A NEW GIANT TURTLE OF THE GENUS *GOPHERUS* (CHELONIA: TESTUDINIDAE) FROM THE PLEISTOCENE OF TAMAULIPAS, MÉXICO, AND A REVIEW OF THE PHYLOGENY AND BIOGEOGRAPHY OF GOPHER TORTOISES

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ABSTRACT—The new giant turtle species *Gopherus donlaloi* is described from a partial skeleton with skull collected in the Rancholabrean deposits in northeastern México. The skull resembles the skull of extant turtles *G. polyphemus* and *G. flavomarginatus* but the new species shows unique skull and shell features. Shell meristic variation of the new species, *G. berlandieri*, and G. laticuneus is discussed denoting problems in the assessment of species based on extremely variable shell characters. Lack of diagnostic features in shells of *G. edae* and *G. hexagonatus* suggests their status as *nomina vana*. A cladistic strict consensus tree suggests that *Gopherus* is a monophyletic group where *G. mohavetus* falls within the outgroup, questioning its status as a member of *Gopherus*. Oligocene *G. laticuneus* is sister to all *Gopherus*, after which Recent *G. berlandieri* and *G. agassizii* branched out paraphyletically. *Gopherus* sensu stricto is monophyletic but the relationships among its taxa are unknown; these include the Miocene *G. brevisternus*, *G. pansus*, and *G. vagus*, the Plio-Pleistocene *G. canyonensis* and *G. donlaloi*, and the Recent *G. polyphemus* and *G. flavomarginatus*. A second analysis excluding most incomplete taxa retains the polytomy of *G. berlandieri*, *G. agassizii*, and *Gopherus* sensu stricto, but resolves the relationships within *Gopherus* sensu stricto. *G. brevisternus* is sister to the rest of the clade, followed by *G. flavomarginatus*, after which there is a polytomy formed by *G. canyonensis*, *G. donlaloi* and *G. polyphemus*. Bootstrap and branch-support analyses indicate that the clades within *Gopherus* sensu stricto are well supported. Reanalysis of biogeographic relationships based on the phylogeny suggests that the origin of *Gopherus* sensu stricto can be traced to the Miocene on the Central Plains, later extending southward from eastern Arizona to Florida and from northern Texas to Aguascalientes during the Plio-Pleistocene. The extinction of giant gopher turtles in Texas and eastern Mexico associated with the invasion of their distribution area by *G. berlandieri* is the best hypothesis to explain the recent disjunct distribution of *G. polyphemus* and *G. flavomarginatus*.

INTRODUCTION

Gopherus is a broadly distributed group of large turtles endemic to North America. Four valid living species are recognized: *Gopherus agassizii*, *G. berlandieri*, *G. flavomarginatus*, and *G. polyphemus* (Auffenberg, 1974), ranging from southwestern Utah in North America, as far south as the Bolsón de Mapimí in Durango, México, and from western California to the Atlantic Coastal Plains in Florida (Ernst and Barbour, 1989).

The genus *Gopherus* has fossil representatives from the Oligocene to the Recent. Taxonomically, it is a very complicated group since most of the known fossil species have been described from fragmentary skeletons to which specific names have been given. Recent reviews of the genus are those of Auffenberg (1974) and Bramble (1982), suggesting several synonymies and allocating species to different tortoise groups, considerably reducing the number of previously recognized species. Despite this, many of the still valid species are represented by remains that lack characters diagnostic of the species or even generic level.

Most fossil species of *Gopherus* are known from fragments and only four are known from complete skeletons with skulls. These are: *Gopherus canyonensis* Johnston, 1937, *G. brevisternus* Loomis, 1909, *G. laticuneus* Cope, 1873, including the skull described by Gilmore (1946) as *G. praeextans*, and *G. mohavetus* Merriam, 1919 (Brattstrom, 1961) of which the skull is poorly known. Since osteological features of most gopher turtles are unknown, the establishment of synonymies and phylogenetic relationships of fossil and living species is far from well understood. A summary of the current status of fossil *Gopherus* is presented in Table 1.

The earliest fossil representatives of gopher turtles date from the early Oligocene, are grouped within the *Scaptochelys* (or *Xerobates*) paraphyletic group (Crumly, 1993), and are considered closely related to *G. agassizii* and *G. berlandieri*. The fossil record of the *Gopherus* sensu stricto group (a monophyletic assemblage that includes *G. polyphemus* and *G. flavomarginatus*), is known from the early Miocene to Recent. Localities with fossil remains are very scattered, making biogeographical trends difficult to establish.

In México, the fossil record of *Gopherus* is sparce. The group had only been reported from one locality, the Pleistocene of Aguascalientes from which *G. auffenbergi*, *G. flavomarginatus*, and *G. pargensis* are known (Mooser, 1972; 1980). Of these taxa, *G. auffenbergi* was referred to *G. berlandieri* by Bramble (1982), and the validity of *G. pargensis* cannot be assessed since it was based on an undiagnostic shell fragment with the left posterior peripherals and attached incomplete pleurals. An almost complete plastron with some peripheral plates and limbs, housed at the Museo Regional de Historia of the Instituto Nacional de Antropología e Historia, in the city of Aguascalientes, is probably Mooser's specimen FC 507 referred to *G. flavomarginatus* (Valencia-Cruz and Guzmán Gutiérrez, 1994). Also known is a recently recovered carapace housed at the Universidad Autónoma de San Luis Potosí (M. Alvarado, pers. comm.), which still needs to be studied.

This paper reports the presence of a new species of a Pleistocene giant *Gopherus* recovered in western Tamaulipas (Fig. 1). After a report from the local people of the Ejido de San Lázaro, fieldwork was carried out in the area. As a result, several sites bearing fossil vertebrates were located and fossil remains were collected. Most of the fossils are moderately well preserved, al-

though there are a few exceptional cases such as the two almost complete carapaces, one of them with skull, presented here. These new findings increase our understanding of various aspects of the historical biogeography of recent *Gopherus* based largely on phylogeny and the fossil record.

Abbreviations—**IGM**, Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. Carapace nomenclature is that of Auffenberg (1976), and manus description is following Bramble (1982). All measurements are in millimeters.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768
TESTUDINES Batsch, 1788
TESTUDINIDAE Gray, 1825
GOPHERUS Rafinesque, 1832
GOPHERUS DONLALOI, sp. nov.
(Figs. 2–5, 7)

Holotype—IGM 6076, Universidad Nacional Autónoma de México, Instituto de Geología, partial, well-preserved, not yet fully ossified young adult with complete skull, anterior half of carapace with most of plastron, right shoulder girdle with scapula and coracoid, left scapula, complete right forelimb with humerus, radius, ulna, carpals, metacarpals, and complete set of phalanges, partial left forelimb with humerus, radius and ulna, broken left femur, proximal portions of right tibia and fibula, six cervical vertebrae (atlas, axis, and vertebrae 3–6), first dorsal unattached to shell, and ten caudal vertebrae.

Paratypes—IGM 6079, almost complete shell of old adult with carapace moderately flattened and separated from plastron, eighth cervical vertebra, almost-complete pelvis, and right humerus and shoulder girdle (coracoid and scapula). IGM 6075, small plastron of juvenile.

Locality and horizon—Lands of Ejido San Lázaro in the Municipio de Villagrán in the northwestern part of the State of Tamaulipas, 80 km north of Ciudad Victoria, México (Fig. 1). The fossil vertebrates were collected from a light yellow clay, which bears remains of *Glyptotherium* sp., *Equus conversidens*, *Mammuthus* sp., and *Bison* sp. The presence of the latter genus suggests a Rancholabrean age.

Etymology—For Don Lalo Martínez, one of the major supporters of vertebrate paleontology in the State of Tamaulipas, an excellent field worker and story teller (he never tells the same one twice).

Diagnosis—An extremely large turtle with maximum known plastron length of 520 mm. The skull is high, with a wide and short temporal region (brachycephalus), similar to *G. flavomarginatus*. The skull shape is the result of the lateral widening of the prootic, opisthotic, and supraoccipital, to shelf an enlarged otic cavity and probably a large otolith. The prefrontals are pronounced, forming a hump, the posteroventral process of the maxilla is enlarged, the skull roof emargination is transversely oriented, the prootic and the opisthotic are in contact, and the quadrate foot is oriented slightly anteriorly. It differs from other *Gopherus* sensu stricto turtle skulls in its larger size (except for *G. canyonensis*), the more oval shape of the external nares, with a broad ventral process of the prefrontal and a wide dorsal process of the premaxilla extending between the nares, a large depression on the antero medial surface of the maxilla within the nares which stretches the premaxillae posterior to the nares dorsal process, a more pronounced hump on the forehead, relatively small eyes, parietals not extended onto the posterior supraoccipital process (crest), a parietal depression on the frontoparietal suture, premaxillary ridge ending in a T-shaped structure (not with a forked Y-shaped end), nasopalatine foramen considerably small and rounded, basioccipital and basipterygoid shortened

anteroposteriorly because of brachycephaly, marginal scutes 5, 6, and 7 of about the same size and shape contacting the second pleural scute, a single inguinal scute separated from the femoral scute by a projection of the abdominal scute, which extends to contact the plastral rim, plastron anterior lobe 1/4 to 1/3 of plastral length with a considerable increment in the anterior projection in some specimens, anterior projection of the plastron rounded, and pisciform probably present.

Description

The Skull—The skull is only known from the holotype specimen (Figs. 2, 3). It is almost complete with the lower jaw attached to the skull but displaced laterally covering the palate transversely. Most of the left jugal, postorbital, and quadratojugal are broken, as well as the right jugal and squamosal. The supraoccipital lacks the dorsal crest.

The skull length is 89.8 mm from the anterior end of the premaxillae to the posterior margin of the squamosal. The standard length of Auffenberg (1976) to the posterior end of the supraoccipital crest cannot be estimated since the crest is broken. Auffenberg's standard width is 84.8 mm, giving a 1:1 skull proportion (brachycephalus) as in *G. flavomarginatus*. Other skull measurements are in Table 2.

The premaxillae form a wide narial projection that divides the external nares. The maxillae are short anteroposteriorly. The premaxillary process is wider compared to that of *G. flavomarginatus* and *G. polyphemus*, resembling the condition of *G. agassizii*. The prefrontal process of the maxilla is also relatively wider compared to extant *Gopherus*, but never as wide as in *G. canyonensis*. The posteroventral process is well extended and obliquely oriented. The postorbital process of the maxilla is broken on both sides. On the medial face of the maxilla forming the narial floor of the air passageway, there is a large anterior depression just posterior to the lateral margins of the external nares separated from a large posterior depression by a well-developed ridge (Fig. 4A). Neither the anterior nor posterolateral depressions of the air passageway were observed in any other gopher turtle, in which the narial floor is flat.

