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ABSTRACT

The pine-oak woodlands of the Sierra Madre Occidental of México extend for about 1100 km from the northern end of the Sonoran-Chihuahuan border southward to the region of the common borders of Zacatecas, Nayarit, and Jalisco. On the eastern side of the sierra the pine-oak woodlands grade into mesquite-grassland on the Mexican Plateau in the foothills. The steep escarpment on the west and its deep *barrancas* allow for complex interdigitation of the pine-oak woodland vegetation and the tropical deciduous forests in the lowlands. The climate of the pine-oak woodlands is of the humid temperate type with cool summers and moderate winters. Most precipitation falls in July, August, and September. Pine-oak woodland vegetation ranges from an oak scrub at the lower limit through mixed pine-oak vegetation at intermediate elevations to pine forest with a mixture of boreal elements at the upper limit.

The herpetofauna of the pine-oak woodlands of the Sierra Madre Occidental comprises 86 species, including 3 salamanders, 17 anurans, 3 turtles, 27 lizards, and 36 snakes. These 86 taxa may be placed in four distributional categories, viz., endemic or nearly so (8 species), widespread pine-oak (17 species), widespread (17 species), and peripheral (44 species). Over 90% of the herpetofauna is shared with one or more adjacent regions in the following order of prominence: Mesquite-Grassland Area (39 species), Pacific Coast Tropical Area (33 species), Cordillera Volcánica Montane Woodland Area (30 species), North American Montane Woodland Area (28 species), and North American Desertscrub Area (23 species).

Four herpetofaunal assemblages may be recognized. These include the Pine-Oak Woodland Assemblage (43 species), most members of which have their ranges centered in the Sierra Madre Occidental or in the Cordillera Volcánica, the Ubiquitous Assemblage (26 species), the Pacific Lowland Subhumid Assemblage (13 species), and the Mesquite-Grassland Assemblage (4 species).

Within the Pine-Oak Woodland Assemblage, three historical elements are represented, viz., the Old Northern, Young Northern, and Middle American elements. Most generic groups in this assemblage belong to the first two elements.

Formation of the Mexican Plateau and the bounding escarpments began at the end of the Cretaceous period. Igneous activity during the Miocene formed the Sierra Madre Occidental. Volcanic quiescence during the Pliocene allowed for peneplanation, followed, in turn, by more vulcanism during the upper Pliocene and on into the Pleistocene. Pleistocene glaciation and interglacial periods brought about alternating expansion and contraction of montane glaciers, coupled with depression and elevation of vegetation zones.

Modernization of the North American herpetofauna was a Mio-Pliocene phenomenon, whereas the Pleistocene involved changes in range brought about by a fluctuating environment.

Pine-oak woodland vegetation in the Sierra Madre Occidental began to develop after the cessation of Miocene orogeny and became established at least by the Pliocene.

Origin and establishment of the Pine-Oak Woodland Assemblage of the Sierra Madre Occidental herpetofauna appears to have involved two major events, viz.: (1) evolution of an endemic Sierra Madre-centered component during events that created the sierra in the Miocene and Pliocene; (2) dispersal of the members of an extra-sierra component into the sierra, primarily from the Cordillera Volcánica, during

Pleistocene glacial depression of highland vegetation zones. Dispersal across deep canyons and plateau terrain now extant between the Sierra Madre Occidental and the Cordillera Volcánica has been primarily unidirectional, as noted above, apparently because most members of the Sierra Madre-centered and endemic component of the Pine-Oak Woodland Assemblage are restricted to more northern regions of the sierra or are restricted to small geographical ranges somewhere in the sierra. Most of the species in the other three assemblages appear to have been involved in Quaternary dispersals into the sierra from adjacent regions.

INTRODUCTION

The Sierra Madre Occidental constitutes one of the major geomorphic features of the country of México. Its relatively remote temperate pine-oak woodlands provide a pleasant respite for the naturalist from the hectic bustle of life on the Mexican Plateau and the Pacific coastal lowlands. It is still possible to camp and work in the more remote areas of these mountains for days on end and see only the occasional *leñero* or *vaquero*. This tranquility and the relative pristine character of the pine-oak woodlands is threatened, however, every time a new road is bulldozed up the slopes in search of *madera* or pasturage. Once the road is built, further development follows; *pueblos* begin to pop up along its length, especially if the road is paved as has been the case with Hwy. 40 through southern Durango. We feel fortunate to have worked in an area of this country of rapid human population growth that is all too fast disappearing.

The literature on the herpetofauna of this section of México includes reports of collections made in different regions of the sierra. Collections from the pine-oak woodlands have been reported or listed from the Yepómera area (Van Devender and Lowe, 1977), Mojarachíc (Taylor and Knobloch, 1940), and the Cerro Mohinora region (Webb and Baker, 1984) in Chihuahua, from western Chihuahua (Tanner, 1985), from the Yécora region in Sonora (Lara-Gongora, 1986), from the Sierra Surutato in Sinaloa (McDiarmid et al., 1976), from eastern Sinaloa (Hardy and McDiarmid, 1969), from the Hwy. 40 region in Durango and Sinaloa (Webb, 1984), from the Pueblo Nuevo area (Webb and Baker, 1962), and Rancho Las Margaritas (Drake, 1958) in Durango. Other information on the herpetofauna of the Sierra Madre Occidental is included in a wide variety of other sources, many systematic in nature.

This paper is an expanded version of one given at a symposium on Mexican herpetogeography in honor of Hobart M. and Rozella B. Smith in Salt Lake City in 1983. We would like to dedicate this published version to them as well.

METHODS

The information upon which this study is based was derived from our own field work and from the literature containing distributional data on the herpetofauna of the Sierra Madre Occidental. An annotated bibliography of this literature will be submitted elsewhere. Separately and together we have spent a total of 132 man-days during the months of July, August, and September working in all regions of the mountain range, except for that in central Durango. Portions of three trips in 1972, 1974, and 1975 were spent working along Hwy. 40 in southern Durango. One of these trips also included a survey of the Sierra de Valparaíso in southwestern

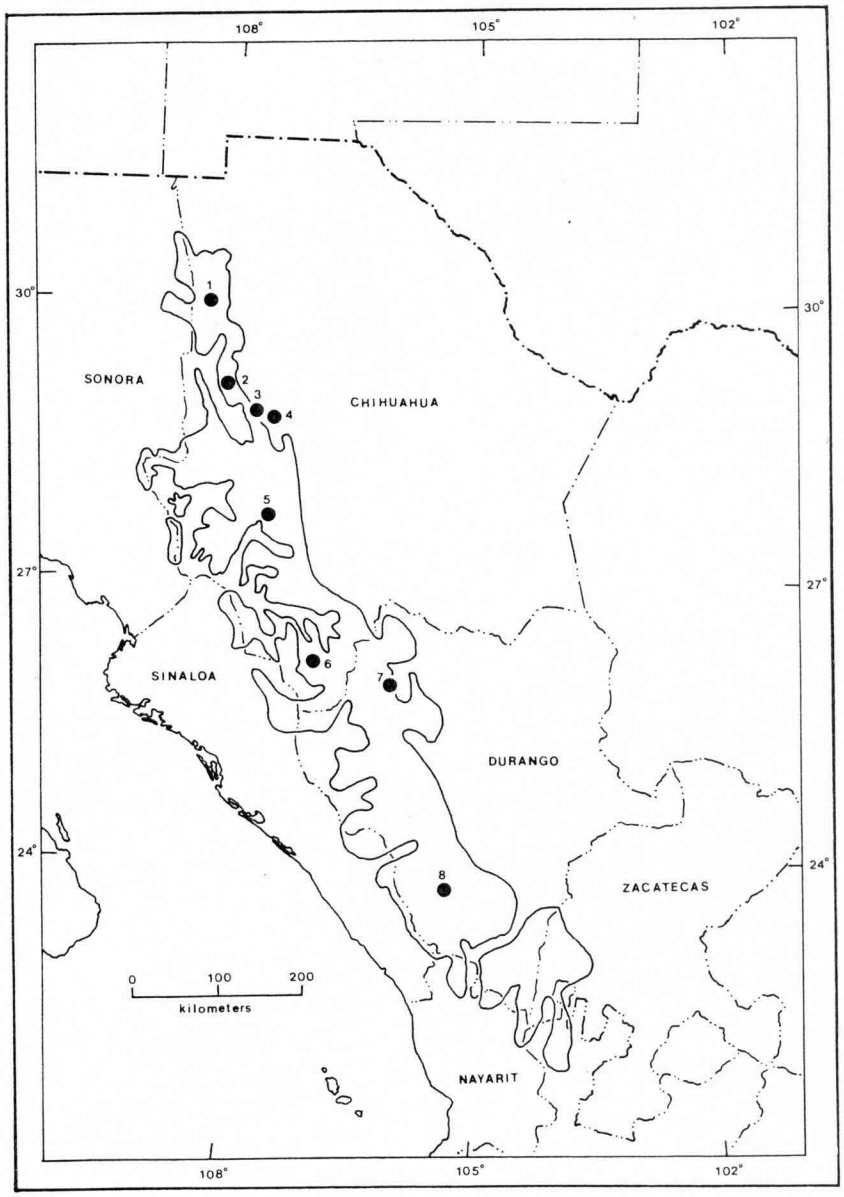

Figure 1. Limits of the pine-oak woodlands of the Sierra Madre Occidental of México (solid lines), as recognized in this study. The bold interrupted line represents the international border. Other interrupted lines are state boundaries. Localities indicated are those used in the analysis of climate, as follows: (1) Colonia García, Chihuahua; (2) Madera, Chihuahua; (3) Temósachic, Chihuahua; (4) Ciudad Guerrero, Chihuahua; (5) Creel, Chihuahua; (6) Guadalupe y Calvo, Chihuahua; (7) Guanaceví, Durango; (8) El Salto, Durango.

