

THE HYDROBIID SNAILS (GASTROPODA: RISSOACEA) OF THE CUATRO CIENEGAS BASIN: SYSTEMATIC RELATIONSHIPS AND ECOLOGY OF A UNIQUE FAUNA

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ABSTRACT

Results of the study of the morphology, systematics, and ecology of the Cuatro Ciénegas hydrobiids are given. Contrary to previous thought, no subfamilies of hydrobiids are endemic to the basin: all taxa studied belong to either the Nymphophilinae or Littoridininae, subfamilies widespread throughout North America. Of the nine genera (five endemic) and 13 species (nine endemic) found while sampling a large portion of the basin drainage, one genus and three species are new (but will be described elsewhere), and two species are new to the basin. The six nominal species of *Mexipyrghus* are reduced to one, *M. churinceanus*.

The diverse fauna is partitioned among three habitat types: species with large, thickened shells inhabit large springs and their outflows; minute, blind, unpigmented species are restricted to smaller groundwater outlets; and a third set of species inhabits smaller streams of the basin. Within large springs, micro-habitat partitioning occurs as separate species predominate either in soft sediment, on aquatic vegetation, or on travertine. At least one species reproduces year-round in the thermal waters of large springs.

Phenetic and phyletic analyses show that three of five endemic genera closely resemble non-endemics found in the basin. The close similarity of endemics to non-endemics, lower level of endemism than once thought, lack of marked differentiation within the basin, and close proximity of the basin drainage to outside waters suggest a local and recent origin for the endemic taxa.

RESUMEN

Se reportan resultados del estudio de la morfología, sistemática, y ecología de los hydrobioides de Cuatro Ciénegas. Contra lo que se había pensado, ninguna subfamilia de hydrobioids es endémica a la cuenca: todos los taxa investigados pertenecen a Nymphophilinae ó Littoridininae, subfamilias extendidas por todo Norte America. De los 9 géneros (5 endémicos) y 13 especies (9 endémicas) encontrados en muestras tomadas sobre una porción grande de la cuenca, 1 género y 3 especies son nuevas, y 2 especies son nuevas para la cuenca. Las 6 especies nominales de *Mexipyrghus* estan reducidas a 1, *M. churinceanus*.

La fauna diversa está repartido entre 3 tipos de hábitats: las especies con conchas grandes y gruesas habitan manantiales grandes y sus desagües; las especies diminutas, ciegas, y sin pigmentación estan restringidas a salidas pequeñas de aguas subterráneas; y el tercer grupo de especies habita arroyos pequeños. Dentro de los manantiales grandes se ve la repartición de micro-hábitat donde especies distintas predominan en sedimento suelto, en vegetación acuática ó en travertino. Por lo menos una especie se reproduce durante todo el año en las aguas termales de los manantiales grandes.

El análisis fenotípico y filético muestra que 3 de los 5 géneros endémicos son muy parecidos a los no endémicos encontrados en la cuenca. La semejanza casi completa de los endémicos a los no endémicos, el nivel mas bajo de endemismo que se había pensado, la falta de diferenciación dentro de la cuenca y la proximidad cercana del drenaje de la cuenca a aguas afuera indican un origen local y reciente de los taxa endémicos.

INTRODUCTION.—Of the various groups of organisms found in Cuatro Ciénegas, the hydrobiid snails have been credited with the highest level of endemism. Taylor (1966a) considered three subfamilies, five genera, and 12 species of these tiny aquatic snails as endemic to the basin. Local endemism of freshwater snail faunas, involving a few species, is common in the arid American Southwest (Taylor 1966b, Russell 1971, Pratt 1977), but the high level of endemism of the Cuatro Ciénegas snail fauna is unique in

North and Central America. Apart from their high endemism, the hydrobiid snails of Cuatro Ciénegas are of interest for the following reasons: 1) the shells of many of the species are relatively large, sculptured, or color-banded (Fig. 1), whereas most hydrobiids have small, smooth shells without color; 2) the high local diversity of the hydrobiid fauna, with nine genera and 12 species found within a 30 x 40 km valley, is unparalleled in North and Central America and compares favorably with that of the

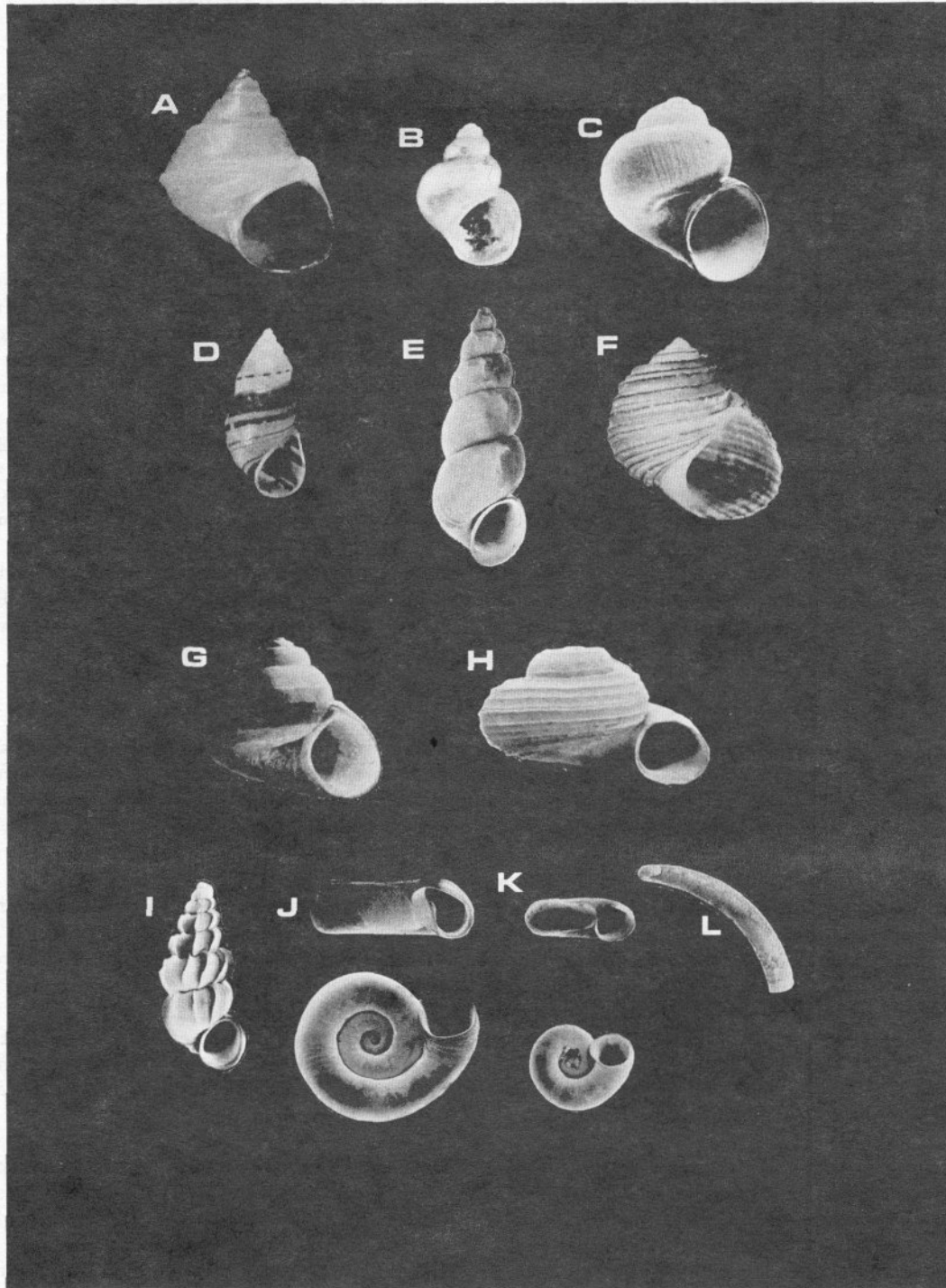


Figure 1. Photographs of shells of hydrobiid species found in the Cuatro Ciénegas Basin. The shells are not printed to the same enlargement. A) *Nymphophilus minckleyi* (shell length, 8.0 mm); B) *Nymphophilus* n. sp. (4.25 mm); C) "*Stiobia*" n. sp. (1.15 mm); D) *Mexipyrgus churinceanus* (3.76 mm); E) *Durangonella coahuilae* (3.60 mm); F) *Mexithauma quadripaludium* (7.83 mm); G) *Cochliopina riograndensis* (shell width, 3.00 mm); H) *C. milleri* (shell width, 3.26 mm); I) *Paludiscala caramba* (shell length, 2.40 mm); J) *Coahuilix* n. sp. (shell width, 1.20 mm); K) *C. hubbsi* (shell width, 0.87 mm); L) *Orygoceras* (?) sp. (shell width, 2.26 mm).

large hydrobiid faunas of ancient lakes (Table 1); and 3) differentiated populations of snails distributed among the insular springs of the valley offer an opportunity to study evolution in a "natural laboratory" (Taylor and Minckley 1966).

