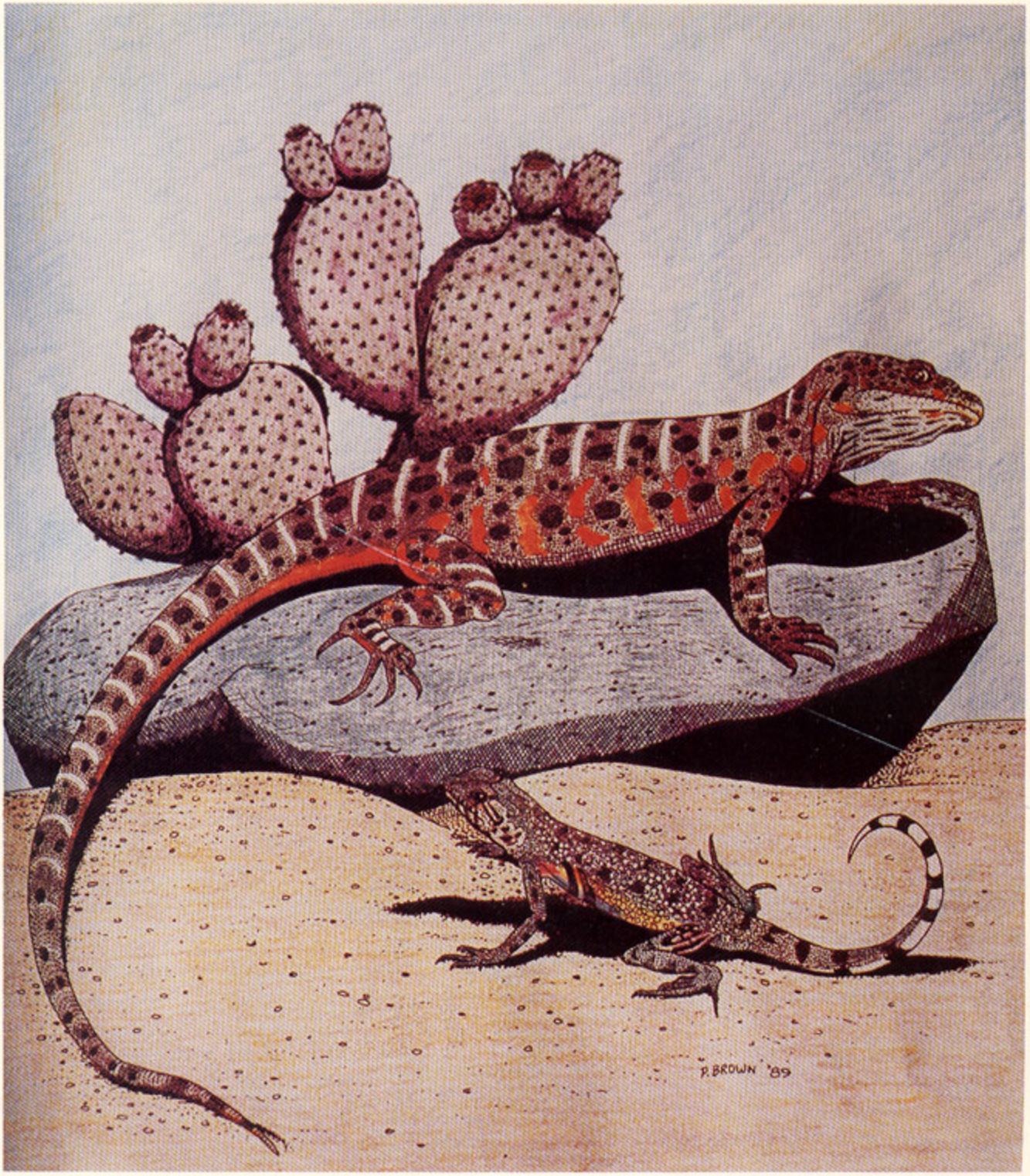
Herpetology of the North American Deserts

Proceedings of a Symposium



Southwestern Herpetologists Society • Special Publication No. 5

Late Quaternary Amphibians and Reptiles from Maravillas Canyon Cave, Texas, with Discussion of the Biogeography and Evolution of the Chihuahuan Desert Herpetofauna

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INTRODUCTION

Trans-Pecos Texas has long been an area of adventure, mystery and wonder for herpetologists. Wright and Wright's (1957) account of collecting *Elaphe bairdi* (Baird's ratsnake) in Green Gulch in the Chisos Mountains in 1934 was certainly of a prized animal in an exotic place. This snake was originally described as *Coluber bairdi* by H. C. Yarrow in 1880 based on an immature specimen collected by von Manteuffel, a hospital steward at Fort Davis in the Apache (=Davis) Mountains. A few years later Edward D. Cope (1886) described a snake from near Ciudad Chihuahua as *Trimorphodon vilkinsoni* (=*T. biscutatus vilkinsoni,* Texas lyre snake) although most subsequent specimens have been taken in Trans-Pecos Texas. Earlier Spencer F. Baird (1859), the director of the Smithsonian Institution in Washington, described *Gerrhonotus infernalis* (=*G. liocephalus infernalis,* Texas alligator lizard) from the Devil's River north of Comstock. This secretive animal was not recollected in the area until the early 1970's!

Near the turn of the century Arthur E. Brown, Director of the Philadelphia Zoological Garden, employed E. Meyenberg of Pecos, Texas, as a collector. Meyenberg's collections in the Davis Mountains led to the description of *Coluber subocularis* (= *Elaphe subocularis,* Trans-Pecos ratsnake; Brown, 1901) and *Ophiobolus alternus* (= *Lampropeltis mexicana alterna,* gray-banded kingsnake; Brown, 1902). The latter was only known from seven specimens as late as 1950 (Conant, 1957). It had such an unusual color pattern for a kingsnake that Blanchard (1921) aligned it with *L. pyromelana* (Arizona mountain kingsnake) but not *L. mexicana* (Mexican kingsnake) or *L. leonis* (now a synonym of *L. m. mexicana)* although he postulated that *L. leonis* was ancestral to *L. calligaster* (prairie and mole kingsnakes). In 1904, Leonhard Stejneger described *Sceloporus merriami* (canyon lizard), a very distinct spiny lizard from near the junction of the Pecos River and the Rio Grande, between Comstock and Langtry.

As the herpetofauna of the United States became relatively well-known, the Trans-Pecos continued to yield interesting new reptiles. *Agkistrodon mokeson pictigaster* (= *A. contortrix pictigaster,* Trans-Pecos copperhead) was described based on a holotype from Maple Canyon in the Davis Mountains and paratypes from the Chisos and Davis mountains (Gloyd and Conant, 1943). In 1950, *Lampropeltis blairi* (= *L. mexicana blairi,* Blair's kingsnake; Flury, 1950) was described based

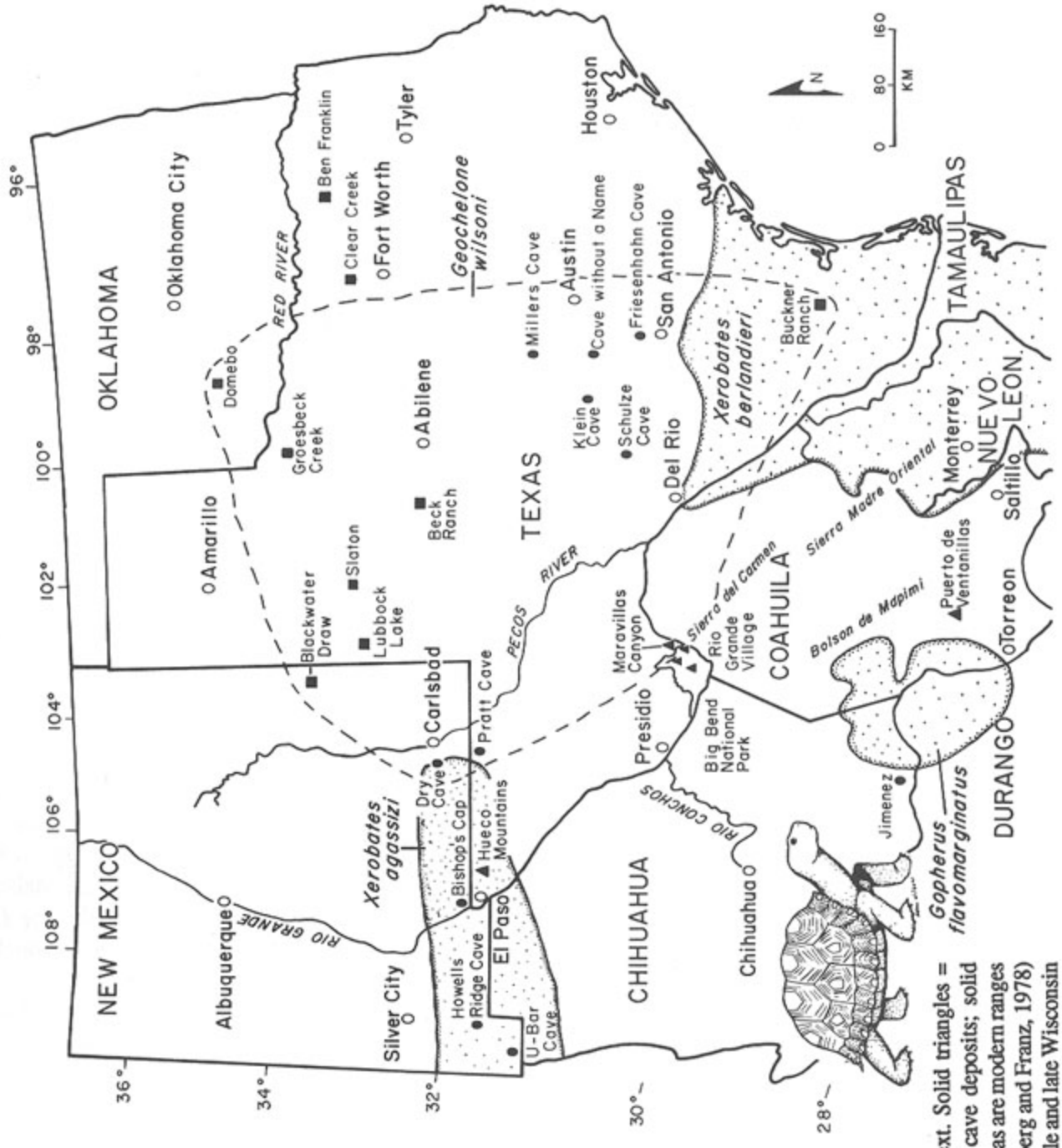

Figure 1. Map of area discussed in text. Solid triangles = packrat midden sites; solid circles = cave deposits; solid squares = sedimentary sites. Stipple areas are modern ranges of *Gopherus flavomarginatus* (Auffenberg and Franz, 1978) and *Xerobates berlandieri* and the middle and late Wisconsin range of *X. agassizi* (Moodie and Van Devender, 1979). Dashed line encloses known middle and late Wisconsin range of *Geochelone wilsoni*.

on a Terrell County specimen. *Tantilla cucullata* (= *T. rubra cucullata,* blackhood snake) was described on a specimen from southeast of Alpine (Minton, 1959), soon followed by *T. diabola* (= *T. rubra diabola,* Devil's River black-headed snake) on a specimen from Dolan Spring's on the Devil's River (Fouquette and Potter, 1961). *Coleonyx reticulatus* (Big Bend gecko) was described by Davis and Dixon (1958) from 760 m elevation in Black Gap Wildlife Management Area. The type and only specimen for a decade or so was taken in a snap trap set for rodents.

In this paper, we report the remains of amphibians and reptiles from a series of fossil packrat (*Neotoma* sp.) middens dated back to 27,800 yr B.P. (radiocarbon years before 1950) from Maravillas Canyon Cave in Black Gap Wildlife Management Area (Fig. 1), and discuss their paleoecological, biogeographical, and evolutionary significance.

MATERIALS AND METHODS

Fossil packrat middens are hard, dark organic deposits found in dry rockshelters or caves in arid and semi-arid areas in the western United States and northern Mexico (Van Devender et al., 1987). Packrat middens are excellent sources of well-preserved plant and animal remains from the deserts of North America (Van Devender, 1990). Abundant plant remains collected by packrats on rocky slopes within about 30-50 m of the rockshelters provide detailed records of the local flora and vegetation. Radiocarbon dates allow individual midden assemblages to be placed in chronological sequences.

Packrat middens were first discovered in Maravillas Canyon Cave by Rogers (1964) and studied by Wells (1966). In this study, thirteen additional middens yielded radiocarbon ages from 27,820 to 1160 yr B.P. (Table 1) providing biotic records for 16,800 years of the last glacial period (the Wisconsin) and the 11,000 years of the present interglacial (the Holocene). A reconstruction of the local vegetation is presented in Van Devender (1990).

Faunal remains in packrat middens are varied. The remains of ground-dwelling arthropods (insects, millipedes, scorpions, etc.) can be relatively common (Hall et al., 1990). These can be local rockshelter inhabitants, on local plants collected by packrats (Elias, 1990), or from fecal material of small mammalian predators, such as *Bassariscus astutus* (ringtail; Mead and Van Devender, 1981). Packrat fecal pellets, and occasionally *Sceloporus* sp. epidermal scales, are the only common to abundant vertebrate remains in middens. Lizard and tortoise epidermal scales and mammal hair are occasionally found. Bones found in packrat middens are usually isolated small elements from different individuals of small animals. Although packrats readily collect larger bones, most of the midden bones are probably from the regurgitated pellets of hawks or owls or mammal feces. Many bones have been partially dissolved in digestion. Middens from caves or rockshelters that are preferred raptor roosts such as Maravillas Canyon Cave often yield substantial numbers of teeth and bones but not the abundances typical of cave fill deposits. Unlike many cave faunas, the midden vertebrates are associated with plant assemblages and radiocarbon. Remains of extinct animals in late Pleistocene middens are rarely found. The accumulation area for vertebrate remains is certainly greater than for the plant remains but probably less than a kilometer.

