FLORIDA MUSEUM OF NATURAL HISTORY

BULLETIN

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Vol. 43, No. 2, pp. 49-77 2000

UNIVERSITY OF FLORIDA GAINESVILLE

Numbers of the **BULLETIN OF THE FLORIDA MUSEUM OF NATURAL HISTORY** are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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Managing Editor of the BULLETIN
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ISSN: 0071-6154 CODEN: BF 5BA5

Publication date: November 15, 2000 Price: $5.00

LANDSNAILS OF THE GENUS *HUMBOLDTIANA* FROM NORTHERN MEXICO (GASTROPODA, PULMONATA, HELICOIDEA, HUMBOLDTIANIDAE)

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ABSTRACT

Seven new species are described from the following Mexican states: Nuevo León: *Humboldtiana porterae* n. sp. and *H. edesma* n. sp.; Zacatecas: *H. bicincta* n. sp.; Durango: *H. latizona* n. sp. and *H. gradyi* n. sp.; Querétaro: *H. pinicola* n. sp.; Coahuila: *H. oreina* n. sp. The description of *H. plana* Metcalf and Riskind 1976 is amended, and the holotype is refigured. Two new subgenera are proposed: *Oreades* n. subgen. (type species: *Humboldtiana porterae* n. sp.) and *Polyomphalus* n. subgen. (type species: *H. oreina* n. sp.). The generic definition of *Humboldtiana* s. s. is amended.

Key words: Landsnail, Gastropoda, Pulmonata, Humboldtianidae, *Humboldtiana*, *Oreades*, *Polymophala*, Mexico.

RESUMEN

Se describen siete especies nuevas para los siguientes estados de Mexico: Nuevo León: *Humboldtiana porterae* n. sp. y *H. edesma* n. sp.; Zacatecas: *H. bicincta* n. sp.; Durango: *H. latizona* n. sp. y *H. gradyi* n. sp.; Querétaro: *H. pinicola* n. sp.; Coahuila: *H. oreina* n. sp. Se corrige la descripcion de *H. plana* Metcalf y Riskind 1976 y se redefine el holotipo. Se proponen dos nuevos subgeneros: *Oreades* n. subgen. (especie tipica: *Humboldtiana porterae* n. sp.) y *Polyomphalus* n. subgen. (especie tipica: *H. oreina* n. sp.) y se corrige la definicion generica de *Humboldtiana* s. s.

TABLE OF CONTENTS

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Thompson, F.G., and F.P. Brewer. 2000. Landsnails of the genus *Humboldtiana* from northern Mexico (Gastropoda, Pulmonata, Helicoidea, Humboldtianidae). Bull. Florida Mus. Nat. Hist. 43(2):49-77.

INTRODUCTION

The purpose of this paper is to describe seven new species and two new subgenera of *Humboldtiana* found in the Mexican states of Nuevo León, Querétaro, Coahuila, Zacatecas, and Durango. Another previously known species from Coahuila is redescribed. Prior to this work the genus *Humboldtiana* contained thirty species and two subspecies. Up to the present twenty-two species and one subspecies have been described from the Mexican state of México. *Humboldtiana* is distributed from Texas south to the states of México and Veracruz. Populations occur in isolated colonies and no colony is known to contain more than a single species. The intrinsic ability for geographic dispersal is limited, as evidenced by the high degree of local endemism. Dispersal probably is the result of long-term passive events associated with tectonic and climactic changes and other adventitious means. Speciation appears to have been a result of genetic isolation from other colonies because of ecological barriers coupled with local processes of natural selection and genetic drift. This produced a large number of morphologically and geographically isolated species of which interspecific competition seems not to have been a factor in their evolution.

Most species of *Humboldtiana* are conservative in the basic plan of the reproductive anatomy (Fig. 7). The genus is characterized by having four dart-sacs surrounding the vagina. Two dart-bulbs are associated with each of the dart sacs. Four dart-glands form a ring around the vagina above the dart-sacs and below the point where the spermathecal duct diverges from the uterus. The spermathecal duct bears an appendix near its distal end. The interior of the penis contains a verge. A great deal of itinerant local variations from this plan may take place. Reduction or modification of any of these structures occurs in various species. Normally the dart-bulbs are imbedded in the wall of the vagina at the base of the dart-sacs and are not visible superficially. In a new subgenus from Coahuila the dart-bulbs are conspicuous at the base of each dart-sac, as they are in the related genus *Bunnya* (Baker, 1942). A most striking departure from the general anatomical plan is found in another new subgenus that lacks dart-glands, dart-sacs, and dart-bulbs on the vagina, lacks an appendix on the spermathecal duct, and lacks a verge within the penis.

Most *Humboldtiana* are known only from shells. Anatomical data for the others are incomplete so that in some instances critical comparisons between species cannot be made. Solem (1974) attempted to determine species boundaries within *Humboldtiana* and to look for patterns of morphological specialization over broader geographic regions. He arbitrarily concluded that populations that differed anatomically from other populations represented distinct species, and populations that differed only in shell characters might or might not be different species. He found no geographically associated patterns of anatomical differentiation. Our observations are nearly consistent with his, except that we recognize two new subgenera which have geographically restricted distributions.

Burch and Thompson (1957) recognized two species groups. Group-I was proposed for those species that have an enlarged epiphallic chamber, have a short, stout verge, and have the dart-glands juxtaposed to the dart-sacs. Presumably this group includes the type species, *H. humboldtiana* (Pfeiffer, 1847), which remains anatomically unknown. Group-II was proposed for those species that have a vestigial epiphallic chamber, a long, slender verge, and have dart-glands separated from the dart-sacs by a distance equal to or greater than the length of the glands. The division of *Humboldtiana* into these two groups is no longer tenable. All the species we discuss below have dart-glands juxtaposed to the dart-sacs and none has an enlarged epiphallic chamber, whereas the verge may be short and stout, or elongate and tubular, or even absent. For purposes of this paper we continue to use group designations for species within the subgenus *Humboldtiana*, but the designations are somewhat arbitrary because of the lack of anatomical information on some previously described species. Also, it is apparent that many species remain to be discovered. Group boundaries and geographic patterns of speciation cannot be resolved until then. Papers dealing with the phylogenetic relationships of the family *Humboldtiana* are presumptive and contribute nothing to our knowledge of its relationships (Cuezo, 1997).

METHODS AND TERMINOLOGY

The shell descriptions of new species are based primarily on the holotype. Meristic data, as well as significant variations pertaining to the paratypes, are also included in the description. Morphological features among the paratypes that differ significantly from the character-states in the holotype are indicated in parenthesis. Individual measurements are listed for the holotype and the paratypes.

In this paper we use the term *lateral expansion rate* as a ratio of the transverse distance from the apex to the outer lip divided by the width of the shell. The ratio is useful for comparisons between species. In the female reproductive system the dart-sacs and dart-glands may be reduced in size or be absent in particular species. Two species may have non-homologous but equal numbers of reduced dart-sacs. For comparative purposes we assign a number (ds_1, ds_2, ds_3, ds_4) for each of the dart-sacs in a clockwise sequence beginning with the dart-sac that faces the atrium and penis (see Fig. 37). Abbreviations for other structures in anatomical figures are as follows:

agl	albumen gland
app	spermathecal appendix
atr	genital atrium
db	dart-bulb
dgl	dart-gland
epi	epiphallus
flg	flagellum
pen	penis
pr	penis retractor muscle
spt	spermatheca
sptd	spermathecal duct
utr	uterus
vag	vagina
vd	vas deferens
vrg	verge

Genus *Humboldtiana* Ihering, 1892
Subgenus *Humboldtiana* s. s.

Type species: *Helix humboldtiana* Pfeiffer, 1847

The shell is helicoid or depressed-helicoid in shape; usually solid; color pattern three-banded. Sculpture variable, smooth, and glossy to coarsely wrinkled; granules when present aligned parallel to axial growth striations. Spermathecal duct slender, about as long as or longer than the combined length of the uterus+vagina; spermathecal duct with an appendix. Vagina bearing dart-glands, dart-sacs, and two dart-bulbs on each side of the dart-sacs; dart-bulbs imbedded in vaginal wall and not apparent externally; dart-glands forming a ring or a partial ring around the vagina above the dart-sacs. Penis bearing a verge internally. Flagellum moderately long.

Distribution.—Widely distributed from the Guadalupe Mountains in Texas south to Puebla and Veracruz. *Humboldtiana* s. s. contains numerous species, which encompass a great deal of morphological variation. Additional subgeneric divisions may be warranted as new material becomes available for study.

Etymology.—The genus is named for the Prussian naturalist Alexander von Humboldt (1769-1859).

The *Humboldtiana buffoniana* species-group

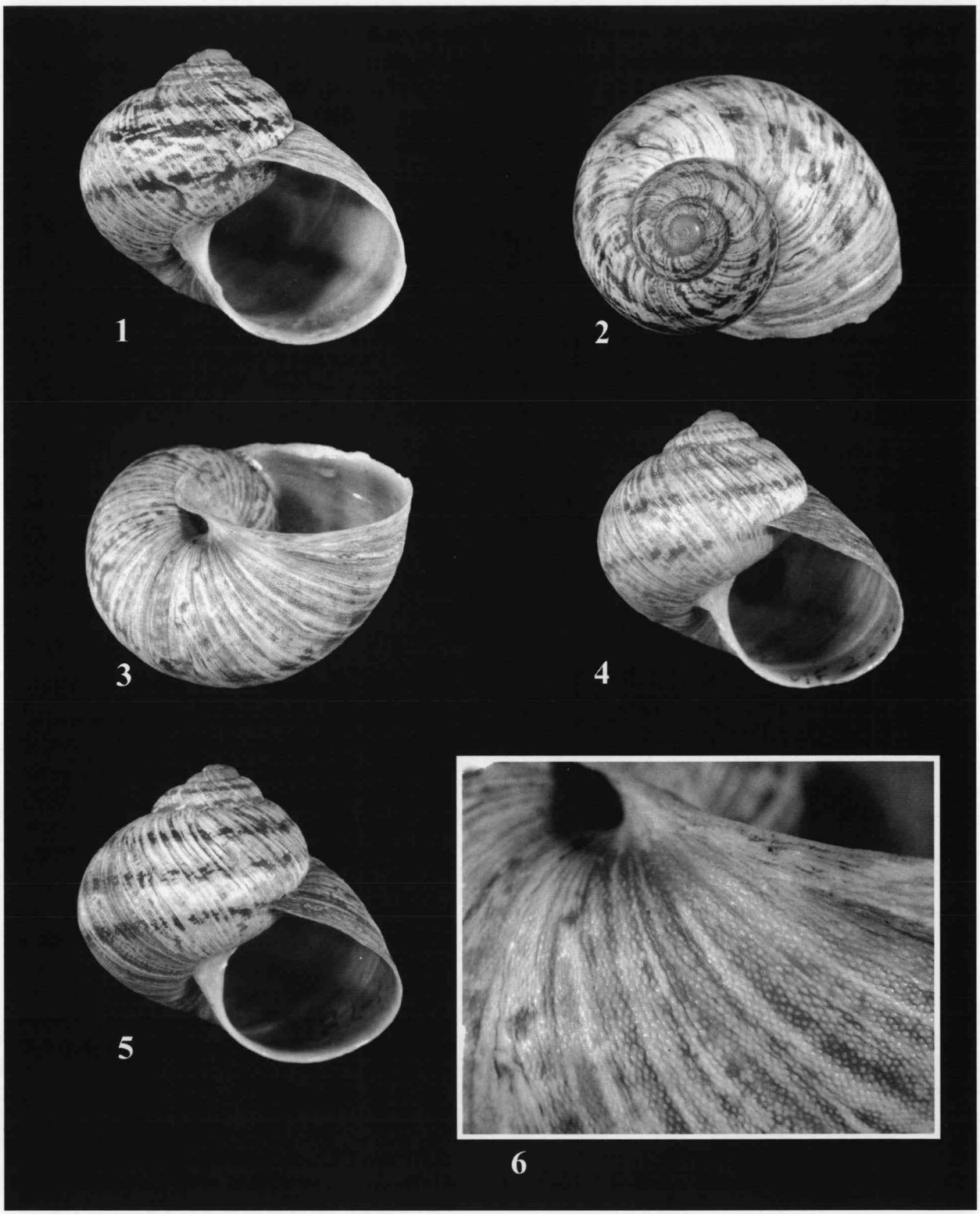
This group of species is discussed in Pilsbry (1927, 1948), and Burch and Thompson (1958). The group is typical of the genus. It is characterized by having dull, lusterless rough shells that are covered for the most part with a dense mesh of granules on and between the rugose incremental striations and wrinkles. The reproductive system has a ring of four dart-sacs on the vagina with the four dart-glands discharging into the vagina between the openings of the dart-sacs. The following two new species belong here.

Humboldtiana gradyi new species
(Figures 1-6, 7-9)

Diagnosis.—A medium-sized helicoid species of the *buffoniana* species-group. Shell about 35 mm wide and with 3.9-4.2 whorls; lateral expansion rate 0.59-0.65. The dull-colored three-banded shell is rugosely sculptured with rough incremental striations and wrinkles. Superimposed upon the wrinkles is a dense mesh of minute granules that cover the last two whorls. The growth wrinkles and the granules are white, and obscure the tan background and the three bands. The translucent interior of the aperture has a light brown wash. The umbilicus is partially open. The aperture lies at an angle of 22-30° to the shell axis. Vagina with four equal-sized dart-sacs. Spermathecal appendix less than length of distal segment of spermathecal duct. Penis bulbous at apical end, with a large tri-lobed verge internally formed from a single fold of tissue pendent from the apex and open along its side. Epiphallus longer than penis. Flagellum 1.2-1.4 times combined length of penis+epiphallus.

Among known species, the shell of *Humboldtiana gradyi* is most similar to *H. durangoensis* Solem, 1954. The latter is larger, has better defined color bands on a lighter background, is not as strongly streaked with white, the suture is more deeply impressed, and the umbilicus is reduced to a rimate perforation. The anatomy of *H. durangoensis* remains unknown.

Shell (Figs. 1-6).—Medium-sized for the genus, 33-37 mm in diameter; helicoid in shape, being 0.89-



Figs. 1-6. ***Humboldtiana gradyi*** **new species.** Figs. 1-3, 6: holotype (UF 267738). Figs. 4-5: paratypes (UF 267720).

