AN EXTANT, INDIGENOUS TORTOISE POPULATION IN BAJA CALIFORNIA SUR, MEXICO, WITH THE DESCRIPTION OF A NEW SPECIES OF *XEROBATES* (TESTUDINES: TESTUDINIDAE)

John R. Ottley[1] and Victor M. Velázques Solis[2]

ABSTRACT.—An extant, indigenous desert tortoise population is reported from the cape region of Baja California Sur, Mexico. This population is described and figured as a new species, *Xerobates lepidocephalus*, distinct from all other North American tortoises including *Xerobates agassizii*, *X. berlandieri*, *Gopherus flavomarginatus*, and *G. polyphemus*. *Xerobates lepidocephalus*, or the scaly-headed tortoise, whose range is known only from an extremely small area in the gulf-drainage mountains just south of La Paz, appears to be a peninsular relict whose closest living relative is probably *X. agassizii*. However, carpal bone affinities connote a close relationship between *X. lepidocephalus* and the Oligocene species *X. laticunea* from Wyoming and Colorado, suggesting that the former species may be one of the more primitive contemporary tortoises of the *Xerobates* lineage. Such evidence indicates that *X. lepidocephalus* is not of vicariant origin resulting from the formation of the cape of Baja California. Scaly-headed tortoises likely ranged, and may yet be discovered, in other medium-elevation mountain ranges of the cape.

The desert tortoise is one of the most recognizable members of the desert biota inhabiting southwestern North America. The most westerly ranging species, *Xerobates agassizii*, has been reported from the deserts of California, Arizona, Nevada, Utah, Sonora, and the extreme northeastern corner of Baja California, Mexico (Van Denburgh 1922, Carr 1952, Stebbins 1966, Auffenberg and Franz 1978a, 1978b). Unfortunately, no confirmed sightings of *X. agassizii* in northeastern Baja California have been made for well over a decade; and, because of the growth of the local human population and the increased use of arable land for farming, the species may no longer exist in this region. Tortoises previously have never been reported from any other portion of Baja California (Norte or Sur).

In early 1987, while seeking information on potential aquatic turtle sites from ranchers residing in the mountain ranges directly south of La Paz, we were told of terrestrial turtle sightings. However, no one with whom we spoke at that time had actually seen a terrestrial turtle nor could they accurately describe where such sightings had been made. We were suspicious of these rumors because, even if substantiated, the occurrence of an indigenous, terrestrial species seemed unlikely, particularly in view of the introduction of slider turtles, *Pseudemys scripta*, into this region by several local families.

In late January 1989 a live tortoise was brought to the La Paz Military Hospital by a rancher who reportedly found the specimen near the Buena Mujer Dam approximately 20 km south of La Paz. In May 1989 we accompanied this rancher to the collecting site and found the fragmented shell of a second tortoise. We made inquiries to residents of that area and were told that although tortoises were only rarely encountered, they were well known in the region. At least two of the families claimed to be direct descendants of homesteaders who arrived in this region during the mid-1800s, all of whom recounted that their ancestors had been familiar with the tortoises, which were wide ranging in earlier time but were now encountered only in the vicinity of a small mountain area known as the Sierra San Vicente. The locals with whom we spoke seemed convinced that the tortoises were indigenous. A comparative evaluation with specimens from other populations convinced us that the Sierra San Vicente population is unique among North American tortoises.

MATERIALS AND METHODS

During the course of this study, in addition to the type material herein described, we

[1]28235 Cobb Lane, Valley Center, California 92082.
[2]Hospital Militar, Calle Revolución, 870 Norte, La Paz, Baja California Sur, Mexico.

Fig. 1. *Xerobates lepidocephalus:* holotype, BYU 39706, from near the Buena Mujer Dam, Baja California Sur.

examined 29 live specimens of *G. agassizii* (5 specimens from Sonora, 24 from California), 6 live *X. berlandieri*, 1 live *G. flavomarginatus*, and 1 live *G. polyphemus*. Photographs of other specimens were also used to aid in our diagnoses and include: 18 *X. agassizii* (11 from USA and 7 from Sonora), 4 *X. berlandieri*, 3 *G. flavomarginatus*, and 5 *G. polyphemus*. Shell terminology was taken from Woodbury and Hardy (1948) and Carr (1952). Bone terminology follows Auffenberg (1966, 1976) and Bramble (1982). Shell measurements were taken following Woodbury and Hardy (1948), using a high-quality, steel meter stick "in planes parallel to or at right angles to a flat surface upon which the tortoise was resting" (Woodbury and Hardy 1948: 154). Head measurements were taken using a Venier caliper at the widest part of the head (width) and from the tip of the snout to the posterior border of the parietal scales (length). Hindlimb length was taken by measuring the distance from the edge of the plastron to the base of the first nail when the limb was fully extended. Figures depicting cranial, vertebral, and carpal characters were taken from radiographs and/or adapted from Bramble's (1982) ink drawings.