Maravillas Canyon Cave amphibian and reptile remains were identified using Van Devender's personal reference skeletal collection, and have been deposited into the vertebrate paleontological collection of the University of Arizona Laboratory of Paleontology (UALP). Arthropod remains from the samples were reported in Elias and Van Devender (1990).

ENVIRONMENTAL SETTING

The Chihuahuan Desert is the arid and semi-arid area on the Mexican Plateau in the rainshadows of the Sierra Madre Occidental on the west and the Sierra Madre Oriental on the east (Fig. 1). More than 70% of the rainfall falls in summer. Summers are hot and winters cool, although occasional incursions of Arctic air masses -- blue northers or nortes

Table 1. Radiocarbon dates, University of Arizona Laboratory of Paleontology locality numbers and paleovegetation for packrat middens from Maravillas Canyon Cave, Brewster County, Texas. A = standard date, AA = tandem accelerator mass spectrometer dates.

Site	Date (yr B.P.)	Lab. No.	Material Dated	UALP Loc #	Paleovegetation
TRV4	27,820 _ 1270	A-1847	*Juniperus* sp. twigs	8537	Pinyon-juniper-oak woodland
TRV11	20,950 _ 780	A-4238	*Juniperus* sp. twigs	8608	Pinyon-juniper-oak woodland
TRV1	20,600 _ 1530	A-1860	*Juniperus* sp. twigs	8535	Pinyon-juniper-oak woodland
TRV3	16,160 _ 330	A-1842	*Juniperus* sp. twigs	8536	Pinyon-juniper-oak woodland
TRV10	12,420 _ 360	A-2992	*Juniperus* sp. twigs	8540	Pinyon-juniper-oak woodland
TRV18	11,960 _ 280	A-4491	midden debris	8601	Pinyon-juniper-oak woodland
TRV2	11,240 _ 160	A-1861	*Pinus remota* needles	8602	Pinyon-juniper-oak woodland
TRV8	10,280 _ 280	A-3135	midden debris	8538	Oak-juniper-woodland
TRV12	10,215 _ 320	AA-1276	*Gymnogyps californianus* bone	8603	Oak-juniper-woodland
TRV16	6020 _ 110	A-4227	*Neotoma* sp. fecal pellets	8611	Succulent desertscrub
TRV15	5790 _ 120	A-4228	*Neotoma* sp. fecal pellets	8610	Succulent desertscrub
TRV13	5110 _ 100	A-4230	*Neotoma* sp. fecal pellets	8609	Succulent desertscrub
TRV9	4680 _ 160	A-2991	*Opuntia phaeacantha*-type seeds	8539	Succulent desertscrub
TRV17	1160 _ 80	A-4229	*Neotoma* sp. fecal pellets	8612	Succulent desertscrub
General	not dated			8613	Various

-- can bring severe freezes throughout the area. The climatic Chihuahuan Desert defined by the de Martonne aridity index (Schmidt, 1986) is a much smaller area than often used by biologists for a broader area best termed the Chihuahuan Biotic Province (Blair, 1950; Morafka, 1977a). Distributions of plant species and communities are better indicators of biotic provinces than animals because their range limits are more closely controlled by climate.

The Bolson de Mapimi, a series of internal drainage basins mostly above 1200 m elevation in Coahuila, Durango, and Chihuahua (Tamayo, 1962), is a subtropical area that supports a desertscrub vegetation with abundant succulents and many endemic species that extends north into the Big Bend of Texas. Morafka's (1977a, 1977b) Mapimian Subprovince of the Chihuahuan Desert was the central of three subdivisions although Schmidt (1979) concluded that the southern Saladan Subprovince receives too much rainfall to be part of the Chihuahuan Desert.

The northern Chihuahuan Desert is drained by the Rio Conchos in Chihuahua, the Rio Grande and Pecos River in Texas and New Mexico, and the Gila River and Rio Bavispe across the Continental Divide in southeastern Arizona and northeastern Sonora. In the northern Chihuahuan Desert, more frequent freezes favor grassland over subtropical desertscrub species. In many places Chihuahuan desertscrub covers rocky slopes adjacent to desert grassland in deep-soiled valley bottoms. Morafka (1977a) called the portion of the northern Chihuahuan Desert in the Pecos and Rio Grande rivers drainages in Texas and New Mexico the Trans-Pecos Subprovince. Typical Chihuahuan desertscrub associations dominated by *Acacia neovernicosa* (Chihuahuan whitethorn), *Atriplex canescens* (fourwing saltbush), *Fouquieria splendens* (ocotillo), *Larrea divaricata* (creosotebush), and *Parthenium incanum* (mariola) extend to an abrupt Chihuahuan-Sonoran Desert transition in the Whetstone Mountains west of Benson, Arizona. The Cochise Filter Barrier (Lowe and Wright, 1968; Morafka, 1977a) was mostly based on amphibians and reptiles entering southeastern Arizona and southwestern New Mexico from Sinaloan thornscrub in northeastern Sonora and not an eastward extension of the Sonoran Desert (Lowe, 1955).

The area between the Davis Mountains and the Pecos River is in the Trans-Pecos Subprovince but not within the climatic Chihuahuan Desert of Schmidt (1986). It was considered to be part of the Chihuahuan Desert based on the herpetofauna although there are few floristic similarities. Along the Rio Grande between the Davis Mountains and the Rio Grande Valley east of Del Rio, elevation decreases and temperature and rainfall increase, opposite of typical Southwestern environmental gradients. The biota is a complicated mixture of Balconian (central Texas), Chihuahuan, Sierra Madrean (Mexican), and Tamaulipan elements (Blair, 1950; Devine, 1969). Climatically the area differs from most of the Chihuahuan Desert in that the summer rainy season is biseasonal with May-June and September-October peaks instead of July-August (Neilson, 1987).

Black Gap Wildlife Management Area is located 90 km south of Marathon near the eastern edge of the Chihuahuan Desert. The limestone Sierra del Caballo Muerto (Dead Horse Mountains) separate Black Gap from Big Bend National Park. Although the Sierra del Caballo Muerto rise to 1770 m elevation and support a relict pinyon-juniper woodland with *Pinus remota* (papershell pinyon), *Juniperus pinchotii* (Pinchot juniper), and *Quercus pungens* (shrub live oak; Wells, 1965), it is a modest north-northeast extension of the massive Sierra del Carmen - Sierra Madre Oriental axis in Coahuila. The Fronterizas portion of the Sierra del Carmen reaches an elevation of 2900 m. The vegetation of Black Gap ranges from xeric Chihuahuan desertscrub in the lowlands to a woodland-chaparral at 1370 m elevation in Big Brushy Canyon on the east side of the Sierra del Caballo Muerto.

Maravillas Creek is the major drainage for the Marathon Basin including the Santiago and Del Norte mountains (the north-northeast extension of the Sierra del Caballo Muerto) and the Glass Mountains north of Marathon. The vegetation becomes a well-developed grassland as elevation rises to 1050-1200 m. In Black Gap, Maravillas Canyon is 1-2 km wide, oriented east-west, and at 460 to 700 m

elevation in the streambed. The Caves are at 610 m elevation in a north-facing limestone cliff about 5.4 km east of the Rio Grande (Rogers, 1964; Wells, 1966).

On the 75 m of relatively steep slopes that separate the cave and the dry streambed, the vegetation is desertscrub dominated by *Bouteloua ramosa* (chino grass), a robust grass exceptionally well-adapted to desert climate, in association with *Agave lechuguilla* (lechuguilla), *Dasylirion leiophyllum* (sotol), *Euphorbia antisyphilitica* (candelilla), and *Leucophyllum frutescens* (Texas silverleaf). The shady cliff base near the caves supports a relatively diverse mesic association with high species richness including plants otherwise only in the riparian community along the wash. The alluvial terraces just above the wash support a more typical Chihuahuan desertscrub with additional xeric shrubs. Water stands in the streambed only after heavy rains.

The general climate of the Big Bend becomes more mesic down the Rio Grande as the elevation decreases: i.e., rainfall increases from 273 mm/yr at 563 m elevation at Rio Grande Village in the National Park to 468 mm/yr at 305 m at Del Rio.

RESULTS

A total of 73 fossil records for 30 amphibian and reptile taxa were identified from 13 Maravillas Canyon Cave packrat middens (Figs. 2 and 3). In the following accounts fossil records are listed from oldest to youngest under Materials. Numbers in parentheses are UALP catalog numbers. Ages are in thousands of years (ka; Table 1). Time period abbreviations are: MW=middle Wisconsin, LW=late Wisconsin, EH=early Holocene, MH=middle Holocene, LH=late Holocene. Detailed information on associated radiocarbon dates, UALP locality numbers, and associated paleovegetation are in Table 1.

CLASS AMPHIBIA
ORDER ANURA
Pelobatidae

Scaphiopus couchi (Couch's Spadefoot). Material - TRV17: l. squamosal (16987); MC Gen.: r. ilium (17019). Age - LW, LH: 1.2 ka. Criteria for the identification of *S. couchi* ilia are given in Van Devender et al. (1985) and elsewhere. The squamosal with its distinctive rugose dorsomedial surface was from a large individual (snout-vent length ca. 70 mm). This medium-sized toad is widespread in grassland, desertscrub, and subtropical thornscrub communities of warm, semi-arid, and arid North America including Black Gap (Axtell, 1959). Other late Pleistocene and Holocene fossil records are from Schultz Cave, Texas (Holman, 1969a); Howell's Ridge and Shelter caves, New Mexico (Brattstrom, 1964; Van Devender and Worthington, 1977); Deadman Cave and Wellton Hills 2 packrat midden, Arizona (Mead et al., 1984; Van Devender and Mead, 1978), and Rancho la Brisca, Sonora, Mexico, (Van Devender et al., 1985).

Scaphiopus sp. (Spadefoot). Material - TRV3: fused urostyle with attached sacral vertebra (16930). Age - LW: 16.2 ka. Identification of this fragmentary specimen was not possible. Both *Scaphiopus couchi* and *S. hammondi* (western spadefoot) occur in Black Gap (Axtell, 1959).

Bufonidae

Bufo cf. *punctatus* (Red-spotted Toad). Material - TRV17: scapula (16988). Age - LH: 1.2 ka. Identification criteria of *B. punctatus* scapulae are given in Van Devender et al. (1985). The "waist" of the scapula is relatively broader than in *Rana, Scaphiopus,* and *Syrrhophus* and more closely resembles *Bufo punctatus* than *B. cognatus* (Great Plains toad), *B. debilis* (green toad), *B. retiformis* (Sonoran green toad), *B. speciosus* (Texas toad), *B. valliceps* (Gulf Coast toad), or *B. woodhousei* (Woodhouse's toad). *Bufo punctatus* is a small rock-dwelling toad found throughout the drier areas of North America including Black Gap (Axtell, 1959).

Other late Pleistocene and Holocene fossil records for *B. punctatus* are from Dry and Howell's Ridge caves, New Mexico (Holman, 1970; Van Devender and Worthington, 1977); Ajo Mountains and Wolcott Peak packrat middens, and Deadman Cave, Arizona (Van Devender and Mead, 1978;

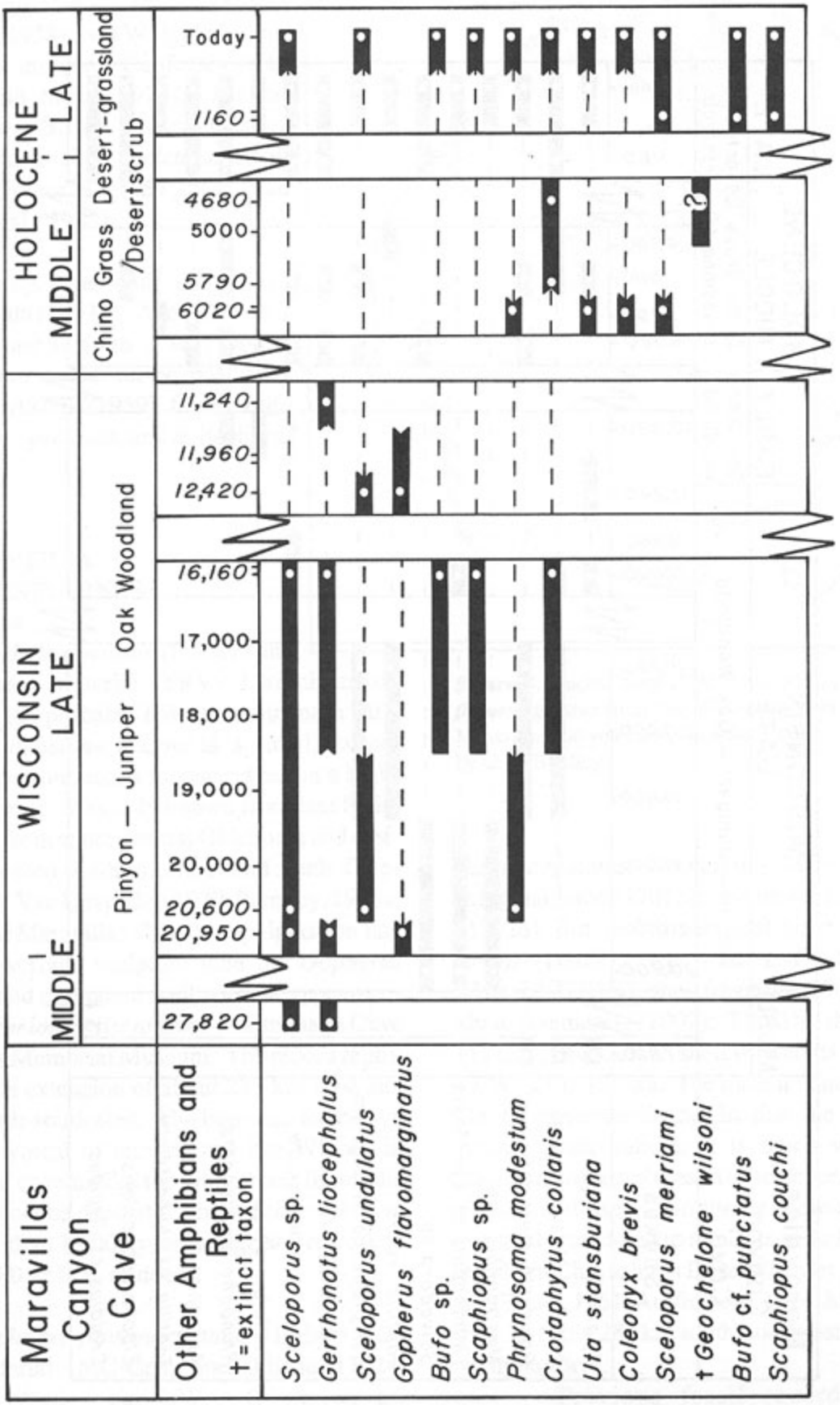

Figure 2. Temporal distribution of amphibians and reptiles exclusive of snakes identified from Maravillas Canyon Cave packrat middens, Brewster County, Texas. Ages are in yr B.P. with radiocarbon dates in italics following Table 1. The 4680 yr B.P. record for *Geochelone wilsoni* is a late Wisconsin contaminant that is probably older than 11,000 yr B.P.

