

# *Mexistrophia*, a new genus of Cerionidae from Mexico (Gastropoda: Pulmonata: Urocoptoidea)

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## ABSTRACT

*Mexistrophia* new genus and three new species of the landsnail family Cerionidae, *Mexistrophia reticulata* new species, *M. obsoleta* new species, *M. inexpectata* new species, are described from northeastern México. The genus is characterized by the absence of lamella or other barriers within the shell. The genus is diagnosed by soft anatomical features as well as shell characteristics. The known distribution of *Mexistrophia* is confined to higher elevations at 2000–2600 meters in the Sierra Madre Oriental in the states of Nuevo León, Querétaro and Hidalgo, where it inhabits cool temperate conifer forests that are subject to seasonal frosts and occasional freezes. Its distribution is disjunct geographically and ecologically from that of *Cerion*, which is confined to the tropical Caribbean region at very low elevations.

*Additional keywords:* Landsnails, biodiversity, endemism

## INTRODUCTION

A prevailing misconception in molluscan biogeography is that the land snail family Cerionidae is an autochthonous West Indian element. *Cerion*, the only extant genus recognized in the family, has undergone extensive speciation, but has never successfully colonized the mainland, even though on at least two occasions species became established in Florida, once in the Oligocene (Dall, 1890), and once by the more recently derived *Cerion incanum* (Binney, 1857). Roth and Hartman (1998) report a probable cerionid, *Cerion archerontis*, from the Uppermost Cretaceous of Montana. However, the type specimen is a fragmented and flattened fossil that defies clear taxonomic characterization.

During the last forty years, while conducting field work in Mexico, occasionally I collected peculiar cylindrical-conical snails that I identified tentatively as "*Cerion*". They were found in habitats uncharacteristic of *Cerion*. They were set aside among undetermined "Urocoptidae" until now. Anatomical and conchological examinations reveal that they are Cerionidae, but that they differ from *Cerion* as a separate genus. Three new species are described.

**Abbreviations and Text Conventions:** The following symbols are used in the illustrations of anatomical structures: **abl**, albumen gland; **atr**, atrium; **app**, appendix; **div**, diverticulum; **epi**, epiphallus; **fovi**, free oviduct; **ovid**, oviduct; **pen**, penis; **prm**, penis retractor muscle; **pro**, prostate; **rom**, right ocular retractor muscle; **spd**, spermathecal duct; **spr**, spermatheca; **vag**, vagina; **vas**, vas deferens; **vrn**, vaginal retractor muscle; Institutional abbreviations: CNMO: Colección Nacional de Moluscos, Mexico; UF: Florida Museum of Natural History, Gainesville.

## SYSTEMATICS

### *Mexistrophia* new genus

**Type Species:** *Mexistrophia reticulata* new species.

**Description:** Shell small, 10–13 mm length. Shell pupiform, with a low dome-shaped apex. Protoconch whorls smooth and do not conspicuously rise above following whorl. Peristome thickened, but only slightly so, not reflected, incomplete across parietal wall. Outer lip and columellar lip connected by thin parietal callus. Outer surface sculptured with fine axial thread-riblets. Internal axis broad and hollow in upper whorls of dome-like apex, then narrowing and becoming narrowly perforate or solid in last two or three whorls. Internal barrier of lamellae or denticles lacking at all growth stages (in contrast with *Cerion*.)

**Anatomy:** General anatomical states typically Cerionidae. Short foot lacking a suprapedal groove. Plain lung, with unbranched pulmonary vein. Kidney short, with very short ureter near the end. Secondary ureter absent.

Reproductive system typically cerionid. Genital atrium moderately long and capacious. Epiphallus poorly differentiated from vas deferens. Epiphallus + vas deferens form very long loop that extends alongside oviduct-prostate. Penis consists of two parts. Epiphallus entering middle of penis. Penis ending in blind diverticulum distal

to epiphallus. Penis retractor muscle inserts on apex of diverticulum. Right ocular retractor muscle passes mesad to genitalia and attaches to right pedal retractor muscle. Spermathecal duct very long, with very long appendix, or lacking an appendix. Spermathecal duct unites with free oviduct to form distinct vagina. Free oviduct stout and slightly longer than vagina. Stout vaginal retractor muscle originates on right ocular retractor muscle and inserts on vagina (Figures 24–25).

Radula of *Mexistrophia* is typical Cerionidae with nearly flat horizontal tooth rows that do not curve upward near margins. Central tooth tricuspid. Lateral and marginal teeth bicuspid with large mesocone and small ectocone. Mesocone of marginal teeth long, extending beyond base of tooth. Laterals and marginals lacking entocones.

**Habitat and Distribution:** *Mexistrophia* are ground-dwelling snails that are found in eastern Mexico in cool temperate coniferous forests at high elevations.

**Etymology:** *Mexistrophia* (f.). The genus name is taken from *Mexi-*, México, and *strophia*, Gr. *στροφία*, a turning point, such as an axis. *Strophia* Albers, 1850 is an earlier generic name that was widely used for *Cerion* (not *Strophia* Meigen, 1832, Lepidoptera).

### *Mexistrophia reticulata* new species

(Figures 1–6, 20, 22, 27, 28, Table 1)

**Diagnosis:** Pupiform shell, moderately robust, about 9–13 mm long. Conspicuous white peristome lacking noticeable callus reinforcing it internally. Sculpture consisting of thread-riblets, with upper ends that weakly crenulate the suture. Spermathecal duct with long appendix.

