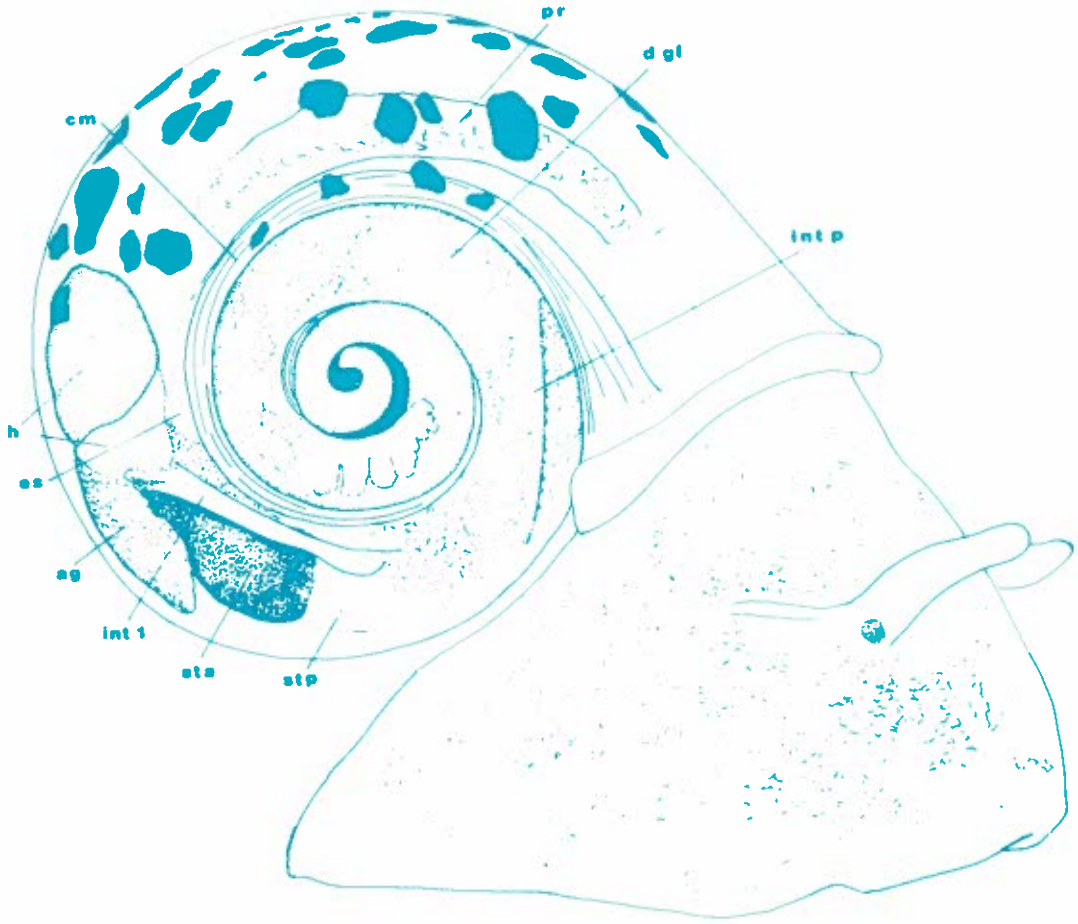
Pecosorbis, a new genus of fresh-water snails (Planorbidae) from New Mexico

by Dwight W. Taylor



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FRONT COVER—See Fig. 2B, p. 7.

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Abstract

Pecosorbis, new genus of Planorbidae, subfamily Planorbulinae, is established for *Biomphalaria kansasensis* Berry. The species has previously been known only as a Pliocene fossil, but now is recognized in the Quaternary of the southwest United States, and living in the Pecos Valley of New Mexico. *Pecosorbis* is unusual because of its restricted distribution and habitat in seasonal rock pools. Most similar to *Menetus,* it differs in having a preputial organ with an external duct, no spermatheca, and a penial sac that is mostly eversible.

Introduction

The novel discovery described here is significant in various ways. Within the context of molluscan studies, scarcely anyone would have expected this new genus in the United States. Fresh-water snails of the family Planorbidae have been studied for a long time in North America, and *Pecosorbis* is markedly distinct in taxonomic characters. Its habitat in seasonal pools and its restricted distribution are unusual. Furthermore, it proves to be a "living fossil," a Pliocene spedes thought to be extinct. Although several Pleistocene species of fresh-water molluscs have been discovered alive, this is the first occasion in North America when a **Tertiary form has been recognized as living. Once again shell features in Planorbidae are shown to give little clue to relationships, and the original generic allocation of the fossils is revised significantly.**

Field work in New Mexico was supported by two agencies whose interests have been amazingly rewarded by discovery of *Pecosorbis.* Principal support came from the New Mexico Department of Game and Fish Endangered Species Program through John P. Hubbard. These studies were intended to identify species of restricted distribution in the state, as a basis for possible classification as endangered or threatened. *Pecosorbis* indeed qualifies as having restricted distribution, because there are only two living populations known thus far. It is the only genus of molluscs limited to New Mexico.

Additional field support came from the New Mexico Bureau of Mines and Mineral Resources through Frank E. Kottlowski, Director, and John W. Hawley. This support has been planned for studies in interpreting environmental significance of fossil mollusc shells in the state. The discovery of *Pecosorbis,* reclassification of the Pliocene species, and recognition that *Pecosorbis* is widespread as a Quaternary fossil, even though so limited today, casts a new light on the known fossils.

At the University of Colorado Museum, Shi-Kuei Wu kindly provided access to collections and field notes by Junius Henderson. Special gratitude is due to A. L. Metcalf, University of Texas at El Paso, for loaning specimens (UTEP catalog numbers) collected by him that represent most of the known localities of *Pecosorbis.*

Materials and methods

The specimens described and illustrated were anesthetized with menthol, fixed in FAA (formalin–acetic acid–alcohol), and transferred to 70% ethanol. One advantage of using menthol as an anesthetic in these and other aquatic pulmonate snails is that often the turgor induced by menthol is sufficient to cause extrusion of the penial complex. Drawings are camera-lucida sketches except as indicated.

Description of *Pecosorbis*

Family PLANORBIDAE
Subfamily PLANORBULINAE
PECOSORBIS, new genus

Generic diagnosis—Planorbidae with unbranched and generally single or paired diverticula of ovotestis; and narrowly elongate prostate with 4-5 diverticula in cross section. Penial complex with a preputial organ projecting from the preputium, and art external duct from that organ to the penial sac; preputium and penial sac **most of everted in copulation. Seminal vesicle compact, without acute projections or numerous lobes. No spermatheca.**

Type *species—Biomphalaria kansasensis* Berry, **1966.**

Distribution—Living in Pecos River valley, New Mexico; late Pleistocene–Holocene in southern New Mexico, Trans-Pecos, Texas, and southeastern Arizona; Pliocene, southwestern Kansas. One species.

Etymology—After the Pecos River, and Latin *orbis,* **m., circle. The generic name is apt in describing its**

modern distribution, and *kansasensis* was apt for the fossil as known previously. The combination is incongruous, however, as the Pecos River is nowhere in Kansas.

Description and illustrations of morphology are based on a large series from Little McKittrick Draw, New Mexico.

PECOSORBIS KANSASENSIS (Berry, 1966)
Figs. 1-11

Segmentina obstructa (Mor.)?: Walker, 1915, p. 4; drift of Cuervo River, San Miguel County, New Mexico.

Planorbula armigera (Say) [misidentified]: Leonard and Frye, 1962, p. 21, p1. 2, figs. 10-12; Pecos River alluvium, Pleistocene, Ward County, Texas.

Biomphalaria kansasensis sp.n.: Berry, 1966, *in* Berry and Miller, p. 266, figs. 3-5; Spring Creek fauna, Meade County, Kansas. Taylor, 1966, p. 9; paleoecological interpretation.

Promenetus umbilicatellus (Cockerell) [misidentified]: Metcalf, 1967, p. 38; late Pleistocene and Holocene, Rio Grande valley, New Mexico-Texas.

Biomphalaria sp.: Metcalf, 1969, p. 159; late Quaternary, Rio Grande valley, New Mexico-Texas. Seager et al., 1975, p. 24; late Pleistocene, Rio Grande valley, Dona Ana County, New Mexico.

? Menetus cf. portlandensis Baker: Leonard and Frye, 1975, p. 21; drift of Arroyo del Macho, Chaves County, New Mexico.

Biomphalaria obstructa [misidentified]: Metcalf, 1977, pp. 57, 60, 65; late Pleistocene, Toyah, Reeves County, and Finlay Mountains, Hudspeth County, Texas. Metcalf, 1982, p. 51; late Pleistocene, Toyah, Reeves County, Texas.

Shell (Fig. 1)

The various modern and fossil samples examined include several large series that agree closely with the original description and illustrations by Berry. Among fresh-water pulmonates, the species is relatively less variable and only supplementary notes will be given.

Periostracum pale tan, the surface texture silky or even shiny. Sharply defined, irregular riblets that develop gradually on the later part of the body whorl are a characteristic feature of the species. Often shells have two variceal ridges, and there may be riblets developed prior to both variceal ridges. This feature varies within samples. Even shells with no varix may have irregular riblets. Shell sculpture is therefore interpreted as a specific character. In the modern samples from southeastern New Mexico shells may be found with 0, 1, 2, or 3 varices, and development of riblets may occur prior to the last varix only, or on earlier parts of the shell as well, or not at all. Shell formed immediately after a varix lacks riblets, as was noted in the original description.

