The Biogeographical Relationships of the Amphibians and Reptiles of the Guadalupe Mountains

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The Guadalupe Mountains of southern New Mexico and adjacent Texas possess an unusually rich and diverse herpetofauna. This is undoubtedly due in large part to the unusual diversity of habitats within the region, but it may also reflect the strategic location of the mountains with respect to biogeographic regions. The Guadalupes are essentially an extension of the more prominent Sacramento Mountains that lie immediately to the northwest, and as such are subject to some biotic influence of the southern Rocky Mountain system. However, the southern Great Plains lie to the east of the mountains, and the great Chihuahuan Desert stretches away to the south. Also, the Pecos River is located only a few miles to the east, and could act as an avenue for the intrusion of some more aquatic species.

The purposes of this paper are to provide a brief summary of the amphibians and reptiles that occur in the Guadalupe Mountains and their immediate vicinity and to analyze the faunal elements represented in the herpetofauna and their relative importance. Needless to say, any conclusions relative to the biogeographic position of the area that are based on the herpetofauna alone may not apply to other groups.

THE HERPETOFAUNA

Bailey (1905) briefly described the vertebrate fauna of the Guadalupe Mountains and wrote (1928) a popular account of the animals found in the vicinity of Carlsbad Caverns. The first serious study of the amphibians and reptiles as such, however, was that of Mosauer (1932), who recorded 18 species from the area. My own field work in the Guadalupe Mountains resulted in the collection of 50 species, together with considerable relevant ecological data (Mecham 1955). Most of this information has not been published, although two taxonomic papers (Mecham 1956, 1957) were stimulated by this new material. Frederick Gehlbach has done extensive work on the ecology and distribution of the herpetofauna, but again much of this work remains unpublished. A mimeographed summary (Gehlbach 1964) of

the amphibians and reptiles of Carlsbad Caverns National Park, however, is available together with two relevant taxonomic papers (Gehlbach 1974; Gehlbach and McCoy 1965) and the contribution in this volume. Many other herpetological records are scattered through the literature. A recent review of the turtles of New Mexico (Degenhardt and Christiansen 1974) provides a useful summary of the distribution of this group in the region. Several studies on late and post-Pleistocene herpetological remains are also of some relevance. These include Holman (1970), Gehlbach and Holman (1974), and Applegarth (1977).

A list of the amphibians and reptiles known from the Guadalupe Mountains or their immediate vicinity is given below, together with brief summaries of their local distribution. Life belts in the sense of Dice (1943) have been used in a loosely descriptive sense, although it is recognized that an altitudinally based classification of habitats in the Guadalupe Mountains is unsatisfactory in some respects. The plains life belt as used here refers to habitats below roughly 4200 ft on the lower slopes and the adjacent desert plains. The roughlands belt encompasses a wide range of habitats in the mountains proper from roughly 4200 ft to 7000 ft or more, and including evergreen woodland (*sensu* Gehlbach 1967). The montane belt includes coniferous forest as may occur on the peneplane above approximately 7200 ft.

Subspecific names have not been used in this account except where relevant. Forms rare in the area (known from only one or two records) are indicated by "R." Forms indicated by an asterisk presumably do not occur within the boundaries of the Guadalupe Mountains National Park; other species listed have been reported from the park or almost certainly occur there. Distributional information is based primarily on Mecham (1955) together with published sources except as otherwise noted.

Amphibia. Recorded species include *Ambystoma tigrinum, Scaphiopus couchi, Scaphiopus hammondi, Scaphiopus bombifrons*, **Hylactophryne augusti* (R), *Bufo cognatus* (R), *Bufo debilis, Bufo punctatus, Bufo speciosus*,**Acris crepitans*, and *Rana berlandieri*. The bullfrog, *Rana catesbeiana*, also is present in the region, but apparently is an introduction. *Ambystoma tigrinum* may occur at all altitudes in ponds or tanks. The *Scaphiopus* species, *Bufo cognatus, B. speciosus*, and *B. debilis* occur primarily in the plains life belt below 4800 ft, whereas the more rock-loving *B. punctatus* ranges from the lower altitudes to above 6000 ft. *Acris crepitans* is known only from permanent water sites on the eastern side of the range, as are southern leopard frogs (*Rana berlandieri*). *Bufo cognatus* is known from a single record south of Dell City on the southwestern side of the mountains (data of Gehlbach). The robber frog, *Hylactophryne augusti*, is known from a single specimen taken northwest of Carlsbad (Koster 1946). This was the only record of the species in New Mexico for a number of years, although another specimen has since been taken near Roswell (Zweifel 1967).