The prefrontals are expanded dorsally, forming the characteristic hump of *G. flavomarginatus* and *G. polyphemus*. The nasal process is considerably wide, giving each naris a more oval shape and preventing the dorsal margin from being confluent as in other *Gopherus*. The prefrontal-frontal suture is more or less straight and reaches the orbital rim, as in *G. flavomarginatus*. This condition differs from that in *G. polyphemus*, in which the orbital margins of the prefrontals extend posteriorly, reaching the postorbital and excluding the frontals from the orbit. Posterior to the dorsal margin of the orbit there is a notch that slightly restricts the frontals. In dorsal view, the lateral margins of the prefrontal and frontals (forming the dorsal margins of the orbit) extend slightly obliquely in relation to the skull main axis, as in *G. agassizii*. This differs from other extant *Gopherus* in which these margins are parallel to one another.

The orbits are relatively small, being only the 25% of the total skull length. The orbit is round but slightly compressed anteroposteriorly, as in *G. canyonensis*; however, in the new species, a dorsal notch in the frontal (and not a ventral shallow constriction) enlarges the orbit dorsoventrally. A similar notch is observed in *G. agassizii*, but the one in *G. donlaloi* is more abrupt. Excluding the notch, all opposite points of the orbital rim are equal in length. The bones limiting the orbit are the maxilla anteroventrally, the prefrontal and frontals dorsally, and the postorbital posteriorly. The length of the postorbital process of the maxilla or whether the jugal is present cannot be estimated; however, judging from the breaking point and outline of both the maxilla and the postorbital, the postorbital bar of the maxilla is thin as in *G. flavomarginatus*.

A small depression is distinguished in the joint of the frontals

TABLE 1. Valid species of *Gopherus* as used in this paper, presented according to the results obtained in the cladistic analysis

	Valid species	Taxa included	Locality	Geologic range	Reference
Gopherus Rafinesque, 1932					
Basal *Gopherus*	*G. laticuneus* Cope, 1873		Weld Co., Colorado	Early Oligocene	
		Testudo praeextans Lambe, 1913	Weld Co., Colorado; Dawes Co. and Sioux Co., Nebraska; Zeibach Co., S Dakota; Niobrara Co., Wyoming	Eocene/Oligocene boundary	Auffenberg, 1974; Gilmore, 1946; Bramble, 1982, Hutchison, 1996.
		T. quadrata Cope, 1884	Weld Co., Colorado		Hutchinson, 1996
		T. thomsoni Hay, 1908	Ziebach Co., S Dakota	Middle Oligocene	Hutchinson, 1996
Xerobates group	*G. agassizii* Cooper, 1863		SE California, SE Nevada SW Utah, S Arizona, Sonora, N Sinaloa. Probably introduced to S Baja California Sur	Recent	Iverson, 1992
		G. agassizii	Doña Ana Co., New Mexico; San Bernardino Co., California	Late Pleistocene	Brattstrom, 1961
		G. agassizii	Clark Co., Nevada	Late Pleistocene	Brattstrom, 1961
		G. agassizii	Doña Ana Co. and Eddy Co., New Mexico	Pleistocene	Van Devender, et al. 1976
	G. berlandieri Agassiz, 1857		S Texas, E Coahuila, Nuevo Leon, Tamaulipas, E San Luis Potosi	Recent	Iverson, 1992
		G. auffenbergi Mooser, 1972	Mpio. de Aguascalientes, Aguascalientes	Pleistocene (Irvingtonian)	Bramble, 1982
Gopherus s.s. group	*G. brevisternus* Loomis, 1909		Laramie Co., Wyoming	Early Miocene	
	G. flavomarginatus Legler, 1959		Bolson de Mapimí: SE Chihuahua, W Coahuila, N Durango	Recent	Iverson, 1992
		G. flavomarginatus	Maricopa Co., Pima Co. and Graham Co., Arizona	Pleistocene	Bramble, 1982
		G. flavomarginatus	Mpio. de Aguascalientes, Aguascalientes	Middle Pleistocene	Mooser, 1980
		G. huecoensis Strain, 1966	Hudspeth Co., Texas	Early Pleistocene	Auffenberg, 1974; Bramble, 1982
	C. canyonensis Johnston, 1937		Randall Co., Texas	Early Pleistocene	
		G. pertenius Cope, 1892	Crosby Co., Texas	Late Pliocene	Bramble, 1982
	G. donlaloi sp. nov. Reynoso and Montellano		Mpio. de Villagrán, Tamaulipas	Late Pleistocene	This paper
	G. polyphemus Daudin, 1802		NE Louisiana, S Mississippi, S Alabama, S Georgia, Florida and probably S South Carolina	Recent	Iverson, 1992
		G. atascosae Hay, 1902	Atascosa Co., Texas	Middle Pleistocene?	Auffenberg, 1974; Bramble, 1982
		G. praecedens Hay, 1916	St. Lucie Co., Florida	Late Pleistocene	Auffenberg, 1974
Gopherus s.s. uncertain relationships	*G. vagus* Hay, 1908		Albany Co., (?), Wyoming	Late Miocene	
	G. pansus Hay, 1908		Weld Co., Colorado	Late Miocene	
Not *Gopherus*	*G. mohavetus* Merriam, 1919		San Bernardino Co., California	Late Miocene	This paper
		G. brattstromi Brattstrom, 1961	Kern Co., California	Late Miocene	Auffenberg, 1974; Bramble, 1982
		Tsetudo milleri Brattstrom, 1961	San Bernardino Co., California		Bramble, 1982
nomina vana	*G. edae* Hay, 1907		Sioux Co., Nebraska	Early Miocene	This paper
	G. hollandi Hay, 1907		Sioux Co., Nebraska	Early Miocene	Auffenberg, 1974; Bramble, 1982
	G. hexagonatus Cope, 1893		Briscoe Co., Texas	Middle to late Pleistocene	This paper

TABLE 1. Valid species of *Gopherus* as used in this paper, presented according to the results obtained in the cladistic analysis

	Valid species	Taxa included	Locality	Geologic range	Reference
nomina vana		*G. laticaudatus* Cope, 1893	Briscoe Co., Texas	Middle Pleistocene (incorrectly Pliocene by Hay)	Auffenberg, 1974; Bramble, 1982
		G. hexagonatus	Willacy Co., Texas	Late Pleistocene	Westgate, 1989
		G. hexagonatus	Brown Co., Kansas	Pleistocene	Hibbard, 1960
		G. hexagonatus	San Patricio Co., Texas	Early Wisconsian, Late Pleistocene	Auffenberg, 1962; Lundelius, 1972
	G. pargensis Mooser, 1980		Mpio. de Aguascalientes, Aguascalientes	Middle Pleistocene-Recent	This paper

and the parietals. This depression resembles in position the pineal foramina of other reptiles. In *G. flavomarginatus* (an adult) this depression is also present, but in an interfrontal position. Posteriorly, the parietals do not extend over the supraoccipital crest, ending anterior to the level of the posterior end of the opisthotic. In other *Gopherus* species, the parietals ride high over the supraoccipital crest. Although broken, the supraoccipital crest appears not to be too pronounced, being similar to that of *G. polyphemus*.

The postorbital bones are as in other species. The postorbital arcade is narrow as in all *Gopherus*, except for *G. brevisternus*, in which it is broad. Seen from above, the emargination for the adductor musculature is short and laterally elongated. This is caused by the anterior displacement of the postorbital, with the concomitant formation of the frontal notch described above. This condition is similar to that of *G. canyonensis*, but the hollow is even narrower anteroposteriorly. Among extant *Gopherus*, only *G. polyphemus* and *G. flavomarginatus* have an anteroposteriorly narrow dorsal hollow, but in these species it is not as narrow and remains obliquely oriented. The quadratojugal is arched as in other *Gopherus*, but in *G. donlaloi*, the exact shape of the bone is not known. However, judging from the outline of adjacent bones, the lateral emargination is pronounced, resulting in a narrow lateral arcade. This arcade can be compared to that of *G. flavomarginatus*, which has the narrowest arcade among gopher turtles, and strongly contrasts with the broad arcade of *G. canyonensis* and *G. brevisternus*.

The dorsal surface of the otic region is considerably less depressed than in other *Gopherus* species. This can be clearly observed in occipital view in which the orbits are barely exposed when seen from behind. This shallow depression causes the quadrate-squamosal dorsal expansion to appear less pronounced. The structure of the otic region is similar to that described by Bramble (1982) for *Gopherus* sensu stricto. The otic chamber is very large, and although the presence of a large saccular otolith cannot be verified, this certainly could be present. The anterior face of the otic region is structured by the prootic and the quadrate only. The participation of the parietal is reduced since there is not an extensive overlap of this bone onto the prootic. The anterior face of the prootic is flat, as in *G. agassizii*, but perpendicular to the main axis of the skull. The surface for the trochlear process of the otic chamber (for the articulation of the *cartilago transiliens*) is reduced relative to the skull size. This surface is about the size of that in an adult skull of *G. flavomarginatus*, which is only about half the size of the holotype of *G. donlaloi*.

The bones making up the otic region are widened laterally as in *G. flavomarginatus* and *G. polyphemus*. The prootic is well exposed anteriorly. Laterally, the otic opening in the quadrate is broad as in all gopher turtles, and certainly does not resemble the "greatly narrowed" condition present in *G. brevisternus* (Loomis, 1909). The quadrate is slightly anteriorly oriented as in *G. flavomarginatus*, *G. polyphemus*, and *G. canyonensis*, but not as much as in *G. agassizii*. The exoccipitals resemble condition 1 or 2 of Auffenberg (1976) in which the basal foramina are open.