**Description:** Shell (Figures 1–6). Shell pupiform. Spire cylindrical, relatively slender, with low domed-shaped apex. Shell wall opaque. Ground color light brown mottled with lighter irregular-shaped spots and streaks that form reticulated pattern. White streaks tend most conspicuous on upper ends of ribs. Peristome and adjacent interior of aperture white. Deeper within, inner wall and axis rust-colored. Shell 10.5–13.2 mm long, 3.9–4.4 mm wide, and 0.31–0.38 times as wide as long. Shell contains 8.0–9.2 whorls separated by weakly impressed suture. Protoconch consisting of two smooth whorls slightly elevated above following whorls. Following whorls sculptured with numerous oblique thread-riblets strongest on apical whorl, but nearly equally developed on spire. Riblets strongest below suture and weakly crenulate suture. Umbilicus imperforate or narrowly rimate. Thick peristome weakly reflected and discontinuous across parietal wall, where it is replaced by thin glaze. Aperture ovate, slightly higher than wide, 0.28–0.33 times shell length, and 0.67–0.80 times shell width. Aperture slightly prosocline in lateral profile (Figure 5). Axis conspicuously enlarged in apical whorls.

Cylindric part of shell axis slightly sinuous, much narrower, and narrowly perforate or solid by last whorl (Figure 6). (Measurements based on the holotype and twelve paratypes are given in Table 1.)

**Anatomy:** Reproductive anatomy (Figures 20–22) (Five specimens examined (UF 211129): Genital atrium (*atr*) moderately long and capacious. Right ocular retractor a narrow slip of muscle that passes mesad to lower genitalia, attaching to vagina in conjunction with vaginal retractor muscle. Stout penis (*pen*) bulbous, consisting of two nearly equal sections. Distal section forming globose, blind diverticulum (*div*). Short penis retractor muscle (*prm*) originating on inner wall of lung and inserting on end of diverticulum. Epiphallus (*epi*) entering middle of penis at base of diverticulum. Epiphallus moderately stout at union with penis, but gradually grading into very long vas deferens. Epiphallus lined internally with simple longitudinal columns. Spermatheca (*spr*) large and elliptical, resting against dorsal side of oviduct at base of albumen gland. Spermathecal duct (*spd*) stout, moderately long, enlarged at base where it is muscular and weakly convoluted. Duct bearing very long appendix (*app*) about as long as spermathecal duct. End of appendix extending to upper end of albumen gland. Spermathecal duct uniting with free oviduct (*fovi*) to form short but distinct vagina (*vag*). Free oviduct relatively stout and slightly longer than vagina. Heavy slip of muscle that is a branch of right pedal retractor inserting on vagina to form vaginal retractor muscle (*vrn*) (Figures 21–22).

Radula (Figures 27–28). Two specimens examined (UF 445301). Radular formula 14-1-14. Transverse tooth rows nearly flat, not curving upward at ends. Transition from lateral teeth to marginal teeth not clearly differentiated morphologically. Eight lateral teeth and 6 marginal teeth present in each half-row. Lateral teeth rising slightly, and marginal teeth becoming nearly horizontal. Central tooth trapezoidal with indented dorsal edge, 18  $\mu$ m wide and 20  $\mu$ m high. Central tooth with large lanceolate mesocone, 15  $\mu$ m long, extending to base of tooth. Mesocone flanked on each side by short acuminate ectocone. Lateral teeth with long, slender mesocone overlapping tooth below, and small ectocone. Marginal teeth with long mesocone and small ectocone.

**Type Locality:** A talus slope 1.0 km east of Pinal de Amoles, Querétaro State, Mexico, 21.15° N, 99.64° W, 2150 m alt.

**Type Material:** Holotype: UF 211128, collected 25 July, 1993 by Fred G. Thompson and Elizabeth L. Mihalcik; Paratypes: UF 435013 (30), CNMO 3379 (5), all from type locality.

**Other Material Examined:** UF 211129; type locality. Specimens preserved in 75% ETOH.

**Habitat:** The dominant vegetation in the area consists of pine forests with scattered small oak trees



**Figures 1–19.** New species of *Mexistrophia*. **1–6.** *Mexistrophia reticulata* new species. **1.** Holotype (UF 211128). **2–6.** Paratypes (UF 43513). **7–10.** *Mexistrophia obsoleta* new species. **7.** Holotype (UF 34296). **8–10.** Paratypes (UF 435015). **11–19.** *Mexistrophia inexpectata* new species. **11.** Holotype (UF 226461). **12–19.** Paratypes (UF 435014). Scale bar for Figure 1 applies to Figures 1–6; for Figure 7 to Figures 7–10; for Figure 11 to Figures 11–19.

(*Quercus* sp.). Snails were found among grasses, mosses and *Sedum* growing among limestone cobbles.

