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Fred G. Thompson

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SOME LANDSNAILS OF THE GENUS *HUMBOLDTIANA* FROM CHIHUAHUA AND WESTERN TEXAS

Fred G. Thompson[1]

ABSTRACT

Humboldtiana (Gastropoda, Pulmonata, Helicoidea, Humboldtianidae) is endemic to higher elevations of central and northern México, and southwestern Texas. The fauna of the Mexican State of Chihuahua is reviewed. Thirteen species are recorded from there. This is estimated to be a small percent of the species that occur in Chihuahua. *Humboldtiana presidii* Pilsbry, 1939 from Texas is redescribed and is elevated to specific status. Formerly it was classified as a subspecies of *H. hogeana* (Martens, 1892). New taxa are *Gymnopallax* n. subgen. for *H. cicatricosa* n. sp. (referred species: *H. sylvania* Thompson & Mejía, 2006); *Clydonacme* n. subgen. for *H. regula* (referred species: *H. spectabile* n. sp., *H. titania* n. sp., *H. oberon* n. sp., *H. princeps* n. sp. and *H. hogeana* Martens 1892); *Aglotrochus* n. subgen. for *H. tanymastix* n. sp. *Humboldtiana balanites* n. sp. and *H. corruga* Thompson & Mejía, 2006 are referred tentatively to the subgenus *Humboldtiana*. The primary types of *H. hogeana* Martens, 1892, *H. presidii* Pilsbry, 1939, and *H. torrei* Pilsbry 1935 are refigured. The subgeneric affinities of *Humboldtiana torrei* Pilsbry, 1935 and *H. eulaliae* Metcalf, 1984 are uncertain.

Key Words: México, Chihuahua, Texas, terrestrial, snails, Gastropoda, *Humboldtiana*.

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INTRODUCTION

The objective of this report is to review the landsnails of the genus *Humboldtiana* in Chihuahua, and to clarify the status of a single species from west Texas that was thought to be subspecifically related to a Mexican species.

The genus *Humboldtiana* are a varied group of landsnails found over a large geographic area of western Texas and México. They tend to live in isolated colonies in rocky habitats, many of which are in arid regions. They have received relatively little attention because many of the rocky places in which they occur are difficult to access, and seasonal weather conditions influence the availability of live specimens. These factors, coupled with the historical paucity of systematic malacologists, have yielded an understudied group of organisms.

This report does not pretend to address adequately the taxonomy of *Humboldtiana* found in the study area. Undoubtedly, only a small fraction of the species of *Humboldtiana* that live in Chihuahua are known. Chihuahua is the largest state in México. Only a few weeks of field work have been devoted to landsnail surveys there, and only a small fraction of the state has been explored for mollusks.

METHODS AND TERMINOLOGY

Descriptions of new species are based primarily on the holotype. Meristic data as well as significant variations pertaining to other specimens also are included in the description. Morphological features among the paratypes that differ significantly from the holotype are indicated in parenthesis.

The shell height (H) is the distance from the apex to the basal lip parallel to the shell axis. The shell width (W) is the greatest distance across the shell transverse to the shell axis. The aperture height (AH) is measured from the basal lip to the point of attachment of the upper lip. The aperture width (AW) is measured from the edge of the outer lip to the inner edge of the columellar lip transverse to the shell axis. Averages (Avg) and standard deviations (SD) include measurements of the holotype as well as paratypes.

Specimens were relaxed in the field with a weak chloral hydrate solution, fixed for 24 hours in 85% ETOH and then preserved in 75% ETOH. Dissections were made in 75 % ETOH with the aid of a Bausch & Lomb 0.7-3.0 sterio-microscope.

In the female reproductive system the dart-sacs and dart-glands may be reduced in size and one or more dart-sacs may be absent in particular species. Two species may have non-homologous but equal numbers of reduced dart-sacs. Thus, for comparative purposes each of the dart-sacs is numbered (ds_1, ds_2, ds_3, ds_4) in a clockwise sequence beginning with the dart-sac that faces the atrium and penis (*see* Fig. 10, 60, 76). The vas deferens ascends along the vagina between ds_1 and ds_4. Abbreviations for other structures in figures of the reproductive anatomy are as follow. agl albumen gland; cae spermathecal caecum; 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_f free vagina; vag_l lower vagina; vag_m middle vagina; vd vas deferens; vrg verge. Internally the penis bears a verge, which is an extension of the epiphallus into the penis chamber. The internal structure of the penis and of the verge are important for discriminating species.

The vagina begins at the union with the penis at the genital atrium and extends upward to the point where the spermathecal duct branches from the uterus. The vagina consists of three segments, the lower vagina (vag_l), the middle vagina (vag_m) and the free vagina (vag_f). The lower vagina is separated from the middle vagina by a ring of dart-sacs. The middle vagina is separated from the free vagina a ring of dart-glands. The relative length of each of the segments is taxonomically significant (Burch & Thompson, 1956).

Species boundaries have become more clearly defined than was apparent in an earlier study (Solem, 1974). Shell characteristics of form, color pattern, embryonic sculpture and postembryonic sculpture constitute valid criteria for species recognition. Anatomical feature, including color patterns and numerous aspects of the reproductive anatomy are useful also for species definitions. Both shell and anatomical features provide bases for showing relationships.

Museum acronyms used in this paper are as follows:

ANSP - Academy of Natural Sciences, Philadelphia, PA.

BMNH - British Museum (Natural History), London.

ITCV - Instituto Tecnologico de Ciudad Victoria, Tamaulipas, Mexico.

UF - Florida Museum of Natural History, University of Florida, Gainesville, FL.

USNM - National Museum of Natural History, Washington, D.C.

Genus *Humboldtiana* Von Ihering, 1892

The genus *Humboldtiana* is in a state of systematic flux. This is, in part, because the genus is very widely distributed through central and northern México and southwestern Texas. Throughout this range the genus has undergone extensive evolution in shell characters and soft anatomy. Thirty-seven species and two subspecies have been described up to now. Almost all are known only from a single locality, and those localities are widely scattered with great distances separating them. From the available data it is apparent that few if any species occur in a geographic area of more than a few km^2. Thus, the known species are isolated both geographically and phyletically. Except for those species from southwestern Texas, geographic patterns of speciation are difficult to discern because of this isolation.

Most helminthoglytoid genera consist of species that are geographically separated by short distances from their nearest relative. Subgenera and species-groups are tightly associated with specific mountain ranges and other physiographic features. Apparent relationships are easily discerned because of anatomical similarities coupled with geographic proximity. Similar local patterns of speciation appear to be the case in *Humboldtiana*, but extensive local field collections that are needed to substantiate these patterns are not available from throughout most of the range of the genus. This has led to major underestimates of species diversity within *Humboldtiana*.

Papers dealing with the anatomy of *Humboldtiana* are Pilsbry 1927, Pilsbry 1939, Pilsbry 1948, Burch & Thompson 1957, Thompson 1967, Pratt 1971, Solem 1974, Fullington & Zimmerman 1977, Metcalf 1983, Thompson & Brewer 2000, Thompson 2006, and Thompson and Mejía 2006. Current investigations of DNA sequencing by Omar Mejía, Instituto Politecnico Nacional, Cd. México, will provide new insight into phylogeny within the genus.

This study recognizes six subgenera of *Humboldtiana*: *Humboldtiana* s. s., *Oreades* Thompson & Brewer, 2000, and *Polyomphala* Thompson & Brewer, 2000, *Gymnopallax* new subgenus, *Clydonacme*, new subgenus, and *Aglotrochus* new subgenus. The subgenera are separated by differences of the shell and of the reproductive anatomy.

Key to the subgenera of *Humboldtiana*.

1a. Dart-glands absent. Dart-sacs absent. Penis without a verge. Vagina undifferentiated into lower, middle and upper segments. ..... *Oreadne* Thompson & Brewer, 2000.

Other characters. Shell without granular sculpture. Embryonic whorls smooth. Shell shape depressed-helicoid. Color pattern banded. Mantle color-pattern uniform. Penis retractor muscle inserting on apex of penis. Genital atrium long. Spermathecal duct short, less than length of uterus. Spermathecal duct without a caecum. Type species: *Humboldtiana porterae* Thompson & Brewer, 2000.

1b. Dart-sacs present. Dart-glands present. Penis with a verge. Vagina differentiated into lower, middle and upper (free) segments. 2a

2a. Mantle mottled with dark-gray spots. Apex of shell denuded; pitted due to erosion. Spermathecal duct without a caecum. ..... *Gymnopallax* n. subgen.

Other characters. Shell without granular sculpture. Apical sculpture smooth. Shell helico-globose. Banding on shell obsolete. Verge long, length of penis. Penis retractor muscle inserting on apex of penis. Genital atrium abbreviated. Middle vagina long, widely separating dart-glands from dart sacs. Dart-glands present; Dart-sacs present. Dart-bulbs at base of dart-sacs externally visible. Spermathecal duct longer than uterus. Type species: *Humboldtiana cicatricosa* n. sp.

2b. Mantle uniform in color. Apex of shell not denuded. Spermathecal duct with a caecum 3a

3a. Shell without granular sculpture..... ..... *Aglotrochus* n.subgen.

Other characters. Embryonic sculpture consisting of straight, very fine transverse striations. Shell shape depressed-helicoid. Color pattern banded with numerous transverse dark streaks, Penis with a large verge. Penis retractor muscle inserting on apex of penis. Genital atrium long. Free vagina short. Middle vagina abbreviated so that the dart-glands are separated from the dart-sacs by a short gap. Dart-bulbs

not visible. Spermathecal duct very long, more than twice the length of the uterus. Type species: *Humboldtiana tanymastix* n. sp.

3b. Shell with granular sculpture on part or all of shell. 4a

4a. Shell sculpture consisting of large nodular tubercles arranged in short rows transverse to the incremental striations. Embryonic sculpture consisting of fine straight radial striations. Shell shape discoidal. Shell banding obsolete. Dart-bulbs exposed. .... *Polyomphala* Thompson & Brewer, 2000.

Other characters. Mantle uniform dark gray. Verge large, eccentric. Penis retractor muscle inserting on base of epiphallus. Genital atrium abbreviated. Free vagina not apparent. Middle vagina abbreviated; dart-glands juxtaposed to dart-sacs. Spermathecal duct longer than uterus. Type species: *Humboldtiana oreina* Thompson & Brewer, 2000.

4b. Shell sculpture without large nodes. Embryonic sculpture different. Shell shape helicoid or depressed helicoid. Shell distinctly banded. Dart-bulbs not apparent. 5a

5a. Embryonic sculpture consisting of wavy trasverse stiations and wrinkles Granular sculpture confined to first post-embryonic whorl..... *Clydonacme* n. subgen.

Other characters. Penis with a short verge that is equal to or less than half the length of the penis. Penis retractor muscle forms a narrow sheath around base of epiphallus. Genital atrium abbreviated. Free vagina short. Dart-glands juxtaposed to, or widely separated from dart-sacs. Spermathecal duct variable in length. Type species: *Humboldtiana regula* n. sp.

5b. Embryonic whorls smooth. Granular sculpture distributed widely over surface of shell. ....*Humboldtiana* Von Ihering, 1892.

Other characters. Verge present. Penis retractor muscle inserting on apex of penis or on base of epiphallus. Genital atrium long. Free vagina abbreviated. Middle vagina abbreviated; dart-glands juxtaposed against dart-sacs. Spermathecal duct longer than uterus. Type species: *Helix humboldtiana* Pfeiffer, 1847.

The subgenus *Humboldtiana* is difficult to define because it includes disparate groups of species, which clearly do not form a single integral unit (Thompson 2006). Most striking of these is the *Humboldtiana bicincta* species group (Thompson & Brewer, 2000). Its shell characters and reproductive anatomy diverge from patterns that otherwise occur widely within *Humboldtiana*. Additional study of the subgenus *Humboldtiana* is required before it can be defined satisfactorily. The new subgenera proposed herein differ by distinct embryonic shell sculpture patters coupled with unique anatomical character states.

Subgenus *Humboldtiana* von Ihering, 1892

Most species of *Humboldtiana* have smooth embryonic shells. It is doubtful that the following three species belong to a single subgenus. They are retained within the subgenus *Humboldtiana* until additional local patterns of species diversity become apparent.

Undetermined species group

Humboldtiana presidii Pilsbry, 1939

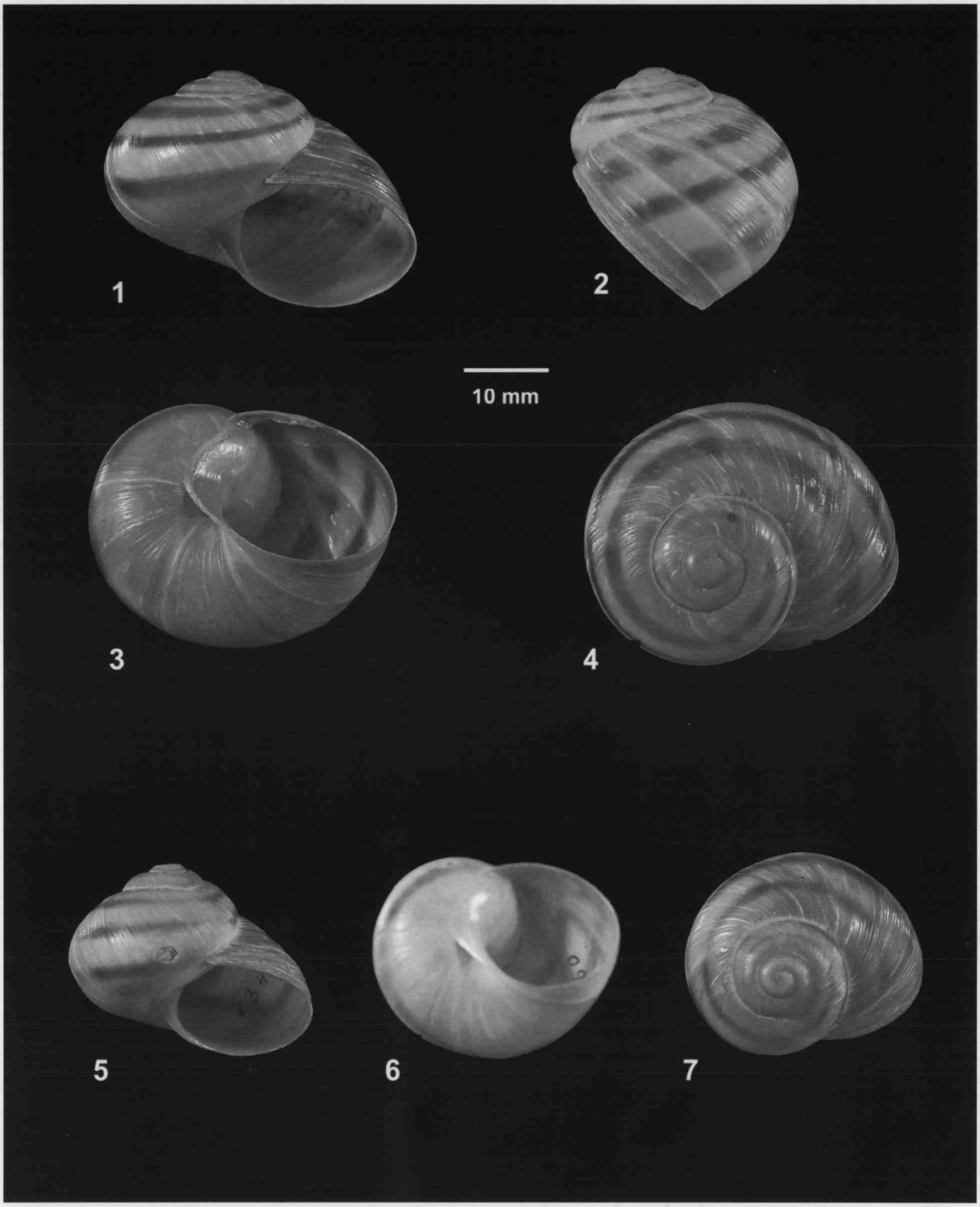
Humboldtiana hogeana presidii Pilsbry, 1939: 402; fig. 269f.

Diagnosis.— See below, Remarks.

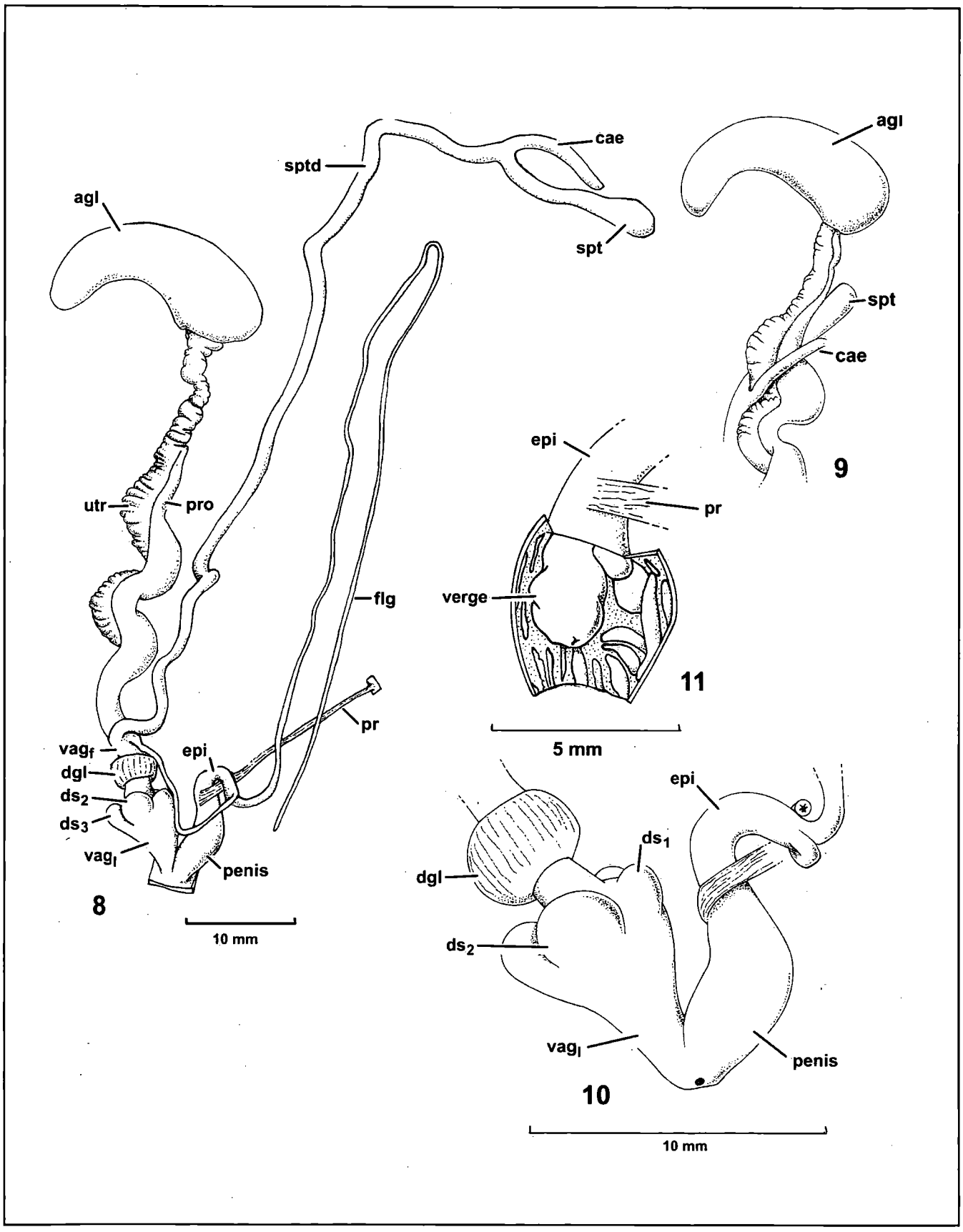
Shell (Figs. 1-7).— The shell is medium size, up to 34.3 mm wide. It is depressed sub-globose in shape, and is 0.74-0.85 times as high as wide.. The 1.5 embryonic whorls are nearly flat and smooth. The following half postembryonic whorl has rather close irregular radial striations. The remaining whorls have fine growth wrinkles and striations, but completely lack granular sculpture. The aperture is strongly oblique (Fig. 2). The peristome is weakly reflected along the upper and basal margins, and broadly reflected over the umbilical region so that the shell is obliquely umbilicate (Figs. 3, 6). The color pattern is light brown with three subequal chestnut bands and occasional whitish transverse streaks. The interior of aperture has a whitish glaze and is banded within..