Early classifications of hydrobioids (i.e., those rissocean snails that resemble *Hydrobia* in morphology of either shell, penis, operculum, or radula) (Berry 1943; Morrison 1949), including that originally offered for the Cuatro Ciénegas fauna (Taylor 1966a), were based on these characters and a few other external morphological features (see Table 2). It now is known that such characters have converged in rissocean taxa that are not closely related on the basis of overall soft-part anatomy (Davis 1979). Such convergences are rampant among hydrobiid snails and study of entire soft-part anatomy is necessary both to recognize these convergences and to clarify systematic relationships (Davis 1979). Endemic freshwater snail faunas frequently include taxa with thickened, sculptured, or otherwise-peculiar shells (Annandale 1919, Vermeij and Covich 1978) that represent adaptations to local ecological conditions.

Classifications weighted in favor of such shell features may inflate the uniqueness of such taxa. Some of the endemic snails of Lake Tanganyika, for instance, have thickened, sculptured, "marine-like" shells and once were considered to be oceanic relicts and classified as members of modern or Jurassic marine families (see Pilsbry and Bequaert 1927; Yonge 1938). Later anatomical studies showed that they were modified members of widespread freshwater cerithiacean families (Leloup 1953): the peculiar shells masked a more conventional soft-part anatomy.

The original description of the Cuatro Ciénegas hydrobiids by Taylor (1966a) stands as a fine contribution for that time period and stimulated my own research. Yet in light of the above, the classification offered for the snails is suspect because it was based largely on shell and external features. Additionally, within the data set used, the numerous subfamilies described do not have distinctive sets of features (see Thompson 1968; Davis 1979). The descriptions of species are suspect also because they were based

Table 1. Comparison of generic and specific diversities among hydrobiid faunas of ancient lakes (from data compiled by Boss 1978) and the Cuatro Ciénegas Basin (Hershler 1983).

Location	Number of genera	Number of species
Lake Baikal, Soviet Union	5	40
Lake Tanganyika, East Africa	3	3
Lake Ohrid, Yugoslavia	5	39
Lake Titicaca, Peru-Bolivia	7	21
Lake Inle, Burma	2	5
Cuatro Ciénegas, Mexico	9	12

on samples from only twelve localities (Taylor 1966a): six allopatric species of *Mexipyrgus* were described from a total of seven localities.

A detailed presentation of the morphology of the Cuatro Ciénegas hydrobiids, together with a systematic revision of the fauna (including descriptions of new taxa), is presented elsewhere (Hershler 1983). The purposes of this paper are: 1) to summarize changes in the classification of the snails and to discuss new taxa (and those new to the basin); 2) to present sampling data and to discuss patterns of distribution of the hydrobiid species among the aquatic habitats of the basin and other aspects of their ecology; and 3) to discuss the origin, evolution, and endemism of the hydrobiid fauna.

METHODS.—Snails were collected from 103 localities in the basin. One hundred localities were concentrated in an arc surrounding the northern tip of the Sierra de San Marcos (Fig. 2) and encompassed parts of four of the five-seven drainages of the basin (Minckley 1969; LaBounty 1974). Soft sediments, largely consisting of snail copropel, were sampled using a fine hand sieve. Bunches of vegetation (*Clara*, *Utricularia*, *Nymphaea*) were collected at random, washed, and the dislodged snails then picked from the residue under a dissecting microscope. Snails were picked from individual travertine pieces and blocks using fine forceps. To collect the tiny snails that frequent groundwater outlets, ordinary domestic (cotton) mops were placed into small springheads to serve as colonization substrates (method suggested by W. L. Minckley). Mops were periodically removed, washed, and the snails picked from the residue under a dissecting microscope. Dissection methods and

Table 2. Diagnostic features listed by Taylor (1966a) for hydrobiid subfamilies found in Cuatro Ciénegas.

Subfamily	Diagnostic features
Cochliopinae	Shell trochoid to planispiral.
Littoridininae	Shell elongate to turritiform; penis with bulbous or elongate lobes.
Nymphophilinae*	Shell large, trochoid; operculum multispiral; penis with elongate filament and blood sinus; vas deferens in elevated ridge along mantle cavity floor.
Mexithaumatinae*	Shell with bristly periostracum; anterior end of pallial oviduct reflected; mantle edge papillate; tentacles with pigment strip along length.
Paludiscalinae*	Shell with lamelliform costae.

*Considered endemic to the Cuatro Ciénegas Basin by Taylor (1966a).