0.98 times as high as wide. Ground color lusterless light tan with three brown bands and numerous close white axial streaks; the upper band is about halfway between the suture and the periphery; the second band is just above the periphery; the lower band is about halfway between the periphery and the base of the body whorl; bands partially obscured by white axial streaks and a dense mesh of white granules; bands become decreasingly distinct on last half whorl; apex cream-colored; peristome white; interior of aperture with a slight brown flush; exterior bands visible inside of shell. Spire conical and straight-sided with a moderately impressed suture. Shell consisting of 3.9-4.2 rapidly expanding whorls; lateral expansion rate 0.59-0.65; embryonic shell smooth (Fig. 2), 4.9 mm in diameter and consisting of 1.5 whorls; first quarter of embryonic shell depressed so that apex appears flat-topped in frontal view; subsequent whorls regularly descending along the periphery; last whorl expanding laterally, and last quarter abruptly descending to the lower band; umbilicus narrowly perforate; about 75 percent covered by the columellar reflection. Sculpture consisting of irregular, closely spaced axial growth threads and wrinkles; superimposed on and between the growth threads are numerous minute axially-elongated granules that are about 0.1 mm in length and tend to coalesce (Fig. 6); striations and granules continuous over surface of post embryonic shell. Aperture prosocline at 22-30° to vertical axis of shell; aperture oblong-ovate in shape; width equal to or slightly greater than height; with a thin, opaque, tan parietal callus; peristome very slightly reflected along base, and more so along the columellar reflection; upper end of outer lip inserted just above the edge of the lower brown band.

Measurements in mm are given for the *Humboldtiana gradyi* n. sp. holotype (UF 267738) and four paratypes (UF 267720) selected to show size variations in mature shells.

Specimen	Height	Width	ApH	ApW	Whorls
holotype	31.3	34.5	23	24	3.9
paratype	30.5	34.0	22	23	4.1
paratype	31.0	35.0	22	23	4.0
paratype	32.5	33.0	22	22	4.1
paratype	34.0	37.0	23	24	4.2

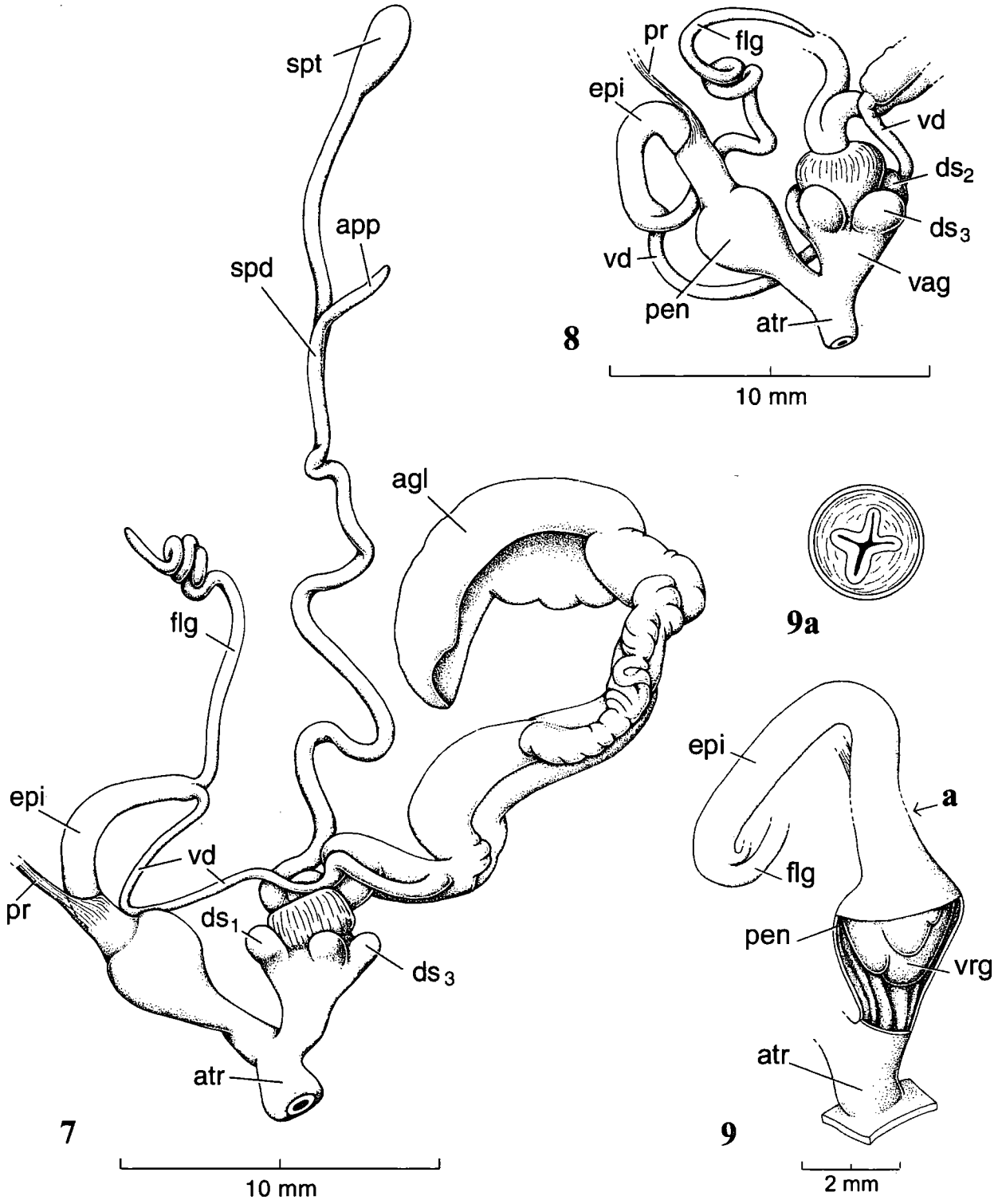
Reproductive Anatomy (Figs. 7-9, Table 1).—Typical for the subgroup of *Humboldtiana buffoniana*. The following description is based on five paratypes (UF 267720). Genital atrium very short, 1-3 mm long. Penis slender at base, upper half bulbous; interior (Fig. 9) with six longitudinal folds and containing a short, stout verge that is formed from a vertical fold of tissue that is trilobed at its lower end and is open along one edge to the roof of the penis. Penis retractor muscle about equal to or slightly longer than the penis; originating on the middle of the inner wall of the lung about one fourth of distance posterior to the mantle collar; inserting on and enveloping the base of the epiphallus. Epiphallus stocky, about half again as long as penis, lined internally with four longitudinal columns of tissue (Fig. 9a). Vas deferens nearly uniform in diameter between prostate and epiphallus. Flagellum about 1.2-1.4 times the combined length of the penis+epiphallus. Vagina relatively short with four equal-sized dart-sacs. Dart-glands juxtaposed to the dart-sacs and coalesced into a ring around the vagina. Spermathecal duct long (Fig. 7), about 1.5-1.7 times the length of the uterus; spermathecal sac elongate-elliptical in shape. Spermathecal appendix short, about 0.2-0.3 times the distal segment of the spermathecal duct; branching from duct at about 0.7-0.8 of the distance from its base. Albumen gland large and elongate. Talon and carrefour imbedded in albumen gland.

Type Locality.—DURANGO: area near the Dos de Diciembre Microwave Tower, 2 km southeast, 5 km east of Dos de Diciembre (24°44.6′ N, 103°32.7′ W); 2080 m alt. The area is on the edge of a knoll in a small range of low hills consisting of metamorphic rocks intruding through limestone and capped with caliche. The vegetation consisted of numerous *Agave americana*, *Dasylirion* sp. (sotal), *Yucca* spp., and occasional mesquite. Snails were found aestivating under *Agave*, dead *Yucca*, and sotal. HOLOTYPE: UF 267738; collected 15 June, 1997, by Grady B. Taylor, Greg P. Brewer, and Fred G. Thompson. PARATYPES: UF 267720 (10), UF 267721 (10, animals of 267720), ITCVZ 8012 (10); same data as the holotype.

Other Localities.—DURANGO: a limestone ridge 2 km SE, and 6.5 km ESE of Dos de Diciembre (24°23.1′ N, 103°30.8′ W); 2010 m alt. (UF 267685, ITCVZ).

Remarks.—The two localities where this species was collected are about 3 km apart. We observe no significant differences between the two populations in the shell or the reproductive anatomy.

The verge of *Humboldtiana gradyi* is unique among



Figs. 7-9. ***Humboldtiana gradyi*** **new species.** Reproductive anatomy of two paratypes (UF 267721). Fig. 7: complete reproductive system. Fig. 8: terminal genital structures of a second specimen. Fig. 9: interior of penis from Fig. 8. Fig. 9a: transverse section of epiphallus in Fig. 9.

known species in the *H. buffoniana* species-group. It consists of a pendent fold of tissue that is open to the apex along one side. Most other species have a tubular verge, although it may be very short, as in the following species.

Etymology.—We take pleasure in naming this species after Grady B. Taylor (San Antonio, Texas) for his companionship in the field and in recognition of his lifelong dedication to and love for shells.

Humboldtiana pinicola new species (Figs. 10-15, 16-18)

Diagnosis.—A large helicoid shell that is about 40 mm wide and consists of 4.4-4.8 whorls. Lateral expansion rate 0.59-0.64. The lusterless shell is relatively rugose with rough white incremental wrinkles and a dense mesh of granules on the last 2.5 whorls. The light brown shell bears three black bands intermittently interrupted by the white growth wrinkle. The aperture is prosocline at an angle of 32-39° to the axis of the shell.

Superficially *Humboldtiana pinicola* is most similar in shell features to *H. fasciata* Burch and Thompson, 1957 from Hidalgo, which has 4.2-4.3 whorls and an aperture that lies at a steeper angle of about 45°. However, the reproductive anatomy of *H. fasciata* is very different in that the penis is elliptical-elongate and the mucus glands on the vagina are widely separated from the dart-sacs. *Humboldtiana fasciata* is placed in the *texana* species-group.

Shell (Figs. 10-15).—Shell conical-globose in shape; medium- to large-sized for the genus, 36.5-42.6 mm wide; 0.85-1.06 times as high as wide. Spire straight-sided, 0.33-0.44 times height of shell. Shell lusterless, ground color light brown with three broad, bold, black spiral bands, of which the middle band is usually the narrowest; interior of aperture with a white flush, but clearly showing the external banded pattern through the thin shell. Suture moderately impressed. Whorls 4.4-4.8; body whorl rapidly expanding, lateral expansion rate 0.59-0.64; last quarter whorl descending below the periphery to the lower band. Embryonic shell (Fig. 11) caramel in color, with 1.6-1.7 whorls; raised and pitted; first whorl 4.2 mm wide and planar and then descending along the suture. Following whorls sculptured with coarse growth wrinkles that tend to be white and which intermittently disrupt the black bands. The last two whorls of the shell are covered with a dense mesh of small oblong-shaped granules, which are about 0.3 mm in size and tend to be aligned axially; granules largest and densest on the growth wrinkles and generally are the same color as their background; granules become weaker near the umbilicus. Aperture broadly ovate, 0.80-1.06 times as high as wide, and about 0.58-0.69 times the height of the shell; plane of aperture prosocline at an angle of 32-39° to the shell axis. Outer lip sharp but slightly reflected; basal lip thicker; columellar lip more broadly reflected and partially obstructing the narrow umbilicus; parietal wall with a thin transparent callus.

Reproductive anatomy (Figs.16-18, Table 1).—The following description is based on five paratypes (UF 268440). Genital atrium long and relatively slender, about equal to the length of the penis. Penis short and stocky, shorter than length of vagina; slightly compressed antero-posteriorly. Interior of penis with a long verge that has three or four twisted terminal lobes (Fig. 18). Verge extending to opening of vagina. Inner wall of distal half of penis with several large, thick transverse fleshy folds, and about 6-8 smaller longitudinal ridges below. Penis retractor muscle long, originating on middle of lung wall just behind mantle collar and inserting on base of epiphallus. Epiphallus short and stout; enlarged at base; entering penis eccentrically due to longitudinal compression of penis (Fig. 18); interior of epiphallus with four longitudinal folds (Figs. 17a, 17b). Flagellum relatively short for the genus (Fig. 17), about 1.7-2.6 times the combined length of the penis+epiphallus. The high ratio is due to very short length of penis and epiphallus. Vas deferens stout, but constricted at epiphallus and again above atrium (Fig. 16). Vagina capacious, almost as long as combined length of penis+atrium; bearing four unequal sized dart-sacs; ds_1 largest; ds_4 second largest; ds_2 smallest. Dart-glands forming a thick ring around vagina juxtaposed to dart-sacs. Spermathecal duct (Fig. 16) moderately long, stout, about 1.04-1.26 times length of the uterus; spermathecal sac small, bulbous; appendix shorter than distal segment of spermathecal duct; branching from duct at about 0.5-0.7 the distance from its base. Albumen gland large, reniform in shape; carrefour imbedded in albumen gland. Talon elongate, exposed.

Type Locality.—QUERÉTARO: southeast side of Cerro Puerto El Pino, limestone outcrop in an oak-pine forest ca. 6 km by road southwest of Pinal de Amoles (21°07.5′ N, 99°38.2′ W); 2650 m alt. The area consisted of sparse forest and open grassy pastures with stone fences and walls along their borders. Snails were found aestivating in crevices in limestone outcrops and stone walls and on pine trees. HOLOTYPE: UF 268441;

Table 1.— ***Humboldtiana***. Comparative measurements of the reproductive anatomy of: 1-5 ***H. pinicola*** **n. sp.** (UF 268440); 6-9) ***H. gradyi*** **n. sp.** (UF 267720); and 10) ***H. gradyi*** **n. sp.** (UF267685).

Legend: PR = penis retractor muscle, PN = penis, EP = epiphallus, FL = flagellum, AT = atrium, VG = vagina, FV = free vagina, UT = uterus, SD = spermathecal duct, SB = base of sper-mathecal duct, SP = end of spermathecal duct, AP = appendix. The length of the spermathecal duct includes the spermatheca. The end of the spermathecal duct includes the spermathecal bulb and that segment of the duct above the appendix. The base of the spermathecal duct includes that segment below the appendix.

	Spec. no.	PR	PN	EP	FL	AT	VG	FV	UT	SD	SB	SP	AP
H. pinicola n. sp. (UF 268440)													
	1	17	12	7	38	4	13	0	61	69	40	29	19
	2	18	9	7	36	4	16	0	63	67	34	33	20
	3	18	8	6	37	3	15	0	57	59	40	19	14
	4	18	8	7	38	4	14	0	49	62	36	26	14
	5	13	11	8	33	3	14	0	48	50	31	19	16
H. gradyi n. sp. (UF 267720)													
	6	11	11	14	33	3	11	2	47	71	54	17	5
	7	5	11	22	41	2	14	2	44	71	59	12	-
	8	22	9	15	33	2	10	2	46	70	55	15	3
	9	16	9	16	30	1	15	3	43	74	54	20	6
H. gradyi n. sp. (UF 267685)													
	10	20	9	9	32	3	16	7	44	69	49	20	8

collected February 1, 1998, by Steven P. Christman, and Fred G. Thompson. PARATYPES: UF 268440 (7), UF 268276 (7), ITCVZ 8013 (6); same data as the holotype.

Distribution.—This species is known only from the immediate vicinity of the type locality where it is found in pine forests and mixed hardwood-pine forests.

