

### PART III. HISTORICAL BIOGEOGRAPHY OF THE BOLSON TORTOISE

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#### INTRODUCTION

How Bolson tortoise populations came to exist only in the Mapimi bolsons and why they are now confined here remains unanswered. Since related tortoises in the genera *Styemys* and *Gopherus* have the most complete fossil record of any extant North American reptile group (Auffenberg, 1971, 1976; Auffenberg and Franz, 1982; Brattstrom, 1961; Messing, 1986), paleontological evidence may yield insights into their evolution and biogeography. While even this substantial record does not provide unambiguous indications of generic (or species group) divergences, or species origins, its closing chapters, the late Wisconsin and Holocene epochs, do provide a detailed and sequential paleoecology for the northern Chihuahuan Desert region. That sequence provides us with an unusually good opportunity to evaluate competing hypotheses about the demise of North America's megafauna, using the declining population of our largest surviving "temperate" terrestrial reptile, the Bolson tortoise, as a test case.

#### THE TERTIARY PERIOD

Late Tertiary environmental changes, especially the repeat orogenies of the Miocene Epoch, may have induced differentiation of the more specialized and fossorial *Gopherus* from a generalized *Xerobates* stock. Bramble (1982) assembled a transformational series of characteristics from head (especially inner ear), neck and forelimb morphology that demonstrated the more fossorial specialization of true "*Gopherus*," its differentiation from the more generalized genus "*Xerobates*" and its special adaptations and historical affinities for semiarid sandy substrates. Others contend that *Xerobates* are not a natural sister group—just primitive *Gopherus*. In light of such criticism, we shall treat *Xerobates* as synonymous with *Gopherus*, employing only the latter term.

Bramble (1982) indicated that the Miocene differentiation of true "*Gopherus*" occurred on the Great Plains and the adjacent emerging Mexican Plateau. Cooling trends, combined with increased aridity and the dilation of seasonal temperature extremes, fostered the development of sandy, well-drained soils. The appearance and proliferation of *Gopherus* was correlated with development of these soils. Axelrod (1950, 1958, 1979; Axelrod and Raven, 1975) also noted the expansion of semiarid vegetation during this same period (originating in late Oligocene and earlier). Morafka (1978) and Van Devender (1986) recognized parallel modernization in the Miocene flora and herpetofauna. During the early Tertiary, a generalized track of semiarid biota began to coalesce into the Madro-Tethyan Geoflora (Axelrod and Raven, 1975). This "track" established an intermittent northeastern American connection with Eurasia and included the now subtropical helodermatid lizards (Hoffstetter, 1957; Stevens et al., 1977).



A second subordinate track of more arid-adapted biota separated from the Madro-Tethyan Geoflora during Mio-Pliocene times. This derivative system involved both sclerophyll and grassland vegetation and may have reached peak aridity (possibly comparable to modern desert conditions) in the early Miocene (Bramble and Hutchinson, 1980; Bramble, 1982; Hutchinson, 1982), late Miocene (Van Devender, 1986) or late Pliocene (Morafka, 1978). The confusion regarding the arid peak chronology stems from the differing empirical bases used, and from a recent revision of the Mio-Pliocene boundary from 11 My to 5.5 My. This latter change placed many formerly Pliocene records within the revised Miocene time (Van Couvering, 1978). This track approximates the Mojavia Geoflora (Axelrod, 1958) in terms of chronology, geography, and ecology.

Southwestern landscapes and climates underwent a second profound modernization. On the Pacific Coast, Baja California emerged (Gastil et al., 1975) while the orogeny of the Coahuila Folded Belt (and the Sierra Madre Oriental) contributed not only to the development of the Mexican Plateau, but also to the recession of the Mississippi Embayment and its associated maritime climates. Orogenic activities in the intervening continental interior accentuated rain shadow effects of the Rocky Mountains upon the Great Plains, and volcanic extrusives contributed significantly to the development of the Sierra Madre Occidental in Mexico (Christiansen and Lipman, 1972; McDowell and Keizer, 1977). Pliocene and early Pleistocene coolings combined with repeated faulting and uplift of existing blocks to separate the modern deserts of North America (Morafka, 1978; Axelrod, 1979).

Tertiary Mojavia was already a temperate, semiarid complex, including thorn scrub, chaparrals and savannas, eventually becoming a desert in the south. These ecosystems were species rich compared to current habitats, and less characterized by single dominants such as the creosote bush (*Larrea divaricata*), which was documented in North America no earlier than 18,000 yr BP. While *Larrea*'s first continental appearance is unknown, its continuous modern occupation of the northern Chihuahuan and Sonoran deserts extends back only some 5000 years (Van Devender et al., 1987). Throughout Mojavia, climates were more mild and more precipitation occurred, even between rainy seasons. The Mojavia landscape was probably an edaphic patchwork of scrub and grasslands grossly similar to current vegetation in the Bolson de Mapimi. The flora and reptile fauna were dominated by extant species or species groups (Morafka, 1978; Van Devender, 1986). From this general region, California to Kansas and south to the Mexican Plateau, the Late Tertiary herpetofauna included modern genera such as the anurans *Bufo* and *Scaphiopus*, the lizards *Gerrhonotus*, *Sauromalus*, *Heloderma*, *Ctenosaura*, *Phrynosoma*, *Crotaphytus*, *Sceloporus*, and possibly *Dipsosaurus*, and the snakes *Nerodia*, *Coluber*, *Heterodon*, *Pituophis*, *Agkistrodon*, *Sistrurus*, and *Crotalus* (Gehlbach, 1965; Auffenberg and Milstead, 1965; Brattstrom, 1955, 1967). The chelonian genera *Terrapene*, *Trionyx*, *Chrysemys*, *Kinosternon*, and *Geochelone* were also represented. The late Tertiary of Mojavia not only included a predominantly modern herpetofauna, but also a shift from browsing to grazing dentition in mammalian herbivores (Stevens et al., 1977; Woodburne et al., 1974). This latter shift was probably a response to the coalescence of patchy, local grassland into major prairies and open woodlands during the Miocene. This transition was paralleled by the shift in jaw morphology (*os transilens* development) associated with the evolution of *Gopherus* from "*Xerobates*" (Bramble, 1971, 1982).

The expanding and increasingly arid communities of Mojavia created an arid



midcontinental track into which diverse species became entrained at different times. Many taxa, including *Gopherus*, probably evolved *in situ* as more arid circumstances overtook them. Farther north, suitable habitats of early Tertiary times in the Great Plains underwent cooling trends, which likely caused the extinction of tortoises (Auffenberg, 1969, 1974).

Bramble (1982) suggested that virtually all Tertiary records for true *Gopherus* were from east of the Continental Divide, while "*Xerobates*" during this time period was from the west. He further suggested that members of the two groups have never been found in the same deposit, even during the late Tertiary Period when true *Gopherus* (Bramble's genus) may have extended west to western Arizona and *G. agassizii* (Bramble's *Xerobates*) occurred east to Texas and New Mexico. Auffenberg (1974) however, reported *G. canyonensis* from the Pliocene (Blancan) of southeastern Arizona. Currently, *Gopherus flavomarginatus* occurs within 150 km of *Gopherus berlandieri* in central Coahuila. If the two genera were once sympatric, different substrate preferences may have segregated the two stocks into microallopatry, producing a pattern of local complementarity. The upland distribution of *Gopherus agassizii* in the eastern Sonoran Desert today may have been reinforced by past coexistence with *Gopherus flavomarginatus*, which seems better adapted to valley floors and margins than does *G. agassizii*. In contrast, historically allopatric *G. agassizii* populations in the Mojave Desert, while topographically widespread, have no particular affinity to upland habitats (Luckenbach, 1982; Jarchow, personal communication).

