

SYSTEMATIC REVISION OF THE HYDROBIIDAE (GASTROPODA: RISSOACEA)
OF THE CUATRO CIÉNEGAS BASIN, COAHUILA, MÉXICO

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ABSTRACT

This study gives detailed morphological descriptions, including aspects of shell and soft-part anatomy, for 12 species of nine genera of hydrobiid snails (Gastropoda: Rissoacea) from the isolated desert spring system of Cuatro Ciénegas, Coahuila, México. Snails were collected from 103 localities in the basin and summaries of the distribution and ecology for each species are given. One new genus and three new species are described.

The six nominal species of *Mexipyrghus* are reduced to one variable species, *Mexipyrghus churinceanus*, as there are no suites of morphological features that can consistently define separate taxa when a large number of populations is studied. A multivariate morphological analysis of *Mexipyrghus churinceanus*, involving 20 morphological characters from 33 populations in the basin, shows that the trends of variation only partly follow the distribution of populations among the drainage systems of the basin.

Contrary to previous thought, there are no subfamilies of hydrobiids endemic to the Cuatro Ciénegas basin; all taxa studied belong to either the Nymphophilinae or Littoridininae, widely distributed subfamilies. Five genera and at least nine species are endemic to the basin. Phenetic and phyletic analyses show that of the five endemic genera, three are more closely related to nonendemic genera found in the basin than to each other, suggesting a polyphyletic origin for the endemic snails. The endemic snails may also be of a more recent and local origin than once thought. Snail taxa from the Pliocene Pebas Formation of Peru, the shells of which are superficially similar to those of the Cuatro Ciénegas endemic taxa, are not Hydrobiidae and thus the conchological similarity is due to convergence.

Four of the Cuatro Ciénegas hydrobiid genera are ovoviviparous. Anatomical studies show that the evolution of this reproductive mode in the Hydrobiidae has involved modifications of the female reproductive system to separate incoming sperm from outgoing embryos, increase the amount of space available for holding embryos, and allow for control of the release of young.

Key words: Hydrobiidae; Cuatro Ciénegas; systematics; morphology; endemism; evolution; ovoviviparity.

INTRODUCTION

The small (30 by 40 km) desert valley of Cuatro Ciénegas, Coahuila, México (Fig. 1) harbors a remarkable endemic biota (Contreras, 1978; Minckley, 1969). Most of the endemic taxa are associated with the extensive spring fed aquatic environments of this closed-drainage basin and include one genus and four species of crustaceans (Cole & Minckley, 1966, 1970, 1972; Holsinger & Minckley, 1971), eight-ten species of fishes (Minckley, 1977), and two species of turtles (Schmidt & Owens, 1944; Webb & Legler, 1960). In addition, three subfamilies, five genera, and 12 species of hydrobioid snails (those rissoacean snails that resemble *Hydrobia* in shell, operculum, penis, or radula) have been considered endemic to the valley (Taylor, 1966).

Apart from their high endemism, the hydrobioid snails of Cuatro Ciénegas are of interest for the following reasons: 1) a number of taxa have large, sculptured or color-banded shells whereas most hydrobioids have small, smooth shells without color bands; 2) several taxa may have been involved in coevolution with snail-eating cichlid fishes in the valley (Vermeij & Covich, 1978); 3) the snails are deployed within a nearly unique variety of spring fed aquatic environments within the desert; 4) differentiated populations of snails are found among the various springs of the valley and offer the opportunity to study evolution in a natural laboratory (Taylor, 1966; Taylor & Minckley, 1966).

The original description of the Cuatro Ciénegas hydrobioids (Taylor, 1966) stimulated this study and stands as an exemplary contribution for that time period. Credit should

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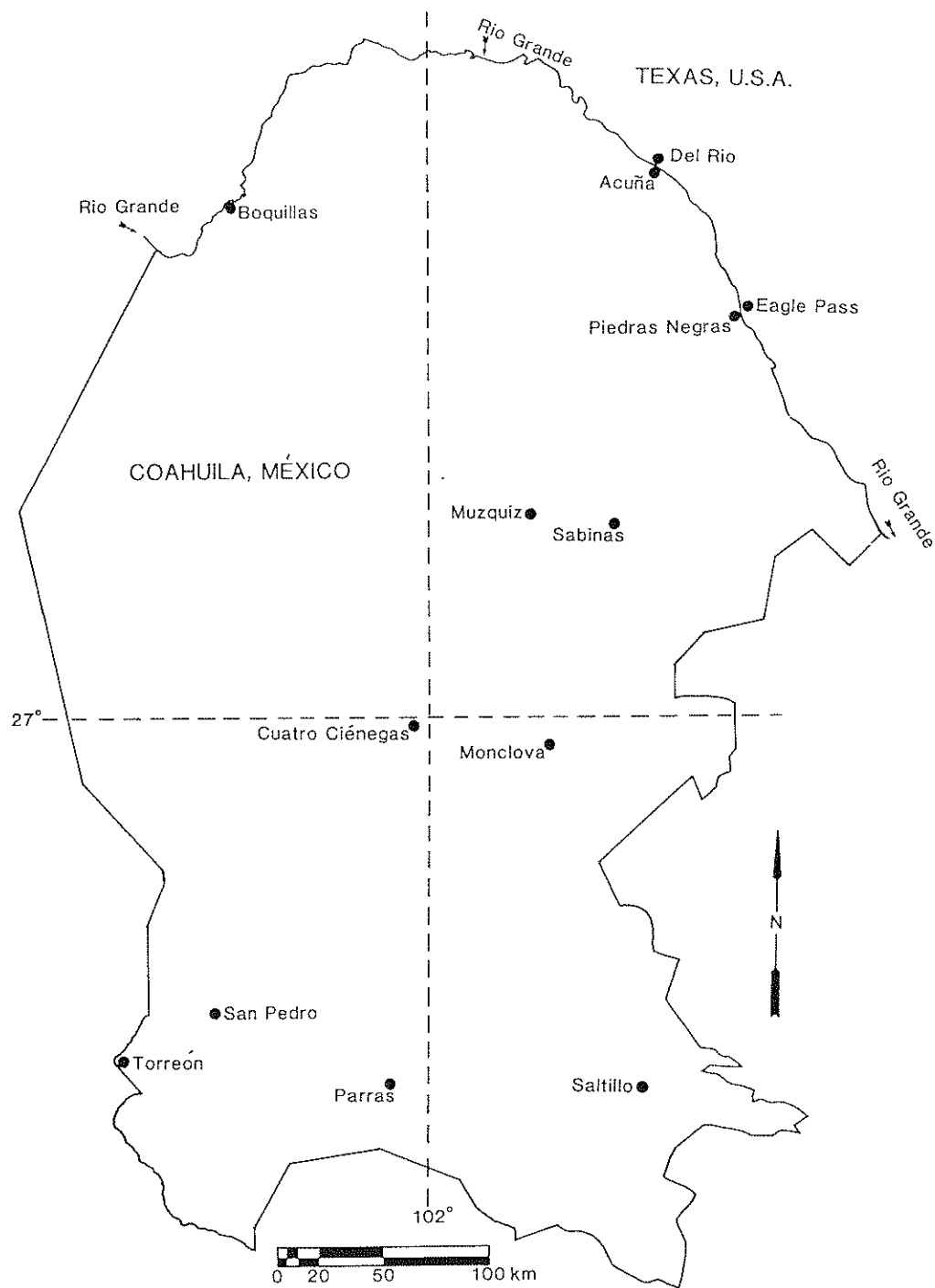


FIG. 1. Map of Coahuila, México, showing the location of the Cuatro Ciénegas Basin. The arrows indicate the direction of flow of the Rio Grande.

be given to that author for recognizing the uniqueness of both the hydrobioid fauna and the environmental setting.

The classification scheme within which the Cuatro Ciénegas hydrobioid snails were described was based on a character set restricted to shell, operculum, penis, and a few other aspects of external morphology (Taylor, 1966). It is now known, on the basis of overall soft part anatomy, that such characters have frequently converged in hydrobioid taxa that are not closely related (Davis, 1979). In a series of papers (Davis, 1968, 1979, 1980; Davis *et al.*, 1976, 1982; Davis & Pons da Silva, 1984) it was shown that the Hydrobiidae (pre-1980) are polyphyletic and that study of all aspects of soft part morphology, particularly the entire female reproductive system, is necessary to recognize convergences and clarify the systematic relationships of hydrobioid snails. As the original descriptions of the Cuatro Ciénegas hydrobioids did not include aspects of internal anatomy, these taxa's classification is suspect. The species descriptions were usually based on collections from single localities, and only 12 localities were sampled (Taylor, 1966).

This paper: 1) presents detailed morphological descriptions of the Cuatro Ciénegas hydrobioid taxa and assesses their systematic affinities, the results of which are frequently at odds with previous classification (Taylor, 1966). One new genus and three new species are described. Morphological data from populations are analyzed to resolve species problems; 2) summarizes the distribution and ecology of each species (103 localities sampled in the valley); 3) discusses the results of the above as they relate to the origin, evolution, and endemism of the hydrobioid snails of Cuatro Ciénegas; 4) discusses the evolution of ovoviviparity¹ in hydrobioid snails.

Environmental Setting

Cuatro Ciénegas lies in the mideastern section of the Chihuahuan Desert (Miller, 1977; Fig. 1). The valley receives less than 200 mm of precipitation annually (Minckley, 1969). The mean annual temperature is 23°C (Morafka, 1977), with midday summer temperatures exceeding 40°C. The valley floor is 740 m above sea level, bounded on all sides by tall (to 3000 m) peaks of the Sierra Madre Oriental. The valley floor is relatively flat.

The basin consists of two lobes, separated by the northern end of the Sierra de San Marcos (Fig. 2). There are far more springs in the eastern than in the western lobe. Springs are particularly concentrated around the Sierra de San Marcos. The springs vary: there are small seeps; small springs with spring pool areas of less than 10 m² that run for only tens of meters; and much larger springs with spring pool areas in excess of 900 m² and depths to 7 m, whose outflows are large streams. While most of the springs are limnocrenes, with spring pools at the heads, there are also rheocrenes, where water rushes out of the ground as flowing streams. Other aquatic environments include playa lakes, receiving flow from large streams; spring fed pools that have no outflows; and extensive spring fed marshes. This great diversity of desert spring fed aquatic environments can only be matched in North America by that seen in the Death Valley-Ash Meadows area (Deacon & Minckley, 1974; Soltz & Naiman, 1978).

Spring levels vary seasonally, as the water table rises in the winter and drops in the summer. The spring water is generally quite hard and high in sulphates (Minckley & Cole, 1968). Most of the springs are thermal (to 34°C), but cooler (14–25°C) springs are also found. The larger springs have fairly constant water temperatures throughout the year (Minckley, 1969), while spring runs and shallow pools can be subject to considerable variation in water temperature. For example, North Spring has a spring pool area of about 230 m² and a maximum depth of 1.5 m. Its waters flow into a second pool and then run as a wide shallow stream for 77 m before disappearing into a hole. The spring is thermal; 10 separate headspring temperature readings during 1981 gave a mean of 32.9°C (29.5–34.5°C). Maxi-mini thermometer readings for four days (beginning 6/18/81) had a variation of 31–34.5°C for the head and 20.6–37.8°C at the hole where the water goes underground. Thus, during this time period, the headspring water temperature varied only 3.5°C while downstream it varied 17.2°C.

The larger springs and their outflows have considerable microhabitat diversity, usually including several types of aquatic vegetation (sedges, *Nymphaea*, *Chara*, *Utricularia*); a soft sediment consisting of snail copropel and/or an algal-detritus mixture; a sand con-

¹By ovoviviparity I mean brooding young without direct tissue connection, following Van der Schalie (1936).

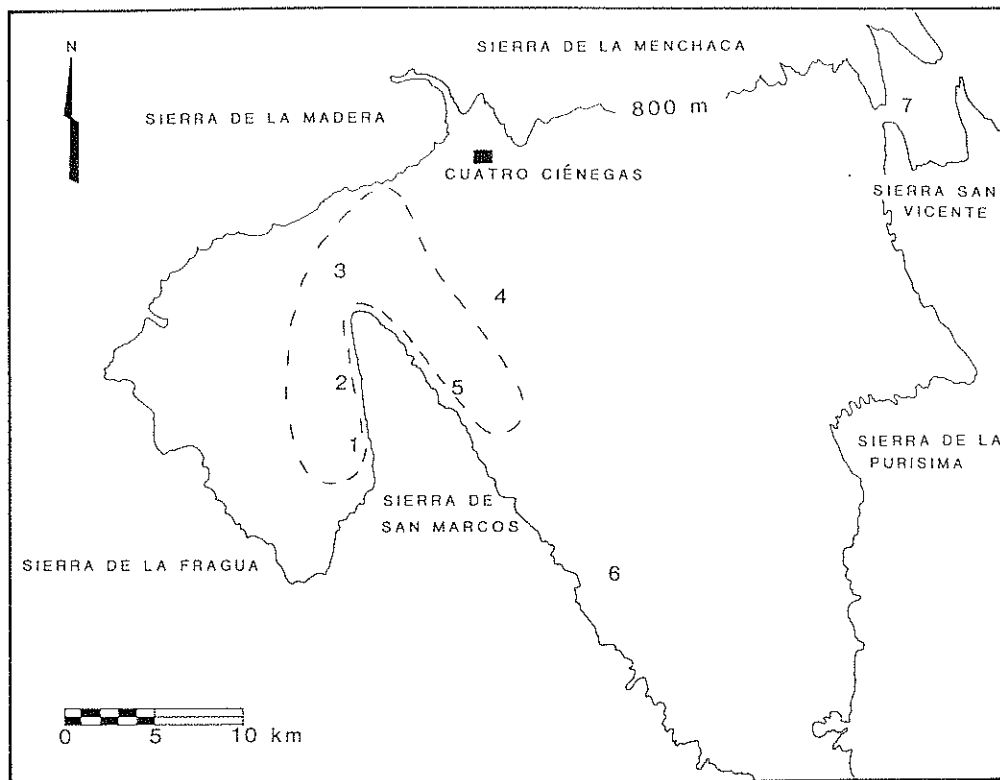


FIG. 2. Map of the Cuatro Ciénegas Basin, showing the portion of the basin that was intensively sampled (area enclosed by dashed lines). The numbers indicate the origins of the seven major drainages of the basin (from Minckley, 1969): 1, the Churince system; 2, the Becerra system; 3, the Rio Mesquites system; 4, Rio Puente Chiquito; 5, Tio Candido; 6, Santa Tecla Laguna; 7, Rio Salado de Nadadores.

sisting of travertine pieces and shell debris; large travertine blocks; and the banks, which can be gently sloping or greatly undercut. The smaller springs and their outflows have fewer microhabitats, typically including a dark organic mud, fine travertine sand, and occasional *Chara* mats.

Five to seven major drainage systems occur in the valley (Fig. 2), with possible natural connections existing between them via underground rivers, or surficial waters during rainy periods (LaBounty, 1974; Minckley, 1969). A number of irrigation canals drain water from the large springs, lowering their levels and destroying peripheral aquatic habitats (Minckley, 1969). Irrigation canals from different drainage systems are often connected, offering opportunities for gene flow between previously isolated populations. The basin currently has no surficial connection to outside drainage, but water has probably

drained from the basin to the nearby Rio Salado de Nadadores (Fig. 2, Locality 7) in the past (Miller & Minckley, 1963; Minckley, 1969). More information on the aquatic environments of the basin can be found in Arnold (1972), Brown (1974), Deacon & Minckley (1974), and Minckley (1969).

MATERIALS AND METHODS

Localities

The waters of only a portion of the valley drainage (dashed line in Fig. 2), encompassing parts of four of the basin drainages, were intensively sampled. One hundred collection localities from this area are shown in Fig. 3 and described in Appendix 1. Three other localities (101–103 in Appendix 1) from other areas were also sampled. The various locali-

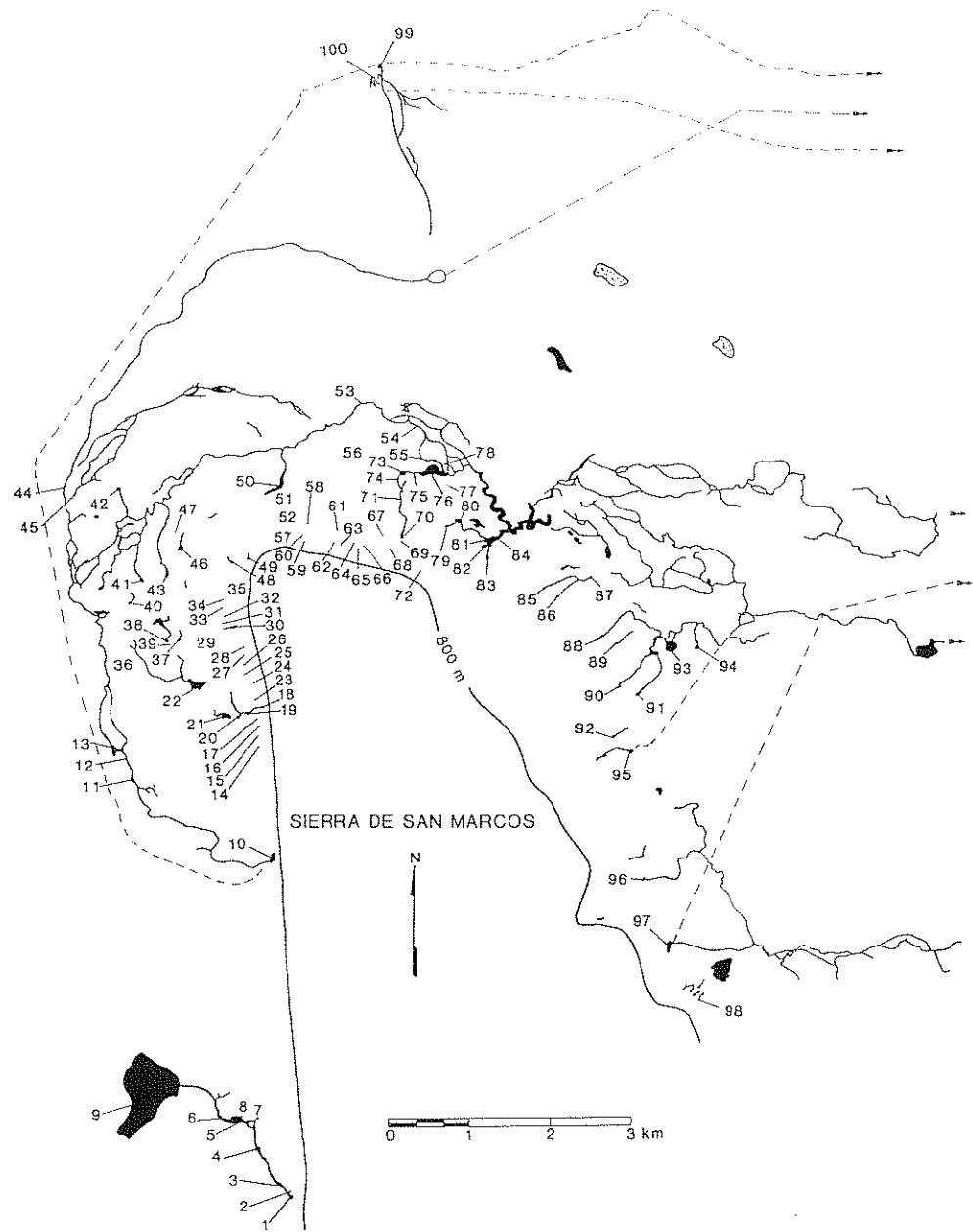


FIG. 3. Map of the portion of the basin drainage that was intensively sampled. The numbers (1–100) refer to collection localities. The dashed lines refer to irrigation canals. The arrows indicate waters that continue to flow toward the east.

ties (and ANSP catalog numbers for the lots) for each species are given in Appendix 2. Snails were collected and studied in the valley during September, 1978; April–August, 1979; April, 1980–June, 1981; and December, 1981.

Collection Methods

Fine hand sieves were used to collect snails from sediments ranging from flocculent copropel to coarse travertine sand. In some cases, the sediment itself was collected and

examined under a dissecting microscope to determine whether very small snails, which would pass through the sieves, were present. Snails were picked off large pieces of travertine using tweezers. Samples of aquatic vegetation were collected and carefully washed in a bucket to remove clinging snails. The material was then sorted under a dissecting microscope. A number of snail taxa are suspected of living in groundwater outlets or subterranean waters of the valley (Taylor, 1966). To collect such snails, ordinary domestic mops were placed into small springheads, removed after a 24 hour period, and then washed in a bucket. The snails that colonized the mops were collected and sorted under a dissecting microscope (method suggested orally by Dr. W. L. Minckley; similar method described in Holsinger & Minckley, 1971). For each small springhead, one to ten mop samples, spread out over a period of months, were taken. This method is crude as it cannot distinguish between snails living at the groundwater outlet and those being washed out from underground. A superior method, sampling only snails from subterranean waters, would be to place a fine mesh net over the groundwater outlet, essentially filtering snails from the water stream; such a method has been successfully used to sample the fauna of artesian wells (Holsinger & Longley, 1980).

Anatomy

Dissection techniques are those of Davis (1979) and Davis & Carney (1973). Several other techniques were also employed. The penis was cut from the male, examined on both sides at 50 \times magnification, and then wet-mounted on a slide with cover slip for study using a compound microscope fitted with an ocular micrometer. The length of the pallial oviduct is the length from the anterior end to the posteriormost point, excluding any length bent back upon itself at the posterior end. The length of the duct from the seminal receptacle is the length from the seminal receptacle body to the junction with the oviduct or sperm duct. The nervous system was studied for species of all genera except *Mexistiobia* n. gen. and *Coahuilix* and showed no variance except in size and concentration of ganglia. Therefore, the measurements of the nervous structures are not presented. For ovoviparous species, shelled embryos were gathered by cracking the shell of an adult

female, removing the brood pouch, and placing it in a drop of CLOROX for several minutes (Davis, 1969b). The embryonic shells were then counted and, in some cases, measured. In addition, the brood pouches of several snails were teased apart so the small, nonshelled embryos could be counted. Shell measurements for the various taxa are from mature adults (those having a complete aperture). The apical whorls of shells were measured using the method of Davis (1967, pl. 3, fig. 6). Radulae and shells were studied and photographed using the SEM facility at the Academy of Natural Sciences of Philadelphia. Statistical techniques, for the most part, are restricted to t-tests and correlation coefficients.

The generic descriptions are necessarily brief, as anatomical data is generally available for only one species per genus (due to monotypy or lack of studies of congeners). The descriptions will have to be altered as more data become available. Only character states unique to the various taxa, or of use in assessing their systematic status, are stressed. Other characters and their character states that are standard for the Rissoacea: Hydrobiidae (Davis, 1966, 1979; Hershler & Davis, 1980) are not mentioned and include, for example, the characteristic loop of the intestine above the style sac, the position of the salivary glands on top of the nerve ring, and the ovoid shape of the fecal pellets. Fifty-one characters and their character states that were used to distinguish genera and generic groups in the Hydrobiidae are listed in Appendix 3 with notations as to where they are figured. Common radular formulas for species studied are given in Table 1. Several characters may be unfamiliar to the reader and require explanation. The bolster and ventral channel of the pallial oviduct are defined and discussed in Davis *et al.* (1982), and Davis & Pons da Silva (1984). The caecal chamber (defined in Davis *et al.*, 1982), while apparently present in all Hydrobiidae, is reduced in some taxa so as not to project posterior to the stomach. Tentacle ciliation is discussed in Davis *et al.* (1982). The digestive gland of hydrobioid snails usually has finger-like tubercles projecting from the main body, but in small sized snails the tubercles may be mere swellings. In resolving species problems, emphasis was placed on whether purported species were sympatric or not, and whether consistent morphological differences between purported species could be found

TABLE 1. Generalized cusp formulas for the four tooth types of the radula of all species studied.

Species	Central	Lateral	Inner marginal	Outer marginal
<i>Nymphophilus minckleyi</i>	$\frac{4(5)-1-4(5)}{3-3}$	2(3)-1-2(3)	12-17	15-20
<i>Mexistiobia manantiali</i>	$\frac{4(5)-1-4(5)}{1-1}$	4(5)-1-3	19-24	22-26
<i>Coahuilix hubbsi</i>	$\frac{3(4)-1-3(4)}{1-1}$	5-1-3(4)	16-21	16-19
<i>Paludiscala caramba</i>	$\frac{4(5)-1-4(5)}{1-1}$	4(5)-1-3	18-24	16-25
<i>Cochliopina milleri</i>	$\frac{4(5)-1-4(5)}{1-1}$	3(4)-1-3	18-25	19-28
<i>Mexithauma quadripaludium</i>	$\frac{4(5)-1-4(5)}{2(3)-2(3)}$	3(4)-1-3(4)	10-14	12-16
<i>Durangonella coahuilae</i>	$\frac{4(5)-1-4(5)}{1-1}$	4(5)-1-4(5)	19-27	20-27
<i>Mexipyrgus churinceanus</i>	$\frac{4(5)-1-4(5)}{2(3)-2(3)}$	4(5)-1-4(5)	21-36	24-38

when numerous populations were studied. The descriptions of taxa not named in this paper are modified from those of Taylor (1966) and Thompson (1979).

For a multivariate analysis of *Mexipyrgus churinceanus* populations the computer program used was the June, 1974 version of the SUNY at Stony Brook numerical taxonomy program, NT-SYS (Rohlf *et al.*, 1972). Characters were standardized in the usual manner (Sneath & Sokal, 1973). In the Q-mode analysis, a taxonomic distance matrix was generated, using the unweighted pair-group method with arithmetic averaging (UPGMA). The minimum spanning tree (MST) and "subsets" components of NT-SYS were used. For the R-mode analysis, character correlations were subjected to Principal Components Analysis (PCA), with the first three components used to yield a matrix of OTU projections in principal component space. These OTU locations in the three-dimensional PCA space were used as the initial configuration for a nonmetric multidimensional scaling (MDS) placement of the Q-mode taxonomic distances between OTUs. The Prim Network was used. As the cluster analysis and phenograms generated are subject to distortion, only the ordination and MDS are presented here. Components were extracted until eigenvalues were less than 1.0. Subset solutions and the minimum spanning tree are superimposed on the ordination diagrams.

SYSTEMATIC FRAMEWORK

The basic features of rissoacean snails are reviewed in Fretter & Graham (1962). Davis (1979) has listed the features that distinguish hydrobioid snails from other rissoaceans. The definitions below are modified from those of Davis (1979, 1980) and Davis *et al.* (1982).

Family Hydrobiidae

These include hydrobioids in which sperm enter the anterior end of the pallial oviduct and pass along an internal, ciliated ventral channel to the bursa copulatrix; or, in which sperm enter a separate spermathecal duct, presumably formed by separation of the ventral channel from the pallial oviduct (not to be confused with the convergent structure of the Pomatiopsidae), and pass through it to the bursa copulatrix. The spermathecal duct is never associated with either the kidney or the pericardium (contrast the Triculinae). The mode of reproduction is oviparity or ovoviviparity. The penis may (Thompson, 1968, fig. 39) or may not (Thompson, 1968, fig. 37) have lobes. The penis may also be without specialized glands (Hershler & Davis, 1980, fig. 4D), or may have glandular ridges consisting of an elevated area in which rows of small glands discharge through a central slit (Thompson, 1968, fig. 42); apocrine glands (Andrews, 1977, p. 82, fig. A); glandular papillae (Hubendick, 1955, fig. 88); or mammiiform

glands (Fig. 44). The latter two gland types are only borne on penial lobes, whereas glandular ridges and apocrine glands can be found on the penis as well (Thompson, 1968, figs. 44, 38, respectively). There is neither a pedal crease nor a suprapedal fold (contrast the Pomatiopsinae); the snails move by ciliary gliding. The mantle collar may or may not have a pallial tubercle, filament, or numerous papillations. The tentacles may or may not have hypertrophied ciliary tufts. The eyes are located in slight swellings at the base of the tentacles. The central tooth of the radula usually has pronounced lateral angles, giving the tooth a trapezoidal shape, and one or more pairs of basal cusps that usually originate from the lateral angles (contrast the Pomatiopsidae). The stomach has a caecal chamber that usually protrudes posterior to the stomach chambers. An anterior digestive lobe may be present. The shell may or may not have wrinkled, pitted apical microsculpture.

Subfamily Nymphophilinae

These include Hydrobiidae in which the pallial oviduct has an internal ciliated ventral channel, and the penis is bilobed and bears one or more elevated glandular ridges. The tentacles do not have hypertrophied ciliary tufts. The apical whorl has wrinkled, pitted microsculpture. The only mode of reproduction thus far reported for this subfamily is oviparity (Thompson, 1968, 1977, 1979).

Subfamily Littoridininae

These include Hydrobiidae in which there is a spermathecal duct separate (at least posteriorly) from the pallial oviduct. The spermathecal duct may be short or long. The pallial oviduct often has three or four tissue types. The penis may be without specialized glands, or with large apocrine glands, glandular papillae, or mammiform glands. The tentacles often have hypertrophied ciliary tufts. The apical whorl may or may not have wrinkled, pitted microsculpture. The mode of reproduction may be oviparity or ovoviviparity.

The subfamilial placement of the Cuatro Ciénegas hydrobioids, based on anatomical study, is contrasted with that of Taylor (1966) in Table 2.

DESCRIPTION OF TAXA

Nymphophilinae

Nymphophilus Taylor, 1966

Type-species: *Nymphophilus minckleyi* Taylor, 1966.

Distribution: endemic to the Cuatro Ciénegas Basin.

Species included: *N. minckleyi*, *N. acarinus* n. sp.

Description

Diagnostic features of *Nymphophilus* include the large (length, 3.5–8.3 mm) trochoid

TABLE 2. Subfamilial placement of the Cuatro Ciénegas hydrobiid genera (based on the results of this study) contrasted with that of Taylor (1966).

Taylor (1966)	This study
Family Hydrobiidae	Family Hydrobiidae
Subfamily Cochliopinae	Subfamily Littoridininae
<i>Coahuilix</i> *	<i>Coahuilix</i> *
<i>Cochliopina</i>	<i>Paludiscala</i> *
Subfamily Littoridininae	<i>Mexithauma</i> *
<i>Mexipyrargus</i> *	<i>Cochliopina</i>
<i>Durangonella</i>	<i>Durangonella</i>
Subfamily Nymphophilinae**	<i>Mexipyrargus</i> *
<i>Nymphophilus</i> *	Subfamily Nymphophilinae
Subfamily Mexithaumatinae**	<i>Nymphophilus</i> *
<i>Mexithauma</i> *	<i>Mexistiobia</i> ¹
Subfamily Paludiscalinae**	Subfamily Unknown
<i>Paludiscala</i> *	<i>Orygoceras</i> ? ²

*Genus endemic to the Cuatro Ciénegas basin.

**Subfamily considered endemic to the Cuatro Ciénegas Basin by Taylor (1966).

¹New genus.

²Systematic status uncertain as anatomy is not yet studied.

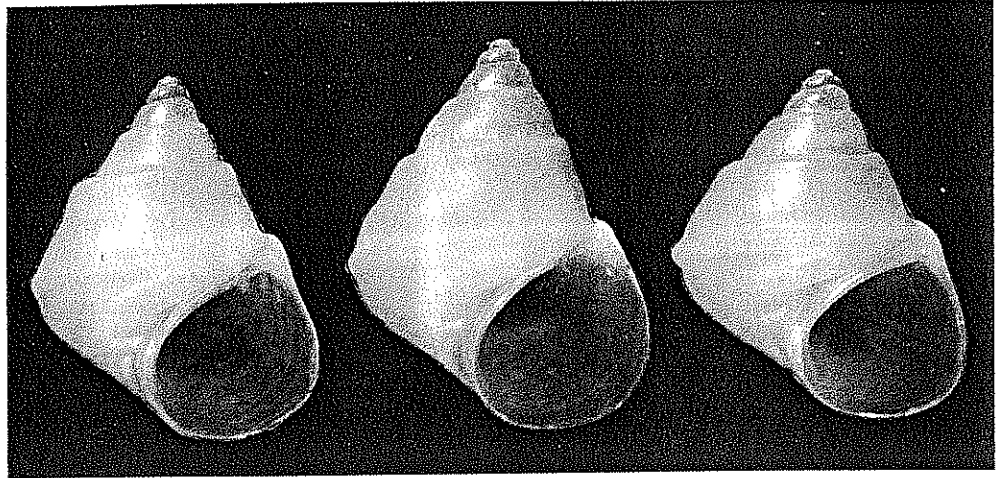


FIG. 4. Shells of *Nymphophilus minckleyi* from Locality 76. The shell on the left is 8.0 mm long; the others are printed at the same enlargement.

shell (Figs. 4, 9), multispiral operculum (Fig. 5B), elongate osphradium (30% of the ctenidium length), and bush-like male gonad (not shown).

The bursa (Bu) is positioned posterior to the pallial oviduct (Figs. 7A, B); the duct of the bursa to the common opening of the albumen gland and ventral channel is elongate; the seminal receptacle (Sr) and oviduct coils (Coi) are located anterior to the bursa (Fig. 7B); the bolster of the ventral channel is well-

developed (Bvc, Fig. 7D); the pallial oviduct opens laterally as a common genital aperture (Cga, Fig. 7E); the penis (Fig. 8A) with massive, folded penial lobe (Plo) bears one to four glandular ridges (Glr) on its ventral surface.

Discussion

Among nymphophilines, *Nymphophilus* is most similar to *Marstonia*, as both taxa have a penis with few glandular ridges (for *Marsto-*

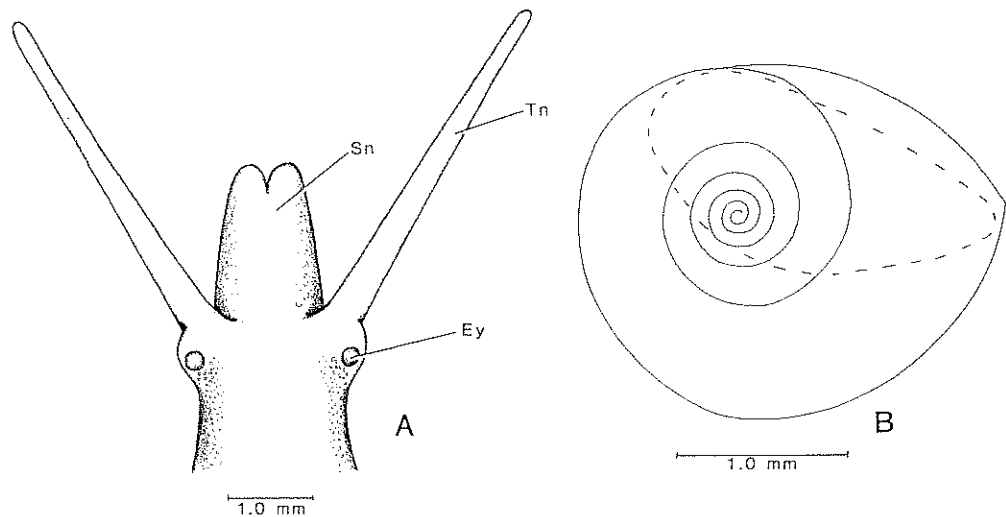


FIG. 5. Head and operculum of *N. minckleyi*. A. Head seen dorsally. B. Operculum, with dashed line indicating attachment area to operculigerous lobe. Ey—eye; Sn—snout; Tn—tentacle.

nia, see Thompson, 1977, figs. 5, 7, 11) and a large bursa positioned posterior to the pallial oviduct (for *Marstonia*, see Thompson, 1977, fig. 10).

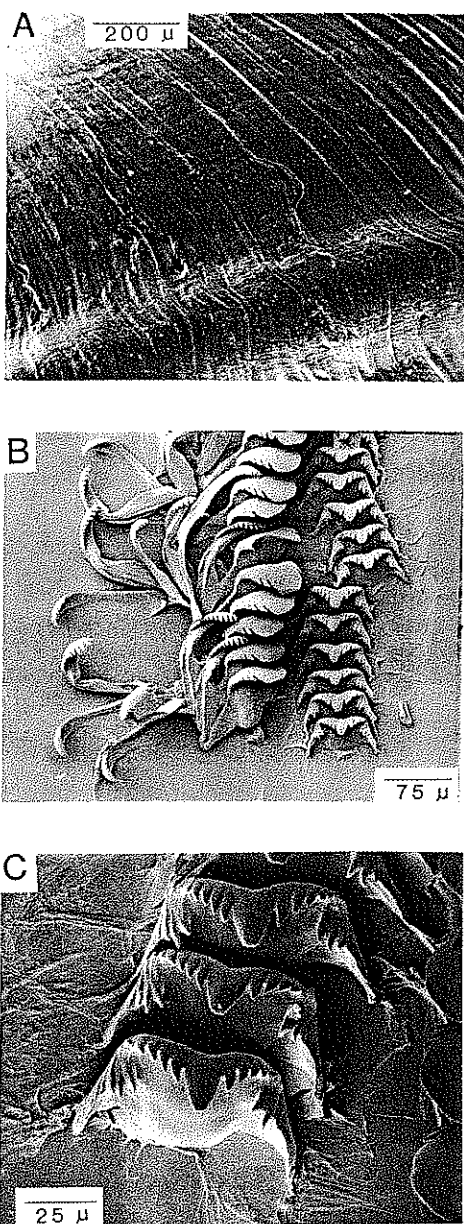


FIG. 6. SEM photos of shell and radula of *N. minckleyi*. A. Portion of body whorl showing the peripheral keel and wavy collabral microsculpture. B. Portion of radular ribbon. C. Several central teeth.

Nymphophilus minckleyi Taylor, 1966

Holotype: UMMZ (University of Michigan Museum of Zoology) 220188.

Type-locality: Locality 53.

Habitat: *Nymphophilus minckleyi* is found in large springs and their outflows. *Nymphophilus minckleyi* was rarely taken from the smaller springs; mops yielded specimens from the heads of only three of 38 such springs. In the large springs, *N. minckleyi* was collected from aquatic vegetation (*Nymphaea*, *Chara*, *Utricularia*), travertine, and, to a lesser extent, from gentle, sloping banks. On a microhabitat scale, this species is occasionally sympatric with *Mexithauma quadripaludium* and *Cochliopina milleri*. It has been suggested (Arnold, 1972) that *N. minckleyi*, as well as *Mexithauma* and *Mexipyrgus*, is nocturnal, moving about at night when the predaceous cichlid fish are inactive.

The egg capsules of this species were found on water lily (*Nymphaea*) leaves from many localities throughout the year. It was not uncommon to find over 100 capsules on a single 15 cm leaf. The capsules were rarely found on the shells of living snails. The egg capsule is hemispherical and is coated with detrital material along the sides, but the top of the capsule is clear of detritus and the yellow-colored embryo is visible inside. Usually, hydrobioid egg capsules are completely coated with either sand or detritus. For 13 egg capsules from Locality 76, the egg capsule diameter is 0.52 ± 0.40 mm. The height of the capsule is about 0.25 mm. The embryonic shells inside have 1.00–1.25 whorls.

Description

Nymphophilus minckleyi is distinctive in having a large shell (Fig. 4), with 5.5–6.0 flattened to slightly rounded whorls. There is a strong spiral keel, at or just above the suture, that fades on the body whorl and is barely noticeable at the aperture.

Shell

The spire is moderately high, the base rounded, and the umbilicus narrow. The sutures are shallow. The aperture is longer than it is wide, somewhat angled adapically, rounded abapically, and with a complete thickened peristome in adults. In adult shells, the aperture is adnate to or slightly separated from the penultimate whorl. The plane of the

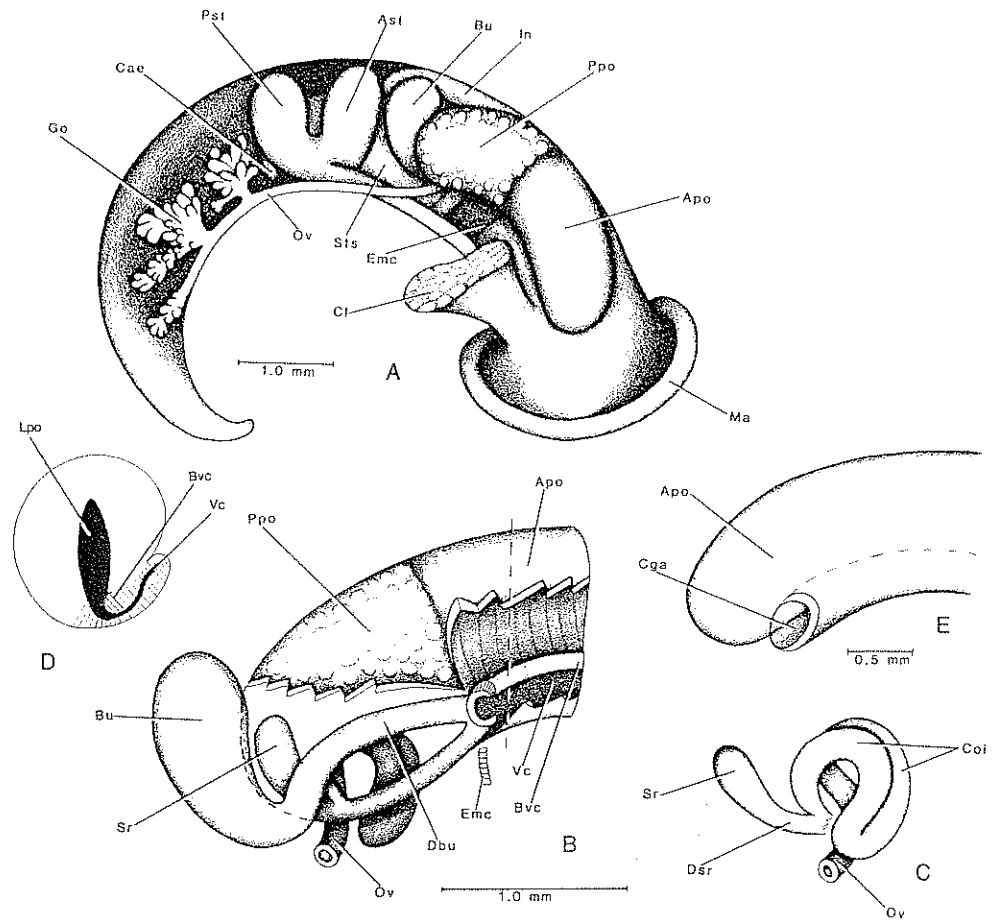


FIG. 7. Female reproductive anatomy of *N. minckleyi*. A. Snail uncoiled, exposing the ventral aspect without head and kidney tissue. Note the position of the bursa (Bu) posterior to the pallial oviduct (Apo + Ppo). B. Oriented as in A, but with a portion of the pallial oviduct cut away to reveal the bursa copulatrix complex, bolster (Bvc), and ventral channel (Vc). The left-hand dashed line indicates the posterior extent of the pallial oviduct. C. Oriented as in B, but with the bursa, its duct (Dbu) and the anterior portion of the duct of the seminal receptacle removed to reveal the oviduct coils (Coi). D. Cross-section of the pallial oviduct (looking anteriorly), cut where the right-hand dashed line indicates in B. Note the thickened bolster (Bvc) and well-developed ventral channel (Vc). E. Dorsal aspect of the capsule gland (Apo) showing the lateral opening of the common genital aperture (Cga). Apo—capsule gland; Ast—anterior stomach chamber; Bu—bursa; Bvc—bolster of ventral channel; Cae—caecum of stomach; Cga—common genital aperture; Cl—columellar muscle; Coi—coil of oviduct; Dbu—duct of the bursa; Dsr—duct of seminal receptacle; Emc—posterior end of mantle cavity; Go—gonad; In—intestine; Lpo—lumen of pallial oviduct; Ma—mantle edge; Ov—oviduct; Ppo—albumen gland; Pst—posterior stomach chamber; Sr—seminal receptacle; Sts—style sac; Vc—ventral channel.

aperture is only slightly tilted away from the coiling axis. The shell is colorless and translucent. The pitted apical microsculpture is shown in Thompson (1979, figs. 4–7). Postembryonic whorls have coarse, wavy growth lines (Fig. 6A), giving the shell a satiny sheen. Shell measurements for three pop-

ulations, all from large springs or streams, are given in Table 3. Shell lengths of males are significantly larger ($p < .01$) than those of females for all three populations. Shells were removed from egg capsules from Locality 76 and their apical whorls measured. For 16 shells, the width of the tip of the apical whorl

TABLE 3. Shell measurements (mm) of males and females from three populations of *Nymphophilus minckleyi*. Snails with the dominant maximum whorl number were used. N = 9, Mean \pm standard deviation. "p" refers to the significance level for the difference between shell lengths of males and females (t-test) for that population.

	Whorls	Length	Width	Length of body whorl	Length of aperture	Width of aperture	p
<i>Locality 76</i>							
♂	6.0	7.88 \pm 0.50	5.90 \pm 0.42	5.99 \pm 0.49	4.38 \pm 0.42	3.53 \pm 0.24	<.005
♀	5.5	6.89 \pm 0.28	5.51 \pm 0.22	5.37 \pm 0.31	3.92 \pm 0.11	3.21 \pm 0.20	
<i>Locality 97</i>							
♂	6.0	7.90 \pm 0.30	5.68 \pm 0.27	5.86 \pm 0.27	4.05 \pm 0.58	3.56 \pm 0.15	<.01
♀	6.0	7.49 \pm 0.32	5.58 \pm 0.20	5.52 \pm 0.26	2.77 \pm 0.24	3.22 \pm 0.18	
<i>Locality 53</i>							
♂	5.5	8.30 \pm 0.36	6.52 \pm 0.37	6.57 \pm 0.39	4.81 \pm 0.27	3.93 \pm 0.19	<.005
♀	5.5	7.79 \pm 0.18	6.33 \pm 0.27	6.08 \pm 0.14	4.45 \pm 0.23	3.71 \pm 0.20	

averaged 0.135 ± 0.017 mm; the width of the first whorl was 0.339 ± 0.040 mm. The width of the first whorl for shells from the type-locality was 0.30 mm (Thompson, 1979).

