

MICROGEOGRAPHIC VARIATION IN THE BANDED SPRING SNAIL  
(HYDROBIIDAE: *MEXIPYRGUS*) FROM THE CUATRO CIÉNEGAS BASIN,  
COAHUILA, MÉXICO

Robert Hershler

*Department of Invertebrate Zoology, National Museum of Natural History,  
Smithsonian Institution, Washington, DC 20560, U.S.A.*

W.L. Minckley

*Department of Zoology, Arizona State University, Tempe, Arizona 85287, U.S.A.*

ABSTRACT

Microgeographic variation is documented among 16 populations of the aquatic snail *Mexipyrgus churinceanus* Taylor from El Mojarral spring system in Cuatro Ciénegas, northern México. Patterns of variation among these snails include a steep cline linking two nominal species, and a gentler one tending to link one of these with a third nominal species from an adjacent spring system.

The form of these clines is apparently explained by the presence or absence of gene flow barriers in the spring system, although alternative explanations are discussed. A review of ideas on the origin of aquatic habitats in the basin suitable for *Mexipyrgus* suggests that the clines represent secondary intergradation, with divergence having occurred in allopatric populations isolated by desiccation of a barriar lake(s) or fragmentation of a massive, continuous spring, and secondary contact made possible by reintegration of habitats. The results, suggesting genetic exchange among distinctive populations having restricted distributions, support an earlier contention that these populations comprise a single, polytypic species.

Key words: Hydrobiidae; Cuatro Ciénegas; springs; morphology; variation; clines.

INTRODUCTION

Aquatic prosobranch snails of the genus *Mexipyrgus* Taylor, 1966 (Gastropoda: Hydrobiidae), endemic to the desert valley of Cuatro Ciénegas, northeastern México, provide outstanding examples of localized morphological differentiation. Distinctive populations are distributed among spring-fed pools and stream outflows of springs in this small, 1200 km<sup>2</sup>, endorheic, intermontane basin (Taylor, 1966; Taylor & Minckley, 1966; Hershler, 1984, 1985). Two contrasting opinions have been put forward regarding their taxonomic status: Taylor (1966) described six species from seven collecting sites; and Hershler (1985) reduced the genus to monotypy (*Mexipyrgus churinceanus* Taylor), based on principal component analysis of data from more than 30 localities. Systematic problems associated with allopatric populations (Mayr, 1963; Wiley, 1981) are thus epitomized by these animals.

While spring-fed pools in the basin are insular in nature, some have outflows interconnecting with other outflows or spring pools, providing possible contact zones between populations. The snail is habitat-specific, occurring only where there are ample and invariable sources of water, gentle or negligible currents, warm and constant temperature, and substrate consisting of an accumulation of soft, flocculent sediments (Taylor, 1966; Hershler, 1984, 1985). Physically connected places that provide continuous habitat of this type are rare. Discovery of a zone of syntopy would be of great value in providing a measure of evolutionary divergence among distinctive stocks.

One interconnected series of large springs and outflows in an area locally known as El Mojarral contains type localities of two nominal species of *Mexipyrgus* (*sensu* Taylor, 1966). Evidence was sought of syntopy, allotropy, and/or intergradation involving these as well as a third nominal species from an adjacent spring system. We here describe

microgeographic variation of snails in the Mojarral area, comparing patterns of morphology in a relatively continuous habitat with those in one with apparent barriers to gene flow. Opportunity also is taken to report additional hydrographic descriptions and interpretations which pertain to origins, age, and evolutionary history of the basin and its unique biota.

### STUDY AREA, MATERIALS, AND METHODS

*Description of the area.* Average annual rainfall of less than 200 mm (Vivo Escoto, 1964), coupled with high temperatures and evaporation rates, disallows other than storm-induced runoff, and permanent aquatic habitats in the Cuatro Ciénegas Basin are fed exclusively by springs (Minckley, 1969). Water rises near ends of bajadas with considerable force, its artesian nature indicating an origin at high elevation such as from precipitation on the eroded, north-plunging Sierra de San Marcos anticline. Massive Cretaceous limestones of surrounding mountains (Baker, 1971) are characterized by permeable strata and solution channels through which water may pass until forced upward by obstructing faults of basin margins.

Minckley (1969) presented a simplistic explanation of origin and succession in most present aquatic habitats of the basin, beginning with development of solution channels. Such channels presumably founded as the basin was dewatered to form pits (*pozos*) that expanded by lateral collapse to form lake-springs or limnocrenes (*lagunas*). Further slumping of banks produced increased surface area and heterogeneity, followed by vegetation invasion and development of marshlands (*ciénegas*). Surface streams were further proposed to represent founded subterranean waterways. Downflow, dune-impounded or otherwise formed lentic habitats developed into terminal, shallow, variably mineralized barrial (basin floor) lakes. With climatic changes toward greater aridity (Van Devender, 1976, 1977; Wells, 1978; Axelrod, 1979) the successional sequence ends in formation of extensive playas, wet only after periods of rainfall.

*El Mojarral.* A series of springs and marshlands comprising El Mojarral is about 11.5 km SW of the town of Cuatro Ciénegas (Minckley, 1969; Fig. 2). The drainage (Fig. 1)

includes three major spring pools: Mojarral West Laguna; "Middle spring," and Mojarral East Laguna. Extensive *ciénegas* lie between and adjacent to pools, and a number of smaller springs, streams, and marshes are upslope (south) of the major part of the system. Drainage of El Mojarral is N and E toward an eastern sump. A surface outflow of Mojarral West enters "Middle spring," whose surface outflow in turn (and in part) enters Mojarral East. There also are underwater outflows (black dots in Fig. 1); one from Mojarral West Laguna is via a large, tubular vent in the eastern end. Underwater inflow (open circles in Fig. 1) and outflows in "Middle spring" are similarly large and tube-like, and a number of smaller springs rise from the floor of the western end of Mojarral East. The surface outflow of Mojarral East receives several small, surface distributaries of the Río Mesquites (arrows in Fig. 1), and ultimately joins that river, the largest in the basin (not included in Fig. 1).

Spring inflows to the Mojarral system are thermal at 30 to 35° C and characterized by hard water of crystal clarity. Depths of pools range from less than 1.0 to 4.7 m. They are unshaded except locally by banks; sunlight penetrates to the bottoms. All may have common groundwater sources or are linked by subterranean conduits, given their linear alignment, proximity, and similarities in water quality. Slight temperature decreases downflow may thus represent cooling of groundwater in travel from its source, or may indicate multiple sources. Reductions in EDTA water hardness downflow from Mojarral West Laguna (to Mojarral East Laguna) indicated by Minckley & Cole (1968) (1254 vs. 1208 mg/l) were probably not significant. Values in the two springs were actually or essentially the same in 1966 and 1968 (1234 mg/l in each and 1236 vs. 1249, respectively; Arnold, 1972; Minckley, unpublished data). Attempts to trace subterranean flow from Mojarral West to "Middle spring" by copious application of fluorescein dye in 1968 and 1970 failed (Arnold, 1972; Minckley, unpublished data). Dye was not detected by eye or through use of activated charcoal collectors examined under strong ultraviolet light at various, presumably appropriate times following repeated dye application. Discharge volumes are great and dye dilution was either too high or subterranean distances and complexities far greater than anticipated.

