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BULLETIN

**THE LAND SNAIL GENUS *EPIROBIA* AND ALLIED GENERA IN
MÉXICO AND CENTRAL AMERICA, WITH THE DESCRIPTION
OF A NEW FAMILY, THE EPIROBIIDAE (GASTROPODA,
PULMONATA, UROCOPTOIDEA)**

Fred G. Thompson

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University of Florida
P.O. Box 117800
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FAX: 352-846-0287
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THE DESCRIPTION OF A NEW FAMILY, THE EPIROBIIDAE
(GASTROPODA, PULMONATA, UROCOPTOIDEA)

Fred G. Thompson¹

ABSTRACT

The species-level taxonomy of three closely related urocoptoid land snails, *Epirobia* Strebel & Pfeiffer 1880, *Propilsbrya* Bartsch 1906, and *Pectinistemma* Rehder 1940, are reviewed and a new family is erected for them. *Gyrocion* Pilsbry 1904 and *Prionoloplax* Pilsbry 1953 may also belong in this new family, but remain unknown anatomically. New species named in this work are *Epirobia subsulca* n. sp., *Epirobia brevior* n. sp., *Epirobia longior* n. sp., *Epirobia interupta* n. sp., *Epirobia adusta* n. sp., *Pectinistemma roesslingi* n. sp., *Pectinistemma gracilidens* n. sp., and *Pectinistemma ceramicum* n. sp. *Epirobia alternans* Thompson 1976 is elevated from subspecific status within *Epirobia swiftiana* (Crosse 1863) to full species rank. **Epirobiidae new family** is recognized as distinct from other urocoptoid families by characteristics of the shell, the reproductive system, the radula, and the genome. Morphology and molecular data support the monophyly of the Epirobiidae and their independence from other groups of urocoptoid gastropods. These data also support the independence and monophyly of the Holospiridae Pilsbry 1946 and the Eucalodiidae Crosse & Fischer 1868.

Key words: *Epirobia*, *Propilsbrya*, *Pectinistemma*, *Stalactella*, *Holospira*, Epirobiidae, Holospiridae, Eucalodiidae, Urocoptoidea, México, Central America, taxonomy.

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¹Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA 32611-7800; <fgt@flmnh.ufl.edu>

INTRODUCTION

Epirobia has remained an enigmatic genus of land snails because it occurs in tropical regions that have seldom been visited by malacologists. The taxonomic status and relationships of *Epirobia* have been variously hypothesized as a subgenus of *Holospira* or as a closely related genus in the Holospiridae (Von Martens 1897; Pilsbry & Vanatta 1898; Pilsbry 1902, 1953; Rehder 1940; Thompson 1976). No review of *Epirobia* has been made since Pilsbry (1902). Fresh material remained unavailable, and very little was known concerning its anatomy until Thompson (1976) described two new species of *Epirobia* from Chiapas, and pointed out the disparate anatomy of the genus compared to *Holospira*. Thompson (2011a) placed *Epirobia*, *Propilsbrya* and *Pectinistemma* in the Eucalodiidae

because of shell similarities. Field work by the author between 1968–2000 in México, Guatemala, and Honduras has yielded numerous additional specimens representing *Epirobia*, *Pectinistemma* and *Propilsbrya*, including critical anatomical material, making it possible to re-examine the systematics of these snails, and re-evaluate their familial relationships. Uit De Weerd (2008) examined the phylogeny of urocoptoid gastropods based on the gene 28S rRNA, and established the superfamily Urocoptoidea for the group. He demonstrated that *Epirobia* is the sister group of all other Urocoptoidea (Fig. 1). Data presented herein support the monophyly of epirobiid genera and their independence from other groups of the Urocoptoidea. The data also support the monophyly and independence of the Holospiridae and Eucalodiidae.

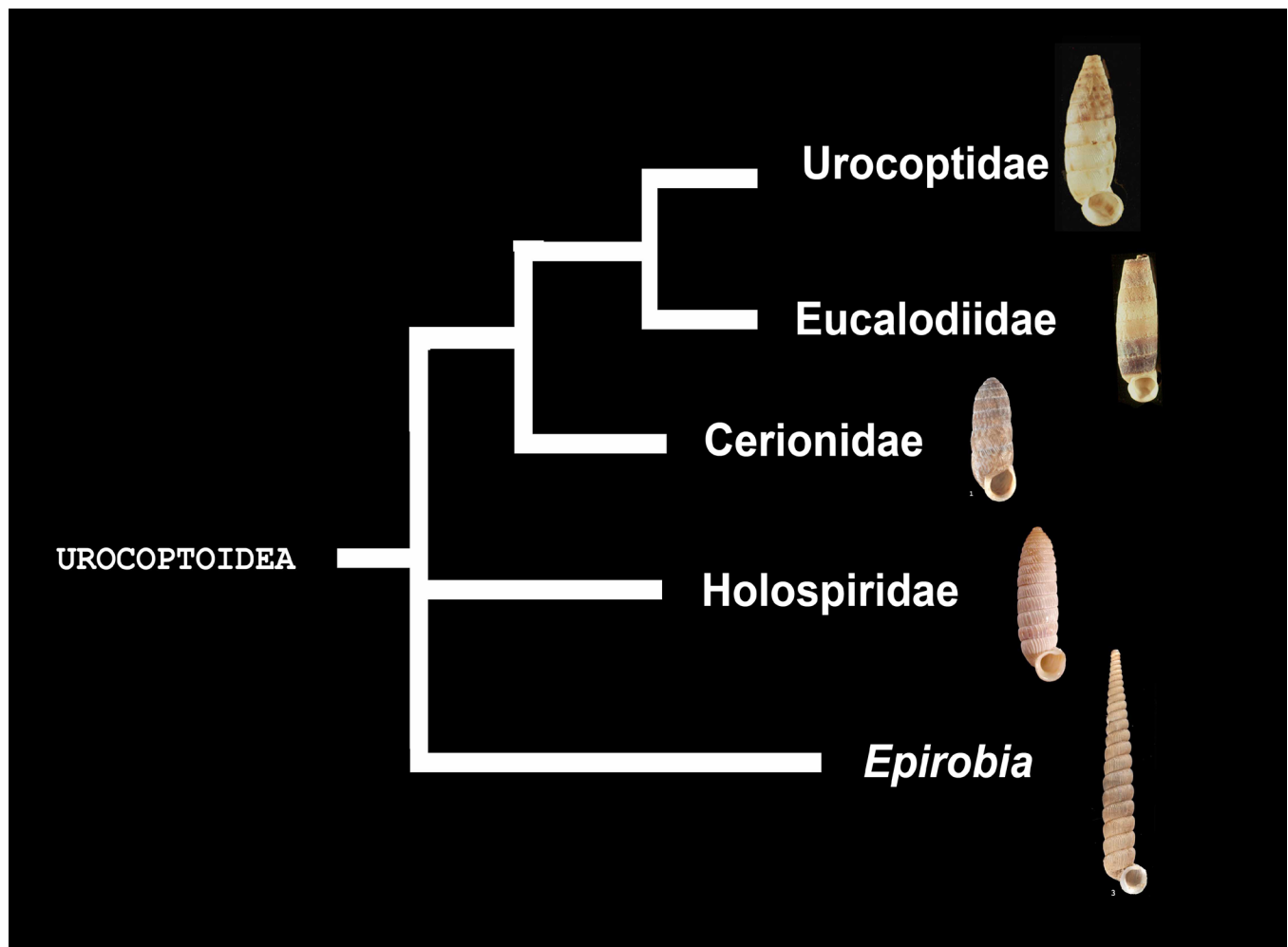


Figure 1. Phylogeny of urocoptoid gastropods based on the gene 28S rRNA (after Uit De Weerd 2008).

MATERIAL AND METHODS

This research is based primarily on specimens in the Florida Museum of Natural History that were collected from México and northern Central America over the last 50 years.

Measurements are standard for cylindrical shells as outlined in Thompson and Mihalcik (2005). Shell length is measured parallel to the axis from the apex to the last whorl, including the peristome. Width is measured perpendicular to the axis of the shell and does not include the neck of the last whorl or the reflected peristome. The axis was examined by filing open the shell and by radiography. Illustrations of radula and jaws are from micrographs taken with an Hitachi 5400 scanning electron microscope. Dissections were made in 75% ETOH with the aid of a WILD microscope.

Acronyms of museum collections for specimens used in this study are: **ANSP**, Academy of Natural Sciences of Philadelphia; **CNMO**, Colección Nacional de Moluscos (México); **NMNH**, Muséum National d'Histoire Naturelle, Paris; **UF**, Florida Museum of Natural History, Gainesville, Florida; **USNM**, United States National Museum of Natural History, Washington; and **ZMB**, Museum für Naturkunde, Humboldt Universität, Berlin.

SYSTEMATICS

UROOPTOIDEA

EPIROBIIDAE new family

Type genus.—*Epirobia* Strebel & Pfeffer 1880.

Referred genera.—*Propilsbrya* Bartsch 1906, *Pectinistemma* Rehder 1940, and tentatively, *Gyrocion* Pilsbry 1904b and *Prionoloplax* Pilsbry 1953. *Epirobia*, *Propilsbrya* and *Pectinistemma* are alike in anatomy and most shell characters. *Gyrocion* has a similar shell as the other three genera, but remains unknown anatomically.

Diagnosis.—The Epirobiidae differs from the Holospiridae and the Eucalodiidae by having a long diverticulum on the penis. The penis retractor muscle attaches to the end of the diverticulum. The epiphallus is very long and is weakly differentiated

from the vas deferens. The central tooth of the radula is wider than the adjacent lateral tooth, and it has a small acuminate ectocone high on each side of the tooth and an enlarged broad mesocone. The lateral teeth have a large mesocone and an ectocone. In the Holospiridae and the Eucalodiidae the central tooth is narrower than the adjacent lateral teeth. In the Holospiridae the central and lateral radular teeth are unicuspid with a large mesocone. In the Eucalodiidae the centrals and laterals possess ectocones. These characters separate the Epirobiidae from other Urooptoidea, except the Cerionidae. The Cerionidae differ in shell morphology by having a short, dome-shaped apex, a solid axis in the lower-most whorls, an incomplete peristome across the parietal wall of the aperture, and a non-reflected outer lip. The right ocular retractor muscle passes mesad to the genitalia, not through the penis-oviducal angle, and the penis retractor muscle originates on the right ocular retractor muscle, not on the inner wall of the lung. The epiphallus is well developed and differentiated from the vas-deferens. The penis has a short diverticulum, and the penis retractor muscle attaches to the apex of the diverticulum.

Additional characteristics which are shared with the Holospiridae and the Eucalodiidae, but separate Epirobiidae from Urooptidae are as follows. The axis is hollow. The jaw is solid. The radular teeth are arranged in nearly straight transverse rows. The penis retractor muscle arises from the inner wall of the lung, and the right ocular retractor muscle passes through the penis-vaginal angle. In the Urooptidae the axis is solid and imperforate, the jaw is multi-plated, and the radular teeth are arranged in V-shaped rows. The penis retractor muscle arises from the right ocular retractor muscle, which passes mesad to the genitalia.

Distribution and habitat.—The family is confined to northern Central America and eastern México as far north as Coahuila, Nuevo León, and Tamaulipas (Figs. 2–3). *Epirobia* occurs in Honduras, northern Guatemala, and the Mexican states of Chiapas and Veracruz. *Propilsbrya* is known from high altitudes in Coahuila and Nuevo León. *Pectinistemma* is found at high altitudes in

Nuevo León and Tamaulipas. *Gyrocion* occurs in a low-altitude mesic situation in southern Nuevo León.

Species of *Epirobia* are highly restricted by slight ecological changes in their local deployment. They are found on damp, shaded, moss-draped limestone outcrops. Colonies are very localized and may be confined to areas of only a few square meters. Populations are severely impacted by deforestation and are extirpated by habitat loss.

Propilsbrya and *Pectinistemma* are found on limestone terrains at moderate or higher altitudes in mesic plant communities that are subjected to periodic forest fires. Their populations are not as localized as are those of *Epirobia*.

Genus *Epirobia* Strebel & Pfeffer 1880

Epirobia Strebel & Pfeffer 1880; Beitrag, IV: 77, 85.- Von Martens 1897; Biol. Cent.-Amer.: 283.- Pilsbry and Vanatta 1898; Proc. Acad. Nat. Sci. Phila., 50: 281.- Pilsbry 1902; Man. Conch., 15: 59-61.- Thompson



Figure 2. Distribution of the Epirobiidae in Mexico and Guatemala.

1976; Nautilus, 90: 41–46.- Thompson 2011a; Bull. Fla. Mus. Nat. Hist., 50: 139.

Type species.—*Cylindrella polygyra* Pfeiffer 1856 (Pilsbry & Vanatta 1898).

Included species.—*Epirobia apiostoma* (Pfeiffer 1856), *Epirobia polygyrella* (Von Martens 1863), *Epirobia swiftiana* (Crosse 1863), *Epirobia berendti* (Pfeiffer 1866), *Epirobia gassiesi* (Pfeiffer 1867), *Epirobia lurida* Thompson 1976, *Epirobia alternans* Thompson 1976, *Epirobia subsulca* n. sp., *Epirobia brevior* n. sp., *Epirobia longior* n. sp., *Epirobia interupta* n. sp., and *Epirobia adusta* n. sp.

Remarks.—Pilsbry (1902) described the radula of *E. polygyra* and Thompson (1976) described the anatomy and radula of *Epirobia lurida* Thompson 1976. The anatomy of *E. polygyra* is described below in detail because it is the type species of the genus.

The shell of *Epirobia* is elongate and slender. It may be entire or decollate. The protoconch is smooth. The teleoconch is sculptured with axial ribs. Spiral sculpture is absent. Internally the shell has a hollow axis that usually is sculptured with oblique, weak axial ribs. Granular sculpture may

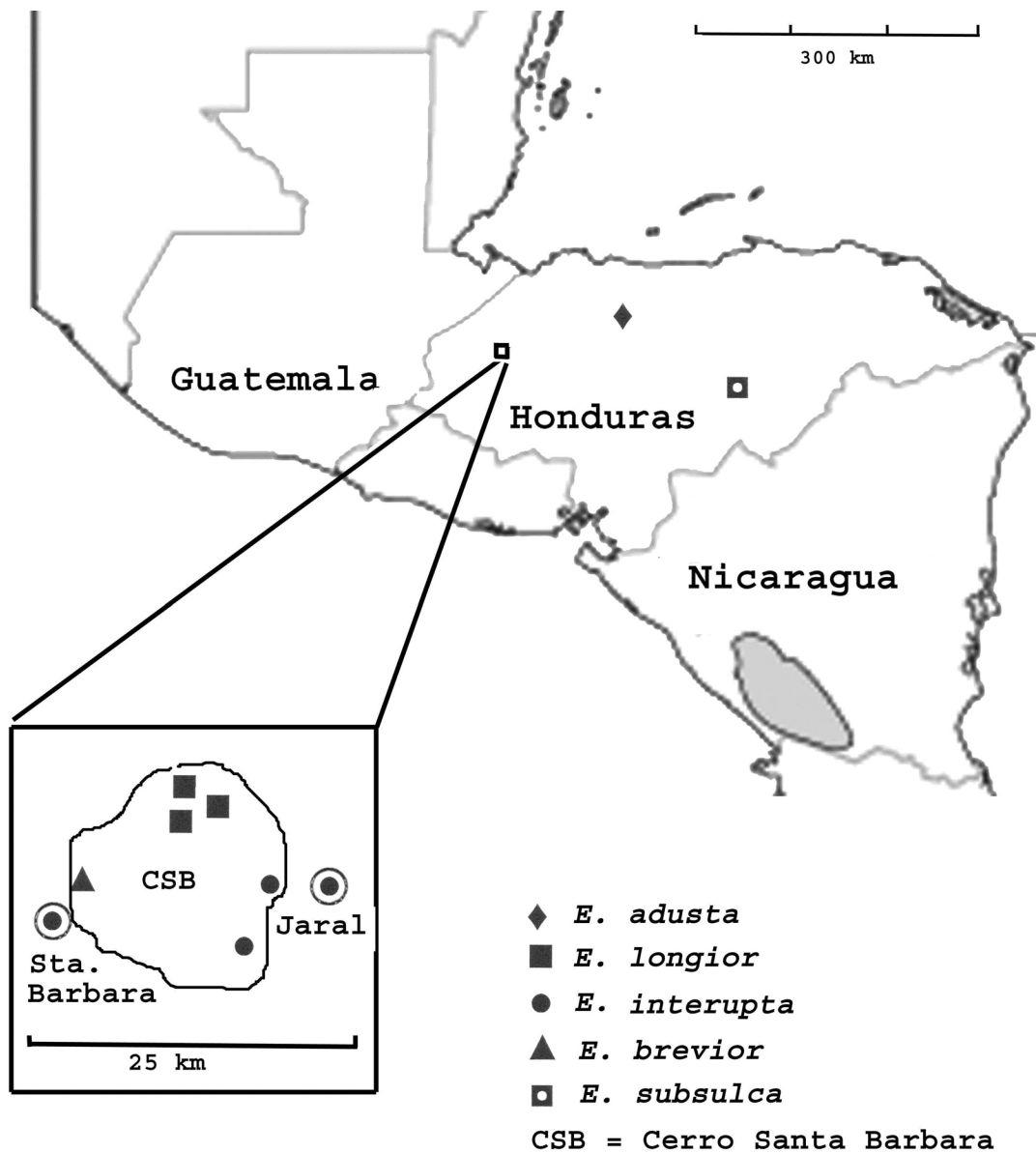


Figure 3. Distribution of species of *Epirobia* in Honduras.

also be present on the axis. The interior of the shell lacks lamellae.

The jaw is solid with 6–8 wide vertical ribs. The central tooth is tricuspid; the mesocone is very broad and long, overlapping the base of the tooth and the top of the succeeding tooth; an ectocone on each side extends above the mesocone. The lateral teeth are bicuspid with a long, broad mesocone and a smaller raised ectocone. The marginal teeth may have multiple ectocones and in some species an entocone.

The gonad is confined to the inner curvature of the lower-most whorl of the digestive gland. The gonad consists of four clusters of 3–6 clavate lobes each. The spermatheca is elliptical and appressed against the middle of the base of the albumen gland. The spermathecal duct is very stout above its junction with the vagina, which is just above the genital atrium. The duct has an appendix shortly below the spermatheca. The penis is long and slender. It has a long stout diverticulum at the apex. The penis retractor originates on the inner wall of the lung and inserts on the apex of the diverticulum. The epiphallus and the vas deferens are very long and slender. In most species the epiphallus and the vas deferens are poorly differentiated.

Strebel and Pfeffer (1880) reported on portions of the reproductive system and the radula of *Epirobia apiostoma* (Pfeiffer 1856) recovered from a dried specimen, but their observations depart significantly from other observations on epirobiid anatomy, suggesting that their material was misidentified (Pilsbry 1902; Thompson 1976).

Epirobia are slender land snails 15–25 mm long found in southeastern México, Guatemala, and Honduras. They have received relatively little study because the geographic areas in which they occur have until recently been poorly explored for mollusks. More collecting needs to be done in many areas within this region.

A misconception concerning the decollate condition of the shell has persisted since the genus was described in 1880. Generally it is stated that the shell is non-decollate. That is, the mature shell retains the entire shell throughout life, and by implication, the entire shell is occupied by the snail's

body. This has led many authors to relate *Epirobia* and allied genera with *Holospira* Strebel & Pfeffer 1880 (Von Martens 1897; Pilsbry & Vanatta 1898; Pilsbry 1902, 1953; Thompson 1976; Schileyco 1999). The study of recently collected specimens from many localities in México, Guatemala, and Honduras prompted a re-examination of the decollate condition of the *Epirobia* shell.

In some species, such as *E. polygyrella* (Von Martens 1863), *E. swiftiana* (Crosse 1863), and *E. alternans* Thompson 1976, the shell is non-decollate and lacks an apical plug (Fig. 4). This character is similar to the Holospiridae, all of which are non-decollate and the snail's body occupies the entire shell (Thompson 1964, 1971, 1988; Thompson & Mihalcik 2005). However, other species of *Epirobia* are decollate, or they have an apical plug within the shell while retaining the entire protoconch (Fig. 5). Such specimens are biologically decollate because the whorls above the apical plug are not occupied by the snail's body and are dead. The decollate state of these *Epirobia* is similar to that found in the Eucalodiidae, all of which are decollate, even though occasional individuals may retain dead whorls above the apical plug (Pilsbry 1902; Thompson 1968, 1976; Thompson & Correa 1994).

The decollate condition has little phylogenetic significance. Uit De Weerd (2008) placed *Epirobia* as ancestral to the Urocoptoidea based on a robust analysis of 28S rRNA sequence data. He related the genus closest to the Holospiridae based on the morphological state of a non-decollate shell, which is true only in some *Epirobia*. The reproductive anatomy and the radula do not support a close relationship with the Holospiridae.

The *Epirobia polygyra* Species Group

The species in this group have delicate, slender shells, and most species are decollate (one species is non-decollate). Shell color is uniform light brown or grayish brown. The whorls bear numerous low, closely spaced ribs that are not broken into clusters. The group is found in southern Veracruz, Chiapas, and Guatemala at low to intermediate elevations.

Epirobia polygyra* (Pfeiffer 1856)*Figure 6A-D**

Cylindrella polygyra Pfeiffer 1856; Proc. Zool. Soc. London: 322; pl. 35, figs. 2–3.- Fischer & Crosse 1873; Miss. Sci. Mex., I: 405; pl. 17, figs. 16.

Holospira (Epirobia) polygyra (Pfeiffer). Von Martens 1897; Biol. Cent. Amer.: 284.