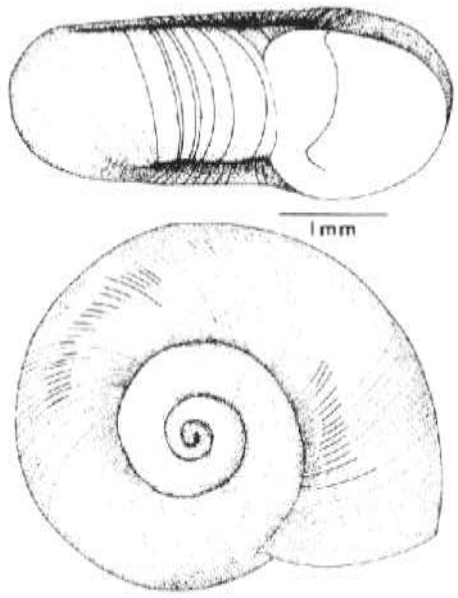

FIGURE 1—*Pecosorbis kansasensis* (Berry), shell from Little McKittrick Draw, New Mexico.

Some of the Pleistocene and Holocene specimens seen attain as large a size as those in the original Pliocene sample, whereas specimens in the two modern series from Eddy County, New Mexico, do not. A subsample of 10 larger specimens from the original Pliocene collection measured 4.82 mm in greatest diameter (range 4.6-5.3), with 4.0 whorls (range 3³/44). Corresponding measurements of 10 larger specimens from Little McKittrick Canyon are 3.59 mm in diameter (3.3-3.8), with 3.4 whorls (3 1/4 - 3 3/4); and from Last Chance Canyon 3.84 mm (3.6-4.0), with 3I/7-3³/4 whorls.

Compared to *Promenetus umbilicatellus*, *Pecosorbis* has a shell of greater relative height; the surface texture is silky to shiny, not dull; and sculpture is usually stronger. *P. umbilicatellus* often has fine riblets also, but these are less prominent, occur over more of the shell, and do not show discontinuity after varix formation.

Animal (Fig. 2A, B)

Pigmentation is sparse, consisting of scattered wisps of melanin in the head-foot and distal part of the mantle. Mostly oval or narrowly elongate melanin patches over the pulmonary cavity are visible readily through the shell. After removal of the shell, additional pigmentation can be seen in the form of sparse melanin wisps on some organs; the anterior chamber of the stomach is the darkest element of the body. Many internal features can be seen even without dissection.

Reproductive system
(Figs. 3-9; 10 specimens dissected)

Hermaphroditic portion—Ovotestis with flask-shaped diverticula that are unbranched, arranged proximally in a single series, then arranged alternately, and distally paired. They are translucent and oocytes are visible even without staining. The collecting canal is continued as a thin-walled tube of relatively large diameter, the ovisperm duct, that constricts abruptly to about one-fifth its diameter **before** entering the seminal vesicle. The vesicle forms a compact mass (Fig. 4) that when stretched (Fig. 6) is revealed as a sinuous tube with bluntly rounded lateral outpocketings. The vesicle is discretely defined proximally but less so distally, as the lateral pouches diminish gradually in size. The distal ovisperm duct is conspicuously longer than the seminal vesicle.

Male portion—The spermiduct leaves the carrefour as a thick-walled tube and narrows gradually as it runs along the right side of the oviduct. The prostate, of about 70 diverticula, is nested in the concave right

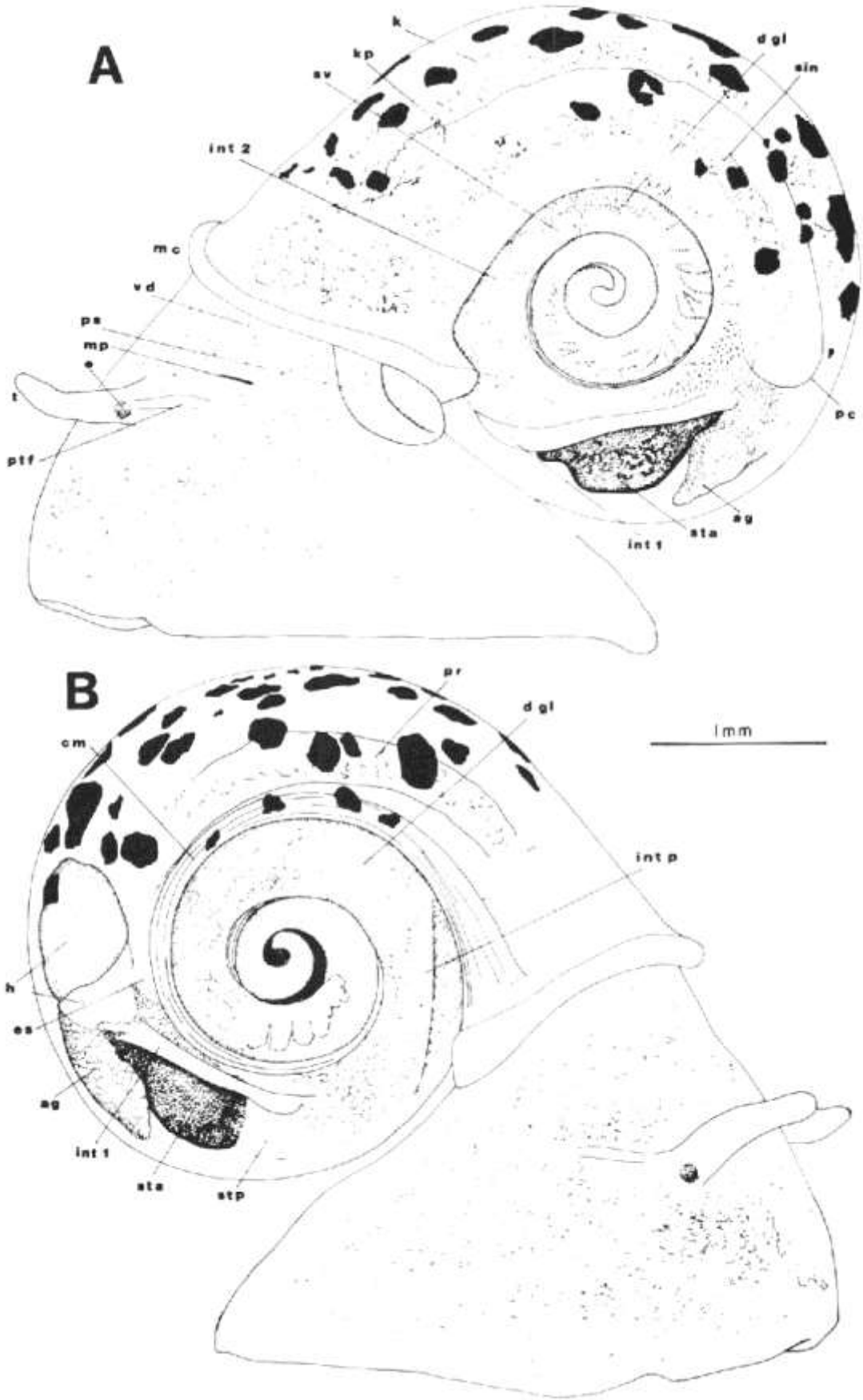

FIGURE 2—*Pacosorbis kansasensis* (Berry), the same specimen in two views (A, B) after removal of shell. Abbreviations: **ag**, albumen gland; **cm**, columellar muscle; **d gl**, digestive gland; **e**, eye; **es**, esophagus; **h**, heart; **int 1**, proximal portion of intestine; **int 2**, distal portion of intestine; **int p**, posterior loop of intestine; **k**, kidney; **kp**, pore of kidney; **mc**, mantle collar; **mp**, male pore; **pc**, posterior end of pulmonary cavity; **pr**, prostate; **ps**, pseudobranch; **ptf**, post-tentacular flap; **sin**, sinus; **sta**, anterior stomach; **stp**, posterior stomach; **sv**, seminal vesicle; **t**, tentacle; **vd**, vas deferens.

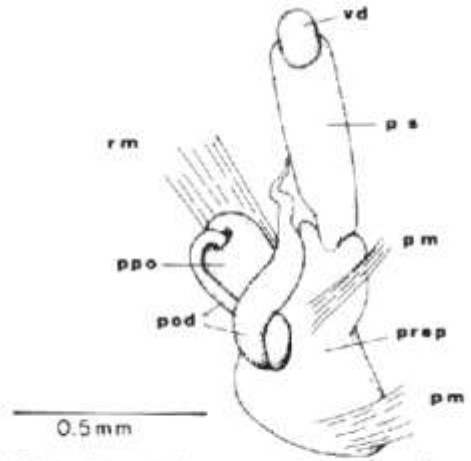

FIGURE 3—*Pecosorbis kansasensis* (Berry), penial complex of specimen in Figs. 1, 2, 4, medial view. Abbreviations: **pm**, protractor muscle; **pod**, preputial-organ duct; **ppo**, preputial organ; **prep**, preputium; **ps**, penial sac; **rm**, retractor muscle; **vd**, vas deferens.

side of the nidamental gland, with the posterior diverticula distal to the end of the oviducal pouch and the anterior diverticula proximal to the narrow anterior portion of the nidamental gland. At midlength of the prostate, where it is of greatest width and height, there are 3-5 prostate diverticula in transverse section. These have a maximum of one branch, and most diverticula discharge directly into the spermiduct.