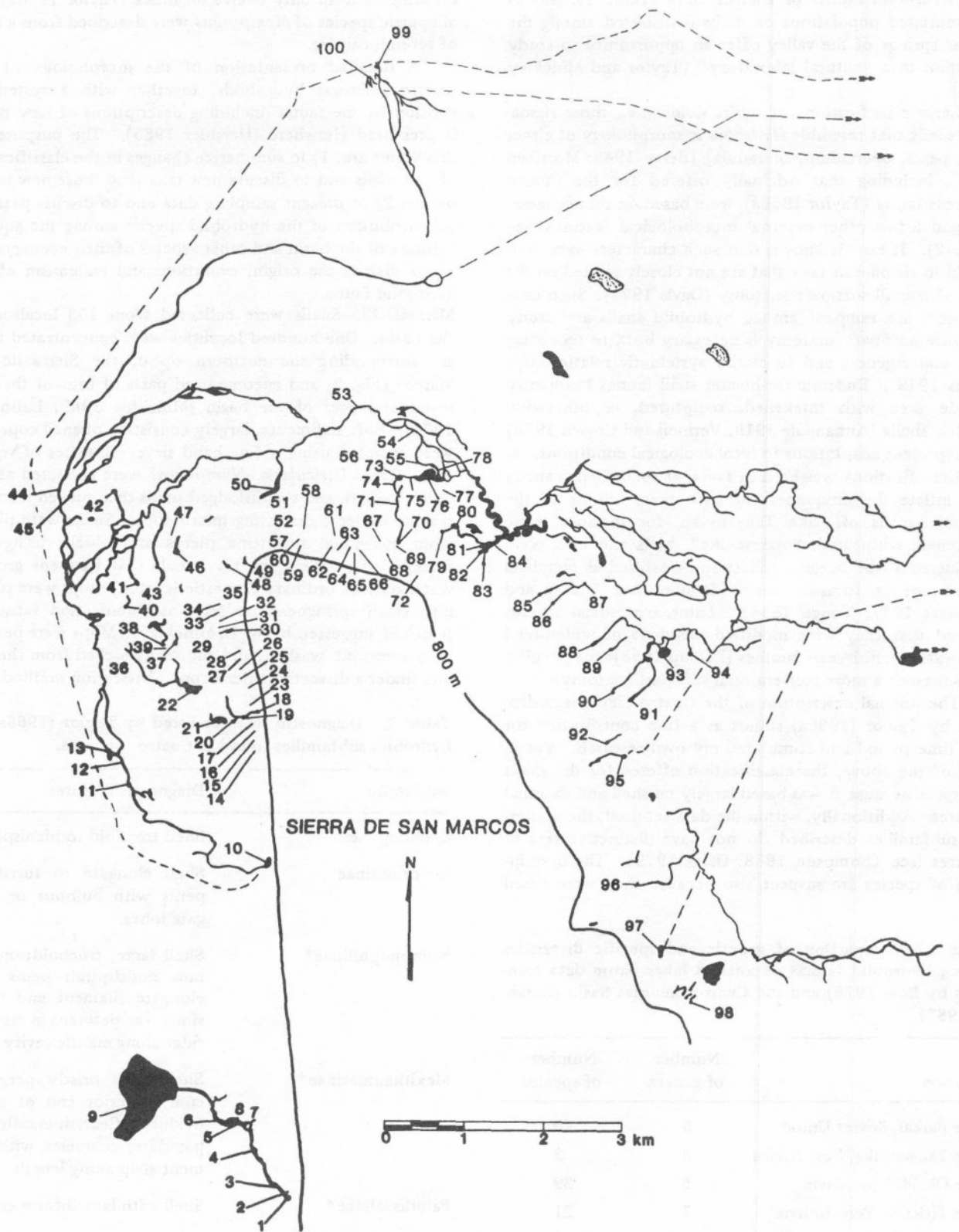


Figure 2. Map of the portion of the basin that was intensively sampled (from Hershler 1983). Numbers (1-100) refer to collection localities. Dashed lines refer to irrigation canals. Arrows indicate waters that continue to flow toward the east.

other techniques of morphologic study are described elsewhere (Hershler 1983).

RESULTS.—Changes in classification. Recent anatomical studies have demonstrated that hydrobioid snails represent a polyphyletic assemblage that includes taxa belonging to the Hydrobiidae and Pomatiopsidae, families characterized by divergent anatomical groundplans (Davis 1979). Among the Hydrobiidae, two basic anatomical groups are seen (Davis et al. 1982, Hershler 1983). One group includes the Hydrobiinae and Nymphophilinae (*sensu* Thompson 1979, Davis et al. 1982), in which sperm are received into the pallial oviduct of the female (Apo + Ppo, Fig. 3A) and travel along an internal ciliated channel (Vc) of the capsule gland (Apo) towards the sperm-receiving bursa copulatrix (Bu) and seminal receptacle (Sr). Nymphophilines are characterized by a penis with glandular ridges (Glr, Fig. 4B), elevated regions with paired rows of small glands discharging through a central slit; whereas species in the Hydrobiinae have a penis lacking specialized glands. In the other group, the Littoridininae (*sensu* Davis et al. 1982), sperm enter a spermathecal duct (Sd, Fig. 3B) of the female, which is at least partly separate from the pallial oviduct (wholly separate in some taxa, Fig. 3D), and travel along

this duct: the pallial oviduct has no ciliated sperm groove in the ventral channel. This penis of littoridinines lacks glandular ridges, but may have other specialized gland types (Figs. 4C, D). Littoridinines also differ from the Nymphophilinae-Hydrobiinae in that their cephalic tentacles often have complex, hypertrophied, surficial ciliary tracts (Ci, Fig. 4A), while the tentacles of the latter lack these complex tracts. This subfamilial classification of the Hydrobiidae, while admittedly based on few characters, does place emphasis on a major difference in overall anatomical groundplan (i.e., ventral channel versus spermathecal duct). This classification is deemed tentative, not only because at least 90% of the North and Central American hydrobiid species are unknown in terms of anatomy, but also because recent work (Ponder 1983) suggests that character-states of the female reproductive system (such as the above) may also have arisen iteratively in the evolution of various rissoacean groups.

Thompson (1979) demonstrated that *Nymphophilus*, endemic to Cuatro Ciénegas and previously considered the sole genus in this subfamily (Taylor 1966a), was similar in anatomy to hydrobiid snails from other parts of North America and added several genera to this subfamily. My

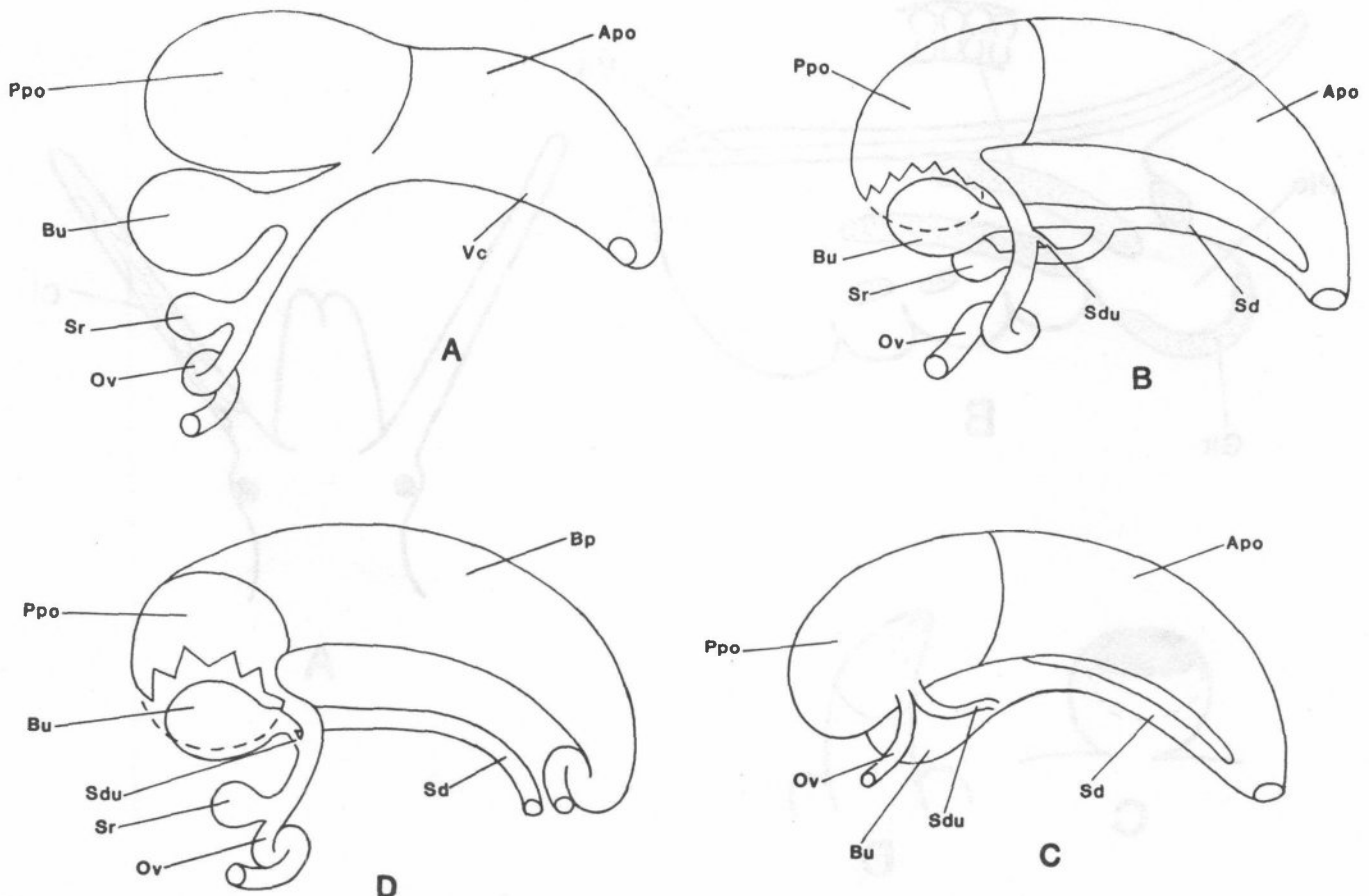


Figure 3. Schematic drawings of the female reproductive morphologies of A) *Hydrobia*, B) *Spurwinkia*, C) *Coabuilix*, and D) *Mexitbauma* (from Hershler 1983). Apo = capsule gland; Bp = brood pouch; Bu = bursa copulatrix; Ov = oviduct; Ppo = albumen gland; Sd = spermathecal duct; Sdu = sperm duct; Sr = seminal receptacle; and Vc = ventral channel.

studies indicate that all Cuatro Ciénegas hydrobiids studied can be placed in the Nymphophilinae or the Littoridininae (also widespread with numerous taxa): there are no subfamilies endemic to the basin. My classification of the Cuatro Ciénegas hydrobiids is contrasted with the original classification in Table 3. The purported distinctive features of the three nominal subfamilies erected by Taylor (1966a), which were considered endemic to the basin (Table 1), are unconvincing. For example, the penis of *Nymphophilus* has glandular ridges as do those of all nymphophilines, and all hydrobiids have the vas deferens in a ridge (of varying height) on the floor of the mantle cavity (Thompson 1968, 1979). The reflected pallial oviduct in *Mexithauma* is found in many hydrobiids and is associated with a viviparous reproductive habit (Hershler 1983). Pigment streaks on tentacles also are common among hydrobiid snails (Fretter and Graham 1962, Hershler and Davis 1980). Lamelliform costae on the shell, seen in *Paludiscala*, also are found in unrelated taxa (e.g., *Lanzaia*).