Testudinata. Turtles recorded include **Chelydra serpentina*, *Kinosternon flavescens*, **Chrysemys picta*, **Chrysemys scripta*, **Chrysemys concinna*, *Terrapene ornata*, and **Trionyx spiniferus*. With the exception of *Kinosternon flavescens*, which is distributed widely in association with permanent and semipermanent ponds and streams, the aquatic turtle species are essentially limited in the area to the Pecos River and to its tributary, the Black River (Degenhardt and Christiansen 1974), which extends to the eastern foothills of the mountains. The only terrestrial species, *Terrapene ornata*, is widely distributed at lower elevations.

Lacertilia. Species recorded include *Eumeces obsoletus, Eumeces multivirgatus, Cnemidophorus exsanguis, Cnemidophorus gularis, Cnemidophorus inornatus, Cnemidophorus tesselatus, Cnemidophorus tigris, Coleonyx brevis, Crotaphytus collaris, *Crotaphytus wislizeni, Cophosaurus texanus, Holbrookia maculata* (R), *Phrynosoma cornutum, Phrynosoma douglassi, Phrynosoma modestum, Sceloporus poinsetti, Sceloporus undulatus, Urosaurus ornatus*, and *Uta stansburiana*.

Holbrookia maculata is reported here in the area for the first time. Specimens in the Texas Tech Museum collection were taken by Mr. Tony Burgess from gypsum dunes on the southwestern side on the mountains near Eclipse Well. *Cnemidophorus tigris, C. inornatus, C. gularis, Crotaphytus wislizeni*, and *Uta stansburiana* are all essentially confined to the desert plains below 4500 ft. *Cnemidophorus tigris* and *Crotaphytus wislizeni* apparently have been collected in the immediate vicinity only from mesquite dunes bordering the salt flats to the southwest. Forms such as *Coleonyx brevis* and *Phyrnosoma modestum* occur in parts of the desert plains but also penetrate lower parts of the roughlands belt. *Phrynosoma cornutum* not only occurs widely in the plains belt, but ranges to nearly 6000 ft. *Eumeces obsoletus, Cnemidophorus tesselatus, Cnemidophorus exsanguis, Crotaphytus collaris*, and the rocky adapted *Cophosaurus texanus* are all common in more open roughlands habitats to approximately 6000 ft. The saxicolous *Urosaurus ornatus* and *Sceloporus poinsetti* have extremely wide altitudinal ranges, and *S. poinsetti*, at least, ranges above 8000 ft. The ubiquitous *Sceloporus undulatus* occurs at all altitudes as does *Eumeces multivirgatus*. *Phrynosoma douglassi* occurs in evergreen woodland and coniferous forest, usually above 6000 ft. The last four species listed all occur in the coniferous forest of The Bowl.

Serpentes. Species recorded include *Leptotyphlops dulcis,*Thamnophis marcianus,*Thamnophis proximus, Thamnophis cyrtopsis, *Natrix erythrogaster, Arizona elegans, Elaphe guttata, Elaphe subocularis, Pituophis melanoleucus, Rhinocheilus lecontei, Salvadora grahamiae, Salvadora hexalepis* (R), *Sonora episcopa, Diadophis punctatus, Gyalopion canum, Lampropeltis getulus, Lampropeltis mexicana* (R), *Masticophis flagellum, Masticophis taeniatus, Opheodrys vernalis* (?), *Heterodon*

nasicus, Hypsiglena torquata, Tantilla atriceps, Tantilla nigriceps, Crotalus atrox, Crotalus lepidus, Crotalus molossus, Crotalus scutulatus (R), and *Crotalus viridis.*

