

# THE *HELICINA UMBONATA* COMPLEX IN THE WEST INDIES (GASTROPODA, PROSOBRANCHIA, HELICINIDAE)

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**ABSTRACT:** The *umbonata* species group is placed in *Helicina* (s.s.) because of characteristics of the radula and embryonic shell sculpture. The group consists of five taxa: *H. u. umbonata* Shuttleworth, *H. u. pitheca*, new subspecies, *H. liobasis* new species, *H. dominicensis* Pfeiffer, and *H. rhips* new species. The latter three species occur on Hispaniola, *H. u. umbonata* on Puerto Rico, and *H. u. pitheca* on Mona Island.

Foraging specialization and habitat selection are discussed as the basis for evolution within the Helicinidae.

**SUMARIO:** El grupo de especies *umbonata* es incluida en el género *Helicina* (s. s.) por las características de la rádula y la escultura de la concha embrionica. El grupo consiste de cinco taxa: *H. u. umbonata* Shuttleworth, *H. u. pitheca* n. sub sp., *H. liobasis* n. sp., *H. dominicensis* Pfeiffer y *H. rhips* n. sp., Las tres últimas especies ocurren en la Isla Hispaniola, *H. u. umbonata* en Puerto Rico y *H. u. pitheca* en la Isla Mona.

La especialización de forage y la selección de habitat son discutidas como bases para la evolución dentro de la familia Helicinidae.

## TABLE OF CONTENTS

PROLOGUE .....	2
ACKNOWLEDGEMENTS .....	2
INTRODUCTION .....	2
HISTORICAL ACCOUNT .....	2
ADAPTIVE RADIATION WITHIN THE HELICINIDAE .....	5
GENERIC RELATIONSHIPS OF THE <i>UMBONATA</i> SPECIES GROUP .....	5
Characters of the <i>umbonata</i> group .....	7
Comparisons with <i>Helicina</i> .....	9
Comparisons with <i>Lucidella</i> (s. s.) .....	9
Comparisons with <i>Lucidella</i> ( <i>Poenia</i> ) .....	9
Comparisons with <i>Alcadia</i> .....	9
Generic relationships .....	10
ECOLOGICAL DEPLOYMENT OF THE <i>UMBONATA</i> SPECIES GROUP .....	11
SPECIFIC RELATIONSHIPS .....	11
SYSTEMATICS OF THE <i>UMBONATA</i> SPECIES GROUP .....	12
<i>Helicina u. umbonata</i> SHUTTLEWORTH .....	12
<i>Helicina umbonata pitheca</i> NEW SUBSPECIES .....	15
<i>Helicina liobasis</i> NEW SPECIES .....	17
<i>Helicina dominicensis</i> PFEIFFER .....	19
<i>Helicina rhips</i> NEW SPECIES .....	21
LITERATURE CITED .....	23

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## PROLOGUE

In May 1974 Howard W. Campbell initiated a study to assess the potential environmental impact of proposed economic developments on Mona Island. A survey of the land snail fauna was made by Campbell and the author. The molluscan fauna had been summarized (Clench 1951), but some taxonomic problems remained to be resolved. One was the generic relationships of the helicinid land snail known as *Lucidella umbonata* (Shuttleworth). The following year a similar trip was organized by Campbell to Saona Island and the adjacent mainland of Hispaniola. Another species of helicinid was discovered that is closely related to *umbonata*. Additional field work in Puerto Rico and Hispaniola yielded critical material that resolves the systematics of *umbonata* and related species. This paper is dedicated to Dr. Howard W. Campbell, who was instrumental in much of my field work in Middle America and the United States. He shall be remembered for his companionship on many field trips and the close friendship I enjoyed since we first met.

## ACKNOWLEDGEMENTS

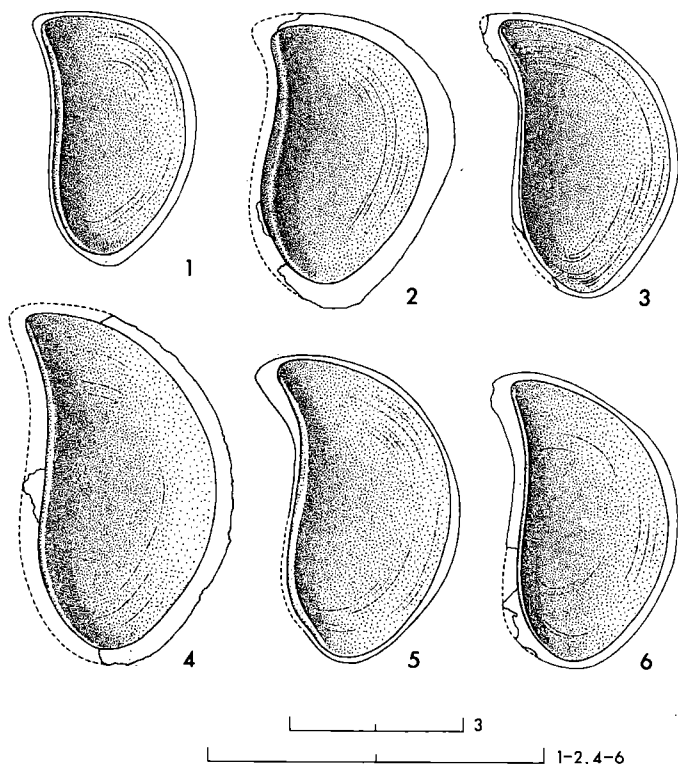
Field work relevant to this study on Puerto Rico and Mona Island was supported, in part, by contracts 14-16-0088-785 and 85911-1400-906-01 from the U.S. Fish and Wildlife Service. Field work on Hispaniola was supported, in part, by National Geographic Society Research Grant No. 1541. I am grateful to the officials of both organizations for the support they have rendered to me. Figures 8-29 were made on a HITACHI S-415-A Scanning Electron Microscope in the Department of Zoology, University of Florida. The following individuals assisted me in the field: Steven P. Christman, Ronald I. Crombie, Richard Franz, Roy W. McDiarmid, and, of course, Howard W. Campbell.

## INTRODUCTION

## HISTORICAL ACCOUNT

This paper concerns a group of moderate-sized operculate land snails of the family Helicinidae that occurs on Puerto Rico, Hispaniola (Fig. 7), and small islands in between. Two are known species. Two others and a subspecies are described as new. Over the years the known species have been shuffled among various genera on the basis of limited data on the shell and operculum. The discovery of the new taxa on Hispaniola and Mona Island requires a reexamination of the others in order to resolve questions about systematic relationships. New data based on embryonic shell sculpture and the radula demonstrate the close relationships among the species and that their generic affinities are different than previously thought.