Spring pools have little substrate diversity,

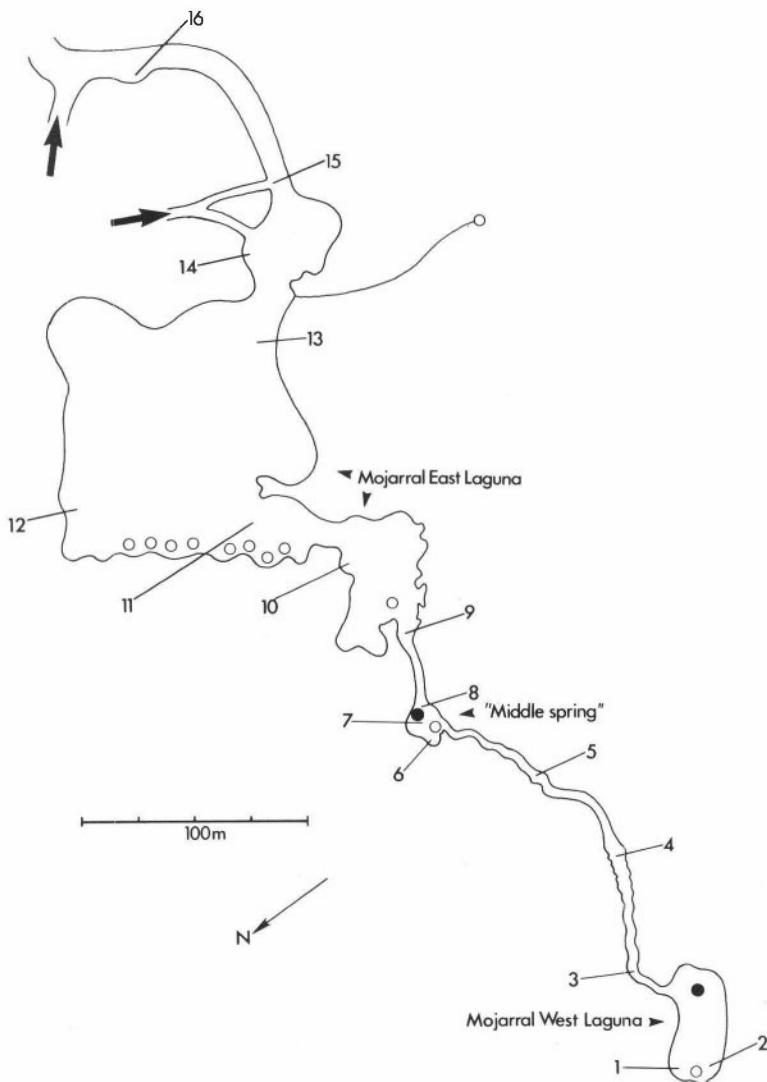


FIG. 1. Map of El Mojarral drainage showing the location of 16 sampling points. Open and filled circles indicate spring orifices and underwater outflows, respectively. The large arrows to the E indicate inflowing branches of the Río Mesquites.

consisting predominantly of flocculent, organic, copropellic sediment less than 1.0 cm to greater than 0.5 m deep that overlies firmer layers of bits of travertine and snail shell. Exposed shell and travertine fragments armor areas where currents remove copropellic materials. Local stands of waterlily (*Nymphaea ampla* [Salisb.]) vegetate some bottoms, sparse beds of sedges are in shallows, and stony travertine deposits comprise shorelines and bottoms adjacent to inflows.

*Nominal taxa.* Three nominal species of *Mexipyrgus* are in the Mojarral area, capsule descriptions for which are as follows (modified from Taylor, 1966).

- 1) *Mexipyrgus mojarralis* Taylor. Shell (Fig. 3A-F) small, 4.5–5.0 mm high; spiral sculpture well-developed on body whorl; periostracal bands few (two to four) in number, with thickened subsutural band usually

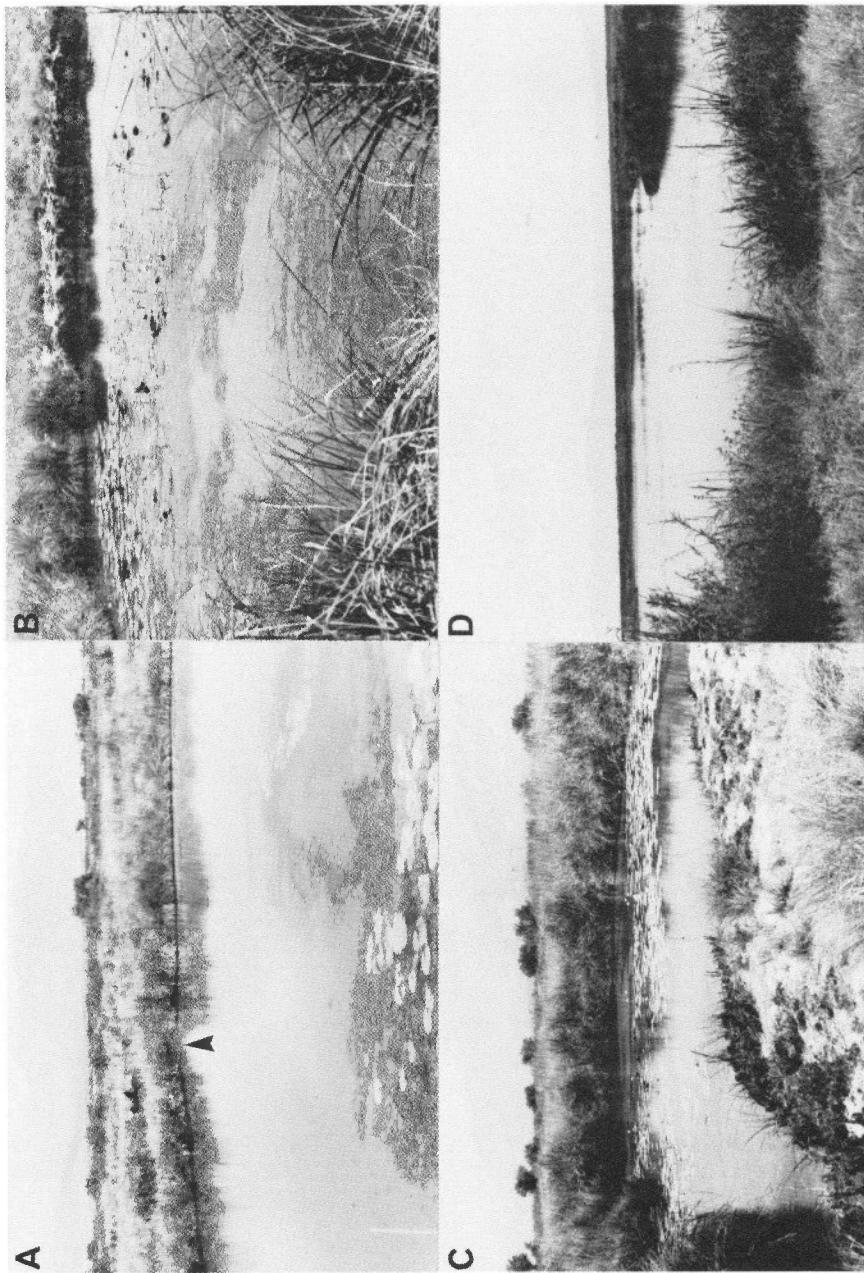


FIG. 2. El Mojarral spring pools. A. SE portion of Mojarral West Laguna. Note the waterlily stand in the foreground and underwater outflow tube to the right. The arrow indicates the surface outflow. B. Northern half of "Middle spring." Note the waterlily stand crossing the spring. C. "Middle spring" viewed from the S. Riparian vegetation in the foreground has been largely removed by a recent fire. The surface outflow is in the lower left. Again note the extensive waterlily stand. D. Mojarral East Laguna, viewed from the N.

