ECOLOGICAL AND ZOOGEOGRAPHIC RELATIONSHIPS OF AMPHIBIANS
AND REPTILES OF THE CUATRO CIENEGAS BASIN

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ABSTRACT

The herpetofauna of the Cuatro Ciénegas Basin consists of 66 native species (8 anuran amphibians, 4 turtles, 23 lizards, 31 snakes) and two introduced species. Ecologically 41 (62%) are desert species, 20% riparian, 9% semi-aquatic, and 9% aquatic. Geographic relationships are predominantly with the Chihuahuan Desert (42 species, 64%). The Tamaulipan (lowland) fauna consists of 18 species (27%), of which four are endemics. The fauna includes 39% mesic-adapted relict populations, and 10% endemics. The endemics range from poorly-differentiated subspecies to strongly divergent species, indicating long persistence of the aquatic habitats and their sequential colonization by waves of invading faunal elements.

RESUMEN

La herpetofauna del Bolsón de Cuatro Ciénegas consiste en 66 especies nativas (8 anfibios anuros, 4 tortugas, 23 lagartijas, 31 culebras) y 2 especies introducidas. Ecologicamente 41 (62%) son especies desérticas, 20% son especies ribereñas, 9% son semi-aquáticas, y 9% son aquáticas. Las relaciones geográficas son principalmente con el desierto chihuahuense (42 especies, 64%). La Fauna tamaulipense (tierra baja) consiste en 18 especies (27%), de las cuales cuatro son endémicas. Dicha fauna incluye 39% poblaciones relictas que están adaptadas a condiciones húmedas y 10% endémicas. Las endémicas varían entre subespecies poco diferenciadas a especies que son muy divergentes. Esto indica persistencia larga de los hábitats acuáticos y su colonización en sucesión por oleadas de elementos faunísticos invasores.

INTRODUCTION.—The Cuatro Ciénegas Basin is an intermontane, closed-drainage valley in the central part of the State of Coahuila, México (approximately 27° N by 104° W). The Basin is small, roughly 30 by 40 km, and its floor lies at an average 740 m elevation. Surrounding mountains rise to elevations near or exceeding 2,500 m. Geology and physiography of the region were thoroughly reviewed by Minckley (1969).

Both climatically and geographically the Cuatro Ciénegas Basin lies within the Chihuahuan Desert, as defined by Morafka (1977), and Schmidt (1979). The climate is arid, as the highly seasonal precipitation averages less than 200 mm annually, and daytime temperatures in summer may exceed 44° C. Vegetation and fauna in the Cuatro Ciénegas Basin superficially appear typical of an arid intermontane basin at the eastern edge of the plateau section of the Chihuahuan Desert, but this impression is vastly misleading. From the floor of the Cuatro Ciénegas Basin a series of major springs arise, and feed a hydrologic system that includes a spectrum of aquatic habitats ranging from flowing rivers to ponds, lakes, and marshes. Moreover, these aquatic habitats are apparently of great antiquity and permanence. Given combined conditions of habitat diversity and permanence, and isolation of the basin (until historic times), elements of the aquatic fauna have undergone explosive adaptive radiation and speciation resulting in swarms of endemic forms. The groups of aquatic organisms that have been studied (reviewed in Minckley 1969, 1978, Holsinger and Minckley 1971, and papers in this volume) show varying degrees of differentiation, ranging from strongly differentiated autochthonous species or species swarms, to undifferentiated populations of widespread species (outside the basin). This recurring pattern of differentiation reveals two aspects of aquatic habitats in the Cuatro Ciénegas Basin: their persistence through time, and their sequential colonization by waves of invading faunal elements.

The aquatic herpetofauna includes one strongly differentiated species, several endemic subspecies, several relict populations, and others that are continuous with and indistinguishable from populations in the remainder of the Río Grande drainage. The overall result is superposition of a rich aquatic and semi-aquatic faunal element, including both differentiated endemics and relictual populations, on an otherwise typical Chihuahuan Desert herpetofauna. Richness of the herpetofauna is further enhanced by the position of the basin on a major faunal boundary, that results in juxtaposition or interdigitation of Tamauli-

pan elements with the Chihuahuan Desert herpetofauna. These two factors, presence of an aquatic and semiaquatic fauna and overlap with Tamaulipan species, produces remarkable diversity.