Two critical biogeographical questions may be addressed in the Tertiary record. First where, and second, when did the speciation of *G. flavomarginatus* occur? While the fossil record reveals an apparent time and setting for the differentiation of the specialized *polyphemus*-*flavomarginatus* group from more generalized antecedents, it yields no such clear pattern for the speciation of *Gopherus flavomarginatus*. Temporally, no unambiguous record for the species exists prior to the late Pliocene Period of West Texas (for the putative conspecific *G. huecoensis*: Auffenberg, 1974, 1976). In this instance, negative data may in fact allow the possibility of a relatively recent history for *Gopherus flavomarginatus*. Late Pliocene fossils from the same region yield *Gopherus pertenuis*, *G. hexagonatus*, *G. laticaudatus*, and *G. canyonensis*. All of these taxa appear to be closer to the extant Florida gopher tortoise *G. polyphemus*, and several may be conspecific with the latter. Meylan (1981) suggested a central Texas-Florida connection between semi-arid adapted reptiles (*Crotalus atrox* and *Crotalus adamanteus* being the particular example) was sustained throughout much of the Pleistocene. During late Wisconsin time oak-hickory-southern pine forest dominated the Gulf Coast Plain (Delcourt and Delcourt, 1985). However, during the short, but frequent, interglacials pine parklands may have circumscribed the northern rim of the Gulf of Mexico, reestablishing this track for semiarid reptiles through glaciopluvial intervals. Van Devender (1986) has documented that similar grasslands occurred on the Mexican Plateau and adjacent West Texas. Therefore, the question remains as to how *G. flavomarginatus* separated from a *polyphemus*-like sister species (*Gopherus canyonensis*) to the east. Sympatric speciation is unlikely, especially in light of the extremely conservative karyotypes of chelonians in general and testudinids in particular (Dowler and Bickham, 1982). Assuming allopatric speciation the late Tertiary uplift, possibly Trans-Pecos Texas ranges (the Guadalupe, Davis and Chisos in the Rio Grande Rift of Baldrige et al., 1984), extending southeast through the Coahuila Folded Belt, and terminating in Sierra Madre



Oriental, might have separated the species. This diagonal series of ridges, established earlier in the Tertiary, may have been uplifted sufficiently to isolate *Gopherus flavomarginatus* from its eastern congeners. Geological time estimates would place some of these uplifts approximately two to three million years ago. Early Pleistocene continuation of these uplifts, and parallel orogenic activity in the Saladan region may have reduced its maximum Pliocene range by 30–50%. Confounding this simple scenario is the presence of late Tertiary *G. canyonensis* in Arizona, far to the west of the alleged vicariant division and antedating its occurrence. Perhaps middle Miocene orogenic activity involving the same landscape was responsible, though both these scenarios are highly speculative.

## THE QUATERNARY PERIOD

### *The Pleistocene Epoch*

Local extinction, fragmentation, and limited dispersal characterize the Quaternary history of the gopher tortoises, unlike the vigorous speciation and expansion of the Tertiary. However, few of the Pleistocene fossils are assigned absolute dates. Available data inscribe only possible distribution, and many have recently been taxonomically reassessed (King and Saunders, 1986). The situation is further confused by uncertain taxonomic relationships of several closely related fossil *Gopherus*. The Pleistocene section summarizes the geographical distribution of *G. flavomarginatus*, describes the paleoecological setting for this distribution, accounts for the Pleistocene and Holocene ecological changes that led to the fragmented modern distribution, and addresses the issue of late Pleistocene mass extinction of the North American megafauna.

Middle to late Pleistocene *G. auffenbergi* (= *berlandieri*) have been reported from Aguascalientes, Mexico (Mooser, 1972), and fossils resembling *G. canyonensis* and/or *G. flavomarginatus* from Phoenix and El Mirage (Bramble, 1982; T. Van Devender, personal communication). D. Bramble (personal communication) observed that the Phoenix fossils appear to be late Pleistocene (Rancholabrean?), based upon their stratigraphic position. Auffenberg (1969) described the Pleistocene range of *G. flavomarginatus* as almost all of the Mexican Plateau, extending at least from southern New Mexico south to Aguascalientes. He further noted a specimen from the middle Pleistocene of Kansas that was structurally similar to both *G. flavomarginatus* and *G. polyphemus*. Maximal distribution was probably achieved in the late Pliocene and was reduced progressively in the first half of the Pleistocene by orogeny in the south. Little is known about the paleoecology of the sites from which these fossils have been reported.

In light of the Pleistocene range of *G. flavomarginatus*, the paleoecology of the Mexican Plateau and adjacent basin and range topography, especially the northern and western parts, will be emphasized. It is also important to note two recent revisions in Quaternary perspectives that greatly influence this account. First, Imbrie and Imbrie (1980), based largely on oxygen 16/18 ratios, proposed that the Pleistocene was subject to 15–20 glacial pulses. Each episode lasted about 90,000 years and had about 10,000 years of interglacial stage. This discovery not only increases the number of Pleistocene alternating climatic intervals in North America to 15–20, but also reduces interglacial episodes to a maximum of 10% of the last two million years, and more likely to 6% (Van Devender, 1986).

The second revision of Pleistocene perspective results largely from analysis of late Pleistocene packrat (*Neotoma*) middens (Van Devender, 1976, 1977, 1978,



1986; Van Devender and Mead, 1978; Van Devender and Spaulding, 1979). Data from middens extending across several North American deserts document that downslope displacement of piñon-juniper woodland due to increasingly cool climate was not universal, nor did a reciprocal replacement of more xeric-adapted species always occur. These discoveries challenge simplistic models that invoke unified and exclusionary displacements of tightly coevolved Pleistocene communities. The glaciopluvial communities described by Van Devender often bore more resemblance in organization to contemporary tropical communities, manifest by high diversity, the presence of more southern taxa, and intercommunity transitions characterized by gradual climatic gradients formed by species specific changes, not by narrow discrete ecotonal boundaries. Thus, these glaciopluvial assemblages may well represent the "norm" for the Quaternary. However, Brackenridge (1978) and Spaulding and Graumlich (1986) questioned this scenario for equability, particularly for the more western (Nevada) desert regions. Modern associations are best treated as temporary and probably short-lived interglacial anomalies. An ecological characterization of the glaciopluvial Mexican Plateau (north of the Transvolcanic Province) is completed by examination of the major, current biotic subprovinces of the Chihuahuan Desert (Morafka 1978): the northern Trans-Pecos (Rio Grande drainage), the central Mapimian, and the southern Saladan.

Pollen analyses from New Mexico (Hafsten, 1961) reveal the fossil record in mild interglacial Wisconsin times. These analyses, when combined with midden records, span the longitudinal axis of the Trans-Pecos Subprovince of the northern Chihuahuan Desert. Cool, moist grasslands, either treeless or with poorly developed pine "parkland" dominated lower elevations (Llano Estacado) of interglacial (33,500 to 22,000 years ago) with vegetation of spruce (*Picea*) and pine (*Pinus*) woodlands at least in upland situations, accompanied by juniper-oak-piñon woodlands and grasslands in lower basins. End-Pleistocene habitats (15,000 to 10,000 years ago) continued to sustain piñon woodlands and oak/grass. Cold scrub (*Artemisia*) probably locally dominated dry slopes and dunes (Harris, 1978) and remained serially dominant even into early Holocene times at least in the northwestern Trans-Pecos extending south specifically to the Hueco Mountains (Texas) according to Van Devender et al. (1987). Evidence from midden and fossil data generally corroborate the reconstruction of glacial Trans-Pecos habitats as cooler in the summer, with more abundant precipitation evenly distributed throughout the year, and less extreme summer and winter temperatures than found today.

The Pleistocene history of the Mapimian Subprovince is based primarily on a pair of midden localities at the eastern edge of the Mapimi bolsons, and a pollen history from Cuatro Ciénegas at the eastern edge of the region. Van Devender and Burgess (1985) discovered a wood rat midden from the Sierra de la Misericordia (near Bermejillo), Durango, showing a past flora of essentially modern desert perennials, of which 50% were succulents. Seventy to 100% of these species currently occur within 1 km of the midden site. However, the reverse was true of trees and woody shrubs. A well-developed piñon-juniper woodland was recorded at this site. Species currently extralimital to this area were derived from all directions, but the largest components came from the south and east. A similar east-to-west expansion of Pleistocene biota has been described for the herpetofauna by Auffenberg and Milstead (1965) and Morafka (1978).