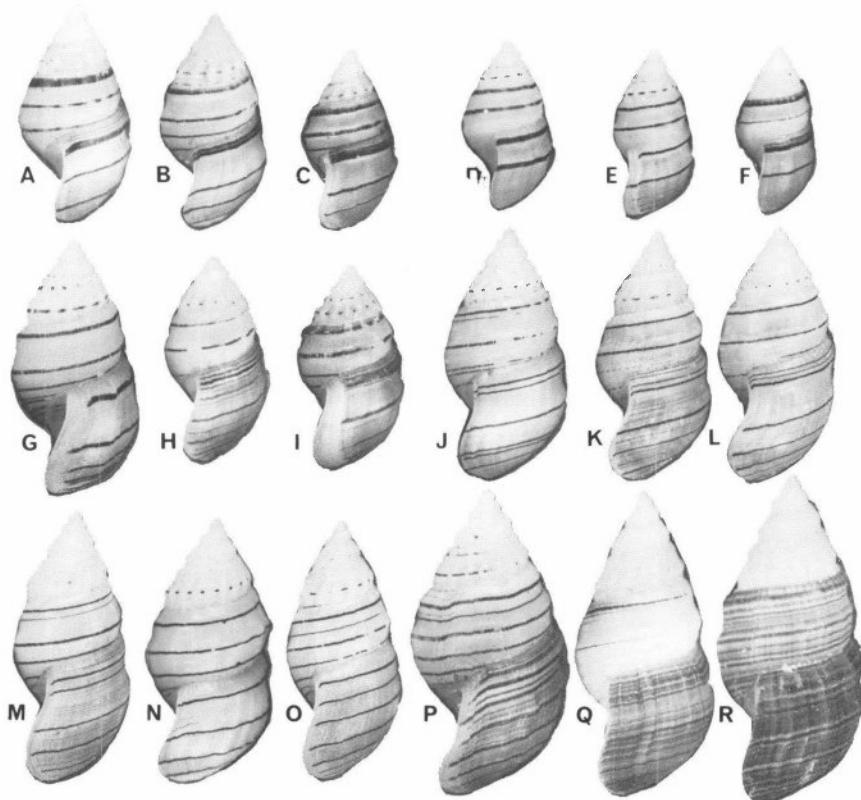


FIG. 3. Photographs of shells of *Mexipyrgus churinceanus* from El Mojarral. The shells are from localities 2 (A-C), 6 (D-F), 9 (G-I), 12 (J-L), 14 (M-O), and 16 (P-R). Shell "A" is 4.89 mm in height and the other photos are printed to the same enlargement.

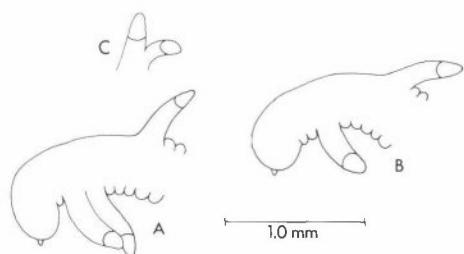


FIG. 4. Penial variation seen among *Mexipyrgus churinceanus* from El Mojarral. Note the variation in number of lobes on the inner curvature (A, B) and occasional presence (C) of an additional lobe on the outer curvature.

present; penis with a single (not two as implied in Taylor, 1966) lobe on the inner curvature (Fig. 4B). Type locality, Mojarral West Laguna.  
 2) *M. multilineatus* Taylor. Shell (Fig. 3J-O) intermediate in size, 5.0–5.1 mm high; spiral sculpture poorly defined on body whorl; up to 20 bands present, with thickened subsutural band absent; penis with one or two lobes on inner curvature (Fig. 4). Type locality, Mojarral East Laguna.  
 3) *M. lugoi* Taylor. Shell (Fig. 3P-R) large, 7.3 mm high; spiral sculpture on body whorl poorly developed; 25–35 bands present, with thick-

TABLE 1. Collection sites for this study, numbered as in Fig. 1, with collection dates and USNM (National Museum of Natural History) catalog numbers for samples in parentheses.

1. Mojarral West Laguna, 16 m S of N end, right offshore of E side, 3 cm deep (3/11/81) (850287).
2. Mojarral West Laguna, 4 m S of NW corner, right offshore, 1 m deep (3/19/81) (850285).
3. Stream from Mojarral West Laguna, 20 m downstream from spring (12/12/81) (850281).
4. Stream from Mojarral West Laguna, 80 m downstream from spring (12/12/81) (850288).
5. Stream from Mojarral West Laguna, 42 m above entrance to "Middle spring" (12/12/81) (850276).
6. "Middle spring," 1 m S of N corner, 5 m W of E side, 2 m deep (12/14/81) (850277).
7. "Middle spring," 8 m S of N tip, 6 m W of E side, in *Nymphaea* "reef," 7 cm deep (12/14/81) (850286).
8. "Middle spring," 1 m N of S tip, 3 m E of W side, 1 m deep (12/14/81) (850282).
9. Mojarral East Laguna, western lobe, at inflow from "Middle spring" (12/14/81) (850279).
10. Mojarral East Laguna, western lobe, 13 m NW of connection to eastern lobe, 0.7 m deep (12/14/81) (850284).
11. Mojarral East Laguna, eastern lobe, 53 m SE of connection to western lobe, 1 m deep (3/18/81) (850274).
12. Mojarral East Laguna, eastern lobe, 11 m S of NE corner, 7 m offshore (2/14/81) (850278).
13. Mojarral East Laguna, eastern lobe, 40 m N of SW corner, right offshore (3/17/81) (850273).
14. Stream from Mojarral East Laguna, 30 m downstream from spring, east side, near inflow from first arm of the Rio Mesquites (12/14/81) (850283).
15. Stream from Mojarral East Laguna, at inflow of the second arm of the Rio Mesquites (12/14/81) (850275).
16. Stream from the Mojarral East Laguna, shallow pooled area, N side of stream, just above inflow of third arm of the Rio Mesquites (12/14/81) (850280).

ened subsutural band absent; penis with two lobes on inner curvature (Fig. 4A). Type locality, Rio Mesquites, one to two km upflow from confluence with outflow of Mojarral East Laguna.

**Specimens examined and methodology.** Specimens of *Mexipyrgus* were collected during March and December 1981 from 16 sampling points along a transect through the El Mojarral system (Fig. 1). Precise locality

data are in Table 1. At each locale 100–300 individuals were secured by repeated sweeps of a fine-meshed hand sieve through soft sediments within a randomly chosen area not exceeding 4.0 m<sup>2</sup>. Snails were relaxed in the field using menthol crystals, fixed in dilute formalin, and preserved in 70% ethanol.

A series of adults, recognized by completion and thickening of the inner shell lip, was chosen from each sample; empty shells were excluded. Relaxed snails were readily sexed by noting presence or absence of the penis. The following features, including all those used in diagnoses of nominal species (excepting shell sculptural pattern), were scored, counted or measured (numbers per sample in parentheses) as follows: presence or absence of banding on the outer shell lip (100); presence or absence of a thickened subsutural band (relative to other shell bands) on the outer lip (50 banded shells); number of bands on the outer lip (50 banded shells); shell length (15 females); and number of lobes on inner and outer curvature of the penis, expressed as an "inner-outer" formula (25 males). In addition, the following shell parameters were measured or counted for 15 individuals of each sex from five of the 16 sampling points (2, 8, 12, 14, and 16; Fig. 1): shell height (SH), shell width (SW), length of body whorl (LBW), aperture height (AH), aperture width (AW), and number of whorls (WLS). Measurements were made at 25× using a Wild M-5 dissecting microscope fitted with an ocular micrometer. All shell bands distinctive at 25× were counted.

