costa Rica; sex-independent mean values were used.

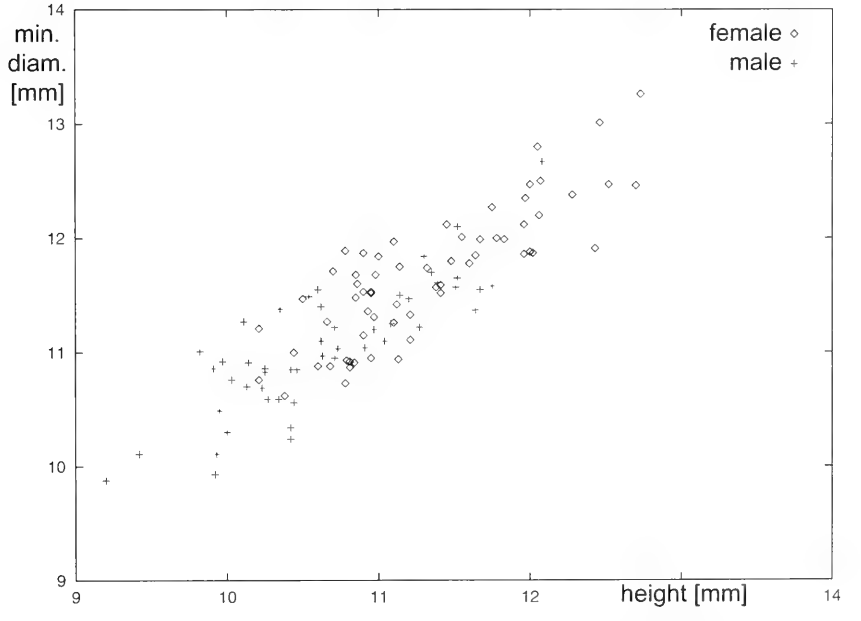


FIG. 32. Range of measurements in females and males exemplary for height and minor diameter in the population from Cahuita.

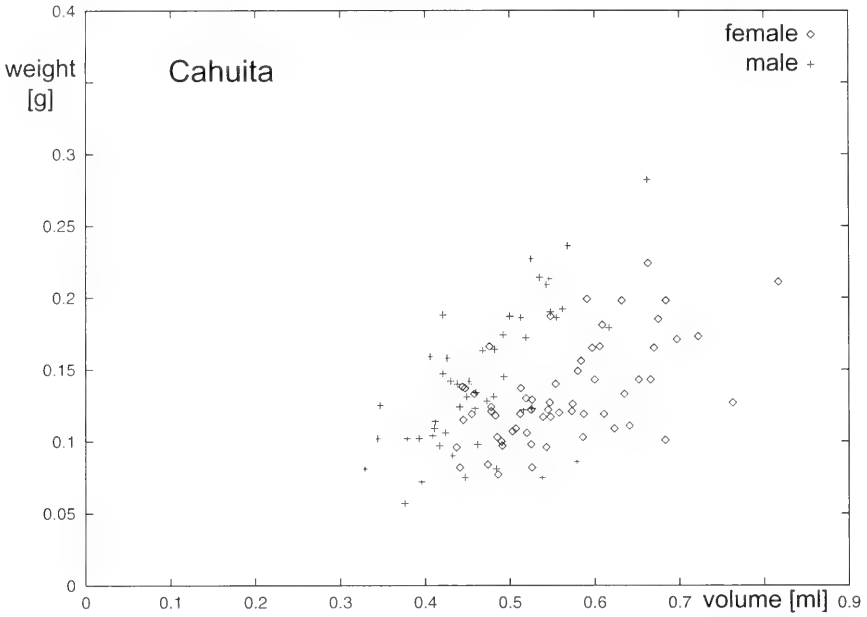


FIG. 33. Relation of weight to volume in females and males of the population of *Helicina funcki* from Cahuita (material according to Table 3).

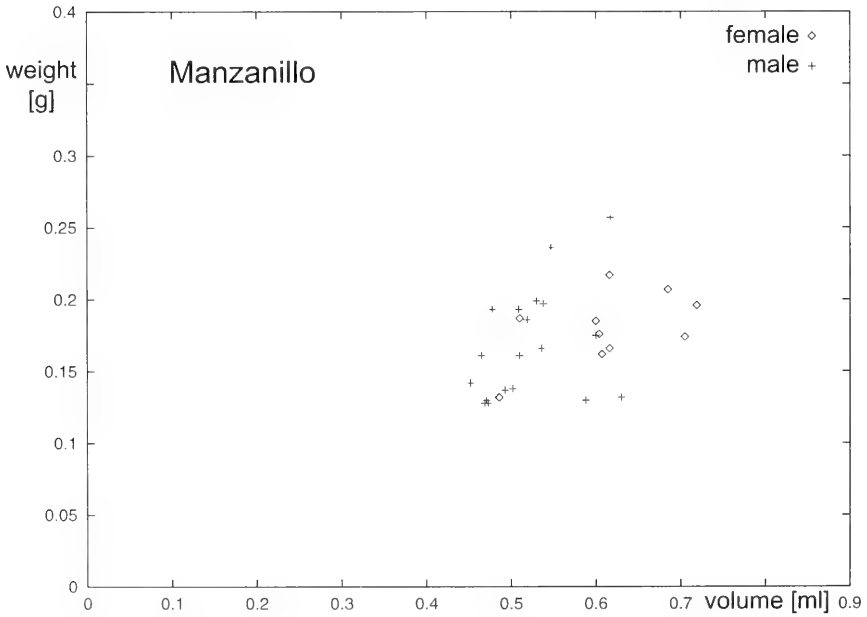


FIG. 34. Relation of weight to volume in females and males of the population of *Helicina funcki* from Manzanillo (material according to Table 3).

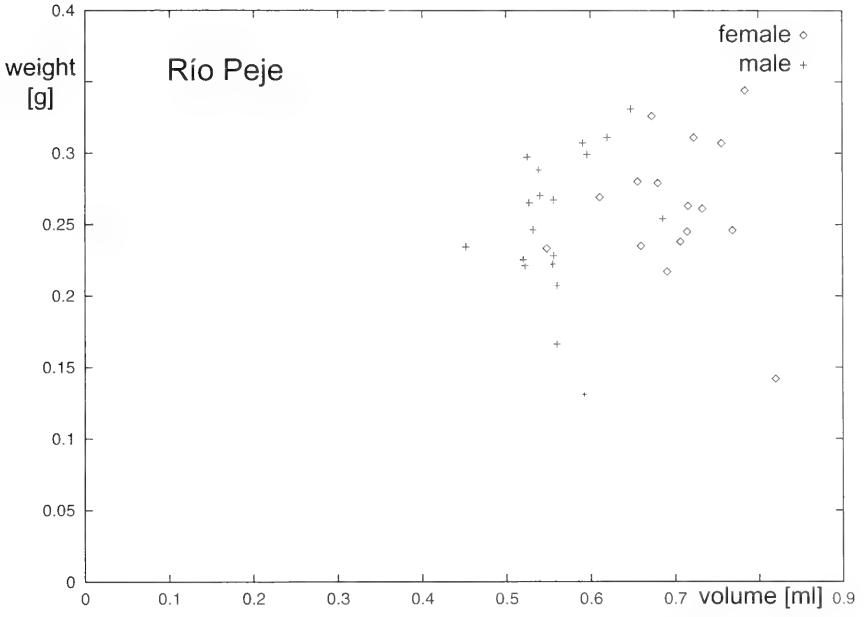


FIG. 35. Relation of weight to volume in females and males of the population of *Helicina funcki* from Río Peje (material according to Table 3).

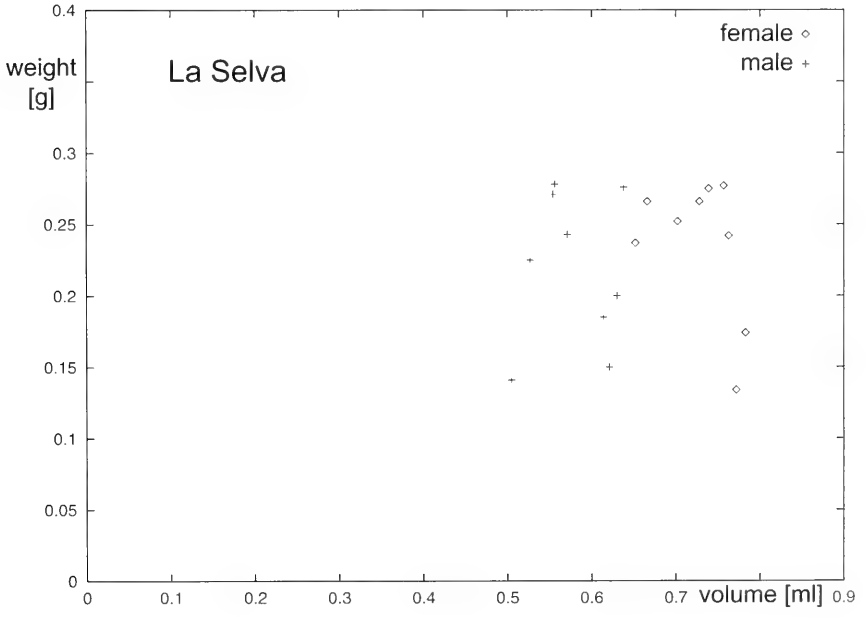


FIG. 36. Relation of weight to volume in females and males of the population of *Helicina funcki* from La Selva (material according to Table 3).

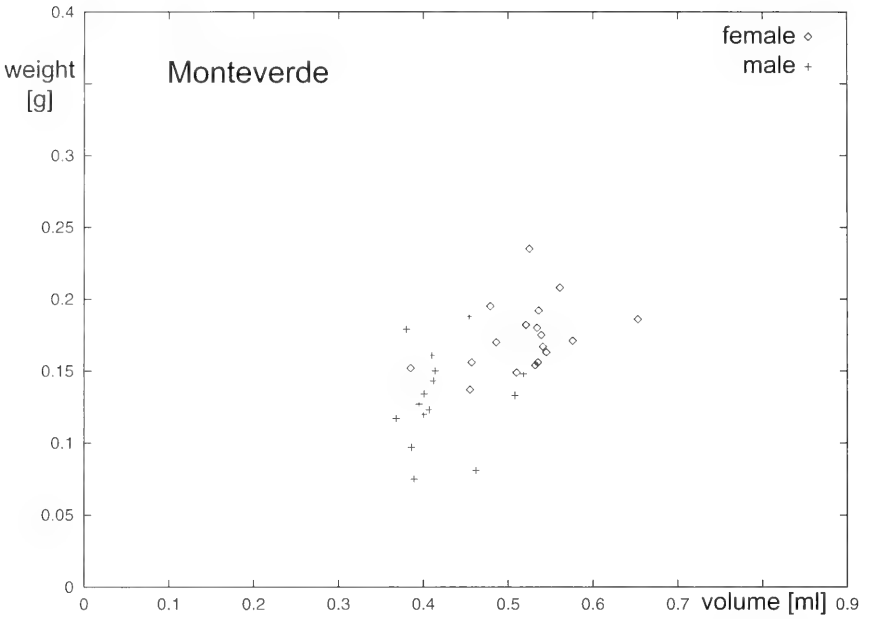


FIG. 37. Relation of weight to volume in females and males of the population of *Helicina funcki* from Monteverde (material according to Table 3).

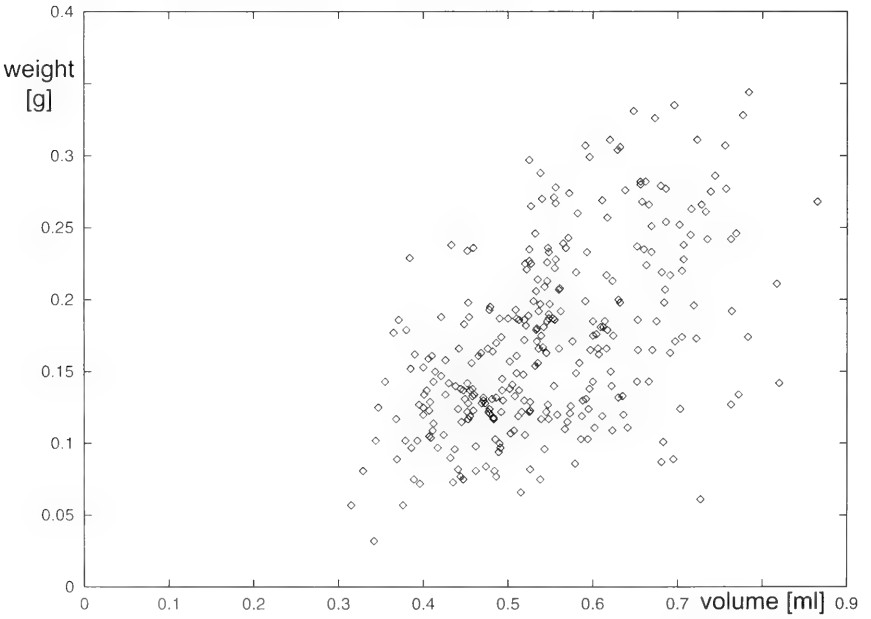


FIG. 38. Relation of weight to volume in adults of *Helicina funcki* in Costa Rica (all material listed in Table 3 included).

Considering the problems connected with the weight measurements, the data (Fig. 28) indeed show contrary results even in otherwise rather similar populations (e.g., upper rows: Rincon de la Vieja to Monteverde). When only looking at the better-supported data – namely Monteverde, La Selva, Río Peje, Cahuita, Manzanillo – the difference between males and females is greater in the population at Monteverde than in La Selva, Río Peje and Manzanillo, whereas at Cahuita this relationship is even reversed. Taking into account the greater size of all females, it seems that in the lowland populations the males invest more material in their shells than females of the same volume do. To test this assumption, the relation of weight to volume is plotted for these populations (Figs. 33–37). Because the mathematical relation between weight and volume is unknown and males and females fall into a different range, the data of all specimens of *Helicina funcki* used in the morphometric analysis were plotted as an adjustment for comparison (Fig. 38). As expected, the latter measurements are widely scattered, but a linear approximation or a function of greater degree would better match the data. A higher volume should result in a higher weight. The Monteverde population clearly demonstrates this relation for both sexes (Fig. 37), whereas the males of the lowland populations on average weigh the same as females with a higher volume (Figs. 33–36). For other localities, the deviations explained above seem to be interposed with the actual results.

Habitat

Biolley (1897) found the species on the trunks of trees, the stems of plantains (*Musa*) and also on the ground. Except for the last habitat, these observations could be confirmed during the field work for this study. Moreover, *Helicina funcki* often crawls and aestivates on the underside or more seldom on the upper side of different kind of leaves. The recognized plants belong not only to Musaceae, Heliconiaceae, and palms, but also to various herbs of the undergrowth. *Helicina.funcki* may even be found on climbing species such as the Araceae *Monstera* spec. Probably because of the relatively large size of the species, it is found on plant species with large leaves. But it lives on trunks, branches and twigs of trees, bushes and tree ferns as well. *Helicina funcki* not only crawls on live leaf surfaces, it was also found in the dead, dried and curled-up leaves, especially those of bananas. In areas of human influence specimens were observed on concrete walls of buildings or wooden fences. Thus, *H. funcki* is a typical arboreal species, having been observed up to 7 m or more above the ground. With regards to alimentation, it was definitely found feeding on the surface of trunks and on living and dead leaves.

Distribution

Helicina funcki is confined to southern Central America. Although for Nicaragua it has thus far only been recorded by Ancey (1897) from Greytown at the mouth of the Río San Juan, with a further unspecified lot in the collection of the UF and a site somewhere along the southern border of the Río San Juan (von Martens, 1901), the distribution range extends at least from southern Nicaragua to the Canal Zone in Panama. It most probably occurs in the eastern Caribbean lowlands further north in Nicaragua as well, because the habitats do not change greatly. Furthermore, the wide distribution in northern Costa Rica and the morphometric data suggest that in this area *H. funcki* has not come close to its distribution limit.

Due to the lack of literature records for the better investigated countries, such as Honduras, Guatemala and Belize, and due to the absence of *H. funcki* in the extensive Central American collection of the UF (checked personally) any occurrences north of Nicaragua can be excluded. The relatively large size furthermore renders the species unlikely to be overlooked. The records from Ylalag (Mexico: Oaxaca) by Wagner (1910a) therefore seems very questionable.

In Costa Rica, the species is fairly widely distributed throughout the Caribbean plain and on the mountain slopes (Fig. 39). The distribution is mainly influenced by the central mountain chains subdividing the country. *Helicina funcki* crosses the northern volcanic mountains (Cordillera de Guanacaste and Tilarán, Cordillera Central), where the upper Pacific slopes are connected to the Caribbean side by various valleys between the separate volcanoes. According to the present data, the species is known to occur up to 1,800 m. A limitation by altitude is furthermore supported

by the decline of the shell size with increasing elevation of the localities. In fact, the southern Cordillera de Talamanca, highly elevated as a continuous mountain chain (approximately 3,000 m), forms a clear barrier in the distribution of *H. funcki*. The exact occurrence on the Caribbean slope of this Cordillera is known only fragmentarily because the area is difficult to reach and has not been investigated. Continuing downhill towards the northern Pacific and in the Valle Central the climate becomes drier (Figs. 2, 3), therefore appearing to be the most important factor limiting the distribution. Except for the most southern Caribbean plain, *H. funcki* does not occur in areas of less than 2,000 mm annual precipitation. On the more humid southern Pacific plains and slopes, *H. funcki* is replaced by *H. pitalensis*.

The single record of *H. funcki* on the Península de Osa (INBio 1486976) seems to contradict the otherwise continuous distribution. Upon request, the data were confirmed by INBio. The specimen is small (9.4/12.1/9.5 mm). There is no reason to question the finding, despite the fact that several collecting efforts of INBio up to now have yielded only one specimen, because species of Helicinidae are extremely rare on Península de Osa.

Biolley in 1897 reports the species as the most common land snail of the country. Nowadays due to the extreme change of the land use (e.g., deforestation in large areas), it probably will be shown that synanthropic snails like *Subulina octona* (Bruguière, 1789), the introduced *Ovachlamys fulgens* (Gude, 1900) (Barrientos, 2000) and *Succinea costaricana* von Martens, 1898, the latter known as pest species in agriculture (Villalobos et al., 1995), are now much more common.

Discussion

The differences of *Helicina funcki costaricensis* to the nominal species mentioned by Wagner (1910a) can be summarized as differences in size and in a more strongly

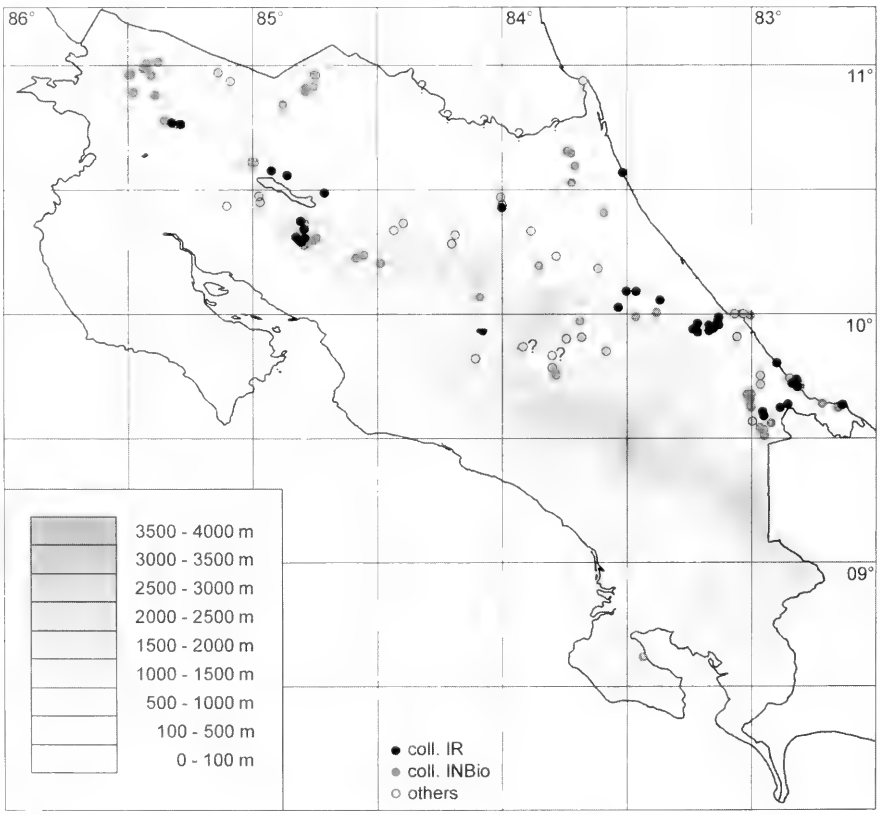


FIG. 39. Records of *Helicina funcki* in Costa Rica.

developed outer lip. The original description of the subspecies does not include any comparison with *H. funcki*. Astonishingly, Wagner (1910a) gives higher dimensions (12–15/15–18/12–14 mm) than in his publication in 1905 (11.0/13.3/11.3 mm), which on one hand clearly are exaggerated, on the other hand the indeed higher values from specimens from San José were most likely included in his measurements. The morphometric investigations of different populations of *H. funcki* suggest that the size depends on environmental factors and is not suitable for the separation of a subspecies in absence of other differentiating characters. The type lots of both the nominal form and the subspecies fall in the range of the Costa Rican specimens (Fig. 24). *Helicina funcki* reaches maximum sizes in lowlands to which the type locality of *H. funcki costaricensis* belongs. The nominal species is described from close to the southern limit of its distribution (Fig. 39), which makes it likely that environmental conditions of this area are less favorable for the species, such as perhaps at high elevations, which may result in smaller shells. Therefore, *H. funcki costaricensis* is regarded as a synonym of *H. funcki*. Regarding the comparably large shells mentioned by Wagner (1905, 1910a) (checked: MIZ 8990: 2 ads.: 13.4/16.0/13.2 mm; 13.9/15.7/12.9 mm) from San José, the locality given without comment is misleading, because one would immediately think of San José, capital of Costa Rica (in the historical times of Wagner a possible locality). But considering the relation of shell size to elevation of the locality (Fig. 31), the site appears to be in contradiction to the shell size because San José is located at about an altitude of 1,160 m. Biolley (1897) reported a small form of *H. funcki* from Cartago (close to San José, at a similar elevation). A closer examination of the map of Costa Rica reveals a second San José in the Alajuela Province, close to Santa Clara, which is here suggested to be the locality "San José". It also supports the localization of "Santa Clara". Under *H. funcki costaricensis*, Wagner (1910a) mentions a somewhat dubious form from Ylalag, Mexico in his collection, which is said to be more elevated and remarkably angulated at the periphery. It could not be checked and therefore cannot be discussed any further, especially because of the outstanding locality for *Helicina funcki*.

The description of *Helicina deppeana parvidens* has to be discussed in the context of material in the ZMB. *Helicina deppeana* von Martens, 1863, was described from Mexico (locality unknown) and was figured later (von Martens, 1865, 1890) together with a variety from Yalalag (State of Oaxaca, Mexico). The study of the original material of the figures stored in the ZMB revealed the following: the typical *H. deppeana* (syntypes ZMB 4571) are not conspecific with *H. funcki*, for example, they do not have the typical ornamentation of lighter patches, and are more solid and unicolored. The specimens of the variety from Yalalag (ZMB 1743) look exactly like specimens of *H. funcki* and thus are specifically different from *H. deppeana*, an observation already remarked on the label by Wagner: "nach meiner Ansicht stellen die vorliegenden Exemplare nur *Helicina funcki* dar" [= in my opinion the specimens only represent *H. funcki*]. Interestingly, Wagner (1910a) completely avoids any comment on this in his monograph, although it is certain that he had seen the collection prior to his publication, because various types of newly described species (e.g., *H. pitalensis*, *H. tenuis pittieri*) are in the ZMB collection. The singular Mexican locality of *H. funcki* is discussed in the paragraph "Distribution". Returning to *H. deppeana parvidens*, it is very likely that when Pilsbry (1920a) published his work on Costa Rican land molluscs, he used the Biologia Centrali-Americana (von Martens, 1890–1901), representing the only comprehensive contribution for the area even today. It therefore appears probable that Pilsbry was misled by this figure and classified part of his Costa Rican material of *H. funcki* as a new subspecies of the Mexican *H. deppeana*.

Helicina (*Tristramia*) *pitalensis*
Wagner, 1910

Helicina funcki – von Martens, 1900: 603–604: Costa Rica: SW-Costa Rica: Bay of Terraba [mouth of Río Terraba, about 09°00'N, 83°36'W, Puntarenas Province], Tocori in the valley of the Río Paquita [NE of Quepos, canton Aguirre, 09°29'43"N, 84°04'52"W, 10 m a.s.l., Puntarenas Province], middle part of the Río Saveque [now: Río Savegre, about 09°29'N, 83°56'W, San José Province] and lower part of the Río Pacuare [now Río Pacuar south of San Isidro de El General [not Río Pacuare on Atlantic slope!], about 09°16'N, 83°39'W, San José Province] (Pittier); El Pital, in the valley of the Río

Naranjo [near Londres? (about 09°27'N, 84°05'W, Puntarenas Province], some specimens banded and others more elevated (Pittier) [in part] [*non* L. Pfeiffer, 1849]

Helicina pitalensis Wagner, 1910a: 308, pl. 61, figs. 17–19

Helicina amoena – Monge-Nájera, 1997: 113: Costa Rica [*non* L. Pfeiffer, 1849]

Original Description

"Gehäuse kegelförmig mit gewölbter Basis, festschalig, leicht glänzend, zitrongelb mit undeutlichen weissen Flecken und Punkten, sowie einer schmalen rotbraunen Binde über der Naht und dem Kiel. Die Skulptur besteht aus feinen, etwas ungleichmässigen Zuwachsstreifen, auch erscheint die Epidermis unter der Lupe sehr fein gerunzelt. Das regelmässig spitzkegelförmige Gewinde besteht aus 5–5$^1/_2$ leicht gewölbten, langsam zunehmenden Umgängen, welche durch eine hell berandete, schwach eingedrückte Naht geschieden werden; der letzte ist beiderseits gleichmässig gewölbt, an der Peripherie deutlich kantig bis stumpf gekielt und steigt vorne nicht herab (unmittelbar vor der Mündung ein wenig hinauf). Die abgerundet dreieckige Mündung ist schief, innen gelb mit durchscheinender Binde. Der leicht verdickte, gelbliche Mundsaum erweitert; der Oberrand schmal und an der Insertion vorgezogen, der Aussen- und Basalrand breit umgeschlagen. Die kurze, abgerundete Spindel ist senkrecht oder leicht nach links gebogen; am Uebergange derselben in den Basalrand der Mündung eine zahnartig vorspringende Ecke. Der sehr dünne, feingekörnelte Basalkallus nur im Umkreise der Spindel deutlich. Das Grübchen in der Nabelgegend undeutlich.
D = 14, d = 11,5, H = 13,5 mm.
Deckel birnförmig mit seitlich gekrümter [sic] Spitze schwarzbraun bis pechschwarz mit lichterem Streifen entlang der Sigmakante; die dünne, feingekörnelte Kalkplatte nur am Spindelrande etwas leistenartig verdickt; in den übrigen Verhältnissen typisch.

Fundort: El Pital im Tale des Río Naranjo im südwestlichen Costarica. Da abgebildete Exemplar im k. Museum zu Berlin.

Von der ähnlichen *Helicina funcki* Pfeiffer unterscheidet sich vorstehende neue Art durch die lebhafte Färbung mit deutlicher Binde, die glänzende Oberfläche mit deutlicheren Zuwachsstreifen, das höhere Gewinde mit deutlich gewölbten langsam und regelmässig zunehmenden Umgängen, den weniger erweiterten, aber deutlich kantigen bis stumpfgekielten letzten Umgang, sowie besonders die abweichenden Verhältnisse der Mündung und des Mundsaumes."

Type Material

ZMB 103240 "El Pital, 200 m, III.1893, Vallée du Río Naranjo, leg. Madame Pittier de Fahega" (the lot contains one specimen)
Because the original description refers to one specimen in the ZMB which matches the figure, it is the holotype (Fig. 40).
Dimensions:
Holotype: 13.0/12.5/14.0/11.2/9.1/10.6/10.0 mm

Type Locality

"El Pital im Tale des Río Naranjo im südwestlichen Costarica"; El Pital could not be

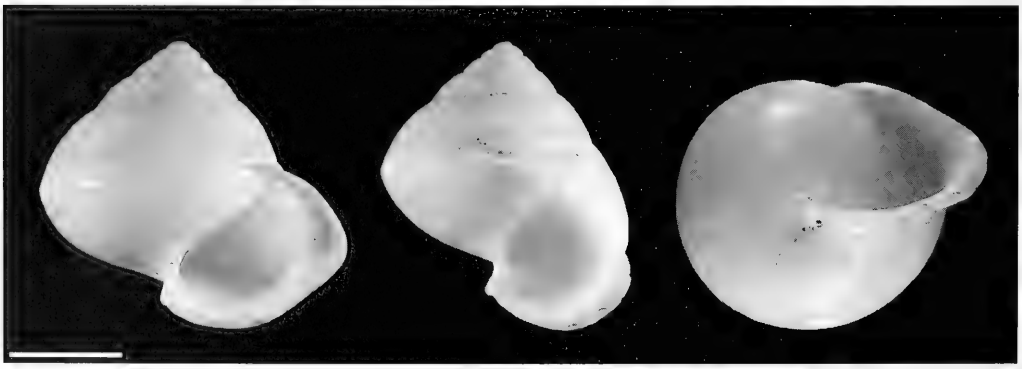


FIG. 40. *Helicina pitalensis*, holotype, ZMB 103240, height 13.0 mm; scale bar 5 mm.

localized on recent detailed maps. The Río Naranjo leads into the Pacific Ocean at the southern border of the Parque Nacional de Manuel Antonio, a little south of Quepos. By the elevation given in the data remaining with the original material, the type locality can be assumed to be located near Londres [about 09°27'N, 84°05'W], Puntarenas Province.

Examined Material

Leg. I. Richling

Puntarenas: S *San Vito*, Wilson Botanical Garden, Las Cruces, sendero a Río Jaba, 08°46'57"N, 82°57'40"W, 1,160 m a.s.l., 27.08.1999: (IR 1013); 28.08.1999: (IR 1016)

N Neily, road from Ciudad Neily to San Vito, open area with a few trees, 08°40'23"N, 82°56'44"W, 180 m a.s.l., N Neily, 23.03.1997: (IR 209)

Fila de Cal, road from Ciudad Neily to San Vito, S Campo Dos, burned area, 08°41'00"N, 82°56'29"W, 630 m a.s.l., 23.03.1997: (IR 191)

Fila Costeña, *north of Bajo Bonito* (locally called Llano Bonito), N of Río Claro, rain forest, 08°44'41"N, 83°02'09"W, 980 m a.s.l., 24.03.1997: (IR 221); 15.02.1999: (IR 579); 29.08.1999: (IR 1028); 06.03.2001: (IR 1485)

INBio Collection

Puntarenas: *Parque Nacional Corcovado*: *Estación Sirena, 08°28'52"N, 83°35'32"W, 5 m a.s.l.*: leg. Mario Chinchilla, 23.03.1995: 1 juv. (INBio 1485050); *Sendero los Espaveles, Sirena, 08°28'49"N, 83°35'42"W, 0 m a.s.l.*: leg. Annia Picado, 25.03.1995: 1 ad. (INBio 1482837); 1 ad. (INBio 1482842); *Sendero Espaveles, 08°29'05"N, 83°35'29"W, 0 m a.s.l.*: leg. Socorro Avila, 23.03.1995: 1 ad. (INBio 1482627); *Sendero Espaveles, 08°29'22"N, 83°35'14"W, 0 m a.s.l.*: leg. Billen Gamboa R., 03.12.1995: 1 ad. (INBio 1485173); *Estación Sirena, Sendero Las Ollas, 08°28'47"N, 83°35'40"W, 5 m a.s.l.*: leg. Alejandro Azofeifa, 25.03.1995: 1 juv. (INBio 1484670); *Estación Sirena, Sendero Las Ollas, 08°28'57"N, 83°35'20"W, 20 m a.s.l.*: leg. Francisco Alvarado, 25.03.1995: 1 s.ad. (INBio 1484221); *Sendero los Patos, 3.5 km al N. de la Estación Sirena, 08°30'46"N, 83°35'56"W, 0 m a.s.l.*: leg. Ramon Angulo, 26.08.1994: 1 juv. (INBio 1480506); *Río Pavo, 08°30'51"N, 83°35'44"W, 20 m a.s.l.*: leg. M. Madrigal, 03.04.1996: 2 ads. (INBio 3542542)

Reserva Forestal Golfo Dulce: *Cerro La Torre, Finca La Purruja, 08°32'04"N, 83°25'53"W, 400 m a.s.l.*: leg. Javier Quesada, 05.05.1994: 1 s.ad. (INBio 1477485); *Agujas, alrededores de la estación, 08°32'13"N, 83°25'33"W, 300 m a.s.l.*: leg. A. Berrocal, 01.11.1998: 1 ad. (INBio 3397130)

Fila Cal: *24 km de San Vito hacia Ciudad Neilly, 08°41'36"N, 82°56'36"W, 780 m a.s.l.*: 29.08.1995: 1 ad. (INBio 1485456); 29.08.1995: 1 s.ad., 1 juv. (INBio 3121204) (all leg. Marianella Segura); *24.5 km S en la carretera de San Vito hacia Ciudad Neilly, 08°40'55"N, 82°56'23"W, 600 m a.s.l.*: leg. Zaidett Barrientos, 21.11.1995: 1 juv. (INBio 1485120)

4.5 km NW de Ciudad Neily, Camino Paralelo al Río Caño Seco, Colectado en hojarasca en helechos, 08°40'50"N, 82°57'25"W, 180 m a.s.l.: leg. M. Chinchilla, 22.11.1995: 1 ad. (INBio 3542525)

Linda Vista, Río Claro: *3 km NE de la Escuela de Llano Bonito, 08°44'54"N, 83°02'04"W*: 920 m a.s.l., leg. Socorro Avila, 24.03.1997: 1 s.ad., 1 juv. (INBio 1494393); 950 m a.s.l., leg. Alexander Alvarado Mendez, 15.02.1999: 1 s.ad., 1 juv. (INBio 3091134)

Other Sources

COSTA RICA

Alajuela: La Paz, Chemin du rivière Sarapiqui [not localized, near Isla Bonita?, about 10°15'30"N, 84°11'W], Biolley, *ex* Godet, 12.1892 received: 1 ad. (ZMB 45501)

Description

Shell (Fig. 335D–E): Conical-subglobose, solid, relatively large, slightly shiny to dull. Color: basic color lemon yellow, sometimes less bright, with slender reddish-brown band between sutures or suture and the periphery respectively, in some specimens very light or obsolete. On account of this band, the upper whorls may appear darker. The periphery is always lighter. As in *Helicina funcki*, the color is overlapped by fine white patches and lines giving the shell a special ornamentation. Surface textured with fine, irregular growth lines and oblique grooves of different individual orientation but of same general direc-

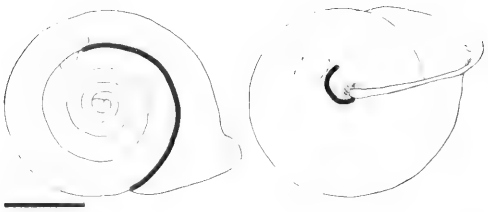


FIG. 41. Axial cleft and muscle attachments of *Helicina pitalensis*, IR 579; scale bar 5 mm.

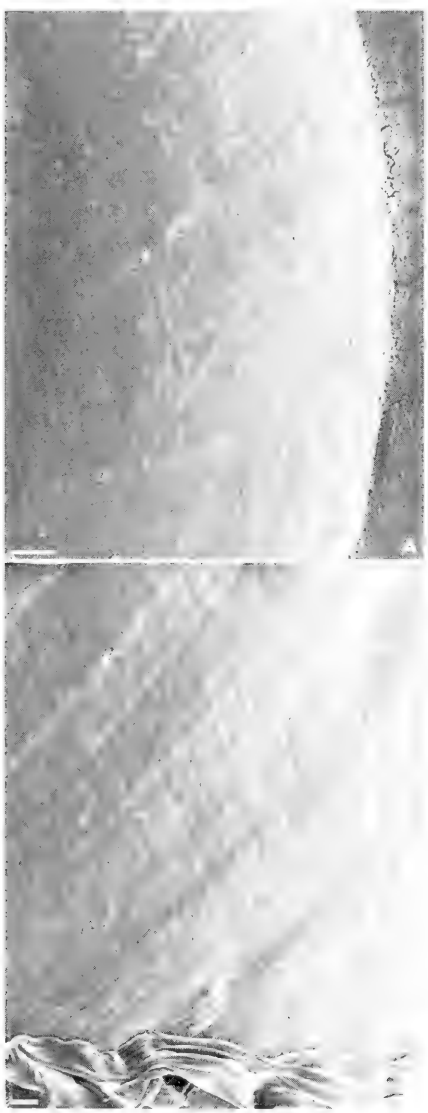


FIG. 42. Teleoconch surface structure of *Helicina pitalensis*. A. On 2nd whorl. B. On 4th whorl; scale bar 100 µm.

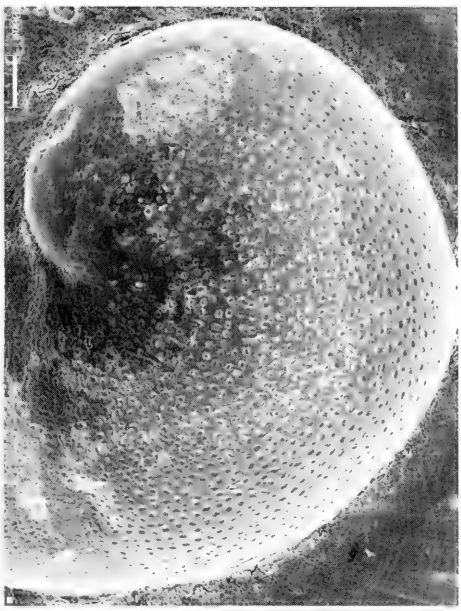


FIG. 43. Embryonic shell of *Helicina pitalensis*; scale bar 100 µm.

tion (Fig. 42), causing the dull appearance. Embryonic shell with about 1 whorl; $4^{1}/_{8}$–$4^{5}/_{8}$ subsequent whorls slightly convex; periphery remarkably angulated; whorls equally extending in size and slightly descending, only towards aperture slightly ascending; spire very regular. Suture slightly impressed and marginally lighter in color. Aperture oblique and nearly straight, inserting a little above periphery. Outer lip yellowish-whitish, very thickened, broadly expanded, only in the upper palatal part a little less strongly developed. Reflection nearly rectangular to

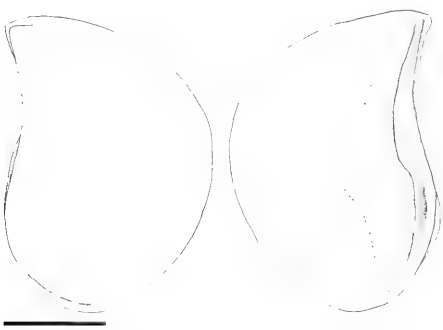


FIG. 44. Operculum of *Helicina pitalensis*, IR 579; scale bar 2.5 mm.

the whorl; transition to columella with a remarkably protruding denticle. Columella short, slightly curved, umbilical area without any groove or impressed line. Basal callus only close to columella present, thin, slightly granulated.

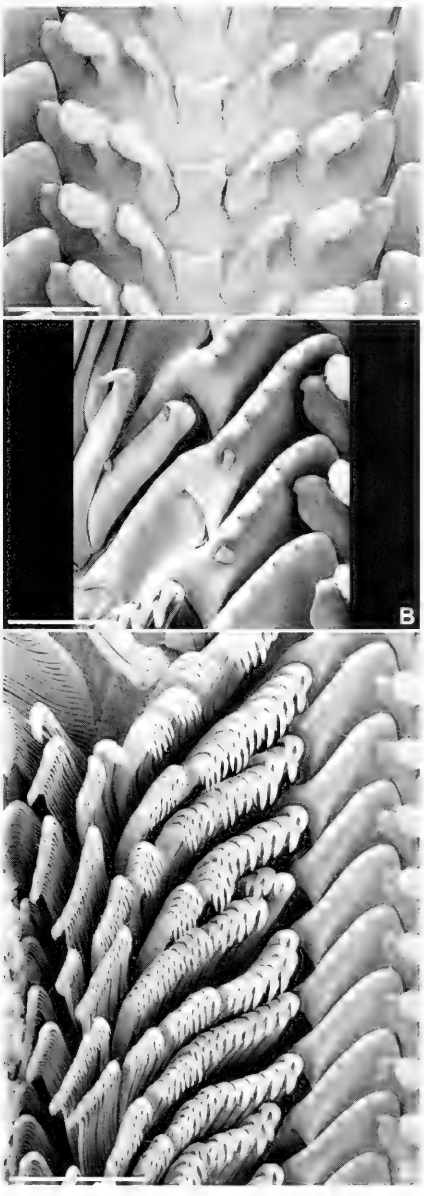


FIG. 45. Radula of *Helicina pitalensis*. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 µm (A, B), 100 µm (C).

Juveniles are roundly angulated, and in some cases a few rows of periostracal hairs are present at the periphery.

Internal Shell Structures: (Fig. 41)

Teleoconch Surface Structure (Fig. 42): The transitional structure is developed, but as in *Helicina funcki* the pattern of oblique diverging grooves continues up to the aperture. In the shell illustrated, the grooves remain finer than in *H. funcki* (see 4th whorl), but this aspect is subject to individual variation.

Embryonic Shell (Fig. 43): The embryonic shell of *Helicina pitalensis* is very similar to that of *Helicina funcki*. The specimens measured came from altitudes of nearly 1,000 m. In comparison with the *H. funcki*-populations, the intermediate size therefore suggests equal dimensions, assuming a similar dependence on altitude.
Diameter: 1,089 µm (± 23) (1,040–1,150) (n = 10) (IR 579, IR 1013, IR 1028, IR 1485).

Operculum (Fig. 44): Slightly calcified, calcareous plate leaving a free margin, thickened towards columellar side. Color dark reddish-brown to even black, only non-calcified margin transparent. Columellar side regularly S-shaped, upper end acute and pointed, lower end well rounded.

Animal (Fig. 337C): Only specimens that were very similarly colored from Bajo Bonito were studied. The foot is whitish-yellowish

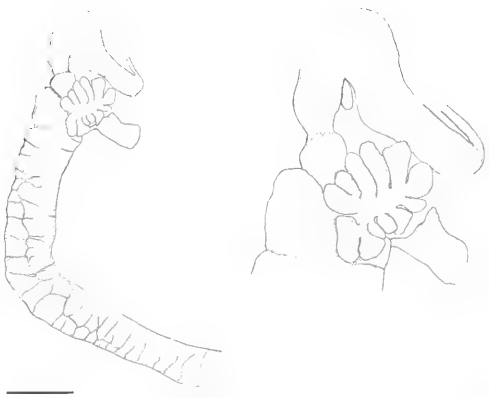


FIG. 46. Female reproductive system of *Helicina pitalensis*, apical complex enlarged, IR 579; scale bars 2 mm (left), 1 mm (right).

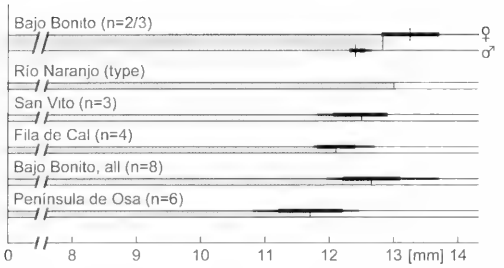


FIG. 47. Shell height of different populations of *Helicina pitalensis* in Costa Rica, according to Table 5; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex.

throughout, the head region, especially around the black eyes and occasionally the upper part of the snout, is distinctly white. The tentacles become gradually darker towards their tips. The mantle has a whitish pigmentation.

Radula (Fig. 45): Only two specimens were investigated. The cusps on the A- and C-central are vestigial, only the B-central bears 5 to 9 cusps. Comb-lateral with 6–8 cusps, cusps on marginals slowly increasing in number. Radula with about 95–99 rows of teeth.

Female Reproductive System (Fig. 46): Only three female specimens were available for dissection. The pallial reproductive system closely resembles that of *Helicina funcki*.

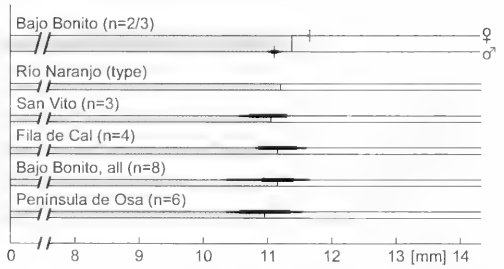


FIG. 48. Minor diameter of shell of different populations of *Helicina pitalensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

The bursa copulatrix differs in that it is as elongated as the whole organ, and the lobes project from a central axis and are much shorter, similar to those in the other species, although they are occasionally further subdivided. The provaginal sac seems to be smaller than in *Helicina funcki*.

Morphometry and Sexual Dimorphism

Despite the number of lots of *Helicina pitalensis*, the material for morphometric analysis is scant because of a high proportion of juvenile shells.

Individuals from the lowlands of the Península de Osa differed from the typical specimens in having a more prominent aperture. The few individual records summarized as "Península de Osa" originate from the same region near Estación Sirena and were compared to populations from "San Vito", "Bajo Bonito" and "Fila de Cal", which are located close to each other in the mountainous country on the southern Pacific side (Fig. 52). The only specimens whose sex was determined belong to the population of Bajo Bonito. Any comparisons in this species can only hint at possible tendencies because of the scanty data.

Morphometry: The different populations show remarkably little differences in their minor diameter (Table 5, Fig. 48), which therefore provides a good reference for the pattern of differences among the populations for other measurements (Figs. 47, 49–51). The population "Península de Osa" displays the highest deviations; the shells are relatively less elevated in every respect (height, height of last whorl and columellar axis), but the aperture and outer lip is much more expanded. This confirms the observations noted above (Fig. 52). In general, the "Bajo Bonito" population best matches the type in proportions and size. This excludes a correlation of the differing shell shape of the "Península de Osa" specimens to the altitude, because the type lot also originates from lowlands (200 m) whereas the other sites are located at 700 to 1,160 m (San Vito). Thus, the special shell shape of the population "Península de Osa" seems to be a local peculiarity. Furthermore, current data do not support a correlation of shell size and altitude as for *Helicina funcki*.

TABLE 5. Measurements of different populations of *Helicina pitalensis* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; only population in last column separated in females and males, these individuals are also included in "Bajo Bonito, all" (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

	"San Vito" (altitude 1160 m) lots IR 1016					"Fila de Cal" (altitude 600–780 m) lots IR 191, 209, INBio 1485456, INBio 3542525				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	12.48	0.47	11.78	12.89	3	12.12	0.30	11.75	12.72	4
Maj. diam.	12.34	0.37	11.78	12.65	3	12.31	0.19	11.96	12.58	4
Min. diam.	11.04	0.34	10.53	11.31	3	11.13	0.30	10.81	11.60	4
Outer lip	8.46	0.08	8.39	8.58	3	8.48	0.27	7.93	8.82	4
Last whorl	10.02	0.31	9.56	10.33	3	9.84	0.25	9.36	10.14	4
Col. axis	9.45	0.40	8.85	9.79	3	9.39	0.48	8.91	9.88	4

	"Bajo Bonito, all" (altitude 920–980 m) lots IR 221, IR 579, IR 1028, IR 1485					"Península de Osa" (altitude 0–20 m) lots INBio 3542542, INBio 1482627, INBio 1482837, INBio 1482842, INBio 1485173				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	12.64	0.45	11.96	13.70	8	11.69	0.50	10.78	12.44	6
Maj. diam.	12.49	0.33	12.07	13.12	8	11.95	0.43	11.30	12.62	6
Min. diam.	11.13	0.27	10.33	11.66	8	10.93	0.40	10.35	11.54	6
Outer lip	8.51	0.27	7.85	9.08	8	8.78	0.42	8.25	9.25	6
Last whorl	10.21	0.29	9.68	10.78	8	9.77	0.39	9.27	10.30	6
Col. axis	9.50	0.33	8.75	10.48	8	8.89	0.52	7.91	9.67	6

	"Bajo Bonito" (altitude 980 m) lots IR 579, IR 1028, IR 1485					
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	13.26	0.44	12.82	13.70	2
Height	m	12.41	0.16	12.29	12.65	3
Maj. diam.	f	13.09	0.04	13.05	13.12	2
Maj. diam.	m	12.34	0.19	12.17	12.63	3
Min. diam.	f	11.64	0.02	11.62	11.66	2
Min. diam.	m	11.08	0.07	10.98	11.18	3
Outer lip	f	8.81	0.28	8.53	9.08	2
Outer lip	m	8.61	0.18	8.35	8.88	3
Last whorl	f	10.67	0.12	10.55	10.78	2
Last whorl	m	10.21	0.15	10.07	10.43	3
Col. axis	f	9.95	0.53	9.42	10.48	2
Col. axis	m	9.43	0.10	9.27	9.54	3
Weight	f	0.074	0.000	0.074	0.074	1
Weight	m	0.121	0.024	0.091	0.156	3
Volume	f	0.603	0.000	0.603	0.603	1
Volume	m	0.507	0.027	0.476	0.547	3

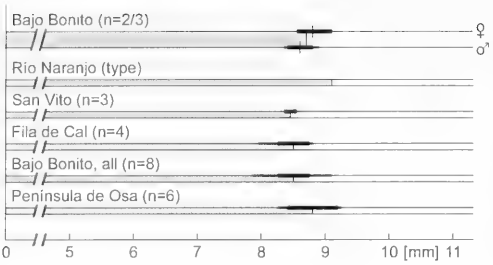


FIG. 49. Expansion of outer lip of different populations of *Helicina pitalensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

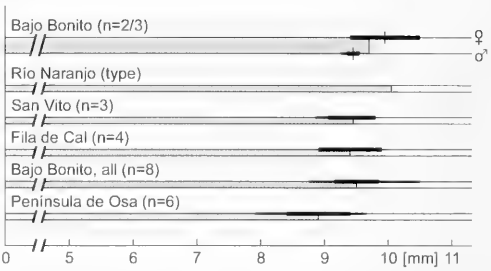


FIG. 51. Height of columellar axis of different populations of *Helicina pitalensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

Sexual Dimorphism: Although not well supported, the data for only two females and three males (Table 5, Figs. 47–51, upper row) suggest that females are bigger. The clear differences between both sexes for height, minor diameter, and height of last whorl may be only a coincidence.

Habitat

My live material came from two localities, near Bajo Bonito and near San Vito. They are characterized by steep mountain forests, probably primary rain forests, the first bordered by secondary growth and small manually tended agricultural areas. *Helicina pitalensis* lives in arboreal environments mainly on the underside of leaves of palms and Heliconiaceae. It was also found in the dried and curled-up leaves of abandoned banana trees. It thus has a very similar habitat as *H. funcki*.

Distribution (Fig. 53)

According to the relatively few records, *Helicina pitalensis* is confined to the southern Pacific slopes and coastal lowlands in Costa Rica. On the Península de Osa and in the Fila de Cruces it is found at various localities. From the area around the type locality and the connecting area to the southern localities there are no recent records. This may be explained by lack of investigations in these areas and the relatively low abundance of the species on one hand, and the fact that the Pacific plains were transformed into agricultural plantations to a large extent starting in the 1950s.

The records of Pittier date back to the end of the 19th century when the areas where largely unexplored and under closed forest cover. Assuming that the interpretation of the records listed in von Martens (1900) is correct, *H. pitalensis* at least was well distributed over the area of the southern Pacific plain, replacing *H. funcki* in this region. In the Fila Cruces area and on Península de Osa, *H. pitalensis* is found sympatrically with *H. talamancensis*.

A typical specimen (ZMB 45501) of *H. pitalensis* is labeled as originating from La Paz, a location at the Río Sarapiqui north of the Cordillera Central on the Caribbean slope. This location seems to contradict the assumed distribution. Pending better knowledge, it is considered here to be erroneous.

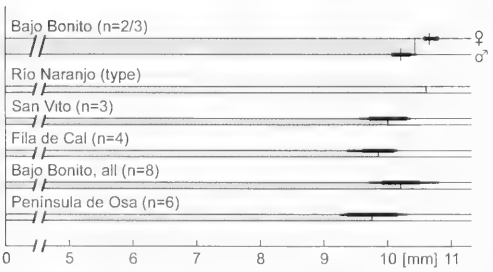


FIG. 50. Height of last whorl of different populations of *Helicina pitalensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

Discussion

The species most resembles *Helicina funcki*, which is of about equal size and shows the same shell ornamentation. *Helicina pitalensis* is relatively higher and has more convex whorls. All specimens of *H. funcki* studied show neither banding nor the distinct angulation of the periphery. The strong denticle at the transition of the basal outer lip to the columella is characteristic for *H. pitalensis*, whereas it lacks the groove or angulation in the transition from the columella into the body whorl. Fur-

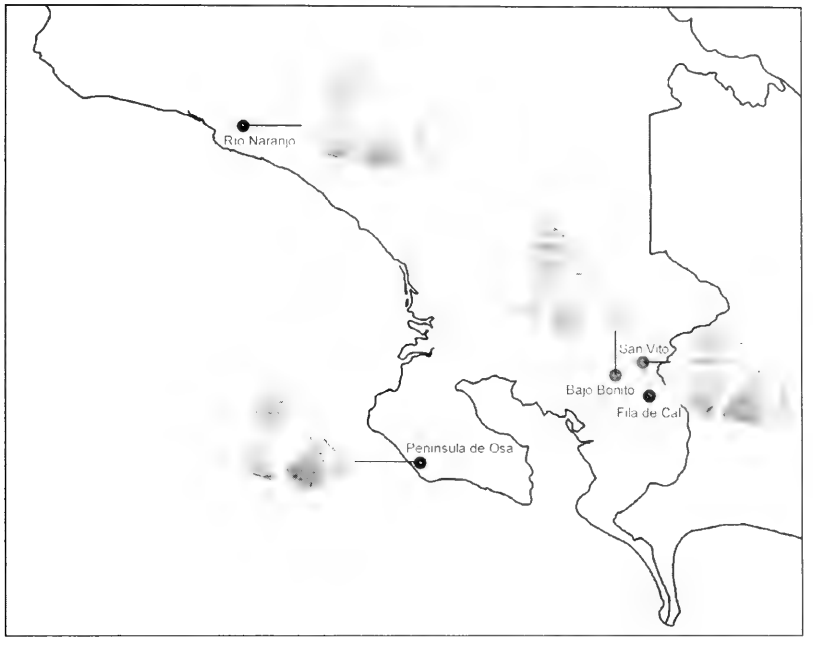


FIG. 52. Variations in Costa Rican *Helicina pitalensis*: shell height in figures reflects the mean value (enlarged), each shell originates from the respective locality.

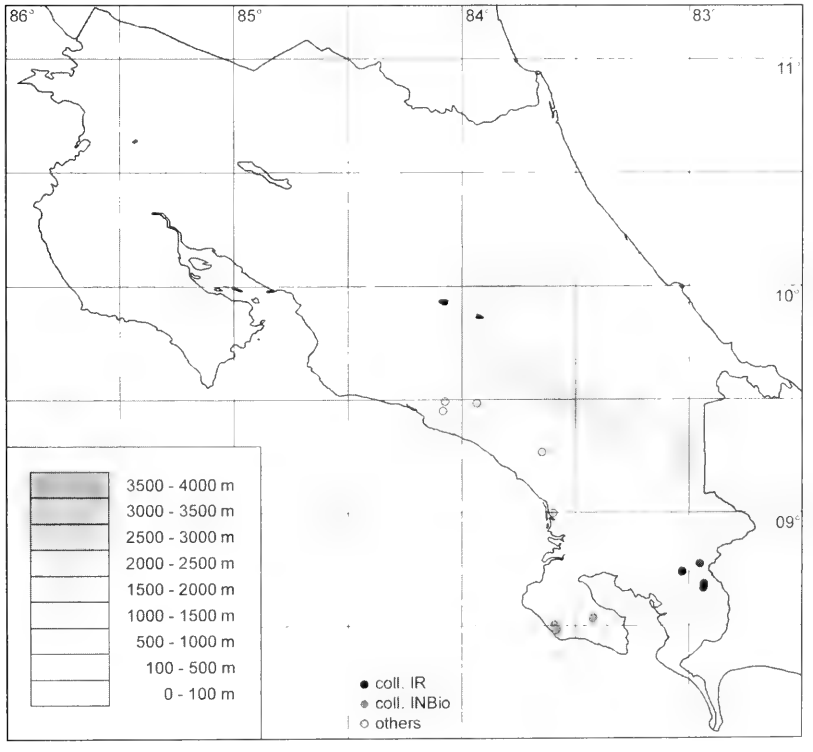


FIG. 53. Records of *Helicina pitalensis* in Costa Rica.

thermore, the soft body color differs and is constantly lighter in *H. pitalensis*.

The interpretation of the additional records of *H. funcki* listed in von Martens (1900) in SW-Costa Rica is difficult, because one of these locations became the type locality of *H. pitalensis* with description of this species by Wagner. Von Martens (1900) remarked: "some specimens banded and others more elevated", obviously for the specimens from El Pital. As here, Wagner saw only the holotype from the ZMB. If the remark of von Martens (1900) also referred to the specimens from the other locations, it would render their identification as *H. pitalensis* very likely. Although other material of Pittier is kept in the ZMB or the MHNN respectively, these lots could, unfortunately, not be found in either of the collections and thus could not be verified. According to personal information of Zaidett Barrientos (INBio), those parts of the historical collections in Costa Rica in the Museo Nacional in San José could not yet be found when she searched for this material. The museum had passed through several crises and the whereabouts of the material is uncertain. Regarding the fact that, according to the present data, *H. funcki* and *H. pitalensis* do not occur sympatrically and the latter species has not been recorded from the southern Pacific plain (except the one doubtful record from the Península de Osa, see: under *H. funcki*) and the questionable interpretation of von Martens' remark, it seems more appropriate, until better knowledge comes along, to refer the records from "Bay of Terraba, Tocori in the valley of the Río Paquita, middle part of the Río Saveque and lower part of the Río Pacuare (Pittier)" also to *H. pitalensis*.

The record of *Helicina amoena* L. Pfeiffer, 1849, for Costa Rica by Monge-Nájera (1997) was based on the material in the INBio collection. The subsequent revision of the material revealed one lot of *H. amoena* (INBio 1485173) collected and determined before 1997, on the basis of which the publication must have been based. This specimen can clearly be referred to *H. pitalensis* in its typical form from the Península de Osa. *Helicina amoena* is distinguished from *H. pitalensis* by its less elevated shell, which is more strongly angulated at the periphery and marked with distinct spiral striations. The color is also different. Except for one doubtful record from Panama by von Martens (1890) ("*Helicina amoena* var. b" from Champion) *H. amoena* has not yet been reported south of the Mosquito Coast of Nicaragua (Fluck, 1906: Mosquito Coast: NW Kukallaya, Wounta River; Jacobson, 1968: Bonanza). The original material of this doubtful record was assumed to be in the collection of the ZMB, as is other material of Champion, but it remains lost, although it was also searched for under other possible designations. It was later cited by Pilsbry (1910, 1926a), but who claimed not to have seen the specimen.

All recent records of *H. pitalensis* refer more to the south than the type locality. The specimens from the area of the Fila Cruces (Linda Vista, Fila Cal, San Vito) at higher altitudes (about 6001,000 m) are very similar to the type material. Only the basic lemon-yellow color is sometimes replaced by light orange-brownish. Specimens from the Península de Osa sometimes lack the band and show certain deviations in shape and a stronger inflation of the whorls immediately below the suture. But because other characteristics do not differ (e.g., color, development of columellar region, protruding denticle at the transition of outer lip to columella, roundly angulated periphery) and adult material from other locations on the Península de Osa is not available, a separation of this form is not yet warranted.

Helicina (*Tristramia*) *tenuis*
L. Pfeiffer, 1849

Helicina tenuis L. Pfeiffer, 1849: 124–125 (not figured)
Helicina vernalis Morelet, 1849: 20 (not figured)
Helicina tenuis – L. Pfeiffer, 1850: 40, pl. 7, figs. 33, 34
Helicina tenuis – L. Pfeiffer, 1852a: 372
Helicina vernalis – L. Pfeiffer, 1852a: 372
Helicina tenuis – L. Pfeiffer, 1852b: 269
Helicina vernalis – L. Pfeiffer, 1852b: 269–270
Helicina vernalis – L. Pfeiffer, 1853: 71, pl. 10, figs. 12–14
Helicina chiapensis L. Pfeiffer, 1856: 237 (not figured); 1857: 380 (not figured)
?*Helicina lindeni* – Tristram, 1862: 5: Guatemala: neighbourhood of Dueñas [according to Tristram, 1864] (Salvin) [*non* L. Pfeiffer, 1849]
?*Helicina lindeni* – Sowerby, 1866: 288, pl. 272, figs. 258260 [*non* L. Pfeiffer, 1849]
Helicina chiapensis – Sowerby, 1866: 288, pl. 272, figs. 255–257

Helicina vernalis – Sowerby, 1866: 288, pl. 273, fig. 273
Helicina tenuis – Bland, 1866: 9
Helicina vernalis – Bland, 1866: 9
Helicina chiapensis – Bland, 1866: 9
Helicina vernalis – Reeve, 1874: pl. 18, fig. 156
Helicina chiappensis [sic] – Reeve, 1874: pl. 13, fig. 110
Helicina vernalis – von Martens, 1875: 649: Guatemala: Coban, Vera Paz
Helicina vernalis – von Martens, 1876: 259: Guatemala: Coban
Helicina lindeni – Angas, 1879: 484: Costa Rica [*non* L. Pfeiffer, 1849]
?*Helicina lindeni* var. *minor* – Ancey, 1886: 258–259: Honduras, Atlantic coast (smaller specimens)
Helicina tenuis – von Martens, 1890: 34–35: Central Mexico: Sayula in Jalisco, Irapuato near Guantajuoto; E-Mexico: Soledad, between Cordova and Orizaba; SE-Mexico: Chiapas; Teapa and San Juan Bautista in Tabasco, Tapinapa; Yucatan; N-Guatamala: Peten Province; Cubilguitz, valley of the River de la Pasion; Coban; San Gerónimo and the neighbouring mountains in Vera Paz; Panzos; Chacoj; San Juan (all in the valley of the Polochic River); Purula; S-Guatemala: Totonicapam mountains 8,500 to 10,500 feet (small variety); El Reposo 800 feet; Las Mercedes 3,000 feet; Cerro Zunil 4,000 feet; San Isidro 1,600 feet, all on Pacific slope; Zapote, on the slope of the Volcan de Fuego; Nicaragua: Toro Rapids?; Costa Rica
Helicina tenuis var. *chiapensis* – Pilsbry, 1892: 339: Mexico: Tabasco: Poana (Rovirosa)
Helicina (*Oligyra*) *lindeni* – Fischer & Crosse, 1893: 416–420, pl. LVI, figs. 1–3: same data as von Martens (1890) [*non* L. Pfeiffer, 1849]
Helicina tenuis – Biolley, 1897: 5: Costa Rica: Turrubares, 200 m [San Pablo de Turrubares, about 09°55'N, 84°27'W, San José Province] and La Paz, 900 m, en el camino del Sarapiquí [along the River Sarapiquí] [not exactly localized, near Isla Bonita?, about 10°15'30"N, 84°11'W, Alajuela Province]
Helicina tenuis – von Martens, 1900: 604: SE-Mexico: Poana, Tabasco; Honduras: East Coast – smaller spec.; NE-Costa Rica: La Paz , on the road to the Río Sarapiqui Sarapiqui [not localized, near Isla Bonita?, about 10°15'30"N, 84°11'W, Alajuela Province] (Biolley); Central Costa Rica: Alajuela, 900–1,000 m [town or province?, town about 10°01'30"N, 84°13'W] (Orosco), SW-Costa Rica: Turubares, 200 m [San Pablo de Turrubares, about 09°55'N, 84°27'W, San José Province] (Biolley); along the Río de los Platanales and the Golfo Dulce [correct: Río de los Platanares, S of Puerto Jiménez, Península de Osa, about 08°31'30"N, 83°18'W, Puntarenas Province] (Pittier)
Helicina vernalis – Wagner, 1905: 233–234, pl. XIII, fig. 13a–c: Guatemala: Petén; Verapaz: Río Polochic
Helicina vernalis verapazensis Wagner, 1905: 234, pl. XIII, fig. 14: Guatemala: Verapaz
Helicina tenuis pittieri Wagner, 1910a: 303–304, pl. 60, fig. 24
Helicina tenuis – Wagner, 1910a: 302–303, pl. 60, figs. 15-23, 25: S-Mexico to Panama: Mexico: Tabasco and Chiapas; Guatemala: Coban, Totonicapan, St. Isidoro, Río Polochic, Mercedes and Vera Paz; Costa Rica: Turrubares [San Pablo de Turrubares, about 09°55'N, 84°27'W, San José Province] and Alajuela [town or province?, town about 10°01'30"N, 84°13'W]
Helicina tenuis var. *lindeni* – Hinkley, 1920: 49, 52: Guatemala: Jocolo plantation on north side of Lake Isabal; Alta Verapaz: Chama between Río Tsalbha and Río Negro [*non* L. Pfeiffer, 1849]
Helicina (*Tristramia*) *tenuis* – Baker, 1922a: 50, pl. III fig. 7, pl. IV, fig. 14 (radula)
Helicina (*Tenuis*) *tenuis* – Baker, 1922b: 35-36: Mexico: S Vera Cruz, near Hacienda de Cuatolapam (Río San Juan – Arroyo Hueyapam, canton of Acayacan (Michigan-Walker-Expedition)
Helicina tenuis – Pilsbry, 1926a: 59, 71: Panama: Los Santos Province: Tonosi (Olsson)
?*Helicina tenuis* var. – Pilsbry, 1930: 339: Panama: Barro Colorado Island (Pinchot-Expedition)
Helicina (*Tristramia*) *lindeni* – Bequaert & Clench, 1933: 543: not found again in Yucatán [*non* L. Pfeiffer, 1849]
Helicina tenuis – Goodrich & van der Schalie, 1937: 12, 15, 32: Guatemala: Petén: region of headwater of Río San Pedro de Mártir, lower Río de la Pasión; Alta Verapaz: upper part of Río de la Pasión
Helicina tenuis – van der Schalie, 1940: 6, 9, 10: Guatemala: Alta Verapaz: Pacala and Chama, 290 m a.s.l., Samac, 1,300 m a.s.l. [W of Coban], Panzamala, 1,250 m a.s.l. [S of Lanquín] (Stuart)

Helicina (*Helicina*) *tenuis* – Haas, 1949: 137–138: Guatemala: Chimaltenango: Yepocapa, 4800 ft.; Zacapa: Santa Clara, valley in the interior of the Sierra de las Minas, N of Cabañas, 5500 ft. (Wenzel &Mitchell)
Helicina tenuis – Bequaert, 1957: 207: Chiapas: Selva Lacandona: Monte Líbano, 600 m, El Real, 600 m
Helicina tenuis tenuis – Thompson, 1967: 228–229: Mexico: Campeche: 10.2 mi E Escárcega, rare (1 spec., dead), Chiapas: 15.8 mi NW Ocozocoautla
Helicina tennuis [sic] – Pérez & Lopez, 1993: 27: Nicaragua
Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* L. Pfeiffer, 1849]

Synonymy

Helicina vernalis Morelet, 1849
Helicina chiapensis L. Pfeiffer, 1856
Helicina vernalis verapazensis Wagner, 1905
Helicina tenuis pittieri Wagner, 1910

Original Description

"Hel. testa, turbinata, tenuissima, vix striatula, pellucida, corneo-albida, rubro obsolete trifasciata; spira conica, acuta; anfractibus 6 vix convexiusculis, ultimo basi planiusculo; apertura fere verticali, triangulari-semiovali; columella brevi, basi retrorsum subdentata, superne in callum nitidum, circumscriptum, dilatata; peristomate tenui, angulatim expanso, margine basali cum columellae basi angulum formante.
Diam. 11, altit. $8^1/_2$ mill.
From Yucatan."

Type Material

BMNH 20010496.1–7 "Yucatan & Barbadoes, coll. Hugh Cuming"
The type lot contains seven specimens, labeled as originating from Yucatan and Barbadoes. The latter locality is not given in the original description. In fact, the lot is a mixture of two species, and only five specimens agree with the description of *Helicina tenuis*. The other two exhibit a less elevated spire, less convex whorls and the first whorls increase more rapidly in size. Furthermore, the shells, lacking the spiral color bands, are colored uniformly whitish, except for a broken nearly transparent thin spiral line above the periphery. Finally, the characteristic denticle of *H. tenuis* at the basal outer lip is less strongly developed. Thus, these specimens (BMNH 20010496.6–7) are excluded from the syntype lot of *Helicina tenuis*, because they do not agree with the original description and the later given figure. It is very likely that the lot was mixed subsequently to the studies of L. Pfeiffer.

The largest specimen is **here selected as lectotype** (Fig. 54), because it best agrees with the figure in L. Pfeiffer (1850). It is the only specimen in the lot with banding, without operculum and about the size given in the description. In comparison with the figure the bands are faded, but it may be an exaggeration in the drawing since they are described as "rubro obsolete trifasciata".
Dimensions:
Lectotype BMNH 20010496.1:
9.8/9.8/10.8/8.9/6.5/7.7/7.6 mm
Paralectotypes BMNH 20010496.2–5:
9.6/9.1/10.4/8.4/6.4/7.5/7.2 mm

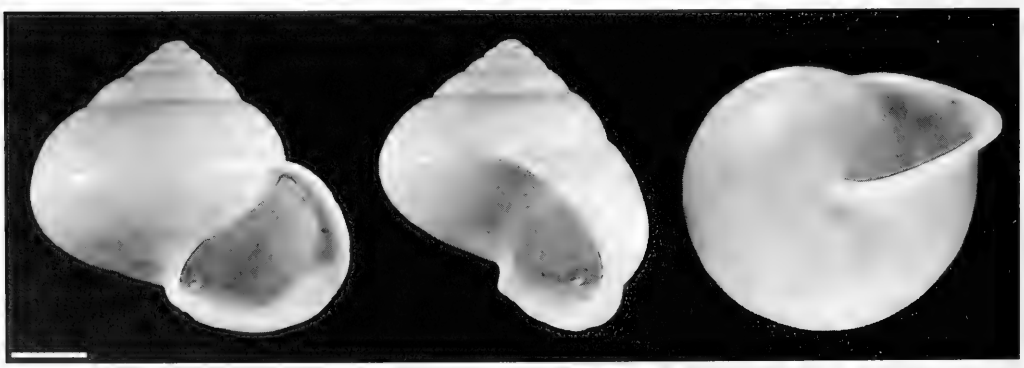


FIG. 54. *Helicina tenuis*, lectotype, BMNH 2001496.1, height 9.8 mm; scale bar 2.5 mm.

8.9/8.7/9.4/8.1/5.6/6.8/7.0 mm
9.8/9.0/10.0/8.3/6.0/7.2/7.5 mm
8.7/7.9/8.7/7.3/5.4/6.4/6.7 mm

It is remarkable that even the type lot shows a comparatively great variation in size and shape (e.g., lectotype and smallest paralectotype).

Type Locality

"Yucatán" [Not clear, whether it refers to the Mexican State of Yucatán or to the whole Yucatán Peninsula, shared by Mexico, Guatemala, and Belize. The present data of distribution suggest its origin rather in the Mexican State of Campeche or the Guatemalan Petén Department.]

Type Material of Synonymous Taxa or Similar Species

Helicina vernalis Morelet, 1849

Type Material: BMNH 1893.2.4.1991–1993: Morelet coll., purchased from H. Fulton
The Morelet collection was bought by H. Fulton and later purchased by the BMNH. Fischer & Crosse (1893) studied the original material in the Morelet collection and figured a shell that can be identified by the mark of a "x" and the clear similarity to the figure. This shell is **here selected as lectotype** of *Helicina vernalis* (BMNH 1893.2.4.1991) (Fig. 55), because it is uncertain whether Fischer & Crosse's comment in the figure caption (pl. LVI, fig. 1, 1a, 1b: "premier type de l' *Helicina vernalis*") can be regarded as a type selection. The lectotype is colored uniformly whitish and still possesses its operculum, whereas the paralectotypes are whitish below the periphery and above tinged reddish-brownish or yellowish with two reddish-brownish bands respectively.
Dimensions:
Lectotype BMNH 1893.2.4.1991:
9.9/9.9/10.8/8.9/6.5/7.7/7.5 mm
Paralectotypes BMNH 1893.2.4.1992–1993:
9.4/9.4/10.3/8.3/6.3/7.5/7.2 mm
9.2/9.2/10.0/8.2/6.2/7.3/7.0 mm

Type Locality: "Petenensis sylvas" [Guatemala, Petén Department]

Helicina chiapensis L. Pfeiffer, 1856

Type Material: Syntype ZMB 65624: leg. Ghiesbreght, *ex* coll. L. Pfeiffer (Fig. 56)
The description of *Helicina chiapensis* was published in two journals. In the earlier publication (December 1856), L. Pfeiffer stated that he had received specimens from Hugh Cuming, leg. Ghiesbreght, which he probably kept in his collection. The second publication (May 1857) refers to material in the collection Hugh Cuming, leg. Ghiesbreght. Thus additional syntypes are possibly in the collection of the BMNH housing the main collection of Hugh Cuming, although they have not yet been found in the type collection.
Dimensions (height/greatest diameter/minor diameter):
Syntype: 10.2/11.4/9.4 mm

Type Locality: "Mexico, Chiapa" [Mexico, State of Chiapas]

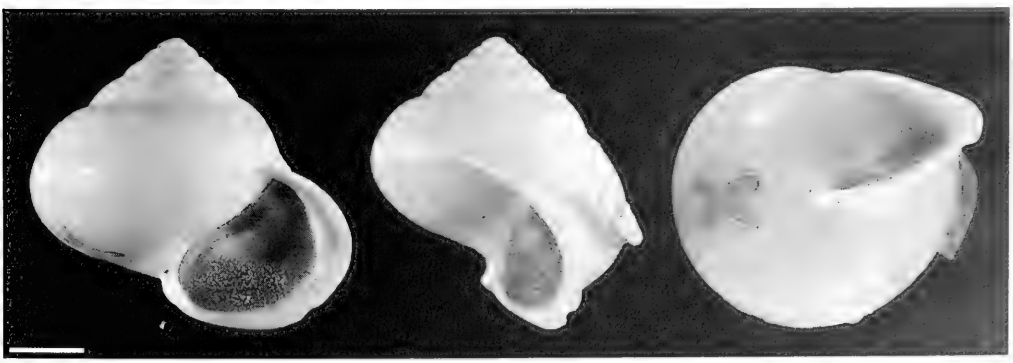


FIG. 55. *Helicina vernalis*, lectotype, BMNH 1893.2.4.1991, height 9.9 mm; scale bar 2.5 mm.

Helicina lindeni L. Pfeiffer, 1849

Helicina lindeni L. Pfeiffer, 1849: 123 (not figured)
Helicina lindeni – L. Pfeiffer, 1850: 52, pl. 8, figs. 25, 26

Material Studied: *Helicina lindeni* var. – BMNH 20010757: Mexico, Hugh Cuming coll., three specimens
The type material could not be located in the collection of the BMNH, although it was listed in the catalogue of the BMNH collection by L. Pfeiffer (1852b: 282) as coming from the type locality Tapinapa, Mexico (leg. Linden).
The specimens in BMNH 20020757 definitely do not belong to *Helicina tenuis*, but rather agree well with the original description of *Helicina lindeni*, especially, because in contrast to *H. tenuis* it is slightly angulated at the periphery and less elevated. None of the shells shows a trace of spiral color bands. The outer lip is more reflexed.

Helicina tenuis pittieri Wagner, 1910

Type Material: Holotype ZMB 103241: leg. Pittier
Because the original description refers to one specimen in the ZMB which also matches the figure it is the holotype (Fig. 57).
Dimensions:
Holotype: 9.2/8.6/9.4/8.0/6.0/7.4/7.1 mm

Type Locality: "Costa Rica, Río de los Plutunales, Golfo Dolce" [correct: Río de los Platanares, S of Puerto Jiménez, Península de Osa, about 08°31'30"N, 83°18'W, Puntarenas Province]

Examined Material

Leg. I. Richling
Guanacaste: *3 km E Nuevo Arenal, 10°31'53"N,84°52'50"W, 640 m a.s.l.*: *property of pension Villa Decary, rain forest*: 03.03.1997: (IR 52); 01.03.1999: (IR 715); 02.03.1999: (IR 722); 31.07.1999: (IR 880); 23.02.2000: (IR 1266); *along small creek E of Villa Decary*: 04.03.1999: (IR 730)
Heredia: S Puerto Viejo de Sarapiqui, *Zona Protectora La Selva*, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1057); (IR 1058); 12.02.2000: (IR 1181)
Puntarenas: *Reserva Natural Absoluta Cabo Blanco, 09°35'16"N, 85°05'45"W, 30 m a.s.l.*: *Sendero Danes and trail from entrance*: 25.08.1999: (IR 1001); (IR 1002); 27.02.2000: (IR 1289); (IR 1291): *Sendero Sueco*: 02.03.2001: (IR 1481)

INBio Collection
Guanacaste: 500 m E de la *Estación Almendros*, 11°02'04"N, 85°31'10"W, 280 m a.s.l., leg. Elba Lopez, 01.08.1994: 1 ad. (INBio 1477167)
Parque Nacional Barra Honda, Los Mesones: 10°10'12"N, 85°21'03"W, 300 m a.s.l., 29.05.1993: 2 ads. (INBio 1463476); 10°10'12"N, 85°20'50"W, 100 m a.s.l., 31.05.1993: 4 ads., 1 s.ad. (INBio 1463452) (all leg. malacological staff of INBio)
Refugio Nacional de Vida Silvestre Bosque Diriá, Sector Diriá: *Sendero Espavel, 10°10'19"N, 85°35'44"W, 220 m a.s.l.*: leg Alexander Alvarado Mendez, 13.05.1999: 6 ads., 4 juvs. (INBio 3096450); 200 m a.s.l.: leg. A. Berrocal, 22.11.1998: 2 ads. (INBio

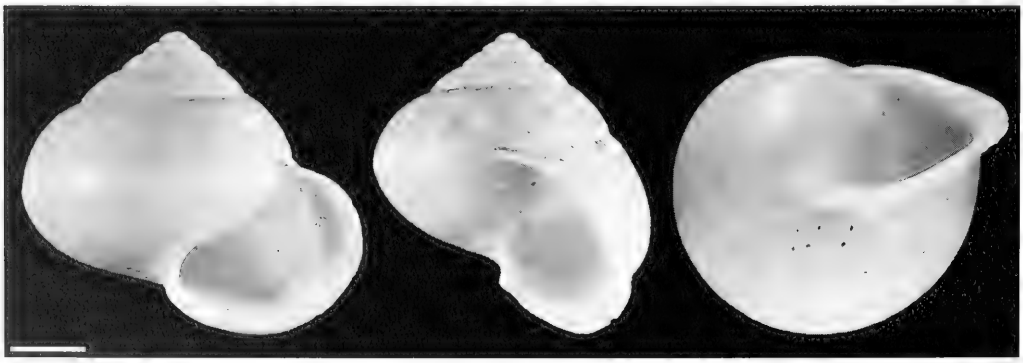


FIG. 56. *Helicina chiapensis*, syntype, ZMB 65624, height 10.2 mm; scale bar 2.5 mm.

3435759); *Camino a Esperanza, 10°10'32"N, 85°35'11"W, 260 m a.s.l.*: 14.05.1999: 1ad., 1 s.ad., 2 juvs. (INBio 1498286); 2 ads. (INBio 1498287) (all leg Alexander Alvarado Mendez)

Puntarenas: *Parque Nacional Carara*: *Quebrada Bonita, 09°46'29"N, 84°36'34"W*: 50 m a.s.l., 03.06.2000: 4 s.ads. (INBio 3324332); 100 m a.s.l., 02.07.2000: 3 ads. (INBio 3129469); *Carara, sendero Laguna Meandrica, 09°48'20"N, 84°35'02"W, 100 m a.s.l.*: 15.07.2000: 1 s.ad. (INBio 3395010) (all leg. malacological staff of INBio)

Parque Nacional Corcovado: *Río Sirena, 08°30'25"N, 83°29'23"W, 545 m a.s.l.*: leg. Enia Navarro, 24.05.1995: 1 ad. (INBio 1484663); *2 km SW del Mirador, 08°32'30"N, 83°30'57"W, 200 m a.s.l.*: leg. Socorro Avila, 22.05.1997: 1 ad. (INBio 1487810)

Reserva Forestal Golfo Dulce: Fila Casa Loma, 1,600 m S de la Escuela de Rincón, 08°41'33"N, 83°29'17"W, 170 m a.s.l.: leg. Socorro Avila, 10.10.1996: 2 ads. (INBio 1487328); Península de Osa, Instalaciones de IDA, 08°41'38"N, 83°29'07"W, 60 m a.s.l.: leg. Ramon Angulo, 07.06.1994: 1 ad. (INBio 1480502)

Reserva Natural Absoluta Cabo Blanco: *Sector Balsitas, Sendero Central, 09°35'02"N, 85°07'26"W, 120 m a.s.l.*: 18.05.1994: 6 juv. (INBio 1473990); 2 ads. (INBio 1475801); 1 ad. (INBio 1475805) (all leg. Zaidett Barrientos); *Sector Cabuya, Sendero Sueco, Río Ariolo, 09°35'16"N, 85°05'41"W, 20 m a.s.l.*: leg. Ulises Chavarría, 08.11.1994: 1 ad. (INBio 1480012); *Sector San Miguel, Sendero Maven, 09°35'09"N, 85°08'12"W, 200 m a.s.l.*: leg. Zaidett Barrientos, 17.05.1994: 1 ad. (INBio 1474149)

Cóbano, Estación *Cabo Blanco*, 09°35'30"N, 85°05'45"W, 15 m a.s.l., leg. malacological staff of INBio, 09.01.1993: 4 ads., 5 s.ads., 3 juvs. (INBio 1465481)

Sendero Camino Maven, orilla de quebrada San Miguel, 09°35'18"N, 85°08'12"W, 100 m a.s.l., leg. Alexander Alvarado Mendez, 21.01.1999: 2 ads. (INBio 1498272); 2 ads. (INBio 1498276)

Quebrada San Miguel, 09°35'15"N, 85°08'15"W, 100 m a.s.l., leg. Socorro Avila, 05.10.1995: 1 ad. (INBio 1484853)

Alajuela: *San Ramón*, 10°05'19"N, 84°29'18"W, 1,060 m a.s.l., leg. malacological staff of INBio, 16.09.1993: 1 ad. (INBio 1464319)

Estación Playuelas, 50 m del Río Frío, 10°57'29"N, 84°44'55"W, 40 m a.s.l., leg. Kattia Martinez, 08.01.1994: 1 ad. (INBio 1479297)

OTHER SOURCES

COSTA RICA

Guanacaste: Las Cascadas, Quebrada San Diego, 10°10'59.5"N, 85°20'18.5"W, leg. D.G. Robinson & J.M. Montoya, 20.09.1998 (APHIS PPQ USDA)

Karst exposure, Cerro Barra Honda, approx. 10°10'10"N, 85°22'10"W, leg. D.G. Robinson & J.M. Montoya, 19.09.1998 (APHIS PPQ USDA)

Nicoya [about 10°08'30"N, 85°27'30"W], leg. H.G. Lee, *ex* G.D. Robinson, W.F. Webb: 1 ad. (UF 166944)

Pederal de Nicoya [about 10°08'N, 85°26'W], leg. Univ. Alabama, M. Smith coll. (MS-15277): 12 ads. (UF 95336)

2.2 mi SE Nicoya [about 10°07'30"N, 85°26'W], 500 ft., leg. F.G. Thompson (FGT-106), 10.08.1964: 1 ad. (UF 214333)

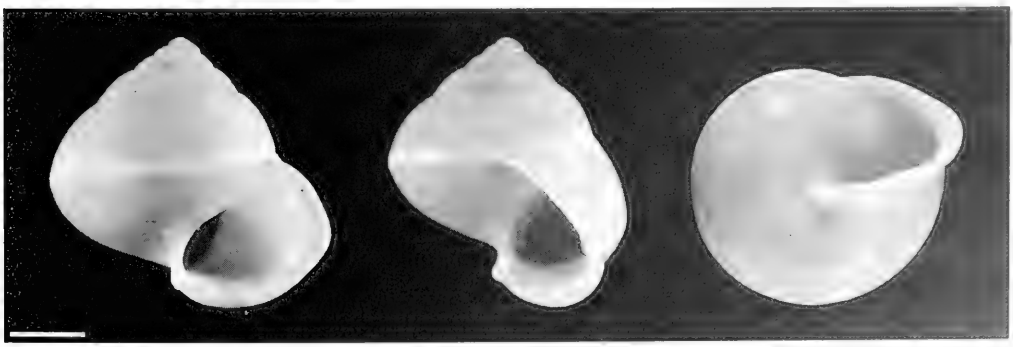


FIG. 57. *Helicina tenuis pittieri*, holotype, ZMB 103241, height 9.2 mm; scale bar 2.5 mm.

3.8 mi S Nicoya [about 10°05'N, 85°28'W], leg. F.G. Thompson (FGT-111), 11.08.1964: 1 ad. (UF 35511)
1.2 mi E Caimital [about 10°04'N, 85°27'W], leg. F.G. Thompson (FGT-109), 11.08.1964: 1 ad. (UF 214332)
Monte Alto conservation area, near Pilangosta, Canton Hojancha, 10°00'48.1"N, 85°24'08.1"W, leg. D.G. Robinson & J.M. Montoya, 19.09.1998 (APHIS PPQ USDA)

Alajuela: "Alajuela" [city or province?, town about 10°01'30"N, 84°13'W], Orosco (ZMB 103247)
La Paz (Chem. du Sarapiqui) [not exactly localized, near Isla Bonita?, about 10°15'30"N, 84°11'W], leg. P. Biolley (#90): 2 ads. (MHNN)
"San José Prov.:" San José [really San José, capital of Costa Rica?, or province later added and originally referring to San José in Alajuela Province, here preferred: 14 km NW of Upala, about 10°58'N, 85°08'W, Alajuela Province], leg. McGinty coll., *ex* Preston & Tomlin: 1 ad. (UF 160158)

San José: Turubares, Versant du Pacifique [San Pablo de Turrubares, about 09°55'N, 84°27'W], 500 m a.s.l., leg. P. Biolley (#140), 06.1893: 21 ads., 1 s.ad. (MHNN)

Cartago: Turrialba [about 09°54'30"N, 83°41'W], coll. C. Bosch, *ex* coll. Rolle, *ex* Wagner: 4 ads. (SMF 180786/4); coll. Rolle: 12 ads. (ZMB 103802)

Puntarenas: Golfito [about 08°39'N, 83°10'W], leg. F.G. Thompson et al., 14.06.1964: 1 ad. (UF 35510)

Costa Rica, without locality further specified: leg: McGinty coll.: 1 ad. (UF 263576); 1 ad. (UF 214331)

GUATEMALA

El Petén: S of Sayaxche, beyond L Petexbatun, leg. J. Polisar, 31.08.1994: 4 ads. (UF 234127)

Huehuetenango: Cave below Finca Chiblac, ca. 5 km W of San Ramon, 15°52'45"N, 91°14'34"W, 700 m a.s.l., leg. F.G. Thompson et al. (FGT-4828), 05.03.1991: 5 ads. (UF 190327); (UF 190329: 1 of 6 spec.)

Alta Verapaz: 2 km WNW of Lanquin, 15°34'38"N, 89°59'19"W, 300 m a.s.l., leg. S.P. Christman (FGT-4791), 21.02.1991: 2 ads. (UF 190068)
4 km W of Lanquin, 15°34'37"N, 90°01'06"W, 330 m a.s.l., leg. F.G. Thompson (FGT-4793), 21.02.1991 (UF 190093: 1 of 5 spec.)
9 km W of Lanquin, 15°35'03"N, 90°03'20"W, 690 m a.s.l., leg. F.G. Thompson et al. (FGT-4787), 20.02.1991: 1 ad. (UF 190036); (UF 190045: 2 of 4 spec.)
11 km W of Lanquin, 15°33'29"N, 90°04'02"W, 1,000 m a.s.l., leg. F.G. Thompson et al. (FGT-4801), 22.02.1991: 2 ads. (UF 190142)
6.5 km SE of Lanquin, 15°32'52"N, 89°57'22"W, 400 m a.s.l., leg. F.G. Thompson (FGT-4796), 21.02.1991: 2 ads. (UF 190108)
8 km SE of Lanquin, 15°32'43"N, 89°56'49"W, 350 m a.s.l., leg. F.G. Thompson et al. (FGT-4797), 21.02.1991: 1 ad. (UF 190116)
2 km ESE Cojaj, 15°33'25"N, 90°06'56"W, 1,250 m a.s.l., leg. F.G. Thompson (FGT-4783), 20.02.1991: 3 ads. (UF 190006)
8 km by road N of Coban, 15°31'30"N, 90°23'11"W, 1,340 m a.s.l., leg. F.G. Thompson et al. (FGT-4776), 18.02.1991: 3 ads. (UF 189950)
4 km E of Coban, 1,260 m a.s.l., leg. F.G. Thompson et al. (FGT-4803), 23.02.1991 (UF 190156: 1 of 2 spec.)

Coban, Sumichrast: 2 ads. (UF 214336); leg. Univ. Alabama, T.H. Aldrich coll. (THA-8198), *ex* Mohr coll.: 2 ads. (UF 095334)
Limestone knoll 11 km S of Coban, 15°24'57"N, 90°24'09"W, 1,350 m a.s.l., leg. F. G. Thompson et al. (FGT-4805), 04.02.1991: 1 ad. (UF 190163)
2.5 km by road NE of Puente Chixoy, 15°21'32"N, 90°39'10"W, 810 m a.s.l., leg. F.G. Thompson (FGT-4781), 19.02.1991 (UF 189988)
Limestone knoll 17.5 km NW of Tactic, 15°21'29"N, 90°25'25"W, 1,330 m a.s.l., leg. F.G. Thompson et al. (FGT-4764), 16.02.1991: 3 ads. (UF 189840)
10.5 km SE of El Tactic, 15°16'59"N, 90°18'11"W, 1,460 m a.s.l., leg. S.P. Christman (FGT-4810), 26.02.1991: 2 ads. (UF 190204)
E of Finca el Volcan, leg. J. Schuster, 22.07.1984: 1 ad. (UF 114090)

Izabal: Río Tameja, 12.9 km SSW Livingston, leg. F.G. Thompson (FGT-54), 04.07.1964: 1 ad. (UF 214330)

Zacapa: La Union, Cerro Mona (N), 1,350-1,500 m a.s.l., leg. E.N. Smith, 20.06.1994: 1 ad. (UF 244447)

Retalhuleu: Retalhuleu, leg. Univ. Alabama, T. H. Aldrich coll. (THA-8197) *ex* Mohr coll.: 2 ads. (UF 95335)

Guatemala, without locality further specified: La Paz [localization?: perhaps Verapaz or in Honduras?], *ex* coll. S. G. A. Jaeckel: 3 ads.

(HNC 39843); leg. Beal-Maltbie coll., *ex* W. Webb coll.: 1 ad. (UF 237376); leg. Beal-Maltbie coll., *ex* W. Webb coll.: 1 ad. (UF 237377)

EL SALVADOR

Ahuachapán: 6 km W of Atiquizaya, on road to Ahuachapán, leg. A. Zilch, 21.09.1951: 4 ads. (SMF)

HONDURAS

Colón: Limestone ridge, 2.6 km SW of La Brea, 15°45'39"N, 86°00'08"W, 100 m a.s.l., leg. F.G. Thompson (FGT-5253), 22.10.1993: 1 ad. (UF 212023)

Olancho: Vicinity of Magua Cave, ca. 15 km SSW of Gualaco, 14°56.5'N, 86°07.5'W, 940 m a.s.l., leg. F.G. Thompson et al. (FGT-5216), 11.03.1993: 4 ads. (UF 194339)

MEXICO

Guerrero: 1 km E Petaquillas, 1158 m a.s.l., leg F.G. Thompson (FGT-1584), 03.11.1970: 9 ads. (UF 217551)
2.2 mi NNE of Mazatlan, 4800 ft., leg. F.G. Thompson (FGT-672), 14.06.1966: 1 ad. (UF 77607)
Limestone hill, 1 km NW of Naranjito, 18°05'03"N, 101°50'45"W, 675 m a.s.l., leg. F.G. Thompson (FGT-5087), 04.11.1992: 1 ad. (UF 200647)

Oaxaca: Lagunas, 259 m a.s.l., leg. F.G. Thompson, 18.07.1966: 2 ads. (UF 214337)
Limestone ridge, 4 km W of Cuauht, moc, 17°05'56"N, 94°54'25"W, 100 m a.s.l., leg. F. G. Thompson et al. (FGT-5271), 02.08.1993: 1 s.ad. (UF 211326)
Limestone knoll, 13 km ENE of Sarabia, 17°05'54"N, 94°56'34"W, 125 m a.s.l., leg. F. G. Thompson et al. (FGT-5269), 02.08.1993: 3 ads. (UF 211316); leg. F. G. Thompson (FGT-5280), 03.08.1993: 2 ads. (UF 211427)

Veracruz: 5 km ENE of Cuauht, moc, Oaxaca, 17°06'59"N, 94°51'10"W, 75 m a.s.l., leg. F.G. Thompson et al. (FGT-5273), 03.08.1993: 1 ad. (UF 211337)
7 km S, 7 km E of Catamaco, 350 m a.s.l., leg. F.G. Thompson et al. (FGT-4608), 03.01.1990: 4 ads. (UF 159375)
Laguna Encontada, 20.08.1962: 1 ad. (UF 214338)
Limestone knoll, 2 km SW of Plan Arroyo, 17°14'15"N, 94°37'36"W, 100 m a.s.l., leg. F.G. Thompson et al. (FGT-5278), 03.08.1993: 2 ads. (UF 211398)

Tabasco: 3 km N of Vicente Guerrero, 17°31'09"N, 92°56'00"W, 160 m a.s.l., leg. F.G. Thompson (FGT-4873), 03.04.1991: 3 ads. (UF 190725)
6.8 km W Teapa, leg. F.G. Thompson (FGT-427), 08.07.1965: 2 ads. (UF 214344)

Campeche: 16.4 km E Escárcega, leg. F.G. Thompson (FGT-406), 19.06.1965: 1 ad. (UF 19296)

Chiapas: 15.1 km W San Cristobal, 2469 m a.s.l., leg. F.G. Thompson (FGT-446), 15.07.1965: 1 juv. (UF 214335); 1 ad. (UF 214340)
18.3 km N Tuxtla Gutierrez, 1372 m a.s.l., leg. F.G. Thompson (FGT-465), 22.07.1965: 1 juv. (UF 214341)
12.9 km N Tuxtla Gutierrez, 1158 m a.s.l., leg. F.G. Thompson (FGT-459), 19.07.1965: 3 ads. (UF 214343)
4.8 km SSE Tuxtla Gutierrez, 823 m a.s.l., leg. F.G. Thompson (FGT-763), 25.07.1966: 2 ads. (UF 214345)
7.5 km NNE Huixtla, 183 m a.s.l., leg. F.G. Thompson (FGT-757), 23.07.1966: 1 ad. (UF 214346)
21.3 mi NW Huixtla, 300 ft., leg. D.R. Paulson et al., 31.07.1965: 2 ads. (UF 214339)
Stream, 44.4 km NW Ocozocoautla, 610 m a.s.l., leg. F.G. Thompson (FGT-464), 21.07.1965: 1 ad. (UF 214342)
25.4 km NW Ocozocoautla, 823 m a.s.l., leg. F.G. Thompson (FGT-462): 20.07.1965: 1 ad. (UF 19295)
34.1 km E, 16.4 km S Comitan, 1524 m a.s.l., leg. F.G. Thompson (FGT-441), 14.07.1965: 1 ad. (UF 214145)
Ruins of Palenque, leg. H.W. Campbell, 04.05.1970: 3 ads. (UF 214334)

Mexico, without locality further specified: leg. Univ. Alabama, T.H. Aldrich coll. (THA-8195): 2 ads. (UF 95291)

Description

Shell (Figs. 58, 335F–I): Conical-globose, semi-fragile to thin, sometimes semitransparent, medium sized and only slightly shiny to dull. Color: basic color yellowish to whitish-opaque to horncolored, with up to three indistinct reddish bands on body whorl: one between suture and periphery and one or two below the periphery. The lower band only very weakly developed or obsolete. Surface textured with fine irregular growth lines and oblique grooves of different indi-

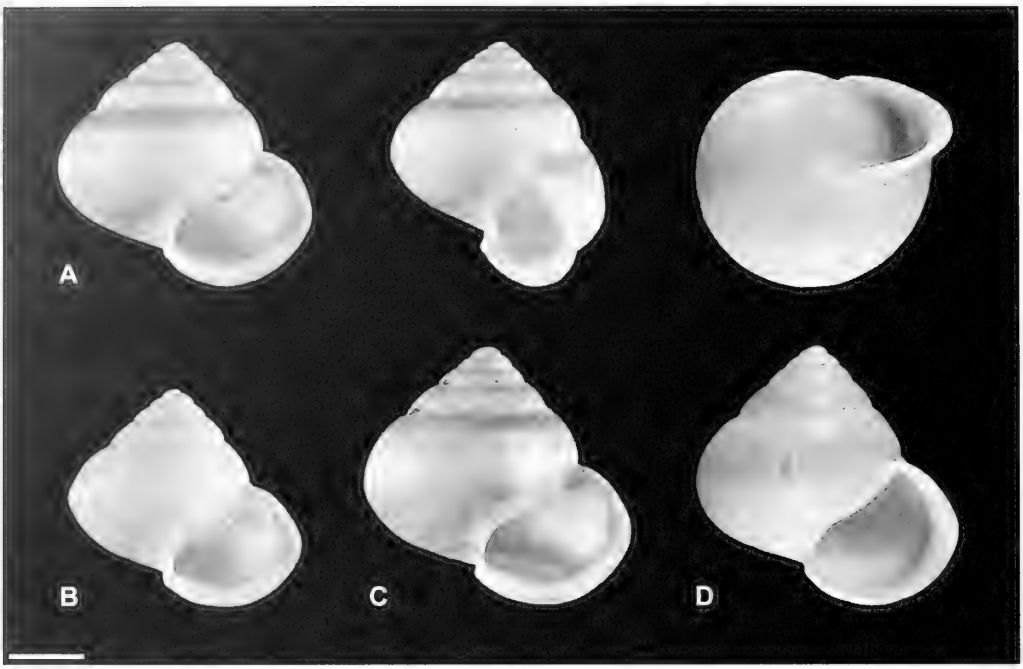


FIG. 58. *Helicina tenuis*. A–C. Cabo Blanco, IR 1001. A. Height 8.3 mm. B. Height 7.3 mm. C. Height 8.5 mm. D. La Selva, IR 1057, height 8.7 mm; scale bar 2.5 mm.

vidual orientation but of the same general direction (Fig. 60), causing the dull appearance. Embryonic shell with about 1 whorl, 4¼–5 (lectotype: 4¾) subsequent whorls well inflated, remarkably convex, the last whorl regularly rounded or sometimes with a slight angulation at the periphery, under the suture slightly shouldered; whorls equally extending in size, forming a very regular conical, pointed spire. Suture deeply impressed. Aperture oblique and nearly straight, last whorl regularly descending and inserting exactly at the periphery. Outer lip always yellowish-white, slightly thickened and broadly expanded. Reflection nearly rectangular to the whorl; transition to columella with a remarkably protruding denticle. Columella short. Basal callus weakly developed and nearly completely smooth or very little granulated, umbilical area without groove.

