THE DESERT TORTOISE *(GOPHERUS AGASSIZI)* IN THE PLEISTOCENE OF THE NORTHERN CHIHUAHUAN DESERT

THOMAS R. VAN DEVENDER, KEVIN B. MOODIE AND ARTHUR H. HARRIS

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THE DESERT TORTOISE (GOPHERUS AGASSIZI) IN THE PLEISTOCENE OF THE NORTHERN CHIHUAHUAN DESERT[1]

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ABSTRACT: New localities (Dry Cave and Robledo Cave) for late Pleistocene *Gopherus agassizi* in southeastern and south-central New Mexico, USA, are 350–550 km east of the nearest modern populations. Plant community reconstructions from radiocarbon-dated fossil packrat middens from nearby areas suggest that the tortoises were living in xerophilous woodland rather than the desert scrub habitats commonly inhabited today. A paleoclimate with mild winters and cooler summers is postulated to explain G. *agassizi* in the late Pleistocene of the northern Chihuahuan Desert.

PLEISTOCENE faunas in the arid southwest and in the southern Great Plains have provided dramatic examples of animals having different geographic distributions under pluvial climates. Many of these are montane forms such as the yellow-bellied marmot (*Marmota flaviventris*), the masked shrew *(Sorex cinereus),* and the bushy-tailed packrat (*Neotoma cinerea)* found as late Pleistocene fossils at lower elevations farther south than they presently occur (Harris, *1970;* Logan and Black, *in press).* Others such as the least shrew *(Cryptotis parva)* and the box turtle *(Terrapene carolina*) formerly lived in southern New Mexico, but now occur no farther west than central and eastern Texas (Harris, et al., *1973;* Milstead, *1967).*

Our purpose in this paper is to discuss a different kind of distributional change. Brattstrom (1961, 1964) reported the desert tortoise (*Gopherus agassizi*) from Shelter and Conkling caves in southern New Mexico. This is a xeric-adapted, desert species presently restricted to the low, hot Mohave and Sonoran deserts. However, this record indicates that during the

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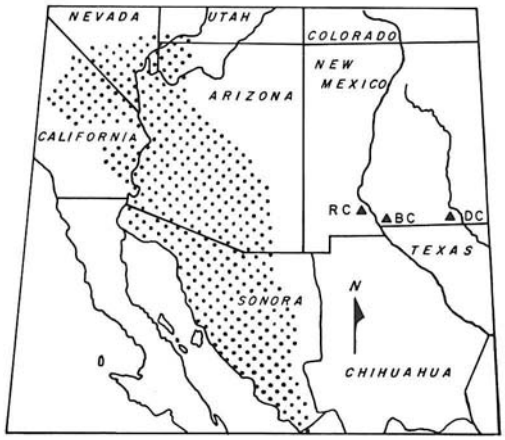

FIG. 1.—Map of the southwestern United States. Stippled area designates present distribution of *Gopherus agassizi* (after Stebbins, 1966). RC = Robledo Cave, BC = Bishop's Cap (Shelter and Conkling caves), DC = Dry Cave.

Pleistocene the species lived in higher, cooler areas in the present Chihuahuan Desert. Here we present new localities for G. agassizi in the northern Chihuahuan Desert (Fig. 1) and reconstruct its habitat using plant macrofossil records from nearby areas.

Shelter and *Conkling* Caves.—Brattstrom's (1961, 1964) G. *agassizi* material came from two limestone caves at the south end of the Organ Mountains, Doña Ana County, New Mexico. The caves are located on the east (Conkling) and west (Shelter) sides of Bishop's Cap (= Pyramid Peak of Brattstrom, 1964) at 1445–1475 m elevation. Bones of extinct mammals, including sloths (*Nothrotheriops* and *Megalonyx*), horse (*Equus*), Llama (*Tanupolama* = *Hemiauchenia* of Webb 1974) and four-horned antelope (*Tetrameryx*) (Conkling 1932; Stock 1930, 1932), were used to support early claims of the contemporaneity of man and Pleistocene fauna (Bryan, 1929). Some of the tortoise bones were burned, suggesting that they were eaten by the Indians, but these deposits have not been radiocarbon dated and the association of the fauna and man is not clear. The deposits are apparently late Pleistocene and Holocene in age, considering Martin's (1973; Long and Martin, 1974) estimate of 11,000 years ago as the final extinction date for most of the megafauna. We have examined a complete plastron of *Gopherus* from Shelter Cave in the Los Angeles County Museum of Natural History (LACM 1010/58912) and concur with Brattstrom's identification of *Gopherus agassizi.*

Robledo Cave

Referred Material.—Right hyoplastron (MALB 74-1); two peripheral bones (MALB 74-1,2).