Descriptive statistics were generated using the computer-mediated SAS program, while ANOVA and Tukey HSD multiple range test ( $p = .05$ ) were performed using SYSTAT (Wilkinson, 1984). CLUSTAN (Wishart, 1978) was used to extract principal components from the correlation matrix of shell morphometry data, with separate analyses for males and females.

## RESULTS

Summary statistics are in Tables 2, 4, and 5, with frequencies or mean values of several characters plotted by collecting station in Fig. 5. Results of Tukey HSD Test for multiple comparisons among means of shell heights are in Table 3.

Several kinds of variation were evident

TABLE 2. Summary data for morphologic features scored or measured for samples from 16 localities. The numbers of individuals used are indicated in parentheses.

Locality	Mean adult shell length (♀, n = 15)	Frequency of banded shells (n = 100)	Mean number of bands on the shell (n = 50)	Frequency of shells with a thickened subsutural band (n = 50)	Frequency of males with the following penial formulae (n = 25):		
					1-1	2-1	Other
1	4.10	99	4.10	78	96	—	4(0-1) (n = 26)
2	4.81	100	4.38	96	96	—	4(0-1) (n = 26)
3	4.71	100	5.76	86	100	—	—
4	5.08	100	6.20	88	100	—	—
5	4.89	96	5.72	94	100	—	—
6	3.96	95	5.12	86	100	—	—
7	4.34	83 (n = 113)	6.66	90	96	—	4(0-1)
8	5.16	73	7.74	60	96	4	— (n = 26)
9	5.70	68	10.0	56	94	3	3(1-2) (n = 33)
10	5.23	41	13.0	0	91	3	3(1-2); 3(2-2) (n = 34)
11	5.28	25	12.1	2	85	6	6(0-1); 3(1-2) (n = 33)
12	5.97	15	8.74	0	83	17	— (n = 30)
13	6.48	19	13.9 (n = 42)	5 (n = 42)	61	36	3(0-1)
14	6.38	50	17.7	2	60	32	4(0-0); 4(1-2)
15	7.30	66	20.8 (n = 38)	3 (n = 38)	32	52	4(0-0); 4(2-0); 8(2-2)
16	7.29	88	22.9 (n = 32)	17 (n = 35)	16	84	—

TABLE 3. Results of the Tukey HSD multiple comparison test among means for shell height. The means (station numbers in parentheses) are ranked by magnitude on the left, and groups of stations containing means that do not differ significantly ( $p = .05$ ) from one another are indicated to the right.

3.96 (6)	6, 1
4.10 (1)	1, 7
4.34 (7)	7, 3
4.71 (3)	3, 2, 5
4.81 (2)	2, 5, 4, 8, 10
4.89 (5)	4, 8, 10, 11
5.08 (4)	11, 9
5.16 (8)	9, 12
5.23 (10)	14, 13
5.28 (11)	16, 15
5.70 (9)	
5.97 (12)	
6.38 (14)	
6.48 (13)	
7.29 (16)	
7.30 (15)	

(Fig. 5). Size (SH), although variable and even differing significantly among sampling points within the relatively small Mojarral West (Table 3), showed a general pattern of gradual increase downflow, with overlap especially common among adjacent, upflow sampling points. Note that significant breaks in size occurred at sampling point 9 and others downflow (Table 3). Numbers of shell

bands increased downflow in a similar fashion. Overlap was again pronounced upflow, with, for instance, no significant differences among any pairs of samples from points 1-8 (Tukey HSD Test,  $p > 0.05$ ). Variation in subsutural banding involved a steep cline, with high frequencies of thickened banding upflow declining sharply to near-zero frequencies downflow (Table 2). Frequency of thickened banding for sampling points 8 and 9 (58%, pooled data) differed significantly with either pooled data from upflow points 1-7 (88%) or downflow sampling points 10-16 (3%) (separate Chi-square tests with continuity corrections,  $p < .001$  for both comparisons).

Snails from not only Mojarral West (sampling (points 1 and 2; Fig. 3A-C), but also its outflow points 3-5) and the two northernmost points in "Middle spring" (points 6, 7; Fig. 3D-F) are clearly referable to *Mexipyrgus mojarralis*. Small size (SH less than 5.1 mm), few shell bands (fewer than 7), high frequency of thickened subsutural banding (greater than 78%), well-developed spiral sculpture on the body whorl, and a "1-1" penial type are characteristic (Table 2). Snails from the next two downflow sampling points (8, 9; Fig. 3G-I) were intermediate between *M. mojarralis* and *M. multilineatus*. Non-thickened subsutural banding, rarely seen in upflow *M. mojarralis*, was common, and a few individuals had the "2-1" penial type not seen

TABLE 4. Shell measurements for females from five localities. For all samples, n = 15. For explanation of abbreviations see p. 362.

Locality		Parameter					
		SH	SW	LBW	AH	AW	WLS
2	̄x	4.80	2.65	3.22	1.79	1.60	6.13
	s	0.167	0.101	0.124	0.087	0.061	0.160
8	̄x	5.16	2.67	3.37	1.93	1.63	6.43
	s	0.456	0.221	0.261	0.178	0.102	0.506
12	̄x	5.97	3.00	3.90	2.17	1.87	6.42
	s	0.464	0.143	0.220	0.123	0.101	0.376
14	̄x	6.38	3.05	3.93	2.19	1.87	6.87
	s	0.346	0.133	0.209	0.125	0.067	0.229
16	̄x	7.29	3.67	4.64	2.65	2.25	6.95
	s	0.361	0.190	0.230	0.172	0.101	0.254

TABLE 5. Shell measurements for males from five localities. For all samples, n = 15. For explanation of abbreviations see p. 362.

Locality		Parameter					
		SH	SW	LBW	AH	AW	WLS
2	̄x	4.14	2.19	2.81	1.63	1.41	6.00
	s	0.210	0.094	0.108	0.057	0.042	0.267
8	̄x	4.61	2.42	3.10	1.85	1.56	6.17
	s	0.207	0.191	0.152	0.119	0.106	0.244
12	̄x	5.67	2.71	3.82	2.19	1.83	6.43
	s	0.243	0.061	0.098	0.102	0.056	0.200
14	̄x	5.82	2.78	3.82	2.15	1.86	6.63
	s	0.262	0.118	0.156	0.128	0.078	0.160
16	̄x	6.28	3.17	4.11	2.52	2.09	6.54
	s	0.276	0.092	0.180	0.128	0.091	0.229

upflow. Widespread character discordance occurred (i.e., individuals with *M. mojarralis* sculpture, yet *M. multilineatus* banding). Separation of snails from these points on the basis of subsutural banding type yielded groups (thickened banding, mean SH = 5.35 mm, N = 21; non-thickened, 5.47 and 20 respectively) that did not differ in size (t-test,  $p > 0.2$ ), further indicating that syntopic taxa were not present.

Snails from sampling points 10–13 resembled *Mexipyrgus multilineatus*, but trends among these points and those further downflow involving increasing size, number of bands, and frequencies of "2-1" penial type, indicated apparent gradation toward a more *M. lugoi*-like snail (Fig. 3J-R). Note that snails from point 16 remained transitional in morphology in that 100% occurrence of the "2-1"

penial type (typical of *M. lugoi*, *fide* Taylor, 1966, and Hershler, 1985) was not present. Again, syntopic taxa were not recognizable at any point.