Internal Shell Structures: (Fig. 59)

Teleoconch Surface Structure (Fig. 60): The transitional structure extends about half a whorl, the subsequent pattern of oblique diverging grooves continues up to the aperture.

Embryonic Shell (Fig. 61): The structure resembles that of *Helicina funcki*, occasionally the pits are somewhat smaller. The embryonic shell size of the Costa Rican specimens agrees fairly well with the larger shells (see "Morphometry") of the type lot of *H. tenuis* which came from the Península de Yucatán. Diameter: 838 µm (± 28) (780–900) (n = 25) (IR 1001, IR 1002); 834 µm (± 27) (800–860)

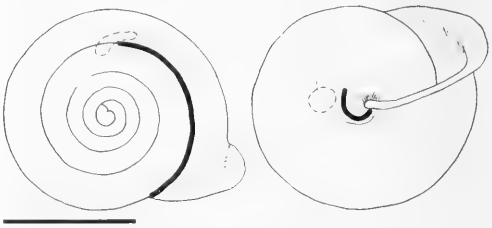


FIG. 59. Axial cleft and muscle attachments of *Helicina tenuis*, IR 1001; scale bar 5 mm.

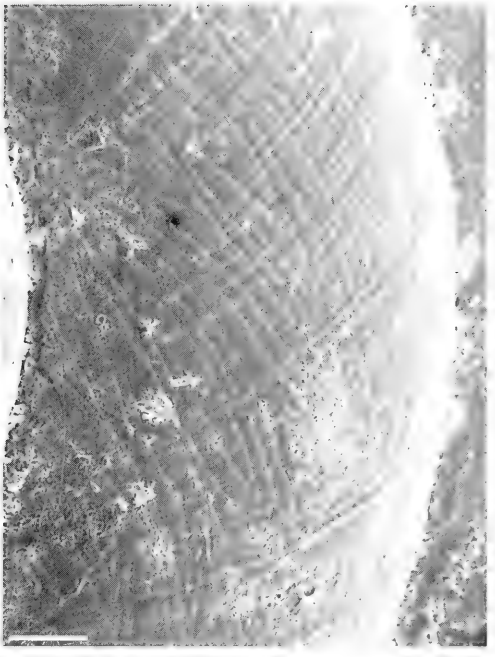


FIG. 60. Teleoconch surface structure of *Helicina tenuis* on 2nd whorl; scale bar 100 µm.

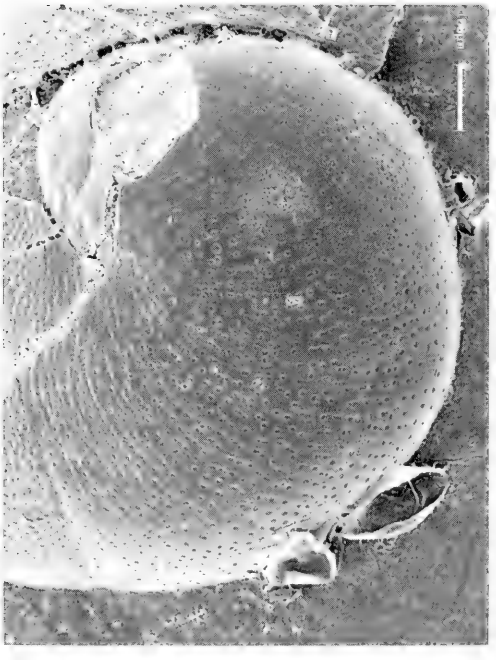


FIG. 61. Embryonic shell of *Helicina tenuis*; scale bar 100 µm.

FIG. 62. Operculum of *Helicina tenuis*, IR 1001; scale bar 2 mm.

(n = 5) (BMNH 20010496.1–5, type lot, lectotype: 860 µm); 813 µm (± 9) (800–820) (n = 3) (BMNH 1893.2.4.1991–1993, type lot of *Helicina vernalis*, lectotype: 820 µm).

Operculum (Fig. 62): Very slightly calcified, calcareous plate leaving a free margin, thickened towards the columellar side. Color reddish horny-amber, only the central area yellowish-transparent. Columellar side nearly regular S-shaped, upper end acute and pointed, lower end continuously changing into outer margin.

Animal (Figs. 337D, E): Foot and head are greyish and become darker towards the dorsal side; tentacles are greyish too. The mantle pigmentation shows a high variability: seldom unicolored light or dark, often basic color light yellowish with two (or seldom one) brown distinct but irregular bands on the last whorl above and below the periphery and more or less irregularly brownish spotted throughout the mantle. The few specimens from Arenal were only brownish spotted with small dots. The pattern is almost always clearly visible through the shell.

Radula (Fig. 63): A-central without well-defined cusps, B-central in most cases with 3–4, C-central only occasionally with up to 6 small cusps. Comb-lateral with 8–9 cusps, cusps on marginals slowly increasing in number. Radula with about 66–86 rows of teeth. Description agrees with Baker (1922a: pl. III, fig. 7, pl. IV, fig. 14).

Female Reproductive System (Figs. 64, 65): The receptaculum seminis is a small, simple drop-shaped sac, the bursa copulatrix pos-

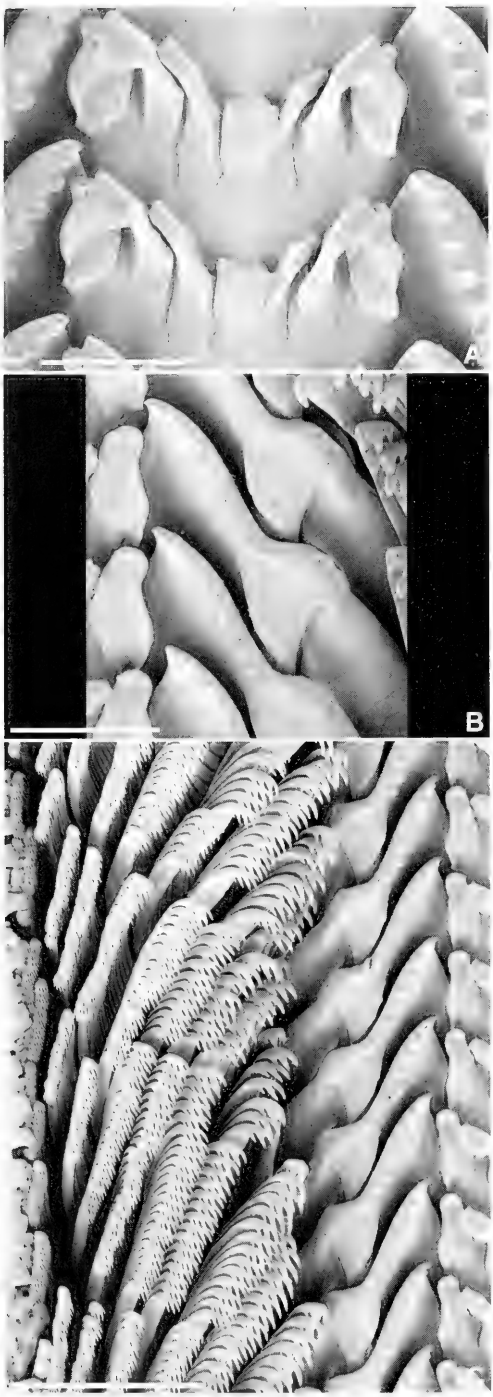


FIG. 63. Radula of *Helicina tenuis*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm (A, B), 100 µm (C).

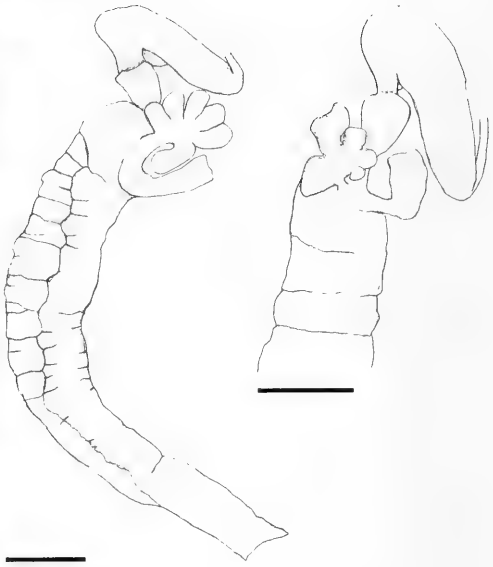


FIG. 64. Female reproductive system of *Helicina tenuis*, IR 1001; scale bar 1 mm.

sesses few rather large simple lobes and is of moderate size. The provaginal sac is oblong and well inflated, its distal end bears a few small processes. It has a slightly greyish-brownish pigmentation. The stalk is shorter than in *Helicina funcki* and rather stout.

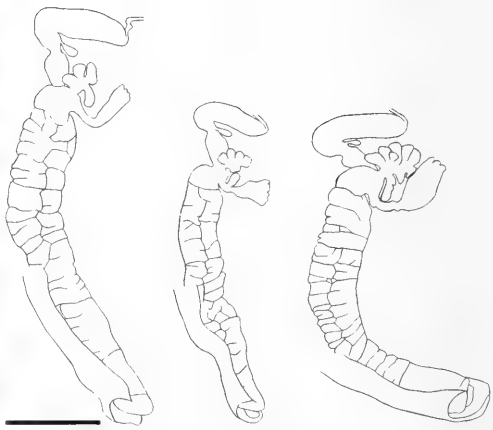


FIG. 65. Variability of the female reproductive system of *Helicina tenuis*, IR 1002; scale bar 2.5 mm.

TABLE 6. Measurements of different populations of *Helicina tenuis* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; only population from "Cabo Blanco" and "La Selva" were determined for the sex (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		"Cabo Blanco" (altitude 30 m) lots IR 1001, IR 1002, IR 1289					"La Selva" (altitude 60 m) lots IR 1057, IR 1181				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.12	0.36	7.28	8.98	54	-	-	-	-	-
Height	m	7.34	0.25	6.71	7.92	30	8.23	0.27	7.83	8.67	4
Maj. diam.	f	7.93	0.29	7.18	8.69	54	-	-	-	-	-
Maj. diam.	m	7.33	0.19	6.90	7.72	30	8.06	0.21	7.75	8.36	4
Min. diam.	f	7.31	0.27	6.67	8.03	54	-	-	-	-	-
Min. diam.	m	6.68	0.18	6.33	7.00	30	7.38	0.14	7.15	7.55	4
Outer lip	f	5.39	0.24	4.81	6.05	54	-	-	-	-	-
Outer lip	m	5.03	0.16	4.49	5.99	30	5.53	0.16	5.37	5.70	4
Last whorl	f	6.43	0.29	5.64	7.24	54	-	-	-	-	-
Last whorl	m	5.83	0.21	5.47	6.24	30	6.39	0.23	6.15	6.67	4
Col. axis	f	6.37	0.26	5.65	7.12	54	-	-	-	-	-
Col. axis	m	5.74	0.19	5.01	6.23	30	6.50	0.18	6.13	6.73	4
Weight	f	0.030	0.009	0.015	0.092	54	-	-	-	-	-
Weight	m	0.027	0.007	0.013	0.048	30	0.053	0.011	0.037	0.065	3
Volume	f	0.159	0.018	0.119	0.207	54	-	-	-	-	-
Volume	m	0.117	0.010	0.100	0.136	30	0.162	0.011	0.145	0.172	3

	"Diriá" (altitude 220–260 m) lots INBio 1498286, 1498287, 3096450					"Barra Honda" (altitude 100–300 m) lots INBio 1463452, 1463476				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	7.89	0.30	7.15	8.43	8	8.48	0.36	7.67	9.02	6
Maj. diam.	7.91	0.22	7.61	8.32	9	8.11	0.29	7.59	8.68	6
Min. diam.	7.14	0.20	6.82	7.48	9	7.55	0.26	6.98	7.98	6
Outer lip	5.19	0.18	5.00	5.85	8	5.50	0.21	5.23	5.43	6
Last whorl	5.99	0.19	5.66	6.36	8	6.42	0.41	5.60	6.93	6
Col. axis	6.27	0.20	5.73	6.68	9	6.88	0.36	6.03	7.34	6

	"Cabo Blanco, INBio" (altitude 15–120 m) lots INBio 1465481, 1475801, 1475805, 1480012, 1484853, 1498272, 1498276, IR 1481					"Turrubares" (altitude 500 m) lot MHNN				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	7.94	0.39	6.92	8.68	22	7.88	0.50	6.91	9.00	21
Maj. diam.	7.95	0.35	7.00	8.60	22	7.90	0.41	7.20	8.80	21
Min. diam.	7.22	0.33	6.32	7.73	21	7.11	0.36	6.49	7.97	21
Outer lip	5.30	0.26	4.65	5.85	22	5.22	0.21	4.85	5.80	21
Last whorl	6.23	0.32	5.30	6.78	22	6.05	0.35	5.40	6.84	21
Col. axis	6.25	0.34	5.29	6.90	22	6.09	0.41	5.30	7.15	21

(*Continues*)

(*Continued*)

	"Carara" (altitude 100 m) lot INBio 3129469					"Osa" (altitude 60–545 m) lots INBio 1480502, 1484663, 1487328, 1487810				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	8.08	0.52	7.31	8.68	3	7.55	0.83	6.70	8.68	4
Maj. diam.	7.60	0.28	7.18	7.93	3	6.98	0.58	6.35	8.06	5
Min. diam.	7.10	0.39	6.51	7.60	3	6.54	0.57	5.88	7.35	4
Outer lip	5.28	0.39	4.70	5.67	3	4.95	0.38	4.51	5.74	5
Last whorl	6.21	0.27	5.81	6.60	3	5.99	0.58	5.44	6.86	5
Col. axis	6.22	0.46	5.53	6.88	3	6.00	0.69	5.24	6.85	4

Morphometry and Sexual Dimorphism

Although *Helicina tenuis* is widely distributed, only data from Costa Rica and the type lot or those of type lots of synonyms, respectively, were included, because the lots studied from other areas consisted of only a very few specimens. Except for "La Selva", the Costa Rican populations originated from the Pacific side. The only southern specimens are those summarized as "Península de Osa" and the holotype of *H. tenuis pittieri* (Table 6, Figs. 66–70).

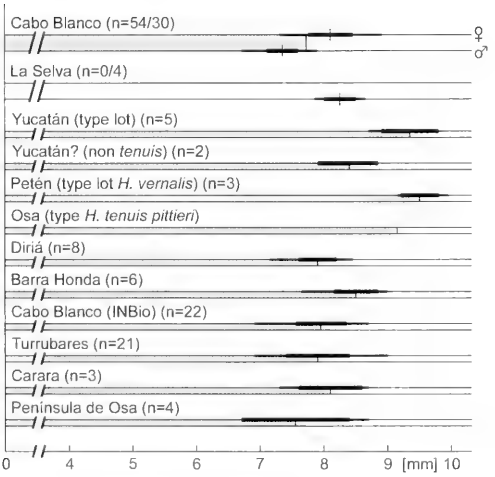


FIG. 66. Shell height of different populations of *Helicina tenuis* in Costa Rica according to Table 6; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex.

Morphometry: Regarding the type lot of *Helicina tenuis*, the non-conspecificity of all specimens is confirmed in the measurements, especially in the height-diameter-relation. *Helicina tenuis pittieri* closely approaches the mean value of the type lot in all characteristics. The same is true for the type lot of *H. vernalis*, which is larger, but otherwise shows similar relations between the different measurements, additionally supporting the status as a synonym.

Except for "Península de Osa", the Pacific populations are remarkably similar to each other in all characteristics. The specimens from Barra Honda have a bigger shell, which is more highly elevated (height, columellar

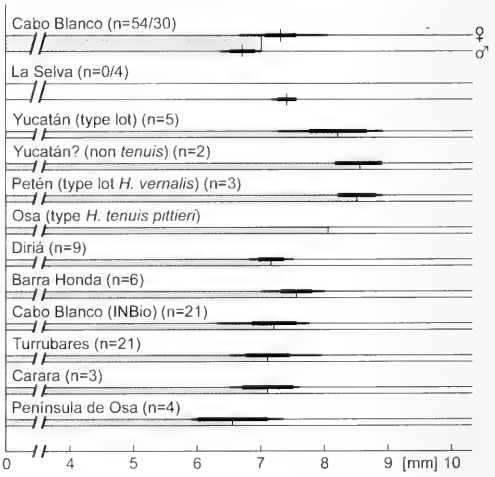


FIG. 67. Minor diameter of shell of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

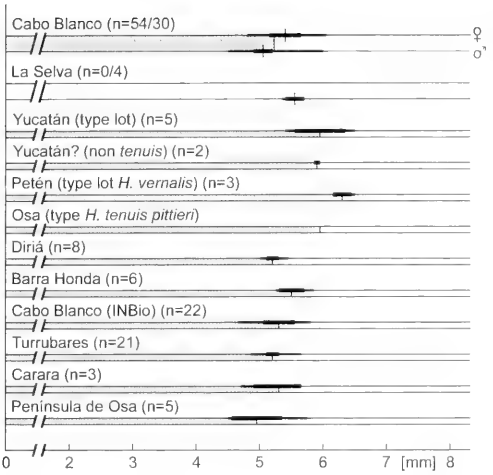


FIG. 68. Expansion of outer lip of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

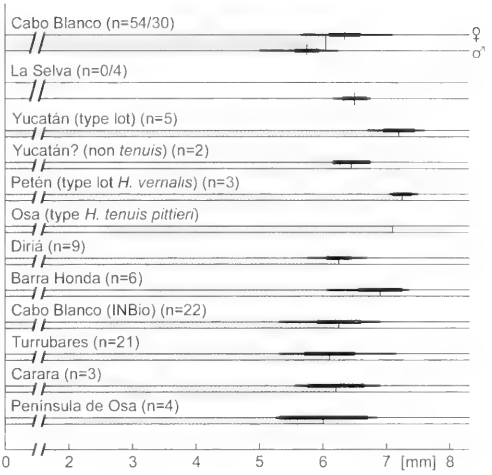


FIG. 70. Height of columellar axis of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

axis). Besides the small sample size, the comparatively high deviations among the specimens from Península de Osa presumably reflect the fact that they originate from different sites on the Península and cannot be considered as a real population the same as the others. Contrary to their small size the type of *H. tenuis pittieri*, collected about 100 years ago on the same peninsula, is exceptional big for the Pacific populations. It suggests that *H. tenuis* displays greater size variation in this area, but the scanty material does not allow further conclusions.

Considering the sexual dimorphism, the average shell height of Caribbean specimens from "La Selva" can be estimated approximately 8.6 mm, thus being bigger than the Pacific populations. This may be caused by the drier climate on the northern Pacific side as compared to the Caribbean plain.

In general, the average of the type lot of *H. tenuis* appears to be typical for the Mexican and Guatemalan areas, since many single specimens from this region were measured and approach a similar size. Nevertheless, smaller specimens were also present, as was the case for the type lot that also may have consisted of specimens from various localities in Yucatán. Goodrich & van der

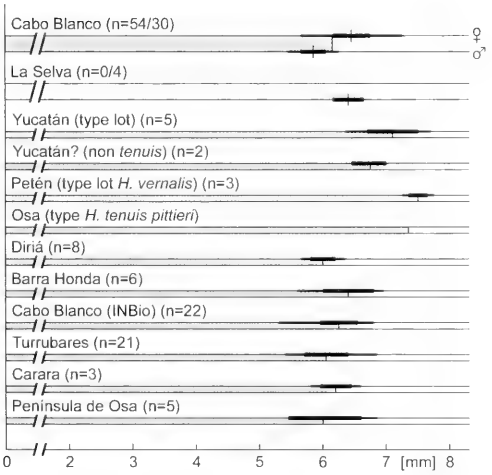


FIG. 69. Height of last whorl of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

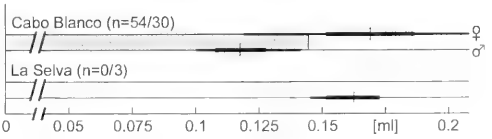


FIG. 71. Shell volume of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

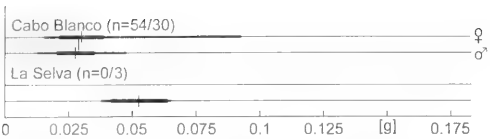


FIG. 72. Shell weight of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

Schalie (1937) state for Péten and North Alta Verapaz, northern Guatemala, that shells from the southern region are a little smaller, unfortunately without giving any measurements. In conclusion, it can be assumed that the shell size of *H. tenuis* varies throughout the whole range of distribution, obviously depending on environmental factors. Near its southern limit of distribution in Costa Rica, the average size is smaller.

Sexual Dimorphism: The 84 specimens of the Cabo Blanco population show clear differences with the average size of females larger than males. The measurements overlap, as shown for height and minor diameter in Fig. 73, but to a smaller degree than in *H. funcki* (Fig. 32). As may be expected, the volume (Fig. 71) best reflects the differences, the average volume of male amounts only 73.6% of the females. The shell weight of both sexes is nearly equal (Fig. 72), therefore males possess relatively heavier shells (Fig. 74).

Habitat

During this study, *Helicina tenuis* was only found in comparatively high abundance during the rainy season in the Cabo Blanco reserve. During the daily rains, the snails were seen crawling on and under living and dead leaves of bushes and palms and on stems. None were collected on the ground. In the same place, *H. tenuis* was nearly "absent" during the dry season, except for very few specimens that were aestivating in folded palm leaves. Two of these seven specimens found were visibly parasitized by larvae of trematodes, whereas no other helicinids ever were found to be infected in this obvious way. It is not clear where the majority of specimens retreat to during the dry period. In addition to the arboreal habitats, searches were conducted in the leaf litter and around the stems of bushes

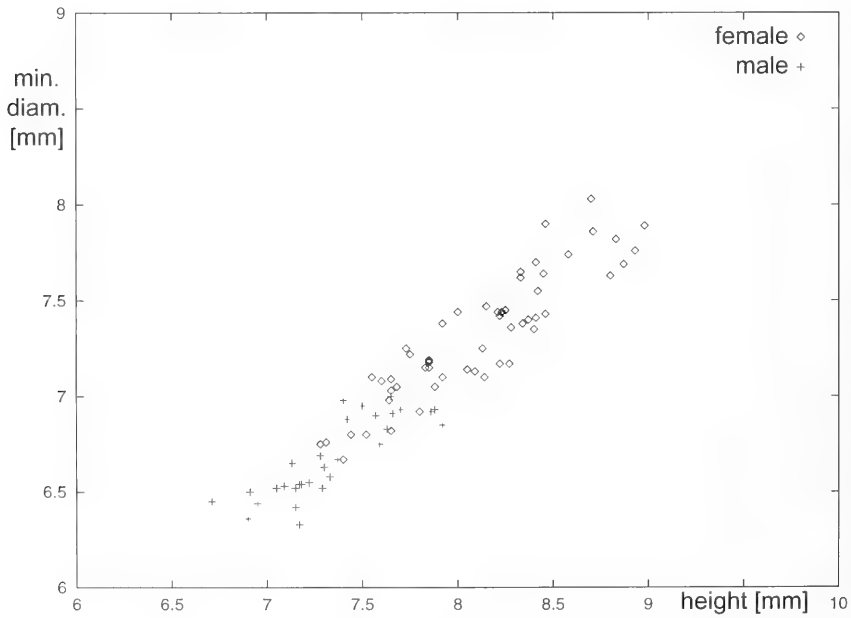


FIG. 73. Range of measurements in females and males exemplary for height and minor diameter in the population from Cabo Blanco.

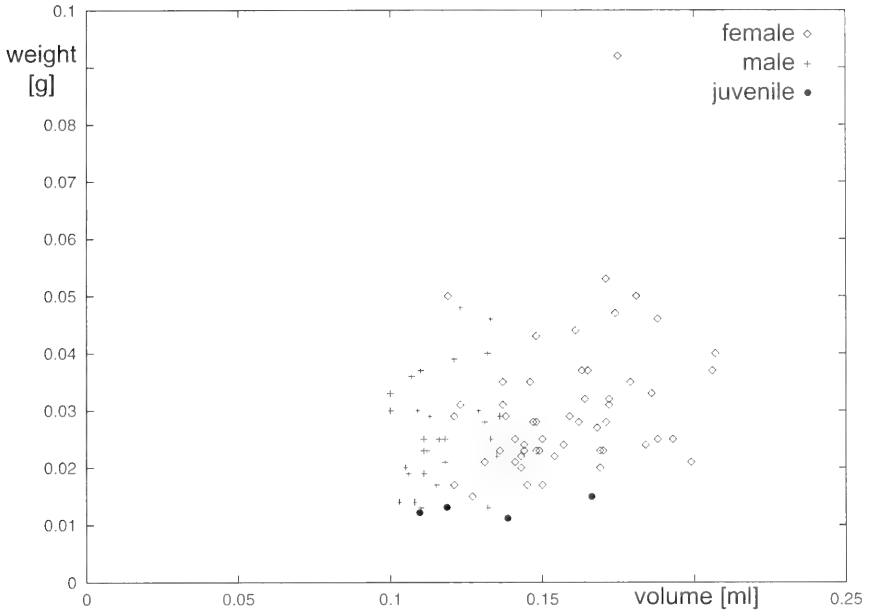


FIG. 74. Relation of weight to volume in females and males of the populations from Cabo Blanco.

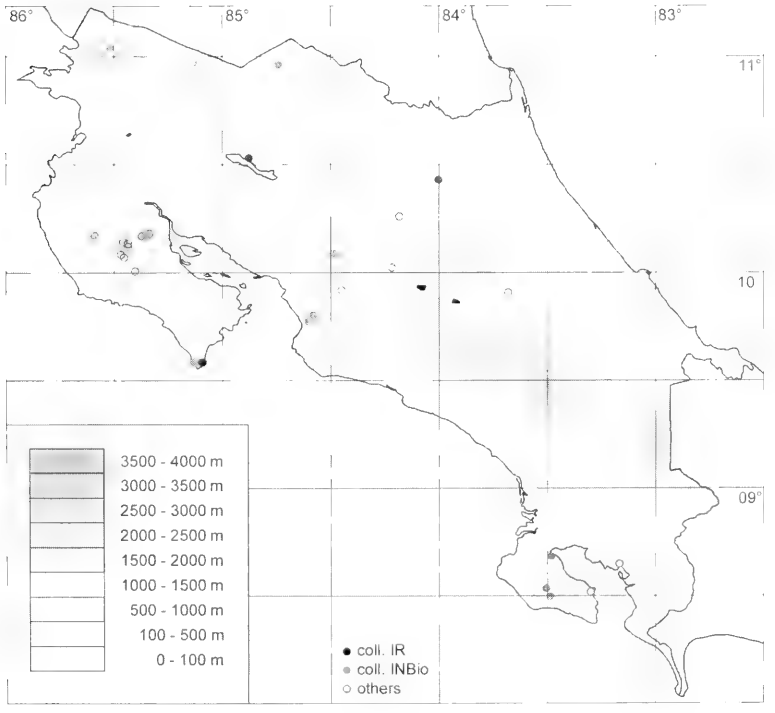


FIG. 75. Records of *Helicina tenuis* in Costa Rica.

and palms on the ground but without success. In other areas without such contrasting seasonal changes (e.g., near Nuevo Arenal, La Selva), *H. tenuis* was only found occasionally during the dry as well during the rainy season. There it was additionally found on the underside of leaves of Musaceae or Heliconiaceae, respectively, which are absent in the drier Cabo Blanco area.

These habitats correspond to those observed by Biolley (1897) for Costa Rica and Baker (1922b) from southern Veracruz in Mexico, who additionally found the species "on the ground and on leaves of shrubs and cacti in the savannah forests". Van der Schalie (1940) reported *H. tenuis* from Alta Verapaz in Guatemala as common and as being found near Panzamala "moving about on the vegetation at night".

With its occurrence on the Península de Nicoya, *H. tenuis* tolerates the highest level of dryness among the Costa Rican Helicinidae and is the only species that can withstand the regular extended dry period during the year. As cited above, it also inhabits the Savannah in association with cacti. This comparatively high ecological tolerance of *Helicina tenuis* among the Helicinidae provides a possible explanation for its remarkably wide distribution.

Distribution

The species reaches its northern limit in southern Mexico (states of Guerrero, Oaxaca, Veracruz) and occurs throughout Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica to western Panama. Even more northern sites in Central Mexico (states of Jalisco and Guantajuato) were listed by von Martens (1890–1901), but the specimens have not been re-examined. The most southeastern record comes from the Tonosi, Los Santos Province, Panama (Pilsbry, 1926a). The specimens from Isla Barro Colorado in the Canal Zone of Panama (Pilsbry, 1930) seem to belong to another species (see "Discussion"). *Helicina tenuis* is found on the Caribbean as well as on the Pacific side of the central mountain chains. Except for *Lucidella lirata*, it is thus probably the most widely distributed species of Helicinidae of the Central American mainland.

In Costa Rica, the species is not common, but was nevertheless found at several distinct localities (Fig. 75). According to the collections, it seems to occur in relatively greater numbers in the Pacific plain, where it also appears to be more widely distributed. Compared with areas investigated and inhabited by other helicinids (e.g., see *H. funcki*), the apparent lack of *H. tenuis* on the Caribbean side at many localities is remarkable, because the species is found in a similar habitat and is comparatively large. In fact, it is completely absent throughout the large province of Limón stretching along the entire Caribbean coast of Costa Rica. La Selva and Turrialba represent the most southeastern localities.

Discussion

The nomenclatural discussion of *Helicina tenuis* is complicated because several confusions have arisen and been maintained in literature.

First, it is important to note that *Helicina tenuis* is not preoccupied by *Helicina tenuis* C. B. Adams, 1849 (now *Stoastomops adamsi* Baker, 1934) from Jamaica, because the latter name was published in September 1849 (Baker, 1934a) and not as stated by von Martens (1890) or Bequaert & Clench (1933) in 1840.

Traditionally, *Helicina tenuis* and *H. lindeni*, both described by L. Pfeiffer in the same paper, the second one page before the other, are regarded as synonyms or varieties of one species. Sowerby (1866) only mentions *H. lindeni*, and his drawing probably represents *H. tenuis*, but both figure and the very short paragraph on the species do not provide sufficient information to assess the status. Von Martens (1890: 34–35) proposed the synonymy without further explanation, except for a statement about the figure of *H. lindeni* in L. Pfeiffer (1850) "not good", and he used *H. tenuis* as the valid name, which also would have established priority because von Martens was the first revising author. Fischer & Crosse (1893) agreed upon the conspecificity, but claimed that *H. lindeni* had page priority and *H. tenuis* became a variety. None of these authors mentions an investigation of the original material (Fischer & Crosse did so for *H. vernalis*), nor did they give reasons for their opinion. Interestingly enough, von Martens (1900: 604) replied in his supplemental part to the French authors, regarding *tenuis* as the most applicable name and remarked on the rather great distinctness L. Pfeiffer attributes to these species (see below). Because both publications

are standard contributions on terrestrial molluscs for Central America, subsequent authors used the one or other name, but commonly adopted the synonymy.

L. Pfeiffer (e.g., 1852a: 372, 388) assigned his two species to different higher groups ("§. 8. Ecarinatae" [*H. tenuis*] and "§. 10. Subcarinatae" [*H. lindeni*]). The descriptions and the subsequently published figures (L. Pfeiffer, 1850) (reprinted here in Fig. 76) are in fact not similar enough to support the synonymy. Obvious differences can be summarized in a less elevated shell in *H. lindeni* ("globosa-conica" instead of "turbinata"; "spira acutiuscula" instead of "acuta" and the measurements). Furthermore, *H. lindeni* is slightly angulated and does not bear color bands, the outer lip is "breviter expanso, reflexiusculo" instead of "tenui, angulatim expanso". L. Pfeiffer's descriptions are short, but very precise in certain details. Regarding the literature, the conclusions of von Martens and Fischer & Crosse can thus not be understood, especially the "not good" figure of *H. lindeni*, because it perfectly matches the written description. Since the type material of *H. lindeni* is still unavailable, possible deviations of the original material (perhaps seen by other authors) from the description that could have explained those conclusions, remain subject to speculation. A variety of *H. lindeni* from the Cuming collection (BMNH 20010757) fits well to the description and figure of *H. lindeni*. In conclusion, *H. tenuis*, for which a lectotype could be chosen in full agreement with the description and the current interpretation, is regarded as specifically distinct from *H. lindeni*. The Costa Rican specimens clearly belong to *H. tenuis*. According to comments and figure *H. lindeni sensu* Fischer & Crosse (1893) is synonymous with *H. tenuis*.

The type material of *Helicina vernalis* and *H. chiapensis* was investigated and the species are confirmed as synonyms of *H. tenuis*. The taxon *H. vernalis verapazensis* proposed by Wagner (1905) was included into the synonymy of *H. tenuis* by himself.

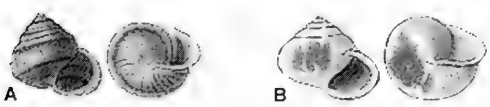


FIG. 76. Reproduction of the figures from L. Pfeiffer (1850) of A. *Helicina tenuis*. B. *Helicina lindeni*.

The present status of *Helicina tenuis pittieri* is doubtful, because comparable material from the Península de Osa is very scarce and the few specimens available show a high variation in size, are always not only smaller, but also belong to different sites. A common feature is the whitish band at the periphery, which is lacking in other Costa Rican populations. Considering the high variation of the widespread *H. tenuis* and the lack of further distinguishing characteristics, *H. tenuis pittieri* is tentatively regarded as a synonym. Wagner (1910a: 303), judging *H. tenuis* as variable and even not constant in local forms, presents only the new subspecies at the southern limit of the distribution as a "auffallender unterschiedene und anscheinend konstante Form" [strikingly different and apparently constant form]. According to the original description and as far as it could be traced in collections (ZMB, SMF, MIZ [Wagner coll.]), it seems very likely that he only knew a single specimen, the holotype of the so-called "constant form". More northern records in Costa Rica Wagner included in the nominal form.

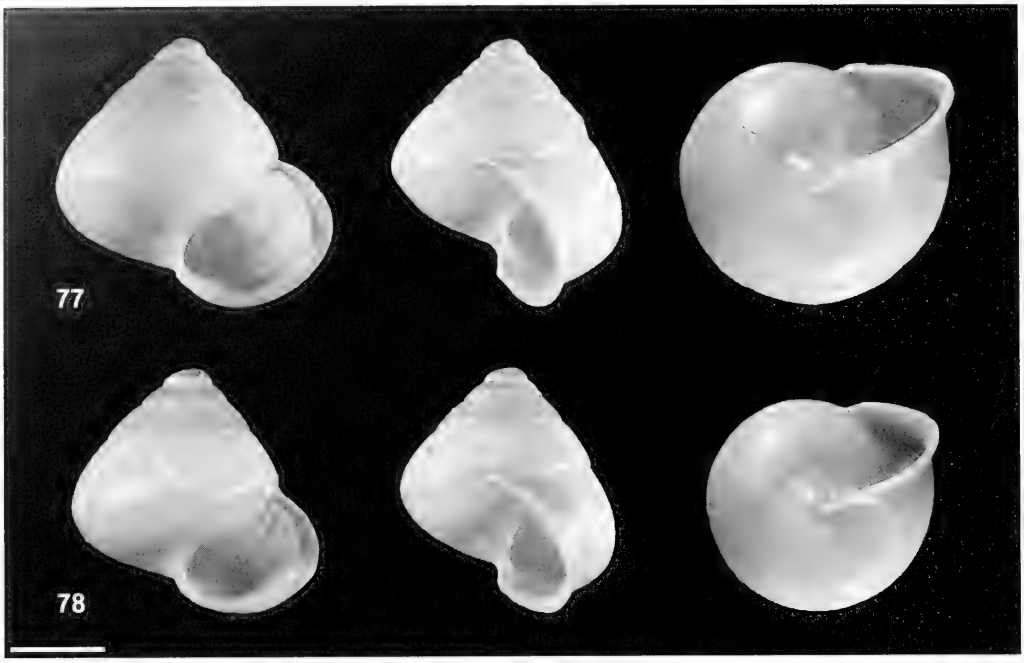
Several records of *H. tenuis* from high elevations (e.g., Cerro Zunil) given by von Martens (1890–1901) likely refer to *H. punctisulcata zunilensis*, in one example cited it is very likely that the record exactly originates from the specimen on which Wagner (1910a) based his new subspecies. The record from the Canal island of Panama (Pilsbry, 1930) seems to be based on another species, because the size of the specimen (5/5.4 mm) is clearly beyond the range of *H. tenuis*.

The record of *H. oweniana* for Costa Rica by Monge-Nájera (1997) was checked in the INBio collection. The lots INBio 1463452 and 1464319 clearly determined before 1997, have to refer to *H. tenuis*. *H. oweniana* is finally distinguished from *H. tenuis* by its orange colored outer lip, a more solid shell, a less impressed suture with its lower margin whitish. *Helicina oweniana* lacks the typical denticle at the transition from the outer lip to the columella.

Helicina (*Tristramia*) *echandiensis* Richling, n. sp.

Type Material

Holotype: INBio 3542520, female (leg. Alexander Alvarado Mendez, 14.11.2001)



FIGS. 77, 78. *Helicina echandiensis* n. sp. FIG. 77. Holotype, INBio 3542520, height 7.2 mm. FIG. 78. Paratype 1, INBio 3542521, height 6.5 mm; scale bar 2.5 mm.

Paratype: INBio 3542521, male (same data as holotype)
Additional paratypes: INBio 3428246: 6 ads., 1 s.ads., 9 juvs., INBio 3574064: 1 s.ad. (same data as holotype)
Dimensions:
Holotype: 7.2/6.8/7.3/6.2/4.4/5.3/5.4 mm
Paratype 1: 6.5/6.1/6.5/5.7/3.9/4.8/5.1 mm

Type Locality

S-Costa Rica, Puntarenas Province, Parque Nacional La Amistad, Sector Las Alturas, Southern Cordillera de Talamanca, S of Cerro Echandi, campamento Echandi, 09°01'33"N, 82°49'12"W, 2,840 m a.s.l.

Etymology

The name refers to the origin of the species, the Cerro Echandi.

Examined Material

INBio Collection

Puntarenas: Zona Protectora Las Tablas, *sector Las Alturas*, campamento de los nacientes del Río Vella Vista, 08°59'39"N, 82°49'18"W, 2,100 m a.s.l.: leg. E. Alfaro, 13.11.2001: 1 ad. (INBio 3505804)

Description

Shell (Figs. 77, 78, 335J–K): conical, thin and fragile, medium to small sized, only slightly shiny to dull. Color: basic color light orange-brownish; apex and upper whorl unicolored, only lighter towards the suture, about the 1.5 last whorls above periphery with a pattern of irregular, mostly parallel distinct white stripes in the same orientation as growth lines, about as wide as interspaces; stripes starting at suture and all ending at the same level a little above periphery. Surface textured with irregular growth lines and oblique grooves of different individual orientation but of same general direction (Fig. 80), causing the rather dull appearance. Embryonic shell with about 1 whorl; $3^{7}/_{8}$ (3½–4) subsequent whorls very straight; last whorl also straight

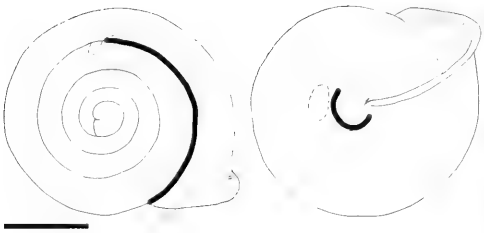


FIG. 79. Axial cleft and muscle attachments of *Helicina echandiensis* n. sp., INBio 3542520; scale bar 2.5 mm.

above and round at periphery and below; whorls equally extending in size, forming a very regular, pointed spire. Suture very slightly impressed. Aperture slightly oblique and straight, last whorl very slightly ascending towards the aperture and inserting just below the periphery. Outer lip of a bright orange, thickened, moderately and equally expanded. Reflection nearly rectangular to the whorl; transition to columella forming a blunt edge with a very small denticle. Columella oblique and rather straight, transition to the body whorl smooth. Basal callus weakly developed, at the base more pronounced and granulated.

Internal Shell Structures: (Fig. 79)

Teleoconch Surface Structure: Helicina echandiensis n. sp. seems to lack the transitional pattern (Fig. 80A), the whole teleoconch exhibits a structure of oblique diverging grooves (Fig. 80B). About the upper half of the beginning of the 1st whorl is occasionally sculptured with fine wrinkles parallel to the growth lines. Overlapping equally spaced periostracal spiral ridges also begin immediately at the teleoconch (Fig. 80A, arrow).

Embryonic Shell (Fig. 81): Faced with the paucity of material for *Helicina echandiensis* n. sp., only one specimen was studied under the SEM (INBio 3574064). The younger part of the embryonic shell appears compressed, as if it developed in slower growth, but this is not likely to be a typical feature. It is probably not related to living conditions at high altitudes where the species is found, because the embryonic shell of *H. punctisulcata*

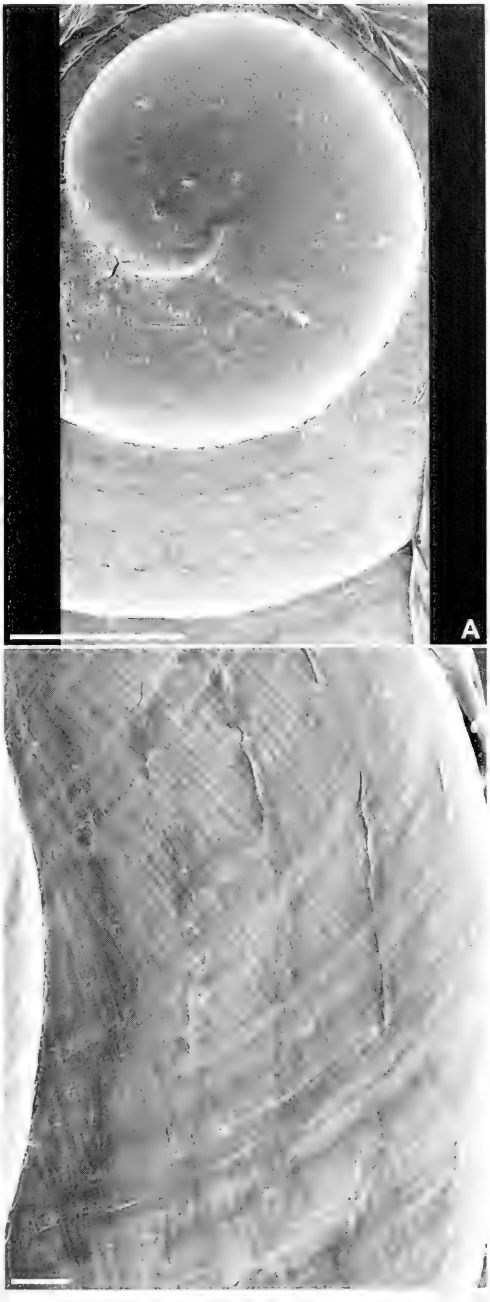


FIG. 80. Teleoconch surface structure of *Helicina echandiensis* n. sp. A. Embryonic shell and begin of 1st and 2nd whorl, arrow indicates exemplarly an early spiral ridge. B. 3rd whorl; scale bars 500 µm (A), 100 µm (B).

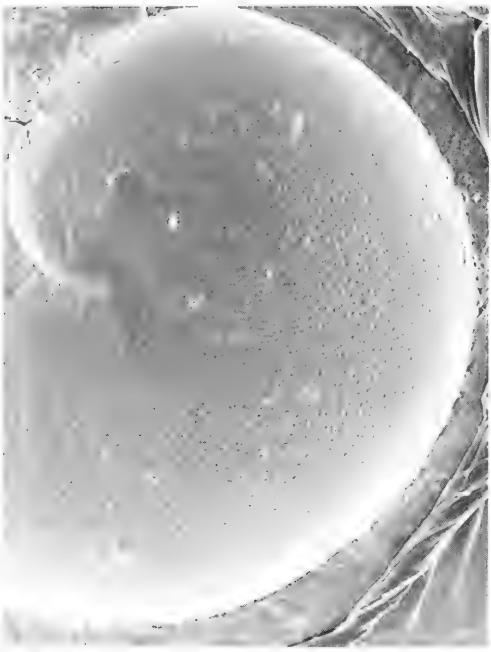


FIG. 81. Embryonic shell of *Helicina echandiensis* n. sp.; scale bar 100 µm.

cuericiensis n. subsp. is normally developed. The arrangement of the pits is less regular than in the previous species, and the pits are relatively smaller. The embryonic shell size is much larger than in *H. escondida* n. sp. of equal shell size and even exceeds that of specimens of *H. funcki* from the lowlands. Diameter: 1,026 µm (± 36) (960–1,120) (n = 9) (INBio 3428246, INBio 3542520, INBio 3542521).

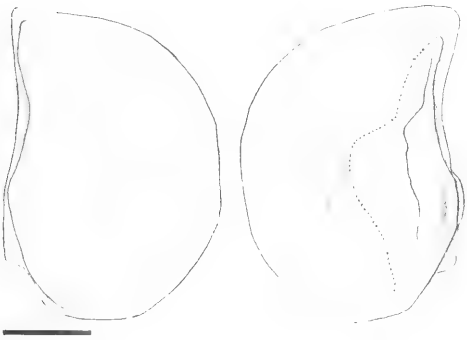


FIG. 82. Operculum of *Helicina echandiensis* n. sp., INBio 3542520; scale bar 1 mm.

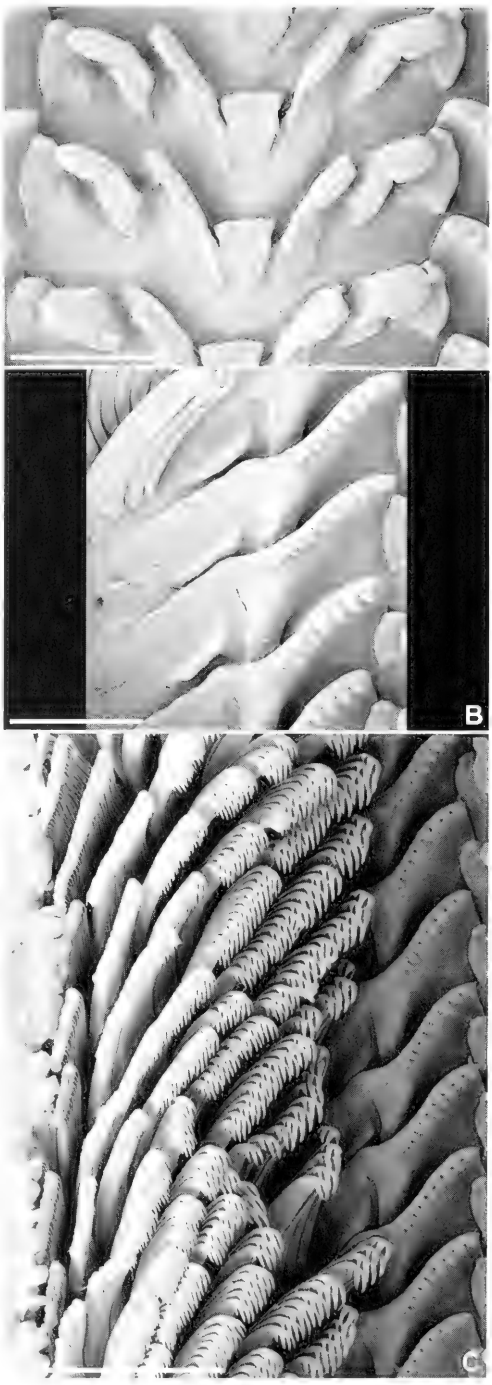


FIG. 83. Radula of *Helicina echandiensis* n. sp. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 µm (A, B), 100 µm (C).

Operculum (Fig. 82): very slightly calcified, calcareous plate covering only part of outer surface. Color horny-amber to orange, only near the columella whitish or transparent. Columellar side slightly irregular S-shaped, upper end acute and pointed, lower end continuously changing into outer margin.

Animal: In the preserved specimens, the soft body is greyish-blackish throughout. Only towards the sides and underside of the foot does the color become lighter. The sides of the foot and parts of the mantle are occasionally only spotted greyish.

Radula (Fig. 83): Due to the lack of material, the radula of only one specimen was investigated. Cutting edges in centrals rather crenulate than bearing cusps, comb-lateral with 10–11 cusps, cusps on marginals slowly increasing in number. Radula with 72 rows of teeth.

Female Reproductive System (Fig. 84): The receptaculum seminis is long and slender and joins the descending limb of the V-organ at the middle of its inner side. The bursa copulatrix is moderately lobed, the flattened provaginal sac is of about equal size. It is clearly demarcated from its short and stout stalk, the distal side is irregularly subdivided. The pallial oviduct is mainly transversally constricted.

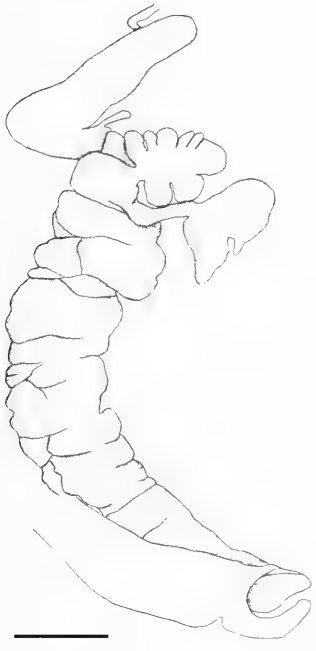


FIG. 84. Female reproductive system of *Helicina echandiensis* n. sp., INBio 3542520; scale bar 1 mm.

Morphometry and Sexual Dimorphism (Table 7, Fig. 85)

The material available is very limited, but because the sex of all these eight adult specimens could be determined (two by removal from the shell, the rest by external inspection enabled by the transparency of the shells), it seems worthwhile including them in the data.

The measurements show a range of deviations that is higher than in the populations of the similarly sized *Helicina escondida* n. sp. for which a comparable number of specimens was analyzed. A sexual dimorphism is indicated with the females being bigger than the males, but the data overlapping slightly. The differences for height and minor diameter in females and males amount less than in such species as *H. gemma* and *H. beatrix* and resemble those of *H. escondida* n. sp. In interpolation from the minor diameter, males have a volume of about 75% that of females.

Habitat

The type locality is located in an area characterized by montane rain forest. The field notes of Alexander Alvarado Mendez state that the specimens were found in very humid, primary

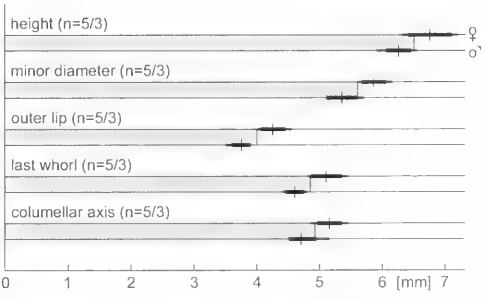


FIG. 85. Measurements of *Helicina echandiensis* n. sp. according to Table 7; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males "; upper line: females, lower line: males; in between and shaded: average of both.

TABLE 7. Measurements of *Helicina echandiensis* n. sp. given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm].

		"Cerro Echandi" (altitude 2840 m) lots INBio 3428246, 3542520, 3542521				
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	6.75	0.34	6.28	7.18	5
Height	m	6.24	0.22	5.92	6.53	3
Maj. diam.	f	6.40	0.23	6.02	6.81	5
Maj. diam.	m	5.78	0.21	5.50	6.10	3
Min. diam.	f	5.87	0.22	5.59	6.15	5
Min. diam.	m	5.34	0.23	5.08	5.68	3
Outer lip	f	4.27	0.19	4.00	4.55	5
Outer lip	m	3.75	0.16	3.52	3.92	3
Last whorl	f	5.09	0.25	4.78	5.45	5
Last whorl	m	4.62	0.14	4.41	4.79	3
Col. axis	f	5.15	0.22	4.86	5.44	5
Col. axis	m	4.79	0.23	4.50	5.13	3

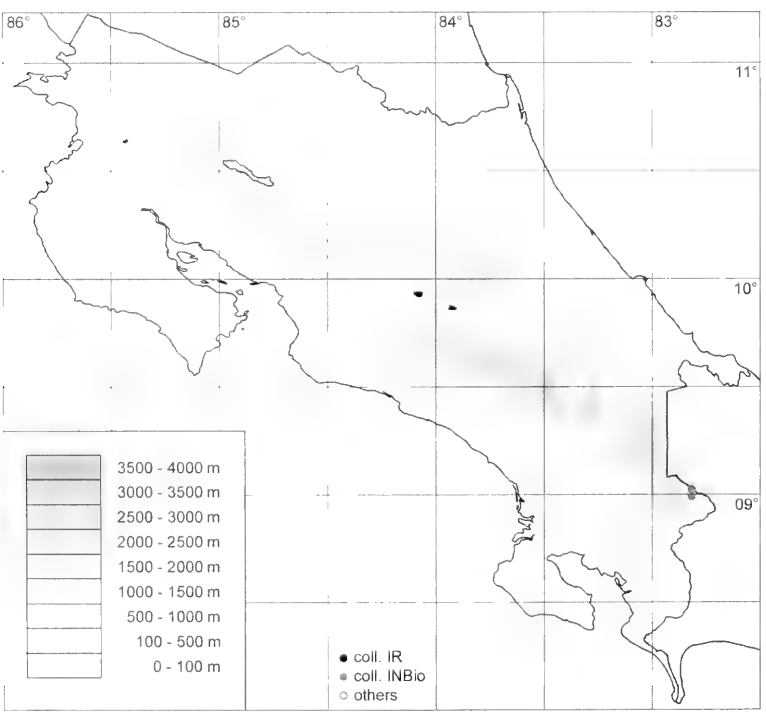


FIG. 86. Records of *Helicina echandiensis* n. sp. in Costa Rica.

forest on black soil. The undergrowth mainly consisted of Heliconiaceae. Considering the shell color and the habitats of comparable species, it seems likely that *Helicina echandiensis* n. sp. was also found on these plants.

Distribution (Fig. 86)

Helicina echandiensis n. sp. is known only from the southern slopes of Cerro Echandi a little below the summit, from altitudes of 2,100 to 2,840 m. The area is part of the central mountain chain of the Cordillera de Talamanca.

Discussion

Helicina echandiensis n. sp. is unique in its combination of characteristics. It can be distinguished from the other species with a bright reddish-orange outer lip – *H. gemma*, *H. beatrix riopejensis* n. subsp. – by the straight and uncurved form of the latter and the surface structure of oblique diverging grooves. Among helicinids of this shape and shell surface texture it is comparable in size only to *H. escondida* n. sp., which has a light yellowish outer lip, a less pronounced surface structure, and more convex whorls. Furthermore *H. escondida* n. sp. lacks the characteristic diagonal white stripes and seems to be restricted to the Caribbean side of the central mountain chains.

Helicina (*Tristramia*) *punctisulcata cuericiensis* Richling, n. subsp.

Type Material

Holotype: INBio 3542622 (leg. A. Picado, 19.01.1996)
Paratype: INBio 3542541, female (09°33'19"N, 83°40'13"W, 2,600 m a.s.l.: colectado mediante sombrereta [collected by beating vegetation], leg. B. Gamboa, 29.10.1995)
Dimensions:
Holotype: 5.9/6.5/6.8/5.8/4.1/4.4/4.8 mm
Paratype: 7.9/7.3/7.7/6.8/4.5/5.6/6.5 mm

Type Locality

Central Costa Rica, San José Province, Cordillera de Talamanca, Estación Cuerici, 4.5 km E de Villa Mills, Sendero el Mirador, 09°33'28"N, 83°40'13"W, 2,700 m a.s.l.

Type Material of Relevant Taxa

Helicina punctisulcata von Martens, 1890

Helicina punctisulcata von Martens, 1890: 36–37, pl. I, fig. 10

Type Material: Lectotype ZMB 103326a: leg. H. H. Smith, additional paralectotypes ZMB 103326b, ZMB 103326c, ZMB 103325
Von Martens based the description on material collected by H. H. Smith, which is in the collection of the ZMB. Four specimens from ZMB 103326 were marked to be figured by von Martens, of which only one matches the measurements given in the original description, the other being much smaller (about 1.3 to 1.8 mm smaller in the greater diameter). Furthermore, it best fits his upper right basal view, with a minute groove in the columellar region. This specimen is **herein selected as lectotype** (Fig. 87).
Dimensions (height/greatest diameter/minor diameter):
Lectotype: 7.2/8.9/7.8 mm

Type Locality: "W Mexico: Omilteme, 8000 ft. on the Sierra Madre del Sur, State of Guerrero, Pacific side of the main cordillera"

FIG. 87. *Helicina punctisulcata*, lectotype, ZMB 103326a, height 7.2 mm; scale bar 2.5 mm.

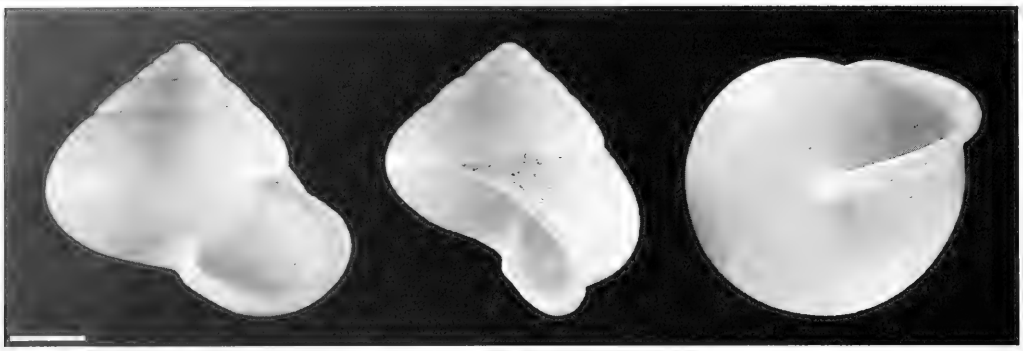


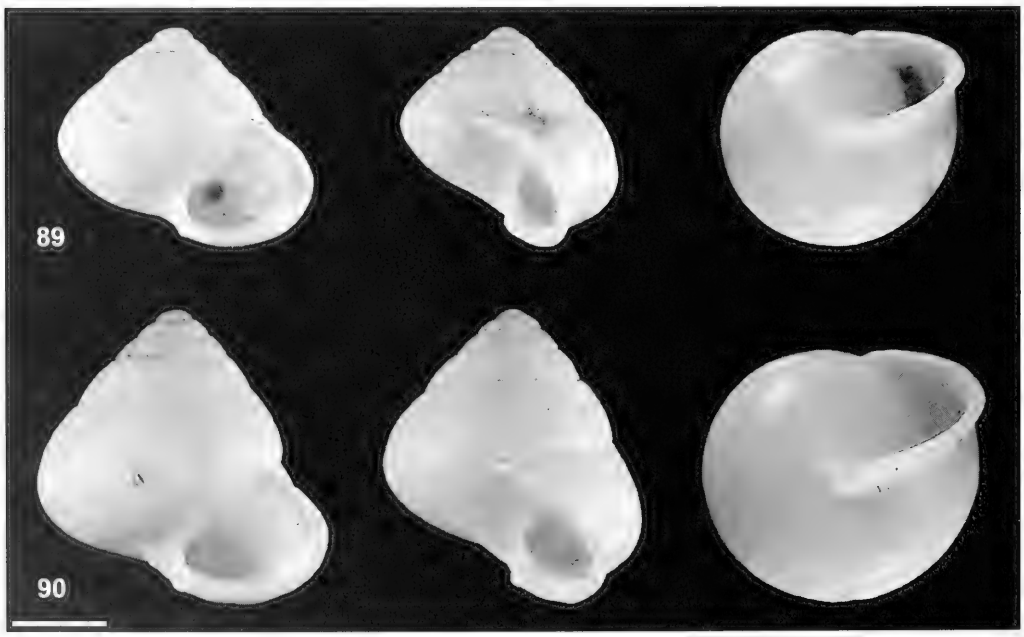
FIG. 88. *Helicina punctisulcata zunilensis*, holotype, ZMB 103324, height 9.2 mm; scale bar 2.5 mm.

Helicina punctisulcata zunilensis Wagner, 1910

Helicina punctisulcata zunilensis Wagner, 1910a: 295, pl. 59, fig. 9

Type Material: Holotype ZMB 103324
Because the original description refers to one specimen in the museum in Berlin, the single specimen matching the figure is the holotype (Fig. 88).
Dimensions (height/greatest diameter/minor diameter):
Holotype: 9.2/10.2/8.7 mm

Type Locality: "Vulkan Zunil in Guatemala" [Guatemala, at border of Quezaltenango and Solola departments, volcano Volcán Zunil]



FIGS. 89, 90. *Helicina punctisulcata cuericiensis* n. subsp. FIG. 89. Holotype, INBio 3542622, height 5.9 mm. FIG. 90. Paratype, INBio 3542541, height 7.9 mm; scale bar 2.5 mm.

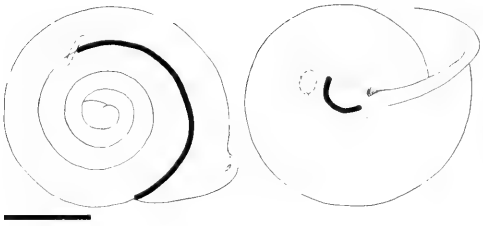


FIG. 91. Axial cleft and muscle attachments of *Helicina punctisulcata cuericiensis* n. subsp., INBio 3542622; scale bar 2.5 mm.

Etymology

The name refers to the origin of the species, the Cerros Cuerici.

Examined Material

INBio Collection

San José: *Estación Cuerici*: *Sendero el Mirador, 4.5 km E de Villa Mills, 09°33'28"N, 83°40'13"W, 2,700 m a.s.l.*: leg. A. Picado, 19.01.1996 (INBio 3542622); 19.01.1996 (INBio 3542527); colectado en una planta [collected on a plant] 26.06.1996, leg. B. Gamboa (INBio 3544828); *2,750 m a.s.l.*: leg. A. J. Mora, 27.11.1995 (INBio 3542528); *09°33'19"N, 83°40'13"W, 2,600 m a.s.l.*: colectado mediante sombrereta [collected by beating vegetation], leg. B. Gamboa, 29.10.1995 (INBio 3542541); recolectado en una rubiaceae caminando [collected crawling on a Rubiaceae], leg. A. Picado, 26.08.1995 (INBio 3542539)

Description

Shell (Figs. 89, 90, 335L–M): Conical, solid, medium to small sized and only slightly shiny to dull. Color: apex and upper whorl dark yellow, becoming lighter with growth and increasingly whitish spotted, towards the aperture changing to whitish with small yellowish spots. Surface textured with irregular growth lines and oblique grooves of different individual orientation but of the same general direction (Fig. 92), causing the dull appearance; last two whorls with 3–4 equally spaced spiral grooves. Embryonic

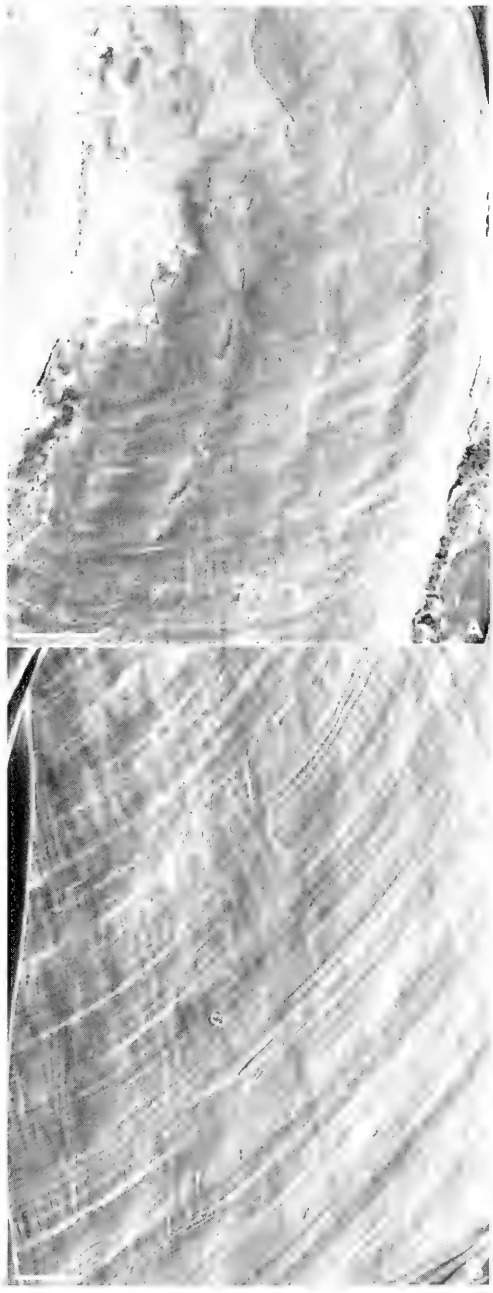


FIG. 92. Teleoconch surface structure of *Helicina punctisulcata cuericiensis* n. subsp. A. 2nd whorl, partly eroded. B. 4th whorl; scale bar 100 µm.

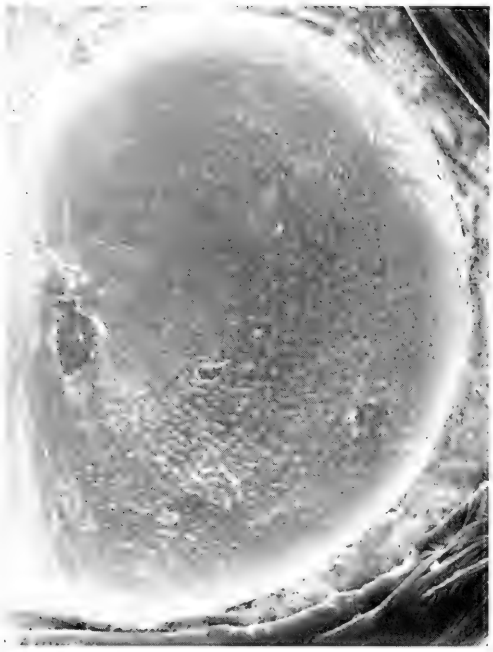


FIG. 93. Embryonic shell of *Helicina punctisulcata cuericiensis* n. subsp.; scale bar 100 µm.

shell with about 1 whorl; $3^{5}/_{8}$ ($3^{5}/_{8}$–$4\frac{1}{2}$) subsequent whorls straight, the last whorl very slightly angulated at the periphery and rounded below; whorls equally extending in size, forming a very regular, pointed spire. Suture moderately impressed. Aperture oblique and straight, last whorl slightly descending towards aperture and inserting below the periphery. Outer lip yellowish, re-

FIG. 94. Operculum of *Helicina punctisulcata cuericiensis* n. subsp., INBio 3542622; scale bar 1 mm.

FIG. 95. Radula of *Helicina punctisulcata cuericiensis* n. subsp. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

markably thickened and equally expanded, edge appearing rounded. Transition to columella protruding, forming a blunt edge with a denticle. Columella very short and curved, transition to the body whorl with sharply impressed line. Basal callus well developed, very pronounced in umbilical area and finely granulated.

Internal Shell Structures: (Fig. 91)

Teleoconch Surface Structure (Fig. 92): In all of the few available specimens, the beginning of the teleoconch is eroded. On the second whorl, the surface is sculptured with oblique diverging grooves continuing throughout the whole teleoconch. This pattern is interposed with distinct, irregular growth lines (Fig. 92B) and spiral grooves, which are characteristic for *Helicina punctisulcata cuericiensis* n. subsp.

Embryonic Shell (Fig. 93): Only a single specimen could be studied. The structure is similar to that of *Helicina funcki*. As in *H. echandiensis* n. sp. the diameter is relatively very large.
Diameter: 1,038 µm (± 15) (1,000–1,060) (n = 5) (INBio 3544828, 3542541, 3542539, 3542528, 3542622).

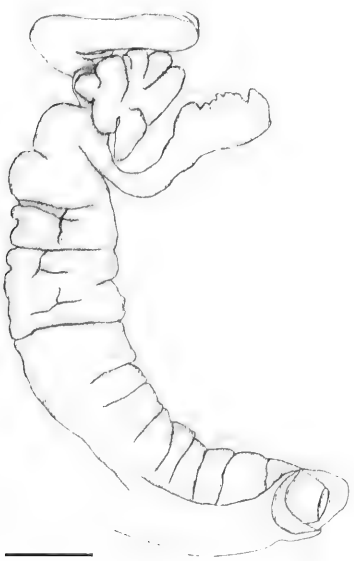


FIG. 96. Female reproductive system of *Helicina punctisulcata cuericiensis* n. subsp., INBio 3542528; scale bar 1 mm.

Operculum (Fig. 94): Very slightly calcified, calcareous plate covering only part of the outer surface. Color horny-amber, at nucleus nearly transparent. Columellar side slightly regularly S-shaped, upper end acute and pointed, lower end rounded, but slightly truncated.

Animal: In preserved specimens, the soft body is greyish-black throughout, only towards the sides and underside of the foot the color becomes lighter to whitish-yellowish. The dark color of the mantle gives the shells of live specimens a greenish tinge.

Radula (Fig. 95): Only two specimens were investigated. The B-central bears 8 well defined cusps, whereas A- and C-central may be a little crenulated. Comb-lateral with 8–11 cusps, cusps on marginals slowly increasing in number. Radula with about 60 rows of teeth.

Female Reproductive System (Fig. 96): The V-organ is comparatively slender, the oblong receptaculum seminis joins its descending limb about the middle of the inner side. The bursa copulatrix is relatively large and compact, it is subdivided in a few simple lobes. The provaginal sac is oblong and finely irregularly lobed at its distal side, a stout, short duct continues to the reception chamber. The sac is blackish pigmented.

Morphometry and Sexual Dimorphism

The amount of material is too limited to be analyzed. The shape of the holotype is representative for all other specimens except for the paratype, which is higher elevated and more evenly rounded at the periphery. The holotype is the smallest specimen, whereas the paratype is the largest.

Two specimens dissected for anatomical studies are females, of which one is the paratype. The other specimen represents the smallest of the four live-collected individuals.

Habitat

The field notes from the collectors of INBio indicate that the species climbs on vegetation, where it was found "en una rubiaceae caminando [crawling on a Rubiaceae]" or by beating vegetation. The type locality is situated in a transitional zone of montane rain forest to paramó vegetation.

Distribution (Fig. 97)

Helicina punctisulcata cuericiensis n. subsp. is only recorded from the main ridge of the northern Cordillera de Talamanca west of the Cerros Cuerici.

Discussion

The specimens were tentatively classified as a new subspecies of *Helicina punctisulcata* because of the resemblance to this species and its subspecies *H. p. zunilensis* in the shell surface structure, color, shell thickness, and development of the outer lip, with a protruding denticle and the impressed line near the columella. In fact, differences are only shell shape, size, and color detail. The comparatively widely spaced spiral grooves are the most remarkable common feature that also distinguishes the "*punctisulcata*"-group from other species of Helicinidae of similar size. The only exception is *H. raresulcata* L. Pfeiffer, 1861, differing in a more globose, slightly angulated and shouldered shape of the shell (rather similar to *H. merdigera* see under *H. monteverdensis* n. sp.), which furthermore occurs on the Caribbean side of Mexico in Veracruz, whereas the subspecies of the "*punctisulcata*"-group all originate from high altitudes in the Pacific or Central mountains. Besides the types of *H. punctisulcata*, similar spirally grooved specimens come from El Salvador (Laguna de las Ranas, 1,730 m a.s.l., leg. A. Zilch, 16.7.1951, SMF), Guatemala, Huehuetenango Department (5 km W of Aguacatan, 15°20'44"N, 91°23'03"W, 1,910 m a.s.l., leg. F. G. Thompson et al.UF 190472, UF 190225), and Honduras, Santa Barbara Department (Cerro Santa Barbara, ridge above El Cedral, 14°54'55"N, 88°07'30"W, 2,800 m a.s.l., leg. J. Polisar, UF 242644). As can be seen, all these specimens also come from high elevations.

Helicina p. cuericiensis n. subsp. is smaller and has a more intense yellow color. Contrary to *H. p. zunilensis*, the spiral grooves are restricted to the upper half of the whorls. The

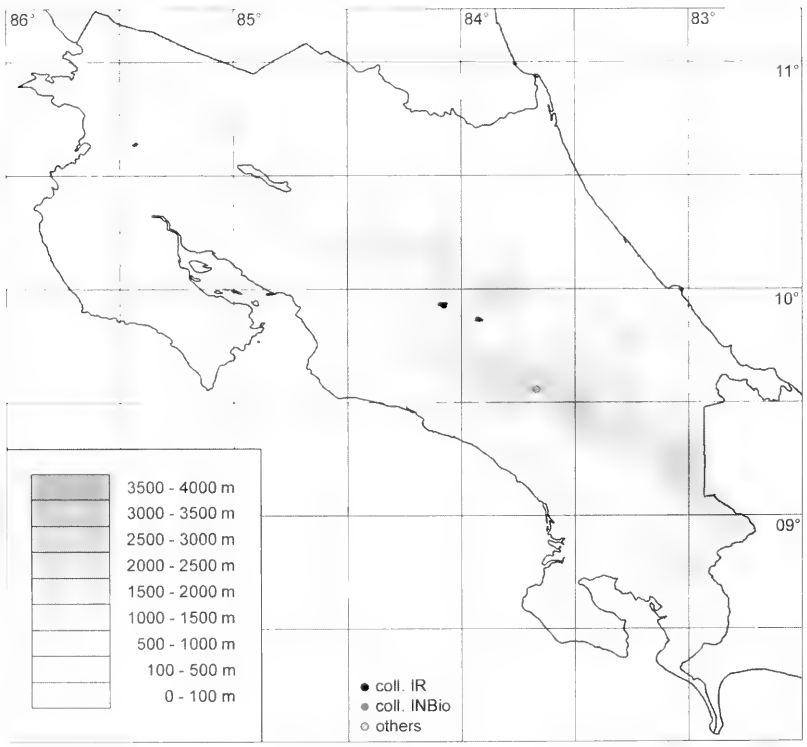


FIG. 97. Records of *Helicina punctisulcata cuericiensis* n. subsp. in Costa Rica.

nominal subspecies appears to be consistently less elevated (broader than high), and the lower margin of the outer lip is less protruding. The few Costa Rican specimens vary remarkably in the relation of height and diameter. But lacking more material for either of the subspecies, the extent of variations, the distribution and ecological data remain only fragmentarily known, which is why the subspecific classification is maintained, although *H. p. punctisulcata* diverges more strongly from the two southern subspecies. Assuming a restriction to higher altitudes, the three subspecies are separated by the low elevations at the Isthmo de Tehuantepec and the Nicaraguan depression respectively.

An additional single specimen from Costa Rica (San José Province, Parque Nacional Chirripó, Fila Cementerio de la Máquina, 4 km E de San Gerardo, 09°27'49"N, 83°33'40"W, 2,200 m a.s.l., leg. Alexander Alvarado Mendez, 08.10.2001, INBio 3428245) is larger than *H. punctisulcata cuericiensis* n. subsp. and is similar to *H. punctisulcata zunilensis*, but, due to the lack of sufficient material, its proper determination must await further comparative data.

Helicina (*"Gemma"*) *beatrix beatrix*
Angas, 1879

Helicina beatrix Angas, 1879: 484, pl. XL, fig. 13
Helicina beatrix – Pilsbry, 1891: 332
Helicina flavida var. – von Martens, 1890: 39
Helicina beatrix – Fischer & Crosse, 1893: 435
Helicina flavida var. *beatrix* – von Martens, 1900: 606: E-Costa Rica: Talamanca (Pittier); Valley of Tuis [about 09°51'N, 83°35'W] (Pittier & Biolley); Santa Clara, 200 m [7.5 km NW of Upala, about 10°56'N, 85°05'W, Alajuela Province] (Biolley); Valley of Alta Coca, near Talamanca, 1,000 m (Pittier) [probably referring to Alto Coén, recently called San José Cabécar, about 09°30'35"N, 83°08'22"W, 500 m a.s.l., Limón Province]; between Uiskur and Mokri [not localized], Alta Talamanca, further in Alta Uren [Alto Urén: 09°23'50"N, 82°59'02"W, 900 m a.s.l., Limón Province], and between Ukatschka and Bruschik, in Alta Taruria [Alto Tararia, about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream, Limón Province] (Pittier)
Alcadia (*Leialcadia*) *beatrix* – Wagner, 1908: 83–84, pl. 14, figs. 19–22
Oligyra (*Succincta*) *beatrix beatrix* – Baker, 1922a: 45
Helicina (*Oligyra*) *beatrix* – Pilsbry, 1926a: 59, 69, fig. 3A, 71: Panama: Bocas del Toro: Mono Creek (Olsson)
?Helicina beatrix – Pilsbry, 1926b: 127: Costa Rica: La Emilia, < 100 ft. [not localized] (Rehn)
Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part]

Original Description

"Shell conical, solid, shining; as seen through the lens, very finely transversely striated; whorls 6, very slightly convex, the four uppermost chestnut, the fifth dark red, with an opaque whitish band below the suture, the last pale olive-green, with a similar opaque band at the suture; outer lip thickened, a little expanded and reflexed; aperture quadrately semilunate. Var. Smaller and straw-coloured thoughout. Diam. $4^1/_2$, alt. 5 lin.

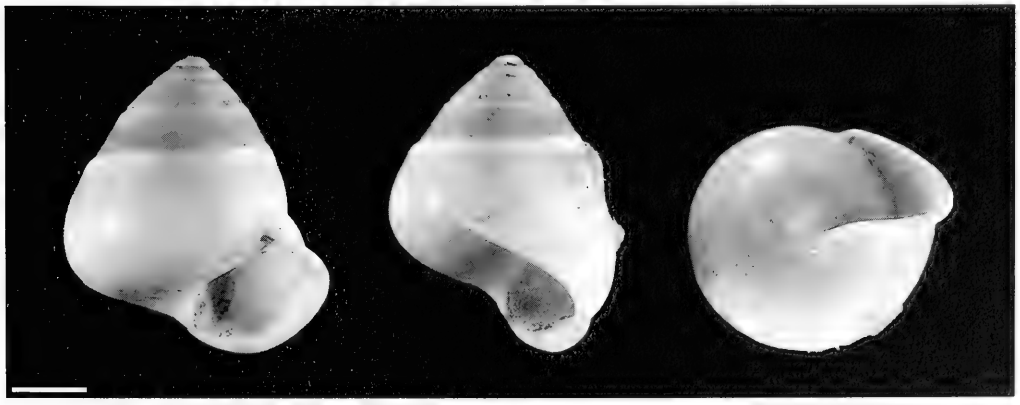


FIG. 98. *Helicina beatrix*, lectotype, BMNH 1879.7.22.29, height 10.1 mm; scale bar 2.5 mm.

Very few specimens. "Found only on the hills up to an elevation of 2,500 feet. Animal dark grey above, sides and foot white" (Gabb). Approaches *H. heloisae*, Sallé, but larger and much more conical."

Type Material

BMNH 1879.7.22.29–31 (leg. Gabb)
Angas (1879: 475) stated that his type material would be placed in the collection of the British Museum, the lot is labeled with "type". Of the three specimens, one represents the dark red opaque whitish banded typical form, the other two the straw colored variety separated by the author. Therefore, the latter two specimens are not regarded as syntypes. The remaining specimen (BMNH 1879.7.22.29), also perfectly matching the figure in the original description, is **here selected as lectotype** of *Helicina beatrix* (Fig. 98). It still bears its operculum and was probably collected live. The two other specimens (one with operculum inside) are much smaller and show a whitish to slightly yellowish color (perhaps faded since the description of Angas), and in one a slight whitish subsutural banding is visible. They are regarded here as *H. beatrix confusa*.
Dimensions:
Lectotype BMNH 1879.7.22.29:
10.1/8.3/8.9/7.7/5.3/7.1/8.2 mm;
BMNH 1879.7.22.30–31 *Helicina beatrix* var. *sensu* Angas, now referred to *H. beatrix confusa*:
7.3/6.9/7.2/6.3/4.3/5.5/5.7 mm
7.0/6.3/6.6/5.9/4.1/5.4/5.6 mm

Type Locality

"Costa Rica, only on the hills up to an elevation of 2,500 feet".

Type Material of Synonymous Taxa or Similar Species

Helicina beatrix nicaraguae (Wagner, 1908)

Alcadia (*Leialcadia*) *beatrix nicaraguae* Wagner, 1908: 84, pl. 14, figs. 23–24

Type Material: MIZ 8408: "Nicaragua"
Wagner did not refer to any type material, but his collection contains only one lot with two specimens. It is labeled to be figured and the larger shell perfectly matches the drawing. It is **here selected as lectotype** (Fig. 99). The paralectotype (MIZ 8408b) is not fully grown.
Dimensions:
Lectotype MIZ 8408a:
10.2/8.7/9.1/8.1/5.3/7.3/8.1 mm

Type Locality: Nicaragua
Unfortunately, the locality Nicaragua is not further specified on Wagner's rewritten label, and an original label is lacking, therefore, it cannot be traced further.

Examined Material

Leg. I. Richling
Limón: *W Guayacán*, abandoned banana plantation, 10°01'53"N, 83°32'14"W, 520 m

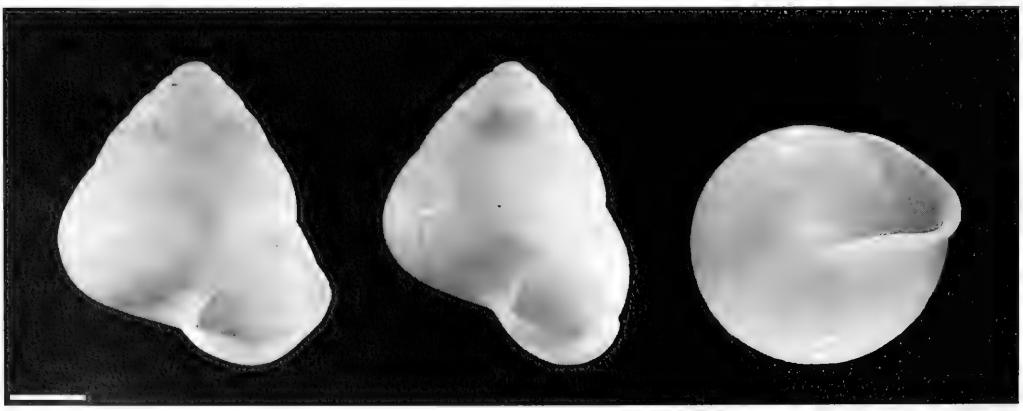


FIG. 99. *Helicina beatrix nicaraguae*, lectotype, MIZ 8408a, height 10.2 mm; scale bar 2.5 mm.

a.s.l., 03.09.1999: (IR 1078); (IR 1081); 12.09.1999: (IR 1087); 15.03.2000: (IR 1360); 17.03.2001: (IR 1606)

INBio Collection

Limón: *Suerre de Jiménez*, 10°11'31"N, 83°44'49"W, 330 m a.s.l., leg. Richard Helling, 26.02.1994: 1 ad. (INBio 1467201)
Reserva Biológica Hitoy Cerere, Sendero Bobócara, 09°40'53"N, 83°04'09"W, 798 m a.s.l., leg. Alexander Alvarado Mendez, 17.06.1999: 1 ad. (INBio 3542522)

Cartago: (determination uncertain) ?*Parque Nacional Barbilla*, bosque secundario, 09°57'52"N, 83°26'59"W, 400 m a.s.l., leg. malacological staff of INBio, 12.01.2001: 1 ad. (INBio 3324279)
?Zona Protectora Río Pacuare, *Sector de la Estación de Barbilla*, 09°58'50"N, 83°27'08"W, 500 m a.s.l., leg. Alexander Alvarado Mendez, 05.09.2000: 1 s.ad. (INBio 3542905)
Zona Protectora Río Pacuare, *Las Brisas de Pacuarito*, 10°02'00"N, 83°28'00"W, 400 m a.s.l., leg. malacological staff of INBio, 29.04.2001: 1 ad. (INBio 3418572)

Other Sources

COSTA RICA

Limón: Finca Los Diamantes, 1,000 ft. [about 10°11'N, 83°37'W], leg. A. Starrett, 22.08.1963: 1 ad. (UF 243509)
Entre Ukatschka et Brushik, Haut Tararia [about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream, Limón Province], leg. H. Pittier, IX.98 (ZMB 103251)

San José: Carillo [?about 10°09'N, 83°57'W], coll. E.R. Sykes (BMNH)

Cartago: Turrialba [about 09°54'30"N, 83°41'W], coll. H. Jaeckel: 1 ad. (SMF 209575/1); coll. H. Rolle, coll. C. Bosch: 3 ads., 1 s.ad. (SMF 180668/4); coll. Rolle: 3 ads. (ZMB 103812); Plattino, Turrialba [about 09°54'30"N, 83°41'W], leg: University of Alabama, M. Smith coll. (MS-15183): 4 ads. (UF 95337)
Tuis [about 09°51'N, 83°35'W], leg. H. Pittier: 1 ad. (ZMB 103252)

Costa Rica, without locality further specified: coll. Wagner (MIZ 8407); leg. P. Biolley: 3 ads., 1 s.ad. (MHNN)

Description

Shell (Figs. 100, 336A): Conical-globose, solid, medium sized and shiny. Color: upper whorls chestnut to reddish-brown, getting darker from apex down, towards last whorl changing to pale olive-green-greyish, towards aperture even opaque, in 2.5 last whorls an opaque whitish band directly below suture. Periostracum very thin, shiny and smooth, except for very fine growth lines. Embryonic shell with about 1 whorl; $4^{3}/_{8}$–5 (lectotype: 5) subsequent whorls very slightly convex; last whorl equally rounded at periphery; upper whorls more rapidly extending in size; whorls rapidly descending, forming a high spire. In the area of the band surface more inflated. Suture slightly impressed. Aperture oblique and in its middle part remarkably curved backwards. Outer lip

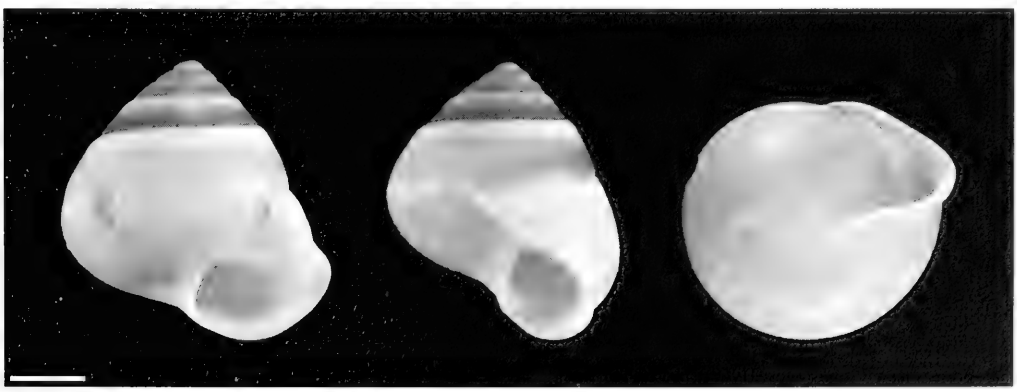


FIG. 100. *Helicina beatrix beatrix*, Guayacán, IR 1087, height 9.4 mm; scale bar 2.5 mm.

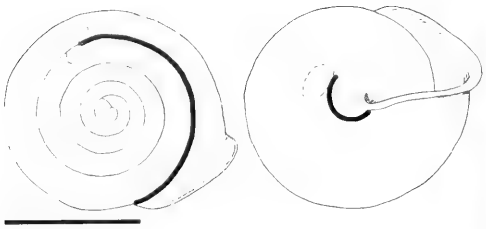


FIG. 101. Axial cleft and muscle attachments of *Helicina beatrix beatrix*, IR 1087; scale bar 5 mm.

always whitish-opaque, similar to the band, thickened and very narrowly reflexed; transition into columella continuous without any notch or only a very small one. Basal callus weakly developed and nearly completely smooth or very little granulated.

Internal Shell Structures: (Fig. 101)

Teleoconch Surface Structure (Fig. 102): The section of the transitional structure encompasses about the first half whorl. A very short zone structured with oblique diverging

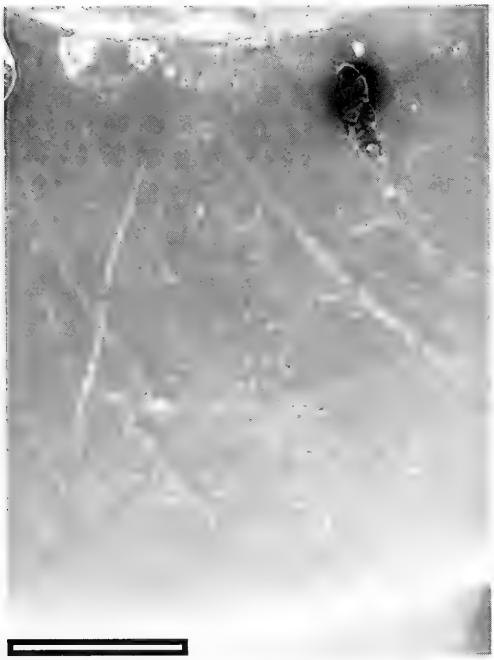


FIG. 102. Teleoconch surface structure of *Helicina beatrix beatrix*, 2nd whorl; scale bar 500 µm.

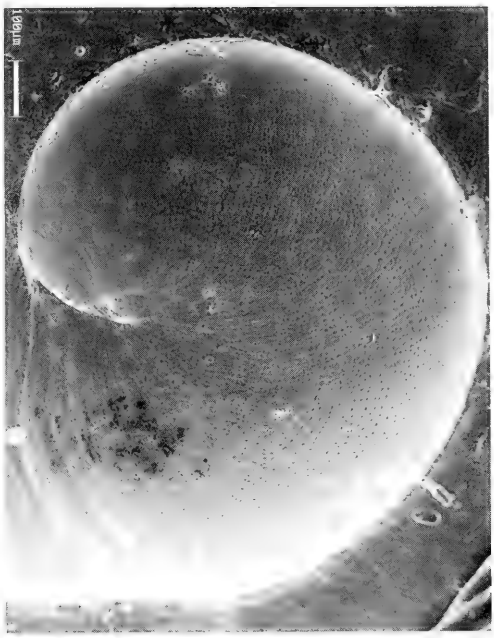


FIG. 103. Embryonic shell of *Helicina beatrix beatrix*; scale bar 100 µm.

grooves a replaced by fine growth lines continuing up to the aperture.

Embryonic Shell (Fig. 103): The spirally arranged pits are consistently much smaller than in *Helicina funcki*, and the interspacial distance exceeds the diameter of the pits. The pattern appears much finer, the smooth surface is more prominent.

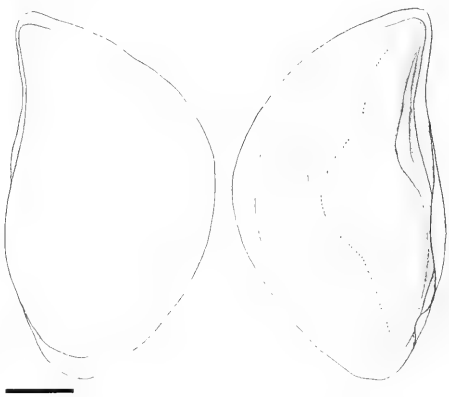


FIG. 104. Operculum of *Helicina beatrix beatrix*, IR 1087; scale bar 1 mm.

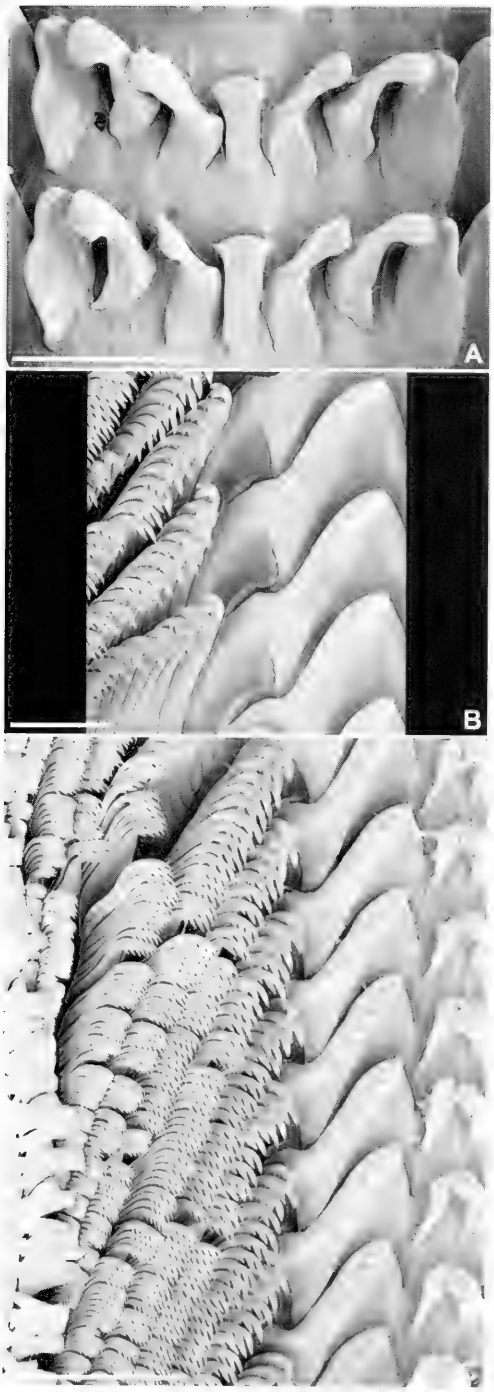


FIG. 105. Radula of *Helicina beatrix beatrix*. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 µm (A, B), 100 µm (C).

Diameter: 963 µm (± 33) (900–1010) (n = 15) (IR 1078, IR 1081, IR 1087, IR 1360, IR 1606); 1,040 µm (BMNH 1879.7.22.29, lectotype).

Operculum (Fig. 104): Very slightly calcified, calcareous plate covering only part of the outer surface, thickened towards the columellar side. Color horny-amber, only near the columella whitish, but still somewhat transparent. Columellar side slightly S-shaped, both ends acute, upper end pointed, lower slightly rounded.

Animal (Fig. 338A): The soft body is unicolored, whitish yellow throughout, only the tentacles may show a tinge of grey, the mantle is whitish pigmented. There is no trace of any dark spots.

Radula (Fig. 105): Because the radulae of the different subspecies are very similar, they are treated under *Helicina beatrix beatrix*. Central A to C may occasionally bear a few cusps, the B-central most frequently. Comb-lateral with 6–8 denticles, only two aberrant forms with a plain edge or 13 cusps respectively. Cusps on marginals rapidly increasing

FIG. 106. Female reproductive system of *Helicina beatrix beatrix*, IR 1087; scale bar 1 mm.

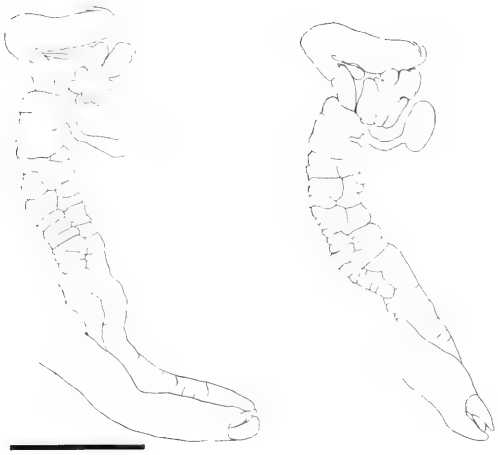


FIG. 107. Variability of the female reproductive system of *Helicina beatrix beatrix*, IR 1087; scale bar 2.5 mm.

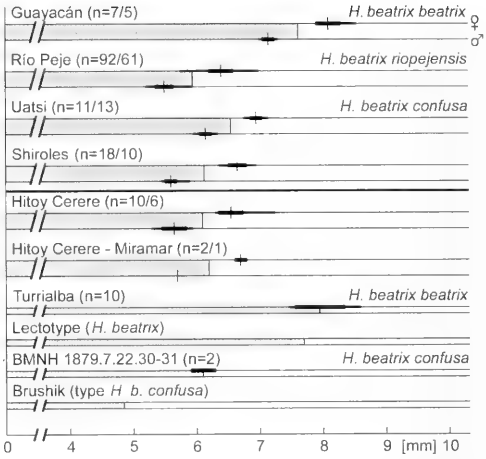


FIG. 109. Minor diameter of shell of different populations of *Helicina beatrix beatrix* and subspecies in Costa Rica according to Table 8; for explanations see Fig. 108.

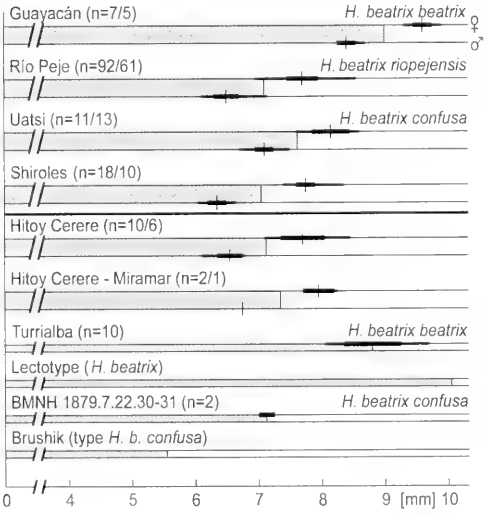


FIG. 108. Shell height of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Hitoy Cerere and Hitoy Cerere - Miramar not determined anatomically (see text).

in number, only in nominal subspecies does a change to more denticles a little more outwards take place, perhaps caused by of the larger size of this form. The same is true for the number of rows of teeth: about 91–138 in *H. b. beatrix*, in the other two subspecies only about 66–79.