Palynological studies of the past 20,000 years in the Cuatro Ciénegas Basin, Coahuila (Meyer, 1973), concluded that the vegetation (Desert Woodland) re-



mained essentially unchanged at lower elevations. Limited midden data from the same region (Van Devender and Burgess, 1985) also yielded some desert flora during late Pleistocene times, but mixed with a significant piñon-juniper component.

Relative to the Trans-Pecos floras, the cooler, mesic woodland assemblages of the Mapimian were probably influenced by even greater equability in temperature (more sheltered from "blue northers") and by more evenly distributed precipitation, especially in winter (Van Devender and Burgess, 1985). In contrast, survival of heliothermic endemic desert lizards such as *Uma exsul* (Pough et al., 1978) along with succulents indicates that sandy and rocky substrates in hot, exposed and well-drained edaphic patches probably persisted throughout the Pleistocene. These taxa survived in warm microclimates through major cooling climatic trends which resulted in lower elevation limits of piñon woodland. Because of the downward superimposition of these woodlands, Van Devender and Burgess (1985) rejected the Mapimi bolson as a refugium for desert biota, based on the mixed nature of the glacial flora relative to modern "pure" desert associations. Refugia, however, do not require survival of a completely intact relict ecosystem. When the Mapimi flora is compared to its widespread Tertiary precursor (at least at the generic level), the Mojavia flora of Axelrod (1958), the Mapimi bolson emerges as a significant, if differential, refugium (Morafka and Lieberman, in press).

Almost nothing is known about Pleistocene conditions in the southern Saladan Subprovince of the Chihuahuan Desert. Harris (1978) described southward range extension of the marmot (*Marmota* sp.), based on Pleistocene fossils from San Josecito Cave in Nuevo Leon (on the periphery of the Saladan Subprovince). He interpreted its presence as indicating increased moisture during winter and spring. Van Devender (personal communication) reported a more extensive small mammal fauna from the same site, including Rocky Mountain, midwestern and tropical species. The high, 1500 to 2000 m minimum relief of the Saladan plains did not favor maintenance of a refugial desert. A few generalized desert species may have survived in complex mild-cool adapted communities of piñon-juniper-oak woodland, chaparral and occasional grassland, paralleling isochronous conditions in the high, cold Great Basin (Mead et al., 1982).

Pliocene climates and topography fostered ecological conditions conducive to a more continuous and extensive distribution for *G. flavomarginatus*, possibly including most of the Mexican Plateau north of the Transvolcanic Axis and north into Texas, New Mexico, and southeastern Arizona. That range has been progressively fragmented and reduced. By the early Pleistocene it may have been reduced to the sites of Trans-Pecos and Mapimi—subprovinces of the modern Chihuahuan Desert. Regional geology presents two interrelated agents with potential for both topographical and ecological fragmentation and extirpation: faulting and lake development. The former was already episodically important throughout Mio-Pliocene periods possibly peaking in the Plio-early Pleistocene.

While the Sierras and Mexican Plateau were largely Oligocene (Oriental) and Miocene (Occidental) in their orogenies (McDowell and Keizer, 1977), there were widespread episodes of mountain rejuvenation throughout the southwest during the late Pliocene and early Pleistocene (King, 1959; Cooper and Silver, 1976; Strain, 1966; Maxwell et al., 1967; Arellano, 1951). Widespread secondary faulting of existing mountain blocks accentuated the basin and range topography that dominates this region. Belcher (1975), among others, has summarized the tectonic



events which led to the evolution of the Rio Grande Rift. Repeated faulting of this landscape does not appear to have excluded *Gopherus* despite the suggestion of Bramble (personal communication) that this would be the case. These processes resulted in closed drainage systems (bolsons) which filled during glaciopluvial precipitation. Rainfall probably increased under these climatic regimes, and standing water had less evaporative loss. Van Devender (1986) suggested that winter precipitation was significant. Furthermore, not all water in these bolsons was from local precipitation. Watersheds in the Rocky Mountains and Sierra Madre Occidental drained to the east of the Continental Divide and produced some of the largest regional lakes. Until the middle Pleistocene, the Rio Grande (the now dominant river of the Trans-Pecos) was a closed basin drainage, terminating in the large playas (lagunas Santa Maria, Palomas, and Guzman) of northwest Chihuahua (Hawley, 1969; Reeves, 1969). Other major glaciopluvial lakes of that northern subprovince included the Estancia Basin, Tularosa Basin, Plains of San Augustin, the Animas and Playas valleys of New Mexico (Kottlewski, 1958), and the Willcox Playa in southeastern Arizona. The Mapimian core of the Plateau also had major lakes in most of its bolsons (Van Devender, 1978). Of particular interest, a massive lake connected the now dry playas of Laguna de Palomas, southeast Chihuahua and Durango (not to be confused with the playa of the same name in northwest Chihuahua) with Coahuila's Laguna del Rey (J. Bartolino, personal communication). As noted previously this combined body of water probably separated the Remedios and Diablo populations of *G. flavomarginatus* intermittently from those south of the lake in what is now the Mapimi core district. Limestone ranges (interspersed with extensive Miocene igneous deposits in the west) combined with bolson lakes to sequester small, isolated tortoise populations along Pleistocene lake shorelines, as illustrated in Fig. 19. Furthermore, the valleys immediately south and east of the Mapimi tortoise district appear to have had extensive flooding, presumably from Laguna Mayran that extended northward toward Tlahualilo and filled (or spilled over into) the Valle de Acatita, Durango. This latter valley is just south and east of the limestone ridges that terminate the Mapimi District. Freshwater mussel shells are found in the extensive sand dunes of the Valle de Acatita, while these sands lack fringe toed lizards (*Uma*) that dominate hummocks both north and south of the Valle. Mussel fragments occur also in the open dunes of Laguna Mayran still occupied by *Uma exsul*. However, Valle de Acatita, unlike Laguna Mayran, is a very narrow and steep walled trough. This region still harbors mud flats and reeds at Los Charcos de Risa. Presumably, the valley was completely inundated by a Pleistocene lake.

Northeast of the Americanos District, the Llano del Guaje appears to be another former wetland barrier. This huge plain borders tortoise populations northeast of Laguna de la Leche, below the north slope of Sierra San Francisco. Almost uniform *Hilaria mutica* grassland covers much of northwestern Coahuila, stretching east to the uplands surrounding Ocampo, and north virtually to the Sierra del Carmen—Big Bend region of the Rio Grande. These plains were probably a marshland or flooded grassland during glaciopluvial times. They may have received heavy summer monsoon rains originating in the Gulf of Mexico (Wells, 1979), if this controversial hypothesis is correct. Even if rainfall cycles and patterns were different, any net increase in precipitation might have produced the immense swale grassland suggested. Today, flooded conditions are somewhat replicated during the summer wet season. Silty soils in the Llano del Guaje also indicate a history of standing flood waters. Farther south, both the Sierra Madre ranges plus the