The inclusion of *Opheodrys vernalis* is based primarily on a recent sight record of the species in the McKittrick Canyon area by Mr. Tony Burgess, although a rancher some years ago gave the writer a good description of what apparently was this species in the vicinity of the ruins of Queen, New Mexico (northern Guadalupe Mountains, 6000 ft). The form is known as a sub-Recent fossil (Logan and Black 1977), and occurs nearby in the Sacramento Mountains. The presence of *Lampropeltis mexicana* is based on a single specimen from the vicinity of Pine Springs (Gehlbach and McCoy 1965), the northernmost record of the species. Inclusion of *Salvadora hexalepis* is based on a specimen in the collection of the Carlsbad Caverns National Park (data of Gehlbach). The listing of only one form of *Diadophis* is an over simplification. Gehlbach (1974) found evidence to indicate that small (*D. p. arnyi*) and large (*D. p. regalis*) forms both occur in the Guadalupe Mountains where they may act as distinct species. The two forms intergrade extensively in other areas of contact, however.

Distributional patterns of the snakes are complex. *Thamnophis proximus, Thamnophis marcianus, Thamnophis cyrtopsis*, and *Natrix erythrogaster* are all confined to the vicinity of permanent water at lower altitudes and drainages on the eastern or northeastern side of the mountains. *Thamnophis cyrtopsis*, a form that is less dependent on permanent water, is more characteristic of the mountains proper and is of wide occurrence. A few species are most characteristic of the plains belt and appear to invade the mountains only at lower altitudes. These include *Arizona elegans, Rhinocheilus lecontei, Heterodon nasicus, Lampropeltis getulus, Tantilla nigriceps, Crotalus viridis*, and *Crotalus scutulatus*. The last form is marginal in the area. The closest record is a specimen taken by Tony Burgess just southwest of the mountains near Eclipse Well. Two saxicolous rattlesnakes (*Crotalus lepidus* and *Crotalus molossus*) are common in the roughlands belt and extend to the highest altitudes. I have found them as high as 7400 and 8200 ft, respectively. Most of the other species of snakes appear to be distributed at lower to intermediate altitudes, spanning parts of both the roughland and plains belts. The bullsnake, *Pituophis melanoleucus*, apparently has the widest ecological tolerance of any of the snakes. I recorded one specimen as low as 3600 ft (in mesquite dunes); Mosauer (1932) found a specimen at about 8000 ft in pine-fir forest.

Other Species. Some additional species as yet unreported from the Guadalupe Mountains may occur there. Possibilities include *Bufo woodhousei, Rana blairi, Leptotyphlops humilis, Coluber constrictor, Lampropeltis triangulum, Thamnophis sirtalis, Trimorphodon biscutatus*, and *Sistrurus catenatus*, among others. The proximity of records for *Bufo woodhousei* strongly suggest that this species does occur in the area, at least in the

vicinity of the Pecos River. The presence of *Coluber constrictor* also is particularly likely. The form occurs nearby in the Sacramento Mountains and has recently been reported to the south in the Davis Mountains (Glidewell 1974). Stebbins (1951) indicated on a map that the canyon treefrog, *Hyla arenicolor*, is present in the Guadalupe Mountains, but this almost certainly was in error. Absence of the species, however, is puzzling in view of the seemingly optimal habitat that is present at several locations, particularly in McKittrick Canyon.

BIOGEOGRAPHICAL RELATIONSHIPS

Dice (1943) and Blair (1950) have placed the upper parts of the Guadalupe Mountains within the Navahonian biotic province, of which they would form the southernmost extension. Lower areas were placed within the Chihuahuan biotic province. The Navahonian, as identified by Dice, is an extensive region that lies between the south-central Rocky Mountains (Coloradan biotic province) and the southwestern deserts. In a sense it is a zone of transition, and inclusion of much of the Guadalupe Mountains in this province emphasizes the northern or montane aspects of the biota. The Chihuahuan biotic province corresponds essentially to the Chihuahuan Desert, although it is more extensive than the desert proper as identified by Shelford (1963) and some other ecologists.