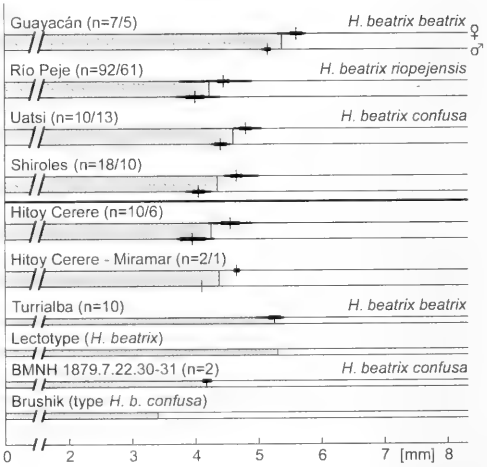


FIG. 110. Expansion of outer lip of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

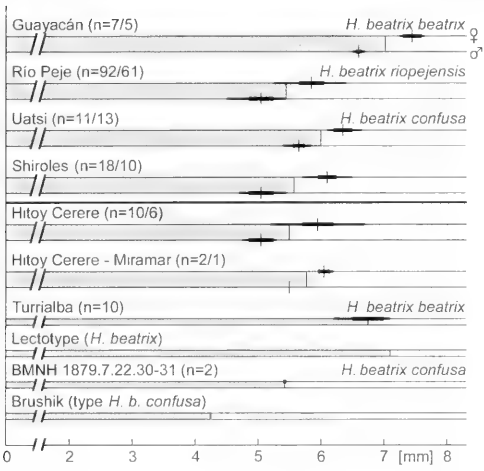


FIG. 111. Height of last whorl of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

Female Reproductive System (Figs. 106, 107): The ascending limb of the V-organ is relatively short and stout. The receptaculum seminis is rather large. The bursa copulatrix consists of a few irregularly shaped lobes; the provaginal sac is somewhat inflated and shows a simple outline, the stalk is short. The pallial oviduct is strongly constricted.

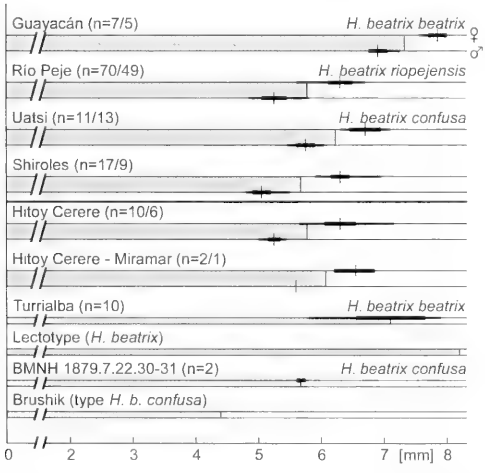


FIG. 112. Height of columellar axis of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

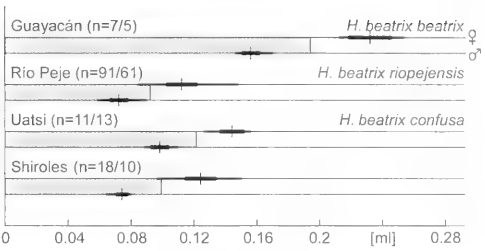


FIG. 113. Shell volume of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

Morphometry and Sexual Dimorphism (Table 8, Figs. 108–114)

For comparison, the different subspecies are all discussed in conjunction with the nominal subspecies. The material available for *Helicina beatrix beatrix* remains very scanty, although during the field work several efforts were made to find the species in greater abundance and at different localities. The only specimens studied anatomically are those from Guayacán. Because the "Turrialba" population is united from lots of three different collections, they may originate from different localities around Turrialba.

The specimens of *H. beatrix confusa* included from the INBio collection (Hitoy Cerere, Hitoy Cerere – Miramar) could not be analyzed for their sex by dissection. To make them nevertheless available for morphometric comparison, the degree of sexual dimorphism found in the dissected populations was used to attribute the probable sex to the specimens in reverse conclusion (see below). These data cannot primarily be used to investigate sexual dimorphism.

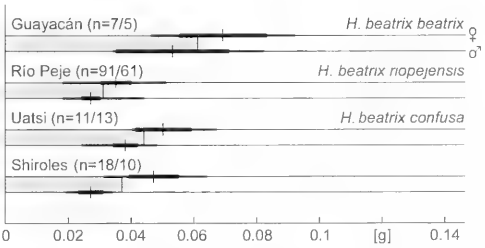


FIG. 114. Shell weight of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

TABLE 8. Measurements of different populations and subspecies of *Helicina beatrix* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals from Hitoy Cerere and Hitoy Cerere – Miramar not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		Helicina beatrix beatrix "Guayacán" (altitude 520 m) lots IR 1078, IR 1087, IR 1081					*Helicina beatrix riopejensis* n. subsp. "Río Peje" (altitude 135 m) lots IR 440, IR 752, IR 1303, IR 1550				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	9.59	0.16	9.31	9.88	7	7.72	0.26	6.95	8.53	92
Height	m	8.39	0.13	8.26	8.71	5	6.51	0.20	6.10	7.17	61
Maj. diam.	f	8.67	0.22	8.33	9.08	7	6.89	0.19	6.00	7.93	92
Maj. diam.	m	7.75	0.08	7.64	7.88	5	5.97	0.15	5.46	6.33	61
Min. diam.	f	8.12	0.21	7.78	8.57	7	6.39	0.18	5.75	7.00	92
Min. diam.	m	7.15	0.10	7.02	7.32	5	5.50	0.14	5.20	5.97	61
Outer lip	f	5.61	0.12	5.31	5.77	7	4.45	0.12	3.75	4.90	92
Outer lip	m	5.13	0.07	5.03	5.22	5	3.98	0.13	3.68	4.40	61
Last whorl	f	7.45	0.13	7.23	7.65	7	5.83	0.18	5.25	6.42	92
Last whorl	m	6.58	0.06	6.49	6.69	5	5.03	0.19	4.53	5.47	61
Col. axis	f	7.83	0.13	7.56	8.01	7	6.28	0.22	5.59	6.88	70
Col. axis	m	6.88	0.15	6.75	7.24	5	5.24	0.19	4.85	5.78	49
Weight	f	0.069	0.014	0.046	0.092	7	0.035	0.005	0.018	0.051	91
Weight	m	0.053	0.018	0.034	0.082	5	0.027	0.003	0.018	0.044	61
Volume	f	0.232	0.014	0.212	0.253	7	0.115	0.009	0.084	0.147	91
Volume	m	0.156	0.006	0.145	0.169	5	0.071	0.005	0.058	0.089	61

		Helicina beatrix confusa "Uatsi" (altitude 30 m) lots IR 1112, IR 1113, IR 1567					*Helicina beatrix confusa* "Shiroles" (altitude 120 m) lots IR 910, IR1327, IR 1594, IR 1600, IR 1646				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.17	0.28	7.59	8.60	11	7.76	0.17	7.40	8.37	18
Height	m	7.10	0.17	6.72	7.50	13	6.35	0.17	6.07	6.67	10
Maj. diam.	f	7.33	0.07	7.20	7.58	11	7.08	0.16	6.77	7.37	18
Maj. diam.	m	6.63	0.16	6.30	6.94	13	6.03	0.13	5.80	6.22	10
Min. diam.	f	6.93	0.10	6.75	7.16	11	6.63	0.17	6.35	6.96	18
Min. diam.	m	6.14	0.11	5.93	6.37	13	5.61	0.12	5.43	5.88	10
Outer lip	f	4.81	0.08	4.61	5.03	10	4.67	0.12	4.47	5.00	18
Outer lip	m	4.42	0.12	4.25	4.63	13	4.04	0.10	3.87	4.25	10
Last whorl	f	6.35	0.16	6.10	6.66	11	6.09	0.14	5.72	6.48	18
Last whorl	m	5.64	0.09	5.42	5.84	13	5.05	0.18	4.72	5.43	10
Col. axis	f	6.68	0.25	6.30	7.08	11	6.32	0.16	5.90	6.96	17
Col. axis	m	5.77	0.15	5.47	6.06	13	5.07	0.17	4.79	5.50	9
Weight	f	0.050	0.009	0.040	0.067	11	0.047	0.008	0.031	0.064	18
Weight	m	0.038	0.004	0.024	0.048	13	0.027	0.004	0.019	0.034	10
Volume	f	0.143	0.007	0.126	0.156	11	0.124	0.010	0.095	0.150	18
Volume	m	0.097	0.006	0.087	0.110	13	0.073	0.004	0.063	0.079	10

(*Continues*)

(*Continued*)

		Helicina beatrix confusa "Hitoy Cerere" (altitude 100–798 m) lots INBio 1473618, 1473833, 1473837, 1475069, 1498277, 1543340, 3096421					*Helicina beatrix confusa* "Hitoy Cerere - Miramar" (altitude 150–300 m) lots INBio 1475230, 1475695, 1476494				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.68	0.34	7.09	8.43	10	7.97	0.26	7.71	8.23	2
Height	m	6.56	0.21	6.10	6.78	6	6.73	0.00	6.73	6.73	1
Maj. diam.	f	6.93	0.20	6.47	7.65	10	7.01	0.04	6.96	7.05	2
Maj. diam.	m	6.04	0.25	5.50	6.46	6	6.04	0.00	6.04	6.04	1
Min. diam.	f	6.56	0.18	6.32	7.23	10	6.68	0.08	6.60	6.76	2
Min. diam.	m	5.65	0.18	5.31	5.94	6	5.70	0.00	5.70	5.70	1
Outer lip	f	4.57	0.17	4.22	4.90	10	4.64	0.04	4.60	4.67	2
Outer lip	m	3.96	0.21	3.69	4.30	6	4.09	0.00	4.09	4.09	1
Last whorl	f	5.95	0.23	5.18	6.68	10	6.07	0.11	5.96	6.18	2
Last whorl	m	5.04	0.21	4.74	5.31	6	5.52	0.00	5.52	5.52	1
Col. axis	f	6.30	0.25	5.64	7.17	10	6.54	0.33	6.21	6.86	2
Col. axis	m	5.26	0.12	5.01	5.46	6	5.59	0.00	5.59	5.59	1

	Helicina beatrix beatrix "Turrialba" lots SMF 209575/1, SMF 180668/4, UF 95337, ZMB 103812				
	Mean value	Deviation	Min	Max	Number
Height	8.81	0.47	8.06	9.70	10
Maj. diam.	7.96	0.42	7.43	8.62	11
Min. diam.	7.39	0.38	6.68	8.00	11
Outer lip	5.24	0.11	4.94	5.41	9
Last whorl	6.75	0.27	6.19	7.08	10
Col. axis	7.11	0.55	5.82	7.90	7

Morphometry: The typical *Helicina beatrix beatrix* clearly possesses the largest shells among the Costa Rican subspecies of *H. beatrix*. Its shells have a similar size at all three localities. The lectotype is more highly elevated, reflected mainly in height and height of the columellar axis, whereas the specimens from Turrialba have relatively the largest minor diameter. Single specimens of *H. beatrix beatrix* not included in the diagrams fall within the same size range.

The populations of the subspecies *H. beatrix confusa* and *H. beatrix riopejensis* n. subsp. show a very constant pattern of differences between the populations for the different measurements, displaying the same relations of the measurements. The specimens of Uatsi have the biggest shells. But they all exhibit a smaller size than the nominal subspecies. The relative constancy within the populations and the nearly equal size of the individuals from Shiroles and Hitoy Cerere (Hitoy Cerere – Miramar) suggest a relation to the distribution, because these localities are closer to each other than Uatsi (Fig. 1). Whereas in measurements the two specimens of *H. beatrix* var. *sensu* Angas match the two subspecies well, the lectotype of *H. beatrix confusa* is much smaller. For the subspecies, the lack of material from additional localities still prevents any investigation of a possible correlation of the size to the altitude which could help to relate the small size of the lectotype (from a much

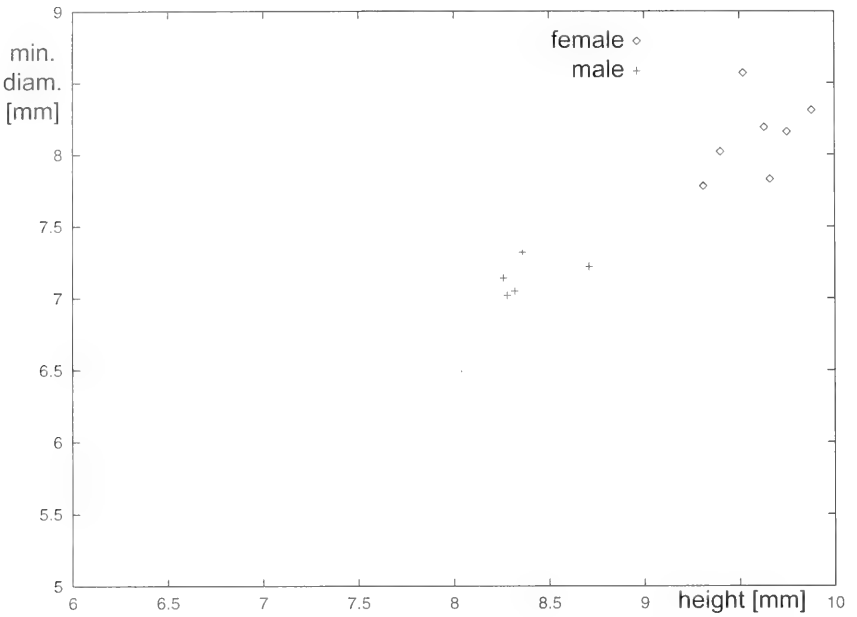


FIG. 115. Range of measurements in females and males of *Helicina beatrix beatrix* exemplary for height and minor diameter in the population from Guayacán.

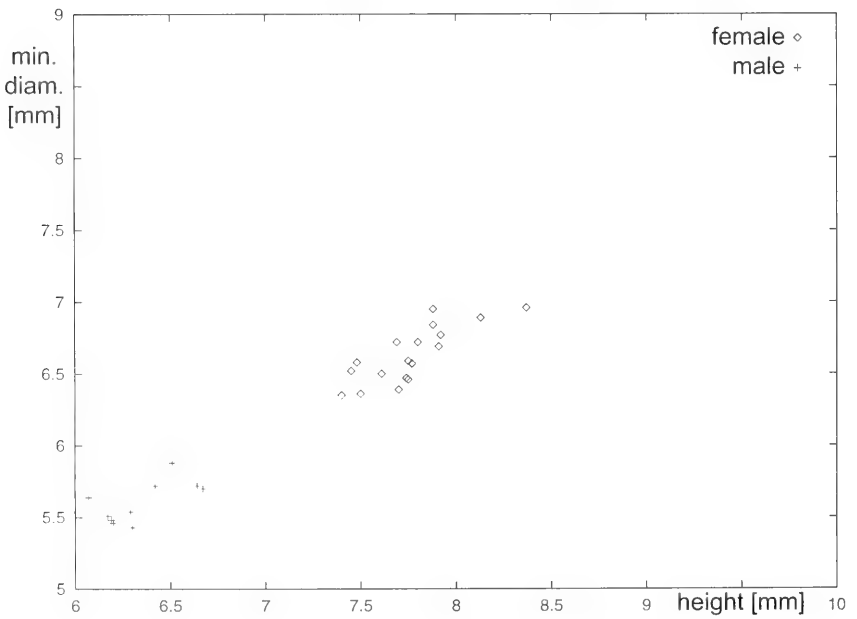


FIG. 116. Range of measurements in females and males of *Helicina beatrix confusa* exemplary for height and minor diameter in the population from Shiroles.

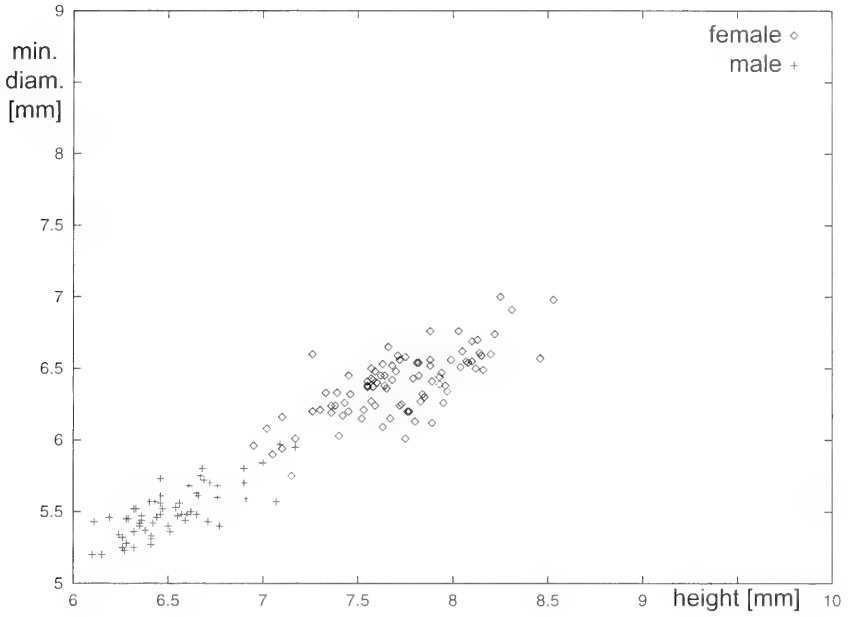


FIG. 117. Range of measurements in females and males of *Helicina beatrix riopejensis* n. subsp. exemplary for height and minor diameter in the population from Río Peje.

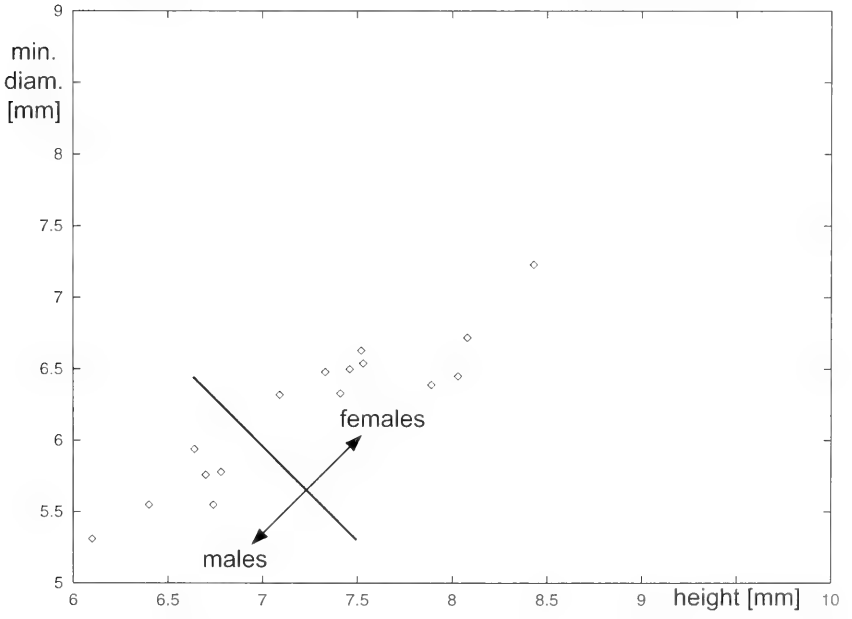


FIG. 118. Plot of measurements for height and minor diameter for individuals of *Helicina beatrix confusa* of unknown sex, exemplary for the population of Hitoy Cerere and the separation proposed.

higher altitude) to the recently collected material. For *H. beatrix beatrix*, the present data do not corroborate a correlation of size with altitude. Within a range from elevations of 330 m (Suerre de Jimenez) to 800–1,000 m (Turrialba) or even up to 2,500? m (Alto Tararia), the size remains nearly constant.

Sexual Dimorphism: All populations and even all measurements show a very clear difference between females and males, in many cases not only within the range of the standard deviation but also for the whole range. This is shown for a population of each subspecies (Figs. 115–117) in data for height and minor diameter, which best separates the sexes. In populations with many individuals (e.g., Río Peje), high extrema are more likely and result in a little overlap. In volume, the males are only about $^{2}/_{3}$ of that (61% to 68%) of females.

The clear difference between both sexes can be used to plot measurements (e.g., minor diameter to height) of specimens of unknown sex (Fig. 118, Hitoy Cerere) in order to attribute them to their most likely sex. But the differences between the populations also demonstrate that this method will only work for specimens from one and the same locality, and the lot from "Turrialba" could not be separated (Fig. 119) because it does not represent a single population.

The differences of the specimens of *H. beatrix* var. *sensu* Angas to the lectotype of *H. beatrix* are out of the range of sexual dimorphism, supporting their exclusion from typical *H. beatrix*.

Habitat

Helicina beatrix beatrix was found by the author at only one locality at Guayacán. There it inhabits a small abandoned banana field on a steep hillside surrounded by secondary growth and partly swampy meadows for cattle. Specimens were aestivating or on the underside of green banana leaves or crawling in curled, dried leaves. Originally the area was covered by rain forest, and it seems to be a relic occurrence of the species. All negative records and the few specimens in collections suggest that *H. beatrix beatrix* is a rare subspecies.

Distribution (Fig. 120)

Although records are scarce, the occurrence shows a remarkable pattern. As already observed by Gabb and cited in the original description, the species is said to occur only on hills up to an elevation of 2,500 feet. In fact *Helicina beatrix* inhabits the Caribbean mountain slopes of the Cordillera Central and the Cordillera de Talamanca. The localities can be attributed to the slopes of three regions: the valley between the volcanoes Barva and Irazú/Turrialba, the Caribbean side of the Valle Central along the Río Reventazón between the Volcán Irazú and northern Cordillera de Talamanca, and the Valle de Talamanca. The verified range of altitude is from about 330 m to 1,000 m or even up to 2,500 m depending on the exact location of "Alto Tararia". The most northern record from Santa Clara near the frontier to Nicaragua is uncertain.

Discussion

Helicina beatrix beatrix is understood as the large whitish-opaque form with reddish-brown upper whorls. The determination of two of the three lots from the Barbilla/Río Pacuare area (INBio 3324279, INBio 3542905) is uncertain; the size of the adult specimen is similar to the nominal subspecies; the color approaches that of *H. b. confusa*. A common feature of *H. beatrix beatrix* and the other subspecies is the general shape as described above and the subsutural opaque band. Furthermore, the outer lip is typically strongly curved backwards, especially in females. Against the background that intermediate forms of the subspecies are lacking and a sympatrical occurrence implying a specific separation is uncertain, the status of subspecies is tentatively maintained or suggested for the population from Río Peje. But certain hints for a sympatrical existence of *H. beatrix beatrix* and *H. b. confusa* have to be mentioned. The type locality of *H. beatrix confusa* (Brushik, Alto Tararia) is probably close to "between Ukatschka and Brushik, Alto Tararia" recorded for *H. beatrix beatrix*, although the exact location is uncertain (see below). Furthermore, a recently collected lot in the collection of INBio from the Sendero [= trail] Bobócara in the reserve Hitoy Cerere contains both subspecies, and the very top of the mountain Cerro Bobócara is given as locality, but is most likely not the source of all specimens. In the extremely mountainous and steep terrain, a short distance of the trail probably already encompasses different habitats at different altitudes. Therefore, the data do not contribute to an assessment of the status of *H. beatrix* and subspecies.

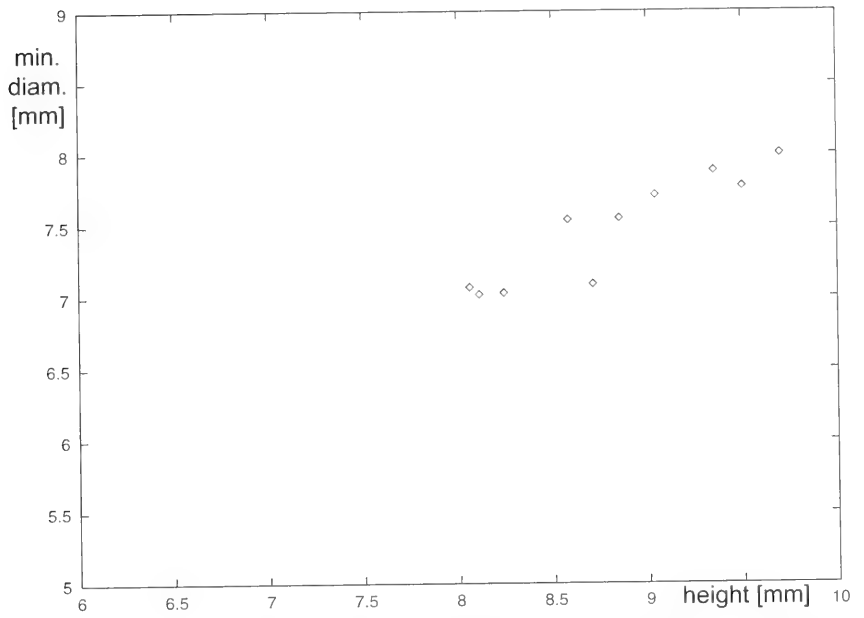


FIG. 119. Plot of measurements for height and minor diameter for individuals of *Helicina beatrix beatrix* of unknown sex, exemplary for the specimens from "Turrialba" (probably not single populations) for which a separation is not possible.

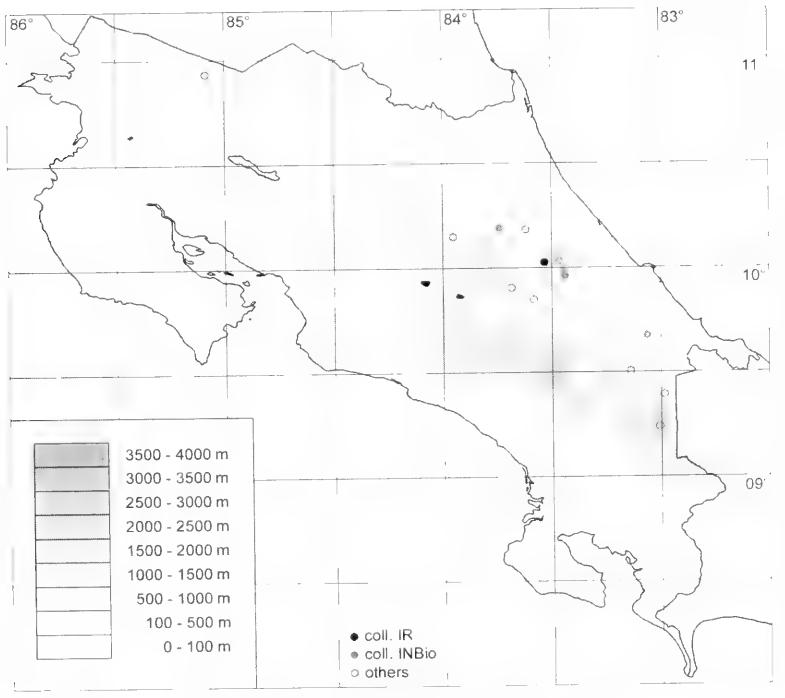


FIG. 120. Records of *Helicina beatrix beatrix* in Costa Rica.

The type lot of *H. beatrix* is of unknown origin and most likely it is also composed of specimens from different localities, because the smaller two belong to a different subspecies. The knowledge of well-localized records of *H. beatrix* is very limited, but among those, the lot ZMB 103251 from high up in the mountains from the Valle de Talamanca (southern Caribbean side) most closely resembles the lectotype in having a high, elevated shell. According to recent and previous findings, populations at Guayacán, Turrialba and Tuis are characterized by more globular shells, thus suggesting that the lectotype probably was not collected in the area of the Río Reventazón and its tributaries between Turrialba and Siquirres, which was comparatively easily accessible at the end of the 19th century as the most direct connection between San José and Puerto Limón on the Caribbean.

The record from Santa Clara remains doubtful, because it is far out of the verified distribution and the original material has not been found. A confusion with *H. gemma* which occurs in this region, can be excluded for three reasons: (1) Biolley (1897) and von Martens (1900) also reported this species for the area as *H. oweniana anozona* and von Martens (1900) as *H. oweniana coccinostoma*, (2) von Martens (1900) characterized the specimens as no less than 10 mm in diameter and 9 in height, whereas *H. gemma* displays a remarkably constant size of about 5 to 7 mm in height, and (3) the orange outer lip of *H. gemma* would rather suggest an identification as *H. oweniana* than *H. beatrix*, exactly as von Martens obviously treated *H. gemma* in his publication. Except for the doubtful record of *H. beatrix nicaraguae*, the species has not been reported from the adjacent Nicaragua. In the face of absence of the original material and the limited knowledge on Nicaraguan Helicinidae, it still remains doubtful.

In *Helicina beatrix nicaraguae*, the whorls very evenly increase in size, forming a regular spire, which is less inflated than in *H. beatrix beatrix*. The whorls are more convex, therefore the suture is more deeply impressed. The whitish band under the suture is less distinct and more slender. The basic color is yellowish, with a tendency to greenish, towards the aperture lighter and changing to opaque.

On account of the poorly investigated Nicaraguan terrestrial molluscan fauna, it is impossible to render any judgement about the possible origin or distribution. According to the Costa Rican records, *H. beatrix* and subspecies are confined to the southern Caribbean slope and coastal plain with its most northern record verified at about Guápiles (10°13'N), or with uncertainty near the Nicaraguan border at Santa Clara. The only record for Nicaragua is that of Wagner (1908) of his new subspecies. Supposing that the record from Santa Clara is attributed to another species and considering that *H. beatrix* and subspecies seem to be absent from the very lowlands, that is, the southern Nicaragua, there appears to be a gap in the distribution towards Nicaragua. Otherwise, specimens from Isla Colón (Isla Colon, Las Gratas, 5 km NNW of Bocas del Toro, 09°23'25"N, 82°16'15"W, 70 m a.s.l., leg. F.G. Thompson (FGT-4724), 17.09.1990: 2 ads. (UF 167532); interior of Colon Island, leg. McGinty coll., 28.03.1953: 1 s.ad. (UF 185607) (Fig. 121), Bocas del Toro Province, Panama, adjacent to the Costa Rica distribution, show a surprising similarity in shape and color. With a height of 9.6 mm, the largest shell nearly reaches the size of the lectotype. An investigation of the Nicaraguan malacofauna would be required to prove whether the type locality of *H. beatrix nicaraguae* is in this country, or whether the lectotype in fact came from Panama.

Von Martens (1890–1901) misinterpreted *H. beatrix* as a variety of *H. flavida* because he had not seen original specimens. Subsequent authors (Pilsbry, 1891; Fischer & Crosse, 1893) stressed the distinctness of *H. beatrix*, and von Martens agreed with this in his supplement.

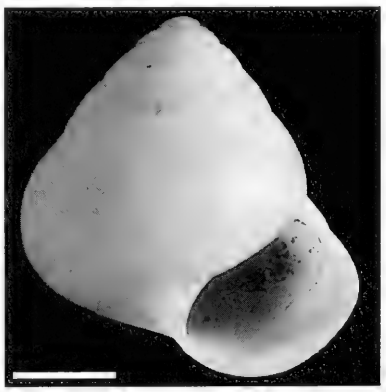


FIG. 121. *Helicina beatrix nicaraguae*, Panama, Isla de Colón, UF 167532, height 8.9 mm; scale bar 2.5 mm.

Pilsbry (1926a) twice mentions *H. beatrix* from Bocas del Toro Province, Panama: specimens agreeing in size with the nominal subspecies from a certain locality and additional individuals not further specified in their origin that are remarkably smaller, thus resembling *H. beatrix confusa* in size. Furthermore, the identification and localization of the Costa Rican record by Pilsbry (1926b) remains doubtful, because altitudes of less than 100 feet would be exceptional for the nominal subspecies.

Helicina (*"Gemma"*) *beatrix confusa* (Wagner, 1908)

Helicina beatrix var. – Angas, 1879: 484, pl. XL, fig. 13 [*non Helicina beatrix* Angas, 1879]
Alcadia (*Leialcadia*) *beatrix confusa* Wagner, 1908: 84, pl. 14, fig. 25
Oligyra (*Succincta*) *beatrix confusa* – Baker, 1922a: 45
Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* Angas, 1879]

Original Description

"Gehäuse viel kleiner [als *Alcadia beatrix*], dünnschaliger, gelbgrün mit rötlichem Gewinde; das niedrigere, konvexe Gewinde besteht nur aus $4^1/_2$ deutlicher gewölbten Umgängen, der letzte ist unten weniger abgeflacht.

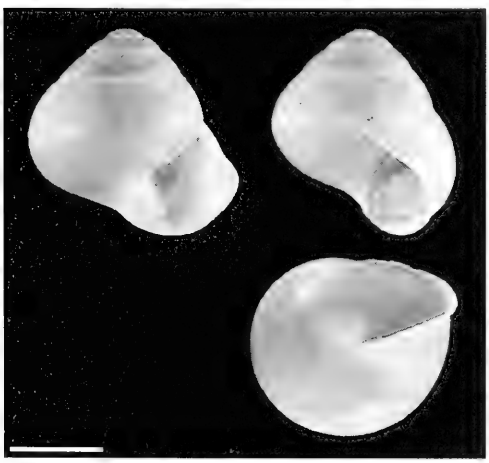


FIG. 122. *Helicina beatrix confusa*, lectotype, MIZ 8409, height 5.6 mm; scale bar 2.5 mm.

D = 7.3, H = 7.2
Deckel wie bei der typischen Form.
Fundort: Costarica."

Type Material

MIZ 8409: "Brusik [sic] Ht. Tararia"
Wagner did not refer to any type material, but his collection contains only one specimen he singled out as type material. It is labeled "to be depicted" and agrees very well with the illustration. The specimen is therefore **here selected as lectotype** (Fig. 122).
Dimensions:
Lectotype: 5.6/5.3/5.7/4.9/3.4/4.2/4.4 mm

Type Locality

"Costa Rica" (figure caption erroneously Nicaragua); restricted by the type selection to Brushik, Alto Tararia [about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream, Limón Province]

Unfortunately, Wagner used to rewrite most of the labels and only occasionally retained the original, thereby not always preserving all information (Riedel, 2000). In the present case, it can be referred to "Brushik, Haut Tararia" [Spanish: Alto Tararia], a source also named by von Martens (1900) for material collected by Pittier. At that time, Pittier was the only one intensively studying the region of the Valle de Talamanca and its adjacent mountain slopes. Despite an intensive search for the locality, it is difficult to rediscover it. It is known that Pittier maintained good relations with the indigenous Cabécar and Bribrí, which inhabit the Valle de Talamanca and settle along the four main rivers – Río Telire, Río Coén, Río Lari and Río Urén – and their tributaries high up in the mountains. Throughout this region, neither Brushik nor Alto Tararia or related names could be found on detailed maps. Much further south a Cerro Tararia ["cerro" = "mountain", 09°09'03"N, 82°58'27"W, 2,690 m a.s.l.] exists, which most likely is not the locality mentioned, because it forms a part of the very central mountain chain and lacks any access route. Furthermore, "Alto" followed by a name of a river usually refers to a main settlement along the river in the mountains, for example, Río Lari – Alto Lari. Therefore, Alto Tararia may mean the upper part of the Río Tararia [about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream], which really exists southeast of Cerro Kamuk. Again, it is difficult

to gain access to the region, settlements or trails are not shown on maps. From Valle de Talamanca, it means following the river Río Lari or Río Urén to their headwaters and to cross the Cerro Kamuk to reach the high region of Río Tararia draining towards Panama. Because other Pittier localities are very reliable, this appears to be the best interpretation, because the material also may have been given to Pittier by indigenous people and probably not all indigenous names and trails were incorporated in maps, and some may even have been forgotten or lost.

Examined Material

Leg. I. Richling

Limón: Southern road from *Bribrí to Shiroles*, small banana plantation near creek, 09°35'17"N, 82°52'46"W, 50 m a.s.l., 15.03.1997: (IR 170)

W Bribri, road to Uatsi, about 09°38'11"N, 82°51'48"W, 30 m a.s.l.: *abandoned field with Heliconiaceae and Eucalyptus*: 17.03.1997: (IR 182); 12.03.1999: (IR 765); 15.09.1999: (IR 1112); (IR 1113); 15.03.2001: (IR 1567); *wooded valley within banana plantation, 50 m a.s.l.*: 15.03.2001: (IR 1585)

N Shiroles: *along Quebrada Kirio, 09°35'38"N, 82°57'20"W*: *120 m a.s.l.*: 15.03.1997: (IR 161); *100 m a.s.l.*: 12.03.1999: (IR 764); 09.08.1999: (IR 910); 06.03.2000: (IR 1327); (IR 1329); 16.03.2001: (IR 1594); (IR 1646); *Cerro Mirador, along trail, 09°36'37"N, 82°57'43"W, 430 m a.s.l.*: 16.03.2001: (IR 1600)

INBio Collection

Limón: *Parque Nacional La Amistad*, Quebrada Cachabri (toma de agua), 09°29'29"N, 82°59'37"W, 360 m a.s.l., leg. Gerardina Gallardo, 26.11.1996: 1 ad. (INBio 1488199)

Reserva Biológica Hitoy Cerere: *Sendero Toma de Agua, 09°40'31"N, 83°01'36"W, 100 m a.s.l.*: 20.04.1994: 5 ads. (INBio 1473837); 1 ad. (INBio 1473618); 2 ads., 1 juv. (INBio 1473833); 13.08.1994: 3 ads., 2 s.ads., 13 juvs. (INBio 1475069) (all leg. Zaidett Barrientos); *Sendero Toma de Agua, 09°40'22"N, 83°01'35"W, 160 m a.s.l.*: leg. Marianella Segura, 14.07.1994: 1 s.ad. (INBio 1478208); 1 juv. (INBio 1478209); *Sector Miramar, Hitoy Cerere, 09°37'50"N, 83°00'52"W, 300 m a.s.l.*: 13.06.1994: 1 ad. (INBio 1476494); 04.07.1994: 1 ad. (INBio 1475695) (all leg. Gerardo Carballo); *Sector Miramar, 09°38'03"N, 83°00'45"W, 300 m a.s.l.*: leg. Zaidett Barrientos, 08.10.1994: 1 ad. (INBio 1475716); *Sendero a Captación de Agua, 09°39'59"N, 83°01'31"W, 200 m a.s.l.*: leg. Alexander Alvarado Mendez, 28.04.1999: 3 ads., 2 s.ads. (INBio 1498277); *Sendero Tepezcintle, 09°40'18"N, 83°01'43"W, 140 m a.s.l.*: leg. Alexander Alvarado Mendez, 28.04.1999: 1 s.ad. (INBio 1496288); *Sendero Bobócara, 09°40'53"N, 83°04'09"W, 798 m a.s.l.*: leg. Alexander Alvarado Mendez, 17.06.1999: 1 ad., 1 s.ad. (INBio 1543340)

Reserva Indígena Talamanca, *Sector Amubri, 09°30'53"N, 82°57'19"W, 70 m a.s.l.*: leg. Gerardina Gallardo, 14.06.1994: 1 ad. (INBio 1477505); 1 ad. (INBio 1477553);

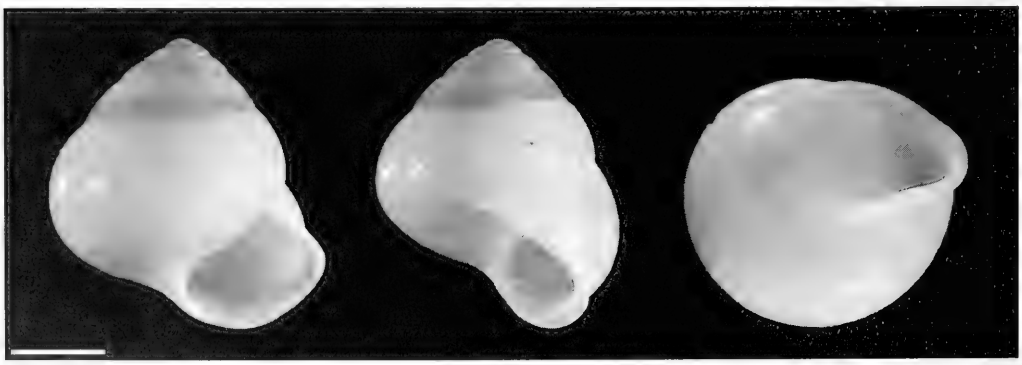


FIG. 123. *Helicina beatrix confusa*, Shiroles, IR 910, height 7.8 mm; scale bar 2.5 mm.

Sector Miramar, Senderos a Río Moín, 09°37'44"N, 83°00'32"W, 150 m a.s.l.: leg. Zaidett Barrientos, 08.11.1994: 1 ad., 1 s.ad., 3 juvs. (INBio 1475230)
Reserva Indígena Tayni, Sendero Tepezcuintle, 09°40'22"N, 83°01'46"W, 180 m a.s.l., leg. Alexander Alvarado Mendez, 22.04.1999: 1 ad. (INBio 3096421)

Other Sources
COSTA RICA
Limón: N of Río Moin [Valle de Talamanca!], 572 000 E, 397 600 S [09°37'45"N, 83°00'38"W], 220 m a.s.l., leg. E.L. Raiser (ELR-086), 11.08.1994: 1 ad., 2 s.ads. (UF 41440)
Costa Rica, without locality further specified: leg. Gabb: 2 spec. (BMNH 1879.7.22.30–31)

Description

Shell (Figs. 123, 336B, C): Conical-globose, rather thin, small sized, shiny. Color: upper whorls yellowish-red, horny changing continuously to yellow at the beginning of body whorl and getting nearly white towards aperture. The opaque whitish band directly below suture very slender. Shell surface shiny and smooth, except very fine growth lines. Embryonic shell with about 1 whorl; 4–5 (lectotype: 3¾) subsequent whorls very slightly convex; last whorl equally rounded at the periphery; upper whorls slightly more rapidly extending in size; whorls regularly descending, forming a nearly blunt spire. Suture slightly impressed. Aperture oblique and in its middle part remarkably curved backwards. Outer lip whitish-opaque similar to the band, slightly thickened and very narrowly reflexed; transition into columella continuous without a very little notch. Basal callus weakly developed and nearly completely smooth or very little granulated, umbilical area whitish.

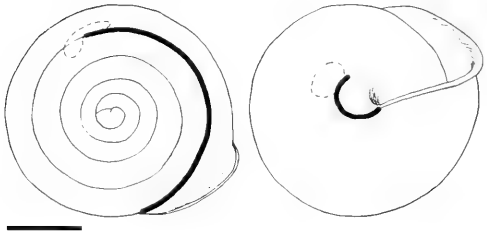


FIG. 124. Axial cleft and muscle attachments of *Helicina beatrix confusa*, IR 1113; scale bar 2.5 mm.

FIG. 125. Teleoconch surface structure of *Helicina beatrix confusa*. A. Changes in the apical part. B. 2nd whorl; scale bars 500 µm (A), 100 µm (B).

Internal Shell Structures: (Fig. 124)

Teleoconch Surface Structure (Fig. 125): Similar to *Helicina b. beatrix*, but the relation between the transitional structure and the pattern of oblique diverging grooves is reversed, the former nearly disappearing.

Embryonic Shell (Fig. 126): Among the specimens investigated, the spiral lines are less numerous than in the nominal subspecies. Otherwise, the embryonic shell structure is similar. The diameter is smaller.
Diameter: 889 µm (± 32) (800–950) (n = 21) (IR 1113, IR 1567); 840 µm (MIZ 8409, lectotype); 900 µm (n = 2) (BMNH 1879.7.22.30–31, *Helicina beatrix confusa*).

Operculum (Fig. 127): Very slightly calcified, calcareous plate covering only part of the outer surface. Color horny-amber, only near the columella whitish, but still somewhat transparent. Columellar side slightly S-shaped, both ends acute, upper end pointed, lower slightly rounded.

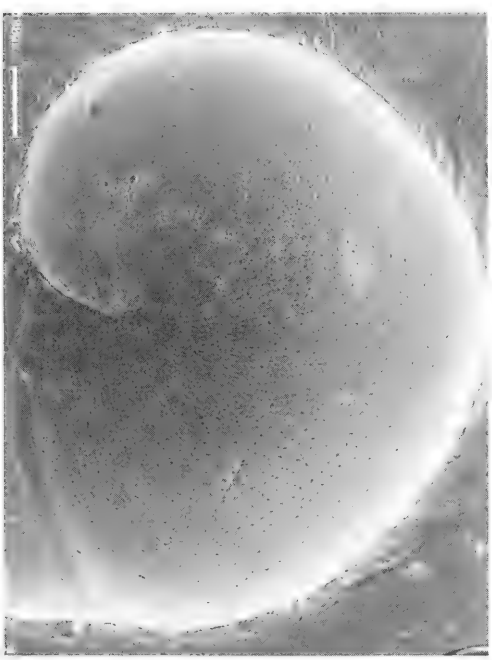


FIG. 126. Embryonic shell of *Helicina beatrix confusa*; scale bar 100 µm.

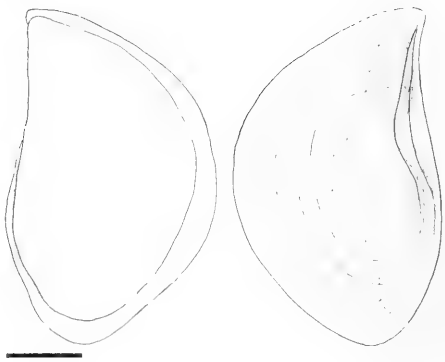


FIG. 127. Operculum of *Helicina beatrix confusa*, IR 1113; scale bar 1 mm.

Animal (Figs. 337F, G): The body color is similar to *Helicina beatrix beatrix*, especially within the yellow-shelled population from Uatsi. In some specimens from Shiroles (more frequently in individuals with orange-brownish tinged shells), the dorsal part of the head region including eyes and tentacles and the foot is more of less grey-blackish and the mantle is greyish pigmented as well.

Radula: See *Helicina beatrix beatrix*.

Female Reproductive System (Figs. 128, 129): The structures are similar to the nominal subspecies; the bursa copulatrix bears even fewer lobes.

FIG. 128. Female reproductive system of *Helicina beatrix confusa*, IR 1113; scale bar 1 mm.

FIG. 129. Variability of the female reproductive system of *Helicina beatrix confusa*, IR 1113; scale bar 2.5 mm.

Morphometry and Sexual Dimorphism

See *Helicina beatrix beatrix*.

Habitat

The population "Uatsi" inhabits an apparently abandoned agricultural area surrounded by small banana fields. The vegetation consists mainly of Heliconiaceae and some bamboo (Poaceae). *Helicina beatrix confusa* was found on the underside of the leaves of Heliconiaceae and occasionally on *Monstera* spec. (Araceae) climbing the few big trees left of the previous forest. By way of contrast, the main site at Shiroles is a small creek in what seemed to be primary forest. Snails were crawling and aestivating on the leaves of various small-leafed plants of the undergrowth along the creek. Two specimens were discovered in the leaf litter. Additionally specimens were found on leaves of lower branches of big trees within the forest. Near Shiroles, *H. beatrix confusa* lives sympatrically with *H. funcki* and *H. escondida* n. sp.

Distribution (Fig. 130)

Helicina beatrix confusa is confined to the southern Caribbean mountain slopes of the northern Cordillera de Talamanca and adjacent hilly areas, namely in the Valle de Talamanca and Valle de Estrella. Like the other subspecies, it seems to be absent near the coast. A more northern occurrence is questionable, a record from the Río Pacuare-

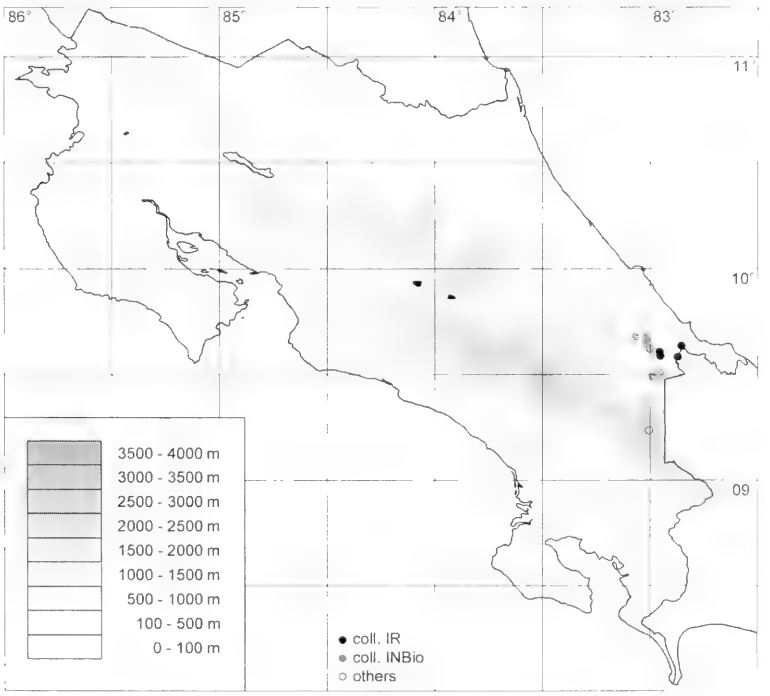


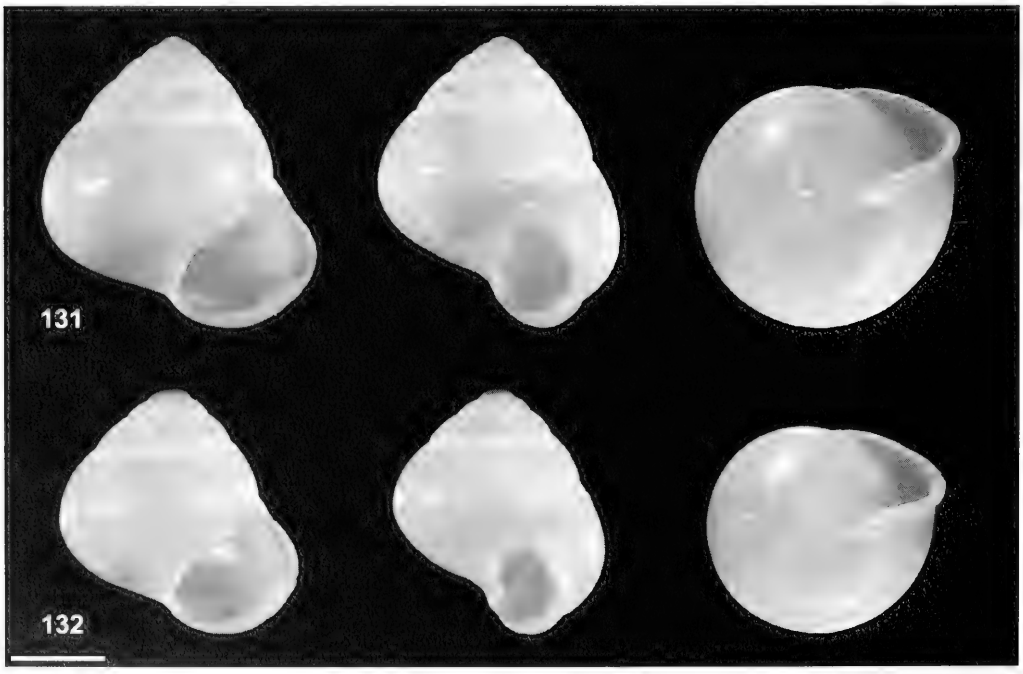
FIG. 130. Records of *Helicina beatrix confusa* in Costa Rica.

Barbilla area at altitudes of 400 to 500 m has tentatively been attributed to the nominal subspecies. The foothills of the Talamanca have otherwise only been poorly investigated, not only because they are difficult to access, but also because the very local and patchy distribution renders the snails difficult to find. There is evidence for a more northerly absence, at least at lower altitudes, because several less elevated sites at Río Siquirres, Río Pacuarito, Río Barbilla, near the road between Siquirres and Limón, were checked with negative results although other Helicinidae at other places inhabiting the same habitats – *H. funcki*, *H. escondida* n. sp., *H. chiquitica*, *H. gemma* – were found.

Discussion

The description given above applies to the lectotype. The specimen is adult, but the outer lip is still not fully developed. The less elevated shell renders is likely to be a male, although it cannot be concluded with certainty due to the lack of comparative material from the same locality. If this assumption is correct, the average size of *Helicina beatrix confusa* would be bigger than indicated by the lectotype. Nevertheless, all specimens studied are clearly bigger. But because the specimens morphometrically studied originate from lower altitudes of sites not far from each other, although comparatively far away from the type locality at presumably higher altitudes, and the shape and the mode of color is similar, they are attributed to this subspecies. The lectotype looks like a reduced form. The distribution within the Valle de Talamanca and adjacent slopes additionally supports this classification.

In the specimens recently collected, the whitish band is like in the nominal subspecies broader, but occasionally it can also be as slender as in the lectotype. The color of the whorls varies within the populations and among them, but the outer lip and umbilical area are constantly whitish-opaque. The individuals from Uatsi possess shells with brownish whorls at the apex that during growth change more or less quickly to a pale or more often bright yellow color above the periphery. At least the beginning of the last whorl is yellow



FIGS. 131, 132. *Helicina beatrix riopejensis* n. subsp., Río Peje. FIG. 131. Holotype, INBio 3542625, height 7.8 mm. FIG. 132. Paratype 1, INBio 3542626, height 6.6 mm; scale bar 2.5 mm.

below the subsutural whitish band. Towards the aperture the color fades to pale yellowish-whitish. Specimens from Shiroles may display a similar color, but in many the brownish-reddish-orange of the upper whorls does not change up to the aperture. Similarly the color becomes lighter below the periphery. In general, the yellow form seems to be more frequent.

Helicina (*"Gemma"*) *beatrix riopejensis* Richling, n. subsp.

Type Material

Holotype: INBio 3542625, female (leg. I. Richling, 09.03.1999, *ex* IR 752)
Paratype 1: INBio 3542626, male (same data as holotype)
Paratype 2: ZMB 103882, female (same data as holotype)
Paratype 3: ZMB 103883, male (same data as holotype)
Dimensions:
Holotype: 7.8/7.0/7.4/6.5/5.9/4.6/6.4 mm
Paratype 1: 6.6/6.0/6.5/5.6/5.0/4.1/5.3 mm
Paratype 2: 8.1/6.8/7.3/6.5/6.1/4.6/6.7 mm
Paratype 3: 6.3/5.9/6.5/5.5/5.2/4.1/5.1 mm

Type Locality

SE-Costa Rica, Limón Province, SW of Liverpool (about 24 km W of Puerto Limón) along Río Peje, 09°55'46"N, 83°13'15"W, 135 m a.s.l.

Etymology

The subspecies is named after its origin, the Río Peje.

Examined Material

Leg. I. Richling
Limón: *SW Liverpool*: *Río Peje and small tributary, 09°56'35"N, 83°14'01"W, 110 m a.s.l.*: 12.03.1997: (IR 125); *along Río Peje, bordering forest with palms, 09°55'46"N, 83°13'15"W, 135 m a.s.l.*: 04.03.1998: (IR 440); 09.03.1999: (IR 752); 03.03.2000: (IR 1303); (IR 1305); (IR 1306); 13.03.2001: (IR 1550)

Description

Shell (Figs. 131, 132, 336D): Conical-globose, rather solid, medium sized, shiny. Color: upper whorls light yellowish-horny-amber, becoming darker from apex down, especially in the course of the last whorl changing to bright orange. A small but very distinct opaque whitish band directly below the suture, color of whorl most intensive towards the band. Shell surface shiny and smooth, only structured with very fine growth lines. Embryonic shell with about 1 whorl; $4^{3}/_{8}$ ($3¾–4½$) subsequent whorls very slightly convex; last whorl equally rounded at the periphery; upper whorls slightly more rapidly extending in size; whorls rapidly descending, forming a high spire. Suture slightly impressed. Aperture oblique and remarkably curved backwards, last whorl regularly descending and inserting exactly at periphery. Outer lip always bright orange in continuation of last whorl, thickened and very narrowly reflexed; transition into columella continuous with a little notch. Basal callus very weakly developed and nearly completely smooth or very little granulated.

Internal Shell Structures: (Fig. 133)

Teleoconch Surface Structure (Fig. 134): Similar to *Helicina b. beatrix*, but the zone of oblique diverging grooves is more pronounced.

Embryonic Shell (Fig. 135): The structure is similar to that of *Helicina beatrix confusa*. Figure 135B shows a common phenomenon also seen in other species: a few spiral lines of pits become indistinguishable.

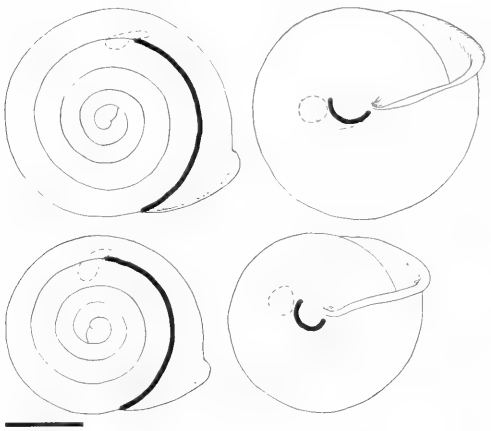


FIG. 133. Axial cleft and muscle attachments of *Helicina beatrix riopejensis* n. subsp., INBio 3542625, 3542626; scale bar 2.5 mm.

FIG. 134. Teleoconch surface structure of *Helicina beatrix riopejensis* n. subsp. A. Embryonic shell to 2nd whorl. B. 1st whorl, zone of transitional pattern and begin of transformation to next structure. C. 1st whorl, pattern of oblique diverging grooves. D. 2nd whorl, smooth surface with growth lines; scale bars 500 µm (A), 100 µm (B–D).

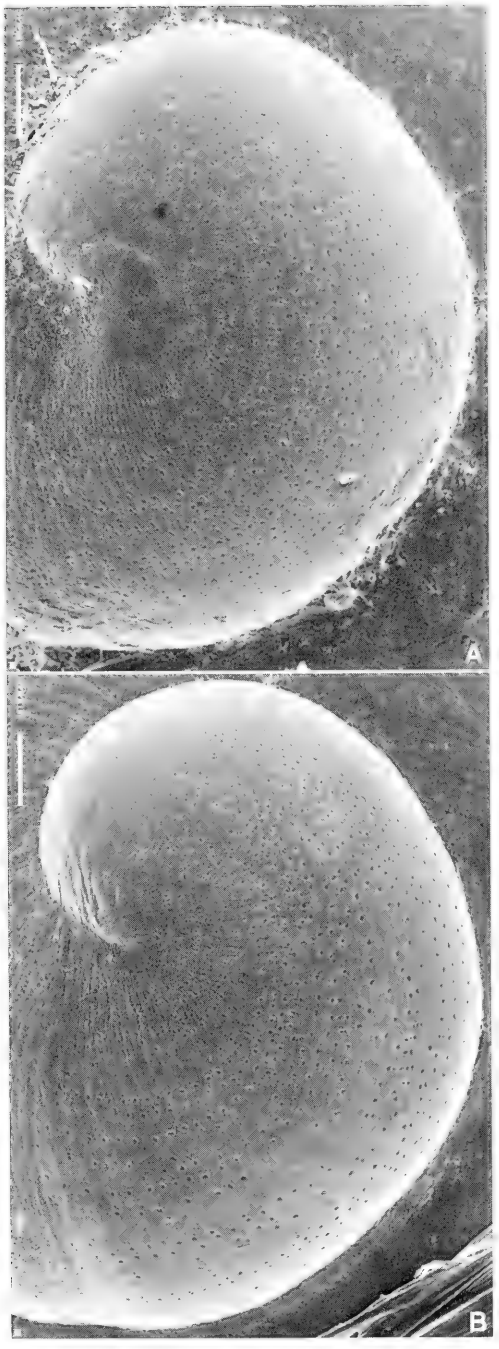


FIG. 135. Embryonic shell of *Helicina beatrix riopejensis* n. subsp.; scale bar 100 µm.

FIG. 136. Operculum of *Helicina beatrix riopejensis* n. subsp., INBio 3542625; scale bar 1 mm.

Diameter: 878 µm (± 31) (800–940) (n = 22) (IR 1303, IR 1550).

Operculum (Fig. 136): Very slightly calcified, calcareous plate covering only part of the outer surface, thickened towards the columellar side. Color orange to dark red, only at columellar side and in the area of the nucleus yellowish-transparent. Columellar side slightly S-shaped, both ends acute, upper end pointed, lower slightly rounded.

Animal (Fig. 337H): As with other subspecies, *Helicina beatrix riopejensis* n. subsp. lacks any spotted pattern on the mantle. But the dorsal and upper lateral sides of head and a median stripe on the posterior foot are black. Only on the middle of the head there is a lighter area. The tentacles are black as well. A greyish-blackish mantle pigmentation gives the semitransparent shell a greenish-brownish appearance, making the white band even more prominent.

Radula: See *Helicina beatrix beatrix*.

Female Reproductive System (Figs. 137, 138): The structures are similar to the nominal subspecies, except for the bursa copulatrix, which is more regularly and deeply lobed; the receptaculum seminis appears consistently smaller.

Morphometry and Sexual Dimorphism

See *Helicina beatrix beatrix*.

FIG. 137. Female reproductive system of *Helicina beatrix riopejensis* n. subsp., apical complex in natural position, dorsal and ventral view, IR 752; scale bars 1 mm (left), 0.5 mm (right).

Habitat

At the type locality, this subspecies is relatively abundant. The undergrowth of the vegetation of the banks of the creek is mainly composed of Heliconiaceae, different palm species, and Araceae. During wet weather, *Helicina beatrix riopejensis* n. subsp. was found crawling nearly everywhere on the leaves with no obvious preference for any particular plants. A higher abundance on leaves of palms and Heliconiaceae may have resulted from the much larger surface of the leaves and the easier search. When aestivating, the specimens were found mainly on the underside of the leaves close to the middle rib. On palms, individuals were observed up to about 5–6 m above the ground. Along the Río Peje, the subspecies lives sympatrically with *H. funcki*, but it was not discovered at several other localities in the area along Río Victoria, Río Blanco, Río René or Río Quito, where *H. funcki* also occurs.

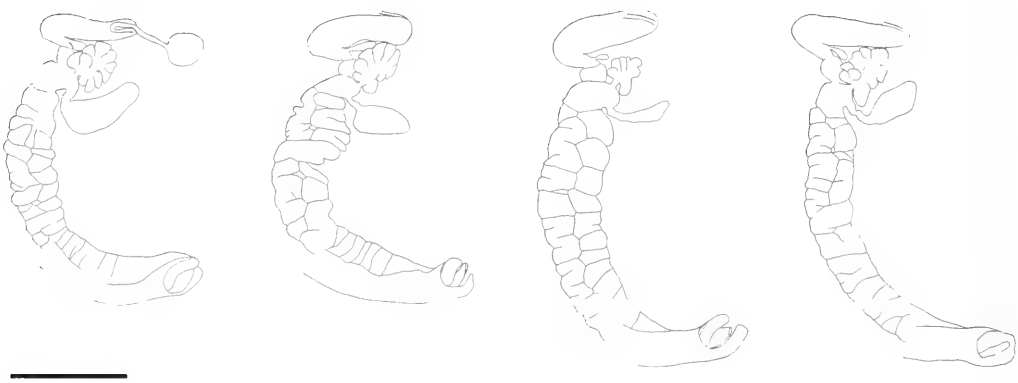


FIG. 138. Variability of the female reproductive system of *Helicina beatrix riopejensis* n. subsp., IR 752; scale bar 2.5 mm.

Distribution (Fig. 139)

Up until now, the subspecies has only been found along the upper part of the Río Peje and a few small tributaries around the type locality. The site belongs to the hilly Caribbean lowlands close to the northeastern foothills of the Cordillera de Talamanca.

Discussion

Few specimens exhibit a dark red spot at the apex. The tinge of orange towards the aperture may be paler or even bright red. Otherwise, the color is very constant within the population investigated.

Helicina beatrix riopejensis n. subsp. differs from the nominal species and other subspecies in the color of the outer lip, which in the other subspecies is consistently whitish, independently of the varying color of the whorls. Furthermore, in *H. beatrix beatrix*, *H. b. confusa*, and *H. b. nicaraguae* the color of the whorls becomes lighter towards the aperture (normally whitish at least in the umbilical area), whereas in *H. b. riopejensis* n. subsp. it turns darker, even in the umbilical area. In general, the whitish band is more slender in *H. b. riopejensis* n. subsp.

With respect to the orange outer lip, the subspecies closely resembles *H. gemma*, but the latter consistently lacks the distinct whitish band under the suture. Its suture seems somewhat more strongly impressed, and the whorls appear to be more convex. Whereas *H. beatrix beatrix* is very clearly distinguished from *H. gemma*, *H. beatrix riopejensis* n. subsp. seems to represent a somewhat intermediate form showing several similarities to both species. Besides the aspects of the shell color, the length of the axial cleft equals the conditions of *H. gemma* and deviates from the other subspecies of *H. beatrix*. On the other hand, *H. beatrix riopejensis* n. subsp. completely lacks the spotted mantle pigmentation of *H. gemma* and, with respect to the morphometry, it would clearly represent the population with the largest specimens. According to all investigated populations of *H. gemma*, the species is much more constant in size than

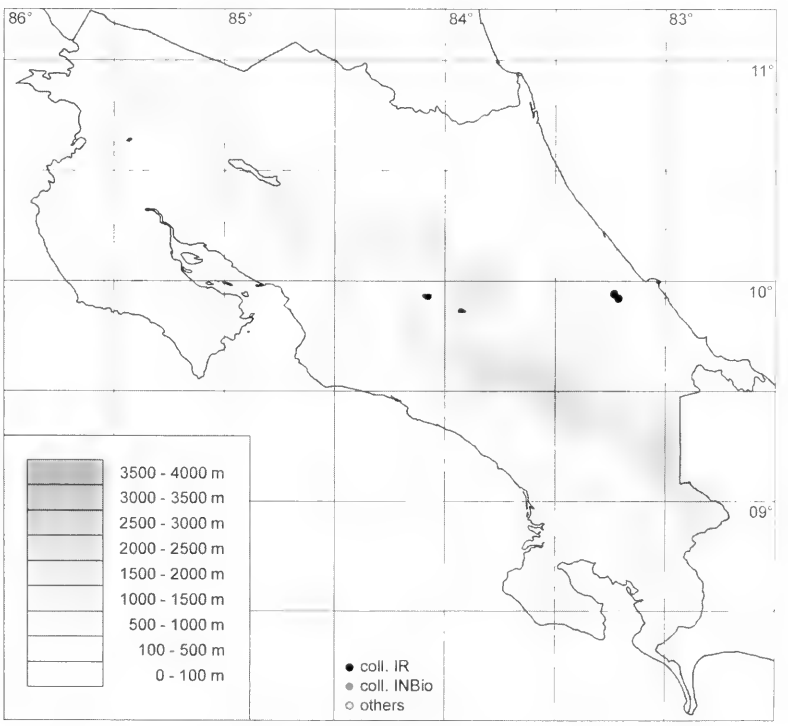


FIG. 139. Records of *Helicina beatrix riopejensis* n. subsp. in Costa Rica.

the other species. At the same locality at the Rio Peje, it reaches its largest sizes, but in Tortuguero, where *H. gemma* occurs sympatrically, the population has a smaller shell size than *H. beatrix riopejensis* n. subsp., making a comparison with the conditions of other species contradictory. With the present state of knowledge, "*riopejensis*" is tentatively referred to *H. beatrix*, but further data may reveal closer affinities to *H. gemma*. Nevertheless, the differences between "*riopejensis*" and both species justify a recognition at subspecific level.

Helicina (*"Gemma"*) *talamancensis* (Richling, 2001)

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* L. Pfeiffer, 1849]
Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* Angas, 1879]
Oligyra talamancensis Richling, 2001: 3–5 (text figure)

Original Description

See "Description".

Type Material

Holotype: INBio 3404978, female (leg. I. Richling, 24.3.1997) (Fig. 140)
Paratype 1: INBio 1494509, female (Puntarenas, 3 km NE de la Escuela de Llano Bonito, 08°44'54"N, 83°02'04"W, 920 m a.s.l., leg. Socorro Avila, 24.03.1997)
Paratype 2: INBio 3389580 (same data as paratype 1)
Paratype 3: ZMB 103368, male (same data as holotype)
Paratype 4: ZMB 103385, probably female, empty shell (from type locality, leg. I. Richling, 29.8.1999)
Paratypes 5–12: INBio 1494642: 7 adults, 1 juvenile (same data as paratype 1)
Paratypes 13–14: INBio 1487761: 2 juveniles (Puntarenas, 3.5 km de la Escuela de Llano Bonito Carretera a San Vito, 08°44'37"N, 83°02'04"W, 840 m a.s.l., leg. Socorro Avila, 24.03.1997)
Dimensions (height/greatest diameter):
Holotype: 9.2/9.2 mm
Paratype 1: 9.1/8.7 mm
Paratype 2: 9.2/8.8 mm
Paratype 3: 8.2/8.3 mm

Type Locality

SW-Costa Rica, Puntarenas Province, Fila Costeña, north of Bajo Bonito (locally called Llano Bonito), north of Río Claro, 8°44'41"N, 83°02'09"W, 980 m a.s.l., probably primary rain forest bordered by secondary growth.

Type Material of Synonymous Taxa or Similar Species

Helicina terryae Rehder, 1940

Helicina terryae Rehder, 1940: 350, fig. 16

Type Material: USNM 536026 (not USNM 539026 as given in Rehder, 1940): holotype (Fig. 141)
Dimensions (given in original description, height/greatest diameter):
Holotype: 8.2/9.8 mm

Type Locality: Panama, Chiriquí Province.

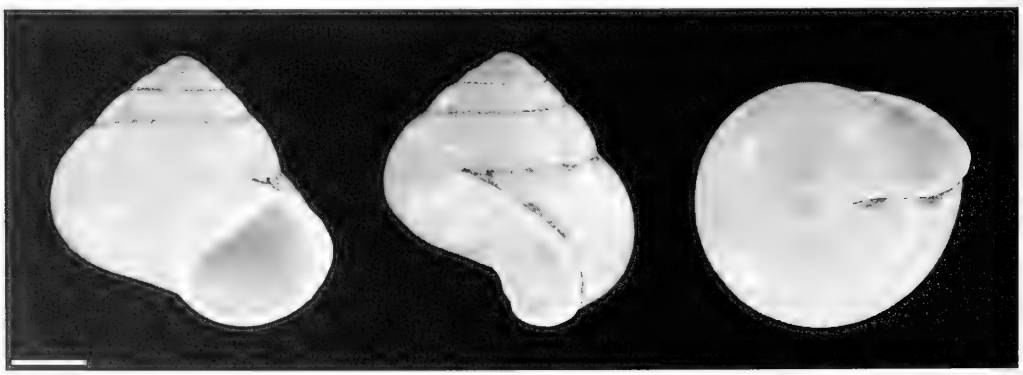


FIG. 140. *Helicina talamancensis*, holotype, INBio 3404978, height 9.2 mm; scale bar 2.5 mm.

Examined Material

Leg. I. Richling

Puntarenas: S *San Vito*, forest opposite the Wilson Botanical Garden, Las Cruces, 08°46'57"N, 82°57'40"W, 1,160 m a.s.l., 29.08.1999: (IR 1018)
N Neily, road from Ciudad Neily to San Vito, open area with a few trees, 08°40'23"N, 82°56'44"W, 180 m a.s.l., N Neily, 23.03.1997: (IR 210)
Fila Costeña, *north of Bajo Bonito* (locally called Llano Bonito), N of Río Claro, rain forest, 08°44'41"N, 83°02'09"W, 980 m a.s.l., 24.03.1997: (IR 222); 15.02.1999: (IR 580); 29.08.1999: (IR 1029), (IR 1661); (IR 1030); 06.03.2001: (IR 1487); (IR 1489)
Refugio Nacional de Fauna Silvestre Golfito, rain forest, 08°39'26"N, 83°10'50"W, 100 m a.s.l., 14.02.1999: (IR 567); 10.02.2000: (IR 1166)

INBio Collection

San José: San Isidro, Area de Conservación la Amistad, *Parque Nacional Chirripó*, Estación Santa Elena, Finca del Gringo, 09°23'31"N, 83°35'42"W, 1,300 m a.s.l.: leg. A. M. Maroto, 29.09.1995: 1 ad. (INBio 3542536)

Puntarenas: *Reserva Forestal Golfo Dulce*: *Cerro de Oro, 08°33'46"N, 83°29'24"W, 150 m a.s.l.*: leg. Eida Fletes, 30.10.1995: 1 ad. (INBio 1498769), 1 ad. (INBio 1498766); *Cerro de Oro, Quebrada Terranosa, 08°34'11"N, 83°30'15"W, 140 m a.s.l.*: leg. Ronald Villalobos, 05.10.1995: 1 ad. (INBio 1485176); *Rancho Quemado, 08°40'35"N, 83°34'33"W, 250 m a.s.l.*: leg. Zaidett Barrientos, 18.03.1994: 1 juv. (INBio 1475394)
Playa Blanca, 08°38'18"N, 83°26'16"W, 0 m a.s.l., leg. Gillermo Mena, 04.09.1995: 1 juv. (INBio 1479918)
Fila Cal: *24 km de San Vito hacia Ciudad Neilly, 08°41'36"N, 82°56'36"W, 780 m a.s.l.*: 14.01.1995: leg. Luis Angulo, 2 ads., 1 juv. (INBio 1480714); leg. Angela Mora Maroto: 2 ads. (INBio 1481246); leg. Socorro Avila: 4 ads., 2 juvs. (INBio 1481353); leg. Marcos Moraga: 1 ad., 1 juv. (INBio 1481564); leg. Alejandro Azofeifa: 1 ad. (INBio 1482605); leg. Francisco Alvarado: 3 s.ads. (INBio 1495690); 29.08.1995: leg. Marianella Segura, 3 ads., 2 s.ads. (INBio 3121201); *740 m a.s.l.*: leg. Ronald Villalobos: 4 juvs. (INBio 1481514); *24.5 km S en la carretera de San Vito hacia Ciudad Neilly, 08°40'55"N, 82°56'23"W, 600 m a.s.l.*: leg. Zaidett Barrientos, 21.11.1995: 4 ads., 1 juv. (INBio 1485120); leg. A. Picado, 21.11.1995: 2 ads., 2 s.ads., 1 juv. (INBio 3542530); leg. M. Segura, 21.11.1995: 2 ad., 1 s.ad. (INBio 3542545)
4.5 km NW de Ciudad Neily, Camino Paralelo al Río Caño Seco, Colectado en hojarasca en helechos, 08°40'50"N, 82°57'25"W, 180 m a.s.l.: leg. M. Chinchilla, 22.11.1995: 4 ads., 1 s.ad. (INBio 3542526)
Jardín Botánico Wilson, Sendero a Río Jaba, 08°47'13"N, 82°58'04"W, 1,160 m a.s.l., leg. Zaidett Barrientos, 10.03.1995: 1 ad. (INBio 1485093)
Estación Pittier: *09°01'32"N, 82°57'46"W, 1,660 m a.s.l.*: leg. Angela Mora Maroto, 15.01.1995: 1 ad., 2 juvs. (INBio 1481397); *Sendero Pittier, 09°01'11"N, 82°57'54"W, 1,540 m a.s.l.*: leg. malacological staff of INBio, 06.11.1995: 4 ads., 1 juv. (INBio 1488141); *Sendero Río Gemelo, 09°01'36"N,*

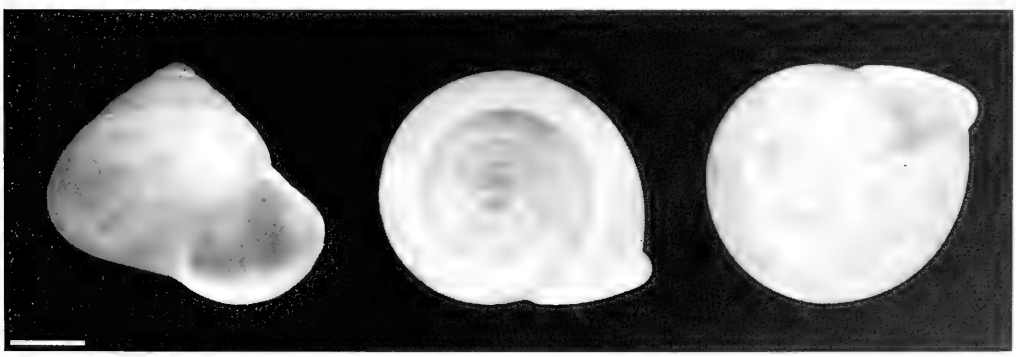


FIG. 141. *Helicina terryae*, holotype, USNM 536026, height 8.2 mm; scale bar 2.5 mm (photograph: R. Hershler).

82°57'26"W, 1,640 m a.s.l.: leg. Annia Picado, 13.01.1995: 1 juv. (INBio 1481168)
Parque Nacional La Amistad, Coto Brus, sendero a Cerro Pittier, 600 m NW de la Estación, 09°01'44"N, 82°57'54"W, 1,750 m a.s.l., leg. Marcos Moraga, 06.11.1995: 1 ad. (INBio 1484619)
Parque Nacional La Amistad, Estación Pittier: Sendero a Cerro Pittier: 09°02'05"N, 82°57'39"W, 1,800 m a.s.l.: leg. Luis Angulo, 06.10.1995: 1 juv. (INBio 1485495); *09°01'43"N, 82°57'54"W, 1,750 m a.s.l.*: leg. M. Moraga, 19.06.1996: 1 ad. (INBio 3542538); *Sendero a Altamira, 900 m NW de la estación, 09°01'52"N, 82°58'05"W, 1,760 m a.s.l.*: leg. Evelio Alfaro, 15.01.1995: 1 ad. (INBio 1480719), 1 ad. (INBio 1480725); leg. Angela Mora Maroto: 2 ads. (INBio 1481219), 1 ad. (INBio 1481236); 1 ad. (INBio 3542544); *Sendero a Río Canasta, 09°01'51"N, 82°58'05"W, 1,740 m a.s.l.*: leg. M. Moraga, 14.06.1996: 1 ad. (INBio 3542540)
Parque Nacional La Amistad, Estación Altamira, Sendero a Estación Biolley: 09°01'59"N, 83°00'39"W, 1,340 m a.s.l.: leg. Marianella Segura, 13.10.1994: 1 ad. (INBio 1485516); *09°01'47"N, 83°01'07"W, 1,300 m a.s.l.*: leg. Alexander Alvarado Mendez, 10.09.2001: 1 ad. (INBio 3394313)
Parque Nacional La Amistad, Cerro Biolley, 09°02'25"N, 83°00'39"W, 1766 m a.s.l., leg. Roberto Delgado, 17.06.1994: 1 ad. (INBio 1467066)
Parque Nacional La Amistad, Cabagra, Puesto Altamira, Sendero a Cerro Biolley, 09°02'12"N, 83°00'39"W, 1,600 m a.s.l., 13.06.2001: 1 s.ad. (INBio 3318186); 3 ads. (INBio 3318194) (all leg. Alexander Alvarado Mendez)
Puntarenas, *Parque Nacional La Amistad, Pittier*, Puesto Altamira, sendero Casa Coca, 09°02'25"N, 82°59'24"W, 1,800 m a.s.l., leg. Alexander Alvarado Mendez, 12.05.2001: 1 ad., 1 s.ad. (INBio 3317088)

Other Sources

COSTA RICA

San José: determination uncertain? 4.3 mi SW of San Isidro del General on Road to Dominical [about 09°20'N, 83°44'W], 01.08.1971: 2 ads. (UF 69848)
Puntarenas: Rincón [about 08°42'30"N, 83°29'30"W], R. Casebeer, 28.06.1963: 1 ad. (UF 243510)

Etymology

The species is named after the southern central mountain chain in Costa Rica, the Cordillera de Talamanca, which forms the greatest remaining undisturbed area of primary forest in the country.

Description

Shell (Figs. 140, 336E): conical-globose, rather solid, medium sized, shiny. Color: yellowish to

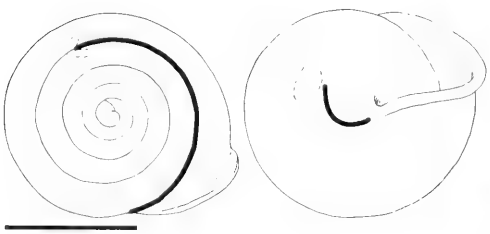


FIG. 142. Axial cleft and muscle attachments of *Helicina talamancensis*, IR 1030; scale bar 5 mm.

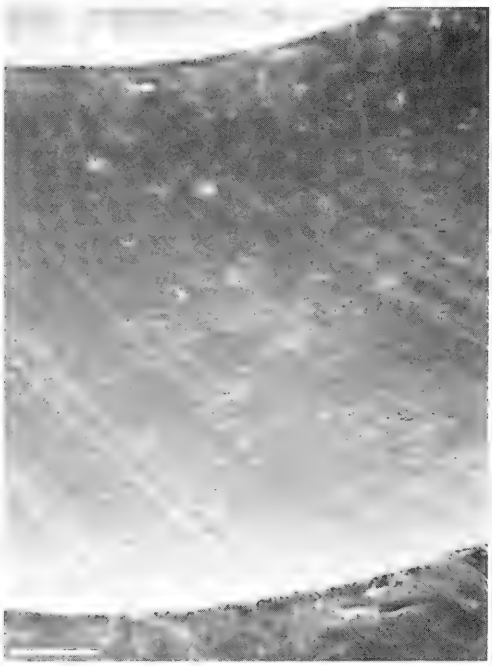


FIG. 143. Teleoconch surface structure of *Helicina talamancensis*, 2nd whorl; scale bar 100 µm.

whitish-opaque (holotype); in some specimens the last whorl yellowish-white and the upper whorls with a more or less strong tendency to a pale orangish-red color. Periostracum very thin, shiny and smooth, except very fine growth lines. Embryonic shell with about 1 whorl; $4^{1}/_{8}$–$4^{3}/_{4}$ subsequent whorls slightly convex; last whorl equally rounded at periphery; upper whorls more rapidly extending in size, so that shell (especially the female's) appears somewhat rounded and less pointed in apical part. Suture slightly impressed. Aperture oblique and in its middle part remarkably curved backwards. Outer lip always whitish, thickened, very narrowly reflexed, appearing somewhat rounded at edge; transition into columella continuous, with a slight notch. Basal callus weakly developed and nearly completely smooth or very little granulated.

Internal Shell Structures: (Fig. 142)

Teleoconch Surface Structure (Fig. 143): The transitional pattern covers only about ¼ of a whorl; the structure is weakly developed. The smooth zone with just the fine growth lines follows directly.

Embryonic Shell (Fig. 144): In comparison with *Helicina beatrix*, the pitted pattern is even less prominent in *H. talamancensis*. The embryonic shell appears nearly smooth. Diameter: 933 µm (± 40) (840–1,000) (n = 18) (IR 222, IR 1028, IR 1030).

Operculum (Fig. 145): Very slightly calcified, calcareous plate covering only part of the outer surface. Color horny-amber, only near the columella whitish, but still somewhat transparent. Columellar side S-shaped, both ends acute, upper end pointed.

Animal (Fig. 338B): The appearance of living *Helicina talamancensis* is striking: the body is whitish-yellow throughout, the mantle pigmentation is also whitish; only the tentacles are deep black. This characteristic color is present in all live and preserved specimens studied.

Radula (Fig. 146): Cutting edge of the centrals smooth or crenulated. Comb-lateral with 8-9 cusps, cusps on marginals rather rapidly increasing in number, but with a similar effect as in *Helicina beatrix beatrix*. Radula with about 60–75 rows of teeth.

Female Reproductive System (Figs. 147, 148): Compared to *Helicina beatrix* the ascending limb of the V-organ is elongated, the receptaculum is drop-shaped. The bursa copulatrix is very irregularly lobed, the elongated provaginal sac shows a simple outline. Its stalk is short and stout. The pallial oviduct is marked by a longitudinal furrow and various transversal constrictions.

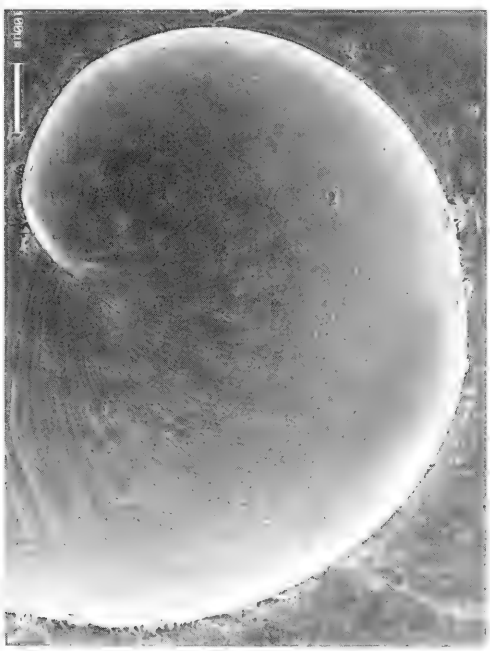


FIG. 144. Embryonic shell of *Helicina talamancensis*; scale bar 100 µm.

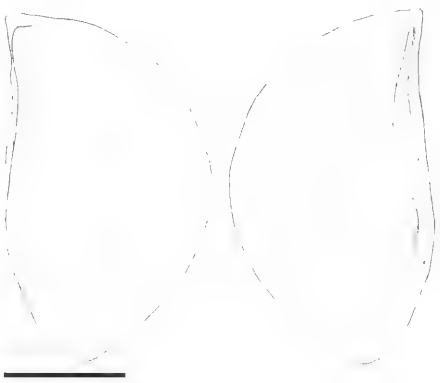


FIG. 145. Operculum of *Helicina talamancensis*, holotype, INBio 3404978; scale bar 2 mm.

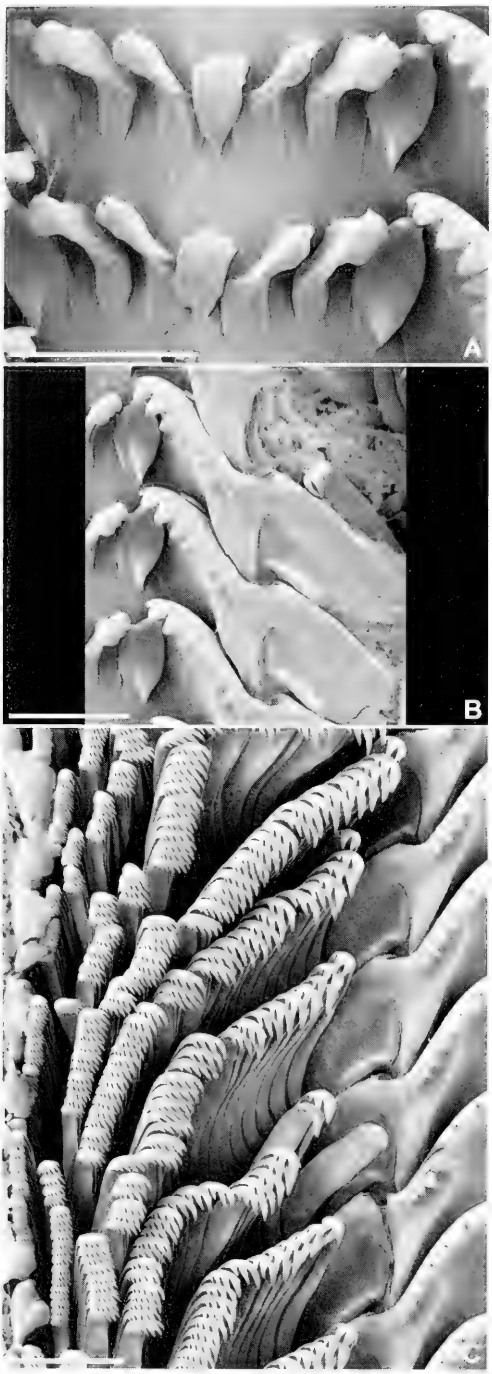


FIG. 146. Radula of *Helicina talamancensis*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

FIG. 147. Female reproductive system of *Helicina talamancensis*, IR 1030; scale bar 1 mm.

Morphometry and Sexual Dimorphism (Table 9, Figs. 149–155)

Helicina talamancensis could not be found in high numbers, the only specimens studied anatomically are those I collected at Bajo Bonito. Populations included from the collection of INBio with sufficient individuals (Fila de Cal, Neily, Amistad, Bajo Bonito) that could not be analyzed for sex were separated as in *H. beatrix* to avoid artificial high deviations of measurements with mixed sexes.

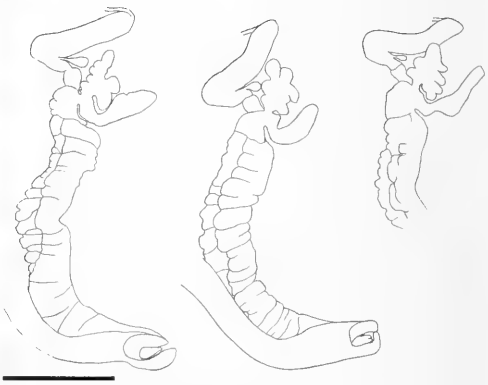


FIG. 148. Variability of the female reproductive system of *Helicina talamancensis*, IR 1030; scale bar 2.5 mm.

TABLE 9. Measurements of different populations of *Helicina talamancensis* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals from Fila de Cal, Neily, Amistad and Bajo Bonito INBio not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		"Bajo Bonito" (altitude 980 m) lots IR 1018, IR 1029, IR 1030, IR 1487				
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	9.03	0.33	8.48	9.61	8
Height	m	7.81	0.18	7.50	8.22	8
Maj. diam.	f	8.54	0.27	8.02	8.92	8
Maj. diam.	m	7.46	0.13	7.16	7.72	8
Min. diam.	f	7.95	0.20	7.60	8.31	8
Min. diam.	m	6.97	0.11	6.75	7.20	8
Outer lip	f	5.61	0.15	5.46	5.91	8
Outer lip	m	5.12	0.17	4.80	5.41	8
Last whorl	f	7.05	0.15	6.58	7.47	8
Last whorl	m	6.17	0.18	5.88	6.46	8
Col. axis	f	7.34	0.26	6.77	7.87	8
Col. axis	m	6.29	0.19	6.03	6.68	7
Weight	f	0.087	0.010	0.056	0.102	8
Weight	m	0.066	0.007	0.055	0.085	8
Volume	f	0.199	0.017	0.172	0.224	8
Volume	m	0.130	0.008	0.115	0.145	8

		"Fila de Cal" (altitude 600–780 m) lots INBio 1480714, 1481246, 1481353, 1481564, 1482605, 1485120, 3121201, 3542530, 3542545					"Neily" (altitude 180 m) lot INBio 3542526				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.73	0.17	7.35	7.98	10	7.75	0.33	7.42	8.08	2
Height	m	6.80	0.21	5.82	7.17	11	6.43	0.04	6.38	6.47	2
Maj. diam.	f	7.14	0.14	6.95	7.42	10	7.42	0.09	7.33	7.50	2
Maj. diam.	m	6.69	0.11	6.45	6.96	11	6.60	0.06	6.54	6.65	2
Min. diam.	f	6.75	0.11	6.55	6.98	10	6.90	0.17	6.73	7.06	2
Min. diam.	m	6.23	0.12	6.08	6.50	11	5.95	0.10	5.85	6.04	2
Outer lip	f	4.71	0.16	4.41	4.87	10	4.78	0.02	4.75	4.80	2
Outer lip	m	4.46	0.08	4.26	4.62	11	4.38	0.11	4.27	4.48	2
Last whorl	f	6.01	0.16	5.70	6.38	10	6.02	0.15	5.87	6.17	2
Last whorl	m	5.50	0.12	5.10	5.83	11	5.15	0.20	4.95	5.35	2
Col. axis	f	6.37	0.29	5.95	7.31	10	6.23	0.23	6.00	6.45	2
Col. axis	m	5.65	0.20	5.29	6.27	11	5.17	0.06	5.11	5.23	2

(*Continues*)

(*Continued*)

		"Amistad" (altitude 1340–1800 m) lots INBio 1467066, 1480719, 1480725, 1481219, 1481236, 1481397, 1484619, 1485516, 1488141, 3317088, 3318194, 3542538, 3542544, 3542540					"Bajo Bonito INBio" (altitude 920 m) lots INBio 1494509, 1494642, 3389580				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.50	0.33	8.06	9.18	11	9.11	0.05	9.00	9.15	4
Height	m	7.26	0.17	6.88	7.67	9	8.10	0.13	7.88	8.28	5
Maj. diam.	f	8.16	0.26	7.78	8.68	11	8.47	0.10	8.33	8.62	4
Maj. diam.	m	7.20	0.21	6.38	7.50	9	7.67	0.17	7.25	7.88	5
Min. diam.	f	7.53	0.23	7.20	7.95	11	7.88	0.09	7.77	8.02	4
Min. diam.	m	6.58	0.15	5.94	6.74	9	7.08	0.12	6.77	7.22	5
Outer lip	f	5.37	0.19	5.08	5.81	11	5.62	0.10	5.42	5.79	4
Outer lip	m	4.76	0.20	4.10	5.15	8	5.14	0.14	4.88	5.40	5
Last whorl	f	6.55	0.19	6.15	6.92	11	7.12	0.07	7.02	7.20	4
Last whorl	m	5.80	0.16	5.49	6.07	9	6.25	0.10	6.09	6.48	5
Col. axis	f	6.94	0.29	6.36	7.63	11	7.29	0.13	7.12	7.55	4
Col. axis	m	5.93	0.15	5.67	6.20	9	6.51	0.08	6.41	6.64	5

		"Península de Osa" (altitude 140–150 m) lots INBio 1485176, 1498766, 1498769					"Chirripó" (altitude 1300 m) lot INBio 3542536				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.06	0.61	7.15	8.82	3	8.16	-	-	-	1
Maj. diam.	f	8.04	0.65	7.07	8.77	3	8.21	-	-	-	1
Min. diam.	f	7.42	0.62	6.50	7.96	3	7.64	-	-	-	1
Outer lip	f	5.26	0.41	4.65	5.66	3	5.27	-	-	-	1
Last whorl	f	6.36	0.45	5.69	6.77	3	6.34	-	-	-	1
Col. axis	f	6.61	0.56	5.77	7.15	3	6.66	-	-	-	1

Morphometry: The populations show remarkable differences in size with the individuals from Fila de Cal and Neily being smallest. For each characteristic, the differences between the populations are similar, implying that the relations are about the same. Although from different altitudes and from localities relatively close to each other, the specimens from Neily and the Fila de Cal are of about the same size, which suggests rather a relation to the sites than to altitude. The few specimens from the lowlands of Península de Osa approach the shells from "Amistad" at much higher altitudes more closely in size than those from Neily or Fila de Cal.

In comparison with *Helicina beatrix beatrix*, the shell volume of the Bajo Bonito population is smaller, but the weight is significantly higher. It confirms the impression of more solid shells in *H. talamancensis*.

Sexual Dimorphism: As in *H. beatrix* the sexes clearly diverge in all measurements, in most cases even without an overlap of the extrema (Fig. 156). The females are much bigger than the males, in volume the males are only $^2/_3$ of the females. This divergence allows the separation of individuals of unknown sex (Fig. 157), as explained under *H. beatrix beatrix*. Although containing only three specimens, the lot from Península de Osa probably consists of two females and one male, because the average is shifted to the higher value.

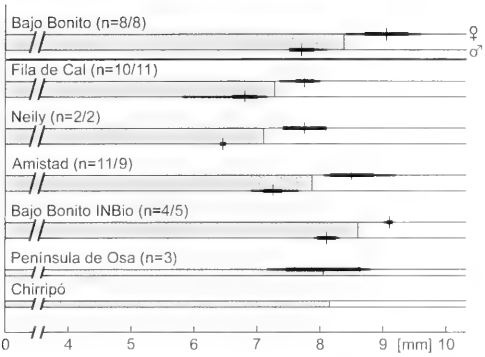


FIG. 149. Shell height of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Fila de Cal, Neily, Amistad, and Bajo Bonito INBio not determined anatomically (see text).

Contrary to most of the populations of *H. funcki* and *H. tenuis*, the smaller males also weigh less than the females.

Habitat

The species is arboreal, at the type locality specimens were found aestivating on the lower side of leaves in the undergrowth, mainly on Heliconiaceae and different species of palms. They were more abundant during the rainy season in August than they were in February and March during the dry period. In rainy weather, individuals were also observed crawling on the upper side of leaves at night near the Wilson Botanical Garden. At several localities, *Helicina talamancensis* occurs sympatrically with *H. pitalensis*.

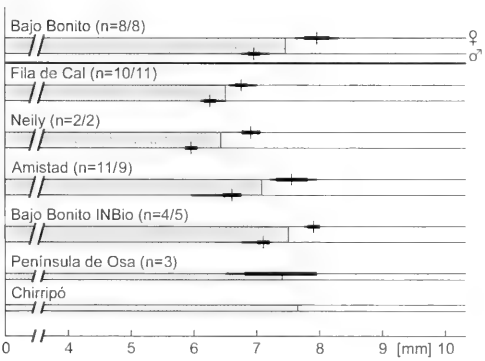


FIG. 150. Minor diameter of shell of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

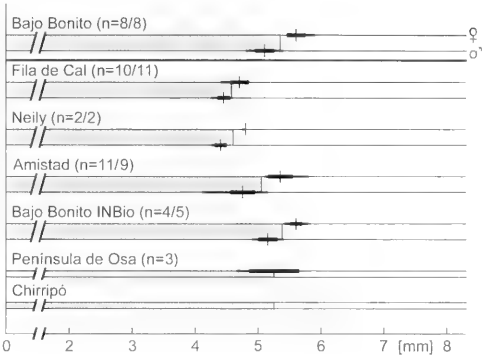


FIG. 151. Expansion of outer lip of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

Distribution (Fig. 158)

Helicina talamancensis is only known from the Pacific slopes in the southern parts of

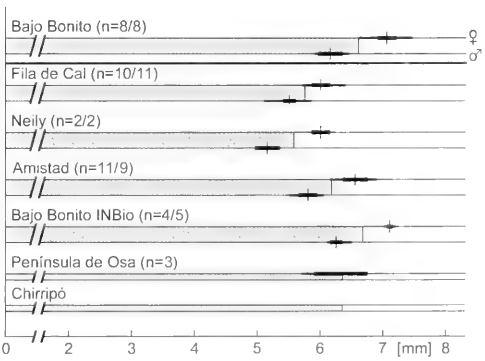


FIG. 152. Height of last whorl of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

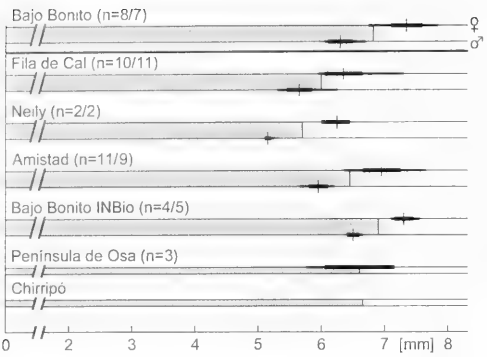


FIG. 153. Height of columellar axis of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

Costa Rica. It occurs in the lowland rain forest on the Península de Osa and near Golfito close to the coast at elevations of approximately 100–250 m. In the steep mountains of Fila Cruces and Fila de Cal and on the slopes of the southern Cordillera de Talamanca, *H. talamancensis* is found on elevations of up to 1,800 m in the cloud forest area. Although corresponding in its distribution to the southern records for *H. pitalensis*, there is no indication and no historical evidence for a more northerly occurrence of this species than the area of San Isidro. With respect to records of Helicinidae, the adjacent area of Chiriqui Province, Panama, is virtually unexplored.