The first biological exploration of the Cuatro Ciénegas Basin was conducted by E. G. Marsh, Jr., in 1899. Schmidt and Owens (1944) reported on Marsh's herpetological collections, which included the type-series of the most spectacular reptilian endemics, the aquatic box turtle Terrapene coahuila. For almost 20 years following Marsh's discoveries, the Cuatro Ciéñegas Basin was bypassed by herpetologists working in Mexico, but in 1958 a field party from the University of Kansas visited the basin and initiated the current period of intensive investigation. A member of that field party, W. L. Minckley, has been the leader in these studies. Although his interests have been primarily in fishes and other aquatic organisms, Minckley and his students have made significant collections of amphibians and reptiles. My own studies of the herpetofauna date from two expeditions to the Basin in 1964. Since then I have made a number of trips to the Basin of 2 to 10 days duration, and a longer visit of 6 weeks. Dozens of other herpetologists have also visited the Cuatro Ciéñegas Basin in the past 25 years, either in search of species of particular interest, or simply lured by prospects of witnessing the adaptational paradox of an aquatic box turtle. The results of their research have been published in nearly 100 scientific papers and articles (Appendix 1). Nevertheless, despite this period of intense study, and the collection of thousands of specimens, some species remain known from only a handful of specimens and others surely remain to be discovered. This analysis, then, must be considered provisional, as it is based on an incomplete sample of a complex and elusive fauna.

METHODS AND DEFINITIONS.—For this analysis the herpetofauna is defined as those species that occur naturally below 1,000 m elevation in the Cuatro Ciéñegas Basin and the adjacent Sacramento Basin, to the immediate east. Above 1,000 m the herpetofauna includes such species as Sceloporus grammicus, Sceloporus ornatus, and Gerrhonotus locephalus (among others), that occur throughout the northern Chihuahuan Desert as montane relicts (Morafka 1977:155). They are not pertinent to analysis of the fauna. Within the area defined 68 species of amphibians and reptiles have been collected. Two of these, Hemidactylus turcicus and Bufo marinus, are introduced exotics. Hemidactylus is well-established in edifacian habitats in the town of Cuatro Ciéñegas de Carranza, as it is elsewhere in northeastern Mexico and southern Texas. Bufo marinus was reported by Schmidt and Owens (1944) from the Marsh collection, but has not been taken since. A third species, Drymarchon corais, may also represent an introduction. It is tentatively included here on the basis of a single specimen. Gopherus berlandieri taken in the vicinity of Cuatro Ciéñegas de Carranza are regarded as escaped pets (W. L. Minckley, pers. comm.). The native herpetofauna includes 8 species of anuran amphibians, four turtles, 23 species of lizards, and 31 species of snakes (Table 1).

Species were categorized ecologically on the basis of modal habitat preference of populations in the Cuatro Ciéñegas Basin, regardless of preferences elsewhere. Four ecological categories are recognized: (1) Desert, (2) Riparian, (3) Semiaquatic, and (4) Aquatic. The ecological category to which each species was assigned is indicated in Table 1. Habitat requirements of species in each category are defined as follows:

Desert (category 1) includes species that are not limited, in distribution or dispersal potential, to aquatic, semiaquatic, or riparian habitats. The category admittedly is broad, and includes many more species than the other three categories. To establish subdivisions within the desert category, such as grassland, sand, or rock face species, would obscure the basic faunal unity of included species.

Riparian species (category 2) are those which, although they do not require aquatic or semiaquatic habitats, are limited within the Basin ecosystem to areas along watercourses or of high subsurface water. These species were categorized by Morafka (1977:155) as "facultative riparian associates." Although their dispersal potential is not limited by stringent aquatic habitat requirements, they tend to be distributed in patterns that reflect drainages and persistent mesic habitats, such as gallery forest and grassland. Species include the skinks Eumeces obsoletus and Eumeces tetragrammus, the snakes Dipsodophis punctatus and Micruropus fulvius, and Bufo valliceps.