Zacatecas. Work in 1976 centered in the northern end of the sierra. A lengthy trip in 1977 explored regions along the length of the cordillera, excluding northern and central Durango. Finally, a short trip was made to the southern Chihuahua and northern Durango portion of the mountain range in 1978. Material resulting from this work has been deposited primarily in the Louisiana State University Museum of Zoology and the University of Texas at Arlington Collection of Vertebrates. Some material remains in our private collection and will be deposited in a permanent collection. The taxon level is that of the species.

Four species listed as rare in Lower Montane Dry Forest (their usage; equivalent to pine-oak woodlands of this study) in the vicinity of Santa Lucía, Sinaloa by Hardy and McDiarmid (1969) were originally included by us in the pine-oak woodland herpetofauna. These four species [*Eleutherodactylus vocalis, Hyla smaragdina, Syrrhophus teretistes* (as *S. modestus*), and *Trimorphodon biscutatus* (as *T. lambda)*] were deleted after Webb's (1984) detailed study of the area showed them to occur in tropical-deciduous forest below the mixed boreal-tropical region (the latter included in the pine-oak woodlands in this study).

LIMITS OF STUDY AREA

The pine-oak woodlands of the Sierra Madre Occidental extend from northwestern Chihuahua and northeastern Sonora southward through western Durango and portions of extreme eastern Sinaloa to southwestern Zacatecas and parts of northern Nayarit and Jalisco (Fig. 1). Our usage of the term pine-oak woodlands includes a variety of forest types and we use the term as a convenience (see section on vegetation). The Río Mezquital valley of southwestern Durango isolates the woodlands of southwestern Zacatecas, adjacent Durango, Jalisco, and part of Nayarit from the woodlands to the north. The map (Fig. 1) was adapted from several published sources (Anderson, 1972; Baker and Greer, 1962; Leopold, 1972) plus our field experience in the area. We chose not to include outlier ranges, such as the Sierra del Nido and the Sierra San Luis of Chihuahua, the Sierra del Tigre and others to the northwest in Sonora. Likewise, outlier ranges to the south were excluded, including the Sierra Morones in Zacatecas and the Sierra Fría in Aquascalientes. The main portion of the woodlands extend approximately 1100 km north to south and is relatively narrow, being no more than 200 km wide at any point. In the north, the lower limits of the pine-oak woodlands are around 1500 to 1800 m. The lower limits of the woodlands generally increases along the eastern slopes as one travels southward. In southern Durango, this limit is about 2100 m, whereas in the Sierra de Valparaíso portion in Zacatecas the lower limit may be as high as 2300 m. To the northwest, the lower limits of the pine-oak woodlands are around 1200 to 1350 m, decreasing slightly in extreme southeastern Sonora. Further south, along the western slopes, these lower limits are around 1500 to 1800 m.

THE SETTING

Physiography . — Most of México north of the Balsas Basin (about 18°N latitude) consists of the Mexican Plateau and bounding mountain ranges and escarpments to the east, west, and south. The mountain ranges and escarpments to the west of this extensive highland plateau are collectively termed the Sierra Madre Occidental. As noted by West (1964), this mountain complex extends approximately from the inter-

Figure 2. Eastern foothills of the Sierra Madre Occidental at Arroyo el Tecuán on Rancho Santa Bárbara, 1.7 km W Los Mimbres on Hwy. 40, Durango, México. Elevation 2220 meters.

national border in the north to the canyons of the tributaries of the Río Grande de Santiago in Jalisco. The formation of the sierra by vulcanism during the Tertiary, faulting and uplift during the Pleistocene, and erosion brought about by Pacific versant rivers and streams have combined to create some of the most spectacular scenery in all of México. The Barranca del Cobre in southwestern Chihuahua rivals the Grand Canyon of Arizona in magnitude and splendor. Driving down over the face of the west-facing escarpment on the fabled Highway 40 from El Salto, Durango, to Chupaderos, Sinaloa, provides for continuous switchback thrills.

According to West (1964), the Sierra Madre Occidental represents "the upturned edges and escarpments of the [western edge of the] plateau proper." From the east (Fig. 2), thus, "the sierra appears to be insignificant, for it rises gradually as a rolling surface to a few hundred meters above the plateau basins" (West, 1964). Viewed from the Pacific coastal plain to the west (Fig. 3), however, "the mountain front rises as a magnificent escarpment to a maximum elevation of 2500-3000 m. above sea level" (West, 1964). This steep escarpment is highly dissected with deep, torturous *barrancas* (Fig. 4) carved by westward-flowing rivers. These *barrancas* or deep canyons may be 1500 to 2000 m. in depth (West, 1964). The highland ridges, however, "form flat-topped mesas with steep, bufa-like cliffs" (West, 1964). These mesas are especially well-developed in southern Durango where much of the area is a relatively level, gently rolling plateau with a general elevation of about 2400 m. The

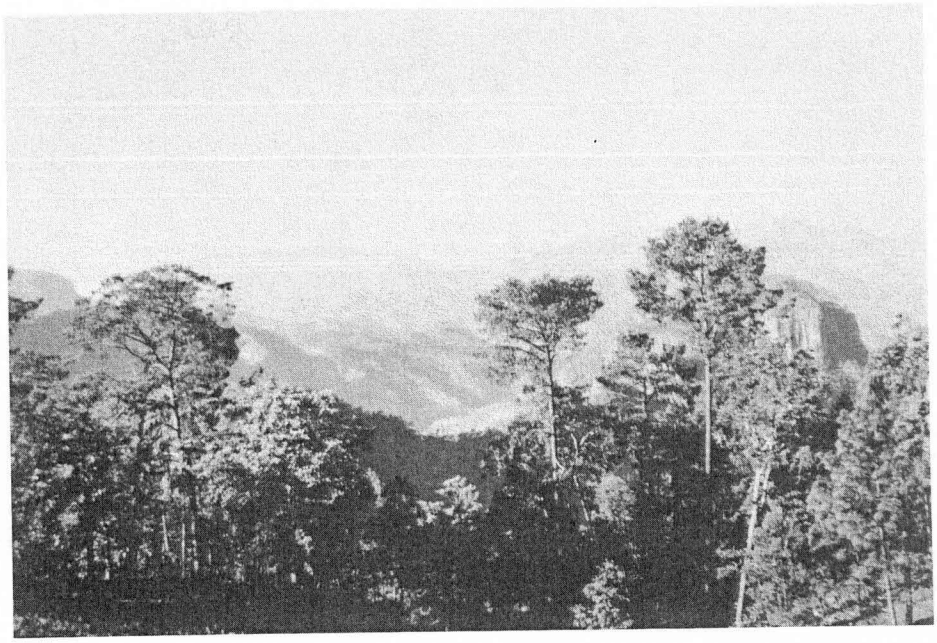

Figure 3. Western periphery of the Sierra Madre Occidental looking west from Los Bancos, 10.2 km W Buenos Aires and about 1 km S of Hwy. 40, Durango, México. Elevation approximately 2300 meters.

highest peak in the sierra is Cerro Mohinora of extreme southwestern Chihuahua near the border with Durango (Rouaix, 1930; Webb and Baker, 1984), notwithstanding the fact that some maps show a higher elevation for the nearby Cerro Chorrera in adjacent Durango. The exact elevation of Cerro Mohinora is uncertain as recorded elevations vary between 3200 and 3418 (Webb and Baker, 1984). To the south and east in Durango, there are several peaks reaching elevations between 3000 and 3200 m, including the cerros Chorrera and Flechas in northwestern Durango, cerros Prieto and Huehuento in west central Durango and Cerro Gordo in southern Durango (Rouaix, 1930). South of the Río Mezquital, the mountains are generally lower. Only one unnamed peak in extreme southern Durango, near the border with Zacatecas, reaches an elevation of 3000 m, with a few other peaks in the immediate area exceeding 2900 m (Centenal, Topográfica, 1:50,000). To the east in the sierra north of Valparaíso, Zacatecas, a single peak, Cerro La Manga, reaches 2900 m, with several others exceeding 2800 m (Cetenal, Topográfica, 1:50,000). In the extreme southern portion of the sierra near Bolaños, Jalisco, a single peak slightly exceeds 2900 m (Cetenal, Topográfica, 1:50,000). To the northwest of Cerro Mohinora, there is, likewise, a decrease in elevation, with the highest peaks being between 2750 and 3000 m. The lone exception is a single peak located near Cerro Mohinora between El Vergel and Guadalupe y Calvo, Chihuahua, with a maximum elevation of 3110 m (Cartográfico Militar, México, 1:250,000).

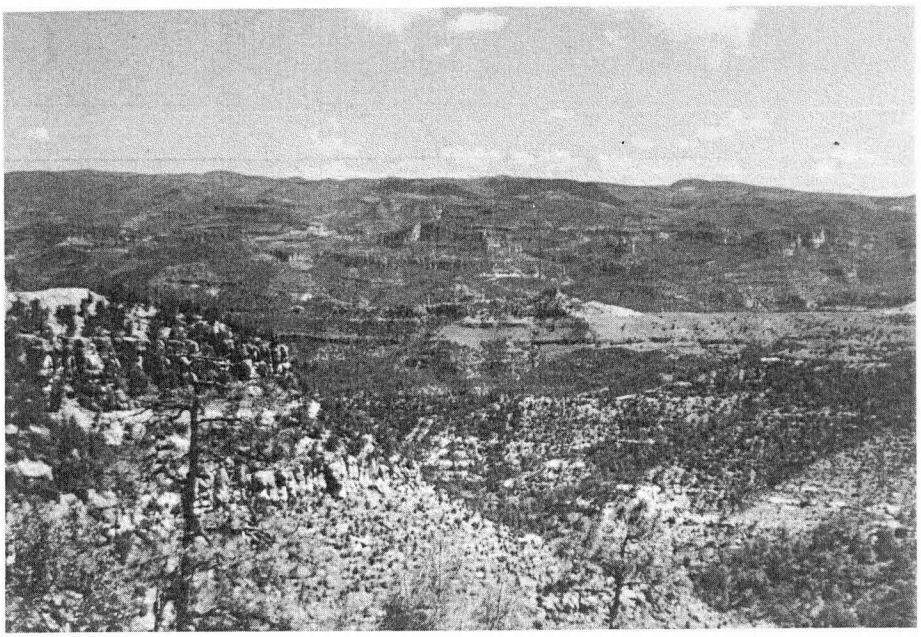

Figure 4. Upper Barranca del Cobre on the Río Urique at the point the road south of Creel crosses the canyon, Chihuahua, México. Elevation 2110 meters.