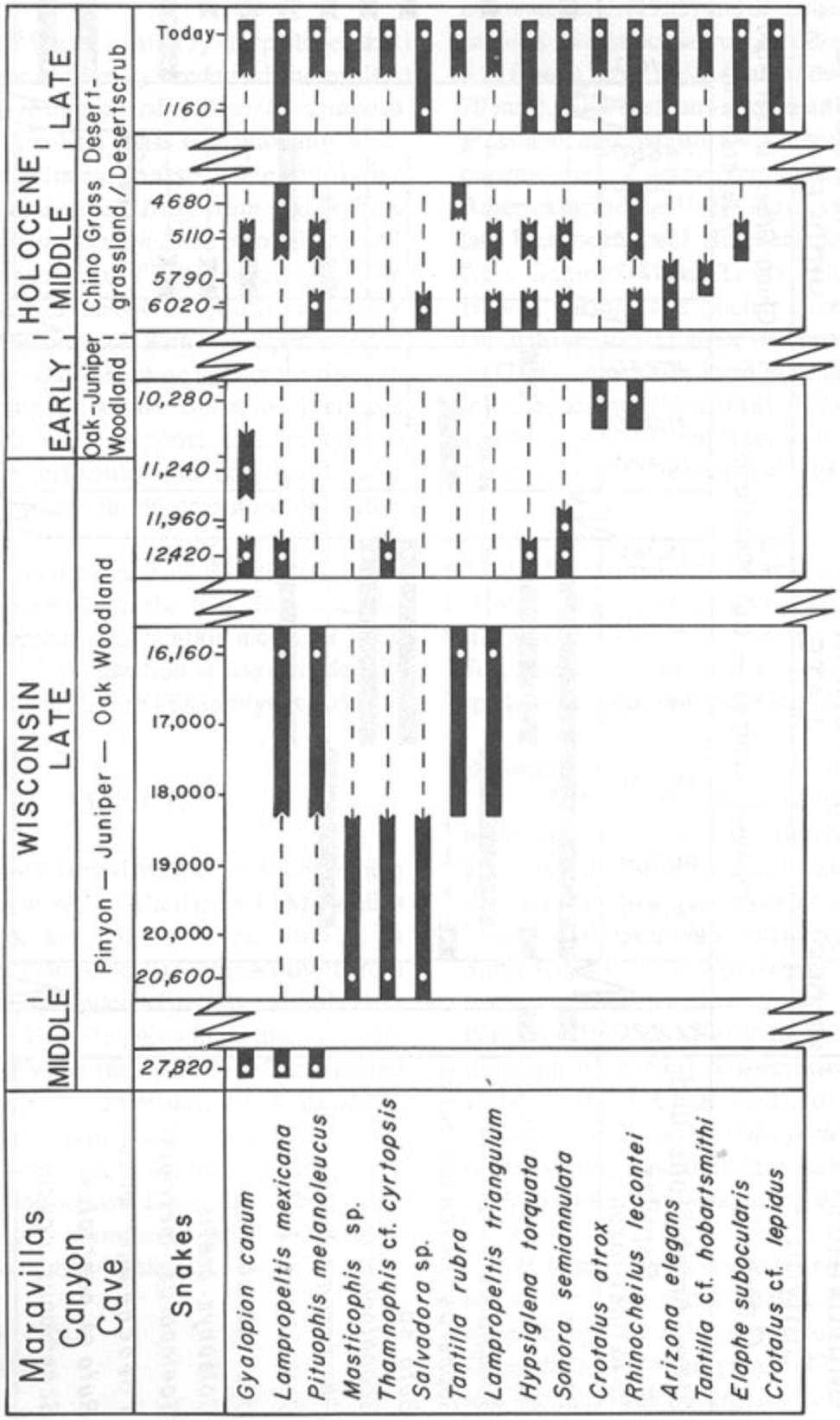

Figure 3. Temporal distribution of snakes identified from Maravillas Canyon Cave packrat middens, Brewster County, Texas. Ages are in yr B.P. with radiocarbon dates in italics following Table 1.

Mead et al., 1984; Van Devender et al., 1991b); Gypsum Cave, Nevada (Brattstrom, 1958); two Whipple Mountains packrat middens, California (Van Devender and Mead, 1978). Humeri from Rancho la Brisca, Sonora, Mexico, were referred to *Bufo punctatus* or *B. retiformis* (Sonoran green toad; Van Devender et al., 1985).

Bufo sp. (true toad). Material - TRV3: scapula (16931). Age - LW:16.2 ka. This bone is from a very young individual and could not be positively identified. Axtell (1959) found *Bufo punctatus, B. speciosus,* and *B. debilis* at Black Gap.

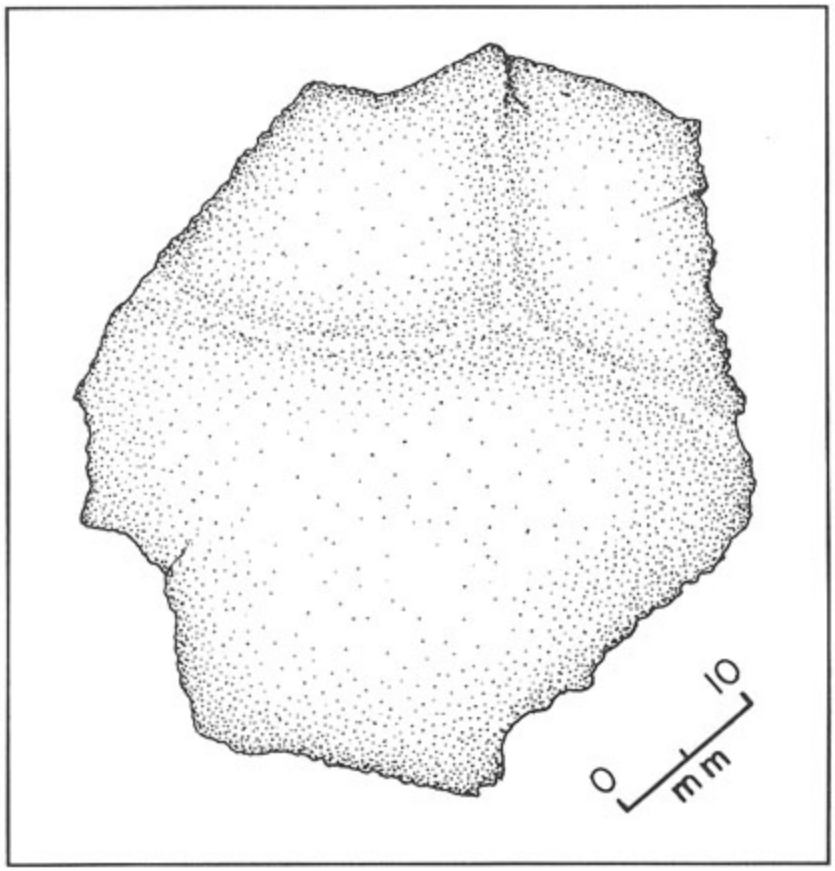

Figure 4. Nuchal bone (UALP 8613/17024) of *Gopherus flavomarginatus* from late Wisconsin floor fill deposits in Maravillas Canyon Cave, Brewster County, Texas. Drawing by G. L. Bradley.

CLASS REPTILIA
ORDER TESTUDINES
Testudinidae

Geochelone wilsoni (Friesenhahn Cave Tortoise). Material - TRV9: l. xiphiplastron (17005). Age - probable LW contaminant in MH: 4.7 ka. *Geochelone wilsoni* is a small, extinct tortoise with pronounced rugose ridges on a high-domed carapace. It is only known from late Pleistocene sites from south-central Oklahoma and eastern New Mexico south to central and south Texas (Moodie and Van Devender, 1979; Parmley, 1986a; Fig. 1). The Maravillas Canyon xiphiplastron had a different surface sculpture than the *Gopherus* specimens and compared well with the type material of *Geochelone wilsoni* from Friesenhahn Cave in the Texas Memorial Museum. The record represents a range extension of about 235 km west and 350 km south-southwest. The bone has the brown coloration typical of mineralized late Wisconsin bones in the cave unlike the white bone in middle and late Holocene deposits. The specimen is most likely older than 11,000 years in age and reworked into the 4680 yr B.P. midden.

Gopherus flavomarginatus (Bolson Tortoise). Material - MC Gen.: nuchal bone (17024; Fig. 4). Age - ca. LW. *Gopherus* cf. *flavomarginatus.* Material - MC Gen.: l. 10th marginal bone (17025); 2nd or 4th r. pleural bone (17026); 3rd or 5th vertebral bone (17028); humerus (17029). Age - ca. LW. *Gopherus* sp. Material - TRV11: shell fragment (17008); TRV10: shell fragment (17007); TRV18: shell fragment (17130); MC Gen.: 6 shell fragments (17027). Age - LW: 21.0-12.0 ka. The nuchal bone is diagnostic for *G. flavomarginatus* in that the sulci for the nuchal scute indicate it is much wider than in *Xerobates agassizi* (desert tortoise) or *X. berlandieri* (Texas tortoise). *Gopherus flavomarginatus* is presently restricted to the Bolson de Mapimi in the southern Chihuahuan Desert (Legler, 1959; Legler and Webb, 1961; Auffenberg, 1974; Morafka, 1982; Fig. 1), about 285 km south-southeast of Maravillas Canyon Cave.

Previous fossil records are from

Aguascalientes, Aguascaliente (Auffenberg and Franz, 1978), and Jimenez, Chihuahua (Messing, 1986), Mexico. In the late Pliocene Blancan Land Mammal Age (2-3 million years ago), fossils of large *Gopherus* called *G. canyonensis* (Auffenberg and Franz, 1978; Johnston, 1937), *G. flavomarginatus* (Bramble, 1982), and *G. huecoensis* (Strain, 1966) have been found from the southern Great Plains in Oklahoma and Texas west to the Colorado River near Parker, Arizona (McCord, 1985; Archer, 1989), and south to near Hermosillo, Sonora. Archer (1989) reported specimens in the present Sonoran Desert from the Phoenix Basin, Arizona, that may be late Pleistocene in age. The Maravillas Canyon records indicate that its range in the Chihuahuan Desert was greater during the late Wisconsin glacial period.

ORDER SQUAMATA
SUBORDER LACERTILIA

Gekkonidae

Coleonyx brevis (Texas Banded Gecko). Material - TRV16: r. dentary of adult (16970; Fig. 5A). Age - MH: 6.0 ka. *Coleonyx brevis* is a small, secretive gecko that prefers dry rocky areas in much of the Chihuahuan Desert including Black Gap (Axtell, 1959). It is smaller and less robust than *C. reticulatus,* the larger species described from a Black Gap specimen (Davis and Dixon, 1958). This is the first fossil record for *C. brevis.*

Iguanidae

Crotaphytus collaris (Collared Lizard) Material - TRV3: frontal (16933); TRV15: l. pterygoid (16965); TRV9: frontal (16943). Age - LW: 16.2 ka, MH: 5.8-4.7 ka. The two frontals resemble *Crotaphytus* rather than *Gambelia* in both their shape and more rugose surface texture. The pterygoid is proportionately narrower than in *Gambelia,* the only other large lizard in the area with a tooth-bearing pterygoid. The frontals and pterygoids of the distant *C. reticulatus* (reticulated collared lizard) of the Rio Grande Valley in south Texas and adjacent Mexico and *C. insularis* (desert collared lizard) of the Great Basin and Mohave deserts from Oregon and Idaho south to Arizona and Baja California cannot easily be separated from *C. collaris. Crotaphytus collaris,* a large, saxicolous lizard of open vegetation from woodland to desertscrub, is widespread in the central and western United States and northern Mexico. Both *C. collaris* and *Gambelia wislizeni* (leopard lizard) occur in the Black Gap area (Axtell, 1959; Treadwell, 1966).

Previous fossil records are from many Pleistocene and Holocene localities in Texas (Gehlbach and Holman, 1974; Holman, 1964, 1966, 1969b; Mecham, 1959; Parmley, 1986a), New Mexico (Brattstrom, 1964; Harris, 1985; Van Devender and Worthington, 1977; Holman, 1970), Arizona (Cole and Mead, 1981; Mead et al., 1984; Mead and Phillips, 1981; Van Devender et al., 1977; Van Devender and Mead, 1978; Van Devender et al., 1991a, 1991b), and Nevada (Brattstrom, 1954; Mead et al., 1982).