Principal components analysis was used to gauge distinctiveness of populations referable to the three nominal species (sampling points 2 and 12 as respective topotypes of *Mexipyrgus mojarralis* and *M. multilineatus* and snails from sampling point 16 as a population trending strongly toward *M. lugoi*) as well as two populations from intermediate geographic positions (points 8 and 14). Scores for the first two principal components are in Fig. 6 (females) and Fig. 7 (males). Topotypes of *Mexipyrgus mojarralis* (sampling point 2) and *M. multilineatus* (point 12) are broadly separated, especially males (Fig. 7), while an intermediate state of specimens

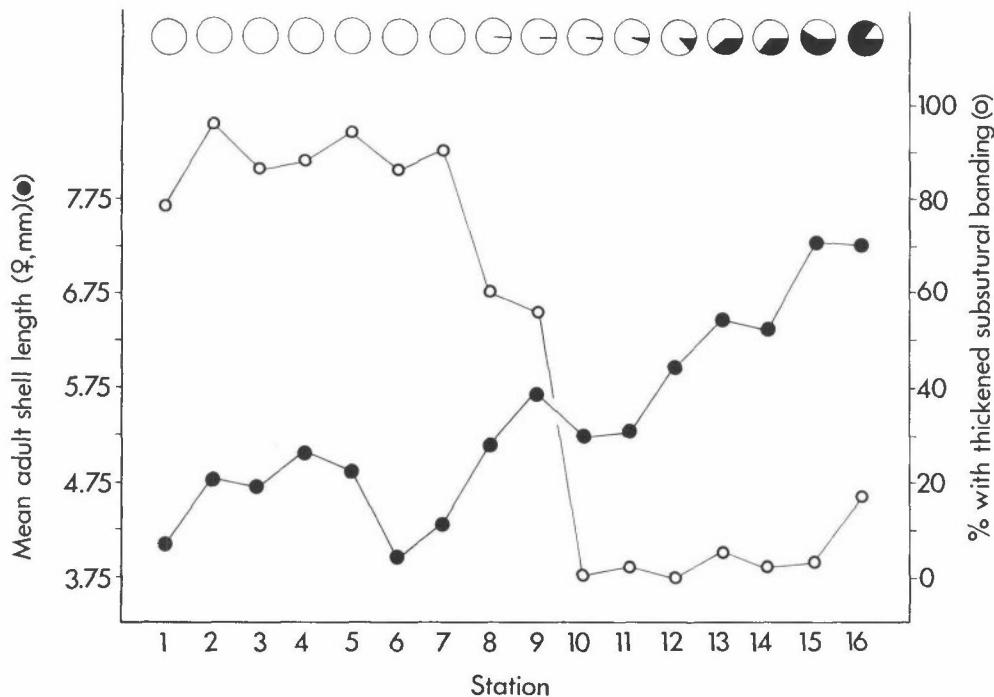


FIG. 5. Variation among localities of mean value of shell length, frequency (%) of occurrence of a thickened subsutural band, and penial lobation (circles above top of plot). Variation in penial lobation is expressed as relative frequency of "1-1" (light) versus "2-1" (dark) types.

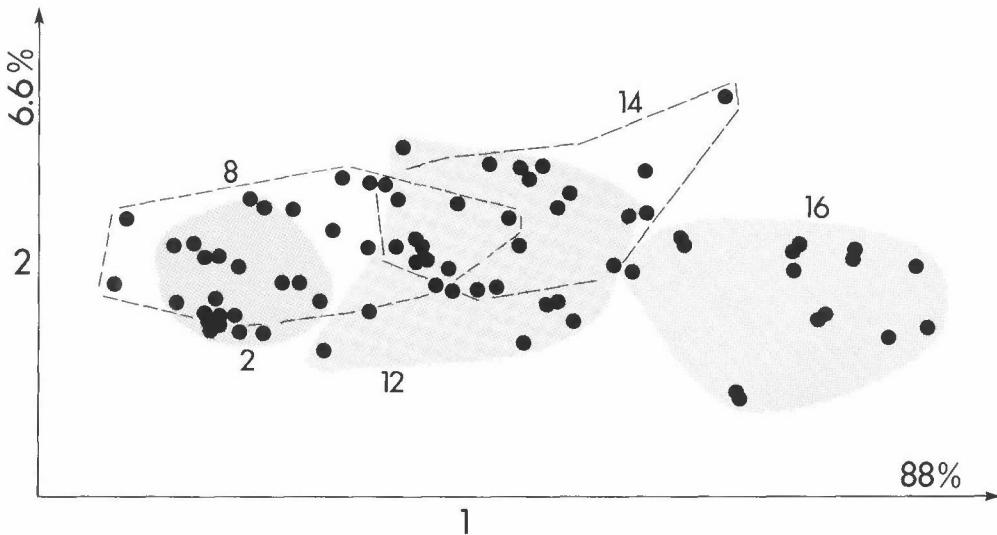


FIG. 6. Plot of scores of first two principal components extracted from the female shell data set.

from point 8 is clearly defined. Variability in the last sample, expressed as mean coefficient of variation for the six shell parameters

(males, 5.74; females, 7.51), also is elevated relative to that seen in animals from sampling points 2 (4.03, 3.74) and 12 (3.31, 5.86).

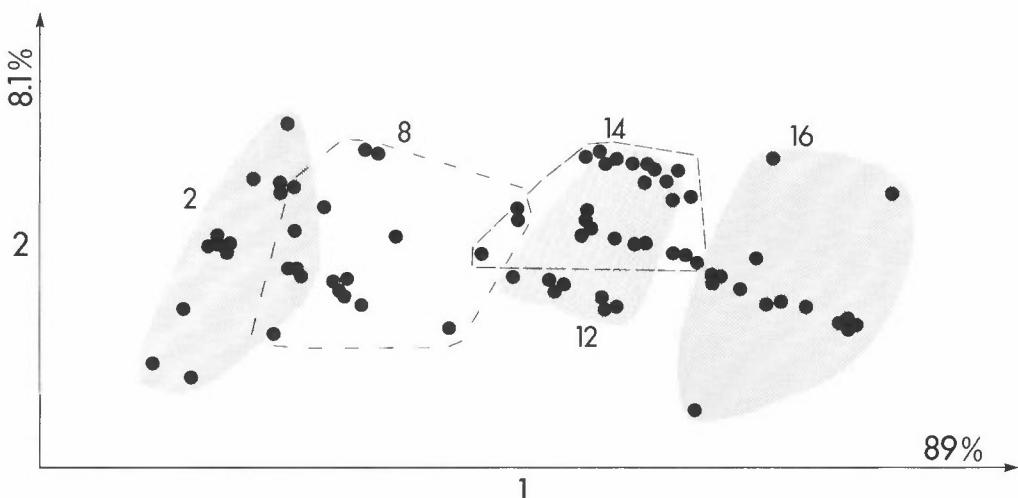


FIG. 7. Plot of scores of first two principal components extracted from the male shell data set.

While topotypes of *Mexipyrgus multilineatus* are less separated from the population trending toward *M. lugoi* (sampling point 16), neither sex from sampling point 14 occupied a morphologically intermediate position, nor did they exhibit elevated variation relative to the other two (locality 14, males 4.22, females 4.62; locality 16, males 4.10, females 4.96; data for locality 12 given above). Separation is largely along the first principal component, which accounts for 88–89% of total variation and is clearly related to size given high positive coefficients of all shell parameters (Table 6). The major role of size or size-dependent shape also is indicated by significant correlations ( $p < .05$ ) between shell height and the other five parameters (males, 78% of possible comparisons significant; females, 92%). Distinctiveness of the *M. lugoi*-like population in this light is largely attributable to the significant increases in size among downflow populations (Table 3).