Nonreproductive Features

Details of the anatomy are from the population from Locality 76 unless otherwise indicated. Measurements of organs and structures are given in Table 4. The snout (Fig. 5A) is 1.77 mm long and relatively squat while the tentacles are thick and elongate (relative to the snout). The snout and tentacles have

embedded in them yellow granules. The eyes are partially surrounded by clear, closely packed granules that extend back along the neck. A light dusting of melanin on the rostrum and tentacles was occasionally seen. The foot is large (relative to that of other species), thickened and dusted with melanin on its dorsal surface and sides. Body pigmentation consists of a dusting of reddish melanin on both dorsal and ventral surfaces. The male gonad occasionally has very dark pigmentation on its ventral surface. The operculum (Fig. 5B) has 5.5–6.0 whorls, and the nucleus is positioned at 39% of the long axis

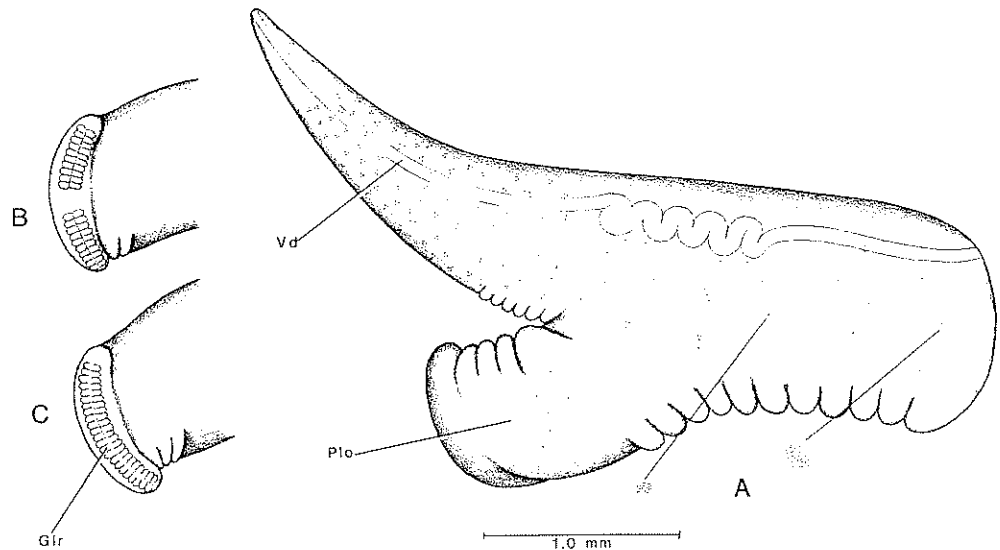


FIG. 8. The penis of *N. minckleyi*. A. Dorsal aspect of the penis. Note the large penial lobe (Plo) with numerous folds in it. B, C. Ventral aspect of the penial lobe showing the glandular ridge(s) (Glr). Vd—Vas deferens.

TABLE 4. Dimensions (mm) or counts of non-neural organs and structures of *Nymphophilus minckleyi*. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	9.30 \pm 0.33	12.40 \pm 0.31
Gill filament number		46.8 \pm 2.17	
Osphradium	L	0.89 \pm 0.13	
Gonad	L	2.49 \pm 0.18	4.76 \pm 0.59
	W	1.09 \pm 0.09	1.19 \pm 0.01
Prostate	L		1.33 \pm 0.12
	W		0.65 \pm 0.08
Penis	L		4.10 \pm 0.46
	W		1.14 \pm 0.15
Pallial oviduct	L	2.96 \pm 0.35	
	W	1.16 \pm 0.13	
Bursa copulatrix	L	1.01 \pm 0.08	
	W	0.44 \pm 0.08	
Seminal receptacle (body) (N = 6)	L	0.51 \pm 0.06	
	W	0.21 \pm 0.03	
Seminal receptacle (duct)	L	0.14 \pm 0.10	
	W	0.12 \pm 0.02	

of the operculum. The operculigerous lobe has a dusting of melanin along its perimeter. The caecal chamber (Cae) extends posterior to the stomach chambers (Fig. 7A).

Radula

The radula is shown in Figs. 6B & C. There are three pairs of basal cusps on the central

tooth, arising from the lateral angles (Fig. 6C). The central cusp of the central tooth is broad and large relative to the cusps on either side. The lateral tooth also has a massive central cusp (Fig. 6B). The marginals have relatively few cusps. Radular statistics and the various cusp arrangements for the four tooth types are given in Tables 5 and 6, respectively.

Female Reproductive Anatomy

The ventral view of the uncoiled female is shown in Fig. 7A. The lobe-like gonad (Go) is short (27%) relative to body length. There are three to five gonad branches, each consisting of small lobes.

The oviduct (Ov) passes beneath the pallial oviduct just at the end of the style sac. A short gonopericardial duct is present (Thompson, 1979, fig. 15). The pallial oviduct is 32% of the body length. The two sections of this organ, the anterior capsule gland (Apo) and the posterior albumen gland (Ppo), are easily distinguishable even in unstained specimens. The posteriormost 20% of the pallial oviduct overlies the style sac (Sts, Fig. 7A). The anterior pallial oviduct ends 1.14 mm from the mantle edge. The relationships between the bursa copulatrix complex and pallial oviduct are shown in Figs. 7B, C. The bursa (Bu) is sac-like and large; 34% the length of the pallial oviduct. The duct of the bursa (Dbu) is

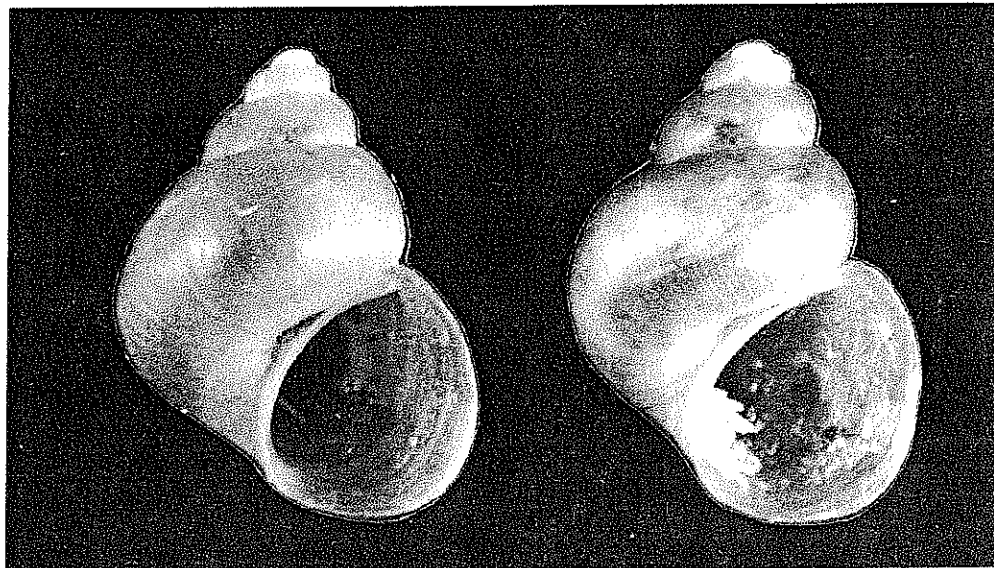


FIG. 9. Shells of *Nymphophilus acarinatorius* from Locality 113. The shell on the left is the holotype (ANSP 355255) and is 4.25 mm long. On the right, printed to the same enlargement, is a paratype (ANSP 355256).

110% of the bursa length (Fig. 7B). The duct of the bursa, seminal receptacle (Sr), and oviduct coils (Coi) lie appressed to the dorsal surface of the albumen gland. The seminal receptacle and oviduct coils are largely anterior to the bursa and dorsal to the duct of the

bursa. The pear-shaped seminal receptacle is relatively large; 50% of the length of the bursa. The oviduct coils twice, with the first coil dorsal to the second one, before receiving the short duct of the seminal receptacle (Dsr, Fig. 7C) and joining the duct of the bursa at the opening to the pallial oviduct (Fig. 7B).

The bursa copulatrix complex has a common opening with the albumen gland and ventral channel (Vc) at the posterior end of the mantle cavity (Fig. 7B). The ventral channel is considerably folded toward the ventral side of the pallial oviduct (Fig. 7D). The bolster of the ventral channel (Bvc) is rounded and thickened (Figs. 7B, D). Sperm masses were found in the ventral channel below the bolster. The walls of the ventral channel do not fuse anteriorly to form a tube separate from the capsule gland (compare Fig. 7C with Davis & Pons da Silva, 1984; fig. 6). The

TABLE 5. Radular statistics from 12 individuals of *Nymphophilus minckleyi*. \bar{X} = mean, S = standard deviation. Measurements are in mm.

Radular feature	\bar{X}	S
Length	1.96	0.11
Width	0.274	0.019
Number of rows	60.7	3.47
Number of rows in formative stage	3.58	1.51
Width of central tooth (N = 28)	0.081	0.0054

TABLE 6. The various cusp arrangements for the four tooth types in 12 radulae of *Nymphophilus minckleyi*, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{3-1-3}{3-3}$	8	2-1-2	33	9	18	15	50
$\frac{4-1-3}{3-3}$	17	3-1-2	17	11	25	16	50
$\frac{4-1-4}{3-2}$	17	3-1-3	75	12	42	17	50
$\frac{4-1-4}{3-3}$	8	3-1-4	8	13	42	18	58
$\frac{4-1-4}{4-4}$	8	4-1-1	8	14	58	19	25
$\frac{5-1-4}{3-2}$	25	4-1-2	8	15	58	20	25
$\frac{5-1-4}{3-3}$	50	4-1-3	58	16	58	21	17
$\frac{5-1-5}{3-2}$	8	4-1-4	17	17	17	24	8
$\frac{5-1-5}{3-3}$	67			18	8		
$\frac{6-1-4}{3-3}$	8						
$\frac{6-1-5}{3-2}$	8						
$\frac{6-1-6}{3-3}$	8						
$\frac{7-1-4}{3-2}$	8						
$\frac{7-1-6}{3-3}$	8						

capsule gland does not open at its anterior tip, but opens as a common genital aperture (Cga), lateral to and 0.3 mm posterior to the tip (Fig. 7E).

Male Reproductive Anatomy

The male gonad is relatively long, 38% of the body length, and extends to the posterior end of the stomach. The gonad has seven branches, each with many small lobes, giving the organ a bush-like appearance. The prostate is quite small, 11% of the body length, and largely posterior to the end of the mantle cavity. The anterior vas deferens exits from the posterior portion of the prostate.

The penis (Fig. 8) is relatively large and thickened, with an elongate penial filament. It is neither ciliated nor does it have an eversible terminal papilla. The single penial lobe (Plo) is positioned on the inner curvature slightly more toward the base of the verge than toward the tip. Thompson (1979, figs. 11–14) illustrates a much stouter penial filament than that shown here, possibly because he was studying preserved material. The penis has no pigment. The vas deferens (Vd) travels near the outer curvature of the penis and coils only during a portion of its length. The penis has numerous Gl₂ glands (see Davis, 1969a, for a discussion of gland types), particularly in the penial filament. The penis has no folds on its outer curvature, while the inner curvature has folds from the base to just beyond the penial lobe.

The penial lobe is quite stout and does not taper appreciably towards its distal end. Numerous folds extend inwards from its sides. The lobe curves both ventrally and towards the tip of the penis. Viewed from the ventral aspect (Figs. 8B, C), the distal edge of the lobe appears as a narrow projection folded above the proximal portion of the lobe. The surface of this distal edge, which cannot

be seen in Fig. 8A, has one to three (see Table 7) glandular ridges (Glr) along its length (Figs. 8B, C). The third ridge (not shown) is often lateral to the other two. Taylor (1966, fig. 21) illustrates a fourth ridge near the base of the penial lobe (ventral surface); this was seen in only one of the 75 specimens studied from three populations.

Nymphophilus acarinatus Hershler, n. sp.

Synonymy: *Nymphophilus* Hershler, n. sp. Hershler in press.

Etymology: the species name comes from the acarinate shell.

Holotype, ANSP 355255, Fig. 9A; paratypes (11); ANSP 355256, Fig. 9B.

Type-locality: Locality 98.

Habitat: *Nymphophilus acarinatus* is known only from empty shells from the type-locality and several specimens collected live from Santa Tecla Laguna (Locality 101). *Nymphophilus acarinatus* is allopatric to *N. minckleyi*.

Description

While there are insufficient anatomical data for a detailed account comparable to that of *N. minckleyi*, this species is placed in *Nymphophilus* because the organization of the bursa copulatrix complex and form of the penis are like those of *N. minckleyi*.

The shell (Fig. 9) differs from that of *N. minckleyi* in that it is somewhat smaller (length, 4.20 mm), has fewer whorls (to 4.8) that are quite rounded, and lacks a peripheral keel, even on early whorls. The growth lines are less pronounced than those of *N. minckleyi*. Measurements of the type and paratypes are given in Table 8.

Discussion

While the differences between *N. acarinatus* and *N. minckleyi* are few and restricted to shell features, there is no blurring of these differences in any of the populations studied. Specimens of *N. minckleyi* from small springs can be as small as *N. acarinatus*, but the whorls remain flattened and the peripheral keel is always present. The consistency of these differences suggests that the taxa are distinct species and not mere allopatric variants.

TABLE 7. Percent of individuals (N = 25) with 1, 2, or 3 glandular ridge(s) on the distal edge of the penial lobe in three populations of *Nymphophilus minckleyi*.

	Number of ridges		
	1	2	3
Locality 76	84	16	0
Locality 97	52	28	20
Locality 53	76	12	12

TABLE 8. Measurements (mm) of the shells of the holotype (ANSP 355255) and paratypes (ANSP 355256) of *Nymphophilus acarinatus*. All shells are from adults with 4.5–4.8 whorls.

	Shell length	Shell width	Length of body whorl	Length of aperture	Width of aperture
Holotype	4.25	3.33	3.37	2.30	1.91
Paratype	3.57	2.89	2.98	2.22	1.71
Paratype	4.13	3.26	3.30	2.38	1.91
Paratype	4.37	3.10	3.45	2.50	1.99

Mexistiobia Hershler, n. gen.

Etymology: the name was formed by adding the prefix Mexi-, referring to distribution within México, to *Stiobia* Thompson & McCaleb, 1978, a very similar nymphophiline from the southeastern U.S.A.

Type-species: *Mexistiobia manantiali* n. sp.

Distribution: thus far known only from the Cuatro Ciénegas Basin and Durango, México (U.S. National Museum of Natural History 351817, labeled "*Valvata*").

Species included: monotypic. The specific status of the Durango population is not known.

Description

Among nymphophilines, the unique features of *Mexistiobia* include the position of the small bursa (Bu) anterior to the seminal

receptacle (Sr, Fig. 14B), the very short duct of the bursa (Dbu), and the position of the male gonad overlying the posterior stomach chamber (not shown).

The shell (Fig. 10) is minute (length, 1.20 mm) and broadly conical; the bolster of the ventral channel is weakly developed (Fig. 14C); the capsule gland opens at its anterior tip as a common genital aperture (Cga, Fig. 14D); the penis has an elongate penial lobe (with one fold in it) bearing a single glandular ridge along its ventral length (Glr, Fig. 13D).

Discussion

Mexistiobia manantiali bears a remarkable conchological resemblance to *Stiobia* Thompson & McCaleb, 1978, a monotypic genus endemic to a spring in Alabama, yet it differs in 11 morphological features (Table 9). Two of these features (4, 6) may have been incorrectly interpreted by Thompson &

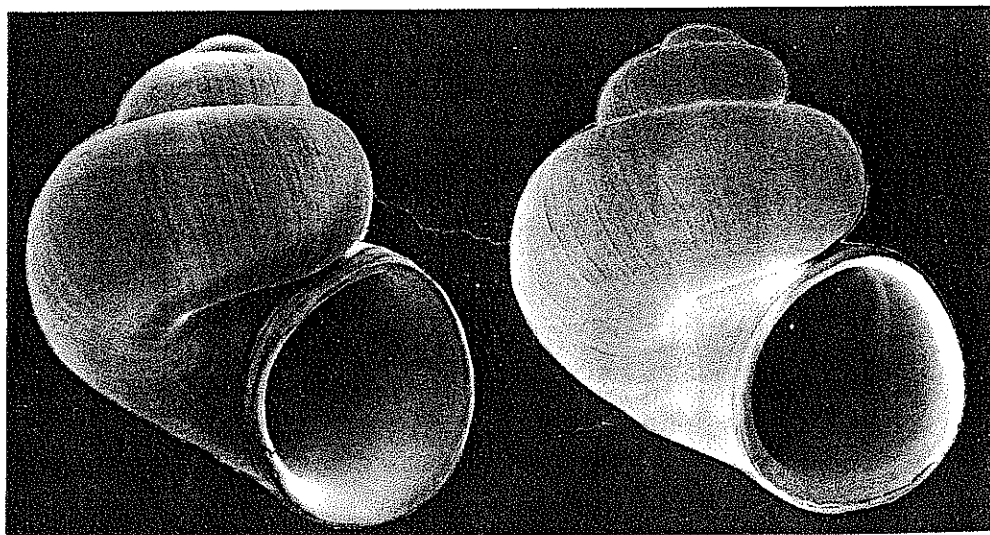


FIG. 10. SEM photos of paratype shells (ANSP A9887d) of *Mexistiobia manantiali* from Locality 51. The shell on the left is 1.15 mm long, that on the right is printed at the same enlargement.

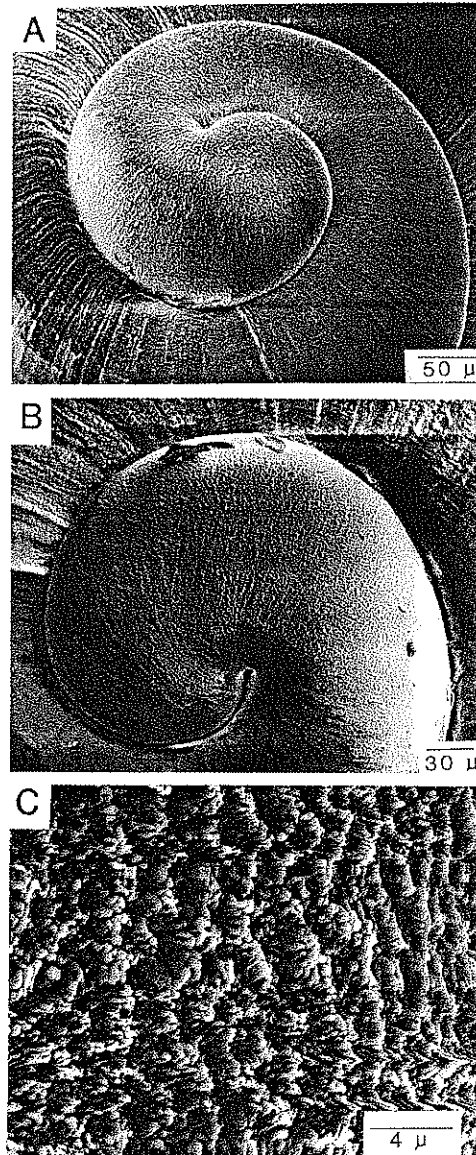


FIG. 11. SEM photos of the apical region of the shell of *Mexistiobia manantiali*, showing the wrinkled, pitted microsculpture at several magnifications.

McCaleb as these would be highly unusual traits for hydrobioid snails. Separate generic status is suggested for these two taxa because of the major differences in the position and organization of the bursa copulatrix complex, and in the form of the penis and number of glandular ridges.

While the stunted appearance of the female reproductive anatomy of *Mexistiobia* is unique among nymphophilines, a penis with few glandular ridges is also seen in *Nymphophilus* and *Marstonia* (see above).

Mexistiobia manantiali Hershler, n. sp.

Synonymy: "*Stiobia*" Hershler, n. sp. Hershler in press.

Etymology: the species name is formed from the Spanish word *manantial*, meaning spring, and refers to the spring-fed habitats of this snail.

Types: holotype, ANSP 355205; paratypes, A9887d, A9888l, 355204, Fig. 10. Because of their small size, the shells had to be photographed using the SEM, which leaves gold coating on the specimens, so the holotype was not used. The paratypes look like the holotype.

Type-locality: Locality 51, a small spring. This species was shown, but undescribed, by Taylor (1966, fig. 4).

Habitat: *Mexistiobia manantiali* is restricted to the smaller springs of the valley. It is found in association with *Durangonella coahuilae*, *Paludiscala caramba*, and *Coahuilix* spp. in the headsprings, and is sympatric with *D. coahuilae* in the spring runs. In terms of microhabitat, *Mexistiobia manantiali* is common in fine organic sediments and *Chara* mats, and prefers a finer sediment than does *D. coahuilae*. While found in mop samples from 20 of 38 small springheads, *Mexistiobia manantiali* probably does not live in subterranean waters as all specimens collected have eyespots and because the species is most adapted for life in open, downstream habitats (see below).

Shell

The colorless shell has rounded whorls and an open umbilicus. Adults have 3.00–3.3 whorls. The whorls sometimes have a very slight angulation at the shoulder. The latter portion of the body whorl frequently pulls away from the preceding whorl in adults. Postembryonic sculpture is restricted to strong growth lines (Figs. 10, 11A). The plane of the aperture is tilted about 10° toward the coiling axis. The apical whorl microsculpture is shown at several magnifications in Figs. 12A–C. Shell measurements from three populations are given in Table 10. The shell length for females is significantly larger than

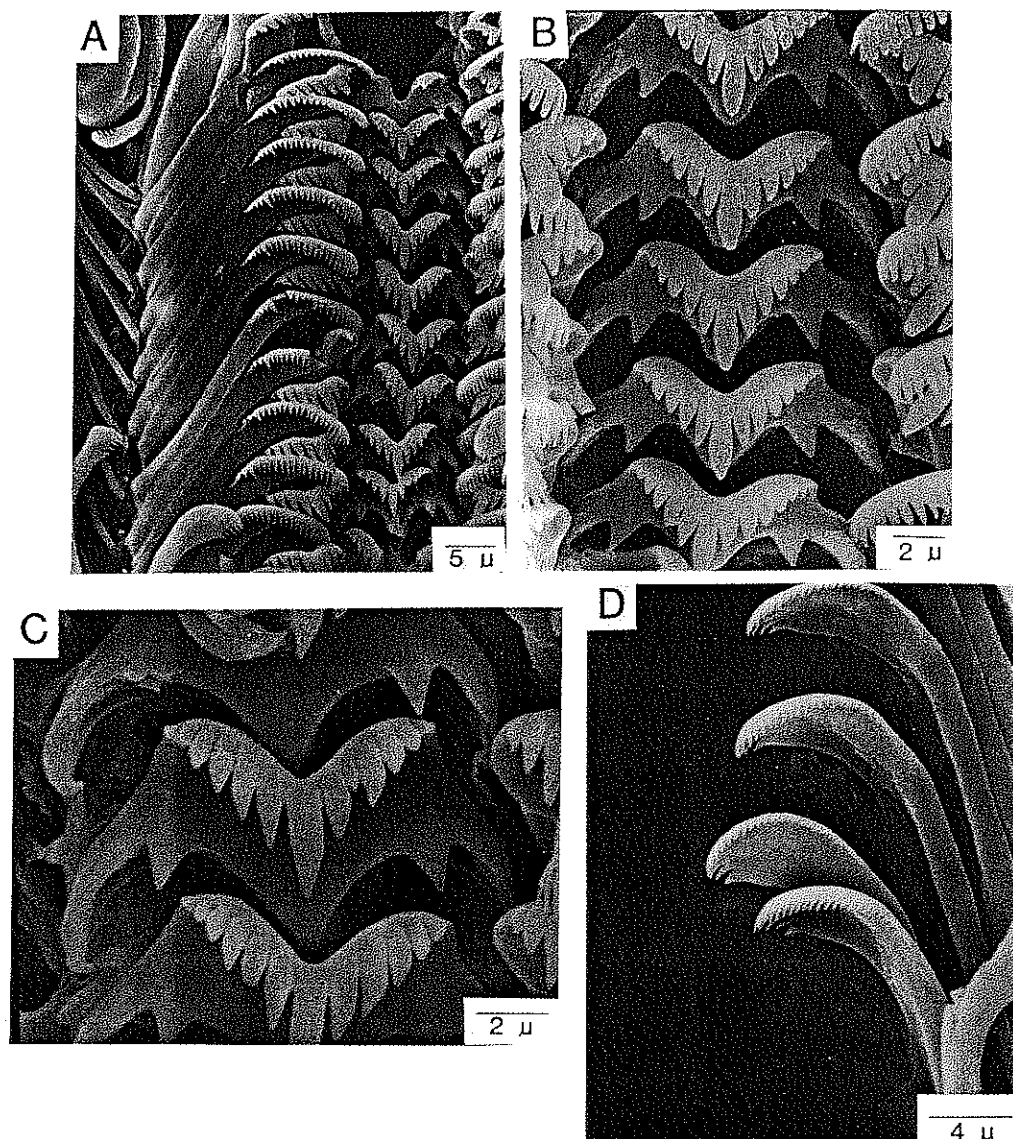


FIG. 12. SEM photos of the radula of *Mexistiobia manantiali*. A. Part of the radula ribbon. B, C. Central teeth. D. Outer marginal teeth.

that for males in two of the three populations (Table 10).

Nonreproductive Features

Observations and data on external features and anatomy are from the type population. Measurements of organs and structures are given in Table 11. The snout is elongate,

while the tentacles are relatively short and thickened (Fig. 13A). A small concentration of granules partially surrounds the eyes. The snout and tentacles usually have a dark melanin dusting. Body pigmentation consists of a dark melanin dusting on the dorsal and ventral surfaces. Adults have only 10–13 gill filaments (Table 11). A prominent caecal chamber (Cae) extends posterior to the stomach

TABLE 9. List of 11 morphological differences between *Stiobia nana* and *Mexistiobia manantiali*. The morphological information on *Stiobia nana* is from Thompson & McCaleb (1978).

<i>Stiobia nana</i>	<i>Mexistiobia manantiali</i>
1. Shell with two spiral keels	Spiral keels absent
2. Wrinkled, pitted microsculpture on all shell whorls	Microsculpture restricted to apical whorl
3. Operculum with 2.5 whorls	Operculum with 3.5 whorls
4. Hypobranchial gland present	Hypobranchial gland absent
5. Lateral tooth of radula with massive, hoe-like central cusp	Central cusp small and dagger-like
6. Bursa and duct of bursa imbedded in the pallial oviduct	Bursa and duct dorsal to pallial oviduct
7. Duct of bursa elongate	Duct is short
8. Seminal receptacle anterior to bursa	Seminal receptacle posterior to bursa
9. Penial filament 35% of penis length	Penial filament 0.45% of penis length
10. Penial lobe massive and stout	Lobe is small and slender
11. Numerous glandular ridges over entire surface of penis	Single glandular ridge on ventral surface of penial lobe

TABLE 10. Shell measurements (mm) of males and females from three populations of *Mexistiobia manantiali*. Snails with the dominant maximum whorl number were used. N = 9, Mean \pm standard deviation. "p" refers to the significance level for the difference between shell lengths of males and females (t-test) for that population.

	Whorls	Length	Width	Length of body whorl	Length of aperture	Width of aperture	p
<i>Locality 51</i>							
♂	3.0	1.19 \pm 0.08	0.99 \pm 0.04	1.08 \pm 0.08	0.64 \pm 0.04	0.53 \pm 0.04	>.10
♀	3.25	1.21 \pm 0.04	1.04 \pm 0.07	1.12 \pm 0.05	0.63 \pm 0.03	0.62 \pm 0.03	
<i>Locality 65</i>							
♂	3.0	0.98 \pm 0.04	0.95 \pm 0.04	0.84 \pm 0.02	0.54 \pm 0.01	0.46 \pm 0.02	<.005
♀	3.25	1.10 \pm 0.05	1.03 \pm 0.05	0.93 \pm 0.04	0.56 \pm 0.03	0.47 \pm 0.02	
<i>Locality 68</i>							
♂	3.0	1.10 \pm 0.05	1.07 \pm 0.04	0.94 \pm 0.04	0.59 \pm 0.03	0.53 \pm 0.02	<.025
♀	3.25	1.15 \pm 0.05	1.11 \pm 0.02	0.95 \pm 0.04	0.60 \pm 0.03	0.52 \pm 0.03	

(Fig. 14A). The operculum (Fig. 13B) has 3.5 whorls, and the nucleus is positioned at 39% of the long axis of the operculum.

Individuals with reduced body pigment were sometimes taken from the mops, while snails from downstream always have dark body pigment. The upstream pigment loss may be because the springhead is usually covered by riparian vegetation, and mimics a subterranean environment. A similar upstream-downstream pigment change is reported for the amphipod *Hyalella* in Cuatro Ciénegas (Holsinger & Minckley, 1971). The usual dark pigmentation of the snails is probably an adaptation to life in the open stream waters that are subject to great insolation.

Radula

The radula is shown in Fig. 12. The central cusps of the central and lateral teeth are blade-like. The marginals have numerous cusps. The central tooth has a single pair of basal cusps originating from the lateral angles (Figs. 12B, C). Radular statistics and the various cusp arrangements of the four tooth types are given in Tables 12 and 13, respectively.

Female Reproductive Anatomy

The organization of the female reproductive system is shown in Fig. 14. The female gonad

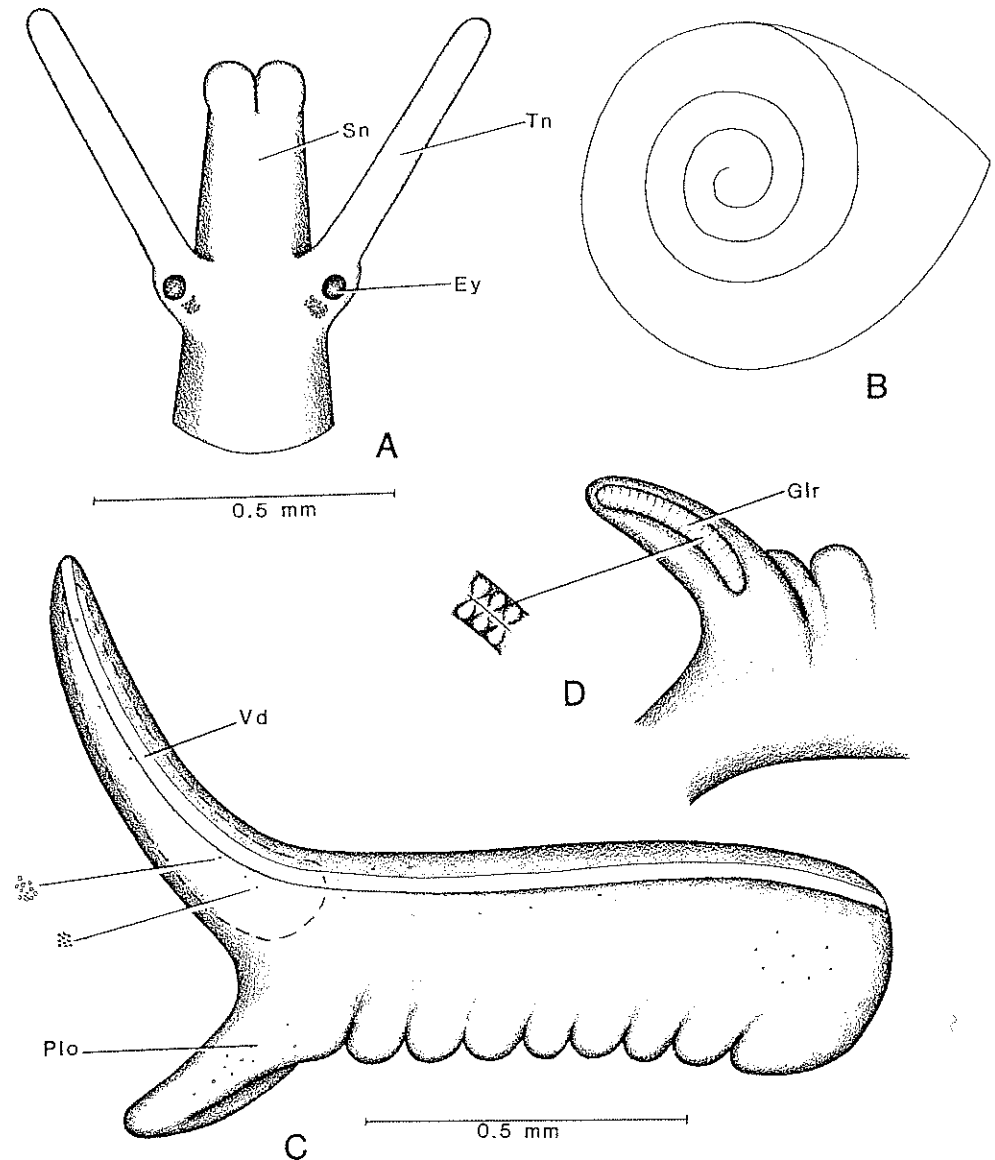


FIG. 13. Head, operculum and penis of *Mexistiobia manantiali*. A. Dorsal aspect of the head. B. Operculum. C. Dorsal aspect of the penis. Note the small, slender penial lobe (Plo). The dashed line indicates the region with melanin. D. Ventral aspect of the penial lobe showing the glandular ridge (Glr), with a close-up of the small glands. Ey—eye; Glr—glandular ridge; Plo—penial lobe; Sn—snout; Tn—tentacle; Vd—vas deferens.

(Go), a single lobed mass, occupies only 17% of the body length. The oviduct (Ov) disappears beneath the pallial oviduct (Apo + Ppo) at the end of the style sac (Sts, Fig. 14A). The pallial oviduct is divided into two equal sections: the albumen gland (Ppo) and the capsule gland (Apo). The pallial oviduct

constitutes 28% of the body length. The posteriormost 30% of the pallial oviduct overlies the style sac. The anterior end of the pallial oviduct is 0.3 mm from the mantle edge.

The relationship between the bursa copulatrix complex and the pallial oviduct is shown in Fig. 14B. The bursa copulatrix complex is

TABLE 11. Dimensions (mm) of counts of non-neural organs and structures of *Mexistiobia manantiali*. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	2.57 \pm 0.18	2.40 \pm 0.20
Gill filament number (N = 7)		11.3 \pm 0.95	
Gonad (N = 7)	L	0.45 \pm 0.06	0.94 \pm 0.11
	W	0.30 \pm 0.02	0.29 \pm 0.03
Prostate (N = 8)	L		0.39 \pm 0.04
	W		0.21 \pm 0.03
Penis	L		1.50 \pm 0.17
	W		0.34 \pm 0.04
Pallial oviduct (N = 8)	L	0.73 \pm 0.09	
	W	0.31 \pm 0.03	
Bursa copulatrix (N = 6)	L	0.15 \pm 0.02	
	W	0.07 \pm 0.02	
Seminal receptacle (body) (N = 7)	L	0.10 \pm 0.02	
	W	0.06 \pm 0.01	
Seminal receptacle (duct) (N = 7)	L	0.09 \pm 0.01	
	W	0.04 \pm 0.01	

TABLE 12. Radular statistics from 12 individuals of *Mexistiobia manantiali*. \bar{X} = mean, S = standard deviation. Measurements in mm.

Radular feature	\bar{X}	S
Length	0.394	0.033
Width	0.069	0.005
Number of rows	56.5	6.5
Number of rows in formative stage	2.83	3.32
Width of central tooth (N = 8)	0.013	0.0004

TABLE 13. The various cusp arrangements of the four tooth types of *Mexistiobia manantiali*, counted from 5 radulae using SEM, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{4-1-4}{1-1}$	40	4-1-3	80	19	20	22	40
$\frac{5-1-5}{1-1}$	60	5-1-3	80	20	40	23	40
$\frac{5-1-4}{1-1}$	20	5-1-4	20	21	60	24	60
$\frac{6-1-5}{1-1}$	20			22	60	25	80
$\frac{6-1-6}{1-1}$	60			23	40	26	60
				24	20		

dorsal to the pallial oviduct. The bursa (Bu) is 21% of the pallial oviduct length, and lies about 0.27 mm anterior to the end of the pallial oviduct. The seminal receptacle (Sr) and single oviduct coil are largely posterior to the bursa. In four of nine females dissected, the tip of the seminal receptacle protruded slightly posterior to the end of the pallial oviduct. The pouch-like seminal receptacle is similar in shape to and only slightly smaller than the bursa, but was easily distinguished by its pink sheen. The duct of the seminal receptacle (Dsr) is short. No gonopericardial duct was seen.

The bursa copulatrix joins the common opening of the ventral channel and albumen gland just posterior to the end of the mantle cavity (Fig. 14B). The ventral channel is only slightly folded toward the ventral side of the pallial oviduct and the bolster is small (Figs. 14B, C). The walls of the ventral channel do not fuse anteriorly (Fig. 14D).

Male Reproductive Anatomy

The male gonad is lobed and is 38% of the body length. The seminal vesicle coils on the posterior stomach chamber. The prostate overlies the mantle cavity. The anterior vas deferens exits from the posterior portion of the prostate.

The penis (Fig. 13C) has a slender, tapering penial filament, and the slender penial lobe is positioned on the inner curvature slightly closer to the tip than to the base of the penis. The penis has neither cilia, nor a ter-

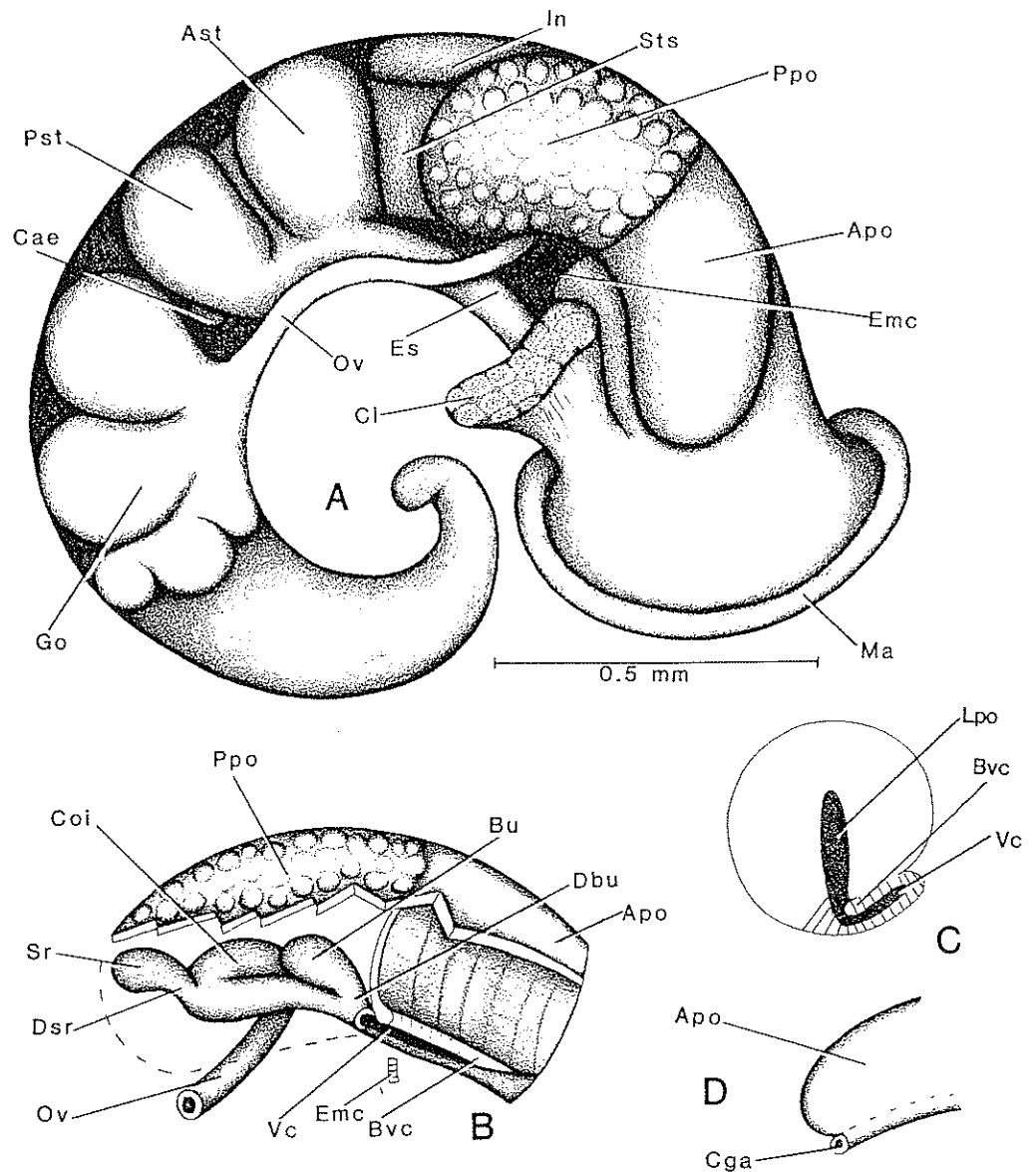


FIG. 14. Female reproductive anatomy of *Mexistiobia manantiali*. A. Snail uncoiled, exposing the ventral aspect without head and kidney tissue. B. Oriented as in A, but with a portion of the pallial oviduct removed to reveal the bursa copulatrix complex, bolster (Bvc), and ventral channel (Vc). C. Cross-section of the pallial oviduct (looking anteriorly), cut just at the common opening of the bursa copulatrix complex and albumen gland. Note the small size of the bolster (Bvc) and reduced ventral channel (Vc). D. Dorsal view of the capsule gland (Apo), showing the opening of the common genital aperture (Cga) at the anterior end of the pallial oviduct. Apo—capsule gland; Ast—anterior stomach chamber; Bu—bursa; Bvc—bolster of ventral channel; Cae—caecum of stomach; Cga—common genital aperture; Cl—columellar muscle; Coi—coil of oviduct; Dbu—duct of the bursa; Dsr—duct of the seminal receptacle; Emc—posterior end of the mantle cavity; Es—esophagus; Go—gonad; In—intestine; Lpo—lumen of pallial oviduct; Ma—mantle edge; Ov—oviduct; Ppo—albumen gland; Pst—posterior stomach chamber; Sr—seminal receptacle; Sts—style sac; Vc—ventral channel.

minimal eversible papilla. The penial filament is darkly pigmented (pigmented area indicated by dashed lines in Fig. 13C) and occasionally the penial lobe is also pigmented. The vas deferens does not coil in the penis. The penis has GI_1 and GI_2 glands. While the outer curvature has no folds, the inner curvature has folds from the base to the penial lobe.

The penial lobe is slender and tapers toward its distal end. Viewed from the ventral aspect (Fig. 13D), the single curved glandular ridge is seen. The ridge is elevated above the ventral surface of the penial lobe and consists of two rows of small glands that discharge through a central slit (see close-up, Fig. 13D).

Littoridininae

Coahuilix Taylor, 1966

Type-species: *Coahuilix hubbsi* Taylor, 1966

Distribution: endemic to the Cuatro Ciénegas Basin.

Species included: *Coahuilix hubbsi*, *Coahuilix landyei* n. sp.

Description

Diagnostic features (unique among littoridinines) include a minute (width, 0.85–1.40 mm) planispiral shell (Figs. 15A–G, I–K); intestine with a coil near its anterior end (Inc, Fig. 17C); basal cusps on the central tooth of the radula arising from the tooth face (Fig. 16C); coiling of the seminal vesicle on the posterior stomach chamber (Sv, Fig. 17C); and position of the prostate posterior to the mantle cavity (Fig. 17A).

The apical whorl has pitted microsculpture (Fig. 16A); the animal is blind (without eyes) and unpigmented; the digestive gland tubercles are reduced to low swellings; the caecal chamber does not protrude posterior to the stomach; gonads of both sexes are a single non-lobed mass (Figs. 17B, C), with that of the female overlying the posterior stomach chamber; the pallial oviduct is divided into three tissue types (Fig. 17B); the oviduct coils, gonopericardial duct, and seminal receptacle are absent (Fig. 17B); the spermathecal duct is elongate and opens separately from the pallial oviduct (Sd, Fig.

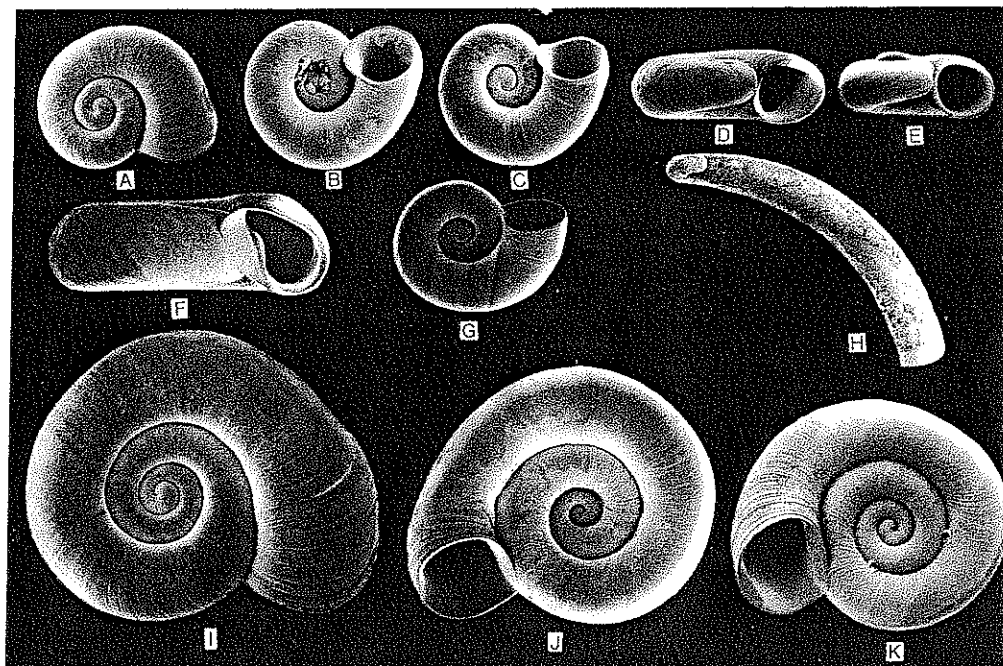


FIG. 15. SEM photos of *Coahuilix hubbsi*, *Coahuilix landyei* and *Orygoceras* (?) sp. Shells A–E are *Coahuilix hubbsi* from Locality 64; shells F, G, I, J, K are paratypes of *Coahuilix landyei* (ANSP 355211) from Locality 64; and shell H is *Orygoceras* (?) sp. from Locality 67. Shell A is 0.871 mm wide, and all others are printed to the same enlargement except H, the tube of which is 2.26 mm long.