Category three, semiaquatic, includes species that live in marshes, sedge mats, and other such habitats peripheral to water courses and lagunas. They are less habitat limited than aquatic species, may be able to survive seasonal or temporary habitat drying, and are capable of dispersal across areas of discontinuous aquatic habitat. Among species in this category are Scincella lateralis, Terrapene coahuila, and Thamnophis proximus.

Aquatic species (category 4) require permanent standing or flowing water. Although some parts of the life history (i.e. nesting in oviparous reptiles) may necessitate emergence, these species live in and disperse only through permanent aquatic habitats. Examples of species in this ecological category are the turtles Trionyx and Pseudemys, and the two species of the snake genus Nerodia. It should be noted that the riparian herpetofauna characterized by Morafka (1977:155) includes species in all three categories (aquatic, semiaquatic, and riparian) as defined above.

There were three major geographic categories established for the analysis: Chihuahuan, Tamaulipan, and ubiquitous. The Chihuahuan fauna is the core desert fauna, and includes species that have distributions centered in the arid northern Mexican Plateau. Tamaulipan species constitute the lowland faunal element; distributions of species in this group center in the Tamaulipan or Austro-riparian zone east of the Cuatro Ciéñegas Basin. Most species in the ubiquitous category have distributions that extend from coast to coast (or nearly so) in the United States, southward onto the Mexican Plateau.
Four further subcategories are recognized in the Chihuahuan category. The first includes forms endemic to the Cuatro Ciénegas Basin, but with affinities in the Chihuahuan fauna. The second includes species geographically limited to the Chihuahuan Desert. Figure 1 shows distribution of one of these Chihuahuan Desert endemics, the gecko Coleonyx brevis. The third subcategory includes species with distributions in both the Chihuahuan Desert and the western Great Plains. Distribution of Eumeces obsOLEius (Fig. 2) illustrates this pattern. The fourth

Table 1. Amphibians and reptiles of the Cuatro Ciénegas Basin, with ecological and geographic category assignments.

<table>
<thead>
<tr>
<th>Amphibia: Salientia</th>
<th>Ecological Category</th>
<th>Geographic Category</th>
<th>Reptilia: Sauria (continued)</th>
<th>Ecological Category</th>
<th>Geographic Category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scaphiopus couchi</td>
<td>1</td>
<td>A-4</td>
<td>Eumeces tetragrammus</td>
<td>2</td>
<td>B-2</td>
</tr>
<tr>
<td>Bufo speciosus</td>
<td>1</td>
<td>B-5</td>
<td>Gerrhonotus higueti*</td>
<td>1</td>
<td>A-1</td>
</tr>
<tr>
<td>Bufo debilis</td>
<td>1</td>
<td>A-4</td>
<td>Ceratophorus inornatus</td>
<td>1</td>
<td>A-2</td>
</tr>
<tr>
<td>Bufo cognatus</td>
<td>1</td>
<td>A-4</td>
<td>Ceratophorus gularis</td>
<td>2</td>
<td>B-2</td>
</tr>
<tr>
<td>Bufo marinus (introduced)</td>
<td>-</td>
<td>-</td>
<td>CeratophorusScalaris*</td>
<td>1</td>
<td>A-1</td>
</tr>
<tr>
<td>Bufo punctatus</td>
<td>1</td>
<td>A-4</td>
<td>Ceratophorus tigris</td>
<td>1</td>
<td>A-4</td>
</tr>
<tr>
<td>Bufo valliceps</td>
<td>2</td>
<td>B-2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hylactophyne augusti</td>
<td>1</td>
<td>A-4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rana (pipiens group)</td>
<td>4</td>
<td>A-3 (?)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Reptilia: Testudines