## GLACIOPLUVIAL DESERT REFUGIA

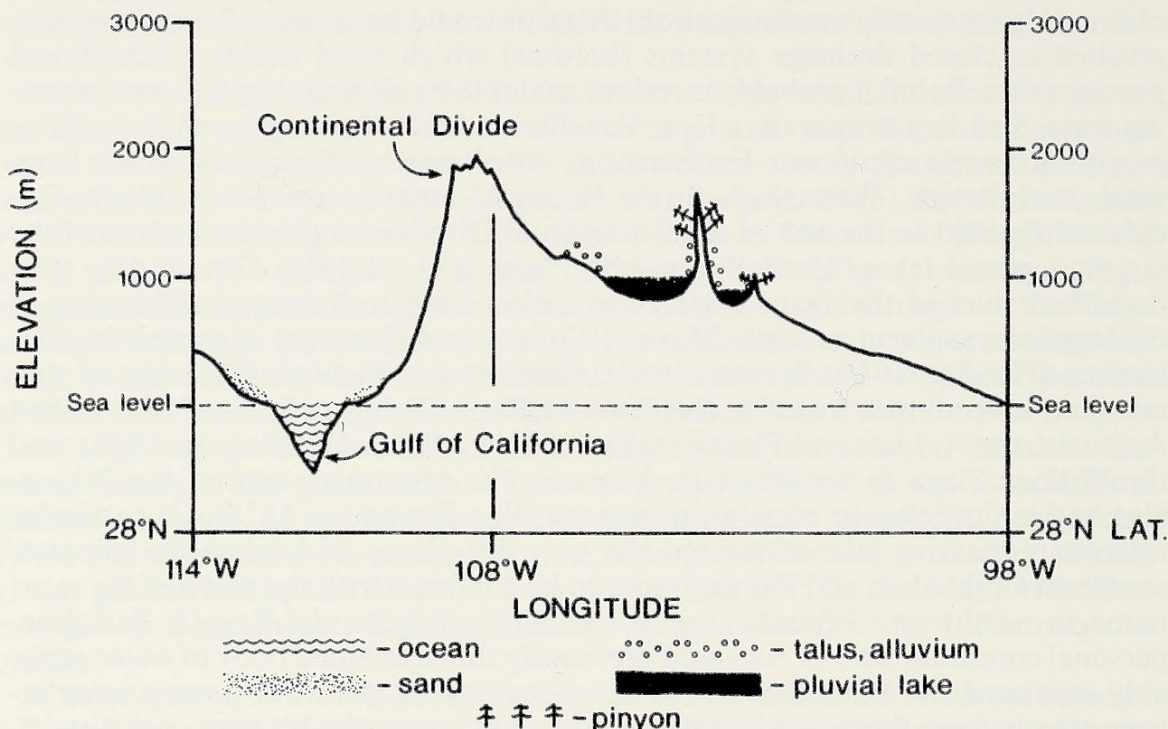


Fig. 19.—Cross-sectional diagram of glaciopluvial North America at the 26th Parallel North, which provides a diagrammatic depiction of the regional fragmentation of the Mapimi refugium.

transverse Anticlinorium of Arteaga fed the lake system of the Parras Basin, which includes the present day lagunas Mayran and Viesca. Despite this double barrier of lakes and 500–1000 m limestone ridges, *G. flavomarginatus* ranged to Aguascalientes, far to the south, possibly during the mid to late Pleistocene (Auffenberg and Franz, 1978). Such a distribution might have been established during Pliocene periods of lower elevation in the Saladan portion of the Plateau (Arellano, 1951), or by a later access to the south along the low Nazas-Aguanaval river valleys bordering the western side of the Parras Basin, where the adjoining uplift (Anticlinorium of Arteaga) is reduced in both elevation and continuity (Cohn, 1965; Morafka, 1978).

### *The Holocene Epoch*

This Holocene Epoch is essentially the last interglacial, representing only a 11,000 year instant within the 1.8 million year old Quaternary. Nonetheless, the Holocene climatic sequence probably recapitulates all of the paleoecological transformations of the 15 to 20 interglacials that punctuated the Pleistocene. In fact, Van Devender (1986) suggested that the Holocene sequence of vegetational replacements in the Chihuahuan Desert may have recapitulated the late Tertiary pattern by which this ecosystem originally developed.

As in the Pleistocene account, any characterization of the region during the Holocene must consider differences between the three Chihuahuan subprovinces. Van Devender (1986) describes the sequence for the Trans-Pecos Subprovince as "... the early Holocene 11,000 to 8,000 years vegetation was a transitional xeric



oak-juniper woodland (Van Devender, 1977). The middle Holocene was a desert-grassland period lacking both woodland and many important Chihuahuan Desert scrub plants. Development of the modern communities was in all cases a late Holocene event. The vegetation changes that mark the boundaries between the early, middle and late Holocene have some temporal variability but were completed 8,000 and 4,000 years ago, respectively."

Van Devender modified this chronology for a Mapimian Subprovince site at Rio Grande Village (Big Bend National Park, Texas) in noting that xeric-adapted Chihuahuan species were already important in Late Wisconsin time, and that the development of desert-grassland was an Early, rather than Middle Holocene event. Messing (1986) noted Pleistocene-Holocene *G. flavomarginatus* from a now extralimital Mapimian site near Jimenez, Chihuahua.

There is no fossil evidence from the Pre-Columbian Holocene of the southern, Saladan Subprovince. Again, by extrapolation from higher elevations and the recently derived desert herpetofauna, its Holocene history, like that of the Trans-Pecos, was presumably marked by reinvasion of desert biota from the Mapimian Subprovince.

Van Devender (1986) indicated that modernization of Holocene plant communities was a stepwise process. Earlier, Van Devender (1978) referred to glaciopluvial conditions, indicating a strong continuity between late Wisconsin and early Holocene conditions (for example, the continuation of widespread piñon-juniper woodlands at lower elevations). Van Devender's middle Holocene "monsoonal" and the Altithermal period (of Antevs, 1948) would appear to be diametrically opposed in their climatic connotations. Van Devender and Worthington (1978) reported no evidence of a hot, dry Altithermal during the middle Holocene at a site near Deming, New Mexico, at the northwest edge of the Chihuahuan Desert. Similarly, Bryant (1978) reported only erosional (no palynological) evidence for an Altithermal climate from the northeastern edge of the Chihuahuan Desert near Del Rio, Texas. Instead, a monsoonal episode may have occurred characterized by strong summer rains from the Gulf of Mexico and gradually warming climates conducive to grassland development. In fact, the conflict is more apparent than real. In all cases, Altithermal correlates with higher middle Holocene temperatures. These induce aridity in the absence of monsoonal precipitation but stimulated them in more mesic/eastern areas where summer rains were already established. Apparently, these same warming trends continued in the Great Basin and Great Plains, areas peripheral to the Mexican Plateau, without the intervention of monsoonal precipitation. In these latter regions, Altithermal warmth and aridity exceeded modern conditions. Van Devender and Worthington (1978) reported that a warm, xeric episode occurred in the late Holocene of southern New Mexico. The delay or suppression of Holocene aridity in the Chihuahuan Desert region by these monsoonal storm tracks is an important consideration in evaluating alternative hypotheses explaining mass extinction of large vertebrates that coincided with the early Holocene. The varying seasonality of altithermals further complicates the correlation of peak arid episodes between regions generally (Davis, 1984). This poses special difficulties for those wishing to invoke climatic change as the common denominator of the extensive and relatively isochronous extinction of the southwestern megafauna. The most dramatic deterioration of regional glaciopluvial equability and grassland vegetation probably occurred only 4000 years ago, long after the demise of the megafauna. However, these latter changes may play an important role in accounting for local extirpation of *G. flavomarginatus*.



## QUATERNARY EXTINCTIONS

During the latest millennium (Wisconsin Glacial), there was a relatively sudden mass extinction of the North American megafauna, removing the majority of larger (44–50 kg) herbivores and their dependent predators from the continent's ecosystems. Even viewed in the larger context of Cenozoic extinction episodes (Webb, 1984) and species turnover rates (Gingerich, 1984), the scope, size-based specificity, and temporal brevity (intensity) of this one extinction episode appear to be unique. Reviews of both hypothetical causes and empirically assessed results of these extinctions are provided by Martin (1967) and the contributions to Martin and Klein (1984). Marshall (1984) provided a particularly lucid overview of the issues, evidence, and the special nomenclature devised to represent them.