Epirobia polygyra (Pfeiffer). Strebel & Pfeiffer 1880: 87; pl. 5, figs. 7a, 7b (shell); pl. 13, fig. 2 (radula).- Pilsbry and Vanatta 1898; Proc. Acad. Nat. Sci. Phila., 50: 281; pl. 17, fig. 2.- Pilsbry 1902; Man. Conch., 15: 64–65; pl. 20, figs. 11, 16–19 (shell); pl. 50, figs. 6, 7 (radula).- Bartsch 1906; Proc. U. S. Nat. Mus., 31: 120.- Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Diagnosis.—The complete shell is about 15–20 mm long. The shell is grayish brown in color. The spire is nearly straight-sided, being slightly concave in shape only along the apical 5–6 whorls. The first whorl is 0.73 mm wide; slightly wider than the following two whorls. The complete shell has 20–25 whorls. The shell develops an apical plug at about 4–6 whorls below the apex and 17–20 whorls above the aperture (Fig. 5A–5D). Mature specimens usually lose some whorls above the apical plug and are decollate, but some individuals, including the lectotype, retain the earlier whorls and

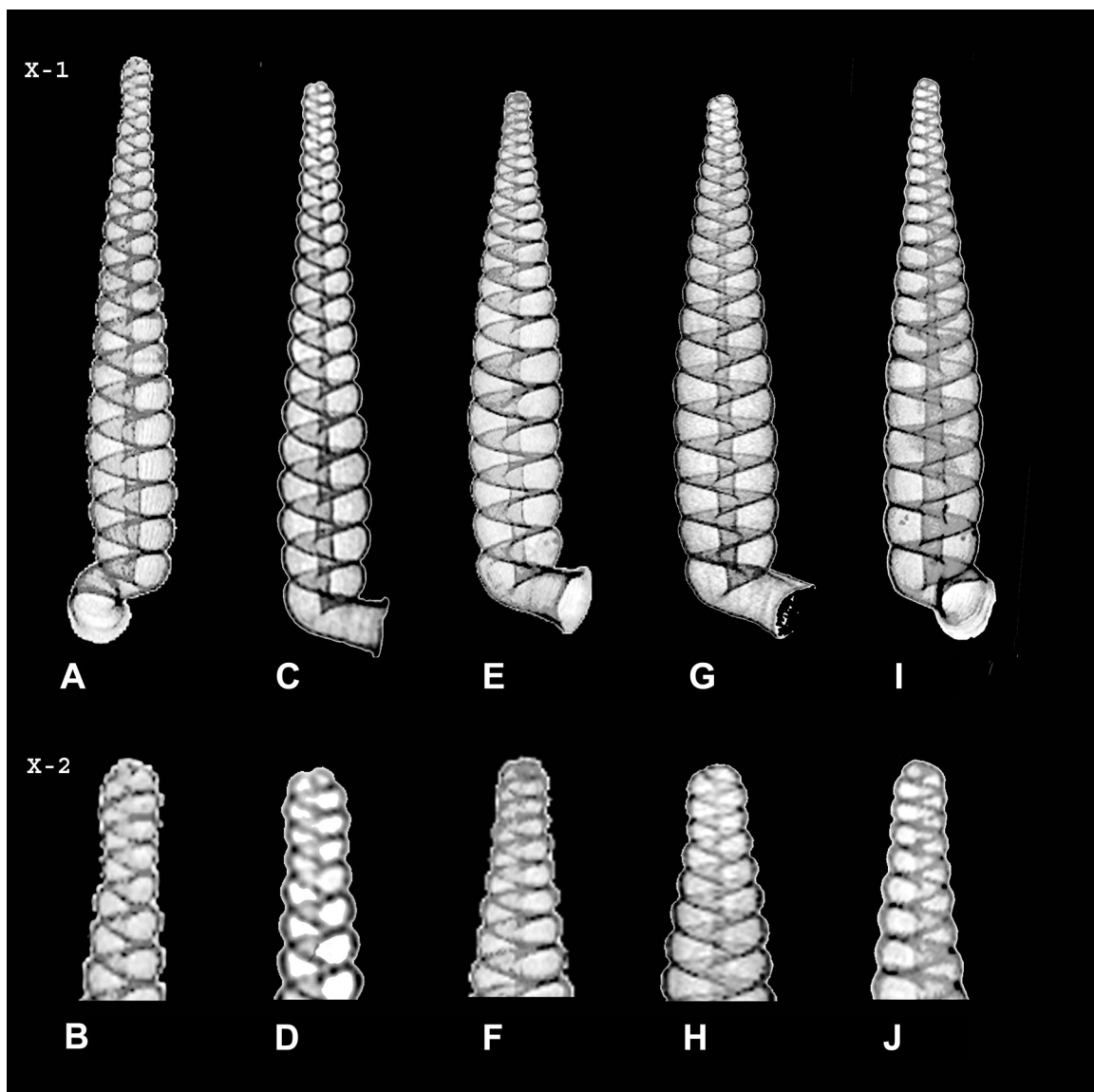


Figure 4. Radiographs of *Epirobia* shells that are non-decollate. **A–B**, *Epirobia polygyrella*, lectotype (ZMB 51157a). **C–D**, *Epirobia polygyrella*, (UF 190152). **E–F**, *Epirobia swiftiana*, lectotype (MNHN 22003). **G–H**, *Epirobia alternans*, paratype (UF 22452). **I–J**, *Epirobia interupta* n. sp., paratype (UF 426760).

have a complete spire. The protoconch consists of three smooth button-shaped whorls. The following whorls are sculptured with relatively evenly spaced prosocline axial riblets. The base of the last whorl has a distinct peripheral angle. The umbilicus is rimate. The axis is narrow and nearly straight-sided. It is slightly twisted in the last two or three whorl, and it bears relatively coarse spicules

that are arranged in oblique rows (Fig. 7G). The aperture projects forward on a short neck for about a fourth of the width of the last whorl (Fig. 6B, 6D). The neck is flattened above. The peristome is thin and moderately reflected, most so along the basal and columellar margin and least so along the parietal and palatal margins.

Measurements of the lectotype and twelve

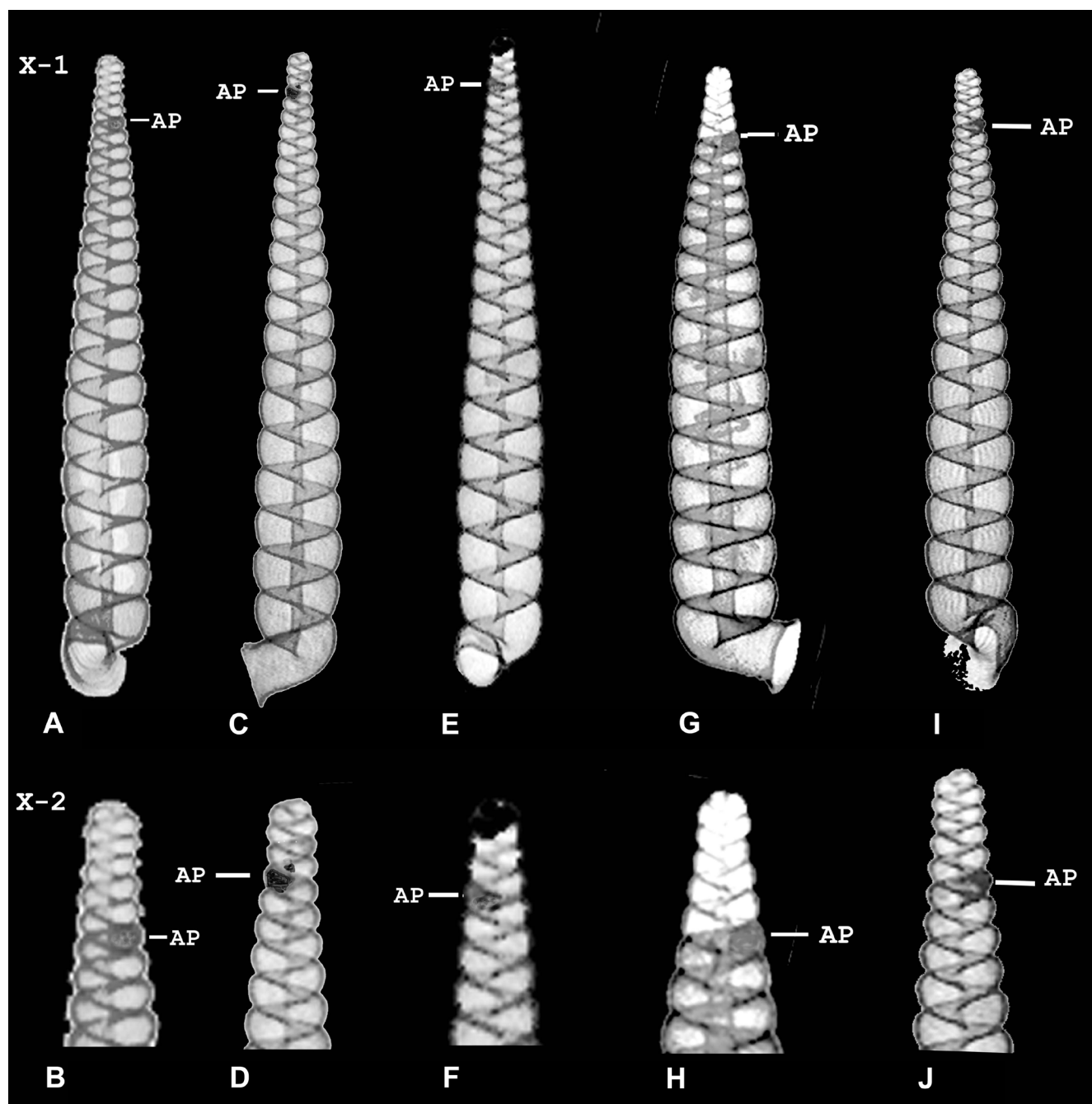


Figure 5. Radiographs of *Epirobia* shells that are decollate. **A-B**, *Epirobia polygyra*, lectotype (MNHN 22006). **C-D**, *Epirobia polygyra*, (UF 190797). **E-F**, *Epirobia apiostoma*, lectotype (MNHN 22004). **G-H**, *Epirobia adusta* n. sp., paratype (UF 426826). **I-J**, *Epirobia lurida*, paratype (UF 22450).

specimens with complete shells are given in Table 1. The back side of the lower five whorls of the lectotype were previously filed open.

Anatomical description.—The contracted animal is 7.5 whorls long. The digestive gland occupies the top three whorls. The lung is three whorls long with a narrow diffuse band of melanophores overlying the lower intestine, and with diffuse black speckling, especially near the mantle collar.

The columellar retractor extends three whorls

up the spire in the contracted animal. Shortly below its origin it gives rise dorsally to a broad pharyngeal retractor that attaches to the posterior base of the pharynx. Then it gives rise to the right and left pedal retractors, which each has a short and narrow ocular retractor. The right ocular retractor passes through the penis-oviducal angle, as in the *Holospiridae*.

The esophagus originates in the center of dorsal side of the pharynx. The salivary glands are fused to form a narrow sheath around the base of

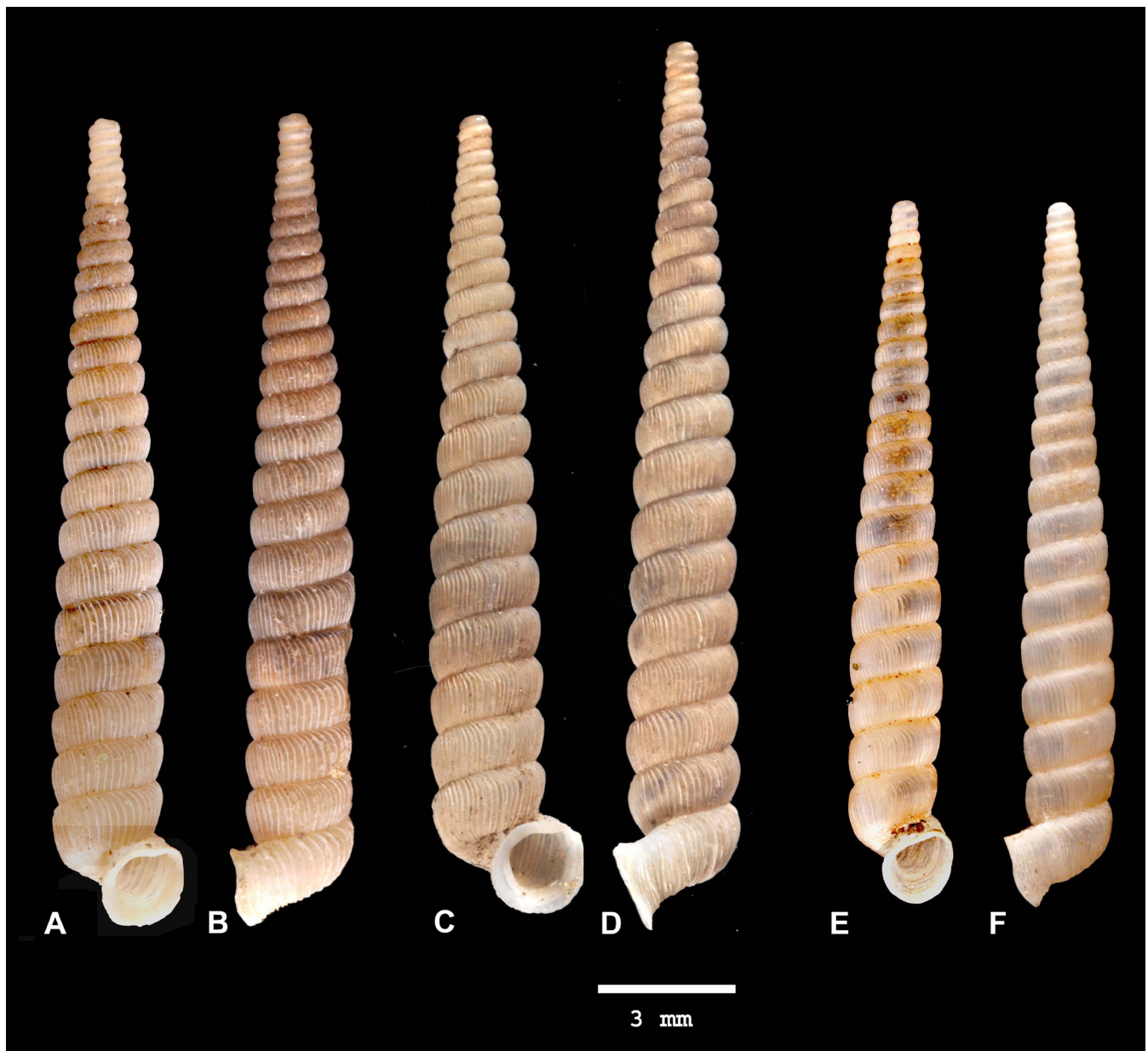


Figure 6. Shells of two species of *Epirobia*. A–D, *Epirobia polygyra* (Pfeiffer 1856). A–B, lectotype (MNHN 22006). C–D, UF 81881. E–F, *Epirobia apiotoma* Pfeiffer 1856, lectotype (MNHN 22004).

the esophagus behind the pharynx.

The arcuate jaw is solid and bears 6–8 large columnar ribs (Fig. 8A). The radular sac is short and is confined to the posterior margin of pharynx. The teeth are in nearly straight transverse rows that are slightly arcuate in the central and lateral fields (Fig. 9B). The radula formula is 10M, 7L, C, 7L, 10M. The central tooth (C) has a large, bluntly rounded mesocone that completely overlaps the face of the tooth. There is a small acuminate ectocone high on each side of the mesocone. The lateral teeth (L) have a large rounded mesocone and a smaller but elongate acuminate ectocone that is well separated from the mesocone. The marginal teeth (M) have a small entocone, a larger acuminate mesocone and 1–2 smaller ectocones. The transition from the laterals to the marginals is gradual in the outer two lateral rows.

The gonad is imbedded in the inner curvature of the lower-most whorl of the digestive gland (Fig. 8B). The gonad consists of four clusters of 3–6 clavate lobes each. The free oviduct is very stout and relatively short. The spermatheca is elliptical and is appressed against the prostate-

uterus just below the base of the albumen gland. The spermathecal duct bears a long appendix shortly below the spermatheca. The spermathecal duct is very stout and muscular above its junction with the free oviduct. The spermathecal duct and the free oviduct unite to form a short, stout vagina just above a short atrium. The penis is long and club-shaped and ends in a more slender diverticulum that is about as long as the penis. The penis retractor muscle originates on the inner wall of the lung and inserts on the apex of the diverticulum. An epiphallus enters the penis at the base of the diverticulum and gradually tapers to the vas deferens. The epiphallus and the vas deferens are poorly differentiated. (3 specimens dissected, UF 81882).

Type locality.—MÉXICO: Veracruz State, Cordova [Córdoba]. Lectotype here designated: MNHN 22006, ex Auguste Sallé (Fig. 6A-B); six possible syntypes are MNHN 22007.

Pfeiffer (1856) described twenty-five specimens from Córdoba collected by the entomologist Auguste Sallé, who collected extensively in the region. The locality is a little ambiguous and is

Table 1. Measurements of shells of *Epirobia polygyra* (Pfeiffer 1856) in mm based on the lectotype and twelve complete specimens. (SL = standard length; SW = standard width; AH = aperture height; AW = aperture width).

	SL	SW	AH	AW	Whorls
Lectotype	17.4	2.4	1.7	1.8	25.1
UF 81881	16.1	2.4	2.0	2.1	20.8
UF 81881	17.3	2.5	2.2	2.0	21.0
UF 81881	17.8	2.7	2.3	2.3	21.5
UF 81881	18.1	2.7	2.0	2.0	21.6
UF 81881	18.1	2.5	2.1	2.1	20.4
UF 81881	20.2	2.7	2.0	2.0	21.9
UF 81881	20.2	2.8	2.0	2.1	21.5
UF 190797	14.4	2.5	1.7	1.7	20.9
UF 190797	15.8	2.4	1.6	1.7	22.0
UF 190797	16.0	2.4	1.7	1.7	21.0
UF 190797	16.8	2.3	2.0	1.9	23.0
UF 190797	17.0	2.5	1.7	1.9	22.7

amended to the vicinity of Córdoba. Syntypes of this species were deposited in the Heinrich Dohrn Collection at the Stettin Museum, which is now in Muzeum Narodowe, Szczecin, Poland. The Dohrn mollusk collection was totally destroyed in the 1939-1945 War (Dance 1986:219). However, Sallé retained specimens of *Cylindrella polygyra* and *C. apiostoma* for his collection, and these are the only known surviving specimens from the original

samples. They are now in the Muséum National d'Histoire Naturelle.

Distribution.—MÉXICO. Known only from central Veracruz (Fig. 2).

Specimens examined.—MÉXICO. Veracruz State: Cerro de Las Palmas, 1 km E of Berlin, 4 km N of Córdoba 980 m alt. (UF 190797, CNMO 3377); Cerro de Las Palmas 2 km ESE of San Rafael Caleria. 0.5 km W of Santa Rosa, 18.590°N.

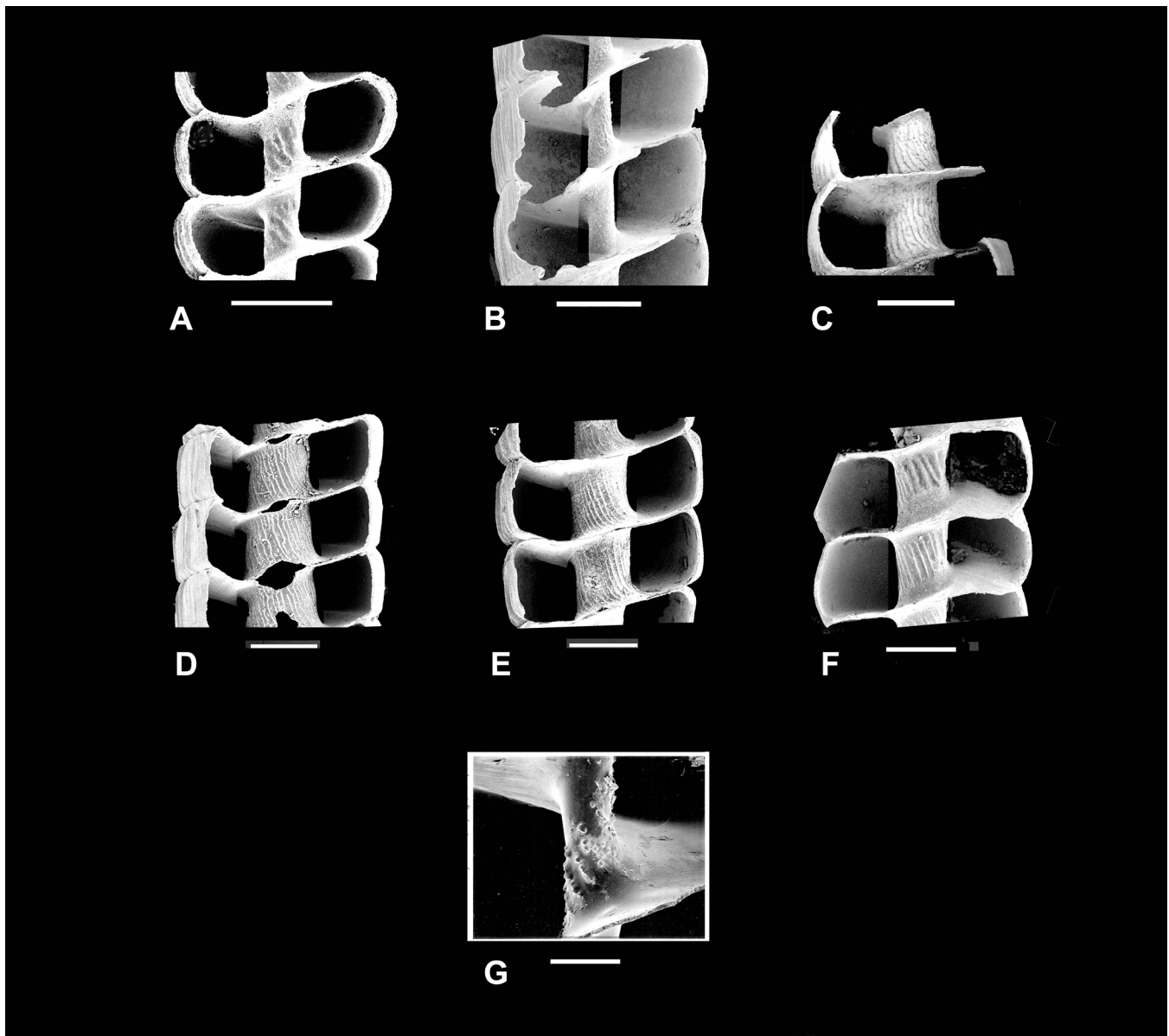
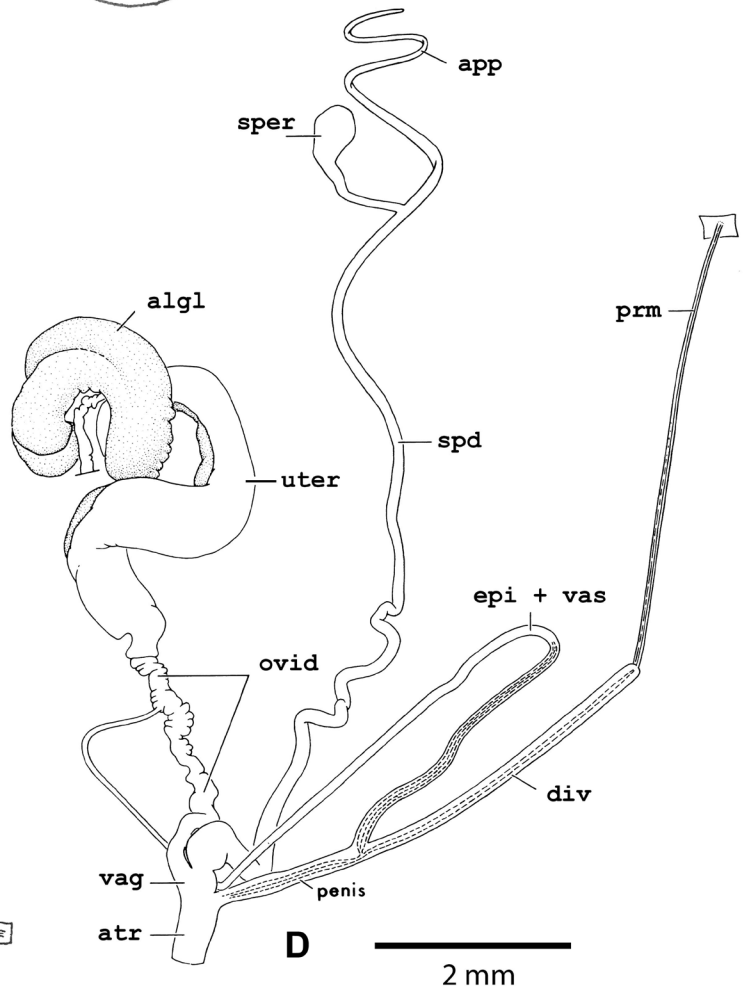
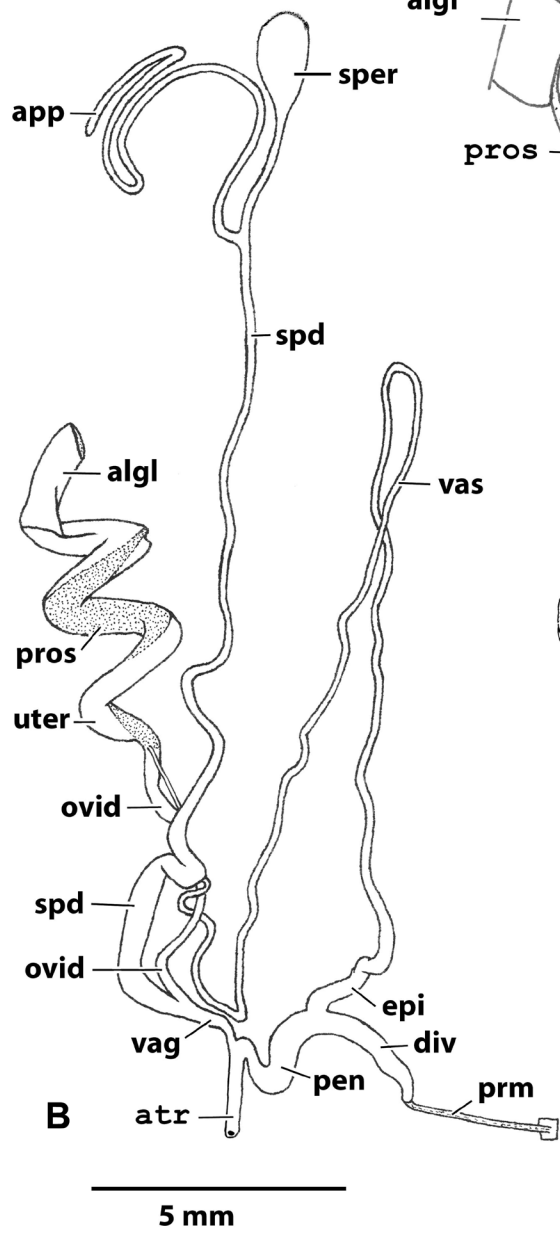
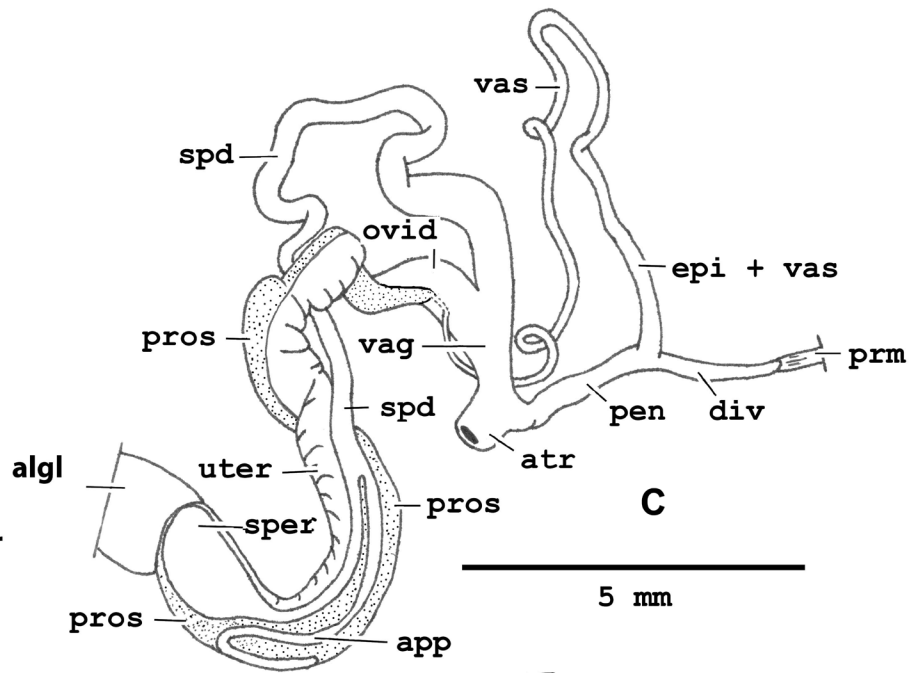
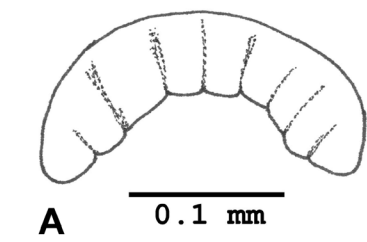


Figure 7. SEM micrographs of *Epirobia* shells showing the axis in the penultimate and antipenultimate whorls. **A**, *Epirobia polygyrella* (UF 180152). **B**, *Epirobia subsulca* n. sp., paratype (UF 426214). **C**, *Epirobia interupta* n. sp., paratype (UF 426760). **D**, *Epirobia longior* n. sp., paratype (UF 426762). **E**, *Epirobia brevior* n. sp., paratype (UF 426761). **F**, *Epirobia adusta* n. sp., paratype (UF 426826). **G**, *Epirobia polygyra*. (UF 81882). Scale bars = 1 mm.