Measurements of the holotype and ten specimens from San Carlos Tunnel, 2.5 mi. N of the Coal Mine Ranch House are given in Table 1.

Anatomy.— A single specimen was available for dissection (UF 354500). Reproductive system (Figs. 8-11). The genital atrium is very short and hardly distinguishable. The penis is short, 4 mm long, and elliptical-ovate in shape (Fig. 10). The inner wall of the penis is lined with short fleshy pilasters. A stout verge extends half the length of the cavity (Fig. 11). The epiphallus is relatively short and stout, 7 mm long, and is slightly less



Figs. 1-7. *Humboldtiana presidii* Pilsbry, 1939.. Figs. 1-4: Texas, Presidio Co., San Carlos Tunnel, 2.5 miles N of Coal Mine Ranch House (UF 354500). Figs. 5-7: Holotype, USNM 134160.



Figs. 8-11. *Humboldtiana presidii* Pilsbry, 1939. Fig. 8: reproductive system (UF 354500). Fig. 9: relationship of spermatheca and caecum to uterus-prostate. Fig. 10: lower genitalia. Fig. 11: interior of penis.

Table 1. *Humboldtiana presidii* Pilsbry, 1939. Measurements in mm of the holotype (USNM 134160) and 10 specimens from San Carlos Tunnel, 2.5 mi. N of the Coal Mine Ranch House (UF 345497/8, UF 345500/2).

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	23.1	28.4	14.9	18.1	3.7	0.81	0.52	0.78	0.82
San Carlos Tunnel									
Min	23.7	31.0	15.8	21.0	3.7	0.74	0.51	0.78	0.75
Max	29.1	34.3	18.9	23.5	4.1	0.85	0.55	0.89	0.86
Avg	26.1	32.7	17.38	21.9	3.9	0.80	0.53	0.84	0.79
SD	1.66	1.31	0.96	0.79	0.11	0.04	0.04	0.03	0.03

than twice the length of the penis. Internally it has four longitudinal folds. The penis retractor muscle is relatively stout, 16 mm long. It originates on the middle of the inner wall of lung midway back from mantle collar and inserts on the base of the epiphallus at the apex of the penis. The flagellum is very long, 86 mm in length, and is about eight times the combined length of the penis + epiphallus. It is lined internally with 6 longitudinal columns of papillae. The lower vagina bears four subequal dart-sacs, of which ds_1 is the largest and ds_3 is the smallest. The dart-glands form a ring around the middle vagina slightly above the dart sacs. The spermathecal duct is very long. The combined length of the duct + the spermatheca is 78 mm. The spermathecal sac is elliptical. The spermathecal caecum is very short. It diverges from the duct at about 8 mm below the base of the sac. The distal part of the spermathecal duct including the spermatheca and the caecum encompass the prostate-uterus just below the albumen gland (Fig. 9). The albumen gland is reniform in shape, and is19 mm long. The carrefour is completely imbedded within the albumen gland.

Type locality.— Near the San Carlos Mine, Presidio County, Texas. Holotype: USNM 134160; collected by J. A. Singley. The San Carlos Mine is located within 300 meters north of the San Carlos Tunnel, which is cut through a granite ridge. The mine is about 2.5 miles (4 km) north of the Coal Mine Ranch House.

Distribution.— Known only from Presidio County, Texas in the immediate vicinity of the Coal Mine Ranch. Pilsbry (1939) records the species from near San Carlos [mine], and from the Rim Rock Mountains, which in part forms the northeast boundary of the Coal Mine Ranch. Texas. Presidio Co.: W edge of Sierra Vieja Rim, Quemada Spring area, ca. 5.8 mi. E of Coal Mine Ranch House (30°25.6'N, 104°40.1'W), 1700 m alt. (UF 354496/7, UF 354498/1); San Carlos Tunnel, ca. 2.5 mi. N of Coal Mine Ranch House (30°27.7 'N, 104°44.2'W), 1280 m alt. (UF 354495/4, UF354497/10, UF 354500/2)

Habitat.— *Humboldtiana presidii* occurs in one of the bleakest areas in Texas. At the San Carlos Tunnel it was found among granite tallus at the base of a high bluff. Along the east side of the ranch at the base of the Vieja Rim the snail was found in similar granite tallus. Both localities were sparsely vegetated with *Opuntia*, scattered grasses, shrubs, and occasional small juniper trees.

Remarks.— *Humboldtiana presidii* was described as a subspecies of *Humboldtiana hogeana* (Martens, 1890). At the time *H. presidii* was described the soft anatomy of neither was known, and the embryonic sculpture of *H. hogeana* was incompletely described. Similar features of the postembryonic shells suggested a close relationship between the two taxa.

The glossy shell of *Humboldtiana presidii* differs from *H. hogeana* by having a nearly flat and perfectly smooth embryonic shell, and by completely lacking granulation on any of the following whorls. The lusterless shell of *H. hogeana* differs by having course transverse wrinkled striations on the embryonic whorls and granular sculpture on the second half-postembryonic whorl. The embryonic sculpture of *H. hogeana* places that species in the subgenus *Clydonacme*.

The anatomy of *Humboldtiana presidii* is characterized by having a short stout penis with a large verge internally. The penis terminates with a shorter epiphallus, which in turn has a very long flagellum. The genital atrium is very short and almost flush with the body wall. The very long spermathecal duct has a short caecum just below the spermatheca. The lower vagina has four subequal dart-sacs, in which ds_2 is conspicuously larger and ds_1 is the most reduced in size. The dart-glands are narrowly separated from the dart-sacs.

Among Texas species *Humboldtiana presidii* re-

sembles *H. chisosensis* Pilsbry, 1927 and *H. fullingtoni* Cheatum, 1972 by having smooth embryonic whorls. The shells have similar depressed-helicoid shapes as well as similar coloration. *Humboldtiana chisosensis* differs anatomically by having a wide gap between the dart-glands and dart-sacs (Pilsbry, 1939: 400, fig. 272), thereby being more similar to members of the *Humboldtiana texana* species group (Burch & Thompson, 1957). *H. fullingtoni* differs from *H. presidii* by having weaker bands, and by having a wide gap between the dart-sacs and the dart-glands.

Etymology.— The name *presidii* refers to Presidio County, Texas, where the species is found.

The *Humboldtiana texana* species-group

In this group of species the dart-glands form a ring around the middle vagina and are widely separated from the dart-sacs (Burch & Thompson, 1957).

Humboldtiana balanites n. sp.

Diagnosis.— The shell is helicoid in shape, and is nearly as high as wide. The shell wall is thin and fragile. The color pattern is lusterless brown with three poorly defined dark bands and numerous oblique light brown stripes that disrupt the bands. The embryonic whorls are smooth and protruding. The postembryonic whorls have a dense mesh of minute granules that are continuously distributed over the surface from the suture to the base. The lower genitalia is robust. The genital atrium is very abbreviated. The penis is large, bulbous and has a long verge internally. The epiphallus is about 1.5 times the length of the penis. The flagellum is about twice the length of the penis + epiphallus. The lower vagina has four equal-sized dart-sacs. The dart-glands are robust and form a ring widely separated from the dart-sacs. The spermathecal duct is very long, being twice the length of the oviduct-prostate. The spermathecal duct bears a small, slender caecum. The mantle is uniformly light grayish brown.

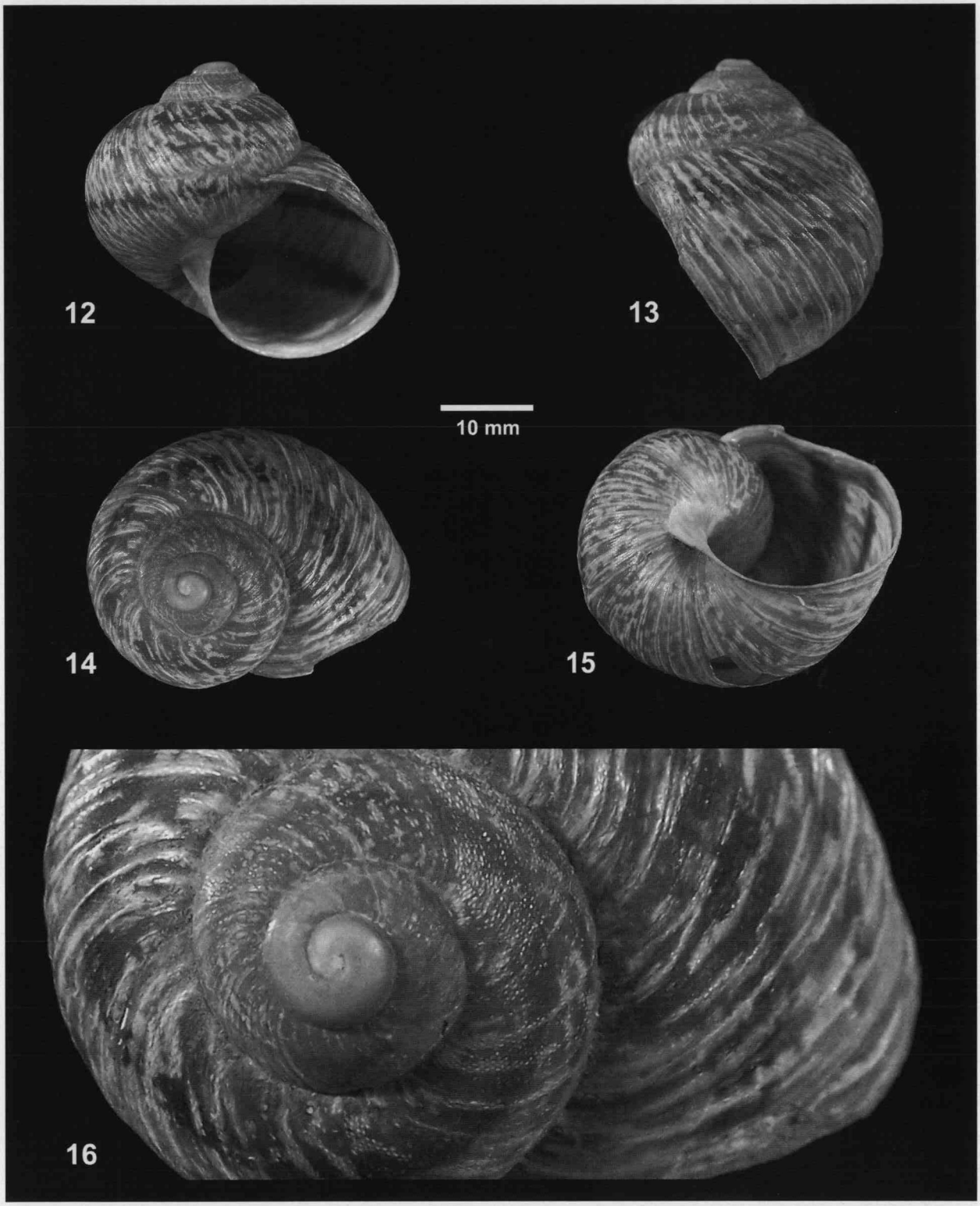
Shell (Figs. 12-16).— This is a moderately sized snail, up to about 33 mm wide with a thin, fragile shell. The shell is helicoid in shape; 0.93 times as high as wide. The periostracum is lusterless. The ground color is dark brown with three nearly black bands. The bands are poorly defined because they are interrupted by numerous oblique light brown stripes and blotches that are aligned with the growth wrinkles. The middle band is the narrowest and the upper band is the widest. The peristome is light purple-brown, and the interior of aperture is brown with a whitish hyaline glaze and banded. The umbilicus is obliquely perforate (Fig. 15). The mature shell has 4.2 whorls, which regularly increase in size, and then descend to the aperture at the last quarter turn. The upper lip of the peristome inserts on or just below the lower band. The embryonic shell consists of 1.6 smooth protruding whorls (Fig. 16). The first embryonic whorl is 4.4 mm wide perpendicular to initial suture. The postembryonic whorls are coarsely striate and wrinkled along the growth lines, and are sculptured with a dense mesh of low, elongate granules that tend to occur in small clusters that are associated with the lighter transverse stripes and blotches. The granules are continuously distributed over the surface of the shell between the suture and the base. The rotund aperture is 0.79-0.91 times as wide as high. The plane of the aperture lies at an angle of 33° to the shell axis (Fig. 13). The peristome is weakly reflected along the upper and basal lips, hardly so along the outer lip, and forms a short triangular patch over the umbilical area.

Measurements of the holotype and two specimens from 6.6 km E of San Ignacio Arareco are given in Table 2.

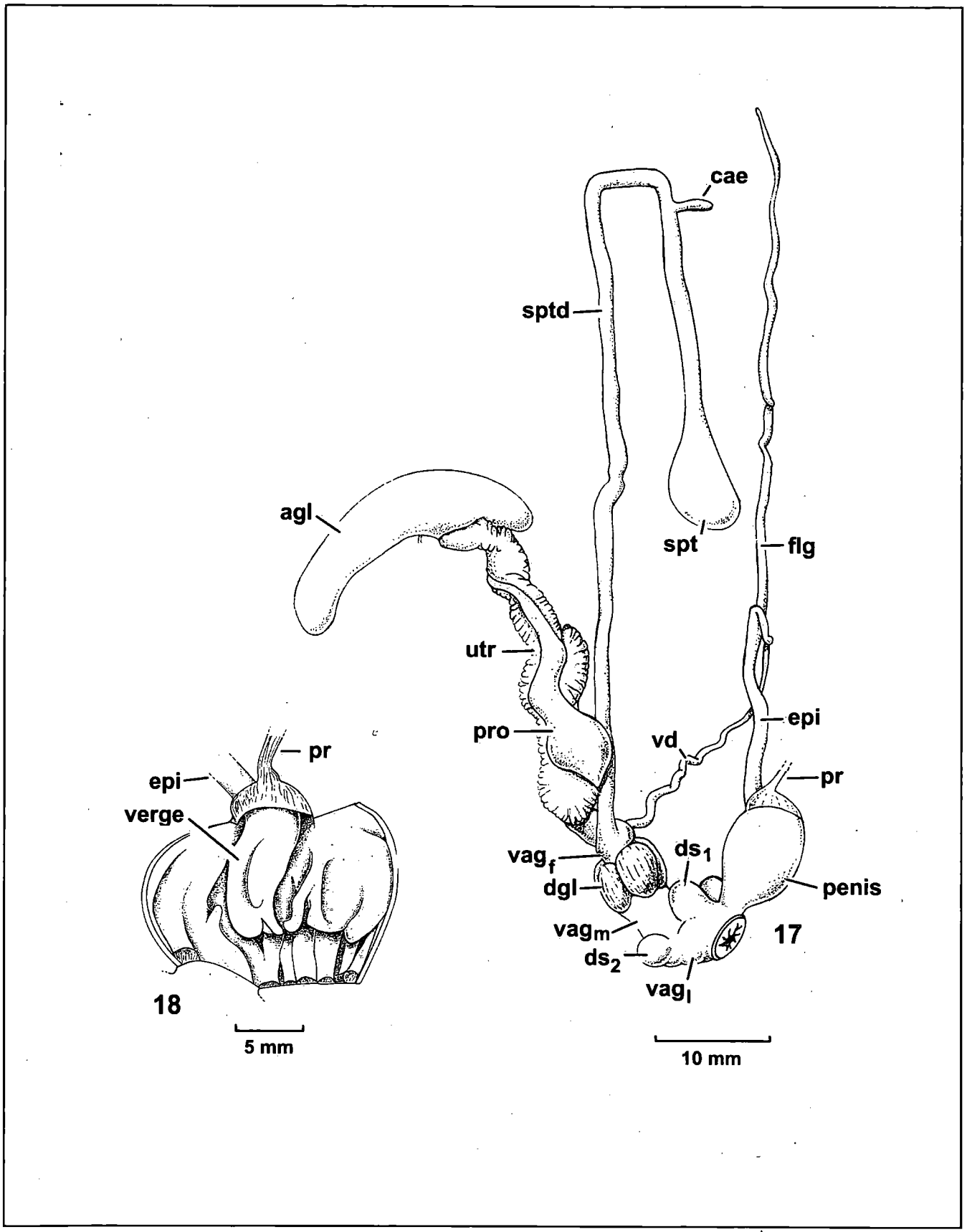
Anatomy.— The head-foot is uniform gray. The sole is light gray. The mantle collar is light gray as is the area of the mantle overlying the uterus-prostate. The mantle is uniform light grayish brown (Fig. 40) as is typical for the genus *Humboldtiana*.

Reproductive system (Figs. 17-18). Two specimens were dissected. The holotype is described and illustrated. A specimen from 6.6 km east of San Ignacio Arareco also was examined. Essentially, the latter specimen did not differ from the holotype. Both specimens had spermatophores in the spermatheca, indicating reproductive activity.