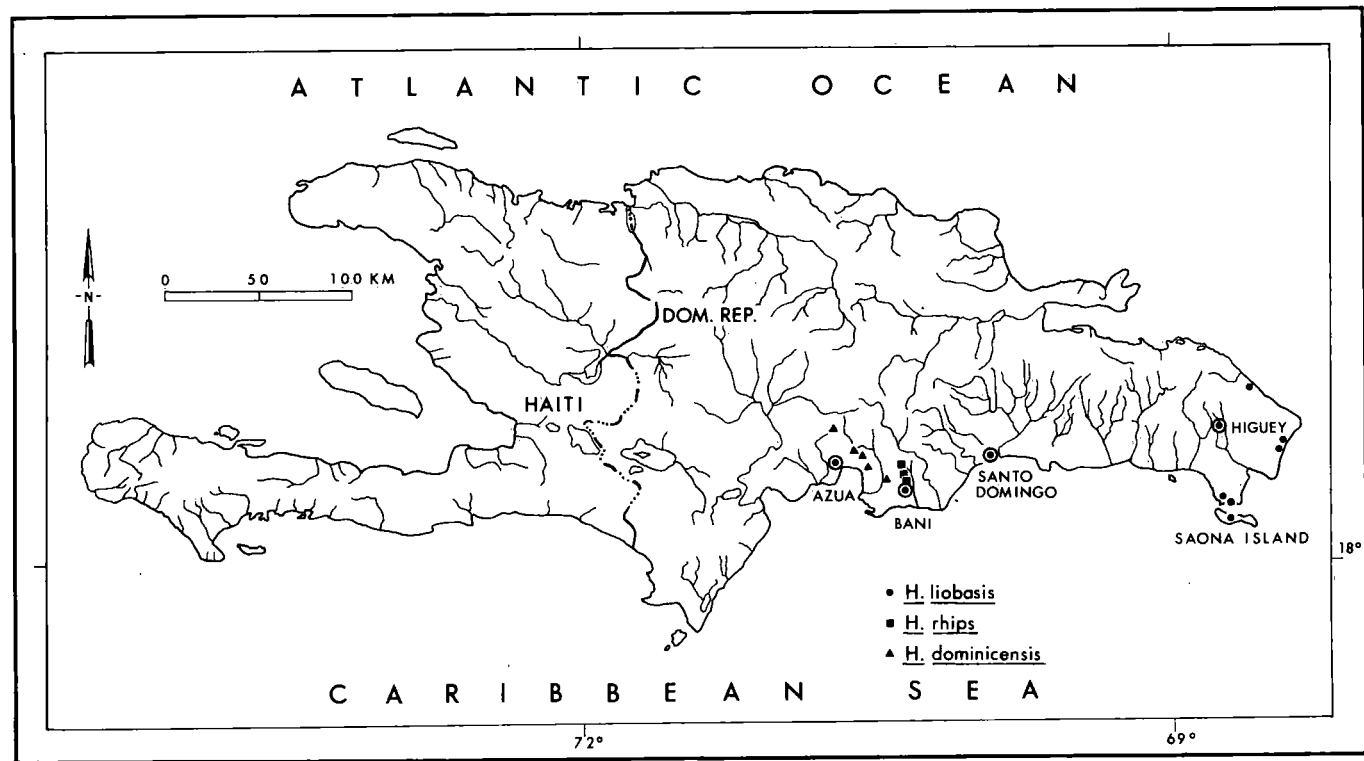
The two known species are *Helicina umbonata* Shuttleworth and *Helicina dominicensis* Pfeiffer 1851. Both were described on the basis of shell and opercular characteristics. Details of the embryonic shell sculpture were not noted, because such data were not utilized in helicinid systematics until now. The radula of neither species had been described.



FIGURES 1-6. — Opercula of *Helicina*. 1 — *H. u. umbonata* Sh. (UF 23139); 2 — *H. u. pitheca* n. ssp. (UF 24064); 3 — *H. rhyps* n. sp., paratype (UF 23234); 4 — *H. dominicensis* Pfr. (UF 23549); 5 — *H. liobasis* n. sp., paratype (UF 25264); 6 — *H. liobasis* n. sp. (UF 25266). Scales equal 2 mm.

*H. umbonata* is a common Puerto Rican snail that has long been familiar to malacologists. Its shell was figured twice (Wagner 1911, van der Schalie 1948), and it is well represented in museum collections. On no occasion has it been misidentified in the literature, nor has any other species been mistaken for it. Wagner (1911:355), in his monograph of the Helicinidae, placed *umbonata* in *Lucidella* because of similar shape and postembryonic shell sculpture to the Jamaican *L. aureola* (Ferrusac), the type species of *Lucidella*. Most subsequent authors followed Wagner. Baker (1962:17) placed *umbonata* in *Lucidella*, subgenus *Poenia* without comment. The present study demonstrates the close relationship of *umbonata* to *Helicina* (s. s.) and not to *Lucidella* (s. l.).

*H. dominicensis* is less well known. It was mentioned only thrice since its original description. Wagner (1911:340) placed *dominicensis* in *Alcadia* on the basis of its operculum. This study demonstrates that *dominicensis* is not related to *Alcadia* but to *Helicina* (s. s.).

FIGURE 7. — Distribution of the *Helicina umbonata* group on Hispaniola.

#### ADAPTIVE RADIATION WITHIN THE HELICINIDAE

Helicinids are anatomically conservative (Baker 1925, 1926; Thompson 1968, 1980). Complex reproductive organs and pallial structures evolved as adaptations for a terrestrial existence, but once they evolved very little differentiation of these organs and structures occurred with further radiation of subfamilies and genera. Subsequent radiation centered about trophic specialization and habitat selection (Thompson 1980). Thus, the most significant morphological features reflecting phylogeny *within* the family are foraging structures that evolved around trophic specialization and external structures that are adaptable to habitat selection. The former involves the radula. The latter involves the shell and operculum.

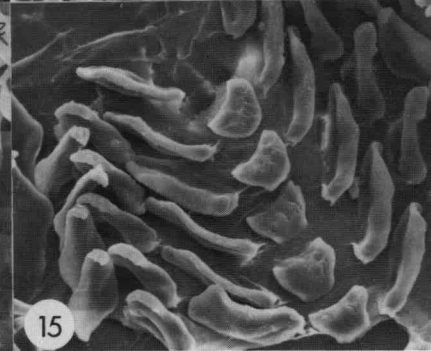
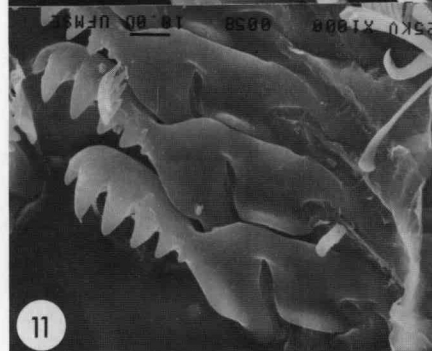
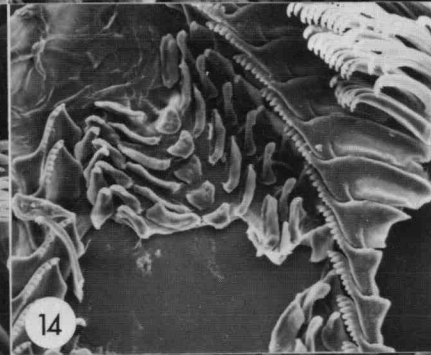
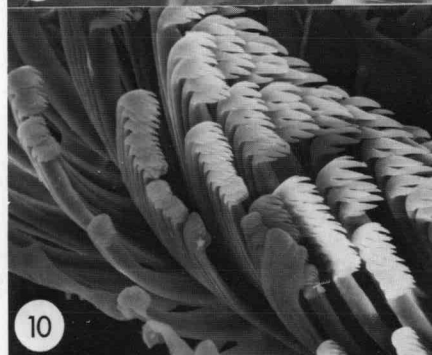
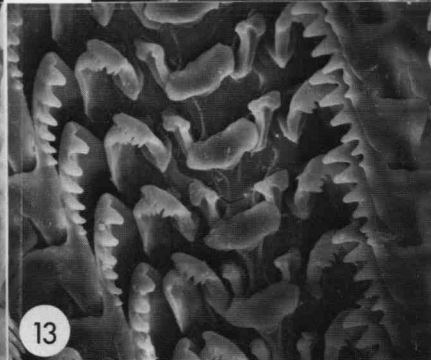
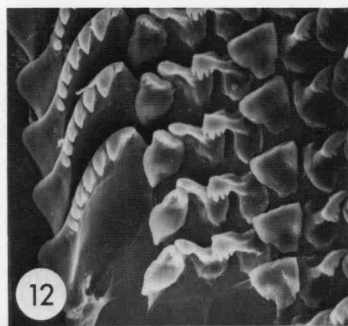
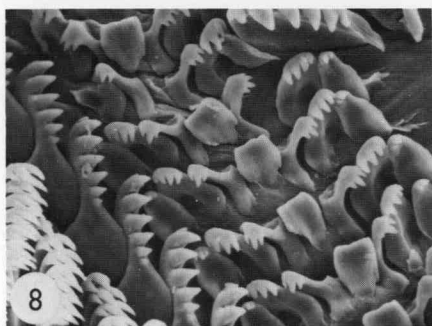
Wagner (1911) proposed a classification based on the postembryonic shell and the operculum. Both organs have intimate contact with the environment and are readily affected by evolutionary pressures associated with habitat selection. These pressures fluctuate constantly and are repetitive in different places and at different times. Wagner's classification does not take into account the phenomenon of convergence. Morphological structures highly adaptable to external environmental pressures provide innumerable opportunities for convergence and have limited application to systematics (Caen 1964).