If the biotic province concept is accepted as a viable method of biogeographical classification, this characterization of the Guadalupe Mountains is definitely misleading as far as amphibians and reptiles are concerned. This is demonstrated by an analysis of the reported forms with respect to their occurrence in the Navahonian and Chihuahuan provinces, together with two other nearby provinces, the Kansan (corresponding essentially to the southern Great Plains) and Balconian (the Edwards Plateau of Texas). As shown by Table 1, the strongest affinities lie with the Chihuahuan, with somewhat lower but nevertheless strong affinities with the Kansan and Balconian. The lowest relationship is with the Navahonian, a finding that is highly inconsistent with the classifications of Dice and Blair. Even if the analysis is restricted to species that penetrate to higher altitudes, say above 6000 ft, the herpetofauna appears to be more Chihuahuan than Navahonian. At least 18 species occur at such altitudes. These include *Ambystoma tigrinum, Bufo punctatus, Cnemidophorus exanguis, Eumeces multivirgatus, E. obsoletus, Phrynosoma douglassi, Sceloporus poinsetti, S. undulatus, Urosaurus ornatus, Diadophis punctatus, Hypsiglena torquata, Masticophis taeniatus, Pituophis melanoleucus, Salvadora grahamiae, Thamnophis cyrtopsis, Opheodrys vernalis, Crotalus lepidus*, and *C. molossus*. Of these, 15 are important in the Chihuahuan, 13 in the Navahonian, 12 in the Balconian, and 7 in the Kansan provinces.

A somewhat different picture emerges if the amphibians and turtles, a greater proportion of which have higher water requirements, are considered separately from lizards and snakes (Tables 2 and 3, respectively). It

TABLE 1. Distribution of amphibians and reptiles of the Guadalupe Mountains in near biotic provinces.

Biotic provinces	Important	Marginal	Total
Kansan	40	4	44
Balconian	41	7	48
Navahonian	31	10	41
Chihuahuan	46	13	59

TABLE 2. Distribution of amphibians and turtles of the Guadalupe Mountains in near biotic provinces.

Biotic provinces	Important	Marginal	Total
Kansan	14	0	14
Balconian	14	2	16
Navahonian	6	3	9
Chihuahuan	8	6	14

TABLE 3. Distribution of lizards and snakes of the Guadalupe Mountains in near biotic provinces.

Biotic provinces	Important	Marginal	Total
Kansan	26	4	30
Balconian	27	5	32
Navahonian	25	7	32
Chihuahuan	38	7	45

may be seen that affinities of the amphibians and turtles are primarily with the Kansan and Balconian provinces, although the importance of the Chihuahuan province still ranks above that of the Navahonian. With respect to the snakes and lizards, the affinities are overwhelmingly with the Chihuahuan province, as would be expected in view of the xeric adaptations of many of these forms.

Another method of analysis is in terms of faunal elements, an approach that involves some arbitrary aspects but does provide a different perspective. At least seven faunal elements (or categories) appear to be represented in the Guadalupe Mountain herpetofauna. These elements (Fig. 1) are listed below.