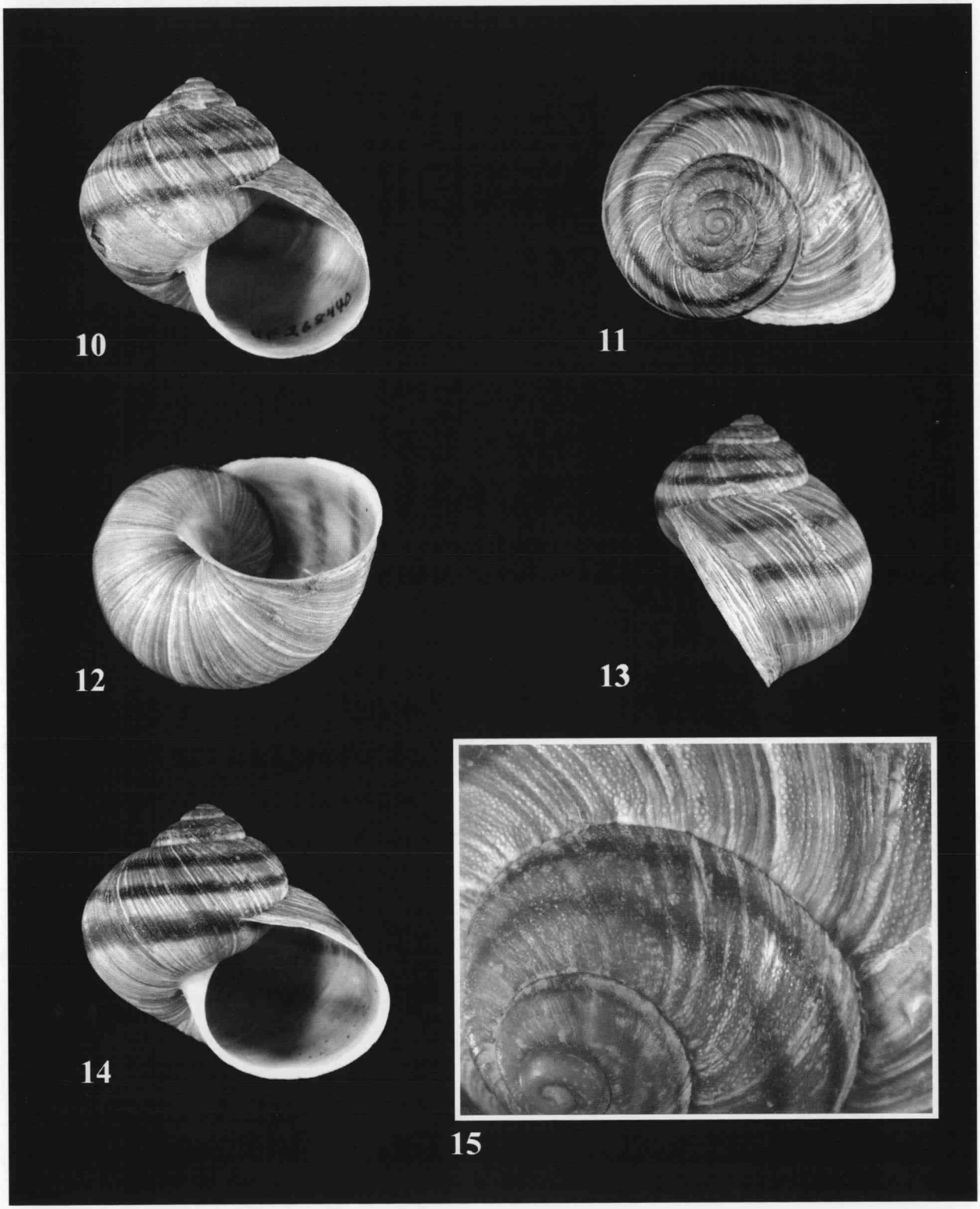
Measurements in mm are given for the *Humboldtiana pinicola* n. sp. holotype (UF 268441) and six paratypes (UF 268440) selected to show variation.

Specimen	Height	Width	ApH	ApW	Whorls
holotype	39.0	42.5	22.5	28.0	4.5
paratype	38.5	42.0	24.3	27.7	4.7
paratype	41.0	40.0	25.5	25.5	4.7
paratype	40.4	42.6	29.0	28.0	4.7
paratype	39.5	37.0	24.2	27.0	4.6
paratype	37.0	42.0	24.8	26.5	4.5
paratype	35.0	36.4	24.0	24.0	4.4

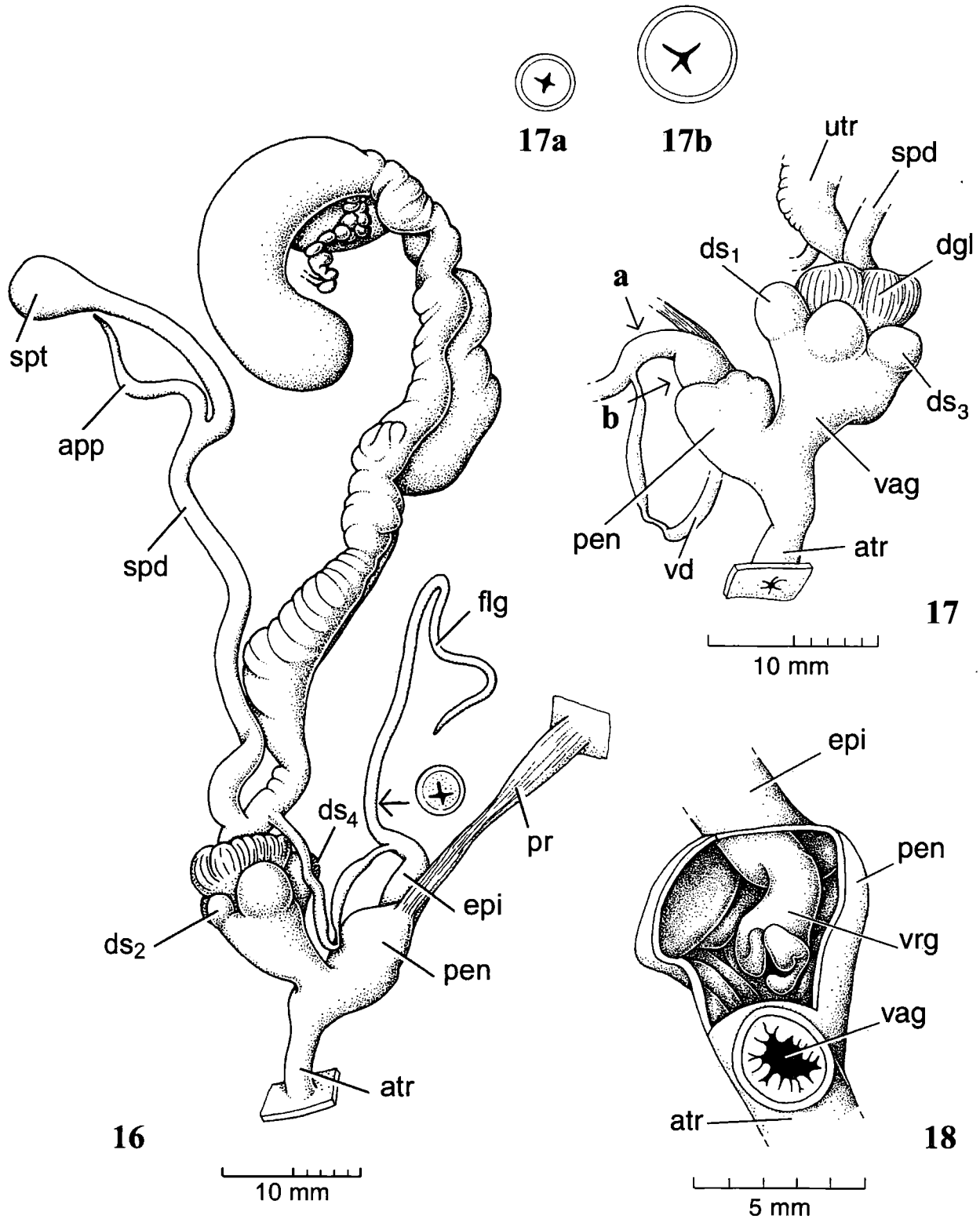
Other records of specimens referred to this species are: Pinal de Amoles, 2,600 m alt. (UF 251482); 2 km S of Pinal de Amoles, 2470 m alt. (UF 218724); 2.5 km NE of Pinal de Amoles, 2170 m alt. (21°18.5′ N, 99°37.1′ W) (UF 200692, UF 268248).

Remarks.—There is little variation among the population samples we have examined. Shells from 2.5 km NE of Pinal de Amoles have darker bands and the ground color is brighter orange-yellow.

This species occurs in the same region as *Humboldtiana queretaroana* (Dall, 1897). The latter has a higher spire, the umbilicus is nearly occluded by the reflected columellar lip, the band-less adult shell has prominent white axial streaks, and the interior of the aperture is dark reddish brown (Solem, 1955: 41). We have examined two juvenile specimens of *H. queretaroana* from Pinal de Amoles (UF 267270), the type locality. We do not have exact geographic coordinates for the locality from which the specimens were collected or the proximity of *H. queretaroana* to known populations of *H. pinicola*. The shells of *H. queretaroana* have faint indications of narrow bands.



Figs. 10-15. ***Humboldtiana pinicola*** **new species.** Figs. 10-13, 15: holotype (UF 268441). Fig. 14: paratype (UF 268440).



Figs. 16-18. ***Humboldtiana pinicola*** **new species.** Reproductive anatomy of a paratype (UF 268440). Fig. 16: complete system. Fig. 17: mesad side of lower genital anatomy; Figs.17a, 17b transverse sections of the epiphallus at points a and b in Fig. 17. Fig. 18: interior of penis.

The sculpture is similar to that of *H. pinicola*, except that the granules are more numerous and more densely packed together.

Etymology.—The species name *pinicola* is from the Latin *pinus*, a pine tree, and *cola*, a dweller, and alludes to its habitat of pine forests.

The *Humboldtiana bicincta* species-group

The following two new species differ from other north Mexican *Humboldtiana* by their depressed, shiny, nearly smooth, light-colored shells, and by the tendency for reduction of the dart-sac apparatus in the female reproductive system.

Humboldtiana bicincta new species
(Figs. 19-24, 25-29)

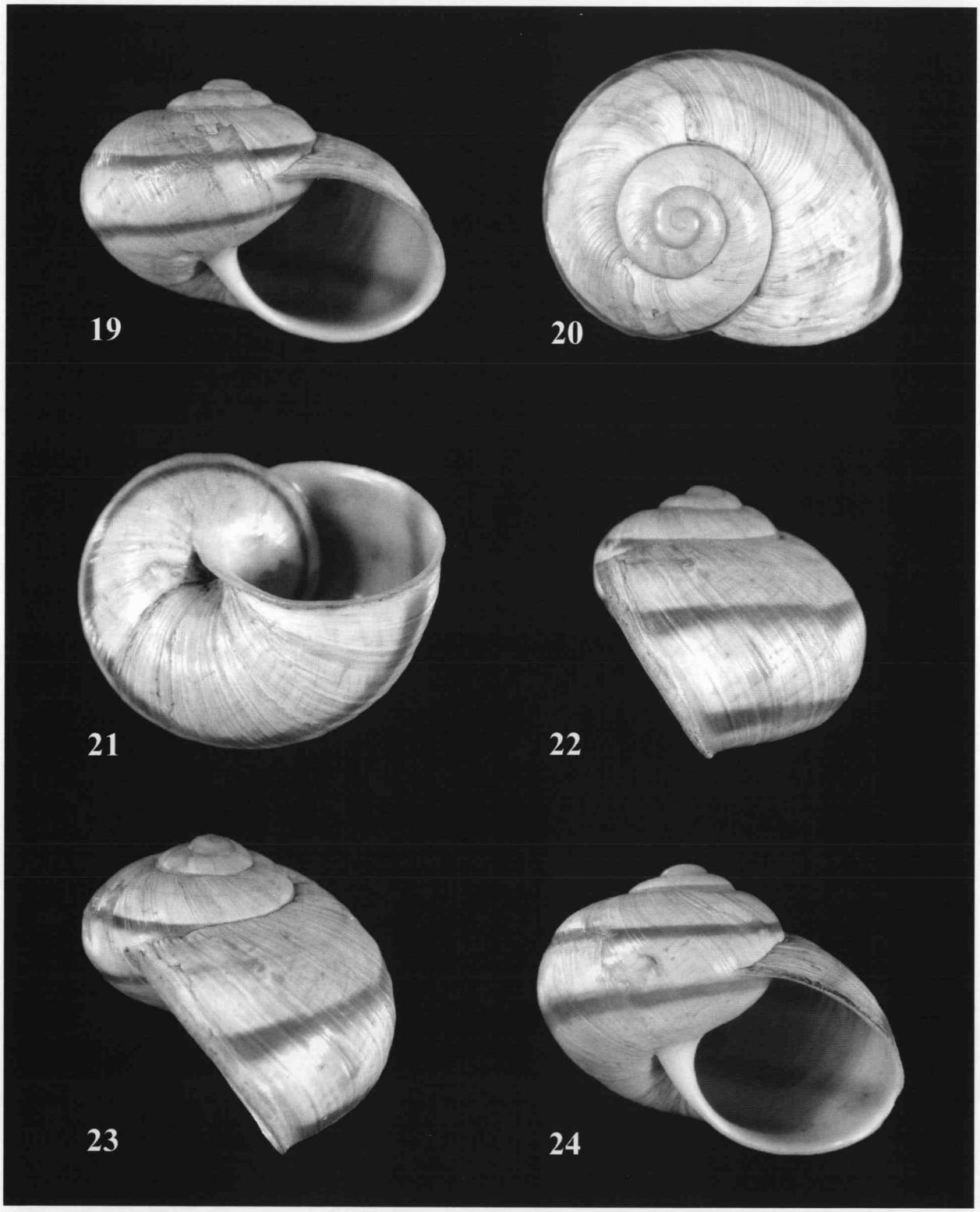
Diagnosis.—A depressed-helicoid shell that is about 30 mm wide, and 0.73-0.80 times as high as wide with an inflated body whorl. The lateral expansion rate is 0.68-0.71. The shell has two prominent peripheral dark brown bands on a lavender-white background. A very faint obsolete third dorsal band is also present. The semi-glossy shell is sculptured with fine but distinct incremental growth striations. Granular sculpture is absent. The vagina has a single functional dart-sac (ds_1) and one vestigial dart-sac (ds_3). The degree of reduction of the dart-sacs and dart-glands is unique within the subgenus *Humboldtiana*, as is also the presence of only three longitudinal folds lining the epiphallic lumen. *Humboldtiana bicincta* also differs from other known species of the subgenus by lacking an appendix on the spermathecal duct, or by having only a vestigial appendix.