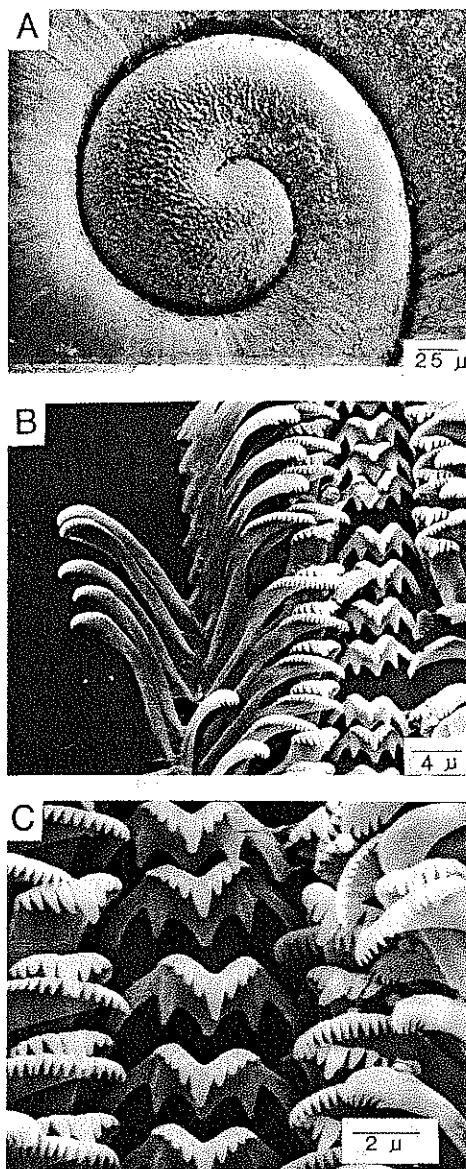


FIG. 16. SEM photos of shell and radula of *Coahuilix hubbsi*. A. Apical shell whorls, showing wrinkled, pitted microsculpture. B. Part of the radular ribbon. C. Central teeth showing the origin of the basal cusps from the face of the tooth.

17B); the females are oviparous; the penis has a bulb-like lobe bearing a large apocrine gland (Agl, Fig. 17D).

Discussion

Within the Littoridininae, *Coahuilix* and *Paludiscala* form a subgroup as they share

numerous features, many related to the small size of the snails and their unique habitat (see Tables 53–55, Figs. 49, 50). The female reproductive system of these snails is characterized by loss of the oviduct coils, gonopericardial duct, and seminal receptacle. *Coahuilix* is distinguished from *Paludiscala* by the unique features listed above and by differences in the secondary sperm storage sacs (*Coahuilix*, absent; *Paludiscala*, present) and the condition of the openings of the spermathecal duct and pallial oviduct (*Coahuilix*, separate; *Paludiscala*, joined).

Coahuilix hubbsi Taylor, 1966

Holotype: UMMZ 2220180

Type-locality: Pozo de la Becerra (Locality 10); only empty shells of this species have been found in this large spring.

Habitat: Living *Coahuilix hubbsi* has been obtained only from mops placed into or just below small springheads. Downstream collecting efforts, with fine hand sieves, never yielded live specimens. Nor were they found when bottom material from the spring runs was collected and examined under the microscope. However, at Locality 64, mops were accidentally placed three meters down from the springhead, where the stream was still completely covered by riparian vegetation, and numerous living specimens were obtained.

Coahuilix hubbsi was only moderately common in the mop samples; while the species was found on mops from 15 of 38 small springheads, it never comprised more than 15% of the snails from the mops from any springhead. Only a few springs yielded more than 10 *Coahuilix hubbsi* per mop.

The fact that *Coahuilix hubbsi* is blind and unpigmented, together with its apparent restriction to groundwater outlets, suggests that the species may also live in subterranean waters in the basin. Other snail taxa in Cuatro Ciénegas with a similar habitat are *Coahuilix landyei*, *Paludiscala caramba*, and *Orygoceras* (?) sp.

Description

The shell (Figs. 15A–E) is less than 1.0 mm wide and has 2.3–2.5 whorls when adult. The last tenth of a whorl is slightly inflated (Fig. 15A). The aperture is inclined about 30° to the coiling axis. A small segment of the inner lip of the aperture is noticeably flared (Figs. 15B, C). Post-embryonic sculpture consists of

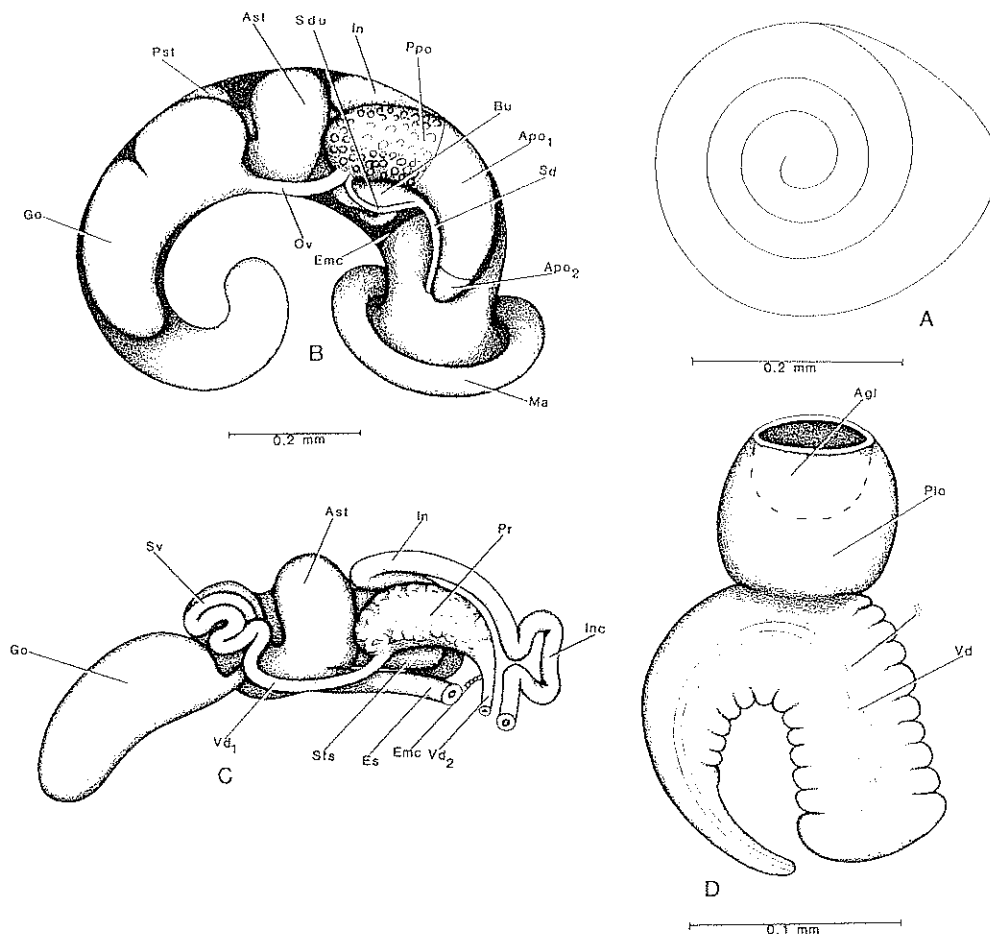


FIG. 17. Aspects of the anatomy of *Coahuilix hubbsi*. A. Operculum. B. Ventral aspect of uncoiled female without head and kidney tissue. Note the simplified gonad (Go), lack of seminal receptacle, and differentiation of the capsule gland into two tissue types (Apo₁ and Apo₂). C. Ventral aspect of uncoiled male without head and kidney tissue. Note the simplified gonad (Go), coiling of the seminal vesicle (Sv) on the stomach, small prostate (Pr) and anterior intestine coil (Inc). D. Dorsal aspect of the penis showing the large bulb-like penial lobe (Plo) with a single apocrine gland (Agl). Agl—apocrine gland; Apo₁—posterior capsule gland; Apo₂—anterior capsule gland; Ast—anterior stomach chamber; Bu—bursa; Emc—posterior end of mantle cavity; Es—esophagus; Go—gonad; In—anterior intestinal coil; Ma—mantle edge; Ov—oviduct; Plo—penial lobe; Ppo—albumen gland; Pr—prostate; Pst—posterior stomach chamber; Sd—spermathecal duct; Sdu—sperm duct; Sts—style sac; Sv—seminal vesicle; Vd—vas deferens; Vd₁—vas deferens from seminal vesicle to prostate; Vd₂—vas deferens from prostate to penis.

weak growth lines. The animal lacks gills, but has an osphradium.

Shell

Shell measurements for specimens from one population (Locality 64) are given in Table 14. The shell widths for females are greater than those for males ($p < 0.05$, Table 14). For each of three other populations

(Localities 58, 38 and 67), shell widths for 20 adult specimens (sexes mixed) were measured with the following means and standard deviations: 0.822 ± 0.055 mm, 0.829 ± 0.056 mm, and 0.799 ± 0.075 mm, respectively.

The shell occasionally has a small spire (Fig. 15E). The last quarter whorl dips abapically away from the preceding whorls. The peristome is complete and slightly thickened.

TABLE 14. Shell measurements (mm) of males and females of *Coahuilix hubbsi* (from Locality 64). N = 9. Mean \pm standard deviation. "p" refers to the significance level for the difference between shell widths of males and females (t-test).

	Whorls	Shell length	Shell width	Length of aperture	Width of aperture	p
♂	2.3–2.5	0.36 \pm 0.02	0.85 \pm 0.04	0.36 \pm 0.02	0.32 \pm 0.02	<.05
♀	2.5	0.37 \pm 0.03	0.89 \pm 0.05	0.36 \pm 0.02	0.33 \pm 0.02	

TABLE 15. Dimensions (mm) of non-neural organs and structures of *Coahuilix hubbsi*. N = 5. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	1.25 \pm 0.08	1.24 \pm 0.08
Gonad	L	0.36 \pm 0.04	0.29 \pm 0.03
	W	0.16 \pm 0.01	0.16 \pm 0.004
Prostate	L		0.19 \pm 0.01
	W		0.10 \pm 0.01
Penis	L		0.35 \pm 0.01
	W		0.10 \pm 0.01
Pallial oviduct	L	0.33 \pm 0.02	
	W	0.13 \pm 0.02	
Bursa copulatrix	L	0.13 \pm 0.01	
	W	0.07 \pm 0.02	

TABLE 16. Radular statistics from 5 individuals of *Coahuilix hubbsi*. \bar{X} = mean, S = standard deviation. Measurements in mm.

Radular feature	\bar{X}	S
Length	0.214	0.011
Width	0.034	0.002
Number of rows	68.8	3.42
Number of rows in formative stage	5.48	0.55

No specimens were found with the extreme flaring of the aperture shown by Taylor (1966, figs. 9, 12). For nine specimens from one population (Locality 64), the width of the tip of the apical whorl averaged 0.081 ± 0.006 mm; the width of the first whorl was 0.138 ± 0.015 mm. No specimen seen had the strong growth lines shown by Taylor (1966, fig. 13).

Nonreproductive Features

Observations and data on external features and anatomy are from the population at Locality 64. Measurements of organs and structures are given in Table 15. The snout is squat and the tentacles are short and thick. The buccal mass, pink-red in color, is visible

through the snout. There is a concentration of white granules and a slight pinkish color where the eyespot normally would be. The tentacles are without hypertrophied ciliary tufts. The operculum (Fig. 17A) has 3.3 whorls and the nucleus is positioned at 42% of the long axis of the operculum. A light pink color and scattered white granules are seen on the operculigerous lobe.

Radula

The radula is shown in Figs. 16B, C. The central tooth has well developed lateral angles, a small basal process, and a dagger-like central cusp. The basal cusp supports clearly arise from the face of the central tooth (Fig. 16C). Radular statistics and the various cusp arrangements for the four tooth types are given in Tables 16 and 17.

Female Reproductive Anatomy

The organization of the female reproductive system is shown in Fig. 17B. The gonad is 28% of the body length. The pallial oviduct extends to the anterior edge of the stomach and is relatively small, comprising 26% of the body length. The oviduct enters the posterior portion of the albumen gland (Fig. 17B). The capsule gland is composed of a large posterior white-colored section (Apo₁, Fig. 17B) and a smaller anterior grey-colored section (Apo₂). The sac-like bursa is positioned dorso-laterally to the pallial oviduct and has its posterior end even with that of the albumen gland. The bursa is 38% of the length of the pallial oviduct. A thin sperm duct (Sdu) issues from the anterior end of the bursa and joins the oviduct at the opening of the albumen gland (Fig. 17B). The posterior portion of the albumen gland, where the oviduct (Ov) and sperm duct (Sdu) jointly enter, has a pink sheen, indicating that sperm is inside. This region differs from the remaining albumen gland in that it is thin-walled and non-glandular: it may be a secondary sperm stor-

TABLE 17. The various cusp arrangements of the four tooth types of *Coahuilix hubbsi*, counted from five radulae using SEM, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{3-1-3}{1-1}$	100	5-1-3	100	16	40	16	20
$\frac{4-1-4}{1-1}$	40	5-1-4	20	17	60	17	60
		6-1-4	20	18	80	18	80
				19	20	17	20
				20	20		
				21	20		

age area (as there is no seminal receptacle). The spermathecal duct (Sd) is usually tightly appressed to the pallial oviduct.

Male Reproductive Anatomy

The male gonad is 23% of the body length. The vas deferens branches off the anterior end of the gonad and the seminal vesicle consists of only a few coils (Sv, Fig. 17C). The anterior vas deferens exits from the anterior tip of the prostate.

The penis has a short penial filament. The penial lobe (Plo, Fig. 17D) is located at 46% of the length of the penis from the base (on the outer curvature), and is slightly taller than it is wide, measuring 0.098 by 0.080 mm. Folds are seen on the outer curvature of the penis from the base to the penial lobe; the inner curvature has folds for 75% of the penis length from the base. The vas deferens does not coil in the penis. Infrequent concentrations of Gl₂ glands are seen in the penis. The penis is neither ciliated, nor does it have a terminal papilla.

The single massive apocrine gland in the penial lobe occupies slightly more than one-half of the height of the lobe. The gland opening is clearly visible and almost circular in cross-section. Its detailed structure is the same as that of *Heleobops* (Thompson, 1968, figs. 38D, E).

Coahuilix landyei Hershler, n. sp.

Synonymy: *Coahuilix*, n. sp. Hershler, in press.

Etymology: named after Mr. J. Jerry Landye, a student of the freshwater molluscs of the southwestern U.S.A., and México.

Types: holotype, ANSP A9894n; paratypes (7), 355211, Figs. 15F, G, I, J, K. Again, because of their small size the shells were photographed using SEM, and therefore the holotype was not used. The paratypes used look like the holotype.

Type-locality: Locality 64.

Habitat: *Coahuilix landyei* has been collected, with one exception, only from mops placed in small springheads. In one spring (Locality 63) several specimens were taken live from *Chara* mats five meters downstream from the groundwater outlet. *Coahuilix landyei* was collected from mops from 13 of 38 small springheads. The species always comprised less than 13% of the collection from any springhead, and never totalled more than four specimens per mop.

Description

While only a few specimens of *Coahuilix landyei* were dissected, all aspects of anatomy seen were basically the same as those of *Coahuilix hubbsi*.

The shell (Figs. 15F, G, I, J-L) differs from that of *Coahuilix hubbsi* in the following respects: 1) adults have one more whorl and are larger (width, to 1.31 mm) than *Coahuilix hubbsi*; 2) the last tenth of a whorl is much more inflated than that of *Coahuilix hubbsi*; 3) the growth lines of the body whorl are much more pronounced than those of *Coahuilix hubbsi*; 4) the last third of the body whorl

TABLE 18. Shell measurements (mm) of adult *Coahuilix landyei* (>3.25 whorls, sexes mixed) from two populations. Mean \pm standard deviation. The shells measured from Locality 64 are paratypes (ANSP 355211).

	Shell length	Shell width	Length of aperture	Width of aperture
Locality 64 N = 9	0.50 \pm 0.04	1.28 \pm 0.02	0.52 \pm 0.03	0.39 \pm 0.04
Locality 67 N = 7	0.49 \pm 0.03	1.31 \pm 0.06	0.49 \pm 0.03	0.41 \pm 0.03

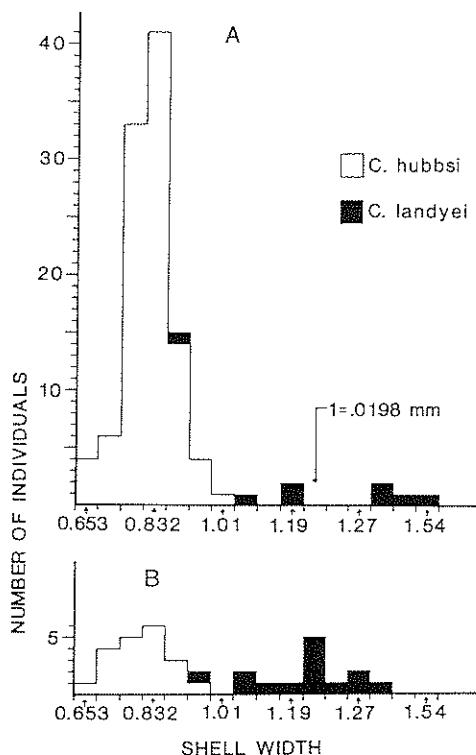


FIG. 18. Shell width frequency distributions from *Coahuilix hubbsi* and *Coahuilix landyei* collected from mops from two localities. A. Locality 67. B. Locality 64. Almost all specimens taken were adults. Note the obvious size difference between the two sympatric species (analyzed in Table 12).

overlaps the preceding whorl (Figs. 15F, J, K), while that of *Coahuilix hubbsi* merely touches the preceding whorl; 5) the aperture is much more inclined to the coiling axis than that of *Coahuilix hubbsi*; and 6) the inner lip of the aperture is much less flared than that of *Coahuilix hubbsi*. The animal has 10–12 gill filaments (*Coahuilix hubbsi* lacks gill fila-

ments). Shell measurements for two populations of *Coahuilix landyei* are given in Table 18.

Discussion

The differences between these two species are all associated with *Coahuilix landyei* having one more shell whorl than *Coahuilix hubbsi*. Separate specific status is suggested by the two taxa being found together on mops at six localities (suggesting sympatry); in these cases the whorl count difference remained pronounced. The shell width frequency distributions (virtually all adult shells) for mop collections of the two species from two of these localities are shown in Fig. 18 and analyzed in Table 19. Note that the differences between the shell width means are highly significant for both localities. Immature *Coahuilix landyei*, with the same size and whorl number as adult *Coahuilix hubbsi*, are distinguishable from the latter as their apertures are neither thickened nor flared (Fig. 15G). Very small immature specimens (<2 whorls), were not found and probably could not be specifically identified.

Other workers have noted two small, planispiral hydrobioid species in Cuatro Ciénegas, and it is likely that the snail referred to but not described or figured as *Hauffenia* sp. (Holsinger & Minckley, 1971, p. 444) is *Coahuilix landyei*.

Paludiscala Taylor, 1966

Type-species: *Paludiscala caramba* Taylor, 1966.

Distribution: endemic to the Cuatro Ciénegas Basin.

Species included: monotypic.

Description

Unique features include the two to three prominent swellings on the coilless oviduct (Fig. 22A) and the disc-like "pouch" that

TABLE 19. Analysis of shell width frequency distributions shown in Fig. 18. "p" refers to the significance level for the difference between shell widths of the two sympatric species (t-test).

		N	Shell width (mean \pm standard deviation)	p
Locality 67	<i>C. hubbsi</i>	20	0.799 \pm 0.075	<.005
	<i>C. landyei</i>	13	1.22 \pm 0.134	
Locality 66	<i>C. hubbsi</i>	103	0.818 \pm 0.024	<.005
	<i>C. landyei</i>	8	1.37 \pm 0.290	

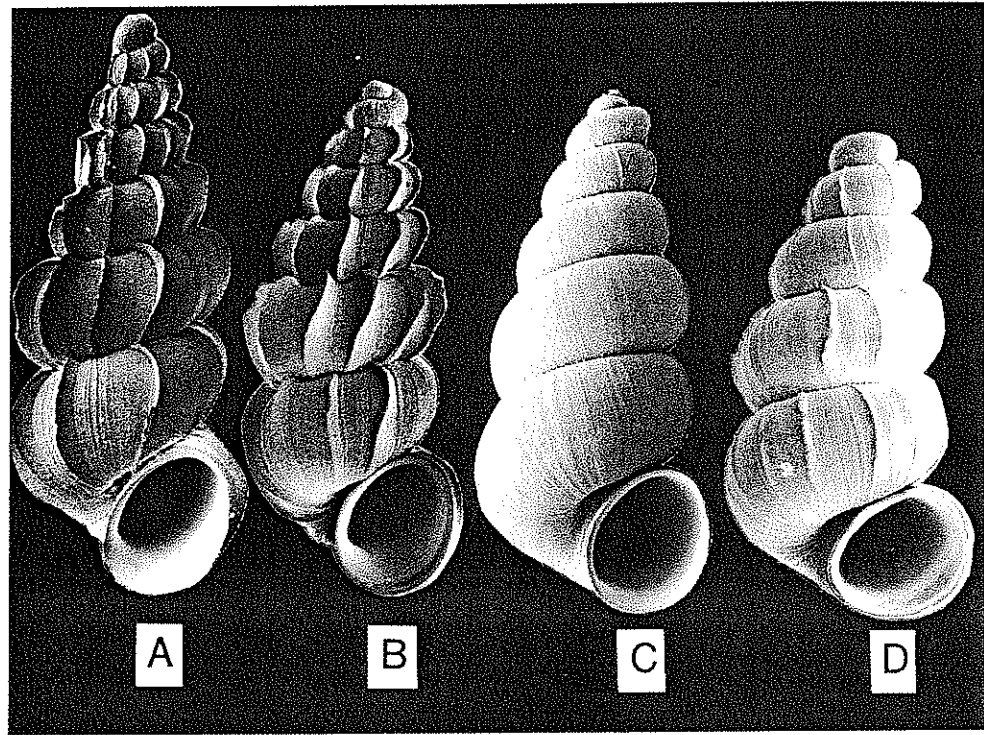


FIG. 19. SEM photos of shells of *Paludiscala caramba*. Shells A and B are from Locality 63, C and D are from Locality 38. Shell A is 2.42 mm long (B is printed to same enlargement), shell C is 1.58 mm long (D is printed to same enlargement).

bulges from the ventral surface of the albumen gland (Figs. 22A, C, D).

The shell (Fig. 19) is small (length, 1.40–2.60 mm) and turriform, with or without lamelliform costae; the apical whorl has pitted microsculpture (Fig. 20A); the animal is blind and unpigmented; the tentacles have *Hydrobia*-like hypertrophied ciliary tufts; the digestive gland tubercles are reduced to low swellings (Fig. 22B); the caecal chamber does not protrude posterior to the stomach

(Fig. 22B); the pallial oviduct contains four distinct tissue sections (Fig. 22A); the seminal receptacle and gonopericardial duct are absent; the spermathecal duct (Sd) is elongate and has a common opening with that of the pallial oviduct (Fig. 22F); females are oviparous; the penis has a bulb-like lobe bearing a large apocrine gland (Agl, Fig. 21C).

Among littoridinines, *Paludiscala* is most similar to *Coahuilix* (see above; Tables 53–55, Figs. 49, 50).

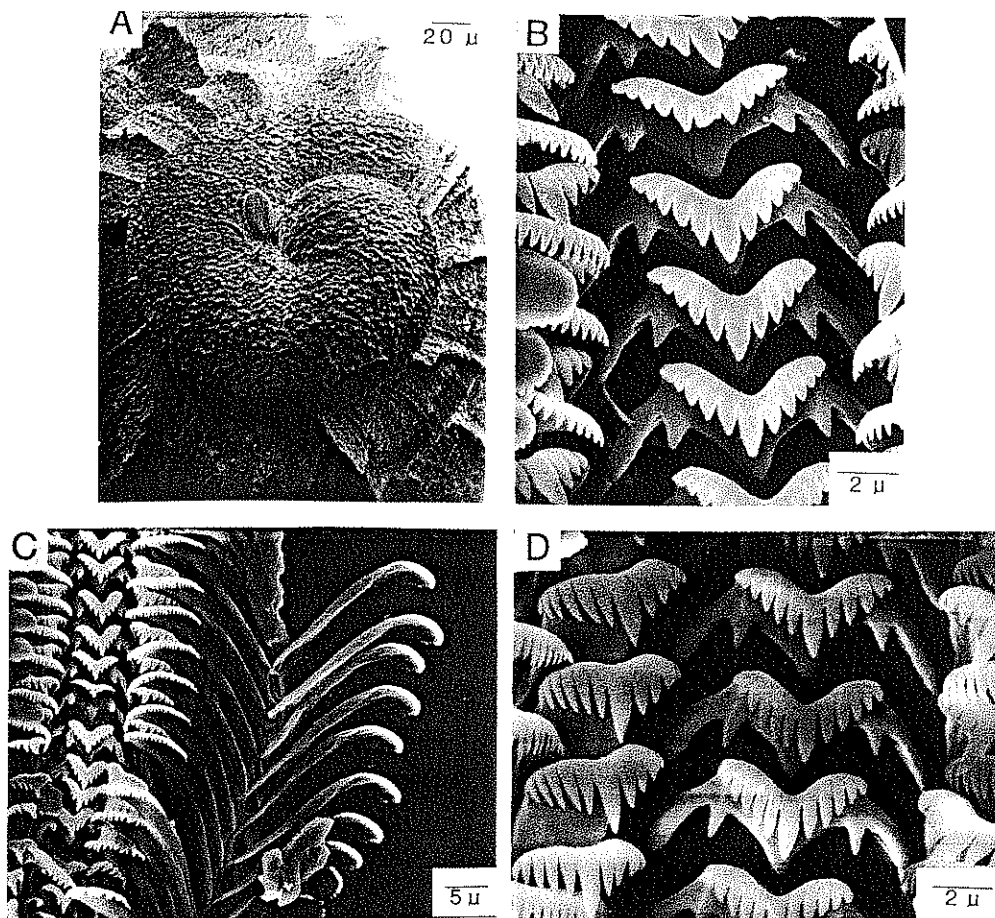


FIG. 20. SEM photos of the apical whorls and radula of *Paludiscala caramba*. A. Apical shell whorls, showing pitted microsculpture. B, D. Central teeth. C. Part of the radula ribbon.

Paludiscala caramba Taylor, 1966

Holotype: UMMZ 220164.

Type-locality: Locality 74. Living *Paludiscala caramba* have not been found at this locality.

Habitat: *Paludiscala caramba* was by far the most common species found in the small springheads; 32 of 38 of these springs yielded this species from mops. Of the 23 springs that yielded more than 100 snails from mop collections, *Paludiscala caramba* comprised greater than 10% of the collection for spring 18, and greater than 50% of the collection for 15. Perhaps more so than *Coahuilix*, *Paludiscala caramba* can extend downstream when there is riparian vegetation covering the stream. At Locality 63, a small thermal (33–

35°C) spring issues into a pool (see Brown, 1974, fig. 5), and then runs 170 m before terminating in a marsh. *Paludiscala caramba* was very abundant on plant and rock surfaces for the upper 83 m, which had virtually complete vegetative cover. Below 83 m the vegetative cover ended and no *Paludiscala caramba* were found, despite intensive collecting which yielded quantities of *Duragonella coahuilae* and *Mexistiobia manantiali*. *Paludiscala caramba* appears to have a similar pattern of distribution in other springs.

Shell

The shell of *Paludiscala caramba* has up to 7.5 rounded whorls. Shell measurements for two populations are given in Table 20. For

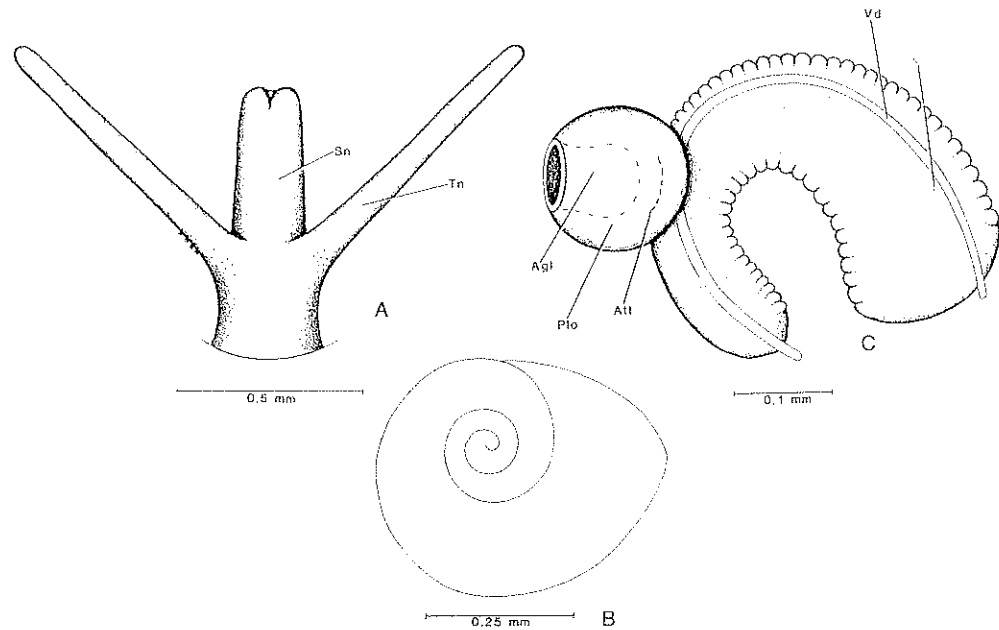


FIG. 21. Head, penis, and operculum of *Paludiscala caramba*. A. Dorsal view of the head. Note the *Hydrobia*-like hypertrophied ciliary tufts on the left tentacle and the lack of eyes. B. Operculum. C. Dorsal aspect of the penis showing the bulb-like penial lobe (Plo) with a single apocrine gland (Agl). The attachment area (Att) of the penial lobe to the penis is hidden by the lobe's curvature. Agl—apocrine gland; Att—attachment of penial lobe to penis; Plo—penial lobe; Sn—snout; Tn—tentacle; Vd—vas deferens.

both populations, there was no significant sexual dimorphism in shell length ($p > 0.1$). For most populations sampled, the shells have fairly tall, thin costae that are curved in profile (Figs. 19A, B). The costae begin after 0.8 whorls and continue to the aperture. Costae spacing is irregular: for 16 shells (sexes mixed) with 7.5 whorls from Locality 63, the penultimate whorl had 9.5 ± 1.7 costae (range of 6–12), and the body whorl had 10.5 ± 1.4 costae (range of 9–13). A few populations (Localities 38, 67) had smaller individuals (6.5 whorls, 1.4 mm shell length) with costae reduced or absent (Figs. 19C, D). The aperture is inclined only 10° to the coiling axis. The peristome is complete, slightly thickened, and adnate to or just free from the preceding whorl. The inner lip is slightly flared.

Nonreproductive Features

The anatomical description and data (Table 21) are from the population from Locality 63. The snout (Fig. 21A) is elongate, as are the tentacles. There are four or five ciliary tufts on

the tentacles and the tufts are restricted to the outer edge of the left tentacle. There is a small concentration of white granules and a pink color in the areas where the eyespots normally would be. Crystalline granules are seen on the ventral body surface. The gills are reduced in number (Table 21). The operculum (Fig. 21B) has three whorls and the nucleus is positioned at 38% of the long axis of the operculum. The operculigerous lobe has a narrow band of crystalline granules and a small area of red-pink color.

Radula

The radula is shown in Figs. 20B–D. The central tooth has a single pair of basal cusps that originate from the lateral angles (Figs. 20B, D). Radular statistics and the various cusp arrangements for the four tooth types are given in Tables 22 and 23.

Female Reproductive Anatomy

The organization of the female reproductive system is shown in Figs. 22A, C, D, E, F. The

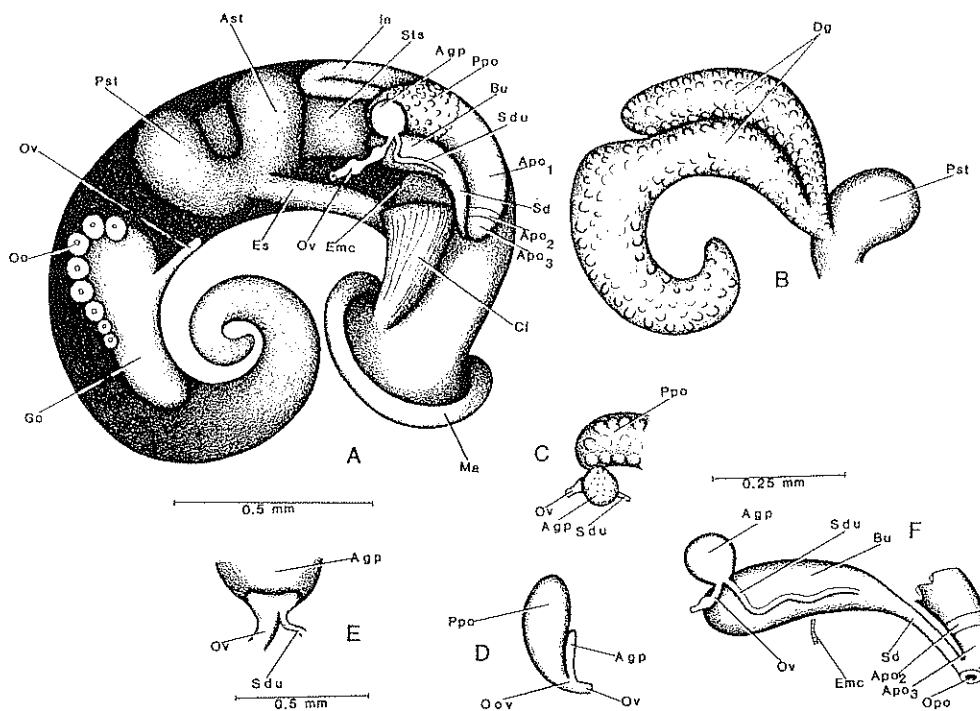


FIG. 22. Aspects of the anatomy of *Paludiscala caramba*. A. Ventral aspect of the uncoiled female without the head and kidney tissue. A section of the oviduct (Ov) has been removed. Note the swellings of the oviduct, the albumen gland pouch (Agp), and capsule gland differentiated into three distinct regions (Apo₁, Apo₂, and Apo₃). B. Ventral aspect of the digestive gland (Dg), showing the tubercles reduced to mere swellings. C. Posterior pallial oviduct oriented as in A, but with the albumen gland pouch (Agp) folded ventrally to expose its basal connection to the main portion of the albumen gland. D. Cross-sectional view of the posterior end of the pallial oviduct showing how the albumen gland pouch (Agp) and oviduct (Ov) jointly open into the albumen gland proper. E. Base of the albumen gland pouch (Agp). Note that the oviduct (Ov) and sperm duct (Sdu) join together at the opening to the albumen gland, which is differentiated from the distal portion of the albumen gland pouch. F. Oriented as in A, but with most of the pallial oviduct cut away to reveal the bursa (Bu). Note that much of the bursa is anterior to the end of the mantle cavity (Emc) and that the spermathecal duct (Sd) joins the pallial oviduct at its anterior end. Agp—albumen gland pouch; Apo₁—posterior capsule gland; Apo₂—middle capsule gland; Apo₃—anterior capsule gland; Ast—anterior stomach chamber; Bu—bursa; Cl—columellar muscle; Dg—digestive gland; Emc—posterior end of the mantle cavity; Es—esophagus; Go—gonad; In—intestine; Ma—mantle edge; Oo—oocyte; Oov—opening of the oviduct; Opo—opening of the pallial oviduct; Ov—oviduct; Ppo—posterior pallial oviduct; Pst—posterior stomach chamber; Sd—spermathecal duct; Sdu—sperm duct; Sts—style sac.

gonad (Go) is a single non-lobed mass that comprises 15% of the body length. The pallial oviduct is 17% of the body length and extends slightly over the style sac. The albumen gland (Ppo) is of normal size. The capsule gland has three distinct tissue sections: a large posterior one (Apo₁, Fig. 22A), a smaller grey-colored one (Apo₂), and a somewhat larger white-colored one (Apo₃). The sac-like bursa lies dorsolateral to the pallial oviduct, and does not extend posterior to it. The bursa is 58% of the pallial oviduct length, and its an-

terior third lies anterior to the end of the mantle cavity (Figs. 22A, F). A thin sperm duct (Sdu) issues from the anterior end of the bursa and coils slightly on its ventral surface (Fig. 22F). The albumen gland "pouch" (Agp) appears as a disc appressed to the ventral surface of the albumen gland (Fig. 22A). When the pouch is pulled away from the pallial oviduct, its basal connection to the latter is readily seen (Fig. 22C). This is also seen in cross-section (Fig. 22D). The oviduct (Ov) and sperm duct (Sdu) jointly enter the

TABLE 20. Shell measurements (mm) of males and females from two populations of *Paludiscala caramba*. Snails with the dominant maximum whorl number(s) were used. N = 9 unless stated otherwise. Mean \pm standard deviation. "p" refers to the significance level for the difference between shell lengths (t-test) for that population.

	Whorls	Length	Width	Length of body whorl	Length of aperture	Width of aperture	p
<i>Locality 63</i>							
♀ (n = 10)	7.0	2.26 \pm 0.08	1.09 \pm 0.08	1.04 \pm 0.05	0.71 \pm 0.04	0.53 \pm 0.04	>.1
	7.5	2.44 \pm 0.09	1.13 \pm 0.10	1.09 \pm 0.07	0.71 \pm 0.03	0.53 \pm 0.03	
♂	7.5	2.41 \pm 0.13	1.11 \pm 0.09	1.07 \pm 0.05	0.71 \pm 0.04	0.53 \pm 0.02	
<i>Locality 27</i>							
♀	7.5	2.50 \pm 0.10	1.18 \pm 0.07	1.08 \pm 0.07	0.74 \pm 0.06	0.57 \pm 0.03	>.1
♂	7.5	2.54 \pm 0.06	1.18 \pm 0.06	1.09 \pm 0.06	0.74 \pm 0.04	0.54 \pm 0.04	

TABLE 21. Dimensions (mm) or counts of non-neural organs and structures of *Paludiscala caramba*. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	3.11 \pm 0.21	3.01 \pm 0.15
Gill filament number		13.6 \pm 0.89	
Osphradium (N=6)	L	0.15 \pm 0.02	
Gonad	L	0.48 \pm 0.07	0.47 \pm 0.08
	W	0.29 \pm 0.04	0.27 \pm 0.03
Prostate	L		0.44 \pm 0.04
	W		0.19 \pm 0.03
Penis	L		0.66 \pm 0.04
	W		0.19 \pm 0.02
Pallial oviduct (N = 7)	L	0.55 \pm 0.06	
	W	0.15 \pm 0.02	
Bursa copulatrix (N = 8)	L	0.32 \pm 0.03	
	W	0.14 \pm 0.02	

TABLE 22. Radular statistics from 5 individuals of *Paludiscala caramba*. \bar{X} = mean, S = standard deviation. Measurements in mm.

Radular features	\bar{X}	S
Length	0.343	0.016
Width	0.050	0.004
Number of rows	72.0	2.0
Number of rows in formative stage	5.2	1.6

TABLE 23. The various cusp arrangements of the four tooth types of *Paludiscala caramba*, counted from five radulae using SEM, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{4-1-4}{1-1}$	80	4-1-3	80	18	20	16	20
$\frac{5-1-4}{1-1}$	40	5-1-3	20	19	20	17	20
$\frac{5-1-5}{1-1}$	80	4-1-4	20	20	20	18	20
$\frac{6-1-4}{1-1}$	20			21	40	22	40
$\frac{6-1-6}{1-1}$	20			22	40	23	80
				23	40	24	40
				24	20	25	20

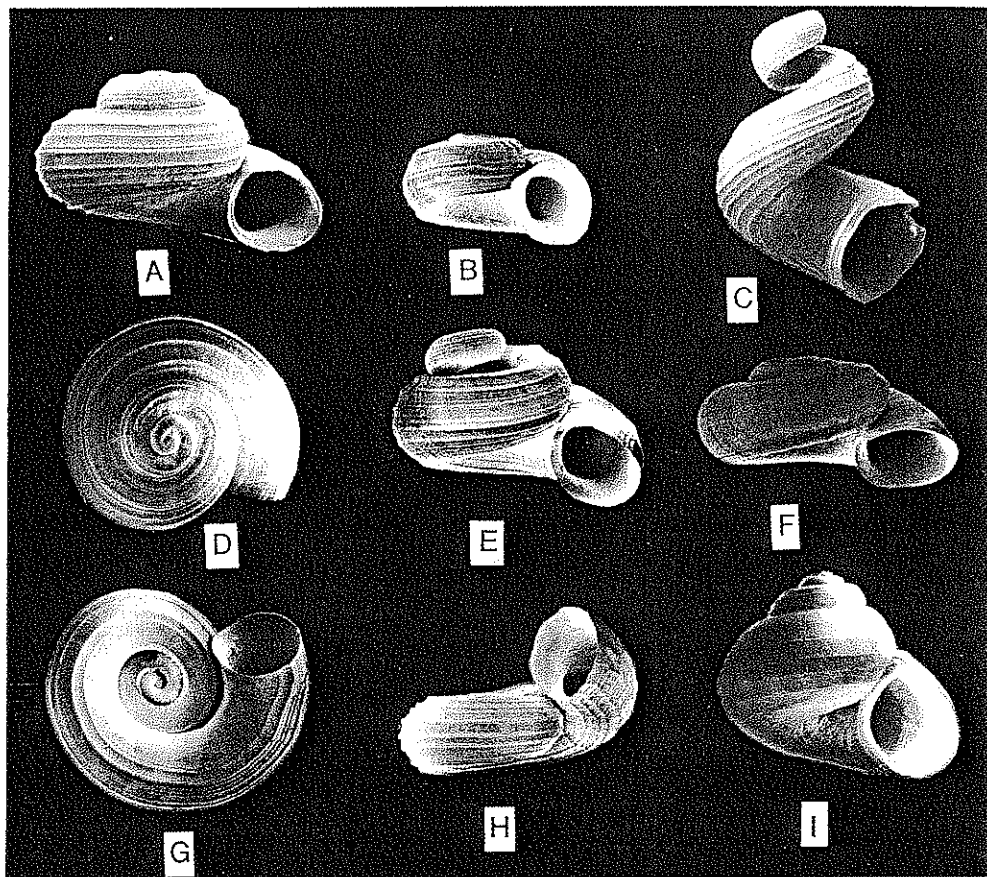


FIG. 23. SEM photos of *Cochliopina milleri* and *Cochliopina riograndensis*. Shells A-H are *Cochliopina milleri* from Locality 38, shell I is *Cochliopina riograndensis* from Locality 101. Shell A is 3.26 mm wide; the others are printed to the same enlargement.

albumen gland at the base of the pouch; this area is somewhat differentiated and appears to be a sphincter (Fig. 22E). There is no seminal receptacle of normal shape or position. The pouch, while non-glandular, is obviously of pallial oviduct origin, yet was seen to hold sperm and probably serves as a secondary seminal receptacle, as may the oviduct swellings. The spermathecal duct (Sd) may be tightly appressed to the columellar side of the pallial oviduct (Fig. 22A) or may be slightly separated from it (Fig. 22F).

The male gonad is a single non-lobed mass. The prostate is relatively large and extends considerably anterior to the end of the mantle cavity. The anterior vas deferens exists from the anterior tip of the prostate.

The penis is bluntly shaped and has neither cilia nor a terminal papilla. The penial lobe (Plo) is located at 67% of the penis length (on the outer curvature) from the base, and has a spherical shape with a diameter of 0.15 mm (Fig. 21C). The lobe overlies its attachment area to the penis, which is short and located on the outer curvature (Att, Fig. 21C). The apocrine gland (Agl) extends for slightly more than one-half of the diameter of the penial lobe. The structure of the gland is precisely that of *Coahuilix*. Folds are seen on the outer curvature of the penis from the base to the penial lobe. The inner curvature has folds for virtually its entire length. The vas deferens (Vd) does not coil in the penis. Infrequent Gl₂ glands are seen in the penis.