The Quaternary megafaunal extinction episode is especially relevant to *G. flavomarginatus* distribution since the morphology, ecology, and vulnerable behavior of the species (criteria from Martin, 1984a) clearly establish it as a member of the collapsing megafauna. Based upon the fossil conspecific *Gopherus* "*huecoensis*" and the *polyphemus*-like ally *G. canyonensis*, isometric predecessors of *G. flavomarginatus* might have been twice the size (linear measurement) and eight times the mass (possibly up to 160 kg) of extant *Gopherus*. As grassland herbivores, tortoises are also similar ecologically to many of the now extinct mammalian megafauna. This tortoise appears to have suffered a recent, rapid, and massive extirpation, from perhaps 80% of its Pleistocene range, even after end Tertiary orogenic reductions to the south are taken into account. Its extirpation may have been paralleled by Holocene diminution of size, very much the parallel of its mammalian analogs.

A wide array of both complementary and contradictory theories have emerged regarding the megafaunal extinctions in North America, and globally. These are: (i) Disease and other pathology based models; (ii) Climatic/ecogeographical models; and (iii) Predation (non-human or human, including the "Pleistocene overkill" hypothesis). Here, we attempt to define each model as it applies specifically to *G. flavomarginatus*. The Bolson tortoise, as a megafaunal component now in the twilight of its survival, provides an interesting test case of the appropriateness of these hypotheses.

*Disease*

Disease and pathological causes are of more historical interest than practical value. At least for North America, there have been few recorded invasions by potential disease vectors in the later Pleistocene other than *Homo sapiens* and the musk ox (*Ovibos*), mammoth (*Mammuthus*), and the bison (*Bison*) which may have made a mid-Pleistocene entrance to North America (Martin, 1967). Paleolithic hunters who entered North America were not a major reservoir of Old World diseases (Hare, 1967). It is unlikely that a single pathogen or even suite of agents would differentially infect large animals regardless of taxon (mammal, bird, and reptile), and spare smaller, more closely-related host species.

Veterinary diagnostic panels for *G. flavomarginatus* blood chemistry and cell differentials, and fecal flotations for parasite (nematode) eggs have revealed no significant pathologies among 50 wild tortoises monitored at the Mapimi laboratory (Morafka et al., 1986). Monitored values were generally within the known ranges of healthy *G. agassizii* (Lieberman and Roszkopf, 1986), even in *G. flavomarginatus* bearing fairly heavy nematode loads (Adest et al., in press).



Similar arguments may be employed in eliminating reproductive or developmental defects (Neuville, 1921; McClean, 1981). Given the diversity of the megafauna, the absence of evidence either past or present, and the uncertainty of climatic extremes that allegedly induced pathologies, defects do not seem a likely explanation. There were few extinctions during the previous 15–20 glacial episodes, thus climate-induced physiological catastrophes appear improbable. In any case such reproductive health models are only credible for mammals with long gestation periods and low fecundity (Kiltie, 1984); neither condition applies to tortoises.

### *Climate*

McClean (1981) linked gestation failure and general physiological failure to hotter summers than either glacial or contemporary climates could produce. The effect of “hot” (and dry) summers was also hypothesized for megafauna extinctions in central Texas (Lundelius, 1967). This simple climatic model invoked reduced equability: higher and drier annual averages than at present, and greater seasonality. Such scenarios depend upon setting major megafauna extinctions at about 8000 years ago, synchronous with the beginning middle Holocene. Geochronology provides little or no support for this hypothesis. When the middle Holocene Altithermal took place, 3000 years after the peak of extinctions, it was regionally specific in its effect. As already observed, Van Devender and Worthington (1978) and Bryant (1978) indicated no vegetational evidence for a New Mexico–West Texas Altithermal. Rather, they found an expansion of the grasslands for which many of the extinct megafaunal species were well-adapted (Mehringer, 1967; McDonald, 1984).

An alternative cold summer shock hypothesis was developed by Axelrod (1967). Its central theme was increased mortality of mammalian herbivore calves in the Great Plains due to polar summer storms moving south through the midcontinental aperture developing between the deteriorating Laurentide and Cordilleran glaciers. A wide variety of large herbivores would have been affected, just as are cattle in the northern plains today. However, the hypothesis does not clarify why climatically sheltered coastal populations (for example, the Rancho la Brea fauna in California), as well as those in the Mexican Plateau and American tropics were simultaneously affected (McDonald, 1984), nor does it explain why equally extreme interglacials (120,000 and 320,000 years ago; Covey, 1984) failed to produce similar results.

The third model for a Holocene climatic catastrophe is the “blue norther.” As in the previous hypothesis, the mid-continental recession of the Laurentide and Cordilleran glaciers opened a southward path for severe polar storms, but in this case the emphasis is placed on winter, rather than summer episodes (Bryson and Wendland, 1967). Unlike the previous explanations, considerable geological and climatological evidence documents inland deterioration of the continental glacier and, consequently, increased seasonality. Harsher winters probably characterized the early and middle Holocene in the middle latitudes and longitudes of North America (Bryson et al., 1969). Furthermore, Van Devender et al. (1976) and Moodie and Van Devender (1979) linked this climatic change directly to the early Holocene extirpation of several chelonians from what is now the New Mexico–western Trans-Pecos region. They suggested climatic extirpation of *Gopherus agassizii*, *Geochelone wilsoni*, and *Terrapene carolina putnami* from the northern Chihuahuan Desert. Prior to the Holocene extirpations, they projected continuous



distributions for *G. agassizii*, *G. berlandieri* and *G. flavomarginatus*. They tentatively attribute primary extirpation of tortoises to colder winters, but do not exclude related vegetational changes or the simultaneous southward advance of Paleo-Indian predators. Of all the Holocene climatic factors proposed, minimum winter temperatures correspond most strongly with current northern limits of tortoises (especially *G. agassizii*). *Gopherus flavomarginatus* were probably tolerant of some cold winters given both their 10-year survival and natural reproduction in a captive population at the Research Ranch, Elgin, Arizona (Appleton, 1978). This site is located in oak grassland habitat at 1500 m elevation. Lowe et al. (1971) documented considerable supercooling capacities for *G. berlandieri* ( $-5.25^{\circ}\text{C}$ ). However, if severe polar storms ("blue northers") did bring hard frosts and snow precipitation, lethal freezing might penetrate even into some burrows, particularly killing hatchlings in their more shallow shelters.

Although these storms may penetrate farther south, even to Mexico City, their duration is more limited. The incursion of northers beyond the Trans-Pecos into the Mapimian refugium was probably a much less frequent event and the effect on local climatic conditions less severe than suggested, as they would have been dissipated by intervening transverse ranges (Davis Mountains), lower latitudes, and lower elevations. Hadley's Cell, a stable subtropical high pressure air mass, may have deflected storms far to the south (Gates, 1976), though early models projecting the climatology of the last glacial, may have underestimated cooling at lower latitudes, a factor which could have eliminated the cell.

### *Vegetational Changes*

Accompanying these climatic scenarios of mass extinction are several secondary effects, especially vegetation changes. These ecogeographical explanations synthesize climatic, vegetational, and faunal evolutionary evidence in various ways, but there is one unifying theme: glaciopluvial communities were restructured and individual species displaced drastically and in unique ways at the end of the Pleistocene. As a result, coevolved stability was thrown into disequilibrium in the new depauperate Holocene communities (Graham and Lundelius, 1984). Ensuing disruptions of food webs resulted in faunal collapses involving both large and small species. Empirical evidence for the previous existence of stable coevolved communities is scant. Already noted, Spaulding and Martin (1979) provide evidence for the opposite. Van Devender et al. (1976) argued effectively against the assumption of static community concepts in their analysis of a Trans-Pecos fossil flora. In a genetically explicit analysis of Baja California herpetofaunal biogeography, Murphy (1983) rejected general application of coevolution in explaining past or present biotic assemblages. For example, the entire southwestern desert biota evolved without its current dominant shrub, creosote (*Larrea divaricata*), which is probably a late invader of North America arriving from Patagonia during some undetermined interglacial or even in the Wisconsin Glacial.