#### DISCUSSION AND CONCLUSIONS

We conclude that upstream to downstream genetic exchange among populations in the Mojarral system is evident: 1) we were unable to demonstrate syntopy between forms; 2) there was an absence of absolute barriers that would promote allotropy and *Mexipyrgus* was almost continuously distributed along a transect of 16 sampling points; and 3) there seems to be ample evidence for clinal

intergradation of morphological characters along geographic and habitat gradients.

*Clinal variation.* Clinal variation among interfertile populations is not surprising (Endler, 1977), especially in a sedentary, ovoviparous animal that lacks broadcast gametes or larvae. However, the two patterns that exist, a steep cline linking *Mexipyrgus mojarralis* with *M. multilineatus* and a more gentle one that tends to connect *M. multilineatus* and *M. lugoi*, require further explanation.

Steep clines predictably occur in areas having reduced (Endler, 1977) or punctuated gene flow, rather than consistent temporal and/or spatial passage of genetic material. The zone of steepness in the Mojarral system, at the southern end of "Middle spring" and entrance into Mojarral East (sampling points 8, 9), occurs coincident with a major habitat discontinuity. Soft substrate is essentially absent in the lowermost 60 m of surface stream from Mojarral West Laguna as well as from the virtual entirety of stream connecting "Middle spring" and Mojarral East. In both cases water flows swiftly over bare travertine. Only unidirectional and perhaps infrequent gene flow is therefore likely, with snails occasionally displaced downstream by currents or drifted with algal mats (at least as young), floating due to accumulation of photosynthetic gasses (Arnold, 1972). Any possible continuity of soft bottom type is further interrupted within "Middle spring" by steep (near vertical) slope of a travertine or travertine-armored, *Nymphaea*-covered reef, that largely sepa-

TABLE 6. Principal components analysis of shell parameters.

Parameter	Females		Males	
	PCI	PCII	PCI	PCII
Shell height	0.428	0.047	0.425	0.038
Shell width	0.420	-0.308	0.417	-0.242
Length of body whorl	0.395	0.076	0.424	-0.089
Aperture height	0.421	-0.231	0.418	-0.263
Aperture width	0.419	-0.322	0.425	-0.166
Number of whorls	0.362	0.860	0.331	0.914

rates the spring into two halves (Fig. 8). This may either represent part of a collapsed roof of the spring or an accumulated travertine postdating such an event. Transport may also occur through subsurface channels possibly connecting at least Mojarral West with "Middle spring" and perhaps Mojarral East. Substrate and other conditions in underground conduits are unknown.

Contrasting lack of evident habitat discontinuity provides an apparent explanation for the uniform cline trending from *Mexipyrgus multilineatus* toward *M. lugoi*. Although much of the western portion of Mojarral East Laguna is floored by travertine, pockets of copropellic sediments are present and bottoms of the eastern two-thirds and the laguna outflow are almost continuously of copropel. The laguna is relatively large, and most currents are from wave action despite a net linear flow from west to east. Such should allow multidirectional active and passive dispersal, and if gene flow occurs it should produce a gradual (net) pattern of influence in the same direction, as was observed in morphology.

Although these explanations appear reasonable, other alternatives exist that merit some speculation. One viable option relates to changes in selection pressure, which can also effect clinal variation (Endler, 1977). In Cuatro Ciénegas, differential predation pressure by a molluscivorous form of the polymorphic fish *Cichlasoma minckleyi* Kornfield & Taylor<sup>1</sup> which feeds heavily on hydrobiids (Taylor & Minckley, 1966; Sage & Selander, 1975; Kornfield *et al.*, 1982), has already been proposed as a major evolutionary force (Vermeij & Covich, 1978). *Cichlasoma minckleyi* is a visual predator, fanning aside soft substrates to expose and eat *Mexipyrgus*, and foraging in vegetation

and over hard bottoms in search of other molluscan prey (e.g. *Mexithauma quadrivalidum* Taylor and *Nymphophilus minckleyi* Taylor). Decreased incidence of periostracal banding on *Mexipyrgus* in Mojarral East (Table 2, 15–18%) compared to upstream sampling points (77–100%) may indicate that unbanded snails appear more cryptic on or in the light-colored sediments in shallow water. Sediments in Mojarral West are comparably light, but the spring is smaller and deeper, with more shading from banks and travertine ledges that may impart a selective advantage to a more heavily banded shell. A significant increase in shell size at the northern end of Mojarral East Laguna could also reflect an increased selective pressure, with increased size reflecting adaptation affording resistance to a crushing predator (Vermeij & Covich, 1978).

Predation by fishes could also influence population sizes of snails, which in turn might be reflected in temporal changes such as stunting or other density dependent factors. Possibly density dependent influences on sculpture, periostracal banding, etc., are not apparent. No quantitative data on *Mexipyrgus* populations other than a maximum density of 49,000 individuals/m<sup>2</sup> (Hershler, 1985) are available. Differential abundance of the molluscivorous form of cichlid relative to another (detritivorous) form, or changes in absolute abundance (and thus influence) of the predator due to variations in year class strength, might also be significant factors in such a system. As for snails, no adequately quantitative data exist on population size of the basin's fishes (see, however, Minckley, 1984). Hershler's (1985) comment that temporal variations in snail size occur at a given locality was based on casual observation and

<sup>1</sup>Minckley (1984) perceived the Cuatro Ciénegas cichlids to comprise a flock of distinct species rather than a single, polytypic form; the history of the discovery of, and research on, this fascinating problem was reviewed and further discussed by Williams *et al.* (1984).

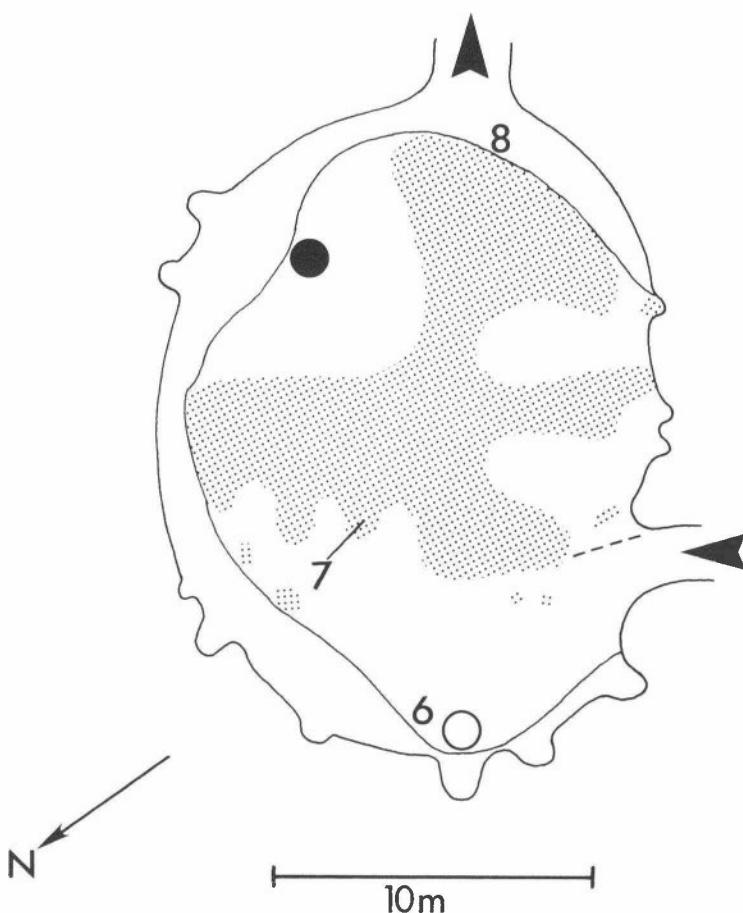


FIG. 8. Map of the "Middle spring." The location of sampling points 6-8 is shown, as are the positions of the large spring orifice (open circle), underwater outflow tube (closed circle), surface inflow and outflow streams (arrows), and extent of the elevated *Nymphaea* reef (stippled). The area in between the outline of the spring and inner line continuing around most of the spring circumference is bare travertine. The N edge of the reef, as well as the area just E of the stream inflow (indicated by a dashed line) are elevated above the bottom of the spring.