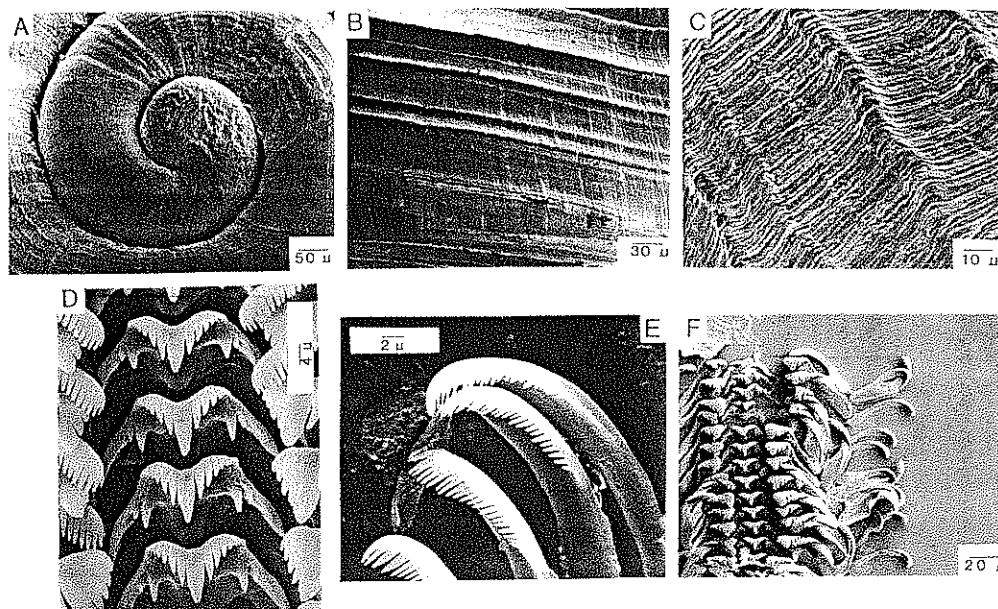


FIG. 24. SEM photos of shell and radula of *Cochliopina milleri*. A. Shell apex, showing wrinkled, pitted microsculpture. B. Portion of the body whorl showing spiral lines and collabral growth lines. C. Close-up of B. D. Central tooth of the radula. E. Outer marginal teeth. F. Part of radular ribbon.

Cochliopina Morrison, 1946

Type-species: *Cochliopina riograndensis* (Pilsbry & Ferriss, 1906).

Distribution: Rio Grande drainage, from Texas south to Panama.

Species included: 20 species listed by Taylor (1966).

Description

Cochliopina has no distinctive unique features, but is recognizable by a combination of character states (see below).

The shell (Fig. 23; Morrison, 1946, pl. 2, figs. 7–9, 11–13) is small (width, 5 mm) and planispiral to low-trochoid in form; the sculpture consists of spiral lines or cords, frequently bearing periostracal bristles; the apical whorl has pitted microsculpture (Fig. 24A); the tentacles have *Spurwinkia*-like hypertrophied ciliary tufts (Figs. 25A, B); females are ovoviviparous; the pallial oviduct has a slight posterior bend; the albumen gland is reduced in size (Ppo, Fig. 26A); the seminal receptacle opens into the oviduct (Figs. 26B, C); the oviduct and anterior end of the bursa are connected by a short sperm duct (Sdu,

Figs. 26B, C); the non-muscular spermathecal duct opens just beyond the posterior end of the mantle cavity (Figs. 26A, C); the anterior end of the brood pouch is muscularized and coiled toward the columellar side (Fig. 26E); the penis is non-lobed, with an elongate penial filament, and lacks specialized glands (Fig. 25D; Morrison, 1946, pl. 3, figs. 9–15).

Discussion

Cochliopina and *Mexithauma* share numerous features (see Tables 53–55, Figs. 49, 50) relating to shell shape, sculpture, tentacle ciliation, reproductive mode, coiling of the pallial oviduct, reduction of the albumen gland size, connection between the seminal receptacle and oviduct, muscularization and coiling of the end of the brood pouch, and the form of the penis (and lack of specialized glands). Distinctive features of the female reproductive system shared by these taxa include the slight posterior bend of the pallial oviduct, the opening of the seminal receptacle into the oviduct, and the well-developed muscularization and coiling of the anterior end of the brood pouch.

The two taxa differ in the following features:

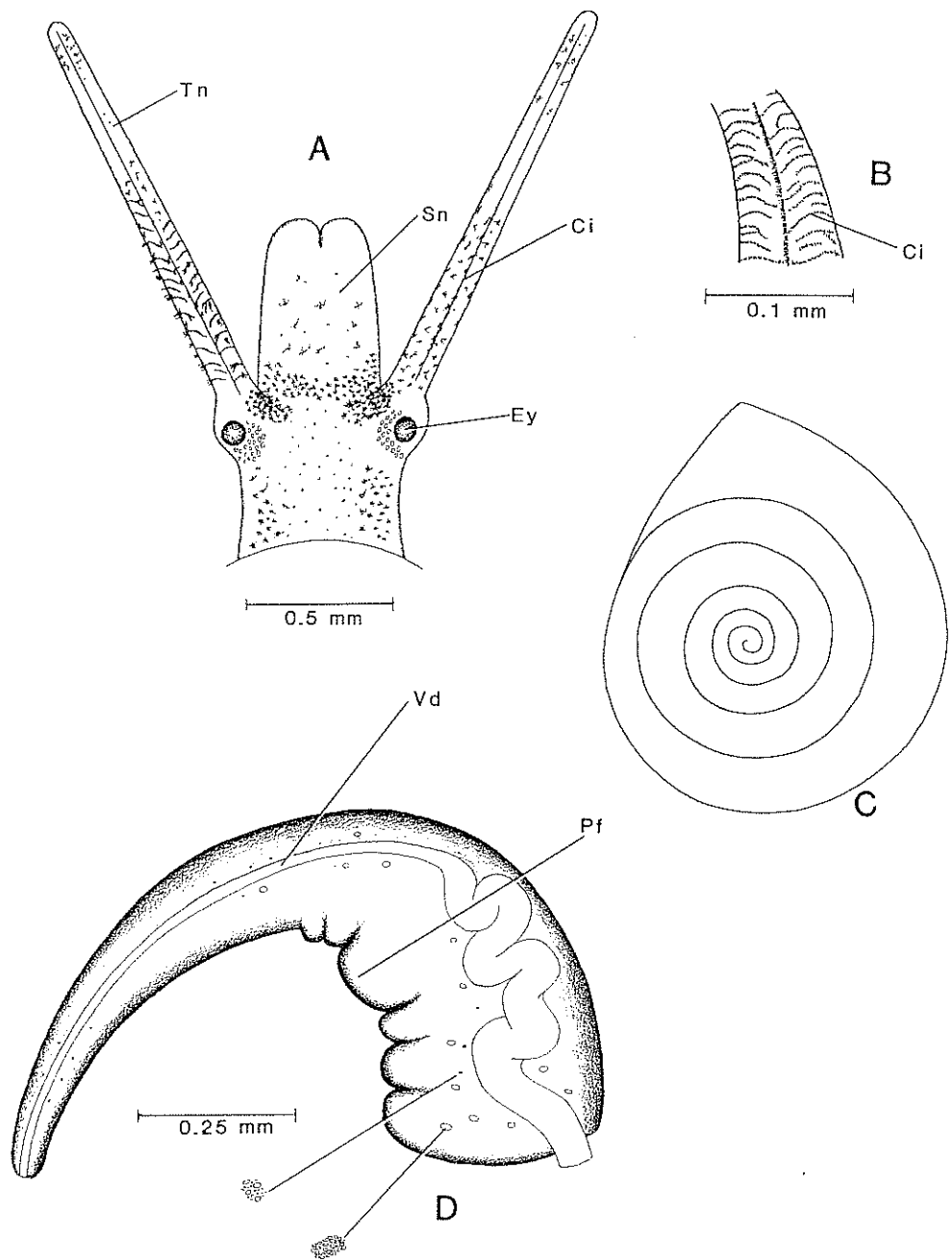


FIG. 25. Head, operculum, and penis of *Cochliopina milleri*. A. Dorsal aspect of the head. Note the *Spurwinkia*-like hypertrophied ciliary tufts (Ci) on the tentacles. B. Close-up of ciliation pattern on left tentacle. C. Operculum. D. Penis with penial folds (Pf), but no lobes. Ci—ciliary tufts on tentacle; Ey—eye; Sn—snout; Tn—tentacle; Vd—vas deferens.

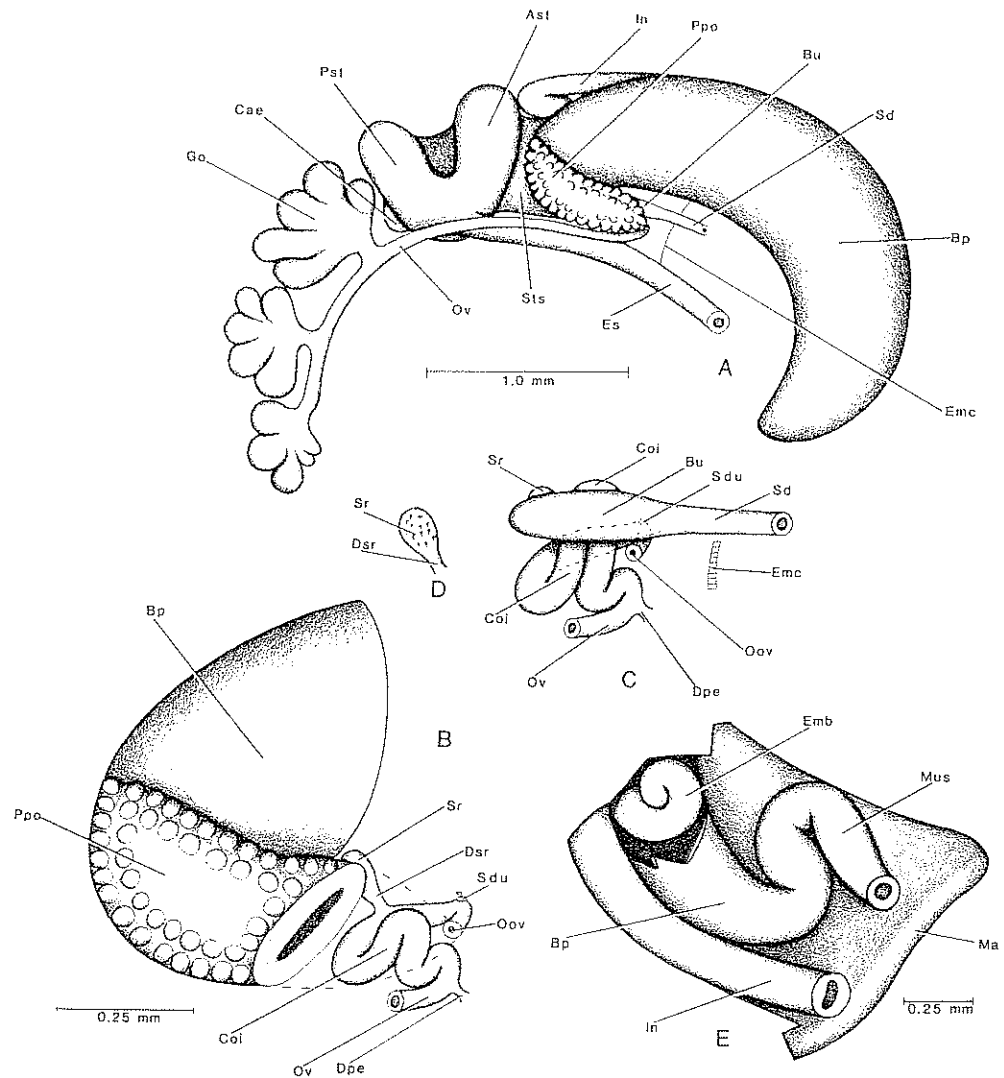


FIG. 26. Female reproductive anatomy of *Cochliopina milleri*. A. Ventral aspect of uncoiled snail without head and kidney tissue. Note the posterior bend of the pallial oviduct. B. Posterior region of the pallial oviduct, oriented as in A, but with a portion of the albumen gland (Ppo) and the bursa cut away to reveal the oviduct coils (Coi), seminal receptacle (Sr), sperm duct (Sdu), and opening of the oviduct into the albumen gland (Oov). C. Oriented as in B, but with the bursa (Bu) in place. D. The seminal receptacle (Sr) with pigment patches. E. Portion of the anterior end of the mantle cavity, showing the muscular coil (Mus) of the anterior end of the brood pouch (Bp). Ast—anterior stomach chamber; Bp—brood pouch; Bu—bursa; Cae—caecum of stomach; Coi—coil of oviduct; Dpe—gonopericardial duct; Dsr—duct of the seminal receptacle; Emb—embryonic shell; Emc—posterior end of the mantle cavity; Es—esophagus; Go—gonad; In—intestine; Ma—mantle edge; Mus—muscular section of the brood pouch; Oov—opening of the oviduct; Ov—oviduct; Ppo—albumen gland; Pst—posterior stomach chamber; Sd—spermathecal duct; Sdu—sperm duct; Sr—seminal receptacle; Srs—style sac.

condition of the mantle edge (*Cochliopina*, smooth; *Mexithauma*, papillate); apical microsculpture (*Cochliopina*, pitted; *Mexithauma*, absent); relative size of the female gonad (*Cochliopina*, large; *Mexithauma*, small); length of the spermathecal duct (*Cochliopina*, short; *Mexithauma*, long); insertion of the sperm duct from the oviduct (*Cochliopina*, to bursa; *Mexithauma*, to duct of bursa); and male gonad morphology (*Cochliopina*, simple lobes; *Mexithauma*, bush-like).

Cochliopina milleri Taylor, 1966

Holotype: UMMZ 220182

Type-locality: Locality 53.

Distribution: endemic to the Cuatro Ciénegas Basin. In the eastern lobe of the basin, it has not been found south of Locality 97 (Fig. 3).

Habitat: *Cochliopina milleri* is most common in the outflows of cool (<28°C) springs, and is usually sympatric with *Nymphophilus minckleyi* on aquatic vegetation, particularly *Chara* and *Utricularia*. *Cochliopina milleri* was rarely found in the large spring pools, and was never found in mop or sieve collections from the small springs.

Description

The generic placement of *Cochliopina milleri* is tentative as the detailed anatomy of the type-species, *Cochliopina riograndensis*, is not known. *Cochliopina milleri* does resemble the type-species in shell form and external anatomy.

The shell (Figs. 23A–H) is thin, relatively small (length, 1.16–1.48 mm), and broadly conical to planispiral, with little whorl overlap; the narrow spiral cords are numerous, prominent, and fringed with light-colored periostracum; the aperture is nearly circular and adnate to or free from the penultimate whorl.

Shell

The shell has rounded whorls and deeply impressed sutures. The aperture is slightly angled adapically and inclined 30–45° to the coiling axis. For the population from Locality 38, coiling abnormalities were frequent and remarkable; varying from a slight loosening of the whorls (Fig. 23E), to a change in coiling direction near the end of the body whorl (Fig. 23H), to near-open coiling (Fig. 23C). Other populations show less coiling variation than that from Locality 38. There are generally 10–20 spiral cords, and numerous spiral lines on the last two whorls. Occasional specimens are almost smooth-shelled (Fig. 23F). The apical whorl microsculpture is somewhat coarser than that seen in other hydrobiid snails (Fig. 24A). Spiral sculpture begins after the first whorl. Close-ups of the spiral sculpture are shown in Figs. 24B, C. There are strong axial growth lines that become especially prominent near the aperture (Fig. 24C).

Shell measurements from the population from Locality 38 (excluding abnormally coiled specimens) are given in Table 24. Females have a greater shell width ($p < .005$) and are also relatively taller (t-test for difference be-

TABLE 24. Shell measurements (mm) of males and females from one population of *Cochliopina milleri* and two populations of *C. riograndensis*. Snails with the dominant maximum whorl number were used. N = 9 unless otherwise indicated. Mean \pm standard deviation. "p" refers to the significance level for the difference between shell widths of males and females (t-test) for that population.

Whorls	Length	Width	Length of body whorl	Length of aperture	Width of aperture	Shell length Shell width	
<i>C. milleri</i> (Locality 38)							
♂	3.0	1.16 ± 0.08	2.29 ± 0.15	1.11 ± 0.10	0.96 ± 0.06	0.89 ± 0.07	0.50 ± 0.03
♀	3.5	1.78 ± 0.10	3.08 ± 0.18	1.57 ± 0.11	1.19 ± 0.10	1.10 ± 0.06	0.58 ± 0.05
p = <.005							
<i>C. riograndensis</i> (Locality 101)							
♂	4.0	2.23 ± 0.10	2.74 ± 0.18	1.84 ± 0.09	1.48 ± 0.09	1.22 ± 0.07	0.82 ± 0.06
♀	4.5	2.78 ± 0.15	3.12 ± 0.28	2.18 ± 0.15	1.59 ± 0.14	1.36 ± 0.10	0.89 ± 0.06
<i>C. riograndensis</i> (Locality 102)							
♂	3.5	1.54 ± 0.04	2.14 ± 0.11	1.34 ± 0.11	1.09 ± 0.09	0.93 ± 0.08	0.72 ± 0.05
♀	4.0	2.21 ± 0.17	2.79 ± 0.15	1.86 ± 0.12	1.43 ± 0.08	1.24 ± 0.08	0.79 ± 0.05
>4.0, <4.5	2.54 ± 0.15	3.06 ± 0.12	2.03 ± 0.08	1.54 ± 0.08	1.33 ± 0.07	0.83 ± 0.03	

TABLE 25. Dimensions (mm) or counts of non-neural organs and structures of *Cochliopina milleri*. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body (N=6)	L	6.47 \pm 0.39	5.15 \pm 0.31
Gill filament number		26.7 \pm 2.28	
Osphradium (N=8)	L	0.35 \pm 0.05	
Gonad (N=6)	L	1.69 \pm 0.09	3.28 \pm 0.15
	W	0.55 \pm 0.05	0.57 \pm 0.03
Prostate	L		0.56 \pm 0.06
	W		0.28 \pm 0.03
Penis	L		1.24 \pm 0.05
	W		0.36 \pm 0.04
Pallial oviduct	L	2.85 \pm 0.28	
	W	0.72 \pm 0.08	
Bursa copulatrix	L	0.27 \pm 0.04	
	W	0.10 \pm 0.01	
Seminal receptacle (body) (N = 6)	L	0.10 \pm 0.01	
	W	0.06 \pm 0.01	
Seminal receptacle (duct) (N=9)	L	0.04 \pm 0.01	
	W	0.04 \pm 0.01	

TABLE 26. Radular statistics from 12 individuals of *Cochliopina milleri*. \bar{X} = mean, S = standard deviation. Measurements in mm.

Radular feature	\bar{X}	S
Length	0.563	0.028
Width	0.106	0.006
Number of rows	45.6	1.96
Number of rows in formative stage	2.36	1.12
Width of central tooth (N = 21)	0.031	0.0014

tween means of shell length/width, $p < 0.005$) than males. This sexual dimorphism is seen by comparing Figs. 23A and B (adult female and male, respectively).

Nonreproductive Features

Details and data concerning anatomy are from the population from Locality 38. Measurements of organs and structures are given in Table 25. The snout is squat and the tentacles are elongate in comparison (Fig. 25A). The left tentacle has 10–12 hypertrophied ciliary tufts protruding from the outer edge and numerous ciliary tracts (Ci, Figs. 25A, B) curving inward toward the center of the tentacle from both sides. These tracts are present for 67% of the tentacle length from the base. The tentacle also has a central ciliary tract

along its length. The right tentacle alone has the central ciliary tract. The snout and tentacles are dusted with melanin to varying degrees. A dark melanin patch at the base of each tentacle, across from the eyespot, is seen in most individuals. Occasional specimens had a dark melanin patch at the tentacle tips. There is a cluster of dull white granules around the eyes and smaller granules are found in the neck, snout, and tentacles.

The sides of the head-foot are sometimes darkly pigmented, and in those specimens a non-pigmented strip was seen extending from the neck to the foot. Body pigmentation for the female consists of small melanin patches on the dorsal and ventral body surfaces that interdigitate with clusters of white granules, producing a mottled appearance. The male is similarly pigmented, but has solid dark melanin on the ventral surface of the gonad. The caecal chamber is prominent.

The operculum (Fig. 25C) has 5.5 whorls and the nucleus is positioned at 42% of the long axis of the operculum. Pigmentation on the operculigerous lobe consists of two to three large melanin patches.

Radula

The radula is shown in Figs. 24D–F. The central tooth has one to three pairs of basal cusps that originate from the lateral angles. The central cusp of the central tooth is dagger-like. The marginal teeth have many cusps. Radular statistics and the various cusp arrangements for the four tooth types are given in Tables 26 and 27.

Female Reproductive Anatomy

The organization of the female reproductive system is shown in Fig. 26. The gonad (Go) has three lobate branches, and occupies 26% of the body length. The pallial oviduct occupies 44% of the body length and overlies most of the style sac. The anterior portion of the pallial oviduct is modified into a thin-walled, non-glandular brood pouch (Bp) for the storage of embryos. The pallial oviduct coils posteriorly, the distance from the posteriormost point of the pallial oviduct and the end of the coil being 0.67 mm. The small albumen gland (Ppo, Fig. 26A) constitutes this coiled portion.

The oviduct (Ov) disappears beneath the anterior portion of the albumen gland (Fig. 26A). There is a short gonopericardial duct

TABLE 27. The various cusp arrangements for the four tooth types in 12 radulae of *Cochliopina milleri*, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{4-1-3}{2-2}$	8	4-1-3	83	17	8	19	40
$\frac{4-1-4}{1-1}$	8	4-1-4	83	18	25	20	40
$\frac{4-1-4}{2-1}$	8	5-1-4	8	19	50	21	40
$\frac{4-1-4}{2-2}$	42	5-1-5	8	20	58	22	60
$\frac{4-1-4}{3-2}$	17	5-1-3	8	21	92	23	80
$\frac{4-1-4}{3-3}$	17	3-1-3	42	22	33	24	60
$\frac{5-1-4}{2-2}$	17			23	58	25	60
$\frac{5-1-4}{3-2}$	8			24	8	26	20
$\frac{5-1-5}{2-1}$	17			25	25	27	20
$\frac{5-1-5}{2-2}$	67			26	8	28	20
$\frac{6-1-5}{2-2}$	25			27	8		
				28	8		

(Dpe). The bursa (Bu) is small, dorsal to, and almost entirely hidden by the albumen gland (Fig. 26A). The elongate seminal receptacle (Sr) is dorsal to and mostly hidden by the bursa. There is usually a light melanin dusting on the seminal receptacle (Fig. 26D).

The oviduct loops several times dorso-laterally to the bursa before receiving the short duct of the seminal receptacle (Dsr, Figs. 26B, C). The minuscule sperm duct (Sdu) enters the oviduct just where the latter turns to open into the end of the albumen gland (Fig. 26B). The spermathecal duct (Sd) extends 0.14 mm beyond the posterior end of the mantle cavity.

The well developed muscular loop (Mus) of the anterior brood pouch is shown in Fig. 26E. For 15 adult females, there was an average of 11.6 ± 2.97 shelled embryos in the brood pouch, as well as another eight to ten very small non-shelled embryos. For 108 shelled embryos, the range of shell width was quite narrow, 0.317–0.475 mm, and the mean was 0.400 ± 0.178 mm. Embryonic shells have up to 1.3 whorls.

Male Reproductive Anatomy

The male gonad consists of 10–12 lobed branches and fills the entire length of the digestive gland, covering the posterior stomach chamber. The gonad is 64% of the body length. The prostate is relatively small, 11% of the body length, but does overlap the mantle cavity. The anterior vas deferens exits from the anterior tip of the prostate.

The penis (Fig. 25D) has numerous folds (Pf) on the inner curvature for one half of the penis length. While one of the folds was sometimes noticeably wider than the others (as in Fig. 26D), it did not project outward as a penial lobe in any specimen. The outer curvature is without folds. Scattered throughout the penis are Gl₁ and Gl₂ gland types. The vas deferens (Vd) coils and thickens from the base of the penis until it is even with the end of the penial folds, after which it narrows and stops coiling. The penis, exclusive of the long penial filament, has a dark brown color that is not an external melanin coating, but colored tissue.

Cochliopina riograndensis
(Pilsbry & Ferriss, 1906)

Holotype: ANSP 91324.

Type-locality: debris of the Rio San Felipe near the Rio Grande, Val Verde County, Texas.

Distribution: Rio Grande drainage of Texas and northeastern México. While this species had been previously known from the Rio Salado de Nadadores, and an adjacent spring, both just east of the Cuatro Ciénegas Basin (Taylor, 1966), the author also collected it at Locality 101 in the southeastern lobe of the basin.

Habitat: This species has been found in springs and spring outlets of various sizes (Fullington, 1978; Taylor, 1966). Locality 101 is a large spring pool (the Santa Tecla Laguna) and *Cochliopina riograndensis* was abundant on unidentified vegetation along its shallow edges.

Description

This species has been amply described by Fullington (1978) and Taylor (1966). Its shell is distinguished from that of *Cochliopina milleri* by its thicker, larger, and relatively taller appearance (see Table 24: note the ratios of

shell length/width). Its whorls overlap greatly and it has a more conical shape than does the shell of *Cochliopina milleri*. The aperture is angled adapically and the inner lip is partly fused to the penultimate whorl. The spiral cords are few in number and lack prominence, but the periostracal bands are darker and wider (especially in the umbilical area) than those of *Cochliopina milleri*.

Discussion

The southeastern lobe of the basin has several nonendemic taxa of undisputed Rio Grande (= Rio Bravo) origin, including the cichlid fish, *Cichlasoma cyanoguttatum* (see Minckley, 1977). The distinctive Rio Grande aspect of the fauna from this portion of the basin contrasts with the more endemic aspect of the fauna from the remainder of the basin. Hubbs & Miller (1965) suggested that the southeastern lobe had a recent surficial connection to the Rio Salado de Nadadores (Fig. 2, Number 7, a Rio Grande tributary), thus explaining this pattern. The discovery of *Cochliopina riograndensis* in the southeastern lobe of the basin supports this hypothesis.

The relationship between endemic *Cochliopina milleri* and non-endemic *Cochliopina riograndensis* is unknown as the internal

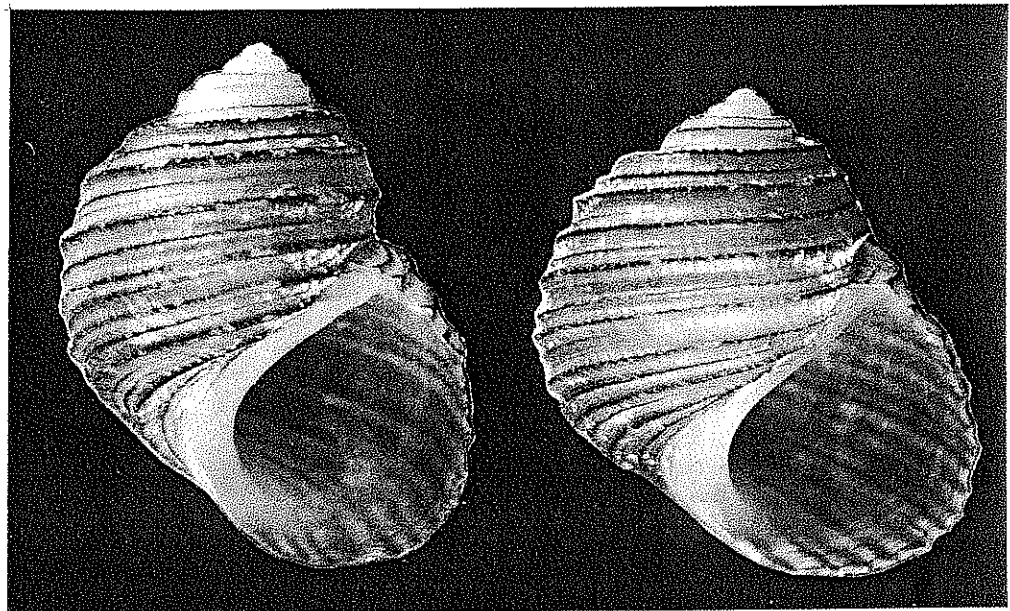


FIG. 27. Shells of *Mexithauma quadripaludium* from Locality 1. The shell on the left is 7.38 mm long, the other is printed at the same enlargement.

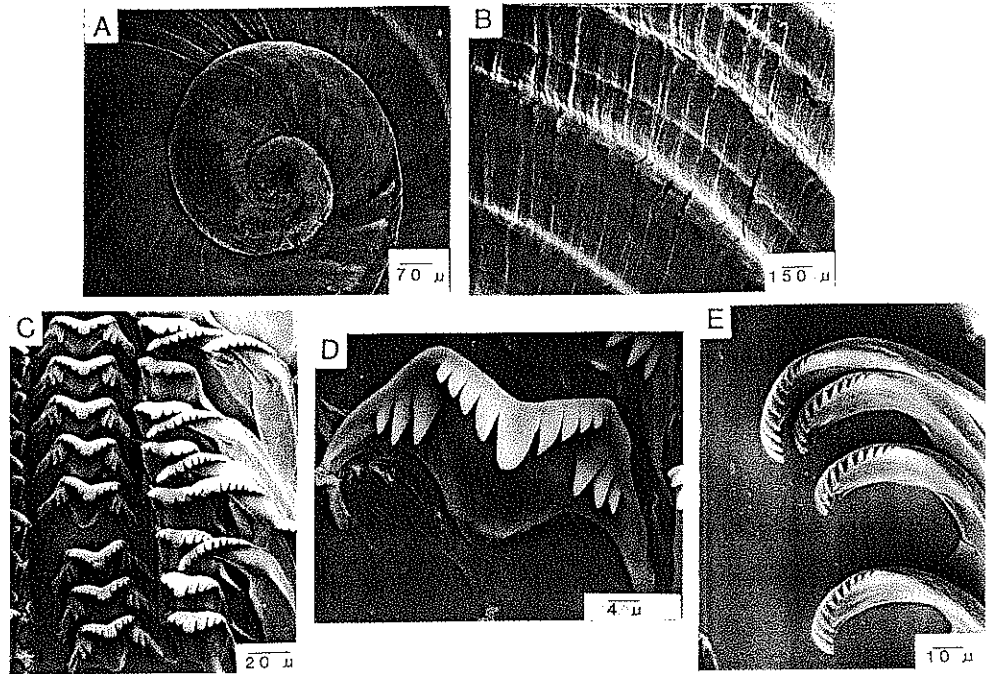


FIG. 28. SEM photos of shell and radula of *Mexithauma quadripaludium*. A. Apical whorls of shell. Note lack of microsculpture. B. Portion of penultimate whorl showing strong spiral cords and collabral microsculpture. C. Part of radular ribbon. D. Isolated central tooth. E. Outer marginal teeth.

anatomy of the latter is not known. The distinctively fragile and loosely-coiled shell of *Cochliopina milleri* may be associated with its restriction to fairly cichlid-free waters (i.e., low predation pressure).

Mexithauma Taylor, 1966

Type-species: *Mexithauma quadripaludium* Taylor, 1966.

Distribution: endemic to the Cuatro Ciéne-gas Basin.

Species included: monotypic.

Description

Distinctive features of *Mexithauma* include the papillate mantle edge of both sexes (Pma, Figs. 30A, 31A) and the open channel (Oc) connecting the openings of the spermathecal duct and pallial oviduct (Figs. 30C, E).

The shell (Fig. 27) is large (length, 7.0 mm), globose, without umbilicus, and with prominent spiral cords fringed with periostracum; the inner lip of the shell is thickened; the

tentacles show *Spurwinkia*-like ciliation (Figs. 29A, B); females are ovoviviparous; the female gonad is very reduced in size (Go, Fig. 30A); a large pallial oviduct overlies the stomach and has a slight posterior bend (Fig. 30A); the seminal receptacle (Sr) is positioned lateral to the bursa and opens into the oviduct (Fig. 30B); the oviduct connects with the duct of the bursa via a short sperm duct (Sdu, Fig. 30B); the anterior end of the brood pouch is muscularized and coiled (Figs. 30C, E); the male gonad is bush-like (Go, Fig. 31A); the penis is non-lobed and lacks specialized glands (Fig. 31B).

Mexithauma is most similar to *Cochliopina* (see above; Tables 53–55, Figs. 49, 50).

Mexithauma quadripaludium Taylor, 1966

Holotype: UMMZ 220214.

Type-locality: Locality 97.

Habitat: *Mexithauma quadripaludium* has been found only in the larger springs and their outflows. It has been collected from all types of aquatic vegetation, sand (composed of

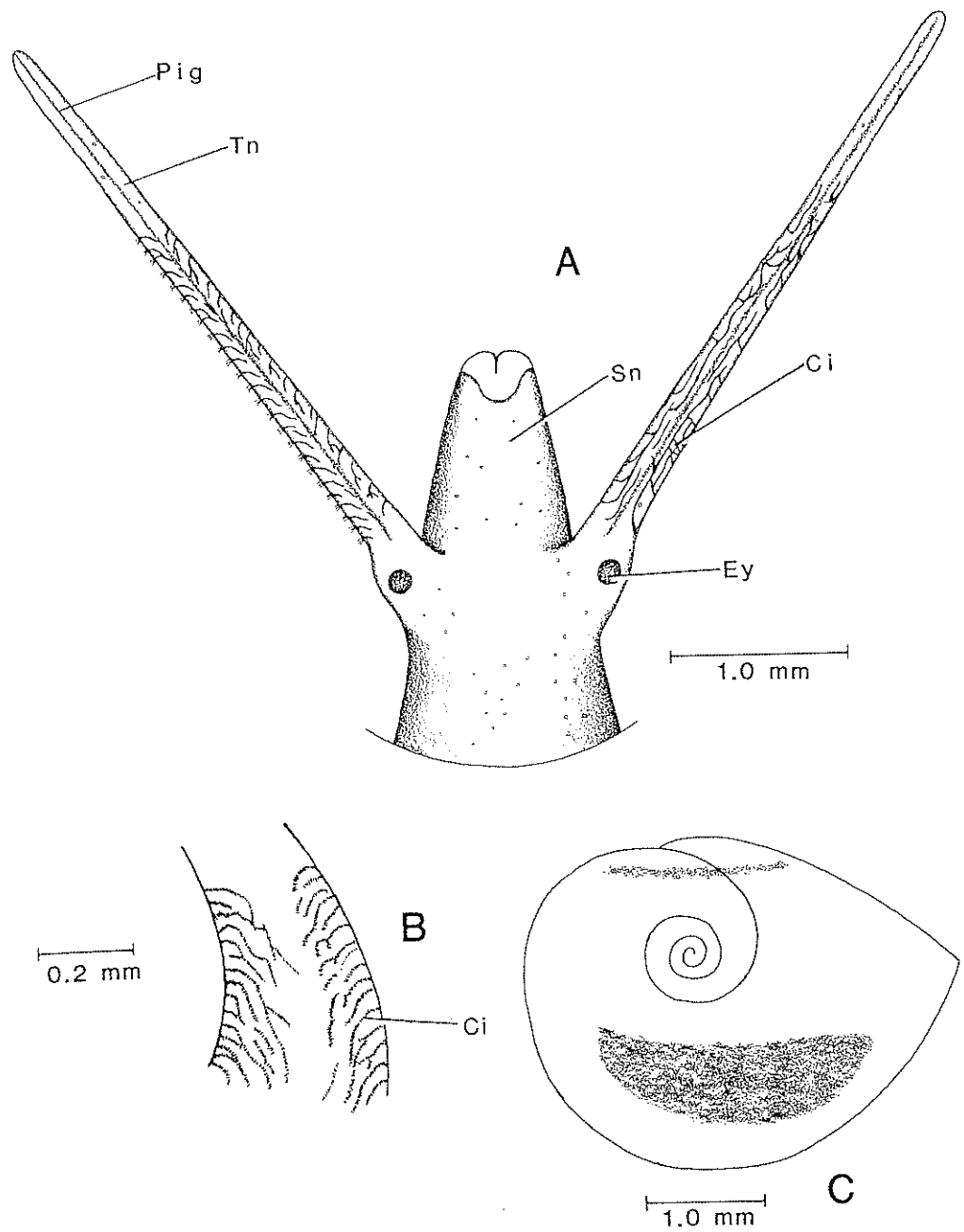


FIG. 29. Head and operculum of *Mexithauma quadripaludium*. A. Dorsal aspect of head. Note the *Spurwinkia*-like hypertrophied ciliary tufts (Ci) and the central pigment streak (Pig) on the tentacles. B. Close-up of ciliation pattern on left tentacle. C. Operculum. The pigment pattern on the operculigerous lobe is also shown. Ci—ciliary tufts on tentacles; Ey—eye; Pig—pigment; Sn—snout; Tn—tentacle.

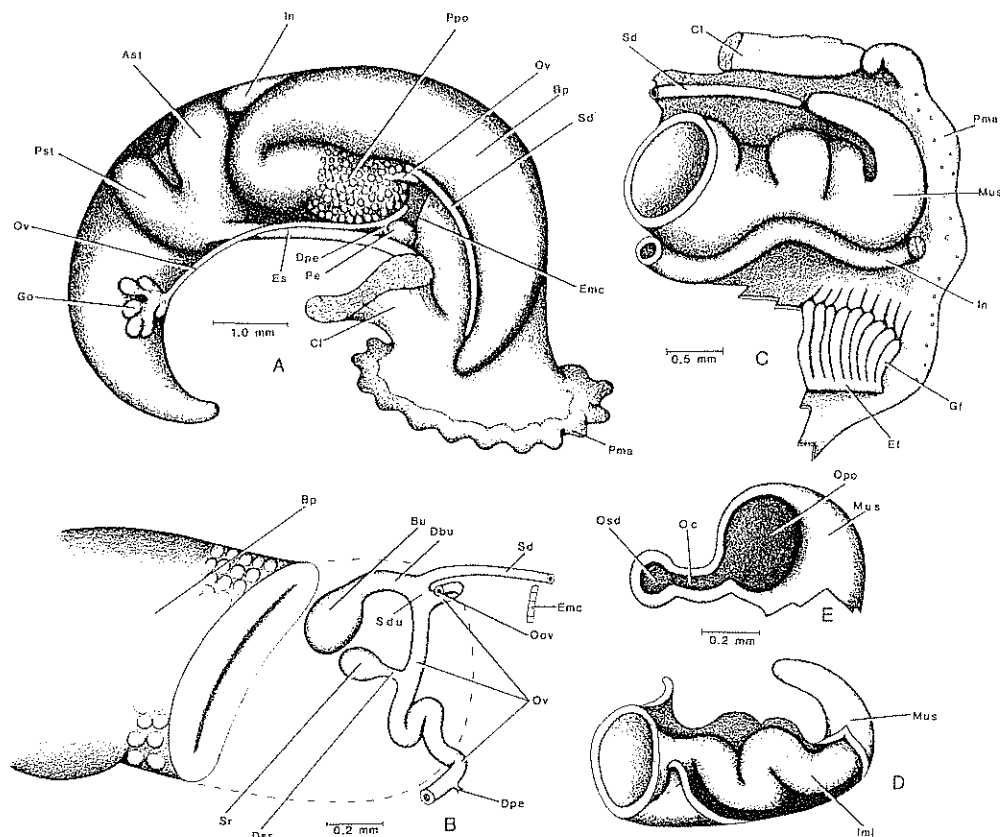


FIG. 30. Female reproductive anatomy of *Mexithauma quadripaludium*. A. Ventral aspect of uncoiled snail without the head and kidney tissue. Note the very small gonad (Go) and large pallial oviduct (Bp + Ppo) with a posterior bend. B. Oriented as in A, but with most of the albumen gland (Ppo) cut away to expose the bursa copulatrix complex. C. Anterior portion of the mantle cavity showing the muscular bend (Mus) of the anterior end of the brood pouch. D. Oriented (and scale) as in C, but with a portion of the epithelium of the anterior end of the brood pouch cut away to expose the inner muscular layer (Iml). E. Oriented as in A, showing the openings of the spermathecal duct (Osd) and pallial oviduct (Opo) connected by an open channel (Oc). Ast—anterior stomach chamber; Bp—brood pouch; Bu—bursa; Cl—columellar muscle; Dbu—duct of the bursa; Dpe—gonopericardial duct; Dsr—duct of the seminal receptacle; Ef—efferent vessel; Emc—posterior end of the mantle cavity; Es—esophagus; Gf—gill filament; Go—gonad; Iml—inner muscular layer; In—intestine; Mus—muscular section of the brood pouch; Oc—open channel; Oov—opening of the oviduct; Opo—opening of the pallial oviduct; Osd—opening of the spermathecal duct; Ov—oviduct; Pe—pericardium; Pma—papillate mantle edge; Ppo—albumen gland; Pst—posterior stomach chamber; Sd—spermathecal duct; Sdu—sperm duct; Sr—seminal receptacle.

travertine pieces and shell fragments), travertine blocks, and the gently sloping banks of spring pools. While *M. quadripaludium* and *Nymphophilus minckleyi* overlap broadly in their microhabitat usage, within any given spring they are largely allopatric on a microhabitat scale. In springs with microhabitat diversity, *N. minckleyi* is most common

on *Nymphaea* and *Chara*, while *M. quadripaludium* is most common in sand or on travertine blocks. However, when one of the species is of reduced abundance or absent, usually in a spring with low microhabitat diversity, the other species may "switch" to other microhabitats, including that usually occupied by the species that is rare or absent.

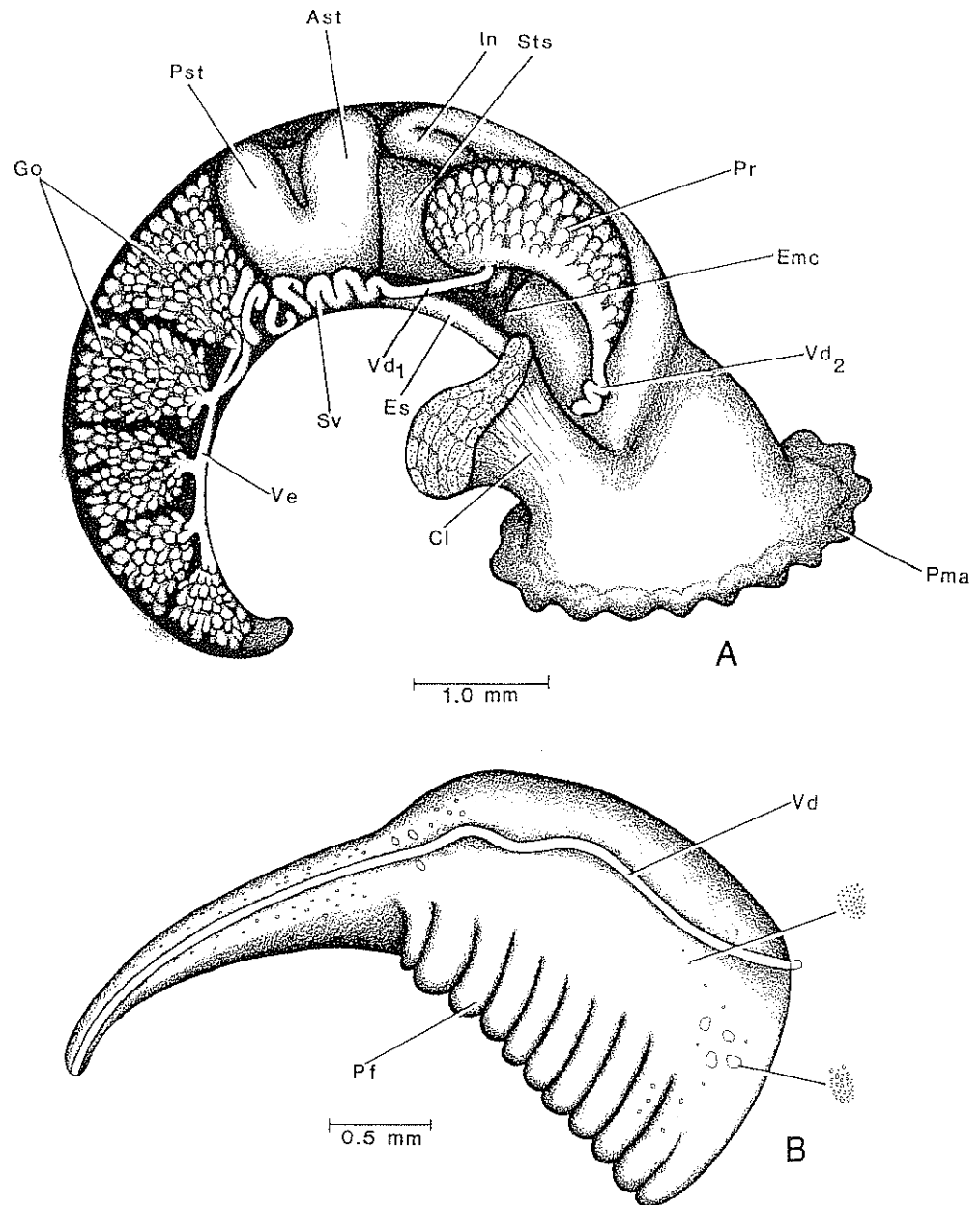


FIG. 31. Male reproductive anatomy of *Mexithauma quadripaludium*. A. Ventral aspect of an uncoiled snail without head and kidney tissue. Note the bush-like gonad (Go). B. Dorsal aspect of the non-lobed penis. Ast—anterior stomach chamber; Cl—columellar muscle; Emc—posterior end of the mantle cavity; Es—esophagus; Go—gonad; In—intestine; Pf—penial fold; Pma—papillate mantle edge; Pr—prostate; Pst—posterior stomach chamber; Sts—style sac; Sv—seminal vesicle; Vd—vas deferens; Vd₁—vas deferens from seminal vesicle to prostate; Vd₂—vas deferens from prostate to penis; Ve—vas efferens.

TABLE 28. Shell measurements (mm) of males and females of *Mexithauma quadripaludium* from Locality 1. The shells measured are from the largest 10% of the population (>4.8 whorls). $N = 9$. Mean \pm standard deviation. "p" refers to the significance level for the difference between shell lengths of males and females (t-test).

	Length	Width	Length of body whorl	Length of aperture	Width of aperture	p
♂	7.28 ± 0.18	6.08 ± 0.19	6.46 ± 0.50	4.89 ± 0.18	3.86 ± 0.31	$>.10$
♀	7.34 ± 0.41	6.30 ± 0.27	6.78 ± 0.31	4.94 ± 0.18	3.84 ± 0.29	

TABLE 29. Frequency distribution for number of spiral cords at the aperture of *Mexithauma quadripaludium* shells. Fifteen shells (sexes mixed) per whorl stage were used. The mean and standard deviation for the shell length of the shells used for each whorl stage are given.