An alternative version of the ecological synthesis has been presented by Guthrie (1984, based in part upon Leopold, 1967), who developed a suite of possible coevolved herbivore to vegetation form dependencies. He suggests that the Holocene was a unique "interglacial," where originally complex Pleistocene floral mosaics were reduced to species-poor zones. The consequence was nutritional inadequacy of locally available forage, combined with reduced primary growing seasons resulting from less equability in climate. Again, little fossil or contemporary supportive evidence exists, especially from regions (for example, Mexico)



of southern North America. Modern Mapimian plant associations sustain a complex mosaic of species, reflecting the continuing equability of the region. Studies of the natural diet of *G. flavomarginatus* (Adest et al., in press) indicate adequate high-protein forage from Mapimi localities which are not overgrazed. The tortoise survives well on a variety of grasses and forbs, provided that protein content (16%) in the juvenile diet is adequate.

*G. flavomarginatus* is a grazer/browser that underwent a Wisconsin-Holocene collapse in distribution, presumably concomitantly with the rest of the megafauna. However, our previous review offers no evidence for alteration of end Pleistocene habitats sufficient to threaten food availability for *G. flavomarginatus*. McDonald (1984) estimated that North American grassland productivity may have undergone a 75% increase during the very time of most megafaunal extinctions. Despite the logical and theoretical attractiveness of synthetic models for extinction, they are probably more appropriate for accounts of progressive individual species extirpation than for the sudden demise of such diverse megafauna. On the other hand, the late Holocene (last 4000 yr) reduction of Trans-Pecos grasslands might have locally extirpated *G. flavomarginatus*. The impact may have been even greater if we assume that vegetational shifts to coarse sand/gravel scrubland favored competitive exclusion of *G. flavomarginatus* by the more xeric-adapted "*Xerobates*" (*G. agassizii/berlandieri*) of Bramble (1982). Ultimately, both climatic and vegetational models of Holocene extinction are extremely vulnerable to the argument that these events were no more severe (hot/cold) than at least three of the preceding 15–20 interglacials (McDonald, 1984) which produced no comparable extinctions.

### Predation

Non-human predation has no empirical basis as a factor in North American Pleistocene extinctions. No single carnivore has emerged as a candidate, and none suddenly appeared or expanded near the time of extinctions. Peak aridity and recent overgrazing may have reduced ground cover so severely as to expose hatchlings to greater predation, but objective demonstration of this has yet to take place.

By elimination of other factors, human induced extinction remains among the few plausible explanations. Further, it has the most explicit fossil evidence as well as a convincing causal relationship still operative in contemporary times.

The timing and geography of Pleistocene extinctions that associate tortoises and human invasion are coupled with a "*modus operandi*" that is distinctly human in character. Circumstantial evidence implies that Paleolithic hunters (Paleo-Indian) are the primary cause of megafauna extinctions. Human hunters may have accentuated extirpations and fragmentations typical of the interglacials into catastrophes from which no subsequent recovery was possible. Six major arguments support the decisive role of human predators in this most abrupt North American extinction:

(1) *Chronology*.—Martin (1958, 1967, 1984b) emphasized a sudden mass extinction of the North American megafauna at 11,000 years ago. This peak, spanning perhaps a thousand years, has been tentatively corroborated by Marcus and Berger (1984) and Mead and Meltzer (1984).

Almost no unambiguous record for humans in North America extends beyond 13,000 years. While MacNeish (1976) and Dillehay (1984) had attempted to establish earlier dates, Berger (1980), and Adovasio and Carlisle (1984) identified



only a single Pennsylvania site (about 19,000 years old) significantly older than the Pleistocene-Holocene boundary. Even the antiquity of this site has been challenged (Mead, 1980). Most evidence indicates several waves of Paleo-Indian invaders from Asia between 14,000 and 8000 years ago and most, if not all, moved south through the mid-Continental corridor (Great Plains) between the Laurentide and Cordilleran glacial masses. After initial human dispersal, some latency period must have taken place before human distribution, density, technology and strategies were sufficient to have major effects. If this assumption is correct, first occurrence of New World humans is not as critical to overkill hypotheses as are their densities and cultural stages. MacNeish (1976), who did not subscribe to the human overkill scenario, still recognized multistage increments in human impact. When differences in reported dates and interpretations are reconciled, the first widespread establishment of human populations in North America correlates well with the demise of the native megafauna. Furthermore, human population establishment is the unique factor which distinguishes the end of the Wisconsin Glacial from several equally severe precursors.

(2) *Geography*.—Geography provides evidence in support of Martin's overkill hypothesis and contradicts climatic alternatives. Geographically, megafaunal extinction occurred only where humans made a sudden first appearance in the Holocene (or very end of the Wisconsin Glacial). In the New World, extinction of the megafauna moved in a north (Bering Strait) to south (Patagonia) wave between 12,000 and 8000 years ago (Martin, 1967), as would be expected if human predation were causal. No climatic or ecological alternative has been suggested that would produce the same pattern.

Insular extinctions in the late Holocene are exceptions that support the overkill rule. Flightless New Zealand and Malagasy birds (Battistini and Verin, 1967; Cassels, 1984) and the larger Malagasy lemuroids and tortoises (Walker, 1967; Dewar, 1984) were refugial insular megafauna subjected to later human invasions. Large tortoises (*Geochelone*) were also subject to these later invasions and extinctions on islands such as Cuba and Mona Island (Williams, 1950, 1952), the Celebes and Malta (Martin, 1967, 1984a) and in historical times, the Galapagos. Giant tortoise populations on Aldabra Island in the Indian Ocean might be viewed as a historical control to the Galapagos experience. In less than 200 years, the Galapagos *Geochelone* suffered a massive decline as a result of human predation and the introduction of rats, dogs, and goats. In contrast, the Aldabra tortoise population remains vigorous on an island that has been spared human intrusion during the 20th century by virtue of the island's lack of harbors, presence of impenetrable scrub, and remote position (Swingland, personal communication; Pritchard, 1979). Again, no climatic-vegetational model rivals the human factor as a common denominator of this global array of Holocene insular extinctions. Only one recently extinct horned "tortoise" (*Meiolania*), from Lord Howe Island in the Australian Realm, appears to have been extinguished by climatic causes, possibly inundation (Martin, 1984a).

(3) *Susceptibility*.—Large slow grazers and browsers appear to have been relatively easy prey for Paleolithic hunters. In North America, mammoths were initially the target species, later replaced by archaic bison (consisting of larger antecedents of existing *Bison* according to some authorities, but including two extinct species in the view of others), and ultimately by the surviving *Bison bison* (Reeves, 1983; Frison and Stanford, 1982; Davis and Wilson, 1978). Selection for large size characterized Paleo-Indian hunting preferences between species and within



species (Edwards, 1967). Chelonians and their eggs were part of the exploited megafauna in the American Southwest. Moodie and Van Devender (1979) reported tortoise shells in association with the artifacts of Paleo-Indians. Fossil tortoises (*Geochelone*) from Florida sinkholes have bone fractures caused by humans, and have been found in association with Paleo-Indian artifacts (Canby, 1979; Holman and Clausen, 1984). Similarly, temperate North America's largest land reptile (*G. flavomarginatus*) is also the most endangered tortoise due to direct human predation. Shell lengths in some *Gopherus* lineages have become reduced by one-half to two-thirds since late Pleistocene times. Edwards (1967) reported that size reduction in response to cooler climates might be expected in heliothermic reptiles, and the opposite should be true for most homeothermic megafauna. However, Van Devender (personal communication) concluded the equable climates of the glacials (mild winters) did favor larger size. The Holocene record has witnessed simultaneous diminution in lineages (*Bufo*, *Sceloporus*, *Procyon*—Van Devender, personal communication) of many physiological types, through varied climates, possibly due to human selection in some taxa, but certainly not in all (*Bufo*). Marshall (1984) proposed a strong correlation between diminution and extinction. King and Saunders (1984) interpreted such a correlation in mastodon chronoclines as the result of "island effects in relictual distribution patterns." However, Shine (1986) and Kowarsky (1982) documented aboriginal human predation directed differentially against larger (female) snakes (*Acrochordus*) and sea turtles, respectively.