Shell features produced during embryonic development within the egg capsule are conservative. They are the consequences of reproductive specializations centering around nidification. They show little variations in species or groups of closely related species living in diverse habitats.

The radula of helicinids is also a conservative morphological system and is a useful indicator of phyletic relationships (Baker 1922). The radular structure of *Helicina* is a generalized state for the family and is relatively primitive in its evolutionary grade. Variations from the *Helicina* grade are derived conditions (Thompson 1980). Characteristics of the radula coupled with embryonic shell features offer great advantage over other structures in showing supraspecific relationships.

#### GENERIC RELATIONSHIPS OF THE *umbonata* SPECIES GROUP

In order to determine the systematic affinities of the *umbonata* species group it was necessary to examine the embryonic sculpture and radula of those genera to which *umbonata* and *dominicensis* have been referred. The embryonic shells of a large number of tropical American species were examined. Five are discussed because of their relevance to the *umbonata* group: *Helicina neritella* Lamarck, *Lucidella aureola* (Ferrussac), *L. (Poenia) depressa* (Gray), *L. (Poenia) lirata* (Pfeiffer) and *Alcadia major*



(Gray). All but *lirata* are the type species for their respective genera or subgenera. Baker (1922) gives data on the radula of many species of helicínids which allow comparisons with the *umbonata* group. The radula of two *Lucidella* are figured in this paper, *L. aureola* and *L. (P.) lirata*.

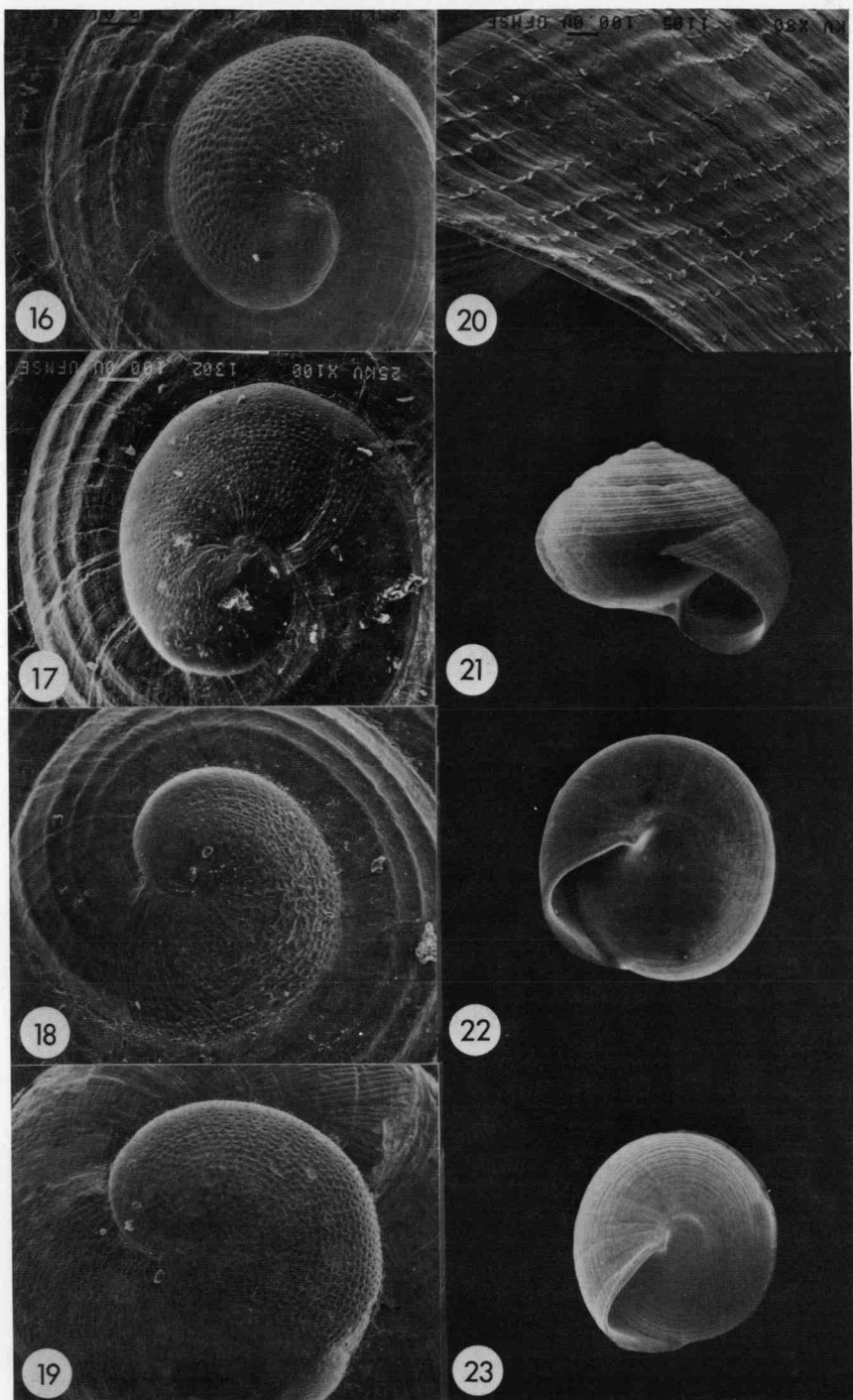
The helicínid radula contains three fields of teeth, the centrals, laterals, and marginals. The central and lateral fields are specialized within different subfamilies and genera for different trophic roles. The marginal fields show less variation. The central field contains seven longitudinal rows of teeth, the rachidian or R-central bordered on each side by the A-central, B-central, and C-central (Figs. 8, 9). The lateral field consists of a complex of two partially fused teeth on each side of the central field, the cusp-bearing comb-lateral and the reinforcing accessory plate (Figs. 9, 11). The marginal field has a large number of slender teeth with acuminate cusps (Fig. 10).

**CHARACTERISTICS OF THE *UMBONATA* GROUP.**—The *umbonata* group includes four species of medium-sized (5-8mm) globose or dome-shaped snails with about 5-6 whorls. All have rugose spiral sculpture on the postembryonic whorls (Fig. 12). The protoconch, or embryonic shell, is about 0.7 mm in diameter and is sculptured with a dense mesh of spirally arranged pits (Figs. 16-18), which are readily distinguishable at 50X with a dissecting microscope.

The operculum is yellowish-orange and narrowly auriculate with a narrow apex hooked to the left (Figs. 1-6). The membranous base extends beyond the edge of the calcareous plate. The calcareous plate has a thin and narrow ridge along the columellar margin. The shape of the apex and the columellar ridge are significant specific characters.

The radula of *H. u. umbonata* (Fig. 12) and *H. u. pitheca* (Figs. 8-11) are described. The central teeth of the radula have projecting cusp-bearing faces (Figs. 8, 9, 11). The A-central has a large pentagonal-shaped base with the face raised on a pedicel like a shelf, and projects laterally with 3-4 cusps. The B-central is erect with a comb-shaped face bearing 4 cusps. The C-central narrows toward the face and bears 3 small cusps. The comb-lateral has 6-7 heavy subequal cusps. The accessory plate has a short base and a narrow laterally projecting appendix; the reflection invests only the outer tip of the comb-lateral without covering any cusps (Fig. 11). The marginal field has about 26 slender, sickle-shaped teeth on

FIGURES 8-15. —Helicínid radulae. 8—*Helicina umbonata pitheca* n. ssp., central field (UF 22896),  $\times 375$ ; 9—Same, central and lateral field,  $\times 400$ ; 10—Same, marginal teeth,  $\times 500$ ; 11—Same, lateral field,  $\times 500$ ; 12—*H. u. umbonata* Pfr., central and lateral field (UF 35133); 13—*Lucidella (Poenia) lirata* (Pfr.), central and lateral field (UF 22988),  $\times 500$ ; 14—*L. aureola* (Adams), hemisection (UF 22987),  $\times 175$ ; 15—Same, central and lateral field,  $\times 375$ .





each side; the innermost teeth have 4 heavy cusps. The outermost teeth have 9-10 very delicate cusps (Fig. 10).

COMPARISONS WITH *HELICINA*. — The protoconch of *H. neritella* is about 0.9 mm in diameter, and has a mesh of spirally arranged pits (Fig. 19) similar to *umbonata*. The radula is described by Baker (1922:52-53; pl. 3, fig. 6; pl. 4, fig. 17). *H. neritella* and *umbonata* are alike. They differ only in the number of cusps on the comb-lateral. *H. neritella* has eight cusps.