Gopherus remains were recovered from Robledo Cave (MALB Loc. No. 74) in the Robledo Mountains northwest of Las Cruces, Doña Ana County, New Mexico. This locality is ≈ 65 km NNW of Bishop's Cap and is on the opposite side of the Rio Grande Valley. Potsherds, charcoal, and bones (some burned) were found with the tortoise bones in a shallow, badly disturbed deposit. No radiocarbon dates are available, but the tortoise material is well-preserved and could be Pleistocene in age. Three different sized individuals are represented. The fragments are not identifiable to species, but probably represent G. *agassizi.*

Dry Cave

Referred material.—Sabertooth Camel Maze (MALB Loc. No. 5): axial portion of right hyoplastron (MALB 5-111); right xiphiplastron (MALB 5-110); right xiphiplastron (MALB 5-252); fragmentary nuchal (MALB 5-253); nuchal (MALB 5-109); Vanishing Floor Room (MALB Loc. Nos. 26 and 27): nearly complete shell missing neurals (MALB 27-88); nuchal (MALB 26-243); left xiphiplastron (MALB 26-231); left xiphiplastron (MALB 26-331).

Dry Cave is located 24 km west of Carlsbad, Eddy County, New Mexico, on the eastern flanks of the Guadalupe Mountains (Harris, 1970). This site is ≈ 175 km east of Bishop's Cap and is the easternmost lo-

TABLE 1.—Radiocarbon dates and locality information of sites mentioned in text.

Site	*Date* (YBP)	Lab. *No.*	*Material dated*	*Elevation* (m)	*Location*
Dry Cave					
Sabertooth Camel Maze	25,160 ± 1730	Tx-1775	Bone carbonate	1290	Eddy County, New Mexico
Vanishing Floor Room	33,590 ± 1500	Tx-1773	Bone carbonate		
Williams Cave #2 Midden	12,040 ± 210	A-1540	Juniper	1495	Culberson County, Texas
Bishop's Cap #1 Midden	10,650 ± 170	A-1571	Juniper	1465	Doña Ana County, New Mexico
Bishop's Cap #2 Midden	10,780 ± 240	A-1572	Juniper	1465	Doña Ana County, New Mexico
Bishop's Cap #3 Midden	10,260 ± 250	A-1573	Juniper	1465	Doña Ana County, New Mexico

cality for Pleistocene *Gopherus agassizi*. Two rooms in Dry Cave (Sabertooth Camel Maze and Vanishing Floor Room) have yielded *Gopherus* fossils (Table 1).

The best specimen is a nearly complete shell that we refer to *G. agassizi* on the following qualitative and quantitative characters. The nuchal scute is wider than long (L/W = 0.93), a character given by Williams (1950) for the genus *Gopherus*. In both the Dry Cave and Shelter Cave specimens examined, the gular scutes are shorter than the humeral scutes along the midline of the pastron (G/H = 0.63 and 0.61, respectively). G/H ratios < 1.0 are characteristic of the *G. agassizi*-group (*G. agassizi* and *G. berlandieri*) rather than the *G. polyphemus*-group (*G. polyphemus* and *G. flavomarginatus*; Legler and Webb, 1961). This ratio in a series of 21 *G. agassizi* from Arizona, California and Sonora, Mexico, in the University of Arizona Department of Biological Sciences Herpetological Collection (UAZ) ranged from 0.40–0.90 with averages of 0.59 and 0.66 for females and males, respectively. The gular projection is relatively better developed in the *G. agassizi* group; the fossils have gular projections very similar to *G. agassizi*. The shell in the Dry Cave fossil is oblong, longer than wide: carapace L/W = 1.22; plastron L/W = 1.38. The L/W ratio for the plastron is identical to the average for a series of *G. agassizi* and greater than the average (1.25) or largest value (1.33) for a series of *G. berlandieri* (Carr, 1952). This ratio for the Shelter Cave plastron is = 1.42. This ratio for the UAZ series of 21 specimens was 1.40–1.65, mean 1.52. The Dry Cave shell was from a female with a carapace length of 252 mm (L/W = 1.22). This is larger than the maximum for *G. berlandieri* (219 mm, male; Auffenberg and Weaver, 1969), but within the range of 230-265 mm for sexually mature females (males are larger) G. agassizi (Woodbury and Hardy 1948). The Shelter Cave plastron was also from a female, but ≈ 14% larger than the Dry Cave specimen. Tables 2 and 3 present the measurements from all fossil specimens.