The six nominal species of *Mexipyrgus* are reduced to one, *M. churinceanus* Taylor (Fig. 1D). The nominal species were described on the basis of minor differences in shell

features. I gathered morphological data on specimens from 33 populations and found that while patterns of geographical variation were evident, the purported differences in shell features among nominal species often were blurred in given populations, or even intergrade, and distinct species thus could not be recognized (Hershler 1983).

New taxa. A list of the hydrobiid species found in the basin is given in Table 4. The new taxa will be described elsewhere (Hershler 1983). *Coahuilix* n. sp. (Fig. 1J) is much larger than *C. hubbsi*, and differs in other shell features as well when sympatric. *Nymphophilus* n. sp. (Fig. 1B) is much smaller in size than *N. minckleyi* and lacks the pronounced basal keel of the shell seen in the latter. These two species are allopatric to one another: *Nymphophilus* n. sp. is known only from the southeast lobe of the basin, whereas *N. minckleyi* is restricted to the northeast and western lobes. "*Stiobia*" n. sp. (Fig. 1C) represents a new genus of Nymphophilinae (also found elsewhere in México), similar to *Stiobia* (Thompson and McCaleb 1978).

Two species new to the basin were discovered during my collecting. *Cochliopina riograndensis* (Fig. 1G), pre-

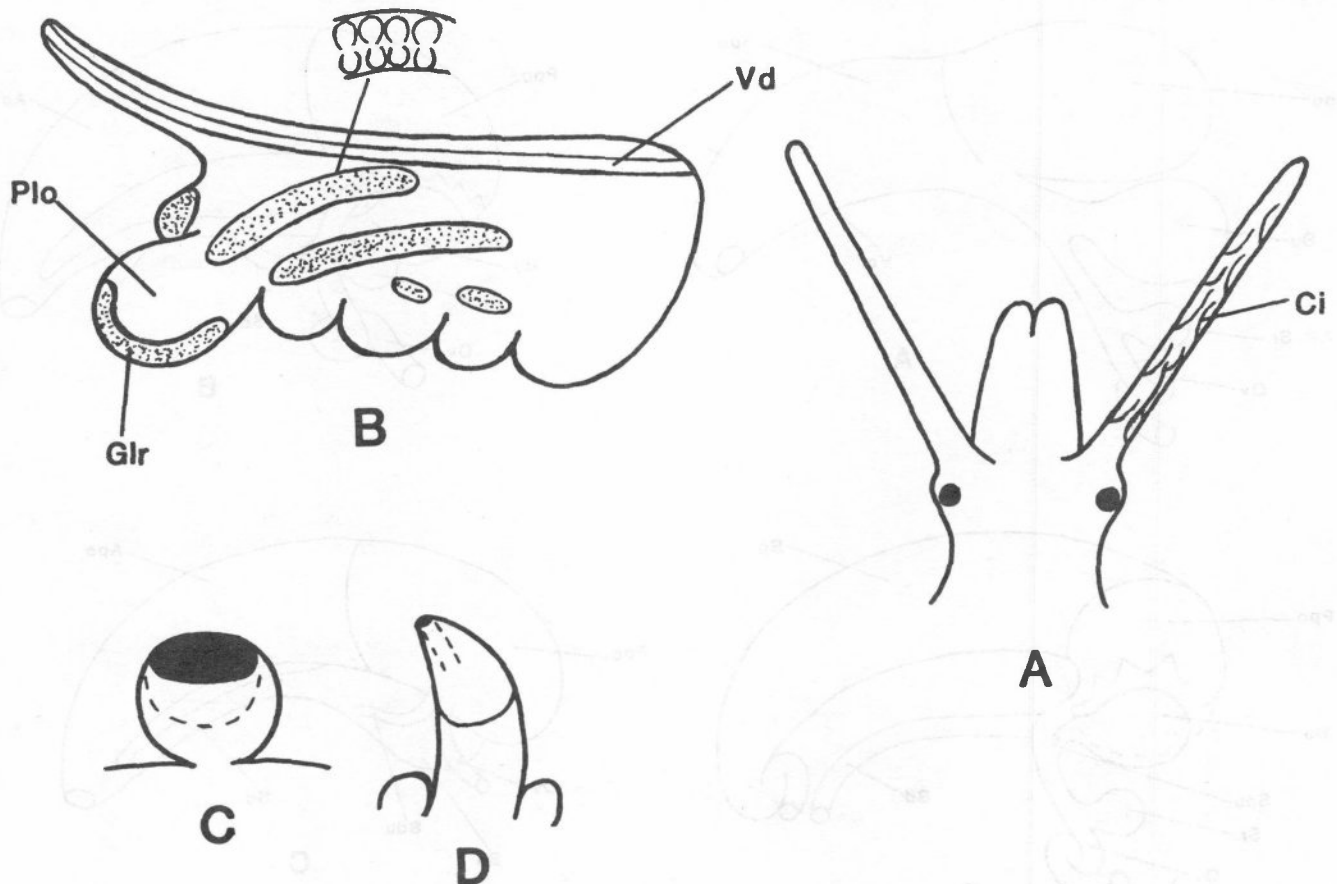


Figure 4. Head, penis, and penial glands of hydrobiid snails. A) Dorsal aspect of the head, showing the hypertrophied ciliary tufts (Ci) on the tentacle; B) Dorsal aspect of the penis, showing glandular ridges (Glr); C, D) Penial gland types (apocrine and mammiform glands, respectively); Ci = ciliary tufts, Glr = glandular ridges, Plo = penial lobe, Vd = vas deferens.

viously known from the nearby Río Salado de Nadadores and other Río Grande tributaries (Taylor 1966a), was collected in Laguna Santa Tecla in the southeastern lobe of the basin. *Orygoceras*(?) sp. (Fig. 1L), previously known from a single spring in western Texas (Taylor 1974), was discovered living in a single small spring in the basin. A fresh shell of this species has been found since at a second locality in western Texas (Davis 1983).

ECOLOGY.—As mentioned above, the hydrobiid fauna of Cuatro Ciénegas also is noteworthy for its high diversity. How are the 12 species distributed among the aquatic habitats of the basin? Most aquatic habitats in the basin are spring-fed, and vary greatly in basic type (i.e., spring pool, stream, marsh, lake), size, and temperature (Minckley 1969). For the purposes of describing the distribution of the various snail species, it is convenient to divide the springs into two classes: small springs, with spring pool areas of $< 9 \text{ m}^2$, whose outflows run as shallow streams for only tens of meters before terminating in a marsh or disappearing underground; and larger springs (Minckley 1969, Figs. 14, 15), with spring pool areas in excess of 900 m^2 , whose outflows are large streams. Discussion is based on intensive collecting at Localities 1-100 (Fig. 2): species not found in this area (*Cochliopina riograndensis* and *Nymphophilus* n. sp.) are discussed only briefly.

Large springs and their outflows. The large springs have considerable micro-habitat diversity, including aquatic vegetation of several types (sedges, *Nymphaea*, *Chara*, Table 3. Subfamilial placement of the Cuatro Ciénegas hydrobiid genera (based on the results of this study) contrasted with that of Taylor (1966a).