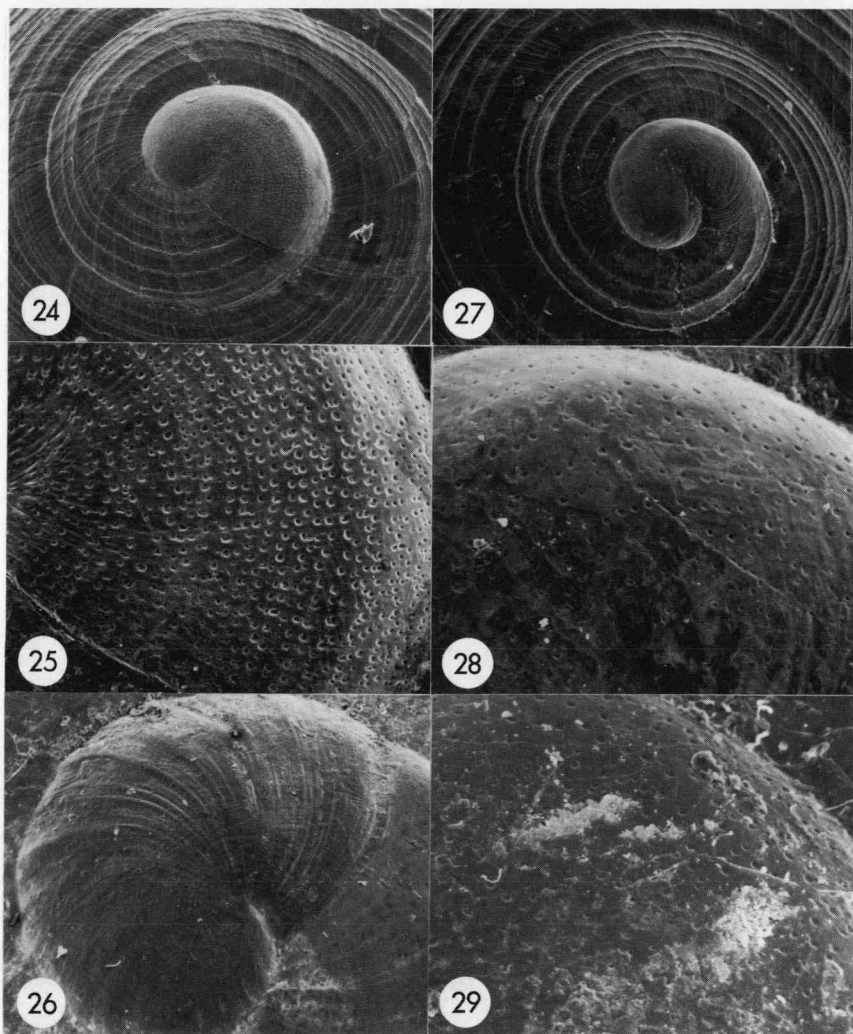
COMPARISONS WITH *LUCIDELLA* (*s. s.*). — The protoconch of *L. aureola* is smaller than *umbonata* (0.5 mm). It is sculptured with very minute pits that are spaced farther apart than their diameters (Figs. 24, 25). The intervening space does not form a mesh, and the pits are not arranged in discrete spiral series. The radula, specialized for scraping fine food particles, is figured in Baker (1922) and in this paper (Figs. 4, 5). The A-central is long, narrow, and oblique; its cutting edge is long, narrow, and lacks denticles. The B-central is shorter and has about 3 rounded knob-like vestigial cusps along the outer edge of the blade. The C-central is spatulate with about 3 poorly defined cusps. The comb lateral has 9 nearly equal cusps. The accessory plate has a very long base bearing a short lateral appendix. The marginals have 2 cusps on the innermost teeth and 4 on the outermost.

COMPARISONS WITH *LUCIDELLA* (*POENIA*). — The protoconch of *L. (P.) depressus* (Fig. 29) and *L. (P.) lirata* (Figs. 27, 28) are illustrated. The subgenus is similar to *Lucidella* (*s. s.*) in the small size of the protoconch (0.4 mm). The pitted sculpture is sparser and finer than in *Lucidella* and is most conspicuous along the periphery. The radula is described and figured by Baker (1922:55; pl. 3, fig. 5; pl. 5, fig. 21) and here (Fig. 13). As in *Lucidella* (*s. s.*) it is specialized for scraping fine substances. The A-central is narrow, elongate, and oblique with a hood-shaped face. The B-central is comb-shaped with about 6 small cusps. The comb-lateral has about 7 cusps. The accessory plate has a long base and a short triangular appendix (Baker, 1922: pl. 5, fig. 21). The inner marginal teeth have 3 cusps. The outer marginals have 4 cusps.

COMPARISONS WITH *ALCADIA*. — The protoconch of *A. major* (Fig. 26) is large (1.0 mm) and is sculptured with coarse, irregularly spaced radial threads. The inner curvature bears a few irregular longitudinal striations.

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FIGURES 16-23. — Electron micrographs of *Helicina* shells. 16 — *H. u. umbonata* Sh., embryonic sculpture (UF 25249),  $\times 60$ ; 17 — *H. liobasis* n. sp., embryonic sculpture (UF 25247),  $\times 50$ ; 18 — *H. rhips* n. sp., embryonic sculpture (UF 22989),  $\times 50$ ; 19 — *H. neritella*, embryonic sculpture (UF 22992),  $\times 50$ ; 20 — *H. u. umbonata* Sh., periostracal bristles on last whorl (UF 25249),  $\times 40$ ; 21 — Same showing postembryonic sculpture and descent of aperture,  $\times 6.5$ ; 22 — *H. liobasis* n. sp., showing smooth base (UF 25254),  $\times 6.5$ ; 23 — *H. u. umbonata* Sh., showing sculpture on base (UF 25249),  $\times 5.5$ .



FIGURES 24-29.—Electron micrographs of helicid embryonic sculpture. 24—*Lucidella aureola* (Adams) (UF 22991),  $\times 50$ ; 25—Same,  $\times 250$ ; 26—*Alcadia major* (Gray) (UF 22980a),  $\times 25$ ; 27—*Lucidella* (*Poenia*) *lirata* (Pfr.) (UF 22990),  $\times 50$ ; 28—Same,  $\times 250$ ; 29—*Lucidella* (*Poenia*) *depressa* (Gray) (UF 35167),  $\times 250$ .

Pitted sculpture is absent. The radula of *A. major* is like that of the Vianinae, not like the Helicininae. Other generic units placed in *Alcadia* as subgenera have Helicininae radula, but a protoconch similar to *Alcadia*.

GENERIC RELATIONSHIPS.—The *umbonata* species group is placed in *Helicina* (s. s.) because of similarities in embryonic shell sculpture and

radular tooth structures. Like *Helicina neritella* the radula is specialized for gouging coarse vegetal food particles whereas the radula of *Lucidella* is specialized for scraping fine substances. Relationships to *Lucidella* (s. l.) and *Alcadia* are not tenable in light of the data presented above. The *umbonata* group is unique among West Indian *Helicina* because of the rugose postembryonic spiral sculpture. Some mainland subgenera placed in *Helicina* have rugose spiral cords, but their embryonic shell sculptures differ. The status of the subgeneric groups associated with *Helicina* needs to be reexamined.

#### ECOLOGICAL DEPLOYMENT OF THE *umbonata* SPECIES GROUP

The *umbonata* group lives in submesic and xeric habitats, although occasionally populations of *H. u. umbonata* occur in mesic stations. The species are adapted to exist in dry habitats through modification of the coloration, sculpture, and microhabitat selection.

Two species, *H. umbonata* and *H. liobasis* are arboreal, foraging and aestivating on trees and shrubs close to the ground. The shells are whitish with conspicuously colored bands and blotches. The markings disrupt the appearance of the light colored shell on a variegated background. Live snails on shrubs are inconspicuous because of the background produced by limbs, vines, leaves, and flowers. The rugose spiral sculpture adds to the visual disruption. Both species also have periostracal bristles (Fig. 20) which usually are worn from adult shells. Presumably these bristles add to visual disruption of the juveniles.