Ventrally the palate is broad and deep. The dorsal projection of the vomer is extensive, even more than that of *G. flavomarginatus* and *G. polyphemus*. The ventral face of the premaxilla has the typical *Gopherus* medial ridge. This ridge contacts the maxillary internal ridge forming a T (or a broad Y) shape, in contrast to the acute Y shape present in *G. flavomarginatus*. The maxillary medial ridges are interrupted at the premaxilla-maxilla
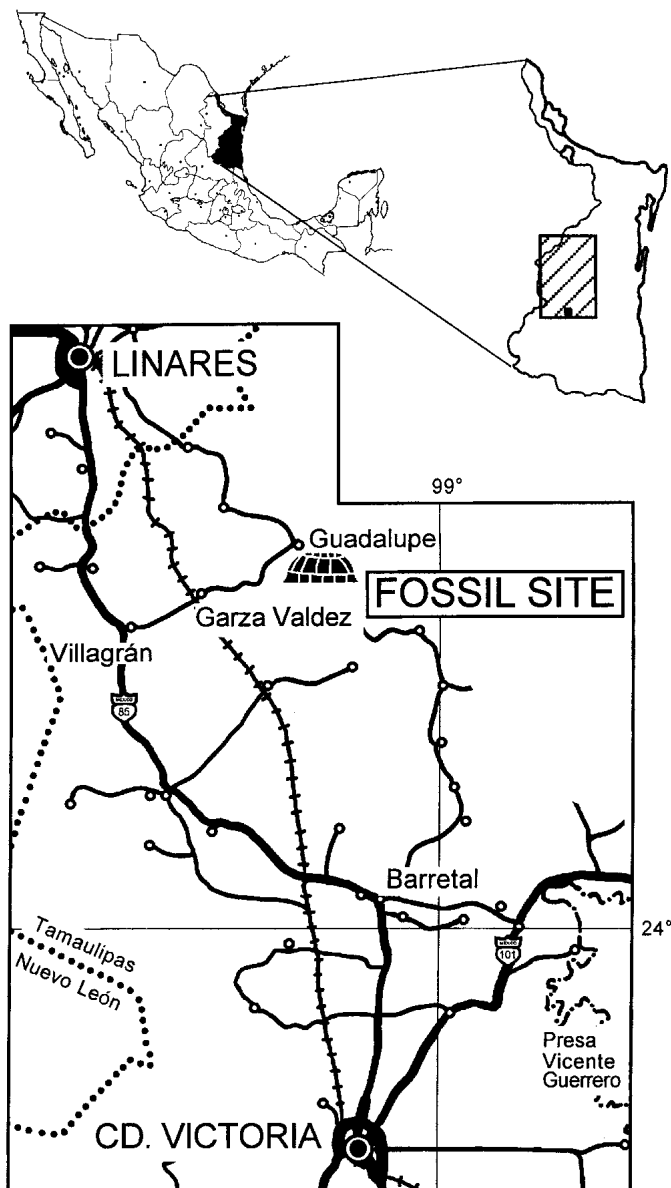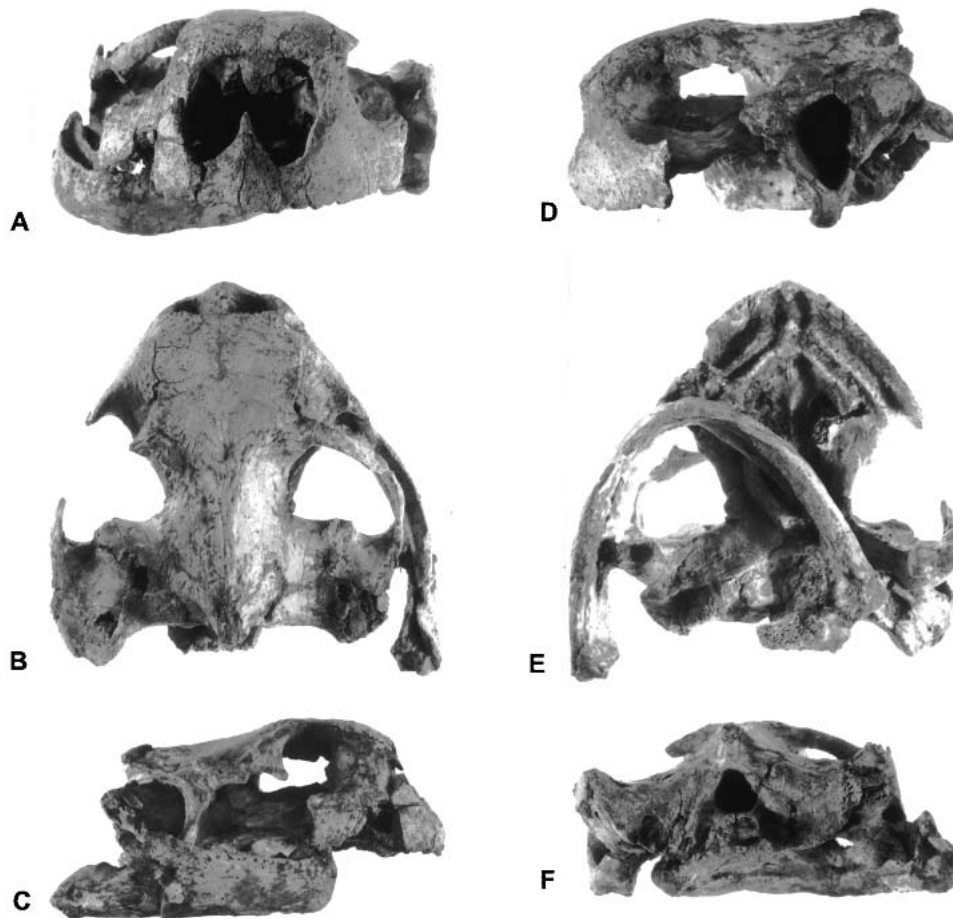

FIGURE 1. Locality map.

FIGURE 2. *Gopherus donlaloi*, IGM 6076 (holotype), skull as preserved. **A**, anterior view; **B**, dorsal view; **C**, right lateral view; **D**, left lateral view; **E**, palatal view; **F**, occipital view. ×2.2.

suture. The anteromedial vomerine aperture is absent and the foramen prepalatinum is large. The prefrontal pit is very similar to that of *G. flavomarginatus* in shape, proportions and position. The orbitonasal foramen is enlarged as in other *Gopherus* species (except *G. laticuneus*), but anteroposteriorly shortened (Fig. 4B). It appears that the reduction of this fenestra is mainly caused by the absence of a deep emargination on the palatine bone, since the emargination on the prefrontal is equal to that of other species. The fenestra is limited laterally by the maxilla; therefore, the palatine and the prefrontal are not in contact within the floor of the orbit. As in *G. polyphemus*, the orbitonasal fenestra is hidden in dorsal view by the prefrontal.

The posterior part of the skull is shorter than in any other known *Gopherus* species. This reduction directly affects the anteroposterior length of the basioccipital and the basipterygoid, which are very short. The basipterygoid does not enter the mid palatal ridge as in *G. flavomarginatus* and *G. polyphemus*.

Cervical and Caudal Vertebrae—Cervical vertebrae are present in the holotype. The atlas was apparently broken in preparation, leaving the anteroventral portion attached to the occipital condyle, but the remaining piece is almost complete and separated. The heavily constructed axis, vertebrae 3 to 6, and first dorsal that was removed from its original attaching point from the shell, are very well preserved. The 8th cervical vertebra is preserved in IGM 6079, which was still articulated before preparation. This vertebra has very elongated postzygapophyses to match the wide and also enlarged prezygapophyses of the first dorsal, giving the head a great capacity of movement.

Ten caudal procoelous vertebrae are preserved but do not appear to be contiguous. Most anterior vertebrae are elongated, of almost about the same size as the cervical vertebrae, and decrease in size posteriorly. Mid-caudal vertebrae are less than half the size of the anterior ones and have small lateral ribs fused to the centrum. The ribs decrease in size in most posterior vertebra, almost disappearing toward the last known vertebra. Some of the mid-caudal vertebrae are shortened anteroposteriorly and slightly flattened, having the zygapophyses somewhat separated.

The Shell—The shell of the larger specimen IGM 6079 probably belongs to an old individual (Fig. 5A, B) with most of its plates fully ossified; the holotype (Fig. 5C, D) appears to be slightly younger, and IGM 6075 is a small juvenile. Shell measurements are presented in Table 3. Both larger shells show some degree of ossification making the outlining of most plates difficult. This problem is increased by the great amount of breaking lines on the carapace and plastron; however, the structure of the shell does not differ to any great extent from that of any of the known species of *Gopherus*, extinct or alive. The pattern of the dorsal plates corresponds to pattern "D" of Auffenberg (1976:fig. 22), the most common among extant species of *Gopherus*, in which oblique sutures separate pleural plates with alternating wide and narrow bases (Fig. 5A, C). The shell is simple, lacking the lateral bony expansion of the posterior peripherals, present in *G. berlandieri* and *G. agassizii*. In the holotype, the 5th, 6th, and 7th peripheral scutes are about the same size and shape, and contact the second pleural scute, as in
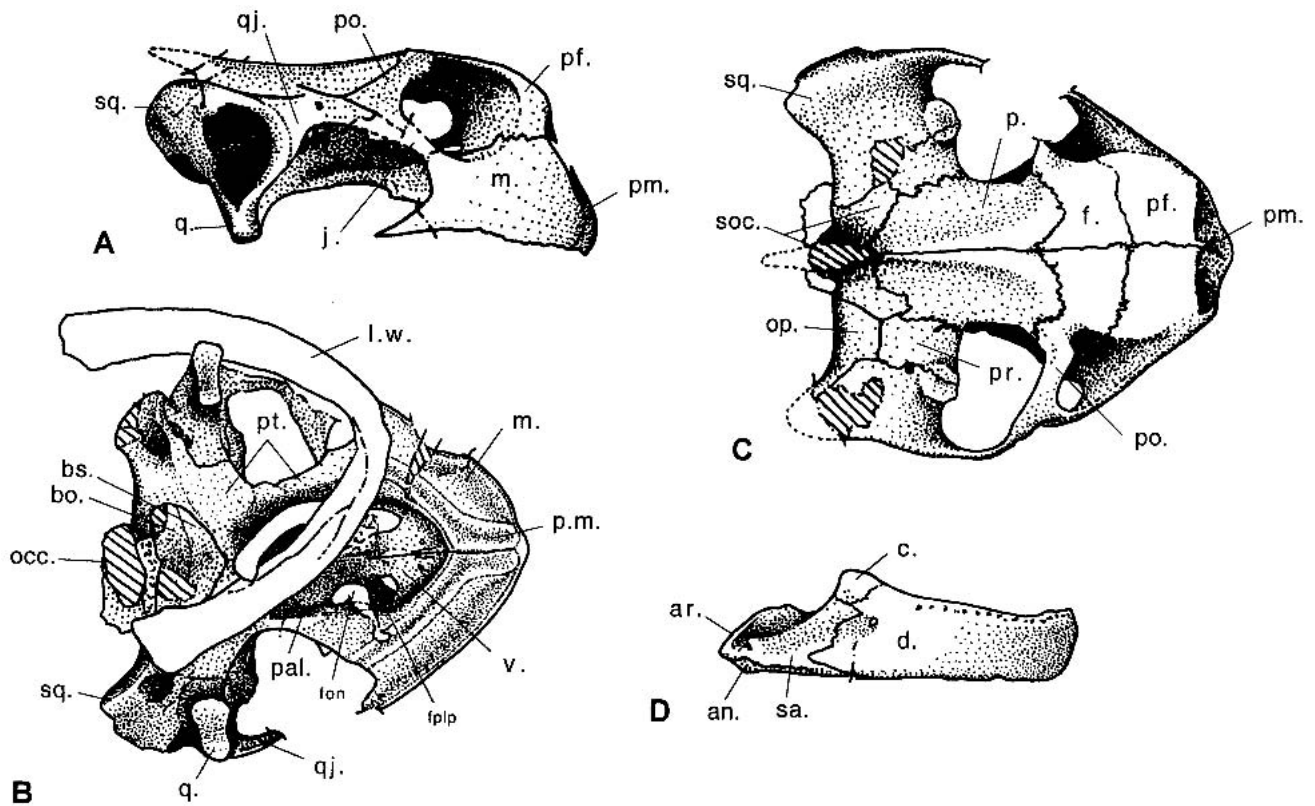
FIGURE 3. *Gopherus donlaloi*, IGM 6076 (holotype), semireconstruction of the skull. **A**, lateral view; **B**, palatal view; **C**, dorsal view; **D**, lateral view of the lower jaw. **Abbreviations**: **an**., angular; **ar**., articular; **bo**., basioccipital; **bs**., basisphenoid; **c**., coronoid; **d**., dentary; **f**., frontal; **fon**., foramen orbitonasale; **fplp**., foramen palatinum posterioris; **j**., jugal; **l.w.**, lower jaw; **m**., maxilla; **occ**., occipital; **op**., opisthotic; **p**., parietal; **pf**., prefrontal; **po**., postorbital; **pm**., premaxilla; **pr**., preorbital; **pt**., pterygoid; **q**., quadrate; **qj**., quadratojugal; **sa**., surangular; **soc**., supraoccipital; **sq**., squamosal; **v**., vomer.