Behavioral vulnerability has also been suggested as affecting the extinct megafauna. Clear documentation of such vulnerability in North American bison (assigned to two extinct, one extinct and/or one living species by different authorities) has been provided by Reeves (1983). Search images, sound cues, and scents which alerted large prey to native predators may not have provided adequate cues to escape human hunters. Certainly tortoises caught away from burrows would have been extremely vulnerable. Based on our estimations of shell strength, and extrapolations from other species, adult shells are adequate defense against most present carnivores (coyotes, foxes, raptors) except the very largest, such as the puma (Moskowitz, personal communication). But these were useless against even the most elemental hunting implements. In fact, tortoises may have even attracted attacks because of the utility of their shells as containers (even today they are used as water bowls and chicken feeders). Taylor (1982) documented parallel modern human exploitation of *G. polyphemus* in north central Florida. However, the burrow provided significant defense. Its extreme depth of two meters or more (Morafka, 1982) is adequate protection against surface predators, even formidable carnivores (for example, bears) that are no longer extant within the range of tortoises. Possibly these long burrows account for the survival of *Gopherus flavomarginatus* while the more widespread but surface-dwelling tortoises (*Geochelone*) became extinct in North America. In apparent contradiction to this line of logic, it might be argued that both *G. agassizii* and *G. berlandieri* are smaller, weaker, more surface active, less protected by deep burrows, and therefore more attractive as potential prey for humans. Why then have they not suffered extinction before the more formidable *G. flavomarginatus*? Human predation typically selects biggest game first, both within and among species. Furthermore, bigger animals often have smaller populations with lower replacement rates. Finally, *G. flavomarginatus* may simply have tasted better and/or yielded more meat than the other members of its genus. Even the differential effects of tribal taboos may



have favored one species over another. Such eclectic selectivity has been exhibited by aboriginal hunters in South America. Some tribes select *Geochelone carbonaria* while others prey only upon the syntopic *G. denticulata* (Moskowitz, personal communication, 1986).

(4) *Lack of ecological replacement.* — In most ecological communities, a declining species is displaced by a more successful competitor or subsequently replaced by an ecological equivalent. This has not occurred in the North American megafauna. Introduction of domestic livestock obscures the truly depauperate condition of native North American megafauna. New or different species should be expected to disperse from adjacent habitats or increase in density in order to exploit the newly available habitat. A terrestrial box turtle (*Terrapene ornata luteola*) now occupies much of the former range of *G. flavomarginatus* in the Trans-Pecos Subprovince of the Chihuahuan Desert. However, this small-sized omnivore in no way fills the burrowing-grazer niche left unoccupied by the extirpated tortoises.

(5) *Human population dynamics.* — Previous quantitative models have shown marked human population growth, oscillations, dispersal, and predation pressure in Paleolithic North America (Martin, 1973; Mosimann and Martin, 1975; Whittington and Dyke, 1984). Although the specific initiation times and patterns of these events have been questioned (Davis, 1978), the models demonstrate the human populations had the potential to grow, disperse, and prey upon the megafauna at rates adequate to explain a mass extinction across the New World in only 2000 years. The validity of the overkill hypothesis does not rest upon these models, but they do enhance its credibility as physically feasible. The credibility of the "overkill/blitzkrieg" hypothesis has been further advanced in this instance by the estimates of Carroll (1968) that 300,000 families occupied the "Great Bolson" of the Chihuahuan Desert (upper Rio Grande Valley) in Pre-Columbian times. Ware (1984) also suggests a 10,000 year human presence in the Rio Grande Valley, characterized by maize-based agriculture for the last 2000 years, presumably conducive to larger resident populations.

Humans are adaptable omnivores and, in the presence of a negative feedback system (especially agricultural societies) that may keep some specialized carnivores in equilibrium with prey, human predation pressure may go unchecked. Because alternative food sources are generally diverse and may be stored, human pressure might have been unrelenting, ultimately causing the extinction of prey populations.

(6) *The uniformitarian argument: human hunter-gatherers in historic times.* — Modern history has recorded frequent and consistent extirpations and extinctions as a result of human predation on large animals. Grizzly bears, condors, and bison appear to have been the last in a series of target species for human hunters in the Southwest. Diamond (1984) provided an excellent set of case studies and patterns of human-induced extinctions that have occurred in historic times. Perhaps the best modern analogue to human invasion of the New World, is our current exploitation of the oceans. At sea, humans still operate as vagrant hunter-gatherers, using essentially refined (and only recently mechanized) snares, nets and spears. The impact of small and temporary human populations has brought about annihilation of the marine megafauna (ranging from auks to sea cows, and the various cetaceans). Just as on land, large sea turtles have not been exempt; their eggs are removed from shore nests while adults are harpooned at sea.

#### POST-COLUMBIAN EVENTS

The historical record for the Mapimian region in north central Mexico is confined to the past 450 years. The major events of this history include the intro-



duction of European people, plants and livestock, and elimination of native hunter-gatherers since 1900. There has been the increasing collection of native plants, in particular, the wax plant, candelilla (*Euphorbia antisiphylitica*), the development of transportation routes and irrigation systems and, more recently, a partly subsidized resettlement program in interior valleys and exploration for petroleum (Morafka et al., 1981).

Irrigation and plowing of desert-grasslands appears to have extirpated tortoises at the southwest edge of their distribution near Tlahualilo, Yermo, and Ceballos, all in Durango. Continued human predation on adult tortoises and, to a much lesser extent on eggs, appears to be a problem throughout the range. Livestock competes for forage and may trample young tortoises.

Interviews with long-time rural residents often yield accounts of deteriorating tortoise populations, even since 1900. Tenneson (1985) interviewed a 50-year-old resident of Ejido la Flor, Durango. He estimated that tortoise populations were currently one-fourth or one-fifth the density his father had seen in the same region 60 years ago. He also remembered bringing ox carts full of tortoises to local markets. One of us (McCoy) interviewed older residents at ranchos and ejidos near Yermo and Ceballos, Durango (see Part I). These informants, men in their 70s and 80s who had lived in the area their entire lives, all related similar scenarios of tortoise population decline. A common element of these histories was that tortoises formerly (50 to 75 or more years ago) were much more abundant, although the limits of distribution were roughly the same. The initial decline in tortoise abundance was invariably attributed to a major change in demography of the local human population: influx of construction workers during the building of Highway 45, the presence of large numbers of mule teamsters during the initial leveling of land destined for irrigation, or the settling of immigrant workers in newly-opened agricultural areas. In each case it was related that hunting pressure on the tortoises was relaxed only when populations became so depleted and individuals so scattered that organized hunts were unlikely to meet with success.

Recently, the impact of PEMEX (National Petroleum Trust of Mexico) exploration roads has been expanding. These dirt strips have been bulldozed across virtually every valley in the Bolson de Mapimi in Durango, southeastern Chihuahua, and to a lesser extent, in western Coahuila. These road building operations have accelerated dramatically since 1977. These roads are unwavering, straight, and totally remove all vegetation in their path. Some capture and reorient local drainages. In March 1982, we discovered roadside campfire sites at Rancho Peñoles, Chihuahua, in which were strewn freshly shattered tortoise shells. The long-term effects of these roads are unknown but at a minimum they generate local losses of adult tortoises due to easier access. At worst, the new roads precede waves of new long-term human colonization, manifest in PEMEX drilling crews, new ejido (cooperative farm) settlements, and drives of livestock into new forage lands.