The vas deferens continues from the prostate as a narrow tube forward to where, behind the male aperture, it leaves the body wall with an abrupt change in course to enter the body cavity. Within the cavity it promptly becomes thicker-walled and of a greater diameter, until it reaches the penial sac. The proximal end is a melanin-flecked bulb. The penial sac is nearly cylindrical but slightly wider proximally, about four times as long as wide, and set off from the preputium by a constriction. Distal to this constriction, the preputium is slightly wider than the sac; the whole form of the preputium is that of a laterally compressed,

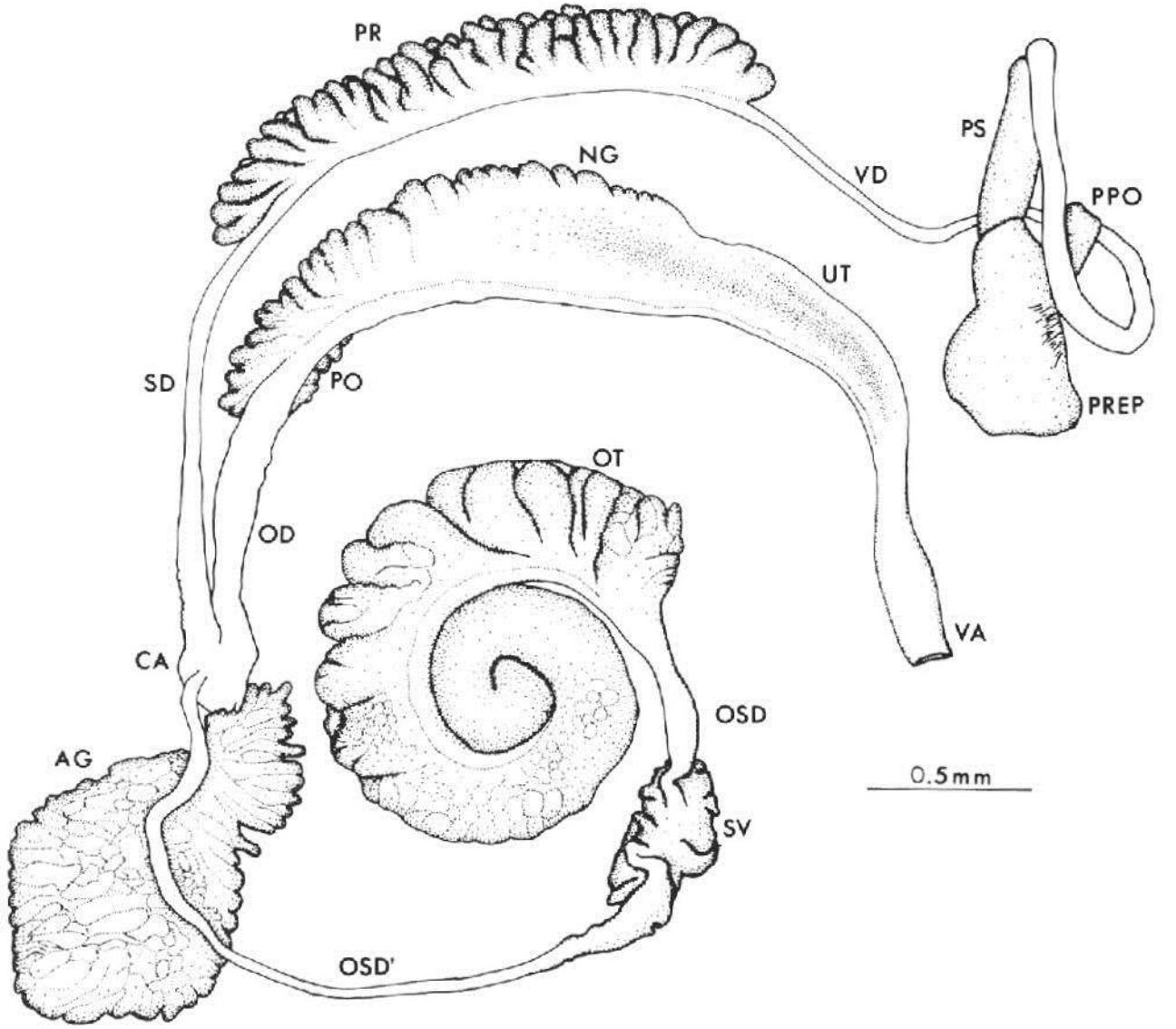

FIGURE 4—Reproductive system of *Pecosorbis kansasensis* (Berry); view from right, except that penial complex (PPO, PREP, PS) has been turned around and shown from left. Same specimen as in Figs. 1–3. Abbreviations: **AG**, albumen gland; **CA**, carrefour; **NG**, nidamental gland; **OD**, oviduct; **OSD**, proximal part of ovisperm duct; **OSD'**, distal part of ovisperm duct; **OT**, ovotestis; **PO**, pouch of oviduct; **PPO**, preputial organ; **PR**, prostate; **PREP**, preputium; **PS**, penial sac; **SD**, spermiduct; **SV**, seminal vesicle; **UT**, uterus; **VA**, vagina; **VD**, vas deferens.

thin-walled tube that widens distally to the male aperture.

The preputial organ projects conspicuously into the body cavity from the preputium. It is a cylindrical body with truncate proximal end, about twice as long as wide. Its duct runs as a thick-walled tube to the medial aspect of the preputium while becoming thicker, then flexes abruptly and courses dorsally, tapering slightly. It then becomes thin-walled abruptly and tapers more rapidly. After a brief sinuous course it enters the posterior aspect of the penial sac at about one-third its length.

Attached to the outside of the preputium are two sets of muscles on opposite sides. A broad retractor muscle originating in the columellar muscle is inserted on the posterodistal aspect of the preputium. Two bands of protractor muscle originate on the dorsal wall of the head cavity, and insert on the anteromedial and distal aspects of the preputium.

Internally, the penial complex is remarkable for its simplicity (Fig. 9). The penial sac is set off from the preputium only by a constriction; there is no velum or sarcobelum. The thin-walled preputium is a sac distended by the preputial organ, lacking the usual pilasters. When retracted within the preputium, the cup of the preputial organ is compressed into folds; these are not permanent and disappear when the organ is everted.

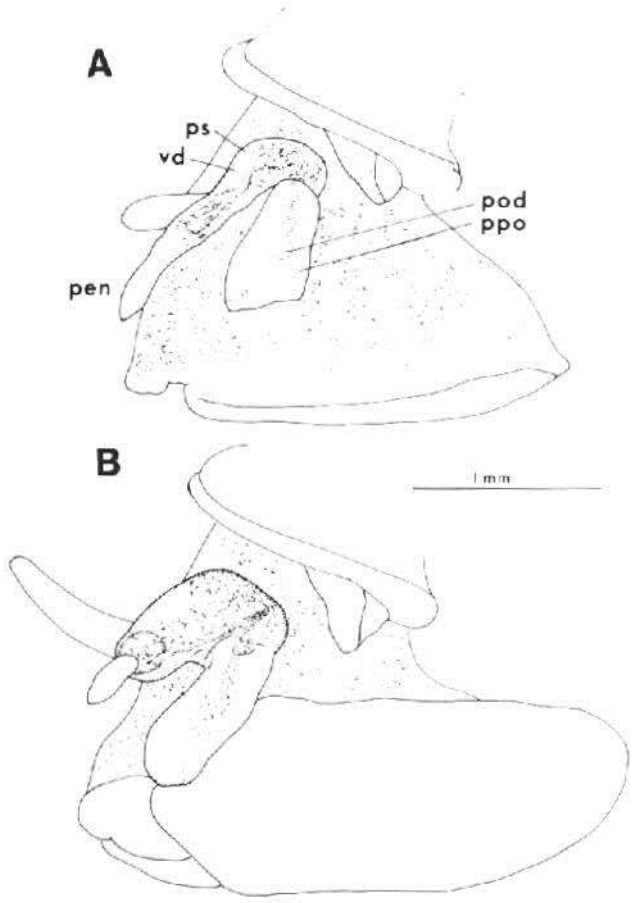

FIGURE 5—*Pecosorbis kansasensis* (Berry), two specimens (A, B) with penial complex extruded. Abbreviations: **pen**, penis; **pod**, preputial-organ duct; **ppo**, preputial organ; **ps**, penial sac; **vd**, vas deferens.

Thirty specimens were preserved with preputium and penis in various stages of eversion and turgor, facilitating observation of the preputial organ, penial sac, and related structures (Figs. 5A, B, 8). In distended state the preputial organ is both longer and bulkier than the preputium. It contains only a few scattered wisps of melanin so that the duct within and the terminal cup are readily visible. The end is noncuticular, distensible and eversible so that the cup may be narrow, broad, or turned inside-out to form a hemispherical end **to** the preputial organ. The duct leads into the preputium, where it becomes about twice as thick and acquires heavier melanin-flecking; then it traverses the ventral lumen of the penial sac to open within the posterolateral face of the proximal bulb of the penial sac. Uniquely, the penial sac is mostly everted along with the preputium, so that its pigmented bulb becomes distal, and the penis is everted for nearly all of its length. The vas deferens is an unpigmented tube of uniform diameter through the preputium and penial sac that opens as a wide slit on the anterolateral face of the penis, proximal to the widest part of that organ and thus at about one-fifth its length. The penis is a fleshy, tapering, symmetrical structure without cuticular covering. Because it is also distensible, the relative position of the exit pore of the vas is affected by degree of turgor.