Phrynosoma modestum (Round-tailed Horned Lizard). Material - TRV16: right angular (16972). Age - MH: 6.0 ka. *Phrynosoma* cf. *modestum.* Material - TRV1: occipital horn scale (17011). Age - LW: 20.6 ka. This small horned lizard is a common inhabitant of desertscrub and desert grassland throughout the Chihuahuan Desert including Black Gap (Axtell, 1959). In the Glass Mountains north of Marathon, *P. modestum* enters pinyon-juniper-oak woodland dominated by *Pinus remota* (T.R. and R.K. Van Devender, pers. obs., 25 March 1986). Previous fossil records of *P. modestum* are from Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977) and Deadman Cave, Arizona (Mead et al., 1984). The latter record represents a 95 km western range extension into the present Sonoran Desert.

Sceloporus merriami (Canyon Lizard). Material - TRV17: r. dentary (16985); frontal (16986). Age - LH: 1.2 ka. *Sceloporus* cf. *merriami.* Material - TRV16: partial frontal (16971). Age - MH: 6.0 ka. The dentary teeth are more slender and less cusped than those of *S. grammicus, S. nelsoni, S. occidentalis, S. pyrocephalus, S. undulatus, S. virgatus,* or *S. woodi.* Indeed the teeth are virtually unicusped with the least development of secondary cusps of any *Sceloporus.* The frontals of *S. merriami*

are more thickened ventrally and the dorsal portion of the posterior half is more depressed than in *S. grammicus* or *S. undulatus.*

This small lizard is a Chihuahuan endemic that can be very common in rocky canyon habitats including Black Gap (Axtell, 1959). The only previous fossil record for *S. merriami* is from a 12,700 yr B.P. late Wisconsin midden from Coahuila, Mexico (Van Devender and Burgess, 1985).

Sceloporus undulatus (Eastern Fence Lizard). Material - TRV1: r. maxilla fragment (17012); TRV10: posterior half of l. dentary (17006). Age - LW: 20.6-12.4 ka. Positive identification of *S. undulatus* from skeletal elements is difficult because closely related species *(S. occidentalis, S. virgatus,* and *S. woodi)* in other geographic areas are very similar. This medium-sized lizard is widespread in a great variety of habitats in the United States west to eastern Nevada and western Arizona and south into Mexico. In more xeric areas including Black Gap (Axtell, 1959), it may be absent or restricted to riparian habitats.

Previous Pleistocene and Holocene fossil records for *S. undulatus* include: Schulze Cave (Parmley, 1986a), Cave Without a Name (Holman, 1968), and Slaton Quarry (Holman, 1969b), Texas, Dry and Howell's Ridge caves, New Mexico (Holman, 1970; Van Devender and Worthington, 1977), Hansen's Bluff, Colorado (Rogers et al., 1985), seven packrat midden sites and Deadman Cave, Arizona (Cole and Mead, 1981; Mead et al., 1984; Van Devender et al., 1977; Van Devender and Mead, 1978).

Sceloporus sp. (Spiny Lizard). Material - TRV4: 22 epidermal scales (17016); TRV11: 6 epidermal scales (17010); TRV1: epidermal scale (16921); TRV3: 3 epidermal scales (17014). Age - MW: 27.8 ka, LW: 21.0-16.2 ka. All of the above scales come from individuals smaller than adult *S. magister* (desert spiny lizard) or *S. poinsetti* (crevice spiny lizard) in the size range of *S. merriami* and *S. undulatus,* all of which occur in Black Gap today (Axtell, 1959). *Sceloporus grammicus* (tree spiny lizard) occurs in the Sierra del Carmen, 20-30 km east across the Rio Grande in Coahuila (Gloyd and Smith, 1942).

Uta stansburiana (Side-blotched Lizard) Material - TRV16: anterior portion of r. dentary (16973). Age - MH: 6.0 ka. The dentary of *U. stansburiana* is like a very small *Sceloporus* with Meckel's canal lateral, closed but not fused, and teeth with secondary cusps very well developed. Other small iguanids such as *Callisaurus, Holbrookia,* and *Urosaurus* have more slender teeth with secondary cusps less well developed. *Uta stansburiana* is a small, ground-dwelling lizard found in arid and semi-arid areas in much of western North America. Previous late Pleistocene and Holocene fossil records include: Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977), five packrat midden sites in Arizona (Mead and Phillips, 1981; Van Devender et al., 1977; Van Devender and Mead, 1978), Smith Creek Cave, Nevada (Brattstrom, 1976), and Rancho la Brea, California (Brattstrom, 1953).

Anguidae

Gerrhonotus liocephalus (Texas Alligator Lizard). Material - TRV4: osteoderm (17015; Fig. 5B); TRV11: osteoderm (17009); TRV#3: osteoderm (16929); TRV2: osteoderm (16928). Age - MW: 27.8 ka, LW: 21.0-11.2 ka. Osteoderms of *G. liocephalus* are distinctive with surface sculpturing on more than half of the dorsal surface. Differences between the osteoderms of *G. liocephalus* and *Ophisaurus attenuatus* (slender glass lizard) are discussed in Parmley (1988a). The osteoderms of *Eumeces* are smooth. *Gerrhonotus liocephalus* is a large anguid lizard with a prehensile tail found in a large area from the Mexican Plateau northward through the Sierra Madre Oriental into central Texas (Smith and Taylor, 1950). Most of Black Gap is apparently too hot and dry for *G. liocephalus* although it is suspected to occur in the higher elevations of the Sierra del Caballo Muerto (Axtell, 1959). Isolated populations are in woodlands in the Sierra del Carmen (15 km E; Gloyd and Smith, 1942) and the Chisos Mountains (20 km SW). Isolated desertscrub records northwest of Big Bend National Park are known from

Terlingua (40 km WSW; Brown, 1950) and 20 km west of Lajitas on Hwy. 170 (70 km W; R. Green, pers. comm., 1987). The nearest Edwards Plateau populations are in the Del Norte Mountains (105 km N; Carignan, 1988) and near the Devil's River north of Comstock (170 km ENE; Devine, 1969).

The only previous fossil records for *G. liocephalus* are from 8,000 yr B.P. Holocene deposits in Klein Cave (Parmley, 1988a). The Maravillas Canyon Cave specimens are the first late Wisconsin record for the species. Both adults and juveniles were represented.

SUBORDER SERPENTES

Colubridae

Arizona elegans (Glossy Snake). Material - TRV16: vertebrae (16982-83); TRV15: 2 vertebrae (16969); TRV17: vertebrae (16999, 17000). Age - MH: 6.0 ka, LH: 1.2 ka. The vertebrae of *Arizona elegans* have a high neural spine that is relatively thin compared to *Pituophis melanoleucus,* a larger snake with very similar vertebrae. Other criteria for the identification of *A. elegans* vertebrae are given in Van Devender and Mead (1971), Mead et al. (1984), and LaDuke (1991).

Arizona elegans is a medium-sized colubrid that prefers open sandy terrain over much of the southwestern United States and northern Mexico. *Arizona elegans* is probably uncommon in the limestone terrain between Big Bend National Park and the sandy soils of the Rio Grande Valley (Devine, 1969; Dixon, 1959). The only record for *A. elegans* in Black Gap is from 16 km west of La Linda on RR 2627 (R. Green, pers. comm., 1987).

Late Pleistocene and Holocene fossil records of *A. elegans* have been reported from seven Texas sites (Gehlbach and Holman, 1974; Hill, 1971; Holman, 1963, 1964, 1966; Parmley, 1986a, 1988a), Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977), Deadman Cave and five packrat midden sites, Arizona (Mead et al., 1984; Van Devender and Mead, 1978; Van Devender et al., 1991a, 1991b), and Rancho La Brea, California (La Duke, 1991).

Elaphe subocularis (Trans-Pecos Ratsnake). Material - TRV13: r. palatine (16964); TRV17: vertebra (16998); MC Gen.: 4 vertebrae, 3 with undated middle Holocene midden material attached (17020-21). Age - MH: 5.1 ka, LH: 1.2 ka.

Elaphe subocularis is a large colubrid snake that is widespread in desertscrub and desert grasslands below 1525 m elevation in the Chihuahuan Desert from south-central New Mexico south into Chihuahua and Coahuila, Mexico (Smith and Taylor, 1945). It is common in many areas of Trans-Pecos including Black Gap (Axtell, 1959; Tennant, 1984). The only previous fossil records for *E. subocularis* are from undated cave deposits on Bishop's Cap, New Mexico, from the northern edge of its range (Brattstrom, 1964).

The vertebrae of *Elaphe guttata, E. obsoleta, Lampropeltis calligaster,* and *Pituophis melanoleucus* resemble each other in a) size and general shape, b) high neural spine, c) high neural arch, and d) centrum not flattened with thin haemal keel. Examination of the vertebrae of *E. flavirufa,* a tropical species with a color pattern similar to *E. guttata emoryi,* places it in this group as well. The vertebrae of *Elaphe subocularis* are easily separated from these taxa because they are wider than long (Parmley, 1986b). Other vertebral characters include: a) centrum wide and flattened, b) haemal keel is low and broad, c) conspicuous depressions formed between haemal keel and subcentral ridge, d) neural spine usually moderately high, e) accessory processes short, sharp and angled to anterior, and f) zygosphene relatively broad and down-curved reflecting potentially large body sizes. Other species with vertebrae wider than long are *E. triaspis* (green ratsnake), a tropical and subtropical ratsnake that enters the United States in the mountains of southeastern Arizona, and *E. rosaliae* (Baja California ratsnake) of Baja California Sur and California. The vertebrae of *E. triaspis* differ from *E. subocularis* in a) their smaller size, b) less flattened centrum, and c) haemal keel thin and sharp. *Elaphe triaspis* is unusual in that females are larger with heavier bodies than males with corresponding size differences in the vertebrae. Reference skeletons were examined from six mature males with snout-vent lengths (SVL) of 641-758 mm (x = 714 mm). The flattened centrum characteristic of *E. subocularis* was only present in a large female *E. triaspis* (SVL=895 mm). Adult *E. subocularis* of

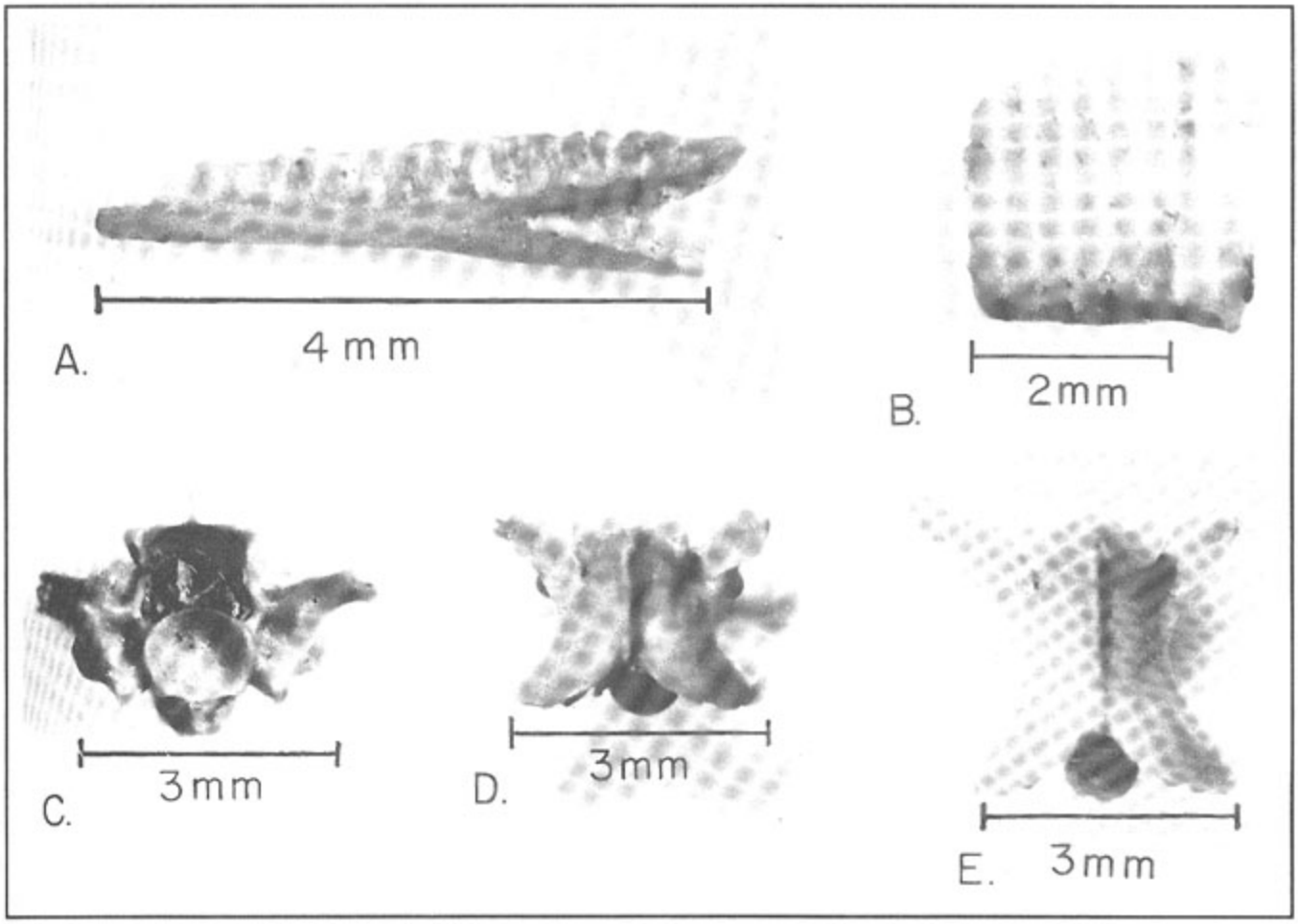

Figure 5.
A. Right dentary (UALP 8611/16970) of *Coleonyx brevis* from MC TRV16 midden dated at 6020 yr B.P.
B. Dorsal surface of *Gerrhonotus liocephalus* osteoderm (UALP 8537/17015) from MC TRV4 midden dated at 27,820 yr B.P.
C. and D. Anterior and dorsal view of *Lampropeltis mexicana* vertebra (UALP 8536/16935) from MC TRV3 midden dated at 16,160 yr B.P.
E. Dorsal view of *Tantilla rubra* vertebra (UALP 8536/16932) from MC TRV3 midden.

both sexes have SVL's greater than 1000 mm. The vertebrae of a captive bred *E. rosaliae* and a wild specimen from Isla Danzante in the Gulf of California (San Diego Society of Natural History #65470) are very similar to *E. subocularis* differing only in a lower neural spine (variable in *E. subocularis)* and a slightly smaller size. The vertebrae of *E. subocularis* and *E. rosaliae* are unique and derived for *Elaphe*.