Bone carbonates from Sabertooth Camel Maze and Vanishing Floor Room yielded radiocarbon dates of 25,160 ± 1730 (Tx-1775) and 33,590 ± 1500 (Tx-1773), respectively. While dates on bone carbonate are not as reliable as those on wood or plant material, these dates serve to place the fossils in the mid-Wisconsinan interstadial from 25,000–35,000 years ago.

DISCUSSION

During the late Pleistocene, G. agassizi lived in the northern Chihuahuan Desert in south-central and southeastern New Mexico. The few records available suggest that G. agassizi was present during the mid-Wisconsinan interstadial and during

TABLE 2.—Measurements (mm) of late Pleistocene *Gopherus agassizi* from Dry Cave, Eddy County, New Mexico. All specimens are in the Museum of Arid Land Biology, University of Texas at El Paso.

Specimen no.	Element	Midline length	Width	
			Max	Across plastron
27–88	Bones: epiplastron	20	46	
	entoplastron	43	42	
	hyoplastron	58	88	
	hypoplastron	50	88	
	xiphiplastron	50	59	
	Sutures: epi-hyoplastral			89
	hyo-hypoplastral			150
	hypo-xiphiplastral			118
	Scutes: gular	30	20	
	humeral	48	57	
	pectoral	13	87	
	abdominal	73	93	
	femoral	32	63	
	anal	26	34	
	Sulci: gulo-humeral			42
	humero-pectoral			114*
	pectoro-abdominal			161
	abdomino-femoral			129
	femoro-anal			67
	Anterior lobe of plastron:	L/W = 60/122 = 0.49		
	Posterior lobe of plastron:	L/W = 49/146 = 0.34		
	Gular notch:	L/W = 9/11 = 0.82		
	Anal notch:	L/W = 10/33 = 0.30		
	Nuchal scute:	L/W = 11/12 = 0.92**		
26–243	Nuchal: bone	L/W = 42/49 = 0.86		
	scute	L/W = 12/14 = 0.86		
5–109	Nuchal: bone	L/W = 40/48 = 0.83		
	scute	L/W = 9/15 = 0.60		
5–253	Nuchal: scute	L/W = 12/15 = 0.80**		
5–252	Right xiphiplastron: bone	L/W = 32/38 = 0.84		
	anal scute	L/W = 19/25 = 0.76		
	anal notch	L/W = 10/20 = 0.50*		
5–110	Right xiphiplastron: bone	L/W = 35/41 = 0.85		
	anal scute	L/W = 20/24 = 0.83		
	anal notch	L/W = 8/24 = 0.33*		
26–231	Left xiphiplastron: bone	L/W = 38/55 = 0.69		
	anal scute	L/W = 19/32 = 0.59		
	anal notch	L/W = 14/26 = 0.54		

* = Estimate.
** = Bone fragmentary.

the latest Wisconsinan of 10,000 to 12,000 years ago. We do not know if *G. agassizi* lived in the Chihuahuan Desert region during the full-glacial period of 18,000 to 21,000 years ago, or if it survived into the Holocene.

The plant macrofossil record of the latest Wisconsinan preserved in ancient packrat or woodrat (genus *Neotoma*) middens in the Chihuahuan Desert can help to reconstruct the Ice Age habitats of the desert tortoise. Three fossil packrat middens collected from between Shelter and Conkling Caves on Bishop's Cap contain a record of a very xerophilous woodland. Woodland species that do not presently occur on Bishop's Cap are juniper (*Juniperus* sp.) and netleaf hackberry (*Celtis reticulata*). A suite of other plant species were associated with them, but the xeric-adapted Chi-

TABLE 3.—Measurements (mm) of late Pleistocene *Gopherus agassizi* from Shelter Cave, Doña Ana County, New Mexico. Specimen is in Los Angeles County Museum of Natural History (LACM 1010/58912).