Two other species, *H. dominicensis* and *H. rhips*, have darker colored shells in which the color pattern is not as distinct. Dark-colored, poorly patterned shells are typical of ground-dwelling land snails. These two species live under terrestrial bromeliads and *Agave* sp. This habitat is protective from desiccation by rosettes of leaves around the base of the plants tightly oppressed against the ground. Presumably the snails forage on but not upon the plants. The matted sculpture of the postembryonic shell adds to the inconspicuous appearance of the snail among dead plant debris. The two species are ecologically segregated further. *H. dominicensis* lives under *Bromelia pinguin* on alluvial substrates. *H. rhips* lives under *Agave* cf. *americana* on limestone substrates.

#### SPECIFIC RELATIONSHIPS

The interspecific relationships of the *umbonata* group are indicated by the shell and opercular structures, and are related to the ecological deployment of the four species. Two subgroups are represented. One consists of two arboreal, brightly colored snails with strong spiral sculpture,

*H. umbonata* and *H. liobasis*. The other consists of two terrestrial, dull-colored snails with matted sculpture, *H. dominicensis* and *H. rhips*. The first species, *H. umbonata*, occurs east of Hispaniola. The other three occur on Hispaniola. The Hispaniolan species are alike in having an auriculate-shaped operculum with a pointed apex strongly hooked to the left (Figs. 3-6). *H. umbonata* has a blunt apex weakly hooked to the left (Figs. 1-2).

Two interpretations of phylogeny can be made. One is that *H. umbonata* and a Hispaniolan prototype diverged morphologically through modification of the operculum and became segregated geographically on Puerto Rico and Hispaniola. Subsequently the Hispaniolan prototype diverged in sculpture, coloration, and habitat deployment to form one lineage leading to *H. liobasis* and the other leading to *H. dominicensis* and *H. rhips*. The latter lineage diverged further through adaptive selection for different plant associations. This interpretation assumes that within the group an arboreal habitat is primitive and a terrestrial habitat is secondarily derived.

A second interpretation of phylogeny is that an Hispaniolan prototype diverged to give rise to two lineages through adaptive selection and modifications of color and sculpture. An arboreal lineage diverged further through minor modifications of sculpture and opercular shape because of geographic isolation, with *H. liobasis* on Hispaniola and *H. umbonata* on Puerto Rico and nearby islands. A terrestrial lineage leading to *H. dominicensis* and *H. rhips* diverged further through adaptive selection for different plant associations. This interpretation permits the Hispaniolan prototype to be either arboreal or terrestrial. Usually among land snails an arboreal existence is a derived condition. A terrestrial prototype is favored, because within the Helicinidae the vast majority of the species are terrestrial. The second interpretation of phylogeny is accepted because it requires the fewest assumptions and is consistent with other patterns of ecological deployment in land snails.

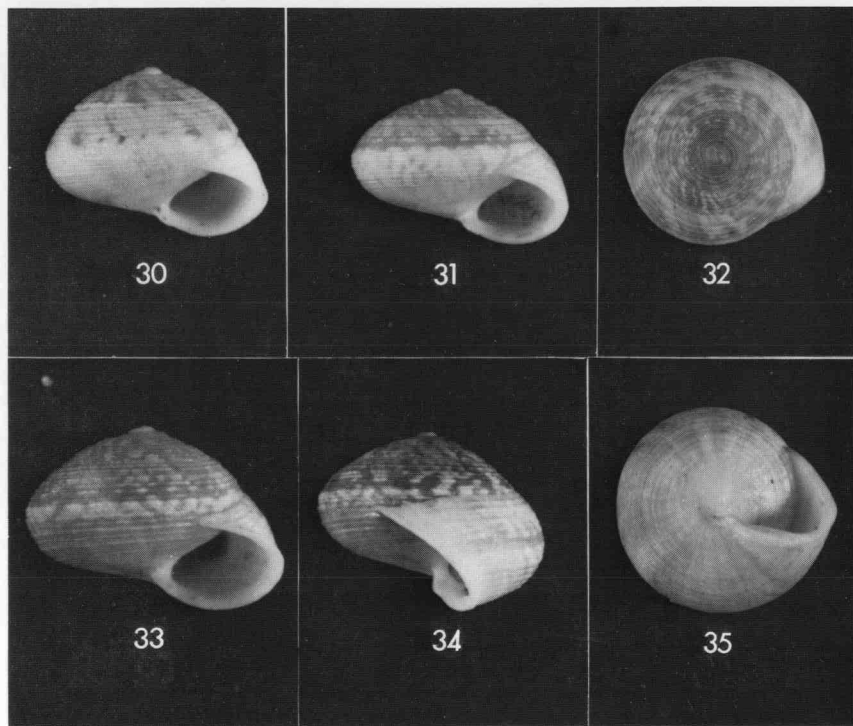
## SYSTEMATICS OF THE *UMBONATA* SPECIES GROUP

### *Helicina u. umbonata* SHUTTLEWORTH

*Helicina umbonata* Shuttleworth 1854; Diagnosen Neuer Mollusken, 6:93. — Pfeiffer 1858; Monogr. Pneumo. Viv.: 187. — Dall and Simpson 1901; Bull. U.S. Fish Comm. (1900) 1:447.

*Lucidella umbonata* (Shuttleworth), Wagner 1911; in Martini and Chemnitz Syst. Conch.-Cab. (Helicinidae): 340; pl. 67:21-24. — van der Schalie 1948; Misc. Publ. Mus. Zool. Univ. Mich. (70):23; pl. 1, fig. 6; map 3. — Boss and Jacobson 1974; Occ. Pap. Moll. 4:37.

*Lucidella (Poenia) umbonata* (Shuttleworth) Baker 1962; Nautilus 76:17.



FIGURES 30-35. — *Helicina u. umbonata* Sh. 30-32, 35—10 km SE of Guanica, Puerto Rico (UF 35139); 33, 34—Cerro de las Cuevas, SE of Juana Diaz, Puerto Rico, 450 m alt. (UF 25008).

**SHELL (FIGS. 30-35).**—Medium-sized, about 5-6 mm in diameter. Depressed dome-shaped, about 0.64-0.75 times as high as wide. Whorls 5.0-5.4. Periphery angulate or carinate; angulation usually accentuated by rugose beaded spiral cords along periphery; occasional specimens rounded peripherally with rugose cords producing angulation. Base of shell flattened around umbilical callus. Protoconch with relatively rugose pits spirally arranged (Fig. 16). Sculpture on subsequent whorls consisting of relatively rugose spiral cords and weaker, irregular axial striations (Fig. 21). The cords on the base become weaker, but are continuous into the aperture (Figs. 23, 25); apical whorls with about 3-10 cords. Cords separated by deep, sharp grooves that are about the same depth as the suture and obscure the suture. Aperture 0.71-0.90 times as high as wide. Outer lip sharp-edged, but internally thickened and very weakly reflected laterally and basally. Columella arched forward, terminating as a low, poorly defined denticle. Color pattern almost always poorly defined. A peripheral band occurs very infrequently. More often the spire contains irregular yellow to rust-colored blotches, spots, and streaks that tend to be

spirally arranged. Interior of aperture light orange. The ground color varies from pinkish-white to light brown. Specimens from mesic habitats are darker with a poorly defined pattern of lighter yellow markings on the spire (Fig. 33, 34). Specimens from xeric habitats tend to be lighter with orange- or rust-colored markings (Fig. 30-32).

**OPERCULUM** (FIG. 1). — Calcareous plate broadly auriculate in shape; apex bluntly rounded, slightly hooked to left; widest at about the middle; evenly rounded below. Columellar margin with a thick, sharp ridge that is highest below and becomes lower toward the apex. Outer surface covered with minute granules.

Measurements in mm based on two population samples, one from a xeric habitat and the other from a mesic habitat, are representative.

	XERIC (UF 35139, 25 specimens)	MESIC (UF 35140, 23 specimens)
Shell width	4.4-5.5	4.9-6.3
Shell height	3.2-3.9	3.2-4.5
Aperture width	1.5-1.9	1.8-2.3
Aperture height	1.9-2.4	2.2-2.8
Whorls	5.0-5.4	4.9-5.4

Aside from slight differences in size and color associated with habitat, no other significant variations are observed.