The genital atrium is abbreviated and barely distinguishable. The large penis is ovate-bulbous, 11 mm long, and widest above the middle. The penis is thick-walled. The inner wall is lined with thick longitudinal fleshy columns (Fig. 18). A relatively slender verge extends nearly the length of the cavity. The end of verge is multi-lobed. The penis retractor muscle is slender. It originates on the center of lung about 8 mm posterior to the mantle collar and inserts on the apex of penis where it forms a short sheath around the base of the epiphallus. The epiphallus is slender and is 16 mm long. It is about half again as long as the penis. The epiphallus is reflected to lie along the side of the penis so that the distal end of the vas deferens is appressed along the genital atrium. The epiphallus has four longitudinal folds internally. The flagellum is very long and slender, being almost twice the combined length of the penis + epiphallus, ca. 40 mm long. The flagellum is lined internally with four longi-



Figs. 12-16. *Humboldtiana balanites* n. sp. Holotype (UF 317170).



Figs. 17-18. *Humboldtiana balanites* n. sp. Fig. 17: reproductive system of holotype (UF 317170). Fig. 18: interior of penis of Fig. 17.

Table 2. *Humboldtiana balanites* n. sp. Measurements in mm of the holotype (UF 317170) and two paratypes (UF 317171, UF 317172).

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	30.9	33.1	19.0	24.3	4.2	0.93	0.57	0.79	0.78
UF 317171	27.0	28.0	15.8	19.6	3.9	0.96	0.56	0.73	0.81
UF 317172	28.0	30.3	16.8	21.6	4.0	0.92	0.55	0.77	0.78

tudinal folds. The lower vagina is very stout, and is slightly less than half the length of the penis. It bears four nearly equal sized dart-sacs, each of which has a bulge on either side of the base caused by the underlying dart-bulbs. The middle vagina is moderately long and bears four dart-glands that form a ring that is widely separated from the dart-sacs. The spermathecal duct is very long; about twice as long as the uterus–prostate. The spermathecal duct + spermatheca is 84 mm long. The bulbous spermatheca is 7 mm long. The spermathecal duct has a short slender caecum that diverges from the duct about a fourth of the distance below the spermatheca. The caecum is relatively short, 3 mm long.

Type locality.— Chihuahua, 0.3 km north of San Ignacia Arareco, ca. 5 km south of Creel (27°43.9' N, 107°37.4'W); 2280 m alt. Holotype: UF 317170; collected 9 August, 2003 by Fred G. Thompson and Elizabeth L. Mihalcik. Paratype: UF 360035 (1) same data as the holotype.

The type locality is at the upper end of a small box canyon ending at a granite wall. *Humboldtiana balanites* was very sparse among dead oak leaves in an open forest of oak and pine at the upper end of a grassy pasture. Only two specimens were found after a two hour search. Apparently this species burrows into the soil to aestivate, because no dead shells or aestivation rings were found along rock ledges or in crevices.

Distribution.— Known only from the type locality and a near-by locality. Chihuahua, 6.6 km E of San Ignacio Arareco, ca. 6 km south, 8 km east of Creel (27°43.9' N, 107°23.5' W), 2280 m alt. (UF 317171, UF 317172).

Remarks.— *Humboldtiana balanites* is similar to *H. durangoensis* Solem, 1954. DNA sequences support this apparent relationship (Omar Mejía, *personal communication*). The latter two species are larger and have better defined bands. They also bear stronger granular sculptures. *Humboldtiana durangoensis* remains unknown anatomically. The spermathecal-duct caecum in *H. balanites* is unusually short within the genus. *Humboldtiana balanitesis* is also similar to *H. corruga* Thompson & Mejía, 2006. Both species have rugosely wrinkled shells with fine granular sculpture over the postembryonic whorls. *Humboldtiana balanites* differs by having a narrower umbilical perforation, a weaker shoulder on the whorls, less inflated whorls, and less clearly demarcated bands. Anatomically *H. balanites* and *H. corruga* have similar large bulbous penises with an elongate verge surrounded by thick glandular folds. *Humboldtiana corruga* differs by having a much longer lower vagina and middle vagina, and a much shorter flagellum.

Among those species that are known anatomically, *Humboldtiana balanites* is similar to *H. texana* Pilsbry, 1927,, *H. chisosensis* Pilsbry, 1927, *H. agavophila* Pratt, 1971 and *H. fullingtoni* Cheatum, 1972, all from Texas, *H. fasciata* Burch & Thompson, 1957 from Hidalgo, *H. globosa* Burch & Thompson, 1957 from Veracruz, and *H. corruga* Thompson and Mejía, 2006 from Chihuahua. This group has in common a dart-gland ring that is widely separated from the dart-sacs, and the species have granular sculpture over part or most of the shell. *Humboldtiana texana* is similar to *H balanites* in color and sculpture, but it is much smaller, and the granular sculpture disappears on the last third whorl and on the base (Pilsbry, 1939: 404). *Humboldtiana globosa* differs from *H. balanites* by its brighter color patters, by its globose shape to the shell, and by having three functional, nearly equal-sized dart sacs, while ds_4 is reduced in size. *Humboldtiana fasciata* differs from *H. balanites* by its larger size and more distinctly banded color pattern.

The commonality of the widely separated dart-glands and the dart-sacs may be a convergent character-state that does not necessarily reflect relationships. *Humboldtiana fasciata* and *H. globosa* are separated geographically from other species by great distances, and the brighter color patterns of their shells are quite unlike the drab patterns found in *H. texana* and *H. balanites*.

Etymology.— The species name *balanites* is from the Classical Greek, βαλανος, an acorn-like object, and alludes to the appearance of this species.

Humboldtiana corruga Thompson & Mejía, 2006

Humboldtiana corruga Thompson & Mejía, 2006; Nautilus, 120, p. 25.

Type locality.— Chihuahua, 0.8 km south, 0.3 km west of Norogachi, (27° 15' 53" N, 107° 7' 49" W), 2280 m alt.. Holotype: UF 358872; collected by Omar Mejía, 25 August, 2003. Found in an open *Pinus-Quercus* woodland. Paratype: ITCV (1); same data as the holotype.

Distribution.— Known only from the type loclality.

Remarks.— This recently described species is found at a locality near that of *Humboldtiana balanites*.

Gymnopallax n. subgen.

Type species.— *Humboldtiana cicatricosa* new species. Referred species: *Humboldtiana sylvania* Thompson & Mejía, 2006.

Diagnosis.— The shell is thin and fragile, and the apex is denuded of the periostracum even in small juveniles. The shell lacks granular sculpture. The embryonic whorls are raised and smooth. The color pattern consists of three poorly defined bands on a light brown background. They are interrupted by numerous dark brown streak and blotches. The outer wall of the lung is light gray and is mottled with numerous small darker gray spots (Fig. 41). A genital atrium is absent due to the abbreviated condition of lower genitalia. The penis has a large multi-lobed verge that extends the full length of the cavity. The flagellum is long. The vagina bears four dart-sacs, each of which has two exposed dart-bulbs. The dart-sacs are widely separated from the dart-gland ring. A free vagina is absent. The spermathecal duct is very long and lacks a caecum.

This subgenus is known only from a small area near Creel, Chihuahua.

Etymology.— The name *Gymnopallax* (f) is from the Classical Greek γύμνος, naked, and πάλάξ, a youth. The name refers to the denuded embryonic whorls.

Humboldtiana (Gymnopallax) cicatricosa n. sp.

Diagnosis.— As for the subgenus.

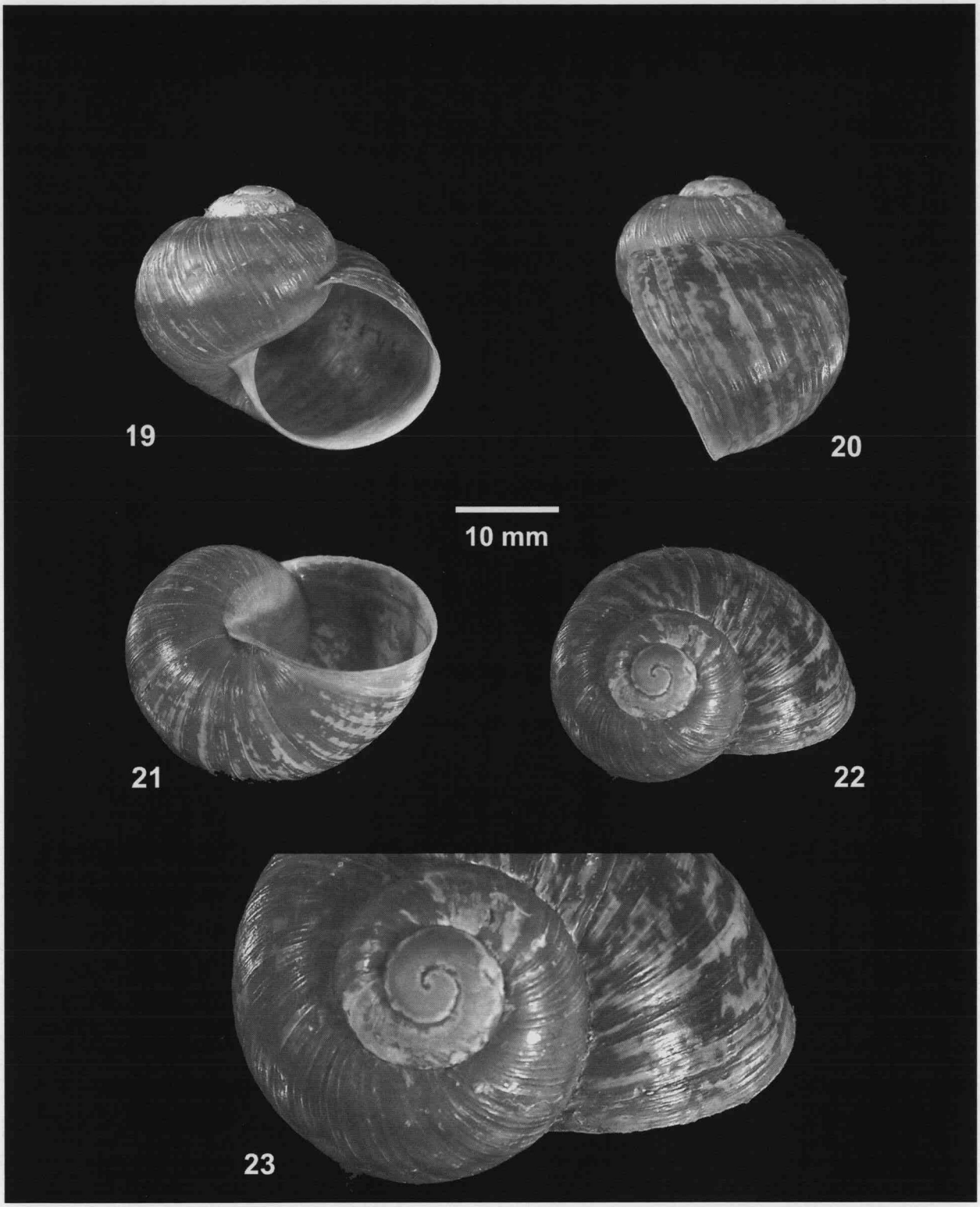
Shell (Figs. 19-23).— The small shell is up to about 28 mm wide. It is helicoid in shape, and is 0.90-0.94 times as high as wide. The shell is thin and fragile. Mature specimens have up to 3.5 whorls. The suture is deeply impressed, forming a narrow channel extending to the aperture. The last quarter whorl descending to the aperture where the upper lip inserts on the lower band. The umbilicus is narrowly rimate. The embryonic shell has 1.7 large, elevated whorls. The first embryonic whorl is 4.9 mm wide transverse to the initial suture. The embryonic whorls are smooth. The apical periostracum is eroded so that by the time the shell approaches maturity the apex is denuded and is strongly pitted from erosion (Fig. 23). The postembryonic whorls are sculptured with coarse incremental threads and striation. Granular sculpture is absent. The color pattern is light, diaphanous brown with three dark brown bands that are interrupted by irregularly spaced alternating dark brown transverse bars and blotches. The upper and lower bands are about equally wide. The middle band is narrower. The aperture is obovate in shape; 0.83-0.86 times as wide as high with its greatest dimension along the vertical axis. The peristome is light gray in color. The interior of the aperture is hyaline brown and banded, and is glossy but rippled beneath the exterior sculpture. The aperture is prosocline, lying at an angle of 40° to shell axis (Fig. 20). The peristome inserts advanced between the middle and upper bands. It is weakly reflected along the dorsal and basal lip, and forms a narrow triangle along columellar lip to nearly occlude the umbilicus (Fig. 21).

Measurements of the holotype and three paratypes are given in Table 3.

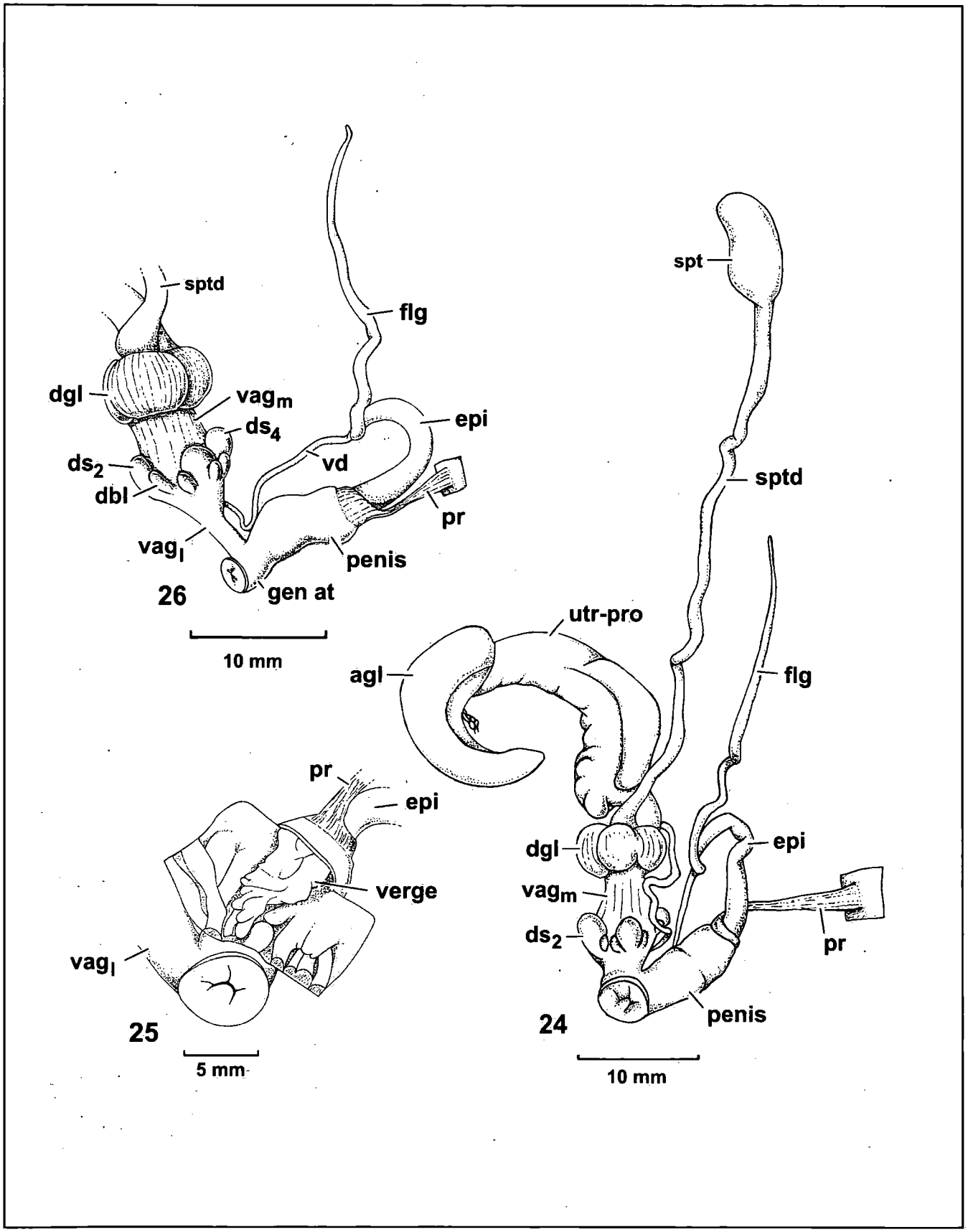
Anatomy.—The head-foot is dark gray in life. The outer wall of the lung is spotted with numerous small gray blotches (Fig. 41).

Reproductive system (Figs. 24-26). Two specimens were dissected. The holotype (Figs. 24, 25) appears to have been in an active breeding state, and the lower genitalia are greatly distended. A paratype (Fig. 26) also is figured. It appears to have been in an inactive sexual state. Measurements are given for the holotype first and the paratype second.

The genital atrium is abbreviated to the extent that it appears to be absent. The penis is very stout, about 10 mm long, and is constricted at the upper third. The inner wall is lined below the constriction with several very heavy longitudinal folds. Above the constriction the inner wall is lined with a few rather indistinct fleshy folds and pads. A very large verge extends nearly the full length of the penis cavity (Fig. 25). The verge ends in several digitiform and follicular processes forming a cluster of lobes. The penis retractor muscle originates on the center of inner wall of lung 3-4 mm behind mantle collar, and inserting on apex of penis where it forming a short sheath around the base of the epiphallus. The epiphallus is almost twice the length of the penis (19, 13



Figs. 19-23. *Humboldtiana cicatricosa* n. sp. Holotype (UF 317169).



Figs. 24-26. *Humboldtiana cicatricosa* n. sp. Fig. 24-25: reproductive system of holotype (UF 317169). Fig. 26: lower reproductive system of paratype (UF 317173).

Table 3. *Humboldtiana cicatricosa* n. sp. Measurements in mm based on the holotype (UF 317169) and the two paratypes. Only the holotype appears to be mature because of its reflected peristome.

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	24.9	27.8	16.3	19.6	3.5	0.90	0.59	0.79	0.83
Paratypes									
UF 317175	24.0	26.2	14.6	17.6	3.4	0.92	0.56	0.73	0.83
UF 317173	25.0	26.5	15.0	17.5	3.4	0.94	0.57	0.70	0.86

mm), It is rather stout and tapers to the flagellum. The epiphallus is lined internally with four longitudinal fleshy columns. The flagellum is slender, and is about equal to the combined length of the penis + epiphallus (29, 28 mm). The interior of the flagellum has four longitudinal fleshy folds. The vagina is about 1.5 times the length of the penis (14, 15 mm). The lower vagina is about half the length of the middle vagina. The free vagina is not visible. The vagina has four dart-sacs near its middle. Each dart-sac has two exposed dart-bulbs. The upper end of the vagina has four discrete dart-glands that form a ring around the top the middle vagina. The dart-glands are widely separated from the dart-sacs. The spermathecal duct is very long. The combined lengths of the duct + spermatheca are 52, 49 mm long. The spermathecal duct lacks a caecum. The spermatheca is bean shaped and 9, 8 mm long.