Discussion

The material of *Helicina talamancensis* contains some specimens that show a completely pale orange color, whereas yellowish specimens are much more common.

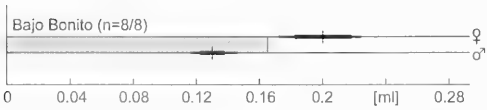


FIG. 154. Shell volume of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

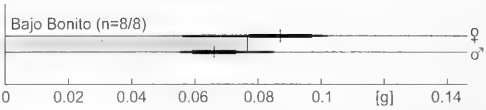


FIG. 155. Shell weight of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

The species most closely resembles *H. beatrix beatrix*, but differs in the form of the peristome. In *H. beatrix beatrix*, the outer lip is less reflexed and thinner, and the aperture is more strongly curved backwards so that the upper part appears somewhat depressed in frontal view. Furthermore, *H. talamancensis* lacks the characteristic white band directly under the suture. The color of the soft body of *H. talamancensis* is unique among Costa Rican Helicinidae.

Helicina terryae is of a nearly similar color and size. Unfortunately, this species was described from the holotype only, with the vague locality of Chiriquí Province, Panama, and there are no other similar specimens in the USNM collection (pers. comm. Dr. R. Hershler, USMN). Examination of photographs of the type (USNM 536026, not USNM 539026, as given in Rehder, 1940; pers. comm. Dr. R. Hershler) revealed that *H. terryae* displays a different outline of the last whorl in having the curvature of the periphery more towards the base. The outer lip is less reflexed, and the spire is lower. Furthermore, the surface of the shell appears to be similar to that of *H. funcki*, for example, with "irregular, oblique, and subspiral grooves", rather than to the smooth and shiny one of *H. talamancensis*.

The material of *H. beatrix* and *H. oweniana sensu* Monge-Nájera (1997) was checked in the INBio collection and was found to partially belong to *H. talamancensis*. The differences to *H. beatrix* are given above. *Helicina oweniana* differs most obviously in the distinct orange color of the outer lip and the less impressed suture.

Rehder (1940) mentioned *H. tenuis* as the most closely resembling species of *H. terryae*. From *H. talamancensis*, *H. tenuis* can easily be distinguished by its shell surface structure, rectangularly expanded outer lip, occasionally developed bands and color of shell and soft body.

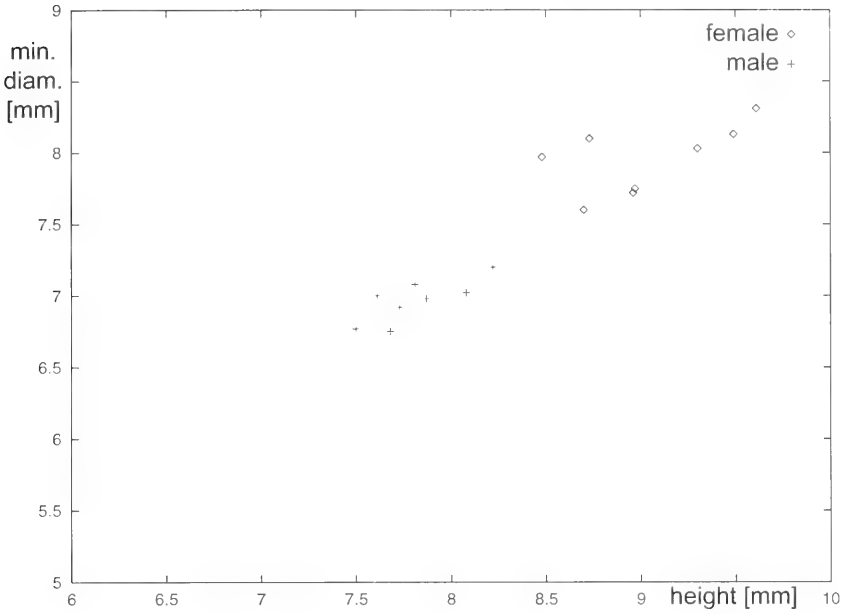


FIG. 156. Range of measurements in females and males of *Helicina talamancensis* exemplary for height and minor diameter in the population from Bajo Bonito.

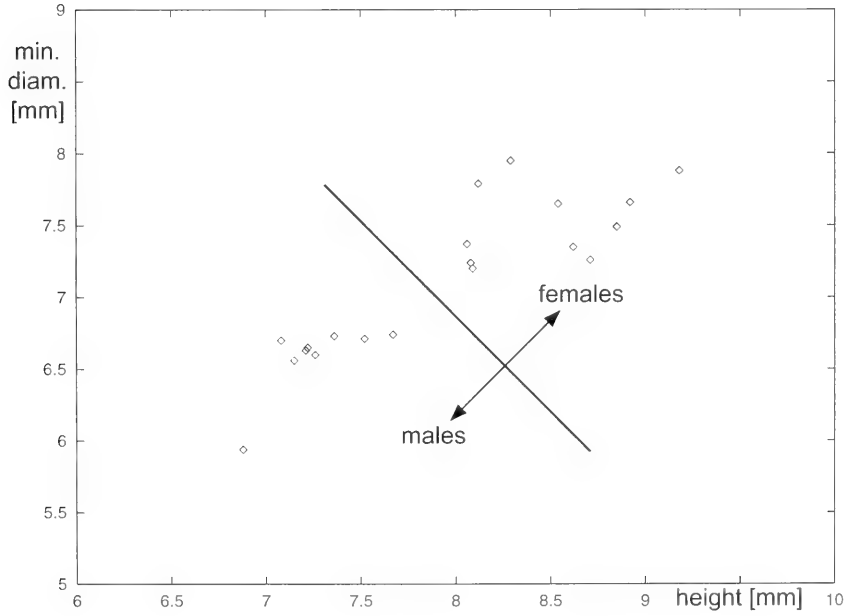


FIG. 157. Plot of measurements for height and minor diameter for individuals of *Helicina talamancensis* of unknown sex, exemplary for the population of Amistad and the separation proposed.

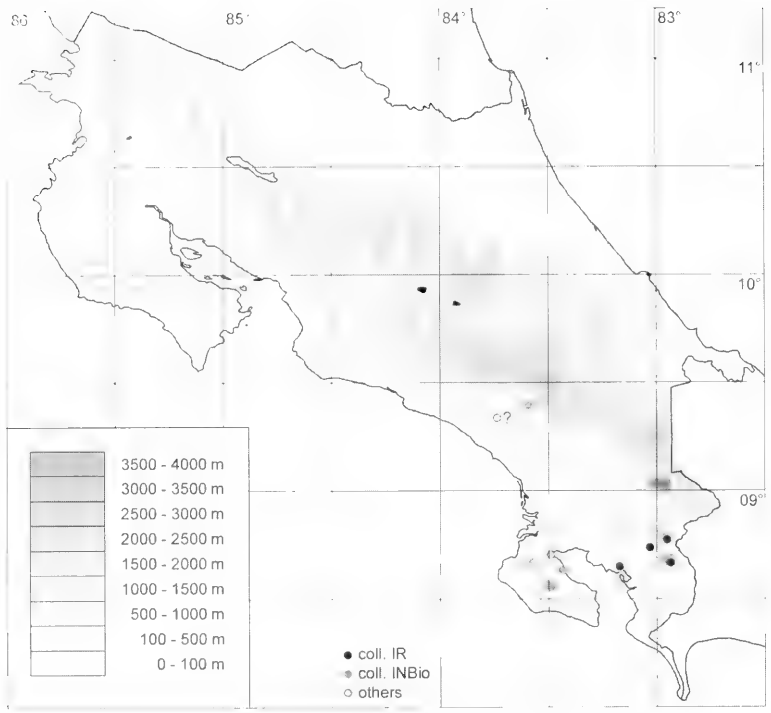


FIG. 158. Records of *Helicina talamancensis* in Costa Rica.

Helicina (*"Gemma"*) *gemma*
Preston, 1903

Helicina oweniana var. *anozona* – Biolley, 1897: 5: Costa Rica: Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] and las Delicias (Santa Clara), 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] [*non* von Martens, 1876]

Helicina oweniana var. *coccinostoma* – von Martens, 1900: 605-606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley) [*non* Morelet, 1849]

Helicina oweniana var. *anozona* – von Martens, 1900: 605-606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley), Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] (Pittier, Biolley) [*non* von Martens, 1876]

Helicina gemma Preston, 1903: 4 (with text figure)

Alcadia (*Leialcadia*) *gemma* – Wagner, 1908: 83, pl. 14, figs. 17–18

Oligyra (*Succincta*) *gemma* – Baker, 1922a: 45

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* L. Pfeiffer, 1849]

Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* Angas, 1879]

Original Description

"Shell conical, elevated, bright yellow, apical whorls crimson, last whorl tinged with orange-scarlet for some distance from the mouth, the outer lip being also of a vivid orange-scarlet colour. Whorls 5, convex, very finely striated with lines of growth. Peristome expanded and slightly reflexed. Aperture rather high and narrow. Operculum reddish-brown, normal.
Diam. maj. 6, alt. 7 millim. Aperture (inside measurement) diam. 2.5, alt. 3 millim.
Hab. – Costa Rica.

A very beautiful and striking shell, whose nearest ally appears to be *H. oweniana*, Pfr., from Mexico; from this, however, it differs in being more globular, in the greater convexity of the whorls and in having one less, in the narrower aperture, and in the color of the outer lip (otherwise similar in both species) extending further up the body whorl than it does in *H. oweniana*."

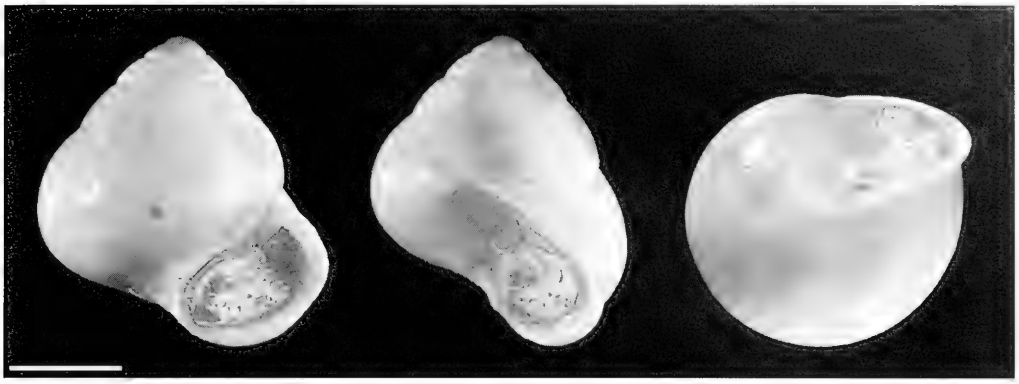


FIG. 159. *Helicina gemma*, lectotype, BMNH 1903.5.4.2, height 7.0 mm; scale bar 2.5 mm.

Type Material

Lectotype BMNH 1903.5.4.2 "San Carlos, purchased from Mr. H.B. Preston"; 1 paralectotype ZMB 53814 "San Carlos, *ex* Preston", 1 paralectotype ZMB 59238 (*ex* Preston); 1 paralectotype ANSP 098181 "Costa Rica, San Carlos River, purchased from Preston as cotype" (Robertson et al., 1986)

According to Dance (1986), most Preston types are in the BMNH collection. Following the advice for type selection of the International Code for Zoological Nomenclature, the specimen BMNH 1903.5.4.2 is **here selected as lectotype** of *Helicina gemma* (Fig. 159). Furthermore, it was labeled by Preston as "type" and is much better preserved than the ZMB specimens suffering from Byne's disease. The specimen still possesses its operculum. I did not study the ANSP specimen.

Dimensions:

Lectotype BMNH 1903.5.4.2:
7.0/6.1/6.5/5.7/3.9/5.4/5.6 mm

Paralectotypes:
ZMB 53814: 6.0/5.4/5.8/5.0/3.5/4.5/4.7 mm
ZMB 59238: 6.7/6.0/6.2/5.5/3.7/5.0/5.4 mm

Type Locality

"Costa Rica", by type selection restricted to San Carlos [on one hand San Carlos is the old name for Ciudad Quesada, about 10°20'N, 84°26'W in Alajuela Province; on the other hand and following the data from the ANSP specimen, a river in northern Costa Rica is called Río San Carlos, bearing the name from the confluence of Río Arenal and Río Peñas Blancas near Boca de Arenal, about 10°33'N, 84°29'W, until it becomes a tributary of the Río San Juan at Boca San Carlos at the Nicaraguan border, about 10°46'30"N, 84°12'30"W in Alajuela Province, thus referring to a more northern area. However, both possible locations share the trait that they are situated on the Caribbean plain in the eastern part of Alajuela Province].

Examined Material

Leg. I. Richling

Guanacaste: *N of Nuevo Arenal: area of primary rain forest, 10°33'32"N, 84°51'40"W, 800 m a.s.l.*: 05.03.1999: (IR 740); *"Las Pavas" (private reserve in preparation), secondary rain forest, about 10°33'30"N, 84°51'53"W, 800 m a.s.l., to 10°33'26"N, 84°51'57"W, 760 m a.s.l.*: 05.03.1999: (IR 741); 17.08.1999: (IR 947); (IR 948): 24.02.2000: (IR 1275); (IR 1277); 27.02.2001: (IR 1460); (IR 1464); 01.03.2001: (IR 1462); 03.03.2001: (IR 1463)

Parque Nacional Guanacaste, *Volcán Cacao*, at southern slope, Estación Cacao, W-Sendero near station, forest, 10°55'35"N, 85°28'06"W, 1,110 m a.s.l., 18.03.1999: (IR 786); 09.03.2000: (IR 1333); (IR 1335)

Alajuela: *Near Volcán Arenal, trail along volcano in rainforest: about 10°29'07"N, 84°42'55"W, 720 m a.s.l.*: 24.02.1998: (IR 387); 03.03.1999: (IR 734); 01.08.1999: (IR 885); 25.02.2000: (IR 1284); *about 10°33'23"N, 84°51'51"W, 800 m a.s.l.*: 05.03.1997: (IR 77); (IR 76)

Limón: Siquirres, along footpath stream up *Río Siquirres* and along a southern tributary, 10°05'37"N, 83°30'32"W, 100 m a.s.l., 11.03.2001: (IR 1536); 19.03.2001: (IR 1618); (IR 1635); (IR 1650; (IR 1652)

Zona Protectora Tortuguero, *near Tortuguero*, N of village, about 10°34'N, 83°31'W, 10 m a.s.l., 16.03.2001: (IR 1621); (IR 1654)

INBio Collection

Guanacaste: *Parque Nacional Guanacaste, Estación Cacao*: 10°55'29"N, 85°28'17"W, 1,100 m a.s.l., leg. Dunia Garcia, 01.12.1995: 1 ad. (INBio 1484977); 10°56'05"N, 85°28'14"W, 1,100 m a.s.l., leg. Dunia Garcia, 13.12.1995: 1 ad., 2 s.ads. (INBio 1488058); 10°55'43"N, 85°28'20"W, 1,000 m a.s.l., leg. malacological staff of INBio, 09.01.1995: 5 ads., 2 s.ads. (INBio 1539438); Sendero Los Naranjos, 10°55'38"N, 85°28'30"W, 1,100 m a.s.l., leg. Dunia Garcia, 13.09.1995: 9 ads., 3 s.ads. (INBio 1487886); Sendero Los Naranjos, 10°55'38"N, 85°28'30"W, 1,020 m a.s.l., leg. malacological staff of INBio, 14.09.1995: 8 ads. (INBio 1539463)

Parque Nacional Guanacaste, La Cruz, 9 km S de Santa Cecilia, Estación Pitilla: *10°59'25"N, 85°25'38"W, 700 m a.s.l.*: leg. Petrona Rios, 22.08.1994: 1 juv. (INBio 1480267); 1 ad. (INBio 1480284); *10°59'33"N, 85°25'46"W, 700 m a.s.l.*: leg. malacological staff of INBio, 10.09.1993: 1 ad. (INBio 1463737); *Lado S del Río Orosí, 10°59'25"N, 85°25'38"W, 700 m a.s.l.*: leg. Calixto Moraga, 23.08.1994: 1 ad., 2 s.ads. (INBio 1480341); leg. Marcos Moraga, 04.04.1995: 1 ad. (INBio 1484672); *Sendero Mena, 400 m W de la Estación Pitilla, 10°59'25"N, 85°25'51"W, 700 m a.s.l.*: leg. Calixto Moraga, 09.01.1994: 1 ad. (INBio 1480045); *Sendero a la Fila de Orosilito, 10°59'24"N, 85°25'38"W, 700 m a.s.l.*: leg. Petrona Rios, 09.01.1994: 1 ad. (INBio 1480270)

Parque Nacional Guanacaste, Sector Orosi (antes: *Maritza)*; sendero Casa Fram, 10°57'40"N, 85°29'45"W, 600 m a.s.l., leg. Zaidett Barrientos, 15.07.1996: 7 ads., 1 s.ad. (INBio 1487835)

Parque Nacional Rincón de la Vieja, Sector Santa María, 10°45'58"N, 85°18'19"W, 800 m a.s.l., leg. Dunia Garcia, 07.11.1996: 1 ad. (INBio 1488039)

Alajuela: *Reserva Biológica San Ramón*, 10°13'30"N, 84°35'17"W, 800 m a.s.l., leg. Gerardo Carballo, 14.12.1994: 1 ad. (INBio 1485501)

Sector Colonia Palmareña, San Ramón, 10°13'56"N, 84°33'12"W, 760 m a.s.l., leg. Gerardo Carballo, 04.11.1995: 1 ad. (INBio 1484803)

Limón: *Estación Cedrales*: *800 m W de la Estación Cedrales, 10°31'39"N, 83°43'33"W, 10 m a.s.l.*: leg. Elias Rojas, 22.11.1996: 1 ad. (INBio 1498586); *Finca Leiva, 1 km W de la estación Cedrales, 10°31'35"N, 83°43'33"W, 10 m a.s.l.*: leg. Elias Rojas, 17.10.1996: 1 juv. (INBio 1501467); 3 ads. (INBio 3398104); *Finca Montaña Grande, 10°31'39"N, 83°43'33"W, 10 m a.s.l.*: 600 m N de la estación Cedrales, leg. Elias Rojas, 18.10.1996: 3 ads., 1 s.ad. (INBio 1501218); 500 m N de la estación Cedrales, leg. Elias Rojas, 18.11.1996: 1 ad. (INBio 1498585)

Orillas del río Aguas Frías, 10°24'05"N, 83°36'00"W, 10 m a.s.l., leg. Elias Rojas, 29.11.1996: 20 ads., 15 s.ads., 8 juvs. (INBio 1487942); 1 ad. (INBio 1488002)

Sector Guápiles, 10°11'51"N, 83°51'22"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 08.03.2000: 1 ad. (INBio 3097951)

Refugio Nacional de Vida Silvestre Barra del Colorado, Barra del Colorado, Estación Sardinas: *10°38'52"N, 83°43'52"W, 50 m a.s.l.*: 10.02.1994: 1 ad., 1 s.ad. (INBio 1484009); 12.10.1994: 1 ad. (INBio 1484371); 16.10.1994: 1 ad. (INBio 1484012); 22.10.1994: 6 ads. (INBio 1485286) (all leg. Flor Araya); *10°39'11"N, 83°44'21"W, 15 m a.s.l.*: 13.01.1994: 2 ads., 1 s.ad. (INBio 1478019); 16.04.1994: 1 ad. (INBio 1477917) (all leg. malacological staff of INBio)

Refugio Nacional de Vida Silvestre Barra del Colorado, Pococí, Colorado, Sector Cerro Cocorí, 30 km N de Cariari, 10°35'39"N, 83°42'59"W: *160 m a.s.l.*: leg. malacological staff of INBio, 10.12.1993: 2 ads. (INBio 1465444); 2 ads. (INBio 1465444); *150 m a.s.l.*: leg. malacological staff of INBio, 04.10.1994: 3 ads. (INBio 1478057); 3 ads. (INBio 1478057); 3 ads. (INBio 1478057)

Cartago: *Parque Nacional Barbilla*: Orilla de río Dantas, cerca de la estación principal, 09°58'23"N, 83°27'03"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 26.10.2000: 1 ad. (INBio 3316138); Sector de la Estación de Barbilla, 09°57'58"N, 83°27'41"W, 480 m a.s.l., leg. Alexander Alvarado Mendez, 06.09.2000: 1 ad. (INBio 3100215)

Puntarenas: *Parque Nacional Corcovado, Estación Sirena*, 08°28'52"N, 83°35'32"W, 5 m a.s.l., leg. Mario Chinchilla, 23.03.1995: 1 ad. (INBio 1485052)

Other Sources

COSTA RICA

Alajuela: Carriblanco [Cariblanco, about 10°17'N, 84°12'W], C.H. Lancester (BMNH 1905.3.31.4)

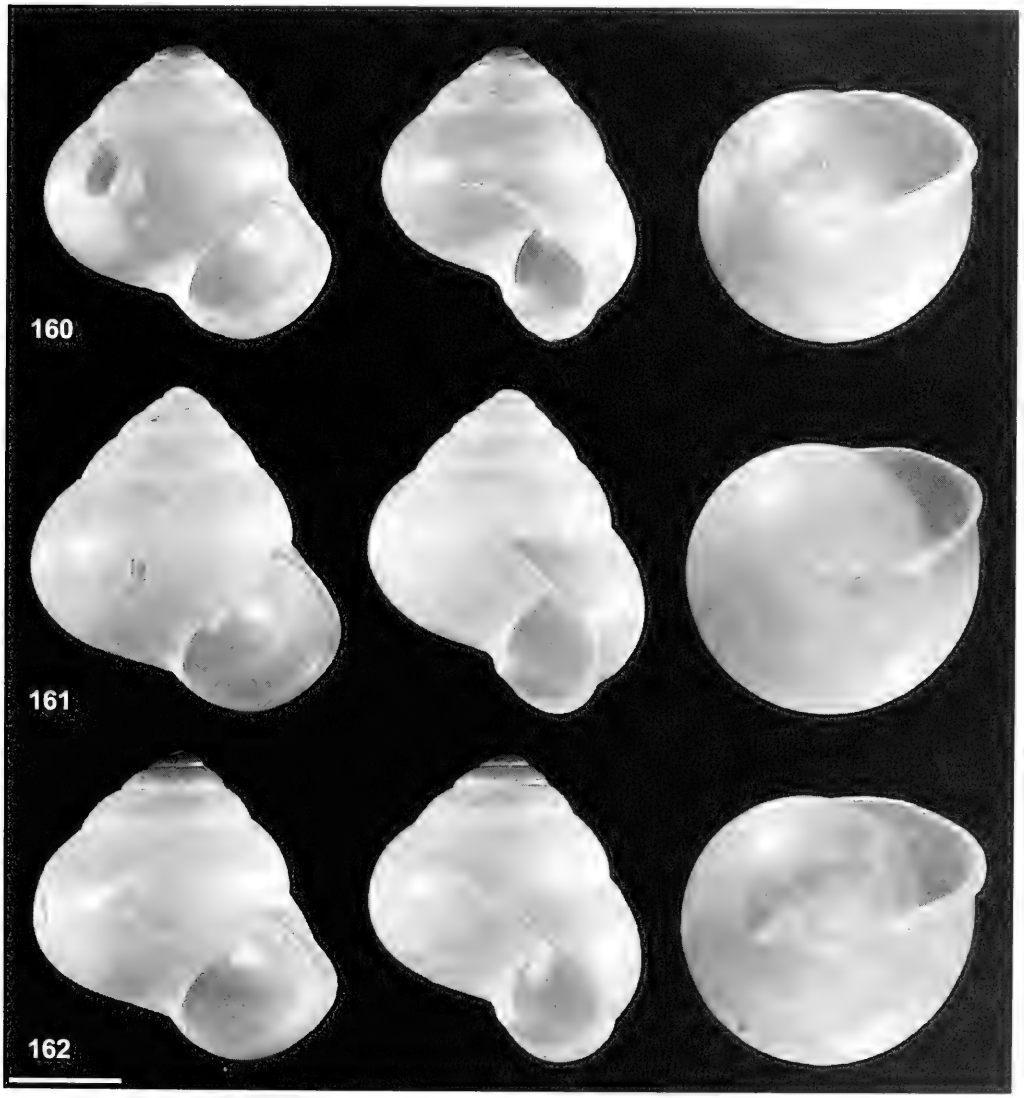
Heredia: Río Frio, Standard Fruit Co., 10°20'N, 83°53'W, leg. Michael J. Corn,

05.12.1969: 1 ad. (UF 217595); Río Frio [about 10°20'N, 83°53'W], leg. Michael J. Corn, 20.02.1970: 1 ad. (UF 217596);
Costa Rica, without locality further specified: *ex* Sowerby & Fulton: 2 ads. (UF 243507: 2 of 3 spec.)

NICARAGUA:
Zelaya Norte: Cerro Saslaya, Bosawas, leg. Zamira Guevara M., 04.1999 (IR 3137)

Description

Shell (Figs. 160–162, 336F–H): Conical, thin and fragile, medium to small sized, semi-transparent and shiny. Color: basic color unicolored, more or less intensively yellow, apical whorls sometimes crimson; last whorl tinged with orange-brownish some distance from aperture, sometimes also at the umbilical area. Surface textured with fine and



FIGS. 160–162. *Helicina gemma*. FIG. 160. Cacao, IR 1333, height 6.6 mm. FIG. 161. Las Pavas, IR 1460, height 7.3 mm. FIG. 162. Siquirres, IR 1536, height 7.0 mm; scale bar 2.5 mm.

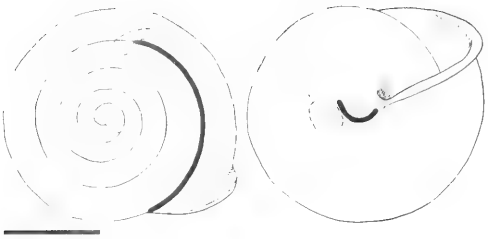


FIG. 163. Axial cleft and muscle attachments of *Helicina gemma*, IR 947; scale bar 2.5 mm.

regular growth lines (Fig. 164), causing the glossy appearance. Embryonic shell with about 1 whorl; $3^5/_8$–$4^3/_8$ (lectotype: 4¼) subsequent whorls convex; last whorl very evenly rounded at the periphery; whorls equally extending in size, forming a very regular, pointed spire. Suture moderately impressed. Aperture oblique and curved backwards, last whorl regularly descending towards the aperture and inserting a little below the periphery. Outer lip in continuation of the whorl of a bright orange color, slightly thickened and very narrowly expanded and reflexed. Transition to columella continuous with a slight notch. Columella slightly curved; transition to the body whorl without any groove. Basal callus very weakly developed and slightly granulated.

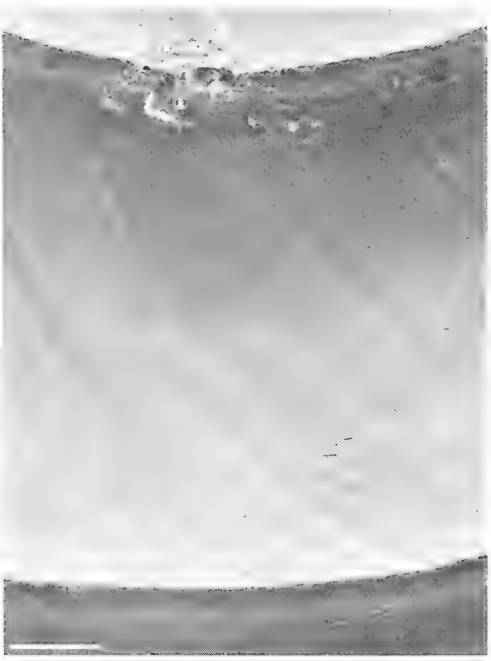


FIG. 164. Teleoconch surface structure of *Helicina gemma*, 2nd whorl; scale bar 100 µm.

Internal Shell Structures: (Fig. 163)

Teleoconch Surface Structure (Fig. 164): The surface structure of *Helicina gemma* is described above representing the general scheme: about ½ whorl exhibits transitional structure and subsequently oblique diverging grooves; the rest of the shell is smooth with only fine growth lines.

Embryonic Shell: The embryonic shell of *Helicina gemma* approaches the structure of *H. funcki* with larger pits and similarly sized interspacings. The pattern is relatively constant within a population as well as at different localities (investigated: Cacao, Las Pavas, Tortuguero, Siquirres) (Fig. 165). The diameter (range and mean value) increases with the altitude of the locality.
Diameter: 925 µm (± 23) (900–960) (n = 10) (IR 786, IR 1333, Cerro Cacao); 845 µm (± 28) (760–900) (n = 24) (IR 1275, Las Pavas); 808 µm (± 25) (740–860) (n = 32) (IR 1635, Siquirres); 800 µm (BMNH 1903.5.4.2, lectotype).

Operculum (Fig. 166): Very slightly calcified, calcareous plate covering only part of the outer surface. Color yellowish to horny-amber-reddish, only near the columella whitish or transparent. Columellar side slightly regular S-shaped, upper end acute and pointed, lower end continuously changing into outer margin.

Animal (Figs. 338C–E): The color of foot and head is constant in all populations, whereas the mantle pattern is subject to variation. The sole is whitish yellow; the dorsal part and upper side of the head region, including tentacles and the dorsal portion of the foot, are greyish to black. In all specimens from the Cerro Cacao and near Volcán Arenal, the mantle is unicolored and pale, whereas in the populations from Las Pavas, Tortuguero and Siquirres such forms are very rare. Instead, the mantle pigmentation displays a special pattern: a greyish-blackish basic color mottled with whitish dots. In most

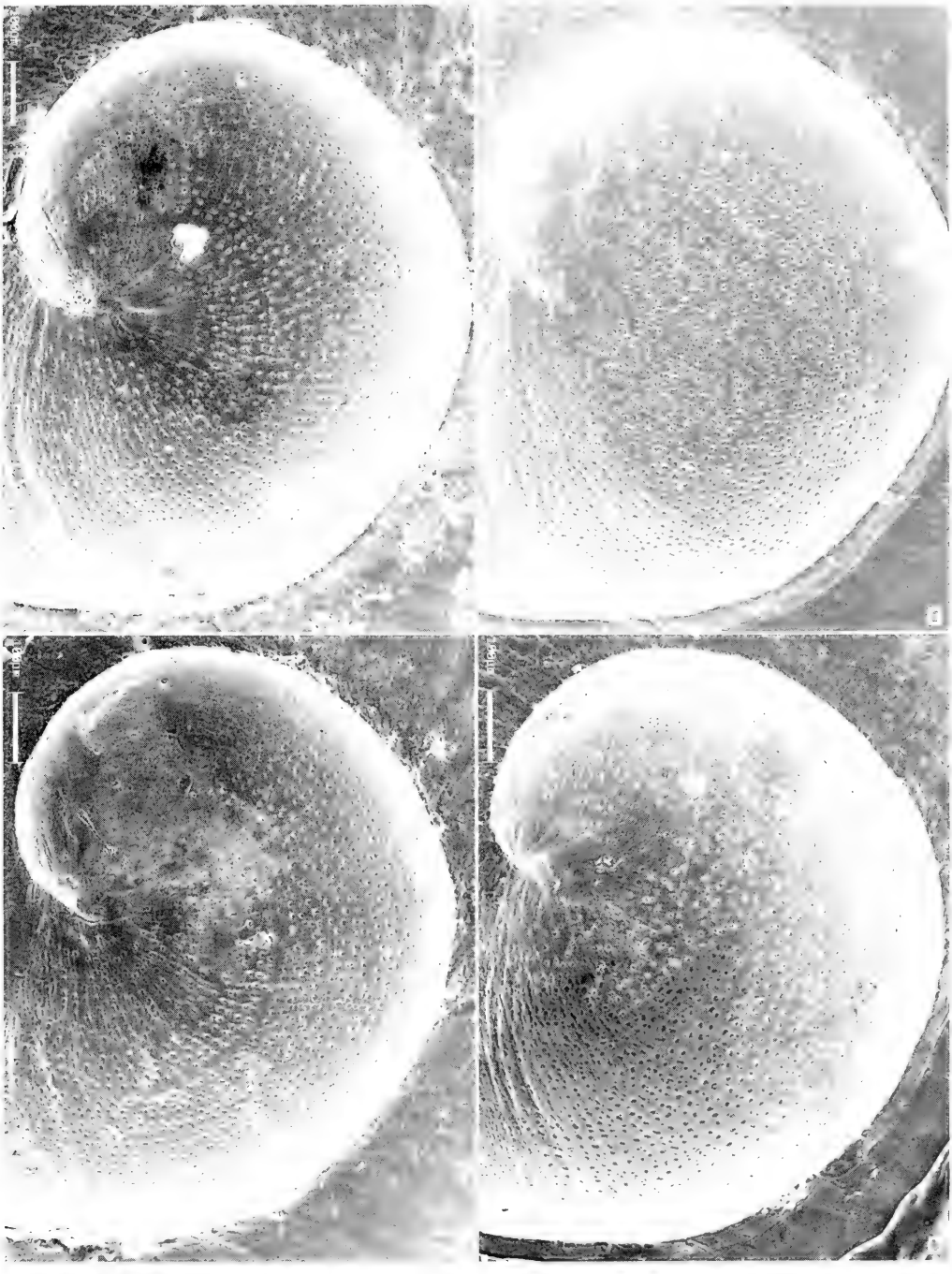


FIG. 165. Embryonic shell of *Helicina gemma*. A. Cerro Cacao, IR 786. B. Las Pavas, IR 1460. C. Tortuguero, IR 1654. D. Siquirres, IR 1618; scale bar 100 µm.

FIG. 166. Operculum of *Helicina gemma*, IR 947; scale bar 1 mm.

cases, these dots are so numerous that only a network of thin dark lines is visible. The mantle pigmentation is clearly visible through the thin shell.

Radula (Figs. 167, 168): Sometimes B- and C-central with 3–7 or about 3 cusps respectively, Figures 167A and 168 show exemplary such variations. Comb-lateral with (7–) 8–9 cusps, cusps on marginals rapidly increasing in number. Radula with about 62–85 rows of teeth.

Female Reproductive System (Figs. 169–171): The receptaculum seminis is quite large and drop-shaped. The prominently developed bursa copulatrix consists of a few relatively large, simple and equal-sized lobes, sometimes further subdivided. They are only occasionally smaller and more numerous. The provaginal sac is simple, and its stout stalk is shorter than in *Helicina funcki*. In comparison to the apical complex, the pallial oviduct is short. It is transversally constricted and often exhibits an additionally longitudinal furrow. Specimens from Las Pavas, Tortuguero and Siquirres are similar; the single female dissected from the Cerro Cacao has a smaller bursa copulatrix (Fig. 170A).

Morphometry and Sexual Dimorphism (Table 10, Figs. 172–176)

The available material of *Helicina gemma* is comparatively comprehensive, and four populations for anatomical investigations from distant sites were collected.

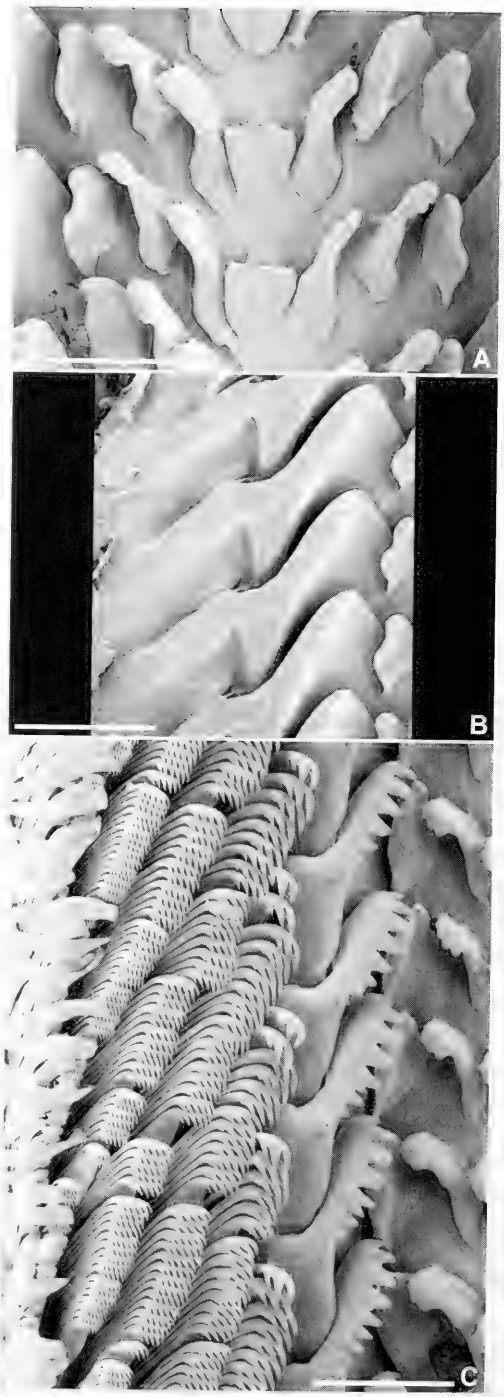


FIG. 167. Radula of *Helicina gemma*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

Whereas the three upper localities of the collection IR and the collection INBio respectively (Figs. 172–176) belong to the northwestern Caribbean slopes, the others come from the eastern plain. The type locality is situated between these sites.

All populations included from the INBio collection (Figs. 172–176, below thick line) that could not be analyzed for their sex were separated, as in *H. beatrix*, to avoid artificially high deviations of measurements with mixed sexes.

Morphometry: The variations among the different populations for the different measurements are quite constant. The size differences correspond to the origin of the specimens. "Cacao" (IR and INBio), "Las Pavas", "Volcán Arenal" and "Orosi" are very similar to each other; only the shell size of the population "Pitilla" is somewhat smaller. Except for Tortuguero which is very close to the sea, *Helicina gemma* becomes bigger in the northeastern Caribbean lowlands. More to the south, near southern limit of known distribution, the size declines (Siquirres). The lectotype, higher than the average shell of the populations compared, has an intermediate size, suggesting that it is a female. As in some samples of *H. funcki*, the corresponding mean values of the two samples from "Cacao" treated separately support the reliability of results gained with small samples sizes.

Following the suggestion that the shells become larger in the lowlands, the average minor diameter was plotted against the altitude of the sites (Fig. 178). The values indicate a slight decline of the size with increasing altitude. The difference amounts about 10% of the shell size of the population with the largest individuals, which is only 5% less than in *H. funcki* but which is yet found up to 1,500 m.

Sexual Dimorphism: All measurements clearly show a different range for both sexes, with the females being bigger. Only in populations with a high sample size (Siquirres, Las Pavas) do the extrema overlap a little, this being illustrated for the original set of data of height and minor diameter for the populations "Las Pavas" and "Siquirres" (Figs. 179, 180). The volume of the males is only about $^2/_3$ of that of the females. The differences displayed for the populations are very constant for each measurement. As explained in *H. beatrix*, the well-developed sexual dimorphism allows a separation of sets of mixed data. (illustrated for Río Aguas Frías, Fig. 181)

The lectotype is assumed to be female, because it seems very unlikely that the type (type lot) is extraordinarily big in a species of low variation. Furthermore, the paralectotypes are smaller.

Habitat

Helicina gemma is an arboreal species, mainly climbing and aestivating on the lower

FIG. 168. Radula of *Helicina gemma*, centrals; scale bar 50 µm.

FIG. 169. Female reproductive system of *Helicina gemma*, IR 1275; scale bar 1 mm.

FIG. 170. Variability of the female reproductive system of *Helicina gemma*, populations from A. Cerro Cacao, IR 786. B. Las Pavas, IR 947, IR 1275; scale bar 2 mm.

and sometimes upper side of leaves. As observed for *H. beatrix*, a special preference of certain plant species could not be observed. The predominant presence appears to depend on the species composition of the undergrowth on whose leaves the species were found. On the Cerro Cacao several small-leafed plants provide a crawling and foraging surface for the snails, whereas in Las Pavas Heliconiaceae and different palms represent a good place to search for *H. gemma*. In Siquirres, specimens were often seen aestivating also on the upper surface of nearly every kind of plant composing the secondary growth near a small creek. On one occasion, the species was found in dead decomposing *Cecropia*-leaves on the ground in the rain forest.

Distribution

The species is limited to southern Central America. The most northern record comes from the Cerro Saslaya in Nicaragua, adjacent to the Costa de Miskitos stretching along the Caribbean coast. The southern limit is reached around Siquirres and Parque Nacional de Barbilla, the northeastern foothills of the Cordillera de Talamanca. *Helicina gemma* possibly occurs a little further the south, but the data suggest that it is finally absent in the Valle de Talamanca or even in the Valle de Estrella, because the lower regions which are normally inhabited by the species have been fairly well investigated, and *H. gemma* has not been reported.

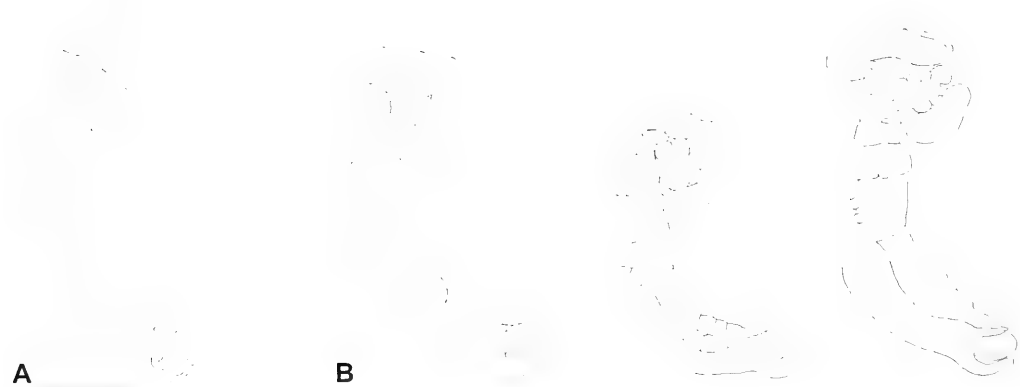


FIG. 171. Variability of the female reproductive system of *Helicina gemma*, populations from A. Tortuguero, IR 1654. B. Siquirres, IR 1652; scale bar 2 mm.

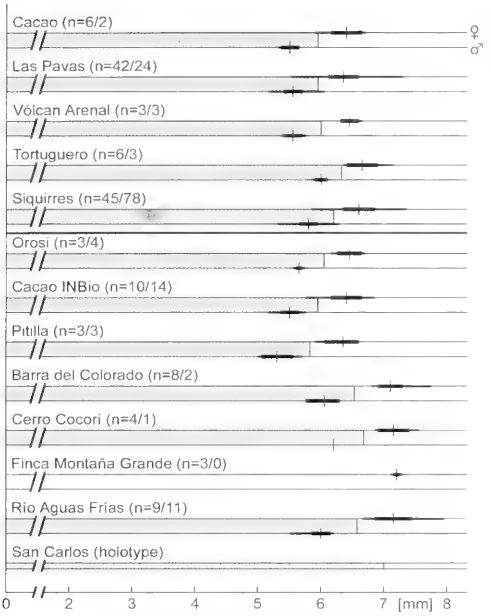


FIG. 172. Shell height of different populations of *Helicina gemma* in Costa Rica according to Table 10; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Orosi, Cacao INBio, Pitilla, Barra del Colorado, Cerro Cocorí, Finca Montaña Grande, and Río Aguas Frías not determined anatomically (see text).

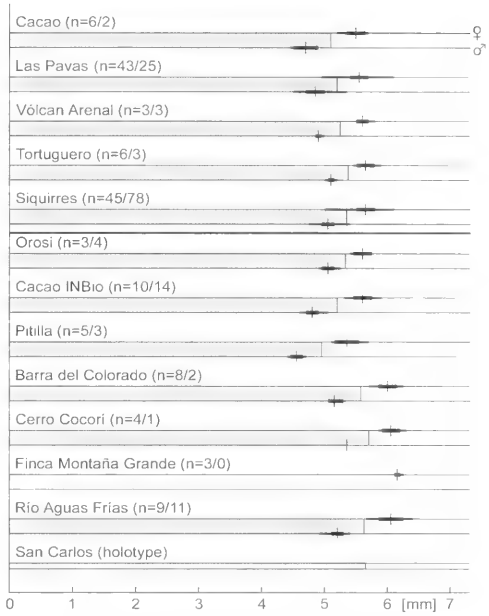


FIG. 173. Minor diameter of shell of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

In Costa Rica, *H. gemma* is confined to the Caribbean plain and the adjacent mountain slopes (Fig. 182). The highest altitude is reached in the northern Cordillera de Guanacaste on the Cerro Cacao at about 1,100 m, where it just crosses the chain of volcanoes. In this region, the higher elevated areas still provide a suitable climate on the otherwise drier Pacific slopes. The absence in the intensively searched area around Monteverde and its presence in the region of the Volcán Arenal and San Ramón at lower altitudes provides evidence that *H. gemma* does not occur much above 1,200 m. In the Caribbean lowlands it is or was probably fairly well distributed although not directly visible on the map. On one hand, vast areas have been deforested and used for agriculture, most probably causing a massive habitat loss, because the species has thus far only been found in pri-

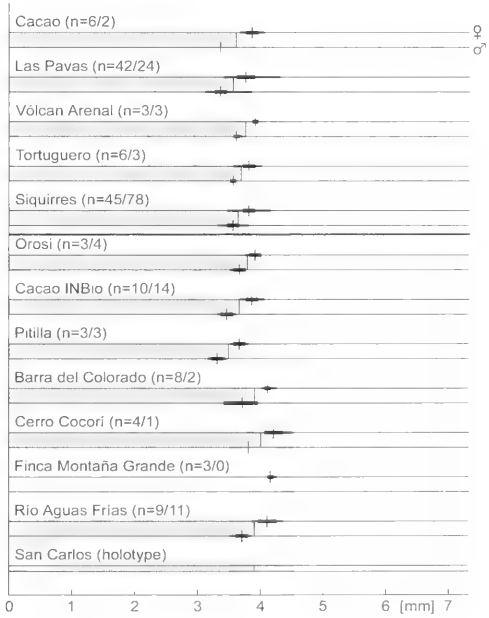


FIG. 174. Expansion of outer lip of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

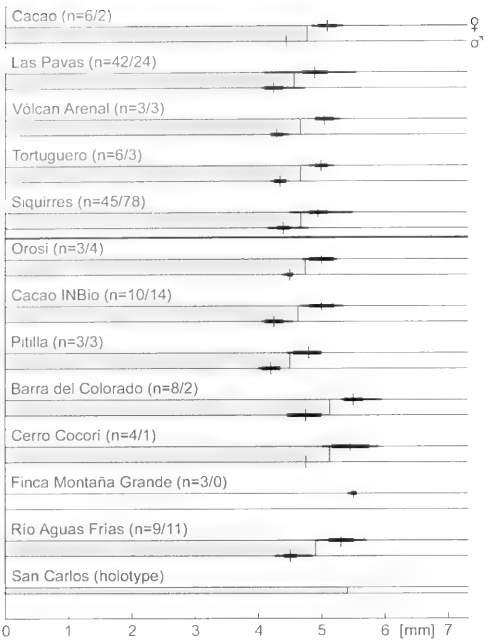


FIG. 175. Height of last whorl of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

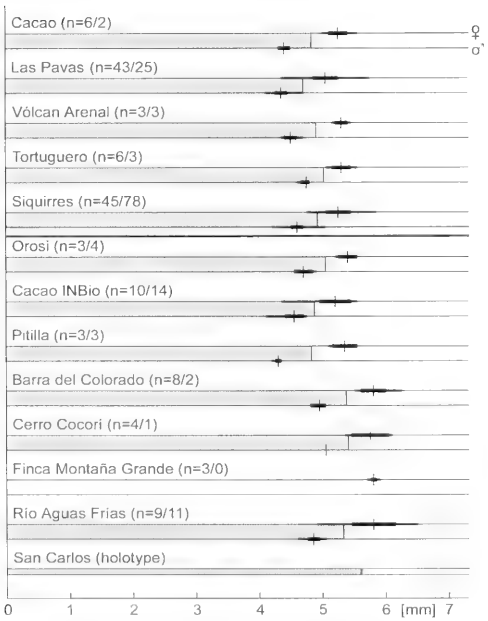


FIG. 176. Height of columellar axis of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

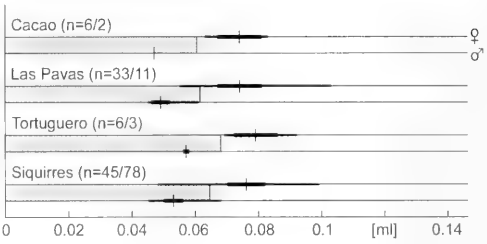


FIG. 177. Shell volume of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

mary or secondary forest or forest-like habitats. On the other hand, investigations (especially INBio's) focus on protected areas compassing mainly mountainous terrain (watersheds and volcanoes). The only exception for the lowlands is the zone of Colorado – Tortuguero on the NE coast. The pattern of distribution is very similar to that of *H. funcki*, except for the fact that the latter has a wider range and obviously a higher ecological tolerance.

Discussion

The color of the shells varies among the different populations in respect to the basic whorl color. Specimens from the Arenal area (volcano and Las Pavas) are pale yellow to even whitish-transparent, whereas the populations of the Caribbean lowlands (Siquirres, Tortuguero, Cerro Cocorí, Barra del Colorado) and Pitilla are bright yellow. Only specimens from the Cacao exhibit a strong tendency towards brownish shells, which is otherwise only very exceptionally observed in the Siquirres population (about 3 out of 120 specimens). The orange aperture is a common and constant character of all specimens, as is the crimson apex of a part of each population.

Preston (1903) compared *Helicina gemma* to *H. oweniana* and recognized the greater convexity (deeper impressed sutures) and fewer whorls. He also stated that the orange color of the outer lip extends further up the last whorl. This is verified by the study of syntypes of *H. oweniana*. Furthermore, *Helicina oweniana* is more solid and larger, the outer lip is very straight and perpendicularly expanded, whereas in *H. gemma* it is narrowly reflexed and curved backwards.

At the time of von Martens' (1890–1901) and Biolley's (1897) reports on the Costa Rican land molluscs, *Helicina oweniana* and subspe-

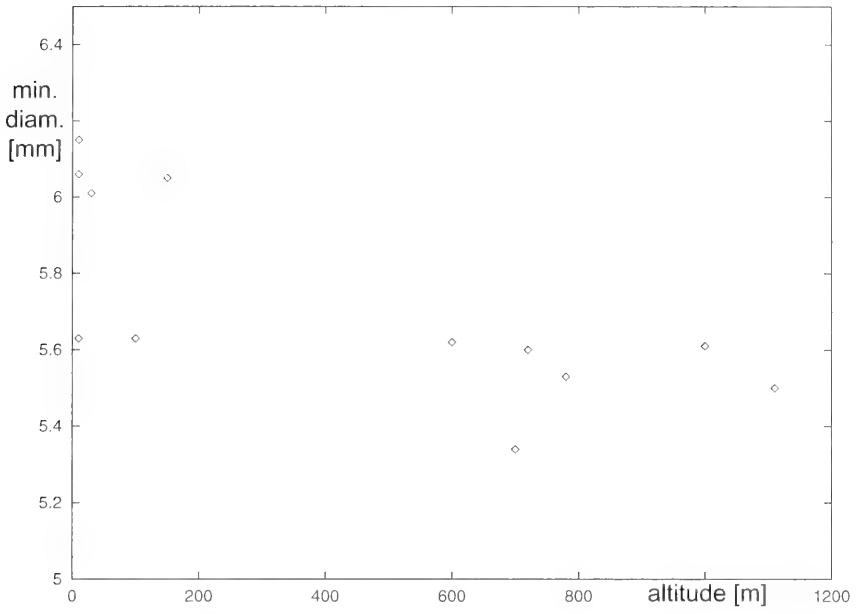


FIG. 178. Relation of minor shell diameter (females used) to altitude of the locality of the different populations of *Helicina gemma* in Costa Rica.

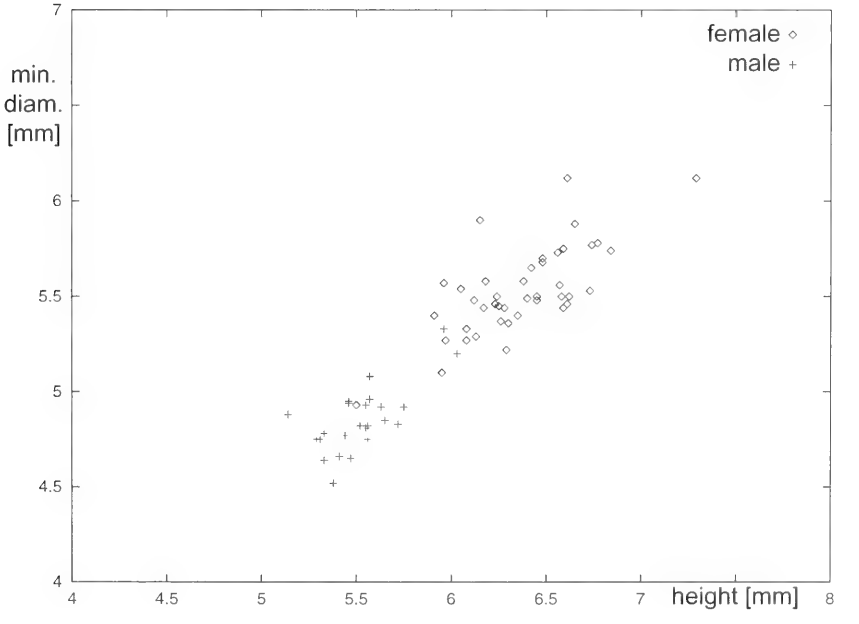


FIG. 179. Range of measurements in females and males of *Helicina gemma* exemplary for height and minor diameter in the population from Las Pavas.

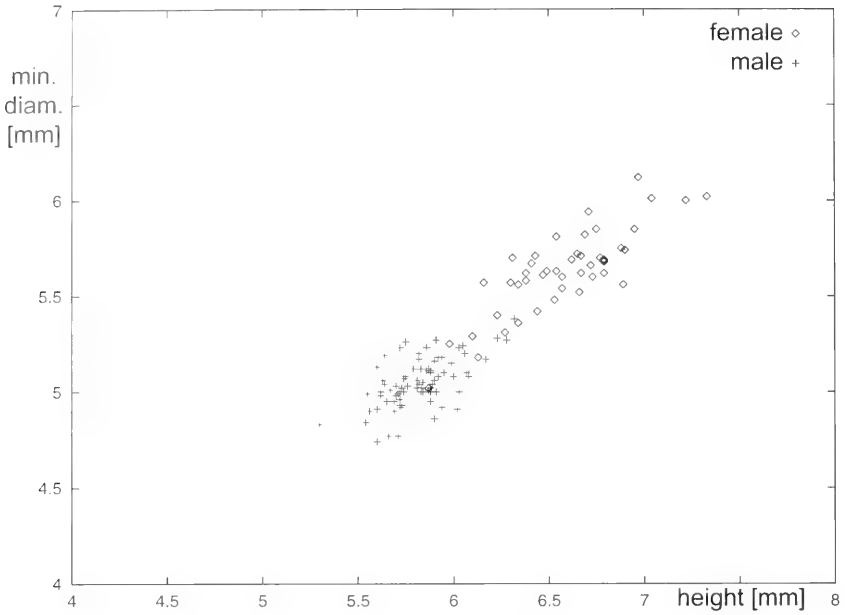


FIG. 180. Range of measurements in females and males of *Helicina gemma* exemplary for height and minor diameter in the population from Siquirres.

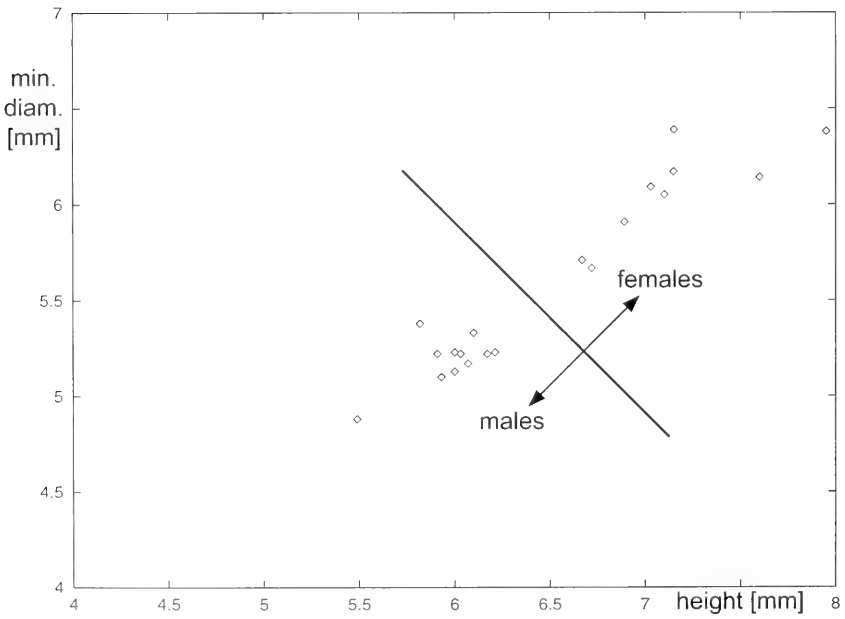


FIG. 181. Plot of measurements for height and minor diameter for individuals of *Helicina gemma* of unknown sex, exemplary for the population of Río Aguas Frías and the separation proposed.

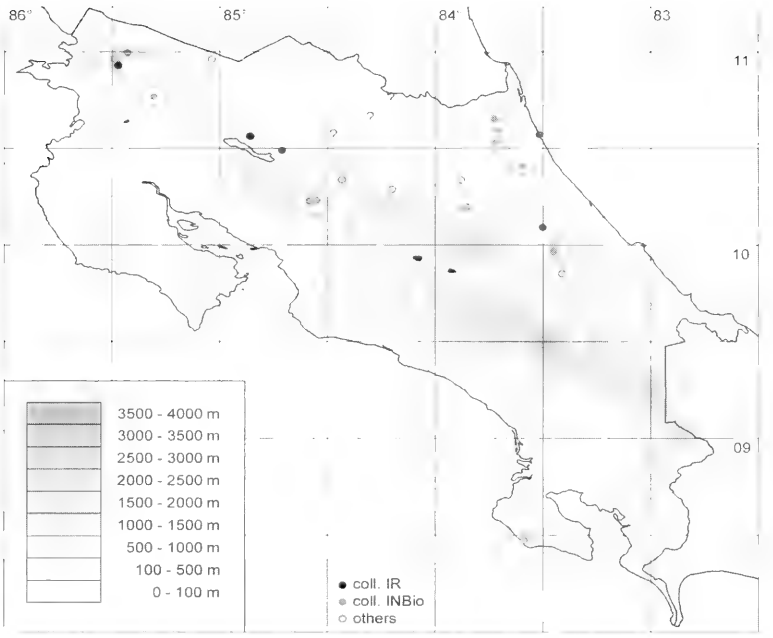


FIG. 182. Records of *Helicina gemma* in Costa Rica.

TABLE 10. Measurements of different populations of *Helicina gemma* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals of all populations included from the collection of INBio (both lower rows and Orosi) not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		"Tortuguero" (altitude 10 m) lots IR 1621, IR 1654					"Siquirres" (altitude 100 m) lots IR 1536, IR 1618, IR 1635, IR 1650, IR 1652				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.67	0.25	6.33	7.13	6	6.58	0.24	5.87	7.33	45
Height	m	6.00	0.09	5.87	6.08	3	5.82	0.14	5.30	6.32	78
Maj. diam.	f	6.05	0.15	5.90	6.28	6	6.06	0.18	5.38	6.55	45
Maj. diam.	m	5.50	0.05	5.43	5.56	3	5.49	0.12	5.20	5.83	78
Min. diam.	f	5.63	0.13	5.45	5.88	6	5.63	0.16	5.02	6.12	45
Min. diam.	m	5.12	0.06	5.02	5.18	3	5.05	0.10	4.74	5.38	78
Outer lip	f	3.80	0.12	3.57	3.98	6	3.81	0.12	3.43	4.13	45
Outer lip	m	3.55	0.05	3.50	3.62	3	3.54	0.08	3.32	3.79	78
Last whorl	f	4.98	0.12	4.82	5.22	6	4.96	0.16	4.48	5.52	45
Last whorl	m	4.34	0.09	4.22	4.47	3	4.42	0.10	4.13	4.81	78
Col. axis	f	5.31	0.17	5.03	5.57	6	5.25	0.19	4.74	5.84	45
Col. axis	m	4.74	0.09	4.60	4.82	3	4.59	0.12	4.19	5.04	78
Weight	f	0.015	0.002	0.012	0.018	6	0.022	0.003	0.012	0.032	45
Weight	m	0.015	0.001	0.014	0.017	3	0.019	0.004	0.011	0.031	78
Volume	f	0.079	0.007	0.069	0.092	6	0.076	0.006	0.048	0.099	45
Volume	m	0.057	0.001	0.056	0.058	3	0.053	0.003	0.045	0.068	78

(*Continues*)

(Continued)

		"Cacao" (altitude 1110 m) lots IR 786, IR 1333					"Las Pavas" (altitude 760–800 m) lots IR 947, IR 948, IR 1275, IR 1460, IR 1462, IR 1463				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.41	0.24	5.90	6.72	6	6.36	0.25	5.50	7.29	42
Height	m	5.48	0.17	5.31	5.64	2	5.53	0.15	5.14	6.03	24
Maj. diam.	f	5.92	0.17	5.66	6.16	6	5.98	0.19	5.42	6.71	43
Maj. diam.	m	5.27	0.10	5.17	5.37	2	5.31	0.16	5.03	5.90	25
Min. diam.	f	5.50	0.16	5.21	5.70	6	5.53	0.17	4.93	6.12	43
Min. diam.	m	4.68	0.22	4.46	4.90	2	4.85	0.13	4.52	5.33	25
Outer lip	f	3.85	0.12	3.65	4.03	6	3.77	0.13	3.38	4.28	42
Outer lip	m	3.37	0.00	3.37	3.37	2	3.37	0.12	3.11	3.86	24
Last whorl	f	5.10	0.14	4.84	5.33	6	4.90	0.20	4.10	5.55	42
Last whorl	m	4.47	0.01	4.46	4.48	2	4.26	0.17	4.03	4.75	24
Col. axis	f	5.25	0.14	5.02	5.57	5	5.05	0.20	4.34	5.77	43
Col. axis	m	4.39	0.10	4.29	4.48	2	4.34	0.12	4.08	4.72	25
Weight	f	0.017	0.004	0.011	0.024	6	0.016	0.002	0.011	0.021	42
Weight	m	0.015	0.003	0.012	0.017	2	0.014	0.003	0.007	0.025	21
Volume	f	0.074	0.007	0.063	0.083	6	0.073	0.007	0.050	0.103	42
Volume	m	0.047	0.000	0.047	0.047	1	0.047	0.003	0.040	0.061	21

		"Vólcan Arenal" (altitude 720 m) lots IR 387, IR 740, IR 885, IR 1284					"Orosi" (altitude 600 m) lot INBio 1487835				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.46	0.16	6.32	6.70	3	6.47	0.20	6.17	6.69	3
Height	m	5.54	0.15	5.35	5.77	3	5.63	0.06	5.56	5.74	4
Maj. diam.	f	6.08	0.10	5.92	6.16	3	6.17	0.24	5.81	6.53	3
Maj. diam.	m	5.39	0.04	5.32	5.43	3	5.49	0.15	5.20	5.75	4
Min. diam.	f	5.60	0.12	5.50	5.78	3	5.62	0.16	5.38	5.77	3
Min. diam.	m	4.92	0.06	4.84	5.01	3	5.04	0.10	4.89	5.24	4
Outer lip	f	3.90	0.05	3.85	3.97	3	3.89	0.09	3.75	3.98	3
Outer lip	m	3.61	0.06	3.54	3.70	3	3.63	0.11	3.48	3.76	4
Last whorl	f	5.07	0.16	4.90	5.31	3	4.98	0.20	4.69	5.25	3
Last whorl	m	4.32	0.10	4.22	4.48	3	4.48	0.07	4.40	4.56	4
Col. axis	f	5.28	0.10	5.13	5.43	3	5.40	0.14	5.19	5.54	3
Col. axis	m	4.50	0.12	4.36	4.68	3	4.68	0.15	4.56	4.90	3
Weight	f	0.022	0.000	0.022	0.022	1	-	-	-	-	-
Weight	m	-	-	-	-	-	-	-	-	-	-

(Continues)

cies were the only known Central American orange-lipped Helicinidae, which is why they most likely assigned their Costa Rican orange-lipped Helicinidae to the subspecies *H. oweniana coccinostoma* or *H. o. anozona*. Both probably synonymous subspecies are more globular, with whorls a little more convex than the nominal subspecies, thus rather resembling *H. gemma*. But the differences to *H. gemma* mentioned above refer to the subspecies as well. Unfortunately, the original material of these records has not yet been rediscovered to check this assumption, but it seems plausible.

(*Continued*)

		"Cacao INBio" (altitude 1000–1100 m) lots INBio 1484977, 1487886, 1488058, 1539438, 1539463					"Pitilla" (altitude 700 m) lots INBio 1463737, 1480045, 1480270, 1480284, 1480341, 1484672				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.38	0.23	5.74	6.84	10	6.33	0.28	5.91	6.59	3
Height	m	5.52	0.15	5.16	5.77	14	5.32	0.24	5.02	5.68	3
Maj. diam.	f	5.99	0.15	5.52	6.22	10	5.75	0.23	5.44	6.10	5
Maj. diam.	m	5.24	0.08	5.03	5.46	14	4.85	0.10	4.71	4.96	3
Min. diam.	f	5.61	0.16	5.29	5.92	10	5.34	0.20	5.08	5.69	5
Min. diam.	m	4.80	0.11	4.60	5.04	14	4.56	0.09	4.42	4.66	3
Outer lip	f	3.85	0.10	3.65	4.04	10	3.64	0.11	3.50	3.81	3
Outer lip	m	3.43	0.08	3.28	3.61	14	3.30	0.10	3.17	3.44	3
Last whorl	f	5.00	0.18	4.67	5.35	10	4.80	0.24	4.44	4.98	3
Last whorl	m	4.27	0.14	4.05	4.53	14	4.22	0.16	3.98	4.37	3
Col. axis	f	5.19	0.23	4.35	5.55	10	5.36	0.18	5.09	5.57	3
Col. axis	m	4.54	0.14	4.10	4.77	14	4.30	0.06	4.21	4.35	3

		"Barra del Colorado" (altitude 15–50 m) lots INBio 1477917, 1484009, 1484012, 1484371, 1485286					"Cerro Cocorí" (altitude 150 m) lots INBio 1465444, 1478057				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.10	0.22	6.81	7.75	8	7.16	0.26	6.83	7.55	4
Height	m	6.03	0.29	5.74	6.32	2	6.21	0.00	6.21	6.21	1
Maj. diam.	f	6.44	0.15	6.07	6.60	8	6.57	0.20	6.32	6.88	4
Maj. diam.	m	5.55	0.17	5.38	5.72	2	5.88	0.00	5.88	5.88	1
Min. diam.	f	6.01	0.14	5.69	6.27	8	6.05	0.16	5.83	6.32	4
Min. diam.	m	5.16	0.13	5.03	5.29	2	5.33	0.00	5.33	5.33	1
Outer lip	f	4.12	0.07	4.02	4.26	8	4.18	0.17	4.03	4.52	4
Outer lip	m	3.68	0.28	3.40	3.95	2	3.82	0.00	3.82	3.82	1
Last whorl	f	5.50	0.17	5.31	5.95	8	5.45	0.28	5.02	5.91	4
Last whorl	m	4.73	0.29	4.44	5.02	2	4.73	0.00	4.73	4.73	1
Col. axis	f	5.80	0.18	5.49	6.23	8	5.77	0.28	5.36	6.12	4
Col. axis	m	4.93	0.13	4.80	5.05	2	5.03	0.00	5.03	5.03	1

		"Finca Montaña Grande" (altitude 10 m) lot INBio 1501218					"Río Aguas Frías" (altitude 10 m) lot INBio 1487942				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.20	0.07	7.10	7.30	3	7.14	0.29	6.67	7.95	9
Height	m	-	-	-	-	-	5.98	0.14	5.49	6.21	11
Maj. diam.	f	6.63	0.07	6.53	6.74	3	6.56	0.10	6.22	6.78	9
Maj. diam.	m	-	-	-	-	-	5.64	0.10	5.30	5.91	11
Min. diam.	f	6.15	0.06	6.12	6.24	3	6.06	0.20	5.67	6.39	9
Min. diam.	m	-	-	-	-	-	5.19	0.09	4.88	5.38	11
Outer lip	f	4.17	0.06	4.08	4.26	3	4.11	0.13	3.86	4.35	9
Outer lip	m	-	-	-	-	-	3.69	0.09	3.48	3.85	11
Last whorl	f	5.48	0.04	5.42	5.53	3	5.32	0.21	4.90	5.72	9
Last whorl	m	-	-	-	-	-	4.50	0.12	4.26	4.84	11
Col. axis	f	5.82	0.06	5.72	5.88	3	5.81	0.35	4.88	6.49	9
Col. axis	m	-	-	-	-	-	4.85	0.11	4.58	5.03	11

The records for *H. oweniana* and *H. beatrix* by Monge-Nájera (1997) were checked in the INBio-collection and partially belong to *H. gemma*. For differences to *H. beatrix riopejensis* n. subsp. and *H. monteverdensis* n. sp. see under these taxa.

Helicina (*"Gemma"*) *monteverdensis* Richling, n. sp.

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* L. Pfeiffer, 1849]
Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [*non* Angas, 1879]

Type Material

Holotype: INBio 3542627, female (leg. I. Richling, 24.02.1999, *ex* IR 634)
Paratype 1: INBio 3542628, male (same data as holotype, 27.07.1999, *ex* IR 844)
Paratype 2: ZMB 103884, female (same data as holotype)
Paratype 3: ZMB 103885, male (same data as paratype 1)
Dimensions:
Holotype: 6.6/6.2/6.5/5.8/3.6/4.8/5.2 mm
Paratype 1: 5.9/5.5/5.8/5.1/3.6/4.6/4.8 mm
Paratype 2: 6.8/6.5/6.8/5.9/4.0/5.0/5.4 mm
Paratype 3: 5.6/5.7/6.1/5.1/3.6/4.6/4.5 mm

Type Locality

NW-Costa Rica, Puntarenas Province, Cordillera de Tilarán, near Monteverde, Zona Protectora Arenal-Monteverde, Reserva Biológica Bosque Nuboso Monteverde, Sendero Bosque Nuboso, about 10°18'08"N, 84°47'41"W, 1,550 m a.s.l., cloud forest.

Type Material of Synonymous Taxa or Similar Species

Helicina merdigera L. Pfeiffer, 1855

Helicina merdigera L. Pfeiffer, 1855: 102: Mexico: Vera Cruz (leg. Sallé, coll. Hugh Cuming)

Type Material: BMNH 20010752: leg. Sallé, coll. Hugh Cuming
The lot contains three specimens, of which one is completely fragmented except for the aperture with the operculum still inside. The two remaining shells are very similar to each other. The species was neither figured by the author nor does the description give any useful hints for the identification of the type. The slightly larger shell is **here selected as lectotype** (Fig. 183), the denticle at the transition of the basal outer lip into the columella is stronger developed. Whereas the paralectotype (Fig. 184) is whitish, it shows a tinge of yellowish-brown.
Dimensions:
Lectotype 20010752.1:
5.0/5.1/5.4/4.7/2.9/3.7/4.0 mm
Paralectotype 20010752.2–3 (latter fragmented): 4.5/5.0/5.3/4.5/3.0/3.4/3.7 mm

Type Locality: "Vera Cruz, Mexico".

Helicina fragilis Morelet, 1851

Helicina fragilis Morelet, 1851: 17 (not figured)

Type Material: BMNH 1893.2.4.809–12, coll. Morelet, purchased from H. Fulton
The Morelet collection was bought by H. Fulton and subsequently purchased by the BMNH. The "type" among the four syntypes (Figs. 185, 186) is marked with an "x" on the shell. This specimen is **here selected as lectotype** (Fig. 185). It matches best the dimensions given by Morelet. It is neither the largest nor the smallest specimen of the type lot.
Dimensions:
Lectotype 1893.2.4.809:
6.0/5.5/5.7/5.1/3.4/4.2/4.9 mm; 5 teleoconch whorls
Paralectotypes 1893.2.4.810–12:
7.2/6.6/7.0/6.1/4.1/5.2/5.9 mm; $4^{7}/_{8}$ teleoconch whorls
5.9/5.6/6.0/5.2/3.5/4.3/4.7 mm; $4^{3}/_{8}$ teleoconch whorls
5.2/5.2/5.6/4.8/3.2/3.9/4.1 mm; 4¼ teleoconch whorls

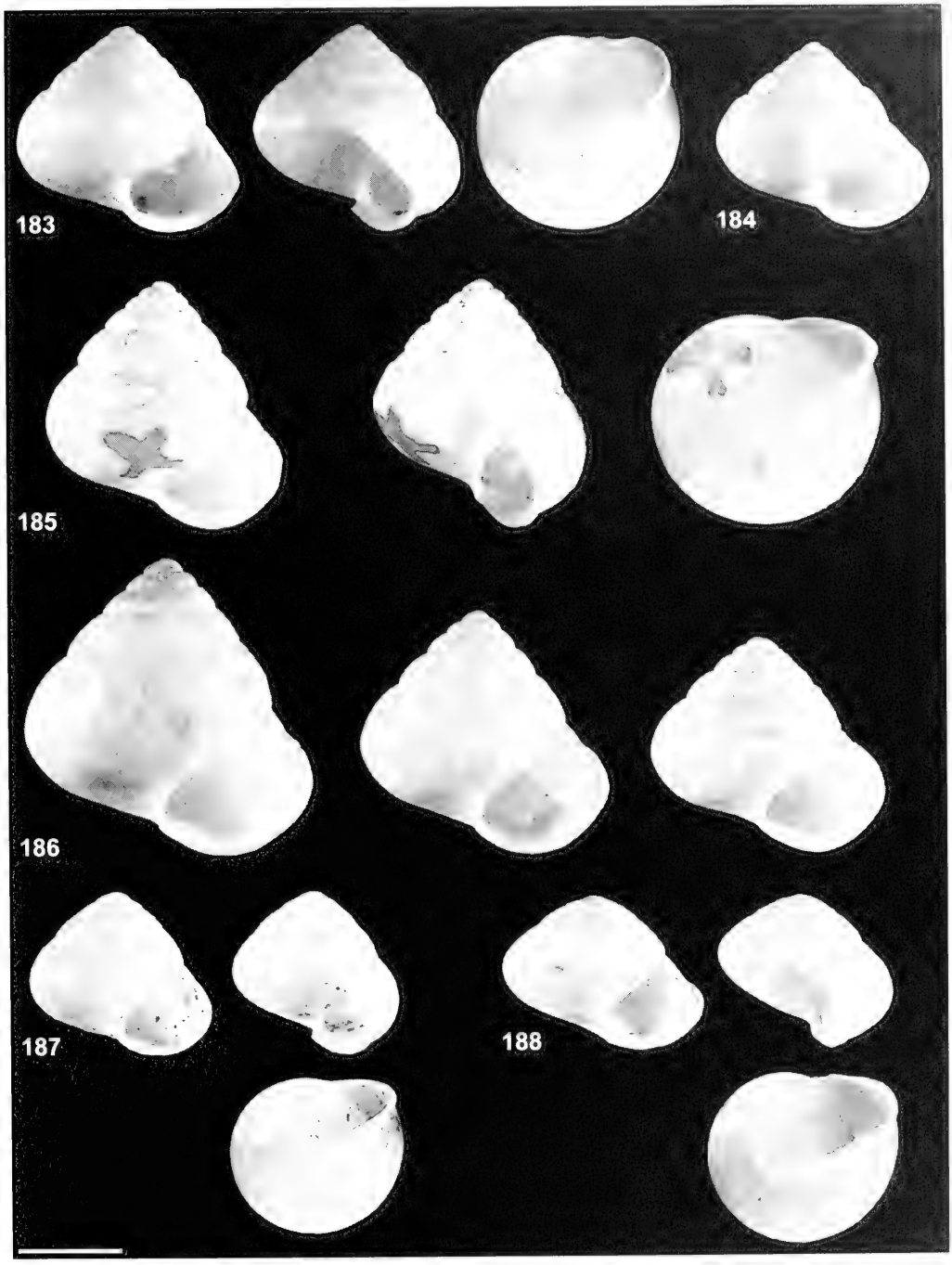
Type Locality: "sylvas Petenenses" [Guatemala: Petén Department].

Helicina mohriana L. Pfeiffer, 1861

Helicina mohriana L. Pfeiffer, 1861: 172–173

Type Material: Not located, probably lost.

Type Locality: Mexico, Orizaba (leg. Mohr) [State of Vera Cruz]



FIGS. 183–188. *Helicina* spp. FIG. 183. *Helicina merdigera*, BMNH 20010752.1, lectotype, height 5.0 mm. FIG. 184. *Helicina merdigera*, BMNH 20010752.2, paralectotype, height 4.5 mm. FIG. 185. *Helicina fragilis*, BMNH 1893.2.4.809, lectotype, height 6.0 mm. FIG. 186. *Helicina fragilis*, BMNH 1893.2.4.810–812, paralectotypes, height 7.2, 5.9, 5.2 mm. FIG. 187. *Helicina elata*, syntype, NHMB 15269, height 4.0 mm. FIG. 188. *Helicina diaphana*, probable syntype, BMNH 196282, height 3.7 mm; scale bar 2.5 mm.

Helicina elata Shuttleworth, 1852

Helicina elata Shuttleworth, 1852: 304

Type Material: Syntype NHMB 15269: leg. Jacot-Guillarmod (Fig. 187)
Shuttleworth stated "specimena pauca vidi", but his collection in the NHMB contains only a single specimen. He probably exchanged the others.
Dimensions:
Syntype: 4.0/4.3/4.3/3.8/2.4/2.9/3.1 mm

Type Locality: Mexico: Vera Cruz: Cordova [Cordoba].

Helicina diaphana L. Pfeiffer, 1852

Helicina diaphana L. Pfeiffer, 1852: 98: Honduras (leg. Mr. Dyson, coll. Hugh Cuming)

Type Material: Probable syntype BMNH 196282: Honduras (It was stated at the time of registration that it was possible that some original labeling from the back of the specimen board was not kept. i.e. MC initials and Dyson as collector.)
The assumption of the type status is supported by the fact that Rehder (1966) refers to a photograph of the syntype in the BMNH, probably the specimen was registered when he requested the photograph; the time period would make this seem likely. The specimen (Fig. 188) shows various details of the original description. The operculum is still inside the shell.
Dimensions:
Syntype?: 3.7/4.8/4.9/4.2/2.7/3.0/3.0 mm

Type Locality: "Honduras"

Examined Material

Leg. I. Richling

Guanacaste: *N Santa Elena, Sendero at Mirador Gerardo*, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l., 28.07.1999: (IR 855); (IR 856); 14.08.1999: (IR 929); (IR 930); 19.02.2000: (IR 1226); (IR 1228); (IR 1229); 24.02.2001: (IR 1416); (IR 1418); (IR 1419); (IR 1420)

Puntarenas: *Near Monteverde*, about 10°17'24"N, 84°48'04"W, 1 km before entrance on road to reserve, 1,500 m a.s.l.: 26.07.1999: (IR 825); 13.08.1999: (IR 920); (IR 921)
Zona Protectora Arenal-Monteverde: *Reserva Biológica Bosque Nuboso Monteverde (about 10°18'08"N, 84°47'41"W, 1,500-1,650 m a.s.l.)*: 27.07.1999: (IR 844); (IR 845); 18.02.2000: (IR 1196); (IR 1197); 25.02.2001: (IR 1436); *Sendero Bosque Nuboso*: 24.02.1999: (IR 634); (IR 636); *Sendero Roble*: 18.02.1998: (IR 302); *Sendero Chomogo*: 18.02.1998: (IR 296)
About 4 km N Santa Elena, Skywalk, 10°18'33"N, 84°49'42"W, 1,330 m a.s.l., 2702.1999: (IR 681)

INBio Collection

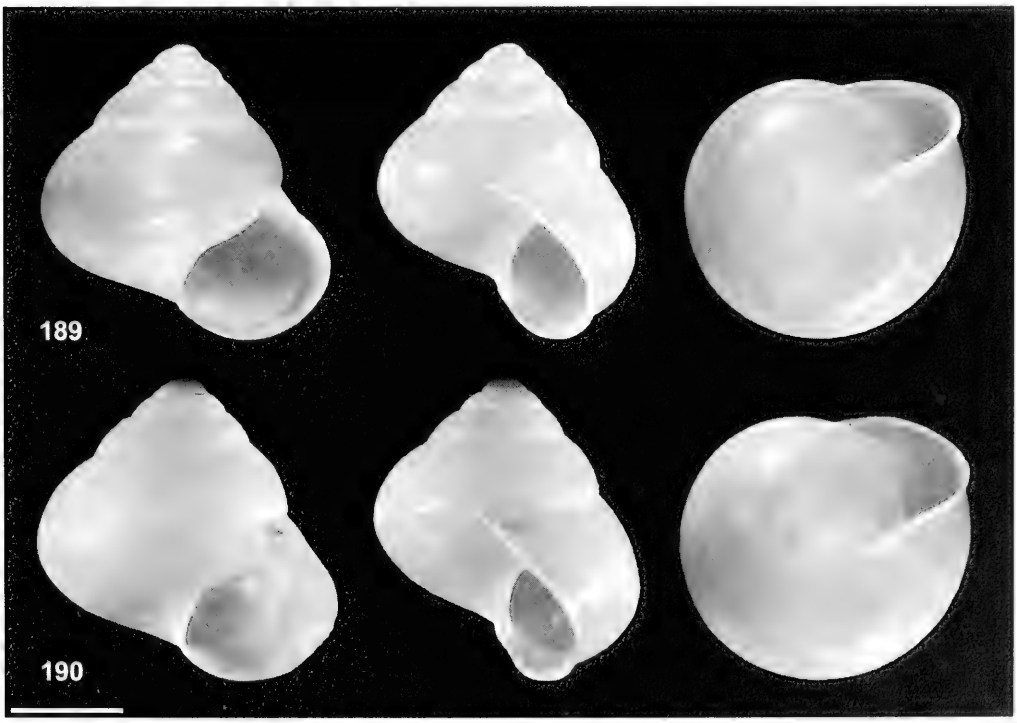
Guanacaste: *Zona Protectora Arenal-Monteverde, Santa Elena*: *Sendero Encantado, 10°21'57"N, 84°47'27"W, 1,400 m a.s.l.*: leg. Kattia Martinez, 13.07.1994: 4 ads., 6 s.ads., 7 juvs. (INBio 1479270); 3 ads., 6 juvs. (INBio 1479273); *Sendero Encantado, 10°21'57"N, 84°47'27"W, 1,200 m a.s.l.*: leg. Kattia Martinez, 21.06.1996: 3 ads., 3 s.ads., 2 juvs. (INBio 1487482); 2 ads. (INBio 1498545); *Sendero Rancho Alegre, 10°21'24"N, 84°47'47"W, 1,440 m a.s.l.*: leg. Kattia Martinez, 13.11.1994: 2 ads. (INBio 1485425); 1 ad., 1 s.ad. (INBio 1485431)
Zona Protectora Arenal-Monteverde: 1km NE de la casa de información Reserva Santa Elena, 10°21'05"N, 84°47'40"W, 1,550 m a.s.l.: leg. Alexander Alvarado Mendez, 12.01.2000: 3 ads., 2 s.ads. (INBio 3098462); Sendero Tabacón, 10°22'55"N, 84°47'40"W, 900 m a.s.l.: leg. Alexander Alvarado Mendez, 03.09.1999: 1 ad. (INBio 1501135)

Alajuela: *Zona Protectora Arenal-Monteverde*: Camino a El Valle, 10°19'44"N, 84°45'55"W, 1,580 m a.s.l.: leg. Kattia Martinez, 20.06.1996: 1 juv. (INBio 1498646); Estación Alemán, 10°18'11"N, 84°44'49"W, 940 m a.s.l.: leg. Dunia Garcia, 10.11.1994: 1 s.ad. (INBio 1475971); Refugio El Valle, 10°19'04"N, 84°46'41"W, 1,800 m a.s.l.: leg. Kattia Martinez, 11.01.1995: 2 ads., 1 s.ad., 2 juvs. (INBio 1498728)
Zona Protectora Arenal-Monteverde, Sector Peñas Blancas, Estación Alemán, 10°18'09"N, 84°44'52"W: *900 m a.s.l.*: leg. Kattia Martinez, 18.08.1994: 1 ad. (INBio 1480178); *1,140 m a.s.l.*: leg. Zaidett Barrientos, 10.11.1994: 2 ads., 1 juv. (INBio 1473354); 1 ad. (INBio 1473359)
Zona Protectora Arenal-Monteverde, *Reserva Biológica Bosque Nuboso Monteverde*: Sendero Pantanoso, 10°18'19"N,

84°47'10"W, 1,620 m a.s.l.: 08.11.1994: 1 s.ad., 1 juv. (INBio 1479473); 15.01.1995: 1 ad., 1 s.ad. (INBio 1498821); 04.04.1995: 1 ad. (INBio 1484024) (all leg. Kattia Martinez); leg. Alejandro Azofeifa, 04.04.1995: 2 juvs. (INBio 1484832)

Cartago: ?*Reserva Indígena Chirripó*, Zona de captación Río Humo, 09°42'47"N, 83°25'52"W, 1,550 m a.s.l., leg. Zaidett Barrientos, 27.06.1996: 1 ad., 4 s.ad.s, 1 juv. (INBio 1498787)

Puntarenas: *Zona Protectora Arenal-Monteverde, Reserva Biológica Bosque Nuboso Monteverde*: *Estación la Casona, 10°18'11"N, 84°47'50"W, 1,600 m a.s.l.*: leg. Kattia Martinez, 30.10.1996: 2 ads., 2 juvs. (INBio 1498680); 1 ad., 2 s.ads., 2 juvs. (INBio 1498684); *Sendero Bosque Eterno, 10°18'22"N, 84°47'40"W, 1,600 m a.s.l.*: 20.01.1995: 1 ad., 1 s.ad. (INBio 1483833); 04.04.1995: 4 ads., 4 s.ads., 1 juv. (INBio 1485231); 04.07.1995: 3 ads. (INBio 1485229); 19.06.1996: 1 ad. (INBio 1498693) (all leg. Kattia Martinez); *Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,600 m a.s.l.*:, 14.06.1994: 2 ads. (INBio 1466785); 16.07.1994: 1 ad., 1 s.ad. (INBio 1479239); 1 s.ad. (INBio 1479860); 16.09.1994: 2 ads., 1 s.ad. (INBio 1480117); 14.01.1995: 3 ads., 1 s.ad. (INBio 1498583); 22.06.1996: 2 ads., 1 juv. (INBio 1498519) (all leg. Kattia Martinez); *Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,520 m a.s.l.*: leg. Zaidett Barrientos, 14.10.1994: 1 ad., 1 juv. (INBio 1468138); 1 ad. (INBio 1468209); *Sendero Bosque Nuboso, 10°17'59"N, 84°47'43"W, 1,520 m a.s.l.*: leg. Alexander Alvarado Mendez, 03.02.1999: 1 ad. (INBio 1501428); *Sendero Chomogo, 10°18'22"N, 84°47'23"W, 1,690 m a.s.l.*: leg. Kattia Martinez, 13.08.1994: 1 ad. (INBio 1480143); 1 juv. (INBio 1480156); *Sendero Chomogo, 10°18'22"N, 84°47'23"W, 1,640 m a.s.l.*: 10.10.1994: 1 ad., 2 s.ads., 1 juv. (INBio 1485418); 25.11.1995: 1 ad. (INBio 1498708); 18.02.1997: 1 ad. (INBio 1498840) (all leg. Kattia Martinez); *Sendero el Río, 10°18'29"N, 84°47'37"W, 1,600 m*



FIGS. 189, 190. *Helicina monteverdensis* n. sp. FIG. 189. Holotype, INBio 3542627, height 6.6 mm. FIG. 190. Paratype 2, ZMB 103884, height 6.8 mm; scale bar 2.5 mm.

a.s.l.: 04.04.1995: 1 ad., 1 s.ad. (INBio 1484664); 04.07.1995: 1 ad., 1 s.ad. (INBio 1484659) (both leg. Alejandro Azofeifa); 15.07.1994: 1 s.ad. (INBio 1480137); 1 s.ad. (INBio 1480151); 16.09.1994: 2 s.ad. (INBio 1480122); 08.12.1994: 2 juvs. (INBio 1480142); 04.07.1995: 6 ads. (INBio 1485230); 29.10.1996: 1 ad. (INBio 1498835) (all leg. Kattia Martinez); *Sendero el Roble, 10°18'16"N, 84°47'27"W, 1,600 m a.s.l.*: leg. Kattia Martinez, 08.11.1994: 1 ad. (INBio 1479363); *Sendero el Camino, 10°18'03"N, 84°47'15"W, 1,560 m a.s.l.*: 23.05.1994: 2 ads. (INBio 1466975); 14.07.1994: 1 s.ad. (INBio 1479374); 1 ad. (INBio 1480153); 13.12.1994: 1 ad., 1 s.ad. (INBio 1484678) (all leg. Kattia Martinez)

Other Sources

COSTA RICA

Guanacaste: 6 mi NNE Tilaran, on road to Arenal [about 10°33'N, 84°59'W?], 17.07.1971: 1 ad. (UF 69855)

San José: Alata la Palma [Alto Palma?, about 10°03'N, 84°00'W], 07.08.1971: 1 s.ad. (UF 69856)

Description

Shell (Figs. 189, 190, 336I–J): Conical, thin and fragile, medium to small sized, semitransparent, shiny. Color: whorls unicolored, whitish-opaque, yellowish to bright yellow or even brownish; apical whorls sometimes with a crimson spot. Surface textured with fine and regular growth lines (Fig. 192), causing the glossy appearance. Embryonic shell with about 1 whorl; 3¾ ($3^3/_8$–4) subsequent whorls convex; last whorl very evenly rounded at the periphery; whorls equally extending in size or last whorl even more rapidly increasing in diameter, forming a pointed spire. Suture moderately impressed. Aperture oblique and curved backwards; last whorl slightly more descending towards aperture and inserting below periphery. Outer lip independently from the color of the whorls always whitish-opaque, slightly thickened and very narrowly expanded and reflexed. Transition to columella continuous with a slight notch. Columella slightly curved, transition to the body whorl without any groove. Basal callus very weakly developed and slightly granulated.

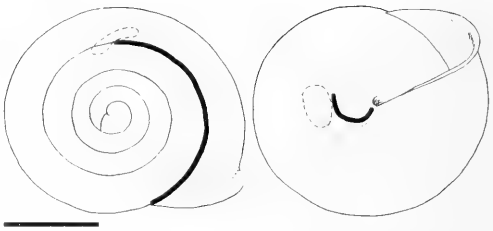


FIG. 191. Axial cleft and muscle attachments of *Helicina monteverdensis* n. sp., INBio 3542627 (holotype) ; scale bar 2.5 mm.

Internal Shell Structures: (Fig. 191)

Teleoconch Surface Structure (Fig. 192): The surface structure is similar to that of *Helicina gemma*.

Embryonic Shell: Among the specimens studied from the populations of Monteverde and Mirador Gerardo, the embryonic shells show large deviations in structure, showing all intermediary variations in pit size from pronounced pits as in *Helicina gemma* to small ones as in *H. beatrix* (Fig. 193A, B). For comparison with *H. fragilis*, a Guatemalan specimen was studied (Fig. 194), but due to the high variations in *H. monteverdensis* n. sp., structural differences cannot be codified. By the way of contrast, the size differs remarkably: the type lot and

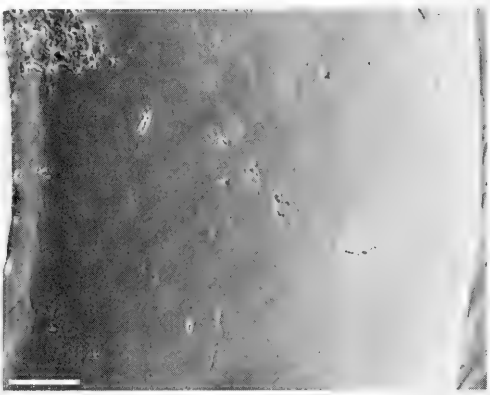


FIG. 192. Teleoconch surface structure of *Helicina monteverdensis* n. sp., 2nd whorl; scale bar 100 µm.

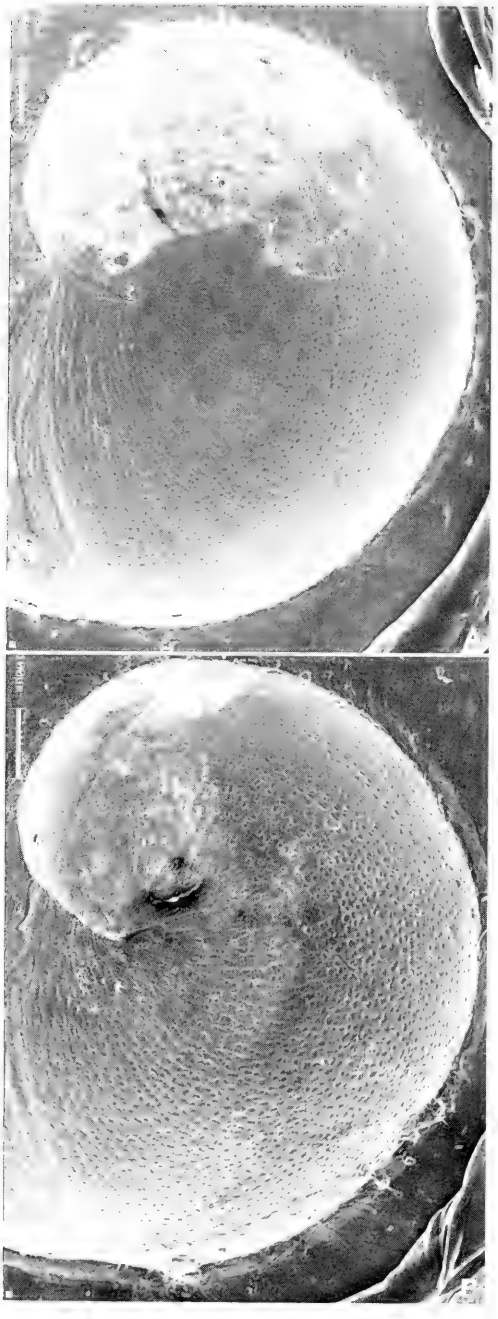


FIG. 193. Embryonic shell of *Helicina monteverdensis* n. sp. A. Mirador Gerardo, IR 1226. B. Same data; scale bar 100 µm.

other Guatemalan specimens show a range of 580 to 760 µm, whereas the embryonic shell of the Costa Rican specimens of *H. monteverdensis* n. sp. is clearly larger (830 to 1,000 µm). These differences clearly exceed the possible deviations caused by effects of altitude, at least as far as the results for *H. gemma* suggest. Furthermore, the specimens from UF 189883 with a small embryonic shell size also originate from an altitude of 1,300 m. The same is true for the type lot of *H. merdigera*, the embryonic shell of which is also remarkably smaller.

The smaller specimens from the population of Mirador Gerardo possess somewhat smaller embryonic shells on the average. The relation of embryonic shell size to the shell size is discussed below.

Diameter: 935 µm (± 25) (900–1,000) (n = 21) (IR 634, IR 844, Monteverde); 897 µm (± 29) (830–990) (n = 15) (IR 1226, Mirador Gerardo); 708 µm (± 44) (620–760) (n = 4) (BMNH 1893.2.4.809–812, type lot of *Helicina fragilis*, lectotype: 620 µm); 610 µm

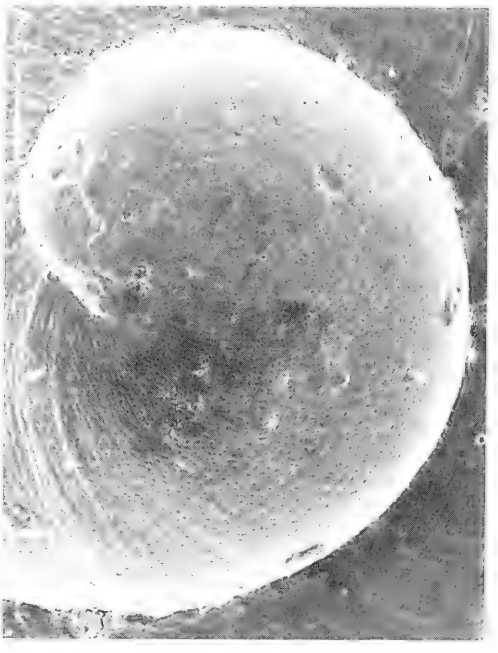


FIG. 194. Embryonic shell of *Helicina fragilis*; scale bar 100 µm.

FIG. 195. Operculum of *Helicina monteverdensis* n. sp., INBio 3542627; scale bar 1 mm.

(UF 190045: Guatemala: Alta Verapaz Department, 9 km W of Lanquin, 15°35'03"N, 90°03'20"W, 690 m a.s.l., leg. F.G. Thompson et al.); 620 µm (± 20) (600–640) (n = 2) (UF 189883: Guatemala, Alta Verapaz Department, 1.5 km SE of (San Juan) Chamelco, 15°24'20"N, 90°18'28"W, 1,300 m a.s.l., leg. F.G. Thompson); 608 µm (± 18) (580–630) (n = 5) (UF 237423: Guatemala: Chama, leg. A.A. Hinkley, *ex* coll. Beal-Maltbie); 650 µm (± 0) (650) (n = 2) (BMNH 20010725.1–2, type lot of *Helicina merdigera*).

Operculum (Fig. 195): Very slightly calcified, calcareous plate covering only part of the outer surface, thickened towards the columellar side. Color whitish-yellow to pale horny-amber, nearly transparent throughout. Columellar side slightly S-shaped, upper end acute and pointed, lower end rounded and continuously changing into outer margin.