Xerobates lepidocephalus, n. sp.
Scaly-Headed Tortoise

HOLOTYPE.—BYU 39706, an adult female collected by Eusebio Villalobos on 15 January 1989 at the western base of the Sierra San Vicente approximately 1 km N of the Buena Mujer Dam, Baja California Sur, Mexico (Fig. 1).

PARATYPE.—BYU 39707, a reconstructed shell (full plastron and 2/3 of the carapace) of an adult female found approximately 300 m SE of the type locality. Collected by Eusebio Villalobos, Victor Velazques S., and John R. Ottley on 23 May 1989.

ETYMOLOGY.—The species name is taken from two Greek nouns, *lepida* = scaly and *cephala* = head, and refers to the characteristically thickened, raised scales on the parietal and temporal regions of the head.

DIAGNOSIS.—*Xerobates lepidocephalus* is distinguished from all other North American tortoise species (*Xerobates agassizii, X. berlandieri, Gopherus flavomarginatus,* and *G. polyphemus*), as well as virtually all testudinids, in lacking enlarged scales on the frontal and prefrontal regions (intersupraoculars); these scales in *X. lepidocephalus* are smooth, small, and subequally sized (with at least four frontal scales separating the orbits; rarely more than two frontals occur in other *Xerobates* and usually only one in *Gopherus*). *Xerobates lepidocephalus* is further distinguished in having thickened, raised, nonsloughing scales covering the parietal and temporal regions of the head. The holotype of *X. lepidocephalus* also possesses well-fused 4th and 5th carpal bones (a characteristic previously observed only in Oligocene *X. laticunea*) and lacks a distinct pisiform (also absent in *G. flavomarginatus* and *G. polyphemus*).

DESCRIPTION OF TYPE.—An adult female with the following measurements: carapace length 229 mm, carapace height 89 mm, carapace width 181 mm, head length 51 mm, head width 37 mm, hind limb length 84 mm. Ratios: carapace height to length .388, carapace width to length .790, head length to carapace length .222, hind limb length to carapace length .367. Coloration (in life) as follows: carapace dusky yellow-brown with slightly darker areolae, anterior halves of lateral marginals slightly lighter; plastron dirty yellowish tan; nonscaly skin around limbs light cream-yellow (most vivid around hind limbs), skin around neck region light yellowish brown, skin with scales darker and scales same color as carapace; heavy scales on limbs and around tail same color as carapace; scales on top of head (parietals, temporals, frontals, and prefrontals) dirty yellowish tan, mottled with slightly darker brown; other portions of head approximate color of carapace. Plastral scutes lack alveoli (excessively worn), carapace scutes with distinct alveoli, but vertebrals and lateral marginals have smooth spots (worn). Head scales on frontal and prefrontal regions small, nearly equal in size, with a minimum of 4 intersupraoculars. Parietal and temporal scales thickened and distinctly raised to as much as 2 mm, abruptly differentiated from other dorsal head scales. Anterior forelimb scales flattened, subequal in size, with a rapid transition to small scales just above the wrist; nails rounded and peglike. Bones of antebrachium as follows (taken from X ray): phalangeal formula 2-2-2-2-1, medial and lateral centrale fused, 1st and 2nd carpals fused, 4th and 5th carpals fused, pisiform appears to be fused with ulnare; radius in contact with 1st and 2nd carpals.

RANGE.—Known only from the Sierra San Vicente region, approximately 1.5 km north of the Buena Mujer Dam, 20 km (by air) south of La Paz, Baja California Sur, Mexico.