#### CONCLUSION

*Gopherus flavomarginatus* is limited geographically and populations are now fragmented. Major topographical features (mountains and playas) account for only a portion of these fragments and limits. Our field data indicate that ecological variables fail to discriminate between sites with and without tortoises. Contiguous and accessible valleys extralimital to the tortoise appear to be nearly identical in their ecological and climatic aspects to localities within the range of the species. While further comparative studies of these peripheral valleys may lead to better



habitat discrimination, our studies point to no environmental factor or set of factors that explain the existing distribution, other than human activities and human settlements. The current range boundaries of the species appear to be a collapsed shadow of the former range, confined to a few remote valleys within the Mapimian Subprovince of the Chihuahuan Desert.

The genus *Gopherus* has the best fossil record of any extant genus of North American reptile. It provides a history of waning distributions beginning in early Miocene times. Early expansions were probably associated with increases in semi-arid grasslands. *Gopherus flavomarginatus* may have become the endemic species of the Mexican Plateau as a result of renewed basin and range development of Trans-Pecos Texas and the Sierra Madre Oriental in late Pliocene times. During the late Pliocene its range may have reached a maximum as grasslands and savannas (*Yucca*, oak, and piñon-juniper) expanded into Arizona and New Mexico. Early Pleistocene uplifts of the Saladan region of the southern Mexican Plateau may have truncated the southern aspect of its range, restricting the tortoise to lower, more western river valleys or possibly isolating entirely the southernmost (late Pleistocene) populations. A single uncertain record for Aguascalientes may extend its presence in the south to Rancholabrean times (500,000 to 180,000 years BP). Subsequent glacio-pluvial lakes and marshes may have also limited tortoises in the south (Parras and Aguascalientes) and east (Llano del Guaje). Cold winters caused a southward retreat from Texas and New Mexico by the beginning of the Holocene Epoch.

End-Pleistocene and early Holocene events induced not only a massive (80%) restriction of the remaining Pleistocene range of *G. flavomarginatus*, but also the sudden mass extinction of many large terrestrial vertebrates in the Western Hemisphere. While a variety of hypotheses have been proposed, only extreme cold winters ("blue northers") and human predation are probable causal agents. The climatic and vegetation changes of the Holocene were probably a repetition of sequences that took place in preceding and occasionally more extreme interglacials. Yet past episodes induced only regional extirpations and dispersals, not mass extinctions. Furthermore, south of the 30th parallel Holocene climatic changes were less extreme, and colder winters were much less pronounced than to the north. Human invasion and expansion in North America appears to be the best documented event that distinguishes the early Holocene from preceding interglacials. Both past and present human hunter-gatherers have been devastating as predators. Turtles and tortoises are documented as food species in both Holocene and historical times. *Gopherus flavomarginatus* might have recovered its lost distribution (at least in Mapimian and Trans-Pecos subprovinces) in middle to late Holocene times had not unremitting human predation kept it in retreat, though continued and increasing "northers" may have also exercised considerable influence.

The tortoise's continued, if limited, survival is probably due to the shelter of its extensive burrow and inaccessibility of the Mapimian valleys (not connected to any major river system) in which it continues to occur. The Mapimi region probably was not as impacted by the mainstream of Paleo-Indian hunters. No archaeological evidence of riparian agricultural communities, for example, has been reported for Mapimi. Relatively infrequent northern winter storms may have helped maintain the equability of climate and diversity and productivity of Mapimian grasslands. Pluvial lake formation may have reduced the vulnerability of shoreline populations (to aboriginal hunters) until relatively late Holocene



times. The absence of surface water in modern, dry bolsons (except immediately after summer storms) may have discouraged recent Pre-Columbian human occupation.

Currently, direct and indirect human pressure continues. Within the last century, approximately 35–50% of the remaining Post-Columbian range of the tortoise was lost, primarily due to irrigation and agriculture in the south (near Torreón, Coahuila) and west (Ceballos, Durango), and continued predation everywhere (especially along major rail and road routes). Within the remaining habitats, population densities continue to be reduced in 80% of examined localities.

Several powerful and contradictory Mexican social trends make a prognosis for the tortoise's survival difficult. Casanova (1980) documented a series of 20th Century socioeconomic patterns that could endanger the quality and stability of Mexican living standards. Between 1900 and 1970 the Mexican population doubled twice, the second time in only 20 years. It reached 80 million people in 1980. Projections for the year 2000 range from 100 to 132 million persons. Economic and distributional factors may either ameliorate or exacerbate population pressure in rural areas. If industrial growth and resulting population migration to urban centers continue to draw off rural populations, net rural densities might actually drop by the year 2000. The rural share of the Mexican population dropped by half (65 to 35%) between 1940 and 1978. If it decreased by another fourth in the next 20 years (1980–2000), the net absolute increase in rural numbers could be less than 10%.

However, cultivation of arable land might undergo an increase independent of rural population growth. The national highway system increased twenty-fold between 1940 and 1977, reaching 200,000 km. Mechanized farming, tapping aquifers, and expanded distribution of ejidos in the Bolson de Mapimi all threaten tortoise populations, regardless of general population trends. Casanova estimated that more than half the population (40 million) had a nutritionally inadequate diet. In arid, rural Mexico, high living costs and inadequate diets might force the population from livestock ranching into episodic hunting and gathering. Such a shift would obviously intensify predation on the tortoise. It might threaten the voluntary program protecting tortoises at the Mapimi Reserve, which has the largest known population.

The reproductive capacity of *G. flavomarginatus* populations is not completely known. G. Aguirre (personal communication) considered clutch size (5.2), frequency (2/yr), survivorship (1 to 5%) and slow maturation time (15–20 yr) in calculating a replacement period of 25–80 yr for a reproducing adult in a colony. Grossly similar estimates for *G. polyphemus* have been made by Auffenberg and Franz (1982). The problem is compounded by our ignorance about reproductive success in scattered (non-colonial) or depleted tortoise populations. We simply do not know whether these low density populations are viable. Perhaps they are composed entirely of non-reproductive adults, isolated survivors.

Some positive events, equally uncertain in their future momentum, have been established. Community cooperation has been protecting tortoises at the MAB Mapimi Reserve since 1978 and continues to expand (G. Aguirre, personal communication, 1987). The World Wildlife Fund assisted Mexico's National Instituto de Ecología in establishing a successful tortoise hatchery in 1983. In 1984, a new tortoise nursery was added to the Instituto Laboratory at Mapimi and it is now fully operational. However, the linked problems of nutrition, growth, and "knobby shell" formation in nursery-raised hatchlings has not yet been overcome, and the



results of the first hatchling reintroductions into natural but ungrazed enclosures remain to be recorded (Adest et al., in press).

In the Sierra del Diablo District of Chihuahua, Ing. Jose Treviño of the Mexican Sub-Secretariat for Urban Development and Ecology (SEDUE) is undertaking a detailed survey of local populations and coordinating a voluntary protection program by local ranchers. Initial results in 1983–84 are encouraging. A second hatchery and nursery has been established at Rancho Sombreretillo, Chihuahua. Also, Ing. Treviño has proposed that the Sierra del Diablo be set aside as a national wildlife refuge. The refuge would include the tortoise populations east of the Sierra (Cerros Emilio, Chihuahua), nearby relict piñon woodlands, and distinctive sand dunes to the south. Organized protection of such a large tract of land, especially when combined with the MAB Mapimi Reserve, would provide a unified conservation program for the Bolson de Mapimi. In the smaller districts at Remedios, Americanos, Yermo, and Diana, conditions continue to deteriorate in absence of any corrective measures. In particular, tortoise populations near Yermo and Diana in Durango may be lost by the end of this century or sooner.

The future welfare of the resident Mexicans and their Bolson tortoise are indivisible. Just as the Holocene collapse of tortoise distribution depended largely upon human conduct, so is its continued survival today. No written political policy will dictate the actions of ranchers and ejido inhabitants. Only the well being, consciousness, and personal values of local Mexicans shall decide whether *G. flavomarginatus* is to become just another late addition to the list of megafauna casualties or whether it will be nurtured and sustained as the centerpiece of the Mapimian desert-grassland which is unique to Mexico's natural heritage.

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