Female portion—The albumen gland is pale yellowish-brown and the most deeply colored organ of the reproductive system. It is roughly pyriform in outline, wider posteriorly. Its outer surface is broadly convex, conforming to the periphery of the body; the inner surface is irregular and adjoining stomach and intestine. Its narrow duct opens into the carrefour on the left posteroventral aspect, opposite the far-larger gonoduct opening on the right posteroventral aspect.

The oviduct leads from the carrefour in a smooth arc as a broad, dorsoventrally compressed tube. After curving through about 45°, it expands into the plicate-walled pouch of the oviduct. This passes with no evident demarcation into the nidamental gland, along whose ventral margin the oviduct runs as a narrow channel. The nidamental gland is convex toward the left, concave on the right, and cradles the prostate. It narrows gradually and merges into the uterus. The spermatheca, usual in higher limnic Basommatophora (Hygrophila), is entirely absent.

The vagina is usually slightly swollen compared to the distal portion of the uterus, but not campanulate, and it is plicate-walled. No trace of other internal structures was seen.

Localities and material examined

(Distribution map, Fig. 10)

Modern

New Mexico—GUADALUPE COUNTY: Small brook in Dakota sandstone 4.5 mi NW of Santa Rosa; coll. **J.** Henderson, 31-VIII-1929 (University of Colorado Museum 17939). **EDDY COUNTY:** Last Chance Canyon, 600 ft W, 2300 ft N, sec. 34, T. 23 S., R. 22 E.; coll. D. W.

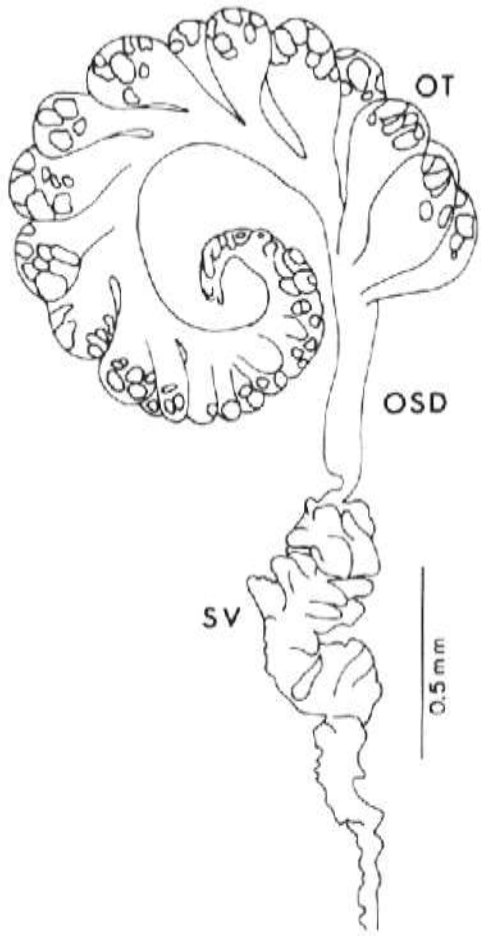

FIGURE 6—*Pecosorbis kansasensis* (Berry), ovotestis and seminal vesicle. Abbreviations: **OSD,** ovisperm duct; **OT,** ovotestis; **SV,** seminal vesicle.

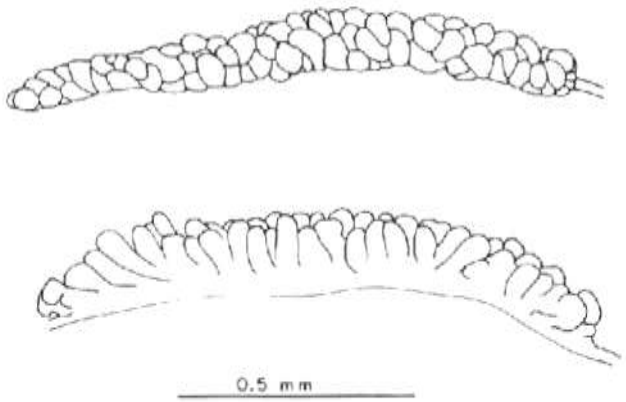

FIGURE 7—*Pecosorbis kansasensis* (Berry), prostate, two views of one specimen.

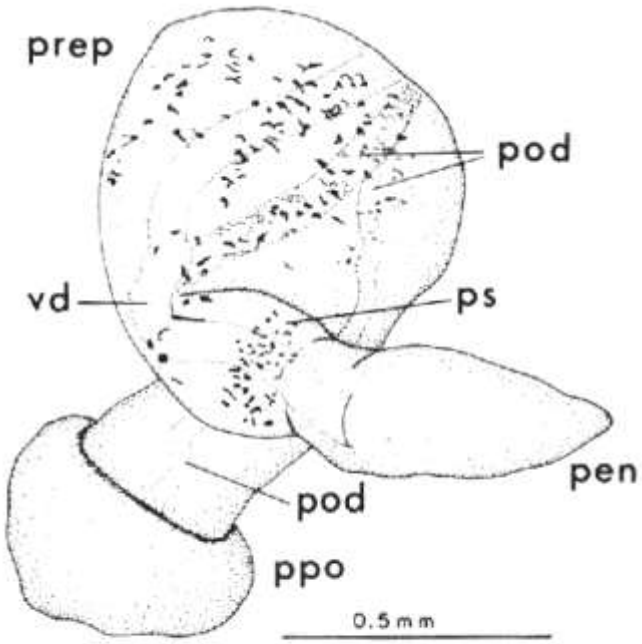

FIGURE 8—*Pecosorbis kansasensis* (Berry), penial complex extruded, with terminal cup of preputial organ everted into a rough hemisphere. Abbreviations: **pen,** penis; **pod,** preputial-organ duct; **ppo,** preputial organ; **prep,** preputium; **ps,** penial sac; **vd,** vas deferens.

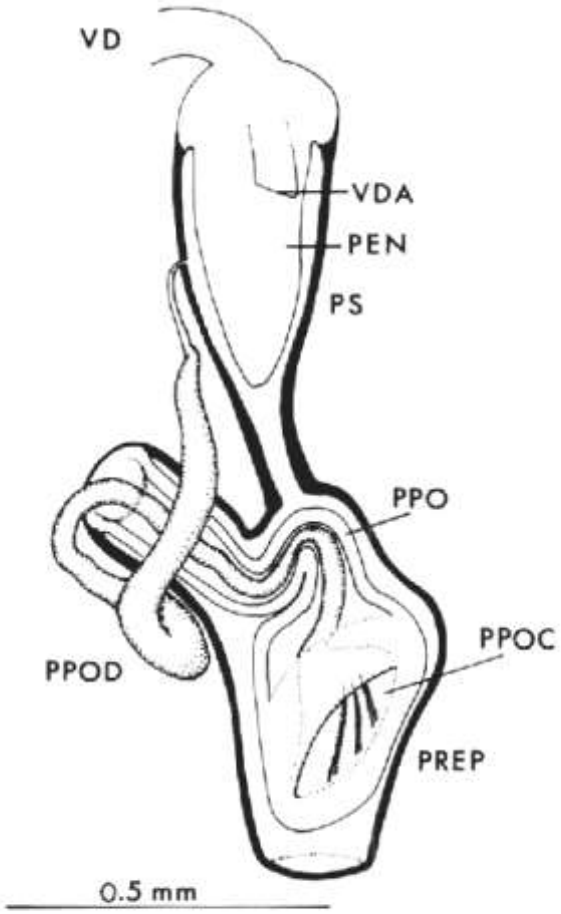

FIGURE 9—*Pecosorbis kansasensis* (Berry), composite diagram of penial complex. Some structures are seen in cross section, others by transparency. Abbreviations: **PEN,** penis; **PPO,** preputial organ; **PPOC,** preputial-organ cup; **PPOD,** preputial-organ duct; **PREP,** preputium; **PS,** penial sac; **VD,** vas deferens; **VDA,** vas deferens aperture.