Taylor (1966a)	This study
Family Hydrobiidae	Family Hydrobiidae
Subfamily Cochliopinac	Subfamily Littoridininae
<i>Coahuilix</i> ¹	<i>Coahuilix</i> ¹
<i>Cochliopina</i>	<i>Paludiscala</i> ¹
Subfamily Littoridininae	<i>Mexithauma</i> ¹
<i>Mexipyrgus</i> ¹	<i>Cochliopina</i>
<i>Durangonella</i>	<i>Durangonella</i>
Subfamily Nymphophilinae ²	<i>Mexipyrgus</i> ¹
<i>Nymphophilus</i> ¹	Subfamily Nymphophilinae
Subfamily Mexithaumatinae ²	<i>Nymphophilus</i> ¹
<i>Mexithauma</i> ¹	" <i>Stiobia</i> " ³
Subfamily Paludiscalinae ²	Subfamily Unknown
<i>Paludiscala</i> ¹	<i>Orygoceras</i> (?) ⁴

¹Genus endemic to the Cuatro Ciénegas Basin.

²Subfamily considered endemic to the Cuatro Ciénegas Basin by Taylor (1966a).

³New genus.

⁴Systematic status uncertain.

Table 4. Hydrobiid species found in the Cuatro Ciénegas Basin.

* <i>Coahuilix hubbsi</i> Taylor 1966a
* <i>Coahuilix</i> n. sp.
* <i>Paludiscala caramba</i> Taylor 1966a
* <i>Mexithauma quadripaludium</i> Taylor 1966a
<i>Cochliopina riograndensis</i> Pilsbry and Ferriss 1906
* <i>Cochliopina milleri</i> Taylor 1966a
* <i>Durangonella coahuilae</i> Taylor 1966a
* <i>Mexipyrgus churinceanus</i> Taylor 1966a
* <i>Nymphophilus minckleyi</i> Taylor 1966a
* <i>Nymphophilus</i> n. sp.
" <i>Stiobia</i> " n. sp.
<i>Orygoceras</i> (?) sp.

*Species endemic to the basin.

Utricularia); soft sediment composed of snail copropel or an algal-detritus mixture, often mixed with small travertine pieces and shell debris; and large-sized travertine pieces (Fig. 5). *Mexipyrgus churinceanus*, *Mexithauma quadripaludium*, and *Nymphophilus minckleyi* are commonly found in the large springs; while *Durangonella coahuilae* and *Cochliopina milleri* are much less common. This may be explained partly by the presence of molluscivorous cichlid fishes in the large springs (Deacon and Minckley 1974, Fig. 7): the former three snails have large and thickened shells, possibly affording resistance to the snail-crushing fish, whereas the latter two species are fragile-shelled.

In all springs sampled, *M. churinceanus* was restricted to soft sediments (in which it burrows), sometimes achieving extremely high densities ranging to $40,000/\text{m}^2$ (data



Figure 5. Photograph showing substrate diversity in Laguna Mojarral East. Note the *Nymphaea* (water lily), soft copropel sediment, and travertine blocks. Vertical distance is 4 m; water depth is 1 m.

from box core sampling). *Nymphophilus minckleyi* and *Mexithauma quadripaludium* usually are found on hard substrates (plant or travertine). The massive foot and trochoid shell of these snails are presumably adaptations to a clinging mode of life. *Nymphophilus minckleyi* may also require a hard substrate on which to deposit its egg capsules (*M. quadripaludium* is viviparous). When *N. minckleyi* and *M. quadripaludium* coexist in a spring that has aquatic vegetation and travertine in abundance, each predominates on the substrate to which it is best adapted (the former on vegetation, the latter on travertine). Data on substrate utilization by the three species in Laguna Mojarral East, a large limnocrone (pool area of about 9,000 m²), are given in Table 5. Only *M. churinceanus* was common in soft sediments; *N. minckleyi* was common and *M. quadripaludium* rare on aquatic vegetation; and *M. quadripaludium* was three times as common as *N. minckleyi* on under surfaces of travertine blocks (the three substrates are shown in Fig. 5). Thus, in a large spring with micro-habitat diversity, each of the three species predominates in a separate micro-habitat. In springs with reduced micro-habitat diversity, either *N. minckleyi* or *M. quadripaludium* is rare or absent, and the species present often "switches" to the micro-habitat usually occupied by the other, suggesting at least a partly competitive basis for patterns of substrate use. In Laguna Churince, for instance, *N. minckleyi* was extremely rare, travertine was largely absent, and *M. quadripaludium* was extremely abundant

Table 5. Relative abundances (%) of snail species within micro-habitats in Laguna Mojarral East (sampling during 4/20-4/30/80).

Species	Micro-habitat			
	Soft sediment ¹	<i>Nympho-aea</i> ²	<i>Chara</i> ³	Travertine ⁴
<i>Mexiphyrus churinceanus</i>	0.99	0.03	—	—
<i>Mexithauma quadripaludium</i>	0.01	0.06	0.11	0.76
<i>Nymphophilus minckleyi</i>	—	0.91	0.89	0.24
Total number of snails collected	3468	1219	251	498

¹From 56-10 minute collecting efforts.

²From 10 samples of plant bunches.

³From 5 samples of plant bunches.

⁴From 110 pieces averaging 12.5 x 30.0 cm.

on dense growths of *Chara* in the deeper portions of the spring.

The other two species occasionally found in large springs, *Durangonella coahuilae* and *Cochliopina milleri*, usually are restricted to soft sediment and aquatic vegetation, respectively. *Cochliopina riograndensis* and *Nymphophilus* n.sp. are on aquatic vegetation in large springs in the Southeastern lobe of the basin.

Prior to man-made alterations, most of the large springs gave rise to large streams that terminated in shallow playa lakes (Minckley 1969). In general, abundances of all of the above species, except *Durangonella coahuilae*, decrease downstream from a spring source. Several environmental changes occur downstream that may account for these decreases. Aquatic vegetation may disappear or become patchy and soft sediments frequently become covered with an algal layer. Water temperature fluctuations may become marked. At Locality 30 (Fig. 2), for instance, water temperatures at the springhead varied from 31.0-34.5°C, over a four-day period during the summer (maxi-mini thermometer readings), while 77 m downstream where water disappeared into a swallet, the temperatures varied from 20.6-37.8°C during the same period. Salts become more concentrated downstream as well (Minckley and Cole 1968). In the Churince system (Localities 1-9, Fig. 2), *M. churinceanus*, *M. quadripaludium*, and *N. minckleyi* have not been found below the large pools (Locality 6), which differ greatly from the springhead in terms of substrate, water chemistry (Minckley and Cole 1968), and water temperature variations. *Durangonella coahuilae*, on the other hand, can tolerate these environmental changes and is abundant not only in these pools, but also in the playa lake, Laguna Grande (Locality 9).

Small springs and their outflows. Small springs also generally have warm water (29-33°C). Riparian vegetation typically covers the springheads and sometimes part of the streams as well. Micro-habitat diversity is reduced relative to the large springs. *Chara* mats and soft sediments composed of mixtures of silt, organic mud and travertine are the only abundant substrates. Of the five species found in large springs, only *D. coahuilae* also is common in the smaller springs. One group of blind, unpigmented species (*Paludiscala caramba*, *Coahuilix hubbsi*, *Coahilix* n. sp., and *Orygoceras*[?] sp.) is restricted largely to heads of these small springs (and possibly subterranean waters), while a second group of species (*D. coahuilae*, "*Stiobia*" n. sp.) abounds not only in springheads, but also in the streams. Species of the second group have dark body pigment that may serve as a "sunscreen" (shells are transparent, as are those of the first group), protecting the vital organs of the snails from the intense insolation of open stream reaches.

Data from the abundances of snail species in mop samples from 38 springheads are given in Table 6. At a given springhead, several mop samples were taken at varying intervals during 1980 and 1981. Snails were picked from each sample until a total of 100 individuals was found. Relative abundances varied little among samples

Table 6. Abundances of snail species in mop samples from 38 small springheads (localities shown in Fig. 2). L = locality, N = number of samples, *Pal* = *Paludiscala caramba*, *C.b.* = *Coabuilix bubbsi*, *C.n.sp.* = *Coabuilix n. sp.*, "S" = "*Stiobia*" n. sp., *Dur* = *Durangonella coabuilae*, *Nym* = *Nymphophilus minckleyi*, *Mex* = *Mexipyrgus cburinceanus*.