has not yet been tested. Another possibility is that sizes of *Mexipyrgus* in Cuatro Ciénegas relate to habitat conditions. The unusually small shell of *M. mojarralis*, for example, could reflect warm water, and the larger shell of *multilineatus* a phenotypic response to cooler or slightly varying water temperatures. Retention of juvenile characters, small size relative to other populations, and various anomalies have been demonstrated in warm-spring fishes (Hubbs, 1959; Miller, 1961; Deacon & Minckley, 1974; Hubbs *et al.*, 1974). However, there seems little correlation among water temperatures and shell size within the Cuatro Ciénegas basin, e.g.

*Mexipyrgus* from Laguna Escobeda, one of the warmest large springs, are not exceptionally small relative to animals from cooler habitats such as Laguna Tío Cándido, and are larger than specimens from slightly cooler Mojarral East (Taylor, 1966; Hershler, 1985, fig. 37, table 48). Further, *Nymphophilus minckleyi* from three diverse habitats do not differ significantly in size (warm, Mojarral East; cool, Laguna Tío Cándido; variable, Río Mesquites; Hershler, 1985, table 3).

*Primary or secondary intergradation?* An answer to the question of primary vs. secondary intergradation necessitates reexamination of ideas on origins of aquatic habitats now

occupied by *Mexipyrgus*. The following scenario was presented for evolution of large laguna systems:

"Development of these complex lake-springs begins with sinkhole formation. Subsequently, in a actively-flowing aquifer-system, foundering and possible dissolution of the banks produce a linear, tortuous channel. In systems on the barrial, far from the mountain fronts, continuing headwater foundering probably produces elongate channels similar to that occupied by the Río Mesquites" (Minckley, 1969: 18-19).

Minckley (unpublished data) is now convinced that aggradation may have played as great an alternative role in formation of present-day habitats as do processes of chemical dissolution, foundering, and erosion. Travertine deposits, often masked by accumulation of evaporites or overgrowth of halophytes in moist areas, are substantially more extensive throughout parts of the basin fed by mineralized water than before realized. Included are linings for waterways that grow to enclose flowing streams, broad cones that elevate springs above surrounding terrain, and travertine shields downslope from outflows. These structures are most readily identified in places desiccated by lowering of water table due to canalization (Minckley, 1969, 1978; S. Contreras-Balderas, 1984) or natural processes. Similar fossil to modern deposits have been described for Miocene to Recent springs of the Verde Formation, Arizona (summarized by Donchin, 1983). Cole & Batchelder (1969) documented incipient roofing of a spring outflow by travertine. Minckley (1973) described isolation of an Arizona spring by formation of a travertine dam, as illustrated by Hendrickson & Minckley (1985, fig. 20). Travertine deposition may be chemical due to changes in pH, physical through release of pressure or evaporation, biogenic through algal activity, or a combination of all three processes (Bathurst, 1975; Hardie *et al.*, 1978).

In Cuatro Ciénegas and elsewhere, migration of spring sources and shifts in outflows have obviously occurred through irregular travertine impoundment. As discharge volumes vary, so do spatial relations of deposition. Springs break out to flow from bases of travertine tubes, domes, and shields so that

source migrations may occur in essentially any direction. Downslope movement of spring sources that might be expected with discharge decrease, for example, might be countered by travertine accumulation, so that sources remain near mountain fronts despite lowering of the basin floor due to dewatering (see below).

Origin of the molluscan fauna of such a system is problematical. Did the progenitor(s) of *Mexipyrgus* populations achieve a wide distribution through active, upflow dispersal over hard bottoms? Was an ancestral form widely distributed in an intermontane lake, then left as relicts as inflowing springs were isolated by dropping water level? Does the present spring complex represent remnants from a formerly massive, single outflow, fragmented by travertine deposition or other factors? Or, did an ancestor(s) arrive and become distributed within the area by passive means, such as in mud on the feet of waterbirds?

*Mexipyrgus* is so remarkably restricted to soft sediments that the first query seems readily rejected. Further, other hydrobiids in the basin that commonly occur on hard surfaces, e.g. *Mexithauma quadripaludium* and *Nymphophilus minckleyi* (Taylor, 1966; Hershler, 1984, 1985), show little intraspecific variation attributable to isolation. They presumably disperse (or dispersed in the past, assuming interconnection of now isolated habitats) at rates adequate to maintain panmixia.

Intermontane lakes were common in northern México during wetter periods of the Pleistocene (Miller, 1981). Some filled to top their basin walls or were captured by headward erosion of adjacent streams (Strain, 1966, 1971), while others had maximum levels controlled by climatic factors since they occupy basins that remain closed today. Highest stages of such lakes corresponded to an exceedingly wet period 22,500-15,000 years before present (ybp) (Wendorf, 1961). Minckley (1969) reported no evidence in the Cuatro Ciénegas basin for high level lacustrine conditions, e.g. wave-cut terraces or beachlines. He favored presence of lower level lakes on the barrial due to persistent (or periodic) drainage through deep, antecedent channels breaching surrounding mountains. Permanent shoreline marks are not necessarily formed in lakes of short duration or when water onlaps fine-grained sediments of bajadas or basin floors.

Perhaps stabilized dunes in the far western and eastern parts of the Cuatro Ciénegas basin (Minckley, 1969) are mute testimony to presence of such a lake(s). Barrial lake conditions were directly indicated in cores drilled by Mexican government workers (verbally reported to Minckley [unpublished data] as intended for petroleum exploration) in the late 1960s. Sediments in three cores drawn from the basin floor 2–3 km southwest of the village of Cuatro Ciénegas were uniformly saturated with water, malodorous, and variably light in color, with only minor interbedding of dark, apparently organic material. Soft, light-colored sediments appeared as alternating crystalline evaporites and dune sands. Other harder, stony materials were apparent marls, showing varve-like banding as in lacustrine beds deposited below depth of wave action. Thicknesses and depths of various layers below surface could not be ascertained, no conglomerate or travertine was seen, and the drillers did not encounter bedrock at maximum depths of 400–600 m.

In contrast, only minor indications of lake sediments appeared in the areas of present springs on or adjacent to bajadas of surrounding mountains. Four holes drilled by Mexican workers within 1.2 km of Sierra de San Marcos yielded fine-grained (calcareous) spring sediments, organic materials, and travertines, interbedded with angular fanglomerates typical of bajada surfaces (Minckley, unpublished data). Again, no depths or thicknesses of sediment layers could be determined, but drillers encountered limestone bedrock at 75 to 250 m. In that same area, Meyer (1972, 1973) documented a sequence of springs, ciénegas, travertine deposits, and adjacent grasslands similar to those existing today in sediments and pollens of two cores (6.2 and 13.9 m long). Varve-like banding was noted in short segments of his cores, but no extensive lake deposits were penetrated. The same evidences of little or no change in aquatic and/or terrestrial habitats and an absence of lake beds were in four additional cores 2.7 to 7.9 m long, taken at the same time at nearby places (Minckley, unpublished data). Radiocarbon dates near the bottom of Meyer's (1973) longest core indicated an age of ca. 30,000 ybp, providing an estimate of minimum age for springs to have been undisturbed by lacustrine inundation in the Cuatro Ciénegas basin.