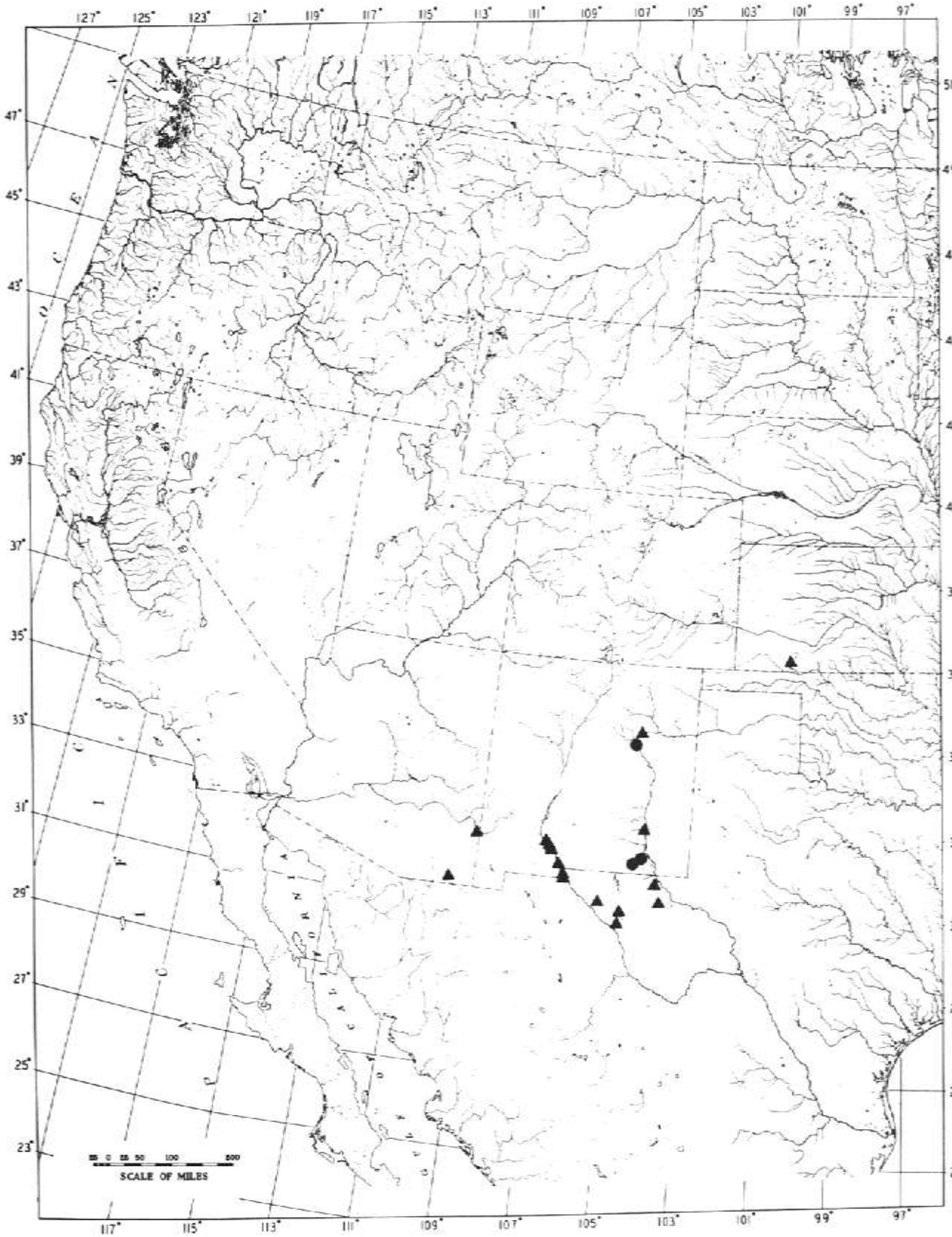

FIGURE 10—Distribution map of *Pecosorbis kansasensis* (Berry). Solid dots = modern localities, triangles = fossil localities; based only on specimens examined; stream-drift samples omitted. Base from the University of Michigan Museum of Zoology drainage map of the United States.

Taylor, 2-XI-1981. Little McKittrick Draw, 100 ft W, 2700 ft 5, sec. 29, T. 22 S., R. 25 E.; coll. A. L. Metcalf, 25-XI-1972 (UTEP 3463), D. W. Taylor, 19-IV-1981.

Quaternary

Arizona—GREENLEE COUNTY: About 1 mi S of Duncan on road to Morenci Pumping Station of El Paso Natural Gas Co.; coll. A. L. Metcalf, 25-X11-1965 (UTEP 7392). COCHISE COUNTY: Banks of Whitewater Arroyo about 12 mi NW of Douglas, Double Adobe fossil locality; coll. A. L. Metcalf, 3-X11-1965, bed *b* (UTEP 6324), beds *d–e* (UTEP 6319).

New Mexico—DONA ANA COUNTY: Picacho alluvium, localities P10, P12, P14, P17, and P22 of Metcalf (1967). Older valley alluvium, sec. 28, **T.** 19 S., R. 2 W., correlative with Tortugas unit. SAN MIGUEL. COUNTY: Holocene alluvium along Conchas River 2 mi N of Cabra Springs Ranch; coll. D. W. Taylor, 14X-1981. CHAVES Cowry: Alluvium along Rio Felix, 1000 ft W, 300 ft N, sec. 34, T. 13 S., R. 26 E.; coll. D. W. Taylor, 30-X-1981.

Texas—EL PASO COUNTY: Picacho alluvium, localities P-24, P-26, and P-27 of Metcalf (1967). CULBERSON COUNTY: 3 mi E of Van Horn along U.S. 80; coll. A. L. Metcalf, 25-X1-1962 (UTEP 7215). JEFF DAVIS COUNTY: Van Horn Creek along Farm Road 2017, 8.5 mi S of U.S. 90; coll. A. L. Metcalf, 23-111-1978 (UTEP 5953). HUDSPETH COUNTY: Finlay Mountains, banks of Campo Grande Arroyo 2 mi WSW of Cavett Ranch; coil. A. L. Metcalf, 10-1-1969 (UTEP 759). REEVES COUNTY: Salt Creek 7.5 mi SW of Orla; coll. A. L. Metcalf, 3-111-1979 (UTEP 6985). South tributary of Billingslea Draw on Saragosa Road; coll. A. L. Metcalf, 1962 (UTEP 3693); dated 12,140 ± 140 B.P. (Metcalf 1977: 59). PECOS COUNTY: Holocene alluvium along Pecos River 2 3/4 mi (straight line) SW of Grandfalls; coll. D. W. Taylor, 21X-1984.

Pliocene

Kansas—MEADE COUNTY: NW 1/4 sec. 14, T. 32 S., R. 29 W., Spring Creek local fauna, Ballard Formation; coll. C. W. Hibbard and others, 1963 (type locality).

Drift specimens have not been itemized because their age is uncertain and the distance of stream transport is speculative. They show the species will be found at other localities, at least as fossils.

Habitat

The two modern localities in Eddy County, southeast New Mexico, are almost precisely the same: seasonal rock pools in limestone ledges. The hollows in the rock are protected from the full force of flood scour, but are low enough along the arroyos to be filled by runoff. At the time of collection the pools were up to six inches deep, 15-20 ft long, with variable accumulations of mud. One pool in Last Chance Canyon was evidently permanent; it **contained** *Chara* **and a narrow-leaved** *Potamogeton.* Associated molluscs were *Planorbella tennis* (Dunker) and *Physa virgata* Gould at both places. Both were associated with *Pecosorbis* also near Santa Rosa, where Junius Henderson collected in 1929. That locality has been destroyed; **it** now lies beneath an interstate highway, but it was evidently similar to those in Eddy County. Henderson's notes specify only "small brook in Dakota ss. 4'12 mi. N.W. of Santa Rosa."

Holocene and older fossils are more widespread than the modern occurrences, and come in some instances from places far removed from any possible rock basins. Presumably, the modern habitat is in such basins because only there does water last long enough for the species to survive. Yet, this does not seem to provide an adequate explanation for the restricted modern range. The fossils likely came from seasonal pools or slow streams. Past episodes of greater or more effective precipitation forming pools along stream valleys in much of the arid Southwest are in keeping with the associated molluscan faunas (Metcalf 1967, 1969, 1974, 1982). The fossils also come from deposits that represent episodes of alluviation in contrast to the present arroyo cutting.

Classification and relationships

Pecosorbis falls within the subfamily Planorbulinae of Planorbidae in the classifications by Baker (1945) and Starobogatov (1967), and within the tribe Planorbulini in Ancyloplanorbidae, Camptoceratinae, according to Hubendick (1978). It is of morphological interest principally because it provides another instance of development of a preputial organ with external duct. Such a structure has been known previously in otherwise separate groups (Planorbidae and Helisomatinae of Baker, 1945), but not in Planorbulinae.

Absence of a spermatheca is striking because this structure is ordinarily present throughout the family. Yet it is lacking also in *Drepanotrema limayanum* (Lesson) as described by Paraense (1976). In that case absence of a spermatheca amounts only to a specific character, because the spermatheca is present in other species of the genus.

When Brown and Mandahl-Barth (1973) proposed the subgenus *Hovorbis* of *Afrogyrus,* they emphasized absence of the spermatheca as one character of the group. Subsequently, Brown (1980) noted that this character was no longer unique in Planorbidae. Nevertheless, absence of a spermatheca is rare in the family; it is known only in *Drepanotrema limayanum, Afrogyrus crassilabrum,* and now *Pecosorbis kansasensis.*

Pecosorbis is most like *Menetus* among the Planorbulinae in the character of an elongate preputial organ with terminal cup and a closed duct. In *Planorbula* and *Promenetus* the preputial organ has a lateral opening and is **roughly spoon-shaped, with an open channel. Comparison of** *Pecosorbis* with *Menetus* **led to a list** of differences (Table 1). *Planorbula* and *Promenetus,* as described by Baker (1945), are like *Menetus* and unlike *Pecosorbis* in having generally heavy pigmentation, a roughly fan-shaped prostate with long, many-branched diverticula, an elongate seminal vesicle with numerous outpocketings, and a spermatheca. Other features common to the three, in contrast to *Pecosorbis,* may be expected with further study. Walter (1971) recorded that *Promenetus* has a campanulate vagina

with a pair of calcareous, claw-like structures; no similar features are found in *Menetus* or *Pecosorbis*, but may be revealed in *Planorbula*. Insertion of the principal penial retractor muscle is on the penial sac in *Menetus*, but on the preputium in *Pecosorbis*, *Planorbula*, and *Promenetus*.