Waters flowing down the eastern slopes of the sierra drain largely into rivers of interior drainage (rios Casas Grandes, Carmen, Nazas, and Aguanaval), as well as into the Río Conchos, a tributary of the Río Bravo (=Rio Grande). However, the eastern slopes of the sierra in southern Durango and the northern slopes of the isolated southern portion considered in this paper are drained by tributaries of the Pacific versant Río Mezquital. Those flowing down the western escarpment collect into Pacific versant rivers (e.g., the rios Yaqui, Mayo, Fuerte, Sinaloa, Culiacán, Mezquital and large tributaries of the Río Grande de Santiago) that have carved the spectacular *barrancas*. These rivers flow out across the coastal plain into the Gulf of California and the Pacific Ocian (Tamayo and West, 1964).

Climate. — The climate of the pine-oak woodlands of the Sierra Madre Occidental is basically of a humid temperate type (Vivó-Escoto, 1964). This climatic type is characterized as having a mean temperature of the coldest month above 0°C and that of the warmest month above 18°C. In México this climatic regime is principally restricted to montane environments (Vivó-Escoto, 1964). Some localities in the Sierra Madre Occidental however, may have temperature regimes in which the mean temperature of the warmest month (June, July, or August) may fall slightly below 18°C (Madera, Creel, and Guadalupe y Calvo — see Table 1).

The precise type of climatic regime is not as easy to determine as might be assumed by examination of Vivó-Escoto's (1964) Fig. 14. That map indicates that the

Table 1

Temperature (°C.) and Precipitation (mm.) Data for Selected Localities in the Sierra Madre Occidental (data from Wernstedt, 1972)

Localities	Elevation (meters)	Monthly Averages J	F	M	A	M	J	J	A	S	O	N	D	Annual
Colonia García, Chihuahua	2100	No temperature data available 9.4	3.6	0.0	1.5	9.4	31.5	76.7	52.6	52.6	15.2	16.0	6.4	274.9
Madera, Chihuahua	2079	6.3° 16.8	7.4° 17.3	10.4° 4.8	12.8° 7.6	14.6° 5.3	17.2° 15.5	17.7° 80.0	17.8° 96.5	16.4° 43.4	16.6° 22.1	13.6° 16.5	8.3° 39.9	12.3° 365.7
Temósachic, Chihuahua	1858	4.3° 8.9	6.6° 4.3	8.7° 7.4	11.7° 6.9	16.6° 11.9	21.0° 27.2	21.8° 109.2	21.2° 128.5	18.7° 64.5	14.0° 30.0	8.2° 14.7	4.8° 40.4	13.0° 453.9
Ciudad Guerrero, Chihuahua	2010	4.1° 9.7	6.0° 10.9	8.2° 4.6	11.7° 5.8	14.9° 12.7	18.5° 33.0	19.3° 117.6	18.2° 119.1	16.8° 81.0	8.3° 23.6	8.4° 10.2	4.8° 29.5	12.2° 457.7
Creel, Chihuahua	2400	3.1° 59.0	4.0° 27.0	6.1° 17.0	9.2° 9.0	12.9° 9.0	17.3° 68.0	17.6° 179.0	16.4° 156.0	14.9° 87.0	11.6° 39.0	6.6° 15.0	3.1° 27.0	10.2° 692.0
Guadalupe y Calvo, Chihuahua	2150	6.0° 60.2	6.9° 56.4	8.0° 34.5	11.3° 6.1	14.4° 23.6	17.6° 83.6	17.1° 256.8	16.5° 221.2	16.7° 156.5	14.1° 64.3	8.9° 29.5	7.2° 83.6	12.1° 1076.3
Guanaceví, Durango	2005	8.8° 17.0	10.4° 13.2	12.4° 13.0	15.5° 7.9	18.2° 14.0	21.7° 64.5	19.1° 145.3	18.6° 155.2	18.0° 116.8	15.7° 38.4	12.2° 13.0	9.3° 49.5	15.0° 647.8
El Salto, Durango	2538	6.3° 36.8	6.5° 34.3	8.0° 7.6	10.6° 2.3	12.8° 36.3	22.2° 153.2	15.4° 193.0	15.5° 188.7	15.2° 129.0	12.8° 61.0	9.3° 22.9	7.2° 59.9	11.4° 925.0

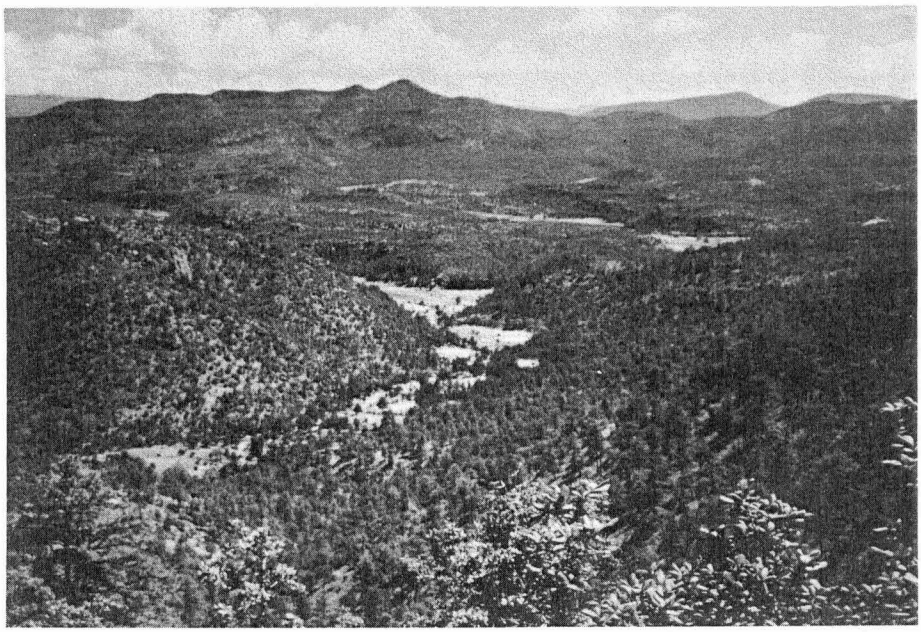

Figure 5. Pine-oak vegetation vista 3.2 km W Ranco Blanco, 26.2 km N San Juancito, Chihuahua, México. Elevation 2410 meters. Elevation of valley, 2150 meters.

higher regions of the sierra possess a Cfb type climate and the slopes have a Cwa type. In the former, according to Vivó-Escoto (1964), there is "rain in every month without a distinct dry period, but usually with most rain coming in the summer or autumn months" and with the "average temperature of the warmest month *below* 22°C." In the latter type there is "a distinct winter dry season and summer rains" and the average temperature of the warmest month is *over* 22°C. In almost all localities for which data are available, there is some amount of rain every month (Table 1) but there is still a distinct dry season. Most of the precipitation in all areas falls in July, August, and September. The percentages range from a low of 64.4% falling in those months at Madera to a high of 77.6% at Colonia García. The least amount of precipitation falls in the months of February through May (Table 1) and these months, in our opinion, comprise a "distinct" dry season. The percentages range from a low of 5.3% at Colonia García to a high of 11.2% at Guadalupe y Calvo.

Some of that precipitation falls as snow in the pine-oak woodlands. Webb (1984) noted that in the Durango highlands "snow may occur for about one third of the year, persisting as small patches in shaded places into June." These data are corroborated by Baker and Greer (1962) who pointed out that "Guanaceví, in the mountains of northcentral Durango, may have 107 days of the year with snow while further south in the mountains at El Salto, 128 days of the year may have snow."