The vertebrae of other sympatric *Elaphe* in Trans-Pecos Texas *(E. bairdi, E. guttata emoryi)* and those of *Pituophis melanoleucus* can be separated from those of *E. subocularis* because they are longer than wide (Parmley, 1986b). The neural spine of *Elaphe bairdi* vertebrae are lower than *E. subocularis. Elaphe vulpina* (fox snake) of north-central United States and *E. rosaliae* are the only other North American species with low neural spines (Holman, 1982; this report). The vertebrae of *E. bairdi* can be separated from those of *E. vulpina* by a) neural spine lower, b) neural arch slightly more flattened, c) zygosphene relatively narrow, d) haemal keel broader, and e) centrum relatively flattened. The vertebrae of *E. rosaliae* differ from *E. bairdi* in a) much wider vertebrae and b) a flatter centrum with strongly excavated depressions between the haemal keel and subcentral ridges. The vertebrae of *E. bairdi* with low neural spines and accessory processes oriented perpendicular to the vertebral axis from above resemble *Lampropeltis*

getulus(common kingsnake) more than other *Elaphe*. The following characters separate their vertebrae: a) vertebrae relatively longer in *L. getulus*, b) zygosphene relatively wider in *E. bairdi,* c) accessory processes more blunt or clavate and horizontally oriented from the anterior rather than dorsally in *L. getulus,* and d) haemal keel lower and broader in *E. bairdi.*

The statement by Dowling and Price (1988) that the vertebrae of *E. rosaliae* and *E. subocularis* are not differentiated from either other *Elaphe* or *Pituophis* is not supported. Although vertebral characters will not separate some colubrid genera, they can be very useful indicators of relationships within a genus such as *Elaphe* (Holman, 1982; Parmley 1984a).

Gyalopion canum (Western Hooknosed Snake). Material - TRV4: vertebra (17017); TRV10: vertebra (16950); TRV2: vertebra (16927); TRV13: vertebra (16963). Age MW: 27.8 ka, LW: 12.4-11.2 ka, MH: 5.1 ka. The vertebrae of *G. canum* have a lower neural spine and a higher neural arch than similar-sized *Hypsiglena torquata* and *Rhinocheilus lecontei* vertebrae (Mead et al., 1984). *Gyalopion canum* is a small burrowing snake common in desert grassland above 770 m elevation (Tennant, 1984). The only Black Gap records for *G. canum* are from 7 km west of La Linda on RR 2627 on 26 June 1986 (R. Green, pers. comm., 1987) and 26 km northwest of the Black Gap Headquarters on RR 2627 (H. K. McCrystal, April 1981).

Late Pleistocene or early Holocene fossils of *G. canum* have been reported from Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977), and Deadman Cave, Arizona (Mead et al., 1984). The latter record was a range extension of 80 km to the north into the present Sonoran Desert.

Hypsiglena torquata (Night Snake). Material - TRV10: vertebra (16951); TRV16: 2 vertebrae (16976-77); TRV13: 2 vertebrae (16954, 16961); TRV17: 4 vertebrae (16989-91, 16993, 17002). Age - LW: 12.4 ka, MH: 6.0-5.1 ka, LH: 1.2 ka. Criteria for the identification of *H. torquata* vertebrae are given in Van Devender and Mead (1978), Mead et al. (1984), Van Devender et al. (1985), and La Duke (1991). This common, small snake occurs in a great variety of habitats from desert to woodland and forest in the western United States including Black Gap (Axtell, 1959) and much of Mexico.

Previous late Pleistocene and Holocene fossil records for *H. torquata* include: Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977), Deadman Cave and seven packrat midden sites, Arizona (Mead and Phillips, 1982; Mead et al., 1984; Van Devender et al., 1977, 1991a; Van Devender and Mead, 1978), Rancho la Brisca, Sonora, Mexico (Van Devender et al., 1985), Smith Creek Cave, Nevada (Mead et al., 1982), and Rancho La Brea (La Duke, 1991) and two Whipple Mountains packrat middens (Van Devender and Mead, 1978), California.

Lampropeltis mexicana (Gray-banded Kingsnake). Material - TRV4: 2 vertebrae (16939-40); TRV3: 2 vertebrae (16935-36; Figs. 5C and D); TRV10: vertebra (16953); TRV13: vertebra (16959); TRV9: vertebra (16948); TRV17: 2 vertebrae (16996-97). Age - MW: 27.8 ka, LW: 16.2-12.4 ka, MH: 5.1-4.7 ka, LH: 1.2 ka. *Lampropeltis mexicana* is a medium-sized kingsnake found in the mountains bounding the Mexican Plateau and the Chihuahuan Desert lowlands. We view the various subspecies in the group as belonging to *L. mexicana* as defined by Gehlbach (1967), and do not consider the characters (iris color, broader head) presented by Gartska (1982) significant enough to elevate *L. m. alterna* to a species. The more triangular heads of *L. m. alterna* and *L. m. blairi* probably reflect their adaptation to subterranean crevice dwelling. The subspecies *L. m. alterna* extends from Coahuila into Texas from the Big Bend to the El Paso area (Miller, 1979). Tanzer (1970) placed the subspecies *L. m. blairi* into the synonymy of *L. m. alterna* based on hatchlings with both color patterns from Val Verde County female and a brief survey of the few specimens available at the time. He thought that the two patterns were color polymorphs represented in similar proportions. However, Miller's (1979) summary of hundreds of specimens indi-

cated that less than 10% of the Val Verde County specimens had typical *alterna* pattern. Extensive collecting near Langtry has shown that the *alterna* pattern is absent or rare in several local populations (B. Ross, pers. comm., 1992). Moreover, the rare *alterna*-type patterns from near Comstock differ from those from the type area in the Davis Mountains in gray versus brownish ground color and the absence of dark flecks on the anterior third of the body. *Lampropeltis m. blairi* is a valid subspecies restricted to the southern edge of the Edwards Plateau east of the Chihuahuan Desert proper. Most of the Black Gap specimens would be considered intergrades (H. K. McCrystal and R. Green, pers. comm., 1987).

The vertebrae of *L. mexicana* are similar to other kingsnakes derived from *L. triangulum (L. pyromelana, L. zonata)* in the low neural spine and well-developed subcentral ridges (Fig. 5C and D; Gartska, 1982). Differentiation of *L. mexicana* and *L. triangulum* presents some problems when the entire range of variation within each species is considered. The northern subspecies of *L. mexicana (alterna, blairi)* are well-adapted to a subterranean existence in rock crevices and have distinctive vertebrae that differ from the small, northern subspecies of *L. triangulum (amaura, celaenops, gentilis,* etc.) in the following characters: a) vertebrae wider than long, b) neural arch flatter, c) zygosphene relatively wide, d) cotyle and condyle relatively larger, e) subcentral ridges less well-developed, and f) neural spine often lower. These characters readily separate the species in the Big Bend. However, the montane subspecies of *L. mexicana (greeri, mexicana, ruthveni, thayeri)* have body forms more like *L. triangulum,* and tropical *L. triangulum (annulata, nelsoni, polyzona,* etc.) reach larger body sizes. Differentiation of all forms within these species will probably prove to be difficult.

The Maravillas Canyon Cave fossils represent the subspecies *L. m. blairi* or *L. m. alterna.* The only previous fossil records for *L. mexicana* are from a 15,300 yr B.P. Late Wisconsin packrat midden from Ernst Tinaja in Big Bend National park (30 km SSE) and from 9180 yr B.P. early Holocene sediments in Baker Cave on the Devil's River north of Comstock (175 km ENE; Miller, 1979).

Lampropeltis triangulum (Milk Snake). Material - TRV16: vertebra (16984); TRV13: vertebra (16960). Age - MH:6.0-5.1 ka. *Lampropeltis* cf. *triangulum.* Material - TRV3: vertebra (16937). Age - LW: 16.2 ka. This small- to medium-sized snake with many subspecies occurs in a great variety of habitats from Canada to northern South America in the largest geographic range of any New World snake. *Lampropeltis triangulum celaenops* (Big Bend milk snake) is a secretive small subspecies that occurs in the Big Bend in desert riparian habitats and mesic areas in the Chisos Mountains. The color pattern of a *L. triangulum* in a photo of a Black Gap animal in Tennant (1984) resembles *L. t. celaenops* while a juvenile from 10 km west La Linda on RR 2627 taken in 1980 was more similar to *L. t. annulata* (Mexican milk snake; R. Green, pers. comm., 1987). The intergrade zone between the two subspecies apparently extends from the northern edge of the Rio Grande Valley in Val Verde County into the eastern Big Bend (Devine, 1969; Tennant, 1984).

The fossils represent a form of *L. triangulum* similar in size to the local *L. t. celaenops.* Previous Pliocene, Pleistocene, and Holocene fossil records include Berends, Oklahoma (Holman, 1986), Beck Ranch (Rogers, 1976), Carrol Creek (Kasper and Parmley, 1990), Cave Without a Name (Hill, 1971), Klein Cave (Parmley, 1988a), Groesbeck Creek, Clear Creek, and Miller's Cave, Texas (Holman, 1963, 1964, 1966), Borcher's, Kentuck, Jinglebob, and Williams, Kansas (Brattstrom, 1967; Holman, 1984), Inglis IA, Florida (Meylan, 1982), Strait Canyon, Virginia (Fay, 1984), and Trout Cave, West Virginia (Holman and Grady, 1987).

Masticophis cf. *flagellum* (Coachwhip). Material - MC Gen.: 5 vertebrae (17030). *Masticophis* sp. Material - TRV1: 3 vertebrae (16925-26, 17013). Age - LW:20.6 ka. Criteria for the identification of *Masticophis* vertebrae are given in Auffenberg (1963), Van Devender and Mead (1978), Van Devender et al. (1985), and La Duke (1991). Separation of the vertebrae of *Masticophis*

and *Coluber* are difficult in some areas because of marked differences in body size in different subspecies of *C. constrictor* (racers). The vertebrae from Maravillas Canyon General are from an individual ca. 1600 mm in snout-vent length and with a total length of probably more than 2000 mm. This would be (1) much larger than *C. c. flaviventris* or *C. c. mormon,* (2) near the maximum size for *M. taeniatus* (ornate whipsnake), but (3) well within the range of *M. flagellum.* The vertebrae of a *Mastigodryas melanolomus* of SVL = 2870 mm from Veracruz, Mexico, are very similar to *Masticophis* and large *C. constrictor* but relatively smaller than the fossil. *Masticophis flagellum* is a large, diurnal snake found in many habitats across the United States and northern Mexico. Both *M. flagellum* and *M. taeniatus* are common in Black Gap (Axtell, 1959).

Previous Pliocene, Pleistocene, and Holocene fossil localities for this large, wide-ranging species include: Inglis IA, Florida (Meylan, 1982), Beck Ranch, Texas (Rogers, 1976), Shelter Cave, New Mexico (Brattstrom, 1964), Gypsum and Smith Creek Caves, Nevada (Brattstrom, 1958, 1976), and Rancho la Brea and Newport Bay Mesa, California (Brattstrom, 1953; Hudson and Brattstrom, 1977).

Pituophis melanoleucus (Bull or Gopher Snake). Material - TRV4: vertebra (17018); TRV11: vertebra (16981); TRV3: vertebra (16938); TRV13: vertebra (16958). Age - MW: 27.8 ka, LW: 21.0-16.2 ka, MH: 5.1 ka. Criteria for the identification of *P. melanoleucus* vertebrae are given in Auffenberg (1963), Van Devender and Mead (1978), Mead et al. (1984), Parmley (1988a), and La Duke (1991). This very large colubrid lives in many habitats throughout the United States and northern Mexico. Axtell (1959) did not find it in Black Gap but has been seen just northwest of Black Gap on RR 2627 (H. K. McCrystal, pers. comm., 1987); it probably occurs there.

The fossil record for this wide-ranging and ecologically very tolerant snake is extensive. Pliocene and Pleistocene fossil localities in Texas include: Friesenhahn Cave (Mecham, 1959), Cave Without a Name (Hill, 1971), Klein Cave (Parmley, 1988), Schulze Cave (Parmley, 1986a), and Beck Ranch (Rogers, 1976).

Rhinocheilus lecontei (Longnosed Snake). Material - TRV8: 3 vertebrae (16942); TRV16: 2 vertebrae (16975, 16978); TRV13: vertebra (16957); TRV9: 3 vertebrae (16945-47); TRV17: 3 vertebrae (16992, 16995). Age - EH: 10.3 ka, MH: 6.0-4.7 ka, LH: 1.2 ka. Criteria for the identification of *R. lecontei* vertebrae are given in Hill (1971), Van Devender and Mead (1978), Mead et al. (1984), and La Duke (1991). This medium-sized snake is widespread in the southwestern United States and northern Mexico in desert, grassland, Sinaloan thornscrub, and tropical deciduous forest habitats. It presently occurs in Black Gap (Axtell, 1959).