The other American group with a preputial organ that has an external duct is *Planorbella*. The reproductive system in *P. trivolvis lenta* is illustrated in Fig. 14. This illustration shows the ovotestis (OT) with numerous crowded and unpaired diverticula that are arranged roughly fan-wise in cross section; therefore, it falls within the Bulinidae in the classification by Starobogatov (1967). Comparison of Figs. 4 and 14 shows the numerous details in which *Pecosorbis* and *Planorbella* differ. Both genera have a preputial organ with an external duct. Comparison of Figs. 9 and 14 shows that in *Pecosorbis* the duct is roughly tubular and that the preputial organ not only distends the preputium but the proximal end projects externally.

TABLE 1. Comparison of *Menetus* and *Pecosorbis*. Abbreviations as in illustrations.

Characteristic	*Menetus*	*Pecosorbis*
Pigmentation	Heavy melanin suffusion, body opaque	Spotted mantle, scattered wisps, body transparent
Ovotestis (OT)	Major follicles branched once and paired	Major follicles unbranched, paired distally
Ovisperm duct, proximal (OSD)	Narrow relative to seminal vesicle, directed posteriorly	Wide relative to seminal vesicle, directed anteriorly
Seminal vesicle (SV)	Elongate, with numerous, bluntly rounded outpocketings	Compact, with fewer, wider chambers
Ovisperm duct, distal (OSD′)	About twice the length of SV, with outpocketings along most of the length	Four to five times the length of SV, outpocketings on proximal half
Oviduct (OV)	Indistinct; pouch of oviduct abuts on carrefour	Elongate; pouch remote from carrefour
Pouch of oviduct (PO)	Blunt-ended, with no crenulate outline	Tapered, with crenulate outline
Nidamental gland (NG)	Smooth dorsal margin	Crenulate dorsal margin
Uterus (UT)	Shorter, stouter	Longer, slender
Spermatheca (SP)	Stout, elongate sac	None
Spermathecal duct (SPD)	Distally enlarged	None
Spermiduct (SD)	Thick bulging walls, shorter	Tapering, slender, elongate
Prostate (PR)	Fan-shaped, with long, several-branched follicles fewer in number	Narrowly elongate, with short, one-branched or unbranched follicles more numerous
Vas deferens (VD)	Distally enlarged, even forming a massive epiphallus	Not enlarged distally
Retractor muscle (RM)	Inserts on penial sac	Inserts on preputium
Penial sac (PS)	About as wide as preputium	Narrower than preputium
Preputium (PREP)	Separated by septum from penial sac; generally tubular; pilasters present	Separated only by constriction from penial sac; swollen distally; pilasters absent
Preputial organ (PPO)	Contained within preputium; distends to about 1/3 the length of the preputium; inserts distally on preputium as extended	Projects into body cavity; distends longer than the preputium; inserts proximally on preputium as extended
Preputial-organ duct (POD, PPOD)	Opens subterminally on penial sac	Opens at 1/3 the length of the penial sac
Eversion of penial complex	Preputium only	Preputium and penial sac
Penis	Thickened tip	Unthickened tip
Pore of vas deferens	Subterminal	Lateral

Description of *Menetus*

Figs. 11-13

Pecosorbis is most like *Menetus* out of the three genera of Planorbulinae described by Baker (1945). Comparison between the two led to the notes and descriptions below.

Genus *MENETUS* H. and A. Adams, 1855

Type species (subsequent designation by Da11, 1870) is *Planorbis opercularis* Gould, 1847; type locality is Rio Sacramento, California.

The genus is restricted to western North America, from southern Alaska to southern California, eastward to northern Idaho. The geologic range is Miocene–Recent. Fossils extend the geographic range to Nevada and western Wyoming.

The number of living species, their differential characters, and nomenclature remain uncertain pending morphological studies. Based on present information, the following synopsis is plausible.

Menetus opercularis (Gould, 1847)—Shell periphery centrally carinate. Reproductive system (Baker, 1945) with vas deferens slightly enlarged at distal end, a short preputial organ, and narrow spermathecal duct. Known only from Mountain Lake, San Francisco, California; now extinct.

Menetus callioglyptus (Vanatta, 1895)—Shell carinate or subangular on the right, so that the right side of the shell is nearly plane. Reproductive system with vas deferens swollen distally, forming a large epiphallus longer than, and nearly as wide as, the penial sac; preputial organ large, filling much of the preputium; distal end of spermathecal duct swollen. Southern coastal Alaska southward to California; along the coast of California as far south as San Francisco; eastward to northern Idaho.

Menetus centervillensis (Tryon, 1871)—Shell with rounded periphery. Morphology unstudied. Oregon to southern California.

Fossil species of *Menet us* are as follows (Taylor and Smith, 1981): *M. carinifex* Taylor, 1981; Pliocene, Nevada. M. *idahoensis* (Yen, 1946), Miocene, Idaho. *M. planulatoides* Henderson and Rodeck, 1934; Miocene, Oregon. *M. vanvlecki* (Arnold, 1910); Pliocene, California.

Scope and rank of *Menetus* and treatment of the nominal species have varied as usual with various authors even in recent times. Baker (1945) regarded *Planorbifex as* a separate genus. The one species, *Menetus vanvlecki,* is distinguished only by the position of the carina, merely a species character *in Menetus;* therefore, it seems unworthy of any higher category (Taylor and Smith, 1981). Baker's subgenus of *Menetus, Micromenetus,* was investigated by Walter (1971), who found it differed widely from *Menetus* in reproductive system, shell sculpture, and other features. Walter advocated separating it, together with the genus *Neoplanorbis* of Alabama, in a separate group of Planorbidae. From cursory dissection of poorly preserved material of *Micromenetus* from California and Texas, it appears that those specimens are in agreement with Walter's data and differ significantly from *Menetus.*

Authors with more conservative views have advocated including *Menetus* in *Planorbula* (Hubendick, 1978; Walter, 1971). Most recently, Burch (1982) ranked *Menetus as* a genus including *Micromenetus* and even expressed doubt that subgeneric rank for the latter is warranted.

Previous descriptions of the morphology of *Menetus* are by Pilsbry (1934) and Baker (1945). Both authors studied the species identified here as *Menetus callioglypt us,* and their illustrations show clearly the relatively enormous epiphallus. Hubendick (1955) ostensibly described the type species, *Menetus opercularis* **(Gould). His material came from Michigan and,** I believe, it was surely *Promenetus exacuous* (Say). Baker's descriptions are perhaps all that will ever be known about *Menetus opercularis,* because the species is extinct. The differences in reproductive system between the two species seem well founded, because the major features Baker described in *M. callioglyptus* are confirmed herein.

At the species level, previous classifications have varied as usual. Baker (1945: 186) listed three species (the same three recognized here) with subspecies, but elsewhere in that work described additional species and subspecies. He studied the morphology of only two, *M. opercularis* **and** *M. callioglyptus.* Burch (1982) considered *Menetus* to include only *M. opercularis;* his illustrations (Burch, 1982, figs. 722, 723) both represent *M. callioglyptus* in the present sense.

The synopsis of the three living species of *Menetus* and their ranges provided above includes corrections of two previous errors, which are discussed below.

Type locality of *Menetus opercularis*—*Gould* (1847) attributed the species to "Rio Sacramento," collected by the U.S. Exploring Expedition in 1841. The species has never been obtained since then except in Mountain Lake, San Francisco. The summary of the Exploring Expedition collections by Carpenter (1857: 211213) lists no small species of Planorbidae from the Sacramento River, but does list a *"Planorbis (flat* and rather fine)" from San Francisco that I believe is the original collection of *Menetus opercularis.* The extraordinary vicissitudes of the Exploring Expedition material, with loss of specimens and data, have been described previously (Johnson, 1964).

Nomenclature of *Menetus callioglyptus*—*Baker* (1945) ranked *Menetus callioglyptus* (Vanatta, 1895) as a subspecies of *M. cooperi* Baker (1941). According to the International Code of Zoological Nomenclature (Article 23, Law of Priority), the oldest name of the species is preferred.