L	N	<i>Pal</i>	<i>C.h.</i>	<i>C.n.sp.</i>	"S"	<i>Dur</i>	<i>Nym</i>	<i>Mex</i>	Total
2	2	1	—	—	—	10	—	—	11
12	2	—	1	—	—	75	—	—	76
14	1	—	—	2	1	13	—	—	16
15	2	—	—	—	17	298	—	—	315
16	9	98	85	1	63	459	—	—	706
17	5	118	—	1	2	23	—	—	144
18	4	6	1	2	—	—	16	—	25
23	2	95	—	—	—	3	—	—	98
24	4	431	—	6	—	23	—	—	460
25	2	14	—	—	1	—	—	—	15
26	1	40	—	—	—	6	—	—	46
27	1	110	—	—	—	—	—	—	110
28	4	237	—	2	41	48	1	—	329
31	3	16	2	1	98	2	—	—	119
32	1	5	—	—	—	—	—	—	5
33	2	200	6	—	—	—	—	—	206
34	2	211	1	—	1	—	—	—	213
35	2	203	2	—	—	6	—	—	211
38a*	4	13	35	1	214	35	—	—	298
b*	2	1	—	—	1	6	—	—	8
40	1	—	—	—	2	—	—	—	2
52	1	2	—	—	131	10	—	—	143
56	1	1	1	—	—	18	—	—	20
57	3	38	—	—	290	—	—	—	328
58	2	19	29	—	3	137	—	—	188
59	2	29	—	—	—	—	—	—	29
60	2	186	—	1	4	4	—	—	195
61	1	100	3	—	—	44	—	—	147
62	2	199	—	—	135	—	—	—	334
63	8	444	—	3	—	—	—	—	447
64	4	450	40	3	—	1	—	—	494
65	6	633	9	3	6	104	—	1	755
66	2	51	8	—	—	—	—	—	59
67**	10	982	119	15	100	—	—	—	1216
68	2	11	8	—	—	—	—	—	19
69	2	142	—	2	—	—	—	—	144
72	2	4	—	—	4	2	1	—	11
77	2	—	—	—	101	27	—	—	128
Total	107	5090	350	43	1215	1354	18	1	8071

*"a" and "b" from small springs joining the larger cool spring at Locality 38.

***Orygoceras*(?) sp. also found in subsequent samples from this spring.

Table 7. Analysis of abundance data from the 23 springs listed in Table 5 from which samples totalled more than 100 individuals. Species abbreviations as in Table 6.

	Species				
	<i>Pal</i>	<i>C.h.</i>	<i>C.n.sp.</i>	"S"	<i>Dur</i>
Number of springs found in (of the 23)	21	11	12	16	14
Number of springs in which species comprised:					
a) more than 0.25 of the sample	14	—	—	6	4
b) more than 0.75 of the sample	12	—	—	3	2

of a given springhead, and data were pooled for each spring. *Paludiscala caramba* was by far the most common species in springheads (Table 7). Of the other blind species, both *Coahuilix hubbsi* and *Coahuilix* n. sp. were less common, and only a few specimens of *Orygoceras*(?) sp. were found in unsorted samples from a single spring. Proof is lacking that the blind, unpigmented species inhabit subterranean waters as well; the mops may be colonized not only by snails washed from underground, but also by surface-dwelling snails living in the springhead (such as *Durangonella coahuilae* and "*Stiobia*" n. sp.). To distinguish between these two sets of snails, a fine mesh net could be capped over the groundwater outlet, filtering snails from the watering stream, but not allowing surface-dwellers to crawl in. This method has been successfully used to sample faunas of artesian wells (Holsinger and Longley 1980).

While blind species were never found in the open reaches of stream, they occasionally extended below springheads when channels were covered by riparian vegetation (mimicking a subterranean environment). At Locality 63, a small thermal (33-35°C) spring issued into a pool (Brown 1974, Fig. 5), then flowed 170 m as a shallow stream before entering a marsh. *Paludiscala caramba* was abundant on plant and travertine surfaces for the upper 83 m of stream, which had complete vegetative cover. Below 83 m, vegetative cover ended and no *P. caramba* were found despite intensive collecting that yielded quantities of *Durangonella coahuilae* and "*Stiobia*" n. sp. At Locality 67, nine mop samples taken 3 m below the springhead, where riparian vegetation completely covered the stream, yielded 67 *P. caramba*, 520 *C. hubbsi*, 10 *Coahuilix* n. sp., as well as quantities of the pigmented species.

The two pigmented species, *D. coahuilae* and "*Stiobia*" n. sp., are abundant in both soft sediments and *Chara* mats of shallow streams. No clear-cut differences were seen in their micro-habitat usage.

Other aquatic habitats. Of all species of the basin, only *Durangonella coahuilae* is common in playa lakes, pools and marshes, habitats with sluggish water circulation and pronounced water temperature and chemistry fluctuations. For example, only *D. coahuilae* was collected from a series of groundwater-fed pools that fluctuated in size as the water table rose and fell (Localities 7, 8). During 1981 water temperatures varied from 9.5-35.6°C in one of these pools;

the snails disappeared only when the pool temporarily dried during drought. *Durangonella coahuilae* does not, however, extend into the saline waters of the basin.

In summary (Table 8), hydrobiid species of the basin are divided into three groups with differing habitat usages: those dwelling in large springs and their outflows, blind species restricted to groundwater outlets, and two species common in the outflows of small springs (one of which also occupies marshes and playa lakes). Predominant species in large springs usually occupy different micro-

Table 8. Summary of the deployment of hydrobioid species among the various habitats in the basin. "++" = common, "+" = rare.

Species	Habitat			
	Large springs and outflows	Small springs Head	Small springs Outflow	Marshes, pools, lakes
<i>Mexipyrgus churinceanus</i>	++	—	—	—
<i>Mexithauma quadripaludium</i>	++	—	—	—
<i>Nymphophilus minckleyi</i>	++	—	—	—
<i>Cochliopina milleri</i>	+	—	—	—
<i>Durangonella coahuilae</i>	+	++	++	++
" <i>Stiobia</i> " n. sp.	—	++	++	—
<i>Paludiscala caramba</i>	—	++	+	—
<i>Coahuilix hubbsi</i>	—	+	+	—
<i>Coahuilix</i> n. sp.	—	+	+	—
<i>Orygoceras</i> (?) sp.	—	+	—	—

habitats. As the fauna is large, partitioning of habitats occurs as expected, with no more than three or four species common at any locality. The diversity of habitats occupied by hydrobiids may be due partly to absence of other groups of gill-breating snails (i.e., viviparids, pleurocarids). Adaptations of the species to their respective habitats and micro-habitats merit more study.