96.932°W, 1000 m alt. (UF 337199); 4 km E of Colonia Toxpan, 18.902°N, 96.902°W, 910 m alt. (UF 337178); 2 km NE of Comalapa, 18.700°N, 96.867°W, 450 m alt. (UF 81881; UF 81882, *in alcohol*).

Remarks.—*Epirobia polygyra* shares with *E. apiostoma* the type locality of “Cordova”. It differs from *E. apiostoma* by being slightly larger, by having much more prominent thread-riblets and by having a more broadly expanded peristome. The axial sculpture is distinct by its interrupted riblets. The axial sculpture of *E. apiostoma* remains unknown.

Specimens from Cerro de las Palmas, 4 km north of Córdoba more closely approximate the lectotype in size and aperture development than do specimens from other populations. Specimens from near Comalapa have a slightly wider peristome.

Epirobia apiostoma (Pfeiffer 1856)

Figure 6E–F

Cylindrella apiostoma Pfeiffer 1856; Proc. Zool. Soc. London: 322; pl. 35, figs. 4–5 (shell).— Fischer & Crosse 1873; Miss. Sci. Mex., I: 406; pl. 17, fig. 15 (shell).

Holospira (Epirobia) apiostoma (Pfeiffer). Von Martens 1897; Biol. Cent. Amer: 283.

Epirobia apiostoma (Pfeiffer). Strebel & Pfeiffer 1880; Beitrag, IV: 88; pl. 5, fig. 6 (shell); pl. 13, fig. 11 (reproductive anatomy?).— Pilsbry 1902; Man. Conch., 15: 63–64; pl. 20, figs. 12–15 (shell).— Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 139.

Diagnosis.—This species has a delicate, subhyalina, grayish shell. An apical plug is formed at 18 whorls above the aperture (Fig. 5E–F). The narrow spire is almost straight-sided. The first whorl is 0.64 mm wide. It is not wider than the following whorl, although it is slightly higher. The whorls are moderately arched between the suture. The last whorl is evenly rounded onto the base and lacks a basal angulation. The sculpture consists of

very fine vertical thread-riblets. The base of the last whorl is evenly rounded and lacks a peripheral angle. The umbilicus is narrowly perforated. The aperture is pear-shaped and extends forward on a short neck that is about a fifth of the width of the last whorl (Fig. 6F). The peristome is weakly expanded, most so along the columellar margin and is narrowest along the parietal margin and the posterior angle. The axis is straight and very slender throughout the length of the shell. It is about a tenth the width of the penultimate whorl (Fig. 5E). Details of axial sculpture could not be resolved from the radiographs. The lectotype has 21.5 whorls.

Measurements of the lectotype are: length, 15.6 mm; width, 2.1 mm; aperture height, 1.5 mm; aperture width, 1.6 mm. 21.5 whorls.

Type locality.—MÉXICO, Veracruz State, Cordova [Córdoba]. Lectotype here designated MNHN 22004, ex Auguste Sallé (Fig. 6E–F).

Distribution.—Known only from the type locality (Fig. 2). *Epirobia apiostoma* was described from the same type locality as *E. polygyra*, Córdoba, Veracruz. Numerous searches in the vicinity of Córdoba by the author between 1966–2004 yielded only the latter species. There can be little doubt that Sallé collected the original samples from the vicinity of Cordoba, but the exact occurrence of the species remains unknown. The lectotype is the only specimen I have been able to locate in a museum collection.

Epirobia lurida Thompson 1976

Figure 10A–B

Epirobia lurida Thompson 1976; Nautilus, 90: 43–45; figs. 1a–b, 2b (shell), 3 (anatomy).— Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Diagnosis.—Medium sized, 15.5–18.3 mm long; 0.15–0.17 times as wide as long. Color light yellowish-gray; lusterless. Whorls 22.5–25.0.



Figure 8. Anatomy of *Epirobia* and *Pectinistemma*. **A**, *Epirobia polygyra*, jaw (UF 81882). **B**, *Epirobia polygyra*, reproductive anatomy (UF 81882). **C**, *Pectinistemma koestneri*, reproductive anatomy (UF 194617). **D**, *Epirobia lurida*, reproductive system (after Thompson 1976). Abbreviations: abgl = albumen gland; app = appendix; atr = genital atrium; div = diverticulum; epi = epiphallus; ovid = free oviduct; pen = penis; prm = penis retractor muscle; pros = prostate; sper = spermatheca; spd = spermathecal duct; uter = uterus; vag = vagina; vas = vas deferens.

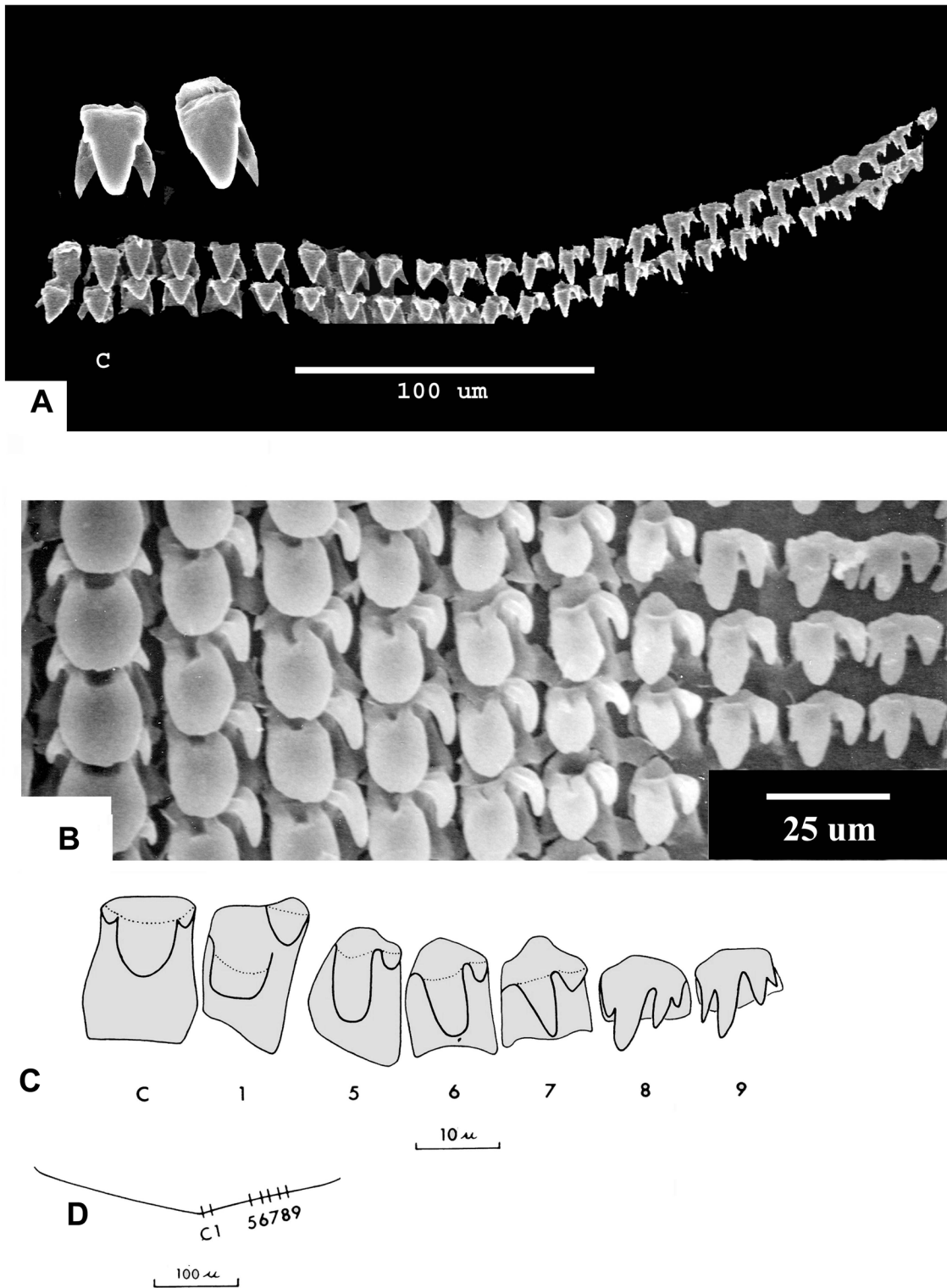


Figure 9. Radula of *Pectinistemma* and *Epirobia*. **A**, *Pectinistemma koestneri* (UF 194617). **B**, *Epirobia polygyra* (UF 81881). **C-D**, *Epirobia lurida* (from Thompson, 1976).

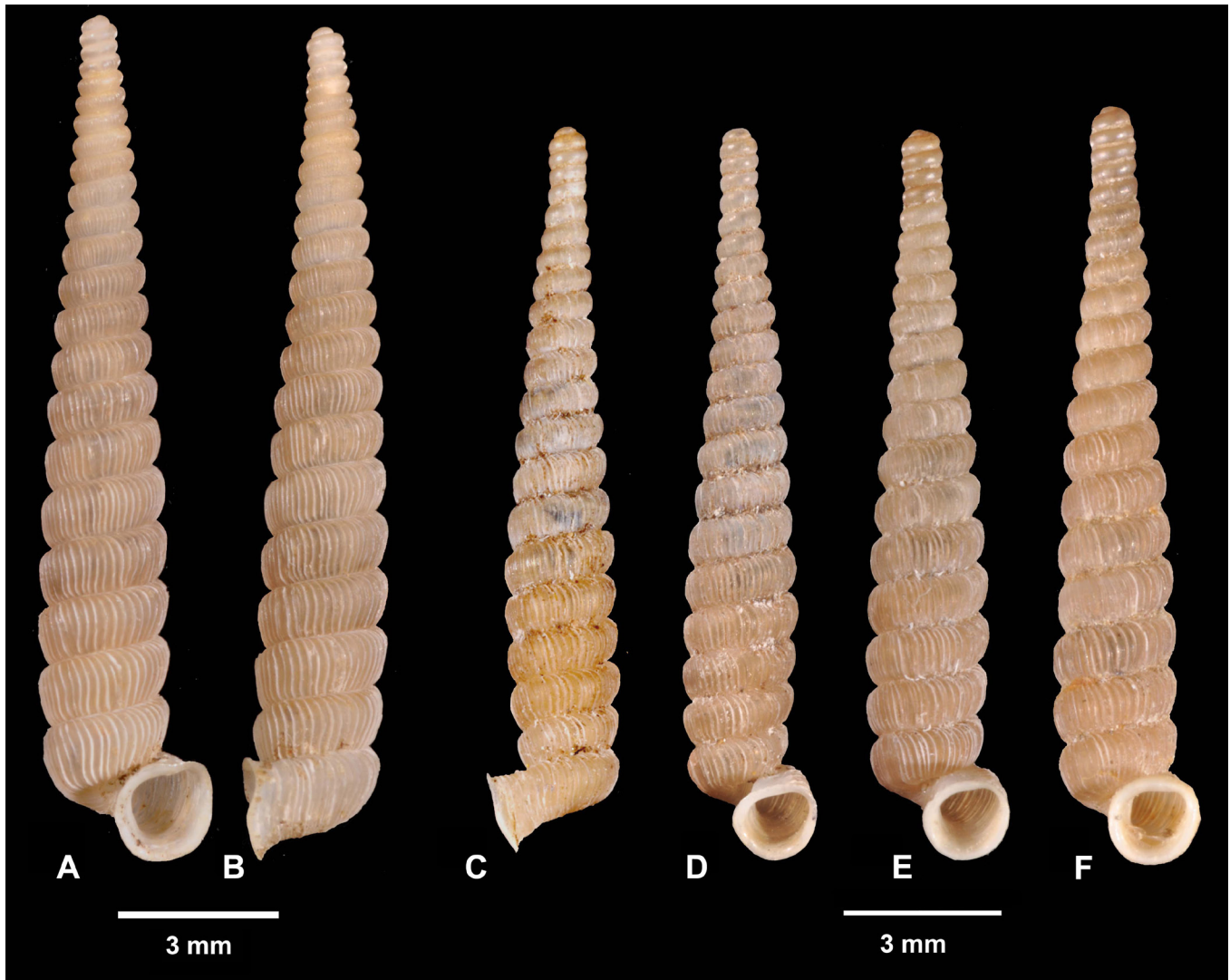


Figure 10. Shells of two species of *Epirobia*. **A–B**, *Epirobia lurida* Thompson 1976, holotype (UF 22449). **C–D**, *Epirobia polygyrella* (Von Martens 1863), lectotype (ZMB 51157). **E–F**, *Epirobia polygyrella* (Von Martens 1863), referred (UF 190152).

Teleoconch sculptured with regularly spaced ribs that are about twice as high as wide and about $\frac{1}{4}$ as wide as their interspaces; penultimate whorl sculptured with 35–49 ribs. Umbilicus rimate. Base of last whorl rounded and lacking a peripheral angle. Axis slender, about $\frac{1}{8}$ the width of the shell; sculpture with small granular spines that tend to form oblique rows.

Anatomy.—Information is taken from Thompson (1976). The radula (Fig. 9C–D) and the reproductive anatomy (Fig. 8D) are figured for comparison with *E. polygyra*.

The anatomy of *Epirobia lurida* and *E. polygyra* are alike in most essential characters.

Epirobia lurida differs from *E. polygyra* by having a relatively smaller mesocone on the central tooth, and smaller ectocones on the central and lateral teeth. Its reproductive anatomy differs by having a longer, more slender penis diverticulum and the epiphallus + vas deferens form a shorter loop.

Type locality.—MÉXICO. Chiapas State, low rolling limestone hills 15.8 mi. [25.5 km] NW of Ocozocoautla on road to Mal Paso, Chiapas; 2700 ft. (830 m) alt. Holotype: UF 22449; Paratypes: UF 22450/114, CNMO 3372/10.

Distribution.—Known only from the vicinity of the type locality (Fig. 2).

Remarks.—The paratype series of this species includes both entire and decollate specimens. Radiographs were made of seven entire paratypes, all of which had apical plugs at 16–20 whorls above the aperture (Fig. 5I–J).

***Epirobia polygyrella* (Von Martens 1863)**

Figure 10C–F

Cylindrella polygyrella Von Martens 1863; Proc. Zool. Soc. London: 411.- Von Martens 1876; Jahrb. Deut. Malak. Ges., 3: 261, pl. 9, fig. 8.

Epirobia morini (Von Martens). Strebe & Pfeiffer 1880; Beitrag, IV: 87, pl. 5, fig. 5 (shell), pl. 13, fig. 2 (radula), pl. 14, figs. 15 a-c (shell).- Bartsch 1906; Proc. U. S. Nat. Mus., 31: 120.

Holospira (Epirobia) polygyrella (Von Martens). Von Martens 1897; Biol. Cent.-Amer: 284; pl. 17, figs. 1–1b (shell).

Epirobia polygyrella (Von Martens). Pilsbry 1902; Man. Conch., 15: 65–66; pl. 20, figs. 8–10 (shell).- Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Diagnosis.—A relatively small species that has a complete shell without an apical plug at maturity. All examined specimens retained the apical whorls. Radiographs were taken of eight specimens (UF 190152). None showed an apical plug (Fig. 4A–D). The shell is about 14–16 mm long, and has 19–21 relatively stocky whorls compared to *Epirobia polygyra*. The shell is unicolor light gray and lusterless. The whorls are strongly arched and are separated by a deep suture. The protoconch consists of four smooth whorls. The second whorl is slightly wider than the following 3–4 whorls.

The teleoconch whorls are sculptured with rather uniformly spaced reversed-sigmoid ribs that are continuous across the whorls and continue onto the last whorl. The ribs are not separated into clusters. The base of the last whorl is rounded and lacks a sub-peripheral angle. The umbilicus is narrowly perforated. The aperture extends forward for about a fourth of the width of the last whorl (Fig. 10C). The aperture is sub-circular and has a wide peristome that is widest along the columellar and palatal margins and is narrowest at the posterior corner. The axis is relatively slender. It is straight-sided within each whorl and is sculptured with relatively widely spaced, sparse oblique riblets that may be broken into short segments (Fig. 7A).

Measurements of the lectotype and six paralectotypes are given in Table 2.

Remarks.—Specimens comprising the type lot (Fig. 10C–D) essentially are identical to specimens from 4 km E of Cobán, 1260 m alt. (UF 190152) (Fig. 10E–F).

The ratio of the whorl height to whorl width provides limited data for discriminating species. These data were used by Von Martens (1897), in part, to distinguish *Epirobia polygyrella* from *E. polygyra*. The ratio he gave for *E. polygyrella* (0.40) is comparable to the ratios for other species described here. The ratio he gave for *E. polygyra* (0.60–0.67) is perplexing. My examination of *E. polygyra* provides ratios of 0.39–0.42, comparable

Table 2. Measurements of shells of *Epirobia polygyrella* (Martens, 1876) in mm based on the lectotype and six complete paralectotypes

	SL	SW	AH	AW	Whorls	SW/SL	AH/AW
Lectotype	14.2	2.26	1.46	1.73	19.0	0.16	0.84
Paralecto.	16.0	2.53	1.73	1.73	20.7	0.16	1.00
Paralecto.	14.8	2.26	1.60	1.86	20.8	0.15	0.86
Paralecto.	14.4	2.26	1.60	1.73	19.8	0.16	0.92
Paralecto.	14.2	2.39	1.60	1.60	18.5	0.17	1.00
Paralecto.	13.8	2.39	1.73	1.86	19.2	0.17	0.93
Paralecto.	13.4	2.26	1.73	1.60	19.8	0.17	1.08
Mean	14.4	2.34	1.64	1.73	19.69	0.16	0.95
SD	0.77	0.10	0.09	0.10	0.79	0.01	0.08

to *E. polygyrella* and other species.

Most previous illustrations are misleading in that they depict a shell with a conspicuously enlarged, knob-shaped apex and a widely expanded peristome (Von Martens 1876, 1897; Pilsbry 1902). The illustrations exaggerate these traits, and they do not match well with any of the syntypes, nor with other specimens I have examined. Strebel and Pfeffer (1880) provided photographs of three specimens from Cobán as *Brachypodella morini* (Morelet 1849). The photographs closely match specimens that I have examined. Syntypes of *Cylindrella polygyrella* are in the Museum für Naturkunde, Humboldt Universität, Berlin. A lectotype and paralectotypes are designated.

Type locality.—GUATEMALA: Dept. Alta Verapáz, Cobán, Lectotype: ZMB 51157a. The lectotype most closely approximates Von Martens' description and measurements among type material that I have examined. Paralectotypes: ZMB 51157b (6 complete shells + 8 incomplete shells and fragments); same data as the lectotype.

Distribution.—GUATEMALA. Known from a narrow zone in the Dept. Izabal west to the Dept. Huehuetenango (Fig. 2).

Specimens examined.—GUATEMALA. Dept. Alta Verapaz: Cobán (UF 179562); 4 km E of Cobán, 1260 m alt. (UF 190152/25); 14 km by rd. N of Cobán, 990 m alt. (15.633° N, 90.327° W) (UF 189923/10); 15 km by rd. N of Cobán, 15.619° N, 90.318° W, 1050 m alt. (UF 189905/20); 2 km ESE of Cajáj, 1050 m alt. 15.555° N, 90.109° W, 1050 m alt. (UF 190009/69). Dept. Huehuetenango: 4.5 km WSW of Tres Ranchos, 15.848° N, 91.253° W, 1300 m alt. (UF 190264/13). Dept. Izabal: microwave tower, Cerro San Gil, 8.5 km WSW Las Escobas, 15.669° N, 88.691° W, 910 m alt. (UF 190564/14).

The *Epirobia subsulca* Species Group

The slender, clavate shell has a weakly concave spire, and is decollate, although individuals may retain dead apical whorls. The lusterless shell is sculptured with white ribs on a brown background. The ribs occur in clusters of 2–6 ribs. The interspaces between the ribs are 1–2 times the width of the ribs. The clusters are separated by smooth intervals

that are equal to or are greater than the width of the clusters. The base of the last whorl is flattened and is bounded by an obtuse peripheral angle. The umbilical opening is broadly elliptical and is about 0.10–0.25 the width of the last whorl. The species are found in the Sierra Agalta and in the environs of Cerro Santa Barbara, Honduras. Three species are recognized.

Epirobia subsulca n. sp.

Figure 11A–C

Diagnosis.—The shell may be superficially non-decollate, but an apical plug is formed at 14–18 whorls above the aperture. The whorls are flattened. The last whorl is weakly sulcate, and is bounded below by a weak basal crest. The sculpture consists of interrupted patches of ribs which coalesce at their upper ends to form a sub-sutural cord. The narrow axis is straight-sided and is smooth except for some minute granules in the lower-most whorls.