Description of *Menetus callioglyptus*

Material examined

Description and illustrations are based on a series of *Menetus callioglyptus* from the Metolius River, River-

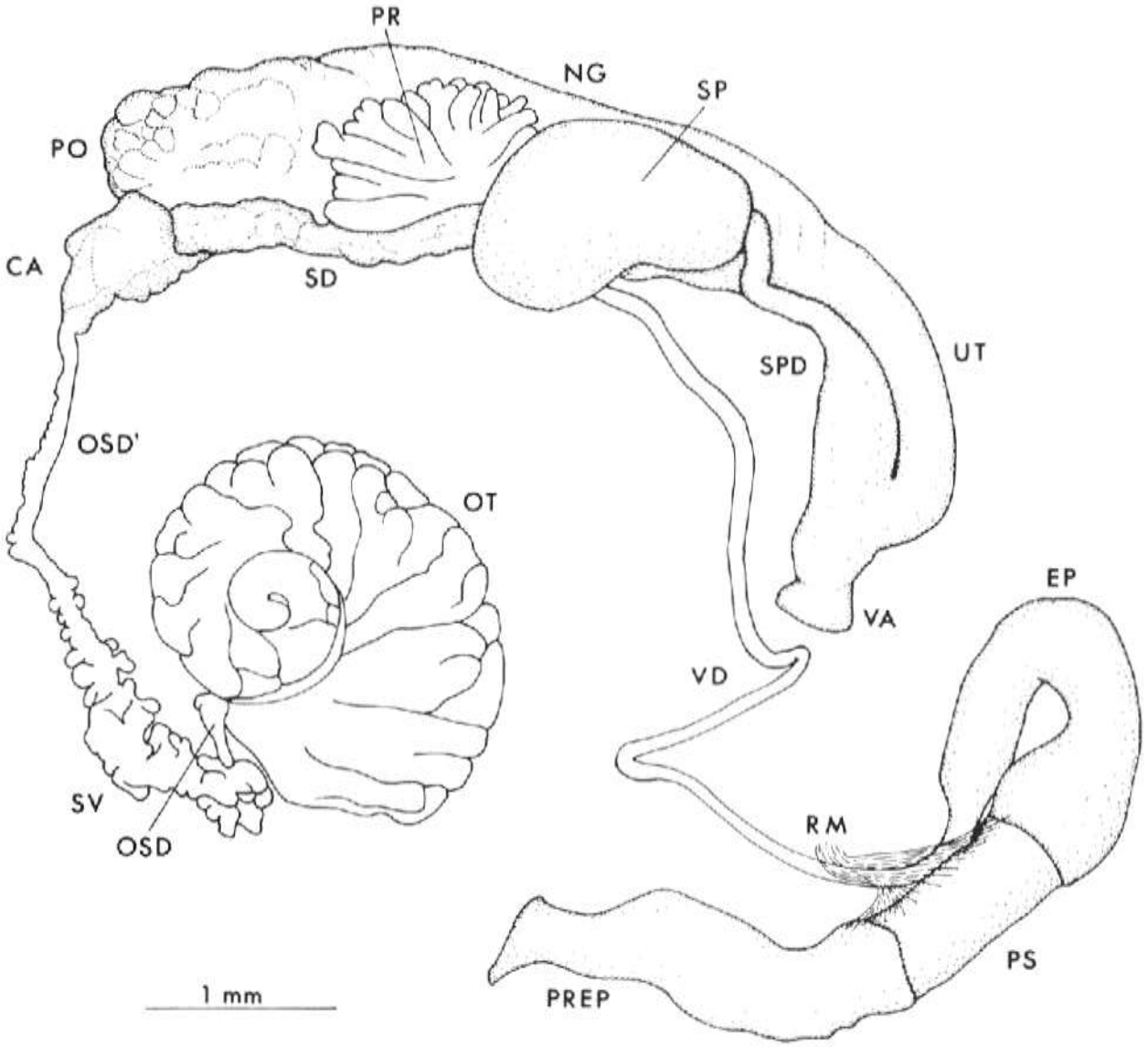

FIGURE 11—*Menetus callioglyptus* (Vanatta), reproductive system. Albumen gland not shown. Abbreviations: **CA,** carrefour; **EP,** epiphallus; **NG,** nidamental gland; **OSD,** ovisperm duct, proximal; **OSD',** ovisperm duct, distal; **OT,** ovotestis; **PO,** pouch of oviduct; **PR,** prostate; **PREP,** preputium; **PS,** penial sac; **RM,** retractor muscle; **SD,** spermiduct; **SP,** spermatheca; **SPD,** spermathecal duct; **SV,** seminal vesicle; **UT,** uterus; **VA,** vagina; **VD,** vas deferens.

side Camp, sec. 15, T. 13 S., R. 9 E., Jefferson County, Oregon, collected by D. W. Taylor, 14—X-1971. The locality is on the eastern slope of the Cascade Range in west-central Oregon, remote from the localities where Baker (1945: 186; as *cooperi* and *callioglyptus)* obtained specimens: Vancouver Island, British Columbia; the Puget Sound area, Washington; and Crescent City, extreme northwest California. The material studied by Pilsbry (1934) came from Corvallis in northwest Oregon, west of the Cascade Range.

Animal

Externally, the body is dark gray to black and opaque from a dense melanin suffusion, but is lighter on the ventral surface. After removal of the shell, the mantle can be seen as varied in intensity of pigmentation. In darker specimens scarcely any organs are visible through the mantle, except that toward the tip of the visceral spire outlines of follicles of the ovotestis can be seen. In paler specimens the stomach, major ves-

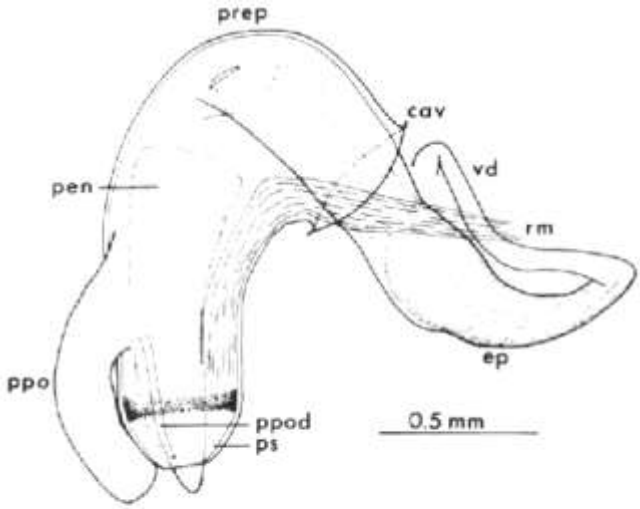

FIGURE 12—*Menetus callioglyptus* (Vanatta), penial complex as everted. Abbreviations: **cav,** wall of body cavity; **ep,** epiphallus; **pen,** penis; **ppo,** preputial organ; **ppod,** preputial-organ duct; **prep,** preputium; **ps,** penial sac; **rm,** retractor muscle; **vd,** vas deferens.

sels, and intestine are seen in outline. Also the large penial complex can be seen through the mantle. The posterior angle of the epiphallus (El? in Figs. 11, 13) reaches L/4 whorl from the mantle collar. Internally, only the reproductive system was studied (10 specimens; Figs. 11-13).

Reproductive system

Hermaphroditic portion—Ovotestis with the major diverticula in pairs except at the posterior tip; the diverticula usually branch once. In peripheral view the tips of the follicles appear to be arranged in three to four transverse rows. The collecting canal discharges into a short ovisperm duct, consistently directed backwards, that leads to the seminal vesicle. The vesicle is discrete and blunt proximally, but the bluntly rounded follicles diminish gradually toward the distal end so that the separation of seminal vesicle from distal ovisperm duct is not precise. Outpocketings of the duct continue most of the way to the carrefour. Neither the albumen gland nor the carrefour are unusual.

Male portion—The stout spermiduct has an uneven, bulging surface and leads to a roughly fan-shaped prostate. In lateral view one to three branches of the follicles are visible; medially more branches are present. The vas deferens is a narrow tube of uniform diameter to the penial complex. It enlarges quickly into a thick-walled epiphallus with a broad, triangular lumen, arched through 180° in the middle or at about three-fourths of its length. Thus the proximal end of the epiphallus may lie along the penial sheath near either its proximal or distal end. The epiphallus enlarges into a muscular swelling around the head of the penis; neither externally nor internally is there a sharp demarcation between epiphallus and penial sac. The proximal part of the penial sac is a symmetrical muscular tube surrounding the stout penis. Distally the sac becomes asymmetrical, receives the duct of