Animal (Fig. 338F, G): The color resembles that of *Helicina gemma*, but varies more strongly. In the individuals originating from Monteverde, the head-foot is usually much paler, only the tentacles are tinged grey; in the mantle pigmentation, the whitish-yellow part is very prominent, but the dark spots very often form an irregular band at the periphery. The pattern in specimens from Mirador Gerardo more closely resembles that of *H. gemma*, but it ranges from nearly black individuals with some very small yellowish-white spots to the reverse, with few slender black lines and spots. In this population, a distinct dark band has never been observed. Usually the dark part of the head-

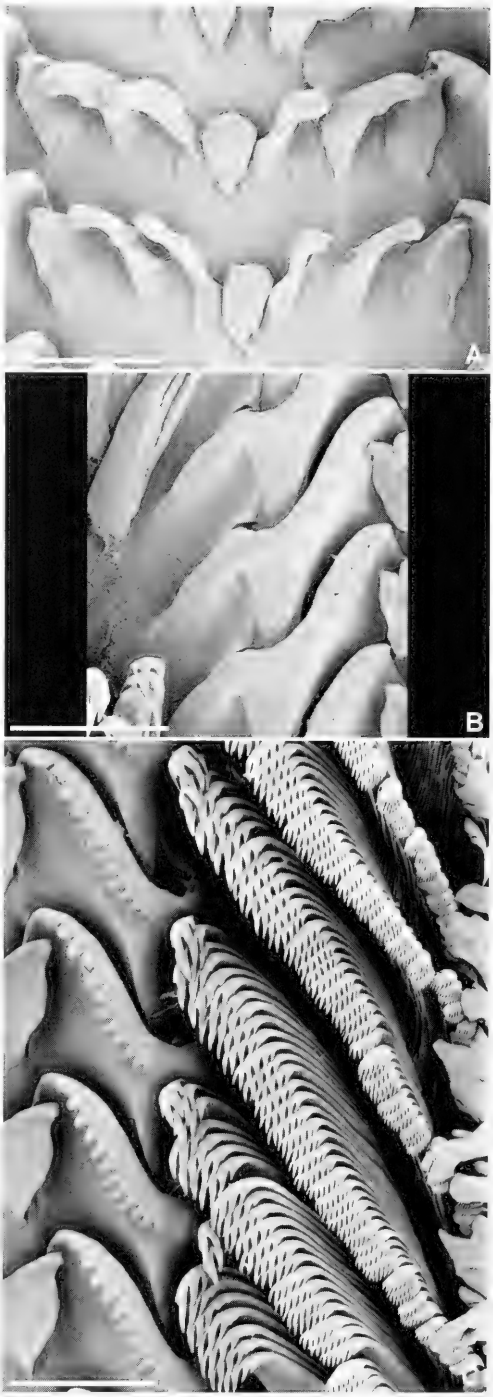
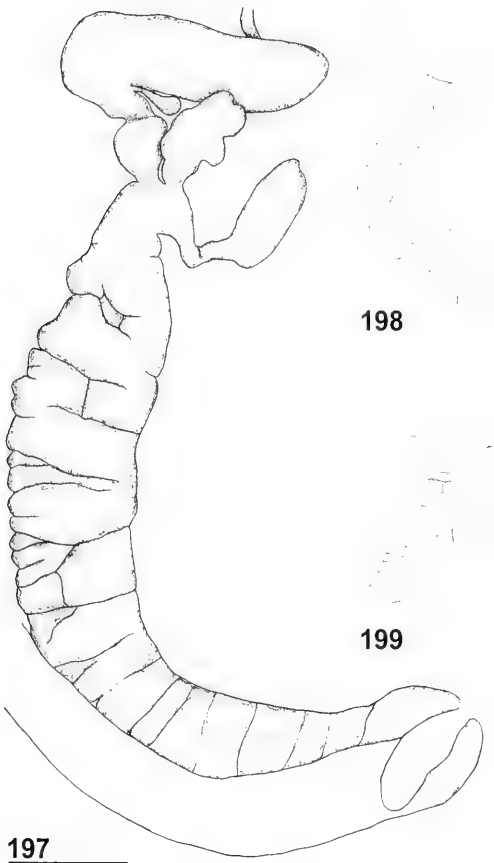


FIG. 196. Radula of *Helicina monteverdensis* n. sp. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

foot is larger and more intensive in specimens with a darker mantle pigmentation. These considerable variations within a population seem to be typical. The few specimens from the Cartago Province are either dark or pale. The mantle pigmentation is clearly visible through the thin shell.

Radula (Fig. 196): All centrals lack well defined cusps. Comb-lateral with 8 cusps, only one exception with 11 or 13 cusps on the other side respectively (Fig. 196C). Cusps on marginals rapidly increasing in number. Radula with about 46–73 rows of teeth.

Female Reproductive System (Figs. 197–199): The reproductive tract of *Helicina monteverdensis* n. sp. is similar to that of *H. gemma* and equal in size and proportions except for the bursa copulatrix. The latter seems to be consistently smaller, although specimens collected during both (dry and rainy) seasons were studied in either species to exclude possible physiological changes. Furthermore, the shape of the bursa copulatrix varies more in *H. monteverdensis* n. sp. Lobes are not always distinctly developed and they are less regular.



FIGS. 197–199. *Helicina monteverdensis* n. sp. FIG. 197. Female reproductive system, IR 844. FIG. 198. Variability of the female reproductive system, population from Mirador Gerardo, IR 1226. FIG. 199. Variability of the female reproductive system, population from Monteverde, IR 844; scale bar 1 mm (Fig. 197), 2 mm (Fig. 198–199).

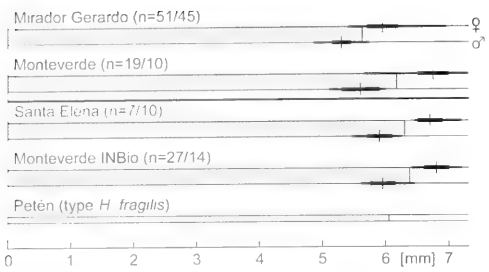


FIG. 200. Shell height of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Santa Elena and Monteverde INBio not determined anatomically (see text).

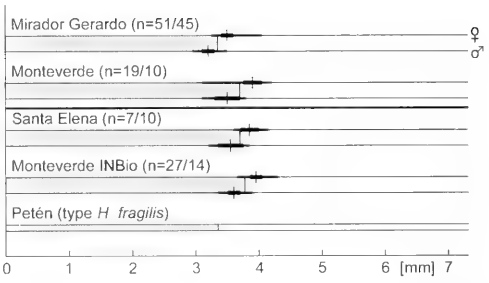


FIG. 202. Expansion of outer lip of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

Morphometry and Sexual Dimorphism (Table 11, Figs. 200–205)

Around the type locality, the species was collected in favorable numbers for the morphometric analysis. Three localities are differentiated from N to S: Mirador Gerardo at the beginning of the northern slope of the Cordillera de Tilarán, the Santa Elena reserve and finally samples mainly in and around the Reserva Biológica Bosque Nuboso Monteverde. The latter are separated in the lots that were anatomically investigated (coll. IR) and INBio's. Both populations included from the latter collection (Figs. 200–204, below thick line), which could not be analyzed for their sex, were separated, as in *Helicina beatrix*, to avoid the artificial high deviations of measurements with mixed sexes. For comparison in the discussion, the lectotype of *H. fragilis* is included in the figures.

Morphometry: The shells of the population "Mirador Gerardo" are remarkably smaller in all measurements than the other populations, which are similar to each other. The constant pattern of differences of the populations for the different measurements suggests the same shape of the shell. In comparison with *Helicina gemma* closely resembling the species, it is remarkable that only the populations with the biggest shells ("Finca Montaña Grande", "Cerro Cocorí") attain the size of the new species from Monteverde, whereas in the closer population "Mirador Gerardo", the average shell

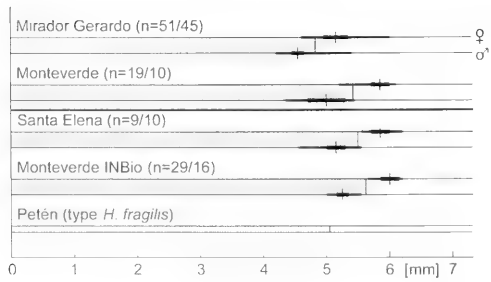


FIG. 201. Minor diameter of shell of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

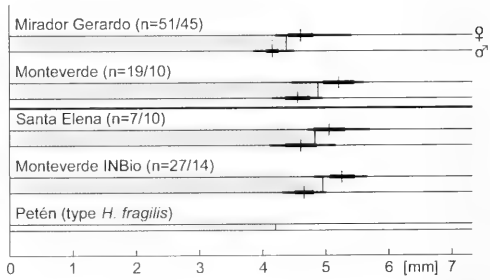


FIG. 203. Height of last whorl of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

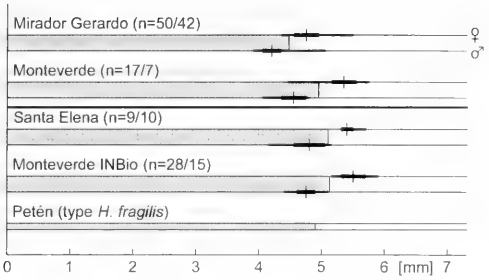


FIG. 204. Height of columellar axis of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

size is clearly smaller than in all *H. gemma*-populations. Thus, *H. monteverdensis* n. sp. displays greater differences in size in just a few closely located and ecological similar populations than does the comparatively widespread *H. gemma* in the several populations investigated. This observation supports the distinctness of the two species.

Sexual Dimorphism: In both populations, the females possess bigger shells. The data overlap only very slightly with the measurements of the males, possibly because of the comparatively high number of specimens included, rendering individual high deviations more likely. The separation of both sexes is additionally shown for the original set of data of height and minor diameter for the population "Monteverde" and "Mirador Gerardo" (Figs. 206–207). In volume, the males only amount to $^2/_3$ or less than the females. The differences displayed for the populations are very constant for each measurement. As explained in *H. beatrix*, the well-developed sexual dimorphism allows a separation of sets of mixed data (illustrated for Monteverde INBio, Fig. 208).

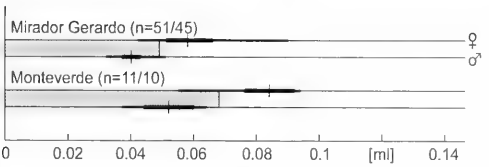


FIG. 205. Shell volume of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

Habitat

Helicina monteverdensis n. sp. has been observed crawling and aestivating on leaves of several small-leafed plants of the undergrowth. Especially at Mirador Gerardo where Heliconiaceae are abundant on the forest margins, it was mainly found on older leaves of plants that were covered with moss and algae. During rainy and cloudy weather, it crawls on both the upper and lower side of the leaves. It has not been seen in leaf litter. In Monteverde and adjacent areas, the species occurs sympatrically with *H. funcki* and *Alcadia hojarasca*.

Distribution (Fig. 209)

Helicina monteverdensis n. sp. seems to be adapted to higher altitudes, most records around 1,500 m. A single exception is the site north of Tilarán (about 700 m?), which can also be located south of or today within the reservoir, because it was collected before the construction of the Embalse de Arenal reservoir. The species occurs in the Cordillera de Tilarán and the Cordillera Central. It is well distributed in the cloud forests of the area of Monteverde – Santa Elena. The record from the northeastern slopes of the Cordillera Talamanca is only tentatively attributed to the new species; further material is required. As the record from the Cordillera Central indicates, the species is probably much more widespread, but many possible sites have either been poorly investigated or not at all. Except for the Cordillera de Guanacaste, *H. monteverdensis* n. sp. replaces *H. gemma* at higher altitudes.

Discussion

The population in Monteverde consists of brightly yellow to whitish shelled specimens, whereas individuals from the Mirador Gerardo within a very limited collection area exhibit a wider range of color, additionally including brownish specimens. The outer lip is always whitish.

Helicina monteverdensis n. sp. most closely resembles *H. gemma* from which it differs by the constantly different color of the outer lip and adjacent part of the last whorl. Besides

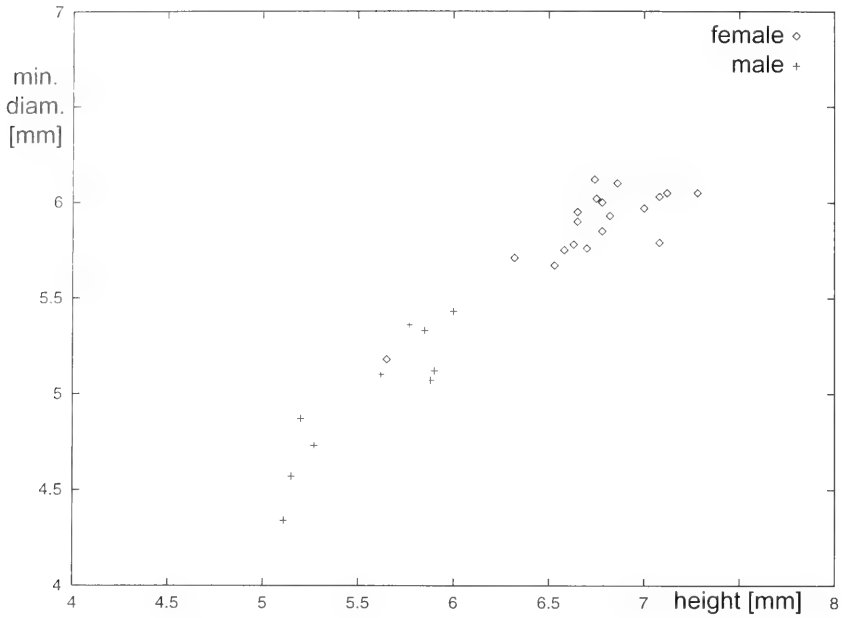


FIG. 206. Range of measurements in females and males of *Helicina monteverdensis* n. sp. exemplary for height and minor diameter in the population from Monteverde.

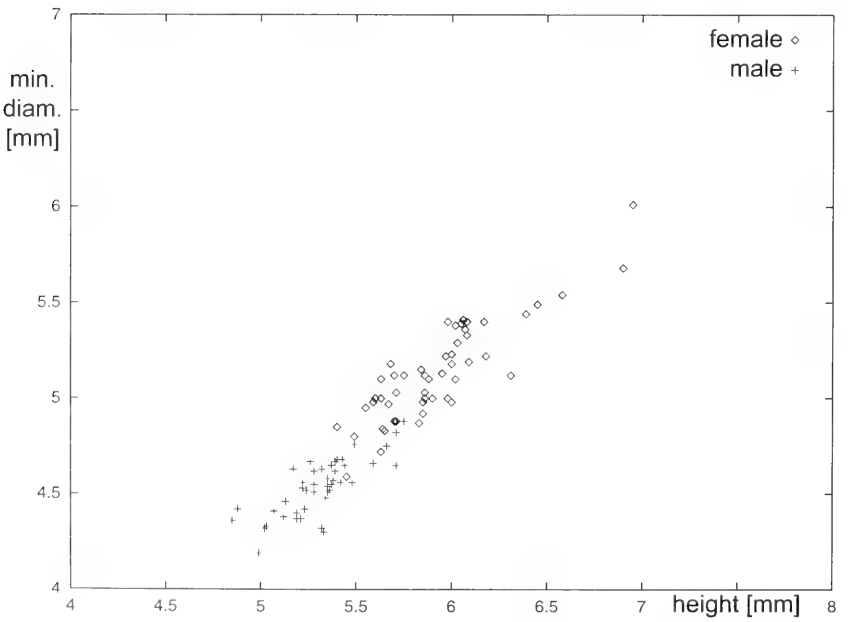


FIG. 207. Range of measurements in females and males of *Helicina monteverdensis* n. sp. exemplary for height and minor diameter in the population from Mirador Gerardo.

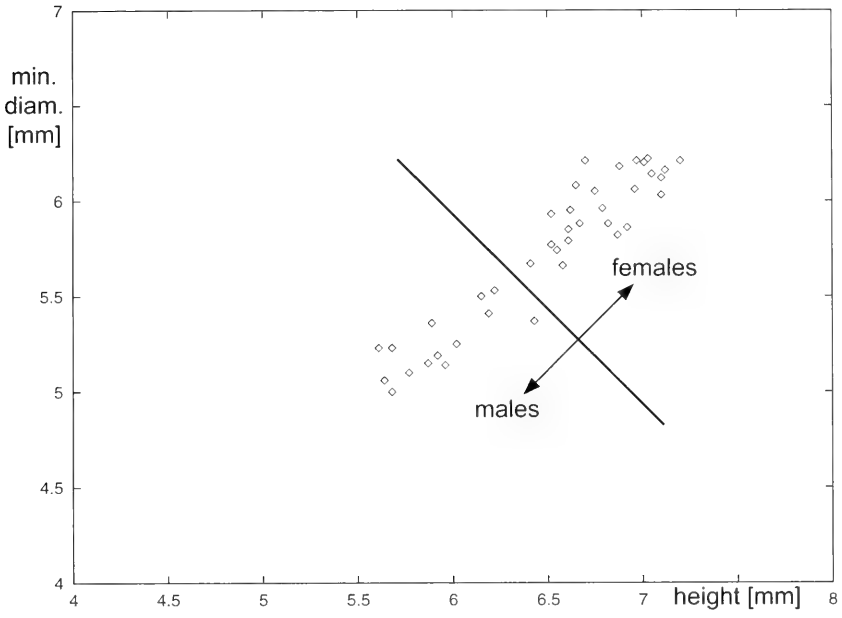


FIG. 208. Plot of measurements for height and minor diameter for individuals of *Helicina monteverdensis* n. sp. of unknown sex, exemplary for the population of Monteverde INBio and the separation proposed.

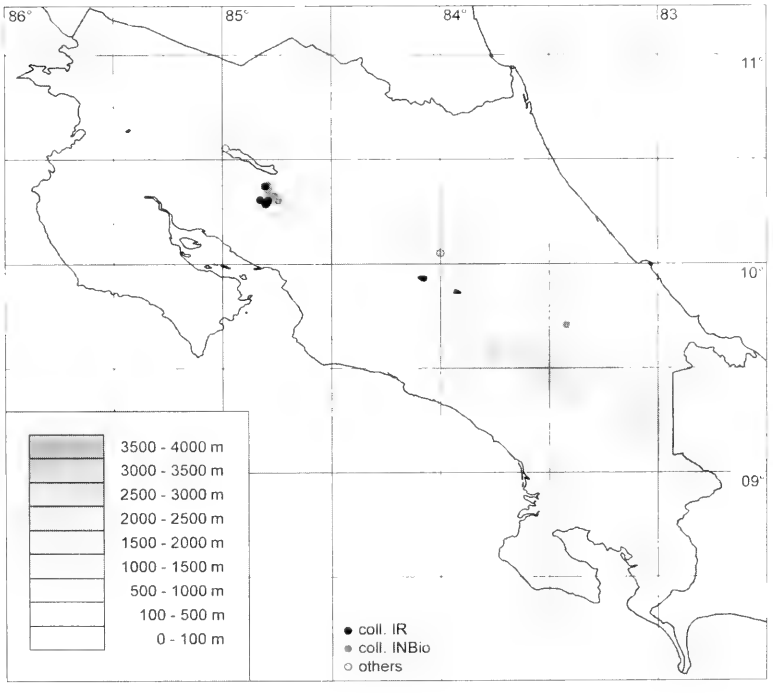


FIG. 209. Records of *Helicina monteverdensis* n. sp. in Costa Rica.

TABLE 11. Measurements of different populations of *Helicina monteverdensis* n. sp. given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals from Santa Elena and Monteverde INBio not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		"Mirador Gerardo" (altitude 1450 m) lots IR 929, IR 1416					"Monteverde" (altitude 1500–650 m) lots IR 296, 634, 825, IR 844, IR 1196				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	5.93	0.24	5.40	6.95	51	6.74	0.23	5.65	7.28	19
Height	m	5.31	0.15	4.85	5.75	45	5.58	0.31	5.11	6.00	10
Maj. diam.	f	5.56	0.23	4.93	6.48	51	6.32	0.17	5.61	6.62	19
Maj. diam.	m	4.96	0.14	4.45	5.41	45	5.46	0.34	4.82	6.02	10
Min. diam.	f	5.14	0.20	4.59	6.01	51	5.87	0.16	5.18	6.12	19
Min. diam.	m	4.54	0.12	4.19	4.88	45	4.99	0.29	4.34	5.43	10
Outer lip	f	3.50	0.11	3.25	4.06	51	3.91	0.15	3.60	4.18	19
Outer lip	m	3.21	0.10	2.95	3.52	45	3.48	0.20	3.10	3.80	10
Last whorl	f	4.62	0.18	4.18	5.40	51	5.22	0.23	4.47	5.58	19
Last whorl	m	4.17	0.12	3.85	4.52	45	4.54	0.21	4.16	4.95	10
Col. axis	f	4.75	0.20	4.37	5.52	50	5.33	0.20	4.45	5.75	17
Col. axis	m	4.22	0.13	3.89	4.57	42	4.56	0.19	4.03	4.80	7
Weight	f	0.013	0.002	0.009	0.022	51	0.016	0.002	0.011	0.019	11
Weight	m	0.011	0.002	0.007	0.017	45	0.013	0.002	0.008	0.018	10
Volume	f	0.058	0.007	0.042	0.090	51	0.084	0.008	0.055	0.094	11
Volume	m	0.040	0.003	0.032	0.051	45	0.052	0.008	0.037	0.064	10

		"Santa Elena" (altitude 1200–1550 m) lots INBio 1479270, 1479273, 1485425, 1485431, 1487482, 1498545, 3098462					"Monteverde INBio" (altitude 1520–1690 m) lots INBio 1466785, 1466975, 1468138, 1468209, 1479239, 1479363, 1480117, 1480143, 1480153, 1483833, 1484024, 1484659, 1484664, 1484678, 1485229, 1485230, 1485231, 1485418, 1498519, 1498583, 1498680, 1498684, 1498693, 1498708, 1498821, 1498835, 1498840, 1501428				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.72	0.19	6.46	7.21	7	6.82	0.20	6.41	7.20	27
Height	m	5.90	0.21	5.43	6.25	10	5.93	0.20	5.61	6.43	14
Maj. diam.	f	6.29	0.17	5.92	6.63	8	6.42	0.19	5.97	6.78	29
Maj. diam.	m	5.58	0.20	5.01	5.99	10	5.70	0.16	5.43	6.10	16
Min. diam.	f	5.84	0.13	5.55	6.19	9	5.99	0.15	5.66	6.22	29
Min. diam.	m	5.13	0.17	4.53	5.56	10	5.25	0.12	5.00	5.53	16
Outer lip	f	3.83	0.16	3.58	4.17	7	3.95	0.12	3.65	4.30	27
Outer lip	m	3.56	0.18	3.18	3.85	10	3.60	0.11	3.33	3.91	14
Last whorl	f	5.07	0.24	4.70	5.70	7	5.24	0.19	4.80	5.66	27
Last whorl	m	4.61	0.23	4.12	5.13	10	4.66	0.14	4.32	5.00	14
Col. axis	f	5.42	0.10	5.29	5.68	9	5.51	0.19	5.13	5.89	28
Col. axis	m	4.79	0.23	4.13	5.15	10	4.77	0.15	4.41	5.08	15

morphometric differences discussed above, the whorls of *H. monteverdensis* n. sp. appear more inflated. The high variation in body color of *H. monteverdensis* n. sp. has not been observed in other species.

Small, thin-shelled, yellowish-whitish-transparent Helicinidae without spiral striations from Central America (mainly Mexico and Guatemala) were normally referred to *Helicina fragilis* or its subspecies *H. fragilis elata* with the synonyms *Helicina merdigera* and the dubious *Helicina mohriana* (e.g., Fischer & Crosse, 1880–1902; von Martens, 1890–1901; Baker, 1922a, 1928). Wagner (1908) did just this when he studied such specimens in the collection of the ZMB from the more southern parts of Costa Rica. Those specimens from the Valle de Talamanca and the neighboring Valle de Estrella were reinvestigated and partly belong to *H. escondida* n. sp., *H. chiquitica* or partly remain dubious in their identification (see under *H. chiquitica*).

To clarify the classification of the small, fragile, whitish Helicinidae from the Monteverde area, the type material of the taxa mentioned above and many lots from Mexico, Guatemala, Honduras and Belize were studied, mainly in the collection of the UF.

Helicina fragilis differs from *H. monteverdensis* n. sp. in having fewer whorls and a much smaller embryonic shell, although the general size of the shells is about the same. The aperture and last whorl is relatively lower, the spire higher. Furthermore, in many specimens of *H. fragilis*, a slight angulation at the periphery (stronger in juvenile stage) is maintained to at least the beginning of the last whorl (e.g., paralectotypes), which in *H. monteverdensis* n. sp. is always rounded. The types were collected under decaying leaves, whereas the new species is arboreal. Baker (1928) observed *H. fragilis elata* on rock ledges, weeds and low brush, but assumed the aestivation on the ground.

The lectotype of *Helicina merdigera* is slightly angulated at the periphery throughout the last whorl, which is a little shouldered below the suture. In comparison with *H. fragilis* and the new species, the shell surface is more roughly sculptured with irregular growth lines and oblique grooves, the outer lip is less reflexed and the thickening is shifted a little inwards. The lower part of the aperture protrudes further, forming a nearly rectangular edge at the transition to the columella, whereas in *H. fragilis* and *H. monteverdensis* n. sp., the transition is continuously or even with a little notch. Other features are similar to *H. fragilis* providing additionally evidence for the distinctness from the new species. Fischer & Crosse (1893) related the observation by Sallé that *H. merdigera* covers its shells with own excrement. It is interesting to note that the fragmented paralectotype shows traces of exactly such encrustation on the shell pieces. If this behavior turns out to be typical for *H. merdigera*, it is also in contradiction to the behavior of the Costa Rican specimens which were never observed to have agglutinated anything on their shiny shells. Considering the differences in the type material, it seems more appropriate to treat *H. merdigera* as specifically distinct from *H. fragilis* until more material is carefully studied, but this is beyond the focus of the current study.

Von Martens (1890), having compared Shuttleworth's typical specimen of *Helicina elata* to a Guatemalan sample, only recognized the smaller size and a more slender peristome. Besides size the syntype at hand differs in a more globose shell, that is, a less elevated spire with a blunt apex, the lower whorls increasing less in diameter. In this respect, it also differs from *H. monteverdensis* n. sp. The figure in Fischer & Crosse (1893) does not match the syntype at all. As described by Shuttleworth and pointed out by Von Martens (1890), *H. elata* exhibits a dentiform prominence at the base of the columella (like *H. merdigera*), which is lacking in the new species. Whether or not *H. elata* has to be treated as a subspecies of *H. fragilis* is a question beyond the scope of this study.

Type material of *Helicina mohriana* could not be located. L. Pfeiffer probably kept it in his own collection, which became part of the collection of Dohrn (Dance, 1986). The latter is said to have been destroyed in the Museum Stettin, Poland, during World War II (Clench & Jacobson, 1971). Wagner (1908) depicted the species for the first time (*Alcadia* (*Leialcadia*) *fragilis mohriana*), but the source of his material is unknown, and the one of two specimens (Wagner, 1908: pl. 14, figs. 14–16) originating from the type locality, Orizaba, represent a not yet fully grown shell. Because he does not give any explanation for this identification and completely ignored "*merdigera*" and "*elata*", it does not contribute to the clarification of the taxon. Thus, it obviously remains a dubious species, which however is differentiated from *H. monteverdensis* n. sp. by a groove in the

umbilical area near the columella mentioned in the original description ("juxta columellam brevem excavatus").

Another dubious species (von Martens, 1891) of this complex is *Helicina diaphana* from Honduras. It has only been depicted very inadequately in Reeve (1874), and it completely escaped the attention of Fischer & Crosse (1880–1902) and Wagner (1907–1911). Rehder (1966) stressed the specific dissimilarity to *Helicina boucourti* Crosse & Fischer, 1869, rendering it more likely to a closer affinity with the "small, thin, fragile, whitish species". The study of the probable syntype shows, on one hand, that *H. diaphana* is clearly different from *H. monteverdensis* n. sp., but, on the other hand, that the taxon does not deserve to be treated as a dubious species, because the description was not based on a juvenile shell. *H. diaphana* is broader than high, appearing depressed, but the periphery is only very roundly angulated, if at all. The suture is very weakly impressed, the apex blunt. The uppermost ¼ whorls of the teleoconch bear widely spaced spiral ridges, subsequently the shell is sculptured with irregular growth lines and an ornamentation of small oblique grooves. The aperture is oblique, inserting below the periphery, the outer lip developed, but only slightly expanded and reflexed. The transition to the columella lacks a notch or denticle.

Considering also *H. chiquitica* and *H. escondida* n. sp., it appears that the Mexican and Guatemalan taxa discussed are not distributed as far southwards as previously assumed.

The original material of the records of Monge-Nájera (1997) for *H. oweniana* and *H. beatrix* was checked in the collection of INBio and can partially be attributed to *H. monteverdensis* n. sp. For differences to these species, compare also the closely related *H. gemma*.

Helicina (*"Gemma"*) *escondida* Richling, n. sp.

Type Material

Holotype: INBio 3542623, female (leg. I. Richling, 12.03.2001, *ex* IR 1543)
Paratype 1: INBio 3542624, male (same data as holotype)
Paratype 2: ZMB 103880, female (same data as holotype)
Paratype 3: ZMB 103881, female (same data as holotype)

Dimensions:
Holotype: 6.2/6.0/6.4/5.4/3.8/4.9/5.0 mm
Paratype 1: 5.9/5.6/6.1/5.1/3.6/4.6/4.5 mm
Paratype 2: 6.8/6.1/6.6/5.7/3.8/5.1/5.3 mm
Paratype 3: 6.6/5.9/6.4/5.5/3.7/4.9/5.3 mm

Type Locality

SE-Costa Rica, Limón Province, approximately 9 km W of Matina, a little upstream on the Río Barbilla from the crossing of the road from Siquirres to Limón, along a tributary of Río Barbilla, 10°03'29"N, 83°22'24"W, 70 m a.s.l., valley of small creek in rain forest (probably secondary forest)

Material Examined

Leg. I. Richling
Heredia: S Puerto Viejo de Sarapiqui, *Zona Protectora La Selva*, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1056)
Limón: About 9 km W of Matina, road Limón to Siquirres, a little stream up the *Río Barbilla*, along a tributary of Río Barbilla, in the valley of a small creek in rain forest, 10°03'29"N, 83°22'24"W, 70 m a.s.l., 12.03.2001: (IR 1543)
N Shiroles, Cerro Mirador, along trail, 09°36'37"N, 82°57'43"W, 430 m a.s.l.: 16.03.2001: (IR 1601)

INBio Collection
Limón: *Sector Hitoy Cerere*: Sendero Bobócara, 09°40'31"N, 83°00'31"W, 200 m a.s.l., leg. malacological staff of INBio, 10.01.1993: 1 ad. (INBio 1466441); 400 m NE de la Estación de Hitoy Cerere, Sendero la "Finca", 09°40'36"N, 83°01'26"W, 110 m a.s.l., leg. Alexander Alvarado Mendez, 27.09.2000: 1 ad. (INBio 3091794)
Reserva Biológica Hitoy Cerere: *Cruce entre Sendero Revienta Pechos y Sendero Espavel, 09°39'12"N, 83°00'58"W, 600 m a.s.l.*: leg. Alexander Alvarado Mendez, 24.04.1999: 5 ads. (INBio 1497850); *Sendero Bobócara*: 09°40'02"N, 83°02'42"W, 500 m a.s.l., 12.06.1999: 1 ad., 1 s.ad. (INBio 3091132); 09°40'53"N, 83°04'09"W, 798 m a.s.l., 17.06.1999: 6 ads., 1 s.ad., 1 juv. (INBio 3542523) (all leg. Alexander Alvarado Mendez)
Reserva Indígena Tayni, Sendero Bobócara, 09°40'28"N, 83°02'12"W, 200 m a.s.l., leg. Alexander Alvarado Mendez, 15.07.1999: 1 ad. (INBio 1498244)

OTHER SOURCES

COSTA RICA

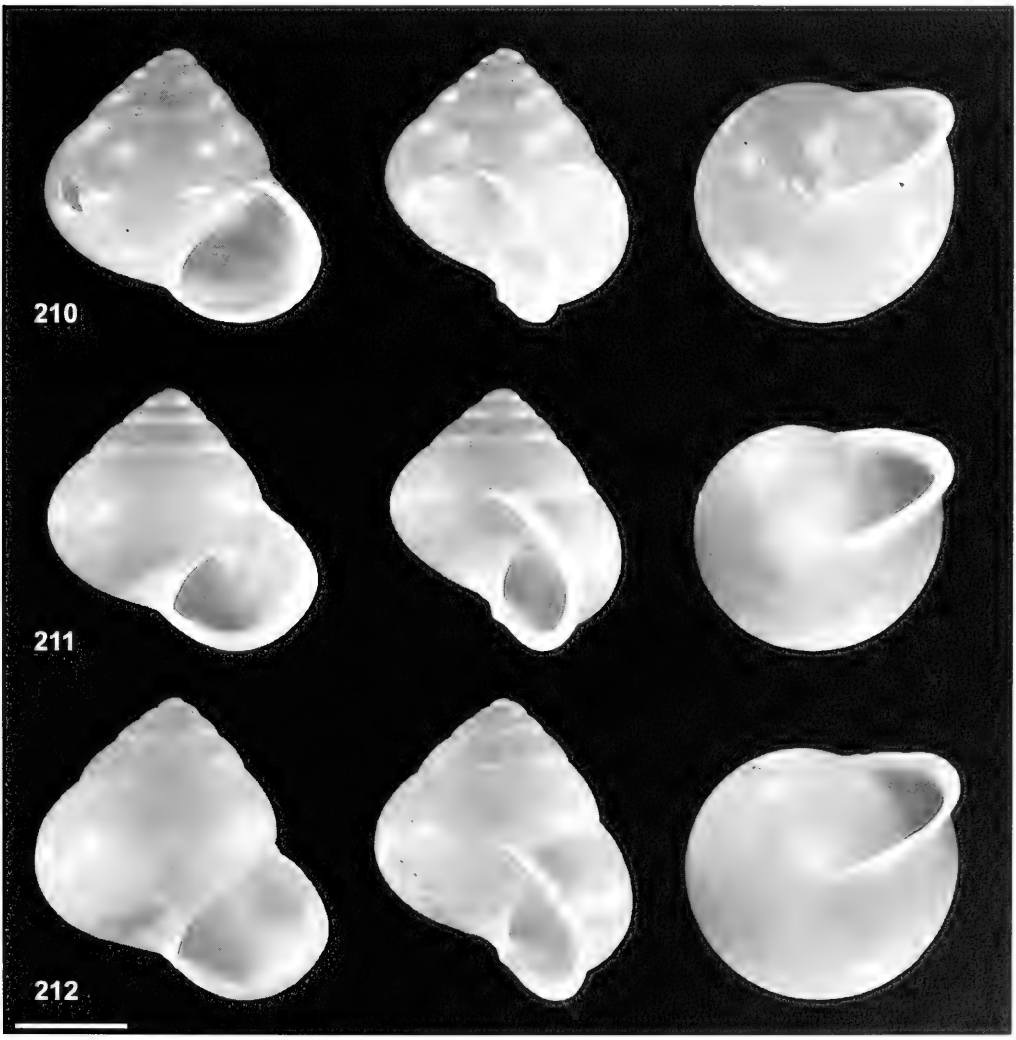
Limón: Los Diamantas Farm [about 10°11'N, 83°37'W], 11.08.1971: 1 ad. (UF 69847); determination uncertain: Los Diamantes Farm, 12 mi SE Guapiles [about 10°11'N, 83°37'W], leg. R.W. McDiarmid, 13.08.1971: 1 s.ad. (UF 217530)

Road cut, along S bank of Río Banano, opposite La Bomba, 09°54'49.7"N, 83°03'56.4"W, leg. D.G. Robinson & J.M. Montoya (Stn. 98 CR-15), 21.09.1998: 2 ads. (APHIS PPQ USDA)

Talamanca, Río Estrella [about 09°43'N, 83°00'W], leg. Pittier (ZMB 103249); Valle del Río Estrella, Talamanca [about 09°43'N, 83°00'W], leg. H. Pittier, III.95 (ZMB 48235) Valleé de Brabri, Talamanca [Bratsi? about 09°33'40"N, 82°53'28"W], leg. H. Pittier, VIII.98 (ZMB 103248)

Cartago: Turrialba [about 09°54'30"N, 83°41'W], International American Agricultural Institute, 2000 ft., leg. F.G. Thompson (FGT-76), 03.08.1963: 2 ads. (UF 214143)

Costa Rica, without locality specified: *ex* Sowerby & Fulton: 1 ad. (UF 243507: 1 of 3 spec.)



FIGS. 210–212. *Helicina escondida* n. sp. FIG. 210. Holotype, INBio 3542623, height 6.2 mm. FIG. 211. Paratype 1, INBio 3542624, height 5.9 mm. FIG. 212. Paratype 2, ZMB 103880, height 6.8 mm; scale bar 2.5 mm.

Etymology

The name represents two aspects of the species: for a long time it has escaped scientific recognition, its occurrence is very "hidden" in natural environments, and the small size and variations of the color render it difficult to find. I had been searching all day without success until I came across some tiny helicinids, which turned out to represent two new species: *chiquitica* and "escondida" (Spanish) = "hidden". The Spanish word is preferred here in homage to its origin and because the Latin translations are occupied by other helicinid species.

Description

Shell (Figs. 210–212, 336K–M): conical, small, fragile and slightly dull. Color: unicolored yellow except for the outer lip and a slight, very thin yellowish-white band directly under suture. Embryonic shell about 1 whorl; $4^{1}/_{8}$ ($3^{7}/_{8}$–$4^{5}/_{8}$) subsequent whorls equally extending in size; last whorl rounded at periphery; only slightly convex, giving the spire a very regular and straight appearance. Periostracum thin, under magnification with very fine equally spaced spiral striations at the periphery (up to about 9 lines) and a texture of fine oblique lines that makes it appear dull. Aperture oblique and very straight. Outer lip independently from color of whorls always yellowish-white, slightly thickened and reflexed nearly rectangularly to the whorls; transition to columella only with a very little denticle. Basal callus very weakly developed, umbilical area finely granulated with a little groove parallel to the columella.

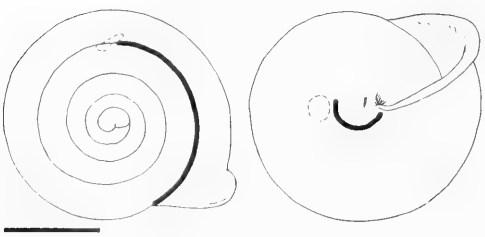


FIG. 213. Axial cleft and muscle attachments of *Helicina escondida* n. sp., INBio 3542623; scale bar 2.5 mm.

Internal Shell Structures (Fig. 213):

Teleoconch Surface Structure: The transitional pattern (Fig. 214A, B) stretches for nearly ¾ of a whorl, the following structure of oblique diverging grooves is only weakly developed, becoming still weaker during growth (Fig. 214C, D), but not disappearing. Furthermore, the surface is sculptured with periostracal spiral ridges that begin in the second whorl.

Embryonic Shell (Fig. 215): Except for size, the embryonic shell closely resembles that of *Helicina funcki*. In the specimens under study, it shows only minor deviations, for example, the lines of pits starting somewhat later.
Diameter: 728 µm (± 25) (680–780) (n = 19) (IR 1543).

Operculum (Fig. 216): Thin and only slightly calcified. Color yellowish and transparent. Columellar margin slightly S-shaped, upper end acute, lower end only weakly angulated, rounded. Inner surface with a little ridge parallel to the columellar margin.

Animal (Figs. 338H, 339A–B): The color of the soft body is variable. The foot is light whitish-yellow and becoming brownish-grey upwards. Dorsal anterior and posterior end and tentacles being darkest, but some individuals are much lighter than other. The mantle color varies from a unicolored greenish to a unicolored dark greyish-brown. Some individuals exhibit a very distinct dark or light band with irregular margins at about the periphery, occasionally the apical part of the mantle is spotted yellowish.

Radula (Fig. 217): The B-central bears 3–4 well-defined cusps; A- and C-central are smooth or crenulate. The comb-lateral remarkably differs from other Costa Rican species in its consistently low number of only 6 cusps. Furthermore, the cusps increase considerably in size inwards. The number of denticles on the marginals increases rapidly. Radula with about 69–78 rows of teeth.

Female Reproductive System (Fig. 218): The receptaculum seminis is very small and spherical. The bursa copulatrix bears a few regular lobes; in one specimen, it is only bi-

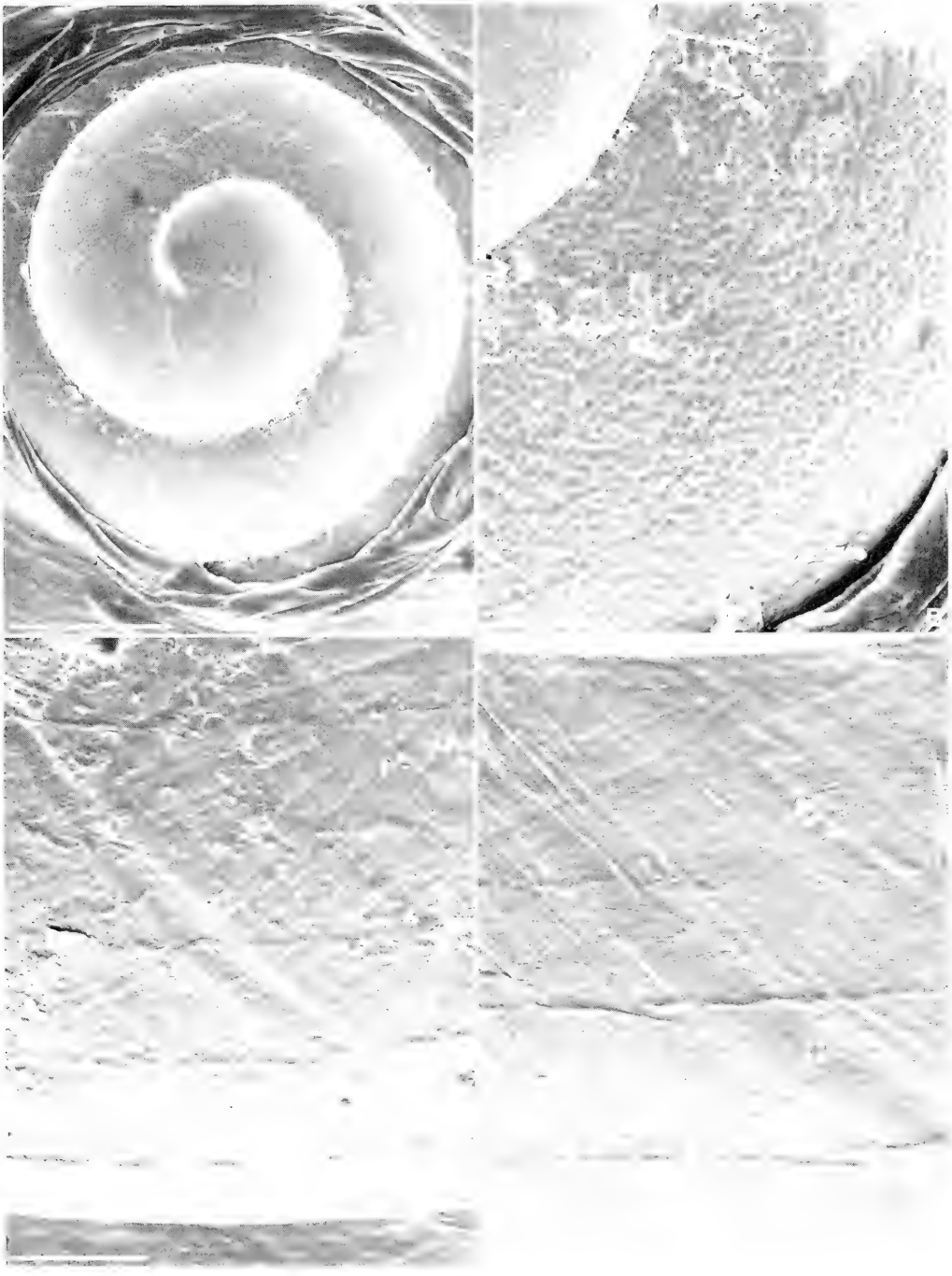


FIG. 214. Teleoconch surface structure of *Helicina escondida* n. sp. A. Embryonic shell and transition of different sections. B. Immediately after embryonic shell: transitional surface structure. C. 2nd whorl. D. 3rd whorl; scale bars 500 µm (A), 100 µm (B-D).

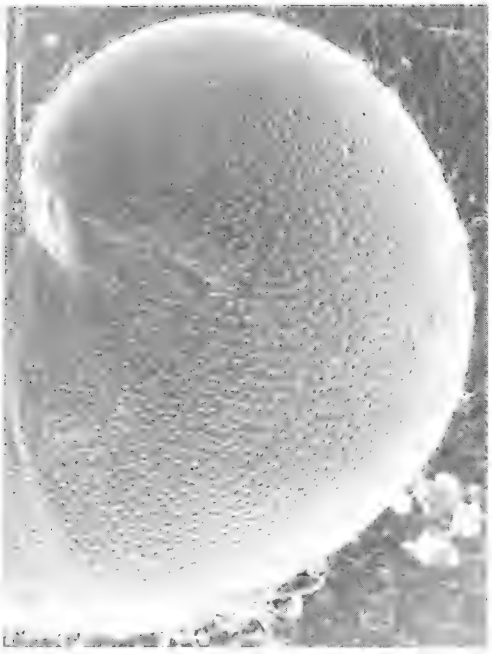


FIG. 215. Embryonic shell of *Helicina escondida* n. sp.; scale bar 100 µm.

lobed. The provaginal sac is elongated and its stout stalk joins the sac about the middle of the long side.

Morphometry and Sexual Dimorphism (Table 12, Figs. 219–223)

The sexes of all specimens from the three areas were determined. Material from INBio allowed the assignment without preparation because of the quite transparent shells.

FIG. 216. Operculum of *Helicina escondida* n. sp., ZMB 103880; scale bar 1 mm.

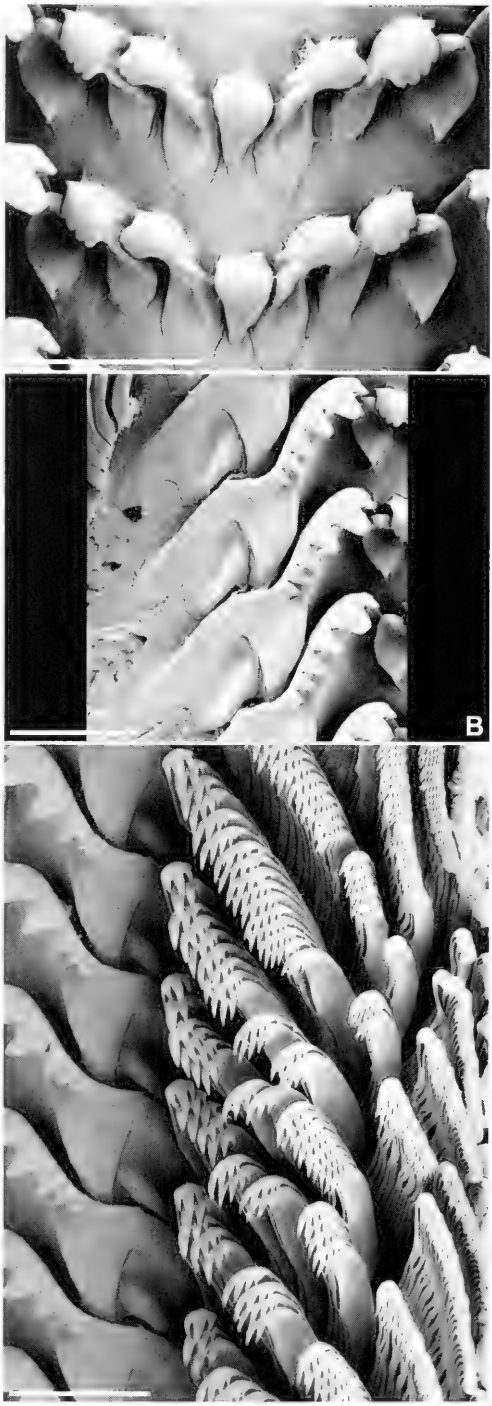


FIG. 217. Radula of *Helicina escondida* n. sp. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

FIG. 218. Female reproductive system of *Helicina escondida* n. sp., ZMB 103880; scale bar 1 mm.

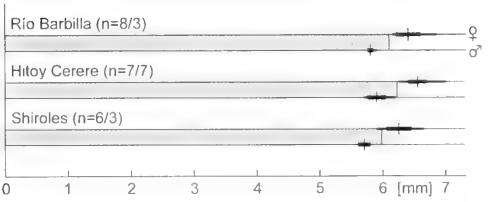


FIG. 219. Shell height of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex.

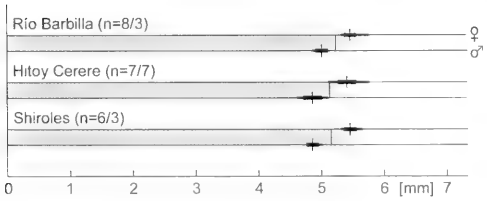


FIG. 220. Minor diameter of shell of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

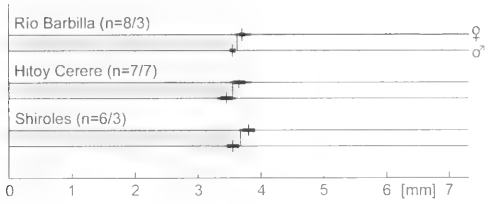


FIG. 221. Expansion of outer lip of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

Morphometry: The populations show only minor deviations among each other and for the different measurements. Only the specimens from Hitoy Cerere are a little more elevated (height and height of the columellar axis).

Sexual Dimorphism: The data show a clear distinction between the measurements for sexes, with the males being much smaller (Figs. 224–226). In interpolation from the minor diameter, males have an average volume of about 74% that of the females, resembling *Helicina tenuis*.

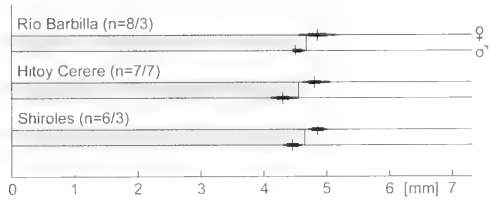


FIG. 222. Height of last whorl of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

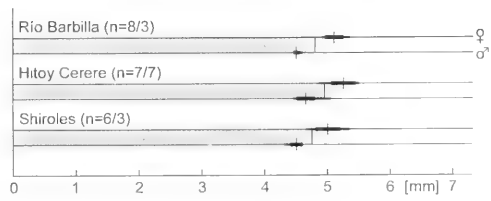


FIG. 223. Height of columellar axis of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

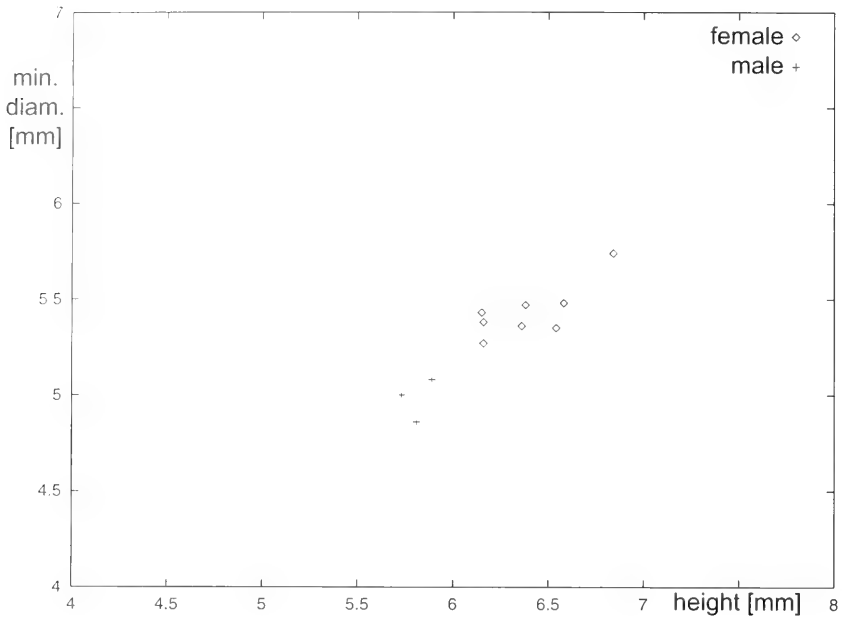


FIG. 224. Range of measurements in females and males of *Helicina escondida* n. sp. exemplary for height and minor diameter in the population from the Río Barbilla.

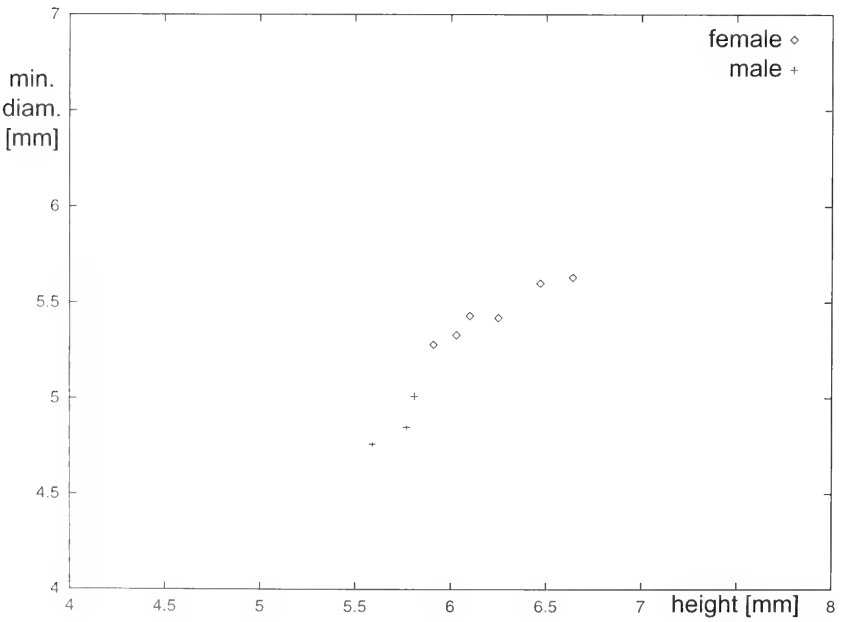


FIG. 225. Range of measurements in females and males of *Helicina escondida* n. sp. exemplary for height and minor diameter in the population from the Shiroles.

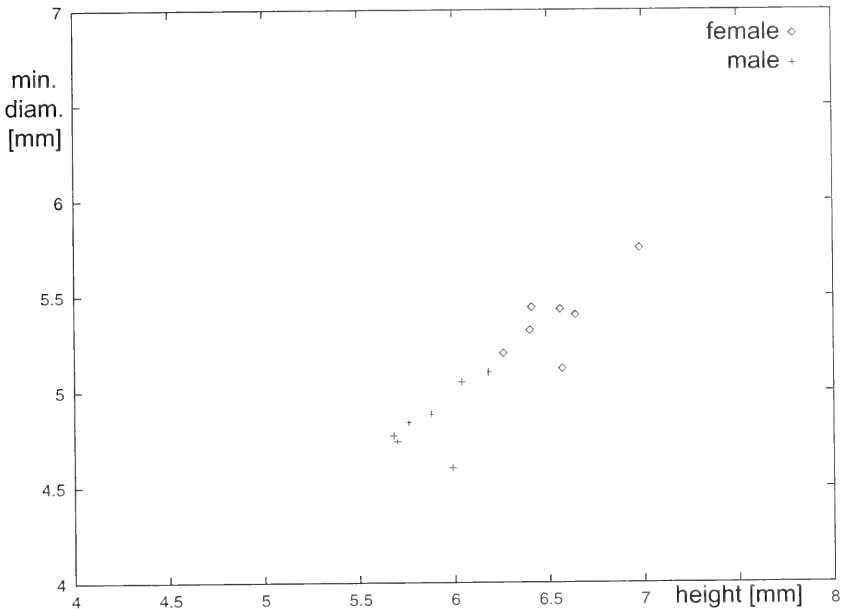


FIG. 226. Range of measurements in females and males of *Helicina escondida* n. sp. exemplary for height and minor diameter in the population from the Hitoy Cerere.

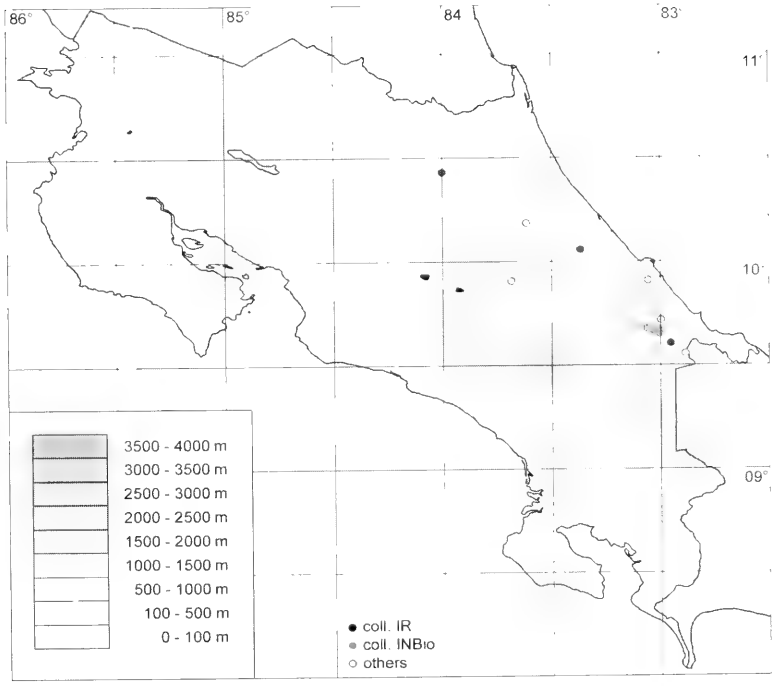


FIG. 227. Records of *Helicina escondida* n. sp. in Costa Rica.

TABLE 12. Measurements of different populations of *Helicina escondida* n. sp. given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm].

		"Río Barbilla" (altitude 70 m) lot IR 1543					"Hitoy Cerere" (altitude 110–798 m) lots INBio 1466441, 1497850, 1498244, 3542523, 3091132, 3091794				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.40	0.19	6.15	6.84	8	6.55	0.16	6.26	6.98	7
Height	m	5.81	0.05	5.73	5.89	3	5.89	0.15	5.68	6.18	7
Maj. diam.	f	5.90	0.10	5.76	6.09	8	5.85	0.19	5.58	6.26	7
Maj. diam.	m	5.44	0.10	5.32	5.59	3	5.30	0.14	4.98	5.58	7
Min. diam.	f	5.44	0.10	5.27	5.74	8	5.38	0.14	5.12	5.75	7
Min. diam.	m	4.98	0.08	4.86	5.08	3	4.85	0.13	4.60	5.10	7
Outer lip	f	3.72	0.07	3.58	3.86	8	3.66	0.11	3.48	3.85	7
Outer lip	m	3.56	0.04	3.52	3.62	3	3.43	0.10	3.28	3.60	7
Last whorl	f	4.84	0.14	4.56	5.13	8	4.82	0.10	4.62	5.04	7
Last whorl	m	4.52	0.08	4.44	4.64	3	4.28	0.10	4.12	4.57	7
Col. axis	f	5.09	0.13	4.89	5.34	8	5.23	0.18	4.87	5.52	7
Col. axis	m	4.49	0.06	4.44	4.58	3	4.67	0.13	4.47	5.03	7

	"Shiroles" (altitude 430 m) lot IR 1601					
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	6.23	0.22	5.91	6.64	6
Height	m	5.72	0.09	5.59	5.81	3
Maj. diam.	f	5.95	0.08	5.86	6.18	6
Maj. diam.	m	5.38	0.09	5.24	5.51	3
Min. diam.	f	5.45	0.11	5.28	5.63	6
Min. diam.	m	4.87	0.09	4.76	5.01	3
Outer lip	f	3.79	0.08	3.67	3.93	6
Outer lip	m	3.56	0.08	3.45	3.66	3
Last whorl	f	4.84	0.11	4.69	5.01	6
Last whorl	m	4.47	0.10	4.32	4.58	3
Col. axis	f	4.99	0.18	4.67	5.37	6
Col. axis	m	4.49	0.11	4.32	4.60	3

Habitat

Helicina escondida n. sp. is an arboreal species that was found on the lower side, more seldomly, the upper side, of small-leafed undergrowth plants. It also was observed aestivating on fronds of ferns. Near the Río Barbilla, the species was only found along a small creek together with *H. chiquitica*. North of Shiroles and probably in Hitoy Cerere, it occurs sympatrically with *H. beatrix confusa* and *H. funcki*. There it was found on a ridge with forest cover.

Distribution (Fig. 227)

The species occurs on the central and southern Caribbean side of Costa Rica at some distance from the coast mainly in the slightly elevated hilly countryside. The most northern occurrence is from the northern foothills of the Cordillera Central; to the south, *Helicina escondida* n. sp. reaches the Valle de Talamanca. Between the neighboring valleys Valle de Estrella and Valle de Talamanca, the species lives up to altitudes of about 800 m.

Because undisturbed areas in this region are still relatively uninvestigated due to their inaccessible nature, it is very likely that *H. escondida* n. sp. can be found at additional localities.

Discussion

Helicina escondida n. sp. was found in at least three different colors within one population (Figs. 210–212, 336K–M): (1) unicolored yellow (represented in holotype, Fig. 336K), (2) reddish-brown, except for the umbilical area, which is whitish (represented by paratype 1, Fig. 336L), or (3) the upper half of each whorl is reddish brown, this may be very light, and the lower half yellow or only with a yellowish band, the transition of both colors exactly at the suture/ periphery, so that the yellow is only seen on last whorl (represented by paratype 2, Fig. 336M). The outer lip is constantly whitish-yellowish.

Helicina escondida n. sp. is distinguished from other small helicinids, such as *H. beatrix*, *H. talamancensis*, *H. monteverdensis* n. sp., *H. fragilis*, and *H. gemma*, by the special surface structure of fine oblique lines and spiral striations. In the species mentioned, it is shiny and smooth. Furthermore, the aperture is straight and not curved backwards. Finally, the groove in the umbilical area is unique for *H. escondida* n. sp. among comparable species. (For further discussion of small, fragile, whitish-yellowish Central American Helicinidae, see the section on *H. monteverdensis* n. sp.) In *H. beatrix*, the whorls are much more convex, and it has a higher spire and a distinct whitish subsutural band. *Helicina gemma* has a orange-scarlet outer lip, whereas in *H. escondida* n. sp. it is yellowish-white. At its type locality, *H. chiquitica* and *H. escondida* n. sp. occur sympatrically, but they are easily separated by their size, color, shape and shell surface texture.

Helicina (*"Gemma"*) *chiquitica*
(Richling, 2001)

Alcadia (*Leialcadia*) *fragilis* – Wagner, 1908: 84–85: Costa Rica: Shirores, Talamanca [in part] [*non* Morelet, 1851]

Oligyra chiquitica Richling, 2001: 1–2 (text figure)

Original Description

See "Description".

Type Material

Holotype: INBio 3404977, female (leg. I. Richling, 12.3.2001)
Paratype 1: INBio 3404981, male (same data as holotype)
Paratype 2: ZMB 103386a, female (same data as holotype)
Paratype 3: ZMB 103386b, male (same data as holotype)
Dimensions (height/greatest diameter):
Holotype: 4.9/4.5 mm
Paratype 1: 4.3/4.2 mm
Paratype 2: 4.6/4.4 mm
Paratype 3: 4.3/4.1 mm

Type Locality

SE-Costa Rica, Limón Province, approximately 9 km W of Matina, a little upstream on the Río Barbilla from the crossing of the road from Siquirres to Limón, along a tributary of Río Barbilla, 10°03'29"N, 83°22'24"W, 70 m a.s.l., in the valley of a small creek in rain forest (probably secondary forest).

Examined Material

Leg. I. Richling
Heredia: S Puerto Viejo de Sarapiqui, *Zona Protectora La Selva*, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1662)
Limón: About 9 km W of Matina, road from Limón to Siquirres, a little stream up the *Río Barbilla*, along a tributary of Río Barbilla, in the valley of a small creek in rain forest, 10°03'29"N, 83°22'24"W, 70 m a.s.l., 12.03.2001: (IR 1539)
S Siquirres, road from Limón to Siquirres, along footpath stream up *Río Pacuarito*, in the valley of a little northern tributary, 10°05'38"N, 83°28'11"W, 110 m a.s.l., 18.03.2001: (IR 1611)

INBio Collection
Cartago: *Parque Nacional Barbilla*, Sector de la Estación de Barbilla, leg. Alexander Alvarado Mendez: 09°58'26"N, 83°27'58"W, 500 m a.s.l., 28.09.2000: 1 ad. (INBio 3100273); 09°58'24"N, 83°27'23"W, 300 m a.s.l., 30.09.2000: 1 ad. (INBio 3104239)
Zona Protectora Río Pacuare, Sector de la Estación de Barbilla, 09°58'50"N, 83°27'08"W, 500 m a.s.l., leg. Alexander Alvarado Mendez, 05.09.2000: 1 ad. (INBio 3103323)

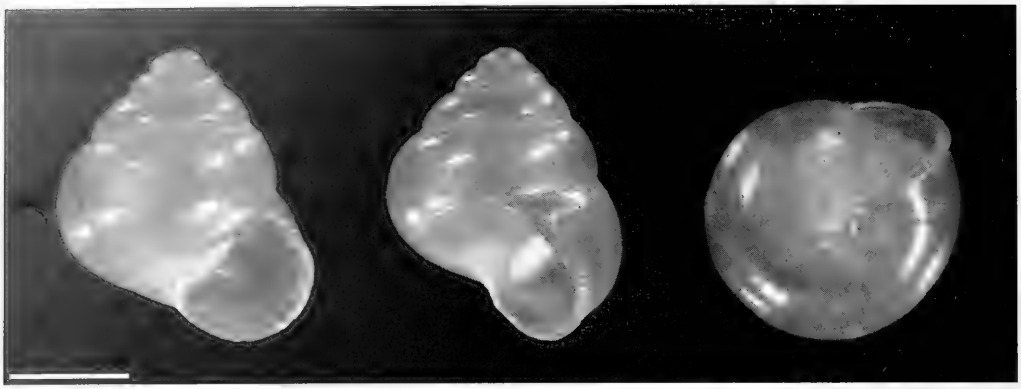


FIG. 228. *Helicina chiquitica*, holotype, INBio 3404977, height 4.9 mm; scale bar 2 mm.

Other Sources

COSTA RICA

Limón: Shirores [Shiroles, 09°35'38"N, 82°57'20"W], Talamanca: leg. H. Pittier (#269): 1 s.ad. (MHNN, part of the lot); leg. H. Pittier (#208), 03.1895: 1 ad., 2 s.ads. (ZMB 48336, part of the lot); leg. Pittier: 1 ad. (ZMB 103250)

Etymology

The species is named for its small size. "Chiquitica" is a diminutive of "chiquita" (Spanish) = "small". In Latin America it correctly would be "chiquitita", but in Costa Rica the diminutive syllable "-tito/a" sometimes is changed to "-tico/a"; the Costa Rican people call themselves also Ticos.

Description

Shell (Figs. 228, 336N): conical-globose, thin, small, shiny. Color: unicolored, reddish-brown, more or less transparent, towards aperture color more intensive. Periostracum very thin, shiny and smooth, except for very fine growth lines. Embryonic shell of about 1 whorl; subsequent $3^{3}/_{8}$ to 4 (holotype: 3¾) whorls slightly convex, equally extending in size; last whorl rounded at periphery. Suture slightly impressed. Aperture oblique and in its middle part slightly curved backwards. Outer lip dark red, thickened, very narrowly reflexed. Basal callus thin, in umbilical area surface scaly-granulated.

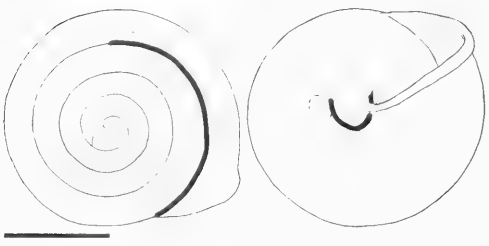


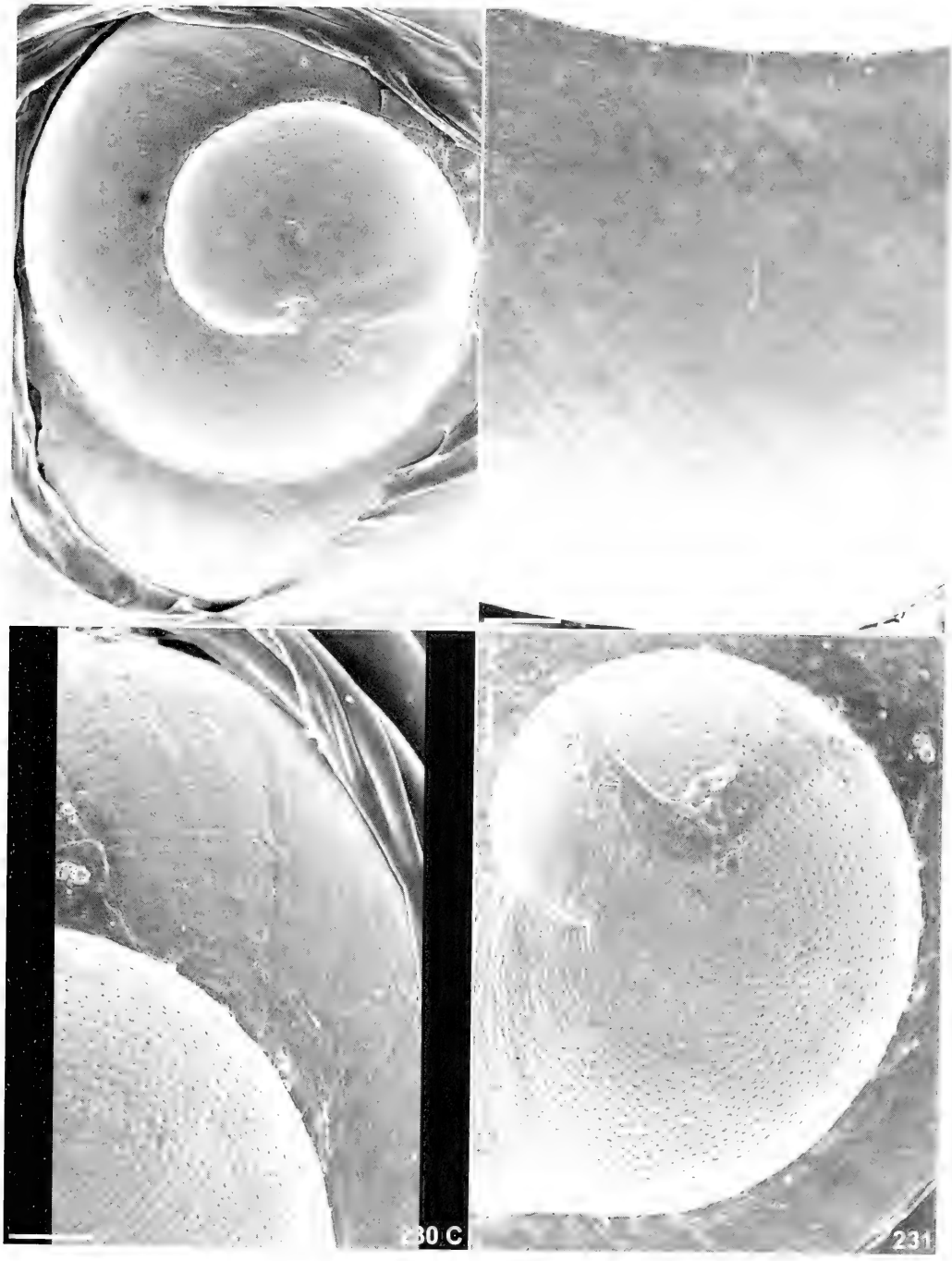
FIG. 229. Axial cleft and muscle attachments of *Helicina chiquitica*, INBio 3404977; scale bar 2 mm.

Internal Shell Structures (Fig. 229):

Teleoconch Surface Structure (Fig. 230): The transitional pattern is well developed (about ½ of a whorl), the subsequent zone with oblique diverging grooves is short. The rest of the teleoconch is smooth, except for fine growth lines.

Embryonic Shell (Fig. 231): The structure does not exhibit peculiarities and closely resembles that of *Helicina gemma*. Compared with the shell size of the latter, the diameter of the embryonic shell of *H. chiquitica* is only slightly smaller. The embryonic shell of the clearly larger *H. escondida* n. sp. is on average even smaller (728 µm) than that of *H. chiquitica*. This shows that embryonic shell size does not always depend on the shell size (see general discussion below).
Diameter: 749 µm (± 28) (660–800) (n = 25) (IR 1539).

Operculum (Fig. 232): Very slightly calcified, calcareous plate not reaching the margin.



FIGS. 230, 231. Shell structure of *Helicina chiquitica*. FIG. 230 Teleoconch surface structure. A. Structure of apical part. B. 2nd whorl. C. 1st whorl: occasional sharp transition from oblique diverging grooves to smooth surface; scale bars 500 µm (A), 100 µm (B–C). FIG. 231. Embryonic shell; scale bar 100 µm.

FIG. 232. Operculum of *Helicina chiquitica*, holotype, INBio 3404977; scale bar 1 mm.

Color horny-amber, slightly transparent. Columellar side S-shaped, upper end acute, lower edge rounded. On inner side, a little ridge parallel to columellar margin. Outer surface granulated.

Animal (Figs. 339C, D): The foot-head region shows a similar color to other species in being greyish-black on the dorsal half including the tentacles. The mantle pigmentation is black throughout or mottled with small pale dots mainly in the apical part. The yellow-shelled form is also much paler in the body color.

Radula (Fig. 233): All centrals lack well-defined cusps and the faces are less pronounced. Comb-lateral with 10–12 pointed cusps, a high number among the Costa Rican species. Cusps on marginals rapidly increasing in number. Radula with about 65–72 rows of teeth.

Female Reproductive System (Fig. 234): The ascending limb of the V-organ is very prominent and stout, the receptaculum seminis is rather small and oblong. The bursa copulatrix is formed by an irregular ovoid sac, which appears to be internally subdivided. The provaginal sac is simple and connected by a short duct. The pallial oviduct is relatively short.

Morphometry and Sexual Dimorphism (Table 13, Figs. 235–239)

Helicina chiquitica is the smallest arboreal species investigated in this study. The few

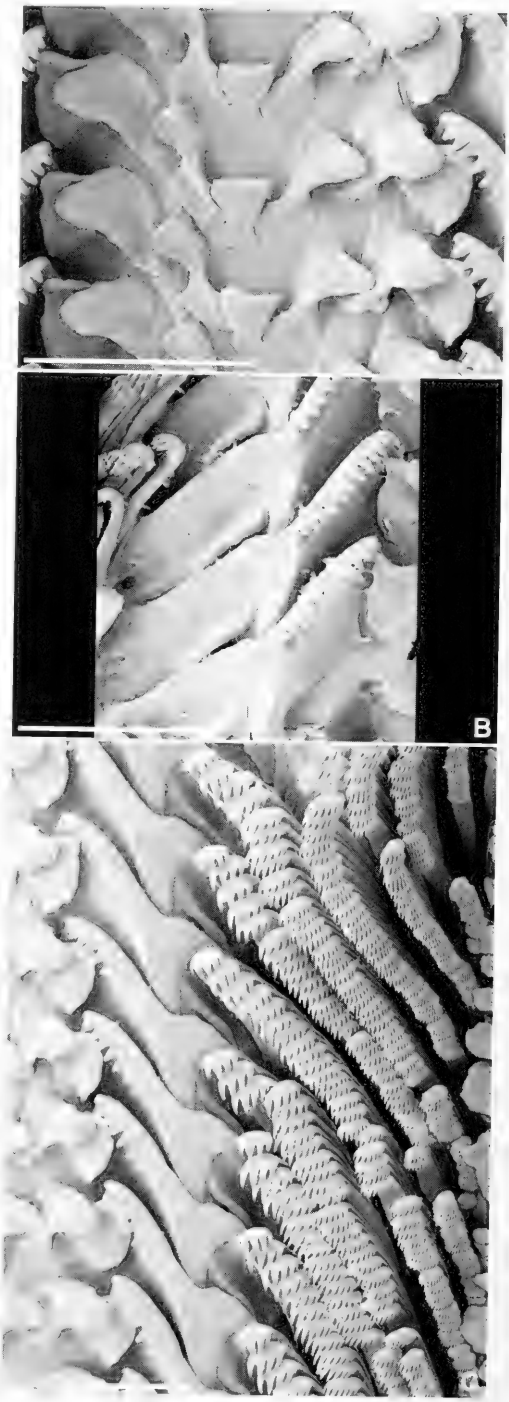


FIG. 233. Radula of *Helicina chiquitica*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

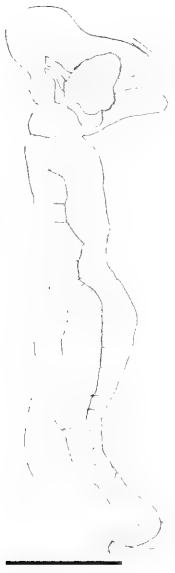


FIG. 234. Female reproductive system of *Helicina chiquitica*, IR 1539; scale bar 1 mm.

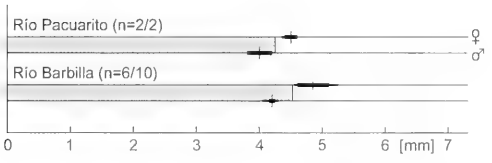


FIG. 235. Shell height of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex.

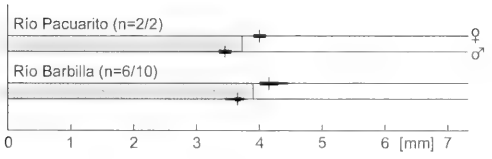


FIG. 236. Minor diameter of shell of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

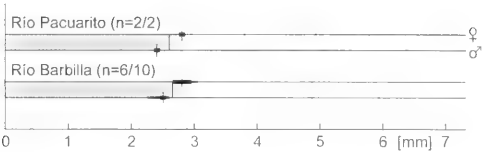


FIG. 237. Expansion of outer lip of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

specimens of *H. chiquitica* from two different localities suggest a smaller shell size for the site "Río Pacuarito", but the sample size is small.

On the other hand, sexual dimorphism is undoubtedly indicated. The clear distinction between the sexes is also illustrated at "Río Barbilla" (Fig. 240). In the interpolation from the minor diameter, males have an average volume of about 65% of that of females.

Habitat

The species has mainly been found on the lower side of leaves of Araceae, occasionally also on the leaves of bushy plants of the undergrowth. At Río Barbilla and Río Pacuarito,

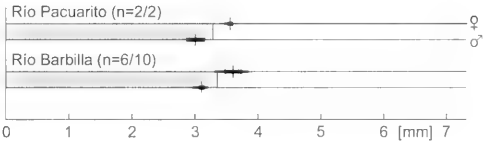


FIG. 238. Height of last whorl of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

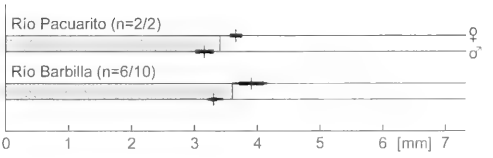


FIG. 239. Height of columellar axis of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

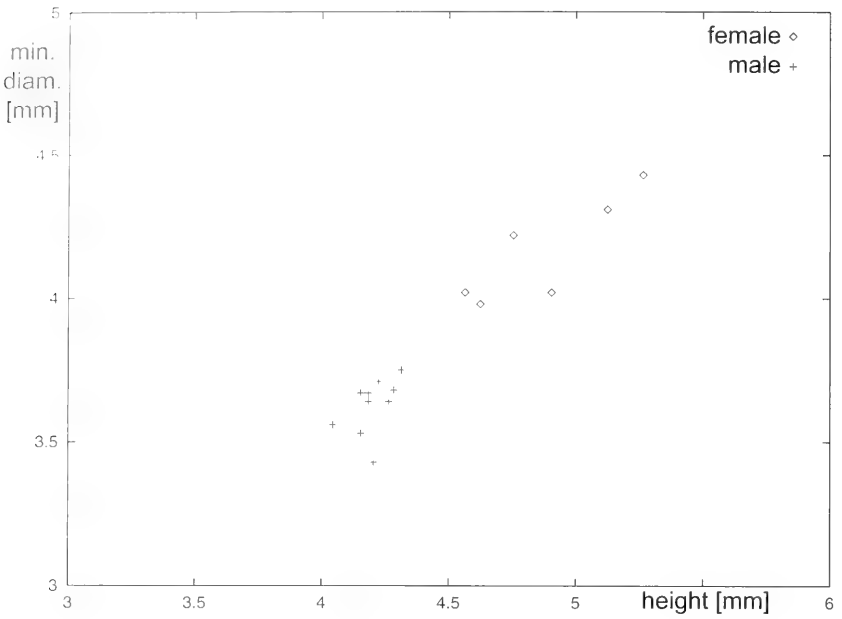


FIG. 240. Range of measurements in females and males of *Helicina chiquitica* exemplary for height and minor diameter in the population from the Río Barbilla.

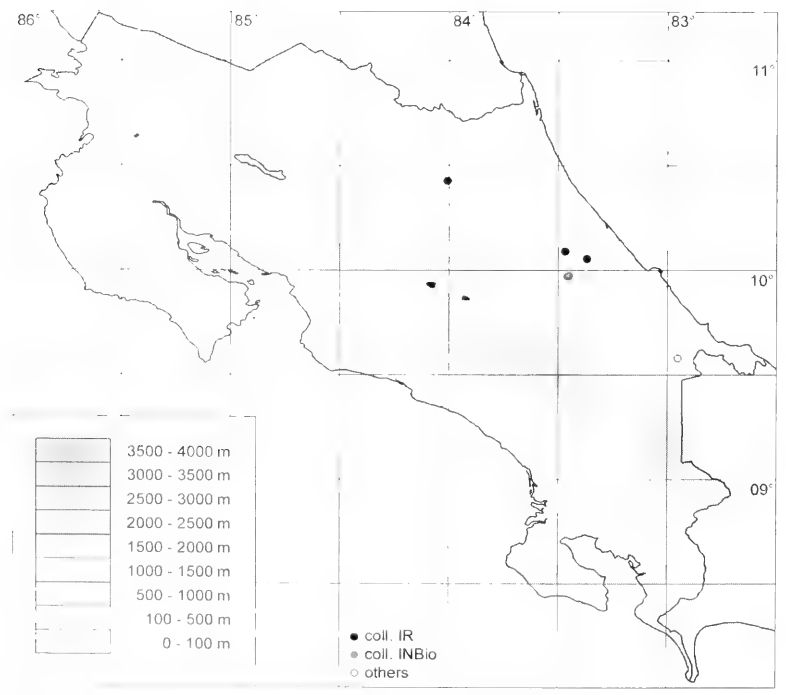


FIG. 241. Records of *Helicina chiquitica* in Costa Rica.

TABLE 13. Measurements of the two populations of *Helicina chiquitica* given as mean value with standard deviation, minimum and maximum0 value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

		"Río Barbilla" (altitude 70 m) lot IR 1539					"Río Pacuarito" (altitude 110 m) lot IR 1611				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	4.87	0.23	4.56	5.26	6	4.49	0.12	4.37	4.60	2
Height	m	4.20	0.06	4.04	4.31	10	3.99	0.21	3.78	4.20	2
Maj. diam.	f	4.48	0.13	4.33	4.68	6	4.33	0.06	4.26	4.39	2
Maj. diam.	m	3.97	0.10	3.73	4.16	10	3.72	0.13	3.59	3.84	2
Min. diam.	f	4.16	0.16	3.98	4.43	6	4.01	0.09	3.92	4.09	2
Min. diam.	m	3.63	0.07	3.43	3.75	10	3.44	0.09	3.35	3.53	2
Outer lip	f	2.82	0.13	2.64	3.04	6	2.78	0.04	2.74	2.82	2
Outer lip	m	2.49	0.07	2.27	2.61	10	2.42	0.04	2.38	2.45	2
Last whorl	f	3.61	0.14	3.38	3.84	6	3.54	0.07	3.47	3.61	2
Last whorl	m	3.10	0.05	2.94	3.20	10	3.01	0.13	2.88	3.13	2
Col. axis	f	3.88	0.18	3.60	4.17	6	3.64	0.10	3.54	3.74	2
Col. axis	m	3.32	0.07	3.18	3.44	10	3.15	0.17	2.98	3.31	2

the occurrence seems to be confined to the vegetation along small, partly steep creeks. At the former locality, *Helicina chiquitica* lives sympatrically with *H. escondida* n. sp.

Distribution (Fig. 241)

Except for the single record northeast of the Central Cordiilera, the few records are in the most northern part of the Caribbean foothills of the Cordillera de Talamanca. *Helicina chiquitica* has only been found some distance from the coast in the hilly countryside from elevations of 70 m to 500 m. The undisturbed areas in this region have scarcely been investigated, because they are difficult to reach. The northern record renders it also very likely that *H. chiquitica* will be found at additional localities.

Furthermore, the small size and the rapid decay of shells in a humid tropical climate provide grounds for assuming that the species has a wider distribution than actually been documented. A study by Barrientos (2000) for *Ovachlamys fulgens* (Gude, 1900) suggests that shells decay in less than five months in the climate of San José with 5–6 dry months per year as opposed to the Caribbean slope, where, lacking dry months, it would take place even faster.

Discussion

In some specimens, the apex is reddish-brown, but the subsequent whorls are yellow. In this case the outer lip is yellow too.

In its shape and shell sculpture, *Helicina chiquitica* is comparable to *H. gemma*, *H. monteverdensis* n. sp., and *H. fragilis*, but *H. chiquitica* is much smaller and has a different color. None of the two species mentioned shows such a dark color in combination with a dark outer lip. The size of the new species is exceptionally small for the known Central American helicinids of this shape. *Helicina strebeli* L. Pfeiffer, 1861, is another small helicinid from Mexico, generally treated as a small subspecies or variety of *Helicina flavida* (see von Martens, 1890; Fischer & Crosse, 1893; Baker, 1928), which clearly differs by its spiral striation. *Helicina mohriana* L. Pfeiffer, 1861, described from Orizaba, Mexico, is discussed as a dubious species or perhaps juvenile stage by Martens (1891) and Fischer & Crosse (1893) or as a synonym of *Helicina fragilis merdigera* by Baker (1922a) respectively. According to the original description, however, it is a little broader than it is high, whereas in *H. chiquitica* all specimens show the reverse relation. Furthermore *H. mohriana* seems to have more whorls (5.5) than the new

species, for which 5 (4 plus about 1 of embryonic shell) whorls are exceptional.

The record of Wagner (1908) for Shiroles in Costa Rica had been based on the material in the ZMB, since the specimens carried determinations written by Wagner. Reexamination of the material revealed specimens of *H. chiquitica*, but the lot (and a similar lot of Pittier stored in the MHNN) consists of two different species, where, unfortunately, all deviating specimens are immature. They exhibit very strong spiral cords, but do not seem to represent *H. escondida* n. sp. which has recently been found at Shiroles, whereas *H. chiquitica* has not as yet been discovered there.

Pyrgodomus microdinus
(Morelet, 1851)

Helicina microdina Morelet, 1851: 18 (not figured)
Helicina microdina – L. Pfeiffer, 1852a: 354
Helicina microdina – L. Pfeiffer, 1852b: 256
Helicina chryseis Tristram, 1862: 5: Guatemala: mountain forests of Vera Paz (Salvin) (not figured)
Helicina microdina – Bland, 1866: 8
Helicina chryseis – Bland, 1866: 10
Helicina chryseis – von Martens, 1890: 39, pl. I, fig. 14
Helicina microdina – von Martens, 1891: 42 (dubious species)
Helicina (*Pyrgodomus*) *chryseis* – Fischer & Crosse, 1893: 440, pl. LVII, fig. 6
Helicina (*Idesa*) *microdina* – Fischer & Crosse, 1893: 438–439, pl. LVI, fig. 9
Helicina chryseis – von Martens, 1900: 606
Eutrochatella (*Artecallossa* [sic]) *microdina* – Wagner, 1908: 138–139, pl. 20, figs. 17–20
Eutrochatella microdina chryseis – Pilsbry, 1920b: 197: Guatemala: Chama
Eutrochatella nicrodina [sic] var. *chryseis* – Hinkley, 1920: 52: Guatemala: Alta Verapaz: Chama between Río Tsalbha and Río Negro Chama: also in river drift
Eutrochatella (*Pyrgodomus*) *microdina microdina* – Baker, 1922a: 61
Eutrochatella (*Pyrgodomus*) *microdina chryseis* – Baker, 1922a: 61 (may be a sex-form)
Pyrgodomus microdinus chryseis – Baker, 1928: 45–46
Pyrgodomus microdinus microdinus – Baker, 1928: 45–46
Pyrgodomus microdina – Goodrich & van der Schalie, 1937: 13, 33: Guatemala: Petén: region of headwater of Río San Pedro de Mártir, lower Río de la Pasión; Alta Verapaz: upper part of Río de la Pasión
Pyrgodomus ? spec. – Monge-Nájera, 1997: 113: Costa Rica

Synonymy

Helicina chryseis Tristram, 1862

Original Description

"T. parvula, conica, transversim minute striata, spiraliter lirata, flava, sursum saturatior. Anfr. 6 convexi, ultimo angulato; columella arcuata, superne callosa, subdilatata. Apertura obliqua, ovalis, margine simplici, recto.

FIG. 242. *Helicina microdina*, lectotype, BMNH 1893.2.3.1986, height 3.8 mm; scale bar 1 mm.

Altit. 4. – Diam. 4.
H. vulgaris prov. Vera-Paz.
Primo aspectu *H. rupestris* Pfr. congruit, quamvis in universum ab ea dissimilis."

Type Material

BMNH 1893.2.3.1986–90: Morelet coll., purchased from H. Fulton
The Morelet collection was bought by H. Fulton and later purchased by the BMNH. Fischer & Crosse (1893) studied the original material in Morelet collection and figured one shell which can be identified by the mark of a "x". This shell is **here selected as lectotype** of *Helicina microdina* (BMNH 1893.2.3.1986) (Fig. 242), because it is uncertain whether Fischer & Crosse's comment in the figure caption (pl. LVI, figs. 9, 9a, 9b, 9c: "Type de l'*H. microdina*") can be regarded as a type selection.
Dimensions (height/greatest diameter/minor diameter):
Lectotype BMNH 1893.2.3.1986: 3.8/3.9/3.5 mm

Type Locality

"Vera-Paz" [Guatemala, Alta Verapaz Department].

Examined Material

Leg. I. Richling
Puntarenas: *N Neily*, road from Ciudad Neily to San Vito, open area with a few trees, 08°40'23"N, 82°56'44"W, 180 m a.s.l., N Neily, 23.03.1997: (IR 209)

Fila de Cal, road from Ciudad Neily to San Vito: *S Campo Dos, burned area and ground with secondary growth and limestone rocks, 08°41'00"N, 82°56'29"W, 630 m a.s.l.*: 23.03.1997: (IR 192); 07.03.1998: (IR 502); 09.02.2000: (IR 1147); *Campo Dos, on Finca, secondary growth and limestone rocks, 08°41'16"N, 82°56'38"W, 700 m a.s.l.*: 07.03.2001: (IR 1517)

INBio Collection
Puntarenas: *Fila Cal, 24 km de San Vito hacia Ciudad Neilly, 08°41'36"N, 82°56'36"W, 780 m a.s.l., 14.01.1995*: leg. Francisco Alvarado: 1 spec. (INBio 1480755); 1 spec. (INBio 1495177); leg. Annia Picado: 2 spec. (INBio 1481148); leg. Mario Chinchilla: 1 spec. (INBio 1481257); leg. Socorro Avila: 3 spec. (INBio 1481361); leg. Ronald Villalobos: 6 spec. (INBio 1481512); leg. Marcos Moraga: 4 spec. (INBio 1481563); leg. Oscar Esquivel: 5 spec. (INBio 1485112); leg. Marcos Madrigal: 2 spec. (INBio 1495685); leg. Enia Navarro: 1 spec. (INBio 1495695); 29.08.1995: leg. Marianella Segura: 11 spec. (INBio 3307036); *24.5 Km S en la carretera de San Vito hacia Ciudad Neilly, 08°40'55"N, 82°56'23"W, 600 m a.s.l.*: leg. Zaidett Barrientos, 21.11.1995: 1 spec. (INBio 1485119)

Description

Shell (Figs. 243, 336R): Conical, high-elevated, triangular in general shape, solid, small sized, dull. Color: bright yellow and on

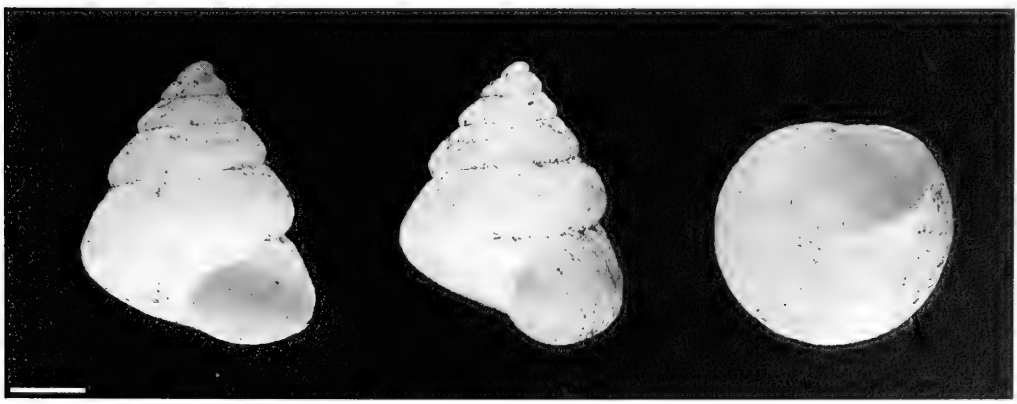
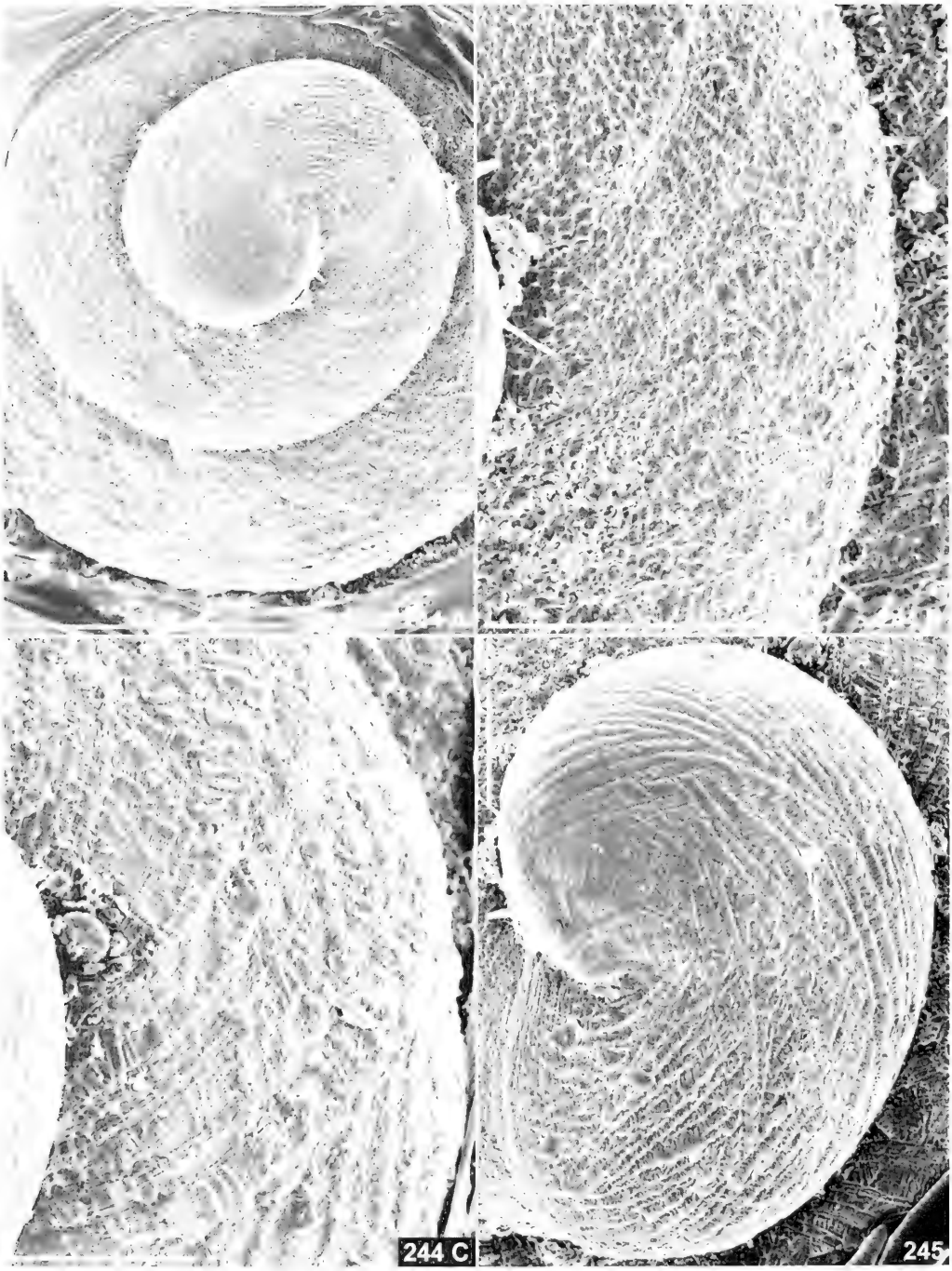


FIG. 243. *Pyrgodomus microdinus*, Fila de Cal, IR 1517, height 3.8 mm; scale bar 1 mm.



FIGS. 244. 245. Shell structure of *Pyrgodomus microdinus*. FIG. 244. Teleoconch surface structure. A. apical part. B. 1st whorl, transitional structure. C. 1st whorl, structure of postembryonic shell; scale bar 500 µm (A); 100 µm (B–C). FIG. 245. Embryonic shell; scale bar 100 µm.

upper side darker colored. Whorls sculptured with spiral ridges, very rough and irregular growth lines and oblique striations. Embryonic shell with about 1 whorl; about 4½ subsequent whorls straight; last whorl angulated on periphery. Whorls equally increasing in size and rapidly descending, always inserting a little below periphery, forming a high, pointed, stepped spire. Suture deeply impressed. Aperture oblique and rather straight. Outer lip of same color as preceding whorls, neither remarkable thickened nor shortly expanded or reflected. Columella short and arched. Basal callus weakly developed.

Internal Shell Structures: Sufficient adult material was not available, especially because the thickness of the whorls would have required cracking the shell in order to examine the internal structures.