Shell (Figs. 19-24).—Shell medium-sized, 23.5-25.6 mm wide; depressed-helicoid in shape with a rotund body whorl, 0.73-0.80 times as high as wide. Spire obtuse, forming an angle of 118-126°. Moderately thick-shelled, semi-glossy, smooth. Suture paralleling upper band until near the last quarter of the body whorl where it abruptly descends to the aperture. Color lavender-white with numerous darker growth streaks and three brown bands. The uppermost band on the dorsal side of the body whorl is faint but persistent. Two prominent bands parallel the periphery, one above and one below, and superficially give the shell a two-banded appearance. Interior of aperture light tan, approaching opaque white toward the peristome; external bands barely distinguishable internally. Suture weakly impressed. Umbilicus rimate. Shell with 3.9-4.1 whorls; lateral expansion rate 0.68-0.71. Embryonic shell tan colored, consists of 1.4-1.5 whorls which are 4.4-4.6 mm wide and have weak radial striation along the suture of the last half whorl. Subsequent whorls with close incremental growth striations; granular sculpture absent. Aperture obovate in shape; 0.96-0.99 times as high as wide; prosocline at an angle of 40-44° to shell axis; parietal callus thin and transparent; slightly convex in outline; peristome white or flesh-colors; slightly reflected along upper, outer, and basal margins, more so along columellar margin, which nearly covers the umbilicus.

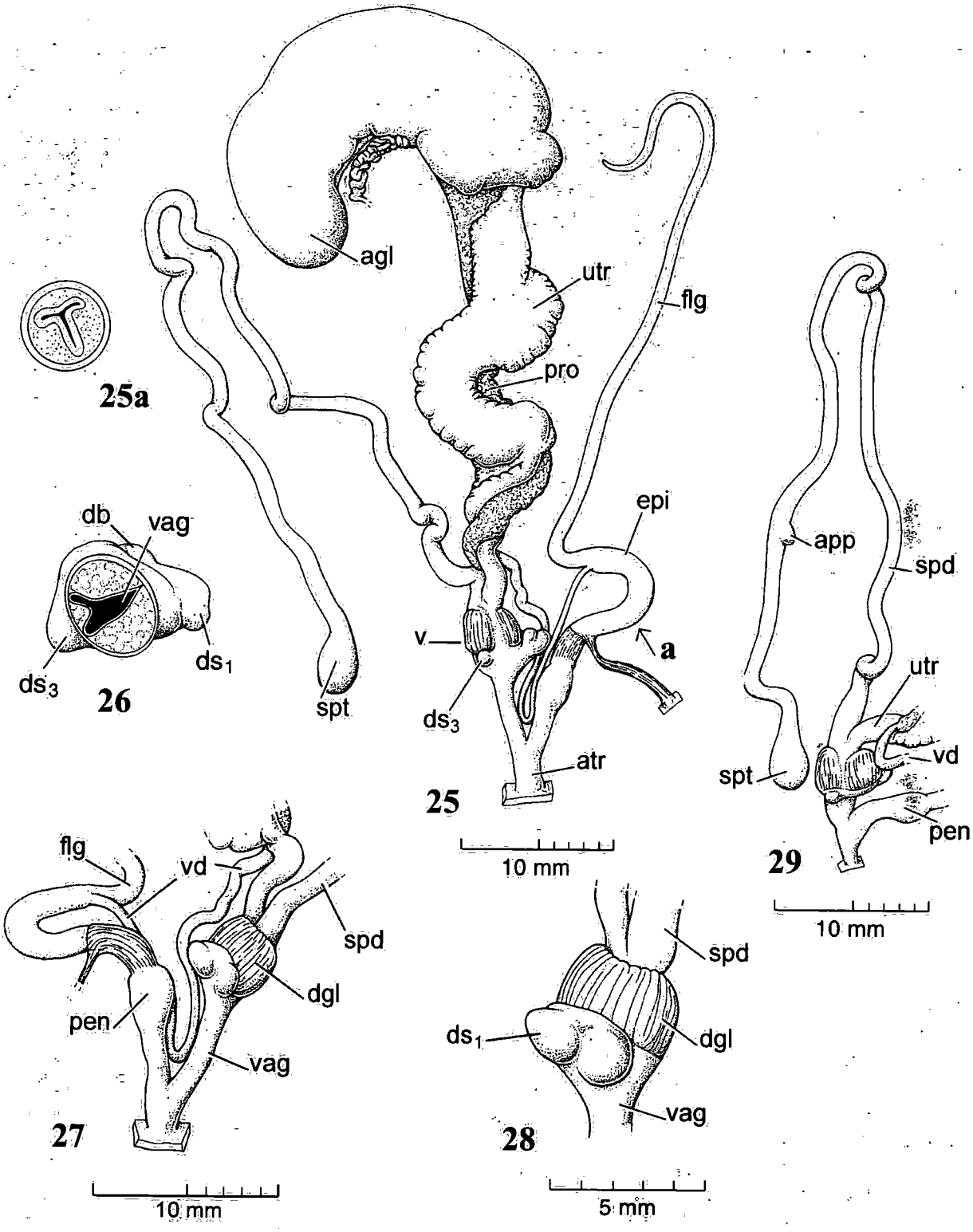
Measurements in mm are given of the *Humboldtiana bicincta* n. sp. holotype (UF 268291) and three paratypes (UF 268289, 268290).

Specimen	Height	Width	ApH	ApW	Whorls
holotype	25.1	33.2	20.1	20.5	4.0
paratype	24.0	33.0	20.5	21.3	3.9
paratype	23.5	29.8	19.1	19.5	3.9
paratype	25.6	32.0	21.0	21.2	3.9

Reproductive system (Figs. 25-29; Table 2).—The following description is based on the holotype and one paratype (UF 268290). Genital opening below right eye-stalk just above margin of foot. Genital atrium short. Penis retractor muscle short and stout; originating on right side of lung just behind mantle collar, inserting on and encompassing lower quarter of epiphallus. Penis elongate; slender below and club-shaped distally; slender base lined internally with five longitudinal folds; interior of distal club-shaped portion with two transverse fleshy folds at the bottom of the cavity; an epiphallic papilla (verge) extends into the cavity almost to its base. The end of the verge has three short lobes. Epiphallus stout and muscular; about three times as long as penis; lined internally with two stout longitudinal folds and one smaller fold (Fig. 25a). Flagellum stout and relatively long, about three times the combined length of penis+epiphallus (Fig. 25). Vagina about as long as penis; basal half of vagina slender, and with six sub-equal longitudinal folds internally; upper portion of vagina greatly enlarged; with only two dart-sacs, ds_1 on the atrial side is large and functional, ds_3 on the opposite side is small and vestigial (Figs. 25, 26); dart-sac ds_1 with two dart-bulbs imbedded in vaginal wall at base of sac (Fig. 26); dart-sac ds_3 without darts or dart-bulbs. Two



Figs. 19-24. ***Humboldtiana bicincta*** **new species.** Figs. 19-23: holotype (UF 268291). Fig. 24: paratype (UF 268290).



Figs. 25-29. ***Humboldtiana bicincta*** new species. Fig. 25: reproductive system of holotype. Fig. 25a: transverse section through epiphallus at point a in Fig. 25. Fig. 26: transverse section through dart-gland and vagina at point V in Fig. 25. Fig. 27: mesad side of lower genitalia in Fig. 25. Fig. 28: dart apparatus in Fig. 27. Fig. 29: partial female system of paratype showing vestigial appendix on spermathecal duct.

unequal-sized dart-glands nearly surround the vagina above and juxtaposed to the dart-sacs (Figs. 25, 26, 29). The larger gland lies above dart-sac ds_1. Spermathecal duct diverging from vagina immediately above dart-glands; spermatheca small and bulbous; appressed to mesad side of uterus just below albumen gland; spermathecal duct very long, about twice or more the length of the uterus+vagina, spermathecal duct *without an appendix* (Fig. 25), *or with only a small vestigial appendix* (Fig. 29). Uterus strongly folded and convoluted. Albumen gland very large and solid, about half as long as uterus. Hermaphroditic duct enlarged and strongly convoluted. Ovotestis imbedded in lower two-thirds of digestive gland; consisting of about three to six, usually four, clusters of multilobed, follicular alveoli.

Type Locality.—ZACATECAS: Sierra de Mascarón, Cuesta de Judas, 4 km south by road from Las Crucitas, 2500 m alt. (24°41.7′ N, 101°39.0′ W). HOLOTYPE: UF 268291; collected February 5, 1998, by Fred G. Thompson and Steven P. Christman. PARATYPES: UF 268290 (1), UF 268289 (2), ITCVZ 8014 (2); same data as the holotype. The Cuesta de Judas forms a narrow east-west oriented ridge which bears a sparse forest of low pines and oaks. Snails were collected at the top of the Cañon de Judas, on the south side of the ridge below the forest zone among dense stands of *Agave* sp. and some *Yucca* sp. Las Crucitas is on the north side of the Sierra de Mascarón on the road to Terminal de Providencia, and is about 37 km west of Hwy 54. The type locality is reached south of the mine Mineral de Nochebuena at Las Crucitas by a very steep mining road with numerous narrow switch-backs.

Distribution.—Known only from the type locality.

Remarks.—The systematic relationship of *Humboldtiana bicincta* is uncertain. It differs from other known species by the combination of its depressed smooth, glossy white shell that is devoid of granular sculpture, by the very much reduced dart-sac complex to one functional dart-sac and one vestigial dart-sac, by reduction of the dart-gland complex surrounding the upper vagina, and by the vestigial appendix on the spermathecal duct. Dart-sac reduction also occurs in such other species as *H. nuevoleonis* Pilsbry, 1927 (*see* Pilsbry, 1948) and *H. fortis* Pilsbry, 1948. Each has only two functional dart-sacs. Pilsbry (1948) does not identify which of the dart-sacs are lost, but interpretations can be made from his illustrations based on the relationship of the dart-sacs to the origin of the spermathecal duct. In *H. nuevoleonis*, dart sacs ds_1 and ds_2 are lost; ds_3 and ds_4 are normal-sized. In *H. fortis*, ds_1 and ds_4 are normal-sized and ds_2 and ds_3 are vestigial. Thus, the functional dart-sacs in *H. bicincta*, *H. nuevoleonis*, and *H. fortis* are not homologous. Dart-gland reductions do not occur in *H. nuevoleonis* or *H. fortis*. Rather, each retains four nearly equal-sized dart-glands that form a ring around the vagina.

The shell of *Humboldtiana bicincta* is similar to *H. torrei* Pilsbry, 1935 from "Chihuahua" and *H. eulaliae* Metcalf, 1984 from the Chihuahua-Coahuila border area near Guimbalete, Chihuahua, 1250 m alt. (27°12.0′ N, 103°47.6′ W). Both these species also lack granular sculpture on the shell. Both are three-banded, and the bands are narrower than they are in *H. bicincta*. *Humboldtiana torrei* and *H. ealaliae* remain unknown anatomically.

Etymology.—The species name *bicincta* is from the Latin *bi-*, two, and *cinctum*, a belt, and refers to the two bold spiral bands that distinguish this species.

Humboldtiana edesma new species
(Figs. 30-34, 36-41)

Diagnosis.—The shell is 30-35 mm wide and has 3.8-4.9 whorls with a lateral expansion rate of 0.66-0.71. The thin shell is depressed, medium-sized, glossy whitish with three uninterrupted bold brown bands. The sculpture consists of numerous growth striations and wrinkles; the dorsal surface of the last whorl has obsolete granular sculpture between the wrinkles. The umbilicus is only partially obstructed by the columellar reflection. The peristome is prosocline at about 42-48°. It is most similar to and geographically closest to the following species. Differences are discussed below. The reproductive system is distinct from other known *Humboldtiana* because of the short bulbous penis and the very short penis retractor muscle that inserts on the lower right side of the mantle collar.

Shell (Figs. 30-34).—Shell small- to medium-sized for the genus; depressed-helicoid in shape; adults 30-35 mm in diameter, and 0.77-0.87 times as high as wide. Spire low and obtuse, forming an angle of 110-122°. Shell smooth, glossy, cream-buff with three uninterrupted strong brown bands. Interior of aperture with a light brown tinge; translucent and showing external dark bands. Suture moderately impressed, descending abruptly just behind aperture (Fig. 33). Umbilicus narrow and partially obstructed by reflected columellar lip. Whorls 3.8-4.0, rapidly expand laterally and separated by a moderately weakly impressed suture; last quarter whorl descending to the lower band. Lateral expansion rate

0.66-0.71. Embryonic shell (Fig. 34) consisting of 1.3-1.4 buff- or cream-colored shiny whorls; 4.1-4.5 mm wide; very weak radial threads along outer edge of the last quarter whorl. The post-embryonic whorls have close growth striations and wrinkles that are strongest and recurved along the suture and become diminished below the periphery. Dorsal side of last whorl has small, weak, granular sculpture aligned radially between the wrinkles. The granules become indistinguishable below the lower band. Aperture obovate in shape and 1.01-1.15 times as high as wide. Upper corners of peristome converging closely. Parietal callus thin and transparent. Plane of aperture prosocline at 42-48° to shell axis. Peristome white or cream-colored, weakly expanded along outer and basal margins, more so along columellar reflection, which covers about half of umbilicus.

Reproductive system (Figs. 36-41, Table 2).—The following description is based on the holotype and two paratypes. Atrium very short and stout, hardly distinguishable. Penis short and bulbous. Interior with a pendant fold of tissue that extends the length of the cavity (Figs. 38, 39, 40) and surrounds a much smaller bi-lobed epiphallic papilla that extends downward as a verge (Fig. 40). Epiphallus relatively stout and about as long as, or longer than, the penis, with four longitudinal folds internally (Fig. 40a). Penis retractor muscle originating on the lower right margin of the lung at the edge of the mantle collar and inserting on the base of the epiphallus; retractor muscle very thick and short, about half the length of the penis. Flagellum long, 3-6 times the combined length of the penis+epiphallus. Vagina bearing four equal-sized dart-sacs and dart-glands. Dart-glands separated from dart-sacs by a distance almost as great as the base of the vagina. Spermathecal duct long; spermathecal sac elliptical; spermathecal appendix about equal to or greater than the length of spermathecal duct (Fig. 36); entering duct at 0.7-0.8 of the distance from its base. Albumen gland stout, reniform; talon and carrefour imbedded in albumen gland.

Type locality.—NUEVO LEÓN: Sierra San Francisco de Desmontes, east slope of Cerro La Mota, Cueva Ahumada 5 km southwest of Los Fierros (25°41.2′ N, 100°42.9′ W); 1,200 m alt. HOLOTYPE: UF 244468; collected by Greg P. Brewer, 13 August, 1995. PARATYPES: UF 271007 (2), UF 271403 (3), ITCVZ 8015 (2); same data as the holotype. Specimens were found crawling on a damp, iron oxide-colored sandstone and under sotal (*Dasylirion* sp.) skirts in a zone densely vegetated with the ubiquitous *Agave lechuguilla* and other low-growing vegetation and grasses. Numerous rodent-gnawed snail shells were scattered about the area.