G. hexagonatus (Cope, 1893). In the larger specimen (IGM 6079), the shell appears to be large and flat; however, this is caused by distortion. Reconstructing the distance between the posterior end of the plastron and the posterior end of the cara-

pace, the shell must have measured about 580 mm. Judging from the holotype, the best preserved specimen, the shell appears to be high, as in extant *Gopherus*. This specimen, however, does show some degree of compression. The arrangement of the

TABLE 2. Measurements of known fossil giant gopher turtle skulls included within *Gopherus* sensu stricto (in mm). *ratio based on the width between quadrates. Measurements in parentheses are approximate

| Measurement	*G. canyonensis*	*G. brevisternus*	*G. donlaloi*
Skull length from anterior end of premaxilla to occipital condyle	124	70	89.4
Greatest skull width	—	77	84.1
Greatest skull height	—	—	(40)
Skull width/length ratio	0.91*	1.1	0.94
Skull length (from anterior margin of prefrontals to supraoccipital crest)	118	80	(82)
Width between posteroventral projections of maxilla	—	(32)	(74.5)
Width between the outer margins of quadrate	129	70	73.9
Width between outer margins of pterygoids	—	—	32.5
Width between orbits	50	25	32.7
Width of palatal fossa	52	—	24.5
Length of the lower jaw	85	—	68.8
Depth of mandible at symphysis	19	—	15.2
Orbit greatest diameter (anteroposterior)	36	23	22.5
Diameter of orbit at right angles to greatest diameter	20	—	22.5
Breadth of occipital condyle	13	—	10.3
Height of foramen magnum	15	—	11.1
Breadth across external nares	44	14	28.5
Depth of skull anterior to orbits	59	—	35.0
Depth of skull at quadrates	50	—	44.7
Breadth of skull between external margin of parietals within temporal vacuities	33	23	28.0
Breadth of palatal shelf	19	—	15.3
Length of ear opening	—	14	16.4
Height of ear opening	—	6	21.7
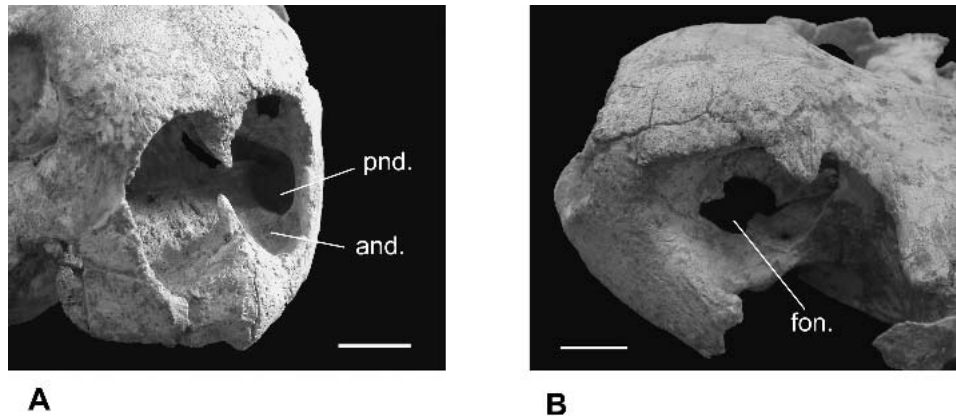
FIGURE 4.   Details of skull features. **A**, nasal view (oblique), anterior and posterior depressions on the floor of the nares air passageway. **B**, orbital view (oblique) showing the short foramen orbitonasale. **Abbreviations**: **and**., anterior nasal depression; **pnd**., posterior nasal depression; **fon**., foramen orbitonasale. Scale bars = 5 mm.

scutes is also similar to that of other gopher turtles with no special differentiation, falling within the known range of variation.

Like the carapace, the plate and scute pattern of the plastron does not differ greatly from that of other gopher turtles. The plastron is elongate, with well-developed anterior and posterior lobes. A rounded anterior projection resembles more the condition observed in *G. polyphemus* and *G. flavomarginatus*, than that of the *berlandieri-agassizii* group in which the anterior projection is bifurcated to different extents. As in most gopher turtles, the gular scute enters the entoplastron, which is rounded, with slight anterior and posterior angulations. This condition is not present consistently in *G. agassizii* and *G. auffenbergi* (the last referred to *G. berlandieri* by Bramble, 1982). The gular scute overlaps the entoplastron ventrally. The pectoral scute is enlarged and narrows anteroposteriorly toward the midline, quite similar to the condition in *G. canyonensis*; however, this bone is never as narrow as that of *G. edae* or *G. brevisternus*. There is a single inguinal scute separated from the femoral scute by an extension of the abdominal scute into the plastral rim.

The epiplastral projection is distinctively large in the older specimen (IGM 6079; Fig. 5B). In the juvenile specimen (IGM 6075), the width/length ratio of the lobe is 0.52, in the holotype it is 0.58, and in the old specimen (IGM 6079) 0.68, showing a progressive increment of slightly less than 25% in this proportion. The increase of the width/length ratio of the epiplastral projection is interesting since the increment is abrupt from the young adult compared to the old specimen. The anterior enlargement of the epiplastral projection mainly causes the increment from 25 mm to 50 mm, being quite distinct in the old specimen

(compare Figure 5B and 5D). The gular scute region of the young adult turtle extends at the most 10 mm beyond the anterior margin of the shell, and in the older specimen 65 mm, changing a major proportion of the plastron/carapace length ratio. Although both turtles have about equal shell width (440 and 460 mm respectively) and an equal anterior lobe width (both of 240 mm), the length of anterior lobe of the plastron varies from 122 to 165 mm.

The shape of the anterior lobe of the young adult turtle resembles that of the holotypes of *G. flavomarginatus*, *G. canyonensis*, *G. mohavetus*, *G. pansus*, and *G. hexagonatus*. As in these turtles, the lobe is rounded with the margin drawing a continuous line all along the sides of the lobes, showing no abrupt change in the margin line at the level of the contact of the gular and humeral scutes. In contrast, in the old specimen, the epiplastral projection projects abruptly as seen in *G. berlandieri*, *G. agassizii*, *G. atascosae* (referred to *G. polyphemus* by Bramble, 1982), *G. laticuneus*, and *G. edae*. Although these differences have been usually considered enough to separate species, the differences can also be interpreted as ontogenetic changes or sexual dimorphism. This conclusion is mainly based on the absence of evidence that two or more species of *Gopherus* could have lived sympatrically, as observed in the extant species (Ernst and Barbour, 1989), and that all specimens here described were collected within an area of 20 km^2 in sediments of the same age. Since most species have been described from unique or very few and fragmentary specimens, not much is known about the variation and ontogenetic change of (fossil) giant gopher turtles. The validity of most gopher turtles based on these characters needs to be reviewed.
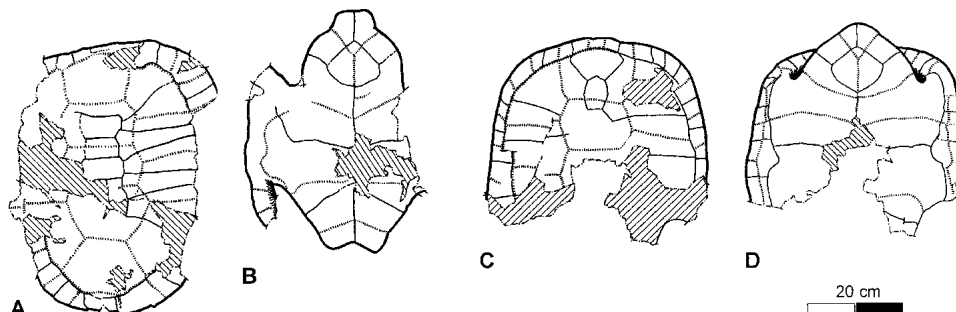

FIGURE 5.   Outline of the carapaces of *G. donlaloi* as preserved. IGM 6079 (paratype) shell (**A**) and plastron (**B**), of an old adult. IGM 6076 (holotype), shell (**C**) and plastron (**D**) of a young adult. The anteroposterior length of the shell of IGM 6079 is distorted because of compression, showing a relatively large shell when compared to the plastron.

TABLE 3. Carapace and plastron measurements of *Gopherus donlaloi* (in mm). Measurements in parentheses are approximate. *underestimated because of compression; **overestimated because of compression

Measurement	IGM 6079	IGM 6076	IGM 6075
Carapace length	580**	—	—
Carapace width	—	451	—
Carapace height	—	178*	—
Median nuchal plate	—	89	—
Median neural 1	—	64	—
Median neural 2	—	—	—
Median neural 3	—	—	—
Median neural 4	—	—	—
Median neural 5	—	—	—
Median nuchal scute	—	29	—
Median vertebral scute 1	—	106	—
Median vertebral scute 2	—	90	—
Plastron length	513	—	245
Anterior lobe length	166	126	68
Plastron width	—	390	205
Anterior lobe width at level of humeral/pectoral plates notch	215	229	105
Posterior lobe length	125	—	56
Posterior lobe width at level of abdominal/femoral scutes notch	(270)	—	118
Length of anterior lip at gulo-humeral notch	—	24	—
Width of anterior lip	—	88	—
Anterior lip thickness	37	34	17.7
Bridge	—	252	—
Anal notch depth	29	—	14
Anal notch width	44	—	18
Median epiplastral length	65	58	16
Entoplastron length	100	95	—
Entoplastron width	109	102	—
Median hyoplastral length	—	97	—
Median hypoplastral length	—	—	—
Median xiphyplastral length	—	—	—
Median gular scute length	88.7	84	31
Median humeral length	—	79	43
Median pectoral length	—	53	17
Median abdominal length	(129)	(144)	(76)
Median femoral length	823	—	(31.6)
Median anal length	41	—	21.8

A similar but more extreme variation is observed in the giant Oligocene *Gopherus laticuneus* of Wyoming (Gilmore, 1946), where two sympatric species were originally described: *G. laticuneus* and *G. praeextans* under the generic name of *Testudo* (Gilmore, 1946). These morphs have been argued to be chronological races by Auffenberg (1974) and synonymous by Bramble (1982) and Crumly (1993), although morphologically and meristically they are distinct, to such a degree that Hutchison (1996) suggested them to be sexual dimorphs. Males would be larger and more robust, with an abrupt enlargement of the epiplastral projection that ends far beyond the shell anterior margin, with almost parallel lateral sides and anterior margin bifurcated; females are significantly smaller (p = 0.002) and less robust, with a less abrupt epiplastral projection that has a rounded outline. If this is true, the larger specimen of *G. donlaloi* (IGM 6079) with large epiplastral projection is expected to be a male, and the holotype, with a shorter epiplastral projection, to be a female. Male *Gopherus* specimens are distinguished from females by the presence of a ventral depression that fits on the carapace of the female during copulation. Specimen IGM 6079 does not show this depression, and therefore cannot be sexed as a male under this criterion.