VARIATION OF CHARACTERS.—Although only one complete specimen of *X. lepidocephalus* is currently available for meristic scale analysis, its head scale characteristics are unique to the extent that there is an extremely low degree of overlap with other species. For example, all North American tortoises (as do virtually all tortoises) have enlarged frontal or prefrontal plates and relatively flattened scales covering the parietal and temporal regions. *Gopherus* spp. generally have two large frontal plates (one in front of the other) that cover most of the frontal (intersupraocular) and prefrontal region, either one of which may be divided. *Xerobates agassizii* and *X. berlandieri* usually possess at least one pair of enlarged frontal plates that may vary in size and shape, and generally cover or partially cover only the frontal region; smaller intersupraoculars (occasionally granular scales) may also be juxtaposed with these plates, with as many as 4 to 6 scales between the supraoculars. One specimen of *X. berlandieri* (collection of S. Veverka) had divided frontal scales to the extent that only one slightly enlarged scale remained. Scales covering the parietal and temporal regions tend to be slightly larger and smoother in *Gopherus* spp. than in *X. agassizii* and *X. berlandieri*, and generally show more signs of sloughing in these latter species; in all of these tortoises the only notable difference in the nature of the scales from the frontal to the parietal regions is a size change. In *X. lepidocephalus* there is a very marked and abrupt change from the flattened frontal scales to the vividly thickened and raised parietals; these latter scales give the appearance of flat-topped cobblestone. Raised and/or thickened parietal and temporal scales are unknown in *Gopherus* spp. and *X. agassizii*; however, one specimen of *X. berlandieri* (collection of L. Greene) had a few slightly raised scales bordering on the parietal/temporal transition.

The fusion of the 4th and 5th carpal bones and the lack of a distinct pisiform observed in the holotype of *X. lepidocephalus* are of uncertain diagnostic value. Both this type of carpal fusion and unfused 4th and 5th carpals are known in Oligocene *X. laticunea* (Bramble 1982). The apparent fusion of the pisiform with the ulnare in the *X. lepidocephalus* holotype may be the result of ontogeny and may vary a great deal within this and other species (Charles Crumly, personal communication, 1989). Whether or not manus bone morphology is of true diagnostic value in *X. lepidocephalus* will depend on the revelations of further study.

Discussion

During the 19th century three species of North American tortoises were described in two genera: *Gopherus polyphemus* Daudin (1801, Auffenberg and Franz 1978e), *Xerobates berlandieri* Agassiz (1857, Auffenberg and Franz 1978c), and *X. agassizii* Cooper (1863, Auffenberg and Franz 1978b). According to Van Denburgh (1922), Stejneger (1893) was the first to consider all three of these forms as congeners, an assessment that persisted for nearly 90 years. Legler (1959) described *G. flavomarginatus* (Auffenberg and Franz 1978d), a species he recognized as being closely related to *G. polyphemus*, but discussed relationships with other North American species in the congeneric sense as well.

More recent compendia on desert tortoise taxonomy have revived arguments for and against recognition of separate genera. Auffenberg (1966, 1976) observed that North American tortoises naturally fell into two species groups. Bramble (1982) took this one step further and placed those groups into separate genera in the following associations: *polyphemus* and *flavomarginatus* under *Gopherus*, and *agassizii* and *berlandieri* under a newly erected genus, *Scaptochelys*. Bramble based this level of recognition on what he interpreted to be eight bilaterally unique, diagnostic characters. The results produced two distinct, functional species groups: specialized burrowers, *Gopherus;* and, more generalized diggers, *Scaptochelys*.

Bour and Dubois (1984) concurred with Bramble's diagnoses for two genera but demonstrated that the position of *Scaptochelys* was already occupied by Agassiz's (1857) genus *Xerobates* (Cooper 1863, True 1882). Crumly (1984, 1985, 1988, personal communication, 1989) noted the uniquely specialized characters shared between *G. flavomarginatus* and *G. polyphemus* but found that *X. agassizii* and *X. berlandieri* did not appear to share a similarly close relationship with one another since they both manifest many of the primitive or "transitional" characters that have become specialized in *Gopherus* (i.e., the presence of a sacular otolith). For these reasons Crumly opted for a single genus, *Gopherus*, to encompass North American tortoises.

The dispute over generic status stems from differing interpretations over the importance of the shared primitive characters. In a strictly morphological sense the shared primitive characters strongly suggest monophyly and therefore the recognition of a single genus. However, when compared with the more derived and shared functional characteristics of each species group, a two-genera interpretation can be argued (Bramble 1982, Lawler 1986, Van Devender 1986, personal communication, 1989). Further, the fossil record indicates that two lineages were distinguishable by the Middle Miocene and have remained largely allopatric since that time (Bramble 1982, Van Devender 1986, Lamb et al. 1989). Lamb et al. (1989) also observed that the qualitative pattern of mitochondrial DNA phylogeny estimates for North American tortoises were substantial, thus adding strength to the recognition of separate genera. At present there is enough evidence to defend either taxonomic point of view; thus the matter of separate genera becomes more a question of how one defines the data. In our opinion, evidence for the recognition of two genera more fully conveys the unique, adaptive histories of each tortoise group: sandy soil burrowers or gopher tortoises, *Gopherus*, and compact soil diggers or desert tortoises, *Xerobates*.