Distribution.—This species is found in the Sierra San Francisco de Desmontes. The sierra is a low, dry limestone range that is aligned NE-SW across the Nuevo León-Coahuila border east of Saltillo. The type locality is at the east end of the range. The following population is referred to this species: COAHUILA: Cuesta de Büey, 5 km NE of Mesón del Norte, 1450 m (25°37.7′ N, 100°55.2′ W) (UF 268317, UF 268318, UF 271008).

Remarks.—No significant shell differences exist among the specimens from the two localities where this species was collected. However, a specimen from northeast of Mesón del Norte differs in the reproductive anatomy from the type population in several conspicuous features (Fig. 41). The penis and vagina complex is larger, the penis has a short neck above the genital atrium, the long slender penis retractor muscle originates on the mid-dorsal margin of the inner lung wall, the epiphallus is proportionally longer and not as stocky, and the flagellum is longer. Otherwise it is similar to typical *Humboldtiana edesma* in development of the bulbous penis and in the configuration of the dart-sacs and dart-glands. We tentatively consider the two populations to be conspecific. *Humboldtiana edesma* is similar to *H. bicincta* because both have relatively smooth, white shells. They differ from each other in many features of the reproductive systems, as are described above.

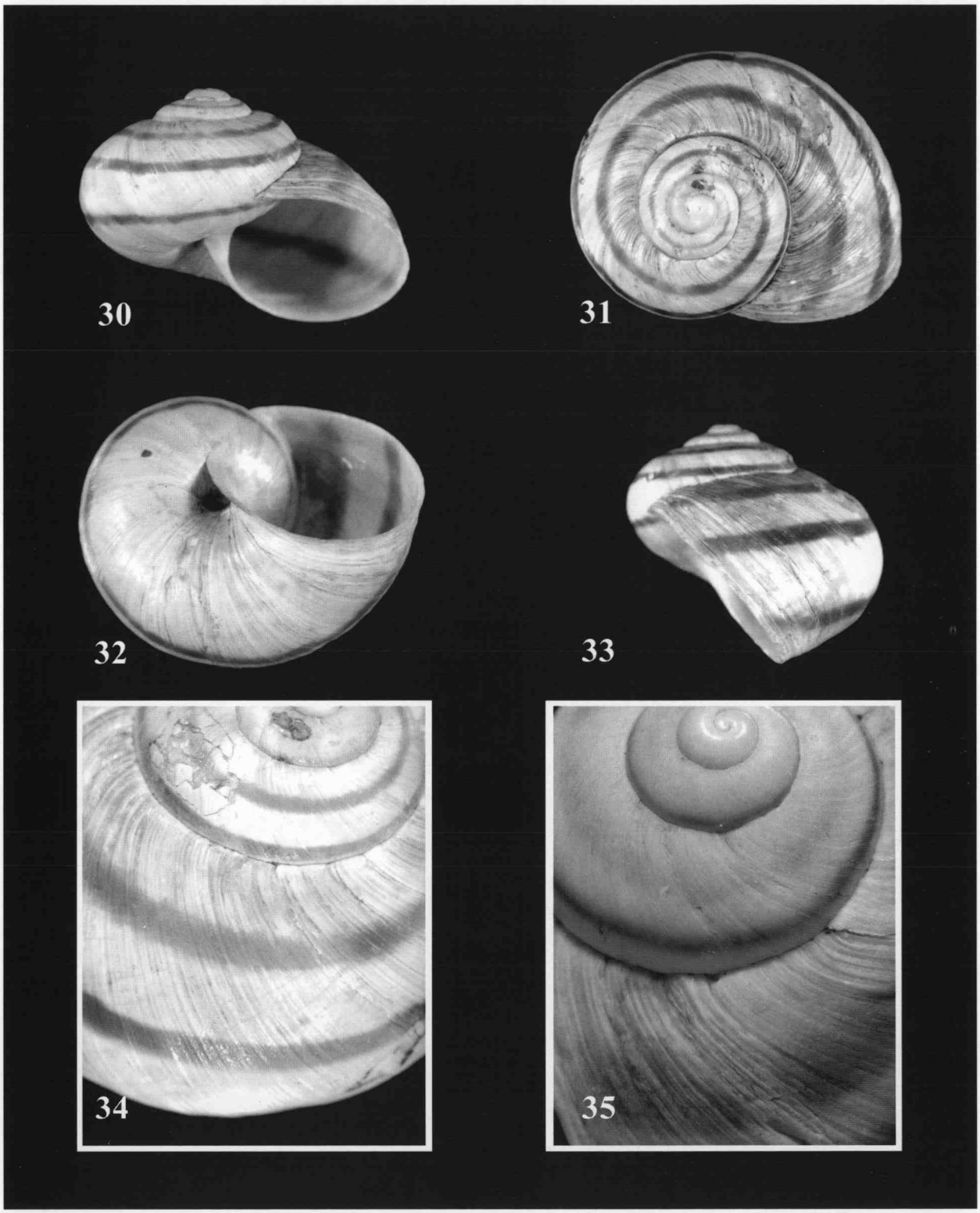
Etymology.—The species name *edesma* is from the Greek εδεσμα, meaning food or edibles such as delectable snacks, and alludes to the fact that this species, like many other land snails, is devoured by rodents.

Measurements in mm are of *Humboldtiana edesma* n. sp. holotype (UF 244468) and three paratypes (UF 271403).

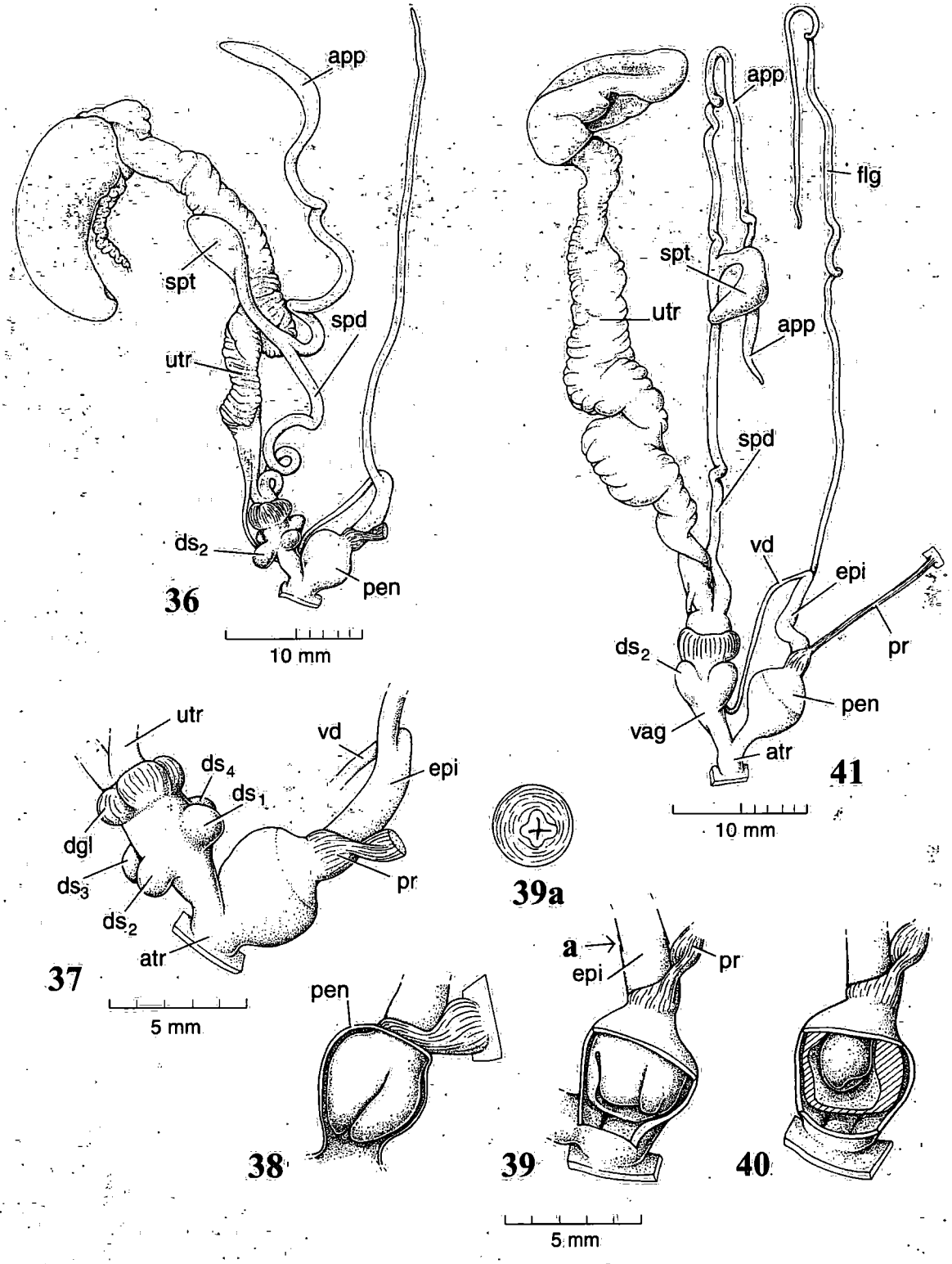
Specimen	Height	Width	ApH	ApW	Whorls
holotype	24.7	35.0	21.1	20.8	4.0
paratype	28.0	32.0	23.0	20.0	4.0
paratype	24.3	30.5	20.5	18.2	3.8
paratype	31.0	24.7	21.0	20.4	3.8

The *Humboldtiana texana* species-group

The following species tentatively is placed in this group. Its anatomy is unknown. The shells of *H. hogeana* (Martens, 1890), *H. torrei* Pilsbry, 1935, and *H. eulaliae*



Figs. 30-35. ***Humboldtiana***. Figs. 30-34: ***H. edesma*** **new species**, holotype (UF 244468). Fig. 35: ***H. latizona*** **new species**, holotype (UF 271009).



Figs. 36-41. *Humboldtiana*. Figs. 36-38: ***Humboldtiana edesma*** **new species**: reproductive anatomy of holotype (UF 244468). Fig. 36: complete system of holotype. Fig. 37: lower genitalia of Fig. 36. Fig. 38: interior of penis showing verge. Fig. 39: interior of penis of a paratype showing outer sheath of verge. Fig. 40: same specimen with verge sheath partially removed. Fig. 41: ***Humboldtiana*** **cf.** ***edesma*** **new species**; reproductive system of specimen from Cuesta de Büey (UF 268817).

Metcalf, 1984 are geographically proximal. They too remain unknown anatomically.

Humboldtiana latizona new species
(Figs. 42-47, 35)

Diagnosis.—This is assumed to be in the *Humboldtiana texana* species-group because of its semi-glossy depressed-helicoid shell, which is a common feature among species of this group, although not diagnostic. It is similar to *H. torrei* and *H. eulaliae* because of its smooth, glossy, light-colored shell. Its medium-sized shell is 31-34 mm wide, with 3.9-4.2 whorls, and is 0.77-0.85 times as high as wide. Its lateral expansion rate is 0.60-0.68. The shell is sculptured with close incremental striations and weak growth wrinkles over which are very fine granules on the dorsal and lateral surfaces of the whorls. The granules continue onto the base but are diminished in size and frequency. This species' most distinctive feature is the color pattern. The shell has three reddish-brown bands on a light tan background. A wide, diffuse rusty zone extends from the suture to the upper band and merges with it.

Shell (Figs. 42-47, 35).—Shell medium-sized, 31-35 mm wide; depressed helicoid in shape, 0.77-0.85 times as high as wide. Shiny, moderately thick. Spire broadly conical, forming an angle of 117-124°. Shell with three reddish-brown bands on a whitish-tan background. The zone between the suture and the upper band is light rust colored and blends with the band, causing the inner margin of the upper band to be poorly defined, and forming a broad sub-sutural rust-colored zone. Middle band variable in width on different specimens, separated from other bands by a light tan zone above and below. Lower band irregular in width along lower margin, and tending to expand and form blotches as it nears the peristome. Base grayish white. Parietal wall and interior of aperture with a transparent wash, clearly showing external color pattern. Umbilicus narrow, obscured by reflected columellar lip. Whorls 3.9-4.2; lateral expansion rate 0.60-0.68. Suture moderately impressed, last quarter whorl descending to the lower band (Fig. 45). Embryonic shell (Fig. 35) with 1.3-1.4 whorls; light tan in color, smooth with fine wavy radial striations along the suture of the last quarter whorl. Lower whorls with fine incremental striations and growth wrinkles, and covered with very fine elongate granules that are axially aligned; granules becoming smaller and more widely spaced on the base of the shell. Aperture obovate in shape, 0.99-1.08 times as high as wide; prosocline at an angle of 40-46° to axis of shell; upper ends of peristome closely converging. Upper and outer lip of peristome not reflected, or reflected very slightly; basal lip weakly reflected; columellar margin of peristome narrowly reflected.

Measurements in mm of the *Humboldtiana latizona* n. sp. holotype (UF 271009) and nine paratypes are as follows.

Specimen	Height	Width	ApH	ApW	Whorls
holotype	26.8	34.8	22.7	22.1	4.0
paratype	26.0	35.0	22.1	23.0	3.9
paratype	27.0	34.2	23.0	21.5	3.9
paratype	30.0	34.5	22.8	22.6	4.3
paratype	27.3	33.0	23.2	23.0	4.1
paratype	27.0	33.0	22.5	21.2	4.0
paratype	26.0	32.0	21.8	21.0	3.9
paratype	26.0	31.0	20.5	20.5	4.2
paratype	25.5	31.2	21.0	20.5	4.0
paratype	29.8	35.0	24.1	23.0	4.2

Type Locality.—DURANGO: Sierra San Lorenzo, Mesitas Coloradas, 7.5 km east of Pedriceña, 1850 m alt. (25°04.4′ N, 103°41.5′ W). HOLOTYPE: UF 271009; collected 27 December, 1969, by Fred G. Thompson. PARATYPES: UF 130585 (5), ITCVZ 8017 (5); same data as the holotype.

Distribution.—Known only from the type locality.