| Trionyx ater*        | 4                   | B-1                 | Leptotyphlops dulis         | 1                   | B-3                 |
| Trionyx spiniferus   | 4                   | B-3                 | Leptotyphlops humilis       | 1                   | A-4                 |
| Pseudemys scripta*   | 4                   | B-1                 | Arizona elegans            | 1                   | A-4                 |
| Terrapene coahuila*  | 3                   | B-1                 | Coluber constrictor        | 2                   | C                   |
|                     |                     |                     | Drymarchon corais          | 2                   | B-2                 |
|                     |                     |                     | Diadophis punctatus        | 2                   | C                   |
|                     |                     |                     | Elaphe obsoleta            | 2                   | B-3                 |
|                     |                     |                     | Elaphe guttata             | 2                   | A-3                 |
|                     |                     |                     | Heterodon nasicus          | 1                   | A-3                 |
|                     |                     |                     | Hypsiglena torquata        | 1                   | A-4                 |
|                     |                     |                     | Lampropeltis alberta       | 1                   | A-2                 |
|                     |                     |                     | Lampropeltis getulus       | 1                   | C                   |
|                     |                     |                     | Lampropeltis triangularum  | 2                   | C                   |
|                     |                     |                     | Masticophis flagellum      | 1                   | C                   |
|                     |                     |                     | Masticophis taoenitians    | 1                   | A-4                 |
|                     |                     |                     | Pituophis melanoleucus     | 1                   | A-4                 |
|                     |                     |                     | Rhinocelus lecontei        | 1                   | A-4                 |
|                     |                     |                     | Sonora seminulata          | 1                   | A-4                 |
|                     |                     |                     | Tortilla atriceps          | 1                   | A-2                 |
|                     |                     |                     | Nerodia erythrogaster      | 4                   | B-3                 |
|                     |                     |                     | Nerodia rhombifera         | 4                   | B-3                 |
|                     |                     |                     | Thamnophis cyrtopsis       | 3                   | A-4                 |
|                     |                     |                     | Thamnophis marcinus        | 3                   | A-4                 |
|                     |                     |                     | Thamnophis proximus        | 3                   | B-3                 |
|                     |                     |                     | Micruroides fulvus         | 2                   | B-2                 |
|                     |                     |                     | Sistrurus catenatus         | 3                   | B-3                 |
|                     |                     |                     | Crotaulus atrox            | 1                   | A-4                 |
|                     |                     |                     | Crotaulus lepidus          | 1                   | A-4                 |
|                     |                     |                     | Crotaulus molossus         | 1                   | A-4                 |
|                     |                     |                     | Crotaulus scutulatus       | 1                   | A-4                 |

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a) 1=Desert, 2=Riparian, 3=Semiaquatic, 4=Aquatic; see text for definitions.

b) A=Chihuahuan (1=Endemic, 2=Chihuahuan Desert only, 3=Chihuahuan Desert and western Great Plains, 4=Widespread, desert and plains); B=Tamaulipan (1=Endemic, 2=Gulf Edge, 3=Plains to desert edge); C=Ubiquitous.

* Indicates endemic species or subspecies.
Figure 1. Distribution of *Coleonyx brevis*, a Chihuahuan Desert endemic species. Approximate location of the Cuatro Ciénegas Basin is indicated by the black square.

Figure 2. Distribution of *Eumeces obsoletus*, a Chihuahuan Desert and Great Plains species. Approximate location of the Cuatro Ciénegas Basin is indicated by the black square.
includes species with wider distributions that include much of the arid southwestern United States and northern México, and the western Great Plains. An example of this type of distribution is that of *Rhinocelus lecontei* (Fig. 3).

In the Tamaulipan category three subcategories are recognized. First is Basin endemics with affinities in the Tamaulipan fauna. The second includes a series of species with distributions extending around the Gulf of México and penetrating the desert *via* extensions of habitat along major river systems. Distribution of *Bufo valliceps* (Fig. 4) illustrates this pattern. The third includes species that are distributed westward across the Great Plains, extending to but not penetrating the Chihuahuan Desert. An example of this distributional pattern is shown in Figure 5, which shows the range of *Bufo speciosus*. Many species in the last group have wider distributions east of the Great Plains than does *B. speciosus*, but all share a characteristic limit at the edge of the Chihuahuan Desert.

**ECOLOGICAL RELATIONSHIPS OF THE HERPETOFAUNA.—**Forty-one (62%) of the 66 native species ecologically are characteristic of deserts (Table 2). More than half of the snake species (58%) and about three-fourths of the lizards (74%) are desert forms. Surprisingly, 6 of the 8 amphibians from the Basin (*Scaphiopus couchi*, *Hylactophryne augusti*, and four species of *Bufo*) also are categorized as desert species.

The next richest fauna in the ecological sense is that of riparian zones. Thirteen species (20%) are classified as riparian (Table 2). Twenty-two percent of the lizards, and the same proportion of snake species are in this category. The only riparian amphibian is *Bufo valliceps*.