Description.—The periostracum is moderately shiny. The shell is light brown with patches of white ribs and a white cord bordering the suture along the upper ends of the ribs. The peristome and the interior of the aperture are white. Complete shells are 18.5–21.0 mm long, 2.5–3.1 mm wide, and 0.13–0.17 time as wide as long. The shell is elongate-clavate in shape with a long, slightly concave apex. It is superficially non-decollate. Complete shells retain 19.6–23.0 whorls. The apical plug is formed at about 14–18 whorls above the aperture. Earlier whorls were lost in only two of 68 specimens examined. The first whorl is as high as wide, and is slightly larger than the following whorl. The following whorls are button-shaped, are slightly compressed and are separated by a deep suture. The lower whorls become weakly arched with a shallow suture and are moderately compressed. The penultimate whorl is 0.41–0.46 times as high as wide. The last whorl is weakly sulcate below the periphery (Fig. 11A) and is bounded below by a basal crest. The first two whorls of the protoconch are smooth. The following whorl is crossed by weak ribs that become fully developed by the 6th whorl. The ribs

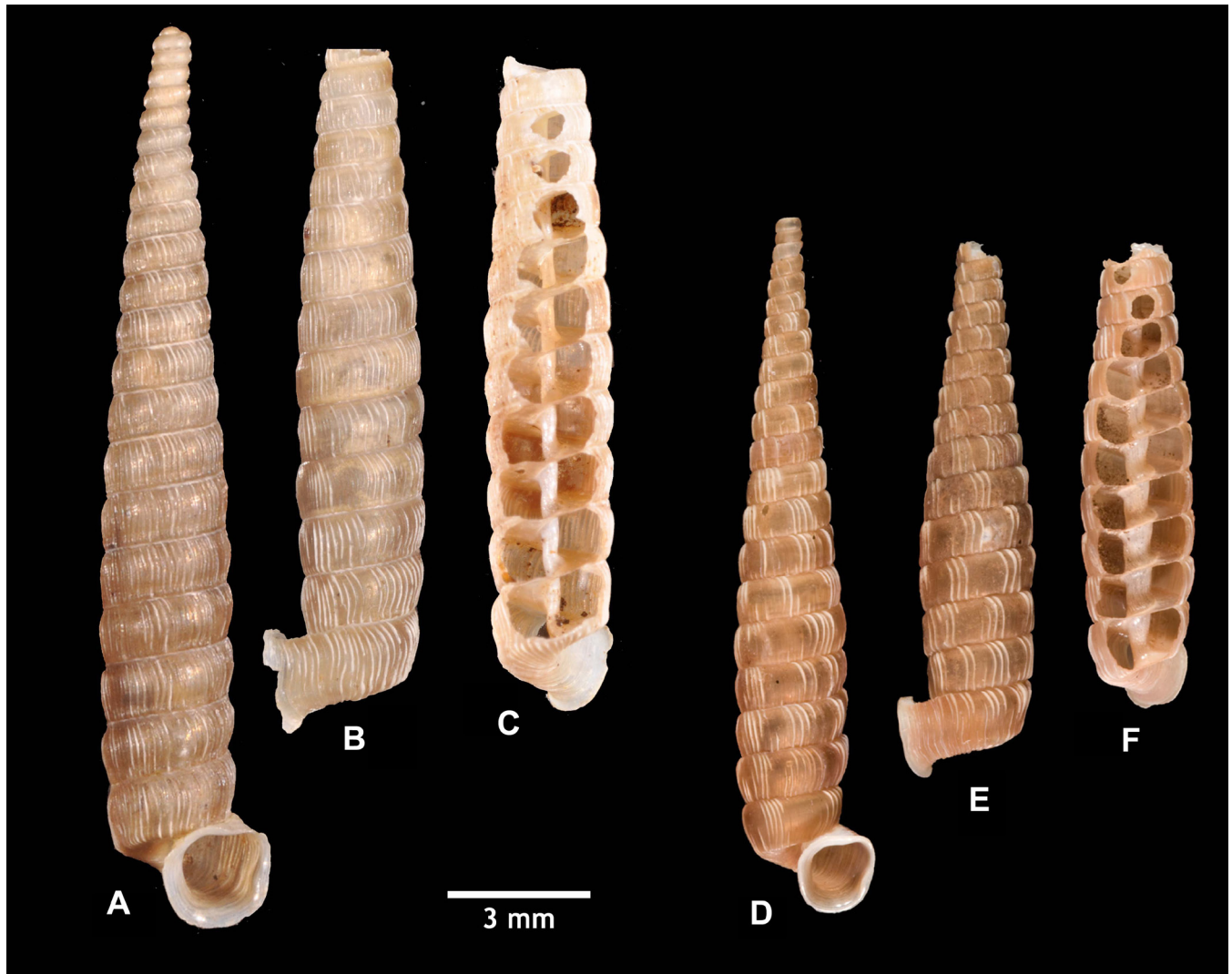


Figure 11. Shells of two species of *Epirobia*. **A–C**, *Epirobia subsulca* n. sp. **A**, holotype (UF 221478). **B–C**, paratypes (UF 426214). **D–F**, *Epirobia brevior* n. sp. **D**, holotype (UF 242756). **E–F**, paratypes (UF 426762).

are weakly reversed-sigmoid in shape, and they are complete across the surface. The ribs are as high as wide with interspaces that are 3–5 times as wide. The interspaces between the ribs are smooth. The ribs occur in patches of a few to many. The patches are separated by narrower smooth irregularly spaced intervals. The upper ends of the ribs tend to coalesce to form a narrow sub-sutural white cord. The ribs continue across the base of the last whorl and are noticeably thicker where they cross the basal crest. The umbilicus is perforated. The hollow axis is straight sided, and is 0.13–0.16 the width of the shell (Figs. 7B, 11C). It is smooth except in the last three whorls where it may bear weak granules.

The aperture is circular-rhomboidal in shape. It is weakly indented along the parietal margin, and is obtusely angular at the posterior corner. It projects forward on a short neck for a distance that is about a tenth the width of the last whorl (Fig. 11B). The peristome is reflected around the aperture. It is narrowest at the posterior corner, and widest along the columellar-basal margin.

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

Type locality.—HONDURAS, Dept. Olancho, Agalta National Park, limestone ridge 6 km NW of Catacamas, ca. 14.88°N, 85.92°W, 1300 m alt. HOLOTYPE: UF 221476; collected by Fred G.

Table 3. Measurements of shells of *Epirobia subsulca* n. sp. in mm based on the holotype and eight paratypes with complete shells.

	SL	SW	AH	AW	Whorls
Holotype	19.3	2.7	2.3	2.4	22.0
Paratype	21.0	2.9	2.4	2.5	21.1
Paratype	20.6	2.8	2.1	---	23.0
Paratype	20.0	2.5	2.3	2.4	22.5
Paratype	19.5	2.9	2.3	2.3	19.6
Paratype	19.4	2.7	2.2	2.4	22.0
Paratype	19.2	2.8	2.0	2.2	20.3
Paratype	18.9	3.1	2.0	2.2	22.0
Paratype	18.5	2.9	2.0	2.3	19.6

Thompson, Steven P. Christman and J. Malcolm Pierson, 19 March, 1994. PARATYPES: UF 426214/67; same data as the holotype.

Distribution.—HONDURAS; known only from the type locality (Fig. 3).

Habitat.—Snails were collected in a coffee grove between two limestone ridges at the edge of a dense secondary thicket of rain forest. They were found on the face of a low limestone ledge that was draped with clusters of mosses.

Etymology.—The species name *subsulca* is from the Latin, *sub-*, less, and *sulcus*, a furrow, and alludes to the shallow sulcus formed below the periphery in the last whorl.

***Epirobia brevior* n. sp.**

Figure 11D–F

Diagnosis.—This species is distinguished by its lamella-like ribs, and its weakly scalariform whorls. The internal axis is widest in the middle whorls, and tapers below in the last two whorls. The species is short and stocky compared to other species in the group.

Description.—The shell is decollate. Only 2 specimens of 20 retained the complete whorls above the apical plug. Non-decollate shells are 17.0–19.1 mm long and have 20.3–21.5 whorls. Decollate shells are 12.5–16.8 mm long, 3.0–3.3 mm wide and have 11.0–15.8 whorls below the apical plug. The whorls are moderately rounded and are separated by a moderately impressed suture.

The lower-most whorls tend to be scalariform. The base is angled at the periphery. The umbilical perforation is elliptical and open. The penultimate whorl is 0.34–0.40 times as high as wide. The ribs are raised and lamellate along their upper ends where they cross the periphery. The aperture is about as high as wide, and varies from ovate to auriculate in shape. It extends forward on a short neck for about a tenth the width of the last whorl (Fig. 11E). The axis is enlarged in the middle of the spire where it is 0.24–0.29 times the width of the shell, and tapers below in the last two whorls. It is slightly concave in outline within each whorl (Figs. 7E, 11F). It is sculpture with low, close, oblique riblets that lack spiculate granules.

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

Type locality.—HONDURAS: Dept. Santa Barbara, Cerro Santa Barbara, limestone bluff on the west slope ca. 2 km north of Huatuso, 14.875°N, 88.133°W, 1460 m alt. HOLOTYPE: UF 242756 (Fig. 11D); collected 28 May, 1995 by John Polisar. PARATYPES: UF 426761/7; same data as the holotype.

Distribution.—HONDURAS; known only from the type locality (Fig. 3).

Etymology.—The name *brevior* is from the Latin, meaning shorter, alluding to fewer number of whorls and shorter shell that characterize this species.

Table 4. Measurements of shells of *Epirobia brevior* n. sp. in mm based on the holotype, a complete (C) paratype, and six decollate (D) paratypes.

	Shell	SL	SW	AH	AW	Whorls
Holotype	C	19.1	3.1	2.2	2.2	21.5
Paratype	C	17.0	3.0	2.2	2.2	20.3
Paratype	D	16.8	3.1	2.0	2.2	15.8
Paratype	D	14.6	3.2	2.2	2.2	14.0
Paratype	D	14.5	3.0	2.1	2.1	14.2
Paratype	D	12.6	3.3	2.3	2.3	11.0
Paratype	D	12.6	3.3	2.0	2.0	12.5
Paratype	D	12.5	3.0	2.1	2.1	12.5

Epirobia longior* n. sp.*Figure 12A–D**

Diagnosis.—This species is distinct from other species of *Epirobia* because of its larger size and the larger number of whorls in non-decollate specimens. The whorls are nearly flat on the spire and are crossed by sparse white ribs. The axis is about a third the width of the whorls and bears fine ribs and spicules.

Description.—The shell is light brown with irregularly spaced white ribs. The interior of the aperture is rust-colored. The peristome is white. The apical whorls, when present, are dull white. The shell is attenuate-clavate in shape. In non-decollate specimens the apex is very slender and is weakly concave between the 2nd and 15th whorls. Non-decollated shells are 23–26 mm long. Decollate specimens are 18–19 mm long below the apical plug. The shell is 3.0–3.4 mm wide. The shell is normally decollated upon terminal growth. Only 2 of 53 specimens examined retained the entire shell. (The holotype retains nearly all of the whorls, except that the first half of the first whorl is missing). Non-decollate specimens have 28.9–29.1 whorls. An apical plug is formed at 17.3–20.2 whorls above the aperture. The apical whorls are rounded with a deeply impressed suture. The first whorl is small and cap-shaped. The second whorl is enlarged and bulbous. The following apical whorls are rounded and are separated by a deep suture. The lower whorls are flattened peripherally and have a shallow suture. The penultimate whorl is 0.34–0.41 times as high as wide. The base of the last whorl is

flattened and is bounded by an obtuse angle. The umbilicus is perforate. The first 5–6 apical whorls are smooth. The following whorls become sculptured with low sparse ribs. The sculpture consists of sparse, irregularly spaced, posteriorly arched ribs that are weakly recurved along the lower suture. The ribs are uniformly low and rounded. They are about as high as wide, except along the lower suture where they tend to become wider and higher and are exaggerated where they cross the basal angle of the last whorl. The ribs are separated from each other by interspaces that are 1–3 times the width of the ribs. The ribs occur in clusters of 2–4 ribs. The intervals between the clusters are about equal to or greater than the width of the clusters. Frequently the ribs are discontinuous across the whorls. The ribs are exaggerated where they cross the basal angle and do not continue to the umbilicus. The aperture extends forward on a short neck that is 0.23–0.33 time the width of the preceding whorl (Fig. 12B–C). The neck of the aperture is flattened above. The aperture is broadly auriculate in shape, and is about as high as wide. The reflected peristome is narrowest along the posterior corner and the palatal margin, and is widest along the baso-columellar margin. Five shells were opened to view the axis. The axis gradually widens to the last 5–6 whorls, at which point it is 0.30–0.32 times the width of shell (Fig. 12D) and then it tapers below. The axis is nearly straight sided within each whorl and is sculptured with close, fine, oblique riblets and spicules (Fig. 7D).

Measurements of the holotype and six

paratypes are given in Table 5.

Type locality.—HONDURAS, Dept. Santa Barbara, east slope of Cerro Santa Barbara, trail southwest of San Luis Los Planes to the summit of the mountain, 14.953°N, 88.156°W; 1640 m alt. HOLOTYPE: UF 242712; collected 24 May, 1995 by John Polisar. PARATYPES: 426762/52; same data as the holotype.

Other specimens examined.—HONDURAS. Dept. Santa Barbara: east slope of Cerro Santa Barbara, trail SW of San Luis Los Planes, 14.947°N, 88.147°W, 1980 m alt. (UF 242691/1); north-east slope of Cerro Santa Barbara, 4 km S of San Luis Los Planes, 1700 m alt. (UF 221074/27).

Distribution.—HONDURAS; known only from the immediate vicinity of the type locality (Fig. 3).

Etymology.—The name *longior* is from the

Latin, meaning longer, alluding to its extended apex, more so than with other *Epirobia*.

The *Epirobia swiftiana* Species Group

The shell is non-decollate, lacks an apical plug, and is relatively obese. The shell is shiny and the sculpture consists of white ribs on a brown background. The ribs are separated into small clusters, as in the *Epirobia subsulcus* species group. This species group is found in the Mexican states of Veracruz, Tabasco, and Chiapas, and in Honduras.

Epirobia swiftiana (Crosse 1863)

Figure 12E–F

Cylindrella swiftiana Crosse 1863; Jour. de Conchyl., 11: 388.- Crosse 1867; Jour. de Conchyl., 15: 200; pl. 5, fig. 5 (shell).- Fischer & Crosse 1873; Miss. Sci. Mex., I: 407; pl. 17, figs. 14 (shell).

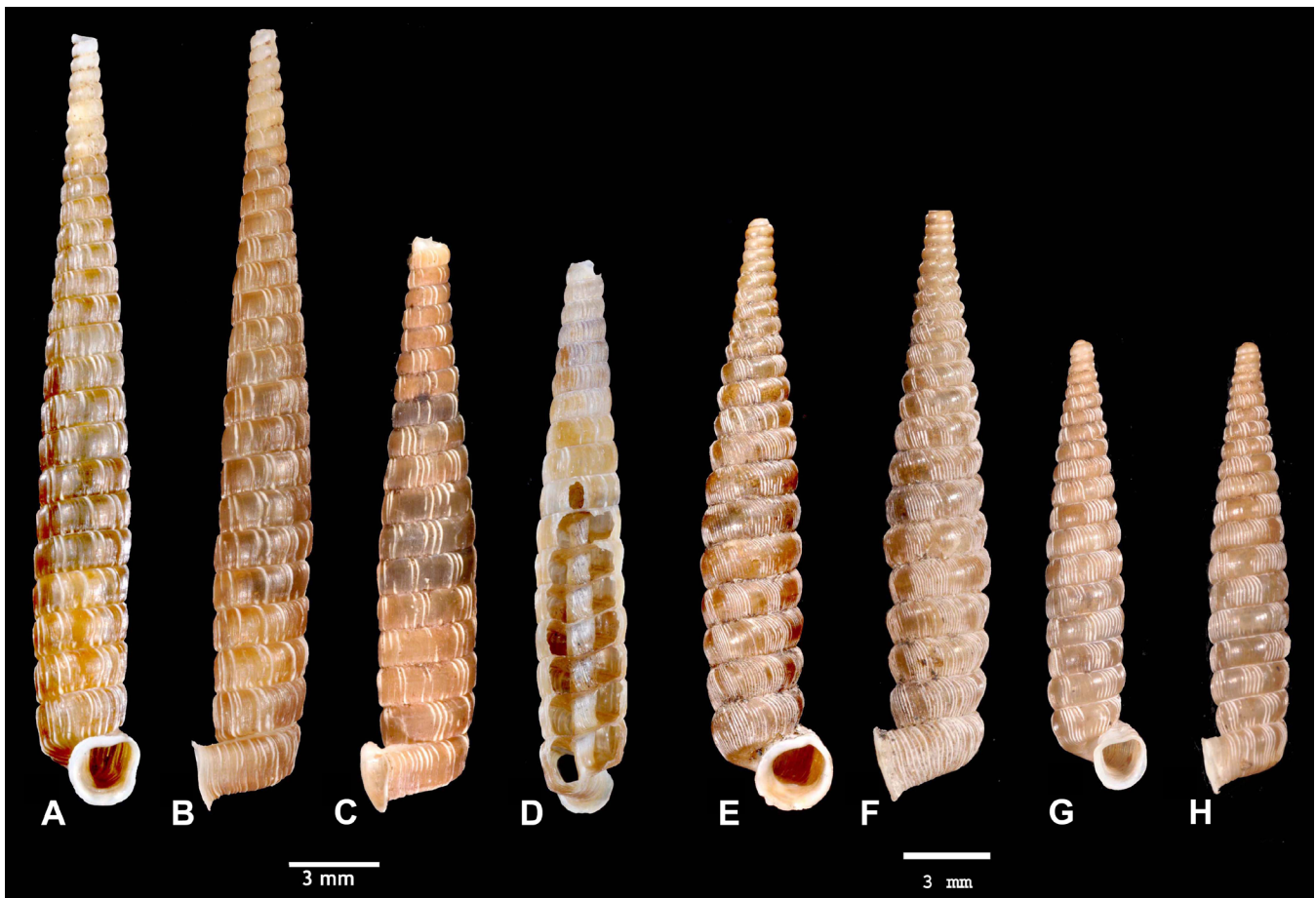


Figure 12. Shells of three species of *Epirobia*. A–D, *Epirobia longior* n. sp. A–B, holotype (UF 242712). C–D, paratypes (UF 426762). E–F, *Epirobia swiftiana* (Pfeiffer 1856), lectotype (MNHN 22002). G–H, *Epirobia alternans* Thompson 1967, holotype (UF 22451).

Table 5. Measurements of shells of *Epirobia longior* n. sp. in mm based on the holotype, a complete (C) paratype, and five decollate (D) paratypes.

	Shell	SL	SW	AH	AW	Whorls
Holotype	C	26.6	3.3	2.2	2.3	28.9
Paratype	C	23.4	3.4	2.0	2.1	29.1
Paratype	D	19.3	3.0	2.0	2.1	20.2
Paratype	D	18.9	3.0	2.2	2.1	18.2
Paratype	D	18.8	3.3	2.3	2.3	18.0
Paratype	D	18.3	3.2	2.2	2.2	17.8
Paratype	D	18.1	3.1	2.1	2.2	17.3

Holospira (Epirobia) swiftiana (Crosse). Von Martens 1897; Biol. Cent. Amer.: 284.

Epirobia swiftiana (Crosse). Pilsbry 1902; Man. Conch., 15: 62–63; pl. 20, figs. 20–22 (shell).

Epirobia swiftiana swiftiana (Crosse). Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 141.

Diagnosis.—The shell is moderately large, 16.0–19.4 mm long and consists of about 20 whorls. The shell is non-decollate and lacks an apical plug (Fig. 4E–F). The whorls are strongly arched and are separated by a deep suture. The protoconch consists of four whorls. The first whorl is 0.70 mm wide and is slightly wider and higher than the following three whorls. The spire consist of about 13 whorls that gradually increase in size and comprises half of the length of the shell. The lower whorls are nearly equal in width until the last whorl which is slightly narrower. The base of the last whorl has a distinct angle along its outer periphery. The oval umbilical perforation is about one-tenth the width of the last whorl. The whorls of the protoconch are smooth. The following whorls are sculptured with strongly prosocline white axial ribs that are about a fourth the width of their interspaces. The ribs occur in clusters of 3–8 ribs that are separated by smooth zones of about the same width. The upper ends of the ribs are recurved forward and weakly crenulate the suture. On the last whorl the ribs end at the basal-peripheral angle. The aperture is slightly wider than high. It extends forward on a short neck for a distance of about one-fifth the width of the last whorl (Fig. 12F). The peristome is conspicuously expanded around the lower palatal, basal and columellar-parietal margins and is narrowest along the posterior angle and the upper

palatal margin. Measurements of the lectotype are: length, 19.4 mm; width, 2.93 mm; aperture height, 2.19 mm; aperture width, 2.26 mm; 20.2 whorls (MNHN 22003).

Two specimens in the Museum of Natural History, United Kingdom are from the DaCosta Collection, but lack other data. One has a broken apex. The second specimen is 16 mm in length and has 20.3 whorls.

Type locality.—Unknown. Lectotype here designated MNHN 22003, ex H. Cuming (Fig. 12E–F).

Distribution.—Unknown. This taxon has not been found since its original description.

***Epirobia alternans* Thompson 1976 new rank Figure 12G–H**

Epirobia swiftiana alternans Thompson 1976; Nautilus, 90: 41–43; figs. 1c–d, 2a. – Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 141.

Remarks.—Ten paratypes were x-rayed to determine the internal structure of the complete shell (Fig. 4G–H). None showed an apical plug.

Epirobia alternans differs from *E. swiftiana* in a number of ways. It is smaller sized even though it has the same number of whorls. Mature specimens are 13.0–14.2 mm long and have 19.5–20.5 whorls. The whorls are less inflated, and the suture is not as pronounced as it is in *E. swiftiana*. The axis is about 0.20–0.23 times the width of the shell. It is weakly concave in outline within each whorl and is sculptured with weak slightly oblique ribs bearing small spines and nodes that are irregularly sized and spaced. The base of the last whorl is narrowly perforate and has a weak sub-peripheral angle. The

aperture is obese pear-shaped and is slightly higher than wide. The peristome is narrowly expanded, more so along the columellar margin, and least so along the posterior corner and the palatal margin (Thompson 1978).

The differences between *Epirobia alternans* and *E. swiftiana* are sufficient to justify recognition of *E. alternans* as a distinct species. When I described *E. alternans* I had not had the opportunity to compare it with specimens of *E. swiftiana*, and I was influenced by their superficial similarity as depicted in the literature.

Type locality.—MÉXICO. Chiapas State: limestone ledge along a ravine 4.5 mi. [10.2 km] N of Jitotól, Chiapas, México; 5400 ft. alt. [1662 m]. Holotype: UF 22451. Paratypes: UF 22452/10; CNMO 3380/2.

Distribution.—MÉXICO: known only from the type locality (Fig. 2).

***Epirobia interrupta* n. sp.**

Figure 13A–C

Diagnosis.—A species resembling *Epirobia swiftiana* and *E. alternans* in size and the number of whorls, and in having non-decollate shells that lack an apical plug, and sculpture consists of whitish ribs arranged in clusters that are separated by smooth intervals. *Epirobia interrupta* differs from *E. swiftiana* by having less rounded whorls, by its more attenuated spire, by its sparser sculpture, by its narrower peristome, and the aperture projects forward not as much. *Epirobia interrupta* differs from *E. alternans* by its more attenuated spire, its less rounded whorls, its wider axis, its narrower peristome and by having the aperture not project forward as much. *Epirobia alternans* is smaller, is less robust and has a narrower axis.