Whorls	Shell length	Number of spiral cords											
		7	8	9	10	11	12	13	14	15	16	17	18
4.0	3.30 ± 0.32	1	3	2	4	4	1	—	—	—	—	—	—
4.5	5.11 ± 0.54	—	—	—	—	—	4	4	2	2	2	1	—
5.0+	7.44 ± 0.34	—	—	—	—	—	—	—	—	1	3	7	2

Shell

Shell measurements for the population from Locality 1 are given in Table 28. The exact number of whorls in large adults cannot be determined as the apex is usually somewhat eroded in such specimens. There is no significant sexual dimorphism in size of shell (Table 28). The spiral cords begin at 2.3 whorls and increase in number with shell size (Table 29). Adults have 15–22 cords on the body whorl that vary in height (Fig. 28B). Strong axial microsculpture, also fringed with periostracum, is present (Fig. 28B). The aperture is large, occupying more than one-half of the height of the body whorl, and is inclined only 10–20° to the coiling axis. The aperture is elliptical in shape, and is somewhat more angled above than below. While the inner lip is greatly thickened, the outer lip is thin. The apical whorl does not have microsculpture (Fig. 28A).

Nonreproductive Features

Anatomical descriptions and data (Table 30) are from the population from Locality 1. The snout (Fig. 29A) is relatively squat, while the tentacles are thickened and elongate. Each tentacle has a central dark pigment strip, extending from just beyond the eye to the tentacle tip (Fig. 29A). On the left tentacle, there are numerous hypertrophied ciliary tufts projecting from the outer edge, as

TABLE 30. Dimensions (mm) or counts of non-neural organs and structures of *Mexithauma quadripaludium*. $N = 5$ unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	11.5 ± 0.48	8.98 ± 0.32
Gill filament number		51.8 ± 1.79	
Osphradium ($N=7$)	L	0.76 ± 0.08	
Gonad	L	0.88 ± 0.07	3.54 ± 0.26
	W	0.65 ± 0.06	1.29 ± 0.12
Prostate	L		1.97 ± 0.24
	W		0.95 ± 0.07
Penis	L		4.12 ± 0.22
	W		1.54 ± 0.13
Pallial oviduct	L	6.72 ± 0.35	
	W	1.91 ± 0.34	
Bursa copulatrix	L	0.26 ± 0.03	
	W	0.19 ± 0.01	
Seminal receptacle (body)	L	0.16 ± 0.01	
	W	0.13 ± 0.02	
Seminal receptacle (duct)	L	0.12 ± 0.01	
	W	0.05 ± 0.01	

well as ciliary tracts curving inwards from both sides. The right tentacle lacks the ciliary tufts projecting from the outer side, and the ciliary tracts run along the length of the tentacle, rather than curving inward. The under-surface of each tentacle also has ciliary tracts running along its length (not figured). Small white granules are scattered in the neck, snout, and tentacles. The snout and neck have a light

dusting of melanin. The foot is large and thickened. There are distinctive pigment streaks just below the eyes and along the sides of the foot. The dorsal body surface has yellow and white pigment granules as well as melanin. The digestive gland is dark brown and has white granules scattered on its ventral surface. A prominent caecal chamber protrudes posterior to the stomach. The operculum (Fig. 29C) has 3.5 whorls and the nucleus is positioned at 41% of the long axis of the operculum. The characteristic pigment streaks on the operculigerous lobe are shown in Fig. 29C.

Radula

The radula is shown in Figs. 28C-E. The central tooth usually has three pairs of basal

cusps arising from prominent lateral angles. The marginal teeth (Figs. 28C, E) have relatively few cusps. Radular statistics and the various cusp arrangements for the four tooth types are given in Tables 31 and 32.

TABLE 31. Radular statistics from nine individuals of *Mexithauma quadripaludum*. \bar{X} = mean, S = standard deviation. Measurements are in mm.

Radular feature	\bar{X}	S
Length	1.42	0.058
Width	0.188	0.008
Number of rows	66.1	2.98
Number of rows in formative stage	4.44	1.01
Width of central tooth (N = 23)	0.047	0.0002

TABLE 32. The various cusp arrangements for the four tooth types in 11 radulae of *Mexithauma quadripaludum*, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{3-1-3}{2-2}$	9	2-1-3	9	10	27	11	9
$\frac{3-1-3}{2-2}$	9	3-1-3	55	11	91	12	64
$\frac{3-1-3}{3-3}$	9	4-1-3	91	12	73	13	82
$\frac{4-1-3}{3-2}$	18	5-1-3	9	13	36	14	82
$\frac{4-1-3}{3-3}$	9	4-1-4	18	14	9	15	45
$\frac{4-1-4}{2-2}$	36			16	9	16	18
$\frac{4-1-4}{3-3}$	45					17	9
$\frac{4-1-4}{3-2}$	27						
$\frac{5-1-3}{3-2}$	9						
$\frac{5-1-3}{2-2}$	18						
$\frac{5-1-3}{3-3}$	18						
$\frac{5-1-4}{3-2}$	27						
$\frac{5-1-4}{3-3}$	18						
$\frac{5-1-4}{2-2}$	9						
$\frac{5-1-5}{3-2}$	18						

Female Reproductive Anatomy

The female gonad (Go) occupies only 8% of the body length and is a mere terminal thickening of the oviduct with a few small lobes. The pallial oviduct is 58% of the body length. The posterior bend of the pallial oviduct extends for 2.5 mm, of which 1.2 mm is albumen gland (Ppo, Fig. 30A). The remainder of the pallial oviduct is a thin-walled brood pouch (Bp). A gonopericardial duct (Dpe, Figs. 30A, B) is present. The sac-like bursa (Bu) is only 4% of the length of the pallial oviduct and is entirely dorsal to the albumen gland (Fig. 30B). The oviduct (Ov) coils once or twice before receiving the short duct from the seminal receptacle (Dsr, Fig. 30B); and then coils to enter the ventral surface of the end of the albumen gland. The spermathecal duct (Sd) is tightly appressed to the columellar side of the pallial oviduct (Fig. 30A).

In Fig. 30D, the muscularized portion of the anterior brood pouch (Mus) is slit open and the epithelium has been cut away to reveal the inner muscular layer (Imi). For 15 adult females, the number of shelled embryos in the brood sac averaged 19.4 ± 4.5 (range of 14–28), and there were an additional 22–35 small, non-shelled embryos packed in the posterior bend of the brood pouch. For 111 shelled embryos, the mean shell length was 0.48 ± 0.37 mm. The range of shell lengths was four-fold, from 0.20 to 0.87 mm. The embryonic shells have up to 2.5 whorls. The embryos have red-brown pigment splotches and yellow-white granules on the dorsal body surface.

Male Reproductive Anatomy

The male gonad (Go, Fig. 31A) has five branches and occupies 29% of the body length, almost filling the digestive gland. The prostate overlaps the mantle cavity and the anterior vas deferens exits from the anterior tip of the prostate. The seminal vesicle coils (Sv) overlap slightly onto the stomach. The penis (Fig. 31B) has an elongate penial filament. There are numerous folds on its inner curvature for slightly more than one half of its length. Where the folds end, the penis suddenly narrows on the outer curvature, giving the penis a peculiar bulging appearance at this point. The penis has numerous Gl₁ and Gl₂ glands. The vas deferens (Vd) only coils slightly in the penis. The penis has neither cilia nor a terminal eversible papilla.

Durangonella Morrison, 1945

Type-species: *Durangonella seemani* (Frauenfeld, 1863).

Distribution: known from isolated drainage systems in arid north-central México.

Species included: five species listed by Taylor (1966).

Description

Durangonella is distinguished from other littoridinine genera by a combination of character states (see below).

The shell (Figs. 32, 33; Morrison, 1945, figs. 1–4) is smooth, slender, turriform, with five to eight slowly increasing, rounded whorls; the tentacles have *Hydrobia*-like ciliation (Fig. 35A); females are ovoviviparous; the female gonad is a very small, non-lobed swelling at the end of the oviduct (Go, Fig. 36A); the pallial oviduct is large and bends posteriorly with several loops in one plane (Fig. 36A); the albumen gland is reduced to a mere glandular smear on one of the loops (Ppo, Fig. 36A); the seminal receptacle (Sr) connects with the oviduct via a short sperm duct (Sdu, Fig. 36D); the spermathecal duct is elongate with an opening separate from that



FIG. 32. SEM photos of shells of *Durangonella coahuilae* from Locality 6. The shell on the left is 3.60 mm long; the other one is printed at the same enlargement.

of the pallial oviduct (Figs. 36A, F, G); the anterior end of the brood pouch is weakly coiled and muscularized (Figs. 36F, G); the penis has a blunt, ciliated tip, a terminal eversible papilla, and one (Fig. 35D) or two (Morrison, 1945, fig. 5) simple lobes that lack specialized glands.

Discussion

Durangonella is most similar to *Mexipyrargus* (see Tables 53–55, Figs. 49, 50), and these taxa share the following distinctive features: pallial oviduct with posterior coil in several loops; albumen gland reduced to a mere

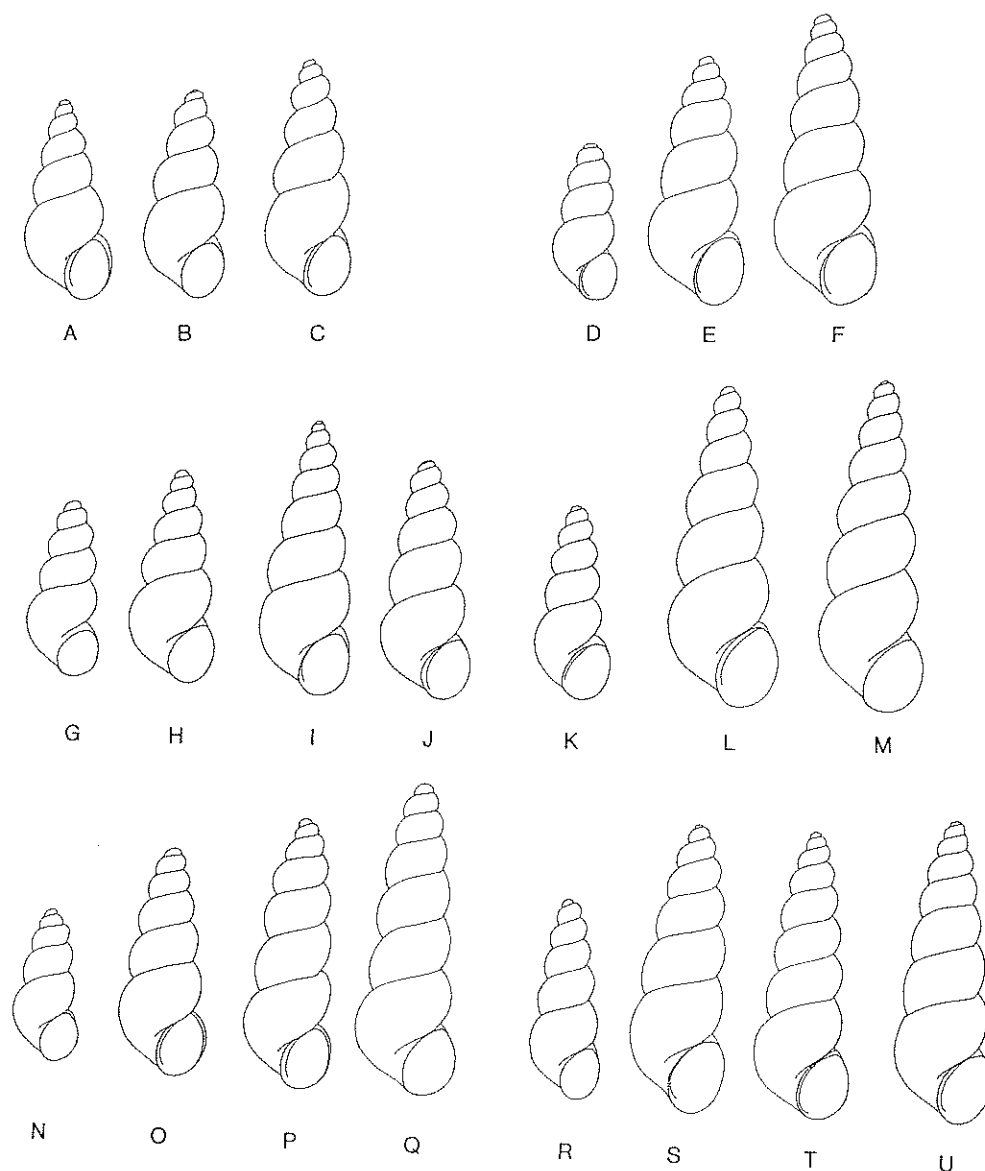


FIG. 33. Camera lucida drawings of shells from six populations of *Durangonella coahuilae*. The shells are from the following localities: A–C, Locality 6; D–F, Locality 14; G–J, Locality 9; K–M, Locality 38; N–Q, Locality 13; R–U, Locality 65. Shell A is 2.42 mm long, and the others are at the same scale.

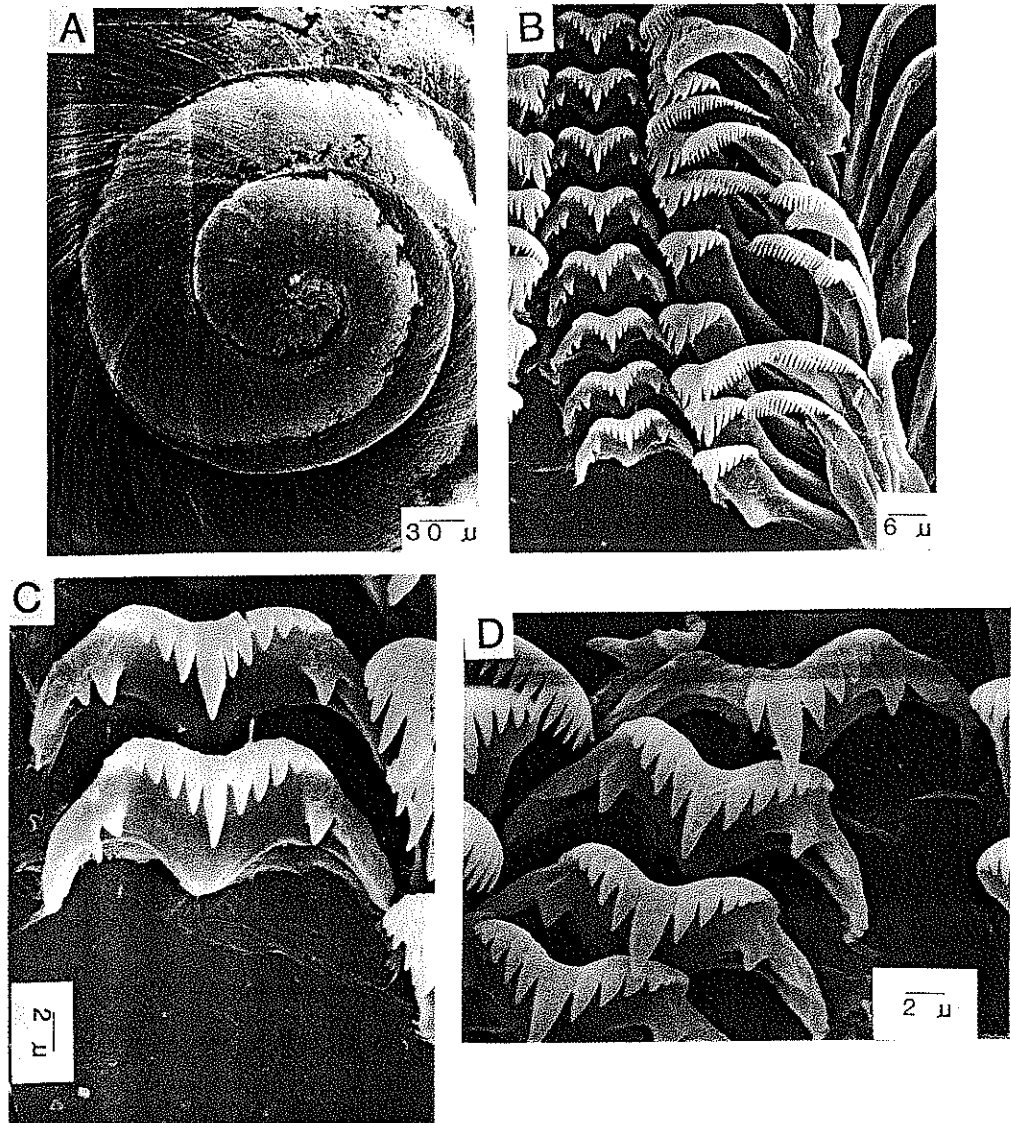


FIG. 34. SEM photos of shell and radula of *Durangonella coahuilae*. A. Apical whorls of the shell. Note the lack of microsculpture. B. Part of the radular ribbon. C, D. Isolated central teeth.

glandular smear; seminal receptacle connected to the oviduct via a short sperm duct; anterior end of the brood pouch weakly muscularized and coiled; penis with a blunt, ciliated tip and a terminal eversible papilla.

Durangonella differs from *Mexipyrus* in the following features: penis glands (*Durangonella*, absent; *Mexipyrus*, mammiform); ciliary tufts on tentacles (*Durangonella*,

Hydrobia-like; *Mexipyrus*, absent); female gonad (*Durangonella*, small and non-lobed; *Mexipyrus*, large and lobed); posterior coils of pallial oviduct (*Durangonella*, in one plane; *Mexipyrus*, in several planes); duct of seminal receptacle (*Durangonella*, not coiled; *Mexipyrus*, coiled); spermathecal duct (*Durangonella*, short; *Mexipyrus*, long).

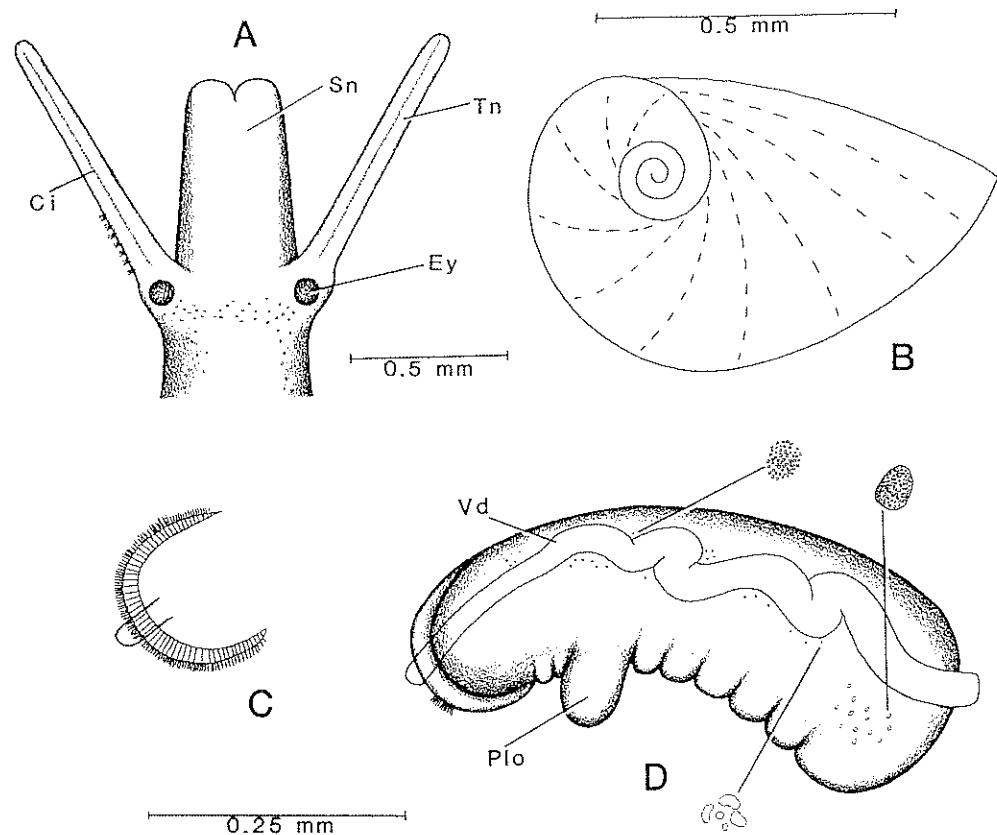


FIG. 35. Head, operculum and penis of *Durangonella coahuilae*. A. Dorsal aspect of head showing the *Hydrobia*-like ciliation of the left tentacle and central ciliary bands (Ci) on both tentacles. B. Operculum. C. Tip of the penis showing the ciliated columnar epithelium. D. Dorsal aspect of the penis showing the blunt tip and small penial lobe (Plo). Note the reduced ciliation (compared to C) of this specimen. Ey—eye; Sn—snout; Tn—tentacle; Vd—vas deferens.

Durangonella coahuilae Taylor, 1966

Holotype: UMMZ 220159.

Type-locality: Locality 9.

Distribution: endemic to the Cuatro Ciénegas Basin.

Habitat: *Durangonella coahuilae* is found in the basin in a wide variety of aquatic environments that include a playa lake, pools formed where the water table is at ground level, small spring-fed pits without outflows, marshes, and springs and streams of all sizes. *Durangonella coahuilae* was found on mops from 23 of 38 small springheads, but, as with *Mexiliobla manantiali*, it probably does not inhabit subterranean waters as it has eyespots and body pigment, and is very common downstream. *Durangonella coahuilae* is most com-

mon in soft organic sediments, but was also found in *Chara* mats and on marl pieces. More so than the other hydrobiids of the basin, *D. coahuilae* is found in waters whose temperatures fluctuate greatly on a diurnal and seasonal basis. For example, *D. coahuilae* was collected from pools with seasonally fluctuating levels (Localities 7, 8) that had water temperature ranges of 9.5–35.6°C during 1980. Snails disappeared from the pools only when they went temporarily dry during an arid period.

Description

The shell (Fig. 33) is not readily distinguishable from those of the other *Durangonella* spp. (Morrison, 1945, figs. 1–4): it varies in

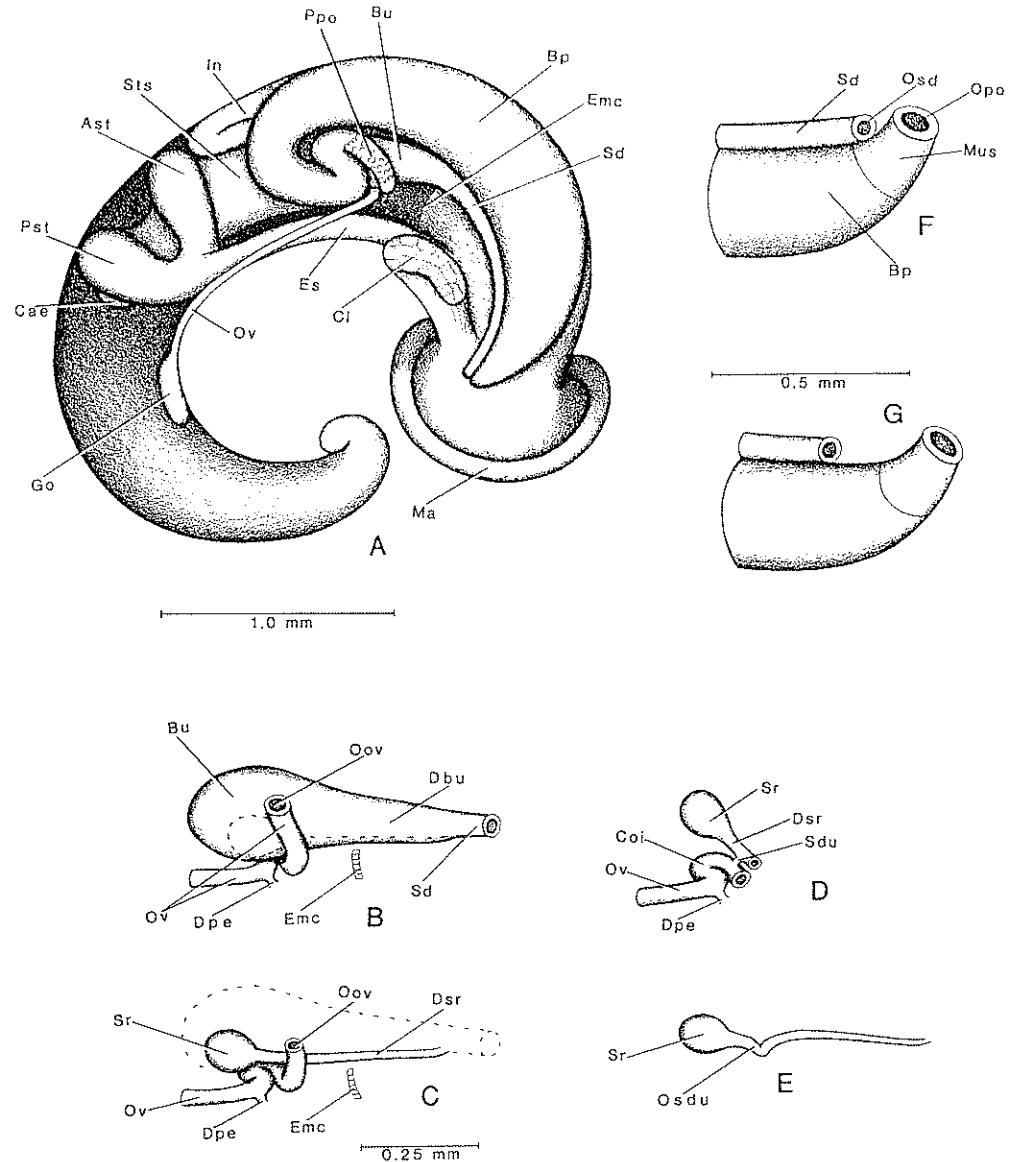


FIG. 36. Female reproductive anatomy of *Durangonella coahuilae*. A. Ventral aspect of uncoiled female without head and kidney tissue. Note the small gonad (Go), posterior coiling of the pallial oviduct (Bp + Ppo), and very small albumen gland (Ppo). B. Oriented as in A, but with the pallial oviduct cut away to expose the bursa (Bu). The spermathecal duct (Sd), which is elongate, has been cut. C. Oriented as in B, but with the bursa removed to expose the seminal receptacle (Sr), its duct (Dsr) and oviduct (Ov). D. Oriented as in C, but with the seminal receptacle (Sr) rotated slightly to expose the short sperm duct (Sdu). E. Frequently-seen kink in the duct of the seminal receptacle. F, G. Variation in the position of the end of the spermathecal duct relative to the opening of the pallial oviduct (Opo). Ast—anterior stomach chamber; Bp—brood pouch; Bu—bursa; Cae—caecum of stomach; Ci—columellar muscle; Coi—coil of oviduct; Dbu—duct of the bursa; Dpe—gonopericardial duct; Dsr—duct of the seminal receptacle; Emc—posterior end of the mantle cavity; Es—esophagus; Go—gonad; In—intestine; Ma—mantle edge; Mus—muscular section of the brood pouch; Oov—opening of the oviduct; Opo—opening of the pallial oviduct; Osd—opening of the spermathecal duct; Osdu—opening of the sperm duct; Ov—oviduct; Ppo—albumen gland; Pst—posterior stomach chamber; Sd—spermathecal duct; Sdu—sperm duct; Sr—seminal receptacle; Sts—style sac.

size, number and roundness of whorls, and depth of sutures to such an extent that individuals can be found that correspond to the types of all of the nominal species.

Durangonella coahuilae does differ from *D. seemani* (the type of the genus) in terms of number of penial lobes (*D. coahuilae*, 1; *D. seemani*, 2), and number of basal cusps on the central tooth of the radula (*D. coahuilae*, 1; *D. seemani*, 2).

Shell

The shell varies in length from 2.30–5.10 mm and has 5.5–8.5 whorls. The aperture is crescent-shaped. The peristome is entire in adults and the end of the body whorl

frequently pulls away from the penultimate whorl. The umbilicus varies from a slight chink to an open slit. Growth lines are prominent (Fig. 34A). Populations vary not only in size of shell and number of whorls, but also in relative shell width, relative size of the body whorl, whorl roundness, suture depth and angle, and degree of sexual dimorphism (Fig. 33). The shell has a smooth apical whorl (Fig. 34A). Shell measurements from nine populations are given in Table 33. For all populations, females are clearly larger than males and have more whorls.

Nonreproductive Features

The measurements of organs and structures for snails from four populations are

TABLE 33. Shell measurements (mm) of males and females from nine populations of *Durangonella coahuilae*. Snails with the dominant maximum whorl number(s) were used. Mean \pm standard deviation. The localities are the following types of aquatic environments: 6, fluctuating pool semi-connected to stream; 9, playa lake; 13, 38, 8, large streams; 14, 51, 74, 65, 43, small streams.

	Whorls	N	Length	Width	Length of body whorl	Length of aperture	Width of aperture
<i>Locality 6</i>							
♂	5.5	7	2.58 \pm 0.17	1.16 \pm 0.07	1.43 \pm 0.10	0.82 \pm 0.06	0.56 \pm 0.03
♀	6.5	9	3.54 \pm 0.17	1.45 \pm 0.04	1.77 \pm 0.07	0.99 \pm 0.05	0.68 \pm 0.04
<i>Locality 9</i>							
♂	6.0	9	2.75 \pm 0.17	1.21 \pm 0.07	1.50 \pm 0.08	0.85 \pm 0.04	0.61 \pm 0.05
	6.5	7	3.11 \pm 0.13	1.31 \pm 0.05	1.62 \pm 0.09	0.91 \pm 0.06	0.63 \pm 0.06
♀	6.5	9	3.40 \pm 0.28	1.44 \pm 0.11	1.78 \pm 0.14	1.01 \pm 0.09	0.71 \pm 0.07
<i>Locality 13</i>							
♂	5.5	10	2.35 \pm 0.14	0.99 \pm 0.06	1.26 \pm 0.08	0.74 \pm 0.05	0.49 \pm 0.03
♀	7.0	10	3.75 \pm 0.16	1.38 \pm 0.07	1.65 \pm 0.08	0.97 \pm 0.05	0.66 \pm 0.05
	7.5	9	4.15 \pm 0.20	1.43 \pm 0.10	1.72 \pm 0.10	1.00 \pm 0.06	0.69 \pm 0.03
<i>Locality 14</i>							
♂	5.5	9	2.51 \pm 0.11	1.07 \pm 0.08	1.37 \pm 0.06	0.80 \pm 0.04	0.58 \pm 0.04
	6.0	7	2.73 \pm 0.11	1.09 \pm 0.05	1.42 \pm 0.08	0.84 \pm 0.06	0.56 \pm 0.04
♀	7.0	9	3.85 \pm 0.17	1.51 \pm 0.06	1.85 \pm 0.08	1.08 \pm 0.05	0.74 \pm 0.03
<i>Locality 38</i>							
♂	6.0	10	2.85 \pm 0.11	1.18 \pm 0.05	1.52 \pm 0.08	0.91 \pm 0.04	0.61 \pm 0.02
♀	8.0	8	4.83 \pm 0.18	1.61 \pm 0.09	2.00 \pm 0.10	1.14 \pm 0.07	0.79 \pm 0.04
	8.5	10	5.08 \pm 0.30	1.58 \pm 0.07	1.99 \pm 0.10	1.11 \pm 0.07	0.79 \pm 0.04
<i>Locality 43</i>							
♂	5.5	10	2.75 \pm 0.18	1.20 \pm 0.08	1.52 \pm 0.09	0.90 \pm 0.05	0.61 \pm 0.04
♀	6.5	9	4.07 \pm 0.19	1.64 \pm 0.07	2.05 \pm 0.10	1.19 \pm 0.07	0.83 \pm 0.04
<i>Locality 51</i>							
♂	7.0	9	3.55 \pm 0.11	1.26 \pm 0.06	1.58 \pm 0.08	0.89 \pm 0.04	0.63 \pm 0.02
♀	7.5	8	4.36 \pm 0.16	1.53 \pm 0.05	1.89 \pm 0.09	1.08 \pm 0.04	0.74 \pm 0.04
<i>Locality 74</i>							
♂	6.5	7	3.06 \pm 0.18	1.14 \pm 0.07	1.48 \pm 0.07	0.82 \pm 0.05	0.58 \pm 0.04
♀	7.0	9	3.96 \pm 0.27	1.47 \pm 0.09	1.86 \pm 0.08	1.04 \pm 0.06	0.72 \pm 0.04
<i>Locality 65</i>							
♂	6.5	12	3.28 \pm 0.19	1.25 \pm 0.07	1.56 \pm 0.10	0.92 \pm 0.07	0.63 \pm 0.04
♀	7.0	10	3.90 \pm 0.25	1.44 \pm 0.09	1.79 \pm 0.11	1.06 \pm 0.07	0.71 \pm 0.05

TABLE 34. Dimensions (mm) or counts of non-neural organs and structures of *Durangonella coahuilae* from Locality 6. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	5.04 \pm 0.39	3.35 \pm 0.12
Gill filament number		26.7 \pm 2.80	
Osphradium	L	0.21 \pm 0.03	
Gonad	L	0.33 \pm 0.08	1.13 \pm 0.09
	W	0.08 \pm 0.02	0.38 \pm 0.004
Prostate (N = 6)	L		0.68 \pm 0.09
	W		0.34 \pm 0.04
Penis	L		0.55 \pm 0.05
	W		0.21 \pm 0.03
Pallial oviduct	L	2.20 \pm 0.23	
	W	0.51 \pm 0.06	
Bursa copulatrix (N = 7)	L	0.33 \pm 0.04	
	W	0.22 \pm 0.01	
Seminal receptacle (body) (N = 6)	L	0.11 \pm 0.01	
	W	0.09 \pm 0.01	
Seminal receptacle (duct) (N = 8)	L	0.04 \pm 0.01	
	W	0.04 \pm 0.01	

TABLE 35. Dimensions (mm) or counts of non-neural organs and structures of *Durangonella coahuilae* from Locality 9. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	5.09 \pm 0.43	4.46 \pm 0.30
Gill filament number		26.4 \pm 1.82	
Osphradium	L	0.20 \pm 0.03	
Gonad	L	0.26 \pm 0.04	1.30 \pm 0.11
	W	0.09 \pm 0.01	0.43 \pm 0.03
Prostate (N = 6)	L		0.72 \pm 0.06
	W		0.34 \pm 0.04
Penis (N = 6)	L		0.56 \pm 0.04
	W		0.21 \pm 0.03
Pallial oviduct	L	2.10 \pm 0.21	
	W	0.53 \pm 0.05	
Bursa copulatrix	L	0.29 \pm 0.02	
	W	0.18 \pm 0.02	
Seminal receptacle (body) (N = 8)	L	0.13 \pm 0.02	
	W	0.10 \pm 0.02	
Seminal receptacle (duct) (N = 8)	L	0.05 \pm 0.01	
	W	0.04 \pm 0.01	

given in Tables 34–37. The anatomical drawings and radula photographs are from specimens from Locality 6. The snout (Fig. 35A) is elongate and the tentacles are relatively short. In addition to the seven to nine hypertrophied ciliary tufts on the outer edge of the left tentacle, each tentacle has a central ciliary tract (Ci, Fig. 35A). Small granules are

TABLE 36. Dimensions (mm) or counts of non-neural organs and structures of *Durangonella coahuilae* from Locality 13. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	5.50 \pm 0.27	4.08 \pm 0.26
Gill filament number		31.5 \pm 1.76	
Osphradium	L	0.21 \pm 0.04	
Gonad	L	0.36 \pm 0.05	1.74 \pm 0.18
	W	0.10 \pm 0.02	0.44 \pm 0.03
Prostate	L		0.74 \pm 0.10
	W		0.32 \pm 0.03
Penis	L		0.42 \pm 0.04
	W		0.16 \pm 0.02
Pallial oviduct	L	2.39 \pm 0.21	
	W	0.47 \pm 0.05	
Bursa copulatrix (N = 9)	L	0.30 \pm 0.03	
	W	0.17 \pm 0.03	
Seminal receptacle (body) (N = 10)	L	0.13 \pm 0.01	
	W	0.10 \pm 0.02	
Seminal receptacle (duct) (N = 6)	L	0.03 \pm 0.01	
	W	0.04 \pm 0.01	

TABLE 37. Dimensions (mm) or counts of non-neural organs and structures of *Durangonella coahuilae* from Locality 14. N = 5 unless stated otherwise. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	6.44 \pm 0.63	4.76 \pm 0.34
Gill filament number		34.7 \pm 1.75	
Osphradium	L	0.21 \pm 0.04	
Gonad	L	0.41 \pm 0.02	1.70 \pm 0.23
	W	0.09 \pm 0.02	0.47 \pm 0.04
Prostate (N = 7)	L		1.00 \pm 0.09
	W		0.40 \pm 0.04
Penis	L		0.46 \pm 0.04
	W		0.21 \pm 0.04
Pallial oviduct	L	2.19 \pm 0.25	
	W	0.59 \pm 0.06	
Bursa copulatrix (N = 6)	L	0.34 \pm 0.04	
	W	0.19 \pm 0.02	
Seminal receptacle (body) (N = 7)	L	0.12 \pm 0.02	
	W	0.11 \pm 0.02	
Seminal receptacle (duct)	L	0.04 \pm 0.002	
	W	0.03 \pm 0.004	

seen around the eyespots and in the neck. The snout may or may not be dusted with melanin. The sides of the head-foot usually have a light melanin dusting, and an unpigmented strip, extending from the eye to the base of the foot, can be seen. Body pigment can be red or black. The male gonad always has dark melanin on its ventral surface. Pop-

ulations may have snails devoid of other body pigment (Locality 6), or with a dark melanin coating (Localities 9, 14), or a spotted pattern (Localities 13, 39) on the ventral body surface. The caecal chamber protrudes posterior to the stomach (Cae, Fig. 36A). The paucispiral operculum (Fig. 35B) has 3.3 whorls and the nucleus is positioned at 26% of the operculum length. The operculigerous lobe has several melanin streaks.

Radula

Radular statistics for specimens from the type-locality (Locality 9) and a second locality (Locality 6) are given in Table 38. The cusp

arrangements for the four tooth types (for specimens from Locality 6) are given in Table 39. The central tooth of the radula has one (and occasionally a second) pair of basal cusps that arise from prominent lateral angles (Figs. 34C, D).

Female Reproductive Anatomy

The female gonad (Go, Fig. 36A) occupies only 6% of the body length. Oocytes were frequently seen in the gonad throughout the year. The pallial oviduct occupies 34-44% of the body length, depending on the population. The length of the posterior bend of the pallial oviduct is 0.6 mm, and the bend extends to

TABLE 38. Radular statistics from individuals of *Durangonella coahuilae* from two populations. \bar{X} = mean, S = standard deviation. Measurements in mm.

Radular feature	Locality 9 (N = 13)		Locality 6 (N = 5)	
	\bar{X}	S	\bar{X}	S
Length	0.444	0.035	0.380	0.023
Width	0.087	0.007	0.074	0.006
Number of rows	48.6	3.25	51.4	2.07
Number of rows in formative stage	3.0	1.3	4.0	1.2
Width of central tooth (N = 14)			0.020	0.001

TABLE 39. The various cusp arrangements for the four tooth types of *Durangonella coahuilae*, counted from 5 radulae using SEM, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{4-1-4}{1-1}$	20	3-1-3	20	19	40	20	20
$\frac{4-1-4}{2-1}$	20	4-1-3	40	20	40	21	40
$\frac{5-1-4}{2-1}$	60	4-1-4	40	22	40	22	60
$\frac{5-1-5}{1-1}$	80	5-1-5	40	23	40	23	40
$\frac{5-1-5}{2-1}$	100			24	40	24	40
$\frac{6-1-5}{1-1}$	20			25	40	25	40
$\frac{6-1-5}{2-1}$	20			26	20	26	20
$\frac{6-1-4}{2-2}$	20			27	20	27	20

within 0.13 mm of the end of the mantle cavity. The albumen gland (Ppo) is no more than a glandular smear on the posterior-most 0.28 mm of the pallial oviduct. The remainder of the pallial oviduct serves as a brood pouch (Bp).

A gonopericardial duct (Dpe) is present (Figs. 36B–D). The sac-like bursa (Bu) is only 12–16% of the length of the pallial oviduct. The seminal receptacle (Sr), dorsal to the bursa, is circular in outline and 44% the length of the bursa. The oviduct (Ov) has a single coil dorso-lateral to the seminal receptacle (Figs. 36B, C) and then receives the short sperm duct (Sdu) from the duct of the seminal receptacle (Dsr). The length of the duct of the seminal receptacle to the opening of the seminal receptacle is short, 0.03–0.05 mm, and then the duct travels (dorsal to and hidden by the bursa) for 0.41 mm until it joins the duct of the bursa (Dbu, Fig. 36C). This junction occurs 0.20 mm anterior to the end of the mantle cavity. The duct of the seminal receptacle often has a kink in it just after the opening of the sperm duct (Fig. 36E). The opening of the spermathecal duct is 0.08–0.20 mm posterior to that of the pallial oviduct (Figs. 36F, G).

Data for number of shelled embryos brooded for females from six populations are given in Table 40. To these numbers can be added one to two non-shelled embryos that were dissolved in the Clorox. For 39 embryonic shells (Locality 6), shell length averaged 0.384 ± 0.158 mm, with an eight-fold range in lengths from 0.079–0.693 mm. The largest embryonic shells have 2.5–2.8 whorls.

Male Reproductive Anatomy

The lobed male gonad has four to five branches and constitutes 29–43% of the body

length. The prostate is 0.16–0.21% the body length, and overlaps the mantle cavity. The anterior vas deferens exits from the anterior tip of the prostate.

The single penial lobe (Plo, Fig. 35D) is located at 61% the penis length from the base. Folds are present on the inner curvature from the base to just beyond the penial lobe. The blunt tip of the penis has tall columnar cells extending back 0.10 mm to where the penial folds end. Ciliation of these cells is variable; for the population from Locality 6, one of the five penes studied had no cilia, and the other four had a small ciliated patch (Fig. 35D). Other populations, particularly those with large-sized males, usually had the entire columnar-celled area ciliated (Fig. 35C). The vas deferens (Vd) coils only slightly in the penis. The penis has both Gl_1 and Gl_2 gland types common. Some populations have males with a small pigmented patch near the penis tip.

Discussion

Among the *Durangonella* species, only *D. coahuilae* has received complete anatomical study. The penis and radula of *D. seemani* have been figured (see above), while the other four species are known only from the shell. Anatomical study of these allopatric species is necessary to resolve their systematic status.

Durangonella coahuilae had been previously known (Taylor, 1966) only from Laguna Grande (Locality 9), the playa lake that is the terminus of the stream from Laguna Churince, a large spring (Locality 1). It has been suggested that other populations in the basin may represent new *Durangonella* species (Holsinger & Minckley, 1971; Taylor, 1966).

The author collected undoubted *D. coa-*

TABLE 40. Data for number of shelled embryos brooded by females from six populations of *Durangonella coahuilae*. The mean shell length (for shells with maximum dominant whorl number) for adult females of each population is also given.

	Mean shell length (mm)	Number of young/females			
		N	X	SD	range
Locality 9	3.40	15	1.87	0.64	1–3
Locality 6	3.54	15	2.60	1.40	1–5
Locality 14	3.85	13	3.77	1.69	1–6
Locality 43	4.07	14	8.14	1.41	6–10
Locality 13	4.15	13	5.64	1.67	2–8
Locality 38	5.08	15	5.60	1.55	2–8

huilae not only from Laguna Grande, but also in pool areas along the stream feeding it (Localities 7, 8), groundwater-fed pools near the stream (Localities 4, 5, 6) and from a mop placed in a small seep near Laguna Churince (Locality 2).

The shells of *D. coahuilae* from populations from the above localities of the Churince system (Figs. 33A–C, G–J), which is currently isolated from other waters of the basin, do differ from shells from other populations (Figs. 33D–F, K–U) in that the females have fewer whorls and smaller shells, and the shells are relatively wider with a relatively larger body whorl (Fig. 33; Table 33). The shell differences may be partly allometric, as the Churince shells are small, but in some cases Churince shells that are smaller (in length) than those from other populations are also absolutely wider.

Despite these differences, the Cuatro Ciénegas *Durangonella* is not being split into several species because: 1) there are no qualitative anatomical differences among the populations studied; 2) the Churince aquatic environments differ from those from which other populations were sampled; and 3) the above shell differences are not always pronounced and the author can not confidently separate out "species" when lots are mixed.

Mexipyrgus Taylor, 1966

Type-species: *Mexipyrgus carranzae* Taylor, 1966.

Distribution: endemic to the Cuatro Ciénegas Basin.

Species included: reduced to monotypy (see below).

Description

Distinctive features of *Mexipyrgus* are as follows: 1) the massive pallial oviduct that extends onto the stomach and then bends into a series of loops that coil progressively dorsal to one another (Figs. 42, 43), partially enveloping the bursa and restricting the space for the kidney (Ki) and pericardium (Pe, Fig. 42A); and 2) the greatly coiled duct of the seminal receptacle (Dsr, Figs. 42B, D, E).

The shell (Fig. 37) is large (number of whorls, 5.5–7.5; length, 3.03–8.45 mm), usually thickened, and elongate-conic in shape; low spiral welts and noded ribs may or may not be prominent on the last two whorls (Figs. 37, 38); periostracal color bands may or may

not be present and (when present) vary from one to thirty distinct bands, to a single wide solid band; the marginal tooth of the radula has numerous cusps (Figs. 39B, C); females are ovoviparous; the albumen gland (Ppo) is reduced to a glandular smear on the dorsal-most loop of the pallial oviduct (Figs. 42, 43); the bursa is enlarged and elongate (Bu, Figs. 42A, 43); the seminal receptacle is dorsal to the bursa and connects with the oviduct via a short sperm duct (Sdu, Fig. 42C); the spermathecal duct (Sd) is short, muscularized, and separated from the bursa by a slight constriction (indicated by arrow in Fig. 42B); the anterior end of brood pouch is weakly muscularized and coiled (Mus, Fig. 41B); the penis (Fig. 44A) has a blunt, ciliated tip, terminal papilla, and lobes (outer curvature, one; inner curvature, one or two) bearing mammi-form glands (Mg, Fig. 44A).

Mexipyrgus is most similar to *Durangonella* (see above; Tables 53–55, Figs. 49, 50).

Mexipyrgus churinceanus Taylor, 1966

Holotype: UMMZ 220150.

Type-locality: Locality 1.