Although head scales (Fig. 2) clearly distinguish *X. lepidocephalus*, comparative similarities of the carpal morphologies (Fig. 3), cranium, and vertebrae (Fig. 4) ally this species with the *Xerobates* group; similarities in shell meristics suggest that its closest living relative is *X. agassizii*. However, the uncommon fusion of the 4th and 5th carpals, a character that *X. lepidocephalus* shares with Oligocene *X. laticunea*, may suggest a close (if not closer) ancestral relationship. Because primitive head scale morphologies are not well known and because *Gopherus* manifests the more primitive manus bone characteristics of North American tortoises, it is unclear whether the head scales and manus bones of

Fig. 2. Dorsolateral view of the head of BYU 39707, showing the small, smooth frontal and prefrontal scales and the abrupt transition to the thickened, raised parietal and temporal scales.

X. lepidocephalus reflect primitive or derived conditions within the genus.

Owing partly to the unresolved taxonomic status of *X. agassizii* populations from Sonora and Sinaloa, the biogeographic origin of *X. lepidocephalus* remains somewhat unclear. Although the known range of *X. lepidocephalus* is limited to the northeastern cape region, the following cursory evidence suggests that it is probably not a cape vicariant: (1) *X. lepidocephalus* may be closely related to *X. laticunea* from Oligocene deposits of Wyoming and Colorado, (2) a population at the southern range terminus of mainland Mexican *X. agassizii* appears to represent a distinct taxon (Lamb et al. 1989) less closely related to *X. lepidocephalus* than this latter species is to northern populations of *X. agassizii*, (3) no fossil tortoises have been found in the Baja California cape or in the region of Jalisco, Mexico, the origin of the cape land mass, and (4) head scale meristics of *X. lepidocephalus* overlap slightly with those of the eastern species *X. berlandieri*. However, because extant *Xerobates* spp. penetrate well into the tropical thorn forest of Sonora and Sinaloa, the possibility of a once more southerly ranging ancestor should not as yet be totally discounted. Despite such arguments, the bulk of current evidence suggests that *X. lepidocephalus* entered Baja California from a more northerly origin, perhaps vicariantly via fragmentation of mid-peninsular land masses and/or at the base. This species is now an isolated relict that may comprise several disjunct peninsular populations.

Although it is surprising that a relatively visible species such as a tortoise passed undetected by naturalists for so long, the discovery of the Baja tortoise is not unlike that of *G. flavomarginatus*. *Xerobates lepidocephalus*, though not currently used as a meat source as is *G. flavomarginatus* (Legler 1959), is well known to the natives; both species occur in areas of considerable human activity. The countryside around the Buena Mujer Dam is dotted with ranches, and the dam itself is visited frequently by residents of La Paz and the San Juan plain. Also, the ranges of both species appear to be restricted to higher

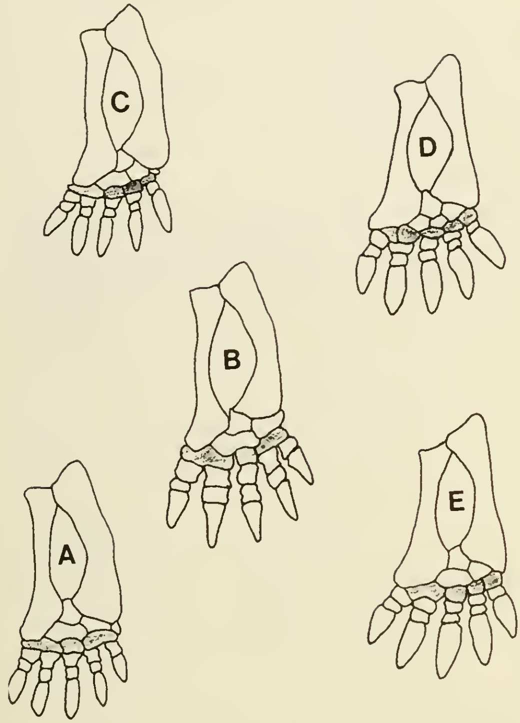

Fig. 3. Comparative morphology of the fused and separate right manus carpal bones (shaded), which number sequentially from left to right, of *Xerobates* and *Gopherus:* A and C, Oligocene *Xerobates laticunea;* B, holotype of *X. lepidocephalus;* C, *X. agassizii* and/or *X. berlandieri;* D, *Gopherus polyphemus;* and E, *G. flavomarginatus.* Figures not to scale.