Description.—The shell is light brown with irregular patches of white ribs. The interior of the aperture is rust colored. The peristome is white. The relatively slender shell is 17.7–21.1 mm long, and 3.1–3.5 mm wide. The shell is non-decollate. All live specimens examined retained a complete spire. Radiographs of seven paratypes showed the absence of an apical plug (Fig. 4I–J). Mature shells have 19.7–23.2 whorls. The shell is clavate

in shape. The last whorl is slightly narrower than the previous whorl. Usually the base is flattened and is bounded laterally by an obtuse angle. The umbilicus is narrowly open. The penultimate whorl is 0.29–0.45 times as high as wide. There are 3 smooth, button-shaped embryonic whorls. The first whorl is cap-shaped. The second whorl is slightly wider than the following whorl, causing the spire to be weakly concave in outline. The following whorls are moderately rounded with a moderately impressed suture. They bear white, low, rounded ribs that are separated by interspaces that are 1–2 times as wide as the ribs. The ribs occur in clusters of 2–6 ribs. The clusters are separated by intervals that are about equal to or greater than the width of the clusters. The ribs are posteriorly arched and are weakly recurved near the lower suture. The upper ends of the ribs may form a weak narrow sub-sutural cord that generally is broken and discontinuous. The aperture extends forward on a short neck that is about one-tenth as long as the width of the last whorls (Fig. 13B). Generally the neck is rounded, but may be flattened above. The aperture usually is higher than wide. It is broadly auriculate in shape with a slightly indented parietal margin. The peristome is broadly reflected; least so along the posterior corner and the palatal lip, and most so along the basal and columellar margins. The axis tapers uniformly to the penultimate whorl where it is 0.25–0.29 time the width of the shell (Figs. 4I, 13C). It bears close, weak, oblique broken ribs and lacks spiculate sculpture (Fig. 7C). The axis is slightly sigmoid within each whorl.

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

Type locality.—HONDURAS, Dept. Santa Barbara, Cerro Santa Barbara, Finca Las Quebradas, 3 km west of El Jarál, 14.643°N, 88.088°W, 1260 m alt. HOLOTYPE: UF 213271; collected 10 October, 1991 by Fred G. Thompson, Harry G. Lee, William Buchanin, and Eric Fernandez. PARATYPES: UF 426760/25; same data as the holotype.

Other specimens examined.—HONDURAS. Dept. Santa Barbara: 4.6 km WSW of El Jaral, 1430 m alt. (UF 213277/11; El Cielo, 14.928°N, 88.104°W, 1700 m alt. (UF 221000/27); 0.5 km

SW of Ocotillo, 15.951°N, 88.098°W, 2100 m alt. (UF 194550/1).

Distribution.—HONDURAS; known only from the immediate vicinity of the type locality (Fig. 3).

Habitat.—Live snails were collected on moss-covered limestone boulders in a densely shaded mountain rain forest.

Etymology.—The species name *interrupta* is from the Latin, meaning interrupted or intervals, alluding to the discontinuous intervals in the ribbed sculpture of the shell.

Species Provisionally Assigned to the *Epirobia swiftiana* Species Group

The following three taxa are assigned to the *Epirobia swiftiana* species-group with reservation. They have obese shells that are quite unlike the more slender shells of other species placed in *Epirobia*.

Epirobia gassiesi (Pfeiffer 1867)

Figure 13D–F

Cylindrella gassiesi Pfeiffer 1867; Jour. de Conchyl., 15: 438.- Fischer & Crosse 1873; Miss. Sci. Mex., I: 410; pl. 17, fig. 17 (shell).

Holospira (Epirobia) gassiesi (Pfeiffer). Von Martens 1897; Biol. Cent. Amer.: 283.

Epirobia gassiesi (Pfeiffer). Pilsbry 1902; Man. Conch., 15: 63; pl. 20, figs. 5–7 (shell). - Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 141.

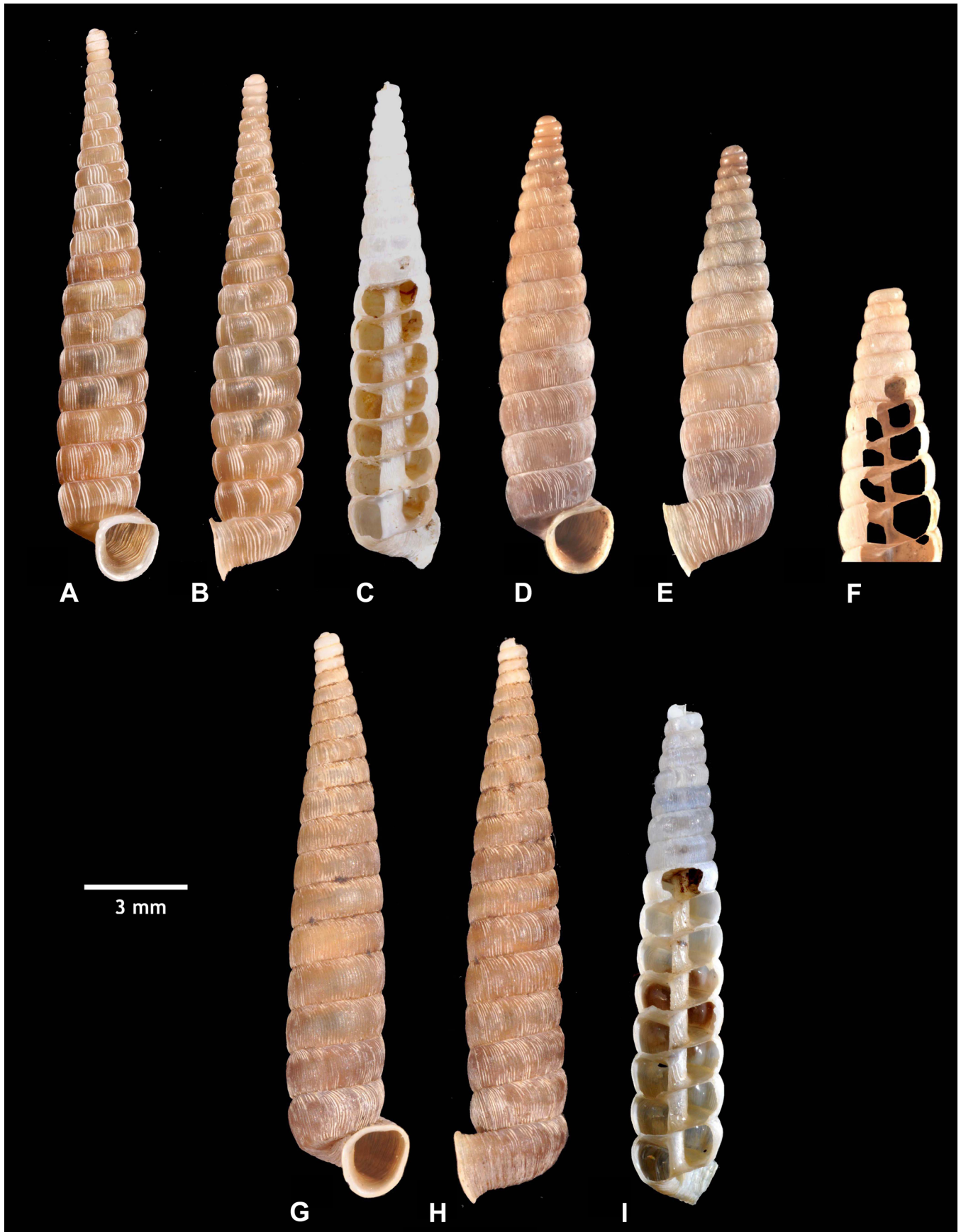
Diagnosis.—The shell is relatively stout, moderately large, and consists of about 14.6–16.4 whorls that are sculptured with fine sinuous thread-riblets. The aperture has a short neck. The umbilicus is rimate. The hollow axis is about one-tenth the width of the shell and is smooth.

Description.—The shell is cylindrical-conic in shape. The periostracum is light livid in color with numerous white thread-riblets on the teleoconch. The peristome is white. The relatively stout shell is 13.9–15.6 mm long, is 3.0–3.3 mm wide and is 0.21–0.23 times as wide as high. The shell is complete and without an apical plug. There are 14.6–16.4 whorls. The base of the last whorl is flattened and is bounded at the periphery with an obtuse angle. The protoconch consists of 1.5 smooth whorls. The apical whorl is noticeable more bulbous than the next whorl. The teleoconch sculpture consists of numerous fine thread-riblets that are weakly sinuous and are about as wide as their interspaces. The sculpture is interrupted with occasional smooth patches. The thread-riblets continue uninterrupted across the whorls and onto the base of the last whorl to the umbilicus.

Table 6. Measurements of shells of *Epirobia interrupta* n. sp. in mm based on the holotype and eight complete paratypes.

	Shell	SL	SW	AH	AW	Whorls
Holotype	C	20.9	3.4	2.7	2.5	22.1
Paratype	C	21.1	3.2	2.2	2.2	23.2
Paratype	C	20.0	3.3	2.2	2.4	22.8
Paratype	C	19.7	3.3	2.3	2.3	22.1
Paratype	C	18.5	3.4	2.5	2.4	21.3
Paratype	C	18.1	3.1	2.4	2.8	21.1
Paratype	C	17.9	3.3	---	---	21.7
Paratype	C	17.7	3.3	2.5	2.4	19.7
Paratype	C	17.7	3.3	2.3	2.4	20.2

Figure 13. Shells of three species of *Epirobia*. **A–C**, *Epirobia interrupta* n. sp. **A**, holotype (UF 213271). **B–C**, paratypes (UF 426760). **D–F**, *Epirobia gassiesi* (Pfeiffer 1867), referred (UF 190526). **G–I**, *Epirobia adusta* n. sp. **G–H**, holotype (UF 420658). **I**, paratype (UF 426826).



The umbilicus is narrowly rimate. The aperture is broadly elliptical in shape and is 0.37–0.40 times the width of the shell. It has a short neck that projects slightly beyond the preceding whorl (Fig. 13E). The top of the neck is flattened and the base is rounded. The peristome is narrowly reflected. It is narrowest at the posterior corner, and is slightly expanded at the baso-columellar angle. The axis is smooth, straight-sided and gradually increases in size to the last whorl where it is one-tenth the width of the whorl (Fig. 13F).

Measurements based on six specimens are given in Table 7.

Type locality.—“Chiapas”. One syntype was examined: MNHN 22005.

Specimens examined.—MÉXICO. Chiapas State: 17 km NW of Teopisca, 16.642° N, 92.538° W, 2290 m alt., leg. F. G. Thompson, 18 March, 1991 (UF 190526/8, CNMO 3376/3).

Distribution.—MÉXICO: known from one specific locality (Fig. 3).

Epirobia berendti berendti (Pfeiffer 1866)

Cylindrella berendti Pfeiffer 1866; Malak. Blätt., 8: 87.- Fischer & Crosse 1873; Miss. Sci. Mex., I: 409.

Epirobia berendti (Pfeiffer). Strebel & Pfeffer 1880: 86; pl. 14, fig. 18 (axis).- Pilsbry 1902; Man. Conch., 15: 61-62; pl. 20, figs. 1–3 (shell), fig. 4 (radula).

Holospira berendti (Pfeiffer). Von Martens 1897; Biol. Cent. Amer.: 281.

Type locality.—Toxpan [Tuxpán?], on the slope to Cerro Matlaguahuitl, near Cordova, Veracruz. [Cerro Matlaguahuitl, 19.083°N, 96.868° W, Municipio Atoyac, east of Córdoba].

This species was based on specimens collected by Auguste Sallé. Pfeiffer’s types of

this species were deposited in the Heinrich Dohrn Collection in the Stettin Museum, which was destroyed in the 1939–1945 war.

Distribution.—VERACRUZ: known only from the type locality (Fig. 2).

Remarks.—Strebel and Pfeffer (1880) reported on the radula. Pilsbry (1902) suggested that their account was based on a specimen of *Holospira goldfussi* (Menke 1847).

Epirobia berendti albida (Fischer & Crosse 1873)

Cylindrella berendti albida Fischer & Crosse 1873; Miss. Sci. Mex., I: 409.

Holospira berendti var. *albida* (Fischer & Crosse). Von Martens 1897; Biol. Cent. Amer.: 281.

Epirobia berendti albida (Fischer & Crosse). Strebel & Pfeffer 1880; Beitrag, IV: 86, 98; pl. 3, fig. 7 (shell).- Pilsbry 1902; Man. Conch., 15: 62. - Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Type locality.—Chiapas.

Distribution.—CHIAPAS: Tabasco (Strebel & Pfeffer 1880).

The *Epirobia adusta* Species Group

The group is distinct from other *Epirobia* by its large, robust shell that is uniformly dull brown and bears numerous close ribs that are interrupted occasionally by short smooth intervals. The shell is decollate. The group consists of a single known species found at higher elevations in the Dept. Yoro, Honduras.

Epirobia adusta n sp.

Figure 13G–I

Diagnosis.—The species differs from other *Epirobia* in its large, robust shell. The color is dull

Table 7. Measurements of shells of *Epirobia gassiesi* (Pfeiffer 1867) in mm based on six complete specimens (UF 190526).

	SL	SW	AH	AW	Whorls
UF190526	13.9	3.0	1.04	1.19	14.6
UF190526	13.9	3.1	1.24	1.19	14.9
UF190526	14.0	3.4	---	---	15.9
UF190526	14.6	3.1	1.19	1.16	15.4
UF190526	14.6	3.2	1.29	1.19	16.4
UF190526	15.6	3.3	1.16	1.22	15.4

tan. The shell is decollate; an apical plug forms at about 14–18 whorls above the aperture. The sculpture consists of coarse, dense, close ribs. The aperture is higher than wide. The axis is coarsely sculptured with oblique ribs that are slightly narrower than their interspaces.

Description.—The periostracum is lusterless dull brown in color. The interior of the aperture is light rust colored. The peristome is white. The adult shell may have an entire apex (Fig. 13G), or it may be decollate (Fig. 13I). About a third (25 of 82) of the mature shells examined had lost whorls above the apical plug. Non-decollate specimens are 17.2–19.1 mm long and have 18.6–20.9 whorls. Decollated specimens are 14.2–18.6 mm long. The apical plug is formed at 14.0–17.9 whorls above the aperture (Fig. 5G-H). The whorls are rounded with a deeply impressed suture. The periphery of the whorls lie at about a third of the distance below the upper suture. The penultimate whorl is 0.39–0.44 times as high as wide. The shell is cylindrical-conical in shape. The body whorl is slightly narrower than the penultimate whorl. The apex is slightly concave in outline. The base is rounded, but is demarcated along its outer margin by an obtuse angle. The umbilicus usually is rimate; occasional specimens may be narrowly perforate or imperforate. The protoconch is smooth, consisting of three whorls. The first whorl is low and cap-shaped. The following whorl is slightly enlarged and higher than the next whorl. The teleoconch

bears numerous posteriorly-arched coarse ribs that are about as wide as their interspaces. The ribs are less crowded on the upper whorls and become more crowded on the lower whorls where they are broken frequently. Occasional smooth spaces the width of 3–5 ribs interrupt the sculpture. The aperture projects forward on a short rounded neck that is about one-fifth to one-sixth the width of the last whorl (Fig. 13H). The aperture usually is higher than wide, and is broadly auriculate or pear-shaped, being weakly indented along the parietal margin. The peristome is not conspicuously thickened, but is moderately reflected, most so along the basocolumellar margin and least so along the posterior corner and palatal margin. The axis was examined in 4 specimens. It is 0.19–0.21 times the width of the shell. It is straight-sided within each whorl, and is almost uniformly equal in width in the spire (Figs. 5G, 13I). It is ornamented with relatively coarse, low, oblique ribs that are slightly narrower than their interspaces (Fig. 7F).

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

Type locality.—HONDURAS, Dept. Yoro, Montaña Macuzál, Finca Macuzál, 7.4 km by air WNW of Yorito, ca. 20 km by road from Yorito, 15.080° N, 87.353° W, 1782 m alt. Holotype: UF 420658; collected 8 April, 2008 by John D. Slapcinsky. Paratypes: UF 426826/81; same data as the holotype.

The type locality is in a closed-canopy

Table 8. Measurements on the shells of *Epirobia adusta* n. sp. in mm based on the holotype and nine complete paratypes.

	SL	SW	AH	AW	Whorls
Holotype	17.8	3.3	2.3	2.1	18.8
Paratype	20.3	3.1	2.5	2.2	20.9
Paratype	19.1	3.0	2.3	2.1	20.4
Paratype	18.8	3.2	2.3	2.1	20.0
Paratype	18.6	3.2	2.2	2.1	19.9
Paratype	18.5	3.2	2.2	2.1	19.8
Paratype	17.8	3.1	2.3	2.1	18.8
Paratype	17.7	3.3	2.3	2.2	18.6
Paratype	17.2	3.3	2.3	2.1	19/2
Paratype	17.2	3.1	2.2	2.2	18.7

mesic forest with limestone boulders and outcrops. Snails were on limestone rock surfaces, usually in depressions in the rock that accumulated leaf litter but not soil.

Distribution.—HONDURAS: known only from the type locality (Fig. 3).

Etymology.—The name *adusta* is from the Latin *adustus*, meaning tanned, brown or swarthy, alluding to the dull tan color of the shell.

Genus *Propilsbrya* Bartsch 1906

Propilsbrya Bartsch 1906; Bull. U. S. Nat. Mus., 31: 121.-Rehder 1940; Jour. Wash. Acad. Sci., 30: 315.-Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 135.-Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Type species.—*Epirobia* (*Propilsbrya*) *nelsoni* Bartsch 1906.

Included species.—*Propilsbrya potosiana* Pilsbry 1953

Diagnosis.—*Propilsbrya* has the basic anatomical structure of the family Epirobiidae. The spermathecal duct and the free oviduct unite to form a vagina above the genital atrium, The free oviduct is long and slender, and the penis bears a long diverticulum. The shell has an entire apex without an apical plug. The lower most two or three whorls have a bold smooth columellar lamella. A thin pectinate parietal lamella extends the entire length of the shell (*P. nelsoni*) or it may be restricted to the lower three whorls (*P. potosiana*).

Distribution.—MÉXICO. At higher altitudes in the states of Coahuila and Nuevo León.

Remarks.—*Propilsbrya* has long been confused with the subgenus *Holospira* (*Stalactella*) because of similar columellar and parietal lamellae (Bartsch 1906; Rehder 1940; Pilsbry 1956). The similarities are due to convergence (Thompson & Mihalcik 2005). The reproductive anatomy and radula place *Propilsbrya* in the Epirobiidae, in contrast with *Stalactella*, which is in the Holospiridae (see below).

Propilsbrya nelsoni (Bartsch 1906)

Epirobia (*Propilsbrya*) *nelsoni* Bartsch 1906; Bull. U. S. Nat. Mus., 31: 122–123; text-fig. 7; pl. 4, fig. 8.

Propilsbrya nelsoni (Bartsch). Rehder 1940; Jour. Wash. Acad. Sci., 30: 316.- Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 136; figs. 3-3b.- Thompson 2011;

Bull. Fla. Mus. Nat. Hist., 50: 140.

Shell.—The shell was adequately described and illustrated by Bartsch (1906) and Pilsbry (1953).

Reproductive anatomy.—The right ocular retractor muscle passes through the penis-oviducal angle (Figs. 14A–B). The genital atrium is relatively long, being about two-thirds the length of the penis. The penis is stout and muscular with a thick wall. It bears an almost equally robust diverticulum that is slightly longer than the penis. The penis and diverticulum bear four longitudinal muscular fold internally. The penis retractor muscle originates on the inner wall of the lung and inserts on the end of the diverticulum. The epiphallus is very slender, and is not distinctly demarcated from the vas deferens. The vas deferens forms a tightly coiled loop over the center of the coelomic cavity. The vagina is about as long as the atrium, and is slightly more ample. The free oviduct is long and slender and is about four times the length of the vagina. The spermathecal duct is very long. It is thick and muscular at its base for a distance about equal to the length of the free oviduct. Internally the base of the duct is thick and muscular and has several longitudinal muscular fold. Above this point it tapers to a narrow tube. The duct bears a slender, elongate appendix close to the spermatheca. The spermatheca is subglobose in shape. It is appressed against the base of the albumen gland, and the appendix is appressed on the dorsal surface of the gland. (ANSP 164212).

Type locality.—MÉXICO: Coahuila State, Sierra Guadalupe. Holotype USNM 187504.

Specimens examined.—COAHUILA: Sierra de Guadalupe; collected by H. A. Pilsbry, 4 August, 1934 (ANSP 164212/4, in ETOH).

Distribution.—MÉXICO: known only from the Sierra Guadalupe in Coahuila State (Fig. 2). In addition to the type locality Pilsbry (1953) recorded the species from 13 km back of the Hacienda Guadalupe, 7500–8500 ft. alt.

Propilsbrya potosiana Pilsbry 1953 Figure 15A–B

Propilsbrya (*Stalactella*) *potosiana* Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105:136–137; pl. 4, figs. 4, 4a,

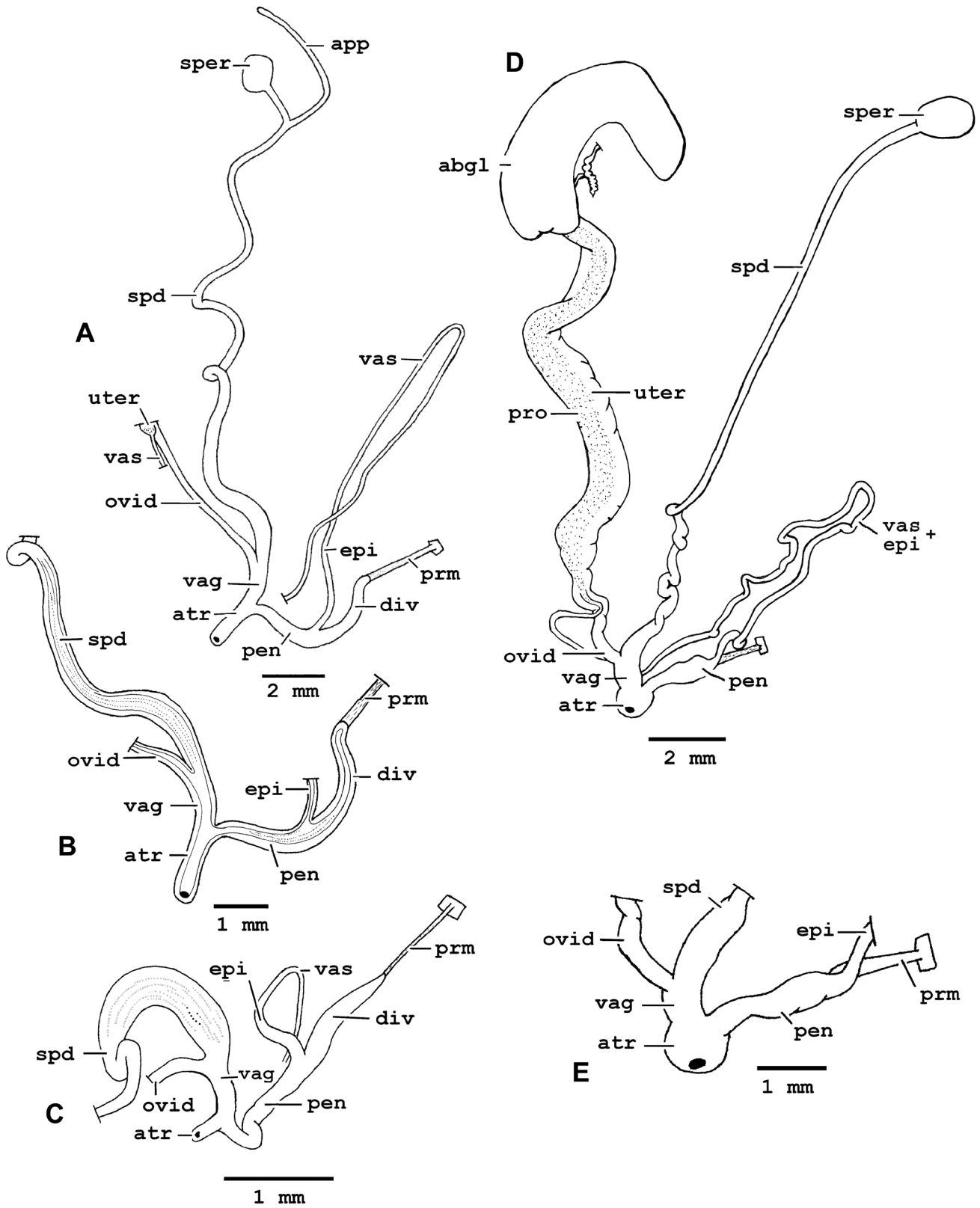


Figure 14. Reproductive anatomy of *Propilsbrya* and *Holospira*. **A–B**, *Propilsbrya nelsoni* (ANSP 164212). **C**, *Propilsbrya potosiana* (UF 198426). **D–E**, *Holospira goldfussi* (UF 270513). Abbreviations as in Fig. 8.