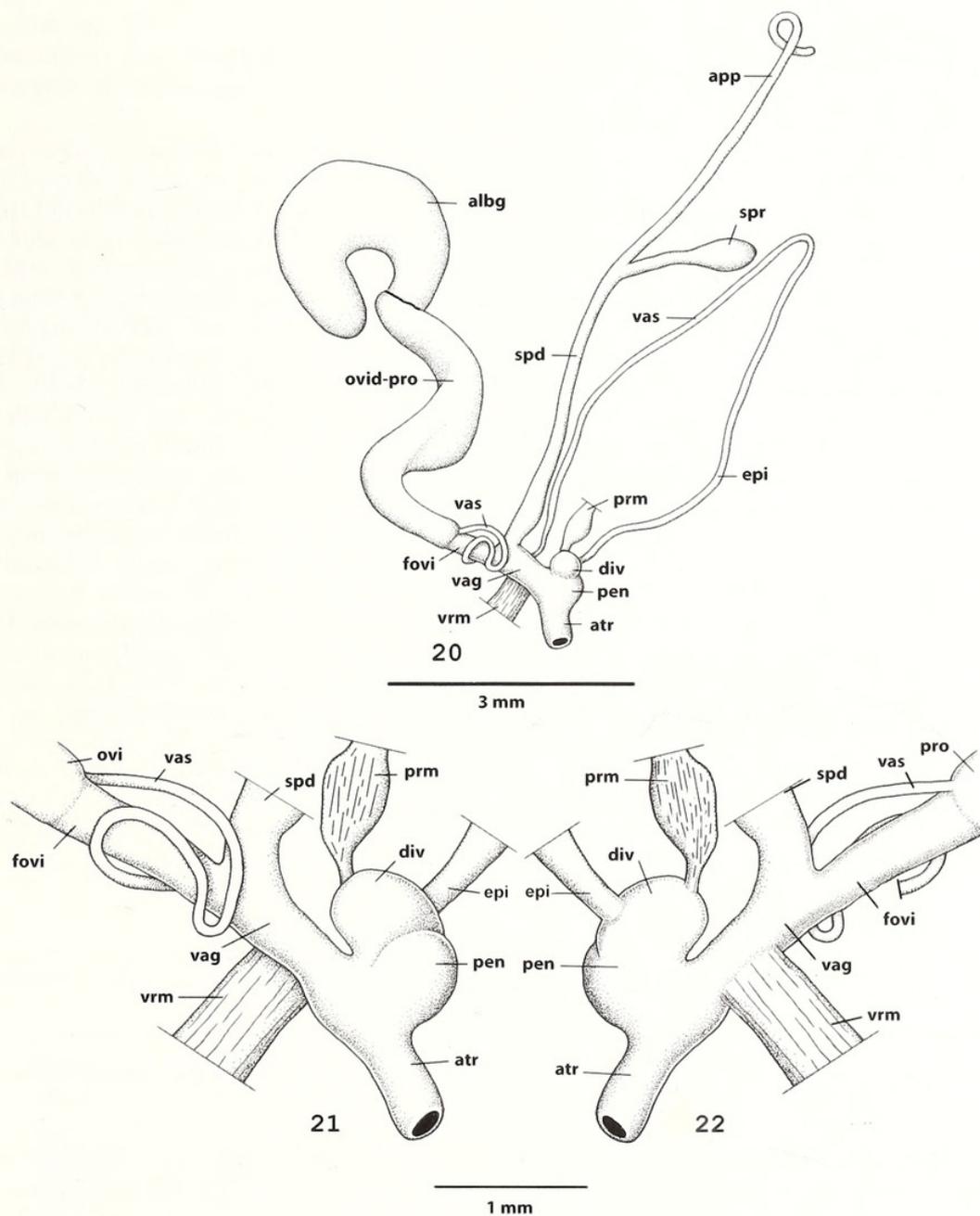
**Distribution:** Querétaro State, Mexico (known only from the type locality.)

**Remarks:** For meristic comparisons with other species see *Mexistrophia inexpectata* new species below.

**Etymology:** The species name *reticulata* (Latin) alludes to the reticulated color pattern of the shell.

**Table 1.** *Mexistrophia reticulata* new species. Measurements in mm of the holotype (UF 211128) and 12 paratypes (UF 435013) selected to show variation. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/SW
Holotype	11.0	3.9	3.6	3.0	8.9	0.35	0.33	0.77
Paratypes								
Min	10.5	3.9	3.2	2.8	8.0	0.31	0.28	0.67
Max	13.2	4.4	3.8	3.2	9.2	0.38	0.33	0.80
Avg	11.55	4.04	3.55	2.98	8.65	0.35	0.31	0.74
STD	0.88	0.14	0.19	0.17	0.41	0.02	0.02	0.03



Figures 20–22. *Mexistrophia reticulata* new species, reproductive anatomy (UF 211129).

***Mexistrophia obsoleta* new species**

**Diagnosis:** Distinguished by obese pupiform shape, obsolescent color pattern, and sculpture in which upper ends of ribs do not crenulate suture and ribs become obsolete or are absent on lower two whorls. Peristome white, relatively narrow, lacking noticeable callus within.

**Description:** Shell (Figures 7–10) obese-pupiform, squat cylindrical spire with low domed-shaped apex with protoconch barely elevated above following whorl. Shell wall opaque. Ground color light tan with obsolescent mottling with lighter irregular spots and streaks that do not form distinct pattern. White streaks most conspicuous on ribs. Peristome and adjacent interior of aperture white. Deeper within aperture, inner wall and axis very light rust-colored. Shell 10.5–12.3 mm long, 4.2–4.8 mm wide, and 0.35–0.41 times as wide as long. Shell contains 8.2–9.1 whorls separated by weakly impressed suture. Protoconch with two smooth whorls. Following whorls sculptured with numerous, relatively strong, oblique thread-riblets nearly equally developed on apex and earlier whorls of cylinder, becoming obsolete on lower two whorls. Upper ends of riblets do not crenulate suture. Umbilicus imperforate or narrowly rimate. Peristome relatively thin, weakly reflected, and discontinuous across parietal wall, where it is replaced by thin callus. Ovate aperture slightly higher than wide, 0.26–0.32 times shell length, and 0.63–0.72 times shell width. Aperture slightly prosocline in lateral profile, not noticeably thickened within. Axis enlarged in apical whorls (Figure 10). In cylindric part of shell axis nearly straight, narrower, becoming narrowly perforate or solid by last whorl. (Measurements based on the holotype and ten paratypes are given in Table 2.)