Figure 6 shows a positive linear correlation between the length and width of the carapace ($r^2 = 0.99$; Fig. 6A) obtained from collection specimens of *G. berlandieri* (scutes removed). This shows that the length of the carapace grows at about the same rate as the width. However, when correlating the length of the carapace and the length of the epiplastral projection, the trend is better explained by an exponential expression ($y = 3.963e^{0.0082x}$; $r^2 = 0.88$; Fig. 6B). This indicates that the length of the epiplastral projection increases at a faster rate than the carapace length throughout ontogeny, indicating that older turtles have a relatively larger epiplastral projection, while the carapace length/width correlation is linear. This suggests that differences in length of the epiplastral projection in the two specimens of *G. donlaloi* are more likely ontogenetic than sexual.

Differences in size between sexes have been noticed in *G. flavomarginatus*, where males tend to be statistically significantly smaller than females of the same ages (Germano, 1993), although normal curves do overlap extensively. This is in contrast to Hutchison (1996), who indicates that there are great differences between sexes in *G. laticuneus*, where males are said to be considerably larger than females (Fig. 6C). This pattern appears not to be expected among *Gopherus* species and confusion may have arisen because juvenile males, like females, do not have plastral depressions.

Appendicular skeleton—The appendicular skeleton is similar to that of any other gopher turtle. Because of gigantism, the limb bones are massive and stoutly constructed, but do not differ greatly from those of the *polyphemus-flavomarginatus* group. The right shoulder girdle with scapula and coracoid, the left scapula, the right forelimb complete with humerus, radius, ulna, carpals, metacarpals and the complete set of phalanges, a partial left forelimb with humerus, radius and ulna, a broken left femur, and the proximal portions of the right tibia and fibula are preserved.

Unfortunately, the manus and pes were prepared by someone else and the bones were removed from their original place before study. However, in the description the bones were arranged to fit original photographs. Some proximal bones were moved laterally in such a way that the bone placed as carpal five is certainly the radiale and the bone placed as the radiale is the lateral

$$y = 0.7169x + 12.521$$
$$R^2 = 0.99$$

$$y = 3.963e^{0.0082x}$$
$$R^2 = 0.88$$

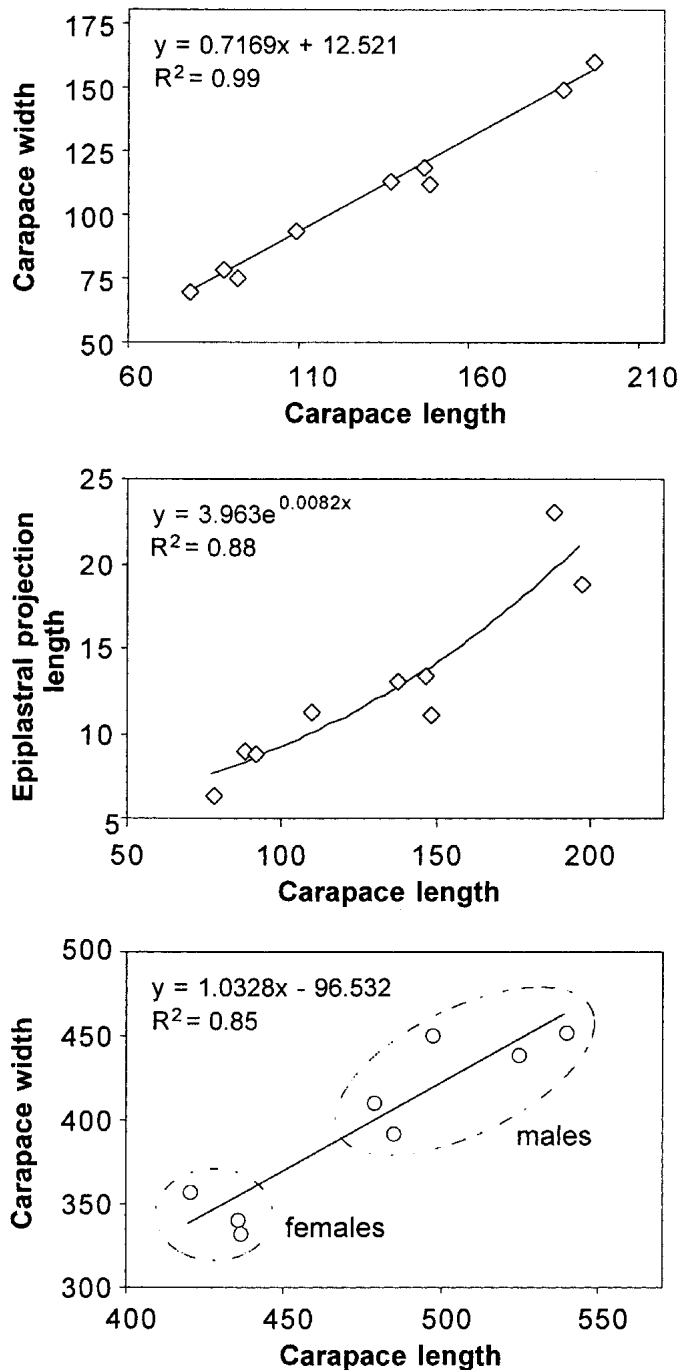$$y = 1.0328x - 96.532$$
$$R^2 = 0.85$$

males

females

FIGURE 6. Trend lines in ontogenetic variation of some carapace measurements of *G. berlandieri*. **A** shows a linear trend in the increment of carapace width / length ratio with growth, whereas the increase of the epiplastral projection length / carapace length ratio (**B**) is better explained as an exponential trend in which the epiplastral projection increases at a faster rate than carapace length with ontogeny. **C**, Size difference among males and females of *G. laticuneus* as suggested by Hutchison (1996).

in which the manus is known, and is very similar to that of *G. polyphemus* illustrated by Bramble (1982:fig. 4G). There is no fusion of either carpal 1 with carpal 2 or the medial with the lateral centrale as in *G. flavomarginatus* and *G. agassizii*. There is a large intermedium, which contacts the lateral centrale and the missing medial centrale ventrally. All carpals and metacarpals are of about the same size, with the exception of carpal I, which is much reduced. Lateral to the ulnare, there is an isolated bone that resembles the pisiform in shape. The presence of a second phalanx in digit five, as in *G. laticuneus* and *G. agassizii* cannot be determined. All remaining second phalanges are ex-
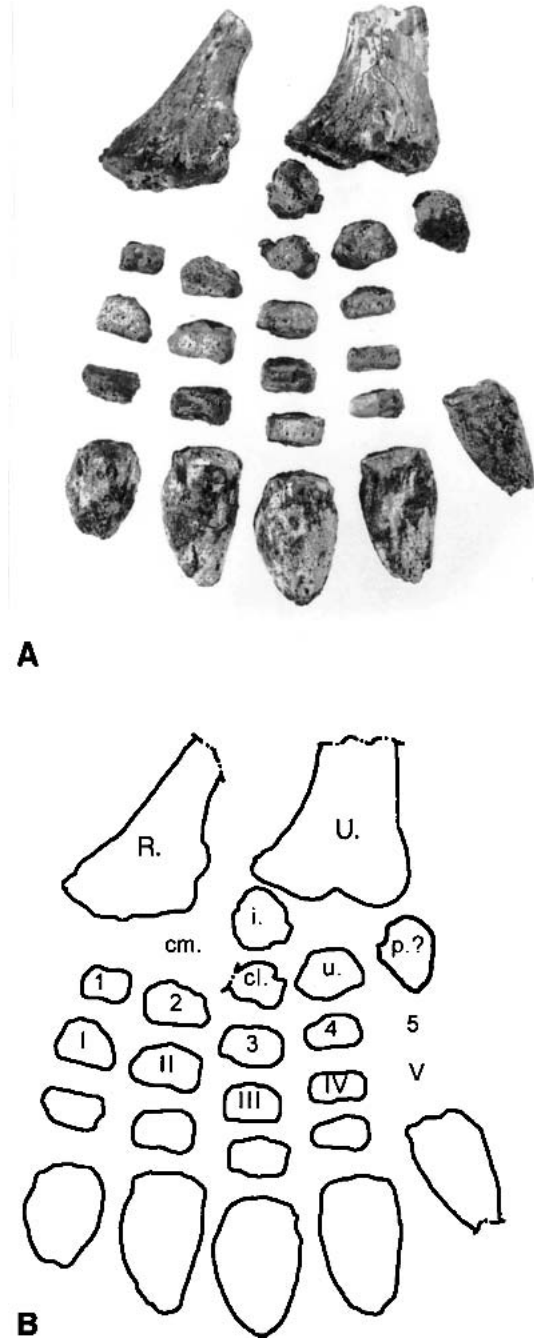

A

B

FIGURE 7. *Gopherus donlaloi*, IGM 6076 (holotype), photograph (**A**) and outline (**B**) of the hand as reconstructed. **Abbreviations**: **cl.**, lateral centrale; **cm.**, medial centrale; **i.**, intermedium; **p.**, pisiform; **R.**, radius; **U.**, ulna; **u.**, ulnare. Arabic numerals are carpals 1–5; roman numerals are metacarpals I-V.

centrale. The medial centrale, carpal 5, and metacarpal V are missing.

The manus is compact, with very short digits (Fig. 7) and long unguals. The set of bones structuring the carpus is complete. The manus probably retains the primitive condition, resembling those of *G. laticuneus* and *G. canyonensis*, two of the fossils

tremely compressed. Distally there are five large, ventrally flattened unguals.

The pes is incomplete and disarticulated. Only four unguals, the second phalanges of the first and second toes, the elongated metacarpals III and IV, and the very shortened tarsal elements can be identified. The astragalo-calcaneum was not preserved.

PHYLOGENETIC RELATIONSHIP OF *GOPHERUS*

The phylogenetic relationships of *G. donlaloi* were studied using maximum parsimony analysis based on Crumly's (1993) original data matrix. Of his 42 characters, only 19 were informative (Table 4). For the analysis, initially all of Crumly's characters were coded for *G. donlaloi*, after which the uninformative characters were deleted. The analysis was executed in PAUP 3.1.1 (Swofford, 1993) using the Branch and Bound algorithm. All characters were unordered and unweighted, and multistate taxa were considered polymorphic. The inclusion of *G. edae* and *G. hexagonatus* in a preliminary analysis resulted in a single huge polytomy either when including all three taxa together or separated one at a time. These taxa were considered too incomplete and therefore excluded from the final analysis. The lack of features defining these taxa suggests their condition as *nomina vana* (Simpson, 1945). The outgroup selected was that of Crumly (1993), including *Manouria*, *Stylemys*, *Hesperotestudo*, and Testudininae. No major corrections to the data set were done.