Reproductive ecology. Near-constancy of water temperatures in large spring pools of the basin is well documented (Minckley 1969, Arnold 1972) and is reflected in the apparent year-round reproduction of *Nymphophilus minckleyi* in Laguna Mojarral East (Fig. 6). A large sample of *Nymphaea* (water lily) was collected from the south-west corner of this spring at 11 monthly intervals during 1980-

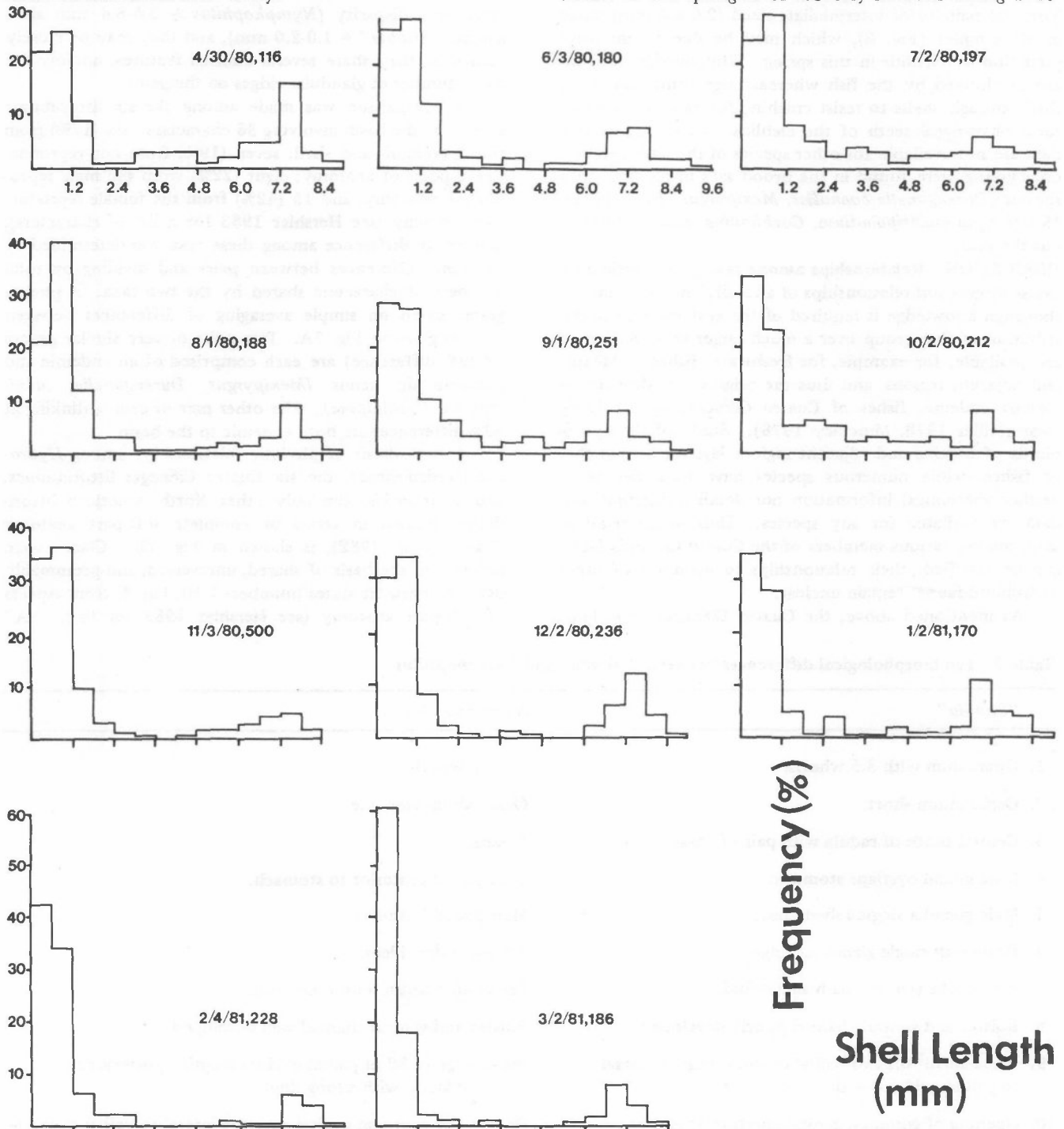


Figure 6. Size-frequency histograms of samples of *Nymphophilus minckleyi* taken from Laguna Mojarral East during 1980-1981. The date of collection and number of snails are given for each histogram.

1981 and washed to remove snails, which were then measured. Water temperatures throughout the year ranged from 26 to 32°C. For all 11 samples, juveniles (shell length <1.25 mm) comprised at least 48% of the total collection (Fig. 6), with a March peak of about 80%. Individuals with mature gonads (seen in dissection), and egg capsules (on *Nymphaea* leaves) were common in all samples. Note the paucity of intermediate-sized (2.0-6.0 mm) snails in all samples (Fig. 6), which may be due to intensive predation by cichlids in this spring. Tiny juveniles perhaps are overlooked by the fish whereas large adults may have thick enough shells to resist crushing forces of the molariform pharyngeal teeth of the cichlids. While comparable data are not available for other species of the basin, embryonic young were found in the brood sacs of all viviparous species (*Durangonella coahuilae*, *Mexipyrgus churinceanus*, *Mexithauma quadripaludium*, *Cochliopina milleri*) throughout the year.

DISCUSSION.—Relationships among taxa. To confidently assess origins and relationships of a locally endemic fauna, a thorough knowledge is required of the systematics and distribution of that group over a much larger area. Such data are available, for example, for freshwater fishes of México and adjacent regions, and thus the origins and affinities of various endemic fishes of Cuatro Ciénegas appear fairly clear (Miller 1978, Minckley 1978). Study of the hydrobioids of México and adjacent regions lags far behind that of fishes; while numerous species have been described, neither anatomical information nor detailed distributional data are available for any species. Thus, while relationships among various members of the Cuatro Ciénegas fauna can be clarified, their relationships to members of other hydrobioid faunas remain unclear.

As mentioned above, the Cuatro Ciénegas hydrobiids

(exclusive of *Orygoceras*?) all belong to either the Nymphophilinae or Littoridininae (Table 3). Of the endemic genera, *Nymphophilus* belongs to the Nymphophilinae, whereas all other are Littoridininae. *Nymphophilus* and "*Stiobia*," the other nymphophiline genus in the basin, differ in at least 10 morphological features (Table 9), but many of those differences are probably correlates of their great size disparity (*Nymphophilus* = 3.5-8.4 mm shell length; "*Stiobia*" = 1.0-2.0 mm), and they may be closely related as they share several unusual features, notably the small number of glandular ridges on the penis.

A comparison was made among the six littoridinine genera of the basin involving 36 characters: six (17%) from the operculum and shell; seven (19%) from non-reproductive aspects of anatomy; eight (22%) from the male reproductive anatomy; and 15 (42%) from the female reproductive anatomy (see Hershler 1983 for a list of characters). Percentage difference among these taxa was determined by counting differences between pairs and dividing by total numbers of characters shared by the two taxa. A phenogram, based on simple averaging of differences between taxa, is given in Fig. 7A. Two pairs of very similar genera (<29% difference) are each comprised of an endemic and non-endemic genus (*Mexipyrgus*, *Durangonella*; *Mexithauma*, *Cochliopina*). The other pair of genera (linking at 49% difference) are both endemic to the basin.

A hypothesis of phyletic relationships among *Hydrobia* (Hydrobiinae), the six Cuatro Ciénegas littoridinines, and *Spurwinkia*, the only other North American littoridinine known in terms of complete soft-part anatomy (Davis et al. 1982), is shown in Fig. 7B. Clades were defined on the basis of shared, unreversed, and presumably derived character states (numbers 1-10, Fig. 8) from aspects of soft-part anatomy (see Hershler 1983 for list). "A"

Table 9. Ten morphological differences between "*Stiobia*" and *Nymphophilus*.

" <i>Stiobia</i> "	<i>Nymphophilus</i>
1. Operculum with 3.5 whorls.	5.5-6.0 whorls.
2. Osphradium short.	Osphradium elongate.
3. Central tooth of radula with 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 (0.21 of pallial oviduct length), dorsal to pallial oviduct, with a short duct.	Bursa large (0.32 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.