**Anatomy:** Unknown.

**Type Locality:** A limestone ravine 15.8 km by road southwest of Pinal de Amoles, Querétaro State, Mexico (21.15° N, 99.65° W), 2585 m alt.

**Type Material:** Holotype UF 34298; collected 27 September, 1970 by Fred G. Thompson; Paratypes UF 435015 (25), CNMO 3373(5); all from type locality.

**Distribution:** Querétaro State, known from the type locality and a nearby locality 2 km ENE of Pinal de Amoles, 2140 m alt. (UF 268262).

**Remarks:** For meristic comparisons with other species see *Mexistrophia inexpectata* new species, below.

**Etymology:** The species name *obsoleta* (Latin) refers to the barely discernable reticulated color pattern on the shell, and its sculpture, which becomes obsolete on the last two whorls.

***Mexistrophia inexpectata* new species**

**Diagnosis:** Relatively slender, pupiform shell with nine or more whorls. Sculpture nearly uniform over shell surface, consisting of fine oblique thread-riblets. Peristome narrowly reflected and reinforced internally by thick callus. Spermathecal duct lacking an appendix.

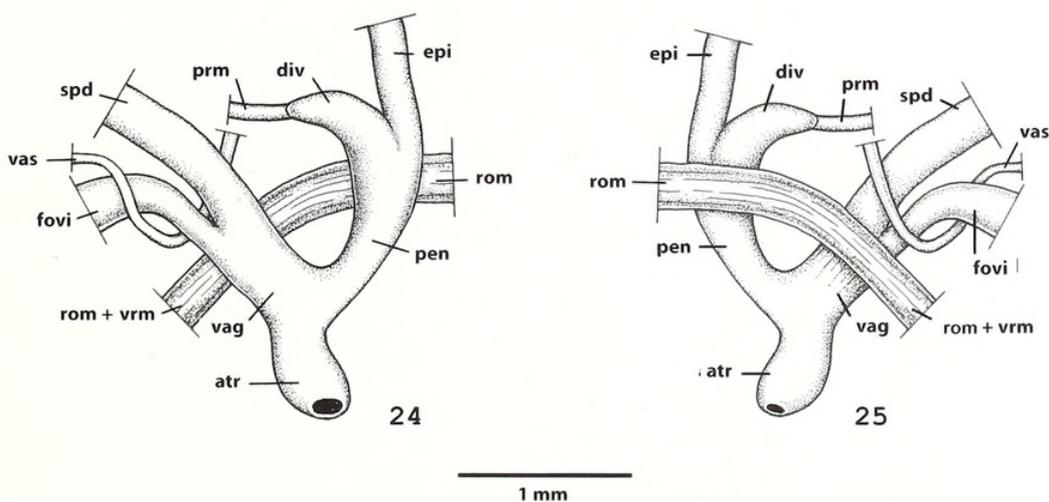
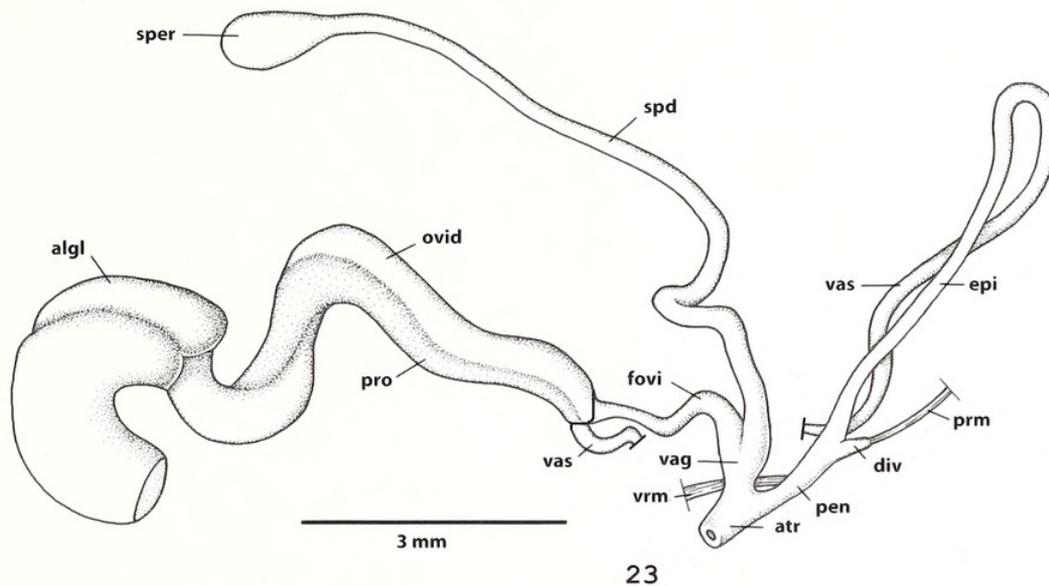
**Description:** Shell (Figures 11–19) pupiform. Cylindrical spire bearing low domed-shaped apex. Shell wall opaque or weakly translucent. Ground color light brown with sparse lighter irregular spots and streaks. White streaks most conspicuous on upper ends of ribs. Peristome and adjacent interior of aperture white. Deeper within inner wall and axis rust-colored. Shell 9.8–12.4 mm long, 3.3–3.5 mm wide, and 0.38–0.35 times as wide as long, with 9.1–11.0 whorls. Suture weakly impressed. Protoconch with two smooth whorls slightly elevated above following whorls. Following whorls sculptured with numerous oblique thread-riblets nearly equally developed over shell surface. Riblets do not crenulate suture. Umbilicus imperforate or narrowly rimate. Thick peristome weakly reflected and discontinuous across parietal wall, where it is replaced by thin glaze. Peristome reinforced internally by thick callus. Aperture ovate, slightly higher than wide, 0.24–0.37 times shell length, and 0.69–0.76 times shell width, slightly prosocline, nearly vertical in lateral profile (Figure 18). Axis conspicuously enlarged in apical whorls, straight in cylindric part of shell, very narrow, becoming narrowly perforate or solid by last two whorls (Figure 19). (Measurements based on the holotype and ten paratypes are given in Table 3.)