Precipitation is lowest in the northern reaches of the sierra and highest in the

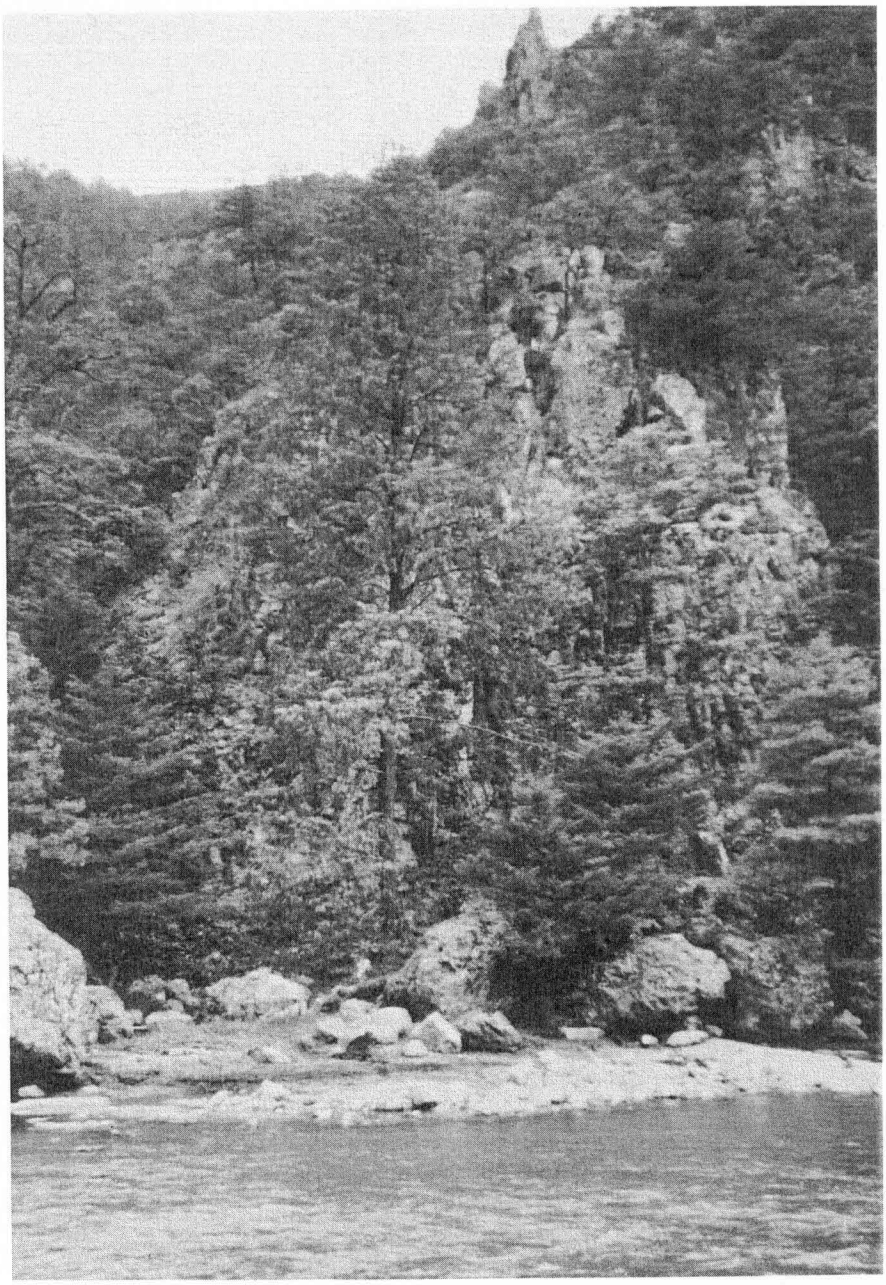

Figure 6. Pine-oak vegetation along Arroyo Santa Rosalia near Guadalupe y Calvo, Chihuahua, México. Elevation 2050 meters.

southern portions. The same relationship exists from east to west in the mountain range (Table 1).

Webb (1984) indicated that "warm, moisture-laden, westerly winds sweep inland from the Pacific Ocean and precipitate most rain on the highest parts of the Sierra Madre [Occidental] that are often shrouded in clouds and where hail storms are not infrequent." Vivó-Escoto (1964), discussing in general the precipitation patterns in highland areas in Middle America, noted that "the rains begin usually in June . . . in the form of violent afternoon thunderstorms, often accompanied by hail, and last through the middle of October." He continued by pointing out that "during the height of the dry season the highlands become parched and winter dust takes the place of summer wind."

The lowest average monthly temperatures occur in December, January, and February in all localities (Table 1). As indicated by Webb (1984), "in winter, cold northerly winds ["*nortes*"] may drop temperatures below freezing." These average monthly temperatures may range as low as about 3°C (= 37°F) in December and January at Creel to as high as 10.4°C (50.7°F) in February at Guanaceví (Table 1). The highest average monthly temperatures occur from June through August and range from 15.4°C (59.7°F) in July at El Salto to 22.2°C (71.9°F) in June at the same locality (Table 1).

Vegetation. — Inasmuch as this paper is concerned with the biogeography of the pine-oak woodlands of the Sierra Madre Occidental, it is important to delimit our use of the term "pine-oak woodland" and to characterize this complex vegetation zone for the purposes of discussing its impact on the distribution of the herpetofauna.

Our use of the term pine-oak woodland includes the "Madrean montane conifer forests" of Pase and Brown (1982) and the "Madrean evergreen woodland" of Brown (1982) and is essentially equivalent to the pine-oak forest of Leopold (1950, 1972), excluding his "piñon-juniper woodland." Thus, we include in our designation his "pine forest," "pine-oak woodland," and "oak scrub." Several authors (including Baker and Greer, 1962; Webb and Baker, 1962, 1984) use the term "pine-oak forest" for these habitat types. Pine-oak woodland to us signifies a forest type in which species of pines and/or oaks occur as the dominant vegetation in varying combinations of composition and diversity. This vegetation type (Figs. 5 and 6) is widespread in northern and central México (Mirov, 1967, Fig. 3-39; Leopold, 1972; Rzedowski, 1983) in mountainous regions at elevations above those supporting mesquite-grassland and tropical deciduous forest.

In general, in the Sierra Madre Occidental "at the lower fringe of the pine-oak zone there is often a belt of stunted oak, growing more like large shrubs than trees" (Leopold, 1972), "adjoining semi-arid foothills or lowland basins" (Leopold, 1950). This *encinal* vegetation grades into the pine-oak vegetation occurring generally at higher elevations. At the northern end of the Sierra Madre Occidental and in the Sierra Madrean outliers, Marshall (1957) noted that "all the species of oaks which comprise encinal of the foothills also grow in the pine-oak woods . . ." The pine-oak vegetation in turn gives way to pine forests or *pinares* which may occur to the tops of the ridges in the sierra or intermingle on scattered peaks with elements of the boreal forest (Webb and Baker, 1962; Leopold, 1972).

The *encinal* vegetation in the foothills of the Sierra Madre Occidental consists of a variety of oaks. Brown (1982) recorded *Quercus chihuahuensis* (Chihuahua oak), *Q. albocincta, Q. emoryi* (Emory oak), *Q. arizonica* (Arizona white oak), *Q. chuchui-*

chupensis, and *Q. santaclarensis* (Santa Clara oak) as the commonly found species in western Chihuahua and adjacent Sonora and *Q. santaclarensis, Q. emoryi, Q. chihuahuensis, Q. grisea* (gray oak), and *Q. durifolia* as the important oaks along the eastern fringe of the sierra in central Chihuahua. In the Yécora region of Sonora, Lowe et al. (1968) indicated that *Q. hypoleucoides* (silver-leaf oak) comprises part of the dominant vegetation. In the Yepómera region of Chihuahua, Van Devender and Lowe (1977) reported *Q. emoryi, Q. arizonica,* and *Q. oblongifolia* (Mexican blue oak). In Durango, Baker and Greer (1962) listed *Q. macrophylla* and *Q. viminea.* Other trees noted as occurring in the *encinal* vegetation by Brown (1982) are *Juniperus deppeana* (alligatorbark juniper), *J. monosperma* (one-seed juniper), and *Pinus cembroides* (Mexican pinyon).

In the pine-oak vegetation at intermediate elevations of the sierra, several of the oaks mentioned above form an admixture with various species of pines, which together form the dominant vegetation. Brown (1982) listed *Q. viminea, Q. hypoleucoides, Q. pennivenia* (hand basin oak), *Q. epileuca, Q. fulva,* and *Q. rugosa* (netleaf oak) as the important oaks and *Pinus engelmannii* (Apache pine), *P. leiophylla* var. *chihuahuana* (Chihuahua pine), *P. ponderosa* var. *arizonica* (Arizona pine), *P. lumholtzii (pino triste),* and *P. durangensis* (Durango pine) as the principal pines of these intermediate elevations of the northern portion of the sierra. In the Yécora region studied by Lowe et al. (1968), *P. engelmannii* and *P. leiophylla* were found. In the Yepómera area inventoried by Van Devender and Lowe (1977), *P. cembroides, P. leiophylla,* and *P. latifolia* (= *P. engelmannii)* occur in the pine-oak zone. Baker and Greer (1962) reported *P. lumholtzii* from the highlands of Durango. In this vegetation zone along Hwy. 40 in southern Durango, Webb (1984) reported *P. leiophylla, P. durangensis,* and *P. strobiformis* (southwestern white pine). We also include here Webb's (1984) "mixed boreal-tropical" zone. Characteristic flora occurring here includes *P. oocarpa, P. teocote,* and *P. lumholtzi* and the oaks *Q. macrophylla, Q. fulva,* and *Q. viminea.* Understory plants in the pine-oak vegetation include Mexican manzanita (*Arctostaphylos pungens),* heavily used for firewood, alligatorbark juniper (*Juniperus deppeana),* madroño (*Arbutus spp.),* and various grasses, especially bunchgrass or *zacatón* (Marshall, 1957; Drake, 1958; Baker and Greer, 1962; Lowe et al., 1968; Leopold, 1972; Van Devender and Lowe, 1977; Webb, 1984).

At higher elevations, pine forest predominates (Fig. 7) and "oaks are subdominant where present at all" (Leopold, 1972). Pines characteristic of the pine-oak zone intrude into these regions, with *Pinus ponderosa* var. *arizonica* "both the dominant montane conifer and commercial tree" (Pase and Brown, 1982: 44) of the pine forest zone (*pinares).*

The highest summits of the sierra are capped by *Pinus ayacahuite* (Mexican white pine), *Pseudotsuqa menziesii* (Douglas fir), *Populus tremuloides* (quaking aspen), and *Pinus ponderosa* (Pase and Brown, 1982). Webb (1984) reported a similar forest in "moist, deep, protected canyons" in Durango. An endemic spruce (*Picea chihuahuana)* occurs on the highest peaks in Durango and on at least one peak in southern Chihuahua (Pase and Brown, 1982).

Figure 7. Pine forest on ridges surrounding highland meadow 12.0 km SW and 8.0 km S El Vergel, Chihuahua, México. Elevation 2430 meters.

COMPOSITION OF THE HERPETOFAUNA

The herpetofauna of the pine-oak woodlands of the Sierra Madre Occidental includes 86 species (with bonafide records), including 3 species of salamanders (3.5% of the total), 17 anurans (19.8%), 3 turtles (3.5%), 27 lizards (31.4%), and 36 snakes (41.9%).