The semiaquatic category constitutes 9% of the total fauna (Table 2). Included species are *Scincella lateralis* and three species of *Thamnophis*, although *T. marcianus* might as easily be classified as riparian. *Sistrurus catesbicus* is also considered semiaquatic, albeit on scanty evidence (Minckley and Rinne 1972). *Terrapene coahuila* is difficult to categorize. Although much of its activity is in semiaquatic habitats (Brown 1974), it is also found in streams and lagunas (Williams et al. 1960, Webb et al. 1963). It is here placed in the semiaquatic category.

Aquatic species also account for 9% of the fauna (Table 2).

**Table 2. Summary of ecological relationships of the herpetofauna, by major taxonomic groups.**

<table>
<thead>
<tr>
<th></th>
<th>Desert</th>
<th>Riparian</th>
<th>Semiaquatic</th>
<th>Aquatic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphibians</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Turtles</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Lizards</td>
<td>17</td>
<td>5</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Snakes</td>
<td>18</td>
<td>7</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Totals</td>
<td>41</td>
<td>13</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>(62%)</td>
<td>(20%)</td>
<td>(9%)</td>
<td>(9%)</td>
<td></td>
</tr>
</tbody>
</table>

Figure 3. Distribution of *Rhinocelus lecontei*, a widespread desert/plains species. Approximate location of the Cuatro Ciénegas Basin is indicated by the black square.
Figure 4. Distribution of *Bufo valliceps*, a Gulf edge species. Approximate location of the Cuatro Ciénergas Basin is indicated by the black square.

Figure 5. Distribution of *Bufo speciosus*, a species that ranges to the edge of the Chihuahuan Desert. Approximate location of the Cuatro Ciénergas Basin is indicated by the black square.
2). The *Rana* sp. (*pipiens* group) is the only aquatic amphibian. *Trionyx ater*, *T. spiniferus*, and *Pseudemys scripta* are the aquatic turtles. There are no aquatic lizards, and *Nerodia erythrogaster* and *N. rhombifera* are the only aquatic snakes.

To summarize, the Cuatro Ciénegas herpetofauna is composed ecologically of about 60% desert species, and 40% aquatic, semiaquatic, and riparian species combined. The presence of extensive aquatic habitats in the Cuatro Ciénegas Basin thus accounts for enhancement of herpetofaunal diversity by roughly a third.

**GEOGRAPHIC RELATIONSHIPS OF THE HERPETOFAUNA.**—Geographic affinities of the Cuatro Ciénegas Basin herpetofauna are summarized in Table 3. A preponderance of the fauna (42 species, 64%) is classified as Chihuahuan. As most of these species are wide-ranging, and not habitat-limited, endemism is rare. Only two forms (*Gerrhonotus lugoii*, *Cnemidophorus scalaris pallidus*) from the Chihuahuan fauna are endemic to the Cuatro Ciénegas Basin. Ten species (7 lizards, 3 snakes) are Chihuahuan Desert endemics, and 5 species (1 amphibian, 2 lizards, 2 snakes) have ranges that encompass the Chihuahuan Desert and western Great Plains. The remaining 25 species (5 amphibians, 8 lizards, 13 snakes) range widely in plains and deserts.

<table>
<thead>
<tr>
<th></th>
<th>Chihuahuan</th>
<th>Tamaulipan</th>
<th>Ubiquitous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphibians</td>
<td>6</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Turtles</td>
<td>0</td>
<td>4 (5)</td>
<td>0</td>
</tr>
<tr>
<td>Lizards</td>
<td>18 (2)</td>
<td>4 (1)</td>
<td>1</td>
</tr>
<tr>
<td>Snakes</td>
<td>18</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>Totals</td>
<td>42</td>
<td>18</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>(64%)</td>
<td>(27%)</td>
<td>(9%)</td>
</tr>
</tbody>
</table>

Table 3. Summary of geographic relationships of the herpetofauna, by major taxonomic groups (number of endemic forms in parentheses).