Teleoconch Surface Structure (Fig. 244): In *Pyrgodomus microdinus*, a structured transitional zone similar to that of the Costa Rican species of *Helicina* is developed for a certain distance at the very beginning of the teleoconch. This zone exhibits a very rough irregular surface of numerous small denticles. The following whorls bear spiral ridges crossed by irregular growth lines that are wrinkled throughout.

Embryonic Shell (Fig. 245): *Pyrgodomus microdinus* displays a greatly different embryonic shell surface structure. Coarse oblique diverging grooves cover the embryonic shell resulting in a very rough surface. Diameter: 530 µm (± 13) (510–550) (n = 4) (IR 192, IR 1517).

Operculum: Calcified portion strongly developed, horny plate very thin and slightly larger, columellar side of calcareous plate slightly convex and thickened. Color whitish and only very slightly transparent. Nucleus nearly in central position, and growth lines almost concentric.

Animal (Fig. 339E): The whole snout and the underside of the foot is whitish-yellowish, the latter darkens gradually to grey towards the upper side. The tentacles are of the same grey, which becomes diffuse at the bases, so that between the tentacles and behind the eyes the head region is tinged with the

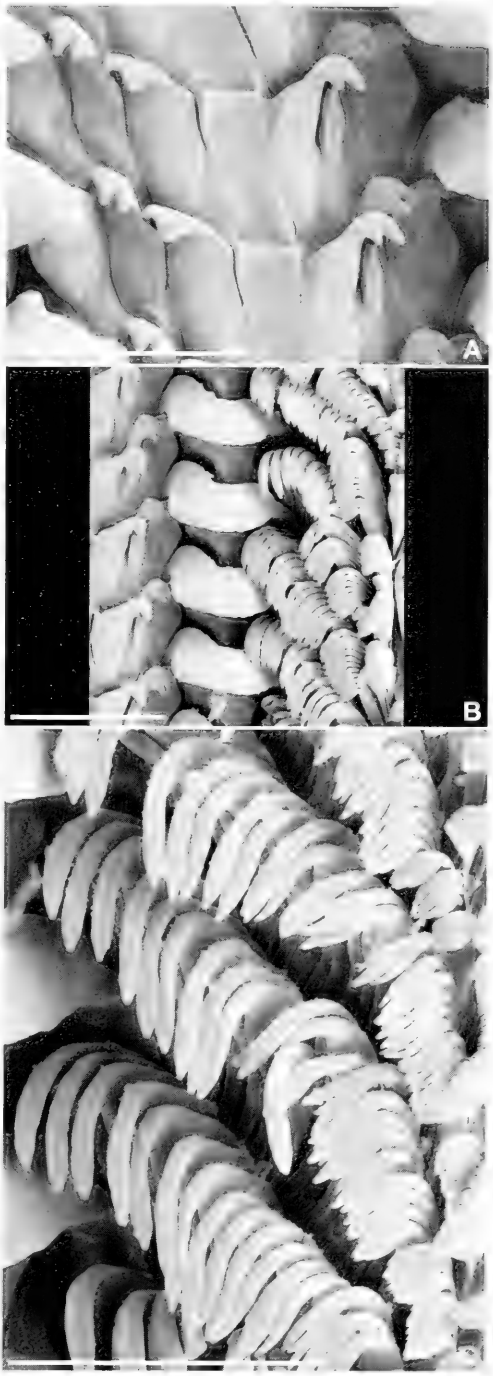


FIG. 246. Radula of *Pyrgodomus microdinus*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

lighter color of the snout. The mantle bears dark patches, which shine through the shells in live specimens and result in a greenish-grey appearance of the animals.

Radula (Fig. 246): Since sufficient Costa Rican material was not available, a specimen from Honduras (Colón Depto., limestone hill, 3 km WSW La Brea, 100 m a.s.l., leg. F.G. Thompson et al. (FGT-5389), 10.03.1994 (UF 221175) was studied.
R-central quadrangular; A- and B-central each bearing 2 sidewards projecting cusps; C-central with 3 denticles. Comb-lateral strong developed and T-shaped with minor crenulations at the cutting edge. Inner marginals unicuspid, outwards slowly increasing number of slender, rather terminal cusps. Radula with about 130 rows of teeth. Baker (1928) studied the radula of the smaller Mexican *Pyrgodomus microdinus abditus* Baker, 1928, and described bicuspid inner marginals, which necessitated a change in the original definition of the subfamily Vianinae with unicuspid inner marginals. Furthermore, the centrals bear each one cusp more, and the denticles on the cutting edge of the T-lateral are more pronounced. It remains questionable whether these deviations are typical for the Mexican subspecies alone, or whether the single specimen investigated in this study is representative at all or if they are subject to individual variation. The increased number of cusps in the smaller Mexican subspecies could also be caused by the phenomenon that smaller specimens/species of Helicinidae independently from their phylogenetic position show a tendency to develop more cusps (see general Discussion).

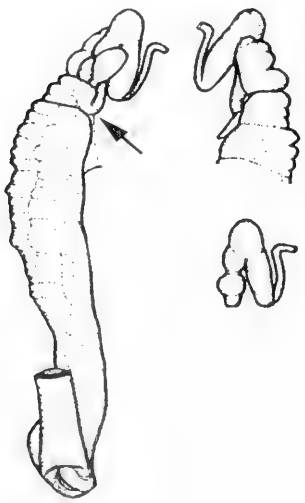


FIG. 247. Female reproductive system of *Pyrgodomus microdinus abditus*, reproduced from Baker (1928: pl. IV, figs. 21–23).

Female Reproductive System: In Costa Rica, no adult live specimens could be found, only some juveniles, therefore their anatomy could not be investigated.
Baker (1928) (reproduced here in Fig. 247) gave a description of the female reproductive system of *Pyrgodomus microdinus abditus*: The apical part of the V-organ is slightly elongated (apical swelling) and the small spherical receptaculum seminis is situated near the middle of the dorsal side of the descending limb (not visible in his figure). The bursa copulatrix is formed by a long ellipsoid sac; the bigger, rounded triangular provaginal sac exhibits coarse lobes on its distal margin. Provaginal duct and vagina are not explicitly mentioned or shown (Fig. 247, arrow), but they are believed to open into the hypobranchial duct, which orifice lies at about $^1/_5$ to $^1/_6$ of the length of the pallial oviduct. In the light of the newly discovered absence of provaginal opening in the Costa Rican species of *Helicina*, this question remains open for *P. microdinus abditus* pending further investigation. The close relationship to *Eutrochatella*, which is indicated by a similar embryonic shell structure, suggests the absence of a provaginal opening, because it is undeveloped in this genus (see under *Eutrochatella* below).

Morphometry and Sexual Dimorphism

Pyrgodomus microdinus was not found in sufficient numbers. In addition, most specimens were not fully grown, making a morphometric investigation impossible.

Habitat

Like related species (e.g., species of the genus *Eutrochatella*), *Pyrgodomus microdinus* lives on limestone rock faces and this obvious dependence characterizes the species as calciphile. Goodrich & van der Schalie (1937)

reported the species from Guatemala as being restricted to limestone outcrops. Under dry weather conditions, it was found aestivating on the underside of larger pieces of rocks or on shaded vertical sides and crevices of rocks.

Live specimens of *P. microdinus* are perfectly adapted to the background, because they possess a camouflage. Small particles of the surroundings are glued on the rough shell surface. This behavior was also observed in Guatemalan specimens by Goodrich & van der Schalie (1937). Only dead specimens show the bright yellow color.

Distribution

The Costa Rican occurrence seems to be limited to the area of the Fila de Cal north of Ciudad Neily (Fig. 248). In view of its ecological requirements, this distribution clearly reflects geological conditions. In Costa Rica, calcareous outcrops are only found in a very few places, such as the Fila de Cal.

The type locality of *P. microdinus* is Alta Verapaz, Guatemala. It has also been recorded from Péten in Guatemala and southern Veracruz, Mexico (as the subspecies *P. microdinus abditus*). For Belize, the different species, *P. simpsoni* (Ancey, 1886), is mentioned by Haas & Solem (1960). The Costa Rican populations seem to represent the most southerly occurrence of *P. microdinus*.

Discussion

Fischer & Crosse (1893) figured the species for the first time on the basis of the original Morelet material. They remarked on the similarity to *Pyrgodomus chryseis*, with the difference that the latter species is more elevated. However, they placed these species in different sections (*Idesa* and *Pyrgodomus*). Wagner (1908) proposed the synonymy of these taxa. Baker (1928) morphometrically compared *P. microdinus*, *P. chryseis* and populations from Veracruz, Mexico. As the result, he attributed the taxa to subspecific rank and raised a new

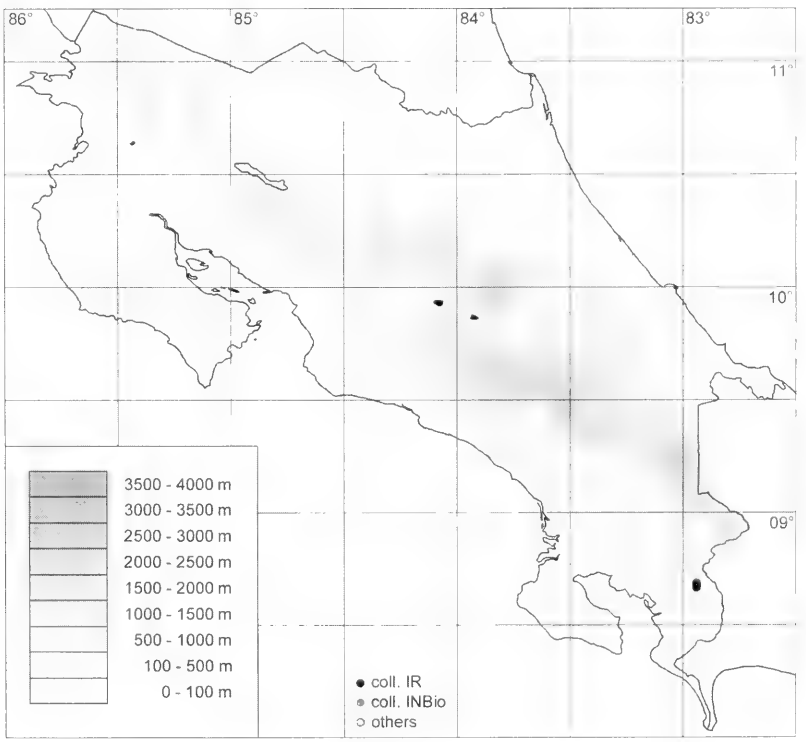


FIG. 248. Records of *Pyrgodomus microdinus* in Costa Rica.

subspecies for Mexican specimens, *P. microdinus abditus* having a smaller size, fewer whorls, and a more depressed shape. He noted that subspecific recognition of *P. microdinus chryseis* was uncertain and required study of a larger series. Ancey (1886) described a quite similar species from Isla de Utila off Honduras, *P. simpsoni*, which Baker (1928) treated as specifically distinct.

The very few adult Costa Rican specimens are remarkably elevated. Therefore, they more closely resemble *P. chryseis*. Against this historic background and because *P. chryseis* and *P. microdinus* both typically originate from the same area in Guatemala, it is more appropriate to regard them as synonymous until better knowledge of the distribution becomes available, thereby treating the Costa Rican specimens as *P. microdinus*. The geographical distance to the northern populations is uncertain due to the lack of extensive investigations of the Nicaraguan malacofauna.

Alcadia (*Microalcadia*) Richling, n. subgen.

Type Species

Helicina hojarasca Richling, 2001

Diagnosis

Shell very small, fragile, with fine spiral striations and rows of periostracal hairs; outer lip of adults not differentiated from the whorl. Calcareous layer of the operculum very thin. Embryonic shell with irregular axial threads and fine oblique grooves crossing each other. Comb-lateral of radula with numerous cusps. Female reproductive system with provaginal opening; provaginal duct very short, thin; bursa copulatrix very prominent; ascending limb of V-organ elongated, curved; receptaculum seminis on descending limb displaced to the ventral side and directed posteriorly.

Etymology

The name refers to the small size of members of this subgenus.

Discussion

The characters of the female reproductive system, in combination with the embryonic shell surface sculpture clearly assign the new subgenus to the genus *Alcadia* and distinguish it from *Helicina* and *Schasicheila*, which also may have been considered. Details about the characteristics of these genera as well as on other Central American supraspecific taxa, are given below.

The only subgenus which has not been included due to its South American occurrence and the absence of material for study is *Trichohelicina* Weyrauch, 1966 (type species by original designation: *Helicina* (*Trichohelicina*) *klappenbachi* Weyrauch, 1966, NE-Argentina, Misiones Province). In the light of the unexpected higher supraspecific diversity among the South American Helicinidae, such as *Angulata*, assignment to *Helicina* by Weyrauch (1966) certainly requires a critical reinvestigation, because it is only based on an impression in the basal callus. The hairy periostracum in both subgenera is regarded as a typical ecological adaptation of several ground-dwelling species and does not primarily indicate a closer relationship. In the absence of further morphological data for *Trichohelicina*, the main differences are the peculiar parietal canal in the upper edge of the aperture and the differentiated outer lip which are absent in *Microalcadia* n. subgen.

Alcadia (*Microalcadia*) *hojarasca* (Richling, 2001)

Helicina hojarasca Richling, 2001: 5–6 (text figure)

Type Material

Holotype: INBio 3404979, (leg. I. Richling, 14.8.1999)
Paratype 1: ZMB 103387 (same data as holotype)
Dimensions (height/greatest diameter):
Holotype: 2.4/2.9 mm
Paratype 1: 2.2/2.8 mm

Type Locality

NW-Costa Rica, Guanacaste Province, Cordillera de Tilarán, about 9 km N of Santa Elena, near Mirador Gerardo, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l., primary cloud forest.

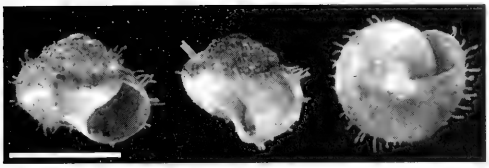


FIG. 249. *Alcadia hojarasca*, holotype, INBio 3404979, height 2.4 mm; scale bar 2.5 mm.

Examined Material

Leg. I. Richling

Guanacaste: About 9 km N Santa Elena, *Sendero at Mirador Gerardo*, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l.: 14.08.1999: (IR 933)

Puntarenas: Punarenas: Zona Protectora Arenal-Monteverde: *Reserva Biológica Bosque Nuboso Monteverde* (about 10°18'08"N, 84°47'41"W, 1,500–1,650 m a.s.l.): 25.02.2001: (IR 1453)

Etymology

The species is named for its habitat "hojarasca" (Spanish) = "leaf litter", it is used as a noun in apposition.

Description

Shell (Figs. 249, 250, 336O): Very small, globose, fragile. Color yellowish-brown. Embryonic shell with about 1 whorl, without clearly marked transition to adult shell; subsequent whorls 3 to $3^1/_3$, regularly increasing in size. Surface with fine spiral cords that are axially crossed by coarse periostracal folds that form hairs at regular distances, so that the whorls bear spiral rows of hairs; 4 rows present on body whorl, on previous whorls the upper 2 rows still present. Hairs rather thick and towards the end extending in breadth, spatula shaped (Fig. 259B). Basal callus whitish and near columella surface granular. Aperture oblique, rather straight. Outer lip not differentiated from whorl, appearing like not fully grown.

FIG. 250. *Alcadia hojarasca*, holotype, INBio 3404979, height 2.4 mm; scale bar 1 mm.

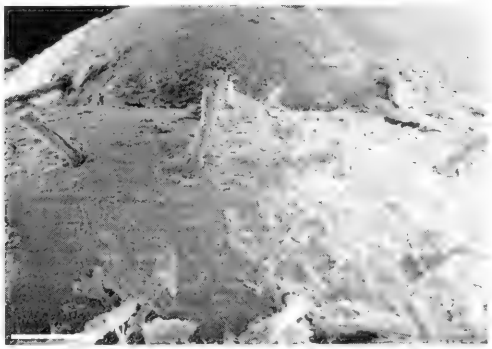


FIG. 251. Teleoconch surface structure of *Alcadia hojarasca*, 2nd whorl; scale bar 100 µm.

Internal Shell Structures: Could not be investigated.

Teleoconch Surface Structure (Fig. 251): The coarse, irregular axial threads on the inner curvature of the embryonic shell continue for about a half whorl on the teleoconch before transforming to the typical, numerous spiral cords.

Embryonic Shell (Fig. 252): The inner curvature is sculptured with coarse, irregular axial threads; the marginal part shows numerous fine, oblique grooves crossing each other. A pitted structure does not occur.
Diameter: 566 µm (n = 1).

Operculum (Fig. 253): Thin, only slightly calcified, calcareous plate only covering the central area. Columellar margin irregularly S-shaped, upper edge acute, but rounded, at lower edge columellar margin continuously changing into outer margin. Nearly transparent, whitish-amber colored. Inner side with a little ridge parallel to the columellar margin.

Animal (Fig. 339F): The color is not very unusual, mantle and upper side of the foot and head region are greyish, towards the underside it becomes paler.

Radula (Fig. 254): Only two specimens were studied and the mounting procedure was

difficult due to the small size and preservation conditions. B-central with 6 small cusps; C-central rather crenulate; R- and A-central not seen. Comb-lateral with 11–12 pointed denticles, accessory plate relatively larger than in other species, about the size of the comb-lateral. Cusps on marginals rapidly increasing in number. Number of rows not counted.

Female Reproductive System (Fig. 255): The ascending limb of the V-organ is elongated and curved; the receptaculum seminis is translocated to the ventral side of the descending limb and directed upwards posteriorly. Bursa copulatrix and provaginal sac exhibit a simple structure, with the former being much larger and approximately reaching the top of the V-organ. Their connections to the reception chamber are very close to each other; at the same point enters a very slender, relatively short provaginal duct.

Morphometry and Sexual Dimorphism

On one hand, the material available is scanty, while, on the other, the peculiar lack of the development of a differentiated outer lip of

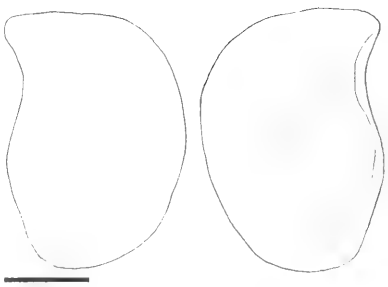


FIG. 253. Operculum of *Alcadia hojarasca*, paratype, ZMB 103387; scale bar 0.5 mm.

FIG. 254. Radula of *Alcadia hojarasca*. A. Comb-lateral. B. Marginals; scale bar 50 µm.

FIG. 252. Embryonic shell of *Alcadia hojarasca*; scale bar 100 µm.

FIG. 255. Female reproductive system of *Alcadia hojarasca*, IR 1242; scale bar 0.5 mm.

the species renders it impossible to recognize mature specimens without closer anatomical studies of the individuals. Furthermore, whether or not mature specimens still increase in shell size remains an unanswered question.

Habitat

Alcadia hojarasca is a ground dweller, it was only found under and between leaves in different stages of decay. The species appears to have a preference for *Cecropia*-leaves. This observation was also made by Zaidett Barrientos for *A. boeckeleri*.

Distribution (Fig. 256)

The species is only known from the type locality and adjacent areas. It is found on the higher elevations of the northeastern slope of the Cordillera de Tilarán.

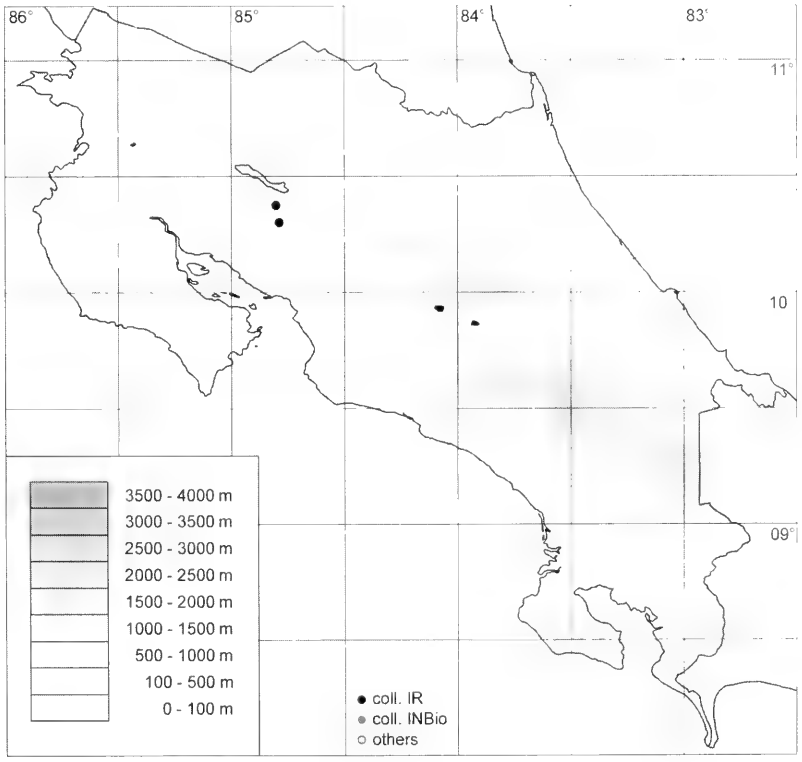


FIG. 256. Records of *Alcadia hojarasca* in Costa Rica.

Discussion

On the Central American mainland there are no other known species of this size that have periostracal hairs persisting in adult stage. The only species with a hairy periostracum on the mainland belong to the genus *Schasicheila*, which is easily characterized by the protruding edges of the operculum, a different embryonic shell structure, and great differences in the female reproductive system (see below).

The only Central American species comparable in size or probably shape is *Helicina exigua* L. Pfeiffer, 1849, described from Honduras. But in the original description, there is no hint given as to periostracal hairs. The surface is described as "subtilissime punctato-striatula", but even eroded periostracal hairs would not leave punctulations because they originate from projections of periostracal folds. Furthermore, *H. exigua* has never been illustrated, and it is treated by von Martens (1891) as a dubious species.

It is rather unusual for helicinids or snails in general not to have a distinctly developed or at least thickened outer lip at the aperture as a sign of maturity and not to further grow in size. In fact, this species looks somewhat immature. On the one hand, field collections revealed specimens of different sizes but even the biggest specimens did not display a differentiated aperture. But on the other hand, dissections of specimens of about the same size as the type have shown that the reproductive system is fully developed, and in the female's receptacula seminis sperm is present, as it is in the male's vas deferens. So there is strong evidence to suggest that the specimens described above represent the adult stage, although it cannot be determined in the case of every individual if it already has reached maturity, because a normal size variation combined with sexual dimorphism still have to be taken into consideration.

For comparison with *Alcadia boeckeleri*, refer to that species.

Alcadia (*Microalcadia*) *boeckeleri* (Richling, 2001)

Helicina boeckeleri Richling, 2001: 6–7 (text figure)

Type Material

Holotype: INBio 3404980, male (leg. I. Richling, 12.3.2000)

Paratype 1: ZMB 103388, female (same data as holotype)

Dimensions (height/greatest diameter):
Holotype: 2.2/2.6 mm
Paratype 1: 2.3/2.7 mm

Type Locality

NW-Costa Rica, Guanacaste Province, Parque Nacional Guanacaste, about 10 km S of Santa Cecilia, Volcán Orosí, near field station Pitilla, 10°59'18"N, 85°25'34"W, 700 m a.s.l., beginning of Sendero Orosilito, primary forest.

Examined Material

INBio Collection

Guanacaste: *Parque Nacional Guanacaste, La Cruz, 9 km S de Santa Cecilia, Estacíon Pitilla*: *10°59'25"N, 85°25'38"W, 700 m a.s.l.*: leg. malacological staff of INBio, 01.03.1995: 9 spec. (INBio 1498481); leg. Evelio Alfaro, 19.04.1995: 1 spec. (INBio 1483310); *10°59'33"N, 85°25'46"W, 700 m a.s.l.*: leg. Dunia Garcia, 10.08.1995: 1 ad. (INBio 1488038); 7 ads., 1 s.ad. (INBio 1488068); *Sector Finca Nacho, 10°58'43"N, 85°25'49"W, 700 m a.s.l.*: leg. C. Moraga, 18.08.1994: 1 ad. (INBio 1480339); *Sendero Mena, 10°59'27"N, 85°25'49"W, 700 m a.s.l.*: leg. malacological staff of INBio, 01.06.1993: 6 spec. (INBio 1466290); *Sendero Los Memos, 11°02'00"N, 85°25'20"W, 700 m a.s.l.*: leg. Calixto Moraga, 02.04.1995: 1 spec. (INBio 1482793)

Etymology

The species is dedicated to Dr. Wolfgang Böckeler who first introduced me to Costa

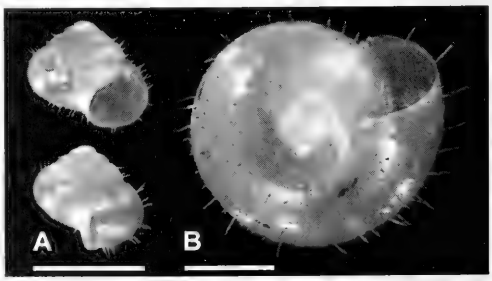
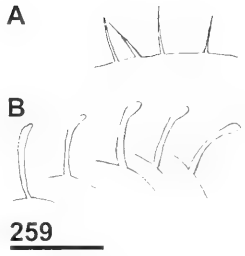


FIG. 257. *Alcadia boeckeleri*. A. Holotype, INBio 3404980, height 2.2 mm. B. Paratype, ZMB 103388; scale bar 2.5 mm (A), 1 mm (B).



FIGS. 258, 259. *Alcadia* spp. FIG. 258. *Alcadia boeckeleri*, holotype, INBio 3404980, height 2.2 mm. FIG. 259. Periostracal hairs of A. *Alcadia boeckeleri*, INBio 3404980. B. *Alcadia hojarasca*, INBio 3404979; scale bar 1 mm (Fig. 258), 0.5 mm (Fig. 259).

Rica and subsequently so often joined me in my search for the hidden helicinids.

Description

Shell (Figs. 257, 258, 336P): Very small, globose and fragile. Color yellowish-brown. Embryonic shell with about 1 whorl, without clearly marked transition into adult shell; subsequent whorls about 3, regularly increasing in size. Surface with fine spiral cords that are axially crossed by very fine threads. On last whorl, 5 rows of periostracal hairs; on previous whorls the upper 2 rows are present. Hairs thin and at the end sharpened (Fig. 259A). Basal callus weakly developed and near columella granulated. Aperture oblique, rather straight. Outer lip undifferentiated from whorl, appearing as not fully grown.

Internal Shell Structures: Could not be investigated.

FIG. 260. Teleoconch surface structure of *Alcadia boeckeleri*, 1st whorl; scale bar 100 µm.

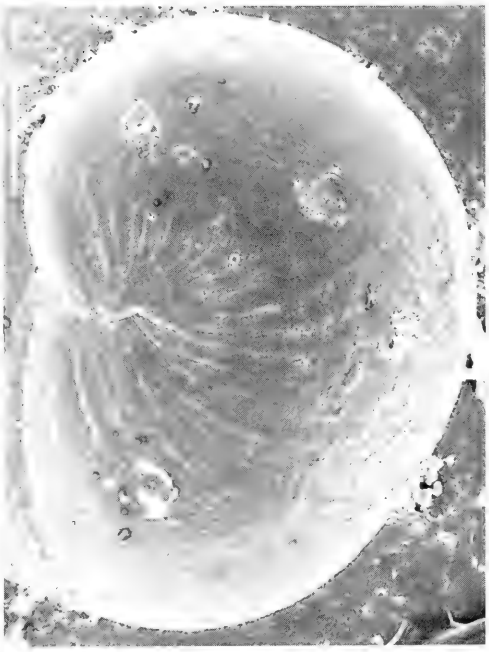


FIG. 261. Embryonic shell of *Alcadia boeckeleri*; scale bar 100 µm.

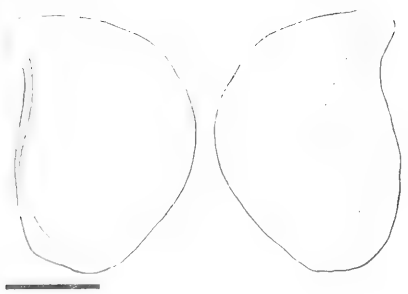


FIG. 262. Operculum of *Alcadia boeckeleri*, holotype, INBio 3404980; scale bar 0.5 mm.

Teleoconch Surface Structure (Fig. 260): A zone of transitional structure of about $^{1}/_{3}$ of a whorl, closely resembling oblique diverging grooves, is continued by numerous spiral cords, crossed only by growth lines.

Embryonic Shell (Fig. 261): The embryonic shell surface structure is similar to that of *Alcadia hojarasca*.
Diameter: 488 µm (n = 1).

Operculum (Fig. 262): Thin, only slightly calcified, calcareous plate only covering the central area. Columellar margin irregularly S-shaped, upper edge acute, but rounded, at lower edge columellar margin continuously changing into outer margin. Nearly transparent, whitish-amber colored. Inner side with a little ridge parallel to the columellar margin.

Animal (Fig. 339G): The color is similar to *Alcadia hojarasca*.

Radula: The radula of *Alcadia boeckeleri* could not be investigated, because sufficient material was lacking.

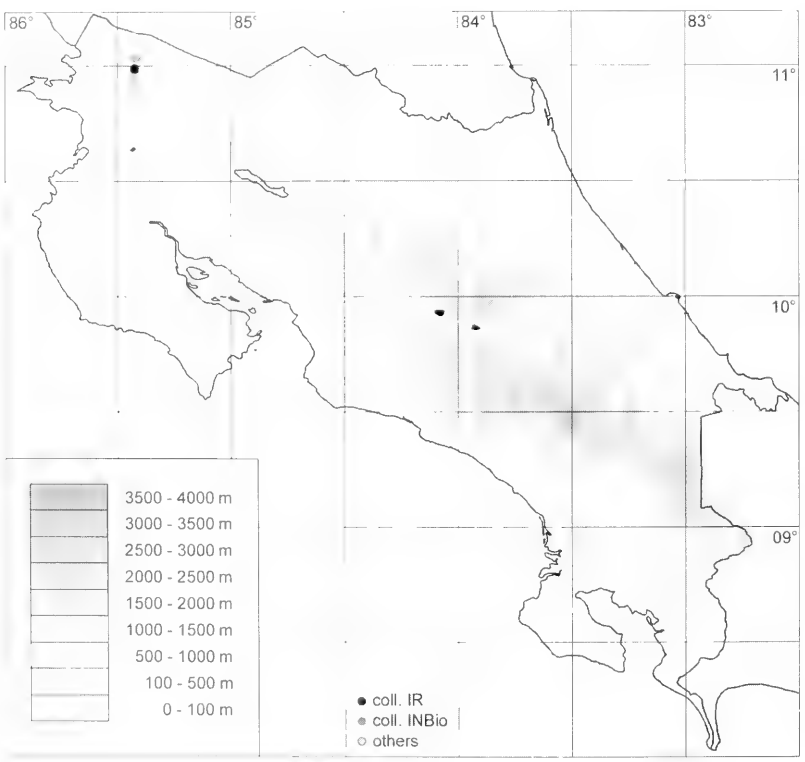


FIG. 263. Records of *Alcadia boeckeleri* in Costa Rica.

Female Reproductive System: The inspection of a single female revealed similar structures as in *Alcadia hojarasca*.

Morphometry and Sexual Dimorphism

See *Alcadia hojarasca*.

Habitat

The species is a typical ground dweller that lives in the leaf litter. See also under *Alcadia hojarasca*.

Distribution (Fig. 263)

The species is only known from the area of the type locality located on the northeastern slope of the Cordillera de Guanacaste, which, together with the volcano Orosí, forms the northern limit of this mountain chain.

Discussion

For general discussion, see *Alcadia hojarasca*.

Alcadia boeckeleri differs from *A. hojarasca* in bearing five instead of four rows of periostracal hairs. Furthermore, the hairs are much thinner and they have a different shape towards the end (Fig. 259). The spire is a little more elevated in *A. boeckeleri*.

Lucidella lirata
(L. Pfeiffer, 1847)

Helicina lirata L. Pfeiffer, 1847a: 150 (not figured)
Helicina lirata – L. Pfeiffer, 1847b: 153
Helicina lirata – L. Pfeiffer, 1848: 83
Helicina unidentata – L. Pfeiffer, 1848: 83 [without description]
Helicina unidentata L. Pfeiffer, 1849: 125 (not figured): Honduras (Dyson, coll. Cuming)
Helicina rusticella Morelet, 1849: 21 (not figured): Island Carmen
Helicina lirata – L. Pfeiffer, 1850: 1415, pl. 4, figs. 40–43: Mexico: Yucatan (Hegewisch)
Helicina unidentata – L. Pfeiffer, 1850: 14, pl. 9, figs. 14–17
Helicina lirata – L. Pfeiffer, 1852a: 341
Helicina unidentata var. – L. Pfeiffer, 1852a: 341
Helicina unidentata – L. Pfeiffer, 1852a: 341
Helicina lirata – L. Pfeiffer, 1852b: 246
Helicina unidentata var. – L. Pfeiffer, 1852b: 246
Helicina unidentata – L. Pfeiffer, 1852b: 246
Helicina lirata – L. Pfeiffer, 1856b: 236: Mexico: Chiapa (Ghiesbreght)
Helicina lirata – von Martens, 1860: 59: Venezuela: near Maracaybo or environs of Merida
Helicina lirata – Tristram, 1864: 413: Guatemala: mountain-forests of Vera Paz (Salvin)
Helicina lirata – von Martens, 1865: 67
Helicina semistriata Sowerby, 1866: 281, pl. 268, fig. 86
Helicina unidentata – Sowerby, 1866: 281, pl. 268, fig. 87
Helicina lirata – Sowerby, 1866: 281, pl. 268, figs. 88–89
Helicina lirata – Bland, 1866: 8
Helicina unidentata – Bland, 1866: 8
Helicina (*Perenna*) *lamellosa* Guppy, 1867: 260, pl. X, fig. 4: Trinidad: Gulf of Paria, islet Cotoras
Helicina semistriata – Tate, 1870: 159: Nicaragua: in the woods and cocoanut groves about Boca del Toro, region Chontales [area around Acoyapa, NE of Lago de Nicaragua]
Helicina lirata – Strebel, 1873: 21, pl. 1, fig. a, pl. 2 fig. 8: Mexico: Bajadas, Veracruz and near Antigua
Helicina lirata – von Martens, 1873: 56: Venezuela
Helicina lirata – Reeve, 1874: pl. 14, fig. 121
Helicina unidentata – Reeve, 1874: pl. 14, fig. 122
Helicina lyrata [sic] – Angas, 1879: 484: Costa Rica (Gabb)
Helicina unidentata – Ancey, 1886: 254: Honduras: Ile d'Utilla (Dyson, Simpson)
Lucidella lirata – Jousseaume, 1889: 232, 235, 256: Venezuela: Caracas, San-Esteban
Helicina lirata – von Martens, 1891: 4142, pl. I, fig. 18 (living animal): E-Mexico: Vera Cruz, at the "bajadas"; S-SE-Mexico: Chiapas, Teapa and San Juan Bautista in Tabasco; Yucatan; N-Guatemala: mountain forests of Vera Paz; S-Guatemala: Retalhuleu; Venezuela
Helicina lirata var. *rusticella* – von Martens, 1891: 41: Yucatan: Island of Carmen, in the Gulf of Campeche
Helicina lirata var. *unidentata* – von Martens, 1891: 41: Honduras; 607: Honduras: Utila Island
Helicina lirata var. *semistriata* – von Martens, 1891: 41: N-Panama: Boca del Toro, Chiriqui

Helicina lirata – Pilsbry, 1891: 332: Mexico: N-Yucatan: Labna; Honduras: Utilla Island (Simpson)

Helicina (*Poenia*) *lirata* – Fischer & Crosse, 1893: 397–399: same data as von Martens, 1891 (for *H. lirata* and *H. lirata* var. *unidentata*) and Mexico: Yucatan, Labna

Helicina (*Poenia*) *lirata* var. *rusticella* – Fischer & Crosse, 1893: 397–399: same data as von Martens, 1891

Helicina (*Perenna*) *lamellosa* – Guppy, 1893: 228

Helicina (*Helicina Perenna*) *lirata* – Guppy, 1895: 74

Helicina (*Helicina Perenna*) *semistriata* – Guppy, 1895: 74

Helicina (*Helicina Perenna*) *lamellosa* – Guppy, 1895: 74

Helicina lirata – von Martens, 1900: 607: S.E. Mexico: San Juan Bautista, garden of the Juarez Institute in the same town; Yucatan: Labna; N-Guatemala: Panzos; SW-Costa Rica: Alto de Mano Tigre, 690 m [not localized] (Pittier)

Helicina lirata var. *rusticella* – von Martens, 1900: 607: SW-Costa Rica: El Pozo, in the shingle (gravices) of the Río Grande de Terraba [not localized: Palmar Norte: 08°57'N, 83°27'W, Puntarenas Province] (Pittier)

Helicina lirata – Pilsbry, 1904: 782: Mexico: Veracruz: Antigua (Rhoads)

Helicina lirata – Pilsbry, 1910: 503: Panama: Canal Zone: Tabernillo (Brown)

Lucidella lirata – Wagner, 1911: 341, pl. 68, figs. 5–7: S-Mexico, Guatemala, Honduras, Venezuela

Lucidella lirata lamelllosa – Wagner, 1911: 341342, pl. 68, fig. 4: Trinidad (island)

Lucidella (*Perenna*) *lirata* – Pilsbry & Brown, 1912: 585

Lucidella lirata var. *lamellosa* – Vernhout, 1914: 26–27: Suriname: Environs of Paramaribo

Lucidella lirata – Hinkley, 1920: 41, 49, 52: Guatemala: Livingston; Jocolo plantation on north side of Lake Isabal: lake drift; Alta Verapaz: Chama between Río Tsalbha and Río Negro: also river drift

Lucidella (*Poenia*) *lirata* – Baker, 1922a: 54–55, pl. III, fig. 5, pl. V, fig. 21 (radula): Mexico-Venezuela; Mexico: Tabasco: San Juan Bautista: Garden of Juarez Institute (Rovirosa)

Lucidella (*Poenia*) *lirata* – Baker, 1922b: 36: Mexico: S Vera Cruz, near hacienda de Cuatolapam (Río San Juan – Arroyo Hueyapam, canton of Acayacan (Michigan-Walker-Expedition)

Lucidella (*Poenia*) *lirata* – Baker, 1923: 22–23: Venezuela: San Esteban, Palma Sola, Aroa, Estación Táchira, La Fría (Michigan-Williamson-Expedition)

Lucidella lirata – Pilsbry, 1926a: 59, 71: Panama: Canal Zone: Tabernilla (Brown), near Darien and Juan Mina (Zetek), Panama City and Taboga Island (Zetek), Bocas del Toro (Gabb)

Lucidella lirata – Pilsbry, 1926b: 127: Costa Rica: Cahuita [09°44'01"N, 82°49'48"W] (Olsson)

Lucidella (*Poenia*) *lirata* – Baker, 1928: 33–34, pl. II, figs. 9–11 (female reproductive system): Mexico: Veracruz: Atoyac, 1300–1475 feet

Lucidella lirata – Pilsbry, 1930: 339: Panama: Canal Zone: roadside in SE of Empire; Taboga Island (Pinchot-Expedition)

Lucidella (*Poenia*) *lirata* – Bequaert & Clench, 1933: 543: Mexico: Yucatan, Chichen Itzá

Lucidella lirata – Goodrich & van der Schalie, 1937: 12, 14–16, 33: Guatemala: Petén: region of headwater of Río San Pedro de Mártir, lower Río de la Pasión; Alta Verapaz: upper part of Río de la Pasión

Lucidella lirata – Richards, 1938: 176: Honduras

Lucidella lirata – Richards & Hummelinck, 1940: 12–13: Venezuela: Margarita Island: Hills SE La Asunción; Cerro del Piache; just above El Valle; La Sierra, El Valle; Toma de Agua del Valle; Toma de Agua de Encañado, San Juan; Los Vagras; between Los Vagras and coast

Lucidella lirata – Bequaert, 1957: 208: Mexico: Chiapas: Selva Lacandona: Laguna Ocotal, 950 m, Laguna Ocotal to El Censo, 1,000 m; Veracruz, Tabasco, Yucatan, Quintana Roo, Guatemala to Panama

Lucidella lirata lamellosa – Bequaert, 1957: 208

Lucidella lirata – Basch, 1959: 8: Guatemala: Petén: Tikal National Park, 17°10'N, 89°25'W

Lucidella lirata – Hubricht, 1960: 83: USA: S-Texas: beach drift

Lucidella (*Poeniella*) *lirata* – Haas & Solem, 1960: 130: British Honduras [Belize]: Río Frio Cave, Cayo District

Lucidella lirata – Branson & McCoy, 1963: 102–103: Mexico: Campeche: Airport, Cuidad del Carmen

Lucidella lirata – Thompson, 1967: 228229: Mexico: Campeche: 8.1 mi SW Champotón, 5.1 mi NNW Dzibalchén, 4.9 mi W Hopelchén, 3.4 mi S Cayál (19°45'N, 90°10'W), 7.2 mi S Pixtún, 10.2 mi E Escárcega, 19.2 mi E Silvituc; Quintana Roo: 4 mi E Xpujil, 7.1 mi NNW Xiatil

Lucidella lirata – Regteren Altena, 1974: 71: Suriname

Lucidella lirata – Tillier, 1980: 35, 36, figs. 20, 21 (operculum): French Guiana: Aouara, Saut Sabbat (Abattis)

Lucidella (*Poenia*) *lirata* – Thompson, 1982: fig. 13 (radula), 27–28 (embryonic shell)

Lucidella lirata – Monge-Nájera, 1997: 113: Costa Rica

Synonymy

Helicina unidentata L. Pfeiffer, 1849
Helicina rusticella Morelet, 1849
Helicina semistriata Sowerby, 1866
Helicina lamellosa Guppy, 1867

Original Description

"T. orbiculato-conoidea, tenuis, acute et confertim concentrice lirata, diaphana, albida; spira conoidea, acuta; anfr. 4,5–5 vix convexiusculi, ultimus carinatus, basi medio impressus; apertura obliqua, rotundato-subtriangularis; columella brevissima, simplex, in callum basalem tenuissimum dilatata; perist. breviter expansum, margine basali medio obsolete unidentato.
Diam. 4, alt. 2 $^{2}/_{3}$ mill.
Habitat in Mexico, Yucatan (Hegewisch)."

Type Material

Not located (assumed to be in the collection of L. Pfeiffer, because it was not otherwise stated, collection L. Pfeiffer having been most likely destroyed in Stettin Museum, Poland during World War II).

Type Locality

"Mexico, Yucatan" [not clear, whether it refers to the Mexican State of Yucatán or the Mexican part of the peninsula of Yucatán].

Examined Material

Leg. I. Richling

Limón: *Parque Nacional Cahuita*, trail from Cahuita to Puerto Vargas, coastal forest with coco palms: about 09°43'27"N, 82°50'28"W, 4 m a.s.l.: 02.03.1998: (IR 418); 10.03.1999: (IR 756); 08.08.1999: (IR 902); 10.08.1999: (IR 913); 04.03.2000: (IR 1314); (IR 1316); 14.03.2001: (IR 1558); (IR 1559); (IR 1640)
Refugio Nacional de Fauna Silvestre Gandoca-Manzanillo, *S Manzanillo*, trail along coast line to S, coastal forest, about 09°38'06"N, 82°38'26"W, 50 m a.s.l., 14.09.1999: (IR 1098); (IR 1124)
W Liverpool, Mexico, at Río Blanco, high water deposit, 09°58'32"N, 83°08'32"W, 35 m a.s.l.: 22.02.1997: (IR 7); 12.03.1997: (IR 113)
N Shiroles, along Quebrada Kirio, 09°35'38"N, 82°57'20"W: *120 m a.s.l.*: 15.03.1997: (IR 162); *60 m a.s.l.*: 03.03.1998: (IR 435)
W Bribri, road to Uatsi, about 09°38'11"N, 82°51'48"W, 30 m a.s.l.: at crossing with Río Carbón, 30 m a.s.l.: 17.3.1997: (IR 187); wooded valley within banana plantation, 50 m a.s.l.: 15.3.2001: (IR 1586)
Southern road from *Bribrí to Shiroles*, small banana plantation near creek, 09°35'17"N, 82°52'46"W, 50 m a.s.l., 15.03.1997: (IR 171)

Puntarenas: *Refugio Nacional de Fauna Silvestre Golfito*, rain forest, 08°39'26"N, 83°10'50"W, 100 m a.s.l., 14.02.1999: (IR 568)

INBio Collection

Limón: *Parque Nacional La Amistad*, Quebrada Cachabri (toma de agua), 09°29'29"N, 82°59'37"W, 360 m a.s.l., leg. Gerardina Gallardo, 26.11.1996: 3 spec. (INBio 1488249)
Reserva Indígena Talamanca: *1 km SW de la Iglesia de Amubri, 09°30'37"N, 82°57'36"W, 70 m a.s.l.*: 19.10.1996: 8 spec. (INBio 1488235); *500 m E de la Iglesia de Amubri, 09°31'06"N, 82°56'50"W, 70 m a.s.l.*: 21.10.1996: 6 spec. (INBio 1488268); *Sector Amubri, 09°30'53"N, 82°57'19"W, 70 m a.s.l.*: 29.11.1994: 1 spec. (INBio 1483399); 30.11.1994: 1 spec. (INBio 1483446); 2 spec. (INBio 1483447); 1 spec. (INBio 1483449); 6 spec. (INBio 1483450); 24.10.1996: 30 spec. (INBio 1487958); 27.11.1996: 1 spec. (INBio 1487352); *Amubri, Sendero Soki, 09°30'53"N, 82°57'19"W, 70 m a.s.l.*: 27.11.1996: 1 spec. (INBio 1487364); 11 spec. (INBio 1488219); 11 spec. (INBio 1493414); *Suirí, orillas del Rio Telire, 09°33'56"N, 82°55'50"W, 30 m a.s.l.*: 25.11.1996: 17 spec. (INBio 1487345) (all

leg. Gerardina Gallardo); *Sector Miramar, Senderos a Río Moín, 09°37'44"N, 83°00'32"W, 150 m a.s.l.*: leg. Zaidett Barrientos, 08.11.1994: 4 spec. (INBio 1475236)

1 Km S de Punta Cocles, 09°38'17"N, 82°43'25"W, 40 m a.s.l., leg. Zaidett Barrientos, 20.08.1996: 1 spec. (INBio 1487843)

Refugio Nacional de Vida Silvestre Gandoca-Manzanillo: Sector Gandoca, 09°35'30"N, 82°36'13"W, 0 m a.s.l.: 29.07.2000: 4 spec. (INBio 3091175); Sector Gandoca, Camino a Gandoca, 09°38'04"N, 82°38'37"W, 10 m a.s.l.: 28.04.2000: 5 spec. (INBio 3097927); Sector Manzanillo, Sendero a Gandoca, 09°38'20"N, 82°39'03"W, 2 m a.s.l.: 30.03.2000: 1 spec. (INBio 3098034) (all leg. Alexander Alvarado Mendez)

Parque Nacional Cahuita: *Sector Puerto Vargas, 09°43'38"N, 82°49'09"W, 0 m a.s.l.*: leg. Alexander Alvarado Mendez, 31.08.1999: 1 spec. (INBio 3091727); 4 spec. (INBio 3091733); *Sendero del limite W del parque, 09°44'00"N, 82°50'25"W, 10 m a.s.l.*: leg. malacological staff of INBio, 11.06.1997: 1 spec. (INBio 1488171)

Reserva Indígena Tayni: *Sendero Tepezcuintle, 09°40'22"N, 83°01'46"W, 180 m a.s.l.*: 22.04.1999: 1 spec. (INBio 3096423); *Sendero Bobocara*: 09°40'28"N, 83°02'17"W, 260 m a.s.l., 01.06.1999: 1 spec. (INBio 1498178); 09°40'28"N, 83°02'12"W, 200 m a.s.l., 01.06.1999: 7 spec. (INBio 1498248) (all leg. Alexander Alvarado Mendez)

Reserva Biológica Hitoy Cerere: *Sendero Tepezcuintle*: 09°40'22"N, 83°01'40"W, 140 m a.s.l., 25.04.1999: 3 spec. (INBio 1497566); 100 m a.s.l., 07.06.1999: 4 spec. (INBio 3096478); 09°40'18"N, 83°01'43"W, 140 m a.s.l., 28.04.1999: 1 spec. (INBio 1497840); *Sendero Bobócara, 09°40'20"N, 83°03'12"W, 620 m a.s.l.*: 14.06.1999: 3 spec. (INBio 3095831) (all leg. Alexander Alvarado Mendez): *Sendero Toma de Agua, 09°40'31"N, 83°01'36"W, 100 m a.s.l.*: 19.04.1994: 1 spec. (INBio 1473669); 2 spec. (INBio 1473674); 58 spec. (INBio 1474306); 30 spec. (INBio 1474336); 20.04.1994: 1 spec. (INBio 1473613) 1 spec. (INBio 1473838); 08.09.1994: 49 spec. (INBio 1475430); 70 spec. (INBio 1475444) (all leg. Zaidett Barrientos); 28.02.1994: 4 spec. (INBio 1476129); 17.07.1994: 70 spec. (INBio 1478443); 30 spec. (INBio 1478459); 06.12.1994: 2 spec. (INBio 1475673) (all leg. Gerardo Carballo); *Estación Hitoy Cerere, 09°40'35"N, 83°01'36"W, 100 m a.s.l.*: leg. malacological staff of INBio, 15.11.1993: 7 spec. (INBio 1463364); *Sendero Chato, 09°40'41"N, 83°01'26"W, 100 m a.s.l.*: leg. Marianella Segura, 17.07.1994: 10 spec. (INBio 1478236); 70 spec. (INBio 1478239

400m NE de la Estación de Hitoy Cerere, Sendero la "Finca", 09°40'35"N, 83°01'26"W: *150 m a.s.l.*: 20.07.1999: 2 spec. (INBio 1495436); *110 m a.s.l.*: 07.05.1999: 3 spec. (INBio 3300038); 27.09.2000: 1 spec. (INBio 3091795) (all leg. Alexander Alvarado Mendez)

Isla Uvita: *frente al muelle de Limón, 09°59'45"N, 83°00'50"W, 5 m a.s.l.*: leg. Alexander Alvarado Mendez, 11.10.2000: 21 spec. (INBio 3315375); 3 spec. (INBio 3315385); *lado N, 09°59'50"N, 83°00'46"W, -10 to 5 m a.s.l.*: leg. A. Berrocal, 06.05.2000: 21 spec. (INBio 3396974)

Puntarenas: *Playa Blanca*, 08°38'18"N, 83°26'16"W, 0 m a.s.l., leg. Gillermo Mena, 04.09.1995: 1 spec. (INBio 1479925)

Isla Pelicanos, 08°36'10"N, 83°08'48"W, 2 m a.s.l., leg. Socorro Avila, 01.11.1997: 1 spec. (INBio 3399211)

Refugio Nacional de Fauna Silvestre Golfito: *Sendero Las Torres, 08°38'37"N, 83°09'54"W, 60 m a.s.l.*: leg. Socorro Avila, 03.12.1997: 4 spec. (INBio 1487712); *150 m al N del Reserva, 08°39'06"N, 83°10'44"W, 40 m a.s.l.*: leg. Alexander AlvaradoMendez, 14.02.1999: 3 spec. (INBio 1501379); *Extremo NW del Aeropuerto de Golfito, 08°39'39"N, 83°11'13"W, 100 m a.s.l.*: leg. Socorro Avila, 03.11.1997: 1 spec. (INBio 1487165); 3 spec. (INBio 1487172)

Parque Nacional Piedras Blancas, Playa San Josecito, 08°39'49"N, 83°15'35"W, 5 m a.s.l., leg. Eida Fletes, 27.10.1996: 2 spec. (INBio 1487318)

Quebrada Benjamin, carretera al tanque del agua 600 m del Barrio Alemania, 08°58'39"N, 83°28'19"W, 100 m a.s.l., leg. Socorro Avila, 08.05.1997: 1 spec. (INBio 1487661); 1 spec. (INBio 1487691)

Palmar Norte, Barrio Alemania, Sendero a Jalisco, 1 Km al NE del Tanque de Acueductos, 08°59'21"N, 83°28'16"W, 400 m a.s.l., leg. Socorro Avila, 08.05.1997: 2 spec. (INBio 1487736); 3 spec. (INBio 1487756)

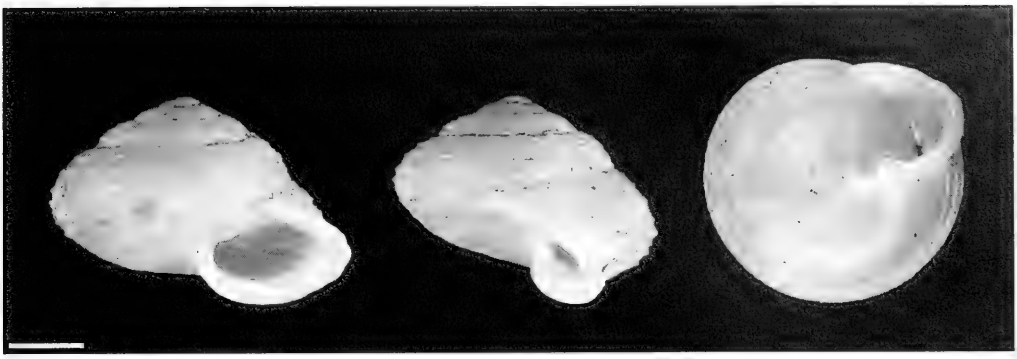


FIG. 264. *Lucidella lirata*, Cahuita, IR 1559; scale bar 1 mm.

OTHER SOURCES

COSTA RICA

Limón: Pandora [about 09°43'N, 82°58'W], leg. F.G. Thompson (FGT-100), 05.08.1964 (UF 214773)

7 km from Valle La Estrella, at Hitoy Cerere National Park [about 09°40'35"N, 83°01'36"W], 152 m a.s.l., E.L. Raiser et al. (ERL 079), 09.08.1994 (UF 41405, UF 41406); E.L. Raiser (ERL 080), 09.08.1994 (UF 41421)

1 km NW of Cahuita, 09°45.5'N, 82°50.9'W, leg. F.G. Thompson (FGT-5616), 25.02.1996 (UF 268476)

NICARAGUA

Matagalpa: 4.5 km. S of Matagalpa, 1,200 m a.s.l., leg. F.G. Thompson, 16.07.1956 (UF 127683)

Description

Shell (Figs. 264, 336Q): Orbiculate-conoidal, depressed, thin, small sized, dull. Color: dark yellowish to brown, diaphanous (whitish: as in original description only faded specimens). Whorls sculptured with a varying number of close-set, prominent, sharp spiral ridges at about equal distance, upper a little wider spaced, some smaller ridges in between. Surface textured with irregular, strong growth lines crossing spiral sculpture. Embryonic shell with about 1 whorl; $3^{5}/_{8}$–4 subsequent whorls slightly convex; last whorl rounded with a slight keel on periph-

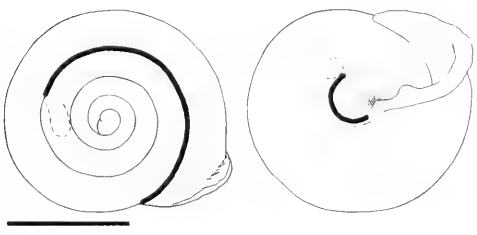


FIG. 265. Axial cleft and muscle attachments of *Lucidella lirata*, IR 1559; scale bar 2 mm.

FIG. 266. Teleoconch surface structure of *Lucidella lirata*, 2nd whorl; scale bar 100 µm.

FIG. 267. Embryonic shell of *Lucidella lirata*; scale bar 100 µm.

ery, umbilical region deeply impressed; whorls rapidly increasing in size and only slightly descending, forming a low spire and a slightly pointed apex. Suture deeply impressed. Aperture oblique and curved backwards towards its base. Outer lip of the same color as the preceding whorls, thickened and narrowly expanded, a slight notch at insertion to body whorl. Reflection very narrow, lower palatal margin with a broad

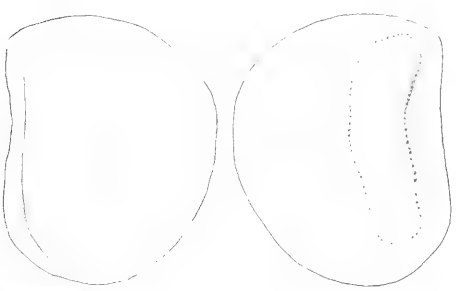


FIG. 268. Operculum of *Lucidella lirata*, IR 1559; scale bar 0.5 mm.

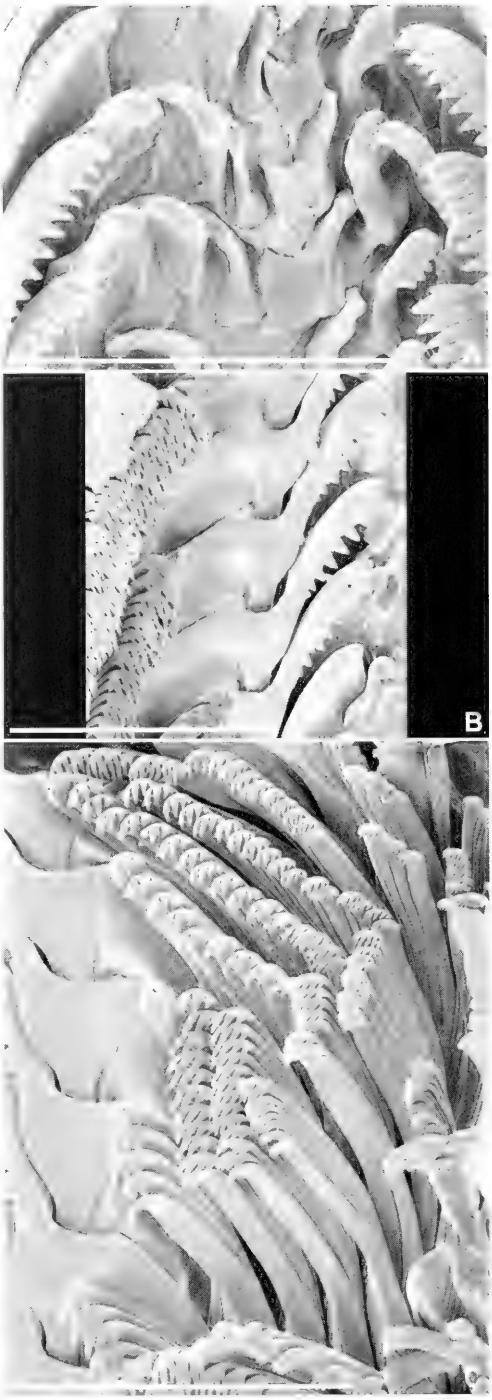


FIG. 269. Radula of *Lucidella lirata*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

tooth that is more or less well developed. Columella short. Basal callus weakly developed and granulated.

Internal Shell Structures (Fig. 265):

Teleoconch Surface Structure (Fig. 266): A transitional pattern is absent, the teleoconch is structured with the typical spiral ridges throughout, the interspaces are smooth except for fine growth line.

Embryonic Shell (Fig. 267): Contrary to the pitted embryonic shells described for species of *Helicina*, the pits of *Lucidella lirata* are not arranged in distinct spiral lines. The interspacial distance exceeds the diameter of the pits, which are more sparcely scattered over the surface. The embryonic shell is even smaller than in the smaller species *Alcadia hojarasca* and *A. boeckeleri*.
Diameter: 426 µm (± 12) (408–465) (n = 13) (IR 756, IR 1314).

Operculum (Fig. 268): Outer surface very slightly calcified, a noticeable ridge only at the columellar side, which is quite straight. Color horny-amber and transparent. Nucleus at a significant distance from the columellar margin. Shape broadly ovoid and only truncated towards the columella.

FIG. 270. Female reproductive system of *Lucidella lirata*, IR 1314; scale bar 0.5 mm.

Animal (Fig. 339H): Only the tentacles are grey, the rest of the body is whitish-yellow. The mantle may be spotted grey, but this is only visible in individuals removed from their shell.

Radula (Fig. 269): A-central elongated and smooth; B- and C-central each bearing about 5–6 cusps. Comb-lateral with 9–12 cusps, cusps on marginals slowly increasing in number. Total number of rows was not counted. Baker (1922a) and (Thompson, 1982) found fewer cusps on the comb-lateral.

Female Reproductive System (Fig. 270): The receptaculum seminis between the two limbs of the V-organ is not developed; it is replaced by an accessory sperm sac on the top of the V-organ or the very beginning of the descending limb respectively, but it is located on the outside of the V-organ. The bursa copulatrix is relatively small and without any lobes. In contrast, the distal side of the provaginal sac is deeply lobed, an additional lobule may occasionally be developed on its stalk. The bursa copulatrix enters the reception chamber via the stalk of the provaginal sac rather than directly. The provaginal duct that continues from the stalk of the provaginal sac is very short and slender. The pallial oviduct is much less folded than in the species of *Helicina*. It receives an additional sac a short distance from the reception chamber, which serves for sperm storage.
The anatomy of the species has already been studied by Baker (1928), but, according to his studies of *Lucidella aureola* (Férussac, 1822), he assumed the existence of a receptaculum seminis as described above for the species of *Helicina* (he had only a single specimen and "it was broken away ..."). The study of serial sections excludes the presence of such an organ. Furthermore, the additional sac on the oviduct escaped Baker's attention.

Morphometry and Sexual Dimorphism (Table 14, Fig. 271)

Sufficient numbers of specimens were found only at Cahuita. Because morphological differ-

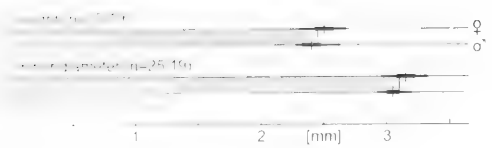


FIG. 271. Measurements of *Lucidella lirata* according to Table 14; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both.

ences between populations cannot be considered here, only height and minor diameter were measured.

The values of males and females widely overlap (Fig. 272), so that statements based on very few shells will only be correct by coincidence (Baker, 1928: 1 female > a few males). On average, females are larger than males. In interpolation from the minor diameter, the males have an average volume of about 92.5% of that of the females, thereby representing the smallest degree of sexual dimorphism found among Costa Rican species of Helicinidae.

Habitat

Lucidella lirata is a typical ground dweller, living in the leaf litter under and between decaying leaves, trunks and fruits. In Costa Rica, it was found abundantly very close to the sea shore in a coconut palm forest on sandy gravel bottom. A semiaquatic behavior (in and at edge of pools, often together with aestivating *Pisidium* and *Planorbis*) described by Baker (1922b) for populations in southern Vera Cruz, Mexico, was not observed. Besides mesic and rain forests, Thompson (1967) also mentions a constantly wet swampy area in Campeche, Mexico as habitats of *L. lirata*.

Distribution

Lucidella lirata is very widespread in Central America. It ranges from southern Mexico to Panama and along the northern coast of South America, where it is found in Venezuela, French Guyana, and Suriname. It inhabits some coastal islands, such as Isla de Utila, Honduras, and Isla de Margarita and Trinidad, Venezuela, but it is absent from the southern Lesser Antilles. In Mexico, *L. lirata* seems to be restricted to the southeastern states Veracruz, Chiapas, Campeche, Quintana Roo, and Yucatán, although it may be rare towards the extreme tip of the Peninsula de Yucatán, because it was only recorded twice from the latter state (Labna and Chichen Itza). According to Correa-Sandoval (2000), it has not been reported north of Jalapa in central Veracruz.

The records for Costa Rica (Fig. 273) are concentrated in two regions, the southern Pacific and the Caribbean plains, but within these areas the species was found at various different sites. According to the quantity of material and the author's own field experience, *L. lirata* occurs more abundantly on the Caribbean side. The distribution stretches along the coast line, where slightly elevated areas are mainly inhabited. In Costa Rica, the species is only occasionally found on altitudes up to 620 m in Hitoy Cerere or up to 690 m in Alto de Mano Tigre on the Pacific side respectively, whereas Bequaert (1957) reported *L. lirata* up to 1,000 m in Mexico.

Discussion

Because Costa Rican populations represent only a small area within the wide distribution of *Lucidella lirata*, and because it is the only species of that genus in Costa Rica, rendering a comparison with other similar taxa within the area of the study unnecessary, it seemed appropriate to investigate and discuss the species to a lesser extent than the representatives of the genus *Helicina* and to accept the interpretations of earlier authors on this subject (e.g., synonymy). For this reason, only Costa Rican material is listed above. A comprehensive revision of the species should encompass samples from the entire area of distribution, something beyond the focus of the present study.

Lucidella lirata varies throughout its area of distribution with respect to the number of spiral ridges and their extent towards the umbilical area, for example, Venezuelan specimens show all intermediates between the typical form and *lamellosa* (Baker, 1923; Regteren Altena, 1974; Tillier, 1980). Furthermore, the elevation of the spire and the dentition of the outer lip are subject to variation. In the Costa Rican samples, the basal tooth is usually well developed, and the upper outer lip is irregularly crenulated, the spiral striation is present only on about half the distance or less from the periphery to the umbilical area.

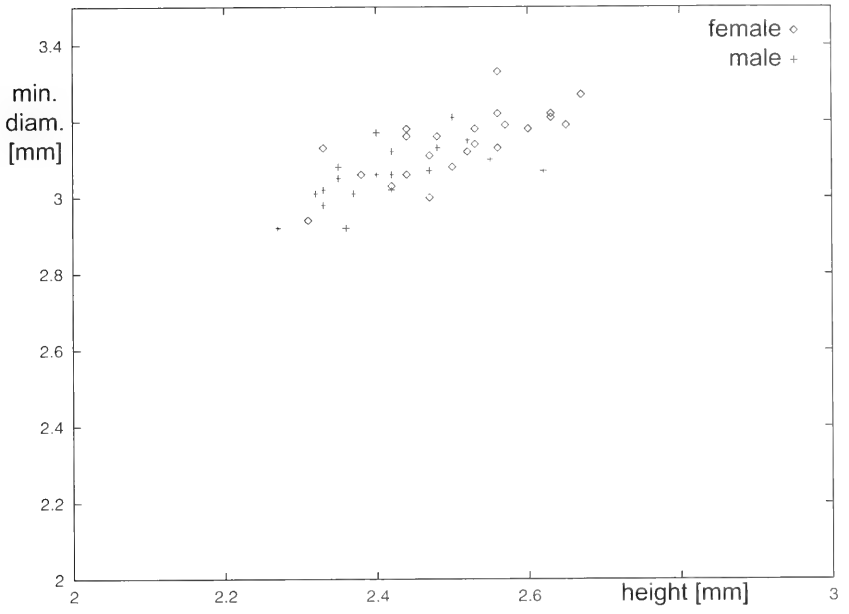


FIG. 272. Range of measurements in females and males of *Lucidella lirata* for height and minor diameter in the population from Cahuita.

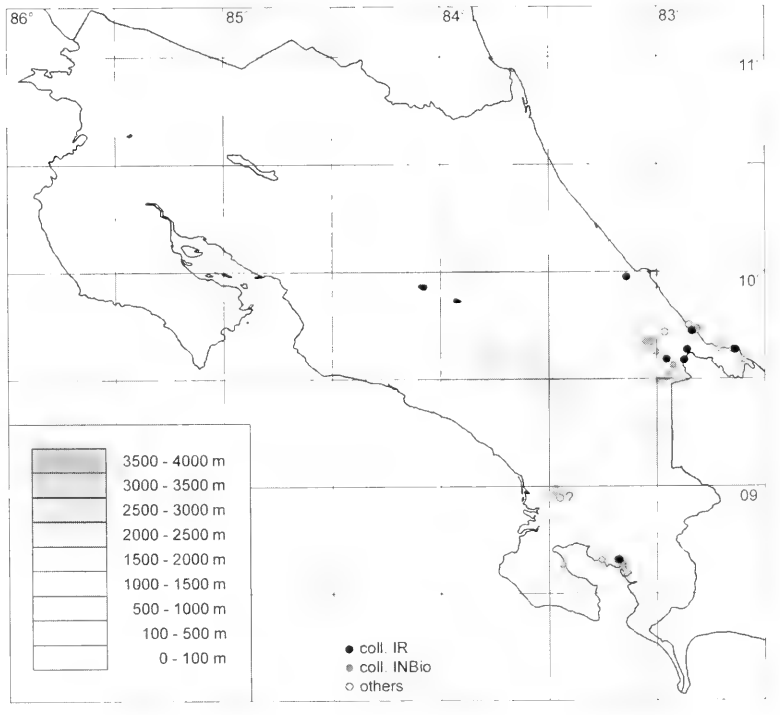


FIG. 273. Records of *Lucidella lirata* in Costa Rica.

TABLE 14. Measurements of the Cahuita-population of *Lucidella lirata* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min. diam. = minor diameter); linear measurements [mm].

	"Cahuita" (altitude 5–10 m) lot IR 1314					
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	2.51	0.08	2.31	2.67	25
Height	m	2.41	0.07	2.27	2.62	19
Min. diam.	f	3.14	0.07	2.94	3.33	25
Min. diam.	m	3.06	0.06	2.92	3.21	19

QUESTIONABLE SPECIES FOR COSTA RICA

Helicina (*Oligyra*) *flavida* Menke, 1828

Examined Material (Fig. 274)

COSTA RICA

Limón: Field cleared of forest vegetation (now soccer field), adjacent to Los Corales III, Puerto Limón, 10°00'06.7"N, 83°02'37.9"W, leg. D.G. Robinson, Summer 1984: 2 ads. (dead collected) (APHIS PPQ USDA)

Distribution

The species is only known for Costa Rica from the two dead specimens collected very near Puerto Limón (Fig. 275). Otherwise, *Helicina flavida* is widely distributed in southern Mexico (states: Puebla, N- to S-Veracruz, Tabasco, Chiapas, Campeche, Quintana Roo), northern Guatemala (departments: Petén, Alta Verapaz, Izabal) and Belize (Cayo district) (von Martens, 1890–1901; Hinkley, 1920; Baker, 1922b; Bequaert, 1957; Haas & Solem, 1960; Thompson, 1967; Correa-Sandoval, 2000).

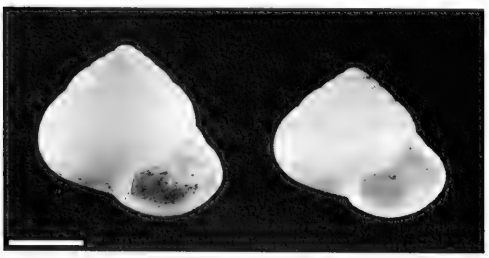


FIG. 274. *Helicina flavida*, Puerto Limón, APHIS PPQ USDA, height 5.9 mm, 5.1 mm; scale bar 2.5 mm.

Discussion

Helicina flavida was originally described from Jamaica, but aside from some records from the Antilles in some mid-19th century publications, almost all subsequent authors treated the Central American mainland species under this name, because a similar species had not been found on the Greater Antilles. Only Wagner (1910a) still retained the use of *flavida* for a non-existent Jamaican species and applied the younger, synonymous name *Helicina brevilabris* L. Pfeiffer, 1856 to the mainland species.

Literature records of *Helicina flavida* var. for Costa Rica (von Martens, 1890–1901) clearly referred to *H. beatrix*. Therefore, the species is newly recorded for Costa Rica, although it remains doubtful whether it still exists in Costa Rica or whether it was even indigenous to Costa Rica in the first place. Having recognized the peculiarity of his discovery, David Robinson re-examined the locality in 1998 but by then it was "totally built over by urban expansion". His examination of some other limestone spots near Puerto Limón where the limestone may have made it possible for the species to exist was unsuccessful (personal communication). On the other hand, Puerto Limón is the only Caribbean port of Costa Rica, where the enormous trade of agricultural

products actually takes place and introduction of foreign species is thereby facilitated. Robinson (1999) lists *H. flavida* among those species that were occasionally imported into the United States. Until better knowledge becomes available, the Costa Rican occurrence of this species remains doubtful.

MISIDENTIFICATIONS FOR COSTA RICA

Helicina amoena L. Pfeiffer, 1849

Helicina amoena – Monge-Nájera, 1997: 113: Costa Rica [*non* L. Pfeiffer, 1849] refers to *Helicina pitalensis*

See under *Helicina pitalensis*.

Helicina oweniana L. Pfeiffer, 1849

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [*non* L. Pfeiffer, 1849] refers to *Helicina tenuis*, *H. talamancensis*, *H. gemma* and *H. monteverdensis* n. sp.

Original Description

Helicina oweniana L. Pfeiffer, 1849: 123 (not figured); L. Pfeiffer, 1850: 40–41, pl. 7, figs. 35, 36

Type Material

BMNH 20010751: 3 syntypes, leg. Mr. Ghiesbright, Hugh Cuming coll. (in original description "Ghiesbreght")

The three syntypes (Fig. 276) are very similar to each other. Compared to most of the Costa Rican species the shells are solid. They are of whitish-yellow color with a very slight touch of green, the lower margin of the suture is whitish; the apex is red; only the outer lip is bright orange. The upper whorls are very straight; the suture very little impressed, whorls regularly descending and extending in size. Aperture oblique, outer lip

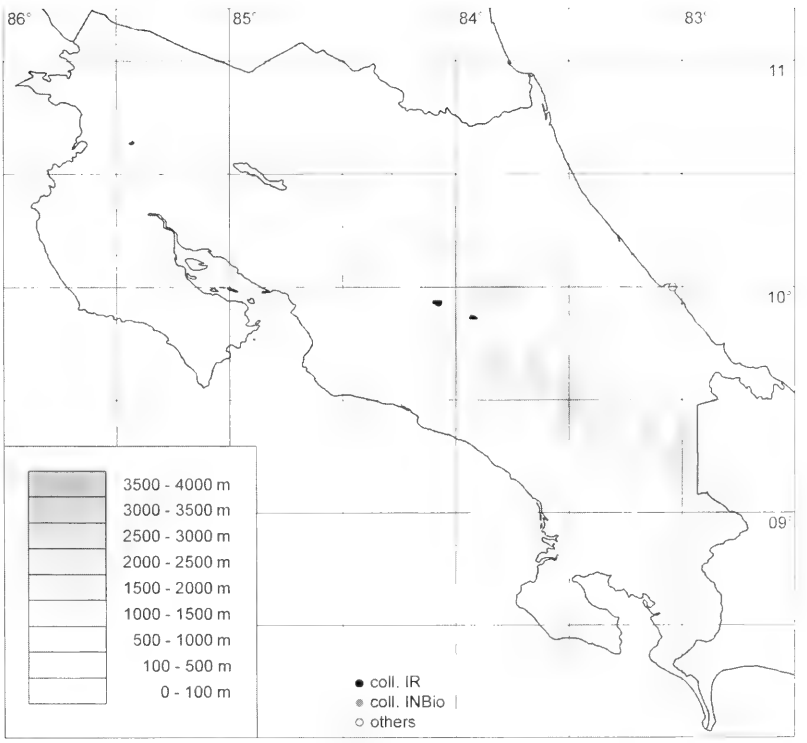


FIG. 275. Records of *Helicina flavida* in Costa Rica.

straight and perpendicularly and flatly expanded, thickened, basal margin with only a little notch. At the columella, a little groove.
Dimensions:
8.3/7.6/8.4/7.1/5.1/5.9/6.6 mm
8.5/7.9/8.6/7.2/5.3/6.2/6.8 mm
8.2/7.4/8.1/6.8/5.2/6.0/6.7 mm

Type Locality

"Chiapas, Mexico".

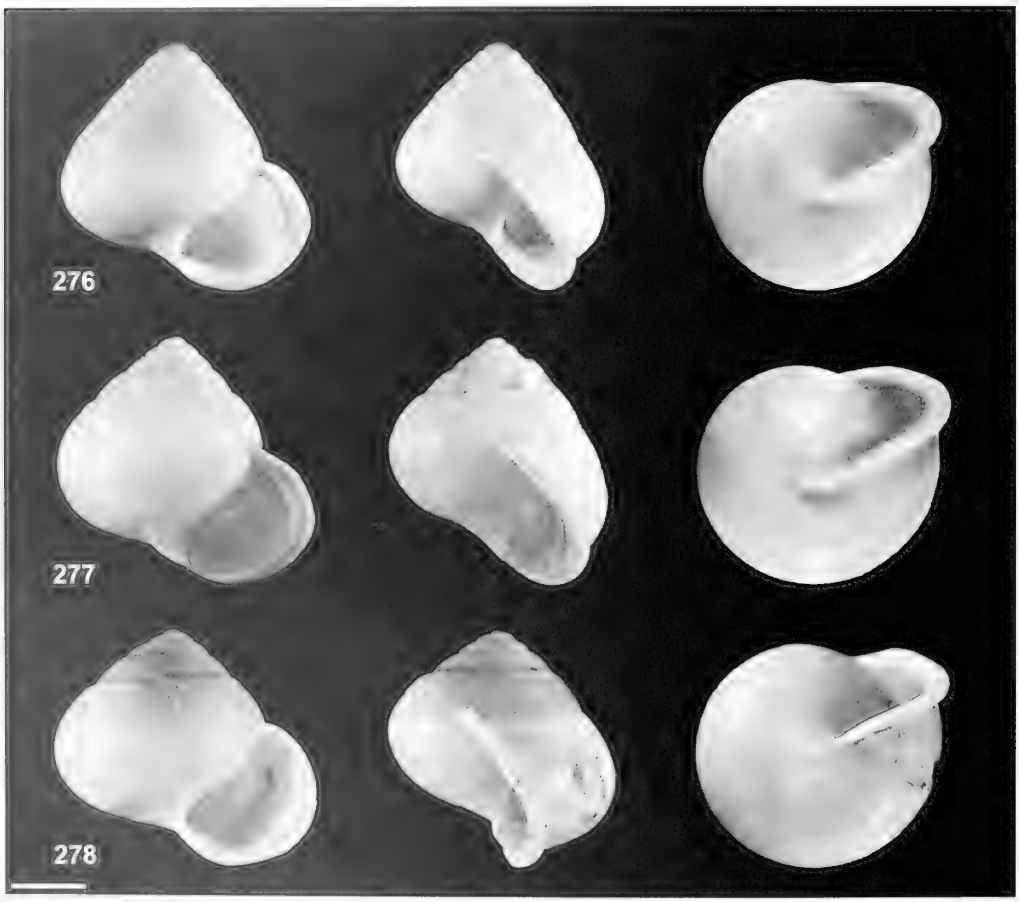
For comments. see under *Helicina tenuis*, *H. talamancensis*, *H. gemma*, and *H. monteverdensis* n. sp.

Helicina oweniana coccinostoma
Morelet, 1849

Helicina oweniana var. *coccinostoma* – von Martens, 1900: 605–606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley) [*non* Morelet, 1849] refers most likely to *Helicina gemma*

Original Description

Helicina coccinostoma Morelet, 1849: 19 (not figured)



FIGS. 276–278. *Helicina* spp. FIG. 276. Syntype of *Helicina oweniana*, BMNH 20010751, height 8.3 mm; scale bar 2.5 mm. FIG. 277. Lectotype of *Helicina coccinostoma*, BMNH 1893.2.4.1605, height 8.3 mm; scale bar 2.5 mm. FIG. 278. Lectotype of *Helicina anozona*, ZMB 25604a, height 7.9 mm; scale bar 2.5 mm.

Type Material

BMNH 1893.2.4.1605–1608, Morelet coll., "Guatemala, Peten, Palenque"
The type lot contains four specimens from the Morelet collection, which was bought by H. Fulton and later purchased by the BMNH. To the shell of one specimen there was glued a small label "type". Because the origin of this label is uncertain and it is obviously not from Morelet himself the specimen is **herein chosen as lectotype**. The paralectotypes do not significantly differ from the lectotype, except for one specimen being less elevated.

The lectotype (Fig. 277) very closely resembles that of *Helicina anozona* in shape. Its color is lighter, yellowish opaque throughout, except for a whitish band directly under the suture and the yellowish outer lip.
Dimensions:
Lectotype BMNH 1893.2.4.1605
8.3/7.9/8.5/6.1/5.3/6.4/6.8 mm
Paralectotypes BMNH 1893.2.4.1606–1608
8.2/7.5/8.1/6.9/5.1/6.1/6.5 mm
7.6/7.8/8.3/6.9/5.1/5.9/5.9 mm
7.2/6.7/7.3/6.1/4.6/5.5/5.6 mm

Type Locality

"Petenensis sylvas" [Guatemala, Petén Department].

The status of the taxon is not further discussed here, because it lies beyond the scope of this study and requires the examination of more comprehensive Mexican and Guatemalan material.

Helicina oweniana anozona
von Martens, 1875

Helicina oweniana var. *anozona* – Biolley, 1897: 5: Costa Rica: Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] and las Delicias (Santa Clara), 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] [*non* von Martens, 1876] refers most likely to *Helicina gemma*

Helicina oweniana var. *anozona* – von Martens, 1900: 605–606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley), Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] (Pittier, Biolley) [*non* von Martens, 1876] refers most likely to *Helicina gemma*

Original Description

Helicina anozona von Martens, 1875: 649 (not figured); von Martens, 1876: 261, pl. 9, fig. 7

Type Material

Lectotype ZMB 25604a (leg. Salvin), 1 paralectotype ZMB 25604b (same data); 4 paralectotypes ZMB 40862 (same data) (present designation); syntypes (now paralectotypes) SNG 2192 (Zilch, 1979)
Von Martens based the description on specimens collected by Salvin housed in the collection of the ZMB, where he was curator at the time. One lot bears von Martens' sign for types, the larger specimen best matches the description and is **here selected as lectotype** (Fig. 278). The figure of *Helicina oweniana anozona* in von Martens (1890) is based on a specimen collected later by Champion (ZMB 103307).

The shell differs from *H. oweniana* in its general shape, a more globular appearance: the whorls are more strongly inflated, the spire is lower, the aperture relatively larger and the whorls are slightly shouldered. Except for the whitish color, the features of the outer lip are very similar.
Dimensions:
Lectotype: 7.9/8.4/8.9/7.5/5.4/6.3/6.3 mm

Type Locality

"Guatemala, vicinity of Coban" [Guatemala: Alta Verapaz].

The status of the taxon is not further discussed here, because it lies beyond the scope of this study and requires the examination of more comprehensive Mexican and Guatemalan material.

Helicina fragilis
Morelet, 1851

Alcadia (*Leialcadia*) *fragilis* – Wagner, 1908: 84–85: Costa Rica: Shirores, Talamanca [in part] [*non* Morelet, 1851] refers partially to *Helicina chiquitica*

See under *Helicina chiquitica* and *Helicina monteverdensis* n. sp.

MORPHOLOGICAL CHARACTERISTICS OF RELATED SUPRASPECIFIC TAXA OF AMERICAN HELICINIDAE

For the discussion of the arrangement of the Costa Rican species and the comparison of morphological characteristics, the following supraspecific taxa were investigated with emphasis on the less investigated features, for example, embryonic shell structure and the anatomy of the female reproductive system. When available, the respective type species were examined, otherwise species were chosen that are assumed to be closely related. The taxa encompass all important genera and subgenera, which include species reported for the Central American mainland and some selected representatives from South America and the Caribbean Islands. Unless otherwise stated, the synonymy given by Baker (1922a) is accepted and not repeated. A detailed listing of the objective synonyms can be found in Keen (1960). From the following taxa, *Helicina*, *Ceochasma*, *Alcadia*, *Lucidella*, *Eutrochatella*, *Pyrgodomus* and *Schasicheila* are commonly recognized at the generic level.

Because the following also gives an overview of these supraspecific taxa and their characteristics, *Succincta* and "*Cinctella*" were added only on the basis of annotated literature data. Furthermore, references for a few radula descriptions were given for completeness.

For the verification of the dissections, histological sections were studied for *Helicina jamaicensis*, *Alcadia hollandi*, *Lucidella aureola* and *Eutrochatella pulchella*. Similar attempts for *Helicina brasiliensis* and *Schasicheila alata* proved to be only partially successful due to the poor condition of the old material.

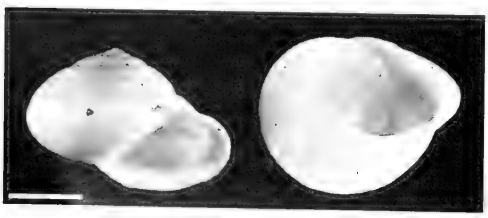


FIG. 279. *Helicina neritella*, IR 3454, height 9.8 mm; scale bar 5 mm.

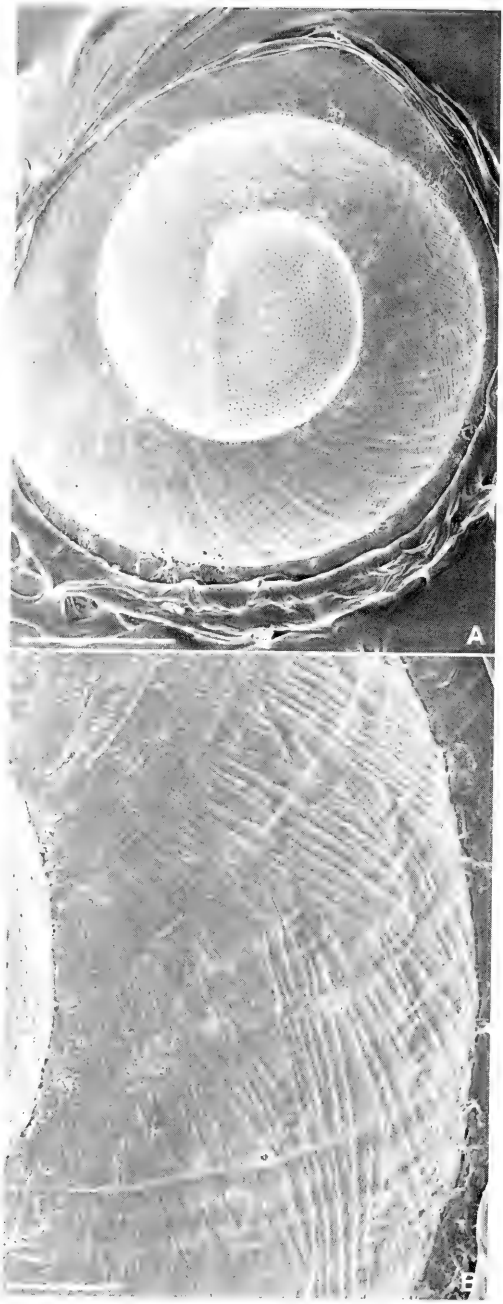


FIG. 280. Teleoconch surface structure of *Helicina neritella*, IR 3857. A. Structure of apical part. B. Pattern of oblique diverging grooves on the 1st whorl; scale bar 500 µm (A), 100 µm (B).

Helicina Lamarck, 1799

Type species

Helicina neritella Lamarck, 1799

Investigated Species

Helicina neritella (Figs. 279, 340A)

Material

Jamaica: Manchester Parish, Mandeville, Caledonia Road, 18°02'11"N, 77°30'44"W, 600 m a.s.l., 28./29.05.2001 (IR 3454, IR 3459); St. Ann Parish, N Ocho Rios, Fern Gully, 310 m a.s.l., 04.06.2001 (IR 3857), leg. W. Böckeler & I. Richling

Morphological Characteristics

Teleoconch Surface Structure (Fig. 280): The first half whorl is sculptured with the transitional pattern, which is followed by strongly developed oblique diverging grooves. This pattern is maintained throughout the teleoconch.

Embryonic Shell (Fig. 281): Densely structured with pits arranged in concentric lines, pits comparatively large. Diameter about 728 µm (n = 3), a little smaller than given by Thompson (1982), other structures equal to his description.

Radula: Figured in Baker (1922a: pl. III, fig. 6, pl. IV, fig. 17).

Female Reproductive System (Fig. 282): Ascending limb of the V-organ elongated, straight, in natural position overlapping with the posterior part of the pallial oviduct. The latter in relation to the apical complex remarkably long, transversally constricted. Small, oblong receptaculum seminis entering inner side of the descending limb. Bursa copulatrix very prominent and elongated with numerous, densely arranged, rather small lobules. Provaginal sac appearing vestigial, long and slender, only slightly demarcated from its much elongated and partially coiled stalk. Provaginal opening absent.

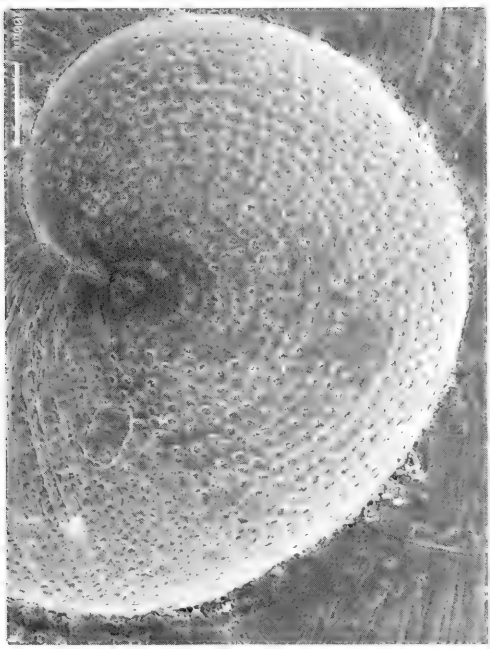


FIG. 281. Embryonic shell of *Helicina neritella*, IR 3459; scale bar 100 µm.

FIG. 282. Female reproductive system of *Helicina neritella*, apical complex enlarged, IR 3454; scale bars 2.5 mm (left), 1 mm (right).

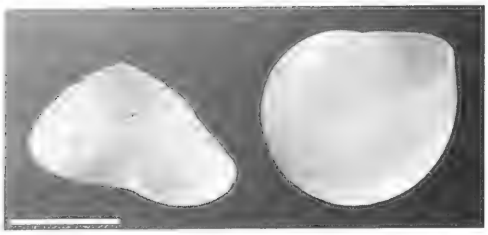


FIG. 283. *Helicina platychila*, UF 259486, height 6.5 mm; scale bar 5 mm.

Investigated Species

Helicina platychila (von Mühlfeldt, 1816) (Figs. 283, 340B)

Material

Dominica: along trail $^{1}/_{8}$ mi. W of Trafalgar Falls, upper end of banana plantation, leg. J. P. E. Morrison (JPEM-2610), 11.10.1965 (UF 259486)

FIG. 284. Embryonic shell of *Helicina platychila*, UF 259486; scale bar 100 µm.

FIG. 285. Female reproductive system of *Helicina platychila*, right figure: dorsal view, UF 259486; scale bar 1 mm.

Morphological Characteristics

Embryonic Shell (Fig. 284): Similar pattern as in *Helicina neritella*, but pits smaller and more numerous. Diameter 890 µm.

Female Reproductive System (Fig. 285): Very similar to that of *Helicina neritella*. Ascending limb of V-organ slightly curved; pallial oviduct relatively shorter and stronger folded. Bursa copulatrix prominent, with less numerous lobes, but the latter larger and elongated. Provaginal sac small, roundly triangular, stalk slightly curved and relatively long. Provaginal opening absent.

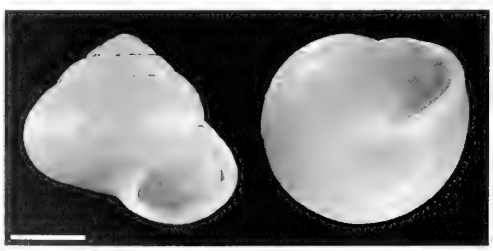


FIG. 286. *Helicina orbiculata*, IR 3361, height 6.5 mm; scale bar 2.5 mm.

Oligyra Say, 1818

Type species

Olygyra orbiculata Say, 1818

Investigated Species

Helicina orbiculata (Figs. 286, 340C)

Material

USA: Florida, Gainesville, Museum Road, near Dickinson Hall, 05.2001, leg. J. Slapcinsky & I. Richling (IR 3359, IR 3361)

Morphological Characteristics

Teleoconch Surface Structure (Fig. 287): Transitional pattern for about $^1/_3$ whorl, subsequently sculptured with oblique diverging grooves up to the aperture. Furthermore widely spaced, slightly impressed spiral grooves with periostracal ridges.

Embryonic Shell (Fig. 288): Scarcely sculptured with pits arranged in concentric lines. Interspaces of lines and pits exceed the size of the pits. Occasionally more densely pitted (Fig. 288B). Diameter 835 µm (n = 4).

Radula (Fig. 289): All centrals with cusps, A-central about 3–4, B-central about 5–6, C-central about 2–4; comb-lateral with 7–8 cusps. Cusps of the marginals rather slowly increasing in number, cusps more distally than laterally arranged. Except for minor deviations, this is in agreement with Baker (1922a).

Female Reproductive System (Fig. 290): V-organ rather stout, pallial oviduct moderately constricted. Receptaculum seminis large, bulbous, entering at inner side of descending limb of V-organ. Bursa copulatrix rather small and weakly lobed, of about the same size as elongated provaginal sac, which is slightly constricted at the distal side, its stalk is short. Provaginal opening absent. The female system was studied and figured by Baker (1926) (Fig. 9). Except for the monaulic (instead of diaulic) conditions, the structures were confirmed. The bursa copulatrix differs in the length of its lobes in the specimens of all three locations (Baker: Miami County, Florida, and San Antonio,

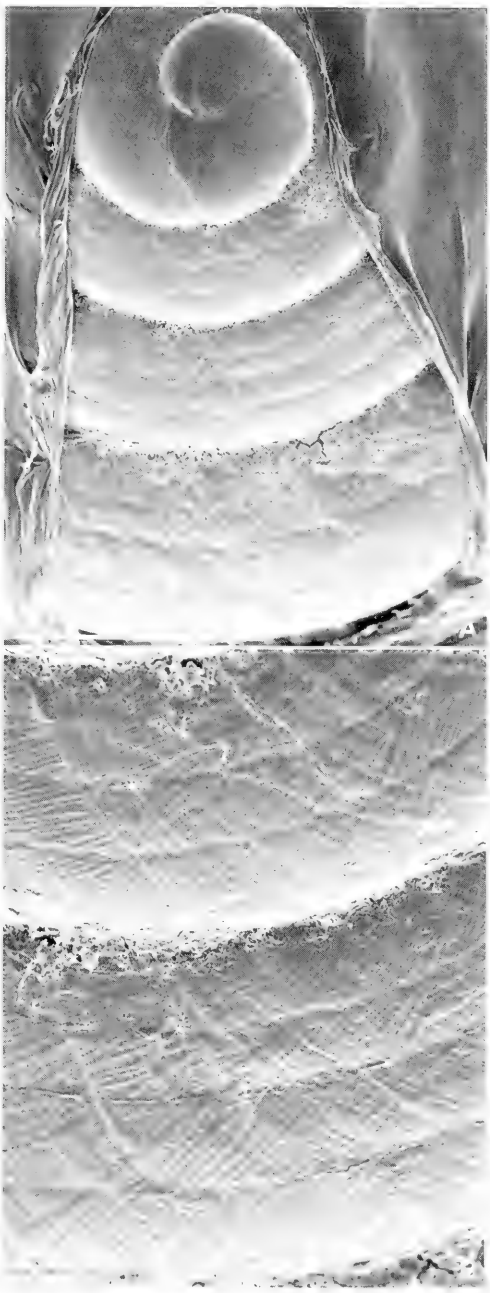


FIG. 287. Teleoconch surface structure of *Helicina orbiculata*, IR 3859. A. Structure of apical part. B. Pattern of oblique diverging grooves and spiral grooves with periostracal ridges on the begin of the 2nd and 3rd whorl; scale bars 500 µm (A), 100 µm (B).

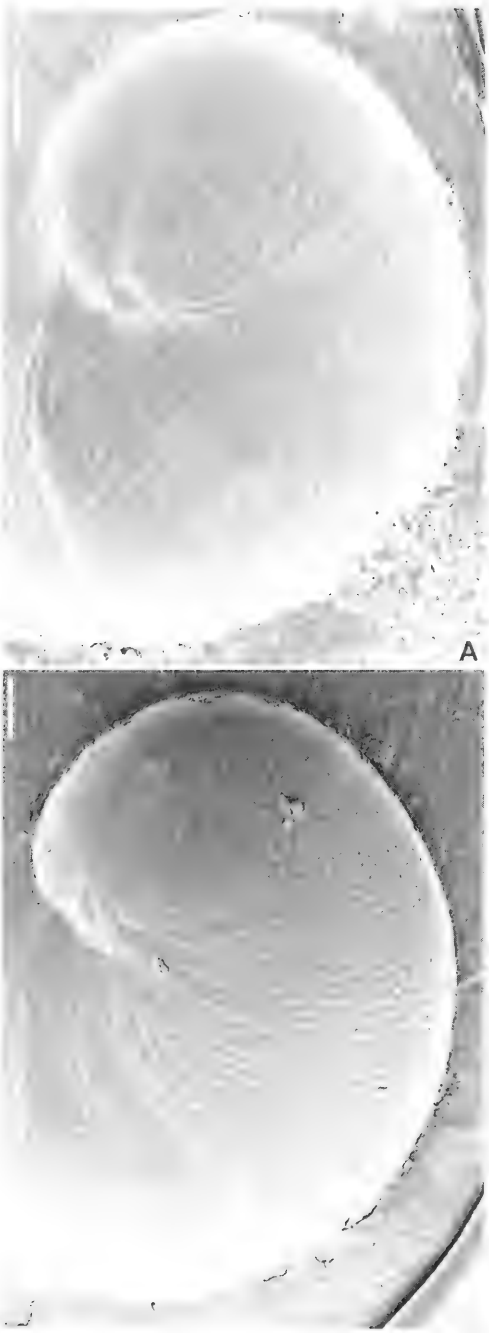


FIG. 288. Embryonic shell of *Helicina orbiculata*. A. IR 3359. B. IR 3361; scale bar 100 µm.