A comparison of these figures to those for the herpetofauna of the Sierra Madrean outliers in southeastern Arizona and southwestern New Mexico shows the two to be nearly identical in percentages of composition. A total of 36 species is recorded from the pine-oak woodlands of these mountains (Bogert and Degenhardt, 1961; Lowe, 1956, 1964), including 1 species of salamander (2.6%), 6 anurans (16.7%), 1 turtle (2.6%), 12 lizards (31.6%), and 16 snakes (44.4%). These figures may also be compared to data for the herpetofauna of the pine-oak woodlands of the section of the Cordillera Volcánica in Michoacán studied by Duellman (1965). He reported a total of 70 species, including 5 species of salamanders (7.1%), 18 anurans (25.7%), 1 turtle (1.4%), 17 lizards (24.3%), and 29 snakes (41.4%).

PATTERNS OF DISTRIBUTION

Distributional Categories. — In analyzing the distribution of the 86 species comprising the herpetofauna of the Sierra Madre Occidental, each species was placed in one of four distributional categories (letters in parentheses used in subsequent discussion) as follows:

1. Endemic (E) — species limited to the Sierra Madre Occidental or nearly so (see definition in Limits of Study Area). A few of these species also occur sporadically in nearby Mexican outlier ranges.
2. Widespread pine-oak (WPO) — species limited, or nearly so, to the pine-oak woodlands in the Sierra Madre Occidental, and in the Cordillera Volcánica, and/or the Sierra Madrean outliers in southeastern Arizona and southwestern New Mexico.
3. Widespread (W) — species widespread in pine-oak woodlands of the Sierra Madre Occidental and also widespread in one or more additional adjacent vegetation zones (other than or in addition to pine-oak woodland).
4. Peripheral (P) — species which barely enter the pine-oak woodlands of the Sierra Madre Occidental.

Eight species are included in the endemic category as follows: *Ambystoma rosaceum, Eleutherodactylus tarahumaraensis, Tomodactylus saxatilis, Barisia levicollis, Eumeces multilineatus, Eumeces parviauriculatus, Adelophis foxi,* and *Thamnophis nigronuchalis*[1]. The membership of the remaining distributional categories is indicated in Table 2. The species included in these four groups are arranged into taxonomic groups and actual and relative numbers calculated in Table 3. Perusal of this table indicates that over half of the members of the herpetofauna have a distribution peripheral to the pine-oak woodlands of the Sierra Madre Occidental and that slightly less than 40% of the species are widespread (both WPO and W categories) in distribution in a generic sense. Only little more than 9% are endemic to the region under study.

Occurrence of Species in Adjacent Vegetation Zones. — Inasmuch as 90.7% of the species in the pine-oak woodlands of the Sierra Madre Occidental are not endemic, it is instructive to denote the distribution of those species in adjacent vegetation zones. The adjacent zones examined are characterized as follows (letters in parentheses used in subsequent discussion):

1. North American Montane Woodland Area (NAMA) — The pine-oak woodland portion of the Sierra Madrean outliers in southeastern Arizona and southwestern New Mexico (Santa Rita, Huachuca, Chiricahua, and Animas Mountains).
2. North American Chihuahuan Desertscrub Area (NADA) — The desertscrub region occurring to the northwest, north, and east of the Sierra Madre below the mesquite grassland zone from southeastern Arizona and adjacent Sonora (the Cochise Filter Barrier of Morafka, 1977) through Durango and into northern Zacatecas.
3. Mesquite-Grassland Area (MGA) — Mesquite-grassland occurs primarily along the eastern base of the sierra below the scrub-oak (*encinal*) zone of the lower slopes and gradually converges with Chihuahuan desertscrub through mixed desert-grassland communities. Mesquite-grassland also occurs sporadically north and northwest of the sierra.

[1] Tanner (1985) recognized *T. nigronuchalis* as a subspecies of *T. rufipunctatus*. In our opinion, his work did not adequately demonstrate the conspecificity of the two and we prefer to recognize them as separate species.

Table 2

Distribution of Widespread Pine-Oak, Widespread, and Peripheral Members of the Pine-Oak Woodland Herpetofauna of the Sierra Madre Occidental in Adjacent Vegetation Zones. See text for explanations of abbreviations.

Distributional Categories	Adjacent Vegetation Zones				
	NAMA	NADA	MGA	PCTA	CVMA
Widespread Pine-Oak[1] (17)					
Bufo microscaphus[2]					
Bufo occidentalis			P	P	x
Rana chiricahuensis	+		R		
Rana tarahumarae	+			R	
Barisia imbricata					x
Elgaria kingii	+	R		R	
Eumeces brevirostris					x
Sceloporus virgatus	+				
Conopsis nasus					x
Crotalus pricei	+				
Crotalus willardi	+				
Geophis dugesii[3]					x
Lampropeltis pyromelana	x				
Rhadinaea laureata					x
Storeria storerioides					x
Tantilla bocourti					x
Thamnophis rufipunctatus		R	R		
	7 (41.2%)	2 (11.8%)	3 (17.6%)	3 (17.6%)	8 (47.1%)
Widespread (17)					
Bufo compactilis			x		
Hyla arenicolor	x	x	x	x	x
Hyla eximia	x		x		x
Scaphiopus multiplicatus	x	x	x		x
Phrynosoma orbiculare			x		x
Sceloporus grammicus			x		x
Sceloporus jarrovii	x		x		
Sceloporus poinsettii		x	x		
Sceloporus scalaris	x		x		x
Crotalus lepidus	x	x	x		
Crotalus molossus	x	x	x		x
Diadophis punctatus	x	x	x		x
Salvadora grahamiae	x		x		
Thamnophis cyrtopsis	x	x	x	x	x
Thamnophis elegans[2]					
Thamnophis eques	x	x	x		x
Thamnophis melanogaster			x		
	11 (64.7%)	8 (47.1%)	16 (94.1%)	2 (11.8%)	10 (58.8%)
Peripheral Species (44)					
Ambystoma tigrinum	x	x	x		x
Pseudoeurycea bellii					x
Bufo punctatus		x	x	x	
Bufo woodhousei		x	x		
Eleutherodactylus occidentalis				x	x
Hyla bistincta					x
Rana magnaocularis				x	

Table 2 Continued on Next Page.

Table 2 (continued)

Distributional Categories	Adjacent Vegetation Zones				
	NAMA	NADA	MGA	PCTA	CVMA
Rana pustulosa				x	
Tomodactylus nitidus				x	x
Kinosternon hirtipes		x	x		
Kinosternon integrum			x	x	x
Kinosternon sonoriense	x	x	x		
Anolis nebulosus				x	x
Cnemidophorus costatus				x	
Cnemidophorus exsanquis	x	x	x		
Eumeces tetragrammus[4]	x			x	
Eumeces lynxe			x		
Eumeces parvulus				x	
Gerrhonotus liocephalus		x		x	
Phrynosoma douglassii	x		x		
Sceloporus bulleri				x	
Sceloporus clarkii	x	x		x	
Sceloporus heterolepis[5]				x	x
Sceloporus nelsoni				x	
Sceloporus spinosus[6]			x	x	
Sceloporus torquatus			x		x
Urosaurus ornatus	x	x	x	x	
Coluber constrictor[2]					
Crotalus basiliscus				x	
Crotalus scutulatus		x	x		
Crotalus stejnegeri				x	
Dryadophis cliftoni				x	
Hypsiglena torquata		x	x	x	
Lampropeltis mexicana			x		
Leptophis diplotropis				x	x
Masticophis mentovarius				x	
Masticophis taeniatus		x	x		
Pituophis deppei			x		
Pituophis melanoleucus	x	x	x	x	
Rhadinaea hesperia				x	x
Salvadora bairdi[7]			x	x	x
Senticolis triaspis	x			x	
Tantilla wilcoxi	x		x		
Trimorphodon tau				x	
	10 (22.7%)	13 (29.5%)	20 (45.5%)	28 (63.6%)	12 (27.3%)
TOTAL (78)	28 (35.0%)	23 (29.5%)	39 (50.0%)	33 (42.3%)	30 (38.5%)

[1] The symbols used in this section of the table have the following meaning: x = range centered in this vegetation zone; + = species also occurs in this vegetation zone; P = peripheral in distribution in this vegetation zone; R = species occurs in riparian habitats in this vegetation zone.

[2] Three species (*Bufo microscaphus, Coluber constrictor,* and *Thamnophis elegans*) are included in this table to eliminate confusion but do not actually occur in any adjacent vegetation zone.

[3] *Geophis dugesii* includes *G. aquilonaris* (see Webb, 1977).

[4] *Eumeces tetragrammus* includes *E. callicephalus* (see Lieb, 1985).

[5] *Sceloporus heterolepis* includes *S. shannonorum* (see Webb, 1969).

[6] *Sceloporus spinosus* includes *S. horridus* (see Boyer et al., 1983).

[7] Tanner (1985) considered this taxon a subspecies of *S. grahamiae*. We prefer to maintain specific status for *S. bairdi* and await a full-scale analysis of the relationship between the two.

Table 3

Frequency of Ordinal Groups of Species of Amphibians and Reptiles in the Sierra Madre Occidental by Distributional Categories (number in parentheses indicates the number of species in that group)

Group	Endemic (E)	Widespread Pine-Oak (WPO)	Widespread (W)	Peripheral (P)
Salamanders (3)	1	—	—	2
	33.3%	—	—	66.7%
Anurans (17)	2	4	4	7
	11.8%	23.5%	23.5%	41.2%
Turtles (3)	—	—	—	3
	—	—	—	100%
Lizards (27)	3	4	5	15
	11.1%	14.8%	18.5%	55.6%
Snakes (36)	2	9	8	17
	5.6%	25.0%	22.2%	47.2%
Totals (86)	8	17	17	44
	9.3%	19.8%	19.8%	51.2%

4. Pacific Coast Tropical Area (PCTA) — The Tropical deciduous forest of the west-facing slopes and thornscrub vegetation of the Pacific coastal plain occurring from southern Sonora southward. These vegetation formations also invade the sierra along the slopes and bottoms of the deep *barrancas* carved from the mountains by the westward-flowing rivers that drain the sierra.
5. Cordillera Volcánica Montane Woodland Area (CVMA) — The pine oak and fir forests of the Cordillera Volcánica from central Jalisco to central Veracruz.