4b.- Correa-Sandoval & Salazar-Rodriguez 2005; Acta Zool. Mex. (n. s.), 21: 61.- Correa Sandoval, N. Strenth & M. C. Salazar-Rodriguez 2007; Acta Zool. Mex. (n. s.), 23: 160.- Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Reproductive anatomy (Fig. 14C).—Dissections were based on three poorly preserved specimens (UF 198426). Aspects of the albumen gland and the uterus-prostate could not be determined completely.

The genital atrium is moderately long and stout. The penis is flexed just above its entrance into the atrium and is stout above this point to the origin of the epiphallus. The penis extends beyond this point as a stout, tapered diverticulum that is about as long as the penis. The penis retractor muscle inserts on the end of the diverticulum and is attached to the inner wall of the lung near the mantle collar. The epiphallus is short and rapidly tapers to

a slender vas deferens, which is short compared to other Epirobiidae. The vagina is relatively long. It is about half as long as and about as wide as the penis. The spermatheca is appressed against the prostate-uterus at the base of the albumen gland. The base of the spermathecal duct is greatly enlarged and muscular. The duct bears an appendix just below the spermatheca (not illustrated).

Type locality.—MÉXICO: Nuevo León State, Cerro Potosí, near Galeana, on boulders in pine forest; 10,500 ft. alt. (3230 m). Holotype ANSP 164586a (Baker 1963).

Specimens examined.—NUEVO LEÓN. Cerro Potosí, pine forest, 24.891° N, 100.227° W, 3100 m alt. (UF 374121/4); Cerro Potosí, NE slope 12 km NW of 18 de Marzo, 24°53'08" N, 100°12'38" W, 2810 m alt. (UF 226425/11); Cerro Potosí, area covered with scrub *Quercus* surrounded by *Pinus*,

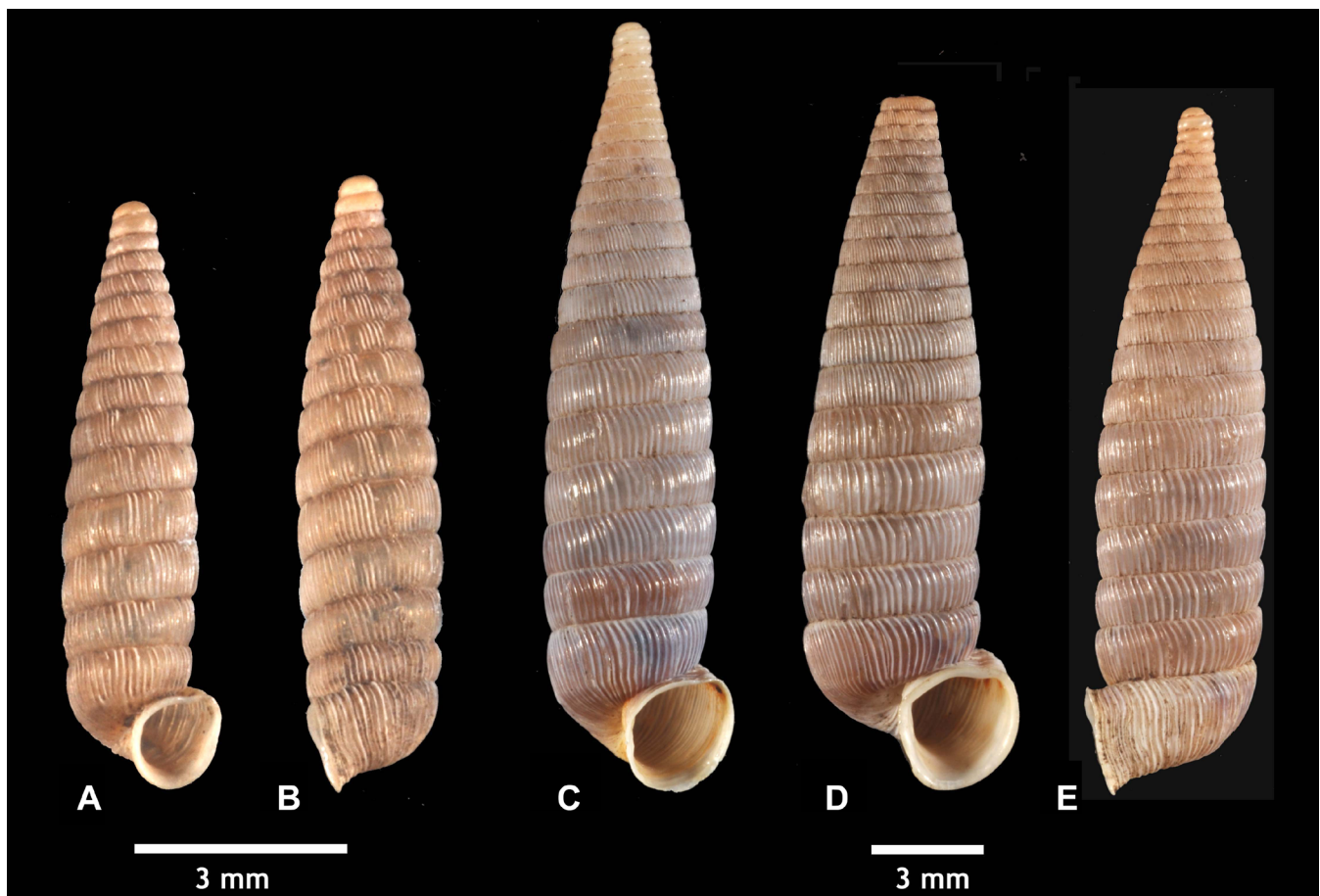


Figure 15. Shells of *Propilsbrya* and *Pectinistemma*. A–B, *Propilsbrya potosiana* Pilsbry 1953, referred (UF 34296). C–E, *Pectinistemma koestneri* (Rehder 1940), referred (UF 180516).

3 km by rd. below microwave tower, 3380 m alt. (UF 34296/42; CNMO 3374/5; UF 198426/5, in ETOH).

Distribution.—NUEVO LEÓN: known only from the immediate vicinity of the type locality (Fig. 2).

Genus *Pectinistemma* Rehder 1940

Propilsbrya (*Pectinistemma*) Rehder 1940; Jour. Wash. Acad. Sci., 30: 315.- Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 135.

Pectinistemma Rehder. Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 141.

Type species.—*Propilsbrya* (*Pectinistemma*) *koestneri* Rehder 1940.

Included species.—*Pectinistemma infernilla* (Pilsbry 1953), *Pectinistemma ceramicum* n. sp., *Pectinistemma roesslingi* n. sp., and *Pectinistemma gracilidens* n. sp.

Diagnosis.—*Pectinistemma* is characterized by having the columellar lamella extend throughout the length of the shell in juveniles as well as adults. A parietal lamella occurs in the lower whorls of the adult shell. Both lamellae are serrated with forward-directed denticles. The shell has an apical plug formed at about 16–18 whorls above the aperture. *Pectinistemma* is here accorded generic status from *Propilsbrya* because of the differences in the internal columellar lamella. In *Propilsbrya* the columellar lamella is smooth.

Distribution.—*Pectinistemma* includes two previously described species, *P. koestneri* (Rehder 1940), and *P. infernilla* (Pilsbry 1953), which are known from high altitudes on Cerro Potosí and Cerro Infiernillo in the state of Nuevo León. Two new species are described from extreme southeastern Nuevo León, and another new species is described from an immediately close locality in Tamaulipas (Fig. 2).

Pectinistemma koestneri (Rehder 1940)

Figure 15C–E

Propilsbrya (*Pectinistemma*) *koestneri* Rehder 1940; Jour. Wash. Acad. Sci., 30: 316; figs. 1–3.- Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 137–138; pl. 4, figs. 1, 1a.- Correa-Sandoval & Salazar-Rodríguez 2005; Acta Zool. Mex. (n. s.), 21: 61.- Correa Sandoval, N. Strenth & M. C. Salazar-Rodríguez 2007; Acta Zool.

Mex. (n. s.), 23: 160.

Pectinistemma koestneri (Rehder). Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 141.

Shell.—An apical plug is formed at about 16–18 whorls above the aperture. The adult shell may be entire or decollate.

Reproductive anatomy.—Three specimens were dissected (UF 194617). The right ocular retractor muscle passes through the penis-oviducal angle and inserts on the right pedal retractor (Fig. 8C). The penis retractor muscle originates on the inner wall of the lung immediately behind the mantle collar and inserts on the apex of the penis diverticulum. The genital atrium is short and broad. The penis is long and robust. The penis ends in a long, stout blind diverticulum that is shorter than the length of the penis below the epiphallus. A moderately long and thick-walled epiphallus enters the penis at the base of the diverticulum. The vas deferens is very long and is compactly coiled over the nape behind the mantle collar. It tapers to the genital atrium and becomes very narrow to the prostate. The vagina is short, stout and thin-walled. The spermatheca is large and elongate. It is appressed against the oviduct at the base of the albumen gland. The spermathecal duct is very long. The base of the duct is thick-walled and is as long and stouter than the penis. The thick portion is about as long as the free oviduct. The spermathecal duct narrows above the enlarged basal portion. Near its distal end the duct bears a very long appendix that forms a flattened sigmoid coil where it rests against the prostate-uterus. The free oviduct is long and stout.

Radula.—Radular formula: 26–1–26. The transverse rows of teeth are straight in the middle field and at the marginals the rows curve upward slightly (Fig. 9A). The central tooth is slightly recessed below the laterals. It is as wide as the laterals and is tri-cuspid. The mesocone is long and acuminate and is bordered on each side near its base by a short acuminate ectocone. The following 7 lateral teeth are bicuspid with a large acuminate mesocone and a small ectocone. The marginal teeth bear a mesocone and a smaller ectocone. On the outer 10 marginals there is an ectocone and an entocone.

Type locality.—MÉXICO: Nuevo León State, Cerro Potosí, Galeana. Holotype USNM 535762.

Specimens examined.—NUEVO LEON: Cerro Potosí, 0.9 mi. [1.5 km] by rd. below microwave tower; 11,300 ft. [3475 m] alt. (UF 180516/43). Cerro Potosí, 2.1 mi. [3.5 km] by road below the microwave tower; 11,000 ft. [3385 m] alt. (UF 180517/40, CNMO 3375/6; UF 194617/7, in ETOH). Cerro Potosí, 1.3 mi. [2.2 km] by rd. below microwave tower; 11,200 ft. [3345 m] alt. (UF 180518/4). NE slope of Cerro Potosí, 15 km W of 18 de Marzo; 3100 m alt. (UF 226432/8). Cerro Potosí, pine forest (24°53'29" N, 100°13'38" W (UF 374122/1 in ETOH).

Distribution.—MÉXICO. Nuevo León State, known only from Cerro Potosí (Fig. 2).

Pectinistemma ceramicum n. sp.

Figure 16A–D

Diagnosis.—A moderately large species with a conical-cylindrical shell that has a weakly concave spire. The background color is bluish-gray with bold white ribs. The shell is about 16–18.5 mm long and has about 18–21 whorls that are sculptured with strong oblique ribs. The obovate-shaped aperture is free from the previous whorl but barely projects forward. The hollow axis bears a denticulate columellar lamella in the lower 4–5 whorls. A smooth parietal lamella may be present or absent. The species is 15.3–18.3 mm long, 4.6–5.1 mm wide, and has 18.4–21.4 whorls.

The bluish-gray ground color of *Pectinistemma ceramicum* has the appearance of fresh clay, which contrasts with the white ribs. The general appearance of the shell is reminiscent of a large *Microceramus* (Urocoptidae). *Microceramus* is readily recognized by its solid shell axis, as well as having an incomplete peristome that is interrupted across the parietal margin.

Shell.—The shell is conical-cylindrical in shape. The conical part of the shell is attenuated and is weakly concave in outline near and below the apex. The lower 3–4 whorls tend to become cylindrical. The shell is bluish-gray in color with bold white ribs. The peristome is white and the

interior of the aperture is rust colored. The shell is moderately large, about 15–18 mm long, and about 0.26–0.32 times as wide as high. The entire shell contains 18.3–21.4 whorls. Normally the shell is entire, although the apical 2–5 whorls are dead and they may be lost (Fig. 16C–D). An apical plug is formed below this point (Fig. 16D, AP). The protoconch consists of two smooth opaque gray whorls. The second whorl is higher and wider than the first and the following whorl. The spire and cylindrical parts of the shell are sculptured with slightly oblique weakly recurved ribs that are almost as wide as their interspaces. There are 49–76 ribs on the penultimate whorl. The ribs are slightly wider at the top and the bottom along the sutures. They become diminished on the base near the umbilicus. The base of the last whorl is rounded. The umbilicus may be rimate or openly perforate. The aperture is obovate in shape and barely projects forward beyond the preceding whorl (Fig. 16B). It is about as wide as high, and about 0.59–0.65 as wide as the preceding whorl. The peristome is free from the preceding whorl and is relatively thick and slightly reflected. The axis is hollow, is widest along the lower whorls of the spire and becomes narrower below (Fig. 16D). It is 0.24–0.27 times as wide as the shell in the penultimate whorl. A columellar lamella is present in the lower 4–5 whorls. The lamella bears long forward-pointed denticles which are most strongly developed in the penultimate and ante-penultimate whorls and rapidly diminish above. A very weak, smooth, parietal lamella may be present or absent in the ante-penultimate whorl. It was present in two specimens of five that were opened.

Measurements of the holotype and ten paratypes selected to show variation are given in Table 9.

Type locality.—MÉXICO: Nuevo León State, Cerro Peña Nevada, an open oak forest on a limestone talus slope, 3 km southwest of La Encantada (23.9214° N, 99.805° W), 2520 m alt. Holotype: UF 226379; collected 17 July, 1994 by Fred G. Thompson, Elizabeth L. Mihalcik and Val J. Roessling. Paratype: UF 434306/45, CNMO 3382/8; same data as the holotype. UF

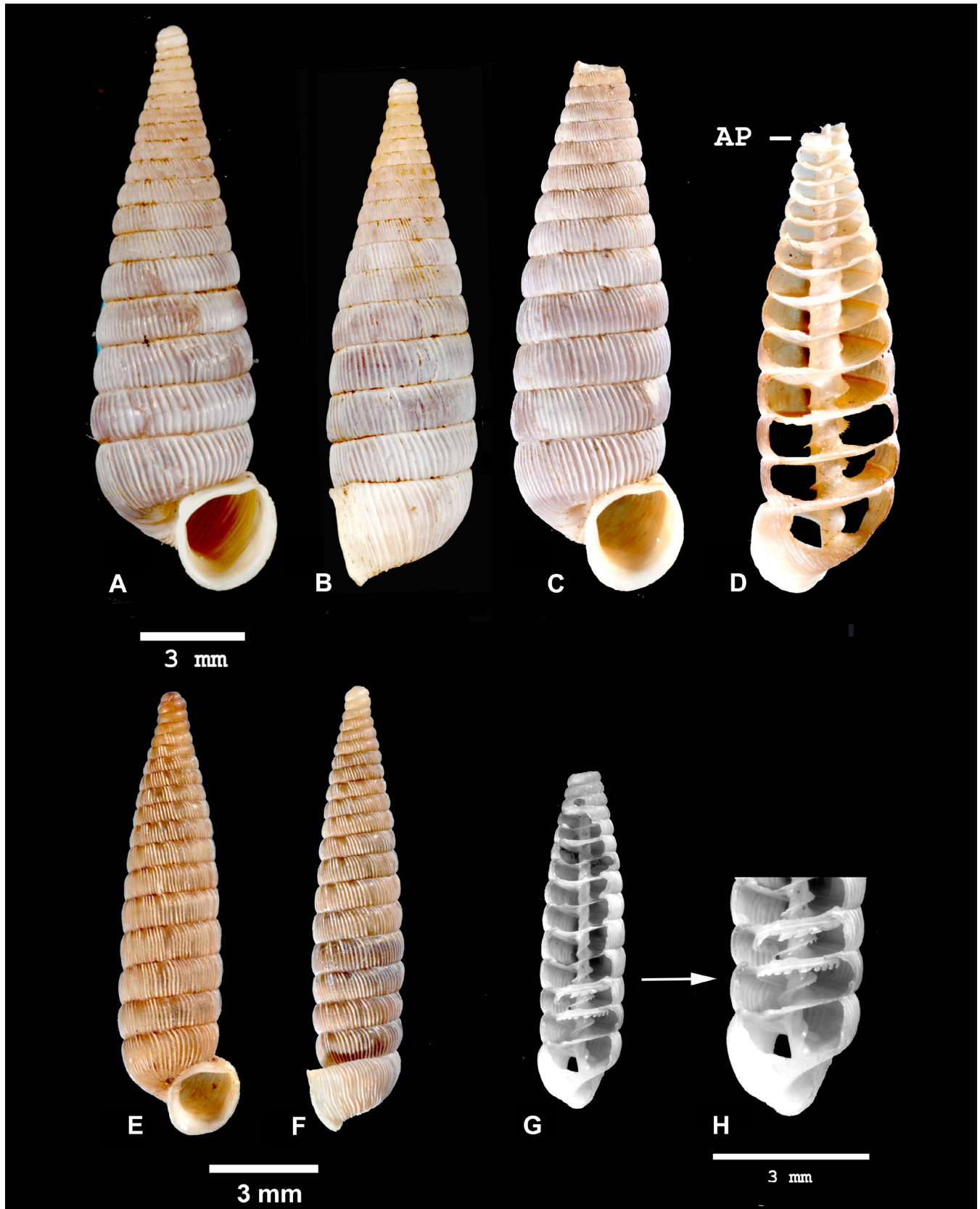


Figure 16. *Pectinistemma ceramicum* n. sp. **A**, holotype (UF 226379). **B–D**, paratypes (UF 434306). *Pectinistemma roesslingi* n. sp. **E–F**, holotype (UF 226415). **G–H**, paratype (UF 267249).

Table 9. Measurements on the shells of *Pectinistemma ceramicum* n. sp. The holotype and ten paratypes (UF 434306) were selected to show variation.

	SL	SW	AH	AW	Whorls	Ribs	SW/SL	AW/SW
Holo.	16.9	5.0	3.2	3.2	18.7	59	0.30	0.64
Para.								
Max.	18.3	5.1	3.2	3.2	21.4	76	0.32	0.65
Min.	15.3	4.6	2.9	2.9	18.3	49	0.27	0.59
Mean	16.7	4.86	3.12	3.07	19.45	64.6	0.29	0.62
SD	0.81	0.19	0.09	0.10	1.20	7.58	0.02	0.02

218723/2; same locality as the holotype; collected 1 September, 1993 by Val J. Roessling.

The species was found in a mesic *Pinus-Quercus* forest among limestone boulders and outcrops where they were exposed, but dormant, among mosses. There appears to be a high rate of predation, judging from the repaired shell fractures seen among most of the specimens examined.

Other specimens examined.—Type locality; preserved specimens in ETOH: UF 219211/6, UF 2226586, UF 226178/15,

Distribution.—MÉXICO. Known only from the type locality (Fig. 2).

Etymology.—The species name *ceramicum* is from the Classical Greek, κεράμικος, earthen. The name alludes to the clay-like coloration of the shell.

***Pectinistemma roesslingi* n. sp.**

Figure 16E–H

Diagnosis.—This species is similar in size and appearance to *Pectinistemma infernilla*. It differs by being smaller, with fewer whorls, and having a longer tapered apex. The shell is sculptured with 51–62 close ribs that have smooth patches below the upper suture. The parietal lamella is shorter. The serrate portions of the columellar and parietal lamella are shorter, and the denticles on the parietal lamella are more pronounced. This species differs from *Pectinistemma infernilla* by its smaller size and having fewer whorls. The shell is sculptured with closer ribs that have smooth patches below the upper suture, and the parietal lamella bears elongate denticles, not blade-like serrations. The

latter species is 12–17 mm long, 3.2–3.7 mm wide, and has 18–24 whorls.

Shell.—The shell is 10.4–13.2 mm long; slender, and 0.23–0.26 times as wide as long. It is conical-cylindric in shape with a elongate tapered spire that increases in diameter to about the last 4–5 whorls. The sides of spire are slightly convex below the second whorl. The background color is light lilac-brown crossed by white ribs. The apical two whorls are light gray. The peristome is white. The shell has 17.7–20.6 whorls that are separated by a moderately deep suture and are moderately arched. The protoconch consists of 2 whorls. The first whorl is slightly enlarged in height and wider than the following whorl. The base of the last whorl is rounded. The umbilicus is rimate or narrowly perforate. The neck of the last whorl extends forward slightly (Fig 16F). It is flattened or indented above and forms a blunt angle along the posterior corner. The aperture is about as wide as high, and is about 0.54–0.71 times the shell width. The aperture is free from the preceding whorl, and is slightly oblique. The peristome is moderately thick and slightly reflected. The outer lip project forward below the posterior corner. The protoconch is smooth. The teleoconch whorls are sculptured with prominent white ribs that arch forward at the upper ends and are about as wide as their interspaces. There are 51–62 ribs on the penultimate whorl. The ribs are complete across the surface of the shell, except along the smooth patches that are 4–6 ribs wide. The patches are formed rather uniformly below the upper suture primarily along the upper half of the whorls and are separated by about 5–10

ribs. The ribs are continuous across the base and neck of the last whorl where they become lamella-like. The hollow axis is about a fifth the width of the shell (Fig. 16G–H). It slowly increases in width in the lower 7–8 whorls. Above this point in the preceding 5–5 whorls the axis is noticeably wider. The axis is noticeably twisted within each whorl. A columellar lamella is located on the middle of the axis in the lower 6–7 whorls. It extends to the last half whorl but is not visible within the aperture. In the preceding two whorls it has narrow forward-directed denticles. Above this point the lamella is low and forms a narrow crest accentuating the twisted axis. There is a thin parietal lamella in the penultimate and anti-penultimate whorls. The lamella bears forward directed blade-like serrations that are larger and wider than the denticles on the columellar lamella.

Measurements based on the holotype and eleven paratypes are given in Table 10. The species is known only from shell specimens.

Type locality.—MÉXICO, Nuevo León State, Cerro Peña Nevada, 1 km north of El Refugio, ca. 19 km south-southeast of Zaragoza (23.9208° N, 99.7194° W), 2350 m alt. Holotype: UF 226415; collected 18 July, 1994 by Fred G. Thompson and Elizabeth L. Mihalcik. Paratypes: UF 267249/18, CNMO 3383/3; same locality as the holotype; collected 18 January, 1994 by Val J. Roessling

Other specimens examined.—MÉXICO. Nuevo Leon State: Cerro Peña Nevada, 1 km S of La Encantada (23.8967° N, 99.7994° W, 2860 m alt. (UF 226371/4, UF 226372/1). A north-south ridge

1.6 km N of El Refugio, ca. 18 km S of Zaragoza (UF 258408/1). Tamaulipas State: road to Nuevo León past Valle Hermoso (23.702° N, 99.827° W), 2737 m alt. (UF 384000, UF 384001, UF 388531, UF 388549).

Distribution.—MÉXICO. Known only from the vicinity of the type locality in Nuevo León State, and from a nearby locality in Tamaulipas State (Fig. 2).

Etymology.—I take pleasure in naming this species after Val J. Roessling, for his assistance with field work on this project.

Pectinistemma infernilla (Pilsbry 1953)

Propilsbrya (*Pectinistemma*) *infernilla* Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 138–139; pl. 4, figs. 2–2c, 6.

Pectinistemma infernilla (Pilsbry). Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 141.

Type locality.—MÉXICO. Nuevo León State, summit of Cerro Infernilla, a mountain above Pablilla, at 10,000 feet [3077 m] elevation. Holotype ANSP 164148a (Baker 1963).

Distribution.—MÉXICO. Nuevo León State; known from several localities on the trail from Pablillo to the summit of Cerro Infernilla (Fig. 2; Pilsbry 1953).

Pectinistemma gracilidens n. sp.