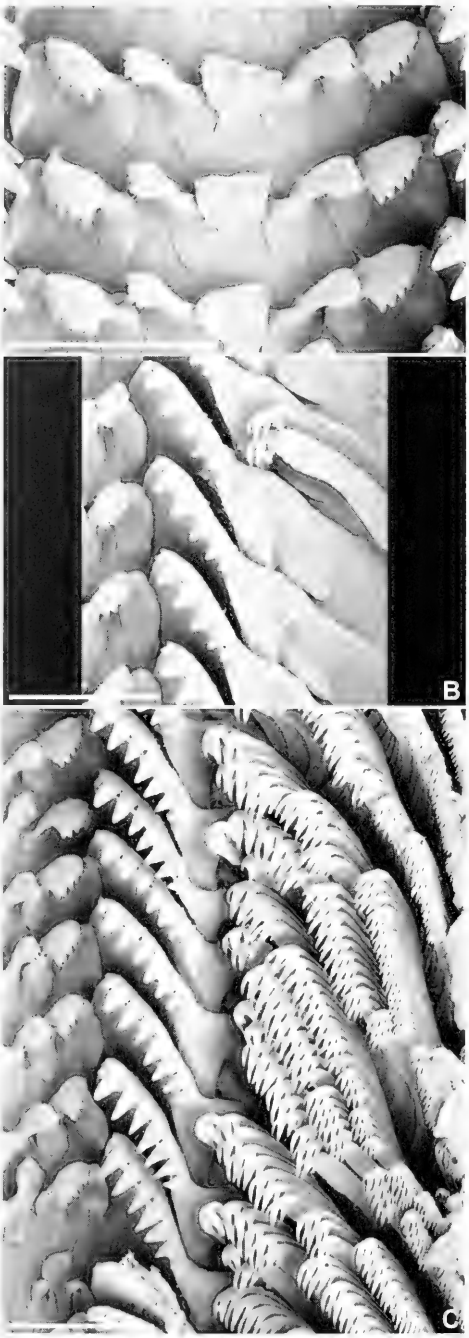


FIG. 289. Radula of *Helicina orbiculata*, IR 3359. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.

FIG. 290. Female reproductive system of *Helicina orbiculata*, IR 3361; scale bar 1 mm.

Texas), the presently studied specimens have furthermore a larger receptaculum seminis. Baker (1926) treated the specimens from Texas as the subspecies *Helicina orbiculata tropica* Jan, 1846, but a recent electrophoretical investigation by Strenth & Littleton (2000) suggests the conspecificity of both taxa, which has been discussed repeatedly.

Succincta Baker, 1922

Type species

Helicina succincta Martens, 1890

Investigated Species

Helicina succincta (investigated by Baker, 1928)

Morphological Characteristics

Radula: Figured in Baker (1928: pl. IV, fig. 26).

Female Reproductive System: Figured in Baker (1928: pl. II, figs. 3, 4): Receptaculum seminis remarkably enlarged and slightly trilobed; bursa copulatrix reduced in size and only bilobed; provaginal sac well developed and distally lobed, stalk quite long. According to the drawing and the results for re-examined mainland species, the provaginal opening is here assumed to be absent.

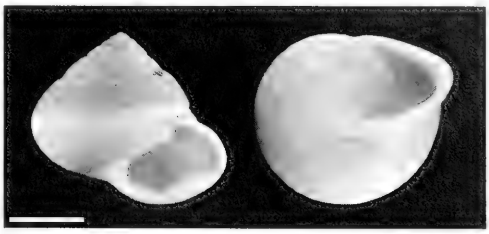


FIG. 291. *Helicina turbinata*, Cordova, ZMB 103315, height 11.7 mm; scale bar 5 mm.

Tristramia Crosse, 1863

Type species

Helicina salvini Tristram, 1861

Investigated Species

Helicina turbinata Wiegmann, 1831 (Figs. 291, 340D)

Material

Mexico: Arisolapa [?], leg. Strebel, #1723 (ZMH 2932)

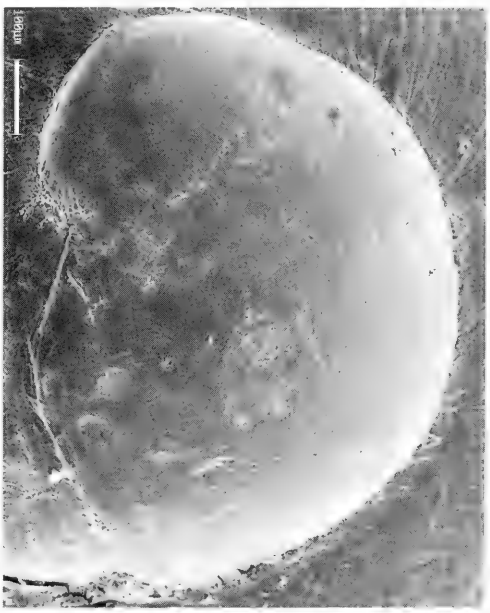


FIG. 292. Embryonic shell of *Helicina turbinata*, ZMH 2932; scale bar 100 µm.

Morphological Characteristics

Embryonic Shell (Fig. 292): The surface is concentrically pitted, but due to the very small size of the widely spaced pits, the surface appears nearly smooth. Diameter 765 µm.

Radula: Figured in Baker for the closely related or synonymous species (von Martens, 1890–1901; Baker, 1922a) *Helicina zephyrina* Menke, 1830 (1922a: pl. III, fig. 9, pl. IV, fig. 13).

Female Reproductive System (Fig. 293): V-organ normally developed; pallial oviduct transversally and partially also longitudinally constricted. Receptaculum seminis very large and bulbous, entering at the inner side of the descending limb of the V-organ, but, due to its unusual size, shifted dorsally. Bursa copulatrix prominent and deeply lobed; provaginal sac with a rather slender stalk (not visible in Fig. 293), large and slightly constricted at its distal side. The provaginal opening is absent. Except for the erroneously assumed provaginal opening the description by Baker (1928) for *Helicina zephyrina* is identical, especially with respect to the shape of the bursa copulatrix and the enlarged receptaculum seminis.

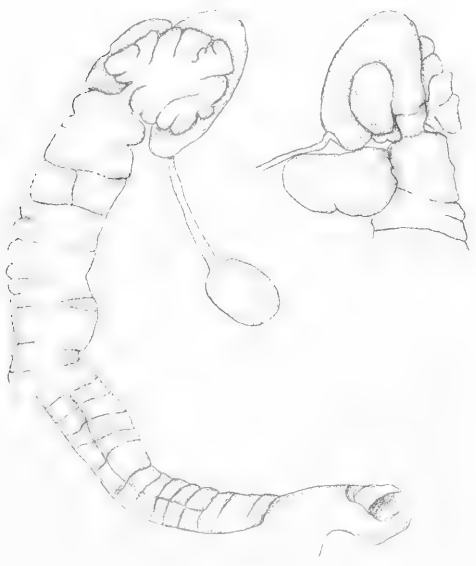


FIG. 293. Female reproductive system of *Helicina turbinata*, right figure: dorsal view, (on account of the poor preservation kept in nearly natural position) ZMH 2932; scale bar 1 mm.

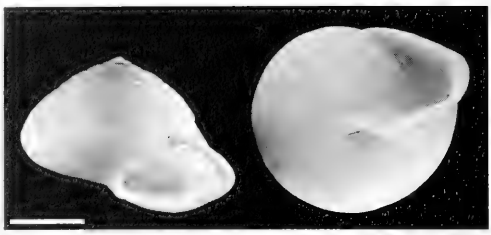


FIG. 294. *Helicina amoena*, ZMB 103345, height 10.6 mm; scale bar 5 mm.

Oxyrhombus Crosse & Fischer, 1893

Type species

Helicina amoena L. Pfeiffer, 1849

Investigated Species

Helicina amoena (Figs. 294, 340E)

Material

Guatemala: Teleman (ZMB 103345)

Morphological Characteristics

Embryonic Shell: The structure is similar to those shown for *Helicina funcki* and *H. pitalensis* (Figs. 15, 43): relatively large pits in concentric lines with their diameter about equal to their interspacial distance. Within the material available, large parts of the embryonic shell were so badly eroded so that it did not seem to be worth figuring. Diameter 860 µm.

Radula: Figured in Baker (1922a: pl. III, fig. 8, pl. IV, fig. 15).

Female Reproductive System (Fig. 295): In general similar to that of *Helicina turbinata*, but receptaculum seminis much smaller, bursa copulatrix with an elongated central axis from which numerous, further subdivided lobes branch off. Provaginal sac much more flattened and more strongly irregularly lobed at the distal side, its stalk of moderate length (not clearly visible in Fig. 295). Provaginal opening absent.

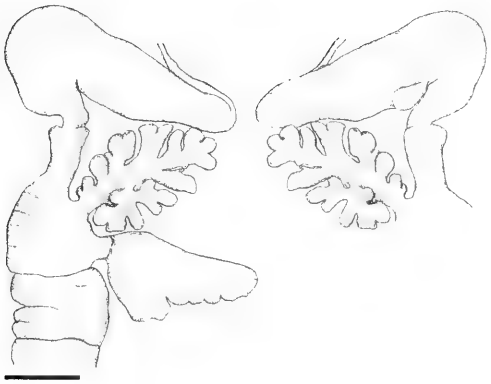


FIG. 295. Female reproductive system of *Helicina amoena*, right figure: dorsal view, distal parts omitted, ZMB 103345; scale bar 1 mm.

Pseudoligyra Baker, 1954

Synonym (objective)

Tenuis Baker, 1922, *non* Barrande, 1881

Type species

Helicina tenuis Pfeiffer, 1849

Investigated Species

Helicina tenuis – see above.

Punctisulcata Baker, 1922

Type species

Helicina punctisulcata von Martens, 1890

Investigated Species

Helicina punctisulcata cuericiensis n. subsp. – see above.

"*Cinctella*" Baker, 1922,
non Monterosato, 1884

Type species

Helicina cinctella Shuttleworth, 1852

Investigated Species

Helicina cinctella (investigated by Baker, 1928)

Morphological Characteristics

Female Reproductive System: Figured in Baker (1928: pl. II, fig. 5): Receptaculum of normal size; bursa copulatrix prominent and having several further subdivided lobes; provaginal sac weakly lobed at distal side, flattened. The provaginal opening is shown in the figure, but its existence is very questionable. Here it is assumed to be absent.

"*Gemma*" Baker, 1922,
non Deshayes, 1853

Type species

Helicina gemma Preston, 1903

Investigated Species

Helicina gemma – see above.

Tamsiana Baker, 1922

Type species

Helicina tamsiana Pfeiffer, 1851

Investigated Species

Helicina tamsiana

Material

Venezuela: Porto Cabello, leg. Martin (ZMB 103314)

Morphological Characteristics

Embryonic Shell: Only a single specimen was studied. It remains uncertain whether the embryonic shell is partially eroded or whether the surface is rather smooth, except for very scarce pits and very slight oblique lines.

Radula: Figured in Baker (1923: p. 20, fig. 20).

Female Reproductive System: Described and figured by Baker (1923: pl. VI, fig. 14): Receptaculum seminis of normal size; bursa copulatrix reduced to a very small, simple sac; provaginal sac very prominent and anteriorly elongated, so that the stalk branches off about the middle of its long side. Provaginal opening is shown in the figure, its existence remains questionable.

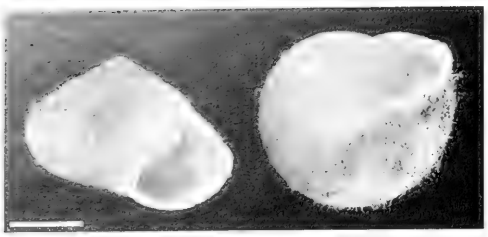


FIG. 296. *Helicina dysoni*, UF 226928, height 5.3 mm; scale bar 2.5 mm.

Analcadia Wagner, 1908

Type species

Helicina dysoni Pfeiffer, 1849

Investigated Species

Helicina dysoni (Figs. 296, 340F)

Material

Trinidad & Tobago: Trinidad Island, Mayaro County, Trinity District, 0.6 km SW junction Trinity Road & Guayaguayare Road (Rushville), 10°07'32"N, 61°03'28"W, 12 m a.s.l., leg. K. Auffenberg et al. (KA-1212), 02.06.1994 (UF 226928)

Venezuela: Margarita Island, Porlamar, just outside town under trees, *ex* Guido Poppe, 1988 (HNC 54607)

Morphological Characteristics

Embryonic Shell (Fig. 297): Surface with a few concentric rows of small, widely spaced pits. Diameter 590 µm.

Radula: Figured by Baker (1923: pl. III, fig. 12).

Female Reproductive System (Fig. 298): Limbs of V-organ rather short, small receptaculum seminis entering at inner side of descending limb. Bursa copulatrix representing a very small sac, its connection to the reception chamber remarkably shifted towards the dorsal side compared to all other species described in this study. Provaginal sac exceptional large and inflated, slightly irregularly constricted at its distal side; stalk short, stout and branching off at the middle of the sac. Directly at junc-

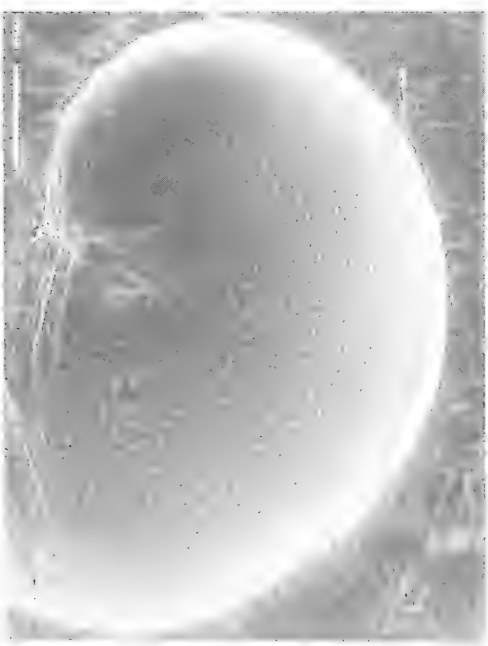


FIG. 297. Embryonic shell of *Helicina dysoni*, HNC 54607; scale bar 100 µm.

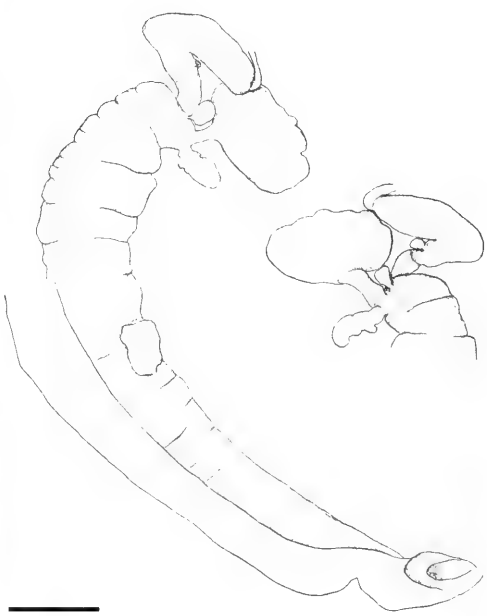


FIG. 298. Female reproductive system of *Helicina dysoni*, right figure: dorsal view, UF 226928; scale bar 1 mm.

tion with the reception chamber is an anterior sac-shaped appendage. Additional sac present at ventral side of the pallial oviduct which seems to be connected to it (remains to be checked histologically). Provaginal opening absent.

Sericea Wagner, 1907

Type species

Helicina sericea Drouet, 1859

Investigated Species

Helicina sericea (Figs. 299, 340G)

Material

Suriname: District Suriname, Bodensavanne [?], mine synagoge, leg. C.O. van Regteren Altena (loc. 51), 14.03.1963 (RMNH 8890)

Morphological Characteristics

Embryonic Shell (Fig. 300): Similar to that of *Helicina dysoni*. Diameter 755 µm.

Female Reproductive System (Fig. 301): V-organ and receptaculum seminis similar to *Helicina dysoni*. Bursa copulatrix of moderate size and subdivided in numerous short lobules. Provaginal sac exceptional large and inflated, nearly kidney-shaped, with its short and stout stalk branching off at about the middle of the proximal side. It bears an anterior basal appendage at the junction with its stalk, which is roundly constricted twice. Provaginal opening absent.

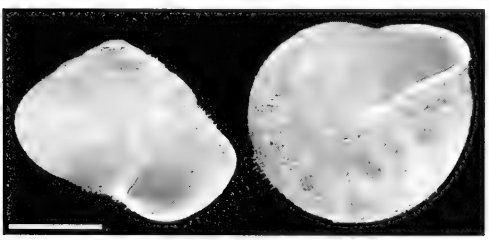


FIG. 299. *Helicina sericea*, RMNH 8890, height 5.1mm; scale bar 2.5 mm.

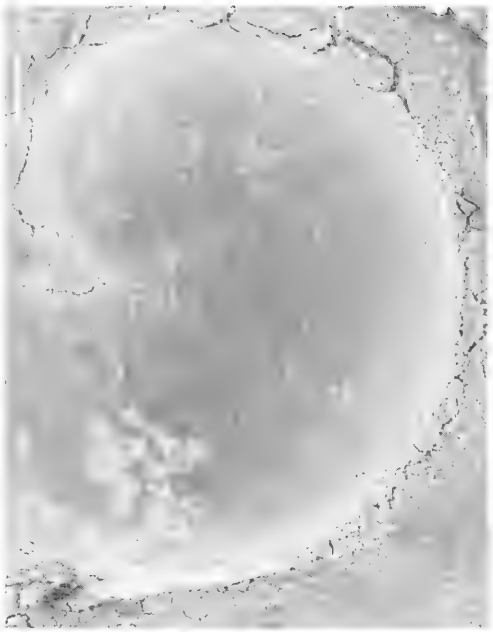


FIG. 300. Embryonic shell of *Helicina sericea*, RMNH 8890; scale bar 100 µm.

FIG. 301. Female reproductive system of *Helicina sericea;* upper, right figure: dorsal view, RMNH 8890; scale bar 1 mm.

Ceochasma Thompson, 1968

Type species

Ceochasma phrixina Thompson, 1968

Investigated Species

Ceochasma phrixina

Material

Mexico: Colima, 0.3 km. SE Tamala, 152 m a.s.l., leg. F.G. Thompson (FGT-777), 02.08.1966 (UF 20139, Paratypes)

Morphological Characteristics

Embryonic Shell: Not examined.

Radula: Figured in Thompson (1968: 49).

Female Reproductive System: Described and figured by Thompson (1968: 49), for this study only reinvestigated with respect to provaginal opening, which was found to be absent.

Angulata Baker, 1922

Type species

Helicina angulata Sowerby, 1842

Investigated Species

Helicina brasiliensis Gray, 1825 (Figs. 302, 340H)

Material

Brazil: Sta. Catharina, Humboldt District, Joinville, Flussgebiet von Itaporu [area of the Río Iguaçu], leg. W. Ehrhardt, purchased 21.10.1910 (ZMH 2931)

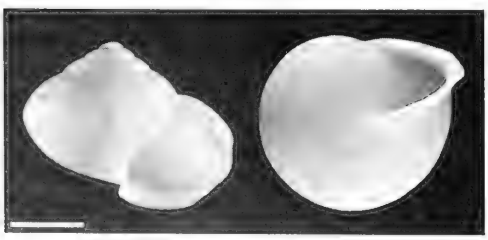


FIG. 302. *Helicina brasiliensis*, ZMH 2931, height 5.6 mm; scale bar 2.5 mm.

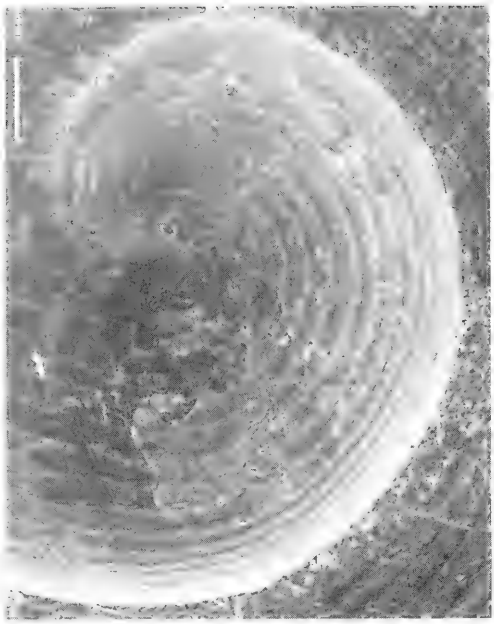


FIG. 303. Embryonic shell of *Helicina brasiliensis*, ZMH 2931; scale bar 100 µm.

Morphological Characteristics

Embryonic Shell (Fig. 303): Sculptured with regular, broad, very slightly raised spiral bands; interspacial distance smaller than the width of these bands, otherwise smooth. Diameter 695 µm (n = 2).

Female Reproductive System (Fig. 304): Receptaculum seminis very small, connected to the inner side of the descending limb of the V-organ; bursa copulatrix large and deeply lobed. Provaginal sac elongated and of somewhat irregular outline, its stalk rather stout. Provaginal duct seems to branch off from this stalk at its most anterior point. Due to the poor preservation of the material, the provaginal duct and opening could not be observed with certainty, but its presence is very likely.

Alcadia Gray, 1840

Type species

Helicina major Gray, 1824

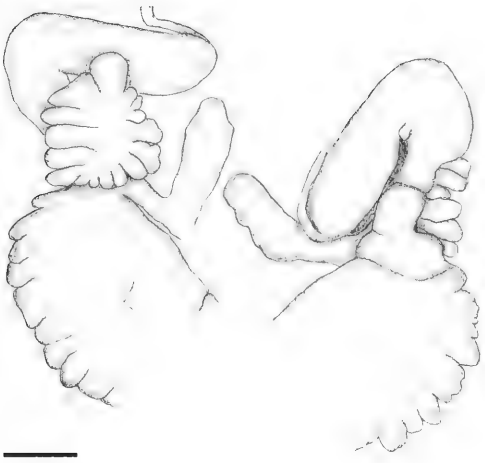


FIG. 304. Female reproductive system of *Helicina brasiliensis*, right figure: dorsal view, (distal parts omitted, provaginal duct and opening likely, but not verified) ZMH 2931; scale bar 0.5 mm.

Investigated Species

Alcadia major (Figs. 305, 340l)

Material

Jamaica: Manchester Parish, Silver Grove, Secondary forest & bordering pasture, limestone & red soil, 18°04.95'N, 77°35.35'W, 880–900 m a.s.l., leg. G. Rosenberg & I.V. Muratov (JBS 113), 02.10.1999 (ANSP 19559)

Morphological Characteristics

Embryonic Shell (Fig. 306): Surface with more or less strong oblique grooves, more pronounced towards the margin, and coarse, irregularly spaced radial threads. Diameter 1800 µm. The embryonic shell had also been studied and figured by Thompson (1982: fig. 26), his specimen shows the oblique grooves within the inner curvature, the diameter is given with 1.0 mm, but a measurement of the figure reveals a more likely size of about 2.2 mm.

Radula (Fig. 307): The centrals completely lack cusps and the cutting edges are reinforced. The "comb"-lateral agrees in its rough outline rather with the denticulated part of the comb-lateral in *Helicina*, but the cutting edge is smooth and thickened and resembles the T-shaped lateral of *Eutrochatella* (vianid radula). The accessory plate seems to be reduced. The tips of the marginals are rounded and show minor crenulations.

The vianid condition of the radula has already been mentioned by Boss & Jacobson (1973) and Thompson (1982), but it has never been figured and described in detail before.

Female Reproductive System (Fig. 308): V-organ with a slight apical swelling, its as-

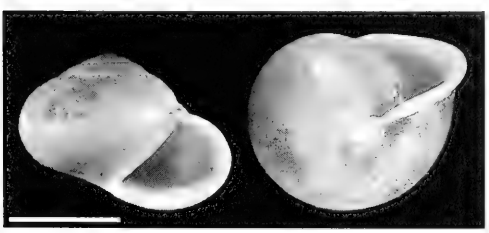


FIG. 305. *Alcadia major*, ANSP 19559, height 14.2 mm; scale bar 10 mm.

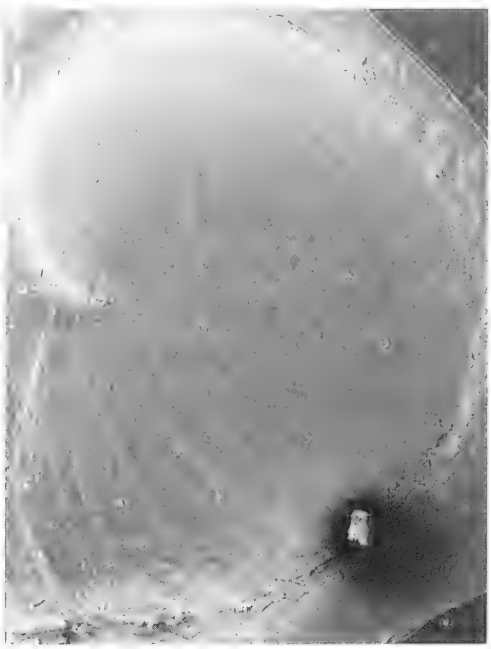


FIG. 306. Embryonic shell of *Alcadia major*, ANSP 19559; scale bar 100 µm.

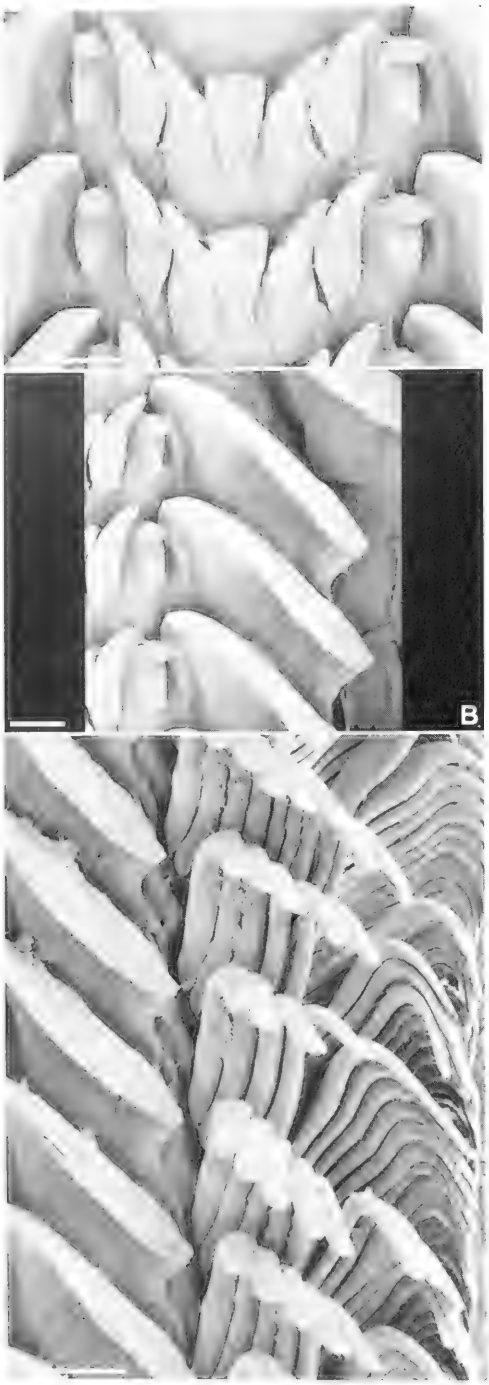


FIG. 307. Radula of *Alcadia major*, IR 3359. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 µm (A, B), 100 µm (C).

FIG. 308. Female reproductive system of *Alcadia major*, ANSP 19559; scale bar 2.5 mm.

cending limb slightly elongated. Receptaculum seminis equal to *Helicina* on the inner side of the descending limb, pedicel well developed. Bursa copulatrix representing a very large, irregularly shaped sac that broadly enters the reception chamber. Close to this connection is a slender provaginal duct that extends up to its opening for about $^{1}/_{3}$ of the length of the pallial oviduct. Close to the reception chamber, the provaginal duct receives the stalk of the medium-sized, oblong provaginal sac. The specimen is not very well preserved and perhaps the visible broad connection of the bursa copulatrix does not reflect the natural condition nor does the weakly demarcated distal end of the reception chamber.

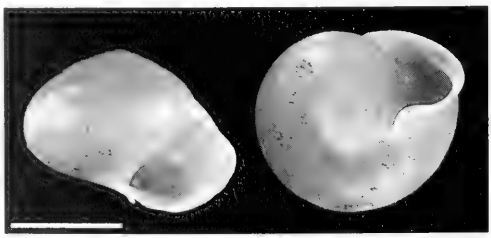


FIG. 309. *Alcadia hollandi*, IR 3579, height 7.4 mm; scale bar 5 mm.

Palliata Baker, 1922

Type species

Helicina palliata C. B. Adams, 1849

Investigated Species

Alcadia hollandi (C. B. Adams, 1849) (Figs. 309, 340J)

Material

Jamaica: Manchester Parish, Mandeville, 600 m a.s.l., Marshall's Drive, 25./27.05.2001, leg. W. Böckeler & I. Richling (IR 3579)

Morphological Characteristics

Embryonic Shell (Fig. 310): Inner curvature with predominant irregular axial threads, towards the margin interposing with strong, very distinct oblique grooves. Diameter 840 µm (n = 2).

Radula: Figured in Bourne (1911: pl. XL, fig. 56). Similar to *Helicina*: with denticulated centrals and marginals, comb-lateral with cusps and accessory plate.

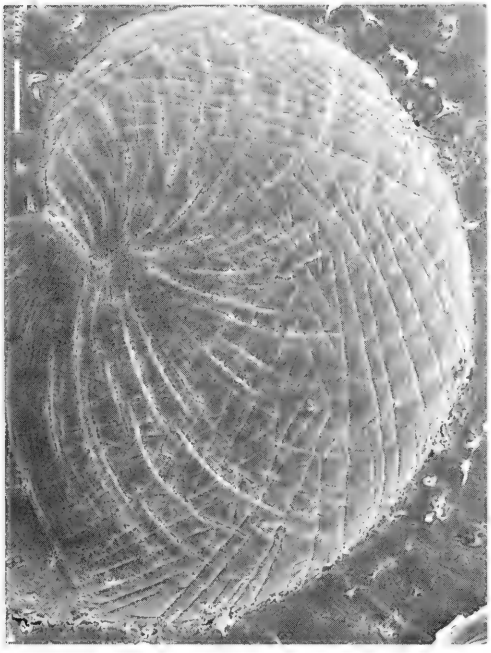


FIG. 310. Embryonic shell of *Alcadia hollandi*, IR 3579; scale bar 100 µm.

FIG. 311. Female reproductive system of *Alcadia hollandi*, IR 3579; scale bar 1 mm.

Female Reproductive System (Fig. 311): Ascending limb of V-organ shorter than in *Alcadia major*; receptaculum seminis small, located on the inner side of descending limb.

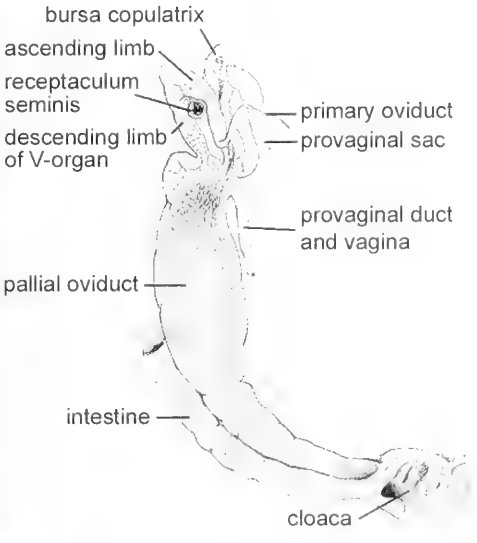


FIG. 312. Female reproductive system of *Alcadia hollandi* (reproduced from Bourne, 1911, explanations modified).

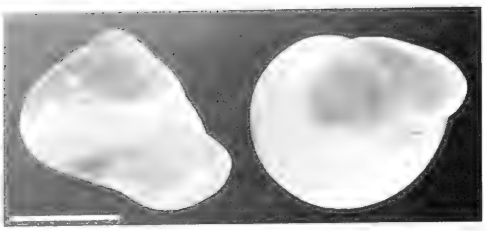


FIG. 313. *Alcadia jamaicensis*, IR 3502, height 8.3 mm; scale bar 5 mm.

Bursa copulatrix representing an oblong sac, longitudinally folded inside. Provaginal sac rather small and at the end of the very long stout stalk or itself stalk-like elongated, entering the reception chamber at nearly the same point as the bursa copulatrix and the provaginal duct. The latter is long and slender and opens at about $^1/_3$ of the way from the beginning of the pallial oviduct. The female system was figured by Bourne (1911: pl. XXXV, fig. 25, reproduced here: Fig. 312), but Baker (1926) questioned its correctness. Bourne's description is verified by the present investigation, only that sperm had not been found within the pallial oviduct, probably due to different physiological conditions.

Investigated Species

Helicina jamaicensis Sowerby, 1841 (Figs. 313, 340K) (belongs to *Alcadia*, an assignment to a subgenus, e.g., *Palliata*, is here not intended)

Material

Jamaica: Manchester Parish, W Bellefield, valley near road to Banana Ground, 18°04'46" N, 77°26'27"W, 580 m a.s.l., 24.05.2001 (IR 3502); Manchester Parish, Mandeville, 600 m a.s.l., Marshall's Drive, 25./27.05.2001 (IR 3574), leg. W. Böckeler & I. Richling

Morphological Characteristics

Embryonic Shell (Fig. 314): Very similar to *Alcadia hollandi*. Diameter 920 µm.

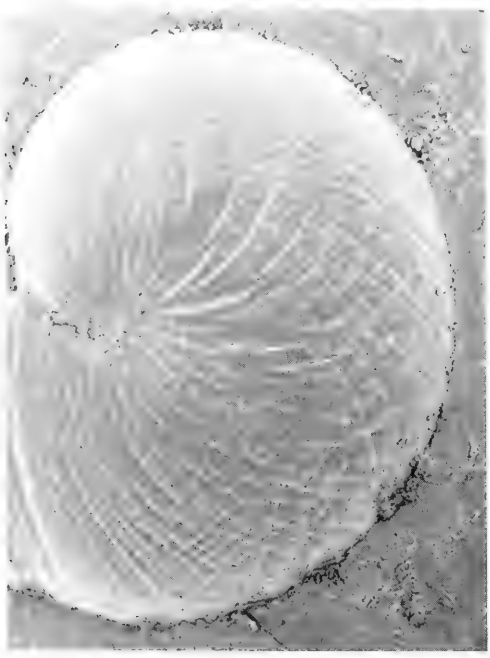


FIG. 314. Embryonic shell of *Alcadia jamaicensis*, IR 3574; scale bar 100 µm.

FIG. 315. Female reproductive system of *Alcadia jamaicensis*, left figure: natural position, right figure: slightly lateral view, IR 3502; scale bar 1 mm.

Female Reproductive System (Fig. 315): V-organ similar to *Alcadia hollandi*; receptaculum seminis larger. Bursa copulatrix, provaginal sac and provaginal duct very closely associated. Bursa copulatrix more prominent than in *Alcadia hollandi*, its position is similar. Provaginal sac of nearly the same size as the bursa copulatrix, forming an elongated sac with a short, stout stalk, which rather connects with the provaginal duct than with the reception chamber. Provaginal duct slightly inflated shortly before its opening at about $^{2}/_{5}$ of the way from the beginning of the pallial oviduct. The latter only with minor constrictions.

Idesa H. Adams & A. Adams, 1856

Synonym (objective)

Leialcadia Wagner, 1907

Type species

Helicina rotunda Orbigny, 1841

Investigated Species

Alcadia rotunda (Figs. 316, 340L)

Material

Cuba: Pinar del Rio, Rangel, leg. M.L. Jaume (ZMB 90412)

Morphological Characteristics

Embryonic Shell (Fig. 317): Sculptured with fine, oblique diverging grooves. Diameter 690 µm.

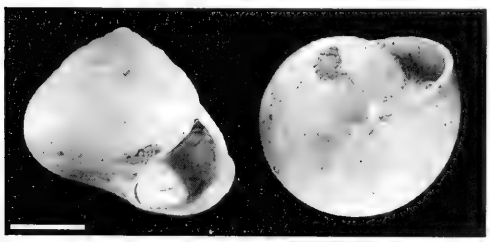


FIG. 316. *Alcadia rotunda*, ZMB 90412; scale bar 2.5 mm.

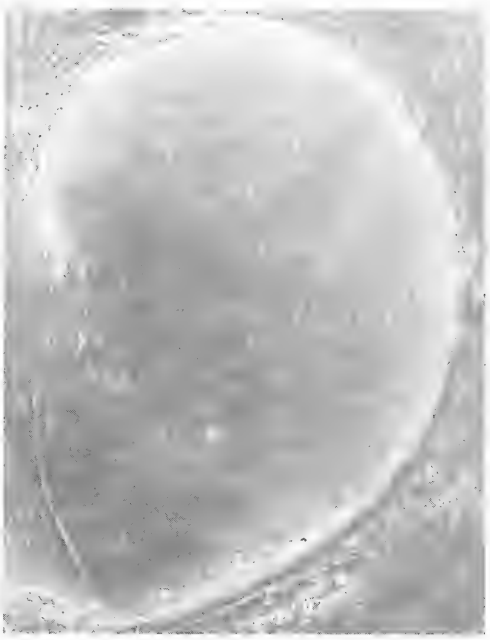


FIG. 317. Embryonic shell of *Alcadia rotunda*, ZMB 90412; scale bar 100 µm.

Radula: Figured by Troschel (1856–1863: pl. V, figs. 10, 11) and Baker (1923: pl. III, fig. 13). Centrals and marginals with cusps, comb-lateral denticulated and with accessory plate.

Female Reproductive System: unknown.

***Microalcadia* Richling, n. subgen.**

Type species

Helicina hojarasca Richling, 2001

Investigated Species

Alcadia hojarasca – see above.

Eutrochatella Fischer, 1885

Type species

Helicina pulchella Gray, 1825

Investigated Species

Eutrochatella pulchella (Figs. 318, 340M)

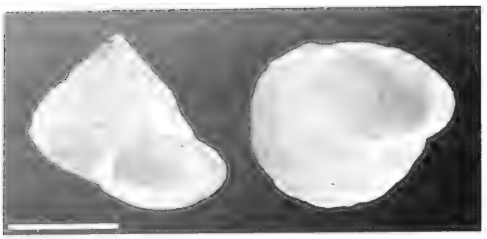


FIG. 318. *Eutrochatella pulchella*, IR 3702, height 7.9 mm; scale bar 5 mm.

Material

Jamaica: Manchester Parish, W Bellefield, valley near road to Banana Ground, 18°04'46" N, 77°26'27"W, 580 m a.s.l., 24.05.2001 (IR 3504); Trelawny Parish, near Burnt Hill, along road to Clarks Town, 18°18'24" N, 77°33'46"W, 510 m a.s.l., 02.06.2001 (IR 3808), leg. W. Böckeler & I. Richling

Morphological Characteristics

Embryonic Shell (Fig. 319): Surface rough, somewhat irregularly wrinkled. These coarse ridges and grooves show an orientation similar to the grooves in *Alcadia*. Diameter 560 µm (n = 3).

Radula: Figured in Bourne (1911: pl. XL, fig. 57) and Baker (1922a: pl. VI, figs. 31–32). All teeth without cusps, except for the outermost marginals, lateral reinforced and T-shaped, accessory plate reduced.

Female Reproductive System (Fig. 320): V-organ of moderate size; receptaculum seminis small and located at the inner side of the descending limb. Bursa copulatrix large, oblong, externally not further subdivided, broadly connected with the reception chamber. Provaginal sac smaller than bursa copulatrix and flattened, lobed at the distal side, its stalk short and slender. The transition of the reception chamber to the pallial oviduct is externally only weakly visible; furthermore, the pallial oviduct of different investigated specimens was remarkably less thickened than in the species of *Helicina* for example, although the specimens were all mature. The provaginal opening is absent. Bourne (1911: pl. XXXV, fig. 26) did not recognize the monaulic condition; furthermore, his figure shows a larger bursa copulatrix.

FIG. 319. Embryonic shell of *Eutrochatella pulchella*, IR 3505; scale bar 100 µm.

FIG. 320. Female reproductive system of *Eutrochatella pulchella*, IR 3808; scale bar 1 mm.

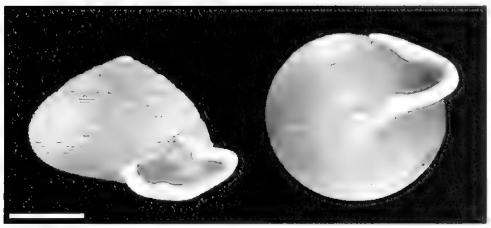


FIG. 321. *Lucidella aureola*, IR 3852, height 5.1mm; scale bar 2.5 mm.

Pyrgodomus Crosse & Fischer, 1893

Type species

Helicina chryseis Tristram, 1861

Investigated Species

Pyrgodomus microdinus – see above.

Lucidella Swainson, 1840

Type species

Helix aureola Férussac, 1822

Investigated Species

Lucidella aureola (Figs. 321, 340N)

Material

Jamaica: Manchester Parish, Mandeville, 600 m a.s.l., Marshall's Drive, 25./27.05.2001 (IR 3578); St. Ann Parish: N Ocho Rios, Fern Gully, 310 m a.s.l., 04.06.2001 (IR 3852), leg. W. Böckeler & I. Richling

Morphological Characteristics

Internal Shell Structures: (Fig. 322)

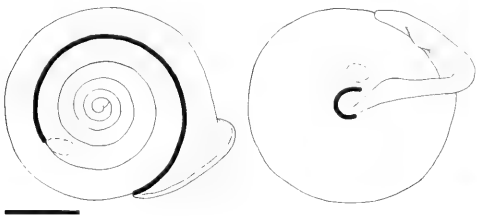


FIG. 322. Axial cleft and muscle attachments of *Lucidella aureola*, IR 3578; scale bar 2.5 mm.

Embryonic Shell (Fig. 323): Sculptured with numerous small pits, which are less regularly arranged than in *Helicina*. Their diameter is smaller than the interspacial distance. Diameter: 515 µm (n = 3). This is in full agreement with the description by Thompson (1982: figs. 24, 25).

Radula: Figured and described by Bourne (1911: pl. XL, fig. 59), Baker (1922a: pl. III, fig. 4, pl. V, fig. 22), and Thompson (1982: figs. 14, 15).

Female Reproductive System (Fig. 324): V-organ with a left-sided apical swelling, limbs rather short. Receptaculum seminis absent. Bursa copulatrix small, simple, broadly connected with the reception chamber. Provaginal sac large, distal side remarkably lobed, stalk branching off at about the middle, short and stout. Provaginal duct short, joining reception chamber nearly together with the stalk of the provaginal sac and the bursa copulatrix, opening at about distal end of the reception chamber. Posterior part (about ¼ to $^1/_5$) of pallial oviduct largely inflated and with numerous internal, longitudinal folds, at the distal end of this

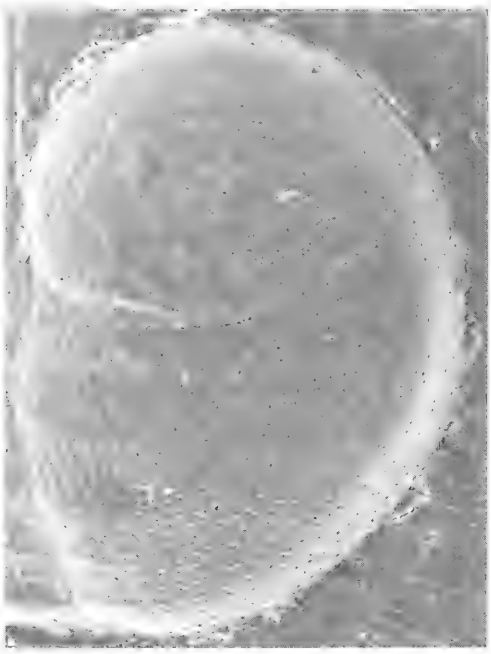


FIG. 323. Embryonic shell of *Lucidella aureola*, IR 3852; scale bar 100 µm.

FIG. 324. Female reproductive system of *Lucidella aureola*, IR 3852; scale bar 0.5 mm.

structure enters an additional, long sac. In both structures, sperm were found. Baker's (1926: pl. VII. fig. 19) description based on badly macerated specimens has to be corrected with respect to the absence of the receptaculum seminis and the additional structures of the pallial oviduct.

Perenna Guppy, 1867

Type species

Helicina lamellosa Guppy, 1867

Investigated Species

Lucidella lirata – see above.

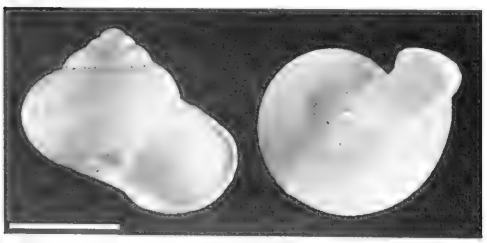


FIG. 325. *Schasicheila alata*, UF 251373, height 8.4 mm; scale bar 5 mm.

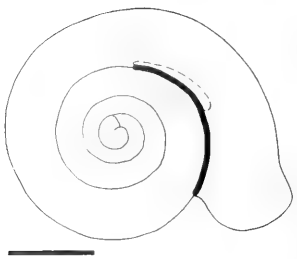


FIG. 326. Axial cleft and right muscle attachment of *Schasicheila alata*, ZMH 2928; scale bar 2.5 mm.

Schasicheila Shuttleworth, 1852

Type species

Helicina alata Pfeiffer, 1848

Investigated Species

Schasicheila alata (Figs. 325, 340O)

Material

Mexico: Agua Caliente, leg. Strebel (#1725) (ZMH 2928); Veracruz, 2.7 mi S Orizaba, 3,800 feet, leg. M.L. Paulson et al., 12.08.1965 (UF 251373)

Morphological Characteristics

Internal Shell Structures: (Fig. 326)

Embryonic Shell (Fig. 327): Sculptured with very regular and prominently raised axial folds. Diameter 1015 µm.

Radula: Figured in Baker (1928: pl. V, fig. 27).

Female Reproductive System (Fig. 328): Both limbs of the V-organ remarkably elongated and curved, a receptaculum seminis developed as in *Helicina*, *Alcadia* and *Eutrochatella* is absent, but in all dissected specimens an accumulation of sperm was found within the oviduct proximal to the weekly separated pedicel. A bursa copulatrix similar to other genera is not present; instead, a large, strongly recurved sac, which seems to be fused with the pedicel extents dorsal to the V-organ, is present. The provaginal sac is rather small and flattened, slightly lobed at the distal side; its stalk is very short. Provaginal duct also very short, opening at

FIG. 327. Embryonic shell of *Schasicheila alata*, ZMH 2928; scale bar 100 µm.

about the beginning of the pallial oviduct. The investigation confirms the description given by Baker (1928: pl. IV, figs. 19, 20).

FIG. 328. Female reproductive system of *Schasicheila alata*, V-organ turned to the left, UF 251373; scale bar 1 mm.

DISCUSSION

Knowledge of Costa Rican Helicinidae

Previous to this study and Richling (2001), six correctly identified species and one correctly identified subspecies (*Helicina funcki*, *H. pitalensis*, *H. tenuis*, *H. beatrix beatrix*, *H. beatrix confusa*, *H. gemma*, *Lucidella lirata*) of Helicinidae were known in Costa Rica. Additionally, a species of "*Pyrgodomus*" had tentatively been listed. The present investigation adds seven new species (*H. escondida* n. sp., *H. echandiensis* n. sp., *H. talamancensis*, *H. monteverdensis* n. sp., *H. chiquitica*, *Alcadia hojarasca*, *A. boeckeleri*) and two new subspecies (*Helicina punctisulcata cuericiensis* n. subsp., *H. beatrix riopejensis* n. subsp.). In addition, previously separated subspecies of *Helicina funcki* and *H. tenuis* were shown to have fallen within the range of intraspecific variability. The new and verified record of *Helicina flavida* remains doubtful in its interpretation. Furthermore, the re-examination of original material and records or their critical consideration demonstrated the absence of the Mexican and Guatemalan species *Helicina amoena*, *H. oweniana* and subspecies and *H. fragilis* from the Costa Rican fauna.

On one hand, the remarkable number of new species reflects the vague knowledge about the discrimination of the described taxa subsequent to the well founded major contributions at the end of the 19th century (e.g., von Martens, 1890–1901; Fischer & Crosse, 1880–1902), that is, the necessity of the examination of the type material. On the other hand, the recent discovery of strikingly different species (e.g., *Helicina echandiensis* n. sp.) in remote areas or the small species *Alcadia hojarasca* and *A. boeckeleri* dwelling in leaf litter illustrates the deficits in the inventory of the fauna, as well the difficulties in finding specimens at all, be it due to the very low abundance or to locally restricted ranges.

Distribution of Costa Rican Species and Faunal Composition

The knowledge of the distribution is limited by the insufficient investigation of the molluscan fauna of the adjacent areas Nicaragua and Panama. Despite considerable collecting efforts, information remains fragmentary for several species within Costa Rica itself. Nevertheless, some general aspects emerge. In the following, "southern Central America" will

refer to the area from the Nicaraguan depression to about the Canal Zone.

The Costa Rican helicinid fauna is composed of the following elements:

(1) widespread species: *Helicina tenuis*, *Lucidella lirata*, *Pyrgodomus microdinus*

(2) species limited to southern Central America: *Helicina funcki*, *H. pitalensis*, *H. beatrix*, *H. talamancensis*, *H. gemma*, *H. monteverdensis* n. sp., *H. escondida* n. sp., *H. chiquitica*

(3) species occurring very locally: *Helicina punctisulcata cueriсiensis*˙ n. subsp., *H. echandiensis* n. sp., *Alcadia hojarasca*¨, *A. boeckeleri*¨

˙ distributional pattern assumed for the taxon because affinities doubtful

¨ distribution too poorly known to be discussed further.

The list shows that most species are endemic to southern Central America. This fact greatly changes the previous idea about the faunal composition with more widely spread and less endemic species due to the exclusion of three misidentified Mexican/Guatemalan species and the recognition of several new taxa.

Considering the distribution of these groups within Costa Rica, it becomes obvious that only the widely spread species occur on the Pacific as well as on the Caribbean side. *Pyrgodomus microdinus* represents an exception, because its distribution is mainly influenced by its strict limitation to calcareous outcrops. The other species can be further subdivided by their restriction to the:

Caribbean side: *Helicina funcki*, *H. beatrix*, *H. gemma*, *H. chiquitica*, *H. monteverdensis* n. sp., *H. escondida* n. sp.

Pacific side: *Helicina pitalensis*, *H. talamancensis*.

Mountain region: *Helicina echandiensis* n. sp., *H. punctisulcata cueriсiensis* n. subsp.

Only the Caribbean species normally cross the continental divide in the Cordillera de Tilarán (e.g., Monteverde) and the Cordillera de Guanacaste, disappearing towards the Pacific plains. The Pacific species are restricted to the southern area and to the northern foothills of the Cordillera de Talamanca. The Península de Nicoya and the central and northern plains and foothills of the Pacific side are virtually uninhabited by any species of the

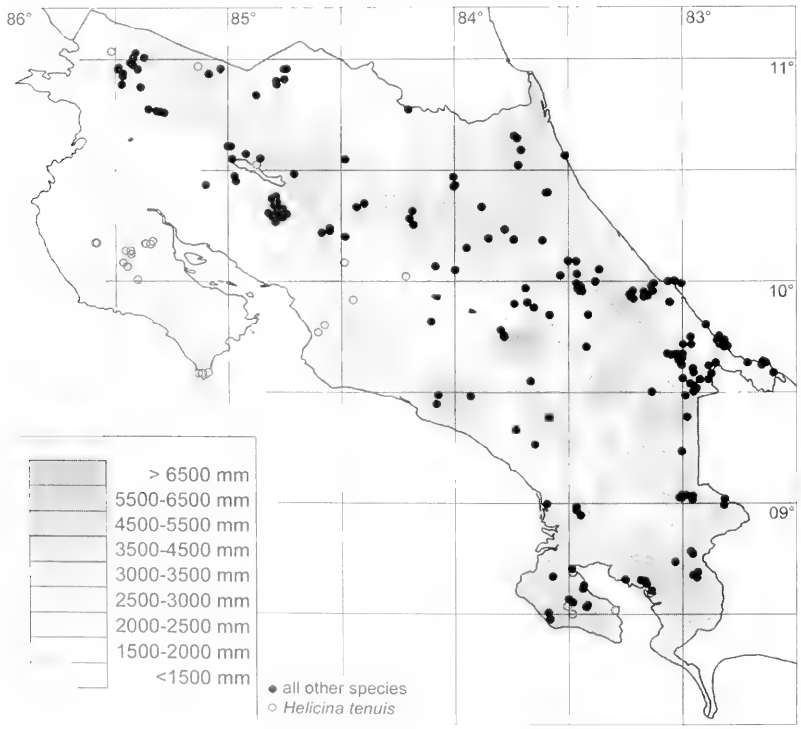


FIG. 329. Costa Rican records of Helicinidae mapped on the annual precipitation [mm/year], *Helicina tenuis* individually marked.

Helicinidae, except for *Helicina tenuis*. This is clearly related to the drier climate.

In conclusion, it can be stated that whereas in southern Costa Rica the continuously highly elevated mountain chain of the Cordillera de Talamanca obviously represents a barrier for the distribution of species; it is replaced more to the north by a dry belt along the northern plains and foothills up to the Valle Central.

The maps (Figs. 329, 330) show the locations of all records of Helicinidae in Costa Rica (*Helicina tenuis* differently marked) mapped on the distribution of the vegetation or the annual precipitation respectively (Ministerio de Agricultura y Ganaderia & Instituto Meteorologico Nacional, 1985). The meteorological data reflect the amount of annual rain and also provide a rough estimation of the real humidity available for the fauna, but do not reflect the strong seasonal changes during the dry period in the northwestern and central parts of the country. These conditions are much better represented by the vegetation, here given in a simplified map (modified after Tosi, 1969), graduated solely according to the humidity-related type of vegetation. As may be expected, the vegetation map actually matches the distribution of the snails in the northwestern part much better. The single dot in the dry forest area (or < 1,500 mm/year rain-area) belongs to an old, subsequently localized record of *Helicina funcki* ("10 mi W of Tilarán"). If it is really correctly plotted, the specimen may also have come from a more humid river valley. On the Caribbean side which lacks such contrasting seasonal changes, a similar correlation cannot be found and the distribution of Helicinidae is probably not limited by climatic conditions.

Morphological Characteristics

In the following section the different characteristics will be discussed under general aspects, their applicability for species differentiation, i. e. mainly for the Costa Rican species, and their value for higher systematics within the Helicinidae.

Teleoconch Shape

The shape and color of the teleoconch are assumed to be directly affected by environ-

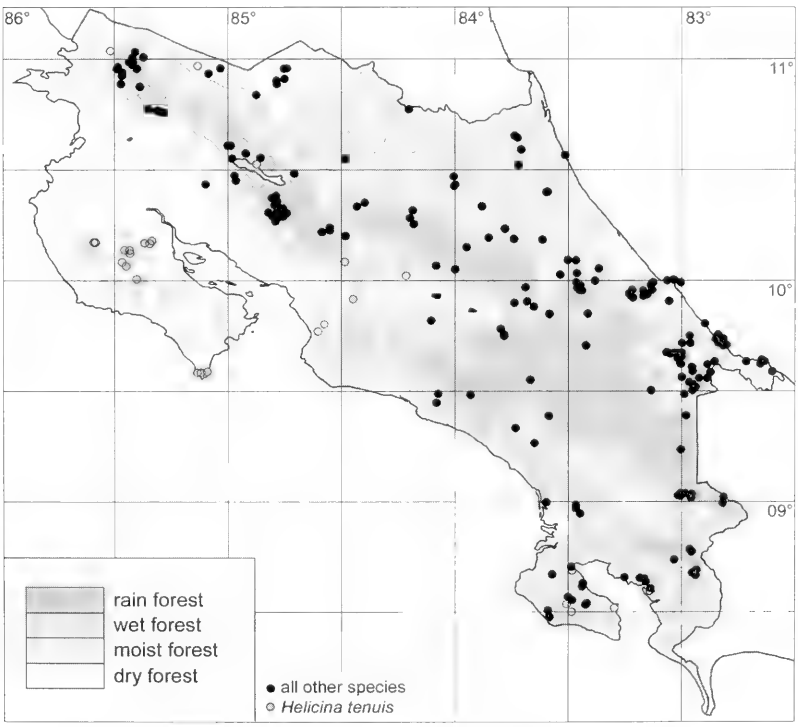


FIG. 330. Costa Rican records of Helicinidae mapped on the types of vegetation, *Helicina tenuis* individually marked.

mental selective pressures and therefore highly adaptable. On one hand, differences may therefore characterize different species, but one the other hand, under different environmental conditions a high plasticity may occur within a single species as well. Likewise, there is a high probability of convergent developments reducing the applicability of these features in higher systematic.

Aspects of the shell color will be discussed separately, along with the soft body color. Due to their practical importance at the species level, also for the determinations, shell characteristics were already discussed in the species accounts. In the following only certain general aspects will be considered.

Despite the outline of the shell, the development of the aperture is an important feature for the differentiation of the Costa Rican species. The aperture is always more or less oblique, but may be straight or curved backwards in its middle portion. The outer lip is flatly expanded or reflexed. The main function of the outer lip of the aperture is obviously the tight attachment to leaves or other surfaces of an aestivating individual. This is especially important for all arboreal species, such as the Costa Rican representatives of *Helicina*. Two different trends are realized to achieve an optimal attachment: (1) the basal part of the outer lip near the transition to the columella is protruded, thus forming a denticle, and is combined with a rather straight aperture (e.g., *Helicina tenuis*), or (2) the basal part is straight or even forms a little notch, but the middle portion of the aperture is strongly curved backwards (e.g., *Helicina beatrix*). Especially the slight basal notch present in all Costa Rican species that Wagner (1907–1911) summarized under the species group "*Gemma*" was used as indication for the inclusion in the subgenus *Leialcadia*. This classification turned out to be wrong, and the similarities can be explained by convergent developments in adaptation to the arboreal life, as is the feature of colorful shells included in the description of the *Leialcadia*. Another striking example for the misleading shell characteristics is illustrated by *Alcadia jamaicensis* (actual arrangement, based on features of embryonic shell and female reproductive system) which has formerly been classified as *Helicina jamaicensis* (e.g., Wagner, 1907–1911).

By the inclusion of *Analcadia* and *Sericea* into *Helicina*, the presence of periostracal hairs adds another example of convergence and shows the unreliability of shell characteristics as an indicator for relationships. Within the family of Helicinidae periostracal hairs are known to occur within at least in four different genera, *Helicina*, *Alcadia*, *Lucidella* (*L. adamsiana* L. Pfeiffer, 1849) and *Schasicheila*, the distinctness of which is strongly supported by characteristics of the female reproductive system and embryonic shell structures. The periostracal hairs seem to be related to a life within the leaf litter, they are also developed in other families of land snails (e.g., Helicidae).

Teleoconch Surface Structure

Among the Costa Rican representatives of the genus *Helicina*, two different traits in teleoconch surface structure can be recognized, a rough surface with oblique diverging grooves or a very smooth shell. Only one species (*Helicina escondida* n. sp.) shows an intermediate characteristic with the former structure only very weakly developed. Because in all species the beginning of the teleoconch (subsequent to the transitional structure) displays a pattern of oblique diverging grooves, the smooth surface is likely to be a derived condition. The rough pattern is furthermore not unique for *Helicina*, it can be observed in different genera worldwide (personal observation), the only otherwise illustrated example is given for an Australian species of *Pleuropoma* Möllendorff, 1893 by Stanisic (1997). The relevance of the structures for revealing relationships remains doubtful, especially due to the problems in the classification of the Central American mainland species (see below). Nevertheless, since the two traits in the Costa Rican species are paralleled by other similarities, although also with intergrades (e.g., shape of the teleoconch, details of the female reproductive system, degree of sexual dimorphism), it may be of importance as a supporting characteristic on a smaller scale.

The distinct transitional structure (youngest portion of the teleoconch) is not developed in all taxa. It is present in all Costa Rican species of *Helicina* and the Jamaican *Helicina neritella*, *Pyrgodomus* and *Alcadia* (*Microalcadia*). In *Lucidella* (*L. lirata* and *L. aureola*), the final pattern of the teleoconch starts directly at its origin. The same applies to *Angulata* in which the embryonic pattern is even identical to that of the teleoconch. The shells available for *Alcadia*

major were all eroded. The study of the figures given for *Helicina umbonata* Shuttleworth, 1854, *H. rhips* Thompson, 1982 and *H. liobasis* Thompson, 1982 by Thompson (1982) show a similar situation as in *Lucidella* and *Angulata*. With the exception of *Alcadia* (*Microalcadia*), the absence of the transitional structure is always combined with a spiral sculpture of the teleoconch, whereas in the other species follows an oblique or irregular pattern. Because the transitional structure in *Helicina* looks like a preliminary stage of the pattern of the oblique diverging grooves produced under different growth conditions (slower or faster), a similar effect simply would not become apparent in a spiral pattern. The lack of knowledge of the life history of Helicinidae reduces possible explanations for the interpretation of the structures. Especially the example of *Helicina umbonata* and related species (verified in its generic position by embryonic shell structures) renders this explanation likely. The systematic relevance of this characteristic by itself is therefore not suggested here, only its occurrence in combination with the pattern of the teleoconch.

Shell and Soft Body Color

Like shell characters, the color of shell and soft body are believed to reflect directly the result of selective processes by the environmental conditions. For example, a study by Johnson (1959) on *Helicina orbiculata* showed that the percentage of a lighter or darker color phase within a population is correlated to the color of the soil and obviously controlled by predation. The color is inconspicuous for species dwelling in the leaf litter, such as *Lucidella lirata*, *Alcadia hojarasca*, and *A. boeckeleri*, which are in fact more or less uniformly brownish or greyish colored. The color of *Pyrgodomus microdinus* supports the camouflage of the shell on rock surfaces. All Costa Rican species of *Helicina* for which the habitat is reported are arboreal. It is known from various examples of different families of land snails, for example, *Liguus* (Orthalicidae), *Amphidromus* (Camaenidae), and *Cepaea* (Helicidae) that colorful and varied patterned or the exceptional greenish shells seem to camouflage the individuals best. In fact all arboreal species investigated have this appearance, but it is realized in two different ways:

(1) heavy, colorful shells, which are more or less variable in their color, the mantle surface is usually unicolored: *Helicina funcki*, *H. pitalensis*, *H. beatrix*, *H. talamancensis*, *H. punctisulcata cuericiensis* n. subsp. (?*H. echandiensis* n. sp.).

(2) slight, nearly transparent shells, except for the colored outer lip, the mantle surface is variously spotted: *Helicina tenuis*, *H. escondida* n. sp., *H. gemma*, *H. monteverdensis* n. sp., *H. chiquitica*.

Thus the development of the remarkable color patterns on the soft bodies of certain species closely depends on the thickness and structure of the shell. The best example is given by *Helicina tenuis* and *H. beatrix confusa*, which nearly equal each other in volume (females), but the shell weight of *H. tenuis* amounts to only $^{3}/_{5}$. Because the arboreal life seems to require a color as described above, the obvious physiological possibility of replacing the shell color by mantle pigmentation first makes the evolutionary development of thin shells possible. This could represent an adaptation to a limited availability of calcium carbonate due to the geological conditions in Costa Rica. *Helicina escondida* n. sp. and *H. funcki* are similar to each other with respect to the presence of greenish specimens besides strongly red tinged (shell) individuals in *H. funcki* or variously spotted (mantle) individuals in *H. escondida* n. sp. *H. chiquitica* represents an exception in so far as most individuals are nearly unicolored black. This may be related to the small size of the species, because in the individuals of *H. monteverdensis* n. sp. from Mirador Gerardo, contrary to the larger ones from Monteverde, the dark share of color prevails. Small juveniles of *H. funcki* are darkly mottled too.

In the single case of *Helicina talamancensis*, the color of the head-foot seems to be characteristic for the species. Assuming the thickness and transparency of the shell to be species-specific, the presence of a color of the soft body as described above is also characteristic because it is shown to be closely correlated with shell conditions.

Internal Shell Structures: Axial Cleft and Muscle Attachment

The absorption of the internal whorls of the spire is a common feature of the families Neritidae, Ceresidae, Proserpinidae, and Helicinidae, which had been described for the latter two families for the first time by Bland (1854). Solem (1983), while studying 15 different species of Helicinidae (worldwide, but not

specifically mentioned), established a relation between the length of the axial cleft and the number of whorls, that is, the length increases with the number of whorls. The total range is about ½ to nearly ¾ of a whorl, and the length of the axial cleft was shown to be species-specific (five specimens of each of two species investigated). His results for *Proserpina* Sowerby, 1839, and *Ceres* Gray, 1856 (in both nearly ½ of a whorl), differ from the description of the respective families given by Thompson (1980), with Ceresidae being about $^{1}/_{10}$ of a whorl and Proserpinidae about ¾ of a whorl. Thompson incorporated this characteristic in his considerations of systematic relationships between the families.

For the Costa Rican material, the present investigation confirms the constancy of the length of the axial cleft for different taxa, but the relation of the number of whorls to the length of the axial cleft cannot be sustained. It may be illustrated at two examples: *Helicina punctisulcata cuericiensis* n. subsp. has $3^{5}/_{8}$ whorls, with an axial cleft of ½ whorl (Fig. 91), whereas *H. gemma* has 4 to $4^{1}/_{8}$ whorls, with an axial cleft of about $^{3}/_{8}$ whorl (Fig. 163). For *H. beatrix riopejensis* n. subsp., shells of both sexes are figured (Fig. 133) that differ in ½ of a whorl, but the axial cleft amounts the same, here $^{3}/_{8}$ of a whorl. The second example, furthermore, shows that a relation of whorl count to the length of the axial cleft is actually in contradiction with the species-specificity, because most species of Helicinidae exhibit a sexual dimorphism in size that is accompanied by a difference in whorl count of females and males. This fact escaped the attention of Solem (1983), but it was noted by Baker (1928).

On the contrary, the length of the axial cleft seems to be characteristic for certain systematic units as the data given by Thompson (1980) suggests, although the differences between his data and Solem's (1983) remain to be checked. From the present investigation, it can be seen that *Lucidella lirata* remarkably diverges from the species of *Helicina*, the axial cleft is ¼ to ½ whorl longer than in all species of *Helicina* studied. Also, with respect to the attachment of the right retractor muscle exclusively on the penultimate whorl, the species differs from *Helicina*. The examination of *Lucidella aureola*, the type species of *Lucidella*, revealed similar conditions (Figs. 265, 322). The same is true for *Schasicheila*, in which an axial cleft shorter than ½ whorl is always combined with the prominent right muscle broadly attached only on the body whorl. According to Baker (1925), the axial cleft of the primitive genus *Hendersonia* Wagner, 1905, encompasses nearly one whorl. In all species of *Helicina* studied, the attachment of the right muscle corresponds to the beginning of the axial cleft and crosses the inner suture and therefore encompasses both whorls.

Within the Costa Rican species of both subgenera of *Helicina* the length of the axial cleft varies from $^{3}/_{8}$ to ½ of a whorl. In species of a very similar shell shape it may differ (e.g., *H. pitalensis* – *H. tenuis*) or be of about the same length (e.g., *H. monteverdensis* n. sp. – *H. chiquitica*). The subspecies *H. beatrix riopejensis* n. subsp. represents a difficult case: it closely resembles *H. beatrix* to which it is tentatively assigned, but the length of the axial cleft is like in *H. gemma* and unlike *H. beatrix*.

Embryonic Shell

Previous to this investigation structures of the embryonic shell of Helicinidae were only applied twice for systematic considerations. Clench & Jacobson (1971) stressed features of the embryonic shell to exclude the subgenus *Striatemoda* Baker, 1940, from the Cuban genus *Emoda* H. & A. Adams, 1856. In a subsequent contribution on the genus *Alcadia* by Boss & Jacobson (1973), the embryonic shell surface is included in the descriptions of various species, but its importance has not been recognized by the authors. Their descriptions are inadequate for a comparison with results gained by SEM studies. Finally, Thompson (1982) successfully used the feature to differentiate the genera *Alcadia*, *Helicina*, and *Lucidella* by investigation of the respective type species.

The results of the present study confirm the applicability of embryonic shell structures for higher systematics in Helicinidae. Furthermore, the significance of embryonic shell features is not only justified by considerations about their conservative nature but verified by well-founded parallel changes in the female reproductive system in all species investigated. The rearrangement of certain subgeneric units of *Alcadia* provides a convincing example. Additional genera (*Eutrochatella*, *Schasicheila* and *Angulata*, newly raised to generic level) can be charac-

terized by their special embryonic shell structures. The close relationship of *Pyrgodomus* to *Eutrochatella* is confirmed. Within the subgeneric level of the genus *Helicina*, embryonic shell structures show high similarities or may vary within a single species to the same degree as between different species (e.g., *H. monteverdensis* n. sp.) so that it can only be occasionally used as a distinguishing characteristic. Among the Costa Rican species, for example, only *H. talamancensis*, *H. beatrix beatrix*, and *H. beatrix confusa* exhibit relatively smaller pits with a more prominent smooth surface.

Implications of the embryonic shell structure on relationships of the different groups within the Helicinidae are by far less obvious and the following examples provide certain evidence that the similar structures are not always homologous developments. The pitted structure of the embryonic shell is known for the genera *Helicina*, *Lucidella* (pits less regularly arranged) and Australian species of *Pleuropoma* (similar to *Helicina*) (Stanisic, 1997), but, with respect to complex characters of the female reproductive system, *Helicina* represents a derived condition compared to *Lucidella*, and the genera of the Australasian region (see female reproductive system, Bourne, 1911). Furthermore, the pitted embryonic shell seems to be absent in primitive members of the family, such as *Hendersonia occulta rubella* (Green, 1832) (personal observation). Studies on embryonic shell structure of other gastropods also point to the difficulties to distinguishing homologous developments (e.g., Ponder & Lindberg, 1997).

Contrary to the structural similarity among closely related species, size provides more information. Size differences of the embryonic shell have not previously been studied for Helicinidae. According to the measurements of the Costa Rican species, size seems to depend on two main factors: (1) the size of the species, and (2) the altitude of the locality of the individuals.

(1) The diameter of the embryonic shell would best be compared with the shell volume, but because this information is not available for all species, it is compared with shell height as well as with the minor diameter of the shells (Figs. 331, 332) to consider the deviations due to different diameter-height-relations, especially for the species of *Lucidella*, *Alcadia* (*Microalcadia*) and *Pyrgodomus*. The embryonic shell size increases with the shell size, although deviations from this general trend are remarkable. On one hand, it is explained by a certain species-specificity of the embryonic shell size as is for example shown for *Helicina chiquitica* or *H. monteverdensis* n. sp.; in the latter species embryonic shell size along with other arguments could be used to distinguish the species. On the other hand, the influence of the altitude (see below) interposes with the relation to shell size. With respect to higher systematics within the family, first data for *Lucidella* and *Eutrochatella* suggest that in these genera (and related like *Pyrgodomus*), the embryonic shell size is relatively smaller than for example in *Helicina*. The specimens investigated for *Lucidella aureola* equal *Helicina gemma* in size, but the embryonic shell is about 285–335 µm smaller, those of *Eutrochatella pulchella* equal *Helicina beatrix confusa* in size, the embryonic shell is about 330 µm smaller.

(2) Since the size of the embryonic shell also seems to reflect a certain species-specificity and not only the influence by the shell size, the measurements of the embryonic shell were directly compared to the altitude (and not as a relation to shell size), but a similar diagram for shell height and diameter to altitude is given to show the general independence of shell size and altitude (Figs. 333, 334). The diagram illustrates a slight increase of the embryonic shell size at higher altitudes independently of the species within the representatives of *Helicina* and also for *Alcadia* (*Microalcadia*), although the results for the latter subgenus are more suggestive in manner than supported by sufficient data. On species level, an increase of the size of the embryonic shell with the altitude is clearly shown for *Helicina funcki* and *H. gemma*.

Faced with a virtually complete absence of data about the natural history of Helicinidae, the results cannot be discussed in this context. The knowledge is limited to a single description of deposited eggs for the species *Viana regina* (Morelet, 1849), which is cited from the observation of a Cuban malacologist by Clench & Jacobson (1968). It seems that these eggs were calcified, because the observer had to break them to examine the embryonic shell. Furthermore, it is known that eggs are released from the ovary into an egg sac at the very beginning of the primary oviduct. In histological sections, these eggs can occasionally be observed in the primary oviduct and in the ascending limb of the V-organ,

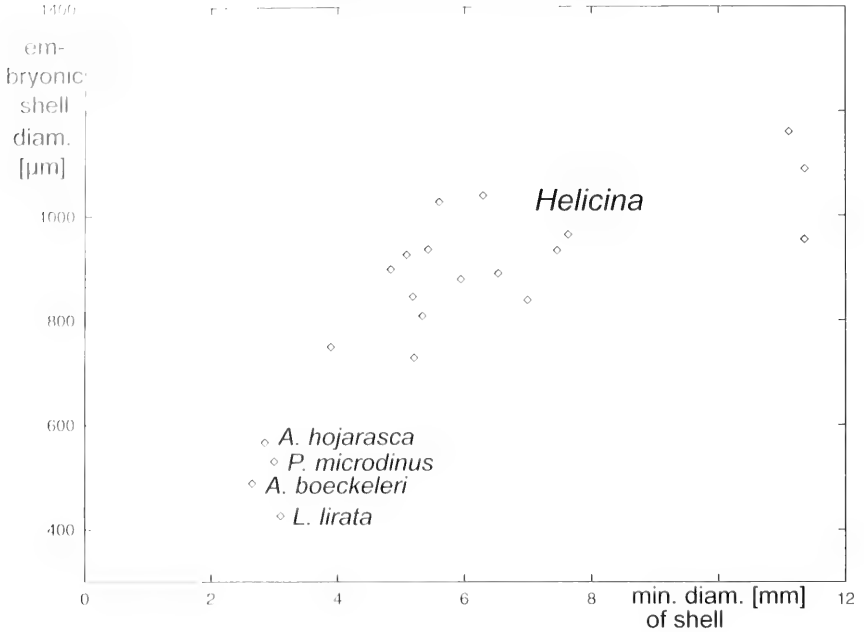


FIG. 331. Relation of embryonic shell diameter to minor diameter of the shell for Costa Rican species (all species included for which measurements of the embryonic shell were given).

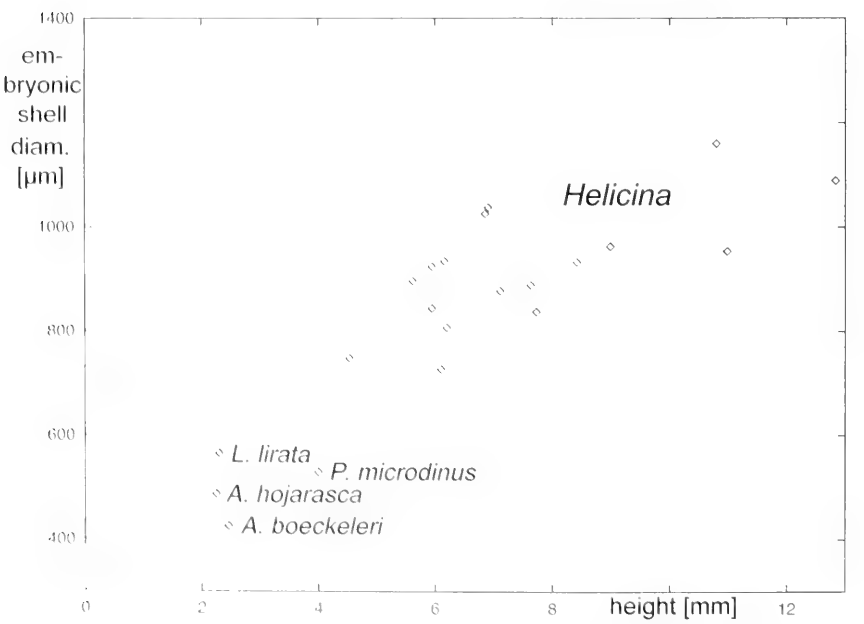


FIG. 332. Relation of embryonic shell diameter to shell height for Costa Rican species (all species included for which measurements of the embryonic shell were given).

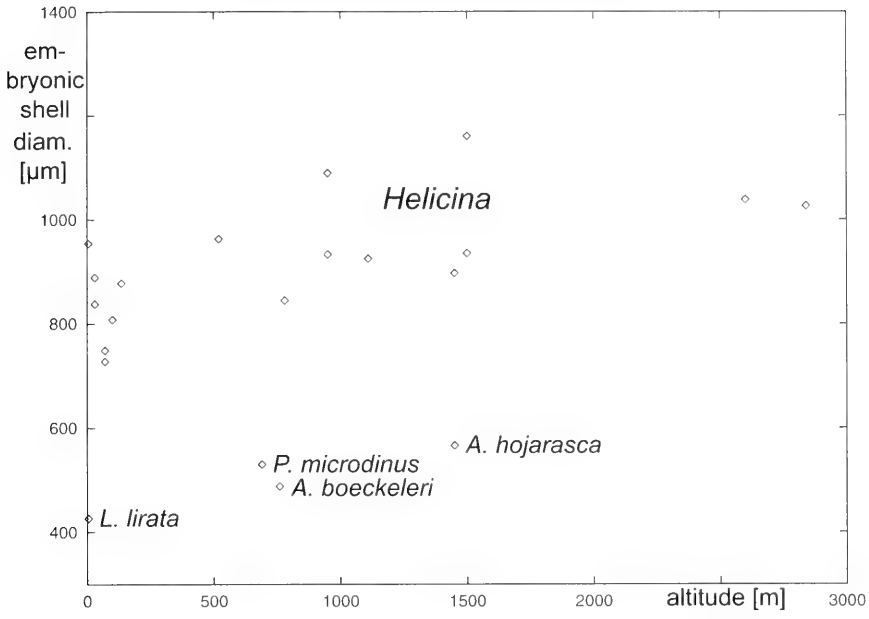


FIG. 333. Relation of embryonic shell diameter to the altitude of the site of the Costa Rican species (all species included for which measurements of the embryonic shell were given).

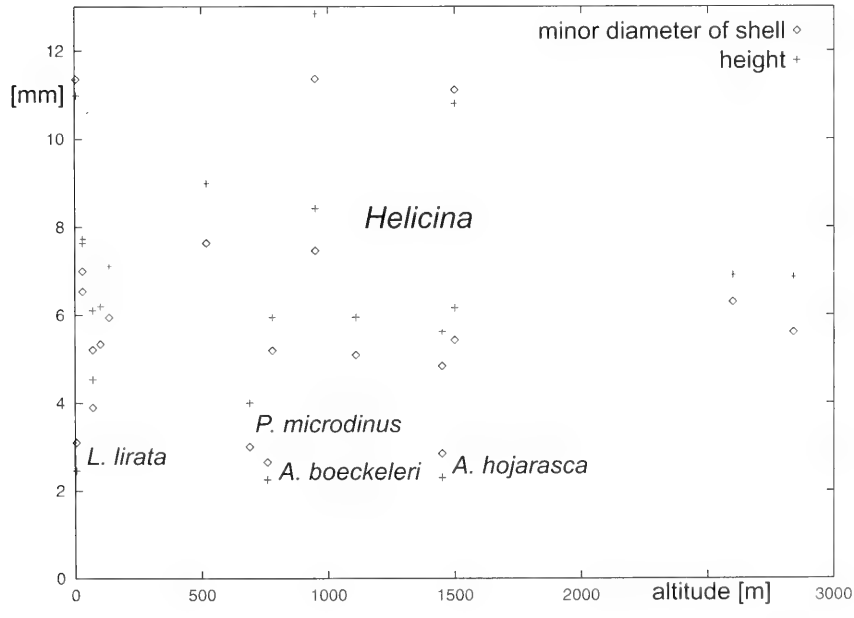


FIG. 334. Relation of shell height or minor diameter respectively to the altitude of the site for the species included in diagram Fig. 333.

but distal to this portion (and therefore fertilized) eggs were never seen or reported by other authors.

Operculum

Wagner's classification represents the first attempt to incorporate the characteristics of the operculum to a large extent. For this reason, the opercula of other than the Costa Rican species are not repeatedly described and discussed. As for shell characteristics, the features on which the operculum closely depend, subsequent studies, including the present one, showed the high flexibility for adaptations to environmental requirements by cases of convergent developments reflected in necessary rearrangements of different taxa. For the genus *Alcadia* from Cuba, Boss & Jacobson (1973) compared the calcification of the operculum in relation to habitat. In arboreal species, the calcareous layer is thinner than in ground-dwellers, the latter possibly requiring stronger protection against small predators.

Aspects of the operculum were successfully applied to recognize and characterize the primitive members of the family by strong traces of a retained paucispiral instead of a concentric condition (Wagner, 1907–1911; Baker, 1922a).

The opercula of the Costa Rican species of *Helicina* are very uniformly developed. Deviations in shape are due to the different shape of the aperture of the shells, for example, the operculum of *H. funcki* is broader than that of *H. beatrix*, because the whorls of the former species increase more rapidly in size. The opercula of *Alcadia hojarasca* and *A. boeckeleri* do not differ from those of *Helicina* species, except for the more irregularly S-shaped columellar edge, reflecting the condition of the strongly rounded periphery of the shells. This illustrates in exemplary fashion that the similarity in the operculum does not necessarily reflect a close relationship between the taxa, especially in the case of certain subgeneric units of *Helicina* and *Alcadia*.

Radula

Because radular characteristics strongly influenced the systematic concepts for the Helicinidae, these structures were described and figured in some detail within the species accounts.

The interpretation of the capituliform complex requires some remarks, because it has caused some past confusion. Originally, Troschel (1856–63) described the accessory plate as a basal appendage, which is always fused with the tooth, but appearing somehow subdivided. Baker (1922a) recognized two plates and paid much more attention to the form of the accessory plate and the point and way of the overlapping of both teeth. His figures give the impression of separate teeth. The peculiar reflexed wing of the accessory plate was corrected in its interpretation by Baker (1926, 1928) as a deposit cementing the two plates together instead of being a kind of a cusp. The plates are said to break upon separation in certain groups of species, whereas in others they "pull apart easily enough". This correction obviously escaped the attention of subsequent authors. Adopting Baker (1922a), Thompson (1980, 1982) still incorporates the characteristic of the wing or reflection of the accessory plate enveloping the end of the comb-lateral for his phylogenetic considerations. This wing is actually not visible in his SEM figures, because it was a misinterpretation of optical microscopic investigations. Stanisic (1997) states that, contrary to certain overseas (= neotropical) species, the comb-lateral and the accessory plate of the Australian species of Helicinidae are always fused together. But in this respect, his SEM figures do not differ from those of neotropical taxa, for example, the Costa Rican species. In natural conditions, the two plates are fused together.

As previously stated, data of this study were gained by SEM-investigations. Despite the great advantages of the higher resolution revealing more exactly the dentition of the marginals and information from the three-dimensional arrangement, the method is accompanied by some disadvantages. On account of the very complex structure of the radula, the numerous marginals always overlap each other, especially the outer ones, rendering an exact count impossible. To a lesser extent, a similar problem exists in analyzing the number of transverse rows, because, especially in small or poorly preserved specimens, the preparation procedure and the necessary positioning may result in losses of parts of the whole ribbon. In optical microscopy especially, the first point simply becomes obsolete by the transparency of the radula. Nevertheless, here the SEM-method is pre-

ferred because drawings from the light microscope reflect rather the interpretation of the author than the real and hereby comparable structures as argued above.

In all Costa Rican species of *Helicina*, the radula displays nearly the same amount of intraspecific and interspecific variations. The only specific differences clearly documented were found in the dentition of the comb-lateral of two species, *H. escondida* n. sp. and *H. chiquitica*. In these species, the number of cusps is constantly strongly reduced or increased, in the former species, the size of the cusps is remarkably enlarged towards the centrals. The differences described for the change in the number of cusps on the marginals are in most cases likely to be related to the size of the species. Evidence is provided by the differences in the subspecies of *Helicina beatrix*. Furthermore, all small-sized species (*Helicina chiquitica*, *Lucidella lirata* and *Alcadia* (*Microalcadia*) *hojarasca*) convergently possess an increased number of denticles on the comb-lateral.

Stanisic (1997), while studying Australian species of the genus *Pleuropoma*, in which the radula in general apparently does not differ remarkably from those shown in this study, points out specific differences of the comb-lateral for certain species analogous to those observed for *Helicina escondida* n. sp. and *H. chiquitica*, and in the cusps of the centrals as well. He relates the divergence in the radula to the habitats of the species – arboreal, ground-dweller and limestone-associated.

The results and interpretation of Stanisic (1997) agree with my own conclusions of seeing the features of the radula more in the light of speciation and adaptations to the substratum the respective species feed on and thus to be subject to convergent development rather than providing a conservative structure useful to indicate phylogenetic relationships. This concept does not exclude the possibility that a certain radiation resulted from the colonization of a special habitat (e.g., *Eutrochatella* and related taxa of the West Indies on calcareous rocks), which is therefore characterized by the obviously necessary adaptation of the radula (e.g., the reinforced T-shaped lateral). On one hand, the fact of the rearrangement of certain groups of Baker's system characterized by radula characteristics provides evidence in itself. On the other hand, additional examples can be given for convergent developments. Boss & Jacobson (1973) and Thompson (1982) had recognized the diverging radula of *Alcadia major* (T-shaped laterals and other features approaching the "vianid" radula instead of the "helicinid" radula typical for other subgroups of *Alcadia*) but hesitated to comment on this "not matching" fact. Because *Alcadia major* lives on "rock bases" (Baker, 1934a) like other species with a "vianid" radula (e.g., *Eutrochatella pulchella*, *Pyrgodomus microdinus*), a convergent foraging structure is very likely and is here favored as an explanation. Outside of the family Helicinidae, a convergent development of the "vianid" radula had already been proposed and accepted by Thompson (1980), namely for the Proserpinidae.

Morphometry and Sexual Dimorphism

The morphometric differences were discussed to some extent in the species account and proved to be useful on the species level, for example, to judge the status of certain subspecies (*Helicina funcki costaricensis*, *H. tenuis pittieri*). Furthermore, a relation to the altitude seems to be specifically different, but data were sufficient only for a few species. A decrease in size at higher altitudes (*Helicina funcki* and *H. gemma*) has also been reported for the Mexican species *H. fragilis elata*, *H. zephyrina zephyrina* and *Pyrgodomus microdinus abditus* by Baker (1928). The study also shows that morphometric analysis of Helicinidae always has to take into account the considerable effects of sexual dimorphism.

Sexual dimorphism in Helicinidae has been known for a long time, but, with very few exceptions, it has never been subjected to detailed studies. Probably the most frequently cited example is the different shape of the shells of both sexes in *Viana regina*, with the males being characterized by a deep notch in the upper outer lip, a fact that was first recognized in this context by L. Pfeiffer (1856a). Wagner (1910b) considered the subject theoretically because he did not have anatomical material available. The species discussed by him were not studied here. Baker (1925) published the first accurate data for differences in size for *Hendersonia occulta rubella*. Although he selected extremes for the measurements expecting the females to be larger, the difference in volume interpolated from his data amounts to about 2% less for the males and both sexes intergrade. Baker (1926) mentioned only the relationships of females to

males of the specimens he had studied anatomically. Baker (1928) analyzed some Mexican species morphometrically, but, with minor exceptions, the number of specimens for each station was limited. According to his results, the sexes intergrade considerably in shape and size, but the shells of males increase more rapidly in diameter resulting in fewer whorls (¼ to ½) and a more depressed shell shape, when sexual dimorphism is developed. The genus *Schasicheila* seems to encompass species with sexual dimorphism (*S. alata*, females > males) and another with intergrading sizes (*S. misantlensis* Fischer & Crosse, 1893, females = males). In later studies on the Jamaican malacofauna, Baker (1934a, b) provided further information, but unfortunately did not include numerical data or the sample size. According to him, all species examined of *Eutrochatella* – *E. pulchella*, *E. tankervillii* (Gray, 1824), *E. nobilis* (C.B. Adams, 1852) and *E. costata* (Gray, 1824) – have males larger than the females, whereas the closely related genus *Pyrgodomus* (Baker, 1928: *P. microdinus abditus*, examination based on several shells) shows the reverse relation. Species of *Lucidella* show all possible relations (<, >, =), and *Helicina* and *Alcadia* are similar in having larger females. A single exception for *Helicina* is given in "*H.* (*Angulata*) *rhynchostoma ernesti*" von Martens, 1873 (Baker, 1926), but this species requires reexamination regarding its systematic affinities.

The data on sexual dimorphism of this study represent the most comprehensive approach to date to analyze the phenomenon for a selected group of species. Against the background of limited material available, the newly developed method of removing the soft body with only minor damage to the shell provides a valuable tool, which made the analysis possible. All species measured exhibit a sexual dimorphism in size of the shell, with females averaging larger than males. Differences are smallest in *Lucidella lirata* (percentage of male's volume about 92%), increase in *Helicina funcki* and *H. pitalensis* (about 80–85%), *H. tenuis*, *H. echandiensis* n. sp. and *H. escondida* n. sp. (about 75–78%) to the greatest values in *H. beatrix*, *H. talamancensis*, *H. gemma*, *H. monteverdensis* n. sp. and *H. chiquitica* (about 61–67(–72)%). This grouping is paralleled by similarities in shell shape, teleoconch surface structure and details of the female reproductive system, suggesting a certain value of the degree of sexual dimorphism with respect to systematic affinities. The group with the highest differences shows furthermore that the dimorphism is independent of the size of the species, because the extrema (*Helicina talamancensis* and *H. chiquitica*) differ in volume by a factor of about 7.

The observation by Baker (1928) that in case of a sexual dimorphism males are more depressed, that is, relatively larger in diameter, could not really be confirmed by the present study. For all species, the different measurements were tested in various relations to each other and no significant differences for both sexes were found. For the relation of height to diameter (here minor diameter), deviations between females and males for acceptable sample size usually range approximately 1% or less for all species, highest differences amount up to 3–4% for very few populations. In more populations, the relative diameter was larger in males than in females, but examples for a reverse relation were found likewise in nearly all species.

The morphometric comparison of different populations clearly demonstrates a certain variability of size for most species and indicates that investigations of the sexual dimorphism will only work with individuals originating from the same population.

The knowledge of the range of size variations within a species due to sexual dimorphism allows a much better judgement of the determination of single specimens, for example, type specimens, and morphometric differences applied for the separation of species or subspecies.

Female Reproductive System

When revising the contributions on systematics of the Helicinidae with respect to the anatomy, especially genitalia, all authors agree in the following: "..., but once they [anatomical structures] evolved very little differentiation of these organs and structures occurred with further radiation of subfamilies and genera" Thompson (1982: 5), or more strictly "This emphasizes the conclusions of Bourne (1911: 777) and Baker (1926: 35) that the general uniformity of the genitalia of the Helicinidae makes them useless for diagnostic purposes" Boss & Jacobson (1974: 6).

The first comprehensive study on the anatomy of Helicinidae based on several species worldwide, combining both dissections and histological studies, was carried out by

Bourne (1911). A similar study was provided only for the primitive species *Hendersonia occulta rubella* by Baker (1925). All previous contributions considered the one or the other detail of different species (Isenkrahe, 1867: first rough anatomy of *Emoda pulcherrima titanica* (Poey, 1851); von Ihering, 1877: nervous system of *Pleuropoma beryllina* (Gould, 1847); Bouvier, 1886: nervous system of *Angulata brasiliensis* and *Emoda sagraiana* (Orbigny, 1842); Thiele, 1902: male reproductive system of *Waldemaria japonica* (A. Adams, 1861); Thiele, 1910: female reproductive system of *Helicina kubaryi* [*nomen nudum?*]). Baker (1926, 1928) studied several American species with emphasis on the genitalia. He clearly states that his intention of finding similar clues for systematic affinities, as in the radula, partially failed, not exclusively because of the considerable uniformity of the structures, but also on account of the scanty and poorly preserved material. Therefore, his contribution is a valuable collection of descriptions for several anatomical features, but the nearly complete absence of conclusions and discussions renders it subject to misinterpretations, as exemplified in the citation above. Subsequent to Baker, only Thompson (1968) described the genitalia of his new genus *Ceochasma* and provided a detailed anatomical study on two species representing the related families Ceresidae and Proserpinidae (Thompson, 1980).

The present anatomical studies focused on the investigation and comparison of the female reproductive system since, on one hand, the discovery of important deviations from the present knowledge promised information relevant for phylogenetic purposes contrary to former assumptions, but on the other hand, it required the re-examination of previously studied species/genera and the assessment of data within the new context.

The study of the Costa Rican species of *Helicina* revealed that all species are similar in the monaulic condition of the female reproductive system. This result is in contradiction with all previous anatomical studies (diaulic system), especially those of Baker (1926) for various Central American species of *Helicina*. Baker (1926) assumed the vaginal opening to be inside the duct of the hypobranchial gland also discharging into the mantle cavity. This is reflected in his figures of the female systems (e.g., fig. 9, *H. orbiculata*). In fact, the hypobranchial duct and gland is closely associated with the apical complex of the female reproductive system, partially enveloping these structures dorsolaterally. In dissection, their separation is not always easy, but the study of histological serial sections finally confirmed the absence of any connection of the reception chamber or associated structures to the hypobranchial duct. Other Central American species, such as *Helicina amoena*, *H. turbinata*, and *H. orbiculata*, the latter also studied by Baker (1926), also constantly lack the provaginal opening. Until more knowledge is available, these results together with the only vague presentation of the provaginal opening in Baker's figures lead me believe that all Central American mainland species commonly referred to *Helicina* are monaulic, that is, that they properly belong to that genus.

Reexamination of several other species studied by Bourne (1911) and Baker (1926) and additional type species of higher systematic units revealed a much higher structural diversity than previously documented. For example, contrary to the results of Bourne (1911) *Eutrochatella pulchella* was found to be monaulic. For *Lucidella lirata* as well as for *L. aureola*, an additional sac on the pallial oviduct for sperm storage was discovered. Furthermore, the receptaculum seminis on the descending limb of the V-organ described by Baker (1926, 1928) turned out to be a misconception. These results add several peculiarities for *Lucidella* and differentiate it more strongly from other genera. The characters of *Schasicheila* (Baker, 1926, 1928) and *Alcadia* (Bourne, 1911) were confirmed.

The changes in the female reproductive system are paralleled by consistently different structures of the embryonic shell and add valuable features in the characterization and differentiation of genera and subgenera, for example, *Alcadia* from *Helicina*. Furthermore, certain changes can be assessed in the direction of the development. The basal members of Helicinidae, such as *Hendersonia occulta rubella*, possess a diaulic system. The basal position is reliably founded on the paucispiral conditions of the operculum and the presence of the vestigial right auricle. The monaulic condition is clearly the derived condition. Furthermore, the diaulic state seems to prevail in most of the genera. Assuming the results of Bourne (1911) for this part to be correct, Australasian species are diaulic as well. At least *Aphanoconia pachystoma ponsonbyi* (E.A. Smith, 1884) from Papua New Guinea,

was re-examined and the structure could be confirmed.

The mon- or diaulic state is expected to be related with functional consequences. But although the morphological structures are fairly well documented, knowledge of functional aspects is limited to the interpretation of morphological features, because other data are not available. Bourne's (1911) observations were not homogeneous for the different taxa and point in different directions. The presence of sperm in the posterior part of the pallial oviduct, the bursa copulatrix, and the receptaculum seminis of *Alcadia hollandi* suggested that the pallial oviduct serves as the copulatory canal. By the way of contrast, two Australasian species of *Aphanoconia* had sperm within the provaginal duct and the provaginal sac, favoring the reception of sperm through this opening. Baker (1925) assumed the provaginal opening to receive the male products in *Hendersonia occulta rubella*, as did Thompson (1980). The monaulic structure only allows the reception of sperm through the pallial oviduct, and therefore demonstrates the physiological possibility. Following this consideration, the provaginal opening could also be functionally vestigial, at least with respect to the reception of sperm, in species with this opening. Under the morphological conditions of *Lucidella* for example (Figs. 270, 324), the reception of sperm through the vagina would require a downward movement to reach the posterior extended portion of the oviduct and its lower appendage, in which sperm were found. The function of the various different structures for sperm storage is even less understood. In most of the different systems there are three structures that are found to be used simultaneously (receptaculum seminis, bursa copulatrix, provaginal sac, ?parts of the pallial oviduct, the appendage of the pallial oviduct or other analogous developments). These aspects remain subject to further studies, possibly ultrastructural analysis.

The variability or specificity of characteristics of the female reproductive system at the species level was studied in detail for the Costa Rican species. Here the applicability is limited, as may be expected for characters useful for higher systematics. Differences mainly occur in the shape and size of the bursa copulatrix and the provaginal sac, as well as in the relation of the apical complex to the pallial oviduct. The latter feature seems to depend more on the size of the species, because the apical complex is not proportionally larger in larger specimens, but the absolute distance to the mantle edge is longer, for example, *Helicina funcki*, *H. pitalensis*. The shape of accessory structures is nearly independent of the developmental stage. Baker (1926) observed that lobules of the bursa copulatrix of immature *Helicina convexa* L. Pfeiffer, 1849, were almost as well developed as those of adults. Dissections of immature *Helicina funcki* confirm this assumption (Fig. 19, right drawing). The main changes connected with maturation take place in the development of the ovary that finally covers large parts of the visceral portion and an enormous thickening of the epithelium of the pallial oviduct (Bourne, 1911; personal observations). Furthermore the content of the accessory structures (empty or filled) does not remarkably influence the shape. Therefore the deviations illustrated are more likely due to intraspecific variability rather than different physiological conditions. Similar to the radula for some species, a certain peculiarity can be recognized, for example, the lobules at the upper end of the provaginal sac of *Helicina tenuis*, the elongated lobes of the bursa copulatrix of *H. funcki*, similarly developed in specimens from Panama (Baker, 1926).

Arrangement of Central American Mainland Taxa

Except for the single species *Pyrgodomus microdinus* and *Lucidella lirata*, the main part of the Costa Rican Helicinidae – namely the species of *Helicina* – was controversially classified and shifted to subgroups of *Helicina* or *Alcadia*. Because this confusion is characteristic for the two genera involving most of the American mainland species and a considerable portion of the Caribbean species, it must be treated to some extent. Subsequently, aspects of the remaining Central American mainland genera will be discussed.

The Genera Helicina and Alcadia

In the following, the different classifications of *Helicina* and *Alcadia* and related subgenera proposed in literature will be presented, critically summarizing the main distinguishing characters of the groups that were stressed by the authors. The respective systematic position of the Costa Rican taxa is indicated. Additionally, all relevant

subsequent contributions on the systematic classifications will be discussed. Finally, the differentiation and characterization of the genera and subgroups and necessary rearrangements will be proposed according to the morphological characters and their partially deviating assessment outlined by this study.

Wagner (1907–1911) – mainly based on features of shell and operculum. The respective assignment of the Costa Rican species is highlighted in bold face style.