Synonymy: *M. churinceanus* Taylor, 1966

M. escobedae Taylor, 1966

M. lugoi Taylor, 1966

M. carranzae Taylor, 1966

M. mojarrales Taylor, 1966

M. multilineatus Taylor, 1966

The name *Mexipyrgus churinceanus*, rather than *M. carranzae* (type of the genus in Taylor, 1966), is applied to this species because the type population for the former has received the most morphological study.

Habitat: *Mexipyrgus churinceanus* is found almost exclusively in the larger springs and streams of the basin. The species was never found in sieve collections from smaller streams, and only a single specimen was taken (Locality 65) from mops from 38 small springheads. *Mexipyrgus churinceanus* is restricted to soft sediments which appear (at 50×) to be composed of snail copropel or decaying plant matter. To a lesser extent, specimens were taken from a mixture of soft sediment and coarse travertine sand. Densities of snails were determined using a box core sampler (22.5 cm square bottom) and ranged up to 49,000/m² (Locality 30). The only species found sympatric with *M. churinceanus* in its microhabitat was *Durangonella coahuilae*.

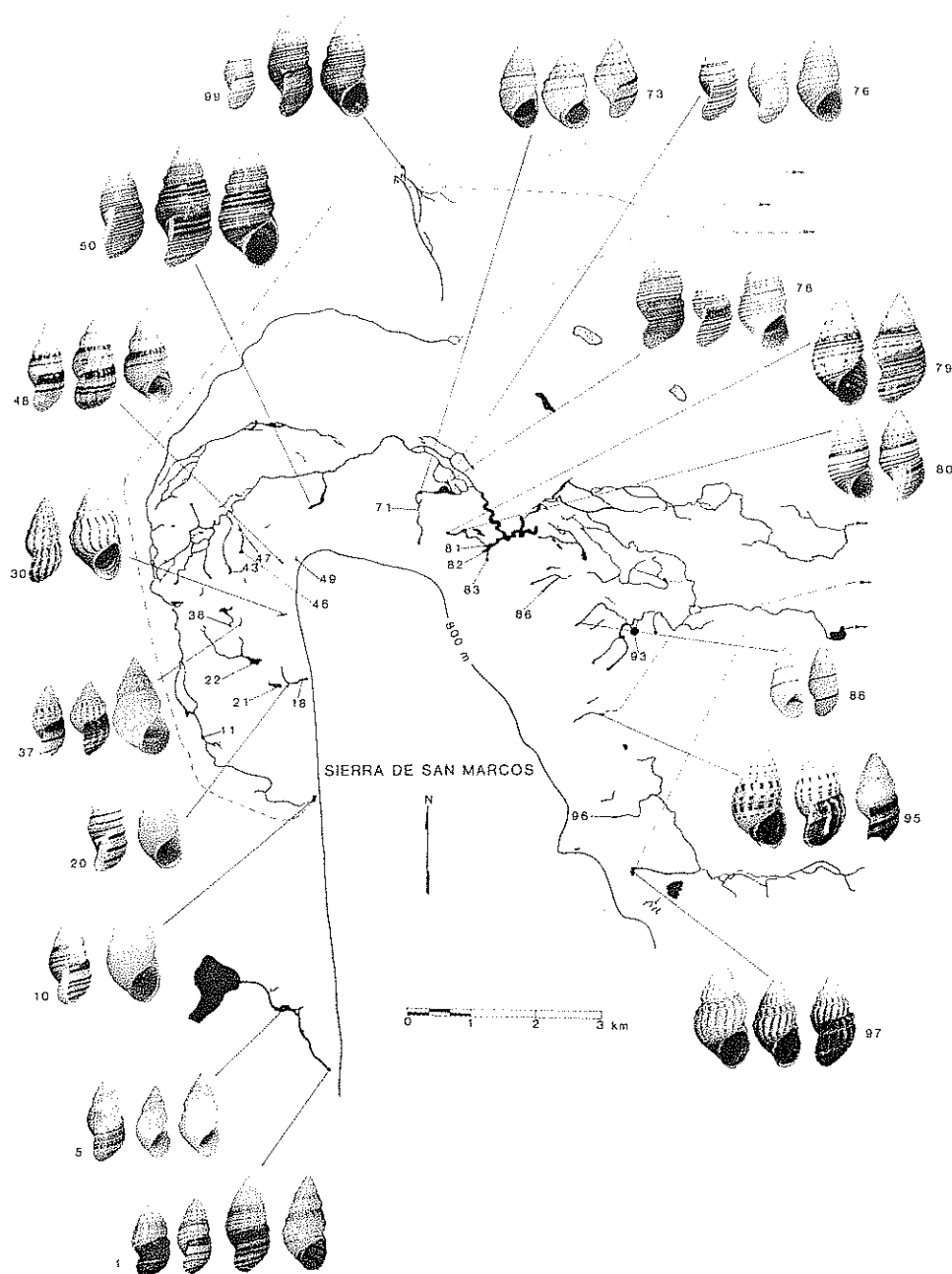


FIG. 37. Localities from which samples of *Mexipyrgus churinceanus* were taken for the multivariate analysis, with photos of shells from selected populations. The photos of shells from Localities 1, 5, 37, 50, 99, 76, 78, 79, 80, and 97 are printed at the same enlargement. The shell on the left for Locality 1 is 5.36 mm long. The photos of shells from Localities 10, 20, 30, 48, 73, 88, and 95 are printed at the same enlargement. The photo on the left for Locality 10 is 4.29 mm long.

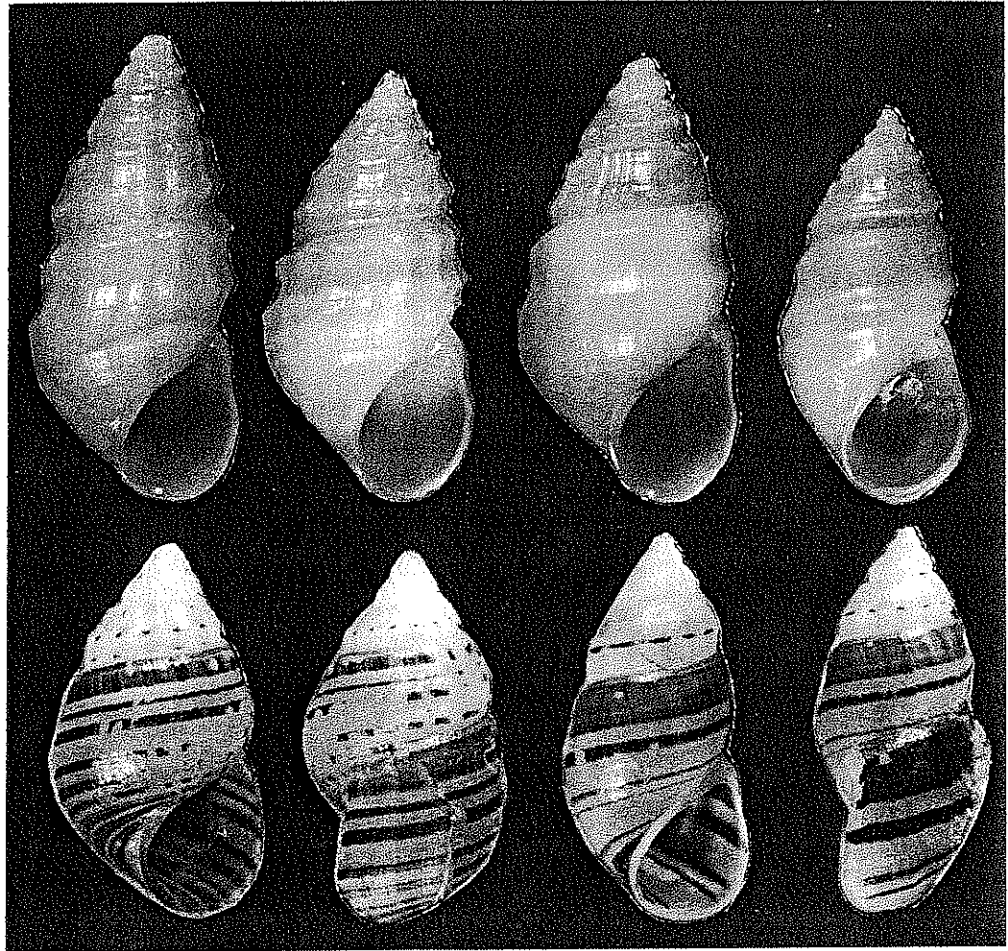


FIG. 38. Photos of shells of *Mexipyrgus churinceanus*. The top row has shells (periostacum removed) from Locality 1, showing sculptural variation. The shell figured on the left is 7.20 mm long. The others in this row are printed at the same enlargement. The bottom row has shells from Locality 90 (eastern lobe of the basin, Fig. 3) showing the thickened sutural periostacal band. The shell on the left is 3.76 mm long and the others in this row are printed to the same enlargement.

Shell

Shell measurements and other data for adults from 33 populations are given in Table 49. The shells are usually white-colored and opaque, but in a few populations they are colorless and transparent. The whorls are flattened and the sutures are not very impressed. The apical whorl is smooth (Fig. 39A). Sculpture begins at or just before the beginning of the third whorl (Fig. 39A). Spiral cords dominate the third whorl while axial ribs predominate on the fourth whorl. Sculpture on

the last two whorls is variable both within (Fig. 38, top row) and among (Fig. 37) populations. After the fourth whorl, noded ribs may be prominent, reduced, or absent; and the spiral sculpture usually consists of two low welts. Cancellate sculpture was rarely seen. In populations with adult shells having prominent axial sculpture, 12–20 ribs were seen on the penultimate whorl. In some cases, a small number of narrow spiral cords is seen below the suture on the body whorl. Sculpture is generally reduced on the body whorl relative to that of the penultimate whorl. Axial growth

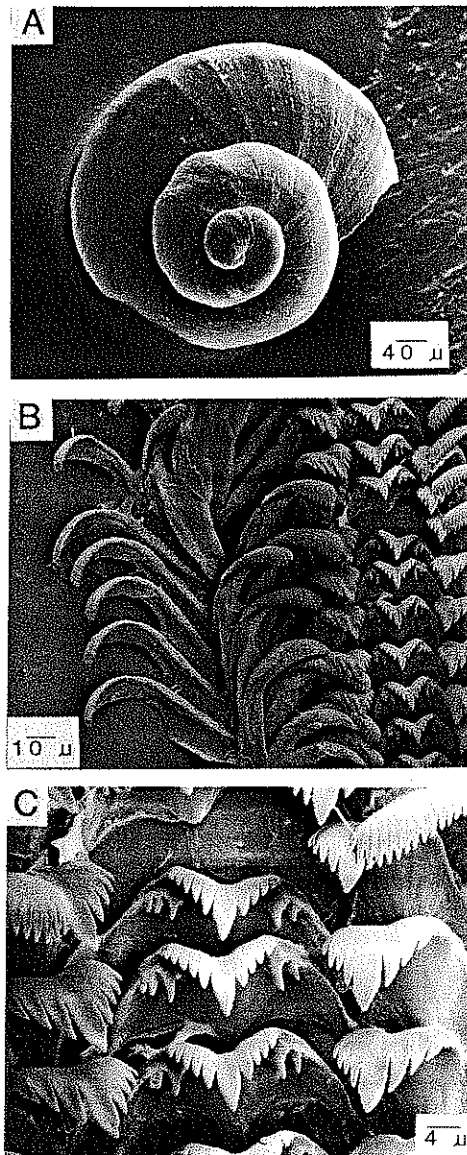


FIG. 39. SEM photos of shell and radula of *Mexipyr-gus churinceanus*. A. Apical view of embryonic shell. Note smooth apex. B. Part of radular ribbon. C. Close-up showing central teeth.

lines are usually prominent. Adult females generally have larger and relatively wider shells than males, as well as more prominent sculpture. The aperture is elongate and somewhat pyriform above. The outer lip usually has a pronounced sinuation. The umbilicus is a narrow slit.

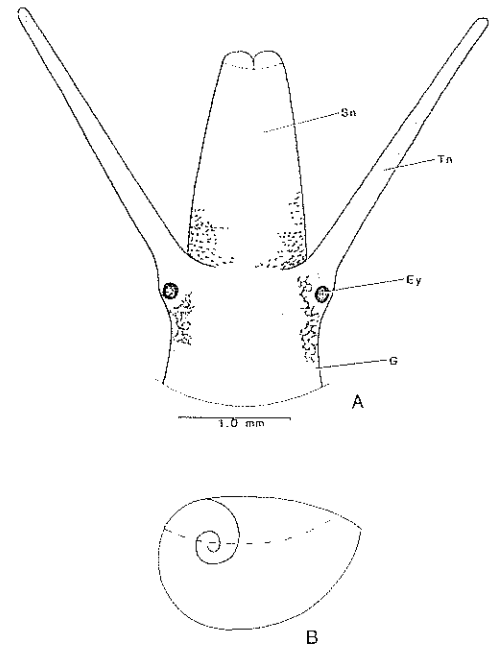


FIG. 40. Head and operculum of *Mexipyr-gus churinceanus*. A. Dorsal aspect of the head. Note the concentration of glandular units (G) and darker color streaks. B. Operculum with the dashed lines showing the attachment area to the operculigerous lobe. Ey—eye; G—glandular unit; Sn—snout; Tn—tentacle.

TABLE 41. Dimensions (mm) of non-neural organs and structures of *Mexipyr-gus churinceanus* from Locality 1. N = 5. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	8.33 \pm 0.36	6.82 \pm 0.34
Osphradium	L	0.30 \pm 0.02	
Gonad	L	1.66 \pm 0.23	2.68 \pm 0.11
	W	0.59 \pm 0.03	0.75 \pm 0.08
Prostate	L		1.50 \pm 0.12
	W		0.90 \pm 0.08
Penis	L		2.61 \pm 0.17
	W		1.15 \pm 0.05
Pallial oviduct	L	4.35 \pm 0.34	
	W	1.08 \pm 0.10	
Bursa copulatrix	L	1.25 \pm 0.16	
	W	0.36 \pm 0.05	
Seminal receptacle (body)	L	0.30 \pm 0.04	
	W	0.09 \pm 0.01	
Seminal receptacle (duct)	L	0.13 \pm 0.01	
	W	0.06 \pm 0.002	

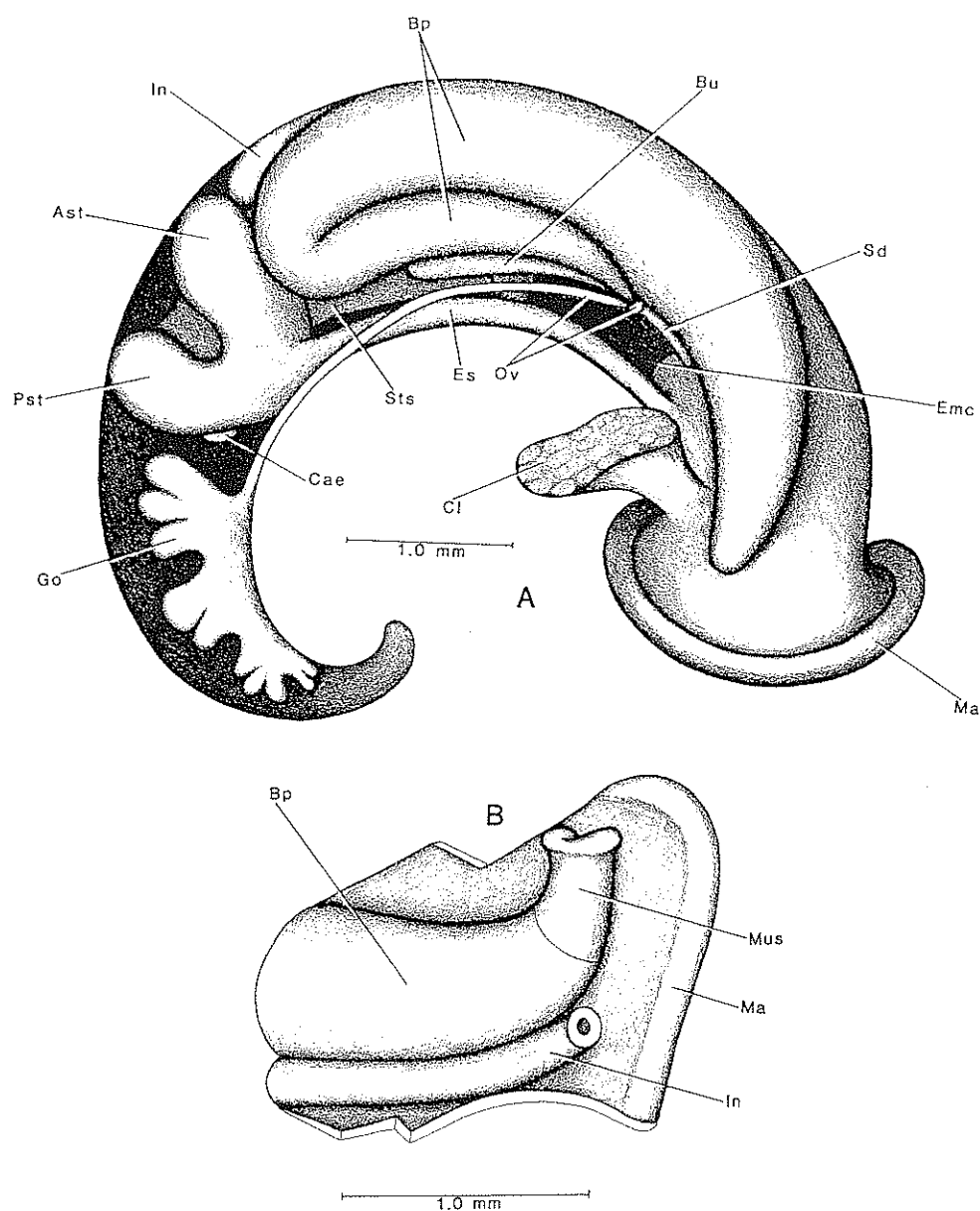


FIG. 41. General organization of the female reproductive anatomy of *Mexipyrgeus churinceanus*. A. Ventral aspect of uncoiled snail without the head and kidney tissue. Note the posterior bend of the brood pouch (Bp). B. Portion of the anterior end of the mantle cavity showing the slight muscular twist (Mus) of the anterior end of the brood pouch. Ast—anterior stomach chamber; Bp—brood pouch; Bu—bursa; Cae—caecum of stomach; Cl—columnellar muscle; Emc—posterior end of the mantle cavity; Es—esophagus; Go—gonad; In—intestine; Ma—mantle edge; Mus—muscular section of brood pouch; Ov—oviduct; Pst—posterior stomach chamber; Sd—spermathecal duct; Sts—style sac.

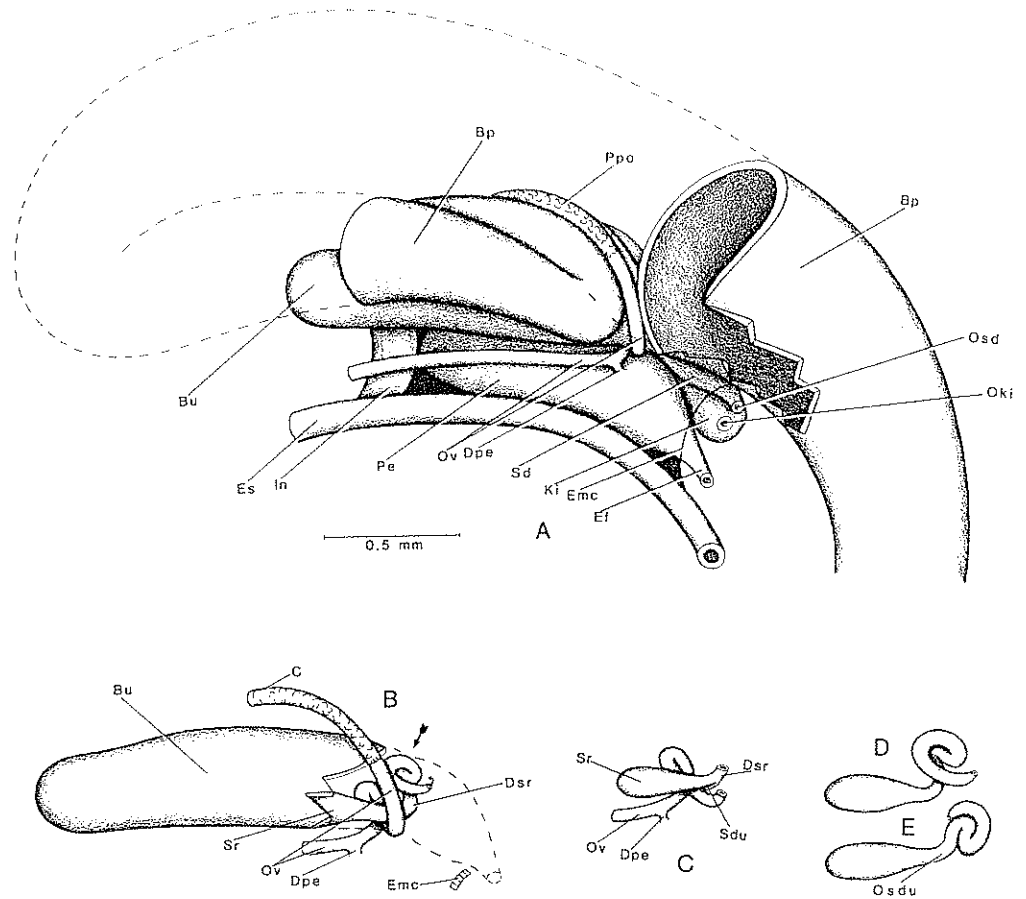


FIG. 42. Female reproductive anatomy of *Mexipyrgus churinceanus*. A. Oriented as in Fig. 41A, but with much of the brood pouch (Bp) cut away to expose the bursa (Bu) and continuation of the pallial oviduct coils dorsal to the part that has been cut away. Note the reduction of the size of the albumen gland (Ppo) and the infringement of the bursa (Bu) and pallial oviduct onto the space occupied by the pericardium (Pe) and kidney (Ki). B. Oriented as in A, but with portion of the brood pouch (Bp) and bursa (Bu) cut away to expose the oviduct (Ov), seminal receptacle (Sr), its duct (Dsr), and the opening of the duct of the seminal receptacle into the dorsal side of the bursa (indicated by small arrow). The large arrow indicates the constriction between the bursa (Bu) and spermathecal duct (Sd). Point C is included for comparison with Fig. 43. C. Oriented as in B, but with part of the oviduct cut to expose the slender sperm duct (Sdu). D, E. Oriented as in C to show variation in the coiling pattern of the duct of the seminal receptacle. Bp—brood pouch; Bu—bursa; Dpe—gonopericardial duct; Dsr—duct of the seminal receptacle; Ef—efferent branchial vessel; Emc—posterior end of the mantle cavity; Es—esophagus; In—intestine; Ki—kidney; Oki—opening of the kidney; Osd—opening of the spermathecal duct; Osd—opening of the sperm duct; Ov—oviduct; Pe—pericardium; Ppo—albumen gland; Sd—spermathecal duct; Sdu—sperm duct; Sr—seminal receptacle.

Nonreproductive Features

Measurements of organs and structures from three populations are given in Tables 41–43. The description of external features and anatomy is largely based on study of the type population (from Locality 1). The snout

(Fig. 40A) is elongate and the tentacles are thin and short by comparison. The tentacles are without hypertrophied ciliary tufts. Large, milk-white granules (G, Fig. 40A) are concentrated in the rostrum and neck. A light dusting of melanin may or may not be seen on the rostrum and neck. The paucispiral oper-

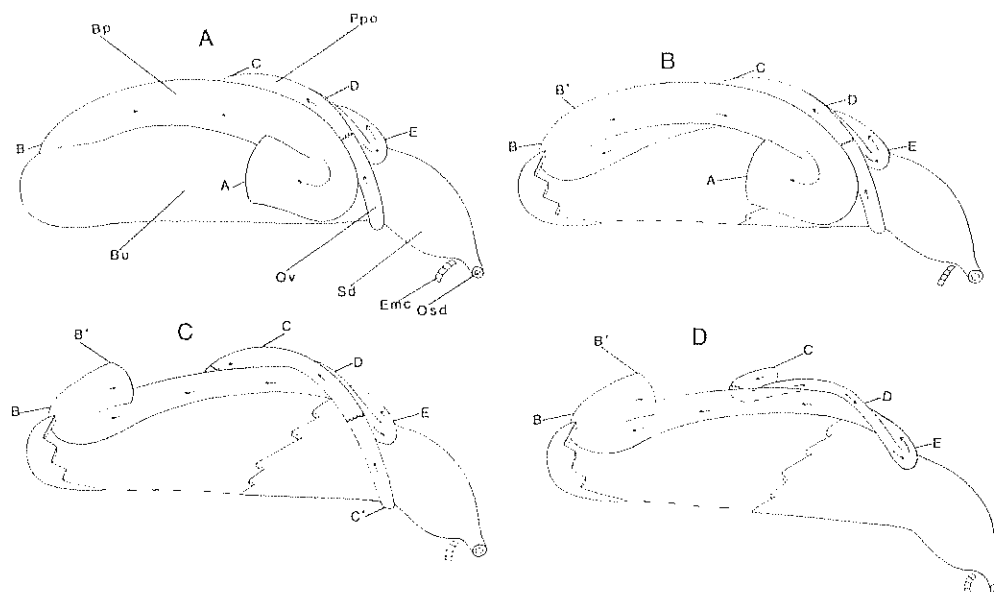


FIG. 43. The nature of the coils of the posterior pallial oviduct as revealed by progressive removal of portions of the coils. Orientation as in Fig. 42A. A. Pallial oviduct cut at point A. B. Part of the bursa (Bu) is cut away to expose the coils on its dorsal side. C. Section A-B' of the pallial oviduct has been removed. D. Section C-C' has been removed. The small arrows indicate the direction of movement of eggs and embryos through the pallial oviduct coils. Bp—brood pouch; Bu—bursa; Emc—posterior end of the mantle cavity; Ov—oviduct; Ppo—albumen gland; Sd—spermathecal duct; Osd—opening of the spermathecal duct.

TABLE 42. Dimensions (mm) of non-neural organs and structures of *Mexipyrgus churinceanus* from Locality 30. N = 5. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	5.46 \pm 0.14	5.01 \pm 0.21
Osphradium	L	0.22 \pm 0.03	
Gonad	L	0.80 \pm 0.06	1.66 \pm 0.10
	W	0.46 \pm 0.05	0.54 \pm 0.07
Prostate	L		1.00 \pm 0.13
	W		0.53 \pm 0.06
Penis	L		1.86 \pm 0.17
	W		0.79 \pm 0.07
Pallial oviduct	L	2.38 \pm 0.14	
	W	0.70 \pm 0.13	
Bursa copulatrix	L	0.80 \pm 0.06	
	W	0.21 \pm 0.03	
Seminal receptacle (body)	L	0.15 \pm 0.02	
	W	0.07 \pm 0.02	
Seminal receptacle (duct)	L	0.10 \pm 0.01	
	W	0.06 \pm 0.01	

TABLE 43. Dimensions (mm) of non-neural organs and structures of *Mexipyrgus churinceanus* from Locality 50. N = 5. Mean \pm standard deviation. L = length, W = width.

		Females	Males
Body	L	9.58 \pm 0.33	9.10 \pm 0.28
Osphradium	L	0.38 \pm 0.13	
Gonad	L	1.42 \pm 0.17	3.26 \pm 0.76
	W	0.73 \pm 0.08	0.76 \pm 0.09
Prostate	L		1.71 \pm 0.11
	W		0.98 \pm 0.06
Penis	L		3.24 \pm 0.23
	W		1.52 \pm 0.23
Pallial oviduct	L	5.43 \pm 0.23	
	W	1.10 \pm 0.08	
Bursa copulatrix	L	1.41 \pm 0.10	
	W	0.38 \pm 0.05	
Seminal receptacle (body)	L	0.36 \pm 0.07	
	W	0.16 \pm 0.02	
Seminal receptacle (duct)	L	0.21 \pm 0.05	
	W	0.08 \pm 0.004	

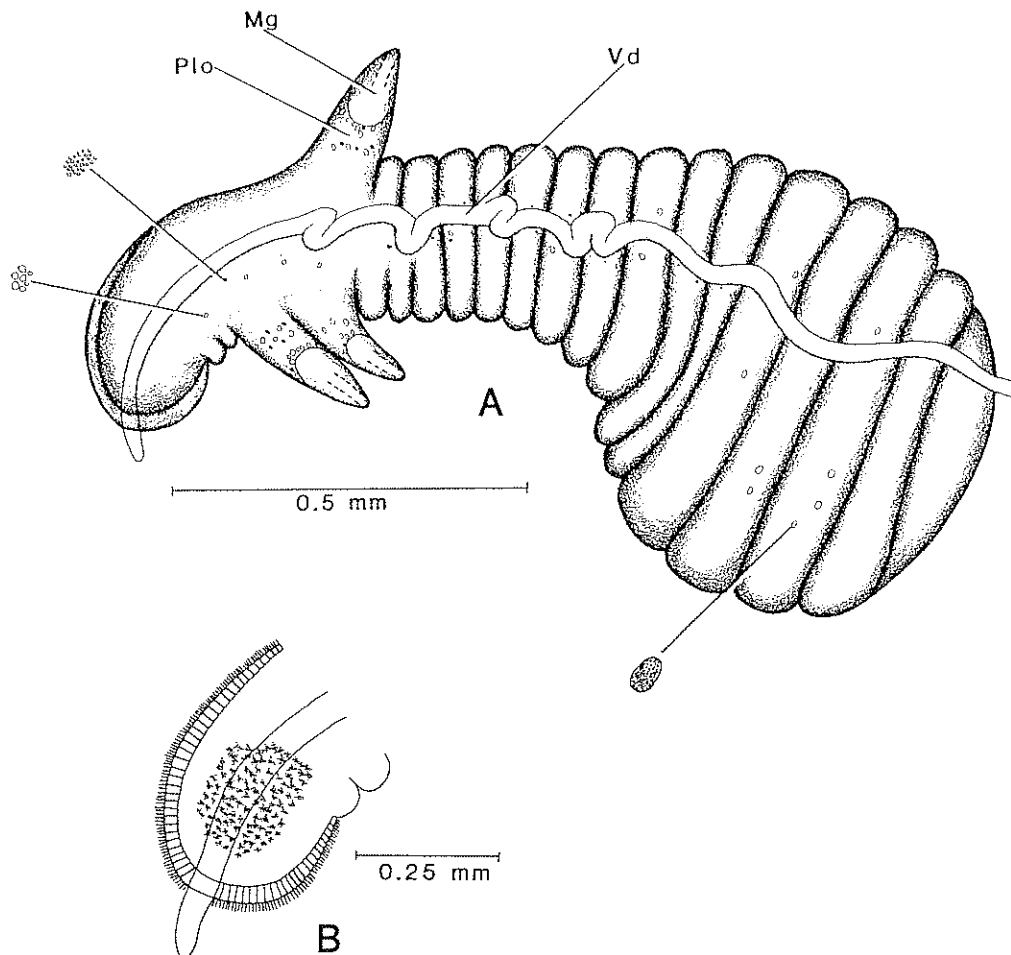


FIG. 44. The penis of *Mexipyrgus churinceanus* from Locality 1. A. Dorsal aspect of the penis. Note the folds in the penis, the blunt tip with ciliated columnar epithelium, and slender penial lobes (Plo) with mammiform glands (Mg). B. The tip of the penis showing the ciliated cells and pigment patch. Mg—mammiform gland; Plo—penial lobe; Vd—vas deferens.

TABLE 44. Radular statistics for females from 6 populations of *Mexipyrgus churinceanus*. Measurements are in mm. Mean \pm standard deviation. "r" and "p" refer to the correlation coefficient (and significance level) between that particular radular feature and mean adult female shell length (from Table 33), for the 6 populations.

	Radular statistics					
	Shell length	N	Length	Width	No. rows	Width of central tooth (N)
Locality 73	4.10	10	0.57 ± 0.02	0.09 ± 0.001	49.4 ± 1.49	0.030 ± 0.0012 (32)
Locality 95	5.29	9	0.65 ± 0.03	0.11 ± 0.006	53.3 ± 2.96	0.033 ± 0.0011 (33)
Locality 76	6.72	9	0.78 ± 0.03	0.13 ± 0.005	54.1 ± 2.76	0.038 ± 0.0017 (27)
Locality 1	7.24	9	0.70 ± 0.03	0.12 ± 0.007	53.2 ± 1.92	0.034 ± 0.0013 (46)
Locality 97	7.51	9	0.71 ± 0.02	0.12 ± 0.005	54.7 ± 1.80	0.034 ± 0.0015 (29)
Locality 50	8.25	9	0.77 ± 0.02	0.14 ± 0.005	54.1 ± 1.96	0.039 ± 0.0018 (22)
			r 0.860		0.833	0.758
			p <.025		<.025	<.05

TABLE 45. The various cusp arrangements for the four tooth types in 18 radulae of *Mexipyrgus churincanus*, with the percentage of radulae showing that arrangement at least once.

Central		Lateral		Inner marginal		Outer marginal	
anterior cusps							
basal cusps	%	cusps	%	cusps	%	cusps	%
$\frac{4-1-4}{2-2}$	6	4-1-4	58	21	11	24	11
$\frac{4-1-4}{3-2}$	17	5-1-4	58	22	6	25	11
$\frac{4-1-4}{3-3}$	28	5-1-5	58	23	33	26	22
$\frac{5-1-4}{3-2}$	33	6-1-4	25	24	11	27	44
$\frac{5-1-4}{3-3}$	44	8-1-4	8	25	33	28	33
$\frac{5-1-4}{2-2}$	22	6-1-5	42	26	56	29	33
$\frac{5-1-4}{2-1}$	11	7-1-4	8	27	61	30	67
$\frac{5-1-5}{2-1}$	6	6-1-6	8	28	56	31	56
$\frac{5-1-5}{2-2}$	28			29	39	32	33
$\frac{5-1-5}{3-2}$	33			30	39	33	39
$\frac{5-1-5}{3-3}$	44			31	17	34	28
$\frac{6-1-4}{3-2}$	6			32	28	35	11
$\frac{6-1-5}{2-2}$	17			33	28	36	17
$\frac{6-1-5}{3-3}$	11			34	17	37	17
$\frac{6-1-6}{2-1}$	6			35	11	38	11
$\frac{6-1-6}{2-2}$	6			36	11		
$\frac{6-1-6}{3-2}$	11						
$\frac{6-1-6}{3-3}$	28						
$\frac{7-1-5}{2-2}$	6						
$\frac{7-1-5}{3-3}$	11						
$\frac{7-1-6}{2-1}$	6						
$\frac{7-1-6}{3-3}$	11						
$\frac{7-1-7}{3-3}$	6						
$\frac{7-1-7}{4-3}$	6						
$\frac{8-1-5}{3-3}$	6						
$\frac{6-1-4}{3-3}$	6						

TABLE 46. Common ($\geq 40\%$ of radulae studied) central tooth cusp formulae for 6 populations of *Mexipyrus churinceanus*.

	Formulae
Locality 73	4-1-4/2-2, 5-1-4/2-2
Locality 95	5-1-4/2-2
Locality 76	5-1-5/2-2, 6-1-5/2-2
Locality 1	5-1-4/3-3, 5-1-5/3-3
Locality 97	5-1-5/3-2
Locality 50	5-1-4/3-3, 5-1-5/3-3

culum (Fig. 40B) has 2.0–2.5 whorls and the nucleus is positioned at 23% of the long axis of the operculum. The body pigmentation consists of thin bands of dark melanin on the dorsal surface, and yellow and white granules on the ventral body surface. The operculigerous lobe has several thin red-purple melanin streaks as well as a large central cluster of white granules. The caecal chamber extends posterior to the stomach (Cae, Fig. 41A).

Radula

The radula is shown in Figs. 39B, C. The central tooth has one to three pairs of basal cusps that arise from the lateral angles. Radular statistics for the type populations of the six nominal species are given in Table 44. Radulae were removed from large females of each population. As seen in Table 44, the length of the radula ribbon, number of rows of teeth, and width of the central tooth are all highly correlated with the average shell lengths of the females for the populations ($p < 0.05$). The cusp arrangement for the four tooth types for the population from Locality 1 are given in Table 45. Common formulae for the cusp arrangements for the central tooth for the same six populations as above are given in Table 46. Note that only the three populations with large-sized females commonly have three pairs of basal cusps.

Female Reproductive Anatomy

The female gonad (Go) consists of four to six lobed branches (Fig. 41A) and is only 15–20% of the body length. The pallial oviduct is 44–57% of the body length, and the posterior coils extend to within 0.38 mm of the end of the mantle cavity. When part of the non-reflected portion of the pallial oviduct is dissected away, it is seen that the posterior bend continues to loop dorsally (Fig. 42A).

Sections of these loops are progressively cut away in Figs. 43A–D to reveal their complex nature and the way that they partially envelop the bursa (Bu).

The bursa is elongate, with a narrowed posterior section, and is 26–34% of the pallial oviduct length. The seminal receptacle (Sr) is appressed to the dorsal side of the bursa near its anterior end (Fig. 42B). The oviduct, after giving off a short gonopericardial duct (Dpe), disappears beneath the bursa and coils once before receiving the narrow sperm duct (Sdu) from the duct of the seminal receptacle (Dsr, Figs. 42B, C). The oviduct then loops back to the ventral side of the bursa to enter the posterior end of the pallial oviduct. The sperm duct is tightly appressed to the duct of the seminal receptacle. After the juncture with the sperm duct, the duct of the seminal receptacle coils variably several times before entering the dorsal side of the anterior end of the bursa (Figs. 42B–E).

The large bursa and massive coils of the pallial oviduct cover the kidney (Ki) and a small portion of the pericardium (Pe, Fig. 42A). The kidney and pericardium are relatively small and flattened compared to those of other hydrobiid snails.

Data for number of embryonic shells obtained from adult females from 10 populations are given in Table 47. Non-shelled embryos were rarely seen in dissected specimens. The correlation between shell length and number of brooded young (data from Table 47) is 0.882 and highly significant ($p < 0.005$). For 100 embryonic shells from females from Locality 1, shell length averaged 0.386 ± 0.190 mm, with a five-fold range from 0.119–0.634 mm. The embryos have red pigment on the dorsal body surface.

Male Reproductive Anatomy

The male gonad has five to six lobed branches, filling most of the digestive gland and comprising 33–39% of the body length. The prostate is 26–34% of the body length, overlaps the mantle cavity, and has the anterior vas deferens exiting from its anterior tip.

The penis is shown in Fig. 44A. It has deep folds over most of its length. The single penial lobe on the outer curvature is located at 67% the penis length from the base. One or (more commonly) two lobes are on the inner curvature, again beginning at 67% of the penis length from the base (Fig. 45). In one population (from Locality 76) a few specimens had a

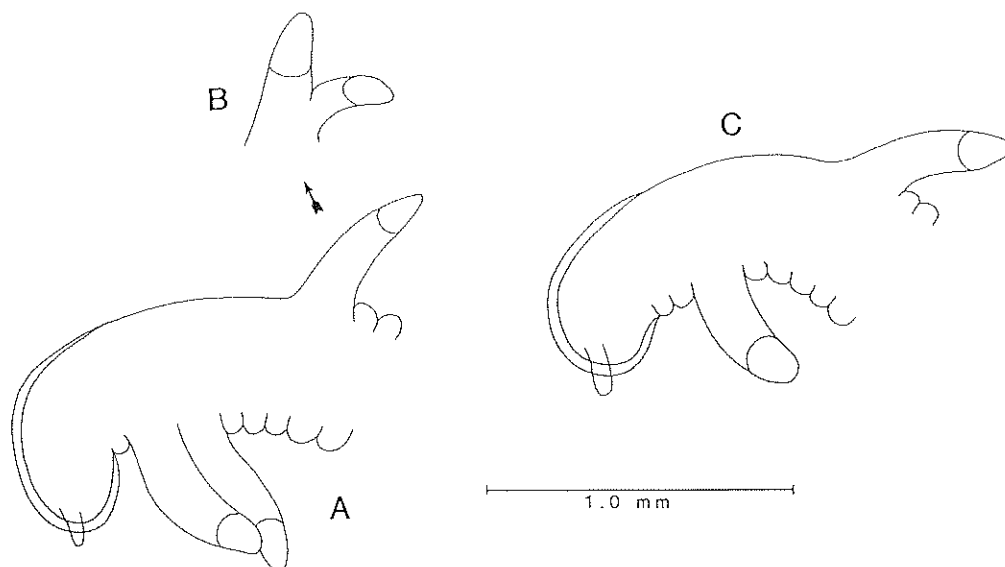


FIG. 45. Variation in the penial lobation of *Mexipyrgus churinceanus*. A. The most common penis type with two lobes on the inner curvature and one lobe on the outer curvature. B. Presence of a second, "bud-like" penial lobe (with mammiform gland) on the outer curvature, seen only in specimens from Locality 76. C. Rare penis type with one lobe on both the inner and outer curvatures, seen only in specimens from Localities 73, 76, and 99.

TABLE 47. Data for number of shelled embryos brooded by females from 10 populations of *Mexipyrgus churinceanus*. The mean shell length (for shells with the maximum dominant whorl number) for adult females for each population is also given.

	Shell length (mm)	Number of young/female			
		N	\bar{X}	SD	range
Locality 6	3.93	16	3.56	1.67	0-7
Locality 16	4.44	15	3.60	3.00	0-12
Locality 10	5.10	14	9.21	3.07	6-17
Locality 18	5.10	17	8.88	3.95	4-17
Locality 21	5.13	15	8.87	3.14	6-18
Locality 11	5.90	13	7.31	2.81	3-14
Locality 5	5.99	14	9.14	1.03	8-11
Locality 22	6.04	16	4.75	1.29	3-8
Locality 1	7.42	15	19.1	3.08	14-24
Locality 50	8.25	15	22.1	5.44	14-35

second small bud-like lobe with mammiform gland on the outer curvature (Fig. 45B).

The mammiform gland occupies about one-half the length of the penial lobe (Mg, Fig. 44A). While an apocrine gland is circular in shape and has both a very large central lumen and large terminal opening (see Thompson, 1968, fig. 38E), the mammiform gland is more conical in shape and has a very narrow

central lumen (surrounded by a muscular layer) and a small, pore-like terminal opening. The penis of *Pyrgophorus coronatus* also has glands that would be considered mammiform (see Fullington, 1978, fig. 16).

The vas deferens (Vd) coils for most of the length of the penis. The tip of the penis has ciliated columnar epithelia extending back to the end of the folds on the inner curvature,

TABLE 48. Data matrix for the multi

Character	1	5	10	11	18	20	21	22	37	38	43	46	47
1. Max. no. whorls, ♂	7.0	6.0	6.0	6.5	6.0	6.0	6.0	6.5	5.5	6.0	5.5	6.0	6.0
2. Max. no. whorls, ♀	7.5	6.5	6.5	7.0	6.5	6.0	6.5	7.0	6.0	7.0	6.0	6.5	6.5
3. Shell length, ♂	5.76	4.77	4.64	5.22	4.14	4.25	4.73	5.48	4.77	5.74	4.58	4.83	4.41
4. Shell length, ♀	7.24	5.99	5.10	5.90	5.10	3.93	5.13	6.04	6.16	7.28	5.69	5.65	5.06
5. Shell width, ♀	3.35	3.04	2.72	3.05	2.72	2.24	2.76	3.16	3.48	4.10	3.46	2.99	2.91
6. Length of body whorl	4.53	3.92	3.47	3.83	3.41	2.78	3.57	4.01	4.30	4.99	4.00	3.85	3.50
7. Length of aperture	2.78	2.45	2.19	2.33	2.17	1.74	2.28	2.36	2.72	3.16	2.69	2.48	2.27
8. Width of aperture	1.79	1.53	1.42	1.60	1.49	1.24	1.51	1.74	1.94	2.19	1.80	1.61	1.60
9. No. of gill filaments	55.0	44.5	52.3	46.0	45.8	45.8	47.0	48.4	50.8	53.4	48.0	50.8	45.2
10. Body whorl with spiral cord	0	0	0	0	0	0	0	0	0	0	0	0	0
11. Shell with periostracal bands	2	0	0	0	1	0	0	0	1	1	2	0	2
12. Banded shells with thick sutural band	2	2	2	2	2	2	1	2	2	2	2	0	2
13. Penis with 1 lobe on inner curvature	0	0	0	0	0	0	0	0	0	0	0	0	0
14. Penis with 2 lobes on inner curvature	1	1	1	1	1	1	1	1	1	1	1	0	1
15. Rostrum pigmented	0	0	0	0	2	0	0	0	2	0	0	1	1
16. No. of periostracal bands	1	1	1	1	0	0	0	1	1	1	1	0	0
17. Freq. of sculpture score—1	.02	0	.14	.02	.03	.33	.03	0	0	0	0	0	.02
18. Freq. of sculpture score—2	.12	0	.33	.14	.13	.48	.46	.02	.10	0	.08	.04	0
19. Freq. of sculpture score—3	.54	.50	.49	.72	.83	.19	.51	.62	.60	.66	.92	.51	.72
20. Freq. of sculpture score—4	.32	.50	.04	.12	.01	0	0	.36	.30	.34	0	.45	.26

and 0.3 mm back on the outer curvature (Fig. 44). A pigmented patch is sometimes seen near the tip of the penis (Fig. 44B.) The penis has Gl₁ and Gl₂ glands.

Discussion

While complete anatomical data are provided for only three populations, specimens from numerous other populations (including those of the types for all nominal species) were dissected as well (see Table 48), yet no qualitative differences in soft-part anatomy were seen. The main difference between populations is in shell features, especially size, and anatomical features correlated with size, such as number of young brooded by females, radular statistics, and number of gill filaments. The purported differences (shell and anatomy) between nominal species are blurred when numerous populations are studied. For example, one of the diagnostic features of *Mexipyrigus mojarrales* (sensu Taylor, 1966), which is considered endemic to Locality 73, is a penis with a single lobe on the inner curvature (the usual number is two). Yet in the Mojarra East Laguna (Locality 76), which has a stream connection with Locality 73, individuals assignable to *M. multilineatus* (sensu Taylor, 1966) may also have this penis type (see Table 49).