Type locality.— Chihuahua, 4 km north-northeast of Rancho Blanco, ca. 31 km NNE of San Juanito, along the highway from La Junta to Creel (28°10.7' N, 107°23.5' W); 2180 m alt. Holotype: UF 317169; collected 8 August, 2003 by Fred G. Thompson and Elizabeth Mihalcik. Paratypes: UF 317175 (1), UF 320068 (1); same data as holotype; UF 317173 (2), 320068 (1), ITCV (1); same locality as holotype; collected 11 August, 2003.

The type locality is on an east-facing slope of a granite bluff along the west side of the highway in a pine-oak forest. There was a heavy ground cover of oak leaves and some pine needles. *Humboldtiana cicatricosa* was very sparse in scattered clusters of damp oak leaves following a rain during the previous night. No association with the granite outcrop was apparent.

Distribution.— Known only from the type locality.

Remarks.— The subgenus *Gymnopallax is* unique within *Humboldtiana* by having a mottled patter of dark spots on the lighter gray mantle. Also, it is unusual by lacking a caecum on the spermathecal duct.The subgenus *Oreades* Thompson & Brewer, 2000 (*H. porterae* Thompson & Brewer, 2000) is like *Gymnopallax* by lacking a spermathecal caecum, but it has few other similarities. *Oreades* lacks a verge, dart glands and dart sacs, and the mantle is uniform gray.

Humboldtiana cicatricosa and *H. sylvania* are unusual by having the early whorls of the shell denuded of the periostracum, allowing the early whorls to become badly pitted from erosion. The periostracum may wear off in other species, but the degree and consistency of this trait coupled with unique anatomical states suggests that the causes of the denuded apexes of these two species are intrinsic and are not due just to wear. *Humboldtiana cicatricosa* differs from *H. sylvania* by lacking distinct bands on the shell, and by having a smaller shell. The latter species has well defined bands and the shell is about 35 mm wide.

Etymology.— The species name is from the Latin *cicatricosus*, meaning scarred, and refers to the pitted condition of the early whorls of the shell.

Humboldtiana sylvania Thompson & Mejía, 2006

Humboldtiana sylvania Thompson & Mejía, 2006; Nautilus, 120, p. 21.

Type locality.— Chihuahua, Corareachi, 4.4 km north, 0.4 km west of Baqueachi (27° 28.45' N, 107°30.93' W); 2000 m alt.. Holotype: UF 353714; collected 31 August, 2003 by Omar Mejía.

Corareachi is a very small village, which is unnamed on the INEGI topographic map series 1:50,000 (G13A32). The type locality is in a *Pinus-Quercus* forest in a grassy glen.

Distribution.— Known only from the type locality.

Remarks.— This recently described species is found in an area that is approximately 100 km south of the type locality for *Humboldtiana cicatricosa*.

Clydonacme, n. subgen.

Type species.— *Humboldtiana regula*, n. sp. Referred species are *Humboldtiana spectabile* n. sp.,

H. titania n. sp., *H. oberon* n. sp., *H. princeps* n. sp., and *H. hogeana* (Martens, 1890).

The embryonic whorls are sculptured with of very fine wavy transverse striation and wrinkles (Figs. 31, 69). Fine granules may be superimposed on the wrinkles. The remainder of shell has incremental striations, and may be with or without fine granules on the first postembryonic whorl. The shell is elevated., with three discreet bands and occasional transverse white streaks on a light brown background. The slender penis has a short verge and heavy columnar fold internally. The penis retractor muscle forms a sheath around the lower part of the epiphallus. The flagellum is stout and moderately short. The dart-glands are closely appressed against the dart-sacs or they may be widely separated. The spermathecal duct is long and bears a short caecum near its end.

This subgenus is known from the Sierra de La Catarina and the Sierra Victorino in north-central Chihuahua, and from areas near Cd. Chihuahua.

Etymology.— The name *Clydonacme* (f.) is from the Classical Greek, κλύδονιον, a ripple, and ακμε, apex, alluding to the fine, wavy transverse striations on the embryonic whorls of the shell.

Species from the Sierra de La Catarina

The Sierra de La Catarina is inhabited by large-sized species that have starkly colored shell. As a group they are characterized anatomically by having a short nipple-like verge, the penis retractor muscle forms a broad sheath around the base of the epiphallus, the epiphallus is narrow and elongate, the genital atrium is very short and abbreviated, the middle vagina is abbreviated so that the dart-sacs are juxtapose to the dart glands, and the spermathecal duct is longer than the uterus-prostate.

Humboldtiana regula n. sp.

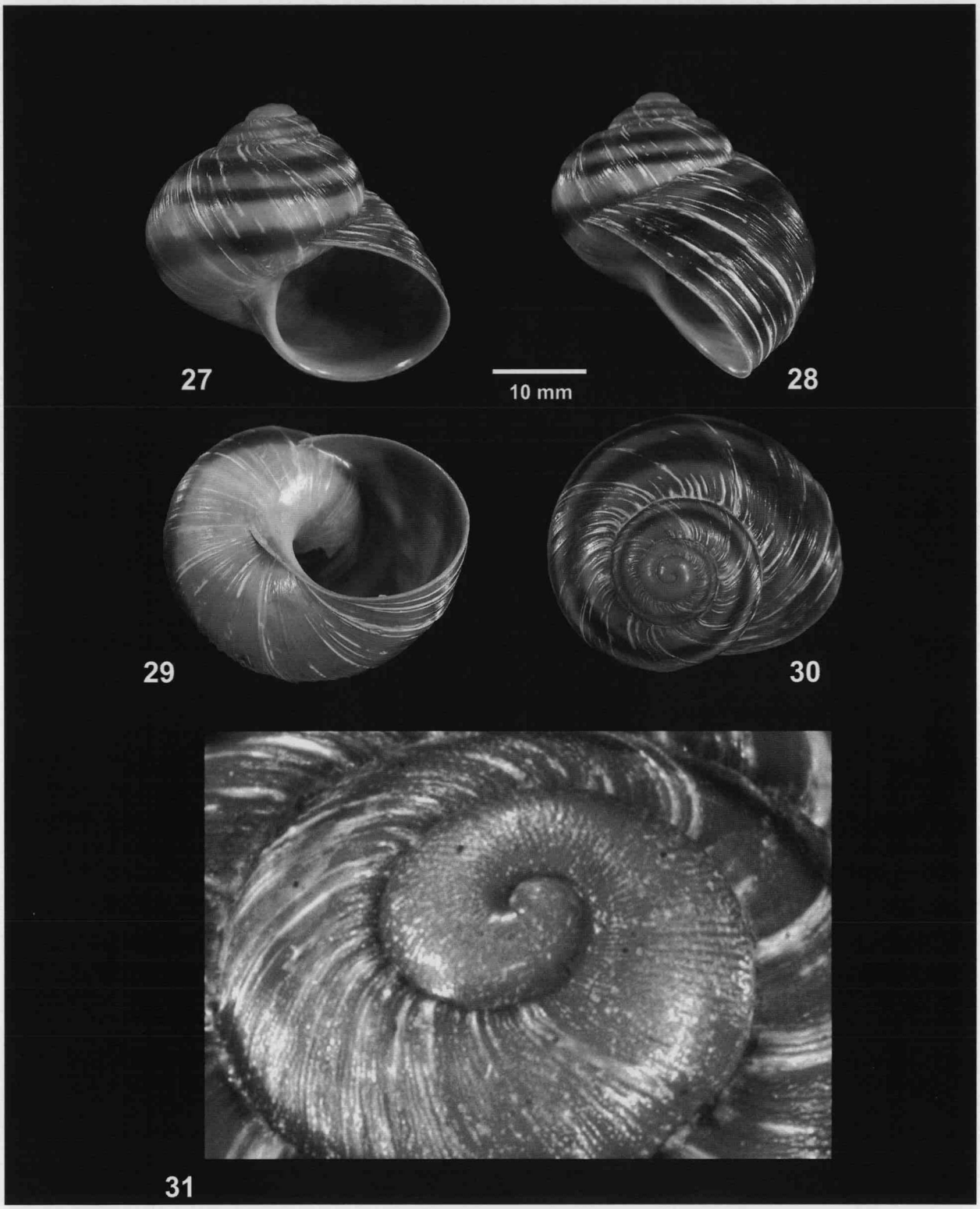
Diagnosis.— The shell is medium sized, globose, and almost as high as wide. The periostracum is shiny light brown with three discreet chestnut-brown bands that frequently are crossed by enamel-white streaks. The embryonic whorls are raised, and sculptured with very fine, wavy, transverse striation. The postembryonic whorls are crossed by irregularly spaced incremental striations. The first postembryonic whorl has very fine elongate granules, which are absent on the following whorls. The genital atrium is very short. The penis is relatively slender. Its inner wall has four heavy longitudinal folds, and its apex bears a short verge. The penis retractor muscle is short and forms a sheath around the lower fourth of epiphallus. The epiphallus is long and stout. The flagellum is short, being about as long as combined length of penis + epiphallus. The first dart-sac (ds_1) is large. The other three dart-sacs progressively decreasing in size. The dart-gland are tightly appressed against the dart-sacs. The spermathecal duct is long and bears a short caecum below the spermathecal bulb.

Shell (Figs. 27-31).— The shell is moderately large, about 29-33 mm wide, conical-globose in shape, and 0.83-1.00 times as high as wide. The periostracum is shiny. The ground color is light brown on the apex and becomes darker toward the aperture. The shell has three discreet chestnut-brown bands. The ground-color and bands are interrupted by frequent transverse enamel-white streaks. The interior of aperture is light brown and banded. Mature shells have 3.8-4.2 whorls. The suture is strongly impressed. The 1.4 embryonic whorls are moderately raised but flattened, and are crossed by fine wavy striations (fig. 31). The following postembryonic whorl has barely distinguishable minute granules that tend to be elongate and aligned between the incremental striations. The remaining whorls lack granular sculpture, but have irregular, distinct incremental striations that are exaggerated at the white streaks. The umbilicus is obliquely rimate and is nearly occluded by the reflected columellar lip. The aperture is rotund, 0.77-0.98 times as wide as high. The plane of aperture lies at 35-45° to the shell axis. The aperture strongly descends along the last quarter turn. The upper lip inserts just below, or on the lower edge of the lower band. The peristome is weakly reflected along the upper lip and strongly reflected along the columellar margin where it nearly obscures the umbilicus. The outer lip is not reflected.

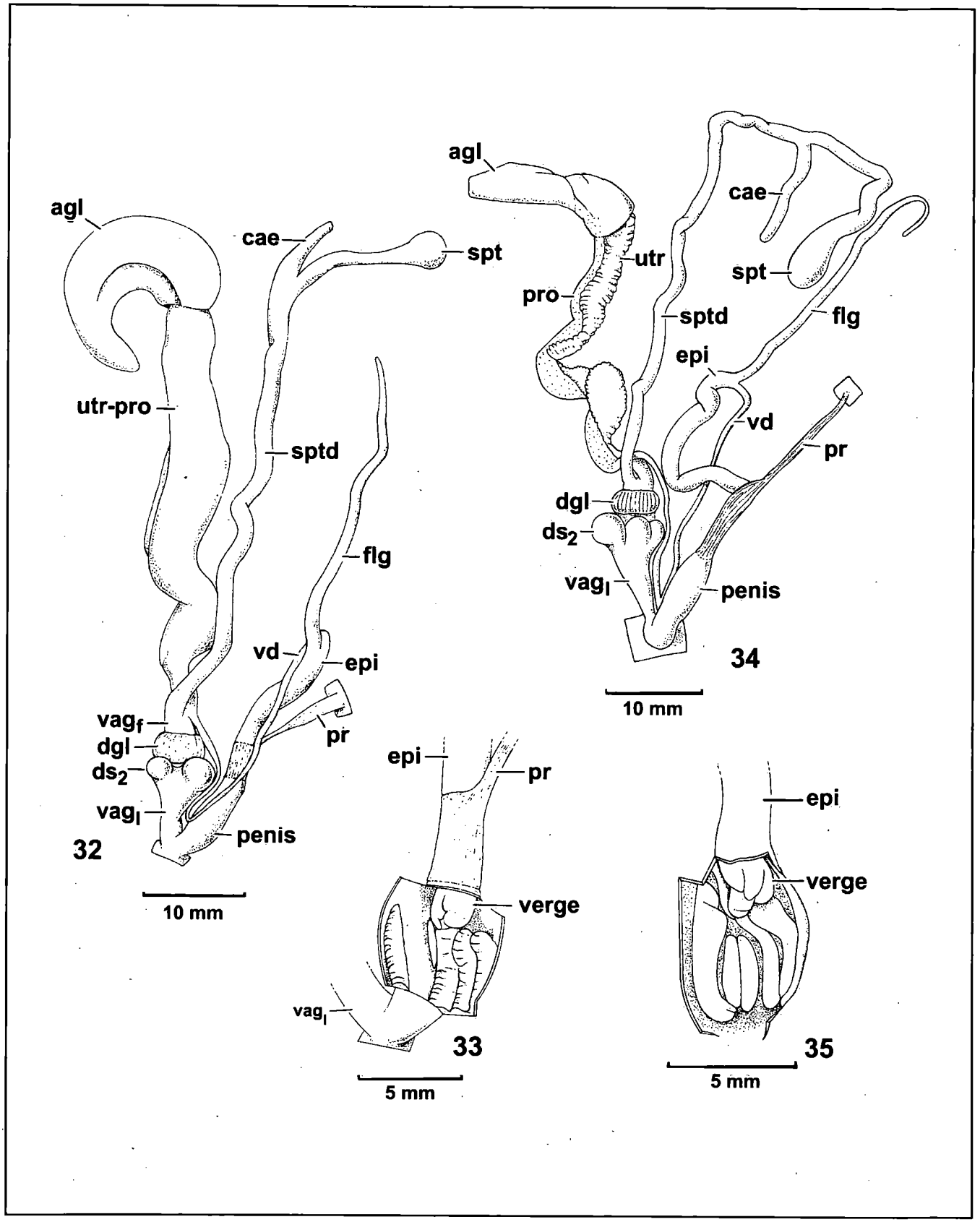
Measurements in mm of the holotype and sixteen paratypes are given in Table 4.

Anatomy (Figs. 32-33).— Two specimens were dissected (UF 317179). One is described below.

The genital atrium is very short. The slender penis is slightly swollen below its middle and is 8 mm long. The interior is lined with four large longitudinal glandular folds, and has a short verge that consists of a thin skirt of tissue (Fig. 33). The penis retractor muscle attaches to and envelops the lower forth of the epiphallus. It originates on the center of mantle floor slightly behind the mantle collar. The epiphallus is almost as stout as the penis and is about twice as long. The lumen of the epiphallus is lined with four longitudinal folds. The flagellum is relatively stout and moderately short, 30 mm long. It is slightly longer than the combined length of the penis + epiphallus. The interior of flagellum is lined with about six longitudinal columns. The lower vagina above



Figs. 27-31. *Humboldtiana regula* n. sp. Figs. 27-30: Holotype (UF 320069). Fig. 31: paratype (UF 317179).



Figs. 32-35. *Humboldtiana* reproductive anatomy. Figs. 32-33. *Humboldtiana regula* n. sp. (UF 317179). Fig. 32: reproductive system. Fig. 33: interior of penis. Figs. 34-35. *Humboldtiana spectabila* n. sp. (UF 358375). Fig. 34: reproductive system. Fig. 35: interior of penis.

the atrium is moderately slender and bears four dart-sacs. The first dart-sac, ds_1, is large and bulbous. The remaining dart-sacs, ds_2, ds_3 and ds_4, are decreasingly smaller. The dart-gland are tightly appressed against the top of the dart-sacs. The free vagina is very short. The spermathecal duct + spermatheca is 61 mm long, is slightly longer than the uterus, and bears a caecum that diverges 16 mm below the end of the spermatheca. The caecum is short, less that half the length of the end of the spermathecal duct above its confluence.

Type Locality.— Chihuahua, Sierra de la Catarina, highway pass ca. 12 km northeast of Ignacio Zaragoza (29°46.0'N, 107°37.8'W); 2250 m alt. Holotype: UF 320069; collected 13 August, 2003 by Fred G. Thompson. Paratypes: UF 317178 (10), UF 317179 (10), ITCV (10), same data as the holotype.

Distribution.— Known only from the immediate vicinity of the type locality. Chihuahua, 21.6 km NE of Ignacio Zaragoza (29°46.4'N, 107°37.5'W), 2280 m alt. (UF 317176); 11 km NE of Ignacio Zaragoza (29°46,0'N, 107°38.2'W), 2320 m alt. (UF 317182).

Ecology.— At the type locality snails were found in tallus along granite outcrops in a sparse submesic piñon-pine and oak forest with sparse clumps of bunchgrasses. Live specimens were aestivating on the underside of large boulders.

Remarks.— In *Humboldtiana regula* the wavy transverse striations on the embryonic whorls are much finer than they are on the following species, and the granular sculpture on the first post-embryonic whorl is finer and not as dense. The shell is considerably smaller, it is darker colored and it bears more numerous white streaks. *Humboldtiana regula* is similar in its anatomy to the following species, and additional collections my reveal that the two are subspecifically related. *Humboldtiana regala* has an epiphallus that is about twice the length of the penis, and the dart-sac ds_1 is enlarged, whereas in the next species the epiphallus is about 5-6 times the length of the penis and ds_2 is enlarged.

Etymology.— The name *regula* is from the Latin *regulus*, a prince, alluding to the regal appearance of the shell.

Humboldtiana spectabile n. sp.

Diagnosis.— The large shell is globose, shiny, and boldly banded. The embryonic whorls are sculptured with numerous wavy transverse striations. The first post-embryonic whorl is densely sculptured with minute granulation overlaying radial striations. The genital atrium is very shot; almost non-existent. The penis is short, stout, and has a short verge. The stout epiphallus is 5-6 times a long as the penis. The penis retractor muscle forms a sheath around the lower third of the epiphallus. The flagellum is short, less the length of the epiphallus. The lower vagina is long and slender. The dart-sacs are sub-equal in size; ds_1 is the largest; ds_3 is the smallest. The dart-glands are juxtaposed against dart-sacs. The free vagina is very short.