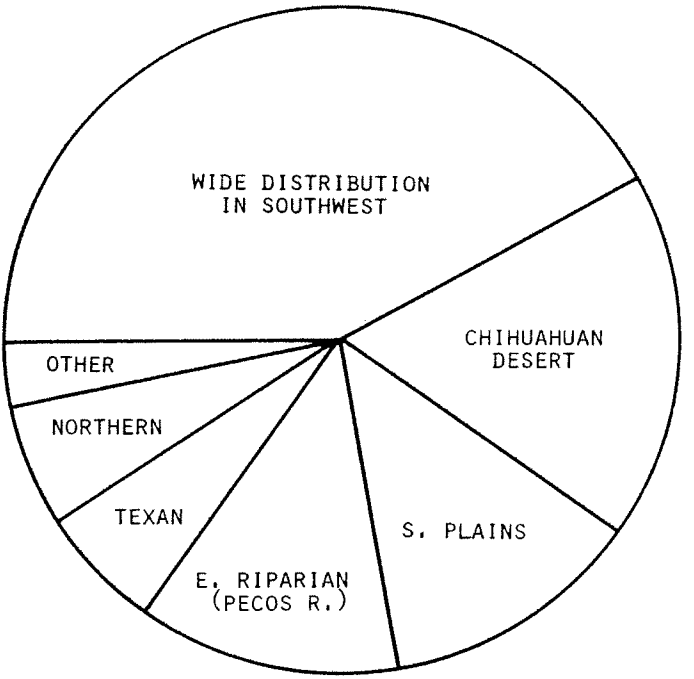

Fig. 1. Relative importance of the herpetological faunal elements represented in the Guadalupe Mountains. Refer to text for further explanation.

Species with Wide Distributions in the Southwest (28 species, 42.4%).—Forms included here are all of such wide distribution that they cannot be assigned to any particular biotic or physiographic region. The greater number occur in the Chihuahuan Desert, but none have their centers of distribution there. Most are limited to arid or semiarid regions in Mexico and the western United States, but some (as *Lampropeltis getulus* or *Ambystoma tigrinum*) range widely in more mesic regions.

Chihuahuan Desert Element (12 forms, 18.2%).—This category consists of forms that are associated with the Chihuahuan Desert, although they may have limited distributions in adjacent areas. Included are *Cnemidophorus inornatus, C. tigris marmoratus, Coleonyx brevis, Cophosaurus texanus,*

Phrynosoma modestum, Sceloporus poinsetti, Elaphe subocularis, Gyalopion canum, Lampropeltis mexicana, Tantilla atriceps, Crotalus lepidus, and *C. scutulatus*. Although *Cnemidophorus tigris* has a much wider distribution, the largely disjunct eastern element of the species (primarily *C. t. marmoratus*) is closely tied to the Chihuahuan Desert and may be used as a biogeographic indicator of that region.

Plains Element (8 forms, 12.1%).—This element is composed of forms that have their distributional centers within the Kansan biotic province (southern Great Plains). Included are *Scaphiopus bombifrons, Kinosternon flavescens, Terrapene ornata, Eumeces obsoletus, Elaphe guttata emoryi, Heterodon nasicus, Sonora episcopa*, and *Tantilla nigriceps*.

Eastern Riparian (Pecos River) Element (eight species, 12.1%).—This distinctive element consists of the aquatic and semiaquatic species of mostly eastern affinities that have been able to invade (or persist in) the area because of the proximity of the Pecos River. All of the forms are associated with permanent water at lower altitudes on the eastern or northeastern side of the mountains. Included here are *Rana berlandieri, Acris crepitans, Chelydra serpentina, Chrysemys scripta, C. concinna, Trionyx spiniferus, Natrix erythrogaster*, and *Thamnophis proximus*.

Northern Element (four species, 6.1%).—This small but heterogeneous group includes forms that approach or attain their southern limits of distribution in western Texas in the Guadalupe Mountains region. Two (*Opheodrys vernalis, Chrysemys picta*) are essentially northern and eastern forms that occur as post-Pleistocene isolates in the Southwest. Populations of the short-horned lizard *Phrynosoma douglassi*, in both the Guadalupe Mountains and the Davis Mountains are disjunct from main elements of the species to the north in New Mexico, and also qualify as relicts. Also included here is the many-lined skink, *Eumeces multivirgatus*. This species is known to occur further to the south in the Chihuahuan Desert, but is primarily associated with the western margin of the Great Plains and the Navahonian biotic province. The subspecies (*E. m. gaigei*) that is found in the Guadalupe Mountains has a distribution that corresponds closely to the Navahonian. The striped phase of this form predominates at higher altitudes, whereas the patternless ("*taylori*") phase is more common at lower altitudes (Mecham 1957).