Previous Pliocene, Pleistocene, and Holocene fossil localities include Gilliland and Slaton Local faunas, Pratt Cave, and Beck Ranch, Texas (Gehlbach and Holman, 1974; Hill, 1971; Holman, 1969b; Parmley, 1988b; Rogers, 1976), Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977), Deadman Cave and seven packrat midden sites, Arizona (Mead, et al., 1984; Mead and Phillips, 1981; Van Devender et al., 1977, 1991a, 1991b; Van Devender and Mead, 1978), Smith Creek Cave, Nevada (Mead et al., 1982), and Rancho La Brea (La Duke, 1991) and a Whipple Mountains packrat midden (Van Devender and Mead, 1978), California.

Salvadora sp. (Patchnosed Snakes). Material - TRV1: vertebra (16924); TRV16: vertebra (16980); TRV17: vertebra (16994). Age - LW: 20.6 ka, MH: 6.0 ka, LH: 1.2 ka. Criteria for the identification of *Salvadora* vertebrae are given in Van Devender et al. (1985). In general *Salvadora* vertebrae are (1) elongate, (2) medium-sized, (3) shorter than *Oxybelis aeneus* (vine snake), (4) larger than *Opheodrys* (green snakes), and (5) smaller than *Coluber, Mastigodryas melanolomus,* and *Masticophis.* The vertebrae are most similar to *Drymobius margaritiferus* (speckled racer) but are slightly smaller with a more elongate, narrow centrum and much narrower zygophene. The vertebrae of *Salvadora grahamiae* (mountain patchnosed snake) and *S. hexalepis deserticola* (Big Bend patchnosed snake) are very similar. Both species

occur in Black Gap (Axtell, 1959).

Sonora semiannulata (Ground Snake). Material - TRV10: vertebra (16952); TRV18: vertebra (17129); TRV16: vertebra (16974); TRV13 vertebra (16962); TRV17: vertebrae (16989, 17001, 17003). Age - LW: 12.4-12.0 ka, MH: 6.0-5.1 ka, LH: 1.2 ka. The vertebrae from *Sonora semiannulata* differ from *Hypsiglena torquata* in a lower, thicker neural spine, and from *Gyalopion canum* in accessory processes oriented laterally or dorsally rather than ventrally when viewed from the anterior (Van Devender and Mead, 1978). *Sonora semiannulata* is a small snake found from the southern Great Plains west to California and south into Mexico in habitats ranging from xeric deserts to mesic mountains including Black Gap (Axtell, 1959).

Previous late Pleistocene and Holocene fossil records (some as *S. episcopa)* are from the William's Local Fauna, central Kansas (Holman, 1984) and Grand Canyon and western Arizona packrat middens (Mead and Phillips, 1981; Van Devender et al., 1977; Van Devender and Mead, 1978).

Tantilla cf. *hobartsmithi* (Blackheaded Snake). Material - TRV15: vertebrae (16966, 16967-68). Age - MH: 6.0 ka. The vertebrae of *Tantilla hobartsmithi* are very small (centrum length less than 1.2 mm) with a very low neural spine and more elongate than in *Chionactis* or *Sonora* (La Duke, 1991; Van Devender et al., 1991). The vertebrae of other small *Tantilla (T atriceps, T. gracilis, T. nigriceps nigriceps, T. planiceps)* are very similar. The vertebrae of the large subspecies *T. nigriceps fumiceps* (Texas black-headed snake) from southwestern New Mexico and southeastern Arizona are larger with centrum lengths of 1.3-1.5 mm or greater. The Maravillas Canyon specimens are from a small species similar to *T. hobartsmithi.*

Tantilla hobartsmithi is a small, secretive snake that is widespread in rocky habitats in a series of isolated populations across the southwestern United States and northern Mexico including Black Gap (Axtell, 1959).

Previous late Pleistocene and Holocene fossil records for small *Tantilla* sp. are from the William's Local Fauna, central Kansas *(T. gracilis* or *T. n. nigriceps;* Holman, 1984), Cave Without a Name, *(T. gracilis* or *T. nigriceps;* Hill, 1971) and Pratt Cave *(T. atriceps = T. hobartsmithi* or *T. nigriceps;* Gehlbach and Holman, 1974), Texas, Howell's Ridge Cave, New Mexico *(T. planiceps atriceps = T. hobartsmithi* or *T. nigriceps;* Van Devender and Worthington, 1977), Picacho Peak packrat midden, Arizona *(T.* cf. *hobartsmithi;* Van Devender *et al.,* 1991a), and Rancho La Brea, California *(T. planiceps;* La Duke, 1991).

Tantilla rubra (Blackhood Snake). Material - TRV3; vertebrae (16932, 16934; Fig. 5E); TRV9: vertebra (16944). Age - LW: 16.2 ka, MH: 4.7 ka. *Tantilla rubra* is a large species of *Tantilla* found from the Pacific slopes of the Isthmus of Tehuantepec northward through central Oaxaca, Puebla, San Luis Potosi, and Nuevo Leon into Texas (Smith and Taylor, 1945). The subspecies *T. r. cucullata* is found in desert-grassland or pinyon-juniper-oak woodland in the Chisos and Davis mountains at 1310-1525 m elevation (Tennant, 1984). A few specimens have been observed in more xeric habitats below 915 m in the Christmas Mountains just north of Big Bend National Park (H. K. McCrystal, pers. comm., 1986). The subspecies *T. r. diabola* occurs below about 475 m elevation east of the Chihuahuan Desert in the northwestern extension of Tamaulipan thornscrub near the junctions of the Devil's and Pecos Rivers with the Rio Grande. Both snakes can reach body lengths over 55 cm. The only Black Gap record for *T. rubra* is from 1.6 km west of the Headquarters on RR 2627 on 3 July 1986 (R. Green, pers. comm., 1987).

The vertebrae of *T. rubra* resemble those of other *Tantilla* but are larger (up to 2.6 mm centrum length). The only southwestern colubrines with vertebrae in this size range are the largest *Hypsiglena torquata* and *Diadophis punctatus,* and small *Salvadora* and *Opheodrys* (green snakes). The vertebrae of *T. rubra* are described as follows: 1) much longer than wide: relatively longer than *Hypsiglena* and *Sonora* but shorter than *Opheodrys,* 2) neural arch moderately flattened: more than small *Salvadora,* less than large *Diadophis,* 3) neural spine long and low with a bifurcate anterior

tip in large adults, 4) zygosphene relatively narrow and modestly down-curved even at large size, 5) accessory processes are longer than in *Salvadora* or *Opheodrys* with an anterior orientation intermediate to them, and 6) haemal keel narrow and sharp with subcentral ridges weakly developed.

The Maravillas Canyon specimens are the first fossil record for the species.

Thamnophis cf. *cyrtopsis* (Black-necked Garter Snake). Material - TRV1: vertebrae (16922-23); TRV10: vertebra (16949). Age - LW: 20.6-12.4 ka. Criteria for the identification of *T. cyrtopsis* vertebrae are presented in Van Devender et al. (1985). These vertebrae resemble *T. cyrtopsis* rather than *T. marcianus* (checkered gartersnake) in that they are relatively longer and the accessory processes are angled more to the anterior in dorsal view. The vertebrae of *T. proximus* and *T. sauritus* are much smaller and more elongate. *Thamnophis cyrtopsis* is a gartersnake that characteristically lives in mountain canyon habitats in much of the southwestern United States and northern Mexico. Intergrades between *T. c. cyrtopsis* and eastern *T. c. ocellata* are relatively common in Black Gap in the rocky streambed in Maravillas Canyon (Axtell, 1959).

Previous late Pleistocene and Holocene fossil records of *T. cyrtopsis* or *T.* cf. *cyrtopsis* are from Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977), and Rancho la Brisca, Sonora, Mexico (Van Devender et al., 1985).

Crotalus atrox (Western Diamondback Rattlesnake). Material - TRV8: vertebra (16941); MC Gen.: vertebra (17022-23). Age - EH: 10.3 ka. Criteria for the identification of *C. atrox* vertebrae are given in Van Devender and Mead (1978) and Van Devender et al. (1985). *Crotalus atrox* is a large rattlesnake found in many habitats throughout the southwestern United States and northern Mexico. It is very common in Black Gap (Axtell, 1959) and enters the woodlands of the southern Edwards Plateau to the east (Devine, 1969).

Previous Pliocene, Pleistocene, and Holocene fossil localities for this large rattlesnake include: Freisenhahn and Miller's Caves, Beck Ranch and Slaton, Texas (Holman, 1966, 1969; Mecham, 1959; Rogers, 1976), Conkling, Dry, Fosberg, and Shelter Caves, New Mexico (Brattstrom, 1964; Holman, 1970), Deadman Cave, Arizona (Mead et al., 1984), a Whipple Mountains packrat midden, California (Van Devender and Mead, 1978), Gypsum Cave, Nevada (Brattstrom, 1954), and Rancho la Brisca, Sonora, Mexico (Van Devender et al., 1985).

Crotalus cf. *lepidus* (Rock Rattlesnake) Material - TRV17: vertebra (17004). Age - LH: 1.2 ka. The vertebrae of *C. lepidus* are relatively small with flattened neural arch, low neural spine, and the hypapophysis strongly angled to the posterior. The vertebrae of *C. molossus* (black-tailed rattlesnake) are similar but much larger. The vertebrae of *C. willardi* (ridge-nosed rattlesnake) are also small and flattened but the neural spine is relatively higher. The vertebrae of *C. pricei* (twin-spotted rattlesnake) are smaller than in *C. lepidus* with neural arch and neural spine moderately higher. Other species of *Crotalus, Sistrurus,* and *Agkistrodon* have higher neural spines and arches, longer and more ventrally-oriented hypapophyses.

Crotalus lepidus is a small rattlesnake of rocky habitats found from southeastern Arizona to south-central Texas and south to central Mexico. Although the western subspecies *(C. l. klauberi)* is predominantly an animal of montane woodlands and forests, *C. l. lepidus* is found in rocky habitats in desertscrub and woodland in much of the Chihuahuan Desert including Black Gap (Axtell, 1959). The only previous fossil record is from a 12,700 yr B.P. Late Wisconsin packrat midden from Coahuila, Mexico (Van Devender and Burgess, 1985).

DISCUSSION

Amphibian, reptile, and plant remains preserved in the Maravillas Canyon Cave middens provide a good reflection of the environmental history of Black Gap in the eastern Big Bend of Texas for 27,820 years of the last glacial/interglacial cycle.

Late Wisconsin.—During the late Wis-

consin glacial age, a mesic pinyon-juniper-oak woodland with *Pinus remota, Juniperus pinchotii,* and *Quercus pungens* grew at Maravillas Canyon Cave. The nearest modern analogs to this woodland are 90 km north in the Glass Mountains, and 215 km east on the southern edge of the Edwards Plateau north of Del Rio. Ice age climates of the Big Bend were very different than today with much cooler summers, mild winters with fewer catastrophic winter freezes, and increased annual rainfall with a shift to winter dominance (Van Devender, 1990).

Geochelone wilsoni was the only extinct species in the fauna. The nearest previous fossil record for it is Schulze Cave on the Edwards Plateau (235 km ENE; Parmley, 1986a). At Dry Cave, New Mexico, *G. wilsoni* was sympatric with *Xerobates agassizi* in middle Wisconsin deposits (Moodie and Van Devender, 1979). In middle and late Wisconsin, the range of the Sonoran Desert *X. agassizi* was 350-550 km further east than today (Van Devender et al., 1976). Near Picacho Peak, Arizona, *X. agassizi* and *Gopherus flavomarginatus* may have been contemporaneous (Archer, 1989). In Maravillas Canyon, *G. wilsoni* was with *G. flavomarginatus. Geochelone crassiscutata,* an extinct giant tortoise, probably occurred throughout the range of *G. wilsoni* prior to 11,000 years ago. In contrast, the four surviving North American tortoises in the genera *Gopherus* and *Xerobates* have widely allopatric ranges.

Gopherus flavomarginatus is today restricted to tobosa grass *(Hilaria mutica)*-honey mesquite *(Prosopis glandulosa)* habitats on the margins of playa lakes well below woodlands in the Bolson de Mapimi in Coahuila, Durango, and Chihuahua (285 km ESE; Morafka, 1982). In the last glacial, the pluvial lakes were full while xeric pinyon-juniper or juniper woodlands with abundant succulents covered the slopes of the adjacent limestone sierras (Van Devender and Burgess, 1985). Although *G. flavomarginatus* was associated with woodland plant remains in Maravillas Canyon Cave, it does not climb well and may not have lived in the slope woodlands. The bones were likely transported to the cave by predators. Even so, the ice age vegetation of more level areas along Maravillas Creek was much more mesic than tobosa grasslands in the Bolson de Mapimi. Equable climates with fewer catastrophic freezes may have allowed it to live in more mesic communities than today or 11,000 years of hunting pressure by native peoples may have artificially restricted it to desertscrub habitats. This tortoise is an Endangered species with the United States Fish and Wildlife Service, protected by Mexico, and on Appendix I (Endangered) of the Convention on International Trade in Endangered Species (CITES). Considering the fossil record, pinyon-juniper-oak woodlands on the southern Edwards Plateau similar to Maravillas Canyon paleocommunities may be good areas to establish refuges to ensure its survival.

Several animals in the Maravillas Canyon Cave fauna reflect more mesic environments and greater faunal exchange between the Edwards Plateau of central Texas and the Chisos Mountains and Sierra del Carmen. Expansion of *Gerrhonotus liocephalus* into lowland woodlands is interesting because this is a Sierra Madrean animal reaching its northern range limits in central Texas. Colder winters with more frequent freezes in the late Wisconsin would probably have displaced most Mexican species out of the area; Black Gap winters were probably no colder than today.