**DISTRIBUTION.** — This subspecies is confined to a narrow coastal belt of calcareous terrain along the western half of Puerto Rico. The specimens examined were collected from within the area reported by van der Schalie (1948:23; map 3) and add little distribution information, except for the specimens from Cerro de las Cuevas. This station is about 50 km east of Ponce. The snail is found most commonly in xeric habitats, but occasionally is found in mesic forests. It is arboreal and aestivates on shrubs, vines, and herbaceous plants within a few meters of the ground. During wet weather it also climbs on limestone rocks (Baker 1962:62).

**SPECIMENS EXAMINED.** — PUERTO RICO: 2 km SSE Guanica (UF 35138); 7 km SE Guanica (UF 35141); 10 km SE Guanica (UF 25249-50; 35139); south slope Cerro de las Cuevas, 3.5 km N, 4.7 km E Juana Diaz, 450 m (UF 25008, 25251, 35138, 35140, 35141, 35165).

**REMARKS.** — *Helicina umbonata* is most closely related to *H. liobasis*, which occurs on the eastern end of Hispaniola and which is geographically most proximal to the two subspecies of *H. umbonata*. *H. umbonata* and *H. liobasis* have similar spiral sculpture on the apex of the shell. The spiral cords are not hatched by conspicuous axial threads, thus differing from the sculpture of *H. dominicensis* and *H. rhips*. *H. umbonata* differs from *H. liobasis* by its sculptured base, depressed shape, relatively wide aper-

ture, and the shape of its operculum. These characters are discussed in greater detail under *H. liobasis*. The enlarged beaded peripheral cords characteristic of *H. u. umbonata* are unique within the species group. Its operculum differs from Hispaniolan species in that its widest point lies above the middle, the columellar ridge is thicker and more rounded, and the apex is rounded.

*H. umbonata* includes two subspecies. The nominate subspecies is confined to Puerto Rico. The other is confined to Mona Island and Monito Island, which lie in Mona Passage between Puerto Rico and Hispaniola. Differences between the two subspecies are discussed below.

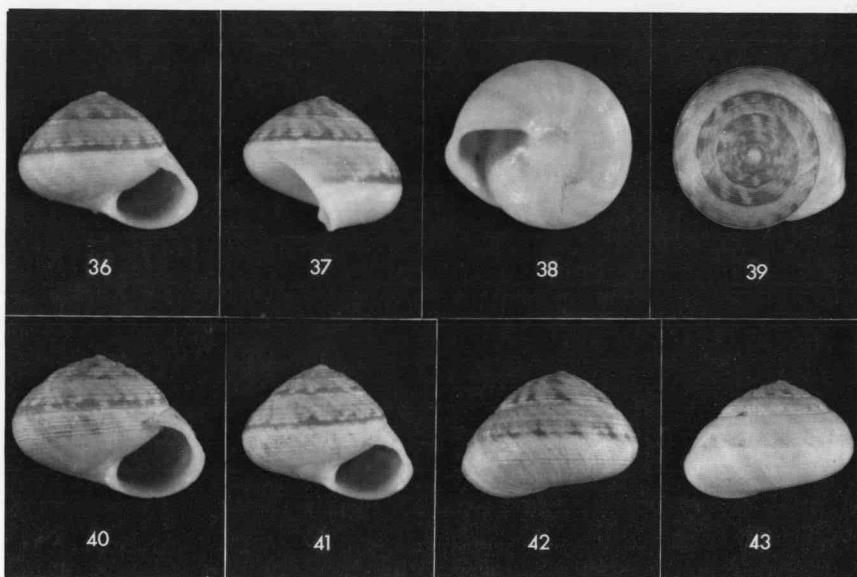
### *Helicina umbonata pitheca* NEW SUBSPECIES

*Lucidella umbonata* (Shuttleworth) Clench 1950; Jour. de Conchyl. 80:271 [Mona Island]. — Thompson 1976; Nautilus 90:152 [Monito Island].

**SHELL** (FIGS. 36-43). — Medium-sized, about 5.1-6.5 mm in diameter. Depressed conical, about 0.7-0.8 times as high as wide; spire low, convex with a protruding apex, about 0.42-0.56 times height of shell. Whorls 5.2-5.7; protoconch with 1.3-1.5 whorls, sculptured as in *H. u. umbonata*. Following whorls sculptured with low spiral lirations that become obsolete on last whorl; *last 1/4-1/2 whorl nearly smooth except for incremental striations. Suture distinct, not obscured by spiral sculpture.* Spiral lirations on base continuing into aperture, diminishing near umbilical callus, which is granular and bordered behind by a strong spiral ridge that continues to base of columella as a slightly projecting, blunt denticle. *Body whorl rounded at periphery and inflated on base.* Aperture broadly auriculate, almost as high as wide; width of aperture 0.41-0.45 times width of shell; height 0.44-0.58 times height of shell. Outer lip sharp-edged, weakly reflected, with a low internal callus. *Aperture slowly descending below periphery along last quarter whorl.* Color yellowish-white with an orange suprapерipheral spiral band that is wavy along its dorsal edge and may be broken into a spiral row of spots and blotches, especially on upper whorls. Occasional specimens white without orange markings. Protoconch yellow. Interior of aperture orange. Outer lip and columella white.

**OPERCULUM** (FIG. 2). — Similar to *H. u. umbonata* except that the columellar ridge is lower, wider, and not as sharp-edged, and the widest point is above the midline.

Measurements in mm of 12 specimens from a mesic habitat, selected from the type lot, are given below (holotype in parentheses). Measurements of 10 specimens from a xeric habitat are also given. These two



FIGURES 36-43. — *Helicina umbonata pitheca* n. ssp. 36-39—Holotype (UF 35168); 40-43—Paratypes (UF 35169).

samples encompass the variation usually encountered, except for occasional gerontic specimens.

	MESIC (UF 35169)	XERIC (UF 24964)
Shell width	5.5-6.5 (6.3)	5.1-5.8
Shell height	4.0-5.0 (4.8)	3.8-4.3
Aperture width	2.0-2.4 (2.7)	2.0-2.3
Aperture height	2.3-2.9 (2.2)	2.1-2.5
Whorls	5.3-5.7 (5.7)	5.2-5.5

TYPE LOCALITY. — MONA ISLAND, Sardinero. HOLOTYPE: (UF 35168); collected 21 May 1974 by Howard W. Campbell and Fred G. Thompson. PARATYPES: UF 35169(89); same data as the holotype.

DISTRIBUTION. — Endemic on Mona Island (UF collections, 17 stations) and nearby Monito Island (Thompson, 1976; UF 35158). They appear to be ubiquitous on Mona Island. Live snails usually are found on plants within a few meters of the ground. The snail aestivates on trees, shrubs, and herbaceous plants.

The specimens from Monito Island are somewhat intermediate in character between *umbonata* and *pitheca*. They have typical *pitheca* sculpture, color, and descent of the aperture.

REMARKS — This is a well-differentiated subspecies that is readily distinguished from *H. u. umbonata* by its color, sculpture, and shape. All