"Texan" Element (four species, 6.1%).—This rather artificial category includes species (*Hylactophryne augusti, Bufo speciosus, Cnemidophorus gularis*, and *Leptotyphlops dulcis*) that are primarily limited to Texas in the United States, although three have extensive ranges in Mexico. New Mexico populations of *Hylactophryne* apparently are isolated from Balconian elements of the species, presumably as a result of a climatic trend toward increased aridity.

Other species (two forms, 3.0%).—Two parthenogenetic whiptails, *Cnemidophorus tesselatus* and *C. exanguis*, do not fit any of the foregoing

categories. Both are about equally distributed between parts of the Chihuahuan and Navahonian biotic provinces.

By way of summary of the various faunal elements, it may be said that aside from the large group of species with wide distributions in the Southwest, the most important contribution is made by the Chihuahuan Desert element, with southern Great Plains and eastern riparian elements following in importance. In addition, there is a small but distinctive northern contribution, and a few forms of importance in Texas–Mexico also reach the area. This picture is not inconsistent with that obtained in terms of biotic provinces. The Chihuahuan Desert contribution was found to be of outstanding importance in both cases, and the northern or Navahonian contribution was found to be relatively minor. The low importance of the latter is not unexpected in view of the decreased importance of terrestrial poikilotherms to the north and in the Rocky Mountains, and should not be viewed as indicative of the composition of the biota as a whole. The plains (or Kansan) affinities were identified as important in both analyses, and both indicated some influence from Texas, although the contribution of the Balconian in the biotic province analysis appears to have been exaggerated by failure to exclude either widely distributed forms or Pecos River elements.

The overall picture that emerges is the extreme diversity of the herpetofauna in terms of its origins, and the critical location of the Guadalupe Mountains at the contact zone between various biotic or herpetofaunistic regions. This is emphasized by the rather remarkable fact that at least 23 of the 66 naturally occurring species reported from the Guadalupe Mountain area reach their limits of distribution in or near there. This includes eight forms of the Chihuahuan Desert, four eastern riparian species, two "Texas" species, two northern forms, and seven other southwestern species.

Some correlations can be seen between the various faunal elements and local distributional patterns. This is most obvious, of course, for the Pecos River element, members of which are confined to permanent water which is found mostly at lower altitudes on the eastern side of the escarpment. Most species of the plains element, with the exception of *Eumeces obsoletus* and possibly *Kinosternon flavescens*, are limited to the plains belt and lowermost part of the roughlands belt. The same is essentially true of the Texan element. Of the northern forms, both *Phrynosoma douglassi* and *Opheodrys vernalis* appear to be restricted to higher and more mesic environments. Although *Eumeces multivirgatus* is found at lower altitudes, it is common in the highest parts of the mountains. Local distribution of the Chihuahuan and other species show no consistent patterns. It is interesting to note in this connection that *Crotalus lepidus* and *Sceloporus poinsetti*, two Chihuahuan Desert species that reach their northern limits of distribution in southern New Mexico, together with *Crotalus molossus*, which ranges only slightly further north, all occur at the highest altitudes in the montane belt.

This striking inconsistency between altitudinal range and northern distributional limits may be the result of continual local dispersal of these saxicolous reptiles from lower habitats. Without this replenishment, the high altitude populations might not be able to maintain themselves over a long period of time.

Finally, attention should be drawn to the fact that there are considerable differences between the herpetofaunas at lower altitudes on the eastern and western sides of the mountains. As already emphasized, the eastern riparian elements essentially are limited to the eastern side, primarily because of proximity of the Pecos River and associated drainage patterns, but also because of the scarcity of permanent water on the western face. *Thamnophis marcianus*, although not included in this element, also conforms to this local pattern. On the other hand, extreme desert habitats including sandy or dune situations near the salt flats on the southwestern side support certain species (*Crotalus scutulatus, Crotaphytus wislizeni, Cnemidophorus tigris, Holbrookia maculata*) that apparently are absent on the immediate eastern side. Limited information suggests that local distribution of some other species is consistent with this dichotomy, but more documentation is needed.

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