The distribution of the non-endemic component among adjacent vegetation zones is indicated in Table 2. Examination of these data illustrates that the species making up the pine-oak woodland herpetofauna of the Sierra Madre Occidental are shared in substantial numbers with all adjacent vegetation zones but most so with the Mesquite-Grassland Area. In fact, almost all (16 of 17) species of the widespread category occur in the Mesquite-Grassland vegetation zone. Of the 17 widespread pine-oak species, none occurs in all three pine-oak woodland areas. Eight widespread pine-oak species have their ranges centered in the CVMA, 8 in the Sierra Madre Occidental, and 1 in mountains north of the sierra. Among peripheral species, the greatest sharing is with the Pacific Coast Tropical Area.

HERPETOFAUNAL ASSEMBLAGES

Based on analysis of present-day geographic and ecological distribution, we established four herpetofaunal assemblages composed of species we feel share similar biogeographic histories. These assemblages, their characterizations, and their members are outlined below:

Pine-Oak Woodland Assemblage. — Included in this assemblage are 43 species that are *predominantly* adapted to montane pine-oak woodlands in western and central México. A few of these species consistently occur outside the pine-oak woodlands along riparian situations (*Rana chiricahuensis*[2], *Kinosternon sonoriense, Elgaria kingii, Thamnophis eques, T. melanogaster,* and *T. rufipunctatus*) or saxicolously in the mesquite-grassland habitat (*Sceloporus jarrovii* and *S. torquatus*). In addition, *Elgaria kingii* has recently been collected in creosote desert scrub (Knight and Duerre, 1987). Eight species are endemic to the Sierra Madre Occidental, 17 are widespread pine-oak species, 11 are peripherals, and 7 are widespread, in terms of distributional category. With respect to major region of occurrence, 19 species have their range centered in the CVMA, with *Hyla eximia* and *Sceloporus scalaris* reaching the NAMA. Nineteen species have their range centered in the Sierra Madre Occidental; nine of these reach the NAMA, one (*Thamnophis eques*) reaches the CVMA, and *Bufo microscaphus*, while not occurring in the NAMA, is found in the mountains to the north of the NAMA. Three species (*Kinosternon sonoriense, Cnemidophorus exsanquis,* and *Lampropeltis pyromelana*) have their range centers north of the Sierra Madre Occidental and none of these species reach the CVMA. It should be added that we are considering the eastern subspecies of *Bufo microscaphus* only. Two species have unusual ranges compared to that of the others in this assemblage. *Sceloporus bulleri* occurs in tropical deciduous forest to the south and southwest of the Sierra Madre Occidental but is most abundant in pine-oak woodland (mixed boreal tropical woodland, in part, of Webb, 1967, 1984). *Lampropeltis mexicana,* although predominately a pine-oak woodland snake, also has been recorded in mesquite-grassland around the southern edge of the Chihuahuan Desert (see Garstka, 1982 for confirmation and for explanation of the name use). The species included in this assemblage are listed below, followed in parentheses by their distributional category. A single asterisk denotes species whose range is centered in the Sierra Madre Occidental; two asterisks denote species whose range is centered in the Cordillera Volcánica Montane Area.

Ambystoma rosaceum (E)*
Pseudoeurycea bellii (P)**
Bufo microscaphus (WPO)*
Bufo occidentalis (WPO)**
Eleutherodactylus tarahumaraensis (E)*
Hyla bistincta (P)**
Hyla eximia (W)**
Rana chiricahuensis (WPO)*
Rana tarahumarae (WPO)*
Tomodactylus saxatilis (E)*
Kinosternon sonoriense (P)
Barisia imbricata (WPO)**
Barisia levicollis (E)*
Cnemidophorus exsanquis (P)
Elgaria kingii (WPO)*

[2] We have followed Hillis et al. (1983) in using the name *chiricahuensis* for the leopard frogs of the upper elevations of the Sierra Madre Occidental. However, Webb and Baker (1984) concluded that the leopard frogs from the sierra in southern Chihuahua were not *Rana chiricahuensis* "as expected."

Eumeces brevirostris (WPO)**
Eumeces lynxe (P)**
Eumeces multilineatus (E)*
Eumeces parviauriculatus (E)*
Phrynosoma orbiculare (W)**
Sceloporus bulleri (P)
Sceloporus grammicus (W)**
Sceloporus heterolepis (P)**
Sceloporus jarrovii (W)*
Sceloporus scalaris (W)**
Sceloporus torquatus (P)**
Sceloporus virgatus (WPO)*
Adelophis foxi (E)*
Conopsis nasus (WPO)**
Crotalus pricei (WPO)*
Crotalus willardi (WPO)*
Geophis dugesii (WPO)**
Lampropeltis mexicana (P)
Lampropeltis pyromelana (WPO)
Rhadinaea hesperia (P)**
Rhadinaea laureata (WPO)**
Salvadora bairdi (P)**
Storeria storerioides (WPO)**
Tantilla bocourti (WPO)**
Thamnophis eques (W)*
Thamnophis melanogaster (W)*
Thamnophis nigronuchalis (E)*
Thamnophis rufipunctatus (WPO)*

Ubiquitous Assemblage. — Included in this assemblage are 26 species that are ecologically and geographically widespread. Seventeen species belong to the Peripheral and 9 to the Widespread distributional categories. Examination of the distribution of the members of this assemblage in the two most adjacent vegetation zones shows that 8 species occur in both the Mesquite-Grassland Area and the Pacific Coast Tropical Area, 11 in the Mesquite-Grassland Area only, and 5 in the Pacific Coast Tropical Area only. In addition, two species, *Coluber constrictor* and *Thamnophis elegans*, are not known from any of the five adjacent vegetation zones discussed above and are considered relicts. The species included in this assemblage are listed below, followed in parentheses by their distributional categories. A single asterisk connotes occurrence in adjacent mesquite-grassland only, two occurrence in adjacent Pacific coast tropical area only, and three asterisks occurrence in both adjacent areas.

Ambystoma tigrinum (P)*
Bufo punctatus (P)***
Bufo woodhousei (P)*
Hyla arenicolor (W)***
Scaphiopus multiplicatus (W)*
Tomodactylus nitidus (P)**
Kinosternon integrum (P)***

Eumeces tetragrammus (P)**
Gerrhonotus liocephalus (P)**
Phrynosoma douglassii (P)*
Sceloporus clarkii (P)**
Sceloporus poinsettii (W)*
Sceloporus spinosus (P)***
Urosaurus ornatus (P)***
Coluber constrictor (P)
Crotalus lepidus (W)*
Crotalus molossus (W)*
Crotalus scutulatus (P)*
Diadophis punctatus (W)*
Hypsiglena torquata (P)***
Masticophis taeniatus (P)*
Pituophis melanoleucus (P)***
Salvadora grahamiae (W)*
Thamnophis cyrtopsis (W)***
Thamnophis elegans (W)
Trimorphodon tau (P)**

Pacific Lowland Subhumid Assemblage. — Included in this assemblage are 13 species predominantly adapted to subhumid habitats in tropical Pacific coastal México. All 13 species belong to the Peripheral distributional category and are restricted to pine-oak woodland habitat in the Sierra Madre Occidental along the western edge of the range. *Anolis nebulosus* has, in addition, apparently gained access to the pine-oak woodlands along the northern edge of the isolated southern portion of the sierra via the Río Mezquital corridor in which it occurs today (Crossin et al., 1973). The species included in this category are as follows:

Eleutherodactylus occidentalis
Rana magnaocularis
Rana pustulosa
Anolis nebulosus
Cnemidophorus costatus
Eumeces parvulus
Sceloporus nelsoni
Crotalus basiliscus
Crotalus stejnegeri
Dryadophis cliftoni
Leptophis diplotropis
Masticophis mentovarius
Senticolus triaspis

Mesquite-Grassland Assemblage. — Included in this assemblage are 4 species predominantly adaped to mesquite-grassland habitats of the Mexican Plateau. Three of the four species belong to the Peripheral distributional category; the fourth is in the Widespread category. All four occur principally in mesquite-grassland communities on the eastern slopes of the Sierra Madre Occidental. The species included in this category are listed below followed in parentheses by their distributional category.

Bufo compactilis (W)
Kinosternon hirtipes (P)
Pituophis deppei (P)
Tantilla wilcoxi (P)

Based on the above allocations, 50% (43 of 86 species) comprising the Sierra Madre Occidental pine-oak woodland herpetofauna belong to the Pine-Oak Woodland Assemblage. The other assemblages comprise, respectively, 30.2, 15.1, and 4.7% of the herpetofauna.

Table 4

Component Genera of Historical Units of the Pine-Oak Woodland Assemblage of the Sierra Madre Occidental (modified after Savage, 1982)

Old Northern (14)	Young Northern (5)	Middle American (7)
Ambystoma	*Hyla* (*eximia* group)	*Bufo* (*occidentalis* group)
Pseudoeurycea	*Cnemidophorus*	*Eleutherodactylus*
Bufo (*americanus* group)	*Phrynosoma*	(*augusti* group)
Rana	*Sceloporus*	*Hyla* (*bistincta* group)
Kinosternon	*Crotalus*	*Tomodactylus*
Barisia		*Geophis*
Elgaria		*Rhadinaea*
Eumeces		*Tantilla*
Adelophis		
Conopsis		
Lampropeltis		
Salvadora		
Storeria		
Thamnophis		

HISTORICAL BIOGEOGRAPHY

Our analysis of herpetofaunal assemblages illustrated that the majority of the species belonging to the Ubiquitous, Pacific Lowland Subhumid, and Mesquite-Grassland assemblages (33 of 43 species or 76.7%) are peripheral in distribution to the pine-oak woodlands of the Sierra Madre Occidental and, therefore, of little aid in determining the historical origin of this herpetofauna. Thus, we have largely restricted our discussion of historical biogeography to analysis of the Pine-Oak Woodland Assemblage of 43 species. Comments on the origin of the other assemblages comprising the herpetofauna are made where pertinent.