Figure 17A–D

Diagnosis.—The shell is small, 12.6–13.0 mm long, conical-cylindrical in shape with a well-defined robust cylindrical spire, and it has 18.1–19.5 whorls. The shell is light brown with a non-decollated grayish-white apex and last half

Table 10. Measurements on the shells of *Pectinistemma roesslingi* n. sp. The holotype and ten paratypes (UF 267249) were selected to show variation.

	SL	SW	AH	AW	Whorls	Ribs	SW/SL	AW/SW
Holo.	12.1	2.9	1.96	2.03	18.3	61	0.24	0.70
Para.								
Max.	13.2	2.9	1.96	2.03	20.6	62	0.26	0.75
Min.	10.4	2.7	1.68	1.75	17.7	54	0.23	0.65
Mean	11.44	2.77	1.79	1.91	18.75	58.4	0.24	0.69
SD	0.69	0.08	0.11	0.10	0.86	3.30	0.12	0.03

of the body whorl. The moderately arched whorls are sculptured with 68–78 fine ribs that are about half as wide as their interspaces. The sculpture is continuous across the whorls and is not disrupted by smooth patches. The large hollow axis is slightly enlarged in the whorls of the conical apex. In the lower whorls it bears a columellar lamella that is weakly serrate with slender forward-directed denticles. A thin parietal lamella is confined to the lower 3 whorls. It bears 7–8 long, slender nearly horizontal denticles in the penultimate whorl and in the ante-penultimate whorl.

Shell.—The shell is 12.6–13.0 mm long, and is 3.0–3.1 mm wide; 0.24 times as wide as high. It is slender, and conical-cylindric in shape with an elongate tapered spire that is slightly concave in outline between the first and sixth whorls. The shell has 18.1–19.5 whorls. The apex is entire, but the first two whorls are dead causing those whorls

to appear nearly white. The whorls are uniformly arched between a moderately impressed suture. The protoconch consists of 2.5 whorls. The first whorl is slightly enlarged in height and wider than the following whorl. The conical apex increases in size to the twelfth or thirteenth whorl. The ground color is light brown with a grayish-white apex and the last half of the body whorl. The apical 2.5 whorls are light gray. The peristome is white. The base of the last whorl is rounded. The umbilicus is rimate or narrowly perforated. The neck of the last whorl extends forward slightly (Fig. 17A–B). It is indented above and forms a blunt angle at the posterior corner. The aperture is about as wide as high and is about 0.60–0.70 times the shell width. The aperture is free from the preceding whorl, and is slightly oblique in lateral profile (Fig. 17A–B). The peristome is moderately thick and slightly reflected. The protoconch is smooth. The teleoconch whorls

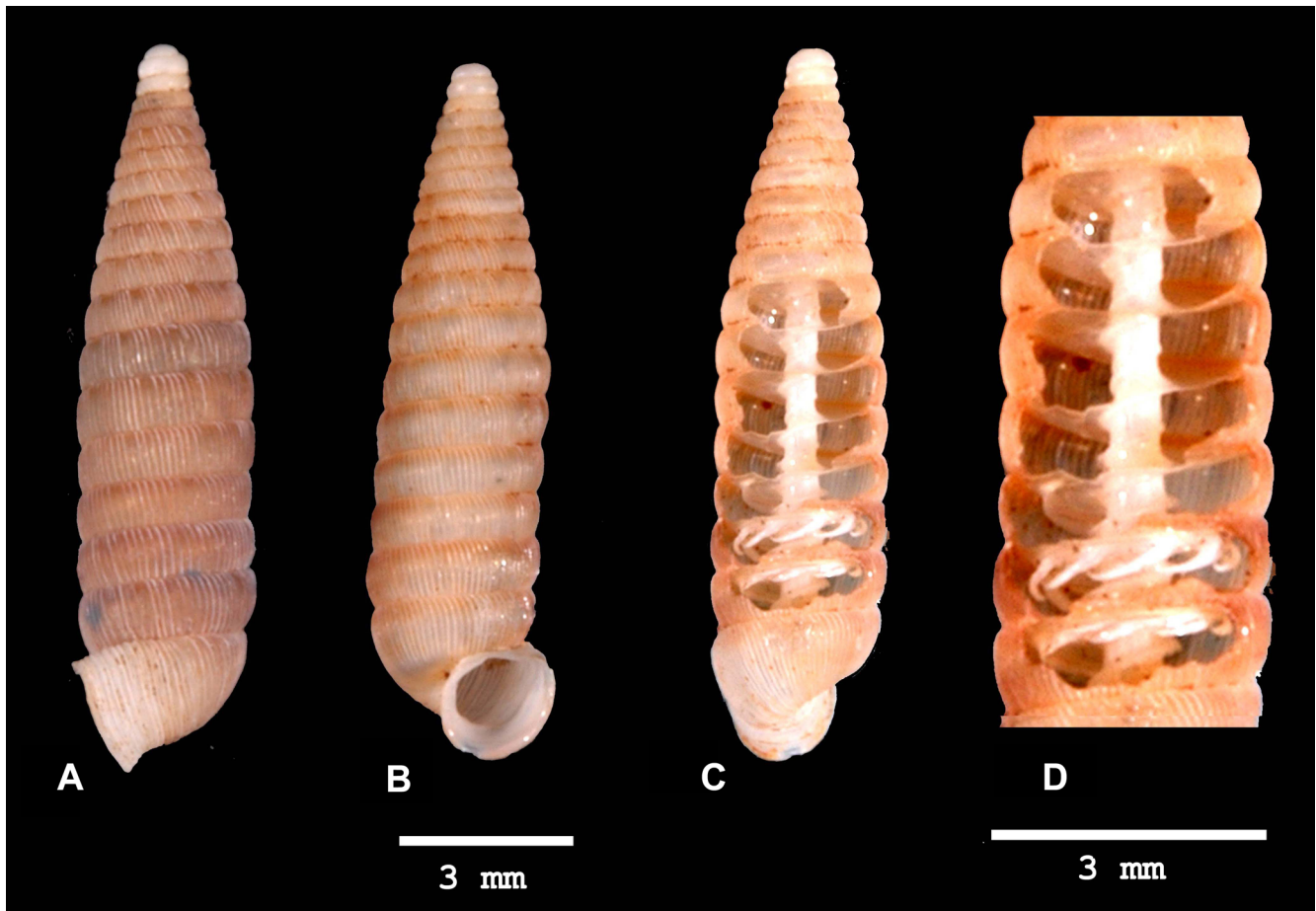


Figure 17. *Pectinistemma gracilidens* n. sp. A–B, holotype (UF 388545). C–D, paratype (UF 435172).

are sculptured with numerous fine ribs that arch forward at the upper ends and are slightly narrower than their interspaces. There are 68–78 ribs on the penultimate whorl. The ribs are only slightly lighter colored than the shell background. The ribs are complete across the surface of the shell and are not interrupted by smooth intermittent patches. The ribs are continuous across the base of the last whorl and extend onto the upper side of the neck where they become thin and lamella-like. The axis is hollow, and is about a fifth the width of the shell (Fig. 17C–D). It is nearly uniform in width in the lower 7–8 whorls. Above this point in the preceding conical whorls the axis is noticeably wider. The axis is nearly straight-sided within each whorl. A columellar lamella is located slightly above the middle of the axis within each whorl and extends the length of the shell and extends to the last half whorl, but is not visible within the aperture. In the lower whorls it has fine, narrow, forward-directed denticles which are obsolete further up the spire. There is a thin parietal lamella in the penultimate and ante-penultimate whorls (Fig. 17C–D). The lamella bears large, forward-directed, nearly horizontal, lanceolate denticles. There are 7–8 denticles per whorl.

Measurements in mm of the holotype and four paratype are given in Table 11.

Type locality.—MÉXICO. Tamaulipas State, Municipio Miquihuana, 3 km past intersection of road to Valle Hermoso and to Nuevo León, 23.702° N, 99.827° W; 2735 m alt. Holotype: UF 388545; collected 21 February, 2006 by Alfonso Correa-Sandoval. Paratypes: UF 435172/6, CNMO 3370/2; same data as the holotype.

Distribution.—MÉXICO. Tamaulipas State; known only from the type locality (Fig. 2). This is the same as the type locality for *Hendersoniella miquihuanae* Thompson and Correa-Sandoval 2011.

Remarks.—*Pectinistemma gracilidens* resembles *P. infernilla* and *P. roesslingi* in general appearance and size. It differs from *P. infernilla* by having on the parietal lamella large, sparse, needle-like denticles that are nearly horizontal in alignment, and the dentate portion of the lamella is confined to the penultimate and ante-penultimate whorls. In *P. infernilla* the denticles are more numerous, they are shorter, and they are nearly erect. *Pectinistemma roesslingi* is less robust with a more attenuated spire (Fig. 16E–F), and it has coarser ribs on the teleoconch. The ribs are white and are disrupted by intermittent smooth patches. The parietal lamella has fine serrate denticles. Superficially, *P. gracilidens* resembles a miniature *P. koestneri* in general appearance, but the latter species differs by its much finer denticles on the parietal lamella as well as its greater size.

Etymology.—The species name *gracilidens* is from the Latin, *gracilis*, slender, and *dens*, a tooth. The name alludes to the long slender teeth aligning the parietal lamella.

Genus *Gyrocion* Pilsbry 1904

Epirobia (*Gyrocion*) Pilsbry 1904; Proc. Acad. Nat. Sci. Phila., 55: 765.- Pilsbry 1953; Proc. Acad. Nat. Sci., Phila., 105: 135.- Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Type species.—*Epirobia* (*Gyrocion*) *mirabilis* Pilsbry 1904).

Remarks.—The status and affinities of

Table 11. Measurements on the shells of the holotype (UF 388545) and four paratypes (UF 435172) of *Pectinistemma gracilidens* n. sp. in mm.

	SL	SW	AH	AW	Whorls	Ribs
Holotype	13.0	3.1	1.8	2.0	18.1	75
Paratype	16.6	3.0	1.8	1.8	19.5	70
Paratype	12.7	3.0	1.8	1.9	19.0	78
Paratype	12.7	3.0	2.0	2.1	18.5	67
Paratype	12.8	3.0	1.8	1.8	19.3	78

Gyrocion are uncertain. The type species is known from two fragments, a juvenile shell consisting of 17 whorls and a segment of 5.5 whorls from the cylindrical portions of another shell. The juvenile shell is similar to that of *Propilsbrya*. The first two whorls are slightly enlarged and button-like. The following whorl is narrower and lower. The subsequent whorls rather rapidly expand producing a concave spire on the earlier whorls. The juvenile shell has a basal lamella in the lower whorls of the tapered apex. The shell attains a diameter of about 2.5 mm (Pilsbry 1904).

Gyrocion was formerly treated as a subgenus of *Epirobia*. I think it is unlikely that a congeneric relationship exists because of the wide geographic gap between the two genera, and the presence of a basal lamella in the early whorls and the shorter concave spire of *Gyrocion* support this interpretation.

***Gyrocion mirabilis* (Pilsbry 1904)**

Epirobia (Gyrocion) mirabilis Pilsbry 1904; Proc. Acad. Nat. Sci. Phila., 55: 765–766; pl. 1, figs. 10, 10a. - Correa Sandoval, N. Strenth & M. C. Salazar-Rodriguez 2007; Acta Zool. Mex. (n. s.), 23: 160.- Thompson 2011; Bull. Fla. Mus. Nat. Hist., 50: 140.

Type locality.—MÉXICO. Nuevo León State, Diente, near Monterey. Lectotype: ANSP 85914a (Baker 1963).

Genus *Prionolopax* Pilsbry 1953

Prionolopax Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 140.

Type species.—*Holospira (Prionolopax) odontoplax* Pilsbry 1953.

Distribution.—Southern Coahuila.

Taxonomy.—One species.

Remarks.—*Prionolopax* may belong to the epirobiid group of genera. It has three lamella confined to the lower four whorls, much like *Holospiridae*, but its apical whorls form an extended spire as with epirobiids, and not a dome as in most *holospirids*. The parietal lamella is serrate or toothed, resembling some *Pectinistemma*.

***Prionolopax odontoplax* (Pilsbry 1953)**

Holospira (Prionolopax) odontoplax Pilsbry 1953; Proc.

Acad. Nat. Sci. Phila., 105: 141; pl. 3, fig. 2.

Type locality.—MÉXICO. Coahuila, first mountain of the Sierra de Penitente on the right side of the road from Saltillo to Diamonte, at the highest pass; 7800–7900 feet alt. Holotype ANSP 164077.

Distribution.—COAHUILA: known only from the type locality.

TAXA INCORRECTLY ASSOCIATED WITH THE EPIROBIIDAE

The following species in the *Holospiridae* have been associated incorrectly with epirobiid genera.

***Coelostemma (Apertaxis) coahuilensis* (Bartsch 1906)**

Epirobia coahuilensis Bartsch 1906; Proc. U. S. Nat. Mus., 31: 121; pl. 4, fig. 2.

Coelostemma (Apertaxis) amplaxis Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 159–160; pl. 3, figs. 3–3b.- Thompson 1971; Bull. Fla. Mus. Nat. Hist., 15: 298–299, fig. 9b.

Coelostemma (Apertaxis) coahuilensis (Bartsch). Thompson & Mihalcik 2011; Archiv für Molluskenkunde, 140: 251.

Type localities.—*Epirobia coahuilensis*: Sierra Guadalupe, Coahuila. Holotype USNM 187505. *Coelostemma (Apertaxis) amplaxis*: Sierra Guadalupe back of the Hacienda Guadalupe, Coahuila; 7500–8000 ft. alt. Holotype ANSP 191189.

Distribution records.—COAHUILA: known only from the Sierra Guadalupe, Coahuila; 2250–2400 m alt.

***Holospira (Stalactella) rosei* Bartsch 1906**

Holospira (Stalactella) rosei Bartsch 1906; Proc. U. S. Nat. Mus., 31: 151–153; text-figs. 11–12; pl. 4, fig. 9.- Thompson & Mihalcik 2005; Bull. Fla. Mus. Nat. Hist., 43: 90–91; figs. 169–171.

Propilsbrya (Stalactella) rosei (Bartsch). Pilsbry 1953; Proc. Acad. Nat. Sci. Phila., 105: 135.

Type locality.—Tehuacán, Puebla. Holotype USNM 188181.

Distribution records.—PUEBLA: known only from the type locality.

Remarks.—Bartsch (1906) correctly associated the subgenus *Stalactella* with *Holospira*. Pilsbry (1953) treated *Stalactella* as a section of

Propilsbrya on the basis of similar columellar and parietal lamellae. Thompson and Mihalcik (2005) recognized *Stalactella* as a subgenus of *Holospira* on the basis of similar shell features. The anatomies of three species of *Stalactella* are described below. They resemble typical *Holospira* in structure. The anatomy of the type species of *Stalactella* (*H. (S.) rosei*) remains unknown, but there can be little doubt that it is essentially like the three species described here because of the strong conchological similarities among species of *Stalactella* and the close proximity of their geographic distributions. The anatomy of *Holospira (Holospira) haploplax* Thompson and Mihalcik 2005 and *Holospira (Holospira) goldfussi* (Menke 1847) are described below for comparisons.

COMPARISONS WITH OTHER FAMILIES OF UROCOPTOIDEA

Epirobiid snails have often been associated with two other families in the Urocoptoidea, the Holospiridae and the Eucalodiidae. The anatomies of these three families are reviewed for comparisons and differences.

ANATOMY OF THE HOLOSPIRIDAE PILSBRY 1946

The following summary is based on Pilsbry (1902): *Coelstemma elizabethae*, *Holospira nelsoni*, and *Metastoma roemeri*; Pilsbry (1946): *Holospira goldfussi*, and *Metastoma roemeri*; Thompson (1964): *Bostrichocentrum*; Gilbertson (1989a, 1993): *Allocoryphe*; Gilbertson (1989b, 2003): *Eudistemma*; Gilbertson (1993): *Eudistemma*, *Sonoraloa*; Gilbertson and Naranjo-Garcia (1998, 2004): *Millerspira*; Thompson and Correa Sandoval (1991): *Hendersoniella*; and Thompson and Mihalcik (2011): *Coelostemma*, *Apertaxis*, and *Goniapex*. New descriptions are provided below for *Stalactella* and *Holospira*.

Shell.—Medium sized, about 10–30 mm long. The apex is entire and dome-shaped. The protoconch consists of 2–3 whorls that protrude above the following whorl, but are shorter than the following whorl. The axis is hollow. The peristome is complete around the aperture, and is free from the preceding whorl. An internal barrier of lamellae

is present or is secondarily absent. The barrier is developed at definitive growth and is confined to the lower four whorls of the spire. The barrier consists of 1) an axial lamella, 2) a basal lamella, 3) a parietal lamella and 4) a palatal lamella, although one or more of these lamellae may be secondarily lost.

Pallial organs.—The kidney is sigmoid-rethrous. The aorta is simple and unbranched.

Jaw.—The jaw is solid and ribbed with 5–7 cusps.

Radula.—The radula is short and broad, 2 L/W. The teeth are arranged in nearly straight transverse rows. The central tooth is as wide as or is wider than the lateral teeth. It has a large, acuminate mesocone. The lateral teeth are subequal in size to the central tooth and bear an acuminate mesocone. The central and lateral teeth lack ectocones.

Retractor muscles.—Penis retractor originates on the inner wall of the lung and inserts on the apex of the penis at the base of the well-developed epiphallus. The right ocular retractor passes through the penis-oviducal angle to attach to the right pedal retractor. The right and left ocular retractors do not form a plate over the pharynx.

Reproductive anatomy.—The reproductive system has a short genital atrium. The penis varies from being short and bulbous to being long and slender. It lacks an internal stimulator (except *Millerspira*). The penis lacks an apical diverticulum (except in *Allocoryphae* and *Eudistemma*). The epiphallus is well developed, usually long and differentiated from the vas deferens. The vagina varies from being short or absent to moderately long and voluminous. The free oviduct is short and relatively stout. The spermatheca is oval or club-shaped. The spermathecal duct has a muscular enlargement near its base. An appendix is present or absent on the spermathecal duct; when present, it originates near the distal end of the duct below the spermatheca.

Evolution in the Holospiridae has occurred through the geographic isolation of colonies, and not through reproductive morphological specialization. Holospirid colonies may be extremely localized. Some species of *Coelostemma*

and *Holospira* are restricted to total distributions of only a few meters in extent (Thompson 1971, 1988; Thompson & Mihalcik 2005, 2011). The reproductive anatomy of *Holospira* does not show significant evolutionary diversity in a genus that has existed since the Upper Cretaceous (Tozer 1956). Clear anatomical distinctions between genera and subgenera are not pronounced in most cases. Exceptions are *Allocoryphe* (Gilbertson 1989a), *Eudistemma* (Gilbertson 1989b), *Eudistemma*, *Sonoraloa* (Gilbertson 1993), and *Millerspira* (Gilbertson & Naranjo-Garcia 1998, 2004).

The Holospiridae has significant variation in its reproductive system, but the anatomy of too few species have been studied for satisfactory phylogenetic analysis. The family includes fourteen genera and subgenera based on shell characters, which overshadow anatomical variation.

A brief characterization of the various genera and subgenera comprising the Holospiridae follows.

Holospira (Holospira) goldfussi (Müller 1847). The free oviduct is short and stocky. The spermathecal duct lacks an appendix. The spermathecal duct and the free oviduct unite to form a distinct stout vagina above the atrium. The penis is long and club-shaped. It lacks a diverticulum. The penis retractor muscle inserts on the apex of the penis at the base of the epiphallus (Strebel & Pfeffer 1880; Thompson this report).

In *Holospira (H.) nelsoni* Pilsbry 1902, *Holospira (Millerspira) milleri* Gilbertson 1989, and *H. (M.) hoffmani* Gilbertson & Naranjo-Garcia 1998, the free oviduct is very long and slender, the free oviduct and the spermathecal duct unite to form a short but distinct vagina above the atrium, The spermathecal duct has an appendix (*H. nelsoni*), or it may lack an appendix (*H. milleri*, *H. hoffmani*). The penis is short and begins at the distal end of the epiphallus. A diverticulum is absent. The penis retractor muscle attaches to the end of the penis at the base of the epiphallus (Pilsbry 1902; Gilbertson & Naranjo-Garcia 1998, 2004) or on the main section of the epiphallus (Gilbertson 1989).

Holospira (Stalactella) marmorata Thompson & Mihalcik 2005, *H. (S.) psectra* Thompson &

Mihalcik 2005 *H. (S.) cremnobates* Thompson & Mihalcik 2005, and *H. (S.) haploplax* Thompson & Mihalcik, 2005 all have a long or moderately long free oviduct, the free oviduct and the spermathecal duct remain separated to the atrium so that a vagina is not formed, the penis is short and ends at the epiphallus and the penis retractor muscle attaches to the penis at the base of the epiphallus (Thompson this report).

In *Metastoma roemeri* (Pfeiffer 1848), the spermathecal duct and the free oviduct are separated to the atrium. A vagina is absent. The spermathecal duct lacks an appendix. The penis is long and slender. A diverticulum is absent on the penis. The penis retractor muscle inserts on the apex of the penis at the base of the epiphallus (Pilsbry 1902).

Bostrichocentrum has a moderately long free oviduct. The spermathecal duct and the free oviduct remain separated to the atrium so that a vagina is not formed. The penis lacks a diverticulum and is very short. The penis retractor muscle attaches to the penis at the base of the epiphallus (Thompson 1964).

Hendersoniella lux Thompson & Correa-[Sandoval] 1991, has a long, slender free oviduct (incorrectly termed vagina in Thompson & Correa-[Sandoval] 1991). The spermathecal duct and the free oviduct remain separate to the atrium so that a vagina is not formed. The penis lacks a diverticulum. The penis is long and slender, and is weakly differentiated from the epiphallus. The penis retractor muscle inserts on the epiphallus.

Anatomical data are very limited for the large genus *Coelostemma*. The genus consists of 5 subgenera and includes 34 described species. The anatomy of *Coelostemma dalli* (Pilsbry 1902) was described by Pilsbry (1902). The anatomy of *Coelostemma costatum* Thompson & Mihalcik 2011, *C. gracilis* Thompson & Mihalcik 2011, *C. cordylum* Thompson & Mihalcik 2011, *C. (Aper-taxis) salpinx* Thompson & Mihalcik 2011 and of *C. (Goniapex) reiteri* Drake 1951 are reported elsewhere (Thompson & Mihalcik 2011.). The genus has a long free oviduct that remains separated from the spermathecal duct, so that a vagina is not formed above the atrium. The penis is moderately

long and slender. A penis diverticulum is absent. The penis retractor muscle inserts on the apex of the penis.

Holospira (Allocoryphe) minima Von Martens 1897, *Holospira (Eudistemma) sherbrookei* Gilbertson 1989, *H. (E.) arizonensis* Stearns 1890, *H. (E.) chiricahuana* Pilsbry 1905, *H. (E.) animasensis*, *H. (E.) metcalfi* and *H. (E.) danielsi* Pilsbry & Ferriss 1915 all have a long, slender free oviduct, the free oviduct and the spermathecal duct unite just above the atrium so that a vagina is hardly formed, the penis has a diverticulum above the entrance of the epiphallus, and the penis retractor muscle inserts on the end of the diverticulum (Gilbertson 1989a, 1989b, 1993, 2003). The retention of *Allocoryphe* and *Eudistemma* as subgenera of *Holospira* is untenable because of anatomical data. Rather, the data suggests that the two groups should be placed in the Cerionidae. However, until more is known about the anatomy of other holospirids, taxonomic changes at this point would cause more confusion than resolution.

Holospiridae is very conservative in reproductive anatomy. Reproductive structure specialization has not been a major evolutionary factor. The reproductive anatomies of *Stalactella*, *Bostrichocentrum* and *Coelostemma* are hardly distinguishable. However, further generic division within the Holospiridae will be necessary when more is known about the anatomy of its numerous species. The retention of a penis diverticulum in *Allocoryphe* and *Eudistemma* suggest a plesiomorphic position within the family. In *Holospira s. s.* the short, stout free oviduct and the formation of a distinct vagina through the union of the free oviduct and the spermathecal duct departs strikingly from other family members.