As there are no morphological criteria by which separate species can be recognized, the six nominal species are reduced to one, *Mexipyrigus churinceanus*. A detailed analysis

of morphological variation of *M. churinceanus*, and its relation to the species problem, is presented below.

Subfamily Unknown

Orygoceras Brusina, 1882

Type-species: *Orygoceras cornucopiae* Brusina, 1882.

Distribution: the single living species is restricted to two localities in the southwestern deserts of North and Central America (see below). Late Cenozoic fossils are known from eastern Europe (Brusina, 1882) and the northwestern United States (Dall, 1925; and others).

Species included: the living species remains undescribed. Numerous fossil species have been described.

Description

The shell is variable in size (width, 2.0–12.0 mm), but always uncoils after a whorl or so, producing a tube-like shape (Fig. 13H). Axial sculpture may (Brusina, 1882, pl. 11) or may not (Fig. 13H) be present.

Orygoceras (?) sp.

Distribution: restricted to Roaring Springs, Real County, Texas (Taylor, 1974); and a single spring in the Cuatro Ciénegas Basin (see below).

variate analysis (measurements in mm).

48	49	30	50	78	99	76	73	71	80	79	81	82	83	86	88	93	95	97	96
6.5	6.5	6.5	7.0	6.5	6.5	6.5	6.0	6.5	6.5	7.0	6.5	6.5	6.5	6.0	5.5	6.5	6.5	7.0	6.0
6.5	7.0	6.5	7.5	7.0	7.0	7.0	6.5	6.5	7.0	7.5	6.5	6.5	7.0	6.5	5.5	7.0	6.5	7.0	6.0
4.25	4.76	4.17	7.03	6.23	5.37	6.03	3.80	5.44	6.24	7.31	5.74	5.96	5.44	4.53	3.14	5.64	4.82	6.58	4.36
4.65	5.54	4.44	8.25	7.34	6.53	6.72	4.10	5.90	6.65	8.45	6.93	6.26	6.96	6.34	3.03	6.53	5.29	7.51	4.51
2.47	2.73	2.43	4.28	3.91	3.28	3.39	2.36	3.34	3.37	4.36	3.84	3.26	3.48	3.47	1.74	3.49	2.76	4.03	2.57
3.02	3.51	2.99	5.45	4.85	4.33	4.47	2.75	4.10	4.41	5.37	4.70	4.21	4.59	4.35	2.08	4.32	3.50	4.87	3.14
1.85	2.18	1.88	3.46	2.99	2.68	2.78	1.66	2.59	2.63	3.41	3.00	2.61	2.73	2.74	1.33	2.73	2.18	3.00	1.93
1.29	1.50	1.32	2.20	2.10	1.80	1.83	1.21	1.76	1.80	2.31	2.04	1.76	1.92	1.90	0.92	1.86	1.51	2.08	1.35
46.8	51.6	44.8	65.6	53.2	58.0	53.4	41.8	53.2	53.8	64.6	51.6	52.6	62.6	63.6	34.2	46.2	47.0	60.6	48.4
0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
2	2	2	2	2	2	0	2	2	0	1	1	0	0	2	0	0	2	2	1
2	2	2	0	0	0	0	1	1	1	0	0	0	1	2	0	1	2	1	2
0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	2	0	0	0	1	0	1	2	2	0	0	0	0	2	2	2
0	0	0	2	2	2	2	0	2	2	2	2	2	1	2	0	1	2	1	1
.08	.04	0	.88	.24	.96	.56	.46	.38	.34	.24	.02	.44	.50	.03	.14	.02	.02	0	0
.24	.23	0	.10	.27	.04	.38	.36	.33	.34	.38	.02	.44	.38	.21	.56	.06	.08	0	0
.66	.73	.18	.02	.46	0	.06	.16	.29	.32	.30	.42	.12	.12	.62	.30	.60	.74	.13	.23
.02	0	.82	0	.03	0	0	.02	0	0	.08	.54	0	0	.14	0	.32	.16	.87	.77

Habitat: restricted to small springheads. Taylor (1974) found one living specimen close to the source of the spring after heavy rains. I collected three live specimens and two empty shells from mops placed at the small springhead at Locality 67. The rarity of live specimens at these localities and the fact that the snail is blind and unpigmented, suggest that its main habitat is subterranean.

Description

The shell (Fig. 13H) uncoils after 1.3 whorls and produces a tube shape that is very similar in all specimens seen. For two specimens from Cuatro Ciénegas, the shell lengths (parallel to the coiling axis) are 1.70 and 1.58 mm, and the widths are 2.26 and 2.06 mm, respectively. Adult Roaring Springs specimens are about 2.0 mm wide (Taylor, 1974). The apical whorl has pitted microsculpture, while the later whorls have strong growth lines. The operculum is paucispiral.

The animal is blind and unpigmented. The buccal mass and operculigerous lobe have a red-pink color similar to that of *Coahuilix* and *Paludiscala*. The intestine has a loop near its anterior end (Taylor, 1974, fig. 1). While not dissected, the animal is hydrobioid in its external appearance.

Discussion

There are three distinct groups of *Orygoceras* species: 1) large (width, to 8 mm),

sculptured species from Late Cenozoic Balkan lake beds; 2) large (to 12 mm), smooth-shelled species from Miocene-Pliocene Idaho lake beds; and 3) the very small (to 2 mm), smooth-shelled living species found in small springheads. The relationships among these three groups remain obscure: the living species is probably not closely related to the fossil taxa as it differs greatly in shell size and habitat.

MORPHOLOGICAL DIFFERENTIATION AMONG POPULATIONS OF *MEXIPYRGUS CHURINCEANUS*

Populations of *Mexipyrigus churinceanus* show considerable variation of shell features (Fig. 37). The six nominal species of *Mexipyrigus* were described by Taylor (1966), all but one from single localities, based on characters involving shell size, shape, sculpture, number and thickness of periostracal bands, and the number of penial lobes. I collected *Mexipyrigus* from over 40 localities in the basin, and noted patterns of variation inconsistent with the species concepts of Taylor (1966). To analyze these patterns of variation and to assess the similarities and differences among populations, a data base of 20 characters (16 from shell, one from body pigment, three from soft parts), including most of those employed in the diagnoses of the nominal species, from 33 populations (OTUs) was subjected to multivariate analysis. These

TABLE 49. Characters used in assessing similarities and differences between populations of *Mexipyrus churinceanus*. Characters 3–9 represent means (of which 4–9 are for females only). In (0, 1) pairs, 0 represents absence of a character-state, 1 represents its presence. Characters 17–20 were also scored only from shells of females as those characters exhibit sexual dimorphism.

1. Maximum number of whorls, males; 2. Maximum number of whorls, females; 3. Shell length, males; 4. Shell length, females; 5. Shell width; 6. Length of body whorl; 7. Length of aperture; 8. Width of aperture; 9. Number of gills; 10. Prominent spiral cord on body whorl (Fig. 37, shells of Locality 73) (0, 1); 11. Shell with periostracal bands (0, 0–33% of shells banded; 1, 34–67%; 2, 68–100%); 12. Banded shells with thick sutural band (Fig. 38, bottom row) (0, 0–33% of banded shells with thick sutural band; 1, 34–67%; 2, 68–100%); 13. Penis with one lobe on the inner curvature (Fig. 45c) (0, 1); 14. Penis with two lobes on the inner curvature (Fig. 45a) (0, 1); 15. Rostrum pigmented (0, 0–33% of population; 1, 34–67%; 3, 68–100%); 16. Number of periostracal bands at the shell aperture (0, <8; 1, 8–14; 2, >14); 17–20. Frequency of shells with the following axial sculpture development at the end of the penultimate whorl; 17. Absent (see Fig. 37, Localities 76, 88); 18. Low ribs of low nodes without ribs (Fig. 37, Locality 48); 19. Moderately high, noded ribs (Fig. 37, Locality 1); 20. High, noded ribs (Fig. 37, Localities 30, 94).

TABLE 50. List of *Mexipyrus churinceanus* populations (used in the multivariate analysis) according to drainage systems.

Drainage	Localities (see Fig. 37)
I	1, 5
Ila	10, 11
Ilb	18, 20, 21, 22, 37, 38, 30, 43, 46, 47, 48, 49
III	99
IVa	50, 78, 71, 73, 76, 79, 80, 81, 82, 83, 86
IVb	88, 93, 95
V	96, 97

characters are listed and explained in Table 49. The entire data set is given in Table 48. The locations of the 33 populations, together with photographs of shells from many of them, are shown in Fig. 37.

The various populations are listed (by locality number), drainage by drainage, in Table 50. Drainage 1, terminating in a shallow playa lake (Locality 9), is currently isolated from other waters of the basin. Drainage 2a consists of the large thermal limnocrone, the Pozo de la Becerra (Locality 10), and its outflow, the Rio Garabatal. Drainage 2b consists of the large number of springs in the area known as El Garabatal, to the north of the Pozo de la Becerra, and to the east of the Rio Garabatal. These springs all flow to the north or west and may have joined the Rio Garabatal in the recent past. While some of these springs flow into the waters of Drainage 4a (see below), the downstream portion of these spring outflows are fast flowing over a hard bottom and no *Mexipyrus* was found in

them during an intensive survey during 1981. Drainage 3 consists of the isolated Anteojo spring complex (Locality 99) which, prior to alterations, may have flowed south to join Drainage 4a. Drainage 4 consists of the large rheocrone, the Rio Mesquites (originating at Locality 50), and nearby springs that flow into it (together constituting Drainage 4a); and the large thermal limnocrone, Laguna Escobedae (Locality 95), and nearby springs that join the Rio Mesquites well downstream (together constituting Drainage 4b). Drainage 5 consists of the large thermal limnocrone, Laguna Tio Candido (Locality 97), and a nearby spring, that flow to the south of Drainage 4.

Five principal components account for 79.93% of the variation. The first component accounts for 40.41%; the second 17.89% (accumulated 58.30%); the third 9.69% (accumulated 68.00%); the fourth 6.66% (accumulated 74.66%); the fifth 5.27%. Character loading for each component is given in Table 51. Characters are considered highly correlated if their load is greater than 0.60. Characters with values of greater than 0.50, but less than 0.60 were assigned to the principal component for which the characters had the highest value.

Characters highly correlated within the first component are number of whorls for males (Character 1, Table 51), measurements from shells of females (Characters 3–8), gill number (9), and number of periostracal bands on the shell (16). This component is one of size: the number of periostracal bands on the shell logically correlates with adult shell length. The second component has highly correlated characters of shell sculpture (10, 17, 19, 20), incidence of a thickened periostracal band (12), and number of penial lobes (13, 14).

TABLE 51. Factor loading of characters for the five principal components that collectively account for 79.93% of the variation in the multivariate analysis.

Character	Principal components				
	1	2	3	4	5
1	0.653	-0.080	0.061	-0.004	0.401
2	-0.406	0.180	0.251	-0.011	-0.527
3	0.947	-0.007	-0.082	0.058	0.001
4	0.969	0.110	0.034	-0.093	-0.106
5	0.951	0.173	0.076	-0.072	-0.132
6	0.971	0.124	0.031	-0.077	-0.158
7	0.958	0.151	0.031	-0.085	-0.156
8	0.945	0.181	0.060	-0.081	-0.170
9	0.865	-0.058	-0.006	-0.143	0.124
10	-0.277	-0.543	0.458	-0.152	-0.006
11	0.147	0.061	0.546	-0.395	0.512
12	-0.477	0.597	0.095	-0.430	0.114
13	-0.006	-0.764	0.421	-0.128	-0.227
14	0.121	0.591	-0.593	-0.011	0.238
15	0.234	0.248	0.177	0.646	-0.022
16	0.765	-0.137	-0.071	0.004	-0.079
17	0.388	-0.826	-0.060	-0.075	0.099
18	-0.158	-0.571	-0.684	0.018	-0.000
19	-0.301	0.690	-0.032	-0.458	-0.261
20	0.016	0.520	0.544	0.511	0.159

These characters do not involve size. The third component includes highly correlated characters of incidence of periostracal banding (11), number of penial lobes (14) and shell sculpture (18). The sole characters highly correlated within the fourth and fifth components are pigmentation of the rostrum (15) and number of whorls for females (2), respectively.

Ordination diagrams following non-metric three-dimensional scaling are given in Fig. 46 (1st vs. 2nd component), Fig. 47 (1st vs. 3rd component), and Fig. 48 (2nd vs. 3rd component). The various populations are referred to by locality numbers in the ordination diagrams. The stress was low (0.0010). The matrix correlation between taxonomic distance and distances in the three dimensional scaling was 0.988.

In Fig. 46, the ordination of component 2 versus component 1, the smaller-shelled populations are in Quadrants I and IV, and the larger-shelled populations are in Quadrants II and III. Populations in Quadrants III and IV are sculptured, have thickened sutural bands and are from four of the drainages, especially Drainages 1 and 2. Populations in Quadrant II are with large, smooth shells, without a thickened sutural band, and sometimes with males

having a single lobe on the inner curvature of the penis (from localities 76, 99); and are exclusively from Drainages III and IVa. In Quadrant I are populations with small-sized shells from Drainages II and IV. Of the nominal species, the populations in Quadrant II would be considered by Taylor as *Mexipyrargus lugoi* or *M. multilineatus* (type populations from localities 50 and 76, respectively). Quadrants III and IV have the type population of *M. churinceanus* (1), *M. escobedae* (95) and *M. carranzae* (97), that differ largely in shell size and sculptural development. The type population of *M. mojarrales* (73) appears as an outlier in Quadrant I as its members have very small shells, with a prominent spiral cord on the body whorl, and males with a single lobe on the inner curvature of the penis.

In Fig. 47, the ordination of component 3 versus component 1, the smaller-shelled populations are again in Quadrants I and IV, and the larger-shelled populations are in Quadrants II and III. Populations with sculptured shells and a high incidence of periostracal banding are in Quadrants III and IV, while smoother-shelled populations with a lower incidence of periostracal banding are in Quadrants I and II. Quadrant II has only populations from Drainage 4 while the other three

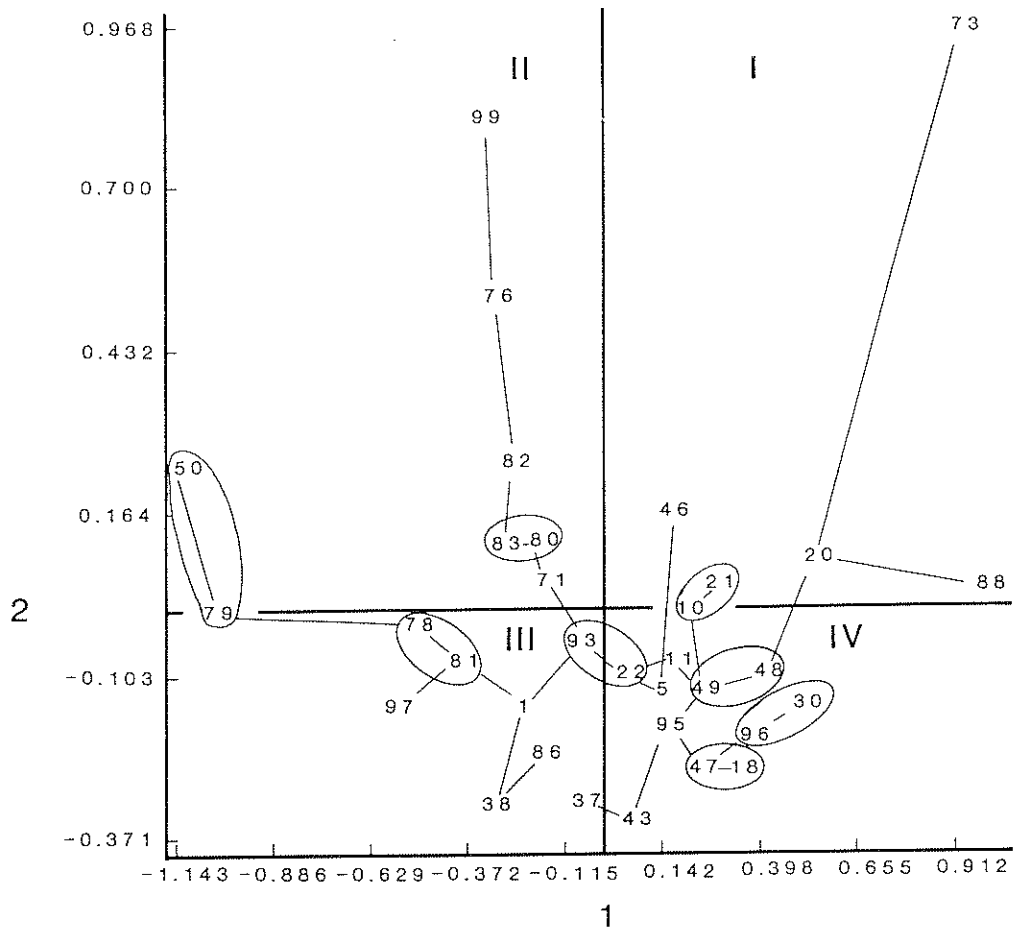


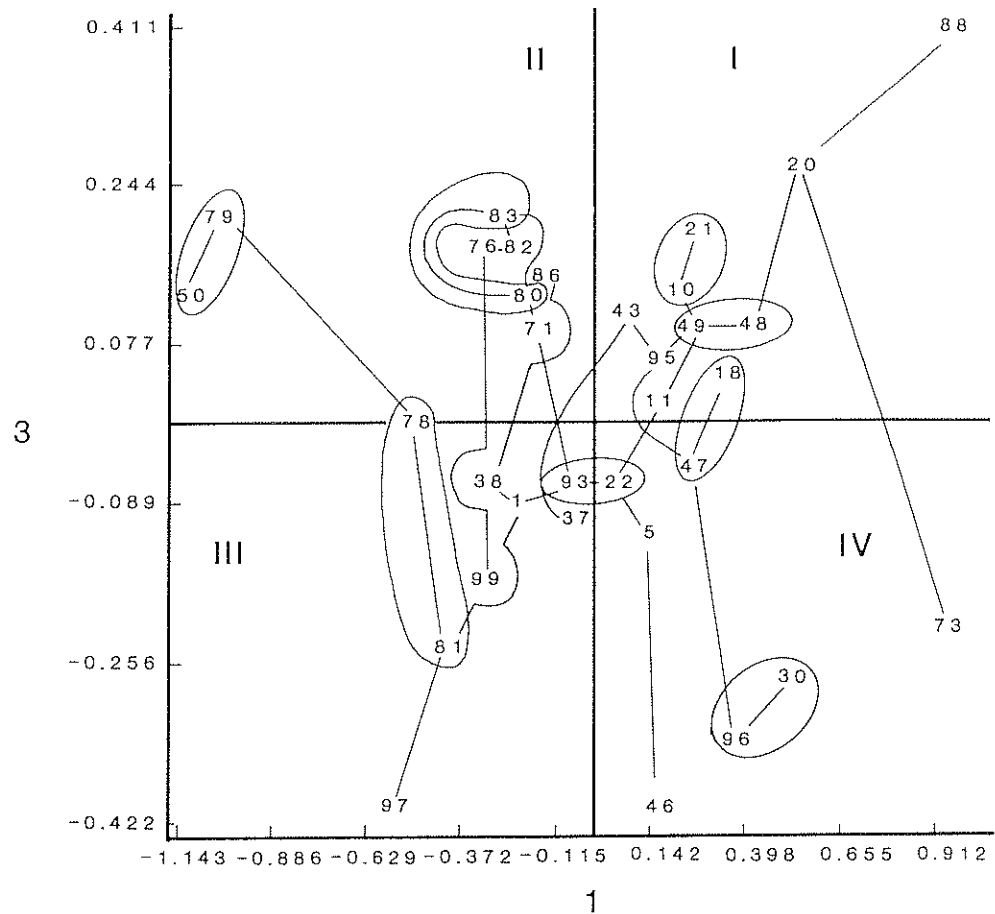
FIG. 46. Ordination diagram of 1×2 principal components, drawn according to non-metric multidimensional scaling. The numbers refer to the 33 populations of *Mexipyrgus churinceanus* (Fig. 37). The minimum spanning tree and subset solutions have been superimposed.

quadrants have populations from several drainages each. The population from Locality 88 appears as an outlier in Quadrant I because its members have a very small, smooth, non-banded shell.

In Fig. 48, the ordination of component 3 versus component 2, the influence of size is removed. In this case, the populations group to an even lesser degree by drainage. In Quadrant I, smooth-shelled populations from Drainage 2 (10, 20, 21) group with those of Drainage 4. In quadrants II and III, populations with sculptured shells with thickened sutural bands are found: note that these include populations from Drainages II, IV and V. The populations from Localities 99 and 73 are

outliers in Quadrant IV as their shells are usually banded and the males have a single lobe on the inner curvature of the penis.

The multivariate analysis indicates that, of the characters used, there is no consistent pattern of geographic variation among the various populations in relation to drainage. Of the eight subsets formed, three are formed among populations of Drainage 2 (10-21, 48-49, 18-47), three are formed among populations of Drainage 4 (50-79, 80-83, 78-81), but two are formed among populations from widely separated drainages: 22-93 (Drainages 2b and 4b) and 30-96 (Drainages 2b and 5); and these two subsets illustrate the problem of recognizing different "species" of

FIG. 47. Ordination diagram of 1×3 principal components.

Mexipyrus. The two populations of Drainage 5 are highly sculptured and are referable to *M. carranzae* (*sensu* Taylor, 1966). Yet one sees a remarkably similar-shelled population (30) from Drainage 2b, on the other side of the tall Sierra de San Marcos, with a low probability of previous connection between the two drainages (Fig. 37). In the other case, while populations from Drainages I and II, in general, are moderately sculptured, with thickened sutural bands, and are referable to *M. churinceanus* (*sensu* Taylor, 1966), populations with similar features are seen in Drainage 4 (71, 78, 81, 86, 93, and Locality 90, Fig. 38, bottom row), supposedly the drainage harboring *M. lugoi* (*sensu* Taylor, 1966, smooth-shelled, without a thickened sutural band). While some of these Drainage 4 populations

(particularly 71) are located close enough to the low, northern tip of the Sierra de San Marcos (Fig. 37) that they could have been founded by snails from western lobe waters (and hence their *M. churinceanus*-like features) given a previously different topography, the other populations (86, 93) are considerably to the south and east of the mountain tip and probably could not have been founded in such a fashion.

One must conclude, therefore, that despite some geographic differentiation of *M. churinceanus* populations, separate species cannot be distinguished, as similar morphological features involving shell size, sculpture and banding pattern have apparently been independently acquired in separated populations. The pattern seen in the ordination

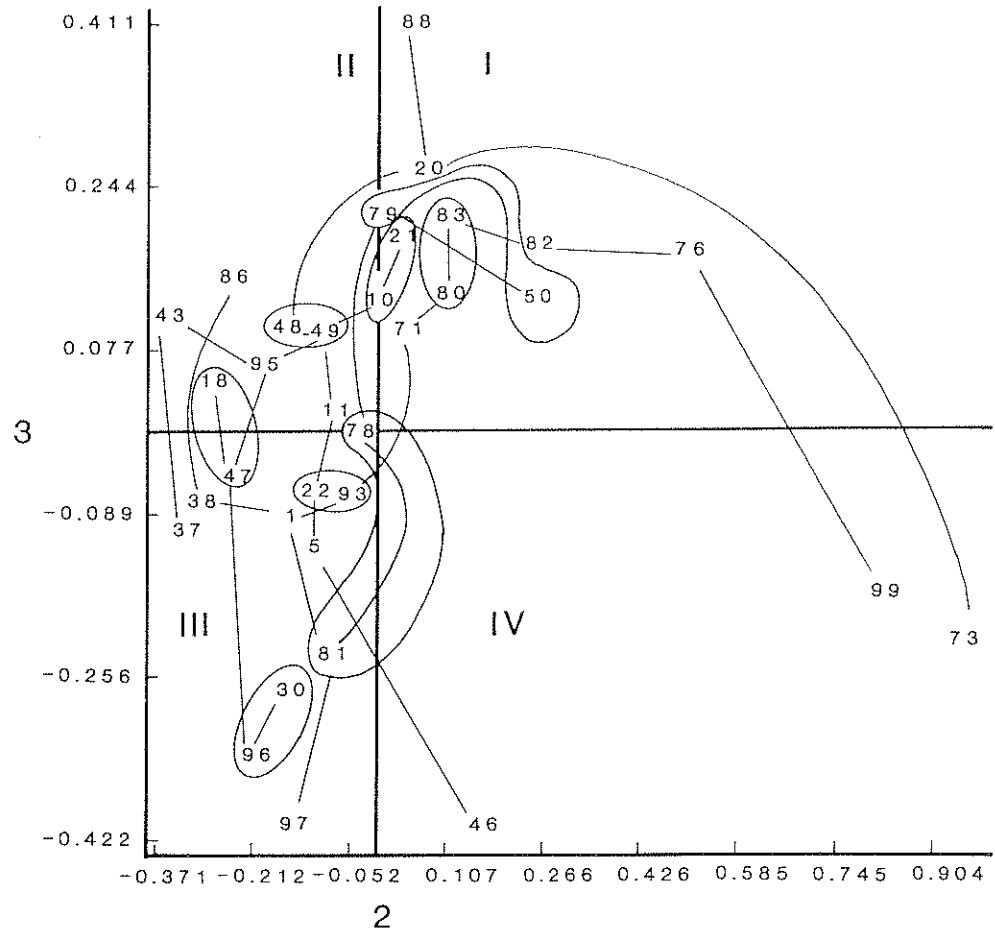


FIG. 48. Ordination diagram of 2 x 3 principal components.

diagrams, with many populations clustered together and a few outliers with unusual features, is one of a single variable species. While the six nominal species must be reduced to one, there may be three races or subspecies, corresponding to *M. churinceanus*, *M. lugoi* and *M. carranzae* (*sensu* Taylor, 1966), as populations assignable to each are concentrated in different portions of the basin drainage; Drainages I and II, III and IV, and V, respectively.

The shell features of *Mexipyrus churinceanus* may be somewhat plastic phenotypically and dependent on environmental factors. While populations located close to one another may be quite similar (such as subset 48-49), in other cases populations from close-by springs (even those with an aquatic connection) are quite dissimilar on shell

characters, especially when the springs differ in size, temperature, or substrate type. For example, the populations from Localities 80 and 79 are from springs (one small-sized and cold, the other large and warm) separated by only 100 m of stream, but differ greatly in shell size and frequency of a thickened sutural band (Table 49, Fig. 37). Populations from Localities 76 and 73 are also from close-by springs (one large and warm, the other small and very warm) with a short stream connection, but differ enough to have been placed in different species (Fig. 37; Taylor, 1966). However, when I collected and studied snails from a transect along the stream connection between the springs, intergradation of the two forms was apparent (Hershler, in preparation). In several cases I visited springs that had been altered by dredging. In these cases

the living specimens differed greatly in size and sculpture from sub-fossil specimens found in the dredged sediment alongside the spring, suggesting that (as the dredging was recent) the habitat change quickly resulted in a shell change.

Shell features may also depend on whether the population lives in a lentic (spring) versus lotic (stream) habitat: note that the spring-head and downstream populations in two instances (from Localities 1 and 5, 10 and 11) differ greatly in size, sculpture, and banding frequency. Banding frequency correlates with substrate color: populations from springs with light-colored sediments are generally unbanded while those from springs with darker sediments are usually banded. A banded shell may appear cryptic in dark sediment, making it more difficult to be seen by predaceous cichlid fish as they disturb and search the sediment when feeding.

RELATIONSHIPS AMONG THE CUATRO CIÉNEGAS HYDROBIIDS

The results of anatomical study of the Cuatro Ciénegas hydrobiids show that all of the taxa belong to the *Nymphophilinae* or *Littoridininae* (see Table 2) are widely distributed subfamilies. Thus while there are endemic genera, there are no subfamilies of hydrobiids endemic to the Cuatro Ciénegas Basin. While the relationships among the various hydrobiid taxa of Cuatro Ciénegas are discussed below, and shed some light onto the origin of the endemic taxa, the discussion is necessarily limited as the hydrobiids of the southwestern

United States, Mexico, and Central America are almost entirely unknown in terms of soft part anatomy, with many taxa still undescribed.

The two nymphophiline genera of the basin, *Mexistiobia* and endemic *Nymphophilus*, differ in at least 10 morphological features (Table 52). However, many of these differences may be simple correlates of the great size difference between snails of these taxa, and the two genera may, in fact, be closely related.

A comparison of the six littoridinine genera of the basin, involving 36 characters, is given in Table 53. Of these characters, six (17%) are from the operculum or shell, seven (19%) are from nonreproductive aspects of anatomy, eight (22%) are from the male reproductive anatomy, and fifteen (42%) are from the female reproductive anatomy. A matrix of percent difference between these taxa is given in Table 54 and was constructed by simply counting differences between taxa pairs and dividing by the total number of characters shared by the two taxa. In instances where for a given character two taxa both share a character state and have a different character state (e.g., 1, 2 versus 1, 3), the difference is scored as 0.5. A phenogram, based on simple averaging of differences between taxa, is given in Fig. 49.

The phenogram (Fig. 49) indicates that there are three groups of littoridinines in the basin, each constituting a pair of genera. Two of the groups consist of very similar genera ($\leq 29\%$ difference), the groups themselves linking at 46% difference. The taxa of the third group, *Paludiscala* and *Coahuilix*, link at 41%

TABLE 52. List of 10 morphological differences between *Mexistiobia* and *Nymphophilus*.

<i>Mexistiobia</i>	<i>Nymphophilus</i>
1. Operculum with 3.5 whorls	5.5–6.0 whorls
2. Osphradium short	Osphradium elongate
3. Central tooth or radula with 1 pair of basal cusps	3 pairs
4. Male gonad overlaps stomach	Male gonad posterior to stomach
5. Male gonad a single lobed mass	Male gonad bush-like
6. Penis with single glandular ridge	1–3 glandular ridges
7. Penial lobe slender, with single fold	Penial lobe stout, with many folds
8. Bolster and ventral channel poorly developed	Bolster and ventral channel well-developed
9. Bursa small (21% of pallial oviduct length), dorsal to pallial oviduct, with a short duct	Bursa large (32% of pallial oviduct length), posterior to pallial oviduct, with a long duct
10. Opening of common genital aperture at end of pallial oviduct	Opening of common genital aperture lateral to pallial oviduct

TABLE 53. Comparison of the six littoridinine genera of Cuatro Ciénegas involving 36 characters. *Pal.* = *Paludiscala*, *Coah.* = *Coahuilix*, *Cochl.* = *Cochliopina*, *Mexith.* = *Mexithauma*, *Dur.* = *Durangonella*, *Mexip.* = *Mexipyrgus*.

Character	<i>Pal.</i>	<i>Coah.</i>	<i>Cochl.</i>	<i>Mexith.</i>	<i>Dur.</i>	<i>Mexip.</i>
Shell						
1. Shape:	3	0	0,1	1	3	2
a) planispiral (0)						
b) trochoid-globose (1)						
c) ovate-conic (2)						
d) turritiform (3)						
2. Sculpture:	0,2	2	1	1	2	0,1
a) ribs (0)						
b) spiral cords (1)						
c) absent (2)						
3. Apical whorl microsculpture:	0	0	0	1	1	1
a) pitted (0)						
b) absent (1)						
4. Shell with periostracal bands (0,1)	0	0	1	1	0	1
5. Shell aperture flared (0, 1)	0	1	0	0	0	0
External Features						
6. Tentacle ciliation:	1	0	2	2	1	0
a) absent (0)						
b) <i>Hydrobia</i> -like (1)						
c) <i>Spurwinkia</i> -like (2)						
7. Snail blind, unpigmented (0,1)	1	1	0	0	0	0
8. Mantle edge papillate (0, 1)	0	0	0	1	0	0
9. Position of operculum nucleus along long axis:	1	1	1	1	0	0
a) <0.30 (0)						
b) ≥0.30 (1)						
Digestive System						
10. Digestive gland tubercles as low swellings (0, 1)	1	1	0	0	0	0
11. Intestine with anterior loop (0, 1)	0	1	0	0	0	0
12. Caecal chamber extends posterior to stomach (0, 1)	0	0	1	1	1	1
13. Origin of basal cusps of central tooth of radula:	1	0	1	1	1	1
a) from face of tooth (0)						
b) from lateral angles (1)						
Male Reproductive Anatomy						
14. Male gonad morphology:	2	2	0	1	0	0
a) simple lobes (0)						
b) bush-like (1)						
c) non-lobed mass (2)						
15. Seminal vesicle coils on stomach (0, 1)	0	1	0	0	0	0
16. Prostate posterior to end of mantle cavity (0, 1)	0	1	0	0	0	0
17. Penis with slender penial filament (0, 1)	0	1	1	1	0	0
18. Penial lobe(s):	1	1	0	0	2	2
a) absent (0)						
b) bulb-like (1)						
c) simple (2)						
19. Penis ciliated (0, 1)	0	0	0	0	1	1
20. Penis with terminal eversible papilla (0, 1)	1	0	0	0	1	1
21. Penis with specialized gland(s) (0, 1)	1	1	0	0	1	1

TABLE 53 (Continued)

Character	Pal.	Coah.	Cochl.	Mexith.	Dur.	Mexip.
Female Reproductive Anatomy						
22. Female gonad overlaps stomach (0, 1)	0	1	0	0	0	0
23. Female gonad:	1	1	0	2	2	0
a) relatively large, lobed (0)						
b) relatively large, nonlobed (1)						
c) relatively small, a mere thickening of oviduct (2)						
24. Reproductive mode:	0	0	1	1	1	1
a) oviparity (0)						
b) ovoviviparity (1)						
25. Length of pallial oviduct/length of body:	0	0	1	1	1	1
a) <0.30						
b) ≥0.30						
26. Length of bursa/length of pallial oviduct:	2	1	0	0	0	1
a) <0.20 (0)						
b) ≥0.20 <0.40 (1)						
c) ≥0.40 (2)						
27. Albumen gland:	0	0	1	1	2	2
a) normal size (0)						
b) reduced in size (1)						
c) very reduced in size (2)						
28. Posterior pallial oviduct:	0	0	1	1	1	2
a) with bend (0)						
b) with simple bend (1)						
c) with complex bend in more than one plane (2)						
29. Normal seminal receptacle present (0, 1)	0	0	1	1	1	1
30. Secondary seminal receptacle present (0, 1)	1	0	0	0	0	0
31. Oviduct without coil (0, 1)	1	1	0	0	0	0
32. Spermathecal duct:	0	0	1	0	0	1
a) long (0)						
b) short (1)						
33. Of ovoviviparous taxa, anterior end of pallial oviduct:	—	—	1	1	0	0
a) with slight muscular coil (0)						
b) with well-developed muscular coil (1)						
34. Of taxa with a normal seminal receptacle, the seminal receptacle opens into:	—	—	0	0	1	1
a) the oviduct directly (0)						
b) the oviduct via a sperm duct (1)						
35. Of taxa with a normal seminal receptacle, the length of the seminal receptacle/length of bursa:	—	—	1	2	1	0
a) <0.30 (0)						
b) ≥0.30 <0.50 (1)						
c) ≥0.50 (2)						
36. Of taxa with a long spermathecal duct, the openings of the spermathecal duct and pallial oviduct are:	1	0	—	2	0	—
a) separate (0)						
b) joined (1)						
c) separate, but with an open channel between them (2)						

TABLE 54. A matrix of percent difference between pairs of the 6 littoridinine genera from Cuatro Ciénegas (based on data from Table 53).

	<i>Paludiscala</i>	<i>Coahuilix</i>	<i>Cochliopina</i>	<i>Mexithauma</i>	<i>Durangonella</i>	<i>Mexipyrus</i>
<i>Paludiscala</i>	—	41	69	73	59	67
<i>Coahuilix</i>		—	77	82	82	84
<i>Cochliopina</i>			—	19	43	44
<i>Mexithauma</i>				—	44	53
<i>Durangonella</i>					—	29
<i>Mexipyrus</i>						—

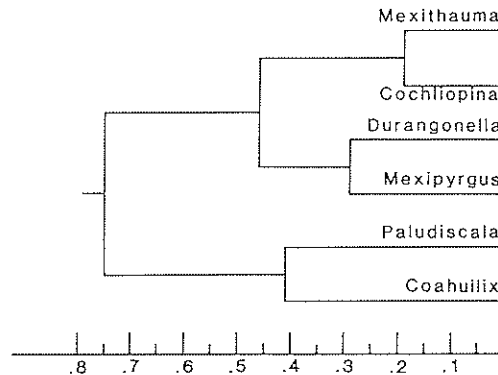
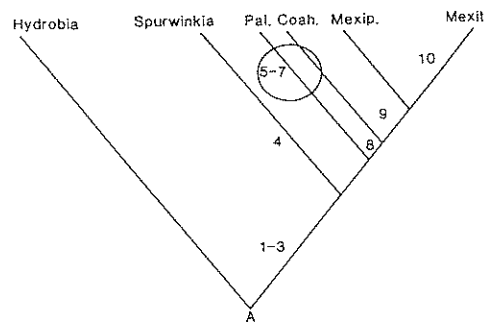


FIG. 49. Phenogram based on distance values derived from Tables 53 and 54.

FIG. 50. Cladogram based on character-states listed in Table 55. Pal. = *Paludiscala*, Coah. = *Coahuilix*, Mexip. = *Mexipyrus*-*Durangonella* group, and Mexit. = *Mexithauma*-*Cochliopina* group. *Paludiscala* and *Coahuilix* share character-states 5-7 (hence the circle enclosing both taxa).

difference. This group links with the other four genera at 75% difference.

An hypothesis of the phyletic relationships among *Hydrobia* (Hydrobiinae), the six Cuatro Ciénegas littoridinine genera, and *Spurwinkia*, the only other North American littoridinine known from entire soft-part anatomy

(see Davis *et al.*, 1982), is shown in Fig. 50. The numbers indicate presumed derived character states, listed in Table 55, used to define clades. Several of these character states, relating to the female reproductive system, are illustrated in Fig. 51. "A" represents an hypothetical ancestral hydrobiid, with the female reproductive anatomy of *Hydrobia*.

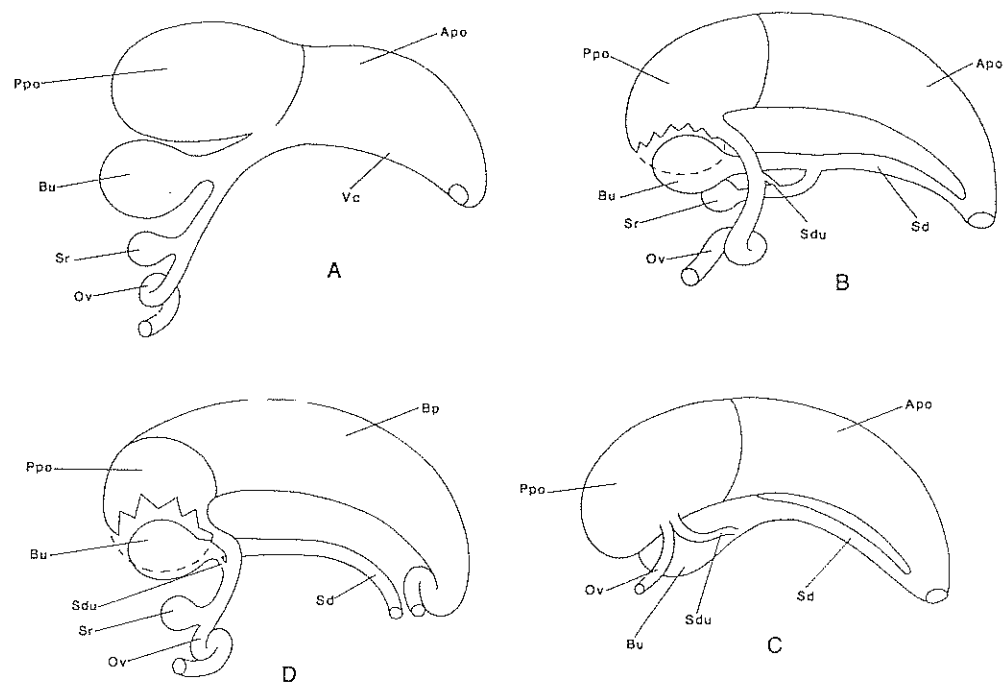
In *Hydrobia* (Fig. 51A), sperm pass along the ciliated ventral channel of the pallial oviduct, which connects with the lumen of the pallial oviduct via a narrow slit. The ventral channel bifurcates at the posterior end of the mantle cavity; one branch leads to the bursa and the other is the anterior end of the oviduct. This groundplan of the female reproductive system is found in all Hydrobiinae, Nymphophilinae and Lithoglyphinae (Davis *et al.*, 1982).

Davis *et al.* (1982) suggest that *Spurwinkia* (Fig. 51B) evolved from an ancestor with an *Hydrobia*-like female reproductive system by having the ventral channel close off and partly separate from the pallial oviduct (character state 1). As the eggs need to reach the albumen gland, a connection to the albumen gland from the oviduct formed (character state 2); and the duct from that point to the duct of the bursa became an extension of the duct of the seminal receptacle (character state 3). The ventral channel is only partly separated from the pallial oviduct, suggesting that *Spurwinkia* is only a step removed from a snail with an *Hydrobia*-like female reproductive system. *Spurwinkia* has the additional derived feature of holding egg capsule chains in the anterior end of the capsule gland (character state 4).

While in *Paludiscala* the ventral channel is still only partly separated from the pallial oviduct, in *Coahuilix* the channel has separated entirely and constitutes a spermathecal duct (character state 8). *Coahuilix* and *Paludiscala*

TABLE 55. Presumably derived character states serving to define clades as shown in Fig. 50.

1. Partial separation of the ventral channel from the pallial oviduct.
2. The oviduct enters the posterior portion of the albumen gland.
3. The duct of the seminal receptacle elongates, connecting to the duct of the bursa. A sperm duct connects the oviduct with the duct of the seminal receptacle.
4. Egg capsule chains are retained within the anterior end of the capsule gland.
5. Loss of eyes and pigment.
6. Loss of oviduct coils.
7. Loss of seminal receptacle.
8. Complete separation of the ventral channel from the pallial oviduct, forming a spermathecal duct.
9. Assumption of ovoviviparity: the anterior pallial oviduct is enlarged and modified into a thin-walled brood pouch, with the albumen gland reduced in size, and with the development of a muscular sphincter at the anterior end of the brood pouch.
10. Shift of ducting: the duct of the seminal receptacle shortens to open directly into the oviduct, and a short duct forms between the bursa (or duct of the bursa) and oviduct.

FIG. 51. Schematic drawings of the female reproductive morphologies of *Hydrobia* (A), *Spurwinkia* (B), *Coahuilix* (C), and *Mexithauma* (D). Lettering as on earlier figures.

are considered closely related and specialized; the evolution of these taxa has involved loss or reduction of morphological features, either associated with the very small size of the snails (character states 6, 7) or associated with the unusual groundwater habitat shared by these taxa (character state 5). Hydrobioid snails with a presumed groundwater

habitat are known from many parts of the world and are frequently small-sized, blind, and without body pigment (Boeters, 1979; Climo, 1974; Ponder, 1966). The bursa copulatrix complex of *Paludiscala* and *Coahuilix* (Fig. 51C) could have been derived from that of *Spurwinkia* by loss of the seminal receptacle and elongation of the sperm duct so as to

connect with the oviduct at the opening into the albumen gland.

The remaining four littoridinines of Cuatro Ciénegas all have the female reproductive anatomy modified as the result of the assumption of ovoviviparity (character state 9). In the *Mexipyrus-Durangonella* group, the organization of the bursa copulatrix complex is basically as in *Spurwinkia*: a short sperm duct connects the duct of the seminal receptacle with the oviduct.

In the *Mexithauma-Cochliopina* group ducting is different: the seminal receptacle opens directly into the oviduct and a short duct connects the bursa (*Cochliopina*) or duct of the bursa (*Mexithauma*, Fig. 51D) and the oviduct. These taxa share a puzzling mosaic of character states: while the opening of the seminal receptacle directly into the oviduct is also seen in *Hydrobia* (but not *Spurwinkia*; see above) and is arguably a primitive character state suggesting a close relationship among these taxa, the spermathecal duct is entirely separate from the pallial oviduct, a derived character state indicating that *Mexithauma* and *Cochliopina* evolved from a *Spurwinkia*-like intermediate. It seems probable that the opening of the seminal receptacle directly into the oviduct, within the littoridine groundplan, is a derived condition and convergent with that of *Hydrobia*. Note that, among littoridinines, this condition has only been found in *Mexithauma* and *Cochliopina*, whereas in other littoridinines from various parts of the world for which the anatomy has been studied, the seminal receptacle connects with the oviduct via a sperm duct (Davis *et al.*, 1982). The latter, more widespread condition is probably the primitive one. The condition seen in *Mexithauma* and *Cochliopina* could have been derived from that of *Spurwinkia* by a shortening of the duct of the seminal receptacle, so as to open into the oviduct, and the development of a duct from the oviduct to the bursa or duct of the bursa (character state 10).

Character states from the female reproductive system have been emphasized in the phyletic analysis because of the complexity of the system (relative to other organ systems in hydrobioid snails), with several organs and ducts functionally organized to receive and hold sperm, fertilize eggs, and provide passage for the eggs or embryos through the pallial oviduct. Precise convergences should be unlikely in such a system. Yet the phyletic analysis indicates that, with the present data

base, character states from the female reproductive system cannot always be confidently scored as primitive or derived; the hypothesized phylogeny is therefore tentative. Anatomical data are needed for more taxa to refine the phyletic analysis. If, for instance, littoridine taxa are found that have the seminal receptacle opening into the oviduct as in *Mexithauma* and *Cochliopina*, but also with the ventral channel only partly separated from the pallial oviduct (as in *Spurwinkia*) then a rearrangement is suggested so that *Mexithauma* and *Cochliopina* are placed closer to "A" than *Spurwinkia*.