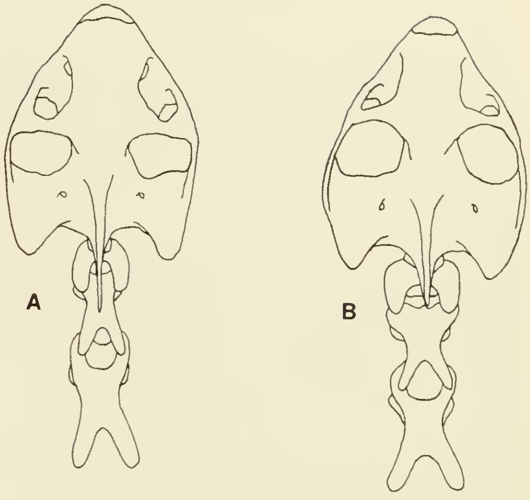

Fig. 4. Dorsal view of the cranium and vertebrae of *Xerobates lepidocephalus:* A, taken from life-size radiograph of the holotype, BYU 39706; B, the cranium and vertebrae of *Xerobates agassizii*, adapted from Bramble (1982). Figures approximate life size.

elevations. Nevertheless, skepticism abounded as to the origin and status of both species. For example, Grant (1960) severely challenged the origin of the type specimens of *G. flavomarginatus* and the taxonomic status of this species. Similarly, local naturalists from La Paz, as did we, initially found it difficult to accept the idea that a geographically restricted tortoise population in the cape region of Baja California was anything other than introduced. Though little is known about the origin and current distribution of *X. lepidocephalus*, its indigenous status is strongly buoyed by its dramatic diagnostic morphology; and, despite the fact that the meristics were taken from a single specimen, the chance that two, and possibly three, heretofore unknown diagnostic characters could be anomalies is probably very low.

Seasonal activity of *X. lepidocephalus* is believed to correspond primarily with the summer and fall rains, an observation corroborated by several local ranchers. The locals also noted that tortoises were infrequently encountered even at that time of the year and that they were usually seen on sloped or hillside areas; no one could recall having seen burrows. Thomas Van Devender (personal communication, 1989) stated that tortoise populations around Tucson, Arizona, are termed "summer rainfall tortoises" because of their seasonal activity; these tortoises are rarely found away from hillsides and do not burrow to avoid water runoff and flooding, particularly during the monsoon season. The late summer activity, suggested habitat preference, and lack of burrows reported by the Sierra San Vicente natives indicate that *X. lepidocephalus* is probably a "summer rainfall tortoise" as well.

At present the range of *X. lepidocephalus* is known only from the rocky foothills of the Sierra San Vicente. This area comprises less than two square kilometers. Eusebio Villalobos told us that during his 15 years in the area he had seen only five or six tortoises. If the observations of the native ranchers are correct, the Sierra San Vicente may house the last vestige of this species in the cape region.

Acknowledgments

We thank Eusebio Villalobos, Jésus Velázques S., Leticia Velázques, and Scott Selstad for their help and companionship in the field. For the loan of specimens and help in obtaining photographs of specimens we thank James Buskirk, Kevin Yates, James and Sandra Veverka, Cuca Espinosa (of San Ignacio, Baja California Sur), and Lillian and Max Greene. Drs. Ron Adair and Steve McHale graciously extended the use of their X-ray lab to us; and, aided by their lab personnel, Laura McDonald and Tammy Whitten, we obtained the radiographs from which the skeletal figures were taken. Dr. Charles R. Crumly graciously shared his provocative and well-founded taxonomic perspectives. We extend our appreciation to Dr. Thomas Van Devender, whose wealth of field observations and insights on desert tortoises he shared with us helped to confirm our meager field data on the Baja California species. The lucid commentaries of James Buskirk, Sandra Veverka, Dr. Charles H. Lowe, Jr., and Howard Lawler also added greatly to this study. Reviews by Dr. Wilmer W. Tanner and Dr. Stephen L. Wood aided the clarity of the manuscript. We are greatly indebted to Jorge Rodríguez R., José Luis Genel G., and Victor Haus V. of the Subdelegación de Ecología Departamento de Aprov. Inspecc. y Vig. Ecologica (SEDUE) of Mexico City, La Paz, and San José del Cabo, in conjunction with Romel Cota and Arturo Gomez C. of the III Ayuntamento de los Cabos, Delegación Municipal of Santiago, as well as the commandant of the La Paz Military Hospital for helping us obtain collecting and export permits (numbers 03.02.257/88 and 01.315/89) for our specimens. We also thank U.S. Customs Service for their cooperation.