Water chemistry of an intermontane lake might have been amenable for *Mexipyrgus* or

its ancestor(s) at a time of high inflow volume or external drainage. Present lakes on the floor of the Cuatro Ciénegas basin are almost certainly too saline and fluctuant in chemistry (Minckley & Cole, 1968; Arnold, 1972) to support the taxon. Climatic conditions might also have been more moderate, allowing for at least seasonal dispersal, yet the region has been at a temperate latitude (Dickinson, 1981) and presumably experienced thermal variations for millenia. Soft bottoms would have been available, or springs may have entered the bottom without or with minimal travertine formation due to hypolimnetic conditions.

Evidence of hydrobiid snails associated with lacustrine habitats of western North America is not uncommon. A possibility thus exists that the progenitor(s) of *Mexipyrgus* attained Cuatro Ciénegas springs through intralacustrine dispersal. In one example, however, an abundance of fossil and subfossil *Tryonia protea* (Gould) and lesser numbers of *Fontelicella longinqua* (Gould) around the Salton Sea, California (Gregg & Taylor, 1965; Taylor, 1981), most probably result from erosional reworking of the Mio-Pliocene Bouse Formation (J.J. Landye, unpublished data). Populations of the former persist in only a few thermal springs (Taylor, 1981). Spring-inhabiting *Fontelicella* spp. (determined by Landye, in Donchin, 1983) were apparently restricted to the vicinity of groundwater inflows in the Mio-Pleistocene Verde Lake, Arizona (Donchin, 1983). Hydrobiids of the genera *Durangonella* Morrison, 1945 and *Tryonia* Stimpson, 1865 nonetheless inhabit lakes, springs, marshlands in and near the Cuatro Ciénegas basin. The former was thought related to *Mexipyrgus* by Hershler (1985), an opinion modified by Hershler & Thompson (1986), who demonstrated a nearer relationship between *Mexipyrgus* and *Tryonia*.

The third alternative, a massive spring that now exists as a series of isolated sources, is perhaps more tenable than the presence of major lake(s) and requires less rationalization of habitats. Cretaceous limestones of Texas of the same origins and cavernous qualities of those in northern México (Baker, 1971) provide aquifers for massive springs (Smith, 1971; Brune, 1981), individuals of which now or in the recent past discharge(d) water volumes surely equivalent to total output of the Cuatro Ciénegas basin. Further, discharges of Cuatro Ciénegas springs must have been greater in times of more precipitation and less evapotranspiration. Higher volumes would

tend to move zones of travertine deposition downflow and resist sealing, diversion, and impoundment of outflows, further maintaining thermal and chemical constancy requisite to *Mexipyrgus* evolution. Fragmentation of such a spring could be piecemeal or systematic, and if the latter could help explain trends in morphology indicated by Hershler (1985: 104) for extant *Mexipyrgus* stocks.

Lastly, passive dispersal of *Mexipyrgus* or its ancestor(s) to and/or within the Cuatro Ciénegas basin cannot be precluded. Waterbirds are abundantly attracted to aquatic habitats in an otherwise hostile desert (Urban, 1959; A. Contreras-Balderas, 1984), and bird movements are evident from place to place within the basin. Founding of new populations by a few individual snails in this manner, if such were documentable, could explain confusing distributions of some morphological types (Hershler, 1985) in the basin. Transport by movements of waterbirds could further explain occurrence of *Mexipyrgus* and other snails in isolated habitats where no access is obvious. On the other hand, if passive dispersal resulted in substantial gene flow, differentiation in *Mexipyrgus* should be suppressed or negated. We cannot further assess this mechanism as a factor in the origin and evolution of the present fauna.

The unlikelihood that *Mexipyrgus* disperses upflow over hard bottoms, as evidenced by its ecology (Taylor, 1966; Hershler, 1984, 1985), seems to preclude possibilities that intergradation in the Mojarral system is primary in nature. Divergence of allopatric populations isolated by desiccation of a barrial lake(s) or progressive fragmentation of a large, continuous spring, seem a viable alternative hypothesis for the origin of differentiation, with reintegration of habitats resulting in secondary contact and intergradation. This does not preclude the possibility for passive dispersal as a contributing factor.

**Systematics.** Taylor's (1966: 189) suspicion that "divergence of the various populations of *Mexipyrgus* may have had nothing to do with reproductive isolation, except through geographic separation" is confirmed, at least in the case of the Mojarral area. Our results clearly demonstrate genetic exchange between two nominal species (*M. mojarralis* and *M. multilineatus*) in the Mojarral system, and provide strong indications of intergradation between *M. multilineatus* of Mojarral East and *M. lugoi* of the Río Mesquites. When one

applies the biological species concept, synonymization of nominal *Mexipyrgus* to a single, polytypic species, *M. churinceanus*, is supported (Hershler, 1985).

The three nominal taxa do, however, conform to the concept of subspecies in that they present arrays of populations with distinctive features and restricted distributions. We stress that differences among these snails are not mere correlates of a downstream trend toward increased size. Number of shell bands, for instance, does not significantly correlate with shell height at any of the 16 sampling points, although an apparently spurious correlation ( $r = .91$ ) occurs when comparing means for these characters among points. As mentioned above, subsutural banding does not appear directly related to size, nor does penial lobation, as seen by a lack of size differences among groups of males having "1-1" (mean shell height, 5.71 mm,  $n = 21$ ) or "2-1" (5.89, 9) penial types (pooled data from sampling points 13 and 14;  $t$ -test,  $p > .05$ ).

Similar morphological characters involving shell sizes, sculpture, and banding pattern have apparently been independently derived in separated populations of *Mexipyrgus* (Hershler, 1985). Or, do characters in common among populations reflect historical processes and events that we do not yet understand? We have not yet devised a way to separate historic vs. derived conditions or states. Even more enigmatic is the question as to why *Mexipyrgus* shows such differentiation while populations of other genera are almost monotypic in the basin. The amount of time required for (or available for) differentiation of the kind seen in Cuatro Ciénegas *Mexipyrgus* also is poorly understood and in debate. Taylor (1966) suggested serious consideration that habitats of the area may have existed since the middle or early Tertiary, and pointed out that *Mexipyrgus* shared characters with *Tryonia* (late Oligocene or early Miocene to Recent) and *Pyrgophorus* Ancey, 1888 (early Pliocene to Recent). Hershler (1985) considered the possibility that differentiation could have been far more rapid, perhaps within the later Pleistocene. There is little doubt that basin and range topography formed in northern México in early Middle Tertiary (Minckley *et al.*, 1986), and that potentials for hydrobiid snail habitat date to that time and before.

Documentation that hybridization occurs between distinct phenotypes of Cuatro

Ciénelas *Mexipyrgus* presents the further possibility of a complex history of differentiation involving genetic exchange as means of disseminating distinctive variation among populations. Perhaps characters or character sets assort independently in hybrids where they are fixed by selection or by chance. If repeated separation and reintegration of aquatic habitats has in fact occurred, as implied by either the presence of a single, large, travertine-mediated spring outflow fragmented into subsystems or by presence of numerous, temporally-separated barrier lakes amenable for dispersal of *Mexipyrgus*, such may be the case. We cannot answer these questions with the current data set or within the framework of the present paper. The "natural laboratory" of Cuatro Ciénelas springs (Taylor & Minckley, 1966) seems to provide an inexhaustible supply of problems to be explored.

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