Convergence is not entirely unknown among features of the female reproductive system of hydrobioid snails: the Pomatiopsidae and Littoridininae both have spermathecal ducts, but of separate ontogenetic origins. The duct of the Pomatiopsidae forms as a bud from the bursa (Davis *et al.*, 1976) while that of the Littoridininae presumably forms as the ventral channel closes off and separates from the pallial oviduct (Davis *et al.*, 1982). The organization of the bursa copulatrix complex of *Mexithauma* (Fig. 30B) is, in fact, virtually identical to that of *Pomatiopsis* (Davis, 1967, pl. 8). This must be because of convergence, as *Mexithauma* lacks the following diagnostic pomatiopsine features: eyes in pronounced swellings at the bases of the tentacles, presence of a pedal crease and suprapedal fold, and basal cusps arising from the face of the central tooth of the radula (Davis, 1979). Character states involved with brooding young are unreliable, in themselves, for defining clades as the evolution of ovoviviparity involves simple, functionally correlated morphological changes (see below), and has occurred iteratively among many groups of gastropods (Fretter & Graham, 1962). Among hydrobioids, ovoviviparity has evolved at least twice: in the littoridinines and in *Potamopyrgus* which have an *Hydrobia*-like female reproductive system (Fretter & Graham, 1962, fig. 186H). Other characters whose character states could be scored as primitive or derived with even less confidence, and hence were excluded from this analysis, include penial form and gland type, length of the spermathecal duct, and tentacle ciliation pattern.

The data (summarized in the phenogram and cladogram) suggest a polyphyletic origin for the endemic hydrobiids of Cuatro Ciénegas. Of the five endemic genera, each of three (*Nymphophilus*, *Mexithauma*, *Mexipyrus*) is more similar to a non-endemic genus

found in the basin than to the other endemic taxa, suggesting that the endemic hydrobiid fauna may be comprised of at least four separate lineages.

ORIGIN OF THE ENDEMIC SNAILS OF CUATRO CIÉNEGAS

The idea that the endemic hydrobiids of Cuatro Ciénegas are an ancient fauna, with most taxa not closely related to other hydrobiids of the region, is prevalent in the literature (Minckley, 1969, 1977; Taylor, 1966). This hypothesis is based on the supposed endemism of subfamilies of snails that have diverged from a common ancestor, necessitating an origin dating back to the Tertiary period based on the usual slow rate of freshwater snail evolution (Taylor, 1966). Does information on the geological history of the region, coupled with the (above) results of systematic study of the snails, support this hypothesis?

It is known from study of fossil plants from packrat middens that the Chihuahuan Desert is of recent origin, the change from woodlands to desert having occurred during the past 12,000 years (Van Devender, 1976, 1977; Wells, 1977). There is faunal and structural evidence that a number of internal drainages of the Chihuahuan Desert once integrated with the Rio Grande system, and have since been isolated, perhaps due to decreased discharges associated with recent aridity (Morafka, 1977; Smith, 1981). The fauna of these now-isolated drainages is characterized by relictualism and local endemism (Miller, 1977; Milstead, 1960; Morafka, 1977).

A good summary of the geological history of the Cuatro Ciénegas area and its effects on isolation of the basin drainage is given by Minckley (1969). While it is known that the Sierra Madre Orientale chain began to form in the early Tertiary, the age of the Cuatro Ciénegas Valley is unknown. It is known, from a study of pollen from cores taken from the valley, that aquatic environments have existed in the valley for at least 40,000 years (Meyer, 1972, 1973). The basin waters have had past connections with the Rio Grande drainage via the Rio Salado de Nadadores, which heads just east of the valley. The fish fauna of Cuatro Ciénegas has numerous Rio Grande elements (Minckley, 1977). Of the snails, *Cochliopina riograndensis*, a species with a Rio Grande distribution, is found in the

basin; and *Nymphophilus*, one of the endemic genera, has been found as a fossil from Pleistocene-Holocene deposits alongside the Rio Monclova (a Rio Grande tributary), 70 km east of Cuatro Ciénegas (J. Landye, personal communication, 1981). Waters from the southern Rio Nazas-Aguanaval system may have also connected with the Cuatro Ciénegas drainage in the past (Conant, 1977; Minckley, 1969). Two of the non-endemic genera of the basin, *Durangonella* and *Mexistibolia*, are known from the Rio Nazas-Aguanaval drainage, but not the Rio Grande.

The above evidence, suggesting that the waters of the basin have had a recent connection to outside drainage, coupled with the discovery of a lower level of endemism than once thought, with no endemic subfamilies and three of five endemic genera closely resembling non-endemic taxa found in the basin, suggests that the endemic snails may be of a more recent and local origin than previously thought.

The Rio Grande drainage of Texas and Mexico, and other waters of southwest Texas, do harbor littoridinine and nymphophiline taxa. Genera from this area assigned to the Littoridininae, on the basis of a penis with stalked, specialized glands (not glandular ridges), include *Texadina* (penis figured in Andrews, 1977: 82-83), *Littoridinops* (Andrews, 1977: 84), and *Pyrgophorus* (Fullington, 1978, fig. 16). The distinctive penis type shared by *Mexistibolia* and *Nymphophilus*, with an elongate penial filament and small number of glandular ridges, is seen in *Fontelicella* (penis discussed in Gregg & Taylor, 1965; figured in Russell, 1971), recently found in a Rio Grande tributary not far from Cuatro Ciénegas (Lytle, 1972). Anatomical study of the above taxa is needed to help determine the origin of the endemic hydrobiids of Cuatro Ciénegas.

I predict that two of the endemic genera, *Paludiscala* and *Coahuilix*, will eventually be found living in waters outside of the basin (see below for discussion of possible *Coahuilix* from Texas). Mexico is undercollected for fresh-water snails and most workers have not employed the methods necessary to collect tiny snails from groundwater outlets. This prediction is supported by the fact that of the three blind, unpigmented crustacean genera originally described from (and considered endemic to) groundwater outlets in Cuatro Ciénegas, two, *Mexiweckelia* and *Mexistenasellus*, were later dis-

covered in cave waters in more southerly parts of Mexico (Argano, 1974; Holsinger, 1973; Magniez, 1972). The discovery of *Orygoceras* (?) sp., previously known from a single spring in southwest Texas, in Cuatro Ciénegas further attests to the potential for a widespread distribution of groundwater-dwelling taxa.

Of the other three endemic genera, one, *Nymphophilus*, may be relict as it has been found fossilized outside the basin, and the other two could have evolved in the basin from the non-endemic taxa that they closely resemble. It is now known that the rate of evolution of fresh-water snails can be quite rapid (Davis, 1979, 1981; Stanley, 1979) and thus one need not invoke an ancient origin for these endemic genera.

The amount of differentiation seen among the snail genera of the basin is slight (only 12 species are known); no genus has more than two species, and only one genus has sympatric congeners. Such minimal differentiation does not support the idea of an ancient snail fauna present in the basin for tens of millions of years, although perhaps in even such a long time span one would not expect great differentiation in so small a basin with apparently plastic drainage patterns.

Members of the endemic Cuatro Ciénegas snail fauna have been linked with those of two other faunas and these possibilities are now discussed. Numerous peculiar-shelled snail taxa have been described from the Pliocene Pebas and other formations from the Upper Amazon Valley in Peru (Boettger, 1878; Conrad, 1871, 1874a, b; Gabb, 1869; de Greve, 1938; Pilsbry, 1944). Some of these taxa have not only been placed in the Hydrobiidae, but have also been considered closely related to some of the Cuatro Ciénegas endemic taxa (Kadolsky, 1980; Parodiz, 1969). These taxa include *Tropidebora* (Pilsbry, 1944), similar to *Nymphophilus*; and *Eubora* Kadolsky, 1980 (= *Ebora* Conrad, 1871), similar to *Mexithauma*. However, examination of types of the Pebas taxa shows that they cannot be hydrobiids as they have a siphonal notch (Fig. 52), or an otherwise peculiarly-angled aperture unknown in living hydrobiids. Similarities between Pebas and Cuatro Ciénegas taxa must therefore be due to convergence.

The Edwards Aquifer in southwest Texas harbors one of the world's most diverse subterranean aquatic faunas (Longley, 1981). Included in this fauna are a number of tiny, blind, unpigmented snails (Karnei, 1978) in-

cluding species with lamelliform costae on the shell that were assigned to *Paludiscala* (Fullington, 1978, fig. 17). Alcohol specimens of these species, stored at Southwest Texas State University, were studied during January, 1982. These snails differ from *Paludiscala* in at least seven features, with the female reproductive anatomy still unstudied: 1) the shell is much smaller (length 1.1 mm) and has only 3.3–3.5 whorls; 2) strong spiral lines, not seen in *Paludiscala*, run between the costae (Fullington, 1978, fig. 17); 3) the aperture is greatly flared all around; 4) the operculum has a slight internal swelling or peg, not known for any other North American hydrobioid; 5) the intestine has an anterior loop; 6) the penis has neither lobes nor specialized glands; 7) there is no ctenidium. These differences rule out there being *Paludiscala*. The shell of these snails is much more similar to that of *Lanzaia* Brusina, 1906 (figured in Bole, 1970, fig. 6), a European hydrobiine.

While *Paludiscala* may not exist in the waters of the Edwards Aquifer, it is possible that *Coahuilix* does. The type of *Horatia micra* (Pilsbry & Ferriss, 1906), described from stream drift (probably washed out of a spring) of the Guadalupe River, New Braunfels, Texas, is remarkably similar to *Coahuilix hubbsi*, with similar slight apertural flaring. *Horatia micra* is also reported from the artesian well at San Marcos, Texas, and a subterranean stream in Manitou Cave, near Fort Payne, Alabama (Hubricht, 1940). Undescribed *Horatia* are reported from Salamander Cave, Travis County, Texas (Reddell, 1965) and Roaring Springs, Real County, Texas (Taylor, 1974).

EVOLUTION OF OVOVIVIPARITY IN HYDROBIOID SNAILS

It has been suggested that the initial step in the evolution of ovoviviparity in hydrobioid snails involves a simple morphologic change: separation of the ventral channel from the pallial oviduct to form a spermathecal duct, thus keeping separate the functions of receiving sperm and storing embryos (Davis *et al.*, 1982). The need for such a prerequisite is suggested by there being numerous taxa worldwide which lack this separation, only one (*Potamopyrgus*) is known to brood young. *Spurwinkia* and *Littoridinops* are apparent intermediates in the evolution of

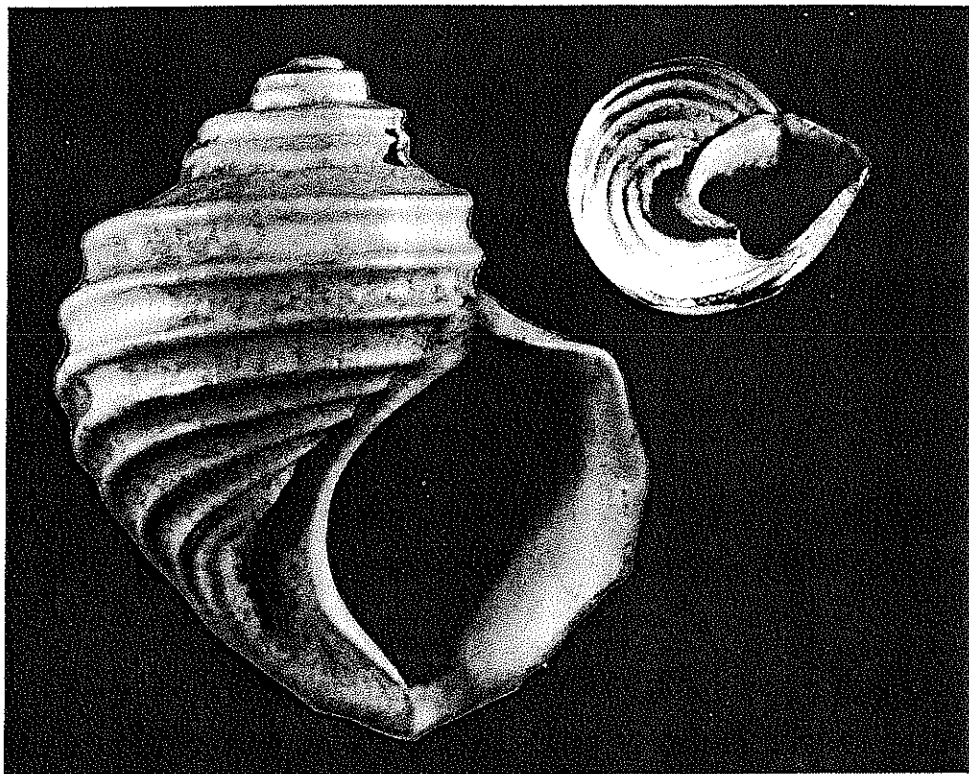


FIG. 52. Holotype (NYSM 9193) of *Eubora bella* (Conrad, 1871). The shell is 7.58 mm long. Note the siphonal notch in the basal view (lower magnification).

ovoviviparity, as they have spermathecal ducts (although that of the former is still connected anteriorly to the pallial oviduct) and, while they do not brood young, they hold egg capsules in the anterior end of the pallial oviduct before depositing them on the substrate (Davis *et al.*, 1982). The littoridinines of Cuatro Ciénegas include taxa that have further modification of the female reproductive system associated with the assumption of ovoviviparity.

Of the six littoridinine taxa of Cuatro Ciénegas, two, *Coahuilix* and *Paludiscala*, are egg layers, but do not hold egg capsules in the anterior pallial oviduct. The other four share features associated with the evolution of ovoviviparity from a *Spurwinkia*-like condition. All have an enlarged pallial oviduct (to 58% of the body length; for *Spurwinkia* it is 40%, Davis *et al.*, 1982) that often overlaps part of the stomach, and that bends posteriorly to varying degrees (*Spurwinkia* has a slight pos-

terior bend of the pallial oviduct). *Mexipyrus* represents the pinnacle of this trend as the length of the brood pouch is vastly increased by a series of coils that are progressively dorsal to one another. Whereas egg laying hydrobioids have a thick walled, glandular pallial oviduct with a slit-like central lumen, the ovoviviparous littoridinines all show at least some reduction in the size of the albumen gland, with the other (much larger) section of the pallial oviduct modified into a thin-walled, non-glandular brood pouch. These features collectively increase the amount of space available in the pallial oviduct for holding embryos. In addition, all of these taxa have the anterior end of the brood pouch muscularized, giving it the ability to stretch as large sized embryos are released, and perhaps the ability to control timing of embryo release. Ovoviviparous snails may not need great egg production at any one time and this may explain why female gonads of three of

the four ovoviviparous taxa are unusually small, filling only a portion of the length of the digestive gland at all times of the year.

The ovoviviparous Cuatro Ciénegas hydrobiids appear to represent two different brooding strategies, each represented by two taxa of the same clade. *Cochliopina* and *Mexithauma* brood a relatively large number of similar-sized embryos, with only a two- and four-fold range in embryo shell lengths, respectively. *Durangonella* and *Mexipyrgus* brood relatively fewer young with a greater (five- and eight-fold, respectively) range of embryo shell lengths. The latter two genera, perhaps holding embryos for long time periods (hence the great range in embryo shell lengths), may require a very long brood pouch, and they do, in fact, have a greater complexity of pallial oviduct coiling than the other two genera. It is not known why the anterior end of the brood pouches of *Cochliopina* and *Mexithauma* is much more reflected and muscularized than in *Durangonella* and *Mexipyrgus*: the former two taxa do not release relatively large young, but perhaps they release numerous young at the same time, necessitating greater stretching of the brood pouch.

Thus the evolution of ovoviviparity in these littoridinines has involved modifications of the female reproductive anatomy to increase the amount of space available for holding embryos, and to allow and control the release of large-sized embryos. Some of these brooding features parallel those described for other fresh-water gastropods. The two brooding strategies outlined above were described for species of the cerithiacean *Semisulcospira* (Davis, 1969b). The great development of posterior pallial oviduct coiling in *Mexipyrgus*, while unique among hydrobioid snails, is paralleled by that seen in several Viviparidae (Rohrbach, 1937).

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APPENDIX 1

Collection localities for this study. Localities 1-100 are shown in Fig. 3. 1. Laguna Churince (southernmost of the three Posos Bonitos), 19.5 km SSW of Cuatro Ciénegas along the highway. 2. small seep feeding the middle of the three Posos Bonitos. 3. Rio Churince, 100 m downstream from Laguna Churince. 4. Rio Churince, wide pool area, 1000 m downstream from Laguna Churince. 5. Rio Churince, very large pool area due E of Laguna Grande. 6. Small pool at NW edge of (5). 7. Small pool in marshy area, N of (5). 8. Small pool in marshy area, W of (7). 9. Laguna Grande, playa lake terminus of Rio Churince. 10. Posos de la Becerra, 4 km S of the tip of Sierra de San Marcos along the highway. 11. Stream from cool springs at Los Chiceros. 12. Small spring feeding stream at Los Chiceros. 13. Stream at Los Chiceros, below warm water inflow from canal from Posos de la Becerra. 14. Small spring, 2.24 km S of tip of Sierra de San Marcos along the highway, at SE corner of the springfield. 15. Small spring, 3 m W of (14), feeding same stream. 16. Small spring, 40 m N of (14). 17. Small spring, 146 m N of (16). 18. Large

spring, 130 m N of (17). 19. Large spring, just W of marsh terminus of (18). 20. Large spring, 10 m W of (19). 21. Large spring, 25 m NW of (20). 22. Juan Santos Laguna, NW of (21). 23. Small spring, 62 m N of (18). 24. Small springhole (no outflow), 370 m NNE of (23). 25. Small spring, 52 m NNW of (24). 26. Small spring, 88 m N of (25). 27. Small spring, 165 m NNW of (26). 28. Small spring at SE corner of vegetated area, 24 m N of (27). 29. Small spring (flowing N), about 300 m W of (28). 30. North Spring, 960 m S of tip of Sierra de San Marcos along the highway. 31. Small spring, 57 m W of (30). 32. Small spring, 27 m N of (31). 33. Small spring, 54 m N of (32). 34. Small spring, 60 m NW of (33). 35. Small spring, 328 m N of (30). 36. Small spring, 300 m NW of (22). 37. Large cold spring, 800 m S, 1 km N of tip of Sierra de San Marcos. 38. Large cold spring, about 50 m W of (37). 39. Small spring hole (no outflow), 10 m S of (38). 40. Small spring, 800 m S, 1.6 km W of tip of Sierra de San Marcos. 41. Large spring, 800 m S, 1.25 km W of tip of Sierra de San Marcos. 42. Large spring, due W of junction of streams from (41) and (43). 43. Large spring, 800 m S, 1.22 km W of tip of Sierra de San Marcos. 44. Rio Garabatal, due W of (42). 45. Small spring, due W of (42). 46. Large spring, 230 m NE of (43). 47. Small spring, just W of marsh terminus of (46). 48. Large spring, 800 m S, 400 m W of tip of Sierra de San Marcos. 49. Large spring, 700 m S of tip of Sierra de San Marcos along the highway. 50. Rio Mesquites, 200 m upstream from junction with springs from the west. 51. Small spring, 100 m S of Rio Mesquites at house of Tierra Blanca. 52. Small spring, just N of highway, 320 m NE of tip of Sierra de San Marcos. 53. Rio Mesquites at the highway, 9.3 km SSW of Cuatro Ciénegas. 54. Rio Mesquites, where small marshy stream branches off the Mojarral area. 55. Small stream branching from (54), due E of (76). 56. Small spring, 320 m S of Rio Mesquites at the highway. 57. Small spring, 370 m S of tip of Sierra de San Marcos along dirt road on the east side. 58. Small spring, due E of (59). 59. Small spring, due E of (60). 60. Small spring, 670 m S of tip of Sierra de San Marcos along dirt road. 61. Small spring, due E of (62). 62. Small spring, 150 m NE of (63). 63. Large spring, 1.12 km S of tip of the Sierra de San Marcos along dirt road. 64. Small spring, 40 m S of (63). 65. Small spring, 72 m S of (64). 66. Small spring, 60 m S of (65). 67. Small spring, 1.4 km S of tip of Sierra de San Marcos along dirt road. 68. Small spring, 1.6 km S of tip of Sierra de San Marcos along dirt road. 69. Small spring, due W of (70). 70. Large spring, 400 m E, 60 m S of (68). 71. Stream from (70), 130 m above marsh. 72. Small spring, 2.7 km S of tip of Sierra de San Marcos along dirt road. 73. Mojarral West Laguna, about 200 m N of (76). 74. Stream draining marsh due W of (73). 75. Stream draining (73). 76. Mojarral East Laguna, 10.2 km S of Cuatro Ciénegas along the highway, 1.4 km S of highway. 77. Small spring, feeding SW corner of (76). 78. Pools 30 m downstream from (55). 79. Large spring, 2.4 km S of tip

of Sierra de San Marcos along dirt road, 900 m E of road. 80. Large spring (receiving flow from 79), 100 m S of (79). 81. Los Remojos, northern spring, 500 m S of (80). 82. Los Remojos, middle spring. 83. Los Remojos, southern spring. 84. Los Remojos, large pool receiving inflows from (81), (82), and (83). 85. Large spring, 1.2 km S of (83). 86. Large spring, 400 m S of (85). 87. Large spring, 115 m SE of (86). 88. Large spring, about 1.2 km S of (86). 89. Large spring, about 100 m S of (88). 90. Large spring, 60 m SW of (89). 91. Large spring, 200 m S of (90). 92. Large spring, about 200 m N of (95). 93. Large spring, due E of (90). 94. Large spring, due SE of (98). 95. Laguna Escobedade, 6.72 km S of tip of Sierra de San Marcos along dirt road, 1 km E of road. 96. Large spring, 6.9 km S of tip of Sierra de San Marcos along dirt road. 97. Laguna Tio Candido, 9.3 km S of tip of Sierra de San Marcos along dirt road. 98. Large spring, 10.7 km S of tip of Sierra de San Marcos along dirt road. 99. Laguna Anteojo. 100. Smaller spring, due W of (99). 101. Santa Tecla Laguna (= La Tecla), 22.2 km S of tip of Sierra de San Marcos along dirt road, 1.6 km SE of road. 102. Spring alongside the Rio Salado de Nadadores, 3.04 km N of Sacramento, Coahuila. 103. Rio Salado de Nadadores, at Carino de la Montana, 3.84 km E of Sacramento, Coahuila.

APPENDIX 2

The material collected by the author and examined during this study is listed below by species. For each species, the lots are listed in order of locality number (1-103), with the catalog numbers and dates of collection following. All of the material is deposited in the Department of Malacology at the Academy of Natural Sciences of Philadelphia (ANSP). The initial letter A refers to specimens in alcohol. Other catalog numbers refer to dry shell lots.

1. *Nymphophilus minckleyi*. 1: A9879-A, 23 Mar. 1979; A9879-E, 17 Dec. 1981; A9878-I, 19 Dec. 1981. 3: A9878-G, 23 Mar. 1979. 5: A9879-B, 16 May 1980. 10: A9878-H, 4 Aug. 1979. 13: A9877-B, 2 June 1979; A9878-A, 17 Nov. 1980; A9878-E, 9 Feb. 1981. 18: A9878-D, 13 June 1979. 30: A9878-F, 9 Apr. 1979. 37: A9878-B, 11 July 1980. 38: A9877-C, 12 Apr. 1979; A9877-F, 18 July 1980. 40: A9877-A, 27 May 1981. 41: A9879-G, 17 Feb. 1981. 42: A9879-D, 10 Apr. 1981. 43: A9878-C, 8 July 1979. 53: 355196, A9877-D, 26 July 1979; A9876, 23 Apr. 1979. 64: A9879-F, 4 June 1981. 71: A9879-C, 1 May 1981; A9879-H, 12 Dec. 1981. 76: A9877-H, 7 May 1979; 355197, A9877-E, 7 Apr. 1981. 79: A9877-G, 3 Apr. 1979. 97: 355195, A9879-J, 21 May 1979.

2. *Nymphophilus acarinatus*. 98: holotype: 355255, 20 Dec. 1981; paratypes: 355256, 20 Dec. 1981. 101: A9929-B, 13 July 1980; A9929-C, 28 May, 1981.

3. *Mexistiobia manantiali*. 14: A9888-E, 25 Nov.

1980. 16: A9887-B, 11–14 June 1979; A9886-K, 5 June 1980; A9888-J, 27 Nov. 1980. 17: A9887-L, 7 Dec. 1980. 25: A9887-G, 11 Feb. 1981. 27: A9888-I, 14 Feb. 1981. 28: A9887-L, 17 Jan. 1981. 29: A9888-B, 7 Apr. 1979. 31: A9887-A, 18 May 1981. 36: A9887-K, 20 June 1981. 38: A9886-I, 8 Jan. 1981; A9887-H, 16 Jan. 1981; A9887-F, 5 Feb. 1981. 43: A9886-M, 13 July 1979. 51: holotype: 355205, 13 July 1979; paratypes: A9887-D, 20 Apr. 1979; 355204, A9888-L, 13 July 1979. 52: A9886-D, 21 June 1981. 57: A9886-C, 15 June 1981. 59: A9886-B, 19 June 1981. 64: A9886-N, 31 May 1979; A9887-E, 30 May 1981; A9886-G, 4 June 1981; A9886-L, 21 June 1981. 65: A9886-H, 31 May 1979; 355206, A9888-F, 28 Apr. 1981. 67: A9886-F, A9887-J, 30 Apr. 1981. 68: A9889-K, 2 May 1981. 72: A9887-C, 19 May 1979. 74: A9888-C, 5 Apr. 1980. 77: A9886-J, 16 June 1981.

4. *Coahuilix hubbsi*. 16: A9892-A, 11–14 June 1979; A9892-M, 5 Jan. 1980; A9882-H, 27 Nov. 1980. 18: A9892-C, 19 Dec. 1981. 24: A9892-J, 14 Dec. 1981. 31: A9892-D, 18 May 1981. 33: A9892-B, 21 May 1981. 35: 355210, 9 May 1981. 38: A9893-C, 8 Jan. 1981. 58: A9892-N, 17 Jan. 1981. 61: A9892-I, 18 June 1981. 64: A9893-B, 26 Apr. 1981; A9892-G, 4 June 1981; A9892-K, 21 June 1981; A9892-E, 13 Dec. 1981. 66: A9892-L, 28 Apr. 1981. 67: 355209, A9893-A, 30 Apr. 1981. 68: A9892-F, 1 May 1981.

5. *Coahuilix landyei*. 16: A9894-M, 27 Nov. 1980. 17: A9894-I, 10 June 1979. 24: A9894-A, 13 Feb. 1981. 28: A9894-L, 7 Apr. 1979; A9894-C, 17 Jan. 1981. 31: A9894-F, 18 May 1981. 38: A9894-E, 8 Jan. 1981. 59: A9894-H, 19 Jan. 1981. 63: A9894-K, 16 Apr. 1981. 64: holotype: A9894-N, 29 Apr. 1981; paratypes: 355211, 27 Apr. 1981. 65: A9894-B, 26 Apr. 1981. 61: A9894-J, 30 Apr. 1981. 69: A9894-G, 6 May 1981.

6. *Cochliopina milleri*. 36: A9884-E, 5 Feb. 1981. 38: A9884-J, 3 Sept. 1978; A9884-C, 10 Apr. 1981; 355200, A9884-K, 5 Jan. 1981. 41: A9884-D, 17 Feb. 1981. 42: A9884-C, 10 Apr. 1981. 43: A9884-B, 8 July 1979. 50: A9884-I, 1 Sept. 1978. 53: A9884-F, 23 Apr. 1979. 55: A9884-G, 7 May 1979. 97: A9884-H, 21 May 1979.

7. *Cochliopina riograndensis*. 101: A9885-D, 10 July 1979; A9885-E, 13 July 1980; 355202, 28 May 1981. 102: 355201, A9885-A, 25 May 1981. 103: A9885-B, A9885-C, 24 July 1979.

8. *Mexithauma quadripaludium*. 1: A9883, 23 Mar. 1979; 355198, A9881-F, 25 Aug. 1980. 10: A9880-E, 9 Apr. 1979; A9881-C, 4 Aug. 1979. 18: A9880-D, 13 June 1979. 20: A9880-G, 20 June 1979. 22: A9880-B, 3 Apr. 1979. 30: A9880-I, 23 Mar. 1979. 42: A9881-E, 10 Apr. 1981. 49: A9881-D, 23 Feb. 1981. 50: A9880-C, 1 Sept. 1978; A9880-F, 26 Feb. 1981. 71: A9880-A, 1 May 1981; A9881-H, 12 Dec. 1981. 76: A9880-H, 9 May 1979; A9882, 26 July 1979; A9881-A, 10 Apr. 1981. 97: 355199, 23 May 1981. 98: A9881-G, 20 Dec. 1981. 99: 355257, 10 Apr. 1981. 100: A9881-B, 10 Apr. 1981. 101: A9880-J, 28 Mar. 1981.

9. *Durangonella coahuilae*. 2: A9922-J, 13 Dec.

1981. 4: A9922-I, 15 May 1980. 5: A9922-G, 16 May 1980; A9924-B, 19 Nov. 1980. 6: A9922-K, 17 May 1980; 355244, A9928-K, 8 Oct. 1980. 7: A9922-H, 20 May 1980. 8: A9922-L, 27 May 1980. 9: A9922-D, 29 Mar. 1979; A9922-B, 16 May 1979; A9922-C, 30 May–10 June 1980; A9922-E, 23 Aug. 1980; A9922-F, 10 Oct. 1980; 355249, 22 Oct. 1980. 12: A9924-L, 19 Dec. 1980. 13: 355250, A9923-B, 13 Nov. 1980. 14: A9923-E, 25 Nov. 1980; 355246, A9928-M, 27 Nov. 1980. 16: A9926-M, 9 June 1979; A9928-J, 27 Nov. 1980; A9925-E, 6 Dec. 1980. 17: A9927-C, A9928-B, 10 June 1979; A9927-K, 7 Dec. 1980. 18: A9923-K, 15 Jan. 1980; A9927-L, 19 Dec. 1981. 23: A9927-A, 8 Feb. 1981; A9927-J, 11 Feb. 1981. 24: A9926-I, 8 Feb. 1981; A9924-I, 13 Feb. 1981; A9928-C, 14 Dec. 1981. 25: A9926-K, 8 Feb. 1981. 26: A9928-H, 14 Dec. 1981. 27: A9927-F, 8 Feb. 1981; A9927-B, 14 Feb. 1981. 28: A9924-N, 7 Apr. 1979; A9926-F, 13 July 1979; A9924-C, 17 Jan. 1981. 29: A9927-D, 14 Feb. 1981. 30: A9925-A, 28 Jan. 1980. 31: A9928-I, 18 May 1981. 35: A9922-A, A9924-G, 9 May 1981. 37: A9926-H, 11 July 1980; A9925-K, 7 Feb. 1981. 38: A9923-D, 15 May, 1979; A9923-F, 18 July 1980; A9924-F, 8 Jan. 1981; 355251, 20 Jan. 1981; A9926-G, 5 Feb. 1981; A9923-C, 5–6 Jan. 1981; A9927-H, 16 Jan. 1981; A9923-H, A9926-J, 6 Feb. 1981. 41: A9925-G, 17 Feb. 1981. 43: A9924-M, 7 July 1979; A9927-I, 13 July 1979; 355245, A9928-L, 17 Feb. 1981. 45: A9926-N, 10 Apr. 1981. 48: A9925-L, 23 Feb. 1981; A9925-J, 5 May 1981. 49: A9925-F, 23 Feb. 1981. 50: A9925-C, A9925-I, 1 Sept. 1978. 51: 355247, A9928-N, 20 Apr. 1979. 52: A9924-D, 21 Jan. 1981. 56: A9928-F, 18 Mar. 1981; A9925-B, 19 Mar. 1981. 58: A9924-A, 17 Jan. 1981. 59: A9923-J, 19 Jan. 1981. 61: A9927-M, 18 Jan. 1981. 62: A9927-N, 15 June 1981. 63: A9926-C, 8 Jan. 1979. 64: A9926-B, A9928-D, 31 May 1979; A9928-A, 21 Jan. 1981; A9926-L, 27 Apr. 1981; A9928-G, 30 May 1981. 65: A9923-A, 22 May 1979; A9924-H, 31 May 1979; 355248, A9923-L, 4 Apr. 1980; A9923-I, 24 July 1980; A9923-J, 1 Oct. 1980. 72: A9927-E, 19 May 1979. 73: 355252, A9926-D, 5 Apr. 1980. 74: A9926-A, 2 May 1979; A9925-H, 12 Apr. 1980. 75: A9925-M, 4 May 1979. 77: A9924-E, 16 Jan. 1981.

10. *Mexipyrgus churinceanus*. 1: A9909-H, 23 Mar. 1979; 355230, 15 Sept. 1980; A9907-I, 20 Sept. 1980; A9909-I, 13 Mar. 1981. 5: A9908-I, 16 May 1980; A9907-H, 24 Sept. 1980; 355231, 5 Oct. 1980. 10: A9909-C, A9911-A, 27 Oct. 1980; 344232, 29 Oct. 1980; A9909-D, 31 Oct. 1980. 11: 355233, 2 Nov. 1980; A9901, 10 Nov. 1980. 13: A9911-F, 8 Nov. 1980. 18: 355220, A9912-I, 12 June 1980; 355216, A9912-E, 12 Aug. 1980; A9911-H, 8 Dec. 1980. 19: A9911-J, 10 Dec. 1980. 20: A9910-G, 26 June 1980; 355234, 10 Dec. 1980; A9907-E, 11 Dec. 1980. 21: 355214, A9912-C, 29 Apr. 1981. 22: A9907-B, 3 Apr. 1979; 355241, 16 Dec. 1980; A9907-C, 18 Dec. 1980. 30: A9911-C, 9 Apr. 1979; A9907-F, 20 Aug. 1980; 355222, A9914, 18 Dec. 1980. 37: 355213, A9912-B, 30 Dec. 1980. 38: 355236, 1 Jan. 1981; A9910-H, 5–8 Jan. 1981;

A9911-B, A9911-D, A9911-E, 16 Feb. 1981; A9910-J, 21 May 1981. 43: A9910-J, 7 July 1979; A9911-G, 16 Feb. 1981. 44: A9911-I, 10 Apr. 1981. 46: A9908-J, 19 Feb. 1981; 3553212, A9912-A, 20 Feb. 1981. 47: 355227, 23 Feb. 1981. 48: A9895, 23 Feb. 1981; 355235, 24 Feb. 1981; A9897, 5 May 1981. 49: A9898, 23 Feb. 1981; 355242, 24 Feb. 1981; A9907-G, 5 May 1981. 50: 355218, A9920, 26 Feb. 1981. 53: A9909-E, 23 Apr. 1979; A9909-F, 6 Mar. 1981. 54: A9909-G, 8 Mar. 1981. 65: A9909-A, 31 May 1979. 67: A9910-E, 4 May 1981; A9910-D, 5 May 1981. 70: A9910-F, 1 May 1981; A9909-J, 2 May 1981. 71: A9910-A, 4 May 1979; 355240, A9910-B, 25 Mar. 1981; A9905, 5 May 1981; A9910-C, 4 May 1981; A9907-A, 12 Dec. 1981. 73: 355219, A9912-H, 11 Mar. 1981. 76: A9906, 16 Mar. 1981; 355239, 17 Mar. 1981. 78: A9907-D, 9 Apr. 1981; 355215, A9912-D, 29 Apr. 1981. 79: A9900, 6 May, 1981; 355237, A9908-F, 8 May, 1981. 81: 355223, A9915, 11 May 1981. 82: 355226, A9918, 11 May 1981. 83: A9902, 9 May 1981; 355243, 11 May 1981. 84: A9908-A, 12 May 1981. 85: A9908-C, 14 May 1981. 86: A9896, 14 May 1981. 87: A9909-B, 16 May 1981. 88: 344229, A9921, 17 May 1981. 89: A9908-B, 17 May 1981. 90: 355225, A9917, 17 May 1981. 91: A9908-G, 18 May 1981. 92: A9908-H, 20 May 1981. 93: A9904, 22 May 1981. 94: A9908-E, 22 May 1981. 95: 355221, A9913, 20 May 1981. 96: 355218, A9912G, 20 Dec. 1981. 97: 355224, A9916, 23 May 1981. 98: A9907-J, 20 Dec. 1981. 99: 355217, A9912-F, 10 Apr. 1981. 100: A9908-D, 10 Apr. 1981. 101: A9903, 28 May 1981.

11. *Orygoceras?* sp. 67: 355254, A9929-A, 19 Dec. 1981.

12. *Paludiscala caramba*. 2: A9890-D, 13 Dec. 1981. 16: A9890-K, 11 June 1979; A9890-H, 5 Jan. 1980; A9889-K, 27 Nov. 1980. 17: A9890-J, 10 Jan. 1979. 18: A9891-J, 19 Dec. 1981. 23: A9889-N, A9891-D, 11 Feb. 1981. 24: A9891-H, 13 Feb. 1981; A9889-M, 14 Dec. 1981. 25: A9891-K, 11 Feb. 1981. 26: A9889-G, 14 Dec. 1981. 27: A9891-L, 11 Feb. 1981. 28: A9880-B, 17 Jan. 1981. 31: A9891-E, 11 May 1981. 32: A9890-L, 18 May 1981. 33: A9889-A, 21 May 1981. 35: A9889-I, 9 May 1981. 38: A9880-H, 16 Jan. 1981; A9890-I, 8 Jan. 1981. 56: A9889-L, 18 May 1981. 57: A9890-M, 15 Jan. 1981. 58: A9889-C, 17 Jan. 1981. 59: A9889-E, 19 June 1981. 60: A9889-B, 19 Jan. 1981. 61: A9890-C, 18 Jan. 1981. 62: A9890-A, 15 Jan. 1981. 63: 355207, A98911, 16 Apr. 1981. 64: A9889-J, 31 May 1979; A9889-F, 26 Apr. 1981; A9890-F, 13 Dec. 1981. 65: A9889-H, 31 May 1979; 355208, 24 July 1980; A9891-I, 26 Apr. 1981. 66: A9891-A, 28 Apr. 1981. 67: A9890-E, 30 Apr. 1981. 68: A9891-B, 1 May 1981. 69: A9891-G, 6 May 1981. 72: A9891-F, 19 May 1979.

APPENDIX 3

Fifty-one characters and their character states are used in this study to distinguish between genera and generic groups of Hydrobiidae. To the right are references to publications in which the various character states have been figured. "H" indicates a figure within this paper.

Shell

1. Shell shape:

- a) planispiral
- b) trochoid-globose
- c) ovate-conic
- d) turritiform

H, Figs. 15A–G, I–K
H, Figs. 4, 9, 27
H, Fig. 37
H, Fig. 33

2. Maximum shell dimension:

- a) <2 mm
- b) ≥2 mm <5 mm
- c) ≥5 mm

—
—
—

3. Shell sculpture:

- a) collabral ribs
- b) spiral cords
- c) absent

H, Fig. 19
H, Fig. 27
H, Fig. 32

4. Apical whorl microsculpture:

- a) wrinkled, pitted
- b) absent

H, Fig. 11; Thompson, 1977, fig. 4
H, Fig. 39A

5. Shell with periostracal bands

H, Fig. 37

6. Shell aperture flared

Boeters, 1974, figs. 9–11; Bole, 1970, fig. 6

External features

7. Tentacle ciliation:

- a) absent
- b) *Hydrobia*-like
- c) *Spurwinkia*-like

H, Fig. 40A
Davis, 1966, fig. 2; Hershler & Davis, 1980, fig. 1A
Davis *et al.*, 1982, fig. 5; H, Figs. 29A, B

8. Animal blind, unpigmented

—

9. Mantle edge papillate

H, Fig. 30A, 31A

10. Osphradium elongate (≥ 0.30 of the ctenidium length) Davis & Pons da Silva, 1984, fig. 6
11. Number of operculum whorls:
 a) < 4 H, Fig. 35B
 b) ≥ 4 H, Fig. 5B
12. Position of nucleus of operculum along its long axis:
 a) $< 30\%$ H, Fig. 35B
 b) $\geq 30\%$ H, Fig. 5B
- Digestive system
13. Digestive gland with reduced tubercles H, Fig. 22B
14. Intestine with anterior loop H, Fig. 17C; Boeters, 1974, fig. 3
15. Caecal chamber extends posterior to stomach H, Fig. 7A
16. Origin of basal cusps of central tooth of radula:
 a) from face of tooth H, Fig. 16C; Davis & Pons da Silva, 1984, fig. 14
 b) from lateral angles H, Fig. 28D
17. Number of pairs of basal cusps on central tooth of radula:
 a) 1–2 H, Figs. 12B, C
 b) ≥ 3 H, Fig. 28D
18. Central cusp of lateral tooth:
 a) massive H, Fig. 6B
 b) small H, Fig. 12A
- Male reproductive anatomy
19. Male gonad morphology:
 a) simple lobes Davis & Greer, 1980, fig. 9A
 b) bush-like H, Fig. 31A
 c) single un-lobed mass H, Fig. 17C
20. Male gonad extends onto stomach —
21. Seminal vesicle coiling:
 a) on stomach H, Fig. 17C
 b) posterior to stomach Davis & Greer, 1980, fig. 9A
22. Position of prostate:
 a) entirely posterior to end of mantle cavity H, Fig. 17C; Davis *et al.*, 1982, fig. 14A
 b) overlaps mantle cavity H, Fig. 31A
23. Anterior vas deferens:
 a) exits from anterior tip of prostate H, Fig. 31A
 b) exits from posterior portion of prostate Davis, 1967, pl. 25, fig. 4
24. Penis with slender penial filament H, Fig. 31B
25. Penis ciliated H, Figs. 35D, 44B
26. Penis with terminal eversible papilla H, Figs. 35D, 44A
27. Penial lobe(s):
 a) absent H, Figs. 25D, 31B
 b) bulb-like H, Figs. 17D, 21C
 c) simple H, Fig. 35D
 d) with folds H, Fig. 8A
28. Gland(s) of penis:
 a) absent —
 b) large, specialized H, Figs. 17D, 21C, 44A
 c) small, in glandular ridges H, Figs. 8B, C; Boeters, 1974, figs. 6, 7; Thompson, 1968, figs. 42–47
29. Of snails having glandular ridges on the penis:
 a) < 4 ridges H, Figs. 8B, C, 13D; Thompson, 1977, figs. 5A, 7A, 11C, 13
 b) ≥ 4 ridges Thompson, 1968, figs. 42–47
- Female reproductive anatomy
30. Reproductive mode:
 a) oviparity —
 b) ovoviviparity —

31. Female gonad morphology:
 - a) relatively large, lobed H, Fig. 41A
 - b) relatively large, un-lobed H, Fig. 17B
 - c) relatively small, a mere thickening at end of oviduct H, Fig. 30A
32. Female gonad extends onto stomach H, Fig. 30A
33. Oviduct without coil H, Fig. 17B
34. Length of pallial oviduct/length of body
 - a) <0.30 H, Fig. 17B
 - b) ≥ 0.30 H, Fig. 30A
35. Posterior pallial oviduct:
 - a) without bend H, Fig. 17B
 - b) with short bend H, Figs. 30A, 36A; Davis *et al.*, 1982, fig. 10A
 - c) with long bend, coiling in >1 plane H, Fig. 43
36. Albumen gland:
 - a) normal sized H, Fig. 17B
 - b) reduced in size H, Fig. 26A
 - c) reduced to a glandular smear H, Fig. 36A
37. Of ovoviviparous taxa, capsule gland:
 - a) with 1 tissue region Hershler & Davis, 1980, fig. 2
 - b) with 2 tissue regions H, Fig. 17B
 - c) with 3 tissue regions H, Fig. 22A
38. Length of bursa/length of pallial oviduct:
 - a) <0.20 H, Fig. 30B
 - b) $\geq 0.20 < 0.40$ H, Fig. 17B
 - c) ≥ 0.40
39. Position of bursa:
 - a) posterior to pallial oviduct H, Figs. 7A, B
 - b) overlapped by pallial oviduct H, Fig. 14B
40. Normal seminal receptacle present H, Fig. 7B
41. Secondary seminal receptacle present H, Fig. 22A
42. Of snails with a normal seminal receptacle, the length of the seminal receptacle/length of bursa is:
 - a) <0.30 H, Fig. 42B
 - b) $\geq 0.30 < 0.50$ H, Figs. 26B, C
 - c) ≥ 0.50 H, Fig. 30B
43. Of snails with a normal seminal receptacle, opening of seminal receptacle into:
 - a) oviduct H, Fig. 30B
 - b) sperm duct H, Fig. 42C
44. Of snails with a normal seminal receptacle, the seminal receptacle is:
 - a) overlapped by the bursa H, Fig. 42B
 - b) lateral to the bursa H, Fig. 30B
45. Female with:
 - a) ciliated ventral channel inside the pallial oviduct H, Fig. 7B
 - b) spermathecal duct H, Fig. 30A
46. Of snails with a ciliated ventral channel:
 - a) pallial oviduct opens at anterior tip H, Fig. 14D
 - b) pallial oviduct opens laterally H, Fig. 7E
47. Of snails with a ciliated ventral channel:
 - a) bolster weakly developed H, Fig. 14C
 - b) bolster well-developed H, Fig. 7D
48. Of snails with a spermathecal duct, the duct is:
 - a) long H, Fig. 30A
 - b) short H, Fig. 26A
49. Of snails with a short spermathecal duct, the duct is:
 - a) muscularized H, Fig. 42B
 - b) non-muscularized H, Fig. 26A

50. Of snails with a long spermathecal duct, the openings of the spermathecal duct and pallial oviduct are:
- a) separate H, Figs. 36F, G
 - b) joined H, Fig. 22F
 - c) separate, but with an open channel between them H, Fig. 30E
51. Of ovoviviparous snails, the anterior pallial oviduct has:
- a) a slight muscular loop H, Fig. 41B
 - b) a well-developed muscular loop H, Fig. 26E