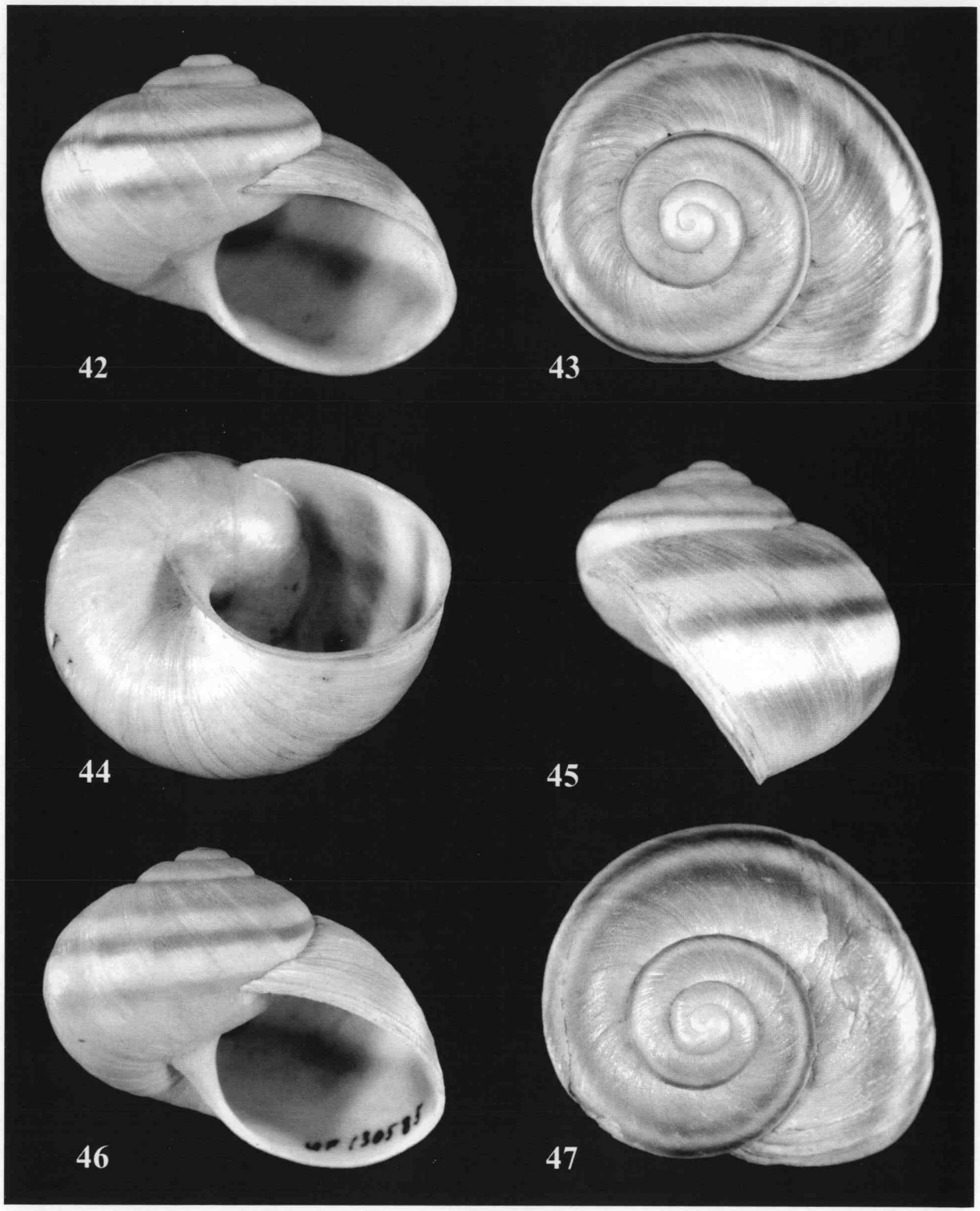
Remarks.—The color pattern of this species is unique within *Humboldtiana*. The broad rusty zone lying between the suture and the upper band, as well as the poorly defined rusty lower band, contrast strongly with other species from adjacent areas with similar shells. In *H. torrei* the three bands are sharply defined, uneven, narrow, and woody-brown (Pilsbry, 1935). The shell is devoid of granular sculpture. The shell of *H. eulaliae* has three very narrow dark brown bands, and it also lacks granular sculpture (Metcalf, 1984).

Etymology.—The name *latizona* is from the Latin *latus*, broad, and *zona*, a belt or girdle. It alludes to the wide reddish zone on the last whorl between the suture and the upper band.

Oreades new subgenus

Type species.—*Humboldtiana porterae* new species

The shell is helicoid in shape; thin and fragile compared to other *Humboldtiana*; color pattern three-banded, as



Figs. 42-47. ***Humboldtiana latizona*** **new species.** Figs. 42-45: holotype (UF 271009). Figs. 46-47: paratypes (UF 130585).

is typical for the genus; sculpture consisting of coarse incremental growth striation and elongate granules aligned parallel to growth striations. Spermathecal duct short and stout; duct lacking an appendix. Vagina lacking dart sacs, dart bulbs, or dart glands. Penis slender, lacking a verge internally. Flagellum very short, about one-third the combined length of the penis+epiphallus.

The reproductive anatomy of *Oreades* differs from that of all other Humboldtianidae by its highly derived apomorphic character states. These include the complete loss of dart sacs, dart glands, and dart bulbs on the vagina; having a short spermathecal duct that is about one-half the combined length of the vagina-uterus; lacking an appendix on the spermathecal stalk; and lacking a verge in the penis. There is a tendency for reduction or loss of various of these structures among particular species within the subgenus *Humboldtiana*, but none approaches the reduced character state that distinguishes *Oreades*.

Distribution.—*Oreades* is known only from the Cañon de Garcia, Nuevo León.

Etymology.—The subgeneric name *Oreades* (f.) is from the Greek ορεαδες, meaning nymphs who inhabit hills, and alludes to the snail's graceful, delicate shell and its natural habitat.

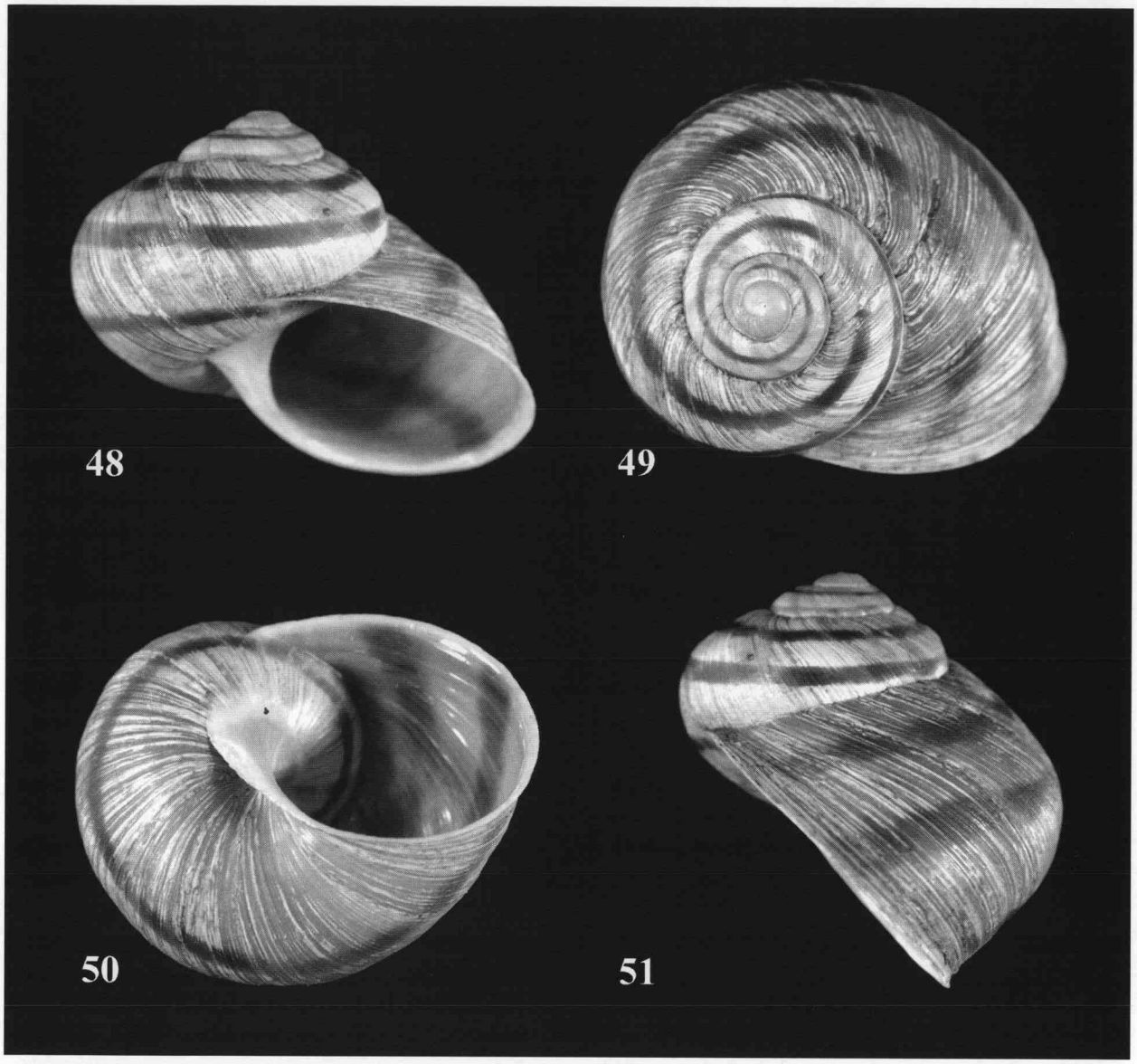
Humboldtiana porterae new species
(Figs. 48-51, 52-54)

Diagnosis.—This species has a large depressed-helicoid shell. It is readily recognized by its color pattern, which consists of three uninterrupted bold chocolate-brown bands overlaying a tan background streaked with numerous transverse white growth wrinkles. The sharply defined spiral bands on the lighter streaked background give this species a very elegant appearance.

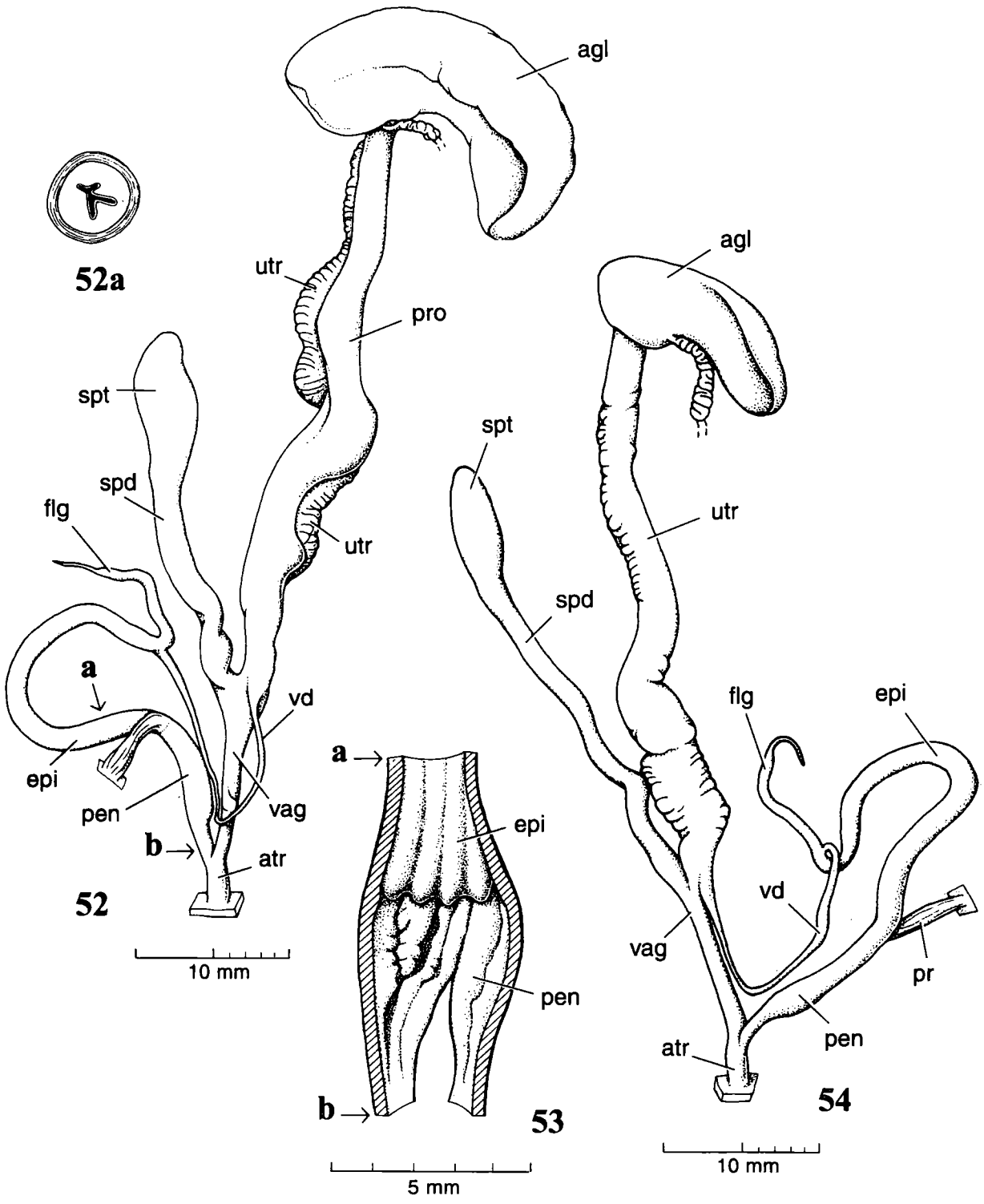
Shell (Figs. 48-51).—Adults 38-41 mm in width, depressed-helicoid in shape, 0.78-0.83 times as high as wide. Thin, shiny. Color pattern consisting of three sharply defined chocolate-brown bands on a chalky-white ground color which becomes increasingly tan toward aperture. Ground color interrupted by numerous transverse, narrow, white-streaked growth wrinkles that do not interrupt spiral bands. Spiral bands are not uniform in width; middle band usually the widest. Peristome light tan. Interior of aperture with a light brown translucent wash showing external bands. Apex low, obtuse, forming an angle of 104-115°. Suture moderately impressed, descending below the periphery on the last quarter whorl. Umbilicus rimate in adults. Whorls 4.1-4.3, rapidly expanding, lateral expansion rate 0.65-0.67. Last quarter whorl descending below the periphery to the lower band. Embryonic shell 5.0-5.3 mm wide, consisting of 1.3 smooth whorls with radial striation along the suture. Postembryonic whorls with rugose transverse striations and wrinkles. The latter bear numerous weak elongate granules that are axially aligned and occur on the last 2.5 whorls; they tend to diminish on the fourth whorl above and below the periphery, but they may occur sporadically into the umbilical area in occasional specimens. Aperture prosocline, lying at an angle of 40-48° to shell axis. Aperture obovate, 0.97-1.04 times as high as wide. Parietal callus thin, transparent. Peristome uniformly reflected along outer and basal lip; columellar lip strongly reflected, appressed, and nearly occluding umbilicus.