**Table 2.** *Mexistrophia obsoleta* new species. Measurements in mm of the holotype (UF 34298) and 10 paratypes (UF 435015) selected to show variation. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/SW
Holotype	11.2	4.2	3.4	3.1	8.3	0.38	0.29	0.81
Paratypes								
min	10.5	4.2	3.2	2.7	8.2	0.35	0.26	0.63
max	12.3	4.8	3.5	3.4	9.1	0.41	0.32	0.71
avg	11.38	4.36	3.33	2.59	8.52	0.38	0.29	0.68
STD	0.56	0.20	0.11	0.18	0.30	0.02	0.02	0.05

**Table 3.** *Mexistrophia inexpectata* new species. Measurements in mm of the holotype (UF 226407) and 10 paratypes (UF 485014) selected to show variation. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

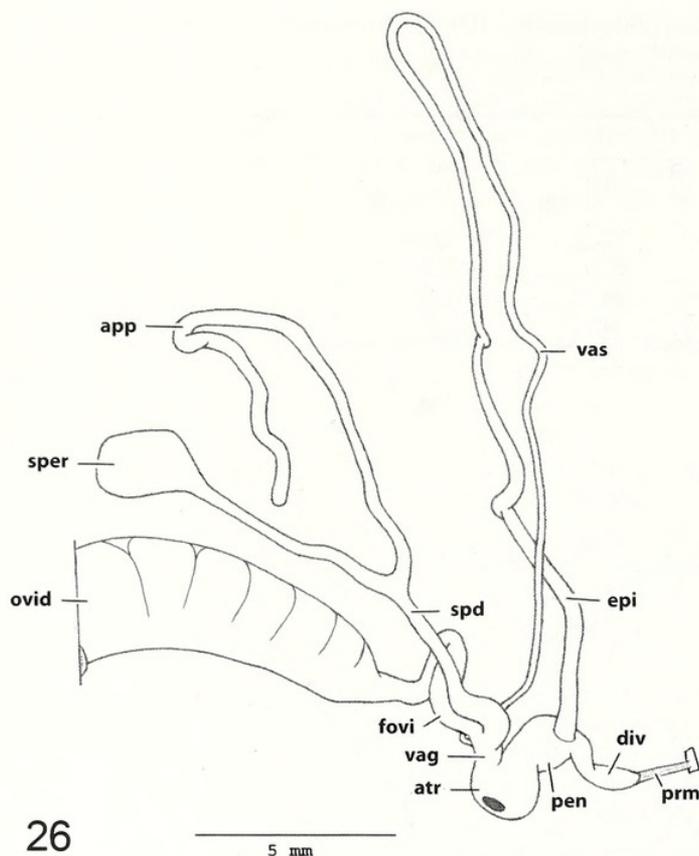
	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/SW
Holotype	11.4	3.5	3.0	2.4	9.2	0.31	0.26	0.69
Paratypes								
Min	9.8	3.3	2.7	2.3	9.1	0.28	0.24	0.69
Max	12.4	3.6	3.0	2.6	11.0	0.35	0.27	0.76
Avg	10.87	3.42	2.84	2.46	9.71	0.32	0.26	0.72
STD	0.70	0.10	0.17	0.09	0.51	0.02	0.01	0.02



**Figures 23–25.** *Mexistrophia inexpectata* new species, reproductive anatomy (UF 226408).

**Anatomy:** Reproductive anatomy (Figures 23–25) (Five specimens examined (UF 226408): Genital atrium (atr) moderately long and stocky. Penis (pen) moderately long and slender, ending in slender, short, blind divertic-

ulum (div). Penis lined internally with six longitudinal columns, lacks verge or stimulator. Penis retractor muscle (prm) long and slender, originating on inner lung wall and inserting on diverticulum end. Right ocular retractor



**Figure 26.** *Cerion uva* (Linnaeus, 1758). Reproductive anatomy (UF 336946).

muscle (rom) passing mesad to genital system and inserting into right pedal retractor muscle, attached to vagina (vag) by short slips of muscle (Figure 25). Epiphallus (epi) entering the penis (pen) shortly below diverticulum, long, stout, and poorly differentiated from vas deferens (vas). Elliptical spermatheca (sper) resting against side of oviduct-prostate at base of albumen gland. Spermathecal duct (spd) relatively stout and lacking appendix. Duct uniting with free oviduct (fovi) to form short but well developed vagina (vag). Free oviduct short but stocky, about as long as combined length of vagina + genital atrium.

Radula (Figures 29–30) (Two specimens examined, UF 226408): Radular ribbon 0.55 mm wide by 1.34 mm long. Radular formula 18-1-18. Transverse tooth rows horizontal, nearly straight, not curving upward at margins. Eighteen lateral + marginal teeth present. Lateral teeth transition without morphological distinction into marginal teeth. Central tooth as wide as adjacent lateral teeth, 16  $\mu$ m wide, trapezoidal, tricuspid. Mesocone acuminate, extending beyond tooth base, bordered on each side by short acuminate ectocone. All seven lateral teeth bicuspid with large acuminate mesocone and smaller acuminate ectocone. Marginal teeth with large lanceolate mesocone and single acuminate ectocone.