Specimen No.	Element		Midline length	Widths	
				Max	Across plastron
LACM 1010/ 58912	Bones:	epiplastron	29	50	
		entoplastron	52	44	
		hyoplastron	66	97	
		hypoplastron	59	97	
		xiphiplastron	50	57	
	Sutures:	epi-hyoplastral			98
		hyo-hypoplastral			183*
		hypo-xiphiplastral			113
	Scutes:	gular	35	23	
		humeral	57	60	
		pectoral	18	92	
		abdominal	83	96	
		femoral	37	63	
		anal	24	37	
	Sulci:	gulo-humeral			46
		humero-pectoral			122
		pectoro-abdominal			180*
		abdomino-femoral			127
		femoro-anal			74
	Anterior lobe of plastron:		L/W = 95/127 = 0.75		
	Posterior lobe of plastron:		L/W = 73/128 = 0.57		
	Gular notch:		L/W = 4/7 = 0.57		
	Anal notch:		L/W = 8/34 = 0.23		

* = Estimate

huahuan Desert species, such as creosotebush (*Larrea divaricata*) and mariola (*Parthenium incanum*) were not found. Radiocarbon dates on juniper seeds and twigs from the middens were 10,260 ± 250 (A-1573), 10,650 ± 170 (A-1571) and 10,780 ± 240 (A-1572) radiocarbon years ago (YBP) (Table 1). This late Pleistocene plant community is probably very similar to those at Shelter and Conkling caves when the fossil *G. agassizi* were deposited.

The late Pleistocene plant communities in the southern Guadalupe Mountains were recently studied using plant macrofossils preserved in a packrat midden and pollen preserved in cave fill from Williams Cave (Van Devender, et al., in press). At 12,040 ± 210 YBP (A-1540, on juniper), the paleocommunity was also a woodland, but was relatively more mesic than Bishop's Cap. Besides juniper, Colorado pinyon (*Pinus edulis*), oak (*Quercus* sp.), and black cherry (*Prunus serotina*) were present. Williams Cave is 55 km SSW of Dry Cave (1330 m elevation) in Culberson County, Texas, at 1495 m elevation. Xerophilous woodland probably extended to the lowest elevations (1075 m) in the valleys surrounding the Guadalupe Mountains at that time. Wells' (1966) study of fossil packrat middens showed that xerophilous woodland occurred as low as 615 m in the Big Bend of Texas 330 km south of the Guadalupe Mountains, and probably covered most of Trans-Pecos Texas at higher elevations. Late Pleistocene *Gopherus agassizi* lived in that woodland and could have been more widespread in the Trans-Pecos than present records suggest. There are no plant macrofossil records for the mid-Wisconsinan interstadial, but the faunal records from Dry Cave imply temperatures slightly more moderate than today with slightly more effective summer precipitation (Harris, 1970, in press). The vegeta-

tion may not have been greatly different from the late Wisconsinan communities.

Gopherus agassizi is a species of the low, hot deserts in its present geographic range; it would rarely, if ever be found in a woodland today. The eastern limits of its present distribution are near Benson, Cochise County, Arizona (Stebbins, 1966; Fig. 1). This is a transitional area where several Chihuahuan species, such as the Texas horned lizard *(Phrynosoma cornutum)* and tarbush (*Flourensia cernua)*, reach their western limits. Sonoran species reaching their eastern limits include the saguaro *(Cereus giganteus)* and the palo verde (*Cercidium microphyllum)*. The present distribution of *Gopherus agassizi* would suggest that it is a cold-sensitive species limited by low winter temperatures to the east. The Pleistocene localities for it are 350 to 550 km farther east. The familiar climatic reconstruction of winters similar to present ones or milder and with cooler summers may help to explain this record, i.e., harsh winters with very low temperatures would kill tortoises even in their burrows; cooler summer temperatures would allow woodland plants to exist at lower elevations. The extirpation of *G. agassizi* from the Chihuahuan Desert is difficult to explain climatically, because it presently lives in habitats as hot and dry as the Chihuahuan Desert today. More severe winters in the Holocene may have been involved, but we hesitate to infer this from negative evidence.

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(TRVD and KBM) *Department of Geosciences, University of Arizona, Tucson, Arizona* 85721, *USA, and* (AHH) *Museum of Arid Land Biology, University of Texas, El Paso, Texas* 77968, *USA*