Results in the analysis (Appendix) agree to a large extent with the results presented by Crumly (1993). However, members of the *flavomarginatus-polyphemus* group collapsed into a polytomy, leaving *G. laticuneus*, *G. berlandieri*, and *G. agassizii* at the base of the tree, the last two with unresolved relationships branching after the first (Fig. 8A). Curiously, *G. mohavetus* falls within the outgroup, suggesting that this taxon may not even belong in *Gopherus*.

Six hard (unambiguous) synapomorphies support the inclusion of *G. donlaloi* within the *polyphemus-flavomarginatus* group: [character 1(1)] pterygoid not in contact with batagurine process, [3 (2)] *cavum labyrinthicum* enlarged to accommodate very large saccular otolith, [4 (2)] prefrontal pit present throughout ontogeny, [5 (1)] trochlear process for adductor musculature reduced, [9 (1)] postzygapophyses of last cervical vertebrae: elongated, [12 (1)] medial centrale and lateral centrale separate or divided by suture, and [13(0)] distal carpals one and two separated. These characters are shared by all members of the clade of *Gopherus* sensu stricto, including: *G. polyphemus*, *G. flavomarginatus*, *G. canyonensis*, *G. donlaloi*, *G. brevisternus*, *G. pansus*, and *G. vagus*. As predicted by Crumly (1993) morphological data indicate

that *G. berlandieri*, *G. agassizii*, and *G. laticuneus* form a paraphyletic assemblage, not forming a "natural" *Scaptochelys* group in the sense of Bramble (1982), although *G. agassizii* and *G. berlandieri* do form a monophyletic "*Xerobates*" group according to mitochondrial DNA sequence data (Lamb and Lydeard, 1994). Hutchison's (1996) subgenus *Oligopherus* is redundant with *G. laticuneus* and need not be used.

A second cladistic analysis was performed only with those taxa for which a skull was preserved, to achieve better resolution within the clade of *Gopherus* sensu stricto. *Gopherus brevisternus* diverged at the base followed by *G. flavomarginatus*, after which there is a trichotomy including *G. donlaloi*, *G. canyonensis*, and *G. polyphemus* (Fig. 8B). In this phylogenetic hypothesis, *Gopherus* sensu stricto is supported by two unambiguous synapomorphies: [5 (1)] trochlear process reduced, and [9(1)] postzygapophyses of last cervical vertebrae elongated. The clade comprising *G. flavomarginatus* + *G. donlaloi*, *G. canyonensis*, and *G. polyphemus* is supported by characters [1(1)] batagurine process not underlapped or contacted by the pterygoid, [3 (2)] enlarged cavum labyrinthicum with very large saccular otolith, and [4 (2)] prefrontal pits always present. The trichotomy including *G. donlaloi*, *G. canyonensis*, and *G. polyphemus* is supported by [12 (1)] medial centrale and lateral centrale separate or divided by suture, and [13 (0)] distal carpals one and two separated (0). Bremer decay indices and bootstrap analysis (Fig. 8B) indicate that the clade *G. flavomarginatus* + *G. donlaloi*, *G. canyonensis*, and *G. polyphemus* and the trichotomy *G. donlaloi*, *G. canyonensis*, and *G. polyphemus* are better supported than any other node in the tree, which require a single step to collapse. Three steps are needed to collapse clade D and 2 steps for clade E. In the bootstrap analysis, 97% of the resultant trees support clade D and 82% clade E. After removing most incomplete taxa, the clade of *Gopherus* sensu stricto becomes less supported than results shown in Figure 8A. The clade was not supported after bootstrap analysis, and it requires a single step to collapse according to Bremer values. The characters that supported *Gopherus* sensu stricto in the first analysis are distributed along the resolved clades in the second analysis, instead of being grouped into a single node. This indicates that the clade of *Gopherus* sensu stricto is not as robust as previously thought and might collapse into *Gopherus* (including *G. berlandieri* and *G. agassizii*) in future analyses.

EVOLUTION OF *GOPHERUS* IN TIME AND SPACE

Stratigraphic evidence largely based on phylogenetic hypotheses points to the origin of all gopher turtles during the Tertiary

TABLE 4. Characters and character states used in the phylogenetic analysis. Characters and states correspond to those listed in the Appendix

| Taxa	Character																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
G. donlaloi	1	1	2	2	1	1	1	0	1	1	0/2	1	0	1	0	0	1	0	2
G. agassizii	0	1	1	1	0	1	1	1	0	0,1	0,2	0	1	1	0,1	0	0	1	0
G. berlandieri	0	1	1	1	0	1	1	0	0	0,1	0,1	0	1	1	0	0	1	1	0
G. brevisternus	0	?	1	1	1	?	0	0	1	?	?	?	?	?	1	0	1	2	?
G. canyonensis	1	?	2	2	1	?	1	0	1	1	1	1	0	?	0	0	1	1	0
G. edae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
G. flavomarginatus	1	1	2	2	1	1	1	0	1	1	0	0	1	?	0	0	1	1	0
G. hexagonatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	2
G. laticuneus	0	?	0	1	?	0	0	1	0	0	0	0	1	?	0	0	1	1	?
G. mohavetus	0	?	?	?	?	?	0	?	?	?	?	0	?	?	0	0	1	1	1
G. pansus	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0	0	1	1	?
G. polyphemus	1	2	2	2	1	1	1	0	1	1	0	1	0	0	0	1	1	1	0
G. vagus	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0	0	1	?	?
Manouria	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0,2	1	0	0,1	0
Hesperotestudo	0	0	0	0	0	0,2	1	0	0	0	2	0	0	?	1	?	1	2	1
Stylemys	0	0	0	0	0	0	0	0	0	0	2	0	0	?	1	1	1	0	2
Testudininae	0	0	0	0	0	0	0	0	0	0,1	0	0	0	1	1	0	1	2	1
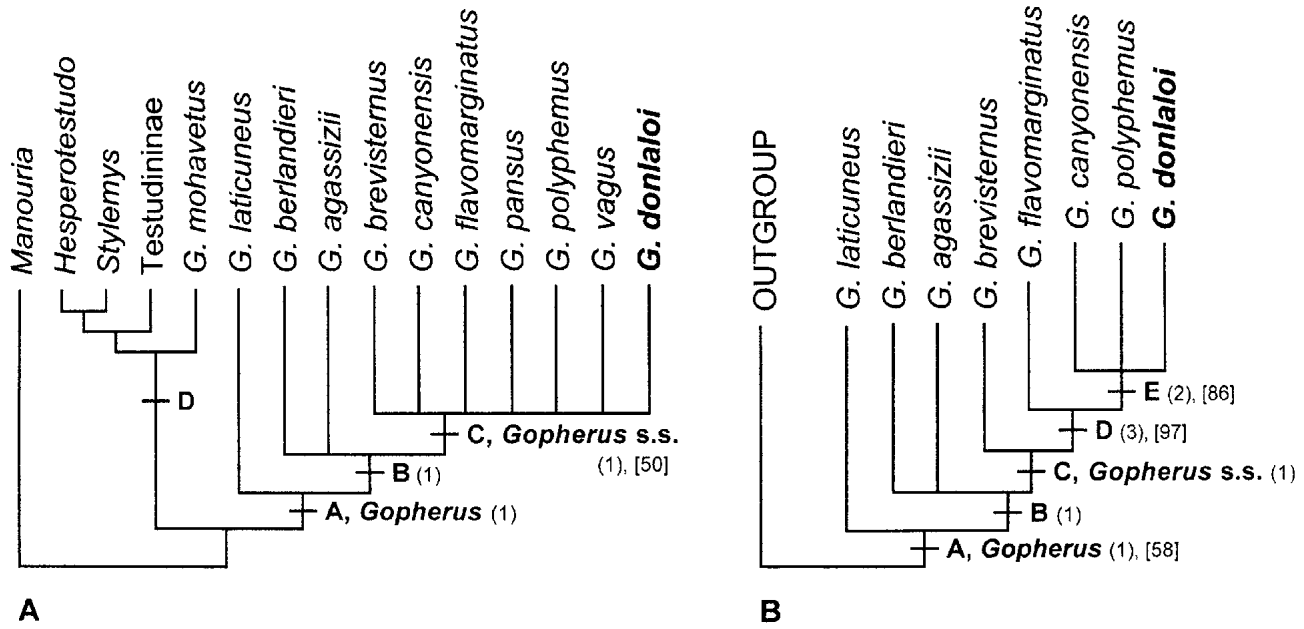
FIGURE 8.   Phylogenetic relationships of *Gopherus*. **A**, including all valid species; **B**, including only those species with known skull. Descriptions of node are listed in the Appendix. Numbers in parentheses following node labels are Bremer's values; numbers in brackets are bootstrap values.

(Fig. 9). *Gopherus laticuneus* from the early Oligocene is the oldest and most primitive known species of *Gopherus*. It derived from a hypothetical ancestor with a long head and a well-developed ear system and was geographically restricted to the central part of the United States, in what is now Colorado, Wyoming, and southwest South Dakota (Fig. 10, 11A). From this clade derived, on the one hand, the ancestor that gave rise to the extant *G. agassizii* and *G. berlandieri* (the *Xerobates* group), and on the other, the ancestor that gave rise to the *Gopherus* sensu

stricto group. The ancient distribution of the *Xerobates* group is uncertain but it likely existed towards the southwestern part of the United States. *Gopherus agassizii* (which has no fossil record) and *G. berlandieri* (whose fossil record goes back just to the Pleistocene) were separated by the displacement of the former to the west to reach its Recent distribution (Fig. 11D); the latter probably could have extended its range to the south, but certainly not into its current distribution (Fig. 11B), occupied until the late Pleistocene by taxa of *Gopherus* sensu stricto.
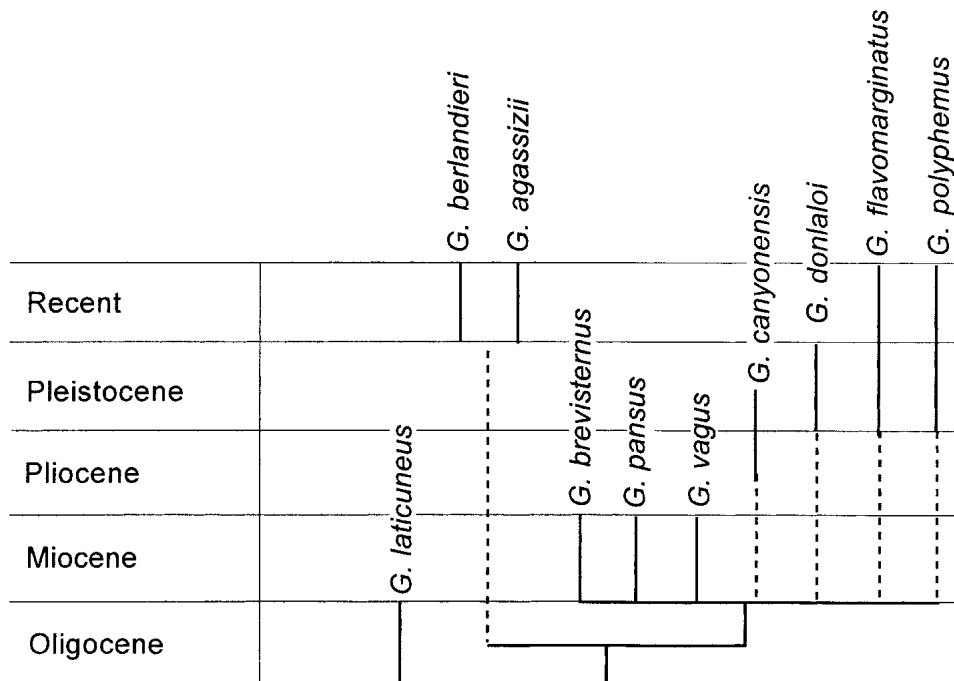

FIGURE 9.   Phylogenetic relationships of *Gopherus* superimposed on time scale. Dotted lines correspond to ghost lineages. Polytomy among *G. berlandieri*, *G. agassizii*, and *Gopherus* sensu stricto was resolved according to DNA results (Lamb and Lydeard, 1994).