Historical Units. — Our current understanding of the historical units comprising the herpetofauna of the Western Hemisphere is based upon the work of a succession of herpetogeographers, culminating in that of Savage (1960, 1966, 1982). Largely utilizing information provided in the last of these papers, we allocated the 24 genera of amphibians and reptiles making up the Pine-Oak Woodland Assemblage to three historical units as indicated in Table 4 (only three of his four historical units are represented). Most of the generic groups involved belong to the Old Northern and Young Northern units, with corresponding limited involvement of genera in the Middle American unit. This conclusion is consistent with that of Duellman (1965) concerning the Michoacán herpetofauna, except that the Pine-Oak Woodland Assemblage contains no genera of South American affinities.

Geohistory. — The geological history of northern and central México is well enough understood in its broad outlines to act as a backdrop against which the origin of the pine-oak woodland herpetofauna of the Sierra Madre Occidental may be discussed. We have drawn primarily from the work of Maldonado-Koerdell (1964), West (1964), Auffenberg and Milstead (1965), and Duellman (1965). Reference below to other pertinent work is made where appropriate. The major geomorphic events that have

shaped the mountains of the Sierra Madre Occidental may be summarized as follows:

1. At the end of the Cretaceous period Middle America entered a phase of intense mountain building and vulcanism (Maldonado-Koerdell, 1964). These geomorphic events resulted from crustal fracturing along and adjacent to which "mountain chains have been thrust upward, large crustal blocks moved horizontally, and in places large masses of volcanic material have been ejected to form ranges and plateaus" (West, 1964). "Coinciding with the Laramide Revolution [also] at the end of the Cretaceous there was an uplift of the Mexican Platéau" (Duellman, 1965). This orogeny occurring at the close of the Mesozoic era "left [a] basic structural pattern for Middle America, on which successive events during [the] Tertiary built its present physical characteristics through emergence, folding and faulting, and erosion" (Maldonado-Koerdell, 1964).
2. The "Miocene [epoch] . . . marked the beginning of great igneous activity which formed the Sierra Madre Occidental . . ." (Maldonado-Koerdell, 1964).
3. "The middle Pliocene transitional epoch was characterized by a long period of volcanic quiescence and intense erosion which peneplained the landscape . . ." (Maldonado-Keordell, 1964). "Pliocene also marked the appearance of the Neovolcanic Axis of Mexico . . ." (Maldonado-Koerdell, 1964). More vulcanism occurred in the upper Pliocene and on into the Pleistocene (Maldonado-Koerdell, 1964).
4. The Pleistocene glaciations and interglacial periods brought about alternating expansion and contraction of montane glaciers, best demonstrated in México in the Cordillera Volcánica (Maldonado-Koerdell, 1964; Duellman, 1965), which brought about depression and elevations of vegetational zones in mountainous regions in México (Duellman, 1965), as well as in Central America (Wake and Lynch, 1976).

Origin of the Herpetofauna. — It has now been amply demonstrated that "modernization of the reptilian fauna of North America is a Mio-Pliocene phenomenon" (Auffenberg and Milstead, 1965). The same may be said for the amphibians (Gehlbach, 1965; Tihen, 1972; Estes, 1981). As noted by Gehlbach (1965), "Miocene forms . . . are so archaic that specific, and in most cases generic, distinctions have been made." This statement is borne out by more recent work (Holman, 1979; Estes, 1983). Gehlbach (1965) went on to say that the Pliocene "seems to have been a period of evolutionary transition with many extinct species placed largely in living genera." With the inception of the Quaternary period, an essentially modern herpetofauna at the species level was already established (Auffenberg and Milstead, 1965; Gehlbach, 1965; Holman, 1969, 1981). Auffenberg and Milstead (1965) pointed out that "the main effects of the Pleistocene on North American reptiles were those changes in range resulting from a fluctuating ecology, along with some speciation, principally at the subspecies level, and some extinction." Duellman (1965) essentially concluded the same about the herpetofauna of Michoacán. Unfortunately, the herpetological fossil record for the Sierra Madre Occidental is very meager. Brattstrom (1955) described an extinct species of toad (*Bufo campi*) from the Yepómera Formation in Chihuahua, and Lindsay (1984) added the iguanids *Sceloporus* nr. *undulatus* and *Phrynosoma* sp. from the same formation. The Yepómera fauna is recognized as a Hemphillian assemblage and was referred to the Pliocene by Brattstrom (1955) and to the early Pliocene by Lindsay (1984). However, Savage and Russell (1983) have placed the Hemphillian assemblage in the late Miocene. This meager fossil history hampers the following discussion, rendering it more speculative in nature. In addi-

tion, the relationships of *Bufo campi* remain obscure (Tihen, 1972).

The evolution of the pine-oak woodlands as a vegetation type is correlated with the geomorphological history of northern and central México. Mirov (1967) noted that "since the Central Mexican Plateau became available to pines only after the Miocene volcanic activity ceased . . . the existence of the pine forests of Mexico . . . does not go farther back than the second half of the Tertiary, possibly the end of that period." He postulated the existence of two dispersal routes, "one along the West Coast ranges, and the other around the Gulf of Mexico." The former route was apparently the more important, as Mirov (1967) stated that "western American pines played a large part in the development of Mexican pines." Thus, pine forests would seem to have been present in the Sierra Madre Occidental at least by the Pliocene, if not before, more or less at the time the herpetofauna was undergoing modernization.

The origin and establishment of the Pine-Oak Woodland Assemblage in the Sierra Madre Occidental is understandable in terms of the following model:

1. The vicariance events involved with the formation of the mountain range appear to have allowed for an upper displacement of ancestral stocks of the endemic species and those whose ranges are centered in the sierra. As noted above, these events occurred during Mio-Pliocene times.
2. Subsequent to the formation of the sierra and the establishment of the pine-oak woodlands at least by the Pliocene, dispersal of stocks that originated outside of the sierra occurred primarily from the Cordillera Volcánica of central México. Pleistocene glacial and interglacial periods initiated alternating depression and elevation of vegetation zones, including that of the pine-oak woodlands (Duellman, 1965; Morafka, 1977). Depression of the zones allowed for establishment of dispersal routes across the now extant mesquite-grassland zone between the southern Sierra Madre Occidental and the western Cordillera Volcánica (Duellman, 1965) and that between the northern Sierra Madre Occidental and the southern Rockies-Mogollon Rim region (the Cochise filter barrier of Morafka, 1977).

The species we believe to have been involved in these two sets of events are listed in Table 5. The criteria we utilized for establishment of this configuration involve present-day distribution, historical element membership, and phylogenetic relationships elucidated in the literature on the component species.

The 21 species thought to have been involved in a Mio-Pliocene upward displacement are in large part either endemic to the Sierra Madre Occidental (8 species) or have their range centered in that sierra (9 species); these species primarily belong to the Old Northern historical element (15 of 21 species), and appear to have evolved *in situ* in the sierra. Almost all of the 22 species considered to have participated in Pleistocene dispersal events have their ranges centered outside of the Sierra Madre Occidental (18 in the Cordillera Volcánica, one south of the Sierra Madre Occidental, one north of this sierra, and only two in the sierra itself), are primarily members of the Young Northern and Middle American historical elements (14 of 22 species), and appear to have evolved outside of the sierra with subsequent dispersal into it. Of the 22 pine-oak woodland assemblage species reaching the Sierra Madre Occidental via Pleistocene dispersal, 18 have dispersed northward from the Cordillera Volcánica, 1 each from the southeast and southwest, and 2 from north of the sierra (Table 5). Only one (*Sceloporus torquatus)* of the 18 species that dispersed northward from the Cordillera Volcánica has not been collected in the sierra north of the Río Mezquital *barranca.* Eight of these 18 species (*Bufo occidentalis, Hyla eximia, Eumeces*

Table 5

Arrangement of the Members of the Pine-Oak Woodland Assemblage of the Sierra Madre Occidental Herpetofauna according to a Two-Step Scenario of Vicariance and Dispersal (see text for explanation). Parenthetical acronyms indicate direction of dispersal from the presumed area of origin into the sierra.

Mio-Pliocene upward displacement	Pleistocene dispersal
Ambystoma rosaceum	*Pseudoeurycea bellii* (CVMA)
Eleutherodactylus tarahumaraensis	*Bufo microscaphus* (N)
Rana chiricahuensis	*Bufo occidentalis* (CVMA)
Rana tarahumarae	*Hyla bistincta* (CVMA)
Tomodactylus saxatilis	*Hyla eximia* (CVMA)
Kinosternon sonoriense	*Barisia imbricata* (CVMA)
Barisia levicollis	*Cnemidophorus exsanquis* (N)
Elgaria kingii	*Eumeces brevirostris* (CVMA)
Eumeces multilineatus	*Eumeces lynxe* (CVMA)
Eumeces parviauriculatus	*Sceloporus bulleri* (SW)
Phrynosoma orbiculare	*Sceloporus grammicus* (CVMA)
Sceloporus virgatus	*Sceloporus heterolepis* (CVMA)
Adelophis foxi	*Sceloporus jarrovii* (SE)
Crotalus pricei	*Sceloporus scalaris* (CVMA)
Crotalus willardi	*Sceloporus torquatus* (CVMA)
Lampropeltis mexicana	*Conopsis nasus* (CVMA)
Lampropeltis pyromelana	*Geophis dugesii* (CVMA)
Thamnophis eques	*Rhadinaea hesperia* (CVMA)
Thamnophis melanogaster	*Rhadinaea laureata* (CVMA)
Thamnophis nigronuchalis	*Salvadora bairdi* (CVMA)
Thamnophis rufipunctatus	*Storeria storerioides* (CVMA)
	Tantilla bocourti (CVMA)

brevirostris, Sceloporus grammicus, S. scalaris, Conopsis nasus, Geophis dugesii, and *Storeria storerioides*) are widespread in the sierra north of the Río Mezquital, one (*Rhadinaea hesperia*) reaches southwestern Chihuahua, one (*Barisia imbricata*) northern Durango, 2 (*Salvadora bairdi* and *Tantilla bocourti*) southern Durango and the Sierra Surutato of northeastern Sinaloa, 4 (*Hyla bistincta, Eumeces lynxe, Sceloporus heterolepis,* and *Rhadinaea laureata*) southern Durango only (and in two cases, adjacent Sinaloa), and one (*Pseudoeurycea bellii*) is represented by a single isolated locality in Sonora. Two of these 18 species (*Hyla eximia* and *Sceloporus scalaris*) have also reached the North American Montane Area. The single species (*Sceloporus bulleri*) that dispersed from southwest of the sierra is known from the sierra only in southern Durango and adjacent Sinaloa. The single species (*Sceloporus jarrovii*) that dispersed from the southeast of the sierra is widespread throughout the sierra and has also reached the North American Montane Area. Of the 2 species that dispersed from the north of the sierra, one (*Bufo microscaphus*) is widespread north of the Río Mezquital and the remaining species (*Cnemidophorus exsanguis*) is confined to the northern portion of the Sierra Madre Occidental.