Shell (Figs. 36-39).— The shell is moderately large, about 32-35 mm wide. It is sub-globose, 0.86-0.96 times as high as wide. The periostracum is shiny, and is colored light brown and bears three bold chestnut-colored bands. The ground color and the bands are interrupted with occasional white streaks. The lower band usually is the widest. The interior of the aperture has a whitish tinge and is banded. The umbilicus is obliquely perforate (Fig. 39). Mature shells have 4.0-4.2 whorls. The suture is deeply impressed. The embryonic shell is raised and consists of 1.5 whorls that are crossed by minute wavy striation. The following complete post-embryonic whorl is densely sculptured with minute granules between and overlying the growth wrinkles and striation. Subsequent whorls lack granular sculpture and are crossed with fine incremental stria-

Table 4. *Humboldtiana regula* n. sp. Measurements in mm for the holotype (UF 320069) and 16 paratypes (UF 317178/7; UF 317179/9).

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	28.0	30.1	16.1	20.8	4.2	0.93	0.54	0.74	0.77
Paratypes									
Min	25.0	28.7	15.2	18.5	3.8	0.83	0.52	0.60	0.77
Max	29.1	33.1	20.4	22.6	4.2	1.00	0.58	0.80	0.98
Avg	27.16	30.18	16.53	20.12	4.0	0.90	0.55	0.75	0.83
SD	1.14	1.16	1.23	0.95	0.12	0.04	0.03	0.04	0.05

tions interrupted by occasional white streaks. The last whorl descends strongly to the aperture to insert at the bottom of the sub-peripheral band. The plane of the aperture lies at about 40° to the shell axis in lateral profile (Fig. 37). The aperture is circular, 0.66-0.80 times as wide as high. The outer lip and the basal lip are very slightly reflected. The columellar lip is widely reflected over the umbilicus. The parietal wall of the aperture has a thin transparent glaze.

Measurements of the holotype and six paratypes are given in Table 5.

Anatomy (Figs. 34-35).— (Paratypes, UF 358375; 4 specimens). The specimens have been preserved for 35 years in 70% ethanol. They are light gray on the head-foot, mantle collar and lung.

The albumen gland is elongate and stout. The carrefour is exposed. The genital atrium is very short, and is separated from the body wall by 1-2 mm. The penis is short, stout and nearly uniform-cylindrical in shape externally. It is 7 mm long, and is demarcated from the epiphallus by a weak constriction. Internally the penis wall is lined with heavy longitudinal pilasters (Fig. 35). The upper part of the chamber bears a short four-lobed verge. The penis retractor muscle is 22-23 mm long, slender. It originates on the middle of the inner wall of lung behind the mantle collar, and inserts on and forms a sheath around the lower third of the epiphallus. The epiphallus is very long, stout and thick-walled. It is about 5-6 times as long as the penis, and it is lined internally with four longitudinal glandular columns. The flagellum is short and stout. It is slightly shorter than the epiphallus and is lined internally with six longitudinal columns of papillae. The vas deferens is moderately stout and is nearly uniform in diameter throughout its length. The lower vagina is moderately long, slender and conical with four unequal-sized dart-sacs radially arranged above. One-dart sac, ds_2 is very large; the other three dart-sacs are much smaller and are sub-equal to each other in size. A stout dart-gland encircles the vagina immediately above, but not appressed against the dart-sacs. The free vagina is almost absent. The spermathecal duct diverges from the vagina just above the dart-glands; it is relatively stout, very long, and bears a short caecum at 0.69-0.75 of the distance from the base. The caecum is about a third or less than the length of the distal spermathecal duct segment. The spermatheca is small and elongate-bulbous in shape. It is oppressed against the upper end of the prostate-uterus at the base of the albumen gland. The spermatheca duct + spermatheca is about twice the length of the uterus.

Type locality.— Chihuahua, a rocky outcrop in the foothills of the Sierra La Catarina, Buenaventura, (29°40' N, 107°30' W); 1850 m alt. Holotype: UF 25129, collected 25 June, 1971 by Jerry J. Landye. Paratypes: UF 358375 (7); ITCV (3); same data as the holotype.

Distribution.— This species is known from the foothills of the Sierra La Catarina, which lies about 20 km southwest of Buenaventura. The range is oriented north-south, and is about 60 km long and about 10 km wide near its middle

Remarks.— The reproductive system differs remarkably from other species of *Humboldtiana* by its very short genital atrium, by its long, slender penis retractor muscle which forms a sheath around the lower third of the epiphallus, and by its very long epiphallus, which is about 5-6 times the length of the penis. The flagellum is short, being less than the length of the epiphallus. The dart glands are associated close to the dart-sacs, and the free vagina is very short

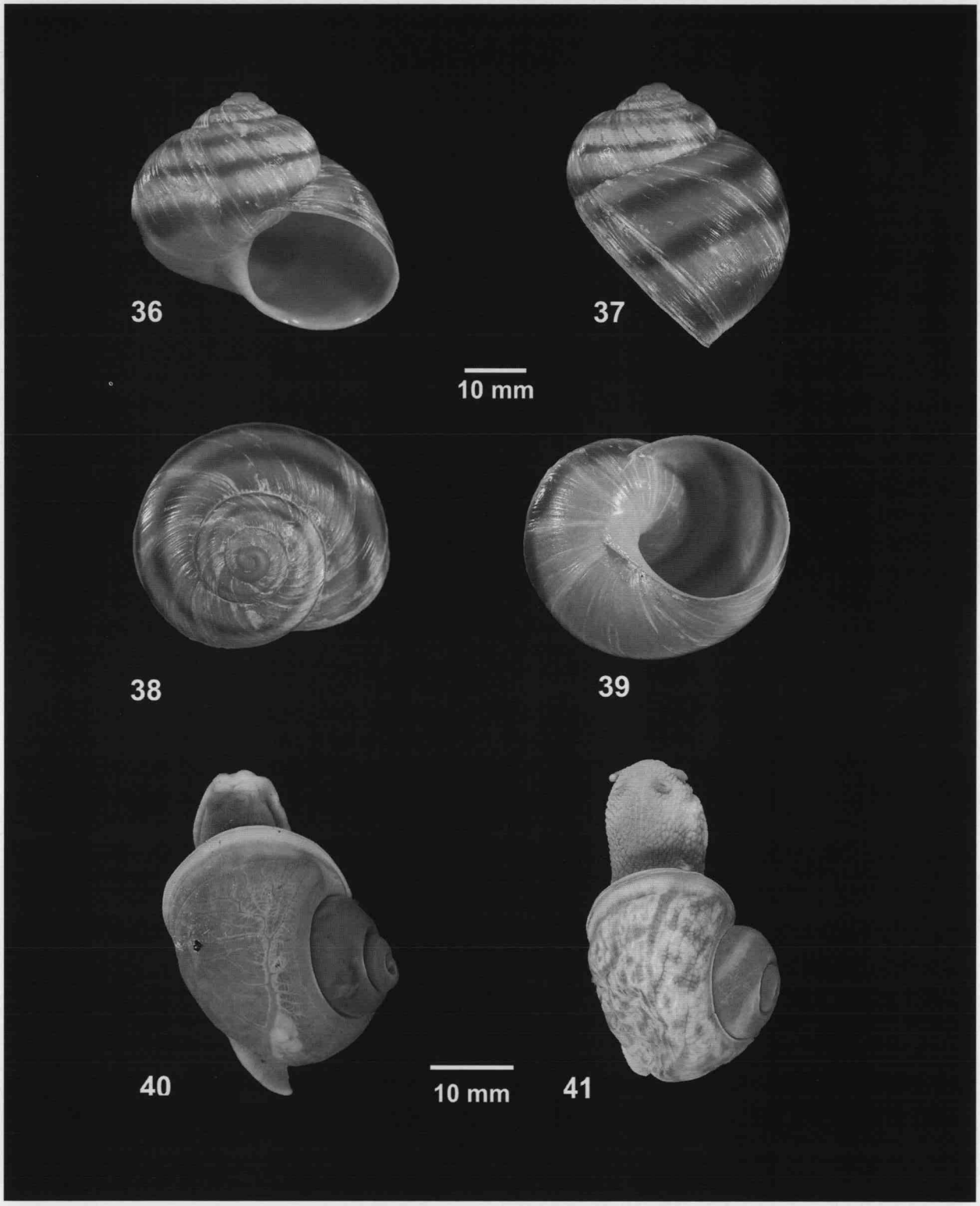
Etymology.— The species name *spectabile* (f.), is from the Latin *spectabilis* (m.), meaning worth seeing, notable or remarkable. The name alludes to the stately appearance of the shell.

Species from the Sierra Victorino

These are large, strongly marked species that are characterized anatomically by a long verge, by having the penis retractor muscle form a narrow collar around

Table 5. *Humboldtiana spectabile* n. sp. Measurements in mm of the holotype (UF 25129) and six paratypes (UF 358375).

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	35.4	38.3	21.1	28.3	4.2	0.92	0.55	0.80	0.75
Paratypes									
Min.	30.6	35.1	19.2	24.1	4.0	0.86	0.52	0.74	0.66
Max.	35.3	37.2	21.1	26.6	4.1	0.96	0.55	0.82	0.80
Avg.	33.13	36.59	19.77	26.46	4.09	0.91	0.54	0.79	0.75
SD	1.59	0.99	0.64	1.63	0.06	0.03	0.01	0.03	0.04



Figs. 36-41. *Humboldtiana*. Figs. 36-39: *Humboldtiana spectabile* n. sp. Holotype (UF 26129). Fig. 40: *Humboldtiana balanites* n. sp. Fig. 41: *Humboldtiana cicatricosa* n. sp.

the base of the epiphallus, by having a short and stout epiphallus, by having an abbreviate genital atrium, by having a long middle vagina that widely separates the dart-sacs from the dart-glands, and by a short spermathecal duct that is less than the length of the uterus-prostate. The flagellum is short and stout compared to species from the Sierra de La Catarina.

Like *Humboldtiana* from the Sierra de La Catarina these snails bear fine transverse striations on the embryonic whorls, but the striations are coarser, though nearly obsolete, and the are not as wavy. The embryonic sculpture is most easily viewed in zones of reflected light.

Humboldtiana titania n. sp.

Diagnosis.— The moderately large shell is depressed-globose in shape, and consists of 4.1-4.5 whorls. The embryonic whorls bear relatively coarse wavy transverse micro-striation. The postembryonic whorls are almost lusterless with rather coarse incremental striations and growth wrinkles. The first postembryonic whorl bears a few scattered granules that mostly are found along the lower suture. The color is light brown with three bold blackish-brown bands and numerous transverse white streaks on growth wrinkles. The peristome is tinged pink. The interior of the aperture is light brown with a whitish tinge and banded. The reproductive anatomy is distinct because of its stout features, including the penis, epiphallus, flagellum, and spermathecal duct. The epiphallus is very short, being about half the length of the penis. The flagellum is moderately short and is lined internally with four longitudinal columns. There are four dart sacs, of which ds_1 is the largest; and ds_3 and ds_4 are vestigial. The dart gland is widely separated from the dart sacs. The spermathecal duct is moderately short with a short caecum nears its distal end.

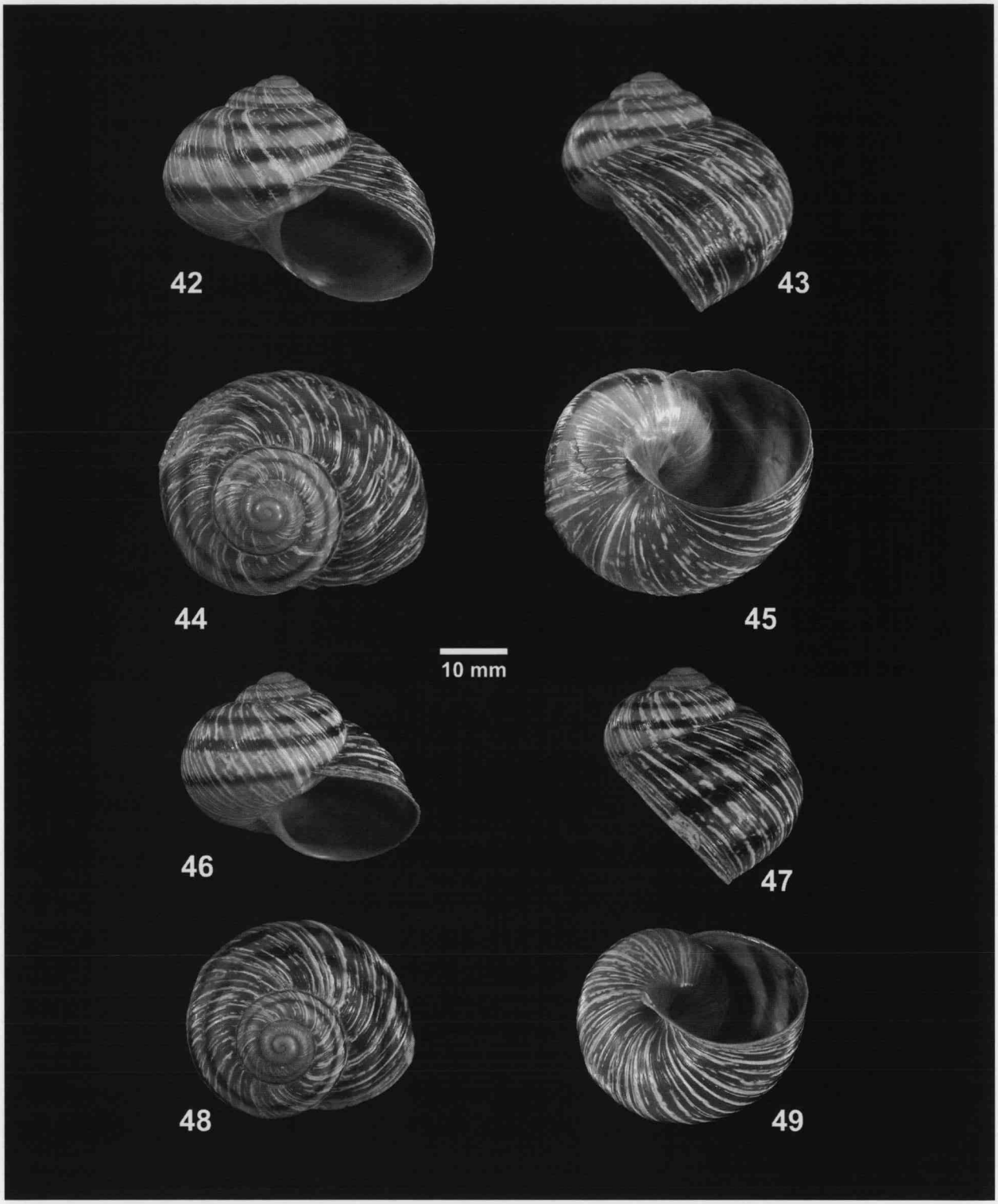
The head-foot is orange-gray in life, and live animals smell like putrid garlic.

Shell (Figs. 42-45).— The shell is large. Mature shells are about 31-39 mm wide, depressed helico-globose in shape, and are about 0.77-0.87 times as high as wide. The whorls are inflated with a deeply impressed suture. The periostracum is smooth but nearly lusterless due to rather strong growth wrinkles. It is light brown in color with three stark blackish-brown bands and numerous transverse white streaks. The bands are subequal in size. The lower band usually is the widest, but not always. The interior of aperture is light brown with a whitish tinge, and is banded. The umbilicus is obliquely perforate (Fig. 45). There are 4.1-4.5 whorls; more often 4.3-4.4. The 1.2 embryonic whorls protrude, but are low. The first embryonic whorl is 4.1 mm wide transverse to the initial suture. The embryonic whorls are sculptured with nearly obsolete transverse wavy wrinkles that are visible mostly in areas of reflected light. The following postembryonic whorls are sculptured with coarse incremental striations and growth wrinkles. The first postembryonic whorl has occasional elongate granules aligned with the growth wrinkles mostly along the lower suture. Granular sculpture is absent on the subsequent whorls. The last whorl strongly descending to the aperture. The upper lip inserts on or just below the sub-peripheral band. The aperture is oblique in lateral profile, lying at an angle of about 34-42° to shell axis (Fig. 43). The aperture is oblong and is 0.77-0.87 times as wide as high. The peristome is slightly reflected along the upper, outer and basal lips; and nearly covers the umbilicus along the columellar margin.

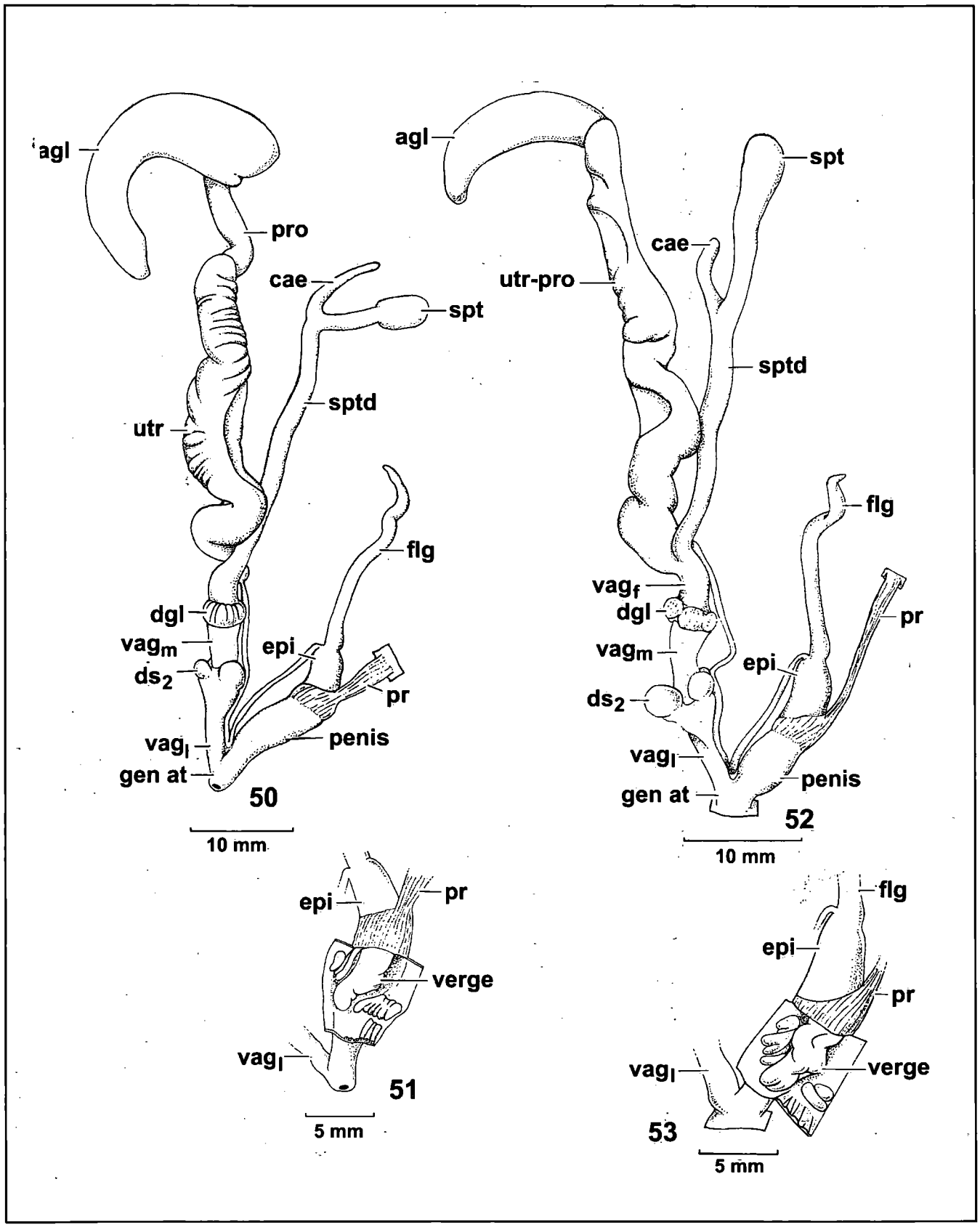
Measurements of the holotype and 14 paratypes are given in Table 6.