ANATOMICAL DESCRIPTIONS OF SPECIES OF *HOLOSPIRA (STALACTELLA)* BARTSCH 1906

Stalactella is confined to the Mexican states of Puebla and immediately adjacent north-eastern Oaxaca (Thompson & Mihalciik 2005). Bartsch (1906) treated *Stalactella* as a subgenus of *Holospira*. *Stalactella* is similar in some of its shell characteristics to *Propilsbrya*. Pilsbry (1953) treated *Stalactella* as a subgenus of *Propilsbrya*

on the basis that *P. potosiana* has an internal shell armature consisting of a smooth columellar lamella and a serrate parietal lamella similar of that of *Holospira (Stalactella) rosei*. This clearly is a case of convergence in shell traits. The anatomy of *Stalactella* is similar to members of the Holospiridae.

The shell of *Stalactella* has a smooth, stout columellar lamella and a serrate parietal lamella in the lower three whorls. The penultimate whorl is conspicuously shorter than the adjacent whorls and is thicker walled. The apical protoconch whorls are aligned at an off-set angle to the shell axis.

The reproductive anatomy of *Stalactella* differs from other *Holospira* by lacking a vagina; the spermathecal duct and the free oviduct enter directly into the atrium. The penis is very short and almost bulbous. The epiphallus + vas deferens form a very long loop.

In order to clarify the relationship between the Epirobiidae and *Stalactella* and between *Stalactella* and *Holospira* the anatomies of three species of *Stalactella* and two other species of *Holospira* are described in detail and illustrated.

HOLOSPIRA (STALACTELLA) CREMNOBATES THOMPSON & MIHALCIK 2005

Reproductive anatomy.—The genital atrium is thick-walled, elongate, tapered- cylindrical and is about 0.5 mm long (Fig. 18C–D). The penis is very short, being slightly longer than wide. The penis retractor muscle inserts on the apex of the penis lateral to the insertion of the epiphallus. Near this junction the epiphallus is almost as wide as the penis. The loop of the vas deferens becomes very narrow at the atrium and from there to the prostate. The free oviduct is very long and moderately stout. The vagina is vestigial and exists as a wide bulge in the atrium. The spermatheca is elongate and club-shaped. The spermathecal duct is highly convoluted for about 2.5 mm above its base at the atrium. The duct is about 10 mm long and bears a long appendix just below the spermatheca.

Specimens examined.—MÉXICO. Puebla, 10 km N of Tehuacán (18°37'23" N, 97°23'35" W), 1990 m alt.; UF 190788 (in 75% ETOH).

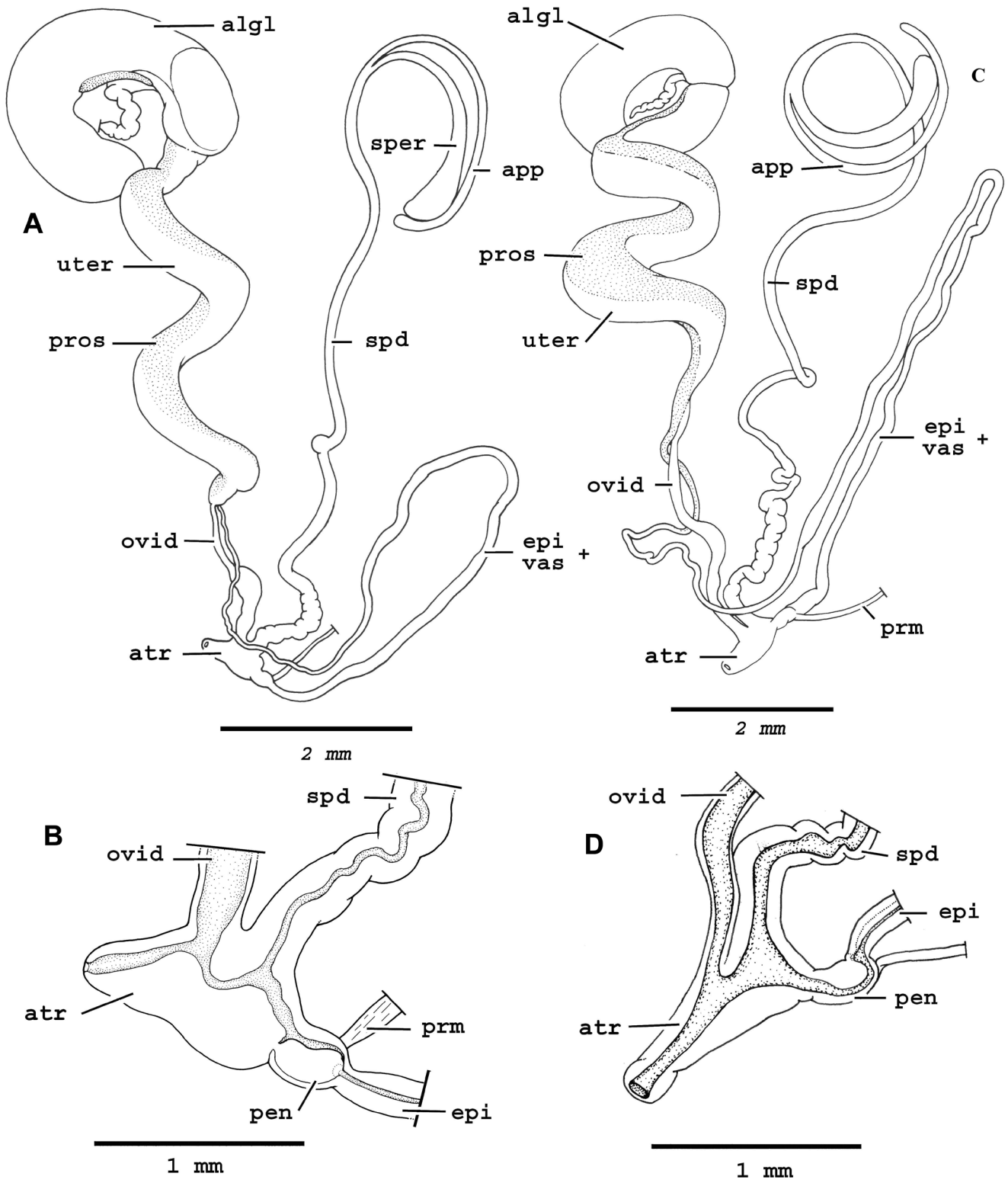


Figure 18. Reproductive anatomy of *Holospira (Stalactella)*. **A–B**, *Holospira (Stalactella) marmorata* (UF 233191). **C–D**, *Holospira (Stalactella) cremnobates* (UF 190788). Abbreviations as in Fig. 8.

HOLOSPIRA (STALACTELLA) PSECTRA THOMPSON & MIHALCIK 2005

Reproductive anatomy.—The genital atrium is cylindrical and stout, and is about 0.7 mm long (Fig. 19A–B). The penis is short, elongate-cylindric, and is about 0.5 mm long. The penis retractor muscle inserts on the apex of penis next to the origin of the epiphallus. The epiphallus is about 12.5 mm long and is slightly narrower than the penis. The demarcation between the epiphallus and the vas deferens is not distinct. At the base of is loop at the atrium the vas deferens narrows from there to the prostate. The free oviduct is about 11 mm long and is very slender. The vagina is vestigial on the atrium opposite the penis. The spermatheca is elongate and club-shaped. The spermathecal duct is enlarged at its base and has a thick convoluted muscular wall. The duct is about 23 mm long and bears a long appendix near the distal end.

Specimens examined.—MÉXICO, Puebla, a limestone cliff on the south slope of Cerro Caolalote, 2 km E of El Carmen, 18° 36' N, 97° 26.01' W; UF 233198 (in 75% ETOH).

Remarks.—The reproductive system is characterized by the elongate epiphallus, spermathecal duct and free oviduct.

HOLOSPIRA (STALACTELLA) MARMORATA THOMPSON & MIHALCIK 2005

Reproductive anatomy.—The genital atrium is very thick-walled, conical and about 0.5 mm long (Fig. 18A–B). The penis is very short, bulbous, and about 0.3 mm long. The penis retractor muscle attaches to the apex of the penis at the base of the epiphallus. The epiphallus is almost as thick as the penis near its base. It forms a long loop with the vas deferens. There is no clear demarcation between the vas deferens and the epiphallus. The vas deferens becomes very slender near the genital atrium. The vagina is vestigial and is not distinct from the genital atrium. The spermatheca is large and is elongate club-shaped. The spermathecal duct near its base is thick walled, muscular, enlarged, is strongly convoluted. It tapers slightly distally. The spermathecal duct bears an appendix distally. The duct is about 8 mm long. The free oviduct is

relatively stout near its base and becomes slender below the uterus. It is about 1.5 mm. long.

Specimens examined.—MÉXICO, Puebla, 3.7 km S of San Vicente Coyotepec, 1880 m alt.; UF 233191 (preserved in 75% ETOH).

Remarks.—The reproductive system differs from other *Stalactella* by the relatively shorter epiphallus-vas deferens loop. Also, the free oviduct is shorter and becomes considerable stouter above the atrium.

HOLOSPIRA (HOLOSPIRA) FORTISCUPTA THOMPSON & MIHALCIK, 2005

Reproductive anatomy.—The genital atrium is very short and wide (Fig. 19C–D). The penis is very short, almost bulbous, and is about 0.5 mm long. The penis retractor muscle inserting on the apex of the penis at the base of the epiphallus. The epiphallus is about 11 mm long and is nearly uniformly slender. The vagina is virtually non-existent at the side of the atrium. The spermatheca is narrow and elliptical. The spermathecal duct is very long (about 24 mm). The base of duct is enlarged and muscular. The duct bears an appendix near its distal end that is about 11 mm long. The free oviduct is very long (about 7 mm) and narrow.

Specimens examined.—MÉXICO, Puebla State: 12.3 km E of Puebla, 2525 m alt. (UF 255392, in 75% ETOH).

Remarks.—*Holospira fortisculpta* is tentatively assigned to the subgenus *Holospira*. *Holospira fortisculpta* differs from *Stalactella* by lacking denticles on the parietal lamella, by having the protoconch whorls normally aligned with the shell axis, and by having a normally proportioned penultimate whorl in which the shell wall is not conspicuously thickened. The reproductive anatomy of this species is very similar to that of *Stalactella*. The very short genital atrium, the very short penis, the very long epiphallus, the absence of a distinct vagina and the very long free oviduct are features in common with *Stalactella*.

HOLOSPIRA (HOLOSPIRA) GOLDFUSSI (MENKE 1847)

Reproductive anatomy.—The right ocular retractor muscle passes through the penis-vaginal angle (Fig. 14D–E). The genital atrium is short and

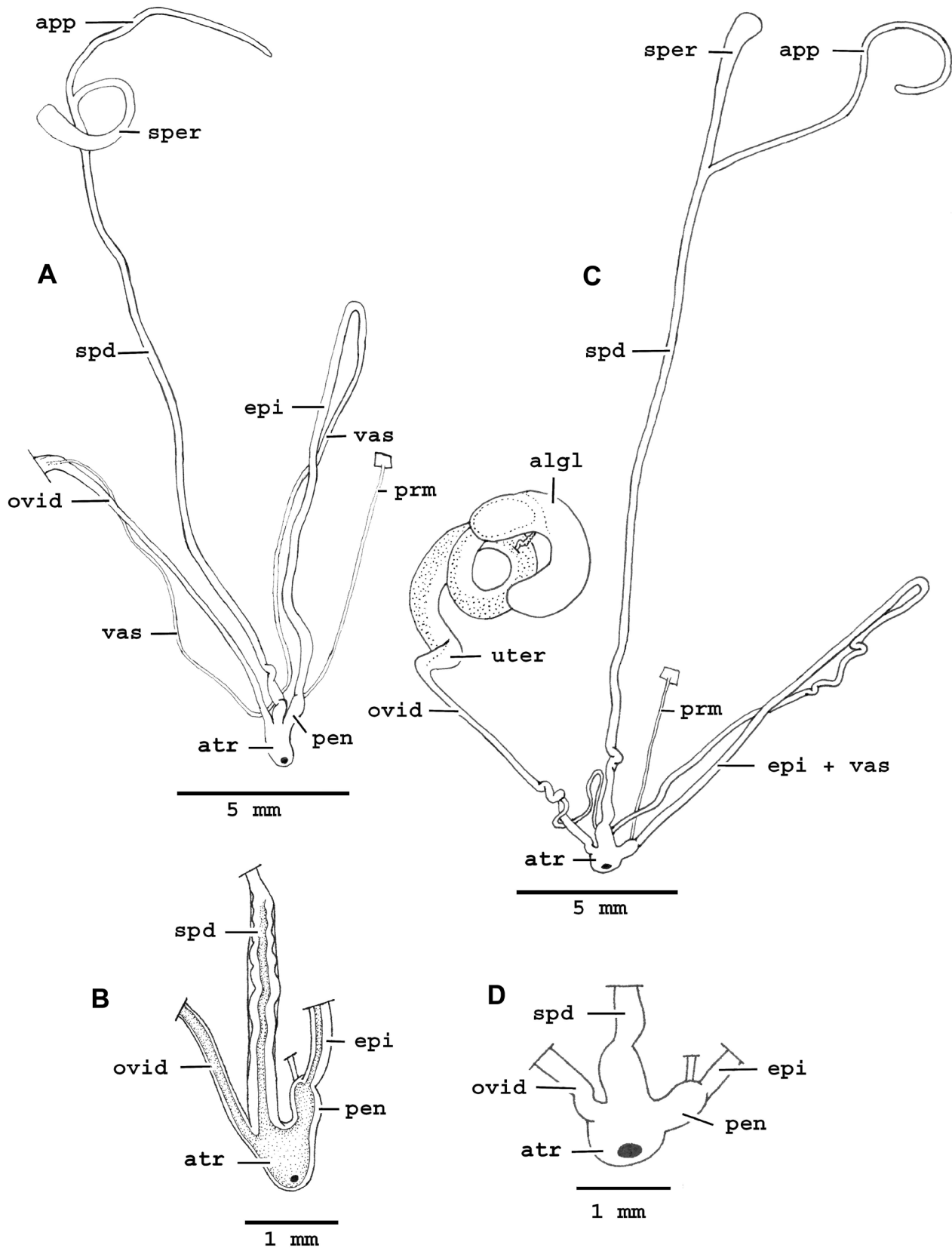


Figure 19. Reproductive anatomy of *Holospira (Stalactella)* and *Holospira (Holospira)*. **A–B**, *Holospira (Stalactella) psectra* (UF 233198). **C–D**, *Holospira (Holospira) fortisculpta* (UF 255392). Abbreviations as in Fig. 8.

thick-walled, but broad, and is about half as long as the penis. The penis is elongate, club shaped, about 1.8 mm long. The penis retractor muscle originates on the inner wall of the lung shortly behind the mantle collar and inserts on the apex of the penis lateral to the epiphallus. The epiphallus is long and slender and is weakly differentiated from the vas-deferens. The epiphallus + vas-deferens loop is about 15 mm long. Spermathecal duct is very long (18 mm); base of duct thickened and muscular followed by a short highly convoluted section of duct. The distinct vagina is relatively ample and is about 1 mm long. The spermathecal duct is thick-walled and convoluted near its base. The duct lacks an appendix. The spermatheca is oval and is appressed against the uterus at the base of the albumen gland. The free oviduct is uniformly wide and is about three times the length of the vagina.

Radula.—The transverse tooth rows are nearly straight. The central tooth is as wide as the lateral teeth, is wider than high, is trapezoidal in shape and is unicuspid. There are 9 lateral teeth and ca. 10 marginal teeth. The lateral teeth are unicuspid and the marginal teeth have a mesocone and a single ectocone.

Remarks.—Salient features of *Holospira goldfuss* are: the free oviduct is short and stout, a distinct vagina is formed below the union of the spermathecal duct and the free oviduct, the spermatheca is broadly elliptical, and spermathecal duct lacks an appendix. These features contrast with those of *H. haploplax*.

Anatomical specimens examined.—TEXAS. Comal Co., Comal Springs State Park, New Braunfels; Coll. 4 Sept., 1998, Gregg Brewer (UF 270513). Panther Canyon, Landon Park, New Braunfels; coll. 18 July. 2010, Val Roesling (UF 444669). Kendall Co., 6.9 mi. S of Kendall, south facing limestone outcrop on Guadalupe River at farm rd. 3160; coll. 26 May, 1996, Gregg Brewer (UF 268908).

ANATOMY OF THE EUCALODIDAE

Data are taken from Strebel and Pfeffer (1880), Fischer and Crosse (1872), Pilsbry (1902, 1903), and Thompson (1963, 1968). The anatomy of the Eucalodiidae remains very poorly documented.

The family includes 15 genera and subgenera and about 70 described species. The anatomies of only a few species have been described in sufficient detail that allow adequate comparisons. These are: *Eucalodium (Eucalodium) decollatum decollatum* Nyst 1841 [as *gheisbregthi*] (Fischer & Crosse 1872); *Eucalodium (Oligostylus) blandianum* Crosse & Fisher 1873 (Strebel & Pfeffer 1880); *Eucalodium (Oligostylus) ausralis* (Thompson 1963); *Anisospira (Anisospira) liebmani* (Pfeiffer 1846) (Thompson 1968); *Anisospira (Anisospira) dalli dalli* (Von Martens 1901) (Thompson 1968); *Anisospira (Trachycion) recticoista townsendi* Pilsbry & Cockerell 1903; *Dissotropis castaneum* Thompson 1968; and *Coelocentrum (Coelocentrum) actispira* (Pfeiffer 1860) (Strebel & Pfeffer 1880).

Shell.—The shell is large, 25–70 mm long; robust, and decollate when adult. The protisiconch whorls are not conspicuously wider or higher than the following whorls. The juvenile shell is attenuated and slender and then the whorls rapidly widen to the adult shell width. The axis is hollow. An internal barrier is rarely present, but when present it consists of a columellar lamella.

Radula.—The teeth are in nearly straight horizontal rows. The central tooth is tri-cuspid with a large mesocone bordered on each side by a small ectocone, and with a narrow rectangular basal plate. The central tooth is as broad as the laterals. The lateral teeth are bicuspid with an long mesocone and a small ectocone.

Jaw.—Arcuate, solid with numerous small vertical plates and cusps.

Pallial organs.—The lung is about four whorls long. The kidney is sigmoid, long and sickle-shaped. The aorta extends unbranched to the mantle collar.

Retractor muscles.—The right ocular retractor muscle passes through the penis-vaginal angle. The penis retractor muscle originates on inner wall of lung and inserting on the apex of the penis at the base of the epiphallus.

Reproductive anatomy.—The genital atrium is moderately long. The penis is well developed and stout, and has a well-developed stimulator

(verge) internally. The epiphallus is stout and well developed. The epiphallus-vas deferens is relatively short between the penis and the prostate. The spermatheca is globose. The base of spermathecal duct is not conspicuously thickened and muscular. An appendix on spermathecal duct, when present, is near the base of the duct. The free oviduct is as long as or longer than the vagina. The vagina is well developed below the junction of the spermathecal duct and the free oviduct.

Salient features that distinguish the Eucalodiidae from epirobiids include the large robust shell. The adult shell is always decollate. The attenuated juvenile shell rapidly expands in its final whorl to the width of the adult shell. The jaw consists of numerous small vertical plates. Differences in the reproductive anatomy are the presence of a verge in the penis, the well-developed epiphallus that forms a shorter loop with the vas deferens to the prostate, the globose spermatheca, and the basal location of an appendix on the spermathecal duct, when present.

ANATOMY OF THE EPIROBIIDAE

Shell.—The shell is elongate with a tapered apex. Sculpture consists of fine incremental ribs. Spiral sculpture is absent. The smooth protoconch consists of two or three slightly enlarged button-like whorls that are wider than the following whorl. The juvenile shell gradually tapers into the adult shell. The first protoconch whorl is imperforate. The shell is decollate or entire. Usually an apical plug is formed shortly below the protoconch. The peristome is complete around the aperture, which is free from the preceding whorl. The axis is hollow. Internal lamella may be present or absent. When present one or more lamella extend the length of the shell in juvenile shells as well as adult shells. Their arrangement and numbers are generically significant. Unlike the Holospiridae, the columellar lamella is developed early in life and extends though the length of the shell. In the Holospiridae the lamella develop only at shell maturity (Thompson & Mihalcik 2005).

Jaw and Radula.—The jaw is solid and ribbed. The radula is long, 4 L/W, and contains about 35

vertical tooth rows. The teeth are arranged in very broad V-shaped transverse rows. The central tooth is wider than the adjacent lateral teeth, which are subequal in size to the central tooth. The central tooth is tricuspid with a large mesocone and has an ectocone on each side of the mesocone. The lateral teeth are bicuspid with an elongate mesocone and an ectocone. The marginal teeth are bicuspid to multicuspid with an elongate mesocone and one or more ectocones.

Pallial organs.—The pallial cavity is about 4 whorls long. The kidney is about $\frac{1}{4}$ whorl long, narrow, reniform, sigmurethrous. The secondary ureter is about equal in diameter to the intestine, and it tightly bound to the latter. The heart is about $\frac{1}{4}$ the length of the kidney. The aorta lies along the left side of the lung and it is weakly branched throughout most of its length. It divides into 5–6 small arterioles just behind the mantle collar (Thompson 1976: *Epirobia lurida*).

Retractor muscles.—The right ocular retractor muscle passes through the penis-oviducal angle and attaches to the right pedal retractor muscle. The right and left ocular retractors do not form a plate over the pharynx. The penis retractor muscle originates on the inner wall of lung and inserts on the end of the penis diverticulum.

Reproductive system.—The genital atrium is short. The penis is elongate and club-shaped. The penis lacks an internal stimulator (verge). The penis bears a long, blind diverticulum onto which the penis retractor muscle inserts. An epiphallus is present, which is poorly differentiated from the vas deferens. The epiphallus + vas deferens form a very long loop. A moderately long vagina is about half the length of the free oviduct. The spermatheca is elongate and has a long duct with an enlarged muscular base. An appendix may be present or absent. When present it enters the duct near its distal end.

The Epirobiidae differ from the Holospiridae and the Eucalodiidae by having a long diverticulum on the penis. The penis retractor muscle attaches to the end of the diverticulum. The epiphallus is very long and is weakly differentiated from the vas deferens. The central tooth of the radula is

wider than the adjacent lateral tooth, and it has a small acuminate ectocone high on each side of the tooth and an enlarged broad mesocone. The lateral teeth have a large mesocone and an ectocone. In the Holospiridae and the Eucalodiidae the central tooth is narrower than the adjacent lateral teeth. In the Holospiridae the central and lateral radular teeth are unicuspid with a large mesocone. In the Eucalodiidae the centrals and laterals possess ectocones. These characters separate the Epirobiidae from other Urocoptoidea, except the Cerionidae. The Cerionidae differ in shell morphology by having a short, dome-shaped apex, a solid axis in the lower-most whorls, an incomplete peristome across the parietal wall of the aperture, and a non-reflected outer lip. The right ocular retractor muscle passes mesad to the genitalia, not through the penis-oviducal angle, and the penis retractor muscle originates on the right ocular retractor muscle, not on the inner wall of the lung. The epiphallus is well developed and differentiated from the vas-deferens. The penis has a short diverticulum, and the penis retractor muscle attaches to the apex of the diverticulum. (Thompson 2011b).

Additional characteristics which are shared with the Holospiridae and the Eucalodiidae, but separate Epirobiidae from Urocoptidae are as follow. The axis is hollow. The jaw is solid. The radular teeth are arranged in nearly straight transverse rows. The penis retractor muscle arises from the inner wall of the lung, and the right ocular retractor muscle passes through the penis-vaginal angle. In the Urocoptidae the axis is solid and imperforate, the jaw is multi-plated, and the radular teeth are arranged in V-shaped rows. The penis retractor muscle arises from the right ocular retractor muscle, which passes mesad to the genitalia.

Among similar appearing groups are the Urocoptidae, subfamily Brachypodellinae, the Eucalodiidae and the Holospiridae. The Holospiridae (except *Allocoryphe* and *Eudistemma*) and the Eucalodiidae lack a penis diverticulum, and the epiphallus is differentiated from the vas deferens. The shell of *Epirobia* resembles

Brachypodella. The later has a solid axis, the first whorl of the protoconch is perforated and the radula consists of just two longitudinal tooth rows.

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