Reproductive system (Figs. 52-54, Table 2).—The following description is based on two topotypes (UF 271399). The shells of both were shattered while extracting the bodies. Atrium moderately short and narrow. The penis retractor muscle originates on the right side of the inner wall of the lung immediately behind the mantle collar and inserts on the apex of the penis. The penis is slender, nearly cylindrical, slightly narrowed near base; undifferentiated externally from epiphallus, except for insertion of the penis retractor muscle. Interior of penis lined with several longitudinal fleshy pilasters (Fig. 53). A verge is absent. The opening from the epiphallus is surrounded by four triangular fleshy papillae that protrude into the penis lumen (Fig. 53). The papillae are short extensions of four longitudinal folds lining the interior of the epiphallus (Fig. 52a). The epiphallus is relatively long, stout, and nearly uniform in diameter throughout its length. It is 2.2-2.5 times the length of the penis. It bears a very short flagellum that ends in a slender filament. The very short flagellum is about one-third the combined length of the penis+epiphallus. The vas deferens is slightly enlarged near the epiphallus, but otherwise is nearly uniformly narrow throughout its length. The vagina is elongate and slender. It lacks dart sacs, dart glands, and dart bulbs. The apex of the vagina is slightly enlarged below the uterus. The spermathecal duct is short and stout, and lacks an appendix. It is appressed against the middle of the uterus and is 0.48-0.82 times the length of the uterus. The spermathecal bulb is elongate-elliptical in shape.

Type Locality.—NUEVO LEÓN, Cañon de Garcia, 7 km northeast of Villa de Garcia (25°50.5′ N, 100°31.5′ W), 950 m alt. HOLOTYPE: UF 39938; collected June 21, 1982, by Fred G. Thompson and Charlotte M. Porter.



Figs. 48-51. ***Humboldtiana porterae*** **new species**, holotype (UF 39938).



Figs. 52-54. ***Humboldtiana porterae*** **new species.** Reproductive anatomy of two topotypes (UF 271399). Fig. 52: complete reproductive system. Fig. 52a: transverse section through epiphallus at point **a** in Fig. 52. Fig. 53: interior of penis and epiphallus between points **a** and **b** in Fig. 52. Fig. 54: reproductive system of a second topotype.

Measurements in mm of the *Humboldtiana porterae* n. sp. holotype (UF 39938) and four mature paratypes (UF 251528, UF 271005) are as follows.

Specimen	Height	Width	ApH	ApW	Whorls
holotype	32.0	39.8	26.5	27.2	4.3
paratype	32.0	41.0	27.7	28.1	4.1
paratype	31.0	38.1	27.2	26.1	4.2
paratype	33.5	41.0	27.0	27.2	4.3
paratype	32.0	38.6	26.1	34.5	4.1

PARATYPES: UF 271005 (2 mature and 4 immature shells); UF 271008 (1 immature), ITCVZ 8016 (2 mature shells), same data as the holotype; UF 251528 (7), collected December15, 1995, by Fred G. Thompson; UF 251528(3), collected February 1, 1999, by Greg P. Brewer. Non-paratypic topotypes: UF 271399 (2, anatomical specimens, shell crushed), collected February 1, 1999, by G. P. Brewer.

The type locality is along the north face of the south rim of the canyon, on a nearly vertical limestone cliff and is on the west side of the pass into the canyon. The xeric vegetation consists of clusters of *Agave lechugilla*, *A. bractiosa*, *Opuntia* sp., *Dasylyrion* sp., *Sedum* sp., *Acacia* sp., and a bunch-grass. Live snails appear to be highly dependent on *Agave bractiosa* for coverage. This small clumping *Agave* was growing out of the north-facing vertical limestone cliffs. Live specimens were attached to limestone under *A. bractiosa* or in rock crevices. We did not find *Humboldtiana porterae* associated with other vegetation.

Distribution.—This species is known only from the type locality.

Etymology.—We take pleasure in naming this species after Charlotte M. Porter, Curator of History of Science, Florida Museum of Natural History, who assisted in collecting the type specimens.

Polyomphala new subgenus

Type species.—*Humboldtiana oreina* new species

The shell is discoidal in shape; moderately thin; color pattern three-banded, obscured by a diaphanous wash in the periostracum. *Sculpture consisting of sparse large nodular tubercles that are arranged in short segments aligned transverse to the incremental growth striations.* Inner wall of aperture rippled by external sculpture. Spermathecal duct slender, longer than the combined length of the uterus+vagina; spermathecal duct with an appendix. Vagina bearing four dart glands, four dart sacs, and two dart bulbs on each side of the dart sacs; *dart bulbs exposed.* Penis asymmetrical; bearing a large verge internally. Flagellum very long, about eight times the combined length of the penis+epiphallus.

The depressed shell, the pustular sculpture arranged into short segments transverse to the growth striations, the asymmetrical bulbous penis, the length of the flagellum, and the exposed dart-bulbs at the base of the dart sacs are unique features among known *Humboldtiana*. In the subgenus *Humboldtiana* dart-bulbs are deeply imbedded in the vaginal wall and are not superficially visible. *Bunnya* Baker, 1942 is the only other genus besides *Humboldtiana* in the Humboldtianidae. It is a slug-like snail with a vestigial shell imbedded in the mantle. Like *Polyomphala*, it too has two superficially visible dart-bulbs associated with each dart-sac.

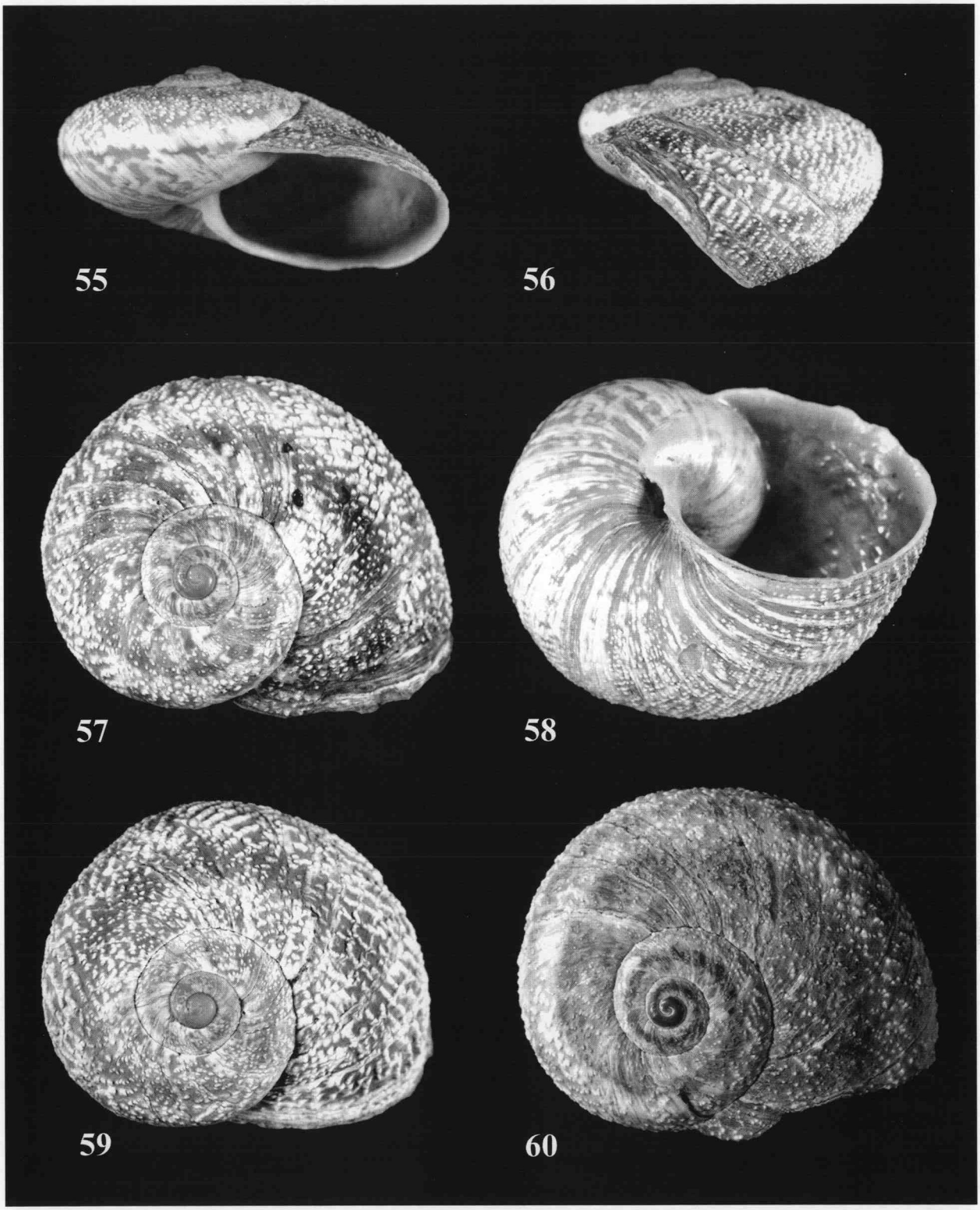
Distribution.—Known only from the Sierra Encantada and the adjacent Sierra Santa Rosa in northern Coahuila.

Etymology.—The subgeneric name *Polyomphala* (f.) is from the Greek πολυ, meaning many, and ομφαλοζ, a knob or boss, and alludes to the coarse, nodular shell sculpture characteristic of this subgenus

Humboldtiana oreina new species (Figs. 55-59, 61-64, 68)

Diagnosis.—A moderately large, nearly planular shell with rugose sculpture that is arranged into elongate pustular ridge-segments along the periphery. The segments are aligned transverse to the incremental growth striations. The sculpture becomes beaded near the suture (Fig. 68), and below the periphery. The base of the shell is smooth. The umbilical perforation is only partially covered by the reflected columellar lip (Fig. 58). The shell has three brown bands that are disrupted and obscured by the white pustular sculpture and by white growth wrinkles. The reproductive system is characterized in the diagnosis for the subgenus *Polyomphala*.

Shell (Figs. 55-59).—Shell moderately large, about 36-41 mm in width; nearly planular, 0.53-0.60 times as high as wide; apex very low and forming an obtuse angle of 136-148°. Shell with 3.9-4.3 rapidly expanding whorls;



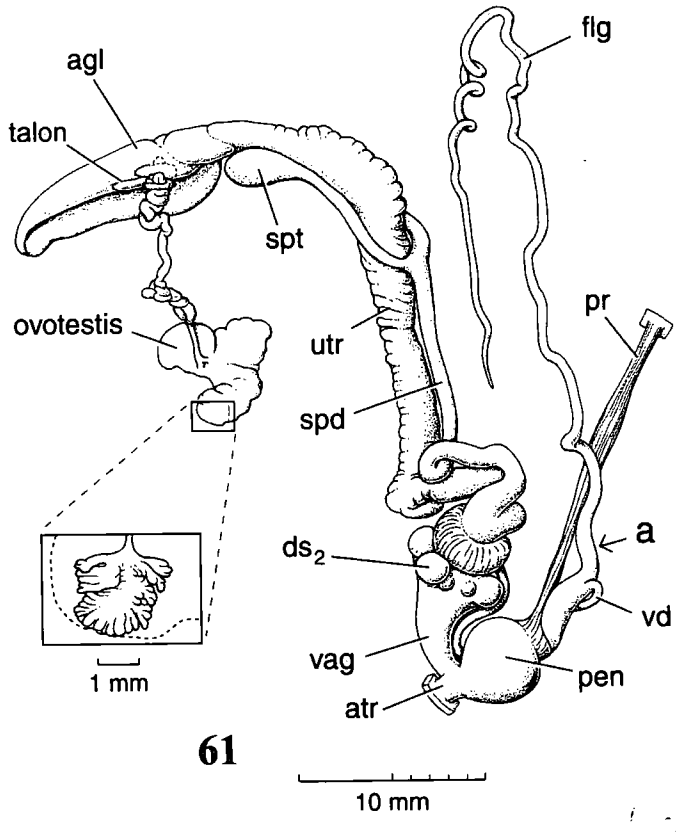
Figs. 55-60. Shells of *Humboldtiana*. Figs. 55-59: ***Humboldtiana oreina*** **new species.** Figs. 55-58: holotype (UF 271518) Fig. 59: paratype (UF 244910). Fig. 60: ***Humboldtiana plana*** **Metcalf and Riskind, 1976,** holotype (DMNH 106681).

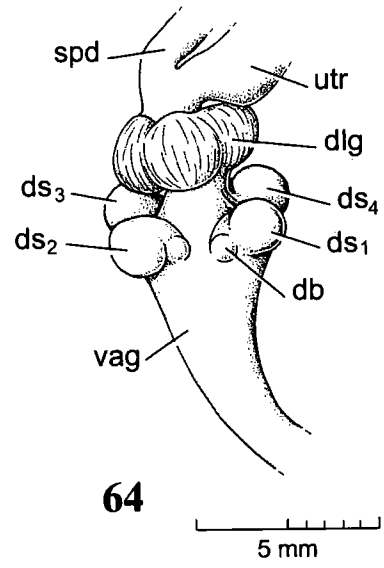
lateral expansion rate 0.59-0.63; last whorl flattened above and forming an obtuse angle at the periphery. Embryonic whorls 1.3, protruding. Last quarter of body whorl descending below lower band (Fig. 55). Suture weakly impressed. Color pattern consisting of three diffuse brown bands on a light gray background above and laterally; base with streaks and patches of diaphanous light brown near umbilicus and peristome. Bands obscured by the white pustular ridge-segments and incremental white growth wrinkles. Dorsal band about as wide as its distance from suture. Middle band lying just above the periphery, and is the least clearly defined. Lower band located just below periphery, narrow and tending to be the most sharply defined of the bands. Peristome whitish. Interior of aperture light magenta-brown, vaguely showing exterior bands, and may appear reticulated due to external pustular sculpture; parietal callus opaque white. Embryonic whorls smooth but with fine radial striations along the suture of the last quarter whorl (Fig. 68). Following whorls sculptured with coarse white granular pustules, which on last whorl form numerous parallel pustular ridge-segments that are aligned transverse to the incremental growth striations (Fig. 59); pustular segments strongest along periphery. Dorsally they become smaller scattered beads near the suture. Below the periphery they are reduced in size to scattered granules; base of shell smooth. Aperture oblong-elliptical in shape; 0.86-0.88 times as high as wide. Peristome reflected along outer lip, becoming narrow along base, and then expanding along columellar margin to partially occlude umbilicus. Plane of aperture lying at 49-59° to shell axis.