Anatomy.— In life the head-foot is orange-gray in color. The color of the mantle is light orange in preservatives. Live snails emitted a strong putrid garlic-like odor.

Reproductive system (Figs, 50-51). The genital atrium is moderately short. The penis is elongate but stout and vase-shaped. The penis wall is thin. The interior of the penis bears a fleshy collar near the middle of the laterad wall with 4 longitudinal folds extending to the atrium. The penis has a large convoluted verge that is about half the length of the penis chamber (Fig. 51). The penis retractor muscle is very short and stout. It is slightly less than the length of the penis. The penis retractor originates slightly behind the mantle collar on the center of nape, and inserts on the epiphallus where it forms a narrow sheath around the lower third of the epiphallus. The epiphallus is very stout and short. It is slightly more than half the length of the penis. Its interior is lined with four fleshy columns. The flagellum is very stout and abruptly tapers at the end. It is short, being slightly longer than the combined length of penis + epiphallus. The interior of the flagellum has four longitudinal fleshy columns. The lower vagina is elongate and tapers narrowly to the atrium. There are four dart-sacs, of which ds_1 is the largest, ds_2 is the second largest, ds_3 and ds_4 are very much reduced in size. The dart-gland are widely separated on the middle vagina from the dart-sacs by a distance about equal to half of the length of the lower vagina. The free vagina is not apparent. The spermathecal duct is stout and is relatively short, being less than the length of the uterus. The spermathecal duct bears a short caecum that is slightly less than the length of the duct + spermatheca above its origin.



Figs. 42-49. *Humboldtiana*. Figs. 42-45. *Humboldtiana titania* n. sp. Holotype (UF 358679). Figs. 46-49: *Humboldtiana oberon* n. sp. Holotype (UF 317164).



Figs. 50-53. *Humboldtiana* reproductive anatomy. Figs. 50-51: *Humboldtiana titania* n. sp. Fig. 50: reproductive system (UF 317164). Fig, 51: interior of penis. Figs. 52-52: *Humboldtiana oberon* n. sp. (UF 317161). Fig. 52: reproductive system. Fig. 53: interior of penis.

Table 6. *Humboldtiana titania* n. sp. Measurements in mm based of the holotype (UF 358679) and 14 paratypes (UF 317163/10, UF 358376/4).

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	32.1	35.1	19.2	24.9	4.2	0.83	0.55	0.83	0.80
Paratypes									
Min	26.3	30.7	16.3	21.0	4.1	0.80	0.51	0.71	0.77
Max	32.7	39.2	20.7	26.0	4.5	0.94	0.57	0.84	0.87
Avg	29.90	35.20	18.99	23.44	4.30	0.85	0.54	0.79	0.81
SD	1.87	2.43	1.13	1.58	0.10	0.04	0.01	0.04	0.04

Type locality.— Chihuahua, Sierra Victorino, 0.6 km southeast of Cumbres Majalca Visitors Center (28°48.1'N, 106°28.8'W), ca. 21 km west of Nueva Majalca; 2060 m alt. Holotype: UF 358679; collected 7 August, 2003 by F. G. Thompson and E. L Mihalcik. Paratypes: UF 358376 (4), UF 317163 (10), ITCV (10); same data as the holotype.

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

Ecology.— The type locality was sparsely forested with oak and a few scattered pines. Snails were collected along a granite ledge. Dead shells were common along the base of the outcrop. Five live specimens were found aestivating deep within crevices from where they were extracted with great difficulty.

Remarks.— The reproductive anatomy of this species is best described as stout in all aspects.

Etymology.— The species name *titania* is from the Classical Literature, Shakespeare, Wm., 1594, *A Mid Summer Night Dream*. Titania is the exquisitely beautiful fairy queen. The name of this species alludes to the beauty of its shell.

Humboldtiana oberon n. sp.

Diagnosis.— The shell is recognized in part by its rich brown ground color with three bold bands and numerous transverse enamel-like white streaks, and by its pink peristome. The surface of the shell is smooth, though interrupted by rather coarse incremental striations and wrinkles. The shell is similar to *Humboldtiana titania*, but it is smaller, and it has a more rotund aperture. It differs further by having stronger transverse wrinkles on the embryonic whorls, by lacking granular sculpture, by being more coarsely wrinkled on the postembryonic whorls, and by having more densely packed transverse white streaks. The genital atrium is almost non-existent. The penis is very short and contains a verge that is almost the length of the penis. The penis retractor muscle is relatively slender and is about as long as the combined length of the penis + epiphallus. The flagellum is about 1.5 times longer than the combined length of the penis + epiphallus. The vagina is slender. The dart-glands are widely separated from the dart-sacs. The dart-sacs are subequal in size; ds_1 is the largest. The head-foot is grayish black in life, and the animal does not exude a distinct odor.

Shell (Figs. 46-49).— The shell is medium to large in size, usually about 25-30 mm wide, but occasional specimens are up to 38 mm wide. It is helico-globose in shape, and is 0.79-0.88 times as high as wide. There are 4.0-4.2 whorls, which are inflated and are separated by a deep suture. The periostracum is smooth but nearly lusterless. The shell has three bold nearly black bands. The ground color in fresh specimens is light brown. The last quarter whorl has a rusty tinge. The ground color and the bands are crossed by numerous transverse enamel-like white streaks and elongate blotches that are located on the growth wrinkles, producing a very handsom appearance to the shell. The peristome is pink. The interior of the aperture is light brown and is banded. The umbilicus is obliquely rimate (Fig, 49). The embryonic shell contains 1.4 whorls that are raised and rounded. The first embryonic whorl is 4.1 mm wide perpendicular to the initial suture. The embryonic whorls are sculptured with relatively wide but vague wavy transverse wrinkles. The postembryonic whorls are crossed by numerous incremental striations and growth wrinkles. Distinct granular sculpture is absent on the embryonic and postembryonic whorls, although occasional growth wrinkles on early whorls may be weakly beaded. The last quarter whorl descending strongly to the aperture. The upper lip inserts on or below the lower band. The aperture is oblong-ovate in shape; 1.03-1.22 times as wide as high, and lies at about 30-35° to shell axis in lateral profile (Fig. 47). The peristome is uniformly, weakly and narrowly reflected. The reflected columellar lip nearly obscures the umbilicus.

Measurements of the holotype and eleven paratypes are given in Table 7.

Anatomy.— The head-foot is grayish-black when alive. The mantle in preservatives is uniformly dark gray. The live animal did not exude a distinct odor when handled.

Reproductive system (Figs. 52-53). Two specimens were dissected. The genital atrium is very short and almost non-distinguishable. The penis is short and stocky, almost ovate-shaped, and 6 mm long. The interior has a long verge that extends nearly the length of the cavity (Fig. 53). The inner wall of penis has a series of folds around the middle and several smaller longitudinal folds below. The penis retractor muscle is slender, 13 mm long. It originating on the middle of inner wall of lung midway behind the mantle collar and inserting on the base of the epiphallus where it forms a narrow sheath around the lower fourth of the epiphallus. The epiphallus is short and stout, and is slightly longer than the penis. Its interior has three longitudinal folds lying opposite a flattened area. The flagellum is stout and tapers abruptly to a point. It is 17 mm long, slightly longer than the combined length of the penis + epiphallus. The interior of the flagellum has four longitudinal folds. The lower vagina is 20 mm long and slender; with four dart-sacs, of which ds_1 is the largest; ds_2 the next largest; ds_3 and ds_4 are subequal in size. The middle vagina is surrounded by a four lobed dart-gland that is widely separated from the dart-sacs. The free vagina is not apparent. The spermatheca + duct is moderately short; about 37 mm long and about the same length as the uterus. The spermathecal duct bears a short caecum that is located at about 0.60 of the distance from the base of the duct. The caecum is about equal in length of duct below the spermatheca and its origin. The spermatheca is elongate and almost elliptical in shape.

Type locality.— Chihuahua, Sierra Victorino, 17 km west of Nueva Majalca (28°47.4'N, 106°27.7'W) 1900-2000 m alt. Holotype: UF 317164; collected 6 August, 2003 by Fred G. Thompson and Elizabeth L Mihalcik. Paratypes: (UF 317160 (15), 317161 (4), ITCV (10); same data as the holotype.

Distribution.— Known only from the type locality.

Ecology.— This species was found on a steep slope in an open sub-mesic oak and juniper forest. Snails were found among dead leaves on the forest floor. It had rained during the previous night, and live specimens were not in aestivation. Apparently this species burrows in the ground during dormancy, because granite ledges near by had no concentrations of dead shells.

Remarks.— *Humboldtiana oberon* is closely related to *H. titania* as is indicated by similar shell features and the reproductive anatomy. Although they appear similar, the two differ substantially in shell features, as well as anatomical structure that distinguish them as separate species.

Etymology.— The species name *oberon* is from the Classical Literature, Shakespeare, Wm., 1594, *A Mid Summer Night Dream*. Oberon is the fairy king.

Species from the vicinity of Ciudad Chihuahua

Low mountain ranges and hills in this region are inhabited by *Clydonacme*. The two known species do not appear to be closely related to other members of the subgenus because of the relatively rugose embryonic shell sculpture. Only one is known anatomically. It differs from other species by having a long genital atrium, a moderately long and stout epiphallus, the penis retractor inserts at the base of the epiphallus, the flagellum is long and slender, the middle vagina is slightly extended, narrowly separating the dart-sacs from the dart-glands, and the spermathecal duct is very long.

Table 7. *Humboldtiana oberon* n. sp. Measurements in mm of the holotype (UF 317164) and 11 paratypes, UF 317160 (7) and UF 317161 (4). A paratype 38.0 mm wide is not included in the table because of a broken apex.

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	27.2	32.7	18.3	20.0	4.2	0.83	0.56	0.74	0.92
Paratypes									
Min.	24.5	30.5	16.6	18.4	4.0	0.79	0.51	0.69	0.82
Max	29.5	34.2	18.3	21.9	4.2	0.88	0.58	0.81	0.97
Avg	26.69	32.04	17.48	20.08	4.12	0.83	0.55	0.75	0.87
SD	1.17	1.17	0.56	0.79	0.10	0.03	0.02	0.03	0.04

Humboldtiana princeps n. sp.

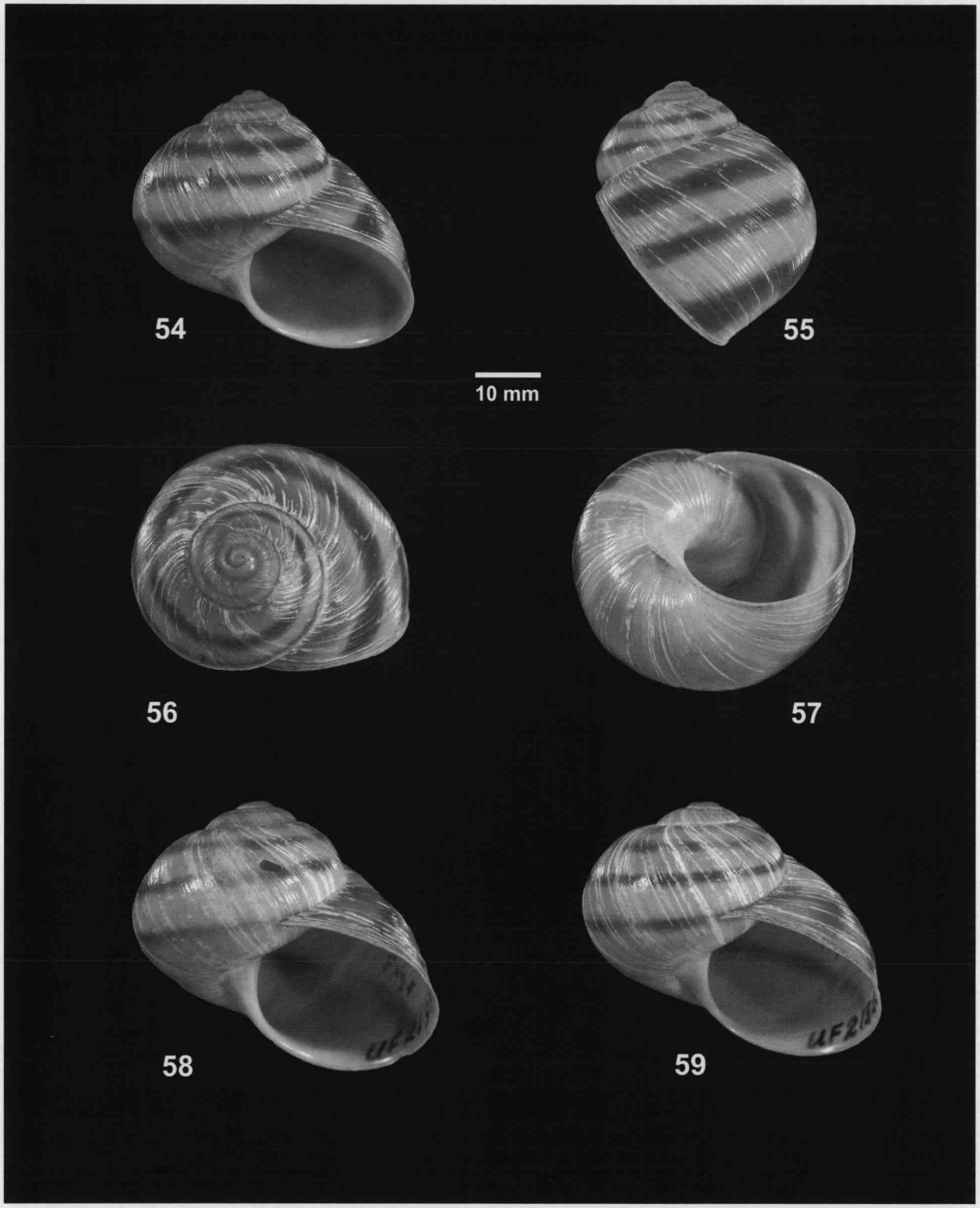
Diagnosis.— The helicoid or depressed-helicoid shell is large, up to 41 mm wide. It is light brown with three chestnut-brown bands and transverse white streaks, and it has a slight luster. The transverse white streaks are less numerous than in other species of *Clydonacme*, and they tend to be broken more frequently. The embryonic whorls bear relatively coarse transverse zigzag threads that are beaded. The postembryonic whorls are sculpture with relatively fine incremental striations and weak growth wrinkles. The first postembryonic whorl bears numerous fine microscopic granules throughout the length of the whorl. The genital atrium is moderately long and slender. The penis is club-shaped with a slight apical constriction; internally it bears a large verge that is half the length of the cavity, and the inner wall is lined with 5-6 heavy fleshy folds. The epiphallus is slightly longer than the penis, and the relatively slender flagellum is slightly longer than the combined length of the penis + epiphallus. The vagina bears four dart-sacs; ds_1 is the largest, and the other three are greatly reduced in size. The dart-glands form a ring around the vagina a short distance above the dart-sacs. The spermatheca + duct bears a caecum and is very long, being about twice the length of the uterus.

Shell (Fig. 54-59).— The shell is up to 41 mm wide, and is helicoid to depressed-helicoid in shape; 0.83-1.02 times as high as wide. There are 4.0-4.2 whorls that are inflated and have a moderately impressed suture. The whorls regularly expand until the last quarter whorl, which rapidly descends to the aperture (Fig. 55). The upper lip of the peristome inserts on or just below the sub-peripheral band. The periostracum is nearly smooth and has a low luster. The umbilicus is narrowly, obliquely rimate (Fig. 57). The ground color is light brown with three chestnut-brown bands. The bands are unequal in width. A lighter chestnut zone usually borders the suture along the upper side of the whorls. Frequent transverse white streaks, which lie on the growth wrinkles, interrupt the underlying color patterns. The interior of the aperture is light grayish-brown and banded. The peristome is light brown, and the parietal callus is hyaline. The 1.5 embryonic whorls are raised. The first embryonic whorl is 3.9-4.1 mm wide transverse to the initial suture. The embryonic sculpture consists of relatively coarse zigzag transverse threads that are beaded by granules. The postembryonic whorls have relatively fine incremental striations and low growth wrinkle. In addition, the first postembryonic whorl has numerous granules that tend to be aligned along the growth wrinkles. The granules occur throughout the length of the whorl, but are densest along the lower ¾ of that whorl. Granular sculpture is absent on the lower whorls. The aperture is broadly obovate in shape; 0.76-0.84 times as wide as high. The plane of the aperture lies at an angle of 40-42° to the shell axis. The peristome is weakly but uniformly reflected along the upper and outer lips; more so along the basal lip, and strongly so over the columellar area.