Therefore, from the above discussion it is obvious that the major route of Pleistocene dispersal has been from south to north. The same condition obtains for the 21 species of Mio-Pliocene upward displacement origin. Only three of these species have reached the Cordillera Volcánica, whereas 10 of the 21 species have reached the North American Montane Area (*Thamnophis rufipunctatus* is included here although it does not occur in the NAMA proper but to the north of it).

The reasons for such inequality in the apparent major directions of dispersal of the 43 pine-oak woodland assemblage species is not easily explainable and then so only in a very speculative manner. Of the 21 species of Mio-Pliocene upward displacement origin, within the Sierra Madre Occidental 8 (*Rana tarahumarae, Kinosternon sonoriense, Barisia levicollis, Eumeces multilineatus, E. parviauriculatus, Sceloporus virgatus, Lampropeltis pyromelana,* and *Thamnophis rufipunctatus*) occur presently only in the northern half of the sierra and 4 others (*Tomodactylus saxatilis, Adelophis foxi, Lampropeltis mexicana*, and *Thamnophis nigronuchalis*) occur only in a restricted geographical area of southern Durango (*T. saxatilis* also occurs in adjacent Sinaloa) north of the Río Mezquital. Thus, these 12 species were not likely to have been in a position for southward dispersal from the Sierra Madre Occidental during the periods of depression of the pine-oak woodlands in the Pleistocene. The 9 remaining species of Mio-Pliocene upward displacement origin are all widespread in the sierra (8 are known from the southern isolated portion south of the Río Mezquital) and could be considered available during some period of the Pleistocene for southward dispersal from the Sierra Madre Occidental Scrutiny of these 9 species shows that three (*Phrynosoma orbiculare, Thamnophis eques*, and *T. melanogaster*) have indeed dispersed into the Cordillera Volcánica from the Sierra Madre Occidental. Four other species are believed by us to be replaced in the pine-oak woodlands of the Cordillera Volcánica by related species. These four species are listed below, followed in parentheses by their Cordillera Volcánica counterpart: *Ambystoma rosaceum (A. ordinarium); Eleutherodactylus tarahumaraensis (E. augusti); Rana chiricahuensis (R. montezumae* species group — see Hillis, et al., 1983); *Crotalus pricei (C. triseriatus*). Thus, of the nine Mio-Pliocene upwardly displaced species seemingly available for southward dispersal from the Sierra Madre Occidental during the Pleistocene, three have successfully done so and four others are believed to be replaced in the Cordillera Volcánica by sister species. The remaining two seemingly available species (*Elgaria kingii* and *Crotalus willardi*) have neither dispersed southward from the sierra into the Cordillera Volcánica nor have an apparent sister species in the CVMA. Information presented by Tihen (1949) indicates an origin in the northern portion of the Sierra Madre Occidental for *Elgaria kingii*. Subsequently, the species has successfully dispersed southward only to northwestern Jalisco, the southernmost occurrence of the genus today. It is unclear why *Crotalus willardi* apparently was never able to cross the barrier between the Sierra Madre Occidental and the Cordillera Volcánica.

The 26 members of the Ubiquitous Assemblage almost all appear to have become part of the herpetofauna of the pine-oak woodlands of the Sierra Madre Occidental as a result of dispersal sometime during the Quaternary (Pleistocene or Holocene) from either the Mexican Plateau (10 species) or the Pacific coastal region (7 species) or both (2 species). Four species may have dispersed into the sierra during the Quaternary from the north and another from the south (Cordillera Volcánica). *Crotalus lepidus* and *C. molossus* do not fit the above pattern for Quaternary

dispersal. Their widespread range within the pine-oak woodlands and outside these areas as relicts in rocky areas suggests that they were involved in the Mio-Pliocene upward displacement phenomenon described earlier.

The four members of the Mesquite-Grassland Assemblage all seem to represent Quaternary dispersals from the Mexican Plateau and all 13 members of the Pacific Lowland Subhumid Assemblage recent dispersals from the Pacific coastal region.

RESUMEN

Los bosques de pino-encino de la Sierra Madre Occidental de México se extienden hasta 1100 km hacia el límite norte de la línea que divide Sonora y Chihuahua, y hacia el sur a la zona en donde se encuentran los límites de los estados de Zacatecas, Nayarit y Jalisco. Sobre la parte este de la sierra, las tierras de pino-encino se van gradando hacia tierras de mezquite y praderas en la meseta central de México. Hacia la parte oeste de la sierra, la pendiente es muy pronunciada, con profundas barrancas que dan lugar a una compleja intergradación de las tierras de pino-encino con el bosque tropical deciduo en las partes bajas. El clima de las tierras de pino-encino es húmedo templado, con veranos frescos e inviernos moderados. Las lluvias tienen lugar, principalmente, entre los meses de julio y septiembre. Las tierras de pino-encino, varían en constitución, de casi matorrales de encino, en las tierras bajas, pasando por una mezcla de pino-encino de diferentes proporciones a elevaciones medias hacia bosque de pino con una mezcla de elementos boreales en el límite superior de la sierra.

La herpetofauna de los bosques de pino-encino contiene 86 especies que incluyen tres salamandras, 17 anuros, tres tortugas, 27 lagartijas y 36 serpientes. Estos 86 taxa se pueden dividir in cuatro categorías de distribución, que son: endémicas o casi endémicas (8 especies), ampliamente distribuídas en bosques de pino-encino (17 especies), de distribución muy amplia (17 especies), y periféricas (44 especies). Más del 90 porciento de la herpetofauna se comparte con una o más regiones adyacentes in el siguiente orden de importancia: Area de Mesquital (39 especies), Area Tropical de la Costa del Pacífico (33 especies), Bosques Montañosos Norteamericanos (28 especies), Area de Bosques de la Cordillera Volcánica (30 especies), y el Area de Matorral Desértico (23 especies).

Se pueden reconocer cuatro grupos herpetofáunisticos los cuales incluyen el conjunto de los bosques de pino-encino (43 especies), la mayoría de los cuales tienen su área de distribución de las cordilleras de la Sierra Madre Occidental o en la Cordillera Volcánica, el grupo ubicuo (26 especies), el grupo de las Tierras Bajas Subhúmedas del Pacífico (13 especies), y el grupo de Mesquital (4 especies).

Dentro del grupo de los bosques de pino-encino se presentan tres elementos históricos que son: el Norteño Antiquo, el Norteño Reciente y los Elementos de Mesoamérica. La mayoría de los grupos genéricos in este conjunto pertenecen a los primeros dos elementos.

La formación de la altiplanicie mexicana y de los acantilados comenzaron al final del periodo cretásico. La actividad volcánica durante el Mioceno formó la Sierra Madre Occidental. La calma en el Plioceno permitió la formación de la peneplanicie (penellanura), seguida por otro período de actividad volcánica durante el Plioceno superior hasta el Pleistoceno. Las glaciaciones del Pleistoceno y los períodos interglaciales produjeron expansiones y contracciones de los glaciares montañosos que se alternaron con depresiones y elevaciones de las zonas vegetales.

La modernización de la herpetofauna norteamericana fué un fenómeno Mio-Pliocénico, mientras que el Pleistoceno produjo cambios en las áreas de distribución debido a las fluctuaciones del ambiente.

La vegetación de los bosques de pino-encino en la Sierra Madre Occidental comenzó a desarrollarse después de terminados los levantamientos y vulcanismo del Mioceno y se estableció para el Plioceno.

El origen y establecimiento de la herpetofauna de la cordillera de los bosques de pino-encino de la Sierra Madre Occidental parece que involucró dos eventos de mayor consecuencia: (1) evolución de un componente endémico y uno en el centro de la Sierra Madre durante el Mioceno y Plioceno como resultado de varios eventos vicariantes que crearon la sierra; (2) dispersión de los componentes extraños a la sierra, principalmente desde la cordillera volcánica, lo cual ocurrió durante las heladas del Pleistoceno, con la depresión de las zonas vegetales in las áreas montañosas. Dispersión a través de los cañones profundos y la altiplanicie, entre la Sierra Madre Occidental y la Cordillera Volcánica, la cual ha sido principalmente unidireccional, aparentemente debido a que la mayoría de los miembros del centro de la Sierra Madre y el componente endémico de las cordilleras de bosques de pino-encino están restringidos a las zonas norteñas de la sierra o viven en zonas geográficas más pequeñas en algunas partes de la sierra. La mayoría de las especies en los otros tres conjuntos aparentemente han estado involucrados en dispersiones durante el cuaternario desde regiones adyacentes.

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