Literature Cited

Agassiz, L. 1857. Contributions to the natural history of the United States of America. First Monograph. Vol. 1. Little, Brown & Co., Boston. li + 452 pp.

Auffenberg, W. 1966. The carpus of land tortoises (Testudinidae). Bull. Florida St. Mus., Biol. Sci. 10: 159–192.

______. 1976. The genus *Gopherus* (Testudinidae). Pt. 1. Osteology and relationships to extant species. Bull. Florida St. Mus., Biol. Sci. 20: 47–110.

Auffenberg, W., and R. Franz. 1978a. *Gopherus* Rafinesque. Gopher tortoises. Reptilia: Testudines: Testudinidae. Cat. Amer. Amph. Rept. 211.1–2.

______. 1978b. *Gopherus agassizii*. Cat. Amer. Amph. Rept. 212.1–2.

______. 1978c. *Gopherus berlandieri*. Cat. Amer. Amph. Rept. 213.1–2.

______. 1978d. *Gopherus flavomarginatus*. Cat. Amer. Amph. Rept. 214.1–2.

______. 1978e. *Gopherus polyphemus*. Cat. Amer. Amph. Rept. 215.1–2.

Bour, R., and A. Dubois. 1984. *Xerobates* Agassiz, 1857, synonyme plus ancien de *Scaptochelys* Bramble, 1982 (Reptilia, Chelonii, Testudinidae). Extrait du Bull. Mens. de la Soc. Linn. de Lyon 53: 30–32.

Bramble, D. 1982. *Scaptochelys:* generic revision and evolution of gopher tortoises. Copeia 1982: 852–867.

Carr, A. 1952. Handbook of turtles: the turtles of the United States, Canada, and Baja California. Cornell University Press. 542 pp.

Cooper, J. G. 1863. New California animals. (Description of *Xerobates agassizii*). Proc. California Acad. Sci. 2: 118–123.

Crumly, C. R. 1984. The evolution of land tortoises (Family Testudinidae). Unpublished dissertation. Rutgers–The State University, Newark. 558 pp.

______. 1985. The genus name for the North American gopher tortoises. Pages 147–148 *in* Proc. Desert Tortoise Council 1984 Symp.

______. 1988. A nomenclatural history of tortoises (Family Testudinidae). Smithsonian Herpetol. Info. Serv. 75. 17 pp.

Grant, C. 1960. *Gopherus*. Herpetologica 16: 29–31.

Lamb, T., J. C. Avise, and J. W. Gibbons. 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizii*), and evolutionary relationships among the North American gopher tortoises. Evol. 43: 76–87.

Lawler, H. 1986. The desert tortoise and its North American relatives. Sonoriensis 7: 6–15.

Legler, J. M. 1959. A new tortoise, genus *Gopherus*, from north-central Mexico. Univ. Kansas Pub. Mus. Nat. Hist. 11: 335–346.

Smith, H. M., and R. B. Smith. 1980. Synopsis of the herpetofauna of Mexico. Vol. VI. Guide to Mexican turtles. Bibliographic addendum III. John Johnson, North Bennington, Vermont. xvii + 1044.

Stebbins, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston. 279 pp.

Stejneger, L. 1893. North American Fauna 7: 161.

True, F. W. 1882. Key to the three species of North American land tortoises. Proc. U.S. Nat. Mus. 4: 434.

Van Denburgh, J. 1922. The reptiles of western North America. Snakes and turtles. Occ. Pap. California Acad. Sci. 2: 9995–1000.

Van Devender, T. R. 1986. The fossil record. *In:* The desert tortoise and its North American relatives. Sonoriensis 7: 8–9.

Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecol. Monogr. 18: 145–200.