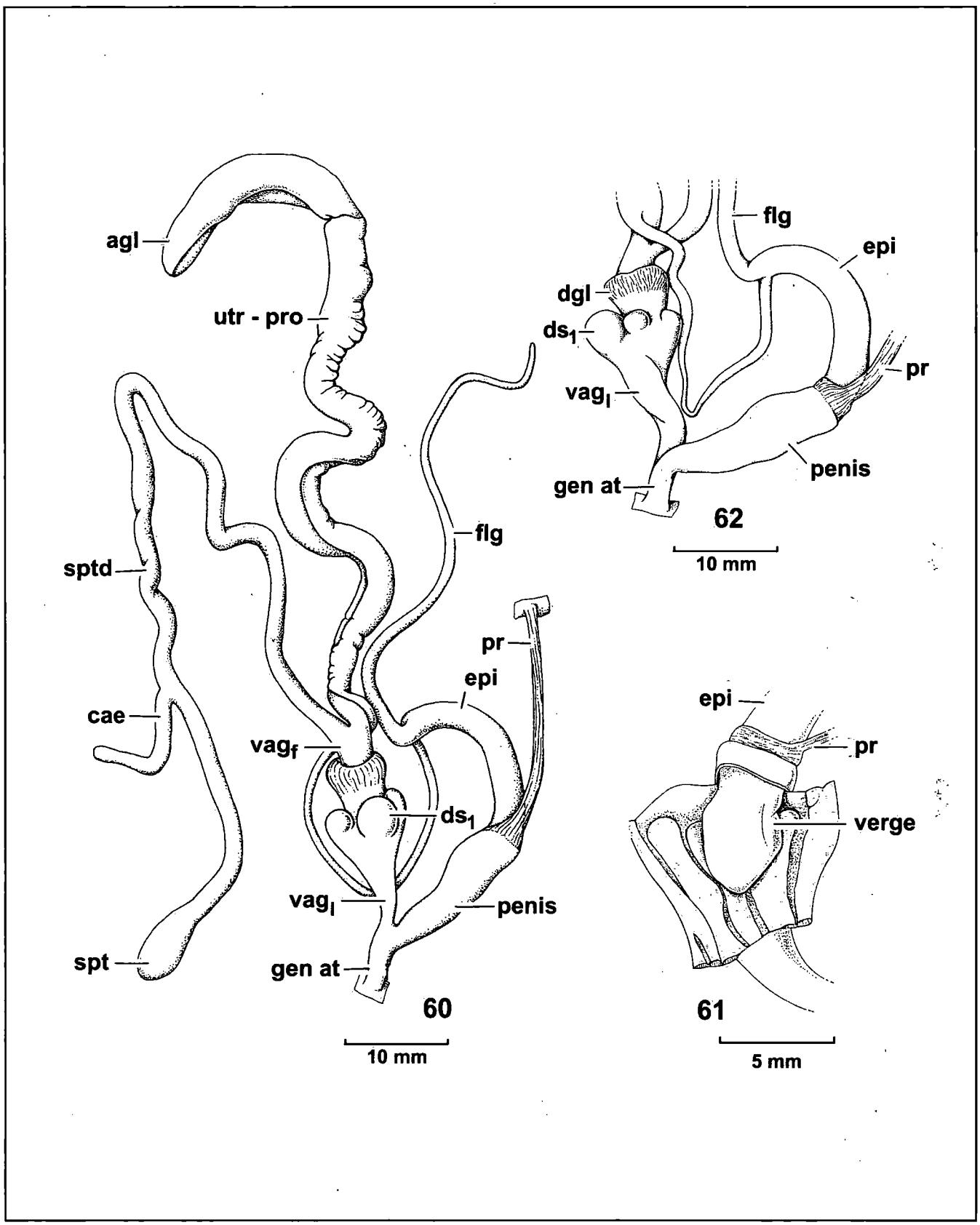
Measurements of the holotype and twelve paratypes are given in Table 8.

Anatomy (Figs. 60-62).— Three specimens were dissected (UF 21331). The genital atrium is 2-3 mm long and slender. The penis is 12-15 mm long and tapered. It is widest below the epiphallus. The upper end of the penis has a slight constriction, which corresponds to the absence of internal folds at that point. The inner wall of the penis has 5-6 longitudinal folds that extend from below the apical constriction to the base. The penis contains a large verge in the upper third of chamber (Fig. 61). The penis retractor muscle is 14-17 mm long and is slightly longer than the penis. The penis retractor muscle originates on the middle of the inner wall of lung about 3-4 mm behind the mantle collar, and inserts on the end of the penis laterad to the epiphallus and forms a narrow sheath around the lower end of the epiphallus. The epiphallus is 15-18 mm long, stout, thick-walled, and is slightly longer than the penis. It is lined internally with four longitudinal folds. The flagellum is 33-42 mm long, relatively slender and is slightly longer than the combined length of the penis + epiphallus. It is lined internally with four longitudinal folds. The vas deferens is moderately stout below the prostate and above the epiphallus, and is very narrow in its middle where it is attached by connective tissue to the genital atrium. The lower vagina is relatively long and is conical and it bears four unequal sized dart-sacs. One dart-sac, ds_1, is large and bulbous; the other three dart-sacs are much smaller and are about equal in size to each other. The dart-glands encircles the middle vagina a few mm above the dart-sacs. The spermathecal duct diverges from the free vagina 1-2 mm above the dart-glands. It is moderately stout and very long. The spermatheca + duct is 97-113 mm long. The duct bears a short caecum at 0.69-0.76 of the distance from the base. The caecum is about half or less than the length of the remaining spermatheca + duct. The spermatheca is small, elongate-bulbous, and is oppressed against the upper end of the uterus-prostate at the base of the albumen gland. The spermatheca + duct is about twice the length of the uterus. The uterus is 47-52 mm long.

Type locality.— Chihuahua, 13 km southwest of Cd. Chihuahua (28°37'N, 106°10'W); 1540 m alt. Holo-



Figs. 54-59. *Humboldtiana princeps* n. sp. Figs. 54-57, Holotype (UF 350039). Figs. 58-59, Paratypes (UF 21331).



Figs. 60-62. *Humboldtiana pinceps* n. sp.: reproductive anatomy of two paratypes (UF 21331). Figs. 60: reproductive system. Fig. 61: interior of penis of Fig. 60. Fig. 62: lower genitalia of a paratype (UF 21331).

type: UF 350039; collected 23 November, 1970 by Fred G. Thompson. Paratypes: 21330 (4), 21331 (7), ITCV (4); same data as the holotype.

Snails were collected from crevices in a granite bluff along the south side of the stream below the Presa Chihuahua. The area was in a submesic forest consisting of a dense growths of thorn scrub above, below and on the side of the bluff.

Distribution.— Known only from the type locality.

Remarks.— The shell of *Humboldtiana princeps* is highly variable in shape and in the width of the bands. Usually the lower band is the widest, but not always. The subsutural reddish zone is absent in one live-collected paratype.

Etymology.— The species name *princeps* is from Latin, meaning first among many, such as a prince or princess. The name alludes to the princely appearance of this snail.

Humboldtiana hogeana (Martens, 1892)

Helix humboldtiana högeana Martens, 1892: 148; pl. 7, figs. 20, 21 (shell).

Humboldtiana hogeana (Martens). Pilsbry, 1927: 179.- Pilsbry, 1935a; Nautilus, 48: 2; pl. 1, fig. 9 (shell).Pilsbry, 1935b: 2; pl. 1, fig. 9 (shell).- Pilsbry, 1939: 402.- Pilsbry, 1948: 202.- Solem, 1954: 5.- Th ompson, 1967: 25.

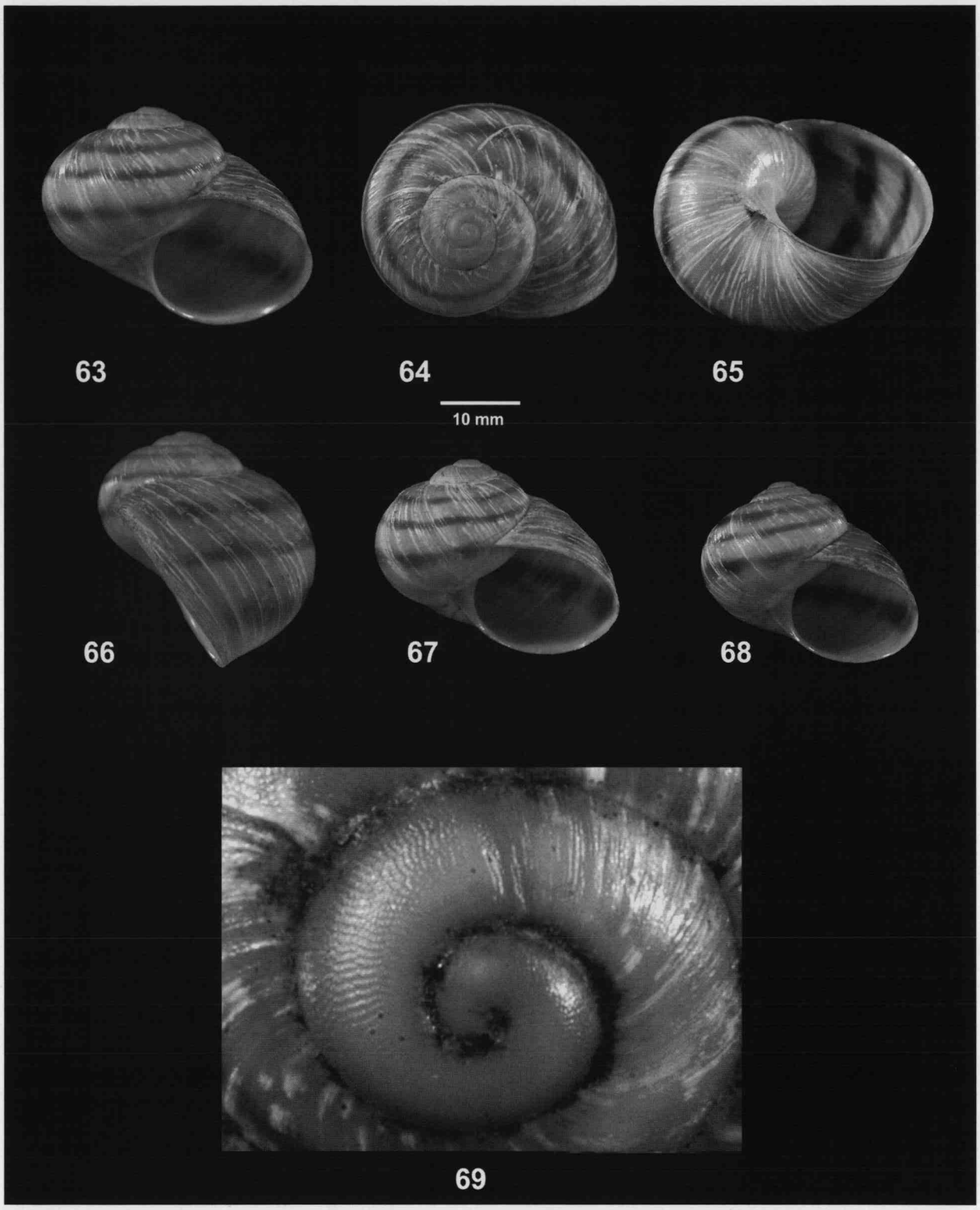
Diagnosis.— The following description is based on the syntypes, which are the only known specimens. A small-sized *Humboldtiana* that is up to about 33 mm wide with a helicoid-shaped shell that is 0.78-0.80 times as high as wide. The aperture is obovate in shape, and is higher than wide. The shell is lusterless, light brown in color with transverse white streaks and three reddish-brown bands. The middle band is the narrowest. The embryonic whorls are smaller than in other species in the subgenus. The embryonic sculpture consisting of distinct transverse zigzag striations. The postembryonic sculpture consists of incremental striation and weak growth wrinkles. The second-half postembryonic whorl bears fine granules.

Shell (Figs. 63-69).— A relatively small-sized species that is up to about 33 mm wide with a helicoid-shaped shell that is 0.78-0.80 times as high as wide. The periostracum is lusterless. The ground color is light brown with three reddish-brown bands. The middle band is the narrowest, and the sub-peripheral band is the widest. The shell bears transverse white streaks that are located on incremental growth striations. The white streaks are not as crowded as in other species in the subgenus. The interior of aperture is light brown with a whitish tinge and banded. The peristome is light brown. Rimate (Fig. 65). The aperture is obovate in shape, and is 0.82 times as wide as high. There are 3.8-3.9 whorls at maturity. Embryonic whorls 1.5. The first embryonic whorl is 3.7 mm wide perpendicular to the initial suture. The embryonic sculpture consists of relatively coarse and well defined beaded zigzag striations (Fig. 69). The following 1/4-1/2 postembryonic whorl bears incremental striation and wrinkles. The next half whorl has in addition, dense fine granules on and between the wrinkles. The remainder of the shell is sculpted with incremental striations and low wrinkles that continue over the surface and into the umbilical chink, but lacks granular sculpture. The whorls are rotund with a moderately impressed suture. They regularly expand in size along the upper edge of the middle band. The last 1/8th whorl descends to the aperture at the upper edge of the sub-peripheral band. The plane of the aperture lies at an angle of 43-48° to the shell axis (Fig. 66). The aperture is obovate in shape and is 0.82 times as wide as high. The peristome is weakly reflected along the upper, outer and basal lips and then expands broadly to nearly occlude the umbilical perforation.

Measurements of the lectotype and the mature paralectotype are as given in Table 9.

Table 8. *Humboldtiana priceps* n. sp. Measurements in mm of the holotype (UF 350039) and 12 paratypes.

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	37.2	38.8	22.5	29.6	4.2	0.96	0.58	0.80	0.76
Paratypes									
Min.	31.6	33.2	18.4	23.0	4.0	0.83	0.54	0.73	0.76
Max	37.2	41.0	23.2	28.4	4.1	0.91	0.57	0.76	0.84
Avg	34.29	37.58	21.27	26.50	4.06	0.91	0.57	0.77	0.80
SD	1.53	2.31	1.57	1.98	0.06	0.05	0.01	0.04	0.02



Figs. 63-69. *Humboldtiana hogeana* Martens, 1892. Figs. 63-66: Lectotype (BMNH 1901-6-22-657). Fig. 67: paralectotype (BMNH 1901-6-22-658). Figs. 68-69: paralectotype.(BMNH 1901-6-22-658).

Type Locality.— Chihuahua. Lectotype by present designation: BMNH 1901-6-22-657; collected in 1880 by H. Höge (Figs. 63-66). The lectotype is figured in Martens, pl. 7, fig. 21. Paralectotype α: BMNH 1901-6-22-658 (1 mature specimen; figured in Martens, pl. 7, fig. 20) (Fig. 67). Paralectotype β: BMNH 1901-6-22-658 (1 immature specimen) (Fig. 68-69). The paralectotypes have the same data as the lectotype.

Martens described this species from "Chihuahua". It is not clear whether the locality is the city or the state. Whether the species actually occurred in Cd. Chihuahua can no longer be determined. The city has expanded since from being a small pueblo of less than 1,500 people then to a vast metropolis of 750,000 people now, and nothing remains there that resembles a natural habitat that could harbor an *Humboldtiana*. The embryonic sculpture, which consists of coarse beaded transverse wrinkled threads, is very similar to *Humboldtiana princeps*, suggesting that the provenance for the species is in or near Cd. Chihuahua.

Distribution.— The provenance of *Humboldtiana hogeana* remains unknown. Pilsbry (1935: 2) cites a specimen from Chihuahua City, which he states is a topotype, but he presents no information about why he considers the city to be the type locality. The specimen (ANSP 162326) is a different species than *H. hogeana* because of its more elevated helicoid shell shape, its glossy periostracum, and its brighter and more discretely banded color pattern. Later Pilsbry (1948: 202) reported *H. hogeana* from northwestern Chihuahua in the Sierra Madre at 3.5 mi. [6 km] above Colonia Juaréz. Specimens collected from there by Pilsbry are in the Florida Museum of Natural History (UF 185700, UF 103138). These represent an undescribed species. They remain undescribed until anatomical material becomes available.

Solem (1974: 363) stated that *Humboldtiana hogeana* was widely distributed in Chihuahua. This is based upon earlier reports in the literature. He cites no specimen records to substantiate the distribution.

Remarks.— The lectotype and the paralectotype α appear to be mature because they each have a reflected peristome. The type specimens were collected in a fresh state, if not alive. Each of them has dried mucus deposits on the exterior surface or the aperture. The lectotype bears an aestivation ring on the upper side of the body whorl. The curvature of the ring matches the contour of the outer lip of the immature paralectotype β.

The relationship of this species is uncertain because of the absence of anatomical information. The shell differs from other *Clydonacme* by its smaller size, coarser embryonic sculpture, higher aperture shape, and banding pattern. These characters are not sufficient to indicate relationships within the subgenus, and without anatomical information taxonomic relationships remain uncertain although the embryonic sculpture is similar to that of *H. princeps*.

Etymology.— Named after H. Höge, who collected the species while traveling in México during 1879-1880.

Aglotrochus n. subgen.

Type species.— *Humboldtiana tanymastyx* n. sp.

The shell is moderately large and depressed-helicoid in shape. It is smooth and shiny. The embryonic whorls are sculptured with very fine, straight, transverse striations. The post-embryonic sculpture consists of incremental striations and wrinkles. Granular sculpture is absent. The color is light brown with three dark brown bands and numerous transverse white streaks. The genital atrium is moderately long. The penis is short and eccentrically clavate in shape. Internally the penis contains a large verge that is about half the length of the chamber. The epiphallus is relatively slender and is about equal to the length of the penis. The flagellum is very long and slender. It is equal to seven times the combined length of the penis + epiphallus. The vagina bears four dart-sacs with ds_1 the largest and ds_4 the smallest. The dart-glands form a ring around the vagina immediately above the dart-sacs. The spermathecal duct is very long, being about as long as the flagellum and about 2.7 times the length of the uterus.