FIGURE 10. Distribution of valid fossil species of *Gopherus* according to published records. Fossil taxa: 1, *G. laticuneus*; 2, *G. agassizii*; 3, *G. berlandieri*; 4. *G. flavomarginatus*; 5. *G. polyphemus*; 6. *G. brevisternus*; 7. *G. pansus*; 8. *G. vagus*; 9. *G. canyonensis*; 10, *G. donlaloi*; 11, *G. edae*; 12, *G. hexagonatus*. Recent taxa: horizontal lines *G. agassizii*; vertical lines *G. berlandieri*; right diagonals, *G. flavomarginatus*; left diagonals *G. polyphemus*. Distribution of fossil taxa does not match those of Auffenberg and Franz (1978); e.g., no reference of *G. laticuneus* from Montana was found; and *G. hexagonatus* from Kansas was collected at Brown Co. located in northeastern Kansas (Hibbard, 1960).

During the Miocene, *Gopherus* sensu stricto rapidly radiated, forming a monophyletic assemblage in which the interrelationships among taxa are uncertain. Stratigraphically, *Gopherus* sensu stricto is divided in two groups (Fig. 9). The first is composed of the Miocene taxa *G. brevisternus*, *G. pansus*, and *G. vagus*, having distributions restricted to the central United States (Fig. 10), and overlapping the distribution of the basal *G. laticuneus* already extinct at the time, and probably forcing the movement of *Xerobates* taxa to the southwest, near their Recent distribution.

Of all Miocene species of *Gopherus* sensu stricto, only *G. brevisternus* shows enough diagnostic characters to be considered a separate species [characters 1(0), 3, 4, 7(0), 15, 18(2) in the Appendix]. The head of this turtle is already brachycephalic, but not as in the Pleistocene *G. donlaloi* and *G. canyonensis*; its saccular otolith is mid sized but it still has the batagurine process in contact with the pterygoid, and lacks the posterior maxillary process. *Gopherus brevisternus* shows the expected intermediate condition between that of basal *Gopherus* species to taxa of late *Gopherus* sensu stricto, and phylogenetic results support this conclusion (Fig. 8B). The spaciotemporal proximity of *G. brevisternus* with *G. vagus* and *G. pansus* (Fig. 11B) may suggest that all three taxa are synonymous with *G. pansus* Hay, 1908, the valid name because of date and page priority. However, a more precise anatomical study needs to be done before drawing final conclusions.

The second group of species of *Gopherus* sensu stricto is that of Pliocene-Pleistocene-Recent gopher turtles. This group comprises:

1. The extinct *G. canyonensis* (Johnston, 1937), which includes *G. pertenius* (Cope, 1892). If *G. pertenius* is certainly a synonym of *G. canyonensis*, as suggested by Bramble (1982), the taxon would range from the late Pliocene (early Blancan) to early Pleistocene (late Blancan), and from the western part of Texas to eastern Arizona (Fig. 10);

2. The extinct *G. donlaloi*, of late Pleistocene age (Rancholabrean), known from the eastern part of northern Mexico, probably ranging as far south as San Luis Potosí (G. Alvarado, pers. comm.) and into Texas;

3. The extant *G. flavomarginatus* including *G. huecoensis*, (Strain, 1966), ranging from early Pleistocene to Recent. Now it is confined to the Bolsón de Mapimí from northeastern Durango to southeastern Chihuahua and southwestern Coahuila, but with a probable ancient distribution to southern New Mexico (Morafka, 1988) and southwestern Texas, and as far south as Aguascalientes (Mooser, 1980) from which fossils with "*flavomarginatus*, *canyonensis*, *polyphemus*" appearance have been reported. However the taxonomy of these specimens still needs to be verified;

4. *Gopherus polyphemus*, including *G. atascosae* (doubtfully according to Bramble, 1982) and *G. praecedens* (Auffenberg and Franz, 1978), ranging from the ? middle Pleistocene (Irvingtonian) to Recent. The current distribution extends along
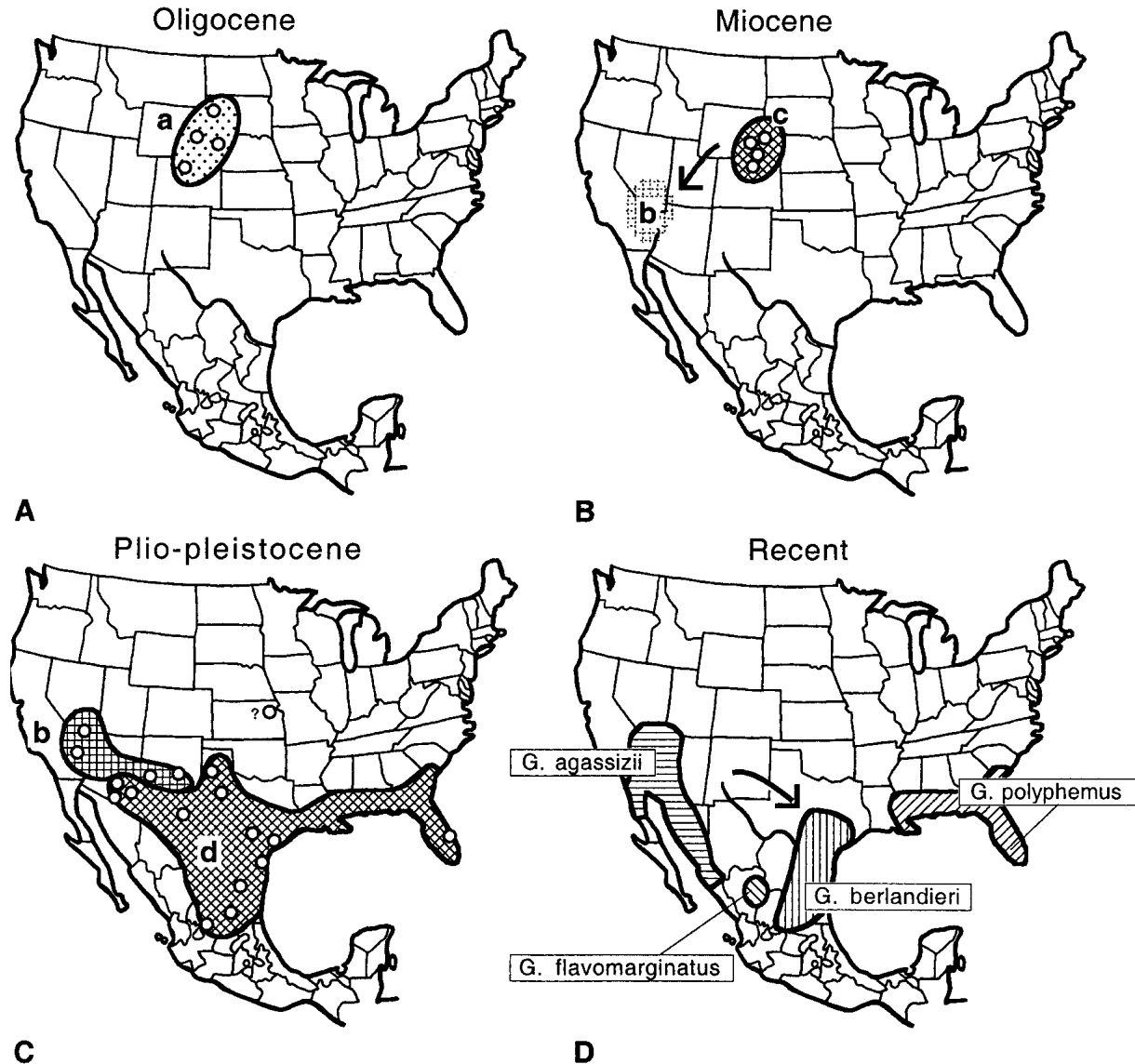
FIGURE 11.   Historical biogeography of *Gopherus* as reconstructed from phylogenetic and stratigraphic data. **A**, The genus *Gopherus* originates in the Oligocene in the Central Plains of the United States in Wyoming, Colorado, Nebraska and South Dakota where the basal *G. laticuneus* occurred. **B**, by the Miocene, an ancestral *G. agassizii-G. berlandieri* clade and *Gopherus* sensu stricto (*G. brevisternus*, *G. pansus*, and *G. vagus*) originated. *Gopherus* sensu stricto settled in the same area as *G. laticuneus*, already extinct, while the *G. agassizii-G. berlandieri* ancestral clade displaced to the west into the northern portion of the current distribution of *G. agassizii*. **C**, During the Plio-Pleistocene, Central Plains species went extinct and *Gopherus* sensu stricto moved south, expanding its range from New Mexico to Florida and from northern Texas to Aguascalientes. **D**, during the late Pleistocene to Recent, giant forms of *Gopherus* sensu stricto (such as *G. canyonensis* and *G. donlaloi*) went extinct, and *G. berlandieri*, branching out from the *G. agassizii-G. berlandieri* ancestral clade, extended its distribution area to the south, separating *G. polyphemus* from *G. flavomarginatus*. **Symbols**: white circles show reported collecting points; dotted area is the reconstructed distribution for *G. laticuneus*, squared areas are for the *G. agassizii-G. berlandieri* ancestral clade, and diamond areas are for *Gopherus* sensu stricto. **a**, *G. laticuneus*; **b**, *G. agassizii-G. berlandieri* ancestral clade; **c**, Miocene *Gopherus* sensu stricto (*G. brevisternus*, *G. pansus*, and *G. vagus*) taxa; **d**, Plio-Pleistocene and Recent *Gopherus* sensu stricto (*G. canyonensis*, *G. donlaloi*, *G. flavomarginatus*, and *G. polyphemus*). In B, the distribution of the *G. agassizii-G. berlandieri* ancestral clade (b) is hypothetical.

the Atlantic Coast Plain from South Carolina throughout Florida, and west along the Gulf Coastal Plain to extreme eastern Louisiana. Fossil *G. atascosae* extended its range to the west to central Texas, although its synonymy with *G. polyphemus* still needs to be reviewed.