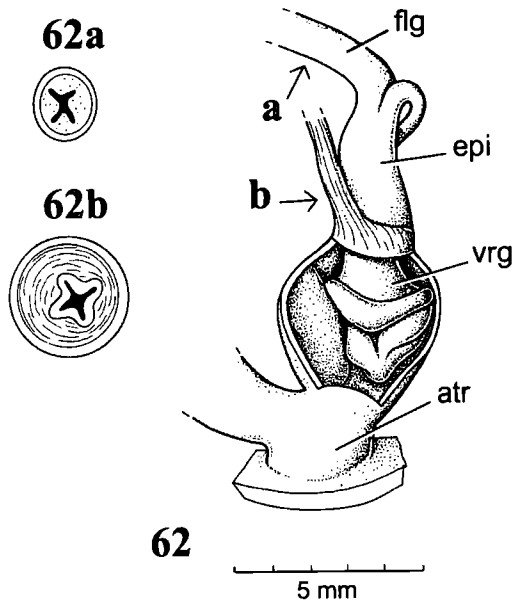
Anatomy (Figs. 61-64).—The following description is based on two topotypic specimens (UF 244911). The shells of both were crushed while extracting the bodies. *External features*. The head-foot is brown, becoming lighter-colored on the nape and darker posteriorly to the end of the tail. The mantle collar is bright orange. The mantle is dark gray. The tail is dorso-ventrally flattened and is covered by very fine granular pustules, which become enlarged along the sides of the foot, and change into large fleshy pebbles on the upper sides and nape. The kidney is elongate and tapers to a narrow rounded point anteriorly. The aorta branches profusely to the mantle collar. *Reproductive system* (Figs. 61-64, Table 1). Genital atrium very short, nearly indistinct. Penis retractor muscle very slender, originating on center of inner wall of lung at edge of mantle collar; inserting on and forming a sheath surrounding base of epiphallus. Penis very short and bulbous; inner wall of penis with three thick longitudinal fleshy pilasters, one or more of which is enlarged, causing the penis to be acentric on one side (Fig, 63). Interior of penis with a large verge that extends nearly to base of penis lumen (Fig. 62). End of verge with a complexly twisted collar and lobes. Epiphallus short and stout, enlarged near penis, lined internally with four longitudinal folds (Fig. 62b). Flagellum very long and slender, about eight times combined length of penis+epiphallus; flagellum lined internally with four fleshy columns (Fig. 62a). Vas deferens uniformly slender. Vagina relatively long and conical compared to most other *Humboldtiana*, bearing four equal-sized dart-sacs, each of which has two distinct dart-bulbs at its base (Fig. 64). Four dart-glands coalesced to form a ring around vagina immediately above dart-sacs. Spermatheca small, elongate-bulbous; impressed against upper end of prostate-uterus at base of albumen gland (Fig. 61). Spermathecal duct very long, diverging from uterus just above dart-glands; bearing a short appendix which originates from spermathecal duct about 0.8 of distance from base of duct (Fig. 63); appendix about as long as distal end of the duct+spermathecal bulb. Albumen gland with a long groove on its ventral surface where it overlays intestine. Talon exposed along axial edge of groove. Carrefour partially exposed at base of hermaphroditic duct. Ovotestis forming a large tri-lobed cluster of acini in third whorl of digestive gland (Fig. 61).

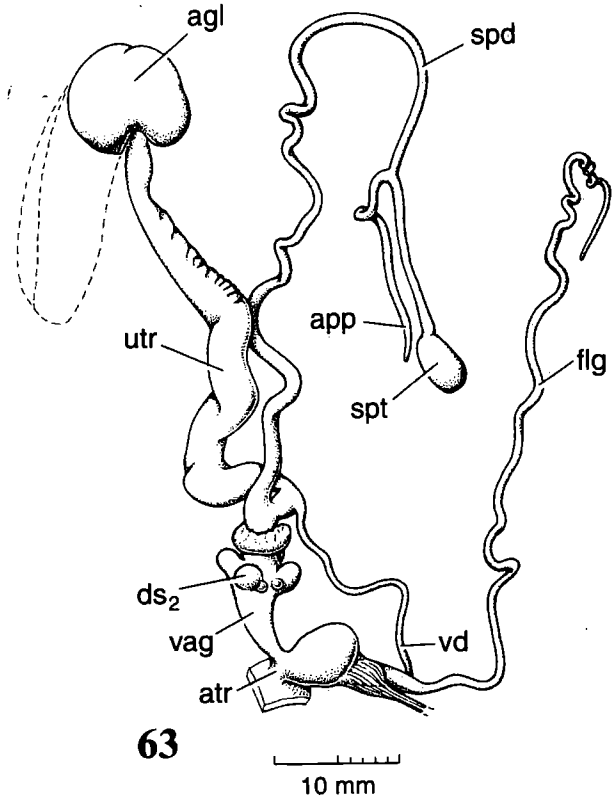
Measurements in mm of the *Humboldtiana oreina* **n. sp.** holotype (UF 271518) and of five adult paratypes (UF 244190) selected to show variation are as follows. Measurements for the holotype of *H. plana* (DMNH 106681) are also included. Exact measurements for *H. plana* are estimated because the last (quarter) whorl is fractured.

Specimen	Height	Width	ApH	ApW	Whorls
holotype	21.0	39.8	23.0	26.0	3.9
paratype	24.0	40.0	22.5	26.0	4.2
paratype	24.2	40.5	23.0	26.0	4.3
paratype	20.2	38.1	21.8	25.0	4.0
paratype	21.0	37.0	20.1	22.8	4.2
paratype	20.0	36.0	21.0	24.0	4.0
H. plana	23.8	42.5	20.1	26.0	4.0









Figs. 61-64. ***Humboldtiana oreina*** **new species.**. Fig. 61: reproductive anatomy of a topotypic specimen (UF 244911). Fig. 62: Lower male genital system of Fig. 61 showing interior of penis. Fig. 62a: transverse section through flagellum at point a in Fig. 62. Fig. 62b: transverse section through epiphallus at point b in Fig. 62. Fig. 63: reproductive system of a second topotypic specimen. Fig. 64: enlargement of vagina in Fig. 63 showing details of dart apparatus.

Table 2.- *Humboldtiana*. Comparative measurements of the reproductive anatomy of: 1-2) *H. bicincta* n. sp. (UF 268291, UF 268290) (1, holotype; 2, a contracted paratype); 3-4) *H. edesma* n. sp. (UF 271007, 2 paratypes); 5) *H. edesma* n. sp. (UF 268317); 6-7) *H. porterae* n. sp. (UF 271399), and 8) *H. oreina* n. sp. (UF 244911).

Legend: PR = penis retractor muscle, PN = penis, EP = epiphallus, FL = flagellum, AT = atrium, VG = vagina, FV = free vagina, UT = uterus, SD = spermathecal duct, SB = base of sper-mathecal duct, SP = end of spermathecal duct, AP = appendix. The length of the spermathecal duct includes the spermatheca. The end of the spermathecal duct includes the spermathecal bulb and that segment of the duct above the appendix. The base of the spermathecal duct includes that segment below the appendix.

	Spec. no.	PR	PN	EP	FL	AT	VG	FV	UT	SD	SB	SP	AP
H. bicincta n. sp. (UF 26891, UF 268290)	1	4	4	12	45	3	13	8	31	82	—	4	—
	2	5	6	13	42	—	—	—	42	77	52	3	2
H. edesma n. sp. (UF 271007)	3	1.5	4	7	34	1	7	2	33	43	34	9	42
	4	2	4	4	48	1	6	3	23	36	26	12	43
H. edesma n. sp. (UF 268317)	5	12	7	11	61	3	12	5	36	31	21	10	39
H. porterae n. sp. (U F 271399)	6	10	12	27	13	4	14	—	41	34	—	—	—
	7	7	12	29	13	3	10	—	36	16	—	—	—
H. oreina n. sp. (UF 244911)	8	15	5	4	72	1	11	0	36	87	71	16	17

Distribution.—Known only from the type locality.

Type locality.—COAHUILA: Sierra La Encantada, La Ventana Cañon de Boquilla, 27 km WNW of Hacienda La Babia, 91 km NW of Melchor Musquíz (28°39.1' N, 102°19.5' W), 1150 m. HOLOTYPE: UF 271518; collected by F. G. Thompson, Scott Ogden, Val Roessling, and Grady B. Taylor 12 September, 1995. PARATYPES: UF 244910 (10), UF 268907 (6), ITCVZ 8018 (5). Other specimens: UF 244911 (3 topotypic preserved specimens).

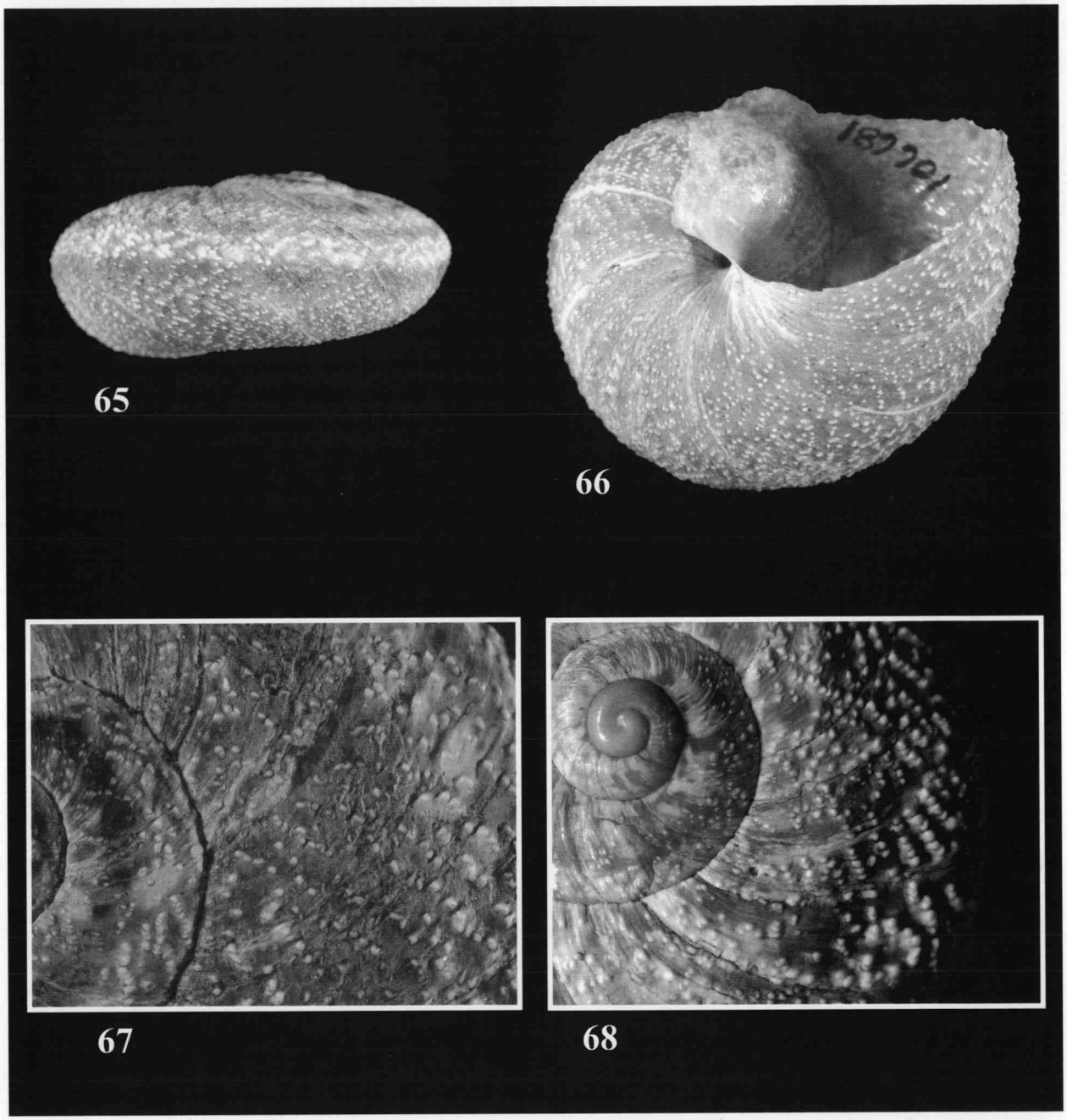
Remarks.—In *Humboldtiana oreina* the long spermathecal duct, the long flagellum, and the bulbous penis with its highly modified elongate verge comprise differences that are unique within *Humboldtiana*. However, these peculiarities of the spermathecal duct, the flagellum, and the penis are differences of degree and may be significant only as species criteria. *Humboldtiana plana* Metcalf and Riskind, 1976 is the only other species assigned to *Polyomphala*. The latter is unknown anatomically (see below).

Etymology.—The species name *oreina* is from the Greek ορεινα, meaning a mountaineer and alludes to the snails habitat.

Humboldtiana plana Metcalf and Riskind, 1976 (Figs. 60, 65-67)

Humboldtiana plana Metcalf and Riskind, 1976; Nautilus 90:99-100; Figs. 1-3 (shell)

This species is known only from the holotype shell which is broken along the last quarter whorl (Figs. 60, 65-67). Its measurements are given with those of the previous species. The shell is slightly larger than that of *Humboldtiana oreina*, it is more depressed (Figs. 65, 56, respectively) and the umbilical perforation is more narrowly rimate because of the reflected columellar lip (Fig. 66). As is typical for the subgenus *Polyomphala*, the sculpture is dominated by large nodular tubercles arranged into short segments along the periphery of the shell. The sculpture of *H. plana* differs from that of *H.*



Figs. 65-68. Shells of *Humboldtiana*. Figs. 65-67: ***Humboldtiana plana*** **Metcalf and Riskind, 1976,** holotype (DMNH 106681). Figs. 68: ***Humboldtiana oreina*** **new species,** paratype (UF 244910).

oreina in that the granules on the dorsal surface of the whorls are smaller and sparser (Figs. 67, 60, respectively), the granules on the base encroach into the umbilical area, and the segments of enlarged tubercles along the periphery are shorter (Figs. 67, 56, respectively).

Type locality.—COAHUILA: Mpio. de Muzquía [Hacienda La Babia], Sierra de Santa Rosa near the summit of Rincón de Maria, in a sheltered mesic cleft on a massive limestone cliff with a northern exposure (28°28'N, 102°04'W). Holotype: Delaware Museum of Natural History 106681; collected by David H. Riskind *et al.* August 23, 1975.

Distribution.—Known only from the type locality.

Etymology.—This species is named after David H. Riskind, who discovered it while searching for Native American rock-paintings.

ACKNOWLEDGMENTS

We wish to express our appreciation to the following people who have assisted us in this study. Timothy A. Pearce, Delaware Museum of Natural History (DMNH), loaned us the holotype of *Humboldtiana plana* for critical comparison to material more recently collected. Our field results were greatly improved because of assistance provided by Scott Ogden, Grady B. Taylor, and Val Roessling, all from San Antonio, Texas, and by Steven P. Christman and Charlotte M. Porter (Florida Museum of Natural History). The anatomical drawings were inked by Susan Trammel. Liath Appleton assisted with numerous tasks relating to the final production of the manuscript. Alfonso Correa Sandoval, Instituto Tecnologico de Ciudad Victoria (ITCV), Tamaulipas, assisted us in the field and in numerous other ways that made this project possible. An anonymous reviewer provided useful comments that significantly improved this paper. We are grateful to each of these people for their help. Funding for field work relating to this project came from the George LaDue McGinty Endowment in Malacology, Florida Museum of Natural History. Field work in Mexico was made possible by authorization of permits DOO 700(2).- 260, DOO 750.- 8939 and DOO 750.- 1895 issued by the Dirección General de la Vida Silvestre, Mexico.

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