Black Gap is presently an intergrade zone for subspecies of *Thamnophis cyrtopsis (cyrtopsis* x *ocellata;* Axtell, 1959), *Lampropeltis triangulum (annulata* x *celaenops),* and *L. mexicana (alterna* x *blairi).* The extreme color pattern variability of *Lampropeltis mexicana* in the Christmas Mountains just north of Big Bend National Park is likely the genetic signature of *L. m. blairi* entering the Big Bend lowlands from the east into the range of *L. m. alterna* during each ice age. In contrast color patterns of animals from near Lajitas on the west side of the Big Bend are more similar to those from the Davis Mountains, especially ground color and dorsal flecking. The expansions of *Pinus remota* woodlands during glacials along the Rio Grande northwest as far as the El Paso area (Lanner and Van Devender, 1981) provided a corridor for *Lampropeltis m. alterna* to establish populations in the Sierra Vieja, Hueco, and Guadalupe mountains (Miller, 1979). In the Holocene, *L. m. alterna* stock

from the Davis Mountains or the Big Bend probably moved eastward broadening the intergrade zone and reducing the range of the *L. m. blairi.*

Tantilla rubra diabola east of Black Gap has a light nuchal collar on the neck. *T. r. cucullata* in the Christmas and Davis mountains have a dark head lacking a light collar. Collins (1991) elevated them to full species status based on their apparent geographic isolation and Frost and Hillis' (1990) species concepts. However, many individuals in the Chisos Mountains just west of Black Gap have incomplete light nuchal collars (Degenhardt et al., 1976) and specimens with middorsal constriction of the collar occur in Val Verde County (Devine, 1969). Additional collecting will undoubtedly show the secretive *T. rubra* to be more widespread in the Big Bend. The present distribution of color pattern characters suggests that the subspecies *T. r. diabola* has repeatedly extended its range into the Big Bend during glacial periods with *T. r. cucullata* or intergrades moving to the east in interglacials.

The highly variable color pattern in Big Bend populations of *A. c. pictigaster* suggests strong gene flow with *A. c. laticinctus* (broad-banded copperhead) during glacials and isolation in interglacials (Van Devender and Conant, 1990; H. K. McCrystal, pers. comm., 1986). A record of *Colinus virginianus* (bobwhite quail) from an undated deposit in Mule Ears Peak Cave in the Park (Wetmore and Friedman, 1933) probably represents a similar late Wisconsin range extension from the Edwards Plateau in to the Big Bend. Considering similar gene flow during glacials for over 90% of the last two million years (Van Devender, 1986), it is not surprising that recognizing subspecies of *A. contortrix, L. mexicana, L. triangulum,* and *T. rubra* in the Big Bend is difficult.

Other animals found in the late Wisconsin middens such as *Gyalopion canum* and *Lampropeltis triangulum* are apparently rare or uncommon today in riparian habitats at the lower, xeric edge of their ecological ranges in Black Gap but are more common at higher elevation in the mountains or on the Edwards Plateau.

Holocene.—The vegetation and climate of Black Gap went through several stages in the Holocene before the modern regime was established. The disappearance of *Pinus remota* and other mesic woodland plants about 11,000 yr B.P. marked the end of the glacial period. At 10,280 yr B.P. a xeric oak-juniper woodland with *Agave lechuguilla* and *Dasylirion* sp. grew around the cave. Pollen records from cave sediments from near the mouths of the Devil's and Pecos rivers (Bryant and Holloway, 1985) indicate that *P. remota* survived for several thousand years in more mesic eastern areas after its disappearance from Chihuahuan Desert. Middle Holocene (8230 to 4200 yr B.P.) and late Holocene (1160 yr B.P.) Maravillas middens record a rich desert grassland with many of the modern plants near the cave. The samples contained a few desert plants now restricted to xeric alluvial terraces well below the cave. The modern chino grass desertscrub on the slopes is apparently a little more mesic than it was a few thousand years ago.

At the beginning of the present interglacial, only three animals disappeared from the Maravillas Canyon herpetofauna. *Geochelone wilsoni* became extinct, *Gopherus flavomarginatus* retreated south into Mexico, and *Gerrhonotus liocephalus* found refuge in woodlands isolated mountains including the Chisos Mountains and Del Norte mountains, Sierra del Carmen, possibly the Sierra del Caballo Muerto, scattered desert relictual areas, and on the Edwards Plateau. Other reptiles including *Crotaphytus collaris, Gyalopion canum, Hypsiglena torquata, Lampropeltis mexicana, L. triangulum, Phrynosoma modestum,* and *Sonora semiannulata* remained in the area as habitats shifted from ice age pinyon-juniper-oak woodland to more modern desertscrub communities. Reptiles such as *Gerrhonotus liocephalus* and *Elaphe bairdi* have been isolated in the Chisos Mountains for at least 9,000 years with no obvious genetic changes. Many other southwestern reptiles have isolated montane populations that have not evolved noticeably, or have differentiated into distinctive demes not recognized as subspecies, although the ranges have been isolated during each of the 15-20 Pleistocene interglacials (Van Devender et al., 1992). Divergence in these montane populations may have occurred in the Holocene, the first interglacial after dispersal, or accumulatively in all subsequent interglacials. Evolutionary changes in species, subspe-

cies, and local demes in response to the many, dramatic climatic fluctuations in the two million years of the Pleistocene have been modest or minimal. Isolation of populations should not be weighted heavily as taxonomic characters considering geographic ranges have been dynamic with gene flow during each glacial periods.

Gymnogyps californianus (California condor) was an interesting member of the early Holocene fauna of Maravillas Canyon. A tandem accelerator radiocarbon date on bone from the humerus (UALP 17098) suggests that it survived in the Black Gap until 10,215 yr B.P. (Van Devender, 1990) while most records for the Grand Canyon of Arizona are older than 11,000 yr B.P. (Emslie, 1987). Bones of *G. californianus* previously reported from Mule Ear Peak Cave in Big Bend National Park (Wetmore and Friedman, 1933) were radiocarbon dated at 12,580 yr B.P. (Emslie, 1987).

A number of species appear in the Maravillas Canyon record for the first time in the Holocene including *Crotalus atrox* and *Rhinocheilus lecontei* in the early Holocene, *Arizona elegans, Coleonyx brevis, Elaphe subocularis, Sceloporus merriami, Tantilla* cf. *hobartsmithi,* and *Uta stansburiana* in the middle Holocene, and *Bufo* cf. *punctatus, Crotalus* cf. *lepidus,* and *Scaphiopus couchi* in the late Holocene. Most of the species could have been in the area earlier but were missed in modest midden samples.

The Klein Cave fauna in Kerr County (340 km ENE) yielded bones of *Arizona elegans, Gerrhonotus liocephalus, Hylactophryne augusti* (barking frog), and *Syrrhophus marnockii* (cliff frog; Parmley, 1988a) indicating that some western and Mexican animals had already dispersed onto the Edwards Plateau by 8000 years ago. At Schulze Cave on the Edwards Plateau, *Elaphe bairdi* displaced *E. obsoleta lindheimeri* (Texas ratsnake) in the Holocene (Parmley, 1986a). The final reduction and fragmentation of ranges of species such as Big Bend reptiles as *Agkistrodon contortrix, Coleonyx reticulatus, Lampropeltis mexicana, L. triangulum,* and *Tantilla rubra* was probably in the last 4,000 years or less.

Paleoecology.—As grasses, especially *Bouteloua ramosa,* recovered from the major drought of 1949 to 1957, the lizards in Chihuahuan desertscrub in Black Gap and Big Bend National Park shifted their relative abundances and microhabitat distributions (Degenhardt, 1977; Milstead, 1977). Similar changes have probably occurred continuously in Maravillas Canyon over the last 27,820 years as the local vegetation shifted from ice age pinyon-juniper-oak woodlands to postglacial oak-juniper woodland, desert grassland, and Chihuahuan desertscrub. The overall stability in the local herpetofauna with relatively few additions to the fauna from the north or east during the Wisconsin glacial is especially interesting. *Gopherus flavomarginatus* is the only animal that formerly lived in habitats no longer occupied today. *Gerrhonotus liocephalus* is the only animal that is mostly excluded from lowland habitats today.

The explanation for the habitat stability is equally interesting. In the Big Bend, climate and biota are strongly zoned along an elevational gradient with hot, dry deserts in the lowlands and mesic woodlands on the mountaintops: i.e., the environmental gradient typical of much of the southwestern United States and northern Mexico. The herpetofauna is variously arranged along this gradient with some animals more or less restricted to desertscrub, desert grassland, montane woodlands, or some combination of habitats. However, from the Chihuahuan Desert east to the Gulf of Mexico rainfall increases as elevation decreases. The limestone lowlands paralleling the Rio Grande in Terrell and Val Verde counties east of the Big Bend support a rich mixture of Chihuahuan desertscrub, Great Plains grassland, Edwards Plateau woodland, and Tamaulipan thornscrub plants. In this equable climate and mixed biota, the desert animals of the Big Bend live in woodlands. The late Wisconsin fauna of Black Gap was probably living in similar equable woodland environments. In general the herpetofauna of the Big Bend has been more conservative than the flora, especially long-lived trees, shrubs, and succulents, in response to a major glacial/interglacial climate change.

Biogeography and Evolution.—The faunal relationship between the Edwards Plateau and the Big Bend with elements from the Balconian, Chihuahuan, and Sierra Madrean biotic provinces

(Devine, 1969) has been established throughout the Pleistocene with westward movements during glacials and eastward movements during interglacials. Milstead (1960) discussed the distributions of 14 species of mesic amphibians and reptiles with relict populations in Trans-Pecos Texas, many between the Pecos River and the Davis Mountains, that indicate wetter climates in the past. The presence of endemic taxa including *Lampropeltis mexicana blairi, Syrrhopus marnockii* (cliff frog), *Tantilla rubra diabola,* and *Thamnophis cyrtopsis ocellata* centered on the southern Edwards Plateau and adjacent Coahuila argues that the area has supported a unique environment for a long time.

The presence of Chihuahuan Desert and Sierra Madrean animals in late Wisconsin woodlands in Maravillas Canyon leads to some interesting conclusions. The Pleistocene with its cool climates and enormous continental glaciers began about two million years ago. The Wisconsin glacial age was previously thought to be the last of four glacial/interglacial cycles. Recent studies of isotopic ratios and planktonic fauna from deep sea cores has demonstrated that there were actually 15-20 cycles in the last 1.8 million years (Imbrie and Imbrie, 1979). Moreover, the glacial periods were about 100,000 years in length compared to 10,000-20,000 years for interglacials. In this context, woodland vegetation and glacial climates with mild winters and cool summers may have been in Black Gap for more than 90% of the last two million years of the Pleistocene (Van Devender, 1986). Although the modern environments may be typical of less than 5% of the Pleistocene, they are probably similar to the original late Miocene Chihuahuan Desert (Axelrod, 1979; Van Devender, 1986; Morafka, 1988)

Because *Gerrhonotus liocephalus, Gyalopion canum, Tantilla rubra,* etc. were present in Maravillas Canyon during the last glacial, the Sierra Madrean component of the Big Bend herpetofauna probably predates the Pleistocene. Most species were not, as is often inferred, displaced southward to Mexican refugia during glacials. Much of the evolution of the Chihuahuan Desert component of the fauna was probably the result of the uplifts of the Sierra Madre Oriental and Sierra Madre Occidental creating the arid Mexican Plateau in the middle Miocene. Axelrod (1979) places the formation of the deserts of North America in general at five to eight million years ago in the latest Miocene. The differentiation of *Coleonyx reticulatus, Elaphe subocularis, Gyalopion canum, Lampropeltis mexicana alterna, Sceloporus merriami,* and *Tantilla rubra cucullata* from their southern tropical ancestors probably dates to this time. *Agkistrodon contortrix pictigaster* and *Elaphe bairdi* are apparently derived from eastern species while *Lampropeltis triangulum celaenops* is close to Great Plains-Rocky Mountains stock.

A number of Chihuahuan Desert reptiles suggest past connections with the Sonoran and Mohave deserts in Arizona, California, Sonora, and Baja California. The east-west faunal similarities reflect several different situations. Many shared species including *Arizona elegans, Crotalus atrox, Pituophis melanoleucus, Rhinocheilus lecontei,* and *Sonora semiannulata* are simply widespread in the warm deserts and semi-arid grasslands of North America. In these widespread taxa, the distribution of subspecies often reflects evolution of infraspecific taxa subsequent to the formation of the modern biotic provinces. Thus regional subspecies may be millions of years old and not newly-evolved, ephemeral entities.

In the Pliocene, *Gopherus flavomarginatus,* or its close relative *G. huecoensis,* was widespread from Texas to Arizona and Sonora (Bramble, 1982; Morafka, 1988). As the warm, wet subtropical climates of the Pliocene gave way to glacial climates in the early Pleistocene about two million years ago, fewer fossils were preserved in sediments. In the Phoenix Basin of Arizona, populations apparently persisted in the present Sonoran Desert into the late Pleistocene, perhaps to the end of the Wisconsin (Archer, 1989). Although the Maravillas Canyon Cave record does document a northward range extension in the late Wisconsin, the absence of more northerly fossils suggests the Chihuahuan and Sonoran populations were widely disjunct. In this case, the glacial climates separated Chihuahuan and Sonoran populations that did not speciate, but has been reduced to a local endemic in the Bolson de Mapimi.