The Tamaulipan or lowland element of the fauna is smaller (18 species, 27%) but includes 4 Basin endemics (*Trionyx ater*, *Terrapene coahuila*, *Pseudemys scripta taylori*, *Scincella lateralis* ssp.). Five of the Tamaulipan species have distributions that skirt the arid northern Mexican Plateau around the margin of the Gulf of México, and extend to or into the Basin via the drainage of the Río Salado. These are *Bufo valliceps*, *Eumeces tetragrammus*, *Cnemidophorus gularis*, *Drymarchon corais*, and *Mierurus fulvius*. Nine species are more widely distributed, in the Great Plains and eastward, and characteristically occur in relict populations located as mesic-adapted isolates at the desert edge.

The geographic relationships of the herpetofauna also relate to the position of the Cuatro Ciénegas Basin at the extreme eastern edge of the Chihuahuan Desert Province. Because of an abrupt topographic boundary at the eastern edge of the Basin, and resulting climatic and ecological transitions, the boundary between the Chihuahuan and Tamaulipan faunal zones is particularly sharp in this area. Sixteen (58%) of the Chihuahuan species reach an eastern range limit at the edge of the Basin. More striking are the Tamaulipan species, of which 77% (14 species) reach their western limit in the Cuatro Ciénegas Basin. Among the aquatic and semiaquatic species only two (*Nerodia erythrogaster*, *Rana* sp.) penetrate farther west, beyond Cuatro Ciénegas into the Chihuahuan Desert (Conant 1969, 1978).

The abruptness of this faunal boundary is emphasized by the distributions of two pairs of lizard species: *Sceloporus olivaceus* and *S. magister*, and *Cnemidophorus gularis* and *C. scalaris*. The two Tamaulipan species (*S. olivaceus* and *C. gularis*) reach their westernmost range limits at the edge of the Cuatro Ciénegas Basin (Puerto Salado), and are replaced by the Chihuahuan representatives. In the case of *Cnemidophorus gularis* and *C. scalaris*, secondary hybridization occurs where the species are in contact (Walker 1981).

**SUMMARY.**—The herpetofauna of the Cuatro Ciénegas Basin superficially is characteristic of the Chihuahuan Desert. This is borne out by analysis of both ecological and geographic relationships of the fauna—62% are desert forms, and 64% have geographic affinities with the Chihuahuan fauna. Although the Tamaulipan fauna constitutes only 27% of the species, a majority of the Basin endemics have geographic affinities there. The Cuatro Ciénegas Basin herpetofauna includes a high proportion of relict populations (59%), as noted by Milstead (1960), and Morafka (1977:157-158). This large relictual element is even more remarkable in that 6 species, almost 10% of the total fauna, are differentiated at some taxonomically recognizable level.

Patterns of differentiation among relict amphibians and reptiles in the Cuatro Ciénegas Basin are fully as varied and complicated as in fishes, mollusks, and crustaceans. At one end of the spectrum is the highly differentiated *Terrapene coahuila*, a species so divergent within the genus that its phyletic relationships continue to be a subject of controversy (Brown 1971, Milstead 1967). An intermediate level of differentiation is illustrated by *Trionyx ater* and *Pseudemys scripta taylori*. Although *T. ater* is distinctive morphologically (Webb 1962) it apparently hybridizes freely in portions of the Basin with invading populations of *T. spiniferus* (Webb 1973). *Pseudemys scripta taylori* intergrades with *P. scripta elegans* in a narrow zone that begins at Puerto Salado and extends downstream perhaps no farther than the Sacramento Basin. "Legler (1960) described specimens from Puerto Salado as intermediate between the two subspecies. Turtles from the eastern end of the Sacramento Basin (El Cariño de la Montaña) are "typical" *P. s. elegans* (M. A. Ewert, pers. comm.). Conant (1969) noted "some suggestions of local endemism" in Basin populations of *Nerodia erythrogaster*. At the other extreme are relictual, but apparently undifferentiated, populations of such species as *Eumeces tetragrammus*, *Coluber constrictor*, *Mierurus fulvius*, and *Sistrurus catenatus*. These differing levels of morphological divergence, as Minckley (1969,
1978) observed, indicate a "mosaic of differentiation," and result from a long history of successive faunal invasions. Reconstruction of this history, which is essential to understanding the complex pattern of differentiation, must await comparative studies of genetic divergence of the relicual populations.

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Appendix 1.

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