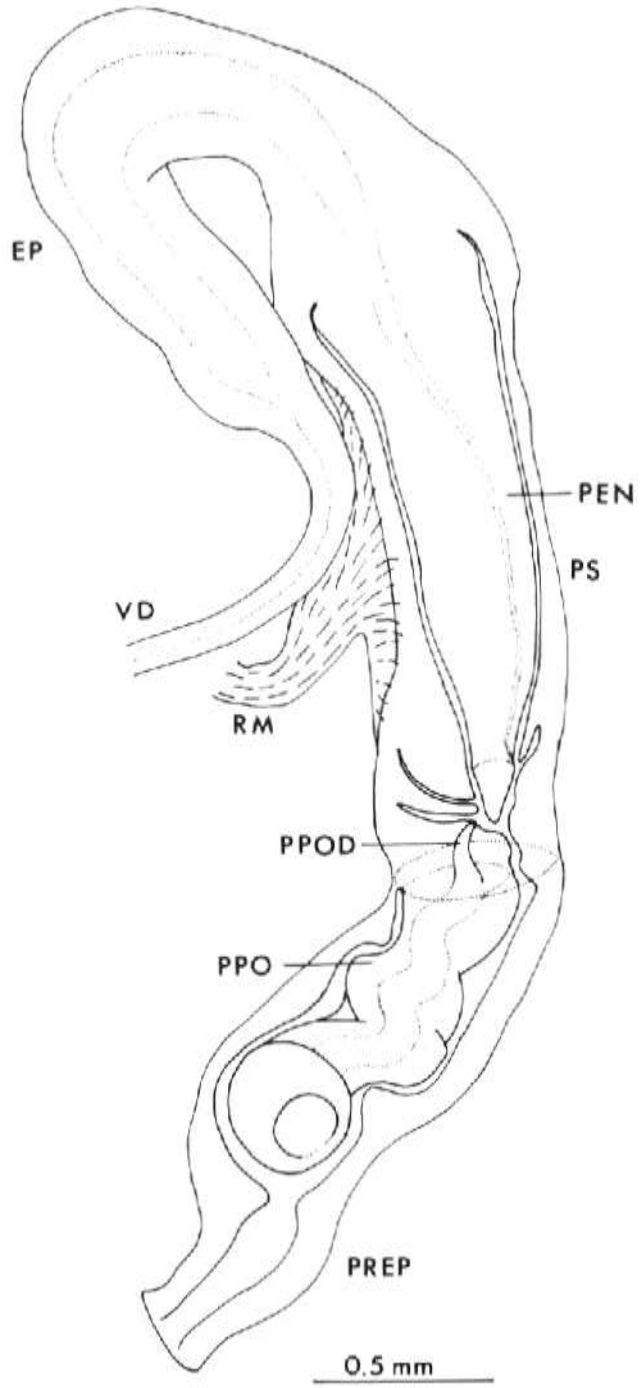

FIGURE 13—*Menetus callioglyptus* (Vanatta), penial complex as retracted. Some structures are seen in cross section or by transparency. Abbreviations: **EP**, epiphallus; **PEN**, penis; **PPO**, preputial organ; **PPOD**, preputial-organ duct; **PREP**, preputium; **PS**, penial sac; **RM**, retractor muscle; **VD**, vas deferens.

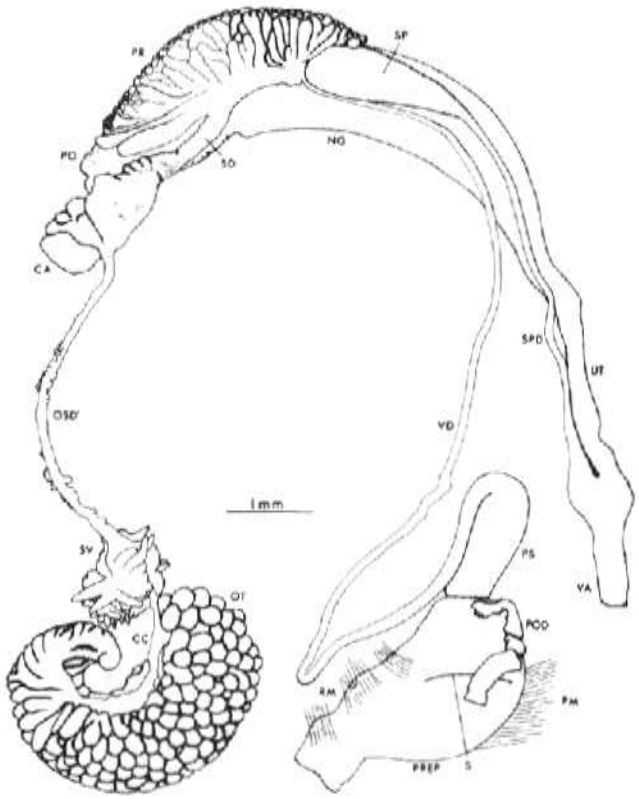

FIGURE 14—Reproductive system of *Planorbella trivolvis lenta* (Say) from West Frio River, Prade Ranch, Real County, Texas. Albumen gland not shown. Abbreviations: **CA**, carrefour; **CC**, collecting canal of ovotestis; **NG**, nidamental gland; **OSD'**, distal part of ovisperm duct; **OT**, ovotestis; **PM**, protractor muscle; **PO**, pouch of oviduct; **POD**, preputial-organ duct; **PR**, prostate; **PREP**, preputium; **PS**, penial sac; **RM**, retractor muscles; **S**, slit in preputium; **SD**, spermiduct; **SP**, spermatheca; **SPD**, spermathecal duct; **SV**, seminal vesicle; **UT**, uterus; **VA**, vagina; **VD**, vas deferens.

the preputial organ, and is separated except for a narrow opening from the tubular preputium.

Five specimens out of the series were preserved with preputium and its organ everted (Fig. 12). The walls of both are transparent. Internally, wisps of melanin form an irregular anastomosing network on the penial sac and outline nerves and vessels on its surface. A ring of heavy melanin surrounds the sac near its distal end.

The preputial organ is a slightly tapering, tubular structure inserted on the preputium about one-third the length from the distal end (as extruded) on the posterolateral aspect. It lacks all melanin. As preserved, the end is a fleshy cup with irregularly folded walls. The duct within discharges just inside the lumen of the everted preputium.

The penis is a stout, narrowly conical body with a firm but non-cuticular tip. The terminal pore of the narrow vas deferens is immediately behind this tip.

Female portion—The pouch of the oviduct is studded with low, globular swellings in contrast to the smooth outline of the nidamental gland. A short uterus meets the duct of the spermatheca at a pronounced angle. The spermatheca is a bulky, elongate sac up to about three times as long as wide. It discharges by a duct that is at first narrow but widens to as much as four or five times that width, and becomes even wider than the distal end of the uterus. This dilated, distal portion of the duct has thick, muscular plicate walls and, because it is in line with the vagina, it may receive the tip of the penis.

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Selected conversion factors*

TO CONVERT	MULTIPLY BY	TO OBTAIN
Length		
inches, in	2.540	centimeters, cm
feet, ft	3.048×10^{-1}	meters, m
yards, yds	9.144×10^{-1}	m
statute miles, mi	1.609	kilometers, km
fathoms	1.829	m
angstroms, Å	1.0×10^{-8}	cm
Å	1.0×10^{-4}	micrometers, μm
Area		
in^2	6.452	cm^2
ft^2	9.29×10^{-2}	m^2
yds^2	8.361×10^{-1}	m^2
mi^2	2.590	km^2
acres	4.047×10^{3}	m^2
acres	4.047×10^{-1}	hectares, ha
Volume (wet and dry)		
in^3	1.639×10^{1}	cm^3
ft^3	2.832×10^{-2}	m^3
yds^3	7.646×10^{-1}	m^3
fluid ounces	2.957×10^{-2}	liters, l *or* L
quarts	9.463×10^{-1}	l
U.S. gallons, gal	3.785	l
U.S. gal	3.785×10^{-3}	m^3
acre-ft	1.234×10^{3}	m^3
barrels (oil), bbl	1.589×10^{-1}	m^3
Weight, mass		
ounces avoirdupois, avdp	2.8349×10^{1}	grams, gr
troy ounces, oz	3.1103×10^{1}	gr
pounds, lb	4.536×10^{-1}	kilograms, kg
long tons	1.016	metric tons, mt
short tons	9.078×10^{-1}	mt
oz mt^{-1}	3.43×10^{1}	parts per million, ppm
Velocity		
ft sec^{-1} (= ft/sec)	3.048×10^{-1}	m sec^{-1} (= m/sec)
mi hr^{-1}	1.6093	km hr^{-1}
mi hr^{-1}	4.470×10^{-1}	m sec^{-1}

TO CONVERT	MULTIPLY BY	TO OBTAIN
Pressure, stress		
lb in^{-2} (= lb/in^2), psi	7.03×10^{-2}	kg cm^{-2} (= kg/cm^2)
lb in^{-2}	6.804×10^{-2}	atmospheres, atm
lb in^{-2}	6.895×10^{3}	newtons (N)/m^2, N m^{-2}
atm	1.0333	kg cm^{-2}
atm	7.6×10^{2}	mm of Hg (at 0° C)
inches of Hg (at 0° C)	3.453×10^{-2}	kg cm^{-2}
bars, b	1.020	kg cm^{-2}
b	1.0×10^{6}	dynes cm^{-2}
b	9.869×10^{-1}	atm
b	1.0×10^{-1}	megapascals, MPa
Density		
lb in^{-3} (= lb/in^3)	2.768×10^{1}	gr cm^{-3} (= gr/cm^3)
Viscosity		
poises	1.0	gr cm^{-1} sec^{-1} *or* dynes cm^{-2}
Discharge		
U.S. gal min^{-1}, gpm	6.308×10^{-2}	l sec^{-1}
gpm	6.308×10^{-5}	m^3 sec^{-1}
ft^3 sec^{-1}	2.832×10^{-2}	m^3 sec^{-1}
Hydraulic conductivity		
U.S. gal day^{-1} ft^{-2}	4.720×10^{-7}	m sec^{-1}
Permeability		
darcies	9.870×10^{-13}	m^2
Transmissivity		
U.S. gal day^{-1} ft^{-1}	1.438×10^{-7}	m^2 sec^{-1}
U.S. gal min^{-1} ft^{-1}	2.072×10^{-1}	l sec^{-1} m^{-1}
Magnetic field intensity		
gausses	1.0×10^{5}	gammas
Energy, heat		
British thermal units, BTU	2.52×10^{-1}	calories, cal
BTU	1.0758×10^{2}	kilogram-meters, kgm
BTU lb^{-1}	5.56×10^{-1}	cal kg^{-1}
Temperature		
°C + 273	1.0	°K (Kelvin)
°C + 17.78	1.8	°F (Fahrenheit)
°F − 32	5/9	°C (Celsius)

Divide by the factor number to reverse conversions.
Exponents: for example 4.047×10^{3} (see acres) = 4,047; 9.29×10^{-2} (see ft^2) = 0.0929.

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