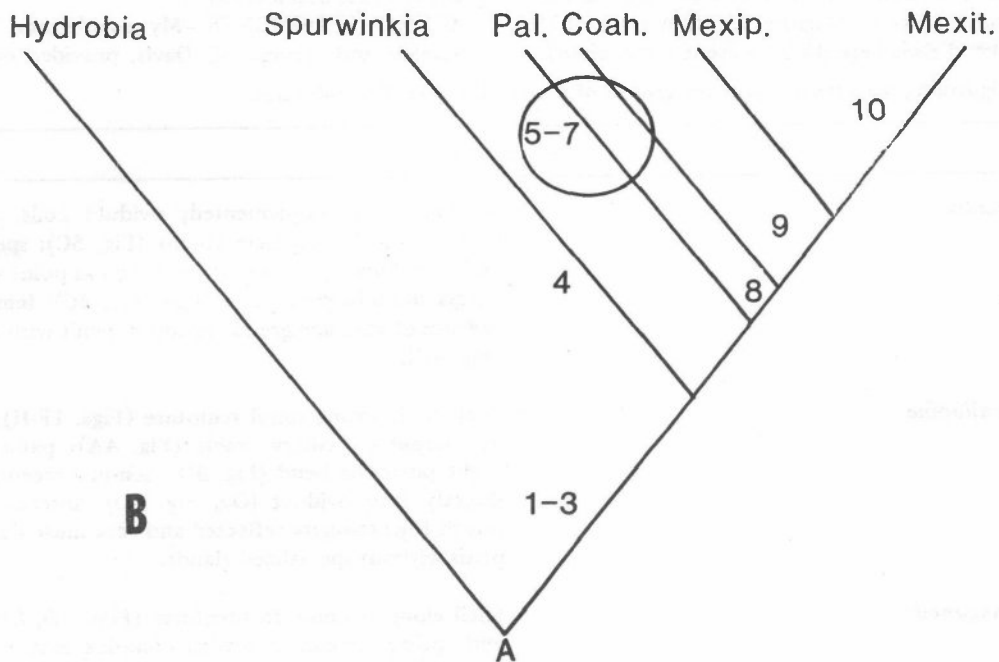
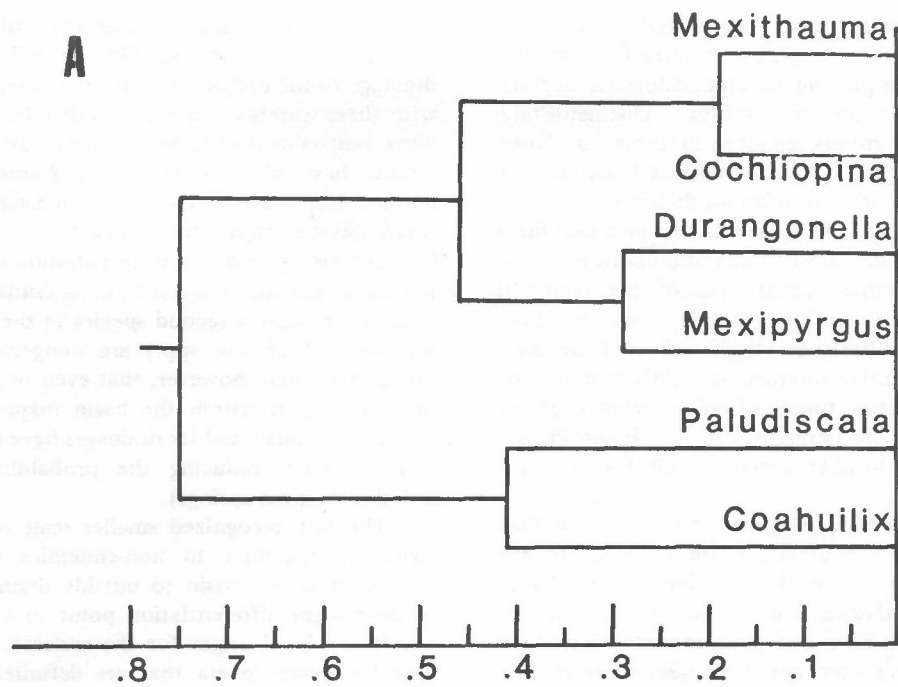


Figure 7. Phenogram (A) and cladogram (B) showing relationships among the littoridinine genera of Cuatro Ciénegas (from Hershler 1983). For the cladogram, Pal. = *Paludiscala*, Coah. = *Coahuilix*, Mexip. = *Mexipyrgus-Durangonella* group, and Mexit. = *Mexithauma-Cochliopina* group. *Paludiscala* and *Coahuilix* share character-states 5-7 (hence the circle enclosing them).

represents a hypothetical, ancestral hydrobiid. The strong concordance between the grouping of Cuatro Ciénegas littoridinine genera in the phenogram and cladogram suggests that the groups constitute true clades. Distinguishing features of these three groups are given in Table 10. Note also that of the six genera, two (*Coahuilix* and *Paludiscala*) are egg-layers while the other four brood their young.

Origin and endemism of the fauna. The idea that most of the endemic snails are ancient (tens of millions of years) relicts unrelated to other extant taxa of the region is prevalent in the literature (Taylor 1966a; Minckley 1969; Parodiz 1969), but was based on classifications of the snails that inflated their seeming uniqueness. Unfortunately no fossil record, documenting timing of colonization(s) of and diversification within the basin, is known. However, my results suggest a more local and recent origin for the endemic snails.

I have shown that endemism is on a smaller scale than previously believed; no subfamilies are endemic to the basin. Of the five genera considered endemic to the basin, I suspect that two, *Paludiscala* and *Coahuilix*, are in fact not so restricted, but have not been recorded elsewhere because the techniques necessary to collect these minute snails from groundwater outlets generally are not used during fieldwork. Snails with shells resembling those of the above are known from the Edwards Aquifer of Texas (Pilsbry and Ferriss 1906, Fullington 1978). Note that two of the three blind, unpigmented crustacean genera originally described from and considered endemic to groundwater outlets in the Cuatro Ciénegas Basin, *Mexiweckelia* and *Mexistenasellus*, were discovered later in cave waters in southern México (Magniez 1972, Argano 1973, Holsinger 1973) and elsewhere (Cole, present symposium).

Table 10. Distinguishing features of the three groups of Cuatro Ciénegas littoridinines.

Group	Features
<i>Paludiscala-Coahuilix</i>	Animal blind, unpigmented; oviduct coils, gonopericardial duct, seminal receptacle absent (Fig. 3C); sperm duct (Sdu) connects bursa (Bu) and oviduct (Ov) at point where the latter enters the albumen gland (Ppo, Fig. 3C); females oviparous; caecum of stomach greatly reduced; penis with apocrine gland (Fig. 4C).
<i>Mexithauma-Cochliopina</i>	Shell with strong spiral sculpture (Figs. 1F-H); tentacles with hypertrophied ciliary tracts (Fig. 4A); pallial oviduct with slight posterior bend (Fig. 3D); seminal receptacle (Sr) opens directly into oviduct (Ov, Fig. 3D); anterior end of brood pouch (Bp) strongly reflected and very muscularized (Fig. 3D); penis without specialized glands.
<i>Mexipyrgus-Durangonella</i>	Shell elongate-conic to turriiform (Figs. 1D, E); pallial oviduct with posterior coil in several complex loops; albumen gland reduced to mere glandular smear; seminal receptacle (Sr) connects with oviduct (Ov) via a short sperm duct (Sdu, Fig. 3B); anterior end of brood pouch (Bp) weakly reflected and slightly muscularized (Fig. 3C); penis with ciliated tip.

The basin drainage, while currently isolated, lies in close proximity to the Río Grande (= Río Bravo del Norte) drainage to the east and has likely had repeated connections with these waters in the recent past (Minckley 1969, 1978). Taxa assignable to the Nymphophilinae and Littoridininae on the basis of penis type (i.e., *Fontelicella* and *Pyrgophorus*, respectively) are found in nearby waters of northern México and southwest Texas.

The lack of marked differentiation of snail taxa within the basin may also suggest a young fauna; only three of the nine genera have a second species in the basin and in only one case (*Coahuilix* spp.) are congeners sympatric. It should be noted, however, that even over a long period of time speciation within the basin might be infrequent as the basin is small and its drainages have continually shifted through time (reducing the probability of continuous isolation of given springs).

The now-recognized smaller scale of endemism, similarity of endemics to non-endemics within the basin, proximity of the basin to outside drainage, and low level of intra-basin differentiation point to a recent (late Cenozoic?) and local origin for the endemic snail fauna. Note that the three genera that are definitely endemic to the basin (*Nymphophilus*, *Mexipyrgus*, and *Mexithauma*) are all inhabitants of large springs. Rapid *in situ* evolution of these genera (from the non-endemics they resemble) could have occurred as a result of intense cichlid predation within the large springs selecting for large, thickened shells, with soft parts changing less so. Rapid evolution of freshwater snail genera has been documented in several cases (Davis 1979, 1981; Stanley 1979).

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