**Type Locality:** A west-facing hillside on a limestone exposure, 0.5 km north of El Refugio, Nuevo León, Mexico (23.921° N, 99.719° W), 2360 m alt. The type

locality is in a grassy open “piñon” (pine) forest with scattered agave and small oaks. Snails were collected from among and under flags of limestone.

**Type Material:** Holotype UF 226407; collected 24 July, 1994 by Fred G. Thompson, Elizabeth Mihalcik, Grady Taylor, and Val J. Roessling; Paratypes UF 435014 (85), CNMO 3371 (10); same data as the holotype; UF 267253 (33); collected January, 1996 by Val J. Roessling; all from type locality.

**Distribution:** Nuevo León State, known only from the type locality.

**Etymology:** The species name *inexpectatus* is from the Latin and alludes to the fact that the reproductive system differs from what I anticipated before dissecting the species.

**Remarks:** Shell measurements of the three species of *Mexistrophia* may be compared as in Table 4. *Mexistrophia inexpectata* is separated from *M. reticulata* and *M. obsoleta* by its slender size and by its larger number of whorls.

#### ADDITIONAL MEXISTROPHIA

Specimens of *Mexistrophia* are available from the localities below. They differ from the new species described above by size, obesity, and whorl count enough to suggest that they represent different species. Their taxonomic status remains undetermined because only shell samples are available for study. These samples indicate that the genus is widespread in northeastern Mexico.

Nuevo León: 1.7 km N El Refugio, 18 km. S of Zaragoza; (UF 258407), collected 4 November, 1995 by Val J. Roessling.

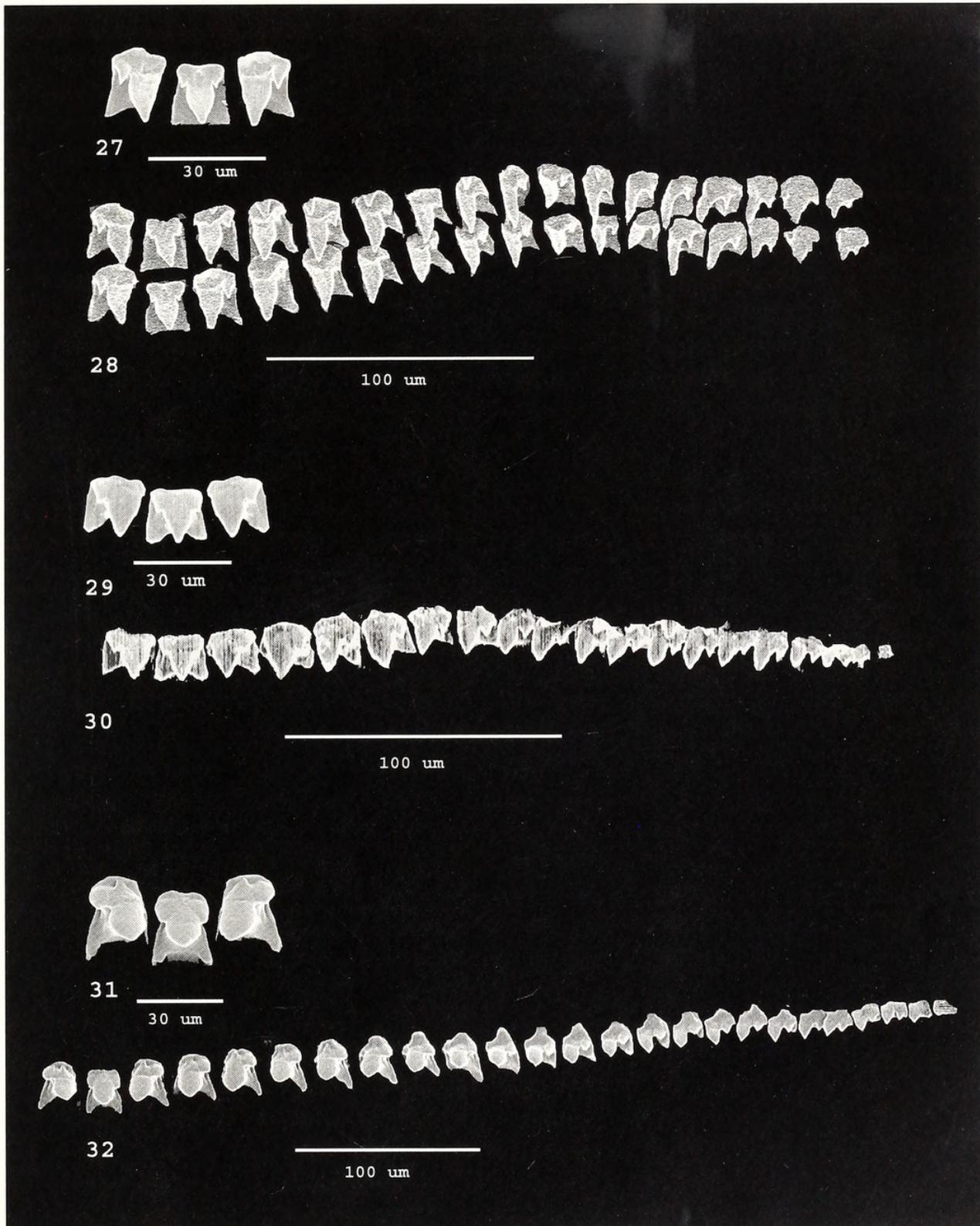
Hidalgo: Ixmiquilpan (20.483° N, 99.233° W) (UF 179719); leg. Gonzalo Halfter, collected 6 March, 1960.