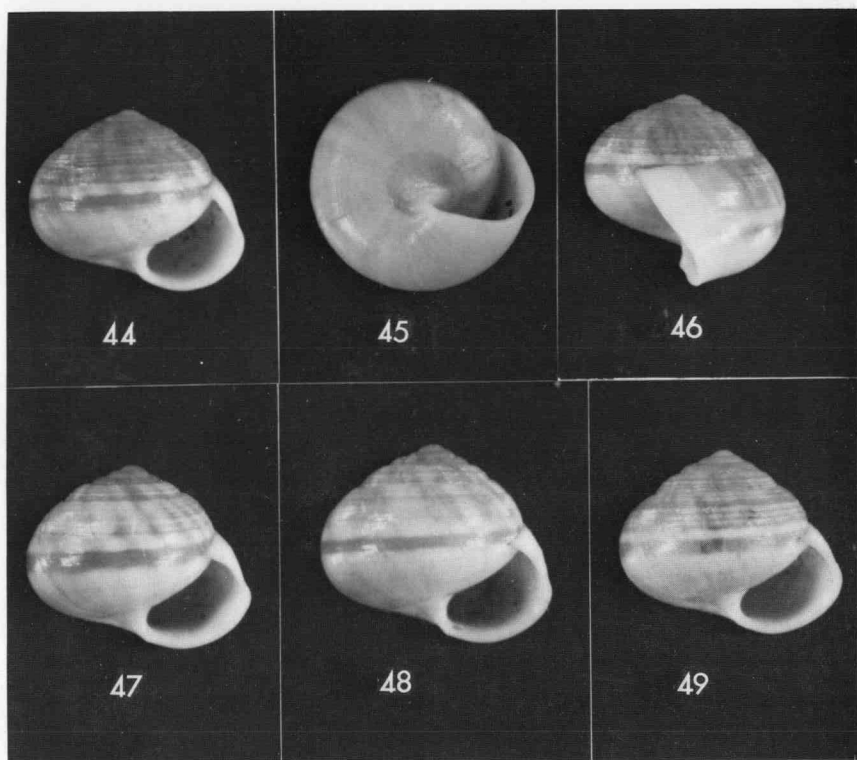


samples of *H. u. pitheca* are dominated by specimens with a distinct suprapерipheral orange band. Some specimens have a spiral series of spots or lack markings on the last whorl. *H. u. umbonata* has a poorly defined color pattern that seldom forms a peripheral band, although the blotches and spots tend to be spirally arranged. In *H. u. umbonata* the spiral lirations are quite heavy and obscure the suture, whereas *H. u. pitheca* has weaker spiral lirations that do not obscure the suture. The *H. u. umbonata* lirations are stronger along the periphery, accentuating the peripheral angle, and the sculpture continues undiminished to the aperture. *H. u. pitheca* has a more inflated body whorl with a rounded periphery and a weakly inflated base, and the aperture descends slightly below the periphery. In *H. u. umbonata* the aperture descends farther along the last 1/10 whorl (Figs. 21, 43).

ETYMOLOGY.—From the Greek *pithekos*, meaning monkey, in this case a patronym for Mona Island; *mona*, from modern Spanish, meaning monkey.

#### *Helicina liobasis* NEW SPECIES

SHELL (FIGS. 44-49).—Medium-sized, about 5 mm in width. Dome-shaped, about 0.78-0.90 times as high as wide; spire convex, raised, about 0.42-0.53 times height of shell. Whorls 4.6-5.1 (5.1 in holotype). Last whorl rounded, descending to aperture below peripheral band. Protoconch with 1.1 whorls; sculptured with fine pits arranged in spiral series (Fig. 17). Subsequent whorls sculptured with about 3-6 low, wide spiral cords that lie above the periphery; cords crossed by variable axial striations which become obsolete on the periphery. Base smooth, or nearly so (Figs. 22, 45); some specimens have occasional faint spiral and axial striations. Whorls inflated; last 1/4 whorl descending below periphery to aperture. Umbilical callus blue-gray in live specimens, finely granular. Color pattern consisting of rust-colored spiral bands on a cream-white background. Lower band distinct, lying along periphery. Upper band poorly defined, lying along middle of shoulder and corresponding part of earlier whorls; separated from suture by a narrow white zone. In some specimens upper band is broken into several narrow bands that lie in grooves between spiral cords. Frequently upper band has superimposed rusty blotches that extend to suture. Protoconch yellow. Lip and columella white. Interior of aperture light orange. Aperture half-moon shaped, oblique and sigmoid in lateral profile; about 0.47-0.58 times height of shell and 0.42-0.46 times width of shell. Lip sharp-edged; internally thickened above and increasingly thicker to base. Outer lip very slightly reflected, bordered behind by a very shallow groove. Columella oblique and curved forward, ending in a very weak basal denticle that is connected to posterior edge of umbilical callus by a weak buttress.



FIGURES 44-49. — *Helicina liobasis* n. sp. 44-46—Holotype (UF 25263); 47-49—Paratypes (UF 25264).

**OPERCULUM** (FIGS. 5-6).—Calcareous plate widest at middle; base bluntly rounded. Apex pointed, strongly hooked to left. Columellar ridge sharp, narrow, highest near base, not reflected laterally.

Measurements in mm of 19 specimens from the type lot are as follow (holotype in parentheses): shell width 4.8-5.4 (5.2), shell height 3.8-4.7 (4.3), aperture width 1.9-2.4 (2.4), aperture height 2.0-2.5 (2.4).

The shell of *H. liobasis* shows little variation aside from size and relative height. The type lot nearly encompasses the full range of variation found in other populations. The series from 4 km SE Punta Cana contains a gerontic shell 6.6 mm in diameter. The series from Punta Palmillos has a preponderance of relatively depressed shells, but the total variation within this series is within the variation of the type lot.

**DISTRIBUTION** (FIG. 7).—Found along the extreme eastern tip of Hispaniola and offshore islands in Departamento (= Dpto.) de Altagracia, Dominican Republic. It appears to be restricted to a narrow zone along the coast. Numerous field collections were made at localities inland from

El Macao, Punta Cana, and Boca de Yuma. No specimens were found except at coastal localities.

*H. liobasis*, like *H. umbonata*, is arboreal. Live specimens were collected on Saona Island, Punta Palmillos, and south of El Macao crawling on coconut palms and shrubs. Other live specimens were found aestivating on tree trunks and shrub stems.

TYPE LOCALITY. — DOMINICAN REPUBLIC, ALTAGRACIA DPTO., north coast of Isla Saona opposite Isla Catalinita. The area consists of a low submesic open forest on a limestone terrain with occasional small clearings. The lower vegetation was heavily browsed by goats. Snail shells occurred under limestone slabs in forest floor litter. Occasional live specimens were found on tree trunks. HOLOTYPE: UF 25265; collected 18 February 1975 by Howard W. Campbell and Fred G. Thompson. PARATYPES: UF 25264 (59), UF 25247 (3), UF 25254 (1); same data as the holotype.

OTHER LOCALITIES. — DOMINICAN REPUBLIC: ALTAGRACIA DPTO.: 1 km SW El Macao (UF 25268, 8); Punta Cana (UF 25276, 1); 4 km SE Punta Cana (UF 25269, 2); Punta Palmillas (UF 25266, 23); Isla Catalinita (UF 25267, 7).

REMARKS. — *Helicina liobasis* is similar to *H. dominicensis* and *H. rhips* in its dome-shaped shell, its narrow pointed operculum, and its color pattern. It differs from *H. umbonata* in these as well as other characteristics, which are discussed under that species. *H. liobasis* differs from the Hispaniolan species by its weaker columella denticle, its sculpture, and its peristome. The sculpture of *H. liobasis* consists of much wider spiral cords and lacks the axial threads that give a matted pattern to the shells of *H. dominicensis* and *H. rhips*. The outer peristome of *H. liobasis* is hardly reflected. What little reflection occurs is accentuated by a weak postlabial groove. In other Hispaniolan species, the outer and basal lips are conspicuously reflected.

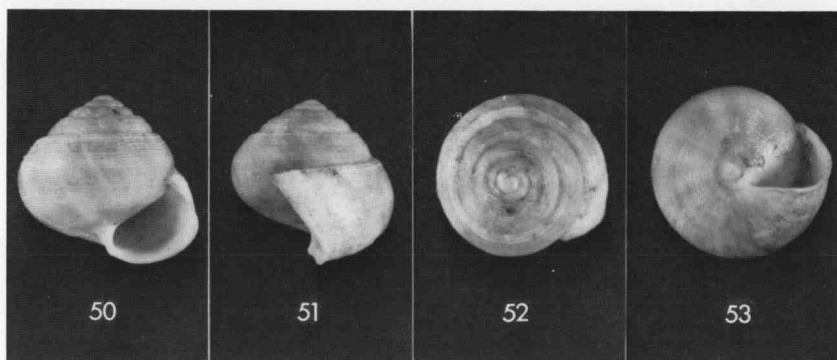
ETYMOLOGY. — *Liobasis*, from the Greek, *leios* meaning smooth and *basis*, meaning base, alluding to the lack of sculpture on the base of the shell.

#### *Helicina dominicensis* PFEIFFER

*Helicina dominicensis* Pfeiffer 1851; Proc. Zool. Soc. (London): 149. — 1852; Monogr. Pneumon. Viv. 1:352. — Crosse 1891; Jour. de Conchyl. 39:185.