Of this clade, *G. flavomarginatus* branched before *G. canyonensis*, *G. donlaloi*, and *G. polyphemus*, maintaining these three taxa as a monophyletic group until late in the Pleistocene. If *G. hexagonatus* is shown to belong to Plio-Pleistocene *Go-*

pherus sensu stricto, the biogeographic scenario for the clade would extend its distribution to northeastern Kansas during the middle to late Pleistocene.

Morafka (1988) has pointed out how difficult it is to explain the disjunct distribution of the Bolsón de Mapimí *G. flavomarginatus* from its extant sister taxon *G. polyphemus* of Florida. He argues that *G. flavomarginatus* separated from *G. polyphemus* and related eastern fossil taxa by the late Tertiary uplift, possibly of the Trans-Pecos Texas ranges, extending southeast through the Coahuila Folded Belt and terminating in the Sierra Madre

Oriental. However, during the late Tertiary, the giant turtle *G. canyonensis* remained in Arizona, far to the west of the mentioned ridges, and within the possible extended range of *G. flavomarginatus*. Later, Morafka stated that towards the Quaternary, fossils resembling *G. canyonensis* and/or *G. flavomarginatus* extended throughout almost the entire Mexican Plateau from Aguascalientes to as far north as southern New Mexico and Kansas. Despite his long discussion, he never concluded how *G. berlandieri*, the sister taxon of *G. agassizii*, transposed into the distribution of *Gopherus* sensu stricto separating *G. flavomarginatus* from *G. polyphemus*.

The monophyletic assemblage that includes all Pleistocene and Recent species of *Gopherus* sensu stricto extended from eastern Arizona to Florida, and from northern Texas to Aguascalientes, never overlapping the distribution of *G. agassizii* with a past known distribution from southern California to southern New Mexico (Fig. 11C). The successful expansion of *Gopherus* sensu stricto during the Pleistocene was followed by a series of extinctions and reduction of the range affecting most of the species. *Gopherus canyonensis* was extinct by the early Pleistocene, leaving only *G. donlaloi* as a connection between the still broad distribution of *G. flavomarginatus* and *G. polyphemus*. As suggested by Morafka (1988), the Trans Pecos Texas chain of mountains and the Sierra Madre Oriental could have played an important role in the separation of *G. flavomarginatus* from other eastern species of *Gopherus* sensu stricto, but could not be the reason for their disjunct distributions.

The extinction of *G. donlaloi*, the last survivor among the giant gopher turtles, played an important role in the broad separation of *G. polyphemus* and *G. flavomarginatus* populations. The reason why *G. donlaloi* went extinct relies on pure speculation; however, it is interesting to notice that its distribution area is now broadly occupied by *G. berlandieri* (Fig. 11D), a turtle supposedly more adapted to dry environments (Morafka, 1988). The biogeographical pattern shows clearly that *G. berlandieri* inhabits an area once occupied by species of *Gopherus* sensu stricto. A plausible scenario could be that the eastern population of a *G. agassizii-G. berlandieri* ancestral clade moved southeastward while differentiating into *G. berlandieri* near the end of the Pleistocene. The extension of *G. berlandieri* into territory of *Gopherus* sensu stricto could only have happened for one of two reasons: (1) because *G. berlandieri* was a better competitor, bringing *G. donlaloi* to extinction, or (2) because the extinction of *G. donlaloi* (caused by any of the possible reasons listed by Morafka, 1988) left an empty space into which *G. berlandieri* expanded its range to the south. If allopatric distribution is a rule among gopher turtles, and only one species can be successful in a given area, the disjunct distribution of *G. flavomarginatus* and *G. polyphemus*, separated by the basal *G. berlandieri*, would be simply explained by the southern movement of *G. berlandieri* into the area previously occupied by *G. donlaloi*.

Toward the Recent, the geographic distributions of both *G. flavomarginatus* and *G. polyphemus* were reduced to their present-day ranges. This appears to represent an ongoing trend that started during the Late Pleistocene, and may lead to eventual extinction.

CONCLUSIONS

Gopherus donlaloi is one of the few relatively complete giant turtles with a preserved skull, from which valuable characters can be discerned. This is not the case for most fossil species of *Gopherus*, in which the skull is unknown. Instead, they have been described from complete or fragmentary shells. The variation in the shell, as seen in *G. donlaloi* and *G. laticuneus*, obscures important taxonomic characters. The taxonomic results of this study are that *G. mohavetus* might not belong in *Gopherus*, and that the lack of diagnostic features in *G. edae* and *G. hexagonatus* suggests these taxa to be *nomina vana*.

Phylogenetic results show that the relationships of *Gopherus* sensu stricto are far from understood. However, the resultant polytomy gives insight into the evolution of the lineage in time and space, providing new information to understand Recent distribution of the genus. The disjunct distribution of closely related *G. flavomarginatus* and *G. polyphemus*, separated by *G. berlandieri*, can now be interpreted as the fragmentation of a previously wide distribution of *Gopherus* sensu stricto along the southwestern portion of the United States and Mexico, where only those species distributed geographically at the extremes survived. The separation of the two extant species of *Gopherus* sensu stricto is more the result of the extinction of the intermediate species and the southward movement of *G. berlandieri* than to the displacement of *G. flavomarginatus* to the west.

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APPENDIX

Characters and character states

List of characters used in the analysis. Numbers in brackets correspond to informative characters presented by Crumly (1993). Numbers in parentheses are character states.

1 [1]. Batagurine process and pterygoid: pterygoid broadly underlaps and contacts batagurine process (0); enlarged cavum labyrinthicum housing saccular otolith, preventing pterygoid from underlapping and contacting pterygoid (1).

2 [2]. Basisphenoid rostrum: radix trabeculae long converging anteromedially, but not in contact (0); radix trabeculae short, robust, converging slightly, but not contacting one another (1); very short radix trabeculae with *dorsum sellae* reduced (2).

3 [3]. Cavum labyrinthicum: about same size or slightly larger than recessus scala tympani (0); cavum labyrinthicum somewhat enlarged with small or large saccular otolith (1); enlarged cavum labyrinthicum to accommodate very large saccular otolith (2).

4 [5]. Prefrontal pit: recess on ventral portion of prefrontal bone in roof of each nasal canal absent (0); pits present only in large adults (1); pits always present (2).

5 [10]. Trochlear process: large (0); reduced (1).

6 [12]. Foramen orbitonasale: moderate to small (0); large (1).

7 [13]. Posterior maxillary process: absent (0); present (1).

8 [15]. Vomerine foramen: absent (0); small unpaired aperture at or near vomero-premaxillary suture (1).

9 [19]. Postzygapophyses of last cervical vertebrae: short (0); elongated (1).

10 [22]. Pisiform: present on lateral edge of manus articulating with ulna (0); absent (1).

11 [23]. Number of phalanges in first and fifth digits: two phalanges in first four digits and only one phalanx in fifth (0); first and fifth digits with single phalanx and middle three digits with two phalanges each (1); two phalanges in all five digits (2).

12 [24]. Medial centrale and lateral centrale: two central bones fused (0); central bones separate or divided by suture (1).

13 [26]. Distal carpals one and two: separated (0); fused (1).

14 [33]. Hip spines: hip spines present as group of protuberant, often pointed scales (0); spines reduced or absent (1).

15 [36]. Pectoral scute shape: rectangular (0); reduced medially to narrow scute crossing plastron to contact opposite pectoral scute (1); medial portion of pectoral scute absent (2).

16 [39]. Gular scute proportions: gular scute longer than wide (0); width equal to or greater than length (1).

17 [40]. Gular scute and anterior entoplastron: gular scute not overlapping or just reaching edge of entoplastron (0); gular scutes broadly overlapping entoplastron (1).

18 [41]. Marginal scutes and second pleural scute: peripherals 5, 6, and 7 about same size and shape and contacting second pleural scute (0); peripherals 4 and 6 enlarged, 4th contacting second pleural scute (1); peripherals 5 and 6 enlarged, 4th not contacting second pleural (2).

19 [42]. Inguinal scutes: multiple and in contact with femoral scute (0); single and in contact with femoral scute (1); single and separated from femoral scute by extension of abdominal scute forming small portion of plastral rim (2).

Analysis

A first analysis was performed with a branch-and-bound search using PAUP 3.1.1 with an initial upper bound computed via a stepwise, furthest additional sequence, and multi-state taxa interpreted as polymorphisms. *Gopherus edae* and *G. hexagonatus* were deleted and *Manouria, Hespe-*

rotestudo, *Stylemys*, and Testudininae were designated as outgroup taxa. The final data matrix had 17 taxa and 19 informative characters, all unordered and unweighted.

Results (Fig. 8A): shortest tree found = 47; number of trees retained = 576.

Most parsimonious tree description: tree length = 47; consistency index = 0.745; homoplasy index = 0.468; retention index = 0.800; rescaled consistency index = 0.596.

List of apomorphies.

Ambiguous characters (*) are interpreted with ACCTRAN character-state optimization.

Node A, *Gopherus*: 2*, 4.

Node B: 3, 6, 7, 10*.

Node C, *Gopherus* sensu stricto: 1, 3(2), 4(2), 5, 9, 12, 13(0).

Node D: 13(0)*, 19.

G. donlaloi: 18(0), 19(2).

G. brevisternus: 1(0), 3, 4, 7(0), 15, 18(2).

G. canyonensis : 11.

G. flavomarginatus: 12(0), 13.

G. polyphemus: 2(2), 14 (0), 16.

G. agassizii: 8, 17(0).

G. laticuneus: 8.

A second analysis was performed including only those taxa with known skull using the same procedure as described above. The data matrix consisted of 13 taxa and 19 informative characters. Decay indices were obtained using the converse constraint option of PAUP, and 100 bootstrap replicates were computed using branch and bound with the initial upper bound computed via stepwise addition with furthest additional sequence.

Results (Figure 8B): Shortest tree found = 47; number of trees retained = 6.

Most-parsimonious tree description: Tree length = 47; consistency index = 0.745; homoplasy index = 0.468; retention index = 0.786; rescaled consistency index = 0.585.

List of apomorphies

Ambiguous characters (*) are interpreted with ACCTRAN character-state optimization.

Most-parsimonious tree description 1 (rooted using user-specified outgroup):

Node A, *Gopherus*: 2*, 4.

Node B: 3, 6, 7, 10*.

Node C, *Gopherus* sensu stricto: 5, 9.

Node D: 1, 3(2), 4(2).

Node E: 12, 13(0).

G. donlaloi: 18 (0), 19(2).

G. canyonensis: 11.

G. polyphemus: 2(2), 14(0), 16.

G. brevisternus: 7(0), 15, 18(2).

G. agassizii: 8, 17(0).

G. laticuneus 8.