Querétaro: 14 km NE of San Joaquín, turn-off from Mexico Highway 120 (18.756° N, 96.189° W), 2400 m alt. (UF 244942); collected by Grady H. Taylor, 8 September 1978.

#### GEOGRAPHIC DISTRIBUTION OF THE FAMILY CERIONIDAE

(Figures 33–34)

*Mexistrophia* is found in eastern Mexico over a north-south linear distance of about 400 km, and inland by about 200 km west of the Gulf of Mexico (Figure 33). It is known from the states of Nuevo León, Querétaro, and Hidalgo, at elevations between 2150–2585 meters. This is about 1600 km west of the nearest locality from where *Cerion* has been reported in the West Indies (Figure 34). *Cerion* is strictly a West Indian genus found in Cuba, Bahamas Islands, Hispaniola, Puerto Rico, St. Croix, and the Cayman Islands (Fahy, 1996). A single



**Figures 27–32.** *Mexistrophia* and *Cerion uva*, SEM micrographs or radula. **27–28.** *Mexistrophia reticulata* new species (UF 445301). **27.** Central and adjacent lateral teeth. **28.** Hemi-sections of two horizontal teeth rows. **29–30.** *Mexistrophia inexpectata* new species (UF 226408). **29.** Central and lateral teeth. **30.** Hemi-section of a horizontal tooth row. **31–32.** *Cerion uva* (UF 249358). **31.** Central and adjacent lateral teeth. **32.** Hemi-section of a horizontal tooth row.

**Table 4.** Comparisons of measurements (mm) and meristic counts among the three new species of *Mexistrophia* described in this article.

	<i>M. reticulata</i>	<i>M. obsoleta</i>	<i>M. inexpectata</i>
SL	10.5–13.2	10.5–12.3	9.8–12.4
SW	3.9–4.4	4.2–4.8	3.3–3.6
ApH	3.2–3.8	3.2–3.5	2.7–3.0
ApW	2.8–3.2	2.7–3.4	2.3–2.6
Whorls	8.0–9.2	8.2–9.1	9.1–11.0
SW/SL	0.31–0.38	0.35–0.41	0.28–0.35
ApH/SL	0.28–0.33	0.26–0.32	0.24–0.27
ApW/SW	0.67–0.80	0.63–0.72	0.69–0.76

species, *C. uva* (Linnaeus, 1758), occurs on the Dutch Leeward Islands. A single species, *C. incanum* (A. Binney, 1857), occurs naturally on the mainland in extreme southeastern Florida. No species of *Cerion* has been found in suitable coastal habitats in eastern Mexico or Central America, although during the last two centuries experienced collectors searched such habitats for non-marine mollusks at numerous localities.

#### ECOLOGICAL DEPLOYMENT OF *MEXISTROPHIA*

The ecological deployment of *Mexistrophia* contrasts strongly with the ecological distribution of West Indian Cerionidae. Nearly all West Indian Cerionidae are found at very low elevations, of only a few meters to tens of meters. Generally they occur at just a few meters to a few kilometers from the nearest shoreline among tropical vegetative associations.

In striking contrast species of *Mexistrophia* occur at elevations of greater than 2000 meters, and are found inland at more than 200 kilometers from the Gulf of Mexico. They occur in cool mesic or submesic temperate coniferous forests. Winter frosts and occasional freezes are normal at localities from where the genus is known.

#### COMPARISONS OF *MEXISTROPHIA* WITH *CERION*

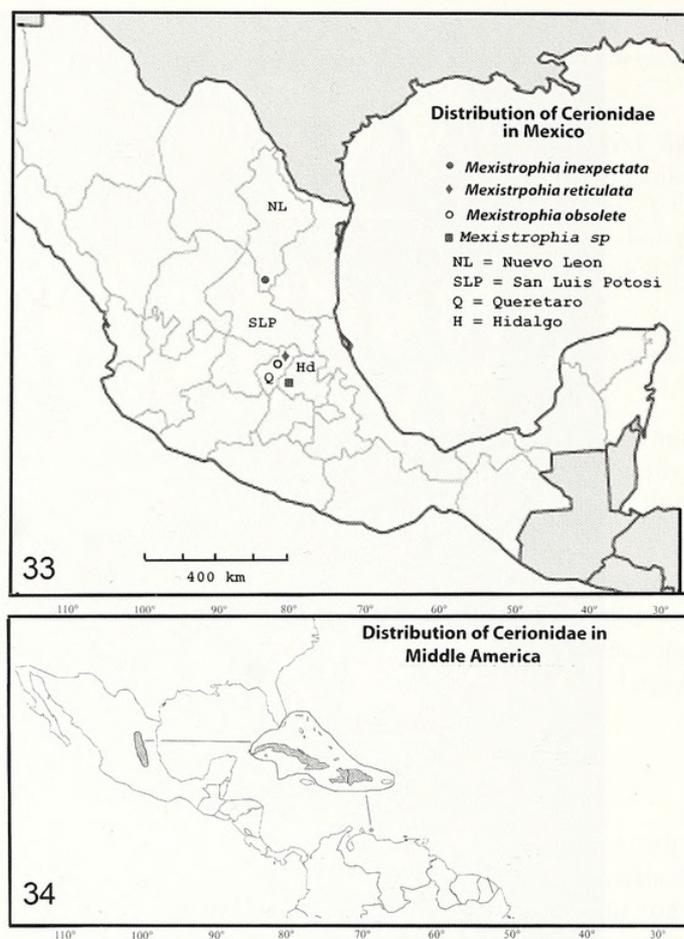
The anatomy of the *Cerion* remains poorly studied. Anatomical information is available for the following species:

*Cerion (Strophlops) incanum* (Binney, 1857): Pilsbry, 1902: 176–178 [radula]; Pilsbry, 1946: 159–161 [reproductive anatomy].