Alcadia
- Subgenus: *Eucaladia* [= *Alcadia*]: Jamaica, Cuba, Bahamas, St. Thomas, St. Jan [= St. John?], Vieque, Puerto Rico, Hispaniola, French Guyana, Suriname, Brazil
  - Formenkreis "*Palliata*": Jamaica, Cuba
  - Formenkreis "*Hispida*": Cuba, Bahamas, St. Thomas, St. Jan [= St. John?], Vieque, Puerto Rico
  - Formenkreis "*Intusplicata*": Hispaniola
  - Formenkreis "*Sericea*": French Guyana, Suriname, Brazil
  - Formenkreis "*Incrustata*": Cuba
- Subgenus: *Leialcadia* [= *Idesa*]: Cuba, Jamaica, Puerto Rico, Hispaniola, Trinidad, Venezuela, Colombia, Costa Rica, Nicaragua, Guatemala, Mexico
  - Formenkreis "*Megastoma*": Jamaica, Cuba, Puerto Rico
  - Formenkreis "*Nitida*": Cuba, Puerto Rico
  - Formenkreis "*Mamilla*": Hispaniola, Cuba
  - Formenkreis "*Bellula*": Cuba
  - Formenkreis "*Ampliata*": Jamaica
  - Formenkreis "*Tamsiana*": Trinidad, Venezuela, Colombia
  - Formenkreis "*Gemma*": Costa Rica, Nicaragua, Guatemala, Mexico: ***gemma, beatrix*, (*fragilis*)**
- Subgenus: *Analcadia*: Guadeloupe, Martinique, St. Lucia, Dominica, Venezuela, Trinidad, Belize, Bonacca (island off Honduras), Nicaragua, Hispaniola, Puerto Rico, Vieque, St. Jan [= St. John?], Tortola
- Subgenus *Emoda*: Cuba

Helicina
- Formenkreis "*Angulata*" and "*Variabilis*": Brazil
- Formenkreis "*Concentrica*": Venezuela, Colombia, Peru, Bolivia
- Formenkreis "*Punctisulcata*": Mexico, Guatemala: ***punctisulcata***
- Formenkreis "*Cinctella*": Mexico, USA
- Formenkreis "*Tenuis*" [= *Pseudoligyra*]: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Bolivia: ***tenuis***
- Formenkreis "*Turbinata*": Panama, Costa Rica, Nicaragua, Honduras, Mexico, Guatemala: ***funcki*, *pitalensis***
- Formenkreis "*Succincta*": Mexico, Guatemala
- Formenkreis "*Festiva*": Hispaniola
- Formenkreis "*Euneritella*" [= *Helicina*]: Cuba, Jamaica, Grenada, St. Vincent, Guadeloupe, Dominica, Bonacca, Martinique, Trinidad, Barbados, Bermuda

The differences between *Helicina* and *Alcadia* given by Wagner (1907–1911) can be summarized as consisting mainly of shell characteristics (in *Helicina*: umbilical area always and constantly with an impressed line or groove, no periostracal hairs; *Alcadia s.s.*: typical basal notch). Furthermore, the operculum of *Helicina* only differs in a less prominent sigma-edge and a nucleus most closely approaching the columellar edge (but this is also attributed to *Analcadia*, *Leialcadia* and *Alcadia s.s.* partially). Wagner (1907–1911) adds that some species of *Alcadia* and Mexican and Antillean species of *Helicina* intergrade or only weakly exhibit the typical characters respectively.

With respect to the characteristics of the operculum, *Analcadia* differs from *Leialcadia* only in a deeper groove near the lower part of the sigma-edge, other differences apply to shell characteristics. *Leialcadia* is typically characterized by the shiny and lasting periostracum and reduced characteristics of aperture and operculum. Both subgenera lack the prominent calcareous plate of the operculum and the deep notch in the basal part of the aperture described for *Alcadia s.s.*

The "Formenkreise" were only used to summarize groups of species, they were introduced without any description or type species.

Baker (1922a) – mainly based on characters of the radula, in combination with some features of the shell and operculum.

Oligyra (tropical and subtropical America)
- Subgenus: *Oligyra*: tropical and subtropical America
  - Section: *Oligyra s.s.*: USA, Bermuda Islands, Mexico
  - Section: *Succincta*: Mexico to South America: ***gemma, beatrix***

Subgenus: *Alcadia*: West Indies to South America
Section: *Idesa*: West Indies
Section: *Analcadia*: Antilles to Central America
Helicina (tropical America)
Subgenus: *Helicina*: West Indies
Subgenus: *Tristramia*: mainland [of tropical America]
Section: *Oxyrhombus*: Central and E-Mexico to South America: ***punctisulcata***
Section: *Tamsiana*: northern South America
Section: *Angulata*: South America to Central America
Section: *Tenuis* [= *Pseudoligyra*]: Mexico to Central America; South America: ***tenuis***
Section: *Tristramia*: Mexico to Colombia: ***funcki***, ***pitalensis***

According to Baker (1922a), *Oligyra* differs from *Helicina* by a well-developed wing at the accessory plate and centrals with always well-developed cusps. The operculum shows intergrading characters. Compared with *Alcadia*, the genus has a light operculum lacking the inferior point fitting in the corresponding notch in the basal outer lip, and A- and B-central do not exhibit heavy backs. It was later maintained that *Oligyra* and *Alcadia* belong to two diverging lines of evolution. It would, however, be extremely difficult to name any very definite characteristics for their separation.

Succincta differs from *Oligyra* in the tendency of reduction of the cusps of the A-central, whereas A- and B-central of *Oligyra* are with well-developed cusps. Additionally, the shell is more globose, and marginals show a wing-like expansions below the tips (otherwise strictly lingulate).

According to Baker (1923) the centrals of the radula of *Analcadia* resemble those of *Oligyra s.s.*, but shell characters approach those of *Alcadia*, suggesting *Analcadia* as a subgenus between the subgenera *Oligyra* and *Alcadia*. The radula of *Oligyra* (*Alcadia* – section: *Idesa*) *rotunda* is said to agree with *Alcadia s.s.* in the centrals and with *Sericea* or *Analcadia* in the comb-lateral.

Tristramia differs from *Helicina* in strictly lingulate marginals (not sickle-shaped with lateral wings near tips), a lacking shelf-like projection bearing the cusps on the A-central and a differing accessory plate (operculum and comb-lateral are equal). The differences between *Oxyrhombus*, *Tamsiana*, *Angulata*, *Tenuis*, and *Tristramia* include shell characteristics (presence or absence of a spiral striation, periphery angular or not) and radula characters not worth mentioning.

All the radula differences within *Helicina* and *Oligyra* (because the main difference "the wing" was a misinterpretation) become reduced to minor deviations in cusp development (presence and shape) on centrals and the comb-lateral and the arrangement and an increase in the number of the cusps on the marginals (more on tip or laterally).

The author erroneously recognized the "Formenkreise" of Wagner (1907–1911) as relevant supraspecific taxa and, by doing so, made them nomenclaturally available (Zilch, 1948); some became objective synonyms of older supraspecific taxa, other were synonymized, but some were accepted as sections. Because there is good reason to suppose that Wagner based the "Formenkreise" on similarities of shell characteristics, it may be said that for the taxa accepted and kept in their position, Baker only attempted to consolidate this system with questionable radula features, instead of having raised it based on these characteristics.

Baker (1926) – system modified to incorporate anatomical characters.

Helicina
Subgenus: *Helicina*
Subgenus: *Oligyra*
Section: *Oligyra s.s.*
Section: *Succincta*: ***gemma***, ***beatrix***
Subgenus: *Tristramia*
Section: *Tristramia s.s.*: ***funcki***, ***pitalensis***
Section: *Tenuis* [= *Pseudoligyra*]: ***tenuis***
Subgenus: *Oxyrhombus*
Section: *Oxyrhombus s.s.*: ***punctisulcata***
Section: *Angulata*
Section: *Tamsiana*
Alcadia
Subgenus: *Alcadia*
Subgenus: *Analcadia*
Subgenus: *Sericea*
Subgenus: *Idesa* (included after Baker, 1923)

Because Baker assumed the anatomy of *Alcadia s.s.* was distinct from *Oligyra* (he studied *Analcadia* and *Sericea*, but did not have adequate material of *Alcadia s.s.* and only very critically interpreted the [correct] figure given by Bourne, 1911, as generalized), he raised *Alcadia* again to generic level and pointed to further investigations to show the

exact line of demarcation between *Oligyra* and *Alcadia*. He stated that shell and radula characters of *Succincta* (*Helicina* (*Succincta*) *cacaguelita* Pilsbry & Clapp, 1902, examined) approach those of *Alcadia*, but the anatomy appears closest to that of the subgenus *Tristramia* (*Helicina* (*Tristramia*) *funcki* examined).

Baker pointed out that anatomical and shell characteristics of *Helicina* and *Oligyra* "intergrade to such an extent, that one meets considerable practical difficulty in any attempt to differentiate the two groups." Therefore, he included *Oligyra* with two sections as subgenus into *Helicina*.

When describing the anatomy of *Helicina* (*Oxyrhombus*) *cinctella*, Baker (1928) remarked that the female genital system is intermediate between those of the species of *Oligyra* and that of *H. concentrica* L. Pfeiffer, 1849 [the only representative for *Oxyrhombus* studied by Baker (1926)], although the structure of the bursa copulatrix distinctly approaches that of *Tristramia*.

Rehder (1966) discussed the systematic affinities of *Helicina bocourti* Crosse & Fischer, 1869, Honduras (formerly regarded as subspecies of *H. dysoni*, Venezuela) applying the characteristics of the radula and concluded that both species belong to the subgenus *Tristramia*, of *Helicina*, synonymizing *Oxyrhombus* and *Tristramia*, because the radula of *H. bocourti* combines characteristics of both groups. Regarding a rearrangement of the subgenus *Analcadia*, of which *H. dysoni* is the type species, to *Helicina* instead of *Alcadia*, Rehder (1966) avoided a direct statement, because he later pointed to the periostracal hairs and the development of the operculum of *H. dysoni* as characteristic of the genus *Alcadia* and mentioned his uncertainty "that radular characteristics alone can be used for subgeneric differentiation".

Boss & Jacobson (1973) revised the Cuban species of the genus *Alcadia*. Considering anatomical studies of the previous authors and combining their own results on the radula with Baker's (1922a), they pointed out that "shell morphology, together with certain features of the operculum still constitute the most reliable method of distinguishing members of the genus". They then proceed to differentiate *Helicina* and *Alcadia* mainly by the basal notch or sinus of the shell and an internal lamella and groove on the columellar edge of the operculum. Nevertheless, it remains doubtful how they define the genus outside of Cuba, that is, the exact line of demarcation between *Helicina* and *Alcadia*, because *Alcadia* in their sense (Boss & Jacobson, 1973: 311–312) occurs on most of the West Indian islands as well as on the mainland from southern Mexico to northern South America. Actually, this distribution only agrees with Wagner's version and not with that of Baker (1922a, 1926), who attributed part of Wagner's *Leialcadia*, namely the species groups "*Gemma*" and "*Tamsiana*", to *Helicina* or *Oligyra* respectively and, by doing so, excludes *Alcadia* from Central America (but not from northern South America). Boss & Jacobson (1973) even assumed the origin of the genus to be in Central America.

Their investigation of the radula of four Cuban species (two of them type species of subgenera) and *Alcadia major* (Jamaica) revealed that it cannot be used as a diagnostic feature for *Alcadia*, at least at the present state of knowledge. Troschel (1856-63), for example, noted a different shape of the R-central in *Helicina* and *Alcadia*, but Boss & Jacobson found it to be too variable in their species studies of *Alcadia*.

Thompson (1982), clarifying the systematic affinities of the species group *Helicina umbonata* from the West Indies, used embryonic shell structures for the first time, because they are of conservative character and show little variations within species or closely related groups. When judging other characteristics for their applicability to systematics, he regarded shell and operculum as being directly affected by evolutionary pressures due to their direct contact with the environment and thus as being subject to convergence. By the way of contrast, Thompson (1982) assumes the radula as a useful, conservative morphological system, citing the studies of Baker (1922a), although it is obviously also under direct selective pressure as foraging organ, and although Thompson (1980) argues that the vianid radula (radula with inner lateral T-shaped) has convergently evolved in Proserpinidae and Vianinae for similar trophic activities.

His results with respect to the embryonic shell show that *Alcadia* clearly differs from *Helicina s.s.* Other generic units placed in *Alcadia* as subgenera are said to agree with *Alcadia s.s.*, whereas some mainland subgenera associated with *Helicina* differ from *Helicina s.s.* thus requiring re-examination. Against the backdrop of the controversial ar-

rangement of subgeneric units of *Helicina* and *Alcadia*, it remains doubtful just what Thompson (1982) refers to. He does not specify any taxa or species on which he based his statement about the subgeneric taxa except for those genera within the actual scope of his study (*Helicina s.s.*, *Alcadia s.s.*, *Lucidella s.s.* and *Poenia*).

To summarize the present state of knowledge, it can certainly be stated, that the discrimination of the genera *Helicina* and *Alcadia* and their associated subgenera remains a controversial topic. Especially the species groups "*Gemma*" and "*Tamsiana*", the former encompassing part of the Costa Rican taxa, were shifted either to the one or other genus. Radula differences turned out to be wrong interpretations or to intergrade or vary. The features of shell and operculum most strongly and constantly influenced the classification since they actually also represented the foundation for later concepts. The anatomy has been regarded as too uniform and conservative even within the Helicinidae, except for some primitive members (e.g., *Hendersonia*). The only definite and first hint for a clear separation of the genera *s.s.* is given by the structure of the embryonic shell.

New Proposed Arrangement

From the results of the present study, the following arrangement is proposed for those taxa investigated. Details of the assessment of the different characteristics were discussed in the foregoing chapter. Contrary to previous attempts, emphasis is placed on differences in the female reproductive system, which agree with changes in the embryonic shell structure.

Helicina[*]
- Subgenus: *Helicina s.s.* (West Indies)
- Subgenus: *Tristramia* (Synonyms: *Oxyrhombus*, *Pseudoligyra* [= *Tenuis*], ?"*Cinctella*") (Central American mainland): ***funcki*, *pitalensis*, *tenuis*, *echandiensis* n. sp., *punctisulcata cuericiensis* n. subsp.**
- Subgenus: *Oligyra* (Synonym: *Succincta*) (Central American mainland)
- Subgenus: "*Gemma*"[**]: ***gemma*, *beatrix*, *talamancensis*, *monteverdensis* n. sp., *chiquitica*, *escondida* n. sp.**
- Subgenus: *Ceochasma* (Mexico)
- Subgenus: *Analcadia* (northern South America)
- Subgenus: *Sericea* (northern South America)
- ?Subgenus: *Tamsiana* (northern South America)

Angulata (South America)

Alcadia[***]
- Subgenus: *Alcadia* (West Indies)
- Subgenus: *Microalcadia* n. subgen. (Central American mainland): ***hojarasca*, *boeckeleri***
- Subgenus: *Idesa* (West Indies)

[*] the South American taxa will be discussed, but they are only included as examples, because they were beyond the actual scope of this study

[**] the taxon *Gemma* is preoccupied, but considering the uncertainty of the this subdivision, it seems unjustified at present to replace the name

[***] other Antillean subgenera are not considered

Helicina is characterized by the embryonic shell structured with pits arranged in concentric lines, the absence of a provaginal opening (i.e., monaulic), and an externally subdivided bursa copulatrix in the female reproductive system.

In *Alcadia*, the embryonic shell exhibits more or less strong oblique grooves and coarse, irregularly spaced radial threads. The provaginal opening of the female system is present (i.e., diaulic) with an elongated provaginal duct. The bursa copulatrix is an oblong sac that is externally not distinctly lobed. Other examples included West Indian subunits (*Palliata*, *Idesa*, and the species *Alcadia jamaicensis*, formerly associated with *Helicina*) that will not be judged as to their final status, but they do show a similar embryonic shell structure, although much more strongly developed and have, in principle, the same arrangement of the female organs.

In *Helicina s.s.,* the embryonic shell is very densely sculptured with large pits. The bursa copulatrix is the predominant accessory organ of the apical complex in the female reproductive system. It is complexly subdivided, whereas the provaginal sac appears simplified and much reduced. The ascending limb of the V-organ is elongated.

With respect to the above-mentioned characteristics the subgeneric units *Tristramia*, *Oxyrhombus*, *Pseudoligyra*, "*Cinctella*", *Succincta* and *Oligyra* were confirmed in their association with *Helicina*.

The species group "*Gemma*" *sensu* Wagner (1908) sharing shell characteristics with sub-

groups of *Alcadia* is now clearly distinguished from that genus and belongs to *Helicina s.l.*

Tamsiana, the second group in questionable position, could not finally be assessed in its relationship since adequate material was not available. A single embryonic shell studied (ZMB 103314) is partially eroded, and the surface can only be described with uncertainty as very scarcely pitted and crossed by very slight oblique lines. The figure of the female system given by Baker (1922a) shows a much reduced bursa copulatrix and a very large provaginal sac. Assuming the provaginal orifice to be incorrect, these characteristics would approach those of *Analcadia* and subordinate *Tamsiana* to *Helicina*, but a reexamination of the female system is still required.

The northern South American subunits *Analcadia* and *Sericea*, both studied by the respective type species, have to be rearranged from *Alcadia* to *Helicina*. They have a less densely pitted embryonic shell in common with a tinge of oblique lines and a strongly enlarged provaginal sac with a basal appendage. Furthermore, *Analcadia* and *Sericea* share the feature of a hairy periostracum, which is absent in other subgroups of *Helicina*. These similarities probably indicate a close relationship of both taxa, but, on account of the differently developed bursa copulatrix and the conspicuous sac on the middle portion of the pallial oviduct of *Helicina* (*Analcadia*) *dysoni*, the taxa are tentatively recognized as separate subgenera of *Helicina*.

Study of the Brazilian species "*Helicina*" *brasiliensis*, closely related to the type species of *Angulata* (*Helicina angulata*), shows a very different embryonic shell structure (broad, regular, concentric lines instead of pits or oblique grooves and radial threads), thus providing sufficient reason to raise *Angulata* to generic level. Older available names do not seem to exist. The anatomy of the female system resembles *Helicina* with respect to the bursa copulatrix, provaginal sac, receptaculum seminis, and the V-organ, but unfortunately the most important feature, the mon- or diaulic condition could not properly be determined due to the poor preservation of the material available. Preliminary studies on other South American species suggest a higher diversity of the female system than in the Central American mainland species of *Helicina* and render the presence of a provaginal opening more likely than its absence. Beside the above-mentioned taxa *Tamsiana*, *Analcadia* and *Sericea* subgrouped to *Helicina*, only four other supraspecific taxa have been based on South American species – *Angulata*, *Variabilis* Baker, 1922; *Concentrica* Baker, 1922; and *Trichohelicina*. *Variabilis* and *Trichohelicina* have not yet been investigated, the latter is discussed above under *Alcadia* (*Microalcadia*) n. subgen. Radula and female reproductive system of *Helicina concentrica* were studied by Baker (1923, 1926). Although the existence of a provaginal opening remains to be re-examined, the anatomical structures with a weakly lobed bursa copulatrix and a strongly enlarged provaginal sac show more similarities to the other species/ subgenera of northern South America (*Analcadia*, *Sericea*, *Tamsiana*) than to *Angulata*.

Because of the similarities of the female reproductive system of *Ceochasma* to *Helicina* and the absence of other distinguishing features, except for the outstanding and characteristic development of the deep slit-like sinus at the suture of the body whorl, the genus is hereby tentatively regarded as a subgenus of *Helicina*.

A subdivision of the Central American mainland species of *Helicina* remains difficult. The following available, non-synonymous supraspecific taxa (unless otherwise stated the synonymy given in Baker (1922a) for Central American mainland supraspecific taxa is accepted here) have to be considered: *Oligyra*, *Succincta*, *Tristramia*, *Oxyrhombus*, *Punctisulcata* and *Pseudoligyra*. The preoccupied "Formenkreis" names of Wagner *Gemma* and *Cinctella* were accepted by Baker (1922a) and type species were designated. Because Baker treated both as synonyms, differentiating features were never formulated.

As shown above, Baker (1926) could not find any anatomical characteristics distinguishing *Helicina* and *Oligyra*. Radula characteristics also do not contribute much to the differentiation of the taxa given above, for example, *Pseudoligyra* is said to differ from *Tristramia* only in the dentition of the C-central (4 cusps or rounded hook).

With respect to the Costa Rican species studied, two groups can be distinguished encompassing the following species:

1st group: *Helicina funcki*, *H. pitalensis*

2nd group: *Helicina beatrix*, *H. talamancensis*, *H. gemma*, *H. monteverdensis* n. sp., *H. chiquitica*

Remaining: *Helicina tenuis*, *H. escondida* n. sp., *H. echandiensis* n. sp., *H. punctisulcata cuericiensis* n. subsp.

The groups can be characterized as follows:

1st group: (a) embryonic shell: diameter of pits equal to interspaces, (b) surface structure of teleoconch with oblique diverging grooves, (c) cusps of marginal teeth slowly increasing in number, (d) provaginal sac irregularly lobed at distal side, (e) bursa copulatrix with numerous, often further subdivided lobes, central axis or lobes elongated, (f) males in volume a little more than 80% of females (in *Helicina pitalensis* not known).

2nd group: (a) embryonic shell: in some species diameter of pits smaller than interspaces and less densely pitted, (b) surface structure of teleoconch smooth, except for fine growth lines, (c) cusps of marginal teeth rapidly increasing in number and cusps more laterally arranged, (d) provaginal sac smooth at distal side, (e) bursa copulatrix with tendency to less numerous lobes, (f) males in volume about 62–70% of females.

Helicina tenuis, *H. echandiensis* n. sp. and *H. punctisulcata cuericiensis* n. subsp. fit in the first group except for (e) the rather simple bursa copulatrix and in (f) being intermediate between the groups with a male's volume about 75% of the female's (in *H. echandiensis* n. sp. only few individuals investigated, in *H. punctisulcata cuericiensis* n. subsp. unknown).

Helicina escondida n. sp. rather approaches the second group except for b) a surface structure similar to that of the 1st group although very slightly developed and in (f) being intermediate between the groups and equal to *H. tenuis* with a male's volume about 75% of the female's.

With respect to the radula, all the species have the common trait that at least the A-central is without well-defined cusps. Only occasionally it is crenulate or, in a single specimen, even denticulate, but not consistently for any species. Other deviations appear rather species-specific, for example, comb-lateral in *Helicina escondida* n. sp.

A comparison of the species investigated for the subgeneric units proposed by earlier authors (the type species of *Oligyra*, *Oxyrhombus*, *Pseudoligyra* and "*Gemma*", possibly related species for *Tristramia* and *Punctisulcata*, for *Succincta* and "*Cinctella*" only literature data were available) does not resolve clearly differentiated groups. At this level, the detailed embryonic shell structure does not seem to be applicable, because it already intergrades among the groups of the Costa Rican species otherwise separated by different characteristics. For the female reproductive system, two main trends can be recognized in the relative development of the bursa copulatrix and the provaginal sac and its stalk, but intergrades can also be found among the Costa Rican species. On one hand, the bursa is relatively large and more complex in its structure, and the provaginal sac is long-stalked and irregularly lobed at its distal side or end. On the other hand, the bursa copulatrix is simply subdivided and more or less reduced in the number of lobes, and the provaginal sac is smooth and more distinct in its outline. The first trend is significantly found in *Tristramia* and *Oxyrhombus*, "*Cinctella*" and to a lesser extent also in *Punctisulcata* and *Pseudoligyra*, sharing also the teleoconch surface structure of oblique diverging grooves. This group most closely resembles *Helicina s.s.* from the West Indies. The other trend is developed in "*Gemma*" in combination with a very smooth shell. *Oligyra* and *Succincta* represent an intermediate stage, with a lobed provaginal sac and a remarkably reduced bursa copulatrix (although not to the same degree within different populations of *Helicina orbiculata*). Furthermore, they share the feature of an enlarged receptaculum seminis and a shell sculptured with spiral grooves. Additionally, at least *H. orbiculata* exhibits the pattern of oblique diverging grooves on the teleoconch. According to Baker (1928), *Helicina* (*Succincta*) *flavida* combines similar characteristics.

Data of Baker (1928) allow the interpolation of the degree of sexual dimorphism for *Helicina zephyrina* (to *Tristramia*) of about 82% (portion: male's of female's volume) resembling the 1st group of the Costa Rican species.

Summarizing, the features of the embryonic shell and female reproductive system are helpful on the generic level, rather than for differentiating within this group of species, although the latter characteristics show tendencies that are probably worth following up for other species. Except for the trends in the denticulation of the marginals, which seems to be more influenced by the specimen size, differences in the radula appear more subjective rather than objective, or they are limited to single species. Although in the data predominantly limited to Costa Rican species, a correlation of shell similarities and the degree of sexual dimorphism is obvious. This fact provides evidence that these characteris-

tics, especially the features of the shell, are useful in recognizing relationships at the subgeneric level when the assignment to the genus is also verified by other features.

Considering the practical taxonomical necessity of assigning the Central American mainland taxa to certain subgroups and since other subgenera of *Helicina* can be recognized properly, although final definitive differentiating characteristics could not be found, the proposed arrangement is tentative and follows the similarities outlined above. *Tristramia*, *Oxyrhombus*, *Pseudoligyra* and ?"*Cinctella*" (the latter not studied) are assumed to be synonymous including the 1st group of the Costa Rican species. The name *Tristramia* has priority. Furthermore, *Oligyra* and *Succincta* are regarded as synonymous with *Oligyra* being the older name, but *Oligyra* and *Tristramia* diverge from the group of "*Gemma*", which encompasses the 2nd group of the Costa Rican species. This name will tentatively be used for the separate subgenus, although it will have to be replaced in case this subdivision must be modified by additional data. Presently, the proposal of a new name seems inappropriate.

The well-defined differences between *Helicina* and *Alcadia* and other subgenera mentioned above, together with the uniformity among the species from the Central American mainland with respect to otherwise distinguishing features, suggest a much closer relationship within the mainland species than was previously assumed. The genus *Alcadia* has been shown to be absent from the Central American mainland and northern South America, except for the newly discovered small species *Alcadia* (*Microalcadia*) *hojarasca* and *A.* (*M.*) *boeckeleri*, which is distinguished from the *Alcadia s.s.* and examples investigated from other West Indian species by the peculiarities outlined in the description of the new subgenus. The presence of only a limited number of small-sized species of a genus on the mainland, as is here shown for *Alcadia*, is paralleled in the genus *Lucidella* and the new world Vianinae (according to the definition of Thompson, 1980; the subfamilial arrangement will not be discussed here) with their main radiation in the West Indies. In this case, only the species *L. lirata* and *L. midyetti* Richards, 1938, or *Pyrgodomus microdinus* and *P. simpsoni* respectively occur on the mainland. By way of contrast, *Helicina* represents the predominant genus on the mainland and is spread over the West Indian Islands, although the exact distribution still remains subject to further studies. This is due to the previous confusion with *Alcadia* according to the characteristics of the post-embryonal shell and the operculum, upon which the only classification including species of the West Indian fauna had been based. But the species *Helicina platychila* from Dominica (Lesser Antilles), included as an example, and the type species *Helicina neritella* from Jamaica (Greater Antilles) clearly confirm the wider distribution.

Other Central American Mainland Genera

Due to insufficient material, the genus *Pyrgodomus* could not be examined for features of the female reproductive system, but the similarities in shell shape and surface structure, embryonic shell and radula confirm the close relationship to the Antillean genus *Eutrochatella*. Especially the size of the embryonic shell appears to be characteristically reduced in these genera compared with *Helicina* and *Alcadia*. The examination of the type species of *Eutrochatella* revealed monaulic conditions in the female reproductive system rendering a closer affinity to *Helicina* likely. Up to now there has been no evidence for assuming that the monaulic condition evolved more than once. The different embryonic shell structure of *Helicina* as well as the radula characteristics of *Eutrochatella* were discussed as being subject to convergent developments. Whether or not the differentiation of *Pyrgodomus* at the generic level is justified, depends on further investigations of the West Indian species and the final re-examination of the anatomy of *Pyrgodomus*. The traditional treatment is therefore tentatively maintained, although, according to the present data, the divergence from *Eutrochatella* probably does not exceed those differences of the mainland subgenera of *Lucidella* and *Alcadia* to their West Indian subunits.

The same applies to *Lucidella* as to *Pyrgodomus*, namely that the main portion of the species inhabits the West Indian Islands and only a few species, such as *Lucidella lirata*, occur on the mainland. Therefore, the discussion will be limited to the typical subgenus and *Perenna* based on the presently investigated species from Costa Rica. According to the system of Keen (1960), which is adopted here, two additional subgen-

era, *Poenia* and *Poeniella*, are established on a species from Jamaica or the Lesser Antilles respectively. The investigation of the female reproductive system of *Lucidella lirata* as well as of *L. aureola* required the corrections of important details given by Baker (1926, 1928). Therefore, it does not only confirm the affinities of *Perenna* to *Lucidella* but also allows the clear differentiation of the genus by peculiar characteristics of the female anatomy. *Lucidella* lacks the receptaculum seminis on the inner side of the descending limb of the V-organ, which bears apical swellings, but possesses an additional sac-like structure for sperm storage at the posterior portion of the pallial oviduct. In the absence of the receptaculum seminis and in the shortness of the provaginal duct, *Lucidella* resembles *Schasicheila*. The differences in the embryonic shell structure outlined by Thompson (1982) were confirmed and, as in other genera, are parallel in the anatomical features. Furthermore, the investigation of the internal shell structures showed the peculiar attachment of the right portion of the retractor muscle on the penultimate whorl and a comparable long axial cleft. As stated above, *Perenna*, although diverging in shell shape, generally agrees with *Lucidella, s.s.*, with respect to embryonic shell and female system, but the bursa copulatrix is more closely associated with the stalk of the provaginal sac than directly with the reception chamber. Additionally, the posterior portion of the pallial oviduct is less inflated and internally folded, thus providing further reasons for retaining the subgeneric separation.

Finally, the genus *Schasicheila* does not occur in Costa Rica and seems to be limited to Mexico and Guatemala, but it is included here to take all Central American mainland genera of the Helicinidae into account. *Schasicheila* is characterized by several peculiarities of the postembryonic shell and operculum (summarized by Wagner, 1907–1911). Its radula does not diverge remarkably from the typical denticulated type of *Helicina*, for example. Concerning its anatomy, Baker (1926, 1928) recognized the genus as one of the most aberrant groups of Helicinidae. Reexamination of the type species confirmed all of Baker's observations, especially with respect to the diaulic condition of the female reproductive system. The embryonic shell structure and the internal shell structure added further distinguishing features.

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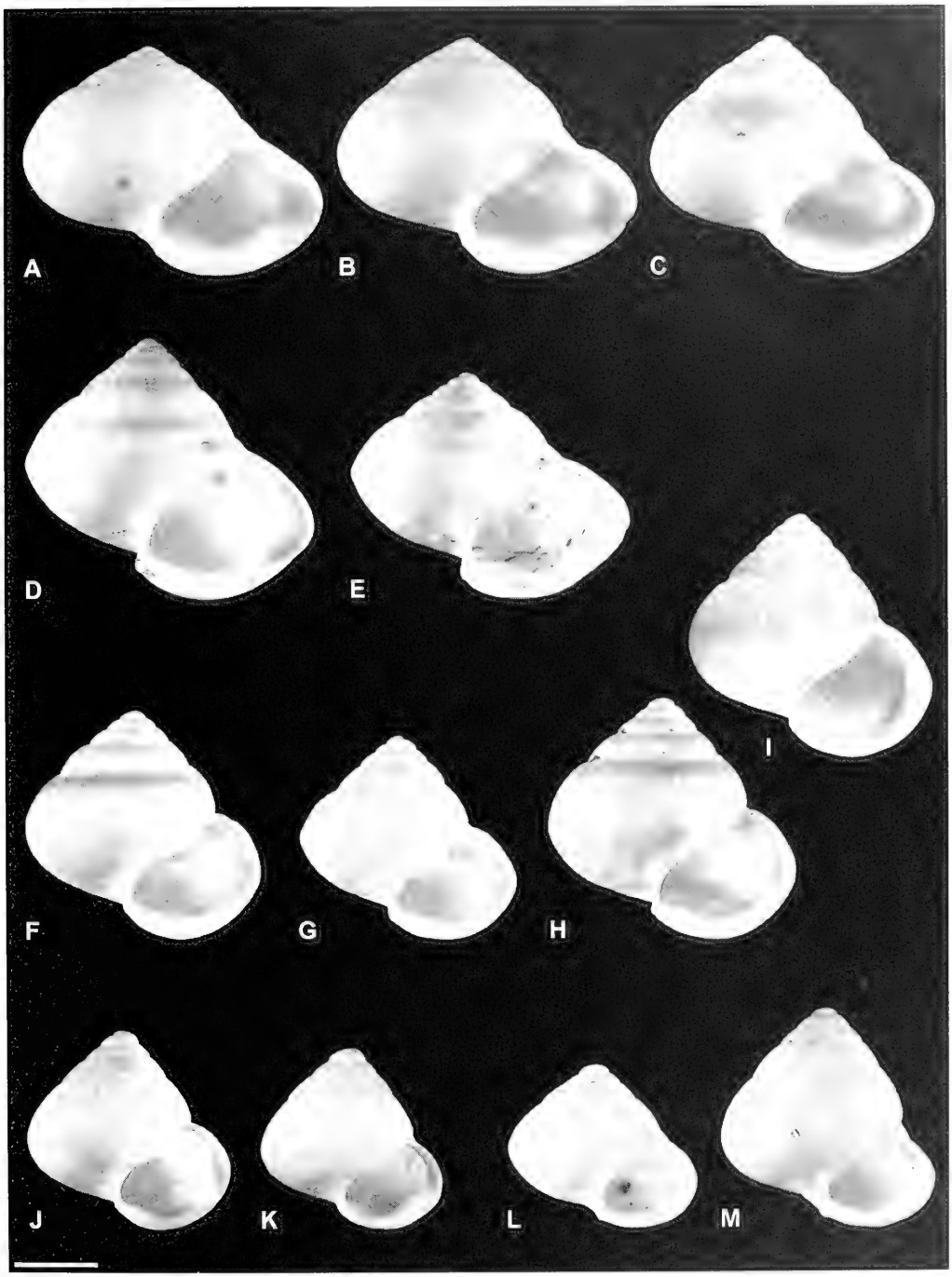

FIG. 335. A-C. *Helicina funcki*. A. Río Barbilla. B. Manzanillo. C. Santa Elena. D–E. *H. pitalensis*. D. Bajo Bonito. E. Península de Osa. F–I. *H. tenuis*. F–H. Cabo Blanco. I. La Selva. J–K. *H. echandiensis* n. sp., campamento Echandi. L–M. *H. punctisulcata cuericiensis* n. ssp., Estación Cuerici; scale bars 4 mm (A–E), 3 mm (F–M).

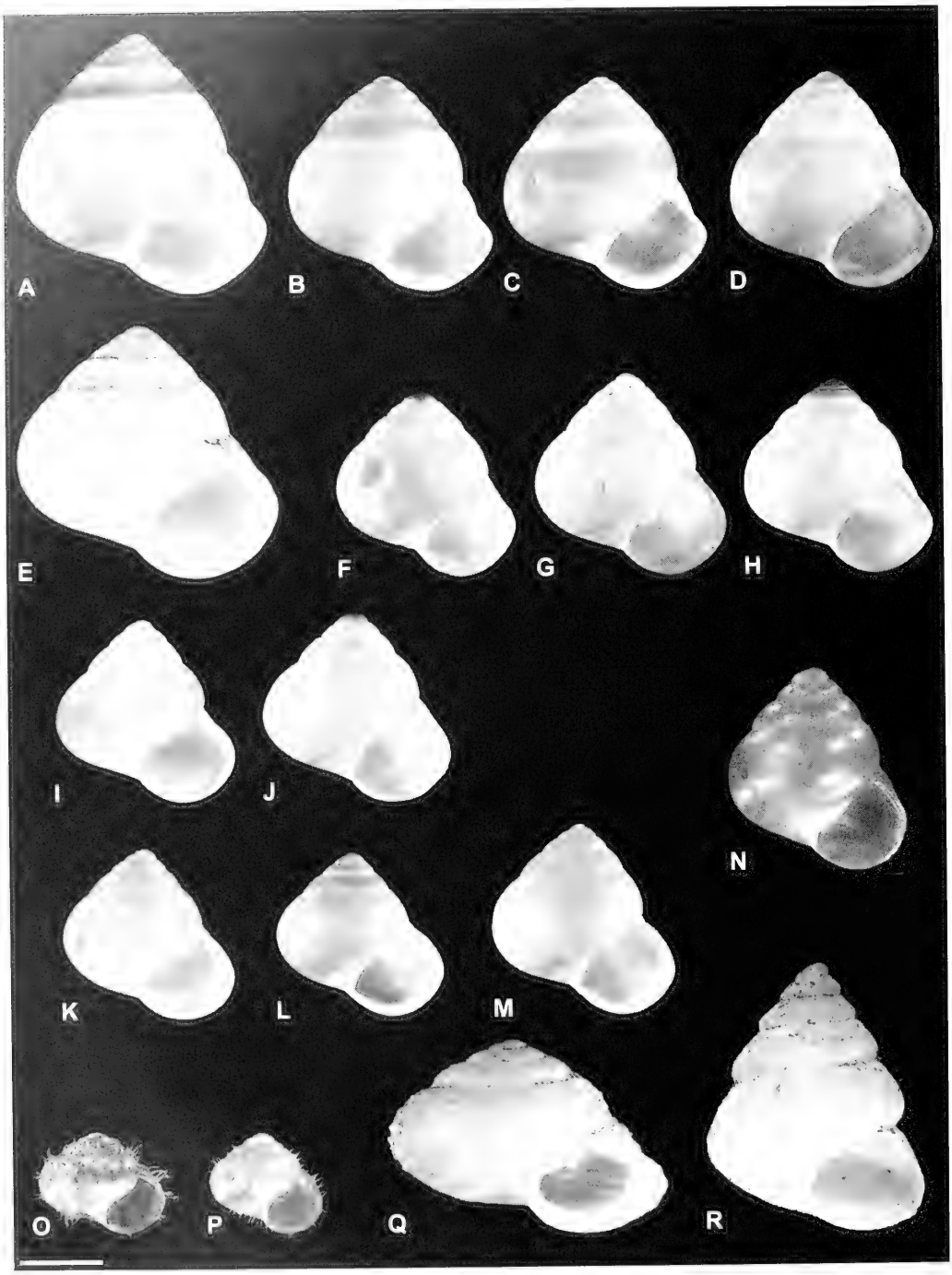

FIG. 336. A. *Helicina beatrix beatrix*, Guayacán. B-C. *H. b. confusa*. B. Uatsi. C. Shiroles. D. *H. b. riopejensis* n. ssp., Río Peje. E. *H. talamancensis*, Bajo Bonito. F–H. *H. gemma*. F. Cacao. G. Las Pavas. H. Siquirres. I–J. *H. monteverdensis* n. sp., Monteverde. K–M. *H. escondida* n. sp., Río Barbilla. N. *H. chiquitica*, Río Barbilla. O. *Alcadia hojarasca*, Mirador Gerardo. P. *A. boeckeleri*, Pitilla. Q. *Lucidella lirata*, Cahuita. R. *Pyrgodomus microdinus*, Fila de Cal; scale bars 3 mm (A–M), 2 mm (N–P), 1.2 mm (Q–R).

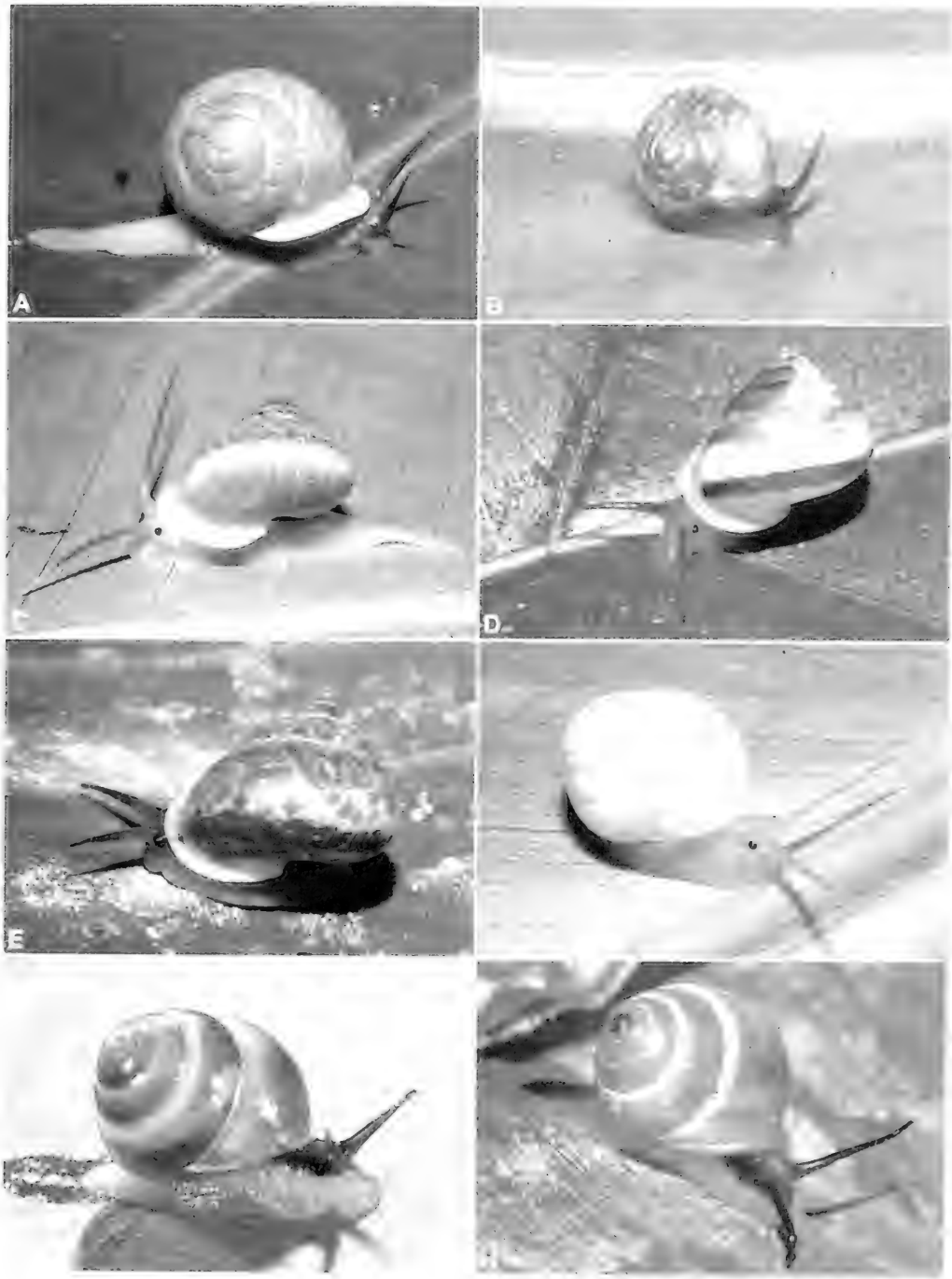

FIG. 337. Living animals of. A. *Helicina funcki*, Cahuita. B. *H. funcki*, juvenile, Uatsi. C. *H. pitalensis*, Bajo Bonito. D. *H. tenuis*, Cabo Blanco. E. *H. tenuis*, La Selva. F. *H. beatrix confusa*, Uatsi. G. *H. beatrix confusa*, Shiroles (photograph: V. Wiese). H. *H. beatrix riopejensis* n. ssp., Rio Peje.

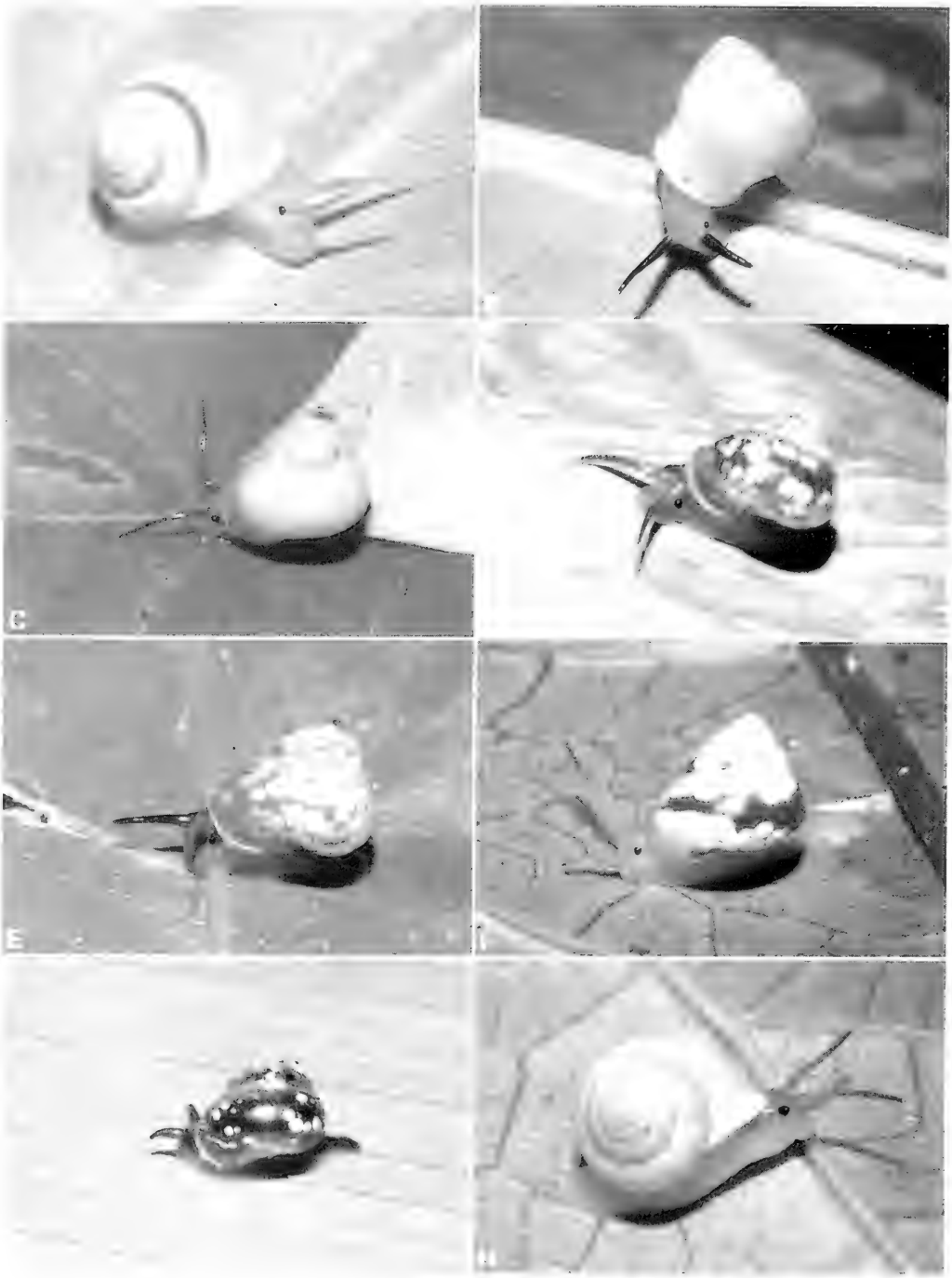

FIG. 338. Living animals. A. *Helicina beatrix beatrix*, Guayacán. B. *H. talamancensis*, Bajo Bonito. C. *H. gemma*, Cacao. D. *H. gemma*, Las Pavas. E. *H. gemma*, Siquirres. F. *H. monteverdensis* n. sp., Monteverde. G. *H. monteverdensis* n. sp., Mirador Gerardo. H. *H. escondida* n. sp., Shiroles.

FIG. 339. Living animals. A. *Helicina escondida* n. sp., Shiroles. B. *H. escondida* n. sp., Río Barbilla. C. *H. chiquitica*, Río Barbilla. D. *H. chiquitica*, Río Pacuarito. E. *Pyrgodomus microdinus*, Fila de Cal (photograph: V. Wiese). F. *Alcadia hojarasca*, Mirador Gerardo. G. *A. boeckeleri*, Pitilla. H. *Lucidella lirata*, Cahuita.

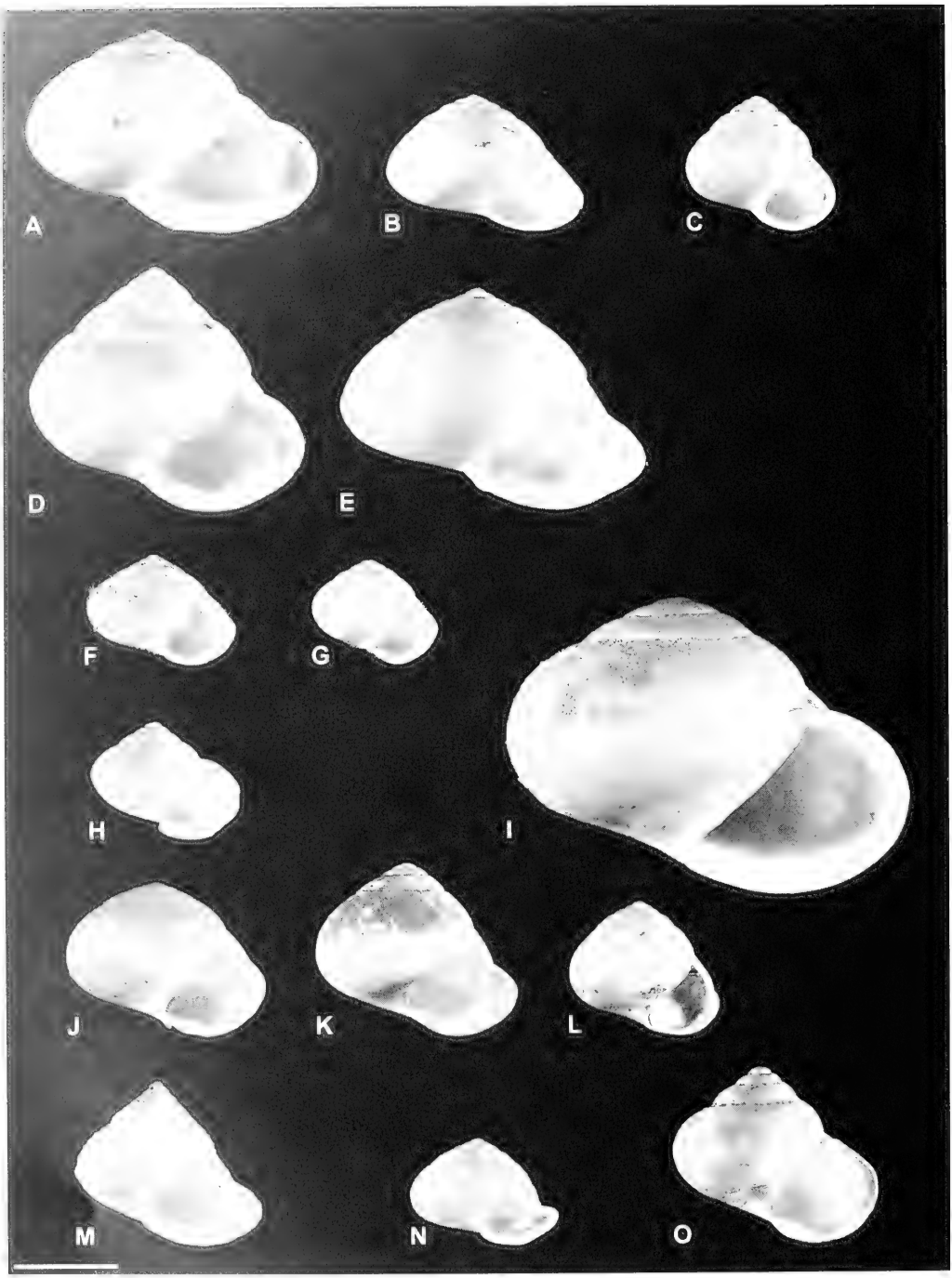

FIG. 340. A. *Helicina neritella*, Jamaica. B. *H. platychila*, Dominica. C. *H. orbiculata*, Florida. D. *H. turbinata*, Mexico. E. *H. amoena*, Guatemala. F. *H. dysoni*, Trinidad & Tobago. G. *H. sericea*, Suriname. H. *Angulata brasiliensis*, Brazil. I. *Alcadia major*, Jamaica. J. *A. hollandi*, Jamaica. K. *A. jamaicensis*, Jamaica. L. *A. rotunda*, Cuba. M. *Eutrochatella pulchella*, Jamaica. N. *Lucidella aureola*, Jamaica. O. *Schasicheila alata*, Mexico; scale bar 5 mm.

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RESEARCH NOTES

MALACOLOGIA, 2004, 45(2): 443–450

REPRODUCTIVE PERIOD AND GROWTH RATE OF THE FRESHWATER SNAIL *HELEOBIA PARCHAPPII* (d'ORBIGNY, 1835) (GASTROPODA: RISSOOIDEA) IN A SHALLOW BRACKISH HABITAT (BUENOS AIRES PROVINCE, ARGENTINA)

Claudio G. De Francesco[1]& Federico I. Isla[2]

ABSTRACT

Heleobia parchappii (d'Orbigny, 1835) is a rissooidean snail very widespread in freshwater environments of Argentina, occurring at salinities < 1‰. In 1998, we found a population of this species inhabiting a brackish canal (10–34‰) located close to the headwaters of the Mar Chiquita coastal lagoon (37°31'07"S, 57°18'30"W, Buenos Aires, Argentina). The aim of the present work is to analyse the reproductive period and growth rate of this species in this saline condition. Monthly collections were made from August 1998 to August 1999. Two hundred snails per sample were measured and size-frequency distributions (SFD) constructed. Data on reproductive periods, growth rates and shell sizes were estimated from comparisons of SFD diagrams along the year. Our results show that *H. parchappii* is able to develop permanent populations in brackish waters. The species exhibits a seasonal cycle of reproductive activity from spring to fall, with two main spawning peaks. Maximum growth rate takes place in fall, whereas it is lower during the rest of the year, and snails attain smaller sizes than in freshwater environments. These results may explain the great abundance of autochthonous concentrations of *H. parchappii* in past estuarine habitats from the same region.

Key words: *Heleobia parchappii*, reproductive period, growth rate, brackish water, Buenos Aires Province, Argentina.

INTRODUCTION

Heleobia parchappii (d'Orbigny, 1835) is a rissooidean snail that is very widespread in freshwater environments of Argentina, being particularly abundant in rivers, creeks, shallow lakes, ponds and streams of the Pampa Region (Gaillard & Castellanos, 1976; Castellanos & Landoni, 1995). In these freshwater habitats, the species has an annual cycle of reproductive activity with development direct to a benthic juvenile. Research on reproduction indicates that it displays a high natality rate towards the late spring and a minor peak in winter (Cazzaniga, 1981a). During this period, egg capsules are laid in the substratum and over shells of the same species (Cazzaniga, 1982). Snails occur on different substrata, such as submerged vegetation, pebbles, muds and serpulid reefs (Cazzaniga, 1981a, b; Darrigran, 1995; De Francesco & Isla, 2003). They are omnivorous, preferentially feeding on the epipelic diatoms, ostracodes, rotifers, ciliates and chironomid larvae associated to the periphyton (Cazzaniga, 1981b).

The genus *Heleobia* Stimpson, 1865, belongs to the family Cochliopidae Tryon, 1866, according to Wilke et al. (2001). However, this genus was included for many years in the worldwide family Hydrobiidae Troschel, 1857, and there are some authors who maintain that they should remain in this family (see Liu et al., 2001). Nevertheless, snails resemble hydrobiids in general features of head/foot and genitalia, as well as in distributional ecology and biology (De Francesco, 2002). For that reason and to avoid future taxonomic confusion, we use here the informal term hydrobioid (that groups all rissooidean snails) for general considerations (Kabat & Hershler, 1993), being clear that the studied snails may belong to either of these two rissooidean families.

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Heleobia parchappii is also found in abundance in holocene freshwater sequences of the Pampa Region, accompanied by other freshwater snails, such as *Chilina parchappii* (d'Orbigny, 1835), *Biomphalaria peregrina* (d'Orbigny, 1835), *B. tenagophila* (d'Orbigny, 1835), *Lymnaea viatrix* (d'Orbigny, 1835), and *Pomacea canaliculata* (Lamarck, 1822) (Ameghino, 1889; Frenguelli, 1945a, b; De Francesco & Prieto, 1999; Zárate et al., 1998). Although *H. parchappii* does not inhabit estuarine environments (De Francesco & Isla, 2003), it is commonly found in estuarine sequences outcropping along the southwestern Atlantic coast. Here, *H. parchappii* gives rise of extensive monospecific deposits (Isla et al., 1986; Farinati & Zavala, 1995; De Francesco & Zárate, 1999; De Francesco, 2002; Espinosa et al., 2003; De Francesco & Isla, 2003). Variations in stable isotope composition of these fossil shells suggested that *H. parchappii* may have been adapted in the past to wide salinity fluctuations as a consequence of the drying of small ponds (Bonadonna et al., 1995). Ecological studies, however, indicate that *H. parchappii* cannot settle permanent populations in mesohaline environments (Cazzaniga, 1982). In such conditions, size decreases and density fluctuates greatly (Cazzaniga, 1981a). These differences between the habitat of living and fossil snails have led to controversial interpretations and, elsewhere, to different paleoenvironmental reconstructions. In this regard, the good preservation, wide range of sizes and low fragmentation observed in *H. parchappii* fossil shells suggest autochthonous concentrations deposited under low energy estuarine conditions (Farinati & Zavala, 1995; De Francesco & Zárate, 1999; Espinosa et al., 2003). However, their presence in littoral marginal deposits where today they are absent leads some authors to interpret them as representing allochthonous material (Aguirre & Farinati, 2000; Aguirre & Urrutia, 2002) transported by currents from creek and river headwaters.

Fortunately, the finding in 1998 of an artificial canal with a high salinity content inhabited by *H. parchappii* provided an opportunity to analyse the reproductive biology and ecology of this species in this saline condition. In previous work (De Francesco & Isla, 2003), we observed that *H. parchappii* was present during the whole sampling period in this brackish

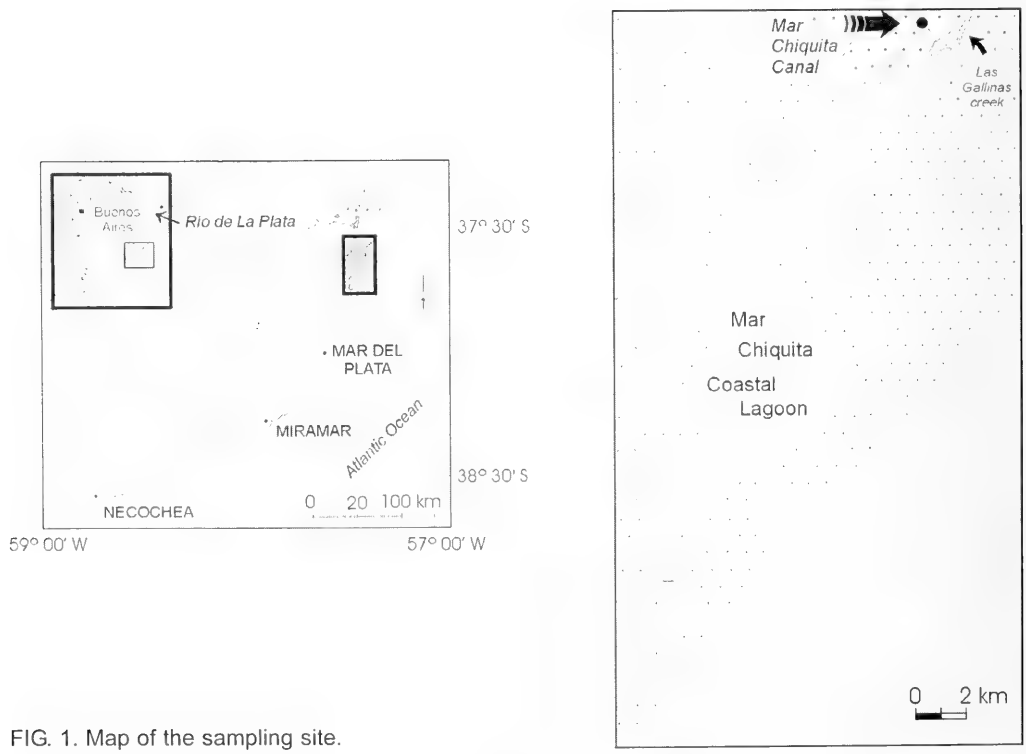

FIG. 1. Map of the sampling site.

canal at mean values between 17‰ and 23‰ (even up to 34‰), and pointed out that this species should be classed equally as a freshwater-brackish species. The purpose of this paper is to analyse in more detail the basic aspects of its life cycle in order to demonstrate the capacity of this species to tolerate and settle permanent populations in brackish waters.

MATERIAL AND METHODS

The brackish canal (37°31'07"S, 57°18'30"W) is located close to the mouth of the Las Gallinas creek (Fig. 1), a shallow stream that flows into the headwaters of the Mar Chiquita coastal lagoon, Buenos Aires Province. It is an artificial canal, approximately 1 m in depth and 3 m in width, characterised by a typical brackish fauna. Reef-like aggregates of the serpulid polychaete *Ficopomatus enigmaticus* (Ten Hove & Weerdenburg, 1978), crabs and shorebirds are among the most abundant organisms. Although the canal is located far from the marine influence, it is carved into holocene marine deposits (Fasano et al., 1982). Consequently, salinity remains relatively high, varying in relation to the balance between precipitation and evaporation in the area.

Snails were collected from reefs of *F. enigmaticus* using three replicate cores of 6 cm diameter x 11 cm height. Samples were sieved gently through 0.35 mm mesh (45 ASTM), and placed in plastic cups. All plastic cups were filled with water from the canal in order to keep snails alive for a correct taxonomic determination in the laboratory. Monthly collections were made from August 1998 to June 1999. Water temperature, salinity, pH, and dissolved oxygen at the time of sampling were also measured (De Francesco & Isla, 2003). In the laboratory, 200 snails per sample were measured under a Wild M5A stereoscopic microscope and size-frequency distributions (SFD) constructed. Total shell length (the distance from the apex to the anterior margin of the aperture) was used as an estimate of size. Estimation of reproductive periods, growth rates and shell sizes were made from comparisons of SFD diagrams during the year. Climatic conditions did not allow us to sample in September 1998 and February 1999. In addition, data on water temperature and salinity could not be recorded in March 1999 because the canal became dry. All specimens are housed in the Micropaleontology Laboratory of the Coastal Geology Research Centre (University of Mar del Plata).

Size-frequency distributions were analysed to recognise dominating size groups using the procedure described by MacDonald & Pitcher (1979). This analysis, termed MIX, uses initial estimates of the distribution mixture by maximum likelihood to find the best fit to the data assuming a normal distribution for each component. The program estimates the proportion of the mixture and the means and standard deviations of the component distributions, as well as the goodness of fit of the model to the data. Results from the MIX were employed to separate cohorts and follow cohort-specific growth. Growth pattern was determined by graphical analysis of the progression of detected components in successive SFD.

RESULTS

Monthly size-frequency distributions of snails fitted a normal distribution in August, November, December 1998, and January 1999, whereas they were bimodal during the rest of the year (Fig. 2). Three cohorts were detected (Table 1, Fig. 3A). The breeding period of *H. parchappii* took place from spring to fall (Figs. 2, 3A). Two main reproductive peaks were recorded, one in early spring and the other during the fall. Egg capsules, however, were present during the whole period, attached to shells of living specimens and over the reef surface. The second peak was more important, according to the higher abundance of youngest snails found (Fig. 2). Both peaks started at temperatures of 20°C and salinities between 20‰ and 22‰ (Fig. 3B). In general terms, temperature and salinity varied during the whole sampling period between 9.45°C and 26.25°C and 10.6‰ and 34‰, respectively (Fig. 3B). The pH was very basic, varying between 7.66 and 9.15 (De Francesco & Isla, 2003).

From August 1998 to January 1999 (late winter-summer) the growth rate of cohorts 1 and 2 was 0.40 mm month^{-1}. There was a period of minor growth between November and December (0.08 mm month^{-1}) that was only recorded in cohort 2 because of the disappearance of cohort 1. This growth trend correlated with the variation in water temperature (Fig. 3B). Significant growth was not recorded

between January and March 1999 (0.05 mm month^{-1}), which coincided with the local drought. After that, the growth rate of cohort 2 rose to the highest values of the cycle (0.52 mm month^{-1}) from March to May 1999 (fall). During the same period, the mean size of juveniles from cohort 3 decreased due to mortality. Finally, during the late fall and early winter, the growth rate of cohort 3 was low (0.085 mm month^{-1}), and the size of cohort 2 gradually decreased (mortality) (Fig. 3A). Size of adult snails varied between 2.11 ± 0.64 mm and 4.02 ± 0.82 mm (Table 1), which corresponded to specimens of 4 and 5 whorls (Fig. 4). The newly hatched snails found in October 1998 and March 1999 attained sizes between 0.65 ± 0.28 mm and 0.83 ± 0.62 mm (Table 1). Density of snails varied between 0.2 and 4.1 individuals per cm^3 during the year.

DISCUSSION

Our results show that *H. parchappii* is able to develop permanent populations in brackish waters with mean salinities between 17‰ and 23‰ during the year. In this circumstance, the species exhibits a seasonal cycle of reproductive activity from spring to fall, with two main spawning peaks. This reproductive pattern is very similar to that of the congeneric species *H. conexa* (Gaillard, 1974) found in Mar Chiquita coastal lagoon, which is mostly influenced by water temperature (De Francesco, 2002). Cazzaniga (1981a) found a similar reproductive pattern with two spawning peaks in *H. parchappii* from freshwater environments of the southern Buenos Aires Province. This similarity observed in life cycles under different saline conditions invites some speculation about the relative importance of this factor in

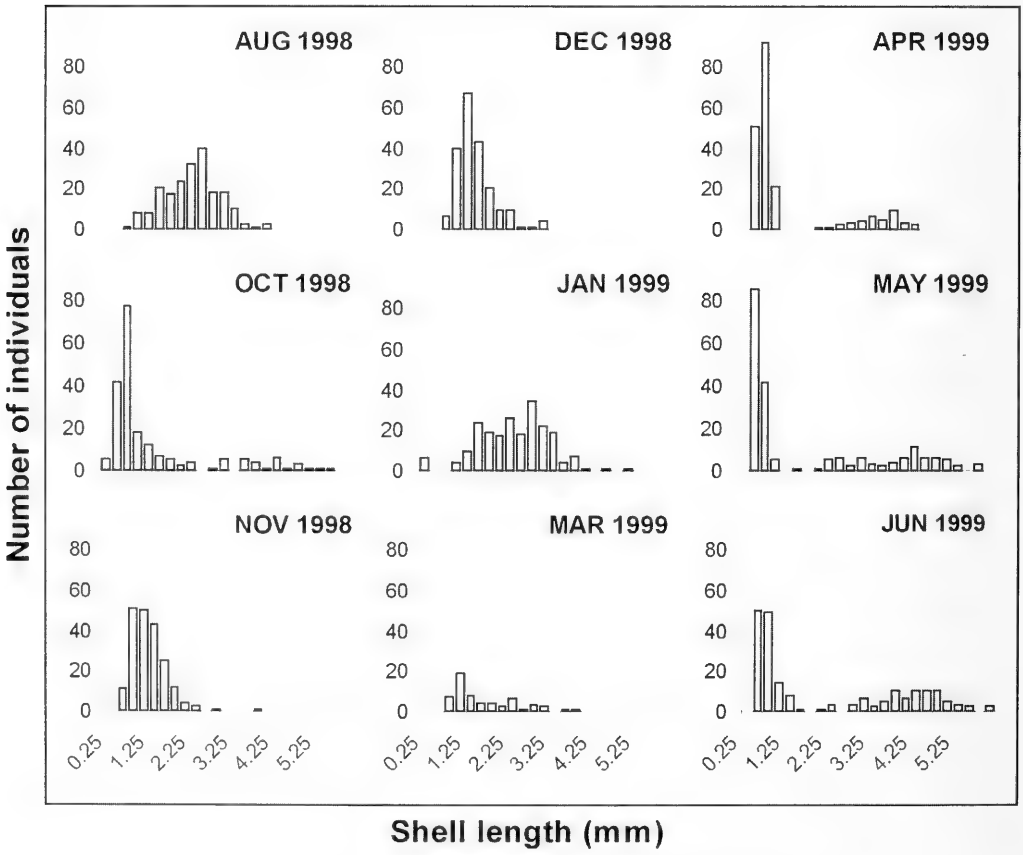

FIG. 2. Size-frequency distributions of *Heleobia parchappii* in the Mar Chiquita canal.

TABLE 1. Mean shell length, standard deviation and proportion of each cohort of *Heleobia parchappii* by month in the Mar Chiquita canal based upon MIX analysis of percent size-frequency histograms (Prop = proportion of a component, SL = mean shell length, SD = standard deviation, X^2 = goodness-of-fit test between observed and expected, df = degrees of freedom, p = significance level for goodness-of-fit test).

	Cohort 1			Cohort 2			Cohort 3						
Month	Prop	SL	SD	Prop	SL	SD	Prop	SL	SD	X^2	df	n	p
Aug 1998	1.00	2.11	0.64		-			-		6.13	4	200	0.19
Oct	0.23	2.95	1.39	0.77	0.65	0.28		-		4.43	5	200	0.49
Nov		-		1.00	1.05	0.38		-		8.32	6	200	0.22
Dec		-		1.00	1.21	0.29		-		9.66	4	200	0.05
Jan 1999		-		1.00	2.28	0.70		-		12.80	5	200	0.03
Mar		-		0.25	2.47	0.57	0.75	0.83	0.62	1.54	2	200	0.46
Apr		-		0.16	3.27	0.55	0.84	0.66	0.28	2.39	3	200	0.50
May		-		0.30	4.02	0.82	0.70	0.40	0.30	3.83	6	200	0.70
Jun		-		0.39	3.98	0.85	0.61	0.57	0.30	5.73	6	200	0.45

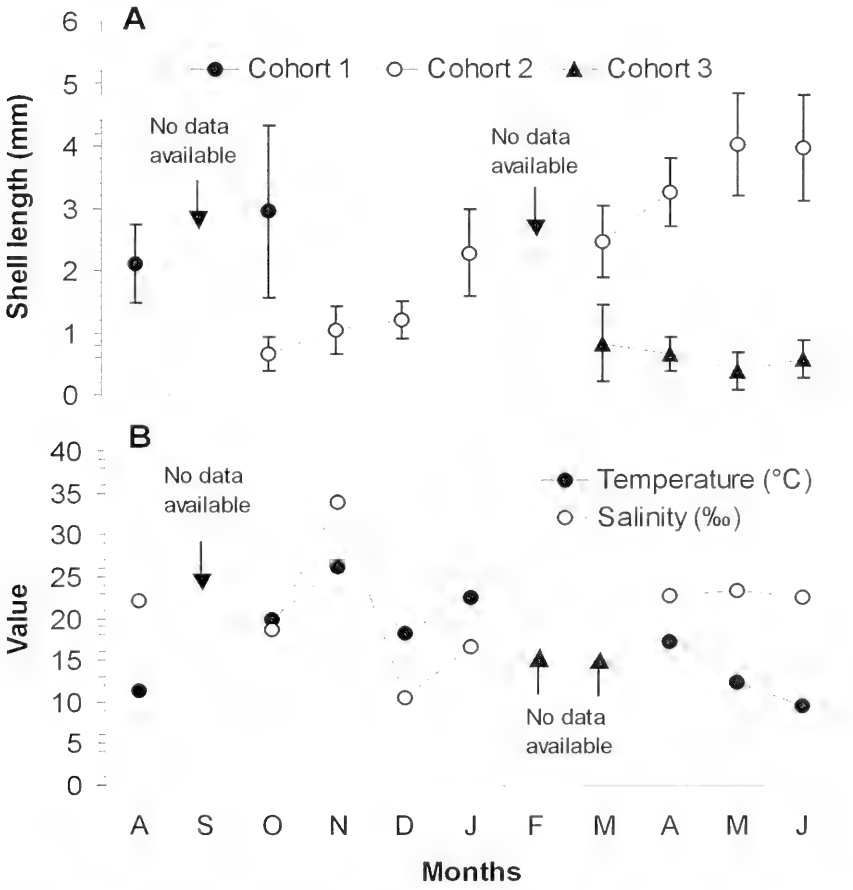

FIG. 3A. Mean shell length and standard deviation from Table 1 of each component of all samples during the sampling period (August 1998–June 1999) based upon MIX analysis of percent size-frequency histograms. B: Annual distribution of temperature and salinity in the Mar Chiquita canal.

conditioning the reproductive activity of snails. Cazzaniga (1982) pointed out that *H. parchappii* experiences a marked fluctuation in density, an unstable size structure and high abundance of young snails in mesohaline environments. In the Mar Chiquita brackish canal, we found that even though the density fluctuates greatly, the size structure remains relatively stable and cohorts can be followed monthly during the year. Thus, it appears that salinity does not have a marked influence on the reproductive activity of *H. parchappii* but does affect population structure.

Cazzaniga (1982) found that sizes between 2.5 mm and 4.1 mm corresponded to pre-reproductive subadults (4 whorls), while adults ranged between 4.1 mm and 5.5 mm (5–6 whorls). The adult snails from the brackish canal show shell sizes that resemble those of pre-reproductive subadults, whereas they coincide with adults in whorl number. These results demonstrate that snails from the brackish canal attain smaller sizes than those found in freshwater environments from the southern Buenos Aires Province. This effect could be related to the influence of the higher salinity content present in the canal. Salinity has been shown to be a key environmental variable controlling the growth and distribution of hydrobioid gastropods in northern Europe. Here, snails inhabiting brackish water reached sexual maturity at a smaller size than those living in fresh water (Forbes, 1991; Jacobsen & Forbes, 1997).

Heleobia parchappii appears to follow a special strategy in the unstable environment of Mar Chiquita canal. It is adapted to drastic environmental fluctuations, such as drying events. It can be seen from the analysis of cohorts that the size structure was not significantly altered by the drying event recorded in February–March 1999. Snails only showed a temporary growth cessation but continued their natural growth after the canal flooded again. It has been seen that snails can remain in an inactive condition in stressed environments for up to a month (De Francesco, unpublished data). Probably, snails remained quiescent among the reef tubes (reefs retain humidity) during the drying period but rapidly

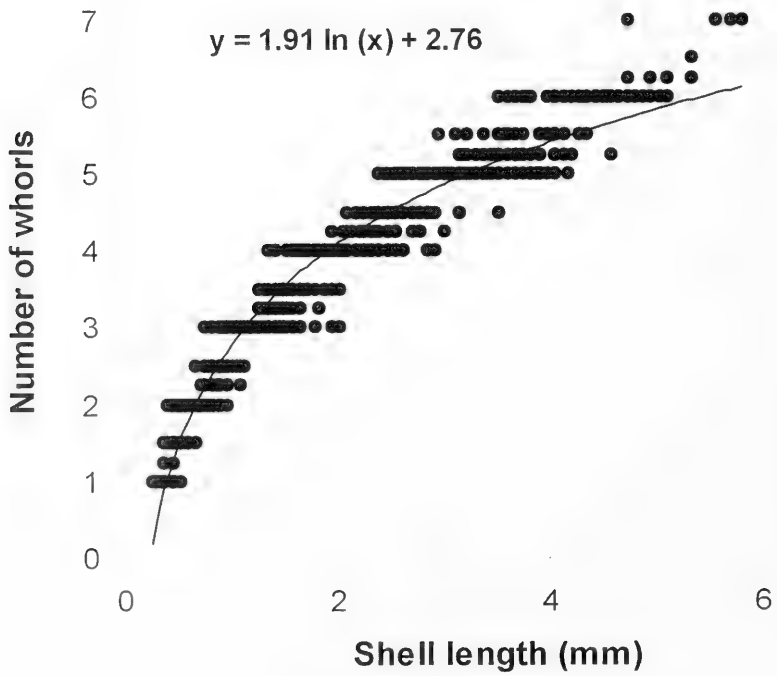

FIG. 4. Scatter diagram for the number of whorls and shell length of *Heleobia parchappii* in the Mar Chiquita canal.

spread as soon as climatic conditions became favourable.

The tolerance of *H. parchappii* to waters with high salinity content may explain the great abundance of autochthonous fossil concentrations of this species found in coastal outcrops on the southeastern Buenos Aires Province (Farinati & Zavala, 1995; De Francesco & Zárate, 1999; De Francesco, 2002; Espinosa et al., 2003). The reason why *H. parchappi* actually occurs only in freshwater environments far away from the marine influence cannot at present be explained. One likely factor in the modern restriction of *H. parchappii* to freshwater habitats is the interspecific competition with *H. conexa.* This species actually inhabits coastal environments similar to those occupied by *H. parchappii* during the Holocene. However, *H. conexa* was not present in this area in the past (De Francesco & Zárate, 1999; De Francesco, 2002), and that probably facilitated the access of the opportunistic *H. parchappii* to estuarine environments. There is evidence that interspecific competition significantly affects the distribution pattern of estuarine hydrobioids mostly in coastal lagoons (Fenchel & Kofoed, 1976; Cherril & James, 1987; Gorbushin, 1996; Grudemo & Bohlin, 2000; Barnes, 1999, among others).

Although it is not possible to consider the generality of the ideas presented in this study with the scattered observations presented here, these data indicate that *H. parchappii* has, in at least some situations, the capability to tolerate and sustain stable populations in environments with high salinity (up to 34‰) in spite of the fact that it generally occurs in freshwater environments. These results demonstrate a greater tolerance than is usually assumed for this species, with important consequences for the reconstruction of past environments.

ACKNOWLEDGEMENTS

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FIRST REPORT OF A TERRESTRIAL SLUG (*ARION FASCIATUS*) LIVING IN AN AQUATIC HABITAT

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The banded slug, *Arion fasciatus* (Nilsson, 1823), was introduced into North America from Europe (Chichester & Getz, 1969), where it is commonly found in damp areas and wet meadows adjacent to streams (Pfleger & Chatfield, 1988). Although best known as farm and garden pests, slugs occupy a variety of habitats, often playing a beneficial role similar to that of many terrestrial snails in the decomposition of forest litter (Mason, 1974; Petersen & Luxton, 1982). In fact, slugs are commonly described as "snails without shells", an appropriate moniker given that they often replace ecologically similar species of snails in habitats with insufficient supplies of calcium for shell formation (Barnes, 1987).

Although there are a number of freshwater pulmonate snails, most of these must come to the surface to obtain air for respiration (Barnes, 1987). Kinzie (1992), however, observed the predaceous snail *Euglandina rosea* (Férussac) immersed in Hawaiian streams and documented them feeding on aquatic snails in the laboratory. Furthermore, several species of deep-water lymnaeid snails appear to have abandoned air breathing entirely, filling the mantle cavity with water, and a few have even evolved a secondary gill (pseudobranch) that consists of series of folds of the mantle near the pneumostome (Pennak, 1953; Barnes, 1987). While the ability of an air-breathing pulmonate to survive underwater was confirmed by Lowell & Carriker (1946) in an experiment in which 20 generations of the pond snail *Lymnaea stagnalis appressa* were raised entirely under water, no species of *terrestrial* slug has ever been recorded as living in freshwater. However, Rollo & Shibata (1991) did find some individuals of the slug *Deroceras leave* Müller submerged on the underside of floating logs in a flooded wetland.

We have observed *A. fasciatus* at three different sites in the headwaters of Spring Coulee Creek and at one site in the headwaters of nearby Poplar Creek, all of which are near the village of Coon Valley (43°40'N, 90°54'W), Vernon County, Wisconsin. The majority of our observations of *A. fasciatus* living in the aquatic habitat are from a single, 2 m^2 riffle site in the upper reaches of Spring Coulee Creek (USCC). These coldwater streams, which are perennial and remain ice-free during the winter, are located in the Driftless Area of southwest Wisconsin, a region that was not covered with ice during the latest period of Pleistocene glaciation.

Although at first we thought that these aquatic slugs might belong to an undescribed species, dissection of the reproductive tract by J.B. Burch of the Mollusk Division of the University of Michigan Museum of Zoology showed them to be *A. fasciatus*. Voucher specimens have been deposited in the University of Michigan Museum of Zoology (UMMZ 300110). This taxonomy was supported by genetic analysis of PCR amplified DNA from the mitochondrial cytochrome c oxidase subunit I gene (GenBank accession number AY321295), which showed that all 584 bases matched perfectly with those previously described for two specimens of *A. fasciatus* (GenBank accession numbers: AY094598 from Lithuania and AF239735 from Georgia, USA).

Slugs at the USCC site were checked at least quarterly since being discovered in 1996 by the first author (RJH). *Arion fasciatus* (normally 15–30 individuals) are observed at USCC throughout the year, although casual observations suggest that slug densities decline during the winter. Annual water temperature fluctuation at this site is very small (~1C°), with temperatures between 9–10°C (Deuschle, 2001). Current velocities in this riffle are moderate and stable throughout the year (mean ± SD = 24.4 ± 7.7 cm/s) (Deuschle, 2001). Dissolved oxygen concentrations in midsummer average 10.56 ± 0.09 mg O_2/l. We believe the USCC site is well aerated throughout the year; brook trout (*Salvelinus fontinalis*) and slimy sculpin (*Cottus cognatus*), two fish that require high dissolved oxygen tensions, are commonly observed. Slugs were observed at depths between 0.5–

10 cm. We have observed both adults and juveniles of all sizes (total body length range: 0.7–6 cm), suggesting that these slugs may complete their life cycles within this stream system. Although we have not yet searched for eggs in the stream, experiments done by Rollo & Shibata (1991) revealed that the eggs of some slug species have a high hatching success when reared underwater.

Sites where slugs have been observed are, with one exception, always beneath shaded highway bridges, and no specimens have been seen in locations exposed to direct sunlight. Individuals occur on submerged rocks as well as sand substrata in gently flowing water. From the grazing trails we observed, the slugs appear to be feeding on periphyton growing on rocks and fallen leaves. We have not observed slugs on the stream bank or in the adjacent woods, although several individuals were seen on rocks partially submerged at the water-air interface. Specimens brought into the laboratory and placed in an experimental flume (Vogel & La Barbera, 1978) have survived over two weeks entirely submerged (until removed for histological examination) and made no attempts during this time to climb onto the sides of the flume or rocks that projected above the water line. Slugs maintained for several days in a plastic jug, however, left the water within 12 h of capture and climbed onto the sides of the container, suggesting that the ability to remain submerged is dependent on a continuous supply of flowing, well-oxygenated water.

These findings run counter to the long-standing presumption that pulmonate slugs are entirely terrestrial. In spite of an extensive literature search, we cannot find a single reference that suggest otherwise, nor are any of the authorities in the field with whom we have spoken aware of a terrestrial slug living in water. As such, this population of stream-dwelling slugs poses a number of interesting questions that remain to be studied in more detail.

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POPULATION STRUCTURE IN *DREPANOTREMA KERMATOIDES* AND *D. CIMEX* (GASTROPODA, PLANORBIDAE) IN NATURAL CONDITIONS

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ABSTRACT

Drepanotrema kermatoides and *D. cimex* are present in the Multiple Use Natural Reserve "Isla Martín García", Argentina. Although these species are endemic to the Neotropical Region, their biology and ecology have been little studied. The purpose of this study was to analyze the main demographic trends of *Drepanotrema* in different seasons under natural conditions. Relative abundance and population structure in nature were compared. Seasonal samples were taken from six environments between 1995 and 1997. Each species was found in three different environments. *Drepanotrema kermatoides* was more abundant in The Stream and *D. cimex* in Tank Quarry. From the population structure observation, we found that the dominant class corresponded to individuals at the onset of reproduction.

Key words: demography, Planorbidae, *Drepanotrema*, Río de la Plata Basin.

INTRODUCTION

The planorbid genus *Drepanotrema* is endemic to the Neotropical Region and includes nine species, with six found in Argentina: *D. anatinum* (d'Orbigny, 1835), *D. cimex* (Moricand, 1839), *D. depressissimum* (Moricand, 1839), *D. heloicum* (d'Orbigny, 1835), *D. kermatoides* (d'Orbigny, 1835), and *D. lucidum* (Pfeiffer, 1839). While they are abundant, their biology and ecology have been scarcely studied (Bonetto et al., 1990; Rumi, 1991; Hamman et al., 1993; Rumi et al., 1997), and their morphology and classification have not received as much attention as have those of other planorbids, especially species of *Biomphalaria*, which are important for human health.

The purpose of this study was to analyze the main demographic trends shown by *Drepanotrema* in natural conditions in the different habitats and seasons by analyzing changes in relative abundances and population structure.

The study was conducted in the Multiple Use Natural Reserve "Isla Martín García" (IMG), Argentina, where intensive biodiversity research has already been conducted (Lahitte & Hurrell, 1988, 1994; Rumi et al., 1996; Armendáriz et al., 2000; Armendáriz & Cesar, 2001). Freshwater gastropods found in the IMG include species of Ampullariidae, Hydrobiidae, Physidae, Chilinidae, Ancylidae, and Planorbidae. The Planorbidae are represented by the genera *Biomphalaria* Preston, 1910; *Antillorbis* Harry & Hubendick, 1963; and *Drepanotrema* Fischer & Crosse, 1880 (Rumi et al., 1996).

MATERIALS AND METHODS

The IMG is located in the Upper Río de la Plata, south of the mouth of the Uruguay River (34°11'25"S; 58°15'38"W) (Fig. 1). It is the only island in the Río de la Plata system that constitutes an outcrop of the Brazilian massif of Precambrian crystalline basement rocks. The

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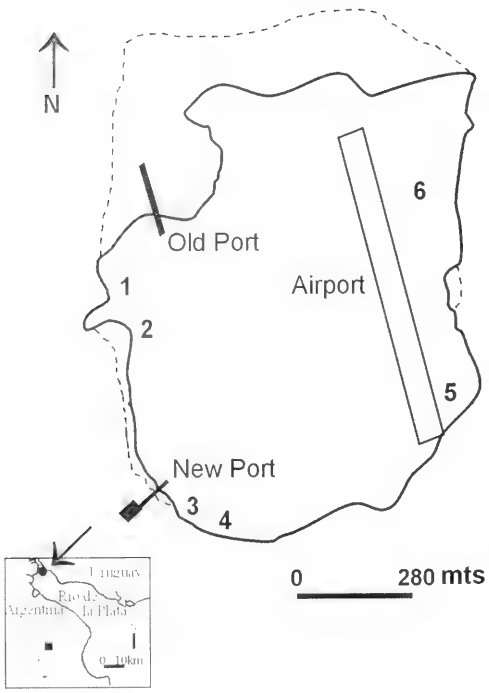

FIG. 1. Isla Martín García map with sampling stations: 1. Rubbish Quarry; 2. Tank Quarry; 3. Big Quarry; 4. Buoy Quarry; 5. The Stream and 6. Intangible Zone.

other deltaic islands are sedimentary. Eight seasonal samplings were carried out between the summer of 1995 and the autumn of 1997 in six environments (Fig. 1). One of them, the Stream is small and drains into coastal pools. It had a depth of no more than 1 m, and a dominant floating plant carpet, especially of *Pistia stratiotes* and *Salvinia biloba*. Another four stations sampled, the quarries used for mineral exploitation of the crystalline basement rock many years ago are now artificial ponds. Except for the Rubbish Quarry (named by local inhabitants because it is close to a garbage dump), they were covered by carpets of free-floating macrophytes, especially the Lemnaceae species, *Salvinia biloba*, *S. minima*, *Azolla filiculoides*, *Limnobium laevigatum*, and *Pistia stratiotes*. The quarries showed strong eutrophication and desiccation in summer. Finally, the Intangible Zone (restricted area) is a flooded sector, which is frequently devoid of water. *Iris pseudacorus* was dominant and surrounded by a xerophylous forest.

Snails were collected in the littoral zone of the stations using sieves of 15 cm diameter and 0.14 mm mesh size. Snail relative abundance was calculated as captures per unit effort (CPUE), that is, specimens/30 min/person. Maximum shell diameter of all specimens was measured with calipers to 0.02 mm precision. For graphic representation of seasonal population structure for each species and environment, numbers of individuals in each 1 mm size class were used. To estimate class differences of each season among the years, the Student's "t" test (two means of matching samples; two tales) was employed. If the obtained differences were not significant, the mean value for each class was used. In cases when the abundance was lower than the number of classes considered, the sample was not taken into account.

RESULTS

Two species were recorded: *Drepanotrema kermatoides* and *D. cimex* (Fig. 2).

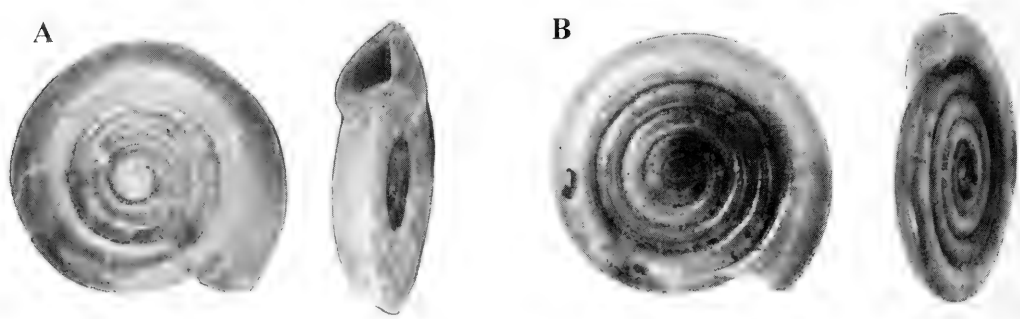

FIG. 2. Dorsal and lateral view of shells of A. *Drepanotrema kermatoides*, diameter = 5.40 mm, and B. *D. cimex*, diameter = 5.25 mm.

TABLE 1. *Drepanotrema kermatoides*. Mean estimations of snail abundance by season and habitat. (-): without samples; N: number of considered seasons. *same value for N register.

	Intangible Zone			Big Quarry			Stream		
	Mean	Range	N	Mean	Range	N	Mean	Range	N
Summer	0	0	3	18.33	0–55	3	314	314*	2
Autumn	24	0–48	2	4.5	0–9	2	36	-	1
Winter	-	-	-	0	-	1	-	-	-
Spring	27.5	5–50	2	53	4–102	2	177.5	59–296	2

Drepanotrema kermatoides (Table 1, Fig. 3): This species inhabited three very different environments. Big Quarry (the largest on the island), despite water-level fluctuations, had sufficient water to maintain snail populations. However, during most of the year, very low densities were recorded. They were somewhat higher in the spring. Considering population structure, adults between 4 and 6 mm predominated. The Stream had, in summer, the most abundant population numbers, in spite of high fluctuations. In cases in which the population structure/season was compared among different years, the results did not show significant differences: summer1995/1997: $t = 0$, $df = 8$, $P > 0.05$ and spring: $t = 2.24$, $df = 8$, $P > 0.05$. Juveniles occurred almost year round. Finally, the Intangible Zone maintained a very low population level. As in Big Quarry, there was a greater representation of adults.

Drepanotrema cimex (Table 2, Fig. 4): Populations of this species were found in three quarries: Tank, Rubbish and Buoy. As with *D. kermatoides*, abundances varied widely. The Tank Quarry showed the most abundant and seasonally stable population. The highest abundance of individuals was

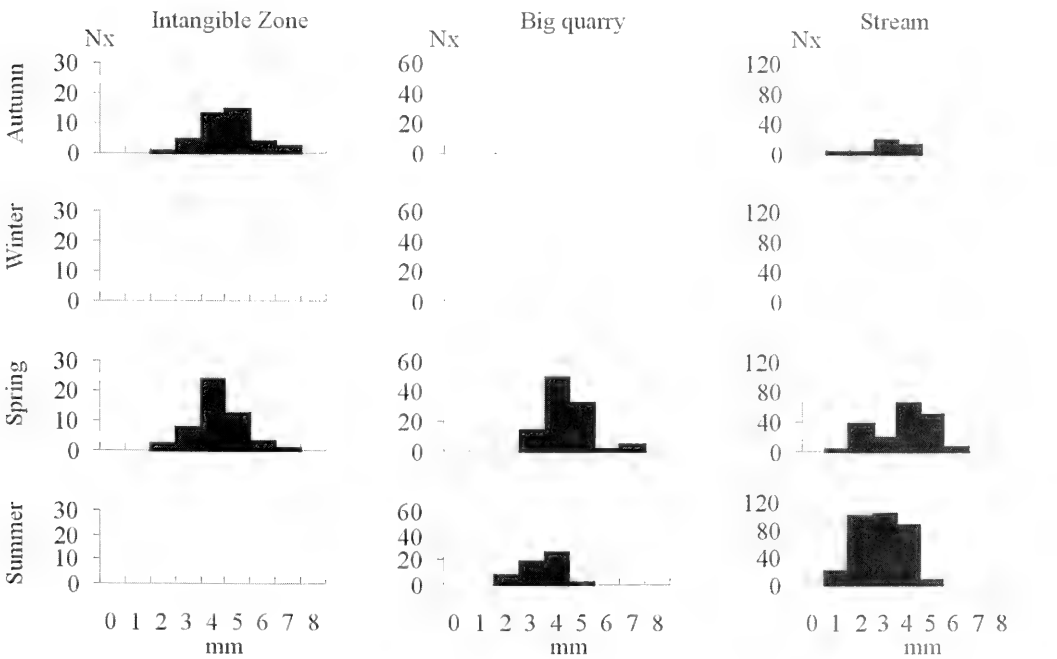

FIG. 3. *Drepanotrema kermatoides*. Population structures by season.

TABLE 2. *Drepanotrema cimex*. Mean estimations of snail abundance by season and habitat. (-): without samples; N: number of considered seasons.

	Tank Quarry			Rubbish Quarry			Buoy Quarry		
	Mean	Range	N	Mean	Range	N	Mean	Range	N
Summer	497	52–942	2	23.33	0–69	3	-	-	-
Autumn	392	0–784	2	184.5	1–386	2	-	-	-
Winter	276	-	1	74	-	1	-	-	-
Spring	86	50–122	2	26.5	4–49	2	52	-	1

observed in summer, decreasing slowly towards the spring. Population structure/season did not differ significantly among different years: summer 1996/1997 $t = 1.86$, $df = 8$, $P > 0.05$ and spring: $t = 0.81$, $df = 8$, $P > 0.05$. Although adult sizes dominated, all juvenile sizes were represented. At the Rubbish Quarry, densities were lower than at the Tank Quarry, with *D. cimex* more abundant in autumn. In 1995, the population was well represented all year. However, in the summer 1996, the quarry dried out and the abundance become very low. The population did not recover. Adults and juveniles, although in a lower proportion, were represented. The Buoy Quarry (called that because of a large red marine buoy half sunken in the center), only sampled in the spring 1996, showed a medium abundance with all sizes represented.

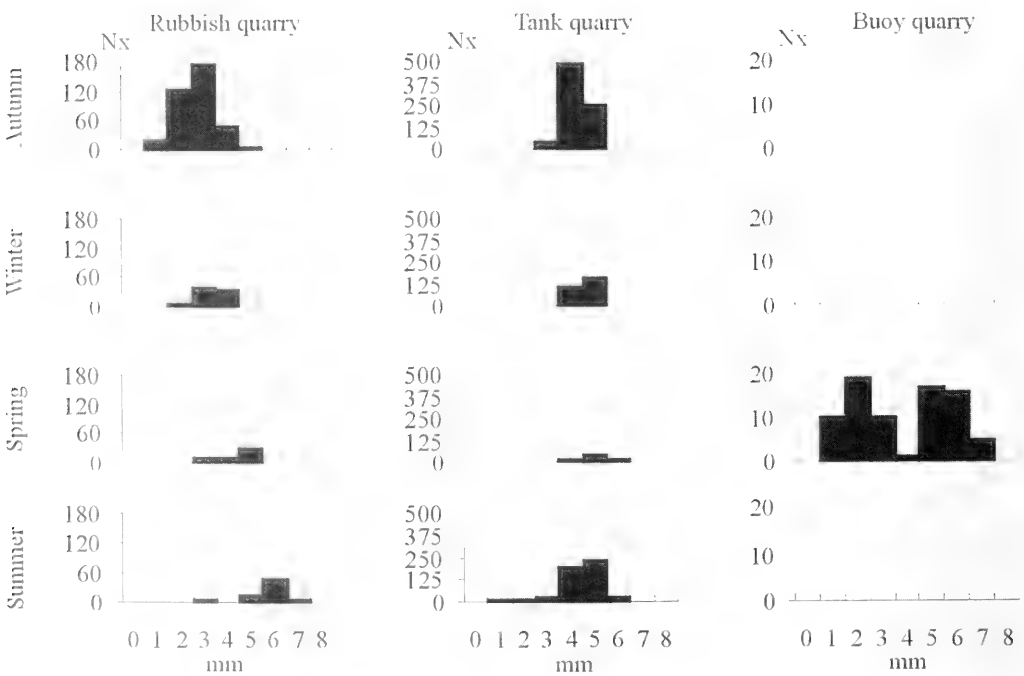

FIG. 4. *Drepanotrema cimex*. Population structures by season.

DISCUSSION

Drepanotrema kermatoides was most abundant at spring and summer in The Stream. This abundance was associated with The Stream's shallow depth and proximity to the river, which backed up into the stream during floods (because of the strong SE winds, mainly in winter), thus favoring the migratory movements of snails, and causing high fluctuations in abundance. By contrast, in the Intangible Zone abundance was very low. This could be due to the fact that this environment during dry seasons suffered total desiccation in summers and autumn 1997 when only empty shells were detected. Recruitment between spring and summer was drastically reduced because of the desiccation effects and negating recovery of population size. The Big Quarry (the largest on the island) with its surface totally covered by carpets of free floating macrophytes, had the lowest snail abundance. This was apparently due to the summer 1995, when the quarry had considerable plant decay, mainly produced by macrophytes, resulting in near anoxia (0.2 mg/l), with high concentrations of soluble reactive phosphorus (SRP) (1,086 µg/l), ammonium (338 µg/l) and organic matter (13 mg/l), and with low concentration of nitrates (7 µg/l).

Drepanotrema cimex was most abundant throughout the sampling periods, especially between summer and autumn. The Tank Quarry showed the most abundant and seasonally stable population. Only once, in autumn 1997, was there a strong desiccation event.

From the observation of population structure relative to size (Figs. 3, 4), we found that the dominant classes (3 to 5 mm) corresponded to the onset of reproduction. In general, *Drepanotrema* species showed the greatest recruitment in autumn and spring. These results agree with reproductive strategies found in other freshwater mollusks in these areas of Argentina (Hamann et al., 1993; Rumi, 1993).

The population structure (Fig. 4) in Buoy Quarry, although having only one sample, seemed to have two cohorts. One presumably originated in autumn (according to the size) and another, of adult individuals in their last growth stages, perhaps carried over from the previous year. Thus, it can be inferred that longevity of this species would exceed one year in natural conditions. Other observations of the Planorbidae (e.g., *Biomphalaria peregrina* (d'Orbigny, 1835)), have also indicated longevities of two years, although under laboratory conditions (Rumi, 1993).

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Taxa in **bold** are new; pages in *italic* indicate figures of taxa.

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