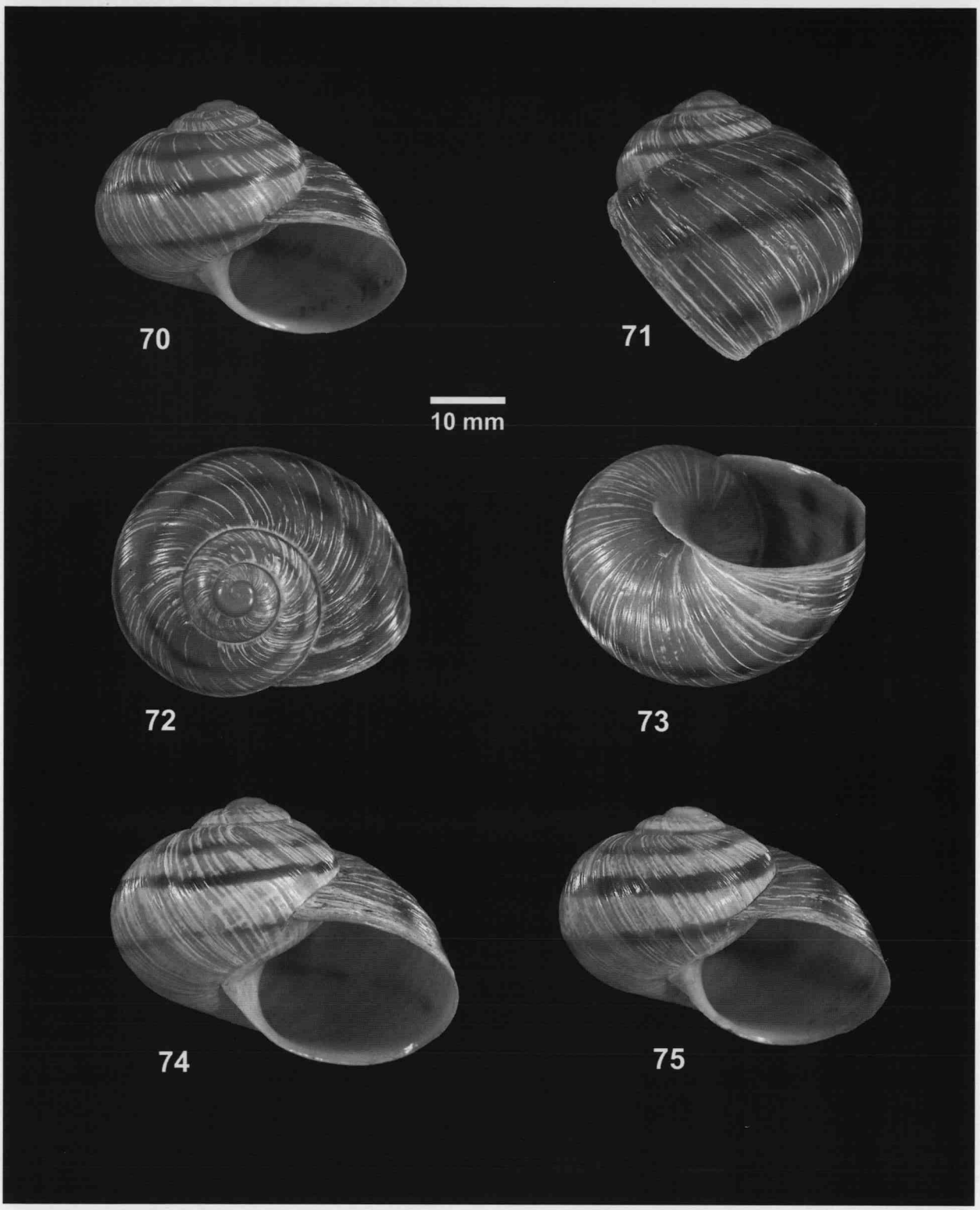
The type species is alone among known congeners because of the very fine transverse striations on the embryonic whorls.

Etymology.— The name *Aglotrochus* (m.) is from the Classical Greek αγλαια, splendor or beauty, and τροχος, a ball. The name alludes to the appearance of the shell.

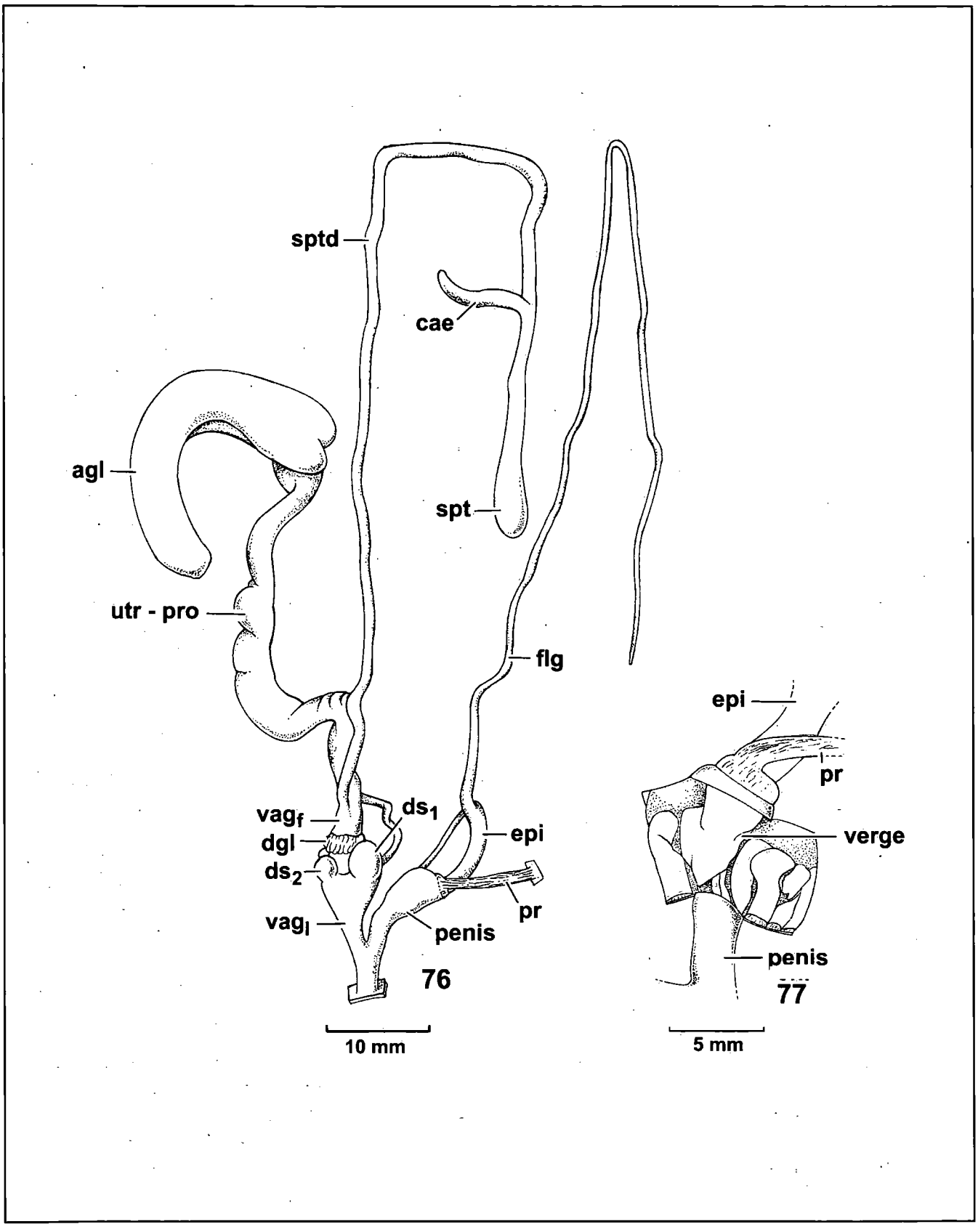
Humboldtiana tanymastix n. sp.

Diagnosis.— Same as for the subgenus.

Shell (Figs. 70-75).— The large shell is about 35-38 mm wide, depressed-helicoid in shape, and 0.73-0.82 times as high as wide. There are 4.0-4.2 rotund whorls that are separated by a moderately impressed suture. The periostracum is shiny. The ground color is light brown with three dark brown bands and numerous transverse white streaks. The middle band is the widest and the darkest. The white streaks are irregularly spaced



Figs. 70-75. *Humboldtiana tanymastix* n. sp.. Figs. 70-73: Holotype (UF 21324). Figs. 74-75: paratypes (UF 21325).



Figs. 76-77. *Humboldtiana tanymastix* n. sp.. Fig. 76: reproductive system (UF 21325). Fig. 77: interior of penis of Fig. 76.

Table 9. *Humboldtiana hogeana* Martens, 1882. Measurements in mm of the lectotype and the mature paralectotype α.

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Lectotype	26.4	32.8	17.7	21.6	3.9	0.80	0.54	0.82	0.82
Paralectotype	22.8	29.4	16.6	20.2	3.8	0.78	0.56	0.89	0.82

on the growth wrinkles. The streaks may be continuous, or they may be broken into shorter segments. The streaks are more numerous and crowed on the apex to the extent that they obscure the light brown ground color. The interior of the aperture is light brown with a whitish tinge and is banded. The peristome is colored the same as the ground color. The parietal callus is thin and hyaline. There are 1.4-1.5 rather low embryonic whorls. The first embryonic whorl is 4.0-4.1 mm wide transverse to the initial suture. The embryonic whorls are sculptured with very fine transverse striations. The subsequent whorls are sculpture with distinct but fine incremental striations and wrinkles that are continuous from the suture into the umbilicus. Granular sculpture is completely absent on the embryonic and the post-embryonic whorls. The umbilicus is rimate (Fig. 73). The whorls regularly increase in size along the middle band until the last quarter whorl and then rapidly descends to the aperture. The upper lip inserting on the lower band. The plain of aperture lies at 41-45° to the shell axis (Fig. 71). The aperture is broadly oval and is about 1.15 times as wide as high. The peristome is very narrowly reflected along the upper, outer and basal lips, and broadly reflected over the umbilicus.

Measurements of the holotype and four paratypes are given in Table 10.

Anatomy (Figs. 76-77).— Three specimens were dissected (UF 21325). The genital atrium is moderately slender and is 4 mm long. The penis is 8 mm long and is clavate in shape with the epiphallus entering the apex eccentrically. The penis contains a stout verge that extends to about the middle of the penis (Fig. 77). The inner wall of the penis has a girdle of 5-6 heavy folds along its upper half. The folds become smaller and subequal in size near the base of the penis. The stout penis retractor muscle originates on the middle of the inner wall of the lung, and inserts on the apex of the penis. It is slightly longer than the penis and forms a narrow sheath around the base of the epiphallus. The epiphallus is moderately stout, uniformly wide, and is about as long as the penis. Its interior is lined with 4-5 longitudinal folds. The flagellum is very long and slender. It is about seven times the combined length of penis + epiphallus, 115 mm. long. The lower vagina is moderately short, and bears four unequal sized dart-sacs, of which ds_1 is the largest and ds_4 is the smallest. The dart-glands form a ring around the middle vagina immediately above the dart-sacs. The free vagina is about 3-4 mm long. The spermathecal duct is very long, being about 110 mm long. It is about as stout as the epiphallus, is about as long as the flagellum, and is about 2.5 times the length of the uterus-prostate. The spermathecal duct bears a caecum that diverges at about 0.8 of the distance above the base of the duct. The caecum is short and is less than half the length of the remaining spermathecal duct + spermatheca. The spermathecal duct gradually expands into the narrow sack-shaped spermatheca.

Type locality.— Chihuahua, Sierra Santo Domingo, 4 km west-southwest of Francisco Portillo (28°36'N, 105°54'W), 1970 m alt. Holotype: UF 21324; collected 27 November, 1970 by Fred G. Thompson. Paratypes: UF 21325 (3), ITCV (2); same data as the holotype.

Francisco Portillo is a mining town located about 21 km ESE of Cd. Chihuahua. It is reached by driving 13 km SE of the city on Hwy. 45 and then ENE on a microwave tower road. The village of Francisco Portillo is 9 km further ENE on the road. Snails were collected behind the Mina Vieja lead-silver mine, approximately 4 km WSW of Francisco Portillo. In 1970 Francisco Portillo was known as Tulalia.

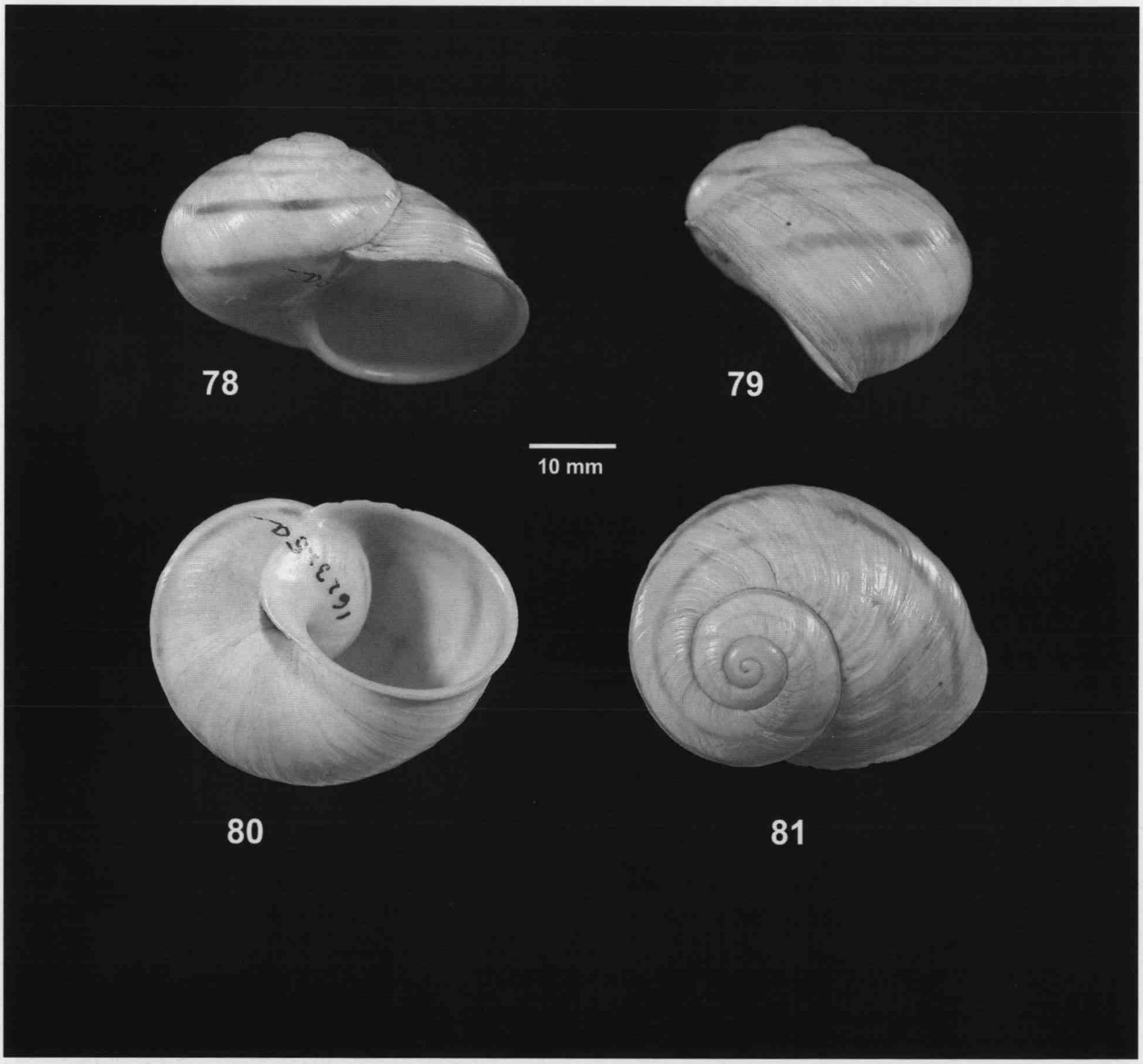
Distribution.— Known only from the type locality.

Ecology.— Snails were collected on limestone ledges where they were aestivating beneath and among leaves of a large species of *Agave* that was growing on the face of the ledge. The lowermost *Agave* leaves form a rosette that is adpressed against the rock, which is cooled by the live plant and provides shelter from predators. Other vegetation in the immediate vicinity consisted of sparse growths of xeric shrubs. The area was very dry at the time of the collection.

Remarks.— This elegant appearing snail is unlike any other *Humboldtiana*. The combination of the glossy, brightly colored shell, the fine transverse striations on

Table 10. *Humboldtiana tanymastix* n. sp. Measurements in mm of the holotype (UF 21324) and four paratypes.

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH
Holotype	31.1	37.9	21.2	24.3	4.1	0.82	0.56	0.78	0.87
Paratype	29.3	38.3	21.3	25.4	4.1	0.77	0.56	0.87	0.84
Paratype	30.1	36.8	20.0	23.0	4.2	0.82	0.54	0.76	0.87
Paratype	26.7	36.6	20.2	23.3	4.0	0.73	0.55	0.87	0.87
Paratype	27.4	35.0	19.1	22.7	4.0	0.78	0.55	0.83	0.84



Figs. 78-81. *Humboldtiana torrei* Pilsbry, 1935. Holotype (ANSP 162325).

the embryonic whorls and the absence of granular sculpture on the postembryonic whorls immediately distinguish it from all other groups within the genus. The species is variable in relative height as well as in the color pattern. Two paratypes (Figs. 74-75) are illustrated for comparison with the holotype (Figs. 70-73).

Etymology.— The name *tanymastix* (f.) is from the Classical Greek τανυ, meaning long and μαστιξ, a whip, alluding to the long flagellum on the epiphallus.

Undetermined subgenus

The following two species from Chihuahua are referred to *Humboldtiana bicincta* species group (*see* Thompson & Brewer, 2000). Both are unknown anatomically, so their placement in this group is provisional. They have a depressed spire that is about 0.7 times the shell width, they have three bands on a white background, and they have smooth shells that lack granular sculpture. In some species of this group the bands may be obsolete or entirely absent.

Humboldtiana eulaliae Metcalf, 1984

Humboldtiana eulaliae Metcalf, 1984; Nautilus, 98: 145-147; figs. 1-4 (shell).

Type locality.— Chihuahua, west side of the Sierra Santa Eulalia (27°12.0'N, 103°47.6'W); 1250 m alt. Holotype USNM 820297; collected by Wally Lippencott (U. S. Department of Agriculture), 23 March, 1982.

Metcalf provides the following information about the type locality ... "is along walls of the canyon debauching southwestward about midway of the Santa Eulalia range. The mouth of the canyon is 1.3 km E of El Pinalero and 7.5 km N and 1.5 km E of El "Penoles" on the Guimbalete quadrangle. The canyon is ca. 2.5 km long heading at 1650 m and debauching at 1250 m".

Distribution.— Known only from the type locality.

Humboldtiana torrei Pilsbry, 1935

Humboldtiana torrei Pilsbry, 1935b: 1; 2; pl. 1, fig. 10 (shell).

Type locality.— Chihuahua, San Antonio y Santa Rosalia, near and south of Cd. Chihuahua. Holotype: ANSP 162325; collected by Carlos de la Torre, about 1899. Paratypes ANSP (1), Carlos de la Torre collection, Havana, Cuba.

Distribution.— Known only from the type locality.

Remarks.— The holotype is re-figured to show all faces of the shell (Figs 78-81).

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