*Cerion (Strophlops) glans* (Kuster, 1847): Richter, 1926: 277–342 [reproductive anatomy]; Jaenicke, 1933.

*Cerion (Strophlops) mumia chrysalis* (Férussac): Pilsbry, 1902: 176–178 [reproductive anatomy].

*Cerion striatellum* (Guerin-Manneville, 1829): Baker, 1961: 33–34 [lung, reproductive anatomy].



**Figures 33.** Distribution of Cerionidae in Mexico. **34.** Distribution of Cerionidae in Middle America.

*Cerion (Cerion) uva* (Linnaeus, 1776): Baker, 1961: 34–35; Thompson, this report; Netherlands Antilles, Curaçao, beach at Christenffel National Park (UF 336946).

#### CHARACTERIZATION OF THE CERIONIDAE

The available data, although limited, allow the Cerionidae to be characterized as follows. The foot is short and lacks a pedal groove. The ureter is confined to the anterior end of the kidney. A secondary ureter is absent. The plain lung has an unbranched pulmonary artery. The reproductive anatomy has a blind diverticulum on the end of the penis (Figure 26). The right ocular retractor is a narrow slip of muscle that passes mesad to the lower genitalia and unites with the right pedal retractor muscle. It is attached to the vagina in conjunction with the vaginal retractor muscle. The penis retractor muscle inserts on the apex of the diverticulum. The epiphallus enters the penis at the base of the diverticulum. The vagina is moderately long. The spermathecal duct bears a very long appendix. The jaw is finely ribbed. The radula differs from other urocoptoid families as follow. The transverse tooth rows are nearly horizontal and are not curved upward at the margins. The central

tooth is tricuspid with a large mezocone bordered on each side by a small ectocone. The lateral teeth and the marginal teeth are bicuspid with a large mesocone and a smaller ectocone. The mesocone is elongate and extends beyond the base of the tooth. Entocones are absent.

**Remarks:** *Mexistrophia reticulata* is typical of the Cerionidae in its anatomical states. *Mexistrophia inexpectata* departs from the general morphology of *Cerion* by lacking a diverticulum on the spermathecal duct. This trait is considered a derived state, because the presence of a diverticulum among stylommatophoran families is so widespread that its presence must be considered plesiomorphic (Nordsieck, 2007). The taxonomic significance of the absence of a diverticulum in *M. inexpectata* remains to be determined because the loss of a diverticulum within families, subfamilies, and genera occurred in several occasions.

*Mexistrophia* differs in shell features from *Cerion* by lacking internal lamellae and denticles at all stages of growth. Juvenile of many *Cerion* species have 2–5 denticles within the early whorls in addition to an axial lamella and a parietal lamella or denticle in the adult stage. A comparison of *Mexistrophia* to subgeneric groups within *Cerion* shows no close relationship to any subgenus.

*Cerion* contains various extant subgenera and a single fossil subgenus, *Eustrophia* Dall 1890. The extant subgenera are found on the Bahamas Islands, the Greater Antilles except Jamaica, St. Croix and the Dutch Leeward Islands. The subgenera differ by the location of the axial lamella and the parietal lamella or denticles. All of the subgenera except the fossil *Eustrophia* have a columellar lamella and a parietal lamella or tooth that is visible within the aperture. *Eustrophia* includes a single species, *Cerion (Eustrophia) anadonta* (Dall, 1890). It is a large, robust, poorly known fossil from the Oligocene Silex beds of Florida. It has been reported from several localities in the Upper Oligocene–Lower Miocene of Florida (Mansfield, 1937), but no information is available concerning the internal morphology of the shell. It was described originally as lacking an axial lamella and a parietal tooth. However, the holotype (USNM 111972) has a parietal tooth (Harasewych, 2009). The absence of an internally confined axial lamella is not confirmed because no specimen has been dissected for examination of this trait.

No close relationship between *Mexistrophia* and a particular subgenus of *Cerion* is evident. A close relationship between *Mexistrophia* and *Eustrophia* is not plausible because of their general dissimilarities. To apply a generic name based on an imperfectly known fossil species to a modern group is of very dubious value.

Roth and Hartman (1998) report a probable species of *Cerion* from the uppermost Cretaceous Hell Creek Formation of Montana. *Cerion acherantia* Roth and Hartman, 1998 is based on a fractured and compressed shell that defies clear characterization. The identity of this species as a cerionid is to some extent supported by the discovery of modern Cerionidae in Mexico.

Speculation in the literature related Cerionidae to the Clausiliidae and other families placed in the Mesurethra (Emberton et al., 1990). Uit de Weerd (2008) demonstrated that the Cerionidae belong in the Urocoptoidea, and that they are most closely related to the Holospiridae on the basis of 28S rRNA sequence data. If Cerionidae are recognized as a distinct family, the Holospiridae and the Eucolodiidae must also be recognized as separate families because their 28S rRNA, soft anatomies, and basic shell structures differ from Urocoptidae as much as or greater than do the Cerionidae.

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