*Alcadia (Analcadia) dominicensis* (Pfeiffer) Wagner 1911; in Martini and Chemnitz, Syst. Conchyl. Cab., Helicinidae: 355; pl. 68, figs. 1-3.

SHELL (FIGS. 50-53). — Medium-sized, about 5-6 mm wide; conico-



FIGURES 50-53. — *Helicina dominicensis* Pfr. (UF 23183).

globose, about 0.85-0.92 times as high as wide. Spire raised, straight-sided, forming an obtuse cone with a blunt apex. Body whorl rotund, uniformly rounded. Suture deeply impressed. Whorls 5.0-5.3. Protoconch with about 1.3 whorls, typically sculptured for group. Whorls regularly increasing in size, shouldered along suture, regularly descending; last 1/10 whorl descending slightly below periphery to aperture. Whorls sculptured with numerous low spiral cords that are crossed by finer, lower radial threads forming a matted surface; spiral cords slightly finer on base of shell than above. Umbilical callus small, about 1/6 diameter of shell, white, granular, with a weak indentation at base of columella. Ground color yellowish-white with a broad spiral dull yellow zone around periphery and on spire. Protoconch light yellow. Interior of aperture light orange. Peristome white. Aperture half-moon shaped; about as high as wide; about 0.49-0.52 times height of shell. Outer lip straight-edged above, weakly reflected laterally and below. Columella concave internally and arched forward below, forming a blunt denticle.

**OPERCULUM** (FIG. 4). — Calcareous plate acutely pointed above and bluntly rounded below. Apex sharp, moderately hooked to left. Widest point of plate at middle. Columellar ridge thick and sharp-crested below, very low along apical half; ridge not projecting sideways beyond margin of basal plate.

Measurements in mm based upon 11 adults are as follow: shell width 5.2-5.8, shell height 4.6-5.3, aperture width 2.4-2.7, aperture height 2.4-2.7.

**DISTRIBUTION** (FIG. 7). — Endemic to Hispaniola where it has a moderate distribution in the Azua basin and occurs as far east as the area near Bani. I found it at only five localities. Its paucity in collections may be due to its apparent habitat preference. I found it only in clusters of the terrestrial bromeliad, *Bromelia pinguin*, which grows in dense thickets on alluvium in xeric areas, and it was not found on limestone outcrops within

the same area. This habitat was infrequently searched for snails because relatively few species occur there compared to the much richer fauna associated with limestone. Subsequent search in the bromeliad habitat may show that the species is more widely distributed.

**TYPE LOCALITY.**—Pfeiffer (1851:149) described this species from specimens collected by August Sallé, and gave Haiti (= Hispaniola) as the type locality. Crosse (1891:39) recorded it from Las Charcas, Dominican Republic, also from specimens collected by Sallé who visited there in 1849. Apparently Sallé did not collect it elsewhere, nor has it been reported from elsewhere. Therefore, the type locality is restricted herein to Las Charcas, Departamento de Azua, Dominican Republic.

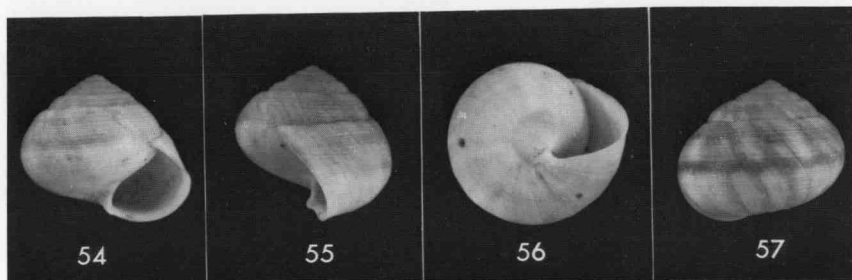
**SPECIMENS EXAMINED.**—DOMINICAN REPUBLIC; AZUA DPTO: 1 km SE Peralto, 510 m (UF 23549.3); 1 km N Estebania, 170 m (UF 23547.1); 2 km N Las Charcas, 80 m (UF 28183.8); 6 km ESE Las Charcas (UF 23063.3). PERAVIA DPTO: 6 km WNW Bani (UF 23548.2).

**REMARKS.**—*H. dominicensis* is very similar to *H. rhips* in shape, color, and sculpture. The two differ in size, whorl count, and aspects of the operculum, as is discussed under the latter species.

### *Helicina rhips* NEW SPECIES

**SHELL (FIGS. 54-57).**—Large, about 7-8 mm in diameter. Conicoglobose, about 0.84-0.92 times as high as wide; spiral convex, raised about 0.45-0.50 height of shell. Whorls 5.5-5.9 in adults. Protoconch consisting of about 1.1 whorls that are sculptured uniformly with small pits arranged in spiral series (Fig. 18). Subsequent whorls with relatively strong spiral chords crossed by finer axial threads creating a latticed pattern; about 3-4 chords on second whorl; about 20-25 chords between suture and lip on last whorl. Chords uniform in size over last whorl. Umbilical callus coarsely granular, about 1/5 diameter of base, light yellow. Color of shell dull cream white to light pink with diffuse light yellow to light orange bands on body whorl; upper band lying about 1/3 of distance from suture to lip insertion; lower band lying just above periphery and lip insertion. Bands coalescing on upper whorls forming a brighter yellow or orange apex. Peristome and columella white. Interior of aperture dark yellow to orange. Aperture semilunar, about as high as wide, about 0.50-0.55 times height of shell and about 0.44-0.48 times width of shell; descending slightly and inserting on body whorl just below periphery. Lip moderately reflected at periphery and along base, not reflected above. Lip oblique and sigmoid in lateral profile. Columella arched and curved forward, ending as a blunt denticle that is connected to posterior edge of umbilical callus by a narrow buttress.

**OPERCULUM (FIG. 3).**—Calcareous plate acutely pointed above, bluntly



FIGURES 54-57.—*Helicina rhips* n. sp. 54-56—Holotype (UF 23064); 57—Paratype (UF 23234).

rounded below, and widest at midpoint. Apex more strongly hooked to left than in *H. dominicensis*. Columellar ridge sharp-edged, and *projecting sideways beyond margin of basal plate*.

Measurements in mm based on 25 mature specimens are as follow (holotype in parenthesis): shell width 7.0-8.4 (8.2), shell height 6.2-7.5 (7.0), aperture width 3.3-4.0 (3.7), aperture height 3.3-3.8 (3.7).

DISTRIBUTION (FIG. 7).—Endemic to Hispaniola where it is known only from a low limestone mountain ridge that extends from Bani northward for about 8 km. The ridge is covered with a dense submesic thorn forest. The snail was not found in adjacent areas where numerous collections were made. No live specimens were found. Dead shells were always associated with *Agave* cf. *americana*.

TYPE LOCALITY.—DOMINICAN REPUBLIC: PERAVIA DPTO., 6 km north of Bani, 100 m elevation. The type locality is along the east side of a limestone mountain ridge about 0.5 km west of the Rio Bani. The area at the base of the ridge consists of a tallus slope of huge limestone slabs and boulders. Specimens were found only along the base of the rock wall forming the ridge, not on the tallus slope. HOLOTYPE: UF 23064, collected 23 January 1980 by Fred G. Thompson. PARATYPES: UF 23234 (23), same data as the holotype; UF 25246 (14), 2 km NE Bani, 100 m; UF 23190 (2), 1 km N Bani, 75 m.

REMARKS.—*Helicina rhips* is closely related to *H. dominicensis* and appears to be a giant replica of the latter. The two species differ in size, whorl-count, and the structure of the opercula. They are considered species for the following reasons. In other species of helicínids such size discrepancies do not occur, even over large geographic areas. In addition to its larger size, *H. rhips* has about a half whorl more than does *H. dominicensis*. Usually in helicínids subspecies differences in size are not accompanied by such differences in whorl count. The reflected columellar ridge on the operculum is unique within the *umbonata* species group, and is a degree of differentiation not commonly found among closely-related species. Finally, no trends toward intergradation occur.

*H. dominicensis* occupies a relatively large geographic area within the Azua basin and is monomorphic in size, whorl-count, and opercular structure throughout the area.

ETYMOLOGY. — *Rhips*, from the Greek *rhips*, a wickerwork, net, or screen in allusion to the sculpture of the shell.

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