The uplift of the Continental Divide and the initiation of glacial climates about two million years ago split the ranges of other reptiles into eastern and western populations (a "vicariance event") that evolved into new species. Examples of such east-west species pairs include *Coleonyx brevis/ C. variegatus, Phrynosoma modestum/ P. platyrhinos,* and *Elaphe subocularis/E. rosaliae. Phrynosoma modestum* is an interesting example of paedomorphism, the evolution of a new species from immature stages of another species. Small *P. platyrhinos* are very similar to more mature *P. modestum.* Montanucci (1987) concluded from a cladistic analysis that *P. modestum* and its sister species, *P. platyrhinos,* evolved from a common ancestor during Pleistocene glacials. In fact, *P. modestum* only differed in characters that reflect maturation at small size (loss of angular bone in most individuals, enlarged gular scales, and enlarged projecting scale at the base of the parietal horn) with a single new state (relatively enlarged postlabial scales). The elaborate ornamentation of the surfaces of the dentary and outer skull bones also appears to us to be derived. *P. platyrhinos* easily could be the ancestor, not the sister, of *P. modestum,* an inference inhibited by the geometry of cladograms and the assumption of the extinction of ancestors.

Elaphe subocularis in the Chihuahuan Desert and *E. rosaliae* in the Sonoran Desert probably also represent species that evolved as Pleistocene climates disrupted a continuous east-west range. We find the arguments to elevate *E. triaspis* to the genus *Senticollis* (Dowling and Fries, 1987) and *E. rosaliae* and *E. subocularis* to *Bogertophis* (Dowling and Price, 1988) unsatisfying and prefer to keep them in *Elaphe.* While the hemipenes of *E. triaspis* appear to be unique and derived, the ranges of scale characters presented (divided anal scale, keeled dorsal scales, total dorsal scales, total ventral scales) overlap with values for *Pituophis* and other *Elaphe,* especially the Mexican species *(flavirufa, phaescens, rosaliae,* and *subocularis).*

Bogertophis was principally characterized by the presence of a row of lorilabial scales and increased numbers of diploid chromosomes (38 in *rosaliae,* 40 in *subocularis).* Most of the other characters examined were variable in other Elaphe and not unique to *Bogertophis.* Rather than *Senticollis* and *Bogertophis* being unique genera not closely related to any other North American colubrids, we view them as well-differentiated species of *Elaphe* that could be grouped in one or two subgenera. The relationship between the three species needs further study considering the vertebral characters discussed above, lack of sexual dimorphism in scutellation (Dowling and Price, 1988), the similar pattern ontogeny (barred juveniles to patternless adults) in *E. triaspis intermedia* and *E. rosaliae,* and the slender bodies of subadult *E. subocularis* and adult *E. triaspis.* Rather than two genera with unknown affinities to other North American colubrids, the species probably represent radiation from a tropical ancestral *Elaphe* as the Sierra Madres were uplifted *(E. triaspis),* the deserts developed (ancestral *E. rosaliae - E. subocularis),* and the beginning of the Pleistocene *(E. rosaliae* and *E. subocularis).*

The third type of east-west species pairs reflect the evolution of similar species from common subtropical ancestors. The vicariance event in this case would be the uplift of the Rocky Mountains and Sierra Madres in the early-middle Miocene restricting tropical forests to lowlands on both coasts of Mexico and increasing aridity on the Mexican Plateau and in the Sonoran Desert lowlands. Many of the behavioral, physiological, and morphological adaptations of amphibians and reptiles to dry seasons in tropical forests preadapted them to the deserts that emerged from them. Ancestral populations in "old" habitats would rarely, if ever, be affected by the selection pressures responsible for creating new species in isolated populations in "new" habitats. Modern species are the results of "natural selection past" and have been rigorously maintained through strong, pervasive, continuous stabilizing selection pressures. Most species have responded to repeated climatic changes with simple shifts in range and not speciation. For example *Coleonyx reticulatus* in the Chihuahuan Desert and of *C. switaki* in the Sonoran Desert were both derived from a subtropical ancestor (very close to *C. mitratus;* Grismer, 1983).

The helodermatid lizards provide an inter-

esting variation of this scenario. The family has an extensive fossil record in the early Tertiary of North America including the extinct genera *Euheloderma* and *Lowesaurus* (Pregill et al., 1986). The living species of *Heloderma* include *H. suspectum* (Gila monster) in the eastern Mohave and Sonoran deserts in Arizona, California, Nevada, Utah, and Sonora, and *H. horridum* (Mexican beaded lizard) in tropical forests on the western coast of Mexico as far north as Sonora (Brown and Carmony, 1991). The substantial morphological differences, notably the more elongate body, limbs, and tail of *H. horridum,* and the overlaps of their geographic ranges and habitats in southern Sonora suggest that the two species evolved in isolation. It is difficult to envision an adequate barrier to separate them as the Sonoran Desert developed out of dry tropical forests in northwestern Mexico (Axelrod, 1979). *Heloderma texanum* was described from early Miocene sediments in the Big Bend of Texas (Yatkola, 1976). This species and *H. horridum* likely evolved from a common tropical ancestor as the Sierra Madre Occidental were uplifted in the middle Miocene. *H. texanum* developed adaptations to aridity as the Chihuahuan Desert formed on the Mexican Plateau, subsequently dispersed to the northwest across the Continental Divide as part of Morafka's (1977a) Mohavia. Continued uplift of the Mexican Plateau and the Rocky Mountains and the onset of glacial climates in the Pleistocene eventually lead to the extinction of *H. texanum;* western populations survived as *H. suspectum. H. suspectum* and *H. horridum* then came into contact for the first time as independently-derived species. In this case, a typical Sonoran Desert animal likely evolved in the present Chihuahuan Desert and not *in situ* as aridity developed in the Miocene. The northern Mohave Desert *H. s. cingulum* may well be the more primitive subspecies.

The genus *Lampropeltis* is an excellent example of a taxon with a complicated phylogeny. In his 1921 monograph, Blanchard placed *L. alterna* close to *L. pyromelana* but not *L. leonis* as suggested by Brown (1902). *L. mexicana* was thought to be a unique form with characters of both *L. calligaster* and *L. triangulum* while *L. ruthveni* was closest to *L. multicincta.* After further taxonomic study, some of these inferred relationships were found to reflect color pattern convergence. Gehlbach and Baker (1962) placed *alterna* and *leonis* into *L. mexicana* along with *blairi, greeri,* and *thayeri.* Gartska (1982) considered *ruthveni* closely allied to *L. mexicana* as well. Webb (1961) considered *mexicana* to be the most primitive *Lampropeltis* and derived the *L. calligaster-getulus* and *L. triangulum* group (including *L. pyromelana* and *L. zonata)* from them, mostly because of color pattern similarities between *leonis* and *L. calligaster.*

We propose an alternative model based on characters in combination with historical biogeography. *L. calligaster* is the most primitive kingsnake based on pattern and vertebral similarities with *Elaphe* (shared primitive characters). *L. getulus* was an early derivative with new characters (black coloration, lower neural spine) that spread across the continent in the early to middle Miocene. Older subspecies survived on the east and west coasts as new subspecies developed in the mid-continent grasslands *(splendida)* and Sinaloan thornscrub *(nigritis). L. triangulum,* another early *L. calligaster* derivative, spread widely across the continent, south into central America, and later into South America. Williams (1988) recognized 25 subspecies of *L. triangulum* in different geographic areas. Within this complex, subspecies found in lowland tropical habitats *(annulata, nelsoni, oligozona, polyzona,* etc.) are less-derived than subspecies found in more recent habitats including the Andes *(andesina),* the Sierra Madres *(arcifera, cambelli, dixoni, smithii),* the Great Plains *(gentilis, multistriata),* and Rocky Mountains-Great Basin *(celaenops, taylori). L. zonata* is a variable western complex of seven subspecies that probably evolved from *L. triangulum* (Zweifel, 1952).

An intriguing idea on the ancestry of *L. mexicana* is suggested by (1) Blanchard's (1921) observation that *ruthveni* was closest to *L. z. multicincta,* (2) apparent sympatry of *ruthveni* and *L. t. arcifera* in Michoacan in the highlands of southern Mexico (Gartska, 1982; Williams, 1988), and (3) high fertility in captivity between *L. mexicana, L. pyromelana,* and *L. zonata* but not *L. triangulum* (S.F. Hale and F. Retes, pers. comm., 1987). *L. mexicana* could be derived from *L. zonata*

isolated on mainland Mexico by the rift of the Baja California Peninsula about 12 million years ago (Axelrod, 1979; Murphy, 1983), and the subsequent uplift of the Sierra Madre Sur. Other subspecies of *L. mexicana* evolved with the uplift of the Sierra Madre Oriental *(thayeri),* Sierra Madre Occidental *(greeri),* and the Chihuahuan Desert *(alterna, blairi). L. pyromelana knoblochi* and *L. p. pyromelana* probably represent independent northern extensions of *L. m. greeri* into temperate forests in Chihuahua, Arizona, New Mexico, Utah, and Nevada. Specimens from the break in their ranges in northern Durango or southern Chihuahua could demonstrate both to be subspecies of *L. mexicana.* We view *L. mexicana* and its descendents, especially *L. m. alterna* and *L. pyromelana,* as the most derived taxa in *Lampropeltis* and not the most primitive.

Thus, the six species of *Lampropeltis* currently recognized are the results of different evolutionary radiations at different times during the modernization of the North American landscape. Taxa such as *L. calligaster rhombomaculata, L. getulus getulus,* and *L. triangulum annulata* that live in old temperate broadleaf or tropical forest habitats certainly could be older and more primitive than taxa such as *L. c. calligaster, L. g. splendida, L. t. gentilis, L. t. cambelli, L. m. alterna* or *L. m. greeri* found in younger, derived desertscrub, grassland, or montane forest habitats. Within widespread polymorphic species such as *L. getulus, L. triangulum,* and *L. mexicana,* the distributions of subspecies reflect regional biogeographic provinces established in the Miocene.

From a historical perspective, the survival of ancestral populations to coexist with their descendants is probably the typical situation in the North American herpetofauna. In the above evolutionary model, ancestors could survive at eight or nine levels in the phylogeny: e.g., *calligaster* → *getulus* and *triangulum* (→ *zonata*→ *ruthveni* → *mexicana*→*thayeri*→*blairi* and *greeri* [→*alterna, knoblochi,* and *pyromelana* [[→ *infralabialis]]).* Behavioral or genetic barriers to natural interbreeding were probably established long ago between *calligaster, getulus,* and *triangulum,* and at secondary contacts between *triangulum* and *mexicana* in Mexico and Texas, and *pyromelana* in Arizona and Utah. There is no reason to think that, as is assumed in most cases in the cladistic phylogenetic methodology (Wiley, 1981; Frost et al., 1992)), that ancestral species become extinct as new ones evolve. Because species are as stable and long lived as the fossil record indicates, the most closely related species are ancestor and descendent(s), which will always have greater genetic similarity and fewer character changes than paired descendents of an extinct ancestor (Van Devender et al., 1992).

Although models such as this are speculative, they present evolutionary hypotheses based on the environmental history of North America, and the realization that evolutionary rates in each lineage are different. Assumptions of ancestor extinction and the equality of all characters in cladistic analysis are also speculative, but have little if any historical support and conflict with most theories of speciation. The equal use of all characters as potential species characters and the disregard for the degree of divergence in atemporal analyses magnifies insignificant and convergent characters unnecessarily to appear more "scientific" or to give the appearance of greater diversity of species (Collins, 1991). The taxonomic implications of uncritical acceptance of cladistic reconstructions of phylogenies are profound. Donoghue (1985) recommended that the biological species definition be replaced by monophyletic species where a population should be recognized as a species if it has ***any*** discernible difference from others. Collins (1991) raised 55 allopatric, differentiated subspecies of North American amphibians and reptiles to species without character analyses following the cladistic philosophy of Frost and Hillis (1990). Each species and subspecies in the current literature represents not only the results, conclusion, and opinion of a taxonomist, but a hypothesis about the relationships of one taxon to others. This body of knowledge should not be lightly cast aside in favor of new taxonomies based on a methodology that cannot separate families from subfamilies, genera from subgenera, species from subspecies, and offers little new, unambiguous knowledge in return. Studies of the evolution and historical biogeography of southwestern amphibians and reptiles should embrace

the fossil record and paleoenvironmental reconstructions incorporating them into reconstructions, and not accept unfounded, non-evolutionary assumptions in their analytical methodology. In our view, testing evolutionary models or phylogenies based on historical biogeography has the best chance of producing realistic and reasonable, but not necessarily the most "parsimonious," phylogenies.

ACKNOWLEDGEMENTS

We thank Jim Scudday and W. Eugene Hall for help with field work. R. Wayne Van Devender and I discovered the Big Bend and its fascinating fauna together in the 1960's, and began a lifelong dialogue on its fauna, natural history, biogeography, and evolution. Hugh K. McCrystal, Rick Green, and Dennie Miller provided invaluable information on the distribution of Big Bend herps. Dave Morafka's review was insightful and stimulating. Ernest Lundelius and Wann Langston compared the *Geochelone wilsoni* specimen with the type material in the Texas Memorial Museum. Greg Pregill, San Diego Natural History Museum, arranged the loan of an *Elaphe rosaliae* skeleton. Stephen F. Hale and R. Wayne Van Devender provided skeletons of *E. bairdi, E. flavirufa,* and *E. rosaliae*. Amadeo M. Rea, San Diego Natural History Museum, identified the *Gymnogyps californianus* humerus. Charles H. Lowe, Jr., allowed us to examine *Elaphe triaspis* in the Herpetological Collection in the Department of Ecology and Evolutionary Biology, University of Arizona. Collecting permits were provided by the Texas Parks and Wildlife Department. Field support in Black Gap was provided by Jerry L. Cooke. Funds were provided by National Science Foundation Grants DEB 80-22773, and BSR 84-00797, to T.R. Van Devender. Helen Wilson drafted the figures. Gene Hall photographed the bones in Fig. 5. Jean Morgan processed the manuscript.

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